FR. J. MATHIESEN

PALAEOBOTANICAL INVESTIGATIONS INTO SOME CORMOPHYTIC MACROFOSSILS FROM THE NEOGENE TERTIARY LIGNITES OF CENTRAL JUTLAND

PART III: ANGIOSPERMS

Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 20, 9



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Synopsis

The angiospermous flora represented by leaves and a few seeds from the Middle Miocene lignitic clay at Moselund and Silkeborg Vesterskov consists of species of the extant families Gramineae, Palmae, Zingiberaceae, Salicaceae, Betulaceae, Fagaceae, Myricaceae, Moraceae, Lauraceae, Aceraceae, Hamamelidaceae, Rhamnaceae, Styraceae, Nyssaceae and Menyanthaceae. The flora is relatively poor in number of species, but rich in specimens allowing investigation of the range in leaf variation verified by anatomical detail.

Remains of palm leaves anatomically corresponding to leaves of a *Nypa* sp. are described under the name *Palmacites nypoides* n. sp. *Brachychilophyllum* sp. and *Ocotea ravnii* n. sp. replace the original names *Musa* and *Laurus* as these were both misleading and inadequate. New species are described as *Myrica cimbrica* and *Nymphaeoidea lignitica*.

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III. Angiosperms

Angiospermous remains, mainly leaves, are copiously represented in the lignitic clays of Moselund and Silkeborg Vesterskov, partly in a satisfactory state of preservation; the Fasterholt lignites only rarely offered determinable angiospermous fossils (F. J. MATHIESEN 1965, Pag. 15 et seq.) and these were mostly extremely fragmentary.

Much of the material allowed an anatomical study; the cuticular structure of the leaves offered details of systematic value, and the seeds and fruits also gave valuable additional information.

Due to the fragmental nature of the matrix the larger specimens were unfortunately often incomplete, and as the dark carbonized leaf substance was inclined to crumble the outline of the leaves were often only faintly set into relief from the dark coloured matrix. In the imprints the margin and venation are often far more easily perceptible. The accompanying sketches are all executed as camera-lucida drawings with the greatest possible exactness. In order to facilitate my idea of the entire shape of the objects in question I have in many instances contrived to complete the margin and venation, but always in such a way that the additions are easily distinguishable. My efforts have concentrated towards gathering morphologically corresponding leaves into specific groups ("Formkreise") and, if possible, corroborating their mutual interdependence by anatomical study, a method which is of growing importance.

As in most cases it has been impossible to obtain transverse sections the structure of the leaf has to be recognized by studying the successive layers as they appear in front view and combining the details to a total image. The disintegration of the crystalline matrix in the mesophyll has not favoured the tracing of minute details.

Only four of the described species can be regarded as new to the fossil floras of Europe. The anatomical details given are supplemental to the morphological diagnoses, mainly supporting the generic position of the fossil. In pointing out extant generic relations to the fossils I have found it useful to accompany the sketches of their salient anatomical features with a figure of the anatomy of the supposed extant species, mostly as a transverse section of the leaf. Some fossils of the floras of Moselund and Silkeborg Vesterskov proved in this way to have been erroneously placed systematically, but in most cases one can only but admire the systematic insight of the former investigators. Where the available characters agree, the original generic and specific names are retained (e.g. *Ficus lanceolata* O. HEER) but in certain cases there is some uncertainty as anatomical detail of most of the previously established species are not available. As a fossil *Nypa* has hitherto only been known by its fruits, and as the foliar remains still seem to be specifically doubtful, *Palmacites nypoides* will perhaps be the adequate designation. The name *Laurus (Laurophyllum)*, used as a collective name for leaves of the type in question, is better restricted to leaves which agree anatomically with those of the genus *Laurus*.

The herbarium of the Botanical Gardens of the University of Copenhagen has placed its rich collections of comparative material at my disposal, and my thanks are due to the staff of this institution as well as to the direction of the 'Botanical Gardens of the University and of the Gardens of the Royal School of Agriculture. The keepers of the Botanical Museum, Dr. A. SKOVSTED and Dr. B. HANSEN, have also with their usual kind attention been good enough to provide herbarium material from abroad.

The photographic plates are based on the work of the photographic laboratory of the Mineralogical Museum. In preparing the photographs Mr. CHR. HALKIER has placed his experience at my disposal in finishing this part of the work. It is suggested that the plates are studied through a reading glass.

Mrs. E. NORDMANN of the staff of the Institute of Historical Geology kindly executed the figures 8 A and B.

I am greatly indebted to the late Professor A. ROSENKRANTZ for the interest he has taken in my work, and to Mrs. H. HELBÆK and Mrs. L. CHRISTIANSEN of the Mineralogical Museum and the Royal School of Pharmacy, respectively, for their careful retyping of the manuscript.

Dr. STUART WATT of the staff of the Geological Survey of Greenland kindly revised my translation into English and read a proof.

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Monocotyledons

Arundo sp. Rhizome Arundo donax (Goeppert) O. Heer

Fossils of this type, evidently fragments of the rhizomes of a monocotyledonous plant, commonly occur in the Neogene Tertiary of Europe. The specimens are mostly considerably flattened by compression. Satisfactory figures are given by G. MÜNSTER (1842, Heft 5, Tab. III and IV) and by F. UNGER (1847) and are referred to the rhizome of a grass (*Calamites goepperti*) a name which O. HEER (1856) amended to *Arundo*.

Small and large fragments frequently occur in the lignitic clay of Moselund; Plate I shows a specimen of considerable size. The tissue is bleached and partly dissolved, the epidermis and the subepidermal layers having mostly totally disappeared. Traces of the scale leaves are hardly visible, their bases forming fine transverse lines, 5 (6) nodes are present. In the plate the surface shows a fine longitudinal striation which in a transverse cut is seen to form a continuous ring enclosing a brown parenchymatous, highly dissolved and altered central tissue. It has not been possible to perform a detailed study of these anatomical features, yet some facts could be made out which unquestionably indicate the rhizome of the extant *Arundo*. The original thickness of the rhizome is estimated to have been 3-4 cm.

Adventitious roots, evidently emerging from the rhizome, with their fine branches can be seen to the left in the figured specimen (Plate I). Scars left by decayed roots are seen on the surface as black dots, marking the connection with the longitudinal striated layer, which is to be considered as a sort of pericyclic ring, thin but exceedingly solid. Outermost to the right in the photograph is found a small piece of the rhizome showing circular low warts, 2–3 mm in diameter, in a few cases they enclose a star-like figure representing the hadromatic radii of the adventitious root, the offspring of which is surrounded by an elevated ring of parenchyma and partly of subepidermal origin.

The pericyclic ring evidently forms the most resistant part of the rhizome, the elements are slender, longitudinally extended and forming small groups, each enclosing some vessels. The groups are tangentially confluent.

Comparisons have been made with recent material from the Botanical Gardens of the University of Copenhagen and some slides of the rhizome of *Arundo donax* from the collections of the Royal School of Pharmacy, Copenhagen (Rhizoma Donacis). The details observable in the fossil agree very well with those of *Arundo donax*. The extant *Arundo* attains a considerable size in the Mediterranean countries, where it locally covers extensive areas in swamps and on moist ground. The rather large leaves show a character all of their own, the venation being composed of numerous delicate veins of equal fineness. Leaves which might be related to *Arundo* are also present at Moselund, but only as impressions.

Palmacites nypoides n. sp.

Leaf debris and imprints of monocotyledonous leaves, anatomically comparable to a palm, probably *Nypa*, were derived from the lignite at Moselund.

Leaf imprints

The leaf imprints give an idea of the size, shape and partly also the venation. A single specimen (figured in Plate IV) shows the venation and also some of the leaf substance but details were difficult to ascertain due to the specimen being mineralized, the colour being in fact a dark ochre. Between the more conspicuous veins (0.5 to 1.0 mm broad), running at a distance of 3-5 mm from each other, a system of 3-5 much narrower veins is locally visible. The specimen in question is lying with its under side turned upwards and the epidermis and most of the mesophyll is destroyed or worn away. To the right in the photograph is found a 3 mm broad, rather faintly pronounced furrow, running most of the length of the object, probably representing the imprint of a longitudinal fold of the lamina, faintly protruding on the under side. There is a corresponding shallow furrow running between two parallel conspicuous veins on the upper side. In some of the smaller fragments these details are far more distinct. Similar structures are characteristic for the extant *Nypa*.

Under the microscope the veins show traces of the stegma cells. Only parts of the layer corresponding to the second hypodermal layer of Nypa are recognizable as an almost uniform brown film, only interrupted by hyaline, distinctly bordered spots, $20-25\mu$ in diameter, evidently representing the borders of hydathode pits. These elements probably owe their preservation to the compact content of tannin.

Anatomy

My attention was drawn to these leaves by the occurrence of a thin flake of a brownish colour, about 2×2.5 cm, washed out of the matrix from the excavation II (F. J. MATHIESEN 1965, fig. 2). Under the microscope the flake shows a layer of almost quadratic elements, most of them filled with a dark brown content; circular lacunae, $20-25\mu$ in diameter, were rather common.

A small coherent mass of debris after maceration appeared to consist mainly of fragments of leaves of the same type as those of the flake mentioned, and are

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clearly those of a palm. Twigs of *Glyptostrobus* were found intermingled with the leaf fragments.

The photograph of Plate II A shows a part of the filmy flake. It is obvious that it consists of two layers. The epidermis is partly intact and appears to be composed of quadratic elements far smaller than those of the underlying hypodermal layer. The lacunae, so easily perceptible in Plates II A and III A, represent pits in the leaf surface sunk to the inner border of the hypoderma. They are surrounded by a ring of epidermal cells and clothed with epidermis. In their bottom a stoma is developed as a hydathode.

The second hypodermal layer, visible below in Plate II A, is also composed of thin-walled elements, often conspicuous by their dark colour, probably due to a tannic content which on drying shrinks and adheres to the wall thus making it appear more or less thickened. The hypoderma is two layered but the first, subepidermal, layer is in most cases destroyed in the fossils by dissolution, and has only here and there left some remains; its transversely extended, prosenchymatic, thick-walled cells are seen in Plate II B near the upper margin. The pointed ends of these prosenchymatic cells are wedged between the ends of their neighbours, thus forming a coherent sclerenchymatic layer. Fig. 1, F, shows details of the hydathode pith in the passage through the first hypodermal layer.

The epidermis of the under side of the leaf is almost totally destroyed, and only traces of the stomata are left which seem to attain a considerable size $(50-60 \mu)$. The mesophyll and the veins have also only left trifling remains. Some of the debris could be referred to the rachis of a palm leaf. Plate III B shows a part of the epidermis and the underlying hypoderma, both composed of quite small elements.

Diagnosis

Fragments of leaf sections and debris mainly from the foliar upper surfaces, referable to the palm genus *Nypa*.

Venation fine with veins 0.5 to 1.0 mm broad running parallel 3–5 mm apart, the interstitial area occupied by a system of 3–5 far more slender veins.

Under the microscope the upper surface of the leaf is markedly pitted. The pits lined with epidermal cells pass into the layers of the thin-walled hypodermis of the second layer. A stoma is developed as a hydathode at the base of the pit traversing the sclerenchyma whose spindle-shaped, thick-walled elements are replaced below the hydathode by thin-walled mesophyll thus forming an elliptic, translucent space.

Affinites

The anatomical details mentioned indicates the extant *Nypa fruticans* VAN WURMB, a palm nowadays widespread in the Far East growing in brackish water, estuaries and by the sea shore. The anatomy has been studied by several investigators, most recently











Fig. 1. Nypa fruticans van Wurmb. Folium. A, transverse section of epidermis and hypodermal layers. B, C and D are hydathodes in transverse and cross-sections. E shows the successive layers of epidermis and hypoderm in front view. (×300). Palmacites nypoides. F, a hydathode and its surroundings. G, the hypodermal layers in front view. (×300). Moselund.

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by P. B. TOMLINSON (1961). The type of hyathodes is particularly characteristic as well as the structure of the hypoderma and the stomata. Curiously enough the parenchymatic second layer of the hypoderm seems to have escaped the attention of some of the investigators; I have demonstrated it in the comparative material. In fig. 1, G, is a drawing of the hypoderma. Fig. 1, B–D show sketches of the hydathodes of the extant *Nypa* in section and front view. It should be noted that hydathodes also appear on the under side of the leaf, but they are here not sunk and are somewhat smaller than those from the upper side. For details concerning the leaf anatomy of *Nypa fruticans* references can be given to the papers of H. KOOP (1907), H. SOLEREDER and F. J. MEYER (1928) and P. B. TOMLINSON (1961). Their descriptions agree with what is ascertained in the fossil. The hydathodes were first described by H. KOOP (1907).

Unfortunately it has not been possible to utilize the anatomical details of the stomata and the stegmatic cover of the surface of the fibres, but the striking parallelism between the fossil and the extant *Nypa*, as far as the anatomical details available allow, seems to indicate generic comparability. Specific concordance, of course, is not proved. The specific name for the leaf *Palmacites nypoides* would possibly be adequate but following the deduction of H. TRALAU (1964) it might perhaps be justifiable to form the name *Nypa* sp. aff. *N. fruticans* van Wurmb, thus emphasising the mutual relation of the fossil and the extant species.

According to TRALAU'S (op. cit.) investigations palms of the Nypa type must have been very common in the Paleogene Tertiary of Europe. He enumerates no less than 50 references to pictured specimens of fruits of Nypa aff. N. fruticans VAN WURMB.

All the fossils referable to *Nypa* are derived from the Eocene except for a few specimens from the Far East where a younger age is suspected. The determination is almost always based on the finds of the very characteristic fruits. TRALAU's paper (1964) illustrates the recent and past distribution and sketches the occurrence of *Nypa* along the Eocene shoreline in Europe. Pollen referable to *Nypa* recorded from New Zealand is of Pliocene age.

A. HELHINEL (1925), according to H. TRALAU (1964), has described some fruits together with leaf fragments as *Nipadites hurtini*. Concerning them H. TRALAU remarks: "Nor do the foliar and fruit fossils from Landenian deposits of Belgium . . . show any reliable characters which make their belonging to Nypa trustworthy. The foliar fossils are so fragmentary and badly preserved that they show almost no recognizable [macroscopic] characters at all." (1964, p. 22).

At any rate our find demonstrates the existence of a *Nypa* in far younger layers than hitherto recorded, probably middle or early Miocene, and perhaps it will prove useful to investigate debris similar to that which has been the subject of the investigation related here. Fruits of *Nypa* have not yet been found in the Moselund lignites.

Some fragments of palm leaves, described and figured by M. E. J. CHANDLER (1929) as belonging to a *Nypa*, are evidently not referable to this genus.

Brachychilophyllum sp.

Fragments of leaves referable to monocotyledons of the order Scitaminales occasionally occur in European layers of Tertiary age, especially in the Neogene. In the lignitic clay at Moselund they are not rare and from the dark bottom layers some specimens were collected in which the leaf substance was fairly well preserved (Plate V). Unfortunately it has not been possible to secure an entire leaf. The leaf size has been considerable according to the fragments with transverse dimensions estimated to be about 10 cm. The leaf has probably had an extended elliptic-lanceolate outline. A fragment in which some of the marginal region is preserved shows close to the margin 3–4 faintly prominent folds running parallel to the border (Plate V C). Numerous fine, close-set veins, steeply ascend from the 3–4 mm broad midrib and are connected by cross anastomoses, traceable through ridges in the surface. The lamina has probably been of a rather thin structure.

Under the binocular microscope the leaf venation appears to be composed of two types, (1) a more vigorous type with a thickness of 0.5 mm and about 8–10 mm apart, and (2) a far more slender type of 0.2 mm in thickness of which the last 3–4 veins run in the intervals between the more vigorous. The veins are immediately adjacent to the epidermis of the under side of the leaf and consequently inseparable from the matrix. In places where the leaf substance could be removed and the veins laid open, details of the venation are very distinct and it is seen that the cross anastomoses are numerous and only about 3–4 mm apart.

The anatomy had to be studied from rather small pieces of debris as the fossil consists of a very brittle, highly carbonized mass. The following description is consequently based on a number of fragments.

The epidermis is mostly dissolved, the remaining rests show thin-walled, almost rectangular elements, with traces of stomata on the under side epidermis. Both the upper and lower sides have a hypodermal layer of thin-walled cells, the hypoderma of the upper side mostly collapsed with groups of elements filled with a brown substance. The assimilation tissue is composed of thin-walled cells and includes a great number of crystals of various sizes soluble in hydrochloric acid. These are probably not of biogenetic origin but were formed during the fossilification processes. Scattered in the mesophyll are small idioblasts with a tannic content (fig. 2, C). Idioblasts of a far larger size accompany the margin of the scleroidic cover of the conducting tissue and are only locally present in the under side of the lower hypoderm. In the mesophyll there are ellipsoidal elements $36-40 \mu$ large which are not collapsed as they are filled with a brownish, finely grained substance. They probably represent oil cells (fig. 2, B). The elements of the mesophyll appear finely grained.

Only the sclerenchymatic cover of the vein tissue is preserved, and the hypoderma of the lower side is partly interrupted below the veins.

The anatomical details, in connection with the morphological characters, indicate a member of the family Zingiberaceae. It is difficult on the basis of the material



Fig. 2. A, transverse section of leaf of *Brachychilus horsfieldii* O. G. Petersen. B and C, details of the mesophyll of *Brachychilophyllum* sp. $(\times 300)$.

at hand to refer the fossils to a distinct genus but most of the available characters indicate similarity to the recent genus *Brachychilus* (*B. horsfieldii* O. G. PETERSEN, R. BROWN). This genus is widespread in the Far East and, according to A. BYRD GRAF (1963), also reaches the southern coast of China.

In the paper of H. SOLEREDER and F. J. MEYER (1930) it is stated (pag. 44) that in the leaf of *Brachychilus horsfieldii* PETERSEN, R. BROWN is found "eine Menge grosse Krystalle im Mesophyll" (cited from W. FUTTERER 1897, p. 44). I have not succeeded in verifying this. In all specimens of the recent *Brachychilus* that I have examined there are numerous, quite small crystals which are common and well developed in the specimens figured (fig. 2, A) from the collection of A. KOSTERMANN (No. 21530, East Borneo), and only here and there are there larger crystals, partly in small clusters. The arrangement and forms of the small tanniferous idioblasts agree

very well in the fossil and living species, they are not noted from other Zingiberaceae. Thus the fossil can be given the generic name *Brachychilophyllum*.

An inspection of some leaf fragments of the type referable to plants of the order Scitaminales, carried out by B. ESKE KOCH and W. L. FRIEDRICH (1971), suggests that a closer determination of them is rather dubious. Among those figured by O. HEER (1869 b, Tab. IV, Fig. 7–10) the venation of *Zingiber* O. HEER is not unlike the Moselund fossil material. The *Musa bilincica* C. v. ETTINGSHAUSEN (1865, Tab. VI, Fig. 11) from Kutchein, Bohemia is also based upon fragments in which the venation is very little pronounced, and to judge by the figure cited, to have had very fine veins. Leaves referred to *Musa bilincica* are not uncommon in layers of Middle Miocene age.

Spirematospermum wetzleri (O. HEER)

A number of seeds referable to *Spirematospermum wetzleri* (O. HEER) are found in the Moselund material. A few capsules of the type figured by B. ESKE KOCH and W. L. FRIEDRICH (1971) are also present.

The authors cited have discussed the possibility of referring these fossils to the type of the recent *Cerulophos* (SCHUMANN) R. E. HOLTUM. Fragments of leaves referable to this species were not present and a closer connection of the seeds with a Zingiberaceae of the type described above was not possible.

Dicotyledons

Salix varians H. R. GOEPPERT

The series of leaves figured at natural size in figure 3 were collected from the lignite of Silkeborg Vesterskov. There is only little variation in shape and venation and they are more or less complete. H. R. GOEPPERT (1855) has given a diagnosis which runs as follows: "Salix folii petiolatis elongato-lanceolatis vel lanceolatisacuminatis basi attennuatis semilatis vel basi integris et apicem versus serrulatis penninervis, nervis secundariis augusto subacrito adscendentibus subexcurrentibus vel in marginum subramosus." Salix varians H. R. GOEPPERT and his five closely related species (S. wimmeriana, S. arcuata, S. acutissima and Salicites dubius) which are now all included in S. varians (R. KRÄUSEL, 1919), all occur in the fossiliferous clay at Schossnitz. They may thus be considered as a group of types which together have a wide variation range. The serrulation of the margin is a variable character. The photographs of R. KRÄUSEL (1919) represent leaves with an entire or almost entire margin, as do the leaves from Silkeborg Vesterskov in which the margin only shows serrulation in a few places giving it a faintly undulating appearance. The special character of venation pointed out by O. HEER (1856, pag. 25) and referred to as "verkürzte Secundärnerven" are displayed on some of the photographs of R. KRÄUSEL (op. cit.). The character consists of slender veins emerging from the main rib in the intervals of the more vigorous normal secondary veins but anastomizing before joining them. Nr. 9



Fig. 3. Salix varians H. R. Goeppert. (1/1). Silkeborg Vesterskov.

The venation is not very conspicuous in our leaves, but at least the offspring of the "verkürzte Secundärnerven" are visible here and there.

Only the carbonized substance of the leaf figured as fig. 3, C has given sufficiently useful anatomical details for determination. R. KRÄUSEL and H. WEYLAND (1954) reproduce photographs of the cuticle of *S. varians* and an instructive drawing. The cuticle of our leaf shows corresponding details: stomata of the *Salix* type and numerous hair bases of small diameter $(4-6\mu)$. Stomata and hair bases are only found on the under side of the leaf. According to the facts available the leaves in question are related to the extant genus *Salix*, though there is still some doubt as to the nearest allied recent species. *Salix fragilis* and *S. triandra*, which have been considered, possess hairs of a far stouter shape with the hair bases measuring $10-12\mu$.

The clay at Schossnitz in now referred to the Upper Miocene (R. KRÄUSEL 1919). Other finds of *Salix varians* are noted from Rixhöft (Samland) and Oeningen (O. HEER 1856). The locality at Rixhöft was formerly referred to the Upper Oligocene but is probably of far younger geological age. According to floristic comparisons by A. JENTZSCH (1909) it probably has an age near to that of fossiliferous layers at Senftenberg: "So erscheint uns jetzt das weite Gebiet der Braunkohlenformation von Senftenberg bis zum Samlande als ein einheitliches Florenreich, welches jünger als die oligocäne Meerestransgression ist". (loc. cit. pag. 61).

Fagus feroniae F. UNGER

A series of leaves were secured from the lignitic clay of Moselund which according to their shape and venation are related to the extant genus *Fagus* and apart from size are only slightly different. Some of the most completely preserved are reproduced in fig. 4. An anatomical verification has not been possible as the fossils present are only preserved as imprints.

The European fossil leaves related to Fagus can probably be separated into two types, though they are not always sharply distinguishable. One type is characterized by its more numerous secondary veins, varying in number from 9–14 and by a rather distinct attenuated tip, the secondary veins running straight to the margin, while the second type is distinguished by shorter, more ovoidal leaves and fewer secondary veins (5–9) running to the margin in a somewhat upward bent curve. The first type is probably present in the extant floras represented by the North American *Fagus ferruginea*, the second by the European *Fagus silvatica* L. According to W. PH. SCHIM-PER and A. SCHENK (1890) the tertiary veins also present a striking contrast; in the leaves of *Fagus ferruginea* forming a network in the interstitia between the secondary veins, while their ramification in *F. silvatica* L. is less marked. These characters are emphasized in the paper of P. MENZEL (1906) in his diagnosis of the fossil "*F. ferruginea* var. *miocenica*", but a combination of the two characters is not uncommon and *F. silvatica* appears as a highly polymorphous species. It is commonly regarded as the climax in development of the older *Fagus* type in which shortening of the lumina, Nr. 9



Fig. 4. Fagus feroniae F. Unger. (1/1). Moselund.

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the almost disappearance of the acuminate tip and the reduction in the number of secondary veins have all taken place. C. VON ETTINGSHAUSEN (1867) united UNGER's four species of *Fagus* in a common circuit of related forms. The series of leaves figured (1867, Tab. XV, Fig. 12–20) agree with the specimens reproduced here as fig. 4, A–E, and consequently indicate a *F. silvatica* type. C. VON ETTINGSHAUSEN (loc. cit.) has chosen the first name given by F. UNGER and designated his fossils as *F. feroniae*.

The leaves figured by R. KRÄUSEL (1919) from the Tertiary of Silesia are undoubtedly related to the type F. ferruginea; they are referred to F. attenuata H. R. GOEPPERT. A thorough discussion is given by P. MENZEL (1906) of the mutual affinities of the numerous fossils designated as Fagus.

The fossils from Moselund are referred to the *Fagus silvatica* type on the basis of the characters mentioned, and maintaining the priority of F. UNGER the name must be given as *Fagus feroniae*.

R. KRÄUSEL and H. WEYLAND (1954) have figured cuticular preparations of F. attenuata H. R. GOEPPERT. The very thin cuticle of the Fagus leaves does not favour photographic reproduction so that the drawing in fig. 4 gives a supplement. The small glands figured here seem to be characteristic of the species. Leaves of the Fagus type are recorded from the Upper Cretaceous and are found in the Tertiary layers up to the Pliocene.

Myrica cimbrica n. sp.

A number of spatula-shaped leaves were obtained from the lignitic clay at Silkeborg Vesterskov. Eight specimens, evidently of the same species are illustrated in fig. 5 with their outlines partly completed.

The cuticle is well preserved, while the tissue of the mesophyll and the veins have almost totally dissolved. By inspection under the binocular microscope the upper and especially the under side of the lamina are finely punctured, a character not shown in the drawings.

Details of the epidermis are given in figure 6, A–C. The lateral walls vary from straight to slightly curved. Stomata are only developed on the under side, the epidermis protruding somewhat under the stomatical apparatus. The course of the side walls are mainly indicated by the small wedges of the cuticle which project into the membrane of the wall while the cellulose thickenings are mostly dissolved.

The conspicuous paired elements, enclosed by a group of stellate arranged cells each denote the base of a glandular hair with the base emerging from the bottom of a shallow pit. They occur on both sides of the leaf, but are far more numerous on the under side. The size of the glandular disks are indicated by the circumference of their cuticles. Figure 6, E and F show the basal cell as well as the four vertical rows of elements which form the short stalk carrying the disk, $70-80 \mu$ in diameter. Only the cuticle of the disk is preserved.

Against the base of the lamina as well as the leaf stalk the surface shows a slight



Fig. 5. Myrica cimbrica n. sp. (1/1). Silkeborg Vestskov.

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Fig. 6. Myrica cimbrica n. sp. A and B, cuticles from the upper and lower surfaces of the leaf, respectively. (×300).
C, stomata and their surrounding (epidermal elements figured at a higher magnification). D-G, glandular hairs. (×400). Silkeborg Vestskov.

furrow, the epidermis of which has carried a few cover-hairs, probably rather thickwalled as might be judged from the remaining basal parts sunk between the surrounding epidermal cells (8–10 μ in diameter).

Diagnosis

Leaves obovate, spathulate, long stalked, decurrent at the base, apex rounded or emarginate, border entire, surface smooth, finely punctured. Glandular hairs of the *Myrica* type on both sides of the leaf. Stomata on the under side only. Epidermal cells thin walled with more or less wavy side walls.

Affinities

The anatomical details indicate the genus *Myrica*. A microphotograph of the epidermis of a fossil species, *M. macrodurensis* (R. KRÄUSEL and H. WEYLAND 1954) and their text figure 10 of *M. integerimea* KRÄUSEL & WEYLAND, as well as the figures of R. LITKE (1968) are similar. The leaf fragments figured by LITKE (op. cit. fig. 3–6) are incomplete but evidently represent a rather broad-leafed type of *Myrica*, while R. KRÄUSEL and H. WEYLAND describe the leaves of *M. macrodurensis* as "small, long-elliptical". A reference to one of the forementioned species or to any of the other numerous fossil *Myrica* species is probably not possible, and so it seems safer to regard our leaves as representing a new species. *M. studeri* O. HEER is somewhat similar to our fossil in the shape and size of the leaves, but anatomical details are lacking. *Myrica cimbrica* would perhaps be an appropriate name for our fossil.

The shape and size of the leaves are critical for the identification of analogous living species. Among living *Myrica* only *M. spathulata* MIRBEL, a species confined to Madagascar, seems to have a close correspondence to the fossil. The fossil leaves agree well with the illustrated living material (cf. MIRBEL 1827, Pl. 28 and J. F. LEROY'S *Flore de Madagascar*, 1952, Fig. 1,16) as well as with the comparative material of *M. spathulata* MIRBEL kept in the Botanical Museum of the University of Copenhagen.

ALF. GRANDIDIER in his Histoire de Madagascar etc. (1892) has figured a specimen mainly characterized by narrower leaves, yet this type is accepted as belonging to the Myrica spathulata MIRBEL by AUG. CHEVALIER (1901–02) as well as by J. F. LEROY (1952). LEROY (op. cit.) has given an abbriviated diagnosis of the species which for the leaves is: "Feuilles longuement pétiolées; pétiole de 6–12 mm. long, canaliculé au dessus, pubérulent; limbe obovale-spatulé, longuement atténué-décurrent à la base, arrondi-obtus, parfois émarginé au sommet, à bords très entiers, ondulés ou crénelés, non révolutés, de 5–9×1,5–3,5 cm., coriace, lisse, souvent brillant sur le dessus, avec puits et glandes nombreux dans le jeune âge . .." (1952, 53e, p. 3).

Our fossil is characterized by its large, spathulate leaves with decurrent lamina. The anatomical details, as far as the state of preservation allows comparison, agrees with that of the living material so that the fossil and the extant *M. spathulata* MIRBEL have at least close anatomical affinities.

Betula and Alnus

Leaves of *Betula* spp. and female catkins of an *Alnus* were collected from the lignitic clay at Moselund. An almost entire leaf of a *Betula* is reproduced in fig. 7, A. In shape, size and venation it agrees with the leaves of *B. brongniarti* figured by C. von ETTINGSHAUSEN (1867 and 1868). The biserrate type denticulation is only faintly pronounced, yet traceable. Glandular hairs of the *Betula* type occur, but are rare. P. MENZEL (1906, p. 37) has given one of his valuable Latin diagnosis of the fossil: "B. foliis petiolatis, basi ovatis vel subcordatis, ovatis vel ovato-oblongis, acuminatis, inaequaliter vel duplicato-serratis; nervis secundariis craspedodromis, in



Fig. 7. A, Betula brongniarti C. v. Ettingshausen. (1/1). B, Betula prisca C. v. Ettingshausen. (2/1). Moselund.

utroque latere 14–15 parallelis, subrectis, infimis ramosis, angulis $50-55^{\circ}$ egredientibus, 3–6 mm inter se remotis, nervis tertiariis tenuibus, transversis." C. von ETTINGS-HAUSEN (1867) has drawn attention to the close resemblance of the *Betula brongniarti* leaves to the leaves of the North American species *B. lenta*. P. MENZEL (1906) discusses the mutual systematic relation of a group of large leaved *Betula* spp. from the Tertiary and concludes that the fossil species *B. dryadum*, *B. brongniarti*, *B. speciosa*, *B. cuspidens*, *B. elliptica* and *B. sachalinensis* are variants of a single species, *B. brong*-



Fig. 8. Alnus sp. female catkins. (2/1). Moselund. (E. Nordmann del.).

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niarti C. von Ettingshausen widely distributed in the Tertiary of Europe and northern Asia.

The fossil species, *B. macrophylla* (H. R. GOEPPERT) O. HEER is also a rather large-leaved type, but it is not so clearly delimited as *B. brongniarti*. Its generic position is even somewhat doubtful. The photographs given by H. REIMANN (1919) are not sufficiently diagnostic so I should prefer to name our fossil *B. brongniarti*. A figure of P. MENZEL'S paper (1906, Tab. VIII, fig. 22) agrees perfectly with our leaf. Imprints of leaf fragments referable to another *Betula* species, perhaps *B. prisca* C. v. ETTINGS-HAUSEN, also occur in the clay at Moselund.

The *Alnus* catkins (fig. 8, A and B) do not allow closer study. Such remains are not rare in the Neogene Tertiary deposits of Europe. *Alnus kefersteinii* (H. R. GOEPPERT) is evidently a widely dispersed fossil species, also present in the Samland deposits. *Alnus* leaves have not been seen in the Moselund deposits.

Ficus lanceolata O. HEER

Leaves of the types reproduced in figures 9, A–F and 10, A–F, are very common in the lignitic clay at Moselund and are equally distributed throughout the whole series. In the upper, yellow part of the layer they mainly appear as imprints, in the dark bottom layer the leaf substance is often preserved as a thin, coaly film which, cleared by treatment with sodium hypochlorite, reveals anatomical details. All the figures are regarded as representing leaves of the same, evidently heterophyllous, species; transitional forms are sometimes found.

The imprints selected for drawing show the venation in a distinct way; the epidermis and details of the mesophyll, especially the latex tubes, are also traceable, but as a whole the tissues appear in a highly hyaline state.

The most common leaf type varies from rather narrow to broad lanceolate in outline, the wedge-shaped basal part gradually tapering over into the short, sometimes slightly thickened petiole. The midrib appears prominent and rather broad. The type, figured 10, B–F, is characterized by its obovate form, more or less oblique with a bluntly rounded or even incised apex. The margin is always found entire. Hair bases could not be seen.

Anatomy

Large leaves such as those figured 9 B and 10 A have mostly been chosen for anatomical study, but all the types figured agree anatomically.

The epidermis of the upper side is composed of thin-walled, polygonal elements. A brown body of crystalline shape was found in many of the cells and was evidently the envelope of a monoclinic oxalate crystal, now dissolved.

A hypodermal layer of rather large, thin-walled, polygonal cells has been developed inside the epidermis but only scattered rests remain. Among the mineral particles



Fig. 9. Ficus lanceolata O. Heer. (1/1). Moselund.

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Fig. 10. Ficus lanceolata O. Heer. (1/1). Moselund.

attention is drawn to the not uncommon occurrence of $4 \mu \log 2 \mu$ broad, cylindrical or conical silica bodies.

In the macerated leaf the palisade layer has strongly compressed, very narrow elements markedly collected in groups separated by broad, hyaline, anastomosing furrows forming a network intersecting the darker groups of palisade tissue. Evidently the hyaline parts had originally also been filled out with palisade cells, now dissolved. The tufts of palisade cells correspond in outline to the vertical borders of an hypodermal element fixed to their bulging and more resistant inner side.

Only a few patches of the lower epidermis were left and of the aerenchyma the most conspicuous elements are the rare fragments of latex tubes easily recognizable by their black contents. Larger pieces occasionally occur in the hyaline tissue of the imprints.

Immediately below the palisade are traceable numerous spheroidal secretary elements with a diameter of $15-20 \mu$.

A peculiar type of lithocyst is found in the lowermost mesophyll layer, often bordering the lower epidermis. They are spherical reaching a diameter of 90μ . They are numerous and crowded in the apex of the leaf but of somewhat smaller diameter. Their walls are rather thin, often totally dissolved, and their existence in this case only marked by a drop of a dark brown substance or one or two globular silica bodies. A coat of small, very thin-walled, hyaline elements sometimes form a sort of halo which throw them into relief in the preparations.

The epidermis of the upper side of the leaf has been extremely rich in monoclinic calcium oxalate crystals. As they are not enclosed in a cutinized cover, they are of course only traceable in the fossils.

Silica containing idioblasts (lithocysts) of the upper side of the leaf of the extant *Ficus diversifolia* were first observed by O. RENNER (1907, pag. 462). On closer examination they show a rather singular structure as will appear from figure 11 C. A cone-shaped feature passing through the hypoderm reveals the palisade lined with narrow, cutinized elements which in its lower part is sometimes filled out with a small spherical or conical silica body. It was of importance for the determination of the fossil that such a structure could be demonstrated in our *F. lanceolata* as their appearance seems to be restricted to the extant *F. diversifolia*, but the leaf substance of the fossil is only available in a highly disintegrated state. As the elements of the small lithocysts are partly cutinized and consequently rather resistant, it should be possible to demonstrate at least fragments of these elements. These can be demonstrated, and here and there also an almost intact lithocyst can be found (Fig. 11, F–H).

Another peculiarity in which the fossil and living species agree is the strand of small, almost isodiametric scleroids, running outside the anastomosis of the veins. Particles of this tissue sometimes occur in the macerated substance of the fossil leaf.

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Fig. 11. A–C, *Ficus diversifolia* Blume (lanceolate leaf type). A, transverse section; B, upper epidermis; C, transverse section of leaf showing the small sunken lithocysts of the upper side of the leaf. (A and $B \times 300$; $C \times 400$).

D-H, Ficus lanceolata O. Heer. D, secretory elements of the subpalisade layer; E, lithocysts from the under side of the leaf; F-H, isolated cutinized tips of the funnel-shaped depressions of the upper side of the leaf. $(D \times 300; E-H \times 600)$. Moselund.

Discussion

The morphology as well as the anatomical characters indicate the genus *Ficus*, nowadays distributed in the tropics and subtropics and is richly represented in eastern Asia. Some species show a remarkable variation of the leaves within the same systematic unit. The plates of the monumental memoir by G. KING (1888), for example, give a striking impression of the variation. The widely distributed *Ficus deltoidea* JACK (*F. diversifolia* BLUME), in particular, represented (loc. cit.) in the plates 174 and 175 show the remarkable range of heterophyllic characters in this species; lancet-shaped

and broad obovate leaves can be borne by the same specimen, sometimes associated with a third type with very broad, triangular laminae and regular bifurcating venation. This third type seems to occur rather commonly but is not found represented among the fossils from Moselund.

An anatomical examination based upon the herbarium material in the Botanical Museum of the University of Copenhagen shows a striking resemblance between the lanceolate leaves of F. deltoidea and the Moselund fossils. The transverse section of such a leaf (fig. 11 A) approaches in size and form that of the fossils illustrated in fig. 9 B and 10 A. The anatomical details of the fossils and the leaf of the extant F. deltoidea almost agree but a closer systematic connection is, of course, not demonstrable. Dicotomous branched veins such as occur in the obovate leaves of the extant F. deltoidea are not found in the fossil material which argues against a closer specific affinity.

O. HEER in his *Flora Tertiaria Helvetica* described and figured some leaves as *Ficus lanceolata* (II, 1856, Pag. 62, Pl. 81, Fig. 2–5) very much like the Moselund fossils, especially those of the lanceolate type. Other specimens referable to *F. lanceolata* are figured by ENGELHARDT (1873) and C. v. ETTINGSHAUSEN (1867). O. HEER in his *Miocene baltische Flora* (1869 a, Tab. XXI, Fig. 9) figured some characteristic objects probably referable to synconia of a *Ficus* sp. These were regarded by O. HEER as fruits of *Nyssa*, which undoubtedly is a misunderstanding; they are very much like small synconia, and their appearance in the layers at Rixhöft together with leaves of *Ficus lanceolata* suggests the presence of a species of this genus in the European Tertiary.

An anatomical study of O. HEER's material is not possible. Yet, for practical reasons it seems most convenient to retain the name given by O. HEER perhaps altering the generic name to Ficophyllum following A. G. NATHORST'S proposal.

Ocotea ravnii n. sp.

Leaves of the type represented in fig. 12, A–C, were collected from the dark coloured bottom layer of the lignitic clay at Moselund. All the remains are fragments but the completed outlines (fig. 12) give an impression of the shape, size and the more salient features of the venation. The leaf substance was preserved in some cases and while the rather thick lamina show the secondary veins distinctly the ramifications of a higher degree were scarcely discernible, the veins being very fine and evidently running in the central part of the mesophyll.

The epidermis of the upper side of the leaf is composed of polygonal, rather thick-walled elements. Below the epidermis there are numerous, large, thin-walled, ellipsoidal cells $(70-120 \mu)$ without any special content (mucilage cells) (fig. 14, A–D), separated from each other by palisades thus forming a mixed layer composed of these large cells and the surrounding palisades. The aerenchyma, which is mostly destroyed, encloses small $(30-40 \mu)$ secretory elements (oil cells) occurring singly or in groups.



Fig. 12. Ocotea ravnii n. sp. (1/1). Moselund.

Some of the palisade cells are of sclerenchymatic nature. Quite small, white dots can be recognized using a binocular microscope and reflected light on the upper side of the leaf, which represent the hyaline tips of the sclerenchymatic palisade cells. They occur singly or arranged in groups, often surrounding a mucilage cell. The sclerenchyma nesting in the upper layer of the aerenchyma is composed of quite small, thick-walled sclereids. Stomata are only found in the epidermis on the under side of the leaf; their intimate structure was not discernible. The prosenchymatic covering of the veins is partly accompanied by crystal-bearing elements.



Fig. 13. Ocotea foetens Aublier. A, transverse section of leaf; B, subepidermal layer in front view. (×300).

Diagnosis

Stalked, lanceolate leaves of the Lauraceous type, lamina fairly thick, slightly chagrinated, venation somewhat obscure, campylodronous.

Upper epidermis composed of polygonal, rather thick-walled elements; a layer of large, thin-walled cells intermingled with palisade cells forms a sort of discontinuous hypoderm. Some of the palisade cells are developed as sclereids as well as occurring in the bordering layer of the aerenchyma, in which scattered nests of small, thickwalled sclereids are found. Secretory elements (oil cells) occur in the aerenchyma.

Affinities

The morphology of the fossil as well as the anatomical detail available indicates the natural family of the Lauraceae. Amongst the members of this family sclereids in the mesophyll accompanied by mucilage cells are only recorded in a few genera,



Fig. 14. Ocolea ravnii n. sp. A and B, clusters of small sclereids in the upper layers of the aerenchyma; C, epidermal cells and outlines of palisade cells intermingled with hyaline tips of the sclerenchymatic palisade cells; D, part of C. (×400). Moselund.

of which *Ocotea* is one. Of the numerous *Ocotea* species only a few have been studied anatomically, principally the species of the New World, and the genus is only scarcely represented in the herbarium of our Museum. Anatomical details are given in the works of H. SOLEREDER (1899, 1908), METCALFE & CHALK (1950) and J. CLAUDITZ (1902). *Ocotea foetens* AUBLIER is endemic in the Canary Islands, and is found fossil (Pleistocene) in Madeira. It is a small tree with leaves highly variable in shape and thickness of the lamina. In the thin leaves the venation as a whole is distinct while in the thicker ones it appears as in our fossils. For comparison sections of the leaf of *Ocotea foetens* are reproduced (fig. 13, A and B). The anatomy of the living and fossil material agrees fairly well, so the assignment of our fossils to the genus *Ocotea* might be justifiable. The specific identity cannot be proved; a salient difference is, e.g. the far more frequent sclerenchyma nests in the upper part of the aerenchyma in the fossil.

As specific name I would like to propose the name *ravnii* in commemoration of the well known, now deceased, keeper of the palaeontological collections of the

Geological and Mineralogical Museum of the University of Copenhagen, J. P. J. RAVN.

If my systematic location of the fossils is correct then the former geographical distribution of this type of *Ocotea* is of interest.

Litsea polymorpha A. BRAUN

Leaves of the types reproduced in figures 15 and 16 are widely distributed in the limnic layers of Europe and North America from Oligocene to Miocene in age. The upper Oligocene and lower Miocene are particularly rich in these fossils. From the papers of H. BANDULSKA (1923, 1926 and 1928) it appears that such leaves are also present in the Eocene at Bournemouth, England. All the leaves reproduced here are from the Moselund lignite.

Folia triplinervia of the lauraceous type occurring as fossils have commonly been referred to the recent genus *Cinnamomum* and a considerable number of species have been established. M. STAUB (1905) compiled a list of their occurrences together with the relevant literature and reproduced many figures from the older publications. This gives a comprehensive view over the variability of the types established as species.

The material from Moselund shows certain differences in shape and size (fig. 15 and 16) so it seems desirable to control the interdependence by an anatomical investigation. The state of preservation of the leaf substance made this possible. Microscope slides showing the cuticle and details of the mesophyll were easily prepared. Most of the leaves figured were anatomically investigated and the specific unity is thus beyond doubt. The lamina of the leaf must have been rather thin.

Anatomy

The epidermis of the upper surface shows straight to somewhat wavy side walls of differing thickness, but without being able to refer this character to a particular leaf type. The epidermal elements of the lower surface are always extremely thin and are less well preserved than those of the upper surface. Stomata are only present on the under side, often forming small clusters in the intervenia, and at a magnification of about 200 times they give the impression, shown in fig. 17 B, of a protruding dome formed by the two accessory cells and almost covering the guard cells. As only the cuticle of the guard cells is preserved only the slit between these is visible. The stomatal apparatus is surrounded by 4–6 ordinary epidermal cells. Figures 17, A and B, are reproduced from the same leaf, the other figures are drawn from various, especially favourable parts of the leaves of the available material. Fig. 17, D, shows a reconstructed stomatal apparatus and its surrounding cells.

A characteristic epidermal feature is the numerous, circular or polygonal thickwalled elements which are found on the under side of the laminae in all the leaves investigated. Their margin is slightly protruding. They represent the basal parts of unicellular, thick-walled cover hairs, wedged in between the thin-walled epidermal







Fig. 16. Litsea polymorpha A. Braun. (1/1) Moselund.



Fig. 17. Litsea polymorpha A. Braun. A, epidermis of the upper surface of leaf; B, clusters of stomata on the under side; C, upper side of leaf with epidermal walls of a thinner walled type; D, reconstruction of the stomatal apparatus and its surrounding cells; E and F, hairs from between the thin-walled epidermal elements of the under side of the leaf; G, transverse section of leaf showing two larger elements (30–100 μ broad) with well preserved walls in the palisade tissue; H, transverse section through the epidermis of the under side of the leaf. (A–C×200, D–F×400, G–H×200). Moselund.

elements. A few hairs were found undamaged (fig. 17 E and F); the leaf must have been densely covered with such hairs most of which are shed.

Larger elements $(30-100 \ \mu \text{ broad})$ with a rather well preserved wall are commonly developed in the mesophyll and predominantly occur between the palisade cells. Figure 17, G, shows part of a transverse section with two cells of this type enclosed between palisades. They represent secretary cells often containing a yellowish-brown

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Fig. 18. Litsea glauca Siebold. A, epidermis of the upper, and B, of the under surface of the leaf; C, a hair, and D, a stoma. $(A-B\times 300; D\times 400)$.

mass, evidently hardened balsam. The mesophyll is almost totally destroyed and the fibres accompanying the conductive tissue of the veins seem to be without crystal chambers. Figure 17, H, shows a section through the epidermis of the under side.

Affinities

According to these statements there seems no doubt that these fossils represent foliage of a plant belonging to the Lauraceae. The folium triplinervium type is widely distributed among the angiosperms, but when the oil cells, cover hairs and the rather specific stomatal apparatus is also considered the systematic probabilities are very limited so that in fact only the Lauraceae can claim consideration. It proves more difficult to relate our fossils to a distinct genus. Attention must be directed to Lauraceae types combining the shape and venation of the leaf, the structure of the laminae and the dense hair covering of the lower side of the leaf.

The studies of H. BANDULSKA (1926, 1928) on the leaf anatomy of *Cinnamomum*, *Lindera* and *Litsea* show that the systematically useful anatomical differences between them are small. The characters of our fossils indicate *Litsea*, but this genus has a very extensive range and it proved impossible to consider all the species.

Probably *L. glauca* SIEBOLD might be regarded as a likely type, yet it differs in anatomical detail: two layers of palisade cells and a hair covering somewhat different. Fig. 18, A–D, shows details of its anatomy. A faint greyish, dewy cover, probably of
a waxy nature, found on the upper surface of the laminae perhaps has its parallel in the fossil, mainly perceptible in the leaves freshly dug out from the lignite.

As specific name the designation *polymorpha* might be employed in spite of the almost total lack of anatomical detail concerning the numerous types collected under this name. It must have been rather common in the Tertiary; the literature list given by M. STAUB (1905) comprises 73 items.

The occurrence of small leaves together with larger ones does not hinder their reference to the same species. The same "cinnamon" species, for example, has been shown by M. STAUB (op. cit.) to have branchlets carrying both leaves of a normal size and shape, and smaller leaves. A considerable range of variation is thus acceptable.

Acer trilobatum A. BRAUN

(Phyllites trilobatus C. v. Sternberg)

The two leaves reproduced in figure 19, A and B, appeared as imprints in the vellow clay dominating the upper layers of the lignite at Moselund. The leaves of this species show a wide range of variation; ALEXANDER BRAUN (1845) distinguished no less than four types (A. productum, A. tricuspidatum, A. trilobatum and A. vitifolium) regarded by him as distinct species. This variation makes it difficult to give a short and concise diagnosis. W. PH. SCHIMPER (1874 p. 130) attempts a combination which runs as follows: 1. Acer trilobatum (Sternberg) Alex. Braun. Foliis longe petiolatis, palmato-trilobis, vel subquinquelobis, lobis plerumque inæqualibus, lobo medio lateralibus longiore et latiore, rarius æqualibus; inciso-dentatis, dentibus inæqualibus, apice longe acuminatis, lobis lateralibus patentibus vel plus minus arrectis, sinubus angulum rectum, subrectum, interdum acutum formantibus. O. HEER (1856) based his description on an extensive collection mainly from the layers at Oeningen (Switzerland), and included the four types of A. BRAUN in one species: A. trilobatum. The leaf type in question was first studied by C. v. STERNBERG (1828, *Phyllites trilobatus*) and figured in his Flora der Vorwelt (Tab. 50, Fig. 8). F. UNGER (1847) notes the species under the name A. trilobatum and figured a series of leaves (op. cit. Tab. 41, Fig. 1-8). Our specimens agree particularly well with the leaves figured by O. HEER (1856, Tab. CXII-CXV) which are distinguished by their tapering, almost wedge-shaped, bases.

The double samaras so characteristic of *Acer* species were not found in the layers of Moselund.

Acer trilobatum is widely distributed in European Tertiary deposits extending from the Oligocene to the Pliocene, with a maximum distribution in the early Miocene. According to A. Pax (1885) it represents a fossil member of his *rubra* section (A. paleo. rubra).



Fig. 19. A and B Acer trilobatum A. Braun. C and D Acer brachyphyllum O. Heer. (1/1). Moselund.

Acer brachyphyllum O. HEER

Leaves referable to Acer brachyphyllum were also found in the Moselund lignite. Figure 19, C and D, show fragments which are sufficiently complete to allow a reconstruction. O. HEER in his *Flora Tertiaria Helvetica* III (1859, Tab. CXVII, Fig. 10–13) figured a series of entire leaves of *A. brachyphyllum* with which our material

agrees very well. In the *Traité de Paléontologie végétale* W. PH. SCHIMPER gives a diagnosis of the leaves which runs as follows: 15. Acer brachyphyllum HEER. Foliis ambitu cordato-subrotundis, trilobes, lobis latis, brevibus, sparsim grosse dentatis, apice acuminatis, sinubus augustum rectum vel oblicum formantibus (III, 1874, p. 137).

The species is noted from the Tertiary of Oeningen (Switzerland), from horizons of an older age such as at Bilin (Austria) and the lignitic layers of the Rhein valley.

A. brachyphyllum is regarded by A. Pax (1885) as representing a Tertiary type of his A. spicata section (Paleo spicata).

Parottia fagifolia (H. R. GOEPPERT) O. HEER

Leaves referable to *Parottia fagifolia* are probably among the most common fossils in certain layers of the Moselund lignites. They are sometimes found heaped so closely together that it was almost impossible to separate individual leaves undamaged as the enclosing matrix with its rich content of carbonized plant debris was incoherent and crumbly. Efforts to obtain whole leaves were successful from the upper yellow layers; the accompanying figures of the large leaves are drawn from imprints. In the dark layers of the fossiliferous clay the leaf substance is more or less well preserved, but strongly carbonized and only present as a thin, crumbly film.

The figures given in the drawings (fig. 20 and 21) show the outlines and venation of some common types of the fossil leaves. They have short petioles, are obovate, more or less acuminate with the base most often somewhat oblique and an outline rounded to almost cordate to acuminate and sometimes wedge shaped. The margin of the upper half is sinuous to sinuous dentate, in the basal part always entire. The two first secondary veins emerge at or at least very near the base of the lamina, opposite or almost so; the other veins alternate and set off at acute angles, craspedodromous, while the tertiary issue at right angles.

H. R. GOEPPERT (1855) referred leaves like these to the genus Quercus (Q. fagifolia), but O. HEER (1859) and C. v. ETTINGSHAUSEN (1869) recognized their real systematic position, and their resemblance to leaves of certain extant Hamamelidaceae, especially those of *Parottia*, *Fothergilla* and *Hamamelis* of which *Parottia* claimed particular attention. In order to support this reference a number of the best preserved of our specimens were studied anatomically. Unfortunately the cell walls of the mesophyll elements, the epidermal cells and the fibres accompanying the veins proved mostly dissolved so that only the epidermal cuticle offered discernable details. According to some remaining traces the side walls of the epidermis were undulating and stomata only found on the under side of the leaf. A fine warting of the cuticle was perceptible.

As is well known, especially through the work of A. REINSCH (1890), certain Hamamelidaceae have cover hairs of a rather peculiar type (fig. 22, A–D). Certain elements of the epidermis are developed as thick-walled cups enclosing the basal parts



Fig. 20. Parottia fagifolia (H. R. Goeppert) O. Heer. (1/1). Moselund.

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Fig. 21. Parottia fagifolia (H. R. Goeppert) O. Heer. (1/1). Moselund.



Fig. 22. A–D, tufts of cover hairs and their epidermal bases in the extant *Parottia persica*, A in front view, D in section. E–G, front view of hair tuft bases in the epidermis of the midrib of *Parottia fagifolia*, (×400). H–I, pseudomorphs of calcium oxalate in the collapsed mesophyll of *P. fagifolia*. (×300). Moselund.

of a tuft of one-celled, tapering, thick-walled hairs. Fig. 22, A and D, show such cups empty as the hairs are shed. In the genera *Fothergilla* and *Hamamelis* hairs of this type are found on most of the lamina, in *Parottia* they are almost exclusively confined to the middle vein.

In the fossil the tuft of hairs have disappeared but the thick-walled cups enclosing the base may be preserved and through their existence a hair covering of the type mentioned can be deduced. Elements of this structure were found in the epidermis of the midrib (fig. 22, E–G). In the epidermis of the intermeria such structures were not found although a considerable number of leaves were examined.

In some Hamamelidaceae, e.g. *Parottia*, small or large crystals of calcium oxalate are found enclosed in the mesophyll tissue, mainly in the palisade layer. In the extant *Parottia* they attain a considerable size and are easily demonstrable in a leaf bleached with sodium hypochlorite. The figures 22, H and I, show parts of the fossil in which some mesophyll is still preserved, but only the crystal-bearing elements have kept their original size and shape due to the crystal filling which is probably a pseudomorph of the original calcium oxalate crystal. They attain a size of about 20μ . In the extant *Parottia* smaller crystals are crowded beside and on the veins, but these cannot be demonstrated in the fossil.

The leaves referred to *Parottia* are of rather variable size; two types are easily recognizable, a larger and a smaller. The extant *Parottia* shows the same feature, the long, slender branches carrying leaves of the first type, while the buds on these slender branches only develop into branchlets with a few leaves of the second type.

Fossil leaves referable to *Parottia fagifolia* (H. R. GOEPPERT) O. HEER are widespread in central Europe from the middle to the upper Miocene (Schossnitz, Silesia).

The recent analogue, *Parottia persica* (DE CANDOLLE) C. A. MEY is found in the mountain region of north-western Persia, where it thrives in damp and sheltered places.

Liquidambar europaeum A. BRAUN

Imprints of a few leaves easily recognizable as a *Liquidambar* are available from the lignitic clay at Moselund. Two types, a large five lobed specimen and a smaller trilobed, both present only as fragments are illustrated in fig. 23 A and B. Leaves and fruiting heads referable to *Liquidambar* are rather common in the Miocene deposits of Europe (P. MENZEL 1906). O. HEER (1856, Tab. LI–LII) figures a collection of leaf types of *L. europaeum* A. BRAUN while H. CZECZOTT and A. SHORGILLO (1959) illustrate buds of what is probably another species, *L. magnilocitata* CZECZOTT & SHORGILLO.

Zizyphus tiliaefolius (F. UNGER) O. HEER

The two leaves figured (fig. 24 A and B) were collected from the lignite at Moselund. As they are only imprints an anatomical verification is not possible. The size, shape and venation is rather characteristic and permits a reference to the genus *Zizyphus*, the extant species of which show leaves of this type. It is found fossil in Neogene Tertiary layers of Europe. In the memoir of E. BAUMBERGER and P. MENZEL (1914) a thorough diagnosis is given which runs as follows: Z. foliis petiolatis subcordatis vel orvato-ellipticis accuminatis, crenatus-seratis, triplinerviis, nervis secundariis infimis basiliaribus vel suprabassilaribus arcuatim adenisentibus extus ramosis ramis in dentes margine exeuntibus vel crenatum conjunctum et ramulis in dentis imittantibus nervis secundariis ceteris angulis acutis primario egretiantibus, nervis tertiariis transversis subparalellis angustis rectis e mediano orientibus, partim ramosis. This diagnosis agrees with our fossil.

This species is noted from the Tertiary of Switzerland (Oeningen) and from the Neogene of Austria (Bilen), Bohemia and Italy. The figures of F. UNGER (1861–1866) as well as the leaves figured by ETTINGSHAUSEN (1867, Tab. 2, Figs. 14, 15, 17 and 18) and also those of VELENOVSKÝ (1881) agree very well and correspond closely to our fossils.



Fig. 23. Liquidambar europaeum A. Braun, A-B, leaves of different types. C, Styraciphyllum sp., leaf. Both (1/1). Moselund.



Fig. 24. Zizyphus tiliaefolius (F. Unger) O. Heer. (2/1). Moselund.

Nyssa disseminata (R. Ludwig) F. Kirchheimer

A number of specimens of carpoliths referable to *Nyssa*, a genus widespread throughout the European brown coal layers, were collected from the lignite of Silkeborg Vesterskov. The state of preservation allowed an anatomical investigation so that a comparison with the monopyrenous drupe of the extant *Nyssa* was possible.

HARTZ (1909, Tab. III, Fig. 14–16) illustrated pyrenes that are 30×18 mm in size. Most of the Moselund material is considerably smaller, and a group of pyrenes figured by KIRCHHEIMER (1957, Tan. 46) are smaller still. Carpoliths from the Eocene London clay have been assigned to four distinct species on the basis of their size difference (C. and E. REID 1915).

In outline the carpoliths are ovoid, compressed and 3–4 mm thick. The pyrenes often split into two halves parallel to the broad sides. The surface shows 10–16 broad, bluntly protruding ribs separated by thin furrows running from the base to the top of the pyrene.

The wall of the pyrene is built up of thick-walled prosenchymatous elements, arranged in groups differing in the arrangement of the component cells (fig. 25 B).



Fig. 25. Anatomical details of the pyrene of the extant Nyssa multiflora, A and C, transverse and longitudinal sections respectively of the innermost part. B and E, transverse and longitudinal sections respectively of the pyrene of the fossil Nyssa disseminata (R. Ludwig) F. Kirchheimer. D, rows of thin-walled parenchyma elements, originally crystallophore, of N. disseminata. (×300). Silkeborg Vesterskov.

Rows of thin-walled, crystal-bearing parenchyma (the calcium oxalate crystals have been dissolved) and tangentially stretched cavities denote the places originally occupied by the vertical conducting tissue of which only a few quite narrow vessels remain.

The inner border layer is composed mainly of axially stretched prosenchymatous elements (fig. 25, E).

Parts of the pyrene of the extant *Nyssa multiflora* are reproduced in figure 25, A and C, for comparison. The similarity to the fossil is striking. The thin-walled parenchyma, of course, shows the original crystal contents.

The genus Nyssa, together with Davidia and Carupotheca, are now regarded as forming a family of their own: the Nyssaceae. Nyssa drupaca of North America is probably the recent analogue of the fossil N. disseminata. Leaves were not found in the Danish lignites. They are recorded by R. KRÄUSEL from the upper Miocene layers of Schossnitz. The specific name 'disseminata', according to F. KIRCHHEIMER (1957), was erroneously given by R. LUDWIG (1858) to a carpolith of quite another origin, a Pinus seed, which later has proved identical with Nyssa pyrenes.

Styraciphyllum sp.

(Pterostyrax sp. ? P. Menzel)

Only one specimen has been noted at Moselund of leaves of the type reproduced in fig. 23, C. P. MENZEL (1906) has figured part of a similar leaf from the Senftenberg layers (op. cit. Tab. VII, Fig. 44). The characteristic denticulation of MENZEL's illustration agrees with those from Moselund, and are suggestive of a tree belonging to the Styraceae. His Latin diagnosis runs as follows: P. foliis membranacei, ovatis; apice acuminatis, margine remote argute denticulatis, nervis secundaries e primarie angulis $40-60^{\circ}$ orientibus, paralellis, sursum arcutatis, camtodromis, ramilos externos in dentis emittentibus, nervis tertiaria angulis acutis egredientibus, maculas oblongas formatibus. (op. cit. pag. 123).

Similar leaves are not uncommon among the Styraceae occurring, for example, in the genera *Halesia* and Styrax, and it will probably not be possible to refer our leaf to a definite genus. A. G. NATHORST (1885) compared similar leaves from the Tertiary of Japan with the leaves of the extant Styrax japonica, and P. MENZEL draws attention to *Halesia (Pterostyrax) cuspidata* SIEBOLD & ZUCCARINI as a possible related species.

Menyanthes tertiaria O. HEER

A number of small, dark coloured seeds, somewhat scattered but still forming a distinct group, were found on a cleavage surface from the bottom layer of the lignitic clay at Moselund. The seeds were of the same size and shape, like small, very thick lenses, 2 mm in diameter and about 1 mm thick. This agrees with the figures given by O. HEER (1859, Pag. 30, Tab. CIV, Fig. 3). The seed coat only encloses a cavity since the contents are totally dissolved. The state of preservation allowed the preparation of very thin transverse and tangential sections, suitable for anatomical study.

Fig. 26, B and C show parts of transverse sections. The epidermis is partly preserved intact showing side walls thickened in such a way that the thickening gradually grows against the outer part of the cell, so that the lumen appears as a pointed arch. Much of the thickening is partly dissolved in the fossil so that only the cuticle and the middle lamella are found intact and the secondary parts of the wall are visible as a greyish shadow (finely dotted in my figures). Fig. 26, B–C show the character of the subepidermal layers which consist of an uniformly developed tissue of polygonal, thin-walled elements, indistinctly pored, and traces of the raphe. In front view the epidermis is composed of longitudinally stretched elements, their ends wedged together and the wall appears distinctly pored where the thickening is preserved, and the lumina often only visible as narrow strips.

The corresponding parts of the extant *Menyanthes trifoliata* L. agree with those of the fossil and with the anatomical detail visible in the photographs of F. KIRCH-HEIMER (1957, Tab. 6, Fig. 35). Thus the seeds in question can be compared to those



Fig. 26. Menyanthes tertiaria O. Heer. A, transverse section of a seed. (30/1); B–D, details of seed coat in transverse and longitudinal sections. ($\times 300$). Moselund.

of the living species, though naturally specific identity cannot be proved. or at any rate a similar species.

The extant genus *Menyanthes*, regarded as representing a family of its own, is nearly allied to the Gentianaceae. The geographical range of *Menyanthes* is borealcircumpolar although in eastern Asia (China and Japan) a *Menyanthes* species has a more southerly distribution.

Nymphaeoidea lignitica n. sp.

The four leaves sketched in our figure 27, A–D, were collected from the dark coloured basal part of the lignitic clay at Moselund. The leaves are all of the same type, a deeply cordate base making them characteristic and indicates a floating leaf. Three of the specimens are almost of the same size; one is notably smaller. A fragment of a far larger leaf is not figured.

The specimens reproduced in the sketches (fig. 27, A–C) may represent the normal size range, but there has probably been considerable variation. All the specimens lay with their upper surfaces upwards. The lamina is intimately connected with the clay so that it is impossible to isolate the leaf as a whole. Thus the anatomy had to be studied partly on fragments and partly in reflected light under the binocular microscope. Some details of systematic value could be ascertained which referred them to the natural group of the Nymphaeoideae.

The remains of the thin stalk is found at the base of the incision. The main rib is distinct but the venation as a whole is very feebly marked and only the basal parts



Fig. 27. Nymphaeoidea lignitica n. sp. A-D, types of floating leaves (2/1); E-G, the upper and lower layer of the air-chambers. In E and F some bases of the internal hair-like sclereids are shown; in G the hydropotes are visible in the epidermis of the under side. (×300). Moselund.

of the lateral veins are discernible while the ramifications are minutely thin. The leaf substance is partly dissolved, but a tendency to successive scaling of the more resistant layers allows an anatomical study of the component elements.

Anatomy

The epidermis of the upper side appears as an almost black film. Its polygonal elements are only distinguished by the fine cracks, corresponding to the side walls of the cells. Traces of the stomata can only be demonstrated by their outer slit which appears as a fine, 20μ long diaphanous dot with the guard cells only occasionally

visible. Only some compressed rests are preserved of the succeeding assimilation layer in which the brown substance is here and there intermingled with white streaks and spots sometimes arranged in small circles which are probably remains of a sclerenchyma.

The subsequent layers are developed as an aerenchyma and are distinctly divided into two types of layers: an upper continuous layer composed of relatively small air-chambers (fig. 27, E, F) enclosed by quite small, rather thick-walled elements, and a lower layer composed of far larger units enclosed by rows of thin-walled cells (fig. 27, G). This lower part of the floating tissue is often totally destroyed and is only recognizable by traces of the walls that are left. Of the epidermis on the under side only patches of quite small $(6-7\mu)$ elements have avoided destruction; they are of various sizes, rounded or elliptical in outline, the larger ones more irregular. The cells composing them are mostly filled with a brown or black substance. These cells form an epidermal tissue of a very peculiar character, and have evidently proved more resistant to dissolution and destruction than the rest of the under side aerenchyma.

Diagnosis

Leaves of the floating type, oblong to almost orbicular, margin entire, base deeply cordate, in the bottom of the incision rests of the slender stalk, venation obscure except for the midrib. Stomata found only on the upper side of the leaf. A subpalisade layer of small, rather thick-walled elements forms the roof of the large under side air-chambers, the bordering layers of which, as well as the cells of the under side epidermis, are built up of extremely thin-walled elements. A hydropote occupies the central part of the epidermis under each air-chamber. The mesophyll as a whole has been traversed by hair-like, ramifying sclereids of which only fragments are preserved in the fossil.

Affinities

The fossil leaves agree very well in shape, size and available anatomical detail with the leaf characters of the extant genus *Nymphaeoidea*, the best known of which is *Nymphaeoidea limnanthenum* commonly kept in the ponds of botanical gardens. E. PERROT has given in his memoir *Anatomie comparée des Gentianacées* (1898) a comprehensive account of the Gentianaceae including the group of the Menyanthoideae which modern taxonomist consider a separate family.

The small group of narrow, resistant elements of the lower epidermis were detected by this author who termed them 'Hydropotes'. They are restricted to the *Nymphaeoidea* group of the extant Menyanthoideae, which includes species with floating leaves, highly variable in size, but mostly far smaller than those of *Nymphaeoidea limnanthenum*. Another generic character present is the occurrence of numerous internal hair-like sclereids, more or less ramified, often emerging from the walls of the air-chambers. The hair-like sclereids are often abundantly branched and so have



Fig. 28. The extant Nymphaeoidea humboltiana. A, transverse section of leaf; B-E, aerenchyma, B, C and E drawn in front view, D in section, and E, shows hydropotes. ($\times 300$). Herbarium material.

a very complicated appearance, often completely filling the air-chambers as a compact mass of entangled branches. On closer inspection hair-like sclereids are not only directed downwards into the larger air-chambers but in some cases also upwards penetrating the palisade tissue. Most of the under side of the fossil leaves is dissolved and the sclerenchymous hair-like protuberances have consequently disappeared and only traces of their basal parts remain (fig. 27, E, F). The upwards directed branches are better preserved by the bordering palisade cells and are sometimes traceable, and when the branches form a candelabrum-like group the transverse section will of course show a small circle of sclerenchymatous elements (fig. 28, A). The well known 4

Biol. Skr. Dan. Vid. Selsk. 20, no. 9.

'internal hairs' of, e.g. *Nymphaea*, may be compared with these sclerenchyma hair-like formations of the Nymphaeoideae.

The Botanical Museum of the University of Copenhagen has placed its rich material of the Nymphaeoideae at my disposal. Several species show a considerable range of leaf variation in both shape, size and thickness of the lamina. In the thin leaves a reduction of the palisade tissue is noticeable and the sclerenchyma hairs are more poorly developed.

Leaves showing a certain similarity with our fossils are described under the name 'Hydrocharis arbicularis' by O. HEER (1859, Tab. C II) and as 'Hydrocharis obovata' by PH. WESSEL & O. WEBER (1856, Tab. XXX). According to the venation the latter might be referred to Hydrocharis.

The genus *Nymphaeoidea* is widely distributed in the floras of the present time, notably in North and South America, where a species extends as far north as Canada, and from Africa and Asia. The extant *Nymphaeoidea humboltiana* from South and Central America shows some parallelism with our fossil.

Apocynophyllum sp. cf. A. helveticum O. HEER

Leaves of the type reproduced in fig. 29 A–I and fig. 30, A–I are rather common in the lignitic clay at Moselund, especially in the dark coloured bottom layer. Similar leaves are figured by O. HEER in his *Miocene Baltische Flora* (1869 a) and in the *Flora Tertiaria Helvetica* (1859) and named *Apocynophyllum helveticum*. They are distinguished from other leaves which O. HEER also referred to *Apocynophyllum* by the short attenuated base, while in the other species the transition from limb to stalk appears to be more gradual. In the *Flora Tertiaria Helvetica* Tab. C IV is figured a branchlet with opposite leaves, a feature common in the Apocynaceae. The state of preservation is rather poor and the lamina appears very thin. The upper surface seems to be somewhat wrinkled while the under side is smooth and glossy.

By inspection under the binocular microscope with intense illumination, the surface shows a singular structure, appearing as composed mostly of small $(20-30 \mu)$ circular elements intermingled with some larger ones and evidently forming an almost coherent subpalisade layer. Under higher magnification they are conspicuous through their dark brown content probably representing hardened latex. Rests of the epidermis and palisade layer were only sparingly found; the tissue of the aerenchyma was also mostly destroyed. Numerous black dots about 10μ in diameter were perceptible. These represent fragments of latex tubes of which larger fragments could be demonstrated especially accompanying the veins and their borders.

The few available details combined with the shape and venation of the leaf indicate a plant of the Apocynacean family. According to C. SPIRE (1905) only a few genera of the family show a continuous layer of latex cells under the palisades. *Echitus, Cleyhornea, Kopsis* and *Taberncemontana* all have such cells but the leaf type of our fossil only agrees with that of *Echitus.* Some material for comparison was by courtesy



Fig. 29. Leaf outlines of A pocynophyllum sp. (1/1). Moselund.

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Fig. 30. Leaf outlines of A pocynophyllum sp. (1/1). Moselund.

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Fig. 31. Schematic cross section of the Miocene of Jutland. After L. B. Rasmussen (1966).

obtained from the herbarium of Kew Gardens. The anatomy agrees fairly well with that of the fossil, so that it seems probable that this represents a type allied to the extant *Echitus*; the generic name *Apocynophyllum* might perhaps be altered to Echitophyllum but the characters of the fossil do not allow a closer interdependence with an extant genus.

Stratigraphic notes

In spite of the efforts in determining the geological age of the Miocene deposits of central Jutland, of which B. ESKE KOCH et al. has given a comprehensive summary (1973), there still remains a few unsolved details. The modern interpretation is expressed by L. B. RASMUSSEN (1966 et seq.) and illustrated by the well known sketch reproduced here as fig. 31. The marine and limnic facies interdigitate, with the marine influence retreating westward on two occasions, viz. between the Lower and Middle Miocene, and again in the upper Middle Miocene, followed by a complete marine transgression. The marine deposits are well dated by the molluscan fauna.

Within the limnic facies the coal layers have been exploited on a large scale at Fasterholt, Salten, Lystrupsminde and Troldhede. These have yielded samples of fossil wood which by xylotomic examination, etc. are referable to *Sequoioxylon*, *Taxodioxylon*, *Glyptostroboxylon*, *Sciadopityoxylon*, *Pinuxylon*, and some *Cupressinoxylon* (F. J. MATHIESEN, 1970). But these are not of much use for age determination.

The Moselund deposit, which has yielded most of the determinable fossil leaves, and the lignites of Silkeborg Vesterskov claim special interest. They are undoubtedly autochthonous lacustrine formations. Both occur as elevated plateaux (Moselund about 80 m above sea level). The plant remains do not bear impressions of having been exposed to attrition by long transport in flowing water. The flora of Moselund is remarkably rich in Pteridophytes and dominated by angiosperms with only a few gymnosperm species. Unfortunately these deposits are not found associated with marine layers.

The presence of species referable to *Nypa*, *Brachychilus*, *Ficus* and *Ocotea* give the flora a striking aspect which perhaps might allow these deposits to be placed geologically somewhat before the bulk of the productive brown coal layers, probably in the upper part of the Ribe Formation. The presence of *Parottia* and *Salvinia bjerringii* is also noteworthy as well as some fern types.

In the search for Miocene floras comparable with the floras of Moselund and Silkeborg Vesterskov attention is drawn, among others, to a paper by H. CZECZOTT (1959) on the fossil floras of the Tertiary rift valley of north-eastern Bohemia which has extremely rich Tertiary floras from the Middle Oligocene to the Middle Miocene. From these floras the author has attempted to give a floristic summary of the different strata. She regards the deposits of Ducheny (Dux) and Vrosovice (Laumy) as the youngest of these floras placing them in the Helvetian series, i.e. Middle Miocene. Attention is drawn to the presence of *Parottia* which according to the author first appears in strata of this age.

Remains of palms are known as late as from the Upper Miocene (F. KIRCH-HEIMER, 1957). The fossil flora of Samland, described by O. HEER (1869 a) as being of Miocene age, shows parallelisms to the Moselund flora. The age is commonly regarded as Upper Oligocene (Aquitanian), but is probably younger, up to the Middle Miocene.

A striking feature of the larger floras, especially those of the older parts of the Miocene, is the mixture of types now restricted to sub-tropical zones with genera more familiar in more temperate climates. Moselund is no exception in this respect showing the same features known from comparable localities. Most of the more common Neogene species show a remarkable horizontal as well as vertical distribution.

If the Moselund and Silkeborg Vesterskov floras are regarded as being of Middle Miocene age it would give a closer connection between these deposits and those of the western brown coal layers.

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PLATES

PLATE I Arundo sp. rhizome. (1/1). Moselund.



PLATE II Palmacites nypoides n. sp. folium. A and B, show epidermal and hypodermal layers. In B, sclereids of the hypodermis are visible. (×175). Moselund.

Pl. II



 $\label{eq:Plate III} Palmacites nypoides n. sp. folium. A, the second hypodermal layer with numerous hydathode pits. B, surface layers of the rachis. ($$\times175$). Moselund.$

PL. III



PLATE IV Palmacites nypoides n. sp. Fragment of a leaf showing the venation. (1/1). Moselund.



PLATE V Brachychilophyllum sp. Fragments of leaves. C, shows 3–4 folds parallel to the border to the left of the arrow. (1/1) Moselund.




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