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Combined view of various tree ring parameters from different forest habitats in Tibet for the reconstruction of seasonal aspects of Asian Monsoon variability

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ABSTRACT

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Tibetan forests cover a wide range of ecological habitats. Three different types of tree limit can be derived from statistical climate-growth relationships: An alpine timberline, where growth is limited by temperature conditions, a semiarid tree limit, where available moisture is the minimum factor for tree growth, and dry, southfacing exposures near the upper treeline, where growth can be limited as well by temperature as by moisture conditions. Trees at each of these sites, which belong to the genera *Pinus, Picea, Abies* and *Juniperus* are sensitive to specific seasonal climatic elements e.g., summer precipitation, summer or winter temperature. The potential for the selective reconstruction of different seasonal aspects of climate is enhanced by considering different tree ring parameters like total ring width (TRW), maximum latewood density (MLD), wood anatomy and the content of $\delta^{13}C$ in wood cellulose. The combination of these seasonal climate related parameters provides a more comprehensive view of climate variability over the year, allowing the reconstruction of synoptic weather conditions. These are much better indicators for wind system dynamics and monsoon variability than one single meteorological factor alone. Since juniper can reach living ages of more than 1300 years in Tibet, dendroclimatological studies offer the possibility to reconstruct monsoon variability on the Tibetan Plateau and adjacent regions during the last millennium.

Key-words—Monsoon, Tibet, Forest, Ring width, Climate.

एशियाई मानसून की परिवर्तनशीलता के मौसमी परिप्रेक्ष्य की पुनर्रचना हेतु तिब्बत के विभिन्न वन आवासीयों से प्राप्त विभिन्न वृक्ष वलय प्राचलों का एकीकृत विश्लेषण

अख़िम ब्राउनिंग

सारांश

तिब्बत के वनों में पारिस्थितिकीय आवासीयों की वैविध्यमयता विद्यमान है। वृक्ष सीमाओं के तीन भिन्न-भिन्न रूप सांख्यिकीय जलवायु-वृद्धि सहसम्बन्धन से प्राप्त किए गए हैं : एक अल्पाइन वृक्ष सीमा, जहाँ वृद्धि तापमान की स्थितियों में सीमित है; एक अर्द्धशुष्क वृक्ष सीमा, जहाँ उपलब्ध आर्द्रता वृक्ष वृद्धि हेतु न्यूनतम कारक है तथा ऊपरी वृक्ष सीमा के

समीप शुष्क उत्तराभिमुख अनावरण, जहाँ वृद्धि को तापमान एवं आर्द्रता की स्थितियों में सीमित किया जा सकता है। इनमें से प्रत्येक स्थलों पर वे वृक्ष, जो *पाइनस, पाइसिया, एबीज़* तथा *जूनीपेरस* वंश से सम्बन्धित हैं, कुछ विशिष्ट मौसमी जलवायुविक तत्वों, जैसे- ग्रीष्म वृद्धि, ग्रीष्म अथवा शीत तापमान के प्रति संवेदनशील हैं। जलवायु के विभिन्न मौसमी पहलुओं की चयनित पुनर्रचना हेतु आवश्यक आधार को विभिन्न वृक्ष वलय प्राचलों, जैसे- सकल वलयी चौड़ाई (टी.आर. डब्ल्यू.), अधिकतम पश्च काष्ठ घनत्व (एम.एल.डी.), काष्ठ शारीर विज्ञान तथा काष्ठ सेलुलोज में $\delta^{13}C$ के तत्व से बल मिलता है। इन मौसमी जलवायु सम्बन्धी प्राचलों का संयोजन साररूपी मौसमी स्थितियों की पुनर्रचना को प्रदर्शित करते हुए सम्पूर्ण वर्ष में जलवायु की विविधता का अपेक्षाकृत अधिक समग्र परिदृश्य प्रदान करता है। ये पवन तंत्र गतिविज्ञान तथा मानसून विविधता हेतु एकमात्र मौसमी कारक की अपेक्षा अधिक उत्कृष्ट संकेतक हैं। चूँकि जूनीपेर तिब्बत में 1300 वर्षों से अधिक जीवनकाल तक ही पहुँच सकता है, अतः वृक्षजलवायुविक अध्ययन से तिब्बत के पठार एवं समीपवर्ती क्षेत्रों में विगत सहस्राब्दि के दौरान मानसून परिवर्तनशीलता का पुनर्सृजन सम्भव है।

संकेत शब्द—मानसून, तिब्बत, वन, वलय चौड़ाई, जलवायु.

INTRODUCTION

USUALLY certain tree-ring parameters like maximum latewood density at subalpine sites or ring width under semiarid conditions, show high correlations with specific seasonal climate elements like summer temperature in the former or summer precipitation in the latter case. Therefore, the majority of dendroclimatic studies are limited in reconstructing one or a few seasonal aspects of climate at best.

The mountain regions of eastern Tibet show a variety of climatic conditions and hence a tremendous diversity of ecological forest types and tree habitats. This allows to combine several wood parameters which are sensitive to different seasonal climate elements. Thus, the reconstruction of climate over the whole course of a calender year may become possible. The identification of changing synoptic weather conditions helps to gain deeper insight into the variation of climate in southern Asia.

CHARACTERISTICS OF CLIMATIC CONDITIONS AND METEOROLOGICAL DATA

The subtropical high plateau of Tibet receives an immense amount of solar radiation in spring and summer and therefore acts as a huge heating surface, resulting in a strong low pressure cell over the plateau (Murakami, 1987). This causes moist air masses over the Indian Ocean and the Bay of Bengal to flow northward and bring moisture to southern and high Asia. As a result, 70 to 80% of the total annual precipitation in Tibet falls during the season of the Indian Summer Monsoon (ISM) between late June and middle of September. However, this general picture is strongly modified by mountain topography (Schweinfurth, 1981). Local diurnal circulation systems cause an ascent of unstable air masses, so that a great amount of summer precipitation is of convective character (Flohn, 1987). The Himalaya-Hengduan Shan mountain chains form a natural barrier for the monsoonal air masses to flow northward. The deeply incised gorges of the upstreams of Nu Jiang (Salween), Lancang Jiang (Mekong), Jinsha Jiang (Yangtze) and Yarlung Tsangpo (upstream of Brahmaputra), therefore act as pathways for the monsoon (Chang, 1981), resulting in a steep moisture gradient from south-east to north-west in Southern Tibet.

During winter, when dry and cold air masses that originate from central Asia prevail, the Tibetan Plateau acts as a heat sink and is colder than the surrounding free atmosphere. Western disturbances bring little precipitation in the form of snow. Apart from Mountain areas, the snow cover usually does not persist due to the immense insolation even in winter. However, the intensity of the Eurasian winter and the depth of the snow cover over Tibet and the Himalaya have a strong influence on the ISM of the following summer, as has long been recognized by British meteorologists (e.g., Walker, 1910). Since the albedo is enhanced over snow, thermal energy is consumed to melt the snow and moist the soil surfaces after snowmelt. Therefore, the heating of the plateau surface is delayed and weakened after severe winters in Eurasia (Barnett *et al.,* 1988, Vernekar *et al.,* 1995). As a consequence, the low pressure cell over Tibet as the driving force for the ISM is not as strong as after a mild winter. Statistically, ISM and Eurasian Snow Cover (ESC) are negatively correlated and reduced amounts of monsoonal precipitation can often be observed after cold winters (Barnett *et al.,* 1988; Khandekar, 1991; Yang & Xu, 1994). Due to the marginal position at the northwestern fringe of influence of the ISM and the seasonal change of two competing circulation systems, the Tibetan Plateau is expected to be very sensitive to variations in the activity of the summer or winter circulation pattern.

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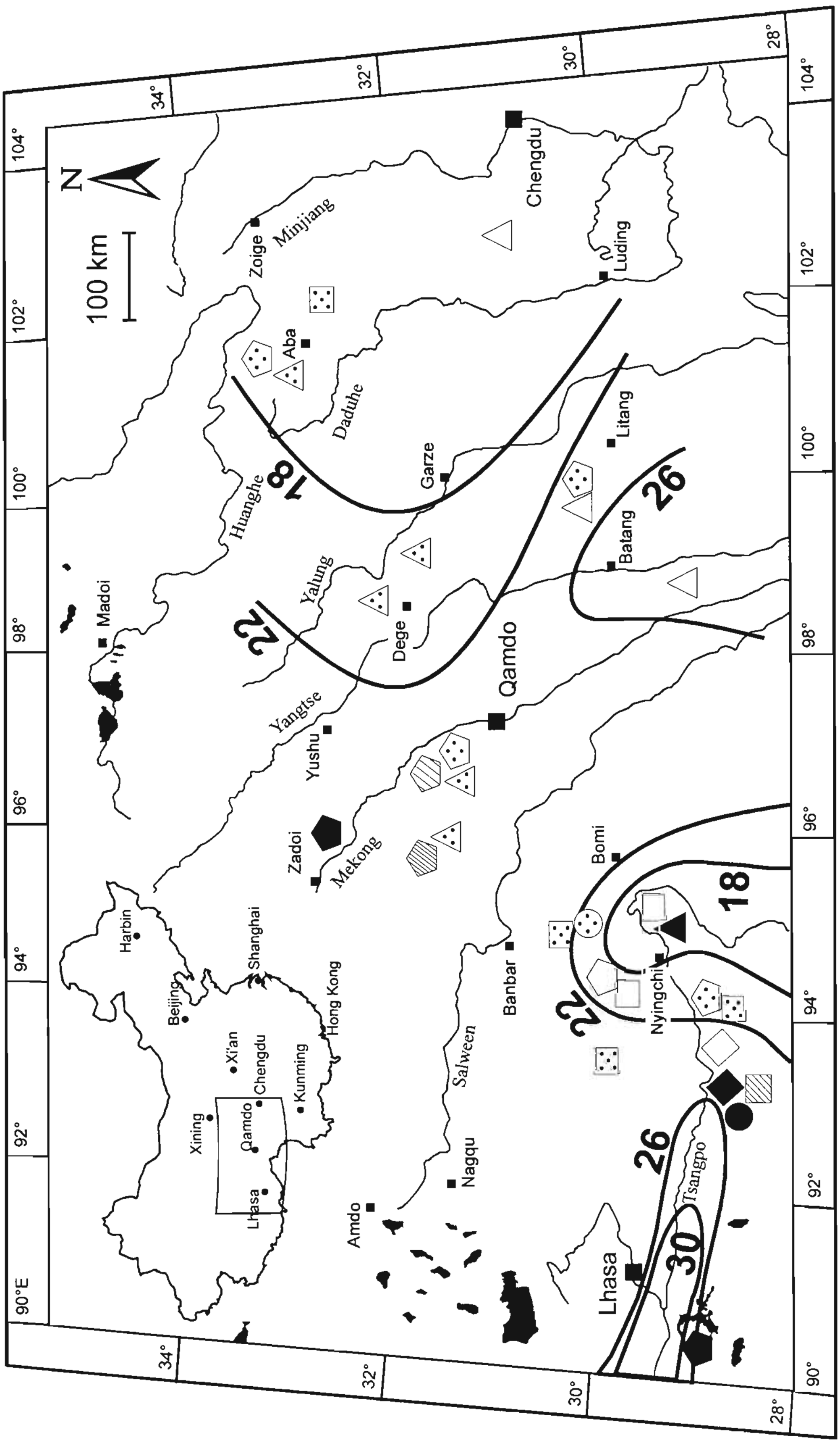
Fig. 1—Coefficient of variation of summer (June-September) precipitation and mean sensitivity (MS) of ring width chronologies.


100 km
N
Zoige
Minjiang
Chengdu
Luding
Aba
Daduhe
Litang
Garze
Huanghe
18
22
26
30
Batang
Yalung
Madoi
Dege
Qamdo
Yangtse
Yushu
Zadoi
Mekong
Bomi
Harbin
Beijing
Shanghai
Hong Kong
Xi'an
Chengdu
Kunming
Xining
Qamdo
Lhasa
Banbar
Nyingchi
Salween
Nagqu
Amdo
Tsangpo
Lhasa
90°E
92°
94°
96°
98°
100°
102°
104°
28°
30°
32°
34°
tree species:
Larix
Juniperus
Pinus
Abies
Picea
mean sensitivity of ring width chronologies:
< 0,10
0,10-0,14
0,15-0,19
0,20-0,24
> 0,25

Site name	Location	Elev. (m)	Tree species*	No. of trees	Time span/years
Wolong	30°53'N/ 102°50'E	3700	*Picea purpurea*	7	1842-1994 (153)
Zhegu	31°34'N/ 102°51'E	3950	*Abies fabri*	13	1737-1994 (258)
Zoige	34°02'N/ 102°43'E	3600	*A.* cf. *fargesii*	10	1830-1988 (159)
Gonggaling	33°00'N/ 103°42'E	3400	*A.* sp.	10	1679-1989 (311)
Aba	32°42'N/ 102°12'E	3850	*A.* sp.	23	1699-1991 (293)
Nianbaoyeze	33°13'N/ 101°16'E	4000	*Picea purpurea*	6	1728-1991 (264)
		4100	*Juniperus* sp.	7	1471-1991 (521)
Lhamcoka	31°49'N/ 99°05,5'E	4350	*Picea balfouriana*	20	1630-1994 (365)
Zagqen	32°07'N/ 98°51'E	4150	*P. balfouriana*	10	1699-1991 (323)
Haize Shan	30°18'N/ 99°30'E	4350	*P. balfouriana*	15	1777-1993 (217)
Haize Shan	30°18'N/ 99°29'E	4400	*Juniperus tibetica*	11	1174-1993 (820)
Gartog	29°40'N/ 98°31'E	4300	*Picea balfouriana*	14	1709-1993 (285)
Qamdo	31°05'N/ 96°57,5'E	4500	*P. balfouriana*	15	1406-1994 (589)
Qamdo	31°05'N/ 96°57,8'E	4600	*Juniperus tibetica*	14	1226-1994 (733)
Qamdo	31°07'N/ 97°02'E	4350	*J. tibetica*	34	449-1994 (1546)
Riwoqe	31°18'N/ 96°29'E	4300	*Picea balfouriana*	28	1673-1994 (322)
Riwoqe	31°17.5'N/ 96°30'E	4400	*Juniperus tibetica*	11	1354-1994 (641)
Zadoi	32°06'N/ 98°51'E	4300	*J. tibetica*	5	1445-1991 (547)
Nam	29°35'N/ 95°10'E	4100	*Abies* cf. *delavayi* var. *motouensis*	28	1740-1989 (250)
Nam		3350	*Picea* sp.	11	1846-1989 (143)
Gyalaperi	29°53'N/ 94°53'E	4000	*Abies delavayi* var. *motouensis*	12	1774-1993 (220)
Gyalaperi	29°54'N/ 94°53'E	3820	*Larix griffithiana*	20	1782-1994 (213)
Nyingchi	29°35'N/ 94°46'E	4300	*Abies delavayi* var. *motouensis*	27	1654-1993 (340)
Nyingchi	29°37'N/ 94°40'E	4300	*Juniperus* sp.	12	1568-1993 (426)
Chi	29°59'N/ 93°59'E	3900	*Abies delavayi* var. *motouensis*	10	1741-1994 (254)
Mainling	29°02'N/ 93°54'E	3430	*Pinus densata*	15	1765-1993 (229)
Mainling	29°04'N/ 93°57'E	4200	*Juniperus tibetica*	10	1047-1993 (947)
Mainling	29°03'N/ 93°57'E	4100	*Abies delavayi* var. *motouensis*	9	1664-1993 (330)
Langhsien	28°59'N/ 93°13'E	3500	*Pinus densata*	12	1760-1993 (234)
Langhsien	28°55'N/ 93°14'E	3700	*Abies* cf. *squamata*	13	1707-1993 (287)
			Larix griffithiana	8	1736-1993 (258)
Nakarze	28°58'N/ 90°28'E	4500	*Juniperus tibetica*	11(8)	1680-1994 (315)

Fig. 2—Tree-ring localities in Tibet referred to in this study.

The meteorological data that are available from the Tibetan Plateau do not extend further back than 1951, and in many cases the period of observations is less than 30 years. The meteorological stations are located near larger settlements in valley floors and are therefore not representative with respect to moisture conditions of most of the tree-ring sites investigated, which lie in a vertical distance of up to 1400 m. Like in other mountain areas, the spatial representativity of the precipitation data is not high and ranges from about 200 to 250 km, whereas temperature data show a correlation coefficient of more than 0.7 within 350 to 500 km (Boehner, 1996). As Vaganov *et al.* (1999) have shown, correlation between maximum latewood density (MLD) and temperature data could be improved from 0·52 to 0·67,by choosing pentads in relation to the beginning of the vegetation period, which can vary within 30 days, instead of monthly means of calendar-related periods. Unfortunately, data for the beginning of the vegetation period in different altitudinal belts are still lacking for Tibet. Moreover, lacking information about the effectiveness of rainfall events and short drought periods, that are not recorded in the monthly means of precipitation data, are further obstacles for a proper calibration between tree growth and climate.

RESULTS

Ecological diversity of tree limits in Tibet

It is known from many dendroclimatic studies that trees from dry forest habitats show a higher growth variability than trees from temperature limited sites. Fig. 1 shows the coefficient of variation for summer precipitation and mean sensitivity of ring width chronologies developed in Tibet. Details about the tree locations examined are given in Fig. 2 in the appendix. There is a general agreement between the precipitation gradient from east to west in northeastern and southern Tibet and increasing sensitivity of the trees. Fig. 3 shows a schematic transect through a mountain range west of Qamdo, indicating that this agreement is not spatially robust. Northern slopes are covered by dense forests of *Picea balfouriana*, and the upper tree limit lies around 4500 m.a.s.l. Southern exposures carry open forests of *Juniperus tibetica* which extends up to more than 4600 m. Below 4400 m, or other than south-facing slopes, the two species form mixed stands. The bottom of Lancang Jiang (Mekong) valley runs at 3200 m, but the lower parts of the slopes are presently devoid of forest. This might be a consequence of human activity, since there are remnants of settlements near Qamdo since neolithic times (Huang, 1994). The meteorological station at Qamdo registers an average annual precipitation of 474 mm which should be high enough to allow tree growth. Therefore, a site of *Pinus densata* from the Tsangpo Valley further to the west, that is supposed to grow under similar conditions, is shown on the left half of Fig. 3. The cut on the slope line and the question mark in the valley symbolize that it is only an assumption, that steppe forests of this type could have been existent near Qamdo as well.

Above the topographic cross-section, correlation functions between tree growth (TRW in case of *Juniperus* and *Pinus*, MLD in case of *Picea*) and the nearest meteorological station are shown (Qamdo in case of *Juniperus* and *Picea*, Tsetang in case of *Pinus*). It can clearly be seen, that MLD of spruce on northern aspects is clearly determined by temperature in August and September, whereas ring width (TRW) of pine shows high positive correlations with precipitation of July of the growth period, and summer precipitation of the year prior to growth, when the carbon storage for the formation of earlywood is assimilated. Correlations with temperature are negative during these months. In contrast to these two sites of very clear climate-growth relationships, there is no such clear dominance of one single climate element on growth at the juniper site. There are positive correlations with spring precipitation and summer temperature (and vice versa), so it can be assumed that dry and warm springs before the monsoon period cause drought stress at this site, while moist and cool summers lead to reduced growth rates at this high elevation. It may therefore be concluded that the growth of juniper for this region is in general controlled by temperature, but is far more sensitive to short-term or episodic drought periods than spruce on the neighbouring northern slopes.

As a consequence, three different types of ecological timberlines can be identified in Tibet, as indicated at the top of Fig. 3: a cold-moist tree-limit, where growth is exclusively limited by temperature conditions, a warm-dry tree-limit, where growth is usually controlled by the available amount of moisture, and a cold-dry tree-limit, where growth is mainly controlled by temperature, but where in dry years the influence of precipitation deficit prevails (Bräuning, 2000). These different ecological forest types can be used for the reconstruction of different climate elements, as it has already been demonstrated by LaMarche (1974) for *Pinus longaeva* in the White Mountains of California.

To support these findings, values of mean sensitivity (MS) which have been averaged for several chronologies of the particular type of tree-limit (number given in brackets in Fig. 3) show the highest sensitivity at the dry valley sites (0·34), the lowest values at the cold-moist sites (0·11) and intermediate values at the cold-dry sites (0·16). Therefore, the inconsistencies between MS and precipitation gradient in Fig. 1 can be explained by the ecological diversification of forest types due to topographic conditions and point to the importance of a proper ecological characterization of the forest types which are investigated.

Reconstruction of Seasonal Climate Elements

In the following paragraphs, the potential of various tree-ring features for the reconstruction of climate is discussed while particular emphasis is laid on the seasonal aspects of the climatic response of the different wood parameters.

Wood anatomical features

As it was shown by Bräuning (1999b), *Pinus densata* shows unusual wood anatomical features near its western limit of distribution, where the amount of available moisture is the growth-limiting climatic factor: in certain years, the majority of trees at this site forms density fluctuations which appear as bands of latewood-like cells within the earlywood (Fig. 4a). It could be shown that these density fluctuations mainly occur in years with deficit precipitation accompanied by warmer temperature in May and June (Fig. 4b). This is indicative of a delayed onset of the summer monsoon in southern Tibet in the corresponding years, causing above-average precipitation in July of the same years (Fig. 4b).In addition to the absolute amount of summer precipitation, that can be reconstructed from the high correlation between TRW

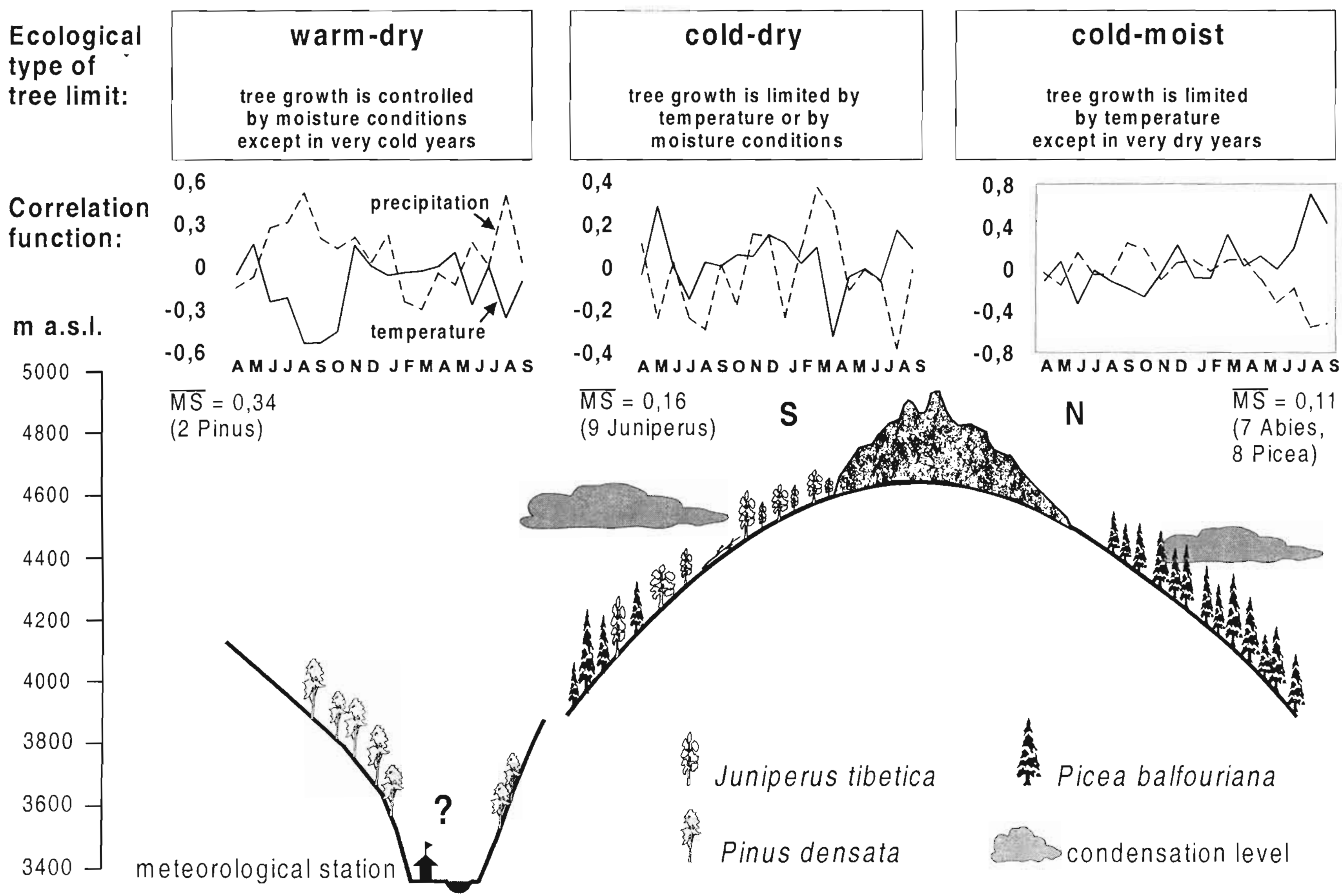


Fig. 3—Idealized profile of ecological forest types through a topographic section in eastern Tibet (Qamdo area, compare Fig. 1). In the upper section correlation functions between tree growth and meteorological data and derived ecological types of tree-limits are shown.

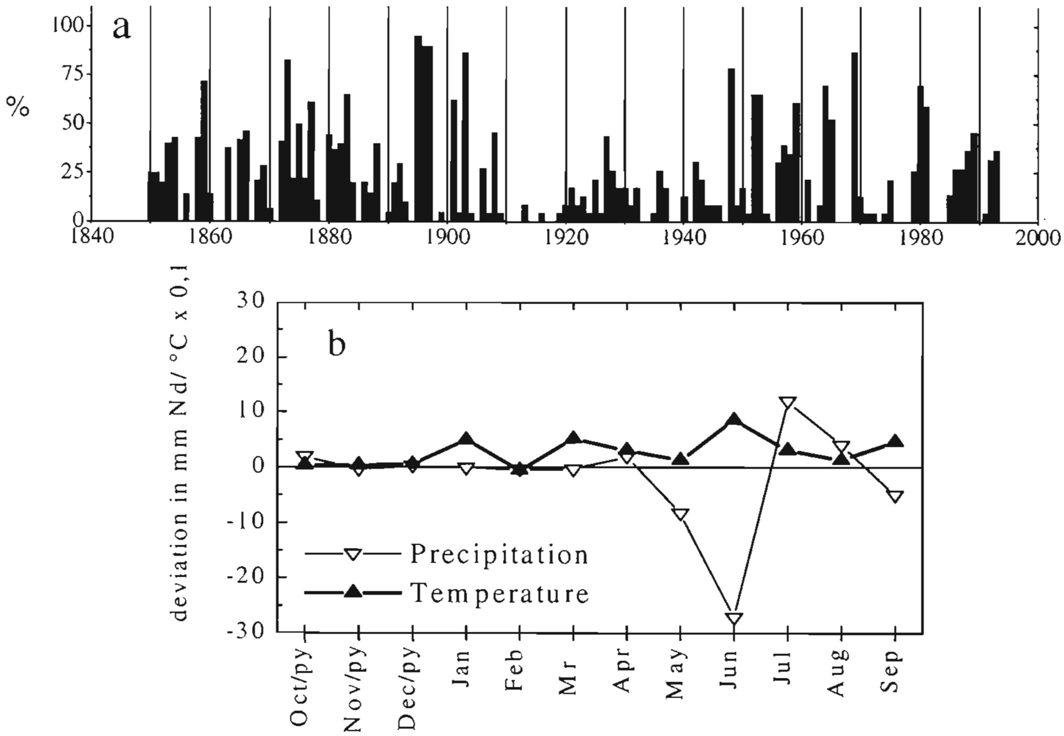


Fig. 4 — *a*. Frequency of density fluctuations (bands of latewood-like cells withing the earlywood) in growth rings of *Pinus densata* from the Tsangpo Valley *b*. Climatological situation at Tsetang (29°15'N, 91°46'E, 3553 m) in years of formation of density fluctuations (mean of the years 1958, 1959, 1964, 1969, 1985-1989, 1992), expressed as averaged deviations of monthly values of temperature and precipitation from October of the previous year (Oct/py.) to September (Sep). From Braeuning 1999b, changed.

and precipitation during summer and late summer in the prior vegetation period (Fig. 3), density fluctuations in trees of drought sensitive forest ecosystems provide information about the activity of the monsoonal circulation system.

Stable Carbon Isotopes

Under drought stress conditions, leaf stomata are closed and the heavy stable carbon isotope ^{13}C is increasingly incorporated into photosynthesis products. Thus, the isotope ratio $^{12}C/^{13}C$ in growth rings can be used as a proxy of climate conditions (Schleser *et al.*, 1999). The ^{13}C content in wood of *Juniperus tibetica* northwest of Qamdo has been measured for the last 1500 years (Zimmermann, 1998; Zimmermann *et al.*, 1997). In general, the isotope ratio follows the long-term trend of ring width at this site and seems to be determined by summer temperature. However, calibration efforts with recent meteorological data are not yet completed, so the results of this study shall be dealt with in detail in another paper.

Maximum Latewood Density (MLD)

In many mountain regions of the temperate zones MLD has proved to be closely linked with summer temperatures (Vaganov *et al.*, 1999; Luckman *et al.*, 1997; Schweingruber & Briffa, 1996). In Fig. 5, a regional master chronology of *Picea balfouriana* from central eastern Tibet is compared to summer temperature (August and September) of a composed meteorological series from the stations Derge and Qamdo (Fig. 1).

Unfortunately, this series covers only 32 years (1953-1984), so there is insufficient data for statistical verification of the results. The high linear correlation ($r = 0{\cdot}74$) explains 55% of the variance of the MLD-chronology and can be used in a simple linear regression to reconstruct summer temperatures in eastern Tibet for the last 400 years (Fig. 5, Bräuning, 1999a, 2000).

Total Ring Width (TRW)

Under extreme site conditions, growth rates are mainly determined by one single climatological factor only. Near the dry distribution limit, growth of the specific tree species is controlled by moisture condition. As the exmaple of the stand of *Pinus densata* near Langhsien demonstrates, ring width chronologies from such sites show high correlations to summer precipitation and can be used to reconstruct summer precipitation (Bräuning, 1999a).

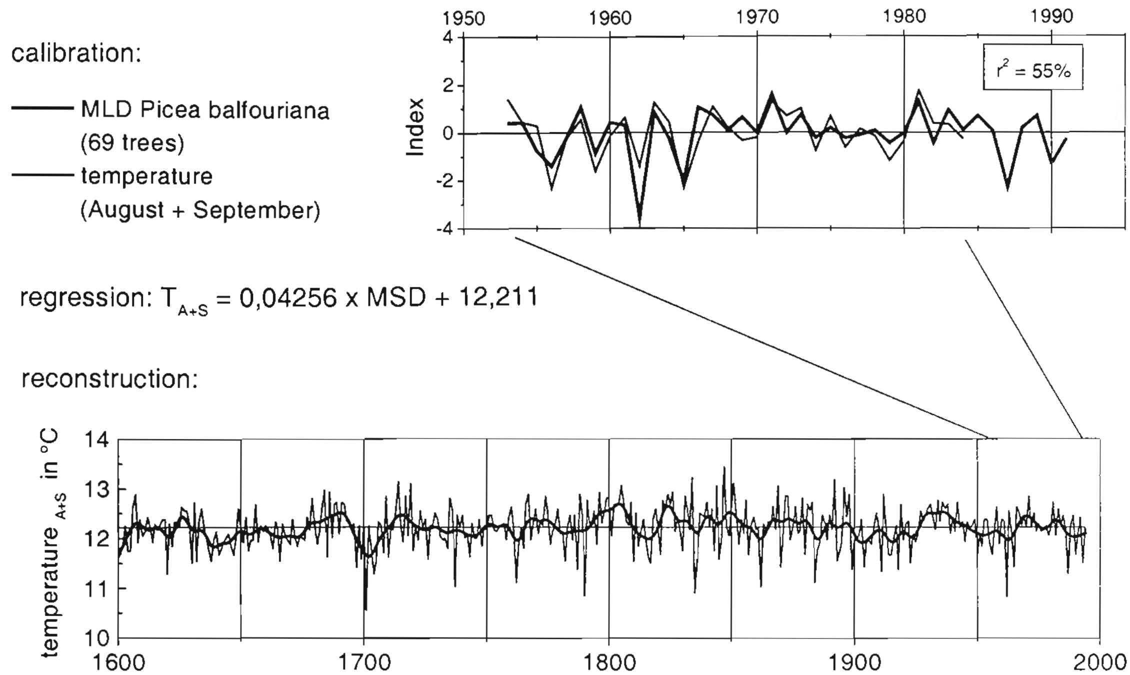


Fig. 5—Comparison between maximum latewood density (MLD) of *Picea balfouriana* and meteorological data and a reconstruction of summer temperature for the last 400 years for central eastern Tibet. Heavy line in the lower graph is the 5-year low-pass filtered series.

In contrast, ring width chronologies from *Picea* or *Abies* species from the upper timberline are sensitive to winter temperatures. The regional master chronology of *Picea balfouriana* from central eastern Tibet shows a correlation coefficient of 0·53 with temperature from November to December prior to the vegetation period (Fig. 6a) which is significant at the 99% confidence level. Cold winter temperatures might cause direct frost damage of the needles or may increase the risk of frost dryness, since solar radiation in subtropical mountain regions is considerable even during winter times. In addition, after cold winters with delayed snow melt, the following vegetation period is shortened, an early start of winter enhances the consumption of stored carbohydrates (Frenzel & Maisch, 1981), which may lead to a reduced earlywood width in the following year.

Many ring width chronologies are developed from tree stands which are not located near the tree limit of one of the two ecological types discussed above. They originate from sites with moderate conditions or from cold-arid timberlines (Fig. 3), where temperature as well as moisture conditions can limit growth in certain years. In such cases, there is no simple linear climate-growth relationship, and correlation coefficients between ring width and monthly climate elements decrease. The use of multiple regression techniques and the development of response functions (Fritts, 1976) can establish statistical relationships between ring width series and meteorological data which are in some cases able to explain more than 75% of the variance of the time series (Wu, 1992; Wu & Shao, 1995). In some cases, however, when a huge number of climatic variables are included into the regression equation, the results are difficult to explain from an ecological point of view.

Two alternative approaches can be applied to gain climatological information from such sites: The first is not to correlate ring width and single monthly meteorological series, but to use more complex climatic series which already integrate seasonal aspects of climate themselves. In Fig. 6b, a regional master chronology from eastern Tibet of *Juniperus tibetica* is compared with the Indian Summer Monsoon Index (ISM) which represents an area-weighted mean of precipitation from June to September over India and the area of snow cover over Eurasia in the preceeding winter (ESC) which has been derived from satellite images (Hahn & Shukla, 1976; Dey & Bhanu Kumar, 1983; Khandekar, 1991). ISM and ESC are negatively correlated (r = -0·55), but in Fig. 6b, the latter has been plotted in a reversed scale for a better visual comparison. The correlation coefficients between ring width index and ISM and ESC are 0·8 and -0·68 respectively and are significant on the 99·9% level. Since these trees represent cold-arid timberline sites (Fig. 3), the results show that warm and moist summers favour growth while cold and dry conditions lead to reduced ring width. In other words, growth rates from subalpine juniper sites can be used as indicators of whether the circulation system of the Indian Summer Monsoon or of the central Asian

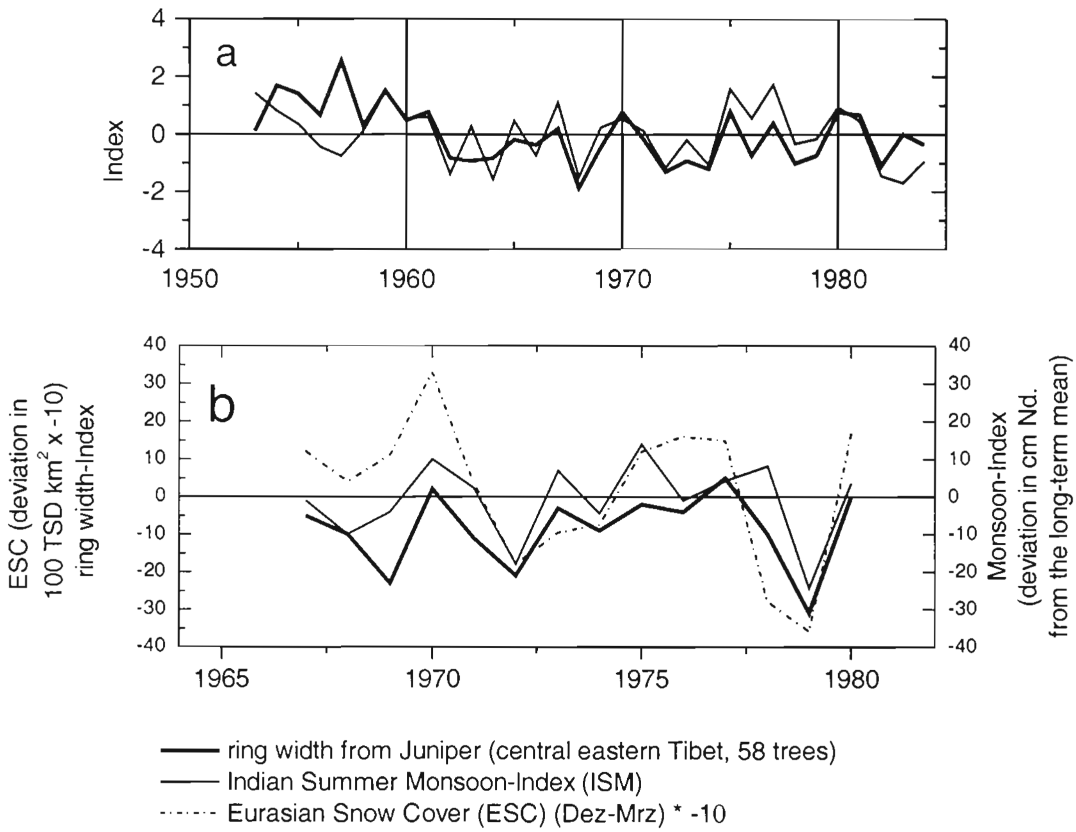


Fig. 6—*a*. Comparison between ring width of a regional master chronology of *Picea balfouriana* for central eastern Tibet and winter temperature. *b*. Correlation between ring width of *Juniperus tibetica* and indices of Indian Summer Monsoon (ISM) and Eurasion Snow Cover (ESC).

Winter Monsoon was more active. This is of special interest, since *Juniperus tibetica* can reach to the ages of more than 1300 years in Tibet (Bräuning, 1994, 1999a) and can thus provide information about the monsoon activity during different climate periods like the Little Ice Age or the medieval climatic optimum. However, it must be mentioned that if the longest existing ISM record of 124 years (1871-1994, Pant & Rupa Kumar, 1997) is compared with the juniper chronology, the correlation coefficient decreases below the 90% significance level. Although it is a well known fact that the relationship between tree-ring parameters and climate is not necessarily stable within periods of changing climate, this point needs further investigation.

This phenomenon is addressed by the second approach that can be applied for the climatological interpretation of ring width series, pointer year analyses. This approach tries to evaluate the climatological response of selected years in which the influence of climate on tree growth is particularly evident. In this study, such years were selected by the criterion of corresponding growth trends among the trees which are included in a local chronology: more than 75% of all trees must show the same growth tendency or interval trend (see Schweingruber *et al.*, 1990; Kaennel & Schweingruber, 1995 for terminology). The strength of the growth signal was calculated as the first difference of the ring width index chronologies from which the natural age trend of the trees was removed by a 50-years Kernal filter (Rinn, 1996), and classified as pointer value 1, 2 or 3 for being below or exceeding the first or second standard deviation, respectively.

In Fig. 7, the spatial pattern of ring width response under different climatological conditions is illustrated for three years (1966, 1968 and 1972). In 1966 (Fig. 7a), southern Tibet received between 28 and 80 mm excess precipitation in June. As a consequence, the dry forest sites in the Tsangpo Valley react with positive pointer intervals with values of 2 and 3, whereas subalpine sites in this area did not profit from the additional moisture. In contrast, 1968 (Fig. 7b) was a very cold year: annual mean temperature was below the long-term mean for about 0·8°C in eastern Tibet and for more than 1·2°C in western Tibet, respectively. Since this temperature depression affected the whole investigation area, the reaction of tree stands is uniformly negative. The most complex pattern is shown in Fig. 7c: In 1972, a bench of below-average precipitation in June stretches from the area south of Lhasa via Qamdo to the northeastern margin of the Tibetan Plateau. Within this area, dry sites in the Tsangpo Valley show reduced

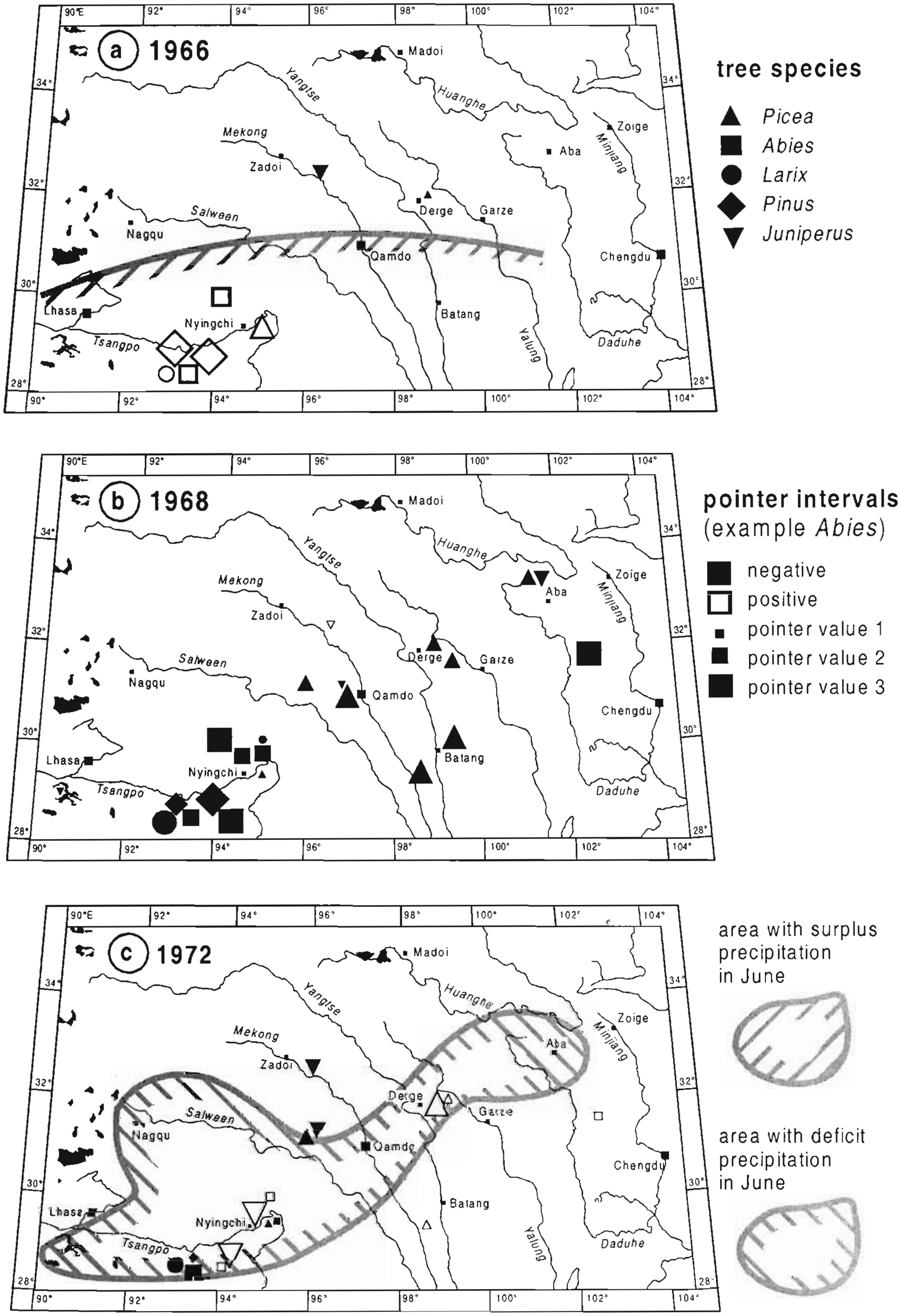


Fig. 7.—Pointer intervals of ring width series and their climatological interpretation.
a. surplus of early summer (June) precipitation in southern Tibet (1966)
b the whole year is cooler than the long-term mean (1968)
c. deficit of early summer (June) precipitation in southern and eastern Tibet (1972)

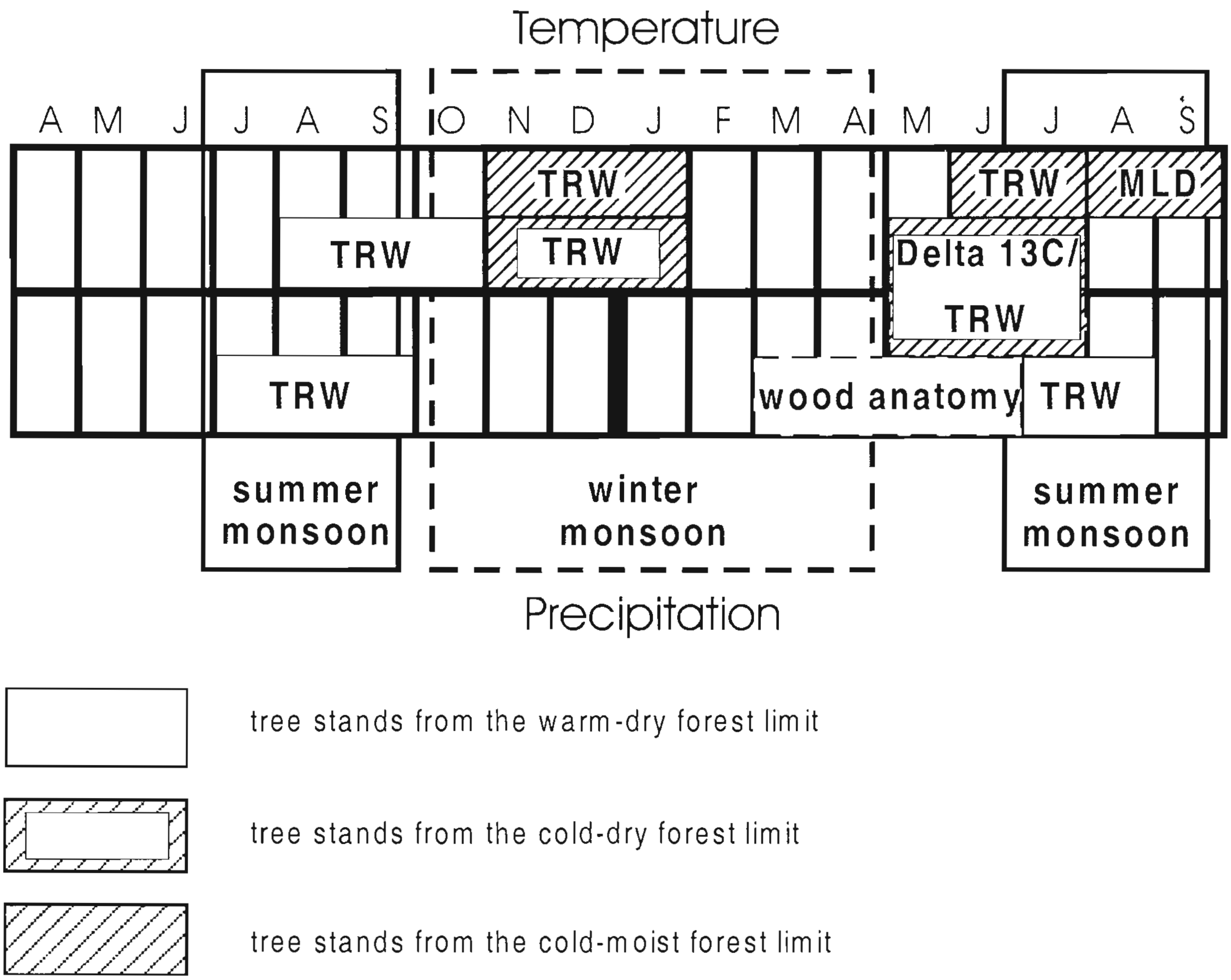


Fig. 8—Contribution of different tree-ring parameters to the reconstruction of seasonal aspects of monsoon variability. TRW = total ring width, MLD = maximum latewood density.

growth rates, whereas subalpine sites near Nyingchi and Derge profit from the drier and warmer conditions during early summer. In conclusion, the geographical pattern of growth reactions can be interpreted in terms of the underlying climatological conditions when forest types with different, well known ecological conditions are part of a sampling network (see Fig. 3 for comparison).

SUMMARY AND CONCLUSIONS

As shown above, several tree-ring parameters like ring width under different site conditions, MLD or wood anatomy can be used to reconstruct seasonal aspects of climate variability, as summarized in Fig. 8. Ring width series from the warm-dry forest limit can be used to reconstruct moisture conditions since they show high correlations with summer precipitation in the year of growth and the preceeding late summer and negative correlations with summer temperature. In distinctive years (therefore hatched lines are used in Fig. 8), wood anatomical features indicate a delayed onset of the summer monsoon in southern Tibet. Ring width and MLD from the cold-moist subalpine tree limit bear information about winter and summer temperatures. Stable carbon isotopes and ring width data from forest stands at the cold-dry tree limit are, in general, indicators of temperature, but in dry years they are also sensitive to a lack of moisture. The geographical pattern of growth changes in pointer years can help to identify the nature of the triggering climatic event.

The combination of these parameters provides the opportunity to gain insight into seasonal aspects of climate during almost 15 months (early summer of the year prior to growth to late summer of the year of growth). Apart from the reconstruction of single climate elements, such as summer temperature or precipitation, the application of combined multiple proxy data can contribute to the reconstruction of dynamic aspects in circulation patterns. In Tibet, this approach offers the possibility to shed light on shifts in the balance of the competing wind systems of the winter and summer monsoon in periods of changing climate, for example during the Little Ice Age or the Medieval Climatic Optimum.

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An improved reconstruction of summer temperature at Srinagar, Kashmir since 1660 AD, based on tree-ring width and maximum latewood density of *Abies pindrow* [Royle] Spach.

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ABSTRACT

Hughes MK 2001. An improved reconstruction of summer temperature at Srinagar, Kashmir since 1660 AD, based on tree-ring width and maximum latewood density of *Abies pindrow* [Royle] Spach. Palaeobotanist 50(1) : 13-19.

Regional chronologies based on conifer ring width and density variables were developed for the region surrounding the Vale of Kashmir. The effects of age/size trend on the raw data were removed by a more conservative technique than in previous work in this region, in the hope of retaining multidecadal climate variability. A reconstruction of split summer temperature (April through September, excluding July) at Srinagar captured 58% of the variance of the instrumental record (56% in validation). Decadal to multidecadal variability was distributed throughout the reconstructed period, but interannual variability was greater in the first century of the reconstruction than later. In particular, there was a higher concentration of the coolest summers before 1770 than after.

Key-words—Latewood, Tree ring, Reconstruction, Summer, *Abies pindrow*.

एबीज़ पिण्ड्रो स्पैक की वृक्ष वलयी चौड़ाई तथा अधिकतम पश्चदारु घनत्व के आधार पर विगत सन् 1660 ई. से आज तक के श्रीनगर (कश्मीर) के ग्रीष्मकालीन तापमान का परिवर्धित पुनर्सृजन

मैल्कॉम के. ह्यूगेस

सारांश

कश्मीर घाटी के आस-पास के क्षेत्र हेतु शंक्वाकार वलयी चौड़ाई तथा घनत्व प्रसरणों के आधार पर क्षेत्रीय कालानुक्रम विकसित किया गया। बहुदशकीय जलवायुविक प्रसरणों को संरक्षित करने के उद्देश्य से विगत अनुसन्धान कार्य के विपरीत इस बार एक अधिक पारम्परिक प्रविधि के माध्यम से अपरिपक्व आंकड़ों से आयु/आमाप रुझानों के प्रभावों को हटा दिया गया। श्रीनगर में विभक्त ग्रीष्म तापमान का पुनर्सृजन (जुलाई के अलावा अप्रैल से सितम्बर तक) कुल प्रभावी अभिलेखों (56% वैध) में से प्रसरण का 58% ग्रहण कर लेता है। सम्पूर्ण पुनर्सृजित अवधि के दौरान दशकीय से बहुदशकीय परिवर्तिता का वितरण किया गया, परन्तु अन्तिम शती की तुलना में प्रारंभिक शताब्दी में अन्तरवार्षिक परिवर्तिता अपेक्षाकृत अधिक थी। संक्षेप में, सन् 1770 ई. से पूर्व ठण्डी ग्रीष्म की तीव्रता बाद की तुलना में उच्चतर था।

संकेत शब्द—पश्चदारु, वृक्ष वलय, पुनर्सृजन, ग्रीष्म, *एबीज़ पिण्ड्रो*.

INTRODUCTION

THE western Himalayan region contains many potentially valuable natural archives of interannual to century-scale climate variability, notably the size, density and isotopic composition of the annual rings of trees growing in subalpine environments (Bhattacharyya *et al.*, 1988; Bhattacharyya & Yadav, 1989, 1996; Borgaonkar *et al.*, 1994, 1996; Hughes, 1992; Hughes & Davis, 1987; Pant, 1983; Ramesh, 1995; Ramesh *et al.*, 1985, 1986a, b; Yadav & Bhattacharyya, 1992; Yadav *et al.*, 1997, 1999). The ring width and maximum latewood density of subalpine conifers are particularly good archives of information on spring and summer temperatures, but they are limited in temporal and frequency range by the life-span of available trees. Here, the applicability of a summer temperature reconstruction for Srinagar, Kashmir, is extended to 1660 AD by the use of the longest available samples of Himalayan silver fir to create regional chronologies of maximum latewood density and total ring width for the mountains surrounding the Vale of Kashmir.

MATERIALS AND DATA USED

Tree-ring materials

The collection and development of the tree-ring materials used to develop this reconstruction was described by Hughes and Davies (1987) and Hughes (1992). Replicated, cross-dated chronologies of *Abies pindrow* were developed from a network of sites distributed in the mountains around the Vale of Kashmir (Fig. 1). All but two of the eight sites used were at elevations between 3100 and 3400 m a.s.l.. The lowest was at 2620 m a.s.l. with an East-Northeast aspect, and all but one of the sites had an aspect between East and North. All but one were on slopes greater than 40 degrees. The earliest dated ring at each site ranged from 1604 to 1777 AD. After crossdating and analysis using X-ray microdensitometry (Lenz *et al.*, 1976; Hughes & Davis, 1987; Hughes, 1992), site and regional chronologies were developed for maximum latewood density (MXD), minimum earlywood density (MND), earlywood width (EWW), latewood width (LWW) and total ring width (TRW). This was done by removing age/size trend from the series of measurements for each core by fitting a spline with a variance reduction function of 50% at two-thirds the length of the series, and taking the quotient of the actual and fitted value for each year as the index. Each series was then prewhitened using a conservatively fit time-series model. The detrended and prewhitened measurement series for the cores were then combined by averaging to produce the site and regional chronologies for four of the five variables. MND was not used because it showed weak correlation between trees at the same site.

Hughes (1992) chose to present reconstructions only as far back as 1780 AD based on the eight TRW and seven MXD series developed from individual site chronologies. These reconstructions are referred to here as being from the 15-series network. This limitation was necessary because the chronologies most strongly weighted in the climate calibrations were poorly replicated in their early decades. However, he also reported that there was a very strong common regional signal in three of the four variables, the percentage of variance accounted for by the first principal component of the network from 1891-1980 AD being: MXD 61%; EWW 29%; LWW 47%; TRW 45%. Fig. 2 gives a graphical representation of

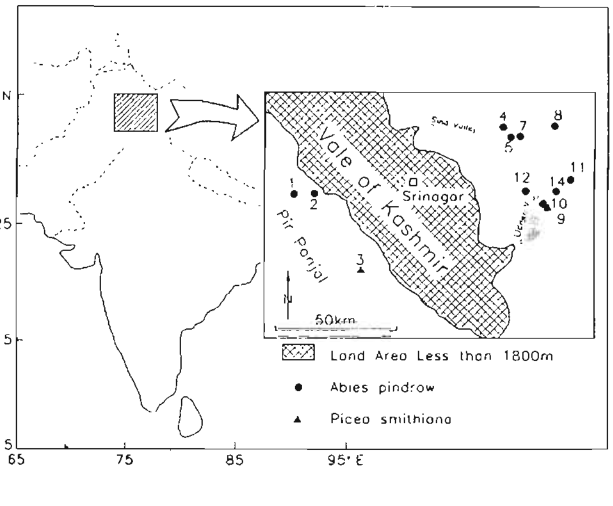

Fig. 1—The location of Srinagar, and of the tree-ring sites used in this paper. The three-letter site codes given in Fig. 2 correspond to numbers on this map thus: GUL-2; KHI-3; SAR-8; SON-7; WSO-4; CHA-11; THI-5; PAH-10. From Hughes (1992).

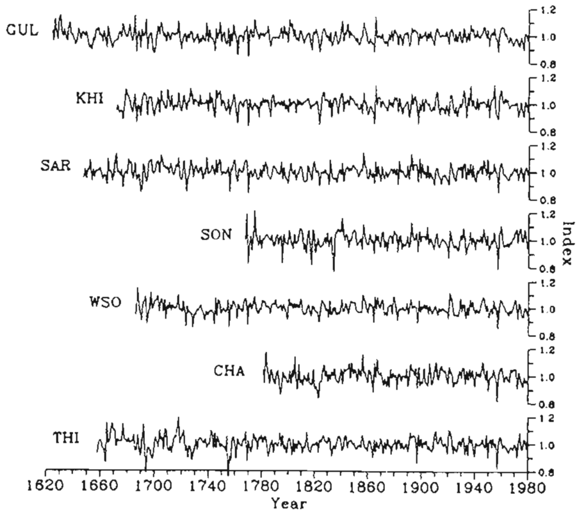

Fig. 2—Maximum latewood density chronologies for seven of the sites shown in Fig. 1. The vertical axes show dimensionless indices produced by standardizing the raw measurements to remove age/growth trend. See text for explanation.

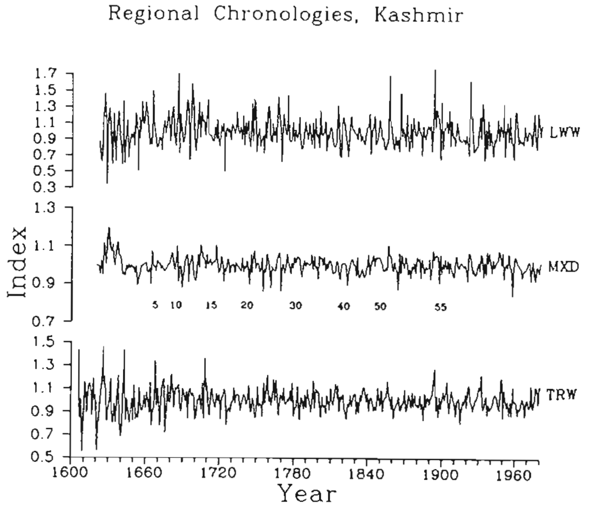

Fig. 3—Regional chronologies developed as described in the text. Each is based on a different tree-ring variable: LWW-latewood width; MXD-maximum latewood density; TRW-total ring width. The numbers over the MXD curve show the number of samples in the chronology at that year. The vertical axes show dimensionless indices produced by standardizing the raw measurements to remove age/growth trend. See text for explanation.

the strength of this regional signal in the case of MXD. This common signal results from a common pattern of climate response as revealed by response function analysis (see below). Therefore Hughes (1992) circumvented the problem of inadequate replication in the early years of site chronologies by calculating mean regional chronologies using the best materials from all the available sites (Fig. 3). The best materials were those with clear cross-dating, maximum length, and strong correlation with measurements from the other trees. All of the original raw data are available on-line at World Data Centre 'A' for Paleoclimatology, International Tree-Ring Data Bank.

Meteorological data

Monthly mean temperature and total precipitation data for Srinagar, Kashmir (34°05' N, 74°50' E, 1587 m a.s.l.) from 1893 AD on were obtained from World Weather Records. Although it is located in a high valley between two major mountain ranges, the summer temperature at Srinagar is well correlated with a region stretching from eastern Iran to the western Tibetan Plateau (Fig. 4).

IDENTIFICATION OF CLIMATE SIGNAL

Response functions

Response functions were calculated according to the procedures developed by Fritts *et al.*, 1971 and Fritts, 1976. The response function is based on an orthogonalized regression of monthly temperature and precipitation on the tree-ring chronology, and permits an examination of the influence of climate variables that may be correlated with one another. The meteorological data from the Srinagar station were used in these analyses. It is clear that MXD and LWW are more strongly correlated with temperature and precipitation than is TRW (Fig. 5). Both MXD and LWW show strong responses to temperature at the beginning (April-May) and end (August-September) of the growing season. This phenomenon has been observed in many other response functions for MXD (e.g., Briffa *et al.*, 1988, 1992; Conkey, 1986). In the case of several of the Kashmir sites, small but significant negative response function elements were found for July temperature in MXD and LWW.

Transfer functions

Hughes (1992) used the earlier version of the MXD regional chronology to reconstruct April-May temperature at Srinagar back to 1690 AD. This reconstruction had a calibration r^2 of 0·37 ($p<0{\cdot}0001$) for 1893-1942, and verification r^2 of 0·29 ($p<0{\cdot}01$) for 1943-1968, compared to 0·53 and 0·40 respectively for the reconstruction based on the 15-series network. As the version of the regional MXD chronology he used contained significant persistence, Hughes (1992) offered both current and next years' MXD chronologies as predictors, but the best model used only the current year values.

In the development of a transfer function using the new version of the regional chronologies, only current year MXD and TRW were offered as predictors, as they had been prewhitened. LWW was not used as it is highly correlated with MXD. As in the earlier work, the period 1893-1970 was used for calibration and verification. A marked decline in correlation between MXD and temperature was noted after 1970 (Hughes, 1992), suggesting a change in the relationship between the two. The mean temperature for a 'split summer' comprising April-September with July omitted was used as predictand. This was done because of the lack of response of the tree-ring variables in July, and because models including July temperature did not perform as well as those without July in terms of calibration and verification statistics. A 'jacknife' calibration-verification scheme was used (Fig. 6), with the periods 1893-1931 and 1931-1970 as complementary calibration and verification periods. Very strong statistics were found for both periods on all tests applied. In addition, the individual terms of the regression equations derived in the calibration stage (not shown) were similar for the two periods, indicating a temporally stable relationship between 1893 and 1970. Therefore, a new calibration was calculated for the whole period 1893-1970 (Fig. 6) with an adjusted r^2 of 0·58 ($F=53{\cdot}52$, $p<0{\cdot}0001$). A leave-one-out approach was used to calculate verification statistics for this calibration, giving an adjusted r^2 of 0·56, and the correct sign of first difference in 63 of the total of 77 years (ST in Fig. 6). The strong relationship between observed split summer temperature and that derived using the transfer function is illustrated in Fig. 7. The tree rings capture the major elements of multi-year to interdecadal variability as well as interannual variability.

THE RECONSTRUCTION

Given these strong diagnostic statistics, the new split summer transfer model was applied to the new versions of the regional MXD and TRW chronologies to produce the reconstruction shown in Fig. 8. This reconstruction may not be directly compared with the spring and late-summer temperature reconstructions reported by Hughes (1992), since they differ from one another as a result of their seasonality. Runs of summers of above-average warmth are reconstructed for the early 18th century, early 19th century, mid-19th century and mid-20th century. Sustained periods of cool summers are reconstructed for the mid-18th century, the early 19th century and from around 1950 to the end of the reconstruction in 1970. Most of the coolest individual summers are reconstructed for the first century of the reconstruction, while the warmest summers are more evenly distributed. It is very unlikely that this is an artefact of the structure of the chronology, as the series is well replicated back as least as far as 1700. A

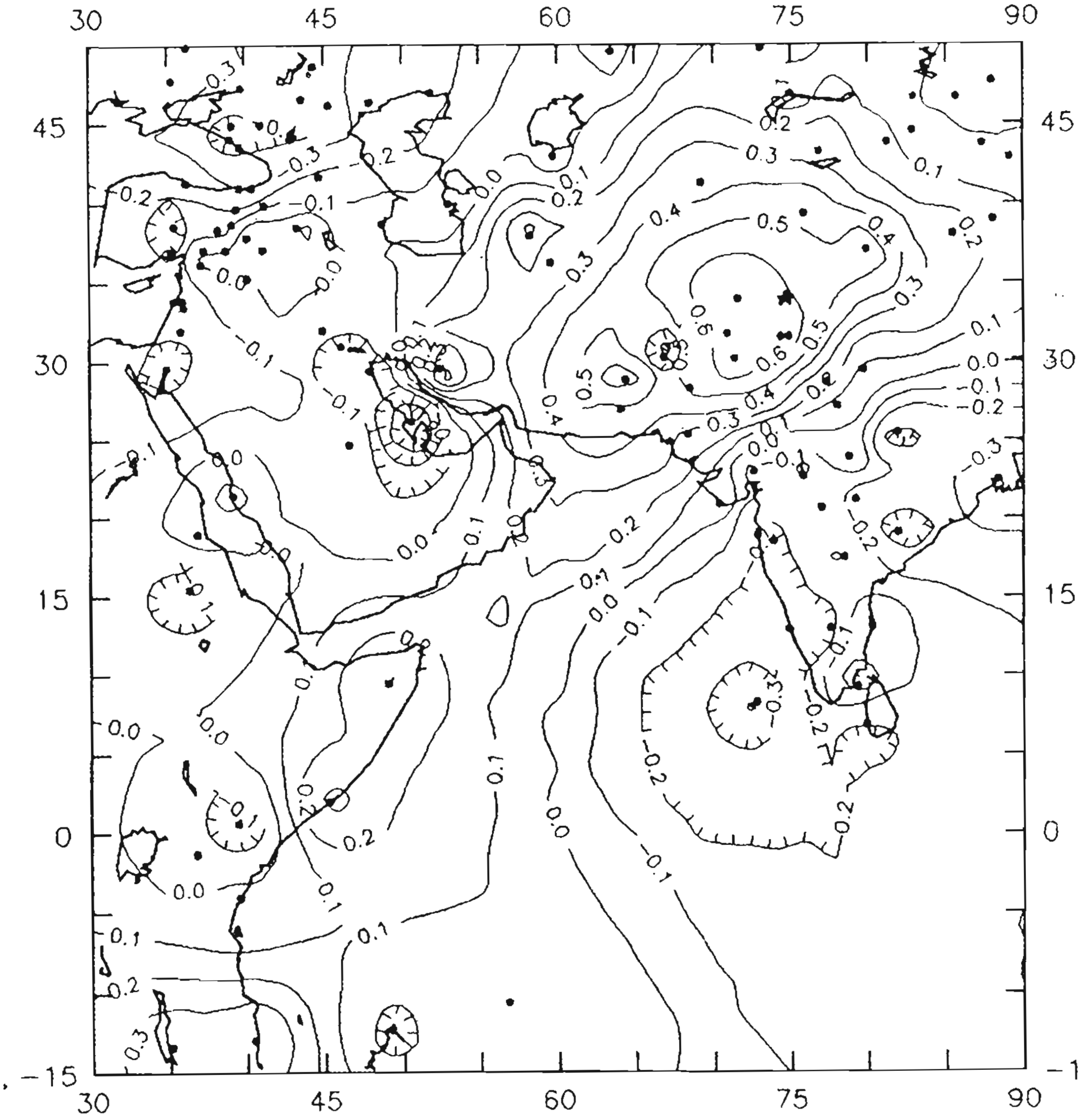

Fig. 4— Correlations between split summer (April-September without July) temperature at Srinagar (shown as a star) and stations throughout west Asia. Symbol sizes are proportional to correlation. Correlations were calculated for the period 1953-1972. All stations were screened for missing data and tested for homogeneity before being included in the data set prepared by G.M. Garfin.

reconstruction produced using only the 10 longest cores, and hence having little change in sample depth along its length, displayed this same feature. This rules out variation in sample depth as the cause of this feature. There is no consistent relationship between the timing of the coldest reconstructed summers and indices of explosive volcanic eruptions in the 24 months prior to the beginning of the growth season in April. This contrasts with work by, for example, Briffa *et al.* (1998a) and Hughes *et al.* (1999).

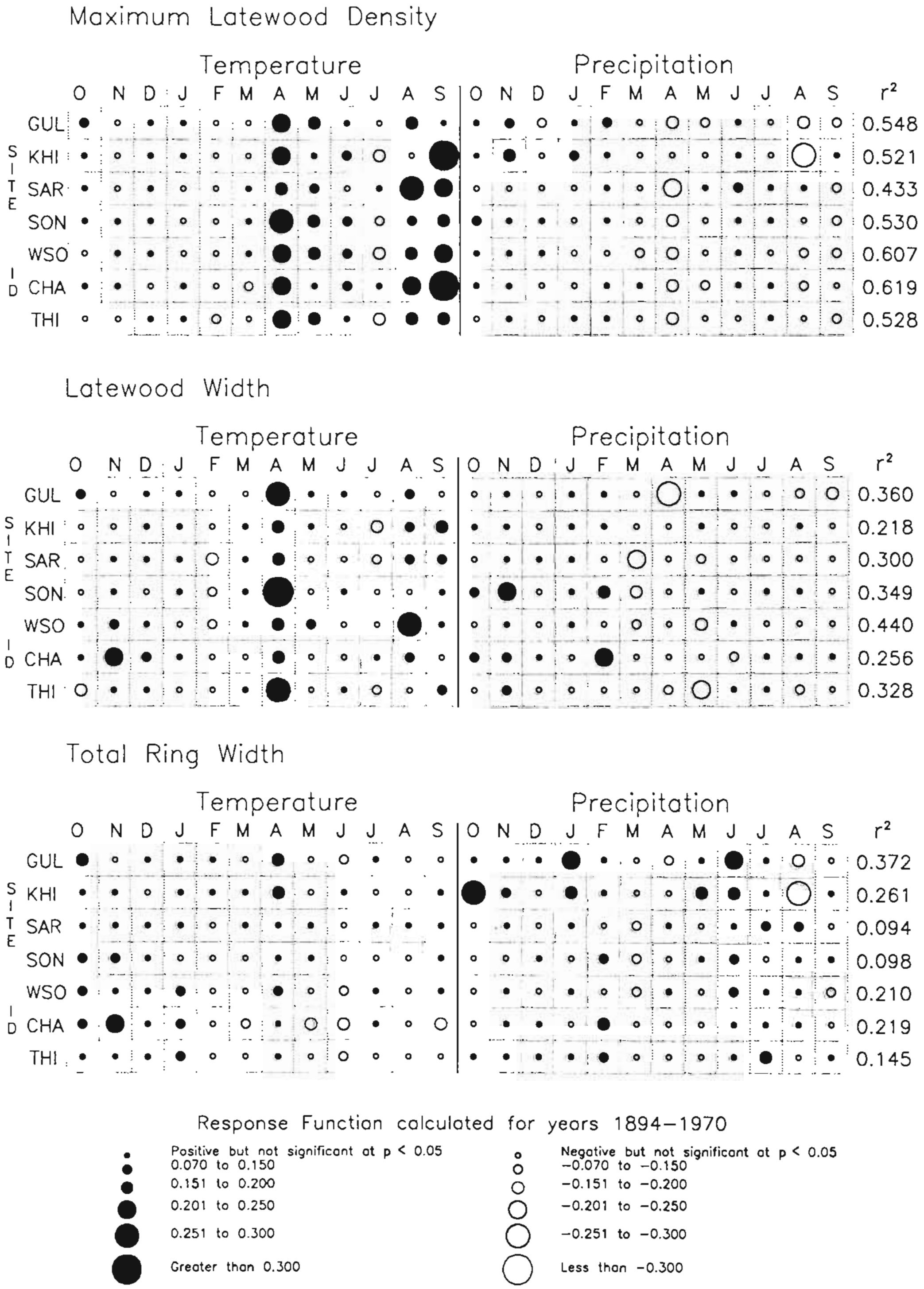

Fig. 5—Response function elements for Maximum latewood density (MXD) top panel; Latewood width (LWW) middle panel; Total ring width (TRW) lower panel.

Period	Calibration		Verification			
	r_a^2	F	r_a^2	ST	CE	RE
1893–1931	0.505	19.30***	0.516***	30/7***	0.343	0.478
1931–1970	0.647	34.44***	0.654***	29/7***	0.522	0.586
1893–1970	0.583	53.52***	0.560***	64/13***	–	–

*** p ≤ 0.0001 ST: Sign Test
** p ≤ 0.001 CE: Coefficient of Efficiency
* p ≤ 0.010 RE: Reduction of Error

Fig. 6—Split Summer Temperature.

DISCUSSION

Why should the correlations between MXD and LWW on the one hand and temperature on the other be strongest at the beginning and end of the growth season, but weak or even negative in July? The strength of correlation between MXD and early growth season temperatures is, at first sight, puzzling. Vaganov (1996), however, has pointed out the crucial role played in ring formation by conditions just after the initiation of cambial activity, including the predetermination of the size of latewood cells. This is also the time at which the size of the new needle mass is determined, which must influence the amount of photosynthate available for cell wall thickening at the end of the season. Similarly, it can be argued that a warm August-September will permit the production of excess photosynthate which could be available for increased thickening of latewood tracheid walls, leading to higher maximum latewood density. It is difficult to find a process of similar importance to the amount and density of latewood taking place in the middle of the season. It should also be borne in mind that, although the climate of the Vale of Kashmir is not strongly influenced by the summer monsoon, July is usually a time of major changes in circulation over this region, and July conditions are generally less strongly correlated with June and August than are other adjacent months in the year.

Since the first reconstructions for Kashmir based on TRW and MXD were published (Hughes, 1992), it has been reported that the relationship between many high-latitude MXD chronologies and temperature has weakened and changed, especially on decadal time scales, starting in the mid-20[th] century (Briffa *et al.*, 1998b). Is the weakened relationship seen in Kashmir since 1970 the result of the same phenomenon, or is there a problem with the instrumental data? This is an important topic for future research.

There are decadal-to-multidecadal features in the reconstruction, but no evidence of long-term trend. Given the shortness of many of the segments making up the chronologies used, this does not necessarily mean that such trends have not occurred. There is a tendency for a higher frequency of cool summers to be reconstructed before 1770 than after. There is no clear relationship between these cool summers and known explosive volcanic eruptions. There is evidence of large-scale spatial coherence between summer temperature in Kashmir and spring temperature several hundreds of kilometers to the southeast in Uttar Pradesh (Yadav *et al.*, 1997), at least on the decadal timescale. Examples of this include periods of cool conditions around 1750 and in the 1810s, and warmth in the 1850s.

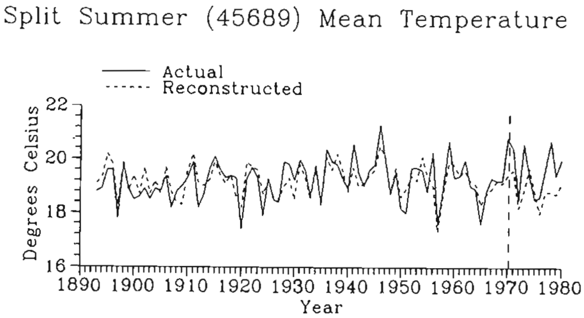

Fig. 7—Split summer temperature as observed at Srinagar (solid line) and as reconstructed in this paper (broken line).

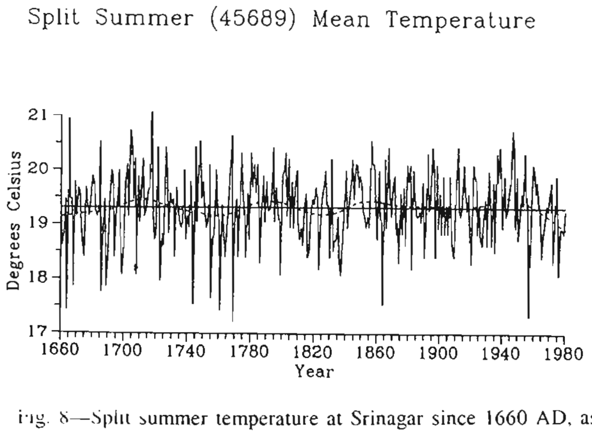

Fig. 8—Split summer temperature at Srinagar since 1660 AD, as reconstructed in this paper.

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Teak vessel chronologies as an indicator of Southeast Asian Premonsoon temperature

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ABSTRACT

Pumijumnong N & Park W-K 2001. Teak vessel chronologies as an indicator of Southeast Asian Premonsoon temperature. Palaeobotanist 50(1) : 21-26.

The presented dendroclimatological study on Teak (*Tectona grandis* L.) was carried out in northern Thailand by using earlywood vessel density and latewood conductive area and other anatomical variables. The vessel density is determined using an image analysis system. The anatomical variables are used to calibrate and verify temperature during the March period. The regression equation explains about 44% of the relationship among calibrated variances. The study also suggests that more detailed study of El Nino via anatomical variables and tree-ring widths might be possible.

Key-words—Anatomical variable, Teak, Image analysis system, El. Nino.

दक्षिण-पूर्वी एशियाई मानसूनी तापमान के संकेतक के रूप में टीक वाहिका का कालानुक्रम

नासुदा पूमिजुमनांग एवं वोन-क्यू पार्क

सारांश

अग्र दारु घनत्व एवं पश्चदारु वाहिनी क्षेत्र तथा अन्य शारीरीय चरों की सहायता से उत्तरी थाईलैण्ड क्षेत्र का वृक्षजलवायुविक अध्ययन किया गया। प्रतिबिम्ब विश्लेषण सिस्टम की सहायता से वाहिका के घनत्व का भी अभिनिर्धारण किया गया है। शारीरीय चरों को मार्च की अवधि के तापमान को अनुसंशोधित एवं अभिप्रमाणित करने हेतु प्रयुक्त किया गया है। समाश्रयण समीकरण अनुसंशोधित प्रसरणों के मध्य लगभग 44% का सहसम्बन्धन व्याख्यायित करता है। अध्ययन से यह भी प्रस्तावित होता है कि शारीरीय चरों तथा वृक्ष-वलय चौड़ाइयों द्वारा एल निनो का अधिक विस्तृत अध्ययन किया जाना सम्भव है।

संकेत शब्द—शारीरीय चर, टीक, प्रतिबिम्ब विश्लेषण सिस्टम, एल निनो.

INTRODUCTION

TEAK (*Tectona grandis* L.) is one of the few species in the subtropical zone in Southeast Asia that has potential for dendroclimatology. Teak tree-ring width has been proven in various studies to have a significant, positive correlation with rainfall. For example, teak growth in Northern Thailand was positively correlated with rainfall during the beginning of the rainy season (Pumijumnong *et al.*, 1995), teak growth in Myanmar was positively correlated

Observation	Variables	Symbol	Description
Earlywood	EWAREA	V1	Earlywood vessel area
	EWD4	V2	Earlywood conductive area
	EWDD	V3	Earlywood vessel density
	EWDIA	V4	Earlywood vessel diameter
Latewood	LWAREA	V5	Latewood vessel area
	LWD4	V6	Latewood conductive area
	LWDD	V7	Latewood vessel density
	LWDIA	V8	Latewood vessel diameter
Total ring	TWAREA	V9	Total ring vessel area
	TWD4	V10	Total ring conductive area
	TWDD	V11	Total ring vessel density
	TWDIA	V12	Total ring vessel diameter
Ring Width	RW	V13	Ring width

Fig. 1—Twelve anatomical variables and ring width.

with April rainfall, which is during the transition period from the dry season to the wet season (Pumijumnong *et al.*, 2001), just as teak growth in Java was positively correlated with rainfall in the transition period between the dry season and the wet season (D'Arrigo *et al.*, 1994), and teak growth in India was positively correlated with rainfall during the previous October (Bhattacharyya *et al.*, 1992). In contrast to rainfall, temperature seems to have a very weak effect on radial growth of teak in this region.

Image analysis was employed as a new technique to obtain certain anatomical variables of tree rings. Methods have been developed to determine vessel size and vessel density in broad-leaf trees of Temperate Zone using this technique (Eckstein & Frisse, 1982; Woodcock, 1989; Sass & Eckstein, 1992; Sass, 1993). For subtropical trees Pumijumnong and Park (1999, 2000) have applied the image analysis method to Thai teak.

OBJECTIVE

The objective of the study is to explore whether or not anatomical variables can be used to produce a better reconstruction of Southeast Asia temperature, as opposed to tree-ring width.

MATERIAL AND METHODS

Twelve anatomical variables (Fig. 1) were derived from five teak trees and two cores per tree from northern Thailand. These were completely measured for the 50 years 1947-1996 using an image analysis system (Image-Pro Plus, Media Cybertic L.P. 1994). These anatomical variables were detrended by fitting first a negative exponential or straight

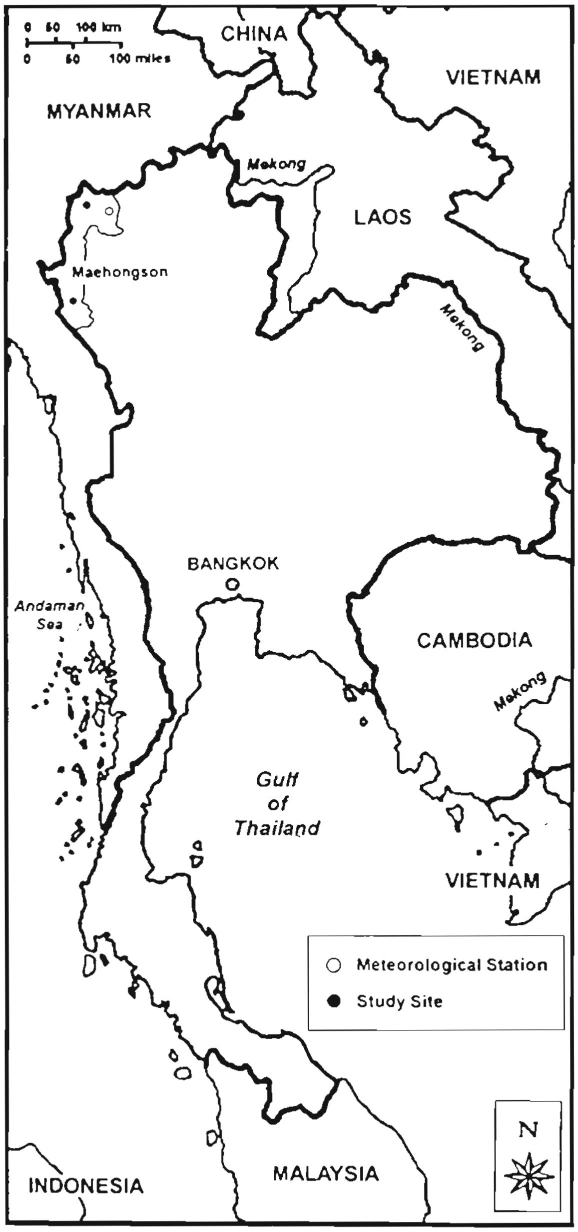

Fig. 2—Map of Thailand and study area. ⟶

line or a cubic spline with a 50% response period of 66 years. An autoregressive model was applied to the detrended series, and the residual series were averaged using the robust mean to obtain the final chronology (Cook, 1985).

Climate data were obtained from the Maehongson Station, situated at a lower elevation (271·68 m a.s.l.) than the tree-ring sites (600-700 m a.s.l.), and about 30 km away from the study site (Fig. 2). Fig. 3 shows a climate diagram of the study area in Maehongson Province. The temperature data extend from AD 1951 to 1997.

These thirteen variables and mean monthly temperature were analyzed by Pearson correlation. We included lagged anatomical variables in $year_{(t0)}$, $year_{(t-1)}$, $year_{(t+1)}$ and $year_{(t+2)}$ in order to consider biological persistence in the series. We finally selected March temperature for reconstruction because it was most highly correlated with ring variables.

Stepwise regression modelling was employed to calculate each significant dependent variable and principal component. Only the significant equations were employed to estimate independent variables. Finally, we calibrated and verified these independent variables. The calibration period was from 1948 to 1972, and the verification period was from 1973 to 1994.

RESULTS AND DISCUSSION

This study chooses temperature data in March as an equation because it showed reasonable relationship among the variables in equation. Although the temperature in May and June revealed a positive correlation with anatomical variables more than data in March, but the results of stepwise analysis using temperature data in May and June were more complicated and hardly to explain such relationship between the variables. Six anatomical variables ($V6_{(t0)}$, $V61_{(t-1)}$, $V3_{(t+1)}$, $V10_{(t+1)}$, $V62_{(t+2)}$ and $V112_{(t+2)}$) were first entered into the equation. The significant variables in the stepwise regression equation for estimated March temperature were ET3 = 260·1150-12·3556 * V61 + 25·6757 * V3 - 11·7864 * V62, where ET3 is estimated March temperature, $V61_{(t-1)}$ is latewood conductive area in $year_{(t-1)}$, $V3_{(t+1)}$ is earlywood vessel density in $year_{(t+1)}$ and $V62_{(t+2)}$ is latewood conductive area in $year_{(t+2)}$. Fig. 5 shows summary statistics for the calibration period and verification period for March temperature.

The percentage of variance (r^2=0·444) that explains the dependent variable of the equation. Pearson correlation indicates the degree of coherence integrated over all frequencies. Calibration and verification periods show a Pearson correlation of 0·4595 and 0·6500, respectively. The reduction of error statistic (RE), a procedure test of the reliability of a climate reconstruction (Fritts, 1976), which can be applied to independent data (e.g., anatomical variables) to measure the association between a series of actual values and their estimates. RE is 0·1789 and 0·4224 for calibration and verification, respectively. Notably, the reduction of error statistic results are all positive, and are equal to or greater than the proposed lower-limit of acceptable RE values. This

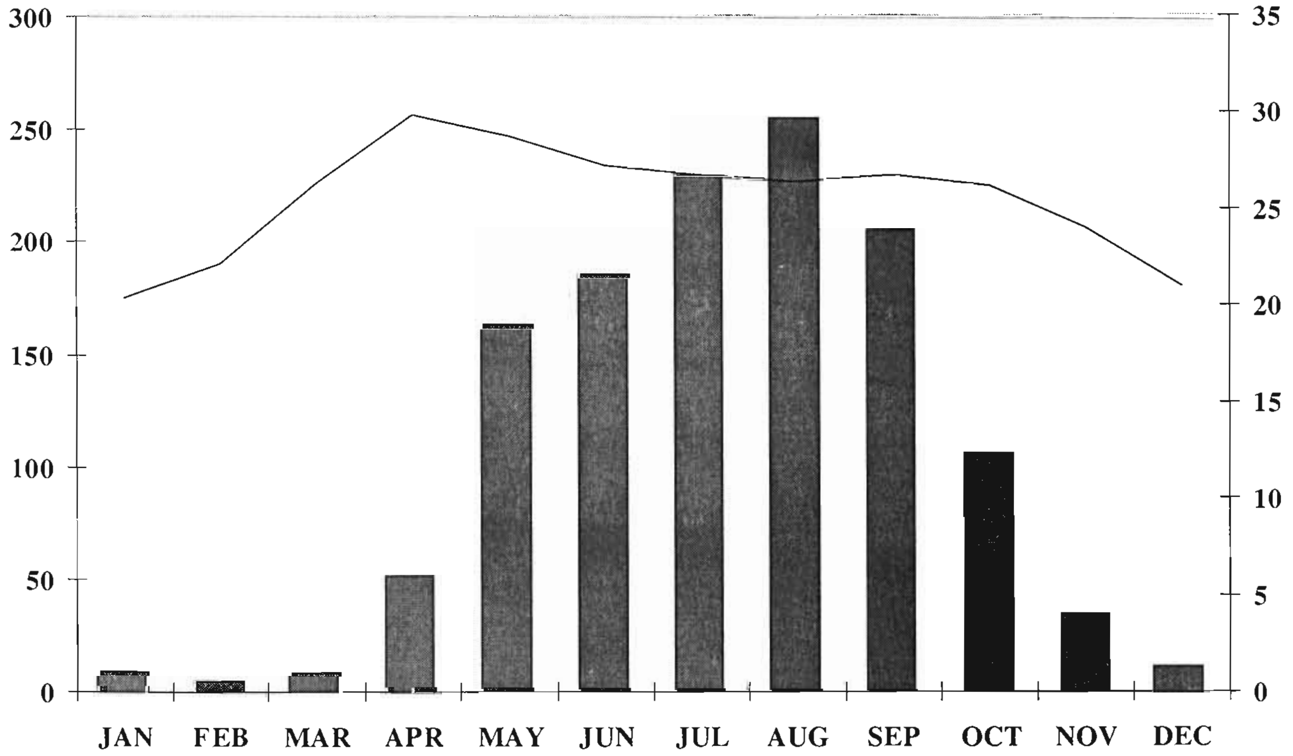

Fig. 3—Climate diagram of Maehongson Province. Bars represent mean annual rainfall (1911-1997); lines represent mean temperature (°C).

Climate	Month	Significant	Variable
Rainfall	Current April	Negative	EWAREA (V1) EWDIA (V4) EWDD (V3) TWAREA (V9) TWDIA (V12) TWD4 (V10)
	Current May	Positive	EWAREA (V1) EWDIA (V4) LWD4 (V6)
		Negative	LWDD (V7) TWDD (V11)
Temperature	Current April	Positive	LWDD (V7) TWAREA (V9) TWDIA (V12) TWD4(V10) TWDD (V11)
	Current May	Positive	LWDD (V7) TWAREA (V9) TWD4(V10)
	Current June	Negative	LWAREA (V5) LWDIA (V8) LWD4 (V6)

Source: Pumijumnong & Park (1999)

Fig. 4—The correlation between climate data and anatomical variable.

Statistic parameters	Calibration (1951-1972)	Verification (1973-1994)
$R^2 = 0{\cdot}444$		
Correlation	0·4595*	0·6500*
Reduction of error	0·1789*	0·4224*
T-value	2·8398*	1·5859>=1·7200
Sign-products	9<=6	5*

ET3 = 260.1150 - 12.3556 * V61 + 25.6757 * V3 - 11.7864 * V62..., where:

ET3, estimated March temperature

V61, latewood conductive area in $year_{(t-1)}$

V3, earlywood vessel density in $year_{(t+1)}$

V62, latewood conductive area in $year_{(t+2)}$

*Significant value at 95% confidence level

Fig. 5—Summary statistics of parameters for calibration and verification periods.

strongly indicates that the calibration and verification are reliable. The T-value, which calculates the products of the deviations and collects the positive and negative products in two separate groups based on their signs. The T-values of the series are 2·8398 and 1·5859. The sign-products test indicates whether or not sufficient similarity exists between the actual and estimated data. For this study, sign-products of calibration and verification periods are 9 and 5.

Fig. 6 depicts actual March temperature versus estimated March temperature derived using the above equation. The estimated March temperature (dotted line) better coincides with actual March temperature during the verification period (1973-1994) than during the calibration period (1951-1972). In 1986, the estimated value exceeds the actual value, although after this their patterns are similar until the year 1973. The calibration period, which has a correlation value of 0·4595, shows some different peaks between the actual and estimated March temperature, such as in 1970, 1967, 1963 and 1955.

The anatomical variables that are negatively correlated with March temperature are $V61_{(t-1)}$ (latewood conductive area in $year_{(t-1)}$) and $V62_{(t+2)}$ (latewood conductive area two years later). The anatomical variable that is positively correlated with March temperature, is $V3_{(t+1)}$ (earlywood vessel density in $year_{(t+1)}$). The role that temperature plays in teak growth may be more difficult to determine than that of rainfall due to steady warm temperature in the subtropical zone, combined

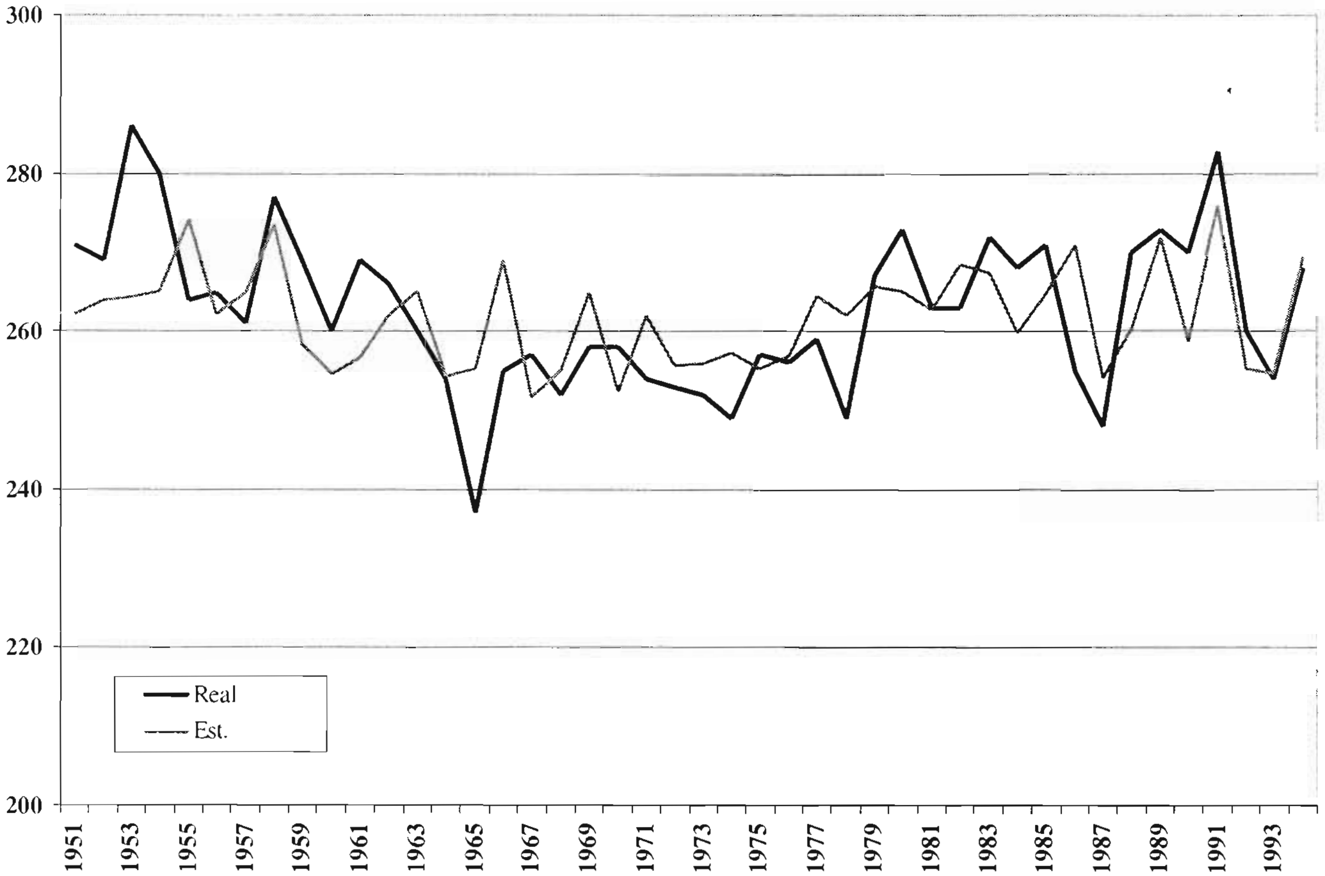

Fig. 6—Depicts current March temperature (thick line) versus estimated March temperature (thin line).

with complex hormonal processes in the tree. Previous studies emphasized that May temperature has a negative correlation with tree-ring width (Pumijumnong 1995). However, in this study tree-ring width was not entered into the stepwise regression model. Still, this may be accounted for, by considering high temperature which usually means less rainfall (i.e., a drought year), causing teak to produce a narrow ring, otherwise containing only a large vessel with one or two lines and no latewood. This coincides with the fact that the regression equation shows a negative correlation between temperature and latewood conductive area (V61). In a normal year optimum temperature combines with adequate rainfall and teak trees form a wider ring, with a large earlywood area and large earlywood vessel density (V3).

Present results using anatomical variables show a correlation with March temperature that we do not see using tree-ring width. Calibration and verification are reliable, as shown by 3 out of 4 statistical measures being at significant levels. The question is: Is it possible that if we examine these variables over a much longer period of time, the statistical parameters will show a higher correlation? Reconstructing March temperatures in Thailand could be important in analysing El Nino events, which begins around the end of December and continues some time into the following year, and warrants further research.

CONCLUSION

In Thai teak, latewood conductive area in year$_{(t-1)}$ and year$_{(t+2)}$ and earlywood vessel density in year$_{(t+1)}$ correlate with March temperature. Drought years cause the teak to have narrow rings with little or no latewood. By contrast, in a year with adequate water and optimal temperature, the teak will develop wide rings with large earlywood and latewood. Further studies will extend these measurements for more years, which will help to reconstruct March temperature for longer period. Besides anatomical variables can be used to determine the effect of El Nino phenomenon on teak growth in Thailand.

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Climatic implications of tree-ring density variations in Himalayan conifers

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ABSTRACT

Borgaonkar HP, Kumar KR, Pant GB, Okada N, Fujiwara T & Yamashita K 2001. Climatic implications of tree-ring density variations in Himalayan conifers. Palaeobotanist 50(1) : 27-34.

The densitometric analysis of Himalayan conifers from six different sites reveals the strong association of ring density parameters with regional climate. Minimum earlywood density and total ring width are major contributors to the tree growth-climate relationship. It also indicates that pre-monsoon (March-April-May) temperature has significant positive relationship with earlywood density and significant negative correlation with total ring width. In case of precipitation, earlywood density gives negative relationship and ring width gives positive relationship with pre-monsoon precipitation. Latewood density parameters do not show any coherent pattern of relationship with climate. A strong association of earlywood density and ring width parameters may be due to severe moisture stress conditions occurring during the early phase of growing season of the conifers over the region.

Key-words—Conifers, Himalaya, Climate, Tree-ring density.

हिमालयी शंकुवृक्षों के घनत्व वैविध्य के जलवायुविक निहितार्थ

एच.पी. बोरगाँवकर, के. रूप कुमार, जी.बी. पंत, एन. ओकादा, टी. फूजीवारा एवं के. यामाशिता

सारांश

छः भिन्न-भिन्न स्थलों से प्राप्त हिमालयी शंकुवृक्षों के घनत्वमिति विश्लेषण से क्षेत्रीय जलवायु के साथ वलय घनत्व प्राचलों का दृढ़ साहचर्य प्रदर्शित हुआ है। वृक्ष वृद्धि-जलवायु सम्बन्धों के मूल्यांकन में न्यूनतम अग्रदारु घनत्व तथा सकल वलयी चौड़ाई प्रमुख भूमिका का निर्वाह करते हैं। इससे यह भी संकेत मिलता है कि मात्र मानसून पूर्व (मार्च-अप्रैल-मई) जलवायु (तापमान एवं वर्षण) का ही अग्रदारु घनत्व एवं सकल वलयी चौड़ाई के साथ महत्त्वपूर्ण सम्बन्ध है जबकि पश्चदारु घनत्व प्राचल जलवायु के साथ कोई प्रभावी सम्बन्ध नहीं प्रदर्शित करते हैं। अग्रदारु घनत्व प्राचलों का दृढ़ साहचर्य इस क्षेत्र में शंकु वृक्षों के वृद्धि करने की प्रारंभिक प्रावस्था के दौरान की भयावह आर्द्र प्रतिबल स्थितियों के कारण हो सकता है।

संकेत शब्द—शंकुवृक्ष, हिमालय, जलवायु, अग्रदारु.

INTRODUCTION

OVER the western Himalayan region numerous tree-ring studies have been done using Himalayan conifers (Pant, 1979, 1983; Pant & Borgaonkar, 1984; Pant *et al.*, 1998; Hughes & Davies, 1987; Borgaonkar *et al.*, 1994, 1996, 1999; Bhattacharyya *et al.*, 1988; Bhattacharyya & Yadav, 1999). Tree-ring width index chronologies from different parts of the western Himalaya show significant relationship with pre-monsoon (March-April-May) temperature and precipitation (Borgaonkar, 1996; Yadav *et al.*, 1999). These results are based on only ring widths. However, ring density parameters are also important in dendroclimatic studies to better understand the tree growth-climate relationship at intra-annual to intra-seasonal scales (Schweingruber *et al.*, 1978).

Preliminary study by Pant *et al.* (2000) on tree-ring density parameters of Himalayan cedar (*Cedrus deodara* D. Don) indicates the important role of earlywood density in dendroclimatic modelling. Though their analysis was limited to a single conifer species from two nearby sites of western Himalaya, it primarily indicates the high potential of earlywood density of *Cedrus deodara* for climate reconstruction. In the present paper, dendroclimatic analysis was carried out using density parameters of four conifer species namely *Cedrus deodara* D. Don., *Picea smithiana* Boiss, *Abies pindrow* Spach and *Pinus roxburghii* Sargent from six different sites of western Himalaya to determine their utility in dendroclimatic reconstructions. This also includes the density chronologies of *Cedrus deodara* from two sites studied by Pant *et al.* (2000) to compare with the density chronologies from other western Himalayan sites.

TREE-RING DATA

Eighty-one tree core samples from four different species of Himalayan conifers were analysed. Fig. 1 summarises the tree-ring site information. Ring density of the cores was measured at Forestry and Forest Products Research Institute, Tsukuba, Japan.

Cores were cut transversely to a thickness of 2 mm with a twin-bladed saw and oven dried. All samples were X-rayed with "soft" X-ray. The X-ray apparatus was EMBW-S type manufactured by SOFTEX. The distance between X-ray source and sample was set to 2·2 m with voltage 14 kV, current 12 mA and exposed time 4 minutes. The densitometric analysis of these x-ray radiographs was carried out on a DENDRO-2003 tree-ring workstation. Six parameters were measured on each tree-ring sample from transmitted image of the x-ray film to produce time series of earlywood, latewood, minimum, maximum and mean densities along with total ring width. The boundary between earlywood and latewood was identified as the mid point between the maximum and minimum density measurement of each ring.

All ring width series were checked with computer programme COFECHA (Holmes *et al.*, 1986) for possible measurement or dating errors. This involves statistical cross dating to test each individual series against a master chronology of the site on the basis of correlation coefficients. Any error in dating was rectified by re-checking/ re-measuring the sample. All chronologies showed good cross matching.

CLIMATE DATA

The network of meteorological stations over western Himalaya is sparse and records are discontinuous. Particularly at higher elevations very few meteorological stations are available. Consequently, it is commonly difficult to locate meteorological stations close to the tree-ring sites for

Site	Location	Elevation in Meter	Date of Collection	Species	Chronology name	No. of cores
Narkhanda (H.P.)	31°12' N 77°14' E	3000	April, 1990	*Abies pindrow*	NARAP	12
				Picea smithiana	NARPS	6
				Cedrus deodara	NARCD	12
Gahan (H.P.)	31°11' N 77°14' E	2500	April, 1990	*Picea smithiana*	GAHPS	10
Kufri (H.P.)	31°07' N 77°10' E	2600	June, 1989	*Cedrus deodara*	KUFCD	15
Kanasar (U.P.)	30°45' N 77°48' E	2200	June, 1989	*Cedrus deodara*	KANCD	9
Dhanolti (U.P.)	30°45' N 78°25' E	2400	April, 1991	*Picea smithiana*	DHAPS	5
Ghansali (U.P.)	30°37' N 78°45' E	2100	April, 1991	*Pinus roxburghii*	GHAPR	12

Fig. 1—Western Himalayan tree-ring sites used for density measurement.

Sr. No.	Station	State	Latitude	Longitude	Elevation(m)	Rainfall Period	Temperature Period
1	Srinagar	J & K	34° 05'	74° 50'	1587	1893-1990	1893-1990
2	Shimla	H.P.	31° 06'	77° 10'	2202	1863-1990	1876-1990
3	Mussoorie	U.P.	30° 27'	78° 05'	2042	1869-1990	1901-1990
4	Dehradun	U.P.	30° 19'	78° 02'	682	1861-1990	1901-1990
5	Pauri	U.P.	30° 08'	78° 55'	1595	1871-1982	—
6	Nainital	U.P.	29° 24'	79° 28'	1953	1849-1982	—
7	Mukteshwar	U.P.	29° 28'	79° 39'	2311	1901-1990	1901-1990
8	Almora	U.P.	29° 35'	79° 41'	1676	1856-1982	—
9	Joshimath	U.P	30° 33'	79° 34'	1875	1871-1990	—
10	Pithoragarh	U.P.	29° 35'	80° 15'	1639	1864-1982	—

Fig. 2—List of meteorological stations of Western Himalaya used in the analysis.

dendroclimatic analysis. In the present analysis monthly rainfall and monthly mean surface temperature anomalies for the period AD 1901-90 were calculated from the data of the stations widely spread over the western Himalaya as listed in Fig. 2. These stations possess continuous data of monthly rainfall and temperature for the period as shown in Fig. 2. Most of the climate time series show significant correlations ($p < \cdot 001$) among the stations (Pant *et al.*, 1999). The regional anomalies have been obtained by arithmetic average of individual station's anomalies from their respective means. Thus, the monthly anomalies of rainfall based on the data of 10 stations and temperature anomalies based on data of 5 stations represent the climate of entire western Himalayan region. These anomaly series were used further in response function analysis for dendroclimatic modelling.

Parameters	Chronology name	Common period	Mean sensitivity	Mean correlation between the trees	Signal to noise ratio (SNR)	% Variance due to first eigen vector	Expressed population signal (EPS)
Ring width	NARAP	1749-1986	·23	·36	6·75	44	·87
	NARPS	1805-1988	·22	·33	2·95	46	·74
	NARCD	1835-1982	·25	·30	5·14	40	·84
	GAHPS	1857-1984	·22	·37	5·87	41	·86
	KUFCD	1899-1984	·23	·42	10·86	45	·91
	KANCD	1878-1986	·29	·38	5·52	46	·85
	DHAPS	1852-1988	·25	·37	2·93	40	·75
	GHAPR	1861-1982	·26	·31	5·39	42	·84
Earlywood Density	NARAP	1749-1986	·11	·32	5·65	42	·85
	NARPS	1805-1988	·08	·39	3·80	47	·79
	NARCD	1835-1982	·10	·28	4·67	38	·82
	GAHPS	1857-1984	·08	·39	6·39	40	·86
	KUFCD	1899-1984	·05	·28	5·83	36	·85
	KANCD	1878-1986	·07	·21	2·39	34	·70
	DHAPS	1852-1988	·05	·40	3·33	41	·77
	GHAPR	1861-1982	·05	·29	4·90	39	·83
Latewood Density	NARAP	1749-1986	·05	·05	·63	23	·39
	NARPS	1805-1988	·04	·05	·5	26	·24
	NARCD	1835-1982	·10	·09	1·18	20	·54
	GAHPS	1857-1984	·07	·11	1·23	25	·55
	KUFCD	1899-1984	·28	·23	4·48	29	·81
	KANCD	1878-1986	·03	·08	·78	22	·41
	DHAPS	1852-1988	·02	·12	·68	18	·40
	GHAPR	1861-1982	·04	·18	2·63	28	·72

Fig. 3—Statistics for residual chronologies of ring width and density parameters of western Himalayan conifers.

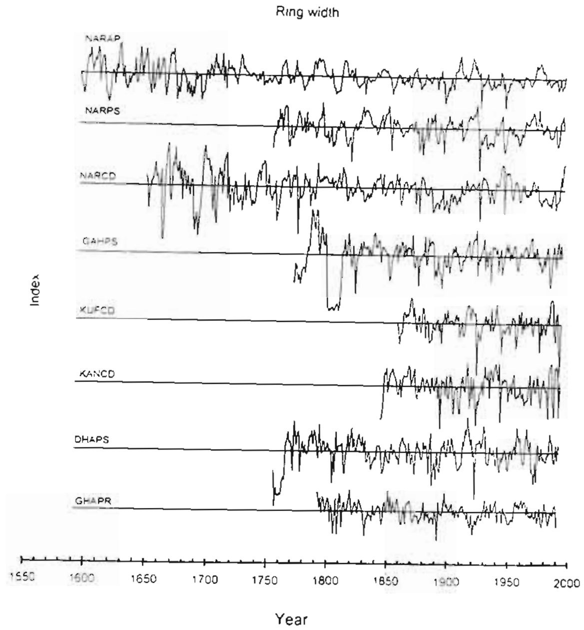

Fig. 4 (a)—Ring width index chronologies from western Himalaya.

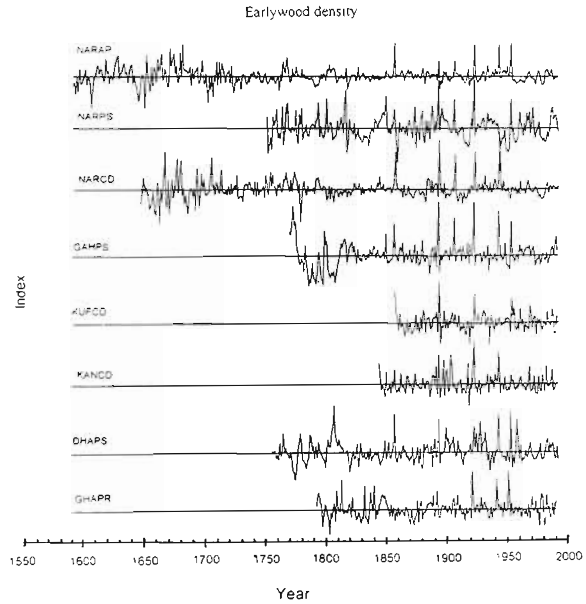

Fig. 4 (b)—Earlywood density index chronologies from western Himalaya.

DENDROCLIMATIC ANALYSIS

Before using the tree-ring series for dendroclimatic modelling, they were standardised using computer programme ARSTAN (Holmes *et al.*, 1986) to remove non-climatic signal and maximise common climatic signal in the series (Fritts, 1976; Cook *et al.*, 1990). All series were standardised by applying a suitable spline as this option gives the optimum signal as demonstrated by Borgaonkar *et al.* (1999) for western Himalayan conifers. Most of the tree-ring series show many occasions of suppression and release of tree growth. This may be due to natural survival competition among the trees, hence cubic spline smoothing is more suitable than other filters, such as negative exponential, linear regression, polynomial etc. Exogenous disturbances (fire, insect, pollution) are less over the sites, therefore, the spline stiffness was selected as 60%N, where, N is series length (Cook *et al.*, 1990; Borgaonkar, 1996). The programme ARSTAN also gives the information about dendroclimatic potential of the series in terms of common variance explained by the individual series, which is attributable to climate. Significant persistence (autocorrelation) in the series is a common feature of Himalayan conifers (Borgaonkar, 1996). The auto-regressive modelling option in the programme ARSTAN was used to remove autocorrelation structure from the series thus forming the residual version of the chronology.

Fig. 3 gives some important common period statistics for total ring width, minimum earlywood and maximum latewood densities of eight different residual chronologies. These statistics are informative to evaluate the dendroclimatic potential of the tree-ring series (Fritts, 1976). It was observed that ring-width chronologies exhibit moderately high values of mean sensitivity (the average relative difference from one ring to the next). Mean correlation between the trees and variance due to first eigen vector, which are the measure of common signal, are relatively higher in ring-width and earlywood density than latewood density chronologies. These high values may be due to a widespread common climate signal. The ring-width and earlywood density series also show large signal to noise ratio. This reveals that earlywood density of Himalayan conifers is climatically more sensitive than the latewood density. These results are similar to those presented by Pant *et al.* (2000) for density parameters of two *Cedrus deodara* sites of the western Himalaya. Fig. 4a and b represent residual chronologies of ring width and earlywood density respectively. The Expressed Population Signal (EPS) given in Fig. 3 quantifies the degree of which the sample size of particular chronology represents the hypothetically perfect chronology. The EPS values of ring-width and earlywood density chronologies are sufficiently high and statistically reliable for climate studies. (Briffa & Jones, 1990).

Response function analysis (Fritts, 1976) was used to study the tree growth -climate relationship. For this purpose, principal components of monthly mean surface temperature and precipitation anomalies of western Himalaya were used as predictor variables in multiple regression analysis (response

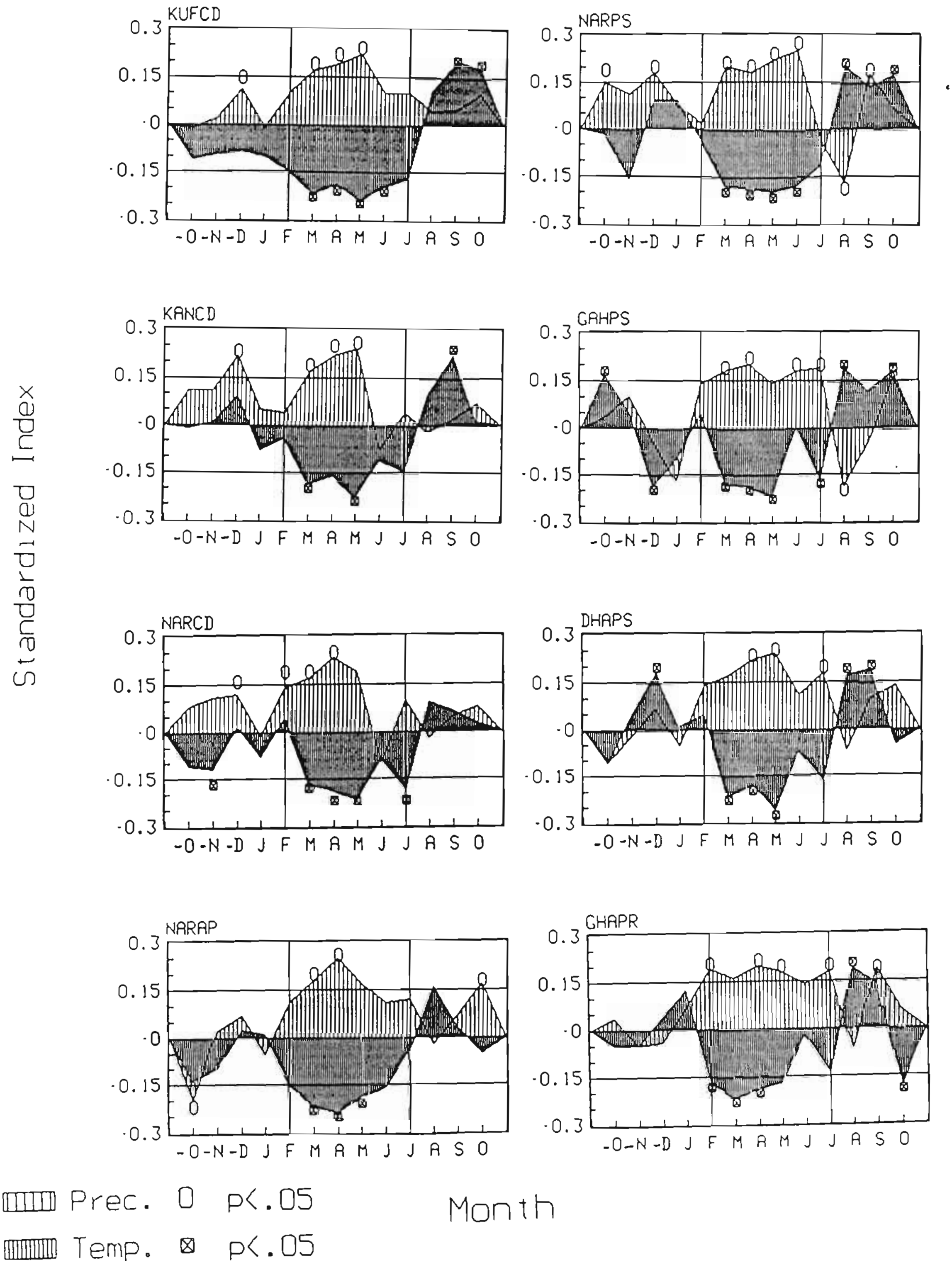

Fig. 5—Response functions of eight ring width chronologies calculated with monthly temperature and precipitation anomalies of western Himalaya. Crossed squares and circles indicate significance level at $p < \cdot 05$.

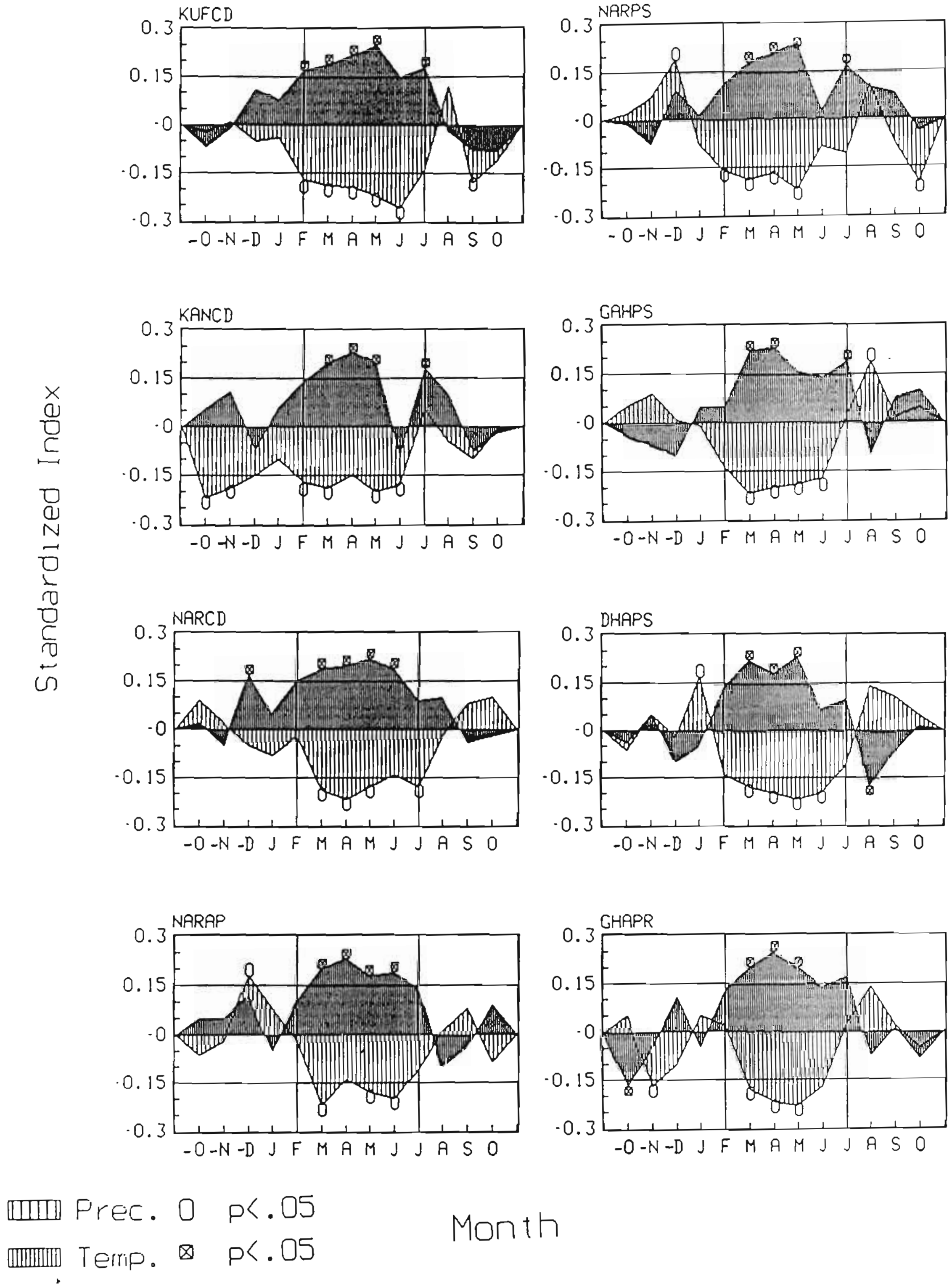

Fig. 6—Response functions of eight earlywood density chronologies calculated with monthly temperature and precipitation anomalies of western Himalaya. Crossed squares and circles indicate significance level at p < ·05.

function) to calculate the effect of each climate variable on tree growth parameters (total ring width and earlywood density). The active growth period of the Himalayan conifers is generally from March to October. Hence the climate variables were selected as previous October (end of prior year's growing season) to current October (end of current year's growing season) as discussed in detail by Borgaonkar (1996). Therefore, a total 26 climate variables, 13 each of temperature and precipitation anomalies for the period 1901-90 were used in the response functions analysis as predictors. The series of rainfall and temperature anomalies for the period 1901-90 were selected in response function analysis, as this period is common both in rainfall and temperature data and cover maximum number of stations. Response functions were constructed with residual chronologies of ring width and earlywood density of each site as predictands. Latewood density chronologies, which do not show any significant common signal related to climate (Fig. 3), were not used in the response function analysis. Calculations were done with Programme PRECON (Fritts, 1997). Figs. 5 and 6 represent the response function results of ring width and earlywood density, respectively, for all the site chronologies of western Himalaya.

It was observed that summer pre-monsoon (March-April-May) temperature and precipitation are the major parameters influencing on tree growth of the each site included in this analysis. Crossed squares and circles in Figs. 5 and 6 indicate the significant relationship at 95% confidence interval for temperature and precipitation respectively. In the case of ring width (Fig. 5), temperature in summer months, particularly in March-April-May shows significant negative relationships over all the tree-ring sites. Precipitation during same months indicates a significant positive relationship. In the case of earlywood density exactly the opposite pattern was observed for all the sites (Fig. 6). Summer temperature shows a significant positive relationship and precipitation shows a negative association. This is mainly because of moisture stress conditions (high temperature and low precipitation) occurring during the early growing season of the Himalayan conifers. However, latewood density parameters did not show significant relationship with the climate.

DISCUSSION AND CONCLUSION

It was first observed by Pant *et al.* (2000) that earlywood density Himalayan Cedar (*Cedrus deodara*) are climatically more sensitive than latewood density in dendroclimatic reconstruction. Many other studies on sub-alpine conifers indicated a greater utility of maximum latewood density and ring-width than the minimum earlywood density in dendroclimatic reconstructions (Schweingruber *et al.*, 1978, 1979; Hughes *et al.*, 1994; Yasue *et al.*, 1997). Hughes (1992) also noted the maximum latewood density of *Abies pindraw* from Kashmir was greatly influenced by the summer temperature. In the present analysis, response of earlywood density and ring width of different conifer species from various parts of western Himalaya indicates strong association with pre-monsoon summer climate. Various statistical parameters of tree-ring chronologies in Fig. 3 also indicate higher dendroclimatic potential of earlywood density and ring width than the maximum latewood density.

The climate of Kashmir is different from the other parts of western Himalaya at lower latitudes including Himachal Pradesh and Uttaranchal. Kashmir is outside the monsoon currents and strongly influenced by extra-tropical western disturbances. Whereas, southern parts of western Himalaya experience moderate influence of monsoon precipitation. Over this part moisture stress condition occur in pre-monsoon months (March-April-May) when temperature is high and precipitation amount is very small (Borgaonkar, 1996). This period coincides with early growing period of the conifers. Hence earlywood density is influenced by the climate during this period. The similar climatic conditions (higher temperature and low precipitation) are observed in May-June-July over Kashmir region which influences later part of growing season of the conifers, hence, latewood density shows significant response to climate of these months as noted by Hughes (1992).

In response function analysis, both ring width and earlywood density show significant relationships with pre-monsoon summer temperature and precipitation. However, the pattern of relationship is exactly opposite in both the cases. Temperature of pre-monsoon months is negatively correlated with ring width and positively correlated with earlywood density. A similar opposite pattern was observed in case of precipitation. As discussed by Pant *et al.* (2000) this is mainly because water deficit in the early growing season suppresses rapid expansion of tracheids (Fritts, 1976). Tracheid diameter contributes to the density variations. Smaller diameter also contributes less ring width, as ring width is the sum of radial diameters of the tracheids. Trees produce narrower tracheids if water is less available. Water deficit in the growing season suppresses enlargement of tracheids. When tracheids become narrower, the proportion of cell wall increases due to the reduction of lumen size. Larger cell wall portion in earlywood gives higher value of density. This explains why narrow rings contribute high values of earlywood density. Xiong *et al.* (1998) also showed the high dendroclimatic potential of earlywood tree-ring parameters (earlywood width and density) of New Zealand pink pine (*Halocarpus biformis* Hook).

This clearly establishes the great performance of density parameters of Himalayan conifers in dendroclimatic studies and indicates that the use of earlywood density parameters jointly with ring width may provide a more robust picture of past climate over the entire western Himalaya than the available reconstructions obtained only with total ring width.

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Teak tree-ring chronologies in Myanmar — A first attempt

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ABSTRACT

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A preliminary dendrochronological study with teak in Myanmar was performed in order to test its potential as a palaeoclimatic archive. There was a strong signal for rainfall in April, i.e., for the transition period between the dry and the rainy season.

Key-words—Teak, Dendrochronology, Myanmar.

म्याँमार में टीक वृक्ष वलय कालानुक्रम सम्बन्धी प्रथम अनुसन्धान कार्य

नासुदा पूमिजुमनांग, डीटर आक्सटाइन एवं वोन-क्यू पार्क

सारांश

एक पुराजलवायुविक संग्रह के रूप में म्याँमार के टीक की प्रभाविता को प्रेक्षित करने के उद्देश्य से वहाँ की टीक का प्रारंभिक वृक्ष वलय कालानुक्रमिकीय अध्ययन किया गया। यहाँ शुष्क एवं वर्षा के मौसम के बीच के संक्रमण काल हेतु अर्थात् अप्रैल माह में वृष्टि के महत्त्वपूर्ण संकेत मिले हैं।

संकेत शब्द—टीक, वृक्षवलयकालानुक्रमिकी, म्याँमार.

INTRODUCTION

TEAK (*Tectona grandis* L.) has been proven for some time to be of great dendroclimatic potential in several areas of its natural distribution: Berlage (1931) and D'Arrigo *et al*. (1994) studied teak in Java, Bhattacharyya *et al*. (1992) and Wood (1996) in India, Pumijumnong *et al*. (1995) in Thailand and Eckstein and Xayvongsa (unpubl.) in Laos. However, in Myanmar teak has not yet dendrochronologically been explored. Since the old-grown teak forests in the whole area from India to Laos are endangered by logging activities, it is high time to rescue the unique source of climatic information archived in those trees. The present paper is the first attempt from Myanmar.

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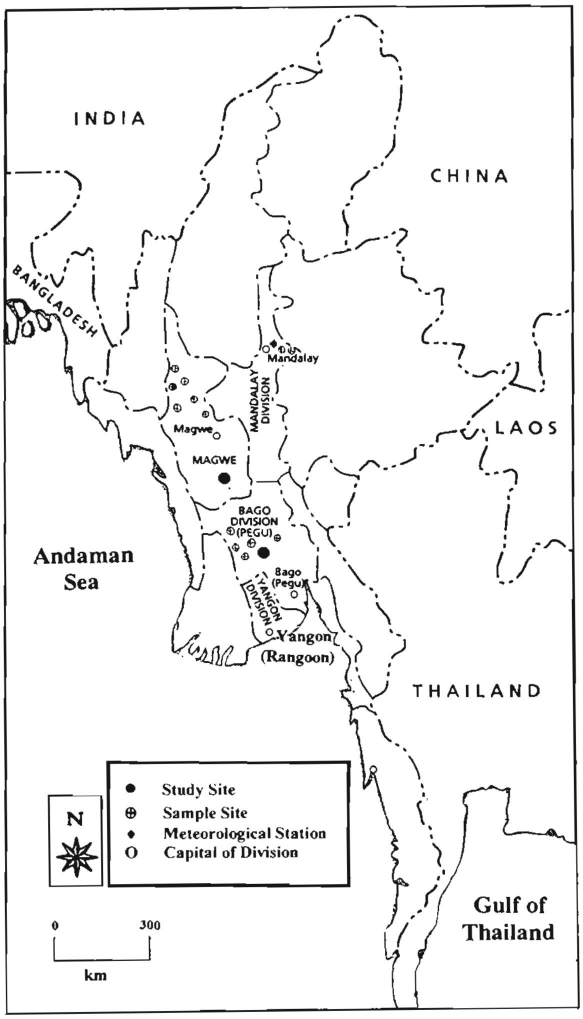

Fig. 1—Map of Myanmar: the two sample sites for the present study are located in the Mandalay Division near the Meteorological Station and the location of the study sites.

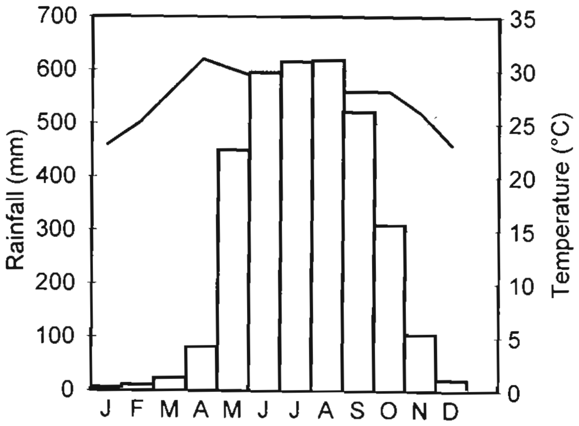

Fig. 2—Climate diagram of the Mandalay Meteorological Station: climate diagram.

STUDY AREA AND SAMPLE SITES

Increment cores were taken from 187 living teak trees in different areas and various forest types in Myanmar (Fig. 1). These are: humid mixed-deciduous forest at Seinye Research Station in the Pago Division, dry mixed-deciduous forest at Moswe Research Station in the Magwe Division and humid mixed-deciduous forest at Pyinoolwin Forest Reserve in the Mandalay Division. The elevation of all sites is in between 300 and 700 m asl., the slopes are moderate and facing to the east, south-east or south, respectively. All sites provide good growing conditions for teak because there is one dry and one wet season per year (Fig. 2). From November to April, monthly rainfall amounts to only 42 mm on average, whereas from May to October the monsoon brings rain with a monthly average of 159 mm. The climate data for the present study are from the Mandalay Meteorological Station. The monthly sums of rainfall extend from 1990 back to 1889 AD, the monthly mean temperatures from 1990 to 1931 AD.

The objective of the present study is to evaluate the dendroclimatic potential of teak in Myanmar using a subsample from two sites, named Mandalay A (MA) and Mandalay B (MB), in the Pyinoolwin Forest Reserve (Fig. 3). On site MA, 12 trees with 36 cores and on site MB, 21 trees with 73 cores were sampled. On average, three cores per tree were taken from the ridges of the often fluted trunks.

METHODS

The tree-ring widths of these cores were measured to the nearest 0·01 mm using a binocular microscope with a linear stage interfaced with a computer. Various routines out of the DPL program package (Holmes, 1994) were applied for the data management and analyses, among them COFECHA (Holmes, 1983) to statistically check the visual cross-dating, and ARSTAN (Cook, 1985) to detrend and autoregressively model the tree-ring series. Finally, the series were averaged for each site to a master chronology using the robust mean function.

RESULTS AND DISCUSSION

A 136-year long chronology covering the time span from 1998 to 1863 (Fig. 4) has been made from the site MA (12 teak trees with 36 cores). The mean tree-ring width is 1·77 mm. The mean sensitivity of the raw tree-ring series is fairly high (0·48) and conversely, the autocorrelation rather low (0·54). The mean correlation of all tree-ring series with the master chronology made from all tree-ring series except the one which is not correlated, is 0·45.

From the site MB, 21 teak trees with 73 cores were included into a 165-year long chronology from 1998 to 1834

Fig. 3—Teak forest in the Pyinoolwin Forest Reserve.

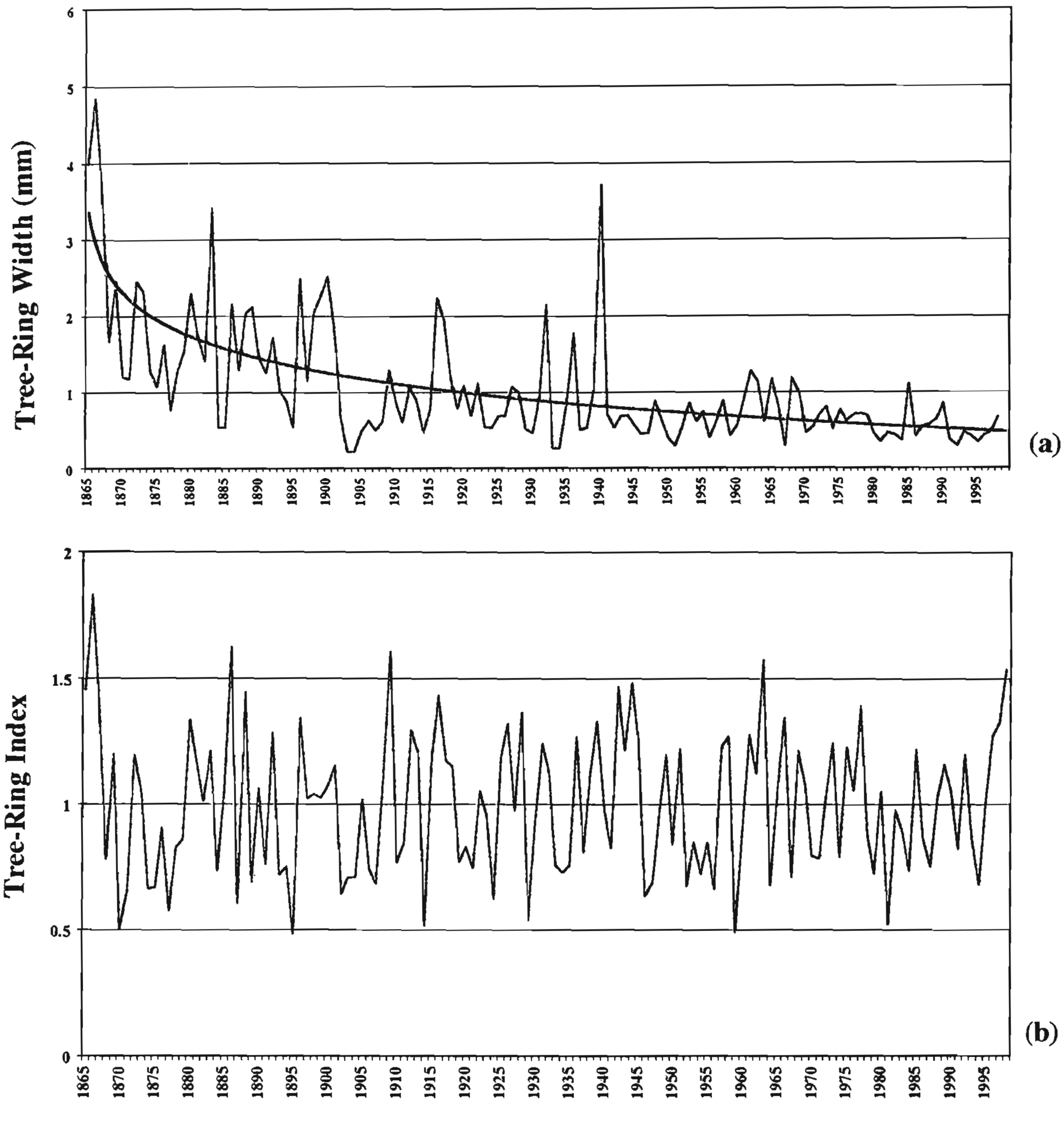

Fig. 4—MA tree-ring width (a) and index chronologies (b).

(Fig. 5). The mean tree-ring width is 2·08 mm, and the mean sensitivity and autocorrelation are 0·50 and 0·49, respectively. The mean correlation is 0·46 (Fig. 6).

To study the climate/growth relationships, the monthly values for rainfall and temperature from October prior to the growing season until current September were correlated with the so-called residual tree-ring chronology, that is the chronology where the autocorrelation has been eliminated by autoregressive modelling (Fig. 7). The highest positive correlation is with rainfall in April, i.e., the transition period from the dry to the wet season. However, there is also an unexpectedly high negative correlation with rainfall in the preceding October, but only for one of the two sites. There is also some correlation with temperature in the previous December, a result which is physiologically not explainable since we know from our studies in N.-Thailand (Pumijumnong *et al.*, 1996) that the cambium is dormant after the beginning of November.

In N. Thailand, the growth of teak is also mainly stimulated by the amount of rainfall during the beginning of the rainy season, although not as strictly concentrated on one single month as in Myanmar. In addition, our results get supported by Pant and Borgaonkar (1983) who found a similar response of teak in India. The climate-growth relationship for

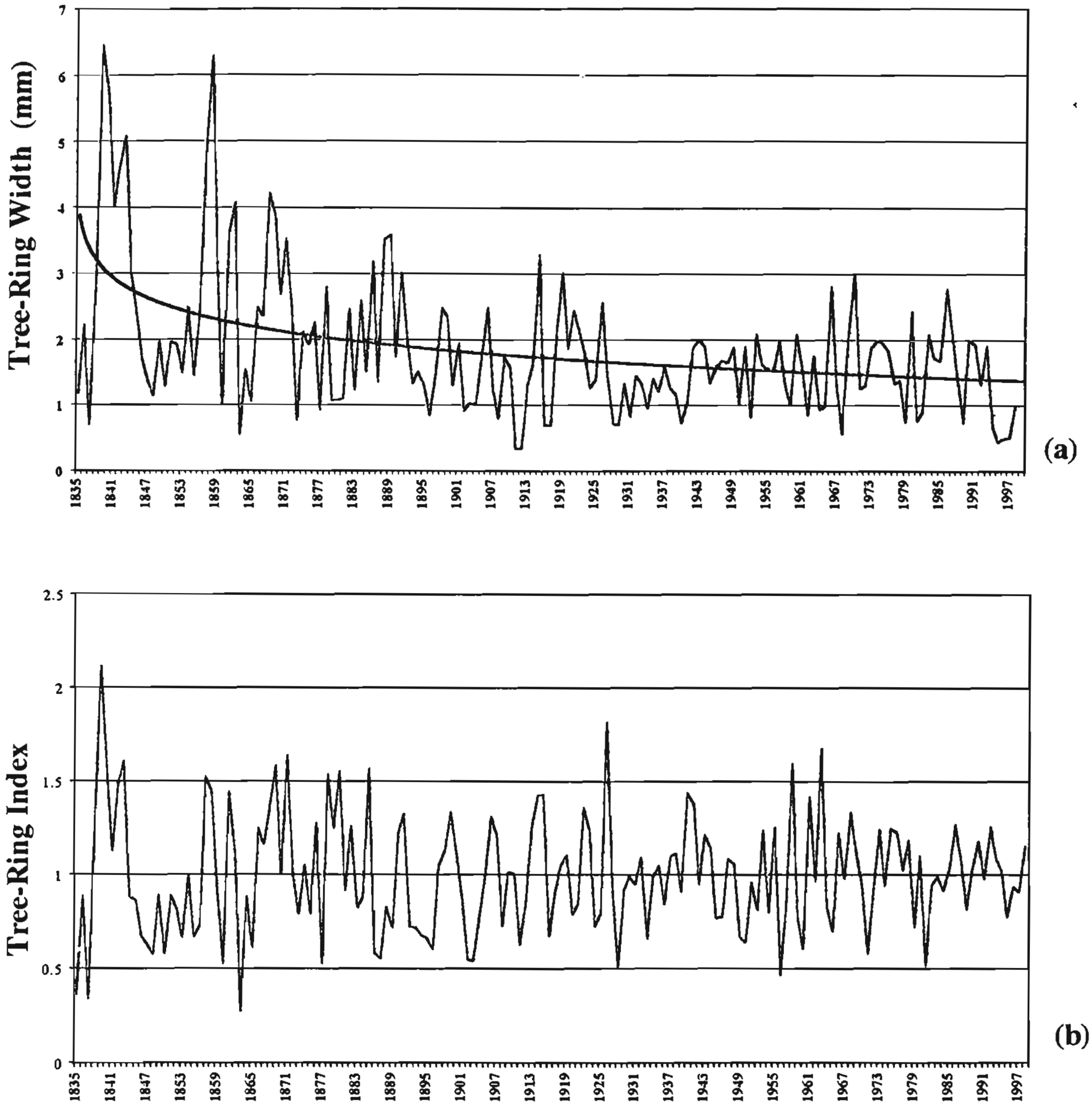

Fig. 5—MB tree-ring width (a) and index chronologies (b).

the teak in Laos has not been studied yet, but from the similarity of its growth pattern with teak in N-Thailand a similar climatic signal can be assumed.

CONCLUSION

Our first attempt to evaluate teak trees in Myanmar as an archive for palaeoclimatic information was successful. Teak

Study site	Trees(n)	Cores(n)	Start/endyear	Age (years)	Tree-ring width(mm)	S.D. (mm)	Auto-correlation	Mean sensitivity	Mean corr. with master chron.
MA	12	33	1863-1998	136	1·77	1·34	·54	·48	·45
MB	21	73	1834-1998	165	2·08	1·53	·49	·50	·46

Fig. 6—Pyinoolwin Forest Reserve: tree-ring statistics of the MA and MB site.

Site	-O	-N	-D	J	F	M	A	M	J	J	A	S
MA_p	-·13	·20	·16	-·09	-·12	-·05	·25**	·04	·16	·12	·08	·11
MA_t	-·19	-·12	·21	·17	-·04	·15	·09	-·13	-·07	-·03	-·04	-·01
MB_p	-·27**	-·15	·11	·07	-·04	·13	·35**	·05	·07	10	·09	-·00
MB_t	-·12	-·06	·26**	·17	·08	·02	·06	·16	·10	·07	-·09	-·06

Fig. 7—Correlation between tree-ring width and climate; T = temperature, P = precipitation; **= significance at 0·05 level.

is a reliable recorder of rainfall in April, which is an important month for the onset of the monsoon. In the nearest future it is urgently necessary to sample old-grown teak trees in Myanmar in order to get tree-ring series extending back into the past as far as possible. With such proxy data we want to contribute to the reconstruction of the variability of the monsoon climate and thus for its better understanding.

Acknowledgements*—We express our thanks to the Thai Research Fund (TRF) and to the German Science Foundation (DFG) for financial support, to Kuaw Tint, Director General, Forest Department, Mehm Ko Ko Gyi, former Coordinator of TEAKNET (Asia Pacific Region), Saw Eh Dah, Coordinator, Forest Department, Yangon/Myanmar, for cooperation during the sampling expedition in March 1998. Many thanks to Surachon Kulvijit, Somiert Pitakkamonporn and Toonsak Valayaphet for their help, as well as to the Faculty of Environment and Resource Studies, Mahidol University/Thailand, for organisational support.*

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Tree ring analysis of teak (*Tectona grandis*) ring width chronology from Mae Na, Thailand

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ABSTRACT

Borgaonkar HP, Pumijumnong N, Buckley BM, Taesumrith O & Chutiwat S 2001. Tree ring analysis of teak (*Tectona grandis*) ring width chronology from Mae Na, Thailand. Palaeobotanist 50(1) : 41-45.

Tree ring analysis of about 39 core samples of teak (*Tectona grandis*) collected from undisturbed natural forest near Mae Na, Thailand was carried out. All samples show good cross matching within the tree and between the trees. Chronology statistics indicate the usefulness of the species in dendroclimatic studies. Tree growth – climate relationship based on correlation and response function analysis revealed the important role of precipitation during the monsoon months.

Key-words—Teak, *Tectona grandis*, Tree ring, Thailand.

थाईलैण्ड के माए ना नामक स्थान से प्राप्त एक टीक वृक्ष (*टेक्टोना ग्राण्डिस*) के वलयी चौड़ाई कालानुक्रम का वृक्षजलवायुविक विश्लेषण

एच.पी. बोरगाँवकर, नासूदा पूमिजुमनांग, ब्रेन्डन.एम. बकले, ओ. तीसुमृति एवं एस. चुटीवाट

सारांश

उत्तरी थाईलैण्ड के माए ना नामक स्थान के समीप के अविक्षुब्ध प्राकृतिक वनों से संग्रहीत किए गए टीक (*टेक्टोना ग्राण्डिस*) के लगभग 39 क्रोड़ नमूनों का वृक्ष वलय विश्लेषण किया गया। सभी नमूने वृक्ष के भीतर तथा वृक्षों के मध्य उत्कृष्ट परस्पर सुमेलन प्रदर्शित करते हैं। कालानुक्रमिकीय सांख्यिकी वृक्ष जलवायुविक अध्ययनों में प्रजातियों के महत्त्व का संकेत करती है। सहसम्बन्धन तथा अनुक्रिया फलन विश्लेषण के आधार पर ज्ञात वृक्ष वृद्धि-जलवायु के सम्बन्ध मानसूनी महीनों के दौरान वर्षण के महत्त्व को प्रदर्शित करते हैं।

संकेत शब्द—टीक, *टेक्टोना ग्राण्डिस*, वृक्ष वलय, थाईलैण्ड.

INTRODUCTION

THE purpose of this study was to investigate the dendroclimatic response of teak (*Tectona grandis*) growing in a largely undisturbed, natural environment in northern Thailand, at the Mae Na Forest Protection Unit (MNFPU), Chiang Dao. Earlier studies (e.g., De Boer, 1951; Murphy & Whetton, 1989; Pant & Borgaonkar, 1983; Jacoby & D'Arrigo, 1990; D'Arrigo *et al.*, 1994; Pumijumnong *et al.*, 1995a, b) clearly demonstrate the usefulness of teak as a proxy source for rainfall variability and broad-scale climate features such as ENSO. This paper reports on a dendroclimatic analysis of teak samples collected as a part of FIELDWEEK 99, a dendrochronology training workshop held in Chiang Mai, Thailand in February, 1999. This programme was co-sponsored by the National Science Foundation (USA) and the PAGES initiative of IGBP. FIELDWEEK 99 was hosted by the Tree Ring Laboratory of Lamont-Doherty Earth Observatory (USA), in conjunction with Chiang Mai University and the Queen Sirikit Botanic Garden in Mae Rim. The purpose of the FIELDWEEK was to provide training in dendrochronological techniques and dendroclimatic analyses to participants from the southeast Asian region. As part of this programme the Mae Na Teak Project was selected by our group to understand the nature of the relationship between radial growth in teak and climate. The results of these analyses, in addition to being a useful learning exercise, also form an important contribution to the growing dendroclimatic database for the region.

TREE RING DATA

Thirty nine core samples were taken from 12 teak trees at the MNFPU, about 80 km north of Chiang Mai, Thailand (Fig. 1). This remnant stand is protected from logging and other major disturbance, and is considered to be growing in a largely natural environment. Nine of the trees were sampled from four directions (primarily along the four cardinal directions where possible) to reduce the effects of within-tree variability that can be quite large in teak (Pumijumnong *et al.*, 1995a). An additional three trees were cored once only, bringing the total number of cores to 39. All cores were glued to wooden core mounts and surfaced with sand paper up to 400 grit, in order to render the tree ring boundaries more clearly visible. Skeleton plots (Stokes & Smiley, 1968) were used in conjunction with visual inspection to facilitate the correct dating of each sample. While none of the samples is more than 100 years old, good crossmatching has been observed both within and between individual trees. Ring width measurement of all 39 cores was carried out by one of the authors (NP) at Mahidol University, Thailand, and a dating quality control check was initiated with the computer program COFECHA (Holmes *et al.*, 1986).

CLIMATIC DATA

Monthly mean temperature and precipitation data from Chiang Mai, about 80 km south of MNFPU, were used for dendroclimatic analysis. Monthly temperature data are available for the period 1951-90 (40 years), whereas monthly rainfall data cover the period 1911-1997 (87 years). Fig. 2 illustrates the monthly variations in temperature and rainfall based on monthly averages of the available periods. The dry period from December to March receives only 5% of the annual precipitation, while 88% falls during May to October monsoon rains. Mean temperature remains above 20°C throughout the year, with April and May being the warmest months.

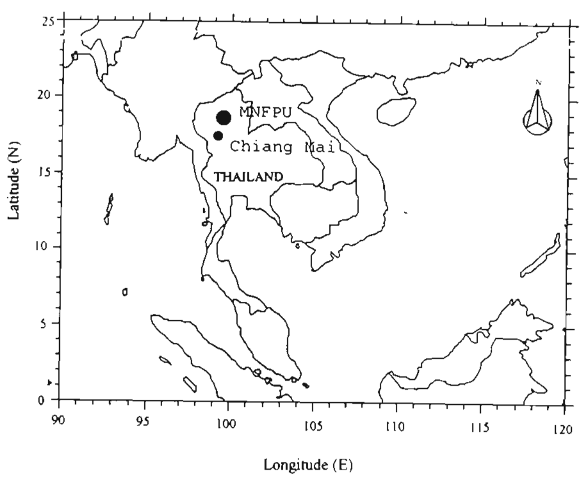

Fig. 1—Location of Mae Na Forest Protection Unit (MNFPU) in northern Thailand.

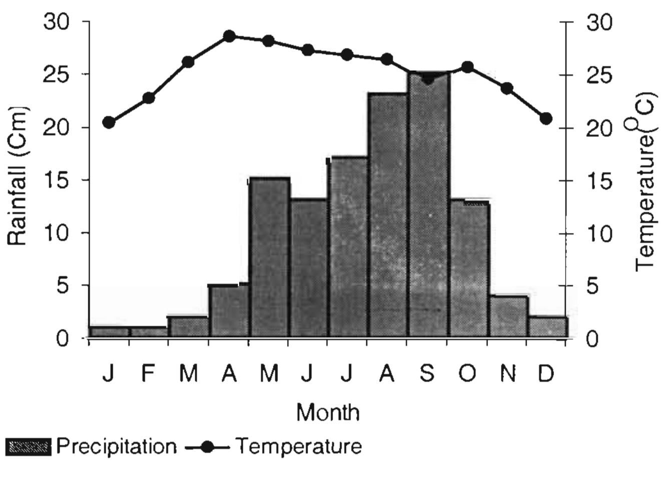

Fig. 2—Monthly variations in temperature and precipitation of Chiang Mai, Thailand based on long-term averages.

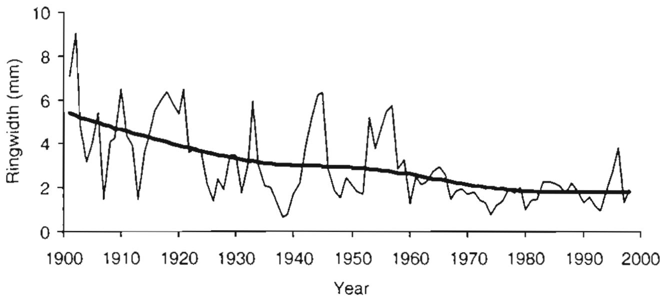

Fig. 3—Teak ring width series at Mae Na along with cubic spline smoothing at a cutoff frequency of 47%N, where N is number of data points.

Sr. No.	Parameter	Standard chronology	Residual chronology
Full chronology period 1901-1998 (98 years)			
1	No. of tree series	12	12
2	Standard deviation	0·26	0·25
3	Mean sensitivity	0·25	0·31
4	Auto-correlation	0·40	-0·05
Common period of the chronology 1924-1995 (72 years)			
5	No. of tree series	12	12
6	Variance (Y%)	28	35
7	Signal to noise ratio	4·6	6·3
8	Variance in 1st eigenvector	34%	41%

Fig. 4—Descriptive statistics of tree ring index chronology of teak at Mae Na, Thailand.

CHRONOLOGY DEVELOPMENT

The oldest teak tree in our study collection spans the 98 years from 1901-1998. Many of our samples exhibit significant persistence (lag-1 autocorrelation) and high values of mean sensitivity, a statistical measure of the degree of change between one value and the next (Fritts, 1976). The sampling strategy of extracting four cores per tree was employed to account for changes in circuit uniformity that are common in teak (Pumijumnong *et al.*, 1995a), and can render any given radius unrepresentative of the overall growth of the tree itself. Circuit uniformity for trees growing at this site was not highly problematic, as within-tree correlations were high between all four directions. However, the temporal length of cores are often different due to obliquity in ring patterns along each radius, likely due to eccentricities in circuit uniformity that caused the core operators to miss the center of the tree. To account for any problems related to the within-tree variability, we averaged all four ring width series from each tree, thereby forming a single series to represent an individual tree. This procedure resulted in 9 averaged series from 9 trees, and 3 series of single cores from the remaining 3 trees. The individual series were then standardised into dimensionless indices in an attempt to optimize the common signal between all trees at the site (Fritts, 1976; Cook *et al.*, 1990).

For standardising ring-width time series we used the computer program ARSTAN (Holmes *et al.*, 1986). Autoregressive modelling was applied to remove the persistence in the series. A cubic spline smoothing (Cook & Peters, 1981) with 47% N years as cutoff frequency (where N is the length of the series) was found to be most suitable for detrending these series. Fig. 3 represents the nature of the ring width series of teak with the cubic spline filter. The ring width index series, derived as the quotient of raw ring width values and the corresponding smoothed values, gives moderately high values of mean sensitivity and common variance explained by the tree assemblage. Good dendroclimatic series are widely considered to have large values of mean sensitivity, large common variance, and low values of lag-1 auto-correlation (persistence) (Fritts, 1976). Fig. 4 gives some key statistics of the standard (with persistence) and residual (without persistence) index chronologies (shown in Fig. 5). In the residual chronology, values for mean sensitivity (0·31) and common variance (35%) have been improved over the standard chronology.

TREE GROWTH-CLIMATE RELATIONSHIP

The simplest method for studying the association between tree growth and climate is through correlation analysis. In the case of teak in Thailand, particularly in northern Thailand, the active growth season is thought to commence some time in April with the onset of rainy season, and end in October when rains cease (Pumijumnong *et al.*, 1995b). Precipitation during these wet-season months largely controls tree growth, however Buckley *et al.* (2001) demonstrated a continued response to rainfall event during the dormant (dry) season that begs further investigation.

The highest rainfall is from June to August, with rains decreasing by October. In contrast, November to March is a mostly dry period with little or no rainfall. Monthly variations of temperature are very small throughout the year, particularly in the rainy season (May-October) when changes in monthly mean temperature are negligible. Therefore, temperature would not appear to exert any obvious limiting control over the radial growth of teak. However, it should be noted that Pumijumnong and Park (2001) note the influence of temperature on the development of earlywood vessels, though have yet to determine whether this is related to an intercorrelation between temperature and precipitation or is truly a response to temperature.

In modelling the tree growth-climate relationship we used monthly climatic data (temperature and rainfall) from Chiang Mai with a dendroclimatic window spanning from the previous October (ending of prior growth season) to the current October (ending of current growth season). In all instances we used the residual (pre-whitened) chronology for

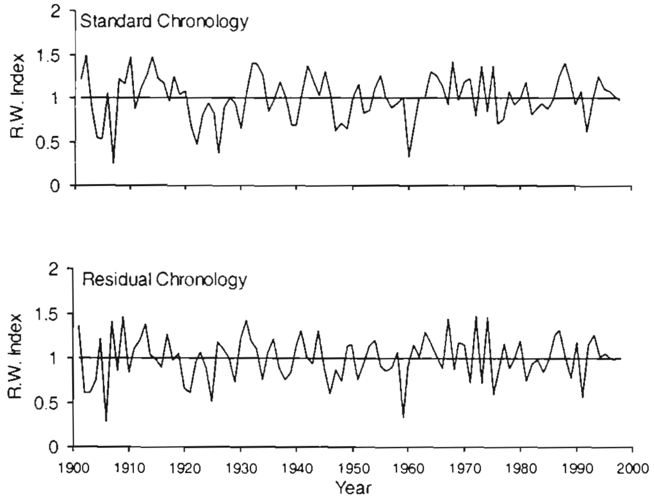

Fig. 5—Teak ring width index chronology at Mae Na representing Standard (with persistence) and Residual (without persistence) versions.

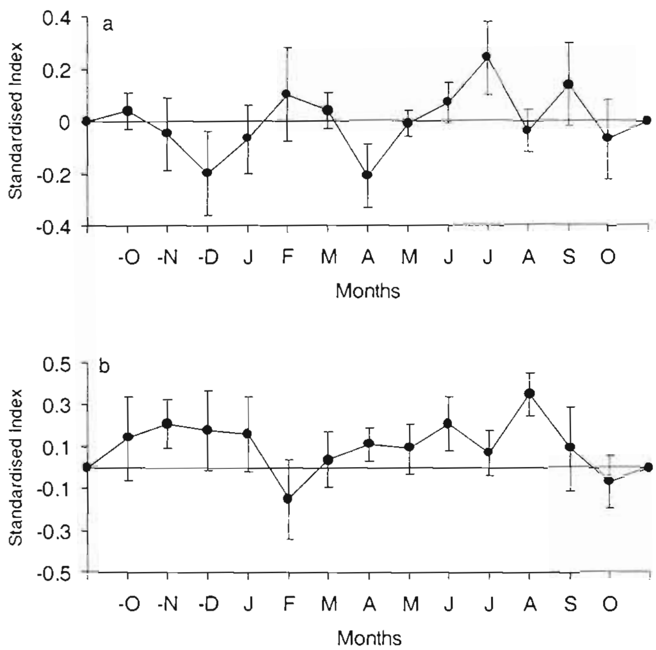

Fig. 7—Response functions using residual ring width index chronology of teak at Mae Na and Chiang Mai temperature (a) and precipitation (b). Vertical bars indicate 95% confidence interval.

comparison. Fig. 6 shows the correlation coefficients between the residual chronology indices and precipitation and temperature for each month. Previous November and current August precipitation have significant ($p<0·05$) positive relationships with tree growth. Previous October-November-December (OND) and current July-August (JA) precipitation also have significant ($p<0·05$) positive correlations with tree growth. None of the temperature parameters indicate significant relationships with the tree-ring chronology.

Another method of studying the dendroclimatic relationship is through response function analysis (Fritts, 1976). This can be a more precise method and gives a quantitative distribution of the response of each climatic parameter independently on tree growth. Response function analysis involves a step-wise multiple regression analysis in which monthly climatic parameters are the predictors and ring widths are the predictand variables. Monthly climatic parameters are generally inter-correlated, so they are first transformed into principle components before entering into the regression equation. Coefficients of the regression equation represent the variance, or the amount of tree growth related to the effect of a particular climate parameter. The use of traditional response function analysis, however, is considered controversial by some researchers (Blasing *et al.*, 1984) due to the subjective nature of screening predictor variables before entering into regression. The possibility for over-inflation of the significance of some parameters is a concern and should be noted.

Fig. 7 represents the results of a response function analysis with a total of 26 variables; 13 each of monthly mean temperature and monthly rainfall from previous October to current October. Each parameter represents its response on tree growth in terms of the amount of variance in the tree-ring index chronology. Previous November and the current rainy season months of April, June and August indicate significant positive relationships with tree growth. Previous December and current April temperature are negatively associated, whereas, June temperature shows positive response.

DISCUSSION AND CONCLUSIONS

The analyses clearly indicate the important role of precipitation in tree growth activity during the monsoon months, as would be expected, and as is noted in previous work with teak. Precipitation in November of the prior season also appears to be an important parameter, with a significant positive relationship ($r=0·4$). These results make biological and physiological sense, because an increase in soil moisture at the beginning of the dry season (December-March) and the

Month	-O	-N	-D	J	F	M	A	M	J	J	A	S	O	-OND	JA
Temp.	·01	00	-·10	·05	·15	·09	-·03	-·02	·04	·09	·11	·18	13	-·06	·08
Ppt.	·12	**·40**	·09	·02	-·06	·20	·08	-·05	·18	·14	**·33**	-·14	-·06	**·31**	**·34**

Fig. 6—Correlation coefficients between the residual tree ring chronology and monthly climate (bold figures indicate significant relationship at $p < ·05$).

carryover effects on the physiological processes of the tree (Fritts, 1976) can both contribute to tree growth. The significant negative relationship with temperature in April (the hottest month of the year) is likely due to moisture stress conditions resulting from high temperature and low precipitation for this month (Fig. 2). Cambial activities in teak are thought to restart during the month of April, though dendrometer band studies presented by Buckley *et al.* (2001) suggest an even earlier start, perhaps as early as February. Higher temperatures will accelerate evapotranspiration causing a lack of moisture during the very early period of growing season when cambial cell division is most rapid. This would create unfavourable conditions for tree growth, and may be responsible for the negative relationship of April temperature with tree growth. Conversely, higher than average precipitation in April is conducive to increased growth.

During the wet season (May to October) temperature does not appear to play any direct role in radial tree growth. Precipitation shows positive response with tree growth during these months, as might be expected. Drought conditions coincide with below average radial growth, hence teak can be very useful for the reconstruction of drought events in the past, and more broad-scale climate features related to variations in monsoon rainfall such as ENSO (D'Arrigo *et al.*, 1994).

The results from this study are based on the chronology from a single stand of teak with limited sample size and temporal coverage. However we derive similar results to the investigations by Pumijumnong *et al.* (1995a, b), carried out over a broad area of northern Thailand.

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Cedrela angustifolia Ses. et Moc. ex Dc., Meliaceae: potential species for tropical dendrochronology

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ABSTRACT

Tomazello FM, Botosso PC, Lisi CS & Spathelf P 2001. *Cedrela angustifolia* Ses. et Moc. ex Dc., Meliaceae: potential species for tropical dendrochronology. Palaeobotanist 50(1) : 47-53.

The characteristics of *Cedrela angustifolia*, i.e., its dendrology, ecology, silviculture and wood anatomy were described. This Meliaceae species naturally occurring in Latin America produces annual growth rings with sensibility to climatic variables, such as rainfall and temperature, showing potentiality to climatic reconstruction. The X-ray densitometry of the wood constitutes, besides the usual wood anatomy analysis, a suitable method to delimit the annual growth rings, as well as, to determine the wood density variation from pith to bark and within the growth rings.

Key-words—*Cedrela angustifolia*, Meliaceae, Dendrochronology, X-ray densitometry, Growth rings.

सिड्रेला एंगस्टीफोलिया सेस. एट् मॉक. एक्स डीसी., मीलिएसी : उष्णकटिबन्धीय वृक्षवलयकालानुक्रमिकी हेतु प्रभावी प्रजाति

मारियो टोमाज़ेलो एफ़, पी.सी. बोतोसो, सी.एस. लिसी एवं पी. स्पेतेल्फ

सारांश

प्रस्तुत शोध पत्र में *सिड्रेला एंगस्टीफ़ोलिया* के अभिलक्षणों, जैसे — वृक्षवलयकालानुक्रमिकी, पारिस्थितिकीविज्ञान, वनवर्धन एवं काष्ठ शारीरविज्ञान का वर्णन किया गया है।। ये मीलिएसी प्रजातियाँ, जो प्रायः लैटिन अमरीका में पाई जाती हैं, जलवायुविक पुनर्रचना से प्रभाविता प्रदर्शित करते हुए जलवायुविक चरों, जैसे — जलवृष्टि एवं तापमान के साथ संवेदनशीलता से युक्त वार्षिक वृद्धि वलयों का उत्पादन करती है। सामान्यतः किए जाने वाले काष्ठ शारीरविज्ञान विश्लेषण के अतिरिक्त काष्ठ की एक्स-रे घनत्वमिति वार्षिक वृद्धि वलयों को सीमांकित करने हेतु तथा वृद्धि वलयों के भीतर एवं मज्जा से छाल वल्क के मध्य काष्ठ घनत्व के निर्धारण हेतु सर्वाधिक उपयुक्त प्रविधि है।

संकेत शब्द—*सिड्रेला एंगस्टीफ़ोलिया*, मीलिएसी, वृक्षवलयकालानुक्रमिकी, एक्स-रे घनत्वमिति, वृद्धि वलय.

INTRODUCTION

CEDRELA constitutes an important neotropical genus occurring from Mexico (latitude 26° N) to northern Argentina and the south of Brazil (latitude 28° S), including all countries of Latin America, except Chile. The *Cedrela* species occur in dry and wet low lands up to an altitude of 1,200 m as well in drained soils of the tropical and subtropical forests usually associated with broadleaves and conifers (Hueck, 1972; Rizzini, 1978). They are highly demanding of sunlight, frequently occurring as a pioneer, with high growth rates in secondary forests (Pennington, 1981). The genus consists of seven species, namely (i) *C. angustifolia*, occurring from Mexico to northern Argentina, except on the Antilles Islands, (ii) *C. fissilis*, from Costa Rica to Argentina, (iii) *C. lilloi*, in Peru, Bolivia and Argentina, (iv) *C. montana*, in Venezuela, Colombia and Equador, (v) *C. oaxacensis*, from Mexico to Panama, (vi) *C. odorata*, from Mexico to Argentina, and (vii) *C. weberbauerii*, in Peru (Smith, 1960; Gonzales, 1976; Ramirez & Styles, 1978; Rizzini, 1978). In Brazil three species of *Cedrela* occur naturally; *C. odorata*, considered the Amazonian forest cedar, *C. angustifolia*, the Atlantic forest cedar, and *C. fissilis*, the dry forest cedar, from the state of Minas Gerais to southern Brazil. According to Rizzini (1978) these species are interpenetrating in their areas of natural distribution in the Brazilian central region. Besides these, a fourth species, *C. lilloi*, is cited as occurring in southern Brazil (Carvalho, 1994).

In this paper particular emphasis is given to review the prospects of tree ring analysis of *Cedrela angustifolia* because of its ecological importance, distribution and dendrochronological applications.

CEDRELA ANGUSTIFOLIA: ECOLOGY, DENDROLOGY AND WOOD ANATOMY

In its area of distribution *C. angustifolia* is designated by an extensive list of common names like, cedro, cedro rosa, cedro branco in Brazil; cedro saltenho in Argentina; cedro blanco in Peru, among others ones (Girardi, 1975; Rizzini, 1978).

In Brazil, *C. angustifolia* is commonly found in all moist Atlantic forests, but frequent in the States of Espírito Santo, Rio de Janeiro, Minas Gerais, São Paulo and Paraná and rare in southern Bahia, and of minor importance in the State of Para. It is a large tree, 20-30 m height, shades leaves during the period of maturation of fruits, July-August; and producing new leaves and flowers in August-September (Rizzini, 1978).

In Argentina, *C. angustifolia* occurs in the oriental boundary of the high mountain forest in the Chaquenho Park, from 1700 to 1900 m of altitude (Villalba, 1995). It also occurs in northwestern Argentina and western Bolivia, in the Tucumano-Boliviana forest, at 28° South latitude and 200-1,900 m of altitude. The trees are co-dominant reaching 40 m high and 1·50 m of trunk diameter, presenting the growth period from September to April - May, followed the period leaves fall (Villalba *et al.*, 1985). In the Tucumano-Oranense forest, (at 22-28° south latitude, 800-1,900 m altitude, 1,400 mm/year precipitation) *C. angustifolia* trees reaches 35 m high and 2·50 m trunk diameter at 800 m of altitude, but are smaller and less abundant in high altitudes (Tortorelli, 1956; Villalba *et al.*, 1987).

Descriptions of *C. angustifolia*, including taxonomy, botany, ecological, phenological and silvicultural and related aspects are presented by several studies (Tortorelli, 1956;

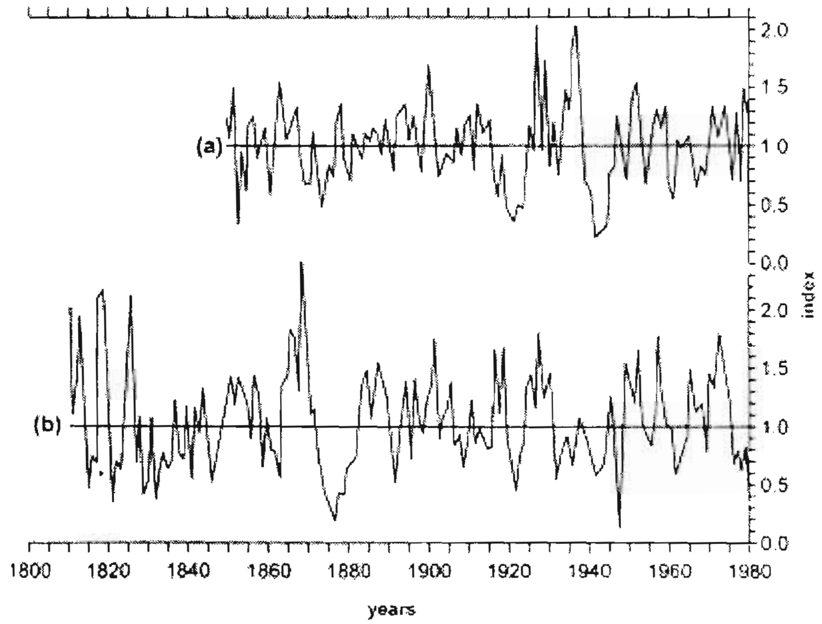

Fig. 1—Chronological series of *Cedrela angustifolia* trees, in Rio Blanco (Jujuy) (a) and Finca del Rey (Salta) (b), Argentina (after Villalba *et al.*, 1985).

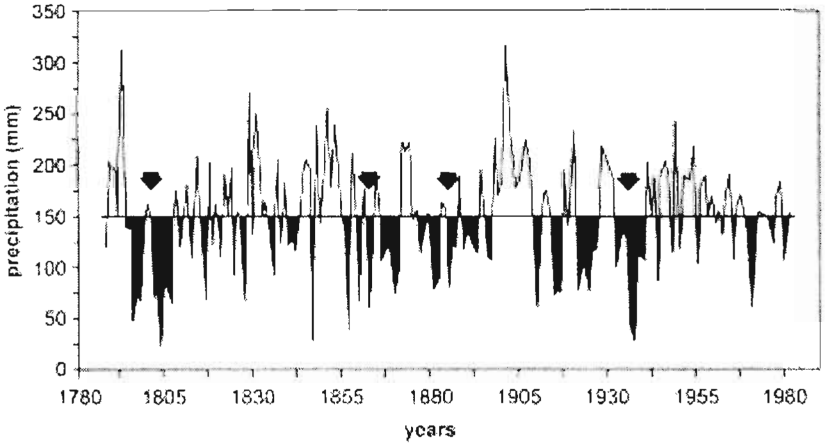

Fig. 2—Precipitation reconstruction of the annual dry period (June-November) since 1788 in Jujuy city, Argentina. Dry periods are indicated by arrows (after Villalba, 1995).

Smith, 1960; Girardi, 1975; Sanchez *et al.*, 1976; Rizzini, 1978).

The wood of *C. angustifolia* has a yellowish-rose coloured sapwood and the heartwood colour varies from reddish-brown to darkened rose beige, depending on the provenance. The wood has a wide utilization in marquetry, carpentry, aeronautics, naval and civil constructions, etc. (Tortorelli, 1956; Rizzini, 1978; Villalba *et al.*, 1985). The anatomical wood characteristics of *C. angustifolia* were described by Peréz Mogollon (1973), Lebacq (1973) and Dechamps (1985), examining wood samples collected from Venezuela, Peru and Brazil, respectively. The presence of well-defined growth rings marked by initial parenchyma bands and vessels forming semi-porous rings have been reported in all these studies.

CEDRELA ANGUSTIFOLIA: POTENTIAL IN TROPICAL DENDROCHRONOLOGY

The Meliaceae is included within the list of many tropical families which seems to be potential for dendrochronological studies with emphasis on its genus *Cedrela* (Chalk, 1983; Tomazello Filho *et al.*, 2000). This tree combines fundamental characteristics like, (i) large trunk diameter and high growth rates, (ii) distinct phenophases with the trees leaf-fall in the dry season, in natural stands and plantations, (iii) wood with important anatomical features, i.e., distinct and well-defined annual growth rings, (iv) medium density wood, permitting the extraction of samples by non-destructive methods. These features make *C. angustifolia* more significant for dendrochronological studies in trees (Villalba *et al.*, 1985, 1987, 1992; Villalba, 1995; Boninsegna & Villalba, 1996).

Two chronologies of *C. angustifolia* were elaborated in Argentina and northern Bolivia from trees growing in low latitude forests, where the growth period is from September to April-May with the fall of leaves and the trees are completely leafless. The distinct and well-defined annual tree rings are formed in response to the phenological phases, presenting a fine uniformity in the cross section of a trunk, which allows to get a high quality cross-dating. For these trees, temperature and precipitation in the beginning of the vegetative growth period seems to induce an increase in the width of growth rings. The statistical analysis of chronologies shows a high average sensitivity and signal-to-noise ratio, with a high percentage of variance explained by the first "eigenvector" and a high correlation between the trees. Consequently, the chronologies have a very strong common signal with a good potential for climatic reconstruction (Villalba *et al.*, 1985) (Fig. 1).

In mountain forests of northwestern Argentina, two chronologies of *C. angustifolia* trees were constructed, establishing the relationship between growth rings and local climatic variations. In xeromorphic environmental conditions the diameter growth of the trees was controlled by temperature and precipitation of spring and beginning of summer. A positive correlation between growth rings and climate was detected in at the upper limits of the occurrence of the species.

Thus, tree ring data of *C. angustifolia* can be used for local climatic reconstruction, like the periodicity of dry periods in northwestern Argentina. In Jujuy city, for example, correlation coefficients between the precipitation of the dry season (June-November) and four tree-rings chronologies were calculated for the period 1909-1979. Then, these correlation coefficients were applied to the growth-ring chronologies until 1788, extending the winter precipitation back to 200 years. The reconstructed climate data reveal extremely dry periods in 1795-1807, 1858-1870, 1877-1892, 1934-1938 (Villalba, 1995) (Fig. 2).

In the transition area of Tucumano-Orense forest and Chaqueño Park, Argentina, tree ring samples were collected from 26 *Cedrela angustifolia* trees. These samples were dated through cross dating technique. Tree growth climate relationship is yet to built. In Cerro Chañar site, 1,600 m a.s.l. and 1,400 mm of annual average precipitation, the trees showed a positive relationship with spring-summer precipitation and a negative relationship with summer temperature. In Río

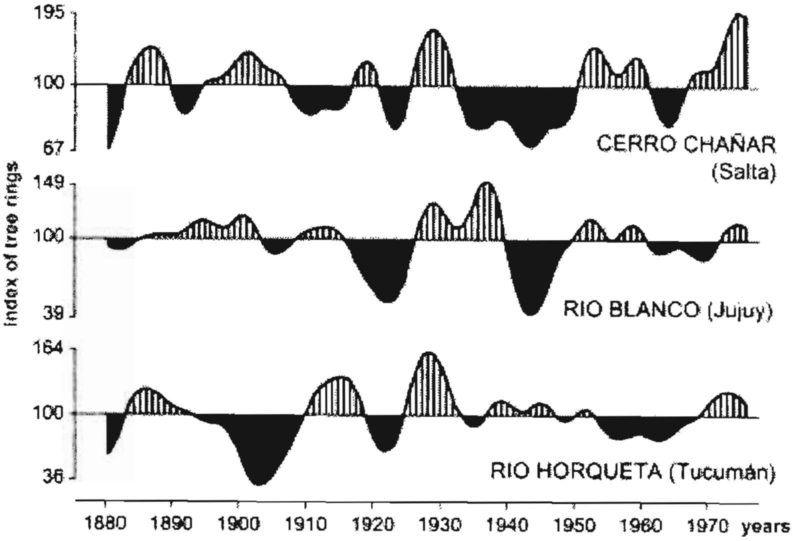

Fig. 3—Chronologies of the growth rings thickness index of *Cedrela angustifolia* trees in Cerro Chanar/Salta and Rio Blanco/Jujuy, Tucumano-Orense forest / Chaquenõ Park, Argentina (after Villalba *et al.*, 1987).

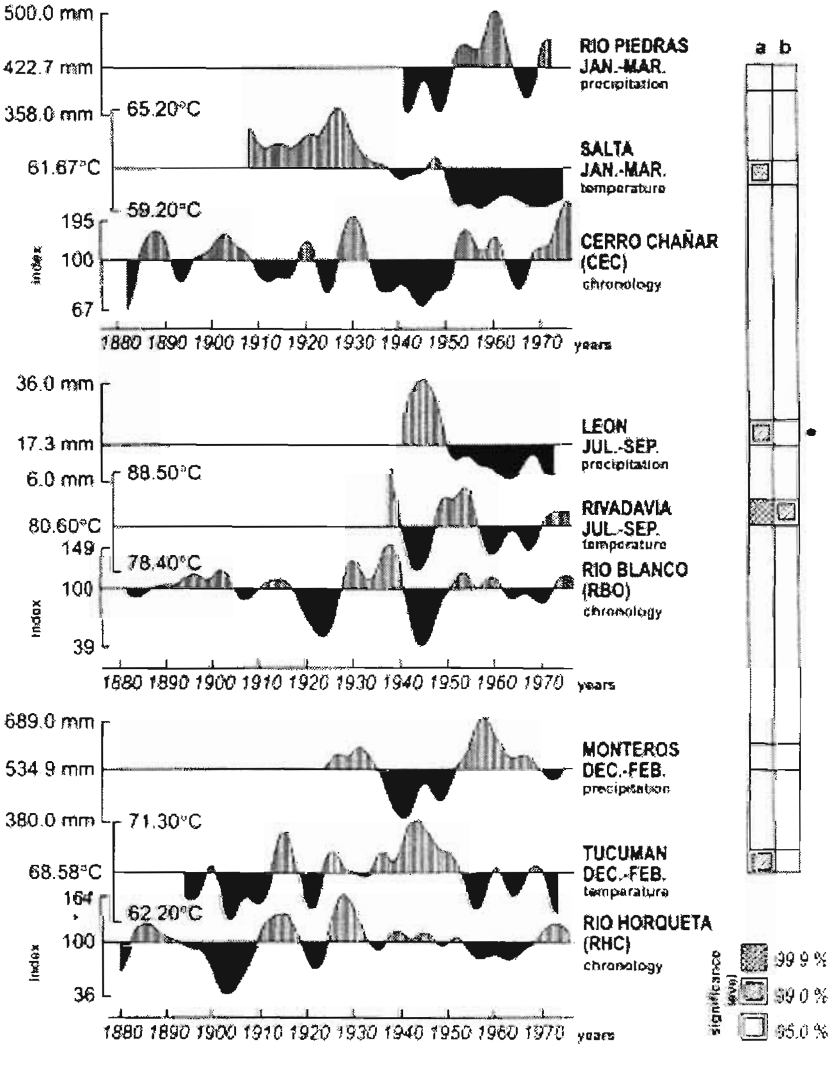

Fig. 4—Comparison of the tendencies of growth ring index of *Cedrela angustifolia* trees in Cerro Chanar e Rio Blanco with seasonal climate. The tendencies were determined by the average of the index with low frequency digital filter. The significance levels are indicated to (a) coefficient of correlation, (b) percentage de acceptance (o) inverse relation (after Villalba *et al.*, 1987).

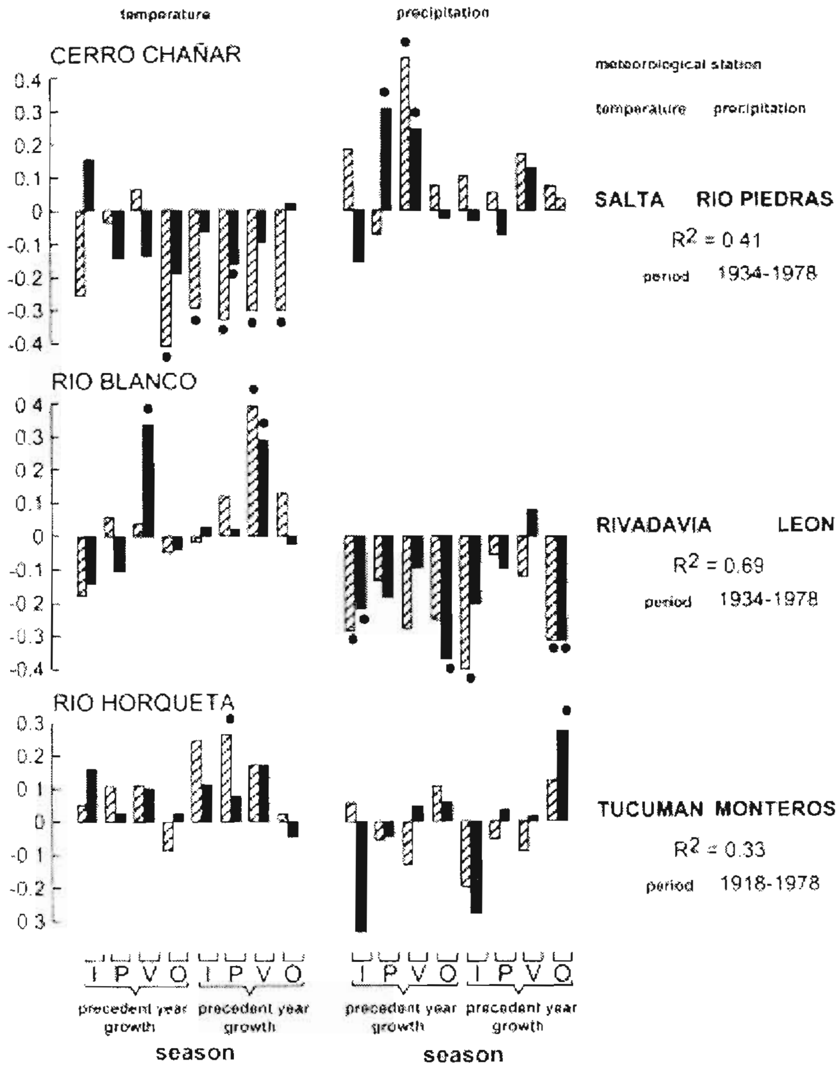

Fig. 5—Correlation function (● and response function (■) to chronologies de *Cedrela angustifolia* in Cerro Chanar e Rio Blanco. Coefficient of correlation and response function significant at 95% (●). To the response functions the % of variance explained by climate is presented (R2). The climatic seasons are abbreviated as I, winter; P, spring; V, summer; O, autumn (after Villalba *et al.*, 1987).

Blanco site, at 1,870 m of altitude, upper limit of distribution of this species, the summer temperature constitutes the primary climatic parameter inducing tree growth. The precipitation of the end of winter and beginning of spring and autumn seems to be negatively related to trees growth, probably due to an indirect effect on the amount of incident radiation (Villalba *et al.*, 1987) (Figs. 3, 4, 5).

In subtropical northwestern Argentina 12 chronologies were made by Villalba *et al.*, (1992) using tree ring data of *C. angustifolia* and *Juglans* and reconstructed the seasonal and annual precipitation explaining 60-80 % of precipitation variance. A recent literature revision of dendroclimatology in the South Hemisphere, Boninsegna and Villalba (1996) concluded that in the tropical region, the growth rings of *Cedrela angustifolia* trees at 24° S produce chronological series with sensitivity to climatic conditions.

In Brazil, the wood anatomical analysis of *Cedrela angustifolia* trees enables the distinction of clearly visible annual growth rings, delimited by initial parenchyma bands and semi-ring porousity. Under stereomicroscopy it was possible to determine the tree age and annual and cumulative increment rates, with significant variations between the 3 different phases of the tree growth, higher at 1-5th and 16-20th and lower at 6-15th years (Fig. 6). The X-ray densitometry can also be applied for the delimitation of annual growth rings and the determination of wood density variation, from pith to bark. Maximum wood density values of latewood of some years, i.e., 15th year (0·90 g/cm^3) were distinct comparing with other, i.e., 3th, 7th (0·45 g/cm^3), probably due to climatic variation. These results show the potentiality of both methodologies in dendrochronological studies of tropical species, i.e., *Cedrela angustifolia*, including tree age

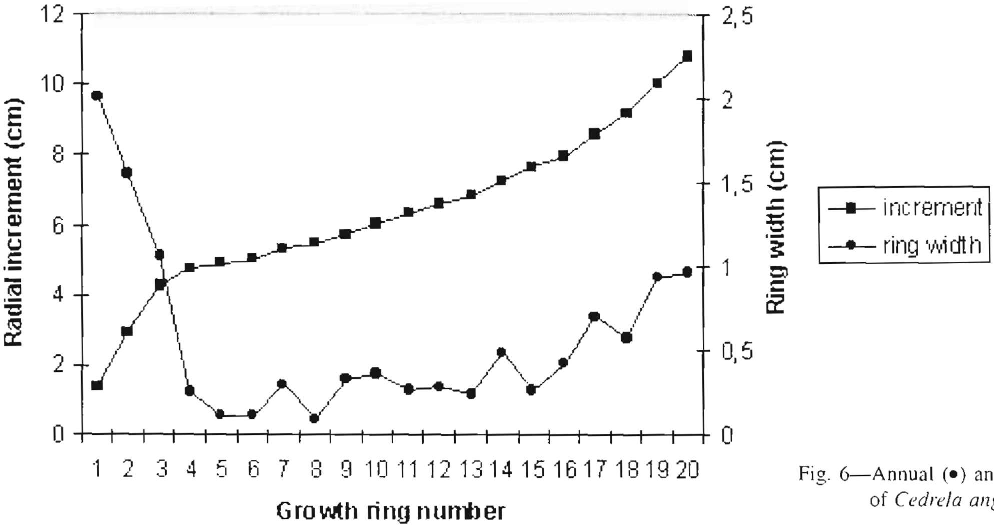

Fig. 6—Annual (•) and cumulative radial (♦) increments of *Cedrela angustifolia* tree.

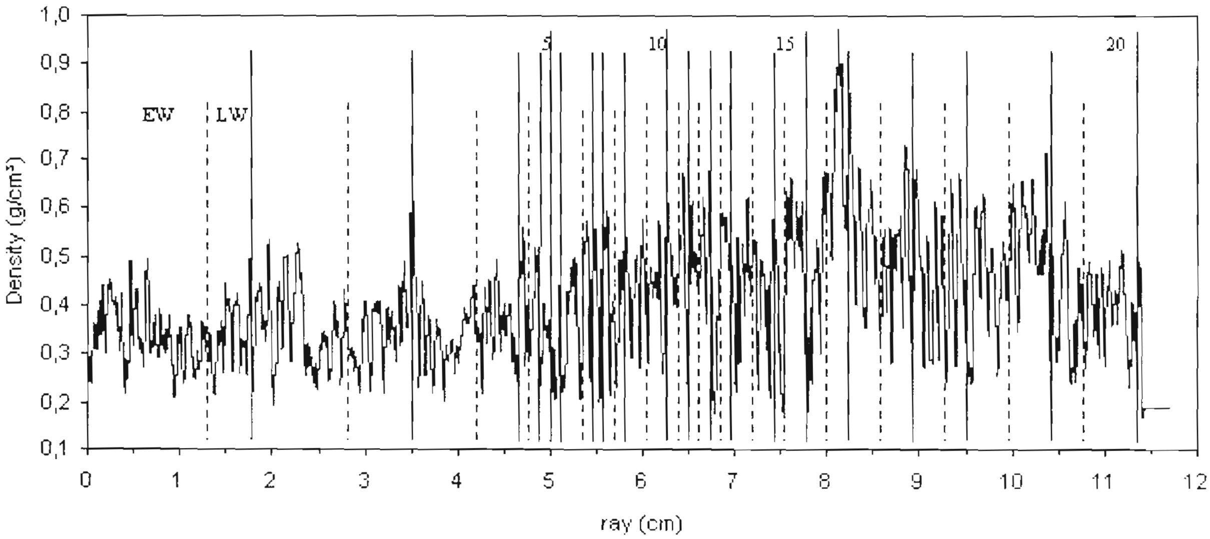

Fig. 7—Wood density profile, by X-ray densitometry, and demarcation of annual growth ring and boundaries of early (EW) and latewood (LW) of *Cedrela angustifolia* tree.

determination, stand dynamics and relationship between climate, etc. (Fig. 7).

CONCLUSIONS

The number of tropical and subtropical species applied in dendrochronology has been increased, allowing the age and growth rate determination through growth-ring analysis. Among the species, emphasis has to be given to *Cedrela*, an important member of the Meliaceae family and, in particular, to *C. angustifolia*. Occurring in large areas of the Latin American continent, in different ecological conditions, *C. angustifolia* produces annual growth-rings with climatic sensitivity used to the construction of chronologies related to climate, population dynamics, phenology, forest management, etc. Usually the tree-ring analysis consisted of the observation and measurement directly on polished wood cross section. However, the X-ray densitometry commonly used in conifer species, can be also applied to *C. angustifolia* for dendrochronological purposes.

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The genus *Toona* (Meliaceae): dendrology, ecology and wood anatomy with reference to its applicability for tropical dendrochronology

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ABSTRACT

Tomazello FM, Botosso PC & Lisi CS 2001. The genus *Toona* (Meliaceae): dendrology, ecology and wood anatomy with reference to its applicability for tropical dendrochronology. Palaeobotanist 50(1) : 55-62.

The potentiality of *Toona* sp. trees, Meliaceae native in Asia and Australia continents, for dendrochronological studies is described, including its silviculture, ecology and wood anatomy. Emphasis is given to the presence of distinct annual growth rings sensitive to climatic variations and detectable by wood cross section analysis and X-ray densitometry technique.

Key-words—*Toona* sp., Meliaceae, Dendrochronology, X-ray densitometry, Growth rings.

टूना वंश (मीलिएसी) : उष्णकटिबन्धीय वृक्षवलयकालानुक्रमिकी हेतु इसकी अनुप्रयोगात्मकता के सन्दर्भ में वृक्षविज्ञान, पारिस्थितिकीविज्ञान तथा काष्ठ शारीरविज्ञान

मारियो टोमाज़ेलो एफ़, पी.सी. बोतोसो, सी.एस. लिसी

सारांश

प्रस्तुत शोध पत्र में एशिया तथा आस्ट्रेलिया महाद्वीप के मीलिएसी मूल के *टूना* प्रजाति के वृक्षों की वृक्षवलयकालानुक्रमिकीय अध्ययन में उपयोगिता का वर्णन अभिप्रेत है। इस अध्ययन में इसके वनवर्धन, पारिस्थितिकीविज्ञान तथा काष्ठ शारीरविज्ञान को समाहित किया गया है। अध्ययन में काष्ठ अनुप्रस्थ परिच्छेद विश्लेषण एवं एक्स-रे घनत्वमिति प्रविधि द्वारा पहचाने जा सकने वाले जलवायुविक परिवर्तनों के प्रति संवेदनशील सुस्पष्ट वृद्धि वलयों की उपस्थिति पर विशेष ध्यान दिया गया है।

संकेत शब्द—*टूना* प्रजाति, मीलिएसी, वृक्षवलयकालानुक्रमिकी, एक्स-रे घनत्वमिति विज्ञान, वृद्धि वलय.

INTRODUCTION

TAXA under Meliaceae occurs in tropical and pantropical regions throughout Africa, America and Asia, grouped in 51 genera and 1400 species with approximately 500 species of economic importance (Lawrence, 1951; Styles, 1972; Girardi, 1975; Holdridge, 1976a; Styles & Khosla, 1976; Barroso, 1984). This family is represented by 8 genera in South America—*Cedrela, Swietenia, Cabralea, Trichilia, Guarea, Carapa, Schmardaea* and *Ruegea* - with the first 6 genera naturally occurring in Brazil. In addition exotic genera introduced from other regions are—*Melia, Azadirachta, Toona* and *Khaya*, etc. (Holdridge, 1976a; Rizzini, 1978; Pennington, 1981; Barroso, 1984). The

Meliaceae family was studied by several researchers, like De Candolle (1878), Kribs (1930), Smith (1960, 1965), Pennington and Styles (1975), Holdridge (1976a, b). In addition there are several reprots from Brazil itself—Pirani (1984), Pastore and Berzaghi (1989) in São Paulo, Amaral (1981) in Goiás, Klein (1984) in Santa Catarina, Girardi (1975) in Rio Grande do Sul and Pinheiro (1986) in Minas Gerais States.

Among the representative species of Meliaceae, in this paper emphasis is given to the genus *Toona,* considering its silvicultural and ecological importance, wood quality and dendrochronological applications in tropical regions of the world.

THE GENUS *TOONA:* DENDROLOGY, ECOLOGY AND WOOD ANATOMY

The systematic classification of the genus *Toona* has been discussed since long time by many authors, because of its similarity to the genus *Cedrela.* According to Smith (1960), 2 genera were initially established by Roemer in 1846: *Cedrela* including the American cedars and *Toona*, the Asiatic cedars. Later, in 1878, De Candolle grouped them as *Cedrela,* because its close similarities and Harms, in 1896, classified 2 different genera, regrouped again by De Candolle in 1908 (Pinheiro *et al.*, 1994).

However classification of Harms was accepted by Smith (1960), pointing of the differences between *Cedrela* and *Toona*. Chevalier and Begemann, cited by Grijpma and Ramalho (1969) relates 11 species, *Toona ciliata* (with 20 varieties), *T. calantas*, *T. fargesii*, *T. microcarpa*, *T. mollis*, *T. multijuga*, *T. paucijuga*, *T. serrata*, *T. serrulata*, *T. sinensis* and *T. sureni.* The most important species for the ecological conditions in Latin America are *T. ciliata* var. *australis*, *T. calantas* e *T. sureni.* Actually, the better revision referring to the genus *Toona* was done by Bahadhur (1988), in India, representing an analysis of the taxonomic knowledge, including descriptions, occurrence, economic uses, habitats, vernacular names, etc.

Toona ciliata Roem. var. *australis* (F. v M.) C. DC.

Toona ciliata has a natural widespread distribution, throughout India, Pakistan, Myanmar, Thailand, southern China, New Guinea, Malaysia, Philippines, Himalayan valleys (up to 1300 m height), Molucas Island, etc. The trees can be found across the river banks and in inclined lands, also in swampy and wet tropical forests, including all the western Pacific region (Grijpma & Ramalho, 1969).

Toona ciliata var. *australis* trees naturally occurs in eastern Australia in New South Wales (Ulladula, southern Sidney) and Queensland States (northern Atherton) and has the synonyms *T. australis*, *Cedrela australis* and *C. toona* var. *australis*. It's denominated "cedro australiano" or toona in Brazil, toona and cedar in Mexico, red cedar, Australian toona, Australian red cedar in all speaking English countries. The trees show monopodial growth and a superficial root system, reaching 30-46 m in height and 1·50-2·00 m trunk diameter and are light tolerant in the juvenile period,

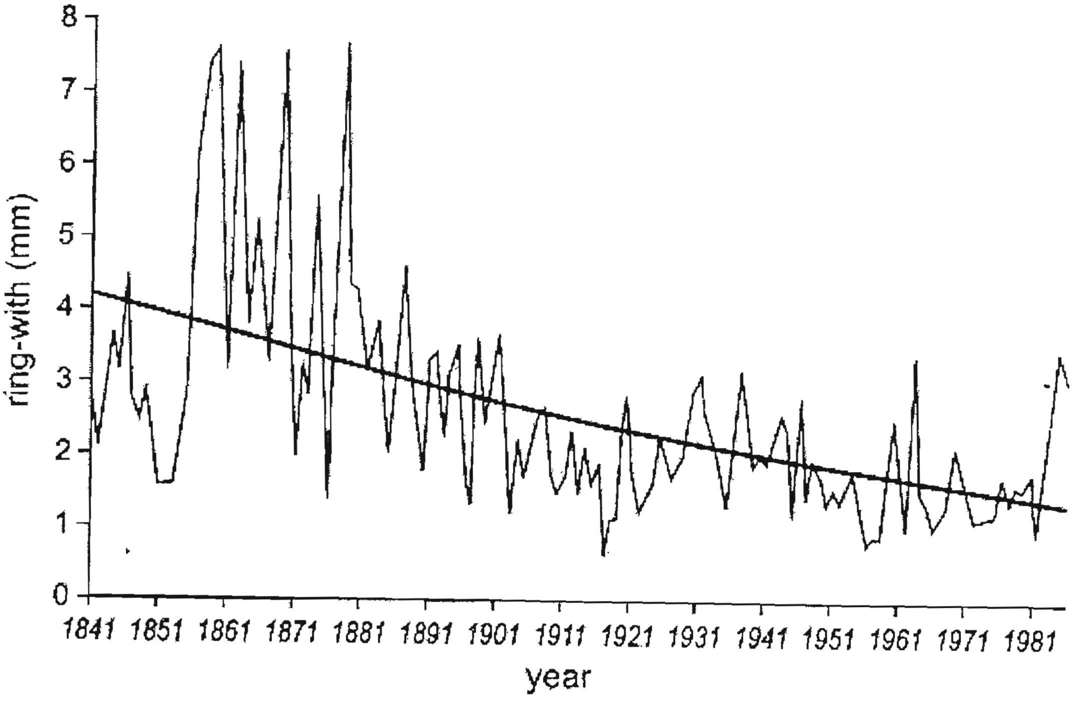

Fig. 1—Curve of growth ring width of *Toona ciliata* tress (after Bhattacharyya *et al.*, 1992).

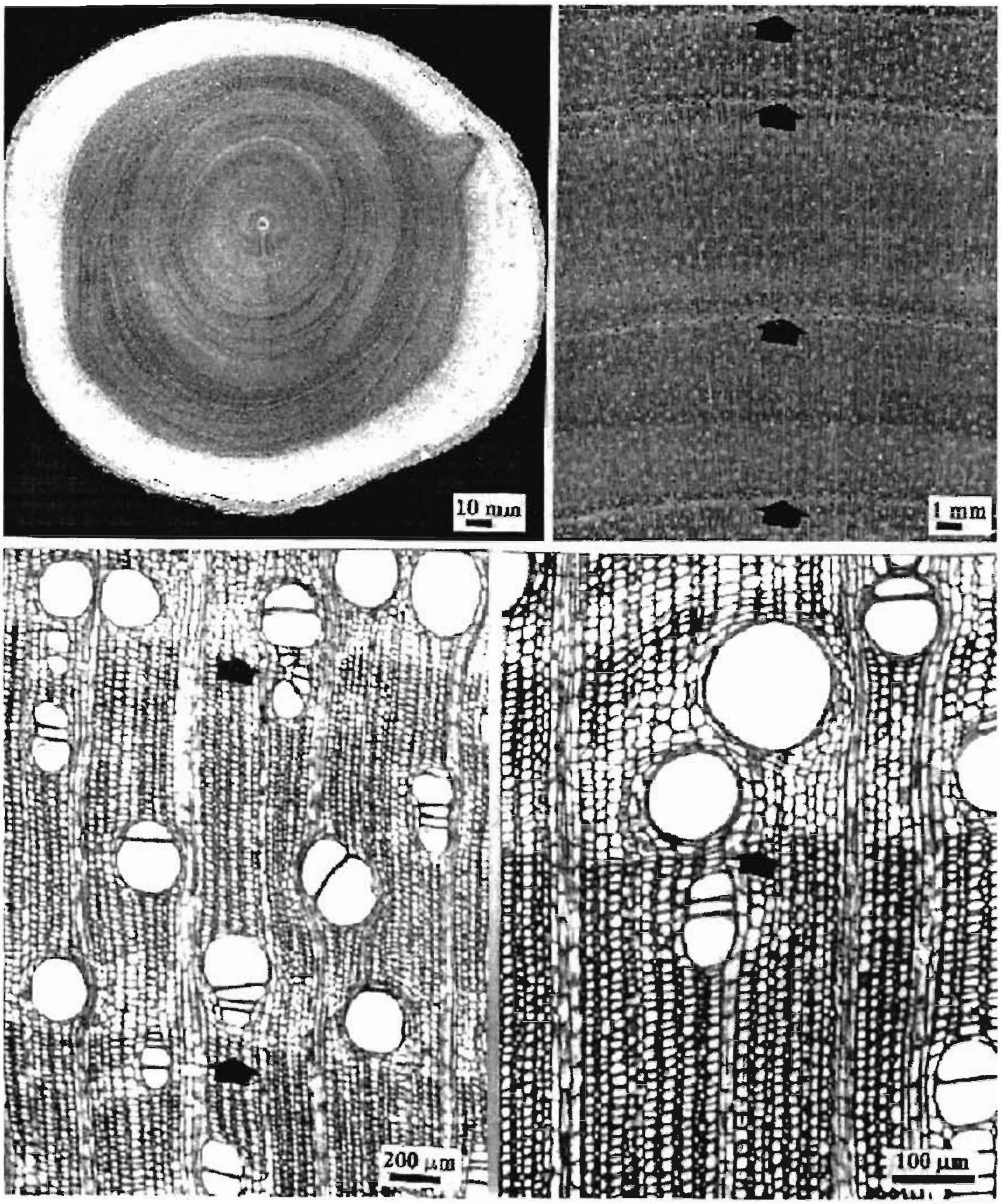

PLATE 1

Wood anatomy and growth rings of *Toona ciliata* var. *australis* tree. Cross section of a trunk (a) and wood (b) showing growth rings, delimited by initial parenchyma bands and semi-porous ring. Cross section (c, d) showing the features of the parenchyma cells, vessel and fiber wall thickness in early and latewood.

demanding sunlight in adult phase. In Australia it occurs in low to median lands, wet to very wet climates, with 1100-4000 mm annual precipitation and a dry period of 3-4 months. Despite their preference to wet soils, the trees can also develop in driest regions, with 800 mm annual precipitation, where the ground water table is accessible to the roots in the dry period. The temperatures can vary from -1 to 43°C, supporting light frosts; in Atherton region the temperature varies from -2 to 28°C. Rich and well-drained soils are ideal for toona, which prefers chalky soils and does not support dense clayish and poor sandy soils (Grijpma & Ramalho, 1969; Walters, 1974; Rocas, 1986; Namikawa, 1988; Pinheiro *et al.*, 1994).

In Central America countries, like Mexico the *T. ciliata* trees were introduced from India and Myanmar and reach 15-17 m height in tropical area plantations (Rocas, 1986). In Costa Rica the trees grow excellent in well-drained and nutrient-rich soils with positive response to mineral fertilization. The pruning of branches is recommended in 15-20 years old trees for higher wood quality (Otarola *et al.*, 1976; Sanchez *et al.*, 1976).

Introduced in Hawaii in 1914, this tree species has been cultivated for its high increment rates, reaching 30-36 m in height and 0·25-0·65 m diameter in 22 years, producing wood with excellent properties. Their phenology is characterized by the flowering in April-June, fruit ripening and seed dispersal in July-October and leaves shading in dry sites with hydric deficit (Walters, 1974).

In South America, *Toona ciliata* var. *australis* trees were introduced in 1969, in Argentina, by Cozzo and Mangieri, with aim to replace the cedar species in a reforestation program, however in Missiones Province, 10 year-old toona plantations suffered from photosynthetic problems (Mangieri, 1972; Sanchez *et al.*, 1992). In 1988, toona was introduced in the Alto Parana region, Paraguay, where the tree plantations show high growth increment rates compared to other species (Serafina *et al.*, 1994).

In Brazil, toona shows good adaptation to several ecological conditions, also presenting resistance behaviour against Meliaceae shoot borer, *Hypsipyla grandella*, while it is attacked in its country of origin by *H. robusta* (Grijpma, 1976). In Minas Gerais State, toona trees reveal good growth increments and well-marked phenological events, flowering in September-November, fructification in January-March and leaves fall in June-July (Pinheiro, 1986). Plantations cited by Ledoux and Lobato (1976) in the Amazonian region prove the potential of toona, despite the great variability between trees. In the same way, plantations in São Paulo and Espírito Santo States demonstrate its potential concerning the wood volumetric increments (IPEF, 1975). The *T. ciliata* var. *australis* descriptions, including taxonomy, botany, ecological aspects, silvicultural features, phenology, etc., are presented by Gripjma and Ramalho (1969) and Pinheiro (1986).

The wood characteristics of *T. ciliata* trees and its variety *australis* are similar, with specific gravity of 0·45-0·64 g/cm³, presenting the same characteristics as *Cedrela* (Record & Hess, 1947). Toona is considered as one of the best quality woods in India, Australia, etc., widely applied in furniture, carpentry, cabinet, etc. The bark can be used in medicine and trees as ornamental in parks and gardens (Grijpama & Ramalho, 1969; Walters, 1974; Rocas, 1986; Namikawa, 1988).

The wood of *T. ciliata* presents sapwood rose-light brown and in the var. *australis* the color is yellowish-white, and the heartwood darkened-brown to reddish. The wood anatomy and properties were studied by many authors (Francis, 1951; Bhat, 1985; Espinoza de Pernia, 1987; Cardoso & Tomazello Filho, 1988; Sudo, 1989; Haslett *et al.*, 1991), including fibers and early and latewood measurements (Bisset *et al.*, 1950). Additionally, dendrochronological studies were developed by Chowdhury (1939), Bhattacharyya *et al.* (1992) and Cardoso and Tomazello (1988), due to the presence of distinct annual growth rings, delimitated by some typical anatomical wood features like initial parenchyma bands, vessel arrangement and fiber wall thickness (PLATE 1).

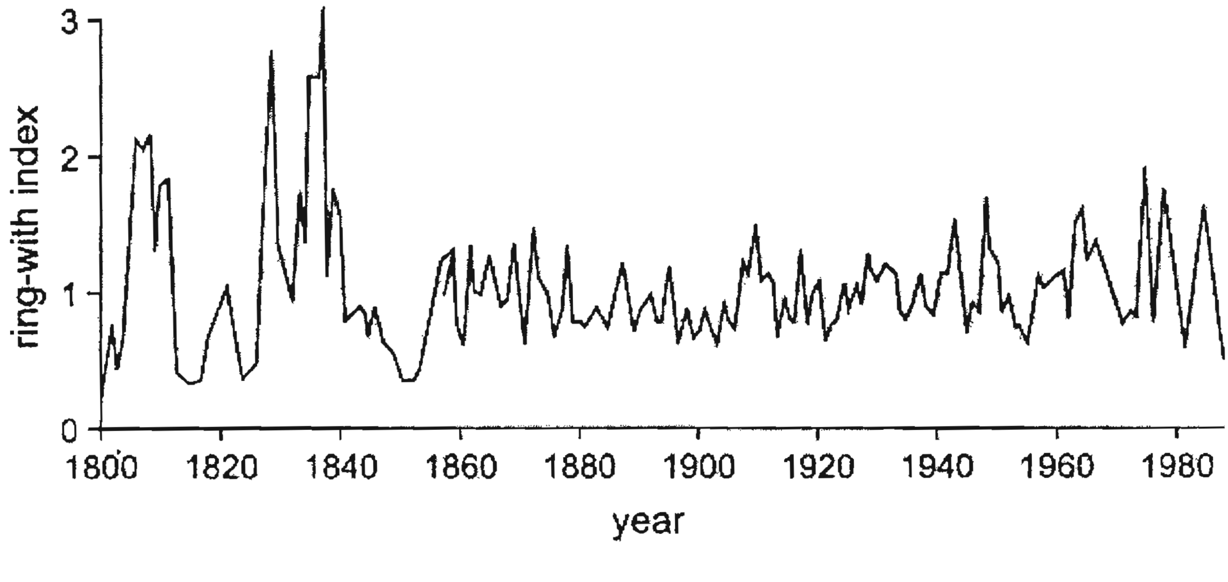

Fig. 2—Chronology of growth ring width index of *Toona ciliata* trees (after Bhattacharyya *et al.*, 1992).

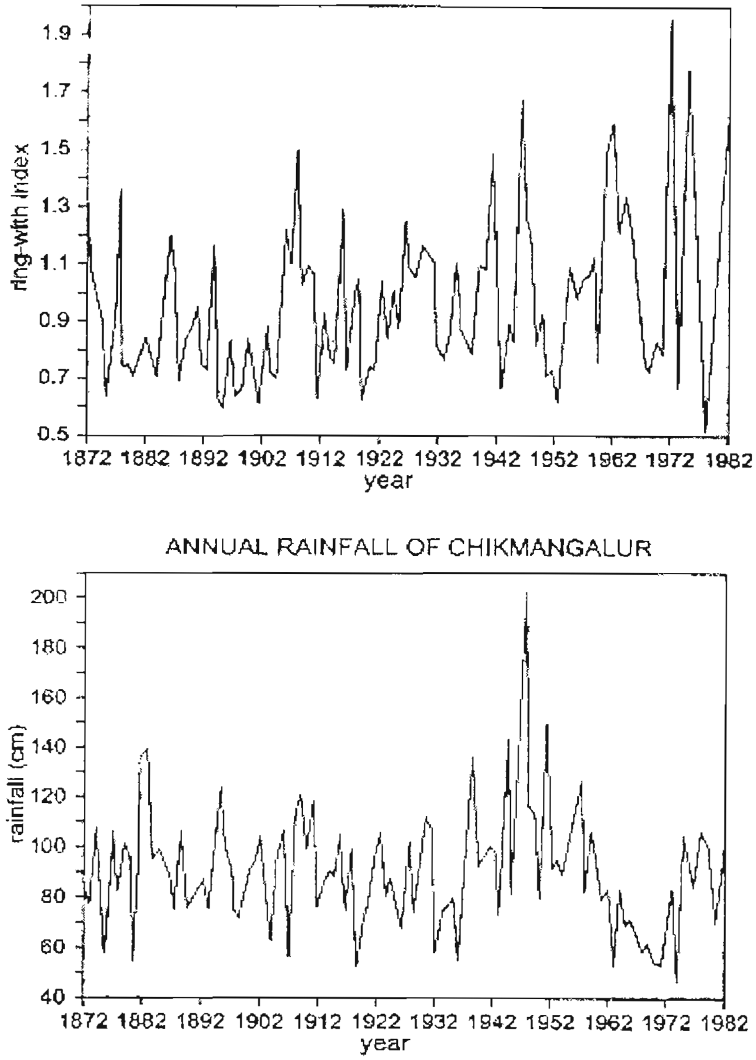

Fig. 3—Chronology of growth ring width index and annual rainfall showing the correlation between *Toona ciliata* tree growth and annual rainfall (aft er Bhattacharyya *et al.*, 1992).

Toona sureni (Bl.) Merril.

This species naturally occurs in low lands up to 1000 m altitude in the dense pluvial equatorial forests of Vietnam, Cambodia, Indonesia, Myanmar and Malaysia. The tree shows high growth increments, reaching 20-40 m height and 0·60-2·00 m diameter, producing high quality wood. The heartwood color is dark-brown, with characteristic odour, 0·39-0·45 g/cm³ specific gravity, usually used in furniture, carpentry, etc. The trees are strongly attacked by *Hypsipyla robusta* in Asia, when growing in plantations. However, the toona trees in Puerto Rico plantations are resistant against *H. gnarled*, reaching 4·3 (2·30-8·30) m height and 7·0 (2·5-13·5) cm diameter in 5·5 years (Gripjma & Ramalho, 1969).

Toona calantas Merril et Rolfe

The species occurs in several provinces of the Philippines, near to the riverbanks and areas periodically inundated. The trees reach 40-50 m height and up to 1·50 m diameter. The straight and cylindrical trunk is free of branches until 50% trunk height. Heartwood light to dark reddish, specific gravity 0·41-0·44 g/cm³. The wood can be easily worked and is applied in furniture, general carpentry, musical instruments, etc. (Gripjma & Ramalho, 1969).

TOONA CILIATA: A POTENTIAL SPECIES IN TROPICAL DENDROCHRONOLOGY

Toona ciliata var. *australis* presents distinct annual growth rings constituted by fibers with length variations

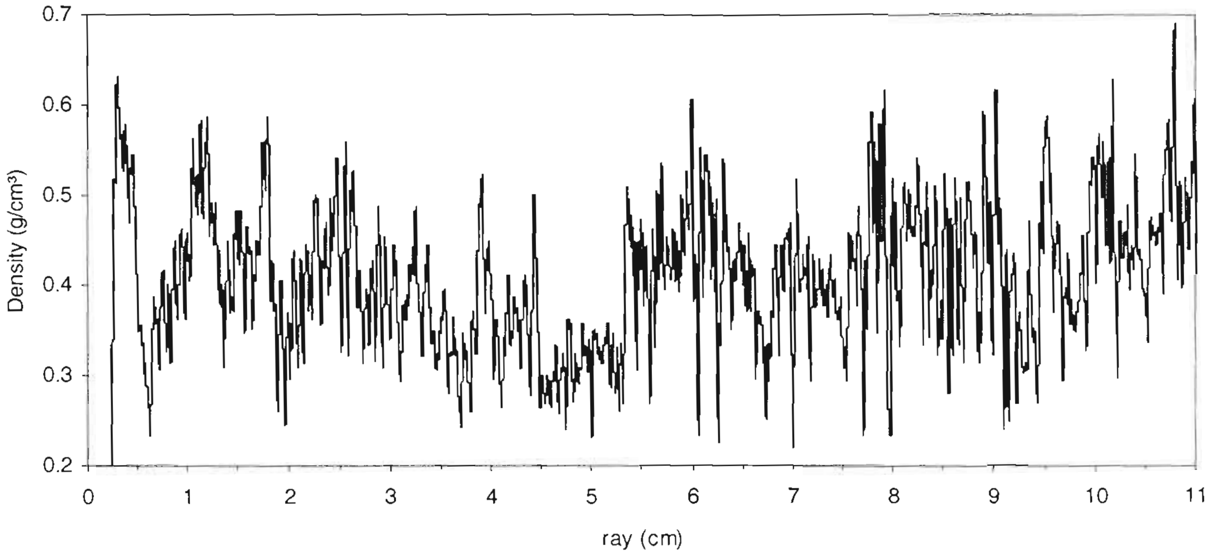

Fig. 4—Wood density profile by X-ray densitometry and demarcation of annual growth ring and boundaries of early (EW) and latewood (LW) of *Toona ciliata* tree (ref., Text-Figure 1).

related to the diameter increment rates. The shorter fibers, at the first earlywood layers, are formed in the beginning of spring, during the period of maximum cambium activity, while the latewood fibers of last layers produced in winter, during the minimum cambium activity are 83% longer (Bisset *et al.*, 1950).

In India, *T. ciliata* is a deciduous tree, starting radial growth only after the renovation of 50% of the canopy with new leaves. In response, the cambium produces distinct annual growth rings, the boundaries of which are delimited by initial parenchyma bands and large diameter vessels forming semi-porous rings, resulting in a period of fast growth followed by a period of lower growth rates (Chowdhury, 1940; Chowdhury & Rao, 1948).

Also in India, *T. ciliata* trees are found potential for dendrochronological studies. They exhibit annual growth-rings sensitive to climatic variations. The growth rings were dated and measured and a reference-chronology of growth ring width from 1800-1987 compared with growth ring width index chronology and annual rainfall. They recorded that the narrow growth rings width was correlated with hydric deficit in the soil, caused by a low photosynthetic activity during the less rainfall years during the peak of monsoon rainy season (June-August), when growth is supposed to be fast. *Toona* trees produce a superficial root system when growing in flat sticky red soils with low water infiltration and deficient drainage, when the water saturation may reduce soil oxygen supply and, consequently, inhibit the root growth (Bhattacharya *et al.*, 1992) (Figs. 1, 2, 3).

In Brazil, *Toona ciliata* trees produce distinct annual growth rings characterized by initial parenchyma bands and semi-porous ring, making possible the determination of tree age and annual increment rates (Cardoso & Tomazello Filho, 1988). Besides direct growth ring measurements on the polished cross section, the X-ray densitometry method can be applied for the delimitation of annual growth rings of toona wood samples. Significant values of maximum wood density between and within growth rings also can be obtained, like 5° and 16° annual rings, with a specific gravity of 0·35 and 0·60 g/cm^3, respectively. These results show the potentiality of both methodologies in the dendrochronological studies of tropical species, i.e., *Toona ciliata*, including tree age determination, stand dynamics and relationship to climate, etc. (Fig. 4).

CONCLUSIONS

Toona ciliata has a great potential for dendroclimatology studies and forest dynamics in natural forests and plantations in its area of natural occurrence and in Asia as well as in tropical areas of Central and South America. In American countries, including Brazil, the phenological characteristics of introduced toona trees are similar to other native Meliaceae species, mainly *Cedrela* and *Swietenia*. In these areas, however, resistant behaviour presented by toona trees against the Meliaceae shoot borer, *Hypsipyla grandella* constitutes the main advantage. In addition these species produces distinct annual tree rings delimitated by a typical initial parenchyma and semi-porous ring, essential for dendrochronological studies. The wood anatomy and X-ray densitometry methodologies can also be applied to the annual growth rings delimitation and to the intra- and inter-tree-ring density determination. However, a limited amount of dendrochronological work has been carried out on toona trees, despite of the confirmed sensitivity of the annual growth rings to climatic variation.

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Similar tree ring pattern in the Gymnosperm woods from Late Permian of Antarctica and India

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ABSTRACT

Bera S & Banerjee M 2001. Similar tree ring pattern in the Gymnosperm woods from Late Permian of Antarctica and India. Palaeobotanist 50(1) : 63-70.

Tree rings revealed in a newly described gymnosperm wood *Araucarioxylon ghoshii* sp. nov. from Raniganj Formation, Raniganj Coalfield, India are similar to the tree rings described in the *in situ* gymnosperm fossil woods from the Late Permian of Antarctica.

The rings of the fossil woods from Antarctica and India have higher proportion of early woods compared to little amount of late wood. Characteristic zigzag pattern of early wood tracheids formed due to collapsing and crushing of tracheid files and false rings occur in the woods recorded from two distant areas. The characters suggest occurrence of rapidly growing young forest in both the continents during Late Permian. Quantitative analysis of growth rings in *A. ghoshii* reveals a CSDM curve with right skewedness +19% suggesting its possible evergreen nature with small to moderate leaf retention time.

Key-words—Late Permian, Antarctica, *Araucarioxylon*.

अण्टार्कटिका एवं भारत के अन्तिम परमियनयुगीन अनावृतबीजी काष्ठों का सममित वृक्ष वलय विन्यास

सुबीर बेरा एवं मंजु बनर्जी

सारांश

भारत के रानीगंज कोयला क्षेत्र अवस्थित रानीगंज शैलसमूह से प्राप्त *अराउकेरियॉक्सीलॉन घोषाइ* नवप्रजाति से तुलनीय नवीनतम अभिलक्षणित अनावृतबीजी काष्ठ में प्रदर्शित हुए वृक्ष वलय अन्तिम परमियनयुगीन अण्टार्कटिका से प्राप्त स्वस्थाने अनावृतबीजी अश्मित काष्ठ के वृक्ष वलयों के समरूप हैं।

अण्टार्कटिका एवं भारत से प्राप्त अश्मित काष्ठों के वलयों में पश्चदारु की अल्प मात्रा की तुलना में अग्रदारु उच्चतर अनुपात में विद्यमान है। दो सुदूरवर्ती क्षेत्रों से अंकित किए गए काष्ठों में संवाहिका (ट्रेकीड) फाइलों एवं कूट वलयों के निपातन एवं संदलन के कारण निर्मित अग्रदारु संवाहिकाओं के अभिलाक्षणिक टेढ़े-मेढ़े विन्यास प्रदर्शित हुए हैं। ये अभिलक्षण अन्तिम परमियन कल्प के दौरान दोनों महाद्वीपों में नूतन वनों की अतिशीघ्र वृद्धि को प्रस्तावित करते हैं। *ए. घोषाई* में वृद्धि वलयों के गुणात्मक विश्लेषण से दक्षिण विषमतल +19 प्रतिशत युक्त सी.एस.डी.एम. वक्र प्रदर्शित हुआ है, जो हल्के से मध्यम पर्ण धारण शक्ति युक्त सम्भावित सदाबहारी प्रकृति को प्रस्तावित करता है।

संकेत शब्द—अन्तिम परमियन, अण्टार्कटिका, *अराउकेरियॉक्सीलॉन*.

INTRODUCTION

TREE growth rings are evidence of growth rhythm in trees. Correspondence of differential rate of cambial activity with climatic condition is considered as the primary factor for the formation of the annual growth rings in plants. Tree ring research thus has attracted the climatologists to assess the pattern of climatic change in the immediate past few thousand years. The climate consideration, mainly the seasonal variations in temperate conditions applied in the geologically older horizons of Palaeozoic eras also. Dendroclimatology, Palaeodendroclimatology have thus equally gained importance in Palaeoclimate research (Brown, 1925; Chaloner & Creber, 1973; Creber & Chaloner, 1984, 1985; Jefferson, 1982, 1983; Francis, 1984, 1986; Ash & Creber, 1992; Taylor *et al.*, 1992; Tidwell & Medlyn, 1993; Chapman, 1994; Yadav & Bhattacharyya, 1994, 1996a, b; Creber & Francis, 1999).

Major support to accept the seasonal climate change in the Permo-Carboniferous supercontinent Gondwana land comes from the distinct growth rings of the most common Lower Gondwana petrified woods identified as species of *Dadoxylon* and *Araucarioxylon*. Emergence and flourishing of the Lower Gondwana forests preceeding millions of years of phases of glaciation, deglaciations are regarded as the obvious reason for a temperate climate influence in the Southern hemisphere coal forming vegetation. However, the factors of morphographic characteristics of the large assemblage of *Glossopteris* species, association of the glossopterid members with the tropical Euramarian flora (Banerjee, 1988) or Euramarian like flora (Banerjee & D'Rozario, 1999) and the typical features of growth rings recorded in the *in situ* Permian petrified wood forest preserved in close association with *Glossopteris*, *Vertebraria* from Antarctica (Taylor *et al.*, 1992) lying in a much higher Palaeolatitude (80° to 85°) are significant data to reconsider the palaeoclimate of the Permo-Carboniferous forests.

In the present paper some permineralised woods collected from Raniganj Coalfield (Raniganj Formation – Late Permian) are described which show the typical growth ring pattern with small late wood and zigzag pattern of collapsing of tracheids in the early wood similar to the Antarctic Late Permian petrified woods.

MATERIAL AND METHODS

The permineralised wood specimens of the present study were collected from Andal Railway Station, Raniganj Formation, Raniganj Coalfield. The logs range from 18-29 cm in diameter, consisting of secondary wood only; its pith, primary xylem, phloem and cortex are not preserved. Woods were studied using ground thin sections.

The radial diameters of successive tracheid cells were measured across each growth increment. Using these data the cumulative algebraic sum of each cell deviation from the mean of the radial diameters was calculated and plotted as a zero trending curve, the CSDM curve after Creber and Chaloner (1984). The percentage skew of the zenith of the CSDM curve with respect to the centre of the plot was calculated (Falcon-Lang, 2000).

DESCRIPTION

Genus—ARAUCARIOXYLON Kraus, 1870

ARAUCARIOXYLON GHOSHII sp. nov.

(Pl. 1·1-4; Pl. 2·1-6)

Diagnosis

Secondary wood with distinct growth rings, Growth rings with scanty (3-6 cells wide) late wood. Xylem rays homogenous, uniseriate or rarely biseriate, 3-29 (mostly 3-15 cells) cells high. Radial walls of tracheids with 3-4 seriate (mostly 3-seriate), contiguous, subopposite to alternate, subcircular to hexagonal bordered pits. Cross field pits weakly bordered, 2-6 (usually 3-4) in number.

Holotype Specimen Number—PPL/PW/1-4.

Locality—Andal Railway Station, Raniganj Coalfield.

Horizon—Raniganj Formation, Upper Permian.

Collected by— A.K. Ghosh 1945.

Repository—Palaeobotany & Palynology section, Department of Botany, University of Calcutta.

Derivation of specific name—The species is named after late Professor A.K. Ghosh, the founder teacher of Palaeobotany & Palynology Section, Department of Botany, University of Calcutta, Kolkata.

Detail Description

This species is represented in the present collection by four specimens of silicified woods (PPL/PW/1-4) showing only secondary wood of 18-29 cm diameter. Pith, primary xylem and extra xylary elements are not preserved in any of the woods.

Growth rings occur with clearly distinguishable zones of early and late woods. 26-33 rings varying between 2·65-5·34 mm in width (mean ring width 3·86 mm) are recorded.

The growth rings show a large amount of early wood with narrow (3-6 cells wide) late wood. In some of the rings a few layers of early wood tracheids have comparatively small radial dimensions. This false late wood is easily recognized for its more thicker walls and appearing more dense than rest of the wood. The ring boundaries are marked by late

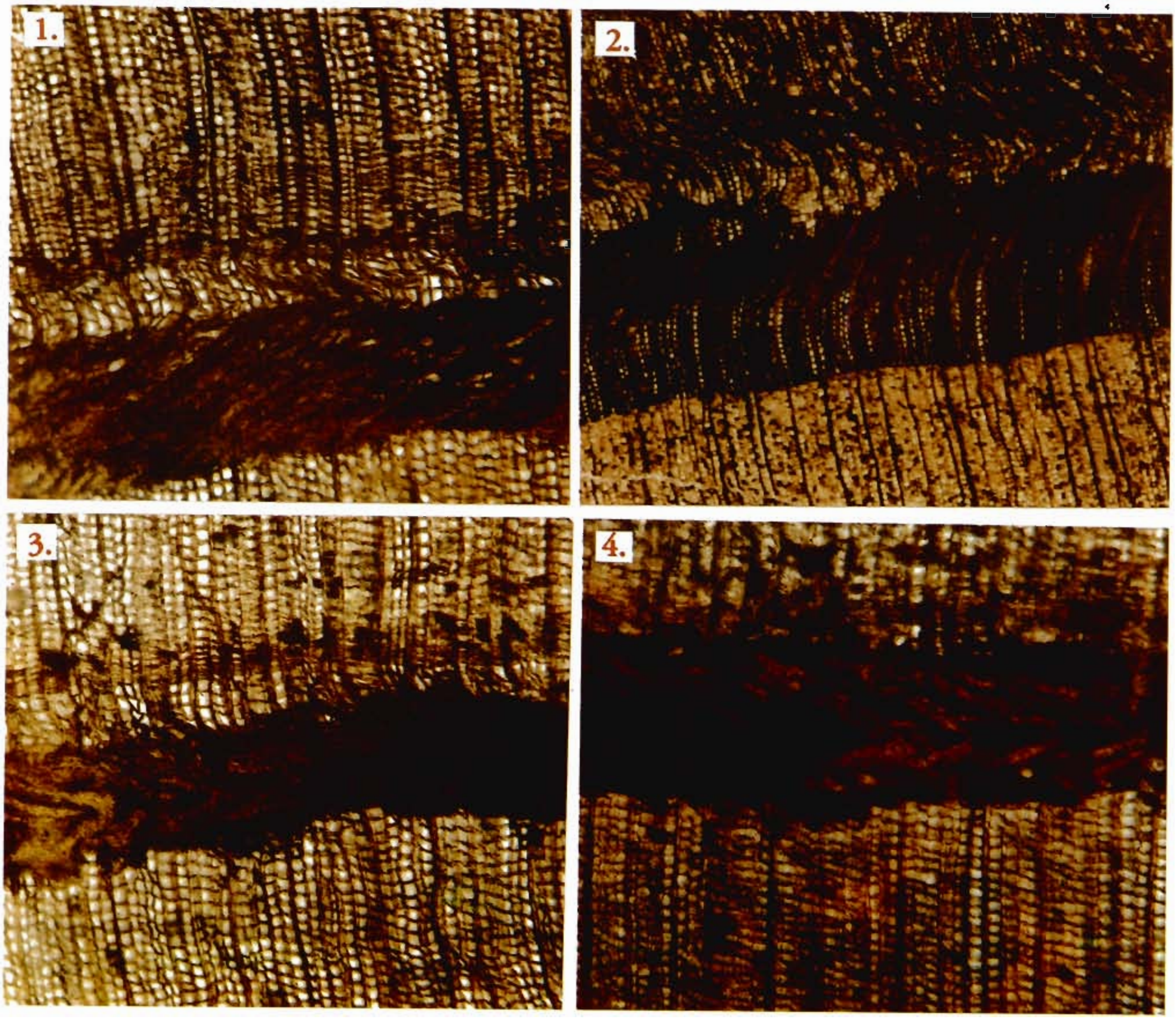


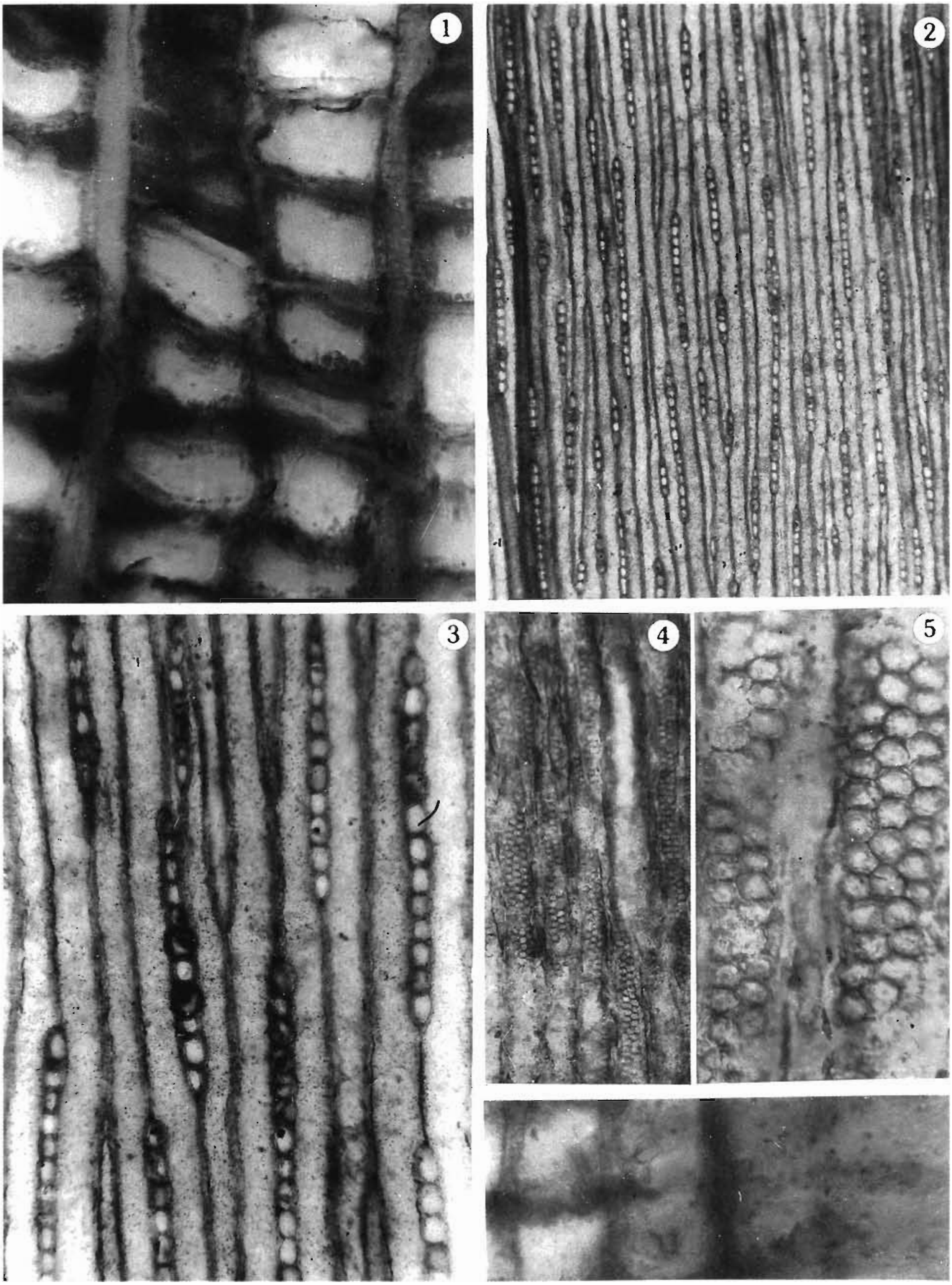
PLATE 1

1. Cross section of *Araucarioxylon ghoshii* sp. nov. showing growth ring boundary and false ring. x 60.
2. Zigzag pattern of tracheid files. x 60.

3 & 4. Cross section of *A. ghoshii* showing arrowhead pattern of tracheid files. x 60.

wood cells with thick walls and narrow lumens. No frost rings are evident at the beginning or end of annual rings. The early wood is characterized by the presence of thick, collapsed and distorted files of tracheids developing arrowhead or zigzag pattern (Pl. 1·1-4) of the growth rings. These features are not reported in the woods described so far from Indian Lower Gondwana (Fig. 1).

The early wood tracheids are polygonal to subcircular in transverse section and range from 35.5-50 μm in radial plane, tracheid walls 4-6 μm thick (Pl. 2.1). The late wood tracheids


1
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Growth ring characters of woods	Mount Acherner wood, Antarctica	Raniganj Coalfield wood, India
Diameter of the wood	9-18 cm	18-29 cm
No. of growth rings	15 (highest number recorded)	26-33
Mean ring width	4·5 mm (Maximum ring width 11.38 mm)	3·86 mm (Maximum ring width)
Proportion of late wood	Very small	Very small (3-6 cells wide)
Frost ring	Absent	Absent
False ring	Present	Present
Zigzag/arrowhead pattern in early wood	Zigzag pattern	Zigzag & arrowhead pattern

Fig. 1—Comparative account of growth ring features of Permian Woods from Antarctica and India.

are more or less rectangular with rounded angles. The radial dimension of the latewood tracheids ranges between 34·5-37·5 µm.

The xylem rays are homogenous, mostly uniseriate or sometimes partly biseriate due to the presence of middle or terminal ray cell pair, 3-29 cells high (commonly 3-15 cells), 34-37/mm^2, tangentially ray cells are 20-26 µm wide (Pl. 2·2, 3).

Radial walls of tracheids with 3-4 seriate (mostly 3 seriate) pits; pits subcircular to hexagonal, contiguous (araucariod), subopposite to alternate, bordered (Pl. 2·4, 5).

The cross-field pits are weakly bordered, 2-6 (usually 3-4) in number; pit pore subcircular to circular, 3-4 µm in diameter (Pl. 2·6).

COMPARISON

Araucarioxylon ghosii sp. nov. has been compared with other Permian species of *Dadoxylon* and *Araucarioxylon* from India and abroad. The presence of araucarian tracheary pitting, uniseriate or rarely partially biseriate rays indicates that the present wood may be a species of *Araucarioxylon*. About fourteen species of the genus *Araucarioxylon* have been described so far from the Indian Lower Gondwana. A comparative analysis of characters of the new species with the known species of *Araucarioxylon* from India and abroad has been made (Fig. 2). *A. ghoshii* differ from all the described species in radial and cross field pitting and characteristic growth ring features.

A new species *Araucarioxylon ghoshii* has been proposed for the presently investigated wood.

DISCUSSION

While comparing with the other Permian woods from India and abroad, the presently described *Araucarioxylon ghoshii* sp. nov. wood shows similar tree ring features in the wood described from the Permian Mount *Glossopteris* Formation, Mount Weaver Formation, Antarctica (Maheshwari, 1972) and Late Permian deposits of Mount Acherner, Antarctica (Taylor *et al.*, 1992). In these woods comparatively fewer numbers of rings are observed some of which are fairly wide. This type of growth ring character is suggestive of a young and rapidly growing forest (Taylor *et al.*, 1992).

In *A. ghoshii* the structure of individual rings with well developed early wood and scant late wood is also comparable to that seen in the Permian polar forest of Antarctica. Another significant feature shared by these woods is the presence of thick tracheid files in early wood developing a zigzag or arrowhead pattern, giving the appearance of growth rings. Scant development of late wood and absence of frost rings in both the woods also suggest a warm climate at the time of deposition. Presence of small amount of latewood suggests sudden cessation of cambial activity at the end of the growing season. This feature coupled with absence of frost rings suggests that late wood production and cessation of cambial

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PLATE 2

1. T.S. of *Araucarioxylon ghoshii* sp. nov. showing early wood tracheids and ray cells. x 450.

2 & 3. T.L.S. of *A. ghoshii* sp. nov. showing distribution and dimension of rays. (2) x 120; (3) x 300.

4 & 5. R.L.S of *A. ghoshii* sp. nov. showing araucariod radial pitting. (4) x 300; (5) x 450.

6. R.L.S. of the same showing cross field pits. x 450.

Name of species	Growth rings	Pitting Radial	Tangential	Xylem rays (in cells) Width	Height	Cross field pits
Araucarioxylon ghoshii sp. nov.	Distinct	3-4 seriate (mostly 3) subcircular to hexagonal, contiguous, araucaroid	Absent	Uniseriate rarely biseriate	1-29 (average 3-15)	2-6, weakly bordered
A. bhivkundense Agashe & Prasad, 1984	Distinct	1-2 seriate in groups of 2, 3, 4	Present	1-2 seriate	1-33 (average 8)	1-8 (commonly 1-2), cupressoid
A. wejgaoense Agashe & Shashi Kumar, 1996	Distinct	1-2 seriate, mostly biseriate	Present	1-2 seriate, mostly uniseriate	2-34 (average 8-12)	1-6 (commonly 2-4), cupressoid
A. parbeliense (Rao) Maheshwari, 1972	Present	1-5 seriate, araucaroid, pit pore circular to oval	Absent	Uniseriate	1-24 (average 2-3)	8-9, bordered pore slit like
A. ningahense Maheshwari, 1965	Distinct	1-4 seriate, alternate or opposite, contiguous, hexagonal	Present	Uniseriate	1-11 (average 2-3)	1-6, bordered, pore oval
A. gondwanense (Maithy) Maheshwari, 1972	Distinct	1-5 seriate, alternate or subopposite, contiguous	Absent	Uniseriate and partly biseriate (13%)	1-43 (average 8-9)	2-8, contiguous or separate, pore circular
A. kharkhariense (Maithy) Maheshwari, 1972	Distinct	1-3 seriate, biseriate pits alternate or opposite, triseriate pits alternate, contiguous	Absent	Uniseriate, biseriate common	1-29 (average 6-7)	2-7, contiguous, pore elliptical
A. loharense Agashe & Gowda, 1978	Present	1-4 seriate, separate or contiguous, hexagonal or circular or elongated	Present	Uniseriate, biseriate common	1-27 (average 11)	2-9; 2, 4, 6 common
A. nandori Vagyani & Raju, 1981	Present	1-3 seriate, araucaroid	Absent	Uniseriate	2-30 (average 8)	2-6, cupressoid, pore circular to oval
A. surangei Agashe *et al.*, 1981	Present	1-4 seriate, separate or contiguous, opposite or alternate, pit pore circular or oblique	Present	Uniseriate and biseriate	1-35 (average 4)	1-11, cupressoid, round to oval
A. lathiense Agashe *et al.*, 1981	Present	1-4 seriate, separate or contiguous, round, oval to hexagonal	Absent	Uniseriate	1-27 (average 3-4)	1-10, cupressoid circular to oval with thin border
A. bengalense (Holden) Maheshwari, 1972	Present	1-3 seriate, araucaroid	Absent	Uniseriate	1-20	2-7 cupressoid
A. bradshawianum Bajpai & Maheshwari, 1986	Distinct	1-5 seriate, araucaroid	Absent	Uniseriate to biseriate	1-21 (average 2-7)	2-4, bordered
A. kumarpurensis Bajpai & Singh, 1986	Distinct	1-2 (rarely 4) seriate, araucaroid	Absent	Uniseriate to biseriate	1-19 (average 3-11)	2-8, cupressoid
A. kothariensis Agashe & Prasad, 1984	Distinct	1-4 seriate, free or contiguous, araucaroid	Present (1-3 seriate)	Uniseriate (55%) or biseriate (43%) or triseriate (< 2%)	1-44 border, cupressoid	1-12, with thin
A. arberi (Seward) Maheshwari, 1972	Distinct	1-4 seriate	Absent	Uniseriate	1-21 (average 6-12)	1-10, oblique
A. meridionale (White) Maheshwari, 1972	Absent	Uniseriate, pit pore oval or oblique	Absent	Uniseriate	1-30	
A. nummularium (White) Maheshwari, 1972	Doubtful	Mostly uniseriate, rarely biseriate	Absent	Uniseriate or often biseriate	1-30 (average 6-7)	many
A. roxoi (Maniero) Maheshwari, 1972	Distinct	1-2 seriate, pore boat shaped	Present	Uniseriate	1-36 (average 9)	2-4 (rarely 5-6)
A. allanii (Kräusel) Maheshwari, 1972	Distinct	1-2 seriate (rarely 3), pits circular to subcircular	Absent	Uniseriate, partly biseriate	1-27 (average 5)	1-6 (rarely 8)
A. africanum Bamford, 1999	Distinct	Mostly biseriate, sporadically uniseriate	Absent	Uniseriate	2-18	2-7, round to oval, araucaroid
A. karooensis Bamford, 1999	Distinct	Mostly biseriate, rarely uni or triseriate	Absent	Uniseriate sporadically biseriate	3-25	2-4, round to oval

Fig. 2—Comparative anatomical features in different species of *Araucarioxylon* from India & Abroad.

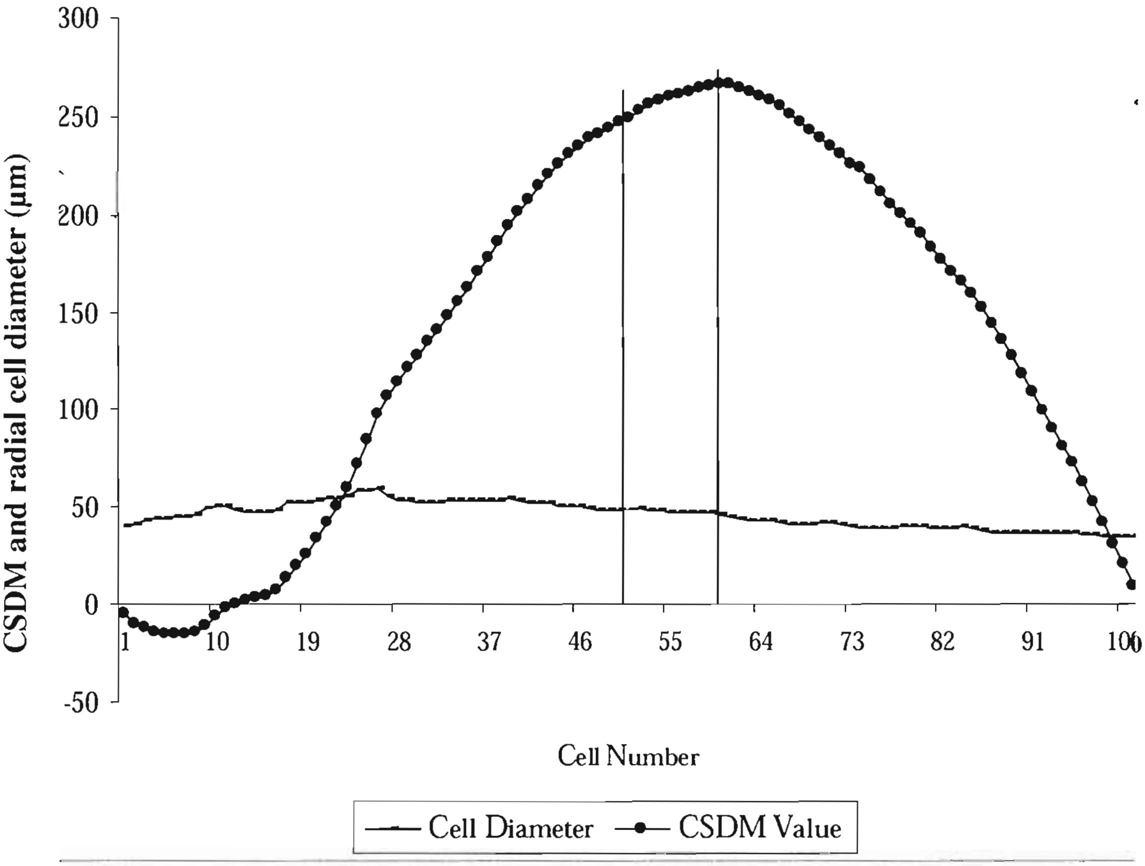

Fig. 3—CSDM Curve skewness data of *A. ghoshii* sp. nov.

activity were a response to lower light levels in the autumn (Taylor *et al.*, 1992). Such a minimal development of latewood points towards a lack of winter hardening of the trees and experienced only short periods of freezing weather, if any (Basinger, 1991).

Recently, Falcon-Lang (2000) outlined a method in which woods of deciduous and evergreen coniferopsids may be distinguished from one another on the basis of a quantitative analysis of growth ring anatomy. He advocated deciduous nature of the conifer woods dominantly with symmetrical or left-skewed CSDM curves and evergreen conifer woods dominantly possess right-skewed CSDM curves. In addition, the magnitude of right skewedness in evergreen conifers seems to be positively related to leaf longevity, i.e., the higher the leaf life span, the greater will be the right-skewedness value (Falcon-Lang, 2000).

Quantitative analysis of growth rings in *A. ghoshii* wood reveals a CSDM curve with right skewedness +19% (Fig. 3). This value suggests that these trees were possibly evergreen with small to moderate leaf retention time (LRT). No CSDM data on the Antarctic woods studied by Taylor *et al.*, (1992) are available. However, Francis (1996) quantitatively analysed growth rings in some glossopterid woods from Allan Hills in the Transantarctic Mountains and found that CSDM curves were symmetrical suggesting their deciduous nature. More CSDM data is required to support this interpretation related to leaf retention time of Permian glossopterid plants.

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Tree ring analysis of *Abies pindrow* around Dokriani Bamak (Glacier), Western Himalayas, in relation to climate and glacial behaviour: Preliminary results

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ABSTRACT

Bhattacharyya A, Chaudhary V & Gergan JT 2001. Tree ring analysis of *Abies pindrow* around Dokriani Bamak (Glacier), Western Himalayas, in relation to climate and glacial behaviour: Preliminary results. Palaeobotanist 50(1) : 71-75.

Analysis of tree ring data of *Abies pindrow* has been made from seven sites (Din Gad Valley) close to the Dokriani Bamak Glacier (Latitude 30°50' to 30°52' N and 78°47' to 78°50' E Longitude). Total 299 cores from 157 trees were collected from seven sites representing different glacially formed geomorphic features and elevation zones to study growth behaviour of trees in relation to climate change and glacial fluctuations in the Western Himalaya. A tree ring chronology of this site for the last 371 years extending from 1625 AD to 1995 AD has been established. Analysis of tree growth trend during this period indicates that the trees of this region experienced several periods of reduced growth that might have coincided with positive mass balance and glacial advance.

Key-words—*Abies pindrow*, Glacial fluctuations, Tree-rings.

पश्चिमी हिमालय के डोकरियानी बामक (हिमनद) के आस-पास की जलवायु एवं हिमनदीय प्रकृति विवेचना हेतु *एबीज़ पिण्ड्रो* का वृक्ष वलय विश्लेषण

अमलव भट्टाचार्य, वन्दना चौधरी एवं जे.टी. गरगन

सारांश

डोकरियानी बामक हिमनद (30°50' से 30°52' उत्तरी अक्षांश पर तथा 78°47' से 7८°50' पूर्वी रेखांश) के समीपस्थ सात संस्थितियों (दिन गाद घाटी) से *एबीज़ पिण्ड्रो* के वृक्ष वलय आंकडों का विश्लेषण किया गया। पश्चिमी हिमालय में जलवायुविक परिवर्तनों तथा हिमनदी उच्चावचनों के सन्दर्भ में वृक्षों की वृद्धि के रूझानों के अध्ययन हेतु भिन्न-भिन्न हिमनदीय रूप वाले भूआकृतिक स्थलों को निरूपित करने वाली सात संस्थितियों तथा ग्यारह मण्डलों से कुल 157 वृक्षों से 299 क्रोड एकत्र किए गए। विगत 1625 ई. से 1995 ई. के मध्य के 371 वर्षों का इस वृक्ष का कालानुक्रम निर्धारित किया गया। इस काल का वृक्ष वृद्धि रूझान विश्लेषण इंगित करता है कि इस क्षेत्र के वृक्षों में अल्प वृद्धि के अनेक चरण इस दौरान आए होंगे, जो सकारात्मक सन्तुलित पुंज तथा हिमनदीय अग्रता के साथ सम्पाति होंगे।

संकेत शब्द—*एबीज़ पिण्ड्रो,* हिमनदीय उच्चावचन, वृक्ष वलय.

INTRODUCTION

EVIDENCE of advancement and retreat of glaciers are significant indicators of past climatic changes. A good amount of work (Jangpangi & Vohra, 1962; Kurien & Munshi, 1972; Vohra, 1981; Chaujar, 1991; Kumar & Dobhal, 1994; and others) has been done on Himalayan glaciers, which document geomorphic evidences of glacial fluctuations. However, constrain in these studies is lack of absolute dates of these features to provide temporal records of glacial fluctuations. Mass balance data selected from a glacier for a long period of time provides sufficient information to make a climatic classification for this region. This type of information is not available for Himalayan glaciers since most of the work on mass balance in the country has been aimed to calculate the net balance of glacier. Even, the mass balance data covering more than 10 years are not available.

In this paper, attempt has been made to discuss dendrochronological potentiality of *Abies pindrow*, a conifer growing in sub-alpine forests of which upper limit is located 800 m downstream from the snout of Dokriani Bamak Glacier. Tree-ring data of this species has been analysed to study relationship of tree growth with climatic changes of this region and glacial fluctuations. This data has also been used to give an approximate date of geomorphic features, which are indicative of glacial fluctuations during the recent past.

LOCATION OF SITE AND MATERIALS

Dokriani Bamak Glacier is a valley type of glacier situated between Lat. 30°50'-35°52' N and Long. 78°47'-78°50' E. It has a glacier area of 7·0 sq km and lies in Uttarkashi District, Uttaranchal State. It is 25 km east of Bhukki Village and nearly 60 km south of Gangotri (Fig.1). Most of the glaciated area in Din Gad Valley is now covered largely by silver fir (*A. pindrow*) intermixed with *Betula utilis* and *Rhododendron* near the timberline broad leaved mixed conifer forest in lower levels.

Tree-ring samples were collected during 1995 field trip mainly from silver fir growing on several glaciated features hundred to several hundred meters below the present position of the snout. A small number of samples of *Pinus wallichiana*, *Taxus baccata* and *Cedrus deodara* growing at lower elevation close to Tela have been collected to understand their suitability for tree ring analysis. Details of sampling sites are:

1. 800 m downstream from the present position of the glacier snout.

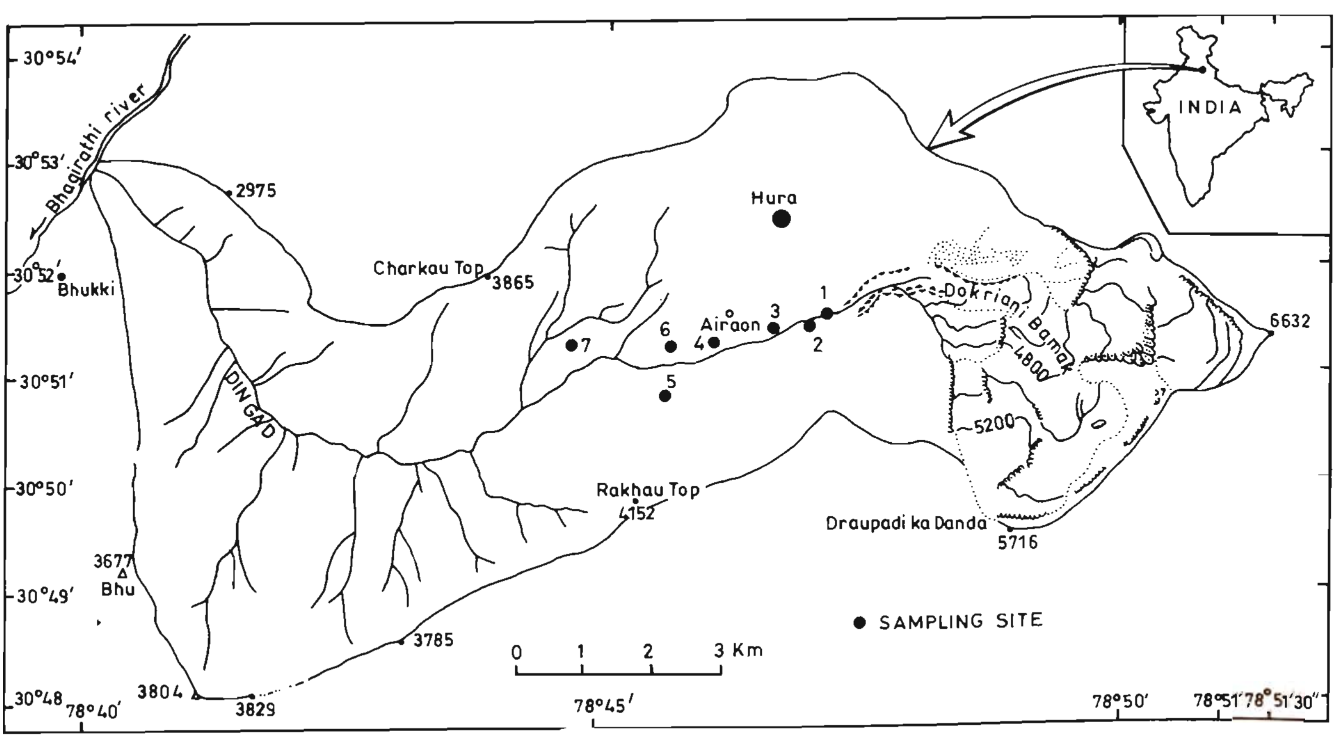

Fig. 1—Location of tree ring sampling sites around Dokriani Bamak Glacier.

2. Island in Din Gad 1600 m downstream from the glacier snout.

3. Palaeo medial moraine of Dokriani Bamak and Hura Glaciers.

4. Trees growing along the margins of marshy meadows of Khera Tappar.

5. Trees growing on northern rocky slope of Rakhau close to the Gujarhut Karauli.

6. Trees growing on margins of meadows on the way to Khera Tal.

7. Trees growing along a lateral moraine close to Khera Tal.

Generally, two cores per tree, one each from opposite direction were collected with the increment borer. Human disturbance is evident throughout the valley region but it is more conspicuous especially around Gujarhut at 3,000 m. Several left-over stumps and the presence of a few hollow trees of huge girth, which have escaped logging, indicate tree felling was common in the recent past.

TREE-RING DATING AND CHRONOLOGY PREPARATION

Samples were mounted and processed using standard procedure of tree ring analysis. Details of the methods of tree ring analysis is published in Stokes and Smiley, 1968; Fritts, 1976; Schweingruber, 1988; Cook & Kairiukstis, 1990; Hughes *et al.*, 1982 and others. Boundaries of rings in these trees are very sharp and neither false rings nor missing rings were recorded. All the samples except from trees growing at lower elevation of 2,500 m asl (Tela) have been dated by 'cross-dating' technique of tree-ring analysis. Oldest dates for these seven sampling sites in descending order are 1858 AD, 1828 AD, 1727 AD, 1704 AD, 1626 AD, 1781 AD and 1593 AD respectively. It has been observed that trees growing over thick soil cover around Khera Tal and Gujarhut are much older. In higher elevation closer to the glacier snout, trees are younger in age. For further analysis, ring widths of each dated core were measured using increment-measuring stage coupled with a microcomputer with 0·01 mm accuracy. These data have been analysed using COFECHA Program (Holmes, 1996). This program performs data quality control by thoroughly checking the tree ring measurements and locating all the portions within a tree ring series showing weak or erroneous cross-dating or measurement errors. Ring width data were standardised to form tree ring indices using program ARSTAN Program (Holmes, 1996). It removes growth trends related to age and stand dynamics while retaining the maximum common signal. Finally, tree ring chronology of this species from seven sites in Din Gad Valley has been established which extends from 1625 AD-1995 AD (Fig. 2).

CLIMATE AND GLACIAL DATA

Long climatic records around Dokriani Bamak Glacier are not available. Regular meteorological monitoring was started only few years back, which is not enough for the detailed analysis of the climate glacier relationship of the region. Even in the Himalayan region in general, the meteorological stations are very few and are situated mostly at lower elevations. This makes it difficult to use the meteorological data for the study of glacial fluctuations. However, a broad idea of the climatic trend (especially for temperature and precipitation) can be visualised at higher elevations during years of positive glacial mass balance reported earlier (Puri *et al.*, 1995) form the climatic records of several stations located at mid-elevations in the Himalaya. Analyses of data from published records (Pant *et al.*, 1999) from these stations indicate that at the beginning of the 20th century, i.e. during 1900 to 1930, summers were much cooler and winters were moist with a peak during 1905-1910. Low winter temperature and higher precipitation has been recorded during 1974-75, 1975-76. Regarding earlier positions of the snout of Dokriani Bamak Glacier relevant information only is available from the Survey of India topographical sheet

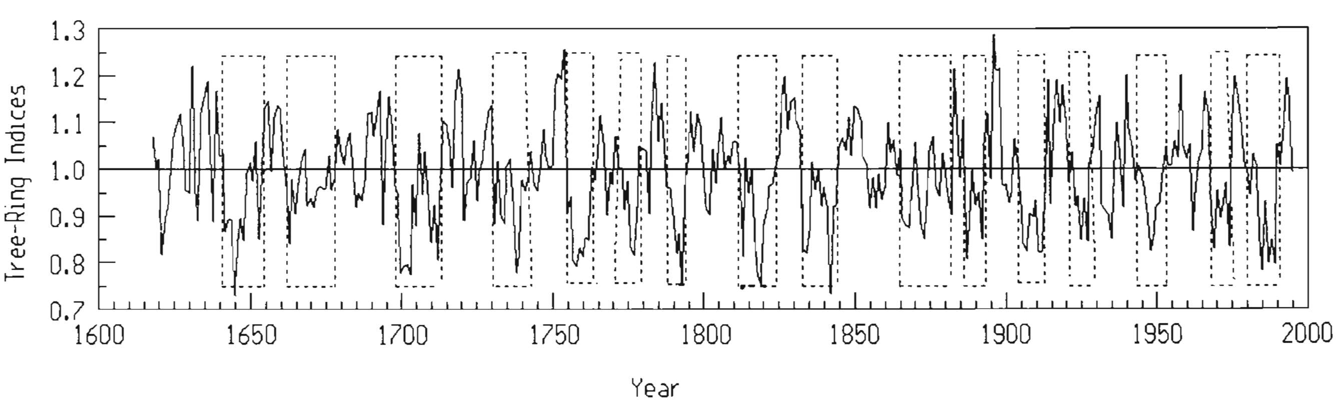

Fig. 2—Tree-Ring Chronology of *Abies pindrow* extending from 1625 to 1995 A.D. (Dotted area shows years of low growth).

(1962-63 edition) on a scale of 1:50,000. In the recent study by Gergan and Dobhal (1996), the total retreat of this glacier between 1962 and 1991 was calculated to 480·1 m (16·5 m/yr average) while during 1991 to 1995, it retreated by 69·9 m (17·5 m/yr average). This glacier like other Himalayan glaciers is in the state of recession during the recent past. There is little information regarding temporal aspects of the history of Himalayan glaciers. Mayeswki and Jeschke (1979) documented year-wise fluctuations of glaciers since 1812 AD, which is based on the percentage of advancement, retreat and stationary positions of several glaciers in the Himalayas and Trans Himalayan region. Until now this is the only report, on glacial fluctuations in terms of absolute dates, from this region.

TREE GROWTH/CLIMATE/GLACIAL FLUCTUATION

Most of these trees have been dated in between 1700 AD and 1995 AD, with the exception of some older trees growing around Khera Tal and Gujarhut at lower elevations are dated before 1700 AD. Absence of older trees might be due to unsuitable climatic conditions prior to eighteenth century for settlement of fir trees at these sites. Oxygen isotopic analysis from ice core of this glacier and surface snow samples suggest that climatic conditions three centuries ago, during the Little Ice-Age period, were much cooler than at present (Nijampurkar *et al.*, 1996).

Year-wise variations of tree growth and their relationship to corresponding year's glacial fluctuation or to the glacial mass balance budget and climate are very complicated. Several non-climatic variables play a significant role in both tree growth and budget of glacial mass balance. However, it is obvious that major climatic conditions required for tree growth and glacial advancement in the mountainous region are inversely related. High winter snowfall and short, cool, cloudy summers generally favour positive mass balance, which on the other hand retard tree growth by inhibiting photosynthetic activity during the growing period of a tree.

The growth behaviour of *A. pindrow* has been compared with the available data on glacial fluctuations, mass balance, precipitation and temperature data of the western Himalaya. Due to non-availability of modern climate data close to the glacier, it has not been possible to analyse tree growth trend in relation to the history of the present glacier. According to available data on glacial fluctuations (Mayewski *et al.*, 1980) and mass balance data of the western Himalayan region (Puri *et al.*, 1995), it has been observed that low tree growth occurs during advancement of glacier and positive glacial mass balance. The years of positive glacial mass balance reported by Puri *et al.* (1995) has been found within the bracket years of low tree growth recorded during 1968-76 and 1981-89.

Tree ring samples from trees growing about 1 km downstream to the glacier snout at 3,600 m. asl. have been dated to 1858 AD, which indicates that at least since that period the snout was higher than the position of trees dated and had not descended lower than the present position of this tree. It is a general observation that cold winds blowing from the glacier play a significant role in reducing the growth of trees in the vicinity. This impact would be more in case of an advancing glacier and could be seen in the growth pattern in trees growing several hundred meters below. These fluctuations might have caused lower tree growth for a considerable period by reducing the growing period. Several periods of suppressed growth lasting for five or more years recorded in the present *Abies* chronology might be linked with glacial advancement or years of positive glacial mass balance. Periods of suppressed growth are noticed during 1640-55, 1662-78, 1698-1713, 1731-42, 1755-64, 1771-80, 1786-94, 1811-24, 1832-44, 1865-82, 1885-94, 1904-13, 1921-29, 1943-53, 1968-76 and 1981-89 in the 371-years tree-ring chronology (Fig. 2). It is significant to note that the lower tree growth during the decade of 1810's might also be associated with the cooling of the Northern Hemisphere temperature resulted due to the eruption of Tambora in April 1815.

CONCLUSION

A. pindrow growing adjacent to snout of Dokriani Bamak Glacier has been found promising for tree ring studies to understand past glacial behaviour. Several periods of suppressed growth in the tree ring chronology covering 371 years seem to correspond to years of positive glacial mass balance of the near-by glacier during this period. Comparative analysis of tree growth with the available fragmentary data on glacial history and mass balance of Himalayan glaciers gives evidence on the interrelationship between mass balance budget and vis-à-vis climatic changes of the Himalayan region. Earlier, another sub-alpine conifer, *Pinus wallichiana* growing in Kinnaur, Western Himalaya, has also been found to have potential for this kind of study (Bhattacharyya & Yadav, 1996). The present study is not substantial; a detailed study is being taken up in the second phase of this work and by using multiple tree-ring chronologies of several conifer taxa of the sub-alpine region and using climatic data from a large number of meteorological stations which would provide a better data base to quantify tree growth/climate/glacial relationship in a longer time scale.

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Dendrochronological analysis of growth decline of Korean conifers in Urban and Rural areas

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ABSTRACT

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This study was conducted to examine the growth trends of the pines growing in three regions of Korea. Two regions, Seoul and Ulsan were selected as polluted areas, and one region, Pyungchang as unpolluted area. From each region, five sampling sites were selected. From each site, two major pine species were chosen and ten dominant or co-dominant trees of each species were sampled. Visual comparison using the pointer-year method was used to quantify abrupt growth changes. Some species indicated short-term decline but we could not find persistent growth declines in all regions. Most of short-term declines appeared to be related to either climate variation or non-anthropogenic factors such as insects. At present, it is uncertain that air pollution reduced the growths of trees.

Key-words—Forest decline, Dendroecology, Growth trend, *Pinus densiflora, Pinus thunbergii, Pinus rigida, Pinus koraiensis.*

कोरिया के शहरी एवं ग्रामीण क्षेत्रों के कोरियाई शंकुवृक्षों के वृद्धि ह्रास का वृक्षकालानुक्रमिकीय विश्लेषण

वोन-क्यू पार्क, सांग-हो चोंग, युंग-ग्यू पार्क एवं रामरतन यादव

सारांश

प्रस्तुत अध्ययन कोरिया के तीन क्षेत्रों में पाए जाने वाले चीड़ वृक्षों के वृद्धि रुझानों के प्रेक्षण हेतु किया गया है। इनमें से दो मण्डल सिओल एवं अल्सान प्रदूषित मण्डलों के रूप में चयनित किये गये तथा एक मण्डल, प्युंगचांग को प्रदूषणरहित मण्डल के रूप में चयनित किया गया। प्रत्येक मण्डल से पाँच नमूने के स्थल चयनित किए गए। प्रत्येक स्थल से दो बड़ी चीड़ प्रजातियों को चुना गया तथा प्रत्येक प्रजाति के दस प्रमुख अथवा सहप्रमुख वृक्षों के नमूने लिए गए। सूचक वर्ष प्रविधि की सहायता से चाक्षुष तुलना द्वारा खण्डित वृद्धि परिवर्तनों की मात्रा की गणना की गई। कुछ प्रजातियाँ संक्षिप्त अवधि के ह्रास संकेतित करती हैं, किन्तु सभी मण्डलों में सतत् वृद्धि ह्रास नहीं प्राप्त किए जा सके। अधिकांश संक्षिप्त अवधि के ह्रास या तो जलवायुविक परिवर्तनों से सम्बन्धित हैं अथवा अमानवोद्भवी कारकों, जैसे-कीटों से सम्बन्धित हैं। वर्तमान में यह अनिश्चित है कि वायु प्रदूषण से वृक्षों की वृद्धि में ह्रास हुआ था।

संकेत शब्द—वन ह्रास, वृक्षकालानुक्रमिकीविज्ञान, वृद्धि रुझान, *पाइनस डेन्सीफ़्लोरा, पाइनस थनबर्गाई, पाइनस रिजिडा, पाइनस कोराइएन्सिस.*

INTRODUCTION

SOME signs of forest damage caused by air pollutants have been detected in industrial regions of Korea since late 1970s. The damages observed were mainly on crown damage, while some studies detected the reduction of radial growths (Kim *et al.*, 1987; Korea FRI, 1988; Lee & Yoo, 1991; Kim, 1991; Kim *et al.*, 1991). Some studies indicated severe growth reduction of pines, just after establishing industrial complexes in Ulsan and Yeocheon (Anonymous, 1988; Kim, 1991). In Seoul, Lee and Yoo (1991) reported growth decline of *Pinus densiflora* and *Quercus* spp. growing at Namsan Mt. and attributed this decline to air-pollution damage. However, a recent study claimed that most of growth reductions of *Pinus densiflora* at Namsan resulted from insect outbreaks and droughts rather than air pollution (Kim, 1994).

Most of the trees in municipal and industrial regions in Korea are young, usually, less than 50 years old. It is difficult to determine the growth decline in the short tree-ring series of such young trees. We can hardly apply appropriate detrending procedures which can remove age-related growth trend in short series. In the present study, we applied the 'point-year' method, proposed by Schweingruber (1986), which can quantify abrupt growth changes persisting for a number of years.

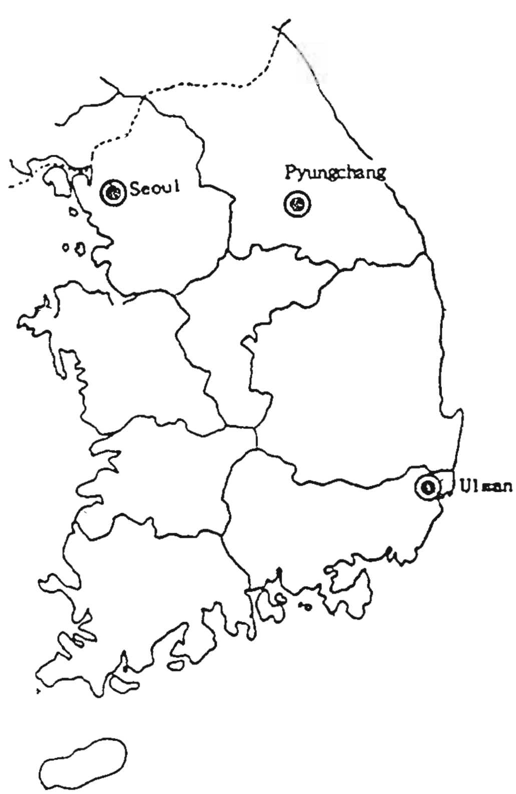

Fig. 1—Study Sites.

STUDY AREAS

Two regions, Seoul and Ulsan were selected as polluted areas, and one region, Pyungchang as un-polluted area (Fig. 1). First region, Seoul is a metropolitan region where more than 10 millions reside and hundreds of industrial factories operate. Smog is frequently observed in the city of Seoul and most concerns are given to increases of emissions from automobiles. The second region, Ulsan is a seaside city, of industrial region where heavy-chemical engineering factories have been operated since the middle 1970s. Some diebacks of pines have been reported in the areas near the factories. The third region, Pyungchang is in a mountainous area. This region is considered to be free from air pollution.

From each region, four sampling sites were selected. From each site, two major conifer species were chosen and ten dominant or co-dominant trees of each species were sampled.

The sites in Seoul located in the Bukhansan National Park, just on the northern boundary of the city of Seoul. The sites are on the exposed slope to the city. The soils of these sites are generally shallow and coarse-sandy. The species chosen in Seoul region were *Pinus densiflora* (Japanese red pine, sonamu) and *P. rigida* (pitch pine). Red pine samples were obtained from natural stands and pitch pines from planted stands. The ages of red pines (50 to 60 years) were little older than pitch pines.

The sites in Ulsan are within 2 km radius from the industrial complex. The sites are rather flat and are exposed to the emissions from the factories when the wind blows from the seaside. The soils are generally deep and fine-sandy. The species chosen in Ulsan region were *Pinus densiflora* and *Pinus thunbergii* (black pine). Both species were obtained from natural stands. The ages of both species ranged from 40 to 60. An additional site (Dudong), which located at 20 km northwest to other sites in Ulsan. This site was considered free of air pollutants from Ulsan.

The sites in Pyungchang located in the rural areas within 10 km radius. The elevations of these sites (about 300 m) are higher than in Seoul and Ulsan. Pyungchang is cold and heavy-snow area. The soils of these sites are generally deep and fine-sandy. The species sampled from Pyungchang were *Pinus*

Region	Species	Names of Site (Site identification)
Seoul	*Pinus densiflora*	Dobong, Jungneung, Sailgu, Bukak
	Pinus rigida	(DB) (JN) (SI) (BA)
Ulsan	*Pinus densiflora*	Hongyung, Dalmat, Sukyu, Yongam, Dudong
	Pinus thunbergii	(HM) (DM) (SY) (YA) (DD)
Pyung-chang	*Pinus densiflora*	Nonggong, Hangdong, Bangrim, Gupo
	Pinus koraiensis	(NG) (HD) (BR) (GP)

Fig. 2—Name of Sites and Species.

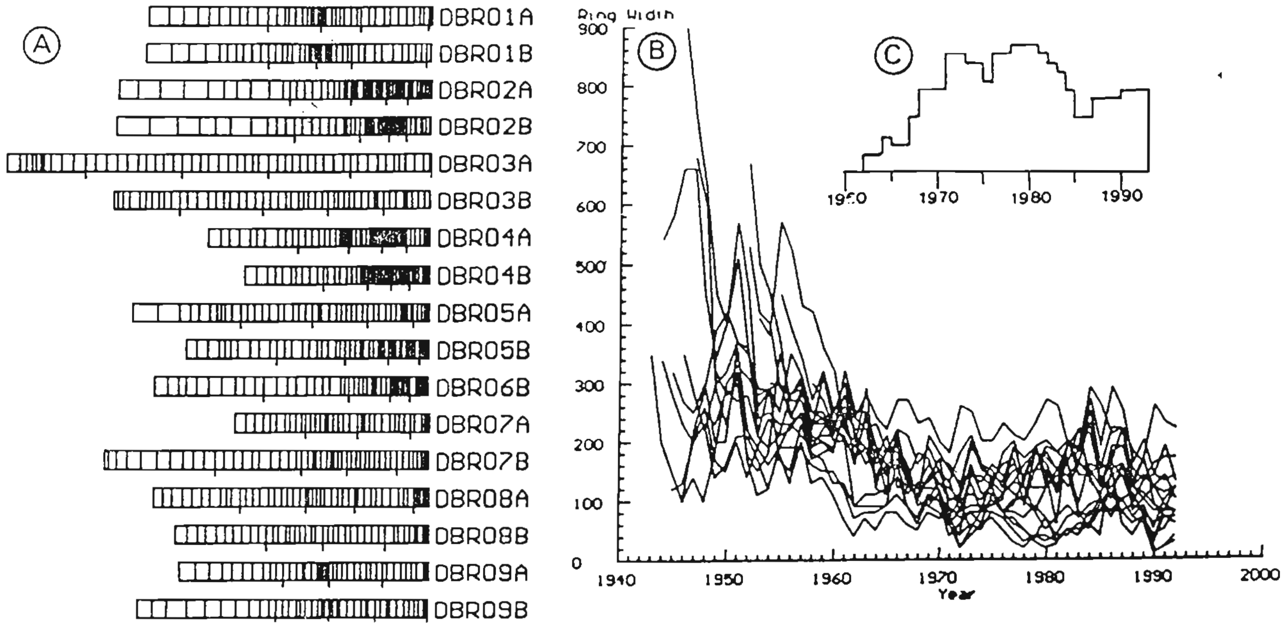

Fig. 3—Ring-width patterns of Dobong pitch pines. **A.** core-beam patterns. **B.** raw series and **C.** phase diagram (pointer-year).

densiflora and *Pinus koraiensis* (Korean pine). Red pines were obtained from natural stands but Korean pines from plantation. The ages of both species ranged from 40 to 55. Fig. 2 summarized the names of the site and species sampled.

METHODS

Two cores from each tree were collected using increment borers at 50 cm above the ground. They were crossdated using the skeleton plot method (Stokes & Smiley 1968).

To evaluate abrupt growth change, we adopt the 'pointer year' method of Schweingruber (1986). Pointer years are the years of annual rings that differ visibly and markedly from the preceding and subsequent rings. There are various kind of pointer years but we count only ones which abrupt growth reduction continues in three consequent years. Duration and intensity of growth reduction were indicated by making a bar graph. For the years when the growth reduced about 50% compared to the previous years, one bar was given, and two bars for about 70% reduction and three bars for more than 90% reduction. The final bar graph ('phase diagram') of each species was made from each site by summing all bars.

Fig. 3 demonstrates how ring-width patterns can be illustrated in different ways. Fig. 3A ('core-beam pattern') illustrates the ring-width pattern of each core. Fig. 3B is an overlaid plot of raw ring-width series. The final phase diagram obtained is given in Fig. 3C. The point-year method was originally developed to examine the growth pattern quickly without measuring ring widths. However, if we want to apply the point-year method for the ring-width data which have already been made, we can easily obtain core-beam patterns from ring-width data using computer graphics such as TSAP (Rinn, 1994). It is much easier to produce phase diagram from core-beam pattern than to re-examine the increment cores.

RESULTS AND DISCUSSION

The phase diagrams for three regions are shown in Figs. 4-6. Each diagram represents the cumulated growth reduction change of each species at one site. In Ulsan, red pines and black pines show different growth patterns (Fig. 4). The most severe reductions of red pines in Ulsan were found during 1965-1980. In most sites, the growths of red pines were recovered after 1980. The growths of black pines did not indicate any prolonged reductions during 1965-1980. Instead, ones from some sites (DMT, YAT and SYT) showed more growth reductions after 1985. It is interesting that the red pines of Dudong site, which is far from the city of Ulsan, also possessed the phase diagram similar to others for the other sites in Ulsan. We could not find any anomalies in monthly temperature and precipitation in Ulsan area during 1965-1980. Growth reductions of the red pines are unlikely attributed to air pollution damages. More likely the causes of growth reduction appear to be related with insect damages. Red pines have been periodically infected by the insects, pine-needle gall midge (*Thecodiplosis pinicola*). Nationwide survey

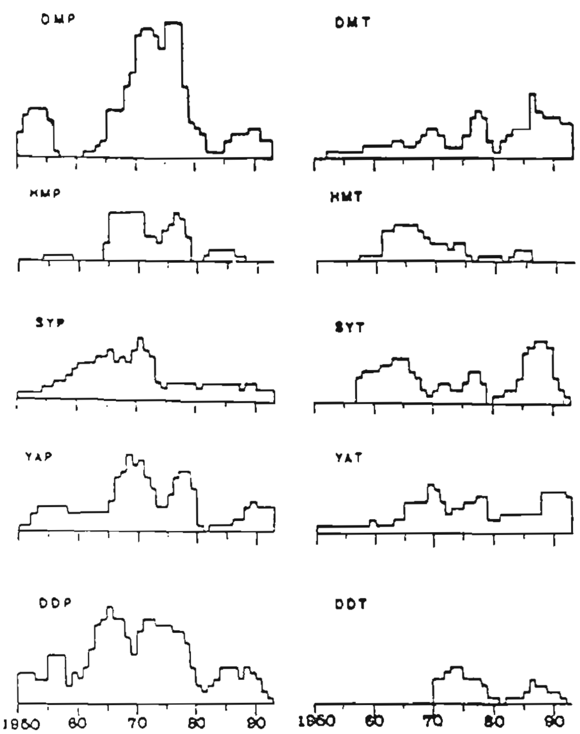

Fig. 4—Phase diagrams for Ulsan (left: red pine, right: black pine). *See Fig. 2 for site abbreviation.

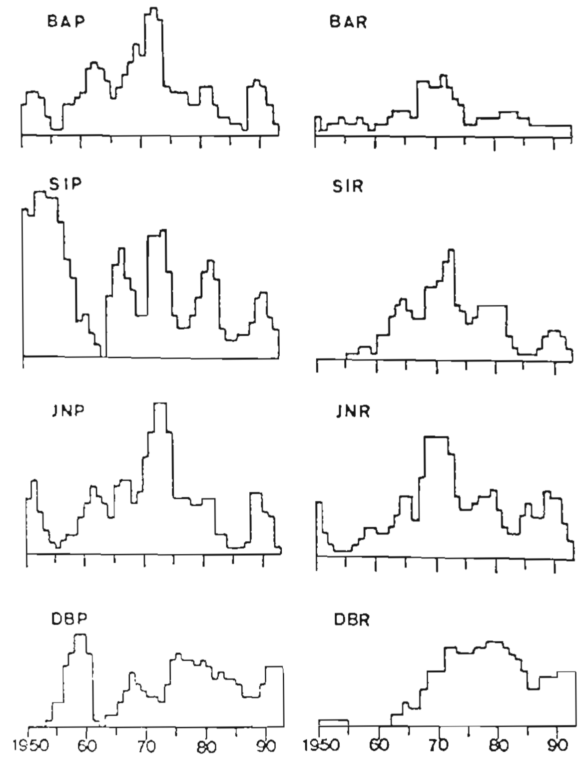

Fig. 5—Phase diagrams for Seoul (left: red pine, right: pitch pine).

indicates that the highest outbreaks of this insect occurred in 1975 and 1976 (Kim, 1994).

Growth declines of black pines in the Ulsan area have been reported in several studies (Korea FRI, 1988; Kim, 1991). They observed abrupt growth reductions around 1975, at the onset of the industrial complex. In the present study, we could not find this abrupt growth changes.

There are three plausible explanations for this discrepancy. First, the sites for the present study is little far from the factories than those for the other studies. Secondly, we might collect only living trees which had survived from the heavy dosages of pollutants and had grown under less competition. Thirdly, the analytical method was different. The previous studies did not use the dendrochronological procedures such as crossdating and detrending method.

In Seoul, the phase diagram patterns of red pines are similar to those for Ulsan's (Fig. 5). Among them, one site (SIP) indicated periodic reductions. This seems to be related with the outbreaks of the pine-needle gall midge. Highest growth reduction occurred in the early 1970s. The strong relationship between soil moisture and the growths of red pines and pitch pines growing in Seoul was found in the previous study (Vaganov & Park, 1992). The annual P-E indices of long-term effectiveness of precipitation for plant growths (Thornthwaite's) in Seoul indicates long-term moisture deficiency during 1965-1975.

Both moisture stress and insect damage seem to be responsible for the growth reductions of red pine. However, the effect of climate should be stronger because the phase diagrams for pitch pines are similar to those of red pines which are non-host trees for the gall midge insects.

The phase diagrams of Pyungchang (Fig. 6) indicate less growth reduction than the other regions but they also possess short-term variations. Both red pines and Korean pines show some growth reduction during late 1960s and late 1980s. Red pines in this regions are known to be infested by gall midge since late 1980. The causes of the reductions during late 1960 should be further studied.

CONCLUSIONS

In this study, we could not find persistent growth decline in the Ulsan, Seoul and Pyungchang regions. Most of short-term declines appears to be related to either climate variation or disturbances such as insects. At present, it is uncertain that air pollution reduced the growths of trees. In future, it is

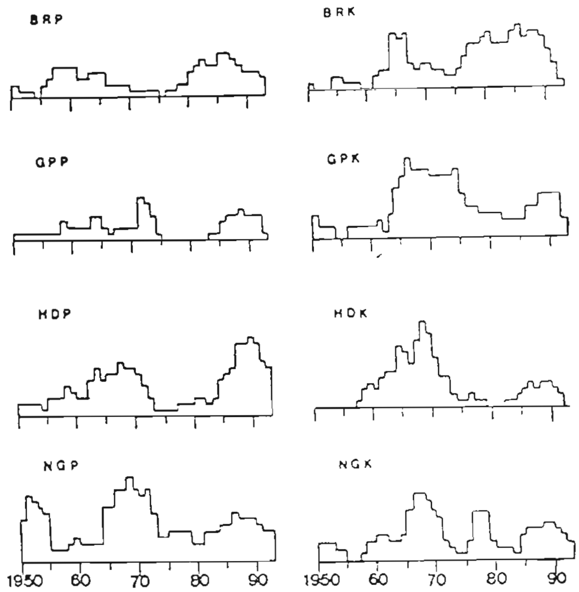

Fig. 6—Phase diagram for Pyungchang Left . red pine, right . Korean pine)

necessary to monitor environmental factors as well as tree growth in these regions.

We found that the pointer-year method was more efficient than the detrending method in determining the growth decline of young stands like most forests in Korea. Based on this finding, we adopted the former method for the 5-years forest decline monitoring project of Korea Forestry Research Institute.

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A dendrometer band study of teak (*Tectona grandis* L.F.) in north Thailand

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ABSTRACT

Buckley BM, Tongjit O, Poonsri R & Pumijumnong N 2001 A dendrometer band study of teak (*Tectona grandis* L.F.) in north Thailand. Palaeobotanist 50(1) : 83-87.

We present results from a dendrometer band study of teak in north Thailand. We track daily circumferential changes for three trees over nearly sixteen months from November 3, 1998 to February 29, 2000. This period encompasses one complete cycle of dry and wet seasons, along with the very important transitions from wet to dry (November) and from dry to wet (April). Circumferential changes were observed for all three stems; decreasing in response to the onset of drought, and increasing following rain events, particularly after leafout and during the wet season. Dry-season rain events also resulted in stem swelling, when the trees were devoid of leaves and thought to be dormant. While these dormant-season fluctuations can be attributed to hydration/dessication of the stem tissue and not cambial cell division, there appears to be a net gain in circumference following a rain event in the middle of the first dry season. We therefore stress the importance of climate/physiology relationships even during periods of dormancy. We recognise the need for more detailed monitoring of environmental and growth factors, to maximise our understanding of the effects of climate on cambial activity and radial growth. This information is critical for understanding the complex relationships between climate and tree growth in these tropical forests, for which precious little data exist.

Key-words—Teak, Dendrometer, Dendroclimatology, Radial growth, Thailand.

उत्तरी थाईलैण्ड से प्राप्त टीक (*टेक्टोना ग्रैण्डिस* एल.एफ.) का डेन्ड्रोमीटर बैण्ड सम्बन्धी अध्ययन

ब्रेन्डन एम. बकले, ओ. टांग्जिट, आर. पूंसरी एवं नासुदा पूमिजुमनांग

सारांश

प्रस्तुत शोध पत्र में हमने उत्तरी थाईलैण्ड के टीक वृक्ष के डेन्ड्रोमीटर बैण्ड सम्बन्धी अध्ययन से प्राप्त परिणामों को प्रस्तुत किया है। इस हेतु हमने 3 नवम्बर, 1998 से 29 फरवरी 2000 तक की सोलह महीनों से अधिक अवधि के दौरान तीन वृक्षों के परिधीय परिवर्तनों का नित्य प्रेक्षण किया। इस कालावधि के दौरान आरम्भ में पूर्णतः शुष्क मौसम था, तत्पश्चात आर्द्र से उष्ण के मध्य का महत्त्वपूर्ण मौसम (नवम्बर माह) था तथा अन्त में शुष्क से आर्द्र (अप्रैल माह) मौसम के मध्य का काल था। हमने पाया कि जैसी सम्भावना थी, उसी के अनुरूप शुष्क मौसम के प्रारंभिक समय में अनावृष्टि के प्रारम्भ में सभी तीनों तनों की परिधि में ह्रास था तथा पतझड़ के पश्चात वर्षा के प्रारम्भ में परिधि में वृद्धि लक्षित होती है। बहरहाल, शुष्क मौसम के मध्य के दौरान, जब वृक्ष पत्तियों से रहित हो जाते हैं तथा प्रसुप्तावस्था में

होते हैं, हमने वर्षा की घटनाओं के परिणाम स्वरूप परिधि में वृद्धि पाई। शुष्क मौसम के मध्य में वर्षा के पश्चात परिधि में एक सकल वृद्धि प्रतीत होती है, जो प्रसुप्तावस्था के दौरान भी जलवायु/भूआकृतिक सम्बन्धों के महत्त्व को दर्शाती है। एधात्मक (कैम्बियमी) गतिविधियों तथा अरीय वृद्धि के प्रभावों को और अधिक समझने हेतु इस अध्ययन के अगले चरण में हमें पर्यावरण एवं वृद्धि के कारकों का और अधिक विस्तृत अनुश्रवण करना होगा। उदाहरण के लिए, सम्पूर्ण वर्ष के दौरान केम्बियमी ऊतकों के नियमित नमूने प्रेक्षित करने का कार्यक्रम एधा (कैम्बियम) के कोशिकीय अनुभागों के प्रारम्भ के काल मापन को अधिक शुद्धतापूर्वक निर्धारित कर सकेगा। हम इस दृष्टिकोण का उपयोग न सिर्फ टीक में कर रहे हैं, अपितु सम्पूर्ण उत्तरी थाईलैण्ड की अन्य अनेक अत्यधिक महत्त्वपूर्ण प्रजातियों हेतु भी कर रहे हैं। ये सूचनाएँ इन उष्णकटिबन्धीय वनों में जलवायु एवं वृक्ष वृद्धि के मध्य के जटिल सम्बन्धों को समझने हेतु अत्यन्त महत्त्वपूर्ण हैं, जिनके लिए इससे पहले बहुत कम आंकड़े ही उपलब्ध थे। इस अनुसन्धान को दीर्घावधि तक जारी रखना अत्यन्त महत्त्वपूर्ण है, क्योंकि यह अध्ययन भविष्य के अनुसन्धान कार्यों हेतु आधार तैयार करेगा।

संकेत शब्द—टीक, डेन्ड्रोमीटर, वृद्धि, उष्णकटिबन्धीय वन, थाईलैण्ड.

INTRODUCTION

THE experiment reported in this paper was implemented as part of FIELDWEEK 99, a training workshop on tropical dendrochronology held in Chiang Mai, Thailand in February, 1999. Teak (*Tectona grandis* L.F.) is one of only three tree species from Thailand (along with two species of *Pinus*) shown to have identifiable annual growth rings that are useful for dendrochronology (e.g., Buckley *et al.*, 1995; D'Arrigo *et al.*, 1997; Pumijumnong *et al.*, 1995a, b, c). Other studies on teak clearly demonstrate its usefulness as a proxy for Monsoon rainfall (e.g., De Boer, 1951; Murphy & Whetton, 1989; Pant & Borgaonkar, 1983; Jacoby & D'Arrigo, 1990; D'Arrigo *et al.*, 1994; Pumijumnong *et al.*, 1995c; Borgaonkar *et al.*, this volume) and as a proxy for the El Nino Southern Oscillation (ENSO) phenomenon (Stahle *et al.*, 1998). As such, teak is arguably the most important tropical tree species for dendroclimatic research, certainly with regards to Monsoon Asia. A more detailed understanding of the physiological response to climate for this important species, throughout its entire annual cycle, is therefore of great interest to dendroclimatologists.

Dendrometer studies have been demonstrated to provide useful information about annual radial tree growth, with particular relevance to the effects of precipitation on cambial activity (e.g., Fritts, 1962; Palmer & Ogden, 1983; Worbes, 1995). We have, accordingly, begun a programme to monitor the radial growth of teak and other proven or promising tropical species for successive seasons, as part of a broader baseline study for understanding tropical tree growth and the effects of climate.

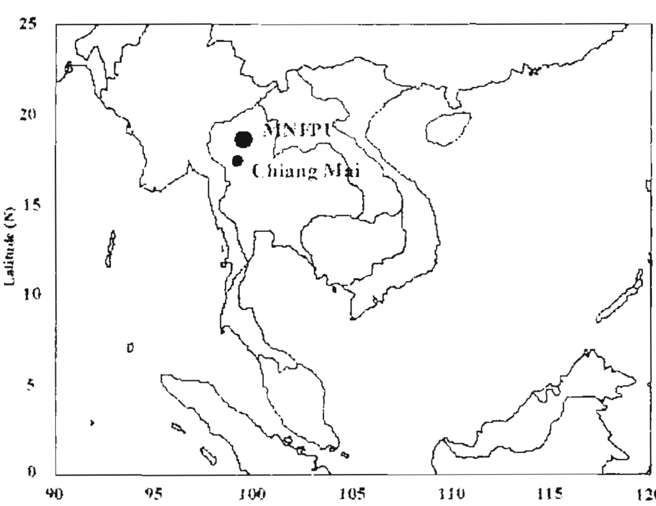

Fig. 1—Location of the Mae Na Forest Protection Unit (MNFPU) in north Thailand.

MATERIAL AND METHODS

We installed manual band dendrometers on three teak trees at the Mae Na Forest Protection Unit (MNFPU), about 80 km north of Chiang Mai, Thailand (Fig. 1). This remnant stand, consisting of approximately 100 stems, survived previous large-scale logging in the Chiang Dao area and is currently protected from further logging and other major disturbance. For purposes of this study these trees are considered to be growing in a largely natural environment, although on-site housing and groundskeeping activities certainly exert an effect on the groundcover. No artificial watering occurs at the site, however, so these trees are entirely dependent on natural rainfall.

The climate of the region can be compared to that of Chiang Mai, the general climate characteristics for which are illustrated in Fig. 2 of Borgaonkar *et al.* (this volume). The dry period north Thailand is from December to March

Fig. 2—A Gensler manual band dendrometer on a teak tree at MNFPU

with nearly 90% of the annual rain falling during the May to October Monsoon. Mean temperature remains above 20°C throughout the year, with April and May comprising the warmest months.

The manual band dendrometer used for this study (Fig. 2) was made by Agricultural Electronics Inc., USA, and are comprised of metal alloy bands that encircle the tree and are connected to a spring-loaded vernier scale. The band material is made of Hastalloy 276, with a coefficient of thermal expansion of 11·2 micrometers/meter/degree C. The vernier scale registers the daily circumferential change to 0·1 mm accuracy. Measurements must be taken manually by visually reading the vernier scale, increasing the possibility for measurement error. Therefore, measurements are checked by two recorders whenever possible. For consistency, we record band measurements at the same time each day, between 8:00 and 9:00 AM. As a further check we record stem circumference just below the band each day at the time of band reading, using a forester's tape measure. This proved to be a valuable calibration check during times when bands needed to be reset due to mechanical reasons.

Along with the dendrometer measurements, we record temperature at the time of measurement, and the occurrence or absence of rainfall during the 24 hours leading up to the time of measurement. (We recently began measuring absolute rainfall amount at the site on February 2, 2001, when we installed two manual rain gauges and a max/min thermometer). In addition to climate variables we also record phenological phenomena (e.g.; date of flowering, and "leaf out") and mechanical problems (e.g.; termite activity that results in band expansion, and stem shrinkage with drought that extends beyond the scale of the bands). In such instances corrections are made and the bands reset.

RESULTS AND DISCUSSION

The dendrometer band measurements for the period November 3, 1998 to February 29, 2000 are shown in Fig. 3. As expected, these data clearly indicate the importance of precipitation for radial growth activity in teak during the monsoon months. Following each rain event, even during the period of dormancy, we recorded circumferential increases that were followed by decreases in stem size as conditions dried out again. This demonstrates that active transport of water through the stem occurs even in the absence of photosynthetic processes, but does not imply that cambial cell division is taking place. There is a net gain in circumference following a three-days rain period from January 16-18, 1999, however, right in the middle of the dry season. After the first leaves appeared on February 27, 1999 additional rain events resulted in further increases in circumference. However, all three stems reached a 3 months low before May 5, 1999 when a heavy rain occurred and the trees swelled in size once again, attaining their largest sizes of the season.

During the 1999 wet season, all three stems swelled beyond the range of the bands on two occasions, thus the "plateau" effect as seen in Fig. 3 (corrections were made using daily tape measurements of circumference as noted earlier). In contrast, a period of reduced rainfall from late June to mid-July resulted in significant stem shrinkage in the midst of the wet season, between the two largest growth periods. By the end of the wet season all three trees decreased in circumference, until receiving rain in late February. By the end of the recorded period a net increase of approximately 10 mm can be seen from the prior year, and is consistent with tape measurements of circumference (Fig. 4) that show increases of 1·5, 1·4 and 2·2 cm for trees 36, 51 and 57,

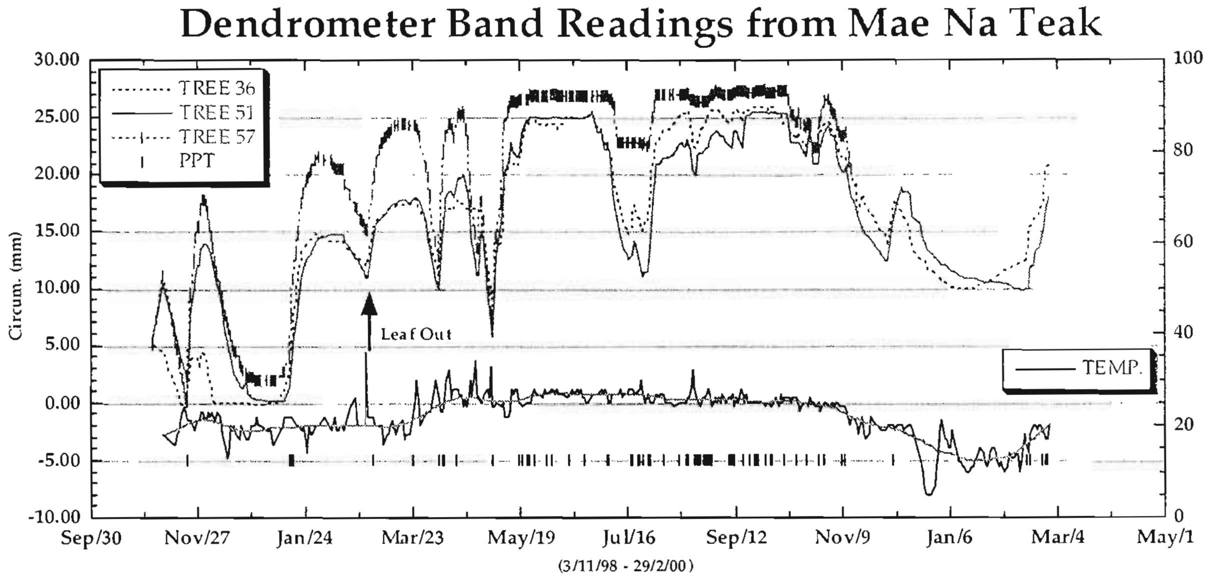

Fig. 3—Dendrometer band measurements from 3 teak trees at MNFPU from Nov. 3, 1998 to Feb. 29, 2000. The shaded area in the center of the graph denotes the "traditional" wet season period from May through October. The arrow marks the day when the first leaves appeared (Feb. 27). The line at the bottom shows daily temperature. The vertical black bars indicate the occurrence of rain events.

respectively. We also cored and measured the year 1999 growth ring for all three trees.

Borgaonkar *et al.* (this volume) demonstrate the importance of precipitation for the MNFPU teak stand through time. Their response function analyses show a significant ($p<0.05$) positive relationship with precipitation for November of the prior season (transitional season from wet to dry), and also during the wet season (May to October). Drought conditions at the stand coincide with below average radial growth, and wetter conditions coincide with increased radial growth over the past 87 years. The authors note that while there is an inverse response between ring width and temperature during the hottest month of April, this may in fact be related to the correlation between temperature and precipitation and not a direct response to temperature, *per se*. However, Pumijumnong and Park (this volume) note a relationship between temperature and earlywood vessel density that suggests that more research is required to address the possibility of temperature influencing some aspects of growth in teak. Prior research by Kaosa-Ard (1977; 1986) demonstrates that temperature does have an effect on teak seedlings. The author notes an optimum range for growth around 30°/25°C.for day/night temperature. Temperatures dipping below 18°C caused a cessation of growth in teak seedlings. It is interesting to note that in the Mae Na teak stand, the first leaves appeared on the first day following the hottest temperature recorded during the course of this study (36°C on February 26). Further exploration of the effects of temperature on teak growth therefore seems warranted.

Tree ID	CBH Jan. 4, 1999	CBH Jan. 20, 2000
Tree 36	149·5	151·0
Tree 51	134·0	135·4
Tree 57	147·8	150·0

Fig. 4—Circumference at band height, in centimeters, for the three teak trees. Measurements were taken just below the band dendrometers with a foresters tape measure, on Jan. 4, 1999 and Jan. 20, 2000, two periods of stem minima.

This preliminary study sheds some light on the annual growth cycle of teak in north Thailand. For example, the onset of shoot development and leaf out, and more importantly cambial activity, is largely considered to be sometime in April (e.g., Pumijumnong *et al.*, 1995a, b). Our results show that the first leaves can appear much earlier, in this instance late February, and that cambial activity may, under some circumstances, begin earlier than previously thought. We are now incorporating other techniques into this study, most notably cambial scarring or "pinning" methods, in order to absolutely determine the date of first cambial cell division. It is necessary to continue monitoring these factors over successive seasons and to incorporate more variables into our experimental design. We are applying this approach to several species in multiple locations in Thailand, an exercise we anticipate will be of immense value in future studies that aim to utilise tree-ring parameters for modelling past environmental changes in the tropics.

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Seasonal temperature reconstruction from central China based on tree ring data

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ABSTRACT

Liu Y, Ma L, Hughes MK, Garfin-Woll GM, Cai Q, An Z & Leavitt SW 2001. Seasonal temperature reconstruction from central China based on tree ring data. Palaeobotanist 50(1) : 89-94.

Mean temperature of March and April for the Qinling Mountains has been reconstructed based on *Abies chensiensis* tree-ring width for the last 250 years, with good chronology replication since 1828 to 1991 AD. The explained variance of the reconstruction was 50·8%. Eight relative cold and 8 warm periods for early spring have been found. Power spectrum analysis displays 24, 21·82, 20·00, 18·46, 2·76, 2·73, 2·26, 2·11 and 2·09 yrs cycles. The reconstruction was significantly negatively correlated to dryness/wetness indices, which were derived from historical documents, with $r = -0{\cdot}297$ ($N_3 = 229$, $p < 0{\cdot}0001$) after 10 years moving average. After 1900, r reached $-0{\cdot}718$ ($N_4 = 75$, $p < 0{\cdot}0001$). This suggests that lower mean temperature of March-April could be a signal of drought for the year, and *vice versa*.

Key-words—Qinling Mountains, China, Ring width, Temperature reconstruction.

मध्य चीन से प्राप्त वृक्ष-वलय मौसमी तापमान के अभिलेख

यू लिउ, लिमिन मा, मैल्कॉम के. ह्यूजेस, ग्रेग एम. गार्फ़िन-वॉल, किउफ़ांग काई, ज़ीशेंग एन. एवं स्टीवन डब्ल्यू. लीविट

सारांश

विगत सन् 1828 से 1991 ई. के दौरान उत्कृष्ट कालानुक्रम पुनरावृत्ति के साथ 250 वर्षों की *एबीज़ चेन्सिएन्सिस* वृक्ष की वलयी चौड़ाई को आधार मानकर क्विनलांग पर्वतश्रेणी के मार्च एवं अप्रैल माह के औसत तापमान का पुनर्सृजन किया गया। पुनर्सृजित तापमान का विश्लेषित औसत प्रसरण 50·8% था। प्रारंभिक बसन्त ऋतु की क्रमशः 8 शीत तथा 8 उष्ण अवधियाँ पाई गईं। ऊर्जा स्पेक्ट्रमी विश्लेषण 24, 21·82, 20·00, 18·46, 2·76, 2·73, 2·26, 2·11 एवं 2·09 वर्ष के चक्र प्रदर्शित करता है। पुनर्सृजन शुष्क/आर्द्र सूचकांकों से ऋणात्मक रूप से सहसम्बन्धित है, जिन्हें 10 वर्षीय गतिशील औसत के पश्चात आर = -0·297 (एन$_3$ = 229, पी. < 0·0001) के साथ ऐतिहासिक दस्तावेजों से निगमित किया गया था। सन् 1900 ई. के पश्चात आर मान -0·718 तक (एन$_4$ = 75, पी. < 0·0001) पहुँच गया था। इससे प्रस्तावित होता है कि मार्च से अप्रैल माह के मध्य निम्न औसत तापमान वर्ष हेतु अनावृष्टि का संकेतक हो सकता है तथा इसी अनुक्रम से आगे के अनुमान भी किए जा सकते हैं।

संकेत शब्द—क्विनलिंग पर्वतश्रेणी, चीन, वलयी चौड़ाई, तापमान, पुनर्सृजन.

INTRODUCTION

WITH their high resolution and reliability, tree rings play a very important role in global climate change study. The CLIVAR (Climate Variability and Predictability) program of the World Climate Research Program especially emphasizes the study of the variations of the Earth's climate over the last 100 to 1,000 years, which should feed directly into a better understanding of climate variability and predictability (The PAGES/CLIVAR Intersection, 1994). The PAGES (Past Global Changes) Project of the International Geosphere-Biosphere Program stresses the extraction of high resolution climatic proxies on similar time scales (PAGES, 1995). Tree-ring research has been listed as an important technique in both programs.

Tree rings are being combined with early instrumental records, historical documents, and other natural archives to build a season by season history of Earth's climate for the last millennium. Recent study reveals that the 20th century is a warm period compared to the last several centuries (Jacoby *et al.*, 1996; Mann *et al.*, 1998). During the steep rise of global warming in the past 20 years, annual spring mean temperature has increased significantly more rapidly than any other season in Northern Hemisphere (Groisman *et al.*, 1994). How about it in China?

The Qinling Mountains stretch more than 1500 km from the east to the west in central China. They form an important climatic demarcation line between north and south. Several dendrochronological contributions have been made for this region (Liu *et al.*, 1990; Wu & Shao, 1994; Shao & Wu, 1994; Yin & Wu, 1995). Hughes *et al.* (1994) reconstructed precipitation variation for April- June and May-July by using *Pinus armandii* in the eastern part of the mountains. It has been demonstrated that the 1920's and 1930's are the distinct dry periods in the past 400 years. By combining tree-ring and documentary data quantitatively, Wu *et al.* (1995) reconstructed total precipitation of April-July more precisely for Mt. Huashan in the east of the Qinling Mountains.

In this paper, we report a reconstruction of early spring (March to April) mean temperature using tree-ring data of *Abies chensiensis* from the central Qinling Mountains. The validation tests, statistical methods and historical documents were employed to verify the reconstruction, and provide objective methods for specifying the degree to which the tree-ring reconstruction replicated the actual instrumental record of climate.

TREE RING MATERIAL

The samples were collected from Eagle Peak (33°5'N, 108°5' E, elevation 2200-2500 m) in Zhen'an county (Fig. 1), Shaanxi Province, central Qinling Mountains, in the summer of 1993, during Chinese-United States joint cooperation.

The trees sampled were growing on north-facing aspects with slopes from 30° to 60°. The soil thickness are of about 10-30 cm with greatest depth at the moistest sites. There are a mixture of mountain-brown-earth and yellow-brown-forest soil. The dominant tree species at the site is *Abies chensiensis* and other trees are *Tsuga chinensis*, *Pinus armandii*, *Betula platyphylla* and *Cupressus funebris*. The stand is fairly open, with 5-10 m between trees and a discontinuous canopy. Three cores were taken from each of 25 trees. Two cores from every individual were used to develop tree-ring chronologies, and the third one was used to do X-ray density analysis, which will be reported elsewhere.

The samples were dried, glued and mounted. The cores were sanded to a smooth surface using sandpaper to 500 mesh (Phipps, 1985; Swetnam, 1985). Then, each growth ring for each core was assigned to the correct calendar year through cross-dating method (Stokes & Smiley, 1968). All samples were measured to within 0·01 mm using a Velmex-1 measuring system. Quality control of cross-dating was performed by a cross-correlation procedure COFECHA (Holmes, 1983), and the cores which did not match the master series well were removed. The program ARSTAN (Cook, 1985) was employed to produce tree-ring chronologies from the cross-dated series. In this paper the raw ring-width series were detrended by fitting cubic spline with a 50% variance reduction function (VRF) at 85 years wavelength (Cook & Kairiukstis, 1990). In the processing, the effects of non-synchronous disturbance events and age-related trend were reduced. Three versions of the chronologies, therefore, were obtained: standard (STD), residual (RES) and 'ARSTAN'(ARS). Fig. 2 shows the statistical characteristics of three kinds of chronologies for the Eagle Peak site. The statistical features of the detrended and residual series are listed in Fig. 3.

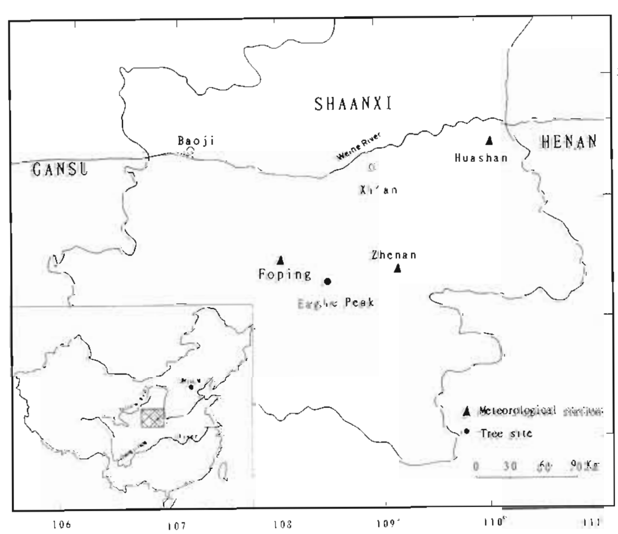

Fig. 1—The location of sampling site and nearby observation stations

	STD[1]	RES[2]	ARS[3]
Mean sensitivity	0·156	0·158	0·150
Standard deviation	0·201	0·147	0·204
First order autocorrelation	0·509	0·052	0·552
Skewness	0·056	0·214	0·208
Kurtosis	1·363	1·212	3·205

[1] Standard chronology
[2] Residual chronology
[3] Arstan chronology

Fig. 2—The statistical characteristics of STD, RES and ARS chronologies.

TRANSFER FUNCTION

Meteorological data were taken from Zhen'an, the nearest observation station (1958-1992, 35°26'N, 109°56'E, elevation 625 m). There were no missing data. These data were used to analyze the relationship between ring-width indices and climate. Homogeneity was tested by both double-mass analysis (Kohler, 1949) and the Mann-Kendall (Mann, 1945) statistical method. Foping (33°32'N, 107°59'E, elevation 1191·8 m), Xian (34°18'N, 108°56'E, elevation 397 m) and Huashan (34°29'N, 110°05'E, elevation 2064 m) stations were used as references. The results show that the Zhen'an data have no inhomogeneity.

Both correlation analysis and response function (Fritts & Wu, 1986) indicated that tree growth is positively influenced by mean temperature of March and April, with r=0·697 (p<0·0001) (Fig. 4). Ring-width at this site had a weak response to precipitation.

Previous work based on various tree-ring variables of *Pinus armandi*, such as ring width (Wu & Shao, 1994), ring width and density variables (Hughes *et al.*, 1994) and tree-ring climate modelling (Yin & Wu, 1995) in the eastern Qinling Mountains revealed that April temperature is a significant factor in limiting tree growth of this region. Our results are quite similar to those studies.

Generally speaking, early spring temperature is a crucial factor for the commencement of tree growth, formation of new needles, and the effective length of the growing season.

Since the STD chronology has the highest correlation with the climatic data, it has been used to do further analysis. Considering that auto-correlation in the STD chronology was more than 0·5, a transfer function between tree-ring-width (predictors) and mean temperature of March to April (predictand) is designed as follows:

	Detrended	Residual
Mean correlation between all series	0·238	0·296
Mean correlation between trees	0·230	0·289
Mean correlation within a tree	0·302	0·355
Signal/noise ratio	3·280	4·470
Expressed population signal (EPS)	0·766	0·817
% Variance in 1st PC	28·1%	32·9%

Fig. 3—The statistical features of detrended and residual series.

$$\hat{T}_{34} = 4{\cdot}919 W_{(t)} - 0{\cdot}962\, W_{(t+1)} + 6{\cdot}655 \qquad (1)$$
(r=0·713, F=16·018, P<0·0001)

Where $\hat{T}_{34}$ is mean temperature of March to April, $W_{(t)}$ and $W_{(t+1)}$ are the indices of the $STD_{(t)}$ and $STD_{(t+1)}$ chronologies, separately. For the calibration period of 1958-1991 (N_1=34), the equation is highly significant. The predictor variables account for 50.8% (and 47.6% when adjusted for loss of degrees of freedom) of the variance in the temperature. Fig. 5 shows the comparison of actual and estimated March to April mean temperature for the interval of 1958-1991.

CLIMATIC RECONSTRUCTION

In terms of the transfer function, we reconstructed the March-April mean temperature for 1741-1991 AD (Fig. 6). However, the chronology is not strongly replicated until 1828 AD, the first year in which the Subsample Signal Strength (SSS) reaches 0·85 (Wigley *et al.*, 1984). The curve displays obvious cold and warm spring variation alternately.

The correlation (r), sign test (S_1, S_2), F value, reduction of error (RE) and product mean (t) (Fritts, 1991) are all significant (Fig. 7), and indicate that the reconstructed data track the independent early spring mean temperature data quite well from 1958 to 1991. S_1 is the general sign test between observation and reconstruction (N_1=34) that measures the associations at all frequencies. S_2, which reflects the high-frequency climatic variations, is a similar test to above (n=33), and it is made for the first differences (Fritts, 1991).

As the possibilities for independent verification are severely limited by the shortness of the instrumental record,

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Mar.-Apr.
STD	0·173	0·166	0·325*	0·687*	0·117	0·123	0·217	0·236	0·264	-0·135	0·697*
RES	0·1	0·062	0·263	0·497*	0·096	0·01	0·186	0·19	0·108	-0·203	0·528*
ARS	0·188	0·139	0·319*	0·648*	0·033	0·096	0·172	0·26	0·21	-0·149	0·668*

Fig. 4—The correlation between observed temperature and ring width.

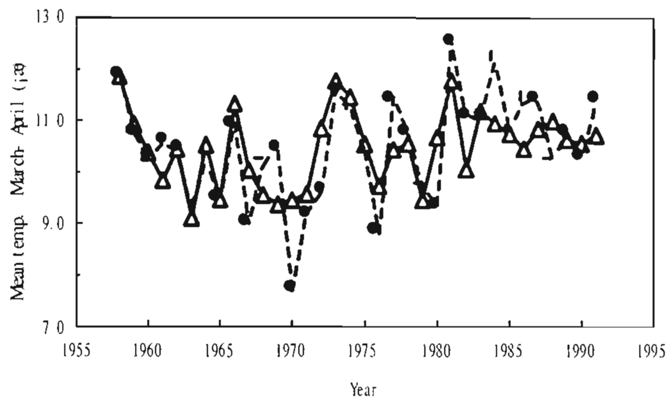

Fig. 5—Comparison of observed (dashed line) and estimated (solid line) March-April mean temperature for the interval 1958-1991.

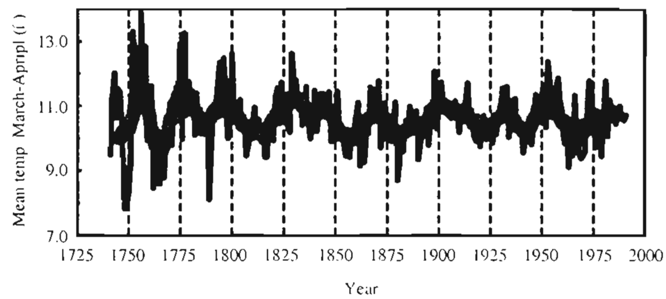

Fig. 6—Reconstructed March-April mean temperature for the period 1741-1991 AD. Smoothed line is the 10 years moving average.

the reliability of the reconstruction is also confirmed by comparison between observation data from meteorological stations nearby, not used in the calibration (Fig. 8).

The other unique independent paleoclimate proxy record, dryness/wetness indices that were generated from abundant Chinese historical documents (Academy of Meteorological Science, 1982), can provide much information to verify our reconstruction. In enormous Chinese historical writings there are abundant climatic descriptions, which are of great value for studying climatic fluctuations. During 1970's, hundreds of climatologists processed these materials from more than 2200 local annals and many other historical writings nationalwide, and abstracted from them more than two million and two hundred thousand characters. The dryness/wetness of each year in the recent 510-years period are classified into 5 grades: grade 1 – wettest, grade 2 – wet, grade 3 – normal, grade 4 – dry, and grade 5 – drought (Academy of Meteorological Science, 1982).

The reconstruction is significantly negatively correlated to the dryness/wetness index at 95% confidence level for the period 1741 to 1980 AD (N_2=239). For the region there are in total 58 level 4 or 5 drought years. Among them 35 years (60·35%) correspond to the mean temperature from March to April lower than the 250 years mean values (10·6°), and 23 years (39·65%) higher than mean. On the other hand, in 86 level 1 or 2 wettest to wetter years of the records, there are 49 years (57%) corresponding to higher temperature than mean, and 37 years (43%) to lower than mean.

It seems that March-April mean temperature provides information on precipitation in forthcoming seasons. Lower spring temperature could hint the drought, and warm springs at warmer seasons.

Drought years are recorded in documents (Shaanxi Meteorological Station, 1976). For example: **1813** severe drought in Zhen'an, reduced harvest (reconstructed temperature 10.0°); **1900** Zhen'an severe drought (10.5°); **1939** drought in Zhen'an (10.2°); **1944** spring drought for a quite long time in Zhen'an (9.9°), etc.

Some spring cold events also appeared in the reconstruction, such as: **1748** black frost in March (8.1°) in Zhen'an; **1884** heavy frost in April in Zhen'an, and 47 hectares wheat frost-bitten (10.6°); **1923** snow disaster in April in Zhen'an, and large-scale crops injured (10.2°), etc.

In order to emphasize decadal fluctuations, the series were filtered with 10 years moving average and the correlation rises

	r	F	$S_1(a, b)$	$S_2(a, b)$	t	RE	R^2	R^2_{adj}
$\hat{T}_{34}$	0·713	16·018	22(24, 26)	26(24, 26)	3·41	0·406	0·508	0·476

Fig. 7—The statistical characteristics of reconstruction (For definitions of symbols please see text. *a*—exceeds the 95% significant confidence level; *b*—99% level).

Station	Period	Observed *vs* observed	Reconstruction *vs* observed
Zhen'an *vs* Huashan	1958-1989	0.616 (<0.0001)	0.391 (<0.027)
Zhen'an *vs* Xian	1958-1990	0.771 (<0.0001)	0.619 (<0.0001)
Zhen'an *vs* Foping	1958-1990	0.694 (<0.0001)	0.576 (<0.001)

Fig. 8—Correlation between reconstructed and observed data from nearby meteorological stations (*r, p*).

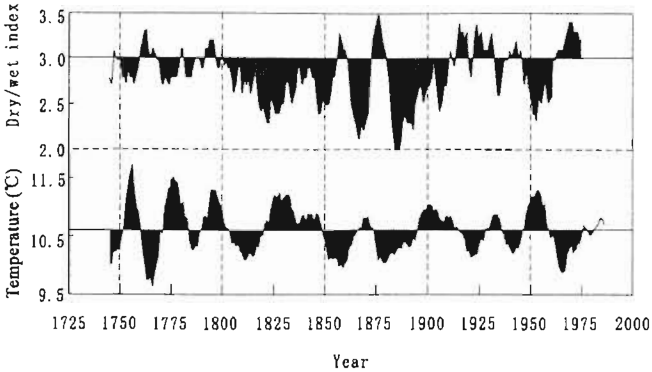

Fig. 9—The comparison between reconstruction and dryness/wetness (D/W) indices derived from historical documents The shading represents dry periods. Two curves were smoothed by 10 years moving average. The dryness/wetness indices were defined as: 1 wettest, 2 wet, 3 normal, 4 dry and 5 drought.

to –0·297 at the 99% significance level (after smoothing, the sample length N_3=229, p<0·0001). It is clear that early spring low mean temperature corresponds to drought (shaded in the Fig. 9), and warm to wet on decadal-scale, especially after 1900. As calculated after 1900, the two curves were highly correlated with r= -0·718 (N_4=75, p<0·0001). For instance, 1920-1930 in north China is one of the periods of greatest reduction in precipitation of the last 400 years, a consequence of reduced strength of the east Asian summer monsoon (Hughes *et al.*, 1994; Liu *et al.*, 1997; Liu & Ma, 1999). Our reconstruction shows a low temperature interval with 10.1°C, (about 5·2% lower than mean) for 1925-1930, including an extreme low value of 9·7°C of 1929, the driest year in 20th century. But during 1950-1960 south Shaanxi Province suffered flooding to the fullest extent, with reconstructed temperature of 11·6°C, 9·3% higher than the long-term mean.

Both the precision and resolution of series derived from historical documents is likely to be higher after 1900, due to many more records being available than in earlier times (Zhang, 1995). The tree ring based reconstruction does not suffer from

Warm			Cold		
	Period	*TEM(°C)*		*Period*	*TEM(°C)*
1	1773-1784	11·6	1	1961-1973	9·8
2	1947-1960	11·5	2	1939-1946	10·0
3	1792-1806	11·3	3	1785-1791	10·1
4	1829-1848	11·3	4	1849-1860	10·1
5	1931-1938	11·1	5	1807-1828	10·2
6	1898-1915	11·0	6	1916-1930	10·2
7	1974-1992	10·9	7	1746-1772	10·2
8	1861-1872	10·8	8	1873-1897	10·3

Fig. 11—Eight warm and eight cold intervals of early spring for the last 250 years in Zhen'an (250 years mean is 10·6°, TEM—Temperature).

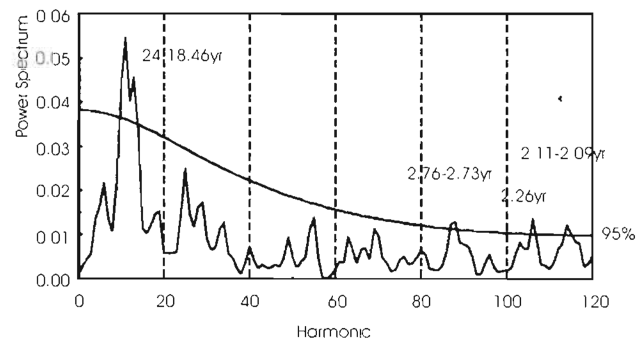

Fig. 10—Power spectrum analysis for reconstruction of early spring temperature (lag years=120, the smoothed line is 95% confidence limit line).

this problem, and this difference should be borne in mind when comparing the two kinds of records.

The reconstruction was tested for periodicities in the power spectrum analysis. The result displays remarkable 24, 21·82, 20·00, 18·46, 2·76, 2·73, 2·26, 2·11 and 2·09 yrs cycles for the past 250 years (Fig. 10). The major periodicity is 24 years. Besides this, 2·76 to 2·09 yrs are quite similar to the quasi-biennial oscillation (QBO). The effects of the QBO exist on the large-scale, and it may indicate sea-land coupling (Qian *et al.*, 1998).

Analysis of the 250 years reconstruction indicates that 16 periods were significantly warmer or colder than the mean (Fig. 11), but greatest confidence should be given to those after 1828, because of the poor replication of the chronology before this date.

Three stages (6, 5 & 7) in the warm intervals (Fig. 11) corresponded separately to abrupt warming in the Northern Hemisphere and globally during the last hundred years: end of 19th century, 1920-1930 and 1970's (Bradley *et al.*, 1987; Zeng *et al.*, 1995; Wang & Ye, 1995; Lin *et al.*, 1995). It indicates that the trend variation of the early spring temperature in the Qinling Mountains is quite synchronous with global variations on these time scales.

CONCLUSIONS

The preliminary work reported here confirms that tree-ring data has great potential to extend modern instrumental data in the Qinling Mountains in north-central China.

Based on well cross-dated ring-width series, mean temperature of March to April for Zhen'an China, was reconstructed. The explained variance of the reconstruction reaches to 50·8%. The data illustrations along with the statistics indicate that the tree-ring reconstruction is valid in reproducing the timing and duration of temperature anomalies. Eight relative cold and eight warm periods for early spring have been identified. Power spectrum analysis displays 24, 21·82, 20·00, 18·46, 2·76, 2·73, 2·26, 2·11 and 2·09 years cycles. The reconstruction can be well verified by historical documents at both high and low frequency. The lower mean temperature of March-April could be a signal of drought for the year and *vice versa*.

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Specifics of tree growth in Lithuania and its dependence on various factors

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ABSTRACT

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Due to a great diversity of tree stand conditions and climate in Lithuania, the response of tree growth to environmental changes differs considerably across the country. It causes difficulties in compiling long dated tree ring records from sub fossil and archaeological wood through cross matching of modern woods.

It was found that changes in long-term radial growth and the recurrence of biennial growth rhythm are the basic features, which distinguish tree stand conditions in Lithuania.

Key-words—Tree-rings, Radial growth, Climatic factors, Geohydrological conditions, Lithuania.

लिथुआनिया में वृक्ष वृद्धि की विशिष्टताएँ एवं विभिन्न कारकों पर इसकी निर्भरता

योनस कार्पाविचस

सारांश

लिथुआनिया में वृक्ष खड़ स्थितियों तथा जलवायु में विविधता के कारण सम्पूर्ण देश के पर्यावरणीय परिवर्तन भिन्न-भिन्न हैं। इस कारण जब पुरातात्विक काष्ठ की उपअश्मीय एवं अरीय वृद्धि के आंकड़े प्रयुक्त किए जाते हैं, तो दीर्घावधिक वृक्ष वलयों की श्रेणी निर्मित करने में अनेक असुविधाओं का सामना करना पड़ता है।

यह पाया गया है कि दीर्घावधिक अरीय वृद्धि में परिवर्तन तथा द्विवार्षिक वृद्धि चक्र ही वे प्रमुख अभिलक्षण हैं, जिनसे लिथुआनिया की वृक्ष खड़ स्थितियाँ अभिनिर्धारित की जा सकती हैं।

संकेत शब्द—वृक्ष वलय, अरीय वृद्धि, जलवायुविक कारक, भूजलीय स्थितियाँ, लिथुआनिया.

INTRODUCTION

SEVERAL tree ring features, such as ring width, wood density and chemical properties are being increasingly applied in various applications of dendroclimatology and dendrochronology. The details of tree ring and its relationship to environmental changes including methodology of such analyses are thoroughly described by Bitvinskas (1974), Fritts (1976), Schweingruber (1988), Cook & Kairiukstis (1989), Lovelius (1979) and others. The works of these authors and others showed, that the radial increments of trees are influenced by a number of factors of both climatic and non-climatic.

It has been recorded that even in such a small territory (65·2 thousand km²) as Lithuania, there is considerable diversity in responses to tree growth to environment. These differences might be related to soil types and changes of ground water level (Kairaitis & Karpavicius, 1996). Moreover, it has also been established that changes in radial growth are also influenced by several climatic factors (Karpavicius *et al.*, 1996).

Due to the relatively short age of trees in Lithuania (200–300 years), it is very difficult to establish reliable tree ring records longer than 300 years. The data could be extended by cross matching with the long tree ring series using subfossil and archaeological wood. However for the building of long tree-ring series of a site and tree species needs the knowledge of peculiarities of tree radial growth of trees of this region. In this paper an attempt has been made to overview the factors influencing the tree growths in Lithuania.

MATERIAL AND METHODS

A dense network of dendrochronological materials from Lithuania has been collected by several workers and these samples are stored our in Dendrochronology Laboratory (Fig. 1).

The species investigated mainly are pine (*Pinus sylvestris* L.), spruce (*Picea abies* (L.) Karst.), oak (*Quercus robur* L.) and larch (*Larix* sp.). For the tree-ring analysis not less than 10 increment cores, one from each tree, at breast height in each experimental plot was collected through increment borer. In some cases samples were taken from more than 100 trees. These large number of tree ring samples were analysed to evaluate which trees are more sensitive to climatic, whether there are missing and false rings and does the growth reduction depend on concurrent conditions in the stand. The investigation has shown that most trees of average and normal selection categories have such qualities (Karpavicius, 1986). The biggest amount of samples for the investigation from trees of selective categories have been taken since then.

After the mounting and processing the samples for tree ring analysis, ring width of all these samples were measured using the stereomicroscope and measuring machine. Pine, spruce and larch samples were measured to 0·05 mm and oak to 0·1 mm accuracy. Each early and late wood width was measured separately. The data from individual samples in each stand were averaged and the prepared tree-ring series were used for the further analysis. During analysis of radial growth it has been recorded that, the data provided earlier in the reports of the National forestry assessment, for the description of local growth condition are inadequate. With the support of the geological bore in stands growing in conditions of normal

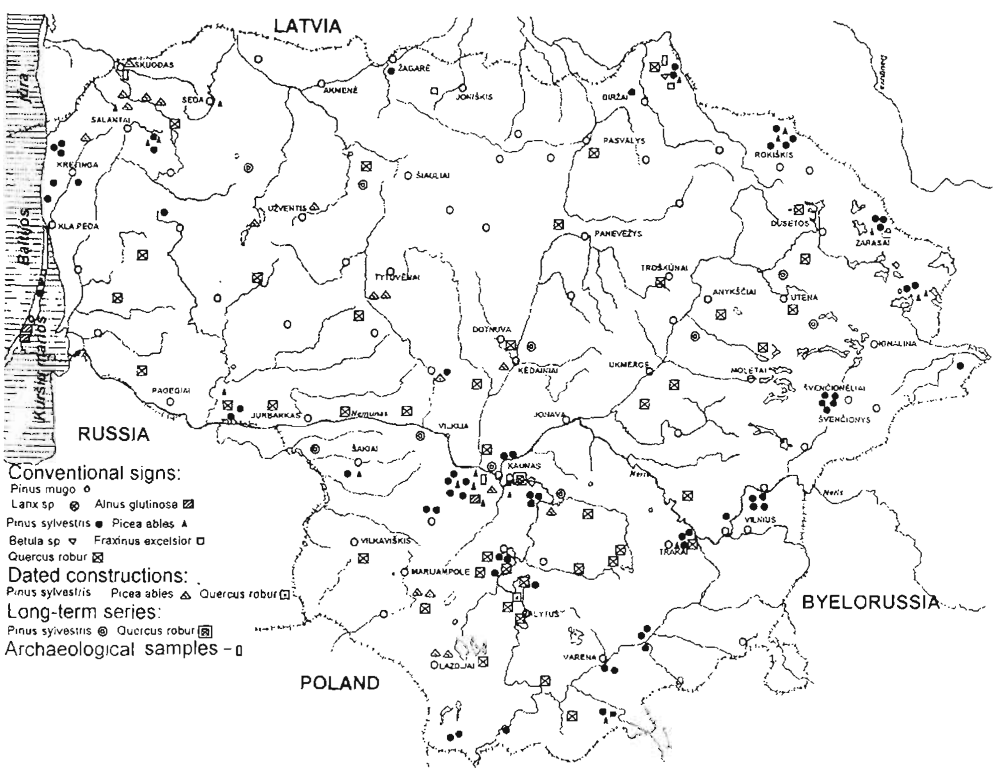

Fig. 1—Location of the experimental plots in Lithuania.

humidity, samples of soil for the supplementary analysis were taken. Attention on the examination of soil composition and ground water level was focused. Where ever possible, the examination was lowered to a depth of 6 m.

Experimental plots, located in bogs, in different localities were selected with regard to the distance from the water reservoirs (river, lake) and from the border of the bog, the thickness of the peat layer, etc., representing different hydrological conditions and forest sites (according to grass cover). These samples were taken from different age groups of trees in order to evaluate the impact of age, to facilitate identification of missing tree rings and also to compare the reaction to climatic factors.

As mentioned earlier, it is not possible to analyse trees covering time span of hundreds or more years, growing in Lithuania. However, one long tree ring series (2200 years), using the series of the radial growth from pine wood, found in "Uzpelkiu tyrelis" has been established (Pukiene, 1997). Dendroscale of subfossil oak, taken out from the ground of river Neris at Smurgainiai (Byelorussia) for 6000 years (Kairaitis, unpubl.) is nearly finished. Dendroscale for about 1000 years of the radial growth of pine wood, found in peat bog "Aukstoji plynia" (Karpavicius, 1998) is also nearly finished. It should be mentioned that all these long-term scales have gaps in certain periods.

While compiling long-term series, one has to face a number of problems. One of these is that, trees growing in different conditions of the geohydrological regime, react to the changes of climatic conditions differently. Therefore, the

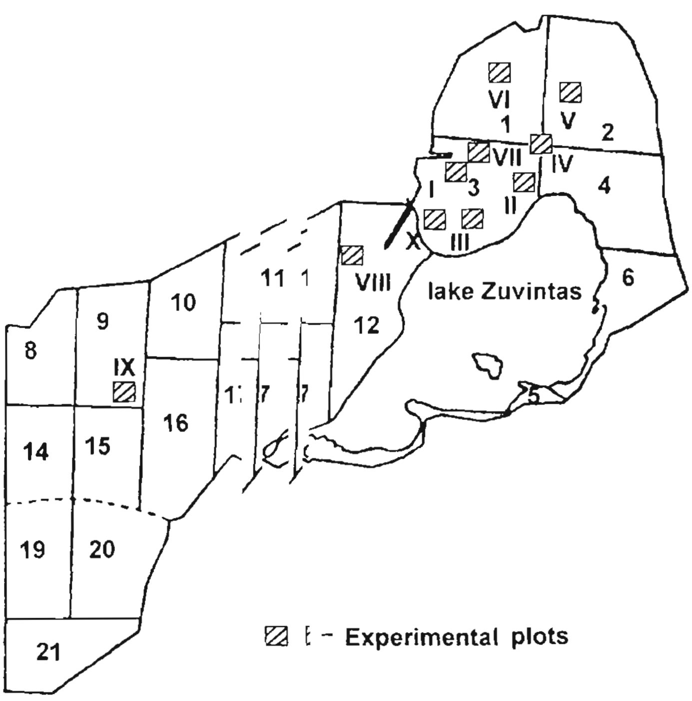

Fig. 2—Scheme of the expt esrirexnental plots in Zuvintas reservation.

data of radial growth could not be used for joint ring-series through cross dating.

Consequently, one of the main goals of our laboratory is to find out the explanation about peculiarities of radial growth of trees, growing in different conditions of the geohydrological regimes and their dependence on the climatic factors. The possibility to identify conditions of the growing site was investigated according to the radial growth patterns of samples from 43 oak stands and over 20 experimental plots, located in the pine forest bogs in Lithuania. The biggest parts of experimental plots (10) from peat bog of the Zuvintas strict reservation were chosen (Fig. 2).

For this investigation, several statistical methods were used. These will be described briefly in the discussion below.

RESULTS AND DISCUSSION

Lithuania, being in the centre of Europe, could be described as a country with great diversity in climate and vegetation. For example, during the period of 1893-1997 average precipitation was 618 mm, ranging from 407 mm in 1911 to 915 mm in 1950 and the average temperature being 6·4 °C. Moreover, a great range of temperature and precipitation comparing the data of different months has been observed. For example, the average winter temperature has varied from –0·1°C in 1925 to –10·3°C in 1940 and the average air temperature of March from +5·2°C in 1921 to –9·0°C in 1952, while the June precipitation from 158 mm in 1901 to 6 mm in 1940.

During the study of radial growth-climate relationships of various tree species more similar responses with climatic factors were found: positive growth-climatic relationships were found with mean annual temperature, temperature of September, October, March and precipitation of June. On the other hand, negative relationships were found with precipitation of September, October, May and temperature of June. The growth – climate relationships with other months are different and depend on various factors. For example, after extremely cold winters radial growth of trees become similar, e.g., after cold winters in 1940-41 and 1979-80 years decrease in radial growth is common as for oaks and pine growing in the soil of normal humidity.

The greatest dependency of growth on climatic factors is associated with soil composition and the depth of ground water. These factors influence not only growth-climatic relationships, but also the tree growth dynamics. Four types of growth-climate responses in Lithuania oak stands have been established (Kairaitis & Karpavicius, 1996): (1) insensitive to both temperature and precipitation; (2) more sensitive to the temperature regime (3) more sensitive to precipitation and (4) sensitive to temperature and precipitation.

Some of oak stands can not be assigned to any of these types. They belong to one type based on coefficients of

Period	Experimental Plot			
	M – 2	M – 3	M – 4	M – 5
until 1943	64·1	64·2	88·3	68·2
1943-1980	50·0	63·2	73·6	39·5
1981-1994	76·9	100	100	92·3

Fig. 3—Percentage of similarity of radial growth patterns of trees from different experimental plots (Minciagires forestry of Aukstaitija National Park).

correlation with meteorological factors during one period, and to another type based on results in another period.

Characteristic of type 1 oak stands is that they grow in sandy or loamy soils, have average or thick soil layers (about 40 cm) with humus, and ground water at the depth of 1·2 to 1·5 m.

Type 2 stands grow in soils characterized by a thin layer of loam or sand at the surface, leading into loam which then graduates in to clay. At some stands, sand is again found below the clay, or sand intermixed with clay. The ground water level is at a depth of 1·2 to 3 m.

Stands with the third type of response, growing in sandy or gravel soil with a deep ground water level.

Type 4 responses characterize oak stands which grow in soils of either pure loam or clay or which have a thin horizontal strip of sand at the surface. Ground water levels of over 6 m are common to the stands.

As it has already been mentioned, for tree growth not only are different types of climatic response common, but the course of growth dynamic as well. The most distinct dynamic of radial growth is found for oaks and pines, which grow in bogs settings closely related with hydrological conditions.

Similar percentage among tree groups, growing in the same bog, reflects the dynamics of radial growth (Fig. 3).

As Fig. 3 shows, the largest percentage of similarity with the growth of pines in the centre of the bog (depth of peat 1·8 m) have pines, growing in such places, where the depth of peat fluctuates from 1 to 1·5 m (e.p. Nr. M – 3 and M – 4), though e.p. Nr. M – 3 trees grow approximately 10 m from peat edge. Moreover, trees growing at the border (e.p. Nr. M – 2), or no less than 10 m away from the edge, but the depth of peat reaching only 0·6 m (e.p. Nr. M – 5) have less synchronisation than those growing in the centre.

It proves once again, that it is not possible to combine tree ring from different hydrological settings. The question arises, is it possible to define the stands where trees grew on the basis of radial growth features?

Research carried out at the laboratory shows that in addition to previously mentioned differences, some radial growth features typical for specific growth conditions exist. These regularities are well investigated for oaks (Kairaitis & Karpavicius, 1996; Kairaitis, 1998) and pines growing in bogs (Karpavicius, 1993, 1998). As pines growing in Zuvintas reservation, radial growth illustrate one of these features is the trend of long- term radial growth (Fig. 4).

As seen in Fig. 4, in 1936-1979 the average amount of precipitation has decreased and the average radial growth of pines has increased in nearly all-experimental plot, compared to the 1893-1935 period. This increase in pine increment varies in different bog localities, due to different hydrological conditions. The radial growth increase of pines was lowest in the most humid forest sites (e.p. Nr. Z-1, Z-7, Z-8) and in one of central peak site of the bog (e.p. Nr. Z-4). Meanwhile, in the e.p. Nr. Z-2, Z-3 and Z-10, which are not far from lake Zuvintas and the River Dovine, the increment was doubled, as the excess water was drained to the lake-river (Fig. 2). On the other hand, the lowest amount of precipitation in e.p. Nr. Z-6, which is located on a sloping area 200 m from the spruce stand located near the border of the bog, had a negative impact.

Although the decrease of precipitation from the mean of 627·2 mm in the period of 1893-1935 to 607·9 mm in the period of 1936-1979 had a positive impact on the radial growth in nearly all experimental plots located in the Zuvintas reservation, in the other bogs impact is negative, except for the pines growing in the central part of the bogs. This can be explained by the distance from the border of the bog and the peat layer thickness.

Such phenomena of radial growth were also found for subfossil wood of pines, excavated from various depths from the peat bog "Aukstoji Plynia" (Karpavicius, 1998).

Another feature of radial growth studies is the two-years rhythm in which the increment of one year is bigger than that of the previous two years. This pattern is mainly characteristic for periods when rainy years were followed by drier years (Karpavicius, 1993). In the 1954-1963 period, in even years the average of precipitation was 600·8 mm and in uneven years it was only 503 mm. This pattern creates different humidity

Period	Experimental Plot									Precipitation
	Z – 1	Z – 2	Z – 3	Z – 4	Z – 6	Z – 7	Z – 8	Z – 9	Z – 10	
1893-1935	0·54	0·46	0·54	0·52	0·63	0·50	0·44	—	0·63	627·2
1936-1979	0·68	0·93	1·04	0·63	0·58	0·51	0·58	0·66	1·35	607·9

Fig. 4—The average radial increment and precipitation of different periods (in mm).

and nutritional conditions in different areas of the bog. If the increase in precipitation in experimental plot Nr. Z-4 and Z-6 results in decrease in increment growth, in the experimental plot Nr. Z-9 the precipitation had a positive impact on growth. It is important to note that this two years pattern is less common for pines growing near the border of the bog where thin layer of peat dominate.

To summarise, the width of radial increment in separate time periods and a characteristic two years rhythm/pattern are reliable indicators that allow us to evaluate the geohydrological conditions of the tree growth.

One more growth features for the pines growing in bogs is that radial growth of young pines reflect the climatic fluctuation the same way like older trees but the absolute values of their increment depend on the climatic conditions in the period the trees started to growth (Karpavicius, 1994). This feature is common not only for the pines growing in Zuvintas reservation, but also for those stands in other bogs, where the depth of peat is more than 1 m and that grow further from the border of the bog.

This feature of young tree radial increment is most characteristic for oaks (Kairaitis, 1998) and pines growing in bogs. That is why, for the formation of long-time series, use of tree-ring data from subfossil wood, is recommended to use absolute quantities. If separate individual increment indices are used for the joining of long-term tree ring series, much information developing hundred-year-old cycle is lost.

CONCLUSIONS

The dynamics of radial growth of trees in Lithuania discussed in this paper has been found to have correlation with diversified environmental variables viz., meteorological factors, soil composition and depth of ground water, moisture regime and a host of other factors. Due to these differences, it is essential to use data from more or less analogous habitats as possible when compiling long-time series of tree growth in Lithuania. It has been recorded that extremely cold winters are one of the basic factors for which different tree species growing in locations of normal humidity react similarly (negatively). Moreover, long-term radial increment changes and constant two-years increment rhythm recurring no less than every 10 years of oaks and pines growing in bogs are basic features, which allow us to distinguish the growing conditions.

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Network of tree-ring series in Estonia connected with north European chronologies

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ABSTRACT

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The present paper describes the course of building up the tree ring network of Scots pine (*Pinus sylvestris* L.) in Estonia. Although the construction timber in this region of the Baltic comes from two tree species, Scots pine and Norway spruce (*Picea abies* Karst.), only the former was used for comparisons between the average tree ring series in Estonia and tree ring chronologies of Scots pine from other neighbouring areas: Sweden, Finland, Latvia and Poland. The dated tree ring series were compared using Student's t-criterion. It appeared that Estonian tree ring series of pine generally showed the greatest similarity with the chronology of Gotland pine in Sweden (the t-value with the average series of growing pines in north-western Estonia reaching 9·59). The similarities with other matched tree ring chronologies were also significant. It can be concluded that Estonia belongs together with other Baltic Sea countries to the same dendroclimatological region of uniform tree growth. This fact enables to use dated tree ring chronologies from the neighbouring areas to confirm the dating of tree ring sequences in Estonia.

Key-words—Tree-rings, Network, *Pinus sylvestris* L., Estonia, N Europe.

एस्टोनिया में उत्तर यूरोपीय कालानुक्रम से सम्बद्ध वृक्ष वलय श्रेणियों का संजाल

अलर लानलेड

सारांश

प्रस्तुत शोध पत्र में एस्टोनिया के स्कॉट्स पाइन (*पाइनस सिल्वेस्ट्रिस* एल.) के वृक्ष वलय संजाल की निर्मिति प्रक्रिया वर्णित की गयी है। यद्यपि बाल्टिक के इस क्षेत्र की काष्ठ स्कॉट्स पाइन एवं नार्वे स्प्रूस (*पाइसिया एबीज़* कार्स्ट) नामक दो वृक्ष प्रजातियों से निर्मित है, परन्तु नार्वे स्प्रूस को कुछ समीपवर्ती क्षेत्रों, जैसे - स्वीडन, फिनलैण्ड, लाटविया एवं पोलैण्ड से प्राप्त स्कॉट्स पाइन की वृक्ष वलय कालानुक्रमिकी के साथ-साथ एस्टोनिया की औसत वृक्ष वलय श्रेणी की तुलना हेतु भी प्रयुक्त किया गया है। स्टूडेण्ट्स टी-क्राइटेरियन की सहायता से वृक्ष वलय श्रेणियों की आयु की तुलना की गई थी। ऐसा प्रतीत होता है कि पाइन की एस्टोनिया वृक्ष वलय श्रेणी सामान्यतः स्वीडन की गॉटलैण्ड पाइन कालानुक्रमिकी (उत्तर-पश्चिमी एस्टोनिया में वृद्धिमय पाइन औसत श्रेणी से युक्त टी-मान 9·59 तक पहुँचता हुआ) के साथ गहन समरूपता प्रदर्शित करती है। कुछ अन्य विदेशी वृक्ष वलय कालानुक्रमिकी के साथ संगति भी महत्त्वपूर्ण है। इससे यह निष्कर्ष निकलता है कि एस्टोनिया बाल्टिक समुद्र के आस-पास अन्य देशों के साथ एक समान वृक्ष वाले उसी वृक्ष जलवायुविक क्षेत्र से सम्बन्धित है। यह तथ्य एस्टोनिया के वृक्ष वलय अनुक्रम के आयु निर्धारण की पुष्टि हेतु समीपवर्ती क्षेत्रों के वृक्ष वलय कालानुक्रम को प्रयुक्त करने के लिए सहायक सिद्ध हो सकता है।

संकेत शब्द—वृक्ष वलय, संजाल, *पाइनस सिल्वेस्ट्रिस* एल., एस्टोनिया, उत्तरी यूरोप.

INTRODUCTION

THE aim is to find out if old buildings in Estonia can be dated on the basis of the tree ring chronologies in other neighbouring countries. In other words, it is the question of geographical extension of a dendroclimatologically uniform region. Some idea of the possible range of dendroclimatologically uniform regions in Scandinavia was obtained from a map presented by Bartholin (1993). According to the map, the uniform region of pine in central part of Sweden covers roughly a north-southward elongated area three times as large as Estonia, which lies not far in the east of that region. One can easily imagine the extension of this region eastward so that it will also cover the area of both Estonia and southern Finland on the eastern coast of the Baltic Sea. In the above-referred paper, Bartholin stated that "in practice these areas are larger" in addition, he gave some examples on successful dating of the Scandinavian tree ring curves by mean curves of Poland and Finland. Presumably, the climate is more uniform in this region along the east-west direction than along the north-south direction. Using similarities between the tree ring series in these regions can prove these considerations.

Estonia, the northernmost of the three Baltic countries in northern Europe, has now its own tree ring network of pines that is connected with the tree ring chronologies of pines in other neighbouring countries (Fig. 1).

The tree ring samples from Estonia came from roof constructions of old buildings, mainly churches, but also from other buildings and extant trees. The common construction timber of this area is Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* Karst.). As pine and spruce have different biology, and they form different tree ring sequences, there was a need to distinguish, firstly, the samples of these tree species, and secondly, to develop separately tree ring averages for these species. Pine and spruce wood has often been used mixed in the same construction, or the framework of a roof is made of one tree species and repaired with another. Borer cores of centuries-old wood sometimes do not reveal visual features of the tree species. Therefore, in all cases the tree species of the cores of the construction wood was

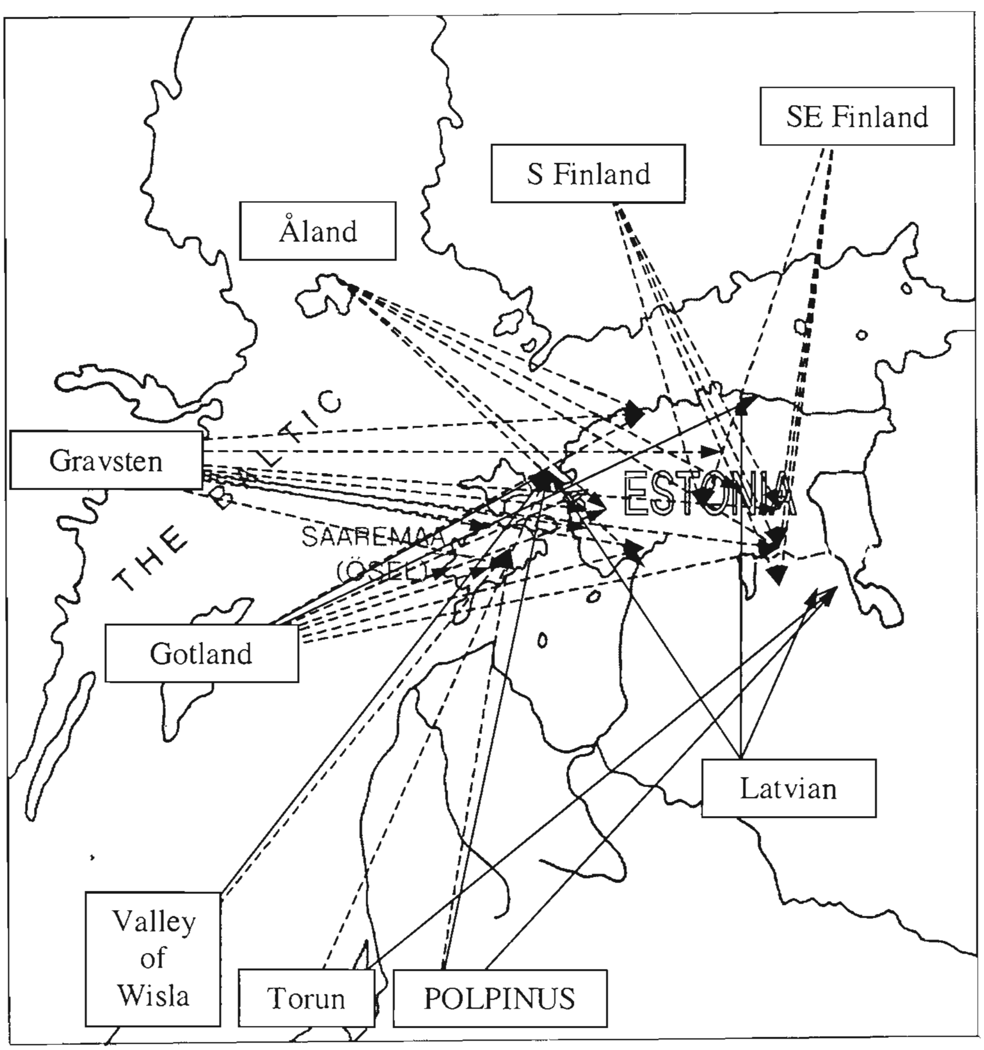

Fig. 1—The location of tree ring series of pine in Estonia significantly correlated with the pine chronologies of the neighbouring areas around the Baltic Sea. The correlation was estimated by Student's t-criterion. The dashed line arrows indicate connections of construction wood, the solid line arrows of growing pines in Estonia. Labels on the map mark the correlated chronologies outside Estonia; details of them are given in the text.

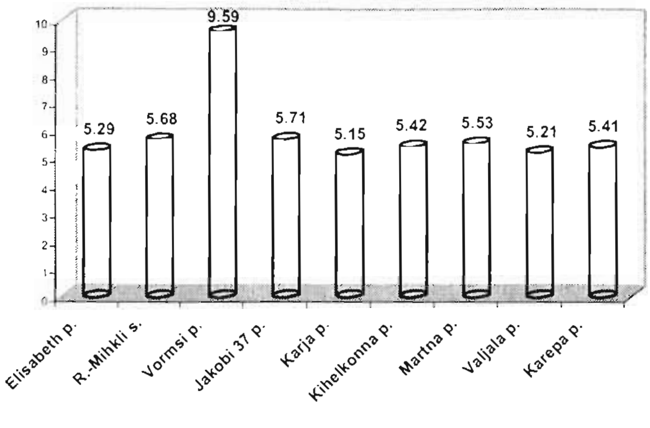

Fig. 2— Student's t-values of Estonian average pine series with Gotland pine chronology (Bartholin, personal commun, 1998). Ordinate: Student's t-values. Abscissa: names (toponymes) of the average tree-ring series. Numbers next to the bars show overlapping of the series in years, at the top of the bars - t-value; p. = pines, s. = spruces. Vormsi pines is a series of extant trees, the rest series come from buildings.

determined microscopically. It appeared that pine and spruce occurred nearly in equal numbers among the sampled construction timber.

MATERIAL AND METHODS

Usually 10 to 30 cores were extracted from different beams of a construction. The tree ring widths were measured and the ring sequences were synchronized between themselves by graphs and Student's t-values. Well synchronizing tree ring curves of the same species were joined into an object average series, consisting usually of 5 to 10 or more initial series. These average series were dated by reference chronologies, using also earlier dated average tree ring series from Estonia (Läänelaid, 1999a, b). Some of the average series were dated by longer Estonian average series of growing pines or spruces. The dated objects located in different parts of Estonia - on the sea islands in the western part, on the continent in north-western Estonia, and in northern and eastern Estonia. Altogether there were about 40 sample locations over Estonia that were involved in the present research (Läänelaid, 1998).

The correlation among the average tree ring series of old buildings in Estonia varies. Some of the series reveal high correlation, and some of them do not correlate at all between themselves. Besides the distance between the sample sites, correlation of the average tree ring series is apparently related to the similarity of the conditions at the sites of the tree stands.

In order to connect Estonian tree ring network with neighbouring areas, the average pine tree ring series of buildings were correlated with available tree ring chronologies in Sweden (pine chronologies of Gotland and Gravsten, both by Bartholin, personal commun, 1998), Finland (pine chronologies of Åland by Bartholin, personal commun, 1991, of southern Finland by Zetterberg, personal commun, 1998, and of south-eastern Finland by Lindholm, personal commun, 1998), Latvia (Bauska church by Zunde, personal commun, 1998; Latvian pine chronology by Špalte, 1979), and Poland (modern pine chronologies of Torun, POLPINUS, northern Poland, and the Valley of Wisla, all by Zielski, personal commun, 1989, 1992a, 1992c, 1995).

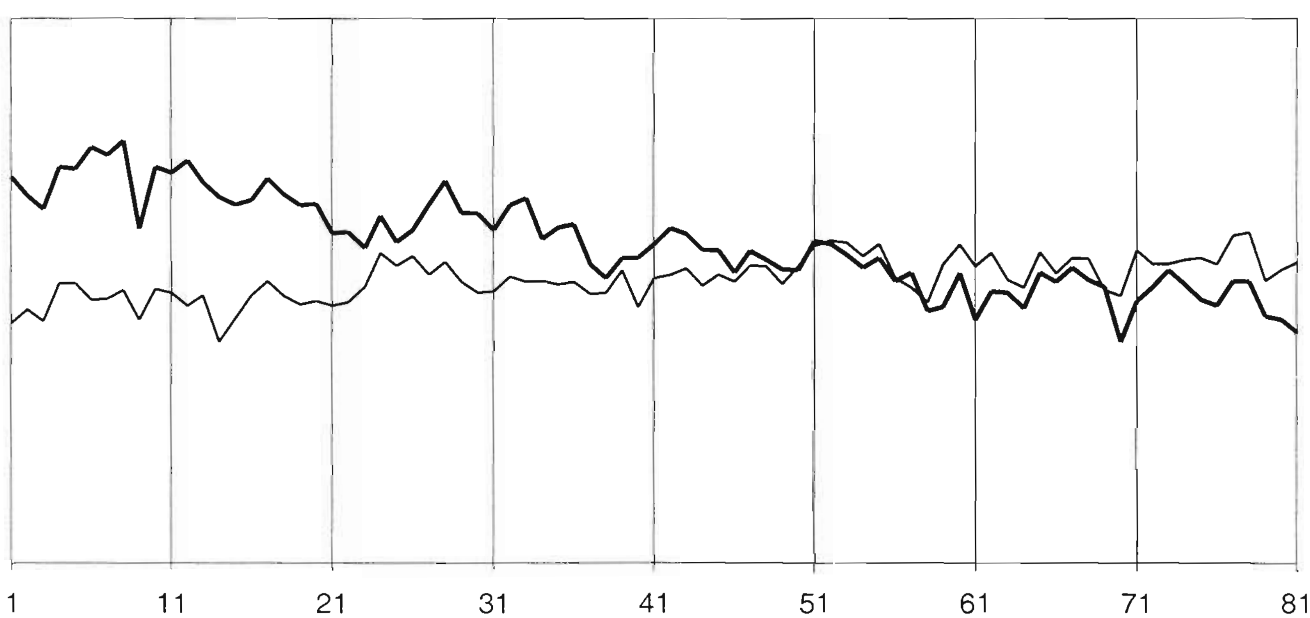

Fig. 3—An 80-year cut of matched tree ring series of extant pines from Vormsi Island, NW Estonia (thick line), and Gotland pine chronology (Sweden). Student's t = 9·59. Abscissa: years. Ordinate: ring widths in logarithmic scale.

RESULTS

It appeared that of these reference chronologies, Gotland pine chronology gave the highest correlation with Estonian object series. The Swedish island of Gotland is situated in southwest from Estonia. The buildings and sites that correlated with Gotland chronology are distributed over Estonia (Fig. 1); however, the connections tend to be presented mostly in the western part of Estonia. This fact may lead to the speculation that the high similarity between the tree ring curves is due to the timber trade as the construction wood for western Estonian buildings was presumably often imported from Gotland in the past. This presumption is however disproved by the highest correlation, t = 9·59, of the series of extant growing pines on Vormsi Island in Estonia with the Gotland pine chronology (Fig. 2). Even an untrained eye can recognize the similarity of the matched graphs of these tree ring series (Fig. 3). Thus, we can conclude that the sampled Estonian construction timber was not necessarily imported from Gotland, but the similarity of the tree ring curves is due to the similar climate on the Estonian and Swedish islands in the Baltic Sea.

Pine chronology of Gravsten, lying west from Estonia, reveals high correlation with the Estonian tree ring series from different parts of the area (Fig. 1). The highest t-value, 5·5, is revealed with some average series in eastern Estonia: Karlova Mansion and Uppsala House in Tartu, and Kursi Church (Fig. 4). Nevertheless, it is much lower than the t-value between Gotland chronology and Vormsi pines (where it is 9·6); hence, it does not allow presuming timber import from Gravsten to Estonia.

Pine chronology of Finnish Åland islands, situated in northwest from Estonia, yields generally lower t-values compared to the Estonian series than the previous reference chronologies. Still, it correlates well with several object series over Estonia. The highest t-value, 7·5, is with long pine series (205 years) of Karuse Church in western Estonia. Nevertheless, it does not mean that the timber was imported from Åland.

The pine chronology of southern Finland that is situated northward from Estonia reveals lower t-values with Estonian object series than the previous references. The highest t-value is reaching to 4·46 with the pine series of Tampere House in Tartu, southeastern Estonia.

The pine chronology of southeastern Finland provides t = 4·58 as the highest, with an average series of four objects from eastern Estonia (Nõo, Palamuse, Pilistvere churches, and Jakobi Street 45 in Tartu). From these similarities it is clear that the investigated Estonian construction timber did not originate from Finland but was rather of local origin.

Tree ring series of Bauska Church, southern Latvia (Zunde, personal commun, 1998), gave considerable correlation with three Estonian series; of them t = 5·73

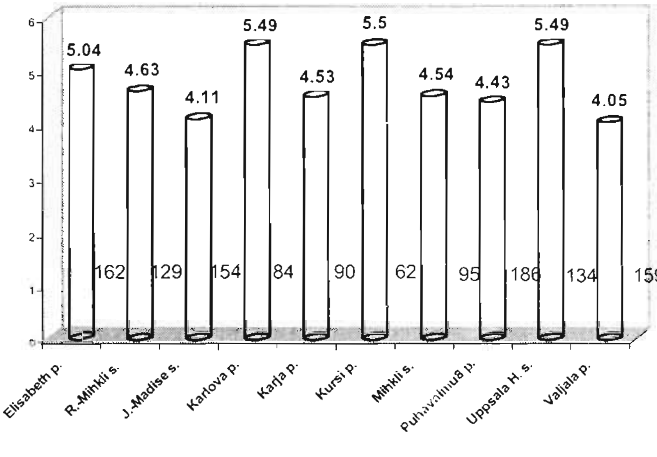

Fig. 4—Student's t-values of Estonian average pine series with Gravsten pine chronology (Bartholin, personal commun, 1998). Ordinate: Student's t-values. Abscissa: names (toponymes) of the average tree ring series. Numbers next to the bars show overlapping of the series in years, at the top of the bars - t-value; p. = pines, s. = spruces. All Estonian tree ring series refer to the construction wood

(overlapping 115 years) with Elisabeth Church pine series of Pärnu being the highest. A general Latvian pine chronology of modern trees dating from 1723-1972 AD (Špalte, 1979) showed significant correlation with series of growing pines in Vormsi, north-western Estonia (t = 8·22), Karepa, northern Estonia (t = 7·19) and Kiidjärve, south-eastern Estonia (t = 6·17), whereas the correlation with the tree ring series of construction timber was more modest (reaching t = 4·79 in case of Martna Church).

As to the Polish pine chronologies (Zielski, personal commun, 1989, 1992a, b, c, 1995), the Torun modern pines gave the highest t-value, 5·01, for growing pines in Vormsi, northwestern Estonia. Modern pines in the Valley of Wisla yielded also high t-value, 4·97, with the Vormsi pines, as well as the Polish chronology POLPINUS (t = 4·99). The northern Poland pine chronology yields somewhat lower t-values with some Estonian object series. It has to be mentioned that Bartholin and Zielski (1992) have found a high correlation between some church chronologies from northern Poland and several other chronologies from Sweden.

DISCUSSION

The fact that the t-values of the foreign reference chronologies are often higher with average series of growing pines than with the series of construction wood in Estonia make one suggest that the higher correlation may be caused to a certain extent by the preserved age trend of the trees both in the last end of the reference chronologies and in the Estonian modern tree ring series. As the average Estonian series of construction wood mainly consist of roughly even-aged tree series, the average series also preserve their age trend. While correlated with a long reference chronology, the Estonian object series that contain age trend match with the middle part of the reference chronology built up by series of various ages and with suppressed age trend. Therefore, their correlation is lower than in the case of the two series that both contain age trend. The next task is to suppress the age trend in Estonian tree ring series by composing longer chronologies of uneven-aged tree ring series.

The relatively high t-values of the foreign reference chronologies with the series of growing pines in Estonia still allows to disprove the suggestion that the construction wood of some Estonian buildings was imported from Sweden. Apparently, the construction wood of the studied church roofs is of local origin. It does not eliminate the possibility of wood import to Estonia for other purposes during the past centuries.

As to the directions of the world, the Estonian tree ring series show generally better similarity with westward chronologies than with northern and southern ones (some available chronologies from Russia in the east did not yield considerable correlation with Estonian series). While attributing the similarity of the tree ring series to the climate, we can note that in the Baltic region the zone of similar climate extends mainly in the west-east direction. As there were no remarkable differences established in the correlation with foreign chronologies between the tree ring series from western and eastern Estonia, we can consider that the whole Estonia belongs to the same dendroclimatologically uniform region as other northern European countries. Tree ring chronologies from southern Finland and especially from Sweden that are situated on the same latitudes as Estonia can be successfully used for dating Estonian object series.

CONCLUSIONS

1. Tree ring chronologies of pine from the central part of Sweden, especially the Gotland pine chronology, correlate well with tree ring series from all over Estonia.
2. Tree ring chronologies of pine from southern and southeastern Finland correlate well with tree ring series from eastern Estonia.
3. Tree ring chronologies of pine from Poland correlate with some tree ring series from western Estonia.
4. The comparison of Estonian tree ring series with Lithuanian and neighbouring Russian tree ring chronologies should be carried out in the future.
5. The correlations allow to conclude that the area of Estonia belongs to the same dendroclimatological region as northern European countries, and the tree ring chronologies from close neighbouring areas, especially from western Sweden, can be used for dendrochronological comparisons and dating of Estonian tree ring series.

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July-August temperature of central Korea since 1700 AD: Reconstruction from tree rings of Korean pine (*Pinus koraiensis*)

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ABSTRACT

Park W-K, Seo J-W, Kim Y & Oh J-H 2001. July-August temperature of central Korea since 1700 AD : Reconstruction from tree rings of Korean pine (*Pinus koraiensis*). Palaeobotanist 50(1) : 107-111.

July-August mean temperatures of 1657-1998 AD were reconstructed using two local chronologies of Korean pine (*Pinus koraiensis*) growing in subalpine regions (1500-1600 m) of Sorak Mountain in the central Korean peninsula. Calibration function for the instrumental period (1909-1949 AD) was obtained by using linear regression with the lagged chronology at t-1. The calibration was verified by independent data of 1953-1995 AD. The reconstruction indicates that the 1700-1730 and 1830-1850 periods were coolest in last 340 years. The warming trend was not found in summer temperature during the 20th century.

Key-words—Global warming, Dendroclimatology, Korean pine, Subalpine trees.

मध्य कोरिया के विगत 1700 ई. से आज तक के जुलाई-अगस्त माह का तापमान : कोरियाई चीड़ (*पाइनस कोराइएन्सिस*) के वृक्ष वलयों से तापमान का पुनर्सृजन

वोन-क्यू पार्क, जिओंग-वुक स्यू, योजुंग किम एवं जेइ-हो ओह

सारांश

मध्य प्रायद्वीप के सोराक पर्वत के उपअल्पाइन क्षेत्रों (1500-1600 मीटर) में उगने वाले कोरियाई चीड़ (*पाइनस कोराइएन्सिस*) के दो स्थानीय कालानुक्रमों की सहायता से विगत सन् 1657-1998 ई. के मध्य के जुलाई-अगस्त माह के औसत तापमान का पुनर्सृजन किया गया। टी-1 पर पश्चायित कालानुक्रम से रैखिक समाश्रयण को प्रयुक्त करते हुए प्रमुख अवधि (सन् 1909-1949 ई.) हेतु अनुसंशोधित फलन प्राप्त किया गया। यह अनुसंशोधन सांख्यिकीय रूप से सन् 1953-1995 ई. की अवधि से तुलनीय है। पुनर्सृजन से संकेतित होता है कि विगत 340 वर्षों के दौरान सन् 1700-1730 ई. तथा सन् 1830-1850 ई. की अवधियाँ सर्वाधिक ठण्डी थीं। 20वीं शताब्दी के दौरान उष्णता सम्बन्धी रूझानों के कोई प्रमाण नहीं प्राप्त हुए हैं।

संकेत शब्द—भूमण्डलीय उष्णता, वृक्षजलवायुविकी, कोरियाई चीड़, उपअल्पाइनी वृक्ष.

INTRODUCTION

GREATER understanding of the global changes, particularly recent climate change, so called 'global warming', due to anthropogenic impacts, has become an increasingly important goal of scientific endeavor in the world which is faced with growing population and increasing pressure on energy, water and ecological values. However, the basic problem is that we do not know enough about the climate and its variations in the past, which is key to study the present and future climate. The records of actual instrumental observations of meteorological stations are too short to examine the climate variations in long term. Fortunately, information about climate prior to the beginning of instrumental observation can be obtained from proxy data such as pollen, sediment, ice cores and tree rings. Among proxies, tree rings provide the data with the highest resolution, at least, in yearly and even in seasonal scales (Fritts, 1976; Hughes *et al.*, 1982; Schweingruber, 1988; Cook & Kairiukstis, 1990).

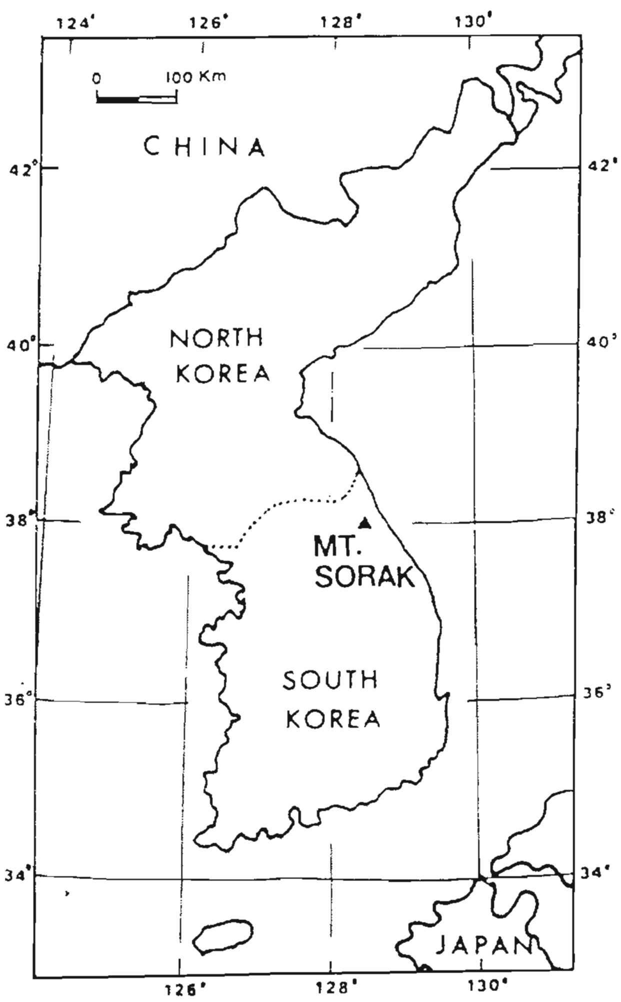

Fig. 1—Location of study site.

Some species reported growing for several centuries in Korea (Kong & Watts, 1993) provide unique opportunities to develop long tree-ring chronologies for climatic reconstructions for this region. Though the area is very important from a climatic view point, only a few high-resolution records of palaeoclimate are available for the Korean region (Park & Yadav, 1998).

The climate of the Korean peninsula within the domain of monsoon system is directly influenced by host of teleconnections with various climatic phenomena operating far remote from the area (Lau, 1992; Dodson & Liu, 1995). Long term high-resolution proxy climate data from such an area where various land-ocean-atmospheric processes interact are very important for assessing the natural variability of Earth's climate system especially in relation to the position of Siberian High, Tibetan High, the Asian monsoon and the western Pacific Warm Pool near Indonesia and New Guinea (Dodson & Liu, 1995).

In the present study, mean July-August temperatures are reconstructed back to the mid 17^{th} century using tree-ring chronologies of Korean pine (*Pinus koraiensis* S. et Z.) growing in subalpine regions (1500-1600 m) of Sorak Mountain in the central Korean peninsula. Korean pine (*Pinus koraiensis*, 5-needle pine) is among the only few trees that live for several hundred years (Kong & Watts, 1993). The objectives of this study are to examine long-term summer temperature variation in central Korea and to compare the 20th century one with that of pre-industry period.

METHODS

Four site chronologies of Korean pine were made from the Sorak Mountain range, which is located in the east coast area of Central Korea (Fig. 1). Two sites (HC & OS) are on the slopes of Taecheongbong, the highest peak of Mt. Sorak and others (HU & HD) on the valley of Hangaerung. The former sites (1500-1600 m) are located at higher elevation than the latter ones (1300-1400 m). Each chronology was made from more than 10 trees. A total of 101 trees were sampled for the present study from dominant ones in each forest site (Fig. 2).

Paired increment cores were taken at breast height using an increment borer from each tree except in a few cases where another side was not approachable due to steep slope. The tree-ring sequences of the mounted and surfaced core samples were crossdated using the graphic method (Schweingruber, 1988). Ring widths were measured to nearest 0·01 mm using a Velmex measuring system. The ring-width plots of each core (log scale) were produced from the ring-width measurements using program TSAP. These plots were used for visual comparison on a light table to date the sample cores within and between the trees. Double-check of dating and measurement accuracies was performed by correlating overlapping 50-years segments of all measured series by using program COFECHA (Holmes, 1983). This helps in identifying segments of a core or group of cores where dating or measurement errors might occur. Thirteen trees could not be crossdated and were not included in further analysis.

Ring-width series were detrended to make tree ring indices using program ARSTAN (Cook, 1985). The detrending methods were chosen to remove age and stand dynamics related growth trends while preserving the maximum common signal with century scale. In most of the cases the cubic spline with 50% variance reduction function at 200 years was found suitable. Site chronologies were obtained by taking robust mean of all index series for each site.

Basic statistical qualities of each site chronology were obtained. Cross-correlation analysis (Briffa & Jones 1990) was conducted to examine the degree to which individual index series agreed with each other; the mean of all correlation among different cores, between-tree correlations, within-tree correlations, Expressed Population Signal (EPS) and the ratio of signal to noise (SNR) were obtained (Fig. 4).

The climate data used for calibration and verification are regional monthly temperatures, the average of 8 station data series obtained from Central Meteorological Service, Korea, 1990. To define an optimum season for reconstruction, we carried out the analysis of correlation between ring indices and monthly temperatures. These indicated generally positive correlations during late growing season and previous dormant season with the tree growth. Based on the correlation profiles, July-August mean temperatures were selected for reconstruction. The calibration and verification periods were chosen as 1909-1949 and 1953-1995, respectively. Multiple linear regression was used for calibration. Lagged predictors were tested for the regression. The lagging process used the ring-width indices for years t-2, t-1, t, t+1, t+2 (where the year of growth is year t) to determine if climatic variations in one year can influence growth in subsequent years due to biological persistence (Fritts, 1976). Various statistical comparisons were used for the verification. These are the correlation coefficients, R^2; sign test, and reduction of error (Fritts 1976).

Site I.D.	HC	OS	HU	HD
Mountain range	Taecheongbong		Hangaerung	
Location	Hwachebong	Osaek	Upper Slope	Down Slope
Elevation	1500	1600	1400	1300
Number of trees (cores)	46(96)	13(23)	13(26)	29(58)

Fig. 2—Site Information.

RESULTS AND DISCUSSION

We developed four sites chronologies (216-342 years) of Korean pine from Sorak Mountain in central Korea (Figs. 3 & 4). The plots of chronologies (Fig. 3) illustrate that the fluctuation patterns agree well with each other. Low growth periods in 1840s and 1900s are apparent. The pointer years, such as 1906, 1917 and 1959, are well matched (Fig. 3). Correlations among the chronologies obtained at similar elevation were high (0·706 between HC & OS, 0·812 between HU & HD for the 1900-1990 period), however, low among different elevation ones (0·354 between HC & HD, 0·183 between OS & HD). The mean correlation among site chronologies was 0·499. Chronology statistics and the results of cross-correlation analysis are given in Fig. 4. Mean sensitivities are 0·144-0·168. These data indicate moderate interannual variation of the tree-ring series. The correlation

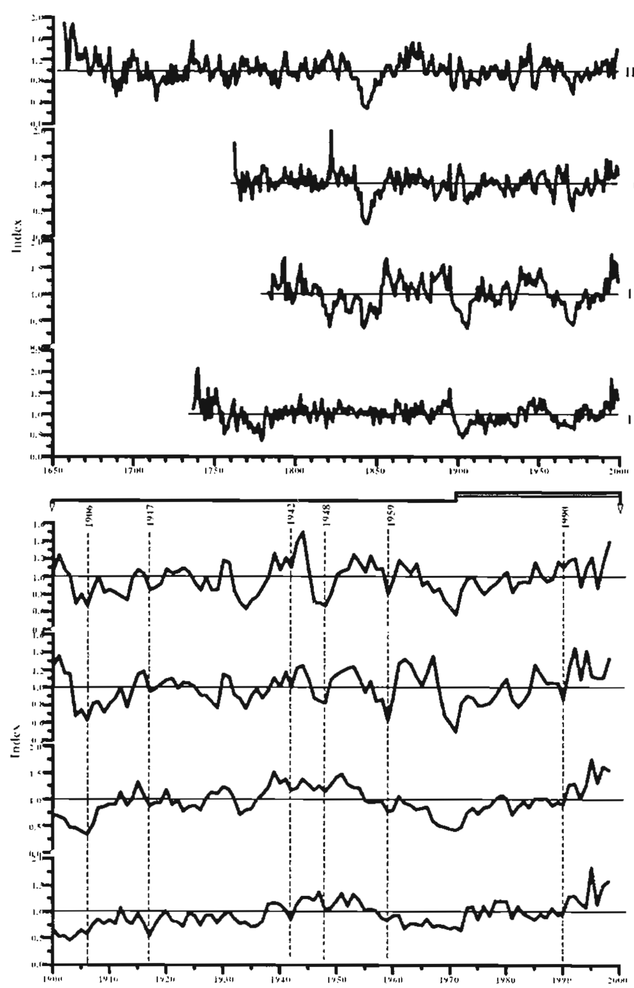

Fig. 3—Tree-ring chronologies of *Pinus koraiensis* of four sites at Sorak Mountain (see Fig. 2 for the chronology abbreviations: The numbers of 200 after site ID indicate the lengths of spline functions used for detrending raw ring-width series)

Site I.D.	HC	OS	HU	HD
Number of trees (cores) analyzed	43(86)	11(20)	13(26)	21(43)
Period (years)	1657-1998 (342)	1762-1998 (237)	1783-1998 (216)	1737-1998 (263)
Mean sensitivity	0·146	0·153	0·144	0·168
Correlation (91 years: 1900-1990)				
Among all radii	0·239	0·216	0·343	0·282
Between trees	0·233	0·206	0·330	0·276
Within trees	0·542	0·411	0·609	0·668
Signal-to-Noise Ratio	11·95	2·59	5·41	6·21
Expressed population signal (EPS)	0·92	0·72	0·84	0·86

Fig. 4—Summary statistics of four sites chronologies.

between trees (0·206-0·330) and the signal-to-noise ratio (2·59-11·95), which provide measures of the strength of common signal in the samples, are rather low. The EPS of three chronologies are higher than the EPS limit (0·85) of acceptable statistical quality suggested by Wigley *et al.* (1984). It implies that the chronologies developed in this study possess common signals.

We obtained mean chronology by taking arithmetic average of two index chronologies obtained at higher elevation sites (HC & OS) to maximize climatic signal. From correlation between climate variables and chronology, July-August mean temperature were chosen for calibration. Five lagged chronologies of t-2, t-1, t, t+1, t+2 years were tried first for the predictors in the stepwise regression, but only one predictor (chronology at t-1) was finally entered into the regression. The lagged predictor results from high autoregression in the chronology. We did not prewhiten the chronology in order to preserve low-frequency variation as much as possible. Final calibration equation for the reconstructions was as follows.

$$T_{J\text{-}A} = 21{\cdot}814 + 2{\cdot}980\ ALL_{t-1}$$

Calibration		Verification				
Period	R^2	Period	r	RE	Sign Test	PMt
1909-1949	0·23*	1953-1995	0·299*	0·05	27/14*	0·267

*R^2 is the square of the correlation coefficient calculated between actual and estimated data; r is the actual/estimated correlation over the verification period; RE is the reduction of error; Sign-test is the sign of paired observed and estimated departures from the mean on the basis of the number of agreements/disagreements; PMt is the t value derived using the product mean test (Fritts, 1976). * $p<0{\cdot}05$, ** $p<0{\cdot}01$.

Fig. 5—Calibration and verification statistics computed for tree-ring and the mean temperature of July to August for two sub-periods. The sub-periods 1909-1949 and 1953-1995 were used for calibration and verification, respectively.

where $T_{J\text{-}A}$ is the mean July-August temperatures; ALL_{t-1} is the ring-width index data at year t-1 for the mean chronology of Mt. Sorak Korean pine.

The calibration and verification statistics are summarized in Fig. 5. Despite the relatively low quality of the calibration ($R^2 = 0{\cdot}23$), all verification tests were significant. The RE (reduction of error), considered as the most rigorous test (Fritts *et al.*, 1990), was larger than zero, which is roughly equivalent to a 95 confidence level for n=20. The verification results indicated the reliability of the reconstruction.

The complete reconstruction is plotted in Fig. 6. Though the reconstruction was made since 1657 AD, the plot was truncated at 1700 AD prior to which sample depth is low. The reconstructed summer temperature (Fig. 1) shows that alternating periods of generally cool and generally warm conditions are typical in summer in central Korea. It indicates also that the 1700-1730 and 1830-1850 were coolest in the last 300 years.

The ancient rain-gauge data in Seoul (1770-1910 AD) records the period 1830-1840 as the wettest period during the last two centuries (Wada, 1917). Highest annual precipitations in the ancient and modern records in Seoul were found in 1839 (3220 mm), 1879 (3148 mm), 1821 (3186 mm) and 1832 (2744 mm). The heavy rains in July brought major floods in 1821 (1410 mm) and in 1832 (1426 mm), which were even much higher than annual mean precipitation (about 1300 mm) (Wada, 1917). In Japan, also very heavy rainfalls brought floods in 1830s (Mikami, 1992). Late 1830s was found one of coolest and wettest summer periods in Northeastern and Central Japan in a study based on the daily weather records in old diaries (Kim, 1992; Mikami, 1992). The present reconstruction indicates that 1840, 1841 and 1842 were the coolest years in the central Korea in the last 300 years. Previous dendroclimatic study also indicated that the years of 1841 and 1842 were coolest years in the same region. We conclude that the 1830-40s cool anomaly is not local but regional aspect, at least in east central Korea.

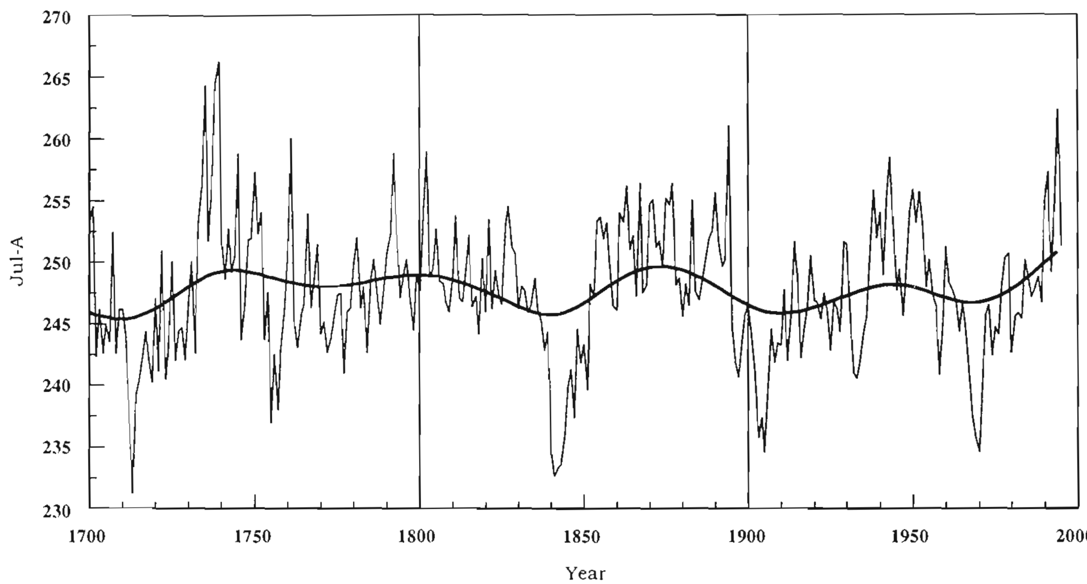

Fig. 6—Reconstructed July-August mean temperature variation. (Y-axis: x 10 celsius degree, bold line is 80-year spline filter)

The warm trend in summer temperature was not found in the last 20th century. In a dendroclimatic study, the warm trend found in the 20th century was less pronounced than the cool periods in the previous centuries. Both studies confirm that the summer-temperature warming trend in central Korea during the 20th century is not obvious.

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Effects of climate on radial growth of *Picea meyeri* in semi-arid grassland, north China

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ABSTRACT

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Dendroclimatic assessment of *Picea meyeri* Rehd. et Wils was carried out on the sandy land in semi-arid Inner Mongolian grassland. Response function analysis was performed to identify climate-growth relationships for *P. meyeri*. The growth of *P. meyeri* exhibits a positive relationships with precipitation in current February and May as well as in prior September. Furthermore, it is showed that several variables among mean monthly temperature and total monthly precipitation from September of current year to August of preceding year can explain about 70% of the variance in the tree-ring width. The results reveal a greater sensitivity of this species to climate conditions in this area, suggesting that *P. meyeri* is a suitable species for dendroclimatic studies.

Key-words—*Picea meyeri*, Dendroclimatology, Semi-arid grassland.

उत्तरी चीन के अर्द्ध शुष्क अन्तर्वर्ती मंगोलियाई घास स्थल में *पाइसिया मीयेरी* की परिधीय वृद्धि पर जलवायु के प्रभाव

एर्युआन लिआंग एवं स्यूमेई शाओ

सारांश

अर्द्धशुष्क अन्तर्वर्ती मंगोलियाई घास स्थल में बलुई स्थल पर *पाइसिया मीयरी* रेड. एट् विल्स का वृक्षजलवायुविक निर्धारण किया गया। *पी. मीयेरी* हेतु जलवायु-वृद्धि सम्बन्धों के अभिनिर्धारण के लिए सहसम्बन्धन फलन विश्लेषण किया गया। *पी. मीयेरी* की वृद्धि वर्तमान फरवरी एवं मई माह तथा सितम्बर के पूर्ववर्ती दिनों में वर्षण की सकारात्मक सम्बद्धता प्रदर्शित करती है। इसके अतिरिक्त यह भी देखा गया है कि पिछले वर्ष के अगस्त माह तथा वर्तमान वर्ष के सितम्बर माह में मासिक औसत तापमान तथा कुल वार्षिक वर्षण के मध्य प्राप्त अनेक प्रसरण वृक्ष वलय चौड़ाई में लगभग 70% प्रसरण की व्याख्या करते हैं। ये परिणाम इस क्षेत्र में इन प्रजातियों की जलवायुविक स्थितियों के प्रति अधिक संवेदनशीलता प्रदर्शित करते हैं, जिससे प्रस्तावित होता है कि *पी. मीयेरी* वृक्षजलवायुविक अध्ययन हेतु एक उपयुक्त प्रजाति है।

संकेत शब्द—*पाइसिया मीयेरी*, वृक्षजलवायुविकी, बलुई भूमि, अर्द्ध शुष्क घासस्थल.

INTRODUCTION

PICEA meyeri Rehd. et Wils is a predominant community of coniferous forest in the mountainous regions in north China. In semi-arid grassland of the Xilin River Basin, Inner Mongolia it has reached the upper latitude margin of its natural range (Zhao *et al.*, 1988). As a climatically relict species, *P. meyeri* forms a special forest landscape on sandy land in semi-arid grassland (Cui & Kong, 1992; Li *et al.*, 1988), which is dominated by perennial dry grass species, such as *Leymus chinensis* and *Stipa grandis*. Thus, small patch of *P. meyeri* forest offers a unique opportunity to conduct dendroclimatic research in the Xilin River Basin. An evaluation of cross-dating characteristics and the responses to climate of unstudied species is the first step in assessing the potentiality of such trees in dendroclimatology (Yasue *et al.*, 1996). In the present study, response function is applied to evaluate the dendroclimatic potential of *P. meyeri* in the Xilin River Basin.

MATERIAL AND METHODS

A small portion of *P. meyeri* natural pure stands (about 2 ha) is located in the north-facing slope of one sand dune (43°42'N, 116°54' E, Elevation 1400 m) (Li *et al.*, 1988). Cambial activity of *P. meyeri* at this elevation and latitude commences at the end of April or the beginning of May (Xu & Zou, 1998; Zhao *et al.*, 1988). *P. meyeri* prefers wet and cold climate in mountainous regions, as a result, spruce growth ceases in August coinciding with high temperature and strong evapotranspiration in this region (Xu & Zou, 1998). The canopy coverage of *P. meyeri* reaches 0·20-0·40 and the height ranges from 5 to 10 m. Soil is woodland sand soil including 80% SiO_2 and low organic matter.

Climatically, this area belongs to continental middle temperate semi-arid zone (Chen, 1988). Winter is cold and dry, while summer is warm and wet. The mean annual temperature is about -0.4°C; the mean of the coldest month, January, is -19.5°C; and one of the warmest month, July, is 20.8°C. On average, the area has 5 months with mean temperature 35°C, May through September, which approximates the length of the growing season. The annual precipitation is about 350 mm and 60–80% of the rainfall occurs in June, July and August. Moreover, this region is characterized by very wide fluctuations in precipitation between year ranging from 150 to 560 mm per year. The annual evaporation is about 4-5 times greater than the total annual precipitation.

Total 42 cores from 21 trees were taken with an increment borer at breast height in opposite directions. All cores were mounted, sanded, and visually cross-dated (Stokes & Smiley, 1968). The ring widths were measured to the nearest 0·01 mm using a linear digitizing tablet coupled to a computer. Then the absolute dating was subsequently verified statistically using COFECHA program (Holmes, 1983). All cores with potential errors were rechecked and corrected if possible. Finally, 3 Cores that showed low correction values with the master chronology were excluded from the site chronology. The measurement series were individually detrended with a cubic smoothing spline (30-years 50% frequency response) to remove tree specific growth trend that resulted from age and size difference, and competition effects of tree growing in closed canopy conditions. The ring-width measurements of each core were divided by the fitted spline values to produce a standardized tree ring series for each core. These individual dimensionless index series were then averaged together using a biweight robust mean to construct a mean standardized chronology (Holmes, 1983; Cook & Kairiukstis, 1990).

Response function analysis was performed to identify the months in which the strongest relation between climatic variables (monthly precipitation and temperature) and growth occurs (Fritts, 1976). For the final analysis, we modelled *P. meyeri* index chronology with the most influential climate variables using multiple regression (Grissino-Mayer & Butler, 1993). The climatic data were from the nearby Xilin Hot Meteorological Station (43°57' N° 116° 04' E), including total monthly rainfall (in mm), average monthly temperature (°C). 5 months of the prior year were used in addition to the data of January through September during the current year. The analyzed period was 1954 to 1994, which was the length in common between the climate record and the chronology. The significantly influenced months were determined at the 95% confidence level.

RESULTS AND DISCUSSION

Primary assessment of chronological characters

One 65-year standardized chronology ranging from 1930 to 1994 was developed and no missing ring was observed in all cores (Fig. 1). The analysis of variance of standard chronology for the period from 1955 to 1994 AD indicated that mean correlation between trees 0·46 and Mean sensitivity 0·18, which is enough to obtain accurate results with response function methods (Rolland, 1993). Relatively high signal-to-noise ratio and percentage of variance accounted for by the first principal component of tree ring index further suggested the suitability of *P. meyeri* standard chronology for climate analysis.

Response function analysis

Response function analysis shows that the precipitations in both February, May of the current year and September of preceeding year are significantly correlated with *P. meyeri*

	Actual	Standardized
Samples Cores/Trees	42/20	39/19
Mean ring width mm	2·500	—
Standard deviation	0·749	0·160
Mean sensitivity	0·245	0·180
First order autocorrelation*	—	-0·019
Mean correlation among all radii*	—	0·474
Mean correlation between trees*	—	0·466
Agreement with population chronology*	—	0·933
Signal-to-noise ratio*	—	13·981
Variance due to first eigenvector (%)*	—	50·12

Fig. 1—General statistics for actual and standardized chronology of *Picea meyeri*. Calculation for the common interval from 1955 to 1994 is indicated by an asterisk.

growth (Fig. 2B). However, no significant relationship can be observed between radial growth and mean monthly temperatures (Fig. 2A).

February precipitation appears to impose a positive effect on radial growth. There are some reports that spring snowfall is close linked to radial growth (Payette *et al.*, 1996; Peterson & Peterson, 1994). However, the significant effect of February

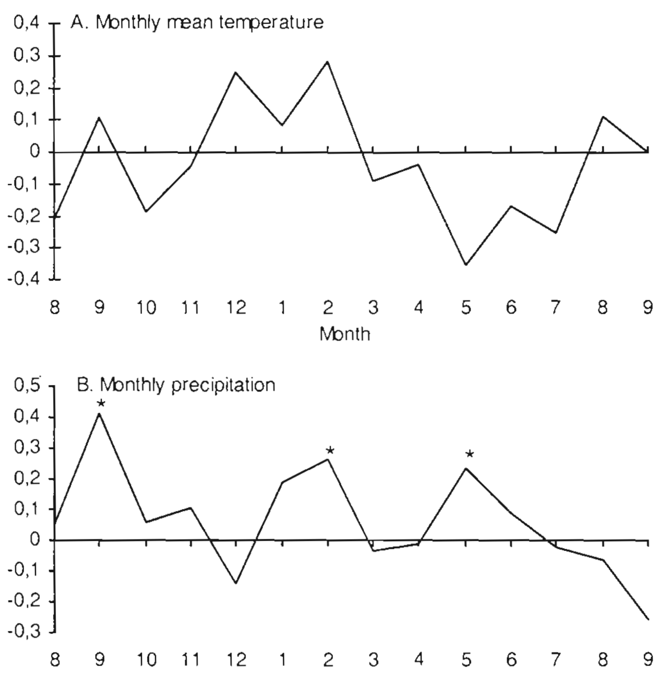

Fig. 2—Response functions for annual tree-ring growth in response to monthly mean temperature (A) and total monthly precipitation (B) from August of the previous year to September of the current year. Vertical scales are dimensionless standardized units.

snowfall cannot be physiologically explained, since the amount of February precipitation is negligible in the Xilin River Basin.

Monsoon rain does not occur in May. Moreover, the prevailing northern and northwestern winds in May probably increase the desiccating effects of the summer heat, resulting in the lowest air humidity in whole year in the Xilin River Basin (Chen, 1988). Soil dryness inversely affects plant growth at all habitats (Oberhuber *et al.*, 1998). In this region with a temperate climate, cell division is usually greater at the beginning of cell distribution phase (early summer) (Hughes *et al.*, 1994), and this is probably the period in which more earlywood is formed. Thus strong moisture stress in May might limit earlywood formation and hence total ring width reflecting the positive influence of the rainfall in May on ring width.

Positive correlation is also evident between spruce growth and precipitation from prior August to prior October, particularly the precipitation in previous year's September. However, other dendroclimatic studies in north China (Hughes *et al.*, 1994; Kang *et al.*, 1997; Liu & Ma, 1999; Shao & Wu, 1994 a, b, 1997 ; Zhang & Wu, 1992, 1997) failed to reveal this phenomenon, which suggests that it is mainly related to sandy substrate in this stand and phenological characters of *P. meyeri* as well as semi-arid climate in the Xilin River Basin. The evapotranspiration decreases obviously in August (Xu & Zou, 1998), while the rainfalls during these 3 months still account for 1/3 of the total annual rainfall. Hence the sandy land forms less surface runoff and can effectively prevent soil water from evaporation relative to grassland chestnut soil (Li *et al.*, 1988). Higher precipitation during this period might likewise control water availability in early spring (Bhattacharyya & Yadav, 1990). The water reservation is crucial for early cambial activity because low rainfall prevails in spring in the Xilin River Basin.

Multiple regression analysis

Because growth of *P. meyeri* is closely associated with climate, we try to describe ring width variation of *P. meyeri* with linear multiple regression. The best model includes 7 climate variables, which produces an R^2 of 0·707. The F-

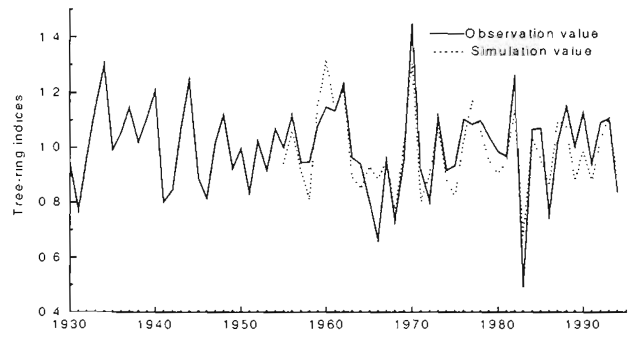

Fig. 3—Time series analysis of tree-ring indices of *Picea meyeri*.

statistic for the model is 11·00 (P<0·05). The model is: $I = 0.743 + 0.00406 R9 + 0.00441 P5 + 0.00277 P6 + 0.0124 T2 - 0.000847 R7 - 0.0323 T5 + 0.0321 T6$.

P5, P6, T5, T6: Total precipitation and mean temperature in current May and June;

R7, R9: total precipitation in prior July and September;

T2: mean temperature in current February.

Predicted tree-ring width index series from 1955 to 1994 against the actual observed values is plotted in Fig. 3. The dotted line representing the simulated values is quite similar to the observed values, which indicates that *P. meyeri* standardized chronology bears a high potential for climate reconstruction in semi-arid grassland of the Xilin River Basin, Inner Mongolia.

CONCLUSION

The present study suggests that *P. meyeri* is a promising species for dendroclimatic studies and a suitable source for the reconstruction of climate-tree growth relationships because of good cross-dating characters and its high sensitivity to the precipitation. The development of *P. meyeri* chronology filled the gap of dendroclimatic investigation in semi-arid grassland, north China. A forthcoming study will identify the linkage between *P. meyeri* chronology in the Xilin River Basin with other chronologies from semi-arid sites in north China, and investigate their spatial response to climate.

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Variability of seasonal $\delta^{13}C$ patterns in Apache Pine from Southern Arizona, USA

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ABSTRACT

Leavitt SW & Baisan CH 2001. Variability of seasonal $\delta^{13}C$ patterns in Apache Pine from Southern Arizona, USA. Palaeobotanist 50(1) : 117-123.

Seasonal $\delta^{13}C$ changes observed in tree rings offer the potential of reconstructing environmental conditions at finer than annual resolution. In the American Southwest, an opportunity to better expose environmental influences on tree-ring $\delta^{13}C$ at seasonal scales is fortuitously afforded by the presence of a time marker within rings. The strong winter-summer bimodal precipitation distribution is conducive to formation of a false-latewood band in the middle of the growing season, approximately June, after which normal growth usually resumes to the end of the growing season. The variability in seasonal $\delta^{13}C$ patterns in the 1991-1993 growth rings of two Apache pine (*Pinus engelmannii*) containing these false rings was investigated by descriptive comparison (1) between radii in a tree, (2) between different vertical heights in the trunks of both trees, and (3) between trees. The patterns of seasonal $\delta^{13}C$ change in tree-ring cellulose were broadly similar between radii, but with differences in amplitude and differences in absolute values of up to nearly 2‰. Between trees, the isotopic patterns were quite similar: concave downward for 1991 and 1993, and continuously increasing in 1992. There were differences of *ca.* 0·5‰ among patterns at different heights within a tree, but there was no common gradient in the isotopic change with height. Comparison of the seasonal patterns with environmental variations suggests that they are more tightly linked to moisture conditions than to temperature or changes in atmospheric $\delta^{13}C$.

Key-words—Tree rings, Carbon isotopes, Drought, *Pinus engelmannii*, False rings, Latewood.

अमरीका के दक्षिणी एरीज़ोना प्रान्त से प्राप्त अपाचे चीड़ में मौसमी $\delta^{13}C$ विन्यास का वैविध्य

स्टीवन डब्ल्यू. लीविट एवं क्रिस्टोफ़र एच. बाइसन

सारांश

वृक्ष वलयों में देखे गए मौसमी $\delta^{13}C$ परिवर्तन वार्षिक वियोजन की अपेक्षा अधिक उत्कृष्ट पर्यावरण स्थितियों के पुनर्सृजन हेतु आधार प्रदान करते हैं। दक्षिण-पश्चिमी अमरीका में वलयों के भीतर समय सूचक चिह्नकों की उपस्थिति से मौसमी पैमाने पर $\delta^{13}C$ वृक्ष वलयों में बेहतर पर्यावरणीय प्रभाव जानने हेतु एक उत्कृष्ट अवसर प्राप्त हुआ है। मजबूत शीत-ग्रीष्म द्विबहुलकीय (बाइमोडल) वर्षण वितरण वृद्धि के मौसम के मध्य में सम्भवतः जून माह में कूट पश्चदारु पट्टिका (बैण्ड) के निर्माण हेतु अनुकूल है, जिसके पश्चात वृद्धि के मौसम के अन्त में सामान्य वृद्धि सामान्यतः आरम्भ होती है। इन कूट वलयों से युक्त दो अपाचे चीड़ (*पाइनस इन्जेलमैनाइ*) के सन् 1991-93 ई. के वृक्ष वलयों में मौसमी $\delta^{13}C$ विन्यास में वैविध्य (1) एक वृक्ष के त्रिज्याओं के मध्य, (2) दो वृक्षों के स्तम्भों में भिन्न-भिन्न ऊर्ध्वाधर ऊँचाइयों के मध्य, तथा (3) वृक्षों के मध्य विस्तृत तुलना द्वारा खोजा गया है। वृक्ष वलय सेलुलोज़ में मौसमी $\delta^{13}C$ परिवर्तन के विन्यास प्रायः त्रिज्याओं

के मध्य एक समान हैं, परन्तु वृक्षों के मध्य आयाम में परिवर्तन एवं लगभग 2‰ तक एकल मान में परिवर्तनों के साथ हैं। समस्थानिक विन्यास पूर्णतः एक समान अर्थात वर्ष 1991 हेतु अवतल अधोमुखी तथा वर्ष 1992 में वृद्धिगामी हैं। वृक्ष के भीतर विभिन्न ऊँचाइयों में विन्यासों के मध्य सी.ए. 0·5‰ की भिन्नताएँ हैं, परन्तु ऊँचाई के साथ समस्थानिक परिवर्तन में कोई उभयनिष्ठ प्रवणता (ग्रेडिएन्ट) नहीं है। पर्यावरणीय विविधता के साथ मौसमी विन्यासों की तुलना से प्रस्तावित होता है कि ये तापमान अथवा वातावरणीय $\delta^{13}C$ तापमान में परिवर्तन की अपेक्षा आर्द्र स्थितियों से अधिक सघनतः सम्बद्ध हैं।

संकेत शब्द—वृक्ष वलय, कार्बन समस्थानिक, अनावृष्टि, *पाइनस एन्जिलमैनाइ*, कूट वलय, अग्र दारु.

INTRODUCTION

MEASUREMENTS of stable-carbon isotopic composition ($\delta^{13}C$) of successive growth increments in leaves (Leavitt & Long, 1982; Lowden & Dyck, 1974; Smedley *et al.*, 1991; Tieszen & Boutton, 1989) and tree rings (Leavitt & Long, 1982, 1985, 1991; Leavitt, 1993; Loader *et al.*, 1995; Ogle & McCormac, 1994; Walcroft *et al.*, 1997; Wilson & Grinsted, 1977) exhibit seasonal changes, perhaps containing a climate signal. For example, empirical results of seasonal intra-ring $\delta^{13}C$ patterns from several field studies (Leavitt, 1993; Leavitt & Long, 1991; Livingston & Spittlehouse, 1996) suggest that soil water conditions, presumably influencing stomatal conductance, are frequently the primary driving mechanism for the seasonal $\delta^{13}C$ observed in tree rings. This is consistent with carbon isotope fractionation models (Farquhar *et al.*, 1982; Francey & Farquhar, 1982) that indicate in addition to $\delta^{13}C_{air}$ of atmospheric CO_2, plant $\delta^{13}C$ is influenced by rates of stomatal conductance and photosynthetic assimilation, both of which can be affected by environmental factors.

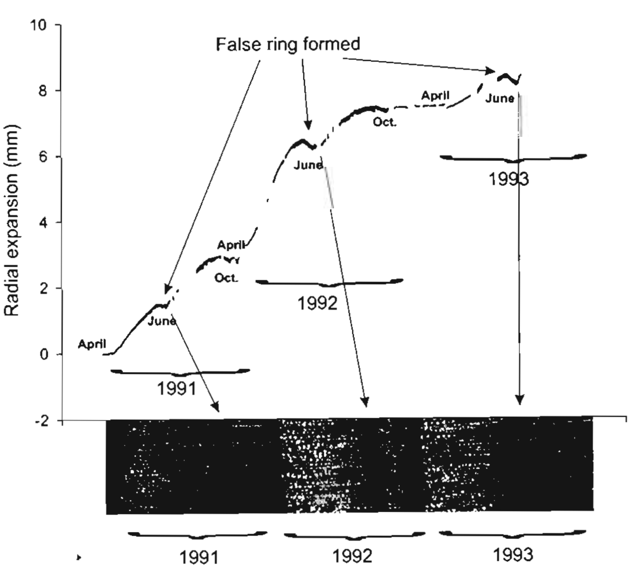

Fig. 1—The 1991-93 daily stem size progression of a nearby *Pinus englemannii* tree monitored by dendrometer, along with photomicrograph of corresponding cell-size patterns. Growth hiatus and stem shrinkage in the second half of June occurs as the false ring (arrows) is formed. Missing data was interpolated.

The southwestern U.S. experiences precipitation from winter frontal storms and summer monsoon airmasses. The late spring-early summer interval between these bimodal precipitation peaks is hot and arid, contributing to the frequent formation of a false latewood band ("false ring") prior to mid-summer re-initiation of cambial growth (Fig. 1). This false latewood provides a time marker (representing approximately the very end of June and beginning of July) with which to more precisely explore timing of correlation between isotopic composition and climate.

The presence of the time marker also offers the potential to help resolve remaining uncertainties about seasonal isotopic patterns in tree rings, including the period they represent and the fidelity of their signal at different locations in a tree. This study expands previous baseline isotopic work on seasonal $\delta^{13}C$ variation in ponderosa pine species in the Southwest, USA (Leavitt *et al.*, 1998, 1999), by exploring seasonal variation of $\delta^{13}C$ in tree rings from different radii, in different years and at various heights in which the false-latewood band is in different locations within the ring or not present at all.

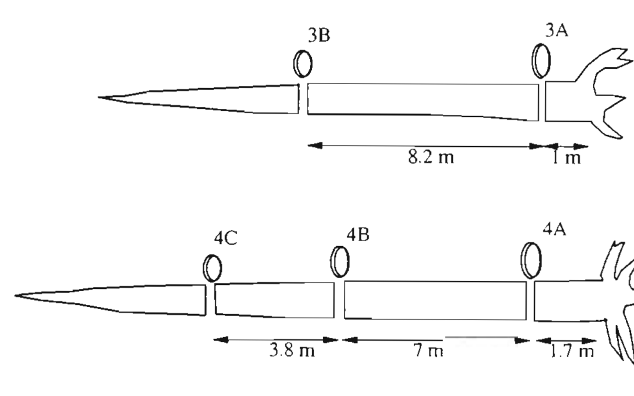

Fig. 2—Location of cross-sections sampled from two trees deposited in flood debris at the lower Rhyolite Canyon Site.

METHODS

The Lower Rhyolite Canyon Site in Chiricahua National Monument (elevation *ca.* 1620 m; location ca. 32·00°N, 109·35°W), southeastern Arizona, was visited on 1 December 1994 to sample Apache pine (*Pinus engelmannii*) trunks of dead trees that had been deposited with debris in and near the streambed by major flooding that occurred the last few days of August 1993. These tree trunks had the disadvantage that we did not know their exact provenience, but it was probably in the lower reaches of the canyon just upstream from the site. It had the advantage that we were free to sample as much material as needed. We sampled cross-sections from different heights of two mature trees (Fig. 2).

The cross-sections were surfaced to enhance growth ring recognition, and the outer rings were cross-dated. Two opposite radii were sampled from each cross-section to minimize effects of circumferential isotope variability (Leavitt & Long, 1984, 1986). The 1991, 1992 and 1993 rings from each radius were sampled by subdividing each ring into 4 equal parts with a razor knife under magnification. The subdivisions from the 2 radii from section 4C were processed separately to determine the extent of circumferential variability. Additionally, the subdivisions from each radial pair (including replicate radial samples from 4C) were pooled to a single series of samples from each cross-section. The holocellulose component of each segment was isolated from ground wood (20-mesh) by removing extractives with toluene-ethanol, treating with hot water, and delignifying in an acetic acid-acidified sodium chlorite solution (Leavitt & Danzer, 1993). Holocellulose was combusted to CO_2 in the presence of excess oxygen in a recirculating microcombustion system. The CO_2 was measured mass-spectrometrically and results are expressed as $\delta^{13}C$ (=$[((^{13}C/^{12}C)_{sample} \div (^{13}C/^{12}C)_{standard}) - 1] \times 1000$) in permil (‰) with respect to the international PDB standard (Craig, 1957). Repeated combustion and analysis of a holocellulose laboratory standard during the study gave a standard deviation of 0.27‰. This value is larger than the long-term reproducibility for analysis of the laboratory standard (*ca.* 0.2‰), but it is still quite satisfactory to distinguish and compare the isotopic patterns in this study.

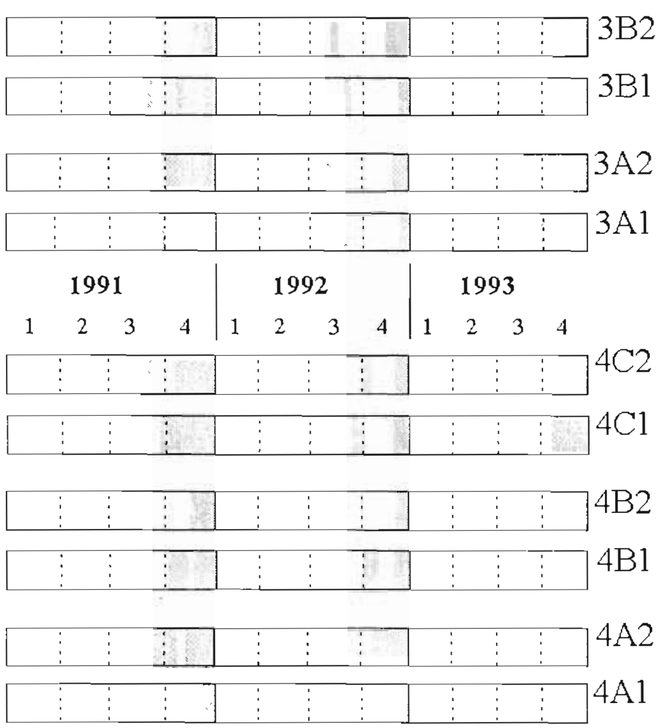

Fig. 3—Position of latewood bands (indicated by shading) in each of the tree rings, with growth proceeding from left to right. The rings were not actually the same width but the 4 subdivisions in each ring (dotted lines) were approximately equal width.

RESULTS AND DISCUSSION

The position of false latewood and latewood bands within each of the radial samples is depicted in Fig. 3. A false-latewood band appears in the majority of the rings, but it was not clearly identifiable in about 25% of the rings. The presence of false rings and at least partial latewood in most of the 1993 rings indicates that this year's xylem growth had nearly been completed by the time of the catastrophic flood. When present, the false-latewood band was always situated in either subdivision 3 or 4. In cross-sections 4A and 4B, false rings in all 3 years were obvious in only one of the two radii. The abundance of false rings in the cross-sections from higher in the trunk is consistent with observations by Fritts (1976) showing a trend of increasing occurrence of false rings with height in a ponderosa pine tree from Flagstaff, Arizona, USA.

The potential value of sampling more than one radius is underscored in the seasonal $\delta^{13}C$ results from the two opposite radii of cross-section 4C (Fig. 4). For the 1992 ring, the patterns are very similar and the absolute differences are small (<1‰). For the 1993 ring, however, the seasonal isotopic shifts are larger in radius 2, and the absolute differences between radii are 1-2‰ for most subdivisions. Many studies have found circumferential variability in the range of 0·5-1·0‰ (Francey, 1981; Leavitt & Long, 1984, 1986; Ramesh *et al.*, 1986) or 1-1·5‰ (Sheu *et al.*, 1996; Stuiver *et al.*, 1984), with variability up to 5‰ reported in the extreme (Tans & Mook, 1980). The mean of the radii at 1·7 m for 1993, however, appears to be fairly representative as suggested by its similarity to the 1993 patterns from the other 2 cross-sections of tree no. 4 and those of tree no. 3 (Figs 5 & 6).

The seasonal $\delta^{13}C$ patterns at most heights are quite similar, with some differences in absolute values (Figs 5 & 6). In tree no. 3, there is the suggestion that higher levels in the tree (8·2 m) are generally less negative than at 1m. In tree no.

4, however, only the 1992 ring shows increasing $\delta^{13}C$ from 1·7 m to 8·7 m to 12·5 m; for the 2 other years the 1·7 m height is most negative, but the 8.7 m height is least negative. Under some circumstances, more negative isotopic values have been found in the foliage of lower branches (Broadmeadow & Griffiths, 1993; Heaton & Crossley, 1995; Medina & Minchin, 1980; Medina *et al.*, 1991; Schleser & Jayasekera, 1985; Sternberg *et al.*, 1989) as a consequence of low light level reducing rates of photosynthesis and the contribution of isotopically light respired CO_2 mixing with the air below the canopy. Within tree rings, vertical $\delta^{13}C$ variability has been typically found in the range of 0·5-1·5% (Heaton, 1999; Leavitt & Long, 1986; Robertson *et al.*, 1995; Schleser, 1992), usually with ambiguous gradient with height. Integrated photosynthetic products dominantly from the upper crown would supply most of the ring development in the trunk, so that gradients are less likely than for leaves, unless there are some lower branches with leaves contributing a significant amount of carbon to part of the associated trunk.

The isotopic patterns for each year are not only consistent among heights in a tree, but they are also consistent between trees, although the $\delta^{13}C$ values of tree no. 3 are generally more negative than tree no. 4. The 1991 and 1993 rings are characterized by a seasonal pattern of increasing $\delta^{13}C$, generally to a maximum in subdivision 3 and then a sharp decline to subdivision 4. Because the false-latewood band is located in subdivision 4 or late in subdivision 3 of these years, the increasing $\delta^{13}C$ of subdivisions 1-3 would be consistent with increased moisture stress through spring and early summer prior to the monsoon onset. The drought relief following monsoon initiation would then be associated with the decline in $\delta^{13}C$. The 1992 ring of both trees shows increasing $\delta^{13}C$ generally sustained over all four subdivisions. This suggests that even after the onset of monsoon-related precipitation, moisture stress persisted. In a related study, living pine trees cored at breast height in 1996 from the lower Rhyolite Canyon in the Chiricahua Mts. (Leavitt *et al.*, 1999) showed similar patterns: $\delta^{13}C$ initially increasing to false-latewood and then decreasing for 1991 and 1993, and increasing throughout the growing season for 1992. The decline at the end of 1993 tended to be larger than in this study, again suggesting that the 1993 ring is not quite complete. In the other study, however, 3 unequal subdivisions were sampled including one after the false-latewood band that contained true latewood and the large-tracheid xylem immediately after the false ring, one containing the false ring, and the third prior to the false ring.

The average monthly climate conditions of the 3 study years (Fig. 7) provide insight into the prevailing environmental conditions at this site. Although the 1991-92 winter seems to have been somewhat cooler than the following winter, minimum and maximum temperatures during the 3 growing seasons do not exhibit distinctive differences. Palmer Drought Severity Index (PDSI) is an integrated climate index representing water status, with values of zero indicative of normal moisture conditions. Numbers above zero are progressively wetter and below zero progressively drier, with –4 being an "extreme" drought condition. The moisture status in 1991 and 1992 is driven largely by winter conditions, with PDSI decreasing from spring to late fall. In 1993, the declining PDSI is interrupted by a major abrupt increase in August. At the Chiricahua National Monument visitor center (near sampling site), it rained *ca.* 25 cm in August distributed over 23 of the 31 days, including 13.1 cm over the last 7 days (with 4.3 cm on the last day). A rainguage in the upper watershed recorded >17 mm on the last 2 days of August alone. The high and sustained August rainfall probably contributed to the strong upturn of PDSI from *ca.* –1 to +1.5.

Many of the features of these isotopic patterns are remarkably consistent with this climatology. The 1991 seasonal tree-ring $\delta^{13}C$ pattern records the monsoon onset with

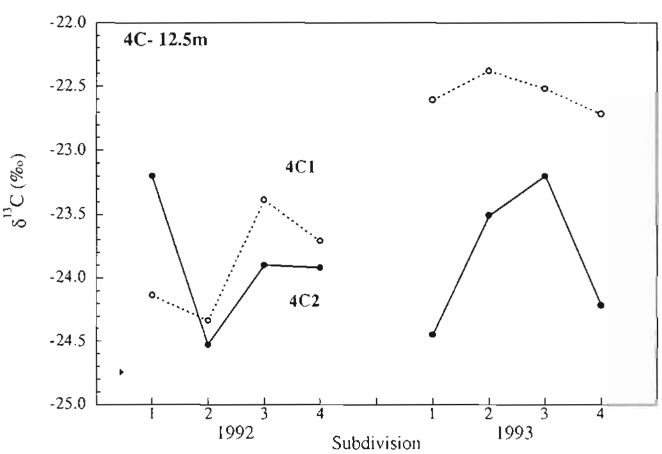

Fig. 4—Isotopic composition of the 1992 and 1993 rings along two opposite radii of the cross-section at 12·5 m above the root crown in Fig. 2.

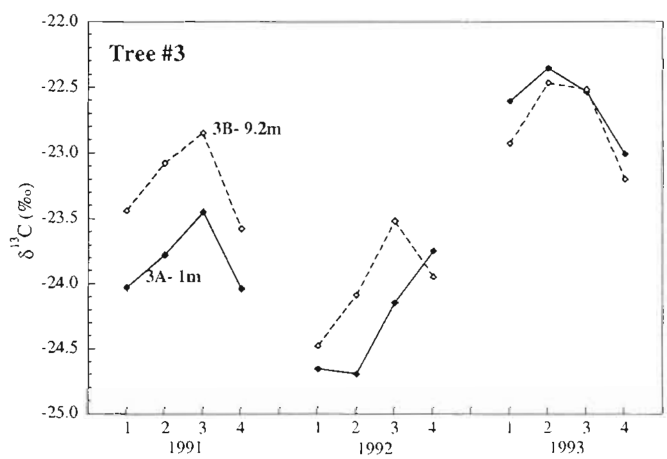

Fig. 5—Seasonal $\delta^{13}C$ patterns in growth rings of tree no. 3 at 1 m and 9·2 m heights in trunk.

declining $\delta^{13}C$ in subdivision 4, even though the monsoon moisture is not sufficiently above normal to increase PDSI. In 1992, the onset of declining spring PDSI was delayed until June, perhaps displayed in the 1992 first subdivision being much more negative than that in 1991 or 1993. Additionally, PDSI declines to lower values at the end of 1992 than either 1991 or 1993, consistent with the continued increase in $\delta^{13}C$ in subdivision 4. Depending on when the trees were killed by flooding, the $\delta^{13}C$ decline in subdivision 4 of the 1993 ring could represent the influence of the sustained August precipitation. Had the trees survived, subdivision 4 may likely have become much more negative than exhibited in our chronology. Also, the first subdivision in 1993 begins at a much less negative value than either 1991 or 1992, consistent with the relatively low spring PDSI values that were already starting to decline after February.

Because $\delta^{13}C_{air}$ can also influence $\delta^{13}C$ of the tree rings, the $\delta^{13}C_{air}$ values (Trolier *et al.*, 1996) at the closest air monitoring site (Niwot Ridge, Colorado, 40.05°N, 105.63°W) were also examined. For 1991-1993, the seasonal $\delta^{13}C_{air}$ fluctuated from *ca.*

−7.65‰ to −8.10‰, representing a range generally lower than the 0.5-1.0 ‰ seasonal variation seen in Figs 5 and 6. The most negative values are in March-April and the least negative values are in August-September. Furthermore, the other tree rings from living trees in Chiricahua National Monument (Leavitt *et al.*, 1999) show an amplitude of seasonal variation from 0.5-1.2‰ for 1991-1993, and 0.5-1.5‰ for 1985-1995. The $\delta^{13}C_{air}$ of local CO_2 undoubtedly contributes to $\delta^{13}C$ of tree rings at lower Rhyolite Canyon, but if Niwot Ridge is representative of the air in southeastern Arizona then it is probably not a first-order effect in the seasonal patterns.

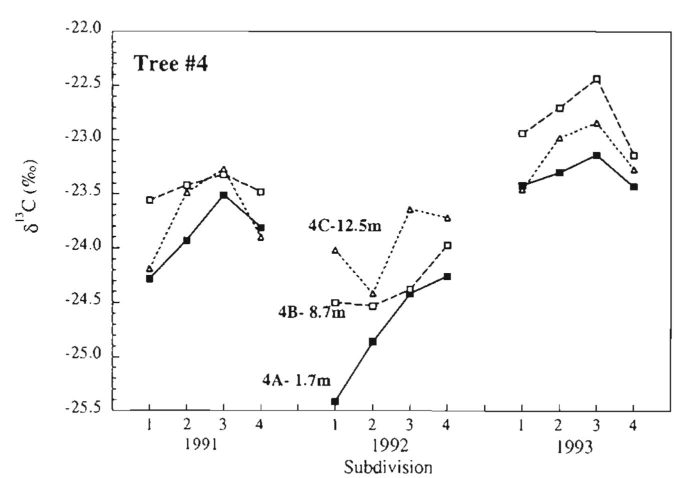

Fig. 6—Seasonal $\delta^{13}C$ patterns in growth rings of tree no. 4 at 1·7 m, 8·7 m and 12·5 m heights in trunk.

CONCLUSIONS

Seasonal tree-ring $\delta^{13}C$ patterns generally have the same shape at different heights, although there are differences in the absolute value and amplitude. This supports sampling all trees at a similar height for a seasonal isotope study.

Uncertainties remain about the exact provenance of both trees. However, the trees show both coherent patterns and similar variations in absolute values over the 3-years period.

The changing absolute values of $\delta^{13}C$ in successive years and the seasonal patterns within each of the 3 years seem best explained by records of drought index and rainfall when supplemented by knowledge of the location of the false ring within each series of subdivisions.

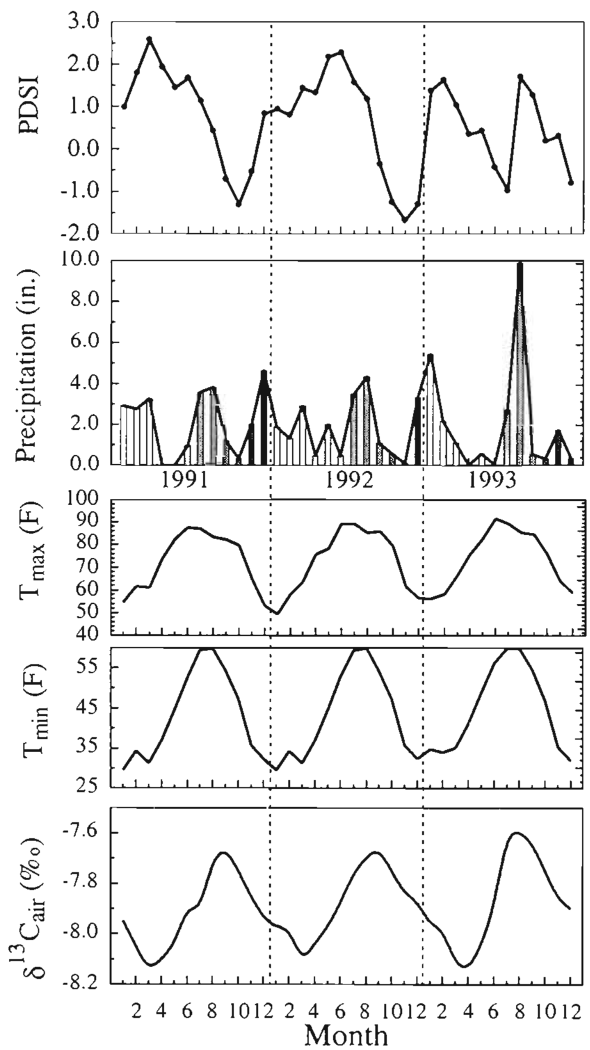

Fig. 7—The $\delta^{13}C_{air}$ of atmospheric CO_2 collected at Niwot Ridge, Colorado (after Trolier *et al.*, 1996), and Chiricahua National Monument climate station monthly mean minimum and maximum temperatures, monthly total precipitation, and Palmer Drought Severity Index (PDSI) for 1991 through 1993.

The $\delta^{13}C_{air}$ of local CO_2 should contribute to the tree-ring isotopic composition but the record available from Niwot Ridge, Colorado, exhibits seasonal variability of *ca.* 0.4‰ that is about one-half of the average seasonal tree-ring isotope variability and the shift may not be synchronous.

The seasonal trends contain environmental information, and given time constraints such as provided by false rings, the environmental information may be more fully exploited. An additional contributing factor, yet to be resolved, is the timing of xylem tracheid expansion versus construction of the cell wall, i.e., although the initial false-latewood cell formation may be timed in response to pre-monsoon hyper-arid conditions, the bulk of cell-wall thickening could occur in subsequent days/weeks. A large lag in these two events would necessitate development of empirical models based on environmental data specific to the period of the bulk of cell-wall formation rather than for the period at which the cells are initially expanded.

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Preliminary relationships between climate and the apical extension, needle production and ring width of *Pinus ponderosa* in Arizona, USA

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ABSTRACT

Hemming D, Jalkanen R & Leavitt SW 2001. Preliminary relationships between climate and the apical extension, needle production and ring width of *Pinus ponderosa* in Arizona, USA. Palaeobotanist 50(1) : 125-131.

Measurements of apical extension (height increment), needle production and ring width from a detailed sequence of measurements on one *Pinus ponderosa* tree from the Santa Catalina Mountains, southern Arizona, USA for the period 1962-1998 are presented. From these measurements the relationships between tree age and height, and tree height and diameter at breast height are determined. These are compared with the overall site trends for the same relationships determined from height and basal age of individual trees, and the site ring width chronology to test whether the growth of the individual tree is comparable with that of other trees at the study site.

Needle production and apical extension are highly correlated (r = 0·67) and show generally similar climate correlations. Ring widths are not significantly correlated with either of these series but all three series are significantly positively correlated with precipitation and dew point temperature during the relatively dry months of March, April and May of the growth year. This seems to be the dominant factor influencing ring width growth. However, needle production and apical extension also appear to be related to both climatological conditions during the year of bud formation as well as during the year of growth. These relationships can be explained by either bud formation processes, depletion of stored carbohydrates that would otherwise be used for bud formation or variations in the rate of apical growth. Further data are required to support some of the climate relationships.

Although there was suppression in the early growth of the individual tree, for the periods when the needle density data and isotope tracer results apply, growth of the individual tree corresponds with average site growth trends. Given this consistency, it is not unreasonable to use the needle production and stable isotope tracer results, which are only available for this tree, to calibrate, verify and parameterise the Tree Ring model.

Key-words—Needle trace method, Apical extension, Ring width, Tree ring model, *Pinus ponderosa*.

अमरीका के एरीज़ोना प्रान्त से प्राप्त *पाइनस पॉन्डीरोसा* की जलवायु एवं शीर्षस्थ विस्तार में सम्बन्ध, सूचिका उत्पादन एवं वलयी चौड़ाई

डेबी हेमिंग, रिस्टो जैकेनन एवं स्टीवन डब्ल्यू. लीविट

सारांश

वर्ष 1962-1998 की अवधि हेतु अमरीका के दक्षिणी एरीज़ोना प्रान्त के सान्ता केटेलीना पर्वतश्रेणियों से प्राप्त एक *पाइनस पॉन्डीरोसा* वृक्ष के अनुमापनों के विस्तृत अनुक्रम से शीर्षस्थ विस्तार (ऊँचाई में वृद्धि), सूचिका उत्पादन तथा वलयी चौड़ाई के अनुमापनों को प्रस्तुत शोध पत्र में प्रस्तुत किया गया है। इन अनुमापनों से वृक्ष ऊँचाई पर वृक्ष की आयु एवं ऊँचाई तथा वृक्ष ऊँचाई एवं व्यास के मध्य के सम्बन्धों को विश्लेषित किया गया है। अध्ययन स्थल के अन्य वृक्षों के साथ इस वृक्ष की वृद्धि तुलनीय है अथवा नहीं, यह जाँचने हेतु इनकी वृक्ष विशेष भी ऊँचाई एवं आधारीय आयु से निर्धारित किए गए, उन्हीं सम्बन्धों हेतु सम्पूर्ण स्थल रूझानों के साथ तुलना की गई।

सूचिका उत्पादन तथा शीर्षस्थ विस्तार उच्चतः सहसम्बन्धित (आर = 0·67) हैं तथा सामान्यतः एक समान जलवायुविक सहसम्बन्धन प्रदर्शित करते हैं। वलयी चौड़ाइयाँ इनमें से किसी भी श्रेणी से महत्त्वपूर्ण रूप से सहसम्बन्धित नहीं हैं, किन्तु वृद्धि वर्ष के मार्च, अप्रैल एवं मई माह के अपेक्षाकृत शुष्क महीनों के दौरान सभी तीन श्रेणियाँ वर्षण एवं ओस बिन्दु तापमान के साथ सकारात्मक रूप से अत्यन्त महत्त्वपूर्ण ढंग से सहसम्बन्धित हैं। यह वलयी चौड़ाई को प्रभावित करने हेतु सबसे प्रमुख कारक है। यद्यपि वर्ष में कली के निर्माण के दौरान तथा वर्ष में वृद्धि के दौरान दोनों जलवायुविक स्थितियों से सूचिका उत्पादन तथा शीर्षस्थ विस्तार भी सम्बन्धित प्रतीत होते हैं। इन सम्बन्धों को या तो कली निर्माण प्रक्रिया अर्थात् संरक्षित कार्बोहाइड्रेटों के ह्रास, जिसे कली निर्माण में प्रयुक्त किया जा सकता था, अथवा शीर्षस्थ वृद्धि की दर द्वारा व्याख्यायित किया जा सकता है। कुछ जलवायुविक सम्बन्धों के समर्थन हेतु और अधिक आंकड़ों की आवश्यकता है।

यद्यपि अवधि के दौरान सूचिका घनत्व आंकड़ों तथा समस्थानिक अनुरेखक (ट्रेसर) के परिणामों को अनुप्रयुक्त करने पर वृक्ष विशेष की प्रारंभिक वृद्धि में लुप्तांगता (सप्रेशन) प्राप्त हुई है, परन्तु वृक्ष विशेष की वृद्धि औसत स्थल वृद्धि रूझानों के संगत है। इस संगति के आधार पर यह तर्कसंगत होगा कि सूचिका उत्पादन तथा स्थाई समस्थानिक अनुरेखक के परिणामों को प्रयुक्त किया जाए, जो मात्र इस वृक्ष के वृक्ष वलय प्रतिदर्श के अनुसंशोधन, अभिप्रमाणन तथा प्राचलीकरण हेतु ही उपलब्ध हैं।

संकेत शब्द—सूचिका अनुरेखक प्रविधि, शीर्षस्थ विस्तार, वलयी चौड़ाई, वृक्षय वलय प्रतिदर्श, *पाइनस पॉन्डीरोसा.*

INTRODUCTION

THE Tree Ring model (Fritts *et al.*, 1999) is a process model that uses daily climatological inputs to estimate various tree functions, including cambial activity and isotopic fractionation. Throughout the development of the Tree Ring model it has been vital to parameterise, calibrate and verify the model with real measurements that are representative of the species and study site that is being modelled. At present, this is done using *Pinus ponderosa* (Ponderosa pine) in the Santa Catalina Mountains of southern Arizona, USA.

For some variables such as ring width and tree height to age relationship, it has been possible to sample and average a representative cross-section of the tree population at the study site. However, for other variables this has not been possible, either because the measurements are destructive or too time consuming to be feasible to measure on more than one or a few trees. In this situation we aim to justify using data that is only available from one or a few trees to provide inputs for the Tree Ring model by checking that the growth of this tree is comparable with that of site averages and consistent with expected climate relationships.

Time series derived from apical extension and ring width for the individual tree in this study are compared with site average curves and, together with time series of needle production, these are compared with climate parameters. If the growth of this tree is shown to be site-consistent, information on photosynthetic allocation from an isotopic tracer experiment conducted on this tree could also be used to verify the modelling of the intra-annual timing of cell development and isotopic composition.

METHODS

An individual ponderosa pine tree from a study site in the Santa Catalina Mountains of southern Arizona, USA (32·42°N, 110·75°W) was felled in February 1999 as part of an isotopic tracer experiment designed to examine the timing of tree ring cell development. This tree was utilised for the present study because sufficient tree material was available for the destructive needle trace density determination.

To check that the growth of the individual tree was indicative of the growth of other trees at the study site a ring width chronology, age versus height curve and height versus diameter at breast height (dbh) curve were constructed using

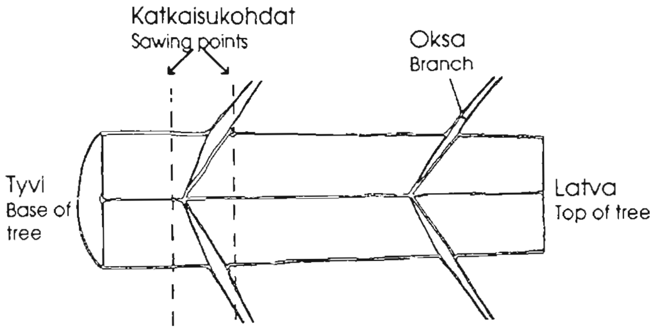


Fig. 1—Sectioning annual branch whorls (After Aalto & Jalkanen 1998)

multiple trees from the site. These were compared with the same measurements made on the individual tree.

Apical Extension and Tree Height

A time series of apical extension was determined on the individual tree by sectioning and measuring the distance between annual branch whorls (Fig. 1), and associating each section with the relevant year of formation and age of pith. By cumulating these apical extension measurements a time series of tree height versus age was also obtained. This individual tree series was compared with a tree height versus age curve for a cross-section of ponderosa pine at the site, which was determined using two techniques:

a) On young trees where annual branch whorls are clearly visible tree age was determined by counting branch whorls from the base. Height was determined with a tape measure.

b) On older trees or where all branch whorls were not clear, measurements of tree age (at coring height ~1.5 m) were estimated from tree cores by adding 20 years to this pith age. Height measurements to the highest visible shoot were made using a clinometer and triangulation.

Needle Production

The Needle Trace Method (Aalto & Jalkanen, 1998; Jalkanen *et al.*, 1998) was used to determine the number of needles that grew on each new apical growth section in each year from 1962 to 1998. This is referred to as needle production. From each of these sections a rectangle of wood approximately 5 cm long was taken surrounding the pith. Using a sharp blade, shavings of wood were removed around the circumference of the pith until a bolt of wood containing the inner-most ring was reached.

As the vascular bundle connecting each dwarf shoot to the new apical stem extends to the pith, and its location is identified after needle shed by a 'scar' (a needle trace), the number of needle traces on the inner-most apical growth ring indicates needle production for that year. To determine needle production the number of needle traces on each bolt was divided by the bolt length to get needle density (needles per unit of apical growth), which was multiplied by length of apical growth.

As with other pine species, ponderosa pine grows needles around the stele at set intervals along a spiral route. If a needle trace seemed to be missing from this spiral further slivers of wood were removed from the section until the trace was exposed.

Ring Widths and DBH

To produce the individual tree ring width series, ring widths were measured on two sides of a disk taken from

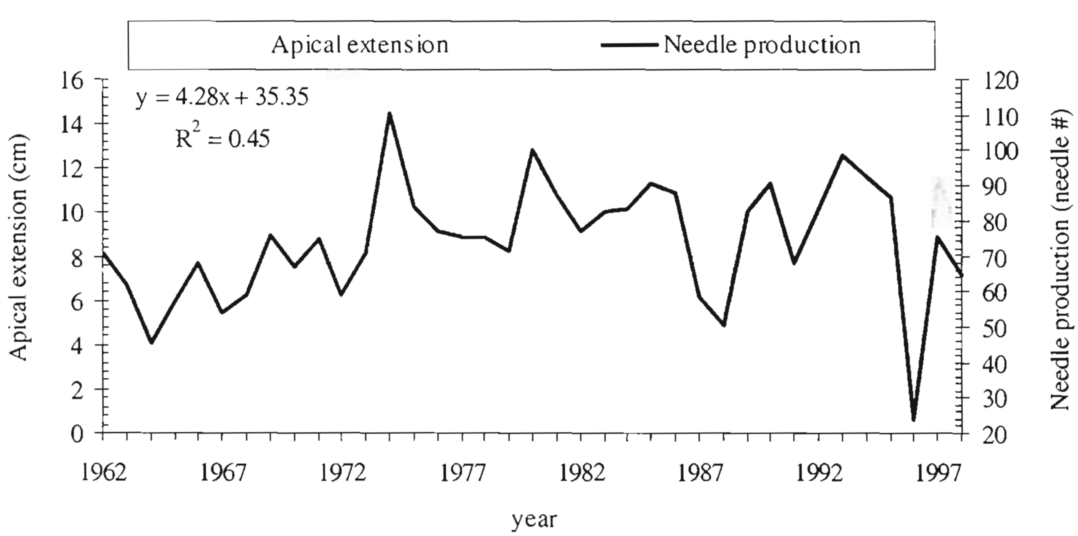


Fig. 2—Time series of apical extension and needle production for a *Pinus ponderosa* in the Santa Catalina Mountains, Arizona, USA.

approximately 1·5 m height. These were averaged to produce a raw ring width series, then an indexed series was produced using a 50 years spline with a 50% cut-off wavelength. The diameter of this disk was assumed to correspond to dbh. A time series of dbh versus height for the tree was constructed by subtracting the cumulative diameter added by each consecutive average raw ring width from this initial dbh measurement and comparing this with the corresponding height measurements. This individual time series is compared with the site series for dbh versus height that was constructed by measuring the dbh of the same trees used to determine the height versus age curve.

The site ring width chronology was constructed by averaging the ring width series of four perpendicular cores from each of nine trees, all between 55 and 133 years old. The resultant series were then indexed, again using 50-years splines with a 50% cut-off wavelength prior to being averaged to form a single chronology.

Climate comparisons

The relationships between the tree growth time series and monthly average climatic parameters are examined by cross-correlation analysis using the monthly climate parameters for the same year and for the year prior to tree growth. The climate parameters used are average, maximum and minimum temperature, precipitation and dew point temperature. For the period 1965 to 1981 the temperature and precipitation records were directly available from the Palisades Meteorological Station, which is approximately 1 km from the study site. Some missing values in this record were reconstructed using regression relationships between the

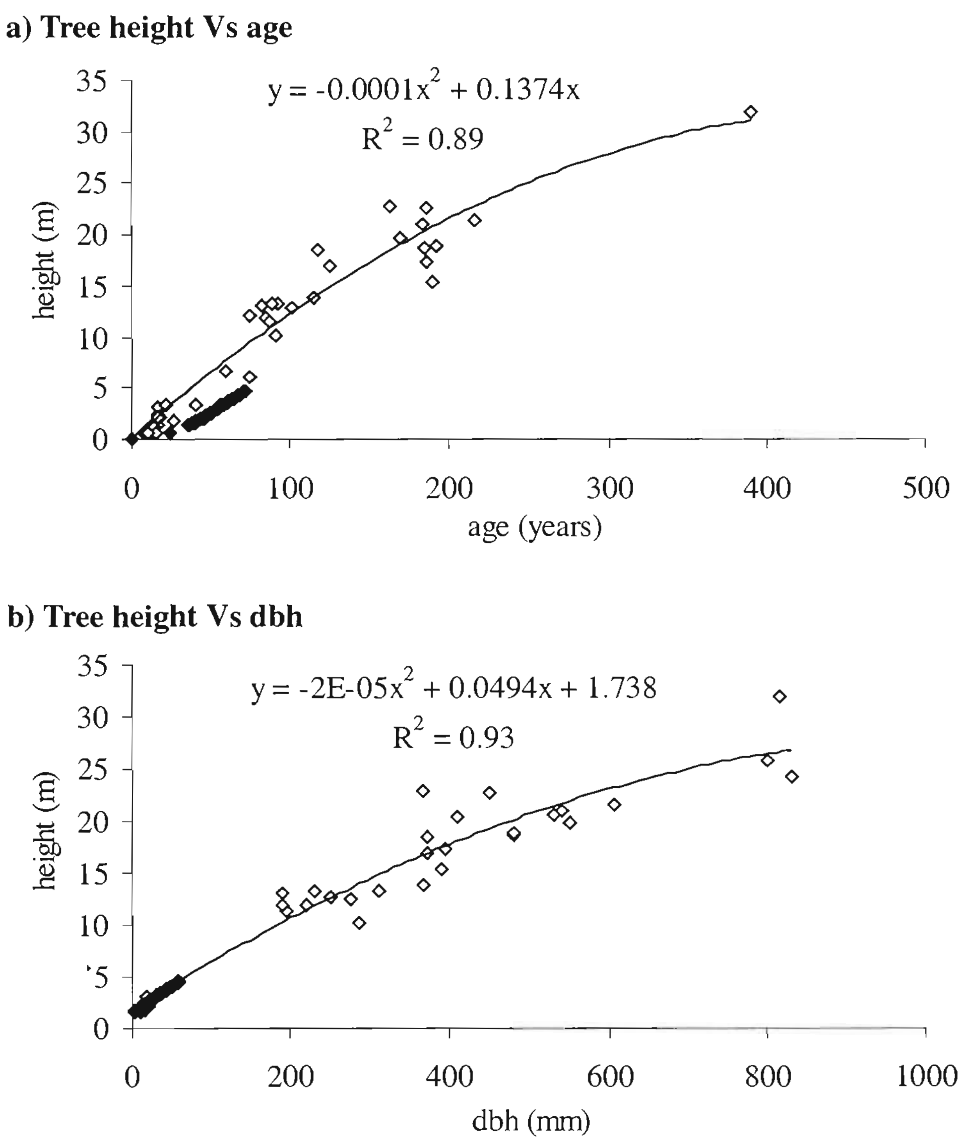


Fig. 3—Relationship between (a) tree height and age and (b) tree height and dbh. The single 'tracer' tree is shown by filled diamonds and the observations from multiple trees at the site are shown by open diamonds. A first-order polynomial is fitted to the multiple tree site data only.

available Palisade data and records from a network of five meteorological stations within a site radius of 25 km.

RESULTS AND DISCUSSION

Tree Measurements

For the individual tree there is a highly significant positive correlation ($r=0{\cdot}67$, $p<0{\cdot}001$) between apical growth and needle production (Fig. 2), but no significant correlation between these series and ring width (raw or indexed). This indicates that the factors, and possibly the timing of factors, influencing apical extension and needle number are similar, but these are different to those factors affecting ring width growth. Poor or non-significant correlations between ring width and apical extension or needle number have also been observed on *Pinus sylvestris* in Finland (Jalkanen, In prep.), and attributed to differences in the time window of climatological influence (Jalkanen, 2000). This is discussed further in the following section.

The relationship between the site curves for height versus age and height versus dbh compared to those for the individual tree are shown in Fig. 3a and b respectively. It is evident from the curve of height versus age (Fig. 3a) that the apical growth of the individual tree was relatively suppressed compared to trees of comparable age in the same stand. The main period of suppression occurred in the first thirty years of growth, until approximately 1960, after which the slope of the height to age curve is nearly parallel with that of the site average, indicating that after initial suppression growth continued at a rate comparable with the site average. This is supported by the close association between the individual tree and the site average curves for height versus dbh (Fig. 3b), which is unaffected by suppressed growth in the individual tree because the height at which dbh is taken (~1·5 m) was not reached until after 1960. The indexed ring width series is highly correlated with a site ring width chronology ($r=0{\cdot}62$, $p<0{\cdot}001$), also indicating that the inter-annual growth of this tree was similar to the site average.

As the isotope tracer experiment was completed in 1998 growth during this period is also outside the period of suppression and appears to be comparable with site averages. It should therefore be reasonable to assume the isotopic responses are similar to those expected from other comparable trees at the site.

Climate and Tree Measurements

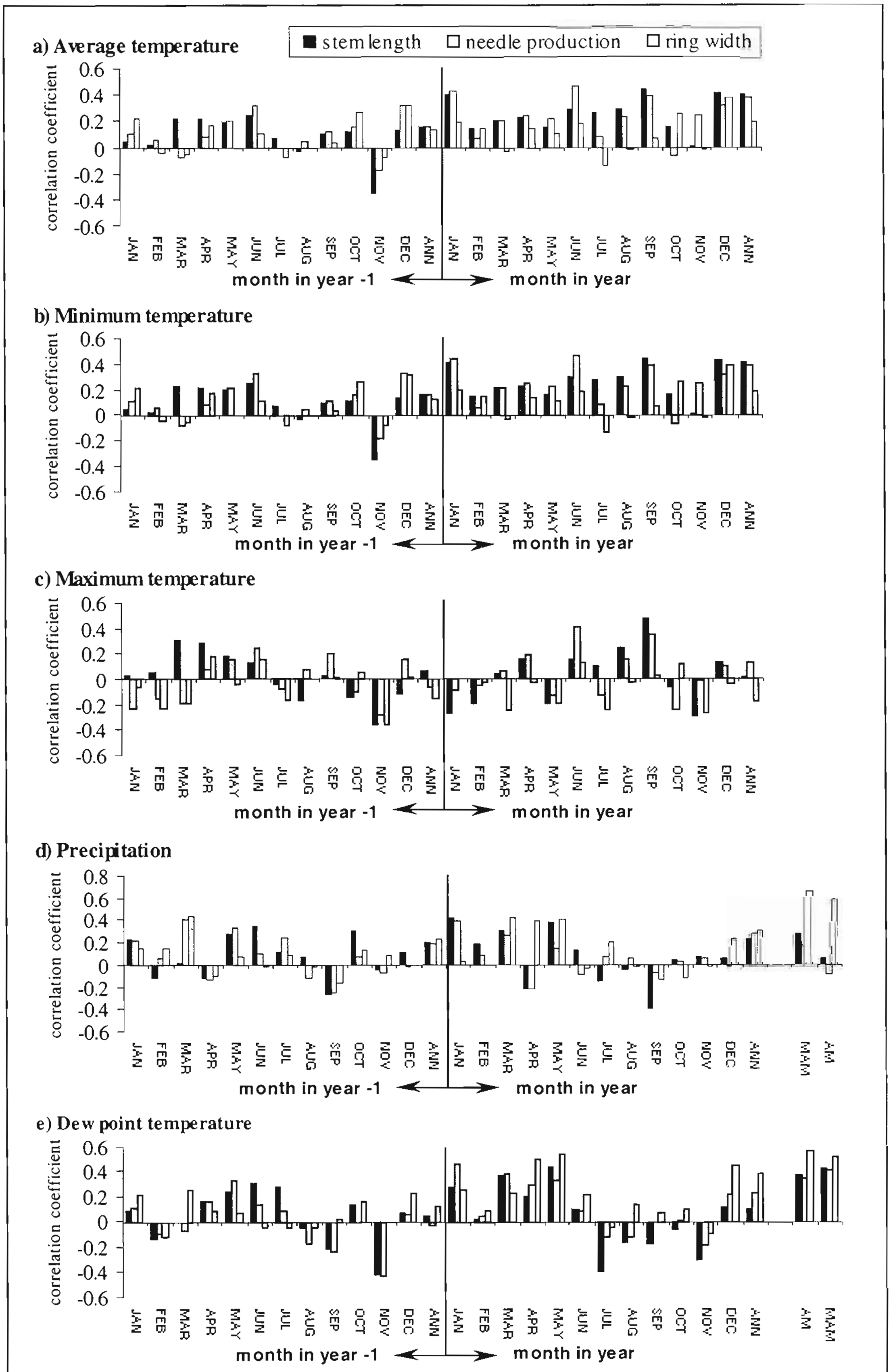
Comparing the series of apical extension, needle production and ring width with climatic parameters (Fig. 4), apical extension and needle production are most significantly correlated with similar climatic parameters and time periods, but these are often different from those most significantly correlated with ring width.

One period when all three tree series are significantly correlated with climate is with precipitation and dew point temperature is during spring (March-May) of the growth year (Fig. 4d & e). This is associated with the initial growth flush in the shoots, needles and stem, and is in agreement with observations of approximately coincident timing between initial height increment and stem diameter growth for *Pinus ponderosa* grown over a two year period in open-top field exposure chambers in California, USA (Tingey *et al.*, 1996). The fact that temperature during this time period does not show significant relationships with any of the tree series suggests that initiation of inter-annual growth is influenced more by moisture availability than temperature. This is supported by the observations that soil moisture is the factor most limiting to growth throughout the geographical range of *Pinus ponderosa* (Burns & Honkala, 1990), and ring widths of this species growing in arid US sites were more dependent on spring precipitation than temperature (Fritts, 1976 p. 240).

Apical extension and needle production are also significantly positively correlated with average and minimum temperature in January and during several of the summer months. As January precipitation is also significantly correlated with these series this relationship may be explained by the amount of winter snow-pack available for initial spring growth. However, the correlations with summer temperature do not seem to be well explained physiologically. It is possible that further smaller growth flushes occur in apical extension throughout the summer, as was observed by Tingey and others (1996) for ponderosa pine however, more observations are required to support this relationship.

Climate variables between the months of March and June of the previous year are generally positively correlated (not always significantly) with both stem extension and needle production. This is the period prior to the initiation of the summer monsoon (which is between early July and October) when stored carbohydrates may be significantly depleted. If conditions are favourable for growth during this time less stored carbohydrate will be depleted and more will therefore be available for bud preparation later that year.

It is also notable that there is a significant negative correlation between November climate (except precipitation) and both stem extension and needle production. This relationship was also noticed for *Pinus sylvestris* in Finland, but for the November two years prior to growth (Jalkanen, 1999; McCarroll & Jalkanen, 1999). It is possible that warm and humid November conditions increase respiration over photosynthesis in ponderosa pine at this location, which will again tend to reduce the carbohydrates available for growth the following season.


a) Average temperature
stem length
needle production
ring width
b) Minimum temperature
c) Maximum temperature
d) Precipitation
e) Dew point temperature
correlation coefficient
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
ANN
MAM
AM
month in year -1
month in year

CONCLUSIONS

Although growth was initially suppressed in the individual tree, during the period 1962 to 1998 it is comparable to that of other trees at the same site. Although not an ideal situation, this justifies the use of data that are only available from this tree during this time period (needle density and isotopic tracer results) for calibration, verification and parameterisation of the Tree Ring model.

Needle production and apical extension are highly positively correlated, indicating that similar factors influence these two variables. However, these factors must be different from those affecting ring width because ring width is not significantly correlated with these series.

Spring moisture during the year of growth is significantly correlated with all three tree series and is the factor most dominant for ring width growth. However, climate relationships with apical extension and needle production appear to be more complex and are related to both climatological conditions during the year of bud formation as well as during the year of growth. These relationships can be explained by either bud formation processes, depletion of stored carbohydrates that would otherwise be used for bud formation or variations in the rate of apical growth.

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Fig. 4—Correlations between climate parameters and apical extension, needle production and ring width for the individual tree. Monthly average climate parameters of (a) average temperature, (b) minimum temperature, (c) maximum temperature, (d) precipitation, & (e) dew point temperature for the year of growth and prior year have been used. Abbreviations of MAM and AM have been used to signify averages for March-May and April-May. Correlations of ±0·34 and better are significant at the 95% level.

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Fire History and Fire Climatology along a 5° Gradient in Latitude in Colorado and Wyoming, USA

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ABSTRACT

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We reconstructed fire chronologies covering the past four to six centuries from fire scars recorded in tree-ring series from 18 sites in the central Rocky Mountains of Colorado and Wyoming. Sites are located in forests containing predominately *Pinus ponderosa*. Median fire-free intervals in fire chronologies are related to latitude, with shorter intervals in southern stands than those in the north. However, strength of this relationship varied through time, with a stronger latitudinal gradient in fire frequency from 1600 to 1800 than from 1700 to 1900. Variability in fire frequency with time may be related to strength of regional climate gradients. Seasonality of fire scars also varied across the latitudinal gradient, from predominately early season fires in the south to late season fires in the north. Superposed epoch analysis of fire years with annual variability in Palmer drought severity indices shows that fire years throughout the gradient were dry, but those in the south were preceded by wet years. This result suggests that fuel amounts may have been limiting in southern forests where fire intervals were shorter, and that longer intervals in the north permitted fuel buildup between fires. All chronologies show a general cessation of fire scars beginning in the latter nineteenth century, coincident with widespread Euro-American settlement of the western US.

Key-words—Chronology, Fire, Forest, USA.

संयुक्त राज्य अमरीका के कोलेराडो एवं वायोमिंग प्रान्त में 5° अक्षांश प्रवणता पर अग्नि का जलवायुविक इतिहास तथा जलवायुविज्ञान

पीटर एम. ब्राउन एवं वेन डी. शेपर्ड

सारांश

हमने कोलेराडो एवं वायोमिंग के मध्य प्रस्तरी पर्वतश्रेणियों के 18 स्थलों की वृक्ष वलय श्रेणियों में अंकित पाँच क्षतचिन्हों (स्कार), जो विगत चौथी एवं छठी शताब्दी के हैं, से अग्नि कालानुक्रम का पुनर्सृजन किया। स्थल प्रमुखतः *पाइनस पॉण्डीरोसा* की प्रमुखता वाले वनों में स्थित हैं। अग्नि कालानुक्रम के माध्य अग्नि अन्तराल उत्तरी खड़ों (स्टैण्ड) की अपेक्षा दक्षिणी खरों में लघुतर अन्तरालों से युक्त अक्षांश से सम्बन्धित हैं, तथापि कालानुसार इस सम्बन्ध की तीव्रता भिन्न-भिन्न होती जाती है। सन् 1700 ई. से 1900 ई. के अन्तराल की अपेक्षा सन् 1600 ई. से 1800 ई. के मध्य अग्नि आवृत्ति में अक्षांश प्रवणता अधिक है। कालानुसार अग्नि आवृत्ति में भिन्नता क्षेत्रीय जलवायुविक प्रवणताओं से सम्बन्धित हो सकती है। दक्षिण में प्रमुखतः प्रारंभिक मौसमी अग्नि से उत्तर में अन्तिम मौसमी अग्नि तक अग्नि क्षतचिह्नों की मौसमिकता भी

भिन्न-भिन्न है। पामर अनावृष्टि भयावहता सूचकांक में वार्षिक भिन्नता से युक्त अग्नि वर्षों के अध्यारोपित युगीन विश्लेषण से प्रदर्शित होता है कि सम्पूर्ण प्रवणता के दौरान अग्नि वर्ष शुष्क थे, किन्तु दक्षिण में यह स्थिति आर्द्र वर्षों के पश्चात आई। इस परिणाम से प्रस्तावित होता है कि दक्षिणी वनों के ईंधन की मात्रा सीमित हो सकती है, जहाँ अग्नि अन्तराल संक्षिप्त थे तथा उत्तर में दीर्घावधिक अन्तरालों के कारण अग्नियों के मध्य ईंधन निर्मित होता रहा होगा। सभी कालानुक्रम सामान्यतः उत्तरवर्ती उन्नीसवीं शताब्दी के प्रारंभ में अग्नि क्षतचिन्हों का अवसान प्रदर्शित करते हैं, जो पश्चिमी अमरीका के दूर-दूर तक फैली हुई यूरो-अमरीकी बस्तियों के सम्पाती हैं।

संकेत शब्द—कालानुक्रम, अग्नि, वन, संयुक्त राज्य अमरीका.

INTRODUCTION

FIRES that burn at the base of a tree may kill portions of the vascular cambium and leave distinctive lesions (fire scars) recorded in the tree-ring series (Fig. 1). By crossdating the tree rings using dendrochronological methods, chronologies of past fires may be reconstructed. Fires can be dated to the year they occurred and often to the season by noting positions of fire scars within annual rings and knowing when radial growth begins and ends during a typical growing season. Long sequences of fire scars often are recorded on individual trees because of repeated burns during a tree's life (Fig. 1).

Studies using fire-scar data from lower and middle elevation forests throughout the western US have shown that frequent, low-severity fires were important forest disturbances prior to the twentieth century (e.g., Swetnam, 1993; Swetnam & Baisan, 1996; Barrett *et al.*, 1997; Brown *et al.*, 1999, 2000, 2001; Veblen *et al.*, 2000). Fires were keystone ecosystem processes (*sensu* Holling, 1992) that influenced forest composition and structure, understorey species diversity and productivity, biogeochemical processes, wildlife habitats, hydrology, and other environmental conditions (e.g., Cooper, 1960; Covington & Moore, 1994). Fire cessation occurred in almost all areas beginning the latter half of the nineteenth century or early in the twentieth century because of land use that accompanied European settlement of the West. Settlement brought intensive livestock grazing which removed grass and herbaceous fuels that promoted fire spread and later, beginning in the early half of the twentieth century, fire suppression by land management agencies, such as the US Forest Service.

Here we describe fire histories reconstructed from fire-scar records in 18 sites that occur along a 5° latitudinal

Fig. 1—Fire scars (arrows) recorded in a cross section from *Pinus ponderosa*. Bottom four fire scars are dormant season (between two rings) while uppermost fire scar occurs early in the earlywood.

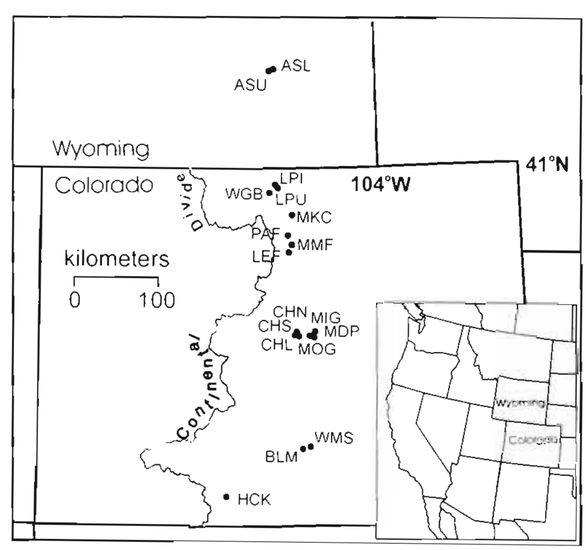

Fig. 2—Locations of 18 Fire History sites in Colorado and Wyoming.

gradient in the Rocky Mountains of Colorado and central Wyoming (Fig. 2). We compare reconstructed fire frequency and fire seasonality to assess shifts in fire-climate relations that occurred along the latitudinal gradient and through different periods covered by the fire chronologies. Our interest is in determining if there are recognizable relations between fire occurrences and variability in regional climate regimes as represented by latitude, and whether or not these relationships remained stable through the period covered by the fire chronologies.

METHODS

We used chainsaws to collect cross sections from fire-scarred trees in montane forests containing predominately *Pinus ponderosa*. Sites range from southern Colorado to central Wyoming along the central Rocky Mountain cordillera (Figs. 2, 3). At each site, we collected cross sections from 10 to 20 trees from forest stands that varied in size from 4 to 20 hectares. Our goal with collection in each site was to reconstruct a comprehensive, long-term fire chronology (Swetnam & Baisan, 1996; Brown *et al.*, 2001). We compiled composite fire chronologies from multiple trees because of the possibility of incomplete fire-scar records on individual trees. It is possible that either a fire that burned at the base of the tree was not recorded at the time of its occurrence or fire scars may have been burned off in subsequent fires or were otherwise erased from a tree's fire-scar record .

Fire-scarred samples were crossdated by matching common patterns of climatically controlled parameters in growth between trees such that absolute dating of tree rings was assured (Stokes & Smiley, 1968). Once tree rings were crossdated on each sample, dates were determined for fire scars. Positions of fire scars within tree rings were also assigned. Dates on individual trees at each site were compiled into fire chronologies and fire frequency was determined using program FHX2 (Grissino-Mayer, 2001).

We used several methods to describe and contrast fire frequency and fire climatology in the 18 stands. Fire frequency in each fire chronology was described by the median fire-free interval (MeFI) during periods of adequate sample coverage. Beginning and ending dates for periods of analysis for MeFI were based on a minimum of four trees in the early part of chronologies and when fires ceased in the late nineteenth or early twentieth centuries. We also calculated MeFI for each chronology for periods from 1600 to 1800 and from 1700 to 1900. We chose these two periods to assess possible differences in fire frequency through time as related

Site Name	Site Code	Elevation Range (m)	Latitude (N)/ Longitude (W)	Dominant Overstory Species [a]	Total Trees/Scars [b]
1. Ashenfelder Lower	ASL	1920-1950	42°20·0'/105°23·0	Pipo	12/68
2. Ashenfelder Upper	ASU	1930-1960	42°20·0'/105°24·5'	Pipo	10/52
3. Lone Pine	LPI	2340-2400	40°49·5'/105°27·5'	Pipo, Psme, Pico	11/17
4. Lone Pine Upper	LPU	2380-2410	40°48·5'/105°27·0'	Pico, Pipo, Psme, Potr	8/15
5. Washout Gulch Burn	WGB	2420-2590	40°44·0'/105°40·0'	Pipo, Psme, Potr	17/47
6. Merrill Kaufmann's Cabin	MKC	2090-2200	40°24·0'/105°12·0'	Pipo	18/86
7. Parachute Hill	PAF	2610-2630	40°14·0'/105°28·0'	Pipo, Psme	21/46
8. Mica Mine	MMF	2220-2250	40°09·0'/105°21·5'	Pipo, Psme	16/71
9. Left Hand Canyon	LEF	2600-2630	40°03·5'/105°28·5'	Pipo, Psme	16/41
10. Cheesman Lake North	CHN	2150-2180	39°11·5'/105°16·0'	Pipo, Psme	13/37
11. Cheesman Lake South	CHS	2160-2230	39°09·0'/105°16·5'	Pipo, Psme	17/56
12. Old Tree Cluster	CHL	2150-2180	39°08·0'/105°18·0'	Pipo	23/78
13. Missouri Gulch	MIG	2630-2670	39°08·5'/105°03·0'	Pipo, Psme, Pico, Pifl	8/18
14. Manitou Old Growth	MOG	2380-2390	39°06·0'/105°06·0'	Pipo	9/41
15. Manitou Demonstration Plot	MDP	2390-2410	39°03·5'/105°04·0'	Pipo	26/124
16. Wet Mountains South	WMS	2670-2690	37°55·5'/105°14·0'	Pipo	20/138
17. Black Mountain	BLM	2720-2740	37°51·5'/105°16·0'	Pipo	10/19
18. Hot Creek	HCK	2590-2640	37°17·5'/106°16·0'	Pipo	17/59

[a] Species designations:
Pipo: *Pinus ponderosa*
Pico: *P. contorta*
Pifl: *P. flexilis*
Psme: *Pseudotsuga menziesii*
Potr: *Populus tremuloides*
[b] Numbers of trees crossdated and fire scars recorded

Fig. 3—Sites collected for Fire History studies in Colorado and Wyoming.

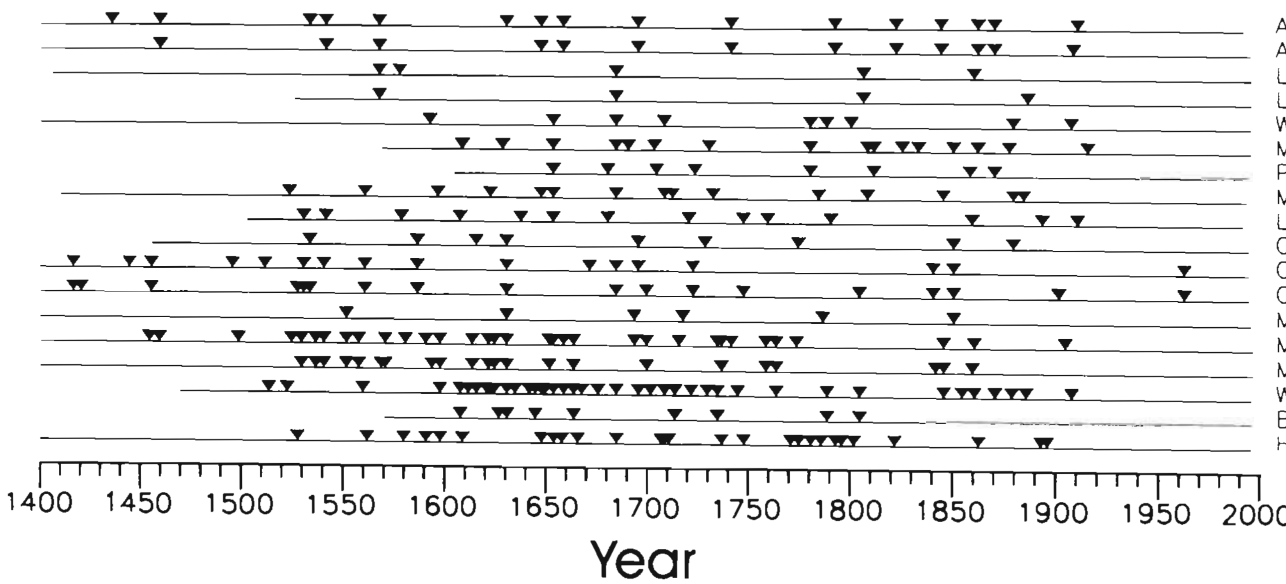

Fig. 4—Summary fire chronologies. Horizontal lines represent time spans of chronologies and inverted triangles represent fire dates.

to variations with latitude. Periods overlap because, contrary to many sites in the southwestern US where fire frequency was very high (fires occurring on average every 3 to 10 years in many forests; Swetnam & Baisan, 1996), fire frequency was lower in most sites and there are not enough intervals for calculation of frequency for all stands for non-overlapping 100-years periods. Linear regressions were used to determine significant relationships between latitude and both MeFI and seasonality of fires. Finally, we used superposed epoch analysis (SEA; Swetnam, 1993) to compare fire occurrences to independent tree-ring based reconstructions of Palmer Drought Severity Index (PDSI; Cook *et al.*, 1996). We used SEA to identify patterns between fire years and an eleven-years window of climate values: six years prior to the fire year, the fire year, and four years following. Significant climate departures were determined using mean climate values and variances calculated from 1000 randomly selected event data sets with the same number of fire dates as the tested data. Reconstructed PDSI values from Cook *et al.*'s (1996) grid points 58 (41° N 104·5° W) and 59 (39° N 104·5° W) were selected based on the grid points' proximity to study locations.

RESULTS AND DISCUSSION

Fire Chronologies

We crossdated a total of 272 trees that recorded 1017 fire scars from the 18 sites. Summaries of fire dates in chronologies are shown in Fig. 4. Fire events were recorded at all sites up until the late nineteenth or early twentieth centuries. As in most areas of the western US, few fire scars were recorded at any site during the twentieth century, reflective of changes in land use that occurred with Euro-American settlement.

Typical fire chronologies from four stands in northern Colorado are shown in Fig. 5. As in all stands sampled for this study, many trees were dead at the time of collection. Resinous heartwood of larger *Pinus ponderosa* trees often persists for several decades after tree death and sampling of remnant trees is a means to extend fire (and climate) chronologies to periods before those of living trees. Most fire-scarred cross sections for this study were removed from stumps left from logging. Many low-elevation forests containing *Pinus ponderosa* were heavily logged because of relative ease of access and proximity to population centers on the Colorado Front Range. Other fire-scarred cross sections were collected from standing dead trees (snags) or logs in addition to those from living trees (Fig. 5).

Stands shown in Fig. 5 occur along a gradient in elevation (Fig. 3) and fire was more frequent in the lowest elevation stand (MKC) than in higher elevation stands (PAF, MMF and LEF). Changes in elevation integrate changes in precipitation and temperature that strongly influence both fuel quantity and its ability to burn. Moister and cooler conditions in upper-elevation forests result in fewer years when fuels are dry enough for fire to spread after ignition (Peet, 1981; Swetnam & Baisan, 1996; Brown *et al.*, 2001). While fire frequency generally decreases with elevation, fire severity may increase because of fuel buildups that result from longer intervals between fires and more productive forests at higher elevations.

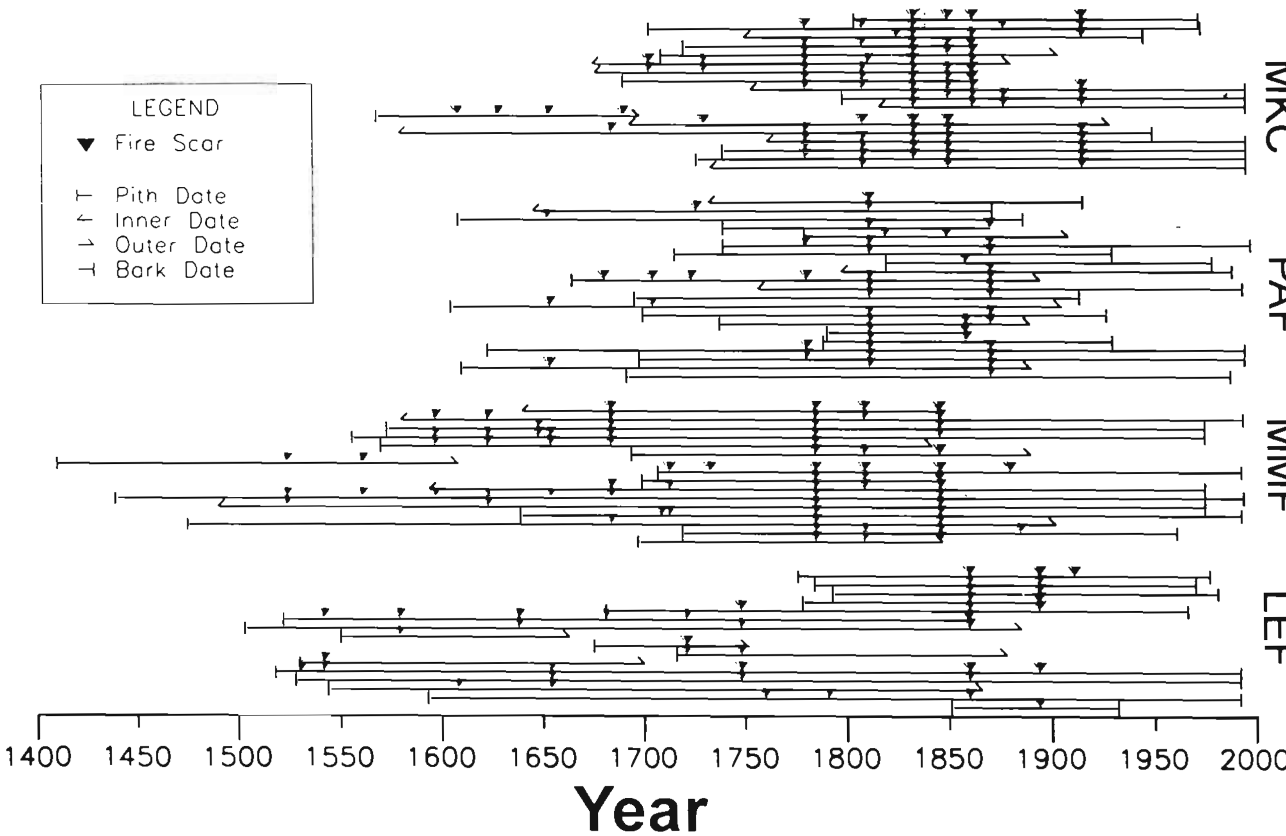

Fig. 5—Composite fire chronologies from four sites in the Colorado Front Range. Sites are arranged from low to high elevation (see Fig. 3).

In several of the higher-elevation areas we sampled for this study, we found evidence of catastrophic crown fires (Brown *et al.*, 1999, 2000). Crown fires likely occurred more frequently and across larger areas in *Pinus ponderosa* forests of our study area than in those of the Southwest because of generally longer intervals between fires (Brown *et al.*, 1999).

In general, we did not find any increase in fire occurrences during the early settlement period of the late nineteenth century as has been found in other fire history studies in central Colorado (e.g., Veblen *et al.*, 2000). This may be the result of either differences in methodologies for developing fire chronologies and/or in locations of stands selected for fire history. Other studies selected primarily living trees for reconstruction of fire history while we collected both living and remnant materials. We have found that living trees in a majority of *Pinus ponderosa* forests in Colorado are relatively young because of past logging that removed larger and older trees. A reliance on living trees that exhibit multiple fire-scar records may bias site selection to areas where fire was more frequent during the early settlement period. Historic records and photographs often document burning that resulted from human ignitions during the settlement period, but we believe that these impacts were limited to specific, more intensively utilized, locations based on fire histories we have reconstructed.

Fire Frequency along the Latitudinal Gradient

While changes in elevation integrate changes in climate regimes at landscape scales (e.g., mountain ranges), changes in latitude integrate changes in climate across larger regional scales. Median fire intervals generally decreased with increasing latitude, although there was a great deal of variability both within and between fire chronologies (Figs.

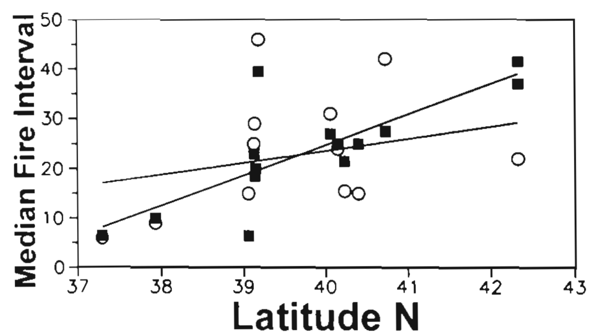

Fig. 6—Box plots of fire interval distributions in fire chronologies. Small boxes are median intervals, large boxes are first and third quartile intervals, and lines are range of intervals in each chronology. Sites are arranged by latitude.

Site	Period of Analysis	No. of Fire Intervals	Median Fire Interval (yr)	Range of Intervals (yr)
ASL	1436-1911	15	26	8 to 74
ASU	1460-1909	12	33·5	8 to 82
WGB	1654-1908	8	29·5	8 to 79
LPI	1568-1861	4	80·5	10 to 122
LPU	1568-1896	3	117	80 to 122
MKC	1609-1878	14	16	3 to 50
PAF	1654-1871	10	21·5	3 to 54
MMF	1524-1885	14	25·5	4 to 52
LEF	1542-1911	13	29	11 to 69
CHN	1534-1880	8	39·5	15 to 76
CHS	1417-1851	15	20	10 to 118
CHL	1325-1851	26	16	3 to 58
MIG	1631-1851	5	64	24 to 79
MOG	1598-1846	10	22·5	2 to 72
MDP	1521-1865	24	7·5	2 to 82
WMS	1514-1908	28	10	4 to 41
BLM	1608-1805	8	19	4 to 54
HCK	1528-1896	26	9·5	2 to 41

Fig. 7—Measures of fire frequency calculated for period of analysis

4, 6 & 7). In northern stands, shorter growing seasons coupled with mostly cooler conditions likely resulted in fewer years during which fires were able to occur. There is also a general decrease in elevation along the latitudinal gradient with lower stands in the north than those in the south (Fig. 3). Decreasing stand elevation with latitude is a result of typical biogeography of species resulting from decreasing temperatures and growing season lengths as one moves north (Richardson, 1998). Intervals between fires found in the sites of this study were generally longer than most *Pinus ponderosa* stands of the Southwest US (see summary of 63 sites from Arizona and New Mexico in Swetnam & Baisan, 1996; Brown *et al.*, 2001) and comparable to those found in *Pinus ponderosa*

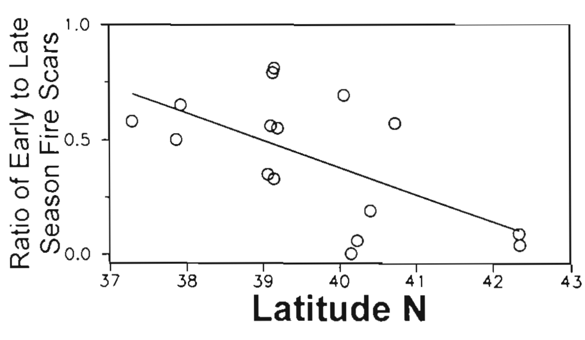

Fig. 8—Median fire intervals (MeFI) by latitude. Squares are MeFI from 1600 to 1800 (MeFI = 6·11 * latitude - 220; R^2 = 0·62) and circles are MeFI from 1700 to 1900 (MeFI = 2·40 * latitude - 72; R^2 = 0·12).

forests of the central Rocky Mountains (Brown *et al.*, 1999, 2000; Veblen *et al.*, 2000).

The relationship of decreased fire frequency with increasing latitude was stronger during the period from 1600 to 1800 ($p < 0·001$) than it was from 1700 to 1900 ($p = 0·21$; Fig. 8). This result highlights instability in fire regimes not only across space but also through time as a result of long-term climate variability. Studies from the Southwest US suggest that climate was less variable on decadal and longer times scales during the seventeenth and eighteenth centuries and, at least in the Southwest, was transitional ca. 1800 to wetter and possibly cooler conditions (Swetnam & Betancourt, 1998; Grissino-Mayer & Swetnam, 2000). It is also likely that generally warmer and likely drier conditions after the end of the little ice age (LIA) of the sixteenth to eighteenth centuries resulted in greater possibility for fires to occur in the more northern stands. Gradients in climate with latitude may have been stronger during the LIA than afterwards, and hence fire occurrences show a stronger gradient in frequency from 1600 to 1800 than from 1700 to 1900. These potential temporal relationships between fire frequency and latitude will be explored with a larger regional dataset from the Southwest (Swetnam & Baisan, 1996; Brown *et al.*, 2001) and northern Rocky Mountains (Brown & Sieg, 1996, 1999; Brown, unpublished data) that spans approximately 13° of latitude.

Latitudinal gradients in fire patterning also are evident in seasonality of fires (Fig. 9) and in relationships with annual drought conditions. Fire scars occurred predominately early in growing seasons in the south and later in growing seasons in the north ($p < 0·001$; Fig. 9). Historic and recent fires in the Southwest commonly occurred during the dry period of May and June and before the onset of summer monsoon moisture during July and August (Swetnam & Baisan, 1996). Fires in more northern stands typically occurred in late July, August, and September after grasses and herbaceous fuels cure at the end of shorter growing seasons than those to the south (Brown & Sieg, 1996, 1999). We found no significant variability in fire seasonality in subsets of fire-scar data based on periods of analysis.

Superposed epoch analysis showed that fires in both northern and southern stands occurred predominately during dry years but that fires in the south often were preceded by wet years. Wet years establish abundant grass and herbaceous understories that are the primary fuels for fire spread. A pattern of wet years preceding dry years has been found in other studies from Southwestern forests (e.g., Swetnam & Baisan, 1996; Brown *et al.*, 2001) and suggests that fire spread in stands was limited as much by fuel amounts as by dry fuel conditions. In more northern stands, fuel amounts were not as limiting to fire spread because of generally longer intervals between fires which permitted fuel buildup.

CONCLUSIONS

Variability in fire frequency in the 18 stands of this study document often strong control by climate regimes that occur along the latitudinal gradient. Variability in fire frequency, fire seasonality, and fire timing in relation to annual variability in PDSI can be related to latitude. Fires in northern stands tended to occur less frequently and later in the summer than those to the south. Fires in the south tended to occur after wet periods that permitted buildup of grass and herbaceous fuels. However, changes in land use accompanying Euro-American settlement at the end of the nineteenth century overrode climatic gradients and led to fire cessation in all stands.

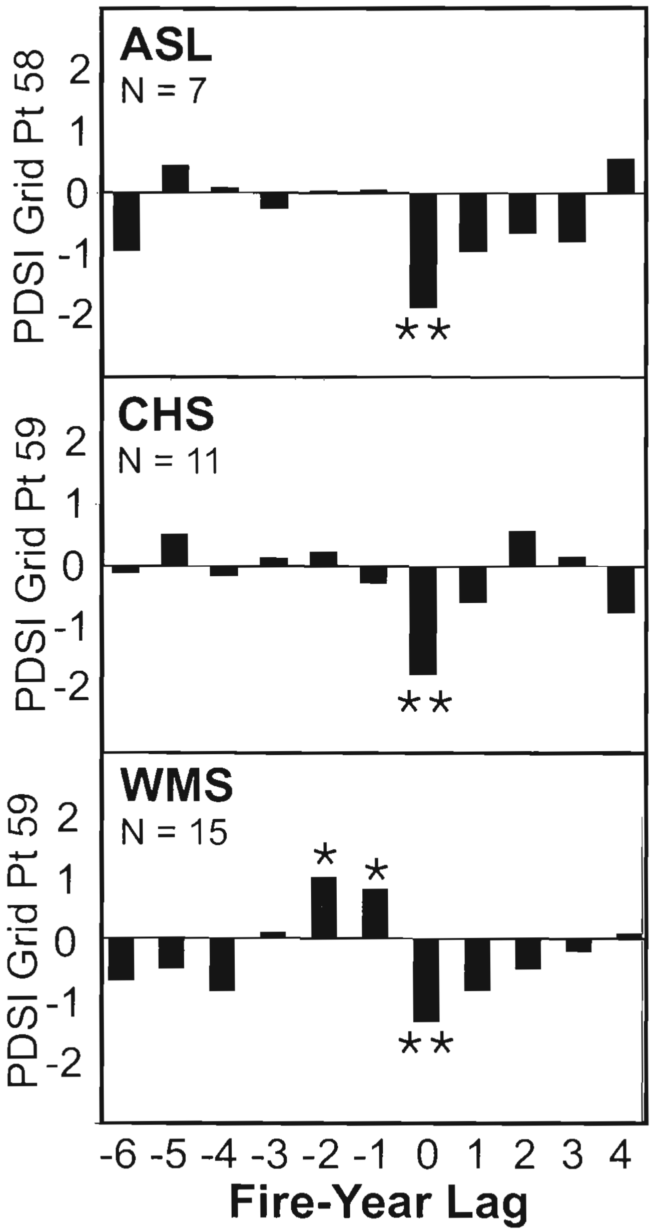

Fig. 9—Ratio of early- to late-season fire scars in fire chronologies by latitude. Ratio in each site is based on fire scars that occur within ring series (i.e., not including dormant season fire scars that occur at the boundary between rings).

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A tree ring reconstruction of climatic extreme years since 1427 AD for Western Central Asia

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ABSTRACT

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Analyses of ring width values of 429 trees from twelve *Juniperus* sites and three mixed sites (*Juniperus, Picea, Pinus*) of the northwest Karakorum in Pakistan and seven *Juniperus* sites of the southern Tien Shan in Kirghizia enable the reconstruction of extreme years since 1427 AD. Extreme growth reactions are classified as (i) event years—reflecting extreme years of individual trees, (ii) site pointer years—reflecting common extreme years within a site, (iii) regional pointer years—reflecting common extreme years within the Karakorum or Tien Shan, and (iv) inter-regional pointer years—reflecting synchronous extreme years between the Karakorum and Tien Shan. A comparison between the Karakorum and Tien Shan results in eight positive inter-regional pointer years (1916, 1804, 1766, 1703, 1577, 1555, 1514, 1431 AD) and 17 negative inter-regional pointer years (1917, 1877, 1871, 1833, 1806, 1802, 1790, 1742, 1669, 1653, 1611, 1605, 1591, 1572, 1495, 1492, 1483 AD). These years are valid for Western Central Asia.

The extreme year reconstructions from the Karakorum and Tien Shan Mountains are dominated by regional pointer years. Regional pointer years result from climatic conditions limiting tree growth independent of site ecology, from the lower, arid, to the upper, humid timberlines, and in different exposures. The seasonal climatic forcing of regional pointer years changes from year-to-year, but temperature variation predominantly limits tree growth. Additional analyses of selected site pointer years, which do *not* belong to regional pointer years, prove temperature signals from sites near the upper timberlines, and precipitation signals from sites near the lower timberlines.

Key-words—Dendrochronology, Climate, Extreme years, Pointer years, Site ecology, Karakorum, Tien Shan, Pakistan, Kirghizia, *Juniperus*.

पश्चिमी-मध्य एशिया हेतु विगत सन् 1427 ई. से आज तक के जलवायुविक चरम वर्षों का वृक्ष वलयी पुनर्सृजन

जान एस्पर, केर्स्टिन ट्रेड्ट, होल्गर गार्टनर एवं बर्खार्ड न्यूविर्थ

सारांश

पाकिस्तान के उत्तर-पश्चिमी कराकोरम के बारह *जूनीपेरस* स्थलों तथा तीन सम्मिश्र स्थलों के 429 वृक्षों (*जूनीपेरस, पाइसिया, पाइनस*) एवं किर्गिज़िया के दक्षिण तिएन शान के सात *जूनीपेरस* स्थलों के वलय चौड़ाई मानों का विश्लेषण विगत सन् 1427 ई. से आज तक के चरम वर्षों का पुनर्सृजन करने हेतु सहायक है। चरम वृद्धि प्रतिक्रियाओं को (I) वृक्ष विशेष के चरम वर्षों को प्रदर्शित करने वाले घटना वर्षों (II) एक स्थल के भीतर उभयनिष्ठ चरम वर्षों को प्रदर्शित करने वाले स्थल संकेतक वर्षों (III) कराकोरम एवं तिएन शान के भीतर उभयनिष्ठ चरम वर्षों को प्रदर्शित करने वाले क्षेत्रीय संकेतक वर्षों तथा (IV) कराकोरम एवं तिएन शान के मध्य समकालिक चरम वर्षों को प्रदर्शित करने वाले अन्तः क्षेत्रीय संकेतक वर्षों के रूप में वर्गीकृत किया गया है। कराकोरम एवं तिएन शान की तुलना करने से आठ सकारात्मक अन्तः क्षेत्रीय संकेतक वर्ष (सन् 1916, 1804, 1766, 1703, 1577, 1555, 1514, 1431 ई.) तथा सत्रह नकारात्मक अन्तः क्षेत्रीय संकेतक वर्ष (सन् 1917, 1877, 1871, 1833, 1806, 1802, 1790, 1742, 1669, 1653, 1611, 1605, 1591, 1572, 1495, 1492, 1483 ई.) परिणामस्वरूप प्राप्त हुए हैं। ये वर्ष पश्चिमी-मध्य एशिया हेतु वैध हैं।

कराकोरम एवं तिएन शान पर्वतश्रेणियों से प्राप्त चरम वर्ष पुनर्सृजन में क्षेत्रीय संकेतक वर्षों की प्रधानता है। जलवायुविक स्थितियों के परिणामस्वरूप प्राप्त क्षेत्रीय संकेतक वर्ष स्थल पारिस्थितिकी के इतर अधो शुष्क से उपरि आर्द्र वृक्षसीमाओं तथा विभिन्न अनावरणों में वृक्ष वृद्धि को सीमित कर देते हैं। क्षेत्रीय संकेतक वर्षों का मौसमी जलवायुविक प्रणोदन वर्ष दर वर्ष परिवर्तित होता है, किन्तु तापमान में भिन्नता प्रमुखतः वृक्ष वृद्धि को सीमित कर देती है। कुछ चयनित स्थल संकेतक वर्षों के अतिरिक्त विश्लेषणों, जो क्षेत्रीय संकेतक वर्षों से सम्बन्धित नहीं हैं, से अधो वृक्ष सीमा के समीप के स्थलों के वर्षण संकेत तथा उपरि वृक्ष सीमा के समीप के स्थलों के तापमान संकेत प्रमाणित होते हैं।

संकेत शब्द—वृक्षवलयकालानुक्रमिकीविज्ञान, जलवायु, चरम वर्ष, संकेतक वर्ष, स्थल पारिस्थितिकी, कराकोरम, तिएन शान, पाकिस्तान, किर्गिज़िया, *जूनीपेरस*.

INTRODUCTION

ANALYSES of tree ring variation enable the reconstruction of climate history on interannual to centennial time scales (overview in Dean *et al.*, 1996; Schweingruber, 1996). Tree ring width or density chronologies are usually transformed into temperature or precipitation series estimated by calibrating and verifying the proxy variation with climatic station data (Fritts & Guiot, 1990; Cook & Kairiukstis, 1990). A commonly used technique to calculate linear models between climatic and tree ring series is response function (Fritts, 1976). Since a tree ring chronology is a sequence of averages from individual trees, the signal strength of chronologies changes from year-to-year and decade-to-decade (Esper *et al.*, 2001a; Wigley *et al.*, 1984). It is widely known that the extreme years of a mean chronology have the highest signal strength (Schweingruber *et al.*, 1991). Analyzing extreme years is therefore an approach to better understand the climate/tree ring relationship.

The high mountain systems of Central Asia are poorly represented on the worldwide map of dendroclimatic reconstructions. There exists only some tree ring studies from Central Asia, a region that might be one of the key areas to understand global climate change (e.g., Bräuning, 1994, 1999; Zimmermann *et al.*, 1997 in Tibet; Cook & Krusic, 2001; Schmidt & Gruhle, 1995 in Nepal; Bhattacharyya *et al.*, 1988; Borgaonkar *et al.*, 1996; Hughes, 1992; Yadav & Bhattacharyya, 1992; Yadav *et al.*, 1997 in India; Graybill *et al.*, 1992 in Kirghizia; Jacoby *et al.*, 1996 in Mongolia). Earlier work showed the importance of decadal and centennial growth variation in Western Central Asia (Esper *et al.*, 1995; Esper, 2000a, b). Common decadal growth variation, observed in the Karakorum and Tien Shan Mountains, reflects mean, annual temperature variability within a range of -0·2 to +0·2°C (Esper *et al.*, 2001b). These mid-term fluctuations are superimposed on centennial trends verifying the existence of faster growth during the Medieval Warm Period, slower growth during the Little Ice Age, and increasing growth rates again in the most recent centuries. However, the growth level in the modern period does not reach the values recorded around 1000 AD (Esper, 2000b; Esper *et al.*, 2001b). To understand the reconstructed climatic variability on broader spatial scales, a group of cooperating scientists was recently established (Amalava Bhattacharyya, Hemant Borgaonkar, Achim Bräuning, Vandana Chaudhary, Edward Cook, Jan Esper, Paul Krusic, Kolli Rupa Kumar, Govind Pant, Amar Sikder, Limin Xiong) to develop a network of tree ring chronologies reaching from Kirghizia in the West to Central China in the East.

This paper focuses on extreme growth years of a tree ring network from the Karakorum (Pakistan) and Tien Shan Mountains (Kirghizia) in Western Central Asia. We present a reconstruction of extreme growth years since 1427 AD and explain the climatic information of extreme years in relation to the ecology of the sampling sites.

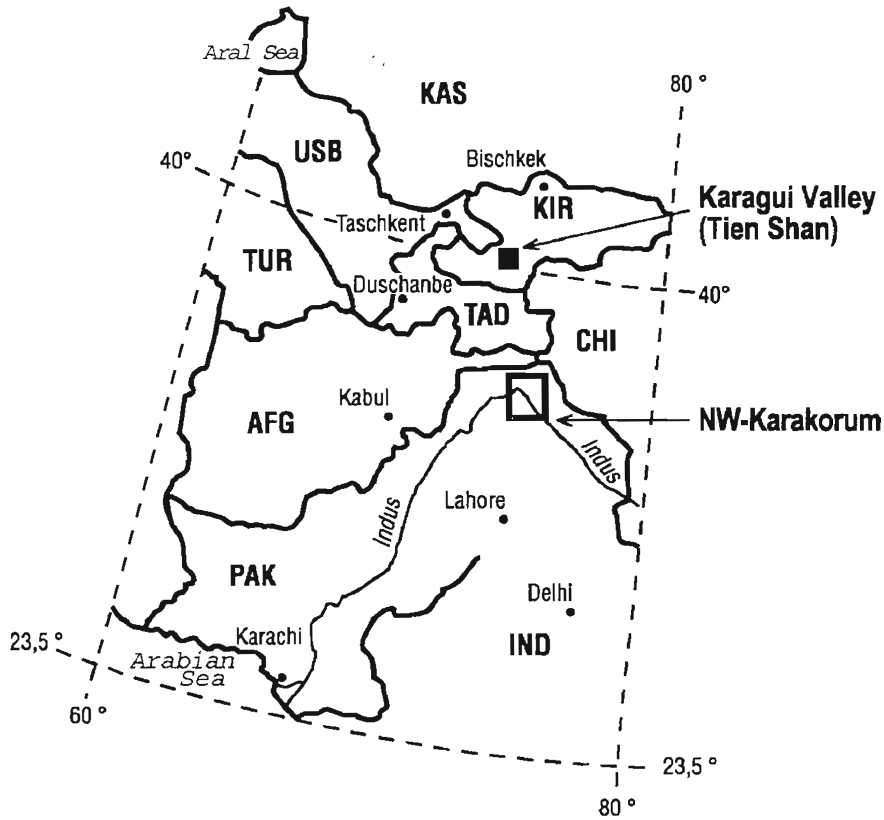


Fig. 1—Western Central Asia region and study areas in the Tien Shan and the Karakorum Mountains.

DATA AND METHODS

More than 2,00,000 ring width values were measured from core samples of 429 *Juniperus* (*J. turkestanica* Kom., *J. seravchanica* Komarov. and *J. semiglobosa* Regel), *Pinus wallichiana* A.B. Jackson and *Picea smithiana* (Wallich) Boiss. trees from the northwest Karakorum of Pakistan and the southern Tien Shan of Kirghizia (Fig. 1). Seven sites were sampled in the Karagui Valley of Kirghizia (K1-K7) and 15 sites from four valleys (P1-P4) in Pakistan. The NNW-facing sites P1a-P1c of the Bagrot Valley are the only mixed sampling locations of *Juniperus*, *Pinus* and *Picea*. All other sites represent pure *Juniperus* samplings (Fig. 2).

Sampling sites reach from 2,700 to 3,900 m asl. in the Karakorum and from 2,550 to 3,200 m asl. in the Tien Shan between the lower, arid, and upper, humid timberlines. Site ecology is also determined by exposure and the distance to monsoonal air masses. The Bagrot Valley (P1) receives the highest amount of rainfall, followed by the Chaprot (P2), the Morkhun (P3) and the Satpara valleys (P4). Elevation, exposure and valley positions enable a classification of the sites within an ecogram (Kaennel & Schweingruber, 1995), such as shown in Fig. 3 for the Karakorum. We presume that tree growth at cold-wet sites is predominantly limited by temperature and at warm-dry sites by precipitation. Tree age at low elevation sites is generally lower than at high elevation sites (Fig. 2).

Even though the distance between the northwest Karakorum (35-37°N/74-76°E) and southern Tien Shan (40°10'N/72°35'E) is only 500 km, different synoptic weather patterns influence each region. The Karakorum sites are affected by westerlies and monsoonal depressions, and the Tien Shan sites by a strong continental climate, without precipitation transport from the Arabian Sea (Böhner, 1996; Flohn, 1958; Reimers, 1992; Weiers, 1998).

Extreme growth reactions within a sequence of i years are classified as follows. Extreme years of individual trees are named »event years« (e_i) (Schweingruber *et al.*, 1990). Synchronous event years of one site result in »site pointer years« (sp_i). Synchronous site pointer years result in »regional pointer years« (rp_i), reflecting common extreme years within the Karakorum region or the Tien Shan region. Synchronous regional pointer years between the Karakorum *and* the Tien Shan result in »inter-regional pointer years« (ip_i).

Event years (e_i) are calculated following a two-step-procedure (Cropper, 1979). First, the residuals (r_i) from a 5-year digital filter, fitted to each individual ring width series, are calculated. This technique removes any low frequency signal. The r_i values are then divided by the standard deviation within a five-year moving-window. This second step scales

Chrono	Valley	Elevation	Exposition	No. of Trees	Max. Age	Aver. Age [yr.]
K1	Karagui	3200 m	SW	30	AD1316	346
K2	40°10'N/72°35'E	3000 m	SSW	25	AD1157	422
K3		2900 m	N	20	AD1346	326
K4		2900 m	SSW	18	AD1591	221
K5		2800 m	W	43	AD1378	227
K6		2600 m	SSW	27	AD1839	93
K7		2550 m	N	13	AD1781	82
P1a	Bagrot	3100 m	NNW	26	AD1535	189
P1b	36°02´N/74°35´E	3300 m	NNW	19	AD1369	268
P1c		3750 m	NNW	5	AD1679	224
P1d		3050 m	S	21	AD1438	236
P1e		3750 m	S	17	AD1240	218
P2a	Chaprot	2700 m	S	14	AD1587	173
P2b	36°20´N/74°02´E	3500 m	S	19	AD1032	481
P2c		3900 m	S	11	AD1144	459
P3a	Morkhun	3900 m	SW	13	AD 476	517
P3b	36°35´N/75°05´E	3800 m	ENE	15	AD 968	510
P3c		3600 m	ENE	20	AD 554	632
P3d		3900 m	SSE	18	AD1069	398
P4a	Satpara	3300 m	NW	13	AD1412	343
P4b	35°10´N/75°30´E	3700 m	S	18	AD 736	755
P4c		3900 m	S	17	AD 388	581
P5	Hunza	single trees		7	AD 568	774

Fig. 2—Western Central Asia tree ring chronologies.

the variance between different periods and series. The resulting e_i values are multiplied by 1000. The highest and lowest e_i values indicate the outliers of individual series. e_i values are then averaged for each site to calculate sp_i sequences. Site pointer years are again classified by ranking the highest and lowest sp_i values of each century, for example, outstanding sp_i values are only reached if e_i values of individual trees are synchronous. The classification of regional and inter-regional pointer years follow the same procedure.

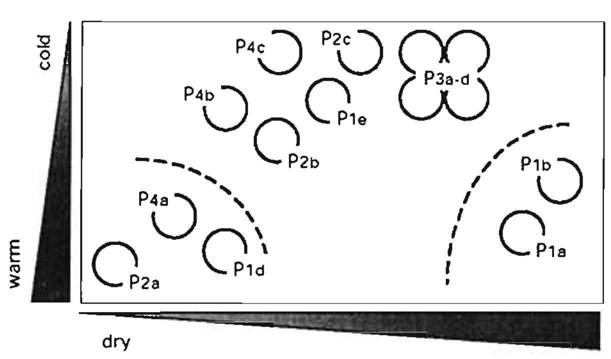


Fig. 3—Classification of the Karakorum sampling sites in an ecogram. Sites near the lower timberlines are »warm and dry«, sites near the upper timberlines are »cold and wet«. Site exposure and valley position likewise specify the location of the sites in the ecogram.

For calibration purposes the monthly mean temperature and precipitation series from the stations Peshawar, Lahore, Murree and Gilgit in Pakistan, and Simla and Ludhiana in India are used. The normalized annual precipitation amounts and annual temperature means of the six stations are shown in Fig. 4. Averaging these stations to regional mean curves is suitable to estimate the conditions at high mountainous tree ring sampling sites. Mountainous climate stations alone are generally less representative and too short to calibrate tree ring variation (Esper, 2000b). This is particularly true for rainfall. While the total average, annual precipitation at Gilgit is only 131 mm, rainfall near the upper timberline of the nearby Bagrot Valley is estimated 800 mm/a and more (Cramer, 2000). The signals in common, recorded by mean, annual precipitation and temperature series (Fig. 4, thick curve), are lower for precipitation than for temperature. The significant rainfall variability over space and with elevation needs to be considered when pointer years are calibrated (Böhner, 1996; Reimers, 1992).

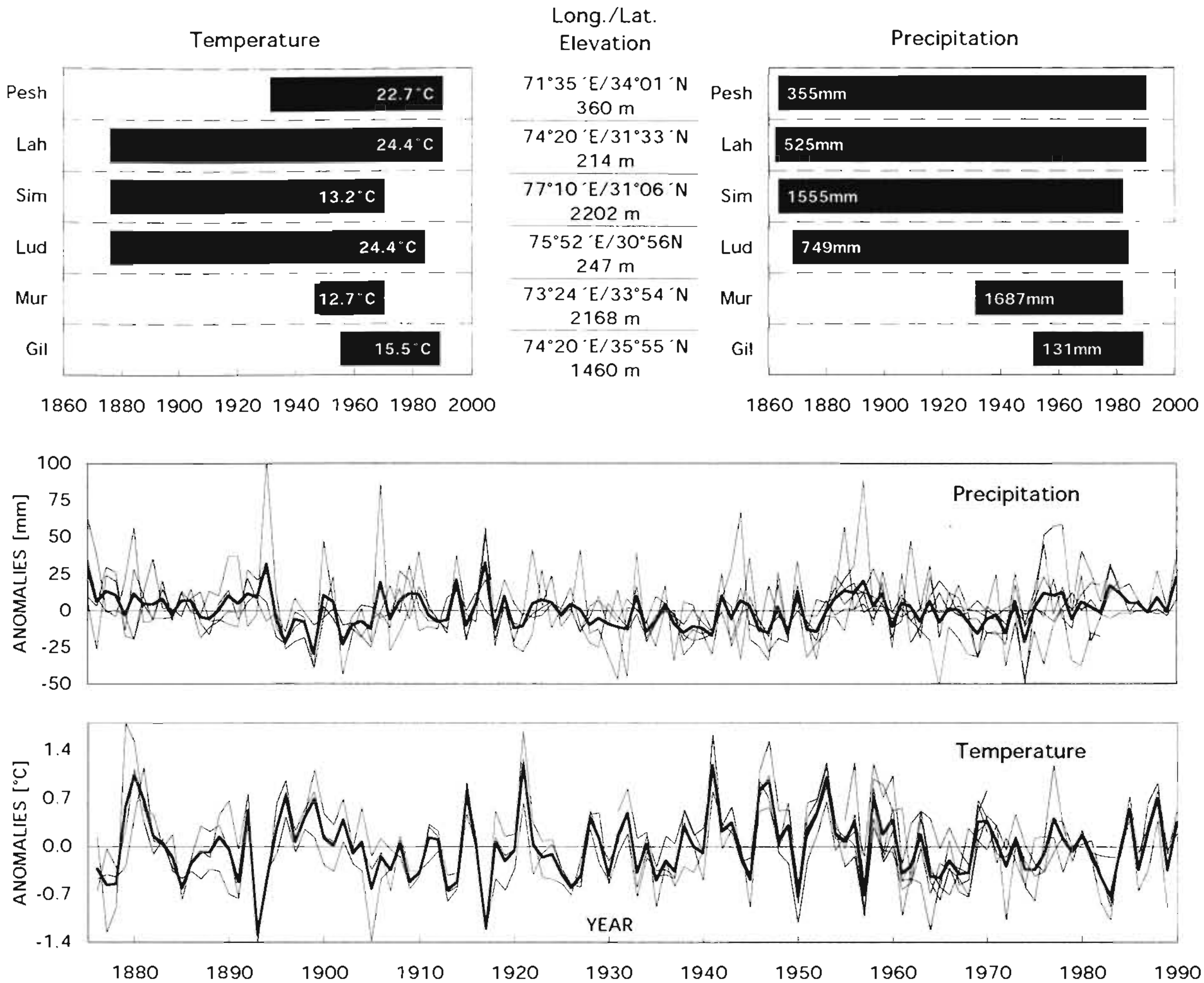


Fig. 4—Length, location and mean values of six climatic station data sets. The curves show the normalized, mean annual precipitation and temperature series (thin curves), and the regional averages (thick curves).

RESULTS

a. Regional and inter-regional pointer years

Fig. 5 shows the reconstruction of regional pointer years of the Karakorum and Tien Shan since 1800 AD. The individual site pointer values (gray and white planes) were divided by the number of sites in each region (Pakistan = 16, Kirghizia = 7), before adding them to regional pointer years. 10 regional pointer years per century are labeled at the top and bottom of the histograms. They only occur, if individual site pointer years appear synchronously. The numbers of trees contributing to regional pointer years are 232 in 1990 AD (221 in 1899 AD) for the Karakorum, and 173 in 1990 AD (145 in 1899 AD) for the Tien Shan.

Regional pointer years refer to climatic conditions forcing the trees of most sites to extreme growth reactions. These reactions are synchronous, even though the sites are located in different exposures, and reach from the lower to the upper timberlines with altitudinal differences of more than 1000 m. Regional pointer years result from climatic conditions limiting tree growth independently of site ecology. Note that the site pointer years are also synchronous between the four sampled valleys of the Karakorum (P1-P4). The distance of these valleys is more than 100 km.

Regional pointer years that are synchronous between the Karakorum and the Tien Shan are labelled bold in Fig. 5. Following this criteria, five positive inter-regional pointer years (1916, 1910, 1878, 1832, 1804 AD) and 10 negative inter-regional pointer years (1936, 1917, 1911, 1877, 1871, 1858, 1833, 1810, 1806, 1802 AD) are reconstructed since

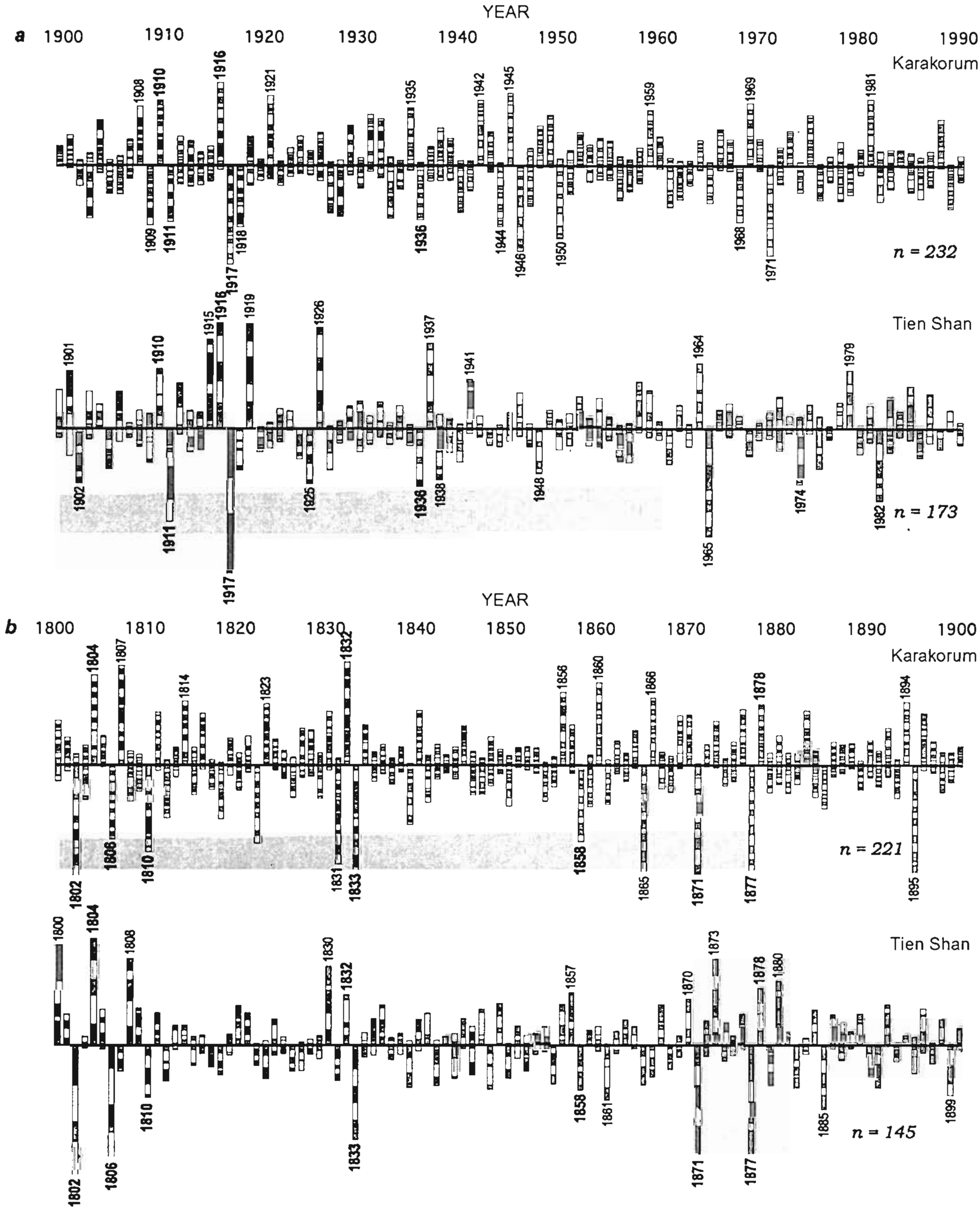


Fig. 5—Pointer year values of 16 Karakorum and seven Tien Shan sampling sites (gray and white planes) AD1900-1990 (*a*) and AD1800-1899 (*b*). Regional pointer years are labeled at the top and bottom of the histograms. Inter-regional pointer years are labeled bold.

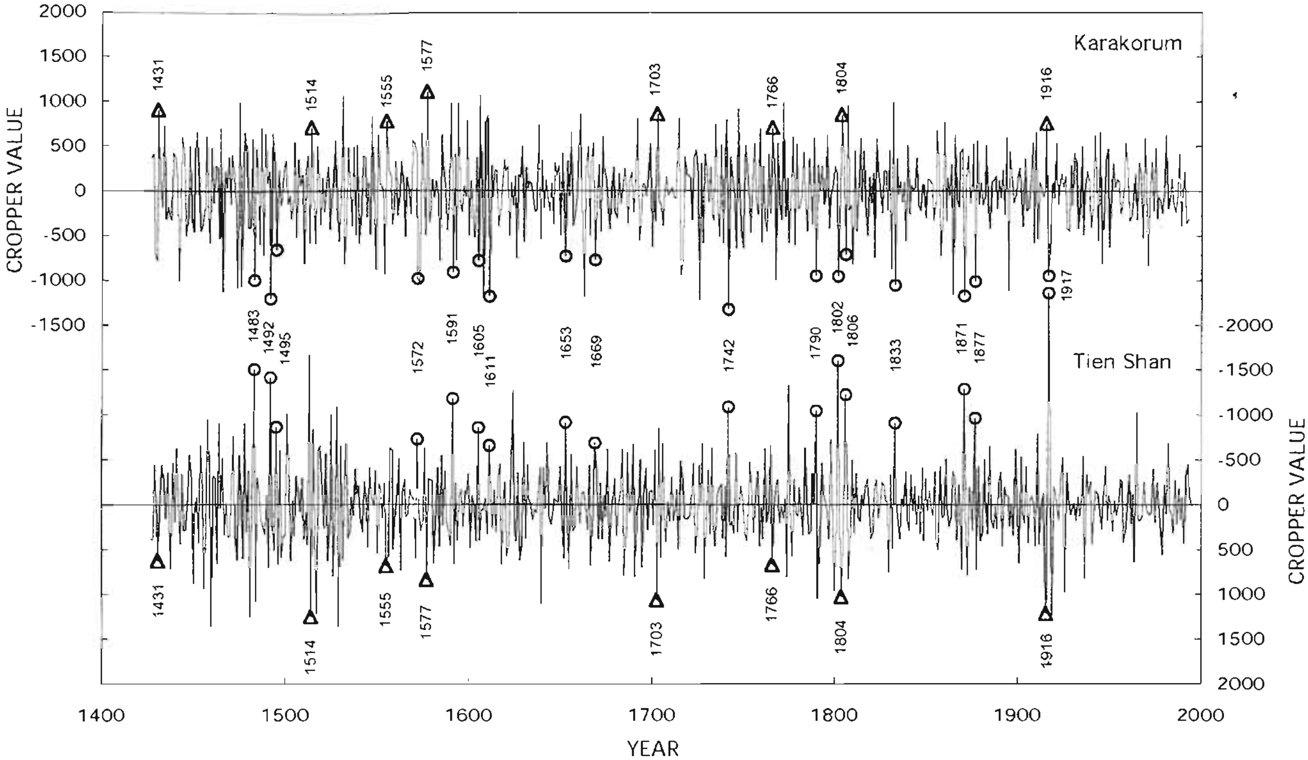


Fig. 6—Inter-regional pointer year reconstruction for Western Central Asia since AD1427. Extreme high and low curve values indicate regional pointer years in the Karakorum and Tien Shan. Synchronous, inter-regional pointer years are labeled with triangles (positive) and circles (negative). Inter-regional pointer years must be among the 50 strongest regional pointer years observed in both the Karakorum and the Tien Shan Mountains.

1800 AD. Negative pointer years are more synchronous within the sites, the regions and in between the regions. Accordingly, they have a higher potential to reconstruct climatic extreme years.

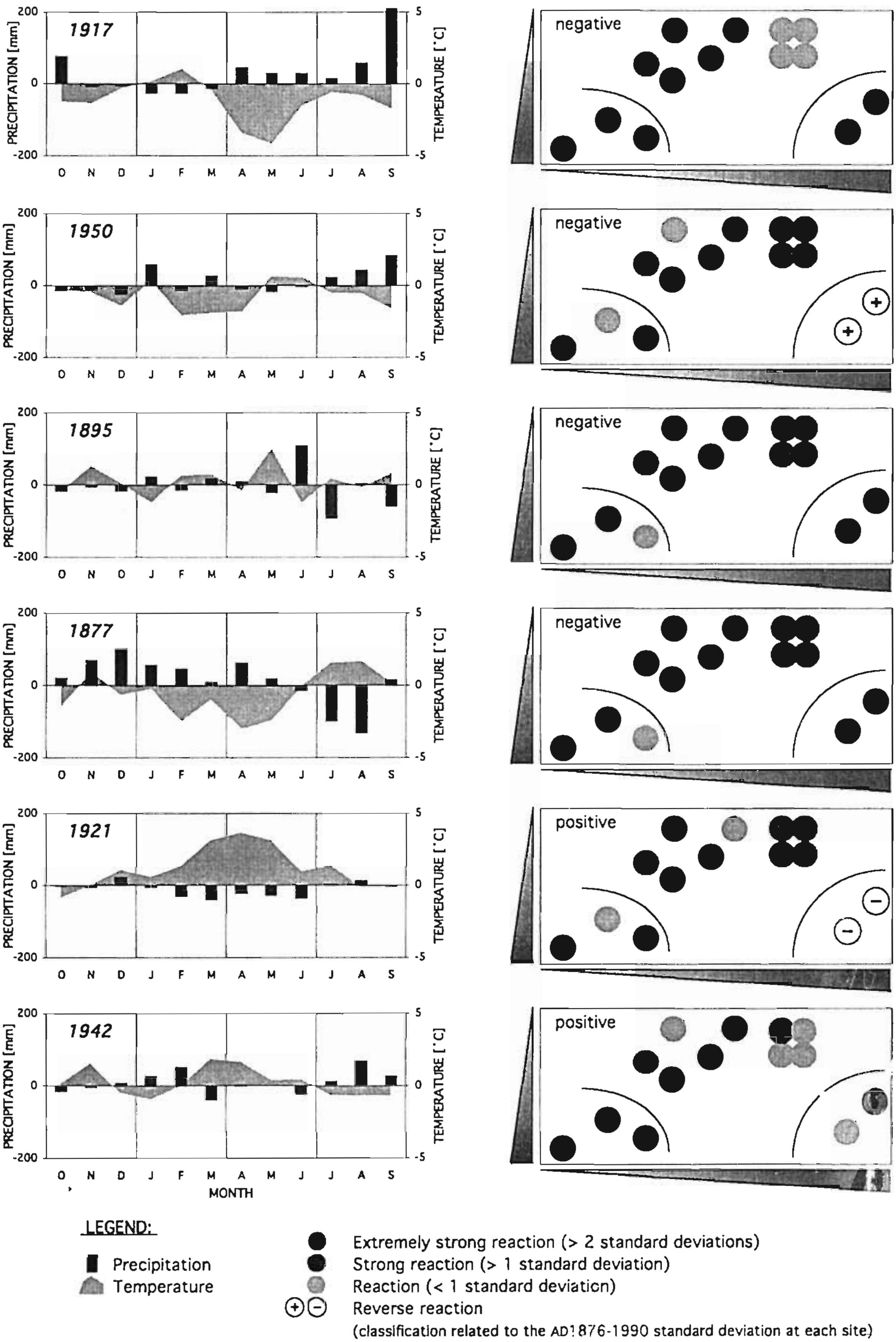
A different, more rigorous approach to reconstruct inter-regional pointer years for Western Central Asia since 1427 AD is shown in Fig. 6. The curves represent regionally averaged pointer values after Cropper (1979) for the Karakorum and the Tien Shan Mountains. Synchronous, inter-regional pointer years from the 50 highest and lowest regional pointer year values are labeled with triangles (positive) and circles (negative). This method is more rigorous than the reconstruction shown in Fig. 5 (less years are labeled in the 19th and 20th centuries), and we recommend using the years labeled in Fig. 6 for calibration purposes with other work, from Nepal, India, or Tibet, for example. Following this strict technique, eight significant positive and 17 negative inter-regional pointer years are reconstructed over the last 564 years. In other words, the chance for a positive pointer year in the Karakorum is increased, if a positive pointer year is reconstructed from the Tien Shan, and vice versa. This chance is again significantly higher for negative regional pointer years.

b. Climatic signals of pointer years

We applied two different techniques to calibrate extreme growth reactions in the Karakorum, (i) analyses of regional pointer years, and (ii) analyses of site pointer years that do *not* belong to regional pointer years.

Fig. 7 shows the site pointer years of the Karakorum in relation to site ecology (right column) together with the temperature and precipitation anomalies from the preceding October to the current September (left column). Site names and ecological parameters are listed in Fig. 2 and Fig. 3. Since negative pointer years are more common within and between the sites, four negative (1917, 1950, 1895, 1877 AD) and only two positive regional pointer years (1921, 1942 AD) are illustrated. The temperature and precipitation anomalies were derived from a maximum of six stations representing regional climatic variability of the northwest Karakorum (see Fig. 4). Site pointer years are ranked by standard deviation units from »reaction«, to »strong reaction«, »extremely strong reaction«, and »reverse reaction«.

1917 AD is one of the most severe negative regional pointer years recorded for the Karakorum. All sampling sites show a negative pointer year, forced by cold conditions during


1917
1950
1895
1877
1921
1942
PRECIPITATION [mm]
TEMPERATURE [°C]
200
0
-200
5
0
-5
O N D J F M A M J J A S
MONTH
negative
negative
negative
negative
positive
positive
LEGEND:
Precipitation
Temperature
Extremely strong reaction (> 2 standard deviations)
Strong reaction (> 1 standard deviation)
Reaction (< 1 standard deviation)
Reverse reaction
(classification related to the AD1876-1990 standard deviation at each site)

the growing season. Temperatures were extremely cold in May. The cambial activity at the sampling sites was reduced, even if the amount of rainfall was sufficient. The reactions were strongest at the wet NNW-facing sites of the Bagrot Valley (ecogram, right corner) and the dry, low elevation sites of the Bagrot, Chaprot and Satpara valleys (left corner). An unexpected result was the strong response of the second group, located close to the arid lower timberline. Prominent work, done along comparable altitudinal transects in the US (e.g., La Marche, 1974), verified a changing response with elevation: drought near the lower timberlines, and cold near the upper timberlines. This conclusion does not hold for the regional pointer years from the Karakorum. The result is confirmed by the low elevation sites of the Tien Shan, which frequently have a missing ring in 1917 AD.

A comparison of the temperature and precipitation anomalies in all four negative regional pointer years indicates that the seasonal climatic forcing is different from year-to-year. Synchronous site pointer years of the Karakorum result from different climatic constellations, a characteristic feature of pointer year analyses (Schweingruber *et al.,* 1991). For example, the temperature and precipitation regimes in 1950 and 1895 AD are very different, but in both years most of the sampled tree ring sites react strongly. In 1950 AD a cold winter with a late start of the vegetation period, and in 1895 AD extreme rainfall conditions in June and July are responsible. The impact of extreme rainfall changes is verified by density fluctuations recorded in the 1895 AD tree ring. 1877 AD is a regional pointer year, caused by severe changes from cold-wet conditions in the pre-season, to warm-dry conditions in the vegetation period.

Even though changing climatic conditions might be responsible for some negative regional pointer years, low temperatures seem to limit tree growth predominantly. This assumption is supported by the positive regional pointer years. 1921 AD is the warmest year of the entire climatic record, and in 1942 AD warm conditions reach from early spring to early summer. In addition, sufficient rainfall is recorded during the generally hot summers of the Karakorum Mountains.

Conspicuous, reverse growth reactions are recorded at the mixed *Juniperus*, *Picea* and *Pinus* sites in 1950 AD and 1921 AD (ecogram, right corner). These years prove the different response of the mixed sampling sites in comparison to the pure *Juniperus* sites sampled elsewhere. Interestingly enough, the mixed sites deviate frequently from the homogenous *Juniperus* sites in years with significant precipitation anomalies (without figure). This result confutes the contention that the NNW-facing, mixed sampling sites of the wet Bagrot Valley are predominantly limited by cold conditions.

To understand the effects of site ecology in greater detail, Fig. 8 lists the pointer years of each Karakorum site that does *not* belong to regional pointer years (column 1). This strategy excludes regional pointer years like 1917 AD, where all sites reacted commonly. Columns 2 and 3 name the sites and, in brackets, the rank of the site pointer year. »III« in row one, for example, means that 1988 AD is the third strongest pointer year at site P3d. The site pointer years ranking first and second belong to regional pointer years. Column 5 discusses significant temperature and precipitation anomalies, and column 6 explains the climatic forcing in relation to site exposure and elevation.

According to Fig. 8, 14 out of 23 site pointer years can be explained, i.e., high elevation sites are limited by temperature and low elevation sites by precipitation, and only nine years do not fit. The site pointer years 1985, 1978, 1931, and 1903 AD can not be readily explained by climatic variation. 1949, 1927, 1892, and 1885 AD are only likely understood, and in 1883 AD a low elevation site apparently reacts to temperature. The analysis shows that the predicted limitation of high elevation sites by temperature and of low elevation sites by precipitation holds only, if different climatic seasons are considered. This evidence limits the obvious tendency that site pointer years near the upper timberline reflect temperature and near the lower timberline precipitation variation.

DISCUSSION

Many of the observed site pointer years are synchronous within one region, causing a frequent occurrence of regional pointer years since 1427 AD. Additional comparison of regional pointer years between the Karakorum and Tien Shan Mountains resulted in eight positive and 17 negative inter-regional pointer years reflecting extreme growth conditions uniform for Western Central Asia. Both results were not expected, since the site ecology changes dramatically within the regions, and the regions belong to different climatic zones. The recorded uniform growth reactions (regional and inter-regional pointer years) question the concept of changing climatic signal strength with changing elevation (e.g., La Marche, 1974) for Western Central Asia, and the differences between the climatic zones outlined in climate atlases (e.g., Köppen, 1918; Troll, 1943).

Even though the analyses of selected site pointer years proved a predominant response to temperature variation at

←

Fig. 7—Temperature and precipitation variation in regional pointer years of the Karakorum. Intensity and sign of the site pointer years reach from »extremely strong reaction« to »reverse reaction«. Ecology of the sampling sites is classified by the location of the sites in the ecogram (see Fig. 3).

YEAR	NEGATIVE	POSITIVE	ELEV./EXP.	TEMPERATURE AND PRECIPITATION	EXPLANATION
1988		P3d (III)	3900 m/SSE	Nov-Feb & Apr-May warm Mar wet	high elevation S-site reacts to **T**
1986	P3c (VI)		3600 m/ENE	Mar-Sep cold	high elevation N-site reacts to **T**
1985	P4a (III)		3300 m/NE	Nov-Apr warm	?
1983		P4a (I)	3300 m/NE	Feb-Jul cold Mar-Apr & Aug wet	low elevation S-site reacts to **P**
1982	P4b (I)		3700 m/S	Feb-Jul cold Mar-May wet, Jul & Sep dry	high elevation S-site reacts to **T** (may be summer drouth)
1978		P2c (IV)	3900 m/S	Mar & Jul cold, May warm Mar & Jun-Jul wet	?
1949		P2b (III)	3500 m/S	Apr-May & Sep warm Aug dry	high elevation S-site likely reacts to spring **T**
1947	P1d (IV)		3050 m/S	Feb-Aug warm Feb-Aug dry, Sep wet	low elevation S-site reacts to **P**
1938		P3b (II)	3800 m/ENE	Mar-Sep warm Mar-Sep dry	high elevation N-site reacts to **T**
1933	P2b (II) P3b (I)		3500 m/S 3800 m/ENE	Apr-May & Aug-Sep cold Aug-Sep wet	high elevation site reacts to **T**
1932		P3a (I)	3900 m/SW	Jan-Apr & Jun warm Jan-Feb & Apr & Jun-Jul dry	high elevation S-site reacts to **T**
1931		P1d (II) P2a (I)	3050 m/S 2700 m/S	Feb cold, Apr & Aug warm Jan-Apr & Jun-Jul dry, Aug-Sep wet	? ?
1930	P1e (III)		3750 m/S	Apr & Jun-Jul cold Jul wet, Aug dry	high elevation S-site reacts to **T**
1927	P2a (II)		2700 m/S	Jan-Mar cold Jan & Mar-Jun dry, Aug wet	low elevation N-site likely reacts to **P**
1914		P1a (IV)	3100 m/NNW	Feb-Jun cold Apr-Jul & Sep wet	low elevation N-site reacts to **P**
1909	P4c (III)		3900 m/S	Dec-Feb & Apr-Sep cold Mar & Aug dry, Apr & Jun-Jul wet	high elevation S-site reacts to **T**
1904		P3c (III)	3600 m/ENE	Apr-Aug warm Mar wet, Apr-Sep dry	high elevation N-site reacts to **T**
1903	P1b (III) P3a (VIII) P3d (IV)		3300 m/NNW 3900 m/SW 3900 m/S	Mar-May cold, Jun-Jul warm Feb & Jun-Jul dry	? ? ?
1892		P4b (III)	3700 m/S	Jan-May warm, Aug-Sep cold Jan-Jun dry, Aug-Sep wet	high elevation S-site likely reacts to spring **T** (or summer **P**)
1885	P2c (IV)		3900 m/S	Feb & May cold Jan & Apr-May wet, Jun & Sep dry	high elevation S-site likely reacts to extreme conditions in May
1884	P1a (IV)		3100 m/NNW	Jan warm Dec-Jun dry, Aug-Sep wet	low elevation N-site reacts to **P**
1883		P1b (IV)	3300 m/NNW	Apr-Aug warm Jan & May & Sep wet, Aug dry	low elevation N-site reacts to **T**
1880		P4c (IV)	3900/S	Mar-Jun & Aug-Sep warm Mar-Apr dry, Mai-Jul wet, Aug-Sep dry	high elevation S-site reacts to **T**

Fig. 8—Temperature and precipitation anomalies in site pointer years of the Karakorum that do not belong to regional pointer years. Column 1 lists the site pointer years, column 2 and 3 the sites, column 4 the elevation and exposure, column 5 the climatic anomalies, and column 6 the tree ring response.

high elevation sites, and to precipitation at low elevation sites, the climatic forcing is not completely understood. Characteristic of the climatic signals in pointer years is the changing forcing seasonality from year-to-year. Some pointer years are caused by climatic anomalies in the pre-season, some in the vegetation period. And even at the low elevation sites, some pointer years are caused by temperature anomalies. This result confirms findings of comparable analyses (e.g.

Schweingruber *et al.*, 1991), which showed that similar pointer years were caused by drought in one year and by cold in another year.

Schweingruber *et al.* (1991) also indicated that single climatic events, like frosts, trigger pointer years as well. These findings point to the climatic data sets available for the Karakorum and Tien Shan region. Single, mountainous stations are not representative to calibrate tree growth at high elevation sites. They are generally located on the arid valley bottoms, and the length of these data sets is limited. Analyses of the impact of single frost events, for example, are not possible on the basis of monthly mean climatic data sets. Calculating regional averages from several climatic stations is the only, but limited, chance to calibrate ring width variation from the Mountains of Pakistan and Kirghizia.

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Conference/Symposia/Workshop Reports

International conference on the Climate and Biota of the Early Paleogene

3-8 July, 2001
Powell, Wyoming, USA

An International Conference entitled, "Climate and Biota of the Early Paleogene" was held at Northwest College, Powell, USA from July 3-8, 2001. The Conference was sponsored by the Smithsonian Institution and University of Michigan. It was the third in a series of conferences on the Paleogene; the previous two were held in Albuquerque, New Mexico (1997) and Goteborg, Sweden (1999).

The conference started with a welcoming reception on July 3rd at the Powell Valley Chamber of Commerce. Oral presentations and poster sessions were held on 4th, 5th and 7th July, bounding a day and a half of field trips in the Bighorn Basin. Posters remained on display throughout the Conference and viewing took place before or after scheduled oral sessions. On July 4 after a full day of technical scientific presentations, all the participants went to the Churchill Farms for the annual 4th of July barbecue. This day is very important in the American history as it happens to be the Independence Day of America.

There were total 170 participants belonging to about 20 countries, namely Argentina, Australia, Austria, Belgium, China, Denmark, Egypt, France, Germany, India, Ireland, Italy, Mongolia, Netherlands, New Zealand, Pakistan, Russia, Spain, Sweden, Switzerland, Syria and United Kingdom, besides the host USA.

The present conference provided an opportunity to all the participants working on Paleogene to interact with each other and to know the latest development on different aspects of palaeobotany. Though most of the papers were on isotopes which are useful in deducing the palaeoclimate, sedimentological studies, palaeomagnetism, macrofossils, pollen, dinoflagellates, nannofossils, foraminifera, molluscs, vertebrates and palaeosols etc. were given due importance. The emphasis was on the causes of global warming that began in the Paleogene, 65 million years ago.

During the oral presentations the role of oceans was discussed in maintaining the warm climate. One of the talks was on K/T and P/E boundaries in dinoflagellate perspective. Some of the important papers were on the impact of Palaeocene-Eocene Greenhouse warming on North American Paratropical forests, testing of canonical correspondence analysis (CCA) and regression models developed to predict mean annual temperature (MAT) using leaf morphology and wood anatomy, Europe - Asia mammalian faunal interchange during the early Eocene, the Early Paleogene climate and leaf flora of New Zealand, the palaeoecology of Eocene insects from Central Europe, chronostratigraphic terminology at P/E boundary and Paleogene West Antarctic climate and vegetational history. The plants from King George Island in Antarctica are the most complete Paleogene terrestrial foliar record in Antarctica. In one of the talks Early Paleogene vegetation of India was presented and position of the Indian Plate during the period was discussed. According to Philip Gingerich of the University of Michigan horses, predators, primates and other mammals emerged during a brief period of extreme warming during the Early Paleogene. Lastly a new locality of K/T boundary was reported which is rich in plant megafossils, pollen, vertebrate and invertebrate.

Powell, the venue of the conference, is surrounded by the best exposed and most intensively studied continental upper Palaeocene- lower Eocene sections in the world and is about 35 miles from the nearest Cody Airport. There were two field trips. The first one was a half day field trip to Cretaceous, Palaeocene and Eocene of Polecat Bench on July 5. Polecat Bench is a flat topped area of high relief north of Powell and the purpose of this trip was to demonstrate the features of the best studied, relatively complete Palaeocene section in the Bighorn Basin. At the east end of Polecat Bench the participants were shown the Maastrichtian Lance Formation, the lower part of the Palaeocene Fort Union Formation and the paraconformable K/T boundary. Historically the K/T boundary in the northern rocky mountains was approximated as the lowest coal bed above the highest dinosaur fossils. More recent work has shown that the onset of coal deposition is always not precisely synchronous with the K/T boundary which is generally recognised by Ir anomaly, shocked quartz and palynofloral change. No Ir anomaly or shocked quartz has been detected in this exposure, but pollen indicates that the K/T boundary is in the carbonaceous shale just below the basal coal of the Fort Union Formation. At the southern end of Polecat Bench the conference delegates examined Palaeocene -Eocene boundary sections of the Willwood Formation. The second field trip was a full day trip to upper Palaeocene- lower Eocene of the Central/ Southern Bighorn Basin on July, 6. On this trip the participants saw the extensive fossiliferous hills striped with red and purple and belonging to middle and upper portions of the Willwood Formation. Thousands of fossils- mammal bones, leaves and shells etc. have already been collected from there and are kept in various museums of USA.

The conference was well organised and successful in its objectives.

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6th International Conference on Biogeochemistry of trace elements

29 July-2 August 2001
University of Guelph, Ontario, Canada

6th International Conference on the Biogeochemistry of trace elements was held at University of Guelph, Ontario, Canada from 29th July to 2nd Aug. 2001. This conference was successively held in Orlando (1990), Taipei (1993), Paris (1995), Berkeley (1997) and Vienna (1999). The conference meeting held after every three years is dedicated to examine contemporary and emerging research in the biogeochemistry of trace elements, an interdisciplinary science linking phenomena, observed in the biosphere to physical and chemical reactions in the lithosphere. About 700 delegates from all over the world gathered here to discuss on issues related to phytoremediation, bioavailability, ecotoxicity etc. of trace metal contaminants. Four important areas of research were highlighted: (1) chemical modelling and speciation, (2) factors controlling the reductive transformations of trace metals and its immobilization by microbes, (3) risk assessment and ecosystem health covered the relevance of reactivity determinants to environmental and Biological Monitoring of the elements and their Inorganic compounds and (4) biological and chemical remediation and the future of 'Green technology' and metal-contaminated ground water were the main concern of the delegates.

Some of the discussions highlighted during the deliberations were—

In the last decade phytoremediation of trace metal contaminants has changed from a conceptual methodology to a practical and commercially-viable technology for environmental clean-up for both organic and inorganic contaminants. Phytoextraction of metal contaminants in soil/ water is potentially an attractive, low cost, '*in situ*' "Green Technology" for the progressive clean-up of metal-polluted soils. Its simplicity has found immediate appeal and acceptance in an environmentally aware and responsible society. The potential is enhanced even further by the excessive costs of existing physico-chemical technology for soil clean-up. It offers the possibility of selectively removing only the metal contaminants leaving a soil in every other way unaffected. Expectations of this developing technology however still far exceed present capabilities.

Worldwide problem of Arsenic, a common toxic metalloid in natural ecosystems and the mining industry was extensively discussed. Its minerals such as Arsenopyrite, Realgar and Orpiment are often associated with coal deposits. The combustion of fossil fuels, particularly lignite, introduces large quantities of arsenic into the environment. Lignite is largely composed of organic matter, but As and other trace elements are connected with inorganic matter. In mineralized rocks it is formed under mesothermal and epithermal conditions. It can be fixed temporarily or permanently with mineral matter or released in solution into the environment. The bioavailability of arsenic in these situations depends on the physical and chemical conditions of specific sites.

Rivers and Streams carrying inland waters towards the deltaic areas in the coastal region are the sink for trace elements brought from the weathered rocks through which the drainage passes. Metal- oxyhydroxides that settle into the lagoons and estuaries along with organic debris either clastic or '*in situ*' create conducive anoxic depositional environment where specially Arsenic and other trace metals are associated with the microbially mediated reactions. My presentation highlighted trace elements problem in Coastal areas. High concentration of trace elements is found in the estuaries and lagoons of India. Mangroves play a significant role in mitigating coastal trace element contamination. The consequences of its slow poisoning and subsequent fatal end has boggled the minds of the researchers to provide safe drinking water to the environmentally aware local inhabitants in the coastal region and Arsenic contaminated sites.

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5th International Conference on Biodeterioration of Cultural Property (ICBCP-5)

12-14 November 2001
Australian Museum, Sydney, Australia

The fifth International Conference on Biodeterioration of Cultural Property was held at the Australian Museum, Sydney, Australia from 12 to 14 November 2001. The conference was organized under the auspices of the International Council for Biodeterioration of Cultural Property (ICBCP) and jointly hosted by the Australian Institute for the Conservation of Cultural Material (AICCM) and the Australian Museum Research Center for Materials Conservation and the Built Environment. The conference was sponsored by Albox Australia Pvt. Ltd., CPM Pest Services, Macmillan Academic & Reference, Australian & Powerhouse Museums. The scientists and museum personnel from many countries such as Japan, Australia, France, Nigeria, Germany, Netherlands, Singapore, Canada, USA, UK, India, etc. participated and discussed the present state-of -art and future strategies on all aspects of biodeterioration and its bioremediation. The conference was held at Australian Museum for three days under fifteen sessions. The level G of the Museum where the auditorium was situated, the large galleries exhibited huge skeletons of dinosaurs and humans in different postures. Level 1 stores a Grand Chapman collection of 850 dazzling minerals. The level 2 showed the ancient megafauna, human evolution, biodiversity and many types of strange and unique Australian spiders, birds and insects.

Earlier conferences were held at India, Japan, Bangkok and Tehran. The present conference was aimed to investigate the causes and control of biodeterioration across a range of cultural property, with a particular emphasis on the application of findings for small museums and developing countries.

My paper entitled "Sampling and estimate of fungal biodeteriogens of Lucknow India", dealt with technique of international standards for qualification and quantification of air-borne microbes. An efficient and reliable sampling is a prerequisite for the proper identification, quantification and management of such problems. Andersen, Rotorod and Burkard air-samplers were employed over a period of one year (January – December, 1997) in both extramural and intramural environments of Lucknow. Certain predominant fungi such as *Alternaria, Aspergillus, Cladosporium Chaetomium, Curvularia, Helminthosporium, Penicillium, Paecilomyces, Torula, Trichoderma* etc. are observed to be associated with the biodeterioration of cultural properties. Both quantitative and qualitative estimates of aeromycoflora have been fruitfully utilized in prediction of various fungal biodeteriogens at particular time and place.

Some of the important papers were Heat Eradication of Insect Infestations: The Development of a Low Cost, Solar Heated Treatment Unit by Andrew Pearce, Australia. Experimental Study of Physical Effects of Freezing Method for Insect Control on Artifact Materials by Takeshi Ishizaki, Japan. The Solar Tent – Cheap and Effective Pest Control in Museums by Agnes W. Brokerh, Netherlands. Monitoring Insect Pests Within Buildings Using Traps – Case Studies of The Use of Traps to Monitor Activity, Spatial Distribution and Efficacy of Pest Control by David Rees, Australia and the present situation of Pest Control of Cultural Properties in Taiwan by Su-Fen Yen, Taiwan.

Hideo Arai of ICBCP, Japan, presented his paper entitled 'Biodeterioration on Angkor site in Cambodia'. He reported severe damage to Angkor site in Cambodia due to bats, plants, lichens and microorganisms. *Gleocapsa, Scytonema, Lyngbya* (Cynophyceae) and *Pyxine,Dirinaria, Lepraria* and *Buellia* (lichens) were found to be main biodeteriorating agents. Nine kinds of lichenocides, algaeocides and biocides were applied as control measures over sandstones. Chiraporn Aranyanark, Bangkok presented her paper entitled 'Biological Agent in the Weathering of Sandstone Sanctuaries in Thailand'. She inferred that apart from lichens and algae, the other biodeteriorating agents are mosses, liverworts, ferns, grasses and dicot plants. Her studies were based on advanced technologies such as optical, polarised, scanning electron microscope and x-ray diffractometer studies.

Robert Child of National Museums and Galleries of Wales presented his paper entitled' Residual Insecticides: The problem with Carriers' He discussed in his paper that most insecticides are combined with a 'carrier' that aids the transmission of the insecticides to the insects. Solvents, carrier gases, powder, etc., are all used, often with other adjutant substances such as emulsifiers and surfactants to improve the insecticides' action. He discussed the effect of such formulation chemistry on the objects of cultural heritage. One of the Indian participant, Shashi Dhawan, Lucknow presented her paper on 'Study of microbial deterioration of paintings of St. Aloysus Chapel, Mangalore, India'. Her data were based on aeroflora and surface flora of murals and canvases of Chapel and informed that fungal form (*Penicillium citrinum*) and algae (*Pleurocapsa & Phormidium*) were the most common and frequently occurring biodetergents of ambient environment and suggested proper control measures for the preservation of valuable paintings.

The conference ended with the realization that lack of conservation centers in different parts of the world and trained personnel are two main bottlenecks in this field. Lack of public awareness and regional literature were also identified as important factors contributing towards biodeterioration of cultural properties. The conference concluded giving emphasis on the need to build up and expand the network among specialists of different disciplines and explore collaborative avenues of research especially on biophysical, biochemical and biological parameters of biodeterioration for long-term preservation of cultural properties.

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17th Himalaya-Karakoram-Tibet Workshop

25-27 March, 2002
Gangtok, Sikkim, India

The first Himalaya-Karakoram-Tibet Workshop was held at Leicester (Great Britain) in 1985. Since then the Himalaya-Karakoram-Tibet Workshops (HKTW) have been held every year in different parts of the world with an aim to exchange and disseminate recently acquired geoscientific information on Himalaya and adjoining regions. It provides the most important forum for the presentation of results by earth scientists working in the Himalaya-Karakoram-Tibet transect where the tectonic evolution has been controlled by the development of the Himalayan mountain range. It is a well known fact that the Himalaya is a "natural laboratory" for scientists studying the geophysical and geological processes involved in collisional tectonics as well as the effects of high mountains and mountain building processes on climate and environment. The 16^{th} Himalaya-Karakoram-Tibet Workshop was held in Graz, Austria from 3-5 April 2001, hosted by the Institut fur Geologie und Palaeontologie, Universitat Graz, Austria. Recently, the 17^{th} Himalaya-Karakoram-Tibet Workshop held in Gangtok, Sikkim, India between March 25-27, 2002- the first ever HKTW held in India and that too during the 'Year of Mountains' of the UN. The 17^{th} HKTW was sponsored by the Department of Science and Technology, Government of India; International Lithosphere Program; Central Scientific and Industrial Research, Delhi, India; Indian National Science Academy, Delhi, India; Coal India Limited, Calcutta, India; Central Ground Water Board, Government of India; Geological Survey of India and Oil and Natural Gas Corporation, India.

The workshop was organized at Hotel Norkhill, Gangtok, Sikkim jointly by the Department of Geology, University of Delhi, India and the Birbal Sahni Institute of Palaeobotany, Lucknow, India. Over 70 participants attended the workshop and delegates came from different parts of Europe, Iran, Japan, Nepal and India. 70 abstracts were published in a Special Supplement of the Journal of Asian Earth Sciences, Volume 20 (4), however, 22 late abstracts have been published separately as addenda abstracts.

Seven technical lecture sessions having about 60 research papers on different parts of the Himalaya-Karakoram and Tibet were covered over three days, and presentations were arranged on the basis of different geoscientific disciplines i.e. (1). Tectonics and the Geodynamics of the Region; (2). Seismicity and Tectonics; (3). Tectonics; (4). Petrology; (5). UHP and related Metamorphism; (6). Mountain Hazards, Geomorphology and Palaeoclimates; (7). Sedimentary Geology and Palaeontology. About 20 posters were also displayed at this workshop.

During the course of presentations, the complex geodynamic evolution of the Himalayan Range has been explained by Prof. G. Mascle on the basis of opening and closing of the Tethyan oceanic realm, and finally by a suturation, with inversion of the Tethyan structures. Prof. Anshu K. Sinha presented the aspect of mountain building processes and evolution of the Himalaya-Karakoram and uplift of the Tibetan plateau. He further highlighted several key issues and suggested new areas of research to be carried-out in near future along the Himalaya-Karakoram-Tibet transect. In a comparative study of mountain uplift between the Nepal Himalaya and the Hidaka Mountains, Japan Prof. K. Arita found that the Himalaya was formed by fold and thrust tectonics in the old Indian continental crust and the Hidaka mountains by steep thrusting along a plate boundary between continent-like and oceanic crusts. Using GPS Geodesy and cosmic ray exposure ages of an offset debris flow in Ladakh, Prof. V.K. Gaur suggested the slip rate on the Karakoram fault is ~4mm/yr. According to him it is likely that Tibet does not behave as a rigid body and that plate tectonics, *sensu stricto*, ought not be applied to Tibet. Quantifying displacement on the South Tibetan Detachment normal fault along the Everest profile Prof. Mike Searle demonstrated approximately 200 km of southward displacement of footwall sillimanite + cordierite gneisses, formed at 600-630^0 C and pressures of 4.0-4.9 kbr (14-18 km depth), beneath the STD which acted as a passive roof fault during southward flow of the hot, viscous, ductile middle crust. The active crustal thickening and high topography in south Tibet took place between 32-18 Ma. Prof. Igor Villa presented data on the amphibolitization of granulitized eclogites from the Kharta region in east Himalaya. The Kharta meta-eclogites occur at the top of the Main Central Thrust Zone in the western limb of the Arun mega-antiform, 30 km east of the Everest-Makalu massif Mineral assemblages, reaction textures and geothermobarometry suggest that two superspposed metamorphic events are recorded. The first event was of eclogite facies, the second event was of medium pressure granulite facies. Prof. S.K. Acharyya presented data on the thrust tectonics, evolution of domal windows and significance of concealed Paleogene foreland basin sediments in the eastern Lesser Himalayas. According to him the largest Siang window located at the eastern syntaxis exposes a duplex of early Paleogene sediments interbanded with the Abor Volcanics beneath the arched up MBT. The Himalayan foreland Tertiary sediments may extend northward up to the belt of Lesser Himalayan domal windows. Prof. S.B. Bhatia presented paper on the age and provenance of the Paleogene sediments of the Himalayan foreland basin. Similarly Prof Ashok Sahni observed ash related catastrophic event at the Subathu-Murree formational boundary.

Similarly, there were several other interesting papers presented by delegates during the three days workshop. The Birbal Sahni Institute of Palaeobotany, Lucknow, India has been represented very well by the participation of six scientists in the workshop. These scientists are Prof. Anshu K. Sinha, Drs. A.K. Srivastava, Neerja Jha, Ram-Awatar, Vandana Prasad and Rajeev Upadhyay. Shri Pawan Katiyar, Technical Officer, supported the projection facility with multimedia projection. Three papers were presented orally whereas other two papers were presented under poster session. Prof. Anshu K. Sinha presented the discovery of the Bathonian-Callovian nannoflora from the eastern Karakoram block. The nannofloral assemblage is dominated by *Watznaueria* spp. However, on the occurrence of marker *Ausulasphaera helvetica*, the presently recorded nannofloral assemblage from the eastern Karakoram Block dates these sediments in the time bracket of

Bathonian-Callovian. Therefore, on the basis of this new findings it is concluded that the Middle Jurassic sedimentary sequence of the eastern Karakoram block and the Reshit Formation of the Chapursan Valley in north Karakoram are equivalent. Similarly, Dr. A.K. Srivastava presented data on morphology, taxonomy and stratigraphical significance of plant fossil assemblages recovered from Permian sequence of Arunanchal Pradesh, Darjeeling and Sikkim areas. Floristic comparison suggest that the plant fossils from Permian sediments of Arunachal Pradesh, Darjeeling and Sikkim of northeast Himalayan region indicates the presence of *Gangamopteris-Noeggerathiopsis* association along with the species of *Glossopteris* in Arunachal and Sikkim. In her presentation Dr Neerja Jha provided additional information on palynological dating of Chhongtash Formation in eastern Karakoram. The palynofloral assemblage suggest typical Gondwana affinity. The dominance of radial monosaccates along with presence of striate and non-striate disaccates suggest an Early Permian age (Late Asselian-Sakmarian). In her poster presentation Dr. Vandana Prasad discussed the palynology and palynofacies analyses as essential clues to assess and identify palaeoenvironment of Subathu Formation, Tal Valley, Garhwal Himalayas in Uttaranchal. According to her the palaeoenvironment curve reflects different environmental conditions varying from brackish swamp, closed lagoon, estuarine and delta plain in the studied section. Similarly, Drs. Ram-Awatar and Rajeev Upadhyay presented their poster on the discovery of the Late Permian and Early Triassic palynofossils from the Cretaceous trench-slope sediments of the Indus Suture Zone, Ladakh Himalaya, India. According to them the palynofossils bearing older Permian and Triassic Tethyan sediments exposed along the northern margin of the Indian plate have been eroded, recycled and redeposited into the tectonically active Cretaceous trench-subduction complex that existed between the Indian and the Asian plates.

Fig. 1—Kanchanjanga Peaks of Higher Eastern Himalaya. A view from Gangtok.

Fig. 2—A Buddhist Monestry, Gangtok.

The afternoon session on day three was followed by the 'General Body Meeting'. It was decided that the 18th HKTW will be held in Switzerland during the April 2-4, 2003. The organizers deserve all the praise for conducting the 17th HKTW for the first time in India in an efficient and successful way.

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Contact Course on Advanced Training in Palaeobotany

03-19 October, 2001

Lucknow (UP) & Jabalpur (MP), India

Palaeobotany helps in understanding the floristic pattern, evolution (through geological time) and extinction of past vegetation and in deciphering palaeoecology and palaeoclimates. The palaeobotanical knowledge is being utilized to identify the source rock potentiality, particularly for oil and coal. Tree-ring analysis, archaeobotany, forensic palynology and isotopic analysis of rocks cover the broader aspects of palaeobotany. Keeping the academic and applied aspects of the subject, a Contact Course on 'Advanced Training in Palaeobotany' was organized, for the first time, at the Birbal Sahni Institute of Palaeobotany (BSIP), in October, 2001 with an objective to train young researchers, teachers and professional scientists of academic and commercial organizations.

The course was co-sponsored by Oil and Natural Gas Corporation Limited and Jabalpur Administration, M.P. Government. The participating scholars were selected from the universities of Allahabad, Ranchi, Kumaun, Garhwal, Lucknow, and Vadodara and from ONGC.

The aim of the course was:

- to disseminate the latest palaeobotanical and allied discipline's knowledge (in Indian context).
- to acquaint the participants with the fundamental and applied aspects of palaeobotany for industrial and societal needs, and
- to provide field knowledge about the collections of plant fossils and need to preserve the fossil sites as national heritage.

The program was designed to cover the areas— Early life, Gondwana geology, Gondwana floristics, Tertiary floristics, coal palynology, coal seam correlation, Intertrappean flora, micropalaeontology, Quaternary vegetation/palaeoclimate, dendrochronology (tree-ring), archaeobotany, aerobiology, forensic palynology, petrography of coal/lignite in relation to quality and CBM, preservation of fossil sites, besides the fundamental aspects of the palaeobotany.

The course was inaugurated (on 3rd October) by Hon'ble Mayor of Lucknow City, Dr. S.C. Rai. In his inaugural message Hon'ble Mayor expressed his pleasure that BSIP is providing latest knowledge of palaeobotany to young generation of scientists and teachers of the country. He very kindly offered to provide space for development of Fossil Park in Lucknow. Prof. A.K. Sinha, Director of the Institute emphasized that during the last 50 years or so palaeobotany has acquired a new dimension and presently the palaeobotanical researches are being utilized in understanding global climatic changes and in prognosticating new source of energy—coal bed methane. He also laid emphasis on classical role of palaeobotany to decipher the floral succession/extinction of different plant groups in geologic past and its application in biostratigraphy, correlation of coal- and oil-bearing strata. Prof. Sinha suggested the participants to derive maximum benefits from important publications of the Institute and advised them to make utilization of library, laboratories, museum, herbarium and workshop facilities.

The course program was designed and managed in three stages. First part dealt to impart teaching and practical demonstrations at the BSIP from October 3-10, in which eminent scientists of the country and scientists of the Institute delivered about thirty lectures in their respective fields of specialization. The second part of the course was related with a one day Field Workshop organized by the Commissioner of Jabalpur Division at Jabalpur (MP) on 12th October. The succeeding phase of course was concerned with an intensive seven days (October 13-19) field training to the participants, in and around Jabalpur to cover the fossil localities of Lower and Upper Gondwana successions and the Infra- and Inter-trappean localities.

The introductory lecture on Gondwana geology, tectonics and terrane accretion highlighted the recent discovery of Gondwana plant fossils in Karakoram region in Himalaya indicating that Karakoram terrane was part of peri-gondwana block. Following the introductory lectures the course was organized to discuss the basic aspects of palaeobotany, i.e. nature and preservation of fossil plants and the various techniques, methodology being used for the study of plant fossils. To cover the palaeobotanical history of plants, the theme related with the earliest record of biota in Precambrian was covered with two lectures on early biosphere and chert microbiota, and Proterozoic carbonaceous macrofossils, highlighting the evolution and adaptations in cyanobacteria and brown, red and green algae. The role of charophyta in geology was also discussed.

The topics related with evolution and radiation of land plants; the *Glossopteris*, *Dicroidium* and *Ptilophyllum* floras of Lower, Middle and Upper Gondwana sequences; comparison of Gondwana flora with contemporaneous floras; origin, antiquity and occurrence of angiosperms; recent advances in fossil pteridophytes; and Tertiary megafossils and palaeopalynological researches carried out in Gondwana and Tertiary basins of India were covered in depth. The application of Quaternary palynology in deciphering palaeoclimate and forest history of Himalayan and peninsular regions were imparted to the participants. Application of botanical knowledge in deciphering palaeoclimate was also highlighted.

The knowledge about new trends of plaeobotanical researches especially application of coal petrology in exploration of coal bed methane, DNA study in palaeobotany, plant remains of archaeological sites and tree-ring analysis were provided. Applied aspects of palaeobotany were also covered with application of palynology in coal exploration, coal seam correlation and boundary problems, and marine micropalaeontology (diatom and dinoflagellate cysts) and its significance in biostratigraphy and oil exploration. The allied topics like dispersed organic matter (DOM) and biodiagenesis of Gondwana and Tertiary coals, isotope dating, the use of electron microscopic techniques in fossil plants, and collision tectonics, uplift and climate change in Himalayas were also covered during the teaching program.

The practical demonstrations were conducted to give training in palaeobotanical techniques, such as maceration method (to liberate pollen-spores from rocks), peel and transfer techniques for cuticular study, preparation of ground thin sections (to observe the anatomical details of petrified material), particulate pellet preparation (for coal/lignite petrographic study), and specialized chemical treatment for the recovery of megaspores, nannofossils, acritarch diatoms and phytoplanktons. The method to prepare palaeobotanical samples for electron microscopic study, geochronological dating, tree-ring analysis and archaeobotanical remains were demonstrated in different laboratories of the Institute by the specialist scientists and technicians.

Fig. 3—Delegates of workshop at Jabalpur.

Fig. 4—Director, BSIP attending to field participants.

The participants were given an opportunity to examine the type and figured specimens kept in the museum and herbarium of the Institute. They were also provided complimentary copies of the valuable reprints of Professor Birbal Sahni, FRS— the founder of BSIP, and some catalogue, monograph and research articles published by the Institute.

Shri Arun Gurtu, Vice-Chancellor of Rani Durgawati University, Jabalpur inaugurated the Field Workshop (on 12th October) and emphasized the significance and importance of fossil plants and expressed his desire to preserve the fossiliferous rich localities of Madhya Pradesh. Dr. Ram Prasad, Director, Institute of Forest Management, MP, Bhopal delivered the presidential address and extended his cooperation for locating and preserving the fossil sites. Shri M.M. Upadhyay, Commissioner, Jabalpur Division in his introductory lecture requested the palaeobotanists to suggest ways and means to develop the National Fossil Park at Ghughua.

During the Workshop, scientists of BSIP presented a detail report about the occurrence of fossils in different geological horizons of Madhya Pradesh. The generic and specific identification of plant fossils preserved at National Fossil Park, Ghughua were discussed. Geologist from GSI presented the geological features of Fossil Park. The biodiversity of the area in relation to plant fossils were also discussed. The forest official, teachers of local university and colleges and general public took keen interest in the scientific deliberations.

The field training programme was conducted by a team of scientists of BSIP to cover the Lower Gondwana coal-bearing rocks of Permian age (*Glossopteris* flora), the Upper Gondwana rocks of Lower Cretaceous age (*Ptilophyllum* flora), and Deccan Intertrappean sedimentary sequences associated with the Deccan volcanic of Upper Cretaceous–Palaeocene age (angiospermous flora). Ganjra Nala and Sher River sections, rocks exposed at Chui Hill, Bara Simla, Pat Baba ridge, Lameta Ghat and Deccan Intertrappean sequence exposed between Padwar and Ranipur were selected and visited for the study. The protected area, containing number of petrified fossil assemblages of wood, fruit, leaves, of National Fossil Park, Ghughua (in Dindori district) were also visited by the participants.

During field programme, the party was explained how to identify the rock sequence and other geological features. They were also provided basic information to use the geological parameter and instruments for examining the orientation of rock beds, measurement of dip and identifying fault and fold. The demarcation of fossiliferous horizon, collection of plant fossils, palynological samples, examination of stratigraphical and lithological successions was amply demonstrated during the field. Interestingly party discovered a sample containing aggregate of 8– 10 eggs from Lameta Ghat Section situated on the right bank of Narmada River about 15 km south west of Jabalpur. The specimen is comparable with dinosaurian eggs, however the smaller size of the eggs make it distinct from all the known records and more likely belongs to egg pouch of avian fauna.

The closing ceremony of the Contact Course was held on October 19^{th} at Jabalpur under the presidentship of the Director, BSIP. The Chief Guest, Shri Rashid Suhail, Chairman, Jabalpur Development Authority exhorted the local public, forest officials and civic administration to protect the fossiliferous sites of Jabalpur area and assured his full cooperation for development of Fossil Park. Commissioner of Jabalpur Division informed that the MP Government has accepted the site plan for the development of National Fossil Park at Ghughua and sought the guidance and cooperation from the Director of BSIP for proper development of the park. Prof. Sinha assured his support and expressed his desire to work jointly for the protection of fossiliferous sites of Madhya Pradesh.

The course was a successful venture. Participants appreciated the efforts made by the BSIP and suggested to organize such program at regular interval in order to acquaint the young scientists with latest developments in the study of fossil plants.

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New Biology towards Socio-economic Progress

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ABSTRACT

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Prof. Birbal Sahni, the founder Director of the Birbal Sahni Institute of Palaeobotany paved the way for systematic developments in this field from botanical and geological aspects. Palaeobotany is the study of ancient life. The Indian sub-continent is bestowed with enormous biodiversity and richness of biological resources. The grave consequence of loss of biological diversity has to be understood on scientific basis. The global biological heritage, both for the present and for the future will have a proven influence on the potential of constructing a sustainable agriculture and forestry system which will produce useful products for the sustenance of human life. The work in new biology and the advent of biotechnology and genetic engineering have given a large number of fundamentals, innovations, tools and techniques. The scientists can produce crops with desired traits, enhance the food productivity and nutritional status of the crops, produce new vaccines and diagnostics, develop packages for environmental restoration and protection of biodiversity. The future advances in new biology offer enormous potential both for economic and societal development.

Key-words—Biology, Technology, Genome, Biodiversity, Protein.

सामाजिक-आर्थिक प्रगति में नवजीवविज्ञान का योगदान

मंजु शर्मा

सारांश

बीरबल साहनी पुरावनस्पतिविज्ञान संस्थान के संस्थापक निदेशक प्रो. बीरबल साहनी ने वानस्पतिक तथा भूगर्भीय परिप्रेक्ष्य से इस क्षेत्र में सुव्यवस्थित विकास के मार्ग का सूत्रपात किया। पुरावनस्पतिविज्ञान मूलतः 'प्राचीन जीवन का अध्ययन' है। भारतीय उपमहाद्वीप में जैवविविधता तथा जैविक संसाधनों का प्रचुर भण्डार उपलब्ध है। जैव विविधता के ह्रास के दुष्परिणामों को वैज्ञानिक दृष्टिकोण से समझा जाना चाहिए। भूमण्डलीय जैव सम्पदा वर्तमान तथा भविष्य दोनों ही के लिए दीर्घकालिक कृषि एवं वानिकी तंत्र को निर्मित करने हेतु आवश्यक है, जो मानव जीवन के पोषण हेतु उपयोगी उत्पाद निर्मित करती है। नव जीवविज्ञान तथा जैव प्रौद्योगिकी के आगमन से अनेक नए सूत्र, अनुसन्धान, उपकरण तथा प्रविधियाँ प्रकाश में आयी हैं। आज वैज्ञानिक इच्छित फसल उगा सकते हैं, खाद्य उत्पादन क्षमता बढ़ा सकते हैं, नए वैक्सीन तथा निदान खोज सकते हैं, पर्यावरण एवं जैवविविधता के संरक्षण हेतु पैकेज विकसित कर सकते हैं। नव जीवविज्ञान में भावी अनुसन्धानों से आर्थिक एवं सामाजिक विकास में अत्यधिक सम्भावनाएँ निर्मित होंगी।

संकेत शब्द—जीवविज्ञान, प्रौद्योगिकी, जीनोम, जैवविविधता, प्रोटीन.

31st Prof. Birbal Sahni Memorial Lecture delivered by Dr (Mrs) Manju Sharma, Secretary, Department of Biotechnology, on 16th November, 2001 at Birbal Sahni Institute of Palaeobotany, Lucknow.

INTRODUCTION

"My own interest in Palaeobotany raises the hope that I may help to bring this fascinating subject more prominently to the notice of my countrymen; and perhaps even succeed in inducing a larger number of them to turn their attention to the rich field that it offers for original investigation".

Prof. Birbal Sahni spoke in one of the sessions of Indian Science Congress in 1920. These words spoken nearly a century ago reflect the genius, the vision and concern about the country of the architect of the field of Palaeobotany in this country and the founder Director of the Birbal Sahni Institute.

Let me share with this audience—an emotion, very precious and personal to me. I received the first real academic distinction in my life in the name of Birbal Sahni Memorial Gold Medal for being the best student of Botany in M.Sc. from the Lucknow University, in 1961. All other previous prizes in school and colleges became second to this prestigious medal which gave me the inspiration, a desire to pursue science as a career. It was my good fortune that Prof. A.R. Rao, my Ph.D. guide, another leading Palaeobotanist had worked under the overall guidance of Prof. Birbal Sahni. Thus you can realize the sentimental value of this lecture for me. I am really grateful to the Director for giving me this opportunity to deliver the Prof. Birbal Sahni Memorial Lecture. I dedicate this lecture to the fond memory of my Guru, Late Prof. A.R. Rao and pay my most respectful tribute to the two great scientists—Prof. Sahni and Prof. Rao.

We have assembled here to commemorate the memory of Prof. Birbal Sahni, a dedicated Scientist and a great philosopher.

His untiring efforts to elucidate the importance of fossil plants both in Botany and in Geology lead to path breaking discoveries. It was due to his selfless, rigorous pursuit that this institute of Palaeobotany came up as a seat of excellence. Since its inception it has tried to live up to his expectations.

Before I proceed to the main topic of my lecture, let me also mention about another great scientist Sir C.V. Raman, who was very close to Prof. Birbal Sahni. The Two were superb communicators of science and certainly Raman had great influence on him.

The Foundation Stone of the new building of this prestigious Institute was laid by nobody less than Pandit Jawaharlal Nehru, on 3rd April 1949, a contemporary of Prof. Birbal Sahni at Cambridge. Let us recall the words of our first Prime Minister emphasizing the importance of science and values while addressing the Indian Science Congress in 1963:

"Without science there is no future for any society; but even with science, unless it is controlled by some spiritual impulses, there is also no future".

Systematic developments in Palaeopalynology from botanical and geological aspects and constantly updating the data for interaction with other allied disciplines have been the hallmarks. It is Palaeobotany which bridges Botany and Geology in order to peep into the evolutionary history of plants which directly or indirectly have a bearing on various aspects of plant life and their geographical distribution with reference to time and space.

Palaeobotany is a major branch of Paleontology – the study of ancient life. The most ancient fossils are those of Archean Era – which are possibly 2.5 billion to 3 billion years old. It involves the study of the origins and development of all plants and plant like organisms from yeast and bacteria to redwoods and orchids. Paleontology, so to say has a great value in Palaeobotany as it levels itself to quantification, age determinations of geologic strata and the correlation of strata from different locations.

The most outstanding and lasting contribution to 19th Century Palaeobotany was made by Dr W.C. Williamson in his studies of British Coal Balls from the precoal stages of peat layers of the lower coal measures. The advent of Precambrian Palaeobotany is one of the most significant developments. Studies on fossil algae have revealed results which have far reaching biological implications about the antiquity of life on earth and the origin of nucleated organisms from which sexual diversification originated.

OUR BIODIVERSITY AND BIOLOGICAL RESOURCES

Today we are in the midst of a revolution of biotechnology and information networking. Before we think of research in New Biology, we must understand the magnitude of our precious Biodiversity. The Indian Sub-continent by virtue of its varied topography, climate and habitat is rich in traditional knowledge of properties and uses of its resources. Biodiversity is a vast variety of living organisms and their products of utility including both flora and fauna with genetic variability not only in animals and plants but also in other organisms like viruses, bacteria, fungi and other microbial populations. It is now recognized as a source of prosperity and livelihood security of millions. The diversity is both in number of different species and at intraspecific levels in the form of races and varieties.

A record of India's plant wealth indicates that there are nearly 17,500 species of angiosperms, 48 species of gymnosperms, 1,200 species of ferns, 6,500 species of algae, 14,500 species of fungi, 2,500 species of lichens, 845 species of liverworts and 1,980 species of mosses. This great diversity of plant wealth thus has a direct bearing on the very existence of humankind and for the ecological security of our Planet. It is here that the great significance of New Biology innovations, biotechniques and discoveries have to be recognized.

In spite of phenomenal advances in discovering new species of flora and fauna on the planet earth, there are 3-27 undiscovered species and yet hundreds of species are discovered and classified by the Biologists every day.

Due to geographic topography there is a decline in diversity from equator to poles. So the losses are even more severe in tropical countries like ours, where human population is expanding at a much alarming rate. One really has to look into a so-called war of humans verses animals and plants. The need for expanding populations and an unequal distribution of wealth has invariably resulted in the unsustainable, exploitative use of naturally existing resources.

One of the grave consequences of this is the loss of biological diversity. A quarter of the earth's total biological diversity amounting nearly to more than a million species is at the brink of extinction in next few decades. Currently nearly more than 35% of the total land of the planet is threatened by desertification. The area of polluted soils and water is expanding exponentially. The green house effect has a direct bearing on world's climate. Both aquatic and terrestrial fauna are rapidly being wiped out and the Mother Earth is threatened of erosion. Hence our concerns about the loss of productivity of agriculture are genuine.

The global biological heritage – the living foundation of existence both for the present and future will certainly have a profound influence on the potential of constructing a sustainable agriculture and forestry system, producing useful products for the sustenance of the human life. India is one of the megacenters of biological diversity. Botanical Survey of India (BSI) has identified more than 45,000 plant species of which nearly 15,000 represent flowering plants, 33% is being endemic and 1,500 species being threatened. Out of 5,000 species studied at length, only 30 are useful in producing 95% of human nutrition. Three main crop species doing this job are maize, rice and wheat. In view of this diversity between and within few plant species it becomes imperative to develop programs of different crop genetic resources both at the National and International levels.

25 hotspots have been identified world over which cover nearly 0.746 million sq. km and houses 0.45 million species. India has 2.4% of the world's area has 8.1% of the world's total biodiversity with a species count of about 0.150 million. Two of the world's hot spots are found in India, namely, the Eastern Himalayas and the Western Ghats, the former being the hottest of the hot spots. In addition, India has 26 recognized endemic centers.

To be agriculturally secure with maximum crop production, the best use of available land has to be made and latest methods of crop improvement have to be brought into practice. A wide range of plant species have been selected over a period of time for their use in agriculture and horticulture. I do not want to elaborate on conventional plant breeding. We all are aware that with just the conventional approaches, it is not possible to improve a specific variety directly either from the viewpoint of productivity or quality. Thus a blending of old and new research techniques is called for.

NEW BIOLOGY

The advent of information technology has given a new dimension, there is a paradigm shift in the areas and strategies for new biology research. Genome technology, today, is an integral part of the new informatics. The latest throughput systems to the bioinformatics set up, high performance computer, DNA amplification and sequencing, genome assembly and gene prediction, proteomics and mass spectroscopy, development of different techniques, gene expression and so on starting with cell biology to modular biology, these are scientific and technological revolutions taking place with a spectacular speed. The scientists have come a long way, there is a thinking in United States, Switzerland and many advanced countries that scientists would be able to make simple "artificial cells from scratch". These can metabolise, replicate and evolve, i.e., to fill the basic criteria for the living entities while they will be truly synthetic. According to Szostak and his colleagues, this would mark, "the beginning of the field of synthetic biology".

There are various modes now available for the new biology studies starting from the genomics study to microbial, proteomics, etc. After all, the world has witnessed, based on the deep knowledge of the fundamentals of new biology and by harnessing the new biotechnological breakthroughs, the genetic profile of the human kind, the information on the blue print of life. The tools generated by the human genome project are applicable and have produced a whole genome catalogues, microbes, plants like *Arabidopsis*, fruit fly *Drosophila melanogaster*, round worm *Caenorhabditis elegans*, etc. It is stated by the scientific community that the complete genome sequences serve as a foundation for the biology of the 21st century. The statement is : "Achieved a fundamental, comprehensive and systematic understanding of health.

The advent of biotechnology and genetic engineering has made it possible to overcome many problems. Biotechnology basically involves the translation of biological theory into engineering. It proclaims attempts to control biological processes for purposes, which are useful and render services for the good of humanity. To design crops with desired traits molecular biology and genetic engineering as a tool have become handy. It is the conglomeration of various molecular techniques that has led to the development of such plants.

OUTCOME AND APPLICATIONS

It is interesting to note that between basic research and its application there is a thin line. Many times, the research concepts and research results are immediately applicable. New biology and biotechnology have been used safely for many years to develop new and useful products in a variety of industries. A large number of products have already been approved for marketing and many more are being developed.

These products include dozens of therapeutics including human insulin for diabetes, growth factors used in bone marrow transplants, products for treating heart attacks, scores of diagnostic kits for AIDS, Hepatitis and other infective agents, enzymes used in food production, etc. The first life saving drug Humulin was produced by recombinant DNA technology and this was followed by a plethora of drugs including Betaseron for treating multiple sclerosis, pulmozyme for cystic fibrosis, activase, a clot dissolving tissue plasminogen activator used for treating heat diseases. It is also possible to produce these biopharmaceuticals in a form identical to the normally occurring ones in the human body but also to design meaningful improvement in activity, stability or bio-availability. Such products are also free from contamination.

Cloning of the exact duplication of specific genes has been an essential tool in biotechnology for more than 20 years. Cloning of human cells, organs and other tissues can produce replacement skin, cartilage and bone tissue for burn and accident victims. This could prove useful for developing internal organs for human transplantation.

The cloning of Dolly and Polly demonstrated that nuclear transfer technology could be used effectively. The breakthrough in developing stem cells holds the potential to control cancer, regenerate spinal cord and brain tissue, and successfully treat many diseases associated with aging. Stem cell Biology has a great potential in saving many lives.

Vaccines are one of the greatest developments of modern biology. They have helped in eradicating diseases like, small pox, pushed polio to the brink of extinction and spared countless people from numerous diseases like, typhus, tetanus, measles, hepatitis A, hepatitis B, rotavirus and other dangerous infections.

But still many other diseases like, malaria, AIDS, herpes, hepatitis C have yet to find a successful vaccine. This gap exists due to the fact that standard immunization methods work poorly or pose unacceptable risks when targeted against a particular illness. Certainly alternate strategies are to be explored. One of the most promising ways is to develop vaccines out of the genetic material either the DNA or RNA. DNA based vaccines will preserve all the positive aspects of the existing vaccines while avoiding the risks. They are easy to design and generate in large quantities using recombinant DNA technology.

Biotechnology offers new opportunities and is the only hope for producing enough food for a growing world population. Malnutrition has been one of the main concerns of the developing world as it results in nearly 12 million deaths every year of the third world children under five. Growing enough staple crops such as corn, rice, wheat, potatoes without further extending the amount of land to be cultivated will require sustained increase in yields per acre. Biotechnological innovations will play a key role in fighting against malnutrition worldwide. Deficiencies of Vitamin-A and iron, for instance are very serious health issues in many regions of developing world, causing childhood blindness and maternal anemia in millions of people whose dietary staple food is rice. Biotechnology has been used to produce a new variety of rice "The Golden Rice" – that contains Vitamin A precursor-carotene and iron. This modified rice is expected to provide nutritional benefits to people suffering from Vitamin-A deficiency related diseases. Adequate Vitamin A intake can also reduce the mortality associated with infectious diseases like, diarrhea and childhood measles by enhancing the activity of human immune system. Genetically modified rice, which boosts yields by nearly 35% has been developed.

Tools of advanced biology to endow plants with genes that help them to resist pests have proved very fruitful. For instance cotton, potato and corn containing the Bt gene from a soil bacterium producing delta-toxin proteins that are selectively toxic to certain kinds of insects are harmless to other insects, humans and animals. Bt cotton has been launched for field trials in India with promising results.

Recently a protein, the first of its kind, that switches in a plant a natural defence against diseases and insects has been approved in US in April 2000 giving farmers an alternative to chemical pesticides. The protein, named Messenger is produced from genetically engineered bacteria. When transformed to a plant, it has shown to increase yields in tomatoes and peppers by 22% besides, making plants more tolerant to drought. This Messenger protein is the first natural product that can turn on the immune systems of crops.

The merging of medical and agricultural biotechnology has opened up new vistas to develop plant varieties with characteristics to improve health. Understanding of how natural plant substances, known as phyto-chemicals, confer protection against cancer and other diseases is amazing. Work is underway that will deliver medicines and vaccines through common foods, which could be used to immunize individuals against a wide variety of enteric and other infectious diseases. This has given birth to Neutraceutical foods. These developments will have far-reaching implications for improving human health worldwide, potentially saving millioń of lives in the poorest areas of the world.

New Biology has paved the way for conservation and sustainable use of biodiversity. Powerful tools for the conservation, evaluation and the use of genetic structure of species are available. Bioremediation employs biological agents to render hazardous wastes into non-hazardous wastes. Even plants have been used for phytoremediation successfully.

The generation of Biofuel cells by making use of catalytic properties of organisms and enzymes for energy conversion holds a great potential. Biofuel cells convert chemical energy into electrical energy. These biocells would be used as specific sensing devices for energy conservation.

Advent of computers has added a new dimension to biological research. With the rapidly evolving superfast computers, improved accuracy in ligand screening, improved combinatorial chemistry designs, virtual explosion in the availability of three dimensional structural information and genome sequence database and the computational techniques will continue to take a center stage in many different aspects of drug design and development process.

Of late biological materials in the form of biochips are going to have a tremendous impact on computer development per se. The biochips would replace the conventional silicon chips used in the computer. The development of biomolecular computers promise to be ten to thousand times smaller than the best super computers with much faster switching times and extremely low power dissipation. Researchers at Advanced Center for Biochemical Engineering College, London have succeeded in obtaining a tiny semiconductor structure from yeast *Schizosaccharomyces pombe*.

Computational tools for mining the genomic data, identifying the potential new drug targets, elucidating and /or predicting the three dimensional structure of targets from the primary structure are at the core of the present day bioinformatics technology. Computational approaches will continue to be essential part of the ongoing and future drug design and development process.

Molecular biology is a technology driven process and numerous new techniques have come up during the last decade. This has totally changed the concept of cloning and studying a single gene at a time. Now one can study a number of genes simultaneously using Microarray or the DNA chip technology. Here one can process thousands of DNA segments for detecting differences in the pattern of DNA sequences or expression pattern of mRNA. Even one can study the overall picture of how genes in all organisms (total genome) function, including the expression profiles at mRNA (Transcriptome) and protein (Proteome). Maps can be made which could eventually help in identifying the defects as well as the positive aspects of concerned gene or a protein. Such are the advantages of using these modern biology tools.

CONCLUSION

Future advances in New Biology offer the promise of an impressive array of new and useful products that will improve crop yield and quality, provide better nutrition, deliver needed vaccines and medicines, produce more desirable fats and oil, extend the shelf life of fruits and vegetables, lower the food costs and create renewable non-food products. These research efforts, innovations and technologies will open up new markets, leading to rapid industrial development and more employment opportunities.

Let me conclude by once again reminding all of you the great potential of the field of new biology and biotechnology which must be to be harnessed for the welfare of humanity and economic progress of the nation. This certainly would depend on the dedicated and concerted efforts of the scientific community, especially the young scientists. We have to recognize that doing the highest quality of science and applying it to generate new products, processes, technologies and systems would form the basis of the socio-economic development of this country in the 21st century. Knowledge in biology can be converted into economic wealth with biotechnological innovations. On this assumption, let us move forward and do the best science.

विज्ञानं ब्रह्मेति व्यजानात्। विज्ञानाद्ध्येव खल्विमानि भूतानि जायन्ते।
विज्ञानेन जातानि जीवन्ति। विज्ञानं प्रयन्त्यभिसंविशन्तीति

तैत्तिरीयोपनिषद् 3/5

Science is Brahma, the almighty. All the living beings are born or are produced through science and at the end while practicing science, they get absorbed into it." (Upanishad)

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Significance of molecular phylogenetic analyses for paleobotanical investigations on the origin of angiosperms

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ABSTRACT

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Molecular phylogenetic analyses have provided increasing evidence that angiosperms are not related to Gnetales, thus contradicting the anthophyte hypothesis based on morphological cladistic analyses and throwing the question of angiosperm relatives back to paleobotanists. Previous analyses of gene sequences based on a molecular clock conflicted with the fossil record in indicating a Late Paleozoic or Triassic origin of the angiosperms, but closer examination suggests that these dates were biased by the use of herbaceous taxa with accelerated rates of molecular evolution. Despite uncertainty on angiosperm relatives, analyses of many genes consistently place *Amborella*, Nymphaeales, *Austrobaileya*, *Trimenia* and Illiciales (the 'ANITA grade') at the base of extant angiosperms, possibly followed by Chloranthaceae. Molecular phylogenies imply that the first crown-group angiosperms had columellar exine structure, suggesting that Hauterivian-Barremian reticulate-columellar monosulcates may be closer to the origin of angiosperms than was thought when granular Magnoliales were believed to be basal. Hauterivian pollen with a verrucate tectum and microspinules is especially similar to *Amborella*. The ANITA lines and Chloranthaceae have ascidiate carpels sealed by secretion and often exotestal seeds, fitting the abundance of such carpels and seeds in Barremian-Aptian mesofloras. Similarities between Aptian angiosperm leaves and ANITA taxa, such as chloranthoid teeth and variable stomatal structure, also suggest that Early Cretaceous angiosperms were more primitive than previously appreciated. Molecular results may help refine search images for extinct angiosperm relatives, away from Gnetales and toward groups such as *Caytonia*, glossopterids, Bennettitales and corystosperms. Since molecular data place the vesselless taxa *Amborella* and Nymphaeales at the base of the angiosperms, the presence of vessels is not evidence that gigantopterids are related to angiosperms. The conclusion that columellar structure is ancestral reaffirms the potential of Triassic reticulate-columellar Crinopolles pollen as angiosperm relatives.

Key-words—Angiosperms, Paleobotany, Cretaceous, Phylogeny, Molecular systematics.

आवृतबीजियों के उद्गम हेतु पुरावानस्पतिक अन्वेषणों में आणविक जातिवृत्तीय विश्लेषणों का महत्व

जेम्स ए. डॉयल

सारांश

आणविक जातिवृत्तीय विश्लेषणों से यह प्रमाणित हुआ है कि आवृतबीजी नीटेलीज़ से सम्बन्धित नहीं हैं। इससे संरचनात्मक क्लैडिस्टिक विश्लेषणों पर आधारित एन्थोफ़ाइट अवधारणा का खण्डन होता है तथा पुरावनस्पतिवैज्ञानिकों के समक्ष आवृतबीजियों के सम्बन्ध में अनेक प्रश्न मुँह उठाए खड़े हो जाते हैं। आणविक घड़ी के आधार पर जीन अनुक्रमों

के अश्मित आंकड़ों के साथ किए गए विगत विश्लेषण, जो आवृतबीजियों हेतु अन्तिम पेलियोज़ोइक अथवा ट्रायसिक उद्गम का संकेत करते थे, विरोधाभासी हैं, किन्तु गहन परीक्षण द्वारा प्रस्तावित किया जाता है कि ये काल निर्धारण आणविक विकास की त्वरित दर के साथ शाकीय वर्गकों के प्रयोग के कारण एकांगी हो गए। आवृतबीजियों के साहचर्यों की अनिश्चितता के बावजूद विद्यमान आवृतबीजियों के आधार पर लगातार *एम्बोरेला, निम्फ़ीलीज, ऑस्ट्रोबेलीया, ट्राइमीनिया* तथा एल्लीसिएलीज़ (ANITA ग्रेड) लगातार अवस्थित पाए गए, जिसके पश्चात क्लोरैन्थेसी उपस्थित है। आणविक जातिवृत्त इंगित करता है कि प्रथम शिखर समूह के आवृतबीजियों की संरचना स्तम्भीय एक्ज़ाइन की भाँति की थी, इससे प्रस्तावित होता है कि हाउटेरेवियन-बैरीमियन जालिकामय-स्तम्भीय एकसकोषी आवृतबीजियों के उद्गम से पूर्व में सोची गई दूरी की अपेक्षा अधिक निकट हो सकते हैं, जब कणिकामय मैग्नोलिएलीज़ आधारीय समझे जाते थे। कणिकामय टेक्टम तथा सूक्ष्म शूलिकाओं से युक्त हाउटेरेवियन परागकण विशेषकर *एम्बोरेला* के समरूप हैं ANITA रेखाएँ तथा क्लोरैन्थेसी उत्सर्जन द्वारा तथा प्रायः एक्सोटेस्टल बीजों द्वारा बन्द की हुई हैं, जो बैरीमियन-एप्टियन मीज़ो वनस्पतिजातों में ऐसे अण्डपों तथा बीजों की प्रचुरता की उपयुक्तता सिद्ध करती है। एप्टियन आवृतबीजी पत्तियों तथा ANITA वर्गकों में क्लोरैन्थॉयड दन्तों तथा परिवर्ती रंध्रीय संरचना जैसी समरूपताएँ प्रस्तावित करती हैं कि पूर्व में समीक्षित किए गए आवृतबीजियों की अपेक्षा प्रारंभिक क्रिटेशस आवृतबीजी कहीं अधिक अपरिष्कृत थे। आणविक परिणाम नेटेलीज़ तथा संगत समूहों, जैसे—*केटोनिया,* ग्लॉसोप्टेरिड्स, बेनीटाइटेलीज़ तथा कोराइस्टोस्थर्मों से विलग विद्यमान आवृतबीजी सम्बन्धियों हेतु परिष्कृत अनुसन्धान प्रतिरूप निर्मित करने में सहायक हैं। चूँकि आणविक आंकड़े वाहिकारहित वर्गकों *एम्बोरेला* तथा निम्फ़ीलीज़ को आवृतबीजियों की तलहटी में रखते हैं, अतः वाहिकाओं की उपस्थिति से प्रमाणित नहीं होता कि जाइगैण्टोप्टेरिड्स आवृतबीजियों से सम्बन्धित हैं इससे यह निष्कर्ष निकलता है कि स्तम्भीय संरचना अपेक्षाकृत प्राचीन है। इससे ट्रायसिक जालिकामय-स्तम्भीय क्राइनोपोलीज़ परागकणों के आवृतबीजियों के सम्बन्धी होने के प्रबल प्रमाण पुष्ट होते हैं।

संकेत शब्द—आवृतबीजी, पुरावनस्पतिविज्ञान, क्रिटेशस, जातिवृत्त विज्ञान, आणविक तंत्र विज्ञान.

INTRODUCTION

Over the past 40 years, paleobotanical studies of Cretaceous fossils, first pollen and leaves, more recently flowers, fruits and seeds in the 'mesofossil' record have provided many indications on the course of early angiosperm evolution, for example supporting the view that 'magnoliids' include the most primitive living angiosperms and 'Amentiferae' are advanced (Crane *et al.*, 1995; Doyle, 1969, 1978; Doyle & Hickey, 1976; Friis & Crepet, 1987; Friis *et al.*, 2000; Hickey & Doyle, 1977; Muller, 1970; Upchurch, 1984; Wolfe *et al.*, 1975). These studies have provided no direct evidence on links between angiosperms and other seed plants, but beginning in the 1980s cladistic analyses of morphological data from living and fossil seed plants appeared to narrow the range of viable hypotheses on this problem, indicating that seed plants and angiosperms are both monophyletic groups and focusing attention on Gnetales, Bennettitales, glossopterids, *Caytonia* and other 'Mesozoic seed ferns' as possible angiosperm relatives (Crane, 1985; Doyle & Donoghue, 1986; Loconte & Stevenson, 1990; Nixon *et al.*, 1994; Rothwell & Serbet, 1994; Doyle, 1996, 1998b).

In the past 10 years, cladistic analyses of molecular data, of necessity restricted to living plants, have provided a vast and completely independent body of evidence on these questions. Although these studies cannot directly address the relationships of fossil taxa to the angiosperms, they do bear on competing hypotheses when these make different predictions on relationships among living taxa. As an observer of both fields, I have been struck not only by conflicts between the two lines of evidence, which have perhaps attracted more attention (Axsmith *et al.*, 1998; Doyle, 1998a; Goremykin *et al.*, 1996), but also by unexpected agreements, and by ways in which insights from one field may suggest new directions for research in the other. This paper will explore both the conflicts and agreements, considering four closely interrelated questions: what the angiosperms came from, when they originated, what the first angiosperms were like, and how answers to the last question may shed light on the first. I will discuss these questions in a cladistic framework, which allows us to generate and test phylogenetic hypotheses in a coherent, explicit fashion.

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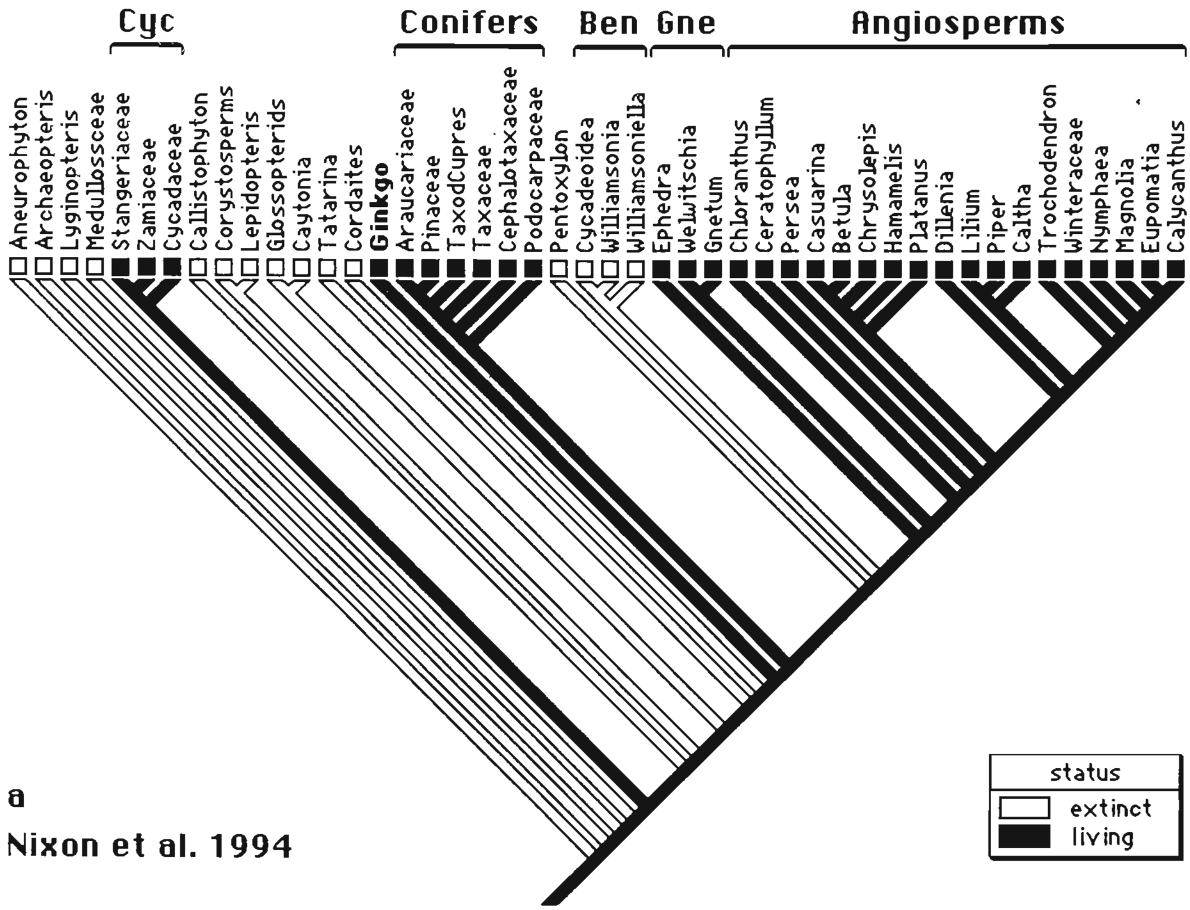
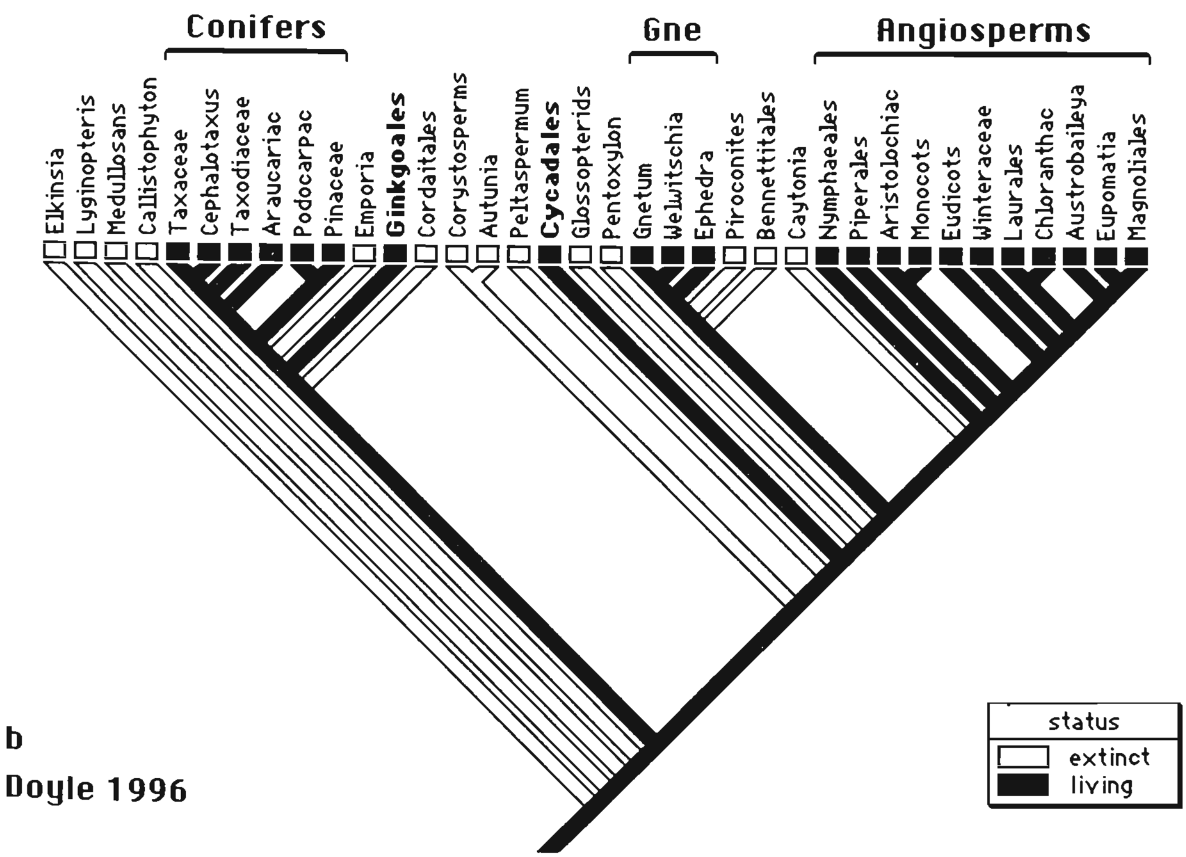
Fig. 1—Representative most parsimonious trees from morphological cladistic analyses of seed plants; (a) Nixon *et al.* (1994), (b) Doyle (1996). Extant lines are indicated in black, extinct lines in white.



a

Nixon et al. 1994



b

Doyle 1996

SEED PLANT PHYLOGENY AND THE ORIGIN OF ANGIOSPERMS

The first question, what the angiosperms came from, can be addressed cladistically by asking how angiosperms are related to other seed plants - what are their closest outgroups - and examining character states shared by these outgroups. This is a case in which most molecular data conflict with morphological cladistic analyses of living and fossil seed plants. Whereas before the application of cladistics there was little agreement on this topic, cladistic analyses all associated angiosperms with Mesozoic Bennettitales and living Gnetales, in a clade called the anthophytes, although they did disagree on just how these groups were related and what other taxa they were related to. Previously, it was widely thought that Gnetales had nothing to do with angiosperms and were instead related to conifers and other coniferophytes (Bailey, 1949; Doyle, 1978; Eames, 1952). The first major analysis, by Crane (1985), identified Gnetales as the sister group of angiosperms, Bennettitales and *Pentoxylon* as the second outgroup, and corystosperms, *Caytonia* and glossopterids as outgroups of the anthophytes. The trees of Doyle and Donoghue (1986) differed in placing angiosperms at the base of the anthophytes, somewhat further from Gnetales. Two of the most divergent results are shown in Fig. 1. In trees of Nixon *et al.* (1994), anthophytes were related to conifers rather than to Mesozoic seed ferns and angiosperms were actually nested within Gnetales (Fig. 1a). In my own latest analysis (Doyle, 1996), *Caytonia* was directly linked with angiosperms, but Gnetales were still their closest living relatives (Fig. 1b). As discussed in Doyle (1994), trees of these different types have very different implications for origin of the angiosperm bitegmic ovule and the carpel. Those that associate anthophytes with *Caytonia* or glossopterids suggest that the angiosperm outer integument is derived from a cupule, whereas those that associate anthophytes with conifers suggest it is homologous with the perianth of Gnetales and derived from scale leaves on an axillary fertile short shoot of the type seen in cordaites and early conifers.

Although molecular analyses cannot shed light on the relationships of angiosperms to Bennettitales, *Caytonia* and other fossils, they can address the relationship between angiosperms and Gnetales: are these groups related at all, and if so, are they monophyletic sister groups, or are angiosperms nested within Gnetales? Early molecular analyses indicated that angiosperms and Gnetales are both monophyletic (Fig. 2), with strong statistical support as measured by bootstrap analysis (Felsenstein, 1985), refuting the view that angiosperms are nested in Gnetales. However, they gave inconsistent results on relationships of the two groups. Some analyses of rDNA indicated that they are sister groups (Hamby & Zimmer, 1992; Stefanovic *et al.*, 1998; Fig. 2a), but this result was weakly supported. Other analyses of rDNA (Hamby & Zimmer, 1992) and the chloroplast gene *rbcL* (Albert *et al.*, 1994) placed Gnetales at the base of seed plants, with angiosperms linked with cycads, *Ginkgo* and conifers (Fig. 2b), or else reversed Gnetales and angiosperms (Hasebe *et al.*, 1992; Fig. 2c). These variations are a function of rooting - where outgroups attach to the seed plant tree; otherwise, the three trees are the same. There is reason to expect that the rooting of seed plants should be difficult: the conifer, cycad and ginkgo lines extend back to the middle Late Carboniferous or the Permian and presumably split not long before and there has been a long time since then for convergences and reversals on the lines leading to living seed plants, resulting in so-called long-branch attraction (Donoghue & Sanderson, 1992; Doyle, 1998a; Felsenstein, 1978). However, in trees first seen in analyses of chloroplast ITS sequences (Goremykin *et al.*, 1996) and 18S rDNA (Chaw *et al.*, 1997), angiosperms are basal in seed plants and Gnetales are linked with conifers (Fig. 2d). With this type of tree, there is no way to reroot seed plants such that angiosperms and Gnetales are related.

In all these studies, bootstrap support for relationships among seed plants was relatively low, so it seemed possible to argue that the morphological evidence for the anthophyte hypothesis could still be accepted (Doyle, 1998a). However, this situation has changed since 1998: many studies based both on single genes and on several genes combined have indicated that Gnetales are more closely related to conifers than to angiosperms, with much higher bootstrap support (Bowe *et al.*, 2000; Chaw *et al.*, 2000; Frohlich & Parker, 2000; Hansen *et al.*, 1999; Qiu *et al.*, 1999; Samigullin *et al.*, 1999; Winter *et al.*, 1999). In fact, the multigene analyses of Qiu *et al.* (1999), Bowe *et al.* (2000) and Chaw *et al.* (2000) actually nested Gnetales within conifers, linked with Pinaceae (Fig. 2e), with most critical nodes supported by bootstrap values of 90-100%. The main variation is that 18S rDNA alone indicates fairly strongly that Gnetales are the sister group of conifers rather than nested within them (Bowe *et al.*, 2000; Chaw *et al.*, 1997), as does the fact that conifers are united by loss of one copy of the large inverted repeat in the chloroplast genome, whereas Gnetales retain both copies (Raubeson & Jansen, 1992). In any case, all these studies are unequivocal in rejecting a relationship between Gnetales and angiosperms (Donoghue & Doyle, 2000). These results are consistent with morphological similarities between Gnetales and conifers cited in pre-cladistic studies, such as linear leaves, lack of scalariform pitting in the primary xylem, circular-bordered pits with tori in the secondary xylem, and compound strobili made up of axillary fertile short shoots (Bailey, 1949; Carlquist, 1996; Doyle, 1978; Eames, 1952), which were outnumbered by anthophyte similarities in morphological cladistic analyses.

These results are not definitive, since other recent studies have produced trees in which Gnetales are the sister group of other living seed plants (Fig. 2b). Sanderson *et al.* (2000) found trees of this sort in parsimony analyses of the chloroplast genes

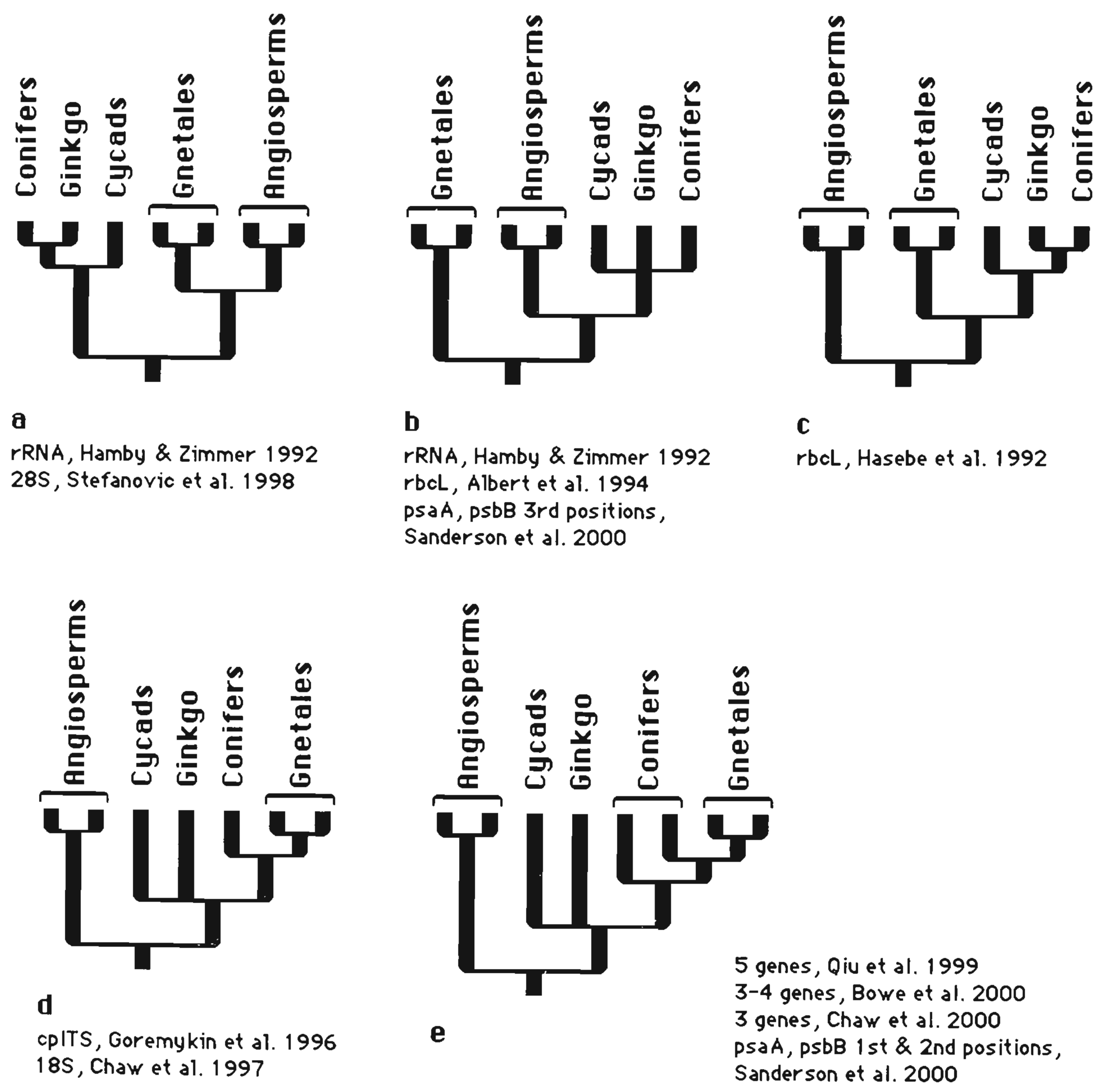


Fig. 2—Seed plant relationships found in analyses of molecular data.

psaA and *psbB*. However, they obtained divergent results when they analyzed different nucleotide positions in each codon: Gnetales nested in conifers based on first and second codon positions, but Gnetales basal in seed plants based on third positions. Since third positions evolve more rapidly, there is reason to suspect that the latter result may be due to long-branch attraction. Consistent with this view, Sanderson *et al.* found Gnetales nested in conifers when they analyzed third positions of *psaA* with maximum likelihood, which is believed to counteract long-branch attraction. Combined analyses of 17 chloroplast genes (Rai *et al.*, 2001) also gave trees with Gnetales basal, but again some subsets of the data and methods of analysis placed Gnetales in conifers. Rydin *et al.* (2002) found trees with Gnetales basal when they analyzed *rbcL* and *atpB* (another chloroplast gene) and these genes combined with 18S and 26S rDNA. However, analysis of *rbcL* and *atpB* with exclusion of nucleotide transitions (which are more common than transversions and therefore more likely to cause long-branch attraction) gave trees with Gnetales nested in conifers. Combined analyses of 18S and 26S linked angiosperms with Gnetales (like some earlier rDNA analyses), but with low support.

Despite these uncertainties, the continued failure of molecular data to support the anthophyte hypothesis suggests that paleobotanists should begin to consider the implications of alternative trees. Trees that link Gnetales with conifers may deserve more attention than those with Gnetales basal, since they are more consistent with the conifer-like morphological features of Gnetales and harder to ascribe to long-branch attraction.

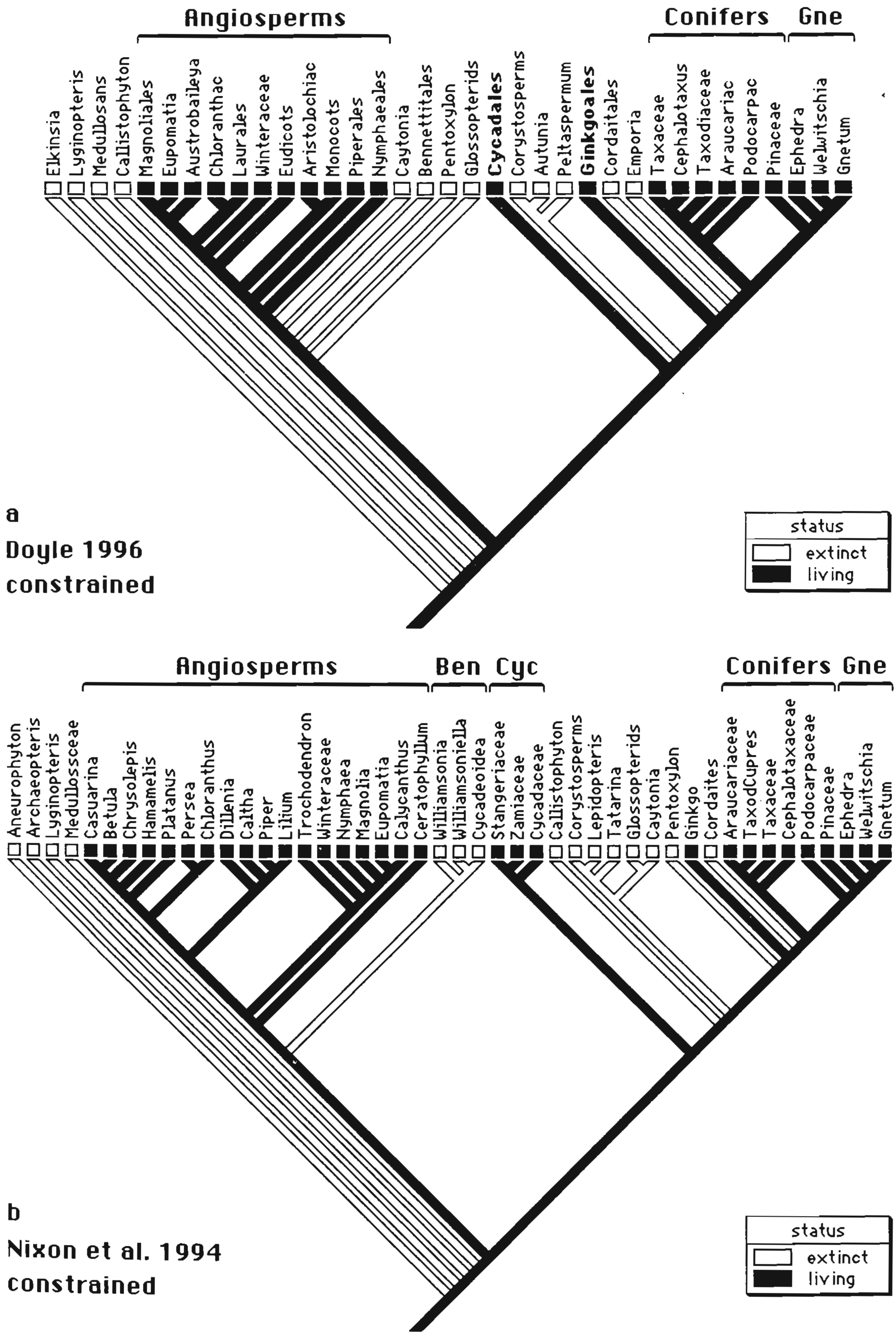
Most molecular studies that associate Gnetales with conifers are also congruent in indicating that living gymnosperms are monophyletic, as the sister group of angiosperms (although this result is not strongly supported - trees with cycads basal or on the line to angiosperms are often almost as parsimonious). Since conifers extend back to the Late Carboniferous, this implies that the line leading to angiosperms goes back this far too - an apparent conflict with the stratigraphic record (Axsmith *et al.*, 1998; Doyle, 1998a). However, this result does not mean that angiosperms and gymnosperms evolved separately from progymnosperms, or that angiosperms originated in the Paleozoic. Since these trees include only living taxa, there could be any number of early seed ferns attached below the split of angiosperms from other living groups, and any number of Permian and Mesozoic fossils attached to the stem lineage leading to angiosperms. This point is illustrated by the tree in Fig. 3a, obtained by analyzing the data set of Doyle (1996) with living gymnosperms constrained to form a clade and Gnetales forced into conifers, and allowing fossils, shown in white, to attach wherever is most parsimonious. The Jurassic fossil *Piroconites*, previously linked with Gnetales, was removed because TEM studies indicate that its supposedly gnetalean exine structure was misinterpreted (Osborn, 2000); this had no effect on unconstrained trees. Late Devonian and Carboniferous seed ferns (*Elkinsia* through *Callistophyton*) still diverge at the base of the tree, and glossopterids, *Pentoxylon*, Bennettitales (in some trees) and *Caytonia* are still associated with angiosperms. Fig. 3b shows a tree from a similarly constrained analysis of the data set of Nixon *et al.* (1994); glossopterids and *Caytonia* are not associated with angiosperms, but Bennettitales are.

Whereas the anthophyte hypothesis suggested that studies of living Gnetales might shed light on the origin of angiosperm features such as double fertilization and endosperm (Friedman, 1992, 1994), molecular results imply that any progress in reconstructing the origin of angiosperms must come from paleobotany. Unfortunately, this task now looks more difficult than it formerly did, since morphological data and methods appear to have given dramatically incorrect results in the case of Gnetales. Before new analyses can be undertaken, we need a complete reappraisal of methods, particularly the way we analyze morphological characters, to understand why previous analyses went so wrong, and whether this could have been avoided. Several characters that seemed to associate angiosperms and Gnetales differ in detail in the two taxa (Donoghue & Doyle, 2000). For example, the tunica in the apical meristem consists of two cell layers in angiosperms but only one in Gnetales; the megaspore wall is thin in Gnetales but completely absent in angiosperms; and double fertilization in Gnetales produces two zygotes, not a zygote and a triploid endosperm nucleus (see references in Doyle, 1996; Doyle & Donoghue, 1986). Another character, granular exine structure, is discussed below. Although in all these cases the gnetalean state could be ancestral to the angiosperm one, the differences could equally well be evidence of convergence. We may also need new data on Mesozoic fossils - either new taxa or new data on characters of known taxa, such as seed cuticles (stressed by Harris, 1954 but generally neglected since then) and stem anatomy. We should also face the possibility that the number of morphological character states in seed plants is too small and the probability for homoplasy during their long evolutionary history too high for reliable cladistic inference ("character state exhaustion", Wagner, 2000), perhaps requiring discovery of new fossils and/or integration of stratigraphic data into phylogenetic analyses. However, molecular data do give indirect indications about groups that need more attention in the search for angiosperm relatives - not Gnetales and related fossils, but rather Bennettitales, *Caytonia*, glossopterids, corystosperms, and more poorly known "seed ferns" in Triassic and Jurassic floras (cf. Anderson & Anderson, 1997).

AGE OF THE ANGIOSPERMS

The second question, when the angiosperms originated, is another case in which fossil and molecular data appear to conflict. Here it is important to distinguish two ages (Doyle & Donoghue, 1993): the time when the stem lineage leading to

Fig. 3—Representative trees based on the data sets of (a) Doyle (1996) and (b) Nixon *et al.* (1994), with extant gymnosperms and angiosperms constrained into a sister-group relationship and Gnetales forced into conifers with Pinaceae, as in recent molecular trees (cf. Fig. 2c). Extant taxa are indicated in black, extinct lines in white.


Angiosperms
Conifers
Gne
Elkinsia
Lyginopteris
Medullosans
Callistophyton
Magnoliales
Eupomatia
Austrobaileya
Chloranthac
Laurales
Winteraceae
Eudicots
Aristolochiac
Monocots
Piperales
Nymphaeales
Caytonia
Bennettitales
Pentoxylon
Glossopterids
Cycadales
Corystosperms
Autunia
Peltaspermum
Ginkgoales
Cordaitales
Emporia
Taxaceae
Cephalotaxus
Taxodiaceae
Araucariac
Podocarpac
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Lyginopteris
Medullosseae
Casuarina
Betula
Chrysolepis
Hamamelis
Platanus
Persea
Chloranthus
Dillenia
Caltha
Piper
Lilium
Trochodendron
Winteraceae
Nymphaea
Magnolia
Eupomatia
Calycanthus
Ceratophyllum
Williamsonia
Williamsoniella
Cycadeoidea
Stangeriaceae
Zamiaceae
Cycadaceae
Callistophyton
Corystosperms
Lepidopteris
Tatarina
Glossopterids
Caytonia
Pentoxylon
Ginkgo
Cordaites
Araucariaceae
TaxodCupres
Taxaceae
Cephalotaxaceae
Podocarpaceae
Pinaceae
Ephedra
Welwitschia
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Nixon et al. 1994
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angiosperms separated from the line to their closest living relatives, and the age of the most recent common ancestor of all living angiosperms, or the crown group. As discussed above, trees of the types in Figs 2c-e imply that the stem lineages of living gymnosperms and angiosperms split in the Carboniferous, but this does not mean that the angiosperm crown group is this old; it could have originated much more recently, and one could argue that the large number of apomorphies separating angiosperms from other groups would take a long time to accumulate. However, the molecular dates being considered here relate specifically to the age of the crown group.

Of course, the age of the angiosperms has also been a topic of controversy in paleobotany. Until the 1960s, many paleobotanists assumed that angiosperms originated long before the Cretaceous, based in large part on identifications of Cretaceous fossils (mostly leaves) with diverse and advanced extant taxa (Axelrod, 1952, 1970). However, this view was challenged by palynological studies, which showed that Early Cretaceous angiosperm pollen was less diverse and more primitive than expected, and that the order of appearance of pollen types agreed with the sequence of evolution inferred from studies of modern plants – monosulcate, as in magnoliids and monocots, tricolpate, the basic type for what are now called eudicots, tricolporate, and finally triporate (Doyle, 1969, 1978; Muller, 1970, 1981). Closer examination of the leaf record and discoveries of fossil flowers and fruits showed a similar pattern of rapid but orderly morphological diversification (Crane *et al.*, 1995; Doyle & Donoghue, 1993; Doyle & Hickey, 1976; Friis & Crepet, 1987; Friis *et al.*, 1994b; Hickey & Doyle, 1977; Upchurch, 1984). Barremian-Aptian mesofossil floras show surprisingly high species diversity, but they do not contradict the picture of low initial advancement (Friis *et al.*, 2000). At present, the oldest definite angiosperm fossils are reticulate monosulcate pollen grains from the Valanginian or Hauterivian (ca. 135 Ma; Brenner, 1996; Hughes, 1994; Trevisan, 1988); a supposedly Jurassic record from China (*Archaefructus*; Sun *et al.*, 1998) has been redated as Barremian-Aptian (Barrett, 2000; Swisher *et al.*, 1999). These data suggest that angiosperms may have originated not long before their appearance in the fossil record, although they do not rule out the existence of older angiosperms if these were rare and plesiomorphic.

Molecular studies on this question have used the concept of a molecular clock, which assumes that gene sequences diverge at a statistically constant rate, to date splits between living groups. This requires at least one calibration point, a split either inside or outside the group that can be dated with the fossil record. Using the gene *gapC* and a rate of molecular evolution inferred from animals, Martin *et al.* (1989) dated the angiosperms, represented by two grasses and seven dicots, as 319 Ma, or mid-Carboniferous. At that time, the most advanced known seed plants were seed ferns more primitive than any living gymnosperms, to say nothing of angiosperms.

Martin *et al.* took this result as support for the views of Axelrod (1952, 1970) and dismissed the concept of a Cretaceous origin as based on negative evidence. However, Crane *et al.* (1989a) argued that the conflict with the fossil record is not so easy to explain away. In particular, Martin *et al.* dated the common ancestor of eudicots as 276 Ma (Permian), but eudicots (which are strongly supported as a monophyletic group: Chase *et al.*, 1993; Qiu *et al.*, 1999; Soltis *et al.*, 1999) are united by tricolpate pollen, which has a dense fossil record, appearing in the late Barremian (Doyle, 1992; Hughes, 1994; Hughes & McDougall, 1990) and becoming ubiquitous in the Albian. Martin *et al.* (1989) did not use any calibration from the plant fossil record, but Martin *et al.* (1993) corrected this deficiency in a study of *gapC* and *rbcL*, which assumed that liverworts split from other land plants at 450 Ma (Late Ordovician); this gave an age of 300 Ma, again Carboniferous. However, younger (though still pre-Cretaceous) ages were found by Wolfe *et al.* (1989) and Laroche *et al.* (1995) - 200 Ma, or Early Jurassic - and by Goremykin *et al.* (1997), based on 58 chloroplast genes - 160 Ma, or Late Jurassic.

Analyses by Sanderson and Doyle (2001) suggest that these dates were biased upward by several factors, especially the fact that molecular evolution is not clocklike and the use of angiosperm taxa with higher than average rates. In addition, previous analyses assumed equal rates across DNA sites (which is known to be incorrect); correcting for this by use of a gamma distribution of rates gives angiosperm ages that are 20-30 Ma younger. Sanderson and Doyle (2001) used *rbcL* sequences from a larger number of taxa, chosen to span the base of the angiosperms and other important nodes. Fig. 4 shows one of their trees plotted against geologic time, calibrated with the divergence of *Marchantia* at 450 Ma, with branch lengths adjusted by a maximum-likelihood program to make molecular evolution as clocklike as possible, and using a gamma distribution. As in other analyses of *rbcL*, Gnetales were basal in seed plants. The estimated age of the angiosperms was 139 Ma, or earliest Cretaceous, close to their first appearance in the fossil record.

A problem with this analysis is that the seed plant relationships in Fig. 4 conflict with other data (as summarized above). Surprisingly, this has little effect on age estimates for angiosperms. When angiosperms and Gnetales were constrained to form a clade, as in the anthophyte hypothesis, the inferred age of angiosperms was 143 Ma, only 4 Ma from that in the previous tree, and the same age was found when Gnetales were forced together with conifers.

These results suggest that ages based on *rbcL* may be more compatible with the fossil record than has been thought. However, ages using the same methods based on 18S rDNA (Sanderson & Doyle, 2001) were still substantially older, varying around 180-190 Ma (depending on seed plant relationships), or Early Jurassic.

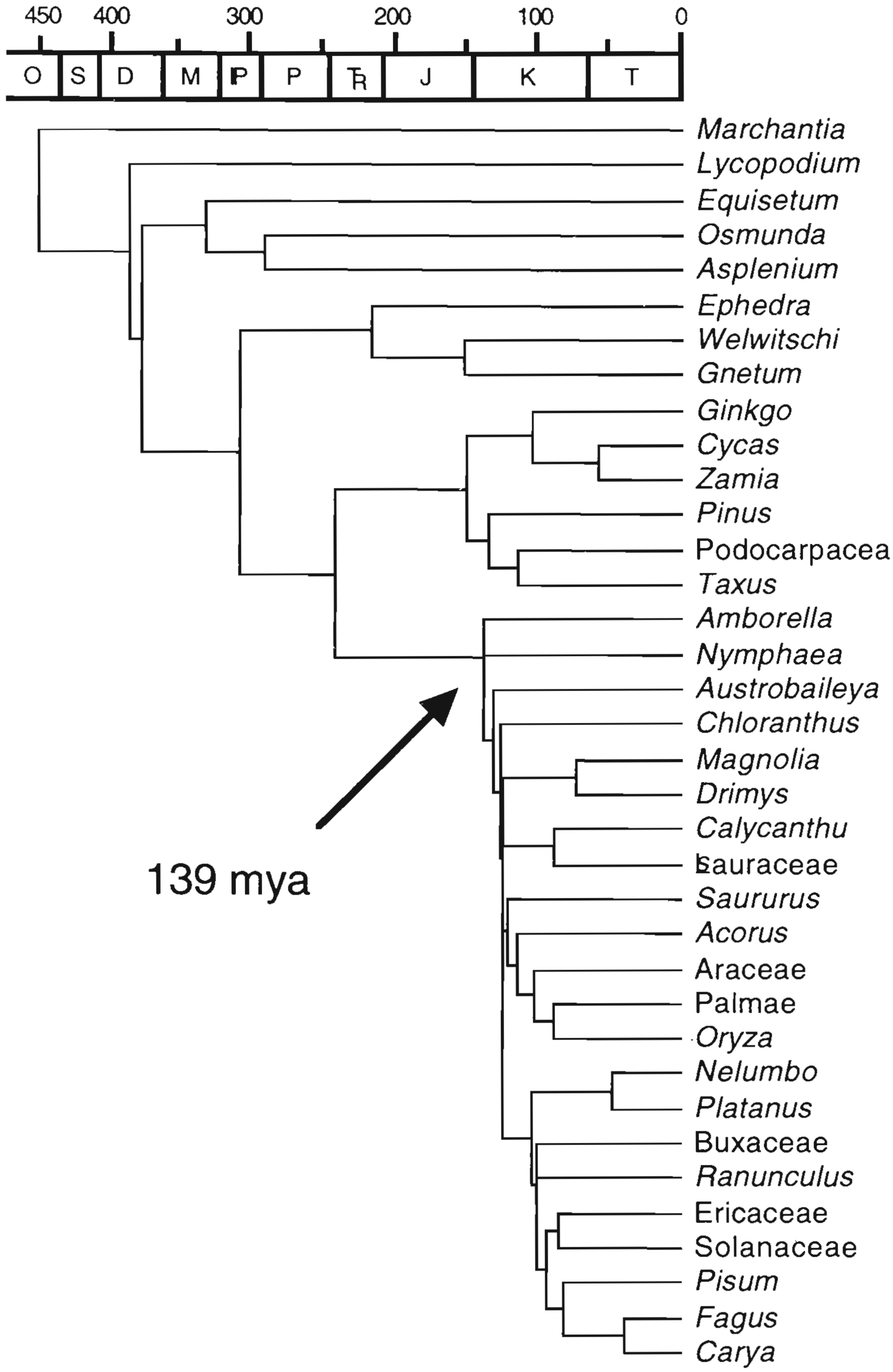

Fig. 4—Seed plant tree based on *rbcL*, with *Lycopodium* forced to the base of vascular plants and conifers forced into a clade, plotted against the geologic time scale, with ages estimated from *rbcL* by maximum likelihood under the assumption of a molecular clock (Sanderson & Doyle, 2001).

Closer examination of the *rbcL* data suggests reasons why previous analyses gave older ages, while warning that the problems are far from solved. Although the ages of angiosperms obtained by Sanderson and Doyle (2001) are consistent with the fossil record, evolution was clearly not clocklike across the tree. In some cases, this gave ages that are too young. Fig. 4 indicates that cycads, *Ginkgo* and conifers split in the Late Jurassic (152 Ma), whereas in fact they go back twice as far, to the Late Carboniferous or Permian. The reasons for this anomaly are clearer in Fig. 5, the same tree presented as a phylogram, with branch lengths proportional to the amount of molecular evolution. Cycads, *Ginkgo* and conifers are unusually short branches; apparently, in pulling the tips of these branches up to the same level as other groups, the likelihood program pulled up their common ancestor too. Some ages within angiosperms are also too young: the split between *Arabidopsis* and *Platanus* was dated as 48 Ma, but the lines leading to both groups are known back to the Albian (100-110 Ma). In contrast, other branches within angiosperms are unusually long—*Oryza*, *Pisum* and *Nicotiana*, all advanced herbaceous taxa. The fact that rates are higher in grasses was already noted by Bousquet *et al.* (1992) and Gaut *et al.* (1992). It happens that earlier clock studies were based largely on such cultivated plants. When Sanderson and Doyle (2001) used *Oryza*, *Pisum* and *Nicotiana* as the only angiosperms in their *rbcL* data set, the estimated age of the group almost doubled - to 252 Ma, or Late Permian.

Sanderson and Doyle (2001) found that age estimates also vary depending on codon positions, with third positions of *rbcL* actually giving angiosperm ages that are too young (Late Cretaceous), and first and second positions giving older ages than the whole sequence. Several previous studies (including Martin *et al.*, 1989, 1993) analyzed amino acid sequences or nonsynonymous substitutions, which involve mostly changes at first and second positions. When Sanderson and Doyle (2001) used *Oryza*, *Pisum* and *Nicotiana* as the only angiosperms on a tree with Gnetales linked with conifers and analyzed only first and second positions of *rbcL*, they obtained a date of 281 Ma, approaching the 300-320 Ma ages of Martin *et al.* (1989, 1993). Thus, taxon sampling and codon positions effectively go far toward explaining the older ages obtained in previous studies. However, this does not indicate which estimates are more nearly correct.

The conflicting ages derived from different genes and the clear inequalities in evolutionary rate among lineages suggest that better understanding of factors influencing rates of molecular evolution and/or development of new methods that deal with unequal rates might reconcile fossil and molecular ages. Unfortunately, the most popular method proposed so far, nonparametric rate smoothing (NPRS, Sanderson, 1997), yields *rbcL* ages for angiosperms that are considerably older than ages based on a clock (Doyle *et al.*, 2001), actually aggravating the conflict. This could mean either that the fossil record is more incomplete than clock-based estimates imply, or that rates of molecular evolution change abruptly rather than gradually (as assumed by NPRS), so that NPRS is even less appropriate than the clock method. These problems should be a topic of continued dialogue between palaeobotanists and molecular evolutionists.

MOLECULAR PHYLOGENIES AND CRETACEOUS ANGIOSPERMS

While molecular data suggest we know less about the outgroups and the age of the angiosperms than we thought, they have greatly clarified the third question - what the first angiosperms were like. In cladistic terms, this is a function of rooting of the angiosperm tree, which depends on character states in the outgroups. In the period of morphological cladistics, it seemed that this problem might not be solved without clear identification of angiosperm outgroups. For example, Donoghue and Doyle (1989) rooted the angiosperms with a hypothetical ancestor based on the seed plant analysis of Doyle and Donoghue (1986). This indicated that Magnoliales were basal in angiosperms, as a result of granular exine structure and other states that they share with Bennettitales and Gnetales, the supposed closest outgroups of angiosperms. In contrast, in trees of Nixon *et al.* (1994; Fig. 1a), in which angiosperms were nested in Gnetales, Chloranthaceae were basal, consistent with their opposite leaves, simple flowers and orthotropous ovules, all gnetalian features. In trees of Doyle (1996, Fig. 1b), in which *Caytonia* was the sister group of angiosperms, Nymphaeales were basal.

In contrast, molecular analyses have converged remarkably on similar rootings of the angiosperms, despite the uncertainties on outgroup relationships discussed above. The main exception was the first large analysis, using *rbcL* (Chase *et al.*, 1993), which placed the aquatic genus *Ceratophyllum* at the base of the angiosperms. The first signs of the present picture came from studies of nuclear rRNA (Doyle *et al.*, 1994; Hamby & Zimmer, 1992) and chloroplast rDNA ITS sequences (Goremykin *et al.*, 1996), which indicated that Nymphaeales were basal. More recent multigene studies have kept Nymphaeales near the base while adding several other taxa around them. The data used included various combinations of *rbcL* and *atpB* from the chloroplast, 18S rDNA from the nucleus, and five mitochondrial genes (Barkman *et al.*, 2000; Parkinson *et al.*, 1999; Qiu *et al.*, 1999; Soltis *et al.*, 1998, 1999, 2000), duplicated phytochrome genes (Mathews & Donoghue, 1999), and 17 chloroplast genes (Graham & Olmstead, 2000). In most of these studies, the first branch was *Amborella*, a vesselless shrub from New Caledonia formerly placed in Laurales; the second was Nymphaeales; and the third was a clade consisting of Illiciales and two Australasian lianas, *Austrobaileya* and *Trimenia* (placed in their own families). These lines were called the 'ANITA grade' by Qiu *et al.* (1999). The main uncertainty concerns the exact relationship of *Amborella* and Nymphaeales. Their placement as successive branches has low bootstrap support and is sensitive to taxon sampling (Graham & Olmstead, 2000; Qiu *et al.*, 2000), and analyses using the RASA method, designed to counteract long branch attraction, unite *Amborella* and Nymphaeales as a basal clade (Barkman

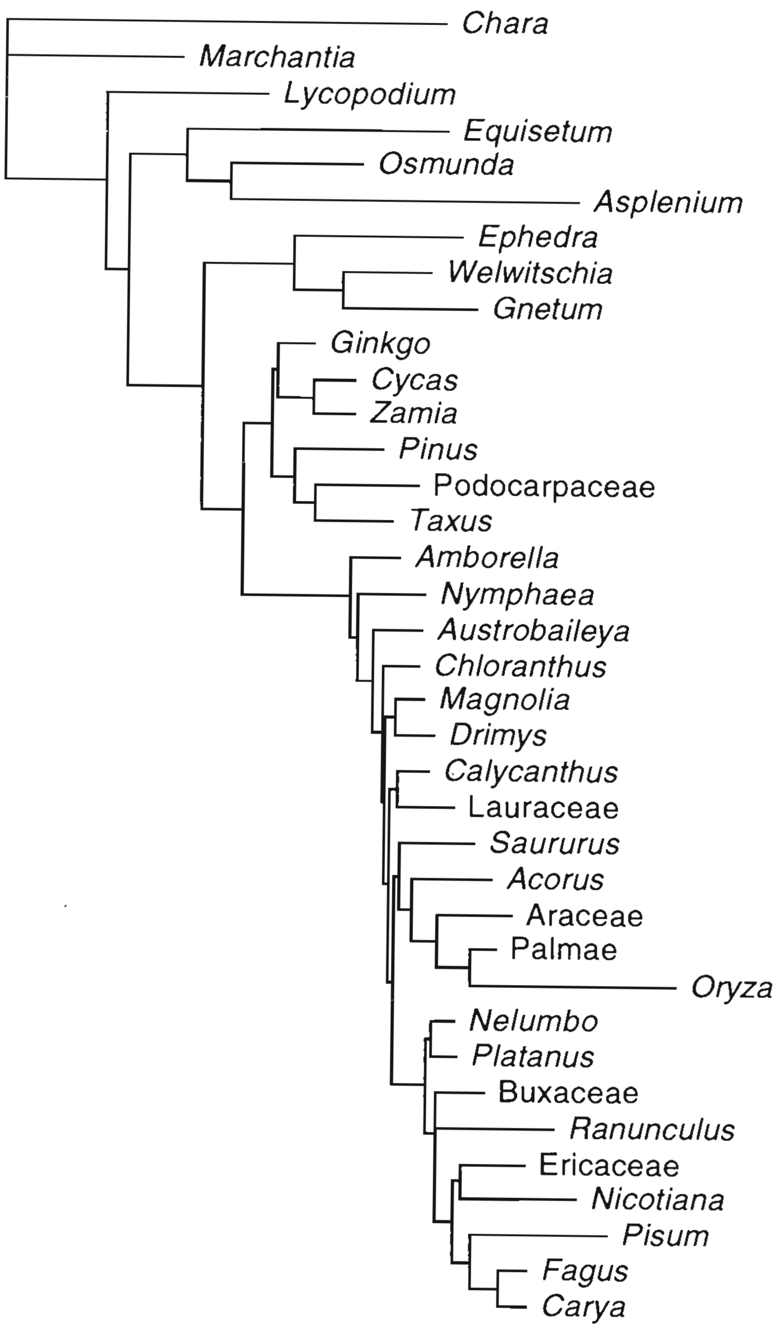

Fig. 5—Tree in Fig. 4 presented as a phylogram, with branch lengths proportional to the amount of molecular evolution (Sanderson & Doyle, 2001).

et al., 2000; contrary to these authors, this has only minor effects on inferred ancestral states). Above the ANITA grade, there are eight major clades, all of which have high bootstrap support, but whose mutual relationships are not completely resolved. Thus, even though living gymnosperms are very distant from angiosperms and their arrangement is uncertain, they appear to provide a strong molecular signal for rooting the angiosperms.

These molecular trees show striking parallels with the Cretaceous fossil record. This point can be illustrated by plotting characters on the tree in Fig. 6, from a study by Doyle and Endress (2000), who combined a new morphological data set with *rbcL*, *atpB* and 18S sequences and specified *Amborella* as the outgroup to other taxa. This 'combined' tree resembles molecular trees in most respects, except in a few places where molecular support was weak. For example, it

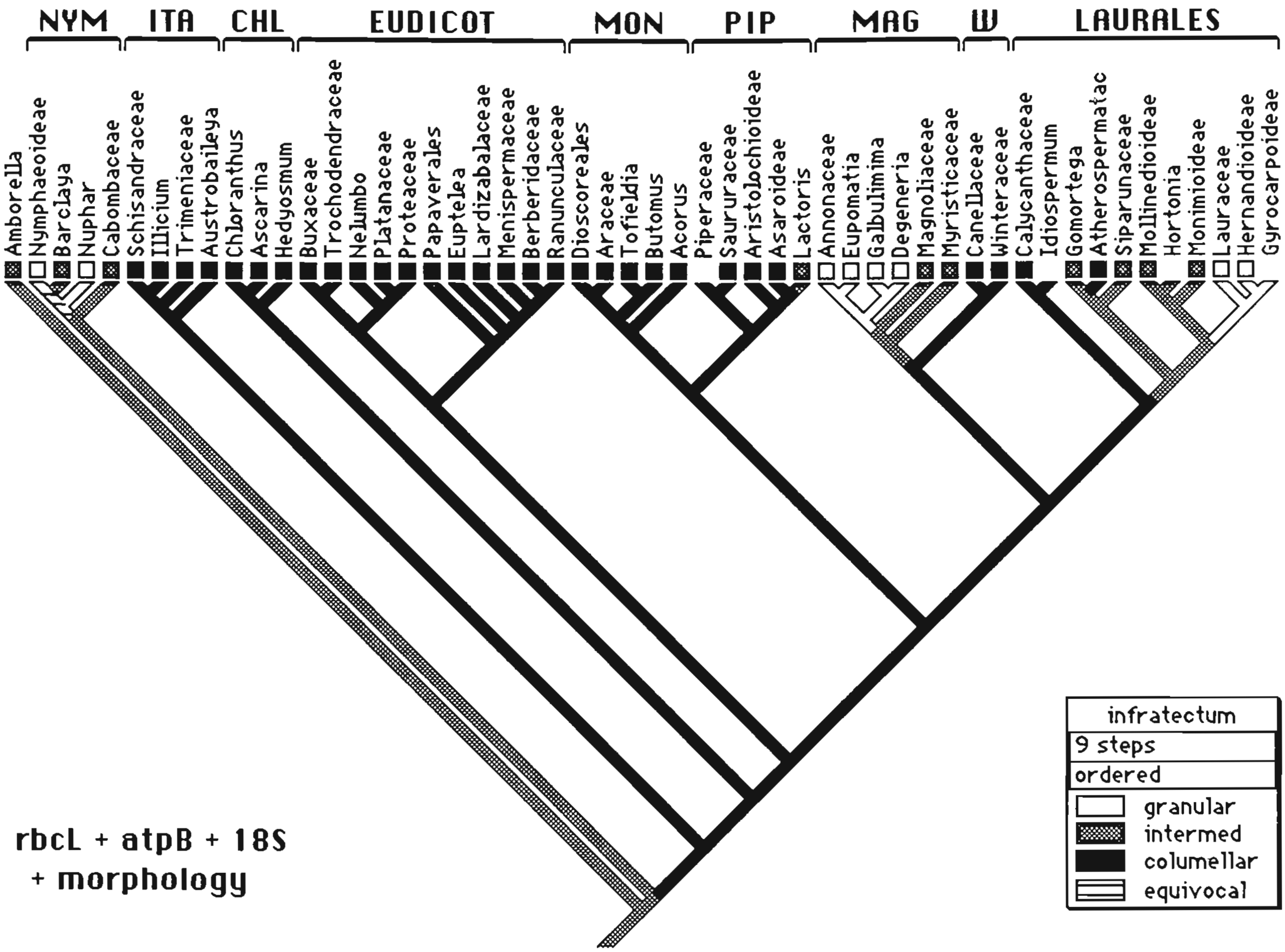

Fig. 6— Single tree found in the combined analysis of Doyle and Endress (2000), based on morphology, *rbcL*, *atpB* and 18S rDNA, showing the inferred evolution of exine structure. CHL = Chloranthaceae, MAG = Magnoliales, W = Winterales, PIP = Piperales, NYM = Nymphaeales, MON = monocots.

links monocots with Piperales (*sensu* APG, 1998, including Aristolochiaceae and *Lactoris*), Winterales with Magnoliales rather than Piperales and Lauraceae with Hernandiaceae rather than Monimiaceae (Monimioideae, *Hortonia*, Mollinedioideae).

Perhaps most interesting is the case of Chloranthaceae, which have occupied several positions in molecular trees, but which morphology helps to place immediately above the ANITA grade. This near-basal position is consistent with the abundance of apparent fossil relatives of Chloranthaceae in the Early Cretaceous, such as the *Clavatipollenites* and *Asteropollis* pollen groups (Couper, 1958; Muller, 1981; Walker & Walker, 1984), flowers and fruits associated with these pollen types (Eklund *et al.*, 1997; Friis *et al.*, 1986, 1994b, 1999; Pedersen *et al.*, 1991), and probably some of the leaves with chloranthoid teeth discussed below. Some Barremian-Aptian fossils (Friis *et al.*, 1994b, figs 3c-f; Friis *et al.*, 1997a, fig. 6.3) appear to be related to the living genus *Hedyosmum*: both groups have pollen with a branched sulcus (*Asteropollis* in the dispersed pollen record) and three tepals fused to the carpel, indicating that the crown group of Chloranthaceae had evolved by this time. Tripartite androecia related to *Chloranthus* are diverse in the Late Cretaceous, and a more problematic example (because of the anomalous orientation of the anthers) is known from the Albian (Crane *et al.*, 1989b; Eklund *et al.*, 1997; Friis *et al.*, 1986; Herendeen *et al.*, 1993).

The new molecular rooting is also significant in suggesting that the earliest Cretaceous angiosperms may be closer to the origin of the clade than previous phylogenetic views implied. A prime example concerns exine structure. The oldest generally accepted angiosperm pollen grains, from the Valanginian of Italy (Trevisan, 1988), the Valanginian-Hauterivian of Israel (Brenner, 1996) and the Hauterivian of

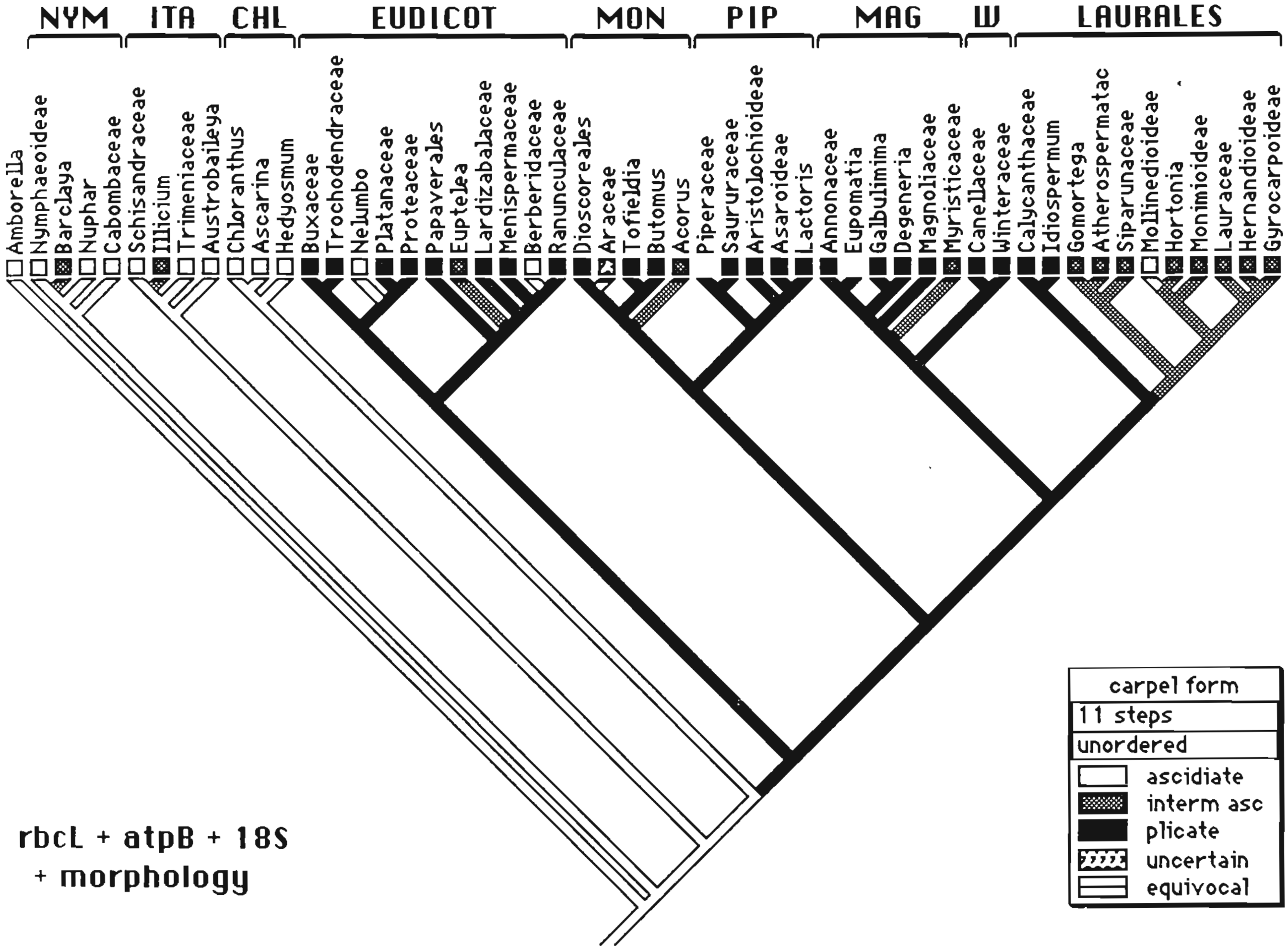

Fig. 7—Tree from the combined analysis of Doyle Endress (2000), showing the inferred evolution of carpel form

England (Hughes, 1994; Hughes & McDougall, 1987; Hughes *et al.*, 1991), are monosulcates and inaperturates with reticulate sculpture and columellar exine structure. It has been argued that the plants producing this pollen were already advanced relative to Magnoliales with smooth pollen and granular exine structure (Muller, 1970; Van Campo & Lugardon, 1973; Walker, 1976; Walker & Walker, 1984; Ward *et al.*, 1989), and this view seemed to be supported by the basal position of Magnoliales in the cladistic analysis of Donoghue and Doyle (1989). Such pollen would be hard to distinguish from that of Bennettitales without TEM study, and it could extend back much earlier without being recognized. However, molecular trees (Fig. 6) indicate that granular structure is actually derived in angiosperms, since Magnoliales and other granular taxa are nested within the group, not basal. The inferred ancestral structure, retained in some Nymphaeales (Cabombaceae, *Barclaya*), had irregular columellae overlain by a continuous tectum; this was called intermediate by Doyle and Endress (2000) but columellar by Osborn *et al.* (1991). Typical columellar structure originated at the third node, along with a reticulate tectum, resulting in pollen like that of *Austrobaileya* (Endress & Honegger, 1980), which would be at home in the Hauterivian. Hence there is no longer reason to assume a long period of angiosperm evolution before the appearance of such pollen.

This conclusion holds all the more if *Amborella* is linked with Nymphaeales (Barkman *et al.*, 2000), since under this arrangement it is equally parsimonious to assume that either tectate-intermediate or reticulate-columellar exines were ancestral. The discovery by Friis *et al.* (2001) of a Barremian-Aptian flower similar to Nymphaeales but with reticulate-columellar pollen may be evidence for the latter view. However, even if the first angiosperm pollen was tectate, the molecular results suggest that it might be more recognizable than pollen of Magnoliales. *Amborella* has monosulcate pollen with verrucate sculpture, small supratectal spinules and sparse, irregular columellae (Hesse, 2001; Sampson, 1993). Hughes

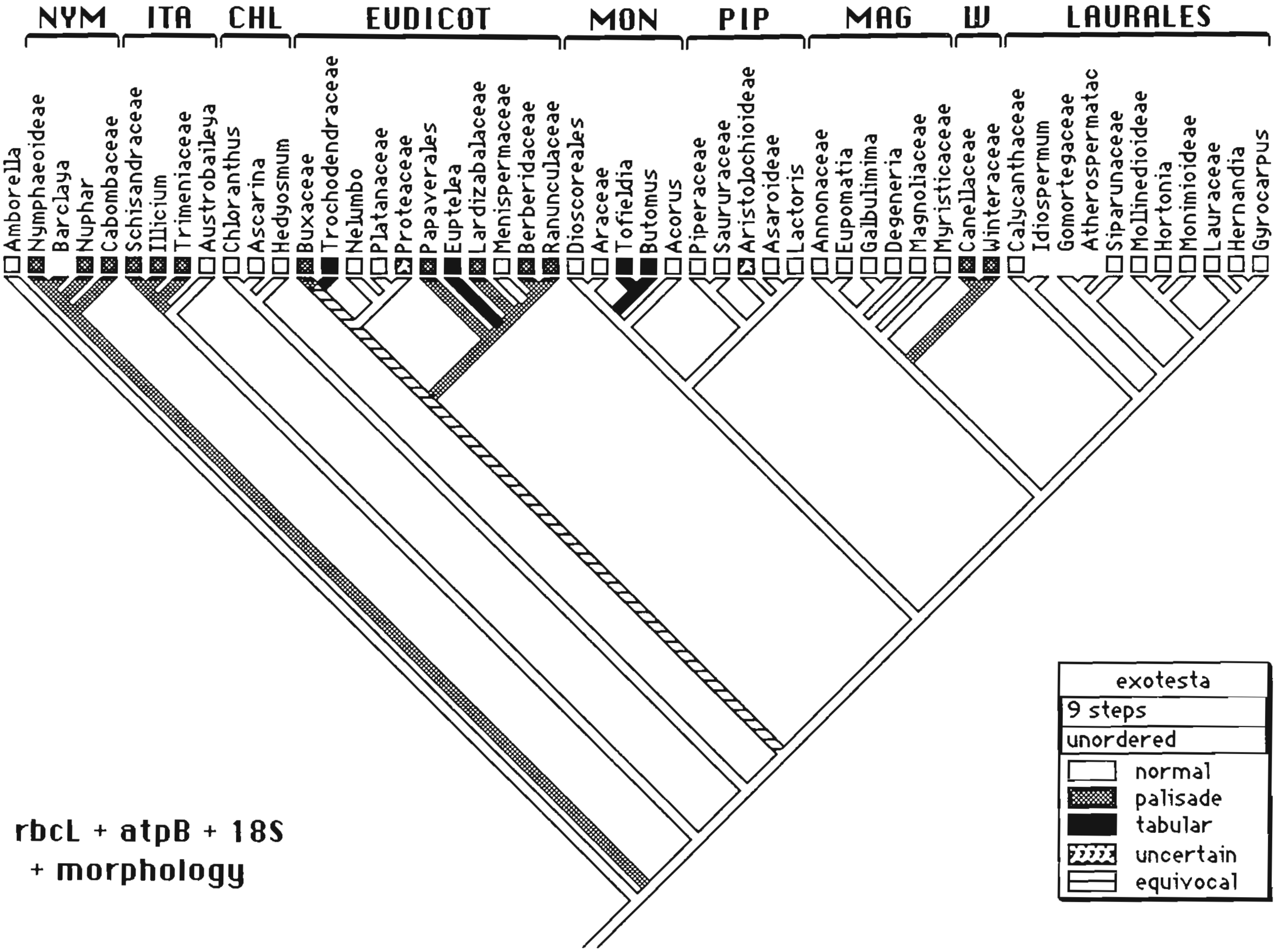

Fig. 8—Tree from the combined analysis of Doyle and Endress (2000), showing the inferred evolution of exotestal structure.

and McDougall (1987) and Hughes (1994) described pollen with almost identical sculpture from the Hauterivian of England as HAUTERIVIAN-CACTISULC. It would be unwarranted to identify this pollen as *Amborella*, but it does show that such pollen existed and can be detected in the earliest angiosperm record.

Other agreements between molecular trees and the Cretaceous record concern carpel morphology. The classical view (especially among American botanists) is that the original carpel was plicate (conduplicate), like a leaf folded down the middle, as in *Degeneria* and Winteraceae (Bailey & Swamy, 1951). However, molecular trees imply that the ancestral carpel was ascidiate, as proposed by Leinfellner (1969) and van Heel (1981). Both carpel types begin their development as a U-shaped primordium. In the plicate type, the two arms of the primordium grow up separately, but in the ascidiate type the cross-zone between the arms becomes meristematic, and the carpel grows up like a tube. At maturity ascidiate carpels are typically barrel-shaped, with a sessile stigma, and they are sealed by secretion rather than postgenital fusion of the margins (Endress & Igersheim, 2000). The combined tree of Doyle and Endress (2000) indicates that the ascidiate state was ancestral and retained up to Chloranthaceae (Fig. 7). This agrees with the fact that most carpels reported by Friis *et al.* (1994b, 1999, 2000) from the Barremian-Aptian of Portugal appear to be ascidiate, judging from their shape, sessile stigma, and lack of evidence for a ventral suture, including both those associated with Chloranthaceae and others. At the fruit stage most had one seed, like *Amborella*, *Trimenia*, *Illicium*, and Chloranthaceae, but a few had several, like other ANITA taxa (Nymphaeales, *Austrobaileya*, Schisandraceae). Friis *et al.* (2000) suggested that both ascidiate and plicate carpels were present, with the latter represented by follicular fruits, but follicles were less common than berries, drupes, nuts and achenes (Eriksson *et al.*, 2000).

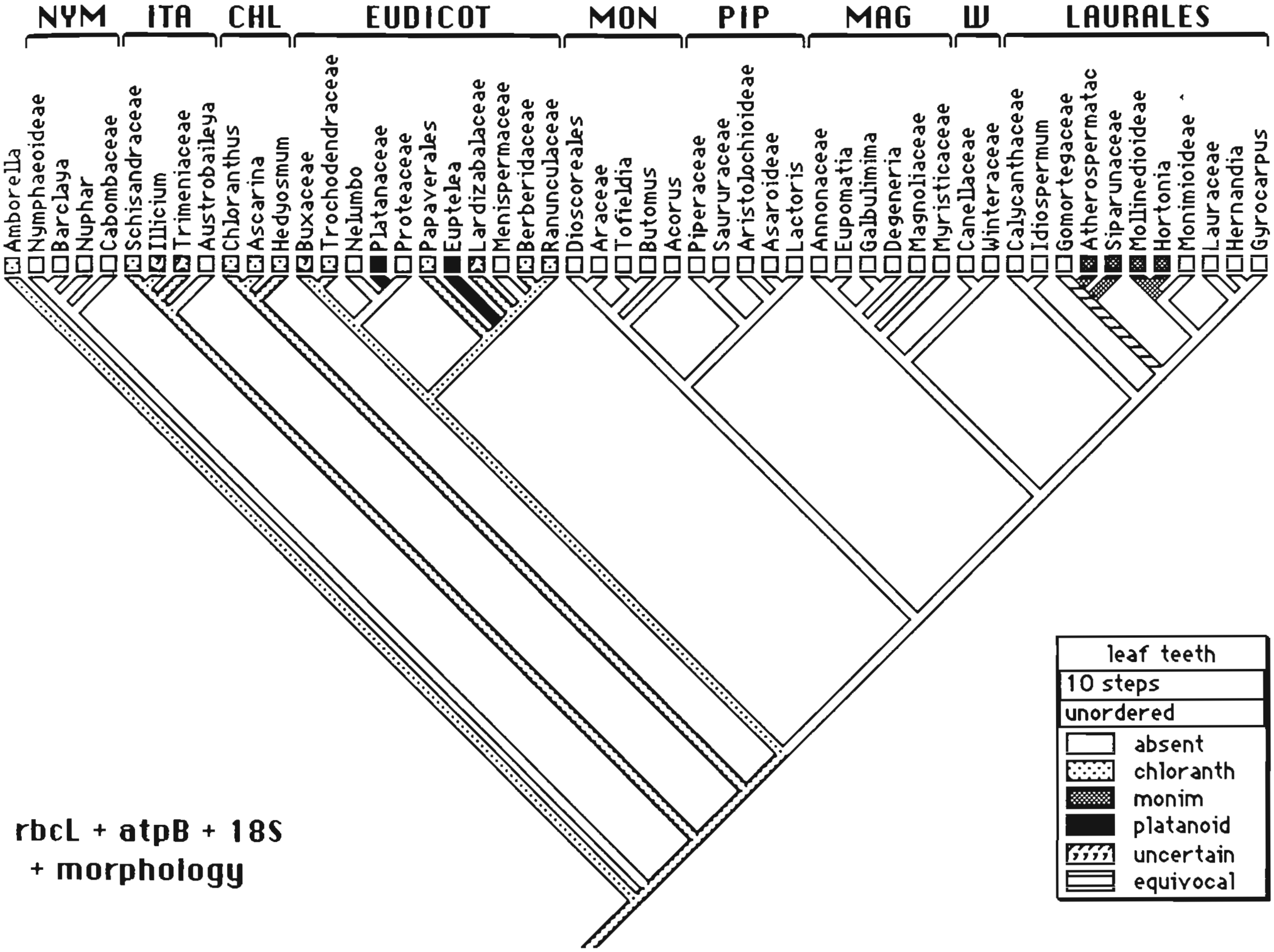

Fig. 9—Tree from the combined analysis of Doyle and Endress (2000), showing the inferred evolution of leaf margin.

Another conspicuous feature of Barremian-Aptian mesofloras is exotestal seed structure, in which cells of the outer epidermis of the outer integument become thick-walled (Friis *et al.*, 1999, 2000). This feature is typical of Nymphaeales, *Trimenia* and Illiciales. It is not inferred to be ancestral on the cladogram in Fig. 8, since it is absent in *Amborella* and *Austrobaileya*, but this may be a function of the relict and specialized (autapomorphic) nature of living ANITA taxa. *Amborella* is autapomorphic in having a hard endocarp derived from the inner carpel wall, *Austrobaileya* in having a fleshy sarcotesta derived from the mesophyll of the outer integument. For functional reasons, origin of either feature might be expected to entail loss of a hard, protective exotesta if this was present in the first angiosperms.

As stressed by Friis *et al.* (2000), Barremian-Aptian mesofloras consist largely of taxa that cannot be associated with any one extant family (except for Chloranthaceae). Many may therefore represent extinct lines on the stem lineages of modern families or the internodes between them. However, as the comparisons made here show, this does not prevent them from contributing to formulation and testing of hypotheses on basic states and character evolution in angiosperms, through comparison with molecular phylogenies and improved data on the distribution of morphological characters.

Similar leaf features are also found at the base of molecular trees and in early angiosperms. An example mentioned above is chloranthoid teeth (Hickey & Wolfe, 1975), with three veins joining below a cap-like apical gland. These occur in modern Chloranthaceae and Barremian-Aptian leaves, such as DBLT no.1 of Upchurch (1984) from the lower Potomac Group (Aptian?) and *Moutonia* spp. of Pons (1984) from the late Barremian or Aptian of Colombia. However, as shown in Fig. 9, chloranthoid teeth are found not only in Chloranthaceae, but also in several ANITA groups and basal eudicots (cf. Hickey & Wolfe, 1975), and Fig. 9 implies that they are ancestral for angiosperms.

Lower Potomac leaves are also notable for their variable stomata, which often vary from paracytic to laterocytic to cyclocytic on the same leaf (Upchurch, 1984). Upchurch suggested that this variation was primitive, like the irregular ("first rank") venation of lower Potomac leaves (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Wolfe *et al.*, 1975). In surveying extant magnoliids, Upchurch (1984) found similar variation in only a few taxa, notably *Amborella*, *Austrobaileya*, *Schisandra* and Chloranthaceae. At the time, this list did not seem particularly significant, but these taxa now stand out as groups located near the base of molecular and combined trees.

The next phases of the angiosperm record also agree with molecular phylogenies by showing new types that can be related to several clades above the ANITA grade, often to basal members of these clades. Among the oldest are monoporate tetrads from the late Barremian of Gabon and the Aptian-Albian of Israel, which resemble Winteraceae in the tetrad habit and ring of endexine around the pore but appear to be more primitive in having finer sculpture (Doyle, 2000; Doyle *et al.*, 1990a, b; Walker *et al.*, 1983).

Tricolpate pollen, which is diagnostic for the eudicot clade, is first seen in the probable late Barremian of Gabon and England (Doyle, 1992; Doyle *et al.*, 1977; Doyle & Hotton, 1991; Hughes, 1994; Hughes & McDougall, 1990), and it has been found in stamens from the Barremian-Aptian of Portugal (Friis *et al.*, 1994b, 2000). The first tricolpates from Gabon have irregularly arranged furrows (Doyle, 1992; Doyle & Hotton, 1991), suggesting they may be on the eudicot stem lineage rather than in the crown group (although similar irregularities occur in the near-basal eudicot *Nelumbo*: Borsch & Wilde, 2000; Kuprianova, 1979). In the lower Potomac Group (Aptian?), there are ternately lobed leaves called *Vitiphyllum* (Berry, 1911; Doyle & Hickey, 1976; Hickey & Doyle, 1977) that are suggestive of Ranunculales, the first eudicot branch in molecular trees.

Other lower Potomac fossils have been compared with monocots (Doyle, 1973; Walker & Walker, 1984): narrow leaves with apically converging venation, known as *Acaciaephyllum*, and monosulcate pollen called *Liliacidites*, with sculpture that grades from coarse in the middle of the grain to fine at the ends, a feature found in many monocots but not known in living magnoliids. These comparisons have been criticized by Gandolfo *et al.* (2000). These authors were correct in arguing that the leaf criteria proposed by Doyle (1973) for separating monocots from gymnosperms do not separate monocots from Gnetales, including the lower Potomac genus *Drewria* (Upchurch & Crane, 1985). Still, *Acaciaephyllum* appears to differ from *Drewria* and extant Gnetales in having spiral rather than opposite leaf arrangement and apical vein fusion. Some pollen types assigned to *Liliacidites* and considered monocots by Doyle (1973) and Walker & Walker (1984), but segregated by Góczán and Juhász (1984) as *Stellatopollis*, differ in having finer sculpture at the proximal pole and sulcus margins rather than the ends of the grain and were therefore questioned as monocots by Doyle and Hotton (1991). As noted by Gandolfo *et al.* (2000), Friis *et al.* (1997b) associated such pollen with carpels (*Anacostia*) that were clearly not monocots (possibly related to Illiciales?). However, more distinctively monocot-like pollen with fine sculpture at the ends of the grain has not yet been found *in situ*. Gandolfo *et al.* cited several other associations of *Liliacidites* with non-monocotyledonous floral remains (e.g., *L. minutus*, associated with *Virginianthus*, discussed below), but all of these are pollen types without sculpture gradation that were assigned to *Liliacidites* by authors who used this genus in a broader sense.

Floral remains representing another magnoliid line, Laurales, are known from the Albian. *Virginianthus* (Friis *et al.*, 1994a), from the upper Potomac Group, appears to be related to Calycanthaceae in having a deep hypanthium and other calycanthaceous features but is more primitive in having monosulcate rather than disulculate pollen. Cenomanian flowers and inflorescences called *Mauldinia* (Drinnan *et al.*, 1990) and associated wood (*Paraphyllanthoxylon*, Herendeen, 1991) correspond in great detail to Lauraceae, and similar but more fragmentary flowers occur in the Albian (Crane *et al.*, 1994). Magnoliales, once considered the most primitive angiosperms but not basal in molecular trees, are not definitely known until the Cenomanian, represented by flowers and leaves of *Archaeanthus* (Dilcher & Crane, 1984), an apparent stem relative of Magnoliaceae. However, Aptian monosulcate pollen with granular exine structure (*Lethomasites*, Ward *et al.*, 1989) and Albian laminar stamens containing smooth monosulcate pollen (Crane *et al.*, 1994, figs 11a, b) may represent this clade.

The Albian marks the explosion of tricolpate eudicot pollen, and many Albian megafossils can be associated with particular eudicot lines. Significantly, all well-reconstructed Albian eudicots appear to be related to groups that molecular phylogenies place near the base of the clade. Many are relatives of *Platanus* and *Nelumbo*, which molecular data unexpectedly unite with Proteaceae in a clade called Proteales (APG, 1998), probably the second branch in eudicots. The oldest are inflorescences of unisexual flowers that resemble those of *Platanus* but are associated with pinnately compound *Sapindopsis* leaves (Crane *et al.*, 1993), and peltate *Nelumbites* leaves and pitted floral receptacles that differ from those of *Nelumbo* in being round rather than flat-topped (Upchurch *et al.*, 1994). Relatives of Buxaceae, another early branch, are represented by inflorescences of unisexual flowers called *Spanomera* (Drinnan *et al.*, 1991). It is not until the Cenomanian that we see definite "core" eudicots (rosids, asterids, and associated smaller groups), such as pentamerous flowers of a rosid type (Basinger & Dilcher, 1984) and the first members of the Normapolles pollen complex (Lang, 1975; Pacltová, 1971, 1981), later members of which have been associated with flowers of "core Amentiferae" or "higher" Fagales (Friis, 1983; Schönenberger *et al.*, 2001; Sims *et al.*, 1999). However, tricolporate pollen, which is probably basic for rosids and asterids, is known from the late Albian (Doyle & Robbins, 1977; Laing, 1975), suggesting that core eudicots had originated by that time.

The fact that the stratigraphic pattern of appearance of pollen, leaf and floral types agrees as well as it does with molecular phylogenies may also be an argument against molecular clock analyses that date the angiosperms as much older than the Cretaceous. If angiosperms had undergone a substantial part of their diversification before the Cretaceous, it is hard to imagine why they "waited in line" and then filed into the Cretaceous fossil record in the same order that molecular evidence indicates they originated long before.

ANGIOSPERM ROOTING AND ANGIOSPERM OUTGROUPS

Although molecular trees do not indicate directly which fossil seed plants were most closely related to angiosperms, they may help indirectly in the search for angiosperm outgroups by suggesting which states are ancestral and thereby refining our search image. For example, the discovery of vessels in Permian gigantopterids (Li & Taylor, 1999; Li *et al.*, 1996) might suggest that these plants were related to angiosperms. However, molecular results (cf. Fig. 6) contradict this argument, since (unlike earlier morphological analyses: Donoghue & Doyle, 1989; Young, 1981) they indicate that the common ancestor of angiosperms did not have vessels: *Amborella* is vesselless, and Nymphaeales either lack vessels or have cells with porose pit membranes that are intermediate between tracheids and vessel elements (Schneider & Carlquist, 1996; Schneider *et al.*, 1995). In contrast, however, the same trees imply that the absence of vessels in Winteraceae and Trochodendraceae is a result of secondary loss. Ecological and biogeographic scenarios for such loss, as a possible consequence of migration into cooler high-latitude areas, have been discussed by Doyle (2000) and Feild *et al.* (2000).

Another example concerns exine structure. As shown in Fig. 6 and discussed above, molecular phylogenies imply that the first angiosperms had columellar structure (either intermediate or well-developed), rather than granular structure, as previously thought (Donoghue & Doyle, 1989; Van Campo & Lugardon, 1973; Walker, 1976; Walker & Walker, 1984). This suggests that paleobotanists should look more closely at Late Triassic monosulcate and related pollen types described by Cornet (1989) as the Crinopolles group, which have reticulate sculpture and conspicuous columellae but a thick, gymnosperm-like endexine (Cornet, 1989; Doyle & Hotton, 1991). Doyle and Hotton (1991) argued that this combination of features might mean that Crinopolles plants were related to but more primitive than angiosperms (i.e., angiosperm stem relatives). This suggestion conflicted with the hypothesis that the first angiosperms had granular exines, which predicted that the gymnospermous endexine was lost before the origin of columellae, but the molecular evidence that columellar exines are ancestral removes this objection. Thus association of Crinopolles pollen with other organs should be a high priority for paleobotanists.

Although it would be most sensational to find angiosperm stem relatives in the Triassic or Jurassic, the possibility that some such plants persisted into the Cretaceous should not be overlooked. A possible candidate is *Archaefructus*, originally described as Late Jurassic (Sun *et al.*, 1998) but redated as Barremian-Aptian (Barrett, 2000; Swisher *et al.*, 1999), an elongate axis bearing numerous well spaced follicles. If *Archaefructus* is a floral axis, as assumed by Sun *et al.* (1998), it is unlike and possibly more primitive than anything in living angiosperms. However, if it is instead an inflorescence, this argument may not hold. Another is *Afropollis* (Doyle *et al.*, 1982), a widespread pollen group in the late Barremian through Cenomanian of Northern Gondwana, which includes coarsely reticulate grains that vary from operculate to zonasulculate and inaperturate. Doyle *et al.* (1990a, b) speculated that *Afropollis* might represent extinct relatives of Winteraceae, but unlike most angiosperms and like the Crinopolles it has a thick, laminated endexine. Friis *et al.* (1999) found *Afropollis* in non-angiospermous microsporangia from the Barremian-Aptian of Portugal, apparently excluding it from the angiosperm crown group, but not necessarily from the stem lineage (Doyle, 2000).

CONCLUSION

It would be presumptuous to argue that paleobotanists should accept molecular phylogenies without question, but these trees are based on a vast and ever-growing body of data that cannot be ignored, and they can be a rich source of hypotheses for future research. Furthermore, molecular trees show remarkable agreements with the Cretaceous angiosperm record. Depending on which line of evidence is considered more reliable, this congruence can be taken as fossil confirmation of molecular results, molecular evidence that the fossil record provides a good picture of the early phases of angiosperm evolution, or both.

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A new peltaspermaceous pteridosperm from the Upper Permian of the Russian Platform

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ABSTRACT

Naugolnykh SV 2001. A new peltaspermaceous pteridosperm from the Upper Permian of the Russian Platform. Palaeobotanist 50(2 & 3) : 189-205.

The paper focuses on the description of a new species of peltaspermalean pteridosperm *Peltaspermopsis polyspermis* Naug. sp. nov. The plant remains were collected from the Upper Permian (Tatarian) of northern part of Russia (N. Dvina River Basin). The species is characterized both by reproductive organs (seed bearing discs and their racemose aggregations) and vegetative organs (stems with nodes of seasonal growth interruptions and *Pursongia*-like lanceolate leaves). The new combination *Peltaspermum parvulum* (Sixtel) Naug. comb. nov. is proposed. General questions concerning *Pursongia* Zalessky, its taxonomical composition, morphological features and relationship with *Glossopteris* are discussed. The species *Pursongia amalitzkii* Zalessky is described on the base of newly collected material.

Key-words—Permian, Pteridosperms, Seed bearing discs, Leaf morphology, *Pursongia, Glossopteris.*

रूसी क्षैतिज आधारभूमि (प्लेटफ़ार्म) पर उपरि परमियन कल्प के नवीनतम पेल्टास्पर्मेशियस टेरिडोस्पर्म

सर्गेइ वी. नाउगोलिन्ख

सारांश

प्रस्तुत शोध-पत्र में पेल्टास्पर्मेलियन टेरिडोस्पर्म की एक नई प्रजाति पेल्टास्पर्माप्सिस पॉलीस्पर्मिस नाउग नव प्रजाति का विवेचन अभिप्रेत है। इस हेतु पादप अवशेष रूस के उत्तरी भाग (एन.ड्वाइन नदी द्रोणी) के उपरि परमियन (तातारियन) कल्प से संग्रहीत किए गए। प्रजाति जननांगों (बीजधारी बिम्ब तथा उनके सभी असीमाक्षी) तथा वनस्पतिपरक अंगों (मौसम वृद्धि अवरोधकों से युक्त गाँठों वाले तने तथा *परसोंगिया* की भाँति की मालाकार पत्तियाँ) दोनों द्वारा ही निरूपित है। अतः नवीनतम संयोजन *पेल्टास्पर्मम* पार्ष्यूलम (सिक्सटेल) नाउग. नव संयोजन प्रस्तावित किया जाता है। इसके अतिरिक्त *परसोंगिया* ज़ैलैक्सी की कुछ सामान्य सी शंकाओं, जैसे- इसका वर्गिकीय संघटन, संरचनात्मक अभिलक्षण तथा *ग्लॉसोप्टेरिस* के साथ इसके सम्बन्धों के समाधान ढूँढने के भी प्रयास इस शोध पत्र में किए गए हैं। नवीनतम संग्रहीत पदार्थों के आधार पर *परसोंगिया अमालिट्ज़काई* नामक प्रजाति का भी विवेचन किया गया है ।

संकेत शब्द—परमियन, टेरिडोस्पर्म, बीजधारी बिम्ब, पर्णसंरचनाविज्ञान, परसोंगिया, *ग्लॉसोप्टेरिस.*

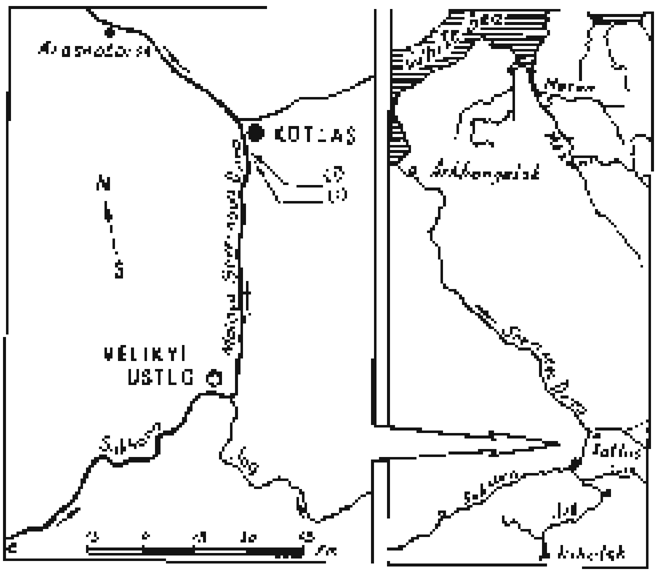

Fig. 1 — Geographical position of the localities studied: 1 - Sokolki, 2 - Zavraje.

INTRODUCTION

INVESTIGATION of the Upper Palaeozoic plants of Angaraland is an interesting and important problem for modern palaeobotany, since Angara and (including Subangaraland ecotonic belt) floras are quite distinctive and considerably different from taxonomic assemblages from other phytogeographical provinces of that time.

The representatives of Peltaspermales were widely spread along external parts of the Angaran continent. There, they were the most abundant plants and represented by high diversity of taxa.

The aim of this paper is the description of a peltaspermalean pteridosperm, which is assigned to new species *Peltaspermopsis polyspermis* Naug., sp. nov. In addition some questions of taxonomy and nomenclature of *Pursongia*-like leaves are discussed.

MATERIAL AND METHODS

The specimens studied originated from two famous localities of plant remains, which belong to the stratotype section of Severodvinskian Horizon of Upper Tatarian substage

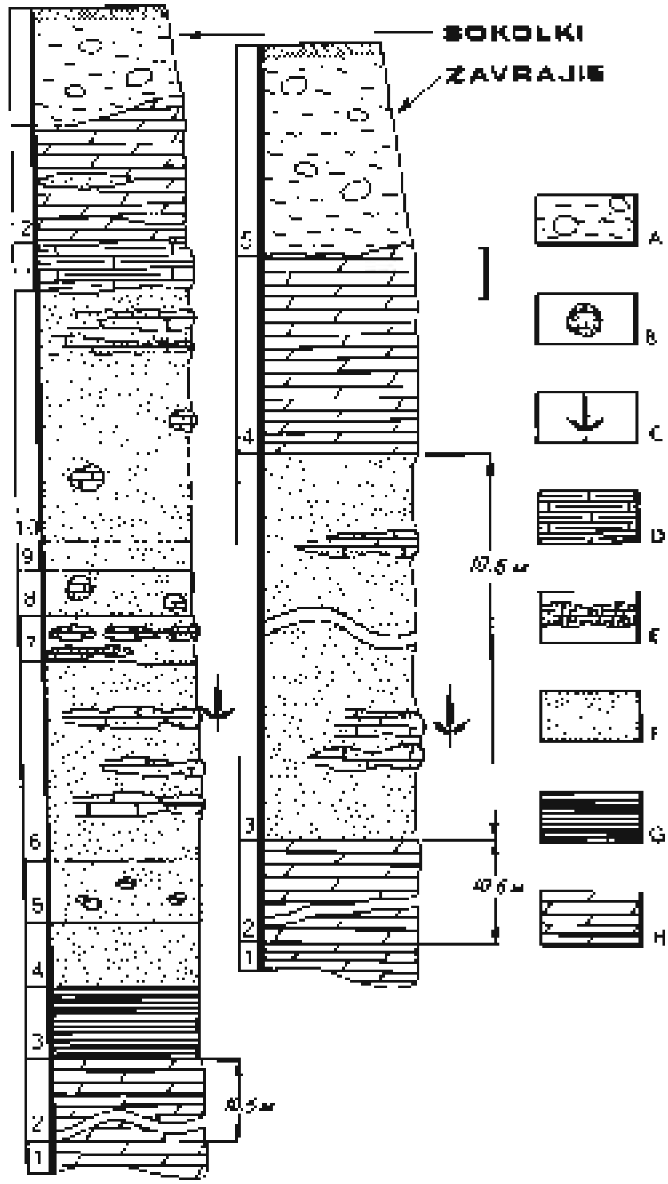

Fig. 2 — Stratigraphical sequences of the localities studied: I - Sokolki, II - Zavraje. Legend: A - quaternary glacial sands and clays, B - spheroid sandstone concretions, C - plant remains, D - marl or argillite with the big amount of carbonate material, E - flattened sandstone concretions, F - sand lenses, G - argillite, H - marl. Scale - 1 m.

PLATE I →

Peltaspermopsis polyspermis Naug., sp. nov.

Seed-bearing discs (1-3, 7-9) and sterile leaves (4-6)

1, 2 — Cross section through the disc stalk with different focus. Specimen no. 4851/3a.

3, 8 — Racemose polyspermic upper disc shows well preserved seed scars. Specimen no. 4851/3.

7 — Seed-bearing disc with numerous (24) radial sectors. Specimen no. 4851/2.

9 — Margin of the disc with the preserved seed scars. Specimen no. 4851/2.

4-6 — Simple lanceolate leaves of *Pursongia* type, associated with the seed-bearing discs. Specimen no. 4851/10 (4, 5) and 4851/12 (6). Zavraje locality. Magnification × 5 (1-3, 7-9), × 3 (4-6).

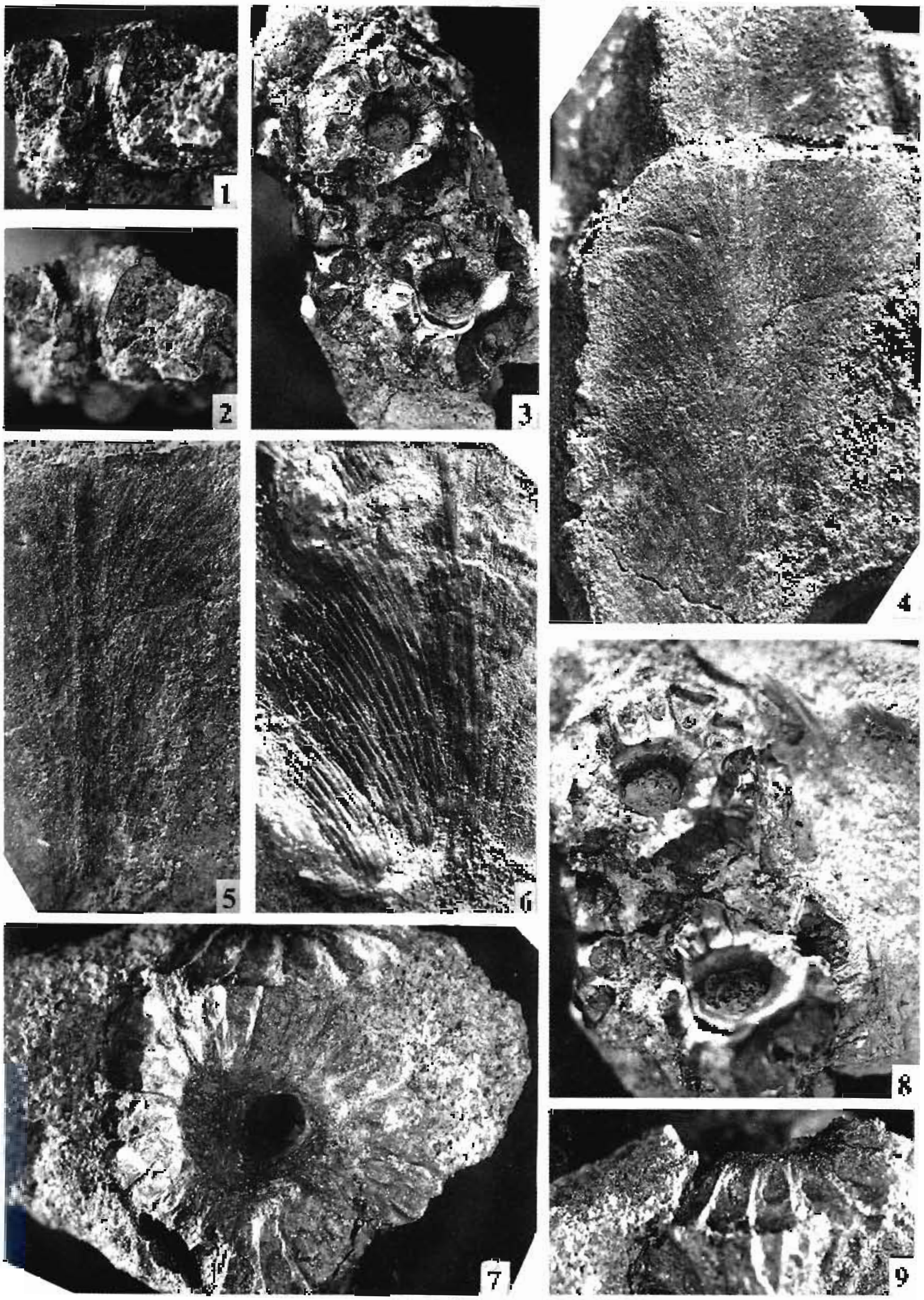

PLATE I

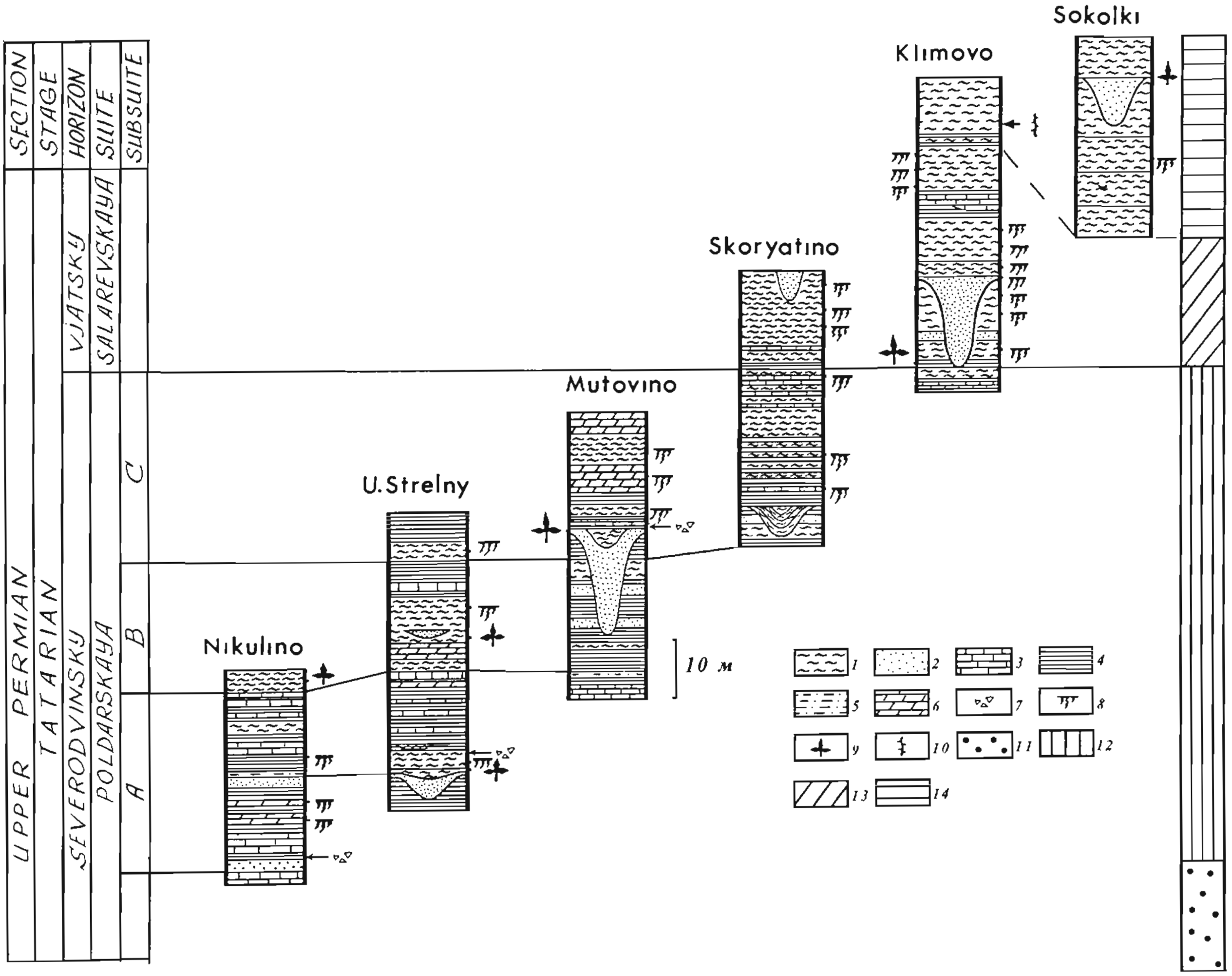

Fig. 3—Correlation between localities studied and the other Tatarian outcrops of the Sukhona-Northern Dvina Basin. Legend: 1 - Clayly aleurolites, 2 - Sands and sandstones, 3 - Mudstone, 4 - Sandy clays, 5 - Sandstones with small influx of aleurolites and argillites, 6 - Marls, 7 - Breccia, 8-9 - Root remains of several types, 10 – Plant megafossils (leaves, stems, fructifications), 11 - Basin deposits of Sukhonskaya Suite, 12 - Subaquious and subaerial deposits of shallow waters and coast lowlands of Poldarskaya Suite, 13 - Paleosol horizons in the lower part of Salarevskaya Suite, 14 - Desert lake sediments with postdiagenetic carbonate encrustations, upper part of Salarevskaya Suite (after Arefiev & Naugolnykh, 1998).

(Gomankov & Meyen, 1986; Arefiev & Naugolnykh, 1998). The localities are disposed on the right bank of the Small Northern Dvina, 10 km upstream of Kotlas City (Fig. 1). Both localities have historical names "Sokolki" and "Zavrajie" (Amalitzky, 1897, 1901, 1922-1924).

These localities are sand and sandstone lenses, which are disposed in marl and clay sediments (Figs 2, 3). The plant remains were found in middle parts of the lenses and, as a rule, occurred in concretions or slightly less consolidated sandstones (Fig. 2).

The specimens were studied under Binocular Microscope MBS-9 and Scanning Electron Microscope Stereoscan 600. Figures were made from photographs (Figs. 7, 11 A-F) and under a binocular microscope with the use of an ocular with grid (Figs 4A-C, E, G-H, J, 5, 7).

The collection is stored in the Geological Institute of the Russian Academy of Sciences (GIN RAS, collection 4851).

SYSTEMATIC DESCRIPTION

Genus—PELTASPERMOPSIS Gomankov, 1986, emend. Poort et Kerp, 1990

1986 Gomankov & Meyen, 1986, p. 56-57.

1990 Poort & Kerp, 1990, p. 20.

Type Species—Peltaspermum buevichiae Gom. & Meyen, 1979; Upper Tatarian, Upper Permian of the Russian platform.

Generic Diagnosis—(after Poort & Kerp, 1990, slightly modified): Genus is used as natural. It includes both vegetative and reproductive organ characteristics. Seed bearing or-

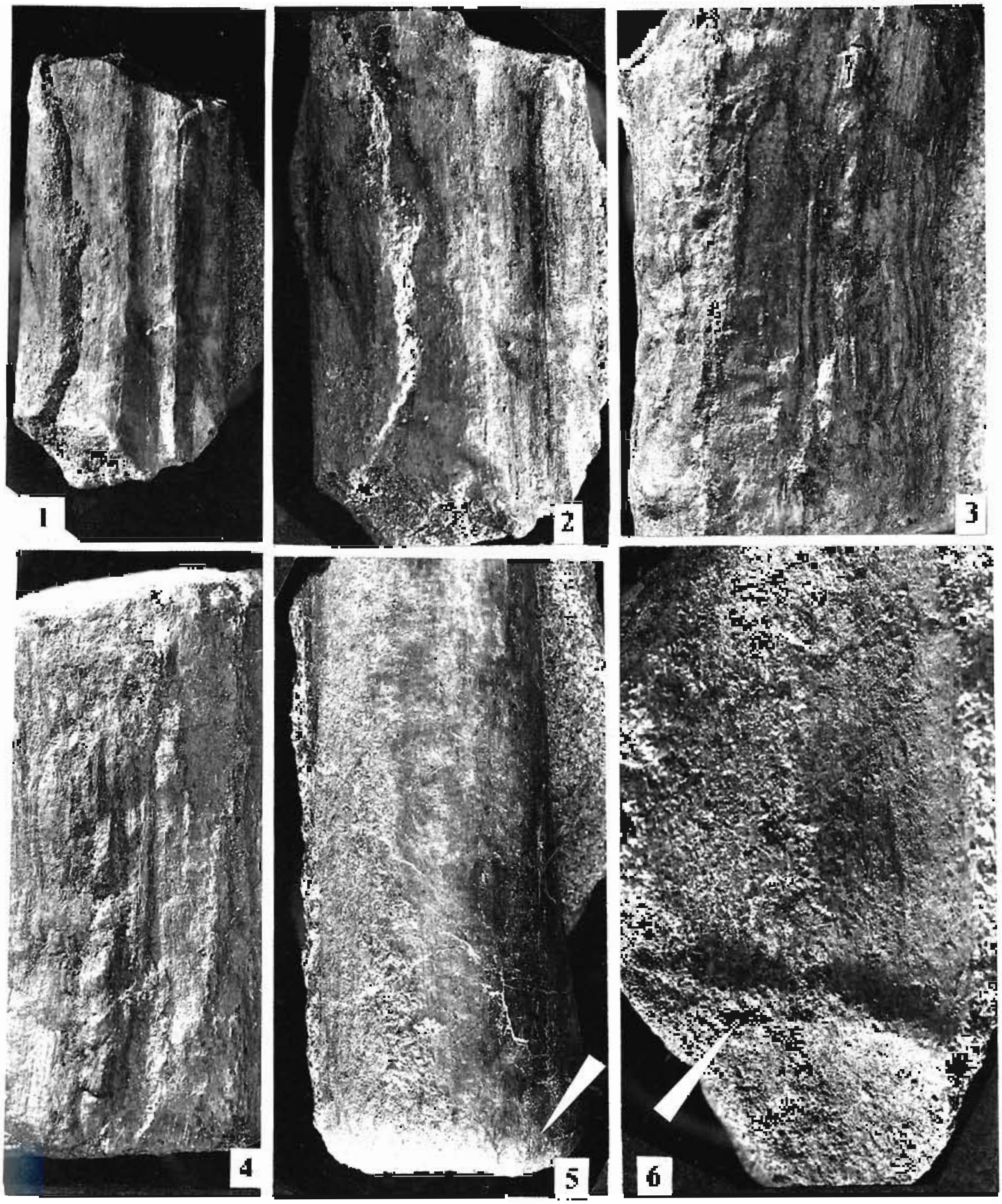

PLATE 2

Permocaulis polyspermis Naug., sp. nov.

Stem fragments. The seasonal growth interruptions are pointed out by the arrows. Specimen Nos. 4851/1 (1, 5), 4851/3 (3, 4), 4851/4 (2), 4851/5 (6). Zav'yalovo locality. Magnifications: ×2 (4), ×3 (1, 2, 6), ×3.5 (5).

gans are compound polysperms with closely disposed elliptical or radially symmetrical umbrella-shaped seed-bearing discs (peltoids). Radially orientated ribs and furrows present on the disc surface. Distal ends of the ribs form marginal lobes. Seeds are attached to lower surface of the discs around central stalk.

Male fructifications consist of several prolonged elliptical sporangia, which were basally fused and form synangia. They produced *Vesicaspora* pollen and pollen of some closely

1	2	3	4	5	6
Triassic	*Peltaspermum parvulum* (Sixtel) Naug., comb. nov.	4-10	10-24	R	*Lepidopteris*
	Peltaspermum petchoricum Chramova	6-7	14-15	?	*Scytophyllum, Lepidopteris*
Upper Permian Zechstein and Tatarian	*Peltaspermum martinsii* (Germar) Poort & Kerp	8-20	11-14	H, R	*Lepidopteris* (al. *Callipteris*) *martinsii*
	Peltaspermopsis buevichiae Gomankov emend. Poort & Kerp	8-12	8-14	H	*Tatarina conspicua*
	Peltaspermopsis polyspermis Naugolnykh, sp. nov.	5-10	24	R	*Pursongia*
Upper Permian Ka-zanian and Ufimian	*Peltaspermum nanshanense* Durante	6-14	16-18	H, R	*Rhachiphyllum* (al *Callipteris*), *Compsopteris* versus *Pursongia*
	Peltaspermum (?) sp. A (Meyen, 1982)	10-14	15-18	R	*Rhachiphyllum* (al. *Callipteris*) *adzvense* *Compsopteris*
	Peltaspermum Sp. (sp. nov.?) Unpublished data, from the Kazanian (?) of Russian Far-East	10-15	15-20	R	*Rhachiphyllum* (al. *Callipteris*) ex gr. *adzvense*
	Peltaspermum (?) sp. „C“, ex Pukhonto & Fefilova, 1983	5-6	8	R	?
Lower Permian	*Peltaspermum retensorium* (Zalessky) Naug. & Kerp	6-25	8-25	H	*Rhachiphyllum* (al. *Callipteris*) *retensorium*

Fig. 4—Selected representatives of *Peltaspermum* and *Peltaspermopsis*: main characters: 1. Age, 2. Female fructifications, 3. Disc diameter (mm), 4. Number of radial sectors, 5. Type of polysperm (R-racemose, H – head-like), 6. Associated leaves.

related striated types (*Protohaploxypinus* etc).

Leaves are simple, disposed on shortened brachyblast-like and unmodified stems in spiral order. Leaf outlines are linear or lanceolate with rounded apex and narrow base. Venation is fan-shaped, with central vein cluster (false midvein). Veins are simple or twice dichotomizing. Venation, as a rule, is not clearly seen.

Distribution—Upper Permian of the Russian platform and Cis-Urals.

Species Composition—*P. buevichiae* (Gom. & Meyen) Gom. emend. Poort & Kerp, *P. polyspermis* Naug., sp. nov.

REMARKS ON GENUS COMPOSITION AND ITS COMPARISON WITH RELATED GENERA

When the genus *Peltaspermopsis* was initially established (Gomankov & Meyen, 1986) the following characteristic patterns were pointed out: (1) compact head-like disposition of peltoids around central axis; (2) relatively small seed scars; (3) relatively large distance between seed scars (distance is over the diameter of the scar). However, as it was justly noted by Poort & Kerp (1990), the type of peltoid position on the fertile axis for the type-species of *Peltaspermum* Harris (*P. rotula*) is still unknown. *P. rotula* polysperms can be

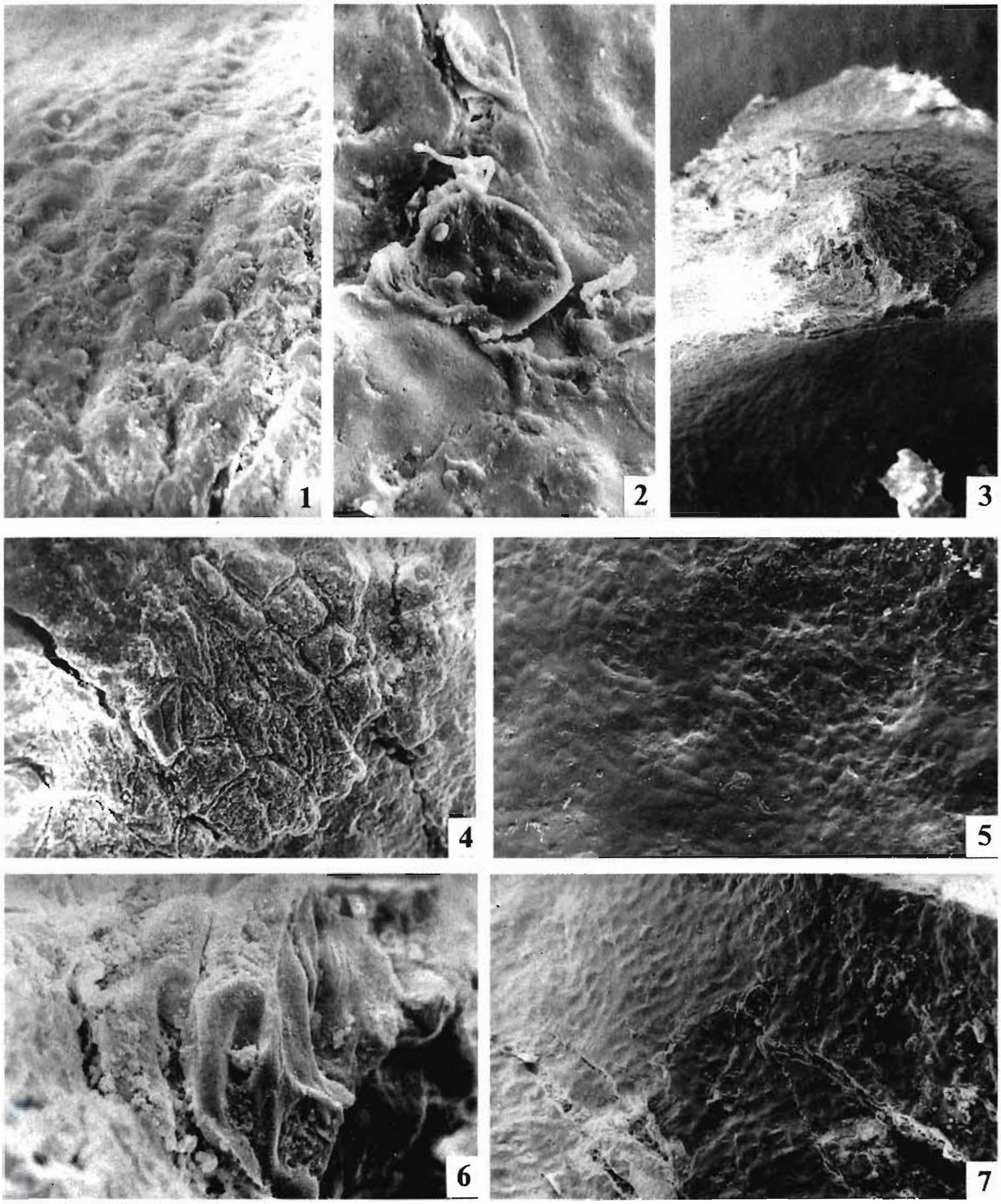

PLATE 3

Peltaspermopsis polyspermis Naug. sp. nov.
Microstructure of seed-bearing disc adaxial surface.

1, 5, 7 Polygonal almost isometrical cells of epidermis;
2, 3 Seed scar microstructure;
4, 6. Microstructure of seed-bearing disc base. Specimen No. 4851/3a. Zavrajie locality. Magnification: x 25 (2); x 50 (3), x 100 (5, 7), x 250 (1, 4), x 500 (2), x 1000 (6).

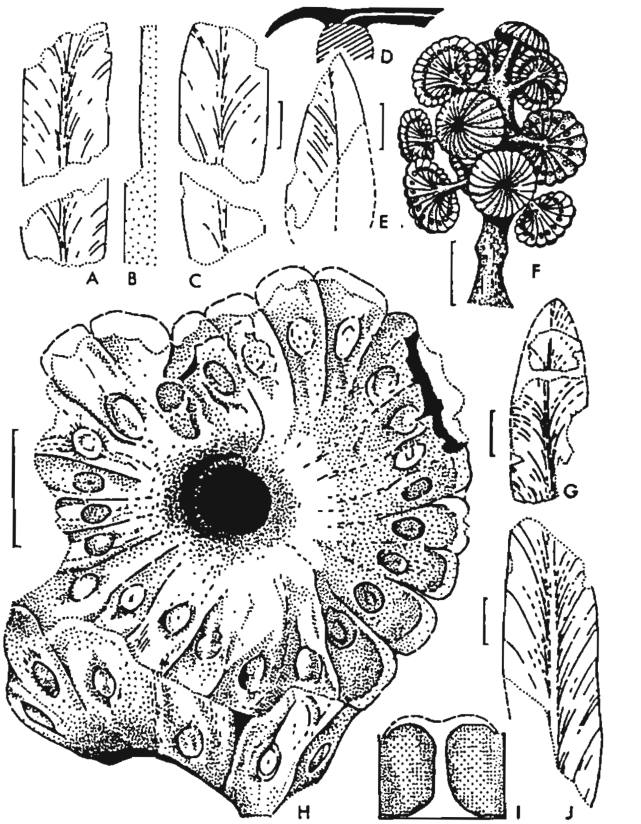

Fig. 5—*Peltaspermopsis polyspermis* Naug. Leaves and ovuliferous disc macromorphology. A-C, E, G, J - Isolated leaves, H – Seedbearing discs, D - Sketch of seed attachment, F - Polysperm reconstruction, I - Mode of preservation, matrix is dotted. Zavrajie locality. Scale bar - 1 mm (H), 1 cm (A-C, E-G, J). D, I - Without scale. Specimens: A - 4851/11a; B, C - 4851/11; E - 4851/18; F – Based on specimen 4851/3; G - 4851/10; H - 4851/2; J - 4851/14.

both compact head-like aggregates and more lax, loose racemose ones. Both types of compound polysperms may sometimes be observed for one and the same species of peltasperm (for example, *P. martinsii*). As for other characteristics, which were used by Gomankov, it should be noted that they are very variable and in various combinations may be observed in many peltasperm species (Fig. 4). For instance, the syndrome of seed-bearing disc characteristics, which were used by Gomankov as generic for *Peltaspermopsis,* is present in *Peltaspermum incisum* Prynada (Stanislavsky, 1976). Seed-bearing discs of *P. incisum* have very small, almost crack-like seed scars with long distances between them (Stanislavsky, 1976, Pl. XXII, 5; Fig. 18). Nonetheless, this plant must be assigned to genus *Peltaspermum* (Poort & Kerp, 1990).

It is clear that *Peltaspermopsis* Gom., as it was introduced by the author of the genus, cannot be sustained on the basis of the characters that are cited in Gomankov and Meyen

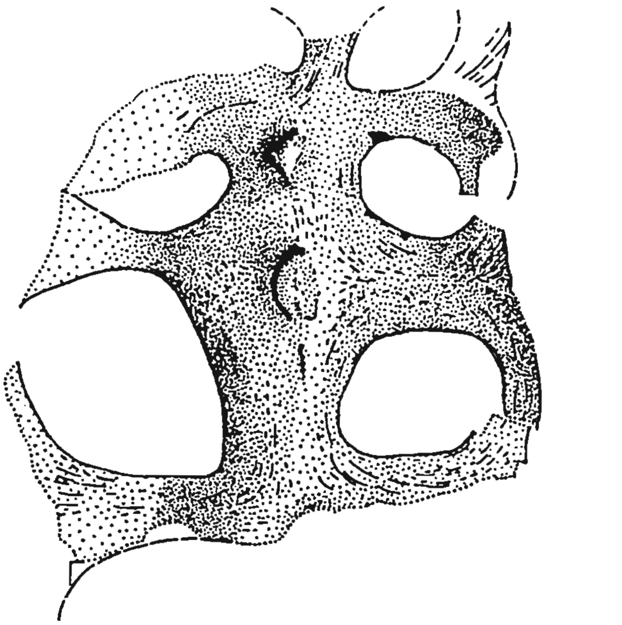

Fig. 6—*Peltaspermopsis polyspermis* Naug. Polysperm axis with attached disc stalks. Zavrajie locality. Scale bar - 1 cm. Specimen 4851/9.

(1986). However, since the relationship between peltoids *Peltaspermopsis buevichiae* and simple lanceolate leaves of *Tatarina*- or *Pursongia*-type is almost well proved, this specific combination of ovuliferous structure and sterile leaves allow us to emend the diagnosis of the genus and fit it in the natural system of vascular plants generally based on reconstructed, well-documented taxa. This procedure with *Peltaspermopsis* was done by Poort and Kerp (1990), who proposed a new fuller diagnosis of *Peltaspermopsis.*

Durante (1992) did not agree with the validity of *Peltaspermopsis* sensu Gomankov either, and used it as subgenus of *Peltaspermum* Harris. As a possibility of moving *Peltaspermopsis* and *Peltaspermum* to the natural system of peltasperm genera, she set out a synthesis of all data about fructifications and associated leaves.

Schweitzer and Kirchner (1998) described a new species *Peltaspermum decipiens* and followed in general the traditional using of nomenclature and taxonomy of *Peltaspermum*-type fructifications and sterile leaves of *Lepidopteris* and *Scytophyllum* type. They criticized Poort & Kerp proposal to unite the genera, and argumented that the genera should be used independently because of uncertain correlation between *Scytophyllum*, *Lepidopteris* and *Peltaspermum*. According to my opinion, we can use both approaches: reconstructed genera *sensu* Poort & Kerp (1990) for general applications like paleophytogeography, paleoecology, and traditional formal genera for field geology and stratigraphy.

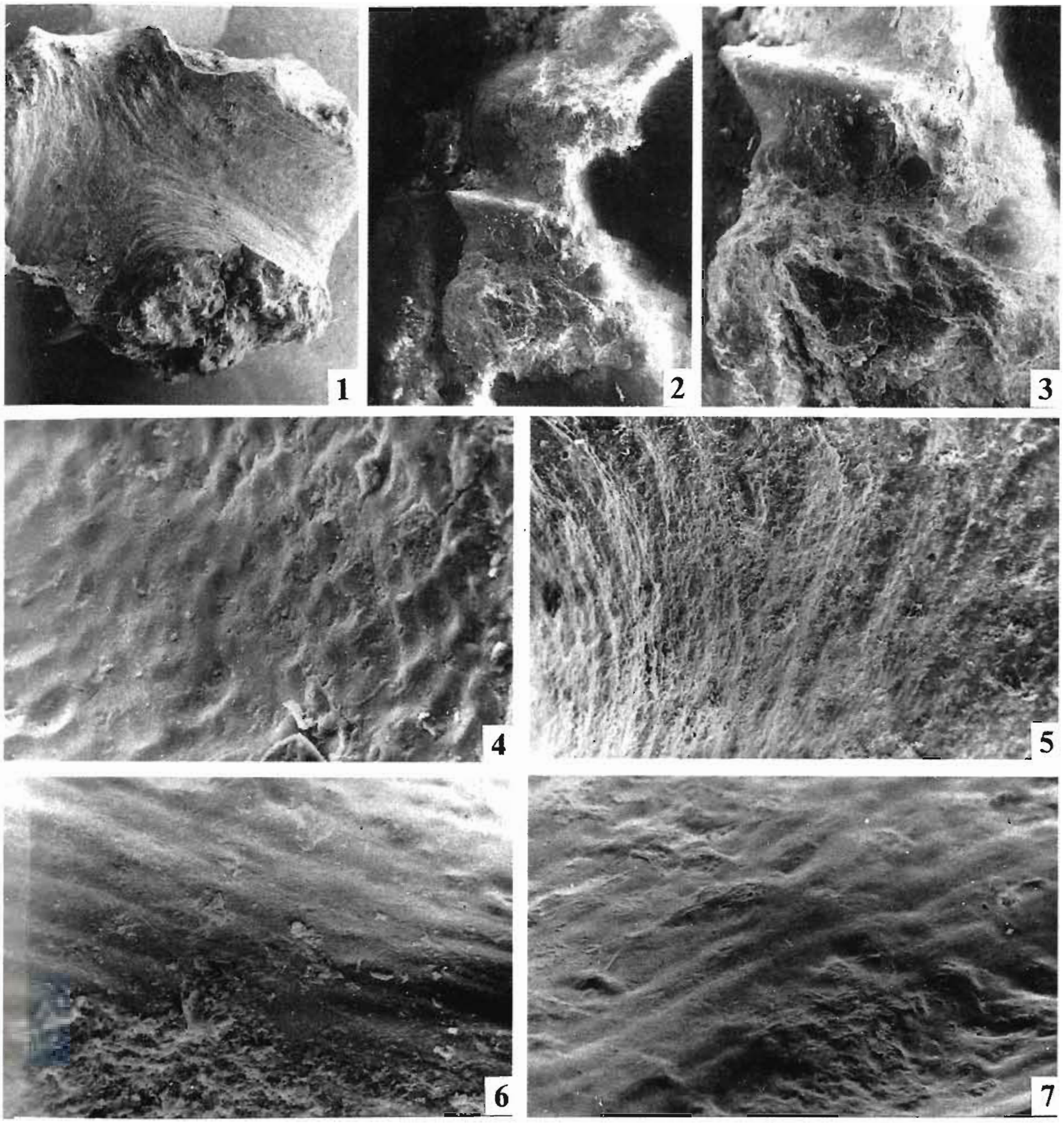

PLATE 4

Peltaspermopsis polyspermis Naug. sp. nov.

Seed-bearing disc and polysperm axes microstructure.

1. Impression of polysperm axis with two seed-bearing disc stalks;
2, 3. Marginal part of seed-bearing disc with two seed scars;
4. Microstructure of seed-bearing disc, adaxial surface;
5-7 Polysperm axis microstructure. Specimen No. 4851/9a (1), 4851/9b (2, 3), 4851/3a (4-7). Zavrajie locality. Magnification: x 10 (1), x 25 (2), x 50 (3, 5), x 250 (4, 6, 7).

Species—**PELTASPERMOPSIS POLYSPERMIS,** sp. nov.
Pl. 1-4.4-8

Diagnosis—Female fructifications are loose racemose aggregates (polysperms) of seed bearing discs (peltoids). Stalks of the peltoids attached to fertile axis in spiral order. The seedbearing disc bears in its central part a depression, which corresponds to position of the stalk attached to the adaxial surface of the disc. The seed bearing discs divided by radial furrows into 20-24 sectors. The seed scars with round outlines, slightly prolonged along radial sectors. The little scarlet of conducting tissues is in the center of seed scar. The margin of seedbearing disc is lobed. The lobes are commonly curved downward (in adaxial direction) and are orientated almost parallel to peltoid stalk.

Sterile leaves are tongue-like or lanceolate, relatively small, with false midvein. The side (secondary) veins curved towards leaf apex.

Description—The studied remains of seed-bearing discs are impressions, which formed as a result of tissue destruction. The sediment matrix conserved "casts" or the outer surface of the fructifications (Fig. 5, 1). Obviously, sediment deposition was very fast and plant remains were deposited before the beginning of the rotting process. A solid iron crust was formed by biogeochemical transformation which was linked with rotting of plant tissues. This crust made possible the conservation of the impressions.

The selected samples include four racemose aggregates (compound polysperms) of seedbearing discs which are preserved to different extents, as well as fifteen fragments and almost complete sterile leaves. The length of polysperm fertile axes is 10-30 mm, but this size is probably only ½ the length of the complete racemose aggregate.

The peltoid stalks are attached to the polysperm axes in loose spiral order (Fig. 6). The basal part of peltoid stalk slightly widens and forms a cone-shaped structure.

Despite the relatively poor preservation of the material (impressions almost without compression) the epidermal characteristics of seedbearing discs were studied by SEM.

The outer microrelief of the epidermis preserved is as negative. The general topography of the cuticle is clearly seen, because cell walls were strongly uplifted under the epidermal surface. Only the microstructure of adaxial surface of the discs with seed scars and the structure of the peltoid stalk were studied.

The main part of adaxial epidermis consists of the isometrical, subrounded cells, sometimes with distinct polygonal outlines (Pl. 3.1, 5, 7; Pl. 4.4). Cell size as a rule is 15 x 20 μm. Slightly bigger cells almost 30 μm in their length occur more rarely. No stomata were found on adaxial surface of the discs. The cells disposed in furrows between disc sectors are more prolonged (Pl. 4.6, 7).

The furrows on the specimens are preserved as ribs (Pl. 4.2, 3). The common size of furrow cells is 15 x 40 μm, sometimes 50 μm in length. The long axes of these cells are orientated along furrows (ribs).

The seed scars are presevved on the impressions as conical- or cupola-shaped protrusions. They consist of loose parenchymatous tissues with unclear cell outlines. The cell walls are slightly curved (Pl. 3.2, 3). The cell size is approximately 10 x 15 μm, i.e., slightly smaller than cells of other parts of adaxial surface of the disc. The seed scar is separated from the sector surface by a distinct line, which apparently corresponds to margins of the scar. The scar often has a narrow

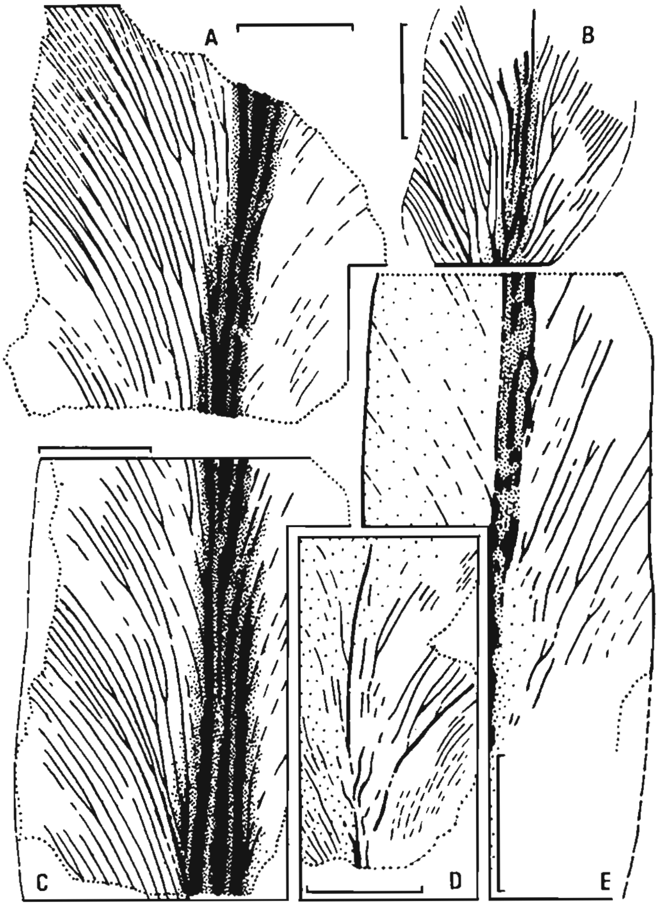

Fig. 7—*Peltaspermopsis polyspermis* Naug. Leaf venation. Zavrajie locality. Scale bar - 1 cm. Specimens: A - 4851/16; B - 4851/15; C - 4851/17; D - 4851/13; E - 4851/14.

marginal limb. Its width is 1/10 of the scar radius. A small protrusion commonly occurs in the central part of the scar, which presumably is the conducting tissue scar.

Not far from the base of the seedbearing disc or at the distal part of peltoid stalk an uncommon microrelief may be seen. This relief is formed by the net of polygonal furrows (Pl. 3.4). The size of the net modules is 20 x 30 μm. These are also probably remains of epidermal cells, but with thicker walls.

Several fragments of stems were found together with the fructifications and sterile leaves of *P. polyspermis*. These stems undoubtedly belong to the same plant, because there are no any other plant remains besides of the stems, peltoids and *Pursongia*-like leaves in the locality. This correlation is also supported by very similar association of *Peltaspermopsis buevichiae* ovuliferous organs and *Tatarina conspicua* leaves, attached to the stems almost identical to the stems found in association with *P. polyspermis* (Gomankov & Meyen, 1986, fig. 28). These stems (Pl. 2.7) are more or less regular cylindrical axes, sometimes slightly narrowing upwards to the supposed stem top. The width of the axes is 11-20 mm. The length

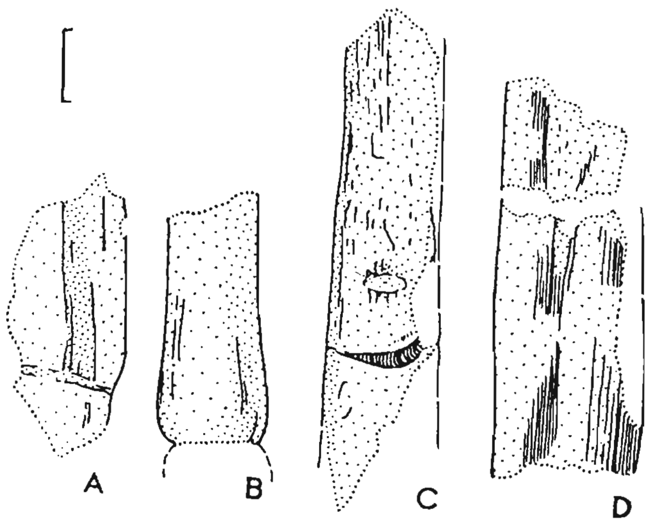

Fig. 8—*Peltaspermopsis polyspermis* Naug. Stems. Zavrajie locality. Scale bar - 1 cm. Specimens: A - 4851/8; B - 4851/4; C - 4851/6; 4851/5.

considerably is more than 10 cm. In cross section the axes are round or ovoid. The ovoid cross-section is secondary and formed by diagenetic compressing of sediment together with the stem.

The stem surface bears elongated folds. Sometimes some rougher and stronger ribs may be observed (Pl. 2.1, 5). In some cases the stem surface may be almost smooth (Pl. 2.2, 6). In addition, there are fine prolonged ribs on the stem surface. These ribs were probably linked with trunk peridermal structure (Pl. 2.3, 4). The rare scars of fallen leaves are sometimes observed. They are elliptical or rhombus-like, elongated across the stem (Fig. 8 C).

One of the important characteristics of these stems is the presence of the nodes (Fig. 8 A-C; Pl. 2.5, 6, marked by arrows), which probably correspond to seasonal interruption of the plant growth.

General morphology of the stems is very similar to young stems of *Ginkgo biloba*, which bear normal leaves arranged in spiral order on the stem when it actively grows, or form a cluster, when the growing is almost stopped during second half of vegetative season (Fig. 9). During winter cold season or extremely hot summer season the leaves were fallen.

The leaves which are associated with generative organs of *P. polyspermis* can be assigned to *Pursongia* Zal. according to formal systematics (see below).

They are relatively small, approximately 5 cm in length. In very rare cases their length is 10 cm. The average width of the leaves is 2 cm. The leaves are entire-margined with parallel margins (Fig. 5 A-C, J), or rarely with gradually narrowing margins from the leaf base to the apex (Fig. 5 E, G). The apex is subtriangular, slightly acute or rounded. The leaf base is also rounded. The venation is fan-shaped or almost pinnate (Fig. 7 A, C, E; Pl. 1.4-6). In the middle part of the leaves the medial cluster of veins is observed. This cluster is formed by several parallel veins, which run together almost up to the leaf apex where they diverge. The cluster itself does not reach the apical 1-1.5 cm. The side (secondary) veins come from the middle cluster at a very acute angle. They commonly dichotomize, first near medial cluster and then closer to leaf margin, forming two or three orders of the side veins. The veins are curved towards the leaf apex. Simple undichotomizing veins also occur. The venation of young scale-like leaves is more complex; the veins may dichotomize four times (Fig. 7, B, D). In some cases such short leaves may have undeveloped basal lobes. Such a lobe has one main vein, which bears dichotomizing side veins.

Etymology —Polyspermis (lat.) – many seeds.

Holotype—GIN RAS, 4851/2.

Occurrence—Salarevskaya Suite, Severodvinsky Horizon, Upper Tatarian, Upper Permian; Russian platform, "Zavrajie" locality.

Discussion—The new species differs from *P. buevichiae* by a big number of the radial sectors, as well as by orientation of the seed scars (the seed scars of *P. polyspermis* are pro-

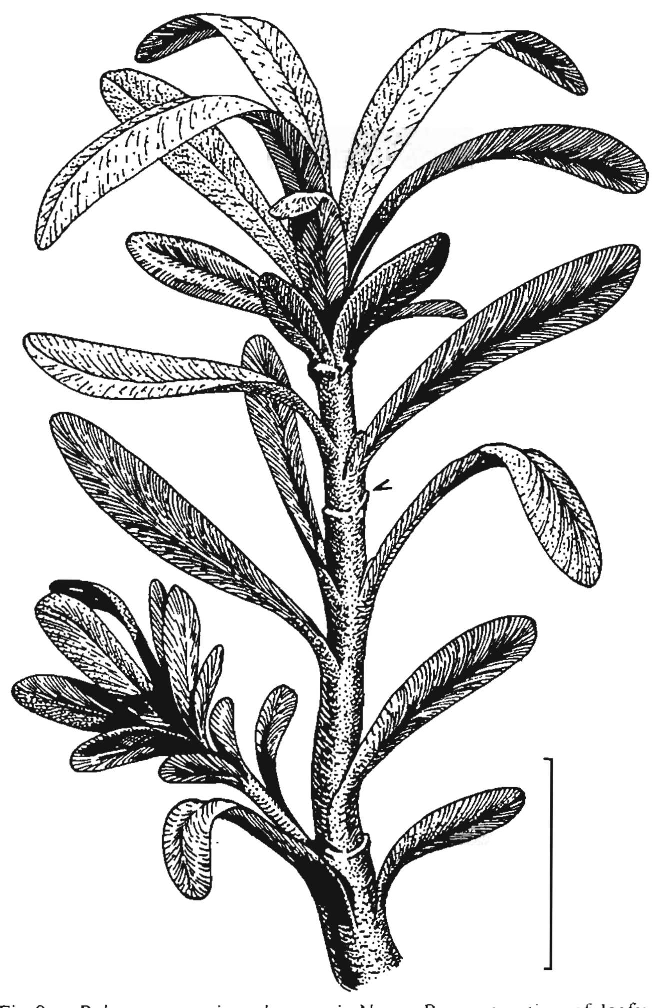

Fig.9— *Peltaspermopsis polyspermis* Naug. Reconstruction of leafy shoot. The season growth interruptions are pointed by arrows. Late Tatarian, West Subangaraland. Scale bar - 10 cm.

longed along sectors) and by the racemose character of the compound polysperms. *P. polyspermis* differs from the *Peltaspermum nanshanense* Durante and *P. multicostatum* Zhang (which were assigned by Durante to *Peltaspermopsis* subgenus) by the smaller size of seedbearing discs in that species and by the racemose character of the polysperms, and also from the *P. nanshanense* by larger number of the radial sectors. The new species is similar to the Lower Permian (Kungurian) *Peltaspermum retensorium* (Naugolnykh & Kerp, 1996) in having a large number of radial sectors. The main difference between these two species is the character of the sterile leaves (leaves of *Peltaspermopsis polyspermis* are simple lanceolate, whereas leaves of *Peltaspermum retensorium* are "fern-like" bi- and tripinnate fronds) and the size of the seed-bearing discs (those of *P. retensorium* are bigger).

An important character of *Peltaspermopsis polyspermis* is seed scar orientation. The scars are prolonged along the radial sectors of the peltoids. By the seed scars position this species clearly differ from the other closely related Upper Permian peltasperms (*P. buevichiae* and *Peltaspermum martinsii*). The seed scars of the last two species are orientated by their long axes across the sectors.

Peltaspermopsis polyspermis is similar to peltoid aggregations from the Kazanian of Pechora Cis-Urals, which were described by Pukhonto & Fefilova (1983) in open nomenclature as *Peltaspermum* sp. "*a*", *P.* sp. "*b*" and *P.* sp. "*c*", by the racemose type of compound polysperms. Sterile leaves associated with *P.* sp. "*a-c*" are still unknown. *Peltaspermopsis polyspermis* differs from the *Peltaspermum* sp."*a*" by the smaller diameter of the discs in beeing three to four times smaller); from *P.* sp. "*b*" and *P.* sp. "*c*" by a considerably larger number of radial sectors; and from the *P.* sp. "c" by the orientation of seed scars, too.

There is quite a big similarity between *Peltaspermopsis* and the compound polysperms associated with *Lepidopteris parvula* Sixtel leaves (Sixtel, 1962) from the Madygenian Suite of Kirgizstan, aged as Middle-Upper Triassic (Dobruskina, 1982). Since the relationship and correlation between these fructifications and leaves *Lepidopteris* may be regarded as proved (Sixtel, 1962), I propose a new combination for the whole plant, *Peltaspermum parvulum* (Sixtel) Naugolnykh, comb. nov. Basionym: *Lepidopteris parvula* Sixtel: Sixtel, 1962, p. 316-319, fig. 9-11, pl. IX, 4-10. Holotype: figured by Sixtel, 1962, pl. IX, 4; spec. 524.

The main difference between *P. parvulum* (Sixtel) Naug. and *Peltaspermopsis polyspermis* is the character of the sterile leaves. The first species has pinnately dissected compound leaves and the latter, simple lanceolate leaves.

The distribution of the taxonomic characteristics among well studied and wide known Permian species of *Peltaspermum* and *Peltaspermopsis,* and also some Triassic peltasperms is shown on Fig. 4.

Genus—PURSONGIA Zalessky, 1933
Species—PURSONGIA AMALITZKII Zalessky 1933
emend. Naugolnykh, emend. nov.
Figs 10; 11 C, D; 12 G (left hand only)

Holotype—figured by Zalessky, 1937, and reproduced here as Fig. 11, C; Upper Tatarian; Russian platform, N. Dvina River, Sokolki locality.

Diagnosis—The sterile leaves with lanceolate outlines, sometimes shortened, scale-like, ovoid or subtriangular. The proportion between width and length is approximately 1/5-1/6. The leaf margin are entire, gradually gathering towards the leaf apex and base. In the middle part of developed leaf the margins are parallel to each other. The false midvein (vein cluster) consists of several strands of vascular tissue. The side (secondary) veins come from the middle cluster. The side veins are simple or rarely 2-3 times dichotomizing. The side veins are arch-like curved and strongly decurrent along the false midvein.

Description—The general leaf morphology of this species is defined by position of maximal leaf width. As a rule, the maximal width is located at lower part of the leaf lamina, or even near the leaf base (Figs 10 C, left; D, F; 10 A, F, 11). Sometimes uncommon aberrant specimens also occur. Their maximal width is in the middle or upper part of the leaf (Fig. 10 G, H). It is interesting to note that the opinion about superficial similarity between macromorphology of *P. amalitzkii* and some Gondwana glossopterids (*Glossopteris crenulata* Brongn., *G. indica* Schimper) appeared after studying such aberrant specimens.

There is no leaf in my collection which bears a completely preserved base. The most complete fragments (Fig. 9 A, G, H) give us sufficient grounds to assume that the leaf base was wedge-like.

The false midvein of our specimens corresponds to shallow furrows (if the leaf is orientated to observer by its adaxial surface) or ribs (if the abaxial surface). The width of false midvein varies from 2-25 mm near leaf base to 05-1 mm near apex. The side veins are very thin and fine, feebly impressed in matrix. They are seen only in indirect light.

In the protologue of *P. amalitzkii,* the author of the species Zalessky noted the presence of anastomoses between the side veins. Such anastomoses (very rare and unclear ones) were shown on Zalessky's figures (see Fig. 11 C, D here). However, our specimens from the type locality "Sokolki" of *P. amalitzki* (i.e., topotypes) do not bear any anastomoses-like structures.

Comparison – P. amalitzkii differs from the other related species of *Pursongia – P. beloussovae* (Radcz.) Gom. & Meyen, *P. elegans* Durante – by considerably bigger leaves. *P. amalitzkii* differs from *P. serrata* (Srebrod.) Meyen by the entire leaf margin.

Remarks – Leaves which probably belonged to

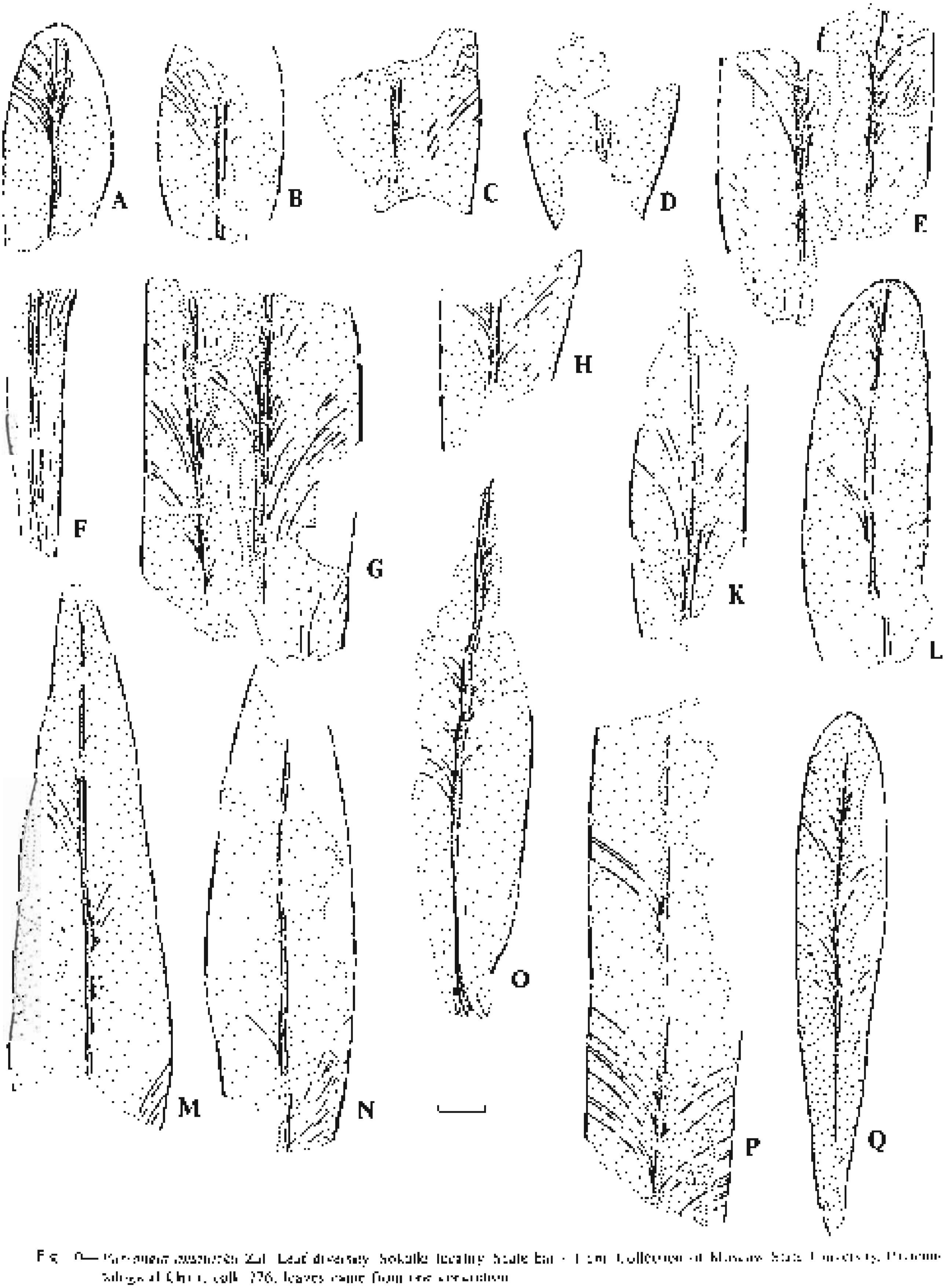

Fig. [illegible].— [illegible] [illegible]. Leaf diversity. Sokolki locality. Scale bar = 1 cm. Collection of Moscow State University, [illegible] [illegible] coll. 276, leaves came from one excavation.

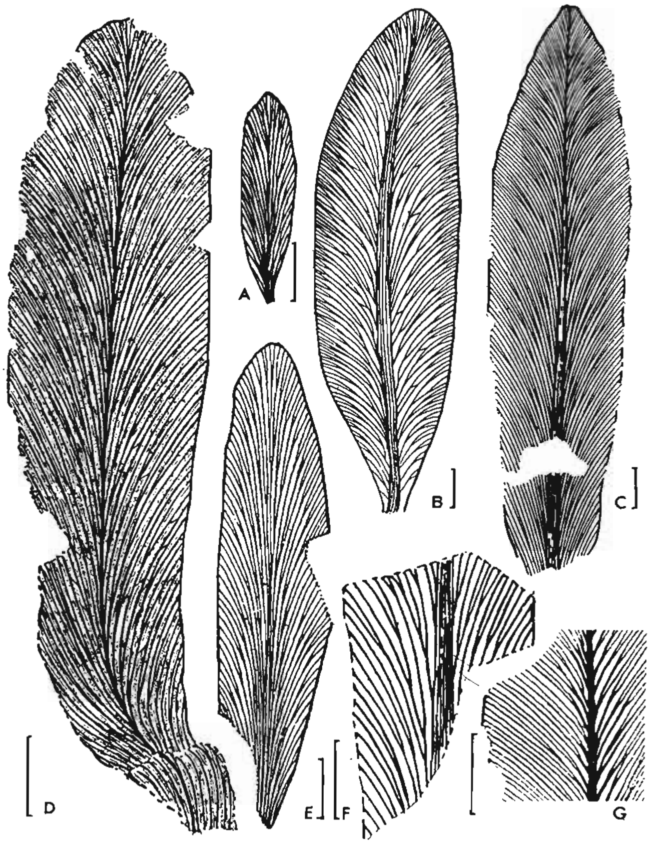

Fig. 11— *Pursongia* and leaves of some related taxa from the Upper Permian of Eurasia, after Zalessky, 1934, 1937 A, E - *Petcheria elongata* Zal., B - *Pursongia asiatica* Zal., C, D - *P. amalitzkii* Zal., F - *Pereborites rarinervis* Zal., G - *Compsopteris tchirkovae* Zal. (this figure is given for comparison, since separated pinnules of this pteridosperm and some related genera similar to *Pursongia*, but differ by the presence of true midvein). Localities: Kuzbass, Ishanovo village (B), Pechora coal basin: Pechora River (A, E), Perebor River (F), Big Synia River (G), Russian platform, Northern Dvina River, Sokolki locality (C), South Cis-Urals, Sakmara River, Kolgumkino village (D). Upper Permian. Scale bar - 1 cm.

Pursongia were described for the first time by Fischer von Waldheim (1840) from the Upper Permian (Tatarian?) of the Orenburg region (Southern Urals). They were assigned by him to some species of *Glossopteris: G. phillipsii* Brongn., *G. crenulata* Brongn. A few years later the last species was noted by Mercklin (1852) from the Upper Permian deposits, presumably of the northern part of Russia.

After half a century the first representative collection of Upper Permian plant remains was obtained by Amalitzky from the Upper Tatarian of Severnaya Dvina Basin. Initially Amalitzky determined a number of typically Gondwanan elements in his possession obviously under the influence of Fischer von Waldheim and Mercklin's papers: *Glossopteris angustifolia* Feistmantel, *G. indica* Schimper, *G. stricta* Bunb., *Gangamopteris cyclopteroides* Feistmantel, *G. major* Feistmantel (Amalitzky, 1901).

The presence of typical Gondwana glossopterid taxa in Amalitzky's localities was in good agreement with the Upper Permian tetrapod fauna of N. Dvina, which was related to the famous South Africa Karroo fauna. Nevertheless, Zalessky restudied Amalitzky's collection a few years later and described similar leaves from the Upper Permian (Upper Kazanian and Tatarian) deposits of Tatarstan under new generic and species names *Pursongia amalitzkii* Zal. (Zalessky, 1929, 1933).

According to Zalessky, the new genus *Pursongia* differs from *Glossopteris* by the presence of hypodermal tissue strands between the side veins. Zalessky thougth that *Pursongia* had anastomoses and net-venation. The genus *Pursongia* with type-species *P. amalitzkii* and some closely related species, *P. angustifolia* Zal. and *P. asiatica*, were assigned by Zalessky to the order Glossopteridales.

Neuburg (1948) noted during redescription of *P. asiatica* Zal. from the Permian deposits of Kuzbass that she could not find anastomoses and hypodermal tissues between side veins. Despite her scepticism about the genus validity, in subsequent works (Neuburg, 1954; Bobrov & Neuburg, 1957) she used this genus widely and even described several new species: *Pursongia tunguscana* Neub., *P. mongolica* Neub. and proposed new combination *P. uralica* (Zal.) Neub. The last species was initially established by Zalessky on a single specimen of leaf fragment from the Kungurian of the Middle Fore-

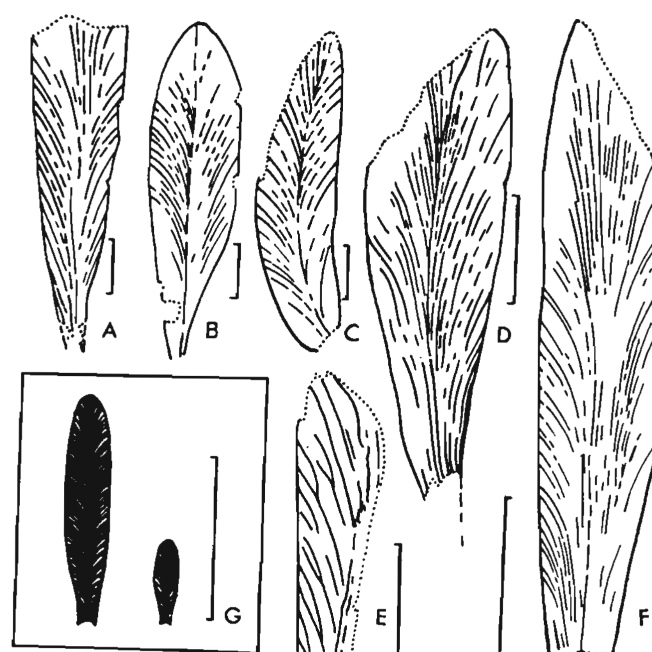

Fig. 12—*Pursongia* and some similar leaves from the Upper Permian of Pechora basin. A-D - *Pursongia* sp., E - *Rossovites* cf. *petschorensis* Zal., F - *Zamiopteris* sp. Pechora Cis-Urals, Yangarey River (A), Paemboy Coal Mines, Talbeyskaya Suite (B-F). G - relationship between middle size leaves of *Pursongia amalitzkii* Zal. (left) and *Pursongia* sp. ex Pukhonto et Fefilova (right). A-F - after Pukhonto, Fefilova, 1983. Scale bar - 1 cm (A-F) and 10 cm (G).

Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Taeniopteris Brongniart, 1828	–	+	–	–	–	–	+	?	+	–	–	–	+		–	+	?	–
Kindbiggea Tate, 1867	–	–	–	–	+	?	+	–	–	–	+	+	–	–	–	–	–	–
Zamiopteris Schmalhausen, 1879	–			+	–	–	+	–	–		+	+	–	–	–	–	+	+
Palaeovittaria Feistmantel, 1876	–	–	+		–		+	?	–		–	–	+	–	–	–	+	–
Euryphyllum Feistmantel, 1879	–	–	–	–	?	+	+	–	–	–	–	+	–	–	+	–	–	–
Lesleya Lesquereux, 1880	+	–	?	–	–		+	–	–	–	–	+	–	–	–	–	+	–
Mesoneckia Johnstone, 1896	+		–	+	?	–	+	–	+	–	–	+	–	–	–	–	–	–
Protoglossopteris Barre, 1903	–		+	–	–	–	–	?			+	–	+	+	–	–	–	–
Glossophyllum Zalessky, 1912	+	–	–	+	+	–	–	+	+	–	–	+		–	–	–	–	–
Lingulifolium Arber, 1913	+	+	–	–	–		+	–	–	–	+	–	–	–	+	–	?	–
Scutaspidium Zalessky, 1925	+	–	–	+	+	–	–	–	–	+	–	–	–	–	–		+	–
Tychtopteris Zalessky, 1930			–	+	+	–	–	–	+	–	–	–	–	+	–	–	+	
Pursongia Zalessky, 1933	+		–	+	+	–	+	–	+		–	+	–	–	–	–	+	
Petcheria Zalessky, 1932	+	–	–	+	+	–	–	–	–	–	–	+	–	–	+	–	–	–
Lanceophyllum Zalessky, 1934	+	+	–	–	–	–	–	–	–	–	+	+	–	–	–	–	+	–
Vittia Frenguelli, 1941	+	+	–				+	–	–	–	+	+	–	–	–	–	+	–
Phyllopteroides Medwell, 1954	–	+	–	–	–		+	–	–	–	+	+	–	–		–	+	–
Evenkiella Radczenko, 1960	–	–	–	+	–	+	+		?	–	?	–	–	–	+			

Fig. 3. The main characters of *Pursongia* and some related leaf genera. 1 – Leaf is simple, entire margined or slightly lobed. 2 – True midvein runs from leaf base to apex. 3 – True midvein is evident only in leaf base. 4 – True midvein is absent. 5 – Vein cluster (false midvein) is present. 6 – Fan shaped venation. 7 – Wedge-like base. 8 – Stalk is present. 9 – Apex is rounded. 10 – Apex is emarginate. 11 – Apex is acute. 12 – Side (or margin) veins are several times (up to 4) dichotomizing. 13 – Side (or margin) veins are simple as a rule. 14 – Developed side lobes are present. 15 – Side veins run at very acute angle to leaf axis (20-30°). 16 – Side veins run at almost 90°. 17 – The angle of side veins is diverse (30-80°). 18 – Epidermal pattern is known for some species. The genera *Pursongiopsis* Sadovnikov, *Gracilophyllum* Kryshtofovich & Prynada, *Mauria* Dobruskina, *Glossophyllum* Kräusel, *Rhabdotaenia* Pant are absent in this table because diagnoses of these genera based on epidermal-cuticular characters.

Urals and first assigned to *Glossopteris*.

Rasskasova (1960) analyzed the composition of *Pursongia*, which contains six species: *P. amalitzkii* Zal., *P. angustifolia* Zal., *P. asiatica* Zal., *P. tungusorum* Neub., *P. mongolica* Neub., *P. uralica* (Zal.) Neub. All of these species originated from the uppermost Lower Permian and Upper Permian of Russian platform and Siberia. She concluded that the genus was heterogeneous and included species with quite different macromorphology. Rasskasova established new monotypical genus *Crapoecia* Rassk. from the Upper Permian (Peljatkinskaya Suite) of Tunguska Basin. The single specimen (holotype) of *C. magnifolia* was an impression of the middle part of simple lanceolate leaf with pinnate venation. The rare anastomoses were observed. The peculiarity of the described leaf does not raise doubts about the validity of the genus *Crapoecia*. However, substantiation of the genus established in the protologue was insufficient because the diagnostic features by which *Crapoecia* differs from *Glossopteris* were not mentioned. In my opinion, the presence of well-developed real midvein and very dense generally pinnate venation may be regarded as such characteristics.

Besides, Rasskasova described new specimens of *Pursongia tungusorum* Neub. in the same paper. These specimens originated from the Upper Permian of Siberia (Ilinskaya Suite of Kuzbass and Peljatkinskaya Suite of Tunguska Basin). The anastomozing of the side veins is very well shown on Rasskasova's photographs and figures. These leaves fully comply with the diagnosis of *Glossopteris*.

After studying Kuzbass species of *Pursongia*, Betekhtina (1965) referred them to three main types of their venation: (1) false glossopteroid venation – *P. uralica* (Zal.) Neub., (2) semi-looped venation – *P. tungusorum* Neub., (3) net-looped venation – *P. mongolica* Neub. According to Betekhtina, the anastomoses are characteristic for all three types of venation. The presence of true anastomoses for Kuzbass leaves assigned by Betekhtina to earlier established species *P. mongolica*, *P. tungusorum* and *P. uralica* f. nana Betekhtina was convincingly documented with the help of good photographs (Betekhtina, 1965, Pl. 2). The leaves of *Pursongia* species without anastomoses in Betekhtina's paper were not discussed.

The presence of real net-venated leaves in Angaran Permian floras was proved by Zimina (1967), who described new species *Glossopteris orientalis* Zim., *Gangamopteris ussuriensis* Zim. and *G. pacifica* Zim. from the Upper Permian of Russian Far-East (Primorie). The floristic assemblage is characterized by generally Angaran taxonomic components. As a possible migration way of glossopterids Zimina pointed Mongolia where glossopterids from the Upper Permian deposits are also known. The new combinations *Glossopteris tungusorum* (Neub.) Zim. and *G. mongolica* (Neub.) Zim. were proposed in the same paper.

The revision of *Pursongia* and plants, which were un-partly assigned to this genus, was impossible for a long time because there were no data about type-species *P. amalitzkii*. The material that I have in my possession let to suggest the main principles of such a revision. The species *P. amalitzkii* (including possible younger synonym *P. angustifolia* Zal.), *P. asiatica* Zal., *P. beloussovae* (Radcz.) Gom. & Meyen, *P. elegans* Durante and related species without anastomoses between side veins should be assigned to the genus *Pursongia*. The species *Glossopteris* [illegible], *G.* [illegible], *G.* [illegible] (two last species were formerly described as *Pursongia*) may be assigned to genus *Glossopteris* according to its formal diagnosis, despite the fact that these Angaran leaves may not necessarily belong to the order Glossopteridales (Dictyopteridiales sensu McLoughlin, 1990, 1995).

A number of genera related to *Pursongia* Zal. by their morphology are known from the Upper Palaeozoic of Angaraland. They are *Listrophyllum* Zal., *Glottophyllum* Zal., *Zamiopteris* Schmalh., *Petcheria* Zal., *Kraeselia* Radcz., *Scapanophyllum* Zal., *Tychtopteris* Zal. They differ from *Pursongia* by the presence of the following characteristics: (1) well developed midvein (*Listrophyllum*), (2) developed stalk (*Listrophyllum*, *Glottophyllum*, *Tychtopteris*, partly some species of *Petcheria*), (3) bifurcated apex (*Scapanophyllum*), (4) developed side lobes (*Tychtopteris*).

It is more difficult to formalize the boundary between *Pursongia* and *Zamiopteris*. There are certain distinctions between the epidermal structure of *Tatarina* Meyen (nomenclatoral variant of *Pursongia* for the species with known epidermal-cuticular structure) and some species of *Zamiopteris* (*Z. neuburgiana* Meyen, *Zamiopteris* sp. ex Meyen, 1969) with known microstructural characteristics. This difference does not allow to suggest that *Zamiopteris* and *Pursongia* are synonyms. However, macromorphologically these genera are very similar. The formal distinctions between *Pursongia* and *Zamiopteris* are stronger venation of representatives of the last genus and, as a rule, their acute apices (the apex of *Pursongia* leaves is commonly round).

A younger synonym of *Pursongia* is *Kirsella* Radcz. as is already noted (Gomankov & Meyen, 1986).

Another undoubted synonym of *Pursongia* is *Pechorites* Zal., which was later redescribed by Pukhonto (in Pukhonto & Fefilova, 1983). Unfortunately, in the description of this genus, Pukhonto did not point out the species composition, though she referred to another species apart from the type-species of *Pechorites*. The comparison with other genera is also absent. In the same work, Pukhonto wrote about the presence of the midvein of *Pechorites*. Judging from the figured holotype (seen here as Fig. 11.1) as well as from Pukhonto's specimens, this latter opinion is obviously mistaken. The incorrect nomenclatorial actions for the choice of lectotype and the reference to neotype (different specimens are taken as neotype) devalue Pukhonto's attempt to modify the diagnosis of *Pechorites* genus and to make it valid.

Kraeselia differs from *Pursongia* by the absence of a midcluster of veins (false midvein) and possibly belongs to *Cordaites*-like plants.

Fig. 15 shows the distribution of characteristics between *Pursongia* and other genera, which are used for simple lanceolate leaves *Lesleya* Lesquereux, *Linguifolium* Arber emend Retallack, *Palaeovittaria* Feistmantel and others.

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Some interesting plant fossils from the Mesozoic of the Rajmahal Hills, India

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ABSTRACT

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Description is given of some interesting plant fossils preserved as petrifactions in the Rajmahal Hills, Jharkhand. These are either new and reported for the first time or an additional information is given on already known earlier description. The fossil taxa belong to algae, lichen, gymnosperms and angiosperms.

Key-words—Petrifactions, Cryptogams, Lichen, Angiosperms.

भारत की मीसोज़ोइक युगीन राजमहल पर्वतश्रेणियों से प्राप्त कुछ दिलचस्प पादपाश्म

बी.डी. शर्मा, डी.आर. बोहरा एवं ओ.पी. सूथर

सारांश

झारखण्ड की राजमहल पर्वतश्रेणियों के अश्मीभवन के रूप में सुसंरक्षित कुछ दिलचस्प पादपाश्मों का वर्णन प्रस्तुत शोध पत्र में अभिप्रेत है। ये या तो नवीनतम हैं, अथवा प्रथम बार प्राप्त किए गए हैं अथवा इनके माध्यम से पूर्व में वर्णित किए गए पहले से ज्ञात पादपाश्मों के विषय में कुछ अतिरिक्त सूचनाएँ प्रदत्त की जा रही हैं। अश्मित वर्गक शैवाल, लाइकेन, अनावृतबीजियों तथा आवृतबीजियों से सम्बन्धित हैं।

संकेत शब्द—अश्मीभवन, बीजलेख, लाइकेन, आवृतबीजी.

INTRODUCTION

PLANT fossils from the Rajmahal Hills have been known for over a century (Oldham & Morris, 1863). Since then a large number of papers have been published by many workers (Feistmantel, 1877; Sahni & Rao, 1933; Ganju, 1946; Sahni, 1948; Gupta, 1954; Mittre, 1957; Bose & Sah, 1968; Sharma, 1974, 1979, 2000; Banerji, 2000). The bulk of the flora includes fossils of ferns, cycads, Bennettitales, Pentoxylales and conifers. Reports are also available on the occurrence of fossil lycopods, Equisetales, pteridosperms, Ginkgoales and angiosperms (Surange, 1966; Sharma, 1971, 1975, 1997; Banerji, 1990, 1993, 2000a). The plant fossils in the northern portion of the Rajmahal Hills are found mostly as impressions whereas, those in the southern part are petrifactions (Gupta, 1966). Incrustations are rare. In the present paper a few petrifactions collected from Sonajori, Nipania and Amarjola are described. These plant fossils are referable to algae, lichens, pentoxylales, conifers and angiosperms.

MATERIAL AND METHODS

Sonajori is a fossiliferous locality situated 4 km from Pakur (Sharma & Bohra, 1976, 1977) on Pakur-Dumka Road. Intertrappean strata are well distinguished from the thick trap depositions. The chert is silicified. It contains fossils of ferns, Pentoxylales, conifers and angiosperms (Bohra & Sharma, 1979; Banerji, 2000a).

Nipania is a well known locality (Srivastava, 1945; Sahni, 1948; Mittre, 1957; Sharma, 1975a) situated 5 km North west of Amrapara. Fossils are preserved in a hard silicified chert. It shows fossils of ferns, Pentoxyleae, conifers and angiosperms. Amarjola is also a well known locality (Sharma, 1972, 1975a). Here the plant fossils are soft and fragile and are taken out by digging the sandy rock. Ferns, Bennettitales, Pentoxylales, conifers and angiosperms are found at Amarjola (Sharma, 1997, 2000). Isolated petrified short shoots of *Pentoxylon* were collected from this locality. Sections through silicified cherts were cut with the help of a diamond edge wheel, while the soft material from Amarjola was boiled in canada balsam prior to sectioning with the help of a wire band-saw. Slides were prepared by the usual techniques involving grinding and polishing and mounted in canada balsam.

DESCRIPTION

Algae

Dark coloured filaments are seen generally scattered in thin sections prepared through Nipania chert. The filaments are of different sizes and thickness. Each filament has multiseriate siphon-like structure (Pl. 1.1). The siphons are of variable lengths. The superficial ones end into a curved or straight spine-like structures which are actually reduced branches as they have distinct transverse septations. Sharma and Harsh (1994) correlated these filaments with the red alga *Polysiphonia*. It has been observed that the thin sections which have polysiphonous filaments also have numerous globular spores with more or less smooth exine (Pl. 1.2). They resemble typical non-flagellate spores of Rhodophyceae (Bold & Wynne, 1985). However, exact morphology of the associated fertile organs is yet to be described.

Lichens

In a thin section prepared through a piece of Nipania chert is seen an elliptical cross section (Pl. 1.3). It measures 4 x 1.5 mm and has a number of dark coloured bodies of various sizes. The bodies are either solitary or in groups of 2-4. Each has a central cavity of 2-4 cavities surrounded by a thick wall (Pl. 1.4) of variable thickness. The dark coloured bodies are embedded in a ground tissue made up of thin walled narrow filaments which give parenchyma like appearance.

It is believed that the black bodies are phycobionts or algal partner of the lichen, which the ground tissue is mycobiont made up of septate mycelium. In some of the lichens there are special modes of asexual reproduction through soridia and isidia (Bold *et al.*, 1987). These are small propogules in which algal cells are surrounded by the fungal filaments (Bold *et al.*, 1987, fig. 10.5 B, C) as in *Parmelia andecans*. The present material is probably a cross section through an isidium of some lichen. Further investigations are required on this material.

Gymnosperms

Pentoxyleae short shoots—In *Pentoxylon* the leaves were described to be restricted to the short shoots (Sahni, 1948). The short shoots in general bear closely arranged, small, spiral, rhomboid leaf bases (Sharma, 1975a, 1979a). This observation was based on study of material from Nipania (Srivastava, 1945; Sahni, 1948; Mittre, 1953, 1957). The authors however were able to collect more than two dozen petrified shoots from Amarjola locality, some of which are figured here (Pl. 1.6). The shoots are of different length and thickness and bear leaf bases of various types i.e., close and rhomboid, close and crescent shaped or sparse and half lunar. They are related to different organs of the pentoxylean plants and performed different function i.e., vegetative shoots, fertile shoots (male & female), etc.

Conifers

Amarjolian young roots—Sharma and Bohra (1975, 1980) described an araucarian root *Araucarioxylon pakurensis* from Sonajori. It has a diarch primary xylem and well developed radial secondary growth. Sharma and Suthar (1980) also

PLATE 1 →

1. Polysiphonous filaments of a red alga with lateral spiny outgrowths. × 38
2. Scattered spores in association with polysiphonous filaments. × 114
3. Elliptical cross section of an isidium of a lichen. × 24
4. Same in portion enlarged showing dark coloured phycobionts embedded in hyaline mycobiont. × 77
5. Cross section of an [illegible] root. Note that epiblema [illegible] cells with [illegible] cells and [illegible] xylem with two exarch [illegible] protoxylem points. × 120
6. Petrified short shoots of Pentoxyleae bearing various types of leaf bases. × 1½
7. Cross section of [illegible] leaf [illegible] smaller and bigger size bundles [illegible] upper side [illegible]. × 48

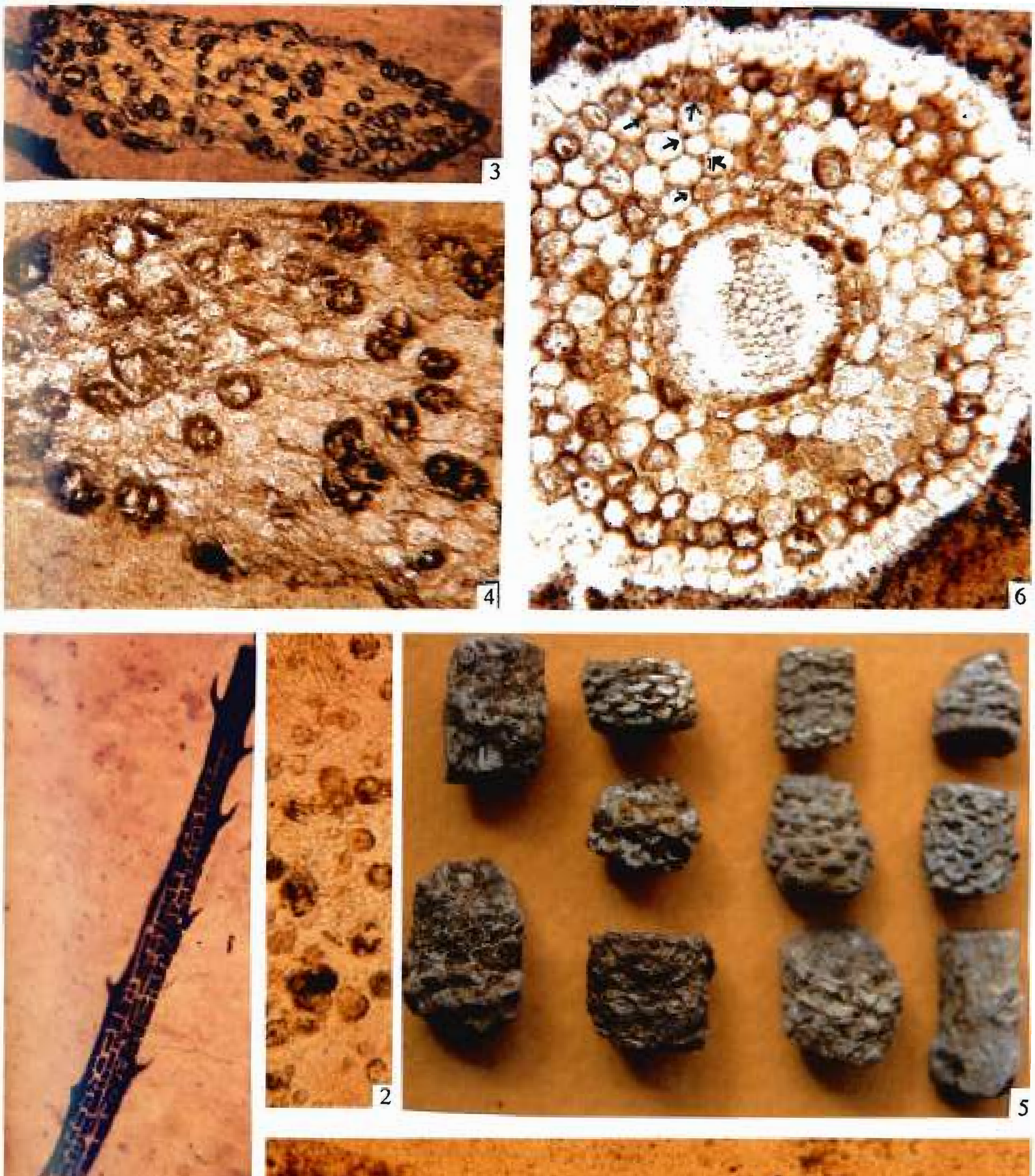

PLATE 1

described an algal association with the young roots of *Araucarioxylon*. In some of the chert pieces from Sonajori araucarian roots are abundant. The present one (Pl. 1.6) is a cross section of a young root of *Araucarioxylon*. There is an epiblema layer, 1-2 cells thick of thin walled cells without cuticle. The cortex is 5-6 cells wide with a few dark staining tannin cells. Poorly preserved inter and intracellular mycorrhizae (arrows) is also visible in the cortex. Endodermis is distinct but made up of narrow cells. It encloses a diarch barrel shaped xylem (Pl. 1.6) with two distinct exarch protoxylem points. Xylem is made up of narrow, closely placed thick-walled tracheids (in T.S.). The xylem is 5-6 cells thick in the middle and reduces towards protoxylem points. Phloem is radial and made up of poorly preserved thin walled cells.

From Sonajori chert a number of diarch filicean roots have also been described e.g., *Gleichenoxarradix diarcha* Bohra and Sharma (1979), *Filicoxarradix conjugatoradix* Bohra and Sharma (1979), *F. acrostichoides* Bohra and Sharma (1979). But these are much different from the present araucarian root in the morphology of the cortex, structure of endodermis and the xylem. Banerji (2000) describes more or less a similar cross section from Sonajori chert and identifies it as a fossil lycopod stem *Lycoxylon sonajoriense* Banerji. She correlates it with *L. indicum* Srivastava (1945) known from the Nipania chert. The latter has a distinct plectostele. A single elliptical xylem plate does not form a plectostele. There should be more than one plate of xylem in order to make a plectostele. The present material is not a stem because leaf bases are absent, the superficial layer of cortex is without cuticle and protoxylem points are exarch, wide and distinct. Presence of mycorrhizae further support under ground portion (may be a root) of the present material. It is a young rootlet of an araucarian root in which neither secondary growth has taken place nor algal association is yet established.

Angiosperm

Monocot leaf—The present material is a cross section of a leaf present in a thin section prepared through a Nipania chert (Pl. 1.7). The two surfaces abaxial and adaxial are quite different from each other. One (abaxial) is straight and is made up of small, narrow rectangular cells while the other (adaxial) is uneven with blunt ridges and furrows resembling those of *Cortaderia selloana* and *Psammochloa villosa* (Metcalfe, 1960). The epidermis of this surface is quite distinct and special, consists of large bulliform-like cells in ridges or raised portions while smaller cells present in the furrows. (The bulliform-like cells were visible in an unmounted slide when examined only in a water film. However, the bulliform cells became invisible on mounting with canada balsam. This feature is common in sections of fossils prepared through Sonajori and Nipania silicified cherts). Probably, the present cross section is of a lamina which had alternating thin and thick veins as is present in many grasses and palms (Metcalfe, 1960, Tomlinson, 1961). The adaxial surfaces of thick veins are covered by bulliform like cells while narrow veins have smaller epidermal cells.

The mesophyll is undifferentiated into palisade and spongy tissues. It is 2-4 cells thick of small more or less isodiametric cells. The leaf has alternate arrangement in a line of smaller and bigger cavities (probably bundles) in correlation with thin and thick veins respectively (Fig. 1). However, the details of 'bundles' are not preserved and only cavities represent them. In gross morphology the cross section looks of some grass. Further investigations are required on this material.

DISCUSSION

The present investigation supports the earlier findings of polysiphoneous filaments and their association with non-flagellate spore. The spores occur not only in large numbers in the chert but are also variable in sizes representing different stages of development. However, cystocarp and other fertile structures are yet to be seen in the Nipania chert. Whether *Polysiphonia*-like plants survived in fresh water lakes of the Rajmahal Hills during the Upper Jurassic or the area had an intrusion of marine water and the red alga came with that from the nearby sea. Venkatachala and Tiwari (1987) have shown marine intrusion and pathway during early Permian through the Rajmahal Hills.

There are not many records of fossil lichens in the world (Taylor & Taylor 1993). If the Fig. 3 identified above as a lichen is correct then this is the first record of a fossil lichen from India and may be from the Mesozoic rocks in the world. In addition to a cross section of an isidium included in the present paper a loose bunch of hyphae and algal cells resembling homoiomerous thallus of a foliage lichen has also been seen in a section through the Nipania chert, description of which will be published elsewhere. Phycobiont is very distinct from the mycobiont. Algal cells are scattered throughout the isidium and no differentiation of a separate cortical portion is visible. This is little different from the isidium of an extant lichens.

Sharma (1973, 1975a, 1974a, 1975a, 1979b, 1996), Suthar & Sharma (1988) and Suthar *et al.* (1988) described the existence of more than one type of short shoots in *Pentoxylon*. A study of external morphology i.e., shape, size and arrangement of leaf bases/bract bases on the surfaces of short shoots collected from Amarjola favour the above statement. It is however, difficult at present to correlate them with their functions like photosynthesis, reproduction, etc. At the same time while suggesting their relationships we must keep in mind that in addition to *Pentoxylon* allied stems like *Guptioxylon* Sharma (1969) and *Purioxylon* Sharma (1971) are also found at Amarjola.

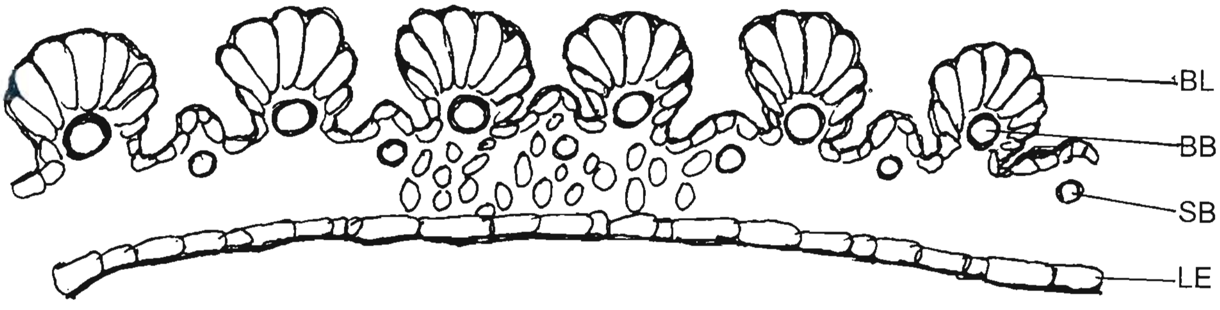

Fig. 1—Cross section of a monocot leaf lamina. Note bulliform-like cells on the adaxial surface with the bigger sized bundles in ridges while furrows have smaller sized epidermal cells. x 60. (BL - Bulliform cells, BB - Bigger bundle, SB - Smaller bundle, LE - Lower epidermis).

The araucarian roots occur frequently in Sonajori chert. These are diarch with many cells containing dark contents in cortex. Secondary growth (Sharma & Bohra, 1975, 1980) is normal except in roots which have algal association (Sharma & Suthar, 1989), a condition identical to the coralloid roots of *Cycas* (Pant, 1973). Some of the young rootlets neither have the secondary growth nor an association of an alga. On the other hand they may show mycorrhizae in their cortical portion, as is seen in the present material. Banerji (2000) identifies a cross section resembling the present figure 6 as *Lycoxylon sonajoriensis* Banerji. It is neither a stem nor similar to *Lycoxylon indicum* and a reconsideration is required.

During recent years a number of fossil angiosperms (Pollen grains and mega-fossils) have been reported from the Rajmahal Hills (Mittre, 1956; Sharma, 1997; Tripathi & Tiwari, 1991; Tiwari & Tripathi, 1995; Banerji, 2000, 2000a). All of them are dicots. But the present leaf has association with monocots. It has alternating thick and thin veins, a character found in the lamina of many grasses and palms. The presence of bulliform-like cells in the adaxial epidermis further supports the monocot angiosperm nature of the present material (Metcalfe, 1960; Tomlinson, 1961; Easu, 1965). A number of sections prepared through the Nipania chert bear cross sections of leaves resembling arecoid palms; descriptions of which will be published else where. The present investigation suggests that both dicots and monocots had already appeared during the Upper Jurassic/Lower Cretaceous in the Rajmahal Hills but with a very low frequency and restricted distribution. The fossil flora of the Rajmahal Hills is not exhausted and needs continuous investigations.

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A note on geological explorations through early expeditions to the Eastern Karakoram, the Shaksgam Valley and the Western Tibet since early half of the Nineteenth Century

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ABSTRACT

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Based on informations available, through early expeditions since the early half of the nineteenth century, on the Central Asian mountain massifs, the present document is aimed towards depicting the significance of these poorly known regions in a larger framework of palaeogeography and accretion of the Indian and Peri-Gondwanian microcontinents with the Asian landmass.

Key-words—Eastern Karakoram, Shaksgam Valley, Western Tibet, Central Asia, Karakoram Fault.

विगत नवीं शती के पूर्वार्द्ध से आज तक पूर्वी कराकोरम, शक्सगाम घाटी तथा पश्चिमी तिब्बत के प्रारंभिक खोज अभियानों में भू-गर्भीय उत्खनन

राजीव उपाध्याय एवं अंशु कुमार सिन्हा

सारांश

प्राप्त सूचनाओं के आधार पर मध्य एशियाई पर्वत श्रेणियों के गिरिपिण्डों (मैसिफ़) के विगत नवीं शती के पूर्वार्द्ध से आज तक हुए खोज अभियानों के आधार पर प्रस्तुत शोध पत्र में इन अल्प ज्ञात क्षेत्रों के पुराभौगोलिक एवं एशियाई भूखण्ड के साथ भारतीय एवं परिगोण्डवाना सूक्ष्म महाद्वीपों के अभिवर्धन को एक वृहत् परिप्रेक्ष्य में व्याख्यायित करते हुए इनके महत्त्व को प्रदर्शित किया गया है।

संकेत शब्द—पूर्वी कराकोरम, शक्सगाम घाटी, पश्चिमी तिब्बत, मध्य एशिया, कराकोरम भ्रंश.

INTRODUCTION

The Karakoram is an ~800 km long, 150 km wide remote region in Central Asia (Fig. 1) and its geology is still partially unknown (Searle, 1991; Gaetani, 1997). The limits of the Karakoram block are still only approximately defined. The western limit of Karakoram with east Hindu Kush is proposed along the Tirich Mir fault or the Chitral fault where serpentinized ultramafic rocks have been found (Gaetani *et al.*, 1996; Zanchi *et al.*, 1997). To the north, the boundary with south Pamirs is poorly defined, as access to the Wakhan part of Afghanistan is still difficult for various reasons. But a limit along the Kilik fault has been proposed (Zanchi, 1993; Gaetani, 1997), as this fault thrusts Permo-Carboniferous sediments over northern Karakoram Cretaceous sediments, and can be followed westwards to the western Karakoram (Kafarskyi & Abdullah, 1976; Buchroithner & Gamerith, 1986). According to Shvolman (1981) and Ruzhentsev and Shvolman (1981) the main Karakoram mountain lies between the Main Karakoram Thrust and the Rushan-Pshart suture zone, which divides the southeast Pamir from the central Pamir (Fig. 1). Terrains located on the eastern side of the Karakoram Fault have been included in the Karakoram by several authors (Desio, 1991, 1977; Gergan & Pant, 1983; Thakur & Mishra, 1984; Searle, 1991; Sinha *et al.*, 1999). But this interpretation is still debated, as Gaetani *et al.* (1990a, b) proposed that the sedimentary successions of the Shaksgam Valley could belong to the south Pamirs, as also supported by descriptions of the Qiangtang area by Chinese scientists. Recently, Sinha *et al.* (1999) proposed that the boundary between the eastern Karakoram and Qiangtang may lie somewhere in the Depsang Plain. However, most Indian geologists consider the area between the Karakoram Pass and the lower Shyok River as eastern Karakoram (Thakur, 1981; Gergan & Pant, 1983; Srimal, 1986; Rai, 1991; Bagati *et al.*, 1994; Sinha, 1997; Sinha *et al.*, 1999). Moreover, it is still open the definition of the eastern termination and connection of the eastern Karakoram to part of the Tibetan Plateau (personal communication with Prof. Gaetani, Italy). To the south, the boundary between the Karakoram block and Ladakh terrain is defined by a complex suture zone closed in the Upper Cretaceous (the Shyok Suture Zone) and reactivated during the Tertiary (Upadhyay *et al.*, 1999; Rolland *et al.*, 2002).

The Karakoram is composed of two east-west striking belts separated by the axial batholith of Mid-Cretaceous to Upper Tertiary age (Debon *et al.*, 1987; Upadhyay *et al.*, 1999). The northern sedimentary belt is formed by Carboniferous to Cretaceous terrigeneous sediments and limestones (Gaetani *et al.*, 1990a, b; Gaetani, 1997; Sinha *et al.*, 1999). The southern Karakoram belt is known as the Karakoram Plutonic-Metamorphic Complex (Searle, 1991; Desio *et al.*, 1985; Sinha & Upadhyay, 1997; Sinha *et al.*, 1999) and the northern sedimentary belt is known as the Karakoram Tethys (Thakur, 1981; Gergan & Pant, 1983; Sinha *et al.*, 1999).

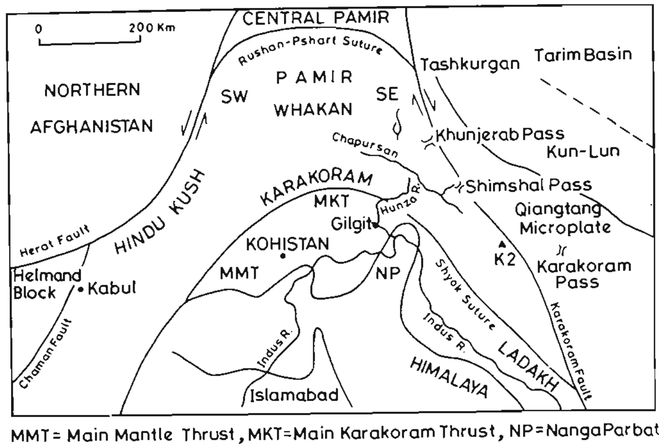

Fig. 1—General tectonic map of Pamir, Kun Lun, Karakoram, Kohistan and Ladakh showing the location of Karakoram fault and different central Asian microcontinental blocks or terranes (modified after Gaetani, 1997).

The Karakoram, located in a central tectonic position of central-eastern Asian blocks, is a key region for a better understanding of the geodynamics of Central Asian blocks during the Lower Palaeozoic (Searle, 1991; Gaetani, 1997; Rolland *et al.*, 2002). Therefore, a detailed geological exploration of the eastern Karakoram mountain system is important to understand the large scale geological processes, palaeogeographic distribution and northern extent of the Gondwana-land and accretion of Peri-Gondwanian Asian microcontinents vis-à-vis India-Asia collision. It is noteworthy to mention here that, as compared to the Himalaya, the geological aspects of the Karakoram mountains are still poorly known, therefore, in the following sections a brief recap of systematic developments of the idea on Central Asian mountain massifs and an understanding of the initial geological explorations through early geological expeditions to the eastern Karakoram, Shaksgam Valley and western Tibet since the early half of the nineteenth century have been provided to understand recent scientific activities, led by different international groups, in these remote regions.

INITIAL EXPEDITIONS

Since the early half of the nineteenth century the eastern Karakoram and adjoining mountain ranges of Central Asia (Fig. 1) have had fascinated the curious explorers and mountain climbers to unravel the occult and mysticsm of these magnificent group of mountains. Therefore, the early explorations were made to identify the Karakoram-Turkestan trade route and to collect first hand information about the large concentration of huge glaciers and mountains, several peaks raising to more than 8,000 m height (K2, 8,611 m), situated in the region.

Systematic record of exploration in the eastern Karakoram mountain could be recapitulated after 1821, when Moorcroft

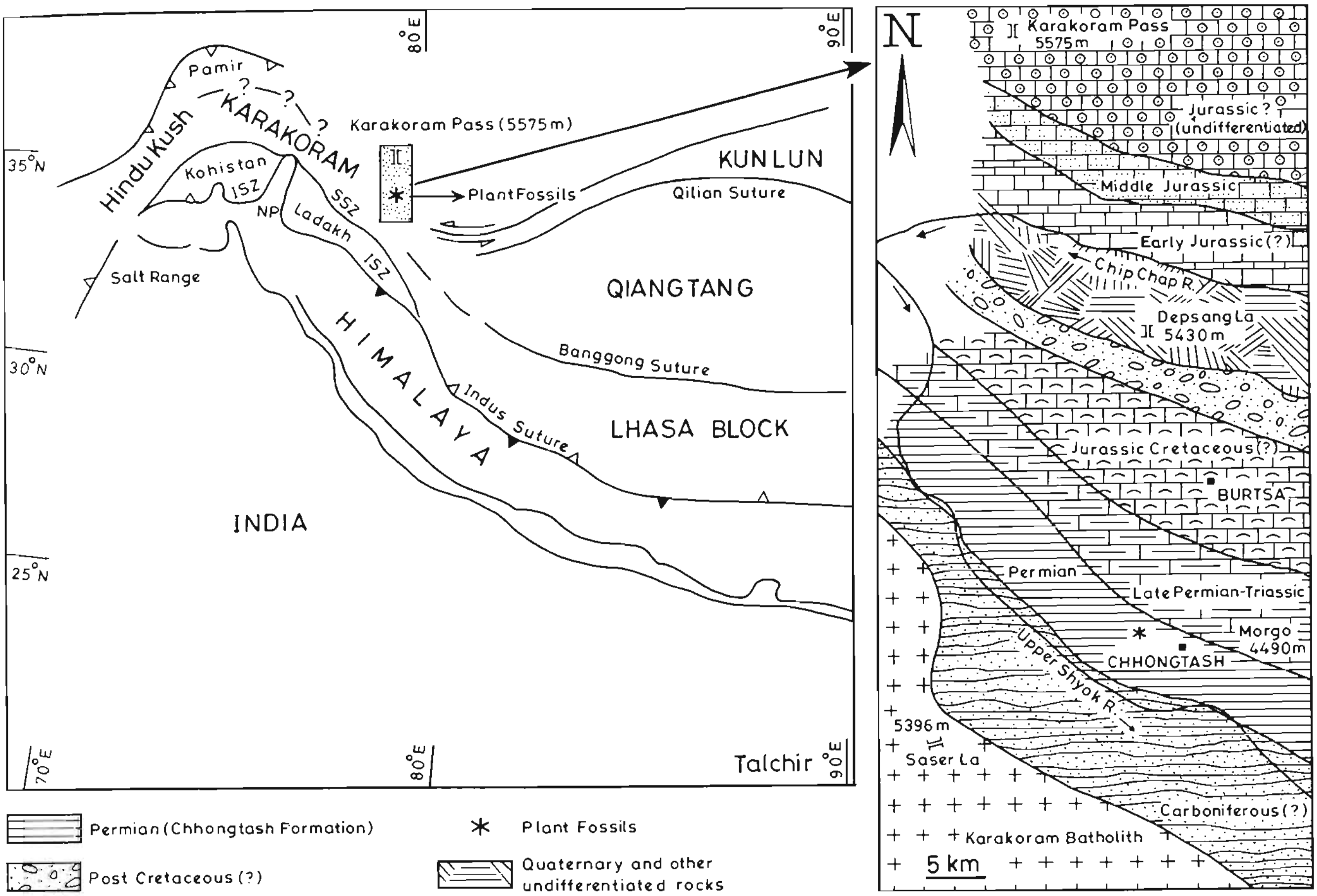

Fig. 2—Left: Simplified geological sketch map of central Asia showing present geotectonic position of western Himalaya, Karakoram, Hindukush, Pamir and Kun Lun mountain ranges; their tectonic subdivisions and location of major sutures, microcontinental fragments (modified after Searle, 1991). Shaded box, study area (Upadhyay *et al.*, 1999); SSZ, Shyok Suture Zone; ISZ, Indus Suture Zone; NP, Nanga Parbat; *Location of the Early Permian plant fossils and palynomorphs (Upadhyay *et al.*, 1999). Right: Simplified geological map of the eastern Karakoram between Saser La and Karakoram Pass showing the geological setting of the plant-bearing Chhongtash Formation and other geological entities in the eastern Karakoram block (Upadhyay *et al.*, 1999).

passed near the snout of the Siachen Glacier. He reported the existence of Siachen Glacier in the Karakoram region. Afterwards, Vigne attempted to reach the Bilafond La in 1835 from the west. It was Strachey who stepped on to the Siachen Glacier in 1848 and Drew in 1849. Significant contributions were made during the second half of the nineteenth century by Von Schlagintweit brothers (1861-66), Lydekker (1883), members of Forsyth expeditions and Drew in 1875. These workers gave the first accurate information on those parts adjoining the Karakoram trade routes, and revealed the presence of marine Mesozoic formations in the region. Earlier, Stoliczka (1865) and later Stoliczka (in Blanford, 1878) for the first time provided valuable geological information collected during his second Yarkand mission. Unfortunately, Stoliczka died on the way back from Karakoram pass, during his second expedition, as a result of his exhaustive traverse (personal communication with Prof. Maurizio Gaetani, Italy) in the most arduous Karakoram and adjoining Central Asia. A monument has been built at Leh in Ladakh by the Geological Survey of India to salute the soldier of geology- the Stoliczka.

The first topographic work in the Chang-Chen Mo and Lingzi-Thang regions of the western Tibet had been done as early as 1858, when Montgomerie of the Survey of India (1922) carried his triangulation series into the upper Indus Valley. Godwin-Austin (1884) and various travellers, including Deasy (1901) and Hedin (1906) had provided enough data for the Survey of India to publish a set of maps on the scale of one inch to four miles. The southern border of the Tibetan Plateau was touched by Hayden's reconnaissance survey of southern Tibet in 1903 and 1922 (Hayden, 1915), and its northern border by the Russian Tibet expedition under the leadership of Pevtsov (Pevtsov *et al.*, 1892-1896). But the geological information of the greater part of the Chang-Thang (western Tibet) is largely the result of one man's work. During his expeditions in the years 1894-1897, 1899-1902, and 1906-1908, Hedin collected systematically specimens of the rocks encountered along his routes, carefully recording their exact position and visible extension, besides preparing the route maps and landscape sketching (Hedin, 1904 -1907). The results of which published in his great work in nine volumes between 1916-1922.

Earlier, Ryall of the Survey of India sketched the lower part of the Siachen Glacier in 1861 and estimated its length as a mere sixteen miles. It is very surprising to learn that when the early explorers and mountain climbers were trying to explore the Siachen Glacier and adjoining region, the neighbouring Shaksgam Valley has remained geographically unknown until 1887. It was Sir Francis Younghusband (1887, cf. Desio *et al.*, 1991) who was travelling with a carvan from Peking, entered the Shaksgam Valley via the Aghil pass and left it via the eastern Muztagh pass. There exist no record whether any other expeditions with scientific purposes had travelled Younghusband's route in Sinkiang, between the Kun Lun mountain chain and that of Aghil, before 1926 (Desio, 1936, Desio *et al.*, 1991). Two years later, Francis Younghusband had a second journey to the Karakoram in 1889. Approaching from the Urdok Valley in the north, he surveyed the massive glacier from Turkestan La and deduced the main axis of the Karakoram range, which later confirmed by Longstaff in 1909. Therefore, Longstaff alongwith Neve and Lt. Slingsby were the first to traverse the length and breadth of the Siachen Glacier. They further established the size of the Siachen up to the Turkestan La, its northern limit. Subsequently, Collins and McInnes of the Survey of India, Worksman and Grant Peterkin surveyed the region during 1911-1912 and marked prominent peaks and glaciers in the eastern Karakoram.

A new era began in the exploration of eastern Karakoram, western Chang-Thang and adjoining Shaksgam Valley with the reconnaissances and multidisciplinary work carried out by the trained geologists of the Italian expeditions under the leadership of Filippo De Filippi in 1912-14; Duke of Spoleto in 1929 alongwith Desio and Umberto Balestreri; Giotto Dainelli (1932, 1933); the Dutch expeditions under Visser in 1922, 1925, 1929-30 (Visser, 1934), the German expeditions under Trinkler in 1927-28 and De Terra (1932) and the British expedition under Shipton in 1937. These scientific expeditions provided the first hand geological account of the eastern Karakoram and adjoining Yarkand region. They further stated the presence of Mesozoic sedimentary rocks around the Karakoram pass and adjoining region. In 1926 the northern slopes of the Aghil were explored by Kenneth Mason's expedition (Mason, 1938). Trying to define the Shaksgam River, Mason crossed the Karakoram pass down to Shaksgam, but he was stopped by the Kyagar Glacier for reaching the upper Shaksgam Valley. Therefore the stretch of valley between Kyagar Glacier and Urdok Glacier had remained unexplored until 1929 (Desio *et al.*, 1991). However, Mason (1938) provided the definition of Karakoram in a geographic sense which was later modified by Desio *et al.* (1991). This definition, though, hardly coincides with the possible boundaries of the 'geological' Karakoram (Gaetani, 1997). Interestingly, in 1929 Duke of Spoleto alongwith Ardito Desio and Umberto Balestreri, however, for the first time explored the remote and geologically unknown region of the Shaksgam Valley. The Duke of Spoleto was the expedition leader and he never crossed the range. He always remained on the Baltoro Glacier (personal communication Prof. Gaetani, Italy). This was followed by Wyss expedition in 1935 and Shipton and Auden expedition in 1937.

The scientific expedition led by Filippo De Filippi in 1912 was one among the largest and most comprehensive before the first world war. It included geodesy, geophysics, geology, meteorology and climatology. Later on, the multidisciplinary geological expedition led by Norin in 1932 was one among the most successful effort as far as preliminary geological and palaeontological investigations are concerned. They for the first time covered an area between Yarkand and western Tibet via Karakoram pass. The detailed geological informations of these remote region were later published in a monograph by Norin in 1946. Similarly, the geological and palaeontological reports and the data obtained from the Shaksgam Valley by various expeditions were published over a large span of time (Desio, 1930a, b, 1936, 1979, 1980; Desio *et al.*, 1991; De Terra, 1932; Auden, 1938; Wyss, 1940; Fantini Sestini, 1965; Gaetani *et al.*, 1990a, b; Gaetani, 1997).

PLATE 1 ⟶

1. Panoramic view of the Indus Suture Zone and the Indus River near Leh in Ladakh. Foreground area belongs to the Ladakh batholith and the background area belongs to Indus Forearc sediments.
2. A view of Shyok Suture Zone along the Nubra River Valley shows tectonic juxtaposition of the Shyok Ophiolitic Melange and the Karakoram batholith.
3. Location of the Karakoram Fault along the Nubra River and field juxtaposition of Karakoram metasediments and the Karakoram batholith.
4. Snow covered mountains, glacier and glacial lake near Saser La in the eastern Karakoram. Snow covered mountains belongs to the Karakoram batholith.
5. A view of Karakoram batholith with glacier, glacial lake and moraines in the eastern Karakoram.
6. Karakoram batholith is intruding into the recrystallized limestone of Saser Brangsa Formation (Carboniferous-Permian) in the eastern Karakoram.
7. Photograph showing the plant fossil and palynomorphs bearing Permian Chhongtash Formation in the eastern Karakoram (Original photography by RU and present displayed version is scanned from the cover page of BSIP, Lucknow Annual Report 1998-1999).

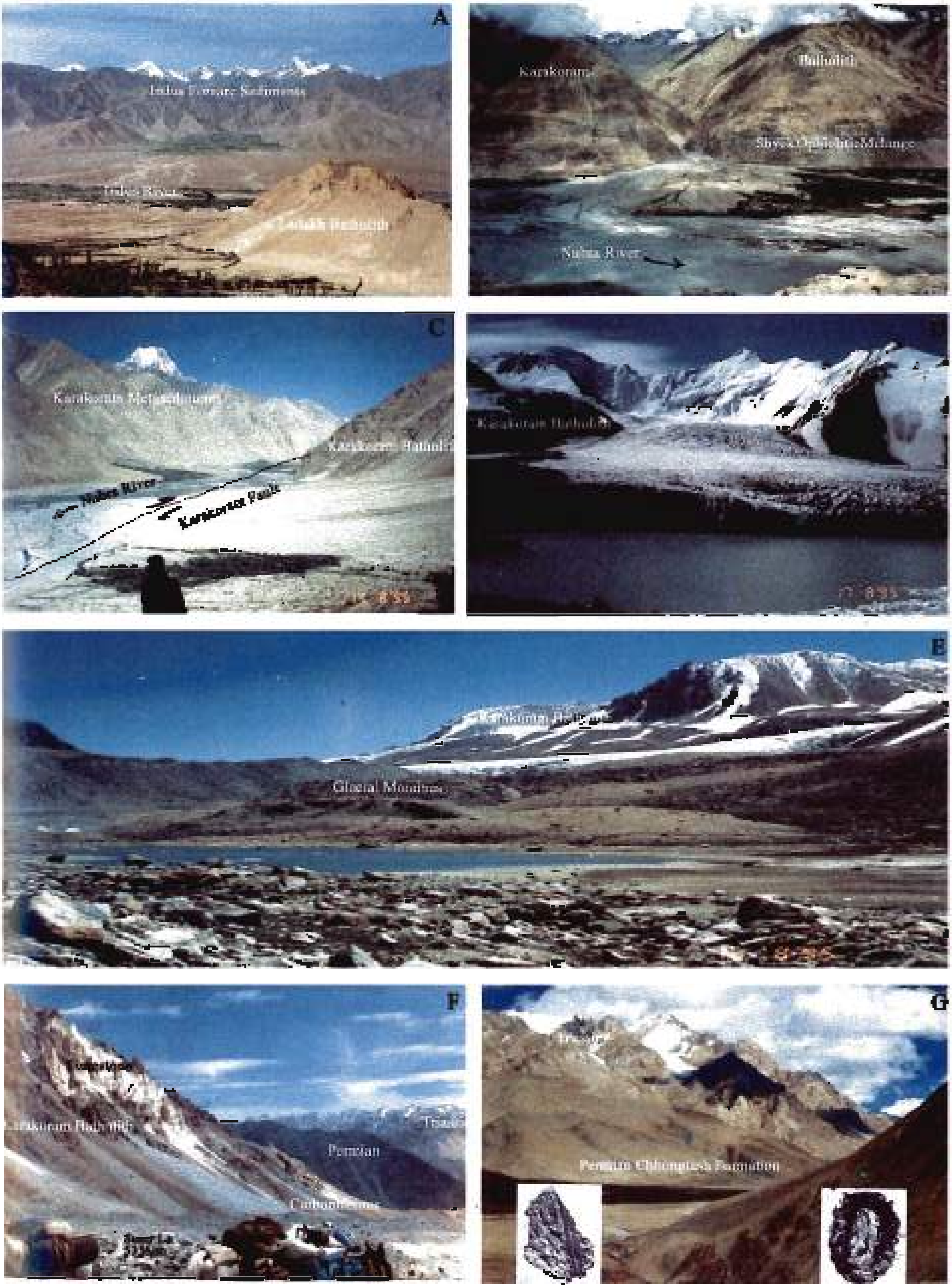
A
Indus River
Ladakh Batholith
B
Karakoram
Batholith
Nubra River
C
Karakoram Fault
D
Karakoram Batholith
E
Glacial Moraines
F
Permian
G
Permian Chhongtash Formation

PLATE I

A NEW ERA WITH NEW DIMENSIONS

Followed by the above mentioned preliminary geological reconnaissance a new era began with the new generation of geoscientists who carried out detailed multidisciplinary expeditions to the remote parts of the Karakoram mountains and Tibetan Plateau. These detailed multidisciplinary investigations indicate that there exists a number of accreted terranes and/or microplates between India-Eurasia collision zone. In the following section a brief highlight of some of these recent scientific information is given.

The Scientific expedition led by Prof. Desio in 1988 is one among the most significant one. The scientific reports of this expedition along with earlier works were published by Desio *et al.* (1991).

It is amazing to note that Prof. Desio—a pioneering stalwart in the geological exploration of the central Asian mountains, worked for more than six decades in the most arduous NW Karakoram and Shaksgam Valley. He is also known for his contribution to unravel the geological mystiques of K2 group of mountains. The summit of K2 has been scaled by Compagnoni and Lacedelli on 31 July, 1954 under the leadership of Prof. Desio's expedition to the Baltoro Basin in the Karakoram. On 18 April 2001 Prof. Desio has actively and successfully seen 104 springs. Unfortunately, on December 12, 2001 the legendary climber, a great geologist and explorer travelling all over the world died at the age of 104 years. Prof. Desio was born in 1897. We salute Prof. Desio—a key figure in the exploration of central Asian mountain massifs, for his outstanding contribution to the earth sciences as a whole. Amazingly, he was a geologist who has seen developments in the earth sciences for three centuries i.e., the later half of nineteenth century, twentieth century and now entered into the twenty first century.

According to Desio *et al.* (1991) the geological transect from Kun Lun to Karakoram could be divided into a number of microplates. These microplates are: 1. *Kun Lun Microplate*—This microplate includes the Kun Lun crystallines and its Late Palaeozoic granitoid intrusions of pre-Jurassic various granitoid types (Matte *et al.*, 1996) and the Palaeozoic Bazar Dara Slates. 2. *Qiangtang Microplate*—The area south of the Kun Lun microplate and east of the Karakoram Fault have been assigned to the Qiangtang microplate (Chang *et al.*, 1986). But recently Parrish and Tirrul (1989) considered this area belonging to the Lhasa microplate. However, Desio *et al.* (1991) decipher the presence of red sandstones and anhydrites of the Surukwat Thrust Sheet as one among the significant unit to represent the Qiangtang affinity. Earlier, Lender *et al.* (1988) assigned that the widespread red sandstone were derived during the Jurassic from the newly formed Kun Lun Range, and considered typical for the Qiangtang microplate within the Shaksgam Valley. 3. *SE Pamir-Karakoram Microplate*—It includes Permian to Triassic and Middle Jurassic Shaksgam Sedimentary belt, the Cretaceous calc-alkaline Sugat Granodiorite and the Sarpo Laggo-K2 Metamorphics. The Karakoram Fault and associated vertical faults are also dissecting the Shaksgam Sedimentary Belt in the region (Gaetani *et al.*, 1990a, b). Desio *et al.* (1991), however, also indicated that the Shaksgam Sedimentary Belt is eventually crossed by the Karakoram Fault alignment east of the Khunjerab pass. As a consequence they proposed that the Karakoram Fault does not represent a microplate boundary between the Karakoram and Qiangtang microplates. They further stated that, if it exists, should lie eastwards of Shaksgam. This is still an unresolved question. To find such answer we have to explore the geology of the Chhungtash—Depsang Plain-Karakoram pass-Loqzung mountains region and adjoining Lingzi-Thang. However, Gaetani *et al.* (1990a, b) and Desio *et al.* (1991) further stated that the Shaksgam Sedimentary Belt shows intermediate affinities between the Karakoram and Qiangtang microplate and its evolution moves from a Karakoram style to a Qiangtang style. In northern Karakoram, Gaetani (1997) provided a 400 Ma record of the evolution of a continental block, largely under marine conditions, from the Ordovician to the Cretaceous. He further identified six tectono-sedimentary cycles in the northern Karakoram.

The 1985 Royal Society Academia Sinica Tibet Geotraverse was organised, between Lhasa-Golmud by a team of geoscientists from United Kingdom and China under the leadership of Profs. Chang Chengfa, Robert Shackleton, John F. Dewey and Yin Jixiang. This multidisciplinary expedition has provided very significant information about the tectonic evolution of Tibetan Plateau. The scientific results of this expedition was published by the Royal Society of London in 1988. According to Dewey *et al.* (1988) the Tibetan Plateau, between the Kun Lun Shan and the Himalaya, consists of terranes accreted successively to Eurasia. The northern most, the Songban-Ganzi Terrane, was accreted to the Kun Lun along

PLATE 2 →

1. A close up view in the vicinity of Jurassic-Cretaceous Burtsa Formation in the eastern Karakoram.
2. Panoramic view of Jurassic-Cretaceous Formations and post-Cretaceous Qazi Langar Formation in the eastern Karakoram.
3. Rimo Glacier, the source of Shyok River near Depsang in the eastern Karakoram with linear crack formations.
4. Depsang La and Depsang Plain (5450 m) periphery of western continuation of Tibetan Plateau.
5. Karakoram Pass (5575 m) as a water divide between the southern Depsang Plateau and northern Yarkand Valley. Background mountains belong to Loqzung Group of mountains of Desio (1934, 1991).
6. A close up view of Karakoram Pass and Loqzung mountains in the eastern Karakoram.

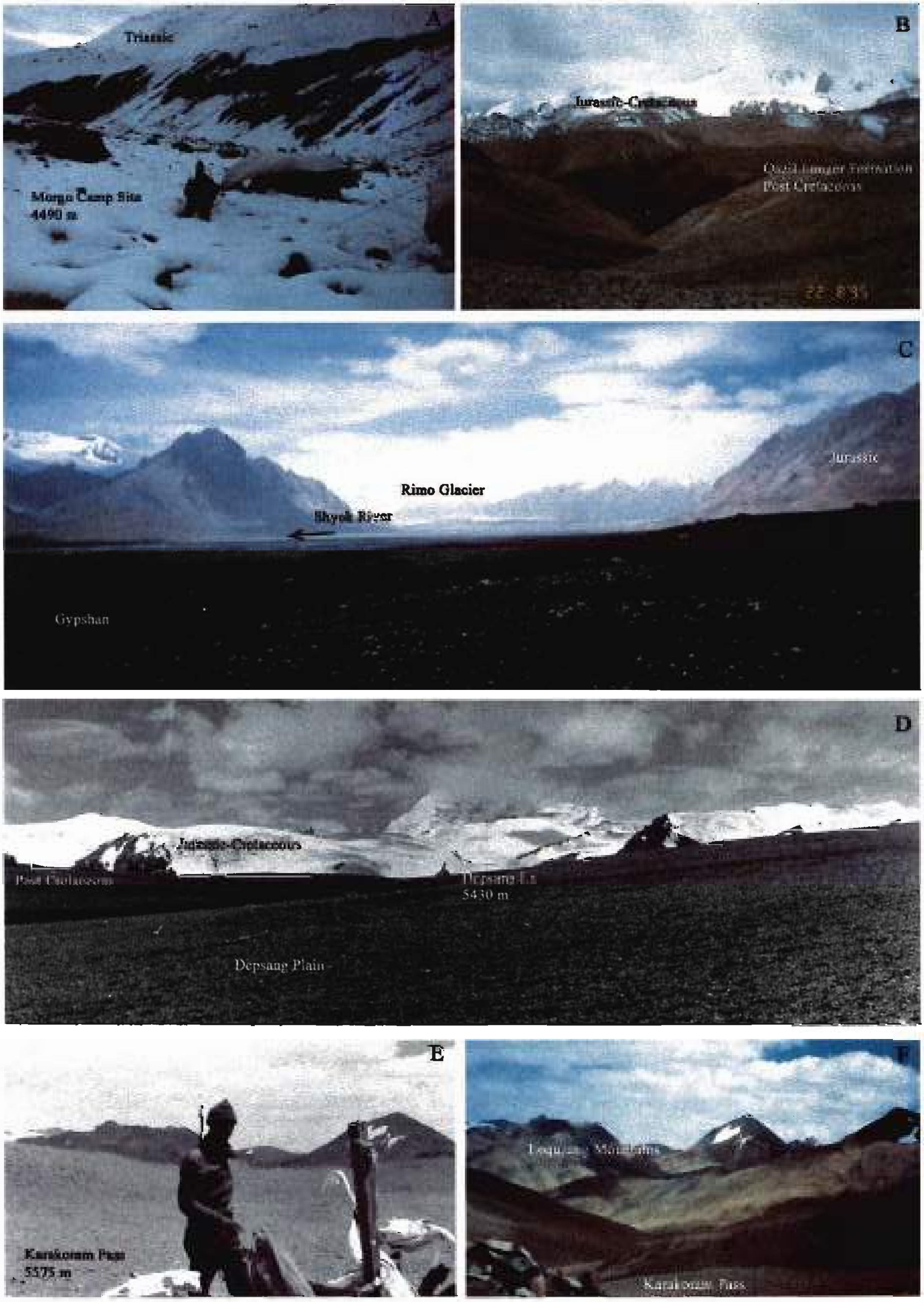
A
Triassic
Murgo Camp Site
4490 m
B
C
Rimo Glacier
Shyok River
Jurassic
Gypshan
D
5430 m
Depsang Plain
E
Karakoram Pass
5575 m
F
Karakoram Pass

PLATE 2

the Kun Lun-Qinling Suture during the Late Permian. The Qiangtang Terrane accreted to the Songban-Ganzi along the Jinsha Suture during the Late Triassic or earliest Jurassic, the Lhasa Terrane to the Qiangtang along the Banggong Suture during the Late Jurassic and, finally, peninsular India to the Lhasa Terrane along the Zangbo Suture during the Middle Eocene. They further proposed that thickening of the Tibetan crust is almost double the normal thickness which may be due to northward-migrating north-south shortening and vertical stretching during the Middle Eocene to earliest Miocene indentation of Asia by India.

In recent years Wadia Institute of Himalayan Geology, Dehradun, India has organised some expeditions to the Eastern Karakoram region. The expedition route lies between the Nubra Valley and Karakoram Pass. Preliminary but significant results of these expeditions were partly published by Gergan and Pant (1983), Bagati *et al.* (1994), Sinha *et al.* (1999). Earlier, Neptune Srimal of the Geological Survey of India also provided important information on the Shyok Suture and eastern Karakoram batholith (Srimal, 1986). According to these expedition reports there exists two major litho-tectonic divisions i.e., (1) Karakoram Plutonic-Metamorphic Complex; (2) Karakoram Tethyan Facies (Fig. 2, Pl. 1, 2). These tectonic divisions are supposed to represent a time span from Carboniferous-Permian to Late Cretaceous (Fig. 2, Pl. 1, 2). The sedimentary sequences between the Depsang Plain and the Karakoram Pass region holds a very close similarity with those exposed in the adjoining Lingzi-Thang and Loqzung mountains. Therefore this region should be considered as one among the most crucial zone to locate the boundary between the Karakoram terrane and Qiangtang microplate. Up-to-date there has been very scanty data available which further enhanced the missing gaps to compare this region with the eastern and western part of the Tibet. However, according to Sinha *et al.* (1999) the sediments of the eastern Karakoram Tethyan Zone are more or less similar to the adjoining Permian-Cretaceous Shaksgam Sedimentary Belt of the NW Karakoram in Sinkiang Province, China and adjoining geological sequences of the western Qiangtang block of western Tibet.

PLANT FOSSILS AND PALYNOMORPHS IN THE KARAKORAM, WESTERN TIBET AND WEST KUN LUN

Significantly, the recent discovery of the Early Permian (Artinskian, ~ 270-265 Ma) marine Gondwana sediments with plant remains and palynomorphs in the Chhongtash Formation of the eastern Karakoram (Upadhyay *et al.*, 1999) suggest that during Early Permian time the Karakoram was a Peri-Gondwanian microcontinent at latitudes of *ca* 35^0 south, somewhere between the Indian Plate and the Qiangtang-Lhasa microcontinent (Upadhyay *et al.*, 1999). The recorded plant fossils are *Noeggerathiopsis*, *Samaropsis* seed, a portion of *Gangamopteris* leaf, some unidentifiable plant types and a portion of a large equisetalean stem (Upadhyay *et al.*, 1999). The plant fossil bearing samples have yielded abundant palynomorphs of Early Permian age (Upadhyay *et al.*, 1999). The Karakoram microcontinent is not a part of the Indian Plate because it lies north of the Shyok and Indus Sutures. The Karakoram microcontinent was welded to Asia around 130-120 Myr ago (Dewey *et al.*, 1988) as part of Peri-Gondwanian collage with the southern margin of Asia (Upadhyay *et al.*, 1999). Unidentified plant remains have also been recorded by Norin (1946) from the Permian Horpatso Formation of western Tibet, deposited ~600 km further east of Chhongtash.

In a similar breakthrough Tongiorgi *et al.* (1994) recorded a sedimentary sequence of the Karakoram microplate which is overlying a granite pluton near Ishkarwaz (upper Yarkhun Valley, Chitral, Pakistan). This sedimentary sequence contains abundant acritarchs of the late early Arenig-early late Arenig (early Ordovician) interval. The palynological assemblages of Karakoram show a marked similarity to the cold water Peri-Gondwana assemblages; i.e., to those of Li Jun's *Arbusculidium-Coryphidium-Striatotheca* 'Mediterranean' Bioprovince (Tongiorgi *et al.*, 1994). Similarly, Amerise *et al.* (1998) recorded new acritarch samples from Vidkot locality, close to the Yarkhun River, to the southeast of Baroghil, Chitral in northwestern Pakistan. According to them the acritarch assemblages confirm the early Arenig age to the lowermost part of the succession. The upper age limit for younger stratigraphic levels at Vidkot could extend up to late Arenig on the occurrence of *Dicrodiacrodium* sp. cf. *D. normale* and *Arkonia tenuata*. The palynomorph assemblages from Vidkot also show clear affinity with the cool water Mediterranean microflora recorded earlier by Tongiorgi *et al.* (1994) from the Ishkarwaz.

Interestingly, while going back to the annales of geological exploration of western Tibet (Norin, 1946) it could be recapitulated that still there exists scant information as far as the floral and palynological records of Central Asian massifs are concerned. However, significant information regarding the presence of plant fossil bearing horizons of these remote regions have been arrived after the publication of a monograph by Norin in 1946. According to him, the Qara-Tagh Highland between the Chipchap Valley and the Qara-Tagh-Su in northewestern Tibet, Wyss (1940) has collected fossils from several Middle and Upper Jurassic horizons at a large number of places but, unfortunately, nothing has as yet been published about the stratigraphy (Norin, 1946). In April 1932, Norin crossed the Qara-Tagh over a pass situated only one or two km to the west of the Qara-Tagh-Davan of Visser and followed the narrow valley of Qara-Tagh-Su and Shu-Lunspo-Lungpa to the Qaraqash Valley. Near the pass where the tributary from pass joins the main valley follow black, richly plant-bearing shales which grade into light grey, gravelly sandstone with a basal conglomerates-several meters thick (Norin, 1946). This plant fossils bearing horizon is situated ~50 km NNE of the Karakoram Pass and ~90 km NNE from the Chhongtash locality from where Upadhyay *et al.* (1999) recorded Early Permian plant remains and palynomorphs. The following plant species were determined by Prof. Halle, Stockholm, in 1934 (Norin, 1946): *Neocalamites* (?) sp., *Klukia exilis*, *Sphenopteris* sp. (one small fragment rather similar to the Wealdon species *Sphenopteris* (*Ruffordia*) *goepperti*), *Cladophlebis* sp., *Nilssonia orientalis*, *Nilssonia* cf. *mediana*, *Ginkgo digitata*, *Ginkgo sibirica*, *Baiera* sp. (*B. gracilis*), *Podozamites lanceolatus*, *Pityophyllum* cf. *nordenskioldii*. This is a typical Mesozoic flora, probably Middle Jurassic (*Klukia*), though it may possibly be younger (Norin, 1946). In additional note on this floral assemblage in 1943, Halle states "According to Oishi (1940) and others, some of the species occur in beds assigned to the Upper Jurassic and even Wealdon. The species determined as *Klukia exilis* may possibly be identical with *Cladophlebis* (*Klukia* ?) *koraiensis* Yabe from the Upper Jurassic Tetori Series".

The development of the western Kun Lun (Norin, 1946) during the early Mesozoic is registered in thick deposits of continental sandstones, shales and conglomerates, the Yarkand Group of De Terra (1932) which are the molasse deposits of the rapidly decaying Variscan ranges (Norin, 1946). In the lower part of Yarkand Group occurs a bed of good coal about 0.5 m thick at the outcrop. The black shale associated with the seam contains plant fossils abundantly. In 1934, Prof. Halle, Stockholm, identified the following species (Norin, 1946): *Cladophlebis* sp., *Nilssonia* cf. *simplex* Oishi, *Nilssonia* or *Pterophyllum* sp., *Phoenicopsis speciosa, Pagiophyllum* ? sp. (cf. *Elatocladus heterophylla* Halle), *Problematicum*. The age of this flora is undoubtedly Mesozoic, most probably Jurassic (Norin, 1946). The upper division of the Yarkand Group begins with reddish sandy shales followed by yellow marls with a Lower or Middle Jurassic flora (*Coniopteris hymenophylloides*, *Taeniopteris vittata*, *T. de Terrae*, *Podozamites lanceolatus* and *Phoenicopsis* cf. *speciosa*). The coal bearing Mesozoic series appears again with entirely different facies near the top of the Kun Lun main range at the head of the Tisnaf Valley below Yangi davan (Norin 1946).

Therefore, on the grounds of above mentioned observations it could be deciphered that up to date there exists two localities of the Ordovician (Arenig) palynomorphs in the marine formation of NW Karakoram (Chitral, Pakistan, Togiorgi *et al.*, 1994; Amerise *et al.*, 1998), one locality of Early Permian plant fossils and palynomorphs in the marine Chhongtash Formation of the eastern Karakoram (Upadhyay *et al.*, 1999), one locality each of Permian and Jurassic plant fossils from the marine formations of the western and the northwestern Tibet (Norin, 1946) and one locality of Jurassic plant fossils bearing continental deposits in the Kun Lun (Norin, 1946).

REGIONAL TECTONIC FEATURES OF THE KARAKORAM, THE WESTERN TIBET AND THE KUN LUN

Based on geological information across western Tibet to Tarim traverse Matte *et al.* (1996) depicted that the Kun Lun was the site of a Mid-Palaeozoic collision. At least three phases of post-Palaeozoic accretion have thickened the blanket of sediments that covers western Tibet. A major part of western Qiangtang have remained stable, since the Mid-Mesozoic. Strike-slip motion along the Karakoram and Altyn Tagh faults has been coeval with overthrusting in the Himalayas and Kun Lun. Such slip partitioning and the volcanism, appear to result simply from northward subduction of India and southward subduction of the Tarim as Tibet is extruded eastwards by India's penetration into Asia (Matte *et al.*, 1996).

Recent geological investigations across Nubra-Shyok River valleys in northern Ladakh (Upadhyay *et al.*, 1999; Chandra *et al.*, 1999) suggest that similarity exists between the Shyok Suture of northern Ladakh and the Northern Suture of Kohistan. It is likely that the Kohistan and the Ladakh units evolved as a single tectonic domain during the Cretaceous-Palaeogene. The Shyok Suture is older than the Indus Suture and closed sometimes between 100-75 Ma. The accretionary processes in the Karakoram region began prior to the final closure of the Indus Suture. Subsequently, collision, suturing and accretion of the Indian Plate along the Indus Suture Zone (50-60 Ma) and the formation of the Nanga Parbat-Haramosh syntaxis separated Kohistan and Ladakh. The different phases of magmatic growth in the Ladakh and the Karakoram have acted as a role of stitching pluton to bind the Indian and Asian plates together. The Holocene-Recent dextral offset along the Karakoram-fault reshaped and rejuvenated the tectonic structures and the architecture of the entire Karakoram, the Shyok Suture and the adjoining Indian Plate region.

The active Karakoram fault with ~120 km dextral offset can be traced along the Shyok Suture in northern Ladakh and adjoining Karakoram and extends further north-west to Pamir. This active, normal-dextral fault is the greatest geomorphic boundary between the Ladakh, Karakoram and western Tibet. The northern segment of the Karakoram fault terminates in the extensional Muji Basin along the border between Tadjzhikistan and Xinjiang (Searle, 1996). Based on geochronological data Zhou *et al.* (2001) indicated that the Karakoram strike-slip faulting occurred from 6.88±0.36 to 8.75±0.25 Ma. The cumulative displacement from Muztag Ata to Muji is about 135 km. The dextral strike-slip offsets of the central part of the Karakoram fault have been accommodated in the north by three splays arcing westward through the central Pamir: the Rangkul, Murghab and Karasu faults (Searle, 1996). In the central Karakoram ranges of north Pakistan and the Shaksgam region of southern Xinjiang, the Karakoram fault slices through the

Permian and early Mesozoic sediments of the north Karakoram terrain and the Karakoram batholith (Desio, 1979; Searle, 1991). The fault runs along the Shaksgam Valley, north of the highest peaks of the Karakoram-K2, Broad Peak and the Gasherbrum range. Across the border in northern Ladakh, the alignment of the 70 km-long Siachen Glacier and the Nubra-Shyok Valley into which it flows has been controlled by the Karakoram fault (Upadhyay, 2001). Based on Ar/Ar dating of micaceous segregation of the sheared Karakoram batholith exposed along the Nubra Valley, Bhutani and Pande (2002) suggested that the age of activation of Karakoram fault in this region is 13.9±0.1 Ma. The slip rate on the Karakoram fault as inferred by Gaur (2001) using GPS Geodesy and cosmic ray exposure ages of an offset debris flow in Ladakh, are ~4 mm/yr. Along the western margin of Pangong Tso Lake, the Karakoram fault splays into two main branches. The eastern splay appears to control, by damming, the outflow channel of the lake, which itself is a drowned river valley (Searle, 1996). There is abundant structural evidence of dextral shear to the south of Pangong Lake in the Nganglong Kangri range, with foliations swinging into alignment with the Karakoram fault (Searle, 1996). Armijo *et al.* (1989) suggested that the Shiquanhe fault branching off the Karakoram fault, transferred displacement along the northern part to a system of minor strike-slip faults and rifts in west central Tibet.

Further southeast, along the floodplains of the Indus and Gar rivers, the NW striking, steeply NE dipping Karakoram fault marks the base of the Ladakh range front. Cumulative scarps tens of meters high across Late Pleistocene moraines, 2 km high triangular facets, and perched glacial valleys attest to rapid vertical throw on the fault (Matte *et al.*, 1996). Dextral offsets of 300-400 m of post-glacial fans and channels imply a Holocene slip rate of the order of 3 cm/yr (Liu Qing, 1993). Such motion has produced the conspicuous ~120 km offset of the Indus River course (Searle, 1996; Liu *et al.*, 1993; Gaudemer *et al.*, 1989). Recent uplift along the fault has exhumed strongly sheared gneisses parallel to the active fault trace in the region.

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Fossil woods from Upper Tertiary sediments of Jammu region (Jammu & Kashmir) North-West India and their significance

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ABSTRACT

Guleria JS, Gupta SS & Srivastava R 2001. Fossil woods from Upper Tertiary sediments of Jammu region (Jammu & Kashmir) North-West India and their significance. Palaeobotanist 50(2 & 3) : 225-246.

Petrified dicotyledonous woods are reported for the first time from the Middle Siwalik sediments of Jammu region (Jammu & Kashmir) in the northwestern part of India. The fossil woods resembling modern woods of *Dipterocarpus* Gaertn.f. (Dipterocarpaceae), *Bischofia* Blume (Euphorbiaceae), *Cassia* Linn. and *Kingiodendron* (Roxb.) Harms (Leguminosae) have been described in detail. Based on the distribution of comparable extant genera and species, prevalence of humid climate and existence of a mixed lowland tropical forest, comprising moist deciduous to evergreen elements, in the area have been deduced. Evidently *Bischofia*, *Dipterocarpus* and *Kingiodendron* existed in the Jammu region during the Late Tertiary time and subsequently shrunk in their distribution due to climatic change. They no longer grow in the area as they require more humid conditions. The occurrence of *Dipterocarpus* is particularly noteworthy as it extends the limit of Dipterocarpaceae in the geological past as far west as Jammu region in the north-west India. The arboreal C_3 forms show that the landscape was well forested.

Key-words—Fossil woods, Xylotomy, Middle Siwalik, Middle Pliocene, Palaeoclimate, Phytogeography, Jammu & Kashmir (India).

उत्तर-पश्चिमी भारत के जम्मू मण्डल (जम्मू तथा कश्मीर) के उपरि टर्शियरी अवसादों से प्राप्त अश्मित काष्ठ एवं उनकी प्रासंगिकता

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सारांश

भारत के उत्तर-पश्चिमी भाग के जम्मू मण्डल (जम्मू तथा कश्मीर) के मध्य शिवालिक अवसादों से प्रथम बार अश्मित द्विबीजपत्री काष्ठ अंकित की गयी है। यह अश्मित काष्ठ आधुनिक काष्ठों *डिप्टेरोकार्पस* गार्टेन. एफ. (डिप्टेरोकार्पेसी), *बिस्कोफ़िया* ब्लूम (यूफ़ोर्बिएसी), *कैशिया* लिन. तथा *किंगियोडेण्ड्रॉन* (रॉक्स बी.) हार्म्स के सदृश है। इसका विस्तृत विवेचन प्रस्तुत शोध पत्र में किया गया है। तुलनीय विद्यमान वंशों एवं प्रजातियों के वितरण के आधार पर क्षेत्र में आर्द्र जलवायु की प्रमुखता तथा नम पर्णपाती से लेकर सदाहरित तत्वों से युक्त एक सम्मिश्र निम्नभूमि ऊष्णकटिबन्धीय वनों की उपस्थिति प्रस्तावित की जाती है। अन्तिम टर्शियरी कल्प के दौरान जम्मू मण्डल में *बिस्कोफ़िया, डिप्टेरोकार्पस* तथा *किंगियोडेण्ड्रॉन*

के होने के प्रमाण मिले हैं, जो जलवायुविक परिवर्तनों के कारण घटते चले गए। आज ये इस क्षेत्र में बिल्कुल भी नहीं पाए जाते हैं, क्योंकि इन्हें वर्तमान की तुलना में अधिक आर्द्र स्थितियों की आवश्यकता होती है। *डिप्टेरोकार्पस* की उपस्थिति यहाँ विशेष रूप से महत्वपूर्ण है, क्योंकि ये भू-गर्भीय अतीत में उत्तर-पश्चिमी भारत में पश्चिमी छोर के जम्मू मण्डल तक डिप्टेरोकार्पेसी का विस्तार दर्शाता है। C_3 वृक्षीय रूपों से प्रदर्शित होता है कि यह क्षेत्र वनों से भली-भांति आच्छादित था।

संकेत शब्द—अश्मित काष्ठ, दारु शारीर, मध्य शिवालिक, मध्य प्लायोसीन, पुराजलवायु, पादप भौगोलिकी, जम्मू तथा कश्मीर (भारत).

INTRODUCTION

THE Siwalik Group in the Jammu and Kashmir State of India comprises a thick and uninterrupted sequence of molassic sediments. The basin of deposition apparently consisted of a series of lakes, swamps and flood plains. The sediments of the area have lately been studied by a number of workers (For earlier references see Bhat *et al.*, 1999; Agarwal *et al.*,1993; Tandon, 1991; Dutta *et al.*, 1975; Gupta, 1997b, 2000; Gupta & Prasad, 2001; Gupta & Shali, 1989, 1990). Gupta and Verma (1988) classified the Siwalik Group of Mansar-Uttarbaini Section, Jammu District, into five formations viz., Mansar (Lower Siwalik), Dewal and Mohargarh (Middle Siwalik) and Uttarbaini and Dughor (Upper Siwalik). They further sub-divided the Uttarbaini Formation into the Labli and the Marikhui members. Gupta (1991, 1997a, 2000) recently proposed the suitability of this classification for the entire Siwalik Group of Jammu and further sub-divided the Mansar Formation into the Dodenal and the Ramnagar members (Fig. 1).

The fossil woods reported in the present paper were recovered from the sediments of Mohargarh Formation. The formation exposed in the fossiliferous areas is characterized by thick-bedded, friable, micaceous sandstone with relatively thinner beds of clay and siltstone. The sandstones are buff, grey and yellowish grey, medium to coarse grained, often pebbly and exhibit channel deposition and torrential current bedding. The sandstone bands at places contain conglomerate lenses and occasionally contain lenses of coal and ferruginous matter. The sandstone/conglomerate make up nearly 90 percent of the entire formation.

Group	Sub-group	Formation	Member	Age
	Terraces (T1 -T3)			Holocene
	----------	Unconformity	----------	
S		Dughor (76 m)		
	Upper Siwalik		Marikhui	Lower Pleistocene
I			(1524 m)	
		Uttarbaini (2524 m)		
W			Labli (1000 m)	Upper Pliocene
	----------	Conformable to Para conformable	----------	
A		Mohargarh		
	Middle Siwalik	(915 m)		Middle Pliocene
	----------	Disconformity (0.82 MY)	----------	
L		Dewal (1753 m)		Lower Pliocene
	Lower Siwalik		Ramnagar	Upper Miocene
I			(1498 m)	
		Mansar (1977 m)		
K			Dodenal (479 m)	Middle Miocene
MURREE				Lower Miocene to Upper Eocene

Fig. 1—Stratigraphic sequence of the Siwalik Group in Jammu region.

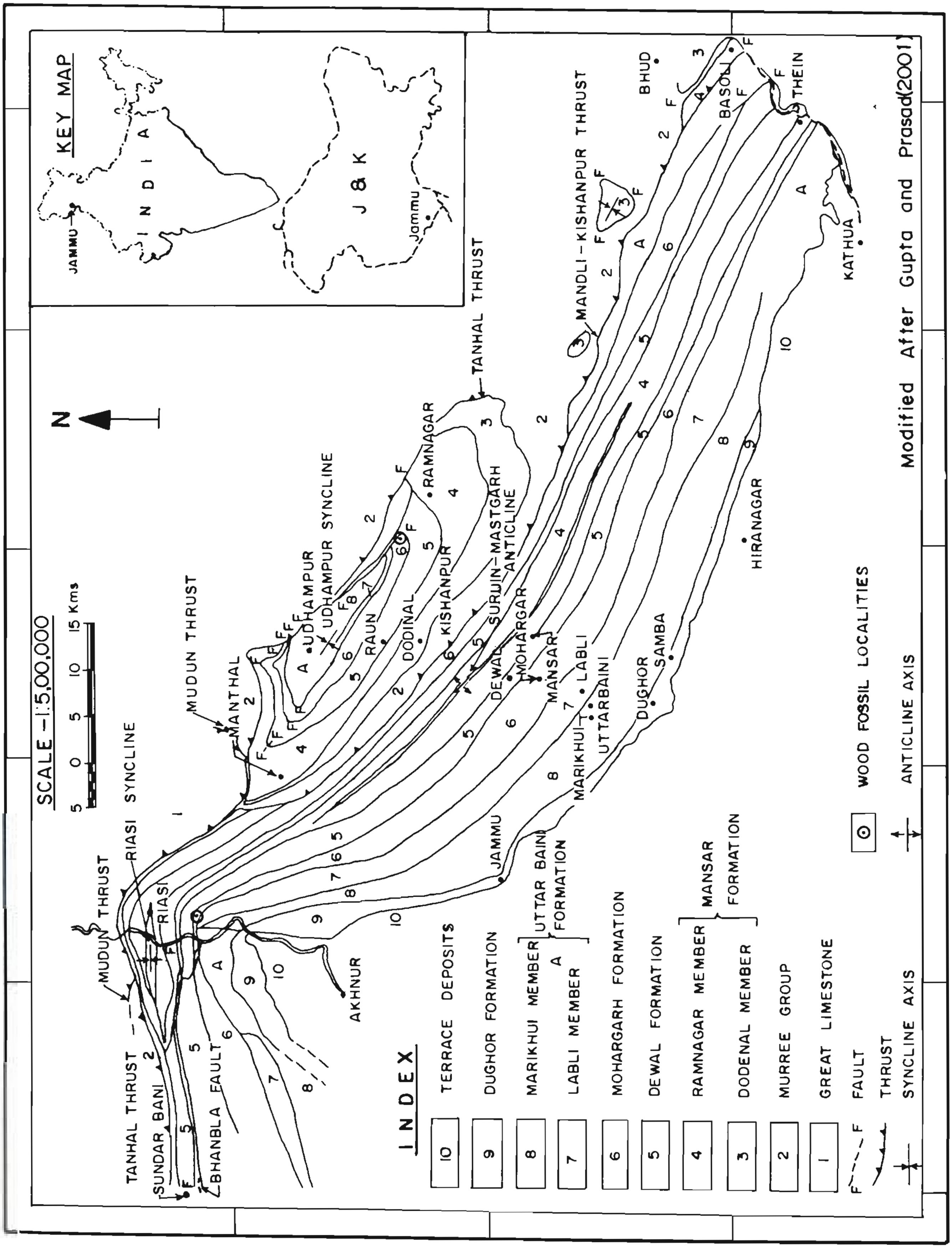

Fig. 2—Geological map of Siwalik Group of Jammu area, J & K, showing fossil wood locations.

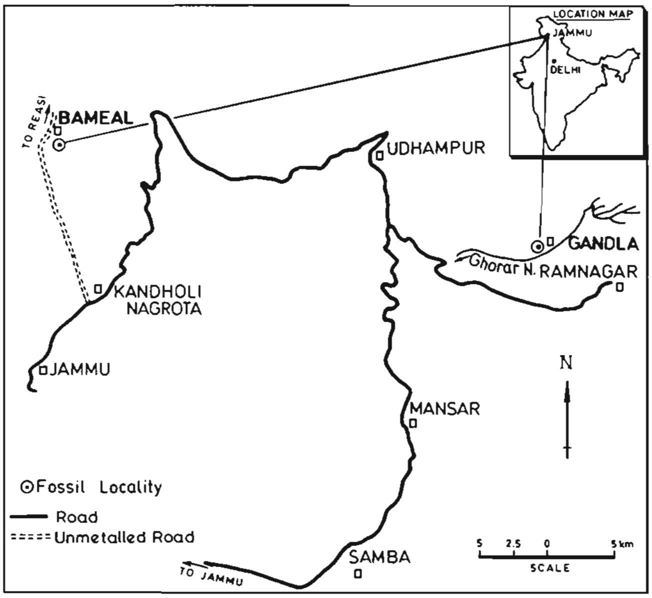

Fig. 3—Map showing fossil wood sites in part of Jammu and Udhampur districts, J & K.

The channel facies sandstone is medium to coarse grained, characterized by large scale trough and planar cross-stratification. Each sandstone unit in a multistoried sandstone body is separated by erosional surfaces which are generally planar but showing scours at places. The latter are generally filled with mud-balls, mud-pellets, calcrete pallets showing tough cross-stratification. The clays occur in thin and widely separated bands and hardly constitute 5 to 10 percent of the Mohargarh Formation. These are generally dark grey, buff, brown and yellowish. Presence of mud-balls along the erosional surfaces suggest the periodic occurrence of strong currents causing reworking of older flood plains. A significant change in sedimentation marked by thick, coarse sediments of Mohargarh Formation suggests an increased fluvial activity and rapid rate of sedimentation along continental fresh water basins. The fossils woods are occasionally found embedded in the sandstone as incomplete logs (Gupta, 2000, p. 58). They are more often encountered in the form of carbonised woody tissues.

There are only a few records of Tertiary plant fossils from the Jammu region. Sahni (1964) reported two species of grass-like leaf impressions of unknown affinities, viz., *Poacites sivalicus* (Sahni, 1964, pp. 8-9, pl. 1, fig. 3) from the Lower Siwalik of Sudnatti Tehsil, Poonch and *P. rajaoriensis* (Sahni, 1964, p. 9, pl. 1, fig. 3) from the Murree sediments of Rajaori, near Poonch and another monocot (plicated parallel veined) leaf impression from the sediments of Murree Series (Miocene) near Rajaori (Sahni, 1964, p. 12, pl. 1, fig. 8). In addition, he described two palm woods, namely, *Palmoxylon wadiai* (Sahni, 1964, pp. 24, 29-30, pl. 1, fig. 12, pl. 2, figs 13-17) and *P. jammuense* (Sahni, 1964, pp. 30-31, pl. 11, figs 75-77) from the alluvial boulder conglomerate deposit (? Pliocene) at the Tawi River, Jammu. *Artocarpus murreecus* is the first fossil dicot leaf reported from this region by Sharma and Gupta (1972) from Thanamandi in Rajaori District, Jammu and Kashmir. Besides, Kumar *et al.* (1979) and Suneja *et al.* (1981a) reported the occurrence of Charophytic gyrogonites represented by *Tectochara meriani meriani, T. meriani huangi* and *Tectochara* spp. in the Lower Siwalik beds (Chinji Formation) of Ramnagar. Suneja *et al.* (1981b) further reported two species of *Chara*, viz., *C. rantzieni* and *C. rantzieni sivalensis* from the Upper Pliocene-Lower Pleistocene sediments of the Tawi Valley, north of Jammu. Lately Bhatia *et al.* (2001) have reported the occurrence of two more charophytic taxa *Hornichara* and *Lychnothamnus* and an angiospermic seed *Boraginocarpus* from the Upper Siwalik sediments of Nagrota Formation. According to Bhatia (1999) the above noted *Tectochara* spp. have been merged under the genus *Nitellopsis* and the *Chara rantzieni sivalensis* under *C. globularis globularis.* Spore-pollen assemblages encountered in the Jammu region have been listed by Mathur (1984). From the above resumé it is clear that no dicotyledonous wood has been reported from this region. Thus, in this paper fossil dicotyledonous woods are being described for the first time from the Jammu region.

MATERIAL AND METHODS

The material for the present study was collected by one of us (S.S.G.) from exposures of the Mohargarh Formation (=Dhokpathan Formation) of Middle Pliocene age (Gupta, 2000). The fossil woods were recovered from two localities, viz., Bameal (32°56'25": 74°52'35") and Gandla (32°50'10": 75°16'00"). The former is situated about 35 km northwest of Jammu near Nagrota in Jammu District; the latter about 25 km southeast of Udhampur town near Ramnagar in Udhampur District of Jammu and Kashmir (Figs 2, 3). The area in general is presently covered by tropical dry mixed deciduous and subtropical pine forests comprising almost pure crop of *Pinus roxburghii* at higher ridges and steep rocky slopes. The angiospermic genera commonly met in the area are : *Acacia, Adhatoda, Aegle, Bauhinia, Butea, Capparis, Cassia, Dalbergia, Dodonea, Ficus, Flacourtia, Lannea, Mallotus, Ougenia, Zizyphus,* etc. (Sharma & Kachroo, 1981). The fossils come from two horizons of the Mohargarh Formation which constitutes 915 m thick sandstone-clay sequence in Bameal Section and 427 m sandstone-conglomerate litho-unit in Gandla Section (Fig. 4). The fossil wood bearing horizons are located 682 m and 194 m above the top of Dewal Formation. In both the localities fossil woods were found embedded in rocks *in situ* and had to be dug out. Occasionally heavy logs were found, which were difficult to carry. From such logs small pieces were removed with the help of a hammer. The fossils comprise only secondary xylem. Preservation of the material is satisfactory to good, though sometimes tissues are highly

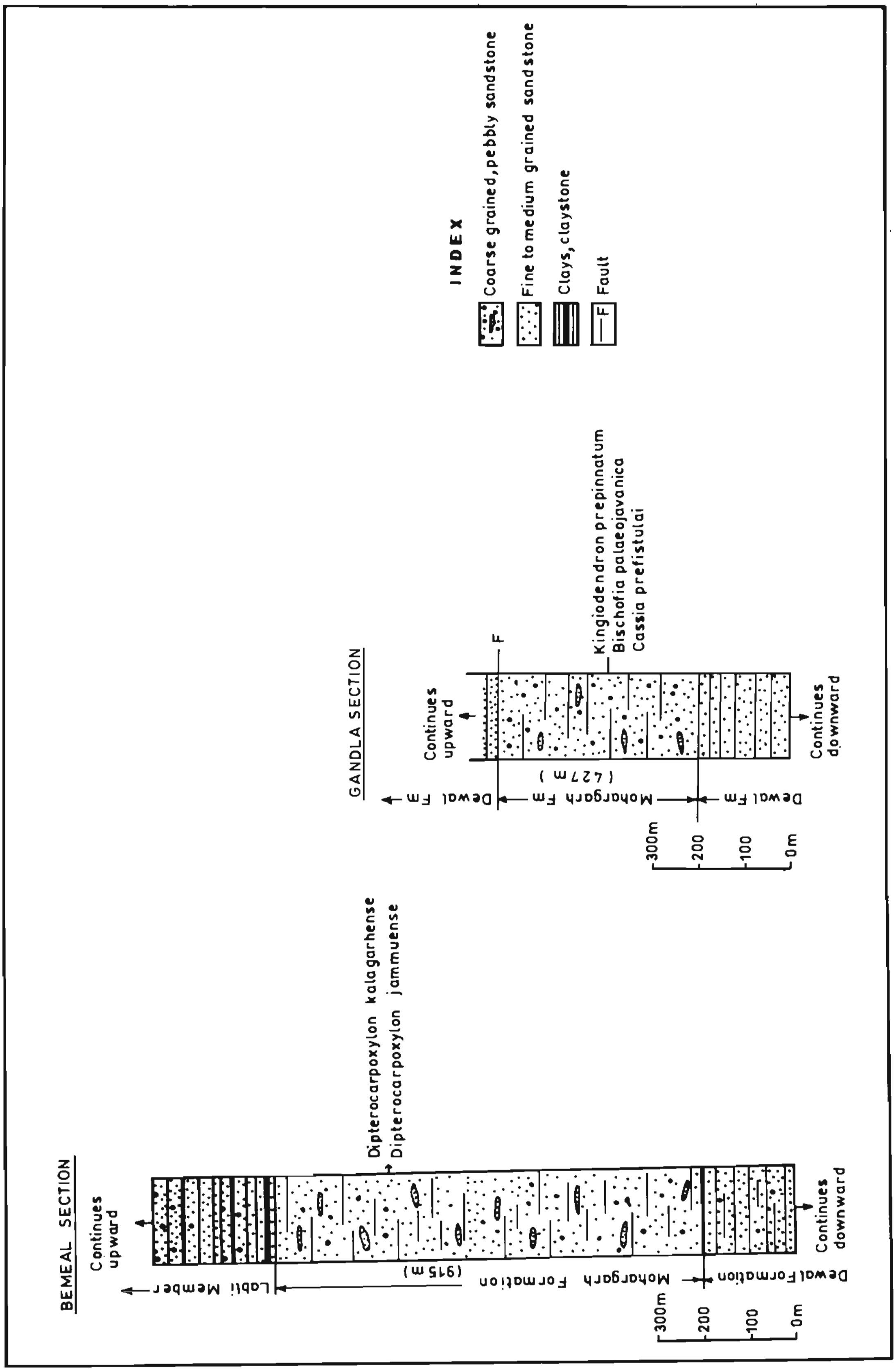

Fig. 4—Litho-columns of Mohargarh Formation showing stratigraphic positions of fossil wood bearing horizons.

degraded. For xylotomical studies the woods were cut into thin slices and transverse, tangential-longitudinal and radial-longitudinal sections were prepared by the usual method of grinding and polishing. The specimens and slides are deposited at the repository of Birbal Sahni Institute of Palaeobotany, Lucknow, India.

SYSTEMATICS

Family—DIPTEROCARPACEAE

Genus—DIPTEROCARPOXYLON Holden emend. Den Berger, 1927

DIPTEROCARPOXYLON JAMMUENSE sp. nov.

(Pl. 1.1-5)

Material—The species is based on a single fairly well preserved specimen 26 cm long and 15.5 cm wide.

Description—*Wood* diffuse-porous (Pl. 1.1). *Growth rings* not seen. *Vessels* small to large (mostly medium sized), tangential diameter 80-260 µm, radial diameter 100-360 µm, evenly distributed, 3-9 vessels per sq. mm; almost solitary (Pl. 1.1), circular to oval, with flattened contact walls when in multiples; tyloses often present; vessel members 240-600 µm long with truncate or oblique end walls; perforations simple; inter-vessel pits not observed. *Vasicentric tracheids* present, intermingled with parenchymatous cells forming thin sheath around vessels, frequently pitted (Pl. 1.4). *Parenchyma* both apotracheal and paratracheal; paratracheal vasicentric, forming uni to biseriate layer with tracheids around vessels; apotracheal scanty, only a few diffuse cells seen, also forming sheath encircling gum canals (Pl. 1.1), cells 48-60 µm in diameter and 28-90 µm in length. *Rays* 1-6 (mostly 3-5) seriate, 5-9 rays per mm, heterocellular (Pl. 1.2, 5); uniseriate rays 2-11 cells or 180-730 µm long, made up of upright cells only or both upright and procumbent cells; multiseriate rays made up of procumbent cells in the centre with uniseriate extensions of 2-12 upright cells at both the ends, sheath cells present on the flanks of multiseriate rays (Pl. 1.3), up to 480 µm wide and 5-45 cells or 200-1,260 µm long; procumbent cells 20-32 µm in tangential height and 40-60 µm in radial length, upright cells 28-48 µm in tangential height and 16-24 µm in radial length, vessel-ray pits simple, many per cell (Pl. 1.5). *Fibres* aligned in radial rows, polygonal in cross section, semilibriform, non-septate, 36-48 µm in diameter, frequently pitted (Pl. 1.4). *Gum canals* vertical, normal, solitary or in tangential groups of 2-4 (5), smaller than vessels, enclosed by parenchymatous sheath, tangential diameter 65-80 µm, radial diameter 75-65 µm (Pl. 1.1).

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow, Geological Survey of India, Jammu.

Holotype—BSIP Museum No. 38305.

Locality—Barneal near Nagrota, Jammu & Kashmir.

Horizon—Nuhargarh Formation, Middle Siwalik.

Age—Middle Pliocene.

Etymology—Specific name is after the Jammu area from where the fossil wood was collected.

Affinities—The important characters of the fossil are: almost solitary vessels with tyloses, vasicentric tracheids, scattered gum canals, solitary or in groups of 2-4 (5), paratracheal parenchyma vasicentric, apotracheal parenchyma scanty, only as few diffuse cells and around gum canals, 1-6 (mostly 3-5) seriate, distinctly heterocellular rays. The combination of all these characters indicate that the fossil belongs to genus *Dipterocarpus* Gaertn. f. of the family Dipterocarpaceae. Thin sections of a large number of extant woods of *Dipterocarpus* available at the Birbal Sahni Institute of Palaeobotany, Lucknow and Forest Research Institute, Dehradun were examined and published descriptions and figures of many other species were also consulted for comparison (Moll & Janssonius, 1906; Kanehira, 1924a, b; Lecomte, 1926; Pearson & Brown, 1932; Reyes, 1938; Desch, 1957; Chowdhury & Ghosh, 1958; Kribs, 1959; Hayashi *et al.*, 1973; Miles, 1978; Ilic, 1991). From the survey of wood slides and literature it was found that the fossil shows close resemblance with the wood structure of *Dipterocarpus indicus* Bedd. (BSIP wood slide no. 5081) and *D. lowii* Hook. f. (BSIP wood slide no. 2,400) as diffuse in aggregate parenchyma is almost absent in these two species. The former, however, differs in having greater frequency of gum canals which are arranged more or less regularly in short or long tangential rows. *Dipterocarpus lowii* shows nearest resemblance with the present fossil in all its characters including frequency and distribution of gum canals.

Comparison and Discussion—A number of fossil wood species referable to the genus *Dipterocarpus* have been described under the artificial genus *Dipterocarpoxylon* Holden emend. Den Berger (1927). About 17 species are known from the Upper Tertiary sediments of Indian subcontinent which includes India, Pakistan, Nepal, Bhutan, Bangladesh, Srilanka and Myanmar (Awasthi, 1996; Awasthi & Mehrotra, 1997;

PLATE 1 ⟶

Dipterocarpoxylon jammuense sp. nov.

1. Cross section showing shape, size and distribution of vessels, parenchyma and gum canals. × 40. Slide no. BSIP 38305-I.
2. Radial longitudinal section showing heterocellular ray tissue. × 200. Slide no. BSIP 38305-III.
3. Tangential longitudinal section showing uniseriate and multiseriate xylem rays. × 40. Slide no. BSIP 38305-II.
4. Radial longitudinal section showing vasicentric tracheids and fibre tracheids. × 200. Slide no. BSIP 38305-III.
5. Radial longitudinal section showing vessel-ray pits. × 400. Slide no. BSIP 38305-III.

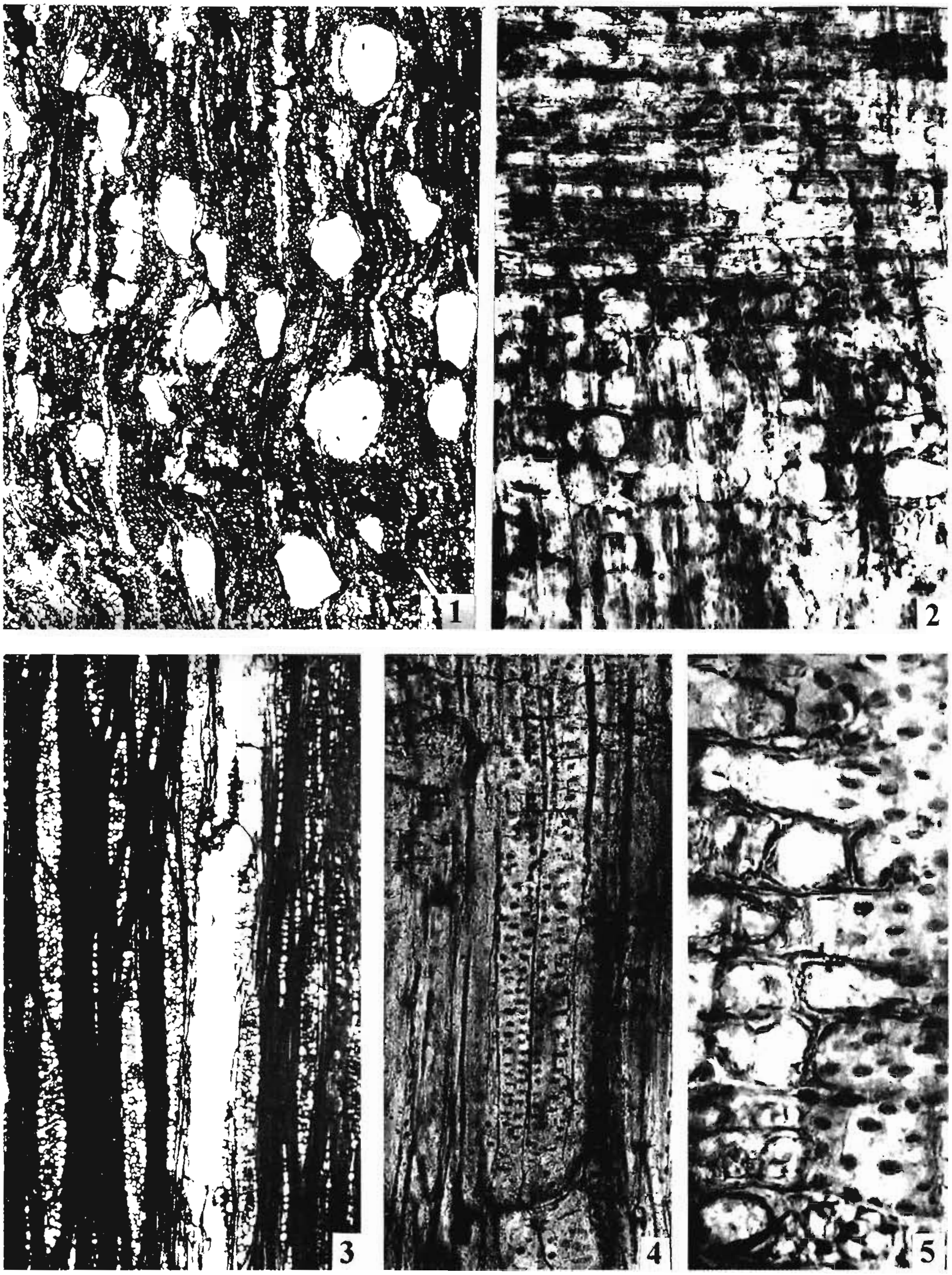

PLATE 1

Guleria, 1996; Prakash *et al.*, 1994, Prasad & Tripathi, 2000, Tiwari & Mehrotra, 2000, Bera & Banerjee, 2001, Srivastava, 2001; references of earlier literature can be seen in these publications). In addition, two fossil woods have been assigned to the natural genus *Dipterocarpus* Gaertn. These have been reported from the Middle Siwalik sediments of Hardwar in Uttar Pradesh and Darjeeling District of West Bengal (Prasad & Khare, 1994; Antal *et al.*, 1999) and compared with the extant wood of *Dipterocarpus* *specioosus* and *D. gracilis*, respectively. Out of the above referred fossil woods, the present fossil shows apparent similarity in gross structure as well as in the near absence of diffuse-in-aggregate parenchyma with *Dipterocarpoxylon pondicherriense* Awasthi, reported from the Upper Tertiary sediments of Pondicherry and Kachchh in Gujarat (Awasthi, 1974; Guleria, 1986). However, in *D. pondicherriense* frequency of gum canals is high and they are more or less regularly arranged in short to long tangential rows. On the contrary frequency of gum canals is low in the present fossil and are mostly scattered, rarely forming groups and hence, can easily be differentiated from *D. pondicherriense*. Since the present specimen differs from the known species of *Dipterocarpoxylon*, a new specific name *Dipterocarpoxylon jammuensis* sp. nov. is assigned to it.

The genus *Dipterocarpus* Gaertn. f. includes about 69 species which are mainly confined to Indo-Malaysian region with maximum development in Borneo, Malaysian Peninsula and Sumatra (Mabberley, 1997, p. 235). The genus ranges in its distribution from India in the West to Philippines in the East. In India, it is found in Assam, the Andamans and the Western Ghats (Chowdhury & Ghosh, 1958; Santapau & Henry, 1973). *Dipterocarpus kerrii* Hook.f. with which the fossil shows nearest resemblance is found in the Malaysian region.

DIPTEROCARPOXYLON KALAGARHENSIS Yadav 1989

(Pl. 2.1-5)

Material—The description is based on a well preserved secondary wood, 46 cm long and 18 cm wide.

Description—*Wood* diffuse-porous (Pl. 2.1-2). *Growth rings* not seen. *Vessels* small to large, tangential diameter 135-315 μm, radial diameter 150-405 μm, almost solitary (Pl. 2.1-2), rarely in radial multiples of two, round to oval when solitary, flattened at the place of contact when in multiples, tyloses present; 1-7 vessels per sq. mm, vessel elements 170-450 μm long with truncate or oblique end walls; perforations simple, inter-vessel pits could not be observed. *Vasicentric tracheids* present, intermingled with parenchymatous cells; forming thin sheath around vessels, frequently pitted (Pl. 2.5). *Parenchyma* abundant, both paratracheal and apotracheal (Pl. 2.1, 2); paratracheal vasicentric, intermingled with vasicentric tracheids forming 1-2 seriate sheath around the vessels; apotracheal abundant, diffuse to diffuse-in-aggregate forming uniseriate broken lines among fibres, fairly conspicuous forming 4-6 celled bands around vertical gum canals (Pl. 2.1, 2); each cell 32-40 μm in diameter and 100-128 μm in length. *Rays* 1-6 seriate, heterocellular, made up of both upright and procumbent cells, 4-7 rays per mm; uniseriate rays 1-16 cells or 145-265 μm long (Pl. 2.3), either made up of upright cells or both upright and procumbent cells; multiseriate 2-6 cells or 40-148 μm wide and 6-55 cells or 240-1,360 μm long, made up of procumbent cells in the centre and extensions of 1-10 upright cells at one or both the ends, sheath cells present on the flanks of multiseriate rays (Pl. 2.3), procumbent cells 20-28 μm in tangential height and 32-60 μm in radial length, upright cells 48-80 μm in tangential height and 24-32 μm in radial length. *Fibres* aligned in radial rows. *Gum Canals* vertical, normal, scattered, solitary or in pairs and sometimes forming tangential groups of 4-6, smaller than the vessels, enclosed by 6-8 seriate apotracheal parenchyma bands (Pl. 2.1), tangential diameter 48-80 μm, radial diameter 80-128 μm.

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow; Geological Survey of India, Jammu.

Specimen No.—BSIP 38306

Locality—Bumeal near Nagrota, Jammu & Kashmir.

Horizon—Mohargarh Formation, Middle Siwalik.

Age—Middle Pliocene.

Affinities—From the survey of modern wood slides and literature it was found that the fossil shows nearest resemblance with the wood structure of *Dipterocarpus obtusifolius* Teysm. ex Miq. (BSIP wood slide no. 2491). Among the fossil species of *Dipterocarpoxylon* already known from the Indian subcontinent, the present fossil cannot be differentiated from *D. kalagarhensis* Yadav, reported from the Lower Siwalik sediments of Kalagarh, Pauri Garhwal District, Uttaranchal (Yadav, 1989). Therefore, it is placed under the same species.

PLATE 2 →

Dipterocarpoxylon kalagarhensis Yadav 1989

1. Cross section showing shape, size and distribution of vessels, parenchyma and gum canals. × 40. Slide no. BSIP 38306-I.
2. Another cross section showing sparsely diffuse-in-aggregate parenchyma. × 40. Slide no. BSIP 38306-I.
3. Tangential longitudinal section showing uniseriate and multiseriate xylem rays, multiseriate rays with sheath cells. × 40. Slide no. BSIP 38306-II.
4. Radial longitudinal section showing heterocellular ray tissue. × 100. Slide no. BSIP 38306-III.
5. Radial longitudinal section showing vasicentric tracheids. × 400. Slide no. BSIP 38306-III.

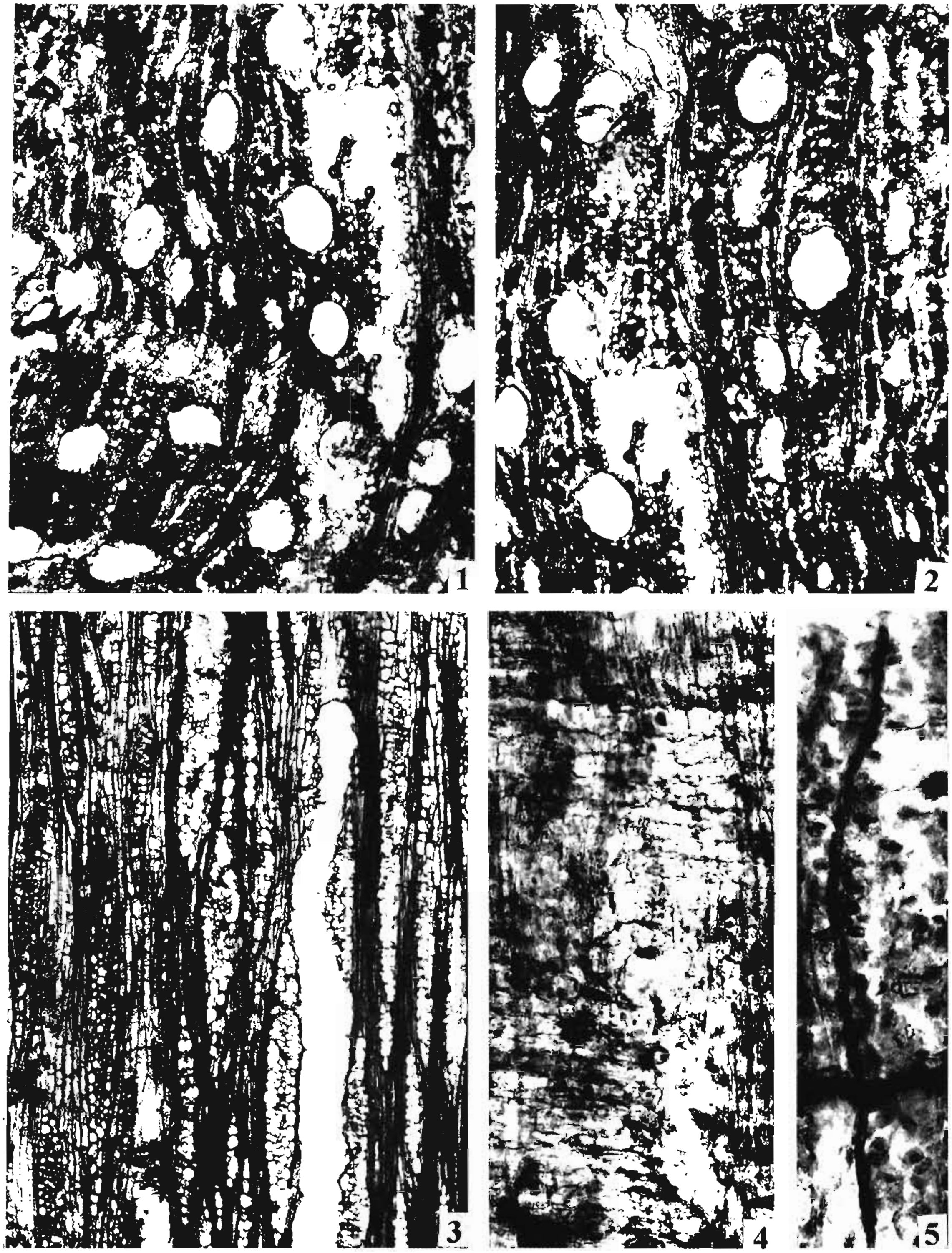

PLATE 2

The species has lately been reported from Neogene sediments of Midnapur District, West Bengal (Bera & Banerjee, 2001).

Dipterocarpus obtusifolius Teysm. ex Miq. with which the fossil shows close resemblance, is a medium to large sized tree and grows gregariously in the lower hill forests of Myanmar up to 900 m above sea level and is found further east in Thailand and Malaysian Peninsula (Chowdhury & Ghosh, 1958 p. 117).

Family—LEGUMINOSAE

Subfamily—CAESALPINIOIDEAE

Genus—CASSINIUM Prakash 1975

CASSINIUM PREFISTULAI Prakash 1975

(Pl. 3.1-5)

1974 *Peltophoroxylon parachonderianum* Kramer p. 124, pl. 28, figs 107, 108, 110-112, 114, 115, pl. 29, fig. 116, text-fig. 14 a-d

1975 *Cassinium prefistulai* Prakash p. 199, pl. 4, figs 14, 16, 17

Awasthi and Srivastava, 1992, p. 151, pl. 4, figs 1-2

1975 *Cassinium variegatum* (Ramanujam) Prakash

Peltophoroxylon variegatum (Ramanujam) Muller-Stoll & Madel 1967

Ramanujam, 1960, p. 120, pl. 22, figs 37-41, text fig. 26.

1975 *Cassinium cassioides* (Prakash & Awasthi) Prakash

Prakash and Awasthi 1970, p. 36, pl. 3, figs 15, 16, pl. 4, figs 19, 20, 21.

Prakash, Vaidyanathan and Tripathi 1974: p 129, pl. 4, figs 30-32; text fig. 9

1979 *Cassinium arcotense* Awasthi p. 159, pl. 2, figs 8, 9, pl. 3, fig. 10.

1981 *Cassinium ballavpurense* Ghosh and Roy p. 285, figs 1-7.

Material—The species is represented by a single specimen with satisfactory preservation, measuring 27 cm in length and 15.5 cm in width.

Description—*Wood* diffuse-porous (Pl. 3.1). *Growth rings* present, delimited by more or less continuous line of apotracheal parenchyma. *Vessels* small to large, tangential diameter 70-325 μm, radial diameter 65-350 μm, evenly distributed, 4-7 vessels per sq mm, usually solitary or in radial multiples of 2-6 (mostly 2-3); circular to oval when solitary and flattened at the place of contact when in radial multiples (Pl. 3.1); tyloses absent, some filled with dark contents; vessel elements 325-500 μm long with oblique to transverse end walls; perforations simple; intervessel pits alternate, hexagonal, vestured with lenticular aperture (Pl. 3.4), 8-10 μm in diameter. *Parenchyma* paratracheal, vasicentric, aliform to aliform-confluent joining adjacent vessels (Pl. 3.1, 2); each cell 35-50 μm in diameter and 60-135 μm long; crystalliferous strands present. *Rays* 1-3 (mostly 3) seriate (Pl. 3.3); 6-12 rays per mm; non storied; homocellular to weakly heterocellular (Pl. 3.4), mostly consisting of procumbent cells, sometimes end cells enlarged and crystalliferous; uniseriate rare, 8-20 cells or 170-550 μm long; procumbent cells 24-36 μm in tangential height and 48-72 μm in radial length. *Fibres* aligned in radial rows, polygonal in cross section (Pl. 3.1), semilibriform, 24-30 μm in diameter, non-septate; interfibre pits not seen.

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow; Geological Survey of India, Jammu.

Specimen No.—BSIP 38307.

Locality—Gandla near Ramnagar, Jammu & Kashmir.

Horizon—Mohargarh Formation, Middle Siwalik.

Age—Middle Pliocene.

Affinities—All the above characters indicate that the fossil wood belongs to the family Leguminosae. On comparing the fossil with a large number of leguminous genera, it was found that on the basis of parenchyma distribution (Ramesh Rao *et al.*, 1972) coupled with other characters, it shows resemblance with the extant wood of the genus *Cassia* Linn. (s.l.). A large number of thin sections of woods of *Cassia* species, viz., *C. aubrevillei* Pellegr., *C. auriculata* Linn., *C. fistula* Linn., *C. grandis* Linn., *C. javanica* Linn., *C. marginata* Roxb., *C. nodosa* Ham. ex Roxb., *C. siamea* Linn. were examined. In addition, published descriptions and photographs of *C. aubrevillei* (Normand, 1950, p. 125, pl. 36), *C. bakeriana* Bailey, *C. fistula* (Ilic, 1991, figs 2061-2062), *C. fruticosa* Willd. (Kribs, 1959, p. 70, fig. 173), *C. javanica*, *C. timoriensis* DC and *C. siamea* (Moll & Janssonius, 1914, pp. 97-108, fig. 150; Kanehira, 1924a, p. 26) were also consulted for comparison with the fossil. It was found that amongst these the fossil shows best resemblance with the woods of *C. fistula*. In both, the fossil wood and the woods of modern *C. fistula*, vessels are small to large, mostly solitary sometimes in multiples with simple perforation plates, intervessel pits vestured; parenchyma terminal apotracheal and aliform to mostly confluent, xylem rays 1-3 (mostly 3 seriate), homocellular to weakly heterocellular, rays and parenchyma cells sometimes crystalliferous, fibres non-septate and thick walled.

PLATE 3

Cassinium prefistulai Prakash 1975

1, 2. Cross sections showing shape, size and distribution of vessels and parenchyma pattern. × 40. Slide no. BSIP 38307-I.

3. Tangential longitudinal section showing 1-3 seriate xylem rays. × 100. Slide no. BSIP 38307-II.

4. Vestured intervessel pits. × 400. Slide no. BSIP 38307-I.

5. Radial longitudinal section showing weakly heterocellular rays. × 100. Slide no. BSIP 38307-III.

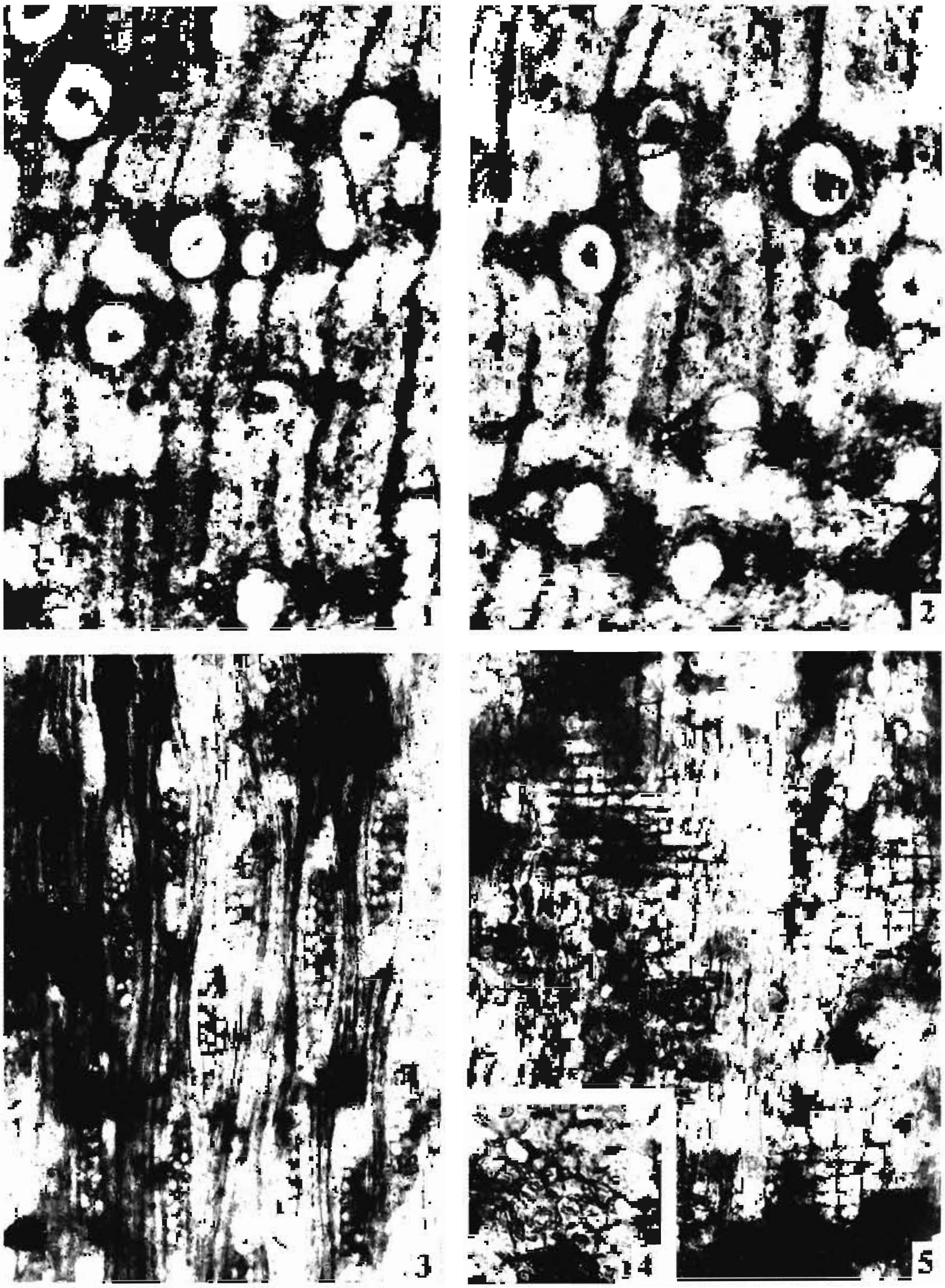

PLATE 3

Comparison and Discussion—Felix (1882) established the genus *Cassioxylon* for the fossil woods showing resemblance with the modern woods of genus *Cassia* Linn. Muller-Stoll and Mädel (1967) while working on fossil woods of Leguminosae re-examined the type slides of *Cassioxylon* and found that the fossil does not show the characters of *Cassia* woods and may not even belong to family Leguminosae. Consequently, they instituted a genus *Peltophoroxylon* to include fossil woods of *Cassia*, *Peltophorum* Vogel and *Xylia* Benth. on account of their close similarity. This genus was further amended by Prakash and Awasthi (1970) and later Prakash (1975, pp. 200-201) further circumscribed the genus *Peltophoroxylon* and instituted a new genus *Cassinium* for the fossil woods showing affinities with the modern woods of *Cassia*. Of the known *Peltophoroxylon* species he transferred four to the new genus *Cassinium* (Prakash, 1975, p. 201). Almost at the same time a fossil wood, *Peltophoroxylon parenchymatosum* showing apparent similarities with the modern woods of *Cassia siamea* was reported from the Southeast Asia by Kramer (1974, p. 124). Since it was published just before Prakash's publication of 1975 and the paper was perhaps not available to Prakash, he could not comment on this species. We take this opportunity to point out that rays in *Peltophoroxylon parenchymatosum* are relatively broad, mostly 3-4 seriate (p. 124, pl. 28, fig. 112) and parenchyma relatively less than in the modern woods of *Cassia siamea*. Woods of *C. siamea* usually possess banded parenchyma and relatively fine 1-2 (3) seriate rays. It seems *Peltophoroxylon parenchymatosum* shows better resemblance with the woods of *Cassia fistula* in the type of parenchyma (Ramesh Rao *et al.*, 1972, pl. 73, fig. 437) and in the width of rays (up to 4 cells wide) have also been observed in this species. Thus in view of close similarity of *P. parenchymatosum* with the woods of *Cassia fistula, P. parenchymatosum* has been transferred under the genus *Cassinium* Prakash, viz., C. *parenchymatosum*. Thus the authors are aware of eleven species of *Cassinium* which are listed in Fig. 5 giving their main anatomical characters. Out of these *C. borooahii* (Prakash) Prakash, *C. ethiopicum* Prakash *et al.*, *C. tripuranum* Acharya and Roy and *C. dongolenese* Giraud and Lejal-Nicol possess banded parenchyma and hence can easily be differentiated from the present specimen. Likewise *C. cassinodosum* Prakash, differs from the present fossil in having relatively narrow rays 1-2 (mostly 2 seriate), bigger vessels (144-400 μm) and septate fibres. The present fossil resembles the remaining six species of *Cassinium*, though it may differ from them in some minor and variable characters. Since the present specimen shows close resemblance with *Cassinium cassioides* (Prakash & Awasthi) Prakash, *C. prefistulai* Prakash, *C. ballavpurense* Ghosh and Roy, *C. variegatum* (Ramanujam) Prakash, *C. arcotense* Awasthi and *C. parenchymatosum* (op. cit.), it forced the authors to re-evaluate the authenticity of these species as they have been instituted on overlapping and variable nature of characters. It is worth noting that inspite of exhibiting minor and variable anatomical differences from each other, the first three species have been compared with the woods of a single extant species, viz., *Cassia fistula*, the fourth, *C. variegatum* (Ramanujam) Prakash has not been compared with the woods of any modern *Cassia* species. Since anatomical features of *C. variegatum* and *C. parenchymatosum* fall within the range of characters observed in the extant woods of *Cassia fistula*, their affinities can easily be assigned to *Cassia fistula*. In 1979, Awasthi instituted a new species *Cassinium arcotense* on the assumption that it shows resemblance with the woods of *Cassia javanica*. However, all the characters of this species can also be seen in the woods of *Cassia fistula*. Awasthi did not mention a single point as to how *C. arcotense* differs from the woods of *Cassia fistula*. The wood characters of *Cassia javanica* and *C. fistula* overlap when a large number of samples were examined and it is difficult to distinguish the two on the basis of anatomical features alone. Prakash *et al.* (1994) while describing *C. cassioides* from the Miocene sediments of Assam have also opined that *C. cassioides* and *C. prefistulai* should be considered as one species although they did not actually merge the two species. Surprisingly they did not mention in their publication about three species of *Cassinium*, namely, *C. ballavpurense, C. tripuranum* and *C. ethiopicum,* specially when the last species was established by Prakash himself in association with Awasthi and Lemoigne. Thus in view of the very close structural similarities in the above referred six species (differences exhibited being of variable nature), it has been considered to merge the following five species, viz., *Cassinium cassioides* (Prakash & Awasthi) Prakash (1975); *C. ballavpurese* Ghosh and Roy (1981); *C. variegatum* (Ramanujam) Prakash (1975); *C. arcotense* Awasthi (1979) and *C. parenchymatosum* (op. cit.) under the type species *C. prefistulai* Prakash (1975). As the present wood specimen also

PLATE 4 →

Kingiodendron prepinnatum Awasthi & Prakash 1987

1. Cross section showing shape, size and distribution of vessels, parenchyma and gum canals. x 40. Slide no. BSIP 38308-I.
2. Tangential longitudinal section enlarged showing mostly 1-3 seriate xylem rays. x 100. Slide no. BSIP 38308-II.
3. Radial longitudinal section showing weakly heterocellular xylem rays. x 100. Slide no BSIP 38308-III.
4. Tangential longitudinal section showing distribution of xylem rays. x40. Slide no. BSIP 38308-II.
5. Vestured intervessel pits. x 400. Slide no. BSIP 38308-II.

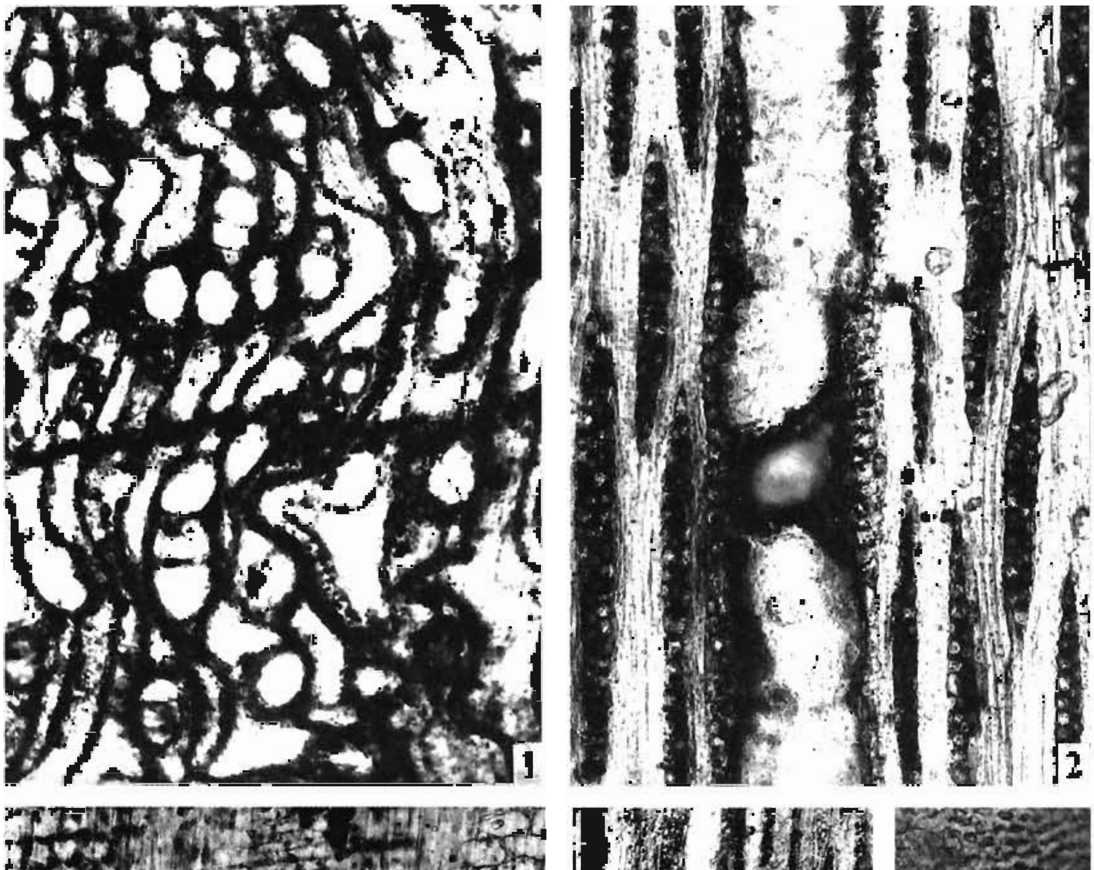

PLATE 4

Name	Vessels	Parenchyma	Rays	Fibres	Modern Comparable Forms	Locality & Age
* *Cassinium varigatum* (Ramanujam, 1960) Prakash 1975	Medium-large, diameter 185-310 µm; solitary and in radial multiples of 2-4.	Terminal and paratracheal confluent bands.	1-3 seriate; homocellular to weakly heterocellular.	Septate.	*Cassia*	Muratandichavadi, South Arcot District; Cuddalore Formation; Miocene-Pliocene.
Cassinium borooahi (Prakash, 1966) Prakash 1975, 1978; Bande & Prakash, 1980; Mehrotra *et al.* 1999; Bera & Banerjee 2001	Medium-large, t.d. 106-380 µm; mostly solitary, sometimes in radial multiples of 2-4; tyloses present.	Paratracheal, banded, aliform confluent bands alternating with fibrous bands.	1-3 seriate, uniseriate rare, homocellular, made up of procumbent cells; 10-30 cells long.	Non-septate; thick walled.	*C. siamea* Lam.	Dimapur-Diphu Road, Assam; Tipam Sandstone; Middle Miocene; Santiniketan, Bolpur District and Uttar Raipur, Birbhum District of West Bengal, Upper Miocene; Subansiri District, Arunachal Pradesh, Late Mio-Pliocene.
* *Cassinium cassioides* (Prakash & Awasthi, 1970) Prakash 1975	Small-large, t.d. 96-240 µm, r.d. 112-320 µm; solitary and in multiples of 2-6 (mostly 2-3); 4-12 per sq mm; tyloses absent.	Paratracheal, mostly aliform to confluent joining many vessels; terminal parenchyma not seen.	1-3 (mostly 2-3) seriate, homocellular consisting of procumbent cells only; 4-24 cells long.	Non-septate; thick walled.	*C. fistula* Linn.	Bhuri-Dehing River bed, near Jaipur, Assam; Tipam Sandstones; Middle Miocene.
Cassinium cassinodosum (Prakash, 1973) Prakash 1975	Medium-large, t.d. 144-400 µm, r.d. 160-416 µm; solitary and in multiples of 2-3 (rarely 6); 2-4 per sq mm, tyloses absent.	Terminal parenchyma appears to be present; paratracheal aliform to confluent forming irregular bands joining many vessels.	1-2 (mostly 2) seriate; homocellular made up of procumbent cells only; 7-34 cells long.	Septate; thick walled.	*C. nodosa* Ham.	Myanmar; Tertiary.
* *Cassinium parenchymatosum* (Kramer, 1974) Guleria *et al.*	Small-large, t.d. 70-300 µm, rd. 70-400 µm; solitary and in radial multiples of 2-3(4); 2-4 per sq mm; mostly empty, tyloses absent.	Terminal parenchyma present; paratracheal aliform to mostly confluent forming undulating bands joining adjacent vessels.	1-4 (mostly 3-4) seriate, homocellular or weakly heterocellular composed mainly of procumbent cells; 15-22 cells or 350-500 µm long; 5 per mm.	Non-spetate; thick walled.	*C. fistula* Linn. and *C. siamea* Lam	South Sumatra and West Java, Indonesia; Tertiary.
Cassinium prefistulai Prakash 1975; Awasthi & Srivastava 1992	Small-large, t.d. 40-240 µm, r.d. 60-300 µm; mostly solitary, sometimes in radial multiples of 2-3; 3-7 per sq	Terminal parenchyma present; paratracheal aliform to mostly confluent forming	1-4 seriate, homocellular or weakly heterocellular	Non-spetate; thick walled.	*C. fistula* Linn.	Khokhra near Nalagarh, Himachal Pradesh and Kalagarh, Uttranchal; Lower Siwalik Series; Middle Miocene;

	mm; mostly empty, sometimes plugged with black-brown deposits.	undulating broad bands joining adjacent vessels.	composed mainly of procumbent cells.			Paddappakara, Kollam District, Kerala; Warkalli Formation; Miocene.
* *Cassinium arcotense* Awasthi 1979	Small-large, t.d. 60-280 μm, r.d. 40-280 μm; solitary and in multiples of 2-4; 4-6 per sq mm; tyloses absent.	Terminal parenchyma present; paratracheal mostly aliform, sometimes confluent.	1-4 (mostly 2-4) seriate, homocelluler, wholly of procumbent cells; upto 25 cells long.	Probably septate; thick walled.	*C. javanica* Linn.	Muratandichavadi near Pondicherry; Cuddalore Series; Miocene-Pliocene.
* *Cassinium ballavpurense* Ghosh & Roy 1981	Small-large, t.d. 160-280 μm, r.d. 200-480 μm; solitary and in radial multiples of 2-5; 3-6 per sq mm.	Paratracheal, aliform-confluent forming undulating bands joining adjacent vessels.	1-4 (mostly 2-3) seriate; homocellular, 15-30 cells long.	Septate; thick walled.	*C. fistula* Linn. & *C. nodosa* Ham.	Ballavpur near Bolpur, Birbhum District., West Bengal; Upper Miocene.
Cassinium ethiopicum Prakash *et al.* 1982	Small-medium, t.d. 30-160 μm, r.d. 25-155 μm; solitary and in multiples of 2-5 (mostly 2-3); 15-30 per sq mm.	Paratracheal banded, bands irregular and wavy, seldom bifurcating.	1-4 seriate; homocellular, 4-27 cells long; 7-12 per mm.	Non-septate; semilibri form, thick walled.	*C. aubrevillei* Pellegr.	Blue Nile Valley, Ethiopia; Mio-Pliocene.
Cassinium tripuranum Acharya & Roy 1986	Medium-large, t.d. 140-268 μm; solitary and in radial multiples of 2-4; 4-8 per sq mm; tyloses absent.	Paratracheal confluent band, wholly or partially encircling vessels; bands 4-10 cells wide.	1-3 (mostly 2) seriate, weakly heterocellular with 1-2 upright cells at the ends, 15-25 cells long.	Non-septate.	*Cassia*	Khowai, Teliamura, Tripura; ? Tipam Sandstone; Upper Miocene.
Cassinium dongolense Giraud & Lejal-Nicol 1989	Medium-large, t.d. 169-206 μm, r.d. 206-356 μm; mostly solitary, rarely in radial multiples of 2-4; 2-6 per sq mm; tyloses present.	Paratracheal forming 3-7(12) cells thick bands.	1-3 (mostly 2) seriate; homocellular; 1-30 cells long.	Non-septate, 18-32 μm in diameter.	*C. siamea* Linn.	Wadi Howar Formation; Northern Sudan; Upper Cretaceous ? or Tertiary.
Present specimen	Small-large, t.d. 70-325 μm, r.d. 65-350 μm; solitary and in radial multiples of 2-3 (rarely 6); 4-7 per sq mm.	Paratracheal, aliform to aliform confluent joining adjacent vessels.	1-3 (mostly 3) seriate, homocellular, 8-20 cells or 170-550 μm long.	Non-septate; semi-libriform.	*C. fistula* Linn.	Ramnagar, Jammu & Kashmir; Middle Siwalik; Upper Miocene.

The age of *C. dongolense* has been mentioned as Upper Cretaceous as well as Cretaceous (?) or Tertiary (Giraud & Lejal-Nicol, 1989, pp. 39, 49). It seems the exact provenance of the fossil is not known. The advanced wood structure of the fossil and our experience on fossil woods says that the age of the species cannot be Cretaceous, it may most probably be Upper Tertiary.
Species marked with * have now been merged under *Cassinium prefistulai*.

Fig. 5—List of *Cassinium* species with their anatomical features and other details.

has characters identical to *C. prefistula* Prakash, it is being placed under the same species. Thus with the merger of the above five species under *C. prefistula* at present there are a total of six valid species of *Cassinium*.

The genus *Cassia* was widespread in India during the Late Tertiary. In the fossil form it is represented by its wood and leaf remains. Its leaf remains have been reported from Bihar, Gujarat, Himachal Pradesh and Uttaranchal (Awasthi & Lakhanpal, 1990; Guleria *et al.*, 2000) and woods have been reported from Himachal Pradesh, Arunachal Pradesh, Uttaranchal, Assam, Tripura, West Bengal, Tamil Nadu and Kerala (see Fig. 5).

Cassia Linn. (*sensu lato*) is a large genus of over 500 species of herbs, shrubs and trees. It is pantropical in distribution. The genus occurs in both the eastern and western hemisphere excluding Europe (Record & Hess, 1943; Willis, 1973). *Cassia fistula* Linn. with which the present fossil shows close resemblance is found throughout the forests of India, Myanmar and Sri Lanka. It is one of the most widespread of the Indian trees ascending up to 1,200 m in the Himalayas and extending further north-west to the hills of Peshawar (Gamble, 1902, p. 308; Ramesh Rao *et al.*, 1972, p. 42).

Genus—KINGIODENDRON Harms

KINGIODENDRON PREPINNATUM Awasthi and Prakash 1987

(Pl. 4.1-5)

Material—The species is represented by a well preserved piece of secondary wood measuring 27 cm in length and 13 cm in width.

Description—*Wood* diffuse-porous (Pl. 4.1). *Growth rings* present, demarcated by narrow 2-3 cells thick parenchyma lines (Pl. 4.1). *Vessels* small to large, mostly medium sized, tangential diameter 80-220 µm, radial diameter 80-340 µm, solitary as well as in radial multiples of 2-3, evenly distributed, 5-8 per sq mm, circular to oval when solitary, with flat contact walls when in multiples, tyloses absent (Pl. 4.1), vessels occasionally filled with dark contents; vessel elements 350-500 µm long with oblique or transverse end walls; perforations simple; inter-vessel pits small, alternate, vestured, 6-8 µm in diameter (Pl. 4.5). *Parenchyma* both paratracheal and apotracheal; paratracheal mostly vasicentric, occasionally aliform to confluent joining adjacent vessels; apotracheal forming 2-3 cell thick terminal lines at growth rings, also encircling gum canals (Pl. 4.1); each cell 25-38 µm in diameter and 32-120 µm long, vessel parenchyma pits larger than intervessel pits, alternate, vestured. *Rays* 1-4 (mostly 2-3) seriate (Pl. 4.2, 4); 6-9 rays per mm, fused rays present, ray tissue heterocellular (Pl. 4.3), uniseriate rays less frequent, made up of upright cells; 4-13 cells or 100-375 µm long, crystals present in ray cells (Pl. 4.5), multiseriate rays made up of procumbent cells in the central portions with few upright cells at the margins (Pl. 4.3), 7-35 cells or 100-980 µm long, procumbent cells 25-30 µm in tangential height and 62-120 µm in radial length, upright cells 60-100 µm in tangential height and 50-75 µm in radial length. *Fibres* aligned in radial rows, moderately thick walled, polygonal in cross-section, 25-30 µm in diameter, nonseptate. *Gum canals* normal, vertical, circular to oval, scattered, aligned tangentially in small groups of 4-8, enclosed by parenchyma cells, almost similar to vessel size (Pl. 4.1).

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow; Geological Survey of India, Jammu.

Specimen No.—BSIP 38308.

Locality—Gandla near Ramnagar, Jammu & Kashmir.

Horizon—Mohargarh Formation, Middle Siwalik.

Age—Middle Pliocene.

Affinities—The most important features of the present fossil wood are, growth rings present, demarcated by thin layer of apotracheal parenchyma, vessels small to large (mostly medium), solitary or in radial multiples of 2-3, intervessel pits vestured; paratracheal parenchyma mostly vasicentric, occasionally aliform, rarely confluent; xylem rays 1-4 (mostly 2-3) seriate, sometimes fusiform, weakly heterocellular, fibres non-libriform, non-septate; gum canals normal, vertical, scattered in small tangential groups, almost of vessel size, surrounded by apotracheal parenchymatous sheath. The combination of these characters is found in leguminous woods. Occurrence of vertical gum canals, which is one of the distinguishing characters of the fossil, has been reported in the secondary woods of a number of leguminous genera, such as *Copaifera* Linn., *Daniellia* Benn., *Detarium* Juss., *Eperua* Aubl., *Gossweilerodendron* Harms, *Kingiodendron* Harms, *Oxystigma* Harms, *Prioria* Griseb., *Pterygopodium* Harms and *Sindora* Miq. Besides, wood of *Crudia* Aubrev and Pellegr. of Simaroubaceae also show apparent similarity with the present fossil (Normand, 1988, pp. 51-55, Pl. LXXVI). However, scanty paratracheal parenchyma, non-vestured —>

PLATE 5

Kingiodendron prepinnatum Awasthi 1987

1. Cross section showing size, shape and distribution of vessels and parenchyma. × 40. Slide no. BSIP 38309-I.
2. Tangential longitudinal section showing xylem rays and vessel segments filled with tyloses. × 40. Slide no. BSIP 38309-II.
3. Tangential longitudinal section enlarged showing fibres as well as broad xylem rays and septate fibres. × 100. Slide no. BSIP 38309-I.
4. Radial longitudinal section showing heterocellular xylem rays. × 100. Slide no. BSIP 38309-III.
5. Magnified radial longitudinal section showing prismatic crystals in xylem ray cells. × 200. Slide no. BSIP 38309-III.

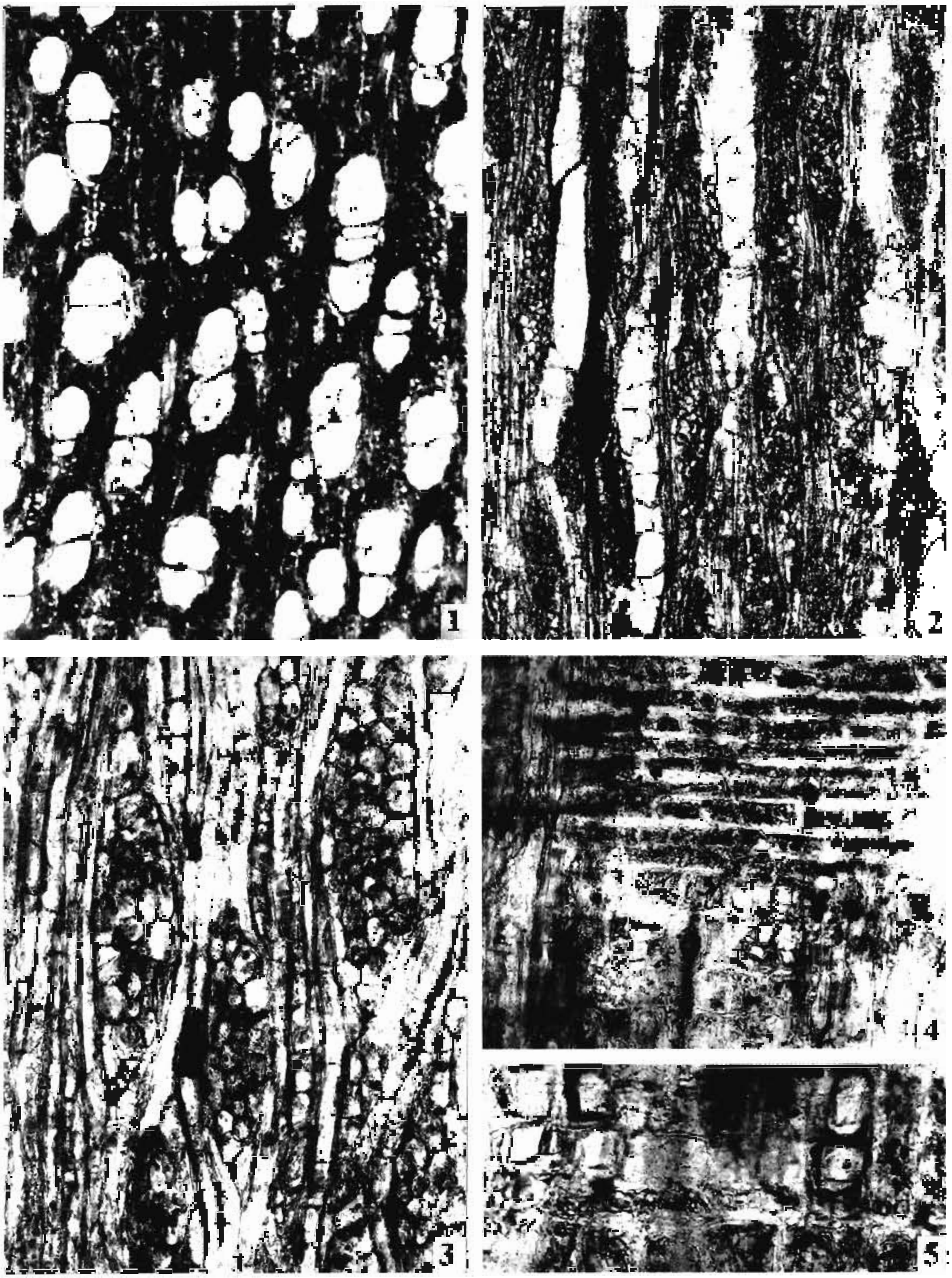

PLATE 5

intervessel pits and taller rays easily differentiate *Gymnostemon* from the present fossil. Among the above mentioned leguminous genera, *Copaifera, Detarium, Eperua,* and *Sindora* and the genus *Gymnostemon* of Simarubaceae, gum canals are found in concentric rows while in the remaining seven genera they are solitary or in pairs or sometimes in short tangential groups. Since the gum canals in the present fossil are scattered and in short tangential groups, it is comparable with the latter six genera, viz., *Daniellia, Gossweilerodendron, Kingiodendron, Oxystigma, Prioria* and *Pterygopodium*. The storied nature of xylem rays, parenchyma and vessel-members in *Daniellia* (Normand, 1950, p. 109, 113, pl. 41; Henderson, 1953, figs 193-194, 201; Kribs, 1959, pp. 77-78, fig. 190) easily separates it from the present fossil. *Gossweilerodendron* differs in having plenty of difffuse-in-aggregate parenchyma forming lines along with homocellular rays (Kribs, 1959, pp. 81-82, fig. 196; Miles, 1978, p. 104; Ilic, 1991, p. 274, fig. 2097). *Oxystigma* and *Pterygopodium* differ in having higher frequency of uniseriate rays and relatively wider gum canals (Kribs, 1959, pp. 90-91, figs 415-416), *Pterygopodium* further differs from the present fossil in having abundant aliform-confluent parenchyma (Kribs, 1959, fig. 416; Miles, 1978, p. 114). Similarly *Prioria* differs from the present fossil in having bigger gum canals (not in tangential groups as in the fossil) and tall rays comprising 30-60 cells (Kribs, 1959, pp. 95-96, fig. 219; Miles, 1978, p. 117). The fossil shows close resembles in its anatomical features with the modern woods of *Hardwickia* Roxb. and *Kingiodendron* Harms (Ramesh Rao *et al.*, 1972, pp. 6-7, 79-82; Ilic, 1991, p. 277, fig. 2109). However, the absence of gum ducts in *Hardwickia* easily differentiates it from the fossil. On examining the slides of modern wood and surveying available literature it was found that the fossil shows best resemblance with the wood of *Kingiodendron* which is characterized by the presence of gum ducts, particularly with *K. pinnatum* (Roxb). Harms (syn. *Hardwickia pinnata* Roxb.) (BSIP wood slide no. 233).

Comparison and Discussion—The authors are aware of only one record of fossil wood of *Kingiodendron*, namely *Kingiodendron prepinnatum* reported by Awasthi and Prakash (1987) from the Mio-Pliocene sediments of Deomali in Arunachal Pradesh, northeast India showing resemblance with the modern woods of *Kingiodendron pinnatum* (Roxb.) Harms. Since affinities of the present fossil wood have been traced to the modern woods of *K. pinnatum* and it also shows resemblance with the only known fossil wood species of *Kingiodendron*, it has been placed under the known species, *Kingiodendron prepinnatum* Awasthi and Prakash (1987).

The genus *Kingiodendron* consists of six species, confined to India, Philippines, Solomon and Fiji islands (Willis, 1973, p. 616; Mabberley, 1997, p. 379). It is represented in India by a single species viz., *Kingiodendron pinnatum* (Roxb.) Harms. It is a large tree occurring in the evergreen forests of Western Ghats from South Kanara to Kerala and Tirunelveli (Ramesh Rao *et al.*, 1972, p. 81) mostly in association with *Vateria indica, Artocarpus hirsutus, Dysoxylum malabaricum, Dipterocarpus indicus, Filicium decipiens, Bischofia javanica, Toona ciliata, Elaeocarpus* sp. and *Hopea parviflora* (Champion & Seth, 1968, pp. 68-69). The occurrence of fossil woods of *Kingiodendron pinnatum* in the northeast as well as in the northwest corners of the country indicate that unlike its present restricted distribution to Western Ghats it was wide-spread in the north during Mio-Pliocene time.

Family—EUPHORBIACEAE

Subfamily—PHYLLANTHOIDEAE

Genus—BISCHOFIA Blume

BISCHOFIA PALAEOJAVANICA Awasthi 1989

(Pl. 5.1-5)

Material—The species is represented by single piece of well preserved secondary wood measuring 30.5 cm in length and 18 cm in width.

Description—*Wood* diffuse-porous. *Growth rings* not seen. *Vessels* small to large, mostly medium sized, tangential diameter 50-220 μm and radial diameter 68-260 μm (Pl. 5.1); solitary and in radial multiples of 2-3; mostly filled with tyloses and some kind of gummy deposits; vessel members 250-550 μm long with truncate or oblique end walls; perforations simple; inter-vessel pits alternate, bordered, hexagonal with lenticular aperture, 10-12 μm in diameter. *Parenchyma* scanty paratracheal, few cells associated with some of the vessels (Pl. 5.1); each cell 30-50 μm in diameter and 80-136 μm long, disjunctive parenchyma present. *Rays* 1-6 seriate (Pl. 5.2, 3), 5-8 per mm; uniseriate rare, 3-8 cells or 170-400 μm long, consists wholly of upright cells; multiseriate rays heterocellular, 2-6 cells or 60-180 μm broad and 8-32 cells or 240-1,275 μm long; made up of procumbent cells in the centre with extensions of 1-9 upright cells at one or both the ends; end to end ray fusion present; sheath cells present on lateral margins; procumbent cells 60-76 μm in tangential height and 100-120 μm in radial length; upright cells 120-156 μm in tangential height and 48-60 μm in radial length; vessel-ray pits many per cell; prismatic crystals present in upright cells (Pl. 5.4, 5). *Fibres* aligned in radial rows; mostly oval to flattered and polygonal (Pl. 5.1), libriform and tracheid like, thick walled, 48-60 μm in diameter in cross section, frequently septate (Pl. 5.3), interfibre pits present.

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow; Geological Survey of India, Jammu.

Specimen No.—BSIP 38309.

Locality—Gandla near Ramnagar, Jammu & Kashmir.

Horizon—Mohargarh Formation, Middle Siwalik.

Age—Middle Pliocene.

Affinities—The important anatomical characters exhibited by the fossil wood are : wood diffuse-porous; growth rings absent; vessels solitary or in multiples of 2-3, medium to large, filled with abundant tyloses, perforations simple; scanty paratracheal perenchyma; rays 1-6 seriate, heterocellular; fibres thick walled, septate, sometimes tracheid like. The combination of these characters indicate that the fossil belongs to the *Glochidion* group of sub-family Phyllanthoideae (Metcalfe & Chalk, 1950) of the family Euphorbiaceae. Among the genera in the *Glochidion* group, the fossil shows best resemblance with the woods of modern genus *Bischofia* Bl. particularly with *Bischofia javanica* Bl. (Pearson & Brown, 1932; Desch, 1957; Ilic, 1991). The genus *Bischofia* is included in the sub-family Phyllanthoideae (Tribe Bischofieae) of the family Euphorbiaceae (Mabberley, 1997 p. 273). In 1960, Ramanujam created the genus *Bischofioxylon,* for a fossil wood resembling *Bischofia,* from near Pondicherry, South India. Mädel (1962) working on euphorbiaceous woods opined that *Bischofioxylon miocenicum* Ramanujam (1960) did not belong to *Bischofia,* instead it showed resemblance with *Bridelia* woods. Accordingly she transferred it to the genus *Bridelioxylon* Ramanujam (1956). Subsequently Bande in 1974 instituted a new genus *Bischofinium* gen. nov. for the fossil woods resembling the modern woods of *Bischofia* Bl. Awasthi (1989, p. 150) critically examined the type slides of both *Bischofioxylon miocenicum* Ramanujam and *Bischofinium deccanii* Bande while describing a fossil wood of *Bischofia* from the Miocene-Pliocene sediments of Arunachal Pradesh, India. He concluded that the exact affinities of these two woods need to be ascertained and that the former belongs neither to *Bischofia* nor to *Bridelia* and the latter also differs from *Bischofia.* He described his fossil wood as a new species of *Bischofia* viz., *Bischofia palaeojavanica* sp. nov. on account of its close similarity with the modern woods of *Bischofia javanica* Bl. (Awasthi, 1989, pp.147-150). This species has since been reported from the Neyveli lignite deposits (Miocene) of Tamil Nadu (Agarwal, 1994, pp. 335-336); Late Miocene sediments of Mon District, Nagaland (Awasthi & Mehrotra, 1990, p. 283), Middle Miocene deposits of Thiruvananthapuram District, Kerala (Srivastava & Awasthi, 1996, p. 96) and Deccan Intertrappean sediments of Kachchh, Gujarat (Guleria & Srivastava, 2001, p. 23). The authors are aware of two more records of fossil woods of *Bischofia,* viz., *Bischofia javanica* Bl. and *B. polycarpa* Airy-Shaw, both reported from the Late Tertiary rocks of Wuhan, Xinzhou County, Hubei Province of China (Qi Guo-fan *et al.*, 1987, pp. 309-313; Yang Jia-ju *et al.*, 1998, pp. 68-76). Of the three fossil woods, *Bischofia polycarpa* can easily be differentiated from the present fossil in having smaller vessels (t.d. 45-78 μm). *Bischofia javanica* shows apparent similarity with the present fossil, nevertheless, it differs in having greater frequency of vessels in radial chains and the vessels without tyloses. It is pointed out that the number of radial multiples of vessels seen in accompanied photographs (Qi Guo-fan *et al.*, 1987, pl. 1, figs 1, 2) is not similar to the wood of *Bischofia javanica* (see Pearson & Brown, 1932, fig. 275; Kanehira, 1924a, b; Lecomte, 1926). The present fossil shows closest resemblance to *Bischofia palaeojavanica* Awasthi (1989) and hence placed in the same species.

The genus *Bischofia* consists of two extant species, viz., *B. javanica* Bl. and *B. polycarpa* Airy Shaw. The former is a tall straight deciduous tree and is mainly confined to Indo-Malaysian region whereas the latter is found in central and south-east China (Willis, 1973, p. 141; Mabberley, 1997, p. 88). In India it occurs in Lower Himalayas up to 1335 m and sub-Himalayan tract from Yamuna River eastward through Uttar Pradesh, Bihar, Assam, Orissa, Tinnevelly and Madurai; Konkan to Nilgiris and also in Andaman Islands (Pearson & Brown, 1932, p. 881; Santapau & Henry, 1973, p. 23). It is apparent from the fossil evidence that like its present day distribution the genus was also wide spread in India during the past.

GENERAL DISCUSSION

The occurrence of *Dipterocarpus* Gaertn.f. and *Kingiodendron* (Roxb.) Harms, in the Middle Siwalik sediments as far west as Jammu region is highly significant in view of their present distribution and climatic requirements. Both the genera are mainly confined to tropical evergreen forests of the Indo-Malaysian region, with their westward limit in India. As far as their distribution in India is concerned, *Dipterocarpus* is found in the Assam, Andamans and Western Ghats and *Kingiodendron* is confined to Western Ghats, South Kanara southwards to Travancore and Tinnevelly (Brandis, 1906; Chowdhury & Ghosh, 1958; Ramesh Rao *et al.*, 1972). Likewise *Bischofia* Blume, a large to very large tree, occurs in sub-Himalayan forests and outer hills up to 1,335 m from Yamuna eastwards to Assam, Orissa, Tinnevelly and Andaman Islands and on the western coast from the Konkan to Nilgiris. It is found scattered and is a characteristic tree of shady ravines, swamps, river banks and also grows in valleys (Gamble, 1902; Pearson & Brown, 1932). Thus its occurrence west of the Yamuna River during the past is significant. *Dipterocarpus* and *Kingiodendron* are typical canopy trees and form the top storey of evergreen to semi-evergreen forests of India. They form a natural association with *Bischofia javanica* and *Artocarpus* in low elevation, evergreen to semi-evergreen forests (Champion & Seth, 1968, pp. 60, 68-69, 87). *Cassia* Linn. is a widespread genus in India and is found in moist deciduous to dry forests. Its occurrence indicates that the area had started experiencing dry climate and the overall assemblage probably represents dwindling components of the semi-evergreen forest. Nevertheless, the fossil records of *Dipterocarpus* species, *Kingiodendron pinnatum* and *Bischofia javanica* indicate the existence of fairly thick vegetation with warm and humid conditions in the Jammu region during the Middle Siwalik time. Based on more or less similar modern analogue as given by Champion and Seth (1968, pp. 87, 89-90), the envisaged mean annual rainfall most probably may have been about 2,000 mm or more and temperature 24° to 25°C in contrast to the present day average annual rainfall of 1,115 mm and average maximum and minimum temperature range of 39°C to 6.8° C (Sharma & Kachroo, 1981). As a result of limited rainfall the area at present is covered by tropical mixed dry deciduous forest. Thus the higher precipitation at the time of fossilization must have supported the occurrence of the above mentioned genera. Their disappearance from the area signifies drastic change in climate. Evidently with the change in climatic conditions from moist to dry during post-Pliocene time, the moisture loving elements like *Dipterocarpus, Kingiodendron* and *Bischofia* died out in the area and only *Cassia* could survive due to its greater adaptability towards drier conditions. It is important to mention that *Dipterocarpus* was a wide spread genus in India during Neogene (Awasthi, 1996; Guleria, 1996). *Dipterocarpus* and *Kingiodendron* are typical Indo-Malaysian genera and have not been reported from the pre-Neogene sediments of India. It seems they entered into India through north-east sometimes in Late Oligocene-Early Miocene when the land connections between India, Myanmar and Malaysia were well established and the Tethys Sea in the Himalayan Fore-deep had completely vanished (Smith *et al.*, 1994, p. 27, map 4). The gradual increase in aridity during post-Pliocene made the environment hostile for the growth of moisture loving plants. The cumulative effect of various factors such as final phase of Himalayan uplift, onset of glaciation, change in drainage patterns of rivers, shift in the course of monsoon currents, etc. perhaps led to change in climatic conditions from warm and humid to dry and cool which adversely affected the past vegetation of this region. Thus the dicotyledonous woods have furnished dependable evidence of existence of favourable climatic conditions with higher precipitation and the occurrence of mixed tropical forest comprising moist deciduous to evergreen elements of C_3 types of plants with swampy and marshy sites in the Jammu region during the Upper Tertiary.

Based on lithology and faunal evidences similar climatic conditions during the Middle Siwalik have been deduced by Badgley and Behremeyer (1980), Gaur and Chopra (1983) and Retallack (1985). Yokoyama *et al.* (1987) have also inferred warm and humid climate in the Jammu region at the time of deposition of Paramandal Sandstone Formation which is now considered equivalent to Mohargarh Formation. However, in view of the available faunal and floral (both mega and microfossils) evidences it can be said that the area was covered by woodland to savanna type of vegetation. The absence of gymnospermous megafossils and lack of distinct upland components in the fossil wood assemblage indicate that the area was occupied by lowland tropical forest. It is apparent from the above plant fossil records that there was no sudden or marked changes in the vegetation from C_3 to C_4 types up to the Late Middle Siwalik in the area and the changes must have been gradual with the progressive increase in desiccation.

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Palynological expression about Permian-Triassic transition in the Talcher Coalfield, Orissa, India

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ABSTRACT

Tripathi A 2001. Palynological expression about Permian-Triassic transition in the Talcher Coalfield, Orissa, India. Palaeobotanist 50(2 & 3) : 247-253.

A Permian-Triassic palynofloral transition is recorded in Borehole TP-8, Talcher Coalfield, Orissa, India. The change of palynoflora from Late Permian to Early Triassic is gradual and not abrupt. The variation in the pattern of changeover of the palynomorph distribution at P/Tr transition in Talcher Coalfield, Mahanadi Basin and Raniganj Coalfield, Damodar Basin is discussed.

Key-words—Palynology, Permian-Triassic transition, Talcher Coalfield, Orissa.

भारत के उड़ीसा प्रान्त के तालचेर कोयला क्षेत्र में परमियन-ट्रायसिक संक्रमण का परागाणविक विवेचन

अर्चना त्रिपाठी

सारांश

भारत के उड़ीसा प्रान्त के तालचेर कोयला क्षेत्र के वेध छिद्र टी.पी.-8 में एक परमियन-ट्रायसिक परागाणुवनस्पतिजातीय अनुक्रम अंकित किया गया है। अन्तिम परमियन से प्रारंभिक ट्रायसिक के मध्य परागाणुवनस्पतिजात में परिवर्तन शनैः - शनैः है तथा यह आकस्मिक नहीं है। प्रस्तुत शोध पत्र में तालचेर कोयला क्षेत्र, महानदी द्रोणी तथा रानीगंज कोयला क्षेत्र, दामोदर द्रोणी में पी./टी. संक्रमण पर परागाणु रूप वितरण के परिवर्तन विन्यास में वैविध्य की चर्चा की गयी है।

संकेत शब्द—परागाणुविज्ञान, परमियन-ट्रायसिक संक्रमण, तालचेर कोयला क्षेत्र, उड़ीसा.

INTRODUCTION

EARLIER palynological analyses of sediments in the Talcher Coalfield have shown the presence of equivalent Late Permian palynofloras (Tiwari *et al.*, 1991; Tripathi, 1996a; Tripathi & Bhattacharyya, 2001). The palynodata corroborate the observation made by Subramanium (1959-1960) of the presence of Upper Permian strata in the Talcher Coalfield on the basis of plant megafossils. The recovery of Early Triassic palynoassemblages in the sediments of Borehole TP-8, Chendipada (Tripathi, 1996a, Fig. 1) overlying the Late Permian palynoassemblage bearing levels prompted the present analysis of the Permian-Triassic boundary in the Talcher Coalfield. Thus the data from closely spaced borecore samples were analysed critically to delineate, if possible, the Permian-Triassic boundary, in this coalfield.

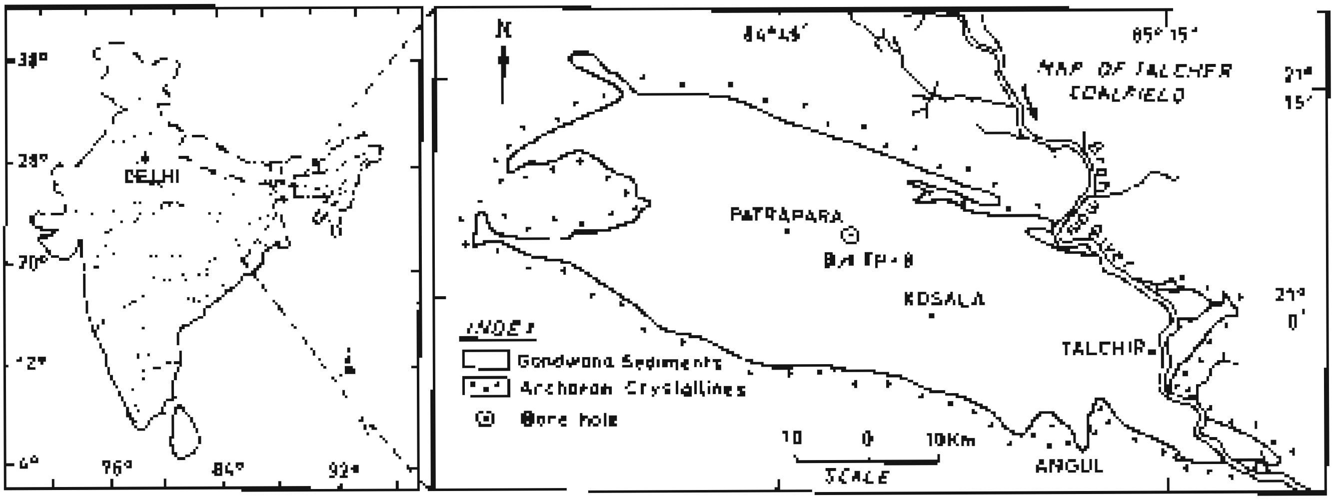


Fig. 1—Map of India with enlarged portion showing location of Borehole TP-8, Talcher Coalfield.

PALYNOLOGICAL OBSERVATIONS

The Borehole TP-8 provided palynoflora considered transitional from Late Permian to Early Triassic. Palynologically, the top-most coal-bearing horizon (374.00-404.00 m depth) is dated as Late Permian while overlying strata at 367.50 m and above are dated as Early Triassic (Tripathi & Bhattacharyya 2001). Detailed analyses of samples between 392.00 and 361.00 m depths (Fig. 2) are plotted in Fig. 3 and Fig. 4. Quantitatively the assemblage (up to 367.50 m) is dominated by striate bisaccate pollen grains while at 361.00 m it is dominated by non-striate bisaccates *Satsangisaccites* Bharadwaj & Srivastava and *Falcisporites* Leschik emend. Klaus. The composition of the palynoflora permits identification of two assemblages (Fig. 6, Pl. 1.1-16). The Assemblage I recorded at depth interval 404-371.50 m has the presence of marker taxa *Navalesporites spinosus*, *Gondisporites raniganjensis*, *Densipollenites magnicorpus*, *Praecolpatites sinuosus* and

S.No.	Depth in m	Lithology	Yield	Preservation	Remarks
1	361.00	Shale band in run of sandstone	Rich	Good	Very rich in other plant tissues
2	367.50	Sandstone with carbonaceous layer	Rich	Good	Very rich in other plant tissues
3	371.50	Grey shale	Common	Poor	Rich in black wood fragments
4	*374.00	Grey shale	Rare	Poor	Rich in black wood fragments
5	*377.00	Grey shale	Rare	Poor	Rich in other plant tissues
6	383.00	Grey shale	Rich	Good	Rich in other plant tissues
7	386.00	Carbonaceous shale	Rich	Good	Rich in other plant tissues
8	*392.00	Coal	Rich	Poor	Other plant tissues rare
9	*404.00	Grey shale	Rare	Poor	Organic matter rare

Fig. 2—List of samples from Borehole TP-8, Talcher Coalfield detailing the lithology together with yield and preservation of palynomorphs and other plant material. The samples marked with an asterisk are analysed qualitatively only, while others qualitatively as well as quantitatively.

PLATE 1

(Scale bar in figure 6 = 10 µm and for all the figures)

1. *Gondisporites raniganjensis*
2. [illegible]
3. *Navalesporites spinosus*
4. [illegible]
5. *Klausipollenites schaubergeri*
6. *Densipollenites densus*
7. *Chordasporites australiensis*
8. [illegible]
9. *Densipollenites magnicorpus*
10. [illegible]
11. [illegible]
12. [illegible]
13. [illegible]
14. [illegible]
15. [illegible]
16. *Leiosphaeridia* sp.

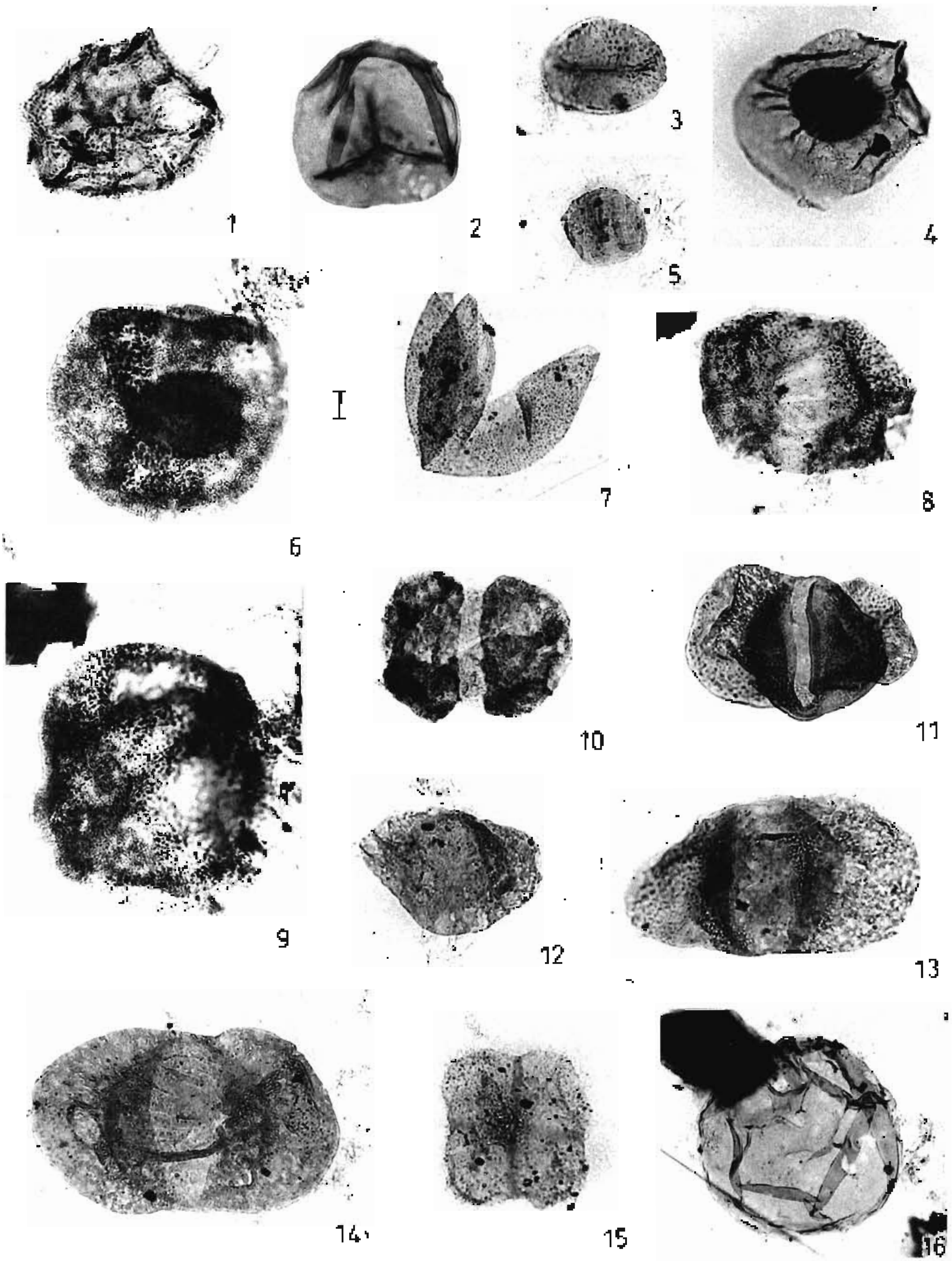


PLATE I

	◄——			Permian			——►	◄—— Triassic	——►
Palynotaxa\Depth of Sample	**404.00**	**392.00**	**386.00**	**383.00**	**377.00**	**374.00**	**371.50**	**367.50**	**361.00**
Striatopodocarpites	+	+	50.0	35.2	+	+	47.0	44.0	11.2
Faunipollenites	+	+	12.0	10.6	+	+	13.0	8.0	1.6
Scheuringipollenites	+	+	9.0	6.0	+	+	3.0	2.0	3.2
Crescentipollenites	+	+	2.0	3.6	+	+	7.0	3.0	
Verticipollenites + *Striatites*	+	+	3.0	+	+	+	4.0		
Densipollenites	+	+	6.0	8.1	+	+	19.0	7.0	
Horriditriletes	+	+	1.0			+			
Cyclogranisporites + *Cyclobaculisporites*	+	+	3.0				3.0		
Satsangisaccites			4.0	10	+	+		2.0	28.0
Falcisporites	+	+	4.0	13.1	+	+		3.0	17.6
Parasaccites + *Plicatipollenites*				0.5		+	1.0		0.8
Weylandites				0.5	+			1.0	11.2
Parasaccites					+	+		6.0	
Callumispora				1.5	+				0.8
Platysaccus + *Cuneatisporites*					+			3.0	1.6
Lophotriletes + *Camptotriletes*			1.0						3.3
Leiosphaeridia	+		2.0		+	+	1.0	1.0	1.0
Quadrisporites	+		3.0	2.5	+	+	1.0	2.0	
Krempipollenites				2.5	+			3.0	3.2
Arcuatipollenites				.05	+		1.0	3.0	1.6
Guttulapollenites								1.0	3.2
Osmundacidites								5.0	4.0
Alisporites								3.0	1.6
Calamospora									0.8
Densoisporites									0.8
Playfordiaspora									4.0
Thymospora				0.5					0.8

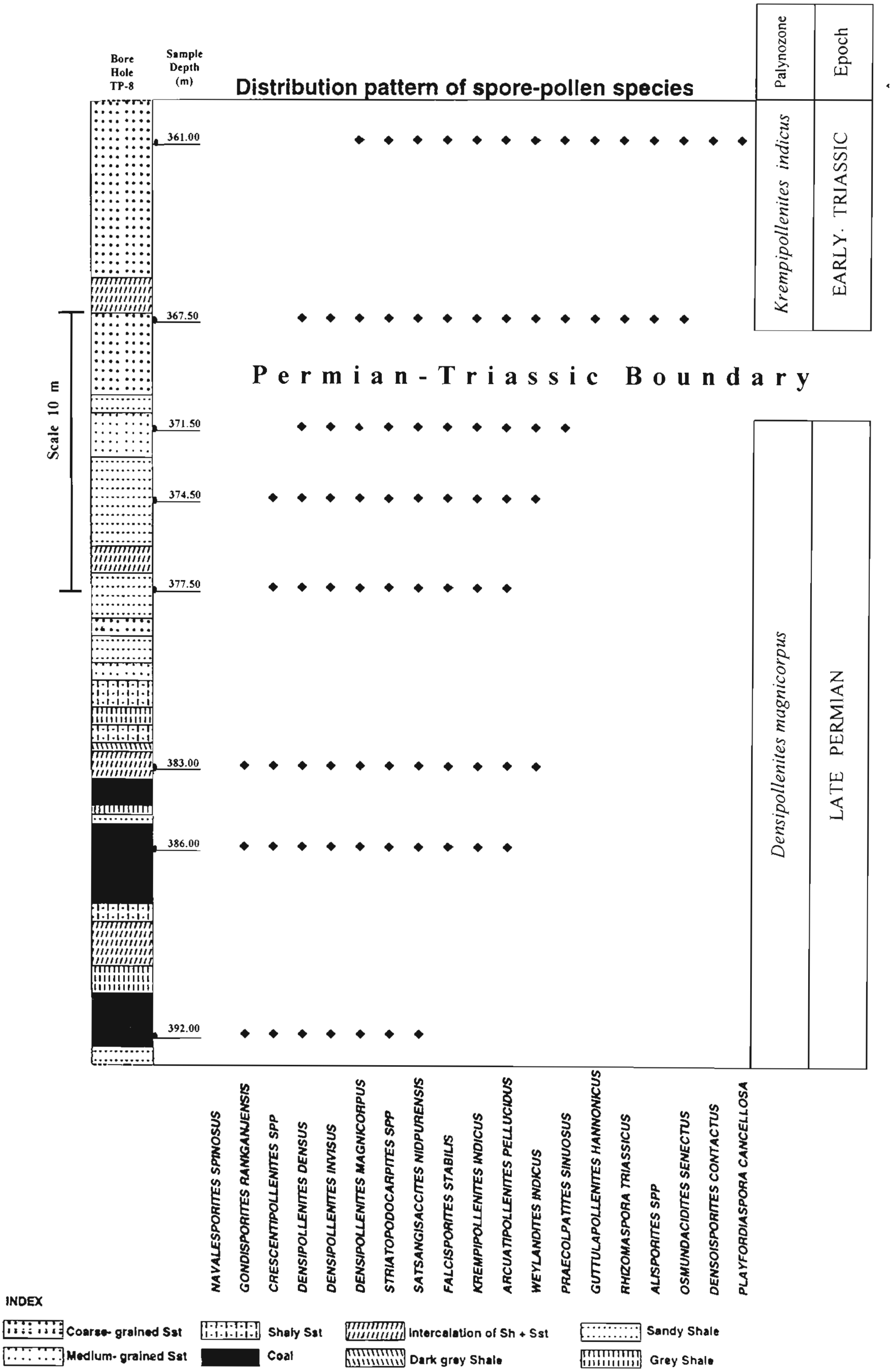
Fig. 3—Relative percentage frequency of spores-pollen in the samples of Borehole TP-8, Talcher Coalfield, Orissa. Counts are based on a total of more than 200 palynomorphs.

Weylandites indicus in striate bisaccate (*Striatopodocarpites*) dominating palynoflora. It is correlatable with the *Densipollenites magnicorpus* Assemblage Zone of Tiwari and Tripathi (1992). The Assemblage I recorded at depth interval 367.50-361.00 m has the Early Triassic marker taxa – *Osmundacidites senectus, Rhizomospora triassica, Arcuatipollenites* spp., *Alisporites* spp., *Playfordiaspora cancellosa* and *Densoisporites contactus* along with abundance/dominance of the nonstriate bisaccate (*Satsangisaccites nidpurensis, Falcisporites stabilis* & *Krempipollenites indicus*). This assemblage is comparable with the *Krempipollenites indicus* Assemblage Zone of Tiwari and Tripathi (1992).

The taxa *Satsangisaccites* and *Falcisporites* make their appearance at 392.00 m and show increased frequencies at 383.00 m with a short decline and rise again to dominance at 361.00 m. A marked change in the palynoflora heralds in the last phase of the coal sequence. Beside these two taxa, other stratigraphically significant forms (*Arcuatipollenites* Tiwari & Vijaya and *Krempipollenites* Tiwari & Vijaya) appear and impart qualitative distinction at 386.00 m. The samples at 367.50 m and 361.00 m contain additional Early Triassic marker forms (*Alisporites* Daugherty emend. Jansonius, *Osmundacidites* Couper); and at 361.00 m *Densoisporites* Weyland & Krieger emend. Dettmann and *Playfordiaspora* Maheshwari & Banerji emend. Vijaya also are introduced. The observed presence of

⟶

Fig. 4—Composite figure showing the lithocolumn of Borehole TP-8 with sample depth analysed, distribution pattern of stratigraphically important spore-pollen species and the palynozones recorded in the sequence. Palynozone after Tiwari & Tripathi 1992.


Bore Hole TP-8
Sample Depth (m)
Distribution pattern of spore-pollen species
Palynozone
Epoch
Krempipollenites indicus
EARLY TRIASSIC
361.00
367.50
Permian-Triassic Boundary
Scale 10 m
371.50
374.50
377.50
383.00
386.00
392.00
Densipollenites magnicorpus
LATE PERMIAN
NAVALESPORITES SPINOSUS
GONDISPORITES RANGANJENSIS
CRESCENTIPOLLENITES SPP
DENSIPOLLENITES DENSUS
DENSIPOLLENITES INVISUS
DENSIPOLLENITES MAGNICORPUS
STRIATOPODOCARPITES SPP
SATSANGISACCITES NIDPURENSIS
FALCISPORITES STABILIS
KREMPIPOLLENITES INDICUS
ARCUATIPOLLENITES PELLUCIDUS
WEYLANDITES INDICUS
PRAECOLPATITES SINUOSUS
GUTTULAPOLLENITES HANNONICUS
RHIZOMASPORA TRIASSICUS
ALISPORITES SPP
OSMUNDACIDITES SENECTUS
DENSOISPORITES CONTACTUS
PLAYFORDIASPORA CANCELLOSA
INDEX
Coarse- grained Sst
Medium- grained Sst
Shaly Sst
Coal
Intercalation of Sh + Sst
Dark grey Shale
Sandy Shale
Grey Shale

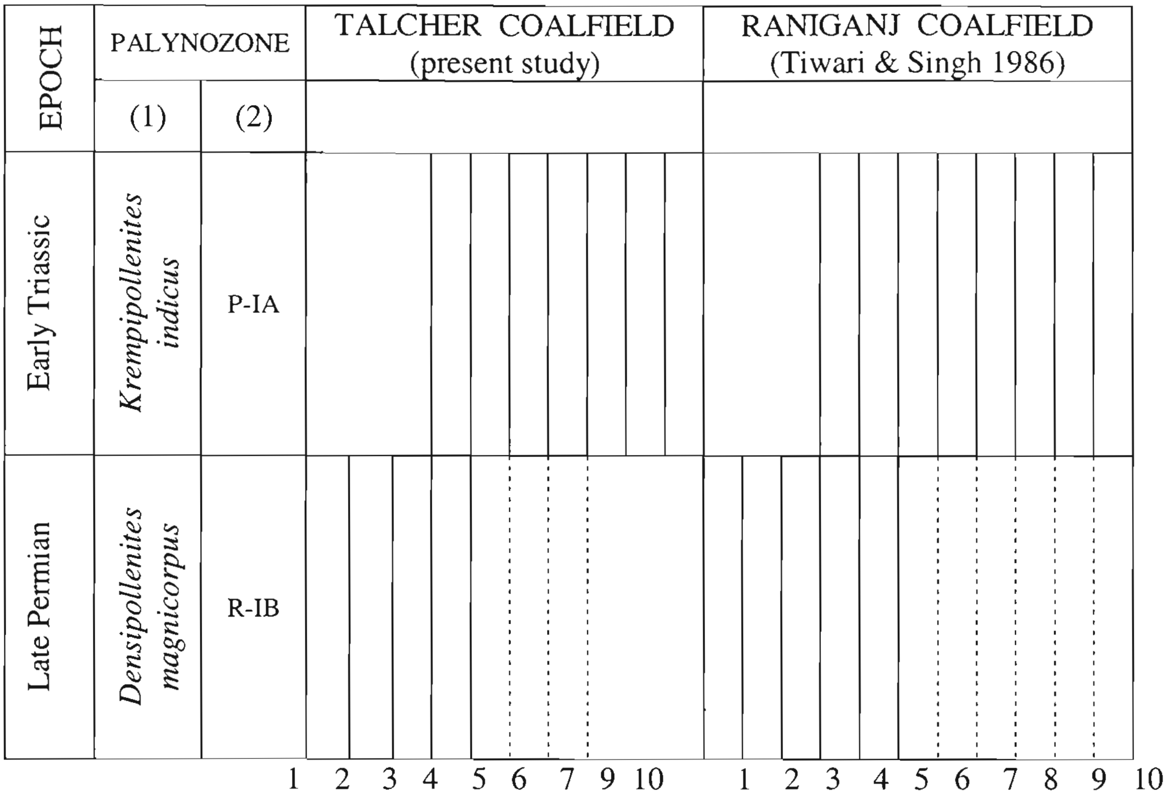


Fig. 5— Pattern of occurrence of marker spore-pollen taxa in Talcher and Raniganj Coalfields across Permian-Triassic boundary. Palynozone (1) after Tiwari & Tripathi 1992; (2) after Tiwari & Singh 1986. Key to numbered genera: 1- *Gondisporites*, 2- *Navalesporites*, 3- *Densipollenites*, 4- *Striatopodocarpites*, 5- *Krempipollenites*, 6- *Satsangisaccites* + *Falcisporites*, 7- *Arcuatipollenites*, 8- *Lundbladispora*, 9- *Densoisporites*, 10- *Playfordiaspora*.

acritarchs throughout the sequence (Fig. 3), though in small quantities, is significant and indicates continuity of the palynoflora and palaeoenvironment. Thus, the palynofloral change from typical Late Permian to Early Triassic is gradual and distinct.

DISCUSSION

The palynological results from Borehole TP-8 indicate that the studied interval represents a transition from Late Permian to Early Triassic (Fig. 4). The change is recorded well within the last phase of the coal-bearing sequence. Palynologically the Permian-Triassic boundary is drawn between the depth interval 371.50-367.50 m. A comparison of the pattern of palynofloral change at the Permian-Triassic boundary in the Talcher and Raniganj coalfields exhibits few differences (Fig. 5). The absence of cavate spores *Lundbladispora* Balme emend. Playford and *Densoisporites* Weyland & Krieger emend. Dettmann in the studied latest Permian palynoflora is striking. These forms reportedly appear in the end-Permian palynoassemblage of the Raniganj Coalfield (Vijaya & Tiwari, 1986). Also, the Early Triassic palynoflora in the Talcher Coalfield has abundant of *Satsangisaccites* to the extent of dominance, instead of *Krempipollenites* Tiwari & Vijaya as reported in the Raniganj Coalfield (Tiwari & Singh, 1983, 1986). These quantitative differences of spores and pollen may reflect climatic differences between the two regions under discussion. A regional provincialism has already been interpreted in the Upper Permian palynoassemblages of various Indian Gondwana basins (Tripathi, 1996b).

Information regarding the yield and preservation of spores-pollen and other plant material from the samples studied here in is presented in Fig. 2. An assessment of this figure shows that the sequence has a good yield of organic matter. The samples from 392.00-383.00 m and 371.50-361.00 m are rich in palynomorphs whereas these are rare in samples at 377.00-374.00 m. The samples from 374.00 and 371.50 m are rich in woody fragments, the remaining samples are rich in other plant tissues. The abundance of other plant tissues has been interpreted to indicate a near shore environment (Pocock *et al.*, 1988; Traverse, 1988). However, no lithological evidence is available for inferring such an environment in Talcher Coalfield. The palynological preservation is poor in the depth interval of 371.50-377.00 m depth, but the other samples (above

Alisporites asansoliensis Maheshwari & Banerji 1975
Alisporites landianus Balme 1970
Arcuatipollenites ovatus Tiwari & Vijaya 1995
Arcuatipollenites pellucidus Tiwari & Vijaya 1995
Crescentipollenites fuscus Bharadwaj, Tiwari & Kar 1974
Crescentipollenites gondwanensis Bharadwaj, Tiwari & Kar 1974
Densipollenites densus Bharadwaj & Srivastava 1969
Densipollenites invisus Bharadwaj & Salujha 1964
Densipollenites magnicorpus Tiwari & Rana 1981
Densoisporites contactus Bharadwaj & Tiwari 1977
Falcisporites stabilis Balme 1970
Gondisporites raniganjensis Bharadwaj 1962
Guttulapollenites hannonicus Goubin 1965
Krempipollenites indicus Tiwari & Vijaya 1995
Nevesisporites spinosus Sarate & Ram-Awatar 1984
Osmundacidites senectus Balme 1963
Playfordiaspora cancellosa (Playford & Dettmann) Maheshwari & Banerji emend. Vijaya 1995
Praecolpatites sinuosus (Balme & Hennelly) Bharadwaj & Srivastava 1969
Rhizomaspora triassica Tiwari & Rana 1981
Satsangisaccites nidpurensis Bharadwaj & Srivastava 1969
Striatopodocarpites decorus Bharadwaj & Salujha 1964
Striatopodocarpites diffusus Bharadwaj & Salujha 1964
Striatopodocarpites magnificus Bharadwaj & Salujha 1964
Weylandites indicus Bharadwaj & Srivastava 1969

Fig. 6—Alphabetical list of spore-pollen species referred in the paper.

and below these depths) show good preservation. This points to a perturbation in the conditions prevailing during deposition of these sediments. Thus palynologically the transitional period from Permian to Triassic evidences a short span of changing palaeoenvironmental conditions.

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Misinterpretations about the 'Pentoxyleae' - A Mesozoic gymnospermous group of plants

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ABSTRACT

Sharma BD 2001. Misinterpretations about the 'Pentoxyleae' - A Mesozoic gymnospermous group of plants. Palaeobotanist 50(2 & 3) : 255-265.

Faulty interpretations on the morphology, anatomy and phylogeny of an extinct plant group 'the Pentoxyleae' are pointed out, and correct descriptions based on the study of large number of specimens and slides are included in the present paper. Reviews and reconstructions based on imaginations are challenged.

Key-words—Unique, Extinct plants, Rajmahal Hills, Reviews, Reconstructions.

मीसोज़ोइक युगीन अनावृतबीजी समूह के पौधे 'पेन्टॉक्सीली' के विषय में कुछ भ्रामक विवेचनाएँ

बी.डी. शर्मा

सारांश

'पेन्टॉक्सीली' समूह के एक विद्यमान पादप समूह के संरचनाविज्ञान, शारीरविज्ञान तथा जातिवृत्त विज्ञान के विषय में कुछ त्रुटिपूर्ण निष्कर्षों को इंगित करते हुए प्रस्तुत शोध पत्र में अनेक प्रादर्शों एवं स्लाइडों के अध्ययन के पश्चात् यथार्थपूर्ण विवेचन प्रस्तुत किया गया है। कल्पना के आधार पर की गयी समीक्षाओं तथा पुर्नसृर्जनों का खण्डन भी किया गया है।

संकेत शब्द—विशिष्ट, सुस्पष्ट पादप, राजमहल पर्वतश्रेणी, समीक्षाएँ, पुनर्सृजन।

INTRODUCTION

IT is after the presentation of a chert piece by Hobson of the Geological Survey of India to Prof. Birbal Sahni that he and his students (Gupta, Rao, etc.) went on an excursion to the Rajmahal Hills, Bihar (now Jharkhand) in 1932 and fortunately they were able to search out the locality (Nipania) from which Hobson probably had collected the chert piece. Sufficient amount of fossiliferous material was collected from Nipania and was given to Rao and Srivastava for investigation (The story narrated by my worthy teacher Late Prof. Gupta, the first research scholar of Prof. Sahni in 1932). Rao (1943a) described in detail the morphology and anatomy of the leaf *Taeniopteris spatulata* which occurs in abundance in the chert (later on renamed as *Nipaniophyllum raoi* by Sahni 1948). Rao (1943) was able to photograph a number of isolated sporangia, spores and seeds, seen in thin sections prepared through the chert. While, Srivastava (1944, 1945) gave descriptions of the anatomy of peculiar stems (*Pentoxylon sahnii & Nipanioxylon guptai*) and seed bearing fructifications (*Carnoconites compactum & C. laxum*) unfortunately Srivastava expired in 1938 and the manuscript (1945) was completed and published by Prof. Sahni with an obituary note). Sahni (1948) instituted a new group of Jurassic gymnosperms—the Pentoxyleae from the Rajmahal Hills on the basis of following characters noted in its fossil plants :-

1. Material permineralised.
2. Branching conifer-like leaves restricted to dwarf shoots.
3. Stem polystelic with generally 5 endocentric steles. Primary xylem mesarch.
4. Pith and cortex parenchymatous with scattered sclerotic nests.
5. Secondary wood compact with growth rings, rays uniseriate and short (2-14 cells high), contiguous uniseriate sometimes biseriate bordered pits on radial walls of tracheids, pits in crossfield large, single per field.
6. Leaf trace many with or without secondary xylem.
7. Leaves simple *Taeniopteris* type, midrib has 5-9 diploxylic bundles in a saucer, stomata on lower surface and syndetocheilic (?).
8. Seeds in globose or elongated infructescence. Orthotropus ovules attached directly to the cone axis. Integument thick heterogeneous nonvascularised. Nucellus free with nucellar pad. Embryo dicotyledonous (?).
9. Relationships suggested with medullosan pteridosperms, cycads, Ginkgoales and the conifers.

Mittre (1953) described the male fructification *Sahnia nipaniensis* bearing a whorl of 12-20, radial simple or branched microsporophylls and large balloon-shaped microsporangia were produced in rows on lateral sides. Spores monocolpate. Mittre (1957) added further to our knowledge about this peculiar group of extinct plants and described stomata haplocheilic (anomocytic).

The author (BDS) and associates were able to collect huge amount of permineralised material of the Pentoxyleae from the original locality Nipania (Sharma, 1975; Suthar & Sharma, 1988; Suthar *et al.*, 1988) and also from other localities like Amarjola (Sharma, 1969, 1973, 1973a, 1974; Sharma *et al.*, 1987) and Sonajori (Sharma & Bohra, 1997). Several hundreds of slides have been prepared of stems, dwarf shoots, leaves and fructifications (both male and seed bearing) and the author has examined each and every slide personally. Many of the figured slides and specimens used in author's publications are deposited now at the Birbal Sahni Institute of Palaeobotany, Lucknow.

Harris (1962) could be able to collect compressions of the pentoxylean seed bearing fructification *Carnoconites cranwellii* from the Jurassic of New Zealand. He correlated it with the *Taeniopteris spatulata* like leaves (Harris, 1962).

Douglas (1969) described from the Jurassic of Victoria (Australia) fertile organs resembling *Carnoconites* and *Sahnia* of the Pentoxyleae. He also related *Taeniopteris daintreei* leaves with the short shoot *Pentoxylon*-like stem. White (1981) while working on the Talbragar Fish Bed flora of New South Wales (Australia) identified the leaf *Pentoxylon australica* and correlated it with *Carnoconites australica*. She writes that the Australian material is quite distinct from that of the New Zealand fossils of the Pentoxyleae. The leaf has incised margin and the seed bearing cone is very large in comparison to Indian and New Zealand material. Drinnan and Chambers (1985) reassessed the leaves of *Taeniopteris daintreei* and related them to the Pentoxyleae.

Bose *et al.* (1985) published a review article "The *Pentoxylon* plant" on the basis of slides and specimens present at the B.S.I.P., Lucknow. The paper has many erroneous descriptions and misinterpretations. Some of the drawings are poor, unlabelled and show nothing e.g., Fig. 3 page 87 while others, are incorrectly assigned and drawn e.g. Fig. 10 page 85. Srivastava's (1945, pl. 4, fig. 38) photograph of R.L.S. of wood does not show separate unequal bordered pits. There are clear cut uniseriate, equal sized contiguous bordered pits on all tracheids.

There are many other indirect publications on the Pentoxyleae which are full of incorrect descriptions and misinterpretations e.g., Stewart (1976), Crane (1985, 1988), Doyle & Donoghue (1986), Stewart & Rothwell (1993), Taylor & Taylor (1993). Probably many of them have neither seen the specimens nor the slides of the pentoxylean fossils from the Rajmahal Hills, India and their faulty descriptions are based on literature and imagination. In taxonomy and morphology one cannot do justice with the description unless and until one examines the specimens (plants growing in nature or herbarium sheet or preserved material) and the slides personally.

Recently, Srivastava and Banerji (2000) have published a very funny review article on the pentoxylean plants with the heading "Pentoxylon plant : A reconstruction and interpretation" in a Journal which publishes mostly articles on plant physiology and cytology. It is full of imaginations and misinterpretation. This is because they have neither examined the specimens nor the slides carefully.

MATERIAL AND METHODS

In addition to the specimens and slides of the pentoxylean plants from Prof. Gupta's collections, the author and associates have also made huge collections of these extinct plants from the well known localities like Nipania, Amarjola and Sonajori. At Amarjola individual fossils are taken out by digging the

PLATE 1

1. *Carnoconites compactus* Longisection seed bearing cone, seeds originating directly from cone axis. X 8.
2. Same. Tangential section showing radiospermic nature of seeds. X 8.
3. Same. Cross section cone with 8-9 seeds attached to the central axis. X 8.
4. *C. rajmahalensis* (?) Long cone with many seeds originating in spiral from the cone axis. X 5.
5. Same. Longisection of a portion of cone with radiospermic seeds. X 8.
6. Same. Cross section with 6 seeds around the cone axis. X 8.
7. *Sahnia nipaniensis*. A microsporophyll with balloon-shaped large microsporangia attached on it. X 30 (Fig. 7 from Suthar & Sharma, 1988).

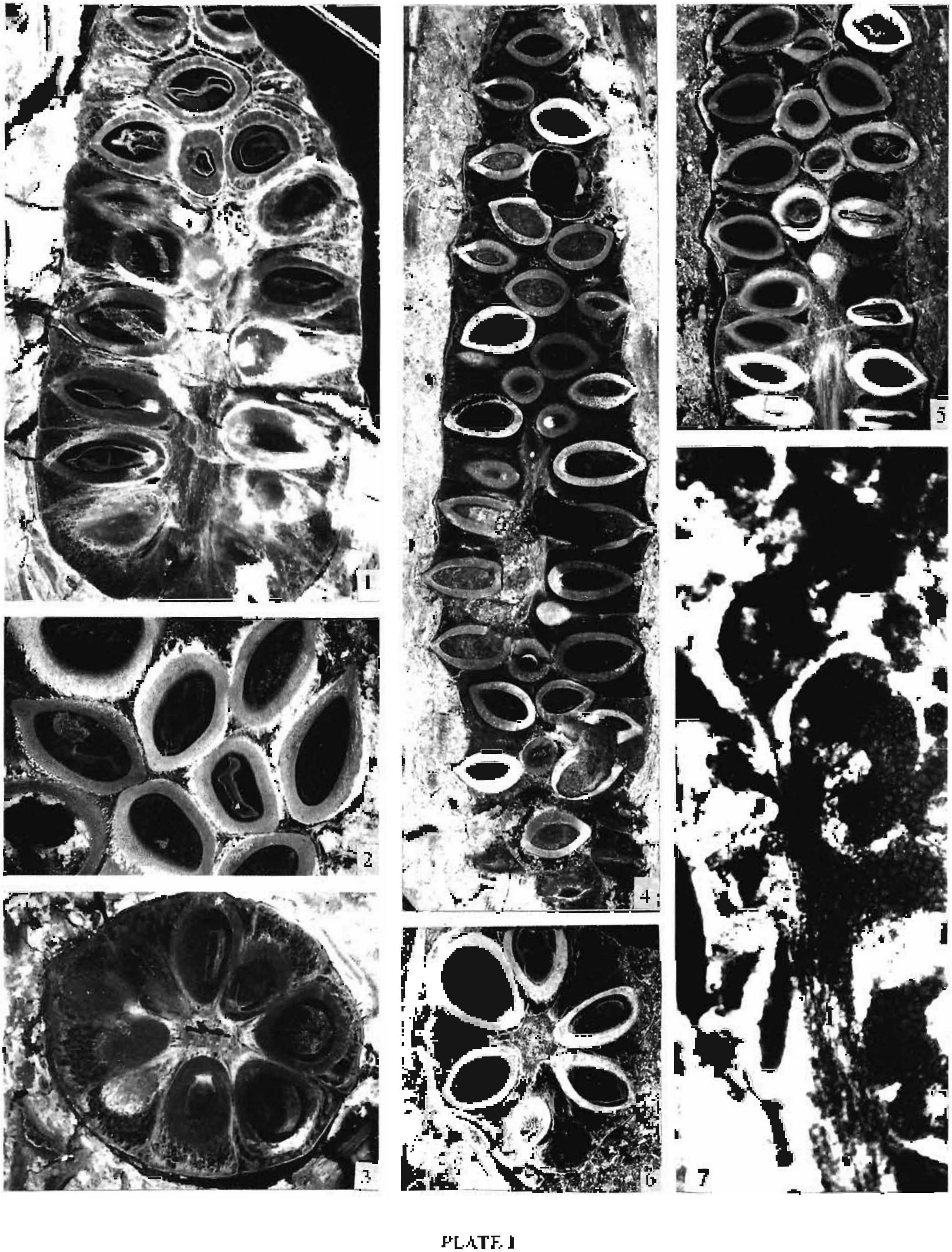


PLATE 1

sandy ferrugenous rock and the specimens are soft and fragile. These are cooked in canada balsam prior to sectioning with a wire bandsaw. Rocks at Sonajori and Nipania are hard and oversilicified. Sections were cut with the help of a diamond edge wheel. Slides were prepared by the usual technique of grinding and polishing methods and mounted in canada balsam. Some of the slides kept unmounted and examined in a water film because sometimes, in silicified cherts, canada balsam makes the section more or less transparent and details of anatomy disappear (Suthar & Sharma, 1988).

OBSERVATION AND DISCUSSION

The organ genera and species now included in the Pentoxyleae are :

Stems

Pentoxylon sahnii Srivastava 1944, 1945
Nipanioxylon guptai Srivastava 1944, 1945
Guptioxylon amarjolense Sharma 1969a
G. endocentrica Sharma 1972
Purioxylon jurassica Sharma 1972a

Leaves

Nipaniophyllum raoi Sahni, 1948
N. hirsutum Mittre, 1957
N. anomozamoides Sharma, 1975
N. hobsonii Bose *et al.* 1985
Taeniopteris spatulata (Harris, 1982)
T. draintreei (Dauglas, 1969; Drinnan & Chambers, 1985)
Pentoxylon australica (White, 1981)

Male fructifications

Sahnia nipaniensis Mittre, 1953
S. laxiphora (Osborn *et al.,* 1991)

Seed bearing infructiscence

Carnoconites compactum Srivastava (1944, 1945)
C. rajmahalensis Bose *et al.* (1984) (*C. laxum* Srivastava, 1944, 1945)
C. cornwelli Harris 1962
C. australica (White, 1981)

Stems

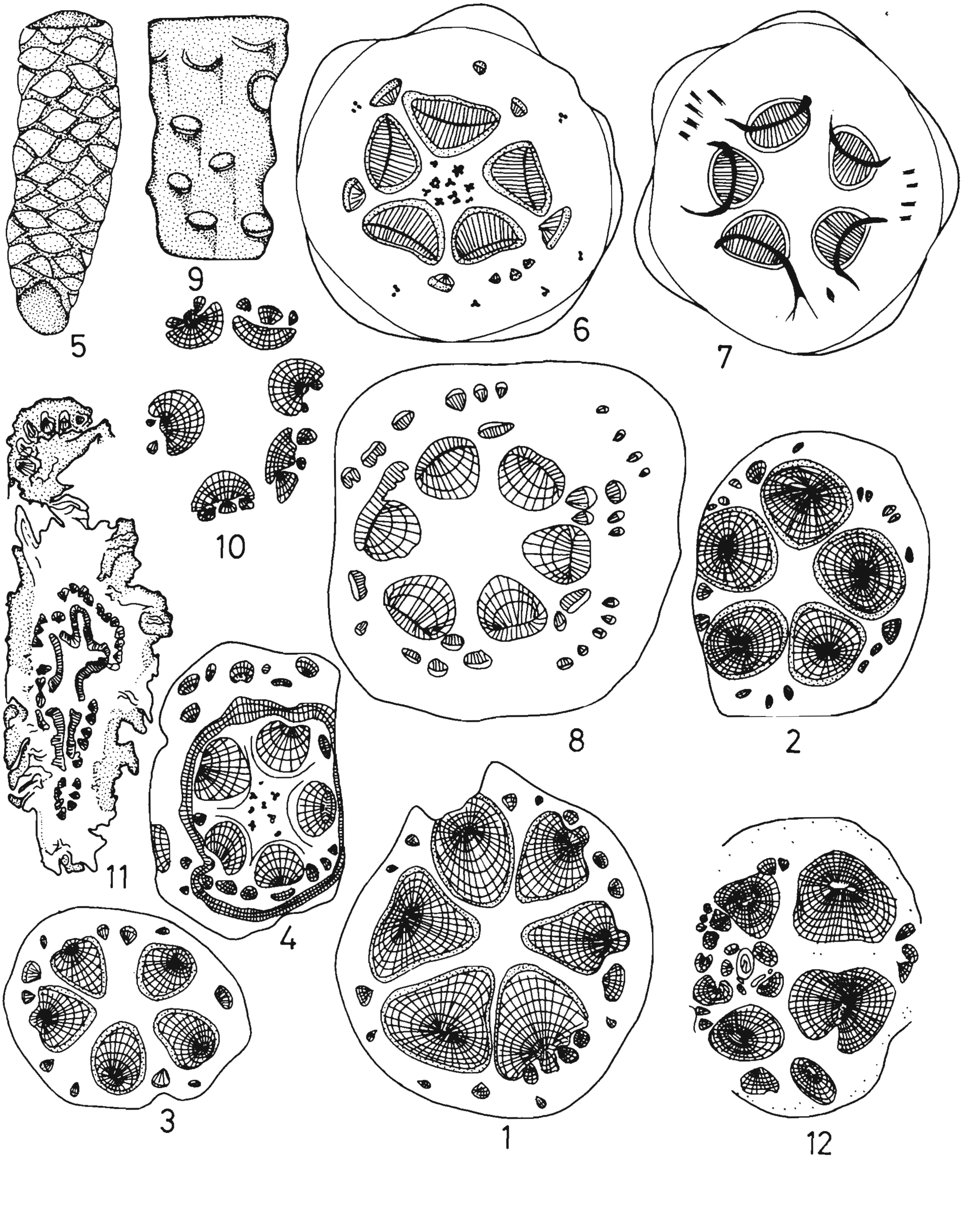
Pentoxylon sahnii Sriv. Hundreds of the pieces of variable sizes (length 1-10 cm and thickness 05-3·5 cm) are present in author's collections, gathered by digging the sandy rock at Amarjola in the Rajmahal Hills. In majority of stems (long shoots) the surface is smooth whereas, close rhomboid leaf bases in helicals (Fig. 5) are present on the dwarf shoots (Sharma, 1973, 1974, 1979). In some of the long shoots distantly placed oval leaf bases (Fig. 9) are present (Sharma, 1973). In an another type of long shoot, a dwarf shoot is seen originating axillary to a decurrent leaf base (Sharma, 1974; pl. 1, figs. C, D). Thick stems may have bases of long shoots on them (Sharma, 1974; pl. 1. figs A, B). Sharma (1996) described various types of shoot systems in *Pentoxylon* plant and confirmed on the bases of anatomy. These are thick stems with either smooth surfaces or have basis of long shoots ; long shoots are of two types, i.e., one may have distantly placed leaf bases and the others produce dwarf shoots axillary to decurrent leaves. Then, the dwarf shoots have close, helical leaf bases and the leaves in majority are produced on them. The fertile shoots are of two types i.e., the male shoot which resembles the vegetative dwarf shoot in general appearance (Fig. 20) but in between leaf bases there are dense growth of hairs (Suthar & Sharma 1988). The seed bearing cones are produced on a peduncle (Figs 14, 15) which in turn is terminal to an another kind of dwarf shoot (Sahni, 1948; Suthar *et al.*, 1988).

Bose *et al.* (1985) also reported the existence of more than dimorphic shoot system in the *Pentoxylon* plant i.e., four types of shoots. However, in support good photographs and camera lucida drawings should have been given. Srivastava and Banerji (2000) in their reconstruction of the *Pentoxylon* plant have shown branches in whorls as well as monopodial, and dichotomy of ultimate branches. Leaves in close spiral are seen on the ultimate dichomotous branches. That is, they did not believe in the origin of vegetative dwarf shoots on lateral sides of the stem and long shoots rather, they considered the dwarf shoots which bear leaves as an extension of long shoots or terminal portion of dichotomised long shoots (Fig. 25). This is not true. Does any body have specimens of dichotomised long or dwarf shoots of *Pentoxylon* ? If yes, how many in number ?

At least this author has neither seen nor has any such specimen in his huge collections of *Pentoxylon* shoots.

Figs 1-12 ⟶

1-11. *Pentoxylon sahnii*. **1-3.** Cross sections long shoots of different thickness, note main steles and origin of cortical bundles. X 6. **4.** Same. Internal periderm encloses 5 steles. X 6. **5.** Dwarf shoot with leaf bases on surface. X 3. **6-8.** Cross sections dwarf shoots showing steles and origin of leaf traces from primary xylem. X 8. **9.** Thin long shoot with sparse leaf bases on surface. X 3. **10.** Cross section fig. 9, cortical bundles (leaf traces) originate from centrifugal portions of steles. X 6. **11.** Cross section fertile shoot (peduncle of *Carnoconites*). X 8. **12.** *Guptioxylon amarjolense* cross section showing steles, medullary bundles and cortical bundles. X 3.
(Figs. 1-3 from Sharma, 1973a; Fig. 4 from Sharma, 1974; Figs 5-7, 9, 10 from Sharma, 1973; Fig. 8 from Sharma, 1979; Fig. 11 from Suthar *et al.*, 1987; Fig. 12 from Sharma, 1969a)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Stewart and Rothwell (1993) write "An armor of leaf bases also spirally arranged, covers the short shoots and the long shoots as well" (Figs 26-13A). In modified reconstruction both long shoots and dwarf shoots are shown covered with close, helical leaf bases (Figs 13, 14). The modification is wrong. In majority, the stems are smooth surfaced and long shoots which produce dwarf shoots have only a few distantly placed leaf bases.

Sharma (1973a) described the anatomy of long shoots, thick and thin and noted that there is no relationship exists between the number of steles (5-8) and the diameter of stem. A thick stem may have 5 and a thin one may have 8 steles. In the majority of steles secondary xylem is more developed towards pith in comparison to that of the centrifugal side (Figs 1, 3). Sometimes, the inner and outer secondary xylem are more or less equally developed (Fig. 2). In dwarf shoots also the number of steles remain constant 5 or 6 throughout the length (Figs 6-8). Stewart and Rothwell (1993, p. 376) write that "The number of vascular segments varies however, from 4 to 10 as a result of branching and anastomosing". Neither in decorted stems nor in serial cross sections cut through many stems could show an anastomosing of steles (vascular segments). There is a definite way of branching of steles in *Pentoxylon sahnii* (Sharma, 1974, 1979). Segmentation or fission of steles is seen in *Guptioxylon amarjolense* Sharma (1969b), an extinct pentoxylean taxon but quite distinct from *Pentoxylon*.

Stewart (1976) described that the vasculature of *Pentoxylon* has originated by fission of an eustele into 5 or more bundles and that is there is no polystelic vasculature in *Pentoxylon*. Has anybody ever seen a eustelic vasculature in any stem or branch of *Pentoxylon* ? Why in the majority of stems are there five vascular segments ? And each segment has its own secondary growth without disturbing others. Segmentation or fission takes place only in secondary xylem of the centrifugal side (Figs 1, 10) for the formation of cortical bundles (Sharma, 1969, 1974) which later on may become leaf traces or branch traces. In *Pentoxylon* the vasculature is not monostelic (Bose *et al.*, 1985; Stewart & Rothwell, 1993) but distinctly polystelic.

Taylor and Taylor (1993, p. 648) write " Young shoots of *Pentoxylon* less than 1 cm in diameter contain only primary vascular bundle in the pith and cortex". Has any body ever prepared such a cross section of *Pentoxylon sahnii*? There is one figured by Srivastava and Banerji (2000, Fig. 2 ID) a poor and unlabelled drawing of axis of a type 3 shoot without mentioning any slide No. or source of drawing. All vegetative dwarf shoots ranging 0.5 to 1.6 cm in diameter have identical anatomy and in each secondary xylem (Figs 6-8) is well developed (Sharma, 1973, 1979). *Pentoxylon* is quite close to conifers in an early activity of the cambium. Secondary xylem of centripetal side develops early and fast in comparison to that of the centrifugal side (Sharma *et al.*, 1987). Due to quick development of secondary xylem, the primary xylem in long shoots is generally seen crushed and details of the primary xylem are yet to be studied.

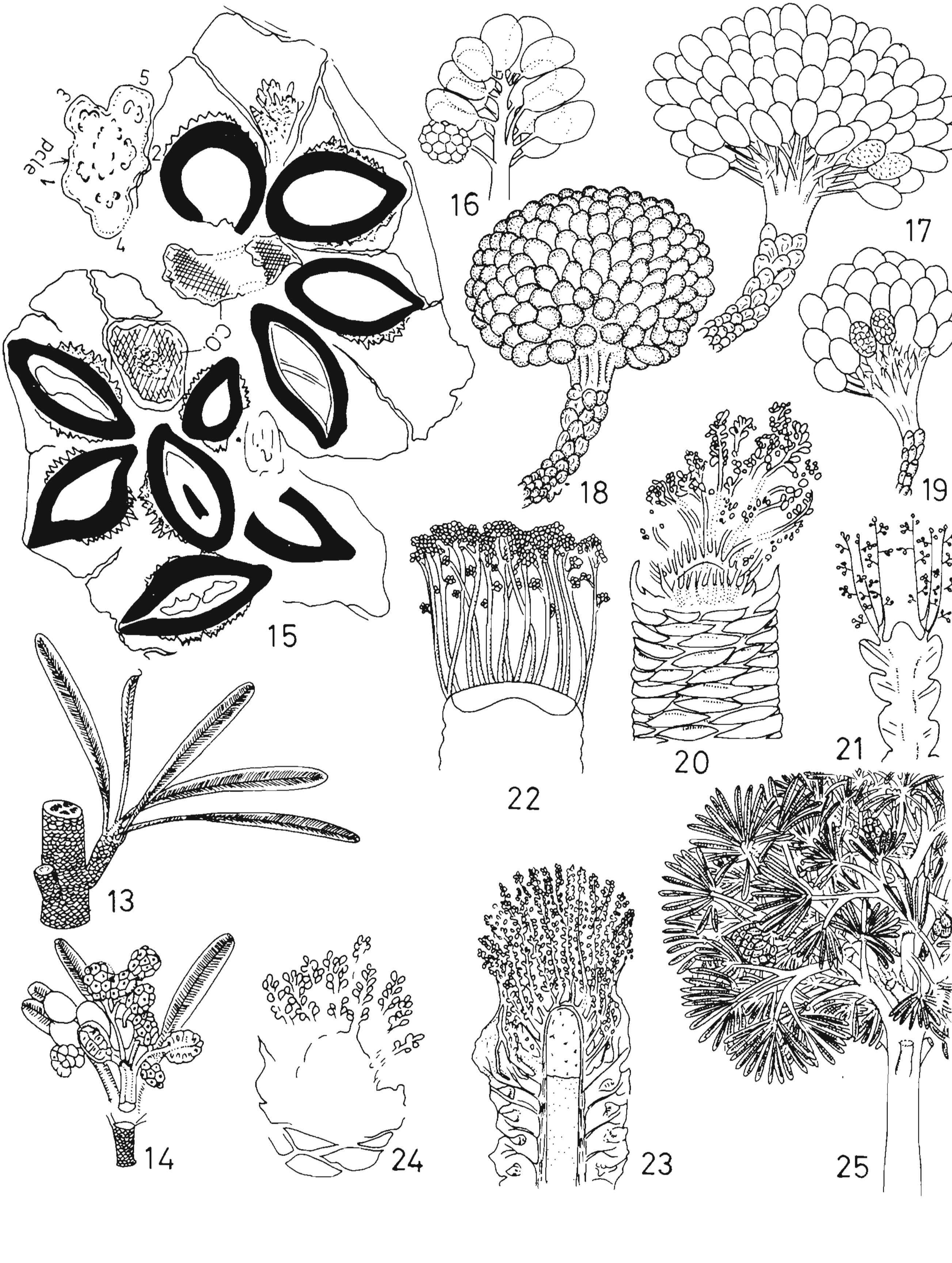
Stewart and Rothwell (1993, p. 376) described the origin of leaf traces "in pair" in *Pentoxylon sahnii*. This is neither true in long shoots (Sharma, 1969, 1973a) nor in dwarf branches (Sharma, 1973, 1979). In the former the cortical bundles originate by fission of secondary xylem of the centrifugal side (Figs 1, 10). While in the later the primary xylem extends laterally (Fig. 7) and cuts off series of endarch traces on either side (Sharma, 1973: Text Figs 5-7, 1979: Text Fig. 2). These are without secondary xylem. Five-8 traces enter a leaf base (Figs 7, 8). How and where the leaf trace bundles become diploxylic is yet to be seen ?

Bose *et al.* (1985) described the structure of secondary phloem of *Pentoxylon sahnii* and write "secondary phloem of *Pentoxylon* is scarcely known apart from a few words of Srivastava (1946)". Probably they did not see a paper by Sharma and Bohra (1977) in which the anatomy of secondary phloem of a long shoot of *Pentoxylon sahnii* is described in detail.

The ground tissue (pith and cortex) is parenchymatous with scattered patches of sclerotic cells. In some of the long shoots of *Pentoxylon* an internal periderm surrounding steles is also observed (Fig. 4). Bose *et al.* (1985, pages 83, 84) described the presence of "small medullary bundles of unknown origin and fate" in type 1 shoots and "also occur especially in the lower part" of "Type 2 shoots". But neither photograph nor drawing is given of the medullary bundles. In hundreds of slides prepared at random and in serial sections, through long shoots and dwarf shoots of all types (polymorphic shoot system described above), the author has not yet seen the presence of medullary bundles in *Pentoxylon*

Figs 13-25 →

13-14. Reconstruction. *Pentoxylon sahnii* and shoot bearing *Carnoconites* cones. Note closely placed rhomboid leaf bases in spirals on stem as well as branches (Stewart & Rothwell, 1993). 15. *Carnoconites compactus* cross section with seeds, cone axis hair and peltately spiral (Sahni, 1948). 16. Reconstruction *C. compactus* infructescence (Mittre, 1953). 17. Same. Reconstruction with hundreds of cones (Bose *et al.*, 1985). 18. Same. Reconstruction more or less similar to fig. 17 (Crane, 1985). 19. Same. Reconstruction with comparatively lesser number of cones (Srivastava & Banerji, 2000). 20. *Sahnia nipaniensis*. Reconstruction male flower (Mittre, 1953). 21. Same. Reconstruction with branched microsporangiophores and microsporangia originate on small lateral branches (Bose *et al.*, 1985). 22. Same. Reconstruction with radial microsporophylls and microsporangia terminal in groups on small lateral branches (Taylor, 1988). 23. Same. Reconstruction with cylindrical receptacle bearing microsporophylls in spiral. Microsporangia in lateral rows (Suthar & Sharma, 1988). 24. Same. Dwarf shoot with a terminal male flower (Srivastava & Banerji, 2000). 25. Reconstruction *Pentoxylon* plant (only one side is shown here) bearing dichotomous long shoots which terminate in leaf producing shoots. Male and seed bearing fructifications originate from long shoots (Srivastava & Banerji, 2000).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sahnii. However, these are present in an allied taxon *Guptioxylon* (*G. amarjolense* Sharma, 1969a & *G. endocentrica* Sharma, 1972).

Nipaniioxylon guptai Srivastava (1944, 1945) instituted the genus for a stem bearing 8-9 steles (bundles) surrounding a wide pith; each has a well developed compact secondary xylem more or less equally developed on either side, i.e., centripetal and centrifugal sides. The ground tissue has scattered nests of sclerotic cells similar to that of *Pentoxylon sahnii*. Sahni (1948) writes in the description of *Nipaniioxylon* Srivastava (page 61) "In any case, there seems no doubt that, if it is a distinct genus, its proper place would be within the group Pentoxyleae". He suspected it a branch system of *Pentoxylon*. Mittre (1957) (based on study of a wrong material probably a conifer stem with anomalous secondary growth) and Sharma (1996) considered *Nipaniioxylon* a distinct stem genus of the Pentoxyleae. Bose *et al.* (1985) believed that it may be a root or twig. The genus needs further investigations.

Guptioxylon amarjolense Sharma (1969a). The stem is a smooth surfaced nearly 2 cm in diameter and is monopodially branched. Four unequal sized steles, each with well developed, compact secondary xylem are present in the ground tissue (Fig. 12). Unequal fission of bundles and presence of medullary bundles are the characteristics of this taxon (Sharma, 1969a, 1974a). Cortical bundles are of various shapes, sizes and nature (exarch, mesarch, endarch, concentric). *Guptioxylon endocentrica* Sharma (1972) is a thick stem with a diameter of 5 cm and has 6 endocentric *Pentoxylon* like steles. Medullary bundles of various size, shape and nature are present. Bose *et al.* (1985, p. 86) considered both the species of *Guptioxylon* described above, equivalent to their "type 2" shoots of *Pentoxylon sahnii*. They believed (without examination of the type specimens, slides and their mode of preservation) that the specimens "are damaged at both ends like ours" and "imagine that these were the bases of the cone bearing branchlets of *Carnoconites*". If it is so, then what would be the thickness of the main stem on which these (2 to 5 cm in diameter shoots) were produced? Secondly their outer surfaces are smooth whereas, "Type 2 shoots" of Bose *et al.* (1985, p. 84) "have persistent leaf base cushions in a crowded helix over the surface". No stem or shoot system of *Pentoxylon* has ever been photographed showing fission of bundles and presence of medullary and cortical bundles of various shapes, sizes and nature. *Guptioxylon* is a distinct taxon from *Pentoxylon* and probably is a link between *Medullosae* and the *Pentoxylon* (Sharma, 1972a).

Purioxylon jurassica Sharma (1972a). It is a smooth surfaced *Pentoxylon* like stem with a fistular pith surrounded by a periderm layer and a ring of collateral, conjoint and endarch bundles. Cortical bundles are of various shapes, sizes and nature and have compact secondary xylem similar to those of *Guptioxylon* or *Pentoxylon*. Sharma (1972a, 1974a) related it in anatomy to Medullosae on one hand and the cycads the other hand.

Leaves

Sahni (1948) named *Nipaniophyllum raoi* for the petrified *Taeniopteris spatulata* like leaves in which the midrib/rachis has 5-9 diploxylic bundles in a saucer or in a row. Stomata hypostomatic, syndetocheilic (?), scattered irregularly between veins and lower epidermal cells were sinuous. Since then three new species from Nipania in the Rajmahal Hills have been created based on presence of few hairs on lower surface (*N. hirsutum* Mittre 1957), revised margin of lamina (*N.* [illegible] Sharma 1975) and comparatively little broader leaves (*N. hobsonii* Bose *et al.* 1985). How valid these parameters are in instituting a new species, needs reconsideration ? Can't these be the different stages of development of the leaves of *N. raoi* ? (young and old). Similarly, should we include in Pentoxyleae or associate with *Pentoxylon* the leaves looking like *Nipaniophyllum* but are found preserved as impressions or compressions, and anatomical details are unknown ?

In *Nipaniophyllum* the stomata are definitely anomocytic (haplocheilic) (Mittre, 1957; Sharma, 1969; Sharma *et al.*, 1987; Bose *et al.*, 1985) and not syndetocheilic. Srivastava and Banerji (2000) developed confusion in the positions of centrifugal and centripetal xylem in a diploxylic bundle of leaf midrib and have drawn an inverted bundle (Fig. 2 J, K).

Male fructification

This material is rare. Mittre (1953) could be able to see longisections through the male fructification and suggested a reconstruction of *Sahnia nipaniensis* Mittre. He believed that radial microsporophylls (12-20) originated in a whorl, on a dwarf shoot (Fig. 20). Balloon-shaped large microsporangia were produced in rows on lateral sides of microsporophylls. Spores were monocolpate with tuberculate exine. Bose *et al.* (1985) interpreted differently on the basis of study of longisections of an another specimen of male fructification (Fig. 21). According to them microsporangiophores branched once or twice in the proximal region and then small lateral shoots were produced on them probably spirally. It is on these small branches that 2-5 balloon shaped (obovate) microsporangia were produced in alternate or opposite arrangements. Suthar and Sharma (1988) published a new reconstruction of *Sahnia nipaniensis* on the basis of longisections of a male fructification collected from Nipania. According to it simple or branched radial microsporophylls were produced in spiral on a cylinderical receptacle terminal to a dwarf shoot (Fig. 22). Large balloon-shaped microsporangia ([illegible]) originated directly on the lateral sides of microsporophylls. Spores monocolpate (monosulcate). Influenced by Bose *et al.* (1985), Taylor (1988) suggested an another reconstruction of *Sahnia* (probably without making any collection and preparation of slides personally). He has shown a number of unbranched radial microsporophylls originating in a whorl from the rim-like collar of a receptacle (Fig. 22). "Each stalk gives rise to secondary laterals that terminate in several stalked pollen sacs". Osborn *et al.* (1991) figure *Sahnia laxiphora* and described origin of large balloon-shaped solitary microsporangia directly on almost entire length of radial microsporophylls. It supports the reconstruction of *Sahnia nipaniensis* suggested by Mittre (1953) and Suthar and Sharma (1988). Srivastava and Banerji (2000) figure a longisection of male fructification (Fig. 24) and show lateral attachment of sporangia in rows on radial microsporangiophores. Further investigations are required for better understanding the structure of the male fructification of the Pentoxyleae.

Crane (1985), Doyle and Donoghue (1986), Stewart and Rothwell (1993) correlate pentoxylean male fructification with *Cycadeoidea* and the bennettitalean fructification *Weltrichia* on the basis of origin of microsporophylls in a whorl and monocolpate (monosulcate) structure of pollen grains. The author considers this correlation purely hypothetical and imaginative. Bennettitales and Pentoxylales are two distinct groups of Mesozoic plants.

Seed bearing fructifications

Srivastava (1944, 1945) described a peculiar, permineralised seed-bearing fructification *Carnoconites* with two species *C. compactum* (Pl. 1.1-3) and *C. laxum* (Pl. 1.4-6). In them orthotropus ovules are produced directly from the cone axis. Seeds are arranged either in compact or loose helicals and each has a thick heterogeneous non-vascularised integument. Nucellus is free and embryo probably was dicotyledonous. Sahni (1948) (Fig. 15), Mittre (1953) and Sharma *et al.* (1987) have figured a number of sections cut in L.S. and C.S. through these cones and added to our knowledge about them. Bose *et al.* (1984) suggested a new combination *Carnoconites rajmahalensis* for *C. laxum* Srivastava on the basis of homology between an earlier described Specimen No. 4514 present at G.S.I., Calcutta (India) and preserved as an impression of *Williamsonia* (?) *rajmahalensis* Wieland (1911). It was collected by Feistmantel (1877) from Mundro in the Rajmahal Hills and had described as a "Cycadeous fructification". They (Bose *et al.* 1984) also write that similar cones preserved in form of an impression were collected earlier from Onthea and Sakarigalighat by Bose (1959), but no description was published. The author wishes to know whether Wieland (1911) has examined the original Specimen (Holotype No. 4514) or if he gave the name *Williamsonia* (?) *rajmahalensis* only on the study of the drawing published by Feistmantel (1877). There are many records in Palaeobotany literature when different names are given to similar fossils based on their mode of preservation e.g., *Trigonocarpus* is a cast or impression or compression of a medullosan seed while similar permineralised seeds are described as *Pachytesta* (Taylor & Taylor, 1993; Stewart & Rothwell, 1993). How justified are Bose *et al.* (1984) in suggesting a new combination *C. rajmahalensis* for *C. laxum*. This needs reconsideration?

Carnoconites compactum is a globose or an oval fructification with compact hexagonal or round ovules in helical arrangement on cone axis (Pl. 1.1-3). Bose *et al.* (1985), Taylor and Taylor (1993), Stewart and Rothwell (1993) and Srivastava and Banerji (2000) have described the seeds/ovules of *Carnoconites* as platyspermic (flat seeds). In majority, the medullosan seeds are radiospermic while in Cordaitales the seeds are designated as platyspermic. In the medullosan seed *Trigonocarpus* or *Pachytesta* the sarcotesta in micropylar portion becomes flat (wing-like) and even then the seed is called radiospermic whereas, in *Carnoconites* only the sclerotesta may become flat (not always) in micropylar region and the seed has been defined as platyspermic. Use of these two terms needs reconsideration. The author considers the seeds of *Carnoconites* to be radiospermic (Pl. 1.1-6).

In *Carnoconites* the vascular supply ends in the basal portion and the nucellus is free with a distinct nucellar pad. Though possible existence of polyembryony has been described in *C. compactum* seeds (Sharma, 1989), yet the structure of the embryo is not definitely know. It is only a hypothesis that the embryo was dicotyledonous (Srivastava, 1945). No drawing or photograph has ever been published showing a dicotyledonous embryo in the *Carnoconites* seed.

A number of reconstructions have been drawn to show the morphology of infructescence of *Carnoconites compactum*. Sahni (1948) made 5-6 stalked globose fructifications arising from a peduncle terminal on a dwarf shoot. While Mittre (1953) believed the presence of 15 to 18, stalked globose fructifications in spiral on a peduncle (Fig. 16). However the attachment of peduncle to stem/branch is not shown. Harris (1962) described *Carnoconites cranwelli* from New Zealand and suggested the presence of 12, long stalked fructifications in a whorl at the stem apex. Bose *et al.* (1985) in a reconstruction beyond imagination of an infructescence of *Carnoconites compactus* (changed from *compactum*, see Bose *et al.*, 1985) have drawn hundreds of globose, stalked fructifications originating in spiral from nearly 12 naked peduncles (Figs. 11, 17) in a whorl at the top of a dwarf shoot (fertile shoot with raised leaf cushion on surface). No body has ever figured a section through Nipania chert bearing such a large number of cones of *C. compactum* or stalks on a peduncle. Maximum 9 or 10 cones have been seen in a bunch. Crane (1985) has also published a reconstruction of *C. compactum* (Fig. 18) resembling more or less that of Bose *et al.* (1985). Interestingly neither Bose nor Crane ever published any account of *Carnoconites* specimens or slides prior to their reconstructions given above. Is it not an imagination? Sahni's reconstruction of *Carnoconites compactum* is more natural than those of others. Srivastava and Banerji (2000) also suggested a reconstruction of seed bearing infructescence of *P. sahnii*. It is similar to that of Bose *et al.* (1985) but with much lesser number of cones on a dwarf shoot (Fig. 19). Leaf bases on dwarf shoot are however shown in whorls, probably this is incorrect.

Pentoxyleae is a synthetic group of Mesozoic gymnosperms which has affinities with the Palaeozoic medullosan pteridosperms in anatomy and structure of seeds. *Guptioxylon amarjolense* and *G. endocentrica* link Medullosales with the Pentoxyleae (Sharma, 1972a). Similar to the medullosan stems, an internal common periderm layer which encircles the steles is also found in many stems and branches of *Pentoxylon* (Sharma, 1974). The seed has thick heterogeneous integument and a free nucellus similar to that of the Medullosae. But the male fertile organs are quite different and distinct in the two groups of extinct plants.

The Triassic stem genus *Rhexoxylon* is close to *Pentoxylon* (Archangelsky & Brett, 1961) in structure of steles and manner of origin of leaf traces. But associated fertile organs of *Rhexoxylon* are yet to be discovered.

The diploxylic bundles of leaf midrib, irregularly oriented amphicyclic stomata on lower surface of lamina and monocolpate pollen grains are identical to those of the cycads (Pant & Mehra, 1963). *Pentoxylon* Sharma (1972a) is a link in derivation of anatomy of cycads from Medullosae.

On cladistic analyses several palaeobotanists place *Pentoxylon* close to the Bennettitales, i.e., a sister group of the clade that includes flowering plants and the Gnetales (Crane, 1985, 1988; Doyle & Donoghue, 1986). Except orthotropous position of ovules and monosulcate pollen grains, there is no other character which may be used in establishing relationship between Bennettitales and the Pentoxyleae. Taylor and Taylor (1993) wrote "the platyspermic ovules, thick sclerotesta and ring of pollen bearing structures suggest affinities with the Bennettitales". The author (BDS) has done enough research work on the bennettitalean seed bearing fructification *Williamsonia* Carruthers but never noticed the platyspermic morphology of ovules and presence of sclerotesta in an integument (Sharma, 1970, 1974, 1980, 1997). Similarly, there is no relationship exists between *Sahnia* and *Weltrichia* (Sharma, 1969b). In *Sahnia* radial microsporophylls are produced in spiral on a cylinderical receptacle (Bose *et al.*, 1985; Suthar & Sharma, 1988), and not in a whorl. Microsporangia in *Sahnia* are large, solitary and balloon-shaped produced directly on microsporophylls. Whereas, in *Weltrichia* microsporangia originate in two rows on finger-like appendages of flat microsporophylls produced in a whorl at the brim of a circular cup-shaped receptacle (Sharma, 1969b; Sitholey & Bose, 1971; Stewart & Rothwell, 1993).

Pentoxylon resembles *Ginkgo* in morphology of dwarf shoots and origin of leaves on them, compact nature of secondary wood, uniseriate, short wood rays and monosulcate pollen grains. Ovules bearing peduncles on dwarf shoots of *Ginkgo* may be correlated but distantly with the cones producing peduncle terminal to dwarf shoot of *Pentoxylon*.

The secondary wood of Pentoxylean stems is compact and made up of squarish tracheids arranged in radial rows. Xylem parenchyma are absent. Tracheids have bordered pittings unior biseriate and contiguous resembling Cordaitales, Araucariaceae, etc. of Coniferopsida.

Comparison of the Pentoxylean fossil plants with Gnetales and the flowering plants is not more than an imagination.

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Palynology of the Late Pliocene sediments of Pinjor Formation, Haryana, India

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ABSTRACT

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Present study highlights the palynoassemblage consisting of algal and fungal remains, pteridophytic spores, gymnosperm and angiosperm pollen recovered from the Pinjor Formation exposed at Nadah, Panchkula, Haryana. The assemblage is dominated by pollen of gymnosperms and angiosperms followed by pteridophytic spores. Algal remains assignable to the Zygnemataceae (*Spirogyra, Mougeotia* and *Zygnema*), fungal spores (*Polyadosporites* and *Frasnacritetrus*), pteridophytic spores *Lycopodiumsporites (Lycopodium)*, *Pteridacidites* (*Pteris*) and *Striatriletes (Ceratopteris)*, gymnosperm pollen *Pinuspollenites* (*Pinus*), *Piceapollenites (Picea)* and *Abiespollenites (Abies)* have been recorded. Angiosperm pollen are mainly represented by *Pinjoriapollis (Magnolia)*, *Retitrescolpites*, *Graminidites*, *Chenopodipollis* and *Malvacearumpollis*. On the basis of their affinities with the modern equivalents, a warm and humid tropical-subtropical climate has been inferred for the Pinjor Formation. The presence of *Spirogyra, Mougeotia*, *Zygnema*, *Lycopodium*, *Ceratopteris*, fungal spores (*Polyadosporites* spp.) and angiosperm pollen (*Malvacearumpollis*) collectively suggest the existence of moist and swampy depositional environment. The presence of grass pollen (Poaceae) indicates the existence of herbaceous flora. The significant drop in grass pollen coinciding with the good proportion of ferns in the middle part of the Pinjor Formation suggests that the vegetation was changed from dry to mainly wet and marshy grassland. Based on the overall palynofloral assemblage, a wet grassland with open and mixed flora during the Pinjor sedimentation has been inferred. The temperate elements viz., *Abies*, *Pinus* and *Picea* appear to be derived from the near by upland areas of the rising Himalaya.

Key-words—Palynology, Palaeoecology, Pinjor Formation, Late Pliocene, Upper Siwalik, Haryana, India.

भारत के हरियाणा प्रान्त के पिन्जोर शैलसमूह के अन्तिम प्लायोसीन अवसादों का परागाणुविज्ञान

मुलागलापल्ली रामचन्द्र राव एवं राजीव पटनायक

सारांश

प्रस्तुत अध्ययन में हरियाणा के पंचकूला क्षेत्र के नादाह में अवस्थित कवकीय एवं शैवालीय अवशेषों और टेरिडोफ़ाइटी जीवाणुओं, अनावृतबीजी तथा आवृतबीजी परागकणों से युक्त परागाणु समुच्चय का विवेचन अभिप्रेत है। समुच्चय में अनावृतबीजी तथा आवृतबीजी परागकणों की प्रधानता है, तत्पश्चात् टेरिडोफ़ाइटी जीवाणु आते हैं। ज़ाइग्मीटेसी (*स्पाइरोगाइरा माउजिओपेटिया* एवं *ज़ाइग्नीमा*) कवकीय बीजाणुओं (*पॉलीएडोस्पोराइटीज़* एवं *फ्रैस्नाक्राइटेट्रस*), *टेरिडोसाइडाइटी*

बीजाणुओं लाइकोपोडियमस्पोराइटीज़ (लाइकोपोडियम), टेरिडासाइडाइटीज़ (टेरिस) एवं *स्ट्रायाट्रायलिटीज़ (सीरेटॉप्टेरिस)*, अनावृतबीजी परागकणों *पाइनसपोलेनाइटीज़ (पाइनस), पाइसियापोलेनाइटीज़ (पाइसिया)* एवं *एबीज़पोलेनाइटीज़ (एबीज़)* से सन्दर्भनीय शैवालीय अवशेष भी अंकित किए गए हैं। आवृतबीजी परागकण मुख्य रूप से *पिन्जोरियापॉलिस (मैग्नोलिया), रेटिट्रेसकॉलपाइटीज़, ग्रैमाइनाइडाइटीज़, चीनोपोडीपोलिस* तथा *माल्वेसीरम्पोलिस* द्वारा निरूपित हैं। आधुनिक समतुल्यों के साथ इनकी बन्धुता के आधार पर पिंजोर शैलसमूह हेतु एक ऊष्ण तथा आर्द्र ऊष्णकटिबन्धीय-उपोष्णकटिबन्धीय जलवायु का अनुमान किया गया है। *स्पाइरोगाइरा, माउजिओटिया, ज़ाइग्नीमा, लाइकोपोडियम, सीरेटॉप्टेरिस*, कवकीय बीजाणुओं तथा आवृतबीजी परागकणों *(माल्वेसीरम्पोलिस)* की संयुक्त उपस्थिति नम तथा अनूपीय निक्षेपणीय पर्यावरण की उपस्थिति प्रस्तावित करती है। घास परागकणों (पोएसी) की उपस्थिति शाकमय वनस्पति जगत की प्राप्ति का संकेत करती है। पिंजोर शैलसमूह के मध्य भाग में फ़र्न के अच्छे अनुपात में होने तथा घास परागकणों में उल्लेखनीय कमी से प्रस्तावित होता है कि इस समय वनस्पति जगत शुष्क से मुख्यतः आर्द्र तथा कच्छ युक्त घास भूमि में परिवर्तित हो गया। समग्र परागाणु वनस्पतिजात समुच्चय के आधार पर पिंजोर अवसादन के दौरान एक विवृत आर्द्र घास भूमि तथा सम्मिश्र वनस्पतिजात का अनुमान किया गया है। शीतोष्ण तत्त्व, जैसे *एबीज़, पाइनस* तथा *पाइसिया* सम्भवतः अग्रायित हिमालय के ऊपरी क्षेत्रों के पास से लिए गए होंगे।

संकेत शब्द—परागाणुविज्ञान, पिंजोर शैलसमूह, अन्तिम पेलियोसीन, उपरि शिवालिक, हरियाणा, भारत।

INTRODUCTION

THE Siwalik Group of rocks forms an important succession in the Tertiary strata of the Indian subcontinent. These continental deposits were laid down in the foredeep on the southern side of the rising Himalaya all along the sub-Himalayan range of India, Nepal and Pakistan. The Group has been divided into Lower, Middle and Upper Siwaliks on the basis of lithology. These were further subdivided into Kamlial, Chinji, Nagri, Dhokpathan, Tatrot, Pinjor and Boulder Conglomerate formations. They are best exposed in Potwar Plateau, Pakistan where most of the type sections of the Siwalik Group but the type sections of the Pinjor and Boulder Conglomerate formations (the middle and the Upper part of the Siwalik subgroup) are best exposed in the vicinity of Chandigarh in India (Pilgrim, 1910, 1913; Gill, 1951). The Siwalik group in general is composed of sandstones, grits, conglomerates, pseudoconglomerates, clays, silts, etc. These fluvial sediments representing age from Middle Miocene to Early Pleistocene (18.4 m.y. to 0.22 m.y., Johnson *et al.*, 1985; Ranga Rao *et al.*, 1985).

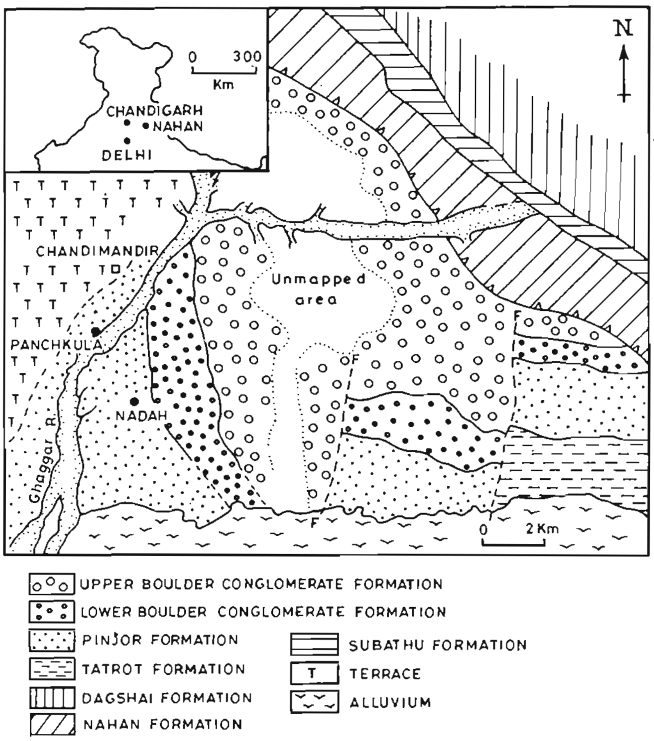

Fig. 1—Geological map showing the Nadah area, Panchkula, Haryana (modified after Kumar & Tandon, 1985).

The Upper Siwaliks in general and Pinjor Formation in particular is very well exposed in the vicinity of Chandigarh (Fig. 1) and are characterized by red, grey mudstones and sandstones. It is sandwiched between the lower Tatrot and upper Boulder Conglomerate formations. These deposits have been extensively studied for sedimentological features (Tandon & Kumar, 1984a; Kumar & Tandon, 1985), fossil fauna (Sahni & Khan, 1959; Nanda, 1973; Raghavan, 1990; Patnaik, 1995, 1997; Patnaik & Schleich, 1998) and Charophyte flora (Bhatia, 1999), Palynoflora (Saxena & Singh, 1980, 1981, 1982a, b; Singh & Saxena, 1980, 1984; Saxena, 1996, 2000), Mathur (1984); Saxena & Bhattacharyya (1987) and Phadtare *et al.* (1994), magnetostratigraphy (Tandon *et al.*, 1984; Azzaroli & Napoleone, 1982; Ranga Rao *et al.*, 1995) and dating of tuffaceous mudstone (Tandon & Kumar, 1984b; Mehta *et al.*, 1993).

The Nadah locality, which has yielded the present flora lies in the Pinjor Formation exposed about 100 meters above the base of the section. The maximum thickness of the section is about 2.5 m but it varies laterally (Fig. 2). Lithologically, the fossiliferous horizon at Nadah is a part of the bluish grey mudstone facies of Kumar and Tandon (1985) contain

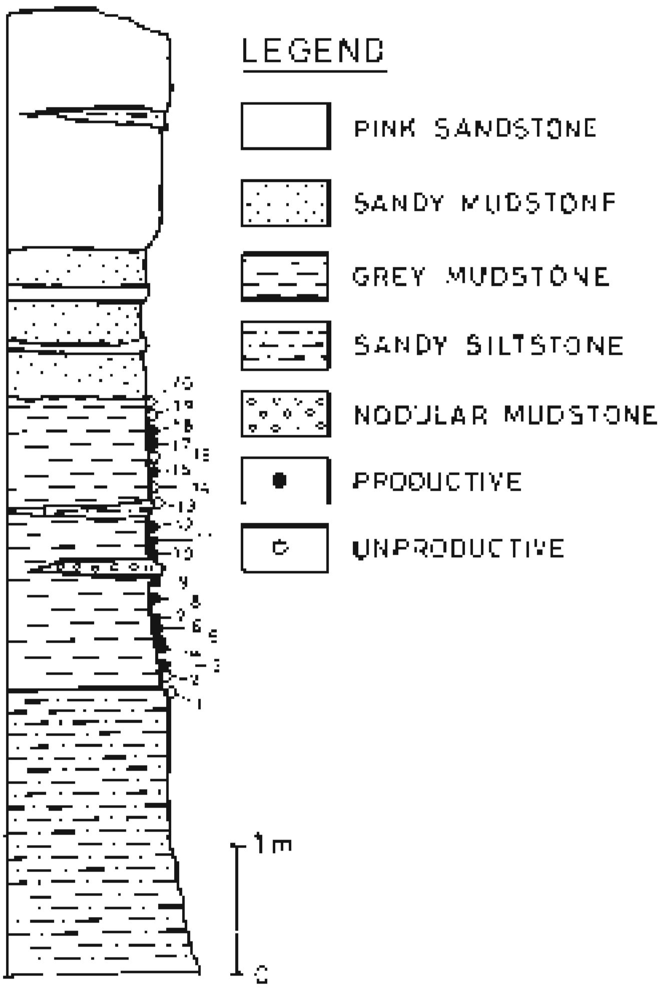

Fig. 2—Lithology of the sampled profile of Pinjor Formation exposed at Nadah section, Panchkula, Haryana.

ferruginous and calcareous nodules, molluscan shells, bioturbation are capped by around 15 cm thick nodular calcium carbonate band indicating presence of shallow seasonal pool of limited aerial extent. In this area, Pinjor Formation conformably overlies the Tatrot Formation characterized by dominant red and grey mudstones and sandstones. Transition between the Tatrot and Pinjor formations is marked by the presence of grey tuffaceous mudstone of 2.14 m.y. (Mehta *et al.*, 1993). In this section, the Pinjor Formation overlain by the Lower Boulder conglomerate Formation. Azzaroli and Napoleone (1982) placed the Nadah section within the Matuyama Epoch spanning between 2.48 and 0.73 m.y. Based on rock magnetic studies, Sangode *et al.* (2001) opined that the Pinjor Formation could also of Pleistocene age. By integrating the zircon fission track dating of the tuffaceous mudstone, palaeomagnetic reversals and rodent assemblages, Patnaik (1997) considered the Nadah deposits of Late Pliocene age (around 2.5 to 2 m.y.).

MATERIAL AND METHODS

The samples were collected from the Pinjor Formation, Upper Siwalik exposed at Nadah, Panchkula, Haryana. Out of 20 samples were collected from the grey mudstone facies, 12 samples yielded palynofossils. Samples were treated with HCL and HF followed by 5% solution of KOH. The slides were prepared in polyvinyl alcohol and mounted in Canada balsam. The material, slides and negatives have been deposited in the Museum of Birbal Sahni Institute of Palaeobotany, Lucknow.

PALYNOLOGY

The palynoflora recorded from the Pinjor Formation (Nadah section) consists of 28 genera and 37 species of algal and fungal remains, pteridophytic spores, gymnosperm and angiosperm pollen. Of these, 5 genera and 4 species belong to algal remains, 2 genera and 2 species to fungal remains, 4 genera and 8 species to pteridophytic spores, 7 genera and 9 species to gymnosperm pollen and 12 genera and 14 species to angiosperm pollen. Besides, some cuticles and tracheids have also been recorded.

LIST OF PALYNOTAXA

Taxa with an asterisk (*) mark have been either described or commented in the text.

Algal remains

*Zygospore of *Spirogyra* type-A (Pl. 1.7)
*Zygospore of *Spirogyra* type-B (Pl. 1.8)
*Zygospore of *Zygnema* (Pl. 1.9)
*Zygospore of *Mougeotia* (Pl. 1.11-12)

Fungal remains

**Polyadosporites* ... sp. nov. (Pl. 1.14-16)
**Polyadosporites* ... sp. nov. (Pl. 3.6, 9)
**Frasnacritetrus* sp. A (Pl. 3.7)
**Frasnacritetrus* sp. B (Pl. 3.8)
*Fungal spore type-A (Pl. 2.18)
*Fungal spore type-B (Pl. 2.19)

Pteridophytic spores

**Lycopodiumsporites* ... sp. nov. (Pl. 1.1-2)
**Lycopodiumsporites* sp. A (Pl. 2.1-2)
**Lycopodiumsporites* sp. B (Pl. 3.1)
**Lycopodiumsporites* sp. C (Pl. 3.4)
**Pteridacidites* ... sp. nov. (Pl. 1.3-4)
**Leptolepidites* sp. (Pl. 2.3)
Striatriletes susannae van der Hammen emend. Kar 1979
S. ... Rao & Singh 1987
*Spore-type (Pl. 1.5-6)

Gymnosperm pollen

Inaperturopollenites ... Saxena & Bhattacharya 1987
**Cycadopites* sp. (Pl. 2.2)

Laricoidites magnus Potonié 1958
Podocarpidites [illegible] Rao 1986
Pinuspollenites [illegible] Rao 1986
**Pinuspollenites nadahensis* sp. nov. (Pl. 2.7-8)
**Pinuspollenites chandraprabhensis* sp. nov. (Pl. 2.12-14)
**Piceapollenites* sp. (Pl. 3.5)
Abiespollenites [illegible] Rao 1986

Angiosperm pollen

[illegible] Singh and Saxena 1984
**Ulmipollenites* sp. (Pl. 3.2)
*[illegible] sp. (Pl. 3.10)
**Nymphaeaceidites* sp. (Pl. 1.13)
[illegible] Ramanujam 1987
[illegible] Saxena & Singh 1981
**Retitricolpites* sp. (Pl. 2.9)
*[illegible] sp. (Pl. 2.6)
*[illegible] sp. (Pl. 3.11)
Malvacearumpollis bakonyensis Nagy 1962
M. grandis Sah 1967
**Malvacearumpollis* sp. (Pl. 2.15-16)
**Graminidites annulatus* sp. nov. (Pl. 1.18-20)
[illegible] Kar & Jain 1981
*Pollen tetrad type-A (Pl. 1.12)
*Pollen tetrad type-B (Pl. 1.17)

SYSTEMATIC DESCRIPTION

SPIROGYRA zygospore type-A

Pl. 1.7

Remarks—Several specimens closely comparable to the zygospores of *Spirogyra* have been recovered. The specimens are oval to rounded elliptical in outline. Size range 75-100 x 45-55 µm. Each specimen is characterized by longitudinal furrow. The walls are 3 µm thick with multiple folds, laevigate.

Affinity—Zygnemataceae (van Geel, 1976).

SPIROGYRA zygospore type-B

Pl. 1.8

Remarks—Zygospores are oval-ellipsoidal in outline. Size range 65-80 x 45-60 µm. The walls are 3 µm thick with very blunt folds, scrobiculate ornamentation.

Affinity—Zygnemataceae (van Geel, 1976).

ZYGNEMA zygospore

Pl. 1.9

Remarks—Zygospores are quadrate in shape, most of them are crumpled. Size range 70-95 x 65-95 µm. A circular depression present in the center of the angles. The retuse angles 2-5 µm in diameter. The walls are 3-4 µm thick, laevigate to finely scabrate ornamentation.

Affinity—Zygospores closely compare with those of extant genus *Zygnema* of Zygnemataceae (Randhawa, 1959).

MOUGEOTIA zygospore

Pl. 1.10-11

Remarks—Zygospores are more or less circular in shape. Size range 65-70 x 60-65 µm. The retuse angles are 2-10 µm in diameter. The walls are 2.5 µm thick, laevigate to finely scabrate. Depression present in the center of the angles.

Affinity—Zygnemataceae.

Genus—POLYADOSPORITES van der Hammen 1954 emend. [illegible], 1991

Type Species—POLYADOSPORITES SUESCAE van der Hammen 1954

POLYADOSPORITES NADAHENSIS sp. nov.

Pl. 1.14-16

Holotype—Pl. 1.14, size 50 x 65 µm, Slide No. BSIP 12611.

PLATE 1

(All photomicrographs are enlarged ca. x 500. Coordinates of the specimens refer to the stage of the BH-2 Olympus microscope no. 2072073)

1-2. [illegible] sp. nov., Slide No. BSIP 12604, coordinates 19.5 x 150.0 (Holotype); 12605, coordinates 21.6 x 154.0.
3-4. [illegible] sp. nov., Slide No. BSIP 12606, coordinates 17.5 x 146.5; 12607, coordinates 9.5 x 139.5 (Holotype).
5-6. Spore type-[illegible], Slide No. BSIP 12606, coordinates 9.5 x 137.5.
7. *Spirogyra* zygospore type-A, Slide No. BSIP 12608, coordinates 9.5 x 147.5.
8. *Spirogyra* zygospore type-B, Slide No. BSIP 12609, coordinates 8.5 x 153.0.
9. *Zygnema* zygospore, Slide No. BSIP 12610, coordinates 15.5 x 157.5.
10, 11. *Mougeotia* zygospore, Slide No. BSIP 12607, coordinates 7.0 x 146.5; 12605, coordinates 8.0 x 157.0.
12. Pollen tetrad type-A, Slide No. BSIP 12605, coordinates 22.0 x 17[illegible].0.
13. *Nymphaeaceidites* sp., Slide No. BSIP 12608, coordinates 5.5 x 141.0.
14-16. *Polyadosporites nadahensis* sp. nov., Slide No. BSIP 12611, coordinates 11.0 x 167.5 (Holotype); 12612, coordinates 9.6 x 159.0; 12613, coordinates 8.0 x 151.0.
17. Pollen tetrad type-B, Slide No. BSIP 12605, coordinates 5.5 x 151.0.
18-20. *Graminidites annulatus* sp. nov., Slide No. BSIP 12604, coordinates 11.4 x 148.0 (Holotype); 12614, coordinates 6.0 x 140.0; 12605, coordinates 22.0 x 151.0.

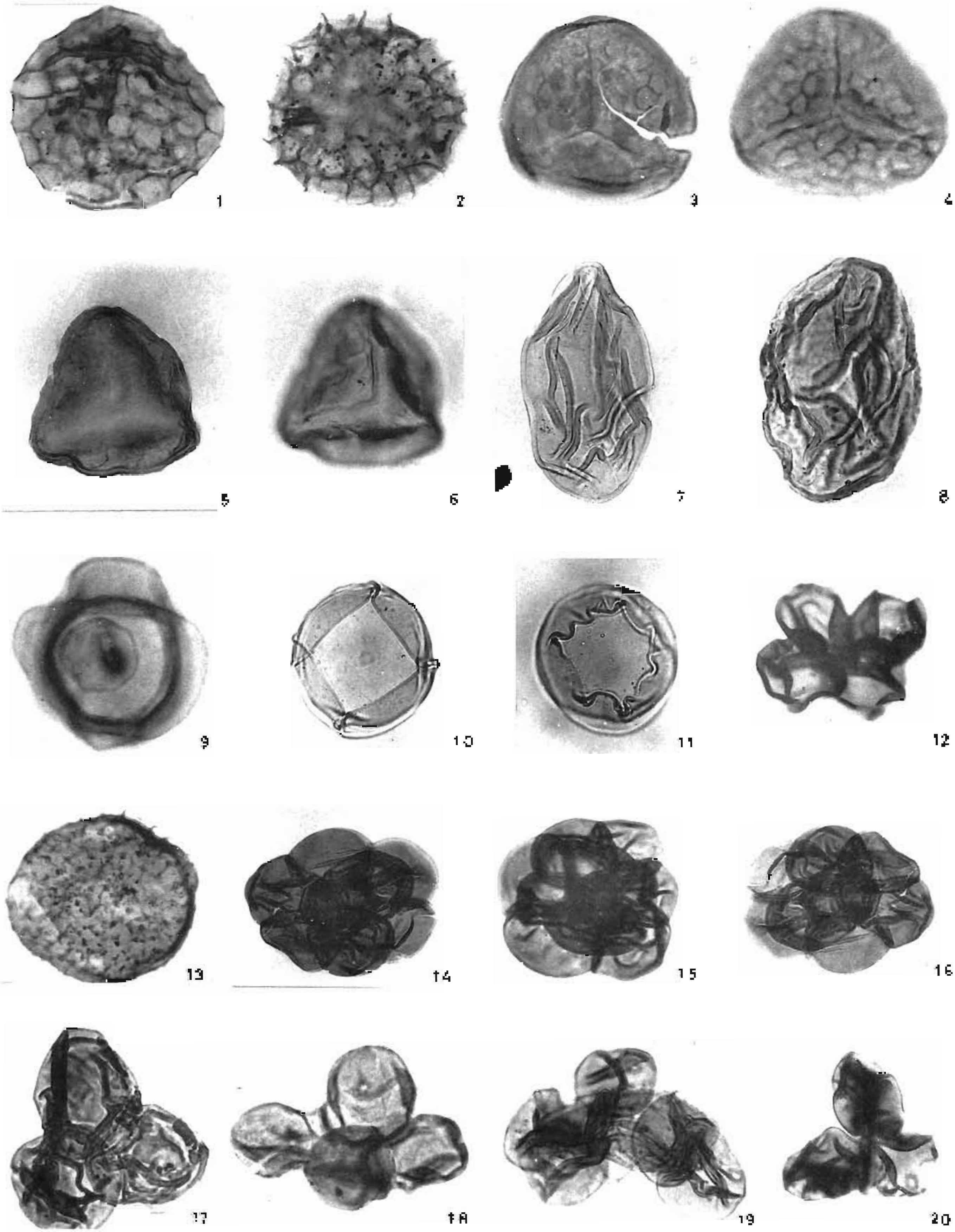

PLATE 1

Type Locality, Horizon and Age—Nadah, Panchkula, Haryana, Upper Siwalik, Pinjor Formation, Late Pliocene.

Diagnosis and Description—Fungal spore colonies composed of number of cells, 16-20 in number. Overall size range 90-130 x 65-90 µm. Inaperturate. Individual cells more or less subspherical in shape, variation in overall shape and size, size range 35-42 x 28-33 µm. Wall 1 µm thick, perforated, surface showing finely pitted reticulate ornamentation.

Comparison—*Polyadosporites [illegible]* sp. nov. is closely comparable with the type species *P. [illegible]* van der Hammen (1954) by its general characters but the latter is differentiated by its smaller size (40-55 µm) and psilate wall.

POLYADOSPORITES SIWALIKUS sp. nov.

Pl. 2.6, 9

Holotype—Pl. 2.6, size 127 x 112 µm, Slide No. BSIP 12620.

Type Locality, Horizon and Age—Nadah, Panchkula, Haryana, Upper Siwalik, Pinjor Formation, Late Pliocene.

Diagnosis and Description—Fungal spores composed of number of individual subspherical cells, cells inaperturate. Size range 127-115 x 112-120 µm. Cell wall thin, septa connecting to 2 or 3 cells, 1-2 µm thick, smooth.

Comparison—*Polyadosporites siwalikus* sp. nov. is distinguished from *Polyadosporites [illegible]* sp. nov. by its bigger size and psilate wall.

Genus—FRASNACRITETRUS Taugourdeau, 1968 emend. Saxena & Sarkar, 1986

Type Species—FRASNACRITETRUS JOSETTAE Taugourdeau, 1968

FRASNACRITETRUS sp. A

Pl. 3.7

Description—Fungal conidia with three processes. Main body rectangular in shape, unicellular, longitudinally septate. Surface finely echinate, evenly distributed all over the body. Processes arise from one end of the body, tubular, wide at the base and gradually tapering towards the apices, nonseptate, wall processes smooth.

Length of conidia—127 µm

Size of the body—35 x 25 µm

Size of the processes—92 µm

Comparison—The present species closely resembles with the *Frasnacritetrus [illegible]* Saxena and Sarkar (1986) by its echinate wall but the latter is differentiated in having 4 processes.

FRASNACRITETRUS sp. B

Pl. 2.8

Description—Fungal conidia with four processes. Main body subrectangular, longitudinally septate. Surface verrucate, verrucae very small, closely placed. Processes arise from one end of the body, tubular, transversely septate, 3-4 septa present in each processes, wall smooth.

Length of conidia—140 µm

Size of the body—30 x 21 µm

Size of the processes—110-115 x 4 µm

Comparison—The present species is closely comparable with the type species *Frasnacritetrus josettae* Taugourdeau (1968) by its shape and general organization but differs in having verrucate body wall.

FUNGAL SPORE type A

Pl. 2.18

Description—Fungal spore subcircular with broad appendage. Size 55 x 95 µm. Appendage tubular, curved, length 65-80 µm. Inaperturate, wall thin, laevigate associated with folds.

Affinity—Spores of *Glomus* (Pirozynski et al., 1988).

PLATE 2 →

(All photomicrographs are enlarged ca. x 500. Coordinates of the specimens refer to the stage of the BH-2 Olympus microscope no. [illegible])

1-2 [illegible] sp. A. Slide No. BSIP 12615, coordinates [illegible].

3 [illegible] sp. Slide No. BSIP [illegible], coordinates [illegible].

4 [illegible] Rao 1958. Slide No. BSIP 12616, coordinates [illegible].

5 [illegible] Rao & Singh 1957. Slide No. BSIP 12615, coordinates [illegible].

6 [illegible] sp. Slide No. BSIP 12606, coordinates [illegible].

7-8 [illegible] sp. nov. Slide No. BSIP 12612, coordinates [illegible] (Holotype).

9 [illegible] sp. Slide No. BSIP 12616, coordinates [illegible].

10 [illegible] Rao 1958. Slide No. BSIP [illegible], coordinates [illegible].

11 [illegible] Rao 1958. Slide No. BSIP 12608, coordinates [illegible].

12-14 [illegible] sp. nov. Slide No. BSIP [illegible], coordinates [illegible]; 12607, coordinates [illegible] (Holotype) 12606, coordinates [illegible].

15-16 [illegible] sp. Slide No. BSIP [illegible], coordinates [illegible].

17 [illegible] 1967. Slide No. BSIP 1260[illegible], coordinates [illegible].

18-19 Fungal spores of *Glomus*. Slide No. BSIP 12609, coordinates [illegible]; 12615, coordinates [illegible].

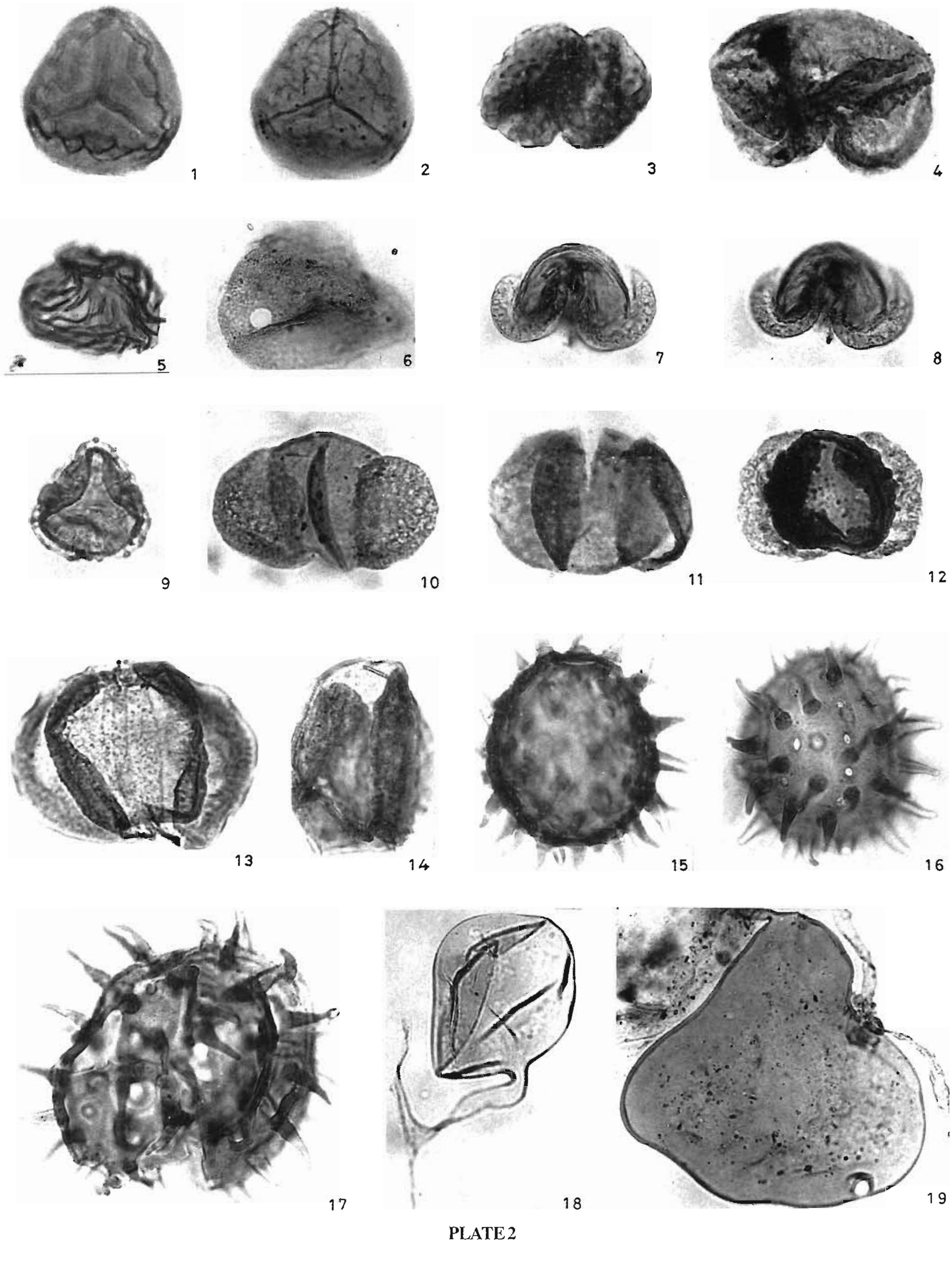

PLATE 2

FUNGAL SPORE type-B

Pl. 2.19

Description—Fungal spore sub-circular with broad appendage. Size 110 x 100 µm. Appendage tubular, coiled, 60 µm long, 4-6 µm wide. Pore present on one side, 4 µm diameter, surrounded by thickening, wall smooth.

Affinity—Spores of *Glomus* (Pirozynski *et al.,* 1988).

Genus—LYCOPODIUMSPORITES (Thiergart, 1938) Delcourt & Sprumont, 1955

Type Species—LYCOPODIUMSPORITES AGATHOECUS (Potonié) Delcourt & Sprumont, 1955

LYCOPODIUMSPORITES NADAHENSIS sp. nov.

Pl. 1.1-2

Holotype—Pl. 1.1, Size 100 µm, Slide No. BSIP 12604.

Type Locality, Horizon and Age—Nadah, Panchkula, Haryana, Upper Siwalik, Pinjor Formation, Late Pliocene.

Diagnosis and Description—Miospores sub-circular in proximal view. Size range 100-118 µm. Trilete, rays indistinct due to heavy reticulation. Exine 1 µm thick, proximal surface psilate while distal surface showing distinct broad reticulate ornamentation, mesh size variable, meshes filled with grana.

Comparison—The present species is distinguished from all the recorded species of *Lycopodiumsporites* from Tertiary sediments of India in having extraordinary size and broad reticulate ornamentation.

Affinity—Lycopodiaceae.

LYCOPODIUMSPORITES sp. A

Pl. 2.1-2

Description—Miospores sub-triangular in proximal view, interapical margins concave, apices broadly rounded. Size range 78-83 x 70-75 µm. Trilete, trilete rays sinuous, raised, reaching almost to the apices. Exine thin, proximal surface smooth. Distal surface showing distinct reticulate ornamentation, meshes big in the centre and small towards apices.

Affinity—Lycopodiaceae.

LYCOPODIUMSPORITES sp. B

Pl. 3.1

Description—Miospore sub-circular in proximal view. Size 150 x 140 µm, Trilete, indistinct due to heavy ornamentation. Exine 3 µm thick. Proximal surface smooth, distal surface showing distinct reticulate ornamentation, meshes 15-25 µm wide, meshes filled with grana. Thin cingulum present around the miospore.

Affinity—Lycopodiaceae.

LYCOPODIUMSPORITES sp. C

Pl. 3.4

Description—Miospore sub-triangular in proximal view, margins concave, apices broadly rounded. Size 110 x 105 µm. Trilete, rays thickened at the centre and narrow towards apices, reaching almost reaching to the equator. Exine 4 µm thick, proximal surface smooth and distal surface showing distinct broad reticulate ornamentation, meshes 10-30 µm wide.

Affinity—Lycopodiaceae.

Genus—PTERIDACIDITES Sah, 1967

Type Species—PTERIDACIDITES AFRICANUS Sah, 1967

PTERIDACIDITES CHANDIGARHENSIS sp. nov.

Pl. 1.3-4

Holotype—Pl. 1.4, Size 95 x 100 µm, Slide No. BSIP 12607.

Type Locality, Horizon and Age—Nadah, Panchkula, Haryana, Upper Siwalik, Pinjor Formation, Late Pliocene.

Diagnosis and Description—Miospores subtriangular with cingulum in proximal view, apices broadly rounded. Size range 93-105 x 85-95 µm. Trilete, open, reaching almost to the

PLATE 3

(All photomicrographs are enlarged ca. x 500. Coordinates of the specimens refer to the stage of the BH2 Olympus microscope no. 217267)

1. *Lycopodiumsporites* sp. B Slide No. BSIP 12616, coordinates 9.0 x 137.4.
2. *Liliacidites* sp. Slide No. BSIP 12607, coordinates 19.5 x 147.0.
3. *Laricoidites magnus* Potonié, 1958. Slide No. BSIP 12607, coordinates 5.0 x 133.0.
4. *Lycopodiumsporites* sp. C, Slide No. BSIP 12607, coordinates 5.5 x 154.3.
5. *Piceapollenites* sp. Slide No. BSIP 12609, coordinates 10.5 x 145.0.
6, 9. *Polyadosporites siwalikus* sp. nov. Slide No. BSIP 12620, coordinates 5.0 x 155.5 (Holotype); 12621, coordinates 19.0 x 166.0.
7. *Frasnacritetrus* sp. A., Slide No. BSIP 12607, coordinates 5.7 x 141.5.
8. *Frasnacritetrus* sp. B., Slide No. BSIP 12622, coordinates 15.0 x 140.7.
10. *Palmidites* sp. Slide No. BSIP 12609, coordinates 10.4 x 157.0.
11. *Psilodiporites* sp. Slide No. BSIP 12623, coordinates 5.0 x 142.0.
12. *Cycadopites* sp. Slide No. BSIP 12604, coordinates 12.0 x 151.4.
13. Angiosperm tracheid, Slide No. BSIP 12624, coordinates 11.0 x 167.0.

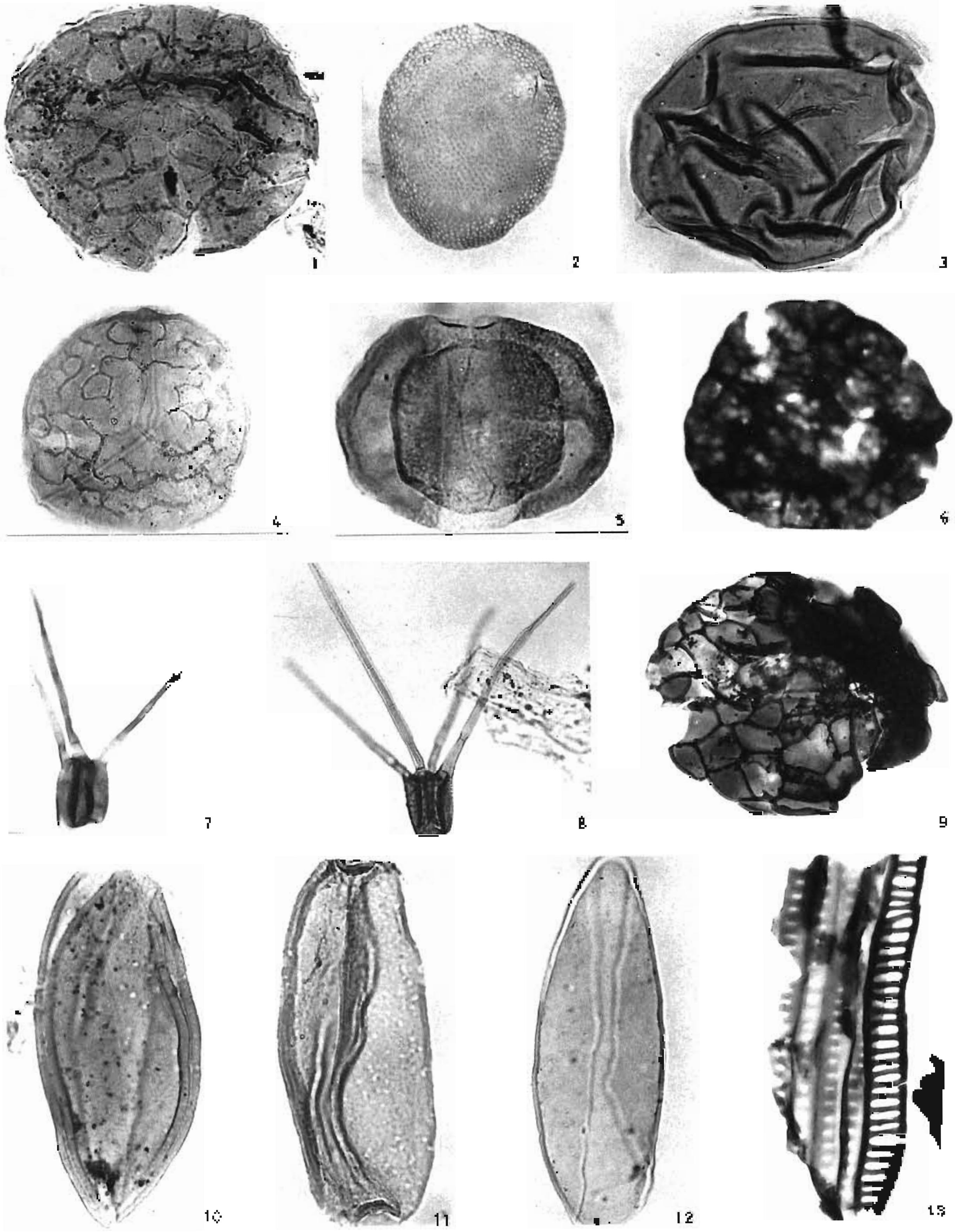

PLATE 3

apices. Exine 1-2 µm thick, proximal surface smooth, distally verrucate, verrucae coalesce to form distinct broad reticulate ornamentation.

Comparison—*Pteridacidites chandigarhensis* sp. nov. is comparable with the type species *Pteridacidites africanus* Sah (1967) by its general characters but the latter is distinguished in its smaller size (55-81 µm), thicker exine and ornamented with fairly large reniform and rounded verrucae. *Pteridacidites vacuus* Sah (1967) is distinct by its more or less circular shape, broader cingulum and in possessing few and large warts. *P. rotundiverrucosus* Sah (1967) differs from the present species in having inter-ray area wholly covered by a small rounded verrucae fused to form a worm-like appearance.

Genus—LEPTOLEPIDITES Couper, 1953

Type Species—LEPTOLEPIDITES VERRUCUS Couper, 1953

LEPTOLEPIDITES sp.

Pl. 2.3

Description—Miospore subtriangular in proximal view. Size 50 x 45 µm. Trilete rays indistinct due to heavy ornamentation. Exine thin, verrucate, verrucae very closely placed. Distal surface showing negative reticulate ornamentation.

SPORE-TYPE

Pl. 1.5-6

Description—Miospore sub-triangular in proximal view, apices broadly rounded, interapical margins concave. Size 85 x 78 µm. Trilete, open, reaching almost to the apices thickening along the rays. Exine 3 µm thick. Proximal surface smooth and distal surface showing distinct reticulate ornamentation.

Affinity—Lygodiaceae.

Genus—CYCADOPITES Wodehouse, 1933

Type Species—CYCADOPITES FOLLICULARIS Wilson & Webster, 1946

CYCADOPITES sp.

Pl. 3.12

Description—Pollen grain oval, elongate in polar view. Size 120 x 61 µm. Monosulcate, sulcus broad at the margin, 15-30 µm wide, and narrow in the center. Exine 3 µm thick, sexine and nexine not differentiated, laevigate ornamentation.

Affinity—Cycadaceae.

Genus—PINUSPOLLENITES Raatz, 1937

Type Species—PINUSPOLLENITES LABDACUS (Potonié) Raatz, 1937

PINUSPOLLENITES NADAHENSIS sp. nov.

Pl. 2.7-8

Holotype—Pl. 2.7, Size 77 x 50 µm, Slide No. BSIP 12612.

Type Locality, Horizon and Age—Nadah, Panchkula Haryana, Upper Siwalik, Pinjor Formation, Late Pliocene.

Diagnosis and Description—Pollen grains bisaccate. Size range 70-77 x 45-55 µm. Central body more or less circular, size range 45-52 x 40-45 µm, margin wavy, thickened in the middle part, up to 4 µm thick, thinning towards the sacci, 1-2 µm thick, central part sunken. Sacci diploxylonoid type, bean-shaped, size range 35-42 x 28-32 µm, marginal crest developed. Surface showing distinct broad reticulate ornamentation.

Comparison—The present species is closely comparable with the type species *Pinuspollenites labdacus* Potonié (1958) by its general organization but the latter is distinguished in having bigger sacci and larger than central body. *Pinuspollenites foveolatus* Rao (1986) is distinct in having smaller size (40-48 x 33-47.5) and foveo-reticulate ornamentation.

Affinity—Pinaceae.

PINUSPOLLENITES CHANDIGARHENSIS sp. nov.

Pl. 2.10-14

Holotype—Pl. 2.13, Size, 122 x 87 µm, Slide No. BSIP 12607.

Type Locality, Horizon and Age—Nadah, Panchkula Haryana, Upper Siwalik, Pinjor Formation.

Diagnosis and Description—Pollen grains bisaccate, size range 90-122 x 60-87 µm. Central body sub-circular to quadrangular in shape, margin wavy, dark brown in colour, size range 75-88 x 58-70 µm, central body bigger than sacci, crest well developed, very thick in the middle and narrow at the attachment of sacci. Sacci kidney-shaped, size range 73-88 x 35-56 µm, ornamented with small meshes, marginal crest developed.

Comparison—*Pinuspollenites chandigarhensis* sp. nov. is distinguished from the *P. nadahensis* sp. nov. by its bigger size and well developed crest on the central body.

Affinity—Pinaceae.

Genus—PICEAPOLLENITES Potonié 1931

Type Species—PICEAPOLLENITES ALATUS Potonié, 1931

PICEAPOLLENITES sp.

Pl. 3.5

Description—Pollen grains bisaccate, oval-elongate in outline. Size range 125-132 x 90-96 µm. Central body sub-circular in shape, size range 90-93 x 80-83 µm, microreticulate. Sacci very closely placed leaving no space in between, hemispherical in shape, size range 88-92 x 40-45 μm, ornamented with small meshes, marginal crest developed, crest gradually thinning to the wings though thickened in the middle.

Comparison—*Piceapollenites alatus* Potonié (1931) differs from the present species in having smaller size (70 μm) and coarser reticulum of the central body.

Affinity—Pinaceae.

Genus—LILIACIDITES Couper, 1953

Type Species—LILIACIDITES KAITANGATAENSIS Couper, 1953

LILIACIDITES sp.

Pl. 3.2

Description—Pollen grain oval in polar view. Size 110 x 90 μm. Monosulcate, sulcus broad and wide. Exine thin, perforated, distinct reticulate ornamentation.

Comparison—*Liliacidites* sp. compares well with *Liliacidites kaitangataensis* Couper (1953) in its general characters but the latter can be distinguished by its differential ornamentation pattern of the reticulate exine (lumina 5 μm at the equator and 1 μm at poles). *Liliacidites baculatus* Venkatachala & Kar (1969) differs in having funnel-shaped sulcus and intrabaculate exine. *Liliacidites keralaensis* Rao (1990) is different in having thicker exine (3.5 μm) and smaller size.

Affinity—Liliaceae.

Genus—PALMIDITES Couper, 1953

Type Species—PALMIDITES MAXIMUS Couper, 1953

PALMIDITES sp.

Pl. 3.10

Description—Pollen grain oval-elongate in polar view. Size 120 x 47 μm. Monocolpate, colpus very long, broad in the middle and narrow at the apex. Exine 7 μm thick, sexine and nexine differentiated, sexine 4 μm thick, perforated, nexine 3 μm thick, smooth, surface showing finely scrobiculate ornamentation.

Affinity—Arecaceae.

Genus—NYMPHAEACIDITES Sah, 1967

Type Species—NYMPHAEACIDITES TYPICUS Sah, 1967

NYMPHAEACIDITES sp.

Pl. 1.13

Description—Pollen grain sub-circular in shape. Size 92 x 82 μm. 1-aperturate, aperture large, operculate, exine 5 μm thick, sexine and nexine not differentiated, sexine provided with sparsely placed spines, spines thin, 6 μm long.

Comparison—*Nymphaeacidites* sp. is differs from *N. typicus* Sah (1967) in having comparatively larger size and absence of suprategellar baculoid processes.

Affinity—Nymphaeaceae.

Genus—RETITRESCOLPITES Sah, 1967

Type Species—RETITRESCOLPITES TYPICUS Sah, 1967

RETITRESCOLPITES sp.

Pl. 2.9

Description—Pollen grain sub-triangular in polar view, apices broadly rounded. Size 60 x 55 μm. Tricolporoidate. Exine 6 μm thick, tectate. Sexine 5 μm thick, pilate, sparsely placed, nexine 1 μm thick, smooth. Distal surface showing distinct broad reticulate ornamentation.

Comparison—The present species is closely comparable with the type species *Retitrescolpites typicus* Sah, 1967 by its retipilate exine but the latter is distinguished in having closely placed pila and thick reticulum.

Affinity—Oleaceae.

Genus—JACOBIPOLLENITES Ramanujam, 1966

Type Species—JACOBIPOLLENITES MAGNIFICUS Ramanujm, 1966

JACOBIPOLLENITES sp.

Pl. 2.6

Description—Pollen grain sub-circular in polar view. Size 72 μm. Monoporate, pore wall thin, 10 μm in diameter. Exine thin, finely reticulate ornamentation.

Comparison—*Jacobipollenites* sp. is closely comparable with *J. magnificus* Ramanujam (1966) by its general characters but the latter distinguished in having coarser reticulum.

Affinity—Sparganiaceae.

Genus—PSILADIPORITES Varma & Rawat emend. Venkatachala & Rawat, 1972

Type Species—PSILADIPORITES HAMMENII Varma & Rawat, 1963

PSILADIPORITES sp.

Pl. 3.11

Description—Pollen grain oval-cylindrical in polar view. Size 120 x 70 μm. Diporate, 15 μm diameter, pore margin thickened, 5 μm thick. Exine 6 μm thick, sexine and nexine differentiated, sexine 2 μm thick, smooth, nexine 4 μm thick, finely scrobiculate ornamentation.

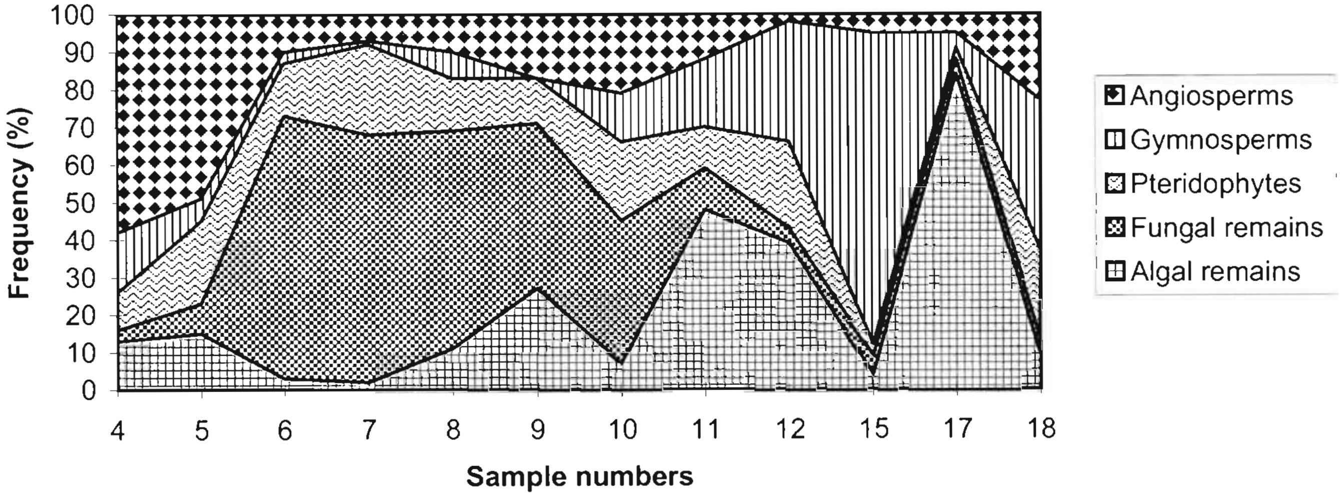

Fig. 3—Representation of different plant groups of Nadah area, Panchkula, Haryana.

Genus—MALVACEARUMPOLLIS Nagy, 1962

Type Species—MALVACEARUMPOLLIS BAKONYENSIS Nagy, 1962

MALVACEARUMPOLLIS sp.

Pl. 2.15-16

Description—Pollen grains sub-circular. Size range 90-100 µm excluding processes. Polyporate, pores more than 12 in number. Exine 6 µm thick, sexine and nexine well differentiated, sexine beset with numerous suprategillar spines, fairly long spines, broad and bulbous base and narrow at the tips, nexine 1 µm thick, smooth. Spines are many, 15-20 µm long, 6-10 µm wide, in between the processes finely fitted reticulate ornamentation.

Comparison—*Malvacearumpollis* sp. closely comparable with the type species *Malvacearumpollis bakonyensis* Nagy (1962) by its general characters but the former is distinguished in having many spines (more than 12) and very bulging bases (bases 6-10 µm). *M. grandis* Sah (1967) is very much larger size (115-139 µm) and many pores.

Affinity—Malvaceae.

Genus—GRAMINIDITES Cookson, 1947

Type Species—GRAMINIDITES MEDIA Cookson, 1947

GRAMINIDITES SIWALIKUS sp. nov.

Pl. 1.18-20

Holotype—Pl. 1.18, Size 110 x 83 µm, Slide No. BSIP 12604.

Type Locality, Horizon and Age—Nadah, Panchkula, Haryana, Upper Siwalik, Pinjor Formation, Late Pliocene.

Diagnosis and Description—Pollen grains in clusters, generally 4-15 in number, connected with 2 or more septa. Size range 70-115 x 70-98 µm. Individual grains sub-triangular to sub-circular in polar view. Size range 40-48 x 32-45 µm. Monoporate, pore surrounded by thick annulus. Exine 2 to 2.5 µm thick, surface showing finely foveo-reticulate ornamentation.

Comparison—The present species is closely comparable with the type species by its porate nature but differs from *Graminidites media* and *G. subreticulata* Cookson (1947) in distinct reticulate ornamentation. *Graminidites assamicus* Sah & Dutta (1968) is distinct by its oval-elliptical shape and ornamentation psilate to faintly structured. *Graminidites chandigarhensis* Saxena & Singh (1982a) is different in having laevigate exine. *G. congoensis* Sah, 1967 is distinct from the present species in having larger size (60-76 µm).

Affinity—Poaceae.

Fig. 4—Possible affinities of palynomorphs recognised in the assemblages and present day distribution. ⟶

Family	Fossil Taxa	Modern equivalents	Preferable habitat	Distribution/ Climate
Zygnemataceae	------------------------	*Zygnema, Spirogyra, Mougeotia*	Commonly found in freshwater of small ponds or temporary pools in wet areas	Cosmopolitan
Lycopodiaceae	*Lycopodiumsporites* spp.	*Lycopodium*	Terrestrial or epiphytes	Cosmopolitan absent in arid areas
Parkeriaceae	*Striatriletes* spp.	*Ceratopteris*	Grows in a variety of aquatic habitats including lakes, ponds, rivers, open swamps and ditches	Widespread distribution though largely confined to warmer regions tropical-subtropical
Pteridaceae	*Pteridacidites chandigarhensis*	*Pteris*	Terrestrial	Worldwide distribution though largely confined to warmer regions, tropical subtropical
Schizaeaceae	*Leptolepidites* sp.	*Schizaea*	Mostly moist forest	Tropical - subtropical
Arecaceae	*Palmidites* sp.	-------	-----------	Tropical-subtropical
Cycadaceae	*Cycadopites* sp.	*Cycas*	Prefers dry places	Tropical subtropical
Podocarpaceae	*Podocarpidites* [illegible]	*Podocarpus*	Plants of mesic forest conditions	Mostly in tropical to warmer occasionally in cool temperate regions
Pinaceae	*Pinuspollenites* spp. *Piceapollenites* sp. *Abiespollenites* [illegible]	*Pinus, Picea, Abies*	Trees of generally poor acidic and either wet or rocky habitats	Widely distributed throughout the temperate parts
Liliaceae	*Liliacidites* sp.	--------------	Mostly herbs, terrestrial	Cosmopolitan
Iridaceae	*Iridacidites markaliensis*	*Watsonia*	--------------	Tropical to temperate
Magnoliaceae	[illegible]	*Magnolia*	Trees and shrubs	Temperate to terrestrial
Oleaceae	[illegible] sp.	--------------	------- -------	Cosmopolitan
Poaceae	*Graminidites* [illegible]	--------------	Almost every type of habitat frequently forming a part of a forest undergrowth in wet or dry places	Widely distributed in all regions of the world
Malvaceae	*Malvacearumpollis* spp.	*Hibiscus*	Terrestrial	Tropical and temperate
Nymphaeaceae	*Nymphaeaceidites* sp.	*Nymphaea*	Aquatic plant	Warm parts of India
Chenopodiaceae	*Chenopodipollis* [illegible]	*Chenopodium*	-------------	Tropical temperate
Sparganiaceae	*Sparganiaceaepollenites* sp.	*Sparganium*	Aquatic	Temperate

POLLEN TETRAD type-A

Pl. 1.19

Description—Pollen grain in tetrad stage, sub-circular in polar view. Size 72 x 85 µm. Individual grains oval-subcircular in shape. Size 40 x 35 µm. Monosulcate, sulcus showing simple cohesion in a tetrad. Exine thin, finely punctate ornamentation.

POLLEN TETRAD type-B

Pl. 1.20

Description—Pollen grain in tetrad stage, sub-triangular in polar view. Size 98 x 93 µm. Individual grains sub-circular in shape, size 57 x 52 µm. Monosulcate, sulcus wide, long and associated with folds. Exine 4 µm thick, sexine and nexine differentiated. Surface showing finely infted reticulate ornamentation.

PALYNOFLORAL ANALYSIS

The palynoassemblage recovered from the Pinjor Formation consists of algal and fungal remains, pteridophytic spores, gymnosperm and angiosperm pollen. Of these *Polyadosporites amethiensis, P. siwalikus, Lycopodiumsporites nahanensis, Pinuspollenites nainitalensis, P. chandigarhensis* and *Graminidites siwalikus* have been proposed as new species.

The gymnosperm pollen is dominant over angiosperm pollen and pteridophytic spores. The frequency of algal remains (zygospores of Zygnemataceae) are low in the lower part of the section and increases in the up section whereas the fungal remains show high frequency in the lower part and progressively decreases towards the top. The frequency of pteridophytic spores especially *Lycopodiumsporites* is dominant in the lower and upper part of the section and decreases at the top of the section. Gymnosperm pollen represented by Pinaceae (*Pinus*) are dominant at the top of the section whereas reverse is the case with the angiosperm pollen (Fig. 3). The possible modern affinities of palynomorphs recognized in the assemblage and their ecological interpretations are given in Fig. 4.

PALYNOSTRATIGRAPHIC ZONATION

Quantitative analysis has been done on the basis of frequencies of palynotaxa in a count of 100 specimens or more specimens per sample and percentage of each palynotaxon or group of palynotaxa was calculated. Percentage frequencies of the selected palynotaxa were plotted under four categories, namely, rare (1-5%), common (6-10%), abundant (11-20%) and predominant (above 20%) (Fig. 5).

Vertical distribution of the palynotaxa clearly indicates that the studied sequence (Pinjor Formation) has been divided into two palynozones—the lower Zone 1 and the upper Zone 2. Recognition of these zones is based on the first (FAD) and last appearance (LAD) of various palynotaxa and their maximum development, decline, restricted occurrence and absence. A description of zones is discussed below:

The characteristic palynotaxa to the lower Zone 1 are *Polyadosporites* spp., *Lycopodiumsporites* spp., *Pregeminipollis lanceolatus* and *Graminidites siwalikus*. The frequency of zygnemataceous spores (*Spirogyra, Zygnema* and *Mougeotia*) is rare to common in the lower part of the section and increases from abundant to predominant at the top of the section. On the other hand, the percentage frequency of *Polyadosporites* spp., *Lycopodiumsporites* spp., *Pregeminipollis lanceolatus* and *Graminidites siwalikus* is abundant to predominant in the lower part of the section and decreases at the top of the section. *Lacrimadites magnus* and *Inaperturopollenites pararudis* are restricted to this zone.

The characteristic feature of Zone 2 is that the *Pinuspollenites* spp. are dominant to predominant in the upper part of the zone. The increased frequency of *Graminidites siwalikus* has been observed at the top of the section. *Abiespollenites, Piceapollenites, Retitrescolpites* and *Chenopodipollis* are restricted to this zone. *Striatriletes* spp. and *Malvacearumpollis* spp. occurring in both the zones of the section (Fig. 5).

PALYNOFLORAL COMPARISON

A comparison of the present assemblage with the known Upper Siwalik assemblages from India and Nepal is discussed below.

Nandi (1975) reported a rich palynoflora from the Siwalik sequence exposed in Jwalamukhi area, Chamba District, Himachal Pradesh and utilized the same in palynostratigraphic zonation. On the basis of qualitative analysis of spore-pollen, she divided the Siwalik sequence into four zones, viz., I-IV. of these Zone-IV represents the uppermost part of the middle and upper Siwalik. This zone has poor representation of *Crassoretitriletes, Alsophilidites, Leptolepidites, Podocarpidites, Pinuspollenites, Monoporopollenites, Abiespollenites* and *Tetradomonoporites*. Of these, *Podocarpidites, Pinuspollenites, Monoporopollenites* (Poaceae) are common to both the assemblages. The comparative study reveals that the dominant elements *Pinuspollenites* and *Monoporopollenites* (Poaceae) are present in both the assemblages showing close resemblance to them.

Singh and Saxena (1981) recorded fungal remains, gymnosperm and angiosperm pollen grains from the Gagret-Bharwain Road section, Una District, Himachal Pradesh. The common genera between the two assemblages are *Pinuspollenites, Lacrimadites, Tricolpites* and *Graminidites*. The above comparison reveals that the palynoassemblage recorded by Singh and Saxena (1981) is broadly comparable to the present assemblage.

Rare □ 1-5% Common ○ 6-10% Abundant ■ 11-20% Predominant ● Above 20%

AGE	PLIOCENE											
FORMATION	PINJOR											
ZONES	ZONE 1							ZONE 2				
SAMPLE NUMBERS	4	5	6	7	8	9	10	11	12	15	17	18
Spirogyra A	○	□	□	□		■	□	●	■		●	□
Spirogrya B	□	○				○	□	○	■		●	□
Mougeotia								○	○		□	
Zygnema	□			□		□	□		□			
Fungal body A	□		●	●	●	●	■			□	□	
Fungal body B	□	○	○	■	○	■	●					
Fungal type										□	●	□
Frasnacritetrus sp.			□					□				
Lycopodiumsporites spp	○	■	■	●	■	■	●	○	■			■
Pteridacidites sp.		□						□	□	□	□	□
Striatriletes susannae	□	□		□	□			□				
Laricoidites major	□	□										
Podocarpidites sp.									□		□	
Pinuspollenites spp.	■	□	□		○		■	■	●	●		●
Piceapollenites sp									□			
Abiespollenites sp.				□					□			○
Inaperturopollenites punctatus		□	□	□	□	□						
Pinjoriapollis lanceolatus	■	■	□	○		■	○	○			□	
Retitrescolpites sp.										□		
Malvacearumpollis spp.						□	□	□	□			□
Chenopodipollis mioceneca										□		
Graminidites spp.	●	●	□	●			□	□	□	□		●

Fig. 5—Palynostratigraphic zonation in the Pinjor Formation, Panchkula, Haryana.

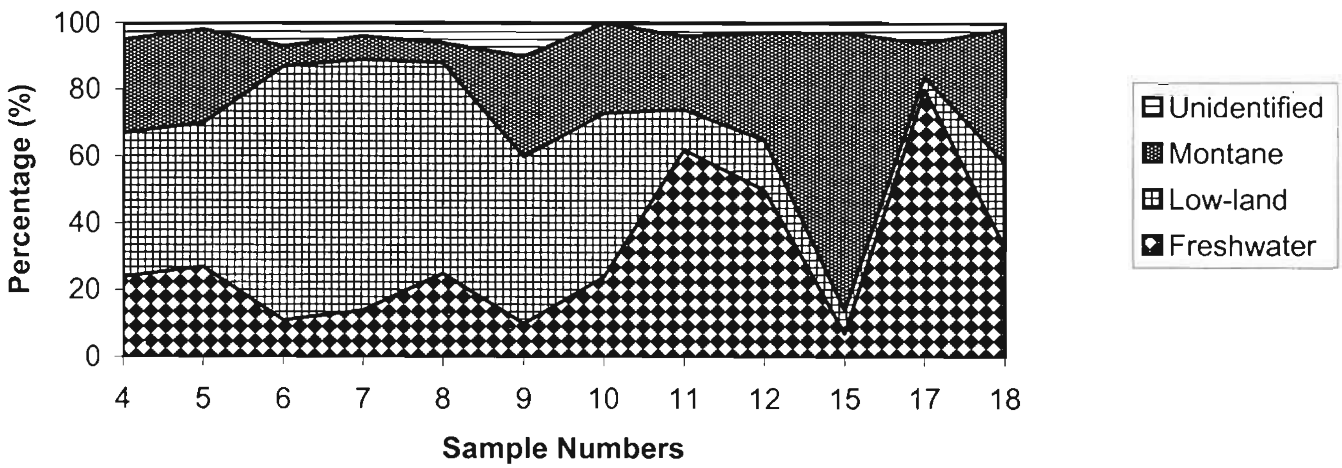

Fig. 6—Percentage of palynotaxa belong to various ecological groups, Pinjor Formation, Haryana.

Saxena and Singh (1982a) recovered palynofossils from the Upper Siwalik sediments exposed along Hoshiarpur-Una Road section, Himachal Pradesh. The common genera between the two assemblages are *Pinuspollenites, Abiespollenites, Laricoidites, Inaperturopollenites, Verrualetes* and *Graminidites*. The palynoassemblage described by Saxena and Singh (1982a) is broadly comparable.

Saxena and Singh (1982b) recorded palynoassemblage from the Pinjor Formation (Upper Siwalik) exposed near Chandigarh, India. The assemblage recorded by them are: *Cyathidites, Lygodiumsporites, Todisporites, Striatriletes, Podocarpidites, Pinuspollenites, Cedripites, Laricoidites, Araucariacites, Retiinaperturites, Palmidites, Psilamonocolpites, Pinjoriapollis, Liliacidites, Favitricolporites, Graminidites* and *Triporites*. Of these, *Striatriletes, Laricoidites, Podocarpidites, Pinuspollenites, Liliacidites* and *Graminidites* are common to both the assemblages. The above comparison indicates that the assemblage recorded by Saxena and Singh (1982b) closely resembles with the present assemblage.

Saxena *et al.* (1984) studied the entire Siwalik sequence exposed along Bhakra-Nangal Road section. The palynoflora recovered from Upper Siwalik are very poor and the genera common to both the assemblages are *Striatriletes, Pinuspollenites* and *Graminidites*. A critical study of the two palynoassemblages reveal that the assemblage recorded by Saxena *et al.* (1984) is broadly comparable with the present one.

Mathur (1984) reported palynoflora from the Upper Siwalik sediments exposed in Malnu-Salwana traverse. The common taxa between the assemblages are *Pinuspollenites, Piceapollenites, Chenopodipollis* and *Graminidites* (Poaceae). The important genera like *Spirogyra, Mougeotia, Zygnema, Polyadosporites* and *Lycopodiumsporites* are not recorded by Mathur (1984), hence, both are not comparable.

Saxena and Bhattacharyya (1987) recorded fungal spores, gymnosperm and angiosperm pollen from the Upper Siwalik sediments exposed along Kala-Amb–Nahan Road section, Sirmaur District, Himachal Pradesh. *Laricoidites, Inaperturopollenites, Pinuspollenites, Pinjoriapollis* and *Monoporopollenites* (Poaceae) are common to both the assemblages. The gymnosperms referable to *Laricoidites, Inaperturopollenites* and *Pinuspollenites* are most dominant element of the assemblage and the same have been recorded from the present study, hence both are broadly comparable.

Phadtare *et al.* (1994) recovered algal and fungal remains, pteridophytic spores, gymnosperm and angiosperm pollen from the Upper Siwalik (Tatrot-Pinjor) sequence of Haripur Khol area, Sirmaur District, Himachal Pradesh. The common genera between the two assemblages are *Pteridacidites, Lycopodiumsporites, Striatriletes, Pinuspollenites Abiespollenites, Graminidites, Chenopodipollis* and *Malvacearumpollis*. According to their study the reduction in *Pinus* pollen and absence of *Ceratopteris, Lycopodium, Chenopodium* have been observed in the Pinjor Formation but reverse is the case in the present study, hence, both the assemblages are not closely comparable.

Saxena *et al.* (1987) recorded fungal remains, pteridophytic spores, gymnosperm and angiosperm pollen from Upper Siwalik (Tatrot-Pinjor) sequence exposed along the Masol-Kiratpur Road, Haryana. The Pinjor palynoassemblage is dominated by gymnospermous pollen (*Laricoidites, Inaperturopollenites* and *Pinuspollenites*). The pteridophytic spores are represented by *Osmundacidites* and *Striatriletes* and angiospermous pollen are represented by *Verrualetes, Pinjoriapollis* and *Cupuliferoipollenites*. The present study has recorded all except *Osmundacidites* and *Cupuliferoipollenites*. The above comparison indicates that the assemblage recorded from Pinjor Formation by Saxena *et al.*, 1987 is broadly comparable with the present one.

Sarkar (1990) recorded palynofossils from Surai Khola of western Nepal and the significant elements of the palynoflora are *Botryococcus*, zygospores of *Zygnema* and *Mougeotia*, *Pediastrum*, *Striatriletes*, *Lycopodiumsporites*, *Monoporopollenites*, *Malvacearumpollis* and *Polyadopollenites*. Except *Botryococcus*, *Pediastrum* and *Polyadopollenites* all the other genera recorded from the present study, hence, the two assemblages are closely comparable.

PALAEOECOLOGICAL INTERPRETATION

The distribution pattern of spores and pollen grains in the Pinjor Formation (Nadah section) clearly indicates the temporal changes in the environment of deposition from the older to younger horizons. The lower part of the section exhibits the presence of aquatic elements viz., *Striatriletes* (*Ceratopteris*) and *Jacobipollenites* (*Sparganium*) that are known to be of freshwater environment. The upper part of the section seems to represent stagnant shallow freshwater conditions in view of the high incidence of zygospores belonging to Zygnemataceae (*Spirogyra*, *Zygnema* and *Mougeotia*). It seems likely that a lowland topography supported the growth of ferns and other herbaceous angiosperms (Poaceae). In the up section the occurrence of algal remains, and pteridophytic spores belong to Lycopodiaceae (*Lycopodium*) gradually decreased and replaced by taxa belonging to upland (*Pinus*, *Picea* and *Abies*) forest communities. The palynofloral population continued from the preceding section shows a remarkable drop in grass pollen and increase the frequency of the spores of *Lycopodium*, collectively indicate the wet climate. The presence of *Striatriletes* (*Ceratopteris*) further supports the existence of marshy muddy condition. The highest percentage of Pinaceae (*Pinus*) pollen in the upper part of the section indicates the possibility of the closeness of temperate vegetation belt.

PALAEOCLIMATE

The Pinjor (Nadah area) palynoassemblage contains algal and fungal remains, pteridophytic spores, gymnosperm and angiosperm pollen. The assemblage has been studied and compared with the modern families and found they are comparable to 18 families. Of these, 5 families restricted to tropical-subtropical, 3 families to tropical to temperate, 4 families to temperate and 6 families are cosmopolitan in distribution (Fig. 4). The pteridophytic spores generally favour moist and shady habitat. *Ceratopteris*, a genus represented by *Striatriletes*, is a water fern growing in tropical region. The presence of fungal spores is indicative of warm and humid condition. The overall vegetational pattern indicates, a tropical - subtropical humid climate during the sedimentation of the Pinjor Formation. The temperate flora belonging to Magnoliaceae (*Magnolia*) and Pinaceae (*Pinus*) appear to be transported from the upland areas in the north.

ENVIRONMENT OF DEPOSITION

Palynological data were thoroughly scrutinized and ecologically significant taxa were selected and segregated for identifying various habitats. Ecological analysis of Pinjor Formation (Nadah area) identifies habitats including low-land, freshwater swamp and water edge and montane elements mentioned below:

Lowland elements—*Polyadosporites*, *Frasnacritetrus*, *Retitrescolpites*, *Graminidites* and *Malvacearumpollis*.

Freshwater elements—*Spirogyra*, *Zygnema*, *Mougeotia*, *Lycopodiumsporites*, *Pteridacidites*, *Striatriletes*, *Nymphaeaceaedites* and *Jacobipollenites*.

Montane elements—*Cycadopites*, *Laricoidites*, *Inaperturopollenites*, *Podocarpidites*, *Pinuspollenites*, *Abiespollenites* and *Piceapollenites*.

The ecological interpretation of recovered spore-pollen reveals that the freshwater forms are dominant over the low-land and montane elements. The percentage frequency of freshwater elements (*Spirogyra*, *Zygnema*, *Mougeotia*, *Nymphaea*) is low in the lower part of the section and progressively increases at the top of the section but reverse is the case with the low land elements. The montane elements belonging to Pinaceae are predominant at the top of the section (Fig. 6).

The presence of zygospores of Zygnemataceae is indicative of stagnant shallow and more or less mesotrophic freshwater habitat (van Geel, 1976; van Geel & van der Hammen, 1978). The presence of the fossil Chara *Lamprothamnium* (i.e., *L. papulosum* and *L. accuminatum*) in the Pinjor Formation suggests that the grey mudstone bed must have been laid down in an oligo-mesohaline environment (Bhatia, 1999). The presence of *Nymphaea* pollen further corroborates the prevalence of lacustrine habitat. A diverse microvertebrate assemblage recovered by (Patnaik & Schleich, 1998) suggest the presence of pond and pond bank communities.

The high incidence of algal and fungal remains, fern spores (*Lycopodium*) and grass pollen indicates that the prevailing flora was mainly of wet, open and mixed nature. The presence of many chlamydospores of *Glomus* reflect the paucity of endomycorrhizal plants and repeated occurrence in these sediments, linked with allochthonous elements representing grassland (Berch & Warner, 1985; Wilson, 1965). The significant drop in grasses pollen coinciding with the good proportion of ferns (*Lycopodium*) and Chenopodiaceae pollen reveal that the flora was changed from dry to mainly wet and marshy grassland. The top most part of the succession exhibits reappearance of graminaceous pollen along with bisaccate pollen, collectively indicate the drier condition during the latter period. The presence of Chenopodiaceae along with the other members of ferns shows that at few places, these plants were thriving for a short period. The gymnosperm pollen possibly were derived from the high mountains nearby in the north. So it may be inferred that the depositional environment of the Pinjor Formation particularly in Panchkula area was deposited in a wet and marshy with open and mixed grassland flora.

CONCLUSIONS

1. The palynoassemblage recovered from the Pinjor Formation (Late Pliocene) is well diversified and contains algal and fungal remains, pteridophytic spores, gymnosperm and angiosperm pollen.
2. *Polypodiisporites nadahensis*, *P. siwalikus*, *Lycopodiumsporites nadahensis*, *Pteridacidites chandigarhensis*, *Pinuspollenites nadahensis*, *P. chandigarhensis* and *Graminidites siwalikus* have been newly proposed.
3. Qualitative and quantitative analyses reveal that the gymnosperm pollen is dominant over angiosperm pollen followed by pteridophytic spores.
4. Stratigraphic distribution of palynoflora revealed that the Pinjor Formation can be divided into lower Zone-1 and the upper Zone-2.
5. On the basis of affinity with modern families, a tropical-subtropical humid climate has been interpreted during the sedimentation of the Pinjor Formation.
6. The assemblage represents a mixture of ecological groups such as low-land, freshwater swamp and water edge, montane and back-mangrove elements.
7. The Pinjor Formation was deposited in a wet and marshy grassland with open and mixed flora.

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Some remarks on the glossopterids and stratigraphical distribution of their fructifications during the Permian on Gondwana Supercontinent

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ABSTRACT

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The paper summarises information available about different organs of the glossopterid group of plants. It has been found that various reconstructions proposed for the glossopterid plant and derivation of its phylogenetic relationships on the basis of cladistic analyses are yet to be validated. The relationship between the families Dictyopteridiumaceae and Eretmoniaceae is discussed. Distribution of various genera of glossopterid fructifications in the Permian of the Gondwana Supercontinent has been tabulated.

Key words—Gondwana Supercontinent, Glossopterids, Fructifications, Biostratigraphy.

गोण्डवाना अधिमहाद्वीप में परमियन कल्प के दौरान ग्लॉसोप्टेरिडों तथा उनके फलन के स्तरिकीय वितरण का विवेचन

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सारांश

प्रस्तुत प्रपत्र में ग्लॉसोप्टेरिड समूह के पौधों के विभिन्न अंगों के विषय में प्राप्त सूचनाओं का समावेश किया गया है। यह पाया गया कि ग्लॉसोप्टेरिड पौधे के विषय में प्रस्तावित विभिन्न पुनर्रचनाएँ तथा क्लैडिस्टिक विश्लेषणों के आधार पर इनके जातिवृत्तीय सम्बन्धों के उद्गम को अभी व्याख्यायित किया जाना शेष है। डिक्ट्योप्टेरिड्यूमेसी तथा इरेटमोनिएसी कुलों के मध्य सम्बन्धन का भी विवेचन किया गया। परमियन कल्प के गोण्डवाना अधिमहाद्वीप के ग्लॉसोप्टेरिड फलनों के विभिन्न वंशों के वितरण सम्बन्धी तालिका भी निर्मित की गयी।

संकेत शब्द—गोण्डवाना अधिमहाद्वीप, ग्लॉसोप्टेरिड, फलन, जैवस्तरिकी.

INTRODUCTION

THE glossopterids are a group of fossil plants that has been known for almost one hundred and eighty years, and which constituted the major part of the Permian vegetation that grew on the Gondwana Supercontinent. However, as yet it has not been possible to reconstruct an indubitable glossopterid plant. The reconstructions proposed by Gould and Delevoryas (1977) and Retallack and Dilcher (1981, 1988), and others show the glossopterid plant as prolifically branched tree, with sparsely distributed leaves. These reconstructions are in fact based on certain presumptions and assumptions, for example, *Vertebraria australis* were the rootlets (roots are not named) and *Arberiella africana,* containing *Protohaploxypinus limpidus* pollen, was the pollen sac of *Dictyopteridium sporiferum* tree (Retallack & Dilcher, 1988, p. 1035). Nothing is said of other striate bisaccate pollen. It is further presumed that the plant was 'probably' wind-pollinated, the ovules were interconnected 'probably' by a good deal of mucilage, by the time of fertilization the fructification 'probably' shrivelled and decayed, seeds were 'probably' scattered by wind. The reason mainly is that, though root, stem, leaf, fertile organs, etc. have been assigned to this group, yet they mostly occur in disjointed condition, and their relationship is based mostly on association. Because of this reason, even the affinities of this group are not well understood. It has very casually been accepted that the glossopterids are pteridosperms, or pteridosperm relatives.

THE GLOSSOPTERIDS

Leaves—The glossopterids are mostly known through leaves that are simple, linear, lanceolate or obovate. Several genera of leaves are on record, some of which have a midrib, and some do not have a midrib, still others have only a partial midrib. Anatomical studies have shown that the midrib is just a concentration of veins identical to the laminar veins (Gould & Delevoryas, 1977; Pigg & Taylor, 1990). The secondary veins emanate either from the midrib or from a central strand of veins, dichotomise, and may or may not anastomose. These leaves also share a similar type of epidermal organisation. The other genera to which the glossopterid leaves are assigned are *Rubidgea* Tate, *Gangamopteris* McCoy, *Glossopteris* Brongniart and *Palaeovittaria* Feistmantel. The probability that leaf genera like *Pantophyllum* Rigby (=*Noeggerathiopsis* Feistmantel), *Euryphyllum* Feistmantel, *Rhabdotaenia* Pant & Verma, *Pteronilssonia* Pant & Nautiyal and *Belemnopteris* Feistmantel may also belong here is low. The leaves of *Pantophyllum* have a typical aspect in their morphology and cuticle (Pant & Verma, 1964; Maheshwari & Singh, 1999), the cuticle of the other genera is also differently organised than that of the glossopterid leaves (Pant & Mehra, 1963; Pant & Verma, 1963; Singh, 1998) and hence none of these genera are considered as belonging to the glossopterid group.

Leaves morphographically indistinguishable from glossopterid leaves are on record from locations outside the Gondwana Supercontinent (Meyen, 1982, 1984; Delevoryas, 1969). However, neither their cuticle is known nor any fertile organ related to the glossopterids is associated with them, hence they are not considered further.

Wood—Many taxa of wood are known from those sediments that contain glossopterid leaves (Kräusel *et al.,* 1961; Prasad, 1982). None of the wood has, however, been found with attached leaves. It is also not expected as the wood is found in decorticated condition, and most of it is known through secondary xylem only, which typically shows annual rings of growth, and has araucarioid pitting on the tracheid walls. The primary xylem is generally endarch, the pith is small, and may contain secretory cells, or canals. Xylem rays are generally uni- or bi-seriate.

Root—The root *Vertebraria*, which some people still argue bore leaves, has a characteristic segmented appearance, the like of which is not known in any of the other contemporary floras. Although *Vertebraria* has not been found in actual attachment with a stem, yet its consistent association with glossopterid leaves leads one to believe that it belongs to this group.

Fructifications—The female fructifications are the only organs that have been found attached to a glossopterid leaf. Male fructification is not known so far. The earliest described glossopterid fructification is *Dictyopteridium.* Feistmantel (1881) who reported this taxon from the Permian sediments of Damodar Graben, India thought it to be a fern pinnule. Chandra and Surange (1976) have convincingly illustrated the association of this fructification with a glossopterid leaf.

Zeiller (1902) described the female fructification *Ottokaria bengalensis* which is probably attached to a leaf of *Glossopteris communis* (Bose MN in Plumstead 1956b; Banerjee, 1978). White (1908) described *Arberia*, a putative glossopterid fructification (Rigby, 1972), from the earliest Permian of Brazil. Plumstead (1952, 1956a, b, 1958) described a host of other fructification genera found attached to leaves of *Gangamopteris*, *Glossopteris* and *Palaeovittaria* from the Permian sediments of South Africa. Since then many fructifications, both in organic connection with leaves and in detached condition, have been reported.

Maheshwari (1965) made a canada balsam transfer of one of the specimens of *Dictyopteridium sporiferum* and demonstrated that the fructification is foliose, bearing ovules on one surface, and showing venation patterns on the other. A somewhat similar pattern is evident in the fructification *Satsangia campanulata* found in the Nidhpuri beds (Srivastava & Maheshwari, 1973). A re-examination of the *Satsangia* fructification shows that it is neither bell-shaped, nor it bore sporangia. The fructification is only partially infolded at the margins, and the scars represent bases of dehisced seeds.

Gould (1975) reported glossopterid fructifications from a Permian petrified peat from Australia. The transverse section of a specimen has vindicated the interpretation of compression material that the fructification was fertile, and bore ovules only on one surface. There now seems to be hardly any scope of doubt in this regard. There is no indubitable evidence to suggest that the glossopterid fructification was a strobilus, or was bisexual, or was covered by a scale leaf (Surange & Chandra, 1975). The ovules/seeds mostly are platyspermic. No indubitable cupular structure has ever been reported. Bisaccate pollen with horizontal striations on the proximal face of the central body has been observed on the integument and in the micropyle of dispersed seeds/ovules (Pant, 1977).

As far as the location of the fructifications is concerned, many believe that it was borne in the axil of a vegetative leaf, while others say that the fructifications were epiphyllous megasporophylls. Very often the pedicel of the fructification was adnate with the midrib or the median strand of veins for some distance; by adherence it became incorporated into the vegetative leaf. Thus the glossopterids seem to belong to the cauliosperms, rather than to phyllosperms.

Seedlings—Srivastava (1978) described *Diphyllopteris verticillata*, a taxon with heterophyllous leaves. The specimen has two oppositely placed *Glossopteris*-type leaves alternating with two dichotomously branched leaves. Pant and Nautiyal (1987) suggested that it was a seedling of the glossopterid plant. Banerjee (2000) is of the opinion that the specimen could as well be young *Rhipidopsis*. Banerjee (2000) described another putative glossopterid seedling *Deogarhia australis*, with two thick cotyledonary leaves and two *Glossopteris* leaves. Earlier Banerjee *et al.* (1991) have reported what they believed was an *in situ Glossopteris* plant with branched stems and spreading roots.

Taxonomic position—Initially regarded as a fern, there is now no doubt that the glossopterids are gymnosperms. But opinions differ as to whether the group merits the rank of a division, a class, an order, or just a family. Some people place the glossopterids in almost as many families as there are genera of female fructifications. Taking into the general organisation of the fructification, all the known fructifications seem to have the same organisation, and hence it is likely that all the glossopterids belong to one family only, that is, the Dictyopteridiumaceae.

The main question that yet remains to be solved is where to place this family? Andrews (1961) classified it as gymnosperms of uncertain affinities, not closely related to any other group. Sporne (1965) placed it under the Pteridospermales. Pant (1962) placed the group at the rank of an order, the Glossopteridales. "The unique leaf attached fructifications of Glossopteridales" suggesting some relation to the Pteridosperms. Some others have suggested that the group represents an independent class - the Glossopteridopsida (Banerjee, 1984). One thing, however, seems certain that the glossopterid group of plants is not closely related to the northern pteridosperms (see Maheshwari, 1990). Some cladistic analyses place glossopterids very close to various seed-fern groups (Crane, 1985). These, however, need further testing as they take into consideration certain premises that are debatable, for example, the occurrence of a cupular structure in the group or the leaf-like nature of the fructification (Schopf, 1976). Doyle and Donoghue (1986, p. 332) observed that Crane "omitted many potentially useful characters", "his interpretation of characters predisposes the analysis toward particular theories" and that "his methods of scoring groups are sometimes questionable". It is not clear as to why Doyle and Donoghue (1986, p. 340, 412) consider pinnately compound leaves/once-pinnate leaves as the derived state in the Glossopteridales, or that "the pinnate arrangement, as in the pollen organs and the ovulate organ *Lidgettonia*, is the basic condition."

Many of us very casually use the term Pteridosperm, like the so-called Mesozoic pteridosperms where nothing is known about the relationship of the leaf and the supposedly related fructification, except that based on similarity of the cuticular organisation. Harris (in Plumstead, 1952, p. 322) had suggested that "such strange plants should not be placed in the Pteridosperms...". Pant (1977, p. 20) remarked that "the Glossopteridales are very different". The glossopterids are thus best placed in the order Dictyopteridiumales in the Class Glossopteridopsida.

IS ERETMONIACEAE, TOO, A GLOSSOPTERID?

Another group of plants, the Eretmoniaceae, has sometimes been placed with the glossopterids. Except for its occurrence in some of those sediments that contain the glossopterids, not much is common between the two. In the Eretmoniaceae, the fructifications are branched 1-4 times; each branch terminates into a head. Both pollen-bearing (*Eretmonia* emend. *Glossotheca* Surange & Maheshwari) and ovule-bearing (*Lidgettonia* Thomas = *Partha* Surange & Chandra) fructifications are known. The leaf to which the fructification is attached is scale-leaf like, which shows reticulate venation but no midrib (Surange & Maheshwari, 1970). Anatomical details are also lacking for this group. At present there is no evidence to suggest that the Eretmoniaceae had a close affinity with the Dictyopteridiumaceae. In fact, some other detached, profusely branched fructifications have been reported from the Indian Gondwana, which are quite unlike the glossopterid fructifications. For example, *Ottokaria dichotoma* (Chandra, 1984), *Veekaeringhia dargavaensis* Maheshwari & Bajpai and *Bebaisabana drimadarshanii* (Bajpai & Maheshwari, 1991).

Thus in Dictyopteridiumales and Eretmoniales we have two different orders of plants that may be related, within the Class Glossopteridopsida.

	Taxon	Australia	India	Africa	South America	Antarctica	Arabian Plate
Late Permian	*Satsangia*	-	+	-	-	-	-
	Utkalia	-	+	-	-	-	-
	Escourtia	-	-	+	-	-	-
	Squamella	+	-	-	-	-	-
	Cometia	+	-	-	-	-	-
	Rigbya	+	-	+	-	-	-
	Nesowalesia	+	-	-	-	-	-
	Eretmonia	+	+	+	+	+	-
	Glossotheca	-	+	-	+	-	-
	Lidgettonia	+	+	+	-	-	-
	Senotheca	-	+	-	-	-	-
	Austroglossa	+	+	-	-	-	-
	Scutum	+	+	-	-	+	-
	Plumsteadia	+	+	+	-	+	-
	Dictyopteridium	+	+	-	+	+	-
	?Arberia	-	-	-	-	-	?
Middle Permian	*Rigbya*	-	-	-	-	-	+
	Eretmonia	-	?	-	-	-	-
	Senotheca	-	-	-	-	-	-
	Hirsutum	-	-	+	+	-	-
	Scutum	-	+	+	+	-	+
	Plumsteadia	+	-	-	+	-	+
	Dictyopteridium	+	+	-	-	-	-
	Ottokaria	-	?	-	+	?	-
	Arberiopsis	-	-	-	+	-	-
	Arberia	-	-	-	+	-	-
	Birbalsahnia	-	+	-	-	-	-
	Veekaysinghia	-	+	-	-	-	-
Early Permian	*Hirsutum*	-	-	-	+	-	-
	Plumsteadia	+	-	+	+	-	-
	Ottokaria	+	+	+	-	-	-
	Arberiopsis	-	-	-	+	-	-
	Arberia	+	+	-	+	-	-

Fig. 1—Distribution of glossopterid and other fructifications, in time and space, on the Gondwana Supercontinent.

STRATIGRAPHICAL DISTRIBUTION OF FRUCTIFICATIONS

Fructifications assigned to the glossopterids have been reported from most regions of the Gondwana Supercontinent. The possible use of these fructifications in biostratigraphy was discussed at a workshop during the 10th Meeting of the Palaeobotanists and Palynologists held at Guarulhos, Brazil during December 2000. No consensus could be arrived at. The main stumbling block seems to be the extreme paucity of the glossopterid fructifications in the sediments throughout, and more particularly so in the South American and Antarctic continents. Rigby (2000) opined that "*Glossopteris* and its fructifications may prove to be better indicators of environmental and climatic conditions than as stratigraphic correlators". Even so, it is possible to arrive at broader zonations based on the available database.

In Australia, McLoughlin (2000) recognises three levels of fertile glossopterids, that is, Lower Permian (containing *Arberia*), Middle-Upper Permian (containing *Dictyopteridium* and *Lidgettonia*) and Upper Permian (containing *Rigbya*, *Cometia* and *Senotheca*). It would thus seem that in Australia *Lidgettonia* appears earlier than *Senotheca*.

In India, too, a similar broad zonation could be recognised (Bajpai, 2000). *Arberia*, supposed to be a fructification of the genus *Gangamopteris* (Rigby, 1972) is restricted to the Talchir and Karharbari formations (Early Permian). *Ottokaria* is known from the lower part of the Barakar Formation (= Karharbari Formation, Early Permian). The reported occurrence of *Ottokaria* in the Raniganj Formation (Banerjee, 1978) and Illawarra Coal Measures (White, 1978) is to be confirmed by further finds. *Dictyopteridium* ranges from late Early Permian to the latest Permian, whereas other foliose fructifications are confined to the Late Permian. Contrary to the situation in the Australian Gondwana, in the Indian Gondwana the genus *Lidgettonia* appears later than *Senotheca*.

In Africa, Anderson and Anderson (1985) have recognised four families of glossopterid fructifications. They have postulated a stratigraphic zonation based on glossopterid fructifications: these zones correspond to the Dwyka, Middle Ecca, Upper Ecca and Estcourt formations, respectively.

A general summary of distribution in time and space of major glossopterid fructification genera is shown in Fig. 1 (data collated from different sources, e.g., Anderson & Anderson, 1985; Archangelsky, 1992; Archangelsky *et al.*, 1981; Banerjee, 1984; Benecke, 1976; Bernardes de Oliveira, 1978; Bose *et al.*, 1990; Broutin, 2000; Chandra & Srivastava, 1981; Cúneo *et al.*, 1993; Holmes, 1974; Lacey & Huard-Moine, 1966; Lacey *et al.*, 1975; le Roux & Anderson, 1977; McLoughlin, 1990a, b; Maheshwari, 1992; Maithy, 1974; Millan, 1967; Rigby, 1972; Schopf, 1976; White, 1964, 1978).

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Micromorphology and Adaptation of leaf epidermal traits in Rhizophoraceae to Coastal Wetland Ecosystem

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ABSTRACT

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The leaf epidermal/cuticular micromorphological feature was studied in four genera viz. *Rhizophora*, *Kandelia*, *Ceriops* and *Bruguiera* of family Rhizophoraceae. While *Rhizophora* has the means to exude excess salt through their stomatal modification (cork-wart-like structure), *Kandelia* shows papillae on the epithelium perhaps for the same reason. No cork-wart like structure was found in *Kandelia*, *Ceriops* and *Bruguiera* species. The epidermal cell size, stomata length and breadth, stomatal index and different areas in the costal and intercostal cell wall pattern are the identifiable traits in all the species studied. *Rhizophora apiculata* and *Bruguiera caryophylloides* shows marked decrease in the epidermal cell size and Stomatal Indices with the varying coastal ecology. During salinity related stress the cork-wart-like structure in *Rhizophora apiculata* on the lower epidermis becomes rudimentary and non-functional while it is well developed and of larger size in normal ecological conditions. *Bruguiera cylindrica* differs with all the species in having undulate cell wall pattern in the costal [illegible] with the stomata and shows closer affinity with *B. gymnorrhiza* (costal cells distinct but with straight anticlinal cell wall) and [illegible] its Syn. *B. caryophylloides* in this respect. The stomatal index (SI) in *Rhizophora mucronata* shows similarity with that of *Bruguiera parviflora* and *B. gymnorrhiza*. However, *R. apiculata* growing in stressed environment shows similar SI as in *Bruguiera cylindrica* and other species of *Rhizophora*, *Ceriops* and *Kandelia*. It is understood that perhaps *Rhizophora apiculata* and *C. decandra* (Syn. *C. roxburghiana*) and *B. cylindrica* (Syn. *B. caryophylloides*) have SI as a non-consistent feature that tends to vary with the changing environment. Mangrove species showing similarity in the epidermal traits and their adaptive features may thrive together in a common coastal environment. Leaf epidermal traits of Rhizophoraceae would help in the identification of fossil cuticles at the species level and their non consistent features adapting to the changing coastal environment would provide potential proxy data for interpreting palaeoecology.

Key-words—Rhizophoraceae, Leaf micromorphology, Coastal ecosystem.

परिवर्तनशील आर्द्रभूमि तटीय पारिस्थितिकीय तंत्र के परिप्रेक्ष्य में राइज़ोफोरेसी कुल के पर्ण उपचर्म लक्षणपुंजों का सूक्ष्मसंरचनाविज्ञान तथा अनुकूलन

अंजुम फारूकी

सारांश

राइज़ोफ़ोरेसी कुल के चार वंशों—*राइज़ोफ़ोरा, कैण्डेलिया, सीरियॉप्स* तथा *ब्रुगुएरा* के पर्ण अधिचर्मीय/सूक्ष्म संरचनात्मक उपचर्मीय अभिलक्षणों का अध्ययन किया गया। *राइज़ोफ़ोरा* अपने स्टोमी (रंध्री) रूपान्तर (कॉर्क-मस्से की भाँति की संरचना) द्वारा अधिक मात्रा में विद्यमान लवण का स्राव करता है, जबकि यह सम्भवतः इसी कारणवश *कैण्डेलिया एपीथीलियम* में दरार प्रदर्शित करता है। *कैण्डेलिया, सीरियॉप्स* तथा *ब्रुगुएरा* प्रजातियों में कोई भी कॉर्क-मस्से के आकार की संरचना नहीं पायी गयी है। अधिचर्मीय कोशिका आमाप, रंध्री लम्बाई तथा चौड़ाई, रंध्री अनुक्रम तथा तटीय एवं अन्तरतटीय कोशिका भित्ति विन्यास में विभेदन सभी अध्ययन की गयी प्रजातियों के अभिनिर्धारणीय लक्षणपुंज हैं। *राइज़ोफ़ोरा एपिक्यूलाटा* तथा *ब्रुगुएरा कैरियोफ़िल्लॉयडीज़* परिवर्ती तटीय पारिस्थितिकी विज्ञान के अनुसार अधिचर्मीय कोशिका आमाप तथा रंध्री अनुक्रमों में वृद्धि/ह्रास प्रदर्शित करते हैं। लवणता सम्बन्धी प्रतिबल के दौरान अधो अधिचर्म पर *राइज़ोफ़ोरा एपिक्यूलाटा* में विद्यमान कॉर्क-मस्से की भाँति की संरचना अल्पवर्धित तथा अक्रियाशील हो जाती है, जबकि यह सुविकसित है तथा सामान्य पारिस्थितिकीय स्थितियों में अपेक्षाकृत बड़े आमाप की है। *ब्रुगुएरा सिलेण्ड्रिका* रंध्री से जड़ित तटीय क्षेत्रों में तरंगित कोशिका भित्ति विन्यास से युक्त सभी प्रजातियों से भिन्न है तथा यह *बी. जिम्नोराइज़ा* (तटीय कोशिकाएँ सुस्पष्ट हैं, किन्तु ये तरंगित अपनतिक कोशिका भित्ति से युक्त हैं) से निकटस्थ बन्धुता प्रदर्शित करता है, जबकि इस सम्बन्ध में यह इसके तुल्य *बी. कैरियोफ़िल्लॉयडीज़* के साथ बन्धुता नहीं प्रदर्शित करता है। *राइज़ोफ़ोरा एपिक्यूलाटा* का रंध्री अनुक्रम *ब्रुगुएरा पार्वीफ़्लोरा* तथा *बी. जिम्नोराइज़ा* के साथ समरूपता प्रदर्शित करता है, जबकि प्रतिबलीय पर्यावरण में उगने वाला *आर. एपिक्यूलाटा, ब्रुगुएरा सेक्सैंग्यूला* तथा *राइज़ोफ़ोरा, सीरियॉप्स* एवं *कैण्डेलिया* की अन्य प्रजातियों के समरूप रंध्री अनुक्रम प्रदर्शित करता है। सम्भव है कि *राइज़ोफ़ोरा एपिक्यूलाटा* एवं *सी. डिकैण्ड्रा* (*सी. टॉक्सबर्गियाना* के तुल्य) तथा *बी. सिलिण्ड्रिका* (*बी. कैरियाफिल्लॉयडीज़* के तुल्य) का रंध्री अनुक्रम एक असंगत अभिलक्षण है, जो परिवर्ती पर्यावरण के अनुसार परिवर्तनशीलता का रुझान रखता है। अधिचर्मीय लक्षणपुंजों तथा उनके अनुकूलित अभिलक्षणों में समरूपता प्रदर्शित करने वाली मैंग्रोव प्रजातियाँ एक उभयनिष्ठ तटीय पर्यावरण में एक साथ फल-फूल सकती हैं। राइज़ोफ़ोरेसी के पर्ण उपचर्मीय लक्षणपुंज एक विशिष्ट स्तर पर अश्मित उपचर्मों के अभिनिर्धारण हेतु सहायक हैं तथा परिवर्ती तटीय पर्यावरण के अनुकूल इनके असंगत अभिलक्षण पुरापारिस्थितिकी के निर्वचन हेतु प्रभावी कूट आंकड़े प्रदान करेंगे।

संकेत शब्द - राइज़ोफ़ोरेसी, पर्णसूक्ष्मसंरचना विज्ञान, तटीय पारिस्थितिकी तंत्र.

INTRODUCTION

IT was in late Silurian- early Devonian Period (400 million yrs ago) that the vascular plants attempted to invade land and acclimatized to the terrestrial environment. Since then plants had to develop features which would help them in adaptation to different ecosystem with special reference to cuticle, stomata and vascular tissue and are considered to have developed simultaneously that led to the emergence and survival of large terrestrial plants (Chaloner, 1970). Such a process is still going on with the number of evidences coming up where the plants adapt to different ecological and edaphic conditions by changing their epidermal traits in order to survive (Stace, 1965a, b; Fahn, 1979; Tukey, 1971; Dilcher, 1974; Farooqui *et al.* 1995, 1997; Farooqui & Bajpai, 1999).

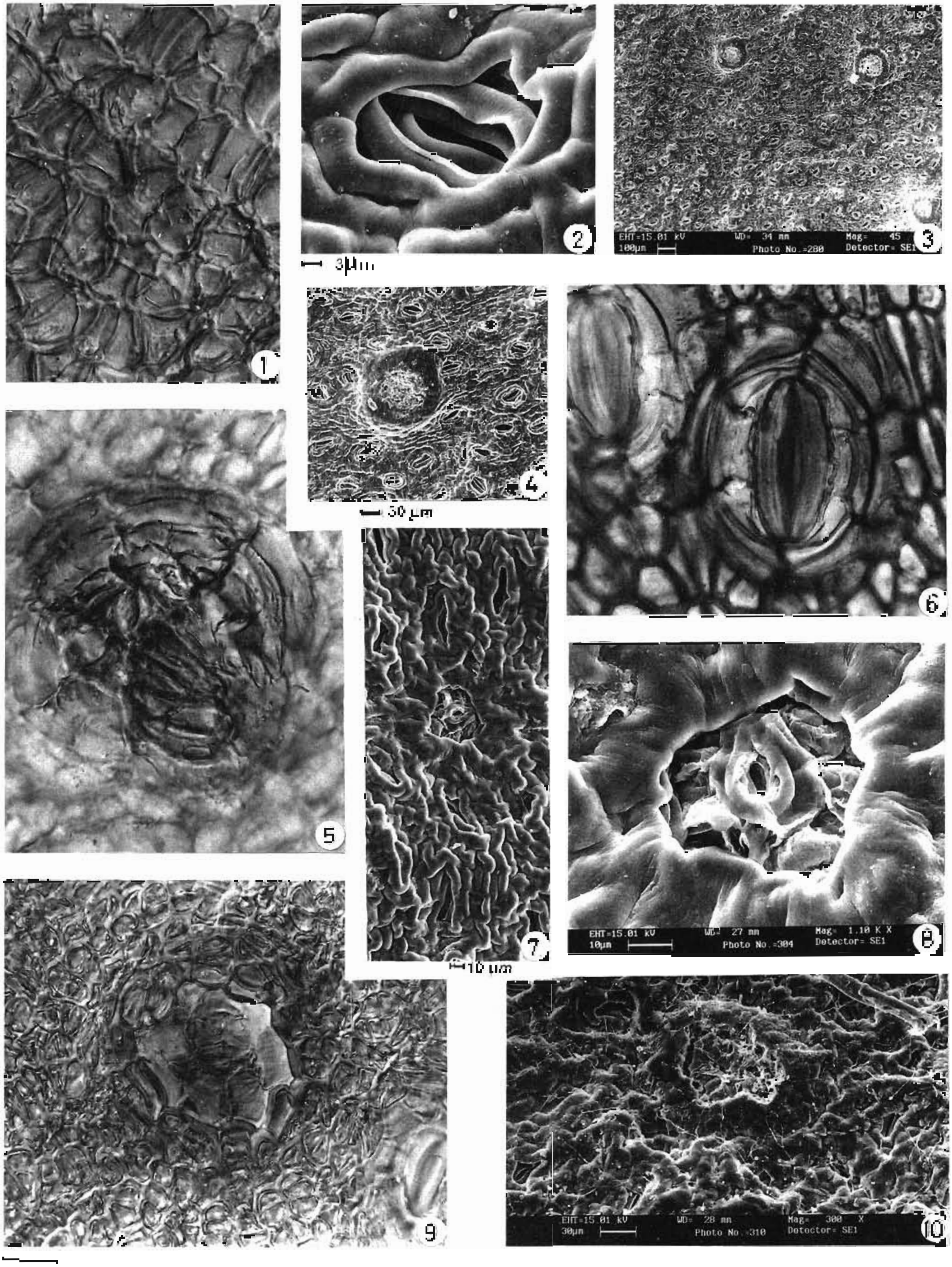
Coastal wetland ecosystems show different ecological zones and each zone is demarcated distinctly by different types of mangrove vegetation (Banerjee, 1994). Any change in the ecology affects the specific zonation of the mangroves depending upon the duration, direction and magnitude of sea-level and climatic fluctuations (Ellison & Stoddart, 1991; Ellison, 1993). It is evident that the distribution of different species is variable along the Indian coastal region and also world wide depending on various factors that also include the geomorphology and geographical distribution (Muller, 1959; Caratini *et al.*, 1973; Blasco, 1975; Chapman, 1977; Tomlinson,

PLATE 1 →

(Scale given below each photoplate is equal to 10 μm unless mentioned otherwise)

Rhizophora apiculata (Specimen Se. No. 1)

1. Upper leaf epidermis showing pentagonal irregular cells with straight- arcuate anticlinal cell walls and underlying hypodermal cells (Light Photomicrographs-LP).
2. Lower leaf epidermis showing sunken stomata, guard cells covered by stomatal legdes (Scanning Electron Microscopic Photomicrographs; SEMP).
3. Lower epidermis (LP) showing compact radially arranged epidermal cells surrounding the reduced stomata that appear highly raised in the surface view called as cork-warts.
4. SEMP of cork-warts in favourable condition.
5. LP of corkwarts.
6. LP of stomata on the lower epidermis.
7. SEMP of cork-warts with reduced stomatal opening in the stress condition (Specimen Se. No. 3).
8. SEMP showing distinct gross features of stomata in the centre of cork-warts.
9. LP of cork-warts in stress condition showing compact and reduced cell size of the stomatal complex.
10. SEMP showing lower epidermis in stress condition with smaller cork-warts and thick epicuticular ornamentation.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EHT=15.01 kV
10µm
WD= 27 mm
Photo No.=304
Mag= 1.10 K X
Detector= SE1
8
9
EHT=15.01 kV
30µm
WD= 28 mm
Photo No.=310
Mag= 300 X
Detector= SE1
10

PLATE 1

NO.	TAXA	I	II	III	IV
1	*Rhizophora apiculata*	C	A	C	B
2	*R. mucronata*	A	C	C	A
3	*R. stylosa*	A	B	B	A
4	*Kandelia candel*	B	C	C	A
5	*Ceriops tagal*	A	C	B	A
6	*C. roxburghiana*	A	A	A	A
7	*C. decandra*	A	B	C	A
8	*Bruguiera parviflora*	B	B	C	B
9	*B. sexangula*	B	B	A	A
10	*B. caryophylloides*	B	A	A	C
11	*B. cylindrica*	C	A	B	C
12	*B. gymnorrhiza*	B	A	A	B

CELL SIZE (µm²) I: A=20-35; B=50-100; C=140-150

STOMATAL LENGTH (µm) II: A=14-15, B=18-21; C=20-21; D=29

STOMATAL BREADTH (µm) III: A=8; B=10-12; C=14-17

STOMATAL INDEX IV: A=7.28-9.9; B=12.8-15.8; C=21.9-29.2

Fig. 1—Affinity between members of Rhizophoraceae with reference to single parameter.

1986; Naskar & Guha Bakshi, 1987; Ellison, 1989; Dagar *et al.*, 1991; Untawale & Jagtap, 1991; Plaziat, 1995; Hoq Hair, 1995; Naskar & Mandal, 1999). Mangroves have been used as biological sea-level indicators since Tertiary period i.e., 65 million yrs (Ellison, 1989). Besides pollen/spores, the cuticular or epidermal microscopic fragments are also abundant in the sedimentary sequence. Reconstruction of former vegetation, climate and environment through palynology alone cannot hope to answer all our questions about palaeoecology and palaeoenvironment. The leaf epidermal traits play a vital role in the adaptation of plants to different environmental conditions. The gross epidermal features along with the adaptive epidermal traits have great potential for understanding various environmental changes (Ball & Farquhar, 1984; Beerling & Chaloner, 1992). However, it is difficult to evaluate the fossil cuticles unless the modern potential specimens are thoroughly investigated in different environment and the variability in the epidermal features is recorded. In an attempt number of workers have evidently compared the modern analogue with that of fossil specimens (Dilcher, 1974; Mehrotra *et al.*, 1998; Cleal *et al.*, 1999). Previous work related to epidermal features of Rhizophoraceae is limited (Metcalfe & Chalk, 1950; Tomlinson, 1986; Das & Ghose, 1996; Naskar & Mandal, 1999) and the understanding of differences in epidermal traits between the genus and between the species is meagre. So far, the data on modern analogue of mangrove cuticle/epidermis and its comparison with the fossil specimens is lacking, although mangrove palynological assemblage in India has been reported since Tertiary Period (Ramanujam & Reddy, 1984). With this objective the present paper puts together the studies related to micromorphology of the epidermal characteristics/traits of the members of Rhizophoraceae and its adapting characters to the changing coastal wetland ecosystem that is directly influenced by sea-level and climatic fluctuations. The study would provide a potential modern analogue for understanding the fossil mangrove cuticle/epidermis *inter alia* dynamics of the coastal palaeovegetation, palaeoecology and palaeoclimate.

MATERIAL AND METHODS

Four genera and ten species belonging to Rhizophoraceae were studied for their leaf epidermal/cuticular micromorphology. These are *Rhizophora apiculata* Bl., *R. mucronata* Lamk., *R. stylosa* Griff., *Kandelia candel* (L.) Druce, *Ceriops tagal* (Perrottet) C.B. Robinson, *C. decandra* (Griff.) Ding Hou (Syn. *C. roxburghiana* Arn.), *Bruguiera parviflora* (Roxb.) Wt. & Arn. Ex Griff., *B. sexangula* (Lour.) Poiret, Bl., *B. cylindrica* (L.) B1. (Syn. *B. caryophylloides* Blume) and *B. gymnorrhiza* (L.) Lamk.

The middle portion from margin to the mid-rib part of the leaf blade was selected for epidermal micromorphological studies in order to minimize variability (Poole *et al.*, 1996). The samples were soaked in 50 per cent (v/v) glycerine overnight

PLATE 1 →

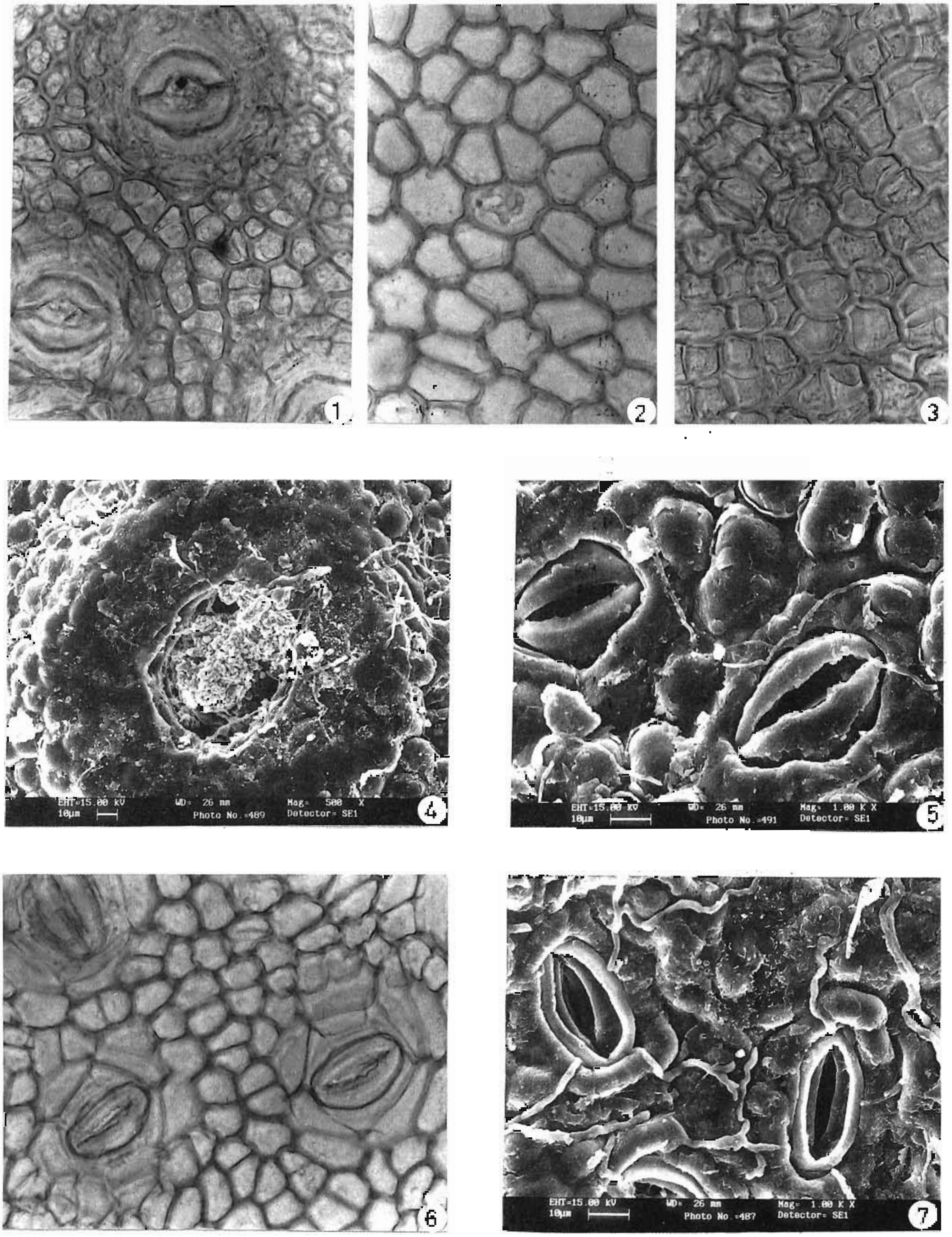
(Scale given below each photograph is equal to 10 µm unless mentioned otherwise)

R. mucronata (Specimen Sr. No. 7)

1. LP of lower leaf epidermis
2. LP of upper leaf epidermis
3. SEMP of cork warts filled with particulate encrustations in the stomatal cavity similar to *R. apiculata*
4. SEMP showing stomatal ledges and flaky fragmented epicuticular wax

R. stylosa (Specimen Sr. No. 8)

5. LP of upper leaf epidermis
6. LP of lower leaf epidermis
7. SEMP of the lower leaf epidermis


1
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3
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10µm Photo No.=489 Detector= SE1
4
EHT=15.00 kV WD= 26 mm Mag= 1.00 K X
10µm Photo No.=491 Detector= SE1
5
6
EHT=15.00 kV WD= 26 mm Mag= 1.00 K X
10µm Photo No.=487 Detector= SE1
7

PLATE 2

Se No	Taxa	Herbarium Specimen No., Name (Collector), Year & Area of Collection
1.	*Rhizophora apiculata* Blume.	HIFP 311, Pascal 1974, Pichavaram
2.	*R. apiculata*	NBRI 88395, Saran & Party 1961, Long Island, Andaman
3.	*R. apiculata*	BSIP 11940, Farooqui 1998, Pichavaram
4.	*R. mucronata* Lamk.	HIFP 312, Pascal 1974, Pichavaram
5.	*R. mucronata* Pichavaram	HIFP 904, Thanikaimoni 1982
6.	*R. mucronata* Pichavaram	NBRI 2652, Ramalingam 1945
7.	*R. mucronata*	BSIP 11941, Farooqui 1998, Pichavaram
8.	*R. stylosa* Griff. Marakkanam	HIFP 494, Thanikaimoni 1979
9.	*Kandelia candel* (L.) Druce	HIFP UT 1154, Thanikaimoni 1979, Mahanadi estuary
10.	*Ceriops decandra* (Griff.) Ding Hou (Syn. *C. roxburghiana* Arn.)	HIFP 1002, Thanikaimoni 1973, Pichavaram
11.	*Ceriops roxburghiana*	NBRI 67212, Srivastava 1960, Sunderbans
12.	*C. roxburghiana*	NBRI 79622, Saran and Party 1961, Long Island, Andaman
13.	*C. roxburghiana*	NBRI 67212, Srivastava 1960, Mahanadi estuary
14.	*C. decandra*	BSIP 4527, Takhtajan & Lakhanpal 1966, Sunderbans
15.	*C. tagal* (Perottet) C.B. Robinson	NBRI 38895, Srivastava 1960, Sunderbans
16.	*Bruguiera caryophylloides* (Burm. F.) Bl. (growing in fish pond)	NBRI 38, Backer 1913, Java
17.	*B. caryophylloides*	NBRI 2653, Swaminathan 1945, Pichavaram
18.	*B. caryophylloides*	NBRI 79463, Saran & Party 1961, Long Island Andaman
19.	*B. gymnorrhiza* (L.) Lamk.	HIFP 493, Ramesh 1984, Pichavaram
20.	*B. gymnorrhiza*	NBRI 86721, Kaul & Party 1965, Cuttack, Orissa
21.	*B. gymnorrhiza*	BSIP 4549, Lakhanpal & Takhtajan 1966, Sunderbans
22.	*B. parviflora* (Roxb.) Wt. & Arn. Ex Griff.	HIFP VKB 12, Legris 1957, Mahanadi estuary
23.	*B. sexangula* (Lour.) Poir	HIFP 1769, Blasco & Thanikaimoni 1974, Sunderbans
24.	*B. sexangula*	BSIP 3224, Lakhanpal 1966, Ceylon
25.	*B. cylindrica* (L.) Blume.	HIFP VKB 1, Legris 1957, Pichavaram
26.	*B. cylindrica*	HIFP 314, Pascal 1974, Pichavaram
27.	*B. cylindrica*	BSIP 4540, Takhtajan & Lakhanpal 1966, Sunderbans

Fig. 2—List of Herbarium specimens studied (HIFP—Herbarium French Institute, Pondicherry; NBRI—National Botanical Research Institute and BSIP—Birbal Sahni Institute of Palaeobotany, Lucknow).

and the leaf epidermis was separated following Ahmad (1974) and Dilcher (1974). The micromorphological description of epidermal features has been followed after Dilcher (1974). The percentage of stomatal index (SI)= Number of stomata (per sq mm leaf area)/ Number of stomata+ No. of non-stomatal epidermal cells per sq mm leaf area x 100 was calculated following Salisbury (1927). The Scanning Electron Microscopic study was carried out after processing the samples through ethanol series and gold-palladium alloy coating before examining in LEO – 430 Scanning Electron Microscope (SEM).

The herbarium samples were obtained from Institut Francais, Pondicherry, National Botanical Research Institute and Birbal Sahni Institute of Palaeobotany, Lucknow. The names of the species with their Synonyms documented in the respective herbarium sheets have been retained in order to

PLATE 3

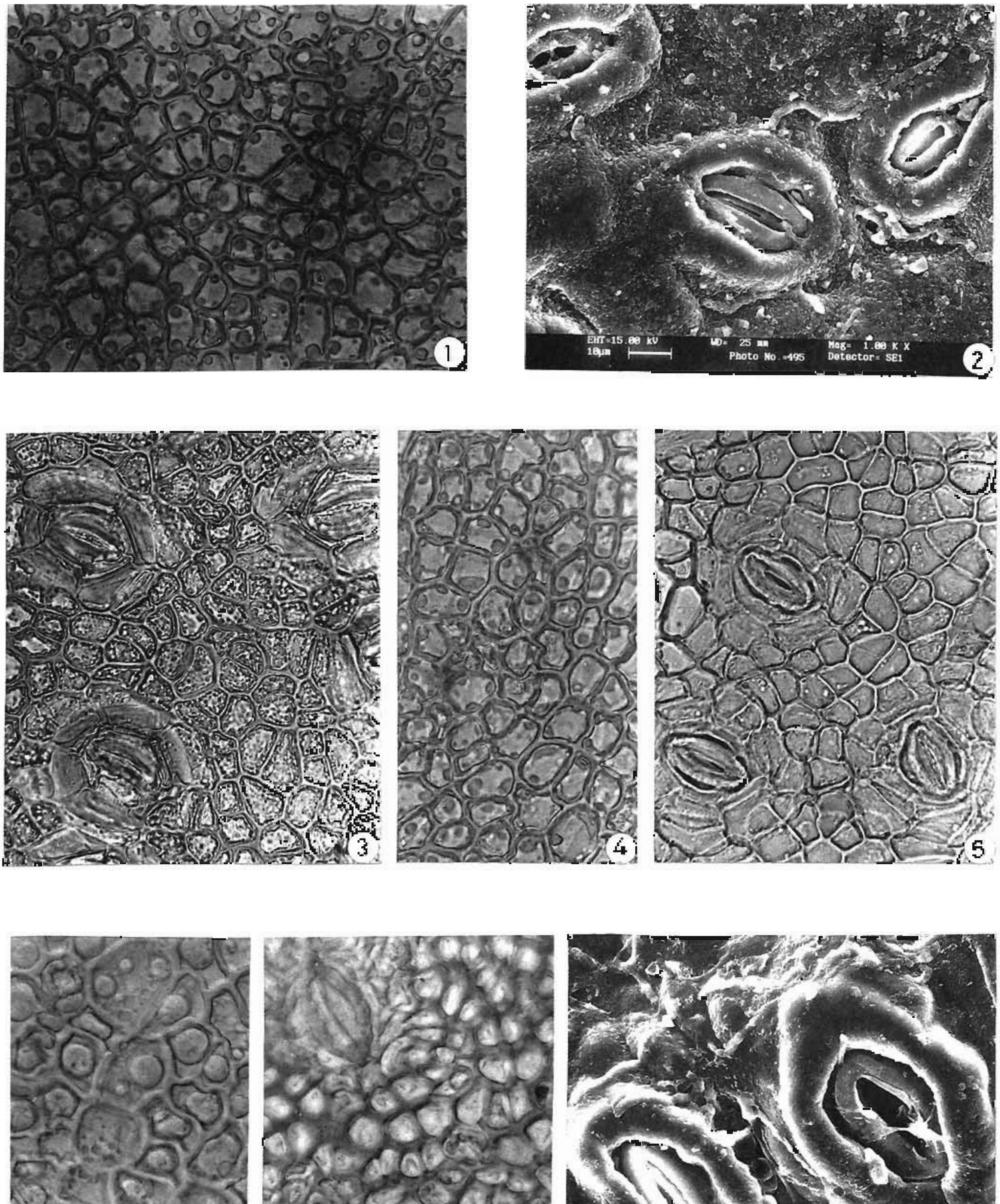
(Scale given below each photoplate is equal to 10 μm unless mentioned otherwise) →

Ceriops decandra (Specimen Se. No. 14)

1. LP of upper leaf epidermis; lower leaf surface.
2. SEMP showing finely lamellated to granular epicuticular ornamentation.
3. As seen under light microscope

C. roxburghiana (Specimen Se. No. 13)

4. LP of upper leaf surface.
5. LP of lower leaf surface; *C. tagal* (Specimen Se. No. 15).
6. LP of upper leaf surface.
7. LP of lower leaf surface.
8. SEMP showing lower leaf surface with typical rhomboid stomatal complex. Finely striated–granular cuticular ornamentation.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Detector= SE1
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7
EHT=15.00 kV
10μm
WD= 25 mm
Photo No.=497
Mag= 1.00 K X
Detector= SE1
8

PLATE 3

study the variation. The list of herbarium specimens is given in Fig. 2.

RESULT AND DISCUSSION

As a barrier to excessive and uncontrollable water loss, the leaf epidermal cells are the most numerous and usually they show considerable variation in size and shape along with number of consistent and non-consistent characteristics (Willmer & Fricker, 1996; Mc Elwain & Chaloner, 1996; Farooqui et al., 1995, 1997; Chaloner & Mc Elwain, 1997; Farooqui & Bajpai, 1999).

Rhizophoraceae (Dahlgren, 1980; Tomlinson, 1986; Naskar & Guha Bakshi, 1987), a pantropical family consists of 16 genera and 120 species. It is in a separate order Rhizophorales: Tribe Rhizophoreae and comprises of four true mangrove genera i.e., *Rhizophora* L., *Ceriops* Arn., *Kandelia* Wt. & Arn. and *Bruguiera* Lamk. These are generally confined to the intertidal zone. Although these thrive well in fresh water ecology but sooner its growth is overpowered by fresh water plant taxa (Chandler & Rabi, 1983).

The number of plant species growing in mangal is small. But, the nomenclature is still a confusing chapter. Most early systematic work was done entirely on the basis of herbarium specimens, so number of descriptions of the same species under different names came into being. Elementary synonymy has been extensively used in the literature (Ridley, 1981; Tomlinson, 1986). During the present study the synonyms of *Ceriops decandra* i.e., *C. roxburghiana* and *Bruguiera cylindrica* i.e., *B. caryophylloides* have been dealt in separately for their significant identifiable difference in leaf micromorphological features in different specimens.

In all the species studied the leaves are dorsiventral and stomata are present on the lower leaf surface. The sunken stomata described by Metcalfe and Chalk (1950) is a mixture of ranunculaceous, cruciferous and rubiaceous type. It consists of guard cells covered by stomatal ledges which are plain and conspicuous. There is no specific subsidiary cell and the epidermal cells surrounding the stomata are arranged radially to form stomatal complex. These are elongated and distinct from other epidermal cells. The size, number, position, its obscurity or distinction from other areas are the identifiable features which vary from species to species.

The upper leaf surface in members of Rhizophoraceae show irregular epidermal cells with insignificant difference in cell wall thickness. The anticlinal cell wall pattern is straight to arcuate in all the species. The costal and intercostal area is well differentiated in *B. cylindrica* (Syn. *Bruguiera caryophylloides*). Other species do not show well defined costal or intercostal areas. The cell size shows a wide range (54-145 mm²) of variability within species. Larger cell size (80-145 mm²) was found in *Rhizophora* (Pl. 1.1; pl. 2.2-3) closely related with *Kandelia* (Pl. 4.1-3). However, *Bruguiera* spp. (Pl. 5.1, 5; Pl. 6.2, 4; Pl. 7.1) differs in having well demarcated costal and intercostal cells that have sinuate anticlinal cell walls. The smallest cell size (50-60 mm²) was found in *Ceriops* spp. (Pl. 3.1, 4, 7) with a slight thickened anticlinal cell wall. The multilayered epidermis is prominent in the surface view only in *Rhizophora apiculata* and *Kandelia candel*.

Fig. shows the characteristic features of the lower leaf surface. The cell size in Group A (20-35 μm²) comprises *Rhizophora mucronata*, *R. stylosa*, *Ceriops tagal* and *Ceriops decandra* (*C. roxburghiana*). The Group B (50-100 μm²) includes *Kandelia candel*, *Bruguiera parviflora*, *B. sexangula*, *B. caryophylloides* and *Bruguiera gymnorrhiza*. The largest cell size (140-150 μm²) was found in *Rhizophora apiculata* and *Bruguiera cylindrica*. The cell size in *Bruguiera caryophylloides* growing in the coastal waters (77±2.5 μm²) and in the fresh water fish pond (48 ± 1.5 μm²) show significant variation with 50 % reduction in the latter. Thus, the cell size varies in different ecology. However, the cell size in *B. cylindrica* was found to be 140±4.9 μm². As *B. caryophylloides* is Synonym of *B. cylindrica* it may be that either the cell size is the non consistent epidermal trait or it should be kept separately while identifying the micromorphological features. Similar feature has also been recorded in *R. apiculata* (Farooqui, 2000) where the cell size reduces in salinity related stress. Thus, *Bruguiera caryophylloides* shows affinity with the *Rhizophora apiculata*. Previously, *B. caryophylloides* Blume was also named as *Rhizophora caryophylloides* Jack Mal. or *B. cylindrica* Linn. (Hooker, 1879).

Affinity between different species with respect to stomatal length and breadth and stomatal index is shown in Fig. 1. It was found that *Rhizophora apiculata* has the longest stomatal length followed by *R. mucronata*, *Kandelia candel* and *Ceriops tagal* (29-31 mm). However, stomata length in *Rhizophora stylosa*, *Ceriops decandra*, *Bruguiera parviflora*, and *Bruguiera sexangula* is 18-21 mm. *Bruguiera cylindrica* (Syn. *B. caryophylloides*) and *B. gymnorrhiza* show only 14-15 mm stomatal length. With respect to stomatal length and breadth *Ceriops decandra* (Specimen No. 10 & 14) and its Syn. *C. roxburghiana* (Specimen No. 11-13) show considerable

PLATE 4

(Scale given below each photoplate is equal to 10 μm unless mentioned otherwise)

Kandelia candel (Specimen No. 9) →

1-3. LP of upper leaf epidermis showing dark patches of thickened epidermal cells distinct from the surrounding cells. Lower leaf epidermis.

4-5. LP showing dark areas of thickened cells.

6. LP showing the dark areas with epidermal ripple in the centre.

7. SEM/LP showing fine granular ornamentation with flakes of epicuticular wax.

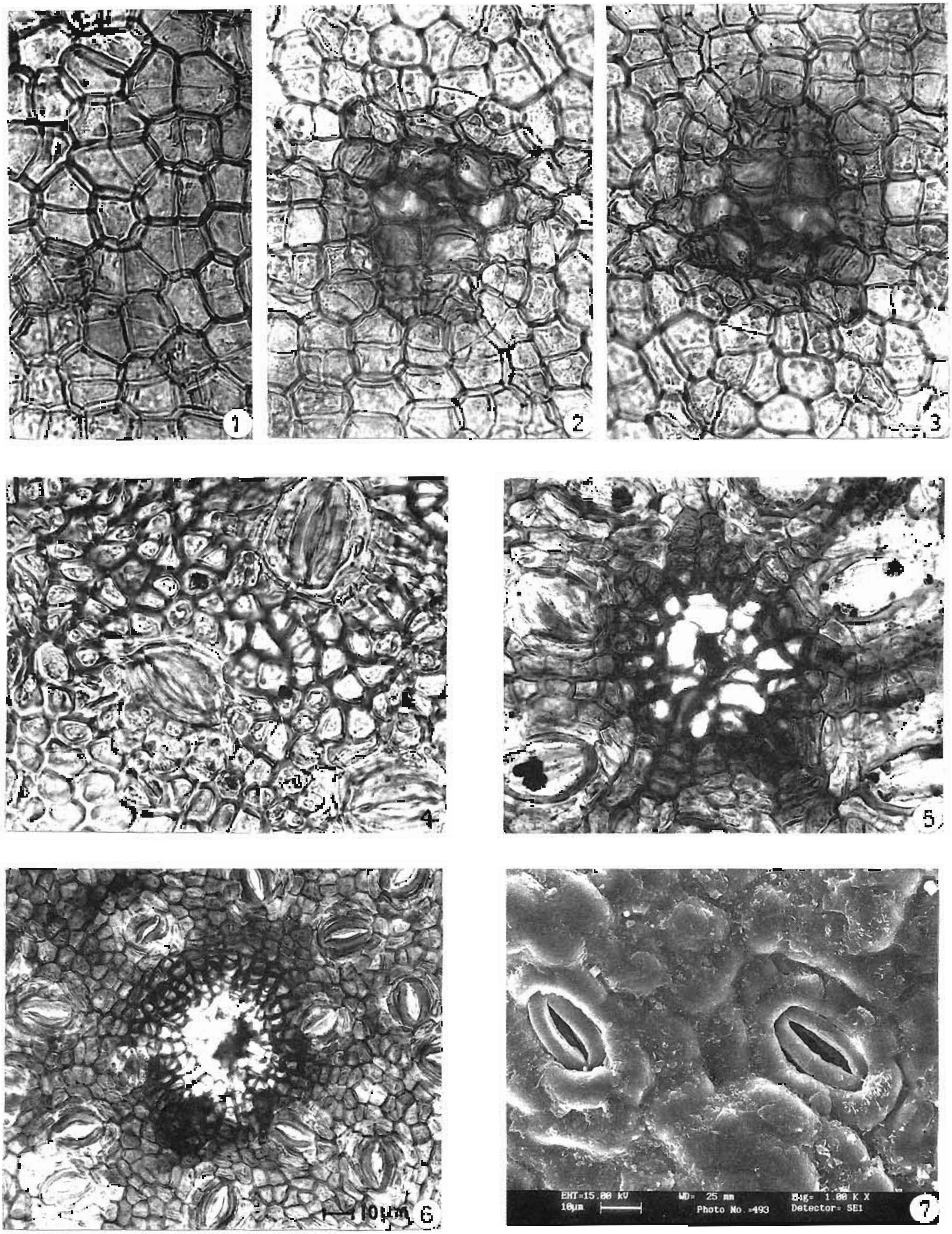
1
2
3
4
5
10µm
6
EHT=15.00 kV
10µm
WD= 25 mm
Photo No.=493
Detector= SE1
7

PLATE 4

variation with significant smaller stomatal length and breadth and larger cell size at 5 per cent error probability in the latter case. This trend is similar to as in *B. cylindrica* (Specimen Se. No. 25-27) and its Syn. *B. caryophylloides* (Specimen Se. No. 17 & 18). Therefore, both the species differ with their synonyms with respect to leaf epidermal micromorphological features. Number of stomata increased in *B. caryophylloides* (Specimen Se. No. 16) while growing in fresh water fish pond than in coastal water (Pl. 5.3-4).

In all the species stomata are sunken covered by the plain and conspicuous stomatal ledges as in *Rhizophora apiculata* (Pl. 1.2), that indicates the xerohalophytic nature of the plants to avoid excess transpiration when the available water becomes physiologically inactive in highly saline ecosystem. There are no salt glands in Rhizophoraceae. Being the salt excluders (Scholander, 1968) they have high sodium and chloride in the xylem sap (Dagar *et al.*, 1991). The excess salt that enters into the plant system has to be excreted by the plants. As studied earlier in *Rhizophora mucronata* by Tomlinson (1986) and Metcalfe and Chalk (1950), *Rhizophora* has cork-wart-like structure to function as hydathodes and help in salt excretion through the leaves. However, the present leaf epidermal studies in *R. apiculata* shows that the cork warts (Pl. 1.3, 4) are the modifications in the stomatal complex (Farooqui & Bajpai, 1999) and these shed off the excess salts excreted by plants during rainy season (Farooqui, 2000). Earlier it was reported (Mullan, 1931) that the excreted salts through cork-warts being hygroscopic absorbs moisture from the atmosphere and supplements the water need of the plant during stress condition. As previously recorded by Stace (1965b) and Fahn (1979), these are either an enlarged stoma or the epidermal rupture. However, our study shows that these are the modifications in the stomatal complex where the stoma reduces to a pore like structure (Pl. 1.6, 7, 8) with a stomatal cavity filled with particulate/salty encrustations surrounded by compact, smaller, elongated and radially arranged epidermal cells around the stomata. These appear as circular, distinct structures placed haphazardly on the lower leaf surface which are highly raised when observed in the surface view (Pl. 1.5). It was also observed that in the exponential phase of the leaf growth, the size and frequency of these cork-warts varies even within a single leaf and different stages of the development in cork-warts is evident (Farooqui & Bajpai, 1999). In *Rhizophora apiculata* these are more active during normal ecological system (strong tidal and fresh water influx) and becomes rudimentary type with small size and low frequency in hypersaline conditions (Pl. 1.9, 10) which in the case of *R. mucronata* was functional. This is perhaps that the Na : K ratio in *R. apiculata* is low and high in *R. mucronata*. According to Kinnade (1999) low levels of K relieved Na toxicity in plants, but low levels of Na enhanced K toxicity. My observations show a high Na : K ratio (4 to 8 : 1) in *R. mucronata* which would have probably lowered the toxic effects of high Na in leaves (Farooqui, 2000) and thus tolerant to a wide range of saline coastal ecology.

The stomatal index (SI) recorded (Fig. 1) remains same in *Rhizophora* species except in *R. apiculata* (12.5) showing higher values comparable to *B. parviflora* and *B. gymnorrhiza* (13.8). *Rhizophora apiculata* (Specimen Se. No. 3) growing in the stress condition has similar SI i.e., 8.27 as compared to *R. mucronata* (8.03) and *R. stylosa* (6.97). *Ceriops tagal*, *Kandelia candel* and *Ceriops decandra* have lowest values as 7.28, 7.30 and 7.69, respectively. However, in *Ceriops roxburghiana* the SI was found to be 10.66 which is quite high as in other specimens of *C. decandra* (Syn. *C. roxburghiana*). It may be that the SI is the non-consistent feature of this species and should be considered while identifying the species through the leaf epidermal micromorphology. Of all the species, SI in *Bruguiera cylindrica* (Specimen Se. No. 25–27) and its Syn. *B. caryophylloides* (Specimen Se. No. 17 & 18) was highest i.e., 29.2 and 21.9, respectively. However, in *B. caryophylloides* (Specimen Se. No. 16) growing in the fish pond the SI was found to be 26.6. *Rhizophora*, *Ceriops* and *Kandelia* have closer affinity with respect to stomatal indices that also shows affinity with *B. sexangula*. But only *R. apiculata* shows affinity with *B. parviflora* and *B. gymnorrhiza*. However, *R. apiculata* growing in stressed environment shows SI similar to as in other species of *Rhizophora*, *Ceriops* and *Kandelia*.

Earlier the SI has served as proxy data for the analysis of past atmospheric changes (Chaloner & McElwain, 1997; Beerling & Woodward, 1997). Palaeoecological interpretations through fossil and modern epidermis has been successfully explained earlier (Palmer, 1976; Upchurch *et al.*, 1985; Upchurch, 1995). Both the atmospheric and palaeoecological changes are generally controlled by modified epidermal cells which surround the stomata (Willmer & Fricker, 1996) with the result plants show varying Stomatal indices (Sparkman *et al.*, 1966; Bell & Farquhar, 1984; McElwain & Chaloner, 1996; Poole *et al.*, 1996a). The comparison of past

PLATE 5

(Scale given below each photoplate is equal to 10 µm unless mentioned otherwise) →

Bruguiera caryophylloides (Specimen No. 17)

1. LP of upper leaf epidermis showing sinuate anticlinal cell wall in the costal area and straight ... in intercostal areas. Lower leaf epidermis.
2. LP showing 4-5 epidermal cells around the bilayered subsidiary cells 2 are lateral to the guard cells and the other 3 on the poles of the guard cells.

B. caryophylloides (Specimen Se. No. 16)

3. LP growing in fresh water fish pond showing increase in stomatal frequency.
4. SEMP showing smooth cuticular ornamentation.

B. parviflora (Specimen Se. No. 22)

5. LP of upper leaf surface.
6. LP of lower leaf surface.

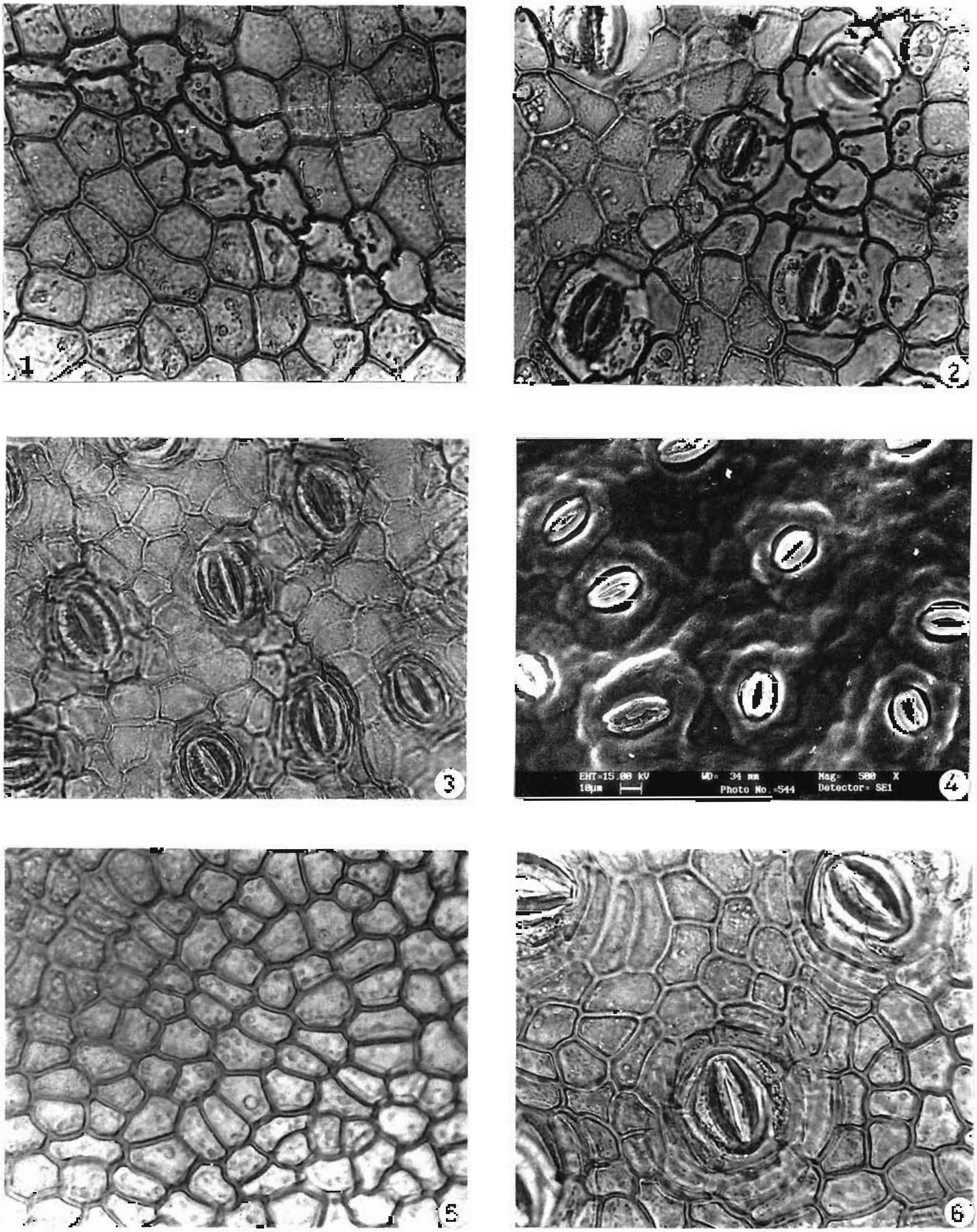
1
2
3
EHT=15.00 kV
10µm
WD= 34 mm
Photo No.=544
Mag= 500 X
Detector= SE1
4
5
6

PLATE 5

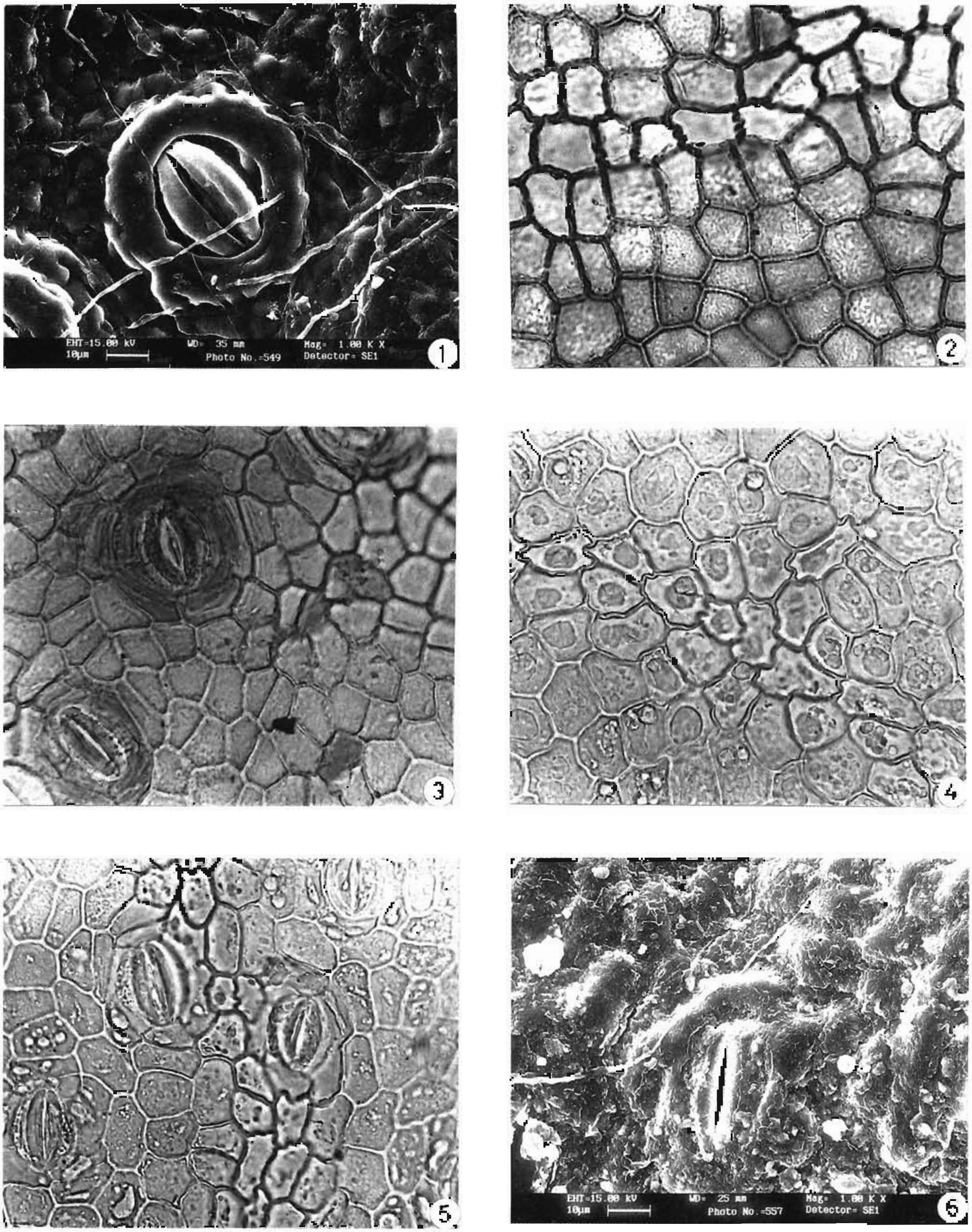
EHT=15.00 kV
10µm
WD= 35 mm
Photo No.=549
Mag= 1.00 K X
Detector= SE1
1
2
3
4
5
EHT=15.00 kV
10µm
WD= 25 mm
Photo No.=557
Mag= 1.00 K X
Detector= SE1
6

PLATE 6

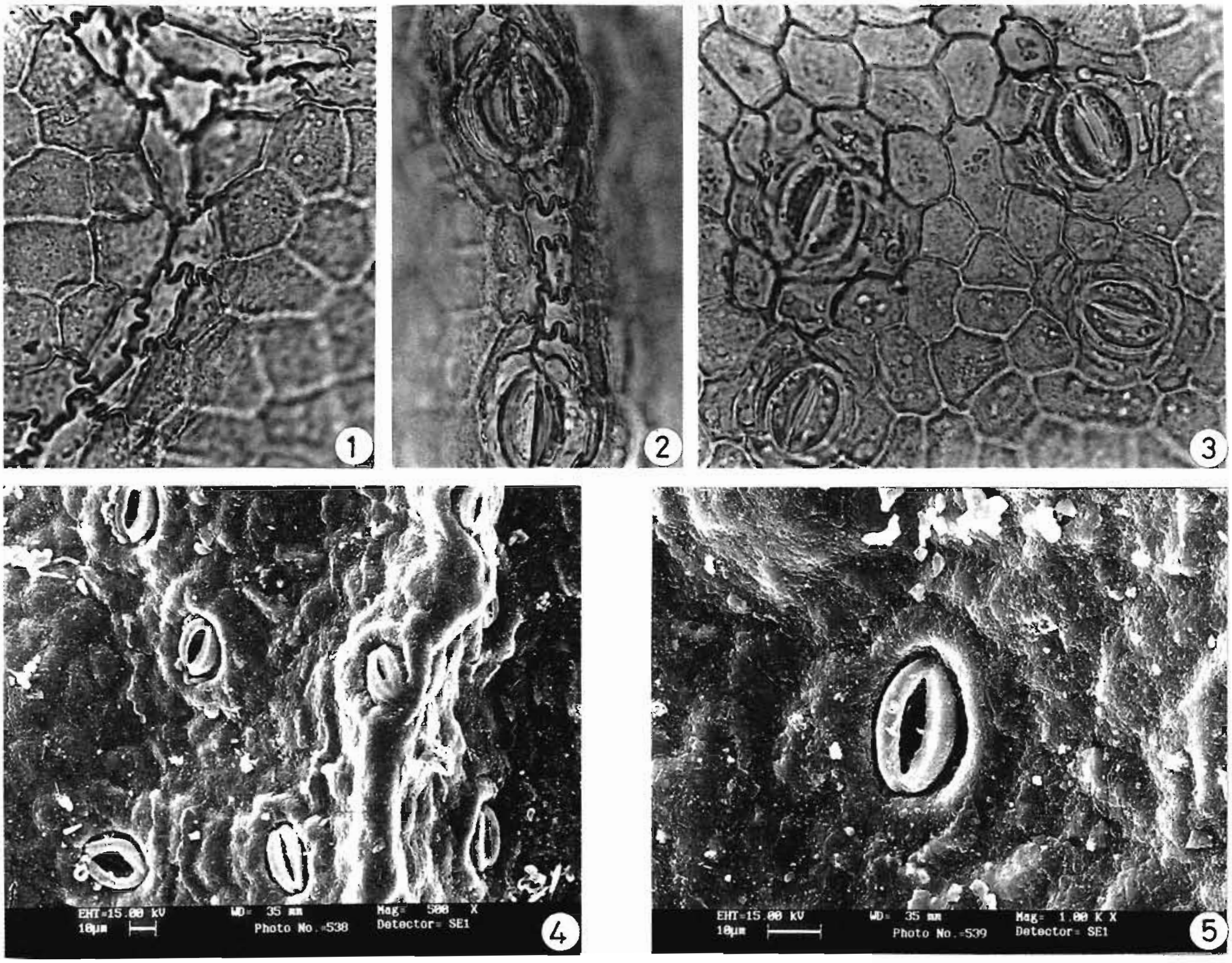

PLATE 7

(Scale given below each photoplate is equal to 10 µm unless mentioned otherwise)

B. cylindrica (Specimen Se. No. 25)

1. LP of upper leaf epidermis showing costal area (sinuate) and intercostal (straight) areas. Lower leaf epidermis.
2. LP showing costal (undulate anticlinal cell wall studded with stomata).
3. LP showing the intercostal areas with the stomata.
4. SEMP upper leaf epidermis showing costal and intercostal cuticular ornamentation.
5. SEMP of lower leaf surface showing stomata and finely striated ornamentation and flaky epicuticular wax.

and present cuticles/epidermis have been studied from Tertiary (Burgh *et al.*, 1993; Kurschner *et al.*, 1996, Mehrotra *et al.*, 1998), Mesozoic (McElwain & Chaloner, 1996; Cleal *et al.*, 1999) Palaeozoic (McElwain & Chaloner, 1995 etc.). The present study shows identifiable variation in the SI of Rhizophoraceae species that would help in the identification of fossil cuticles at the specific level. Adaptive epidermal traits in species would help in the interpretation of palaeoecology.

PLATE 6

←

(Scale given below each photoplate is equal to 10 µm unless mentioned otherwise)

1. SEMP of lower leaf surface in *B. parviflora* showing granulated cuticular ornamentation.

B. sexangula (Specimen Se. No. 24)

2. LP of upper leaf surface with costal (sinuate) and inter costal straight to arcuate anticlinal cell wall.
3. LP showing lower leaf surface

B. gymnorrhiza (Specimen Se. No. 21)

4. LP of lower leaf surface with costal (sinuate–arcuate) and intercostal straight to arcuate anticlinal cell walls.
5. LP of lower leaf surface showing distinct costal (sinuate) and inter costal (straight-arcuate) anticlinal cell walls.
6. SEMP of lower leaf surface showing finely striated ornamentation and flaky epicuticular wax.

The size of the stomatal complex is the largest in *Rhizophora apiculata* while it is comparatively smaller and equal in *R. mucronata* and *R. stylosa*. The anticlinal cell walls of the surrounding epidermal cells are arcuate and elongate, quite distinguishable from rest of the epidermal cells lined parallel to the guard cells with 3 cells each on either side (Pl. 1.6). The poles of the guard cells are slightly occluded (Pl. 1.2) which is not in *R. mucronata* and *R. stylosa* (Pl. 2.1, 6). The surrounding epidermal cells radial to the stomata are 5 in number in *R. stylosa*. The anticlinal cell walls adjacent to the guard cells are straight and not arcuate as in *R. apiculata*. Therefore, 2 cells lie parallel on either sides of the guard cells and one cell covers one of the poles to form a pentagon, which is a distinct identifiable feature (Pl. 2.6).

In *C. decandra* (Pl. 3.5) the stomatal complex resembles *R. stylosa*. The surrounding epidermal cells radial to stomata are not distinguishable in *Rhizophora stylosa*, *Ceriops tagal* and *Kandelia candel* (Pl. 4.4). In *Kandelia candel* the patches of thickened small epidermal cells are observed on both the leaf surfaces that appear ruptured in the later stages (Pl. 4.1, 2, 3, 5). Initially a single cell wall is thickened which is gradually surrounded by number of radially arranged cells to appear as a dark patch of small thickened cells (Pl. 4.6). Although, this is the normal feature of the plant, these become much more active during the stress condition and probably behave like hydathodes through which the salts are exuded. The present study shows that while in *Kandelia* this feature is an epithelium rupture, it is the stomatal modification in *Rhizophora* through which the excess salts are shed off.

The stomatal complex in *Bruguiera caryophylloides* show only 4-5 surrounding cells. Out of which 2 lie parallel and 2 on either side of the poles of the guard cells (Pl. 5.2) in case of 4 cells surrounding the stomata. The anticlinal cell walls are straight to arcuate. Similarly as in Pl. 5.3 *B. caryophylloides* growing in fresh water pond show increase in stomatal frequency. The costal and intercostal cells are not well distinguishable with only few cells showing slightly sinuate anticlinal cell walls. These features resemble to that in *B. parviflora* (Pl. 5.6) and *B. sexangula* (Pl. 6.3). However, in *B. gymnorrhiza* (Pl. 6.5) the costal cells are well demarcated by sinuate anticlinal cell walls on the lower leaf surface. The stomata are lined along on either sides of the costal area. However, the stomata in *B. cylindrica* are lined in the costal area (Pl. 7.2) and also in the intercostal areas (Pl. 7.3). The cells in the costal area show undulate anticlinal cell wall pattern and appears distinct and quite raised in the surface view (Pl. 7.4) which is completely different micromorphological feature when compared with its synonym *B. caryophylloides* (Pl. 5.2-3) or other species in Rhizophoraceae. Fine cuticular striations on the lower leaf epidermis are observed in *B. gymnorrhiza* and *B. cylindrica*. Therefore, with respect to leaf epidermal micromorphological features these two species are closely related and perhaps may show similar pattern of leaf adaptivity to changing coastal ecosystem.

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Palaeocene Rhodophycean Algae from the Ninniyur Formation of the Cauvery Basin, southern India

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ABSTRACT

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The sediments of the Ninniyur Formation, Ariyalur are characterised by exceptionally rich assemblages of algae, of which the coralline algae constitute a major component. The present paper documents 32 species of coralline algae, distributed among eleven genera and five unnamed members of sub-family Melobesioideae, from the algal beds of this formation from Ninniyur and the neighbouring areas. An attempt is made to discuss the depositional environment, using actualistic interpretation of the ecological data on the recovered red algae and the associated fossils in conjunction with information on geological aspects gathered from the existing literature. Based on these, it is inferred that the deposits of the Ninniyur Formation were laid down in a transgressing sea within the neritic zone marked by deposition of biogenic accumulations.

Key-words—Rhodophycean algae, Palaeocene, Ninniyur Formation, Cauvery Basin, India.

दक्षिण भारत की कावेरी द्रोणी के निनियूर शैलसमूह से प्राप्त पेलियोसीन युगीन रोडोफाइसी शैवाल

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सारांश

अरियालूर के निनियूर शैलसमूह के अवसाद शैवालों के अत्यधिक सम्पन्न समुच्चयों द्वारा अभिलक्षणित हैं, जिनमें प्रवाली शैवालों की प्रधानता है। प्रस्तुत शोध पत्र में प्रवाली शैवालों की उपप्रजातियों का उल्लेख किया गया है, जो निनियूर तथा समीपवर्ती क्षेत्रों के इस शैलसमूह के शैवालीय संस्तरों में ग्यारह वंशों तथा मेलोबीसिआइडी उप कुल के पाँच अनाम सदस्यों के मध्य संवितरित हैं। विद्यमान साहित्य से प्राप्त विभिन्न पारिस्थितिकीय परिप्रेक्ष्यों की सूचना के आलोक में खोजे गए लाल शैवाल तथा सहचारित जीवाश्मों के पारिस्थितिकीय आंकड़ों के वास्तविक निर्वचन की सहायता से निक्षेपणीय पर्यावरण की विवेचना का प्रयास इस शोध पत्र में हुआ है। इनके आधार पर यह अनुमान किया जाता है कि निनियूर शैलसमूह के निक्षेप जीवजनित संचयन के निक्षेपण द्वारा सूचित नेरिटांचल के भीतर अतिक्रामी समुद्र में शायित थे।

संकेत शब्द—रोडोफाइसी शैवाल, पेलियोसीन, निनियूर शैलसमूह, कावेरी द्रोणी, भारत।

INTRODUCTION

THOUGH carbonate facies is generally poorly developed globally in the Danian successions, the Tiruchirapalli area of the Cauvery Basin has the distinction of preserving some excellent carbonate build-ups of this interval. They are made up mainly of calcareous algae, foraminifera and other organisms which have attracted the attention of the earth scientists for long but have not been studied in sufficient details to make interpretations concerning palaeoenvironment and depositional history. Despite previous efforts of several palaeontologists mentioned below, the taxonomic inventory of the Niniyur fossil algal forms has largely remained inconclusive and this has resulted in a limited progress of the studies on the stratigraphy and depositional environment of these build-ups. Sustained efforts therefore have to be put in to enlarge the taxonomic database of the algae and the associated fossil forms.

Globally, Johnson (1961, 1969), Maslov (1956), Lemoine (1917, 1923, 1939), etc. have given excellent account of Tertiary algae from different parts of world (cf. Wray, 1977). Braga and Martin (1988) have written a field trip guide book on algal reefs in S. Spain. However, in the taxonomy of recent coralline algae some additional vegetative and reproductive characters have been considered significant (Poignant, 1984; Woelkerling, 1988; Braga *et al.*, 1993; Braga & Aguirre, 1995; Aguirre *et al.*, 1996; Rasser & Piller, 1999; Bosence, 1983, 1984, 1991; Bassi 1995a, b, 1997; Basso *et al.*, 1996, 1997). These workers have also revised the previously documented fossil taxa in the light of these taxonomic concepts. Their revision has helped immensely in the understanding of palaeobotanical and palaeogeographical implications of the above thallophytes with respect to their area of occurrence and distribution in various depositional realms.

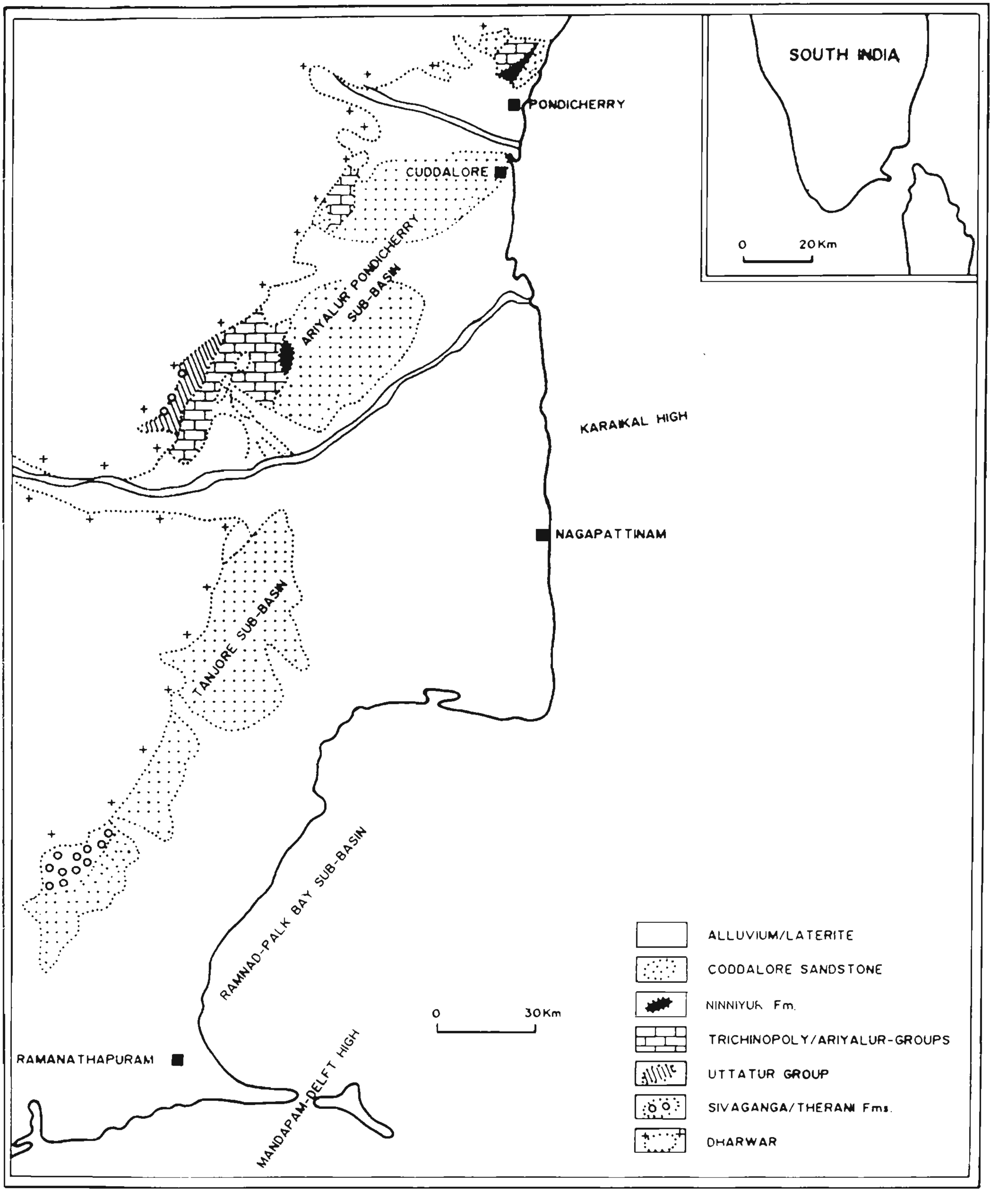
Rao (1951, 1956, 1958), Rao and Pia (1936) and Varma (1952) described 15 taxa of green and red calcareous algae from the Niniyur Formation of Tiruchirapalli District. Gowda (1978) mentioned the occurrence of two dasycladaceous and two Rhodophycean specimens from the Niniyur Formation. Three unnamed species belonging to *Sporolithon* (=*Archaeolithothamnium*), *Lithothamnion* and *Mesophyllum* were reported from the Upper Cretaceous of Ariyalur in Tiruchirapalli District by Manigam *et al.* (1968). Misra and Kumar (1988) described 31 species of Cyanophyceae, Chlorophyceae and Rhodophyceae from the Upper Cretaceous beds of the Varagur area. Rajanikanth (1991) enumerated the calcareous algae from the Niniyur area of the Cauvery Basin. The ecological implications of Cretaceous-Tertiary algae were discussed by Rajanikanth (1992). Ghosh and Murthy (1995) recorded six species of an artificial algal group called the Porostromata from the Cretaceous of Sendurai, Tiruchirapalli District. As the taxonomic contents of these works are based on older morphological criteria, taxonomic observations on the South Indian fossil algal flora need reconsiderations. The present paper is a detailed account of the taxonomic composition of the red algae recovered from the carbonates of the Niniyur Formation and presents palaeoecological interpretations of the documented taxa and the associated fossil groups in the light of known geological factors.

GEOLOGICAL SETTING

The study area forms a part of the Cauvery Basin which falls in the southernmost portion of the Coromondal shelf regime of India (Fig. 1). The basin, situated 160 to 460 km south of Chennai, covers an area of 25,000 sq km on land and about 35,000 sq km of the offshore shelf (Gulf of Mannar, Palk Strait and Coromondal Coast between India and Sri Lanka). The basin evolved as a pull-apart basin as a consequence of rifting along the pre-existing fracture zones of eastern continental margin of Indian craton sometime during the Late Jurassic. The basement faults which have given rise to a series of horsts and grabens, trend NE-SW. The grabens and the faulted depressions in the early stages were filled up with the Upper Gondwana sediments. The marine transgression occurred in the Early Cretaceous, initiating a depositional cycle with a paralic environment which was followed by accumulation of dominantly the marine sequences. After the Deccan Trap outpourings, during the early Tertiary, another phase of marine transgression occurred in response to tectonic and oscillatory movements. These resulted in a shift of depocenters to the east during a series of transgressions and regressions in the Cauvery Basin (Kumar, 1983; Govindan *et al.*, 1998; Banerji, 1972; Sastri *et al.*, 1973). The exposed sedimentary sequence includes continental sediments (Sivaganga Formation) overlain by the marine successions of Cretaceous and Palaeocene ages. The latter are followed by the continental deposits referable to the Cuddalore Sandstone which contains lignite deposits at Neyveli.

The part of the basin which includes the study area has been termed the Ariyalur-Pondicherry Depression. This depression is located in the northern part of the basin and is bounded, on the west, by the granites and gneisses of the Dharwar Supergroup (Archaean) and, on the south-east, by the subsurface ridge, referred to as Kumbhakonam-Shiyali Ridge. The outcrops of the Cretaceous sediments are developed near the western margin of the depression and exhibit facies change from the shelf carbonates near

Fig. 1—The geological map of the Cauvery Basin. The inset shows position of the study area in India (after the document "Stratigraphy of Indian petroliferous basins: Cauvery Basin, 1995" published by ONGC).



SOUTH INDIA
0 20Km
PONDICHERRY
CUDDALORE
ARIYALUR PONDICHERRY SUB-BASIN
KARAIKAL HIGH
NAGAPATTINAM
TANJORE SUB-BASIN
RAMNAD-PALK BAY SUB-BASIN
0 30Km
RAMANATHAPURAM
MANDAPAM-DELFT HIGH
ALLUVIUM/LATERITE
CODDALORE SANDSTONE
NINNIYUR Fm.
TRICHINOPOLY/ARIYALUR-GROUPS
UTTATUR GROUP
SIVAGANGA/THERANI Fms.
DHARWAR

Tiruchirapalli to the shales in the deeper part of the basin. Tertiary sequence is not developed extensively as outcrops but is well represented in the subsurface. During the Tertiary (Palaeocene), extensive carbonate platform environment prevailed because of reduction of clastic supply due to peneplanation of the source area as well as reduced rates of subsidence; in some areas, the fine clastics, however, accumulated alongside the carbonates because of fluctuating conditions of local tectonics (Kumar, 1983).

STRATIGRAPHY

Blanford (1862) was first to study the sedimentary rocks of the Tiruchirapalli area and considered the youngest beds exposed near Sendurai and Ninniyur to be part of the Upper Cretaceous Ariyalur Group. Subsequent work by Rao and Pia (1936) showed that these beds were deposited during an independent transgressive event and hence could be referable to a distinct stratigraphical unit which was designated as the Ninniyur division. Among the subsequent contributions to the stratigraphy of the Tiruchirapalli area, the important ones include Krishnan and Jacob (1959), Banerji (1979), Kumar (1983), Govindan *et al.* (1996), Malarkodi and Nagaraj (1997, 1998) and Govindan *et al.* (1998). Currently, the sequence of fossiliferous marine beds conformably overlying the Kallameedu Formation (Ariyalur Group, Fig. 2) (Upper Cretaceous) is recognised as the Ninniyur Formation. It is well exposed at Sendurai Village (11°15' N : 79°10' E), Adanakkurichchi Village (11°21' N : 79°15' E) and at Periyakurichchi mines (11°17'30" : 79°12') over a NNE-SSW strike between Vellar River in the north and Coleroon River in the south limited between Latitudes 11°08' - 11°22' N and Longitudes 79°10' - 79°17' E (Fig. 2).

Fig. 3 gives some stratigraphic details of the Ninniyur Formation. The most distinguishing feature of this formation is its lithology and fossils, especially the rich representation of the fossil algae (Rao, 1958). Three distinct units can be recognised in the Ninniyur Formation: lower fossiliferous limestone, middle subcrystalline shelly limestone; and the upper argillaceous gritty nodular limestone.

The lowermost unit is exposed at Adanakkurichchi mines, hence called the Adanakkurichchi Limestone. It comprises marl, off-white to yellowish limestone which is moderately compact and richly fossiliferous and noted for the rich miliolid assemblage (Malarkodi & Nagaraj, 1997); however, its algal association is poorly developed (Figs 3, 5). The middle unit is very well exposed at Periyakurichchi and is a dominantly recrystallized, hard, compact, variegated limestone. It is less fossiliferous as compared to the lower unit so far as the mega-invertebrate fossils are concerned; its fauna is largely disintegrated and characterised by the frequently occurring *Hercoglossa danica* Schlotheim along with gastropods, bivalves, ostracods and foraminifers. However, its algal associations are very rich and highly diversified in comparison to that of the lower and upper units (Figs 3, 5). The uppermost unit outcrops at Sendurai Village (about 1.5 km towards Mattur) in a well cutting located near the 1 km milestone on the right side of the main road leading to Adanakkurichchi mines. It is an argillaceous, fine to gritty nodular limestone with nodules ranging in diameter from 2 to 5 cm. It is richly fossiliferous and contains abundant corals, bivalves and gastropods but has less diversified algal association (Figs 3, 5). It is characterised by numerous irregular voids filled with calcite cement. *Cardita beaumonti* Douvillé is the most common fossil of this unit.

The Ninniyur Formation was assigned to the Danian (early Palaeocene) on the basis of *Hercoglossa danica* Schlotheim considered to be characteristic of this stage (Blanford, 1862; Rao & Pia, 1936; Rao, 1956). Subsequent work revealed the presence of planktic foraminifera in the Ninniyur Formation. Sastry *et al.* (1965) suggested an early Palaeocene age for these beds on the basis of *Globorotalia (Truncorotalia) mckannai* Hofker. Malarkodi and Nagaraj (1997, 1998), however, document several species of benthic and planktic foraminifera from different units of the Ninniyur Formation. The age-diagnostic taxa in their assemblage include *Morozovella praecursoria* (Morozova), *Acarinina spiralis* Bolli, *A. mckannai* (White) and the species of *Thalmannita* which indicate that it ranges from early to late Palaeocene (Danian to Thanetian) in age. The distribution and significance of these microfossils in the chronobiostratigraphic context have been examined by Misra *et al.* (2000). Based on this information each of the three units of the Ninniyur Formation can be precisely dated.

The lower unit is characterised by *Acarinina spiralis* Bolli, *Morozovella praecursoria* (Morozova) and *Planorotalites chapmani* (Parr). Of these, *A. spiralis* is diagnostic of zone P2, i.e. late Danian (Malarkodi & Nagaraj, 1997). The lower unit, on this basis could be considered to be late Danian (early Palaeocene) in age. The age-diagnostic planktic foraminifera of the middle unit are *Acarinina mckannai* (White) and *Planorotalites pseudomenardii* (Bolli).

PLATE 1

1-3, 5	*[illegible]*	5	Magnified view of sporangia. X [illegible]
1, 8	Showing isolated sporangia and many conceptacles. X [illegible]	6	*[illegible]* sp. Johnson & Tafur 1952. X 75
2, 3	Conceptacles under low magnification. X 35	7	Thallus attached to coral
4, 5	*Archaeolithothamnium* sp. 4	9	*Solenopora* sp. X [illegible]
4	Thallus with sporangia.		

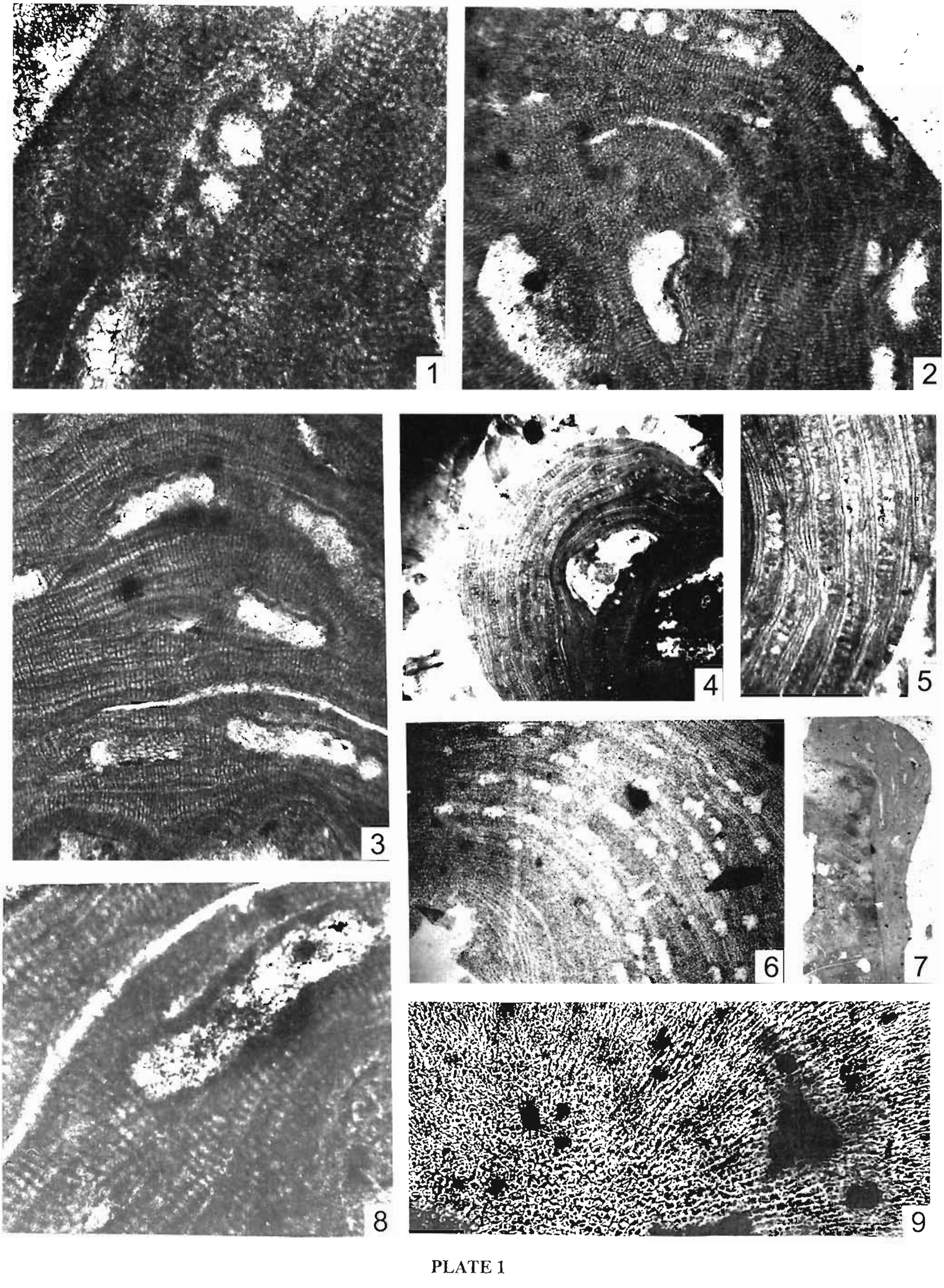


PLATE 1

While *A. mckannai* extends from zone P3 to zone P5, *P. pseudomenardii* is confined to zone P4 (Malarkodi & Nagaraj, 1997). These forms indicate that the middle unit corresponds to zones P3-P4, i.e., Thanetian (late Palaeocene). The upper unit, though marked by the absence of planktic foraminifera, includes some benthic foraminifera, in which *Gavelinella danica*, a Palaeocene marker (Brotzen), is prominent. The upper unit appears to correspond to the Thanetian in view of its position in sequence.

The geological data and sample collections have been made from the following sections.

Adanakkurichchi Section—The lower unit of the Ninniyur Formation is exposed here. However, as compared to its thick subsurface succession, the outcrops are very thin. The studied section exposed at Adanakkurichchi shows a 3-4 m thick sequence of the carbonate rocks with few marly horizons which are characterised by well preserved megafossils (Fig. 5); however, the associated calcareous algae are present only as thin horizontal bands.

Periyakurichchi Section—It represents the middle unit of the Ninniyur Formation and is exposed at Periyakurichchi mines in Ninniyur Village. The measured section is 6-7 m in thickness and comprises subcrystalline to crystalline shelly limestone. The general lithology shows compact, hard limestone at the base which grades into marl beds above. The algal composition of these rocks is rich and varied (Fig. 3).

Mattur Section—This section exposes a sequence which is quite similar to that exposed at the Periyakurichchi mines. However, it is also partly exposed in the well cuttings in and around Ninniyur Village (Fig. 2).

Ninniyur Section—The sequence exposed here is similar to that of the Sendurai Section in general lithology and fossil contents. In this section, the Cuddalore Sandstone overlies the upper unit of the Ninniyur Formation (Fig. 2, 3).

Sendurai Section—This section belongs to the upper unit of the Ninniyur Formation but its exposures are rare and the samples were taken mainly from an unlined well cutting. The exposed surface was only 3.5 to 4.0 m thick. The calcareous algae usually occur as rounded to irregular white patches.

The present investigation has revealed the presence of 32 species grouped under 10 genera of the red alga. The genera recorded in this study are presented in a check-list along with their diagnostic characters. The number of species of these genera are indicated in parentheses as below : *Parachaetetes* (1), *Solenopora* (1), *Kymalithon* (1), *Sporolithon* (8), *Lithothamnion* (9), *Melobesioideae* gen. et spec. indet (5), *Mesophyllum* (1), *Neogonolithon* (1), *Lithophyllum* (1), *Polystrata* (2), *Thaumatoporella* (1).

All the thin sections and peelings are preserved at the Algalology Laboratory, Botany Department, University of Lucknow, Lucknow.

SYSTEMATIC DESCRIPTION

Division—RHODOPHYTA Wittstein, 1901

Class—RHODOPHYCEAE Rabenhorst, 1863

Order—CORALLINALES Silva & Johansen, 1986

Family—SOLENOPORACEAE Pia, 1927

Genus—SOLENOPORA Dybowski, 1878

Species—SOLENOPORA sp.

(Pl. 1.9)

Description—Encrusting, nodular masses are common growth forms of this genus. In vertical section, the filaments show radiating walls between them. Septations between cells of filaments are absent. In transverse sections, cells are rounded to polygonal, averaging 30-50 μm in diameter. Reproductive organs not seen.

Sample No.—B/Mt/A3.

Slide No.—M/CB-33.

Locality—Mattur.

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—This genus is known from Cambrian to Miocene. It occurs rarely in the Ninniyur Formation.

Genus—PARACHAETETES Deninger, 1906

PARACHAETETES ASVAPATII Rao & Pia, 1936

(Pl. 3.4; Pl. 4.6; Pl. 6.2, 9)

1936 *Parachaetetes asvapati* Rao & Pia, p. 32, pl. 3, fig. 1.

1982 *Parachaetetes asvapati* Beckmann, p. 138, pl. 15, figs 4-7.

1991 *Parachaetetes asvapati* Kuss & Conrad, p. 877, figs 5.17.

PLATE 2 →

1. *Sporolithon* sp. 1. X 50.
2. *Sporolithon aschersonii*. X 100.
3. *Sporolithon* sp. 6. X 30.
4. *Sporolithon* sp. 3. X 150.

5, 7, 9. *Sporolithon* sp. 7.

5. Thallus with sporangia. X 20.
7. Group of sporangia forming conceptacle-like structure. X 50.
9. Magnified view of conceptacle. X 150.

6, 8. *Sporolithon aschersonii*.

6. *Sporolithon aschersonii*. X 150.
8. *Sporolithon aschersonii*. 2 X 50.
10. *Lithothamnion* cf. *caravellense*. X 50.

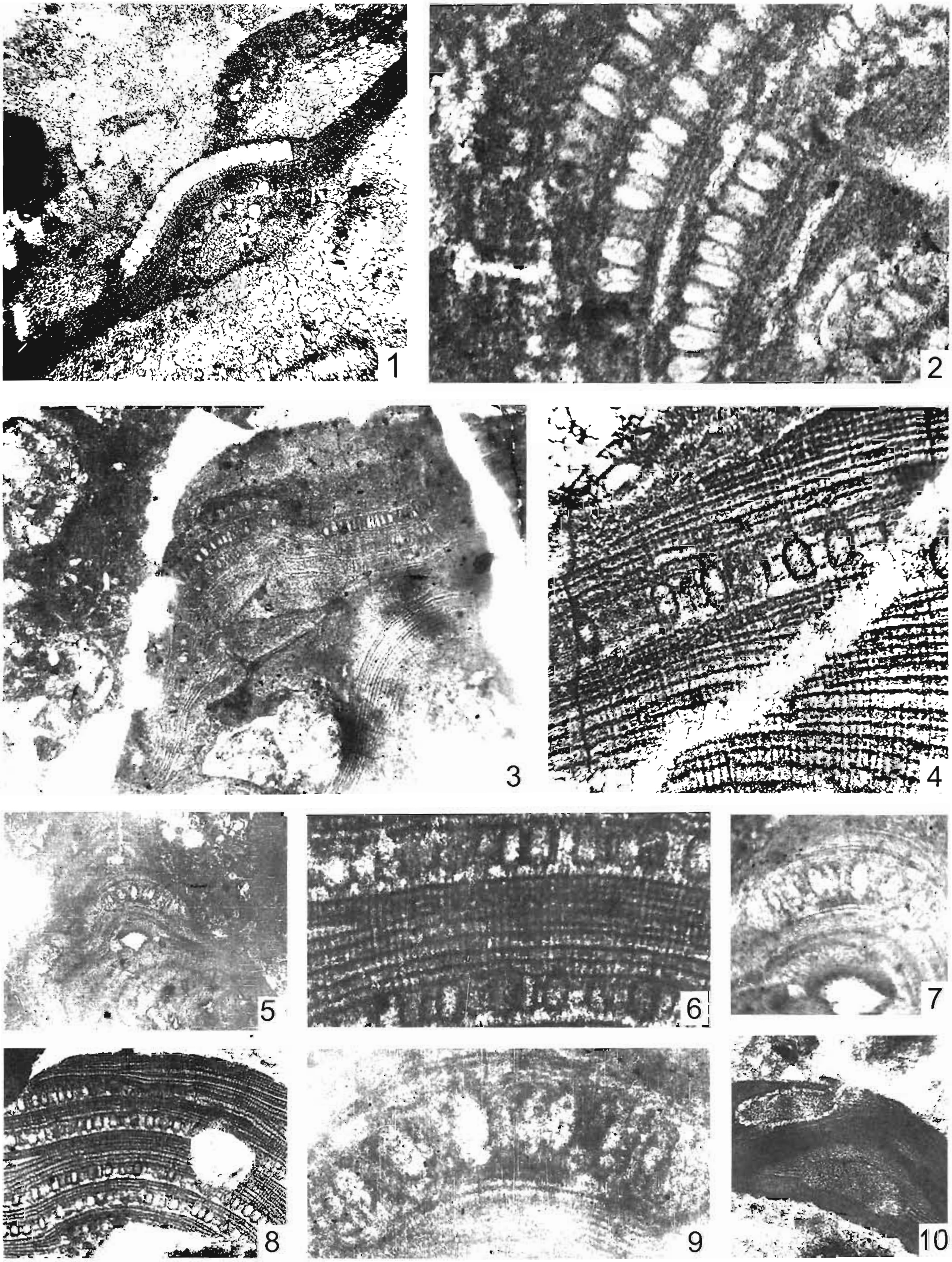


PLATE 2

Description—Thallus encrusting, transparent. Cells are arranged in rows. Cell septations prominent at few places. The diameter of the cells ranges from 40 to 60 µm. The length of the cells vary from 40 to 120 µm.

Sample No.—B/Ad/A5, B2, B/Nn/A4; B/M/A15, B/Per/A10, B6, B/Sn/A24, B3, C3.

Slide No.—SRCB-19, 48, 23, 29.

Locality—Adarakkunichern, Mattur, Sendurai.

Occurrence—Lower, Middle, Upper Unit, Niniyur Formation.

Discussion—Rao and Pia (1936) have reported segregated specimens of this species from Niniyur Village which is very close to Sendurai. In the present work, the fragments are associated with coralline algae. Beckmann *et al.* (1982) recorded this taxon from the Palaeocene of the Monte Giglio, Italy. Kuss and Conrad (1991) reported this species, together with other coralline algae, from the Middle-Late Maastrichtian of the Eastern Desert of Egypt.

Family—SPOROLITHACEAE Verheij, 1993

Genus—*Sporolithon* Heydrich 1897

(=*Archaeolithothamnium* Rothpletz ex Foslie, 1898)

(=*Archaeolithothamnion* Rothpletz ex Foslie 1898)

Archaeolithothamnium Rothpletz 1891; *Archaeolithothamnion* Rothpletz 1891 ex Foslie 1898a. Woelkerling (1988, p. 203, 220), Moussavian and Kuss (1990) and Ghosh and Maithy (1996) treated the genus *Archaeolithothamnium* as synonym of *Sporolithon*.

Species—SPOROLITHON ASCHERSONII (Schwager) Moussavian & Kuss 1990

(Pl. 2.2, 6, 8)

1990 *Sporolithon aschersonii* Moussavian & Kuss, p. 934, pl. 1, figs 1-5.

1995b *Sporolithon aschersonii* Bassi, p. 14, figs 3-5.

1998a *Sporolithon* cf. *aschersonii* Bassi, p. 20, pl. 8, figs 3-6, pl. 9, figs 1-6.

1998b *Sporolithon aschersonii* Bassi, pl. 33, figs 2, 3, 5.

Description—Growth form encrusting, with few protuberances; core filaments generally reduced and poorly preserved; peripheral filaments with small cells. Tetrasporangia cylindrical to club-shaped, densely arranged in a zone, separated by 1-3 sterile filaments (paraphyses); fertile tetrasporangia bearing areas prominently raised. The cells are generally longer than wide, 8-15 µm in length and 6-12 µm in width. Sporangia 120-130 µm in length and 70-85 µm in width. Sporangia usually arise from a basal layer of elongated cells.

Sample No.—B/Per/A5.

Slide No.—PrCB-18, 26.

Locality—Perialkanichern.

Occurrence—Middle Unit, Niniyur Formation.

Discussion—The present specimens are included in *S. aschersonii* on the basis of thallus morphology and prominently raised tetrasporangia bearing areas, but in the present specimens they are not clearly delimited. Segonzac (1961) described this species as "*A. aschersonii*" from the Thanetian limestone of Pyrenees. Moussavian and Kuss (1990) found it in the Palaeocene limestones of the eastern and western parts of Egypt. Bassi (1995b, 1998a, b) has reported this species from the Eocene of Northern Italy.

Sporolithon sp. 2

(Pl. 2.1)

Description—Growth form encrusting. Cells of the peripheral filaments 9-14 µm in length and 8-15 µm in width and cells of core filaments not preserved. Cell fusions indistinct. Sporangial conceptacles arranged in sori. Individual sporangial compartments are rectangular with rounded corners, compactly arranged. They are 50-70 µm in length and 35-45 µm in width. Sporangia usually do not arise from a basal layer of elongated cells.

Sample No.—B/M/A27.

Slide No.—MCB-5.

Locality—Mattur.

Occurrence—Middle Unit, Niniyur Formation.

Discussion—This specimen resembles *Sporolithon bertalleri* Lemoine (c.f. Johnson, J.H., 1964a, p. 205, pl. 1, fig. 1) in shape and size of sporangia. However, sporangia are arranged in sori, while in *S. bertalleri* they are segregated.

PLATE 3 >

1	*Sporolithon* sp. 2. × 30.
2, 11	*Polystrata alba*. × 50.
3	Melobesioideae gen. et sp. indet. 2. × 40.
4	*Paraclavi...* [illegible]. × 25.
5	Melobesioideae gen. et sp. indet. 4. × 50. Showing ... [illegible] conceptacle.
6	*Sporolithon* sp. 2. × 20. Thallus with a row of sporangia.
7	*Distichoplax biserialis*. × 25.
8	*Neogoniolithon* sp. × 25.
9, 10	*Lithothamnion* sp. 2.
9	Magnified view of conceptacle. × 125.
10	Fragmentary thallus with conceptacles. × 50.
12	*Spongites* ... [illegible]. × 25. Conceptacle in perithallus.
13	*Sporolithon* sp. 3. × 100. Showing branching of thallus.

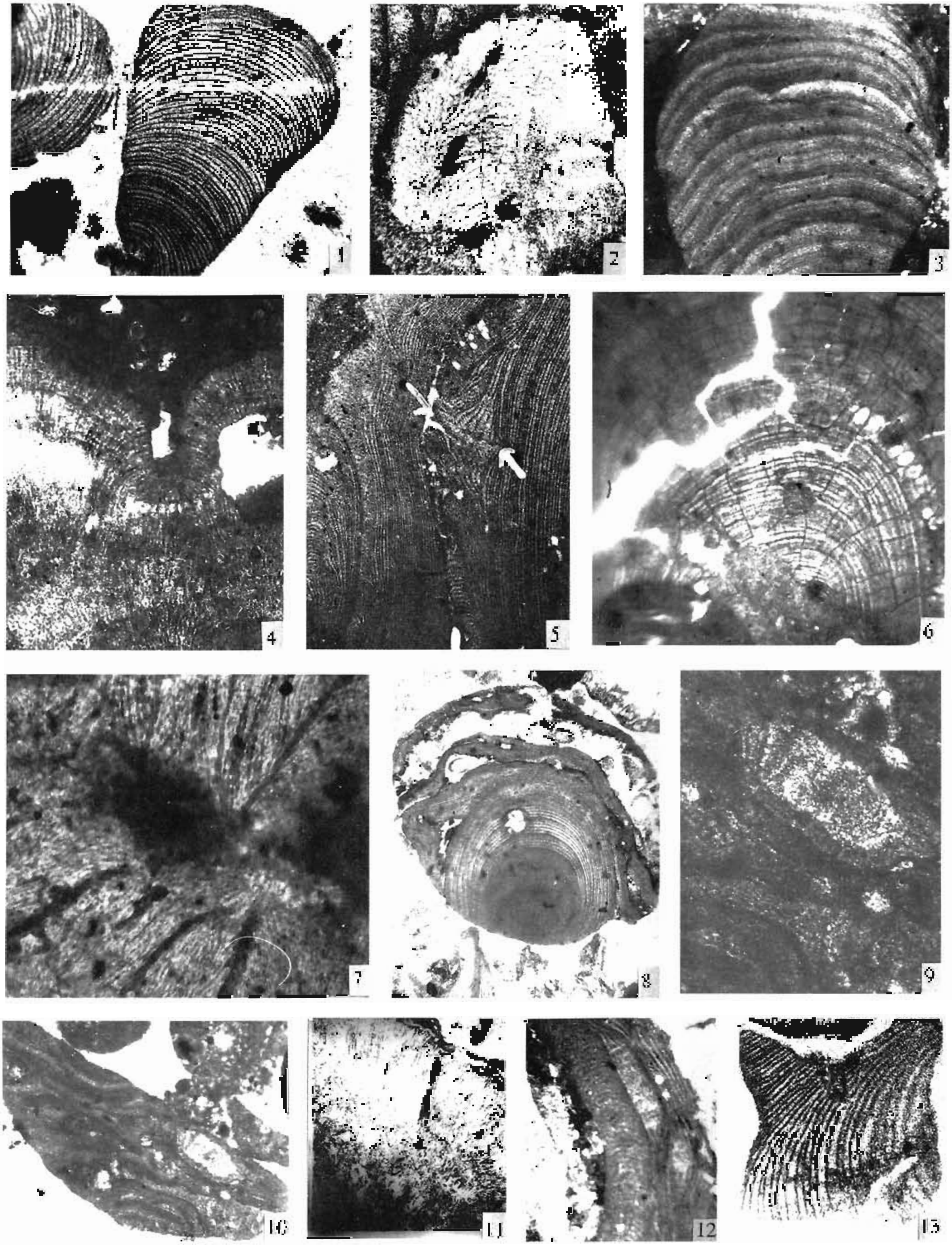


PLATE 3

Sporolithon sp. 2

(Pl. 6, fig. 11)

Description—Growth form encrusting to lumpy with short protuberances. Cells of peripheral filaments 15-28 µm in length and 8-12 µm in width. Peripheral filaments regular with thick horizontal partitions forming concentric lines. Filament walls much thinner and not conspicuous. Sporangia arranged in a row, ovoid in shape, 91-108 µm in length and 53-67 µm in width.

Sample No.—B/Ad/34

Slide No.—A/CB-69

Locality—Adanakurichchi

Occurrence—Lower Unit, Niniyur Formation.

Discussion—This species resembles *Sporolithon parisiense* (Gumbel) Lemoine in thallus organisation and shape of sporangia. However, only few sporangia are preserved in our specimen and their outline is not prominent. *Sporolithon parisiense* (Gumbel) Lemoine has been reported by Johnson (1964a) from the Palaeocene beds of Sirwan Balambo, northern Iraq.

Sporolithon sp. 3

(Pl. 2, fig. 1; Pl. 3, fig. 13)

Description—Growth form encrusting to lumpy, with thick irregular protuberances or short branches. Core filaments poorly developed or absent. Cells of peripheral filaments are 11-28 µm in length and 8-15 µm in width. Sporangia numerous, normally in well defined layers or rows, ovoid to spherical in shape, 35-50 µm in diameter, 75-90 µm in height. Sporangia usually arise from a basal layer of elongated cells.

Sample No.—B/Per/A8.

Slide No.—P/CB-76

Locality—Periyakurichchi

Occurrence—Middle Unit, Niniyur Formation.

Discussion—This species is comparable with *Sporolithon nummuliticum* (Gumbel) Rothpletz but differs from the latter in the shape and size of sporangia and cells of peripheral filaments.

Sporolithon sp. 4

(Pl. 4, fig. 5)

Description—Growth form encrusting. Peripheral filaments are arranged in regular cell rows and horizontal cell walls are more distinct than vertical ones. The peripheral filaments have cell dimensions of 10-24 µm in length and 6-8 µm in width. Several concentric rows of sporangia may occur within one thallus and usually they arise from a basal layer of elongated cells. Sporangia are relatively small and narrow, ovoid to oblong, 40-64 µm in length, 24-32 µm in diameter.

Sample No.—B/Per/A21

Slide No.—P/CB-7

Locality—Periyakurichchi

Occurrence—Middle Unit, Niniyur Formation.

Discussion—This algal specimen is comparable with *Sporolithon longgneinsis* Sripada Rao in arrangement and morphology of sporangia. Beckmann *et al.* (1982) reported *Sporolithon* [illegible] Sripada Rao from the Palaeocene of Monte Giglio, Italy.

Sporolithon sp. 5

(Pl. 3, fig. 6)

Description—Growth form encrusting. Core filaments poorly developed and badly preserved. Peripheral filaments fairly regular in some areas but showing alternate layers of long and short cells in some portions. Horizontal cell walls are more distinct than vertical ones. Cells are 12-14 µm in length and 6-10 µm in width. Sporangia in groups, tightly packed in irregular rows, measuring 75-90 µm in length and 45-60 µm in diameter. Sporangia does not arise from the basal layer of elongated cells.

Sample No.—B/Per/A17

Slide No.—P/CB-70

Locality—Periyakurichchi

Occurrence—Middle Unit, Niniyur Formation.

Discussion—The present specimen differs from *Sporolithon* sp. 3 and other species of the genus mainly in the sporangia not originating from the basal layer of thallus. Though broadly similar to *Sporolithon oscendens* Raineri in shape, size and arrangement of its cells and sporangia, this specimen has slightly larger sporangia. Johnson (1964b) reported *S. oscendens* from the Miocene of Lalak, northern Iraq.

Sporolithon sp. 6

(Pl. 2, fig. 3)

Description—Growth form encrusting. Cells of core filaments not measurable due to bad preservation, peripheral filaments with cells 8-14 µm in length and 12-15 µm in width.

PLATE 4 ⟶

1	*Lithothamnium* [illegible] × 25	3, 8, 9	× 125
2	*Lithothamnium* [illegible] × 35	4	*Lithothamnium* sp. 3 × 40
3, 5, 7, 8, 9	*Sporolithon* [illegible]	6	[illegible] × 15
5, 7	× 50		

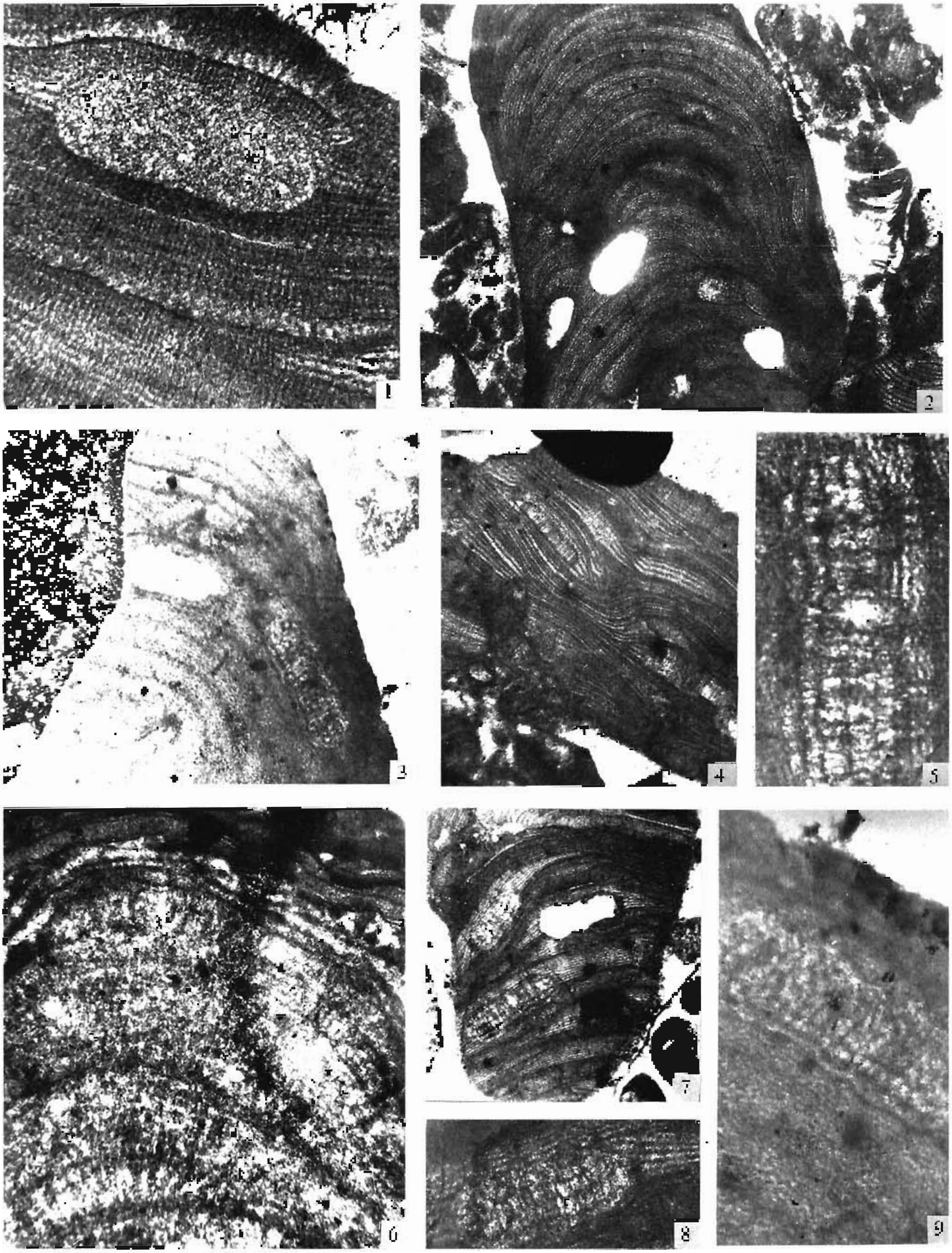


PLATE 4

with rows of oval to elliptical sporangia, 45-50 µm in length and 25-35 µm in diameter.

Sample No.—B/M/2A5

Slide No.—M/CB-8.

Locality—Mattur.

Occurrence—Middle Unit, Nimmayur Formation.

Discussion—Only one specimen of this species was found and could not be compared with any known species of the genus *Sporolithon* Heydrich.

Sporolithon sp. 7

(Pl. 2.5, 7, 9)

Description—Growth form encrusting to lumpy with small protuberances of different shapes. Peripheral filaments with concentric growth zones. Peripheral cells 8-12 µm in length and 10-15 µm in width. Core filaments poorly preserved. Sporangia arranged in saucer-shaped clusters reach 40-60 µm in diameter and 90-120 µm in height.

Sample No.—B/Sn/B3

Slide No.—SCB-25

Locality—Sendurai.

Occurrence—Middle Unit, Nimmayur Formation.

Discussion—The saucer-shaped grouping of sporangia initially appears to be a conceptacle but there is no definite outline of the conceptacle wall and the sporangia are clearly separated from each other. This specimen does not match with any of the known species of the genus *Sporolithon* Heydrich.

Sporolithon sp. 8

(Pl. 3.1)

Description—Thallus encrusting, with curved rows of cells of peripheral filaments. Cells 12-15 µm in length and 8-10 µm in width. Sporangia not preserved.

Sample No.—B/Sn/B6

Slide No.—SCB-59.

Locality—Sendurai.

Occurrence—Upper Unit, Nimmayur Formation.

Discussion—This specimen has narrow elongated cells. The cells of peripheral filaments resemble that of other species of this genus, but it lacks sporangia, hence the specific identification is not possible.

Family—CORALLINACEAE Lamouroux, 1812

Genus—KYMALITHON Lemoine & Emberger, 1967

KYMALITHON BELGICUM Lemoine & Emberger, 1967

(Pl. 1.1, 2, 3, 7, 8)

1967 *Kymalithon belgicum* Lemoine & Emberger, p. 1-11, pl. 4.

1969 *Kymalithon belgicum* Johnson, p. 10, pl. 6, figs 1-3, pl. 23, figs 1-2, pl. 24, figs 1-2.

Description—Growth form encrusting, thickness of encrusting thalli up to 3.75 mm. Thallus organisation monomerous. Core filaments non-coaxial, core portion 75 µm thick. Cells 16-22 µm in length and 10-15 µm in width. The cells of the peripheral region 20-30 µm long and 12-18 µm wide. Cell fusions present. Tetrabisporangia present in small groups within the outer part of peripheral tissue. At places, sporangia unite to form flat, rectangular conceptacles which are multiporate and contain rounded sporangia in small clusters. Conceptacles 140-160 µm in height and 350-400 µm in diameter.

Sample No.—B/Sn/C3

Slide No.—SCB-6

Locality—Sendurai.

Occurrence—Upper Unit, Nimmayur Formation.

Discussion—The south Indian specimens are referable to *K. belgicum* Johnson (1969), and Lemoine and Emberger (1967) reported this species from the Lower Cretaceous (Aptian) of Guatemala. The present record of this species from the Palaeocene indicates its probable extension up to early Tertiary period. In the present specimen, sporangial initials develop as a small group and later unite to form a multipored conceptacle. Hence, it differs from the genus *Lithothamnion* and is being referred to *Kymalithon* Lemoine & Emberger.

Subfamily—MELOBESIOIDEAE Bizzozero, 1885

Genus—LITHOTHAMNION Heydrich, 1897

Species—LITHOTHAMNION FLOREABRASSICA (Millet) Lemoine, 1923

(Pl. 4.2)

1923 *Lithothamnion floreabrassica* Lemoine, 1924, p. 154, fig. 5.

PLATE 5

1, 2. [illegible]
3, 7. [illegible] × 100.
5. × 50.
4. *Lithothamnion* sp. 7 [illegible]
5, 8. *Lithothamnion* [illegible] × 125.
8. [illegible] × 25.
6, 9. [illegible] × 150.
9. [illegible] × 80.

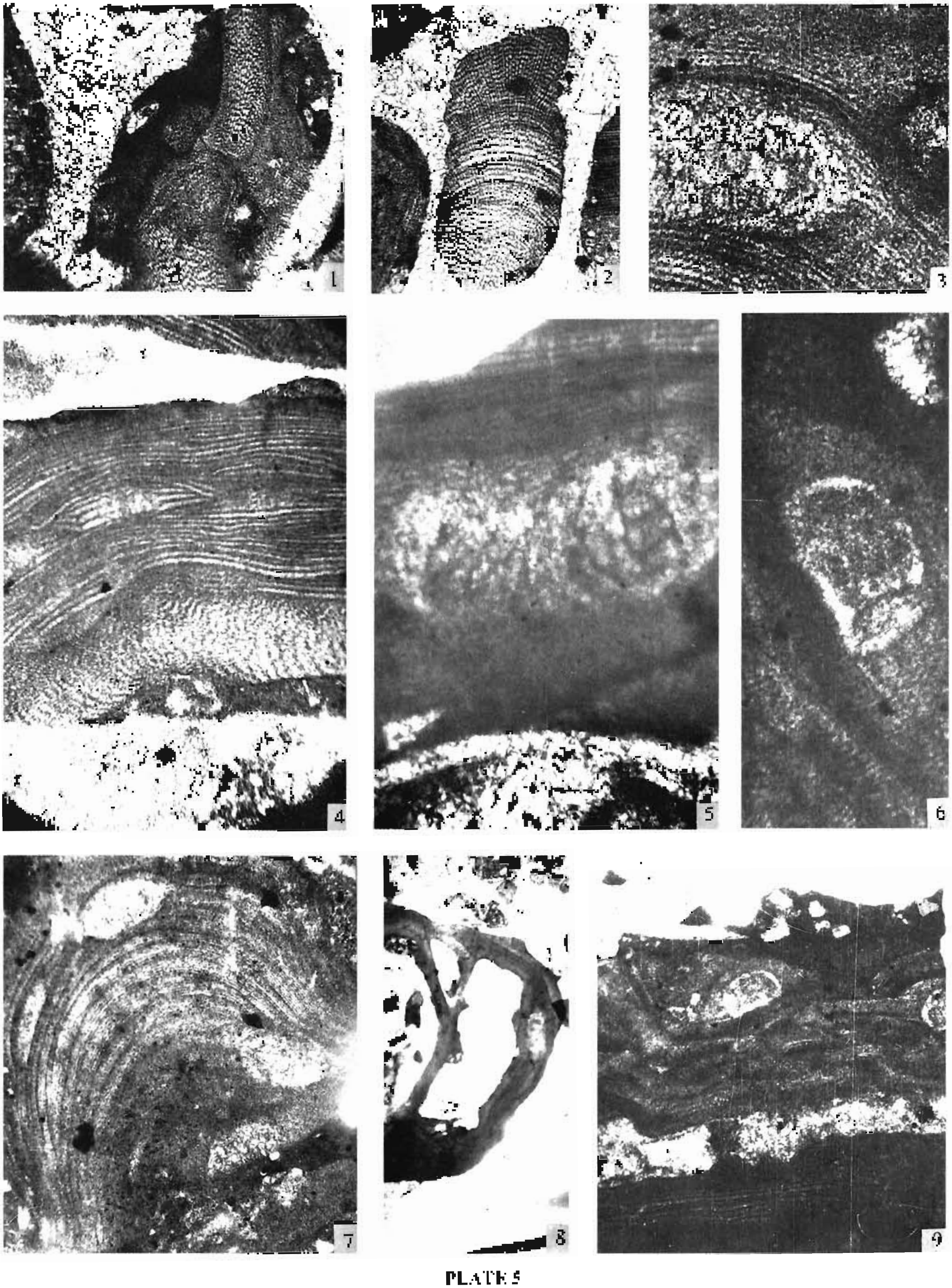


PLATE 5

Description—Growth form encrusting to warty. Thallus organisation monomerous. Core filaments non-coaxial, core portion usually 80-100 µm thick. Filaments curved towards the dorsal surface. Filaments show strong irregular growth zones, with a more or less layered structure. Cell size may vary from zone to zone. Cells 14-23 µm in length and 8-14 µm in diameter. Tetra/bisporangial conceptacles 325-375 µm in diameter and 153-225 µm in height.

Sample No.—B/Nr/A14

Slide No.—NPCB-53

Locality—Ninniyur

Occurrence—Middle Unit, Ninniyur Formation

Discussion—At few places, the conceptacles appear to be multiporate but pores are not prominent. However, this specimen agrees well with *L. floreabrassica* (Miller) Lemoine in general shape and size.

LITHOTHAMNION MANNI Johnson & Stewart 1953

(Pl. 4.1; Pl. 6.8)

1953 *Lithothamnion mannii* Johnson & Stewart, p. 133, pl. 15, fig. 4.

1982 *Lithothamnion mannii* Beckmann, p. 134, pl. 11, figs 9, 10, 11.

Description—Growth form encrusting, thallus thickness about 870 µm. Thallus organisation monomerous. Core filaments non-coaxial about 105 µm in thickness, with cells 10-15 µm in length and 8-12 µm in width. Peripheral region with cells 8-12 µm in length and 6-10 µm in width. Cell fusions present. Tetra/bisporangial conceptacles multiporate, 190-205 µm in height and 350-375 µm in width.

Sample No.—B/Per/A26

Slide No.—PPCB-76

Locality—Periyakurichchi

Occurrence—Middle Unit, Ninniyur Formation

Discussion—This specimen differs from *L. floreabrassica* (Miller) Lemoine in the encrusting nature of the growth form and obovoid conceptacles. Thallus organisation and conceptacle morphology of these specimens show resemblance to *L. mannii*. Conceptacles in the present specimens are slightly broader than in the type recorded by Beckmann *et al.* (1982) from the Palaeocene of Monte Giglio, Italy, but their size is similar to that reported by Johnson & Stewart (1953) from the Eocene beds of the Meganos Formation, California.

LITHOTHAMNION ANDRUSOVI Lemoine 1934

(Pl. 4.3, 5, 7, 8, 9)

1934 *Lithothamnion andrusovi* Lemoine, p. 274, fig. 2.

Description—Growth form encrusting to warty. Thallus organisation monomerous. Core filaments non-coaxial, core portion 150-180 µm thick. Cells 10-15 µm in length and 5-12 µm in diameter. Filaments of peripheral region thick, compact, with small cells (8-10 µm in length and 4-7 µm in width). Tetra/bisporangial conceptacles multiporate, 300-450 µm wide and 140-180 µm high.

Sample No.—B/Mt/A27

Slide No.—MPCB-68

Locality—Mattur

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—The south Indian specimen is referable to *L. andrusovi* Lemoine reported from the Palaeocene to Middle Eocene of Massif of Akros, Massif of Mastrosoum, Massif of Klokova and Massif of Lapithos, Greece (Johnson, 1965). It is also comparable to *Lithothamnion wallisium* Johnson & Stewart, 1953, p. 134, pl. 16, fig. 1 in general shape, irregular growth zones and arrangement of conceptacles, but the latter can be distinguished by small protuberances and smaller and somewhat oblong conceptacles.

LITHOTHAMNION ORBICULATUM Krisanne Hutter 1961

(Pl. 5.5, 8)

1961 *Lithothamnion orbiculatum* Krisanne Hutter XCI. 4, 432-441.

1989 *Lithothamnion orbiculatum* Buscmi *et al.*, p. 141, pl. 2, figs 5-8.

Description—Growth form encrusting, thallus thickness about 2.1 mm. Thallus organisation monomerous. Core filaments non-coaxial, about 180 µm in thickness, with cells 10-14 µm in length and 9-12 µm in width. Peripheral region with cells 8-12 µm in length and 6-9 µm in width. Cell fusions present. Conceptacles multiporate, 200-240 µm in height and 440-495 µm in width. All conceptacles are buried in the thallus. Conceptacles sunken and elongated with rounded margins.

PLATE 6 >

1.	Melobesioideae gen. et sp. indet. 1. X 50	5.	[illegible]. X 50. [illegible] view
2, 9.	[illegible]. X 15	6.	[illegible]. X 50. Side view
9.	X 25	8.	*Lithothamnion mannii*. X 50
3, 7.	*Lithothamnion* sp. 1. Enlarged view of conceptacles. X 50	10, 11.	*Sporolithon* sp. 2. X 50
3.	Thallus with cells of hypothallus and conceptacles. X 15	10.	Thallus showing branching and sporangia. X 90
4.	*Polystrata* sp. X 50		

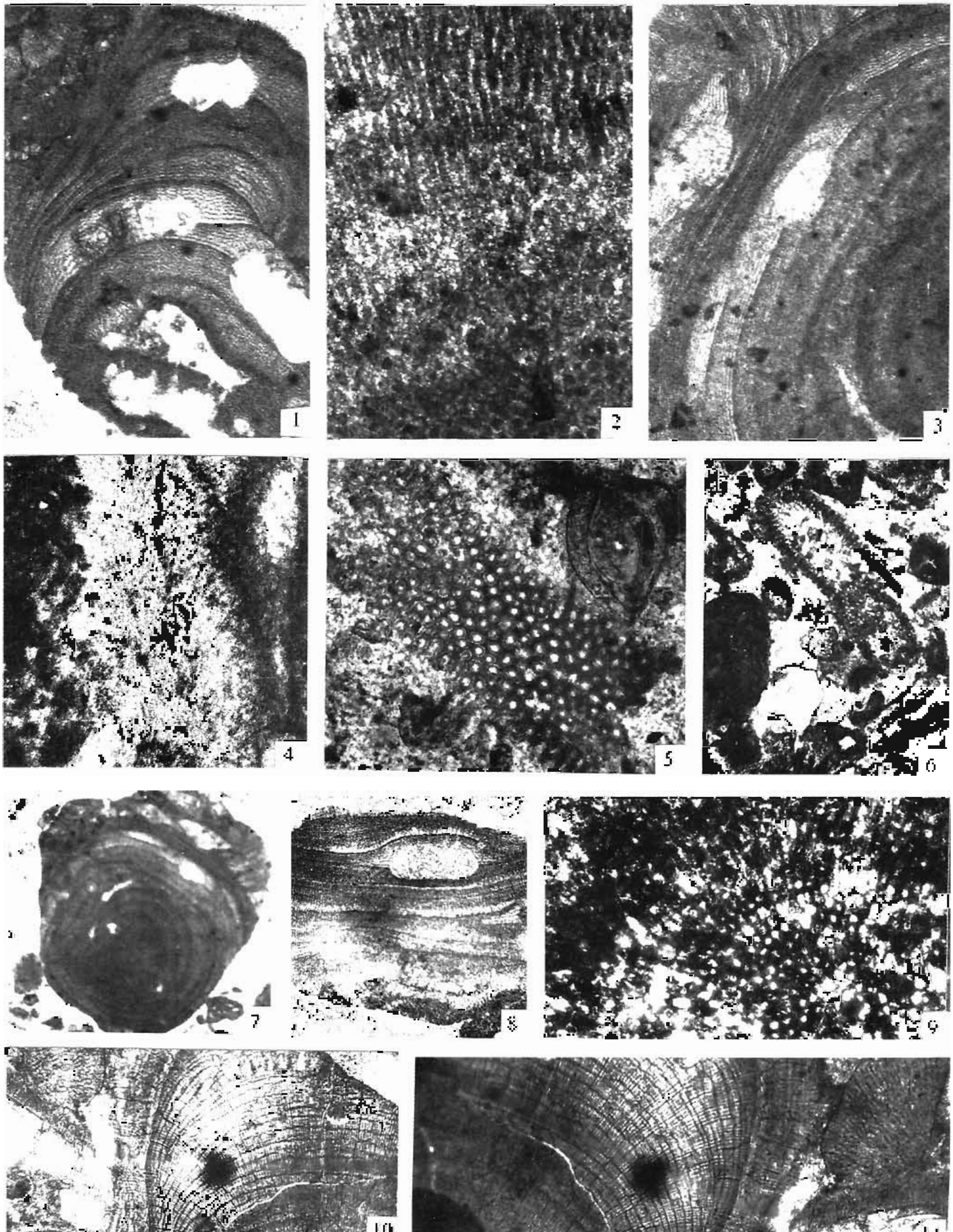


PLATE 6

apparently bisporangia/tetrasporangia, each with four tetraspores.

Sample No.—B/Sn/C4.

Slide No.—S/CB-1.

Locality—Sendurai.

Occurrence—Upper Unit, Ninniyur Formation.

Discussion—The present specimen is comparable with *L. colliculosum* Krivanne on the basis of morphology and conceptacles. However, in the present specimen conceptacles possess zonated tetra/bisporangia, each probably with four tetraspores. However, in the Krivanne's species sporangia have not been reported.

LITHOTHAMNION WALLISIUM Johnson & Tafur 1952

(Pl. 5, 6, 9)

1952 *Lithothamnion wallisium* Johnson & Tafur, p. 538, pl. 62, fig. 3.

1953 *Lithothamnion wallisium* Johnson & Stewart, p. 143, pl. 16, fig. 1.

1982 *Lithothamnion wallisium* Beckmann *et al.*, p. 134, pl. 12, figs 3-4.

Description—Growth form encrusting with variable thickness. Thallus organisation monomerous. Core filaments non-coaxial, parallel to the surface, core portion usually 60-70 μm thick, with cells of 10-25 μm in length and 6-10 μm in diameter. The peripheral filaments is distinct but irregularly zoned; its cells are 7-15 μm in length 6-9 μm in diameter. The conceptacles occur in irregular clusters; more or less reniform and measure 185-250 μm in width and 140 μm in height.

Sample No.—B/Per/A11.

Slide No.—P/CB-65.

Locality—Periyakurichchi.

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—The present specimens appear to be identical with the type species in filament organisation and shape of conceptacles, though the type specimens from California and those described from northwestern Peru (Johnson & Tafur, 1952; Johnson & Stewart, 1953) have larger conceptacles. Beckmann *et al.* (1982) reported this species from the Palaeocene of Monte Giglio, Italy.

LITHOTHAMNION CF. L. CARAVELLENSE Lemoine 1939

(Pl. 2, 10)

1939 *Lithothamnion* cf. *L. caravellense* Lemoine, p. 68-69.

1965 *Lithothamnion* cf. *L. caravellense* Johnson & Kaska, p. 27, pl. 39, figs 2-3.

Description—Growth form encrusting, thallus thickness about 850 mm. Thallus organisation monomerous. Core filaments non-coaxial, about 105 μm in thickness, with cells 8-15 μm in length and 8-12 μm in width. Peripheral region thicker than the core region, with prominent growth zones having cells 12 μm in length and 10 μm in width. Tetra/bisporangia conceptacles apparently multiporate, ovoid to reniform chambers 400-450 μm in diameter and 140-150 μm in height.

Sample No.—B/Per/B19.

Slide No.—P/CB-36.

Locality—Periyakurichchi.

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—Though broadly similar to *Lithothamnion* cf. *L. caravellense* reported from the Miocene of Guatemala by Johnson and Kaska (1965), the present specimens have slightly larger conceptacles than those of the Miocene specimens. Moreover, the multipored roof of the conceptacle in the present specimens is indistinct, it is, therefore, presently described as *Lithothamnion* cf. *L. caravellense* Lemoine.

LITHOTHAMNION sp. 1

(Pl. 6, 9)

Description—Growth form encrusting to lumpy. Thallus organisation monomerous. Core filaments not preserved. It is surrounded by the peripheral filaments, whose cells are arranged in layers parallel to the surface and are 25 μm in length and 18 μm in diameter. Tetra/bisporangia conceptacles, usually present in protuberances, and 212-230 μm long and 136-145 μm wide.

Sample No.—B/Nin/A12.

Slide No.—N/CB-8.

Locality—Ninniyur.

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—The growth form and thallus organisation of this specimen resembles that of *L. valens* Foslie as described by Basso *et al.* (1997) who have given a detailed account of morphotaxonomy of *L. valens* and *L. ramosissimum* (Gumbel non Reuss) Conti, 1946.

LITHOTHAMNION sp. 2

(Pl. 5, 9, 10)

Description—Growth form encrusting. Core filaments non-coaxial, core portion 70-120 μm thick and has cell dimensions 10-15 μm in length and 8-10 μm in diameter. Cells of peripheral filaments not measurable due to bad preservation of filaments. Conceptacles more or less rectangular or box shaped, pore indistinct, 280-310 μm wide, 110-125 μm high. Sporangia not preserved.

Sample No.—B/Per/B15.

Slide No.—P/CB-21.

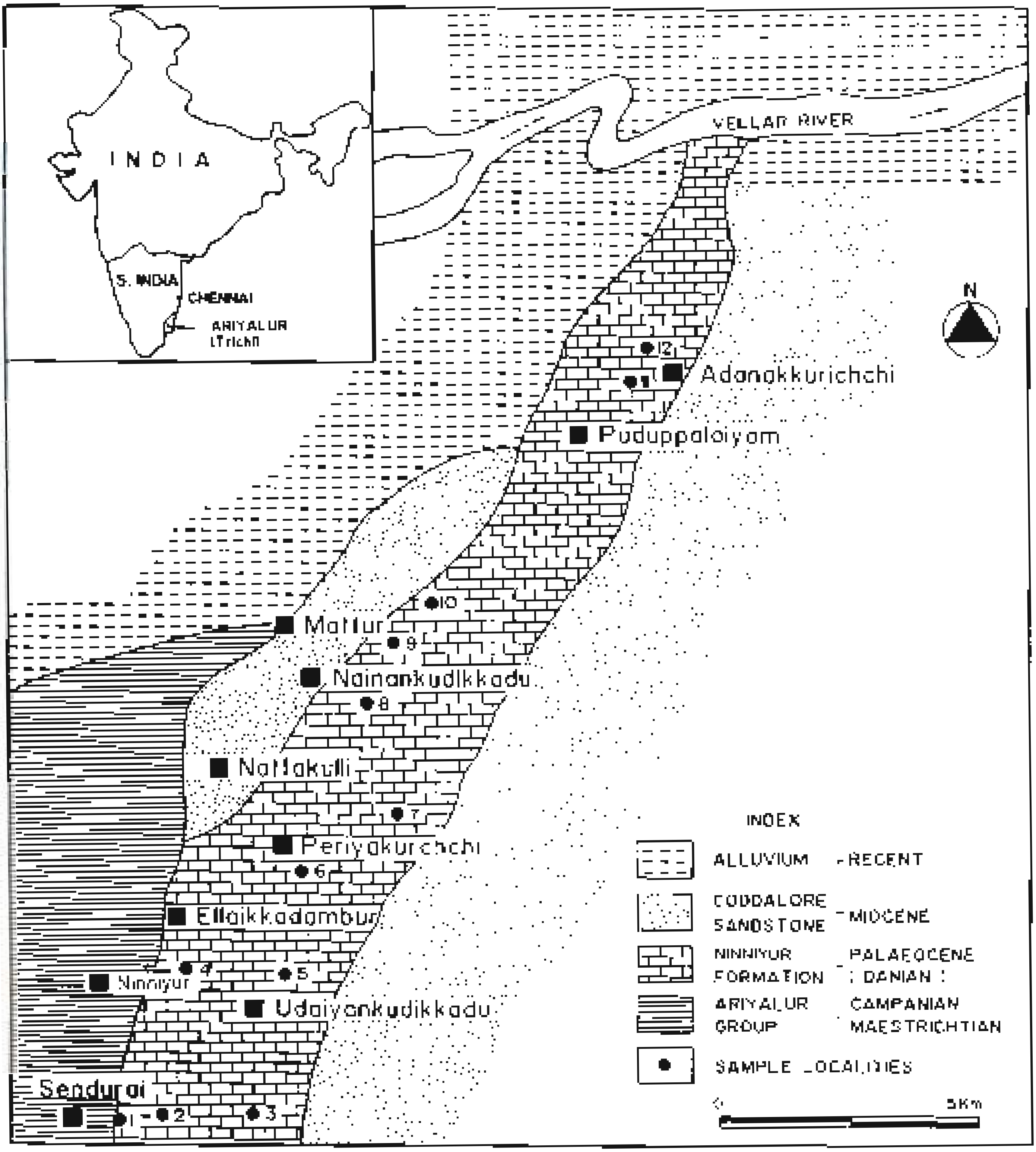


Fig. 2—The geological map of the Ninniyur area, Cauvery Basin, Tamil Nadu (modified after Malarkodi & Nagaraj, 1997)

Locality—Periyakurichchi.

Occurrence—Middle Unit, Niniyur Formation.

Discussion—This species differs from the *Lithothamnion aethiopum* Johnson and Tafur in shape and size of conceptacles. It does not show presence of sporangia. The morphological variation of conceptacles may be due to sectioning of thallus through different planes, but bands of thallus are distinct and the shape of conceptacles appears to be definite.

LITHOTHAMNION sp. 3

(Pl. 4.4; Pl. 5.4)

Description—Growth form encrusting. Thallus organisation monomerous. Core filament non-coaxial, core portion usually 0.16 mm thick, cell fusions occur. Cell tissues 12-20 μm in length and 7-10 μm in width. Peripheral cells rectangular or squarish, distinct, arranged in somewhat undulating rows, about 12-14 in length and 6-10 μm in width. In the peripheral region, the horizontal walls are more distinct than the vertical ones. Conceptacles immature, showing various developmental stages, sunken, 160-210 μm wide, 70-100 μm high.

Sample No.—B/Peri/A30.

Slide No.—PCB-52.

Locality—Periyakurichchi.

Occurrence—Middle Unit, Niniyur Formation.

Discussion—This specimen is comparable with *Palaeothamnium archaeotypum* Conti in the immature conceptacles. Basso *et al.* (1997) reported morphologically similar specimens from the Miocene of Leithakalk and assigned them to *Palaeothamnium archaeotypum* on the basis of developmental stages of conceptacles. Aguirre *et al.* (1996) and Basso (1997) recommended that identification of different species of the genus *Palaeothamnium* Conti be made not only on the basis of developmental stages of conceptacles but also on the growth form, flat epithallial cells, long subepithallial initials and peripheral region. However, the majority of the workers still give due importance to the developmental stages of conceptacles (c.f. Moussavian, 1991). Aguirre *et al.* (1996) have considered the genus *Palaeothamnium* Conti as the younger heterotypic synonym of the genus *Lithothamnion* Heydrich. Hence, the Niniyur specimen is being considered here under the genus *Lithothamnion*.

Subfamily—MELOBESIOIDEAE Bizzozero, 1885

MELOBESIOIDEAE gen. et spec. indet. 1

(Pl. 6.1)

Description—Growth form encrusting. Thallus organisation monomerous. Core filaments non-coaxial, core portion usually 140-180 μm thick, filaments curved towards the dorsal surface. Cells 15-20 μm in length and 9-12 μm in width. The peripheral filaments consist of irregular zones composed of rectangular cells. The cells measure 25-32 μm in length and 7-10 μm in width. Numerous large conceptacles occur irregularly through the tissue. They are 300 μm in width and 150 μm in height. The roof is pierced by numerous openings.

Sample No.—B/Peri/B16.

Slide No.—PCB-45.

Locality—Periyakurichchi.

Occurrence—Middle Unit, Niniyur Formation.

Discussion—The core filaments of this specimen are non-coaxial and epithallial cells are not preserved. Hence, it can be referred either to the genus *Lithothamnion* or to the genus *Phymatolithon*. The taxonomic concept of this form is based on the work of Rasser and Piller (1999) from the Austrian Molasse zone.

MELOBESIOIDEAE gen. et spec. indet. 2

(Pl. 5.3, 7)

Description—Growth form encrusting, with short, slender protuberances. Thallus organisation monomerous. Ventral core filaments poorly developed, non-coaxial, core portion usually 100-140 μm thick, filaments curved towards the dorsal surface. Cells rectangular, measuring 15 μm in length and 12 μm in width. Conceptacles large and prominent, measuring 440-570 μm in diameter and 190-285 μm in height. Roof apparently multiporate.

Sample No.—B/Peri/A30.

Slide No.—PCB-52.

Locality—Periyakurichchi.

Occurrence—Middle Unit, Niniyur Formation.

Discussion—The core filaments of this specimen are non-coaxial and epithallial cells are not preserved. Hence, it can be referred either to the genus *Lithothamnion* or to the genus *Phymatolithon*. The taxonomic concept of this form is based on the work of Rasser and Piller (1999) from the Austrian Molasse zone.

MELOBESIOIDEAE gen. et spec. indet. 3

(Pl. 5.1, 2)

Description—Growth form encrusting, which maintains a fairly constant thickness. Thallus organisation monomerous. Core filaments non-coaxial, 160-250 μm in thickness, with cells 18-24 μm in length and 6-12 μm in width, cell fusions

Fig. 1—The lithostratigraphic representation of the Niniyur Formation in the Ariyalur-Pondicherry area showing position of fossil-bearing samples.

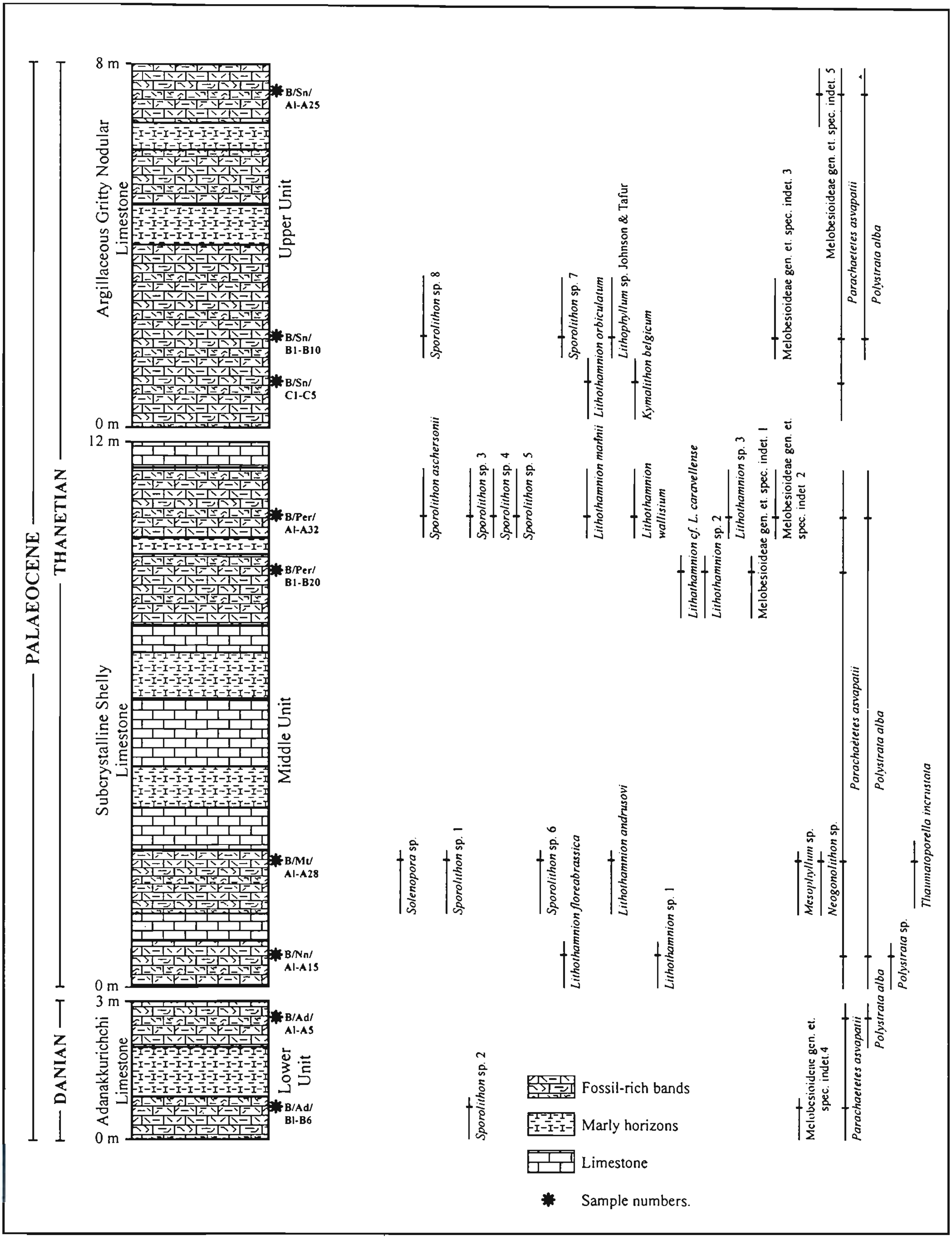

PALAEOCENE
DANIAN
THANETIAN
Adanakkurichchi Limestone
Lower Unit
Subcrystalline Shelly Limestone
Middle Unit
Argillaceous Gritty Nodular Limestone
Upper Unit
0 m
3 m
0 m
12 m
0 m
8 m
B/Ad/ B1-B6
B/Ad/ A1-A5
B/Nn/ A1-A15
B/Mt/ A1-A28
B/Per/ B1-B20
B/Per/ A1-A32
B/Sn/ C1-C5
B/Sn/ B1-B10
B/Sn/ A1-A25
Sporolithon sp. 2
Melobesioideae gen. et. spec. indet.4
Parachaetetes asvapatii
Polystrata alba
Polystrata sp.
Solenopora sp.
Sporolithon sp. 1
Sporolithon sp. 6
Lithothamnion floreabrassica
Lithothamnion andrusovi
Lithothamnion sp. 1
Mesophyllum sp.
Neogonolithon sp.
Thaumatoporella incrustata
Sporolithon aschersoni
Sporolithon sp. 3
Sporolithon sp. 4
Sporolithon sp. 5
Lithothamnion marlnii
Lithothamnion wallisium
Lithothamnion cf. L. caravellense
Lithothamnion sp. 2
Lithothamnion sp. 3
Melobesioideae gen. et. spec. indet. 1
Melobesioideae gen. et. spec. indet 2
Sporolithon sp. 8
Sporolithon sp. 7
Lithothamnion orbiculatum
Lithophyllum sp. Johnson & Tafur
Kymalithon belgicum
Melobesioideae gen. et. spec. indet. 3
Melobesioideae gen. et. spec. indet. 5
Fossil-rich bands
Marly horizons
Limestone
Sample numbers.

Fig. 3

present. Peripheral region with cells 7-12 µm in length and 6-9 µm in width, the thickness of peripheral cells variable and its cells are arranged in horizontal layers. Cell fusions present. Tetra/bisporangial conceptacles not present.

Sample No.—B/Sn/B5.

Slide No.—S/CB- 75.

Locality—Sendurai.

Occurrence—Upper Unit, Ninniyur Formation.

Discussion—Thallus morphology does not resemble any known genus of family Corallinaceae. In the absence of conceptacles, the generic identification of this specimen is not possible. The presence of cell fusions in the thallus and non-coaxial core filaments suggests its relationship with subfamily Melobesioideae.

MELOBESIOIDEAE gen. et spec. indet. 4

(Pl. 3.5)

Description—Growth form encrusting. Thallus organisation monomerous. Core filaments, coaxial, and its cell dimensions 16-26 µm in length and 12-18 µm in width. Peripheral filaments consist of very thin regular rows of long rectangular cells. Cells 15-17 µm in length and 18-25 µm in width. There is a slight alteration of cells near conceptacles; they are smaller and more irregular. Cell fusions not observed. Tetra/bisporangial conceptacles immature.

Sample No.—B/Ad/B1.

Slide No.—A/CB-11.

Locality—Adanakkurichchi.

Occurrence—Lower Unit, Ninniyur Formation.

Discussion—The present specimen possesses immature conceptacles which makes its identification difficult at generic level. Due to the presence of coaxial core filaments, this form seems to be comparable with the genus *Mesophyllum* Lemoine. Since pores of conceptacles are not clear, the present specimen is being placed under subfamily Melobesioideae.

MELOBESIOIDEAE gen. et spec. indet. 5

(Pl. 3.3)

Description—Thallus encrusting. The differentiation of core and peripheral filaments not distinct. Cells 11-16 µm in length and 6-8.5 µm in width. Tetra/bisporangial conceptacles not present.

Sample No.—B/Sn/A19.

Slide No.—S/CB-76.

Locality—Sendurai.

Occurrence—Upper Unit, Ninniyur Formation.

Discussion—Since this vegetative specimen possesses an encrusting growth form and lacks erect or articulated morphology, it is being placed under sub-family Melobesioideae in this study.

Genus—MESOPHYLLUM Lemoine 1928

MESOPHYLLUM sp.

(Pl. 3.8)

Description—Growth form encrusting, formed by more or less well-defined "layers" of cells, showing irregular growth zones. Thallus organisation monomerous. Core filaments coaxial about 75 µm in thickness. Cells 15-20 µm in length and 10-15 µm in width. The layers vary in thickness. The cells of different zones vary considerably in size. Peripheral region with cells 8-12 µm in length and 6-10 µm in width. Tetra/bisporangial conceptacles not preserved.

Sample No.—B/Mt/A23.

Slide No.—M/CB-22.

Locality—Mattur.

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—The present specimen is without reproductive structures but growth form and coaxial nature of core filaments indicate its affinity with *Mesophyllum varians* Johnson (1965) reported from the Palaeocene of Massif of Akros, Greece.

Subfamily—MASTOPHOROIDEAE Setchell, 1943

Genus—NEOGONOLITHON Setchell & Mason, 1943

Species—NEOGONOLITHON sp.

(Pl. 3.12)

Description—Growth form encrusting, thallus 450 µm in thickness. Thallus monomerous. Core filaments coaxial, about 180 µm in thickness, with cells 15-30 µm in length and 8-12 µm in width. Peripheral region with cells 14-20 µm in length and 12-22 µm in width. Cell fusions present. Tetra/bisporangial conceptacle pore indistinct, 380-460 µm wide, 80-95 µm long.

Sample No.—B/Mt/A24.

Slide No.—M/CB-10.

Locality—Mattur.

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—Rasser and Piller (1999) recognised the possibly with similar features as *Neogonolithon* on the basis of uniporate nature of conceptacle and coaxial core filaments. Following these authors, the present specimen is described here as *Neogonolithon* in view of its coaxial core filaments and apparently uniporate nature of conceptacles. Hence, it is being treated as unnamed species of the genus *Neogonolithon* Setchell & Mason. Rasser & Piller (1999) reported *Neogonolithon* sp. from the late Eocene of the Austrian Molasse Zone.

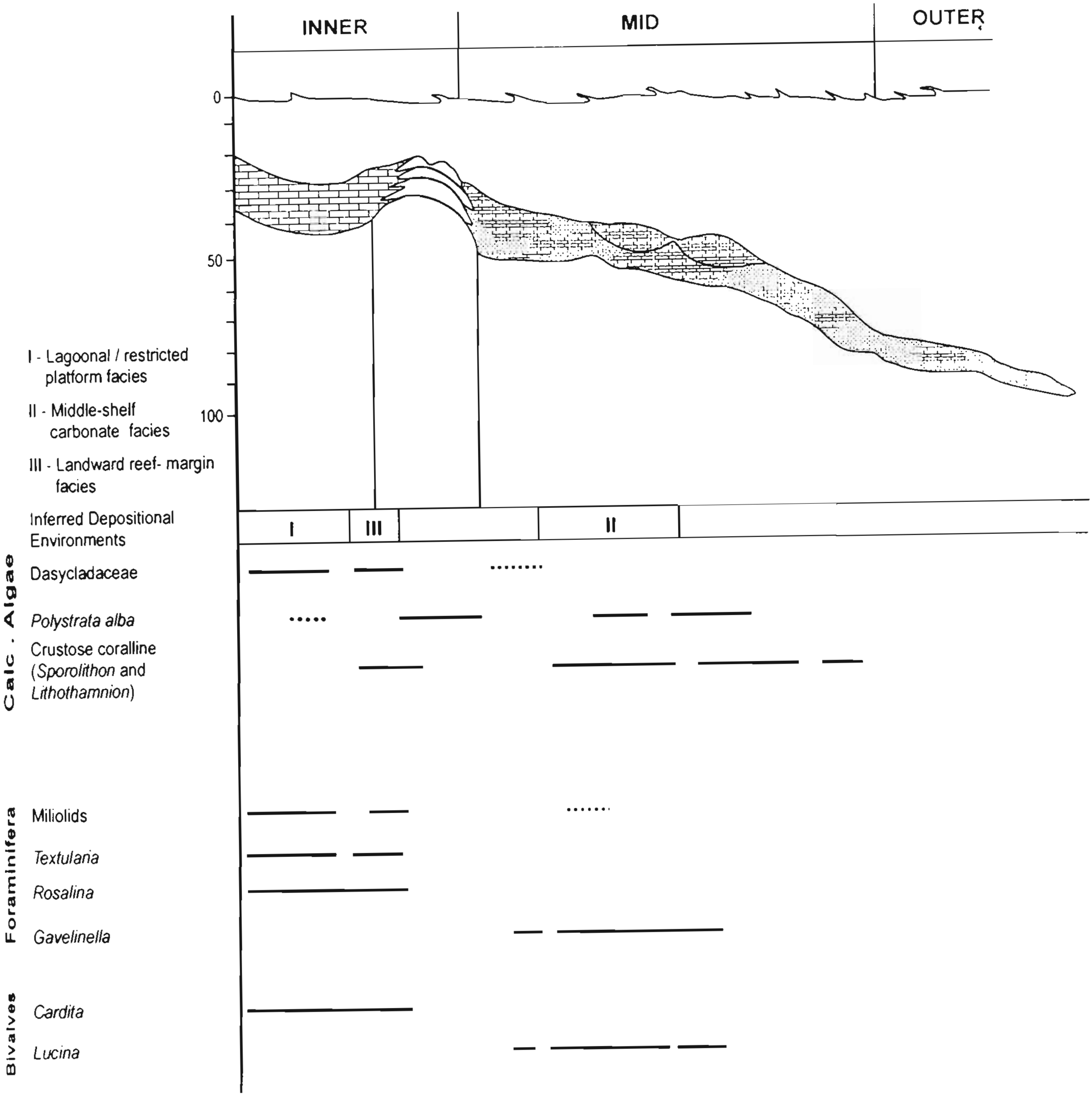


Fig. 4—Conceptual depositional framework of the environmental setting during accumulation on the Ninniyur Formation.

Subfamily—LITHOPHYLLOIDEAE Setchell, 1943

Genus—LITHOPHYLLUM Phillippi, 1837

Species—LITHOPHYLLUM sp. Johnson & Tafur, 1952

(Pl. 1.6)

Description—Growth form encrusting. Core filaments poorly developed, peripheral filaments thin and cells 14-20 µm in length and 16-25 µm in width. Tetra/bisporangial conceptacles small, ovoid or more or less triangular, uniporate, shape variable, 40-70 µm in height and 45-54 µm in width.

Sample No.—B/Sn/B5.

Slide No.—S/CB-75.

Locality—Sendurai.

Occurrence—Upper Unit, Ninniyur Formation.

Discussion—The Ninniyur specimen agrees well with an unnamed species, *Lithophyllum* sp. Phillippi 1837 reported by Johnson and Tafur (1952) from the Atascadero Limestone (Eocene). The present specimen shows poorly developed core filaments, but the nature of uniporate conceptacle and its smaller size suggest its closeness with the Atascadero form.

Family—PEYSSONNELIACEAE Denizot, 1968

Genus—POLYSTRATA Heydrich, 1905

Species—POLYSTRATA ALBA (Pfender) Denizot, 1968

(Pl. 3, figs 2, 7, 11)

1936 *Pseudolithothamnium album* nov. gen. nov. sp. Pfender, p. 304-308; pl. 19, figs 1-5.

1968 *Polystrata alba* (Pfender); Denizot, p. 475-476; pl.9, fig.4.

1965 *Ethelia alba* Johnson & Kaska, p. 69, pl. 15, figs 1, 2.

1997 *Polystrata alba* (Pfender); Denizot, Bassi, p. 311-316; figs 1-4b.

Description—Thallus filamentous, strap or ribbon shaped, consisting of a central part formed by elongated cells which give rise to branched filaments radiating outwards. These filaments are curved outwards and form postigenous tissue. Sporangia not seen. Length of cells 35-40 μm; diameter of cells 20-25μm.

Sample No.—B/Ad/B4; B/Nn/A13; B/Per/A7;B/Sn/A10, B4.

Slide No.—N/CB-48.

Locality—Adanakkurichchi, Ninniyur, Sendurai.

Occurrence—Lower, Middle, Upper units, Ninniyur Formation.

Discussion—As cited in Bassi (1997), *P. alba* is a widely occurring species in the Eocene limestone of Europe. Bassi (1997) re-examined and redescribed the material from the type section (Calcare di Nago Formation, Southern Alps) and pointed out its anatomical analogies with non-geniculate corallines. In the study area, it usually occurs as crusts in association with other corallines such as *Sporolithon*, *Lithothamnion*, etc.

POLYSTRATA sp.

(Pl. 6.4)

Description—Thallus blade-like, bilateral, comprising large elongated cells at the centre, slightly bending outwards, to form postigenous filaments. Sporangia not preserved. Length of cells 55-70 μm width of cells 30-45 μm.

Sample No.—B/Nn/A10.

Slide No.—N/CB- 35.

Locality—Ninniyur.

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—In this species, the thallus is blade-like and has longer cells, while that of *P. alba* is ribbon-shaped and comprises relatively shorter cells. Hence, this specimen is being described as *Polystrata* sp.

Incertae Sedis

Genus—THAUMATOPORELLA Pia, 1927

Species—THAUMATOPORELLA (POLYGONELLA) INCRUSTATA Elliott, 1957

(Pl. 6.5, 6)

1927 *Thaumatoporella parvovesiculifera* (Raineri) Pia, p. 69.

1957 *Lithoporella elliotti* Emberger, p. 625, 629, pl. 32.

1957 *Polygonella incrustata* Elliot, p. 230, pl. 1, figs 11-12.

1965 *Thaumatoporella (Polygonella) incrustata* Johnson & Kaska, p. 59, pl. 16, fig. 2.

Description—Thallus thin, encrusting, a single layer of long polygonal prismatic cells about 55-112 μm in length, 20-40 μm in width.

Sample No.—B/Mt/A2.

Slide No.—M /CB-14,17.

Locality—Mattur.

Occurrence—Middle Unit, Ninniyur Formation.

Discussion—De Castro (1990) described the genus *Thaumatoporella* Pia as a member of the family Thaumatoporellaceae of the order Thaumatoporellales, apparently a green algal form. However, we do not find any convincing reason to assign this genus to green algae because it lacks their typical branching pattern. In the present study, it is described as a form under *Incertae Sedis*.

ANNOTATED CHECK LIST OF GENERA

Genus—SOLENOPORA Dybowski 1878

Thallus encrusting with more or less radiating filaments, cross-partitions are widely spaced or absent in this genus. If the partitions are present, they are considerably thinner than the vertical cell walls. Conceptacles unknown.

Genus—PARACHAETETES Deninger, 1906

Thallus in the form of thin crust with small protuberances. The genus is characterised by strong, numerous, regularly spaced cross partitions that give the tissue a grid-like appearance in longitudinal section. Conceptacles unknown.

Genus—SPOROLITHON Heydrich 1897

Epithallial cells with flattened and flared cells and tetrasporangial conceptacles separated by interspersed calcified filaments (paraphyses) (Woelkerling, 1988); conceptacles arranged in sori (Verheij, 1993).

Genus—KYMALITHON Lemoine & Emberger 1967

Growth form encrusting. Crustose portion composed of a core of non-coaxial filaments and a peripheral region where distal portions of core filaments or their derivatives curve outwards towards the thallus surface. The core filaments are similar with narrow flexible undulating threads of cells with thin walls. There is no suggestion of a regular horizontal layering of the cells. The peripheral filaments in both the basal crust and around the branches show a well-developed "layering" of the cells with thin continuous partition walls. Sporangia develop in the outer part of the peripheral region, in small groups, often containing rounded spores, each sporangium having an individual canal extending to the surface for the discharge of spores. A few examples of sexual conceptacles have been observed.

Genus—LITHOTHAMNION Heydrich 1897

Growth form warty to fruticose. Thallus monomerous, peripheral region is well developed with distinct zonation. Filaments radially organised inside the protuberances, cell fusions conspicuous. Tetra/bisporangial conceptacles multiporate.

Genus—MESOPHYLLUM Lemoine 1928

Growth form crustose to fruticose, composed of flattened lamellae or cylindrical to compressed protuberances. Filaments each consisting of a terminal or subepithallial initial which can produce epithallial cells outwardly at the thallus surface and additional vegetative cells inwardly; palisade cells lacking. Some but not all cells of contiguous filaments joined by cell fusions. Tetra/bisporangial conceptacles multiporate, tetra/bisporangia with mucilaginous plugs. Except for the occurrence of mucilaginous plugs, all these characters can be preserved and observed in fossil specimens. However, according to Woelkerling and Harvey (1992, 1993) *Mesophyllum* is delimited from other genera of Melobesioideae by a combination of eight features, four of which concern the formation of the spermatangial conceptacles and other spermatangial characters, which cannot be observed in the fossils in which the thallus contains a core of coaxial filaments. However, the remaining four characters (haustoria absent, internal construction monomerous, outer-most walls

	Lithological units	Lithology	Study area
CUDDALORE FORMATION			
NINIYUR FORMATION	Argillaceous gritty nodular Limestone (Upper)	Limestone interbedded with marl and clay, contains calcareous algae, corals, polyzoans, bivalves, gastropods and miliolid foraminifera in large number (8 m)	SENDURAI
	White Compact Sublithographic Shelly Limestone (Middle)	Limestone containing broad, rounded patches of calcareous algae with [illegible] (12 m)	PERIYAKKURICHCHI
	Adanakkurichchi Limestone (Lower)	Argillaceous Limestone with intercalated marl and clay. Large number of small, rounded white [illegible] of calcareous algae present in association with bivalves, foraminifera, polyzoans etc. (7 m)	ADANAKKURICHCHI
ARIYALUR GROUP			

Fig. 5—Showing the succession of the Niniyur Formation in the area of study (modified after Muthuramu & Nagaraj, 199?)

of epithallial cells rounded or flattened but not flared; vegetative initials usually longer than cells immediately subtending them), though observable in fossils, are not sufficient to delimit *Mesophyllum* from other genera of Melobesioideae. Therefore it is necessary to use a combination of the above-mentioned characters, together with a predominantly coaxial morphology of the ventral core of cell filaments, to identify fossil specimens of *Mesophyllum*.

Genus—NEOGONOLITHON Setchell & Mason, 1943

Thallus non-endophytic, lacking haustoria and palisade cells; core filaments coaxial (Woelkerling, 1988; Braga *et al.*, 1993). Some cells of contiguous filaments joined by cell fusions. Tetra/bisporangial conceptacles uniporate and clearly delimited.

Genus—LITHOPHYLLUM Philippi 1837

Growth form crustose to fruticose composed entirely of protuberances. Crustose portion of plants and lamellae dorsiventral and dimerous, monomerous, or both dimerous and monomerous. Cell fusions unknown. Tetra/bisporangial conceptacles uniporate and clearly delimited.

Genus—POLYSTRATA Heydrich 1905

Plant growth epigenous, consisting of thin lamellae forming variously shaped thalli lacking in protuberances. The thallus is pseudoparenchymatous, composed of filaments and organised in a bilateral-radial manner. In longitudinal section, each thallus consists of a single eccentric row of primigenous filaments. Postigenous filaments arise plumosely from the outer surface of the cells of primigenous filaments both upward and downward. Within a primigenous filaments, all the successive cells are joined by primary pit connections. Successive cells of postigenous filaments are not joined by primary pit-connections (Basso, 1997).

Genus—THAUMATOPORELLA Pia 1927

Thallus crustose or encrusting, consisting of a single layer of large polygonal cells which may be prismatic in shape. Fertile structures not seen.

STRATIGRAPHIC SIGNIFICANCE

Of 32 taxa of the red algae identified in the present material from the Palaeocene rocks of the Niniyur Formation, seven species are known from the Palaeocene deposits of other parts of the world, and two are known to extend from the Palaeocene to the Eocene. However, this study extends the stratigraphic ranges of a few younger (Oligocene–Miocene, Pleistocene) forms to the Palaeocene (e.g., *Lithothamnion wilsonianum*) and documents for the first time some Jurassic and Middle-Upper Cretaceous taxa (e.g., *Kymalithon belgicum*, *Thaumatoporella* sp., etc.) from the geologically younger Niniyur Formation. Among the Niniyur forms, those which are restricted to the Palaeocene outnumber others and support the Palaeocene age for the Niniyur Formation.

PALAEOECOLOGY

The fossil assemblages of the Niniyur Formation show presence in abundance of the fossil algae, foraminifera, ostracods and mega-invertebrates which can be used as a means to interpret the depositional environment in which the three lithounits of this formation were deposited. The foraminifera and the invertebrates have been used in the previous studies for this purpose, but the ecological potential of the fossil calcareous algae, as indicated in Wray (1978), has not been effectively realised for palaeoenvironmental interpretations because the taxonomic database of the coralline algae from the area of study is inadequate. The present study shows that the taxonomic composition of the calcareous algae of the Niniyur Formation is varied and quite useful for palaeoecological interpretations.

Among the various biotic groups, coralline algae constitute the major components of the assemblage of fossils of the Niniyur Formation. The majority of red algae from the Niniyur Formation are of crustose type and crusts are usually thick and only few thalli show branches. However, the composition of the coralline algal taxa is not uniform in the sequence and shows variation in their distribution in the three units of the formation (Fig. 3).

Adanakkurichchi Limestone Unit

An argillaceous limestone unit dominated by shale and marl, it is characterised by poor development of calcareous algae and other fossil groups. It is the basalmost unit of the Cenozoic succession in the area following the unfossiliferous Kallamedu Formation of the terminal Cretaceous. The not-so well-developed fossil forms of this unit possibly represent the early phase of evolution of the Palaeogene marine life after the terminal extinction event of the Late Cretaceous. Poor diversity and limited development of the algal flora of the lower unit could be explained in terms of gradual regeneration of carbonate platform environments in the post-Cretaceous times. The recovery of benthic communities in the Cenozoic was not quick and did not occur until the stable, stress-free, warmer, oligotrophic environments became available following the climatic warming, high sea-level, low influx of terrigenous supply, reduced upwelling, etc. during the Thanetian (Keller, 1988; Hottinger, 1987; Jauhri, 1997). The signatures of such environments are seen in the middle unit where the different animal and floral groups appear in very high diversities and show extensive development.

The red algae are represented only by fragments of *Sporolithon*, *Parachaetetes*, *Polystrata* which are not significant. Their limited development seems to be due to influx of clastic material received from the coast as indicated by presence of fine clastic sediment and dominance of miliolids. The latter are known to thrive in near-shore environment (Malarkodi & Nagaraj, 1997). Dasycladacean elements referable to *Indopolia satyavanti* Rao & Pia are present in noticeable numbers. *Indopolia* is indicative of shallow shelf facies (back-reef) as it has been reported from the deposits of lagoonal/restricted platform facies of Greece (Deloffre *et al.*, 1991), Ras Al Hamra, Oman (Rácz, 1979) and Iraq (Elliott, 1968). Occasional episodes of storms have washed in elements of relatively deeper-water (middle-shelf) planktic foraminiferal species which are present in some horizons of this unit (Malarkodi & Nagaraj, 1997). From the above facts, it is suggested that Adanakkurichchi unit represents a shallow "back-reef" (lagoonal/restricted platform) facies (Fig. 4) possibly laid down during a gradually transgressing sea within the near-shore, inner-neritic zone characterised by relatively low-energy conditions.

Subcrystalline shelly Limestone Unit

It is a relatively pure carbonate unit characterised by abundant bivalve and gastropod shells and foraminifera. The dominant megainvertebrate fossil species is *Lucina perovata*. The algal group shows maximum representation of crustose type of coralline and other red algae which are dominated by *Sporolithon* and *Lithothamnion*. *Polystrata*, *Parachaetetes* and some indeterminate elements of Melobesioideae also occur in this unit.

The algal crusts appear to be the commonest growth form in the Niniyur algal flora of the middle unit except for a few lumpy forms with protuberances. The encrusting forms were the sediment binders and might have produced the algal boundstones commonly seen in this unit. The dominance of algal crusts, high algal diversity, presence of sporolithaceans and melobesioids in abundance and coarse bioclastic sediment with some carbonate mud all point to a relatively deeper environment of open shelf comparable to that of the algal Rhodolith pavement and Rhodolith mounds facies of Bassi (1998b). The *Sporolithon* rich flora in association with acervulinid foraminifers has been found to be characteristic of the depth range 20-40 m in the northern Red sea, Egypt (Rasser & Piller, 1997). Previous records of *Sporolithon* and *Lithothamnion* have been made from the deposits interpreted to be representative of reef-margin conditions and deeper parts of middle shelf carbonate environment (Schaleker, 1968; Ghose, 1977; Rácz, 1979).

Another important feature of the coralline algal facies of the middle unit of the Niniyur Formation is the association of *Polystrata* in appreciable number. Bassi (1998b) reports that *Polystrata* forms encrustations on hard or soft substrates, either alone or in consortium of non-geniculate corallines and encrusting foraminifera. In the mid and the uppermost outer ramp environments of the Lessini Shelf characterised by low-energy conditions present below normal wave base and normal storm wave base. The studied samples of the middle unit show low amount of miliolids and presence of carbonate mud supporting a relatively deeper environment of low-energy conditions.

In the present context the ecological information on the lucinoid bivalves predominant in this unit is very significant. They are detritus feeders which burrow relatively deeply and suck organic matter accumulated on the sediment surface by means of mucus-lined tubes. Their occurrence in abundance in this unit gives indications of soft but firm substrates where the organic matter would settle on sediment surfaces due to low-water energy and low rates of sedimentation because of very little influx of clastic material.

From the above discussion, it appears that the subcrystalline shelly limestone was deposited in a middle-shelf, low-energy carbonate environment which promoted the formation of patch-reefal organogenic accumulations referred to as "banks" by Banerji (1979) (Fig. 4).

Argillaceous gritty nodular limestone Unit

Among the numerous mega-invertebrate fossils such as corals, bivalves and gastropods, *Cardita beaumonti* is one of the most common forms of this unit. This unit shows influence of terrigenous clastic material during its deposition. The carbonate deposits of this part of the succession, therefore, are comparatively impure and show relatively thinner populations of megainvertebrates, foraminifera, etc.

Among the microfaunal elements, ostracods are predominant in comparison to foraminifera. Three common genera of foraminifera noticed in this unit are *Gavelinella* referable to *G. danica*, *Textularia* and *Rosalina* (Malarkodi & Nagaraj, 1997). *Gavelinella* is a common component of Palaeocene benthic shelf assemblages with textularids and *Rosalina*. These forms usually flourish in an environment marked by high input of clastic material (Berggren & Aubert, 1975).

The red algal association is not as abundant and diversified as that of the preceding unit and is not helpful in providing precise information about palaeo-environmental reconstruction. The genera present in this unit are *Sporolithon*, *Lithothamnion*, *Polystrata*, *Lithophyllum* and *Parachaetetes*. However, the algal association broadly indicates deposition in patch-reefal environment in close proximity to near shores, lagoonal to tidal, medium energy environment. This interpretation is supported by ecological data on the associated foraminifera (e.g., *Gavelinella*, *Rosalina* and *Textularia*) which indicate deposition of this lithounit in the presence of clastic material received from the shore.

The associated dasycladaceans, better represented in this unit than the lower and the middle, include *Cymopolia* sp., *Indopolia satyavanti* Rao & Pia, *Indopolia* sp. and "*Neomeris*" sp. (Misra *et al.*, 2000) which have usually been reported from the lagoonal and restricted platform deposits of Europe and the Middle East (Barattolo, 1998). They support the interpretations based on red algal forms and foraminifera. This depositional environment seems to be similar to the landward reef-margin facies of Basso (1998) (see Text-fig. 4).

CONCLUSION

The algal assemblage studied here is distinguishable into three algal associations in the Niniyur Formation. These associations allow to interpret the depositional environment which prevailed during the Palaeocene in the Niniyur area.

Thirty two taxa of the red algae have been recognised (Fig. 3), of these, seven species are characteristic of the Palaeocene deposits in different parts of the world and two extend from the Palaeocene to Eocene. Others are long ranging and are known either from the geologically older or younger successions. The most common genera are *Sporolithon*, *Lithothamnion* and *Mesophyllum* gen. et. spec. indet.

The Niniyur Formation represents a progradational cycle of the post-Cretaceous transgression which extended from early to late Palaeocene. It was deposited in a carbonate environment with the facies mosaic comparable to that of the Palaeocene deposits of other areas in the Tethys (e.g., Iraq, Oman). The deposits of the Niniyur Formation are characterized by three depositional facies: a near-shore, lagoonal facies with moderate influence of clastic sedimentation, the middle shelf low energy carbonate facies with abundant algal flora and the associated fauna promoting patch-reefal build ups, and the landward "reef margin" facies marking deposition in inner-shelf environment having access to near-shore to tidal conditions and influence of terrigenous clastic deposition. The latter points to the regressive phase of sea in the study area.

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Taxonomic revision of tricolpate pollen from Indian Tertiary

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ABSTRACT

Mandal J & Rao MR 2001. Taxonomic revision of tricolpate pollen from Indian Tertiary. Palaeobotanist 50(2&3) : 341-368.

Tricolpate pollen have been described under 32 genera and 98 species from the Tertiary sediments of India. Some of these genera are either nomenclaturally illegitimate or invalid but still are being used by different palynologists. Moreover, circumscription and the diagnoses of some genera/species are overlapping each other and thus they need a thorough taxonomic revision to make them more useful in stratigraphy. With this objective, holotypes and related specimens of the tricolpate pollen taxa housed at Birbal Sahni Institute of Palaeobotany Museum have been restudied and in part photodocumented. Character assessment and reallocation of the remaining taxa have been done on the basis of available literature and illustrations. Each taxon has been evaluated and demarcation of morphological limits have been attempted to make them more useful and applicable for stratigraphy and age correlation. In addition, the distribution of different species has been recorded to know their stratigraphic range.

Key-words—Palynology, Tricolpate pollen, Tertiary, India.

टर्शियरी कल्प के भारतीय त्रिकॉल्पसी परागकणों का वर्गिकीय पुनरावलोकन

जगन्नाथ प्रसाद मण्डल एवं मुलागलापल्ली रामचन्द्र राव

सारांश

भारत के टर्शियरी अवसादों से प्राप्त त्रिकॉल्पसी परागकणों को 32 वंशों तथा 98 प्रजातियों के अन्तर्गत विवेचित किया गया है। यद्यपि इनमें से कुछ वंश या तो नामकरण के आधार पर विधिसम्मत नहीं है अथवा अयोग्य हैं, किन्तु फिर भी भिन्न-भिन्न परागाणुविद् इन्हें अभी भी प्रयुक्त कर रहे हैं। इसके अतिरिक्त कुछ वंशों/प्रजातियों के परिसीमन तथा विश्लेषण परस्पर विरोधाभासी हैं। अतः इन्हें स्तरिकी हेतु उपयोगी बनाने के लिए इनका गहन वर्गिकीय पुनरावलोकन आवश्यक है। इस उद्देश्य को दृष्टिगत रखते हुए बीरबल साहनी पुरावनस्पतिविज्ञान संस्थान के संग्रहालय में संरक्षित त्रिकॉल्पसी परागाणु वर्गकों के आदि प्ररूपों तथा सम्बन्धित प्रादर्शों का पुनः अध्ययन हेतु छायाप्रलेखन किया गया । प्राप्त साहित्य तथा पारदर्शियों के आधार पर शेष वर्गकों का अभिलक्षण मूल्यांकन तथा पुनः स्थान निर्धारण किया गया। इन्हें स्तरिकी तथा आयु सहसम्बन्धन हेतु अधिक उपयोगी बनाने के उद्देश्य से प्रत्येक वर्ग का मूल्यांकन किया गया तथा इनकी संरचनात्मक सीमाओं के अंकन का प्रयास किया गया। इसके अतिरिक्त इनकी स्तरिकी सीमाओं को ज्ञात करने हेतु विभिन्न प्रजातियों के वितरण भी अंकित किए गए।

संकेत शब्द—परागाणुविज्ञान, त्रिकॉल्पसी परागकण, टर्शियरी, भारत.

INTRODUCTION

THE tricolpate pollen are very abundant and diversified in the Tertiary sequences of India and are represented by 98 species belonging to 32 genera. It has been observed that some of these tricolpate palynotaxa are not properly described. Also, some generic diagnoses overlap with others, e.g., those of *Retitrescolpites*, *Tricolpites* and *Tricolpopollis*. Moreover, the genus *Tricolpites* has been used as dumping place for tricolpate forms irrespective of their qualitative characters. Further, a number of species have been erected on only minute difference of characters, and have been recorded only once by their original authors, viz., *Tricolpites dentimarginatus*, *Retitrescolpites regularis*, *Clavatricolpites gracilis*. Many other species have not been properly identified and different taxa have been lumped together. Consequently, these appear long ranging in the stratigraphic column (e.g., *Tricolpites reticulatus* and *Lakiapollis ovatus*) and have lost significance. In some instances palynologists from different centers have followed nomenclature of their own school, and thus one taxon has several names, e.g., synonyms of *Tricolpites reticulatus*.

Genera like *Polleniricolpites*, *Retitricolpites* are nomenclaturally illegitimate (Jansonius & Hills, 1976) and should be merged with the existing genera or given a new name. Similarly, although holotypes of *Tricolpopollenites* and *Retitrescolpites* are reported to be colporate, still some tricolpate species are being assigned to these genera. Furthermore, there are no genera to accommodate the forms having a margo (*Tricolpites margocolpites*), granulose exine (*Tricolpites granulatus*) or warty exine (*Tricolpites verrucosus*). All these nomenclaturally confusing factors conspire to limit the importance of this group of pollen in correlation and determination of precise age.

These anomalies can be eliminated by studying the holotypes or other specimens for their character assessment and correct placement. With the above objectives, Thanikaimoni *et al.* (1984) and Venkatachala *et al.* (1989, 1996) restudied, described and illustrated some selected taxa. They are *Crassoretitriletes vanraadshooveni* Navale & Misra, 1979, *Dakshinipollenites trisulcatus* Navale & Misra, 1979 emend. Singh & Misra, 1991, *Iraquipollenites spinulosus* Navale & Misra, 1979, *Paravuripollis* [illegible] Kar, 1978, *Pinnatisporites* [illegible] Navale & Misra, 1979, *Tricolpites reticulatus* Cookson ex Couper, 1953, *Crototricolpites* [illegible] Rao & Ramanujam, 1982, *Intrareticulites brevis* (Sah & Kar, 1970) Kar, 1985, *Lanagiopollis elegans* Rao & Ramanujam, 1982 and *Barleriapollenites* [illegible] Ramanujam & Rao in Thanikaimoni *et al.*, 1984.

In the present study, we have endeavoured to evaluate the morphological limits, nomenclatural and taxonomic status of the tricolpate species recorded from Indian Tertiary sediments. Only three species from the above mentioned taxa have been incorporated here. For these purposes holotypes and other specimens available at the museum of Birbal Sahni Institute of Palaeobotany, Lucknow have been examined and photodocumented. The critical evaluation and taxonomic reallocation are based on the examination of specimens, descriptions and illustrations from published literature. Simultaneously, the stratigraphic ranges of different species have been tabulated on the basis of records of their occurrences.

SYSTEMATIC DESCRIPTION

Genus—ALBERTIPOLLENITES Srivastava, 1969a

Type species—*Albertipollenites crassireticulatus* Srivastava, 1969a

Original Diagnosis—Tricolpate, angulaperturate, oblate to spheroidal, colpi short or long, meridional; amb triangular to circular, sides straight to convex; sexine thick, tectate. Ornamentation reticulate, reticula of uniform size all over the pollen body; lumina size 1 μm or larger.

ALBERTIPOLLENITES AQUIFOLIACEAEFORMIS (Biswas, 1962) comb. nov.

Basionym—

Tricolpopollis aquifoliaceaeformis Biswas, 1962. Bull. geol. min. metall. Soc. India 26: 38, pl. 5, fig. 18.

Original Description—Equatorial compression; exine moderately thick, with minute rods, tricolpate; 21 μm.

Occurrence—Early-Middle Eocene, Tura Formation, Meghalaya (Biswas, 1962).

Remark—The photograph (pl. 5, fig. 18) shows that reticula are more than 1 μm in diameter and uniformly present all over the surface.

PLATE 1 >

1. *Polleniricolpites* [illegible] Kar *et al.*, 1994, Slide No. BSIP 10922 (E 33/2), Holotype.
2-3. *Albertipollenites* [illegible] (Sah & Kar, 1970) comb. nov., Slide No. BSIP 5336 (E 29/1), Holotype in different foci.
4. *Dipterocarpuspollenites* [illegible] (Kar & Jain, 1981) Kar, 1992, Slide No. BSIP 5550 (J 39/1).
5 & 6. *Lakiapollis ovatus* [illegible] Comp. (Mathur & Jain, 1980) figs 5-6, Slide No. BSIP 4563 (E 33/3) in different foci; fig. 6, Slide No. BSIP 4563 (N 42) in equatorial view.
7-8. *Dakshinipollenites trisulcatus* Navale & Misra emend. Singh, 1991, Slide No. BSIP [illegible] in different foci.
10-11. [illegible] Saxena, 1979 comb. nov., Slide No. BSIP 12931 (P 37).
12. [illegible] Muller, 1968, Slide No. BSIP 12 [illegible]

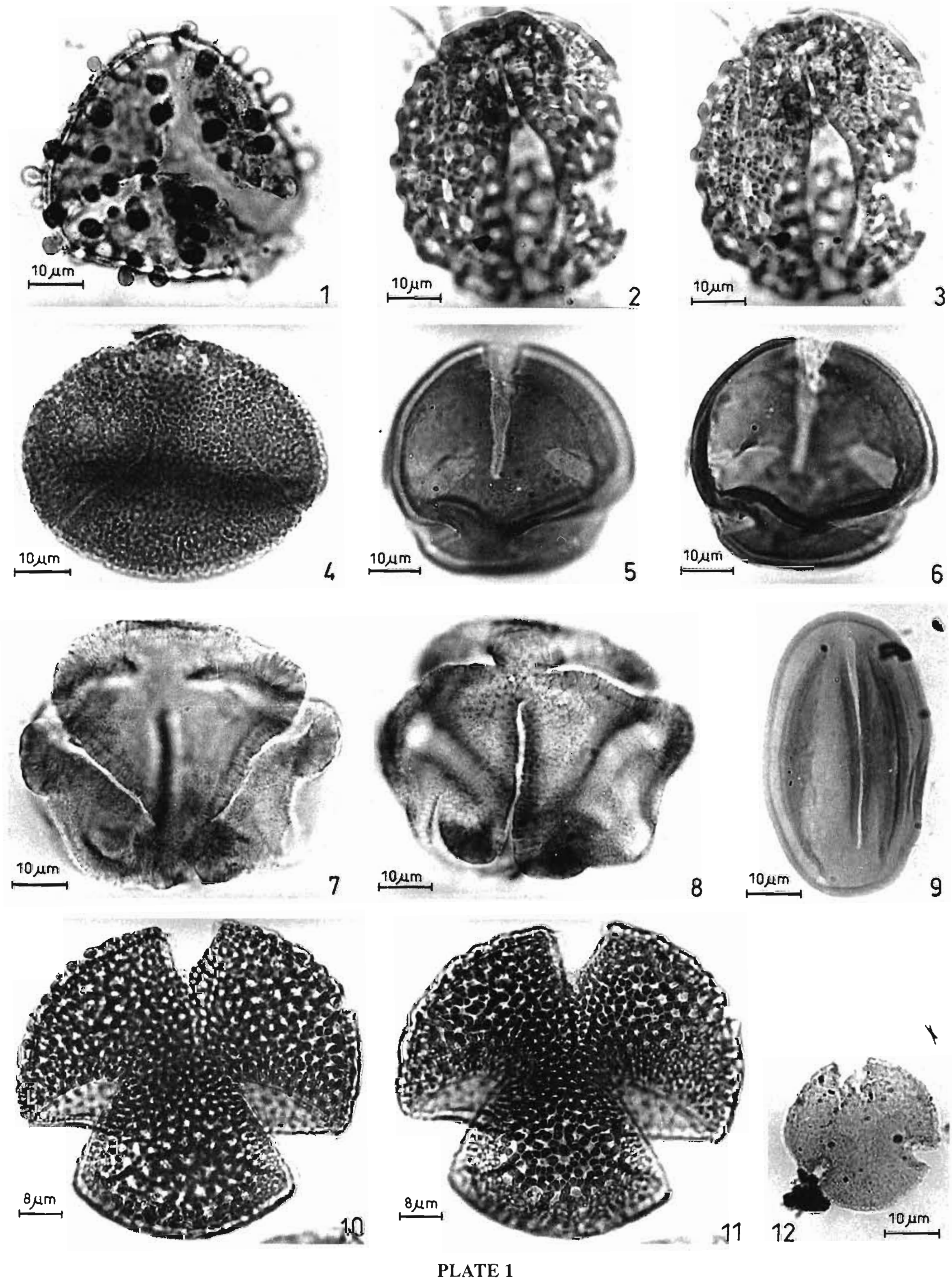
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PLATE 1

ALBERTIPOLLENITES BACULATUS (Jain *et al.*, 1973) comb. nov.

Basionym—

Tricolpites baculatus Jain *et al.*, 1973, Geophytology 3: 155, pl. 1, figs 23-26, 34, 36. *Illegitimate junior homonym* [illegible] *Tricolpites baculatus* Kar & Jain, 1981, Palaeobotanist 27: 120, pl. 3, fig. 81 (now *Dipterocarpuspollenites retipilatus*).

Original Description—Pollen grains tricolpate, spherical, 30-35 µm, colpi long. Exine moderately thick, tegillate, surface baculate-verrucose. Sculptural elements up to 3 µm high.

Occurrence—Palaeocene, Barmer clay Bed, Rajasthan (Jain *et al.*, 1973); Palaeocene, Matanomadh Formation, Kutch (Saxena, 1979).

Remark—Holotype is missing.

ALBERTIPOLLENITES CRASSIRETICULATUS (Dutta & Sah, 1970) comb. nov.

Basionym—

Tricolpites crassireticulatus Dutta and Sah, 1970, Palaeontographica 131: 32, pl. 6, figs 9-12.

Synonym—

1973 *Tricolpites crassireticulatus* Venkatachala and Rawat, Palaeobotanist 20: 244, pl. 4, fig. 9.

Original Description—Size range 25-37 µm, holotype 32 µm, amb roundly triangular to sub-spheroidal, tricolpate, colpi with bulging mesocolpia; exine rather thick, sexine as thick as nexine, pilate, tegillate, surface sculpture coarsely reticulate, crassimurate.

Occurrence—Palaeocene, Cherra Formation, Meghalaya (Dutta & Sah, 1970); and subsurface Oligocene-Miocene sediments, Cauvery Basin (Venkatachala & Rawat, 1973).

Remarks—*Tricolpites crassireticulatus* described by Saxena (1979, Palaeobotanist 26, pl. 2, fig. 23) and Kar and Kumar (1986, Pollen Spores 28, pl. 8, figs 9, 12, 14) are over 60 µm in size and reticula gradually decrease towards pole. These taxa have been placed under *Rousea*.

ALBERTIPOLLENITES GRACILIS (Salujha *et al.*, 1972) comb. nov.

Basionym—

Tricolpites gracilis Salujha *et al.*, 1972, Proc. Sem. Palaeopalynol. Indian Stratigr., Calcutta, pp 279, pl. 3, figs 59, 60.

Original Description—Golden-yellow, rotundly triangular to subcircular with three equidistant furrows, size 20.8-40 µm, tricolpate, colpi 5.4-7.2 µm deep, ±4.8 µm wide, exine textate ± 1.5 µm thick, reticulate, muri over 1 µm wide, with an equally wide lumina, muri slightly protruding at the margin.

Occurrence—Palaeogene sediments, Meghalaya (Salujha *et al.*, 1972); Oligocene, Meghalaya (Salujha *et al.*, 1974); Early Miocene, Bhuban Formation, Tripura (Salujha *et al.*, 1977).

ALBERTIPOLLENITES KARII sp. nov.

Pl. 5, 8-9 (holotype)

Holotype—*Tricolpites* sp. A, in Kar & Kumar, 1986, Pollen Spores 28: 196, pl. 9, fig. 1, slide no. 9495 (reillustrated here, Pl. 5, 8-9).

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Type Locality and Age—Shillong-Cherra Road Section, Meghalaya, Late Palaeocene.

Description—Pollen grain subprolate, 58 × 70-66 × 75 µm in equatorial view. Tricolpate, colpi 52 µm long, margin smooth. Exine 5-6 µm at equator, gradually decreases to 3 µm at poles, nexine almost uniform, 1-1.5 µm, columellae short, 3.5 µm long, 1 µm broad at base and gradually widens upwards, tips 1.5-2 µm, 2-4 µm apart near equator, closer (1-1.5 µm) at poles, tectum smooth, nearly uniform, 1.5 µm. Surface reticulate, reticulum nearly squarish all over the surface, uniform in size, muri simplicolumellate, 1-1.5 µm thick, lumina 4 × 4 µm, free columellae rarely present within lumina.

Comparison—*Albertipollenites karii* compares *A. [illegible]* having large size, thick exine and long colpi. But

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PLATE 2

(All photographs are [illegible] magnification)

1-2. [illegible] (Tripathi & [illegible], 1995), Slide No. BSIP [illegible], Holotype in different focus.

3-7. [illegible] comb. nov., Slide No. BSIP [illegible], Holotype in different focus.

4, 14. [illegible] sp. nov., fig. 4, Slide No. BSIP [illegible] in [illegible] fig. 14, Slide No. BSIP [illegible], Holotype.

5-6. [illegible] (Sah & Dutta, 1966) Mathur & [illegible], 1980, Slide No. BSIP [illegible], [illegible] in different focus.

8-9. [illegible] (Sah & Kar, 1970) [illegible], Slide No. BSIP [illegible], Holotype in different focus.

10-11. [illegible] Sah & Kar, 1974, Slide No. BSIP [illegible], Holotype in different focus.

12. [illegible] sp. (Kar & Kumar, 1986), Slide No. BSIP 9445.

13. [illegible] (Kar & Jain, 1981) Kar, 1985, Slide No. BSIP [illegible], Holotype.

15-16. [illegible] Kar & Jain, 1981, Slide No. BSIP [illegible], Holotype in different focus.

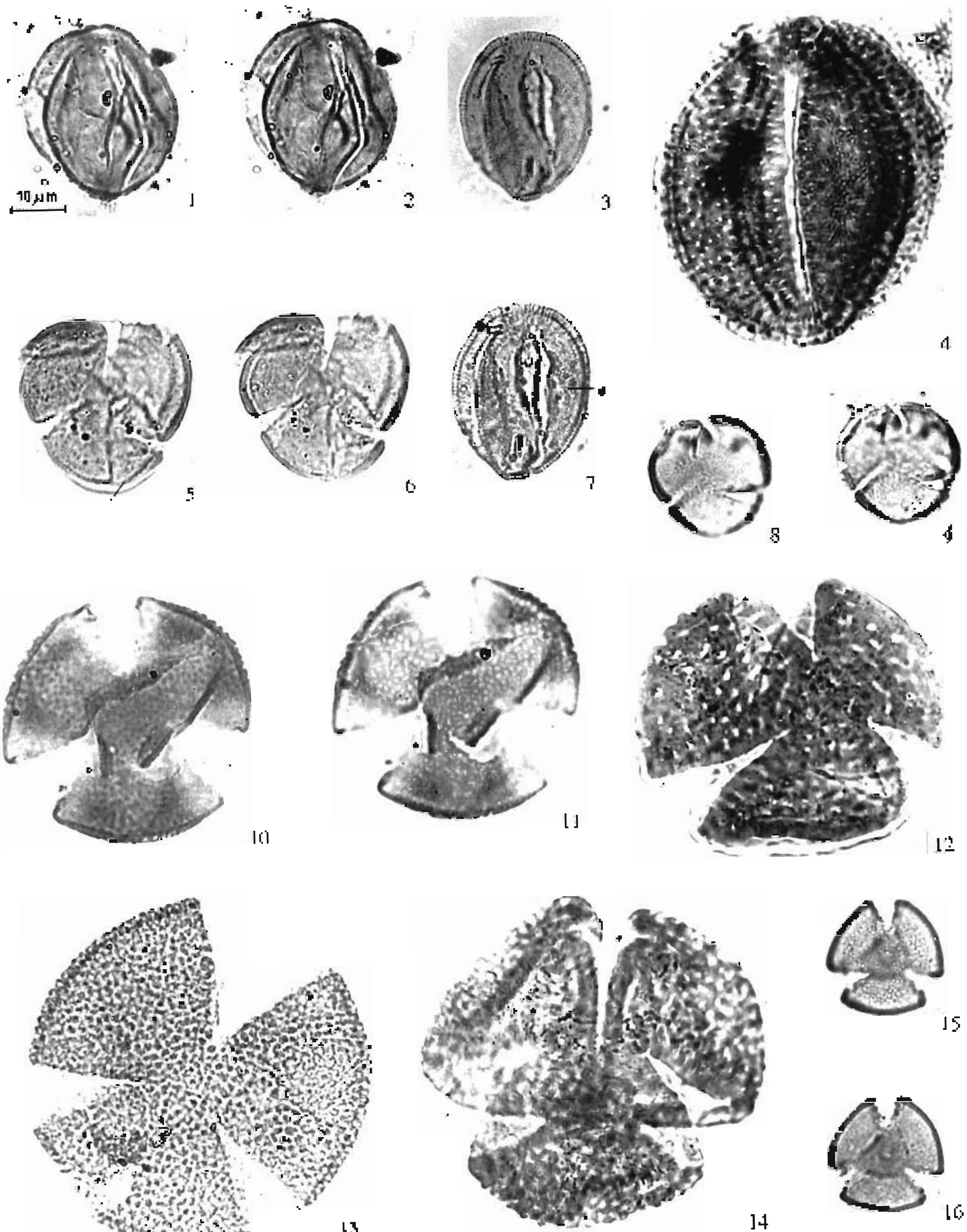

PLATE 2

A. kari differs possessing nearly squarish large reticula and well spaced columellae (2-4 µm).

Occurrence—Late Palaeocene, Lakadong Sandstone Member, Meghalaya (Kar & Kumar, 1986).

ALBERTIPOLLENITES KUMARII sp. nov.

Pl. 4.6-8 (holotype)

Holotype—*Tricolpites* sp. B in Kar & Kumar, 1986, Pollen Spores 28, 198, pl. 9, fig. 8, slide no. 9400 (reillustrated here, Pl. 4.6-8).

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Type Locality and Age—Shillong-Cherra Road Section, Meghalaya, Late Palaeocene.

Description—Pollen grain 100 µm (polar axis) and 61 µm (folded equatorial axis) in equatorial view. Tricolpate, colpi 95 µm long, nearing to poles, margin smooth. Exine 5.5 µm thick at equator, 4.5 µm at poles, nexine uniformly thick, ca. 1 µm; tectum smooth, 1-1.5 µm thick, columellae two types, one set supports tectum, 2.5-3 µm long, 1-1.5 µm broad, 2-3.5 µm apart, other set mainly present in equatorial areas between two long columellae, smaller, 2 µm long, 1 µm broad and does not touch tectum (free). Surface reticulate, reticula vary in size, muri 1.5-2 µm broad, simplicolumellate; lumina vary in shape (oval-elongated) and size, largest lumen 4 x 3 µm, 1-3 free columellae within each lumen.

Comparison—The taxon is very large (100 µm polar axis), has two sets of columellae and bear free columellae within each lumen. These characters distinguish *Albertipollenites kumarii* from known species of *Albertipollenites*.

Occurrence—Late Palaeocene, Lakadong Sandstone Member, Meghalaya (Kar & Kumar, 1986).

ALBERTIPOLLENITES KUTCHENSIS sp. nov.

Pl. 4.3-5 (holotype)

Holotype—*Tricolpites crassireticulatus* Dutta & Sah, 1970, in Kar & Saxena, 1981 (non Dutta & Sah, 1970), Geophytology 11, pl. 3, fig. 56, slide no. 6351 (reillustrated here: Pl. 4.3-5).

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Type Locality and Age—Near Ratadia (sub-surface), southern Kutch, Gujarat, Middle-Late Eocene.

Description—Pollen grain spherical in polar view, 85 x 85 µm. Tricolpate, longicolpate, colpi 32 µm deep, wide at equator. Exine thick, 7 µm at mesocolpium and gradually thins out towards colpi, 4 µm at colpi margins, nexine as thick as or thicker than sexine, tectate, columellae 3.5 µm long mixed with pila, capita 1.5 µm broad, closely placed. Surface uniformly reticulate, lumina elongated 1.5-2.5 µm, muri simplicolumellate.

Comparison—The present species resembles *Albertipollenites crassireticulatus* in their crassireticulate sculpture but differs in being very large in size and having thick exine. Tips of columellae are occasionally swollen (pilate) in *Albertipollenites kutchensis* but not in *A. crassireticulatus*.

Occurrence—Middle-Late Eocene, southern Kutch (Kar & Saxena, 1981).

ALBERTIPOLLENITES MEDIRETICULATUS (Mathur, 1966) comb. nov.

Basionym—

Retitricolpites medireticulatus Mathur, 1966, Q. J. geol. Min. metall. Soc. India 38: 41, pl. 1, fig. 18.

Original Description—Isopolar, radiosymmetric, amb almost round, 36.5 µm in diameter, tricolpate, colpi long, 11 µm broad, margins not smooth. Exine 2 µm thick, sexine almost as thick as nexine with medium size reticulations. Nexine slightly thickened near the colpi, yellow.

Occurrence—Palaeocene (Supratrappeans), Kutch (Mathur, 1966).

ALBERTIPOLLENITES PROBOSCIDEUS (Biswas, 1962) comb. nov.

Basionym—

Tricolpopites proboscideus Biswas, 1962, Bull. geol. min. metall. Soc. India 26: 42, pl. 8, fig. 44.

Original Description—Polar compression, exine thick, uniformly reticulate; tricolpate.

Occurrence—Palaeocene, Tura Formation, Meghalaya (Biswas, 1962).

PLATE 3

1-2. *[illegible]* Mandal *et al.*, 1994, Slide No. BSIP 11002 (J 32/4), Holotype in different foci.

3. *[illegible]* Mandal *et al.*, 1994, Slide No. BSIP 11006 (K 52/2), Holotype.

4-6. *[illegible]* (Saxena 1979) comb. nov., Slide No. BSIP [illegible] (O 22), in different foci.

7-8. *[illegible]* (Saxena 1979) comb. nov., Slide No. BSIP 4953 (F 40), Holotype in different foci.

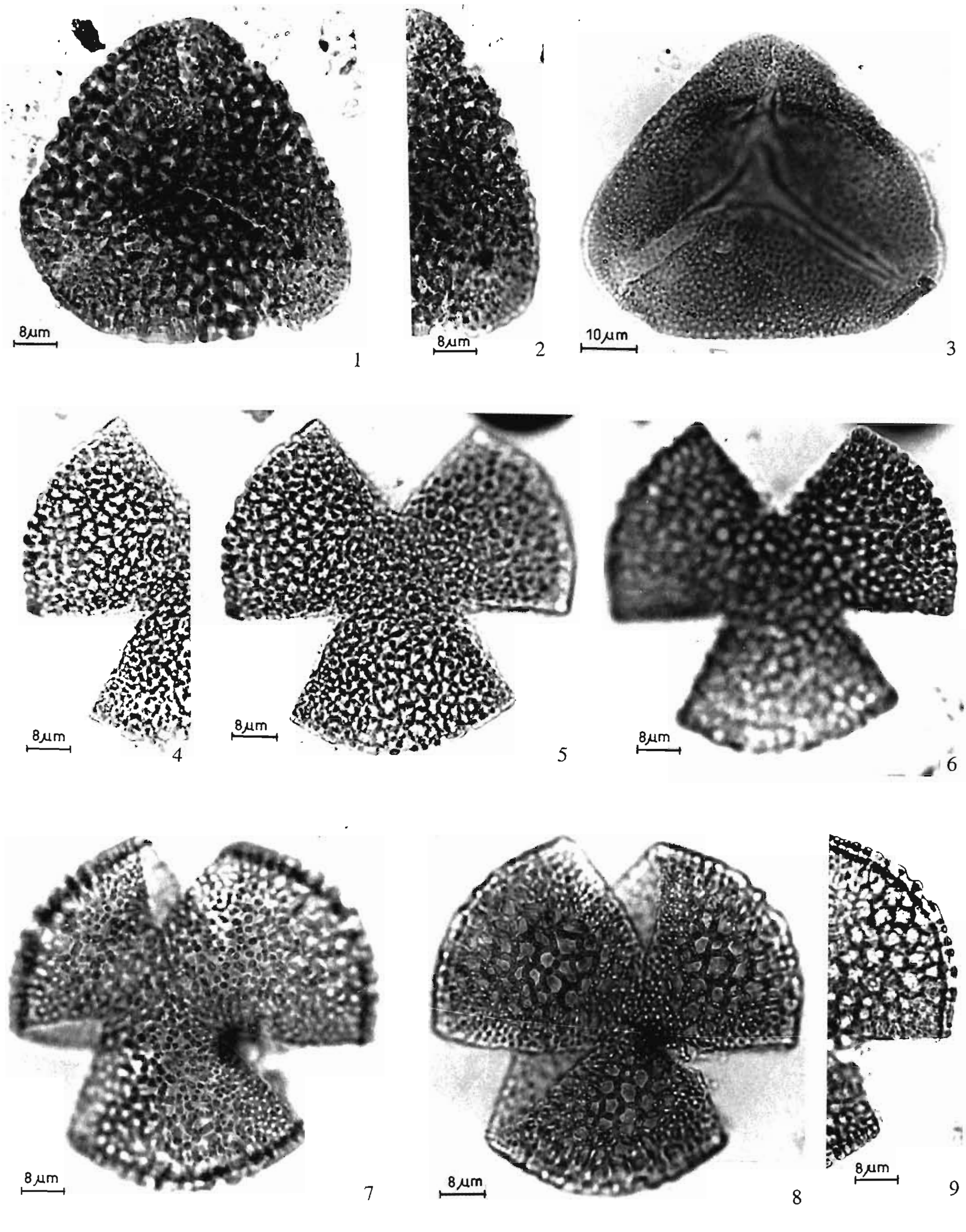

PLATE 3

ALBERTIPOLLENITES RETIBACULATUS (Saxena, 1979) comb. nov.

Pl. 3.4-6

Basionym—

Tricolpites retibaculatus Saxena, 1979, Palaeobotanist 26: 133, pl. 2, figs 27-28.

Original Description—Pollen grains subcircular-subtriangular in polar view, 58-114 µm. Tricolpate, colpi long, well-developed, mesocolpia wide. Exine 2.5-7 on surface view.

Description (Present study)—Pollen grains subtriangular in polar view, 88 x 90 µm. Tricolpate, colpi wide at equator, 38 µm deep. Exine 3 µm thick, sexine thicker than nexine (1 µm), uniformly thick, tectate, columellae slender, 2-3 µm apart, 1.5 µm long, capita 1.5 µm in diameter, mostly fused. Surface retipilate, reticulum almost uniform, lumina irregular, 1-3 µm, muri simplicolumellate, 1.5 µm wide.

Occurrence—Palaeocene, Matanomadh Formation, Kutch (Saxena, 1979); subsurface Middle to Late Eocene sediments, Kutch (Kar & Saxena, 1981).

ALBERTIPOLLENITES ROBUSTUS (Sah & Kar, 1970) comb. nov.

Pl. 1.2-3 (holotype)

Basionym—

Retitricolpites robustus Sah & Kar, 1970, Palaeobotanist 18: 131, pl. 1, fig. 30.

Original Description—Pollen grains subcircular, 40-54 x 38-52 µm. Tricolpate, colpi well developed. Exine thick, reticulate, meshes duplibaculate.

Description (present study)—Pollen grain oblate, 44 x 60 µm in equatorial view. Tricolpate, colpi long, 30 µm, end pointed. Exine 4 µm thick, sexine uniformly thick, about 3 µm ; nexine layer not very distinct at all places, about 1 µm at mesocolpia, tectate, tectum 2.5 µm thick, smooth, columellae slender, 1 µm long and 1.5 µm apart. Surface reticulate, muri mostly duplibaculate, 2 µm wide, lumina oval to elongate, 2.5-4.5 µm, smaller on apocolpial areas.

Occurrence—Early Eocene, Naredi Formation, Kutch (Sah & Kar, 1970).

Genus—BACUBREVITRICOLPITES Rao & Ramanujam, 1982

Type Species—Bacubrevitricolpites rotundus Rao & Ramanujam, 1982.

Original Diagnosis—Pollen grains subprolate equatorially, amb rounded, tricolpate, brevicolpate, colpi narrow, exine intectate, beset with numerous prominent bacules, heads of bacules generally rounded in surface view.

BACUBREVITRICOLPITES ROTUNDUS Rao & Ramanujam, 1982

Original Description—Pollen grains isopolar, amb rounded, subprolate equatorially, polar diameter 21-26.5 µm; tricolpate, brevicolpate, colpi narrow, margins thin, ends blunt. Exine 2-3 µm thick, intectate, baculate, bacules fine, densely distributed all over, up to 2.2 µm high, heads of bacules usually rounded in surface view.

Occurrence—Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

Remark—The aperture is tricolpate and not zoniaperturate.

Genus—BEAUPREAIDITES Cookson, 1950 ex Couper, 1953

Type Species—Beaupreaidites elegansiformis Cookson, 1950 ex Couper, 1953.

Original Diagnosis—This spore type is characterized by its medium size, straight sides, colpoid apertures, tapering exine, and finely reticulate sexine.

Emended Diagnosis (after Martin, 1973)—Pollen grains triaperturate, subangular to semiangular in polar view, oblate or nearly so in equatorial view, more or less isopolar, apertures forming short colpoids, meridionally elongated, with irregular thin margins and tapering exine, angles smoothly rounded, internally the aperture bounded by an area or zone ('Solution', Thomson & Pflug, 1953) of roughened, foveolate or warty endexine corresponding to the postatrium of a porate grain; annulus, vestibule and costae absent; exine reticulate, foveolate or areolate, often the reticulum combined with raised low verrucae; size of grain medium to rather large.

After Milne (1998)- Pollen grains tricolpate to tricolpoidate, angulaperturate, isopolar or subisopolar, oblate to peroblate; amb triangular with straight or gently convex or concave sides. Colpi meridionally aligned, sides more or less straight, termini sharp if grain well preserved. Exine stratified, ektexinous; nexine thicker than or equal to sexine,

PLATE 4

⟶

1-2. *Perfotricolpites neyvelii* (Navale & Misra, 1979) Mandal & Kumar, 2000, Slide No. BSIP 10992 (F 26), Holotype in different foci.

3-5. *Albertipollenites kutchensis* Mandal and Rao sp. nov., Slide No. BSIP 6351(O41/2), Holotype in different foci.

6-8. *Albertipollenites kumarii* Mandal and Rao sp. nov., Slide No. BSIP 9400 (P52/1), Holotype in different foci.

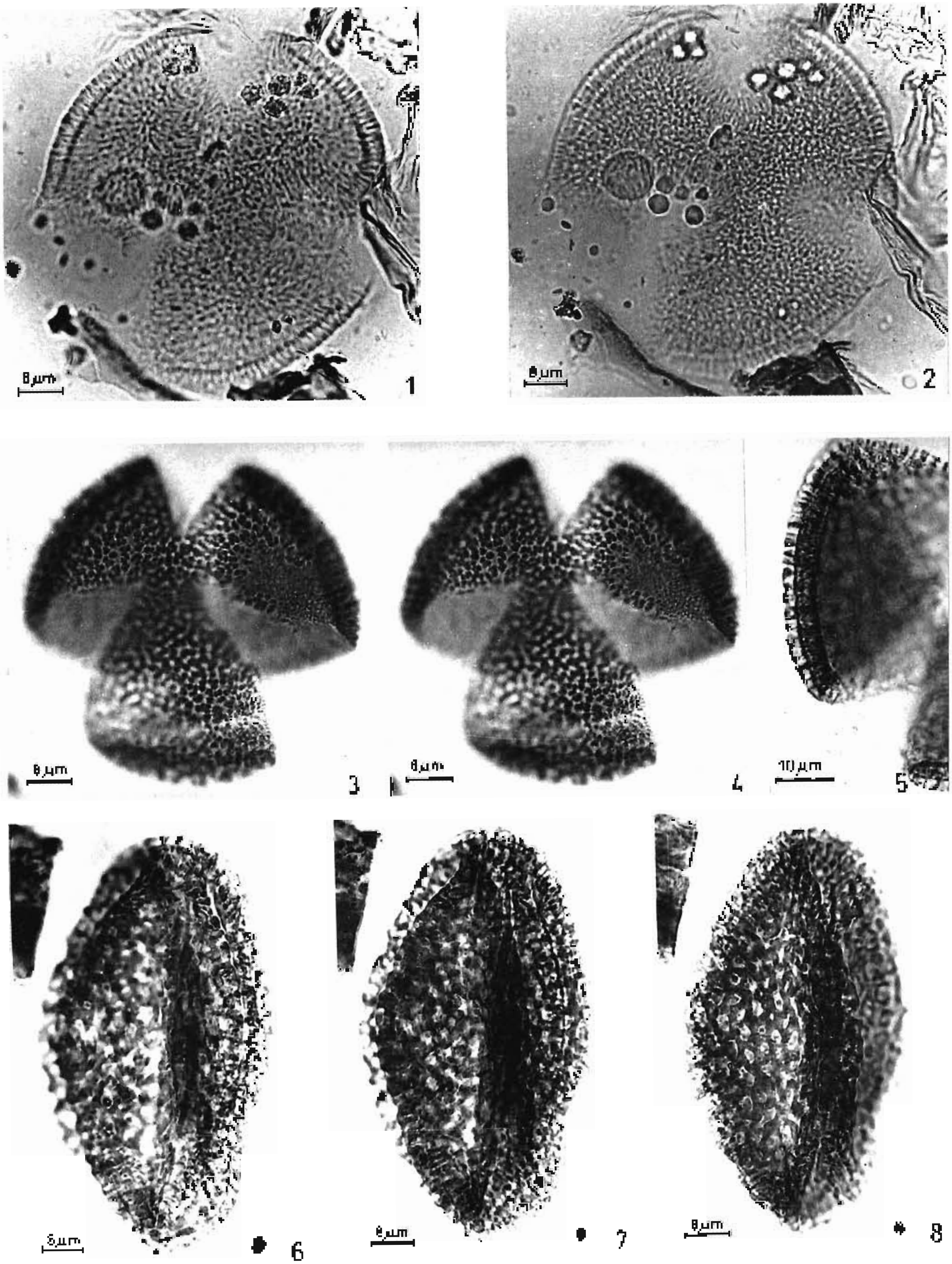

PLATE 4

infratectum thin and densely columellate. Apertural exine thinner than mesocolpial exine. Nexine homogeneous in mesocolpia: thinning abruptly adjacent to colpi termini delineating base of aperture area, then tapering to aperture margin, may partially fragment in aperture area. Tectum of similar width overall or tapering towards grain apices before nexine thin, infratectum same width over grain or thinning slightly in aperture area. If exinal thinning pronounced, apertural area pale in colour compared to rest of grain. Sexine columellate, tectate-perforate or semi-tectate, tectum surface perforate, microreticulate, reticulate, fossulate or foveo-areolate; with or without irregular tectal thickenings, verrucae and/or gemmae. Sculptural elements diminished in aperture area, uniformly developed over remainder of grain or coarser at poles and finer in mesocolpia.

BEAUPREAIDITES TEGILLATUS Venkatachala & Rawat, 1973

Original Description—Pollen grain roundly triangular with slightly convex sides and rounded angles; 23.2 x 23.7 µm in polar view; tricolpate, angulaperturate. Colpi very short, slit like. Exine about 1.5 µm, sexine thicker than nexine except at aperture region where nexinous thickenings are prominent; puncti tegillate, puncta 0.5 to 1.0 µm in diameter forming a reticulate surface.

Occurrence—Subsurface Oligocene-Miocene sediments, Cauvery Basin (Venkatachala & Rawat, 1973).

Genus—CLAVASYNCOLPITES Rao & Ramanujam, 1982

Type Species—*Clavasyncolpites gracilis* Rao & Ramanujam, 1982.

Original Diagnosis—Pollen grains with triangular-rounded triangular amb, tricolpate, syncolpate. Exine intectate, clavate, clavae locally seen in a reticuloid alignment.

CLAVASYNCOLPITES GRACILIS Rao & Ramanujam, 1982

Original Description—Pollen grains isopolar, amb triangular to rounded triangular, sides convex, polar diameter 22-32 µm, tricolpate, syncolpate, colpi wide and gaping at equatorial region, margins slightly thickened and beset with clavate-baculate processes. Exine 1.5-2.5 µm thick, sexine thicker than nexine, intectate, clavate, clavae 1.5-2 µm high, locally mixed with baculae, densely and uniformly distributed all over, here and there seen in reticuloid alignment.

Occurrence—Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

Remark—The specimen is tricolpate and not zonaperturate.

Genus—DAKSHINIPOLLENITES Navale & Misra, 1979; emend. Singh & Misra, 1991

Type Species—*Dakshinipollenites tripakshii* Navale & Misra, 1979, emend. Singh & Misra, 1991.

Original Diagnosis—Pollen grain isopolar, triangular to subtriangular (in polar view), subprolate to suboblate (equatorial view), 48-70 x 48-66 µm in size. Tricolporate, angulaperturate, colpi long, narrow and deep, apocolpi small. Ora faint to indistinct, lalongate, slit like. Exine thin (1-5 µm) in middle part of the mesocolpi where it is projected out like a hump, gradually thickens laterally, being thickest (3-4.5 µm) on the colpal margins. Surface microgranulate to granulate, granulation more prominent towards colpi margins.

Emended Diagnosis (Singh & Misra, 1991)—Pollen isopolar, tricolpate, triangular to subtriangular in polar view, prolate-oblate, spheroidal or sub-spheroidal in equatorial view, exine thin in the middle of mesocolpium where ambitus shows a bulge, gradually thickening towards colpi and thickest at colpus margins, exine composed of a perforate tectum, columellate layer and unstructured nexine, columellae shorter at mesocolpium gradually becoming longer towards colpi margins; ornamentation finely granulate to finely reticulate as gaps between the granules appear like pits or lumina.

DAKSHINIPOLLENITES TRIPAKSHII Navale & Misra, 1979, emend. Singh & Misra, 1991

Pl. 1.7-8

Original Description—Isopolar pollen grain, subprolate to suboblate in equatorial view, triangular to subtriangular in polar view. Size range 48-70 x 48-66 µm. Tricolpate, angulaperturate, longicolpate, colpi deep and narrow, extending quite up to the poles, apocolpium small. Pore obscure, lalongate, like a slit. Exine thin (1.5-2 µm) in the middle part of the mesocolpi (clearly visible in the polar view) projecting outwards like a hump, gradually thickening laterally, being thickest (3-4.5 µm) at the colpi margins.

PLATE 5

1	*Rousea meghalayaensis* Mandal and Rao sp. nov., Slide No. BSIP 9598(K52): Holotype.	8-9	*Albertipollenites* [illegible] Mandal and Rao sp. nov., Slide No. BSIP 9595(J37): Holotype in different foci.
2-4	[illegible] (Sah & Kar) Kar, 1985, Slide No. BSIP 5348 (F34/3): Holotype in different foci.	10-11	*Tricolpites reticulatus* Cookson ex Couper, 1953, Slide No. BSIP 3348 (M31) in two foci.
5-7	*Tricolpites reticulatus* Cookson ex Couper, 1953, Slide No. BSIP 3350(Q 42) showing exine reticulation.	12-14	*Rousea* [illegible] Mandal and Rao sp. nov., Slide No. BSIP 9596(L9): Holotype in different foci.

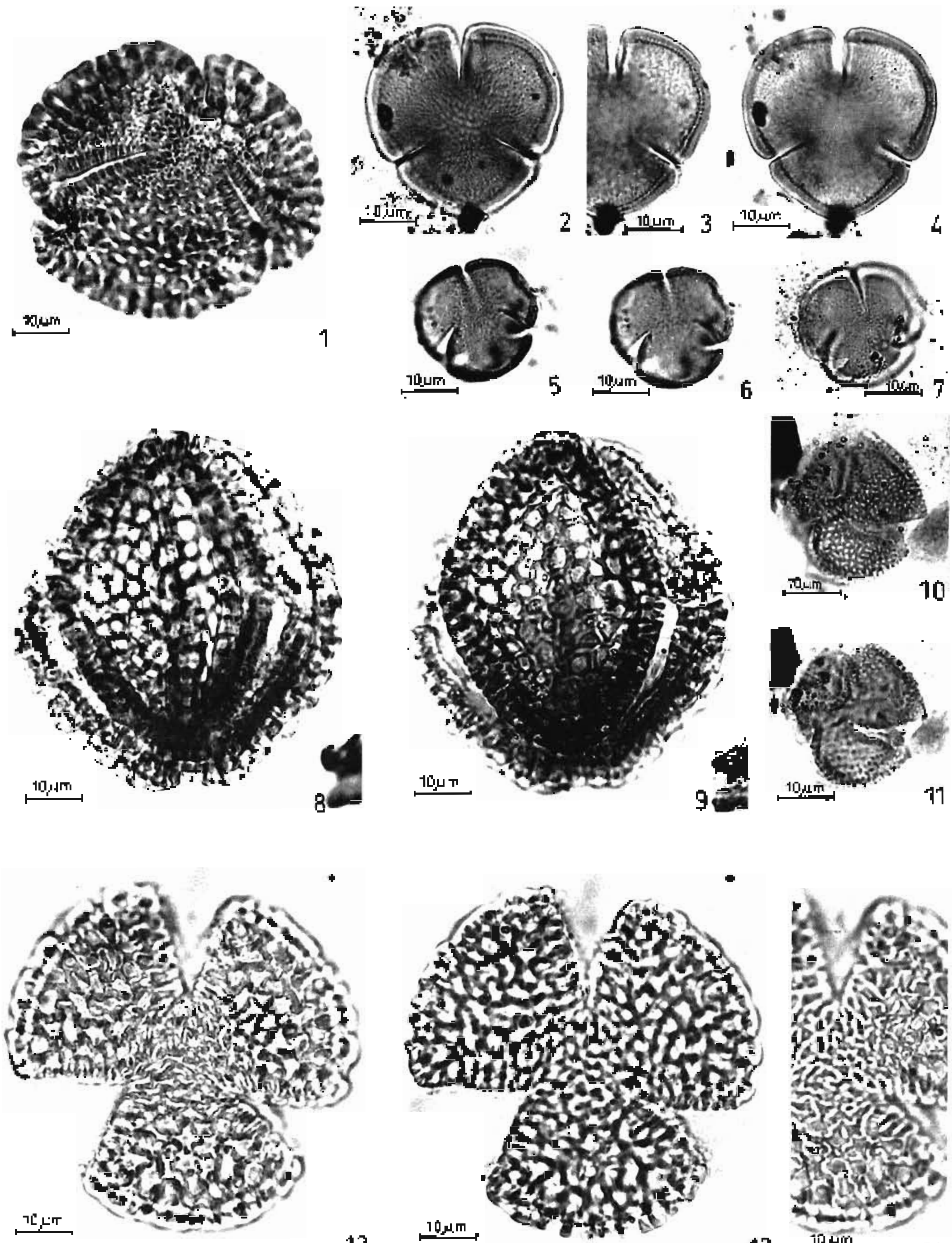

PLATE 5

Microgranulate to granulate, granulation becoming more prominent towards colpi margins.

Emended Description (Singh & Misra, 1991)—Pollen 40-90 μm, isopolar, triangular to subtriangular in polar view, prolate-oblate spheroidal to sub-spheroidal in equatorial view, tricolpate, colpi medium to long; exine comprised of a perforate tectum, columellae layer and unstructured smooth nexine; exine 1-4 μm in the middle of mesocolpium, gradually thickening towards colpi and 3-8 μm at colpus margins, where exine is 2-4 times thicker than at the equatorial bulge; nexine smooth, gradually thickens towards the margin, sexine and nexine thickness is ± equal; surface ornamentation finely granulate to finely reticulate.

Occurrence—Miocene, Neyveli lignitefield, Tamil Nadu (Navale & Misra, 1979; Singh & Misra, 1991).

Genus—DIPTEROCARPUSPOLLENITES Kar, 1992; here emended

Type Species—Dipterocarpuspollenites retipilatus (Kar & Jain, 1981) Kar, 1992.

Original Diagnosis—Pollen grains subcircular and oval in polar and equatorial views respectively. Size range 51-68 μm. Tricolpate, very rarely tricolporoidate, colpi long. Exine 1.5-3.5 μm thick, pilate, pilae up to 3 μm long, 1-1.5 μm broad, closely placed, sometimes fused together, pila provide pseudoreticulate appearance in surface view.

Emended Diagnosis—Pollen spheroidal in polar and subprolate in equatorial view. Tricolpate, longicolpate; sexine thicker than nexine. Exine columellate, with (strongly) perforate tectum, which tends to pushed up between each two columellae. Surface pseudoreticulate at lower focus and verrucate at top focus.

DIPTEROCARPUSPOLLENITES RETIPILATUS (Kar & Jain, 1981) Kar, 1992

Pl. 1.4; Pl. 2.13 (holotype)

Synonyms—(after Kar, 1992)

1981 *Tricolpites baculatus* Kar and Jain, Palaeobotanist 27: 120, pl. 3, figs 81-82.

1982 *Retitricolpites dipterocarpoides* Rao and Ramanujam, Palaeobotanist 30: 69-70, pl. 1, fig. 3.

Non: *Tricolpites baculatus* Jain, *et al.*, 1973 (now *Albertipollenites baculatus*)

Original Description—Pollen grains subcircular in equatorial view, 56-66 μm. Tricolpate, colpi long, prominent, wide in polar view. Exine up to 2 μm thick, sexine thicker than nexine, reticulate, forming negative reticulum.

Description (present study)—Pollen grain rounded triangular in polar view and subprolate in equatorial view, 45-50 x 49-62 μm. Tricolpate, longicolpate, colpi 19.5 μm deep, often gaping at equator. Exine 2 μm, uniformly thick, sexine thicker than nexine, tectate, columellae 1.5 μm long, with strongly perforate tectum, which tends to be pushed up between each two columellae. Surface appear pseudoreticulate at low focus and verrucate at top focus.

Occurrence—Miocene, Kerala Basin (Kar & Jain, 1981; Rao & Ramanujam, 1982).

Genus—DISCOIDITES Muller, 1968

Type Species—Discoidites borneensis Muller, 1968.

Original Diagnosis—Tricolpate disc-shaped pollen grains with short colpi and a columellate wall structure covered by a tectum, through which the tops of the columellae project slightly in a finely verrucate pattern. Columellae may be arranged in a reticuloid pattern.

DISCOIDITES BORNEENSIS Muller, 1968

Pl. 1.12

Original Description—Tricolpate, peroblate, disc-shaped; equatorial contour circular or slightly triangular; colpi fairly short, flat, reaching less than halfway to the poles; wall ± 1.5 μm thick; endexine very thin; columellae indistinctly visible, ± 1 μm long, < 1 μm in diameter, slender, straight, covered by and partly projecting through a psilate to finely verrucate tectum.

Occurrence—Miocene, Ratnagiri (Phadtare & Kulkarni, 1984), Mio-Pliocene, Upper Assam (Mandal & Kumar, 2000).

Remark—Indian specimens range between 34-36 μm in diameter.

DISCOIDITES BENGALENSIS Mathur & Chopra, 1987

Original Description—Pollen grains tricolpate, disc shaped, amb circular to oval, diameter 22-25 μm; colpi narrow and short, with 1-2 μm thick margo, extending less than half the distance to the poles; tectate, columellate, columellae distinct, columellae tops projecting slightly through the tectum; exine finely scabrate, giving microreticulate surface pattern.

Occurrence—Subsurface Late Miocene-Early Pliocene sediments, Bengal Basin (Mathur & Chopra, 1987).

Remarks—*Discoidites bengalensis* differs from *D. borneensis* (specimen from Assam 34.5 x 36 μm) in being smaller in size and having comparatively longer colpi with margo.

Genus—FOVEOTRICOLPITES Pierce, 1961

Type Species—Foveotricolpites sphaeroides Pierce, 1961.

Original Diagnosis—Tricolpate, colpi elongate with conspicuously thickened aperture margins; subprolate, 18 x 21.5 μm; three polar and one equatorial planes of symmetry;

exine *ca.* 1.5 μm thick, tectate; foveolate, foveolae small, closely placed.

Remarks—The diagnosis presented by Pierce (1961) is too short. While dealing with the Indian foveolate species we observed that colpal characters show variation, otherwise they resemble *Foveotricolpites.*

FOVEOTRICOLPITES ALVEOLATUS sp. nov.

Pl. 2.4, 14 (holotype)

Holotype—Foveotricolpites alveolatus Couper, 1953; *in* Tripathi & Singh, 1985, Geophytology 15: 164, pl. 3, fig. 46, slide no. 8784 (reillustrated here, Pl. 2.14)

Non: *Tricolpites alveolatus* Couper, 1953

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Type Locality and Age—Therria Formation, Meghalaya, Palaeocene.

Description (Present study)—Pollen grains subprolate to subspheroidal, 60-71 μm. Tricolpate, colpus 50.5 μm long, wide. Exine 3.5-4.5 μm thick, nexine about 1 μm, sexine pilate, pila ± 3 μm long, capita 2.5-3 μm broad, pila head generally fused forming 2.5 μm thick perforated tectum. Surface foveolate, lumina circular, ± 1 μm, 2-3 μm apart, interfoveolate space smooth.

Occurrence—Palaeocene, Therria Formation, Meghalaya (Tripathi & Singh, 1985).

Remarks—Elsik (1968) studied the holotype of *Tricolpites alveolatus* Couper, 1953 and found it to be colporate. He transferred the same to *Tricolporopollenites baculoferis* Pflug, 1953. The specimen recorded by Tripathi and Singh (1985) is colpate and has foveolate exine, hence we transfer it to *Foveotricolpites.*

FOVEOTRICOLPITES INIQUUS (Salujha *et al.*, 1974) comb. nov.

Basionym—

Tricolpites iniquus Salujha *et al.*, 1974, Palaeobotanist 21: 276, pl. 2, figs 52, 53.

Original Description—Golden yellow, roundly triangular to subcircular, size 19.8-34.6 x 18.2-28.6 μm, tricolpate, colpi 5.2-9.6 μm wide, extending to almost ½ the radial distance; exine over 1 μm thick, smooth to sparsely foveolate, uneven, giving a mat-like appearance.

Occurrence—Middle Oligocene, Jenam Formation, Assam (Salujha, *et al.*, 1974).

FOVEOTRICOLPITES PERFORATUS van der Hammen & Garcia de Mutis, 1965

Occurrence—Subsurface Oligocene-Miocene sediments, Cauvery Basin, Tamil Nadu (Venkatachala & Rawat, 1973).

FOVEOTRICOLPITES PIERCEI Rao & Ramanujam, 1982

Original Description—Pollen grains isopolar, amb rounded, lobes distinct, polar diameter 16-33 μm, tricolpate, brevicolpate (colpoidate), colpi margins thin, ends rounded or blunt. Exine 1.8 μm thick, sexine thicker than nexine, tectate, tectum perforated, surface foveolate, foveolae of uniform size all over, locally coalescing, up to 3 μm in diameter.

Occurrence—Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

FOVEOTRICOLPITES PROLATUS Rao & Ramanujam, 1982

Original Description—Pollen grains isopolar, amb triangular to rounded triangular, lobes distinct, prolate equatorially, 26-38 x 17.5-32 μm; tricolpate, longicolpate, colpi gaping wide at equator, margins uneven, thin, ends pointed. Exine 1.8 μm thick, surface foveo-reticulate, foveolae small, closely placed.

Occurrence—Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

FOVEOTRICOLPITES SIJUENSIS (Baksi, 1962) comb. nov.

Basionym—

Tricolpopites sijuensis Baksi, 1962, Bull. geol. min. metall. Soc. India 26: 16, pl. 1, fig. 6.

Description—Equatorial compression; larger diameter 32 μm, surface ornamentation granular to punctate; tricolpate, colpi wide.

Occurrence—Lower-Middle Eocene, Meghalaya (Baksi, 1962).

FOVEOTRICOLPITES SIMPLEX (Rao & Ramanujam, 1982) comb. nov.

Basionym—

Retibrevitricolpites simplex Rao & Ramanujam, 1982, Palaeobotanist 30: 71, pl. 1, fig. 9.

Original Description—Pollen grains isopolar, amb triangular to rounded triangular, sides convex, polar diameter 25-42 μm; tricolpate, brevicolpate, margins thin, ends pointed. Exine 1.8 μm thick, sexine as thick as nexine. Surface reticulate, brochi small ± 1μm in diameter, finer at mesocolpia.

Occurrence—Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

Remark—The photograph (pl. 1, fig. 9) shows reticula nearly circular and can be termed as foveolate.

ORIGINAL NAME	NEW COMBINATION
Tricolpopites aquifoliaceaeformis	*Albertipollenites aquifoliaceaeformis*
Tricolpites baculatus	*A. baculatus*
T. crassireticulatus	*A. crassireticulatus*
T. gracilis	*A. gracilis*
Retitricolpites medireticulatus	*A. medireticulatus*
Tricolpopites proboscideus	*A. proboscideus*
Retitricolpites robustus	*A. robustus*
Tricolpites retibaculatus	*A. retibaculatus*
T. alveolatus	*Foveotricolpites alveolatus*
T. iniquus	*F. iniquus*
T. paucireticulatus	*F. paucireticulatus*
Tricolpopites sijuensis	*F. sijuensis*
Retibrevitricolpites simplex	*F. simplex*
Trifossapollenites constatus	*Ladakhipollenites constatus*
Tricolpopites prolatus	*L. prolatus*
T. shortii	*L. shortii*
Tricolpites horridus	*Retitrescolpites horridus*
Retitricolpites megareticulatus	*R. gareticulatus*
R. robustus	*R. robustus*
Tricolpites globus	*Rousea globus*
T. matanomadhensis	*R. matanomadhensis*
Retitricolpites sitholeyi	*R. sitholeyi*
R. delicatus	*Tricolpites delicatus*

Fig. 1—List of realloted species with original names and new combinations.

FOVEOTRICOLPITES sp.

Pl. 2.12

Description—Pollen grains tricolpate, isopolar, subprolate, 3-lobed, 52- 60 µm. Exine 2-3 µm thick, foveolate, lumina deep.

Occurrence—Palaeocene, Cherra Formation, Meghalaya (Kar & Kumar, 1986).

Remark—The specimen having large size, thick tectum and irregular foveolae are not comparable to any known species.

Genus—INTRARETICULITIS Kar, 1985

Type Species—*Intrareticulitis brevis* (Sah & Kar, 1970) Kar, 1985.

Original Diagnosis—Pollen grains subcircular-subtriangular in polar view. Tricolpate, colpi distinct, long. Exine intrareticulate-intraretibaculate, structural elements restricted to base of exine.

INTRARETICULITIS BREVIS (Sah & Kar, 1970) Kar, 1985

Pl. 5.2-4 (holotype)

Original Description—Pollen grains subcircular-subtriangular in polar view, 23-34 x 20-32 µm. Tricolpate, colpi distinct, long. Exine 1-3 µm thick, sexine much thicker than nexine, intrareticulate-intraretibaculate, ornamentation confined only to basal part of exine.

Description (present study)—Pollen grains subtriangular, 23 x 25.5-34 x 38 µm in polar view, amb lobate, one lobe angular, mesocolpia convex. Tricolpate, colpi long, 11 µm, pointed, rarely gaping at equator, inconspicuous thickening about 2 µm around colpi especially at polar end. Exine 2 µm at mesocolpia which gradually thickens to 2.5 µm at colpus margins; sexine thicker than nexine, mesocolpial sexine 1.5 µm, both sexine and nexine little thicker near colpi; columellate, columellae distinct, slender, closely placed, 0.5 µm long, longer near colpi; tectate, tectum smooth, 1 µm thick uniformly. Surface granular on top focus and faintly microreticulate in polar area with discontinuous striations in equatorial areas on low focus; lumina nearly circular, about 0.5 µm, muri low.

Occurrence—Early Eocene, Naredi Formation, Kutch (Sah & Kar, 1970; Venkatachala & Kar, 1969; Kar, 1985).

Remarks—Venkatachala *et al.* (1989) treated *Intrareticulitis brevis* as *Tricolpites reticulatus*. But the study of holotype shows that *I. brevis* is distinct possessing thicker sexine than nexine, thick tectum and weak reticulation in polar area and discontinuous striations in equatorial areas. Few specimens illustrated by Kar (1985, pl. 14, figs 1, 2) as *I. brevis* are *Tricolpites reticulatus* having weak reticulation all over the surface.

Genus—LADAKHIPOLLENITES Mathur & Jain, 1980

Type Species—Ladakhipollenites levis (Sah & Dutta, 1966) Mathur & Jain, 1980.

Original Diagnosis—Pollen grains oblate to subspherical, generally preserved as polar compressions, oval, circular to subcircular; tricolpate, colpi long and not brevicolpate, fairly broad, ends generally pointed; exine laevigate to faintly and obscurely sculptured under high magnification (x 1000).

Remarks—Mathur and Jain (1980) instituted *Ladakhipollenites* for psilate, tricolpate pollen and selected *Tricolpites levis* Sah & Dutta (1966) as its type species. The holotype of *T. levis* Sah & Dutta (1966) is not traceable. Here, we select the specimen recorded by Sah & Kar (1974) as neotype.

Mathur & Jain (1980) transferred the following species to *Ladakhipollenites*:

Tricolpites brevis Sah & Kar 1970;

T. levis Sah & Dutta 1966;

T. longicolpus Sah & Dutta 1966;

T. minutus Sah & Kar 1970;

T. pachyexinus Couper 1953;

Kar (1985) instituted *Intrareticulitis* by selecting *Tricolpites brevis* Sah & Kar (1970) as holotype. The specimens referred to this species are, therefore, placed accordingly.

LADAKHIPOLLENITES CONSTATUS (Dutta & Sah, 1970) comb. nov.

Basionym—

Trifossapollenites constatus Dutta & Sah, 1970, Palaeontographica, 131: 27, pl. 6, figs 21-23.

Original Description—Size 32 μm (this value was obtained from a count of 36 pollen grains), amb ovoid, oval-elongate or sub-spheroidal; tricolpate, colpi long, tenuimarginate; sexine thicker than nexine, surface ornamentation psilate to faintly scabrate.

Occurrence—Palaeocene, Cherra Formation, Meghalaya (Dutta & Sah, 1970); Early Miocene, Bhuban Formation, Meghalaya and Assam (Rao *et al.*, 1985).

Remarks—The description of this taxon (Dutta & Sah 1970, pl. 6, figs 21-23) does not conform with the diagnosis of *Trifossapollenites* as the lateral two colpi are not shorter than the middle one.

LADAKHIPOLLENITES ELONGATUS Tripathi & Singh, 1985

Pl. 2.1-2 (holotype)

Original Description—Pollen grains prolate to perprolate in equatorial view; tricolpate, colpus narrow, long; exine 1-1.5 μm thick, tectate, indistinctly sculptured, exine thickened at the two poles.

Occurrence—Palaeocene, Therria Formation, Meghalaya (Tripathi & Singh, 1985).

LADAKHIPOLLENITES LEVIS (Sah & Dutta, 1966) Mathur & Jain, 1980

Pl. 2.5-6 (neotype)

Holotype—Sah and Dutta, 1966, pl. 2, fig. 9, slide no. 3/3.

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow; not traceable, and presumed lost.

Neotype—Sah and Kar, 1974, Palaeobotanist 21: 169, pl. 2, fig. 41. slide no. 4364/4, (here designated).

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Type Locality, Horizon and Age—Mawkma, Khasi Hills, Meghalaya, Cherra Formation; Palaeocene.

Original Description—Size 24-30 μm, amb spherical to subspherical; tricolpate, longicolpate, furrows thin, exine also thin, less than 1 μm, smooth, in some specimens a faint sculpture is discernible under oil immersion.

Description (present study)—Pollen grain spherical in polar view, 30 x 32 μm. Tricolpate, longicolpate, colpi 7.5 μm deep, pointed at poles. Exine 2 μm thick and slightly thicker near colpi margins, sexine-nexine not separable, columellae indistinct. Surface smooth and intrastructured under high magnification.

Occurrence—Palaeocene, Cherra Formation, Meghalaya (Sah & Dutta, 1966); Early Eocene, Naredi Formation, Kutch (Sah & Kar, 1970); Early Eocene, Palana lignite, Rajasthan (Sah & Kar, 1974); Palaeocene-Eocene, Akli lignite, Rajasthan (Naskar & Baksi, 1978); Palaeocene, Dras volcanics, Ladakh (Mathur & Jain, 1980); Late Cretaceous-Palaeocene, Subsurface Bengal Basin, W. Bengal (Baksi & Deb, 1980); Palaeocene, Mikir Formation, Meghalaya (Mehrotra, 1983), Subsurface Early Miocene sediments, Meghalaya (Nandi & Sharma, 1984), Oligocene, Barail Group, Meghalaya and Assam (Singh *et al.*, 1985, 1986).

Remarks—*Ladakhipollenites levis* compares with *Tricolpites reticulatus* in shape, size and in the presence of exinal thickenings near colpi. However, nearly smooth surface in *L. levis* separates the two taxa.

LADAKHIPOLLENITES LONGICOLPUS
(Sah & Dutta, 1966) Mathur & Jain, 1980

Original Description—Size range 23-28 µm; grains spherical to lobate in polar view; tricolp (or) ate, tenuimarginate, colpi long, extending to more than ¾ the radial distance; exine up to 3.5 µm thick, surface ± smooth to finely matted.

Occurrence—Palaeocene, Cherra Formation, Meghalaya (Sah & Dutta, 1966); Palaeocene, Dras volcanics, Ladakh (Mathur & Jain, 1980).

LADAKHIPOLLENITES MINUTUS (Sah & Kar, 1970) Mathur & Jain, 1980

Pl. 2.8-9 (holotype)

Original Description—Pollen grains subcircular-subtriangular, 18-25 x 17-24 µm, tricolpate, brevicolpate. Exine thin, laevigate-finely scrobiculate.

Description (present study)—Pollen grain nearly circular in polar view, slightly bulging at mesocolpia, 24 x 24 µm. Tricolpate, colpi pointed, minutely gaping at equator, 6.5 µm in diameter. Exine 2 µm, slightly thickens at colpi margins, sexine-nexine uniformly thick, nexine thicker near colpi, tectate, columellae not distinct. Surface uniformly scabrate at high magnification.

Occurrence—Early Eocene, Naredi Formation, Kutch (Sah & Kar, 1970); Palaeocene, Matanomadh Formation, Kutch (Saxena, 1979); Oligocene, Barail Group, Assam & Meghalaya (Singh *et al.*, 1985, 1986).

Remarks—*Ladakhipollenites minutus* resembles *Tricolpites reticulatus* in shape, size and exinal characters i.e., sexine thicker near colpus but surface reticulation is not distinct as *Tricolpites reticulatus*.

LADAKHIPOLLENITES PACHYEXINUS (Couper, 1953) Mathur & Jain, 1980

Pl. 1.5-6, 9

Original Description—Free, isopolar, tricolpate, occasionally tetracolpate, colpi long, broad. No trace of ora. Grains spheroidal to prolate-spheroidal. Exine very thick, 2.5-3 µm, psilate.

Description (present study)—Pollen subcircular in polar view, 44 x 58 µm; prolate in equatorial view, 38 x 48 µm. Tricolpate, colpi 44 µm long, end rounded, margin moderately thick. Exine 2 µm thick, sexine as thick as nexine, columellae indistinct. Surface psilate.

Occurrence—Palaeocene, Cherra Formation, Meghalaya (Dutta & Sah, 1970); Early Eocene, Palana lignite, Rajasthan (Sah & Kar, 1974).

LADAKHIPOLLENITES PROLATUS (Baksi, 1962) comb. nov.

Basionym—

Tricolpopites prolatus (nom. corr. pro *T. prolati*) Baksi, 1962, Bull. geol. min. metall. Soc. India 26: 19, pl. 4, fig. 44.

Description—Equatorial compression; longer diameter 19 µm, surface more or less smooth; tricolpate, colpi thick and straight, extend from pole to pole, no pores visible.

Occurrence—Oligocene, Barail Group, Meghalaya (Baksi, 1962).

LADAKHIPOLLENITES SHORTII (Baksi, 1962) comb. nov.

Basionym—

Tricolpopites shortii Baksi, 1962, Bull. geol. min. metall. Soc. India 26: 19, pl. 4, fig. 45.

Description—Equatorial compression; longer diameter 18 µm; surface rough; tricolpate; colpi comparatively thin; do not extend from pole to pole.

Occurrence—Miocene, Surma Group, Meghalaya (Baksi, 1962).

Remark—Photograph (pl. 4, fig. 45) shows psilate exine.

Genus—PERFOTRICOLPITES Garciá Guzmán, 1967

Type Species—*Perfotricolpites digitatus* Garciá Guzmán, 1967.

Original Diagnosis—Tricolpate pollen grains with perforate tectum, digitate columellae and psilate-scabrate sculpture.

PERFOTRICOLPITES NEYVELII (Navale & Misra, 1979) Mandal & Kumar, 2000

Pl. 4.1-2 (holotype)

Original Description—Isopolar pollen, oblate to spheroidal, 60-95 x 60-70 µm in size. Tricolpate, colpi longicolpate, deep but do not reach the poles, mesocolpi are rounded at the periphery. Exine 5-7 µm thick, sexine thicker (2-3 times) than nexine, gradually thinning towards the colpi margins. Distinct rod layer is present in the sexine, rods are long, papillate to clavate forming a granulate to finely microreticulate surface structure.

Description (Mandal & Kumar, 2000)—Pollen grains spheroidal, 52.5-58 x 57-59 µm. Tricolpate, colpi 50 µm long, extended near to the poles. Exine 4.5µm thick, sexine 3.5 µm, nexine thin, 0.5 µm; columellae 2.5 µm long, 1.2 µm broad, occasionally digitate. Tectum thin, perforate; surface appears perforate-microreticulate.

Occurrence—Miocene, Surma Group (Baksi, 1962), Boldamgiri Formation (Saxena & Rao, 1996), Miocene, Warkalli Formation, Kerala (Rao & Nair, 1998), Oligocene, Kutch Basin (Kar, 1985); Oligocene, Barail Group (Mandal & Kumar, 2000).

Remarks—Oligocene forms are comparatively smaller in size and may represent different species.

Genus—PILATRISYNCOLPITES Kar *et al.*, 1994, emended here

Type Species—*Pilatrisyncolpites triangulatus* Kar *et al.*, 1994.

Original Diagnosis—Pollen triangular in polar view, trisyncolpate, colpi long, distinct. Exine up to 2 µm thick, sculpture pilate, interpilar exine ornamentation pseudomicroreticulate.

Emended Diagnosis—Pollen triangular-subtriangular in polar view; trichotomosulcate, colpi long and join at pole. Exine moderately thick, sculpture pilate, interpilar exine ornamentation pseudomicroreticulate.

PILATRISYNCOLPITES TRIANGULATUS Kar *et al.*, 1994; emended here

Pl. 1 (holotype)

Emended Description—Pollen grains triangular in polar view, size range 36-52 × 34-50 µm, apices rounded, interapical margin convex. Trichotomosulcate, colpi distinct, broader at equator and tapering at pole. Exine pilate, pila 4-8 µm long, 2-5 µm broad, narrow at base and swollen at tip, sparsely placed, interpilar exine granulose, very closely placed forming pseudoreticulate ornamentation in surface view.

Occurrence—Oligocene, Barail Group, Assam (Kar *et al.*, 1994); Early Eocene, Naredi Formation, Kutch (Mandal, 2000).

Genus—POLYGONACEAEPITES Baksi, 1962

Type Species—*Polygonaceaepites zonoides* Baksi, 1962.

Original Combined Description—Equatorial compression; long (polar) diameter 34 µm, body zoned, outward portion appears like a flange which becomes appreciably wider near the poles, a few discrete radiating striae mark the flange, otherwise more granular-reticulate than the main body, tricolpate, colpi extend from pole to pole (colpi limit the inner margin), adjacent.

POLYGONACEAEPITES ZONOIDES Baksi, 1962

Occurrence—Miocene, Surma Group, Meghalaya (Baksi, 1962).

Genus—RETITRESCOLPITES Sah, 1967

Type Species—*Retitrescolpites typicus* Sah, 1967.

Original Diagnosis—Grains tricolpate or colporoidate, spheroidal to sub-spheroidal to rounded triangular. Exine retipilate to sometimes reticulate.

Remarks—Generic diagnosis proposed by Sah (1967) is very broad and overlaps circumscription of *Tricolpites*, *Albertipollenites* and *Rousea*, we have assigned tricolpate/colporoidate pollen having strongly retipilate to retibaculate ornamentation under this genus.

RETITRESCOLPITES BELLUS Sah, 1967

Original Description—Known size range 24-42 µm; amb spheroidal to sub-spheroidal; tricolpate, brevicolpate, tenuimarginate. Exine rather thin, sexine slightly thicker than nexine, retipilate.

Occurrence—Palaeocene, Dras Volcanics, Ladakh (Mathur & Jain, 1980).

RETITRESCOLPITES HORRIDUS (Singh *et al.*, 1974) comb. nov.

Basionym—

Tricolpites horridus Singh *et al.*, 1974, Palaeobotanist 21: 276, pl. 2, figs 54, 55.

Original Description—Brown, roundly triangular with three prominent slits, size 25.6-36.6 µm, tricolpate, colpi 5-6.5 µm deep, exine 2-2.5 µm thick, pilate, pila 2.5-3 µm long with globular heads, closely spaced, occasionally coalescing to give a reticulate appearance.

Occurrence—Oligocene sediments, Assam (Singh *et al.*, 1974).

RETITRESCOLPITES MEGARETICULATUS (Mathur, 1966) comb. nov.

Basionym—

Retitricolpites megareticulatus Mathur, 1966, Q. J. geol. Min. metall. Soc. India 38: 41, pl. 1, fig. 19.

Synonym—

1982 *Retitrescolpites indicus* Rao and Ramanujam, Palaeobotanist 30: 70, pl. 1, fig. 6.

Original Description—Polar view: Isopolar, radiosymmetric, amb trilobed, lobes deep and broad, 42 µm in diameter, tricolpate. Colpi 17 µm broad and long, margins smooth. Exine 3 µm thick, reticulate, lumina large, ca. 2 µm, muri with a beaded appearance.

Occurrence—Palaeocene (Subathu equivalent) Kutch (Mathur, 1966); Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

Remarks—Rao and Ramanujam (1982) commented that *R. indicus* resembles *R. typicus* Sah (1967) except in the

Name of Taxa	Late Palaeocene	Early Eocene	Middle Eocene	Late Eocene	Oligocene	Miocene	Pliocene
Albertipollenites aquifoliaceaeformis		++++++	++++++				
A. baculatus	++++++						
A. crassireticulatus	++++++	———	———	———	———	++++++	
A. gracilis	++++++	++++++	++++++	++++++	++++++	++++++	
A. medireticulatus	++++++						
A. kutchensis			++++++	++++++			
A. karii	++++++						
A. kumarii	++++++						
A. proboscideus	++++++						
A. retibaculatus	++++++	———	++++++	++++++			
A. robustus		++++++					
Bacubrevitricolpites rotundus						++++++	
Beaupreaidites tegillatus					++++++	++++++	
Clavasyncolpites gracilis						++++++	
Dakshinipollenites tripakshi						++++++	
Dipterocarpuspollenites retipilatus							++++++
Discoiditesborneensis	++++++	++++++					
D. bengalensis						++++++	++++++
Foveotricolpites alveolatus	++++++						
F. iniquus					++++++		
F. perforatus					++++++	++++++	
F. piercei						++++++	
F. prolatus						++++++	
F. sijuensis		++++++	++++++				
F. simplex						++++++	
Intrareticulitis brevis		++++++					
Ladakhipollenites constatus	++++++					++++++	
L. elongatus	++++++						
L. levis	++++++	++++++	++++++	++++++	++++++	++++++	
L. longicolpus	++++++						
L. minutus	++++++	++++++	———	———	++++++		
L. pachyexinus	++++++	++++++					
L. prolatus					++++++		
L. shortii						++++++	
Perfotricolpites neyvelii					++++++	++++++	
Pilatrisyncolpites triangulatus		++++++	———	———	++++++		
Polygonaceaepites zonoides						++++++	
Retitrescolpites bellus	++++++						

R. howardii					+–––++		
R. megareticulatus	–++++–+	—	———	—	–	++–+++	
R. minor	–+++–++						
R. minutus						––++++	+++++–+
R. sangalensis						––+++++	
R. splendens						––+++++	
R. typicus		+––+++	++++++	–+++–++			
Retitrescolpites communis		+––+++					
R. ilanagai		+++++––					
Rousea globus	–+++++						
R. marginata						+––+++	
R. mahamanendilensis	++–––++						
R. meghalayensis	++–––++						
R. rarensis	++–––+–						
R. valiaiensis						+––+++	
Striatopollis bellus	+++––++	++++++–+	+++++++	———		+––++++	
S. indicus						++–––++	
Tricolpites delicatus					+++++–+		
T. densiornatus	––+++++–	+––++++	+++++++–	++–––+++			
T. levis			+––+++	———		+–+––+	
T. incisoquerus						+–++––+	
T. microreticuloides						–++–––+	
T. minor					+–++++–		
T. pauciornatus	–+++–+						
T. parareticulatus		––++++					
T. reticulatus	+++–––+	++++––+	–++––++	———	–++–++	++–+––	
Retitricolpites perreticulatus	+++–––+					+–++––	

Fig. 2—Range chart of studied tricolpate species from India: + Present; — Not recorded.

possession of a wide gap between the colpi. A further comparison of them reveals that they also differ in their surface sculpture.

RETITRESCOLPITES MINOR Dutta & Sah, 1970

Original Description—Size range 22 to 38 µm, amb ± spheroidal to subprolate in polar view, tricolpate, colpi long, exine thick, sexine thicker than nexine, pilate, non-tegillate, surface sculpture retipilate, reticulum formed of thick, irregular muri and small lumina.

Occurrence—Palaeocene, Cherra Formation, Meghalaya (Dutta & Sah, 1970).

RETITRESCOLPITES MINUTUS Saxena *et al.*, 1984

Original Description—Pollen grains subcircular in polar view, size range 25-30 µm. Tricolporoidate, colpi small, thin, pore small in size, circular in shape. Exine ± 2.5 µm thick, stratified, sexine thicker than nexine, retipilate, pila very small, pin-head like, closely placed, imparting a pseudoreticulate appearance.

Occurrence—Mio-Pliocene, Lower Siwaliks, Himachal Pradesh (Saxena *et al.*, 1984).

Remarks—The study of the holotype reveals that it has a reticulate exine that is thicker in the intercolpium region.

RETITRESCOLPITES SINGULARIS Rao & Ramanujam, 1982

Original Description—Pollen grains isopolar, amb subspheroidal to rounded triangular, lobes prominent, polar diameter 20-28 µm, zonaperturate, tricolpate, longicolpate, colpi reaching poles but not meeting, colpal surface finely granular. Exine up to 4 µm thick, sexine much thicker than nexine, surface irregularly retipilate, heterobrochate, brochi hexa- to polygonal, 3-5 µm in diameter, circumscribed, lumina irregular with free baculoid processes.

Occurrence—Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

Remarks—From the illustrations and description it appears that *R. angulatus* Rao & Ramanujam (1982) is similar to *R. splendens* Sah (1967) in exomorphic characters but the latter is bigger in size (57-78 µm).

RETITRESCOLPITES SPLENDENS Sah, 1967

Original Description—Size range 57-78 µm, amb ± spheroidal to sub-prolate; tricolpate, colpi fairly long, sexine thicker than nexine, retipilate, oligobrochate, muri of reticulum formed of free pila.

Occurrence—Subsurface Early Miocene sediments, Meghalaya (Nandi & Sharma, 1984), Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

RETITRESCOLPITES TYPICUS Sah, 1967

Original Description—Size range 50-65 µm, amb spheroidal to sub-spheroidal in equatorial and sub-oblate in lateral view, tricolpate (or tricolporoidate) fossaperturate, exine well stratified, retipilate, pila prominent, surface sculpturing reticulate, polybrochate.

Occurrence—Subsurface Eocene sediments, Kerala (Saha *et al.*, 1967).

Genus—RETITRISYNCOLPITES Mandal *et al.*, 1994, emended here

Type Species—*Retitrisyncolpites reimannii* Mandal *et al.*, 1994.

Original Diagnosis—Pollen grains trisyncolpate, sometimes colporoidate, triangular-subtriangular in shape. Colpi distinct, long, occasionally funnel shaped or bifurcated at tips. Exine thick, sexine thicker than nexine, tectate, tectum perforated, infratectum columellar, columellae either of same size or coarser at polar and inter-apertural areas. Surface reticulate.

Emended Diagnosis—Pollen trisyncolpate, rarely colporoidate, colpi join together at pole; other characters are as above.

RETITRISYNCOLPITES REIMANNII Mandal *et al.*, 1994 emended here

Pl. 3.1-2 (holotype)

Emended Description—Triangular-subtriangular pollen, size range 41-47 µm. Trisyncolpate, sometimes open, funnel shaped, rarely seems to be colporoidate. Exine tectate, perforate, size of perforation variable, infratectum columellar, columellae stronger at polar and interapertural region. Columellae 1-2 µm long and 1-1.5 µm broad, 0.5-0.8 µm long at corners. Exine 1-2.5 µm thick, sexine thicker than nexine, nexine very thin, 0.5 µm, always not distinct. Surface reticulate, meshes coarse and irregular, muri ± 1 µm high.

Occurrence—Early Eocene, Middle Andaman (Mandal *et al.*, 1994).

RETITRISYNCOLPITES THAUNGII Mandal *et al.*, 1994 emended here

Pl. 3.3 (holotype)

Emended Description—Trisyncolpate-tricolporoidate pollen grains with size range of 31.5-45.5 µm, triangular in shape. Colpi meet at poles, sometimes open at equatorial end. Exine 0.7-1 µm thick, tectate, perforate, perforation more or less same size, ± 0.7 µm high. Sexine and nexine not separable. Surface reticulate, lumina circular, ±0.5 µm, more or less equal in size.

Occurrence—Early Eocene, Middle Andaman (Mandal *et al.*, 1994).

Genus—ROUSEA Srivastava, 1969a

Type Species—*Rousea subtilis* Srivastava, 1969a.

Original Diagnosis—Tricolpate, angulaperturate, colpi long, reaching polar area; amb subtriangular or rounded, sides convex; sexine thick, reticulate, lumina larger in mesocolpia becoming smaller at colpus margins and apocolpia.

ROUSEA GLOBUS (Dutta & Sah, 1970) comb. nov.

Basionym—*Tricolpites globus* Dutta and Sah, 1970, Palaeontographica 131: 35, pl. 7, fig. 28.

Original Description—Known size range 15-20 µm, holotype 18 µm, amb lobate, triangular in polar view, oblate-spheroidal to spheroidal in equatorial, trizonaperturate, colpate, colpi tenuimarginate, fairly long, extending to more than ⅔ the distance to the poles, exine thin, sexine pilate-tegillate, surface sculpture coarsely reticulate, meshes forming the reticulum decrease in size towards the aperture.

Occurrence—Palaeocene, Cherra Formation, Meghalaya (Dutta & Sah, 1970).

ROUSEA MATANOMADHENSIS (Saxena, 1979) comb. nov.

Pl. 1.10-11; Pl. 3.7-9 (holotypes)

Basionym—

Tricolpites matanomadhensis Saxena, 1979, Palaeobotanist 26: 134, pl. 2, fig. 29.

Original Description—Pollen grains ± subcircular in polar view, 72 µm. Tricolpate, colpi well-developed, long. Exine 2-4 µm thick, retibaculate to retipilate, duplibaculate/pilate, tegillate, bacula closely placed, almost joined with each other, forming a perfect reticulum, meshes larger in mesocolpate region.

Description (present study)—Pollen grain subspherical in polar view, 65 × 68 µm. Tricolpate, colpi nearly 40 µm deep, widely gaping at equator. Exine 4.5 µm, sexine as thick as nexine, thins out towards colpi, tectate, pilate; columellae 2.5 µm long, 1 µm broad, 1-3 µm apart, closer near colpi, capita up to 2.5 µm in diameter. Surface reticulate, reticulum bigger at mesocolpia (4.5 µm), narrower towards colpi and apocolpia (1 µm), lumina irregular shape, muri simplicolumellate, 2 µm broad.

Occurrence—Palaeocene, Matanomadh Formation, Kutch (Saxena, 1979).

ROUSEA MEGHALAYAENSIS sp. nov.

Pl. 5.1 (holotype)

Holotype—*Tricolpites crassireticulatus* Dutta & Sah, 1970, in Kar & Kumar, 1986, Pollen Spores 28, pl. 8, fig. 9, slide no. 9398 (reillustrated here, Pl. 5.1).

Non Tricolpites crassireticulatus Dutta & Sah, 1970, Palaeontographica 131 (now *Albertipollenites crassireticulatus*).

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Type Locality and Age—Upper Cherrapunji, Meghalaya, Late Palaeocene.

Description (Present study)—Pollen grain spheroidal, 56.5 x 60 µm in polar, 60 x 63 µm in equatorial view, mesocolpia convex. Tricolpate, colpi long, 50-52 µm, narrow and gaping at equator, margin uniformly 7 µm thick and smooth. Exine 5-6 µm thick, tectum at mesocolpia 2-2.5 µm, columellae robust, 2-2.5 µm long, 1 µm broad, 1-1.5 µm apart, capita 1.5-2.5 µm broad. Surface crassireticulate, reticulum larger at equator and gradually narrow towards pole, muri simplicolumellate, 1.5-2.5 µm wide, narrower near pole, lumina oval to elongated, 1-2 µm long, 1 µm wide at mesocolpia, wall smooth, nearly circular (less than 1 µm) at poles.

Comparison—*Rousea meghalayaensis* differs from other species of *Rousea* having thick muri, smooth lumina wall, small circular reticula at poles and thick colpi wall.

Occurrence—Late Palaeocene, Lakadong Sandstone Member, Meghalaya (Kar & Kumar, 1986).

ROUSEA SAXENAE sp. nov.

Pl. 5.12-14 (holotype)

Holotype—*Tricolpites crassireticulatus* Dutta & Sah, 1970, in Saxena, 1979, Palaeobotanist 26: 133, pl. 2, fig. 23, slide no. 4980 (reillustrated here, Pl. 5.12-14).

Non Tricolpites crassireticulatus Dutta & Sah, 1970, Palaeontographica 131 (now *Albertipollenites crassireticulatus*).

Repository—Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Type Locality and Age—Near village Matanomadh, Kutch Basin, Gujarat, Late Palaeocene.

Description (Present study)—Pollen grains spheroidal, 68 x 70 µm in polar view, mesocolpia convex. Tricolpate, colpi long, 24 µm, gaping at equator, margin minutely wrinkled. Exine 4.5 µm, sexine 3 µm, nexine uniformly 1.5 µm; semitectate, tectum 1.5 µm at equator, less thick at colpus margins; columellae, baculate to club-shaped, 1.5 µm long, 1 µm broad and about 1 µm apart, capita 1.5-2.5 µm wide. Surface reticulate, reticulum larger at equator and colpi margins, smaller at poles, larger reticula often broken, muri wavy, 1-1.5 µm thick, often broken at mesocolpia, simplicolumellate; lumina irregular, narrow and elongated at poles, larger lumina 5 µm long.

Comparison—The taxon distinguishes from other species of *Rousea* possessing large reticula at equator and colpi margins, wavy muri and club-shaped columellae supporting thick tectum.

Occurrence—Late Palaeocene, Matanomadh Formation, Kutch Basin (Saxena, 1979).

ROUSEA SITHOLEYI (Ramanujam, 1966) comb. nov.

Basionym—

Retitricolpites sitholeyi Ramanujam, 1966, Pollen Spores 8: 163, pl. 2, fig. 30.

Original Description—Pollen grains isopolar, suboblate, triangulicolpate, equatorial diameter 26-30 µm. Amb rounded, 3-lobed, lobes not bulging. Colpi broadly gaping at equator, ends sharply pointed, longicolpate. Exine 2-2 µm thick, sexine thicker than nexine, columellae faint, surface reticulate, meshes polygonal, larger at poles, smaller at mesocolpia, muri simplibaculate, look finely beaded under high magnification.

Occurrence—Miocene, Neyveli lignite, Tamil Nadu (Ramanujam, 1966).

Genus—STRIATOPOLLIS Krutzsch, 1959

Type Species—*Striatopollis sarstedtensis* Krutzsch, 1959.

Original Diagnosis—(English translation from Jansonius & Hills, 1976, card no. 2775)—With three colpi; side view oval-rhombic; amb subcircular but with rather deep and up to 5 µm wide gaping colpi (figura fusiform); wall outside the colpi relatively thick (c. 2 µm or more); wall two layered, outer layer with a coarse rib sculpture, the ribs being separated by narrow, deep incisions, the ribs are not smooth, but have an extrapunctate sculpture (which is not a "corrosion sculpture", but a primary feature); the ribs are vertical (meridians), about 5-8 per sector, crossing the equator; their number reduces toward the poles in such a manner, that those of two sections are continuous, those of third section cutting and joining them, or ending before reaching the polar area. The colpus area is free of sculpture, and has a very thin inner wall layer, probably each germinal has a narrow opening (slit) of 6-8 µm length, differentiation of the inner layer in the equatorial plane could not be observed. Polar axis, so far measured, 18-20 µm.

STRIATOPOLLIS INDICUS Mathur and Chopra, 1987

Original Description—Pollen grains tricolpate, amb spheroidal, diameter 15-18 µm, colpi streak-like, long, exine ca. 1 µm thick, striate, ridges and furrows of almost equal breadth, ridges broken near the poles.

Occurrence—Subsurface Late Miocene sediments, Bengal Basin (Mathur & Chopra, 1987).

Remarks—Comparing the characters and illustrations of *Striatopollis indicus* Mathur and Chopra (1987) and *S. catatumbus* (Gonzalez Guzman) Mathur and Chopra (1987) appear closely comparable, but *S. indicus* is much smaller in size.

Genus—TRICOLPITES Cookson, 1947 ex Couper, 1953

Type Species—*Tricolpites reticulatus* Cookson 1947 ex Couper, 1953.

Original Diagnosis—Free, isopolar, tricolpate. Exine variable in thickness and sculpture. Size variable.

Emended Diagnosis—(After Potonié, 1960): Shape spherical to ovoid, tricolpate, mesocolpium bulging, colpi broad, exine on either side stronger, causing the equator to be trilobate, exine finely reticulate.

After Belsky, *et al.*, 1965. (English translation from Jansonius & Hills, 1976): The diagnosis as given in Potonié 1960 should be changed so that also strongly reticulate forms may be included, as well as forms in which the exine is not thickened at either side of colpi, overall shape oblate to subspheroidal.

After Jarzen and Dettmann 1989: Pollen grains free, tricolpate, isopolar, oblate to subprolate; amb circular to trilobate with convex mesocolpia. Colpi meridionally aligned, parallel-sided, but often gaping, margin entire; membrane absent or reduced, without free standing baculia. Exine stratified, sexine baculate, semitectate with reticulate surface. Reticulum regular, composed of smooth-crested muri and elongate to equidimensional lumina that are of uniform size and less than 1 µm in diameter over entire surface of grain.

Remarks—*Tricolpites* was diagnosed by Couper (1953) to accommodate tricolpate pollen with variable ornamentation. Potonié (1960) emended its diagnosis to accommodate only finely reticulate forms. Srivastava (1966, p. 547) discussed at length the nomenclatural and taxonomical status of *Tricolpites* and *Retitricolpites*. Srivastava (1969a, p. 55) accepted the emendation of Potonié 1960, and proposed to include pollen having meshes larger than 1 µm under *Albertipollenites* and *Rousea*.

TRICOLPITES DELICATUS (Kar 1979) comb. nov.

Pl. 2.3.7 (holotype)

Basionym

Retitricolpites delicatus Kar, 1979, Palaeobotanist 26: 38, pl. 2, figs 31, 42.

Original Description—Pollen grains mostly found in equatorial view, 18-36 x 14-30 µm. Tricolpate, colpi narrow, extending almost from one margin to another. Exine microreticulate.

Description (present study)—Pollen grain prolate, 27 x 36 µm in equatorial view. Tricolpate, colpi long, 24 µm. Exine 2 µm thick, sexine-nexine not separable, semitectate, columellae distinct, 1.5 µm long, slender, closely placed. Surface microreticulate, lumina irregular in shape, less than 1 µm in size, muri thin and low.

Occurrence—Oligocene, Kutch Basin (Kar, 1979).

TRICOLPITES DENSIORNATUS Venkatachala & Rawat, 1972

Original Description—Pollen grain roundly triangular, 35.4-39.6 x 35-41.7 µm; tricolpate. Colpi long, wedge-shaped, 15 µm deep in polar view, not reaching the poles. Exine about 3.5 µm thick, slightly thickening towards apertural region, sexine thicker than nexine, closely pilate forming a pseudoreticulum.

Occurrence—Subsurface Palaeocene-Eocene sediments, Cauvery Basin (Venkatachala & Rawat, 1972).

TRICOLPITES FOXII (Biswas, 1962) Ramanujam, 1966

Original Description—Longer diameter 42 µm, exine moderately thick, reticulate, furrows deep, extending to the subpolar region.

Emended Description (Ramanujam, 1966)—Pollen isopolar, spheroidal, 34 x 25 µm. 3-zonocolpate. Amb prominently 3-lobed, lobes widely spaced. Colpi deep, long, ends pointed. Exine 1.8 µm thick, surface minutely reticulate.

Occurrence—Lower-Middle Eocene, Um Sohryngkew River section, Meghalaya (Biswas, 1962); Miocene, Neyveli lignite, Tamil Nadu (Ramanujam, 1966).

TRICOLPITES INCOGNATUS Kar & Jain, 1981

Pl. 2.15.16 (holotype)

Original Description—Pollen grains subtriangular-subcircular in equatorial view, 15-22 µm. Tricolpate, colpi long, funnel shaped in equatorial view. Sexine as thick as nexine, scrobiculate.

Description (present study)—Pollen subtriangular in polar view, 22 x 24 µm. Tricolpate, colpi 7.5 µm deep, gaping at equator, colpi margin irregular, triangular shaped apocolpial area slightly thickened (not parasyncolpate). Exine 1.5 µm, sexine thicker than nexine, uniformly thick, tectate, columellae

0.5 µm long, slender, uniformly spaced. Surface uneven, uniformly microreticulate, lumina circular, nearly 0.5 µm, muri less.

Occurrence—Miocene, Warkalli Formation, Kerala (Kar & Jain, 1981).

TRICOLPITES MICRORETICULOIDES Ramanujam, 1966

Original Description—Pollen grains isopolar, prolate spheroidal, 26 x 24 µm. Tricolpate. Poles rounded. Colpi long, almost reaching poles, of uniform breadth for greater part. Exine 2.5 µm thick, columellae and stiner, surface microreticulate.

Occurrence—Miocene, Neyveli Lignite, Tamil Nadu (Ramanujam, 1966).

Remarks—From the photograph (pl. 2, fig. 26) the nature of reticulation is not discernible.

TRICOLPITES MINOR Sah, 1967

Original Description—Size 23-29 µm; amb spheroidal, tricolpate, colpi tenuimarginate, sexine pilate, surface sculpturing finely microreticulate.

Occurrence—Oligocene, Barail, Meghalaya (Singh *et al.*, 1985).

TRICOLPITES PARVIRETICULATUS Sah, 1967

Original Description—Size range 36-42 µm, amb prolate-spheroidal to sub-prolate, tricolpate, colpi deep, exine sculpture finely reticulate.

Occurrence—Palaeocene, Matanomadh Formation, Kutch (Saxena, 1979; Kar, 1985).

TRICOLPITES PAUCIRETICULATUS Sah & Kar, 1974

Pl. 2.10-11 (holotype)

Original Description—Pollen grains subcircular-circular, 38-46 µm; tricolpate, colpi broad, colpi margin laevigate. Exine reticulate only in middle part of mesocolpate region.

Description (present study)—Pollen grain circular-subcircular in polar view, 50 x 54 µm. Tricolpate, colpi 16.5 µm deep, end pointed, wide at equator. Exine 2.5 µm thick at mesocolpia and gradually thins out towards colpi margin (0.5 µm), nexine as thick as sexine, semitectate, columellae distinct at mesocolpia 1 µm in length and width, indistinct near colpi margins. Surface reticulate, lumina nearly circular, larger (1 µm) at mesocolpia and apocolpia, almost absent at colpi margins, muri simplicolumellate, thin, narrow, smooth.

Occurrence—Early Eocene, Palana lignite, Rajasthan (Sah & Kar, 1974).

TRICOLPITES RETICULATUS Cookson ex Couper, 1953

Pl. 3.5-7, 10-11

Synonyms

1966 *Retitricolpites microreticulatus* Mathur, Q. J. geol. Min. metall. Soc. India 38: 41, pl. 1, fig. 17 (non van der Hammen & Wymstra, 1964).

1972 *Tricolpites longicolpatus* Venkatachala and Rawat, Proc. Sem. Palaeopalynol. Indian Strat. Calcutta, pp 301, pl. 2, figs 16-19.

1974 *Retitricolpites perdilatus* in Baksi and Deb (non Muller, 1968), Geophytology 10: 205, pl. 1, fig. 8.

1985 *Psilatricolpites brevis* (Sah & Kar) Kar, *in part*, Palaeobotanist 34: 40, pl. 14, figs 1-2.

Original Description (Couper, 1953)—Free, isopolar, tricolpate. Exine variable in thickness and sculpture. Size variable.

Emended Description (Jarzen & Dettmann, 1989)—Pollen grains tricolpate, fossaperturate, isopolar, radially symmetrical, suboblate to prolate spheroidal. Amb lobate with convex mesocolpia and inset apocolpia. Colpi meridionally aligned, incised 1/2-3/4 distance to pole, often gaping at equator, margins entire, composed of thickened nexine that projects beyond sexine. Exine 0.8-1.2 µm thick at mesocolpia slightly thicker and beveled at colpal margins. Sexine baculate, semitectate, 0.5-0.8 µm thick, surface with even meshed reticulum. Nexine as thick as, or slightly thinner than, sexine, thickest and protruding beneath sexine at colpal margins. Surface reticulum composed of smooth-crested, simplibaculate muri ca. 0.2 µm wide that enclose angular, almost isodiametric to elongated lumen up to 0.8 µm in maximum dimension.

Occurrence—Miocene, Neyveli lignite, Tamil Nadu (Ramanujam, 1966); Palaeocene, Matanomadh Formation, Kutch (Saxena, 1979); Palaeocene, Mikir Formation, Meghalaya (Mehrotra, 1983); Subsurface Early Miocene sediments, Meghalaya (Nandi & Sharma, 1984); Lower Eocene, Naredi Formation and Middle Eocene, Harudi Formation, Kutch (Kar, 1985); Oligocene, Barail Group, Meghalaya and Assam (Singh *et al.*, 1985, 1986); Late Cretaceous-Palaeocene, Jalangi Formation, Bengal Basin (Baksi & Deb, 1980); Palaeocene, Supratrappean, Kutch (Mathur, 1966) and subsurface Pleistocene to Holocene sediments, Bengal Basin (Mathur & Chopra, 1987).

Remarks—A few specimens show very weak reticulation in comparison to holotype of the species (Pl. 5.5-7). Moreover, some of the specimens described under this species are large in size with larger reticula and they have been transferred to *Albertipollenites* and *Rousea*. *Retitricolpites microreticulatus* Mathur, 1966 described by Rao & Ramanujam (1987) appears as colporate from the photograph (pl. 1, fig. 4). The specimens recorded by Sah and Kar (1974, slide no. 4353/25), Kar (1985 slide nos. 3363/14, 3370/2) and Kar & Kumar (1986, slide no. 9376) as *T. reticulatus* are colporate.

Genus—VERRUTRICOLPITES Pierce, 1961

Type Species—Verrutricolpites sphaeroides Pierce, 1961
Original Diagnosis—Verrucate tricolpate pollen.

VERRUTRICOLPITES PERVERRUCATUS
Ramanujam, 1966

Original Description—Pollen grains isopolar, prolate, 3-zonicolpate, 26 x 22 µm. Amb rounded. Colpi short, with ends blunt. Exine 1.5 µm thick, loosely verrucate. Verrucae not much raised from the surface, 1.5 µm high.

Occurrence—Miocene, Neyveli Lignite, Tamil Nadu (Ramanujam, 1966); Palaeocene, Matanomadh Formation, Kutch (Saxena, 1979; Kar, 1985).

TENTATIVE ASSIGNMENTS

CRANWELLIA INDICA Venkatachala & Rawat, 1972

Original Description—Pollen grain roundly triangular in polar view, angulaperturate, sides convex; 59.4 x 60.0 µm. Tricolpate, colpi short, about 10.0 µm deep in polar view, tapering, broader in the equatorial region, about 6.6 µm wide. Exine about 4.6 µm thick, tectate; sexine thicker than nexine, formed of pila with rounded distal heads; surface striated. Striation about 1 µm thick, closely placed running from pole to pole, sometimes bifurcating and dwindling at the poles, giving a linear pseudoreticulum to the surface.

Occurrence—Subsurface Palaeocene-Eocene sediments, Cauvery Basin (Venkatachala & Rawat, 1972).

Remarks—The photograph of the holotype shows striate ornamentation formed by round- headed pila. The species appears to be closer to *Striatopollis* Krutzsch (1959) than to *Cranwellia* (interapical margins are also not concave, as found in *Cranwellia*). But the present species is larger in size than holotype of *Striatopollis*.

RETITRICOLPITES MARGINATUS van Hoeken Klinkenberg, 1966; *in* Rao and Ramanujam, 1982

Description (after Rao & Ramanujam)—Pollen grain isopolar, amb rounded to subcircular, polar diameter 24-29 µm; zonaperturate, tricolpate, medicolpate, colpi often obscured by heavy sculpturing, margins thin, ends pointed. Exine 2.5 µm thick, sexine thicker than nexine, surface reticulate, heterobrochate, brochi larger at poles, smaller along a margin around colpi, polygonal, muri simplibaculate, lumina angular with 1-5 free bacules.

Occurrence—Miocene, Quilon Formation, Kerala (Rao & Ramanujam, 1982).

Remarks—The specimen described by Rao & Ramanujam (1982) is different from *Retitricolpites marginatus* van Hoeken Klinkenberg (1966) and should be treated as new species under *Rousea* as *Retitricolpites* is invalid. However, Rao & Ramanujam's specimen is not available for examination at present and thus it is kept in tentative assignment.

RETIBREVITRICOLPITES SEMILUNARIS
Ramanujam *et al.*, 1985

Original Description—Pollen grains isopolar, radially symmetrical, oblate, amb triangular, 36-55.5 µm in diameter, apices ± truncate, sides straight to concave; zonaperturate, angulaperturate, tricolpate, brevicolpate, colpi narrow slit-like with conspicuous costae (nexinous thickenings) surrounding them, costae up to 4.5 µm thick; exine up to 5 µm thick, subtectate, mesocolpia with prominent semilunar, cushion-like nexinous thickenings (up to 3.5 µm) sweeping from aperture to aperture, surface finely reticulate, muri high, meshes polygonal, lumina smooth.

Occurrence—Miocene, Neyveli lignite mine-II, Tamil Nadu (Ramanujam *et al.*, 1985).

Remarks—The present species is unique in the possession of straight to concave amb, prominent semilunar, cushion-like nexinal thickening and conspicuous costae bordering the short colpi. Since these are qualitative characters, we feel that this taxon should be placed under a separate genus.

STRIATOPOLLIS BELLUS Sah, 1967

Original Description—Size range 50-54 x 64-76 µm, amb sub-spheroidal to oval; tricolpate, brevicolpate; sexine thicker than nexine, tegillate, striate.

Occurrence—Subsurface Palaeocene-Eocene sediments, Cauvery Basin (Venkatachala & Rawat, 1972); Subsurface Miocene sediments, Meghalaya (Nandi & Sharma, 1984).

Remark—Striatopollis bellus is larger in size than *Striatopollis sarstedtensis* and thus *S. bellus* needs suitable placement.

STRIATOPOLLIS CATATUMBUS (Garciá Guzmán, 1967) Mathur & Chopra, 1987

Original Description—Pollen grain tricolpate, prolate; furrow C 1 - 2, C 1, C 1; sculpture type striate. Width of striae about 1 µm, but finer at the poles. Sometime furrows show a margo. Thickness of exine about 3 µm; ectexine thicker than endexine. Grains semitectate. Polar area 3 µm. Size of holotype 53 x 41 µm.

Occurrence—Subsurface Late Miocene sediments, Bengal Basin (Mathur & Chopra, 1987).

Remarks—Mathur and Chopra (1987) merged *Striatocolpites* (van der Hammen, 1956) Garciá Guzmán (1967) into *Striatopollis* because the former is illegitimate and a later synonym of *Acer* (Jansonius and Hills, 1976). The size of the present species is larger than the holotype of *Striatopollis*.

TRICOLPITES MARGOCOLPITES Venkatachala & Rawat, 1972

Original Description—Pollen grain triangular in polar view, sides straight to convex; 35.7-37 x 37 µm; tricolpate, angulaperturate. Margocolpate, colpi long, 15.2 µm deep in polar view, reaching almost to the poles, wide in the equatorial region, margo about 2.7 µm thick. Exine 1.5 µm thick, thickening towards the pore region; sexine as thick as nexine or slightly thicker, intrapunctate, surface finely reticulate.

Occurrence—Subsurface Palaeocene-Miocene sediments, Cauvery Basin (Venkatachala & Rawat, 1972, 1973).

Remarks—Presence of margo is very characteristic feature and does not come within the circumscription of *Tricolpites*.

TRICOLPITES MINUTUS Jain *et al.*, 1973

Non: *T. minutus* Sah & Kar, 1970

Description—Pollen grains tricolporoidate, spheroidal, 15-25 µm in diameter, prolate, sexine thicker than nexine, surface ornamented with warts, 0.5-1 µm in height.

Occurrence—Palaeocene, Barmer Hill, Rajasthan (Jain *et al.*, 1973).

Remarks—Holotype of this species is missing. This taxon is junior homonym of *Tricolpites minutus* (now *Ladakhipollenites minutus*) but distinct having warty exine.

TRICOLPITES STRIGOSUS Salujha *et al.*, 1974

Original Description—Golden yellow, subcircular, measuring 24-35.2 x 22.4-30.8 µm; occasionally bearing folds; tricolpate, colpi 2.5-4.5 µm deep with a 2-3 µm wide thickening; exine ± 1.2 µm thick, finely granulate, grana ± 1 µm in diameter.

Occurrence—Palaeogene sediments, Meghalaya (Salujha *et al.*, 1974)

Remarks—Salujha *et al.* (1974) mentioned that *T. strigosus* has 2-3 µm thick colpus margins which is not clear from the photograph. Since this species has granulate exine, it differs from other species placed under *Tricolpites*.

TRICOLPITES OVATUS Salujha *et al.*, 1974

Original Description—Golden yellow, oval, size 30.6-38.4 x 21.2-27.8 µm; occasionally bearing folds, tricolpate, colpi 2-3.5 µm wide extending almost from one pole to the other; exine ± 1.5 µm thick, granulose, grana ± 1 µm wide, closely placed.

Occurrence—Palaeocene-Eocene, Disang Group, Meghalaya (Salujha *et al.*, 1974); Early Miocene, Bokabil Formation, Tripura (Salujha *et al.*, 1977).

Remarks—Since this species has granulose exine, it should not be placed under *Tricolpites*.

TRICOLPOPITES GRANULOSUS Baksi, 1962

Description—Polar compression; longer diameter 26 µm, surface dense granular to slightly spinulose, tricolpate, colpal furrow extending right up to the pole.

Occurrence—Miocene, Surma Group, Meghalaya (Baksi, 1962).

TRICOLPOPITES SPINOSUS Baksi, 1962

Description—Oblique equatorial compression; longer diameter (without spines) 44 µm, spines medium based; more or less obtuse termination; infrequent; tricolpate.

Occurrence—Oligocene, Barail Group, Meghalaya (Baksi, 1962).

DISCUSSION

In this paper 98 species of tricolpate pollen recorded from Tertiary sediments of India have been compiled. The taxonomic study reveals that the characters overlap among the genera *Tricolpites, Tricolpopites* and *Retitrescolpites*. The genus *Tricolpites* has been conceived here as per emended diagnosis of Jarzen & Dettmann (1989). The segregation of the genus *Tricolpites* (*sensu lato*) into *Albertipollenites, Rousea* and *Tricolpites* (*sensu stricto*) is followed here after Srivastava (1969b) and the species are reallocated accordingly. *Tricolpopites* Biswas, (1962) was not validly proposed (Jansonius & Hills, 1976) and the genus shows characters identical with *Tricolpites*. The species described under *Tricolpopites* are transferred to different genera. Similarly, species of *Retitricolpites* and *Retibrevitricolpites* are also placed under different genera according to their characters (Fig. 1). *Retitrescolpites* is delimited here as colpate/colporoidate pollen having strongly retipilate to retibaculate exine. Still, the distinction with other genera is not sharp. While dealing with the genus *Ladakhipollenites* it is found that *Ladakhipollenites minutus* lies in the border of *Ladakhipollenites* and *Tricolpites* because in *L. minutus* surface structure appears as muri but they do not join to form reticulum. A few species viz., *Tricolpopollenites microhenriei* (Ambwani, 1982), *Retitrescolpites africanus* (in Saxena *et al.*,1984), *R. assamicus* (Dutta & Sah, 1970), *Retibrevitricolpites foveolatus* (Venkatachala & Rawat, 1972), *Tricolpites matauraensis* (in Sah & Kar, 1974), *T. thomasii* (in Ramanujam, 1966) and *T. speciosum* (Ramanujam, 1966) are found to have colporate aperture on reexamination of specimens and/or from the illustrations.

Dicolpopollis spp., *Incrotonipollis* and *Tricolpites reticulatus* have been dealt here because new information have emerged since Thanikaimoni *et al.* (1984) and Venkatachala *et al.* (1989) studied them. The three species *Tricolpites ornatus*, *T. scrapeus* and *Tricolpopollenites granulosus* are characterized by granular ornamentation and do not compare with the circumscription of existing tricolpate genera. Same is the case with *Tricolpites marginalis* where a margin is very prominent along the colpi. Similarly, *Tricolpites spinosus* and *T. verrucatus* bear spinulose and warty exine respectively. *Retibrevitricolpites vanderhammenii* also shows characteristic mesial thickening and does not come within the circumscription of any known genus. Similarly, *Striatopollis bellus*, *S. crassiundulus* and *Cranwellia indica* show striate exine and appear close to *Striatopollis* but are much larger in size. *Retitricolpites marginatus* needs proper taxonomic treatment. We could not place them properly without examining the types and thus listed them at the end as "Tentative assignments".

The above study is partly based on holotypes and other specimens available in Birbal Sahni Institute of Palaeobotany. Help of literature has been taken for rest of the taxa. Still few distinct taxa could not be reallocated properly and kept under tentative assignments. These taxa require examination of the original specimens for suitable assignment. However, this evaluation has enabled satisfactory taxonomic placement of majority of unsorted tricolpate taxa from India.

The stratigraphic ranges of the studied species, on the basis of their records of occurrence, are presented in Fig. 2. However, it should be noted that some species show long vertical distributions by bringing together in this chart shorter distributions documented from individual basins, e.g., *Tricolpites reticulatus*, that cumulatively translate into a long range. The role of shifting ecology and climate in this phenomenon has not yet been analyzed.

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Dispersed angiosperm cuticles from a lignitic clay bed, Sindhudurg Formation (Miocene), Maharashtra : an interpretation on taxonomy, biodegradation and environment of deposition

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ABSTRACT

Tewari R, Kumar M, Anand-Prakash, Shukla M & Srivastava GP 2001. Dispersed angiosperm cuticles from a lignitic clay bed, Sindhudurg Formation (Miocene), Maharashtra : an interpretation on taxonomy, biodegradation and environment of deposition. Palaeobotanist 50(2 & 3) : 369-380.

A detailed morphotaxonomic study of dispersed leaf cuticles in relation to the effect of various degradational processes have been carried out from a lignitic clay bed exposed at Amberiwadi, Maharashtra. During the investigations, cuticles under various stages of degradation caused mainly by the microbial activity were observed. Such changes have been affected in the foliage dominated organic matter during early stages of diagenesis. These studies also provide an insight into the land plant diversity and help in tracing relationship between well preserved fossil cuticles and the flora still forming a part of the forests in coastal Maharashtra. It is suggested that the deposition of organic matter took place in a shallow niche present over a narrow coastal strip.

Key-words—Dispersed cuticles, Morphology, Taxonomy, Palaeoenvironment, Sindhudurg Formation.

महाराष्ट्र के सिन्धुदुर्ग शैलसमूह के लगुडांगारीय मृत्तिका संस्तर से प्राप्त परिक्षिप्त आवृतबीजी उपचर्मों का वर्गिकीय, जैवनिम्नीकृत तथा निक्षेपणीय पर्यावरण के आधार पर निर्वचन

रजनी तिवारी, माधव कुमार, आनन्द प्रकाश, मनोज शुक्ल एवं गजेन्द्र प्रताप श्रीवास्तव

सारांश

विभिन्न निम्नीकरण प्रक्रियाओं के प्रभावों को ज्ञात करने के उद्देश्य से महाराष्ट्र के अम्बेरीवाड़ी में अनावरित लगुडांगारी मृत्तिका संस्तर से प्राप्त परिक्षिप्त पर्ण उपचर्मों का विस्तृत आकारवर्गिकीय अध्ययन किया गया । अध्ययन के दौरान मूलतः सूक्ष्म जैविक गतिविधियों के कारण निम्नीकृत होने वाले उपचर्मों की विभिन्न अवस्थाओं को प्रेक्षित किया गया। प्रसंघनन की प्रारंभिक अवस्थाओं के दौरान पर्णसमूह की प्रचुरता वाले कार्बनिक पदार्थ में ये परिवर्तन हुए हैं। ये अध्ययन भूमि पादप वैविध्य हेतु एक मार्गदर्शक का कार्य करते हैं तथा इनसे समुद्रतटीय महाराष्ट्र के वनों में अभी तक उग रहे वनस्पतिजातों तथा सुसंरक्षित अश्मित उपचर्मों के मध्य सम्बन्धन स्थापित करने में भी सहायता मिली है। यह प्रस्तावित किया जाता है कि स्थापित कार्बनिक पदार्थ का निक्षेपण एक समुद्रतटीय पट्टी पर उपस्थित एक उथले गर्त्त में हुआ होगा।

संकेत शब्द—पादपाश्म उपत्वचा, आकारविज्ञान, पारिस्थितिकी, पुरापर्यावरण, सिंधुदुर्ग शैलसमूह।

INTRODUCTION

THE Sindhudurg Formation (Miocene), Maharashtra consists of impure lignite, carbonaceous clay, laterite, iron stone bands and gritty clay. Within this sedimentary sequence lignitic clay contains abundant angiospermous cuticles and other types of organic matter. It appears that the source material was very much dominant in foliage. Such a kind of source material generally forms paper coal if other conditions remain favourable. Dispersed cuticles have recently been reported from Sindhudurg Formation (Miocene) of Ratnagiri District, Maharashtra (Tewari & Agarwal, 2002; Agarwal *et al.*, 2002) and from Upper Pliocene-Pleistocene of West Kameng District of Arunachal Pradesh (Joshi *et al.*, in press).

The vegetation growing around Ambarwadi contributed to the primary production of leaf litter and woody fragments, which were deposited in a shallow basin. The abscissed leaves and small wood fragments initially accumulated over the forest floor before being transported to the site of deposition. The cuticular features are helpful in characterization of various fossil taxa. They are also helpful in correlation of beds and in biostratigraphy.

The dispersed cuticles yield information on nature of vegetation and tree types. They also preserve many features (viz., shape and arrangement of epidermal cells, their arrangement around stomata, nature of anticlinal and surface walls, type of stomata, type of guard cells and nature of subsidiary cells) which are linked with the habitat, climate, environment of deposition, phases of degradation and relationship with microorganisms.

So far, little information is available on fungal action on leaf fragments and its role in the preservation of organic matter in the sediments. The decaying processes show differential rate of degradation over cellulose, lignin, lipid, proteins and carbohydrates that are the main constituents of organic matter.

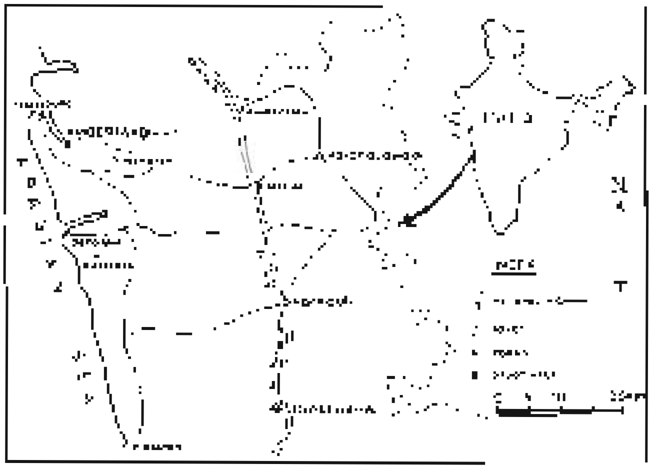

Fig. 1—Location Map

Primarily, these substances are associated with the protective covering in the epidermal tissues. Under various catabolic processes in the sediments they are transformed in to biomonomers, geopolymers and also in some inorganic compounds during diagenesis and peat formation (Berner, 1980). However, some of the plant cuticles retain their original features due to the adaptability against various microorganisms while some display biodegraded stomata and presence of hyphal mats over the cells (Pl. 2.6, 7, 9; Pl. 3).

MATERIAL AND METHODS

The cuticles were isolated from lignitic clay samples by a combination of standard preparation methods suggested for the study of dispersed organic matter which include treatment with dilute HCl and HF acids and sieving through 500 mesh sieve. The residue obtained is smeared over a cover slip mixed with polyvinyl alcohol solution and dried at 60°C. The cover slips are mounted with the help of canada balsam. After the

PLATE 1 →

1. Cuticle of lower surface of the leaf showing straight walled isodiametric to polygonal cells with several fungal fruiting bodies attached and large oval irregularly oriented and distributed stomata. Slide no. BSIP 12450, M 34, x 450.

2, 4, 8. Cuticular pieces showing rectangular to polygonal cells with thick straight to arched walls, oval to rounded, irregularly distributed and oriented paracytic stomata, thickened areas on surface walls (figs 2, 4) and biodegradation of cells (fig. 8). Slide nos BSIP 12452, M 44; 12451, H 42; 12457, L 41, x 500.

3, 5. Cuticle of lower surface of leaf showing polygonal cells with straight to arched anticlinal walls, oval, anomocytic, irregularly distributed and oriented stomata. Slide nos. BSIP 12452, F53; 12453, Y 33, x 500, x 450.

6. Cuticle of lower surface showing polygonal to rectangular cells with sinuous to straight anticlinal walls, elliptic to oval paracytic stomata and surface walls with thickened areas. Slide no. BSIP 12457, L 33, x 500.

7. Cuticle showing rectangular to polygonal cells, deeply sinuous anticlinal walls with speckled thickening and round to oval paracytic stomata. Slide no. BSIP 12454, W25 x 250.

9. Cuticle showing straight to arched walls, isodiametric cells and longitudinally distributed and oriented stomata arranged in rows. Slide no. BSIP 12452, T 36, x 500.

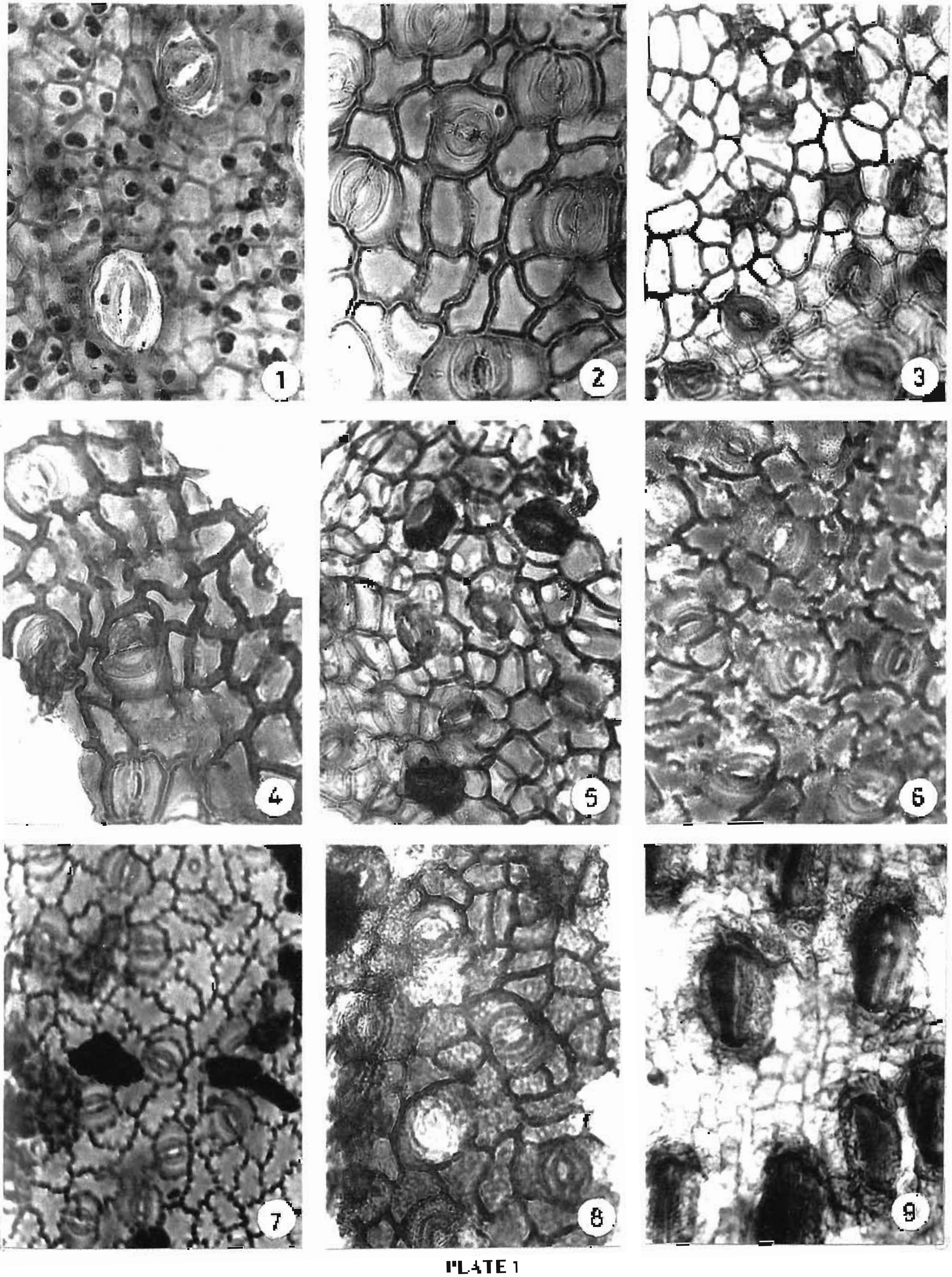

PLATE 1

preparations, the cuticles are studied considering the cells, cell walls, stomata, guard cells and subsidiary cells. The stomatal index is calculated following the methods of Dilcher (1974) and Dilcher and Daghlian (1977).

GEOLOGICAL SETTING

A sedimentary sequence forming part of Sindhudurg Formation is exposed at Amberiwadi (Lat. 16°30'20" N; Long. 73°23'20" E) near Tirot Village in Devgarh Taluk of Sindhudurg District (Fig. 1). Saxena *et al.* (1992) and Saxena (1995) made a detailed lithostratigraphic study of a number of outcrops, well and mine sections etc. of Ratnagiri and Sindhudurg districts of Maharashtra. The generalised sequence of sedimentary deposits is as follows :

Laterite (5 m)

————Unconformity————

Iron stone band (0.1 m)

Grey clay mixed with ferruginous matter

Lignite (1 m)

Gritty clay (0.1 m)

————Unconformity

Laterite (Base thickness not known)

The Sindhudurg Formation overlies Precambrian rocks on Deccan Traps and the contact is marked by an erosional unconformity. A part of lignite is mixed with soft plastic clay and contains carbonised wood remains and yields rich palynoflora of Miocene age.

SYSTEMATIC DESCRIPTION

The dispersed cuticle assemblage recovered from lignitic clays of Sindhudurg Formation shows dominance of dicotyledons and also represents a monocotyledonous family. Based on morphological features, the dispersed cuticles were assigned up to family level only and not up to generic or specific level because of uncertainty about the validity of several species and the preservation of characters in fragments. However, the present taxonomic study is likely to provide a base for evaluating the characters of dispersed fossil angiosperm cuticles and shall also help in the interpretation of palaeovegetation and environment of deposition. A detailed study based on morphotaxonomy of the dispersed cuticle is being carried out and will be published later.

The cuticles of leaves exhibit characters of internal anatomy which can be used for classification or identification of species. The leaf surfaces also show a range of cell arrangement, stomatal structure and cuticular sculpturing which can distinguish one species from another. The analysis of cuticular structures is helpful in reconstructing palaeovegetation of a specific habitat. The cuticles of moist, sheltered, shady habitats are clearly distinct from those of arid/dry conditions. The leaf development and its cuticular morphology depends on genotype and on environment.

On the basis of epidermal characters, the cuticles are referred to seven dicots and one monocot families. Among dicotyledons, the cuticles are assignable to Lauraceae, Magnoliaceae, Myrtaceae, Moraceae, Caesalpiniaceae, Loranthaceae and Symplocaceae, while Dioscoreaceae of Liliflorae represents monocotyledons.

The epidermal characters of different types of dispersed cuticles recovered from Sindhudurg Formation, Amberiwadi and their affinities are given in Fig. 1.

The families described here are mostly characterised by hypostomatic and occasionally amphistomatic cuticles, cells are either differentiated or not differentiated into vein and mesh areas and are usually elongate, polygonal to rectangular and sometimes isodiametric in shape. The lateral walls are both

PLATE 2

1, 2. Cuticle showing rectangular to polygonal cells of mesh area with sinuous anticlinal walls, surface walls with numerous small rounded structures and irregularly distributed and oriented anomocytic stomata. Note "P" present in pores. Slide no. BSIP 12451, G 23, x 450.

3. Cuticle showing rectangular, pentagonal, hexagonal cells with straight to undulate walls and anomocytic stomata with wide stomatal slit. Slide no. BSIP 12456, F 51, x 500.

4. Cuticle showing polygonal thick walled cells and "algal colonies". *[illegible]*. Slide no. BSIP 12456, F 56, x 450.

5. Cuticle showing small isodiametric cells with thin areas on surface and a circular trichome base. *[illegible]*. Slide no. 12450, G 37, x 450.

6. Parenchymatous cells showing circular opening. Slide no. BSIP 12457, K 25, x 450.

7. Cuticle showing polygonal thick walled cells. *[illegible]*. Slide no. BSIP 12452, J 45, x 450.

8. Cuticle showing rectangular to polygonal cells with straight to arched anticlinal walls, surface with thickened areas, large oval irregularly distributed and oriented stomata with wide stomatal slits and indistinct subsidiary cells. Slide no. BSIP 124527, L 41, x 500.

9. Magnified cuticle fragment showing hexagonal epidermal cells with [illegible] and disrupted parenchymatous cells. Slide no. BSIP 12457, M 33, x 250.

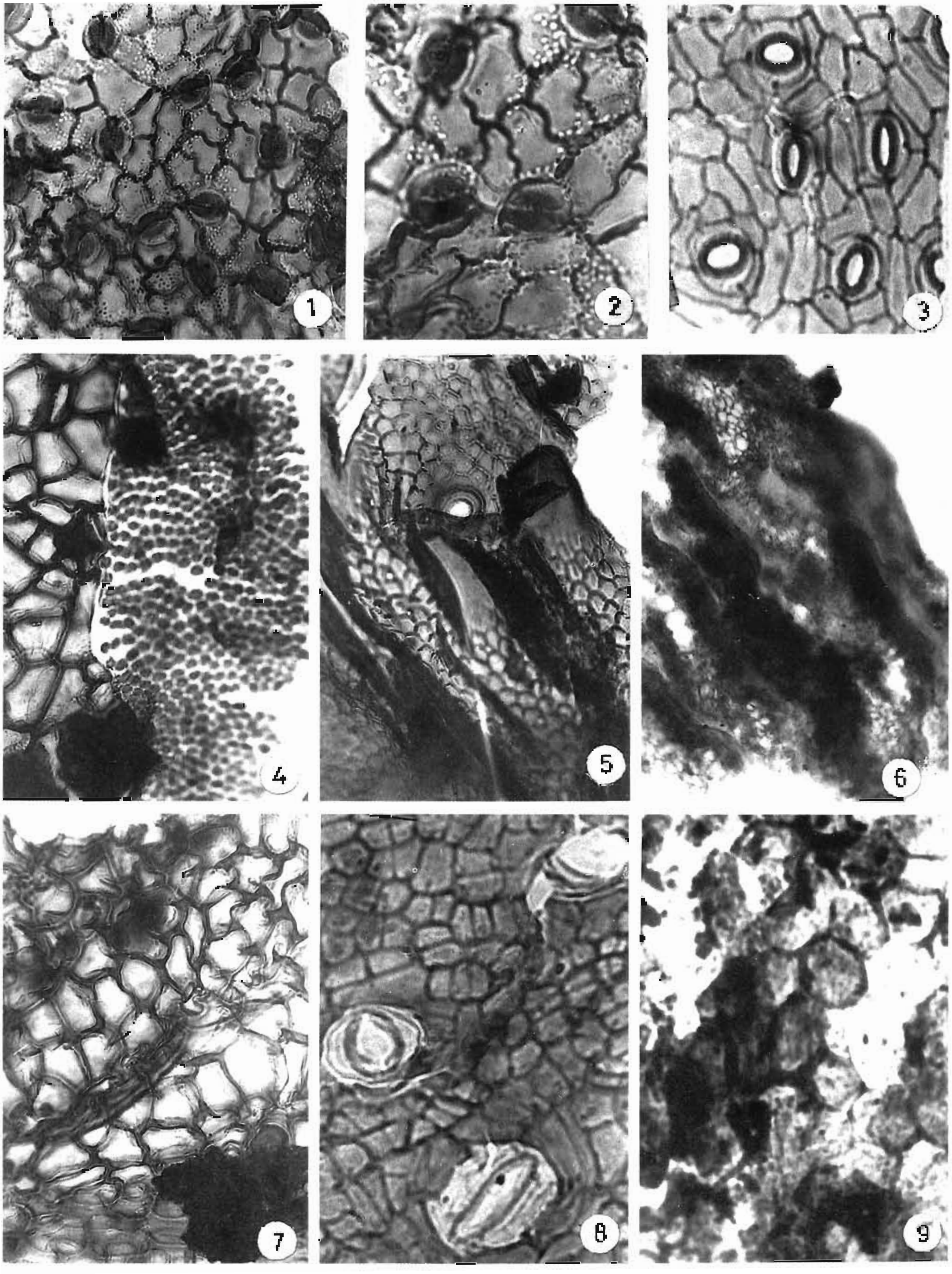

PLATE 2

straight and sinuous and sometimes thickened. The surface walls are usually non-papillate. However, when papillae are present they are either single, dome shaped or numerous, small and rounded on each cell. The stomata are usually oval, anomocytic, rarely paracytic, irregularly distributed and oriented. Sometimes, they are also rounded to semi-circular in shape and distributed in longitudinal rows (in case of monocot family). The guard cells are usually superficial, sometimes thickened, and with distinct 'T' pieces at poles. Stomatal index varies between 1.2–5.1. The subsidiary cells are unspecialised.

Cuticular characters like shape and size of cells, straight, arched and sinuous lateral walls, types of papillae on surface walls, stomatal size, type of stomata (whether anomocytic or paracytic), distribution and frequency, presence of trichomes and their organization and type of subsidiary cells are useful diagnostic characters which are often considered of great taxonomic importance. All these characters are genetically controlled (Stace, 1965). However, some epidermal characters are of eminent ecological significance, for example, large epidermal cells are found in leaves of humid and shaded conditions (Yapp, 1912; Salisbury, 1927; Watson, 1942) and reduced cell size is characteristic of dry conditions (Oxell, 1932).

Similarly, thick cuticle, sunken stomata with raised lobes overarching the suprastomatal cavity, high frequency of stomata, straight cell walls, high trichome density, sunken guard cells, rough surface walls, strong papillae and distinct papillate subsidiary cells with papillae overarching stomata are important xeromorphic characters. These features provide protection against water loss and are particularly efficient in assisting water movement when there is an adequate supply. The rough surface assists reflection and scattering of light and heat and helps the plants from overheating. On the contrary, characters like thin cuticle, undulate cell walls, smooth surface walls, fewer epidermal hairs, superficial, large stomata and unspecialised subsidiary cells are mesomorphic characters found on leaves which grow in moderate and humid habitats (Stace, 1965; Cutler, 1982).

The cuticular characters observed in the present study are clearly indicative of moderate ecological conditions, since they reflect both humid and dry climates, e.g., thin cuticle, undulate to sinuous lateral walls, non-papillate or smooth surface walls, fewer epidermal hairs, normal stomata and unspecialised subsidiary cells indicate tropical conditions with sufficient rainfall. Hypostomatic nature too, reflects heavy precipitation, humidity and shade. However, some cuticular pieces show xeric characters like straight anticlinal walls, papillate surface walls and high frequency of stomata. Presence of both xeric and mesic characters in some plants indicates intermediate habitat, i.e., plants grew under both exposed and humid conditions. Such a condition may also reflect on the capability of plants to adapt during unfavourable climate.

DEGRADATIONAL CHARACTERISTICS

Plant cuticles and wood fragments preserve several anatomical features characteristic of the nature and habitat of parent plants. The degradation of cuticles at various stages indicates the effect of environmental factors and their relationship with other organic remains present in the sediments.

Broadly, three types of degradational agencies exist, namely physical, chemical and biological.

(i) Physical

The organic matter is degraded physically during its transport to depositional sites and abrasion due to clastic material. The degree of mechanical degradation is proportional to the distance travelled and energy of the agency of transport. Physical degradation causes tearing, fracture, abrasion and breakage of larger particles in small pieces.

(ii) Chemical

The breakage, pitting and dissolution of cellular parts observed on epidermal surfaces are apparently caused by the chemical precipitation of salts, calcite, dolomite and formation of pyrite etc. The physical or chemical reaction may also occur between portions of the cell walls and the adjacent pore fluids resulting in precipitation, impregnation, dissolution, etc. (Cohen & Spackman, 1980).

PLATE 3 →

1 Highly biodegraded organic matter with black debris and terminal zoosporangium with hyphae. Slide no. 12452, H 51, × 190.

2, 3 Biodegraded organic matter showing fungal fruiting bodies and hyphae. Slide no. BSIP 12452, Q 33, 40H, × 350.

4 Biodegraded matter showing fruiting bodies (*Phragmothyrites* sp.), ascomata and hyphae embedded in the cells disrupting the tissues. Slide no. BSIP 12452, H 15, × 500.

5 Leaf surface showing hyphal net. Slide no. BSIP 12452, H 45, × 500.

6 Biodegraded terrestrial organic matter with net-like structures of septate dark hyphae. Slide no. BSIP 12452, H 43, × 500.

7 Leaf tissue showing *Meliolinites* sp. with fruiting bodies. Slide no. BSIP 12455, Q 20, × 250.

8, 9 Infected wood fragment showing net-like structure of hyphae and fruiting bodies. Slide nos. 12452, K 27, × 250.

10 Showing biodegraded stomata and accessory cells. Slide no. BSIP 12451, K 51, × 190.

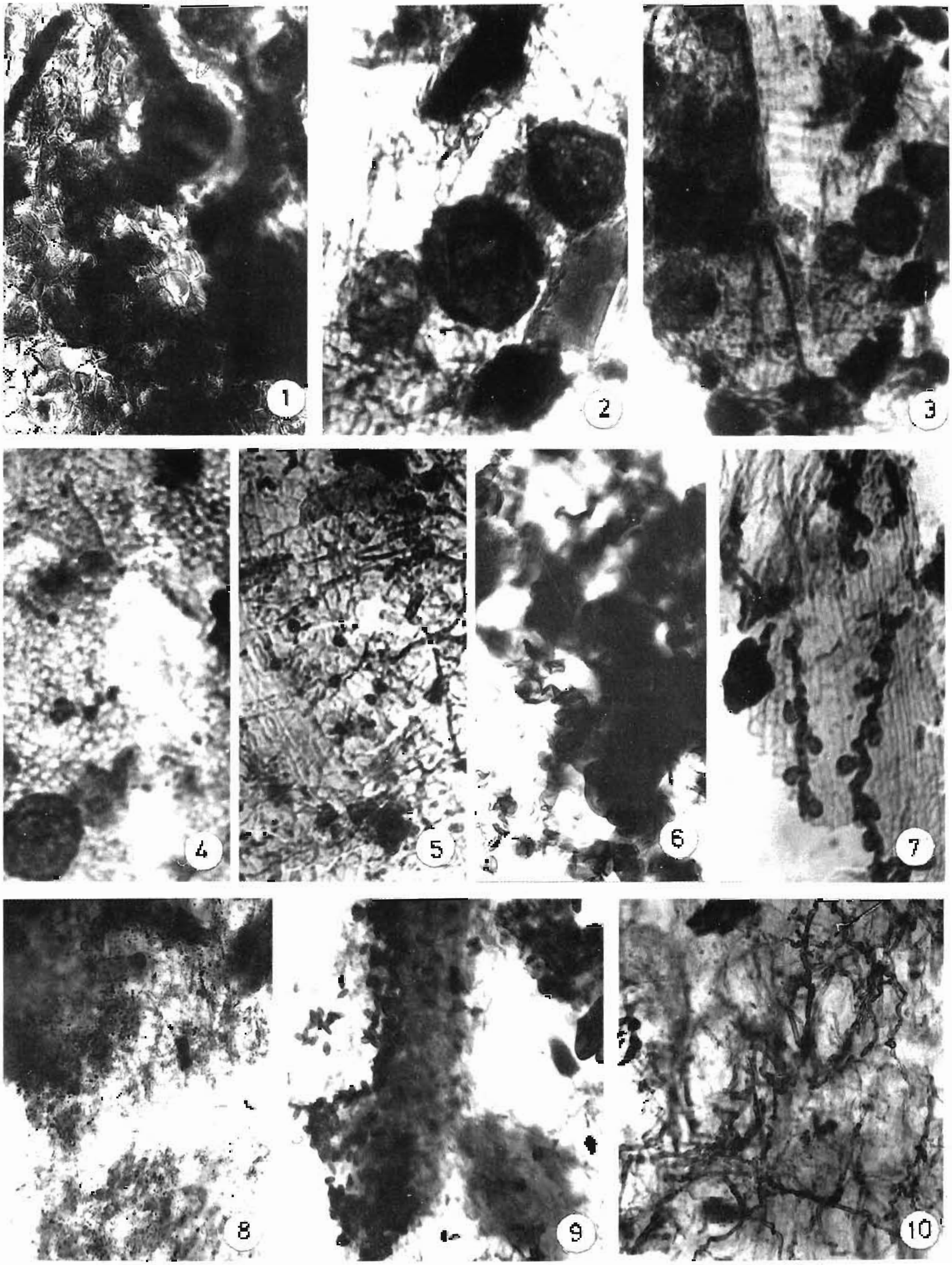

PLATE 3

Cuticle	Nature of cells	Nature of anticlinal walls	Nature of surface walls	Type of stomata	Size of stomatal apparatus	Guard cells	Size of stomatal slit	Stomatal Index	Subsidiary cells	Probable affinity
Type I A	Isodiametric cells, undifferentiated into vein and mesh areas; size of cells of upper surface 24-33 x 15-21 μm; size of cells of lower surface 12-33 x 9-21μm	Straight; 1·5-6 μm wide	Non-papillate	Large, anomocytic, irregularly distributed and oriented	33-51 x 33-48 μm	Superficial 33-51 x 9-12 μm in size; width of guard cell wall 9 μm	24-33 x 3-9 μm	1·2-3·8	Indistinct	Family Lauraceae (Dilcher, 1963, 1974; Giessen, 1971)
Type I B Pl. 2.3	Narrow, elongate, polygonal to rectanguloid cells, undifferentiated into vein and mesh areas; size of cells 24-30 x 6-7·5 μm	Straight, 1 μm wide	Non-papillate	Oval, paracytic, irregularly distributed and oriented	30-36 x 12-15 μm	Thickened guard cells with distinct 'T' pieces at poles; 30-36 x 3-6 μm in size	15-27 x 9-10·5 μm	13	2, parallel to guard cells	Family Lauraceae (Dilcher, 1974)
Type I C Pl. 1.3, 5	Cells divided into vein and mesh areas, cells over mesh areas are irregular to polygonal, irregularly arranged, 12-33 x 9-24 μm in size; cells over vein areas rectangular to elongate, polygonal and arranged end to end in rows, 18-42 x 6-15 μm in size	Undulate to arched, 3 μm wide	Rarely papillate, papillae dome-shaped, each cell with a single papilla, 6-7·5 μm long, 4·5 to 6 μm wide at base, 3 μm wide at apex	Oval to round, anomocytic, irregularly distributed and oriented	18-39 x 15-30 μm	Thickened guard cells with distinct 'T' pieces at poles; 18-39 x 6-9 μm; width of guard cell wall 3 μm	9-30 x 3-9 μm	2·6-14	5-6 in number, like other epidermal cells	Family Lauraceae (Dilcher, 1963)
Type I D Pl. 2.5	Cells undifferentiated into vein and mesh areas; elongate, rectanguloid, hexagonal, pentagonal, arranged irregularly; size 15-30 x 15-21 μm	Straight to undulate, 3 μm wide, undulations 'U' and 'V'-shaped	Non-papillate, sometimes trichome bases measuring 15-48 x 18-39 μm in size are present	Oval to elliptic; anomocytic; irregularly distributed and oriented	24-27 x 27-30 μm	Superficial 24-27 x 12-15 μm; width of guard cell wall 3 μm	12-15 x 4·5-18·5 μm	13	5 in number, like other epidermal cells	Family Lauraceae (Dilcher, 1963, 1974)
Type I E Pl. 1.6 Pl. 2.1, 2	Cells undifferentiated into vein and mesh areas;	Sinuous, 3 μm wide,	Surface wall with numerous,	Semi-circular to oval;	21-24 x 15-21 μm	With laminar thickening and	12 x 3-6 μm	18	5 to 7 in number, like	i) Family Lauracea

	rectanguloid to polygonal, arranged irregularly; 15-36 x 15-24 μm in size	sinuosities 'U' and 'V' shaped	small rounded structures (papilla)	anomocytic, irregularly distributed and oriented		sometimes with distinct 'T' pieces at poles; 21-24 x 6-9 μm in size, width of guard cell wall 3 μm			other epidermal cells	(Litke, 1968) (ii) Family Magnoliaceae, (Baranova, 1972)
Type II Pl. 1.2, 4, 8	Cells undifferentiated, tetragonal, pentagonal, hexagonal, polygonal, irregularly arranged, measure 27-39 x 27 μm in size	Straight to arched, 4·5-7·5 μm wide	With thickened areas, non papillate	Biconvex, paracytic, irregularly distributed and oriented	30-39 x 27-42 μm	Superficial, 30-39 x 9 μm, width of guard cell wall 3-4.5 μm	27-33 x 3μm	15		Family Loranthaceae (Peters, 1963)
Type III	Cells differentiated into vein and mesh areas, cells over mesh areas irregular, rectanguloid to polygonal, arranged irregularly, measure 12-30 x 9-21 μm in size; cells over vein areas elongate, polygonal, arranged end to end in rows, 15-33 x 12-15 μm in size	Straight to undulate, 1.5 μm wide	Non-papillate with thin areas	Squarish to irregular, anomocytic, irregularly distributed and oriented	13·5-18 x 12-18 μm	Indistinct	3-9 x 3-4·5 μm	20	5 in number, similar to other epidermal cells	Family Myrtaceae (Bandulska, 1931)
Type IV Pl. 1.7 Pl. 2.8	Cells undifferentiated, rectanguloid to polygonal, arranged irregularly, measure 30-60 x 18-39 μm in size	Deeply sinuous, sinuosities 'U' shaped, numerous, small knobbed thickenings, measuring 3 μm in diameter present on cell walls	Non-papillate	Round to oval, paracytic, irregularly distributed and oriented	30-33 x 24-27 μm	Thickened, 30-33 x 6-9 μm in size, width of guard cell wall 6 μm	15 x 9 μm	13	2, parallel to guard cells	Family Caesalpiniaceae (Peters, 1963)

Type V	Cells undifferentiated, irregular, rectanguloid to polygonal, arranged irregularly, 18-45 x 12-18 µm	Sinuous to undulate, sinuosities 'U' & 'V' shaped, 3 µm wide	With thickened area	Elliptic to oval in shape, paracytic, appear rectanguloid together with subsidiary cells, irregularly distributed and oriented	21-24 x 18-21 µm	Superficial, 21-24 x 6-9 µm, width of guard cell wall 3 µm	18 x 3 µm	31	2, parallel to guard cells	Family Symplocaceae (Litke, 1968)
Type VI Pl. 1.1	Upper and lower surfaces present, hypostomatic, cells of upper surface undifferentiated, isodiametric to rectanguloid, polygonal, arranged irregularly, 24-33 x 15-21µm; cells of lower surface undifferentiated, isodiametric to polygonal, arranged irregularly, measure 12-24 x 12-18 µm in size	Straight, 3 µm wide	Upper surface papillate, with numerous, rounded knobs (papillae); lower surface non-papillate, attacked by fungal spores	Large, oval, irregularly distributed and oriented	33-51 x 36-48 µm	Superficial, 33-45 x 9-10 µm	24-27 x 9 µm	4	Indistinct	Family Moraceae (Peters, 1963)
Type VII Pl. 1.9	Cell outlines not clear	Papillate, papillae biconvex, arranged in longitudinal row, orientation of papillae straight, parallel to cell surface, measure 6-7·5 x 3-4·5 µm in size	Large, oval, longitudinally distributed and oriented							Family Dioscoreaceae (Peters, 1963)

Fig. 2—Epidermal characters of dispersed cuticles recovered from Sindhudurg Formation, Amberiwadi and their affinities.

(iii) Biological

The microorganisms play a critical role in the degradation of cuticular pieces in the aerial, sub-aerial and under water conditions. These organisms (fungi & bacteria) affect plant tissues and change them from structured tissues to non-structured amorphous. The fungi and bacteria grow quickly in aerobic conditions. During the initial burial stages the meshes of fungal hyphae spread over the cuticles (Pl. 3.1, 4, 6) and enter the spongy mesophyll and palisade layers through stomatal slit (Pl. 3.1). They start degrading entire leaf parts and cuticular layer. Apparently, they reproduce here and convert these tissues in to an amorphous structureless mass (Pl. 3.3). This is evident by the presence of several fruiting bodies, which are found embedded in the biodegraded tissues of leaf and wood fragments (Pl. 3.2, 3, 5, 7 & 8-10). Later, when oxygen supply becomes limited or is exhausted, anaerobic bacteria (Demaison & Moore, 1980) continue the degradation process.

The bacteria present on outer cell membrane accelerate exchange of cellular substances across this membrane. This, in turn, enhances degradation of cell membrane. It can also be presumed that a considerable amount of metabolic activities accelerated the process. During metabolism the complex biopolymers, e.g., cellulose, lignin, proteins, lipids and carbohydrates which are present mostly in leaves, stems, and roots, transform into monomers such as amino acids, fatty acids and some inorganic compounds. These compounds are finally transformed into geopolymers such as fulvic and humic acids during the process of peat formation (Berner, 1980).

PALAEOVEGETATION

Amberiwadi lignitic clay contains rich cuticles and woody fragments. Leaf fragments occurring here are probably the part of accumulated litter formed by falling of leaves. The woody fragments are the part of stems that were broken from the tree and transported to a nearby depositional site. These entities suggest an autochthonous accumulation of vegetal matter, which yields information on plant types and palaeovegetation in the area prior to deposition. The plants of families Lauraceae, Moraceae and Myrtaceae, Caesalpiniaceae are woody trees, while Loranthaceae, Symplocaceae and Magnoliaceae are represented by trees/shrubs. The only monocot family Dioscoreaceae identified here is a climber in nature. The plants of these families widely occur in tropics and subtropics to warm temperate areas (Cullen, 1997). Saxena (1995), Saxena and Misra (1990) and Saxena *et al.* (1992) recorded palynofossils of 25 angiosperm families from Sindhudurg Formation, of which 14 families were of tropical to subtropical region and others of cosmopolitan habitat.

DEPOSITIONAL ENVIRONMENT AND DIAGENESIS OF ORGANIC MATTER

The cuticles and other types of dispersed organic matter recovered from Sindhudurg Formation, Amberiwadi show affinities with the plants growing along the Maharashtra Coast. The basin appears to be a brackish water body within access to sea as well as to fresh water. Small streams contributed fine clastic sediments with silty clayey material. These streams also brought large quantity of abscissed leaves from vegetation growing around the basin. A number of woody fragments, biodegraded and amorphous organic matter observed at the base of the section indicates that this layer was formed at near shore region. A few marine dinoflagellate cysts (Dr MR Rao, personal communication) and algal colony (Pl. 2.4) have also been recorded in this section which further affirms the marine influence.

The channel connected with the depositional area was affected by the cyclic tidal influx of brackish water from Arabian sea. During the deposition of middle layer, foliage from the nearest forested area was transported to the depositional site along with fine argillaceous matter. Thus, due to short transport the plant fragments were often preserved in their original form. This indicates that the swamp area was subjected to periodic overflows and occasional dewatering which reduced the size of humic detritus and also allowed less biodegradation of plant material in comparison to that of basal part. The leaf fragments present in this sequence reveal exclusive dominance of angiospermic remains. It suggests that the incursion of forest litter was higher than the material brought by the other sources to the depositional site. This resulted in the formation of lignitic clay deposit of Amberiwadi, Maharashtra Coast. However, the nature (lensoid shape) of lignitic clay bed shows that the deposition seems to have taken place in a shallow depression located close to the shoreline. Further the thickness and lateral extent of the lignitic clay indicates that the sedimentation could not have continued for a long time. Probably, the basin became shallower and shallower due to the regional uplift of the western coastal margin of India. Saxena (1995) and Saxena *et al.* (1992) suggested that the substrate was not much wet for a longer time or may be seasonally flooded here.

The cuticles of some plants of Lauraceae, Myrtaceae and Moraceae are apparently more resistant to degradation than the plants of other families probably because of the richness of biopolymers in their cellular parts. Chemically, the cuticles of higher plants are heterogeneous in nature. They consist of wax fraction, soluble in common organic solvents and an insoluble cuticular matrix forming the framework of the cuticle. Two biopolymers viz., cutin and cutan exhibit different behaviour when subjected to degradation processes that affect during diagenesis. They show resistance against fungal and bacterial decays (Tegelaar *et al.*, 1991). Cutin is an insoluble lipid polyester and is a main constituent of cuticular membrane associated with protective covering of aerial parts of leaves, fruits and non-woody stems (Holloway, 1982). The plants of Lauraceae and Myrtaceae contain aromatic oil-glands, whereas, milky juice is found in the plants of Moraceae (Hutchinson, 1973; Cullen, 1997). The cuticles of these plants are preserved with original features which indicates that the aromatic compounds and milky sap make epidermal tissues more resistant to decay.

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Studies in fossil gymnospermous woods—Part X; Three new species of *Araucarioxylon* from Lower Gondwana Strata of Chandrapur District of Maharashtra, India

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ABSTRACT

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Recent paleobotanical expedition to several Lower Gondwana (Permian) localities occuring in Chandrapur District of Maharashtra has brought to light several well preserved petrified gymnospermous woods. In the present paper three new species of *Araucarioxylon* i.e., *A. aravii* sp. nov., *A. chandrapurensis* sp. nov. & *A. shailae* sp. nov. are described based on distinct anatomical characters.

Key-words—Fossils, Gymnospermous woods, Lower Gondwana, *Araucarioxylon*, Permian.

भारत के महाराष्ट्र प्रान्त के चन्द्रपुर जिले के अधो गोण्डवाना स्तर से प्राप्त *अराउकेरियॉक्सीलॉन*

श्रीपाद एन. अगाशे एवं एम.एस. शशि कुमार

सारांश

महाराष्ट्र के चन्द्रपुर जिले में अवस्थित विभिन्न अधो गोण्डवाना (परमियन) संस्थितियों के हाल ही में किए गए पुरावानस्पतिक भ्रमण से अनेक सुसंरक्षित अश्मीभूत अनावृतबीजी काष्ठ प्राप्त हुई हैं। प्रस्तुत शोध पत्र में सुस्पष्ट शारीरिक अभिलक्षणों के आधार-पर *अराउकैरियॉक्सीलॉन* की तीन नयी प्रजातियाँ, *ए. अरावाइ* नव प्रजाति, *ए. चन्द्रपुरेन्सिस* नवप्रजाति तथा *ए. शैलाइ* नवप्रजाति अभिलक्षणित की गयी हैं।

संकेत शब्द—पादपाश्म, अनावृतबीजी काष्ठ, अधोगोण्डवाना, *अराउकैरियॉक्सीलॉन,* परमियन.

INTRODUCTION

EXTENSIVE paleobotanical investigation has been done on Lower Gondwana petrified woods occurring in the Lower Gondwana Strata of central, north and north eastern part of India such as Assam, Bengal, Bihar, Madhya Pradesh and Maharashtra. The main contributions to our knowledge of Lower Gondwana woods from India include the works of Greguss (1955, 1967), Lepekhina (1972), Maheshwari (1972), Lakhanpal *et al.* (1977), Agashe and Gowda (1978), (1973), Ramanujam (1978), Varadpande (1978), Agashe *et al.* (1981), Prasad (1982, 1986), Agashe and Prasad (1984, 1989), Agashe and Shashi Kumar (1996).

The genus *Araucarioxylon* Kraus seems to be well represented in the Lower Gondwana formations in various parts of the world. Kraus (1870) reported *A. carbonaceum* as type species from Czechoslovakia. The first report of *Araucarioxylon* from India was made by Schenk (1882), when he reported *A. robertianum* from Asansol. Stopes (1914) reported *Araucarioxylon* from New Zealand. Lepekhina (1972) reported 24 species of *Araucarioxylon* from Northern Eurasia. She also gave a list of 24 genera of palaeozoic woods belonging to the group *Dadoxylon* along with the description of all genera. All these woods were classified on the basis of secondary wood characters. Maheshwari (1972) reported 12 new species of *Araucarioxylon* from various Lower Gondwana formations of the world. He reported *A. araucanum*, *A. meridionale*, *A. santamariense* and *A. vozzii* from S. America, *A. allanii* from Antarctica, *A. agathioides* from India and Antarctica, *A. arberii* from Australia, *A. gondwanense*, *A. bengalense*, *A. prarelectense*, *A. jharkhandense* and *A. barakarense* from various localities of Lower Gondwana formations in India. Lakhanpal *et al.* (1977), described *A. mohgaonense* from Mohgaon kalan beds of Madhya Pradesh (Early Tertiary formations).

Earlier it was confined only to Miospore analysis of coal samples from Nagpur District. Later on thorough investigations of petrified woods from Chandrapur District gained much momentum. The main contributions on Lower Gondwana petrified woods from Maharashtra include the discoveries of Agashe *et al.* (1972-1998).

Agashe and Gowda (1978) described *Araucarioxylon loharense* from Lower Gondwana localities i.e., Lohara of Chandrapur District. Agashe *et al.* (1981) described two new species of *Araucarioxylon* i.e., *A. wadgei* and *A. lathiense* from Lathi of Chandrapur District. Agashe and Prasad (1984) described *Araucarioxylon kothariensis* from Wejgaon of Chandrapur District. Agashe and Prasad (1989) described *Araucarioxylon bhiskundense* from Bhiskund of Chandrapur District. Agashe and Shashi Kumar (1996) described *Araucarioxylon wejgaonense* from Wejgaon of Chandrapur District. Vagyani and Rajput (1981) described *Araucarioxylon nandorii* from Nandori of Chandrapur District. Murthy (1965) made some observations and gave some remarks on *A. dadoxylon* Chapman. Pant and Singh (1987) reported *A. mulhoensianum* from Raniganj Coalfield.

The above reports indicate that *Araucarioxylon* is the highly diversified genera in the Lower Gondwana beds.

AREA OF INVESTIGATION

Chandrapur District is encompassed roughly by latitude 18°15'-15°15' N and longitude 78°55'-80°55' E. The district is bounded on the north by Nagpur and Bhadra districts and on west by Wardha, Yeotmal and Andhra Pradesh, and to the south by Andhra Pradesh and on the east by Madhya Pradesh (Geology & Mineral resources of Maharashtra, 1975).

All the rock formations starting from the Archean to the Upper Cretaceous are met in Chandrapur District. The important rivers flowing in Chandrapur District are Wardha, Wainganga and Pranahita (Fig. 1). Stratigraphically and structurally the entire area of Chandrapur District forms a part of the peninsular shield.

It can be seen in Fig. 1 that Sironcha, Chimur, Brahmapuri and many localities near Chandrapur like Bhandak, Lohara, Ballarpur, Sasandi, Camp IV, Wejgaon, Lathi, Kanhargaon, Rangenapalli and Medaram come under the Lower Gondwana formations. These represent the lower most formations in the Gondwanas deposited during the Glacial Period. Deposition started during the Talchir Period, which comprises boulders, pebbles, rock fragments, mud stones, greenish shales, greenish to brown sandstones and clays.

Subsequently there was a thick series of fluviatile deposition of sandstones, shales and coal seams. This group is called as Barakar Series. This series is overlain by rocks of Kamthi Series, which comprises brown shale white shales and clay. These three series are generally met in all the coalfields of Maharashtra. In these areas abundant plant fossils like petrifactions, impressions and compressions occur.

MATERIAL AND METHODS

Numerous well preserved petrified woods were collected from different Lower Gondwana localities of Chandrapur District of Maharashtra during our palaeobotanical field trips for the past five years. The present paper deals with the detailed anatomical investigation of three well preserved decorticated petrified woods selected among many species collected.

The petrified woods described in the present paper were collected from Wejgaon, which is a small village situated at a distance of about 60 km south east of Chandrapur and also from Wejgaon-Arasi nala on the outskirts of the village in open fields and dried-up nalas. In nalas the fossil woods have been transported by water to the present place from surrounding areas in past. Many of them might have preserved *in-situ*. Three new species of petrified woods are described in this paper, are numbered as B.U.P.W. Nos. 2018, 2028 and 2090. After thorough microscopic observations the three fossil woods were assigned to *Araucarioxylon*.

Nature of preservation of petrified woods—Although most of the petrified woods investigated in the present work were of silicified type, they were extremely well preserved in certain parts with lot of organic matter. Before sectioning the woods the different measurements of each wood like length, breadth and diameter were recorded as in Fig. 5. In certain cases where the specimens were very big, the woods were

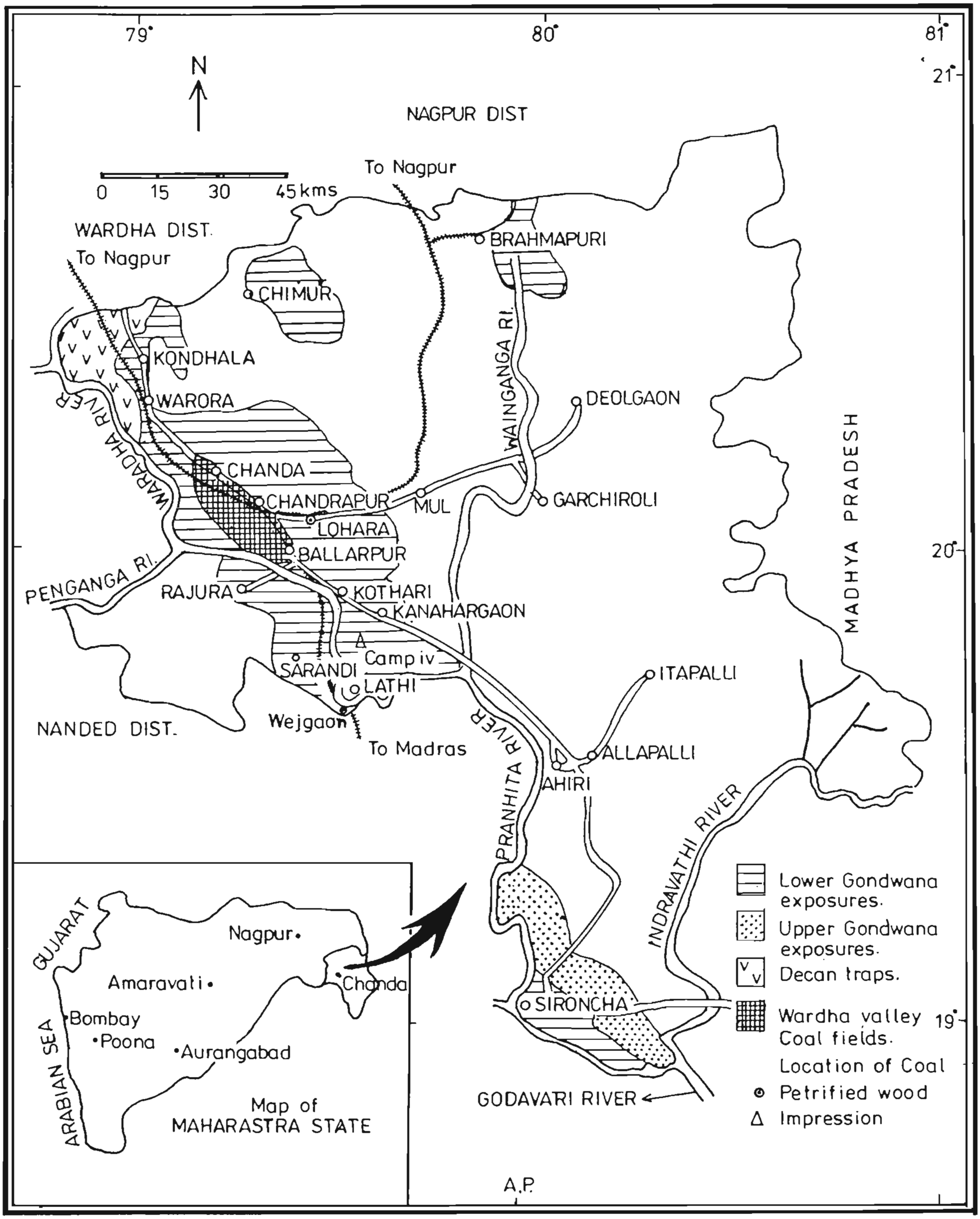

Fig. 1—Geological Map of Chandrapur District of the Maharashtra.

broken down into small pieces of convenient size using geological hammer. Only well preserved portion of the wood was selected for further sectioning and investigation. Usually woods which are brownish to blackish or part of the wood showing brownish to black colour were well preserved with lot of organic matter. After selecting the woods, several sections in different planes like T.S., T.L.S., R.L.S. were made by employing standard methods of sectioning by using Diamond saw cutting machine and later grinding and polishing the sections by using carborundum powder of grades no. 100 and 400 on grinding lap.

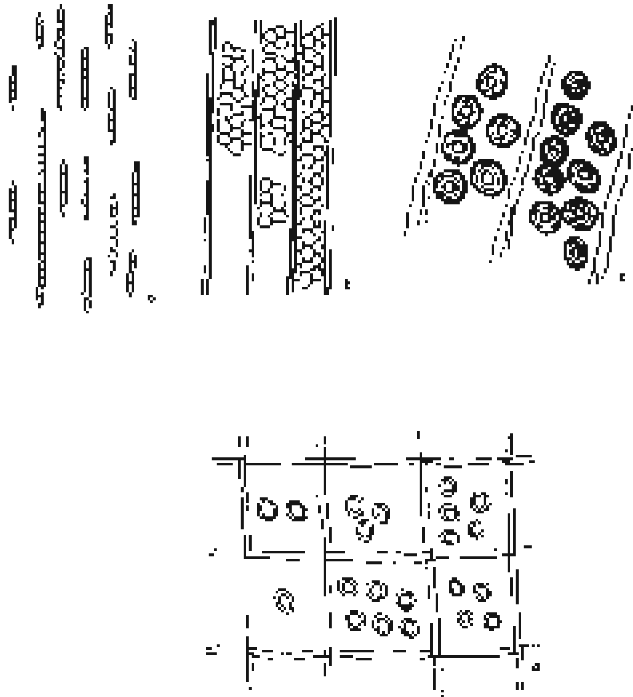

Fig. 2—*Araucarioxylon aravii* sp. nov.: a. T.L.S. showing medullary rays × 100, b. R.L.S. showing hexagonal biseriate alternate pits × 100, c. R.L.S. showing circular biseriate alternate and opposite pits × 250, d. Cross field showing two, three, four, five, six and single field pits × 250.

RESULT

Anatomical description of petrified woods—After detailed anatomical investigations and comparison, the woods were designated as the new species of *Araucarioxylon*. The detailed anatomical description of each petrified wood selected in present study along with some of the salient features of the genera to which they are assigned are given below.

Araucarioxylon is a commonly occurring genus of Lower Gondwana gymnospermous woods reported from India in general and Chandrapur District of Maharashtra in particular. It differs from *Dadoxylon* in the absence of a pith and primary xylem (Lepekhina, 1972). As far as we know, more than 51 species of *Araucarioxylon* occur in various parts of world, 15 of these species are reported from India.

Reports of the occurrence of *Araucarioxylon* species from Chandrapur District of Maharashtra are mainly due to the investigations of Agashe *et al.* (1972-1998) from Palaeobotany Research Laboratory, Department of Botany, Bangalore University, who described *A. indicum*, *A. suvarnum*, *A. kolhicense*, *A. kothariense*, *A. bhadravatiense*, *A. wejgaonense*. Nagvani and Rajo (1981) described *A. nagaloo* from Chandrapur District.

Emended generic diagnosis of *Araucarioxylon* (Kraus, 1870) emend Maheshwari (1972)

Growth rings distinct to absent, tracheidal radial pitting of araucarian type, usually multiseriate alternate, hexagonal, sometimes uniseriate and contiguous, cross field pits cupressoid, spiral thickening in tracheids are absent, xylem rays are uniseriate, partly biseriate.

ARAUCARIOXYLON ARAVII sp. nov.

Pl. 1. 1-8, Fig. 2

Specific Diagnosis—Decorticated secondary wood with distinct growth rings, rays 1-3 seriate, 2-15 cells high, 3 seriate rays being rare, tangential pits present, radial pits 1-3 seriate, araucarioid, cross-field pits 1-6 cupressoid.

Holotype—B.U.P.W. no. 2013 with slides deposited in Paleobotany and Palynology Laboratory, Department of Botany, Bangalore University, Bangalore.

Locality—Wegaon – Araviwada, Chandrapur District, Maharashtra, India.

Etymology—The present new species of wood has been described as *Araucarioxylon aravii* sp. nov., the specific epithet being derived from Araviwada from where the fossil wood was collected.

PLATE 1

Araucarioxylon aravii sp. nov.

1. Transverse section showing growth rings with early wood × 100.
2. Radial wall showing biseriate hexagonal alternate pits × 250.
3. Radial wall showing biseriate, partly triseriate hexagonal alternate bordered pits × 250.
4. Radial wall showing alternate, hexagonal biseriate pits × 250.
5. Radial wall showing circular biseriate alternate pits with elliptic pits in centre × 1000.
6. Radial wall showing circular, biseriate alternate pits × 1000.
7. Cross field showing two, three, five cupressoid field pits × 1000.
8. Cross field showing six cross field pits × 1000.

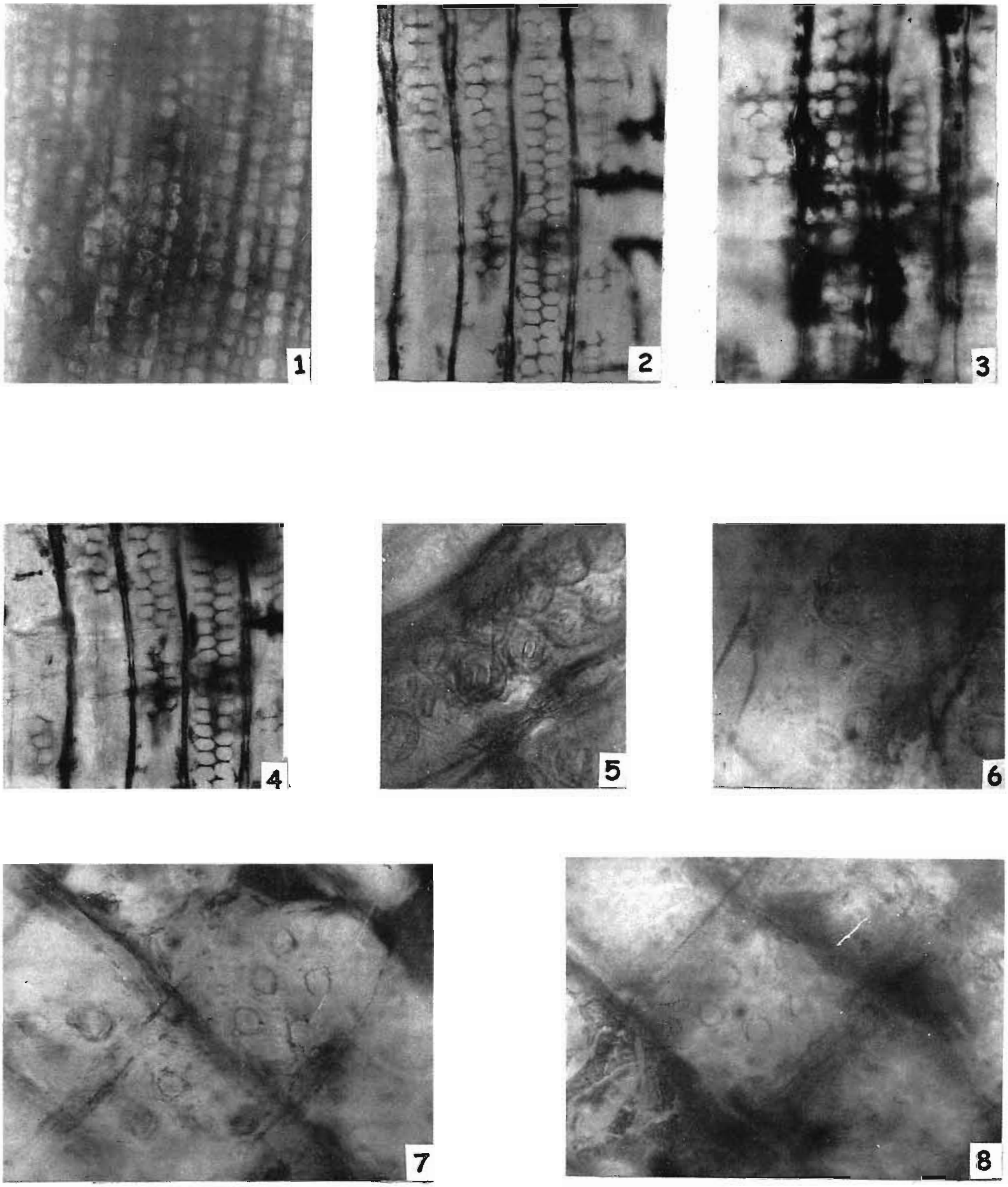

PLATE 1

Geological Age—Lower Gondwana (Permian).

On the basis of generic characters the present wood is assigned to *Araucarioxylon*, it is evident that the present wood belongs to a new species of *Araucarioxylon* as explained below.

Anatomical Description—The material consists of a decorticated secondary wood measuring 8 cm in length and 4 x 3.5 cm in thickness. In T.S. the secondary wood shows distinct growth rings (Pl. 1.1). The early wood tracheids are 120-180 cells thick and are mostly rectangular in shape. The tracheids of early wood measure 1.35 x 2.57 mm in size whereas late wood tracheids are comparatively narrower, squarish 4-5 cells thick measuring 0.16 x 0.28 mm in size.

Tangential longitudinal section shows the medullary rays which are 1-3 seriate, commonly uniseriate, 3 seriate rays being rare (Fig. 2a) and 2-15 cells high with average height of the rays being 5-8 cells. Tangential pits are distinct.

Radial longitudinal section reveals the radial pits which range from 1-3 seriate, mostly 2 seriate araucarioid, sometimes pits are found in groups of 2 or 3. The bordered pits are arranged in various manners. Biseriate and triseriate hexagonal pits are alternate or sub-opposite (Pl. 1.2-4; Fig. 2b). Biseriate circular pits are opposite, uniseriate (Pl. 1.5, 6; Fig. 2c), radial pits are contiguous. The bordered pits are circular as well as hexagonal with distinct border. The maximum diameter of bordered pit is 11.2 mm and shape of pit pore is spherical and diameter of pit pore is 4 mm. The cross field pits are 1-6 cupressoid, spherical – oval in shape, commonly 2-5 pits occur per field. The average diameter of cross field pit is 6.2 mm (Pl. 1.7, 8; Fig. 2d).

Discussion and Comparison–The petrified wood described above shows generic diagnostic characters of *Araucarioxylon* Kraus (1870), emend Maheshwari (1972) in having cupressoid cross-field pits and araucarioid radial pits.

The present specimen or B.U.P.W. no. 2018 differs from all the described species of *Araucarioxylon*, but resembles some species of *Araucarioxylon* in some of the anatomical characters. In having a maximum number of 6 cross-field pits the present specimen resembles *A. nandori* (Vagyani & Raju, 1981) and *A. wejgaoense* (Agashe & Shashi Kumar, 1996) but differs from the described species in medullary ray and radial wall pitting characters.

However, this new species of wood does not have any resemblance with *A. mohgaoensis* (Lakhanpal *et al.*, 1977) in cross-field pitting and medullary ray characters. The only similarity is in radial wall pitting. In both *A. mohgaoensis* and the present wood, the radial pits are 1-3 seriate mostly 2 seriate.

The present newly described wood differs from *A. kothariensis* (Agashe & Prasad, 1984) in radial wall pitting and cross-field pitting characters. In both *A. kothariensis* (Agashe & Prasad, 1984) and in *A. aravii* sp. nov. medullary ray is 1-3 seriate with the average height of 8 cells. The comparison of new species with all the described species of *Araucarioxylon* has been shown in comparative Fig. 5.

The present new species of wood has been described as *Araucarioxylon aravii* sp. nov., the specific epithet being derived from Aravi *nala* from where the fossil wood was collected.

ARAUCARIOXYLON CHANDRAPURENSIS sp. nov.

Pl. 2.1-9; Fig. 3

Specific Diagnosis—Decorticated secondary wood with distinct growth rings, 1-2 seriate medullary rays, mostly uniseriate, 2-36 cells high, tangential pits present, 1-3 seriate araucarioid radial pits, cross-field pits 1-7 cupressoid type.

Holotype—B.U.P.W. no. 2028 along with slides deposited in Paleobotany and Palynology Laboratory, Department of Botany, Bangalore University, Bangalore.

Locality—Wejgaon – Aravi *nala*, Chandrapur District, Maharashtra, India.

Etymology—The present wood is described as a new species of *Araucarioxylon, A. chandrapurensis* sp. nov., the specific name is given after Chandrapur District, from where the wood is collected.

Geological Age—Lower Gondwana (Permian).

On the basis of generic characters the present wood is assigned to *Araucarioxylon*. It is evident that the present wood belongs to a new species of *Araucarioxylon* as explained below.

Anatomical Description—The material consists of decorticated secondary wood measuring 10.4 cm in length and 5.2 x 4.9 cm in thickness with distinct growth rings. In T.S. the growth rings are clear (Pl. 2.1). The early wood tracheids are 80-120 cells thick and rectangular in shape. The tracheids of early wood measure 2.20 x 2.62 mm in size, whereas late wood tracheids are comparatively narrower, 2-4 cells thick measuring 0.14 x 0.46 mm in size.

PLATE 2 ⟶

Araucarioxylon chandrapurensis sp. nov.

1. Transverse section showing growth rings with early wood. x 100.
2. TLS showing uniseriate and biseriate medullary rays. x 100.
3. Cross field showing one, two, three, four cross field pits. x 250.
4. RLS showing hexagonal biseriate, triseriate alternate radial pits. x 250.
5. Cross field showing two, three cupressoid pits. x 250.
6. Cross field showing two, three, four, five, circular oval pits. x 250.
7. Cross field showing two, four, five, seven cupressoid field pits. x 250.
8. Cross field showing three, four, five, seven cupressoid field pits. x 250.
9. Cross field showing two, three, four field pits. x 250.

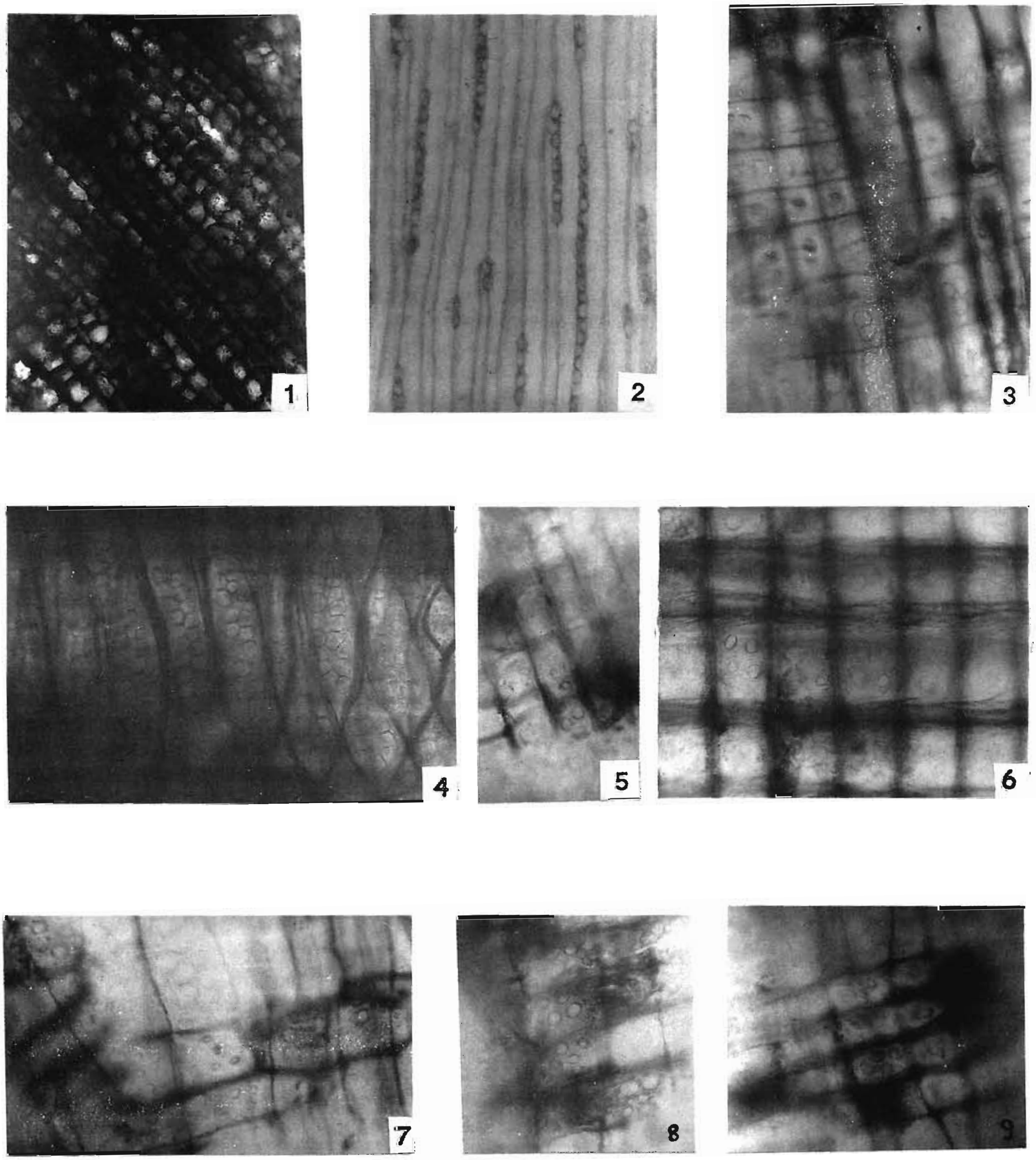

PLATE 2

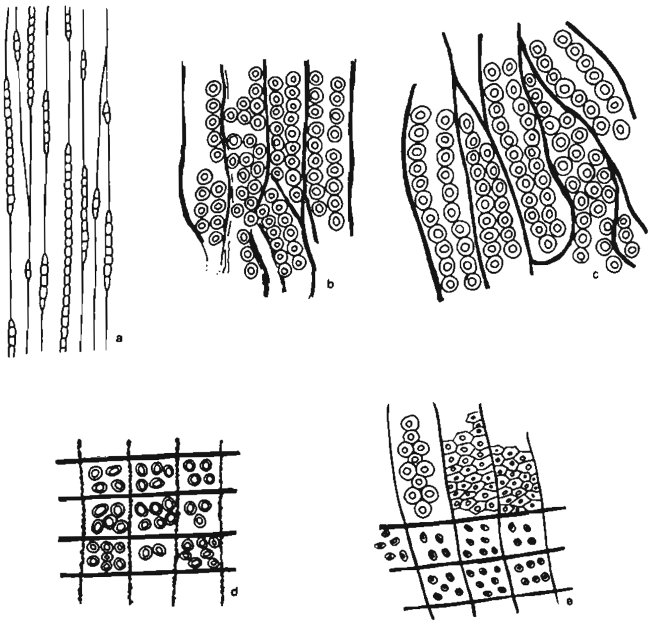

Fig. 3—*Araucarioxylon chandrapurensis* sp. nov. **a**. T.L.S. showing uniseriate medullary rays. x 100. **b**. R.L.S. showing uniseriate, biseriate and triseriate circular alternate pits. x 250. **c**. R.L.S. showing uniseriate, biseriate, triseriate circular alternate and opposite pits. x 250. **d**. Cross field showing two, three, four, five, six and seven field pits. x 400. **e**. RLS showing uniseriate/ partly biseriate circular pits and three-four seriate hexagonal alternate pits and cross-field showing four, five, six and seven field pits. x 250.

Tangential longitudinal section shows medullary rays which are 1-2 seriate, mostly uniseriate 2-36 cells high on an average height of 15 cells. Tangential pits are distinct (Pl. 2.2; Fig. 3a).

Radial longitudinal section reveals the radial pits which are 1-3 seriate, araucarioid mostly 2 seriate with distinct pit pore in centre. Radial pits are arranged in various manner. Biseriate circular pits are alternate or sub-opposite, but biseriate circular pits are oppositely placed in some areas. Triseriate circular pits are alternately placed. Uniseriate pits are contiguous, while biseriate and triseriate hexagonal pits are alternate (Pl. 2.4; Figs 3b, c, e). The maximum diameter of radial pit is 10 mm and that of pit pore is 3.84 mm. The cross-field pits are 1-7 cupressoid, spherical, oval, commonly 2, 4, 5 pits occur per cross field (Pl. 2.3, 5-9; Figs 3d, e).

Discussion and Comparison—The petrified wood B.U.P.W. no. 2028 is assigned to *Araucarioxylon*, as it shows the diagnostic characters of *Araucarioxylon* by having cupressoid cross-field pits and araucarioid radial wall pits. The present specimen differs from all the described species of *Araucarioxylon* by having a maximum number of seven cross field pits, but it resembles few described species of *Araucarioxylon* in other anatomical characters.

The new Araucarian wood resembles *A. mohgaoensis* (Lakhanpal *et al.*, 1977) in medullary ray and radial wall pitting characters, but differs from *A. mohgaoensis* (Lakhanpal *et al.*, 1977) in cross-field pitting characters. In new species of wood and *A. mohgaoensis* (Lakhanpal *et al.*, 1977), medullary ray is uniseriate 2-36 cells high, the average height of the ray is 8-15 cells. Radial wall pits 1-3 seriate, mostly 2 seriate, contiguous alternate. The new species of fossil wood resembles *A. surangei* (Agashe *et al.*, 1981), *A. nandori* (Vagyani & Raju, 1981), *A. bhivkundense* (Agashe & Prasad, 1984), *A. wejgaoense* (Agashe & Shashi Kumar, 1996) in medullary ray characters, but differs from all the four species of *Araucarioxylon* in radial pitting and cross-field pitting characters. The new species of Araucarian wood and *A. nandori* (Vagyani & Raju, 1981), *A. surangeii* (Agashe *et al.*, 1981), *A. bhivkundense* (Agashe & Prasad, 1984), *A. wejgaoense* (Agashe & Shashi Kumar, 1996) resemble each other in having 1-2 seriate medullary ray mostly uniseriate 2-35 cells high on an average height of the ray is 8-15 cells. The comparison of new species of wood with all the described species of *Araucarioxylon* prompted us to describe the present wood as a new species of *Araucarioxylon* as shown in comparison Fig. 5.

ARAUCARIOXYLON SHAILAE sp. nov.

Pl. 3.1-10; Fig. 4

Specific Diagnosis—Decorticated secondary wood with distinct growth rings, 1-2 seriate mostly uniseriate, 2-46 cells high medullary rays, tangential pits are distinct, 1-3 seriate araucarioid radial pits, 1-8 cupressoid cross-field pits.

Holotype—B.U.P.W. no.: 2090 along with slides deposited in Paleobotany and Palynology Laboratory, Department of Botany, Bangalore University, Bangalore.

Locality—Wejgaon Village, Chandrapur District, Maharashtra, India.

PLATE 3 ⟶

Araucarioxylon shailae sp. nov.

1. Transverse section showing growth rings with early wood tracheids. x 100.
2. TLS showing uniseriate and biseriate radial pits. x 250.
3. TLS showing uniseriate and biseriate medullary rays and tangential pits. x 400.
4. RLS showing uniseriate and biseriate circular radial pits biseriate radial pits are opposite, uniseriate / partly biseriate pits are opposite. x 1000.
5. RLS showing biseriate circular radial pits in groups of 2, 3, 4 and uniseriate circular contiguous pits. x 250.
6. RLS showing biseriate circular opposite pits. x 250.
7. RLS showing 3, 5 cupressoid cross field pits. x 1000.
8. RLS showing 2, 4 circular cupressoid cross field pits. x 250.
9. RLS showing 2, 4, 6 circular cupressoid cross field pits. x 400.
10. RLS showing 4 circular cupressoid cross field pits. x 1000.

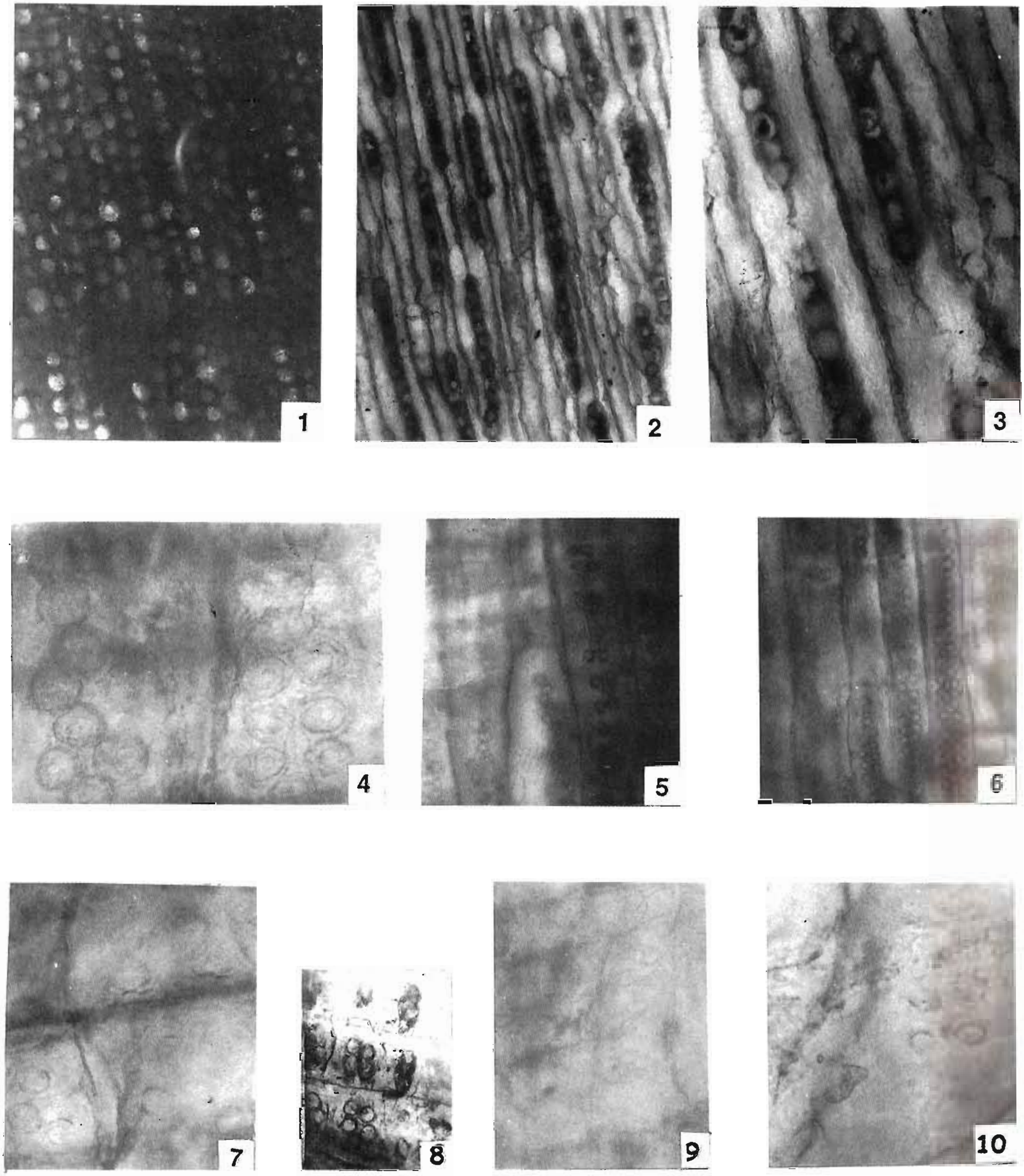

PLATE 3

Sl. No.	Name of the Genus & Species	Geological Age	Growth ring	Medullary ray	Tangential pits	Border pitting on radial walls	Cross field pits	Locality
1.	*A. arberi* (Seward, 1919) comb. nov. Maheshwari 1972	Upper Carboniferous	Distinct	1-21 cells high, usually 6-12 cells high	Absent	1-4 seriate, circular	1-10 oblique	Australia
2.	*A. manieroi* (Krausel & Dolianiti, 1958) comb. nov. Maheshwari 1972	Upper Carboniferous	Distinct	1-47 cells high, on an average of 9-10 cells high	Absent	1-4 seriate, pore elliptical	1-9, sometimes in groups	Brazil
3.	*A. mohgaoensis* Lakhanpal *et. al.*, 1977	Early Tertiary	Distinct	Uniseriate, 2-30 cells high, mostly 8-15 cells	Absent	1-3 seriate, mostly 2 seriate, contiguous alternate / hexagonal	1-2 bordered, cupressoid, circular-oval in shape	Mohgaon - Kalan Chindwara Dist., M.P.
4.	*A. gondwanense* (Maithy, 1964) comb. nov. Maheshwari 1972	Lower Permian	Distinct	13% rays are 2 seriate. 1-43 cells high, average of 9-10 cells high	Absent	1-5 seriate, alternate / sub opposite	2-8 contiguous / separate, circular - oval in shape	Jharia C.F. (Bihar)
5.	*A. parbeliense* (Rao, 1935) comb. nov Maheshwari 1972	Permian	Distinct	1-24 cells high, mostly 2-3 cells high	Absent	1-5 seriate, pore circular - oval	8-9 bordered, pores oblique slit like	Parbelia colliery, Bengal
6.	*A. loharense* Agashe & Gowda, 1978	Permian	Distinct	1-2 seriate, 2-27 cells high, on an average height of 11 cells high	Present	1-4 seriate, round - hexagonal with distinct border	2-9, most commonly 2, 4, 6 pits / field	Lohara, Chandrapur, M.S.
7.	*A. lathiense* Agashe *et al.*, 1981	Permian	Distinct	Uniseriate, 1-27 cells high on an average height of 5 cells	Absent	1-4 seriate, alternate / separate, contiguous	1-10 cupressoid, circular-oval with thin border	Lathi, Chandrapur, M.S.
8.	*A. surangeii* Agashe *et al.*, 1981	Permian	Distinct	1-2 seriate, commonly 1 seriate, 1-35 cells on an average of 4 cells high	Present	1-4 seriate alternate, separate contiguous hexagonal	1-11 cupressoid, commonly 2, 4 round-oval	Lathi, Chandrapur, M.S.
9.	*A. nandori* Vagyani & Raju, 1981	Upper Permian	Distinct	1-2 seriate, mostly uniseriate 2-30 cells high	Absent	1- multiseriate, free contiguous / hexagonal	2-6, cupressoid	Nandori, Chandrapu: M.S.
10.	*A. bhivkundense* Agashe & Prasad, 1984	Permian	Distinct	1-2 seriate free, 1-33 cells high with an average height of 8 cells	Present	1-2 seriate free / contiguous sometimes in groups of 2, 3, 4	1-8 cupressoid, commonly 2, 4 pits occur / field	Bhivkund, Chandrapur, M.S.

11	*A. kothariensis* Agashe & Prasad, 1984	Permian	Distinct	1-3 seriate, 1-44 cells high with an average height of 8 cells	Present	1-4 seriate, araucarioid free / contiguous radial pits in groups of 2, 3, 4	1-12 cupressoid, with thin border commonly 4-8 field pits occur / field	Wejgaon, Chandrapur, M.S.
12.	*A. semibiseriatum* Pant & Singh, 1987	Permian	Distinct	Uniseriate or partly biseriate, 1-24 cells high, rarely up to 38 cells on an average height of 2-9 cells	Present	1-4 seriate, rarely 5 seriate, circular/oval pits, contiguous, sub-opposite or alternate pits	4-16 cupressoid, usually 6-12 pits occur / field	Raniganj Coalfield
13.	*A. wejgaoense* Agashe & Shashi Kumar, 1996	Permian	Distinct	1-2 seriate free, 2-34 cells high, with an average height of 8-12 cells, mostly uniseriate	Present	1-2 seriate, mostly 2 seriate contiguous / alternate sub-opposite may be in groups of 2, 3, 4	1-6 cupressoid, commonly 2-4 pits occur / field	Wejgaon, Chandrapur, M.S.
14.	*A. aravii* sp. nov. Agashe & Shashi Kumar, 1998	Permian	Distinct	1-3 seriate, uniseriate condition is common, 2-15 cells on an average height of 5-8 cells	Absent	1-3 seriate, araucarioid, hexagonal, alternate, bars of sanio seen, mostly hexagonal, biseriate pits are alternate	1-6 cupressoid, circular-oval, commonly 3 pits occur / field	Wejgaon, Chandrapur, M.S.
15.	*A. chandrapurensis* sp. nov. Agashe & Shashi Kumar, 1998	Permian	Distinct	1-2 seriate, mostly uniseriate, 2-36 cells high on an average of 15 cells	Present	1-3 seriate, araucarioid mostly 2 seriate with distinct lumen in center. Circular-hexagonal. 2 seriate pits are alternate / sub-opposite	1-7 cupressoid, commonly 2, 4, 5 pits occur commonly / field	Wejgaon, Chandrapur, M.S.
16.	*A. shailae* sp. nov. Agashe & Shashi Kumar, 1998	Permian	Distinct	1-2 seriate, mostly uniseriate, 2-46 cells high on an average height of 20 cells, uni - 60% bi - 40%	Distinct	1-3 seriate araucarioid, mostly 2 seriate uniseriate circular pits are contiguous, biseriate circular pits are oppositely placed, 3 seriate pits are also alternately placed / oppositely place 2 seriate hexagonal pits are alternately placed	1-8 cupressoid, circular, commonly 2, 4, 5 pits occur / field	Wejgaon, Chandrapur, M.S.

Fig. 5—Comparative anatomical characters of different species of *Araucarioxylon*.

Geological Age—Lower Gondwana (Permian).

Etymology—The present wood is described as a new species of *Araucarioxylon, A. shailae* sp. nov., the specific epithet is given in honour of Dr Shaila Chandra, Palaeobotanist at the Birbal Sahni Institute of Palaeobotany, Lucknow, for her significant work on Lower Gondwana megafossils.

On the basis of generic characters the present wood is assigned to *Araucarioxylon*, it is evident from the present characters, the wood belongs to new species of *Araucarioxylon* as explained below.

Anatomical Description—The material consists of decorticated secondary wood measuring 7 cm in length and 5·8 x 3 cm in thickness showing distinct growth rings (Pl. 3·1). The early wood tracheids are 40-80 cells thick, they are rectangular in shape. The early wood tracheids measure 0·5 x 2·0 mm in size, whereas late wood tracheids are 2-4 cells thick measuring 0·075 x 0·125 mm in size.

Tangential longitudinal section shows medullary rays which are 1-2 seriate, mostly uniseriate, 2-46 cells high with an average height of 20 cells. Uniseriate medullary rays represent 60% and biseriate medullary rays are represented by 40% of total rays. Tangential pits are distinctly circular, contiguous (Pl. 3.2, 3; Figs 4a, b).

Radial longitudinal section reveals the radial pits which are 1-3 seriate, mostly 2 seriate, araucarioid with distinct pit pore in the centre. Radial pits are arranged in various manners. The uniseriate circular pits are contiguous, biseriate; triseriate circular pits are alternately placed. Sometimes radial pits are found in groups (Pl. 3.4-6; Figs 4c-e). The maximum diameter of radial pit is 10·27 mm and shape of the pit pore is spherical and diameter of pit pore is 4 mm. The cross-field pits are 1-8 cupressoid, circular, 2, 4, 5 pits occur/field. The average diameter of cross-field pits is 6·7 mm (Pl. 3·7-10; Figs 4f, g).

Discussion and Comparison—The petrified wood described above shows generic diagnostic characters of *Araucarioxylon* by having cupressoid cross-field pits and araucarioid radial wall pits. The present specimen differs from all the described species of *Araucarioxylon*, but resembles some species of *Araucarioxylon* in certain anatomical characters.

The new araucarian road closely resembles *A. manieroi* (Krausel & Dolianiti, 1958 ; comb. nov. Maheshwari, 1972) in medullary ray characters, but differs from it in other anatomical characters (radial wall pitting and cross-field pitting characters). In both *A. maneroi* and the present wood medullary rays are 2-46 cells high.

The present wood also resembles *A. mohgaoensis* (Lakhanpal *et al.*, 1977) in radial wall pitting characters but differs from *A. mohgaoensis* (Lakhanpal *et al.*, 1977) in other anatomical characters. In both *A. mohgaoensis* and present wood radial pits are 1-3 seriate.

In both *A. bhivkundense* (Agashe & Prasad, 1984) and present wood similarity in cross-field pitting is seen, but it differs in other anatomical characters. In both *A. bhivkundense* (Agashe & Prasad, 1984) and present wood cross-field pits are 1-8 cupressoid.

Although present wood resembles some species of *Araucarioxylon* as discussed above, but it differs from all the described species of *Araucarioxylon* in medullary ray, radial wall pitting and cross-field pitting characters. Hence this wood is described as a new species of *Araucarioxylon* as shown in Fig. 5.

DISCUSSION

Paleobotanical exploration of Maharashtra which was carried out during the past 5-6 years has brought to light several new fossil bearing localities suggesting strongly the existence of highly diversified flora during the Lower Gondwana Period. The real picture of past vegetation may be reconstructed by studying the organic remains of the plants in various forms. Petrified plant material forms the best evidence of the past plant life because of the varied anatomical characters which can be studied from it.

The secondary xylem is very well preserved in all the three species of fossil woods. Pith, primary xylem or cortical tissues are not preserved properly. The xylotomical studies of

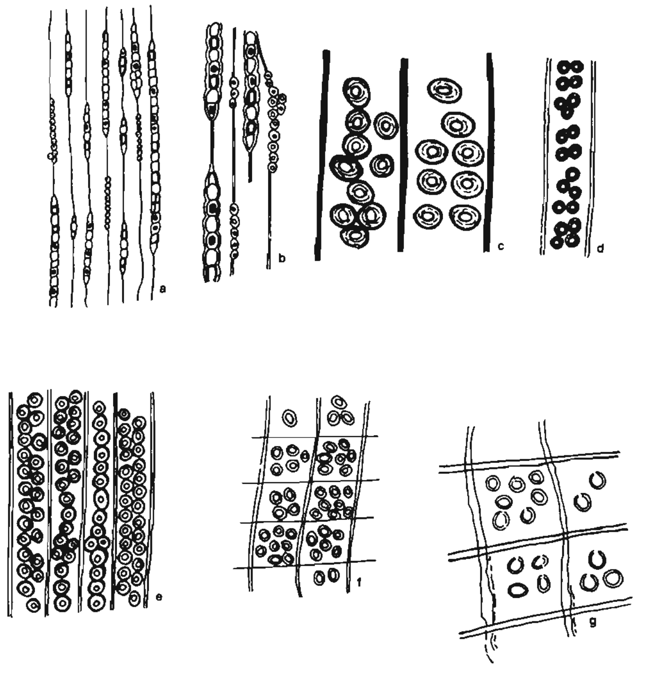

Fig. 4—*Araucarioxylon shailae* sp. nov. **a**. T.L.S. showing uniseriate and biseriate medullary rays. x 100. **b**. T.L.S. showing uniseriate medullary rays and tangential pitting. x 250. **c**. R.L.S. showing circular biseriate opposite pits and pits in groups of two and three. x 400. **d**. R.L.S. showing circular biseriate opposite pits in groups of two, three and four. x 100. **e**. R.L.S. showing uniseriate contiguous pits and biseriate alternate pits. x 250. **f**. Cross field showing one, two, three, four, five, six, seven and eight field pits. x 250. **g**. Cross field showing two, three, four, seven field pits. x 400.

woods from Wejgaon and Wejgaon-Arasi nalas exhibit remarkable resemblance. These woods were characterised by distinct growth rings uniseriate to biseriate nature of rays (uniseriate being most common), Uniseriate to multiseriate border pits which are mostly typically araucarioid type in nature i.e., horizontally compressed and hexagonal arranged in groups and cupressoid cross field pits with thin borders. On account of the presence of these characters all the three species of fossil woods have been assigned to genus *Araucarioxylon* Kraus. However, these three woods differ from each other in characters such as thickness and height of medullary rays and number of cross-field pits and hence differs from all the described species of *Araucarioxylon*. The occurrence of these three new species of *Araucarioxylon* and also *A. latiporosum*, *A. surangei*, *A. jalnaense*, *A. bhandakense*, *A. kothariensis* and *A. wejgaonense* by Agashe *et al.* (1978-1997) from Lower Gondwana Horizon of Chandrapur District suggests that *Araucarioxylon* was rather a well established conifer in Chandrapur District during the Lower Gondwana Period. This discovery of 3 new species of *Araucarioxylon* adds to the diversity of gymnospermous vegetation of Lower Gondwana.

Acknowledgements—*We are thankful to the Department of Science and Technology for financial assistance to the major research scheme entitled "Macrofossil investigation of Lower Gondwana Strata occurring in Maharashtra" during which the above work was carried out. Assistance of Dr P R N Gowda and Mr K P Nagaraj in collection of material and Dr Mary Sesidha J G and Dr Mini Susan Philip in preparation of manuscript and Mr Indukar P in preparation of photographic plates are gratefully acknowledged.*

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Fossil wood of *Dryobalanops* from Pliocene deposits of Indonesia

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ABSTRACT

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The present paper gives a detailed account of anatomical features of petrified wood showing affinities with the modern genus *Dryobalanops* Gaertn.f. of the family Dipterocarpaceae. The fossil wood was found as a big tree trunk in volcanic sediments near Bogor, West Java (Indonesia). The distribution of extant *Dryobalanops* is restricted to tropical evergreen rain forests of Malaysia and Indonesia (Sumatra & Borneo). Today it is absent in the natural forests of Java, although the broad climatic setting has not changed much since Pliocene times. Reasons for its absence in the island are discussed.

Key-words—Anatomy, petrified wood, *Dryobalanops*, Dipterocarpaceae, Pliocene, Java (Indonesia).

इण्डोनेशिया के प्लायोसीन निक्षेपों से प्राप्त ड्रायोबैलेनॉप्स का अश्मित काष्ठ

रश्मि श्रीवास्तव एवं नोरिको कागेमोरी

सारांश

प्रस्तुत शोध-पत्र में डिप्टेरोकार्पेसी कुल के *ड्रायोबैलेनॉप्स* गार्टेन. एफ. नामक आधुनिक वंश के साथ सादृश्यता प्रदर्शित करने वाली अश्मीभूत काष्ठ के शारीरीय गुणों का विस्तृत विवेचन किया गया है। यह अश्मित काष्ठ इण्डोनेशिया के पश्चिमी जावा में बोगोर के समीपस्थ स्थल के ज्वालामुखीय अवसादों में स्थित एक बड़े वृक्ष स्तम्भ से प्राप्त किया गया है। विद्यमान *ड्रायोबैलेनॉप्स* का वितरण मलेशिया एवं इण्डोनेशिया (सुमात्रा तथा बोर्नियो) के ऊष्णकटिबन्धीय सदाहरित वृष्टिमय जंगलों में सीमित है। यद्यपि प्लायोसीन कल्प से लेकर आज तक यहाँ के जलवायुविक रुझानों में बहुत अधिक परिवर्तन नहीं हुए हैं, तथापि वर्तमान में यह जावा के प्राकृतिक वनों में अनुपस्थित है। प्रायद्वीप में इसकी अनुपस्थिति के कारणों का समुचित विवेचन भी इस शोध-पत्र में किया गया है।

संकेत शब्द—शारीरविज्ञान, अश्मीभूत काष्ठ, *ड्रायोबैलेनॉप्स*, डिप्टेरोकार्पेसी, प्लायोसीन, जावा (इंडोनेशिया).

INTRODUCTION

SOUTHEAST Asia is of special interest for botanists dealing with antiquity and evolution of angiosperm floras. Plant megafossils are reported from the Cenozoic sediments of Southeast Asian countries like Myanmar (Prakash, 1973; Prakash & Bande, 1980), Thailand (Endo, 1963; Prakash, 1979; Vozenin-Serra & Privé-Gill, 1989; Vozenin-Serra *et al.*, 1989), Cambodia (Boureau, 1950, 1950a,1952); Malaysia (Warburg, 1897) and Vietnam (Boureau, 1950, 1950a, 1952; Vozenin-Serra, 1981). From Indonesia (Java, Sumatra, Borneo, Ciram and other islands) a large number of fossil leaves and wood were reported by many workers, namely, Göppert (1854); Heer (1876); Gayler (1875, 1887); Crie (1888); Den Berger (1923, 1927); Tobler (1923); Kräusel (1926); Edwards (1931); Schweitzer (1958); Kramer (1974a, b); Sukiman (1977); Vozenin-Serra (1980).

In a comprehensive review of the Tertiary flora of Southeast Asia, Bande and Prakash (1986) gave an almost complete list of fossil records with remarks on phytogeography, migration and palaeoenvironment of the Indo-Malaysian region. In the present paper, present status of diperocarps in Indonesia and probable reasons for disappearance of *Dryobalanops* along with few other members from the natural forests of Java are being discussed.

MATERIAL AND METHODS

Indonesia is an archipelago in the Indian and Pacific oceans across the equator off the coast of Southeast Asian mainland. The fossil wood reported here was collected from Pliocene volcanic sediments of Leuwiliang, about 20 km westward from Bogor, in Western Java, Indonesia. (Fig. 1). The fossil is a piece of a tree trunk measured 60 cm long and 66 x 43 cm in diameter. The preservation is good showing all the xylotomical characters.

Sections of the fossil wood in transverse, tangential-longitudinal and radial-longitudinal planes were cut and ground to obtain thin sections. A few peel sections were also prepared by etching the surface of the fossil wood with Hydrofloric Acid and then after thorough washing cellulose acetate film was placed on it. The fossil wood and microscopic slides are deposited in the Xylarium of the Wood Research Institute, Kyoto University, Uji, Kyoto, Japan. For identification of the fossil wood, slides of extant species of *Dryobalanops* present in the Xylaria of Birbal Sahni Institute of Palaeobotany, Lucknow, India and Forest Research Institute, Dehradun, India were examined carefully.

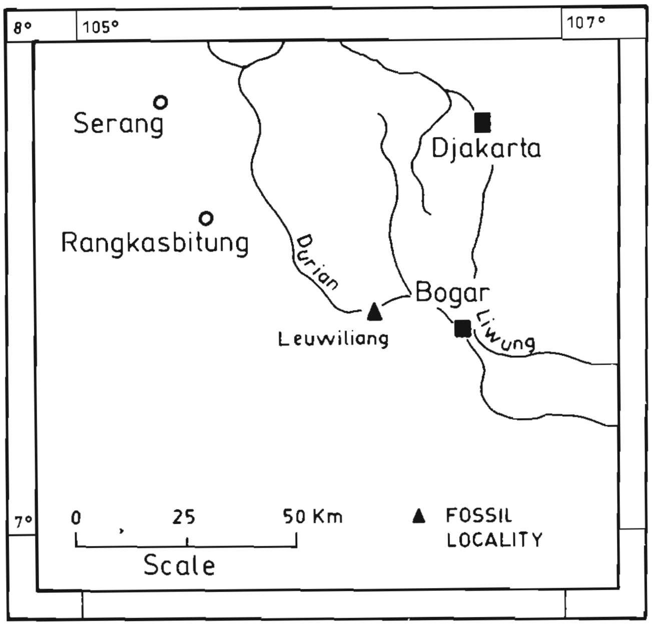

Fig. 1—Map of Bogor, West Java showing fossil locality.

SYSTEMATICS

DICOTYLEDONS

Family—DIPTEROCARPACEAE

Genus—DRYOBALANOXYLON Den Berger, 1923

DRYOBALANOXYLON BOGORENSE sp. nov.

(Pl. 1.1-6)

Description—Wood diffuse porous (Pl. 1.1). *Growth rings* absent (Pl. 1.1). *Vessels* evenly distributed, 3-4 per sq mm; almost exclusively solitary, rarely in radial or oblique pairs, round to oval in cross-section (Pl. 1.1); medium to large, tangential diameter 120-286 (average 203) mm, radial diameter 165-336 (average 250) mm; tyloses commonly present (Pl. 1.4); vessel elements 308-572 (average 500) mm long; end walls transverse to oblique (Pl. 1.2); perforation plates simple; intervessel pits not observed. *Parenchyma* both paratracheal and apotracheal; paratracheal vasicentric to aliform forming 2-3 cells thick sheath which extends laterally joining 2-3 vessels (Pl. 1.1); apotracheal associated with vertical gum canals forming 2-4 cells thick sheath or bands encircling gum canals (Pl. 1.1); each cell 32-36 mm in diameter and 90-164 mm long; ? silica-like particles present in parenchyma cells (Pl. 1.6). *Vasicentric tracheids* present, intermingled with vasicentric parenchyma, bordered pits present in double rows in tangential and radial walls. *Fibre tracheids* constitute ground mass of the wood, polygonal or rectangular in cross-section, 30-40 mm in diameter, walls 7-8 mm thick; nonseptate, single row of small bordered pits present (Pl. 1.2, 3). *Gum canals* vertical; normal; smaller than the vessels; forming tangential rows; embedded or encircled in 2-3 cells thick apotracheal parenchyma bands (Pl. 1.1) ; 33-100 mm in tangential diameter and 55-130 mm in radial diameter. *Rays* 1-6 seriate,

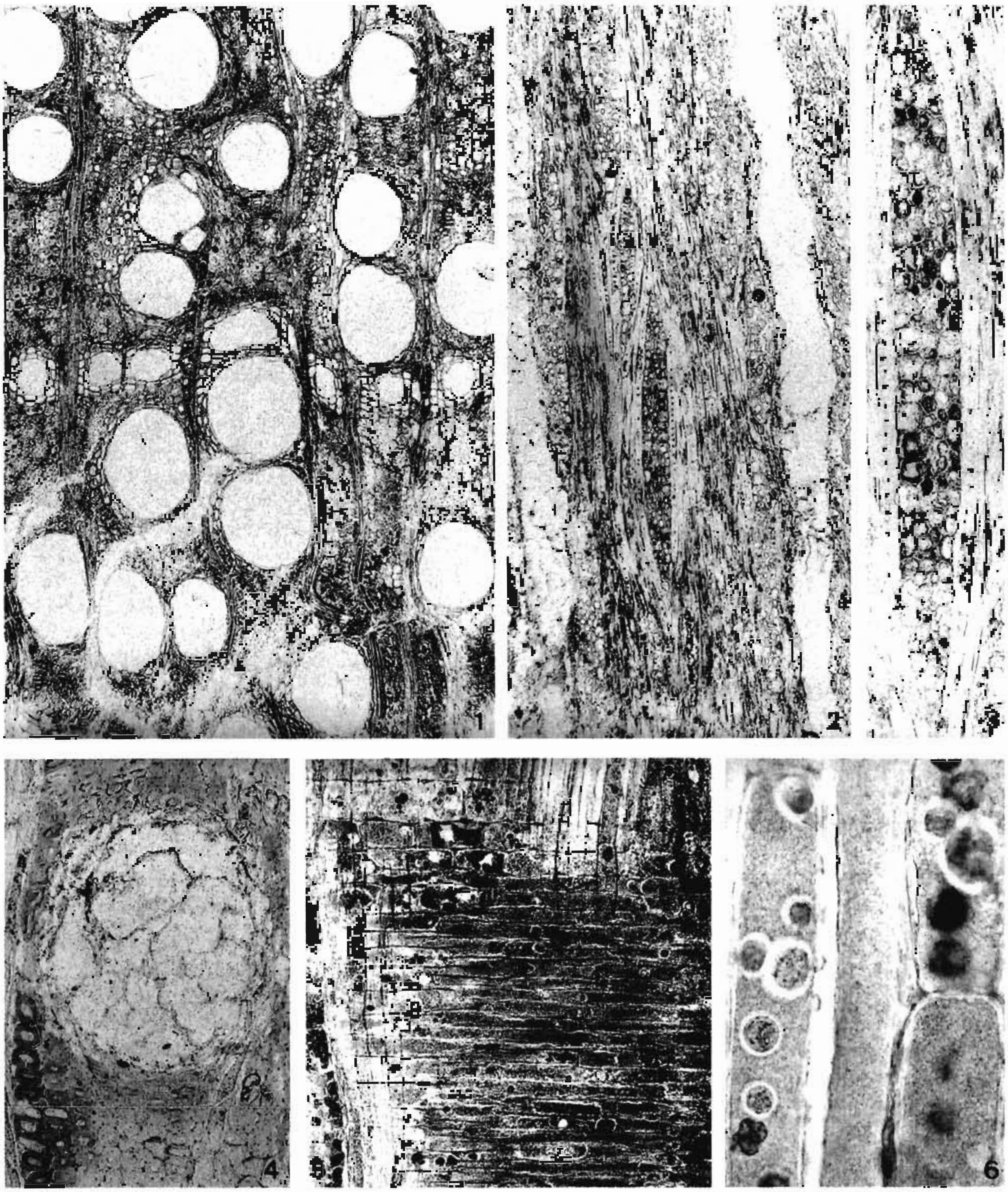

PLATE 1

[illegible] sp. nov.

1. Cross section of fossil wood showing distribution of vessels, parenchyma and vertical gum canals. × 5.
2. Tangential longitudinal section showing distribution of rays and fibre tracheids. × 31.
3. Same section magnified showing multiseriate ray and pits on fibre tracheids. × 125.
4. Cross section magnified showing tylosed vessels. × 125.
5. Radial longitudinal section showing heterocellular rays and vessel-ray pits. × 125.
6. Tangential longitudinal section showing oil-cell-like particles in parenchyma cells. × 315.

heterocellular composed of both upright and procumbent cells (Pl. 1.5); uniseriate rare, composed of upright cells only; multiseriate made up of procumbent cells in the centre with 1-4 marginal row of upright cells at one or both the ends, 11-50 cells or 500-1500 mm tall; upright cells 38-51 mm in both tangential height and radial length, procumbent cells 16-38 mm in tangential height and 83-115 mm in radial length; vessel ray pits simple, many per cell; ? gummy infiltration or some deposit present in ray cells (Pl. 1.2, 3, 5).

Holotype—Specimen no. KYO F2, Wood Research Institute, Kyoto University, Kyoto, Japan.

Locality—Leuwiliang, about 20 km from Bogor, West Java, Indonesia.

Age—Pliocene.

Etymology—Specific name is after Bogor, a place in west Java where fossil locality is situated.

Number of specimen examined—One large piece of petrified wood.

Affinities—The presence of normal vertical gum canals in tangential rows, medium to large, almost exclusively solitary vessels occluded with tyloses, heterocellular rays, vasicentric tracheids and fibre tracheids clearly indicate affinity of the present fossil with the woods of Dipterocarpaceae, particularly with the genera *Balanocarpus*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Isoptera*, *Parashorea*, *Pentacme* and *Shorea* (Metcalfe & Chalk, 1950; Desch, 1957; Chowdhury & Ghosh, 1958; Hayashi *et al.*, 1972; Lin, 1991). However, the presence of exclusively solitary vessels or nearly so and thick-walled fibre tracheids with distinctly bordered pits shows close similarity with the genus *Dryobalanops* and differentiate it from rest of the genera. In order to find out nearest modern counterpart of the fossil, a detailed comparison with thin sections as well as published descriptions and photographs of modern woods of *Dryobalanops*, namely, *D. aromatica* Gaertn. f., *D. beccarii* Dyer PS, *D. lanceolata* Burck, *D. keithii* Symington, *D. oblongifolia* Dyer, *D. rappa* Becc. was made. The fossil wood shows gross resemblance with all these species. In *D. aromatica* the size of vessels, tyloses and parenchyma pattern matches the fossil wood, however, in a few modern specimens ripple marks are present due to storied nature of rays while in others rays are not storeyed (Desch, 1957, p.194). Among the examined species, in *D. beccarii* (BSIP W 2112) the vessels and rays are slightly smaller than the present fossil wood while in *D. lanceolata* (BSIP W 1497) the vessels are larger and tyloses are more frequent. In *D. keithii* (BSIP W 2420) the rays are taller than the fossil while in other specimens of the same species (BSIP W 2105) the vessels are larger, apotracheal diffuse parenchyma in greater amount and rays are taller than the wood under consideration. In *D. oblongifolia* the vessels are larger, tyloses less developed and rays are broader. *D. rappa* (BSIP W 2356) differs in having less developed tyloses and vessels in pairs are frequent with some solitary ones.

Comparison with fossil species—Den Berger (1923) instituted the genus *Dryobalanoxylon* for the fossil woods showing resemblance with modern *Dryobalanops* Gaertn. f. So far three species have been reported from the Neogene of India and 13 species are reported from Neogene and Quaternary deposits of Southeast Asia (Fig. 2). *Dryobalanoxylon bangladense* differs from the present fossil wood in having large amount of apotracheal parenchyma and homocellular, 1-5 (mostly 3) seriate rays ranging from 4-70 cells in height, while in *Dryobalanoxylon* cf. *bangladense* parenchyma is less abundant and rays are up to 10 seriate. *D. holdenii* has 1-4 seriate rays with occasional occurrence of sheath cells. Vessel size and parenchyma pattern matches with the present fossil wood. In *D. indicum* the rays are taller (up to 90 cells or 1900 mm) and have uniseriate extensions of 1-15 upright cells at both the ends. In *D. javanicum* the vessels are slightly smaller (t.d. 125-225 mm, r.d. 125-275 mm) and rays are 2-9 (mostly 4-5) seriate. *D. borneense* differs in having less amount of paratracheal vasicentric parenchyma. In *D. kachinense* vessels are smaller (t.d. 100-200 mm) and rays are broader and shorter (1-8 seriate; up to 700 mm long). *D. mirabile* differs in having smaller vessels (t.d. 75-175 mm, r.d. 100-275 mm), homocellular rays and large gum canals (t.d. 60-200 mm). In *D. marginale* also the vessels are smaller (t.d. 60-200 mm, r.d. 60-150 mm) and xylem rays are 1-4 (mostly 2-3) seriate. In *D. mollucanum* both the apotracheal and paratracheal parenchyma is scanty, rays are homocellular and very broad (4-18 seriate). *D.* [illegible] differs from the present fossil in having abundant parenchyma and rays are 1-4 (mostly 2-3) seriate and homocellular. In *D. spectabile* the vessels are smaller (t.d. 95-200 mm, r.d. 125-275 mm), paratracheal parenchyma very scanty and apotracheal only associated with gum canals, while rays are 1-4 (mostly 3) seriate. *D. sumatrense* differs in having smaller vessels (t.d. 75-200 mm) and taller rays (up to 90 cells). In *D. lunaburense* also vessels are smaller (t.d. 125-275 mm), mostly solitary but groups of 2-4 also present (13%), gum canals are very small (t.d. 22.4-57.8 mm) and spiral thickenings on the tracheids are found. Vessel multiples up to 4, spiral thickenings and intervessel pits are not observed in modern *Dryobalanops*. The general look also does not match *Dryobalanops*. In *D. tobleri*, vessels are 150-200 mm in tangential diameter, paratracheal parenchyma sparse and apotracheal parenchyma associated with gum canals, rays are 1-5 (mostly 3-4) seriate.

The fossil wood under consideration either differs in vessel size or in ray character from all the known species, hence it is described as *Dryobalanoxylon bogorense* sp. nov. The specific epithet indicating its occurrence in Bogor in West Java.

Name of Fossil Species	Age	Horizon/Country	References
Dryobalanoxylon bangkoense *Schweitzer*	Quaternary	Central Sumatra, Indonesia; *Southwest Bangkok, Thailand*	Schweitzer 1958
Dryobalanoxylon cf. bangkoense *Schweitzer*	Quaternary	Central Sumatra, Indonesia; *Southwest Bangkok, Thailand*	Schweitzer 1958
D. borneense Schweitzer	Miocene	Borneo, Indonesia	Schweitzer 1958
D. holdeni (Ramanujam) *Awasthi*	Miocene-*Pliocene*	Cuddalore Sandstone, India	Awasthi 1971
D. indicum (Ramanujam) *Awasthi*	Miocene-*Pliocene*	Cuddalore Sandstone, India	Awasthi 1971
D. javanicum (Kräusel) *Den Berger*	Pliocene	West Java, Indonesia	Den Berger 1927; *Schweitzer 1958*
D. keralaensis Awasthi & Ahuja	Miocene	Warkalli Formation, India	Awasthi & Ahuja 1982
D. khmerinum Boureau	----------	Combodia, Indo-China	Boureau 1952; Schweitzer 1958
D. mirabile Schweitzer	Quaternary	Central Sumatra, Indonesia; South Bangkok, Thailand.	Schweitzer 1958
D. musperi Schweitzer	Early-Late Pliocene	West Java, Indonesia	Schweitzer 1958
D. neglectum Schweitzer	Quaternary	Central Sumatra, Indonesia; Southwest Bangkok, Thailand	Schweitzer 1958
D. rotundatum Schweitzer	Quaternary	Central Sumatra, Indonesia; Southwest Bangkok, Thailand	Schweitzer 1958
D. spectabile (Crié) Den *Berger*	Pliocene	West Java; between Batavia and *Rangkas-Bitoeng, Indonesia*	Den Berger 1923; *Schweitzer 1958*
D. sumatrense Schweitzer	Late Pliocene	Central Sumatra, Indonesia	Schweitzer 1958
D. tambouense Vozenin-Serra	Pliocene	South Vietnam	Vozenin-Serra, 1981
D. tobleri (Kräusel) Den *Berger*	Pliocene	West Java; between Batavia and *Rangkas-Bitoeng, Indonesia*	Den Berger, 1923; *Schweitzer, 1958*
D. bogorense sp. nov.	Pliocene	Bogor, West Java, Indonesia	----------

Fig. 2—Fossil species of *Dryobalanoxylon*.

DISCUSSION

Dipterocarpaceae is the most important family in the present day flora of Southeast Asia as most of the genera are confined to this area (Awasthi, 1996). In view of its earliest authentic record from the Oligocene of north-west Borneo (Muller, 1970, 1981), and its abundance in modern flora of Malaysian region, it is believed that the family had originated in western Malaysia during the Early Tertiary (Merrill, 1923; Bancroft, 1933; Ashton, 1969; Lakhanpal, 1974). Fossil records of *Dipterocarpus* and *Hopea* leaves are reported from younger horizons (probably Eocene) of Sumatra and Borneo (Heer, 1876; Geyler, 1875, 1887), but their age and affinities need confirmation. Brandis (1895) and Bancroft (1933) have already suggested that Geyler's records should not be taken into account in the geological history of the family.

To evaluate the diversity of fossil floras in West Java, a preliminary survey of three fossil localities, namely, Ciampea, Leuwiliang and Jasinga was carried out by Mandang and Martono (1996). Among the wood examined (199), 81.4% (162) belong to the family Dipterocarpaceae. With in the dipterocarps, 19.4% belong to *Dryobalanops* while the rest (18.6%) belong to *Alstonia* (Apocynaceae), *Calophyllum* (Cluciaceae), *Dillenia* (Dilleniaceae), *Ochanostachys* (Olacaceae), *Terminalia* (Combretaceae) and some legums. Dipterocarps are less abundant (both in generic diversity and number) in the present day natural forests of Java (Prawira, 1976) and are represented by *Anisoptera, Dipterocarpus, Hopea, Shorea* and *Vatica* while in the fossil assemblage *Dryobalanops, Rubroshorea* and *Cotylelobium* are also present in addition to these genera. The fossil assemblage in western Java is similar to present day flora of Sumatra and Kalimantan where dipterocarps are in abundance (Directorate of Forestry Planning, 1981).

The deterioration of dipterocarps (both in generic diversity and number) can be explained by Molengraaf Theory (Van Bemmelen, 1949). According to that theory until Early Pleistocene, Sunda Platform (Java, Sumatra, Kalimantan & intervening smaller islands) was united with the mainland of Asia. But after the last ice age, during the Late Pleistocene, melting of polar ice along with volcanic activity due to tectonic disturbances, resulted separation of Java, Kalimantan and Sumatra. Due to volcanic activity, natural forests were buried under lava and some of the genera viz., *Dryobalanops*, *Cotylelobium*, *Anisoptera*, etc. failed to regenerate. Thus they became extinct in the natural forests of Java.

The genus *Dryobalanops* Gaertner f. consists of 7 species restricted in present day tropical evergreen rain forests of Indonesia (Sumatra and Borneo) and Malaysia (Merrill, 1923; Foxworthy, 1946; Mabberley, 1993). However, it was more widely distributed in the geological past (Fig. 2) as its fossil records are known from India and other Southeast Asian countries like Cambodia and Vietnam and it has also been reported from Java in Indonesia.

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Pollen analytical study of late-Holocene sediments from Trans-Yamuna segment of Western Doon valley of Northwest Himalaya

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ABSTRACT

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A trench across a Quaternary fault in a berm was dug out at Sirmuri Tal in the Trans-Yamuna segment of Western Doon valley in Himachal Pradesh. Pollen analytical investigation of 4.90 m deep trench profile from Sirmuri Tal has shown that between 2800 to1800 years BP, mixed open vegetation comprising chiefly grasses, sedges, Cheno/Am, *Artemisia* and Ranunculaceae together with sparsely distributed trees viz., *Emblica officinalis*, *Shorea robusta*, *Holoptelea*, *Mallotus*, *Grewia*, Meliaceae, etc. grew in the region under dry climatic regime. The lake did exist, but it was small in dimension as indicated by the meagre presence of aquatic taxa such as *Typha* and *Potamogeton*. Subsequently, between 1800 to 400 years BP, mixed deciduous forests were established as reflected by the improvement in *Emblica officinalis*, *Mallotus*, *Grewia*, etc. as well as invasion of *Terminalia*, *Adina cordifolia*, *Acacia* and *Syzygium* in the region. The overall increased diversity in the forest floristics signifies that the moist climatic condition prevailed in the region during this period. Lake became wider in expanse as implied by the improved frequencies of *Potamogeton* and *Typha* and first encounter of Dinoflagellate cysts in good number. Since 400 years BP and onwards, the climate deteriorated as evidenced from the decline in the vegetation cover. The lake transformed into a swamp as evidenced by the increase in sedges and Chen/Am and a simultaneous decline in aquatic vegetation. The excessively high frequencies of *Pinus* pollen denotes its transportation by wind and water from nearby subtropical belt where chirpine forests occur luxuriantly.

Key-words—Pollen analysis, Palaeofloristics, Late-Holocene, Sirmuri Tal, Western Doon valley.

उत्तर-पश्चिमी हिमालय की पश्चिमी दून घाटी के ट्रान्स-यमुना अंश से प्राप्त अन्तिम होलोसीन कल्प के अवसादों का परागाणु विश्लेषणात्मक अध्ययन

मोहन सिंह चौहान, गोविन्दराज राजगोपालन, एम.पी. साह, जी. फिलिप एवं एन.एस. विरदी

सारांश

हिमाचल प्रदेश की पश्चिमी दून घाटी के ट्रान्स-यमुना अंश में स्थित सिरमुरी ताल के एक बर्म में क्वाटरनरी भ्रंश के चारों ओर एक गर्त्त खोदी गयी। सिरमुरी ताल की 4.90 मीटर गहरी गर्त्त परिच्छेदिका के परागाणविक विश्लेषण से प्रदर्शित होता है कि विगत 2800 से 1800 वर्ष पूर्व के बीच शुष्क जलवायु के अन्तर्गत क्षेत्र में विरलतः वितरित वृक्षों, जैसे-*एम्बलिका ऑफ़िसिनेलिस, शोरिया रोबस्टा, होलोप्टीलिया, मैलोटस, ग्रीविया,* मीलिएसी इत्यादि के साथ-साथ सम्मिश्र

विवृत वनस्पतियाँ, जिनमें घासें, प्रतृण, चीनो/एम, *आर्टीमीज़िया* तथा रैननक्युलेसी उगती थीं। यहाँ झील भी विद्यमान थी, परन्तु यह कम विस्तृत थी, जो *टाइफ़ा* तथा *पोटामॉजीटॉन* जैसे जलीय वर्गकों की अल्प उपस्थिति द्वारा इंगित है। तत्पश्चात् विगत 1·800 से 400 वर्ष पूर्व के मध्य में सम्मिश्र पर्णपाती वन स्थापित हुए, जो क्षेत्र में *एम्बलिका ऑफ़िसिनेलिस, मैलोटस, ग्रीविया* इत्यादि में सुधार तथा *टर्मिनेलिया, एडीना कॉर्डीफ़ोलिया, एकेशिया* एवं *साइज़ीज़ियम* के विस्तार द्वारा प्रदर्शित है। वन वनस्पतिजात में सकल वर्धित वैविध्य इंगित करता है कि इस काल के दौरान क्षेत्र में आर्द्र जलवायुविक स्थितियाँ विद्यमान थीं। *पोटामॉजीटॉन* एवं *टाइफ़ा* की बेहतर आवृत्तियों तथा उत्कृष्ट संख्या में प्राप्त घूर्णीकशाभ पुटियों द्वारा झील का फैलना इंगित होता है। विगत 400 वर्ष पूर्व तथा तत्पश्चात् से जलवायु बिगड़ने लगी, जो वनस्पति आच्छादन में ह्रास से पुष्ट होता है। फलतः झील एक अनूप में परिणत हो गयी, जो प्रतृणों एवं चीनो/एम की वृद्धि तथा जलीय वनस्पतियों में तत्समय हुए ह्रास से अभिप्रमाणित है। *पाइनस* परागकण की अत्यधिक उच्च आवृत्तियाँ इसका समीपवर्ती उपोष्ण कटिबन्धीय बेल्ट से पवन तथा जल द्वारा परिवहन संकेतित करती हैं, जहाँ चिरपाइन के वन प्रचुर मात्रा में विद्यमान थे।

संकेत शब्द—परागाणविक विश्लेषण, पुरावनस्पतिजातविज्ञान, अन्तिम होलोसीन, सिरमुरी ताल, पश्चिमी दून घाटी.

INTRODUCTION

Tropical deciduous forests, which constitute a major part of vegetation wealth in central India and plains of northern India, have not been adequately studied for their antiquity and climatic fluctuations that they have experienced during the Quaternary period. The available information on this aspect includes investigation on a few megafossils recovered from Siwalik bed of Himachal Pradesh (Tiwari *et al.*, 1979; Prasad *et al.*, 2002) and pollen analysis of some sediment cores from Doon valley, Uttaranchal (Rawat, 1984) and the plains of Uttar Pradesh (Gupta, 1978; Chauhan *et al.*, 1990) and north-eastern part of Madhya Pradesh (Chauhan, 1995, 2000) and a few clay samples from Siwalik bed of Himachal Pradesh (Tiwari *et al.*, 1979). In the present communication an attempt has been made to understand the vegetational and climatic succession in the Siwalik region through the pollen analytical investigation of a Quaternary section exposed at Sirmuri Tal, Sirmur District (H.P.).

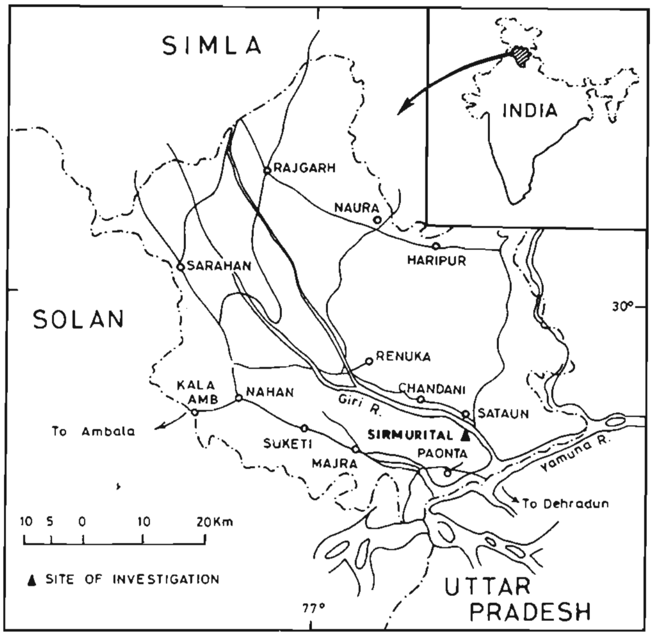

Fig. 1—Map of Sirmur District (H.P.) showing the site of investigation.

Sirmuri Tal is situated about 65 km west of Dehra Dun between 77°39'45" E and 30°32'5" N at an altitude of 580 m a.s.l. on the right bank of Giri River (Fig. 1). Reactivation of fault in Sirmuri Tal area in the Trans-Yamuna segment during Quaternary Period resulted in dislocation of many landforms like river terraces, alluvial fans, stream and ridges and the formation of other morphotectonic features such as sag ponds, berms, triangular facets, pressure ridges, controlled drainage, etc. (Philip & Sah, 1999). Sirmuri Tal presently is a flat cultivated area, in the Western Doon valley. The morphotectonic features as well as the lithological sequence of the dug out trench (15 x 5 x 4 m) have provided ample evidence for the existence of a lake in the past, which was formed as a sag pond in the vicinity of an active fault known as Sirmuri Tal Fault (STF). The hill slopes adjacent to the area are gentle and possess a large number of boulders, conglomerates and gravels. Presently, this ancient lake basin is in the form of a berm (Philip & Sah, 1999).

GEOLOGICAL SETTING

The Trans-Yamuna segment of the Doon valley lies in a tectonically active zone between a number of faults, such as the Main Boundary Thrust (MBT)/Krol Thrust, the Himalayan Frontal Thrust and the Main Boundary Fault/Bilaspur Thrust. The lithotectonic setting and the regional geological map of the area (Fig. 2) exhibit that there are three geological units, i.e., the pre-Tertiary, Tertiary and Quaternary (Fig. 3). The pre-Tertiary rocks are exposed to the north of the Giri River. The Tertiary sediments range from marine shale limestone through the fossiliferous limestone of the Subathu (Paleocene-Eocene age) and the brackish water Dagshais (red, purple and green mudstones and sandstone) to the molassic Siwalik Group. The

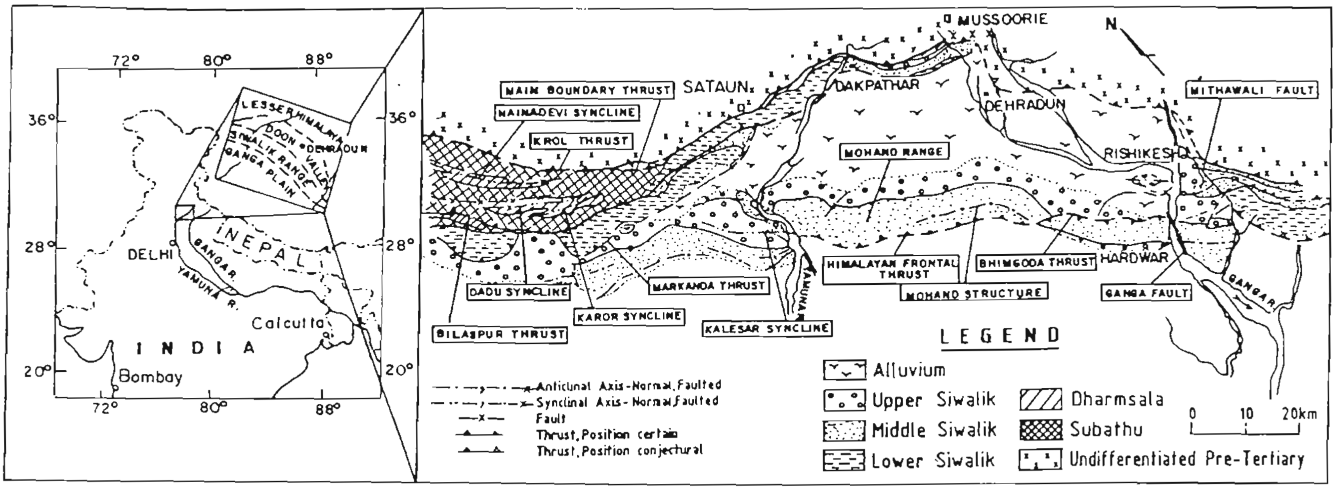

Fig. 2—Geological map of the Trans-Yamuna segment of Western Doon valley (after Karunakaran & Raja Rao, 1979).

Quaternary sediments, which are derived chiefly from the Tertiary rocks, occur as a cover over the Tertiary formations, mainly the Upper Siwalik (Karunakaran & Ranga Rao, 1979; Raiverman *et al.*, 1983). Although, the Tertiary and pre-Tertiary have been mapped by several workers, however, little attempt has been made to map the Quaternary formations in this valley. These deposits are the best indicators of the processes involved in the Quaternary landform evolution of the area,

Age		Group	Lithology
Quaternary		Undifferentiated Post-Siwalik sediments	
	-----	——— Himalayan Frontal Thrust ———	
		Siwalik	Conglomerates, Sandstones and clays
	LOWER	——— Main Boundary Fault / Bilaspur Thrust ———	
TERTIARY		Kasauli	Shales, sandstones, red, purple and green mud
	TERTIARY	Dagshai	stones and Limestone
		Subathu	(fossiliferous)
		——— Main Boundary Thrust ———	
		Tal	Limestones
Pre-Tertiary		Krol	(mainly)
		Infra Krol	
		Blaini Boulder bed	
		Nagthat	Quartzites
		Chandpur	Phyllites
		Mandhali	Limestones

Fig. 3—Lithotectonic setting in the Trans-Yamuna segment of the Doon valley.

and also demonstrate different phases of active tectonics (Philip & Sah, 1999).

VEGETATION

Sirmuri Tal area is characterized by the presence of a mixed type of vegetation. *Grewia oppositifolia*, *Celtis australis*, *Mallotus philippensis*, *Melia azedarach*, *Ficus* ..., *F. roxburghii*, *F. palmata*, *Murraya* sp., *Bauhinia variegata*, *Zanthoxylum alatum*, etc. are the common trees around the site investigated. Scattered thickets of *Adhatoda vasica*, *Vitex negundo*, *Zizyphus jujuba*, *Carissa opaca*, *Lantana camara*, *Berberis asiatica*, *Rubus ellipticus*, *Rosa moschata*, *Colebrookea oppositifolia* and *Woodfordia fruticosa* can be seen throughout the area.

The herbaceous vegetation includes *Oxalis acetosella*, *Rumex hastatus*, *Ageratum conyzoides*, *Micromeria biflora*, *Potentilla sikkimensis*, *Indigofera* sp., *Boerhaavia diffusa*, *Anemone parviflora*, *Polygonum plebeium*, *Geranium nepalense*, etc.

The southern hill slopes adjacent to the site of investigation support sal (*Shorea robusta*) forests. Apart from sal, *Lagerstroemia parviflora*, *Adina cordifolia*, *Buchanania lanzan*, *Anogeissus latifolia*, *Terminalia tomentosa*, *Semecarpus anacardium*, *Ehretia laevis* and *Bauhinia* sp. occur frequently in these forests, whereas *Emblica officinalis*, *Olea glandulifera* and *Lannea coromandelica* are met with occasionally. Few *Syzygium cumini* trees are seen along the bank of the streams.

MATERIAL AND METHODS

A 4.90 m deep trench was dug at Sirmuri Tal, Sirmur District (Himachal Pradesh) to collect samples for pollen analytical investigation. Upper part of the section comprised mainly bouldery hillside slope scree and reworked sediments and hence not considered for sampling. Forty samples were picked from the remaining 3.05 m column at different intervals, depending upon the visible change in the lithology of the section. In addition, samples for radiocarbon dating were also collected from the trench.

The exposed section comprised broadly six lithozones (Fig. 4). The topmost zone is constituted of bouldery hillside scree and reworked material. This overlies the sand with pebble zone, which is fluvial in origin. Below this are the zones of peat with sand and sandy clay. These are supposed to be deposited in a ponding environment. A good number of charcoal pieces were also encountered in these lithozones. Underlying these are sandy and clayey-sand zones and they are fluvial in nature.

To calibrate the sedimentation rate for this trench profile the two radiocarbon dates, i.e., 610±100 years BP (3.60 m) and 2280±110 years BP (4.15 m) have been taken into consideration (Fig. 5). The upper part (2.90-3.60 m) of the profile has the high sedimentation rate of 75 cm/100 years, whereas in the lower part (3.60-4.30 m) it declines to 7 cm/100 years. These sedimentation rates have been used for the extrapolation of three more dates, i.e., 2800 years BP at 4.30 m depth, 1800 years BP at 4.00 m depth and 400 years BP at 3.25 m depth for the precise demarcation of alterations in the vegetational composition and corresponding climate in a chronological order.

The standard procedure of acetolysis (Erdtman, 1943) through the use of 10% aqueous KOH solution, 40% HF and acetolysing mixture (9:1, acetic anhydride and concentrated H_2SO_4) was followed to extract pollen/spores present in the sediments. Only the samples analysed from the middle part of the section constituted of peat and sticky clay have yielded appreciable number of pollen. The upper and lower parts of this section, composed of sand with small pebbles and sand with clay, respectively, have proved palynologically barren.

The pollen sums range between 100-356, depending upon the pollen productivity of the samples analysed. The percentage frequencies of the recovered pollen taxa have been calculated in terms of total land plant pollen. The plant taxa have been grouped as trees, shrubs, herbs, ferns and dinoflagellate cysts and are put in the same order in the pollen diagram.

Depth	Lithology
0-1.85 m	Bouldery hillside scree and reworked material
1.85-2.95 m	Sand with pebbles
2.95-3.50 m	Alternate bands of peat and sand
3.50-4.30 m	Sticky sandy clay with charcoal pieces and nodules
4.30-4.60 m	Sand
4.60-4.90 m	Clayey sand

Fig. 4—Depth-wise lithostratigraphical details.

Depth	Lithology	Radiocarbon dates
2.90 m	Sand with pebbles	BS-1315 Modern
3.60 m	Sticky sandy clay with charcoal pieces and nodules	BS-1382 610±100 years BP
3.80 m	—do—	BS-1383 1310±90 years BP
4.00 m	—do—	BS-1374 1550±120 years BP
4.15 m	—do—	BS-1447 2280±110 years BP

Fig. 5—Radiocarbon dates for the investigated trench profile.

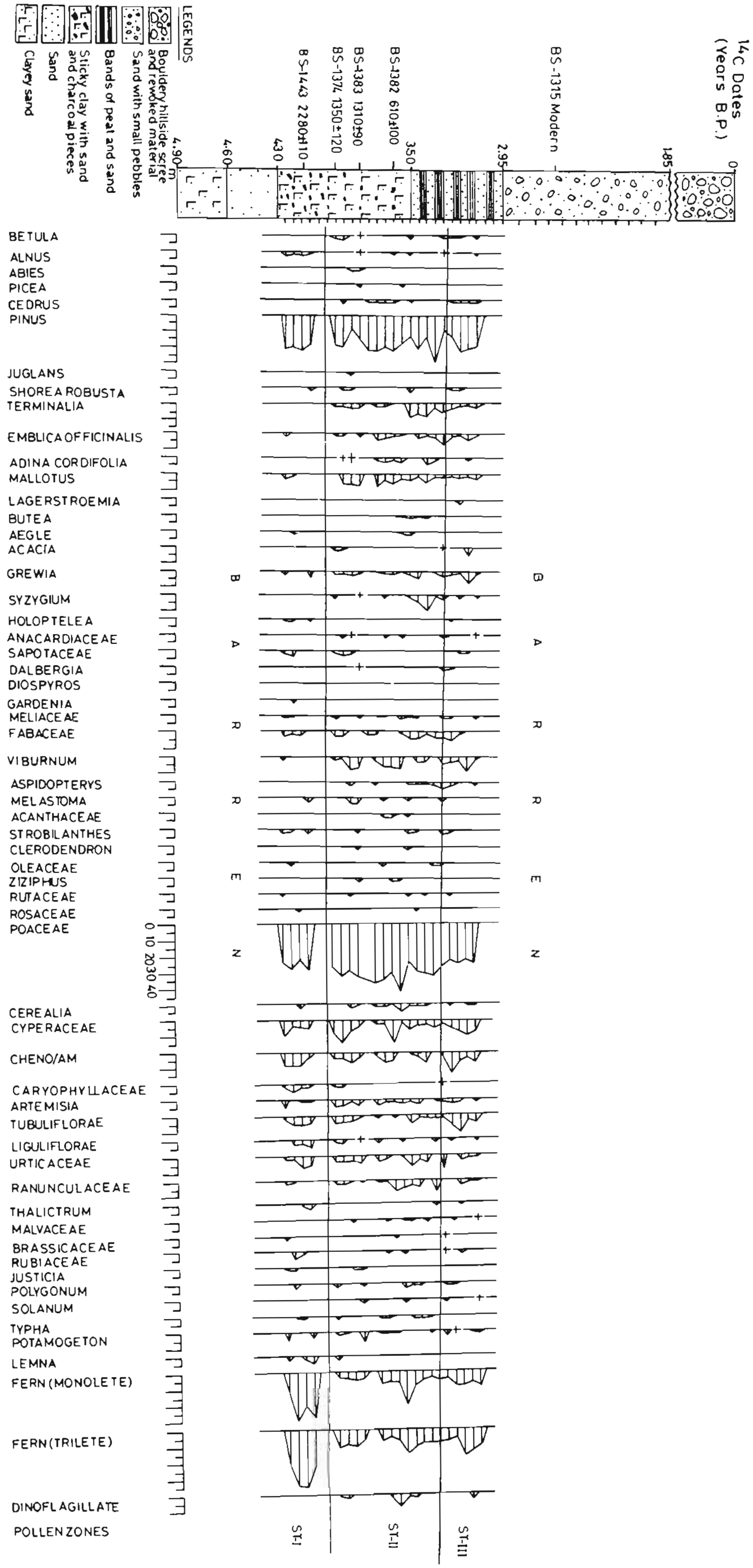

Fig. 6—Pollen diagram from Sirmuri Tal. District Sirmur (Himachal Pradesh).

POLLEN ANALYSIS

To understand the sequential alterations in the palaeofloristics and climate in the region, the pollen diagram constructed from Sirmuri Tal has been divided into three distinct pollen zones from bottom to top, based on the fluctuations in the frequencies of some prominent arboreals and non-arboreals (Fig. 4). These pollen zones are prefixed with the initials 'ST' after the name of investigated site.

Pollen Zone ST-I (4.30-4.00 m): Poaceae-Cyperaceae-Cheno/Am-Mallotus-Holoptelea-Fern Assemblage

This pollen zone with a radiocarbon date of 2780±110 years BP (4.15 m), covering the time span of 2800 to 1800 years BP, depicts high values for non-arboreals and poor representation of arboreals. Among the non-arboreals, Poaceae (grasses 21-30%), Cyperaceae (sedges 5-12%), Cheno/Am (Chenopodiaceae/Amaranthaceae), Urticaceae and Tubuliflorae (3-8% each), Liguliflorae (3-5%) and *Artemisia* (1-3%) are consistently represented with good frequencies. *Thalictrum* and Rubiaceae (2-5% each), Cerealia (2%), the aquatics *Potamogeton* (3-5%) and *Lemna* (2-5%) are met with sporadically. Fern spores monolete (21-30%) and trilete (20-35%) are quite frequent.

The arboreals, *Mallotus*, *Grewia* and Sapotaceae (1-3% each) and *Holoptelea* (1-2%) are low and sporadic, whereas *Emblica*, *Emblica officinalis*, *Shorea robusta*, *Aegle* and Meliaceae are marked by the stray occurrence. The shrubby elements viz. Fabaceae (2-4%) and *Sambucus* (1-2%) are better represented than those of Rosaceae, Oleaceae and Rutaceae.

The Himalayan element, *Pinus roxburghii* (20-25%) is encountered in high frequencies whereas *Alnus* (1-3%) is also represented consistently in low values.

Pollen Zone ST-II (4.00-3.25 m): Terminalia-Mallotus-Syzygium-Emblica officinalis-Poaceae-Cyperaceae Assemblage

This pollen zone dated to 1550±120 years BP (4.00 m), 1310±90 years BP (3.80 m) and 610±100 years BP (3.60 m) and encompassing a time interval of 1800 to 400 years B.P. is characterised by the abrupt improvement in both arboreals and non-arboreals. The arboreals, *Mallotus* (2-8%), *Emblica officinalis* (2-7%), *Grewia* (2-6%) and Meliaceae (2-4%) have much enhanced values than in Pollen Zone ST-I. On the other hand, *Terminalia* (2-8%), *Syzygium* (1-10%) and *Adina cordifolia* (2-5%) appear in high frequencies for the first time together with sporadically represented taxa such as *Bauhinia*, *Acacia* (2% each), *Dalbergia* and *Diospyros* (1% each). The shrubby taxa such as *Ricinus* (2-10%), Fabaceae (3-5%) and *Melastoma* (1-4%) are recorded in increased frequencies.

The non-arboreals such as Poaceae (25-42%), Cyperaceae (2-15%), Ranunculaceae (2-10%), Urticaceae and Tubuliflorae (3-8% each), Cheno/Am (2-7%), *Artemisia* (2-6%) and Cerealia (1-5%) are better represented than in Pollen Zone ST-I. The aquatic elements, *Potamogeton* (1-7%) and *Typha* (1-3%), also have increased frequencies than in the preceding pollen zone. Fern spores (monolete 5-21% and trilete 6-14%) show reduced values in contrast to previous pollen zone. Dinoflagellate cysts (2-10%) are recorded frequently for the first time.

Pinus (2-30%) is recorded in more improved values than in the Pollen Zone ST-I. *Betula* (5%), *Cedrus*, *Abies* and *Picea* (2% each) turn up sporadically for the first time.

Pollen Zone ST-III (3.25-2.95 m): Emblica officinalis-Terminalia-Fabaceae-Mimosa-Poaceae-Cyperaceae-Cheno/Am Assemblage

This pollen zone, with a temporal range of 400 years BP to the present, exhibits a decline in the number as well as frequencies of both arboreals and non-arboreals. The tree taxa viz. *Emblica officinalis* (2-5%), *Mallotus* (1-4%), *Terminalia* (2-3%) and *Syzygium* (1-2%) are consistently represented in reduced frequencies. However, *Grewia* (1-5%) and *Acacia* (6%) are recovered in somewhat improved values, though sporadically. *Shorea robusta*, *Holoptelea* and Meliaceae are scantily present.

Among the herbaceous components, Poaceae (22-35%) followed by Urticaceae (2-10%), Ranunculaceae (3-5%) and Cerealia (2%) are met with in a decreasing trend in contrast to preceding pollen zone. On the other hand, Cheno/Am (4-15%), Cyperaceae (5-17%) and Tubuliflorae (3-10%) show an increasing trend. *Artemisia* (1-5%) remains more or less static. *Potamogeton* (5-7%), *Typha* and Dinoflagellate cysts become more sporadic. Fern spores (monolete 5-10% and trilete 7-20%) maintain their high frequencies. *Pinus* (8-21%) declines considerably in this zone.

DISCUSSION

The pollen analytical investigation of a 4.90 m deep trench profile exposed at Sirmuri Tal, Sirmur District (Himachal Pradesh) has provided some important pollen proxy data for reconstructing the changing vegetational scenario and climatic events in the region during late-Holocene. The pollen sequence generated has demonstrated that around 2800 to 1800 years BP, the open mixed vegetation chiefly composed of grasses together with good proportion of sedges, Chenopodiaceae/Amaranthaceae, *Artemisia*, etc. existed in the region. A few tree taxa such as *Mallotus*, *Emblica officinalis*, *Holoptelea*, *Grewia*, *Shorea robusta*, Meliaceae, etc. and thickets of *Strobilanthes*, *Viburnum*, Oleaceae and Fabaceae grew scantily in the open vegetation. In general, the overall vegetational mosaic reflects that the region was under cool and dry climatic regime during this phase. The presence of fragmentary charcoals in high concentration in the sediments envisages the occurrence of fire in the region, which is often associated with drier climate. The lake did occur, but it was small in expanse as evidenced from the meagre presence of aquatic taxa such as *Potamogeton*, *Lemna* and *Typha*. The sediments comprising clay with fine sand also seem to be accumulated in a pond or small lake on the riverside plain. The geomorphological study of Trans Yamuna segment of the Western Doon valley (Philip & Sah, 1999) has shown that the lake sedimentation commenced about 4000 years BP. The area in the vicinity of the lake was under the impact of anthropogenic activities, more particularly agricultural practices as deciphered by the frequent representation of culture pollen taxa viz., Cerealia, Caryophyllaceae, Chenopodiaceae/Amaranthaceae, *Artemisia*, etc. during this time.

The abundance of *Pinus* pollen in the sediments could be attributed to its transportation by wind or water from nearby mountains where chirpine forests probably occurred profusely.

Between 1800 to 400 years BP, the mixed tropical deciduous forests got established as a consequence of improvement in *Emblica officinalis*, *Grewia*, *Mallotus*, Meliaceae, etc. as well as simultaneous invasion of moist deciduous trees such as *Terminalia*, *Adina cordifolia* and *Syzygium* in the region. The shrubby vegetation comprising *Viburnum*, *Acanthaceae* and *M. koenigii* also flourished well. Thus, the increased diversity in the forest floristics reveals that the area experienced more precipitation, which led to the prevalence of moist climatic condition during this phase. This is also manifested by the low charcoal concentration in the sediments. Furthermore, in response to increased precipitation in the region, the lake also had wider spread than before as indicated by the first record of Dinoflagellate cysts in good numbers and improvement in aquatic taxa viz., *Potamogeton* and *Typha*. This is also substantiated by the presence of sticky clay as well as the bands of peat and fine sand in the upper part of lithocolumn during this phase. Local and historical information indicates that a lake at Sirmur Tal was breached in 1092 AD or about 900 years ago (Philip & Sah, 1999).

With the inception this phase, the expansion of agricultural practices also took place in the region, which is inferred by the better representation of the culture pollen taxa viz., Cerealia, Chenopodiaceae/Amaranthaceae, *Artemisia* and Urticaceae. The remnants of the palace of king of Sirmur located near Sirmur Tal Village and legends associated with palace also reveal the acceleration of anthropogenic activities, particularly agricultural practice in the region as a consequence of increased human population around 1082 AD or 868 years BP (Gazetteer of Sirmur State, 1934 (reprinted 1996)).

The increased frequencies of *Pinus roxburghii* imply that the chirpine forests grew more luxuriantly in the adjoining subtropical belt during this time.

Later on, around 400 years BP and onwards the forests became sparse as well marked by the reduced frequencies of most of the tree taxa viz., *Terminalia*, *Emblica officinalis*, *Adina cordifolia*, *Mallotus* and *Syzygium*. Likewise, the shrubby vegetation, in general, also turned more scanty. Hence, the overall decline in the forest constituents might have occurred under the impact of deterioration of climate, which most probably became cool and dry during this phase. However, the illicit and selective felling of arboreals, particularly trees by the local inhabitants cannot also be ruled out. The ground vegetation remained almost identical in composition, as it was earlier, however, the expansion of sedges and Chenopodiaceae/Amaranthaceae and a corresponding decline in aquatic elements as well as Dinoflagellate cysts signify that the gradual transformation of lake into swamp commenced by this time. The land tenure records of 100 years show that the Giri River gradually migrated southward due to fluvial dynamics and tectonic activity (Philip & Sah, 1999). This change in the river course led to the choking of water source to Sirmur Tal, which ultimately got vanished in due course of time. The agricultural practice continued in the region at a more or less same pace, as before, since most of the culture pollen taxa do not exhibit any conspicuous change in their representation during this phase.

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Short Communication

Occurrence of Glossopteris Flora, Pisdura Nand-Dongargaon Sub-Basin

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PLANT evolution witnessed many innovations. Origin and extinction of plants can be understood through the study of plant fossils preserved in ancient sediments. Geological records exemplify both biological and physical changes and subsequent hydrocarbon resource formation. Occurrence of vegetal debris in the continental environment of Gondwana basins filled in with detrital sediments becomes much significant due to the presence of economically exploitable coal.

Pisdura, a treasure for vertebrate fossils (Mohabey & Udhoji, 2000) hitherto, has been brought into the palaeobotanical gambit. Plant fossils showing affinity with coal forming vegetation have been recorded for the first time from the red sandstones underlying the famous Lameta Formation (Maastrichtian) known for dinosaurian fossils (Mohabey, 1996). Megafossils of Glossopteridales, Cordaitales and equisetales characterized by leaf and stem fossils have been reported enriching the knowledge on the occurrence of gondwanan plant fossils in the Wardha Valley. Further efforts to supplement plant fossil data are needed to understand floral evolution and its contribution to hydrocarbon resource.

The Wardha Valley has been known for coal deposits, animal and plant fossils of gondwanan affinity. The geological inputs were made by Blanford (1868), Hughes (1877), Oldham (1880), Ramanamurthy (1979) and Raja Rao (1982). Pisdura, a small village in the Chandrapur District, Maharashtra (refer Mohabey, 1996 for locality Map) falling in the inland Nand-Dongargaon Sub-Basin within the Wardha Valley has been a paradise for vertebrate palaeontologists. Classic dinosaurian and other vertebrate fossil sites belonging to the Lameta Formation from this locality are known (Jain & Sahni, 1983; Mohabey, 1991, 1996; Mohabey & Udhoji, 2000). However, gondwanan fossils are not studied from this locality. Plant fossils, particularly petrified woods along with leaf impressions have been recorded from other areas of the Wardha Valley (Lakhanpal *et al.*, 1976; Chandra & Tewari, 1991; Agashe & Prasad, 1989; Agashe & Shashi Kumar, 1996). Present communication brings out the necessity to investigate unexplored areas and trace the geographical extent and evolutionary ramifications of Glossopteris Flora during the Gondwana times.

Taxa	Early Permian	Middle Permian	Late Permian	Early Triassic
Equisetalean stem	+	-	−	−
Glossopteris angustifolia	+	+	−	+
Glossopteris browniana	+		-	
Glossopteris communis	+	+	+	+
Glossopteris [illegible]		-	+	+
Glossopteris indica	+	+	+	
Glossopteris [illegible]		-	+	-
Glossopteris [illegible]	+			+
Glossopteris [illegible]	+		-	−
Glossopteris rhabdotaenioides	−	-	+	-
Glossopteris stenoneura	-	+	+	-
Glossopteris [illegible]	-	+	-	
Glossopteris longicaulis	+	-	+	

In addition, *Gangamopteris* sp., *Glossopteris* sp. and *Noeggerathiopsis* sp. are also present in the assemblage.

Fig. 1—Check list of plant fossils from Pisdura and their stratigraphic range.

The Gondwana sediments (Permian-Triassic) in the Pisdura region are characterized by red brown variegated sandstones, reddish siltstone and red shale. They show a disconformable contact with the Lameta Formation (Fig. 2). Plant fossil impressions have been recovered from the sandstones from a section (79°8' 20°18') exposed at about 2 km northeast of the village.

Articulated equisetalean stems (Pteridophytes) with alternating ridges and furrows, a leaf assemblage of Glossopteridales with tongue shaped leaf impressions with variable morphologies viz. *Gangamopteris* sp., *Glossopteris angustifolia*, *G. browniana*, *G. lanceolatus*, *G. longicaulis*, *G. rhabdotaenioides*, *G. stenoneura*, *G. subtilis*, *G. tenuifolia*, *Glossopteris* sp. and Cordaitales viz. *Noeggerathiopsis* sp. are reported in the present note (Pl. 1). This constitutes an addition to the petrified wood data known from the Wardha Valley. A cursory glance at the check list (Fig. 1) suggests an affinity of this flora with the Permian-Early Triassic (250-210 million years) floras known from the Son-Mahanadi, Damodar and related coal basins (Chandra & Tewari, 1991). It corroborates occurrence of Glossopterid forests in the Wardha Valley during Permian-Triassic times which contributed to the rich coal deposits in the Chandrapur and Umrer regions of Maharashtra. A detailed floristic study is in progress to corroborate the present inference.

The Late Permian-Early Triassic Lower Gondwana sediments in the Wardha Valley are assigned under the Kamthi and Mangli beds. Further, detailed systemic studies shall confirm the stratigraphic significance of the Glossopteris Flora reported in this communication. A comparative analysis of the present assemblage with Raniganj/Kamthi palaeobotanical records demonstrates a closer affinity with the latter. Further, the terminal Permian Period witnessed a dramatic change in the global climate with a glaciated to completely non-glaciated state. As leaf fossils are excellent signatures of past atmospheric changes due to their direct contact with outside environment, it is essential to build up fossil leaf database from various niches and interpret past climate patterns.

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Recent	Alluvial sands and clays
Deccan Trap/Intertrappeans	Basalt with thin intertrappean beds containing sandstones and silty clay
Lameta Formation	Laminated clays and shales interbedded with limestones and sandstones, red and green clays, planar and cross bedded sandstone, grey marls, yellow laminated clays and shales
Gondwana Group	Red brown variegated sandstones, reddish siltstone and red shale
Pre-Cambrian	Conglomerates with igneous intrusions

Fig. 2—Stratigraphic sequence of Nand-Dongargaon Sub-Basin.

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PLATE 1 ——>

1. *Glossopteris rhabdotaenioides* Pant & Singh. A portion of leaf showing venation. Specimen No. BSIP 38321. x 2.
2. *Glossopteris gigantea* Chandra & Surange. Specimen No. BSIP 38322. x 2.
3. *Glossopteris subtilis* Pant & Gupta. Specimen No. BSIP 38323. x 2.
4. *Glossopteris indica* Schimper. Specimen No. BSIP 38324. x 2.
5. *Glossopteris communis* Feistmantel. Specimen No. BSIP 38325. x 2.5.
6. Equisetalean stem. Specimen No. BSIP 38324. x 2.
7. Specimen showing the presence of two leaf types, *Glossopteris angustifolia* and *G. indica*. Specimen No. BSIP 38325. x 1.
8. *Glossopteris browniana* Brongniart. Specimen No. BSIP 38326. x 2.
9. *Glossopteris stenoneura* Feistmantel. Specimen No. BSIP 38327. x 2.

10, 11. *Glossopteris tenuifolia* Pant & Gupta. Specimen Nos. BSIP 38328, 38329. x 1.

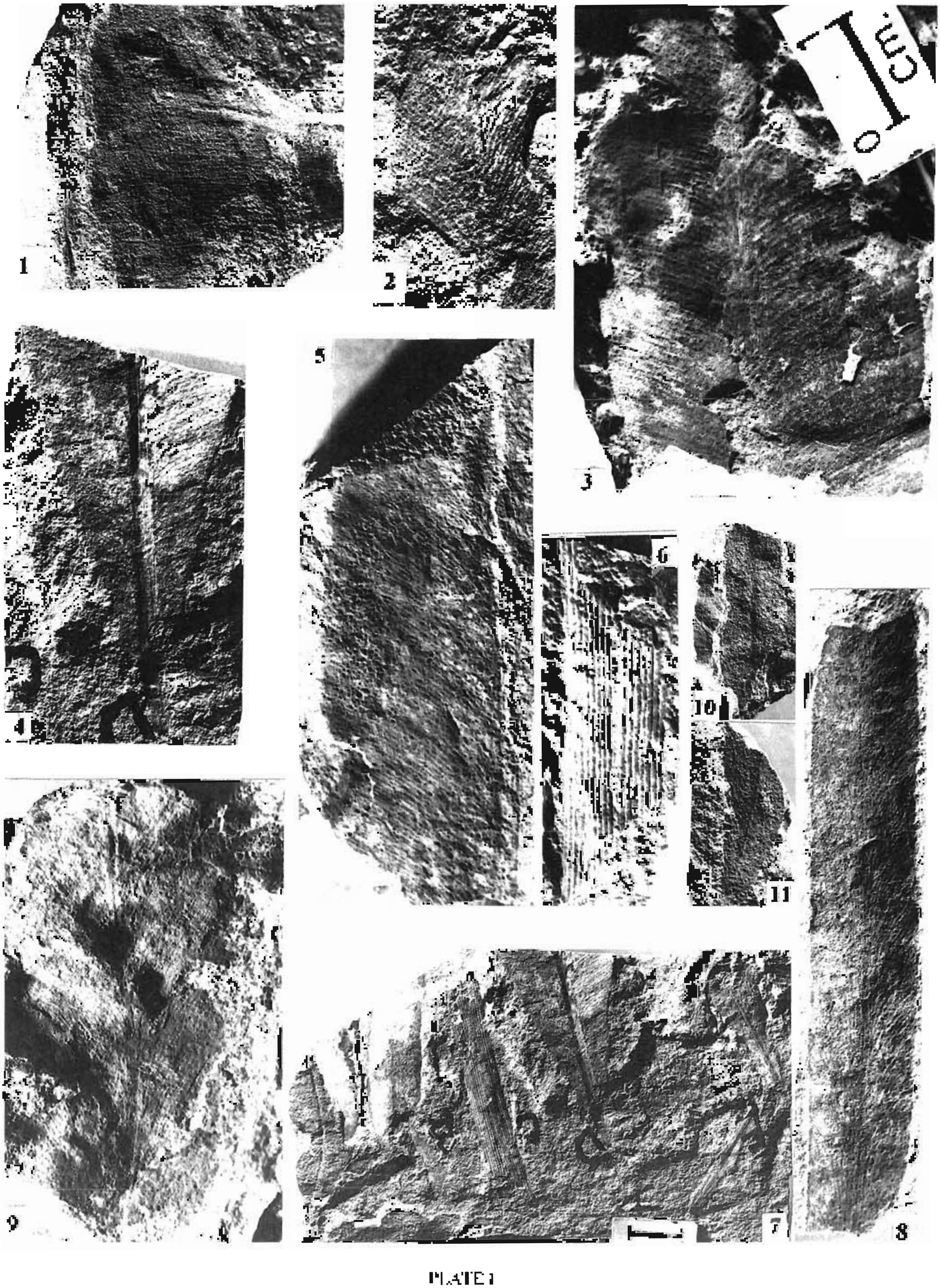

PLATE 1

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