

## CURRENT TRENDS IN PALEOBOTANY

CHESTER A. ARNOLD

*Department of Botany, University of Michigan, Ann Arbor, Mich. (U.S.A.)*

### SUMMARY

The remarkable growth of paleobotany within recent years is revealed in the expanded body of literature and by the increase in number of languages in which it is written. New techniques are involved in the use of cuticles and the electron microscope.

Precambrian rocks, once regarded as essentially without fossils, have been found to contain a variety of micro-organisms, and compounds believed to be decomposition products of chlorophyll have been identified in rocks three billion years old.

Some new ideas have developed concerning the morphology and relationships of some of the very old vascular plants. The original reconstruction of *Psilophyton* embodied more than one plant, and *Asteroxylon* now appears to be a lycopod. The Hyeniales and *Pseudosporochnus* belong to the Cladoxylales. *Archaeopteris* and *Callixylon* are the foliage and woody trunks of the same plant which has been designated a “progymnosperm”. Seeds now appear to have been recognized in the Upper Devonian, and a considerable number of primitive seeds have lately been found in the Lower Carboniferous calciferous sandstone.

Decreased coal mining has curtailed the supply of Carboniferous compressions. In North America outstanding progress has been made in the study of petrified plants in coal balls.

Studies of the *Glossopteris* flora have been extended into Antarctica. Continental drift seems to be the only hypothesis that satisfactorily explains the position of the fragments of ancient Gondwanaland at the present time.

Reinvestigations of the inflorescences of *Cycadeoidea* have shown that the structure of the staminate disc was originally misinterpreted. It is a complex synangium that encircles the gynoecium, rather than being a whorl of pinnate stamens.

The occurrence of angiosperm leaves in the Lower Cretaceous of Greenland is questioned. Some investigators now believe that angiosperms originated at high altitudes in the tropics during the Permian Period. Others would derive them from the Glossopteridae during the same period. Fruits and seeds have proved quite useful in accurate determination of Tertiary angiosperms. Petrified woods create special problems in identification and nomenclature.

## INTRODUCTION

Paleobotany, along with other divisions of natural science, has expanded during recent years to an extent that was quite unanticipated a few decades ago. An approximate measure of this expansion may be seen by comparing the number of titles included in the six issues of the *World Report on Palaeobotany* that cover the interval from 1950 to 1965 (BOUREAU, 1956–1966) as shown in Fig. 1. It is true that beginning with the second issue each report contains a number of titles that had been omitted in previous issues, but these belated listings fall far short of accounting for the increase shown throughout.

In addition to the aforementioned *World Report on Palaeobotany*, other publications essentially paleobotanical in function are *The Palaeobotanist* (Lucknow), *Review of Palaeobotany and Palynology* (Amsterdam) and *Acta Palaeobotanica* (Warsaw). The *Traité de Paléobotanique* (Paris) will, when the projected nine volumes are published, cover fossil plants of all groups. It will be the most comprehensive paleobotanical work in modern times.

The upsurge in the tempo of paleobotanical research that has become so apparent since 1950 has been due partly to the increased awareness of the importance of natural science in our culture and economy, and it is only a logical consequence that paleobotany should receive its share of attention along with other phases of botany and geology. Another important factor in this growth has been the greatly increased availability of research funds which have been used to subsidize graduate students and research associates and to purchase equipment.

Before 1950 the bulk of the paleobotanical literature published each year was in English, French, and German. Today Russian has become one of the languages of paleobotany. Then the greatly accelerated paleobotanical research in South America has resulted in a substantial number of titles appearing annually in Spanish and Portuguese. Moreover, a perusal of the Sixth Report reveals contributions in Polish, Rumanian, Czech, Swedish, Hungarian, Hebrew, Slovak, Italian, Japanese, Chinese, Hindi, and Turkish.

Because the rocks of the earth continue to yield new fossil plants, paleobotany is a dynamic science. The steady accumulation of more information causes rapid obsolescence of subject matter. Textbooks need frequent revision. However, without this constant inflow of new and fresh information, paleobotany would soon become stagnant.

The intent of this paper is to present and emphasize some of the new developments in paleobotany, particularly those that have come about through new or modified techniques, and which may foretell significant developments in the future. No effort is made to summarize all of the important developments during the last few decades. Such a compilation would fill a large volume.

Many of the new developments have arisen from the discovery and description of new plant forms, or from significant additions to our knowledge of

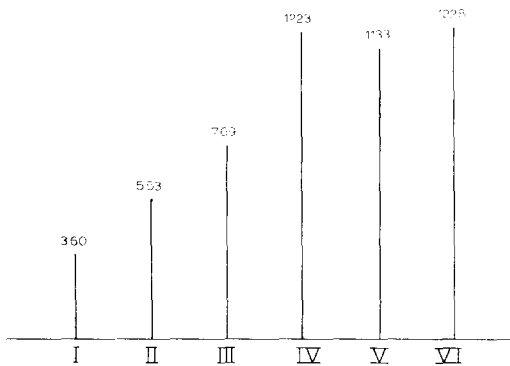


Fig. 1. Chart showing the average annual output of paleobotanical papers listed in the six issues of the *World Report on Palaeobotany*.

Part I—1950-1954; part II—1955-1956; part III—1957-1959; part IV—1960-1961; part V—1962-1963; part VI—1964-1965.

already known ones. Both of these add substantially to the main body of paleobotanical knowledge. Entirely new concepts of relationships may result from the chance discovery of some organ of a fossil plant that was previously unknown, a striking example being Beck's discovery (BECK, 1960a, 1960b) of the stem of *Archaeopteris*, which led to the creation of a new class of plants.

#### USE OF CUTICLES IN PALEOBOTANICAL RESEARCH

The ever-increasing search for new taxonomic characters in fossil plants has led to the frequent incorporation of cuticular characters in diagnoses of new taxa. The use of these is not new, but it has increased markedly within recent years. It has been found that "compression" fossils have retained traces of the cuticle more often than paleobotanists of a generation ago realized. Much cuticular structures can often be revealed by use of proper techniques.

By "cuticles" the paleobotanist usually refers to fragments of leaf epidermis in which the cell walls had become impregnated and the surfaces covered with cutin during development. Cutinization, however, is not confined to leaves; other organs may be similarly affected. Stem cuticles of the Paleozoic lycopods are familiar to paleobotanists and they sometimes accumulate into layers of measurable thickness. Cutinized cell walls are extremely resistant to decay, and they are often preserved when all other parts of the plant have disappeared.

There are two methods in common use for the study of plant cuticles. One is the bulk maceration method, where pieces of fossiliferous rock are disintegrated in acid (usually hydrochloric or hydrofluoric) and then treated with alkali. The residue, which usually contains an assortment of heterogeneous plant fragments, is then collected on a sieve. The different types are then sorted out.

The other method, which is selective, consists of removal of pieces of epi-

dermal fragments from more or less complete leaf compressions. They may be released from the rock matrix by maceration, or by various modifications of the film transfer method. Rather striking results are sometimes attained with the latter. Large portions of fronds and whole leafy shoots can sometimes be removed mostly intact from fine-grained rock. The compressions in the Middle Jurassic deltaic rocks of Yorkshire are especially suited for treatment in this manner (HARRIS, 1961–1964).

The most extensive and successful cuticle studies have been on Mesozoic cycadophytes and coniferophytes. Cuticle studies have played a much lesser role in Paleozoic paleobotany, but to judge from the results achieved from limited investigations, this has been a neglected field. The cuticles of Paleozoic conifers and cordaites have lately been examined by LEDRAN (1962), MEYEN (1963), and BARTHEL (1964). BARTHEL (1962) has also described and figured the epidermal patterns of a number of pteridosperm fronds.

Some of the cuticular characters used in taxonomy are the relation between the guard cells and the subsidiary cells, extent of cutinization of the guard cell walls, the shape of the epidermal cells on the upper and the lower epidermis, presence or absence of cuticular papillae and hairs, whether the cell walls are straight or not, and the distribution of the stomata on the different leaf surfaces. A synopsis of useful cuticular characters has been prepared (ARBEITSGRUPPE "CUTICULAE" DER C.I.M.P., 1964). For the most part cuticle characters apply only at the generic or specific levels. Only after extensive experience can an investigator use them for separation of higher taxa. One of the most productive uses of cuticles is where they provide evidence of identity of detached organs, since the different organs of a plant usually have similar cuticles. For example, THOMAS (1925) relied heavily on similarities in the cuticles when he assigned the separate organs *Caytonia*, *Caytonanthus*, and *Sagenopteris* to one unnamed plant and created the order Caytoniales.

A promising field for investigation that is at present only partially developed is the application of cuticle characters to identification of angiosperm leaves preserved in Tertiary clays and shales. Since many Tertiary angiosperms have close living relatives, and most of those from the Mid and Late Tertiary even appear identical with living species, the fossil cuticles can sometimes be matched with cuticles of living plants, which greatly facilitates accurate identification of the fossils. Unfortunately in the extensive volcanic ash beds of western North America, the cuticles of leaves are seldom well preserved but in strata of different composition such as the delta muds of the Wilcox Group, cuticles can often be recovered (DILCHER, 1963). Excellent cutinized material, including whole leaves of *Symplocos hallensis*, have been described and figured by BARTHEL et al. (1966) from the Middle Eocene. The most extensive recent work on fossil angiosperm cuticles is by KRÄUSEL and WEYLAND (1950, 1954) who studied material from the Tertiary lignites of Germany.

## ELECTRON MICROSCOPY IN PALEOBOTANICAL RESEARCH

Although there are a number of references in the literature to electron microscopy in paleobotanical research, it is still in the experimental stage and it remains to be shown how widely it can be applied to paleobotanical problems. Its potential value lies in the ability of the electron microscope to resolve structural details that lie below the visual range of the optical microscope. For ordinary morphological interpretations, therefore, it has few advantages. Its use is dependent upon an operator trained in the use of the instrument and especially prepared mounts. The instrument is also expensive and therefore not available in all institutions. It seems safe to predict that future use of the electron microscope in paleobotany will be of supplementary nature rather than a replacement of the ordinary microscope. The recently developed scanning electron microscope, which to an extent bridges the gap between the conventional and the older type of electron microscope, may broaden somewhat the use of the electron beam in paleobotany.

The most promising results achieved so far in the application of the electron microscope to paleobotanical problems have been in revealing the ultra-structure of spore exines of fossil plants and in rendering minute surface features visible. It is quite probable that information having taxonomic value may be gained in this way. Mention is made subsequently of the electron microscopy of bacteria-like organisms in 3 billion year old Precambrian chert.

Another application of electron microscopy may be in investigations of the nature of petrification processes. Nobody has told us yet exactly how wood petrifies. The old doctrine of replacement molecule by molecule of the substance of the wood with mineral matter, and still supplied to students in some textbooks, is quite at odds with the simple facts of elementary chemistry and the results obtained when a "peel" section of a coal ball is prepared. A few studies in the ultra-structure of the cell walls of silicified wood have been made with the hope of gaining some understanding of the process of petrification (EICHE, 1954), but these are only preliminary. SCHMID (1967) in a recent paper on electron microscopy of *Callixylon* and *Cordaites* tracheids gives a fairly complete and up-to-date bibliography of the subject.

## EARLY PLANT LIFE

Very little was known about Precambrian life until rather recently. The foundation rocks of the geologic column were repeatedly declared non-fossiliferous, and the rather slender evidence that had been assembled for Precambrian life was mostly indirect. There are, in fact, many Precambrian limestones that bear much resemblance to algae reefs. Some graphite deposits are accounted for on the

assumption that they represent metamorphosed coal seams, and there are minute dark spots in some rocks that look like bacterial chains. But no one had been able to show positively that these were the results of living organisms. The lack of clearly defined fossil remains was believed to be due to the fact that during Precambrian time organisms had not evolved parts sufficiently durable to be preserved, or that if such did exist, they were destroyed by the strong forces of metamorphism that altered the physical characteristics of most of the rock containing them.

Some recent discoveries have changed these beliefs rather drastically. While most Precambrian rocks are quite barren of fossils, certain cherts formed during this remote time have been found to contain remarkably well preserved organisms. They are, however, of microscopic size and they become visible only when the chert is ground into thin sections or prepared for examination under the electron microscope. There are a variety of unicellular organisms, some of which appear to be spores or sporelike bodies, while others may be protistids and unicellular algae. Also there are numerous filamentous forms that appear to represent algae and fungi. Persistence of such delicate structures in rocks that are more than a billion years old is due to the excellent preservative properties of chert. Once sealed in this substance an organism may remain with little outward change as long as the chert itself exists. Because of its durability chert is less readily metamorphosed than other sedimentary rocks.

The oldest organisms ever discovered to date are unicellular bodies resembling bacterial cells and unicellular algae in the cherts in the Early Precambrian Fig Tree Series of South Africa. Their calculated age is 3.1 billion years (BARGHOORN and SCHOPF, 1966; SCHOPF and BARGHOORN, 1967). Somewhat younger but significant because of the variety of forms preserved are the 1.9 billion year old microorganisms in the Middle Precambrian Gunflint Chert along the north shore of Lake Superior in Ontario (BARGHOORN and TYLER, 1965). Altogether eight genera and twelve species of plantlike organisms in the Gunflint Chert have been named and described.

One of the organisms preserved in the Gunflint Chert is *Kakabekia*, a minute body with an umbellate crown borne on a stalk attached to a rounded body. *Kakabekia* is of special interest because a very similar living organism has been found in ammonia-containing soil samples (SIEGEL and SEIGEL, 1968). Its nature, whether algal, fungal, or something else, is unknown, but its tolerance of ammonia renders plausible the hypothesis that the Gunflint Chert was formed at a time when the composition of the atmosphere was different than at present.

Except for a few spores of uncertain source isolated from sandstones and shales, no remains attributable to plants higher than thallophytes have been found in the Precambrian. As far as we can interpret the fossil record, algae and possibly protistids and fungi were the principal forms of Precambrian plant life. Some investigators believe that most of the evolution within the algae, probably as much as 85%, was completed before the beginning of Paleozoic time.

Paleobiochemistry is not exactly a new science though it has not been extensively developed. It has been known for a long time that some of the original calcium carbonate has been retained in geologically ancient shells. Cellulose and lignin has been found in silicified wood, and substances resembling cutin and chitin were long known to exist in other ancient fossils. With the development of paper chromatographic methods, however, such readily destructible compounds as amino acids can still be detected in the armour plates of 300 million year old fish remains (ABELSON, 1956). More surprising still are some organic extracts found in the Early Precambrian cherts (MEINSCHN, 1965). These include alkanes, pristane, and phytane which are believed to be decomposition products of chlorophyll. The presence of these compounds indicate that some of the Early Precambrian organisms did carry on photosynthesis, and that free oxygen was then being released into the atmosphere. Within the last decade and a half a considerable body of literature on the organic components of fossils has accumulated.

#### EARLY LAND PLANTS

The terms "land plants" and "vascular plants" are often used interchangeably, the assumption being that they are essentially the same. However, some of the Early Devonian vascular plants appear to have been aquatics (*Zosterophyllum rhenanum*, KRÄUSEL and WEYLAND, 1935; *Barinophyton obrutshevii*, ANANEV, 1954). Even the Rhynie Chert plants were marsh inhabitants that presumably had retained some of the features of their aquatic forebears. So the question is, which developed first, the vascular system or life out of water? The answer is uncertain.

World-wide interest in early land plants, which was highly stimulated by the discoveries in the Rhynie Chert more than 40 years ago, has been nourished by numerous later made discoveries, and the body of literature that has accrued is large.

The Rhynie discoveries were followed by significant ones in the Middle Devonian near Elberfeld in western Germany, and the plants from there were described in a series of papers by KRÄUSEL and WEYLAND (1935). More recently, important works have appeared on the Devonian floras of Spitzbergen by HØEG (1942), of Belgium by LECLERCQ (1951) and LECLERCQ and BANKS (1962), and of New York State by BANKS (1966) and GRIERSON and BANKS (1963). SURANGE (1967) has summarized what is known of the sparse pre-Carboniferous plant remains of India, and PLUMBSTEAD (1967) has reviewed the considerably larger Devonian floras of the Cape System of South Africa. These are small, however, as compared with northern Devonian floras. Several authors have described South American Devonian plants (FRENGUELLI, 1951; MENENDEZ, 1965), and TACHIBANA (1950) reported the first Devonian plants to be found in Japan.

For a century and a half the extensive Middle and Upper Devonian deposits of New York State have been known to contain fossil plants but until relatively recently there had been no concentrated efforts to study them. The several and rather recent publications by BANKS (1966), BECK (1967), HUEBER and GRIERSON (1961) show that the New York Devonian contains a flora of considerable size. However, to date only the lycopods (GRIERSON and BANKS, 1963) and *Callixylon* (ARNOLD, 1929) have been systematically treated. A complete list of literature citations, many of which deal with single species, would be too long to include here.

Most of the plant remains in the Devonian of New York State are fragmentary compressions and casts. In some, enough mineralization of the tissues had taken place to retain some of the internal structure. Significant examples are *Callixylon*, *Cladoxylon*, *Eddyia*, *Tetraxylopteris* and *Xenocladia*.

Vascular plants have been reported from the pre-Devonian periods but in no epoch older than Late Silurian has proof in the form of preserved vascular tissues been forthcoming. There are, for example, *Aldanophyton* (KRISHTOFOVISH, 1953) from the Cambrian, *Boiophyton* (OBRHEL, 1959) from the Ordovician, *Eohostimella* (SCHOPF et al., 1966) from the Early Silurian, and *Saxonia* (ROSELT, 1962) from the Late Silurian. All except *Eohostimella* are entirely devoid of preserved tissue of any kind. *Eohostimella* shows a layer of subepidermal supporting tissue but nothing else. *Baragwanathia* and *Yarravia*, long hailed as Middle Silurian vascular plants, and of an age believed to be attested to by invertebrate remains, have now been "lifted" to the top of the Lower Devonian.

The Psilophytales, long looked upon as the most primitive of vascular plants, and usually placed at the bottom in phylogenetic diagrams, have of late lost much of their former evolutionary significance. This has been due partly to the growing realization that the group was a highly artificial one containing many unrelated forms. Then a second reason for rejecting it as ancestral to other groups is because plants believed to be true lycopods, arthropytes, primitive ferns, and members of other rather advanced but extinct taxa are known to have existed contemporaneously with the psilophytes. The psilophytes could not have been ancestral to these.

The concept of the Psilophytales was first developed by KIDSTON and LANG (1917) in their well-known series of papers on the plants from the Rhynie Chert. The two plants they included in this group were *Rhynia gwynne-vaughani* and *Psilophyton princeps*, having derived most of their information on the latter from the descriptions and figures that Dawson had published several years before. The reconstructions of *Rhynia gwynne-vaughani* and *R. major* remain virtually unaltered today as KIDSTON and LANG (1921) prepared them 40 years ago, and as these authors defined the Psilophytales, this group remains today the closest approach to the hypothetically simplest plants of which we have any precise knowledge.



The suggestion made by MERKER (1958, 1959) and by PANT (1962) that the underground parts of *Rhynia* and *Horneophyton* may be gametophytic bodies does not alter in any essential way the assumed simple status of these plants. If anything, it points out a closer relationship with the living Psilophytales in which vascularized gametophytes have been observed.

The situation regarding *Psilophyton* has changed somewhat because very little of the internal structure of the material on which DAWSON (1888, p.64) based his reconstruction of *Psilophyton princeps* was revealed. Furthermore, the evidence for Dawson's restoration had never been critically examined. HUEBER and BANKS (1967) have recently redescribed the plant with an emended diagnosis of the genus. They retain the aerial portion of *P. princeps* essentially as Dawson drew it, but the fossilized axes that he thought represented the rhizomes have been found to belong to *Taeniocrada*, a different plant. The new diagnosis is more limited than the older one and excludes some forms that had been included in *Psilophyton*. For instance, the spiny stems that Dawson called *P. princeps* var. *ornatum* belong to a new and as yet unnamed genus that is probably lycopodiaceous, and HOPPING (1956) has made *P. robustius* the type of the genus *Trimerophyton*.

BANKS (1967) has recently proposed that "Psilophytales" be abandoned as a formal taxon, and that the plants formerly placed in it be distributed among three new subdivisions that he would call Rhyniophytina, Zosterophyllophytina, and Trimerophytina. The Rhyniophytina would include, along with some others, *Rhynia*, *Horneophyton* and *Psilophyton princeps*, thus conforming to KIDSTON and LANG's (1917) original concept of Psilophytales. This class is conceived as being a holdover of the pre-Devonian ancestral stock and occupying essentially the position formerly awarded the Psilophytales. The other two subdivisions would include various forms that have from time to time been placed in Psilophytales but which are not close relatives of *Rhynia* or *Psilophyton* as the latter genus has been redefined. The Zosterophyllophytina may represent an early stage in lycopod evolution, and Trimerophytina may have contained the ancestors of the ferns and seed plants. This three-fold classification of early vascular plants may serve until a better one is found.

LYON (1964) has reopened the Rhynie Chert quarry in Aberdeenshire after several years during which it was not exploited and has found stems of *Asteroxylon mackiei* with sporangia borne laterally among the leaves. This discovery confirms the long held belief that the naked fertile axes that Kidston and Lang attributed to this plant belong in all probability to some other plant. It also shows that the affinities of *Asteroxylon* are probably with the lycopods. FAIRON (1967) has re-evaluated KRÄUSEL and WEYLAND's (1926) restoration of *Asteroxylon elberfeldense* and presents evidence that more than one plant was incorporated into it.

The Devonian Hyeniales, based upon *Hyenia* and *Calamophyton*, have long been referred to as the oldest order of the ArthropHYTA (Sphenopsida). The fertile appendages have been homologized with the equisetalean sporangiophore, thus

deducing the origin of the sporangiophore from fertile telomic units. Recently LECLERCQ and SCHWEITZER (1965) described a stem of *Calamophyton* having the *Cladoxylon* type of structure. Apparently, therefore, *Calamophyton* belongs to the Cladoxylales, an extinct group of polystelic spore-bearing Paleozoic plants of unknown relationships. There are few, if any, differences between *Calamophyton* and *Hyenia*, and if it is necessary to remove *Calamophyton* from the Arthrophyta, it seems doubtful that the order Hyeniales can be maintained.

LECLERCQ and BANKS (1962) have found that *Pseudosporochnus nodosus*, from the Middle Devonian of Belgium, has cladoxylalean anatomy, so this genus is removed from the Psilophytales where it was often placed. With the acquisition of *Calamophyton*, *Hyenia* and *Pseudosporochnus*, the Cladoxylales become a group with eight genera.

A series of three discoveries made independently by different investigators had resulted in the Devonian plant *Archaeopteris* becoming one of the best known of Paleozoic plants. The first discovery was made about three decades ago when it was found that *Archaeopteris latifolia* bore microspores and megaspores (ARNOLD, 1939). It was therefore evident that one species at least of *Archaeopteris* was a cryptogam though not a fern of the usual type, or even a pteridosperm, as some paleobotanists had believed.

The second discovery consisted of BECK's (1960a, 1960b) finding of vegetative and fertile parts of *Archaeopteris macilenta* attached to a stem having the *Callixylon* type of secondary wood. Since *Callixylon* trunks 5 ft. in diameter had been observed, *Archaeopteris* was not a small fernlike plant, but a large tree. However, the foliage and reproductive organs of *Callixylon* were unknown up to that time. It had been previously classified with the Cordaitales because of its size and anatomical structure. *Archaeopteris* and *Callixylon* thus became names for different parts of the same plant, but *Archaeopteris*, having priority, became the valid name for the whole plant.

The third discovery was reported by CARLUCCIO et al. (1966) when they showed that the alleged rachis of *Archaeopteris* has the structure of a stem. The *Archaeopteris* "frond", therefore, appears to be a determinate branch system bearing simple leaves. The so-called "pinnae" of *Archaeopteris* may be analogous to the ultimate leafy branchlets of the Taxodiaceae.

A reconstruction of *Archaeopteris* by BECK (1962) shows a tree with a trunk about 5 ft. in diameter at the base and a calculated height of 75–100 ft. Its excurrent habit is not unlike that of *Abies* or *Picea*. Its leaves, however, were quite different, being flat with numerous small veins.

The woody stem and small simple leaves of *Archaeopteris* effectively exclude this plant from the fern category, regardless of the fact that reproduction was by spores. However, it is impossible to assign it to any established class of plants. Beck has filled this vacuum in classification by proposing the new class Pro-gymnospermopsida (BECK, 1960a) which includes *Aneurophyton*, *Tetraxylopteris*,

*Pitus*, and *Protopitys* along with *Archaeopteris*. According to Beck's concept, the "progymnosperms" preceded the true gymnosperms, being their spore-bearing precursors.

Paleobotanists have long believed that seed plants had come into existence before the end of the Devonian Period, though no structures that can unquestionably be called seeds had ever been found in rocks older than Mississippian. All evidence for Devonian seeds, therefore, was indirect. This consisted of conifer-type wood structure in the trunks of *Callixylon* and other plants, the determinate leafy branches that were mistaken for pteridosperm fronds, and a few husklike bodies that might have been seed cupules.

In addition to morphological evidence, which is well known, there is now direct evidence from fossils that the seed evolved from a megasporangium during Devonian time. The initial step was the separation of the sexes in the spores. In fossils this is revealed by spores of two distinct sizes on one plant, the well-known phenomenon of heterospory. We actually know of a few cases of heterospory in Devonian plants. The oldest is in *Svalbardia boyi* from the upper Middle Devonian (KRÄUSEL and WEYLAND, 1960). Heterospory became more prevalent in the Upper Devonian, and has been reported a few times in *Archaeopteris* (ARNOLD, 1939; PETTITT, 1964), in *Barinophyton* (PETTITT, 1964), and in a fructification attributed to *Enigmophyton* (HÖEG, 1942). However, it is not at all certain that any of these plants were direct ancestors of seed plants.

In the quest for Devonian seeds some significant discoveries have recently been recorded. MASLOV (1957) found a body (*Hirsutocarpon*) that bears some resemblance to a *Lepidocarpon*, but his description and figures give but an imperfect idea of its form. CHALONER and PETTITT (1964) then described a seed megaspore, *Cystosporites devonicus*, from the famous Late Devonian "Fish Cliffs" at Scaumenac Bay in Quebec, which resembles a lepidocarp spore. Still more recently PETTITT and BECK (1967) reported seed megaspores with cupule-like structures that were described several years ago from Upper Devonian *Archaeopteris*-bearing shales of Pennsylvania. When first found these cupules were attributed questionably to *Archaeopteris*, but this was abandoned when the microspores and megaspores of that plant were found. At present, these cupules cannot be attributed to any particular plant.

Further research by PETTITT and BECK (1968) has revealed what appear to be nucellar and integumentary tissues around the large seed megaspores within the cupules. It thus appears that the existence of seeds during Late Devonian time has actually been demonstrated.

Much interest has centered on seeds and cupulate organs recently found in the Cementstone Group of the Calciferous Sandstone, of Lower Carboniferous age, of Berwickshire and other places in southern Scotland. Close to twenty different types are now known, some having been described over the years by BENSON (1914) and GORDON (1941), but others more recently by WALTON (1949),

SMITH (1959) and LONG (1960a, 1960b, 1960c). The contributions by Long have been especially outstanding. *Genomosperma kidstoni* (LONG, 1960a) consists of an apically borne elongate nucellus that is partially enclosed by a rudimentary integument. The latter consists only of a whorl of 6–8 terete lobes that arise below the nucellus and extend upward for considerable distance beyond the apex. They do not converge over the apex of the nucellus as do most lobed or unlobed integuments, but spread apically forming a narrow bell-shaped organ. In an associated species, *Genomosperma latens*, the integument lobes converge rather than diverge over the apex. These two species of *Genomosperma* reveal two early stages in the evolution of an integumented ovule from a megasporangium.

Were it not for the presence of a lagenostome at the apex of the nucellus in *Genomosperma kidstoni*, we could hardly call the organ an ovule. It would be only a megasporangium, and not a very highly specialized one at that. But in the pteropsid group of plants it is the lagenostome that marks the transition to the ovule stage. This device aided pollination before the micropyle existed.

In *Eurystoma* (LONG, 1960b), *Geminitheca* (SMITH, 1959), and *Stamnostoma* (LONG, 1960c) we find evidence that cupules developed from telomes represented as portions of fronds. Certain authors (WALTON, 1953; SMITH, 1964) have concluded that the telomic concept best explains the lagenostome-like cupule and the integumentary complex in these and later ovules.

#### UPPER CARBONIFEROUS PLANTS

Decreased coal mining in Europe and North America within the last 30 years has sharply curtailed the number of Carboniferous plant compressions that can be collected from the mines. These fossils had always received less attention in North America than in Europe except for a period at the end of the last century when Leo Lesquereux and David White were active. Unfortunately, their achievements were not perpetuated much after 1900. During the interval including the first half of the present century when Paul Bertrand in France, Walter Gothan and Henry Potonié in Germany and Robert Kidston in Great Britain were advancing our knowledge of Carboniferous floras, the subject for the most part lay quite dormant in North America. There are a few exceptions, however, that should be noted. W. A. Bell became active in Canada, and in 1944 he published the third and last part of his comprehensive studies of the Carboniferous plants of Nova Scotia (BELL, 1944). At this time A. C. Noé collected widely in Illinois, but his greatest contribution was the discovery of coal balls in that state in 1923. American coal balls have recently received the attention of a number of paleobotanists, among whom are Andrews, Balbach, Baxter, Delevoryas, Eggert, Hall, Leisman, Phillips, Taylor and Stewart. Significant contributions were also made by Darrah, Graham, Morgan, Streidtmann and others. During the last two decades the study of plants in coal balls has been the most actively pursued phase

of Carboniferous paleobotany, and some outstanding results have been achieved.

In Great Britain Kidston's unfinished studies of the Carboniferous floras were continued by CROOKALL (1959–1964). In France studies of fern and pteridosperm frond types that reached an advanced stage under Bertrand have been pursued by CORSIN (1951), DANZE-CORSIN (1953), DANZE (1956) and DOUBINGER (1956). In Germany Gothan has been followed by REMY and REMY (1959) and DABER (1959). WAGNER (1966) has carried out extensive investigations of Carboniferous floras in northwestern Spain, and thereby has promoted paleobotanical research in an area previously little known.

Studies of the Late Paleozoic floras of the Kuznetsk Basin in Siberia, and extensively pursued by M. D. Zalessky, were resumed by the late NEUBURG (1948) and collaborators. She has also investigated a large Permian flora in the Pechora Basin (NEUBURG, 1965). This flora is characterized by a large number of cordaites which are represented by numerous leaf forms and seeds. Of special interest, however, are two species of the new genus *Vojnovskya* which typifies the order Vojnovskyales. This is an order of extinct seed plants whose relationships to other seed plant groups is unknown.

The study of Carboniferous plant compressions and the remains in coal balls involves separate techniques and to a large extent separate nomenclature. Moreover, a specialist in one field does not necessarily qualify as a specialist in the other, even though both may be working with material of the same age and belonging to the same natural groups.

In spite of the fragmentary state of most coal ball plants, it has been possible to find out something of the manner of development of some of the plants that grew in the swamps. When material of a certain plant is abundant, as it often is in such horizons as the Calhoun and Herrin Coals of Illinois, or the Bevier and Fleming Coals of Kansas, the slight structural differences displayed in a series of specimens may be due to developmental differences in parts of the individuals. For example, some specimens may be from the older basal parts of stems, while others with lesser amounts of certain tissues may have come from nearer the tips or from the branches. Significant ontogenetic studies have been made in four groups of coal swamp plants. They are the lepidodendrids, *Calamites*, the tree fern *Psaronius*, and *Medullosa*.

Ontogeny in the lepidodendrids has been studied by ANDREWS and MURDY (1958), EGGERT (1961) and LEMOIGNE (1966). The main trunk of the plant developed a large pith and a certain amount of secondary wood. Branching in *Lepidodendron*, *Lepidophloios* and other genera was dichotomous, though in many instances slightly unequal. Each successive dichotomy not only produced axes of smaller diameter, but a smaller pith, less secondary wood and smaller leaves. The ultimate branches were small protosteles devoid of secondary growth and bearing small leaves that resemble those of small *Lycopodium* stems. In former times many specimens representing these growth stages were described as different species.

Similar quantitative tissue reductions have been observed in the main trunks and branches of *Calamites* (EGGERT, 1962), though otherwise the stems of *Calamites* are constructed quite differently from those of the lycopods. Then in the Late Paleozoic tree fern *Psaronius* (MORGAN, 1959) has shown that in passing from the base to the apex of the unbranched trunk an orderly series of changes occurred in the vascular pattern and in arrangement of the fronds.

DELEVORYAS (1955) has described ontogenetic changes in *Medullosa* stems. In a monograph of the American species of the genus, he has reduced the number from 14 to 6, with the rejected species merely being stages in development of other species. *Medullosa noei* is represented by the most complete series of specimens, and much of the information that has been assembled concerning stem ontogeny in this species is doubtlessly applicable to other species. Due to its abundance in coal balls, *Medullosa noei* is the most completely known species of the genus. Its seeds, foliage, petioles, and microsporangiata organs have been identified with reasonable certainty.

Even studies of shoot apices, which were much in vogue for living plants a short time ago, have been possible in a few fossil plants (DELEVORYAS, 1964). A striking instance is a description of a *Calamites* stem tip by MELCHIOR and HALL (1961) where the apical cell is preserved along with several progressively lengthened internodes. A close similarity to the *Equisetum* shoot is noted.

In reinvestigating the development of *Lepidocarpon*, some details of which had not been well understood, BALBACH (1962) found that the "integument" is an outgrowth of the margin of the sporophyll and that it developed along with the megasporangium. The unintegumented sporangia that SCOTT (1901) described, were not young lepidocarps but belonged to different plants.

Some newly described pteridophytic fructifications found in coal balls have broadened our concepts of the morphology of certain plant groups. BAXTER (1963) has described *Calamocarpon*, a calamitalean strobilus that is anatomically similar to *Calamostachys*. This fructification paralleled *Lepidocarpon* in the retention of one large megaspore within the megasporangium, and then by shedding the whole organ as a unit. Thus among the ancient ArthropHYTA we find at least one attempt to "experiment" with seed production, as did some of the ancient lycopods.

Our understanding of the Coenopteridales has expanded, and along with it there has developed a realization of closer relationships to true ferns, largely from observations of fructifications attached to frond parts. There now exists substantial evidence that some species of *Botryopteris*, *Anachoropteris*, *Ankyropteris* and *Zygopteris* are extinct members of the Filicales (EGGERT, 1964; EGGERT and TAYLOR, 1966; EGGERT and DELEVORYAS, 1967).

Remains of the Cordaitales preserved in coal balls have received less attention within recent years than have some other groups. This neglect has not been due to lack of material as stems, foliage, inflorescences and seeds are often

preserved in abundance. Probably the outstanding contribution has been CRIDLAND's (1964) restudy of *Amyelon*, a cordaitan root.

Among the recent contributors to our knowledge of coal ball plants from Great Britain and Europe, HOLDEN (1955), LEMOIGNE (1965) and GALTIER (1967) should be mentioned. In the Soviet Union SNIGIREVSKAYA (1962, 1964) has resumed studies initiated many years ago by Zalessky of the coal ball flora of the Donets Basin. In general, however, European paleobotanists have been more concerned with compressions than with petrifications.

#### THE *Glossopteris* FLORA

The *Glossopteris* flora has been and is currently receiving the attention of paleobotanists located at several places including the Birbal Sahni Institute of Palaeobotany at Lucknow, the University of the Witwatersrand at Johannesburg, and the Institute for Polar Studies at Ohio State University at Columbus. The most extensive of recent accounts of the *Glossopteris* flora is by PLUMBSTEAD (1962) who reports on the fossil plants collected by the Trans-Antarctic Expedition of 1955-1958. The *Glossopteris* flora is by far the largest fossil flora in Antarctica, though plants ranging in age from Devonian to Tertiary have been found there.

SURANGE and SRIVASTAVA (1956) have shown that the characters usually used to distinguish *Glossopteris*, *Gangamopteris*, and *Palaeovittaria* merge when numerous specimens are compared, making separation of these genera difficult or impossible. This leads to the conclusion that they are not natural genera, but represent diversified types camouflaged by similarity in external form. On the basis of cuticular characters Surange and Srivastava arranged 23 named species of the three genera into six groups which may more nearly approximate natural genera. However, they are not formally named.

The fructifications of *Glossopteris* and *Gangamopteris* have attracted much attention following the discoveries announced by PLUMBSTEAD (1952). These plants are now classified in the order Glossopteridales, class Pteridospermopsida, though the fact remains that the pteridospermous nature of the fructifications is only inferred. The true morphology of its fructifications is obscure.

Foliage that resembles *Glossopteris* leaves has been reported by DELEVORYAS (1966) from the Jurassic of southern Mexico. The identifications, however, have not been supported by cuticles or by fructifications. This occurrence of *Glossopteris*-like plants is not only outside the known limits of Gondwanaland, but is a whole system higher in the geologic column than the level at which *Glossopteris* occurs in Gondwanaland. Since the *Glossopteris*-like leaves in Mexico are associated with cycadeoids and other typical Jurassic plants, rather than with typical Gondwanaland genera, they cannot be interpreted as evidence of a Jurassic extension of the *Glossopteris* flora into Mexico.

Any consideration of the *Glossopteris* flora usually brings up the controversial and much discussed idea of continental drift, which in recent years seems to have found increased support in discoveries concerning the structure of the ocean floor, paleomagnetic research and radiometric age determinations (RUNCORN, 1962; HURLEY et al., 1967; HURLEY, 1968). These discoveries, along with the observations on which the theory was originally based, constitute an impressive body of evidence.

Investigators tend to lean more and more toward continental drift as the best explanation of the vegetation of Gondwanaland during the Paleozoic Era (PLUMBSTEAD, 1962; SURANGE, 1966). They claim that drifting continents offer the only explanation in accord with the facts. Less sympathetic are paleobotanists involved with floras of northern latitudes, and with Arctic floras in particular (CHANEY, 1940; AXELROD, 1963; KREMP, 1964; SMILEY, 1967). Northern floras show circumpolar distributional patterns during the Middle and Late Mesozoic and Tertiary that are not essentially different from present day patterns. The main differences are in the relative widths of the tropical and temperate climatic belts at different times. Therefore, before any unqualified acceptance of the drift hypothesis is possible, the conflicting evidence must be reconciled.

#### MESOZOIC FLORAS

Research on Mesozoic floras is widespread, and it is not feasible to attempt a comprehensive survey of them here. Moreover, Mesozoic plants are referred to at several places in connection with other topics.

The Jurassic flora of Yorkshire is one of the greatest of all fossil floras, and a succession of eminent paleobotanists have worked on it for more than a century and a half. As a suitable termination to a long career of research in Mesozoic paleobotany, Professor T. M. Harris is bringing together the voluminous information on this flora. Two projected volumes have already been published (HARRIS, 1961–1964) and two more are scheduled. Harris states emphatically that research on this flora is not finished, and already VAN CITTERT (1966) has found *Angiopteris* in it, which is the first known occurrence of this fern in the fossil state.

DELEVORYAS' (1963) modified interpretation of the inflorescence of *Cycadeoidea* (*Bennettites*) is a splendid example of the desirability of an occasional reexamination and reappraisal of the evidence upon which the subject matter of the science of paleobotany is based. Such reevaluation is especially desirable when the original research was carried out by one individual in an isolated environment. When erroneous interpretations are accompanied by illustrations that appeal to textbook writers, they become still more firmly entrenched. For several years WIELAND'S (1906) restorations of the cycadeoidean "flower" have been accepted without question as authentic, and the figures have been reproduced again and



again without essential modification. Subsequent to the original publication in 1906, nobody had critically examined a "flower" of *Cycadeoidea*.

Wieland's restorations, which are too familiar to require redescription, were obviously based upon the older interpretation of the so-called "flower" of *Williamsonia gigas* that WILLIAMSON (1870) depicted in some detail. This "flower" is shown as having an expanded staminate disc, but no such structure has ever been seen in a silicified cycadeoid. The expanded androecium shown in Wieland's restoration was merely assumed to have existed.

DELEVORYAS (1963, 1968) has recently reexamined the material on which the description of the flower of *Cycadeoidea* was based, and he found that the microsporophylls remained folded in a ring around the central ovuliferous receptacle, and that they formed, in fact, a closed fleshy structure much like that which has been described for *Williamsoniella coronata* from the Jurassic of Yorkshire. So the resemblance to the *Magnolia* flower, which has been so much emphasized by authors during the past, is virtually non-existent. The cycadeoid inflorescence represents an independent evolutionary development among reproductive organs that was quite apart from trends in living plants where it finds no close counterpart. The plants that bore these bizarre inflorescences became extinct at the close of the Mesozoic Era.

Those who have worked with the cycadeoids have become increasingly conscious of the striking peculiarities of these plants. Few paleobotanists regard them as close to the Cycadales and some claim that they are quite unrelated to them.

#### CRETACEOUS AND TERTIARY FLORAS

Recent stratigraphic studies of the Cretaceous and Tertiary sequence in western Greenland (KOCH, 1963, 1964) have thrown new light on some of the Arctic floras described by Oswald Heer (see bibliography by KOCH, 1964) almost a century ago. HEER'S (1874) identification of angiosperm leaves in the Lower Cretaceous Kome Formation, which contains a flora otherwise much like that of the European Wealden, has often been cited as evidence of an early appearance of flowering plants in the Arctic (SEWARD, 1931). KOCH (1964) has concluded that the leaf impressions Heer assigned to the Kome had either fallen from a higher stratum or had been placed with the Kome fossils by mistake. He does not believe that Heer's *Populus primaeva* (and later placed in *Cercidiphyllum*) actually came from the Kome.

Questions have also arisen concerning the stratigraphic relations of some of the beds that Heer assigned to the Upper Cretaceous (KOCH, 1964). Some of them are probably Early Paleocene which contains a large and diversified flora of *Ginkgo*, *Metasequoia* and angiosperms.

In no area of comparable size is there such a complete sequence of plant-

bearing Tertiary deposits that have been so thoroughly investigated as in Japan. The floras of these deposits reveal a series of climatic changes during the Cenozoic Era that correspond in general to those of western North America and western Europe (CHANEY, 1963; TANAI and HUZIOKA, 1967). These changes involved maximum warmth during the Eocene and a corresponding spread of tropical floras to the north. The floras retreated southward during the Oligocene, made a temporary advance northward during the Miocene, but retreated again and for the last time during the Pliocene. This last retreat continued into the Pleistocene ice age. However, the maritime climate of Japan forestalled the extremely low temperatures that prevailed in mid-continental Eurasia and North America. Consequently, the present day floras of Japan have retained more of their Tertiary constituents.

To the Japanese paleobotanists goes the credit for the initial discovery of *Metasequoia* in the Pliocene of their country a few years before it was found still growing in China. The subsequent recognition of this taxodiaceous genus in Cretaceous and Tertiary floras of North America has eliminated much of the confusion that formerly existed regarding the geological history of *Sequoia* and *Taxodium* (CHANEY, 1951).

AXELROD (1965) has shown that floras from different altitudes may show differences that correspond in some respects to those from different latitudes or of different ages. An example is the Middle Miocene Trapper Creek flora of southern Idaho (AXELROD, 1964) which can be quite satisfactorily dated from the position of the beds. On the basis of a high percentage of montane conifers, the flora is estimated to have flourished at an altitude of about 3,000 ft. Were it a lowland flora at the same latitude and with the same conifer content, it would be assigned to the Upper Miocene. The Trapper Creek flora is an example of the complications that may be encountered when assessing the age of almost any Tertiary flora. It shows the distinct advantage in possessing large collections.

Some of the most notable advances in Tertiary paleobotany during recent decades have been made from studies of fossil fruits and seeds. The outstanding contribution has been REID and CHANDLER's (1953) *London Clay Flora*, a magnificently illustrated work that included material from the Island of Sheppey and Hearne Bay at the mouth of the Thames River. More recently Miss Chandler has extended the investigation to include other parts of southern England (CHANDLER, 1960-1964). SCOTT (1954) has described similar seeds from the Clarno Formation of Oregon. Both of these floras reflect the maximum spread of Eocene tropical floras into northern latitudes. CHESTERS (1957) has described Miocene seeds and fruits from an island in Lake Victoria in Kenya which represent the only known Tertiary flora in southern Africa. Mention should be made of KIRCHHEIMER's (1957) book *Die Laubgewächse der Braunkohlenzeit* which brings together the results of prolonged research on the seeds and fruits of the German Tertiary Braunkohle.

Fruits and seeds are valuable supplements to leaf impressions in Tertiary floras, a fact that has been long recognized. The late BROWN (1935) made extensive use of them in his studies of western American Tertiary floras. Identification, however, often presents problems, especially if they represent tropical floras with families and genera with which one is not intimately familiar. Very few herbaria have fruit and seed material adequate for this purpose.

#### THE PROBLEM OF ORIGIN AND ANCESTRY OF ANGIOSPERMS

This problem appears to be no nearer solution than it was a century ago. If anything, its complexities and uncertainties have increased.

It has been suggested many times that angiosperms probably originated during the latter part of the Paleozoic Era (presumably the Permian), which would allow time for the diversification of the group that is exhibited by the variety of leaves displayed in Cretaceous rocks. Two recent protagonists of this view are D. J. Axelrod and E. Plumbstead, both using separate lines of evidence. AXELROD (1959, 1961) has proposed that angiosperms originated in moist tropical uplands where they remained until much later. Then about mid-Mesozoic time they descended into the lowlands, and from there they spread to all habitable parts of the earth. This theory of course has no direct support in the fossil record. The assumption is that the upland habitats were not suitable for preservation of fossils, and this is given as the reason for the almost total lack of unquestionable remains of pre-Cretaceous angiosperms.

The main obstacle to this theory is that if angiosperms originated so early, why did they remain in seclusion in their highland habitats for so long. Places like the broad Jurassic deltas of Yorkshire would certainly have been ideal sites for angiosperms to have gained footholds had they been in existence then. However, no traces of angiosperms, not even pollen, have been found in the large well preserved Yorkshire Jurassic flora.

PLUMBSTEAD (1962, p.124) would derive angiosperms from the glossopterids of Gondwanaland. She says: "It has been shown that the *Glossopteridae* fulfills almost every condition, and possessed almost every quality suggested by paleobotanists as either necessary or desirable in the ancestral stock of angiosperms". The basis for this statement is the stalked, presumably two-valved bisexual fructification that was found on the midribs of some specimens of *Glossopteris*. As it was interpreted the fructification is close to the hypothetical "gonophyll" that MELVILLE (1960) substitutes for the carpel in floral evolution.

Whether *Glossopteris* actually had anything to do with angiosperm evolution is entirely problematic. Unfortunately, *Glossopteris* fructifications are preserved only as imprints and none have been found that show the morphology of the organs in an unequivocal manner. Until they are found, it remains impossible to recognize

in them any characteristics whereby *Glossopteris* can be looked upon as a pro-angiosperm.

Any hypothesis of pre-Cretaceous origin of angiosperms meets firm opposition from palynologists. They point out the total absence of angiosperm pollen below the upper Lower Cretaceous (SCOTT et al., 1960; BRENNER, 1963). They also insist that the few and scattered angiosperm-like leaves that have occasionally been reported from Lower Cretaceous horizons do not necessarily prove the existence of Lower Cretaceous angiosperms, but they may be some kind of advanced gymnosperm (possibly Gnetales). This, however, needs substantiation, and it harkens back to the old belief that each class of living plants originated from that class directly below it in the scale of morphological complexity. Be what it may, the absence of recognizable angiospermous pollen below the uppermost Lower Cretaceous should certainly be heeded. Of course no one knows what the pollen of the ancestral angiosperms might have looked like, and it is not impossible that it has been collected, examined, and described many times without having been recognized.

The lack of positive recognition of angiospermous pollen in pre-Cretaceous rocks is only one facet of the whole problem of angiosperm origin. Although botanists as a rule have no difficulty recognizing the living members of this class, and the myriads of leaf impressions and pieces of silicified wood in Late Cretaceous and Tertiary rocks are equally diagnostic, the "proangiosperms" of earlier periods present problems that are entirely different. The main one, and one that is even more significant than the disconnected state of the fossils, is that angiosperms themselves show so few characters that are constant throughout the class or are confined exclusively to them. Angiosperms of course are "plants with flowers" but we do not know how the flower originated nor are we unanimous concerning its basic morphology. Least of all do we know what kind of organ preceded it. Almost the only distinctive features shown by angiosperms are the peculiar embryo sac and double fertilization, and even these show great variation within the class. If we had some means of finding out when and in what plants these phenomena first came into existence, we would make a long stride toward solution of the problem.

Following this very brief analysis of the situation, a logical and reasonable question is whether there is any chance that the fossil record can contribute materially toward the solution of the problem of angiosperm ancestry and origin. The possibilities appear bleak but we do not know, and the search will go on.

#### FOSSILIZED WOODS

Petrified (mineral infiltrated) woods present difficult problems to paleobotanists, and for that reason they are often ignored. For woods older than

Cretaceous, which belong mostly to extinct gymnosperms, special means of classification usually have to be devised, and the suffix “-oxylon” is often part of the generic name. It is usually difficult to compare these with living woods. The problems presented by Tertiary and Quaternary woods are usually different because they may represent genera or at least families still living. For their study a large collection of living woods is essential just as a herbarium is necessary for the study of leaf impressions of these periods.

The literature on fossil wood is extensive. Much of it is very old, and the taxonomy is often confusing. Identifications of genera and species vary widely due to different states of preservation and to the knowledge of the investigators. It is rare that the wood, the foliage and the reproductive organs of the same plant can be recognized. Paradoxical as it may seem, paleobotanists have been more successful in bringing together detached organs of Paleozoic plants than those of later times.

Of special interest is a large group of Mesozoic gymnosperms with wood showing combined characteristics of the Araucarineae and the Abietineae (the latter being a term formerly used for most of the non-araucarioid conifers). The late Professor E. C. Jeffrey aptly referred to these as the “transition conifers” (JEFFREY, 1912–1913). KRÄUSEL (1949) has designated them the “Protopinaceae”. VOGELLEHNER (1967), however, correctly points out that the group is not a natural one because it includes several phyletic lines.

VOGELLEHNER (1964) has also attempted a taxonomic treatment of the older woods of the *Dadoxylon* complex that are mostly assumed to be cordaitan. He maintains that such genera as *Araucarioxylon*, *Pinites*, *Cordaioxylon*, *Cordaites* and *Araucarites* should be abandoned in favor of *Dadoxylon*.

LEPEKHINA and YATSUENKO-KHMELEVSKY (1966) have invented a revised classification of the pycnoxylic Paleozoic woods (including those from the Devonian). They would separate all woods with preserved pith and primary wood (i.e., *Callixylon*) from those in which secondary wood alone is present (i.e., *Desmoporoxyton*). Due to the limited number of diagnostic characters often displayed by secondary wood, this may be a logical course to pursue. Their work represents an attempt to alleviate the confusion that now exists in the nomenclature and taxonomy of fossil woods, but much more remains to be done.

Due to the influence of the late Professor Birbal Sahni, the fossil woods of India have received much attention. KRÄUSEL et al. (1961) have summarized the woods from the Late Paleozoic that show primary structure. BOSE and DAS SAH (1954) have reexamined the Jurassic age *Homoxyton rajmahalense* and have concluded that it is not a vesselless angiosperm but a cycadeoid. They placed it in a new genus, *Sahnioxylon*. PRAKASH (1960) has reviewed the silicified flora of the Deccan Intertrappean Series. Though best known for its flowers, fruits and seeds, the flora also contains trunks of palms and dicotyledonous trees. The largest display of silicified tree trunks, however, occurs in the Cuddalore Sandstone,

of Late Tertiary age, in South India. They represent several families but those best represented are the Dipterocarpaceae, Euphorbiaceae and Leguminosae.

The Mesozoic woods of North Africa have lately been investigated by Boureau and other French paleobotanists (see bibliography by BATTON, 1965). The Permian woods of South America have received attention from KRÄUSEL and DOLIANITI (1958), and SCHÖNFELD (1947) has studied some of the later woods. For accounts of central European woods the numerous publications of GREGUSS (1961, 1967) should be consulted. PRAKASH and BARGHOORN (1961) have described several Miocene age woods from the Columbia Basalts of Washington State.

#### REFERENCES

- ABELSON, P. H., 1956. Paleobiochemistry. *Sci. Am.*, 195: 83–92.
- ANANEV, A. R., 1954. On the Lower Devonian flora of the southwestern part of western Siberia. *Vopr. Geol. Azii.*, 1: 287–324 (in Russian).
- ANDREWS, H. N. and MURDY, W. H., 1958. Lepidophloios – and ontogeny in arborescent lycopods. *Am. J. Botany*, 45: 552–560.
- ARBEITSGRUPPE "CUTICULAE" DER C.I.M.P., 1964. Entwurf für eine einheitliche diagnostische Beschreibung von Kutikulen. *Fortschr. Geol. Rheinland Westfalen*, 12: 11–24.
- ARNOLD, C. A., 1929. The genus *Callixylon* from the Upper Devonian of central and western New York. *Papers Mich. Acad. Sci.*, 11: 1–50.
- ARNOLD, C. A., 1939. Observations on fossil plants from the Devonian of eastern North America, 4. *Contrib. Museum Paleontol. Univ. Mich.*, 5: 271–314.
- AXELROD, D. I., 1959. Evidence for a tropical center of angiosperm evolution. *Bull. Geol. Soc. Am.*, 70: 1707.
- AXELROD, D. I., 1961. How old are the angiosperms? *Am. J. Sci.*, 259: 447–459.
- AXELROD, D. I., 1963. Fossil floras suggest stable, not drifting, continents. *J. Geophys. Res.*, 68: 3257–3263.
- AXELROD, D. I., 1964. The Miocene Trapper Creek flora of southeastern Idaho. *Univ. Calif. (Berkeley) Publ. Geol. Sci.*, 51: 1–181.
- AXELROD, D. I., 1965. A method for determining the altitude of Tertiary floras. *Palaeobotanist*, 14: 144–171.
- BALBACH, M., 1962. Observations on the ontogeny of *Lepidocarpon*. *Am. J. Botany*, 49: 948–989.
- BANKS, H. P., 1966. Devonian flora of New York State. *Empire State Geogram*, 4: 11–24.
- BANKS, H. P., 1967. Current status of Psilophytales. *Am. J. Botany*, 54: 650.
- BARGHOORN, E. S. and SCHOPF, J. W., 1966. Microorganisms three million years old, from the Precambrian of South Africa. *Science*, 152: 758–763.
- BARGHOORN, E. S. and TYLER, S. A., 1965. Microorganisms from the Gunflint Chert. *Science*, 147: 563–577.
- BARTHEL, M., 1962. Epidermisuntersuchungen an einigen inkohlten Pteridospermenblättern des Oberkarbons und Perms. *Geologie*, 11: 1–140.
- BARTHEL, M., 1964. Coniferen- und Cordaiten Reste aus dem Rotliegenden des Döhlener Beckens. *Geologie*, 13: 60–89.
- BARTHEL, M., KOVAČEK, Z. and RÜFFLE, L., 1966. Symplocaceen-Blätter im Eozän des Geisaltales. *Monatsber. Deut. Akad. Wiss. Berlin*, 8: 354–359.
- BATTON, G., 1965. Contribution à l'étude anatomique et biostratigraphique de la flore du Continental Intercalaire Saharien. Paléobotanique Saharienne. *Centre Natl. Rech. Sci. Géol.*, 6: 7–96.
- BAXTER, R. W., 1963. *Calamocarpon insignis*, a new genus of heterosporous petrified calamitean cones from the American Carboniferous. *Am. J. Botany*, 50: 469–476.

- BECK, C. B., 1960a. Connection between *Archaeopteris* and *Callixylon*. *Science*, 131: 1524–1525.
- BECK, C. B., 1960b. The identity of *Archaeopteris* and *Callixylon*. *Brittonia*, 12: 351–368.
- BECK, C. B., 1962. Reconstruction of *Archaeopteris*, and further consideration of its phylogenetic position. *Am. J. Botany*, 49: 373–382.
- BECK, C. B., 1967. *Eddyia sullivanensis* gen. et sp. nov., a plant of gymnospermous morphology from the Upper Devonian of New York. *Palaeontographica, Abt. B*, 121: 1–22.
- BELL, W. A., 1944. Carboniferous rocks and fossil floras of Nova Scotia. *Geol. Surv. Can., Mem.*, 238: 1–119.
- BENSON, M., 1914. *Sphaerostoma ovale*, a Lower Carboniferous ovule from Pettycur, Fifeshire, Scotland. *Trans. Roy. Soc. Edinburgh*, 50: 1–15.
- BOSE, M. N. and DAS SAH, S. C., 1954. On *Sahnioxylon rajmahalense*, a new name for *Homoxylon rajmahalense*, and *S. andrewsii*, a new species of *Sahnioxylon* from Amrapara in the Rajmahal Hills, Bihar. *Palaeobotanist*, 3: 1–8.
- BOUREAU, E. (Editor), 1956–1966. *World Report on Palaeobotany, I–VI*. Utrecht, 898 pp.
- BRENNER, G. J., 1963. The spores and pollen of the Potomac Group of Maryland. *Maryland Board Nat. Resources, Dept. Geol., Mines Water Resources, Bull.*, 25: 1–207.
- BROWN, R. W., 1935. Miocene leaves, fruits and seeds from Idaho, Oregon and Washington. *J. Paleontol.*, 9: 572–587.
- CARLUCCIO, L. M., HUEBER, F. M. and BANKS, H. P., 1966. *Archaeopteris macilenta*, anatomy and morphology of its frond. *Am. J. Botany*, 53: 719–730.
- CHALONER, W. J. and PETTIT, J. M., 1964. A seed megaspore from the Devonian of Canada. *Palaeontology*, 7: 29–36.
- CHANDLER, M. E. J., 1960–1964. *The Lower Tertiary Floras of Southern England, I–IV*. British Museum of Natural History, London, 847 pp.
- CHANEY, R. W., 1940. Bearing of forests on theory of continental drift. *Sci. Monthly*, 51: 489–499.
- CHANEY, R. W., 1951. A revision of fossil *Sequoia* and *Taxodium* in western North America based on the recent discovery of *Metasequoia*. *Trans. Am. Phil. Soc.*, 40: 171–263.
- CHANEY, R. W., 1963. Introduction to Tertiary floras of Japan. Miocene floras. *Collaborating Assoc. Commem. 80th Anniv. Geol. Soc. Japan, Tokyo*, pp.3–8.
- CHESTERS, K. I. M., 1957. The Miocene flora of Rusinga Island, Lake Victoria, Kenya. *Palaeontographica, Abt. B*, 101: 30–71.
- CORSIN, P., 1951. Flore fossile du bassin houiller de la Sarre et de la Lorraine, 4. Pécopteridées. *Étude Gîtes Min. France*, 1951: 177–370.
- CRIDLAND, A. A., 1964. *Amyelon* in American coal-balls. *Palaeontology*, 7: 186–209.
- CROOKALL, R., 1959–1964. Fossil plants of the Carboniferous rocks of Great Britain. *Geol. Surv. Gt. Brit., Mem. Geol. Surv. Gt. Brit., Palaeontology*, 4: 85–354.
- DABER, R., 1959. Die Mittel-Visé Flora der Tiefbohrungen von Doberlug-Kirchhain. *Geologie*, 26: 1–83.
- DANZE, J. E., 1956. *Contribution à l'Étude des Sphénoptéridées. Les Fougères sphénoptéridiennes du Bassin houiller du nord de la France. Étude géologique pour l'Atlas topographique souterraine*. Serv. Géol., H.B.N.P.C.-I. Flore Fossile, 2: 568 pp.
- DANZE-CORSIN, P., 1953. *Contribution à l'Étude des Marioptéridées. Les Mariopteris du nord de la France. Étude géologique pour l'Atlas topographique souterraine*. Serv. Géol. H.B.N.P.C.-I. Flore fossile, 1: 269 pp.
- DAWSON, J. W., 1888. *The Geological History of Plants*. Appleton, New York, N.Y., 290 pp.
- DELEVORYAS, T., 1955. The Medullosae—structure and relationships. *Palaeontographica, Abt. B*, 97: 14–167.
- DELEVORYAS, T., 1963. Investigations of North American cycadeoids: cones of *Cycadeoidea*. *Am. J. Botany*, 50: 45–52.
- DELEVORYAS, T., 1964. Ontogenetic studies of fossil plants. *Phytomorphology*, 14: 299–314.
- DELEVORYAS, T., 1966. Hunting fossil plants in Mexico. *Discovery*, 2(1): 7–13.
- DELEVORYAS, T., 1968. Investigations of North American cycadeoids: structure, ontogeny and phylogenetic consideration of cones of *Cycadeoidea*. *Palaeontographica, Abt. B*, 121: 122–133.
- DILCHER, D. L., 1963. Cuticular analysis of Eocene leaves of *Ocotea obtusifolia*. *Am. J. Botany*, 50: 1–8.

- DOUBINGER, J., 1956. Contribution à l'étude des flores autuno-stéphaniennes. *Mém. Soc. Géol. France*, 35: 1–180.
- EGGERT, D. A., 1961. The ontogeny of Carboniferous arborescent *Lycopside*. *Palaeontographica, Abt. B*, 108: 43–92.
- EGGERT, D. A., 1962. The ontogeny of Carboniferous arborescent *Sphenopsida*. *Palaeontographica, Abt. B*, 110: 99–127.
- EGGERT, D. A., 1964. The question of the phylogenetic position of the Coenopteridales. *Mem. Torr. Bot. Club*, 21: 38–57.
- EGGERT, D. A. and DELEVORYAS, T., 1967. Studies of Paleozoic ferns: *Sermaya*, gen. nov. and its bearing on filicinean evolution in the Paleozoic. *Palaeontographica, Abt. B*, 120: 169–179.
- EGGERT, D. A. and TAYLOR, T. N., 1966. Studies of Paleozoic ferns: on the genus *Tedelea* gen. nov. *Palaeontographica, Abt. B*, 118: 52–73.
- EICHE, R., 1954. Elektronmikroskopische Untersuchungen an verkieselten Coniferen. *Palaeontographica, Abt. B*, 97: 36–46.
- FAIRON, M., 1967. L'*Asteroxylon elberfeldense* KRÄUSEL et WEYLAND porte-t-il des axes terminaux du type *Hostimella hostimensis* POTONIÉ à Bernard? *Ann. Soc. Géol. Belg., Mém.*, 4(10): 1–30.
- FRENGUELLI, J., 1951. Floras Devonian de la Precordillera de San Juan. Nota preliminar. *Rev. Asoc. Geol. Arg.*, 6: 83–94.
- GORDON, W. T., 1941. *Salpingostoma dasu*—a new Carboniferous seed from East Lothian. *Trans. Roy. Soc. Edinburgh*, 60: 427–464.
- GREGUSS, P., 1961. Permische fossile Hölzer aus Ungarn. *Palaeontographica, Abt. B*, 109: 131–146.
- GREGUSS, P., 1967. Fossil gymnosperm woods in Hungary from the Permian to the Pliocene. *Akad. Kiado, Budapest*, 1967: 1–136.
- GRIERSON, J. D. and BANKS, H. P., 1963. Lycopods of the Devonian of New York State. *Palaeontol. Am.*, 4: 217–295.
- HARRIS, T. M., 1961–1964. *The Jurassic Flora of Yorkshire*. British Museum of Natural History, London, 1: 212 pp; 2: 191 pp.
- HEER, O., 1874. Nachträge zur Miozänen Flora Grönlands. *K. Svenska Vetensk. Akad. Handl.*, 13: 1–29.
- HØEG, O. A., 1942. The Downtonian and Devonian flora of Spitzbergen. *Norg. Svalb. Ishavs-Und. Skrifter*, 83: 1–228.
- HOLDEN, H. S., 1955. On the occurrence of secondary thickening in Paleozoic ferns. *J. Linn. Soc. London (Botany)*, 55: 271–278.
- HOPPING, C. A., 1956. On a specimen of "*Psilophyton robustius*" DAWSON from the Lower Devonian of Canada. *Proc. Roy. Soc. Edinburgh, Sect. B.*, 66: 10–28.
- HUEBER, F. M. and BANKS, H. P., 1967. *Psilophyton princeps*: the search for organic connection. *Taxon*, 16: 81–85.
- HUEBER, F. M. and GRIERSON, J. D., 1961. On the occurrence of *Psilophyton princeps* in the early Upper Devonian of New York. *Am. J. Botany*, 48(6): 473–479.
- HURLEY, P. M., 1968. The confirmation of Continental Drift. *Sci. Am.*, 218: 53–64.
- HURLEY, P. M., DE ALMEIDA, F. F., MELCHER, G. C., CORDANI, U. G., RAND, J. R., KAWASHITA, K., VANDOROS, P., PINSON JR., W. H. and FAIRBAIRN, H. W., 1967. Test of Continental Drift by comparison of radiometric ages. *Science*, 157: 495–500.
- JEFFREY, E. C., 1912–1913. The history, comparative anatomy and evolution of the *Araucarioxylon* type, I–IV. *Proc. Am. Acad. Arts Sci.*, 48: 529–571.
- KIDSTON, R., 1923–1925. Fossil plants of the Carboniferous rocks of Great Britain. *Geol. Surv. Gt. Brit., Mem. Geol. Surv. Gt. Brit., Palaeontology*, 2: 1–681.
- KIDSTON, R. and LANG, W. H., 1917. On Old Red Sandstone plants showing structure, from the Rhynie Chert bed, Aberdeenshire, 1. *Rhynia gwynne-vaughani*, KIDSTON and LANG. *Trans. Roy. Soc. Edinburgh*, 51: 761–784.
- KIDSTON, R. and LANG, W. H., 1921. On Old Red Sandstone plants showing structure, from the Rhynic Chert bed, Aberdeenshire, 5. Restorations of the vascular cryptogams, and discussion of their bearing on the general morphology of the Pteridophyta and the origin of the organization of land-plants. *Trans. Roy. Soc. Edinburgh*, 52: 831–854.
- KIRCHHEIMER, F., 1957. *Die Laubgewächse der Braunkohlenzeit*. Wilhelm Knapp, Halle, 783 pp.



- KOCH, B. C., 1963. Fossil plants from the Lower Paleocene of Agtdalen area, central Nügssuaq Peninsula, northwest Greenland. *Medd. Grønland*, 172: 1–120.
- KOCH, B. E., 1964. Review of fossil floras and nonmarine deposits of west Greenland. *Geol. Soc. Am., Bull.*, 75: 535–548.
- KRÄUSEL, R., 1949. Die fossilen Koniferen-Hölzer. II. Kritische Untersuchungen zur Diagnostik lebender und fossiler Koniferen-Hölzer. *Palaeontographica, Abt. B*, 89: 83–203.
- KRÄUSEL, R. und DOLIANITI, E., 1958. Gymnospermenhölzer aus dem Paläozoikum Brasiliens. *Palaeontographica, Abt. B*, 104: 115–137.
- KRÄUSEL, R. und WEYLAND, H., 1926. Beiträge zur Kenntnis der Devonflora, 2. *Abhandl. Senckenberg. Naturforsch. Ges.*, 40: 115–155.
- KRÄUSEL, R. und WEYLAND, H., 1935. Neue Pflanzenfunde im Rheinischen Unterdevon. *Palaeontographica, Abt. B*, 81: 171–190.
- KRÄUSEL, R. und WEYLAND, H., 1950. Kritische Untersuchungen zur Kutikular-Analyse tertiärer Blätter, 1. *Palaeontographica, Abt. B*, 91: 7–92.
- KRÄUSEL, R. und WEYLAND, H., 1954. Kritische Untersuchungen zur Kutikular-Analyse tertiärer Blätter, 2. *Palaeontographica, Abt. B*, 96: 106–163.
- KRÄUSEL, R. und WEYLAND, H., 1960. Drei neue Pflanzen aus dem Devon. *Palaeontographica, Abt. B*, 107: 65–82.
- KRÄUSEL, R., MAITHY, P. K. and MAHESHWARI, H. K., 1961. Gymnospermous woods with primary structures from Gondwana rocks—a review. *Palaeobotanist*, 10: 97–107.
- KREMP, G. D. W., 1964. Antarctica, the climate of the Tertiary, and a possible cause of our ice age. In: R. J. ADIE (Editor), *Arctic Geology—Proc. Intern. Symp. Antarctic Geology, 1st, Cape Town, 1963*, pp. 736–746.
- KRISHTOFOVISH, A., 1953. Discovery of lycopodiaceous plants in the Precambrian of eastern Siberia. *Dokl. Akad. Nauk S.S.S.R.*, 91: 1377–1379 (in Russian).
- LECLERCQ, S., 1940. Contributions à l'étude de la flore du Dévonien de Belgique. *Acad. Roy. Belg., Classe Sci., Mém.*, 12: 1–65.
- LECLERCQ, S., 1951. Étude morphologique et anatomique d'une fougère du Dévonien Supérieur: le *Rhacophyton zygopteroides*. *Mém. Soc. Géol. Belgique*, 9: 1–62.
- LECLERCQ, S. and BANKS, H. P., 1962. *Pseudosporochnus nodosus* sp. nov., a Middle Devonian plant with cladoxylalean affinities. *Palaeontographica, Abt. B*, 110: 1–34.
- LECLERCQ, S. and SCHWEITZER, H. J., 1965. *Calamophyton* is not a sphenopsid. *Bull. Acad. Roy. Belg., Sér. 5*, 60: 1395–1403.
- LEDRAN, C., 1962. Sur la structure anatomique de quelques feuilles de cordaites. *Bull. Soc. Bot. France*, 109: 63–75.
- LEMOIGNE, Y., 1965. La moelle et son évolution en un chyme chez les Lépidophytales arborescentes du Paléozoïque. *Ann. Sci. Nat. (Botan.)*, 6: 315–338.
- LEMOIGNE, Y., 1966. Les tissus vasculaires et leur histogenèse chez les Lépidophytales arborescentes du Paléozoïque. *Ann. Soc. Nat. Botan.*, 12, 7: 445–474.
- LEPEKHINA, V. G. and YATSENKO-KHMELEVSKY, A. A., 1966. Classification and nomenclature of woods of Paleozoic pycnoxylic plants. *Taxon*, 15: 66–70.
- LONG, A. G., 1960a. On the structure of "*Calymmatotheca kidstoni*" CALDER (emend) and "*Genomosperma latens*" gen. et sp. nov. from the Calciferous Sandstone Series of Berwickshire. *Trans. Roy. Soc. Edinburgh*, 64: 29–44.
- LONG, A. G., 1960b. On the structure of "*Samaropsis scotica*" CALDER (emend) and "*Eurystoma anglare*" gen. et sp. nov., petrified seeds from the Calciferous Sandstone Series of Berwickshire. *Trans. Roy. Soc. Edinburgh*, 64: 261–280.
- LONG, A. G., 1960c. "*Stannostoma huttonense*" gen. et sp. nov.—a pteridosperm seed and cupule from the Calciferous Sandstone Series of Berwickshire. *Trans. Roy. Soc. Edinburgh*, 64: 201–215.
- LYON, A. G., 1964. Probable fertile region of *Asteroxylon mackiei* K. and L. *Nature*, 203: 1082–1083.
- MAMAY, S. H., 1954. Two new plant genera of Pennsylvanian age from Kansas coal balls. *U.S., Geol. Surv., Profess. Papers*, 254D: 81–93.
- MEINSCHEIN, W. G., 1965. Sudan Formation: organic extracts of Early Precambrian rocks. *Science*, 150: 601–605.

- MELCHIOR, R. C. and HALL, J. W., 1961. A calamitean shoot apex from the Pennsylvanian of Iowa. *Am. J. Botany*, 48: 811–815.
- MELVILLE, R., 1960. A new theory of the angiosperm flower. *Nature*, 188: 14–18.
- MASLOV, V. P., 1957. A newly discovered reproductive organ of a Devonian plant. *Dokl. Akad. Nauk U.S.S.R.*, 114: 417–418 (in Russian).
- MENENDEZ, C. A., 1965. *Archaeosigillaria conferta* (FRENGUELLI) nov. comb. del Devonico de la Quebrada de la Chavela, San Juan. *Ameghiniana*, 4: 67–69.
- MERKER, H., 1958. Zum fehlenden Gliede der Rhynienflora. *Botan. Notiser*, 111: 608–618.
- MERKER, H., 1959. Analyse der Rhynien-Basis und Nachweis der Gametophyten. *Botan. Notiser*, 112: 441–452.
- MEYEN, S. V., 1963. Leaf anatomy and nomenclature of Angarian cordaites. *Paleontol. Zh.*, 3: 96–107 (in Russian).
- MIKI, S., 1941. On the change of flora in eastern Asia since Tertiary Period. *Japan J. Botany*, 11: 237–303.
- MORGAN, J., 1959. The morphology and anatomy of American species of the genus *Psaronius*. *Illinois Biol. Monograph*, 27: 1–108.
- NEUBURG, M., 1948. Late Paleozoic floras of the Kutznetsk Basin. *Paleobotanika (Akad. Nauk S.S.S.R. Moscow)*, 12(2): 1–342 (in Russian).
- NEUBURG, M., 1965. Permian flora of Pechora Basin. Pt. III. *Tr. Akad. Nauk S.S.S.R.*, 116: 1–144 (in Russian).
- ORRHILL, J., 1959. Ein Landpflanzenfund im mittelböhmisches Ordovizium. *Geologie*, 5: 535–541.
- PANT, D. D., 1962. The gametophyte of the Psilophytales. *Proc. Summer School Botany, Darjeeling, June 2–15, 1960*: 276–301.
- PETTIT, J. M., 1964. Two heterosporous plants from the Upper Devonian of North America. *Bull. Brit. Museum*, 10: 83–92.
- PETTIT, J. M. and BECK, C. B., 1967. Seed from the Upper Devonian. *Science*, 156: 1727–1729.
- PETTIT, J. M. and BECK, C. B., 1968. *Archaeosperma arnoldii*—a cupulate seed from the Upper Devonian of North America. *Contrib. Museum Paleontol. Univ. Mich.*, 22: 139–154.
- PLUMBSTEAD, E., 1952. Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves. *Trans. Geol. Soc. S. Africa*, 55: 281–328.
- PLUMBSTEAD, E., 1962. *Fossil Floras of Antarctica. Trans-Antarctic Exped. Comm. (1955–58) London, Rept.*, 9: 1–154.
- PLUMBSTEAD, E., 1967. A general review of the Devonian fossil plants found in the Cape System of South Africa. *Palaeontol. Africana*, 10: 1–83.
- PRAKASH, U., 1960. A survey of the Deccan intertrappean flora of India. *J. Paleontol.*, 34: 1027–1040.
- PRAKASH, U. and BARGHOORN, E. S., 1961. Miocene woods from the Columbia basalts of central Washington, 2. *J. Arnold Arboret.*, 42: 347–358.
- REID, E. M. and CHANDLER, M. E. J., 1933. *The London Clay Flora*. British Museum (Natural History), London, 561 pp.
- REMY, W. and REMY, R., 1959. *Pflanzenfossilien*. Akademie Verlag, Berlin, 285 pp.
- ROSELT, G., 1962. Über die ältesten Landpflanzen und eine mögliche Landpflanze aus dem Ludlow Sachsens. *Geologie*, 3: 320–333.
- RAMANUJAM, C. G., 1960. Silicified woods from Tertiary rocks of south India. *Palaeontographica, Abt. B*, 106: 101–140.
- RUNCORN, S. K., 1962. *Continental Drift*. Acad. Press, New York, N.Y., 338 pp.
- SCHMID, R., 1967. Electron microscopy of wood of *Callixylon* and *Cordaites*. *Am. J. Botany*, 54: 720–729.
- SCHÖNFELD, G., 1947. Hölzer aus dem Tertiär von Kolumbien. *Abhandl. Senckenberg. Naturforsch. Ges.*, 475: 1–53.
- SCHOPF, J. M., 1962. A preliminary report on plant remains and coal of the sedimentary section in the central range of the Horlick Mountains, Antarctica. *Ohio State Univ., Inst. Polar Studies, Rept.*, 2: 1–61.
- SCHOPF, J. W. and BARGHOORN, E. S., 1967. Alga-like fossils from the Early Precambrian of South Africa. *Science*, 156: 508–511.

- SCHOPF, J. M., MENCHER, E., BOUCOT, A. J. and ANDREWS, H. N., 1966. Erect plants in the Early Silurian of Maine. *U.S., Geol. Surv., Profess. Papers*, 550-D: 69–75.
- SCOTT, D. H., 1901. On the structure and affinities of fossil plants from the Palaeozoic rocks, 4. The seed-like fructifications of *Lepidocarpon*. *Phil. Trans. Roy. Soc. London, Ser. B*, 194: 291–333.
- SCOTT, R. A., 1954. Fossil nuts and seeds from the Eocene Clarno Formation of Oregon. *Palaeontographica, Abt. B*, 96: 66–97.
- SCOTT, R. A., BARGHOORN, E. S. and LEOPOLD, E., 1960. How old are the angiosperms? *Am. J. Sci.*, 258A: 284–299.
- SEWARD, A. C., 1931. *Plant Life through the Ages*. Macmillan/Univ. Press, London, 601 pp.
- SIEGEL, S. M. and SEIGEL, B. Z., 1968. A living organism morphologically comparable to the Precambrian *Kakabekia*. *Am. J. Botany*, 55: 684–687.
- SMILEY, C. J., 1967. Paleoclimatic interpretations of some Mesozoic floral sequences. *Bull. Am. Assoc. Petrol. Geologists*, 51: 849–863.
- SMITH, D. L., 1959. *Geminitheca scotica* gen. et sp. nov.: a pteridosperm from the Lower Carboniferous of Dunbartonshire. *Ann. Botany (London)*, 23: 477–491.
- SMITH, D. L., 1964. The evolution of the ovule. *Biol. Rev.*, 39: 137–159.
- SNIGIREVSKAYA, N. S., 1962. On the morphology and taxonomy of the genus *Botryopteris*. *Paleontol. Zh.*, 2: 122–132 (in Russian).
- SNIGIREVSKAYA, N. S., 1964. An anatomical study of the plant remains from the Donets coal-balls, 1. *Lepidodendraceae*. *Tr. Botan. Inst., Akad. Nauk S.S.S.R., Ser. 8, Paleobotan.*, 5: 1–37 (in Russian with English summary).
- SURANGE, K. R., 1966. Indian fossil pteridophytes. *Council Sci. Ind. Res., New Delhi, Botan. Monograph*, 14: 1–209.
- SURANGE, K. R. and SRIVASTAVA, P. N., 1956. Studies in the *Glossopteris* flora of India, 5. Generic status of *Glossopteris*, *Gangamopteris*, and *Palaeovittaria*. *Palaeobotanist*, 2: 9–17.
- TACHIBANA, K., 1950. Devonian plants first discovered in Japan. *Proc. Japan Acad.*, 26: 54–58.
- TANAI, T. and HUZIOKA, K., 1967. Climatic implications of Tertiary floras in Japan. In: *Tertiary Correlations and climatic Changes in the Congr. Pacific—Pacific Sci. Assoc., 11th, Tokyo, 1966*, pp. 89–94.
- THOMAS, N. H., 1925. The Caytoniales: a new group of angiospermous plants from the Jurassic rocks of Yorkshire. *Phil. Trans. Roy. Soc. London, Ser. A*, 213: 299–363.
- VAN CITTERT, J. H. A., 1966. New and noteworthy Jurassic ferns from Yorkshire. *Acta Botan. Neerl.*, 15: 284–289.
- VOGELLEHNER, D., 1964. Zur Nomenklatur der fossilen Holzgattung *Dadoxylon* ENDLICHER. *Taxon*, 13: 233–237.
- VOGELLEHNER, D., 1967. Prodomus zu einer Monographie der Protopinaceae. 1. Die protopinoïden Hölzer der Trias. *Palaeontographica, Abt. B*, 121: 30–51.
- WAGNER, R. H., 1966. Palaeobotanical dating of Upper Carboniferous folding phases in north-west Spain. *Mem. Inst. Geol. Minero Espana*, 66: 1–66.
- WALTON, J., 1949. *Calathospermum scoticum*—an ovuliferous fructification of Lower Carboniferous age from Dunbartonshire. *Trans. Roy. Soc. Edinburgh*, 61: 719–728.
- WALTON, J., 1953. The evolution of the ovule in pteridosperms. *Advan. Sci.*, 10: 223–230.
- WIELAND, C. R., 1906. American fossil cycads, 1. *Carnegie Inst. Washington Publ.*, 34: 284 pp.
- WILLIAMSON, W. C., 1870. Contribution toward the history of *Zamia gigas* LINDLEY and HUTTON. *Trans. Linn. Soc. London*, 26: 663–674.

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