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Palaeocene-Eocene marker pollen from India and tropical Africa

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The Palaeocene-Eocene epochs have witnessed a great floral diversification in tropical areas, which is also reflected in the pollen spectra. The important Indian stratigraphical marker taxa have been examined and a comparative study with extant material has provided botanical affinities to some of the taxa. Their comparison with those recorded in Africa leads to reflection on their palaeogeographical distribution. The stratigraphic ranges have been shown in the range chart. Some of the taxa common to India and Africa are: *Retistephanocolpites williamsi, Spinizonocolpites* spp., *Tricolpites reticulatus, Proxapertites* spp., *Anacolosidites luteoides* and *Marginipollis* spp. A number of Indian as well as African taxa are not recorded beyond the terminal Eocene; some of them could have migrated from India to other countries such as *Gonystylus* (*Cryptopolyporites*) to Malaysia and *Gunnera* (*Tricolpites reticulatus*) to Australia. The relative location and motion of India during these epochs could explain the singularity of the Early Tertiary Indian palynoflora.

Key-words—Palynology, Palaeogeography, Continental Drift, Palaeocene-Eocene, India, Africa.

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साराँश

भारत एवं उष्णकटिबन्धीय अफ्रीका से पुरानूतन-आदिनूतन सूचक परागकण

बेंगलूर श्रीनिवासा वेंकटाचाला, सी. करातिनी, सी. तिसत् एवं रंजीत कुमार कर

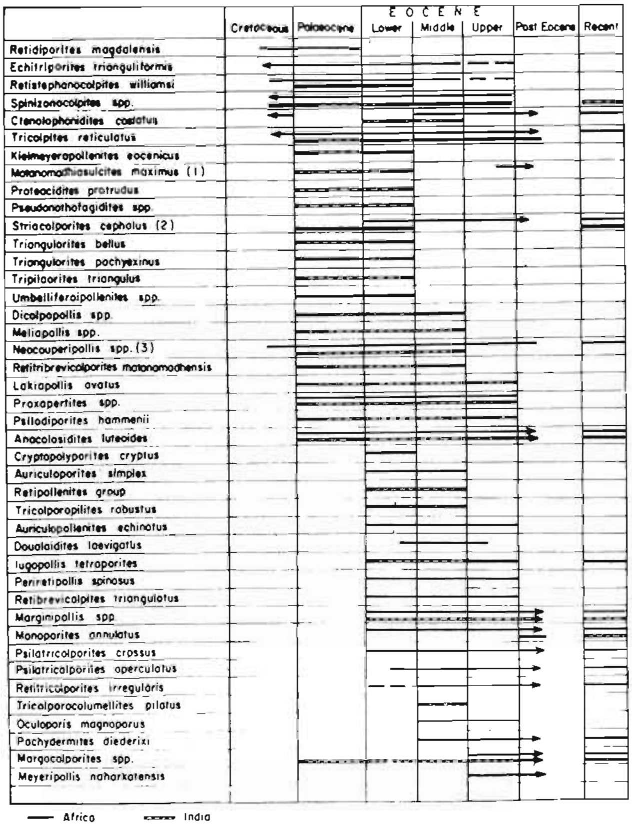
पुरानूतन-आदिनूतन कल्पों से उष्णकटिबन्धीय क्षेत्रों में अत्याधिक वनस्पतिजातीय विविधता के प्रमाण मिलते हैं। यह विविधता परागकण-स्पेक्ट्रमों से भी व्यक्त होती है। इस शोध पत्र में महत्वपूर्ण भारतीय स्तरिकीय-सूचक वर्गकों का अध्ययन किया गया है तथा वर्तमान वर्गकों से तुलनात्मक अध्ययन करने पर कुछ वर्गकों की वनस्पतिक सजातीयता भी प्रेक्षित की गई है। इन वर्गकों की अफ्रीकी वर्गकों से तुलना करने पर इनके पुराभौगोलिक वितरण पर प्रकाश पड़ता है। विस्तृति-तालिका में स्तरिकीय प्रसार दर्शाये गये हैं। **रेटिस्टीफ़ेनोकॉल्पाइटिस विलियमसाई, स्पाइनीजोनोकॉल्पाइटिस** जातियाँ, **ट्राइकॉल्पाइटिस रेटिकुलेटस, प्रोक्सापर्टाइटिस** जातियाँ, **ऐंनाकोलोसिडाइटिस ल्यूटिऑयडिस** एवं **मार्जिनीपॉलिस** जातियों के कुछ वर्गक भारत एवं अफ्रीका दोनों में ही सामान्य हैं। अनंतिम आदिनूतन के बाद अनेक भारतीय एवं अफ्रीकी वर्गक नहीं मिलते; इनमें से कुछ भारत से अन्य देशों में स्थानान्तरित हो गये हैं जैसे **गोनीस्टाइलस (क्रिप्टोपोलीपोराइटिस)** मलेशिया में तथा **गुन्नेरा (ट्राइकॉल्प्पाइटिस रेटिकुलेटस)** ऑस्ट्रेलिया में। इन कल्पों में भारत की आपेक्षिक स्थिति तथा स्थानान्तरण से प्रारम्भिक तृतीयक कल्प में भारतीय परागाणुवनस्पतिजात की यथार्थता अन्वेषित की जा सकती है।

THANIKAIMONI *et al.* (1984) made an attempt to establish the relationship between Indian and African Tertiary pollen. This paper concerns with the same theme but restricts its investigation to the Lower Tertiary, viz., Palaeocene and Eocene. These two periods witnessed maximum development and subsequent diversification and spread of angiosperms in many directions. They registered a gradual decline in Upper Eocene and later in Lower Oligocene at a time when many global changes are recorded (Pomerol & Premoli-Silva, 1986). New groups of plants appeared while some faced extinction. Stratigraphic markers of India and western Africa (from Senegal to Gabon) are discussed. Reflections on floristic provinces in relation to the continental drift have been made.

COMPARATIVE STRATGRAPHIC RANGES IN INDIA AND AFRICA

The enclosed distribution chart (Text-fig. 1) is a result of detailed study of Palaeogene stratigraphic markers used in India and Africa. Certain difficulties were encountered in making this comparison as the taxonomic treatment is different in the two regions. With the publication of the atlas of Tertiary pollen by Thanikaimoni *et al.* (1984), some of the differences have been narrowed down It is hoped that with the publication of this comparative account this would further be narrowed down. to cite examples: African palynologists are familiar with the generic name *Echimonocolpites* which known as *Neocouperi-pollis* in India while *Longapertites brasiliensis* is known as *Matanomadhiasulcites*. We have not attempted any nomenclatural change till detailed comparative studies are accomplished.

Significant Indian marker pollen have been restudied either in Thanikaimoni *et al.* (1984) or in this paper. The geological background and the location of the sedimentary basins are detailed in Thanikaimoni *et al.* (1984)



Text-figure 1—Range chart of Palaeocene-Eocene stratigraphic markers in India and Africa: (1) = *Longapertites brasiliensis*, (2) = *Striatricolpites catatumbus*, (3) = *Echimonocolpites* spp.

The morphological complex of polycolpate pollen despite its high value for Eocene stratigraphy has not been considered here since a great taxonomic confusion does exist in this group which needs serious investigations (Caratini, 1983).

In Africa, the main features of the phytogeographical divisions in the Early Tertiary have been tentatively reconstructed by Raven (1978) and Smith *et al.* (1981). More recently, Bonnefille (1987) has insisted on the distinction between western and eastern parts of Africa because of the differences in the formation of the sedimentary basins. For this reason and because of only a few investigations carried out in the east compared to a large number of studies available on the western continental margin, only the west part is considered here. The African palynological data have been compiled mainly by Germeraad *et al.* (1968) and later in the papers published by numerous authors cited in the references.

RELATIONSHIP BETWEEN INDIAN AND AFRICAN PALYNOFLORA

There is only some similarity between the Early Palaeogene pollen flora of Africa and India since most of the taxa have been recorded only in either of the two countries. It is striking that the common taxa are mainly pantropical such as *Retistephanocolpites williamsi, Spinizonocolpites* spp., *Tricolpites reticulatus, Proxapertites* spp., *Anacolosidites luteoides* and *Marginipollis* spp. which exhibit almost the same stratigraphic range in both the countries. Nevertheless, certain species considered as pantropical by Germeraad *et al.* (1968), *Echitriporites trianguliformis*, for example, have not been recorded in India.

Other taxa occurring in both regions correspond to large morphological groups of extant genera, hence these have no definite botanical significance; *Margocolporites* as well as *Striacolporites-Striatricolpites* may have several living generic counterparts within Caesalpiniaceae. *Ctenolophonidites costatus* appears as a characteristic taxon since it occurs both in India and Africa but has not been recorded either in South America or in South-East Asia. No major phytogeographic conclusions can be drawn on this basis alone.

The dissimilarities of Palaeocene-Eocene floras of India and Africa could be explained due to continental position during this period (Text-fig. 2). India and Africa were distinctly apart as early as Late Cretaceous, and the gap between them did not favour the continuity and exchange of vegetation. A perusal of the chart eloquently exhibits an important feature in the pattern of extinction of many species in the terminal Eocene both in India and Africa. This also corroborates with the distributional pattern in other tropical areas (Germeraad *et al.*, 1968). Significant global events must have influenced such an extinction. Nevertheless, it will be demonstrated further that in India local causes have also contributed to such an extinction.

EVOLUTION OF THE PALAEOCENE-EOCENE PALYNOFLORA IN INDIA

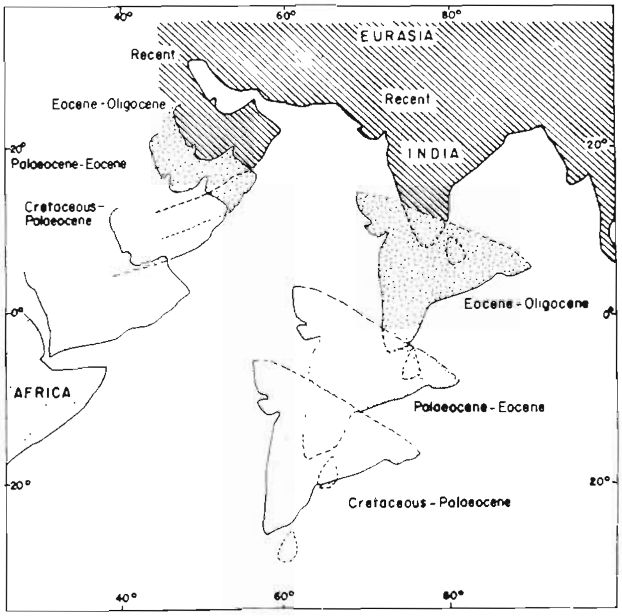
A careful analysis of the chart exhibits that during the Early Palaeogene the flora of India has been subjected to numerous changes. Many genera which are recorded in India during Palaeocene-Eocene either migrated or faced extinction. The extant genus *Durio* (Bombacaceae) may be cited here as an example. This modern genus represented by the pollen genus *Lakiapollis* is found in Palaeocene-Eocene sediments in several regions: Kutch, Kerala, Meghalaya and Assam. Post Eocene records of this pollen in India are absent till to-day. Nevertheless, pollen comparable to *Durio* have been recorded in Miocene and Post-Miocene sediments of Malaysia where the genus is now well established (Anderson & Muller, 1975; Barré de Cruz, 1982).

Similar examples of taxa which habitated in India during Eocene, became extinct in the Post-Eocene period, but are found in other continents even today, for example *Cryptopolyporites* (= *Gonystylus*, Gonystylaceae) now restricted to Malaysia, *Ctenolophonidites costatus* (= *Ctenolophon englerianus*, Ctenolophonaceae) presently in Africa or *C. philippinensis* in South-East Asia, *Retistephanocolpites* (= *Ctenolophon parvifolius*) now in South-East Asia. *Tricolpites reticulatus* (= *Gunnera*, Gunneraceae) and *Proteacidites* (= Proteaceae) now in Australia constitute examples of taxa that disappeared from India and established in disjointed areas: Malaysia, Africa, South America for the former; Australia and South Africa for the later.

Kielmeyerapollenites eocenicus Sah & Kar 1974 from the Palaeocene-Eocene appears closely comparable to extant pollen of the South American *Kielmeyera* (Clusiaceae). Other records of disjointed distribution between fossil and corresponding extant taxa are also known such as *Regnellidium* (Salviniaceae). This fresh water fern which was a common fossil of the Upper Cretaceous-Eocene Deccan Intertrappean flora (Sahni & Rao, 1943) is now restricted to South America. The extinction pattern in India may be related to two main causes:

1. Continental drift

India has been migrating northwards after Cretaceous-Palaeocene (Text-fig. 2). The changes in



Text-figure 2—Location and relative motion of Africa and India from the Cretaceous-Tertiary boundary to Recent (after Olivet *et al.*, 1987).

the latitudinal position and the resulting variations in climate may have been responsible for such extinction in India but these genera continued to live in other regions. While India was drifting and moving away from the equator, Malaysia attained more or less the same position during Oligocene-Miocene and this placement of Malaysia perhaps favoured the migration and subsequent settlement of genera such as *Durio* or *Gonystylus*. The relative position of Malaysia and India may have enabled intercontinental migration as advocated by Axelrod (1979).

2. Palaeogeographical condition of sedimentation

The Palaeocene-Eocene Indian palynoflora is recorded mainly from coal and lignite deposits of Meghalaya, Assam, Kutch, Cambay, Rajasthan and other basins. This palynoflora is fairly characterised by certain swamp dwellers such as the fossil pollen corresponding to *Barringtonia (Marginipollis)*, *Durio (Lakiapollis)*, *Gonystylus (Cryptopolyporites)*, *Nypa (Spinizonocolpites)* as well as associated floral elements including evergreen forest representatives related to Ctenolophonaceae (*Ctenolophonidites* and *Retistephanocolpites*), Olacaceae (*Anacolosidites*), Caesalpiniaceae (*Margocolporites* and *Striacolporites*). This swampy ecological condition did not dominate in these basins after Oligocene. The Neogene sediments of India are predominantly riverine deposits and the change in edaphic condition could have also led to the temporary disappearance of the swampy vegetation which occurred during the Palaeogene sequence. This is likely the explanation for the absence of *Spinizonocolpites-Nypa* during the Upper Palaeogene and the Lower Neogene. It occurs again in the Quaternary sediments of India (Thanikaimoni, 1987), and *Nypa* is still growing now-a-days in some parts of the Indian coastal areas such as Sunderbans and Andaman Islands. This riverine depositional process might also explain the occurrence of Permian, Early Cretaceous and Palaeogene reworked pollen in the Neogene basins. These reworked pollen have been the reason for apparent extension of some of Palaeogene taxa into Neogene.

SYSTEMATIC PALYNOLOGY

Inaperturate

Genus—*Retipollenites* González Guzmán 1967

Pl. 1, figs 1-6; Pl. 2, figs 1-6

Original diagnosis—"Pollen grains with a heavy reticulum that is apparently not placed on a basal layer. Apparently there are no apertures. There seems to be no clear similarities with other genera."

Species studied—*Retipollenites confusus* González Guzmán 1967 and *R. confusus* Rawat *et al.* 1977 (*Cheilanthoidspora monoleta* Sah & Kar 1974, illustrated in Kar, 1985, pl. 22, fig. 1 and *C. enigmata* Sah & Kar 1974, illustrated in Kar, 1985, pl. 22, fig. 2 are here attributed to *Retipollenites* sp.).

Description :

Symmetry and form: Subsphaeroidal to oval.

Dimension :	50-85 μm.
Aperture :	Inaperturate.
Exine :	Tectate
Sexine :	Broadly reticulate, meshes 8-15 μm broad, forming subcircular-rhomboidal-various shaped meshes, muri 2-4 μm thick displaying prominent attachment to the nexine, lumina 4-15 μm wide.
Nexine :	± 1 μm thick, continuous.
Variability :	Quite variable in shape and size; the reticulate pattern is loose to strictly adhered to the body.

Occurrence—Very common in Middle Eocene sediments in western India.

Remarks—*Spirosyncolpites* González Guzman 1967, *Retipollenites* González Guzmán 1967, *Praedapollis* (Boltenhagen & Salard) Legoux 1978, *Periretitricolpites* Jan du Chêne *et al.* 1978 and *Cambonaepollenites* Kedves 1986 share in common the overall organization consisting of a subsphaeroidal body enmeshed in a broad reticulum. *Spirosyncolpites* according to González Guzmán (1967) is "syncolpate", the furrow forming a helix which is often not clearly visible.

Praedapollis is triporate as exemplified by Salard-Cheboldaeff, 1977 (pl. 19, fig. 10) but Legoux (1978) in her emendment of the genus *Praedapollis* opines that the pollen is triaperturate with sometimes reduced colpi or apertures not discernible. *Periretitricolpites* Jan du Chêne *et al.* 1978 is tricolpate.

In a large number of specimens of *Retipollenites* studied, the authors have not been able to recognize any aperture. Some specimens of *Cheilanthoidspora monoleta* and *C. enigmata* described by Kar (1985) exemplify a clear disposition of the body bearing the columellae structure supporting the reticulum; the body is never seen detached or free of reticulum. These specimens not showing germinal apertures are now attributed to *Retipollenites*. However, *Cheilanthoidspora monoleta* (Sah & Kar, 1974: pl. 1, figs 11-14) and *C. enigmata* (Sah & Kar, 1974: pl. 1, figs 7-10) show distinct monolete and trilete apertures. It is possible that some of the *Cheilanthoidspora* could also show alete disposition. The attribution of individuals either to *Cheilanthoidspora* or *Retipollenites* rests on the nature of exine stratification.

Fossil Records :

India :

Kutch

Lower Eocene, Middle Eocene to ? Upper Eocene, *C. enigmata* Kar 1985, pl. 22, fig. 2.

Middle Eocene to ? Upper Eocene, *Cheilanthoidspora enigmata* Kar & Saxena 1981, pl. 2, figs 22, 23.

Cambay

Lower-Middle Eocene, *Retipollenites confusus* Rawat *et al.* 1977, pl. 3, figs 108, 109.

Affinity—Unknown.

Monosulcate

Genus—*Matanomadhiasulcites* Kar 1985

Pl. 3, figs 1-4; Pl. 4, figs 1-13

Original diagnosis—"Pollen grains oval-elliptical in shape. Monosulcate, sulcus distinct to indistinct, almost extending end to end. Exine retipilate-retibaculate".

Species studied—*Matanomadhiasulcites maximus* (Saxena) Kar 1985, *Matanomadhiasulcites kutchensis* (Saxena) Kar 1985, and *Matanomadhiasulcites* sp., Pl. 3, figs 1-4.

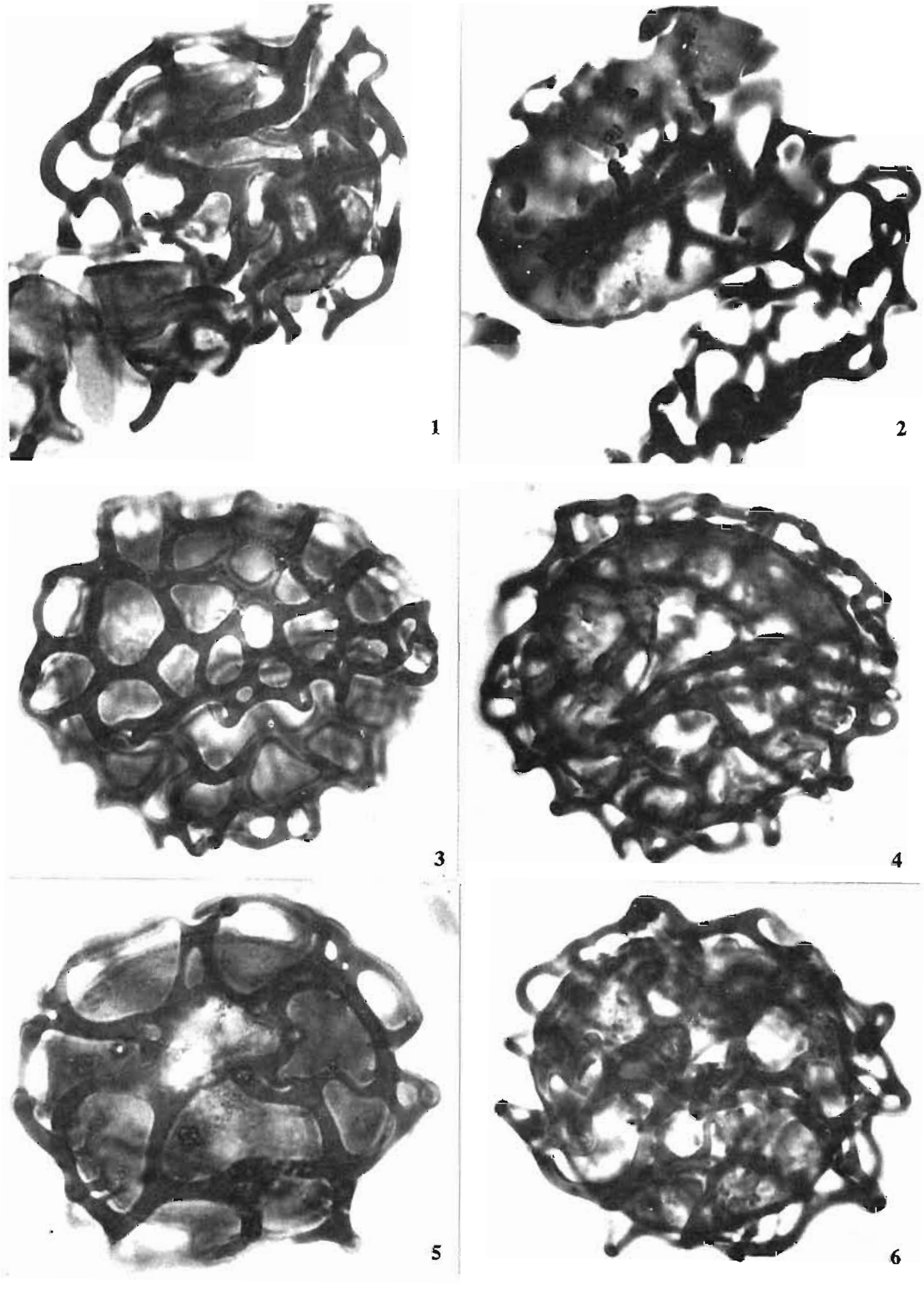


PLATE 1

(All photomicrographs magnified, × 1000)

1-6. *Retipollenites confusus,* Lower to Middle Eocene, Kutch

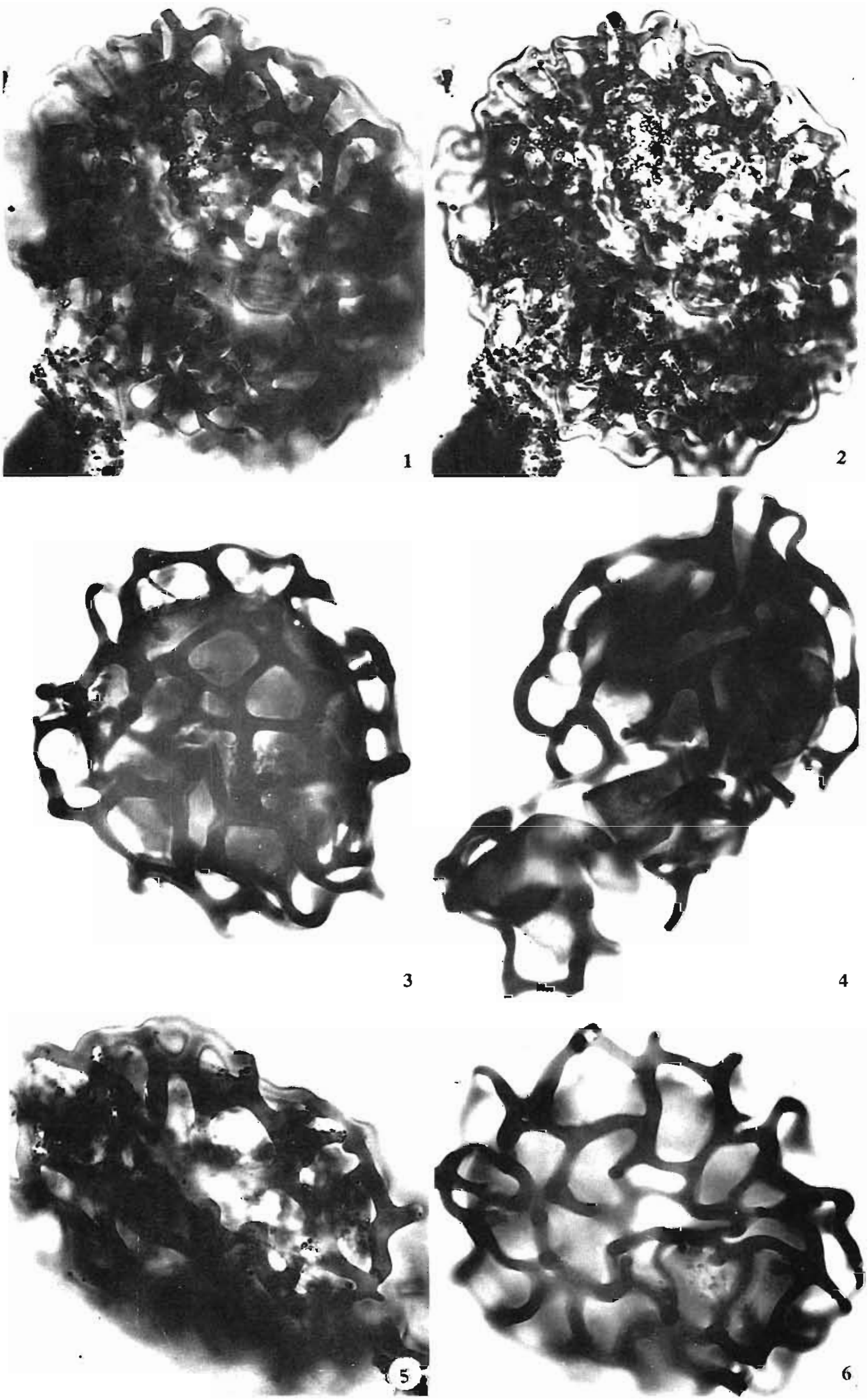


PLATE 2

(All photomicrographs magnified, × 1000)

1, 2. *Retipollenites confusus*, Lower to Middle Eocene, Cambay 3-6. *R. confusus*, Lower to Middle Eocene, Kutch

Description :

Symmetry and form: Heteropolar, oval to elliptical in shape, rarely observed in tetrad.

Dimension : 60-205 × 35-145 μm.

Aperture : Single, in shape of furrow, often simulating a sulcus, or ill-defined as it may occur in isolated monads showing scar from the original tetrad.

Exine : Tectate.

Sexine : Tectum 2-4 μm thick, perforate, size of perforations variable; infratectum columellar; columella 3-8 μm thick, 1-2, 5 μm broad, closely placed.

Nexine : Discontinuous.

Variability : Quite variable in size and shape; the texture of the sexine is more or less constant in individual specimens though variations are observable between two individuals.

Occurrence—*Matanomadhiasulcites* is common (up to 5%) in the Palaeocene of India. It is rare in Africa and America.

Remarks—The genus *Matanomadhiasulcites* has not been accommodated in *Longapertites* since the type species *L. marginatus* defined by van Hoeken-Klinkenberg (1964) has two types of reticulation pattern on the exine, coarser on the distal area opposite the aperture and thinner on the rest of the area and on the proximal side. Moreover the diagnosis of the genus *Longapertites* is broad enough to accommodate all the fossil pollen with "one aperture longer than half the greatest circumference of the grain". It is necessary to closely circumscribe genera and hence *Matanomadhiasulcites* has been maintained.

Tetrads have rarely been found in India; González Guzmán (1967) mentions tetrads as common in *Longapertites brasiliensis*.

Fossil Records :

India :

Kutch

Palaeocene, Liliacidites kutchensis Saxena 1979, pl. 1, figs 9, 10.

Matanomadhiasulcites maximus Kar 1985, pl. 3, figs 1, 2.

Lower Eocene, *Liliacidites baculatus* Venkatachala & Kar 1969, pl. 1, fig. 17.

cf. *Liliacidites* Sah & Kar 1970, pl. 1, fig. 21.

Matanomadhiasulcites maximus Kar 1985, pl. 10, fig. 3.

Meghalaya

Palaeocene, *Matanomadhiasulcites maximus* Kar & Kumar 1986, pl. 5, fig. 5 and pl. 6, fig. 1

Liliacidites microreticulatus Dutta & Sah 1970 from Palaeocene of Meghalaya does not show a reticulate exine with smaller meshes near the ends, as stated in the original diagnosis of *Liliacidites* (Couper, 1953) and is regarded belonging to the genus *Matanomadhiasulcites*.

Africa :

Niger (Sougheera)

Upper Eocene, *Matanomadhiasulcites* sp., Pl. 3, figs 1-4; Pl. 5, figs 5-13 (Thanikaimoni *et al.*, in press).

The illustrations given by the following authors can be considered as corresponding to pollen belonging to this same morphological group.

Eocene, *Liliacidites* cf. *L. vaneendenburgi* Boudouresque, 1980, pl. 5, fig. 14a.

Longapertites brasiliensis Boudouresque 1980, pl. 6, figs 1a, 1b.

Cameroun

Eocene and Oligocene, *Longapertites brasiliensis*, Salard-Cheboldaeff, 1977, pl. 7, fig. 6, p. 156.

South America :

Venezuela

Palaeocene, *Proxapertites maracaiboensis*, Muller *et al.*, 1987, pl. 2, fig. 1.

Eocene, cf. *Liliacidites* sp. B Muller *et al.* 1987, pl. 1, fig. 7.

Columbia

Middle Eocene, *Longapertites brasiliensis* González Guzmán 1967, pl. 25, figs 1-1a.

North America :

Texas

Palaeocene, *Schizosporis palaeocenicus* Elsik 1968, pp. 284-285, pl. 5, fig. 3, named in Elsik 1970 as *Annona ?paleocenicus* (p. 99) after the fossil recorded by Warter (1965) in the Lower Eocene from Mississipi.

Affinity—González Guzmán attributes affinity with Annonaceae for *Longapertites brasiliensis*. Some specimens of *Matanomadhiasulcites* studied and illustrated here (Pl. 3, figs 1-4; Pl. 4, figs 5-13) are comparable to some genera of Annonaceae, particularly *Annona* (Pl. 3, figs 5-7) because of the general structure of the exine and the shape of the aperture (A. Le Thomas, in *litt.*), but for most of them, a monocotyledonous affinity (*i.e.* Liliaceae, Agavaceae, etc.) may be stated. Muller (1981) has rejected the affinity with *Annona* given by Warter (1965) and Elsik (1970) for the Palaeocene fossils from Mississipi and Texas.

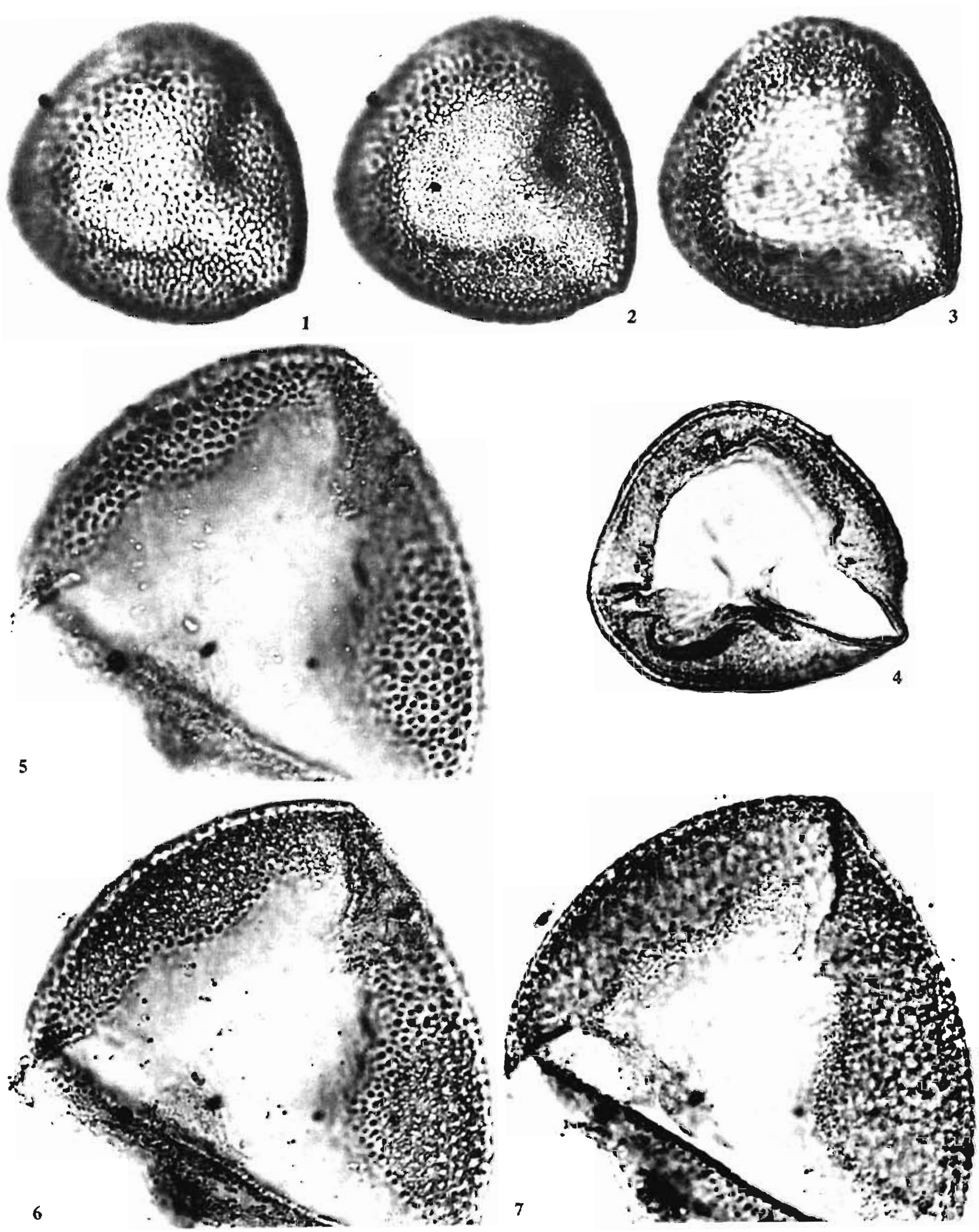


PLATE 3

(All photomicrographs magnified, × 100)

1-4. *Matanomadhiasulcites* sp., Upper Eocene, Sougheera, Niger: 1-3. distal side; 4. proximal side

5-7. *Annona longiflora* S. Wats (slide HIFP 20232)

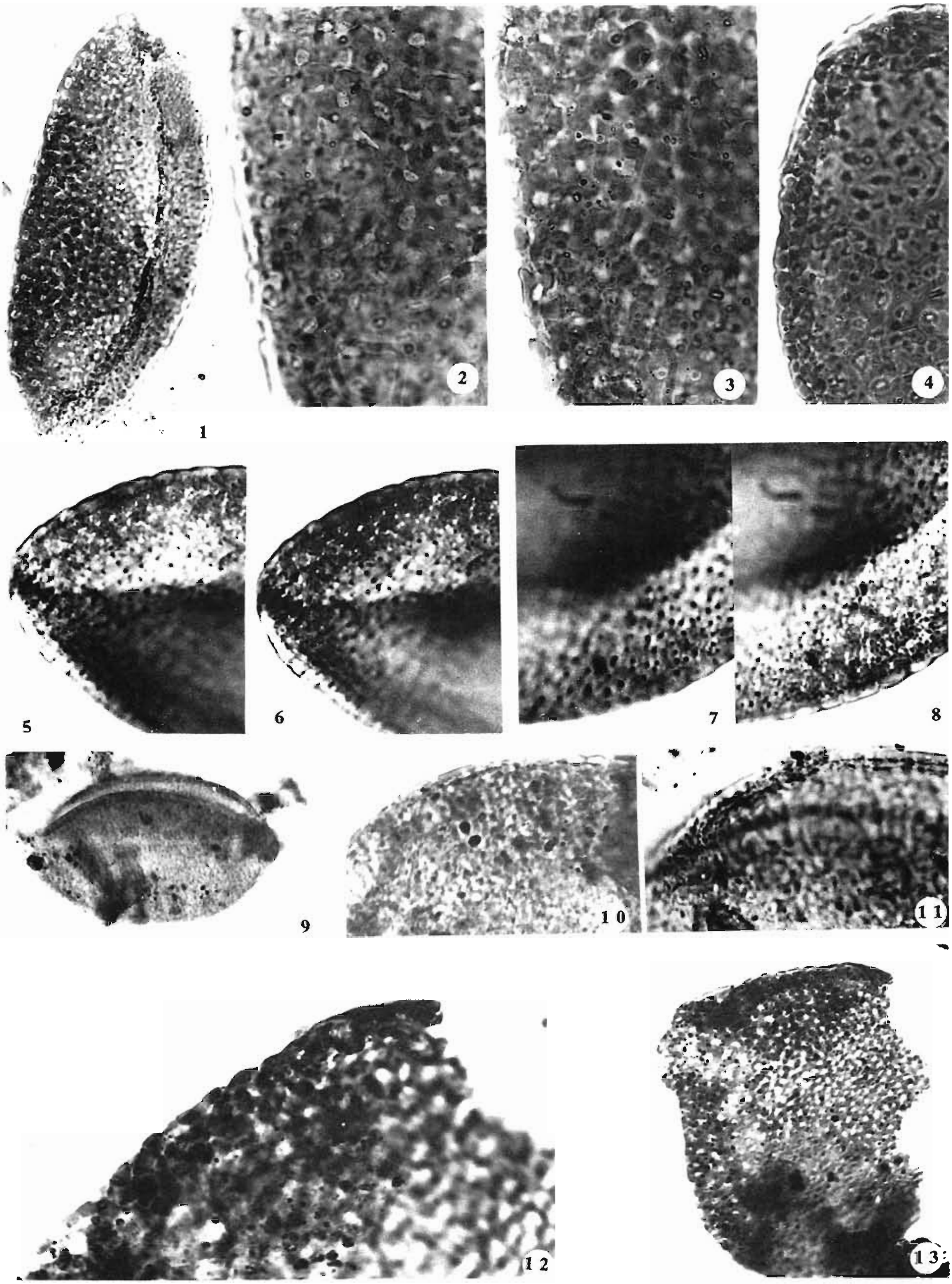


PLATE 4

1-4. *Matanomadhiasulcites maximus*, Palaeocene, Meghalaya, India (1, × 400; 2-3 × 1000)

5-13. *Matanomadhiasulcites* sp., Upper Eocene, Sougheera, Niger (5-8, 10-12), × 1000; 9, 13, × 400)

Tricolpate

Genus—*Tricolpites* Cookson (1947) ex Couper (1953) emend. Potonié 1960

Pl. 5, figs 1-11

Species studied—Tricolpites reticulatus Cookson 1947.

Description :

Symmetry and form : Subprolate to oblate, circular in polar view, often trilobate.
Dimension : 17-30 μm.
Aperture : Tricolpate, colpi long forming a small polar triangle.
Exine : ± 1.5 μm; reticulate, reticulum fine.
Sexine : ± 1 μm, reticulate; infratectum columellate.
Nexine : Continuous, as thick as sexine and thicker near the colpi.
Variability : Not much neither in shape, size nor ornamentation.

Occurrence—Common in India.

Fossil records—T. reticulatus is a very well known morphological taxon, pantropical, ranging from Turonian to Recent (for further details see Kemp & Harris, 1977 or Muller 1981, besides other authors).

In India, *T reticulatus* is a fairly good stratigraphic marker of Palaeocene and Eocene, named differently by various authors (listed below). Well documented pollen having the general organization and reticulate ornamentation of *Gunnera* type as exemplified in the type species is considered here.

India :

Kutch

Palaeocene-Eocene, *Intrareticulites (Tricolpites) brevis* Kar 1985, pl. 14, figs 1, 2.
Lower Eocene, *Tricolpites* sp. Venkatachala & Kar 1969, pl. 2, fig. 50.
T. brevis Sah & Kar 1970, pl. 1, fig. 6.

Cauvery

Palaeocene-Miocene, *Retitricolpites peroblatus* Venkatachala & Rawat 1972, pl. 2, figs 20, 21.
Tricolpites longicolpatus Venkatachala & Rawat 1972, pl. 2, figs 16-19.

Ladakh

Eocene-Miocene, *Tricolpites* sp. Bhandari *et al.* 1977, pl. 2, figs 1-5, 10.
T reticulatus Mathur & Jain 1980, pl. 1, fig. 17

Meghalaya

Palaeocene, *Tricolpites reticulatus* Kar & Kumar 1986, p. 179 (not illustrated).

Affinity—Gunnera (Gunneraceae); see Praglowski (1970) and Muller (1981), besides other authors, for a detailed discussion.

Ecology and present distribution—Palkovic (1974) and Jarzen (1980) provided data on *Gunnera* ecology (herbs of tropical and south temperate super humid environment) and present distribution (Kenya, Tanzania, South Africa, Malagasy Republic, Malaysia, Solomon Islands, Tasmania, New Zealand, Hawaii, Mexico southward to Chile and Argentina); for distribution map, see Good, 1953, p. 116.

Triporate

Genus—*Proteacidites* (Cookson, 1950) ex Couper 1953

Pl. 6, figs 1-3

Species studied—Proteacidites protrudus Sah & Kar 1970.

Original diagnosis—"Pollen grains triangular, 50-60 × 48-55 μm, 3 porate, pore distinct. Exine finely scrobiculate".
Holotype illustrated in Sah and Kar, 1970, pl. 2, fig. 61.

Description :

Symmetry and form : Isopolar, triangular in polar view.
Dimension : 50-60 μm.
Aperture : Triorate, ora situated at the extremities of the triangle, 6-8 μm large.
Exine : Tectate, reticulate
Sexine : 1 μm thick, finely reticulate, meshes < 1 μm; simplicolumellate, columellae long.
Nexine : Continuous, 1 μm thick, becoming thinner near the apertures.
Variability : Not much.

Occurrence—Commonly observed in Palaeocene-Lower Eocene sediments, rare in Middle Eocene.

Fossil records :

India :

Kutch

Palaeocene, *Proteacidites protrudus* Saxena 1979, pl. 3, fig. 55.
Lower Eocene, *P protrudus* Sah & Kar 1970, pl. 2, fig. 61.

Affinity—Proteaceae. Martin and Harris (1974, p. 109) included this species in the genus *Proteacidites* Cookson & Couper 1953 (emend. Martin & Harris, 1974) and compared it with the extant species of the tribes Proteae and Personieae. *Proteacidites dehaani* Germeraad *et al.* 1968, marker

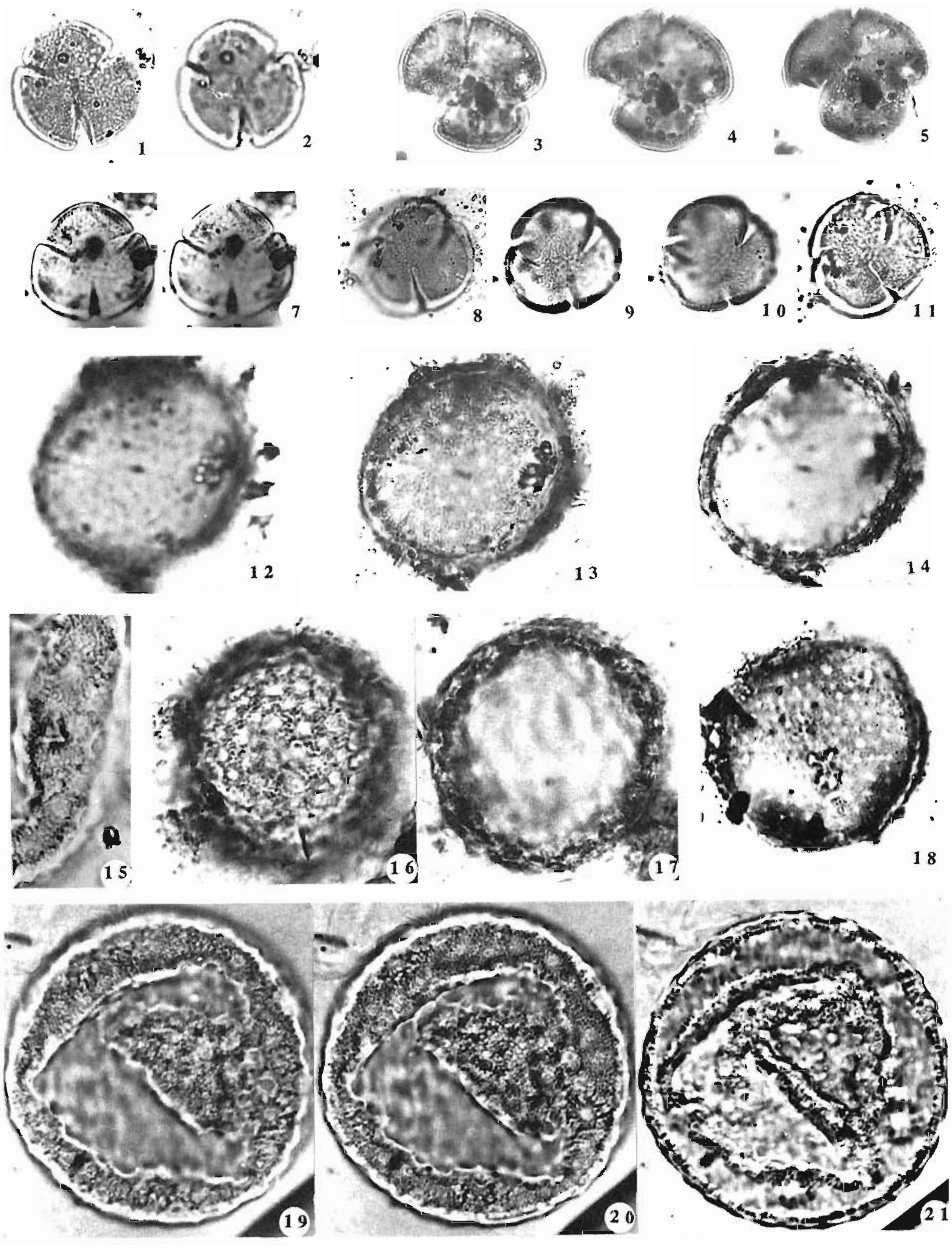


PLATE 5

(All photomicrographs magnified, × 1000)

1-11. *Tricolpites reticulatus*, Lower Eocene, Kutch

12-14. *Cryptopolyporites cryptus*, holotype, Lower Eocene, Kutch

16-18. *C. cryptus*, Lower Eocene, Kutch

15, 19-21. *Gonystylus maingayi* Hook. f., Recent

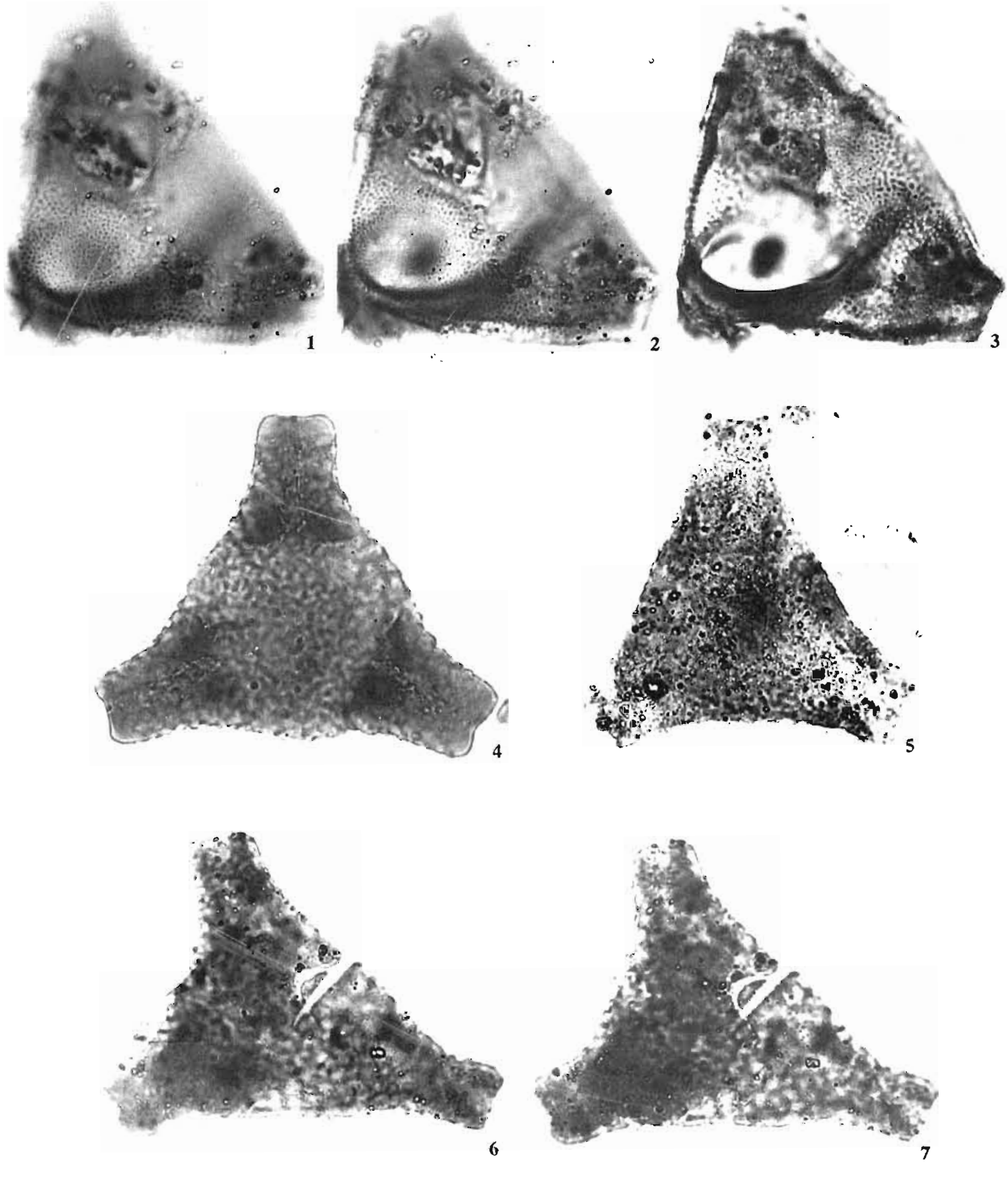


PLATE 6

(All photomicrographs magnified, × 1000)

1-3. *Proteacidites protrudus*, Lower Eocene, Kutch

4. *Triangulorites pachyexinus*, holotype, Palaeocene, Meghalaya

5-7. *T pachyexinus*, Palaeocene, Meghalaya of Maastrichtian in Africa, is different since it is duplicolumellate, with smaller pores.

Genus—*Triangulorites* Kar 1985
Pl. 7, figs 1-8

Original diagnosis—"Pollen grains triangular-subtriangular in polar view, tri- to tetraorate, ora distinct, present on each extended arm. Exine granulose-conied, forming negative reticulum in surface view".

Species studied—Triangulorites bellus (Sah & Kar) Kar 1985; Holotype is illustrated in Sah & Kar, 1970, pl. 2, fig. 70; Kar, 1985, pl. 19, figs 7, 8 and in this paper, Pl. 7, figs 1-4.

Description :

Symmetry and form : Generally isopolar, triangular-subtriangular in polar view with a circular central body and three projecting arms.

Dimension : Pollen body without apertures, 35 × 60 μm; arms 10-35 μm long and 10-18 μm broad.

Aperture : Generally triorate, may be rudimentarily tetraorate; ora situated on atrium-extended tubular processes. Os ends mostly opening in the form of a bowl.

Exine :

Sexine : ± 1 μm thick, granular, forming negative reticulum, more pronounced and specially concentrated at the base of the arms.

Nexine : ± 1 μm thick on the pollen body and 2-3 μm thick at the base of the arm in the form of arcuate angular thickenings in sectional view.

Variability : Variable in size, number and length of extended arms.

Occurrence—Common in Palaeocene-Lower Eocene pollen assemblages of India.

Remarks—*Hakeidites martinii* Khan 1976 (fig. 22), is described from the Pliocene of Papua and New Guinea. This is a grossly comparable pollen with *Guettarda* and *Timonius*. *Hakeidites* is tectate, columellate with concentration of structure on the body region. The apertural arm is also distinctly different. *Propylipollis* Martin & Harris 1974 (fig. 2G), from Lower Tertiary, Australia, has an atrium not protruding as in *T. bellus* and the reticulum is simplior pluricolumellate.

Fossil records :

India :

Cambay

Lower Eocene, *Triorites* cf. *T. inferius* (Dutta & Sah) Rawat *et al.* 1977, pl. 2, fig. 81.

Kutch

Palaeocene, *Triorites bellus* Saxena 1979, pl. 3, fig. 53.

Palaeocene-Lower Eocene, *Triangulorites bellus* Kar 1985, pl. 4, fig. 7 and pl. 19, figs 6-8.

Lower Eocene, *Triorites bellus* Sah & Kar 1970, pl. 2, fig. 70.

Meghalaya

Palaeocene, *Triorites communis* Sah & Dutta 1966, pl. 2, figs 34, 36-38; this taxon seems to belong to the same species but could not be confirmed as the type slide is missing).

Proteacidites excertus Dutta & Sah 1970, pl. 9, figs 25, 26; this taxon also seems to belong to the same species but could not be confirmed as the type slide is missing.

Triangulorites bellus Kar & Kumar 1986, pl. 10, figs 13, 14, 16.

Kerala

Lower Eocene, *T. bellus* Raha *et al.* 1986a, pl. 1, fig. 14.

Rajasthan

Lower Eocene, *Triorites hirsutus* Sah & Kar 1974, pl. 2, fig. 53.

Bengal

Palaeocene-Lower Eocene, *Proteacidites* sp. Baksi 1972, text-fig. 2.

Affinity—Unknown. Some proteaceous types, more particularly within Grevilleae tribe, show a grossly comparable general aspect, but in *Triorites bellus*, the structure of the apertures, with long and strong extended arms, is distinct; besides, the exine ornamentation is granulose-conied instead of reticulate.

Polyporate

Genus—*Cryptopolyporites* Venkatachala & Kar 1969
Pl. 5, figs 12-14, 16-18

Original diagnosis—"Pollen grains circular in polar view. Panporate. Pores hidden, not easily recognisable, covered with baculate processes as in non-porate region".

Species studied—Cryptopolyporites cryptus Venkatachala & Kar 1969.

Description :

Symmetry and form : Sphaeroidal.

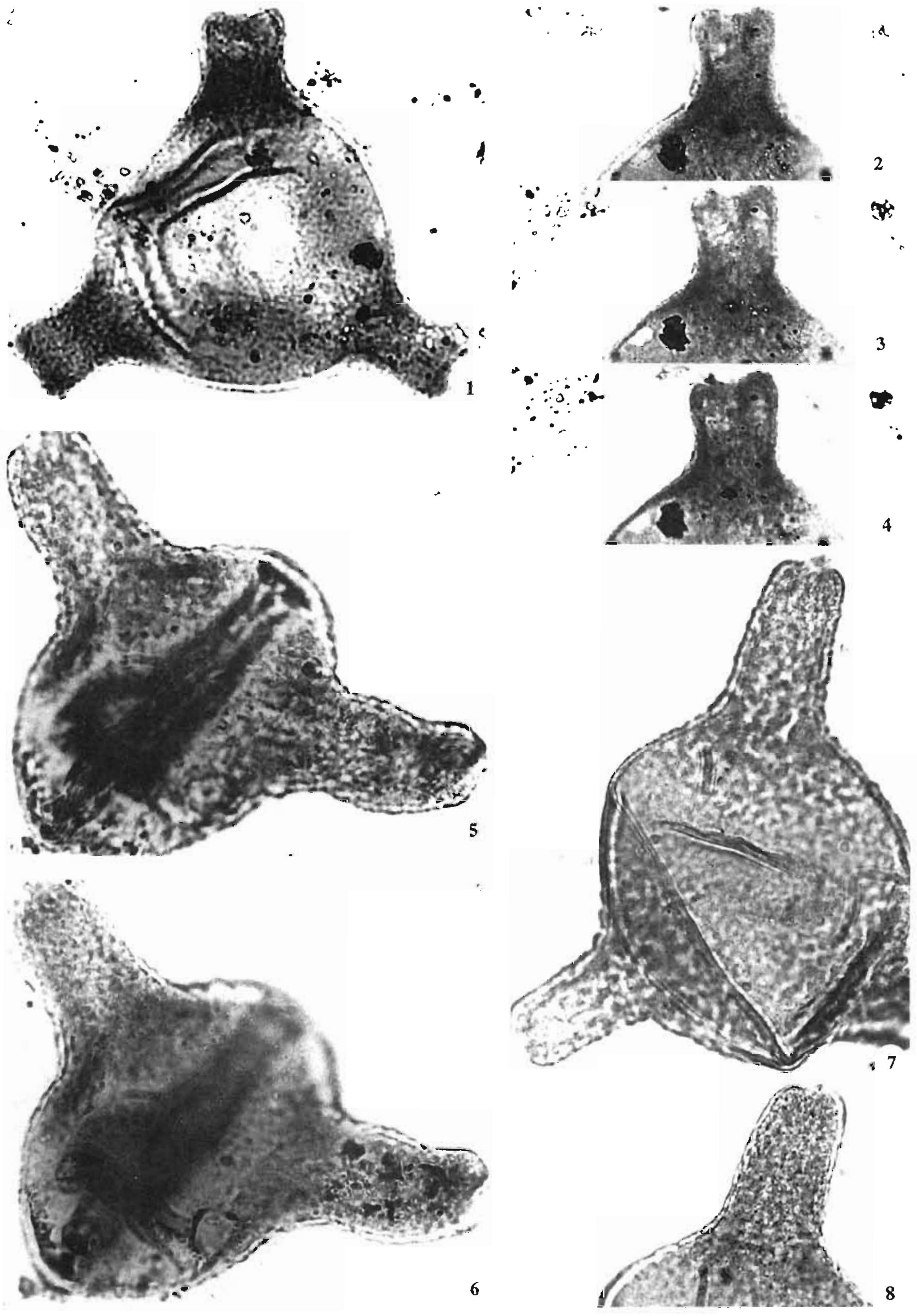


PLATE 7

(All photomicrographs magnified, × 1000)

1-4. *Triangulorites bellus*, holotype, Lower Eocene, Kutch. 5-8. *T. bellus*, reworked in Miocene, Tripura.

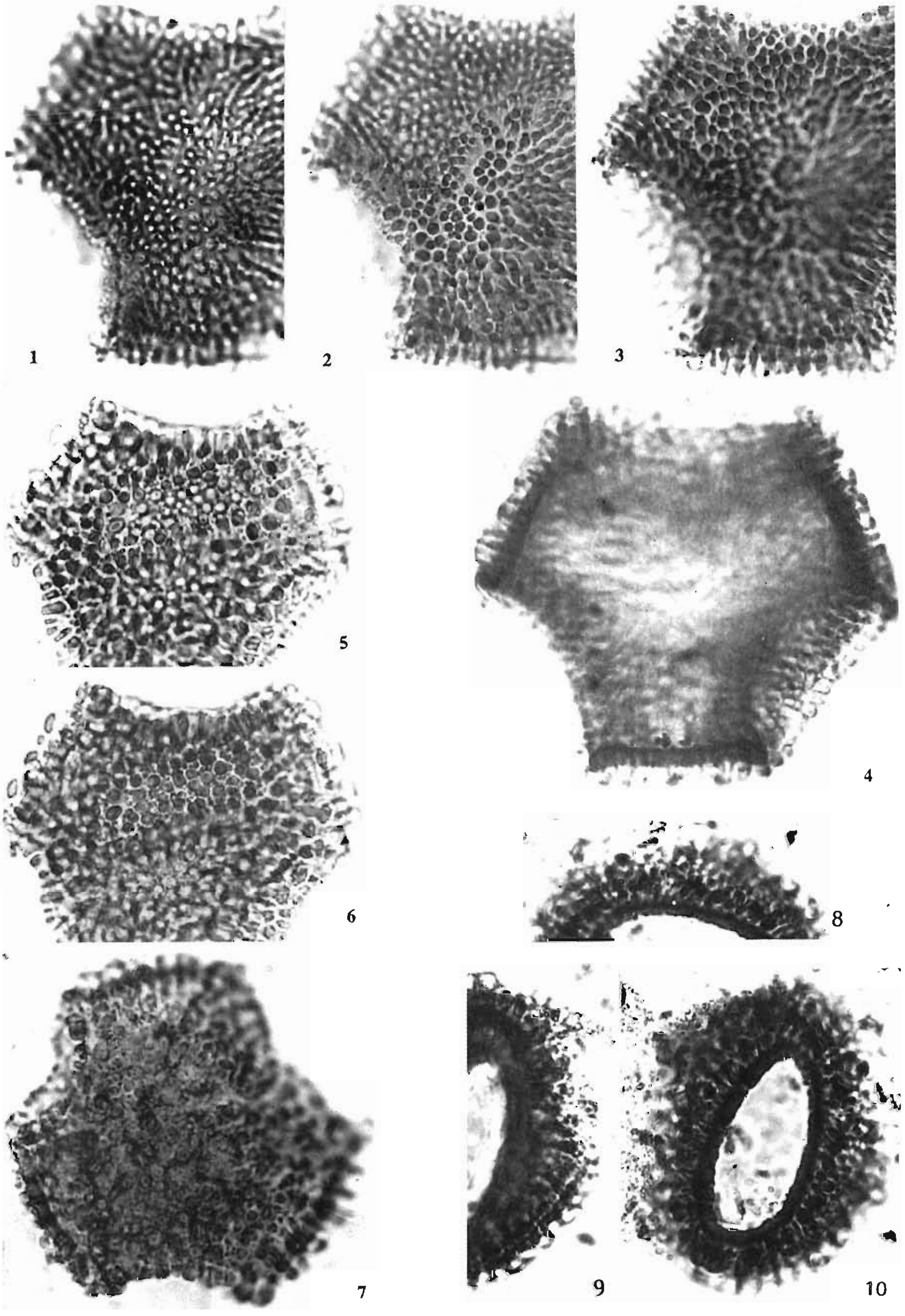


PLATE 8

(All photomicrographs magnified, × 1000)

1-10. *Tripilaorites triangulus*, Miocene (reworked), Tripura

8-10. Showing details of the ora.

Dimension : 40-50 μm.
Aperture : Periporate, it is difficult to discern the number of pores, not uniformly distributed; pores 1-2 μm, sub-circular-circular, obscured in the structure.
Exine : 2-3 μm, tectate.
Sexine : Foveolate, tectum undulating; infra-tectum columellar
Nexine : Not as thick as sexine, seems to be discontinuous.
Variability : Negligible.

Occurrence—Rare.

Fossil records :

India :

Kutch
Lower Eocene, *Cryptopolyporites cryptus* Venkatachala & Kar 1969, pl. 2, fig. 28.

Affinity—Gonystylaceae (Pl. 5, figs 15, 19-21). According to Nowicke *et al.* (1985) this family has a uniform type of pollen The oldest occurrence of fossil pollen is from Oligocene of Borneo (Muller, 1972).

Ecology and distribution of modern genera—Fresh water peat swamp forests from Malaysia to Solomon and Fiji. Now-a-days, this family is no more represented in India.

Genus—*Triangulorites* Kar & Kumar 1986
Pl. 6, figs 4-7

Holotype—Illustrated in Kar & Kumar, 1986, pl. 10, fig. 18.

Species studied—*Triangulorites pachyexinus* Kar & Kumar 1986.

Description :
Symmetry and form : Isopolar, triangular-subtriangular in polar view with three projecting arms.
Dimension : Pollen body without aperture 30-40 μm, arms 20-25 μm long and ± 15 μm broad at basal part.
Aperture Generally triorate, ora situated on extended tubular atrial processes. Os ends opening, slightly broadening.
Exine :
Sexine : ± 1.5μm thick, reticulate, reticulum not uniform; muri sinuous, larger at the base with a more or less dome-shaped section, about 1 μm wide, narrower than lumina.
Nexine In central body 1.5 μm thick and up to 10 μm thick at the base of the arm, thickening restricted and uniform in arm.
Variability : Not much.

Occurrence—Common in Palaeocene of Meghalaya.

Fossil records :

India :

Meghalaya
Palaeocene, *Triangulorites pachyexinus* Kar & Kumar 1986, pl. 10, figs 11, 17, 18.
Triorites sp. Sah & Dutta 1966, pl. 2, fig. 35.

Cauvery
Palaeocene-Lower Eocene, *Triorites tubiferus* Venkatachala & Rawat 1972, pl 3, fig. 33.

Affinity—Unknown.

Genus—*Tripilaorites* Kar 1985
Pl 8, figs 1-10

Holotype—Illustrated in Sah & Kar, 1970, pl. 2, fig. 53.

Original diagnosis—"Pollen grains triangular in polar and oval in equatorial view; Triorate, ora very large, distinct. Exine pilate-baculate"

Species studied—*Tripilaorites triangulus* (Sah & Kar) Kar 1985.

Description :
Symmetry and form : Hexagonal in polar and oval in equatorial view.
Dimension : 28-55 μm.
Aperture : Triorate, ora elliptical occupying the entire concave side of the hexagon.
Exine : 5-7 μm, pilate.
Sexine : 1.5-3 μm, pilate; pila 3-5 μm long with broad heads, 2-4 μm apart, interpilar space granulate.
Nexine : 1-3 μm, continuous.
Variability : In size but not in shape or ornamentation.

Occurrence—Common in some Lower Eocene sediments

Fossil records .

India ·

Kutch
Palaeocene Lower Eocene, *Tripilaorites triangulus* Kar 1985, pl. 19, figs 1, 2.

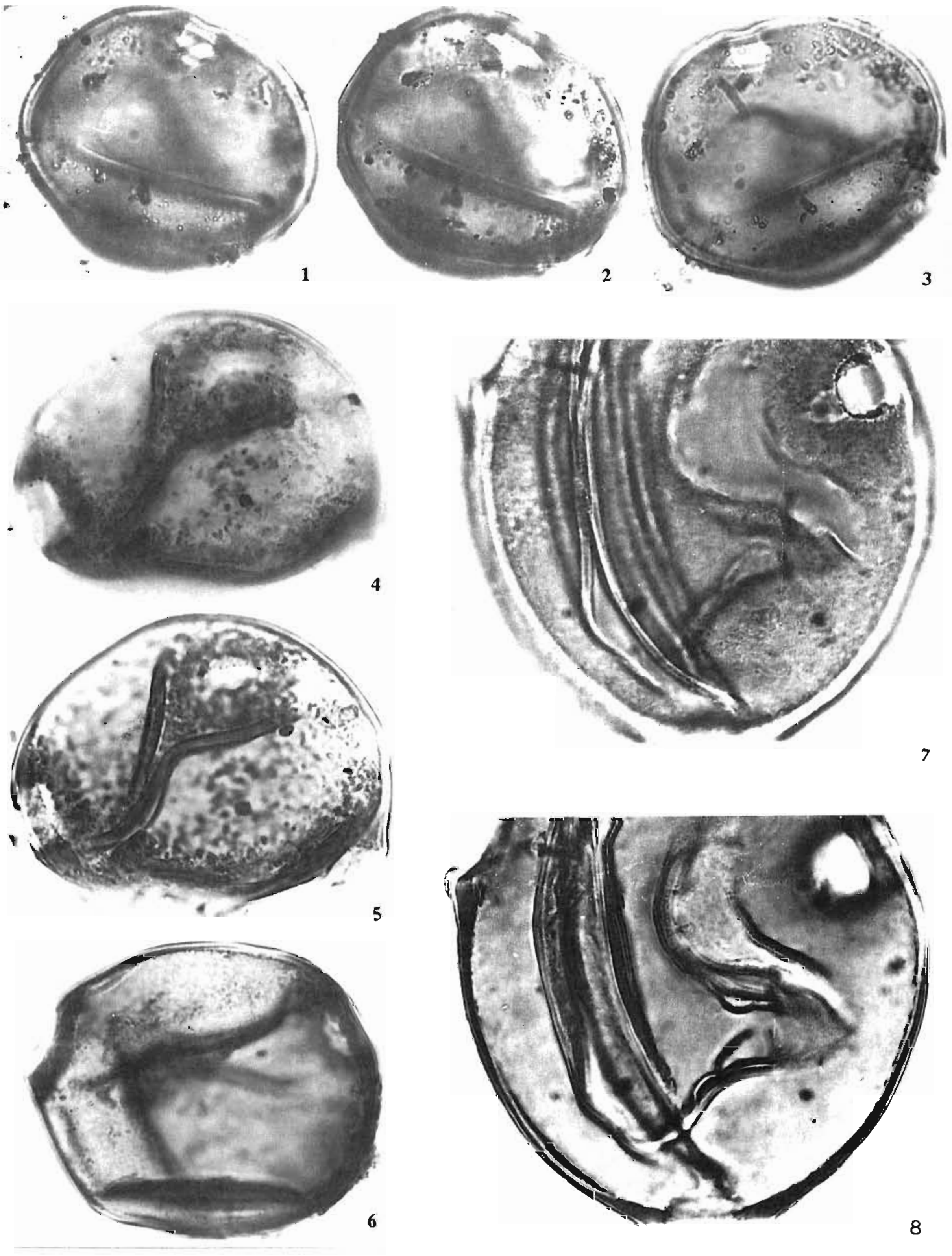


PLATE 9

(All photomicrographs magnified, × 1000)

1-6 *Lakiapollis ovatus*, Lower Eocene, Kutch

7, 8. *Durio conicus* Beccari, recent

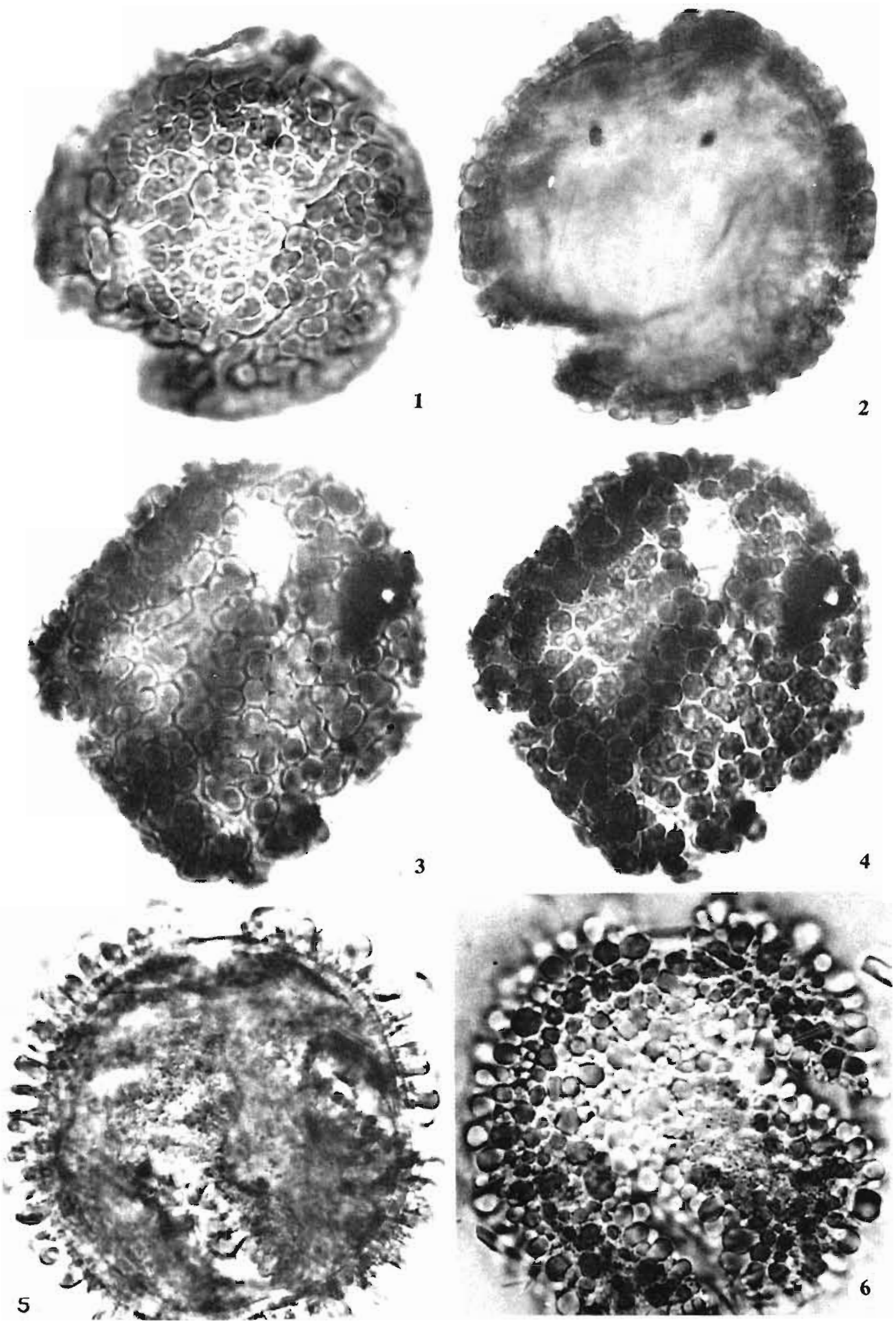


PLATE 10

(All photomicrographs magnified, × 1000)

1-4. *Tricolporopilites robustus*

5, 6. *Alangium villosum*, recent

Lower Eocene, *Tripilaorites triangulus* Sah & Kar 1970, pl. 2, fig. 53.

Tripura

Miocene, as reworked (Kar, unpublished report).

Remarks—Cranwellipollis tortuosus Martin & Harris 1974 is comparable but is distinguished by its ± sphaeroid shape and smaller oral area while *Tripilaorites* is hexagonal with ora occupying the entire breadth of a side of a hexagon. The differences with *Triorites magnificus* Cookson 1950 have been discussed in Kar, 1985 (p. 88). Pocknall and Crosbie (1988) published (pl. 12, fig. 5) a pollen grain attributed to *Beaupreaidites verrucosus* Cookson 1950 which shows a general resemblance to *Tripilaorites triangulus* in overall shape but the former is distinguished by its main features and particularly by consistent microreticulation and tricolpoid aperture.

Affinity—Unknown.

Tricolporate

Genus—*Lakiapollis* Venkatachala & Kar 1969

Pl. 9, figs 1-6

Original diagnosis—"Pollen grains subcircular-circular in polar view. Tricolporate, brevicolpate, colpi narrow. Pores well-developed, oval-elliptical in shape, broader than the colpus. Exine laevigate and infra-structured". For description and ecology, see Thanikaimoni *et al.*, 1984, p. 39. The type species *L. ovatus* Venkatachala & Kar 1969, pl. 3, fig. 77 is reillustrated here.

Species studied—L. ovatus Venkatachala & Kar 1969.

Occurrence—Common in India.

Remarks—Venkatachala and Kar (1969) included pollen grains with both smooth as well as ornamented pattern under *Lakiapollis*. *Lakiapollis* is now restricted to psilate-scabrate pollen as stated in the original diagnosis. *L. matanamadhensis* earlier accommodated under this genus has been transferred to *Retitribrevicolporites* Kar 1985, since *L. matanamadhensis* has a reticulate exine while *L. ovatus* has a psilate exine.

Fossil records :

India :

Kutch

Palaeocene, *Lakiapollis matanamadhensis* Saxena 1979, pl. 2, fig. 37 and pl. 3, fig. 38.

Palaeocene-Lower Eocene, *L. ovatus* Venkatachala & Kar 1969, pl. 3, figs 77-78.

Palaeocene-Lower Eocene, *L. ovatus* Kar 1985, pl. 17, figs 7-9.

Eocene, *L. ovatus*, in Thanikaimoni *et al.*, 1984, pl 20, figs 301-305 and pl. 21, figs 306-309.

Lower Eocene-Middle Eocene, *L. ovatus* Kar 1978, p. 163 (not illustrated).

Middle Eocene-? Upper Eocene, *L. ovatus* Kar & Saxena 1981, pl. 4, fig. 67

Assam

Eocene, *L. ovatus*, Kar, unpublished report.

Meghalaya

Palaeocene, *L. ovatus* Kar & Kumar 1986, pl 8, fig. 3.

Upper Eocene, *L. ovatus* Trivedi (unpublished).

Kerala

Lower Eocene, *L. ovatus* Raha *et al.*, 1986a, pl. 1, figs 17, 19 and 1986b, pl. 1, figs 7, 8.

Miocene (reworked), *L. ovatus* Kar & Jain 1981, pl 3, fig. 9 and pl. 4, fig. 125.

Borneo :

Oligocene, *Durio* type, Muller 1972 (not illustrated).

Miocene, *Durio* type, Anderson & Muller 1975, pl. 1, fig. 4.

Miocene, *Durio* type, Barré de Cruz 1982, pl. 12, fig. 12.

Affinity—Muller (1981) remarks that "*Lakiapollis ovatus* by Venkatachala & Kar (1969) from the undifferentiated Eocene of Kutch (India) appears closely similar to the *Durio* (Bombacaceae) type. If confirmed, this would extend the record at least into the Upper Eocene". Naredi Formation in Kutch from where this species was first recorded is now dated as Early Eocene (Biswas & Raju, 1971). Subsequently, *L. ovatus* was recorded from the Matanomadh Formation of Palaeocene age by Kar (1985). This pollen was also recorded from the Lakadong Formation, Meghalaya (Kar & Kumar, 1986), also dated as Palaeocene by Biswas (1962). A study of pollen of *Durio conicus* Beccari (Pl. 9, figs 7, 8) confirms the contention of Muller (1981).

Genus—*Tricolporopilites* Kar 1985

Pl. 10, figs 1-4

Holotype—Illustrated in Kar, 1985; pl. 23, fig. 1

Original diagnosis—"Pollen grains triangular-subcircular in polar and subcircular-oval in equatorial views. Tricolporate, colpi short-long, pore well developed, margin generally thickened. Exine heavily pilate, pila robustly built, interpilar space granulate, sculptural elements furnish negative reticulum in surface view". The specimens have

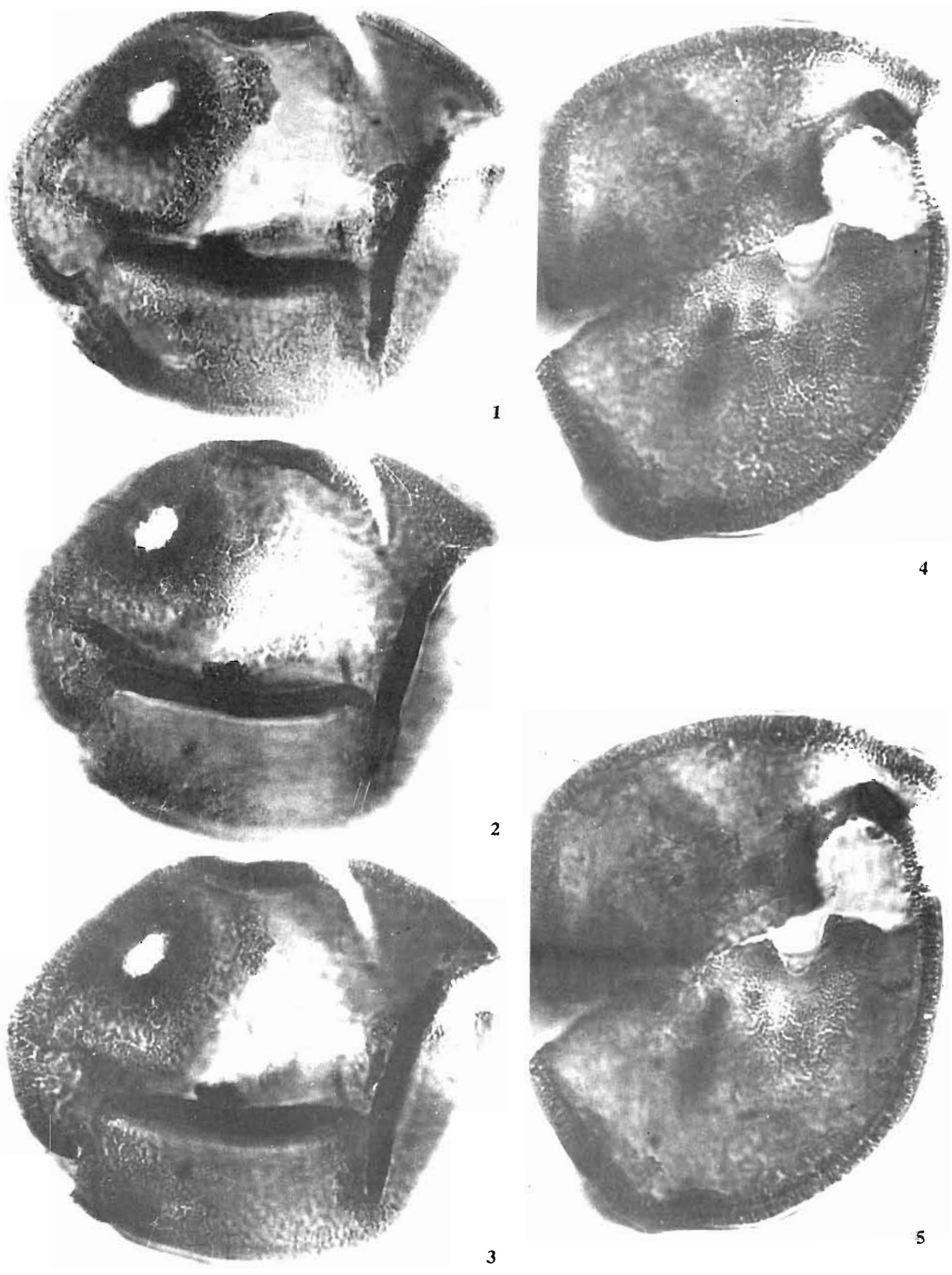


PLATE 11

(All photomicrographs magnified, × 1000)

1-5. *Tricolporocolumellites pilatus*, Eocene, Kutch.

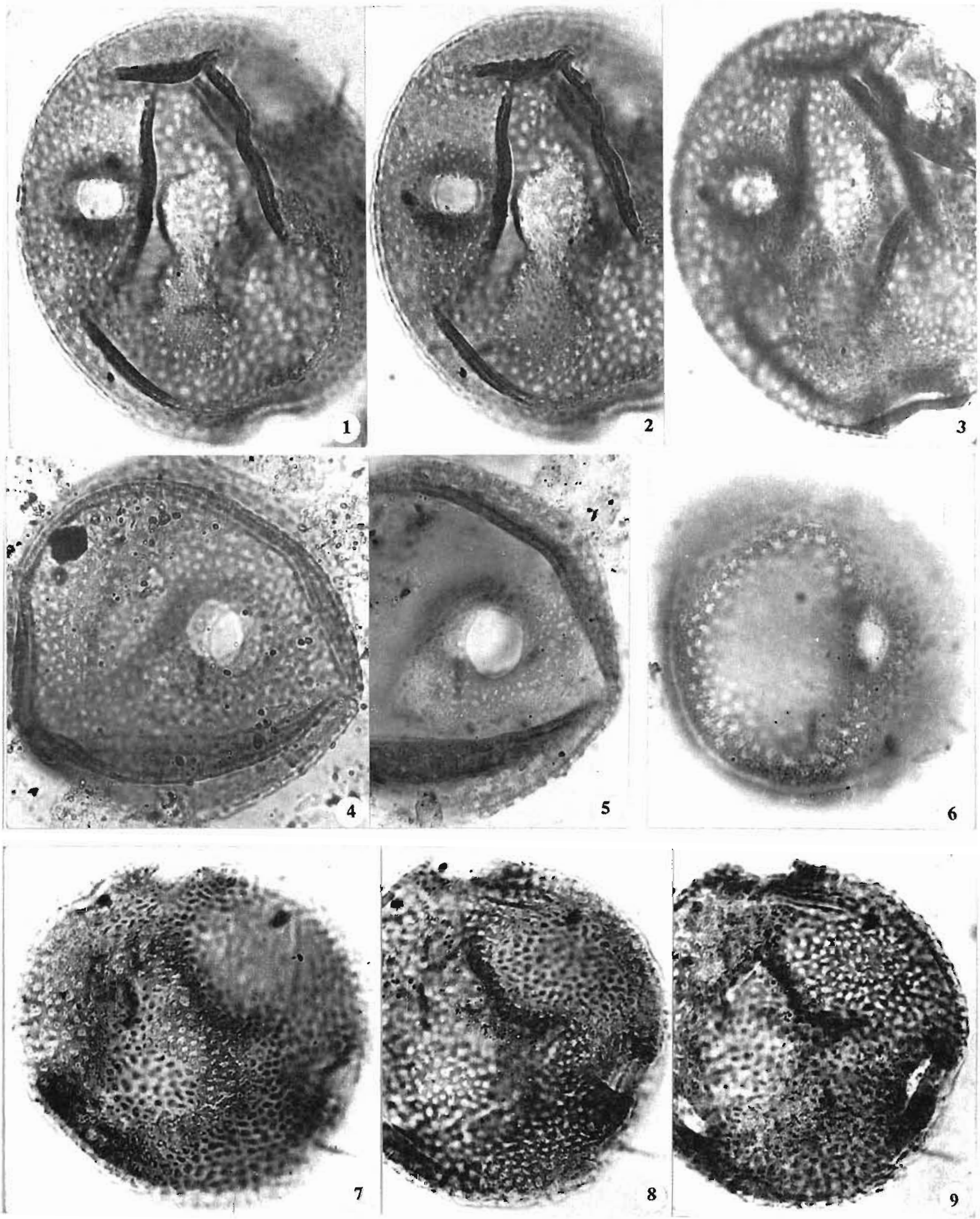


PLATE 12

(All photomicrographs magnified, × 1000)

1-9. *Retitribrevicolporites matanamadhensis*, Lower Eocene, Kutch.

been restudied here and they are distinctly tricolporate (Jansonius & Hills, 1987).

Species studied—Tricolporopilites robustus (Kar & Saxena) Kar 1985.

Description :

Symmetry and form : Subsphaeroidal, triangular-subcircular in polar and subcircular-oval in equatorial view.
Dimension : 55-96 × 50-85 μm.
Aperture : Tricolporate (Pl. 10, fig. 2).
Ectoaperture : Elliptic, short, ends pointed.
Endoaperture : ± rounded, costate.
Exine : 3-6 μm thick.
Sexine : Much thicker than nexine, gemmate, gemmae often coalescing to form irregular mounds, 4-7 μm long, 2-5 μm broad at top, supported by 2 or more columellae.
Nexine : Continuous, thick.
Variability : In size, but not much variable in ornamentation pattern.

Occurrence—Common in India.

Fossil records :

India :

Kutch

Middle Eocene-?Upper Eocene, *Retitrescolpites robustus* Kar & Saxena 1981, pl. 3, figs 59, 60.

Middle Eocene-? Upper Eocene, *Tricolporopilites robustus* Kar 1985, pl. 23, figs 1, 2

Kerala

Lower Eocene-Middle Eocene, *Tricolporopilites pseudoreticulatus* Raha *et al.* 1986b, pl. 1, figs 1-6.

Incertae sedis, in Thanikaimoni *et al.*, 1984 (figs 653-661), from the Miocene of Assam are referred to this genus, however, these pollen grains are interpreted to be reworked, as Eocene pollen in the Miocene of Assam Basin are common.

Affinity—Unknown. Comparisons can be made with certain species of *Alangium*, particularly *A. villosum* (Bl.) Wang (Pl. 10, figs 5, 6). Affinity with Bombacaceae is not ruled out because of the closely comparable apertural features.

Genus—*Tricolporocolumellites* Kar 1985

Pl. 11, figs 1-5

Holotype—Illustrated in Kar, 1985, pl. 23, fig. 4.

Original diagnosis—"Pollen grains subcircular-oval, tricolporate, brevicolpate, pore margin thickened. Exine columellate, pila forming negative reticulum in surface view"

Species studied—Tricolporocolumellites pilatus Kar 1985.

Description :

Symmetry and form : Subspheroidal to oval, generally not observed in polar view.
Dimension : 70-94 × 70-88 μm.
Aperture : Tricolporate, occupies subequatorial position.
Ectoaperture : Short, elliptical, 10-18 × 6-14 μm.
Endoaperture : Distinct, circular-oval, more or less of same size as those of ecto-aperture, costate.
Exine : Tectate, ± 4 μm thick.
Sexine : Thicker than nexine, columellate, columella closely placed.
Nexine : Continuous, cracked.
Variability : In size but not in ornamentation pattern.

Occurrence—Common in Middle Eocene of Kutch.

Fossil records :

India :

Kutch

Middle Eocene-?Upper Eocene, *Lakiapollis matanamadhensis* Kar & Saxena, 1981, pl. 4, fig. 68.

Tricolporocolumellites pilatus Kar 1985, pl. 23, figs 4, 5.

Affinity—Extant equivalents have not been encountered by the authors, however, on analogy, a Bombacaceous affinity is suggested.

Genus—*Retitribrevicolporites* Kar 1985

Pl. 12, figs 1-9

Original diagnosis—"Pollen subcircular, tribrevicolporate, colpi and pore more or less of same size, pore margin thickened. Exine reticulate".

Species studied—R. matanamadhensis (Venkatachala & Kar) Kar 1985 (illustrated in Thanikaimoni *et al.*, 1984, pl. 20, figs 295-300 under the name of *Lakiapollis matanamadhensis*). The holotype could not be located, so a lectotype has been selected from the same material in the slide no. 3353/2.

Description :

Symmetry and form : Sphaeroidal-subsphaeroidal.
Dimension : 30-58 × 35-56 μm.

Aperture : Tribrevicolporate, apertures mostly found in subequatorial position.
Ectoaperture : ± 10 μm large, round to elliptical in shape.
Endoaperture : Round, ± 10 μm large. Costae pronounced.
Exine : Tectate, ± 4 μm thick, sexine thicker than nexine.
Sexine : Reticulate, pluricolumellate, pronounced.
Nexine : Continuous.
Variability : Not much variation.

Occurrence—Common in India.

Remarks—*Retitribrevicolporites* is distinguished from *Lakiapollis* by its reticulate texture and by the pluricolumellate structure of the sexine. The aperture consisting of exo- and endoaperture is closely comparable to that of *Lakiapollis.*

Fossil records :

India :

Kutch

Palaeocene, *L. matanamadhensis* Saxena 1979, pl. 3, fig. 39.

Palaeocene-Eocene, *Retitribrevicolporites matanamadhensis* Kar 1985, pl. 3, fig. 5; pl. 9, fig. 7; pl. 13, figs 1, 2.

Lower Eocene, *Lakiapollis matanamadhensis* Venkatachala & Kar 1969, pl. 3, figs 79, 80.

Meghalaya

Palaeocene, *Tricolporopollis decoris* Dutta & Sah 1970, pl. 9, figs 10, 11.

T. rubra Dutta & Sah 1970, pl. 9, figs 13, 14.

Retitribrevicolporites decoris Kar & Kumar 1986, pl. 8, fig. 19.

R. matanamadhensis Kar & Kumar 1986, pl. 8, fig. 17

Assam

Palaeocene, Lower Eocene, *Retitribrevicolporites matanamadhensis* Kar (unpublished).

Affinity—Unknown.

Conclusion on the morphological group Tribrevicolporate pollen

Lakiapollis, Tricolporopilites, Tricolporocolumellites and *Retitribrevicolporites* share in common the apertural feature consisting of a pronounced costate pore and a short colpi which is mostly distinct. The ornamentation is variable from smooth to variously ornamented :

—*Lakiapollis ovatus* exemplifies psilate to scabrate exine;

—*Tricolporopilites* is gemmate;

—*Tricolporocolumellites* has distinctly columellate exine structure with cracked nexine;

—*Retitribrevicolporites* is reticulate, pluricolumellate.

The columella in *Tricolporocolumellites* and *Retitribrevicolporites* are distinct and also shows varied diversification ranging from obscured to well-pronounced. Some of these tribrevicolporate pollen show clear relationship with Bombacaceous genera, *i.e. Lakiapollis* with *Durio* and *Cullenia,* while *Tricolporopilites* seems closer to some Alangiaceae such as *Alangium villosum.* This group appears to show a trend of diversification from psilate to distinct structured exine. But, in the recent pollen, these corresponding morphological types are manifested in different families.

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