THE RELATIONSHIPS OF CYCADALES ON THE BASIS OF THEIR XYLOTOMY, BRANCHING AND LEAF EPIDERMIS

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ABSTRACT

In the opinion of the author recent Cycadaceae may be looked upon as intermediate forms between Filicinae, Pteridospermae and Monocotyledons. Modern paleontologists, as Remy, Leclerq and others, divide the species of Psilophyta according to the form of their ramification into three groups, called monopodial, dichotomic and verticillate types. Dichotomy is a phyletic feature which may be ascertained from Psilophyta (*Asteroxylon*) through Cycadaceae till monocotyl plants, e.g. in palms or in *Dracaena, Yucca* species. Dicotyledonous trees of perfect dichotomic ramification do not exist, this phenomenon occurs only among ferns, Cycadaceae and Monocotyledons. Apart from anatomical characteristics, also the epidermis of leaves and especially the form and structures of stomata constitute a proper basis to conclude to certain family relations.

THE Cycadales are gymnosperms and as highly developed Cormophytes seem to represent a transitional state of evolutionary history between the less developed Cormophyte with spores in the narrower sense of the word, i.e. between Psilophyta, Pteridophyta, seedy Pteriodospermae on the one side and Chlamydospermae and Angiospermae on the other (*see* PLS. 2 & 3).

If, however, we subject these degrees of evolutional history to closer inspection we can distinguish in all of them without exception several types substantially differing from each other. Another important statement is that *simultaneous* occurrence of these several different types is most significant from the aspect of evolutionary history because from this the possible polyphyletic history of evolution of the vegetable kingdom may be concluded. Thus, Remy in his latest work on Psilophyta definitely distinguishes from each other *Rhynia*, *Protopteridium*, *Asteroxylon* and Calamophyta, first of all on the strength of their branching, more exactly on the basis of (1) the monopodial Protolycopsidae, (2) the dichotomous Psilophytopsida and (3) Protoarticulatae of verticillate branching.

Similar is the position among the Pteridophyta, more developed than the Psilophyta, where we can definitely distinguish (1) the microphyllous Lycopsida, (2) the macrophyllous Pteropsida and (3) the verticillate Sphenopsida.

By and large the same situation repeats itself in the fossil Pterodospermae within which we can also distinguish (1) the microphyllous Lepidocarpa, (2) the macrophyllous Miadesmia etc. and (3) the verticillate Calamocarpa.

Within Gymnosperms (1) the macrophyllous Cycadales and Ginkgoales sharply differ from the (2) microphyllous strobilaceous Coniferae (Pinaceae, Taxodiaceae) and similarly within Chlamydospermae there is a strict separation between (1) Gnetales, (2) Welwitschiales and (3) Ephedrales and finally within Angiospermae we find (1) Monocotyledons, (2) Dicotyledons and (3) Verticillatae.

Now the question arises whether Cycadales in their totality, on the basis of their external and internal morphology, in the first place their wood anatomy, branching, and leaf epidermis structures can be brought to a greater or lesser extent into genetical relationship with some of the recent and fossil types recorded representing different developmental stages, whether Cycadales up to their present comparatively high grade of evolution preserved such ancestral anatomical properties which they carry in themselves right from their simplest state of cormophytes or from which it may be presumed that they developed further during the evolutional history of several million years and as such remained in the most developed cormophytes in the Angiospermae unchanged or in a modified form. These problems raised are in some cases very difficult to answer adequately since it was not possible as yet to elucidate all xylotomical features in the simpler forms extinct for a long time. Therefore in the establishment of relationships with these we are in a very uncertain position.

In spite of these deficiencies we are already in possession of such anatomical observations on the basis of which we can conclude, with high probability, on the relationships of Cycadales both up- and downwards. As it will appear from the following considerations, the living Cycadales carry many such xylotomical and branching features, the perfect copy or at least similar form of which can be found not only in the forms of the simplest cormophytes, i.e. Psilophyta but also in the types of the most developed spermatophytes, i. e. the Angiospermae.

1. THE RELATIONSHIPS BETWEEN CYCADALES AND PSILOPHYTA

Psilophyta which lived in the Devonian, are separated, as we have seen above, by Remy (*l.c.*) into types of monopodial, dichotomous and verticillate branching. Also Henes (1959) distinguishes in the xylem, as to the structure of the tracheids two main types different from each other. One is represented by *Rhynia* and *Hornea* in the central stele of which the tracheid walls are spirally or angularly thickened. Such thickenings can be observed in Cycadales at most in the protoxylem elements, never in the secondary wood.

In the other type, the *Asteroxylon*, several such xylotomical features are found which — strange as it may sound — permit to conclude on closer relationships of Cycadales. The fact that the young shoots of *Asteroxylon* are curved in as a crozier, as the young leaves of some Cycadales (*Cycas circinnalis*, *Bowenia*), that in *Asteroxylon* the tracheids of the central vascular xylem elements are essentially not aligned stellately but essentially dichotomously, (*see* PL. 1, FIG. 1) which mode of branching is also a characteristic feature of Cycadales not only for the branchings of the stem (PL. 2, FIG. 15) but among others also for the last branchings of the leaf veins, reminds us not to leave all these out of consideration when establishing possible relationships (*see* PL. 2, FIGS. 14, 15).

Besides these two interesting characteristics, however, the most important is the perfectly similar structure of the tracheids of *Asteroxylon* and Cycadales. In *Asteroxylon* the wall of the tracheids is thickened identically, according to the scalariform pattern as can be observed in a number of recent Cycadales, particularly in *Zamia* species which develop subterranean rhizomes similarly to *Asteroxvlon* and are in general dichotomously branching. Fig. 2 of Pl. 1 refers to *Asteroxylon* while Fig. 3 of about the same magnification to the recent *Zamia muricata*. The similarity in structure is so considerable that even on the strength of a strict comparison one might conclude a close relationship.

The single scales can both in *Asteroxylon* (PL. 1, FIG. 2) and in the living *Zamia muricata* (PL. 1, FIG. 3) branch dichotomously (Leistengabelung-*Henes*). In *Asteroxylon* no so-called modern pittedness can be found, exactly as in the living *Zamia*. With all this we by no means want to say that the Cycadales originated directly from the Devonian *Asteroxylon*; we merely want to direct attention to the high grade of similarity and identical structure which undoubtedly exist between the tracheids of *Asteroxylon* and of the living Cycadales. Thus between them, between the individual types of Psilophyta, the relationship can be assumed with high probability.

2. THE RELATIONS OF THE LIVING CYCADALES TO THE RECENT AND FOSSIL PTERIDOPHYTA, PTERIDOSPERMAE AND GYMNOSPERMAE

Within the three classes of Pteridophyta — not including Sphenopsida — polystely is characteristic of Lycopsida and Pteropsida, although it appears in a somewhat different form in Lycopsida and in several Pteropsida. In the procumbent stems of Lycopsida the individual steles are generally of lamellar structure. In Pteropsida the single steles (more hadrocentric bundles) are often arranged dispersely and in the middle part of the stem sometimes a rather well separated pith system develops (*Isoetes*, *Stylites*). In the tracheid walls only scalariform thickenings occur, but neither araucarioid nor modern bordered pits develop.

As to the thickening of the tracheid walls both Lycopsida and Pteropsida could be brought in some genetical relationship with Cycadales, particularly Pteropsida, in whose tracheids not only scalariform thickenings but also scalariform performations occur on the ends so that these essentially contact each other not as tracheids but as tracheae. In this respect, the scalariform perforation of *Pteridium aquilinum* and *Lepidozamia hopei* is very interesting, between which there is a high grade of similarity, almost identity. Such high grade of similarity or identity can be assumed only among relatives. If we add that within Pteridophyta the young leaves of Filicinae curl similarly as also in *Bowenia* or *Cycas circinnalis*, and that the terminal branching of the leaf veins are in both dichotomous (PL. 2, FIGS. 16-19; PL. 3, FIG. 25) and that in both there are polyciliated spermatazoids and in the embryos at the formation of octant no suspensors develop, and many other features are common, then the relationship between Filicinae and Cycadales can be well assumed and will hardly be contested by anybody.

This genetical relationship is still more corroborated by the comparison of the xylem of the Carboniferous Pteridophyta and Cycadales; here first of all the huge-sized *Sigillaria*, not the Lepidodendrons, enter into consideration (PL. 1, FIG. 4) for various basic anatomical characteristics. The Lepidodendrons had generally a central stele so that the xylem part was located in the axis of the wood (*see* ZIMMERMANN, 1959; MÄGDEFRAU, 1953). On the other hand *Sigillaria* had exactly such developed pith system as the recent Cycadales which is illustrated by the annexed drawing No. 2 and photograph.

Another similarity is that the stems of the living *Alsophila* (PL. 2, FIG. 16), of recently discovered *Stylites* and also of the extinct *Sigillaria* (FIGS. 20, 21) generally did not branch and if so — particularly in older age — the branching was characteristically dichotomous exactly as in some of the living Cycadales and in the monocotyledonous *Dracaena*, *Yucca* (PL. 3, FIG. 29).

The similarity is complete in that the tracheid walls, e.g. in *Sigillaria saullii* are exactly so scalariformly thickened as it is observed among the living Cycadales, particularly in *Stangeria* and *Zamia*. All these are strikingly illustrated by the opposed photos and drawings (PL. 1, FIGS. 4, 5).

As among the living Cycadales several genera can be distinguished, the xylem structure and particularly the pittedness of the tracheids somewhat differs from each other; similar differences existed among the woody ferns not only of the Carboniferous but also of the subsequent Permian. It is interesting to note, however, that these one-time woody ferns in their inner anatomy — especially in the pittedness of their tracheids — are so strikingly suggestive of the anatomical structure of some genera of the recent Cycadales, that confronting the two structures it can be hardly decided whether they originate from recent Cycadales or from Carboniferous or Permian ferns. So the tracheids with scalariform thickenings of the *Sigillaria saullii* referred to, almost perfectly agree with similarly scalariform thickened tracheids of recent Cycadales, viz. *Zamia* and *Stangeria* (PL 1, FIGS. 4, 5).

This should not mean of course that the present Cycadales originated from *Sigillaria*, but the common origin is evidenced beyond doubt.

In the woody and spermatophytic ferns of the Carboniferous and the Permian — and also in the gymnospermous *Dadoxylon* and *Cordaites* — in the tracheid walls the borded pits are fitting together in several rows and according to a honeycomb-like pattern. The photos and drawings on the tracheids of these and the bordered pittedness of the tracheids in some of the recent Cycadales exhibit a strikingly similar, almost identical structure. On the basis of the photos and drawings put besides each other it is difficult to decide which type of pitting originated from a Carboniferous *Cordaites* or a Permian *Dadoxylon* fossil and which from recent Cycadales (PL. 1, FIGS. 8, 9).

We cannot proceed further in the discussion of the relationships of Cycadales before giving a thought to the relationships of the recent Cycadales, *Stylites* belonging to the order Isoetales and discovered five years ago in Peru and the relationships between *Pleuromeia*, and *Nathorstiana*. The genetical relationships among *Sigillaria*, *Pleuromeia*, *Nathorstiana* and *Isoetes* is recognized and stated by almost all geneticists. The question is whether the recent Cycadales are somehow related first of all to Isoetales. The answer is yes, and the relationship is very close as it convincingly appears from the following (PL. 2, FIG. 20).

According to the more exact anatomical and xylotomical examinations, *Isoetes* and the closely related *Stylites* have such anatomical features which, in our opinion, necessarily imply that Isoetales in the future can be no more placed in the Lycopsida because both can belong only to the Pteropsida. The short stem of the *Stylites* is dichotomously branching exactly as that of the Carboniferous *Sigillaria* or of some recent *Cycas*. The adventitious roots arising from the short stem at their ends also branch dichotomously. *Stylites* and *Isoetes* have polyciliate spermatozoids exactly as Cycadales. *Isoetes* and *Stylites* do not develop embryo suspensor (as the forms belonging to Lycopsida) but both develop further at the development of the embryo without suspensor, similarly to Filicineae. All these are characteristic features and not present in these forms by mere chance.

A further similarity of *Stylites* and *Isoetes* to the Cycadales is that in the interior of the stem of all three there is a rather extensive pit and at the boundary of the pit transfusion cells are aligned with a gradual transition to tracheids, the reticular cell-wall thickenings of which perfectly agree with the cell-wall thickenings of the similar transfusion cells of Cycadales. Transfusion cells of such structure only occur in Cycadales and *Ginkgo*.

At the end of this chapter it can be thus stated that besides the wood-anatomy of both the recent ferns, first of all Isoetales, the extinct *Sigillaria*, *Cycadeoidea*, *Callixylon*, *Protopitys*, *Medullosa* etc. and the recent Cycadales there are many other morphological properties on the basis of which it may be concluded with reason on the close relationship of the above series and such relationship can be almost regarded as certain.

From the living or extinct Gymnosperms it is first of all Dadoxyla (*Cordaites*) with which mainly by the araucarioid pittedness of the tracheids the Cycadales can be brought in some genetical relationship (Pl. 1, Fig. 8).

With the strobilaceous conifers in the narrower sense (Pinaceae, Taxodiaceae) the Cycadales, in our opinion, have no closer genetical relationships. Only *Ginkgo* as well as *Araucaria* and *Podocarpus* can possibly enter into consideration. They can be brought in connection with *Araucaria* first of all by their araucarioid pitting since in the tracheidal walls of *Araucaria* the bordered pits are aligned according to a perfectly identical pattern, in 1-4 longitudinal rows, fitted closely besides each other, according to the honeycomb pattern, as can be observed in some living Cycadales, particularly in the genus *Cycas*. It is surely no mere chance either that in the broad leaves of some *Araucaria* and *Podocarpus* the leaf-veins at their ends branch dichotomously as is observed also in some Cycadales or that most recently in the pollen grains of some *Araucaria* such traces of blepharoblasts, i.e. of the polyciliate spermatozoids were detected as can be observed in the living *Cycas* and *Ginkgo*; this, however, is definitely filicinian character.

Besides Araucariaceae a certain genetic relationship can also be assumed between *Ginkgo* and Cycadales. In some tracheids of *Ginkgo* the bordered pits besides uniseriate arrangement, fit together in 2-3 rows although not quite closely and according to the honeycomb pattern but more loosely in a way as it may be observed in some species of *Encephalartos*. If we add to all these that *Ginkgo* and *Cycas* pollen can be hardly distinguished on account of the high grade of similarity, and in the pollen of *Ginkgo* at fertilization polyciliate spermatozoids are released exactly as in *Cycas* and in the wood and leaves of the young *Ginkgo* the same sort of mucilaginous ducts are running as in the *Cycas*, further that in their dichotomously branching leaf blade the leaf veins are branching manifoldly and perfectly dichotomously as in *Cycas* and that in *Ginkgo*, exactly such calcium oxalate crystal druses occur as in *Cycas* — crystal druses never appearing in conifers in the strict sense of the word — then the idea may well arise that a genetic relationship can be assumed between Cycadales and *Ginkgo* and Araucariaceae also on the basis of the xylotomical properties.

3. THE RELATIONSHIPS BETWEEN CHLAMYDOSPERMAE AND CYCAS

The living Cycadales show some relationship with members of Chlamydospermae, particularly with *Welwitschia* and *Bennettites*. In the cross section structure of *Welwitschia* — although it has no developed pith system — the vessels from the centre are definitely aligned dichotomously following each other and running towards the cambium ring (Pl. 3, Fig. 27) where in the single vascular bundle the phloem bundles corresponding with the xylem bundles are located in one or more rings. In the phloem bundles the structure of the phloem fibres is perfectly similar to the phloem bundles of some Cycadales. The similarity of the tracheids is still enhanced by the fact that in the vessels of *Welwitschia* the bordered pits are never fitted together according to the modern but to the araucarioid pattern and also the apertures of the bordered pits are horizontal, which is also a frequent phenomenon in the tracheids of Cycadales (Pl. 1, Fig. 10). The phenomenon can not be left out of consideration either that in the two foliage-leaves of *Welwitschia* the leaf veins run parallel which always can be traced back to dichotomous branching (Pl. 3, Fig. 28) and that the short stem of the aged *Welwitschia* at its tip always separates into two equal parts which can also be interpreted as a somewhat concealed dichotomous phenomenon (Pl. 3, Fig. 26).

4. THE RELATIONSHIPS BETWEEN THE LIVING ANGIOSPERMAE AND THE CYCADALES

Finally let us examine whether there are between the recent Cycadales and the Angiospermae such xylotomical properties which they brought with them from the gymnospermous state and preserved up to now and from which it might be possibly concluded on their .relationship. Apart from the fact that some monocotyledonous woody plants, e.g. Palmae or Dracaenae, Yuccae, if they are very seldom branching (Pl. 3, Fig. 29) the branching is also dichotomous, exactly as we have observed in Cycadales, in the leaves of monocotyledonous plants the leaf veins run parallel, which phenomenon can be traced back in every case to dichotomous branching although as an abnormality furcated branching occurs also (Pl. 3, Fig. 30), etc.

The vessels are always annularly, spirally or scalariformly thickened and so-called modern pitting hardly occurs in them (Pl. 1, Fig. 12). Their perforation is always scalariform which phenomenon as we have seen, occurs also in some Cycadales. In our opinion the Cycadales show relationships more towards Monocotyledons than towards Dicotyledons in which partly the branching of the stem and partly the final branching of the leaf venation is always monopodial and never dichotomous. *No dichotomously branching dicotyledonous tree exists and this is not due to mere chance.*

Also the interesting phenomenon should not be left out of consideration that when, e.g. the root hairs of the monocotyledonous plants are branching this is always dichotomous and never monopodial (Pl. 3, Fig. 31). But the true dichotomous branching is characteristic not only of Filicinae and Pteridospermae, but also of Cycadales. It seems that this ancestral form of branching (*Vaucheria dichotoma* is also one cell branching dichotomously) also in the most developed seed plants appear always in the youngest organs and even in the ultimate branchings of these, that is partly in the ultimate branchings of the root hairs and partly of the leaf veins.

Summing up what has been said above, in author's opinion the Cycadales living today are on the strength of their more important anatomical and mainly xylotomical features in most probable relationship from the Psilophytes of simpler organism first of all with *Asteroxylon*, *Protopteridium* (not with *Rhynia*), from the Pteridophytes with Eufilicinae and particularly with the heterosporous *Isoetes* and *Stylites* (not with Lycopsida), from the plants of the Carboniferous with *Sigillaria*, *Pleuromeia*, *Nathorstiana* (not with Lepidodendrons) from Pteridospermae with *Medullosa*, *Cycadeoidea*, *Williamsonia*, from Gymnosperms with *Callixylon*, *Actinopodium*, *Völkelliella*, further with *Cordaites* and partly with *Araucaria*, *Podocarpus* (not with the conic Coniferae), from the more developed Chlamydospermae with *Welwitschia*, *Bennettites*, from the most developed Angiospermae with the Monocotyledons, in the first place with Palms and in no case with Dicotyledons.

[Author expanded this view for the first time as early as in 1918 in his study: Ein Gedanke zur polyphyletischen Entwicklung der Pflanzenwelt (Beih.z.Bot. Centralbl. 1918) and for the second time in his work: A phylogenetic system of the Gymnosperms in the light of xylotomy (1955).]

5. THE RELATIONSHIP AMONG RECENT CYCADALES ON THE GROUNDS OF THEIR EPIDERMAL STRUCTURE

Andrews, Arnold, Florin, Cookson and other eminent paleontologists in a number of studies examined the leaf epidermis of the fossil Cycadofilices and the recent Cycadales established that the leaf epidermis of some forms of fossil ferns or Pteridospermae in many respect are suggestive of or even completely agree with the epidermal structure of some forms of recent Cycadales. So, for instance Cookson (1953) described from the Australian tertiary under the name of *Lepidozamia hopeites* a fossil, the leaf epidermis of which almost completely agrees with the leaf epidermis structure of the recent *Macrozamia hopei*. It is difficult to separate both forms from each other although by very exact investigations the identity of the two forms can not be established. Cookson (*l.c.*) made this statement on the strength of the leaf epidermis structure of the living *Macrozamia hopei* and *M. peroffskyana*. This single but characteristic data in itself shows how important it is to become acquainted with the epidermis structure of the recent Cycadales. To justify this claim basides the case of *M. hopeites* we refer to a few more data noting that quite a number of convincing examples could be mentioned beyond those listed here.

On Pl. 4, Fig. 32 refers to the recent *Zamia muricata* while the other of the same magnification confronted to it is *Lyginodendron oldhamium* from Lower Westphalian (FIG. 33). On the two photographs form and size of stomata and subsidiary cells are so convincingly similar that we are inclined to subscribe to the assumption that there might have been or exists perhaps some relationship between the one time Lyginodendrons and the *Zamia* of our days.

The same statement can be made on *Macrozamia miquellii* (FIG. 36) the epidermal structure of which on the other hand is highly suggestive of that in *Elatocladus amblus* of the Jurassic (FIG. 37); from this again some relationship if not identity can be assumed.

Still more characteristic is perhaps the similarity of the epidermis of *Dioon edule* to *Elatocladus punctatus* originating from the English Jura. The form of the guard cells is characteristic of *Dioon edule*. None of recent Cycadales has a stoma of such structure (cf. FLORIN, p. 68). The adjacent photograph is of *Elatocladus punctatus* where the shape of the subsidiary cells and the dimensions of the hexagonal aperture developed almost the same way as can be seen on the photograph of the same magnification on the epidermis of the recent *Dioon edule*. On the evidence of such high degree of similarity or almost identity it can be properly assumed that there is some sort of relationship between *Dioon edule* and *Elatocladus punctatus* (PL. 4, FIGS. 34, 35).

The same statement can be made on the high degree of similarity between the leaf epidermis cells of *Encephalartos lehmannii* and *Callipteris maternsii*. The two stomata as well as form and size of the adjacent subsidiary cells are remarkably reminiscent of each other and thus a possible relationship can be properly assumed.

But perhaps the greatest interest and similitude presents itself between *Stangeria paradoxa* and *Ctenis* from the Rhaetic. The undulation of the epidermis walls of *Stangeria paradoxa* and the curl shape and arrangement of the cuticular laths is so characteristic that it is not suggestive of the epidermis of any form of recent *Cycas*. The epidermal structure of the fossil *Ctenis*, however, (*C. nathorsti*, *C. wilsoni*, *C. minuta*, *C. latepinnata*) and particularly the shape and arrangement of their cuticular laths is so conformable to the shape of the epidermis cells of recent *Stangeria* that if it were not known to us that one photograph is of the fossil *Ctenis minuta* while the other of the recent *Stangeria*, we might on the evidence of the photographs easily take one for the other. (PL. 4, FIGS. 38, 39)

These few examples taken at random might sufficiently verify how much paleontologists need to know the epidermial structure of recent Cycadales. Without such knowledge and comparative recent material the determination of the fossil Pteridospermae or Cycadales respectively on the strength of the epidermal structure of the leaves was very uncertain or even impossible up to now.

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EXPLANATION OF PLATES

Plate 1

1\. *Asteroxylon mackiei* Kidston & Lang. In the interior of the little stem the elements of the xylem bundles are not aligned stellately but dichotomously which is a primitive trait of branching. Observe the direction of the white lines which show the whole dichotomous arrangement of the elements. On the right and left side of the middle line the xylem and phloem bundles are the reflections of each other. To the xylem part No. 1 corresponds 1_a, to 2-2_a to 3-3_a, to 4-4_a. To phloem a corresponds a^1, to b-b^1, to c-c^1, to d-d^1, to e-e^1. Thus the ancestral dichotomous branching appears already in the vascular bundle arrangement of Psilophyta. (After Zimmermann) × 70.

2\. *Asteroxylon mackiei* Kidston & Lang. Longitudinal section detail of the metaxylem. The tracheids show scalariform thickenings. (After Henes).

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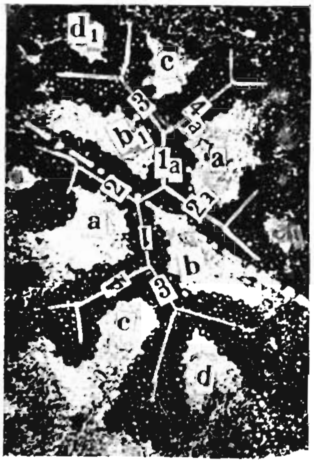

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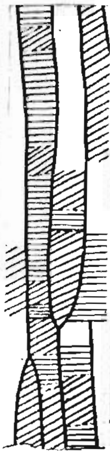

1. Psilophyta (Asteroxylon)

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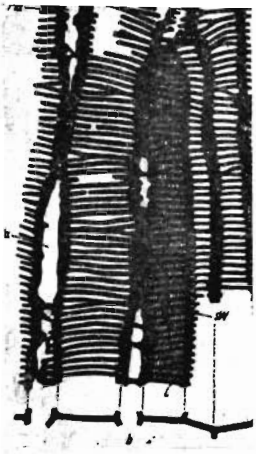
Cycads (Zamia)

4



2. Pteridophyta (Sigillaria)

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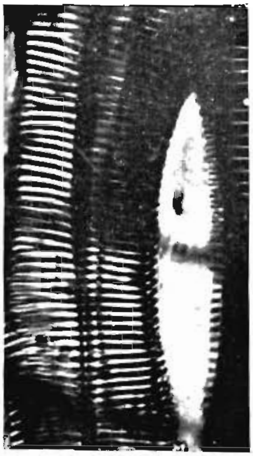

Cycads (Stangeria)

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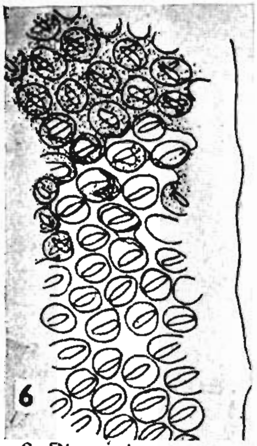

3. Pteridospermae (Lyginopteris)

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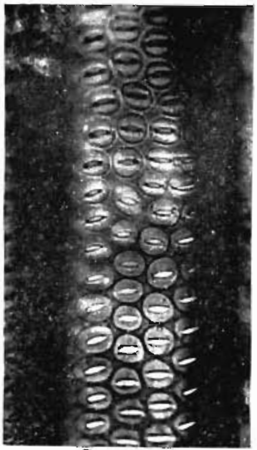

Cycads (Macrozamia)

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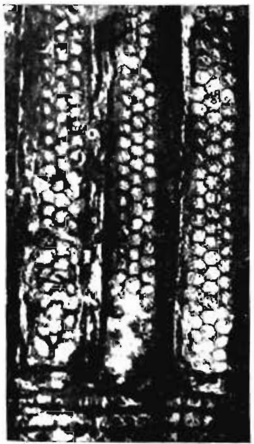

4. Gymnospermae (Dadoxylon)

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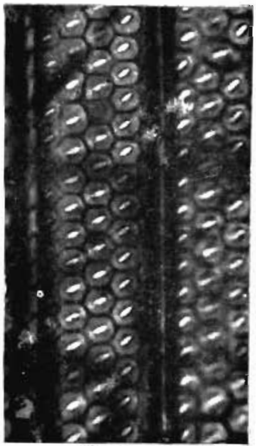

Cycads (Cycas siam.)

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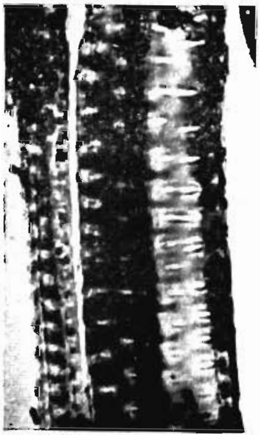

5. Chlamydospermae (Welwitschia)

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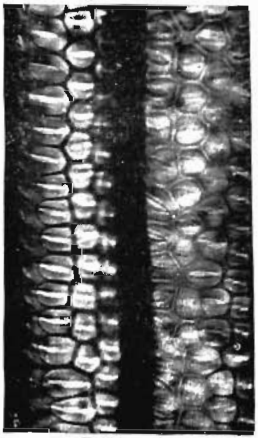

Cycads (Encephalartos)

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6. Angiospermae (Palmae)

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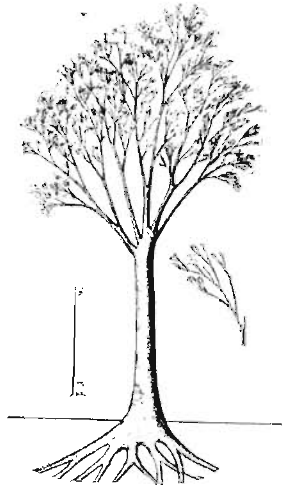
Cycads (Microcycas)

Psilophyta

Pteridophyllopsida



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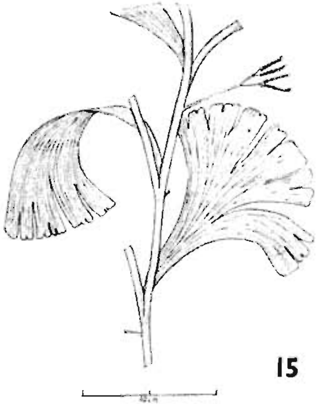

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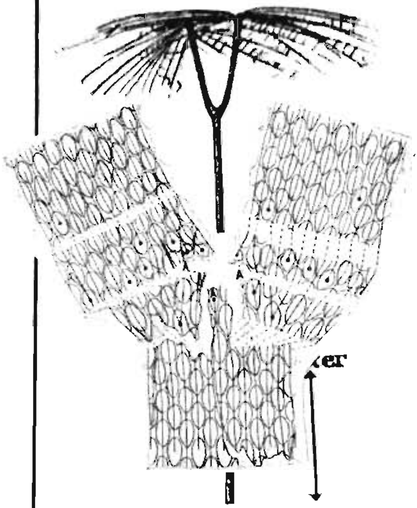
Pteridophyta

Filicinae



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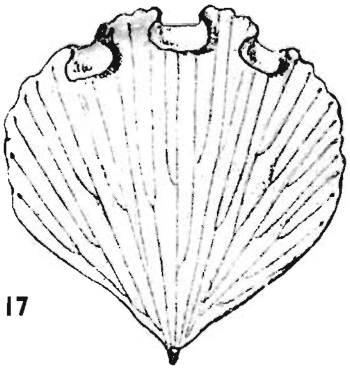

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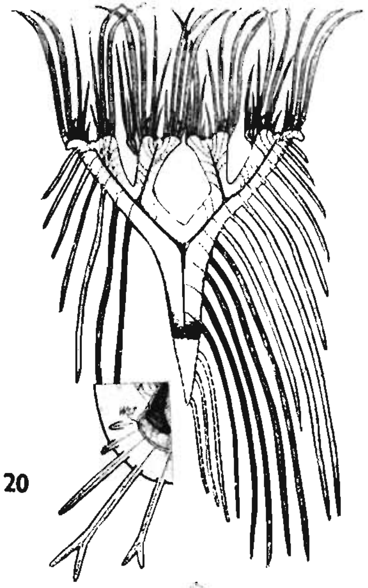
Isoetales



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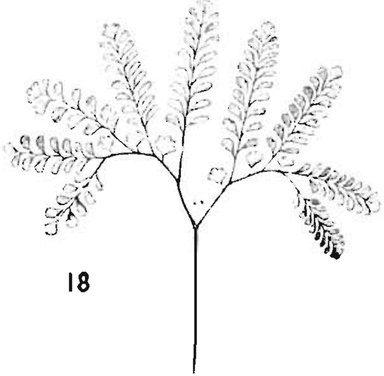

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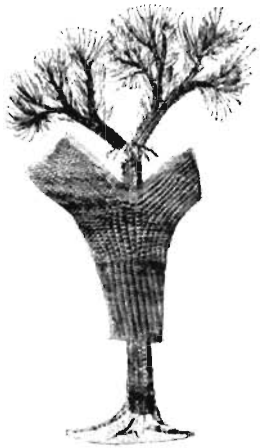
Sigillariaceae



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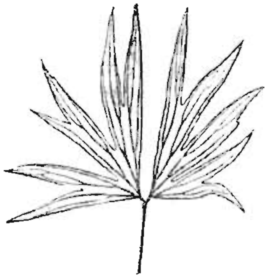

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Pteridospermae
Lyginopteridaceae

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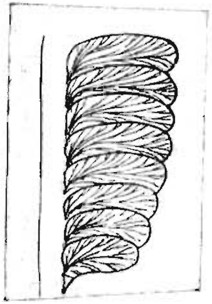

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Gymnospermae
Cycadales

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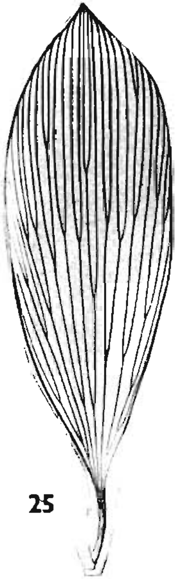

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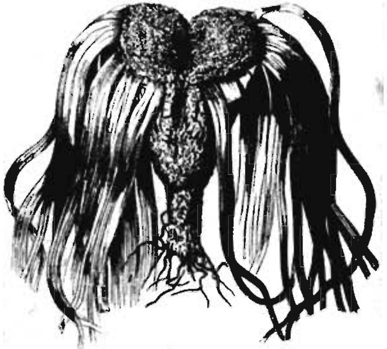
Chlamydospermae
Welwitschiales



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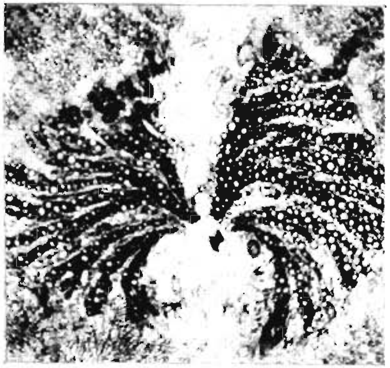

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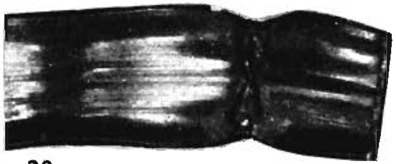

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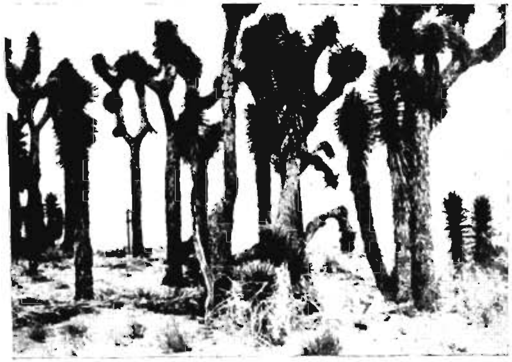
Angiospermae
Monocotyledones



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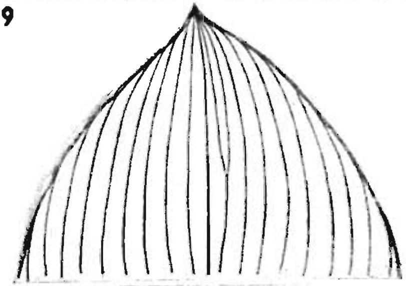

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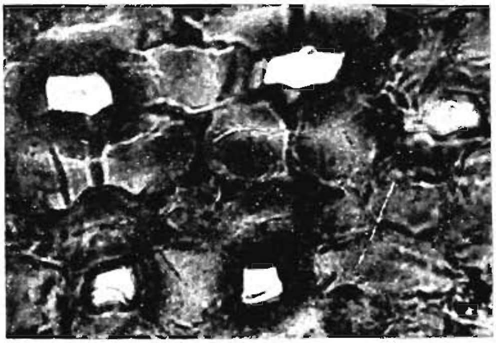
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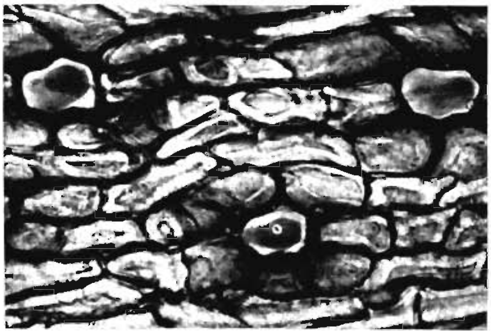
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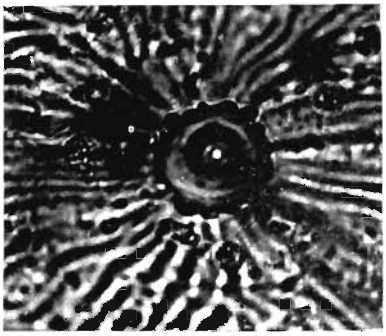
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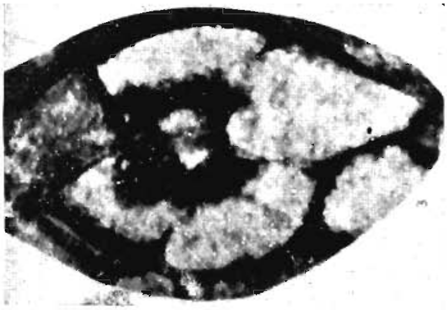
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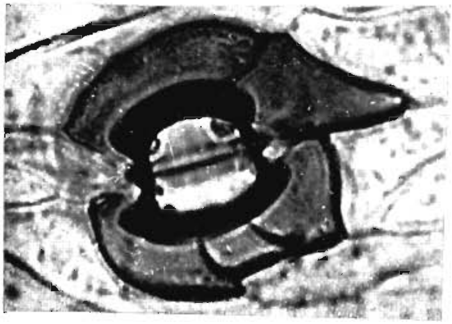
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34

3. *Zamia muricata.* The structure of wood is very similar and can be even regarded as identical to *A. mackiei.* × 250.

4. *Sigillaria saullii* Brgt. In the secondary xylem the tracheid walls show scalariform thickening, the scales are furcate as seen in *Asteroxylon* or in the recent *Stangeria paradoxa.* (After Henes) × 240.

5. *Stangeria paradoxa.* In the walls of the tracheids the scalariform thickenings are also branching furcately. × 250.

6. *Lyginopteris oldhamia* (Binney) Seward. In the tracheids the bordered pits are not closely but loosely arranged besides each other, not in definite longitudinal rows. (After Henes). × 350.

7. In the tracheids of the recent *Macrozamia* the shape and size of the bordered pits, the direction of their aperture and their position to each other is perfectly similar. × 250.

8. *Dadoxylon brandlingi.* In the tracheid walls the bordered pits are arranged according to the araucaroid pattern and in 3-4 rows after each other. (After Zimmermann),

9. In the tracheids of the recent *Cycas siamensis* the arrangement of the bordered pits is very similar. × 250.

10. In the walls of the vessels of *Welwitschia mirabilis* the bordered pits are arranged according to the araucarioid pattern, often the apertures of two bordered pits merge in transverse direction.

11. The same phenomenon is similarly frequent in the recent *Encephalartos.* × 250.

12. The walls of the vessels of Palms show scalariform thickening, the scales are furcately branched as e.g. in *Sigillaria.*

13. The pitting in the living *Microcycas* is also similar. × 250.

PLATE 2

14. On the top of the short stem of the Psilophyte *Pseudosporochnus kreicii* the branches are dichotomously branching, also the endings of the branches are dichotomous.

15. The leaf-like branch or leaf of the Psilophyte *Enigmophyton superbum* and also the leaf veins were dichotomously branching.

16. In Pteridophytes the stem of *Alsophila* is dichotomously branching. The perfect dichotomy is also verified by the arrangement of the cicatrices.

17. In the leaflet of *Adiantum capillus veneris* the leaf veins are dichotomously branching.

18. The composite petioles of the fern *Adiantum pedatum* and also the leaf veins in the leaflet are dichotomously branching.

19. The petiole of the tropical fern *Dryopteris conjugata* the leaf blade and in the blades the leaf veins are dichotomously branching.

20. The short stem of the *Stylites* branches dichotomously also the root ends.

21. The stem of *Sigillaria* of the Carboniferous if it branched it branched dichotomously. On the surface of the stem the number and direction of the cicatrices evidences perfect dichotomy.

PLATE 3

22. The climbing stem of the Peridosperm *Lyginodendron oldhamium* and also the leaf veins in the leaflets have branched dichotomously.

23. In the leaflet of the pteridosperm *Neuropteridium imbricatum* the leaf veins are dichotomously branching.

24. Both the stems above and below the earth of the gymnospermous Cycadales are dichotomously branching.

25. In the *Zamia wallisii* the leaf veins run initially dichotomously, later parallel.

26. The short stem of *Welwitschia mirabilis* separates into two equal parts which is due to dichotomy.

27. In the stem of *Welwitschia mirabilis* the xylem bundles are arranged, not only in their mass but also in their details, dichotomously.

28. In the leaves of *Welwitschia mirabilis* the leaf veins are parallel which is due to the dichotomous branching.

29. The stem of the monocotyledonous *Yucca arborescens* if branching, branches dichotomously. The same phenomenon occurs among the monocotyledonous *Palmae* and *Dracaena.*

30. The leaf veins of the monocotyledons are generally parallel but sometimes at the ends of the leaf veins (e.g. in *Funkia cordata*) the veins are dichotomously branching.

31. When the root hairs of the monocotyledons are branching, they also branch dichotomously (*Triticum vulgare*). Thus dichotomy as a phylum trait always existed from the simplest cauline plants the Psilophyte until the angiospermous *Monocotyledons* and as phylum trait remained also in the most developed phanerogamous plants.

PLATE 4

The similar structure of the stomata in the extinct and recent Cycadales.

32. From the recent *Zamia muricata.*

33. From *Lyginodendron oldhamium* originating from the Lower Westphalian (Florin.)

34. *Dioon edule.*

35. Similar structure of *Elatocladus punctatus* (Jurassian, Florin).

36. From the recent *Macrozamia miquelli.*

37. From *Elatocladus amblus* (Jurassian, Florin).

38. Epidermis cell wall thickening from the recent *Stangeria paradoxa.*

39. Cuticular lath thickenings from *Ctenis minuta* (*Jurasian*). All × 250.