"This paper is dedicated to Professor Ove Arbo Hϕeg, in the year of his 90th Birthday.

THE FOSSIL HISTORY AND PHYLOGENY OF THE CYCADALES

DIVYA DARSHAN PANT

Department of Botany, University of Allahabad, Allahabad

Abstract

Fossil remains attributed to the Cycadales include stems, leaves, scales, fructifications, seeds, pollen grains, and an exceptional plant fossil, *Leptocycas gracilis,* showing leaves, scales and a cone attached to a stem. A critical assessment of Palaeozoic fossils attributed to the group suggests that all of them are doubtful and some, like *Phasmatocycas,* even appear to be based on erroneous reconstructions. The oldest undoubted cycads like *Antarcticycas schopfii* and *Leptocycas gracilis* and some others occur in the Lower and Upper Triassic. A few of these early cycads had compound leaves but other contemporaneous ones had simple leaves so that neither of the two kinds of leaves can be regarded as ancestral. Mesozoic cycads are generally referred to extinct genera but a few forms resembling *Encephalartos* (or *Zamia*) can be traced back to the Triassic and a Cretaceous leaf is actually referred to *Encephalartos*. *Cycas*-like leaf forms called *Cycadites, Pseudocycas* and *Paracycas* go back only to the Jurassic but the oldest *Cycas*-like megasporophylls called *Cycadospadix* are Triassic. Tertiary cycad leaves are mostly assigned to extant genera on the basis of the close similarity of their external form although in some cases even their cuticles are comparable. The only notable exceptions among Tertiary leaves which have been lately referred to extinct genera are *Dioonopsis nipponica, Eostangeria saxonica* and two species of *Pterostoma*. The last mentioned species are assigned here to *Macrozamia* as *M. zamioides* (Hill) comb. nov. and *M. anastomosans* (Hill) comb. nov. due to the resemblance of their cuticles as well as their external form with those of *Macrozamia*.

The contrasting distribution of living and fossil cycads show that while all the 11 genera of extant cycads are confined to the tropical and subtropical regions of the earth, the fossils of the group show a much wider geographical scatter where their distribution extends into the present temperate regions and even into areas near the north or the south poles. The author believes that this poleward distribution may particularly suggest subsequent drifts of the fossil localities instead indicating a capacity of past cycads for cold tolerance.

Diverse views about the phylogeny and relationships of the group are reassessed. It is pointed out that even though the numerous similarities between cycads and preceding pteridosperms point towards their pteridospermous origin yet so far no particular pteridosperms can be regarded as ancestral to them. The similarities of cycads with other groups of gymnosperms are also discussed and it is concluded that none of them can presently be regarded as closely related to the cycads.

I am deeply conscious of the honour which has been bestowed on me by the Palaeobotanical Society by choosing me as the first Indian to receive the coveted award of their International Medal and I am equally conscious of the honour which you have done me, Ladies and Gentlemen, by your ominous presence here. It is, therefore, my first duty to begin this talk by offering my heartfelt thanks to the Palaeobotanical Society. Offering thanks to you reminds me of the debt I owe to my teachers, colleagues, students and associates in research who have helped me in completing my cherished aims and projects which have shaped my ideas and perspectives in different aspects of Botany which are limited to three dimensions and those of Palaeobotany which extend into the fourth dimension of time. In thanking my associates I must especially mention the names of two of my former students, Dr D. D. Nautiyal and Dr D. K. Chauhan who have helped me in spite of their own difficulties and discomfitures in shaping this talk.

I must also thank my students Dr Rita Singh and Kavita Das for their assistance in checking the references.

Before I begin my talk I must also say that when you choose an abstruse person like me for an award which has to be followed by a lecture, it is presumed that the awardee must give a talk on a topic of special interest to him but since such a topic is bound to lie outside the primary interests of a majority of the members of his audience he must present his ideas in easily comprehensible language. This is a difficult task and, therefore, if at any stage I fail to come up to your expectations you will kindly hear and bear me with patience and sympathy.

The topic which I have chosen for to-day's lecture is "The fossil history and phylogeny of the Cycadales", a group of strange "living fossils" reminescent of the Palaeozoic seed ferns which lived nearly 300-350 million years ago.

Early History

Nothing definite can be said about the origin and early history of the Cycadales. The earliest fossils which have been attributed to the group are reported from rocks of the Carboniferous and Permian times and it has therefore been suggested that the group originated during the Palaeozoic times. Diverse plant fragments which are sometimes believed to be the first traces of the group include pollen grains, stems, leaves, and seed-bearing or microsporangiate fructifications.

Among the above remains, dispersed pollen grains of (*Cycadopites* Wodehouse, 1933 Ex Wilson & Webster, 1946) and allied forms (Text-fig. 1A, B) date back to the Carboniferous and they also occur in all subsequent higher strata. However, Palaeozoic *Sporae dispersae* of this kind could equally well belong to the Pteridosperms, Ginkgoales or Coniferales and similar pollen grains occurring in the Mesozoic or Cainozoic strata could even be attributed to the Bennettitales and angiosperms.

Renault (1893, 1896) and others have described some Palaeozoic stems called *Cycadoxylon* (Text-fig. 1C) and *Ptychoxylon* (Text-fig. 1D) which are sometimes suspected to be cycadean because they resemble stems of modern cycads more closely than those of their Palaeozoic contemporaries like *Lyginopteris*, *Medullosa* and *Sutcliffia*. The Permain species, *Cycadoxylon fremyi*, for example, shows cycadean features like indistinct primary xylem strands, mucilage canals in the pith and a vascular ring in the cortex but its leaf traces are not preserved and its foliage and reproductive parts are unknown. Accordingly, it is not possible to assign it to the Cycadales with any certainty.

Typical Mesozoic cycadophytic leaf forms like *Pterophyllum*, *Plagiozamites* and *Sphenozamites* have often been reported from the Palaeozoic (Renault, 1893, 1896 ; Thomas, 1930) and according to Thomas (1930), the cuticle of *Pterophyllum grand'euryi*, from Upper

Text-fig. 1—**A**, *Cycadopites* (Wodehouse) Ex Wilson & Webster 39 μm; **B**, *Ginkgocycadophytus* Somoilovicz 50 μm; **C**, part of transverse section of *Cycadoxylon robustum* Renault ×12; **D**, transverse section of decorticated stem of *Ptychoxylon levyi*; **E**, *Cycadospadix millereyensis*. (C, D, E from Scott, 1923 after Renault); **F**, reconstructed cone of *Lasiostrobus polysacci* (after Taylor, 1970); **G**, reconstruction of megasporophyll of *Phasmatocycas* (after Mamay, 1969); **H, I**, reconstruction of dorsal and ventral views of megasporophylls of *Phasmatocycas* made by Gillespie & Pfefferkorn, 1986; **J-N**, diagrams showing effect of compaction of *Phasmatocycas* (after Gillespie & Pfefferkorn, 1986); **O**, reconstruction of metasporophyll of *Archaeocycas whitei* partly cut open to show seeds covered by lamina, shape and extent of sterile distal lamina hypothetical (after Mamay, 1976); **P**, *Pteronilssonia gopalii* (after Pant & Mehra, 1963) ×1/2; **Q**, *Rhabdotaenia danaeoides* ×1/2; **R**, a stoma from cuticle of *R. danaeoides* ×200 (after Pant, 1958).

ADDENDUM

The most interesting of these seed-fern-like cycads is *Cycas* whose female plants lack a cone and whose megasporophylls are not only like modified leaves but are produced in the same phyllotactic spiral as the vegetative leaves alternately by apices of female plants. In addition, all cycads are unique among living gymnosperms in having fern-like compound leaves, circinate vernation and anatomy. Above all their multiciliate sperms are altogether fern-like but unlike filicinean spermatozoids they never swim in external water. Clearly these features seem to be vestiges of their fern-like ancestry. Unlike the conifers which are the cold tolerant modern gymnospermous dominant tree constituents of temperate forests, the cycads are cold intolerant gymnosperms inhabiting the tropical and warm subtropical regions. They are never dominant and so much depleted in numbers that one of them, the monotypic *Microcycas calocom* of West Cuba, is on the verge of extinction. Indeed, all cycads have been declared endangered plants whose protection is being sought by cycad societies in all progressive countries like U. S. A., South Africa and Australia where they grow. This need of protection seems to have been realised by the plants themselves and all of them have developed toxic glycosides like cycasin and its analogues in all their parts. When animals eat them the glycosides are broken by their intestinal microbial enzymes to release methyl-azoxy-methanol (MAM) and ultimately they release formaldehyde, methanol and nitrogen. When repeatedly eaten by cattle they cause a disease called "rickets" or "wobbles" which results in serious incapacity of limbs and ultimate death. Their unboiled seeds and uncooked parts cause vomitting, diarrhoea, convulsions and cramps in humans and even well prepared starch of cycads causes amylotropic lateral sclerosis and Parkinsonism dementia and mental deficiency by prolonged use. It has also been reported that cycad food is carcinogenic and causes hepatoma in guinea pigs. The only animals capable of consuming cycad leaves without any toxic effects are some leaf eating butterfly caterpillars having 3 glycosidase in their digestive tracts and this breaks down the azoxyglucosidase to MAM which should kill them but they remain unaffected by attaching a glucose to it to form a stable cycasin. This stable cycasin is not excreted by the caterpillar and kept stored so that the worm becomes poisonous to birds and animals eating it. Cycasin is thus a marvellous defence mechanism for cycads as well as for their few successful foragers.

Till 1987, only 10 living genera of these curious plants were known although the distribution and numbers of their species were not fully explored. This incompleteness of our knowledge is vividly shown by the fact that we have lately discovered many new species of the various genera and Stevenson has discovered an entirely new genus, *Chigua*, only a few months ago. He suspects that he is about to discover another new genus.

Please read the following with the matter on p. 128 after First Para (from top).

Zhifeng Gao (1987) too has reported some Lower Permian cycadean fossils from Eastern Hill, Taiyuan, China. Two of them called *Yuania chinensis* and *Tianbaolinia* are described as foliar organs; the first having a stipe and an expanding pulvinus at the base while the second has circinated leaves. The overall similarity of *Tianbaolinia* with *Yuania* is believed to suggest that it may be a juvenile stage of that genus. Zhifeng Gao has also assigned *Primocycas chinensis* Zhu & D'u to a new genus. *Crossozamia*, as *C. chinensis* comb. nov. and also described its three species, viz., *C. cuculata* (Halle) comb. nov., *Crossozamia* sp. and *C. minor* sp. nov. The megasporophylls are reportedly attached spirally to an axis as a strobiloid structure. However, their structure and cuticles are not preserved and their reference to the Cycadales is doubtful.
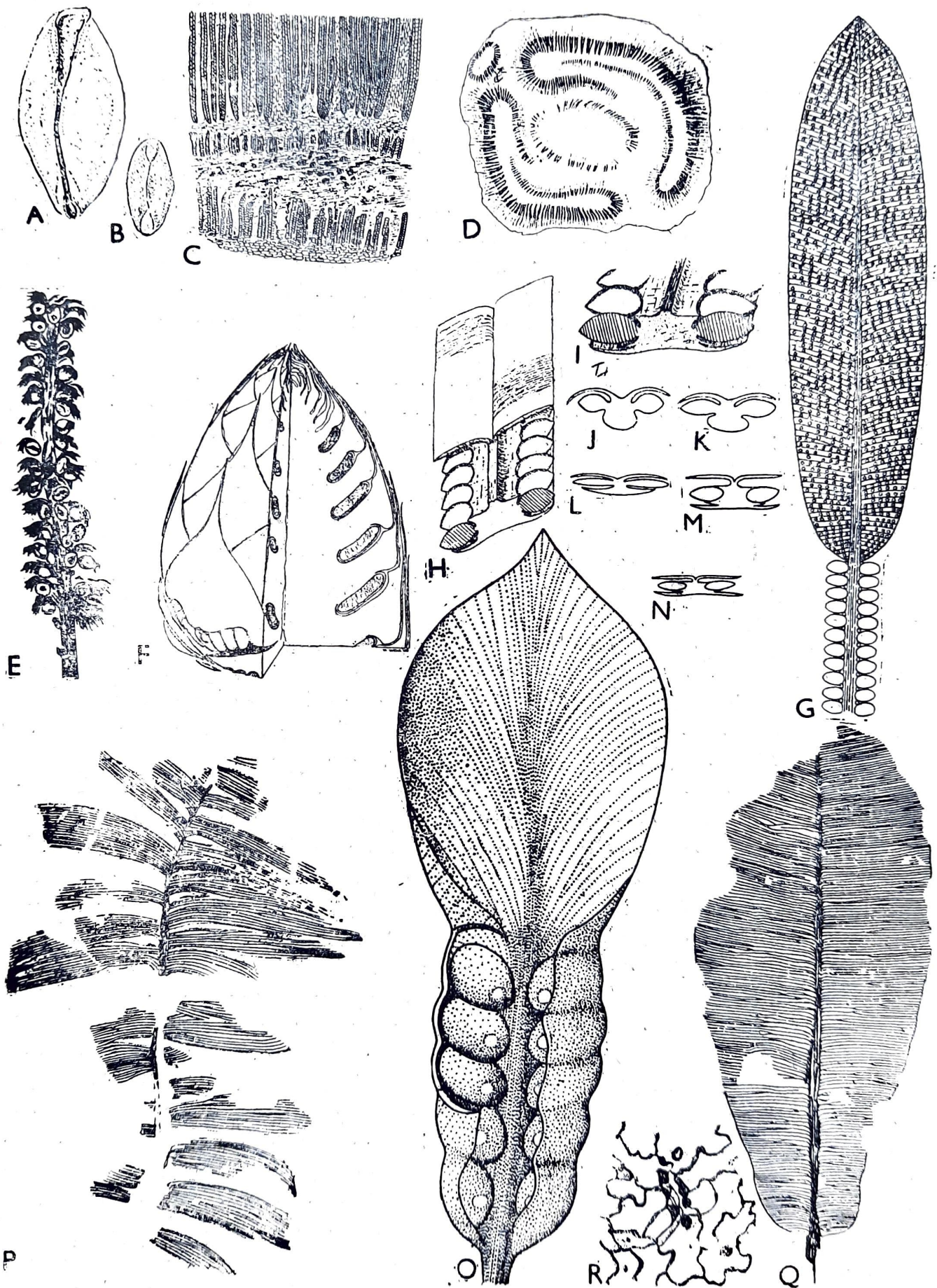
Text-fig. 1

Carboniferous of France, resembles that of the Mesozoic cycadean form *Nilssonia*. A *Nilssonia*-like leaf has been reported by Halle (1927) from the Permian of China under the name *Dioonites densinervis* apparently to indicate its cycadean affinities. Pant and Mehra (1963) have reported another pinnate leaf *Pteronilssonia gopalii* (Text-fig. 1P) from the Lower Gondwanas of India. The epidermis of *P. gopalii* shows haplocheilic stomata with irregular papillate subsidiary cells. The external form and the epidermal structure of the Premo-Carboniferous leaves of *Rhabdotaenia* (Text-fig. 1Q, R—see Pant, 1958; Pant & Verma, 1963) also resemble those of the cycadophytes although these Lower Gondwana leaves are more closely comparable with the associated Glossopteridales. However, the mere occurrence of leaves resembling those of the Cycadales, even when cuticles are preserved, is insufficient proof of the existence of the group during the Palaeozoic because our knowledge of the plants bearing them is far from being complete and their reproductive parts are unknown.

No doubt Zhang and Mo (1981) and Zhu and Du (1981) have described some cycadophytes from the Permian of China which include taeniopterid leaves called *Cladotaeniopteris* occurring in association with a cycadean type of megasporophyll inclusive of a new cycad named *Primocycas chinensis* but in these fossils the cuticles and structure are not preserved and their reference to the Cycadales is doubtful. The only other exceptional Palaeozoic fructifications attributed to the Cycadales are : *Lasiostrobus polysaccii* Taylor, *Cycadospadix millereyensis* Renault, *Phasmatocycas kansana* Mamay, *Archaeocycas whitei* Mamay, *Sobernheimia jonkeri* Kerp. All the above fossils present certain cycadean features but as discussed below their precise affinities are presently quite uncertain.

The first of the above Palaeozoic fructification is *Lasiostrobus polysacci* Taylor (1970) which was described as a possible cycadean male cone from the Pennsylvanian of North America (Text-fig. 1F) but the cone produces polysaccate pollen grains (Pl. 2, figs. 7, 8) which are quite unlike those produced by any living or definitely known fossil cycad. Its attribution to the cycads is therefore extremely doubtful.

The fructification called *Cycadospadix millereyensis* (Text-fig. 1E) was reported by Renault as early as 1893 and 1896 from the Lower Permian of Autun in France along with some cycadophytic leaves and stems called *Cycadoxylon*. It was described as a cone with a slender axis bearing fimbriated, biovulate sporophylls (see Seward, 1917), and Scott (1923) thought that it could even represent a pteridospermous megasporophyll. In any case the cycadean nature of *C. millereyensis* becomes doubtful.

As reconstructed by Mamay (1969, 1976) *Phasmatocycas kansana* (Text-fig. 1G) has a fertile axis bearing two rows of naked orthotropous ovules and spherules regarded as glands on the axis with a nectariferous function. Associated fragments of *Taeniopteris* leaves having interstitial rows of glands are believed to be the distal sterile ends of *Phasmatocycas* axes which is thus presumed to be a primitive type of cycadean megasporophyll. Mamay believes that his *Phasmatocycas* is derived from an ancestor like *Spermopteris* as described by Gridland and Morris (1960), through reduction in the number of seeds and of lamina in the basal ovule bearing part. Gillespie and Pfefferkorn (1986) have now found taeniopterid laminar fragments with attached seeds which they identify as those of *Phasmatocycas* and suggest that their specimens confirm Mamay's reconstruction of its megasporophyll. Instead, the specimens described by Gillespie and Pfefferkorn are obviously quite different from Mamay's reconstructed *Phasmatocycas* in having their ovules attached to the abaxial side of the midrib which bears a taeniopterid lamina above them, on their adaxial side (see Gillespie & Pfefferkorn, 1986, p. 103, pl. 1, figs, 1, 2, 4, and the reconstructions of megasporophylls seen in Fig. 1—see also Text-fig. 1 H-N of this paper)

where as Mamay's reconstructed megasporophyll depicts the ovules to be attached to a non-laminar basal part like that of the megasporophylls of *Cycas*. Therefore, instead of confirming Mamay's reconstruction, the newly discovered specimens of *Phasmatocycas* prove to be quite different and they are so much unlike the megasporophylls of *Cycas* that the suffix of their name makes them misnomers. In fact glandular taeniopterid leaves from the Triassic of Nidpuri, India, called *Glandulataenia* Pant (1987) neither bear any seeds nor they are associated with *Spermopteris*-like ovule bearing organs (see Text-fig. 2A, B) and they suggest that such leaves could be of diverse affinities.

The second megasporophyll described by Mamay (1976) was called *Archaeocycas whitei* (Text-fig. 1O). It existed almost simultaneously with *Phasmatocycas* and is also somewhat similar to its but its forked lateral veins cross the lamina at smaller angles and its seeds are attached to a basal inrolled lamina which, at least partially, encloses them. The attached distal end of the megasporophyll is sterile. Mamay suggests that *Archaeocycas* may be a further step in the evolution of a *Cycas*-like megasporophylls or it may be a stage in the evolution of a carpel-like organ since the ovules are partially enclosed. The specimens of *Phasmatocycas* discovered by Gillespie and Pfefferkorn (1986) clearly indicate that the latter alternative may be preferable so that both these Permian forms can fit into the gap at the starting point in the conception of a gonophyll (Melville, 1962-1963) but they are rather far from the megasporophylls of *Cycas*.

Sobernheimia jonkeri too is a megasporophyll described by Kerp (1982-83) from the Lower Permian of Nahe area in West Germany. The lateral margins of the megasporophyll are produced into linear lobes alternating with seed-like bodies. Kerp attributed *Sobernheima* to the Cycadales due to its resemblance with *Phasmatocycas* but, as pointed out above, since Mamay's reconstruction of that fossil as a *Cycas*-like megasporophyll apperas to be incorrect, the attribution by *Sobernheimia* to the Cycadales becomes equally erroneous and we are left with no undoubted vegetative or reproductive remains of the cycads in the Palaeozoic.

Mesozoic Forms

There are, on the contrary, a number of fossils in the Mesozoic which are regarded as definitely cycadean, although such affinities of many others of the same era are more or less doubtful. The earliest undoubted cycads are reported from the Triassic but according to Karassilov (1978) the true cycads first appeared only in the late Cretaceous. For convenience in description, the Mesozoic fossils attributed to this group are discussed here under the following heads :
(a) Plants whose vegetative as well as reproductive parts are known and reconstructed, (b) Fructifications, (c) Stems, and (d) Leaves.

(a) *Plants whose vegetative as well as reproductive parts are known and reconstructed*—These include *Leptocycas gracilis*, *Diooniticarpidium pennaeforme*, *Palaeocycas integer*, *Baenia gracilis*, *Baenia mamayii* and *Androstrobus prisma*.

Among all hitherto described fossils of the Cycadales *Leptocycas gracilis* (Delevoryas & Hope, 1971) as described from the Upper Triassic of North Carolina, is unique for having left the remains of its stems, leaves, cataphylls (Text-fig. 21) and a cone in connection (Pl. 2, fig. 5). Its slender stems are only 3 to 5 cm thick and they bear loosely arranged terminal crowns of petiolate leaves of *Pseudoctenis* type intermixed with cataphylls. Persistent bases of petioles are present below the crown of leaves but farther down the stem is wrinkled and without the typical cycadean armour of leaf bases. The cuticle of leaves

is of the cycadean type showing straight-walled epidermal cells and haplochielic stomata. Attached to the stem apex in one specimen, is seen a structure which seemingly resembles a drooping male cone of cycads although the pollen grains or cuticles are not preserved.

Diooniticarpidium (Lilienstern, 1928; Kräusel, 1949, 1953), described from the Triassic (Keuper) beds of Germany is reconstructed as a pinnate megasporophyll, about 20 cm long, which bears two rows of narrow somewhat sickle-shaped pinnae and one or two pairs of oval seeds near the base (Text-fig. 2E). Harris (1964) points out that the bodies, interpreted as seeds, appear sunken unlike seeds of *Cycas* or *Dioon* which are projecting. In some specimens they appear like sacs enclosing small seeds although in others they look like seeds. A reconstruction of the plant of *D. pennaeforme* by Lilienstern (Text-fig. 2D) shows a crown of simple vegetative leaves of *Danaeopsis angustifolia* type below a cluster of six ovulate sporophylls. The leaves are attributed to the sporophylls merely on the basis of association in the field. The interpretation of the megasporophyll as that of cycads is doubtful. The structural details of *Diooniticarpidium* and its stem are unknown. Its true affinities are therefore uncertain.

Palaeocycas (*Cycadospadix*) *integer* (Nathorst) Florin described from the Rhaetic of Sweden (Text-fig. 2F, G, H), Florin (1933) reconstructed its female plant on the model of modern *Cycas* due to the resemblance of the reconstructed megasporophylls of *Cycadospadix integer* (Text-fig. 2G) with those of *Cycas*. Large simple taeniopterid leaves named *Bjuvea simplex* (Text-fig. 2F) which occur in association with the above megasporophyll remains are assigned to each other on account of the resemblance of their cuticles. However, as already pointed out by Harris (1961), in this otherwise impressive reconstruction, the stem is entirely imaginary and not even one of the megasporophylls shows attached seeds. The swellings in their stalks no doubt suggest attachment points of seeds but this needs confirmation. The male parts of *Palaeocycas* are unknown.

The fourth plant, *Baenia gracilis* is described from the Jurassic of Yorkshire. On the basis of close association in the field and resemblance in cuticular structure, Harris (1941) attributes the leaves of *Nilssonia compta* (Text-fig. 2K, L), scale leaves of *Deltolepis crepidota*, and male cones of *Androstrobus manis* to *Baenia gracilis*. The female strobilus of *Baenia* shows peltate biovulate sporophylls arranged in a lax spiral round the cone axis (Text-fig. 2 M, N) *Androstrobus manis* (Text-fig. 2O) has small strobili with spirally arranged somewhat flattened sporophylls bearing sporangia on the underside as in *Cycas* and other cycads (Text-fig. 2 P, Q). The spores and sporangia are typically cycadean.

Text-fig. 2—**A**, *Glandulataenia glandulosa* fragment of middle portion of leaf showing glands (black dots) between veins ×2; **B**, a stoma from cuticle of same ×150 (both after Pant, under publication); **C**, megasporophyll of *Cycadospadix hannoquei* (from Pant, 1973, after Saporta & Marion, 1878); **D**, *Diooniticarpidium pennaeforme* reconstruction of plant showing apical cluster of megasporophylls above a crown of *Danaeopsis angustifolia* leaves; **E**, basal fragment of a megasporophyll of *Diooniticarpidium pennaeforme* showing basal swellings (seeds) ×1/2. (D, E, after Lilienstern, 1928); **F**, reconstructed leaf of *Bjuvea simplex* ×ca 1/6; **G**, reconstructed megasporophyll of *Palaeocycas integer*, the seeds have not been found attached ×ca 1/5; **H**, reconstructed plant of *Palaeocycas* showing an apical crown of megasporophylls above a crown of *Bjuvea simplex* leaves borne on an imaginary stem ×ca 1/30 (F, G, H, after Florin, 1933); **I**, *Leptocycas gracilis* reconstruction of a plant about 1.5 m tall (after Delevoryas & Hope, 1971); **J**, reconstructed plants of *Nilssonia tenuinervis* bearing male cones of *Androstrobus wonnacottii* (left) and young and old female cones of *Baenia mamayi* (right). The stem is imaginary (after Harris, 1961); **K, L**, basal and apical parts of leaves of *N. compta*, respectively (from Pant, 1973); **M**, *Baenia gracilis*, reconstructed cone ×1/2; **N**, longitudinal section of megasporophyll with one of the two seeds attached ×1; **O**, cone of *Androstrobus wonnacottii*; **P, Q**, microsporophylls of same in adaxial and abaxial views, respectively (M-Q after Harris, 1941).

The peltate megasporophyll of *Baenia* resembles that of modern *Zamia*, but it has a long slender stalk. The ovules too are just like those of modern cycads. The leaves, *Nilssonia compta*, have pinnae which are not attached on the flanks of the rachis but near its upper side. They are parallel-veined and hypostomatic; their stomata are haplocheilic and epidermal cells are straight-walled. Another similar plant had megasporophylls called *Beania mamayi*, male cones called *Androstrobus wonnacottii* and leaves called *Nilssonia tenuinervis*. Harris (1961) built reconstructions of the plants with imaginary stems (Text-fig. 2J) and refers them to a separate family, the Nilssoniae under Cycadales.

Thomas and Harris (1960) have ascribed the leaf *Pseudoctenis lanei* to the male cone *Androstrobus prisma* on the evidence of association in three localities in Yorkshire and agreement in their cuticular structure. The leaves and the male cones of this plant agree closely with those of modern cycads like *Zamia* and *Encephalartos*. The pinnate leaf shows parallel veins rarely anastomosing and haplocheilic stomata. The massive male cone has microsporophylls with abaxial sporangia arranged in sori. Harris (1964) believes that the plant of *Adorstrobus prisma* may have been closely similar to that of *Zamia* or *Encephalartos*.

(b) Fructifications

Some Mesozoic fructifications which are often assigned to the Cycadales on account of their apparent resemblance with cycadean cones on sporophylls are mentioned in Table 1 below :

Table 1—Some Mesozoic fructifications of Cycadales

Name of fructification	Horizon	Comparable living forms
Zamioidea keuperiana Schuster 1931	Triassic	Resembles the megasporophyll of the Zamioideae
Z. macrozamioides Schuster 1931	Lias	
Lepacyclotes triphyllus Emmons 1856 (Heer) Schuster (See Schuster, 1932)	Triassic	Resembles the megasporophylls of Cycadales
Androstrobilites triassicus Schuster 1932	Rhaetic	Probable male cones apparently resembling those of Cycadales
Cycadospadix Schimper 1870 C. *hannocquei* (Pomel)/Schimper 1870	Jurassic	Megasporophylls like those of modern *Cycas*
C. *pasinianus* Zigno 1885, Saporta 1891, Seward, 1917	Jurassic	
Diooniticarpidium keuperianum Krausel, 1949 D. *pennaeforme*	Keuper	Megasporophylls like those of modern *Cycas* but with much larger sterile end.
Carpolithus sp. Seward, 1895-*Sewardocarpus ecclesbournensis* Schuster 1932	Wealden	Probable seeds of Cycadales but they could even belong to other groups like Ginkgoales.

Fructifications like *Cycadospadix hannocquei* (Text-fig. 2 G) are remarkably like the megasporophylls of *Cycas* but most of the above isolated fructifications are imperfectly known and their reference to the Cycadales is presently uncertain.

(c) *Stems*

The earliest definitely assigned stem of the Cycadales is *Antarcticycas schopffi* Smoot et al. (1985) from the Lower Triassic Fremouw Formation in the Beardmore Glacier area in Antarctica. The stem is rather slender, about 3.7 cm wide. It is monoxylic having a wide pith, a wide cortex and scanty wood with plentiful parenchyma and wide rays between the vascular bundles. It is also monoxylic (see Pant, 1973) and shows a single ring of vascular bundles like that found in the stems of present day *Zamia, Dioon, Ceratozamia, Microcycas* and *Stangeria*. Other cycadean characteristics of the stem are presence of numerous mucilage canals, transfusion tracheids in the pith, cycadean type of vascular elements and the characteristic tangentially traversing girdle traces in the cortex besides the radial traces (*see* Pl. 1, figs. 2, 3, 4).

Another fossil stem which may be included among the fossil Cycadales with equal certainty is *Michelilloa waltonii*. Under this name, Archangelsky and Brett (1963) have described a silicified stem about 10 cm in diameter from the Triassic of Argentina. The stem shows a wide pith with ducts. At its periphery are situated groups of tracheids separated from the surrounding monoxylic xylem cylinder by large parenchyma cells. The xylem cylinder is divided by leaf gaps into wedges. In tangential sections the leaf gaps appear fusiform. Tracheids of xylem cylinder show alternate multiseriate bordered pits. Leaf traces are collateral and their tracheids are scalariform. Their full course as girdles could not be traced but they pass through the cortex obliquely curved like girdles. Their structure and origin are also similar to those of modern cycadean leaf traces. The stem surface shows a ramentum of long filamentous hairs. *Michelilloa* thus presents a number of characters which resemble those of the recent cycads including the presence of the characteristic girdle traces although their full course requires confirmation.

A third petrified trunk described from the Late Triassic Chinle Formation of Arizona and New Mexico is *Lyssoxylon grigsbyi* (Gould, 1971) which has an axis about 7 cm thick, having a central pith and surrounding monoxylic and manoxylic cylinder with secondary xylem showing growth rings like those reported by Chamberlain (1935) in some cycads, crowded persistent leaf bases and girdling leaf traces. The epidermis produces bicelled hairs which form a dense mat around petiole bases. The stem closely resembles the stems of modern *Dioon*.

Yet another petrified stem referred to the Cycadales is *Fascivarixylon mehtae*. The species is based on a single specimen having a diameter of 2.3 cm which has been found in the Jurassic beds of Rajmahal Hills in Bihar (Jain, 1964). The stem shows medullary bundles which Jain compares with those of *Encephalartos* and *Macrozamia* but it is referred to the cycads in the absence of the characteristic girdle traces.

Under the name *Nilssoniocladus* Kimura and Sekido (1975) have described some Early Cretaceous slender stems showing widely spaced lateral short shoots which bear clusters of *Nilssonia* leaves. These authors have assigned *Nilssoniocladus* to a new family Nilssoniaceae which they think is distinct from the old Nilssoniales. However, the above stems which have been attributed to the Cycadales seem to present a contrast with those of most modern Cycadales in being slender (see Text-fig. 3).

Some other Mesozoic cycadean stems may have been described under the name *Bucklandia* Presl, but when properly used that is a name for stem casts or moulds of cycadophytes and it may even include stems belonging to the Bennettitales or to other groups.

Text· fig. 3—Part of an ultimate shoot of *Nilssoniocladus nipponense* with spirally arranged dwarf shoots ×4/5 (after Kimura & Sekido, 1975).

(d) Leaves

The great abundance of cycadophytic leaves during the Mesozoic era led early authors to suggest that the Mesozoic was the "Age of the cycads" because it was then believed that most of them belonged to the Cycadales. Later work has shown that quite a few of them are those of Mesozoic pteridosperms while a large majority belong to the Bennettitales. Exomorphic features of bennettitalean leaves are so similar to those of Cycadales that some of them were given names like *Dioonites*, *Otozamites*, *Anomozamites*, etc. to indicate their relationships with cycadean genera. The confusion regarding the leaves of the two groups was cleared as a result of the work of Nathorst (1902, 1909), Thomas and Bancroft (1913), Florin (1931, 1933), Harris (1932, 1950, 1952), Pant and Nautiyal (1963) and others when it became evident that the leaves of the two groups could usually be distinguished on the basis of their distinct cuticular structure, which is, as a rule, well preserved in fossil leaf compressions. However, while leaves having bennettitalean epidermal features including syndetocheilic stomata are confined to the Bennettitales and Gnetales, those with haplocheilic stomata are of widespread occurrence among the gymnosperms, e.g. in

Coniferales, Ginkgoales, Ephedrales, Taxales, Cycadales and Pteridospermales. In recent years, the allocation of an increasing number of cycad-like pinnate and non-pinnate leaves to the Mesozoic pteridosperms has created another problem. The chief difficulty now is in identifying leaves of the Cycadales from those of the co-existent pteriodosperms. Accordingly, the haplocheilic leaves mentioned below are only provisionally included in the Cycadales (except in cases where their reproductive parts are known) and some of them may well prove to belong to the peteriodosperms or some very different hitherto unknown plants.

Mesozoic leaves with haplocheilic stomata could again be divided into two categories, (i) leaves whose form and structure are different from those of any of the modern genera, and (ii) leaves which are closely comparable with those of some of the modern genera. Among the leaves of the first category are the form genera *Nilssonia, Ctenis, Pseudoctenis, Mesodescolea, Bjuvea, Doratophyllum, Rhabdotaenia, Glandulataenia* and *Pseudopterophyllum*. Under the second category come the leaf forms *Cycadites, Dioonites borealis, Pseudocycas, Paracycas, Moltenia, Walkomia* and *Almargemia* and a leaf described as *Encephalartos* on account of its resemblance with the modern leaves of that genus. Brief descriptions of some of these leaves are given below.

Nilssonia—Some leaves of this type have already been discussed in connection with *Baenia*. There are, however, a number of other species which remain unassigned to their reproductive parts, e.g. *N. princeps* (Oldham & Morris) Seward from the Jurassic of India (and possibly also from Transcaucasia), *N. kendallii* Harris from the Jurassic of Yorkshire, *N. grandifolia* Delle, *N. variabilis* Pryn, and *N. vittaeformis* Pryn, from the Middle Jurassic of Transcaucasia.

Ctenis—This name includes unipinnate leaves where the pinnae are broadly attached and often decurrent. Their veins are parallel or almost so with cross connections here and there (Text-Fig. 4A-E). The stomata are haplocheilic but the epidermal cell walls may be straight or occasionally wavy; some of the well known species are *C. sulcicaulis* (Phillips) Ward and *C. reedii* Harris from the Jurassic of Yorkshire and *C. kaneharai* Yokoyama which occurs in the Jurassic of Yorkshire and Manchuria (Harris, 1964). It is also found in the Lower Cretaceous of Japan. A species called *C. pontica* Delle (1967) is found in the Middle Jurassic of Transcaucasia.

Pseudoctenis—is like *Ctenis* but the cross connections are absent. The stomata are haplocheilic although sometimes transversely oriented (see Fig. 5A, B). A number of species of the genus are reported from Yorkshire. These include *P. harriesi* Harris, *P. locusta* Harris and *P. lanei* Thomas (see Harris, 1964). The leaf of *Leptocycas gracilis* is also of *Pseudoctenis* type.

Mesodescolea—Under the name *M. plicata* Archangelsky & Petriella (1971) have described some Lower Cretaceous compound leaves from Argentina. Their lobed pinnules are net-veined (Text-fig. 7 B-D). The genus is assigned to the Stangeriaceae on the basis of resemblances in cuticular structure.

Bjuvea—Some large taeniopterid leaves previously included in *Macrotaeniopteris* were separated by Florin (1933) under *Bjuvea*. They have cycadean type of cuticular structure with haplocheile stomata and Florin believes that they belong to *Palaeocycas* as already discussed.

Doratophyllum—Under this name Harris (1932) includes spatulate simple leaves of *Taeniopteris* type. A midrib is present and from its two sides arises the lamina. The lateral veins are often furcate but never anastomose. They cross the lamina almost
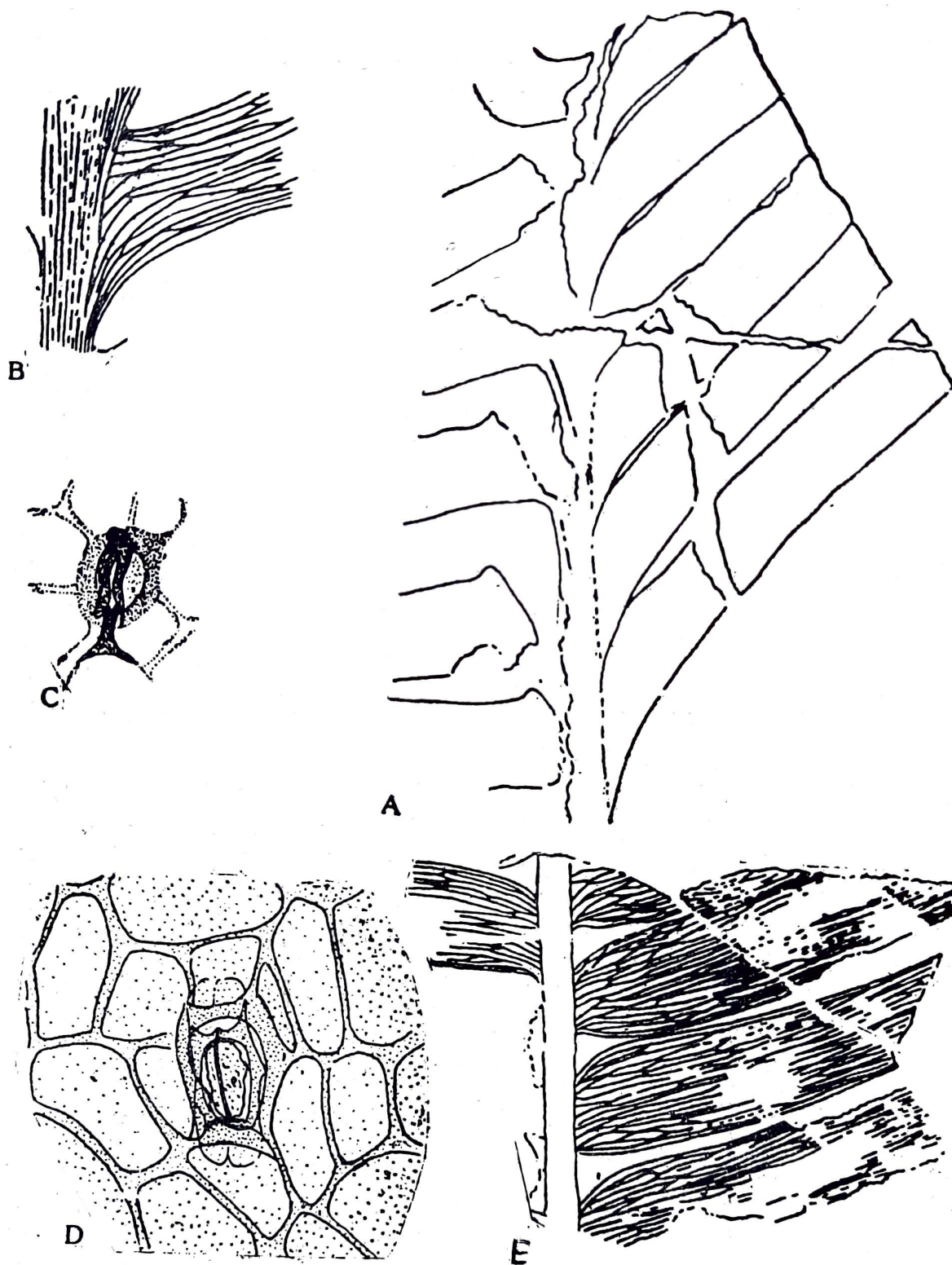
Text-fig. 4—**A-D**, *Ctenis sulcicantis;* **A**, pinnae from upper part ×1/2; **B**, base pinnae ×2/4; **C**, stoma showing guard cell thickenings in an unmacerated epidermis ×300; **D**, a more protected stoma ×300; **E**, *Ctenis kaneharai* middle region of leaf showing venation ×3/4 (all after Harris, 1964).
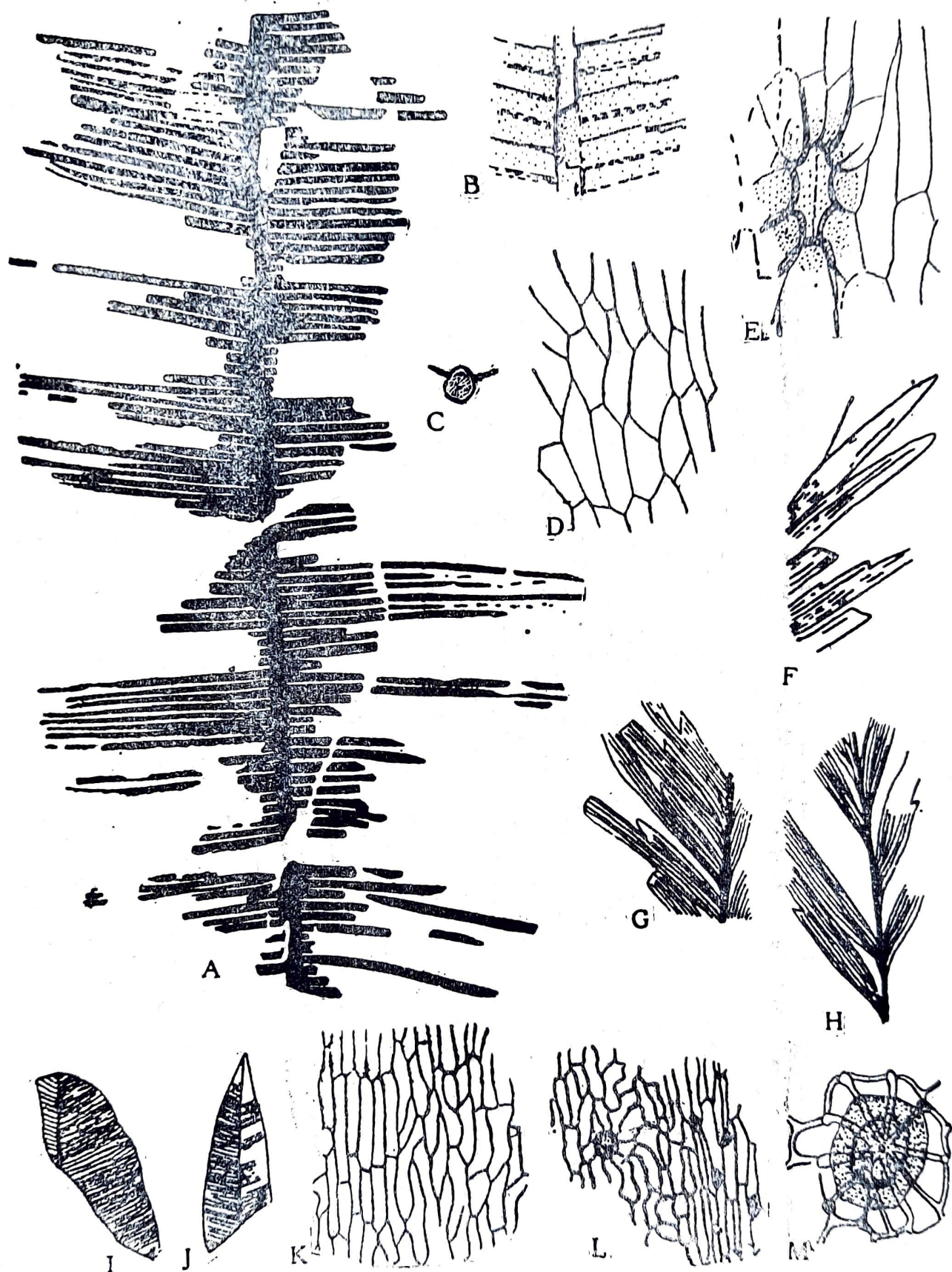
Text-fig. 5—**A-E,** *Paracycas cteis* (after Harris, 1964) : **A,** leaf fragment ×ca 3/4; **B,** rachis and pinnae of the same; **C,** imaginary cross section through rachis with thickness restored; **D,** upper cuticle ×ca 150; **E,** lower cuticle showing a stoma ×ca 300; **F-H,** *Almargemia dentata,* leaf fragments showing venation × ca 3/4 (after Florin, 1933); **I-M,** *Doratophyllum astartensis* (after Harris, 1932). **I, J,** apices of broad and narrow leaves ×ca 3/4. **K,** portion of upper cuticle ×ca 75; **L,** lower cuticle showing a stoma and hair cells ×ca 75; **M,** a stoma ×ca 300.
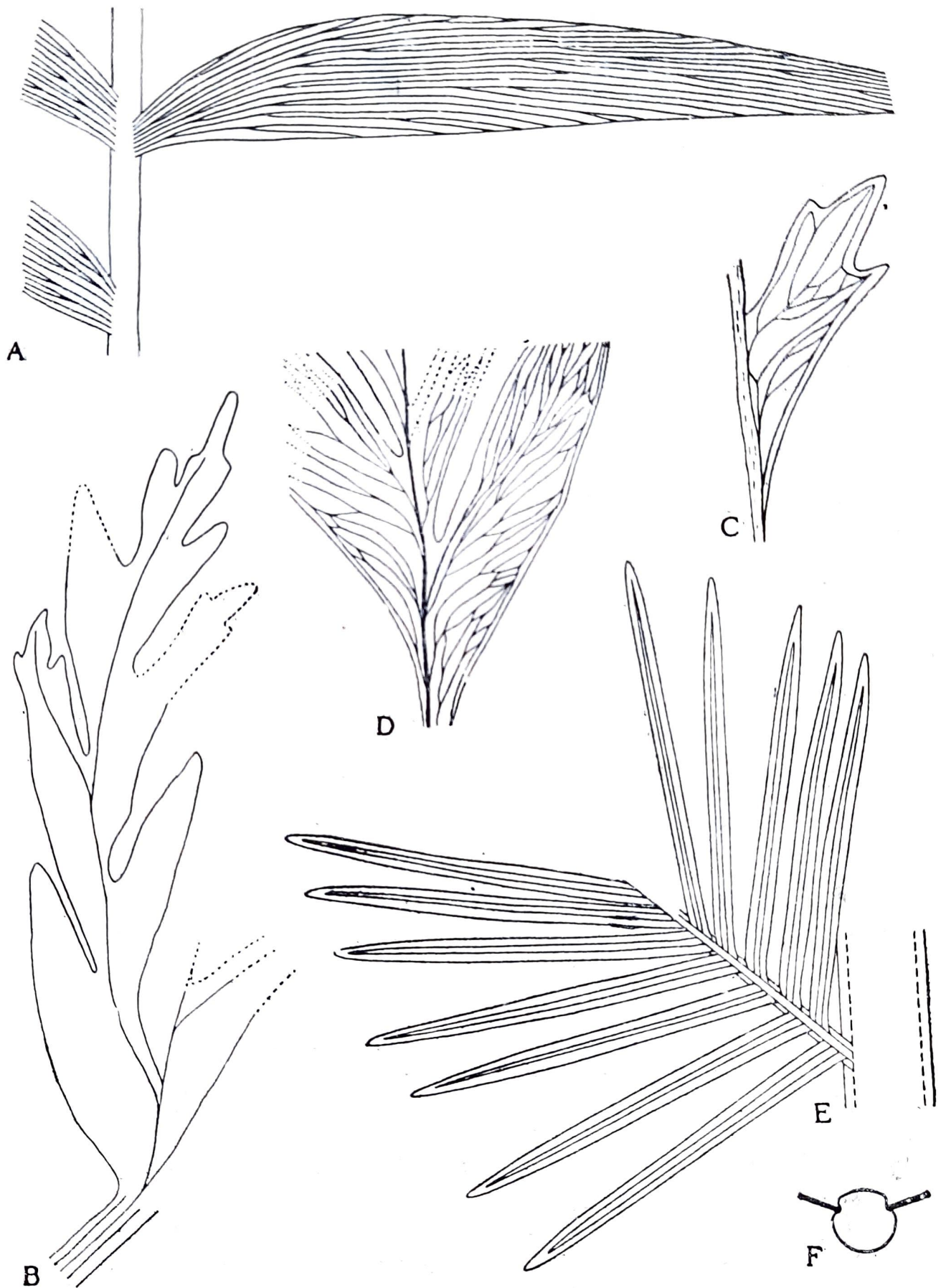
Text-fig. 6—**A-F**, portions of leaves showing venation : **A**, *Macrozamia zamioides* (Hill) comb. nov. (after Hill, 1980); **B-D**, *Mesodescolea plicata* × 1 (after Archangelsky & Petriella, 1971); **E, F**, *Tetoria endoi* (after Kimura & Sekido, 1974), E, posterior portion of penultimate pinna × 1. F, imaginary cross section with thickness restored.

at right angles. The subsidiary cells form a regular ring round the stoma (see Text-fig. 6 I-M). One of the oldest species is *D. astartensis* described from the Rhaetic of East Greenland by Harris (1932).

Rhabdotaenia Pant (1959)—Is another similar genus of taeniopterid leaves but the stomata of its leaves show a rather irregular ring of subsidiary cells. The earliest species of the genus are of Permian age. Their occurrence in the Glossopteris flora and the resemblance of their epidermal characters with those of *Glossopteris* have led to their being assigned to the Glossopteridales (Pant, 1982).

All the same the genus persists into the Triassic and some leaves of same kind now called *Glandulataenia glandulosa* n. comb (Pant, 1987) have a glandular lamina (Text-fig. 2A, B) just like of Mamay's *Taeniopteris* which according to him forms the terminal part of megasporophyll of his *Phasmatocycas*. However, leaves of *Glandula taenia glandulosa* are never associated with any fertile seed bearing remains which could belong to a *Phasmatocycas* like fossil. Indeed the specimens of *Phasmatocycas* described by Gillespie and Ptefferkorn (1986) and *Glandulataenia glandulosa*, as already discussed, may suggest that Mamay's reconstruction of *Phasmatocycas* is erroneous.

Pseudopterophyllum—Under this name Florin (1933) includes leaves with laterally attached pinnae whose length is more than twice their width. The veins are parallel and non-anastomosing. The stomata are haplocheilic. A single species *P. cteniforme* (Nath.) Florin, was described from Sweden. According to Harris (1964), this is a species of *Pseudoctenis*.

The leaf forms described as *Moltenia dentata* Du Toit (1927) from South Africa and *Walkomia feistmantelii* (Johnston) Schuster (1931) from Tasmania are both of Triassic age. The pinnae of *M. dentata* resemble those of some species of *Encephalartos*, *W. feistmantelii* is similar to *Moltenia* but the pinnae are non-decurrent and lanceolate, *Almargemia dentata*, is a Cretaceous leaf fragment described by Florin (1933) from Portugal (Text-fig. 6F-H). The subopposite pinnae have parallel veins and a typically cycadean cuticle. *Almargemia* probably belongs to the Zamioidae.

Among the various Mesozoic forms referred to extinct genera of leaves, a leaf described by Lesquereux (1892) from the Cretaceous of Dakota as *Encephalartos cretaceous* is remarkable in being referred to a modern genus. *Dioonites borealis* Dawson (1883) from the Cretaceous of Northwest Territory in Canada is regarded by Hollich (1932) to be closely related to his *Dioon inopinus* and *D. prosespinuosum* from the Tertiary of Alaska.

The genus *Cycadites* Sternberg (1825) at one time included most of the Mesozoic leaves which had a superficial resemblance with leaves of *Cycas*. Many of these have now proved to be very different in their cuticular structure from those of *Cycas*. The affinities of other leaves are uncertain. Some of them have been shown possess a double median vein and for all such leaves of uncertain affinity Nathorst (1907) proposed the name *Pseudocycas*. Subsequently the name *Cycadites* became reserved for fossil leaf remains which were externally similar to those of *Cycas* and showed a *Cycas*-like cuticular structure. As a result two Mesozoic leaves, *Cycadites cteis* (Harris, 1952) from Yorkshire and *C. blomquistii* Antevs (Florin, 1933) were almost the only ones left in the genus. Lately Harris (1964) has referred *C. cteis* and *C. blomquistii* to a new genus *Paracycas* (Text-fig. 6A-E), which is supposedly related to modern *Cycas*. Subsequently Delle (1967) has reported an additional species of the genus under the name *P. brevipinnata* from Transcaucasia and among others Deludenko and Orovskaya (1976) have reported three more species, *P. raripinnata*, *P. harrisii* (Pl. 2, fig. 6) and *P. intermedio* from Karatau in U.S.S.R.

The separation of *Paracycas* from *Cycadites* has resulted in the latter name being used

only for impressions of *Cycas*-like leaves whose cuticle is not available and which do not show a double midrib. Some leaves which still remain in *Cycadites* are *C. ractangularis* Brauns reported by Delle (1967) from the Jurassic of Transcaucasia ; *C. rajmahalensis* Oldham (see Bose & Banerji, 1981) from the Jurassic, *C. jabalpurensis* Pant & Pant (1987) from the Cretaceous of India (Text-fig. 8A, B) and a Tertiary leaf called *C. escheri* Heer (1955) from Miocene of Switzerland. The occurrence of the above *Cycas*-like forms in widely scattered parts of Europe and Asia may indicate that plants of the Cycadaceae were in the past more diversified and more widespread in the Northern Hemisphere.

Kimura and Sekido (1974) have described a pinnate cycadean frond *Tetoria endoi* from Lower Cretaceous of Japan. Its pinnules are uninerved like those of *Cycas* but it resembles *Bowenia* in being bipinnate (Text-fig. 7E, F). The internal structure or cuticles of *Tetoria* are unknown but Kimura and Sekido believe that it is close to *Cycas*. Perhaps the gap between *Cycas* and *Tetoria* could be bridged by a species like *Cycas micholitzii* which has divided pinnae.

Tertiary Forms

Fructifications

The only Teritiary cone ascribed to the Cycadales is *Zamiostrobus saportanus* Schimper 1870 from the Miocene of France, but its structural details and exact affinities are unknown. Some Tertiary seeds occurring in the Morewell brown coalmine in Victoria, Australia are attributed to *Lepidozamia peroffskyana* by Chapman (see Hill, 1980) but they are only about half the size of the seeds of the living species and their structural details are unknown. Shukla (1947) described a petrified seed, *Gymnovulites* from the Eocene or uppermost Cretaceous of Deccan Intertrappean Series of India, which resembles a young cycadean seed in showing a three-layered integument and a nucellar beak.

Stems

Kräusel (1928) has described some well defined fossil cycadean trunks from the Miocene of Germany under the name *Bucklandia niersteinensis* which, he suggests, may be the stems of *Encephalartos* and Hollick (1932) mentions some Miocene American fossil trunks whose internal structure is not preserved but which could perhaps be referred to the genus *Bucklandia* of Presl in Sternberg, 1825 and may possibly belong to the Cycadales.

Well preserved cycadean petrified stems have also been described from the Lower Tertiary of Argentina under the names *Manucoa cazaui* (Petriella, 1969), *Bororea andreisii* and *B. anzulvichii* (Petriella, 1972, Text-fig. 8a). Both the genera include stems showing a persistent armour of leaf bases and typical manoxylic cycadean stem-anatomy characterised by a wide pith, a wide cortex and intervening rings of vascular bundles having scanty wood and wide parenchymatous rays. The stems show more than one vascular bundle ring (polyxylic), numerous medullary and cortical bundles, mucilage canals and two kinds of leaf traces, i.e. the radial and girdle traces. The polyxylic character of the above stems makes them comparable with those of some modern forms like *Cycas*, *Bowenia*, *Encephalartos* and *Macrozamia* but their medullary bundles eliminate the possibility of their

Text-fig. 7—**A, B,** *Cycadites jabalpurensis* ×3/4 (after Pant & Pant, unpublished); **C,** *Bororoa anzulovichii,* topographic sketch of a sector of transverse section of stem ×3/4 (after Petriella, 1972). **B,** leaf base, C-cortex, **m. c.**—mucilage canal; **p**—pith, **ph**—phloem, **v. b.**—vascular bundle, **x**—xylem.
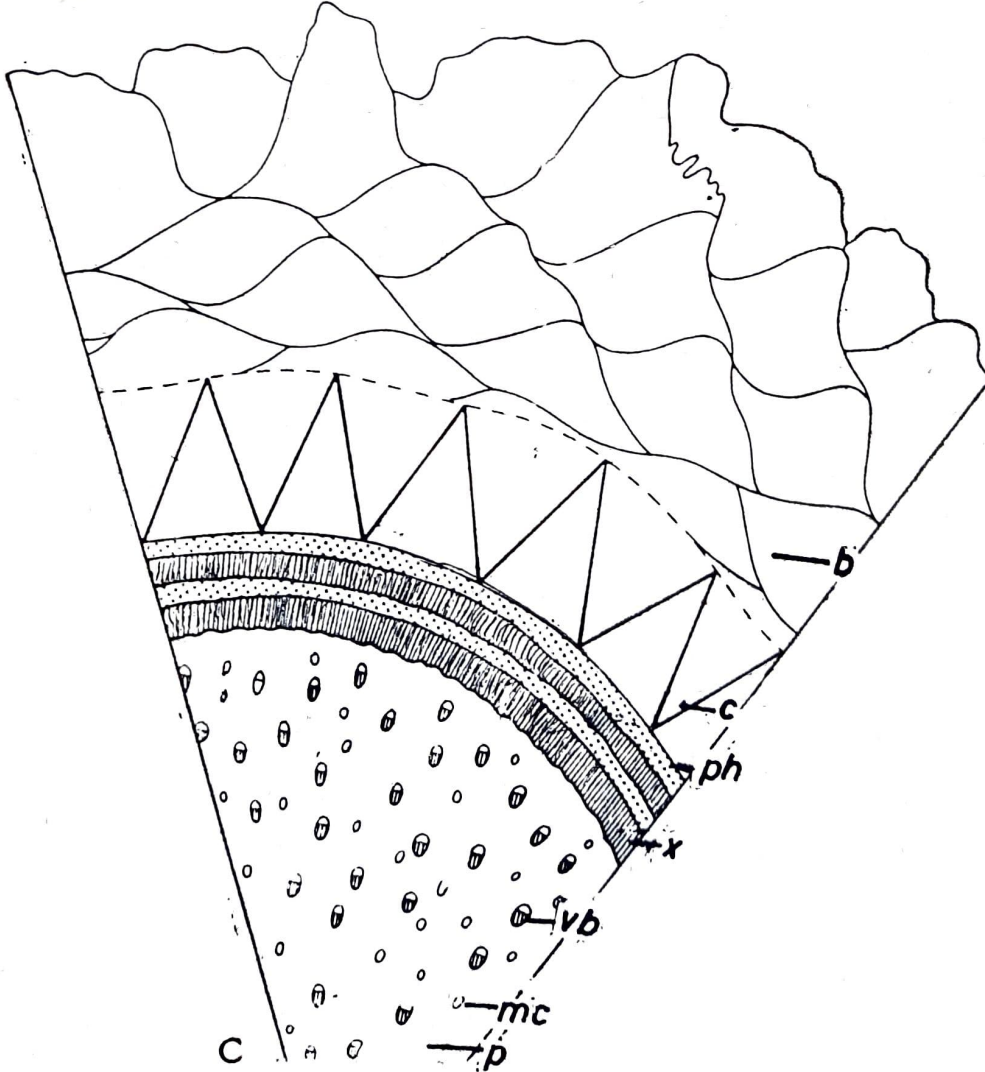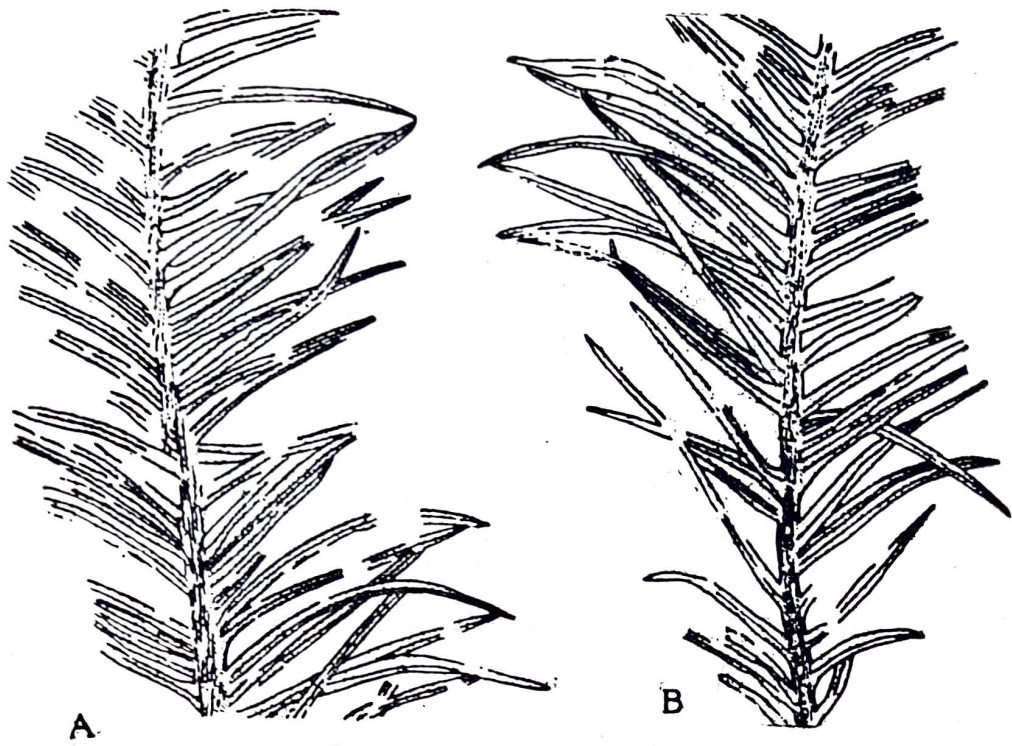
Text-fig. 7

being closely compared with the first two genera leaving only *Encephalartos* and *Macrozamia* among their nearest living forms.

Leaves

Reviewing the accounts of cycad leaves from the Tertiary rocks, Kräusel (1928, 1930) and Hollick (1932, 1936) found that out of numerous fossils described from various parts of the world only a few actually belonged to the group. Based on these assessments and later work an up to date list of Tertiary leaves, which have been assigned to Cycadales, is given in Table 2 below :

Table 2—Tertiary leaves of Cycadales

Name of fossil	Horizon	Locality	Suggested nearest living form
1	2	3	4
Anomozamites muelleri Ettingshausen 1888	Eocene	New South Wales	
Bowenia eocenica Hill 1978	Eocene	Eastern Australia	*Bowenia serrulata* (W. Bull) Chamberlain
B. papillosa Hill 1978	Eocene	Eastern Australia	*B. serrulata* (W. Bull) Chambarlain
Ceratozamia hoffmanrii Ettingshausen 1888	Miocene	Austria	*Ceratozamia* Brong.
C. wrightii Hollick 1932	Eocene	Alaska	*C. mexicana* Brong.
Ceratozamites vicetinus Meschinelli 1889	Oligocene	Italy	*Ceratozamia* Brong.
Cycas fujiana Yokoyama 1911	Eocene	Japan	*C. revoluta* Thunb.
Cycadites escheri Heer 1855	Miocene	Switzerland	*Cycas* L.
Dioon inopinum Hollick 1932	Eocene	Alaska	*Dioon* Lindl.
D. praespinulosum Hollick 1932	Eocene	Alaska	*Dioon spinulosum* Dyer
Dioonopsis nipponica Horiuchi & Kimura 1987	Palaeogene	Japan	*Dioon spinulosum* Dyer
Encephalartos gorceixianus Saporta 1875	Miocene	Greece	*E. altensteinii* Lehm.
Fostangeria saxonica Barthel 1976	Middle Eocene	Germany	
Lepidozamia foveolata Hill 1980	Eocene	Australia	*Lepidozamia* Regel
L. hopeites (Cookson 1953) L.A.S. Johnson 1959	Oligocene	Victoria, Australia	*Lepidozamia hopei* Regel

Table 2 *(Contd.)*

1	2	3	4
Macrozamia anastomosans (Hill 1980) comb. nov.	Eocene	Australia	*Macrozamia communis* L. Johnson, *M. cylindrica* Andre and *M. moorei* Muell.
M. zamioides (Hill 1980) comb. nov.	Eocene	Australia	*Macrozamia communi* L. Johnson, *M. cylindrica* Andre and *M. moorei* Muell.
Zamia australis Berry 1928 (see Hollick 1932)	Oligocene or Upper Miocene	Argentina	*Zamia* L.
Z. collazoensis Hollick 1928	Upper Eocene or Oligocene	Puerto Rico & Virgin Is.	*Z. integrifolia* Jacquin and *Z. salicina* Britton
Z. coloradoensis (Knowlton) Brown 1962	Palaeocene	U.S.A.	*Zamia* L.
Z. mississippiensis Berry 1916	Lr. Eocene	Mississippi	*Z. floridana* D.C.
Z. noblei Hollick 1928	Upper Eocene or Oligocene	Puerto Rico & Virgin Is.	*Z. pumila* L., *Z. umbrosa* Small and *Z. integrifolia* Jacquin.
Z. praecedens Ettinghausen in Krasser 1903 (nom. nud.)	Pliocene	Brazil	*Zamia* L.
Zamia tennesseana	Lr. Eocene	Tennessee	*Z. angustifolia* Jacquin.
Z. tertiaria Engelhard 1891	Lr. Miocene	Chile	*Z. integrifolia* Jacquin.
Z. wilcoxensis Berry 1916	Lower Eocene	Louisiana	*Z. pumila* L.
Z. wyomingensis Brown 1962	Palaeocene	U.S.A.	
Z. sp. Berry 1929	Oligocene	Columbia	
Zamiphyllum sambiense Caspary & Klebs, in Caspary 1907	Miocene	Germany	
Zamites epibius Saporta 1864 (vide Saporta 1867)	Miocene	France	
Zamites ? palaeocenicus Saporta & Marion 1878	Palaeocene	Belgium	
Z. (Dioon ?) tertiarius Heer 1855	Miocene	Switzerland	

The Tertiary remains of Cycadales listed in the Table 2 above are mostly referable to extant genera or closely allied forms. In particular the fossils of *Cycas fujiana* Yokoyama (1911) are reported to be so similar to modern *C. revoluta* that they are almost indistinguishable from it (Pl. 1, fig. 1). The material of *Lepidozamia (Macrozamia) hopeites* described

by Cookson (1953) is fragmentary but its identification is based on the close similarity of its cuticle with that of the existing *L. hopei.* The cuticles of the leaves of *Bowenia eocenica, B. papillosa, Dioonopsis nipponica, Lepidozamia foveolata, Pterostoma zamioides* and *P. anasato-mosans* are also known. Even though Hill (1980) found that the architecture of the leaves of *Pterostoma zamioides* (Text-fig. 7A) and *P. anastomosans* is similar to that of leaves of *Macro-zamia* and *Lepidozamia,* he referred them to a new genus because their cuticle showed sinuous-walled epidermal cells (Pl. 3, figs. 9, 10) which were according to him, not seen in the two living genera. However, as Pant and Nautiyal (1963) have described such sinuous-walled epidermal cells in three species of *Macrozamia,* viz., *M. communis, M. cylin-drica* and *M. moorei* and since Hill, has himself admitted that Tertiary cycads which resemble extant genera should be referred to them if their cuticles also resemble, I am assigning both his species of *Pterostoma* to *Macrozamia* and renaming them *M. zamioides* (Hill) comb. nov. and *M. anastomosans* (Hill) comb. nov. (see Pl. 3, figs. 9-14). The identity of the rest of the fossils is based merely on the close exomorphic resemblance of the fossils with the leaves of one or more species of the respective living genera and this needs to be confirmed by comparing the cuticles of better preserved fossils. In some cases, even the generic iden-tifications are doubtful, e.g. *Ceratozamia wrightii* Hollick (Text-fig. 10 E) is referred to *Dioon* by Schuster (1932). The same is true of *Zamites (Dioon ?) tertiarius* Heer 1855 described from the Miocene of Switzerland. Further, generic names like *Ceratozamites, Zamites* or *Zamiphyllum* were themselves indicative of uncertainty in referring the fossils to the living genera. A name like *Anomozamites muelleri* is even more uncertain. Among fossils which have been compared with extant cycads there are two exceptional species assigned to two extinct genera, viz., *Eostangeria saxonica* and *Dioonopsis nipponica,* and if these are correctly determined they may indicate that the group had a greater generic diversity till as late as the Eocene times.

A critical appraisal of the above mentioned fossil history of the Cycadales (see also Table 3) makes it abundantly clear that all hitherto described Palaeozoic members of the group are either doubtful or based on erroneous reconstructions. It also shows that the first undoubted cycads appeared in the Triassic period as indicated by the occurrence of petrified stems showing undoubted cyadean features like *Antarcticas schopfii* Smoot *et al* from the Lower or Middle Triassic of Antartica, *Michelilloa waltonii* Archangelsky & Brett

Table 3—Reported fossil record of Cycadales

Era age	Fossils showimg connected vegetative and reproductive parts	Stems	Leaves	Fructifications
Pliocene		*Bucklandia nierstei-nensis*	*Zamia praecedens*	
Miocene		*Bucklandia niersteinensis* *Bucklandia* sp.	*Ceratozamia hoffmaii* *Cycadites escheri* *Encephalartos gorceixianus* *Zamia tertiaria, Z. wil-coxensis, Zamiphyllum sambiense, Zamites epibius, Zamites (Dioon?) tertiarius*	*Zamiostrobus saportanus*

Table 3 (Contd.)

Era	Period				
	Oligocene			Ceratozamites vicetinus Lepidozamnia hopeites Zamia australis, Z. collazoenis, Z. noblei, Dioonopsis nipponica	
C A I N O Z O I C	Eocene		Menucoa cazaui, Bororoa andreisii, B. anzulovichii	Bowenia eocenica, B. papillosa, Cycas fujiana Ceratozamia wrightii Dioon praespinulosum Eostangeria saxonica Lepidozamia foveolata Macrozamia anastomosans M. zamioides, Zamia tennesseeana, Z. mississippiensis Z. wilcoxensis	Gymnovulites
	Palaeocene			Zamia coloradoensis Z. wyomingensis Zamites palaeocenicus	
M E S O Z O I C	Cretaceous		Nilssoniocladus	Dioonites borealis Almargemia dentata Mesodescolea plicata Tetoria endoi Enceph alartos cretaceous Cycadites jabalpurensis	Sewardocarpus ecclesbournensis
	Jurassic		Fascivarioxylon mehtae	Deltolepis crepidota, Nilssonia incl. N. compta, N. tenuinervis Paracycas Cycadites rajmahalensis Ctenis, Pseudoctenis P. lanei Doratophyllum, Glandulataenia Moltenia dentata Walkomia feistmantelii Pseudopterophyllum cteniforme Pseudoctenis	Baenia mamayi Androstrobus manis Androstrobus wonnacottii Cycadospadix pasinianus Androstrobus prisma Zamiostrobus stenorachis Androstrobilites triassicus
		Leptocycas gracilis	Michelilloa waltonii Lyssoxylon grigsbyi		
	Triassic		Antarcticycas schopfii	Danaeopsis angustifolia Bjuvea simplex	Diooniticarpidium Palaeocycas integer Cycadospadix
P A L A E O Z O I C	Permian		Ptychoxylon Cycadoxylon	Rhabdotaenia Pteronilssonia Dioonites densinervis Pterophyllum Sphenozamites Cladotaeniopteris Yuania tianbaolinia	Sobernheimina jonkeri Phasmatodycas kansana Archaeocycas whitei Cycadospadix millereyensis Crossozamia (Primocycas) chinensia, C. cuculata, C. minor, Crossozamia sp.
	Carboniferous			Pterophyllum grand' euryi grand' euryi	Lasiostrobus polysaccii

and *Lyssoxylon grigsbyi* Gould from the Upper Triassic of Argentina and Arizona, respectively or by the compressed remains of *Leptocycas gracillis* Delevoryas and Hope from the Upper Triassic of North Carolina which show a columnar stem with attached scales, a crown of cycad-like compound leaves and a terminal cone. Simple leaves of *Bjuvea simplex* or those of *Danaeopsis angustifolia* have also been assembled in crowns with those of cycad-like megasporophylls of *Palaeocycas integer* and *Diooniticarpidium*, respectively, to give reconstructions which appear like modern *Cycas* plants but the assemblies of the fossils are largely author made. The simple leaves in the above reconstructions of *Palaeocycas* and *Diooniticarpidium* have led many an author to suggest that the early ancestors of cycads were simple leaved although as mentioned above compound leaves attributed to the cycad are as old as the simple ones. The sequence in the evolution of unipinnate compound leaves of Cainozoic Cycadales from simple ones in the Palaeozoic through variously lobed leaves in the Mesozoic (Text-fig. 9) as suggested by Mamay (1976) are highly conjectural and they also fail to account for the evolution of bipinnate leaves.

Besides, some other Triassic leaf remains have been attributed to the Cycadales on the evidence of their showing cycad-like epidermal characters although the evidence is equivocal and some of these fossils could even belong to the pteriodosperms. This may be particularly true of leaves resembling Mesozoic cycadophytic foliage reported from the Palaeozoic strata. However, there are a few leaf remains towards the end of the Triassic, e.g. *Moltenia dentata* and *Walkomia feistamantelii*, which look very much like leaves of living *Encephalartos*. Such fossils can be taken to suggest that even cycads having leaves like those of present day genera had come into existence towards the end of the Triassic. Besides others the first *Cycas*-like leaves called *Cycadites* and *Paracycas* are reported from the Jurassic although *Cycas*-like megasporophylls called *Cycadospadix* or *Palaeocycas* go back to the Triassic. Female cones of *Baenia* which are rather lax but otherwise resemble modern cycadean female cones in having similar biovulate megasporophylls, as well as fairly large or much smaller male cones, going under the name *Androstrobus* also occur in the Jurassic of Yorkshire. A petrified Jurassic stem from India called *Fascivarioxylon* is also attributed to the cycads although it lacks girlde traces.

Cycad fossils described from the Cretaceous mostly include leaf remains which can usually be compared rather closely with the leaves of modern genera like *Zamia, Bowenia, Cycas* or *Encephalartos* (some leaves have been actually assigned to *Encephalartos*). Slender twigs called *Nilssoniocladus* have also been assigned to the Cycadales.

The Tertiary record of Cycadales consists mainly of leaves which have been referred to fossil species of modern genera although so far there are no reports of fossil leaves of *Chigua* Stevenson, *Stangeria* and *Microcycas*. Instead, the Tertiary fossils include leaf remains of two extinct genera, *Eostangeria* and *Dioonoposis* (Text-fig. 11 C, D.). Tertiary fossil stems possibly belonging to the Cycadales have been described under the name *Bucklandia* but petrified stems indubitably assigned to this group are reported from the Lower Tertiary of Argentina under the names *Menucoa* and *Bororoa*. A strobilus called *Zamiostrobus saportanus* from Eocene and a seed called *Gymnovulites* from uppermost Cretaceous of Eocene age are also attributed to the Cycadales.

Palaeoecology and past distribution

The palaeoecology and past distribution of the Cycadales has to be discussed in relation to the ecology and present day distribution of their extant members and in order to make our account easily comprehensible we shall consider the distribution of fossil cycads by proceeding backwards in geological time beginning with the recent.
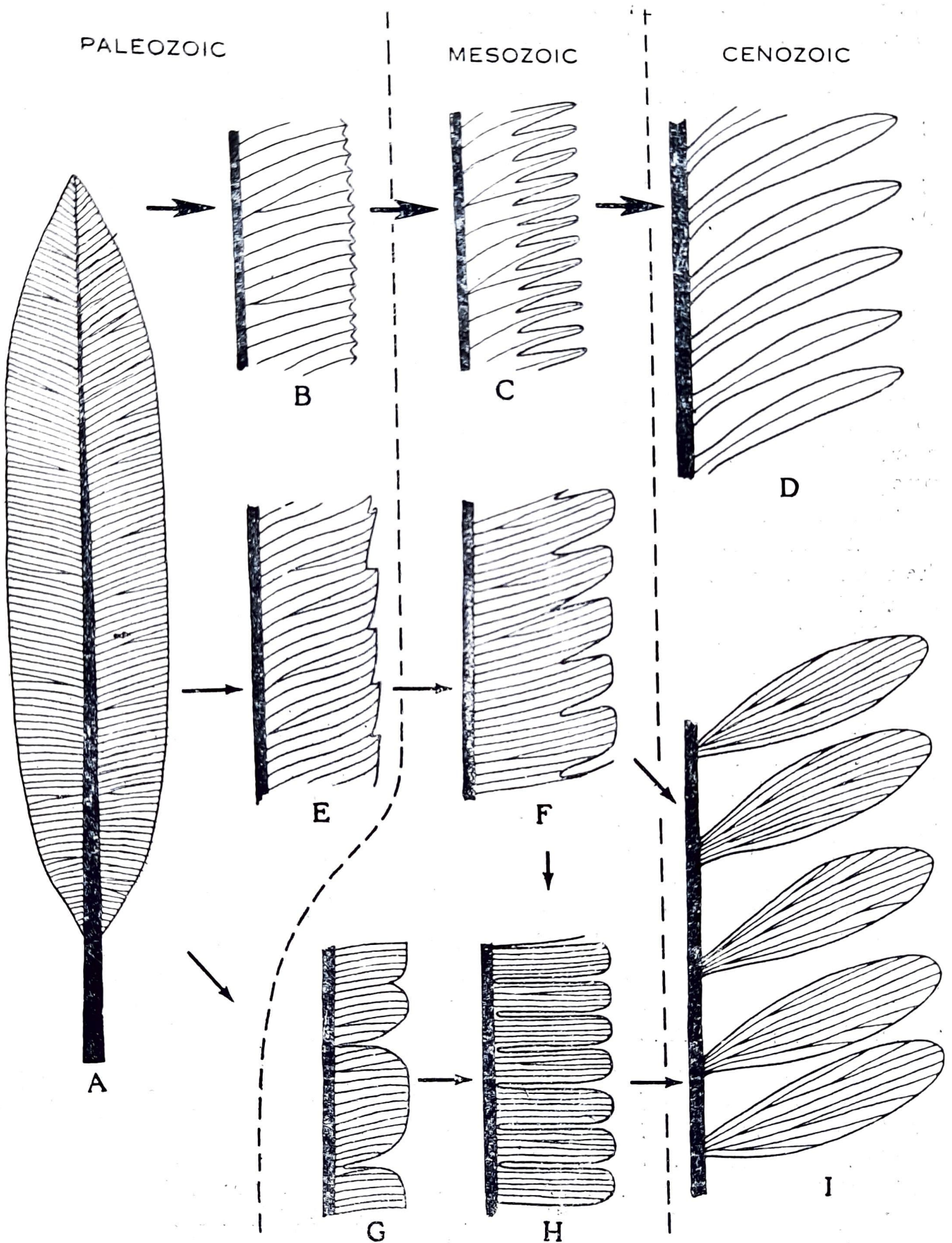
Text-fig. 8—Speculated sequence of evolution of compound cycadalean leaves in Mesozoic and Cenozoic from simple leaves in the Palaeozoic (after Mamay, 1976).

It is well known that all living members of the group are confined to the tropical and subtropical regions of the northern and southern hemispheres, since all of them are warmth loving plants which are usually unable to withstand exposures to frost or temperatures near the freezing point during winters.

In their natural habitats, cycads often grow mixed up with other kinds of vegetation consisting of trees or shrubs or among grasses in a grassland. Sometimes they form pure growths like those of *Macrozamia diplomera* in New South Wales where the plants grow so closely crowded that they leave no room for others. Very often the cycads grow in isolated groups or clumps consisting of plants of the same sex which arise from bulbils of the same parent stock by vegetative means. The plants of the group generally inhabit rocky areas in sloping hilly terrain and exhibit a number of xerophytic features in their physiognomy. Some cycads like *Dioon* and *Cycas circinalis* can withstand extreme xerophytic conditions and can thrive in situations where they are exposed to the blazing tropical sun but others like *Ceratozamia* or *Cycas beddomei* prefer the dense shade or the filtered sun-shade of trees. Some of them like *Stangeria* exhibit different growth forms when they grow under the shade of trees or in open grassland. Due to the fleshy character of their overground columnar trunks or of underground tuberous stems they can even be termed as stem succulents. All the same many cycads grow in areas which are subject to occasional heavy precipitation and abundant rain but the soil and sloping terrain where they grow must be such that their roots do not become waterlogged.

Out of their eleven living genera, three, viz., *Cycas*, *Encephalartos* and *Zamia* occur in the northern as well as the southern hemispheres; four, viz., *Bowenia*, *Macrozamia*, *Lepidozamia* and *Stangeria* occur only in the southern hemisphere while the remaining four genera, viz., *Dioon*, *Ceratozamia*, *Microcycas* and the newly discovered Colombian genus *Chigua* are exclusively northern.

Among the genera which occur on both sides of Equator, the genus *Cycas* is distributed north of Equator up to about 35°N, from southern Japan to the mainland of Asia, in China and South East Asia. On the mainland it becomes confined to areas which are generally south of about 30°N and its distribution shows a further southward dip in India and Africa. Perhaps the warmer maritime climate of Japan is responsible for its slight northward extension in that region. South of Equator the distribution of *Cycas* in eastern Australia extends up to about 35°C, and in Madagascar, Zambesi delta and other Islands its distribution does not generally extend beyond the Tropic of Capricorn. A Tertiary species of *Cycas*, *C. fujiana* Yokoyama (Pl. 1, fig. 1) which is closely similar to modern *C. revoluta* has been reported from 33°C in Japan so that the distribution of the fossils of this species is almost the same as that of its living plants. If, however, we go down into older geological strata we find that *Cycas*-like leaves had a much wider distribution particularly during Jurassic when leaves called *Cycadites* and *Paracycas* have been recorded from Yorkshire, Transcaucasia, Georgia, Rajmahal Hills in India and other places. We also find that *Cycas*-like leaves having only a single midvein in the pinnae are first found in the Jurassic and this may indicate that such forms are not as old as the parallel veined forms like *Encephalartos* or *Zamia* which had come into existence during the Triassic.

The distribution of *Encephalartos* extends to about 14°N in Africa but southwards it reaches about 35°S. I presume that the northward distribution of the genus is presently checked by the desert barrier of Sahara and the mountains of East Africa. However, during Eocene a species, called *Encephalartos gorceixianus* (Text-fig. 10 A, B) was growing at Eubosa Is. in Greece which lies around 38°N. *Encephalartos*-like leaves are also geologically very old. One such leaf form described from the Cretaceous is actually recognised as a
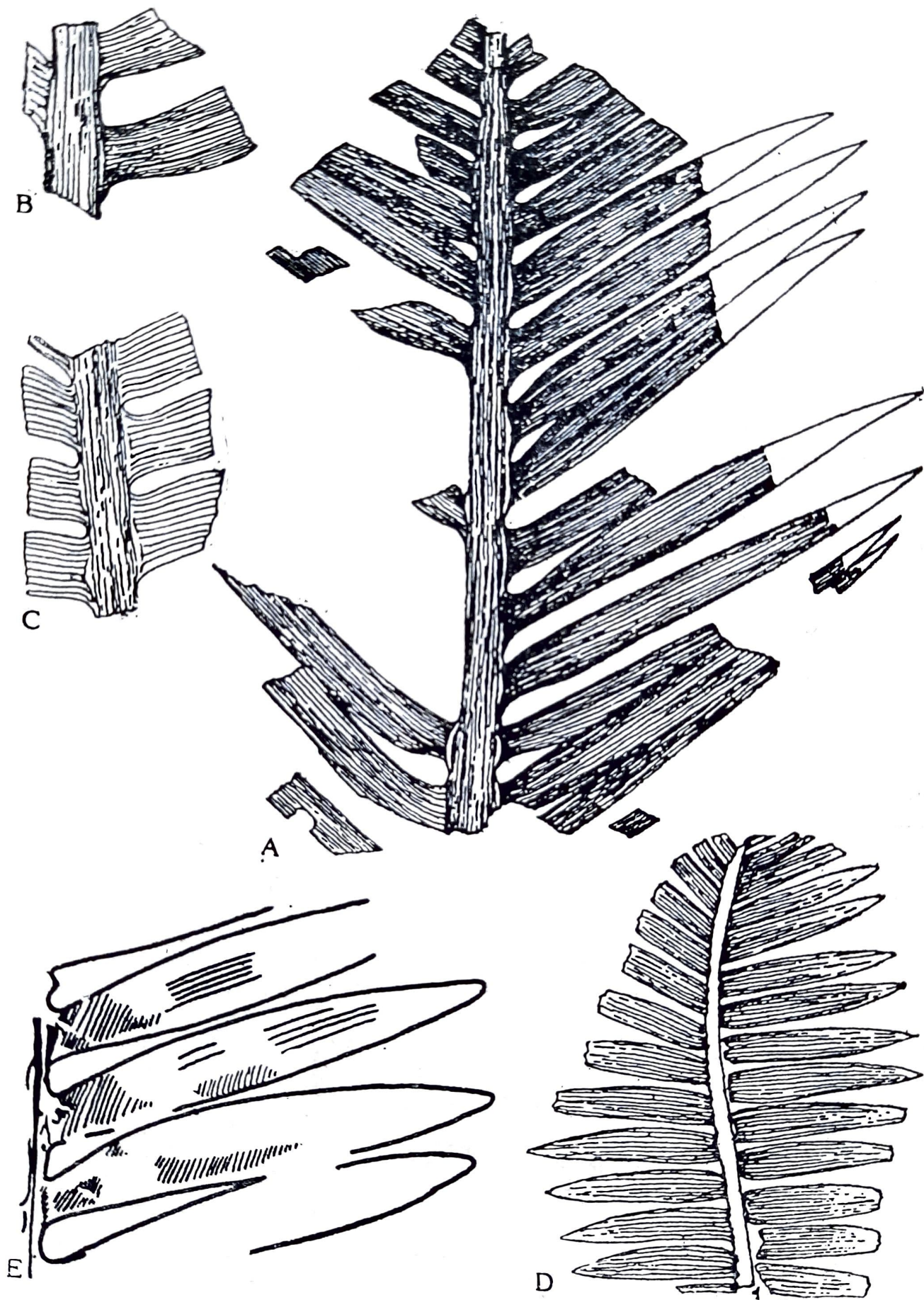
Text-fig. 9—Leaf fragments showing veins : **A, B,** *Encephalartos gorceixianus* ×1; **C, D,** *Zamites epibius* ×1; **E,** *Ceratozamia wrightii* ×1 (all after Hollick, 1932; E, drawn from photograph).
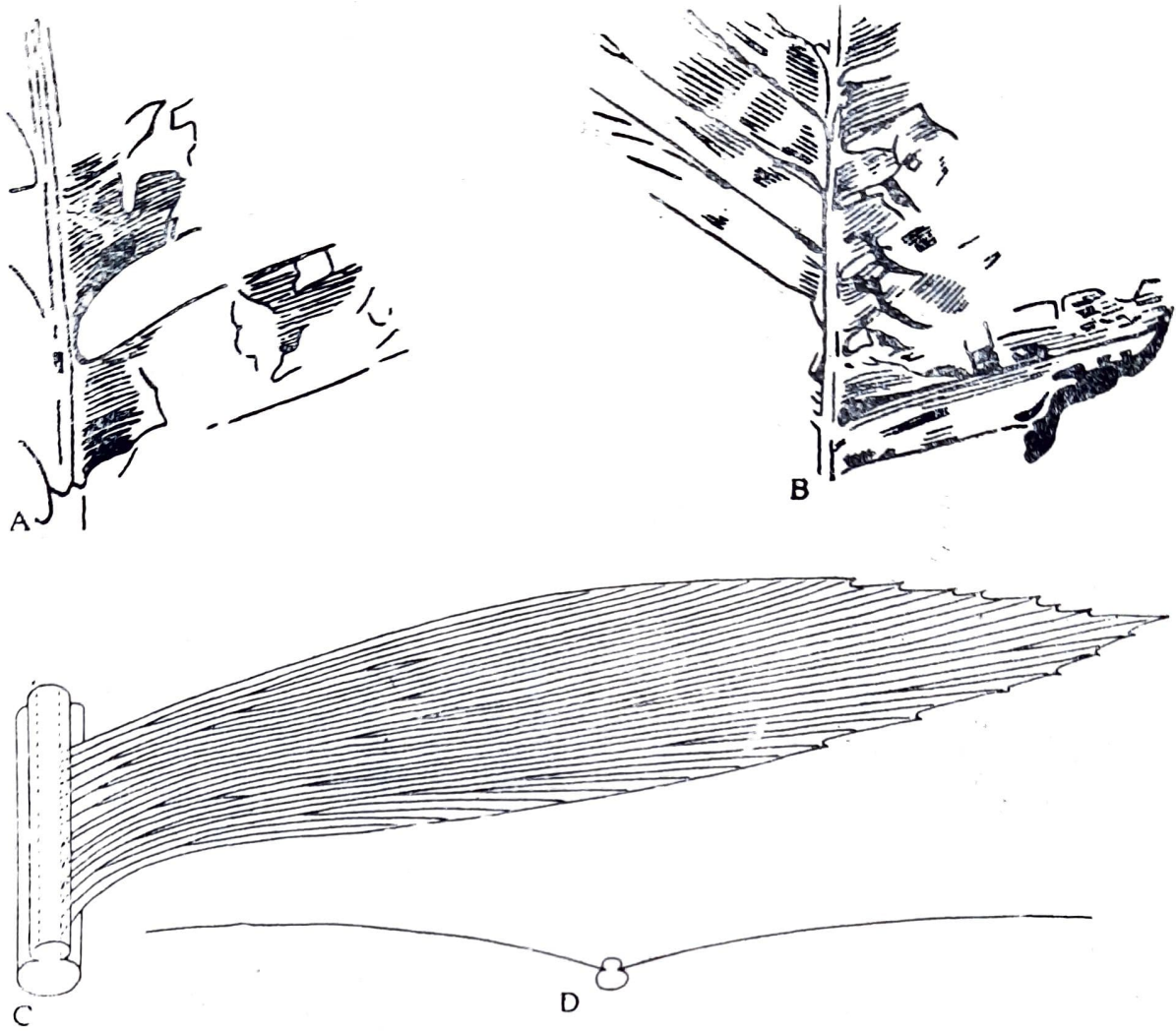
Text-fig. 10. A-C—Portions of leaves : **A,** *Dioon mopinus* ×1; **B,** *D. praespinulosum* ×1; **C,** *Dioonopsis nipponica* × ca 1; **E,** imaginary cross section of leaf with thickness of rachis restored × ca 1. (A, B after Hollick, 1932; C, D, after Horiuchi & Kimura, 1980).

species of the modern genus and called *E. cretaceous.* Another Cretaceous leaf called *Almargemia dentata* (Heer) Florin is described from Portugal. These leaves indicate that *Encephalartos* or closely similar forms were at this time growing as far as 40°N. Besides, a similar looking form called *Moltenia dentata* duToit and *Walkomia feistmantelii* (Johnston) Schuster are described from the Triassic beds of South Africa and Triassic-Jurassic beds of Tasmania, respectively. These fossils indicate firstly that *Encephalarots*-like leaf forms are the oldest among leaf remains which resemble those of modern genera and secondly that they were distributed far and wide during this time when some of them were growing as far south and east Tasmania besides South Africa. The occurrences of petrified stems called *Menucoa* and *Bororoa* which are polyxylic and have medullary bundles like those of modern *Encephalartos* and *Macrozamia* indicate that such forms had a much wider distribution during the Tertiary when they occurred in Argentina. Thomas and Harris (1960) have pointed out that *Pseudoctenis lanei* and *Androstrobus prisma* from the Jurassic of Yorkshire could have belonged to a plant resembling modern *Encephalartos* or *Zamia.*

A genus of Australian cycads, *Lepidozamia* is distributed only in Queensland and New South Wales up to about 35°S but a fossil species, *Lepidozamia hopeites* which was originally described as *Macrozamia hopeites* (Cookson, 1953) has been reported from Bacchus Marsh

in Victoria far to the South of the present home of the nearest living species *L. hopei*. Another species called *L. foveolata* is reported from the Eocene beds in Southern New South Wales around 35°S.

The only genus of cycads which is not found in the tropics but confined to the sub-tropics is *Stangeria* and it occurs in localities which lie between 30°S and 35°S in South Africa. So far no fossils referable to the genus have been reported.

An exclusively northern genus of cycads which is confined to the western part of the Island of Cuba around latitudes 22°N is *Microcycas*. This genus too lacks a fossil record.

Out of the exclusively northern genera, *Dioon* is confined to areas between 17°N and 30°N in Central America and *Ceratozamia* occurs between 17°N and 25°N in the same region. Two species of *Dioon*, *D. inopinus* Hollick and *D. praespinulosum* Hollick (Text-fig. 11A, B) and one species of *Ceratozamia*, *C. wrightei* Hollick (Pl. 4, fig. 15) have been reported from 57°N in Alaska (Hollick, 1932) very far towards the north of the present home of the two genera, *Dioonopsis nipponica* (Text-fig. 11 C, D) which is reportedly similar to *Dioon spinulosum*, has been described from Japan and this also indicates that *Dioon*-like forms had a much wider northward distribution in the past. Yet another species, *Ceratozamia hoffmanii* has been described by Ettinghausen (1888) from Switzerland which is situated around 47°N while *Ceratozamites vicetinus* Meschinelli has been described from Italy from a locality around 45°N, both places are much to the north and far towards the east of the present localities of *Ceratozamia*.

The American cycad, *Zamia* which shows the widest distribution, has its species distributed almost equally, towards the north and the south of Equator, from about 31°N in Florida to about 22°S in South America. One of its fossil species *Z. australis* Berry has been reported from the Oligocene of Argentina, another species *Z. tertiaria* is reported by Ettinghausen from the Late Miocene of Chile and both the localities lie farther south of its present range and two more species, *Z. tennesseeana* Berry is reported from the Lower Eocene of Tennessee while *Z. wilcoxensis* is described from the Lower Miocene of Lousiana and these occur much towards the north of the present range of *Zamia*. Indeed *Zamites epibius* is reported from Miocene of France, further north around 43°N (Text-fig. 10 C, D).

The genus *Bowenia* which has two species, is confined to North Queensland in Australia, one of its species, *B. spectabilis* occurring around 17°S and the other *B. serrulata* around 22°S. Two fossil species of the genus *B. eocenica* and *B. papillosa* have been reported by Hill (1978) from localities which lie far to the south of the present homes of the two living species one around 35°S in New South Wales and the second beyond 38°S in Victoria.

Past distribution indicates drift of former localities

On the whole the past distribution of cycads from the Tertiary backwards up to the Triassic shows that the plants of this group had a much wider distribution in the past and what is unusual about the distribution of many fossil cycads is their occurrence in regions of the earth which are now-a-days so cold and so near the poles that no living cycads can be expected to survive there. This anomalous poleward distribution of fossil cycads can be explained either (1) by assuming a past capability of cycads to withstand cold or (2) by envisaging that the localities or land masses where the fossil cycads are found have since drifted towards the poles. The first alternative is ruled out by the occurrence of extant genera of cycads amongst the fossils since none of their living species can withstand even near freezing point winter temperatures. This leaves us only with the second alternative explanation and in this case we have the supporting evidence of the Permian Glossopteris flora as well as the Triassic flora of Antarctica and also the Rhaetic floras

of Greenland and northern Europe. Obviously the polar localities of fossil cycads were situated near the tropics of their day and have subsequently drifted polewards.

Phylogeny and relationships

It is generally agreed that the Cycadales have evolved from some of the Palaeozoic pteridosperms because both these groups possess typical cycadophyte characters like short sparsely branched trunks, monoxylic stem structure and pinnately compound leaves. The relatively more slender stems of fossil Cycadales may also point towards their pteridospermous affinities. Their foliar bundles and, sometimes the bundles of their cone peduncles show centripetal xylem which is often presnt in the vegetative stems and other parts of the pteridosperms. The seed structure of the cycads resembles that of some of the pteridosperms (e. g. *Trigonocarpus* or *Lagenostoma*). The lobes of sclerotesta observed around the micropyle of some cycad seeds (see Haan, 1920) may indicate that the integuments of radiospermic cycadean seeds (other than those of *Cycas*) may have been formed by the fusion of a circlet of sterile telomes around the nucellus as is vividly seen in a series of Palaeozoic pteridosperm seeds (see Long, 1966 ; Pant, 1966). In the remarkable megasporophyll of *Cycas* (from which the megasporophylls of other cycads can be easily derived) we find the typical leaf-borne ovules of Palaeozoic pteridosperms surviving up to the present day. Mamay (1969) has gone so far as to drive *Cycas*-like sporophylls (and even angiospermous carpels) from some Lower Permian taeniopterid forms like *Spermopteris* (Cridland & Morris, 1960) and other pteridospermous fossils. Absence of an organised female cone in *Cycas* is another pteridospermous feature. The presence of cycad sperm like bodies in pollen chambers of seeds of Medullosales may provide another argument in favour of pteridospermous origin of cycads although the presence of similar ciliated sperms in *Ginkgo* may suggest that this could be due to homoplasy.

The upholders of this theory also emphasize the close resemblance between seeds of cycads and a medullosan seed like *Trigonocarpus* and explain the fused character of the integument and nucellus by assuming that they may have fused in the course of evolution or it could possibly be due to a later intercalation as envisaged by a theory proposed by Oliver (1903) and modified by Sahni (1920). The difference between the organisation of the seed of *Lagenostoma* and that of cycads is explained according to this theory by assuming that the outer fleshy layer of cycad seeds is morphologically equivalent to a cupule fused with the integument. The theory emphasizes the fully integumentary character of the inner set of bundles in the seed.

The resemblance between a pteridosperm seed like that of *Trigonocarpus*, whose integument shows three layers corresponding with those of cycad seeds, is no doubt close but its nucellus is free from the integument right up to the base (in cycads the two structures are free only for a short distance at the micropylar end). Moreover, the nucellus of *Trigonocarpus* has a well developed mantle of nucellar tracheids. On the contrary the seed called *Lagenostoma* has no outer fleshy layer in its integument although its nucellus and integument are fused for most part as in the Cycadales. Stopes (1904, 1905) points out that the inner set of bundles which lies in the fused integument-nucellus complex, may embrace the nucellus but is truly integumentary (like the integumentary bundles of *Lagenostoma*). However, Kershaw (1912), Reyonolds (1924) and Shapiro (1951) emphasize that the inner set of bundles extends into the free part of the nucellus and Pant and Nautiyal (1963) found that even in the fused integument-nucellus-compex the bundles lie between the inner cuticle of integument and the nucellar membrane, so that they are truly speaking neutral. The recent work of Long (1966), Smith (1964) and others on the seeds of some

Palaeozoic pteridosperms indicates that the integument and cupule of their seeds are homologous structures derived by the coalescence of a surrounding whorl of telomes. In some forms like *Lagenostoma* the whorl of surrounding telomes has not only fused with each other but also with the wall of the central megasporangium (nucellus). The lobes in the sclerotesta of some cycad seeds may indicate a fusion of the same kind (*see* Haan, 1920).

Therefore, the derivation of cycad integument by assuming fusions on both sides of an inner integumentary whorl may not be regarded as a case of wild fancy. At the same time it is not necessary to assume a dual nature of the cycad integument since forms like *Trigonocarpus* (where it shows a similar differentiation of soft and hard layers), it appears to have arisen from a single whorl (Walton, 1964).

There are three main theories about the origin of the Cycadales from the pteridosperms. One of these views was proposed by Worsdell (1896, 1998, 1900a, 1900b, 1906). After detailed anatomical studies of the cycads he suggested that they are descended from medullosae having hollow stelar cylinders, e.g. *M. stellata*, by a progressive loss of the centripetal portions of the stelar rings and by the complete elimination of the central "star rings". Worsdell believed that the tertiary arcs of inverted bundles occasionally found in *Macrozamia* and *Bowenia* are the vestiges of the centripetal arcs of medullosan steles. Similarly the two or more smaller steles which are sometimes seen round a larger central stele in some seedlings of the cycads, e.g. in *C. siamensis* were regarded by Worsdell of corresponding with similar arrangement of steles in form like *Medullosa porosa*. He points out that the system of concentric cortical bundles seen in *Cycas* is to be regarded as further proof of the modullosan ancestry of the cycads. In addition, he regards the irregular arrangement of bundles, seen in the peduncles of *Stangeria*, as corresponding to the sinuous steles of *M. leuckartii* but these too had lost their centripetal portions of vascular tissue in a similar manner. The resemblance of the three layers of integument and simple pollen chamber in *Trigonocarpus* seems to support this theory although the freedom of the nucellus up to the chalazal end may disfavour it.

The second theory was suggested by Scott (1923, 1924) who thought that some of the Lyginopterideae, e.g. *Lyginopteris* with their monostelic stems were more likely to have given rise to the cycads (which are often monostelic) rather than the Medulloseae which are always polystelic. He also supported this theory on the basis of greater resemblance between seeds of modern cycads and *Lagenostoma*, e.g. in the fused character of the nucellus and integument up to very near the micropyle although the seed of *Lagenostoma* has a complex pollen chamber and an integument without a fleshy outer layer (unless the cupule is taken as its free equivalent). This theory seems to be supported by the record of fossil cycad stems which shows that their earliest Triassic remains like *Antarcticycas*, *Lyssoxylon* and *Michelilloa* or a Jurassic form called *Fascivarioxylon* are all monoxylic and mono xylic like the stems of modern *Zamia*, *Dioon*, *Ceratozamia* and *Microcycas* (all western genera), but *Fascivarioxylon* shows medullary bundles comparable with those of *Encephalartos* and *Macrozamia*, indicating thereby that such forms were existing in India during the Jurassic. The Lower Tertiary stems described from Argentina called *Menucoa* and *Bororoa* are on the contrary, polyxylic-like the stems of *Cycas*, *Bowenia*, *Macrozamia* and *Encephalartos*. In fact they resemble the stems of *Macrozamia* and *Encephalartos* more closely in having medullary bundles although the Tertiary fossils are reported from an area which lies nearer to the present home of monoxylic genera without medullary bundles. Could then interpret the above facts as suggesting that monoxylic forms showing a single persistent cambium are phytogenetically older than forms which are polyxylic. If the reply

is in the affirmative the ideas of Worsdell about the origin of cycads from polystelic forms are contradicted while those of Scott about their origin from monostelic forms supported.

The third view, held by De Fraine (1912), is a sort of compromise between the ideas of Worsdell and Scott. She regards the Carboniferous protostelic *Sutcliffia* as combining the characteristics of both monostelic forms like *Heterangium* and the polystelic Medullosae. In her theory *Sutcliffia*, which has a large central protostele and numerous similar subsidiary steles, is presumed to have given also on the one hand to the monostelic Lygino-pterideae and Cycadales, and to the polystelic Medulloseae on the other. She derives the monostelic cycads from *Sutcliffia* by assuming the medullation of the main stele and a modification of the subsidiary steles into the peripheral concentric rings and accessory bundles. Bancroft (1914) regards De Fraine's theory as the most plausible.

In recent years Arnold (1953) has supported the theory proposed by Scott because it is simple and more direct while Stewart and Delevoryos (1956) have favoured Worsdell's view of the medullosan origin of the cycads on account of the intermediate type of stem structure presented by stems like *M. stellata* and *Colpoxylon aeduense* amongst the *Medulloseae*; in *M. stellata* the 'star rings' are enclosed in a single peripheral cylindrical stele while in *Colpoxylon aeduense* even the "star rings" have been eliminated.

Against all these ideas of a pteridospermous origin of cycads, Andrews (1961) has struck an emphatic dissenting note and pointed out that beyond certain features, which are common between the stems of the medullosan seed ferns and the cycads, he is unaware of any other significant similarities between the two groups more especially in their reproductive organs. He believes that at a very early stage they evolved independently as seed plants from ancestors which he does not specify.

The reconstructions of *Phasmatocycas* and *Archaeocycas* made by Mamay (1976) were at first taken as the examples of the "significant similarity" wanted by Andrews between the reproductive organs of pteridosperms and the cycads. However, contrary to such expectations, the reconstructions of *Phasmatocycas* and *?Archaeocycas* seem to be erroneous and they can no longer be taken to bridge the gap between the two groups. In fact, Mamay's own belief about the primitive cycadean leaf being simple runs counter to the derivation of cycads from the Palaeozoic pteridosperms which are mostly compound leaved.

Lack of a female cone in *Cycas* and its leaf-like megasporophylls undoubtedly appear to suggest pteridospermous affinities for the cycads but the terminal male one of *Cycas* is well organised like that of all other cycads and is rather far from the pteridosperms. It is therefore possible, as Harris (1976) has also pointed out, that in the ancestors of *Cycas* the female cone too was well organised like that of other cycads and the stem of the female plant was sympodial. At a later stage in evolution the apex of the female plant became more vigorous and continued its growth after the production of the megasporophylls. As a result the stem became monopodial by continuing its growth throughout life and by repeatedly alternating the vegetative and reproductive phases. However, this concept would not be able to explain the presence of primitive looking leaf-like megasporophylls in a female cone which is regarded as advanced and also the repeated reversions of vegetative and reproductive phases in the plant as advanced when similar reversions are regarded as more primitive in the "selago" condition of *Lycopodium*.

Among other points which strike against the derivation of the cycads from the pteridosperms, is the lack of girdle traces in the latter group. However, the sporophyll traces in cycads are all direct and if, as is usual, the reproductive parts are to be regarded as more primitive, the girdle traces of the vegetative leaves may be taken to be a later achieve-

ment. The absence of intermediate types of male fructifications between the two groups is another difficulty but this may not pose any serious problem since the microsporophylls of the cycads are admittedly homologous to their megasporophylls. Our main difficulty in deriving cycads from pteridosperms lies in the lack of transitional synthetic forms which can be regarded as ancestral.

Leaf forms like *Rhabdotaenia* (Pant, 1958 ; Pant & Verma, 1963) and *Pteronilssonia* (Pant & Mehra, 1963) having haplocheilic stomata could be regarded as links between Cycadales and Glossopteridales. However, the pycnoxylic wood, leaf attached fructifications, seeds without an outer fleshy layer and disaccate pollen grains of glossopterids and their possible seedlings with two twice forked epigeal cotyledons (Pant & Nautiyal, 1987) are very different from those of Cycadales.

The differences between cycads, Cordaitales and Ginkgoales are so numerous and important that their resemblances are at once overlooked. Yet the venation (parallel and furcate) and anatomy of the pinnae of cycads (other than *Cycas*, *Chigua* and *Stangeria*) and the leaves of *Cordaites* and Ginkgoales, the platyspermic seeds of *Cycas* and those of Cordaitales and *Ginkgo* must be mentioned even if these are ultimately rejected as instances of symplastic developments. In this connection a glance at Fig. 12A may suggest a strange, though fanciful, resemblance between Chamberlain's hypothetical ancestral megasporophyll of cycads and the female flower of *Cordaianthus zeilleri* (or *Lebachia*). However, the ancestral ovulate leaf as well as the modern megasporophyll of *Cycas* are planated nonaxillary organs, unlike the flowers of *Cordaianthus* (and *Lebachia*) which are radially organised and axillary. The only exceptional radially organised structures reported among the cycads are some abnormal leaves and megasporophylls which bear four rows of pinnae and ovules (Pant, 1953). If these are assumed to be reversions, they may suggest that the cycad leaf and megasporophyll could be derived from a radially organised structure but it would still remain extra-axillary and leave us entirely to surmise about the relationship between Cordaitales and Cycadales. The ciliated motile sperms of *Ginkgo* may also be mentioned among the resemblances between Ginkgoales and Cycadales although they can hardly be regarded as evidence for relationships.

The Bennettitales, which resemble Cycadales in their habit and vegetative characters, are sometimes regarded as directly related to the Cycadales, e.g. Chamberlain (1935) derives the single stalked ovule of the Bennettitales from a large megasporophyll like that of *Cycas* by a gradual reduction in the number of ovules and the size of the sporophyll (see Text-fig. 12). On account of its laterally borne strobili Chamberlain (1913) regards *Macrozamia moorei* as a connecting link between the living cycads and the Bennettitales. Any close relationship between the two groups is, however, out of the question because of the absence of girdle traces in Bennettitales and their presence in Cycadales, the distinct stomatal structure of the two groups (haplochielic in cycads and syndetocheilic in Bennettitales) and very different bisexual or unisexual fructifications in Bennettitales and dioecious plants with unisexual strobili in cycads. Whatever resemblances they show in their body could therefore be the result of a common ancestry or parallel evolution. If this latter view is correct, then the lines leading to Cycadales and Bennettitales have neither any lateral connections nor any further course. The two groups can perhaps be traced back to the Triassic but their relative antiquity too is difficult to decide.

We may, therefore, conclude that while the early traces of these primitive seed plants fail to give any definite clue about their ancestry, their later representatives remain equally ambiguous about their relationships. In any case the living members of Cycadales conti-
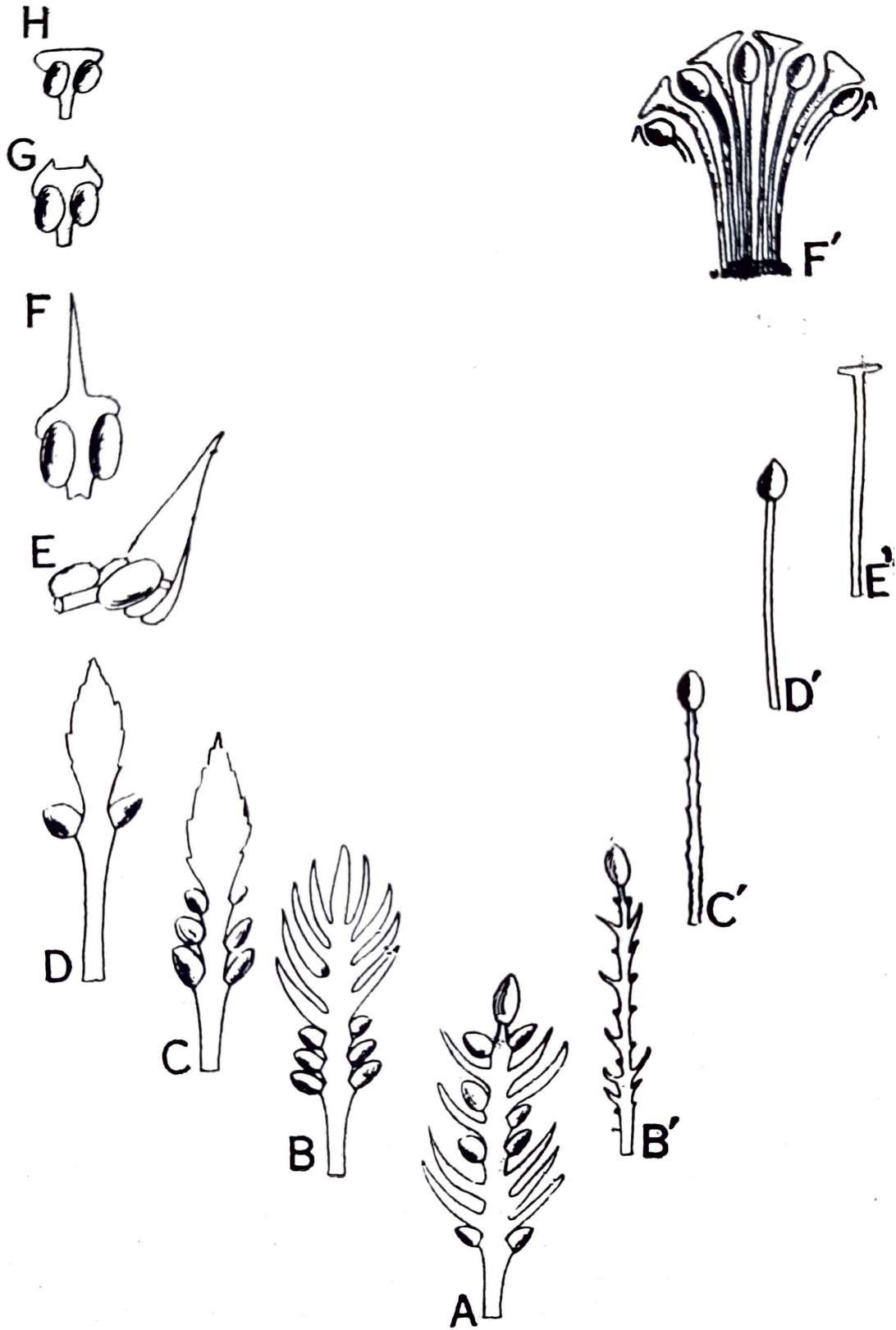
Text-fig. 11—Evolution of megasporophylls in Cycadales and Bennettitales. **A,** theoretical ancestor; **B,** *Cycas revoluta;* **C,** *C. circinalis;* **D,** *C. normanbyana;* **E,** *Dioon edule;* **F,** *Macrozamia;* **G,** *Ceratozamia;* **H,** *Zamia;* **B, C,** hypothetical stages in reduction of megasporophyll of Bennettitales; **D, E, F,** ovule, interseminal scale and their arrangement, respectively in the Bennettitales (from Pant, 1973 after Chamberlain, 1935).

nue as significant survivals of the past ages, presently without any missing links between them and other gymnosperms. Indeed the megasporophyll of *Cycas* makes it a living fossil, virtually like the pteridosperms of the Palaeozoic which lacked strobili and produced ovules on their leaves.

Basic science versus thrusting of "Thrust areas"

Lastly, before I end my talk I would like to say a few words to the critics of basic science, who are exponents of the so-called "thrust areas" in which they even include techniques but raise questions about the utility of work on basic science since they may say that work on cycads and particularly on their fossil history is not needed at a time when we are in urgent need of developing hi-technology, new sources of energy and solving problems of environment besides other things which are of interest to their own selves. Lewis Thomas (1985) has already answered such criticism by saying that science works primarily with our fumblings around ideas and by giving us unexpected surprises. He points out that the elusive search for transmutation of elements or Alchemy (a hybrid word derived from Arabic article *al* and Greek *khemia* for Egypt) led to the foundation of two of the most important branches of modern science-physics and chemistry. May I add that Wegener's Theory of Continental Drift, which was ridiculed as a figment of imagination, has led to the discovery of Plate Tectonics and to the best explanations of earthquakes and volcanoes and to their prediction ? Connected research on sea floor is giving us new sources of minerals and who knows it may lead us to new sources of energy! Fossil cycads too seem to be fumbling around ideas of Continental Drift. Indeed the ideas of Continental Drift are ever drifting and fumbling in new directions. Already the cracks in sea bottom have yielded bacteria which live in extremely hot water at a temperature of 300°C under extremely high pressure, where proteins and DNA would fall apart, enzymes would melt away and anything alive would die. These bacteria have all essential characters of the class like cell walls, ribosomes, etc. It is being suggested that they are the original archaeobacteria. The latest information is that there is a tremendous density of life in the hydrothermal vents of sea bottom where the extremely toxic hydrogen sulphide coming out of the vents is the life giving gas for the organisms which live in utter darkness. The chemosynthetic bacteria oxidise the hydrogen sulphide and they live as endosymbionts inside peculiar tube worms called *Riftia* which form dense colonies in the sea bottom rifts. The *Riftia* worms are eaten up by calms which live on them (Childress *et al.*, 1987).

As Lewis Thomas (1985) points out the principal discoveries of this century can be regarded as the glimpses of the depth of our ignorance about nature which means that mankind must not restrict research on basic aspects of nature since that alone may bring surprises leading to useful discoveries. Let us therefore continue with renewed vigour in our work in Palaeobotany and on cycads.

References

ANDREWS, H. N. (1961). *Studies in Palaeobotany*. New York.

ARCHANGELSKY, S. & BRETT, D. W. (1963). Studies on Triassic fossil plants from Argentina. 2. *Michelilloa waltonii* nov. gen. et sp. from the Ischigualasto Formation. *Ann. Bot.* (*N. S.*), **27** : 147-154.

ARCHANGELSKY, S. & PETRIELLA, B. (1971). Notas Sobre la Flora Fosil de la Zona de Tico, Provincia, de Santa Cruz. IX. Nuevos Datos Acerca de la Marfologia Foliar de *Mesodescolea olicata* Arch. (Cycadales, Stangeriaceae). *Bot. Soc. Argentina*, **15** : 88-94.

ARNOLD, C. A. (1953). Origin and relationships of the cycads. *Phytomorphology*, **3** : 51-65.

BANCROFT, N. (1914). Pteridosperm anatomy and its relation to that of the cycads. *New Phytol.*, **13** : 41-86.

BARTHEL, M. (1976). Farne und Cycadeen. In : Eozäne Floren des Geiseltales. *Abh. Zent. Geol. Inst. Berlin. Palaontol. Abh.*, **26** : 439-498.

BERRY, E. W. (1916). The Lower Eocene floras of southeastern North America. *U. S. Geol. Survey Prof. Paper*, **91**, 481 p.

BERRY, E. W. (1929). Tertiary fossil plants from Colombia, South America. *U. S. Natl. Mus. Proc.* **75**, Pub, 2795 : 1-12.

BERRY, E. W. (1930). Revision of the Lower Eocene Wilcox flora of the Southeastern States with descriptions of new species chiefly from Tennessee and Kentucky. *U. S. Geol. Surv. Prof. Paper*, **156** : 1-144.

BOSE, M. N. & BANERJI, J. (1981). Cycadophytic leaves from Jurassic Lower Cretaceous rocks of India. *Palaeobotanist*, **28-29** : 218-300 (1979-80).

BROWN, R. W. (1962). Palaeocene flora of the Rocky Mountains and Great Plains. *U. S. Geol. Surv. Pap.*, **375**, 119 pp.

CASPARY, R. (1907). Die Flora des Bernsteins und anderer fossiler Harze des ostpreussischen Tertiars. *Preus. Geol. Landesanst. Abh.* new ser. **4** : 1-181.

CHAMBERLAIN, C. J. (1913). *Macrozamia moorei*, a connecting link between living and fossil cycads. *Bot. Gaz.*, **55** : 141-154.

CHAMBERLAIN, C. J. (1935). *Gymnosperms, Structure and Evolution.* Chicago.

CHILDRESS, J. J., FELBECK, H. & SOMERO, G. N. (1987). Symbiosis in the deep sea. *Sci. Amer.* **256**(5) : 106-112.

COOKSON, I. C. (1953). On *Macrozamia hopeites*, and early Tertiary cycad from Australia. *Phytomorphology*, **3** : 306-312.

CRIDLAND, A. A. & MORRIS, J. E. (1960). *Spermopteris*, a new genus of pteridosperms from the Upper Pennsylvanian Series of Kansas. *Amer. J. Bot.* **47** : 855-859.

DAWSON, I. W. (1883). On the Cretaceous and Tertiary floras of British Columbia and Northwest Territory. *Trans. Roy. Soc. Canada* **1** : 24 (1882)

DE FRAINE, E. (1912). On the structure and affinities of *Sutcliffia* in the light of a newly discovered specimen. *Ann. Bot.*, **26** : 1031-1066.

DELEVORYAS, T. & HOPE, R. C. (1971). A new Triassic cycad and its phyletic implications. *Postilla*, **150** : 1-21.

DELLE, G. V. (1967). The Middle Jurassic flora of the Kvarchelian coal basin (Transcaucasia). *Bot. Trans. Akad. Sci. U. S. S. R.*, **8** (6).

DOLUDENKO, M. P. & ORLOVSKAYA, E. R. (1976). Jurassic flora of the Karatau. *Trans. Acad. Sci., U. S. S. R.*, **284** : 1-264.

DU TOIT, A. L. (1927). The fossil flora of the Upper Karroo beds. *South African Mus. Annals*, **22** : 289-420.

DICHLER, A. W. (1889). Cycadaceae in Engler, A. & Prantl, K. *Die naturlichen Pflanzenfamilien* II. **1** : 6-26.

EMMONS, E. (1856). Geological report of the midland counties of North Carolina. *North Carolina Geol. Surv.* : 1-347.

ENGELHARDT, H. (1891). Über Tertiarpflanzen von Chile : *Senechenbergische naturf. Gesell. Abh.* **16** : 629-692.

ENGELHARDT, H. (1922). Die alttertiare Flora von Messel bei Darmstadt. *Hesse geol. Landesanst. Abh*, **7** (4) 17-128.

ENGLER, A. & PRANTL, K. (1926). *Die naturlichen Pflanzenfamilien*, Bd. 13, Leipzig.

ETTINGHAUSEN, C, (1887). Beiträge zur Kenntnis der fossillen Flora Neuseelands. *Kgl. Akad. Wiss. Wien. Denkschr.*, V. **53** : 143-192.

ETTINGHAUSEN, C. (1888). Die fossile Flora von Leoben in Steiermark. *Kgl. Dankschr Akad. Wiss. Wien. Math. nat.* **54** : 261-318.

FLORIN, R. (1931). Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. *Kungl. Svenska Vetensk Akad. Handl.*, III, **10** (1) : 1-588.

FLORIN, R. (1933). Studien über die Cycadales des Mesozoikums. *Kungl. Svenska Vetenska Aked. Handl.* III, **12** : 1-134.

GILLESPIE, W. H. & PFEFFERKORN, H. W. (1986). Taeniopterid lamina on *Phasmatocycas* megasporophylls (Cycadales) from the Lower Permian of Kansas, U. S. A. *Rev. Palaeobot. Palynol.*, **49** : 99-116.

GOULD, R. E. (1971). *Lyssoxylon grigsbyi*, a cycad trunk from the Upper Triassic of Arizona and New Mexico. *Amer. J. Bot.*, **58** : 239-248.

HAAN, H. R. M. DE (1920). Contribution to the knowledge of the morphological value and phylogeny of ovule and its integuments. *Rec. Trav. bot neerl.*, **17** : 219-324.

HALLE, T. G. (1927). Palaeozoic plants from Central Shansi. *Palaeont. Sin.*, Ser. A.2 (Fasc. 1) : Peking.

HARRIS, T. M. (1932). The fossil flora of Scoresby Sound, East Greenland, Pt. 3 Description of seed plants

Incertae sedis together with a discussion of certain cycadophyte cuticles. *Med. om Greenland,* **85** (5) : 1-114.

HARRIS, T. M. (1941). Cones of extinct Cycadales from the Jurassic rocks of Yorkshire. *Phil. Trans. R. Soc. Lond.,* **B 231** : 75-98.

HARRIS, T. M. (1950). Notes on the Jurassic flora of Yorkshire, 46-48. *Ann. Mag. Nat. Hist.,* Ser 12, **3** : 1001-1030.

HARRIS, T. M. (1952). Notes on the Jurassic flora of Yorkshire, 55-57. *Ann. Mag. Nat. Hist.,* Ser 12, **5** : 614-627.

HARRIS, T. M. (1961). The fossil cycads. *Palaeontology,* **4** (Pt. 3) : 313-323.

HARRIS, T. M. (1964). The *Yorkshire Jurassic Flora.* 2. *Caytoniales, Cycadales and Pteridosperms* Brit. Mus. (*Nat. Hist.*), London.

HARRIS, T. M. (1976). The Mesozoic gymnosperms. *Rev. Palaeobot. Palynol.,* **21** : 119-134.

HEER, O. (1855). Flora tertiaria Helvetiae, Winterthur, **1**, 117 p.

HILL, R. S. (1978). Two new species of *Bowenia* Hooker ex Hook. f. from the Eocene of eastern Australia. *Austr. J. Bot.,* **26** : 837-846.

HILL, R. S. (1980). Three new Eocene cycads from eastern Australia. *Austr. J. Bot.* **28** : 105-122.

HOLLICK, A. (1928). Palaeobotany of Porto Rico : *New York Academy of Sciences Scientific Survey of Puerto Rico and Virgin Islands,* **7** pt 3 : 177-238.

HOLLICK, A. (1932). Descriptions of the new species of Tertiary cycads, with a review of those previously recorded. *Bull. Torrey bot. Cl.,* **59** : 169-189.

HOLLICK, A. (1936). The Tertiary floras of Alaska, *U. S. Geol. Surv. Prof. Pap.,* **182**, 185 pp.

HORIUCHI, J. & KIMURA, T. (1987). *Dioonopsis nipponica* gen. et sp. nov, a new cycad from the Palaeogene of Japan. *Rev. Palaeobot. Palynol.,* **51** : 213-225.

JAIN, K. P. (1964). *Fascivarioxylon mehtae* gen. et sp. nov., a new petrified cycadean wood from the Rajmahal Hills, Bihar, India. *Palaeobotanist,* **11** (3) : 138-143 (1962).

JOHNSON, L. A. S. (1959). The families of cycads and the Zamiaceae of Australia. *Proc. Linn. Soc. N. S. W.* **84** (1) : 64-117.

KERP, J. H. F. (1982). Aspects of Permian Palaeobotany and Palynology. I. *Sobernheimia jonkeri* Nov. Gen., Nov. Sp., A new fossil plant of cycadalean affinity from the Waderner Gruppe of Sobernheim. *Rev. Palaeobot. Palynol.* **33** : 173-183.

KERSHAW, E. M. (1912). Structure and development of the ovule of *Bowenia spectabilis. Ann. Bot.,* **26** : 625-646.

KIMURA, T. & SEKIDO, S. (1974). Bipinnate cycadean fronds newly found from the Lower Cretaceous Itoshiro sub-group, the Tetori group, Central Honshu, Japan. *Symp. Morph. and Stratigr. Palaeobot.,* **2** : 23-27. Birbal Sahni Institute of Palaeobotany, Lucknow.

KIMURA, T. & SEKIDO, S. (1975). *Nilssoniocladus* n. gen. (Nilssoniaceae n. fam.), newly found from the early Lower Cretaceous of Japan. *Palaeontographica,* **B 153** : 111-118.

KRASSER, F. (1903). Konstantin von Ettinghausen's Studien über die fossile von Ouricanga in Brasilien. *Akad. Wiss. Wien Sitzungsber,* **112** : 852-860.

KRASSILOV, V. A. (1978). Late Cretaceous gymnosperms from Sakhalin and the terminal Cretaceous event. *Palaeontology,* **21** : 103-106.

KRÄUSEL, R. (1928). Über eine Cycadee aus den Cerithienkalten von Nierstein und über die tertiare Verbreitung der Cycadeen. *Senckenbergiana,* **10** : 103-111.

KRÄUSEL, R. (1930). Über tertiare Cycadeen. *Senckenbergiana,* **12** : 30-31.

KRÄUSEL, R. (1949). Koniferen und anderen Gymnospermen aus der Trias von Lunz, Niedr-Ostereich. *Palaeontographica,* **B 89** : 36-79.

KRAUSEL, R. (1953). Ein neues *Diooniticarpidium* aus der Trias von Lunz. *Senckenbergiana,* **34** (1/3) : 105-108.

LESQUEREUX, L. (1892). The flora of the Dakota group. *U. S. Geol. Survey Monograph,* **17** : 1-256.

LILIENSTERN, R. H. (1928). *Dioonites pennaeformis* Schenk, eine fertile Cycadee aus der Lettenkohle. *Palaeont. Z.,* **10** : 91-107.

LONG, A. G. (1966). Some Lower Carboniferous fructifications from Berwickshire, together with a theoretical account of the evolution of ovules, cupules and carpels. *Trans. R. Soc. Edinb.,* **56** : 345-375.

MAMAY, S. H. (1969). Cycads : fossil evidence of late Palaeozoic origin. *Science,* **164** : 295-296.

MAMAY, S. H. (1976). Paleozoic origin of the cycads. *U. S. Geol. Surv. Prof. Paper,* **934** : 1-48.

MELVILLE, R. (1962-63). A new theory of the angiosperm flower, Part I. *Kew Bull.,* **16** : 1-50.

MELVILLE, R. (1963). A new theory of the angiosperm flower Part II. *Kew Bull.,* **17** : 1-63.

Mescainelli, L. (1889). Studio sulla flora fossili di Monte Piano : *Soc. veneto-trentino. sci. nat. Atti.,* **10** : 274-297.

Nathorst, A. G. (1902). Beiträge Zur Kenntniss einiger mesozoischen Cycadophyten. *Kungl. Svenska Vetensk. Akad. Handl.,* **36** (4) : 1-28.

Nathorst, A G. (1907) Paläobotanische Mitteilungen. *I. Pseudocycas* eine neue Cycadophytengattung aus den cenomanen Kreideablagerungen Gronlands. *Kungl. Svenskavetenskapsakad. Handl.,* **42** : 1.11.

Nathorst, A. G. (1909). Über die Gattung *Nilssonia* Brongn. mit besonderer berücksichtigung schwedischer Arten. *Kungl. Svenska Vetensk Akad. Handl.,* **43** (12) : 1-40.

Oliver, F. W. (1903). The ovules of the older gymnosperms. *Ann. Bot.,* **17** : 451-476.

Pant, D. D. (1953). Notes on *Cycas* plants growing at Allahabad. *Jour. Indian bot. Soc.,* **32** : 145-156.

Pant, D. D. (1958). The structure of some leaves and fructifications of the Glossopteris flora of Tanganyika. *Bull. Brit. Mus. (N. H.),* **3** (4) : 127-175.

Pant, D. D. (1966). Origin of ovules or seeds and their integuments. *Proceedings of Autumn School in Botany, Mahabaleshwar :* 237-253.

Pant, D. D. (1973). *Cycas and the Cycadales.* Allahabad.

Pant, D. D. (1977). The plant of *Glossopteris. J. Indian bot. Soc.,* **56** : 1-23.

Pant, D. D. (1982). The Lower Gondwana gymnosperms and their relationships. *Rev. Palaeobot. Palynol.* **37** : 55-70.

Pant, D. D. (1987). On the genus *Glandulataenia* nov. from the Triassic of Nidhpuri, India (under publication).

Pant, D. D. & Mehra, B. (1962). *Studies in Gymnospermous Plants—Cycas.* 1st Edn. Allahabad.

Pant, D. D. & Mehra, B. ('963). On a cycadophyte leaf *Pteronilssonia gopalii* gen. et sp. nov. from the Lower Gondwanas of India. *Palaeontographica,* **B 113** : 126-134.

Pant, D. D. & Nautiyal, D. D. (1963). Cuticular and epidermal studies of some modern cycadean leaves, sporangia and seeds. *Senck. Biol.,* **44** (4) : 257-347.

Pant, D. D. & Nautiyal, D. D. (1987). *Diphyllopteris verticillata* Srivastava, the probable seedling of *Glossopteris* from the Palaeozoic of India. *Rev. Palaeobot. Palynol.,* **57** : 31-36.

Pant, D. D. & Pant, R. (1987). On *Cycadites jabalpurensis* sp. nov. from the Lower Cretaceous beds of Jabalpur Series, India. (Under publication).

Pant, D. D. & Verma, B. K. (1963). On the structure of leaves of *Rhabdotaenia* Pant from the Raniganj Coalfield, India. *Palaeontology, London,* **6** (2) : 301-314.

Petriella, B. (1970). *Menucoa cazavi* nov. gen. et sp., Fronco petrificado de Cycadales, Provincio de Rio Negro, Argentina. *Ameghiniana,* **6** : 291-302.

Petriella, B. (1972). Estudio de Madereas Petrificados del Terciario Inferior del Areas Central de Chubut (Cerro Boroco). *Rev. Mus. La Plata* (n. s.), Sec. Paleontol. **6** : 159-254.

Pomel, A. (1849). Materiaux pour servir à la flore fossile des terrain jurassiques de la France. *Deutsch. Naturf. Acrtzte Amtliche Ver* **25** : 332-354.

Renault, B. (1893). *Bassin houiller et permien d'Autun et d'Epinac. Etudes Gites Min. de la France.* Paris, Atlas (vol. of plates),

Renault, B. (1896). *Bassin houiller et Permien d'Autun et d'Epinac. Etudes Gites Min. de la France.* Paris.

Reynolds, L. G. (1924). Female gametophyte of *Microcycas. Bot. Gaz.,* **77** : 391-403.

Sahni, B. (1920). On certain archaic features in the seed of *Taxus baccata* with remarks on the antiquity of the Taxineae. *Ann. Bot.,* **34** : 117-133.

Saporta, G. (1867). Études sur la vegetation du sud-est de la France à l'époque tertiaire. *Annales Sci. nat., Botanique,* 5th Ser., **8** : 1-136.

Saporta, G. (1875). *Paléontologie francaise ou descripiion des fossile de la France, plantes jurassiques :* Paris, 2, *Cycadees :* 289-352.

Saporta, G. (1891). *Paléontologie francaise.* Types Proangiospermiques.

Saporta, G. & Marion, A. F. (1878). Revision de la flore Heersienne de Gelinden. *Mem. cour. et Mem. sav. etrang.* (Acad. h. Sci. etc. Belg.) **41** (3) : 1-112.

Schimper, W. P. (1870). *Traité de paléontologie végétale ou la flore du monde primitif.* Paris. **2** : 1-522.

Schimper, W. P. (1872). *Traité de paléontologie végétale ou la flore du monde primitif.* Paris. **2** : 523-968.

Schuster, J. (1931). Über das Verhältnis der systematischen Gliederung der geographischen Verbreitung und des paläontologischer Entwicklung der Cycadaceen. *Bot. Jahrb.,* **64** : 165-265.

Schuster, J. (1932). Cycadaceae in Engler, A. & Diels, L. *Das Pflanzenreich,* **4** (1): 1-168, Leipzing.

Scott, D. H. (1923). *Studies in Fossil Botany.* **2,** 3rd Edn. London.

Scott, D. H. (1924). *Extinct plants and Problems of Evolution.* London.

SEWARD, A. C. (1895). *The Wealden Flora*, Pt 2—Gymnospermae. *Catalogue of the Mesozoic Plants in the Department of Geology, British Museum (Natural History)*, 2 : XII + 259 pp. London.

SEWARD, A. C. (1917). *Fossil Plants*, 3. Cambridge.

SHAPIRO, S. (1951). Stomata on the ovules of *Zamia floridama*. *Amer. J. Bot.*, **38** : 47-53.

SHUKLA, V. B. (1947). A new angiosperm flower and gymnospermous ovule from Mohgaon Kalan, *in* Palaeobotany in India VI. *J. Indian Bot. Soc.*, **26** (4) : 259.

SMITH, D. L. (1964). The evolution of the ovule. *Biol. Rev.*, **39** : 137-159.

SMOOT, E. L., TAYLOR, T. N. & DELEVORYAS, T. (1985). Structurally preserved fossil plants from Antarctica. I. *Antarcticycas* gen. nov., a Triassic cycad stem from the Beardmore Glacier Area. *Amer. J. Bot.*, **72** (9) : 1410-1423.

STERNBERG, G. K. (1825). Versuch einer geognostischen botanisbin Darstelliug der Flora der Vorwelt. Leipsig u. Prague, **1** (4) : 1-48, Tentamen p. i-xiiio.

STEWART, W. N. & DELEVORYAS, T. (1956). The medullosan pteridosperms. *Bot. Rev.*, **22** : 45-80.

STOPES, M. C. (1903). Beiträge zur kenntniss der Fortpflanzungsorgane der cycadeen. *Flora*, **93** : 435-482.

STOPES, M. C. (1905). On the double nature of the cycadean integument. *Ann. Bot.*, **19** : 561-566.

TAYLOR, T. N. (1970). *Lasiostrobus* gen. nov. a staminate strobilus of gymnospermous affinity from the Pennsylvanian of North America. *Amer. J. Bot.* **57** : 670-690.

THOMAS, H. H. (1930). Further observations on the cuticle structure of Mesozoic cycadeen fronds. *Trans. Linn. Soc. London*, Ser. 2, *Bot.*, **48** : 389-415.

THOMAS, H. H. & BANCROFT, N. (1913). On the cuticle of some recent and fossil cycadean fronds. *Trans. Linn. Soc. London*, Ser. 2, *Bot.*, **98** : 105-204.

THOMAS, H. H. & HARRIS, T. M. (1960). Cycadean cones of the Yorkshire Jurassic. *Senck. Leth.*, **41** : 139-161.

THOMAS, L. (1985). *Late Night Thoughts*. Univ. Press, Oxford.

VAKHRAMEEV, V. A. (1962). New Early Cretaceous Cycadophytes from Yakutia. *Paleont. Zh.*, **3** : 123-129. (in Russian)

WALTON, J. (1964). The Pteridosperms. *Trans. Bot. Sc. Edin.*, **39** : 449-459.

WIELAND, G. R. (1906). *American Fossil Cycads*. Washington.

WILSON, L. R. & WEBSTER, R. M. (1946). Plant microfossils from a Port Union coal of Montana. *Amer. J. Bot.*, **33** : 271-278.

WODEHOUSE, R. P. (1933). Tertiary pollen II. The oil shales of the Eocene Green River Formation. *Bull. Torrey Bot. Cl.*, **60** : 479-524.

WORSDELL, W. C. (1896). Anatomy of the stem of *Macrozamia* compared with that of other genera of Cycadaceae. *Ann. Bot.*, **1** : 601-620.

WORSDELL, W. C. (1898). The vascular structure of the sporophylls of the Cycadaceae.. *Ann. Bot.*, **12** : 203-241.

WORSDELL, W. C. (1900). The comparative anatomy of certain species of *Encephalartos* Lehm. *Trans. Linn. Soc. London*, II (5) : 445-459.

WORSDELL, W. C. (1900b). The anatomical structure of *Bowenia spectabilis*. *Ann. Bot.*, **14** : 159-160.

WORSDELL, W. C. (1906). The structure and origin of the Cycadaceae. *Ann. Bot.*, **20** : 129-155.

YOKOYAMA, M. (1911). Some Tertiary fossils from the Miike coalfields. *J. Colloq. Sci. Imp. Univ., Tokyo*, **27** (20) : 1-16.

ZHANG, SHAN-ZHEN & MO, ZHUANG-GUAN (1931). On the occurrence of cycadophytes with slender growth habit in the Permian of China. In : Carl Teichert, Lu Lieu and Pei-ju Chen (Editors), Palaeontology in China. *Geol. Soc. Amer. Spec. pap.*, **187** : 237-242.

ZHIFANG, GAO (1987). The oldest cycads from the Lower Permian of China. Copy of manuscript without illustrations kindly sent by Dr M. N. Bose.

ZHU, JIA-NAN & DU, SIAN-MING (1981). A new Cycad—*Primocycas chinensis* gen. et sp. nov. from Lower Permian in Shansi, China and its significance. *Acta Bot. Sin.* **23** : 401-404.

ZIGNO, A. (1885). *Flore fossilis formationis oolithicae*—Ce piante fossili dell'oolite, **2**.

Explanation of Plates

PLATE 1

Cycas fujiana

1. Portion of leaf (from Yokoyama, 1880).
   Antarcticycas schopfii (all from Smoot *et al.*, 1985)
2. Transverse section of vascular bundle with secondary xylem, secondary phloem (P) and intervening vascular cambium (VC). ×41.
3. Radial section through secondary xylem showing ray cells (R) and pitting on tracheids. ×312.
4. Longitudinal section at junction of pith (PI) and xylem showing short barrel shaped transfusion tracheids (arrow). ×400.

PLATE 2

5. *Leptocycas gracilis* : distal part of plant showing petiole base (lower left), cataphylls and drooping terminal cone. ×1.25 (from Delevoryas & Hope, 1971).
6. *Paracycas harrisii* Deludenko & Orlovskaya ×1 (from Doludenko & Orlovskaya, 1976).
7, 8. Photomicrographs under SEM of *Lasiostrobus* pollen grains showing multiple sacci and wall ornamentation. ×2000 (from Taylor, 1970).

PLATE 3

9. *Macrozamia zamioides* (Hill) n. comb. apical portion of leaf. ×1 (from Hill, 1980).
10. Inner face of lower cuticle of *M. anastomosaus* (Hill) n. comb. ×120 (from Hill, 1980).
11. Inner face of stoma of *M. anastomosaus* (Hill) n. comb. ×1400 (from Hill, 1980).
12. Inner surface of upper cuticle of *M. zamioides* (Hill) n. comb. ×120 (from Hill, 1980).
13. *Macrozamia cylindrica*, upper epidermis showing deeper sinuosities in epidermal cell walls near outer edge. ×240 (from Pant & Nautiyal, 1963).
14. *Macrozamia cylindrica*, upper epidermis from basal region showing stomata and sinuous-walled epidermal cells. ×240 (from Pant & Nautiyal, 1963).

PLATE 4

15. Leaf of *Ceratozamia wrightii*. ×1 (from Hollick, 1932).

15