

Importance of palaeobotany in the study of botany, zoology, geology and archaeology

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WITH the presently mounting emphasis on inter-disciplinary studies of Science, Palaeobotany should rank very high among such areas of Botany. Indeed, it should become far more important than what it has been in the past since it stands not only between the various branches of Botany but also between other subjects like: Zoology, Geology, Archaeology and Ancient History. A palaeobotanist has to be a generalist in Botany before he can claim to be a specialist. Instead of claiming a mastery of any particular branch of botany or a particular group of plants he must have a deep understanding of plants of diverse groups ranging from bacteria to angiosperms, because all of them may occur mixed up in a fossiliferous bed. At the same time he has to be a specialist on diverse plants of such a high order than he can identify them in their fragmented and distorted condition in which not only the plants but even their organs are broken down and preserved with or without structure, in a state where they lie helter skelter and mixed up with those of similar or very diverse other organisms and organs. Sometimes the fossils may be isolated single cells or groups of cells, at other times the broken remains may be more or less distorted fragments of particular stages in the life cycles of past plants, their ecotypes, mutants or polyploids and at other times the fossils may not be morphological but degraded chemical remains or chemical fossils of past forms of life. From such fragmentary and mutilated remains of plants, a palaeobotanist may have to reconstruct not only the entire plants but the entire floras or the ecological conditions in which they lived, their relationships with past and present day forms of life and on that basis reconstruct even the geography of the time which they lived. Although Palaeobotany has links with the diverse aspects of Botany, Geology, Zoology, Palaeontology and Archaeology. A

knowledge of Palaeobotany is therefore important, nay, essential for a study of these subjects.

Therefore, I wish to discuss this importance and the recent achievements in the ever widening vistas of Palaeobotany in the present lecture.

FUNDAMENTAL IMPORTANCE OF PALAEOBOTANY

In dealing with the importance of Palaeobotany, in the study of Botany, one has to remember that the basic theme of all biological studies is evolution and the only direct proof of evolution is supplied by palaeontological studies, all other evidences being indirectly inferred conclusions. The branches of biology called palaeobotany and palaeozoology are therefore of fundamental importance for all biological studies.

In this connection it is also important to mention that many aspects of living plants particularly morphology and anatomy, received a phillip from palaeobotanical studies because a palaeobotanist needs intricate knowledge of living plants for interpreting his fragmentary and often mutilated material of fossil plants. In fact, Williamson, Lang, Bower, Arber, Scott, Oliver, Seward, Sahni, Florin, Chaney, Solms-Laubach, Walton, Thomas, Harris and so many others have contributed as much to the knowledge of living plants as they did to that of Palaeobotany. In particular anatomical studies, especially cuticular, epidermal and xylem studies of living plants and palynology attained their present status more from the work of palaeobotanists than from that of workers on living plants. Indeed, wherever one needs intricate knowledge of parts or fragments for identification, as in forensic science it needs the methodology of Palaeobotany.

MISCONCEPTIONS BASED ON PREJUDICES

A misconception about the subject claims that Palaeobotany is a very old subject where, using the familiar Bonner metaphor, "all the oil in the old oil well has exhausted" and there is very little scope for further research. In this connection one has to point out that palaeobotany is actually younger than many of the fashionable areas of Botany like Plant Physiology, Cytogenetics or Plant Pathology and Molecular Biology, etc. which are believed to be new and full of scope for further research (see Table below).

EARLY HISTORY OF DIFFERENT BRANCHES OF BOTANY

<i>Palaeobotany</i>	—1820 Sternberg, <i>Flora der Vorwelt</i>
	—1828 Brongniart, <i>Histoire des Vegetaux</i>
	—1831 Lyell, <i>Principles of geology</i>
	—1833, 1868 Witham, Binney- <i>Fossil plant anatomy</i>
<i>Taxonomy</i>	BC 287 Theophrastus
	—AD 77 Dioscorides, <i>Materia Medica</i> , described 600 plants
	—1300 Albertus Magnus, <i>On plants</i>
	—1753 Linnaeus <i>Species Plantarum</i> (1st May)
<i>Plant Anatomy</i>	—1672 Grew <i>Anatomy of vegetables begun</i>
	—1672 Malpighi <i>Anatomy Plantarum</i>
<i>Embryology</i>	—1694 Camerarius, <i>Letter on sex in plants</i>
	—1823 Amici sees pollen tube approach ovary
<i>Pathology</i>	—1546 Fracastoro, <i>De contagione</i> first scientific

	statement about transmission of infections
	—1658 Kircher sees "Innumerable worms" under microscope
<i>Plant Physiology</i>	—1648 Van Helmont experiments on plant nutrition
	—1727 Hales measures root pressure
	—1772 Priestley concludes that plants give out oxygen
	—1779 Ingenhousz concludes that plants utilize CO ₂ and produce O ₂ in light
<i>Cytogenetics and Molecular Biology</i>	—1665 Hooke gives first drawing of plant cell
	—1750 Mäupertis foresees chromosomal basis of heredity
	—1765 Trembley makes first drawing of cell division
	—1866-69 Mendel's paper on heredity
	—1869 Meischer discovers nucleic acid
	—1875 Strasburger describes chromosomes and reduction division.

As for the oil in the oil well becoming exhausted let me ask people who know even a little of palaeobotany to name a single fossil plant which is completely known. Even one of the most studied fossils like *Lyginopteris* or *Calymmatotheca* is incompletely known. Its earliest remains were discovered before 1828, named by Brongniart in 1828 but still after the lapse of more than 160 years its parts are imperfectly known and its microsporophylls, male gametophytes, embryology and seed germination are entirely unknown. Let me therefore assert that the oil in other wells may dry up but it is not likely to dry up easily in the well of Palaeobotany. In fact, as we dig deeper the oil seems to be welling up with ever increasing force.

PLATE 1

1. *Lepidocarpon lomaxi*: Longitudinal section showing vascularized embryo embedded in tissue of megagametophyte Phillips.
2. L. S. of *Callospermarion* ovule with pollination droplet, Rothwell.
3. Embryo of *Botbrodendrostrobis mundus* Stubblefield & Rothwell.

- 4, 5. Germinating *Samaropsis* seeds, Krassilov.
6. Seedling of *Samaropsis* Krassilov.
7. Median longitudinal section of apical meristem of *Sphenophyllum* Good & Taylor.
8. Saccate pollen grain of a Cordaite with large central body. Taylor & Millay.
9. Structure of phloem cells showing sieve plates (from Smoot).

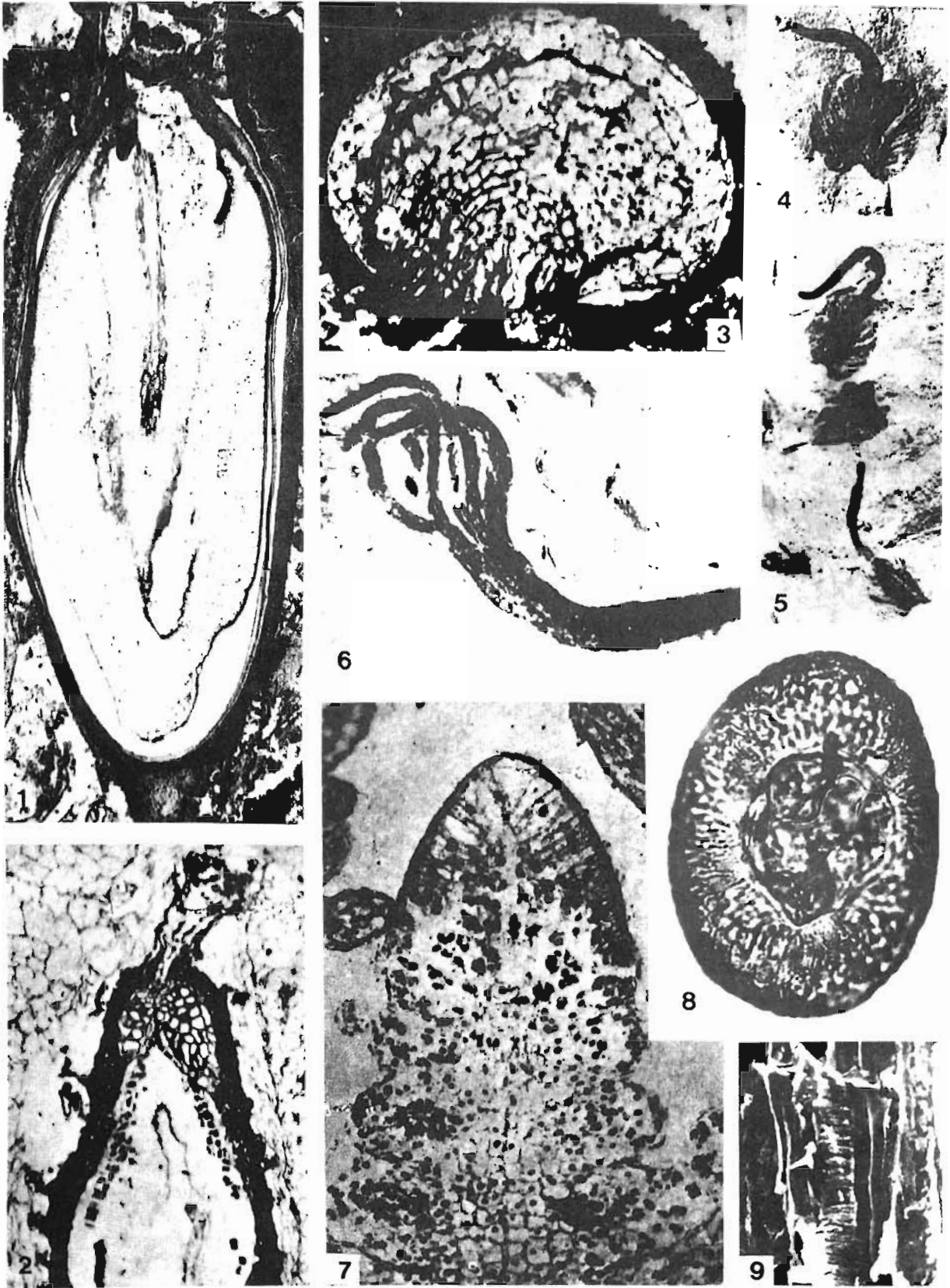


PLATE 1

EVER INCREASING SCOPE OF PALAEOBOTANY

As for the scope of research in palaeobotany it is my assertion that it is becoming greater and brighter every day than that of many other fields of botany and science in general. The importance of the discoveries in palaeobotany is so great that they have changed some of our fundamental concepts about life on earth and brought forth indubitable evidence in support or against ideas that had been prevailing about plant life on earth.

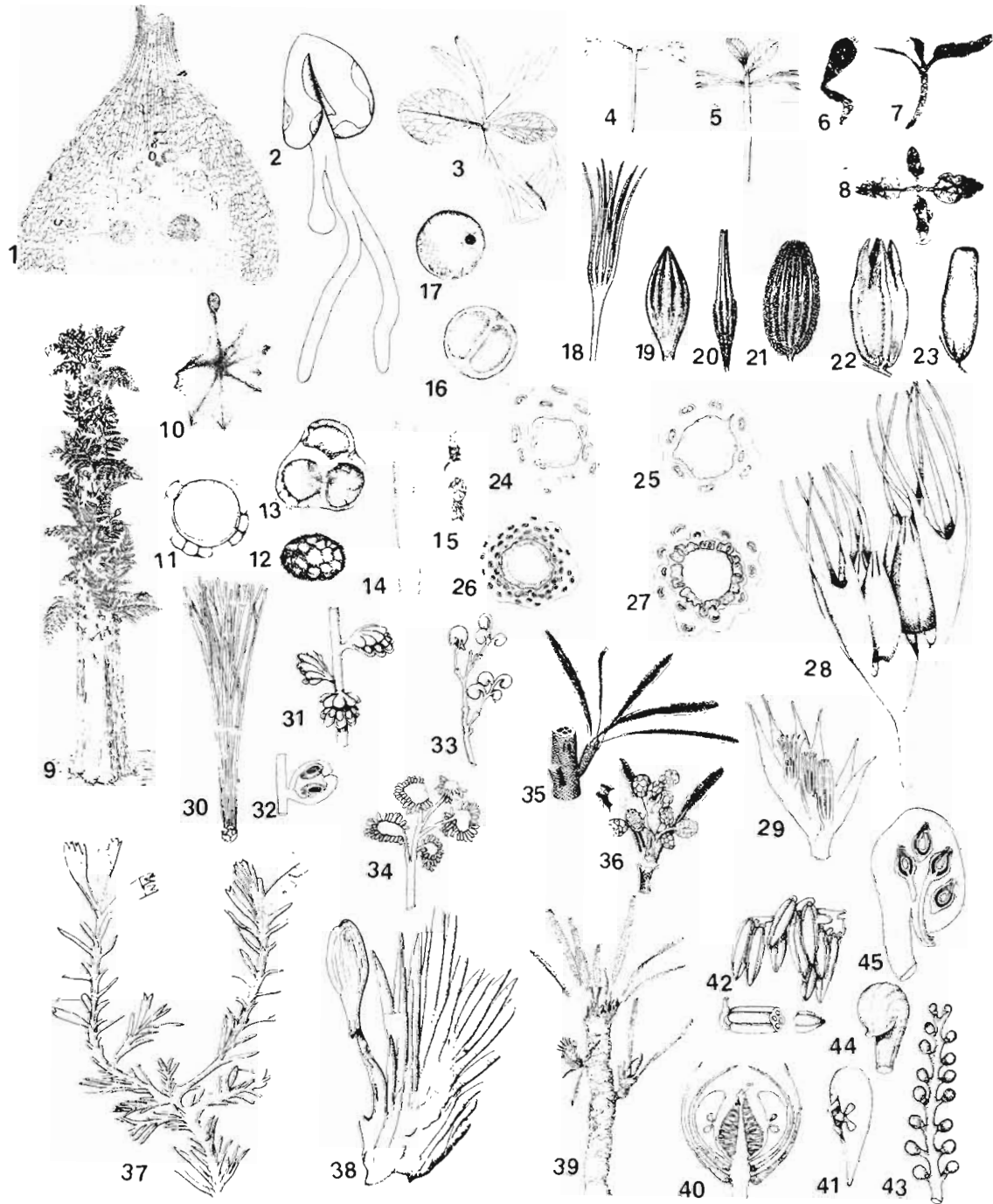
Impact of new techniques and discovery of better preserved material

Before I cite examples in support of the above contentions made by me I must mention something about the new techniques which have become available to the palaeobotanist to enlarge his scope for research. Besides the techniques which were developed by Walton (1928, 1930) like the peel-section method and its later improvements which can enable us to cut serial sections or even circumferential sections of petrified fossils quite expeditiously, the transfer (Walton 1923), celloidin pulls (Lang, 1926) and mass maceration techniques (Harris, 1926), excavation and plastic embedding (Leclercq & Noel, 1953) preparation of latex and rubber casts (Chaloner & Gay, 1972; Watson & Alvin, 1976) and the use of scanning electron microscope and improved techniques of light microscopy like fluorescent, phase contrast, Nomarsky interference microscopy infrared and X-ray photography (Walton, 1936; Schaarschmidt, 1985) and chipping technique (Croft & George, 1958) have given us far greater insights in the structure of fossils. Collection of more specimens increased the chances of finding better preserved remains and this has been another source of greater information about fossils. The new techniques and better material have provided unexpected details of fossils like nuclei and chromosomes—see Pl. 3, figs 1, 2, 6, 7 (Darrah, 1938; Vishnu-Mittre, 1969; Brack Hanes & Vaughn, 1978) and stroma/grana in chloroplasts—see Pl. 3, fig. 2; possible nuclei and mitochondria in Miocene angiosperm leaves (Niklas & Brown, 1981)—see Pl. 2, fig. 4 petrified starch grains (Baxter, 1964) or palisade, spongy mesophyll, and vascular tissues in compressed leaves of *Glossopteris* (Pant, 1958) and other plants, starch grains and archegonia in compressed seeds (Pant & Srivastava, 1964), and vascular cambium in Carboniferous plants (Cichan, 1986). Sieve cells in a Devonian progymnosperm and even sieve areas have been identified in the

Carboniferous phloem of cordaitean axes—see Pl. 1, fig. 9; Pl. 2, fig. 1 (Taylor, 1988), fungi—see Pl. 3, figs 8, 9; mycorrhiza (Stubblefield *et al.*, 1987); pollination drops—see Pl. 1, fig. 2 (Rothwell, Miller & Brown, 1973), formation of pollen, spores and their intrasporic germination as well as gametophytes or embryos in Carboniferous pteridophytes and pteridosperms—see Pl. 1, figs 1, 3; Pl. 3, fig. 6 (Rothwell, 1981), archegonia, pollen tubes and megaspores and embryos inside prothalli of seeds and germinated seedlings—see Text-fig. 1, figs 1-8 (Krassilov, 1987). Some of them show cotyledons which may have been photosynthetic (Pant & Nautiyal, 1987). Bundle sheaths like those of grass leaves seen around bundles of *Glossopteris talbragarensis* (Pant & Nautiyal, 1984) have led these authors to suspect that it could have C₄ plant. We have greater insights now on the pollination and ecology of fossil plants.

Surprises in the diversity and unexpected strangeness of fossil plants

Palaeobotanists have repeatedly come across rather strange fossils in the geological record whose form and nature are so unexpected and so odd that they are unable to fit them in any known group of plants or in any accepted scheme of classification of the plant kingdom. At first, they call them *genera incertae sedis* which can be regarded as riddles of classification till they discover clues about their evolution and affinities. Some of these fossils emphasize the greater diversity of past plants many of which have become extinct. It seems as if Nature was experimenting in different directions and many of its experiments failed to make the forms extinct. Examples of this kind are the Bennettitales, Caytoniales, Glossopteridales (Text-fig. 5: figs 1-19), Czeckanowskiales, Pentoxylales, Corytospermaceae, *Buriadia*, *Rhexoxylon*, Cheirolepidaceae, *Tempskya* and a host of other forms and groups (Text-fig. 1: figs 9, 30-45). Sometimes these fossils temporarily misled us into imagining that we had discovered in them the ancestors of some of our living plants. At other times they seem to complete the picture of plant evolution by fitting in as missing links in the evolution of known groups, e.g., Progymnosperms, *Buriadia*, *Lebachia*, Palaeozoic seeds like *Genomosperma*, *Physostoma*, *Stamnostoma*, and others (Text-fig. 1: figs 18-23, 28-29). Some of them like the seeds of *Lagenostoma* even emphasize the wrong functional notions which we once had about their nine chambered canopy of vascular bundles which was claimed as forming a copious vascular supply at the micropylar end to supply water to



Text-figure 1—figs. 1-45. 1. Seed of *Callospermum ovalis* Pant, Nautiyal & Tiwari showing archegonia, $\times 22.5$; 2. *Vesicaspora* type of pollen grain with branched pollen tube from Rothwell, $\times 650$; 3, 4, 5. Seedlings of *Glossopteris* (*Diphyllopteris verticillata* Srivastava), 3×2 ; $4, 5 \times 1$; 6, 7, 8. Seedlings of *Joffrea speirsii* Crane & Stockey, 6×3.5 ; 7, 8 $\times ca 2$; 9. *Tempskya* reconstruction of plant after Andrews & Kern. 10. *Kakabekia* Barghoorn & Tyler 11. *Eosphaera* Barghoorn & Tyler 12. *Huronispora* Barghoorn & Tyler 13. *Eotetradedrion* Schopf & Barghoorn. 14. *Animikiea* Barghoorn & Tyler. 15. *Archaeonema* Schopf & Barghoorn. 16. *Eozygion*, Schopf & Blacic. 17. *Glenobotrydion* Schopf & Blacic. 18. *Genomosperma kidstonii* Long. 19. *G. latens* Long. 20. *Salpingostoma dasu*. 21. *Physostoma elegans*. 22. *Eurystoma angulare*. 23. *Stannostoma buttonense* Long. 24. *Grammatopteris rigollotii*. 25. *Thamnopteris guynne-vaughanii*. 26. *Zaleskia gracilis*. 27. *Plaeosmunda playfordii*. 28. Cupule of *Archaeosperma arnoldii* Pettitt & Beck; 29. Cupule of *Moresnetia zaleskyi* Rothwell & Scheckler; 30. *Czechanouskia* short shoot; 31, 32. *Leptostrobus longus* Harris; 33. *Umkomasia macleani* Thomas; 34. *Pteruchus africanus* Thomas; 35. Shoot of *Pentoxylon* Srivastava; 36. *Carnoconites* Srivastava; 37, 38. *Buriadia heterophylla* Seward & Sahn; 39. *Williamsonia sewardiana* Sahn; 40, 41. *Williamsoniella coronata* Thomas; 42. *Caytonanthus* Harris; 43, 44, 45. *Caytonia* Thomas.

ciliated motile sperms. As it appears now the nine chambers of hard tissue enclosing soft tissue and vascular bundles represent vestiges of nine telomes which fused to form the integument.

Precambrian life

Before 1965, we had no authentic records of morphological fossils to support the existence of plant life during the Precambrian times although we had come to know that the earth was about 4.5 to 5 billion years old. Definite morphological plant fossils extended backwards in time only up to 0.6 b.y. or 600 million years. No doubt Oparin (1924—see Oparin, 1953) and Haldane (1929) had speculated on the origin of life on the basis of biochemical pathways and experimental support for their ideas was supplied by Miller (1953) but we had no direct proof on palaeontological or palaeobotanical grounds in favour or against the theory. Likewise some people thought that procaryotes were more primitive than the eucaryotes but direct evidence from fossils in favour of such notions was completely lacking. However, Barghoorn and Tyler (1965), Schopf (1968) and subsequent workers on Early Precambrian Fig Tree Formation and Swaziland System of Africa (ca 3.3-5 b.y.), Middle Precambrian Gunflint Chert of Canada (ca 2 b.y.) and Bitter Springs Formation of Australia (0.9-0.8 b.y.) brought forth direct evidence to show that the first forms of life found in Early Precambrian were simple bacteria-like procaryotes called *Eobacterium*, some present day mycoplasma-like bodies called *Eoastrion* and a number of types of cyanobacteria. Some biota like *Kakabekia umbellata* which have since been found in the living state in ammonia rich environments of today could even

confirm the ideas of Oparin and Haldane about the primeval atmosphere of the Precambrian times being rich in ammonia (Text-fig. 1: figs 10-17). Later work on Precambrian fossils from various areas has tried to reassess the evidence of Precambrian biota. Doubts were cast by some workers on the presence of eucaryotes in the Bitter Springs Formation of Australia but these have been dispelled by more critical assessments. The overall impact of this later work has been to carry the earliest fossil record still further back to 3.5 billion years.

Bacteria, Algae, Lichens, Fungi and Bryophytes of later periods

Palaeobotanical knowledge of the above groups of plants is rather scanty and accordingly the evolutionary history of these groups is poorly known and there are doubts about the origin and evolution of their diverse forms. The classification of the living bacteria, algae and lichens is mainly based on their reproductive organs, chemistry or staining reactions or pigments which are difficult to find among their fossils. The classification of fossil algae in particular is chiefly based on their siliceous or calcareous skeletons and it is therefore useful for combining botanical and geological approaches. There is need for intensive search of the fossils of these diverse groups to arrive at definite conclusions about their evolution. The relationships between the various groups of bryophytes like Marchantiales, Jungermanniales, Anthocerotales, Sphaerocarpaceae, Bryales and Sphagnales are obscure and it is difficult to decide whether they represent a reduced or progressively advanced group of plants. Recent reports of Ordovician spores which have been attributed to the Bryophytes may give us some clues

PLATE 2

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- 1 Sieve cell in phloem of *Medullosa noei*—showing elongated sieve areas on radial wall. × 850. from Smoot.
2. TEM photograph of chloroplast showing details of grana. from Niklas & Brown.
3. TEM photograph showing double membranes in cells of Miocene leaf. from Niklas & Brown.
4. Starch filled cells in the female gametophyte of *Cardiocarpus spinatus*. from Baxter.
5. Insect, *Ceroxyela* with pollen grains in the gut. from Krassilov
6. *Vitimipollis* pollen grain from the gut of insect in fig. 5, from Krassilov.
- 7 *Kallospora extrudeus* spore with gelatinous contents (cytoplasm?) extruding from proximal surface. from Hall.
8. Cytoplasm belonging to egg or zygote in the archegonium of a pteridospermous ovule. from Stewart.
9. Longitudinal section of seed showing megagametophyte (G) with two archegonia (arrows), embryos are present within archegonial chambers. from Smoot & Taylor.
10. Longitudinal section of *Lagenostoma ovooides* ovule with well-developed cellular female gametophyte and archegonial cavity. from Taylor & Millay.
- 11 Longitudinal section of apical half of *Taxospermum undulatum*. ovule showing female gametophyte with 'tentpole' and archegonium. from Taylor & Millay.
12. Sperm like contents of a monolete pollen grain. from Stewart.
13. Transverse section of an archegonium showing neck canal (c) and neck cells (n). from Brack-Hanes.

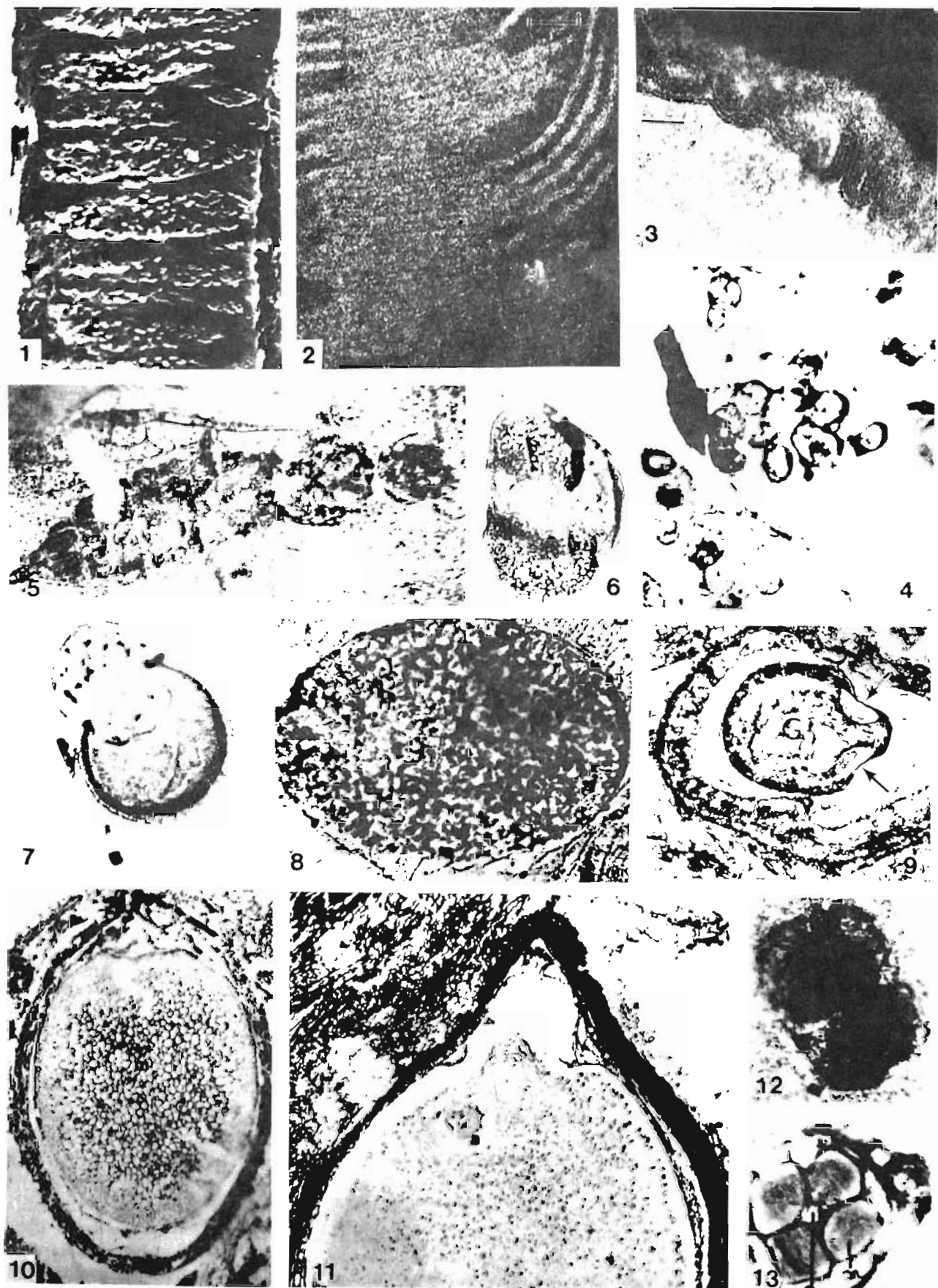
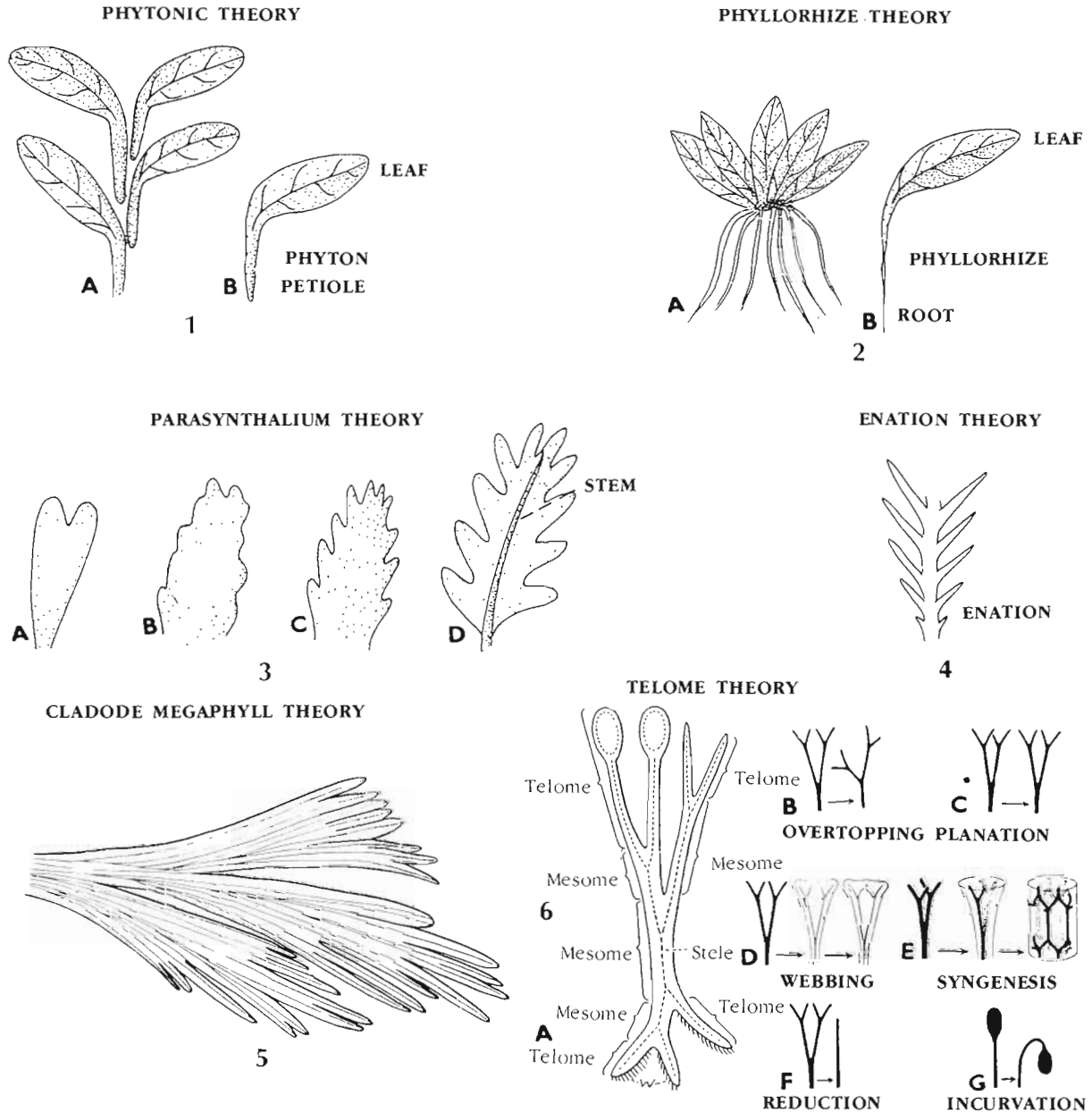


PLATE 2

IDEALIST MORPHOLOGY
FUNDAMENTAL CATEGORIES OR PARTS

CAULOME	PHYLLOME	RHIZOME	TRICHOME
STEM	LEAF	ROOT	HAIR



Text-figure 2—figs. 1-6. Diagrams to illustrate various idealistic theories of plant construction and the Telome Theory.

about the evolution of this group but we need more information.

Origin of land plants

Till 1919, we had only vague ideas about the "Thallesiophyta and Subaerial Transmigration" on land as suggested by Church and others but these were only ideas or theories lacking any direct proof.

Beginning with Dawson's (1859) early work and the later publications of Kidston and Lang (1917-1921) on structurally preserved Psilophytales which was continued subsequently by Høeg (1942), Banks and a host of other botanists we arrived at indubitable evidence about the origin of land plants from algae so much so that Arber (1921) characterised the first land plants by the title "Vascular Thallophytes".

Characters of first land plants

Palaeobotanical discoveries of Late Silurian and Early Devonian plants have shown that early land plants evolved by donning waxy or fatty waterproof coats (cuticles) over their exposed parts to protect them from drying in dry subaerial environments. Their cells could now remain in an active state of growth (algae too can remain alive under dry conditions but their cells hibernate and become inactive). Accompanying their water proof impervious coat land plants also developed pores or stomata for gaseous exchange and inside their axes they developed a core of conducting cells with water proof lignified walls to conduct water from the prostrate axes which grew over wet soil or under it. They absorbed water through their rhizoids and conducted it right up to their actively growing tips. The spores of these plants started being formed in sporangia held high at the ends of fertile axes so that their dissemination by wind had better chance and the spores too became coated with a cuticle for their protection in dry air.

Theories of plant construction

There was a time when morphologists were theorizing and debating the evolution of various plant organs of ideal plants. The idealistic concepts indulged in arguments like hen first or egg first about the organs of the plant body which came first and which came later. Some idealistic morphologists thought that the first plants were made of phyllorhizes or leaf-roots (Phyllorhize theory), others thought that they were wholly fertile (Strobilus theory) or made up of phytoms or leaf-petioles (Phytonic theory), still others thought that the first plants were protocorms or undifferentiated corm-like structures or thallus-like bodies whose lobing gave rise to leaves (Parasynthalium theory—see Eames, 1936). The discoveries of *Rhynia* and *Cooksonia* and other early vascular plants showed that those who believed in idealistic morphology were viewing things upside down. They were usually trying to interpret the structure of simple plants on the basis of more complex plants which had a differentiation of organs like a stem or caulome, a leaf or phyllome and a root or rhizome, a hair or trichome besides other accessory organs for reproduction which were believed to be modifications of one or the other of the aforementioned organs. The discovery of early vascular plants gave us the clue that the bodies of earliest land plants were not differentiated into organs like leaves and roots but they consisted merely of an axis system. Ultimately a new theory

based on such plants called the 'Telome theory' was proposed by Zimmermann (1930) and now instead of looking downwards from complex to simple plants we started looking upwards from simple to complex plants (Text-fig. 2 : figs 1-6).

Evolution of Stelar System and ontogenetic studies

The evolution of the stelar system cannot be understood without the help of the stelar systems of fossil plants (Text-fig. 1 figs 24-27). We know now that those who interpreted the pith as an "invasion" or invagination of the cortex into the centre of stele were proved to be incorrect by fossil forms like *Thamnopteris* and *Zaleskia*. A host of other forms showed that a parenchymatous pith was gradually evolved in-situ from a solid protostele. It was a developmental diversion of central cells (Kidston & Gwynne-Vaughan, 1907, 1909). Ontogenetic studies of fossil plants started by Walton (1934) and continued by Morgan (1959), Eggert (1961, 1962), Good (1971a, 1971b), Good and Taylor (1972) and others have also helped in understanding stelar evolution and apical structure.

Spore evolution

The stages in the evolution of spore sculpturing and heterospory have also been elucidated by recent palaeobotanical discoveries. It appears that spores of diverse early vascular plants were all equal in size or homosporous and their surface was to begin with smooth but thereafter plants started producing unequal spores and their coats started becoming variously ornamented. An intermediate stage in the evolution of heterospory was incipient heterospory when the spores started becoming unequal inside one and the same sporangium and the sporangia of such plants could not be called mega— or micro-sporangia. Some of the present day mosses have stopped at such a stage which bryologists call anisospory but later diverse vascular plants became heterosporous by producing two kinds of sporangia, the mega-sporangia and micro-sporangia which produced unmixed megaspores and microspores. Recent work has suggested that megaspores of some *Lepidocarpon*-like plants called *Achlamydocarpon* had both functional and aborted megaspores and they developed a spongy mass of sporopollenin like that of modern *Azolla* or *Salvinia* and they were floating in water and were fertilized by spermatozoids from microspores which too were swimming in water. Well-developed archegonia with eggs or embryos have been recognised by Galtier (1964, 1970) in *Lepidocarpon* and the entire life cycles of these plants are now known.

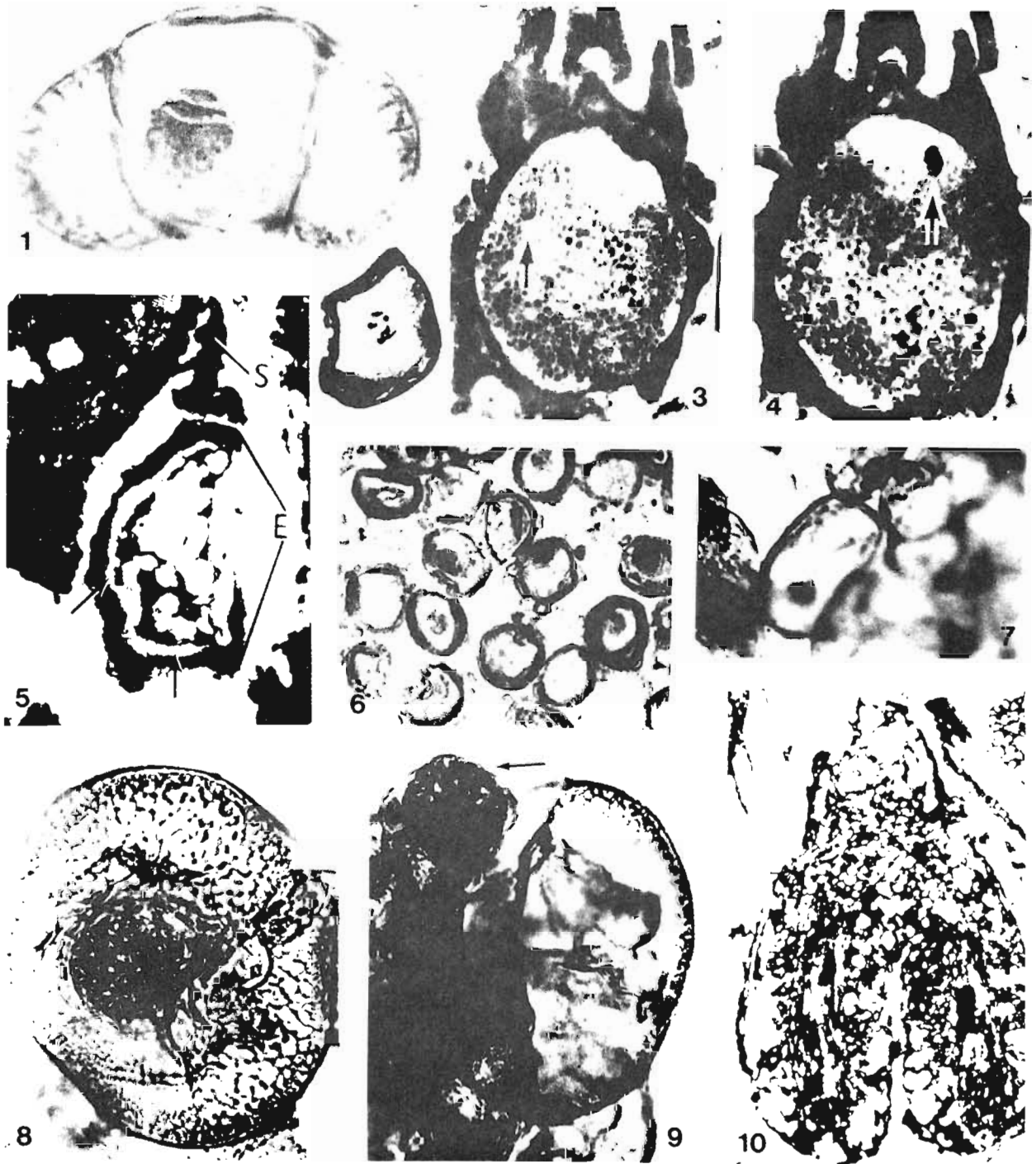


PLATE 3

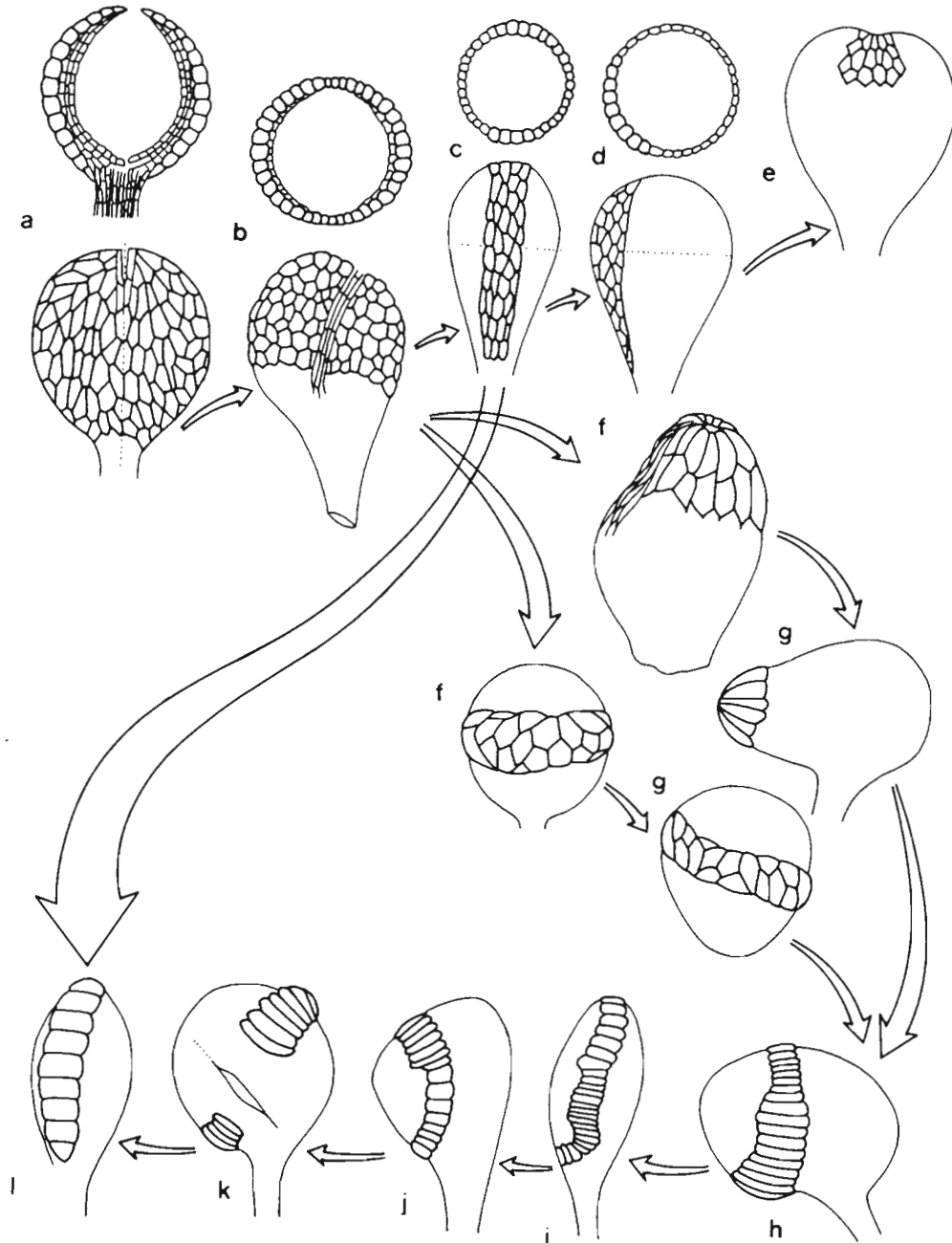
1. *Vesicaspora* pollen grain showing three celled stage of microgametophyte, from Millay & Eggert.
2. Microspore showing prophase, from Brack-Hanes.
- 3, 4. Ovules of *Hydrasperma tenuis* showing archegonia (arrow), from Matten *et al.*
5. Archegonium with multicellular embryo (E) and suspensor (s), from Smoot & Taylor.
6. *Lasiostrabus polysacci*, pollen grains showing microgametophyte development, from Taylor.
7. Nuclei in the monolete spores of *Peltastrobus reedae*, from Baxter
8. *Sullisaccites* pollen grain with zoosporic fungi within the central body, from Taylor
9. Pollen grain with epibiotic sporangium extruding from saccus wall-cap, from Taylor
10. Possible Lower Carboniferous embryo with two cotyledons, from Taylor & Millay

Evolution of sporangium, annulus and sorus

The evolution of a leptosporangium from a eusporangium, the phyletic slide of annulus (Text-fig. 3 : figs a-l), the evolution of a sorus from a monangial condition and the phyletic slide of sorus in ferns too had to be understood in the light of fossil plants (Bower, 1935).

We were again having vague conjectures about the origin of gymnosperms from some

heterosporous ferns through pteridosperms. These ideas were disputed by Thompson (1927) and Doyle (1953) who pointed out that the seed plants were not heterosporous but only heterothallic. In support of this contention Thompson pointed out that the seed spores of some gymnosperms are smaller than their pollen spores and Doyle emphasized that the oldest seed plants antedated the earliest heterosporous ferns or pteridophytes. They thought that the seed plants seemed to have descended from



Text-figure 3—Possible alternative modes of phyletic slide of annulus (after Pant & Khare): **a**, *Stauropteris oldhamia*; **b**, *Botryopteris globosa*; **c**, *Etapteris laccae*; **d**, *Botryopteris forensis*; **e**, *Osmunda*; **f**, *Senftenbergia*; **g**, *Lygodium*; **f**, *Damudopteris*; **g**, *Sermaya*; **h**, *Gleichenia*; **i**, *Plagiogyria*; **j**, *Loxosoma*; **k**, *Hymenophyllum*; **l**, *Leptochilus*.

homosporous but heterothallic ancestors among the ferns or pteridophytes. Subsequent palaeobotanical work has shown that heterospory came into existence in the Lower Devonian while the first seeds (or seed plants) appeared in the Upper Devonian. The origin of gymnosperms can now be traced to the heterosporous Progymnosperms like *Archaeopteris* whose compound fern-like leaves have now been shown to be of the nature of short shoots bearing simple leaves. Its long shoots or trunks could become 5 feet or more in thickness, and with abundant secondary xylem of gymnosperm type. Some species of *Archaeopteris* were heterosporous but at least one of them seems to be closely associated with seeds called *Archaeosperma arnoldii*. Such a unique plant was earlier unimaginable since some of its species are like pteridophytes in reproduction while other species could have been gymnosperms if their association with seeds has any meaning. Beck (1960a, 1960b, 1961, 1970, 1976) has termed such plants as Progymnosperms and they possibly are at the beginning of gymnosperms. Palaeobotany has thus supplied a very much wanted clue about the origin of seed plants.

Origin and evolution of seeds and cupules

The organs called seeds had themselves formed a morphological riddle after the work of Wilhelm Hofmeister (1851) indicated that they could be regarded as integumented megasporangia. The manner of the evolution of the integument was, however, problematic but the work of Long (1960a, 1960b, 1966) and others has shown that the integument has been formed by the fusion of 2 or more sterile telomes in the gymnosperms whereas the seed-like structures of *Lepidocarpon* and *Miadesmia* have integument-like envelopes formed by the megasporophylls. The seeds described lately by Long and others have thus vividly shown the steps in the evolution of the integument from sterile lobes of megasporophylls around the megasporangia (Text-fig. 1 : figs 28, 29) and they also show that seed-like structures or seeds evolved along several parallel lines. May be we discover more lines of evolution, e.g., the evolution of the vasculatureless double integumented seeds of modern angiosperms.

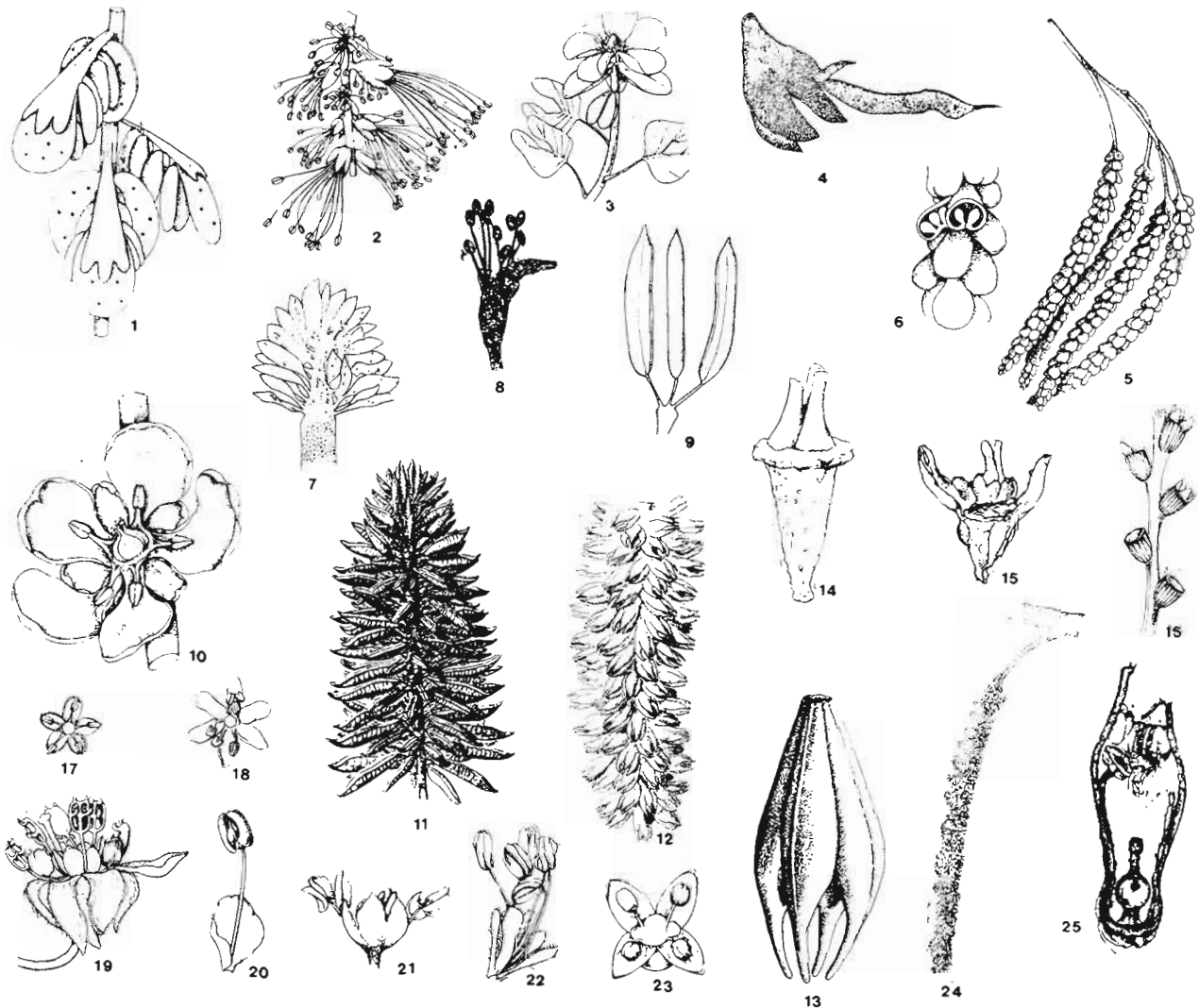
Nature of the female cone of conifers

Likewise an age old riddle about the morphological nature of the female cone of conifers could be solved by the epoch making work of Florin (1939-1945, 1951) and others on fossil conifers

which conclusively showed that the so-called ovuliferous scale was an axillary shoot and the female cone of Coniferales was a compound strobilus.

Origin of Angiosperms

Darwin termed the origin and evolution of Angiosperms to be an "abominable mystery". We were all the time depending on ideas based on comparative morphology and the result has been a multiplicity of classifications of the flowering plants. Some authors like Engler (see Engler *et al.*, 1954) believed that naked unisexual anemophilous flowers like those of the Casuarinales were the most primitive, others like (Arber & Parkin, 1907) and Hutchinson (1959) suggested that bisexual complete flowers having indefinite number of parts like those of the Magnoliales-Ranales complex were most primitive. Some authors derived the angiosperms from the Caytoniales or the Bennettiales, others from the conifers or Gnetales. Unlike the blind man who meant to see the elephant and could not see it whole but only felt its parts, the botanists who were searching for clues about the origin and evolution of angiosperms were sure that they had functional eyes but they were not aware that they needed the light of fossils to solve the problem. Faint glimmers of this light have started coming from the discoveries of a few fossil reproductive parts of angiosperms in the Uppermost Lower Cretaceous, Upper Cretaceous and Eocene beds. So far we were under the impression that we could only see pollen grains and leaves of angiosperms which are preserved as fossils and we thought that floral parts were too delicate to be found in the fossil state but thanks to the work of Dilcher and Crane (1984), Doyle (1978), Hickey and Doyle (1977), Crepet (1979) and their co-workers in U.S.A., Friis (1983, 1984, 1985), Skarby and Friis (1982) in Sweden, Vakhrameev and Kotova (1977), Vakhrameev and Krassilov (1979) and others in U.S.S.R., a number of well-preserved fossil angiospermous gynaecia, androecia, flowers and inflorescences have been discovered in the Middle Albian (105 m.y.) beds (Text-fig. 4 : figs 1-25). These include *Caspiocarpus* and *Hyrcaanthus* which are gynaecia attributed to the Magnoliidae (Chloranthaceae), gynaecia attributed to Hammamelidae, Platanaceae, *Archaeanthus* are just the beginnings of a new field of work (see also Friis *et al.*, 1987). So far we have only found Archichlamydeous flowers in the Cretaceous to be able to say only tentatively that even during the Eocene most of the angiospermous genera were



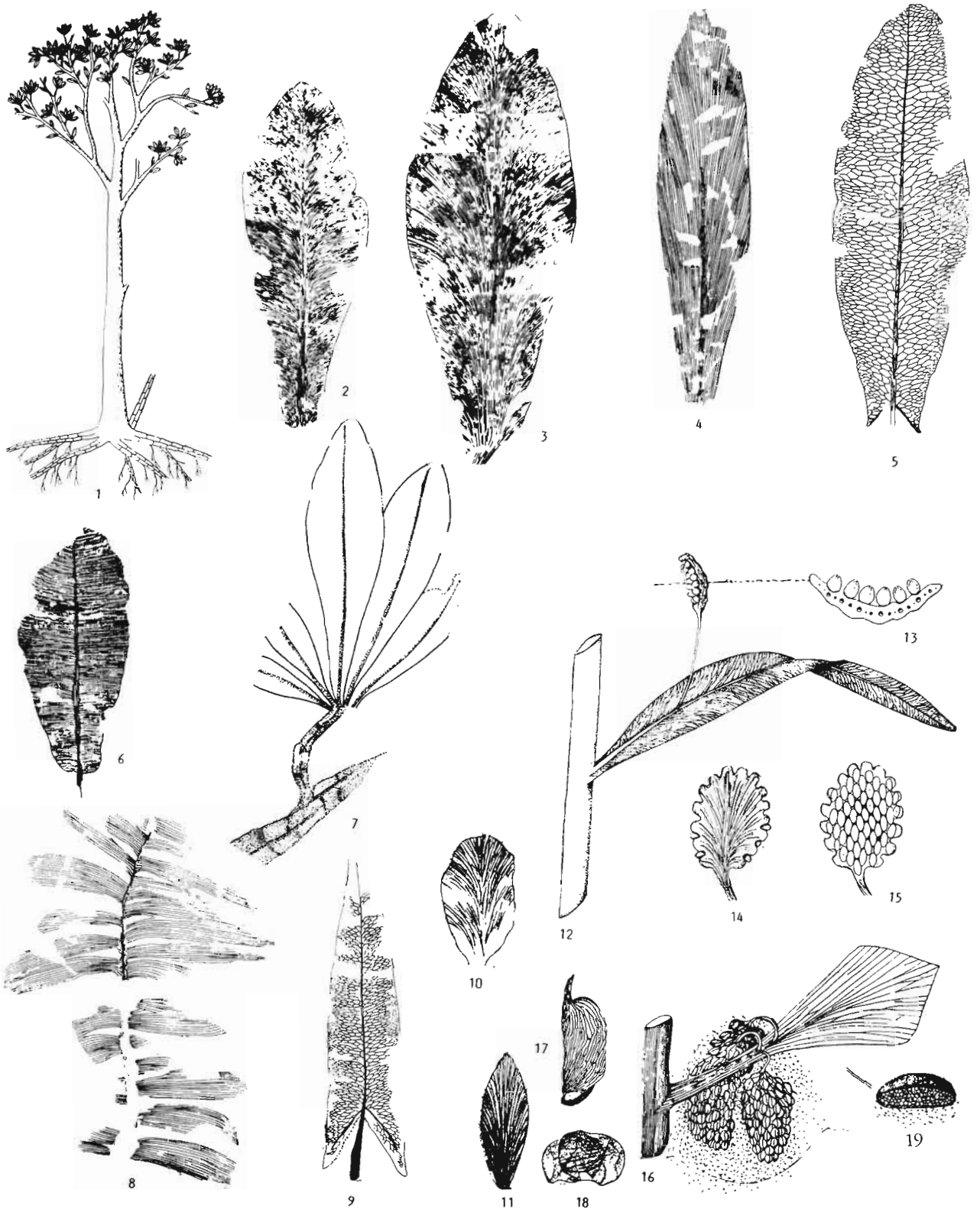
Text-figure 4—figs. 1-25. 1. *Eokachyra aeolia* Crepet, Dilcher & Cotter; 2. *Eomimosoidea* Crepet & Dilcher; 3. *Archaeanthus linneanbergeri* Dilcher & Crane; 4. A papilionoid legume flower with pod Crepet & Taylor; 5,6. *Prisca reynoldsii* Retallack & Dilcher; 7. Magnolialean multicarpellate fruit Crane & Dilcher; 8. *Protomimosoidea b Buchananensis* Crepet & Taylor; 9. *Triplicarpus purkynei* Velenovsky & Viniklar; 10. Unnamed flower from Dakota Formation, Cretaceous, Basinger & Dilcher; 11. *Archaeanthus linneanbergeri*, fertile axis bearing spirally, arranged conduplicate carpels, Dilcher & Crane; 12,13. Catkin-like inflorescence with spirally arranged four parted florets; 14. Epigynous saxifragalean flower with three stout styles, Friis & Skarby; 15. *Scandiantbus costatus* Friis & Skarby; 16. *Leptospermum macrocarpum* Velenovsky; 17. *Berendtia primuloides* Conwentz; 18. *Sambucus succinea* Conwentz; 19. *Cinnamomum prototypum* Conwentz; 20. *Forskobleanthium nudum* Conwentz; 21. *Quercus taeniatopilosa* Conwentz; 22. *Quercus meyeriense* Conwentz; 23. *Myrsinopsis succinea* Conwentz; 24. *Caloda delevoryani* Dilcher & Kovach; 25. *Sabniantbus parijai* Shukla.

different although some of them would be assigned to modern families or to families which combined characters of more than one modern family. Indeed, flowers and fruits of angiosperms started being described in India by Sahni, Shukla (1944) and others in the forties.

Origin and evolution of plant-animal relationships in pollination and insectivory

Connected with the new field of research on fossil flowers is another novel area of research on

pollination studies in living and fossil plants and on animal-plant relationships. This carries us further into the field of palaeoecology since we know that megafossils of plants occur in terrestrial deposits which have been largely neglected by palaeontologists and geologists since they are mostly interested in marine sediments and marine animals. We are aware, however, that right from the Devonian or Silurian, animals were existing in association with plants and Carboniferous onwards a fauna of phytophagous insects existed in the forests



Text-figure 5—figs. 1-19. 1. Reconstructed plant of *Glossopteris*, from Pant, 1971; 2. *Glossopteris major*; 3. *Gangamopteris cyclopteroides*; 4. *Palaeovittaria raniganjensis*; 5. *Sagittophyllum verticillatum* Pant, Nautiyal & Chauhan; 6. *Rhabdotaenia danaeoides*; 7. Bunch of *Glossopteris* leaves attached to a branched *Vertebraria* axis from Pant; 8. *Pteronilssonia gopalii*; 9. *Belemnopteris sagittifolia*, 10. *Rubidgea obovatum*; 11. *Euryphyllum*; 12, 15. *Ottokaria zeilleri*, from Pant & Nautiyal; 12. Reconstruction of a stem bearing a fertilizer; 13. T.S. of head; 14, 15. Sterile and fertile sides of head, respectively; 16. Reconstructed axis with attached fertilizer of *Eretmonia* raining pollen; 17. A single sporangium, *Arberliella* of *Eretmonia*; 18. Bisaccate pollen grain of *Arberliella*; 19. Disc of *Nesowalesia* bearing *Arberliella* with its presumed stalk.

throughout geological time. We know of coprolites containing cuticles and pollen of *Caytonia*-like those described by Harris (1946, 1964). We also have reports of some fossil insects with pollen grains in their alimentary canals and pollen grains sticking to fossil insect legs—see Pl. 2, figs 5, 6 (Krassilov, 1987) but what we need to do is to concentrate our efforts on extending such work. Who can say that it will be stereotyped.

Palaeophytogeography, palaeoecology and taphonomy

Work on the study of palaeofloras from the point of view of demarcating the boundaries of palaeofloristic provinces or phytochoria of the Indian region, their palaeoecology and taphonomy require a great deal of our attention.

History of present day floras

An almost untouched field of research in this country is the study of the history of our present day floras. We do not even know the kinds of forests which existed in various parts of India before the advent of man and how our shoreline has receded or extended and how man has changed the vegetation by extending cultivation. Work of this kind has been done in England by Godwin and his coworkers and it is epitomised in the *History of British flora* (Godwin, 1956). Some workers have taken up such studies in India also (Banerjee & Sen, 1984, 1985, 1986) but who cares for such work in a country mimicking advanced countries and wasting vast sums of money on its space programme that brings repeated failures and at the same time leaves no funds for basic science which can achieve wonders with relatively modest amounts of expenditure.

History of present floras has another aspect which can give us clues about the origin of our cultivated plants or medicinal plants and about the centres of diversity of such plants. Archaeological sites would be particularly useful for such research. Dendrochronology of our archaeological woods too needs our attention.

Continental drift

One of the great achievements of Palaeobotany has been the impetus it gave to the ideas of 'Continental Drift' (Wegener, 1924). At one time people, mainly physicists, were ridiculing the idea for lack of motive force but today it has culminated in plate tectonics, oceanographic research, mineral and biological wealth under the sea, demarcation of volcanic and earthquake prone areas, and the motive

force has been supplied by the physicists themselves.

Palaeobiochemistry and ultrastructure

Palaeobiochemistry and ultrastructure are yet other fields which are grossly neglected aspects of fossil study requiring the attention of Indian palaeontologists and palaeobotanists (Niklas, 1981, 1982; Niklas & Brown, 1981).

Experimental palaeobotany

A relatively new field of palaeobotany may be called experimental palaeobotany. A paper published by Walton (1936) could be regarded as one of the earliest studies of this kind. In this work Walton made observations and experiments on the formation of compression fossils. Subsequently, Oehler and Schopf (1971) and others have performed experiments on the formation of petrifications but this important field needs to be worked out more thoroughly by experiments and observations on the formation of diverse fossils and their beds by experiments under a variety of conditions.

Mineral prospecting

A field of palaeoecological research which is still largely untouched is mineral prospecting with the help of fossils. Coal and oil are no doubt correlated and even prospected with the help of pollen analysis but we know now that microorganisms and even plants of different groups are associated with rocks or minerals of different kinds. There are, for example, sulphur and iron bacteria, copper mosses, calcicoles and calciphobes. There are also associations of algae with minerals of various kinds like calcareous or silicious algae and if we can determine the preferences of fossil plants for particular soils or substrates for rock building, we can use them as palaeoindicators for mineral prospecting.

Sedimentology and stratigraphy

Sedimentology and stratigraphy derived immense help from palaeobotanical studies. A vivid manner in which deposition of sediments can record past events is furnished by the Sunday Stone, a piece of chalky mud kept in the British Museum (Pl. 4, fig. 1). Since it is evidently recorded that the Sunday Stone was formed in a small pool or "horse trough" in a British coalmine in South Shields, County of Tyne and Wear about 1880. Into the pool was flowing a little stream after passing through a chalky

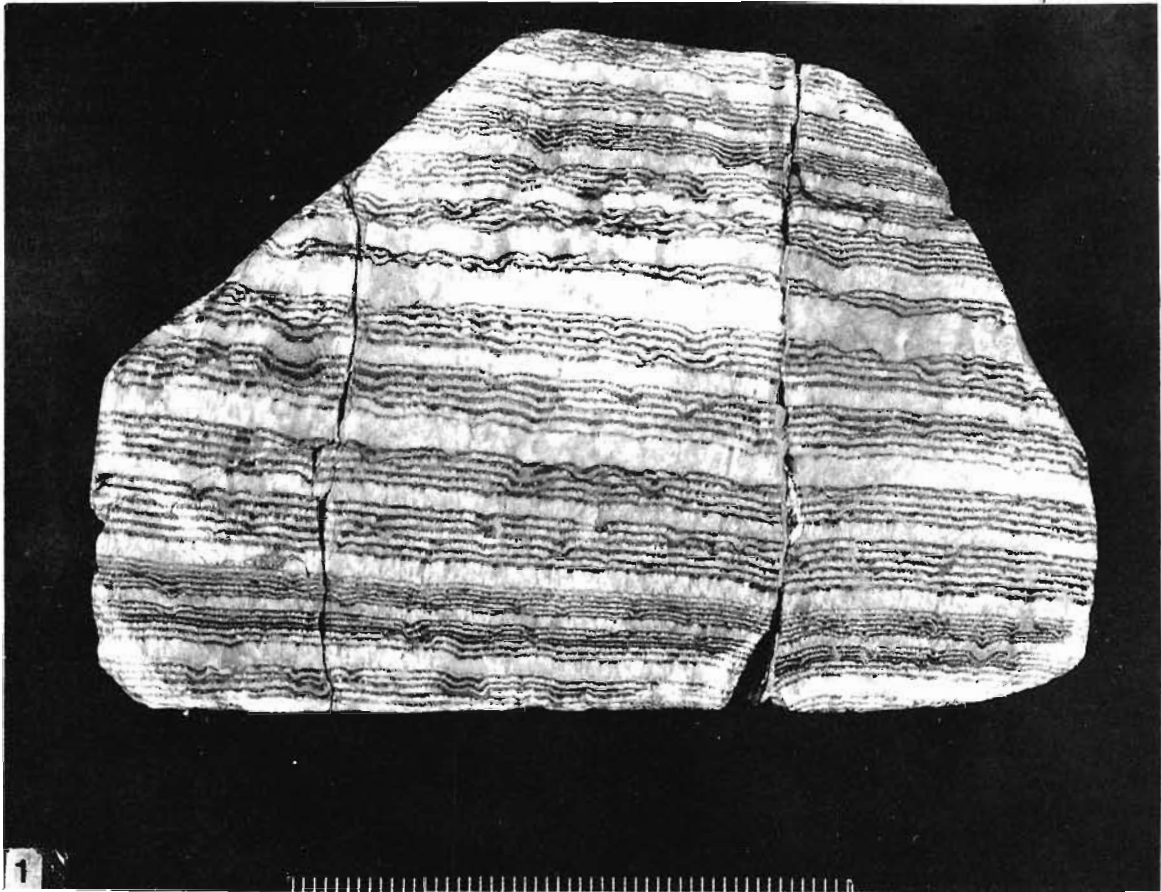


PLATE 4

"Sunday Stone", Specimen no. BM 1988 Pl, formed in a "horse trough" in a British coalmine in South Shields, County of Tyne and Wear about 1880 (Photograph through kind courtesy of Dr C. Hill of British Museum).

bed and depositing chalky sediment at its bottom or it could have been barium sulphate which was used to reduce the risk of fires spreading in the mine. During the days, when the coalmine was working the air was full of coal dust which settled over the water and got mixed up with the chalk or BaSO_4 to settle at the bottom of the trough and the deposit of chalk or BaSO_4 became dark. During the nights the air was relatively free from coal dust and the nocturnal deposit was whiter. The six week days are thus marked by darker layers in the Sunday Stone which alternate with lighter layers formed in the nights following week days up to Friday but after the deposit formed on Saturday there is a thicker white band beginning with Saturday night, Sunday and Sunday night. Thus the thicker white bands in the layered stone represent Sundays and also holidays. Hereafter, it is easy to understand the importance of fossils in recording the past history of life. Since spores and pollen grains can float in the air like coal dust and settle down on land or water, they furnish a

vivid record of past life. Fortunately, they have a resistant, sporopollenin coat which furnishes clues about the plants which produced them. They are frequently used in correlation in sedimentology but can be readily preserved even when other parts of plants are not preserved. Another fortunate feature of spores and pollen is the characteristic sculpturing of their outer coats which often helps us in identifying the plants which produced them. Now since different periods in earth's history were having their characteristic forms of life, palynology is of immense help in dating and correlating rocks. Indeed the same is true of megafossils. Palynology has been extensively used by geologists but they also need to study megafossils and thus palaeobotany too can help us in determining the vertical and horizontal geographic location of various strata in different parts of the world. Radioactive dating, may be useful in absolute age determinations, lithology and petrology too may be useful in dating rocks but palaeobotany and

palaeozoology form the most convenient and cheapest method of dating and locating rocks.

I could have proceeded further in stressing the importance of palaeobotany but limitation of time prevents me from doing so. Therefore, I must end by saying that the importance of palaeobotany which I have mentioned should be enough to open the eyes of those who prevent palaeobotany in getting its due share in funds and posts in the University Departments since they are actually harming the progress of Science. We must remember that scientists at our Institutes also receive their initial training in the Universities.

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