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PALAEOBOTANY'S CONTRIBUTION TO NEOBOTANY

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Dr. Marie Stopes, a colourful personality of great intelligence and ability, amused herself—and others—by publishing a sort of mock palaeobotanical journal titled "The Sportophyte". It comprised a short series of issues which appeared very erratically. The journal was witty, but as always with wit of any value, the words might often have a serious meaning hidden between the lines. Thus in one place she wrote (I quote from memory) : "The ordinary botanist should remember that the material with which the palaeobotanist has to work, is called 'stones' by the layman".

No doubt her intention was to remind the neobotanist (a much better term than "ordinary botanist") that our specimens are fragments which have undergone many sorts of hardships before becoming embedded in a sediment and somehow saved from the usual fate of such organic material, that is to say, complete destruction and mineralization. The Rhynie chert and Carboniferous coalballs are extremely rare exceptions.

What chance would there be of a good result if we were asked to reconstruct the original and entirely unknown vegetation from a mere bucketful of rubbish raked up from the ground in a forest, or from the mud at the bottom of a lake ? All the odds seem to be against the palaeobotanist. But even so, patience, optimism, technical skill, and occasionally a grain of good luck have given results so exciting that neo- and palaeobotanists alike ought to be full of admiration.

However, the question is : To what extent has the study of fossil plants given results of direct value to the understanding of the form, structure and function of the plants of today ? Let us consider a few aspects of the question, and the possible answers.

What I am about to say is well known to palaeobotanists, but perhaps not, to the same extent, to neobotanists. They are occupied with their, shall we say half-million, species of living plants, and are not entirely certain that palaeobotanists, with these peculiar stones of theirs, are botanists in the *true sense of the term*.

PHYLOGENY

Phylogeny ought to be based on palaeobotany. But though we hate to confess it, that idea has not been realized so far, and this holds good for the angiosperms at least as well as for any other group. The fossil record is far too incomplete and raises almost as many problems as it solves. It has given us spotlights rather than a flood-light.

Apart from the occasional finds of fossil wood and an abundance of pollen (to both of which I shall return later), by far most of the angiosperm fossil material consists of leaves, very often without even a trace of cuticle preserved. To identify such material is difficult, and many errors have been committed. However, the general impression obtained from it is clear enough. The angiosperms seemed to appear on the stage almost suddenly in the early part of the Cretaceous period, and, what is particularly striking, even the oldest angiosperms known are in no way archaic. The problem of the origin of the angiosperms, with their two integuments, double fertilization, and many characteristic features in the vegetative body, still seems as "abominable" as when Darwin, as the first, used that often-quoted adjective to characterize it.

Perhaps, however, this view is too pessimistic. Research during the last ten years or so, chiefly by American workers and on American material, has indicated that remains of reproductive organs of angiosperms from the Cretaceous onwards may be accessible in greater quantity than known before. This fact gives base for hope that palaeobotany will in future throw new and unexpected light on the phylogeny of the angiosperms. In their comprehensive and valuable article on palaeobotanical "perspectives in 1980" KNOLL AND ROTHWELL (1981) give references to relevant literature. RETALLACK AND DILCHER have recently (1981) given strong support for the idea that the ancestors of the angiosperms are to be sought among or near the glossopterids.

With regard to the oldest dicotyledons there is a striking frequency of forms believed to belong to genera, or at least families, of the Ranales (Polycarpicae), thus corroborating the current view of which order must be regarded as most primitive among living angiosperms. Also the Amentiferae seem to appear early, a fact which does not conflict with the opinions arrived at on the basis of living flora. However, there is nothing to give the slightest hint of any common ancestry for the Ranales and the Amentiferae.

Fossils have thrown no light on the origin of the monocotyledons and their relationship to the dicotyledons. The fact that the palms make an early appearance and are nearly as old as any other angiosperms known to us, is striking, but does not simplify the problem. Do the palms simply seem to be older than other monocotyledons because their chances of being preserved as fossils are much better than those of herbaceous plants ? Or, were these woody forms really older than their herbaceous relatives, as often seems to be the case ?

(Allow me to digress : Until a few generations ago, by far the majority of the botanists who laid the foundations of taxonomy and systematics of the higher plants, were born and educated in the Northern Temperate Zone. Most of them were probably well over twenty years old before they saw a palm growing in any habitat other than a tub, and some of them probably never did. *Pandanus* and other woody monocotyledons would probable seem even still more strange and unusual in their eyes. To them, the typical monocotyledons were all the herbaceous liliales, orchids, grasses, sedges and various groups of water plants, while the woody monocotyledons appeared to be strange aberrants, secondary in relation to the "normal" herbaceous types. There may have been a certain danger in this attitude. It was subconsciously accepted as correct, and any query would require rethinking and perhaps an abandoning of standpoints).

The situation is quite different if we turn from the angiosperms to the other vascular plants. Certainly we have to admit that, also here, the intermediate forms representing links between major groups are still missing. But consider to what extent the extinct forms, revealed to us by the fossils, have widened our knowledge of the various groups. What would have been our mental picture of the Gingkophytes, Cycadophytes, Taxales, and the Conifers *s. str.* without the testimony of the fossils ? The Pteridophytes too would have been like the emerging tips of icebergs, if we had known nothing of the parts hidden below.

A good example of a morphological and phylogenetical problem solved through palaeobotany is the seed-cone of the conifers, for instance that of pine or spruce. It had puzzled botanists all through the 19th century and far into the 20th : Should it be regarded as a flower, that is, an unbranched condensed shoot with leaves or bracts; or as an inflorescence, that is, a shoot with spirally arranged (or sometimes opposite or verticillate) side-branches bearing specialized leaves or bracts? RUDOLF FLORIN (to whom we shall return in connection with the cuticles and stomata) solved the question in favour of the second alternative. He proved that the ovuliferous scale could have been derived from a shoot. He found that the fructifications of *Cordaites*, especially certain species, showed how one of the ancestors of the pine cone might have been constructed. A few opponents have disagreed with Florin, at least in details, but on the whole there is consensus of opinion on his main point, viz. that the conifer cone is an inflorescence.

The complete picture of any plant also involves the phytogeographical aspect. Our knowledge and understanding of a plant-like *Metasequia glyptostroboides*, discovered in 1941 as a living tree in a small area in Szechwan, is immensely enlarged in the light of the fossils. It is not merely a rare and isolated species. From the day it became known to botanists it stood out as a typical example of a living fossil, the last remnant of a genus whose other members, all of them now extinct, were in the Tertiary period widespread in the Northern Hemisphere, even as far north as Greenland and Spitzbergen. Other well-known examples are *Sciadopitys*, Cycads and *Gingko*, and many pteridophytes.

Our understanding of species or genera with dijunct distributions is incomplete without the historical perspective provided by the fossils. Examples are—genera like *Platanus*, *Liriodendron*, *Morus*, *Magnolia*.

THE TELOME THEORY

The telome theory is inseparably connected with the name of WALTER ZIMMERMANN (1884-1980), who published it in 1930. For the rest of his life he remained faithful to his ideas, which he continued to expound, enlarge and defend.

To say that his greatest achievement lay in the creation of a new word may sound absurd and perhaps even slightly flippant. But this can be said quite seriously, and without detracting from the respect that is due to him.

His term *telome* was the best possible example of the value of a well-chosen new word. Such a word may, as in this case, facilitate discussion, clarify ideas, and open eyes not only for concepts but also for specific objects. In this case the word telome had the advantage of being short, it was easy to combine with prefixes and suffixes, and could be absorbed into most languages.

ZIMMERMANN introduced the word as the name for the ultimate, unbranched, undifferentiated shoots of the primitive terrestrial plants which, in the 1920s and 1930s, went by the name of psilophytes. Of these, *Rhynia* was often considered the most typical representative.

It was easy to follow ZIMMERMANN in his theoretical deductions, when he explained the evolution of the various plant organs from telomes or telome-systems through simple changes. According to his theories the megaphyll, for instance, came into existence through planation, overtopping, "webbing" and limitation in longitudinal growth; similarly various reproductive organs through changes of telomes, each with an apical sporangium.

Most of us of older generations have been taught these ideas or have ourselves lectured on them to our students. They seemed so clear, convincing, satisfying. Unfortunately they may have been too clear, too simple, and too generalizing.

Since then our picture of the earliest vascular plants has become more diversified and complex than appeared to be the case just after the discovery of the Rhynie plants.

The concept of the telome has not disappeared, however. If the word is no longer often used, it is there at the back of our minds when we see or discuss the earliest vascular land plants. The discovery of these plants has had a revolutionary influence on our way of thinking as regards the morphology and phylogeny of the other vascular plants, so the telome still has its value, at least indirectly.

It still happens even, that the telome concept is applied in attempts to explain the origin and development of angiosperm organs, particularly parts of flowers. To what extent this has been successful is a matter of opinion, but it is an interesting fact that the word occurs even today in the titles of publications on the flowers of angiosperms, and in academic text-books.

In connection with ZIMMERMANN's "Theory" it is tempting to refer to HAECKEL's "Biogenetisches Grundgesetz" (Biogenetic Fundamental Law, also called Law of Recapitulation), of 1866. Its creator and his adherents claimed that it had universal application and was valid for all living organisms. Its main point was that "ontogeny recapitulates phylogeny". That is to say, during development from fertilized egg to adult individual, every organism passes through stages resembling the more primitive animals or plants which, according to the theory of evolution, were among the ancestors of the organism in question. HAECKEL was a zoologist and his *Grundgesetz* was concerned mainly with the Animal Kingdom, where he found most of his arguments. His adherents were also zoologists and so were most of his numerous opponents and critics. The botanists as such took very little interest in HAECKEL's "Law". Nevertheless, the idea of recapitulation could well have been expected to crop up, for instance in connection with the development of the various flower parts. But this evidently did not happen. There might have been a new opportunity for consideration of the "Law" when ZIMMERMANN's "Theory" was published and immediately became the centre of discussion. Certainly ZIMMERMANN himself, when he published his "Theory" (in "Die Phylogenie der Pflanzen") included a few pages with rather philosophical remarks on HAECKEL's "Law". Very few other botanists seemed to take any serious interest in this point, however. Evidently HAECKEL's ideas had almost entirely disappeared from the arena of scientific argument.

WOOD ANATOMY

At the start of the 18th century, the knowledge of the inner structure of plants had reached an impressive level, considering the primitive optical instruments the anatomist had at their disposal. Most prominent among the fathers of plant anatomy were NEHEMIAH GREW (1628-1711) and MARCELLO MALEPIGHI (1628-1694).

The 18th century, however, was marked by the genius of LINNAEUS. His interests turned his thoughts and outstanding abilities—and evidently those of most other botanists—towards the living plant as found in nature. Anatomy and physiology were subjects scarcely, if ever, touched upon in his publications or in those of his numerous pupils. This must be the reason, or one of the reasons, why very little progress was made in plant anatomy, including wood anatomy, in the 18th century.

In the first part of the 19th century a renewed interest in wood anatomy was given an impetus from the palaeobotanical side, but was also furthered by the current improvements in the microscope and microscopical techniques.

Fossil wood occurs in all geological formations from the Devonian to the Quaternary. Specimens may consist of anything from large stems and stumps down to minute fragments, and the preservation and fossilizations may vary to the same degree. Some remains, like those found in lignites, are simply carbonized and can be cut with a knife, while others are totally impregnated with a chemical compound, usually silica or calcium carbonate, so that the whole cell structure is visible.

William Nicol (1768-1851), famous for the invention of the double-refracting lens bearing his name, also found a way to prepare thin sections for microscopic study of rocks, by cutting (sawing), grinding, polishing and mounting in Canada balsam. Nicol's principles are still followed today.

Henry Witham ("of Lartington") was the first (as early as 1831) to apply this new method to samples of petrified fossils. He was soon followed by other palaeobotanists. One of them, H. R. Göppert, understood that a prerequisite for a correct description and identification of fossil wood was a solid knowledge of the wood of living trees. So in 1841 he published a book in Latin, "On the Anatomical Structure of Conifers", one of the classics of wood anatomy. Numerous palaeobotanists have followed in his steps. We can safely say that the palaeobotanists provided the foundation for the knowledge of conifer wood anatomy and the appraisal of the taxonomical value of the anatomical features.

Fossil dicotylodon wood occurs more sparingly, both geographically and chronologically, though it is plentiful in certain places and horizons, at least from the late Lower Cretaceous onwards. The study of this material has helped to elucidate the problems of climate and phytogeography in earlier periods, and of the age and distribution of various interesting families which are living still.

Among fossil wood of monocotyledons the *Palmoxylon* predominates. Just as present-day palms morphologically, and therefore also taxonomically, form a very characteristic and somewhat isolated group (to which Endlicher in 1837 gave the appropriate name of *Principes*), the fossil palm stems are nearly always easily identified as such. But characterization and identification as species is usually difficult, even when the material is well preserved, as is often the case. A major part of the research on stem anatomy of recent palms has been conducted by palaeobotanists (a fact which people in Lucknow do not need anybody from far away to tell them).

CUTICLES AND STOMATA

Considering the striking picture presented by stomata under the microscope, it is surprising how slowly the knowledge of these structures developed. Along certain lines the palaeobotanist kept step with the neobotanists, and were in fact ahead of them at the start

Scattered observations on fossil cuticles were published in the 1840s and 1850s, but comparisons with living plants and attempts at identifications made by the authors were uncritical and of no value. An exception was J. G. Bornemann's description (1856) of cycads from the Lettenkohlengruppe (Lower Keuper, Triassic) from Thuringia. He found cuticles so well preserved that he could study the outlines of the epidermis cells without any special preparation.

The further study of the fossil cuticles and stomata depended, however, on the new maceration reagent introduced, in 1861, by Franz Schulze (1815—1873, Professor in Rostock). As students of botany well know, "Schulze", still used in laboratories all over the world, consists of nitric acid and potassium chlorate and can be used, inter alia, for making preparations of plant cuticles after removal of other tissues.

In the 1860s and a few years afterwards, some quite extensive publications appeared on stomata and other epidermal structures of living plants, and the taxonomic values of their various forms were discussed. The same happened in the world of palaeobotany. A maceration technique was applied to fossil material by A. SCHENK in the 1860s, but was little used in the years that followed until reintroduced by A. NATHORST in the first part of the present century (published chiefly in his *Paläobotanische Mitteilungen* 1-11, 1907—1912). He demonstrated the great difference in the epidermis structure within the Cycadophytes. NATHORST used this name as a joint designation for the Cycadales and Bennettitales, the sterile leaves of which had often been indistinguishable. He now found that the wall thickness and the shape of the epidermis cells as seen in cuticle preparations gave a reliable clue.

Important work along the same lines, but with greater emphasis on stomata, was carried out in the years that followed by H. H. THOMAS and NELLIE BANCROFT, T. G. HALLE, T. M. HARRIS, R. FLORIN and others.

RUDOLF FLORIN (1894-1965), a student of NATHORST, was active in many fields of palaeobotany, but his name is above all connected with gymnosperms, both living and extinct, on which he did a tremendous work. More than anyone else, he studied the forms, ontogenetic development and taxonomic value of the stomatal apparatus in the various families, genera and species, always taking into account all other characters on which the taxonomic system can be based.

One example : He found a fundamental difference in the stomatal characters of *Taxus* and its nearest relatives on one hand and those of the true conifers on the other, and maintained that this difference, together with all other characters, made it necessary to separate the Taxales from the true conifers, an opinion now generally accepted.

It has been suggested that within individual conifer species there may be more variations in the stomata than FLORIN assumed. Also, that mature stomata from different species may look alike, even though they have developed differently. This has been especially emphasized by TOMLINSON (1970: 282 seq.), but, nevertheless, he also gives due credit to FLORIN for the pioneer character of his enormous work.

There have been many attempts to employ stomatal characters to clarify taxonomical problems connected with angiosperms. The results, however, have been far less spectacular than in the case of the gymnosperms. Palaeobotanists have been able to contribute very little, if anything, since the cuticles of most angiosperms are so thin and perishable that almost nothing is left after fossilization.

POLLEN ANALYSIS, PALYNOLOGY

During the early years of development of the microscope, pollen grains were among the objects studied, admired, and described by the microscopists (not always professional scientists). Books on pollen grains were printed, with descriptive text, sometimes adorned with exquisite drawings reproduced in copper plate or, after 1800, lithography (fine examples are the books by C. J. FRITZSCHE in the 1830s). Problems connected with the ontogenetic development of pollen grains, as well as their function and place in the life cycle of flowering plants were studied and to a large degree solved. But it was only in our century that pollen grains became the basis of a new branch of science. They became tools in a field which is important not only from an academic point of view but which has developed into a typical applied science involving large economic interests.

In the course of this development the study and use of pollen grains have been extended to include also the spores of vascular cryptogams, the spores of "lower" plants, as well as other minute bodies of organic origin found floating in air or water. "Pollen analysis" was no longer an adequate name, and was replaced by *Palynology* (HYDE, 1927: from Greek *pale* meal, dust).

It all started on a small scale and in a haphazard fashion in the 19th century. The remarkable German scientist EHRENBERG (more about him below) observed and identified pollen grains from deposits of Tertiary age already in 1838, as did the prominent palaeobotanist GÖPPERT in 1841. The Swiss geologist J. FRÜH (1885) was one of the first to publish work on the various species of pollen grains found in peat. He was followed by the German C. A. WEBER, the Dane G. SARAUW, and various Swedes, among whom G. LAGREHEIM was especially important. He improved the methods and introduced quantitative analyses. With full justification he has been called "the spiritual father of pollen analysis." However, it was LENNART VON POST (1884-1951) who laid the real foundation of modern pollen analysis, differential counting of the pollen grains, in various levels at regular vertical distances in the porfile, combined with careful and detailed stratigraphical observations. All these data were presented in pollen diagrams, which VON POST was the first to draw and publish. He gave the first full account of his methods and results in a paper on the history of Swedish forests, read to the 16th meeting of Scandinavian Natural Scientists in Oslo in 1916. The paper immediately aroused great interest. The new method of research spread rapidly to other countries and has gradually been extended in time, that is, to older strata, as well as in content and application.

As mentioned above, pollen grains of Tertiary age and older had been occasionally observed and identified already early in the 19th century, but there was no systematic research until after VON POST's first publications. In the second half of the 1920s and in the 1930s, many papers were published on the pollen flora of lignite and other deposits of Tertiary age, and this line of research was gradually extended downwards in the geological time scale to the early Palaeozoic, and even beyond.

The development was immensely furthered when petroleum geologists started to use pollen, spores, plankton organisms and microscopic fragments of plants for correlation and dating of geological strata.

All this intense activity served the interests of micropalaeontologists, but its value to the neobotanists is undeniable. Without it, we would know far less about the morphology of pollen grains as seen with a light microscope and their wall structure as revealed by electron microscopy ; about the quantities produced by the different plant species ; how the grains are released from the pollen sacks and transported by the various agents ; their role in atmospheric pollution and allergy ; their taxonomic value, as well as all the other problems which may arise and be tackled when one specific part of a plant is submitted to intensive comparative study. G. ERDTMAN (1897-1973), who may be called a student of VON POST, began a systematic investigation and description of pollen grains, and his pioneer work has developed into a world-wide activity by hundreds of palynologists, using the best electron microscopes and other equipment, and resulting in true pollen floras. On the evidence of pollen, some genera have been split and others united.

DINOFLAGELLATES

In this last section we shall turn to the dinoflagellates, a plant group which, until recently, palaeobotanists hardly regarded as possible objects for palaeobotanical research. This group has existed for hundreds of million of years and has been preserved as microfossils which have turned out to be as important as they are numerous. They are important from a practical point of view, and also because they have thrown light upon obscure points in the morphology and life cycle of their living relatives.

In their usual haploid stage the dinoflagellates are unicellular, motile, autotrophic algae. They form an important component of plankton in sea and freshwater, well-known to marine biologists and limnologists, all over the world. They have a cellulose wall consisting of plates arranged in a system characteristic for each species. They multiply by simple division.

Only relatively short time ago it was found that sexual processes and formation of resting spores, called cysts, take place in some species and under certain conditions. It was, however, only through the study of fossil material that the cysts became fully known.

Already in the 1830s, micropalaeontologists had been intrigued by a number of small fossil bodies which some people thought represented remains of a special group of micro-organisms now extinct (Hystrix, Hystricospheres, etc.), while others, rightly, understood that they comprised all sorts of things, like spores of plants, eggs of animals, etc. It was the merit of W. R. Evitt that he, in 1961, on the basis of a large material of Mesozoic and Tertiary age, proved that many of them were empty cysts of dinoflagellates. Some of them showed indications of the plate patterns characteristic of the dinoflagellates. They always had an opening whose form and position were characteristic and constant for each species. This opening, which he called arkeopyle, was the way through which the living contents of the cell escaped when germinating.

The surface of the cyst is sometimes smooth, but often provided with spines etc. of various shapes. The wall itself consists of sporopollenin, in contrast to the cellulose walls of the planktonic forms. This fact at first made it difficult to accept that these cysts were those of dinoflagellates.

Later on, however, it has been found that some living dinoflagellates form cysts built similarly and with walls of sporopollenin, while other genera (like the well-known *Ceratium*), are evidently unable to form them.

These fossil cysts have not with certainty been found in strata older than the Triassic. However, from this period onwards they are common. Sometimes they are found in enormous numbers (thousands per gram of sediment). Being widespread geographically and easily recognizable, they are much used for dating and correlation of layers, particularly in oil geology.

The full knowledge of the cysts has been a valuable addition to the understanding of the life cycle of dinoflagellates and has solved problems in connection with their biology. Thus the presence of great numbers of cysts in the bottom mud explains how it is possible that certain species of dinoflagellate plankton sometimes appear in certain waters in surprisingly short time.

What has been said here does not pretend to be a complete treatment of the whole subject. Only a selection of topics has been presented, and most, or all, of them may be familiar to the palaeobotanists. The addressees are rather the neobotanists. If also they could say : "But all this is well known to us", then nothing could be better.