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THE MIOCENE FLORA OF KREUZAU,
WESTERN GERMANY

I. THE LEAF-REMAINS

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SUMMARY

The geology of the plant-bearing deposits from Kreuzau is related to the geology of the Lower Rhine Basin as a whole. The available evidence would suggest a Middle Miocene age for the Kreuzau sediments. The preponderance of leaf-remains in the deposit is discussed in the light of experiments on leaf transport. Much weight is placed on the use of cuticle analysis in the grouping of the leaf-remains into taxa and as an aid in the determination of the affinities of the fossils. Special emphasis is placed on the need for care in the interpretation of the leaf-remains in terms of living taxa. Of the 77 taxa described, 65 would appear to be referable to the Dicotyledoneae. However, of these 65 taxa only 29 could be referred to a family and 17 to living genera. Only one of these 65 taxa was considered to deserve a specific epithet. The presence of 15 dicotyledonous families could be confirmed. These were the Aceraceae (1), Aquifoliaceae (1), Cercidiphyllaceae (1), Fagaceae (2), Hamamelidaceae (2), Juglandaceae (1), Lauraceae (7), Loranthaceae (1), Myricaceae (1), Platanaceae (1), Rhamnaceae (1), Rosaceae (2), Salicaceae (4), Schisandraceae (1), and Ulmaceae (3). The figure in brackets after each family indicates the number of representatives within the family. The Monocotyledoneae were represented in the deposit by 5 taxa, two of which were taken to belong to the Liliaceae. Three taxa were referred to the Coniferopsida and one each to the Musci, Filicales and Salviniaceae. While the proper affinity of many of the taxa composing the assemblage must remain uncertain, it is pointed out that the assemblage can be interpreted in climatic terms with a fair degree of accuracy. Evidence derived from a quantitative study of leaf characters within the Dicotyledoneae would suggest a fairly humid, warm-temperate or subtropical climate during the deposition of the Kreuzau sediments.

ZUSAMMENFASSUNG

Geologisch gehören die Pflanzenreste enthaltenden Schichten von Kreuzau denen der niederrheinischen Bucht an. Die vorhandenen Anhaltspunkte weisen auf mittelmiozänes Alter hin. Das Überwiegen von Blattresten in den Ablagerungen wird im Lichte von Versuchen über Blatt-Transport besprochen. Für die Unterscheidung der Blattreste und das Feststellen ihrer systematischen Verwandtschaft wurde viel Gebrauch von der Kutikularanalyse gemacht. Es wird jedoch betont, dass beim Zuordnen zu rezenten Taxa grosse Vorsicht geboten ist. Von den 77 beschriebenen Taxa könnten 65 zu den Dicotyledoneae gehören; von ihnen lassen sich nur 29 in einer bekannten Familie und nur 17 in einer rezenten Gattung unterbringen; nicht mehr als eines konnte bis zur Art bestimmt werden. Folgende Dicotyledonenfamilien sind vertreten: Aceraceae (1), Aquifoliaceae (1), Cercidiphyllaceae (1), Fagaceae (2), Hamamelidaceae (2), Juglandaceae (1), Lauraceae (7), Loranthaceae (1), Myricaceae (1), Platanaceae (1), Rhamnaceae (1), Rosaceae (2), Salicaceae (4), Schisandraceae (1), und Ulmaceae (3). Die Zahlen in Klammern geben die Anzahl der gefundenen Vertreter an. An Monocotyledoneae fanden sich nur 5 Taxa, wovon zwei vermutlich Liliaceae. Die Coniferopsida sind durch 3, die Musci, Filicales und Salviniaceae durch je 1 Taxon vertreten. Wenn auch nicht von allen Taxa die Verwandtschaft festgestellt werden konnte, lässt das Material doch gewisse Rückschlüsse klimatologischer Art zu. Quantitative Untersuchungen von Blattmerkmalen an Dicotyledoneae zeigen deutlich, dass die Kreuzauer Schichten unter ziemlich feuchten, warm-gemässigten oder subtropischen klimatischen Bedingungen abgelagert worden sind.

RÉSUMÉ

La géologie des dépôts de Kreuzau peut être comparée avec celle du bassin du Bas-Rhin. Les arguments disponibles semblent indiquer un âge Miocène-moyen pour les dépôts de Kreuzau. L'abondance relative de feuilles dans les sédiments et des expériences mécaniques réalisées au laboratoire suggèrent que le matériel a été remanié. C'est surtout l'examen morphologique des cuticules foliaires qui a servi de critère pour grouper les feuilles dans des taxons. Cet examen a été également très utile pour déterminer les affinités des fossiles avec les genres actuels. Néanmoins il y a lieu de prendre garde lors de l'identification des feuilles fossiles. Des 77 taxons décrits, 65 sont référés aux Dicotyledoneae. Toutefois, de ces 65 taxons, uniquement 29 peuvent être déterminés jusqu'au niveau de la famille, tandis que 17 peuvent être attribués à des genres récents. C'est seulement à un des 65 taxons qu'un nom d'espèce a pu être donné. On peut confirmer la présence de 15 familles appartenant à des Dicotyledoneae: Aceraceae (1), Aquifoliaceae (1), Cercidiphyllaceae (1), Fagaceae (2), Hamamelidaceae (2), Juglandaceae (1), Lauraceae (7), Loranthaceae (1), Myricaceae (1), Platanaceae (1), Rhamnaceae (1), Rosaceae (2), Salicaceae (4), Schisandraceae (1), et Ulmaceae (3). Le chiffre, se trouvant entre parenthèses derrière chaque nom de famille, indique le nombre des taxons appartenant à celle-ci. Les Monocotyledoneae sont représentés dans le dépôt par 5 taxons, dont deux peuvent être envisagés comme appartenant aux Liliaceae. Trois taxons peuvent être correlés avec les Coniferopsida, un avec les Musci, un avec les Filicales et un autre avec les Salviniaceae. Malgré l'incertitude de déterminer avec précision plusieurs taxons rencontrés dans l'ensemble des restes foliaires, il est possible d'attribuer avec un certain degré de certitude un caractère climatique à l'ensemble. Une étude quantitative des caractères foliaires, limitée aux Dicotyledoneae, qui constituent la presque totalité de l'ensemble, suggère l'existence d'un climat chaud-temperé ou subtropicale, relativement humide pendant la formation des sédiments de Kreuzau.

THE PLANT-BEARING BEDS OF KREUZAU

Plant-remains have been known from the Tertiary of the Lower Rhine Basin for a long time. These plant-remains not only attracted the attention of German naturalists, for at an early date the attention of specialists from countries other than Germany was noticeable. The descriptions and illustrations of fruit- and wood-remains by the French naturalist FAUJAS-DE-SAINT-FONDS (1797) and the leaf-remains from Pützberg mentioned by LINDLEY (1833) are witness of this early interest. A short discussion of the plant-remains found in the lignite and associated sediments was given by LYELL (1833, p. 200) in his *Principles of Geology*. This interest has continued up to the present day (compare, e. g., the publication by the American palaeobotanist BROWN in 1953). A summary of the results of work on the Tertiary macroscopic plant-remains from the Lower Rhine Basin is given by KILPPER (1969).

The Lower Rhine Basin ("Niederrheinische Bucht" of German authors) forms a low-lying area surrounded on three sides by hilly country. The topography reflects something of the geology of the area. The hilly country is largely composed of rocks having a pre-Tertiary age, while the intervening low-lying land is underlain by a great thickness of Tertiary sediments. In the deepest part of the Lower Rhine Basin these Tertiary sediments reach a thickness of over 1,000 m. In the Rur Graben the sequence would appear to be most complete. In the lower part of the Tertiary succession supposed Palaeocene, Eocene, Early- and Middle Oligocene sediments have been encountered. However, the greater part of the sediments are younger in age. These deposits contain large seams of lignite which are exploited by means of open-cast mining. In German literature these seams are referred to as Flöze. These seams represent important points of reference in stratigraphical considerations. The main lignite seam is termed the Hauptflöz. In the northern part of the Lower Rhine Basin the Hauptflöz is interdigitated with clastic sediments. The resulting three seams are termed in ascending order, Flöz Morken, Flöz Frimmersdorf and Flöz Garzweiler. Any seam under the Hauptflöz or its equivalents is referred to as Unterflöz and that above the Hauptflöz is termed the Oberflöz. For a general account of the geology of the area one is referred to *Die niederrheinische Braunkohlenformation* (GEOLOGISCHES LANDESAMT NORDRHEIN-WESTFALEN, 1958) and *Geologische und bergbauliche Übersicht des rheinischen Braunkohlenreviers* (DEUTSCHE GEOLOGISCHE GESELLSCHAFT, 1966)

DESCRIPTION OF THE SITE

The locality yielding the leaf-remains described in this paper is situated to the east of the village of Kreuzau (fig. 1). Kreuzau is located in the Rur Graben on the western margin of the Lower Rhine Basin.

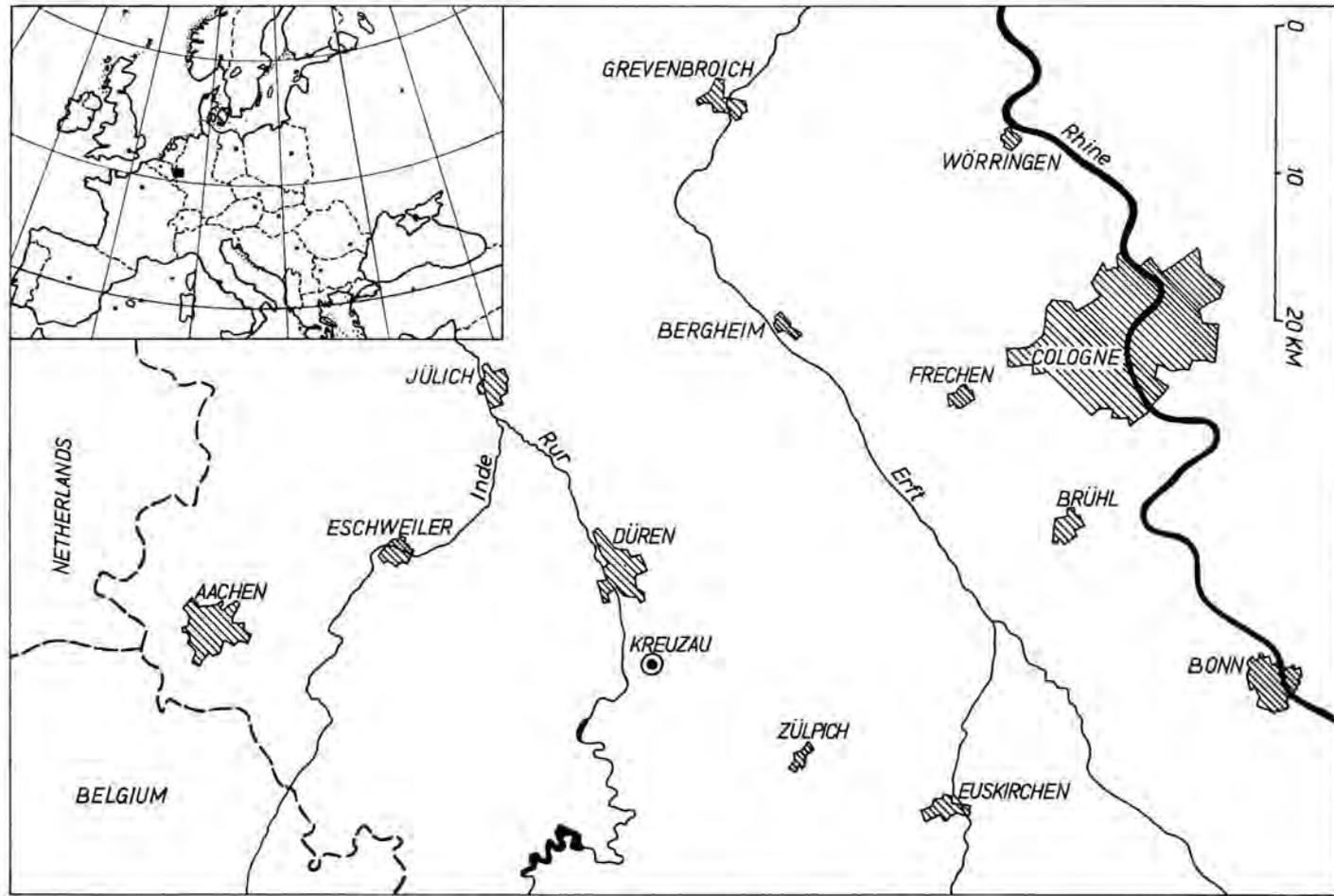


Fig. 1. Map showing the geographical location of Kreuzau.

Although SINDOWSKI (1939 b, p. 422) states in a footnote that the Kreuzau assemblage was discovered by G. Fliegel in 1910, A. Quaas had collected material from the site as early as 1902 and 1903. Early records of the plant-remains from Kreuzau are to be found in FLIEGEL and STOLLER (1910) and QUAAAS (1910). The site later became well-known through the work of WEYLAND (1934). At present plant-remains are still to be found in the sand-pit, now exploited by Wilhelm Pütz.

The lithological section of the Kreuzau sand-pit as exposed in Summer 1966 is shown in Table 1.

TABLE I
Section exposed in the Kreuzau sand-pit.

<i>Units</i>	<i>Lithology</i>	<i>Thickness (m)</i>
<i>D</i>	Boulder bed (Hauptterrasse) (<i>disconformity</i>)	max. 3
<i>C</i>	Lignite	max. 2.8
<i>B</i>	Flat-bedded light grey clays and whitish sands	2.25-4.5
<i>A</i>	Cross-bedded sands and grits, including clay-silt lens 2.9-3.5 m thick; minor clay lenses, light grey in colour, also present	max. 25

While BREDDIN (1935, p. 861) believed that the sands associated with the lignites were free from traces of ferruginous compounds, the cross-bedded sands *A* are, in fact, ferruginous. These sands are ochrous in colour when fresh, although weathering a whitish colour. The large clay-silt lens intercalated in *A* is iron-stained in the top 60 cm and to a lesser extent at its base. It is this lens which has yielded most of the plant-remains found. Some forty years ago the exposed thickness of this clay-silt lens was only 0.5-1.0 m (c.f. WEYLAND, 1934). The light grey lenses in *A* also contain sporadic plant-remains, but not in such a good state of preservation as those in the large clay-silt lens.

In *B* there is an increase in the percentage of clay towards the junction with *C*. Just under the lignite poorly preserved leaf-remains have been found. Near the base of *C* the lignite has a high percentage of clay, such that the junction between *B* and *C* cannot be sharply defined. Due to the disconformity the lignite is only present in the south western extremity of the sand-pit.

The sediments do not give the impression of being markedly disturbed, although PRANGE (1958) was able to demonstrate that the nearby sands and clays of Drove had been affected by faulting in two directions. Moreover, post-depositional warping of the Kreuzau beds has been evidenced by a gradual change of the strike of the flat-bedded sediments (*B*) within the sand-pit.

CONSIDERATIONS WITH REGARD TO CORRELATION

In the almost complete absence of any animal-remains which can be relied on in a faunal zonation of the continental deposits of the Lower Rhine Basin one must revert to information obtainable from plant-remains. This information can be considered under two headings, viz. (a) evidence from plant macrofossils, and (b) palynological evidence.

Evidence from Plant Macrofossils

Despite the large number of localities yielding plant macrofossils in Europe, it has proved difficult to make a satisfactory stratigraphical zonation on the basis of these plant-remains. Within a given stratigraphical sequence such macrofossils are only of sporadic occurrence and any correlation attempted must be based on a comparison with assemblages often found at some distance from the site under consideration. One must be very careful in correlating assemblages of plant macrofossils simply on the similarities or differences in the specific composition of the assemblages from other localities. In the past the stratigraphic position of a new site has frequently been determined as that of the locality or localities showing the greatest number of specific names in common with those of the new site. Such correlations not only rely on the trustworthiness of the taxonomic work, but also on the extent to which the plant-remains have been collected at a given locality. Furthermore, as has been pointed out at an earlier date (FERGUSON, 1967, p. 74), a great deal of the Tertiary palaeobotanical literature from Europe is concerned with plant-remains of supposed Miocene age. Any straight-forward comparison with the literature will therefore tend to have a certain inherent bias in favour of a Miocene age.

With regard to the plant-remains from Kreuzau certain specimens collected by A. Quaas in 1902-1903 were labelled as being Miocene in age. However, in early works dealing with the Kreuzau deposits (FLIEGEL and STOLLER, 1910; QUAAS, 1910) these were considered to have an Early Pliocene age. This conclusion was the result of a certain amount of inadequate reasoning, among which the supposed Mediterranean nature of the floral assemblage and the inclusion of the sediments in the Kieseloolith-Schichten. At that time the Kieseloolith-Schichten were invariably considered to represent the Lower Pliocene (compare, however, the work of, e.g., JURASKY, 1928; RICHTER, 1934; SINDOWSKI, 1939 b; WÖLK, 1941).

During a revision of the assemblage, H. Weyland (in PHILIPP and WEYLAND, 1934; WEYLAND, 1934) came to the conclusion that the Kreuzau deposits were Late Oligocene in age. This was based to a fair extent on a comparison with the macrofloral assemblage found at Rott in the Siebengebirge, south east of Bonn. WEYLAND (1934, p. 29) considered the deposits of Rott to belong to the Upper Middle Oligocene. In the past much emphasis has been placed on the presence of *Microbunodon minimum* (Cuvier) Déperet found within these beds. This mammalian fossil has been made use of as a guide fossil and referred either to the Upper Stampian or Chat-

tian (compare, e.g., SINDOWSKI, 1939 a, 1939 b; SCHWARZBACH, 1952; TEICHMÜLLER, 1958). However, ZÖBELEIN (1960) has pointed out that Oligocene mammals continued on as relicts into the Aquitanian Stage, while TOBIEN (1960) referred to *Microbunodon minimum* in a supposed Late Aquitanian mammalian assemblage. Furthermore, the K/A age determination of the Drachenfels trachyte, which is only slightly younger than the beds at Rott containing *Microbunodon minimum*, would suggest an age of 22.8 m.y.B.P. (LIPPOLT, 1961). This is equivalent to Early Miocene in the Geological Time Scales of HOLMES (1959) and FUNNELL (1964). However, according to BERGGREN (1969) the Oligocene/Miocene boundary is to be taken as 22.5 m.y.B.P..

Thus, since there seems to be agreement that the Kreuzau deposit is younger than that of Rott, a Late Oligocene age is by no means ascertained and one has to reckon with the possibility that the beds may, in fact, be Miocene in age.

Palynological Evidence

The application of pollen-analysis to the correlation of the lignites of the Lower Rhine Basin is an approach which has been largely developed since the Second World War. Pollen-analysis has the advantage over macro-fossils such as leaf-remains, that, whereas the latter are only locally present in appreciable numbers, a small sample of lignite is sufficient to yield hundreds of pollen grains and spores. Much of the work on the lignites has been carried out at the Geological Survey of Nordrhein-Westfalen at Krefeld, where in a period of ten years some 45,000 samples were investigated (REIN, 1961). This work, which is still in progress, has resulted in the erection of diagrams summarizing the succession of palynological assemblages in Central Europe from Oligocene to Pliocene (REIN, 1956, 1961; VON DER BRELIE, 1961, 1967).

For stratigraphical purposes the palynological assemblage is divided up into a number of taxonomic groups. Taxa of only sporadic occurrence in the preparations are usually excluded from the resulting pollen diagram. The chronostratigraphical interpretation of such diagrams must be made with care, since the composition may be affected by influences of an ecological nature. One has to bear in mind that the Lower Rhine Basin was an area undergoing subsidence. Where subsidence was greatest the formation of peat would not always keep abreast with the rise in the water table. A change of this nature would result in a change in the nature of the vegetation. The Lower Rhine Basin was furthermore an area prone to inundation by the sea. In cases of slow transgression by the sea one would expect to find similar vegetational changes to have taken place in the north as well as in the south of the area, but differing in age. This is a point emphasised by PFLUG (1958, p. 92). This theme was developed by JUX and PFLUG (1958 a, 1958 b). However, one of the factors leading to the formation of the great thickness of lignite in the Lower Rhine Basin would

appear to be the rapidity with which the area subsided (TEICHMÜLLER, 1958). It therefore seems possible to accept the premise (VON DER BRELIE and REIN, 1958, p. 559) that within a limited area the changes in the vegetation were no doubt synchronous. Thus the palynological zones established would appear to be of use in chronostratigraphical correlation.

The clayey intercalations exposed in the Kreuzau sand-pit were found to contain a palynological assemblage. However, because of the differences in facies, this assemblage cannot be adequately compared with the results of German authors, who have largely restricted their investigations to lignitic seams. Any comparison must be based on the pollen assemblage found within the lignite (C) of the Kreuzau succession. A detailed palynological study of this lignite was carried out by GELJSKES (1965), the results of which are summarised in fig. 2. In order to facilitate a comparison with the Krefeld diagrams the taxonomic concepts made use of are those to be found in VON DER BRELIE (1961, 1967). The sequence in which the relative percentages are presented is that of VON DER BRELIE (1961). The following taxa have been taken into consideration (the numbers correspond to those in the diagram):

- (1) *Inaperturopollenites emmaensis* (Mürriger et Pflug) Thomson et Pflug
- (2) *Engelhardtoidites microcoryphaeus* (R. Potonié) R. Potonié, Thomson et Thiergart

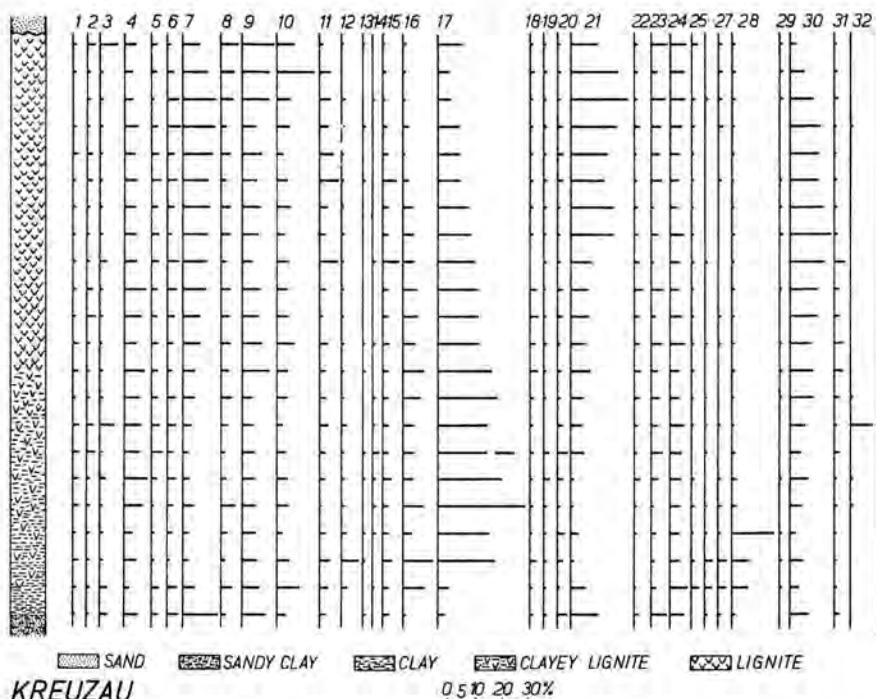


Fig. 2. Pollen diagram of the Kreuzau lignite (after GELJSKES, 1965). The levels sampled were spaced at 10 cm intervals. The numbers refer to those taxa mentioned in the text.

- (3) *Triatriopollenites rurensis* Thomson et Pflug
- (4) *Quercoidites henricii* (R. Potonié) R. Potonié, Thomson et Thiergart
- (5) *Quercoidites microhenricii* (R. Potonié) R. Potonié, Thomson et Thiergart
- (6) *Cupuliferoideaepollenites liblarensis* Thomson
- (7) *Cupuliferoideaepollenites fallax* R. Potonié
- (8) *Cupuliferoideaepollenites villensis* (Thomson) R. Potonié
(= *Tricolporopollenites villensis* (Thomson) Thomson et Pflug)
- (9) *Rhooidites pseudocingulum* (R. Potonié) R. Potonié, Thomson et Thiergart
(= *Rhoipites pseudocingulum* (R. Potonié) R. Potonié)
- (10) *Tricolporopollenites cingulum* (R. Potonié) Thomson et Pflug
- (11) *Tricolporopollenites megaezactus* subsp. *bruehlensis* (Thomson) Thomson et Pflug
- (12) *Araliaceoipollenites euphorii* (R. Potonié) R. Potonié
- (13) *Tricolporopollenites marcodurensis* Pflug et Thomson
- (14) *Tsugaepollenites*
- (15) *Inaperturopollenites dubius* (R. Potonié et Venitz) Thomson et Pflug
- (16) *Taxodiaceaeipollenites hiatus* (R. Potonié) Kremp
- (17) *Sequoiapollenites polyformosus* Thiergart
- (18) *Sciadopityspollenites serratus* (R. Potonié et Venitz) R. Potonié
- (19) *Caryapollenites simplex* (R. Potonié) Raatz
- (20) *Liquidambarpollenites stigmosus* (R. Potonié) Raatz
- (21) *Tricolporopollenites megaezactus* subsp. *exactus* (R. Potonié) Thomson et Pflug
- (22) *Araliaceaeipollenites edmundii* (R. Potonié) R. Potonié
- (23) *Nyssapollenites*
- (24) Bisaccate pollen
- (25) *Tripoporopollenites coryloides* Pflug
- (26) *Trivestibulopollenites betuloides* Pflug
- (27) *Ulmipollenites undulosus* Wolff
- (28) *Alnipollenites verus* R. Potonié
- (29) *Polyporopollenites carpinooides* Pflug
- (30) *Salix*
- (31) *Ilicipollenites*
- (32) Spores

A comparison of the present diagram with those of VON DER BRELIE (1961, 1967) would indicate that the closest resemblance is to be found with diagrams from the upper part of the Hauptflöz and Oberflöz i.e. zones D and E of VON DER BRELIE (1967).

CONSIDERATIONS ON THE AGE

While only little work has been done on the palynological assemblages occurring in marine sediments, preliminary work by VON DER BRELIE

(1958, 1961) has shown that the direct correlation of terrestrial sediments with the Tertiary marine sequence of Germany is by no means easy. Qualitatively and quantitatively the marine sediments are much poorer in pollen grains and spores than their terrestrial equivalents, with the result that much would appear to depend on chance occurrence. Moreover, one is faced with the problem of reworking to a greater extent than in terrestrial deposits. VON DER BRELIE (1958, p. 200) was therefore only able to distinguish large intervals of time on the basis of the palynological assemblages found. A solution to the problem of correlation must therefore be sought through the application of other means.

Traditionally the interdigitation of terrestrial sediments with marine sediments in the northwestern part of the Lower Rhine Basin has acted as the key to the age determinations of the lignites and associated sediments. At an early date FLIEGEL (1907, p. 94) was able to show by means of borings that the Hauptflöz lies on top of marine sediments of Late Oligocene age and that this lignite is overlain by marine sediments of Miocene age in Limburg in The Netherlands. Fliegel was of the opinion that the Hauptflöz was therefore Early Miocene in age. BREDDIN (1932), however, came to the conclusion that the lignites interdigitated with what would appear to be the lateral continuation, more or less lacking in fossils, of Late Oligocene sediments. While most authors were elaborating on Breddin's opinion, MULLER (1943) indicated that the lignite interdigitated with marine sands of Middle Miocene age. BREDDIN (1952) accepted the implications of this work and developed the ideas on the basis of the numerous borings available to him. BREDDIN (1952, p. 102) considered the Neurath sands, which occur above Flöz Frimmersdorf, to be represented in the Dutch Peel area by greensands with a Late Miocene fauna. He therefore referred Flöz Garzweiler and its equivalent, the upper part of the Hauptflöz, to the Upper Miocene and Flöz Frimmersdorf and Flöz Morken to the Middle Miocene. The work of FABIAN (1958) on the boring Straeten 1 from the northern part of the Rur Graben has confirmed Breddin's later work. Between marine sediments referred to the Middle Miocene on the basis of their faunal assemblages, lignites were found yielding palynological assemblages such as found in the Morken and Frimmersdorf lignites. Although JUX and PFLUG (1958 b) state that the presence of the Erkelenzer Swell (= Jackerather Horst) prevents a direct correlation of the lignites found in the Straeten boring with Flöz Frimmersdorf and Flöz Morken, this appears difficult to believe. The third lignite encountered in the boring Straeten 1 was considered to be equivalent to Flöz Garzweiler and may be referable to either Middle or Upper Miocene. The pollen assemblage contains more "Miocene" forms (see VON DER BRELIE, 1959, p. 30) than the Fischbachschichten, which are either referred to the Upper Miocene (VON DER BRELIE, 1959, 1961) or Lower Pliocene (PFLUG, 1957, 1963) on the basis of their pollen assemblage.

The faunal assemblages found in the boring Straeten 1 under the two

lowermost lignitic horizons were considered by FABIAN (1958) to be probably equivalent to those found in the Hemmoor Stufe. Above the two lignites a rich faunal assemblage possibly equivalent to that of the Reinbek Stufe was found. Both the Hemmoor Stufe ("Hemmoorian") and the Reinbek Stufe ("Reinbekian") are units made use of in the marine succession of Northern Germany. In recent German literature these units are frequently applied in a chronostratigraphical sense (compare, e.g., GRIPP, 1961). This classification has even been applied to the terrestrial deposits of the Lower Rhine Basin (c.f. ANDERSON, 1966). VON DER BRELIE (1967) has placed the Neogene palynological zonation of Central Europe within this chronostratigraphical classification. In his diagram zones C, D, and E are taken to correspond to the Hemmoor Stufe and Reinbek Stufe. However, the actual value of the German classification in chronostratigraphy is by no means ascertained (compare, e.g., BOEKSCHOTEN, 1970 who has emphasised the principally lithostratigraphical character of the units). Moreover, a correlation of these units with the Standard Sequence of Miocene Stages in Southern Europe is by no means straight-forward. As to the precise age of the Kreuzau sediments within the Miocene little can be stated with certainty, although it is worth pointing out that a very early or very late Miocene age would appear unlikely.

ENVIRONMENTAL CONDITIONS WITH PARTICULAR REFERENCE TO THE KREUZAU DEPOSITS

The amount of relief in the Lower Rhine Basin at the beginning of the Neogene would appear to have been slight. In the Rur graben close to the present border of the Eifel, the sediments were not conglomeratic nor did they show any signs of contorted bedding (VON DER BRÉLIE and WOLTERS, 1958). The area would appear to have been low-lying, as evidenced by

- (a) Marine intercalations in otherwise terrestrial sediments (e.g. BRED-DIN, 1932; JUNGHANS, 1958).
- (b) The presence of widespread lignite deposits in the area.
- (c) The none too coarse nature of the sediments.
- (d) The large number of plant taxa recorded from the Kreuzau sediments.

SINDOWSKI (1939 b) described the sandy sediments at Kreuzau. He stated that the coarse sands at the bottom of the profile give way to fine and medium grained sands and that the standard deviation (reflecting the grade of sorting) varied from 0.34 at the bottom of the sequence to 1.38 above. These sands would appear to have been laid down in fresh-water conditions for the following reasons:

- (a) The kyanite/staurolite ratio in the Kreuzau sands is only 0.6–0.8. In the marine sediments of the Lower Rhine Basin the ratio is almost invariably more than 2 (see SINDOWSKI, 1939 b, Abb. 14).
- (b) When cross-bedded the sands display lenticular cross-bedding. DUN-BAR and RODGERS (1957, p. 106) consider lenticular cross-bedding to suggest stream action, while deltaic sediments are characterized by tabular cross-bedding.
- (c) FRIEDMAN (1961) considers it possible to distinguish dune, beach and river sands on the basis of the distribution of their grain size, etc. He has shown that the distribution of the grain sizes gives a negatively skewed curve in the case of beach sands and a positively skewed curve in the case of dune and river sands. Making use of the data provided by SINDOWSKI (1939 b) one finds that the distribution of the Kreuzau sands is positively skewed. One would therefore assume that these were either dune or river sands. It can always be argued that this distribution curve only reflects the environment of the parent sediment. However, many negatively skewed distributions are encountered in the sands of the area immediately to the north of Kreuzau, an area showing marine influence. This would suggest that the distribution curves do, in fact, reflect the environment at the time of deposition. Although the data from Kreuzau, when plotted on Friedman's Fig. 5 (mean size plotted against standard deviation), fall within the field of overlap between river and dune sands, there are reasons for believing that the Kreuzau sands represent river-laid deposits. The cross-bedding encountered in dunes is generally on a much larger scale

than that found at Kreuzau. Furthermore, the angle which the cross-stratum makes with the horizontal would tend to be greater than that actually found in the Kreuzau deposits.

The direction of stream flow can be discovered by an analysis of the cross-bedded sands. The orientation of the cross-bedding was measured at a number of sites within the Kreuzau sand pit. In order to arrive at the original orientation of the cross-bedding the figures were rotated back using the figures for the present dip indicated by the overlying flat-bedded sands and clays (*B*). The orientation of the cross-bedding planes (fig. 3) would indicate a roughly South-North flow (c.f. KURTZ, 1938, p. 141) and renders the reconstructions of Kreuzau and environs presented by SINDOWSKI (1939 b, Abb. 1) and WÖLK (1941, Abb. 2) as open to doubt.

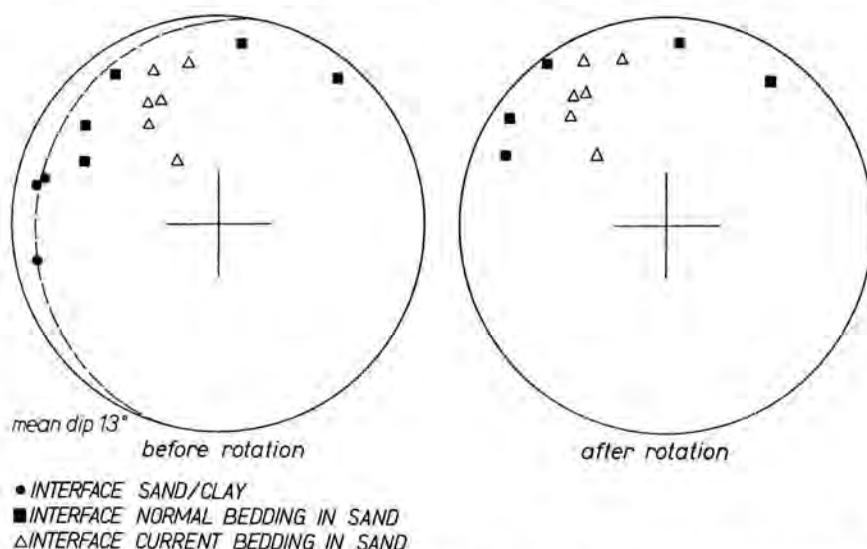


Fig. 3. The orientation of the interface in normal- and current-bedded sands (A) from Kreuzau before and after rotation.

The large clay-silt lens in *A* may represent an infilled ox-bow lake. The greater part of this lens is finely banded, which would suggest deposition in fairly still water. This would appear to be borne out by the following evidence:

- (a) The leaf-remains found in the sediment are rarely accompanied by wood-remains. In areas subject to strong river currents branches and even whole trees are often carried along. Twigs are, however, rare in the clay and only one branch as much as 6 cm wide (in a crushed state) has been recorded in the course of much collecting.
- (b) The presence of *Salvinia*, sometimes in the form of a more or less complete plant, i.e. probably autochthonous, would suggest stagnant or sluggish water for at least part of the time.

- (c) In some cases leaf-remains are to be found in which the veins are accompanied on either side by symmetrical ridges of clay apparently formed by the lateral squeezing out of the sediment as the leaves settled into the sediment.

THE ALLOCHTHONOUS NATURE OF THE MAJORITY OF THE LEAF-REMAINS

Although it is not infrequently assumed that leaf-remains represent a more or less autochthonous element, there seems good reason for assuming that the greater part of the leaf-remains described in this account have undergone a certain amount of transport. The allochthonous nature of these leaf-remains may be inferred from:

- (a) The absence of soil profiles.
- (b) The obvious dominance of leaf-remains. If these remains were autochthonous one would expect to encounter a complete assemblage of plant-remains (numerous fruits and seeds mingled with branches and leaves) Few seeds are present in the clay (E. K. Kempf, personal communication 1967) and most of these would appear to have belonged to aquatic plants. Seeds other than these are almost all winged. It would appear as if these winged seeds are only to be found along with the leaf-remains by way of having a similar specific weight.
- (c) The large number of taxa into which the leaf-remains can be divided would suggest that most of these were allochthonous, since these were probably leaves originating from woody species (see under). The setting would apparently represent floodplain conditions in the environs of Kreuzau. However the vegetation of a flood-plain tends to be open and only colonised by a few species and fewer woody species.

LEAF TRANSPORT-CONSIDERATIONS AND EXPERIMENTAL EVIDENCE

It seems reasonable to consider that most of the leaves found in the clay dropped from plants as a result of natural processes i.e. deciduous species during the autumn. If leaves do not fall directly into water they are liable to undergo a period of decay and prone to a certain amount of displacement in gusts of wind. The factor of wind can be an important factor in a somewhat arid climate with few permanent streams and the amount of movement undergone by the leaves will tend to depend on the weight per unit area of these leaves. Needle-shaped leaves being relatively heavy are not carried far by wind. In a humid climate on the other hand wind transport will be much less important for the following reasons:

- (a) The leaves will be heavier as a result of additional moisture and because of this moisture they will tend to be more difficult to dislodge from each other and the substrate.
- (b) The humidity will tend to encourage a plant cover, which will act as an obstacle to any wind-blown leaves.

- (c) The increased humidity will tend to promote a well-developed river-system and this will take over a certain part of the role played by wind-action in dispersal.

With regard to (c) it should be noted that the actual distance of the plants from the site of deposition would not appear to be as important as the closeness of these plants to a river. One can therefore expect a certain over-representation on the part of river- and lake-side plants.

Those leaves reaching or falling directly into a river are expected to undergo a certain amount of microbial decay and attrition during transport. Microbial decay is greatest in stagnant water or slow-moving streams. This aspect of the subject is under investigation at the present time. However in moderate to fast flowing streams this factor will be minimal. The factor of attrition in such streams has been considered by some authors as extremely important. CHANEY and SANBORN (1933) considered that a thin leaf has only half the chance of entering the fossil record as a thick-leaved form, all other things being equal. It was considered worthwhile testing this opinion experimentally. The flow of water in a stream was simulated using revolving cylinders driven by an electric motor. The diameter of the cylinders was 16 cm and these were filled with a mixture of 750 cc water and a third of this volume of Kreuzau sand.

To this mixture was added a total of 100 circular fragments of leaves of particular species. These leaf fragments, which were taken from freshly fallen leaves, were all 9 mm in diameter. The aim behind this was to enforce a certain uniformity, for factors such as leaf shape and size may also play a certain role. In this case the author was only interested in testing any differences which could be related to differences in leaf thickness. The species tested were: *Acer campestre* L., *A. pseudoplatanus* L., *Alnus glutinosa* (L.) Vill., *Betula utilis* D. Don, *Carpinus betulus* L., *Celastrus orbiculata* Thunb., *Fagus sylvatica* L., *Populus* × *canadensis* Moench, *Quercus robur* L., *Rhododendron brachycarpum* D. Don, and *Ulmus carpiniifolia* Gled.. Each of these species was submitted to 3 runs of 100 hours. The cylinders revolved at a rate of 34–35 revolutions per minute. A ledge at the bottom of the cylinders helped to give a somewhat lateral movement to the water in addition to the forward motion, just as one might expect in a stream.

A criticism that can be levelled at the use of such an apparatus is that it does not simulate nature in every detail. Thus the sand, which in a stream would move at a slower rate than the water, actually moves somewhat more rapidly in the apparatus. However the results, in as far as they are applicable, are interesting. Even after 100 hours (equivalent to approximately 80 km) the various species showed little signs of wear and tear and it was therefore not possible to make any correlations between thickness and resistance to attrition. All species appeared to show the same reaction to transport. Although it is necessary to test these results in

a number of streams, it seems possible at this stage to make two provisional conclusions:

- (a) that the leaves found in the Kreuzau deposit may have travelled 80 km or more before their deposition and
- (b) that all other things being equal mesomorphic leaves have a more or less equal chance of entering the fossil record as xeromorphic leaves.

Because selection of the various forms appears to be a less important factor than previously assumed, the fossil assemblage may be taken to give a moderately good cross-section of the original vegetation. A certain over-representation of lake- and river-side plants and under-representation of evergreen plants is, however, to be expected.

EVIDENCE FOR CLIMATIC CONDITIONS

“Seeing to what an extent the palaeobotanist has to content himself with detached leaves of plants, it would be extremely helpful if he were able to depend upon their shape, venation or internal structure as guides in settling the question as to the climatic condition under which the plants flourished” A. C. SEWARD, 1892, p. 59.

Evidence for palaeoclimates is to be found in many apparently unrelated fields of geology (SCHWARZBACH, 1963). Climatic evidence from the Tertiary of the Lower Rhine Basin has been summarised by TEICHMÜLLER (1958) and SCHWARZBACH (1952, 1968). Teichmüller considered that the temperature decrease during the Tertiary was gradual. He considered that the climate during the deposition of the sediments at Rott was subtropical (TEICHMÜLLER, 1958, p. 743), and referred to floras from the upper part of the Middle Miocene as being subtropical as well. It is, however, by no means clear what was meant by this, for he considered the plant assemblage of Rott to be somewhat similar to the flora of Southern Japan. This flora is considered temperate by most standards. SCHWARZBACH (1968) has sharply criticised the so-called tropical nature of the climate at certain periods within the Tertiary. Both Schwarzbach and Teichmüller, however, agree that the climate during the period of widespread formation of lignite was humid. SCHWARZBACH (1968, pp. 46–47) considered that the total rainfall was certainly more than 1000 mm per year and that the rainfall was equally spread over the whole year with the possible exception of 2 or 3 months in the year during which little rain fell.

PLANT-REMAINS AS PALAEOCLIMATIC INDICATORS

In early papers on Tertiary plant-remains conclusions regarding the climate were only possible once the plant-remains had been determined. The conditions under which the related plant taxa are growing at the present day were examined. The climate was then determined as the common denominator of the conditions under which the various relatives live at the present-day. It follows that if the plant determinations were unreliable that the conclusions regarding climate would tend to be unreliable too. A glance at the comments of authors such as BOMMER (1903), BEYN (1940), SUESSENGUTH (1942, 1944), BERGER (1953) and SCHWARZBACH (1968) should be enough to convince one that many of the generic names given to plant-remains are untrustworthy. This is the result of “failure to preserve a due sense of proportion under the stimulus of the passion for the search” as SEWARD (1931, p. 431) put it. One would therefore welcome an alternative means of determining the climate should this exist. As yet no-one has come up with another means of determining

the climate from a pollen assemblage or assemblages of wood-, fruit- or seed-remains. The possibility of determining the climate from the morphological characters displayed by an assemblage of leaf-remains, as forecast by SEWARD (1892, p. 59) has, however, become a fact. BERGER (1952, 1953) has proposed a means of determining the climate based on a combination of leaf size and the nature of the leaf margin. The leaf assemblage is divided into three basic types: Betulaceous type, Lauraceous type and Leguminous type. This approach has been applied by a number of European authors and differs but little from the present approach.

Characters of Primary Importance

Over fifty years ago I. W. BAILEY and SINNOTT (1916) showed that a relationship existed between the nature of the leaf margin of living dicotyledonous species and the climate in which these species grew. Thus the number of species having an entire leaf margin increases towards the tropics. The relationship is most marked in trees and shrubs and less noticeable in herbs. There are, however, the following reasons for considering that herbs, with the exception of aquatic species, are unlikely to be represented in the form of leaf-remains in the fossil record in general and at the Kreuzau site in particular:

- (a) The number of leaves per plant is much greater in woody plants than in herbs.
- (b) Although transport of leaves through the air is much less important than water transport, the greater height of a tree or shrub will give such plants an initial advantage over their herbaceous neighbours.
- (c) The fact that no well-developed abscission layer is present at the junction of the petiole and the shoot in herbs will tend to have the effect of cutting down the chances of herbaceous taxa entering the fossil record in the form of leaf-remains. Rather, the leaves will tend to wither while still attached to the plant. In woody species, on the other hand, a well developed abscission layer is not uncommonly present at the base of the petiole.

For these reasons the figures for the fossil assemblage have only been compared with figures based on the woody element of the living floras examined. Since the climate is unlikely to be uniform over a large area an attempt was made to base the figures for the living assemblages on local floras. Such floras cover areas small enough to allow one to assume a certain amount of uniformity regarding the climate and at the same time large enough to give a reliable figure.

Before comparing the figures for fossil assemblages with those of living floras it is important to bear in mind some of the factors influencing the figures. While one may assume that few woody species will have been missed on the collecting trips which act as the basis for the published Floras, the taxonomic approach adopted in these Floras may well affect the results. Different approaches to the treatment of critical genera such

as *Rubus* may be expected to cause a difference of a few percent. However, in general, when the Flora is the work of a single author, as is usually the case here, this affect is liable to even itself out as a result of the splitting or lumping of the remaining taxa. The same problems of lumping and splitting apply to the fossil assemblages as well, as mentioned on p. 31. Furthermore, results based on a fossil assemblage consisting of only a few dicotyledonous taxa are liable to be unreliable. The Kreuzau assemblage, which includes 65 dicotyledonous taxa should, however, act as a fairly reliable basis for comparison.

The percentage of dicotyledonous taxa in the Kreuzau assemblage having an entire leaf margin was found to be 47%.*) Allowing for a small margin of error this assemblage was compared with Floras with a woody element having a figure between 45% and 50%. Floras having such a percentage only occur in a relatively narrow belt running through the Mediterranean region, past the Caspian Sea, along the Himalayas and into China. In North America this belt runs from California to the Gulf of Mexico and passes through Florida. This belt is stippled in fig. 4. It can be argued that the percentage of leaves with an entire margin is actually on the low side, for there is the possibility that certain evergreen woody plants were not represented in the Kreuzau assemblage. Such evergreen species not uncommonly have leaves with an entire margin. However, it will be obvious from fig. 4 that the raising of the figure to 55% would have little affect on the climatic conclusions to be drawn. The results indicate a warm temperate to subtropical climate at the time of the deposition of the Kreuzau sediments. BERGER (1955) considered that the Kreuzau assemblage consisted of warm elements (38%) and temperate forms (38%).

It will be obvious that the zone stippled in fig. 4 is characterized by various climatic regimes at the present day. The zone passes through Afghanistan with its very arid climate as well as the Himalayas and China, which tend to have a rather humid climate. In order to identify the climate which existed during the deposition of the Kreuzau sediments more closely, one must make use of other leaf characters. Leaf length lends itself to an application of this kind for leaf size is apparently controlled to some extent by the factor of humidity. WALKER and DUNN (1967) have shown experimentally that a reduction of the relative humidity from 58% to 50% in combination with a greater variation in temperature results in smaller leaves in *Pisum sativum* L. 'Alaska'. While these differences in leaf size might be correlated with temperature affects (c.f. AXELROD and H. P. BAILEY, 1969), this factor alone would not appear to explain all the observed phenomena satisfactorily. One will notice in fig. 5B that in areas having a hot arid climate, that the leaves rarely reach a

*) The term "leaves" is throughout used in its colloquial sense and includes organs more properly referred to as leaflets. However, leaflets may not be recognizable as such when in a detached state.

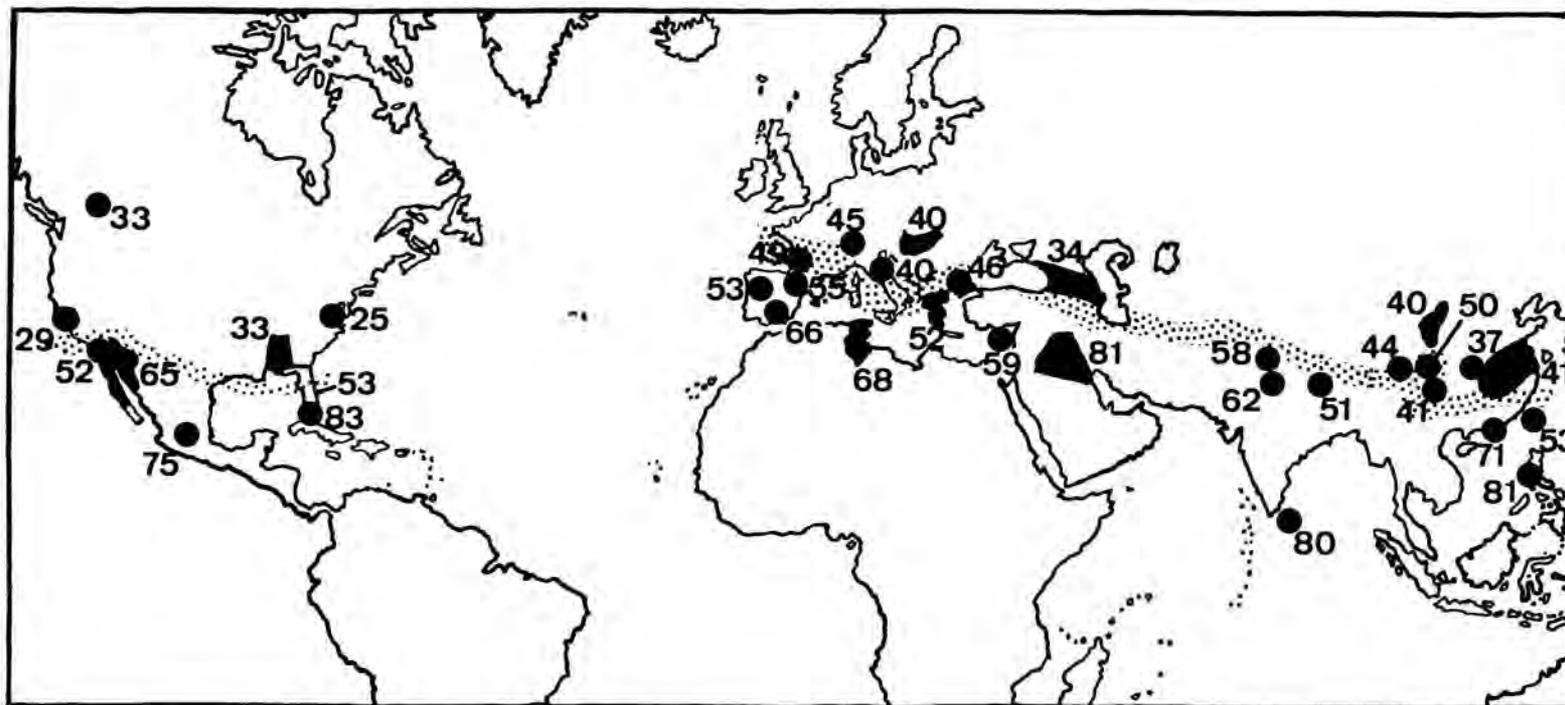


Fig. 4. The percentage of woody species with leaves or leaflets having an entire margin. Compiled from AHRENDT, 1954-56; BAEHNI, 1957-58, 1959-61; I. W. BAILEY and SINNOTT, 1916; BERNARDI, 1962-63; BONNER, 1959-61; BONNET and BARRATTE, 1896; DE HALACSY, 1900-08; DIELS, 1900; ESPAÑA, 1949; FARR, 1907; FRANCHET, 1888; GALIANO and HEYWOOD, 1960; HITCHCOCK and STANDLEY, 1919; HOLMBOE, 1914; HOWELL, RAVEN and RUBTZOFF, 1958; JÁVORKA, 1924-25; JEANJEAN, 1961; LI, 1963; LOPEZ, 1952; MAHESHWARI, 1963; MASCLANS I GIRVÈS, 1966; MOHR, 1901; PAMPANINI, 1911, 1930; RECHINGER, 1964; SHREVE and WIGGINS, 1964; SMALL, 1933; SOMMIER and LEVIER, 1900; STEWARD, 1958; STOYANOV and STEFANOV, 1948; THOMMEN, 1951; WALKER, 1941; WEIBEL, 1957-58, 1959-61.

length of more than 10 cm. A comparison of the figure for Lowland Iraq, which has a hot arid climate, with the figure for Java with its monsoon and tropical rain forests, or there again the dry west coast of North America with the wetter east coast should make this relationship clear. The character of leaf length is apparently more or less independent of the nature of the leaf margin. In all 37.5% of the dicotyledonous taxa from Kreuzau have leaves reaching a length of more than 10 cm. Within the zone delimitable on the grounds of leaf margin only China (and no doubt the part of the Himalayas bordering on China) and Florida have comparable figures. Since leaf length is a character which is not always mentioned in Floras, certain of the figures given in fig. 5B had to be obtained indirectly.

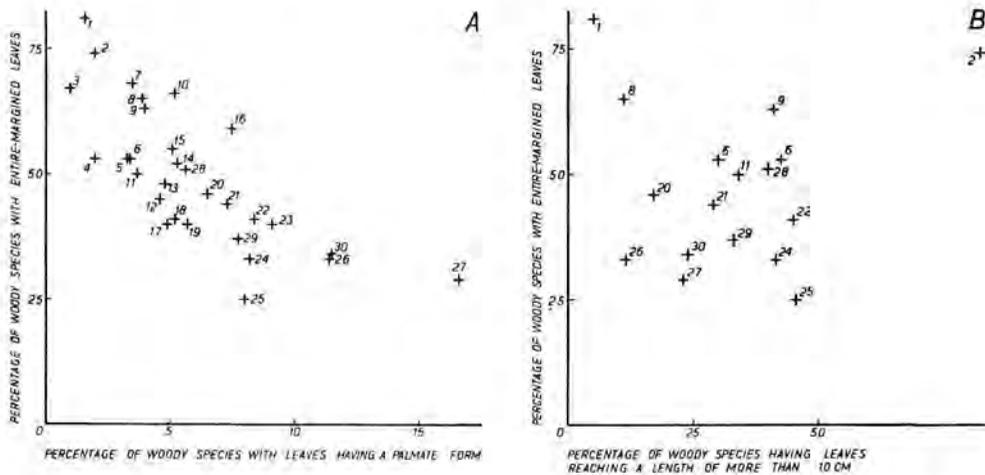


Fig. 5. The percentage of woody species with entire-margined leaves compared (A) with the percentage of woody species with leaves having a palmate form and (B) the percentage of woody species having leaves reaching a length of more than 10 cm. The data was derived from the following sources:

1. Lowland Iraq, RECHINGER, 1964; 2. Java, BACKER and BAKHUIZEN VAN DEN BRINK, 1963-68; 3. Hawaii, I. W. BAILEY and SINNOTT, 1916; 4. Zamora province, Spain, ESPAÑA, 1949; 5. Florida, U.S.A., SMALL, 1933; 6. Taiwan (Formosa), LI, 1963; 7. Tunisia, BONNET and BARRATTE, 1896; 8. Sonoran Desert, U.S.A., SHREVE and WIGGINS, 1964; 9. New Dehli, India, MAHESHWARI, 1963; 10. Jaen province, Spain, GALIANO and HEYWOOD, 1960; 11. Central China, Western District, DIELS, 1900; 12. Switzerland, THOMMEN, 1951; 13. Gironde, France, JEANJEAN, 1961; 14. Greece, DE HALACSY, 1900-08; 15. Lérida, Spain, MASCLANS I GIRVÈS, 1966; 16. Cyprus, HOLMBOE, 1914; 17. Southern Mongolia and Kansu Province, China, WALKER, 1941; 18. Lower Yangtze Valley, China, STEWARD, 1958; 19. Hungary, JÁVORKA, 1924-25; 20. Bulgaria, STOYANOV and STEFANOV, 1948; 21. Moupine province, Tibet, FRANCHET, 1888; 22. Central China, Southern District, DIELS, 1900; 23. San Marino, PAMPANINI, 1930; 24. Alabama, U.S.A., MOHR, 1901; 25. District of Columbia, Washington, U.S.A., HITCHCOCK and STANDLEY, 1919; 26. Selkirk Range, Canada, FARR, 1907; 27. San Francisco, California, U.S.A., HOWELL, RAVEN and RUBTZOFF, 1958; 28. Nepal, AHRENDT, 1954-56, BAEHNI, 1957-58, 1959-61, BERNARDI, 1962-63, BONNER, 1959-61, WEIBEL, 1957-58, 1959-61; 29. Hupeh, China, PAMPANINI, 1911; 30. Caucasus, SOMMIER and LEVIER, 1900.

The figures for the Chinese floras are based on REHDER (1927), unless other measurements were given in the original paper. In the case of the Bulgarian flora and that from Florida the figures were based on herbarium material of species recorded from these areas and present in the Utrecht herbarium. Although the maximum figure for the fossils may be somewhat on the low side due to sampling it is likely that this is compensated for by the expected over-representation of lake- and river-side plants, which because they grow in damper conditions are liable to have somewhat larger leaves.

The choice of characters such as leaf length and the nature of the leaf margin in a determination of the climate rests not so much on the fact that these characters are intrinsically more useful in determining climate. More important is the fact that these characters (a) do not present problems of definition and interpretation, (b) comparative data from living floras is moderately accessible, (c) the characters are of more than limited application in the fossil assemblage. Other characters which may prove to be equally useful are at present of only secondary importance, since they do not fulfil the above conditions.

Characters of Secondary Importance

While less trustworthy than characters of leaf margin and leaf length other characters, which can be used in a confirmatory sense, deserve to be mentioned here. Characters such as leaf shape, the nature of the leaf apex, venation pattern, hairiness and other epidermal features may be considered under this heading.

SINNOTT and I. W. BAILEY (1915) showed that dicotyledonous plants having leaves which are palmate in form are more common in temperate zones and less common in the sub-tropics and tropics. This character shows a close relationship to that of leaf margin (see fig. 5A). However, while the percentage of species having such leaves at the present day rarely exceeds 10%, percentages of up to 20% are encountered in leaf assemblages from the Tertiary. SINNOTT and I. W. BAILEY (1915) considered that this indicated that palmate leaves were to be considered more primitive. However, this does not account for the fairly low percentages in the Palaeogene and high percentages in the Neogene of Central Europe. It is not unlikely that the high percentage of species having palmate leaves in the fossil assemblages is the result of taxonomic splitting, which is unavoidable when forms intermediate between simple and palmate leaves do not exist in a deposit. As a result of this uncertainty the percentage of palmate leaves present in a deposit can only be made use of in a comparison of various fossil floras and not in a direct comparison of fossil with living assemblages.

Although the presence or absence of drip-points (caudate leaf apices) has been made use of in climatic analyses, the results are not fully reliable, since the figures are influenced by a certain amount of personal opinion. When

the length/breadth ratio of the leaves is small this feature is easily defined, while a precise definition is impossible in lanceolate leaves. However, while it is not possible to give exact figures, the fact that SCHWARZBACH (1952, p. 29) mentions the not uncommon occurrence of drip-points at the time of the lignite formation would appear to confirm that the climate at that time was fairly humid.

The nature of the venation would also appear to be a guide to the climatic conditions existing during the deposition of the sediments containing the leaf-remains. Thus one finds, for example, more species with an actinodromous or craspedodromous type of venation in temperate, rather than in subtropical or tropical regions. At the same time, the presence of forms with a marginal vein would appear to be more typical of such subtropical and tropical areas. The inaccessibility of data concerning these features prohibits the use of these features in palaeoclimatic analyses at the present time.

ZEUNER (1932) and MANZE (1968) have pointed out the relationship which exists between the closeness of the fine net venation and the environment. The closeness of this venation is found to increase with:

- (a) greater exposure of the leaves, either at greater altitudes or higher up a tree.
- (b) increase in the intensity of the sun's rays. In temperate parts of the Northern Hemisphere measurements have shown that the leaves on the north side of a tree have a somewhat more open net venation than those facing south. This affect is not as great in the tropics due to the different angle made by the sun with the earth's surface.
- (c) decrease in humidity

This method, which may prove to be of great importance in the future, suffers at present from two drawbacks:

- (a) That the finer venation is only sometimes well enough preserved in the leaf-remains to allow reliable measurements to be made. BEYN (1940, pp. 399-400) comments that the thickness of the cuticle may prevent measurement of this kind and suggested that the solution to this problem might be sought by examining the fine venation reflected in the cuticle. However, as STACE (1965) has pointed out, the finest venation is not always reflected in the cuticle. Measurements could therefore be misleading.
- (b) In the absence of sufficient data from assemblages of plants living under known climatic conditions, one is as yet restricted to that part of the fossil assemblage which is comparable with living genera. This, in itself, introduces a certain factor of uncertainty into the results.

Although a general increase in hairiness with an increase in temperature or wind or a decrease in rainfall can generally be confirmed, characters of hairiness cannot be used to any great extent for the following reasons:

- (a) Although one only expects mature leaves in the deposit the possibility exists that a number of immature leaves may, in fact, be present. While mature leaves may be glabrous, the young stages are often hairy.

- (b) The information from the fossil assemblage is only based on a small percentage of the total assemblage, which may be considered atypical for the whole. While the impression of hairs may occasionally be present in the sediment most of the information is derived from those species yielding cuticles.
- (c) Little comparable data is available from living floras.

Most of the taxa lending themselves to a study of this nature had few or no hairs. This could suggest a fairly humid climate, although the evidence being based on the taxa yielding a cuticle (generally xeromorphic forms) may be somewhat misleading.

Certain features observable in the cuticles may have some climatic significance e.g. size of epidermal cells, stomatal index, thickness of the cuticle. At the present state of knowledge these characters can only be made use of once the affinity of the fossils is known. Other characters such as the presence of sunken stomata, which appear to be connected with aridity, may be possible to interpret directly. The fact that only a few taxa have markedly sunken stomata would suggest that the climate was humid rather than arid. STACE (1965) has mentioned the possibility that characters such as markedly undulate cell walls and the presence of stomatal ledges on the guard cells may be associated with aridity. Of the Kreuzau assemblage only 17.6% of the taxa had markedly undulate cell walls and no more than 5.7% stomata with stomatal ledges. However, with regard to the undulate cells, it is by no means certain that a direct relationship exists between this and climate. WALKER and DUNN (1967) submitted *Pisum sativum* L. 'Alaska' to various conditions of temperature, humidity and sunlight. The amount of undulation observed in the cell walls under "tropical", "mesic" and "desert" conditions remained constant. Similar experiments on an inbred line of *Datura stramonium* (SHARMA and DUNN, 1969) indicate that while the epidermal cell walls were undulate under humid and mesic conditions, growth under xeric conditions resulted in straight-walled cells. A general criticism to be levelled at the use of epidermal characters in reconstructing palaeoclimates is that they are only of limited application. Many leaf-remains do not yield cuticles. Furthermore, if one is making use of characters such as cell size and stomatal number it is essential that the cuticle is removed from a comparable position on the various specimens. This is a requirement that can rarely be fulfilled when dealing with plant-remains which are often fragmentary.

CONCLUSIONS

In conclusion the climate which existed at the time of the deposition of the Kreuzau sediments would appear to have been humid and equable and most closely resembling that found in parts of China and Florida. The closeness to the sea and the resulting water table near the surface were probably contributing factors. A humid climate has been generally accepted (e.g. THOMSON, 1956; TEICHMÜLLER, 1958; MANZE, 1968; SCHWARZ-

BACH, 1952, 1968) for the Lower Rhine Basin during this period. However, differences in opinion exist as to the details. THOMSON (1956) compared the climate prevailing during the formation of the great thickness of lignite with that found in the western part of the Iberian peninsula at the present day. However, since the percentage of woody species having leaves with an entire margin in the Iberian peninsula is higher than that of the Kreuzau assemblage, this conclusion seems unlikely. SCHWARZBACH (1968, p. 57), while considering the temperature during the formation of the lignite as similar to that now found in Mediterranean area, pointed out that the climate differed in having a greater rainfall. He considered the climate best compared with Köppen's Cfa climate, which according to Köppen is only to be found on the east coast of the continents at the present day. The only point on which Schwarzbach's concept differs from that of the present author is that Schwarzbach considered the climate of present-day Florida to be warmer than that indicated by the assemblages from the lignite formation. This opinion was apparently based on the high percentage of woody species with entire leaves which are to be found in the Florida Keys. It should, however, be pointed out that the climate of Florida as a whole is rather variable. On the basis of the leaf characters made use of in the present work a fairly close resemblance would appear to exist between the flora of Northern Florida and the fossil assemblage.

PROBLEMS OF TAXONOMY AND IDENTIFICATION OF THE LEAF-REMAINS

"The basic problem before us is to determine as correctly as possible the affinities of the remains, and their naming is of secondary importance. The value of a name can be no greater than the accuracy with which the plant is determined. . ." U. PRAKASH and R. DAYAL, 1965, p. 23.

The investigation of leaf-remains is only one aspect of the study of fossil floras and should be looked upon as complementary to wood-, seed-, and pollen-analysis. These various lines of evidence may be used in constructing a bio-stratigraphical column and give an idea of the vegetation at a particular place and time in the past. One of the aims of investigating leaf-remains is to bring to light the existence of taxa which might simply remain undiscovered, if other lines of approach were applied.

TAXONOMIC APPROACH WITH REGARD TO THE LEAF-REMAINS

Between 1964 and 1967 some twelve trips were organized to collect plant remains from the sand pit to the east of Kreuzau. For storage purposes the leaf-remains were divided into a small number of groups on the basis of a superficial examination. Some four months were then spent making nearly 1200 cuticle preparations from these leaf-remains and on the basis of the features of the cuticles and those of shape, dissection and venation of the leaves these groups were subdivided. In this way the author hoped to prevent himself from grouping the specimens on gross-morphological characters into taxa, further subdivided at a later date on the basis of the cuticles only. Care was taken to check possible transitions between the original groups. In all just over two thousand specimens were collected. The aim of this mass-collecting was not only to reveal the presence of rarely occurring forms but to aim at a better circumscription of the more common forms as well. For instance, mass-collecting enables one to extrapolate more easily, so that even though a new specimen may not fit entirely within one of the descriptions one can more easily determine whether or not the difference(s) fall(s) within the same pattern. One further advantage of repeated collection from the same locality is that one expects, even allowing for some variation in the samples, a certain amount of agreement between the one collection and another. If this is not apparent one's taxonomic concept is in all probability too narrow.

The grouping of the specimens into working units, or taxa, should be done on the basis of the total assemblage of characters, and evidence for the taxonomic limits should be to a large extent based on the fossils themselves. Knowledge of living taxa may however act as a guide, when a choice as to the drawing of the boundaries exists. For purposes of infor-

mation storage and rapid comparison much use was made of punch cards. It will, however, be obvious that the task of producing punch cards for every specimen (up to 5 cards, each with 133 holes, per specimen, depending on the nature and preservation of the fossil in question) would have been too time-consuming in practice. Only when dealing with type material or with groups of specimens closely resembling each other in venation, cuticle, etc. was each specimen individually described. However, in cases in which the taxa had a distinctive cuticle and/or venation etc. a single set of punch cards was produced covering all the specimens then available. Altogether 1,027 punch cards were used in the present undertaking. The most unsatisfactory taxa treated here will, in general, be those having a limited number of characters. The very small leaves were frequently found to be without any trace of a cuticle, and detailed features of the venation were often found to be lacking. Should these specimens be worth considering at all one is faced with the problem of trying to group them satisfactorily with one another and/or the larger and better preserved forms.

In the initial stages a rather narrow taxonomic concept was held to, in order to guard against the possibility of classifying similar, simply convergent, forms within the same taxon. In connection with recent plants DAVIS and HEYWOOD (1963) have pointed out that this attitude is not necessarily a bad one in preliminary studies. It is easier to combine such taxa at a later date than to attempt to unravel an assemblage originally lumped. Only after the collections in Berlin and Cologne had been studied was a certain amount of lumping of taxa undertaken.

It is unfortunate that one cannot examine all the specimens simultaneously, for the order in which the fossils are examined can play a role in the grouping of specimens into taxa. One takes as a starting point one or more specimens, which act as a basis for a taxon. Should a large number of intermediate forms be found to exist between two or more of these taxa, then in all likelihood one would combine these into a single taxon. If, however, the number of intermediates is smaller and the first intermediate specimens encountered resemble the one taxon more than the other these will tend to be included in the first taxon. The result is that the known range of variability of this taxon increases, while that of the latter remains unchanged. The chances are that any specimens, which would have been considered exactly intermediate between the two taxa as originally defined, will be included in the taxon displaying the large amount of variability. If such specimens should be encountered early on in the investigations, one would be aware of the possible transition or overlap between the entities and the final circumscription might well be different.

COMPARISON WITH RECENT TAXA

In the past leaf-remains have been determined empirically, i.e. determined simply on the basis of similarities with living plants, without consideration of other factors. While such an approach may be applicable

to conifers where it is possible to cover the 50-odd living genera, it is only applicable to angiosperms on a very limited scale. The palaeobotanist is very much limited by his own insufficient experience, when it comes to making a comparison of fossil leaves with those of recent plants. The descriptions of leaves appearing in most taxonomic works dealing with recent plants are sketchy on the whole and can be made little use of. With the exception of the published work of VON ETtingshausen (e.g. 1861) on the leaves of recent plants, there exist no detailed reference works on this subject. The uncertainty of some of the determinations, changes in nomenclature and the important role played by cuticle analysis in modern works dealing with leaf-remains have, however, rendered this work of limited value. MÄDLER (1950) has suggested a way in which one can cut down on the number of possibilities to some extent.

- (a) It is usually possible to limit oneself to a comparison with tropical, sub-tropical or temperate areas on the basis of the climatological features of the assemblage.
- (b) Earlier works, although by no means full-proof, have indicated that Older Tertiary floral assemblages from Western Europe show the greatest resemblance to those now found in Southern Asia and Central America. Younger Tertiary assemblages on the other hand resemble the floras found in Eastern Asia and Eastern North America at the present day.
- (c) Herbs, with the exception of aquatic species, are unlikely to enter the fossil record in the form of leaf-remains (see p. 22). This means that one can largely restrict oneself to a comparison with woody species.

The fact that the climate most closely resembled that of present-day Florida and China would suggest that one must seek the living relatives of the fossil taxa in these areas. However, before accepting this as proven the author made a point of examining the present distributions of five very distinctive genera to be found in the Kreuzau deposit. This concerns the leaves of the water fern *Salvinia* and of the conifer *Amentotaxus*, the fruits of *Carpinus* and *Acer*, as well as shoots referable to the genus *Rosa*. The only part of the world where one finds all five in the same area is in Central China (fig. 6). This would appear to confirm the validity of an approach based on the climatic features inherent in the dicotyledonous leaves.

Having come to the conclusion that the Kreuzau assemblage showed the greatest similarity with the flora of China and to a lesser extent with the flora of Florida, one is then faced with the job of detailed comparison with the floras of these areas. The results of such a comparison are only reliable if the coverage is fairly complete. In the Utrecht herbarium (U) the author was able to find 214 of the 267 woody dicotyledonous genera mentioned by SMALL (1933) as being native to Florida. That represents a coverage of 80%. Of the 546 species of woody dicotyledons described by J. K. Small from Florida the author has been able to cover 65%, in other words 352 spe-

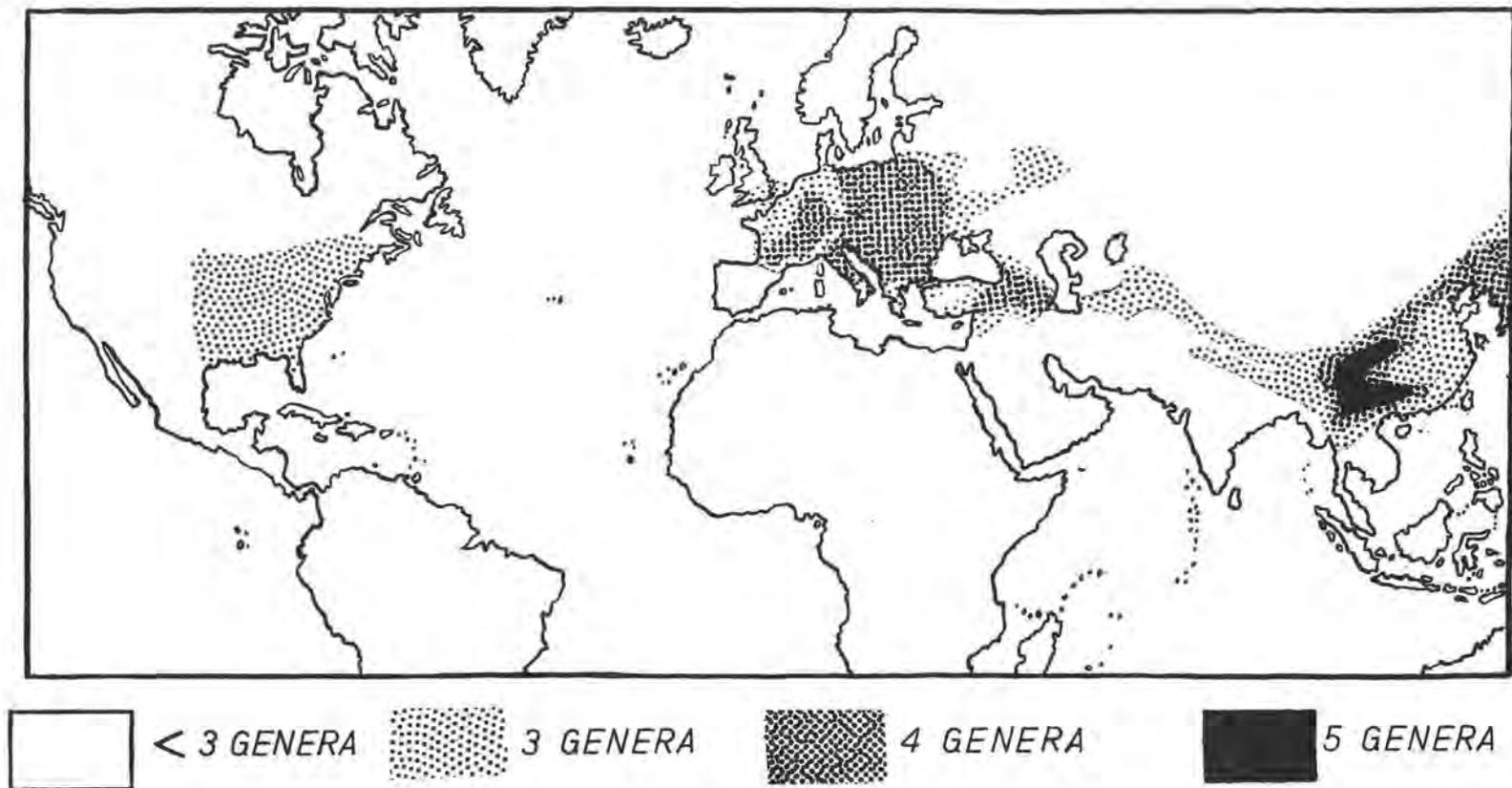


Fig. 6. Map showing the areas where the geographical ranges of *Acer*, *Amentotaxus*, *Carpinus*, *Rosa* and *Salvinia* overlap (largely based on PAX, 1902; FLORIN, 1963; MEUSEL, JÄGER and WEINERT, 1965).

cies in all. Since material from Eastern Asia is poorly represented in Utrecht a trip was made to Edinburgh (E) where a number of important collections from China, including those of Hector Léveillé and George Forrest, are housed. In the case of the Chinese flora, Chung's "Catalogue of Trees and Shrubs of China" was used as a basis for comparison. Of the 728 genera of dicotyledonous plants mentioned by CHUNG (1924), the author was able to sample 469, and 2041 of the 4715 species. Species which are only known from Mongolia and the extreme northern provinces of China such as Kansu and Shansi, or taxa confined to the southern provinces of Kwangtung and Hainan, were not taken into consideration. For the remaining provinces of China the coverage at the specific level is therefore well over the 50% mark. With few exceptions only material which had been seen by a monographer or material determined by one of the authorities on the Chinese flora, e.g. Merrill, Rehder and Handel-Mazzetti, was examined. Some material from Nepal was also examined. The restriction to the above areas was motivated by practical considerations. It seems worth pointing out that one must always bear in mind the possibility of exceptions. Certain fossils e.g. No. XXIII suggest the presence of a European element in the Kreuzau flora. Because other possibilities may have been overlooked, rather full descriptions and lists of those species which have been compared in detail with the fossils are given. This should make it possible to check the determinations more readily. Once the fossils had been compared with the leaves of recent plants it became obvious that some of these were relatively easy to identify, while the affinity of others was more or less uncertain. Others remained completely unidentifiable, since they resembled a large number of the living taxa examined. Unless a case can be made out for considering such fossils of some stratigraphical importance, an entity which cannot be pigeon-holed at a botanical level would be better left without a binomial. This opinion was held by JABLONSKY (1915, p. 253):

"Um die riesige Menge der nichtssagenden Namen nicht unnötig zu vermehren, blieb unter solchen Umständen natürlich eine grosse Anzahl von Blattfragmenten unbestimmt".

APPROACH APPLIED TO DETERMINABLE REMAINS

Fossil botany has its own nomenclatural problems and it is unfortunate that the Code of Botanical Nomenclature does not give a more definite opinion as to the way in which these problems should be tackled. There is more to it than simply identifying the affinities of the fossils. With regard to the nomenclature to be applied to fossils and particularly those from younger sediments, there are two schools of thought: those who refer the plant-remains to recent taxa and those who consider that certain organs concerned in reproduction, e.g. fruits and seeds, may be classified within recent taxa, while other organs, because they are not widely used in the classification of recent plants, should be attributed to form- or organ-genera. GRAHAM (1939) considered that "Form genera should be used for all

leaves that are not accompanied by such [determinative] fructifications" and that "leaves from the same locality and horizon as those accompanied by fructifications should be referred to the modern genus, but similar leaves coming from another region or horizon should be referred to the form genus". Such an approach puts much weight on the accuracy of the determinations of the fructifications, a problem complicated by their often poor preservation in leaf-bearing deposits. One should not overlook the fact that there is often enormous difficulty encountered in the identification of fossil fruits and seeds, even though these are investigated anatomically. Out of a total of 314 species of comparatively well-preserved fruits recognised by REID and CHANDLER (1933) in the London Clay (Eocene), 59 could not be referred to a family at all and a number of other attributions were considered doubtful by these authors. Even assuming that fruits and seeds are generally well-determined, one still faces the problem of correlating the leaf- and seed-remains, a problem complicated by their different dispersal and reaction to transport. This practice of correlating the various organs was one followed amongst others by some authors in the middle of last century and is not to be encouraged. Leaves and fruiting parts and even wood were given the same specific name on the assumption that they were from the same species. Because of nomenclatural reasons, these specific names must often be retained even though the various organs may not be considered as belonging to the same species at all. On the other hand one does agree that the finding of plant-remains other than leaf-remains may give a lead as to the proper affinity of the leaves under investigation or vice versa.

It is certainly true when modern generic names are employed for the fossils in question, that there is a tendency to push the determinations too far. Furthermore, the practice of certain authors to apply a specific name to fossil leaves attributed to a living genus, whose species cannot be separated from one another on leaf characters, is not to be upheld. This approach can be very misleading. The attribution of such leaf-remains to a single specific entity, albeit possibly originating from more than one taxon, can give a false picture of the representation of this genus in the past. However, while the reference of fossils to living genera is not without dangers, the use of form- and organ-genera tends to lead to a certain amount of slackness in determination as does the use of "c.f.". A plant family can often be divided up into a certain number of types and sub-types when this family is examined as to its seeds, or cuticles, or pollen only. The practice of tacking on an ending such as *-ites* or *-phyllum* to the name of a family of recent plants to denote a fossil may therefore have the effect of forming a very unsatisfactory organ-genus. This descriptive method as practised by N. D. Mchedlishvili and S. R. Samoylovich has already been criticized by ZAKLINSKAYA (1962). The danger of this approach is that it tends to conceal the degree to which a determination is possible. The present author feels that the names employed should, to some extent at

least, reflect to what extent it is possible to identify the fossil. Certain authors consider that one should be required to use another - fossil - name for an angiospermous entity because it is necessarily incomplete. However, this seems to the present author to be carrying the case a little too far. In much the same way one can refer to herbarium material, and especially to that of woody plants, as incomplete. Herbarium material, when not in flowering or fruiting condition, may in some cases be considered indeterminate, but one certainly does not apply another name to the material in the vegetative state, at least not on purpose!

TRAVERSE (1957) considered that if the characteristics of the organ fall within the circumscription of only one recent genus, that the fossil should be allocated to this genus. This approach is followed in the present work. One should, however, add that in such a system there is the possibility that in the case of older fossils, for example those from the Cretaceous and Lower Tertiary, that the particular organ belonged to a whole whose circumscription was different from that of the recent genus. Only where there exist various organs each separately determinable as belonging to the same genus is one more certain that the fossil did belong, or was closely allied to, the recent taxon. The tendency to specialization in palaeobotany has, however, unwittingly resulted in the turning out of work which is consequently less reliable from this point of view.

THE CHOICE OF LEAF CHARACTERS

A character is an attribute of an organism and in complex organisms e.g. the Angiosperms, there may be an almost infinite number of such attributes. For the present purposes, however, it was necessary to keep the number of characters made use of at a practical level. The initial choice of characters was based either on their prior usage (straight or in modified form) or on direct experience on a small number of herbarium specimens.

PETIOLE, LEAF SHAPE AND LEAF MARGIN

Although the absolute length of the petiole or the ratio of the length of the petiole to the length of the lamina may be of use in works dealing with recent plants, little emphasis has been placed on these features in the present study. This is a direct consequence of the difficulty in ascertaining whether or not the petiole was preserved *in toto*.

Leaf shape is a character made use of to some extent in taxonomic works dealing with living plants. While relatively constant in certain taxa, a wide range of variation is to be encountered in other taxa, which renders leaf shape of little value in these groups. Leaf shape is liable to change by mutation, in the process of ontogeny and to be altered by a variety of environmental factors, or show seasonal polymorphism. The actual angles formed by the leaf margins at the base and apex of the lamina have sometimes been used for taxonomic purposes (e.g. WOODSON, 1947; JENTYS-SZAFEROWA, 1949, 1950). However, since the angle is difficult to measure and so often does not accurately reflect the actual shape of the leaf it was omitted in the present study.

In various species of *Acer*, *Hedera* and *Platanus* simple and palmate leaves may be found on the same plant. This feature would appear to have a certain climatic significance (see p. 26). In leaves with a palmate form the amount of dissection round the primary veins was estimated by joining the apices of the central and lateral lobes by means of a line. The mid-point along this line was joined to the point of origin of the lateral primary veins. The percentage of the total distance between these two points which was not occupied by leaf substance was taken to represent the amount of dissection.

The nature of the teeth in leaves with a non-entire leaf margin is of great importance from a systematic point of view. Unfortunately, the nature of such teeth is often such as to defy adequate description. The nature of the leaf margin bears a certain relationship to climate as pointed out in the section dealing with climatic conditions. While this generally applies to the assemblage as a whole, rather than to individual taxa, the same species growing under different climatic conditions may display somewhat different leaf margins (compare, e.g. CHIKHLADZE, 1958).

VENATION

In a series of publications a century or more ago VON ETTINGSHAUSEN (1854 a, 1854 b, 1856, 1857, 1858 a, 1858 b, 1861, 1865, 1872 a) described the venation pattern in a number of angiosperm families. However, while the occasional work on leaf venation still continued to be published e.g. ERTL (1932), little attention was paid to this aspect of botany in the following 80 years. A revival of interest in venation patterns and their significance from a systematic point of view is largely the result of the stimulus given by FOSTER (1950 a, 1950 b, 1951, 1959, 1966, 1968).

In his monograph on the venation of dicotyledons VON ETTINGSHAUSEN (1861) divided angiosperms into various types on the basis of their venation. These types have been made use of in the present account. In leaf-remains displaying craspedodromous or camptodromous venation the number of secondary veins occurring on either side of the midvein may have a certain diagnostic value. It is therefore important to be able to establish the actual number present with some degree of accuracy. Since the most proximal and the apical secondary veins are frequently weakly developed, these may prove difficult to specify. For this reason the number given in the descriptions excludes those occurring in the apex, when this is acuminate.

In palaeobotanical works reference is often made to the angle at which the secondary veins arise from the primary veins. The angle is that between any secondary vein and that part of a primary vein distal to the point at which the two veins meet. Since the course of the secondary vein may change somewhat along its length, the angle must be measured over a unit distance (in this case some 5 mm). This angle has not proved to be of much use in the present study. On the other hand, the distance between successive secondary veins, measured along the midvein from base to apex, has proved to be of value in separating various taxa (c.f. MELVILLE, 1960). Not only the trend, if any, but the irregularity encountered would appear to be important. However, it ought to be pointed out that while the distance between the secondary veins has been measured along the midvein, the length of the lamina has been taken as the shortest distance from the base to the apex of the leaf. In cases where the midvein is curved or sinuous apparent discrepancies are liable to exist. In those forms having craspedodromous venation the lengths of successive secondary veins were measured (c.f. MELVILLE, 1960), although this character was found to be less valuable than the distance between successive secondary veins.

The intermediate veins are those veins arising from the primary veins just as secondary veins, but unlike the latter do not normally extend to the margin, close to the margin or to the marginal vein. When they do fulfil one of these conditions they may be distinguished from the secondary veins in being finer or in having a more variable course. Intermediate veins may occur in markedly different configurations (compare, e.g. CORNER, 1958). The maximum amount of extension, measured at right

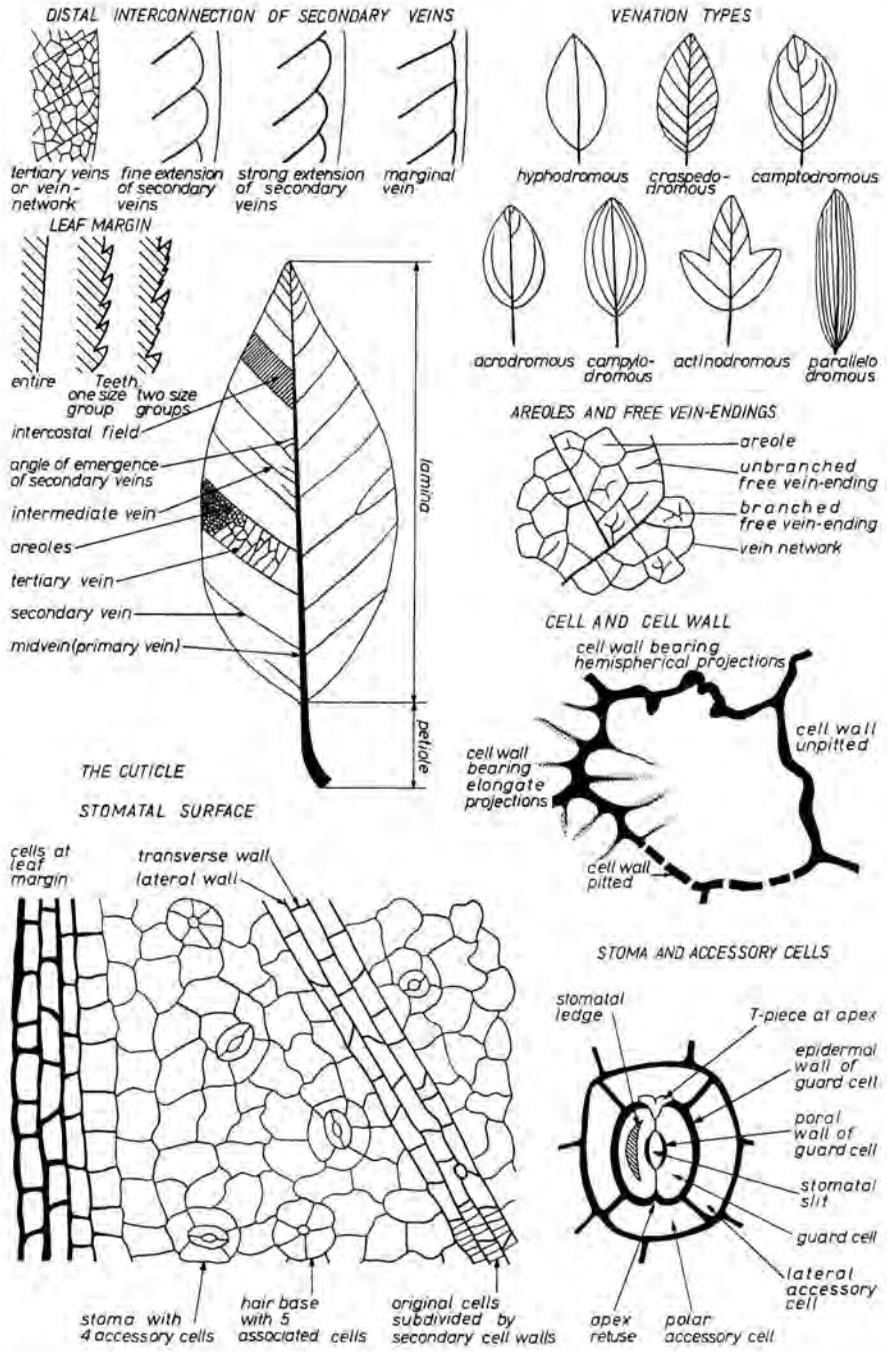


Fig. 7. Illustrations of some of the leaf characters made use of in the present account.

angles to the midvein, although varying somewhat from one intercostal field to another, may have a certain diagnostic value.

The angle of emergence of the tertiary veins was made use of by MEYERHOFF (1952) in his study of the venation in the Betulaceae. This angle, measured in the same way as for the secondary veins, varied within the same limits in all the species initially examined by the present author and therefore appears to be of limited value taxonomically. In the present account the number of tertiary veins per 1 cm secondary vein is given, this being the number on the acroscopic or basiscopical side of the secondary veins and not the combined total. This number has been found to be moderately useful, but should the tertiary veins be much branched and grade into the vein network the actual number is difficult to estimate. In such cases the figures should not be applied too rigidly.

The fine vein reticulum completely surrounds areas of the lamina known as areoles. In living plants the number of these areoles per unit area may be fairly constant per species (LEVIN, 1929; HALL and MELVILLE, 1954) and the number sometimes differs considerably between one species and another. Their number is, however, to some extent related to climatic conditions (see MAXIMOV, 1929; ZEUNER, 1932; WYLIE, 1939, 1947; PLYMALE and WYLIE, 1944; MANZE, 1968). Measurements were made by counting the number of areoles within a circular aperture 10 mm² in diameter. Successive counts on different leaves of a single herbarium specimen gave similar results. One factor which may reduce the value of this feature is the insufficient preservation of the leaf substance in certain cases. It is this factor that prevents one from making much use of the nature of the free vein-endings, a feature of not inconsiderable importance in living plants (CARLQUIST, 1961).

CUTICLE AND EPIDERMIS

HOFMANN (1932) considered cuticle analysis as major a development in palaeobotany as pollen-analysis. Not only can cuticle preparations act as a guide to the separation or grouping of fragmentary fossils, but may be made use of in any determination of the affinity of the plant-remains. Within a small piece of cuticle an almost complete range of epidermal characters may be reflected.

The preparation of cuticles

The preparation of cuticles from both leaf-remains and herbarium material was carried out by oxidation in Schulze's reagents (Potassium Chlorate and Concentrated Nitric Acid). In the case of herbarium material the fragment of lamina removed was taken half way along the length of the lamina. This was rarely possible in the case of fossil material and preparations were made from that part of the lamina most likely to give results. While it was occasionally possible to ease the cuticle from the leaf-remains by means of a dissecting needle, it was generally necessary to remove the cuticle

along with a certain amount of matrix. The amount of matrix should be kept to a minimum, so as to reduce the chance of contamination by means of *cuticulae dispersae*. After treatment in Schulze's reagents the leaf material was washed in a little water and a 10-25% solution of Ammonia (NH₄OH) added. This solution has the effect of clearing the preparation and staining the cuticle a somewhat darker colour. Thus the use of additional staining techniques is generally unnecessary. After renewed washing in water the cuticle preparations were poured into a petri-dish. In the case of fossil material the cuticle is rarely intact and the fragments require to be transferred from the petri-dish onto a slide by means of a fine sable paint-brush. To prevent contamination care should always be taken to clean the brush thoroughly after each preparation. In the case of intact fossil material and recent material the upper and lower surfaces had to be separated first before these could be finally mounted for examination. The mounting medium made use of was either glycerine or glycerine jelly.

Cuticles can also be prepared from fossil material by means of collodium. This method consists of coating the part of the fossil to be removed with a layer of elastic collodium. This is allowed to dry and any large bubbles formed during this process should be removed with a needle. The drying process takes a minute or two and should not be allowed to go too far in which case contraction of the drop of collodium occurs. This increases the possibility of damage to the cuticle. The area covered by the collodium is then removed along with some of the matrix and placed in a small plastic container with Hydrofluoric Acid (HF). The acid has the effect of freeing the leaf substance from the matrix in which it is embedded. One must make sure that the collodium is almost hard when placed in Hydrofluoric Acid, for the collodium otherwise becomes white and loses its transparency. Once the leaf substance is freed from the matrix the collodium layer with its leaf substance rises to the surface and should first be washed in water before undergoing treatment in Schulze's reagents. The reacting mixture should not be allowed to stand for more than a few hours, since collodium is slowly attacked if left in the reagents, with the result that it loses its transparency and becomes brittle. The limit as to the reaction time is one of the greatest disadvantages of the collodium method. Furthermore, the refractive index of collodium is fairly close to that of the cuticle itself, which results in a loss of contrast. Preparations made in this way suffer from undulations caused by a certain amount of shrinkage and the presence of bubbles, and when both upper and lower cuticles are present their mutual interference adds to the difficulty of interpreting the structures. On the other hand this method has the advantages of (a) retaining the cuticle entire if and when the cuticle is thin and/or shattered (b) ruling out the possibility of contamination either during the removal of the leaf substance from the matrix or resulting from an insufficiently cleaned test-tube or paint-brush. This method was therefore not only used for leaf-remains with poorly preserved cuticles but used in confirming the association of a

particular epidermal pattern with a given taxon, when this was only represented in the deposit by a small number of specimens.

Epidermal characters

The cells of the epidermis as reflected in the cuticle may have walls that are straight or undulating. While climatic conditions may influence the amount of undulation exhibited e.g. in *Datura stramonium* (SHARMA and DUNN, 1969), this is not always the case (compare, e.g., WALKER and DUNN, 1967). ROMANOVICH (1960) considered it possible to recognize certain genera and even species of the Solanaceae on the basis of this character. The cell wall was found to show a certain amount of variation as regards continuity, ornamentation and thickness.

In some cases the trace of the cell wall is more or less continuous, while in other cases it is pitted to such an extent as to resemble a dotted line. Furthermore the cell wall may be thickened at intervals in the form of hemispherical bodies or long protrusions projecting into the cell space. Neither form occurred to any extent in the fossils under investigation, but would appear, when present, to have a certain diagnostic value. The actual thickness of the epidermal cell wall as reflected in the cuticle varied somewhat, but was rarely found to be of value taxonomically. Not only does it appear to vary with the maturity of the leaf, but it may have been affected by changes during fossilization. DE VRIES, BREDEMEIJER and HEINEN (1967) have shown that decay caused by fungi and bacteria brings about a gradual thinning of the cell walls sometimes preceded by an initial swelling of their boundaries. Should decay continue the cell walls break down and a structureless mass, the final stage before complete destruction of the cuticle, results.

The size of the epidermal cells may have a certain value in distinguishing various taxa from one another. However, since an increase in size may be directly connected with an increase in ploidy or atmospheric humidity, too much importance should not be attached to minor differences in cell size. Moreover, cell size is dependant to some extent on the position on the leaf chosen for examination. This factor must be borne in mind when dealing with fossil material, for the various preparations may not originate from comparable parts of the lamina. In the present undertaking the size of the cells has been indicated by counting the number occurring within 0.1 mm². Some authors have given actual measurements, but since individual cells can vary so much in size it was felt better to abstain from this practice altogether.

The exchanges of gases between the leaf and the surrounding medium is usually carried out largely by means of stomata when present. The stomata may be present on one or both sides of the lamina. The stomata show variation in their number, arrangement and form, which may be in part a response to environment. A decrease in the number of stomata per unit area may be the result of decreasing exposure and/or increase in humidity

or level of ploidy. However, since such changes go hand-in-hand with a decrease in the number of epidermal cells, stomatal number expressed as a percentage of the total number of epidermal cells (*Stomatal Index*) should represent a fairly satisfactory constant. Experiments (SHARMA and DUNN, 1968, 1969) have shown the Stomatal Index to be generally reliable, except under extreme conditions under which the plants probably would not have survived in nature. When dealing with fossils it is important to bear in mind that when the cuticle is fragmentary or poorly preserved the stomatal index may not be able to be defined as accurately as in recent material. The general arrangement of the stomata would appear to be of some importance taxonomically. DUNN, SHARMA and CAMPBELL (1965) have pointed out that the stomata are mostly arranged in more or less the same direction in Monocotyledons, while Dicotyledons usually have the stomata orientated randomly. In the Angiosperms this may, in part, be related to leaf form and venation pattern. Within the conifers both types are known to occur. The dimension parallel to the stomatal slit is regarded as the length of the stoma, whether or not this was the longer dimension. In most cases the length/breadth ratio appears to vary somewhat, but in some cases this ratio shows a large variability, which may be of some taxonomic value. Stomatal size has been used by a number of authors and while this may hold in certain groups, e.g. Cycadophytes and Monocotyledons, DUNN, SHARMA and CAMPBELL (1965) have shown that in Dicotyledons the size of the stomata, which develop at different times during the growth of the leaf, is liable to vary somewhat. Stomatal size may be correlated with the level of ploidy (e.g. HARRIS, 1969) and an investigation by NESTEROVICH and PONOMAREVA (1961) has shown that the size of the stomata may increase with an increase in soil moisture. A great range of stomatal size within a single leaf has been confirmed in the present study and the use of the length or breadth of stomata in separating taxa is only of limited value. Stomatal size classes and mean stomatal size would appear to be better constants (c.f. SHARMA and DUNN, 1969). All measurements made on the stomata, including those made on the stomatal slit, were carried out under a magnification of $600\times$.

Studies on recent Gymnosperms and Angiosperms have suggested that the number and arrangement of the accessory (subsidiary) cells may be of major importance. The accessory cells may either originate from the same initial as the guard cells or represent modified epidermal cells. In extreme cases the accessory cells differ markedly in size and arrangement from the rest of the epidermal cells. Nonetheless, the presence of accessory cells may sometimes prove difficult to recognize and their number may be hard to specify. METCALFE and CHALK (1950) considered Dicotyledons to be divisible into four principal types on the number and arrangement of their accessory cells (see also BOUREAU, 1954; ESAU, 1960). However, SHAH (1968) has pointed out that up to three of these types may occur in the same leaf. The value of this character, while certainly of some impor-

tance, is possibly of less taxonomic value than the text-books would suggest.

Trichomes are an important feature of recent plants (for review see UPHOF, 1962) and while the trichomes themselves have mostly disappeared the base of the appendage is usually present in the fossil state. The mode of attachment of the trichomes and the specialization of nearby epidermal cells shows much variation (STACE, 1965, pp. 50-55) and has been found of much value in the classification of the leaf-remains.

In living plants the subcuticular structures may sometimes be valuable taxonomically. The nature of these structures such as preserved in the fossil material under consideration did not appear to lend itself to taxonomic study, since the structures were not found to show much variation. However, the presence and frequency of internal resinous bodies, such as were retained after treatment in Schulze's reagents, did appear to vary and is recorded. Crystals were sometimes met with in the examination of the cuticles, but as there appeared to be no easy means of distinguishing the original crystals from those formed during maceration crystal shape had to be left out of consideration in the present undertaking.

GLOSSARY OF TERMS

- Accessory cells* [Epidermis] Epidermal cells immediately surrounding the guard cells and differing from the other epidermal cells in their shape, size and/or arrangement.
- Acrodromous* [Venation] Venation pattern in which the lateral primary veins present only radiate from their point of origin for a short distance before turning inwards in the direction of the leaf apex. The number of lateral primary veins is usually limited to two.
- Acroscopic* [Lamina] That portion of the lamina distal to a given vein.
- Actinodromous* [Venation] Venation pattern in which the lateral primary veins present radiate from the point of their origin.
- Areole* [Lamina] An area of the lamina surrounded on all sides by high-order veins.
- Basisopic* [Lamina] That portion of the lamina proximal to a given vein.
- Brochidodromous* [Venation] Venation pattern of a camptodromous type in which the secondary veins are interconnected distally by prominent loops.
- Camptodromous* [Venation] Pinnate venation pattern in which the secondary veins do not reach the leaf margin.
- Campylodromous* [Venation] Venation pattern in which a number of primary veins (5 or more) arising at or close to the leaf base run in a fairly strongly curved arc and meet again at the leaf apex.
- Craspedodromous* [Venation] Pinnate venation pattern in which the secondary veins or at least the thicker secondary veins terminate at the leaf margin.
- Guard cells* [Epidermis] Cells of the epidermis, (1-2) in number, composing the stomatal apparatus.
- Hyphodromous* [Venation] Venation pattern in which veins other than the midvein are not apparent or only poorly visible externally.
- Intercostal field* [Lamina] An area of the lamina bounded by a number of veins or certain veins and the leaf margin. In this account applied in a restricted sense to an area of the lamina bounded above and below by a secondary vein, on a third side by the midvein, and on the fourth side by the leaf margin or by the distal extension of the more proximal of the two secondary veins.
- Intermediate veins* [Venation] Those veins arising from a primary vein just as secondary veins, but unlike the latter not normally extending to the leaf margin, close to the leaf margin or to the marginal vein. When one of these conditions is fulfilled they may be distinguished from the secondary veins in being finer or in having a more variable course.
- Lamina* The blade of a leaf or leaflet.
- Parallelodromous* [Venation] Venation pattern in which the veins are orientated along the length of the lamina and almost parallel to one another.
- Petiole* The proximal extension of the midvein of a leaf devoid or almost devoid of any laminar tissue. In the present account also made use of if there is no evidence whether particular fossil lamina represent leaves or leaflets.
- Primary veins* [Venation] The largest veins traversing the lamina and distinguished by their greater width and/or length.
- Secondary veins* [Venation] Major veins arising from a primary vein.
- Stomatal Index* [Epidermis] The ratio of the number of stomata to the total number of epidermal cells expressed as a percentage.
- Stomatal ledge* [Epidermis] A longitudinal thickening of the cuticle in the form of a ridge developed on a guard cell.
- Subsidiary cells* [Epidermis] see Accessory cells.
- Tertiary veins* [Venation] Major veins arising from a secondary vein.

SYSTEMATIC PART

The order and circumscription of the taxa is that adopted in Engler's *Syllabus der Pflanzenfamilien* ed. 12 (1954, 1964). Certain of the authors cited by WEYLAND (1934) in connection with the binomials applied by him to the leaf-remains are incorrect or open to doubt. Any mistakes have been corrected in straight-forward cases, but the names left as cited by WEYLAND (1934) in cases requiring a more thorough analysis. Should determinations made by J. Stoller or H. Weyland be reduced to synonymy in a given case this does not mean that the author necessarily considers the taxon as conceived by its original author to be synonymous with the taxonomic entity under consideration. The binomials referred to under "Herbarium material examined in detail" are those occurring on the sheets examined and do not necessarily represent modern taxonomic opinion. However, this approach facilitates any re-checking of the examined material.

I. CLASS MUSCI

Description:

Shoots somewhat curved or sinuous, somewhat branched, branches arising at 60° – 90° , terminal shoots c. 9–c. 12 mm long, shoot axis 0.15–0.45 mm in diameter.

Leaves numerous, isophyllous, overlapping and apparently spirally arranged, 1.0–2.0 mm long and 0.15–0.40 mm wide, attached without constriction to the shoot axis and possibly slightly decurrent. Leaves simple, falcate, arising initially at 35° – 55° , tapering at apex into sharp point. Leaf margin entire.

Epidermis poorly preserved, possibly composed of narrow rectangular to spindle-shaped cells.

Specimens examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3854, 3855.

Discussion:

The delicate nature of the leaves on the shoots would tend to indicate that the remains are those of a moss. The branched shoots, leaf shape etc. might suggest that one is dealing with a member of the Hypnobryales. In the absence of more details a more exact determination is not possible to date.

CLASS FILICES

II. ORDER FILICALES

Description:

Fronde sterile, compoundly pinnate. Major rachis not channelled, 1.0 mm wide, giving rise at 9 mm intervals to rachis bearing pinnules. This rachis,

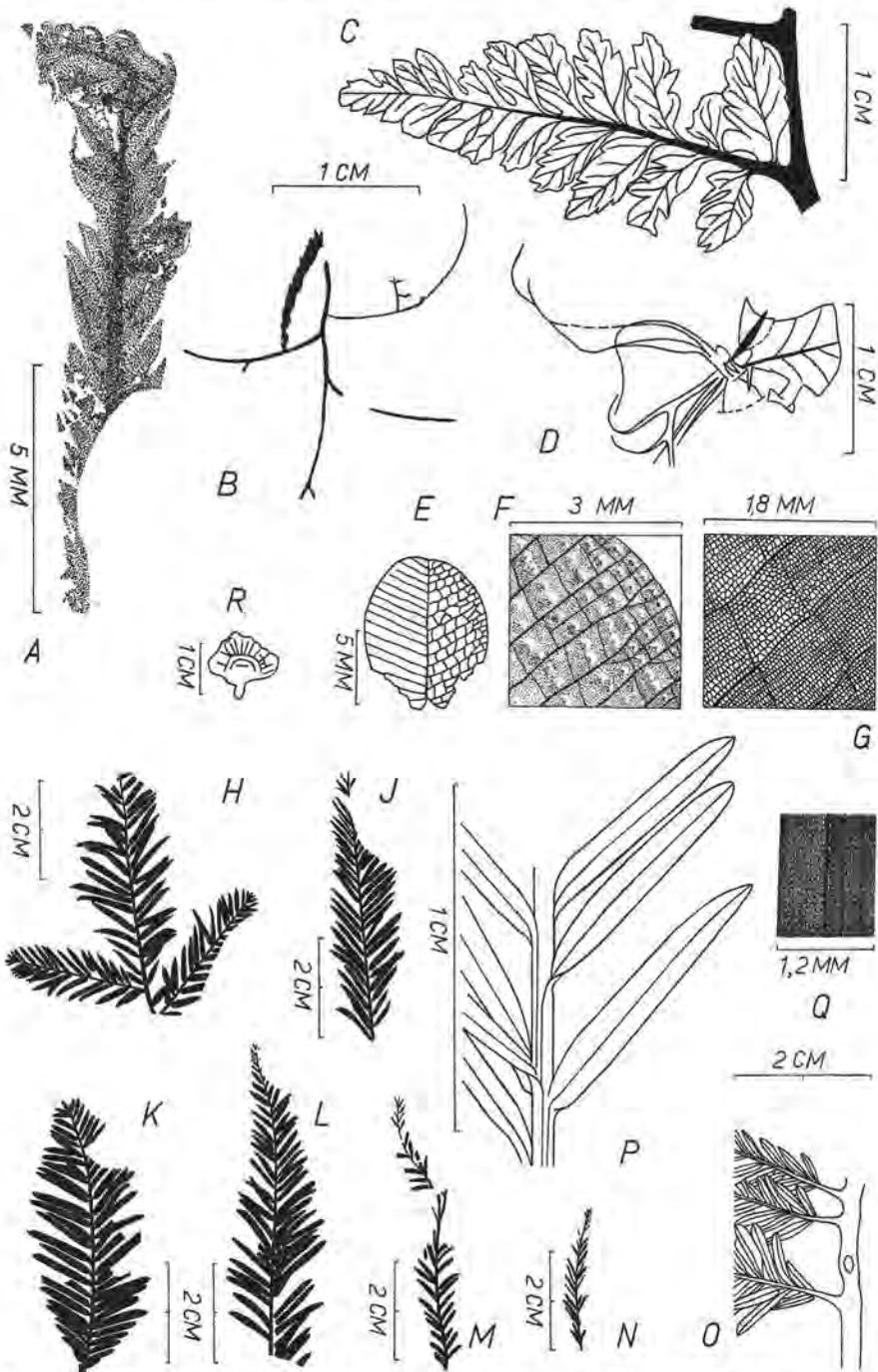


Fig. 8. A-B = I: Utrecht 3854. C = II: Cologne s.n. D-G = III: D = Cologne, Coll. H. Weyland 1636-1636a; E-G = Utrecht 3848. H-R = IV: H = Utrecht 3435 (drawing based on specimen and its counterpart); J = Utrecht 3410 A; K = Utrecht 3397; L = Utrecht 3398; M = Utrecht 3408; N = Utrecht 3405; O = Utrecht 3404; P = detail showing the attachment of the leaves to the shoot; Q = detail showing part of a leaf and its midvein; R = Cologne, Coll. H. Weyland 1702, cone scale.

30 mm long and 0.6 mm wide at base, tapering markedly along length, arises from the major rachis at an initial angle of 45° – 60° , slightly recurved, bearing 11–12 pinnules per side. Pinnules 1.3–9.5 mm long and 0.85–5.0 mm wide, length decreasing successively along rachis from base to apex, having an apparently anadromic arrangement, alternately arranged, spaced on rachis at successively decreasing intervals. Most distal 4–5 pinnules entire, pinnules thereafter dissected to an increasing degree, the maximum number of lobes per pinnule 4 on the proximal side and 5 on the distal side, the lobes alternating, the number on the proximal side of the pinnule always one less than on the distal side; lobes acute, sinuses acute. Basal pinnule unspecialized. Midvein straight or somewhat irregular in course, giving rise to 1–2 secondary veins per side in entire pinnules and 2–6 secondary veins per side in non-entire pinnules, veins arising at 30° – 60° , straight or forwardly arched, opposite or alternately arranged. In larger pinnules secondary veins giving rise at 30° – 45° to 1–2 branches per side. Inset of midvein in pinnule asymmetrical, closer to the proximal than the distal surface. The nature of the epidermal cells unknown.

Specimen examined: Geol. Inst. Cologne: s.n.

Discussion:

Although certain plant groups other than the Filicales may have foliar organs somewhat resembling the fossil e.g. Umbelliferae, the regularity of the structure would suggest a fern. In the fossil the ordering of the pinnules on the rachis is the same as that encountered within the pinnules themselves. In the absence of fertile material a more exact determination proved to be impossible.

ORDER SALVINIALES

FAMILY SALVINIACEAE

III. *Salvinia*

Synonyms: *Salvinia formosa* Heer
Salvinia mildeana Goepfert
Salvinia sp.

WEYLAND, 1934, p. 38!
 SHAPARENKO, 1956, p. 30!
 Coll. H. Weyland 1636–1636 a,
 det. F. Kirchheimer!

Description:

Leaves arranged in clusters on a base also giving rise to simple or branching rootlets.

Petiole 1.2–1.3 mm long and 0.45–0.60 mm wide, more or less parallel-sided, straight.

Lamina circular or sub-circular, 0.6–1.04 cm long, 0.6–0.8 cm wide, the length/breadth ratio being 1.0:1–1.3:1. Leaf apex rounded, leaf base obtuse or rounded.

Leaf margin entire.

Venation craspedodromous, midvein straight, tapering along length, 0.1 mm wide at mid-point between base and apex of the lamina. Midvein

bearing 9–15 secondary veins per side, the most proximal vein arising at 120°–140°, arising in the remaining part of the basal third of the lamina at 55°–110°, in the median third at 40°–70°, in the apical third at 45°–65°. The angle at which the veins arise constant or somewhat increasing initially. The spacing of the veins more or less constant. Secondary veins opposite or subopposite and rarely alternately arranged, hardly tapering along their length, c. 0.025 mm wide at mid-point, interconnected distally by tertiary veins. Intermediate veins absent. Tertiary veins 15–17 per 1 cm secondary vein, straight and unbranched. Papillae, 2 in number, present per tertiary vein interval. A vein, running parallel to the secondary veins, occasionally present between a pair of papillae.

Specimens examined: 5, among which the numbered specimens:

Geol. Inst. Cologne: Coll. H. Weyland 1636–1636a Bot. Mus.
& Herb. Utrecht, Div. of Palaeobot.: 3847, 3848.

Discussion:

The shape of the leaves and the presence of papillae would suggest that one is dealing with the remains of *Salvinia*. However, an attempt to refer the material to a specific entity met with difficulties. In his key to the species of *Salvinia* based on vegetative characters SHAPARENKO (1956, p. 15) not only made use of characters such as leaf size and shape, but the presence, size, shape and uniformity of pilae and papillae and whether the lamina is or is not keeled. The impossibility of observing certain of these features in the present specimens consequently prevented their reference to a specific entity. In this connection it is of interest to note that Dr. E. K. Kempf (personal communication, 1967), who has examined the spores from the Kreuzau deposits, considers it possible to recognize more than one species of *Salvinia*.

Herbarium material examined in detail:

<i>Salvinia auriculata</i> Aubl.	Coll. F. Drouet 2391	(U)	det. C. A. Weatherby
	Coll. R. M. Tryon Jr. 5025	(U)	det. R. M. Tryon Jr.
<i>Salvinia natans</i> (L.) All.	Coll. F. Florschütz, F. P.	(U)	_____
	Jonker & E. T. Nannenga		
	7-10-1938		
	Coll. Z. Wisniewska &		
	H. Blaszczyk 15-8-1952	(U)	_____
<i>Salvinia radula</i> Bak.	Coll. A. C. Smith 2229	(U)	det. C. A. Weatherby
<i>Salvinia rotundifolia</i> Willd.	Coll. P. Weatherwax 232	(U)	det. W. H. Wagner Jr.

CLASS CONIFEROPSIDA

Artificial key to the Taxa:

- | | |
|---|----|
| 1 Leaves linear-lanceolate, generally not appressed to the shoot, cuticle non-papillate | 2 |
| – Leaves decussate, appressed to the shoot, cuticle locally papillate | VI |
| 2 Leaf c. 40–90 mm long and 2.8–7.8 mm wide, bearing a pair of strongly marked stomatal bands on lower surface, stomata mostly orientated parallel to length of leaf, accessory cells (4–) 6–10 (–12) | V |

- Leaf 1.5-2.2 mm long and 0.4-2.1 mm wide, stomata arranged in a number of bands macroscopically indistinct, stomata variously orientated, accessory cells 4 (-5) IV

FAMILY TAXODIACEAE

IV. *Taxodium*

Synonyms: *Sequoia langsdorffii* (Brongniart) Heer WEYLAND, 1934, p. 39!

Taxodium distichum (L.) Rich. QUAAS, 1910, p. 983!

Taxodium distichum miocenicum Heer WEYLAND, 1934, p. 39!

Description:

Shoots 27-70 mm long, 0.20-0.25 mm in diameter at apex of shoot, gradually increasing in diameter away from apex and reaching a maximum diameter of 1.1 mm in leaf-bearing state.

Leaf arrangement alternate, 30-72 leaves or possibly more per shoot, arising from the shoot at 30°-65°, spaced at intervals of 0.5-3.5 (-10.5) mm, equivalent to 4-15 per side per 10 mm, gradually increasing in length up to the sixth to fifteenth leaf from the shoot apex on either side of the shoot, leaf width but slightly increasing away from the apex of the shoot.

Leaves straight or sometimes recurved with midvein 0.07-0.40 mm wide. Leaves mostly linear-lanceolate, although those most proximally on shoots sometimes reduced and scale-like, 1.5-2.2 mm long and 0.4-2.1 mm wide, either tapering to a fine point or more or less parallel-sided ending somewhat abruptly in acute apex, the length/breadth ratio being 4:1-22:1. Leaf base sessile or apparently short petiolate due to a twisting of the leaf base.

Epidermis over midvein composed of c.200 rectangular or spindle-shaped cells per 0.1 mm², cell wall 1-3 microns thick, largely unpitted, straight. Epidermis in stomatal condition composed of c.110-c.150 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1-5:1. Cell wall 0.6-2.0 microns thick, unpitted or pitted, more or less straight. Stomata 16.8-39.2 microns long and 13.6-22.4 microns broad, breadth 50-80% length, 5-10 per 0.1 mm²; stomatal index 6-10%. Stomata variously orientated, slightly depressed, apices non-retuse, sometimes characterized by the presence of a T-shaped piece. Stomatal slit c.75% stomatal length. Accessory cells 4 (-5), symmetrical with 2 polar and 2(-3) lateral cells, similar in size or smaller than the rest of the epidermal cells.

Specimens examined: 221, among which the numbered specimens:

Geol. Inst. Cologne: Coll. H. Weyland 1372, 1637, Excursion 14-5-1949 and E 100.

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.:

3397, 3398, 3399, 3400, 3401, 3402, 3403, 3404, 3405, 3406, 3407, 3408, 3409, 3410A, 3411, 3412, 3413, 3414A, 3415, 3416, 3417, 3418, 3419, 3420, 3421, 3422, 3435, 3459B, 3746B, 3788B.

Discussion:

The general appearance of the leaf-bearing shoots could suggest an affinity with any of a number of living genera e.g. *Taxus*, *Podocarpus*

(*P. andinus*, *P. spicatus*), *Sequoia*, *Glyptostrobus*, or *Taxodium*. However, while the leaves of *Taxus*, *Podocarpus andinus* and *P. spicatus* generally reach their maximum length a few nodes away from the apex of the leafy shoots, *Sequoia*, *Glyptostrobus*, *Taxodium* and the leaf-remains under consideration display a more gradual increase in the leaf length (fig. 9). Moreover, *Taxus*, *Podocarpus andinus* and *P. spicatus* differ from the fossil in having a thicker axis (0.5–0.9 mm wide) at the apex of the shoot and a different epidermis (see FLORIN, 1931). With respect to the axis of its leafy shoots *Sequoia* resembles the above-mentioned species of *Podocarpus* and *Taxus*. At the apex of the shoots the axis is 0.5–0.7 mm in diameter. The leafy shoots of *Sequoia*, moreover, differ from the leaf-remains in having leaves with a length/breadth ratio which rarely exceeds 8:1, the maximum being 11:1.

While the epidermides of the Taxodiaceae are fairly uniform (FLORIN, 1931; SVECHNIKOVA, 1963), differences can be recognized between those of *Glyptostrobus* and *Taxodium*. In the leaves of *Glyptostrobus* the stomata are aligned more or less parallel to the midvein. In *Taxodium*, on the other hand, the stomata are either aligned transversely to the length of the leaf or orientated in various directions. In this respect the available cuticle preparations made from the leaf-remains would suggest an affinity with *Taxodium* rather than *Glyptostrobus*. The fossil resembles the shoots of *Taxodium distichum* (L.) Rich. and *T. mucronatum* Tenore. However, since no features were found separating the shoots of these two species, a reference of the fossil to a specific entity did not prove to be possible.

In view of the presence of certain shoots with recurved leaves, such as found in living material of *Glyptostrobus*, the possibility that this genus was also represented in the Kreuzau assemblage must not be overlooked. However, in the lack of evidence in the form of cuticle preparations the presence of this genus could not be confirmed.

FAMILY TAXACEAE

V. *Amentotaxus florinii* Kräusel

Synonym: *Echitonium sophiae* Weber WEYLAND, 1934, pp. 110–111!

Description:

Leaves linear-lanceolate, straight or falcate, c.40–90 mm long, 2.8–7.8 mm wide, the length/breadth ratio being c.10:1 – c.16:1. Leaf apex acute, leaf base acute. Leaf margin entire, sometimes slightly revolute. Midvein, 0.6–1.0 mm wide, raised on upper surface, not projecting on lower surface but sometimes marked by a zone of discontinuous striae within otherwise smooth central area. Central area, 0.8–2.4 mm wide, flanked on either side by a stomatal band, 0.4–0.9 mm wide in central part of lamina. Marginal to the stomatal band is a band, 0.6–1.3 mm wide, (1–) 1.5–2.7 times as broad as the stomatal band.

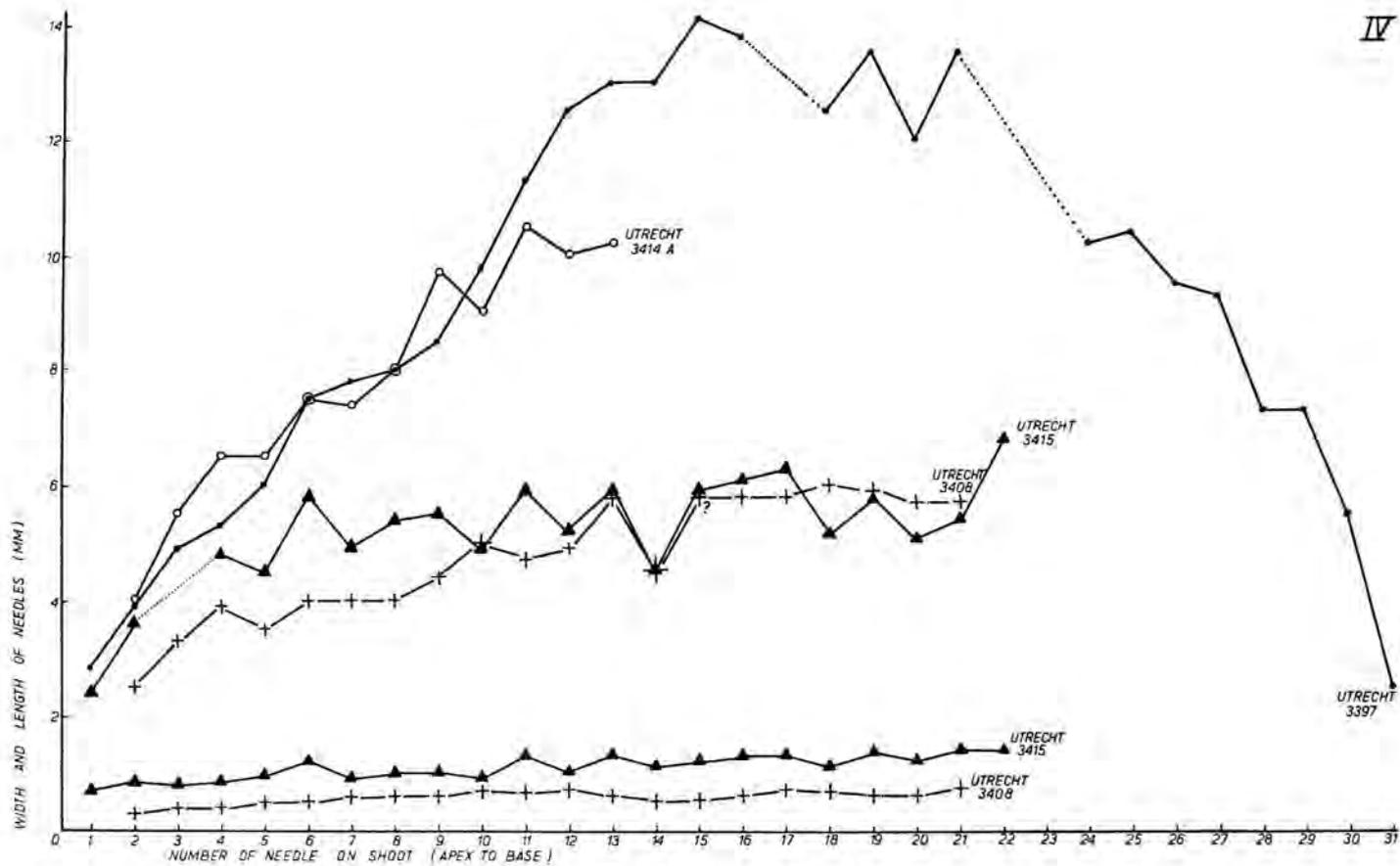


Fig. 9. Graph IV.

Upper epidermis composed of 75–90 square, rectangular or polygonal cells per 0.1 mm², the length/breadth ratio being 1 : 1–2 : 1 (–4 : 1). Cell wall 1–2 microns thick, largely unpitted, more or less straight. Cells over midvein similar to the rest of the epidermal cells.

Lower epidermis above marginal band composed of 60–90 square, rectangular, or more or less polygonal cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–5.5 : 1. Cell wall 1–2 microns thick, largely unpitted, more or less straight. Cells over midvein composed of 90–95 cells per 0.1 mm², elongated parallel to the length of the leaf, the cell length/cell breadth ratio being 1 : 1–6 : 1. Stomatal bands composed of 120–150 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3.5 : 1. Cell wall 1.0–3.5 microns thick, largely unpitted, straight. Stomata c.56 microns long and 18–34 microns broad, breadth 32–60% length, 19–23 per 0.1 mm²; stomatal index 20–21%. Stomata generally orientated with their length parallel to the length of the lamina, depressed, more or less equidistant, apices non-retuse. Stomatal slit 40–45% stomatal length. Accessory cells (4–) 6–10 (–12), symmetrical with 2–4 polar and (2–)4–6 (–8) lateral cells resulting in a star-like appearance of the whole. The walls adjoining the stomata slightly thickened.

Specimens examined : Deutsche Akad. Wiss. Berlin : s.n. (K 153)

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot. : 3471, 3472, 3473, 3474, 3547A.

Discussion :

Although initially referred to *Echitonium sophiae* Weber (WEYLAND, 1934), the leaf-remains did not display the secondary veins present in the type specimen. Cuticle analysis carried out by the present author proved that these remains were, in fact, coniferous. The similarity displayed by the cuticle of the fossil and that of leaves of living species of *Amentotaxus* would indicate that the fossil should be referred to this genus (see KRÄUSEL, 1935; WEYLAND, 1947; FERGUSON, 1967). The cuticles of the various species of *Amentotaxus* would appear to be uniform and are unique amongst living conifers in the presence of numerous accessory cells combining to give a star-shaped appearance. Until recently this genus was considered to be monotypic, but H. L. Li's work on the genus has proved it to consist of four species. LI (1952), in his revision of the genus, made much use of leaf characters and relied in particular on the width of the stomatal bands to separate the various species. In living species the stomatal bands are 1.2–2.5 mm wide mid-way along the lamina, while the comparative figure for the fossil is 0.4–0.9 mm. The reference of the fossil to a separate specific entity would therefore appear to be warranted.

The material was provisionally referred to as *Amentotaxus florinii* Kräusel (WEYLAND, 1947). However, while FLORIN (1940) considered that *Amentotaxus campbellii* (Gardner) Florin (= *Podocarpus campbellii* Gardner) from Ardtun Head (Mull, Scotland) could be recognized as a separate

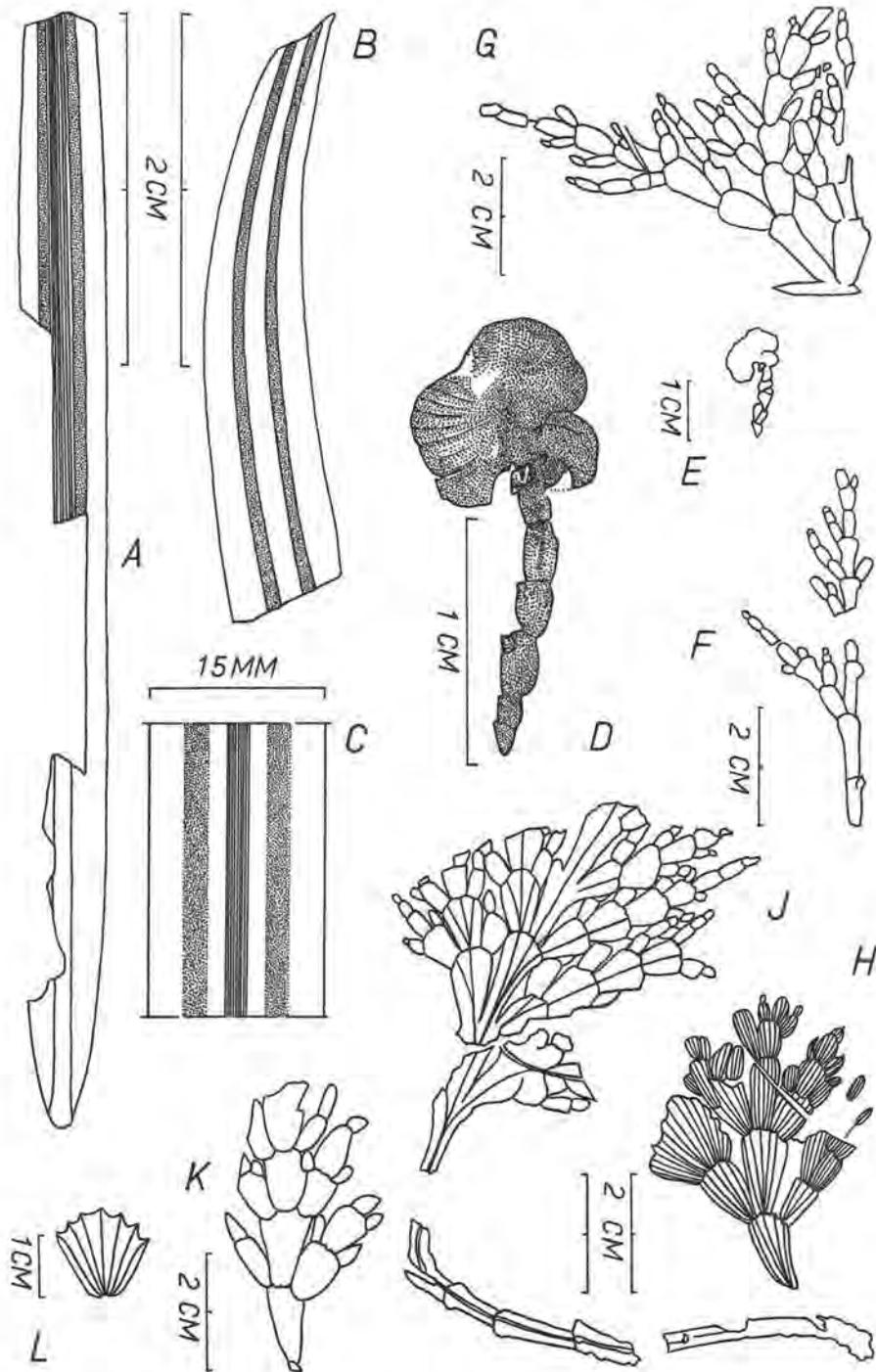


Fig. 10. A-C = V: A = Utrecht 3473; B-C = Utrecht 3474. D-L = VI: D-E = Utrecht 2055, cone; F = Utrecht 3643; G = Utrecht 3641; H = Utrecht 3642; J = Utrecht 3652; K = Utrecht 3646; L = detail of isolated leaf whorl showing distal projections.

species, WEYLAND (1947) suggested the possibility that this taxon might prove to be identical to *Amentotaxus florinii*. Should this indeed prove to be the case the name *Amentotaxus florinii* would have to be reduced to synonymy. The percentage of dicotyledonous taxa from the Ardtun beds having leaves with an entire margin would certainly suggest that the climate at the time of deposition of these beds was similar to that during the deposition of the Kreuzau sediments. Material of *Amentotaxus campbellii* collected by the author from the type locality was found to resemble *A. florinii* in the width of the lamina, the width of the stomatal bands as well as in the size, shape and arrangement of the stomata. In the two specimens of *Amentotaxus campbellii* examined neither leaf apices nor leaf bases were observed. FLORIN (1940) considered the nature of the leaf apices and leaf bases of importance in specific determination. While the importance attached to these characters is questionable, the specific identity of *Amentotaxus florinii* and *A. campbellii* is complicated by two additional considerations. In the first place, the preservation of the material of *Amentotaxus campbellii* available to the present author was not sufficient to enable the outline of the accessory cells to be made out. Secondly, it is important to bear in mind the large gap in time existing between the Ardtun beds (Palaeocene) and the Kreuzau deposits (Miocene). In the meantime, in the absence of a detailed study, *Amentotaxus florinii* is retained as a specific entity.

Herbarium material examined in detail:

Amentotaxus cathayensis Li Coll. W. K. Hu 9209 (E) det. H. L. Li

CONIFEROPSIDA INCERTA SEDIS

VI *Hellia salicornioides* Unger

Synonyms: *Libocedrus salicornioides* (Unger) Heer WEYLAND, 1934, p. 39!

Tetraclinis brongniartii (Endlicher) Coll. H. Weyland 1739, det.
nov. comb. ined. H. Weyland!

Description:

Branchlets flattened dorsi-ventrally, composed of whorls of 4 leaves up to 1.9 cm long and 1.2 cm wide, the base of the whorl concave. Each whorl may give rise to 1-3 whorls distally.

Leaves decussate, marginal leaves slightly shorter than the facial leaves. Facial leaves without median ridge, ending distally in 0-7 small sharp apices separated from each other by shallow rounded sinuses. Marginal leaves small, non-imbricate, entirely fused (at immature stage) to almost entirely fused (in the mature whorls) to the facial leaves, in the latter case ending in a sharp apex. Leaf whorls transversed by 3-5 major vascular bundles, 0.1-0.3 mm in diameter.

Epidermis of facial leaves composed of 85-160 non-papillate or papillate cells per 0.1 mm², the cell length/cell breadth ratio in areas without stomata 1 : 1-9 : 1, more or less rectangular and orientated parallel to the length

of the leaf, the cell length/cell breadth ratio in close proximity to the stomata 1 : 1-2 : 1, the cells variously orientated. Cell wall 0.6-2.5 microns thick, unpitted or somewhat pitted, sometimes bearing elongate projections or being irregularly thickened, straight. The distal lobes of each leaf and in particular the apex of the marginal leaves papillate. Leaves hypostomatic, the number of the stomata on the one surface being 2-3 times greater than on the other surface. Stomata 30-40 microns long and 18-28 microns broad, breadth 50-83% length, 0-11 per 0.1 mm²; stomatal index 0-6.25%. Stomata variously orientated, somewhat depressed, apex non-retuse characterized by the presence of a T-shaped piece, stomata arranged in rows parallel to the length of the leaf or in groups. Stomatal slit 30-50% stomatal length. Accessory cells 4-7, mostly symmetrical with 2-4 polar and 2-4 lateral cells, although sometimes radially arranged. Accessory cells smaller than the rest of the epidermal cells, inner wall somewhat thickened. Marginal leaves similar to the facial leaves in the number and shape of cells and in the nature of the cell wall. The stomata, similar in other respects to those of the facial leaves, occur singly.

Cone ± spheroidal, 0.8 cm long and 1.0 cm wide, composed of 8 (?) cone-scales radiating from a central point of origin. Tissue of cone-scales composed of 90-220 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1-5 : 1. Cell wall 1.5-6.0 microns thick, largely unpitted, straight. Stomata c.30 - c.36 microns long and 21.6-27.0 microns broad, breadth 60-88% length, 0 - c.5 per 0.1 mm²; stomatal index 0-5.5%. Stomata variously orientated, somewhat depressed, arranged in groups. Accessory cells 4-5, symmetrical with 2-3 polar and 2 lateral cells, or radial in arrangement. Accessory cells similar in size to or somewhat smaller than the rest of the epidermal cells, inner wall unthickened.

Specimens examined : 65, among which the numbered specimens:

Geol. Inst. Cologne: Coll. H. Weyland 1369 (K 1), 1721 (K 1),
1722 (K 1), 1739, Coll. M. Schwarzbach 19-5-1944
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 2055, 3641,
3642, 3643, 3644, 3645, 3646, 3647, 3648, 3649, 3650, 3651,
3652, 3653, 3654, 3655, 3656, 3743B.

Discussion :

While Weyland referred Weyland 1739 to *Tetraclinis* this specimen was not found to differ in any respect from vegetative shoots referred to by him as *Libocedrus salicornioides*. Both are here included in the same taxon.

As pointed out by FERGUSON (1967) the taxon under consideration is somewhat anomalous. While generally referred to the Cupressaceae, it differs from members of this family with regard to the leaf whorls. In the species of Cupressaceae examined [*Austrocedrus chilensis* (D. Don) Florin et Boutelje (= *Libocedrus chilensis* (D. Don) Endl.), *Calocedrus decurrens* (Torr.) Florin (= *Libocedrus decurrens* Torr.), *Chamaecyparis lawsoniana* (A. Murray) Parlatore, *Thuja occidentalis* L., *T. plicata* D. Don, *T. standishii* (Gordon) Carrière] the leaves are arranged in the same decus-

sate manner as those of the fossil. However, in the above members of the Cupressaceae the outer imbricate pair of leaves is free to the base, while the inner pair is distally free but proximally fused. In the fossil, on the other hand, the marginal leaves are much reduced and fused to the facial leaves for the greater part of their length. In this respect and with regard to the large size of the leaf whorls, the fossil differs from living representatives of the Cupressaceae.

However, even though the affinity of the fossil is uncertain, the taxon represents a very distinctive entity and would therefore appear to warrant the use of a binomial. The present taxon has been referred to in the past as *Hellia salicornioides* Unger, *Thuyites salicornioides* (Unger) Unger, *Libocedrites salicornioides* (Unger) Endlicher, *Libocedrus salicornioides* (Unger) Heer and *Cupressinocladus salicornioides* (Unger) Seward. In the light of our present knowledge regarding the structure of the fossil all generic names, with the exception of *Hellia*, must be regarded as unsuitable, since they suggest a direct relationship with living conifers.

ARTIFICIAL KEY TO THE ANGIOSPERM LEAF REMAINS

1 Leaves filiform	LXXVII
- Leaves not filiform	2
2 Lamina palmately lobed	3
- Lamina simple	13
3 Leaf margin entire	4
- Leaf margin non-entire	8
4 Leaf base acute to obtuse, angle formed by joining the apex of the central lobe via the primary sinus to the apex of one of the lateral lobes 50°-85°, lateral primary veins arising at some distance above leaf base	XX
- Leaf base obtuse, rounded or cordate, angle formed by joining the apex of the central lobe via the primary sinus to the apex of one of the lateral lobes 75°-130°, lateral primary veins arising at or near the leaf base	5
5 Amount of dissection round primary sinuses 28-c.65%, percentage of the lamina on the basiscopic side of the lateral primary veins 20-31%	6
- Amount of dissection round primary veins up to 28%, percentage of the lamina on the basiscopic side of the lateral primary veins c.30-47%	7
6 Amount of dissection round primary veins c.65%, distance from the origin of the lateral primary veins to the primary sinuses 1.3-1.7 cm	XXXVI
- Amount of dissection round primary veins 28-62%, distance from the origin of the lateral primary veins to the primary sinuses 1.45-3.60 cm	XXXIII
7 Petiole 0.4-1.1 mm wide at mid-point, lamina 3.4-8.8 cm long, the distance from the origin of the lateral primary veins to the primary sinuses 3.4-5.9 cm, lateral primary veins 57-65% the length of the central primary vein, cuticle finely striate	XXXVII
- Petiole c.1.6-5.0 mm wide at mid-point, lamina c.8.5-18.5 cm or more long, the distance from the origin of the lateral primary veins to the primary sinuses 6.5-7.0 cm or more, lateral primary	

veins c.70-87% the length of the central primary vein, cuticle not striate	XXXVIII
8 Lamina with only occasional lobe	XXXIII
- Lamina with toothed margin	9
9 Leaf margin crenulate, in central lobe secondary veins interconnected distally by extensions of secondary veins	XXX
- Leaf margin not crenulate, in central lobe secondary veins interconnected distally by tertiary veins or rarely at apex of lobe by fine extensions of secondary veins	10
10 Lamina length/breadth ratio 0.9 : 1, teeth fall into two size groups	XXXIX
- Lamina length/breadth ratio 1.05 : 1-1.8 : 1, teeth of one size group	11
11 Primary sinuses acute, leaf margin \pm crenate, areoles (5-)15-30 per 10 mm ²	XL
- Primary sinuses angular or rounded, leaf margin dentate or serrulate-denticulate, areoles 30-70 per 10 mm ²	12
12 Lamina length/breadth ratio 1.8 : 1, leaf margin serrulate-denticulate, lateral primary veins 50-52.5% the length of the central primary vein, the spacing of the veins on the basiscopic side of the lateral primary veins, with the exception of slight irregularities, successively decreasing from base to apex	XLI
- Lamina length/breadth ratio 1.05 : 1-1.57 : 1, leaf margin dentate, lateral primary veins 74-93% the length of the central primary vein, the spacing of the veins on the basiscopic side of the lateral primary veins reaching a maximum mid-way	XXVIII
13 Leaf margin entire	14
- Leaf margin non-entire	81
14 Lamina pinnatifid	LX
- Lamina not pinnatifid	15
15 Leaf apex rounded	16
- Leaf apex not rounded	20
16 Venation, including midvein, obscure	XVIII
- Venation, or at least midvein, obvious	17
17 Petiole alate, 2.0-3.2 mm wide at mid-point, lamina 10.8-c.12.5 cm long, length/breadth ratio c.3 : 1-3.4 : 1	XLIX
- Petiole non-alate, 0.6-1.2 mm wide at mid-point, lamina 0.88-3.2 cm long, length/breadth ratio 1.45 : 1-2.2 : 1	18
18 Leaf base obtuse, venation other than midvein obscure	XLII
- Leaf base rounded, venation other than midvein obvious	19
19 Secondary veins 3 per side, the spacing between them reaching a maximum proximally	XLIV
- Secondary veins 6-8 per side, the spacing between them never reaching a maximum proximally	XLIII
20 Venation camptodromous	21
- Venation not camptodromous	71
21 Lamina length/breadth ratio more than 4.9 : 1	22
- Lamina length/breadth ratio less than 4.9 : 1	27
22 Secondary veins few, 3-6(-8) per side	23
- Secondary veins numerous, c.13-c.35 per side	24
23 Lamina 1.4-2.75 cm wide, secondary veins well-developed, epidermis glandular	XXIV
- Lamina 0.57-0.85(-1.3) cm wide, secondary veins poorly visible, epidermis glandular	XLVII

24 Epidermis glandular	VII
– Epidermis eglandular	25
25 Lamina 2.40–4.65 cm wide	XII
– Lamina 0.55–2.30 cm wide	26
26 Cuticle thin, cells of upper epidermis elongate (length/breadth ratio 2.5:1–6:1) over veins, stomata 10.8–19.8 microns long and 5.4–10.8 microns wide, stomatal slit 75–95% stomatal length	XI
– Cuticle thick, cells of upper epidermis but little elongate (length/breadth ratio 1:1–2:1) over veins, stomata 19.8–32.4 microns long and 14.4 microns or more broad, stomatal slit 37.5–60% stomatal length	XXII
27 Tertiary veins generally orientated at $\pm 90^\circ$ to midvein	28
– Tertiary veins rarely orientated at $\pm 90^\circ$ to midvein	33
28 Tertiary veins 9–26 per 1 cm secondary vein	29
– Tertiary veins 2–9 per 1 cm secondary vein	30
29 Tertiary veins 9–13 per 1 cm secondary vein, little or much branched	LVIII
– Tertiary veins 9–26 per 1 cm secondary vein, little branched	XXXV
30 Lamina oblong, leaf base with narrow extension of lamina along petiole	LIV
– Lamina not oblong, leaf base without narrow extension of lamina along petiole	31
31 Secondary veins never more than 7 per side, the spacing of the veins reaching a maximum distally	XLVI
– Secondary veins sometimes more than 7 per side, the spacing of the veins either showing no trend or reaching a maximum midway, rarely apically	32
32 Leaf base acute or nearly so	XLV
– Leaf base obtuse, rounded or slightly cordate, rarely acute	LVIII
33 Leaf base attenuate or acute	34
– Leaf base obtuse, rounded or cordate	55
34 Epidermis glandular	35
– Epidermis eglandular	36
35 Lamina thin, c.2.2–c.4.5 cm long	XLVII
– Lamina thick, 3.6–>15 cm long	VII
36 Hair bases present, large, compound, 30–60 microns in diameter	37
– Hair bases absent, or when present small, simple, 2–18 microns in diameter	38
37 Upper epidermal cell wall \pm straight, within hair base central cell separated from the surrounding cells by cell wall 0.5–1.5 microns thick	LII
– Upper epidermal cell wall rarely straight, usually highly undulate, within hair base central cell separated from the surrounding cells by cell wall 5.5–20 microns thick	XXIX
38 Secondary veins 3–8 per side	39
– Secondary veins 9–c.30 per side	46
39 Spacing of secondary veins reaching a maximum distally, fine vein reticulum not pronounced	XLVI
– Spacing of secondary veins rarely reaching a maximum distally, or when reaching maximum distally vein reticulum very pronounced	40
40 Stomatal ledges present on guard cells	XXI
– Stomatal ledges not present on guard cells	41
41 Cuticle over guard cells markedly thicker than that over accessory cells	XLVIII

- Cuticle over guard cells thinner or as thick as that over accessory cells	42
42 Stomatal index 0-5%	43
- Stomatal index 6-20%	44
43 Fine vein reticulum pronounced, lower epidermal cells somewhat domed, epidermal wall of guard cells obvious in cuticle, hair bases present on lower epidermis over and between veins, 0-14 per 0.1 mm ²	XXV
- Fine vein reticulum not pronounced, lower epidermal cells not domed, epidermal wall of guard cells often obscure in cuticle, hair bases only occasionally present on lower epidermis over veins, 0(-1) per 0.1 mm ²	LVIII
44 Accessory cells narrow, ringing the stomata, internal resinous bodies absent	L
- Accessory cells similar in size to or somewhat smaller than the rest of the epidermal cells, not narrow and ringing the stomata, internal resinous bodies present	45
45 Spacing of secondary veins greatest between most proximal secondary veins	XXIV
- Spacing of secondary veins never greatest between most proximal secondary veins	LI
46 Guard cells with markedly thickened epidermal walls	47
- Guard cells without markedly thickened epidermal walls	48
47 Lamina elliptical, secondary veins c.16-c.30 per side, interconnected distally by marginal vein, stomata 25-40 per 0.1 mm ² , mostly orientated roughly parallel to the midvein	LVII
- Lamina oblong, secondary veins 9-c.11 per side, interconnected distally by fine extensions of secondary veins, stomata 3-10 per 0.1 mm ² , variously orientated	LV
48 Cuticle over guard cells markedly thicker than that over accessory cells	XLVIII
- Cuticle over guard cells thinner or as thick as that over accessory cells	49
49 Accessory cells narrow, ringing the stomata	50
- Accessory cells when present similar in size or somewhat smaller than the rest of the epidermal cells, not narrow and ringing the stomata	51
50 Petiole alate, midvein 0.6-1.0 mm wide at mid-point between base and apex of lamina, secondary veins sometimes obscure, 15-20 per side	XLIX
- Petiole non-alate, midvein 0.1-0.6 mm wide at mid-point between base and apex of lamina, secondary veins generally prominent, 9-13 per side	L
51 Cell wall highly undulate, stomata frequently rhombic in shape	XXIII
- Cell wall straight or only somewhat undulate, stomata rarely rhombic in shape	52
52 Stomatal index 0-5%	53
- Stomatal index 9.5-20%	54
53 Fine vein reticulum pronounced, lower epidermal cells somewhat domed, epidermal wall of guard cells obvious in cuticle, hair bases present on lower epidermis over and between veins, 0-14 per 0.1 mm ²	XXV
- Fine vein reticulum not pronounced, lower epidermal cells not domed, epidermal wall of guard cells often obscure in cuticle,	

hair bases only occasionally present on lower epidermis over veins, 0(-1) per 0.1 mm ²	LVIII
54 Secondary veins numerous, the spacing somewhat irregular, showing no trend, stomatal ledges present on guard cells at least sometimes	XXII
- Secondary veins rarely more than 9 per side, the spacing reaching maximum proximally or mid-way, stomatal ledges never present	LI
55 Secondary veins 4-8 per side	56
- Secondary veins 9-c.30 per side	63
56 Leaf base truncate or markedly cordate, lamina length/breadth ratio 1.0:1-1.7:1	XXXVII
- Leaf base generally obtuse or rounded, when slightly cordate lamina length/breadth ratio >1.7:1	57
57 Spacing of secondary veins reaching maximum distally, fine vein reticulum not pronounced	XLVI
- Spacing of secondary veins rarely reaching maximum distally, or when reaching maximum distally fine vein reticulum pronounced	58
58 Hair bases large, associated with marked thickening of the cuticle	XXIX
- Hair bases absent, or when present small, without undue thickening of the cuticle	59
59 Stomatal index 0-5%	60
- Stomatal index 6-20%	61
60 Fine vein reticulum pronounced, lower epidermal cells somewhat domed, epidermal wall of guard cells obvious in cuticle, hair bases present on lower epidermis over and between veins, 0-14 per 0.1 mm ²	XXV
- Fine vein reticulum not pronounced, lower epidermal cells not domed, epidermal wall of guard cells often obscure in cuticle, hair bases only occasionally present on lower epidermis over veins, 0(-1) per 0.1 mm ²	LVIII
61 Spacing of secondary veins at maximum proximally, lower epidermal cells somewhat to much domed, accessory cells similar in size or somewhat smaller than the rest of the epidermal cells, not ringing the stomata, internal resinous bodies not uncommon	XXIV
- Spacing of secondary veins reaches maximum (proximally -) mid-way or is irregular without any recognizable trend, lower epidermal cells not domed, accessory cells narrow, ringing the stomata, internal resinous bodies absent	62
62 Petiole 25 mm long, secondary veins obscure, lower epidermis much striate, trichome bases rarely present	LVI
- Petiole 2.5-10 mm long, secondary veins generally prominent, lower epidermis not striate, trichome bases always present	L
63 Leaf base with narrow extension of lamina along petiole	LIV
- Not so	64
64 Hair bases large, associated with marked thickening of the cuticle	XXIX
- Hair bases absent, or when present small, without undue thickening of the cuticle	65
65 Cells of upper epidermis 115-160 per 0.1 mm ² , those of leaf margin 100-110 per 0.1 mm ² , guard cells with markedly thickened epidermal walls	LV
- Cells of upper epidermis 170-700 per 0.1 mm ² , those of leaf margin c.260-c.1050 (-c.2000?), guard cells without markedly thickened epidermal walls	66

66	Accessory cells narrow, ringing the stomata	L
-	Accessory cells similar in size, somewhat larger or somewhat smaller than the rest of the epidermal cells, not narrow and ringing the stomata	67
67	Cell wall highly undulate, stomata frequently rhombic in shape	XXIII
-	Cell wall straight or only somewhat undulate, stomata rarely rhombic in shape	68
68	Secondary veins >13 per side, guard cells bearing stomatal ledges at least sometimes, stomatal index 9.5-11.25%	XXII
-	Secondary veins 9-13 per side, guard cells never bearing stomatal ledges, stomatal index 0-8.6%	69
69	Fine vein reticulum pronounced, lower epidermal cells somewhat domed, hair bases present on lower epidermis over and between veins, 0-14 per 0.1 mm ²	XXV
-	Fine vein reticulum not pronounced, lower epidermal cells not domed, hair bases only occasionally present on lower epidermis over veins, 0(-1) per 0.1 mm ²	70
70	Lower epidermal cells 390-720 per 0.1 mm ² , epidermal walls of guard cells often obscure in cuticle	LVIII
-	Lower epidermal cells 190-360 per 0.1 mm ² , epidermal walls of guard cells obvious in cuticle	LIII
71	Lamina length/breadth ratio >6 : 1, venation parallelodromous	72
-	Lamina length/breadth ratio 1.0 : 1-5.5 : 1, venation not parallelodromous	73
72	Lamina elliptical or obovate, 0.60-0.82 cm wide	LXXV
-	Lamina strap-like, 1.0-3.3 cm wide	LXXVI
73	Venation hypodromous or nearly so	74
-	Venation acrodromous, campylodromous or actinodromous	75
74	Lamina c.2.2-c.4.5 cm long and 0.57-0.85(-1.3) cm wide, epidermis glandular	XLVII
-	Lamina 6.9 cm long and 1.95 cm wide, epidermis eglandular	XLVIII
75	Venation actinodromous	76
-	Venation acrodromous or campylodromous	77
76	Petiole 0.4-1.1 mm wide at mid-point, lamina 3.4-8.8 cm long, cuticle finely striate	XXXVII
-	Petiole c.1.6-5.0 mm wide at mid-point, lamina c.8.5-18.5 cm or more long, cuticle not striate	XXXVIII
77	Leaf base truncate or cordate	78
-	Leaf base acute, obtuse or rounded	79
78	Primary veins 3, higher order veins between primary veins usually arising at less than 90°, stomata 0-4 per 0.1 mm ²	LXXII
-	Primary veins 9, higher order veins between primary veins arising at ±90°, stomata 20-30 per 0.1 mm ²	LXXIV
79	Venation campylodromous, primary veins on either side of the central primary vein extending the whole length of the lamina	LXXIII
-	Venation acrodromous, primary veins on either side of the central primary vein extending for 44-75% the length of the lamina	80
80	Secondary veins 3-6(-8) per side, areoles 80-100 per 10 mm ² , lower epidermal cells hardly to markedly domed, hair bases absent	XXIV
-	Secondary veins 1-3(-7) per side, areoles 120-240 per 10 mm ² , lower epidermal cells never domed, hair bases present	XXVI
81	Venation craspedodromous	82
-	Venation camptodromous	104
82	Teeth fall into 2 size groups	83

- Teeth of one size group	90
83 Lamina length/breadth ratio 2.75 : 1-4.4 : 1	84
- Lamina length/breadth ratio (1.1 : 1)-1.4-2.75 : 1	85
84 Secondary veins 14-27 per side, leaf margin serrulate	LXVII
- Secondary veins 5-13 per side, leaf margin with stump-like teeth	LVIII
85 Leaf margin sinuate	LXIX
- Leaf margin not sinuate	86
86 Leaf base highly asymmetrical, on one side of the midvein acute, on the other side cordate	XVI
- Leaf base symmetrical or only slightly asymmetrical	87
87 Leaf margin with stump-like teeth	LVIII
- Leaf margin serrate or serrulate	88
88 Secondary veins not uncommonly dichotomising, spacing of the secondary veins somewhat irregular, reaching maximum mid-way or apically	XV
- Secondary veins do not dichotomise, spacing of the secondary veins fairly regular, reaching maximum proximally or mid-way	89
89 Leaf base sometimes cordate, leaf margin with 0-8 teeth per intercostal field, teeth mucronulate	LXVIII
- Leaf base never cordate, leaf margin with 0-4(-5) teeth per intercostal field, teeth not mucronulate	LXX
90 Lamina length/breadth ratio 4.1 : 1-7.4 : 1	91
- Lamina length/breadth ratio 0.93 : 1-c.3.4 : 1	92
91 Leaf base acute, spacing of the secondary veins greatest proximally	LXVI
- Leaf base obtuse or rounded, spacing of the secondary veins more or less constant throughout length	LXV
92 Tertiary veins orientated at $\pm 90^\circ$ to midvein	93
- Tertiary veins rarely orientated at $\pm 90^\circ$ to midvein	94
93 Leaf margin constricted above terminations of secondary veins, tertiary veins 9-26 per 1 cm secondary vein, little branched	XXXV
- Leaf margin with stump-like teeth, tertiary veins 9-13 per 1 cm secondary vein, little or much branched	LVIII
94 Leaf margin dentate or denticulate	95
- Leaf margin serrate, serrulate or with stump-like teeth	99
95 Lamina length/breadth ratio 2 : 1-c.3 : 1	96
- Lamina length/breadth ratio 0.93 : 1-1.8 : 1	97
96 Lamina 3.0 cm wide, teeth 0.4-1.3 mm wide	XIII
- Lamina 3.8-9.0 cm wide, teeth 1-7 mm wide	XIV
97 Leaf base making an angle of c.90°, teeth 0.2-0.8 mm across, not restricted to the terminations of the secondary veins	XLI
- Leaf base obtuse, rounded, truncate or cordate, teeth 0.4-4.0 mm across, mostly restricted to the terminations of the secondary veins	98
98 Secondary veins 3-5(-8) per side, spacing of veins on basisopic side of most proximal secondary vein showing an initial decrease, cuticle of epidermis in stomatal condition never finely striate	IX
- Secondary veins 7-11(-14), spacing of veins on basisopic side of most proximal secondary vein showing no initial decrease, cuticle of epidermis in stomatal condition generally finely striate	XXVIII
99 Leaf base attenuate, teeth 3-7 per side, 1.2-4.0 mm across	LIX
- Leaf base (acute-) obtuse, rounded or cordate, teeth (0-) 7-c.55 per side, 0.05-1.8 mm across	100
100 Teeth mostly restricted to terminations of secondary veins, intermediate veins extending from 0 to 1/4-1/3(-1/2) the distance from the midvein to the leaf margin	XVII

- Teeth rarely restricted to terminations of secondary veins, intermediate veins extending from 0 to 1/6-9/10 the distance from the midvein to the leaf margin	101
101 Secondary veins 13-30 per side	VIII
- Secondary veins 5-13 per side	102
102 Eight higher order veins borne on basiscopic side of most proximal secondary vein	XLI
- No higher order veins borne on basiscopic side of most proximal secondary vein	103
103 Lamina sessile, 1-c.3.2 cm long	XXXI
- Lamina petiolate, (1-)3-c.1.7 cm long	LVIII
104 Lamina with >20 teeth per side	105
- Lamina with <20 teeth per side	112
105 Secondary veins (10-)13-30 per side	106
- Secondary veins 4-10 per side	110
106 Lamina obovate, leaf margin sinuate, secondary veins interconnected by loops far from the leaf margin	LXIII
- Lamina ovate, elliptical or oblong, rarely obovate, leaf margin serrulate or crenulate, secondary veins interconnected by loops close to the leaf margin	107
107 Leaf margin crenulate	108
- Leaf margin serrulate	109
108 Lamina 0.55-2.30 cm wide	XI
- Lamina 2.40-4.65 cm wide	XII
109 Teeth apiculate	VIII
- Teeth acute (-rounded)	LXII
110 Lamina oblong or elliptical, length/breadth ratio 2:1-3:1, leaf margin serrulate	XXXII
- Lamina suborbicular or ovate, length/breadth ratio 0.8:1-1.75:1, leaf margin \pm crenulate or sinuate	111
111 Leaf apex obtuse or leaf margins meeting at 90°, leaf base markedly cordate, secondary veins 4-6 per side, spaced at rapidly decreasing intervals	XVII
- Leaf apex acute or acuminate, leaf base rounded or slightly cordate, secondary veins 5-10 per side, spaced somewhat irregularly, not uncommonly with two maxima, one proximally and one distally	X
112 Lamina length/breadth ratio 2.6:1-7.4:1	113
- Lamina length/breadth ratio 0.8:1-2.4:1	115
113 Lamina 3.0-3.05 cm long, teeth relatively numerous, 0.10-0.35 mm across	LXIV
- Lamina (2.65-)3.6->15 cm long, teeth widely spaced, 0.1-2.0 mm across	114
114 Leaf base attenuate or acute, teeth (acute-) rounded, tertiary veins (1-)4-12 per 1 cm secondary vein, the glands present having 2 basal cells	VII
- Leaf base obtuse or rounded, teeth acute, tertiary veins 10-21 per 1 cm secondary vein, the glands present having a single basal cell	LXV
115 Lamina suborbicular or ovate, length/breadth ratio being 0.8:1-2.0:1	116
- Lamina elliptical or obovate, length/breadth ratio being 2.15:1-2.4:1	117
116 Petiole up to 60 mm long, lamina 2.6-9.5 cm wide, length/breadth ratio 0.8:1-1.75:1, leaf base rounded or slightly cordate, leaf	

? <i>Ficus</i> sp.?	Coll. H. Weyland 1665, det. H. Weyland!
<i>Myrica lignitum</i> (Unger) Saporta	WEYLAND, 1934, pp. 44-45, Tafel 2, figs. 3, 4, 7, 8!; GOTHAN and WEYLAND, 1964, p. 406, Abb. 280 d!
<i>Myrica marcodurensis</i> Kräusel et Weyland	KRÄUSEL and WEYLAND, 1950, pp. 41-42, Abb. 8-9, Tafel 4, figs. 5-6!
<i>Myrica vindobonensis</i> Ett.	WEYLAND, 1934, p. 46, Tafel 2, fig. 5!
<i>Quercus neriifolia</i> A. Braun	WEYLAND, 1934, pp. 54-55, Tafel 6, figs. 3-5!
<i>Quercus pseudocastanea</i> Goepfert	WEYLAND, 1934, p. 60!
<i>Sapindus falcifolia</i> Unger	WEYLAND, 1934, p. 95, Tafel 17, fig. 5!

Description :

Petiole (2.4 -) 9-20 mm long and 0.7-2.0 mm wide at mid-point, straight or slightly curved, sometimes making somewhat of an angle with the midvein.

Lamina ovate, elliptical, obovate or oblong, 3.6-> 15 cm long, 0.7-3.1 cm wide, the length/breadth ratio being 2.6 : 1-6.6 : 1 (fig. 11), sometimes undulating in a vertical plane to give the impression of large gently rounded lobes interspersed with acute or rounded sinuses when viewed from above. Leaf apex acute to acuminate, leaf base attenuate or acute, sometimes oblique.

Leaf margin entire or non-entire, sometimes bearing acute or more commonly rounded teeth 0.1-2.0 mm across, 0-c.20 per side, alternating with acute, angular or rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein straight or curved, hardly to markedly tapering along length, 0.2-1.0 mm wide at midpoint between base and apex of lamina. Midvein bearing c.7-c.35 secondary veins per side, the most proximal vein arising at 35°-45° (-70°), arising in the remaining part of the basal third of the lamina at 45°-90°, in the median third at 45°-90°, in the apical third at 30°-100°. The angle at which the veins arise increasing, constant or decreasing within the first few mms. The spacing of the veins somewhat irregular, either showing no trend at all, or reaching a maximum mid-way along the lamina (fig. 11). Secondary veins opposite to alternately arranged, hardly tapering along their length, 0.05-0.20 mm wide at mid-point, interconnected distally by strong or fine extensions of secondary veins, or tertiary veins. Intermediate veins 0-6 per intercostal field, arising from midvein at 45°-135°, running more or less parallel to each other or converging/diverging, the spacing between them being more or less constant, increasing distally or irregular. The intermediate veins similar in width or increasing in width with increase in length, extending from 0 to 1/2-9/10 the distance from the midvein to the leaf

margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins (1-) 4-12 per 1 cm secondary vein, somewhat to much branched. Areoles (50-) 70-c.130 per 10 mm², with some to many free vein-endings, these being unbranched and branched.

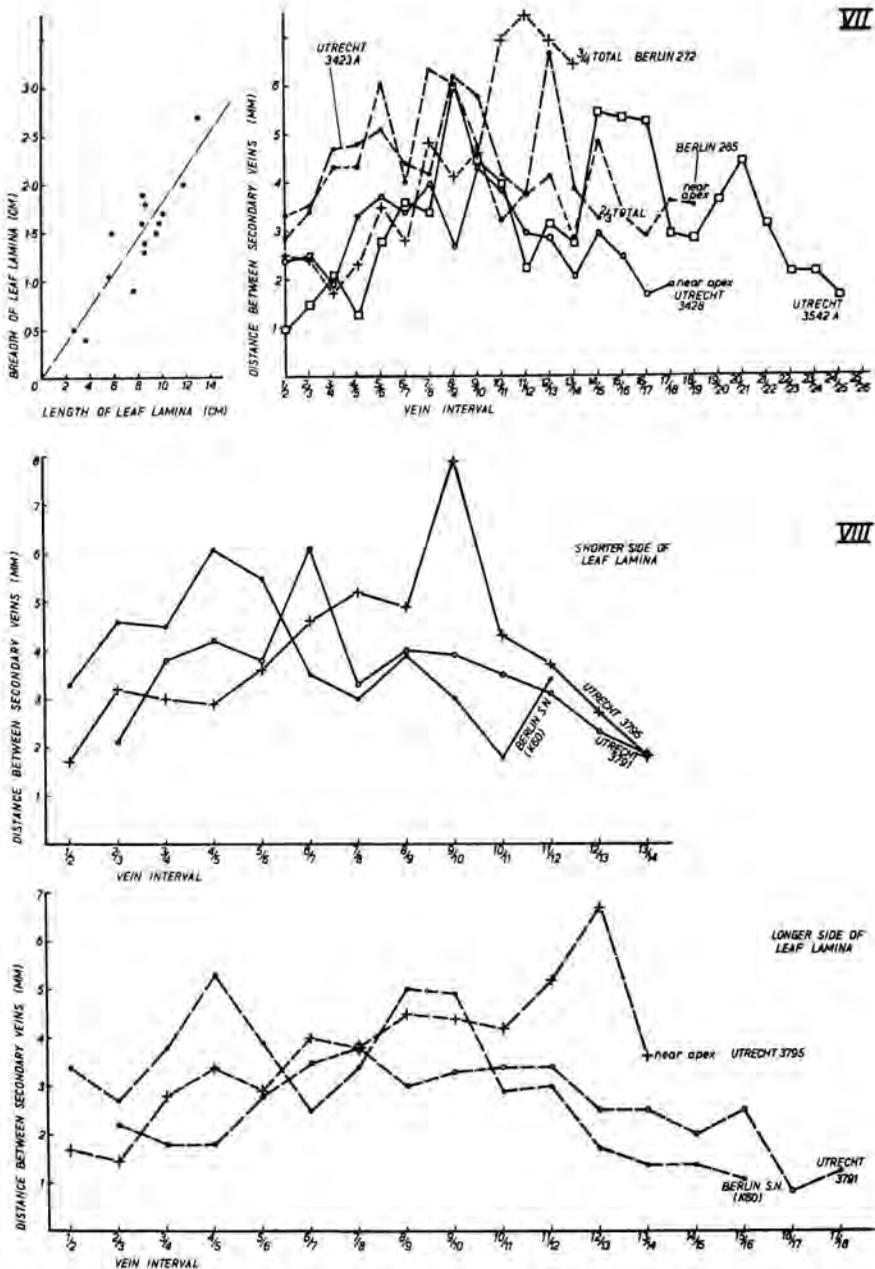


Fig. 11. Graphs VII and VIII p.p.

Epidermis in non-stomatal condition composed of 600–1115 more or less polygonal cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–4 : 1. Cell wall 0.45–2.0 microns thick, largely unpitted to very finely pitted, straight. Cells over veins narrow elongate, the cell length/cell breadth ratio being 1 : 1–5 : 1. Glands c.77–c.91 microns in diameter, resting on 2-celled base 13–18 microns in diameter, present, 0(–1) per 0.1 mm². Epidermis in stomatal condition composed of 570–1140 more or less polygonal cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3 : 1 (–5 : 1). Cell wall 0.3–1.2 microns thick, unpitted or pitted, cell wall straight or occasionally undulate with 0 (–1) lobe per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 4.5 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–10 : 1. Finer veins reflected in cuticle. Stomata 12.6–32.4 microns long and 10.8–27.0 microns broad, breadth 47–120% length, numerous, up to 96 per 0.1 mm²; stomatal index up to 13%. Stomata variously orientated, undepressed, tending to be somewhat grouped, apices commonly retuse. Stomatal slit 40–67 (–82)% stomatal length. Accessory cells 5–7 in number possibly present, although in shape and size the cells in immediate proximity to the stomata resemble the other epidermal cells. Glands, 50–120 microns in diameter, resting on 2-celled base 14–25 microns in diameter present over and between the veins. Internal resinous bodies rare.

Specimens examined : 328, among which the numbered specimens:

Deutsche Akad. Wiss. Berlin: 266(K 90), 275(K 130), 276(K 90), 279(K 90), 281(K 121), 285(K 90), 289(K 147), 292(K 74), 308(K 95), 317(K 141).

Geol. Inst. Cologne: Coll. H. Weyland 1379(K 90), 1381(K 90), 1389(K 121), 1390(K 121), 1413(K 147), 1540(KA 2), 1541(KA 2), 1641(K 90), 1642(K 90), 1643(K 90), 1645(K 90), 1646, 1647(=Coll. W. Jansen 70), 1718a-f(K 96)

Senckenberg Museum, Frankfurt-am-Main: 6290/1

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3235, 3236, 3423, 3424, 3425, 3426, 3427, 3428, 3429, 3430, 3431, 3432, 3433, 3434, 3436, 3437, 3438, 3439, 3440, 3441, 3442, 3443, 3444, 3445, 3446, 3447, 3448, 3449, 3450, 3451, 3452, 3453, 3454, 3455, 3456, 3457, 3458, 3459A, 3460, 3461, 3462A, 3462B, 3463A, 3464A, 3465, 3466, 3467, 3468, 3469, 3470, 3479B, 3539, 3540, 3541, 3542A, 3729B, 3811B, 3838B, 3849, 3850.

Discussion :

While leaves outwardly resembling those referred to by WEYLAND (1934) as *Myrica lignitum* are to be found in taxa other than *Myrica*, the leaf-remains indeed showed glands such as are present in members of the Myricaceae. In this family these glands are borne on a 2 (–3) celled base. Leaves with glands having this number of basal cells are of rare occurrence outside the Myricaceae. In the revision of Weyland's account certain specimens referred by him to families other than the Myricaceae were found to bear such glands.

While pointing out that some doubt existed as to their proper generic assignation, WEYLAND (1934, p. 55) referred certain specimens from Kreuzau to *Quercus neriifolia* A. Braun. The specimen figured by Weyland as Tafel 6, fig. 4 proved to have a cuticle with glands, 60–78 microns in diameter, borne on a 2-celled base. In much the same way the specimen figured by Weyland as Tafel 6, fig. 3 (Berlin 281) had glands, 72–96 microns in diameter. In this case the preservation of the material was not sufficient to enable the number of basal cells to be made out. This specimen and Berlin 292, which did not yield a cuticle, were sufficiently similar in other respects as to be included in the present taxon. Berlin 292, figured by Weyland as Tafel 6, fig. 5, was only found to differ from the other two specimens figured as *Quercus neriifolia* in the greater width of the lamina (2.1 cm as opposed to 1.1–1.55 cm) and the smaller length/breadth ratio of the lamina (2.6:1 as opposed to c.5:1). No other differences could be recognized and the obovate appearance of the lamina, commented on by WEYLAND (1934, pp. 54–55), is simply the result of leaf curl in the proximal part of the lamina. This can be recognized by the abrupt termination of the most proximal secondary veins near the leaf margin. The venation proved to be similar in all three cases. Another specimen from Kreuzau determined by Weyland as *Quercus pseudocastanea* was found to bear glands and moreover resembled the present taxon as regards venation. This specimen was only found to differ from the remaining specimens in the degree to which the lamina was lobed. Although the leaves of certain *Quercus* species may resemble these specimens in outward appearance, glands are rarely encountered in the Fagaceae e.g. *Castanea sequinii* Dode. Furthermore, when present, these glands have only a single basal cell.

Berlin 289, described as *Andromeda protogaea* and figured by Weyland as Tafel 22, fig. 2 was found, in the course of an examination of its gross-morphology, to bear the impressions of glands. A cuticle preparation indeed confirmed that the leaf bore glands such as found in material referred to *Myrica lignitum*. This specimen and Weyland 1413, determined as *Andromeda protogaea* by Weyland, not only agreed in the presence of glands but in gross-morphology as well. In making use of the binomial *Andromeda protogaea* Unger (= *Leucothoë protogaea* (Unger) Schimper) WEYLAND (1934) did not make it clear which concept of the genus *Andromeda* he adopted. The leaves of *Chamaedaphne calyculata* (L.) Moench. (= *Andromeda calyculata* L.) and *Lyonia ferruginea* (Walt.) Nutt. (= *Andromeda ferruginea* Walt., *Xolisma ferruginea* (Walt.) Heller) bear glands. On the other hand the leaves of *Andromeda glaucophylla* Link., *Leucothoë axillaris* (Lam.) D. Don (= *Andromeda axillaris* Lam.), *Leucothoë racemosa* (L.) Gray (= *Andromeda racemosa* L.), *Lyonia ovalifolia* (Wall.) Drude (= *Andromeda ovalifolia* Wall., *Pieris ovalifolia* (Wall.) D. Don), *Neopieris mariana* (L.) Britton (= *Andromeda mariana* L.), *Pieris japonica* (Thunb.) D. Don (= *Andromeda japonica* Thunb.), *Pieris nitida* (Bartr.) Benth. et Hook. (= *Andromeda nitida* Bartr.) and *Xolisma fruticosa* (Michx.) Nash (= *An-*

dromeda ferruginea Walt. var. *fruticosa* Michx.) only bore unicellular or multicellular hairs. A reference to *Andromeda* sensu latissimo cannot be ruled out on the basis of the only poorly preserved material determined by WEYLAND (1934) as *Andromeda protogaea*. However, the similarity of this material to that having epidermides such as found in *Myrica* (and unlike those of *Andromeda* s.l.) would suggest that this material i.e. Berlin 289, H. Weyland 1413, ought not to be considered as that of a separate taxon. None of the other members of the Ericaceae examined were found to have leaves resembling the fossil. In other members of the Ericaceae having leaves bearing glands e.g. various *Rhododendron* species, the number of specialized cells underlying the glands may vary from 2-4 (-6) e.g. *Rhododendron lutescens* Franch., *R. micranthum* Turcz., *R. polylepis* Franch., or be 4-10 or more in number e.g. *Rhododendron nivale* Hook. f. In all cases the leaves of species bearing glands were found to have an upper epidermis with undulate cell walls. Furthermore, when only a relatively small number of specialized cells are present underlying the glands, these cells are characterized by having a highly thickened cell wall.

In the absence of a more suitable name, WEYLAND (1934, p. 95) determined certain specimens as *Sapindus falcifolia*. Of the nine specimens recorded by WEYLAND (1934, p. 20) as present in the Berlin collection only one (Berlin 308, figured by Weyland as Tafel 17, fig. 5) was available to the present author. This specimen yielded a cuticle in which the presence of glands with 2-celled bases could be demonstrated. Other material (Weyland 1718) determined by Weyland as probably that of *Sapindus falcifolia* (or *Salix* sp.) was found to possess a similar cuticle. While the leaves of certain species of *Sapindus* e.g. *Sapindus mukorossii* Gaertn. and *S. saponaria* L. resemble the material referred to as *Sapindus falcifolia* in gross-morphology, the cuticles of these species were found to differ from that of the fossil. The only trichomes present in the living material are club-shaped multicellular hairs. Glands are present on the leaves of other members of the Sapindaceae e.g. *Dodonaea viscosa* Jacq. However, these glands, unlike those of the fossil, have a marked cellular structure and are underlain by 4-12 very small epidermal cells.

Although lacking any trace of a cuticle, certain leaf-remains would appear to be referable to the present taxon. The specimen figured by Weyland as Tafel 17 fig. 4 was referred with certain reservations to *Dodonaea pteleaefolia* (Weber) Heer (= *Rhus pteleaefolia* Weber). No differences were noted between this specimen and material referable to *Myrica*. Berlin 275 was considered by Weyland to be sufficiently different from material he referred to *Myrica lignitum* to warrant the use of a separate binomial. He referred the specimen to *Dryandroides undulata* Heer. WEYLAND (1934, p. 48) stated that this specimen differed from those of *Myrica lignitum* in that it had fewer secondary veins, arising at a more acute angle. In the material available to the present author these differences were

found to break down. Moreover, the apparently undulate leaf margins in Berlin 275 would appear to be largely the result of curling of the leaf prior to fossilization. Undulation on a smaller scale was, however, observed in other material referred to the present taxon.

Weyland 1665, which Weyland determined as *Ficus* sp.? is, however, similar to leaves of species belonging to *Berberis* group Wallichiana. It is true that Weyland 1665 has sharp teeth and relatively large intercostal fields separating somewhat arched secondary veins in the distal part of the lamina, features not entirely in agreement with other specimens included here. However in the absence of any further evidence in the form of a cuticle preparation it was felt wiser to refer this specimen to the present taxon.

In the foregoing discussion mention has been made of a number of families in which certain of the species have leaves bearing glands. Glands are also found on the leaves of certain members of the Acanthaceae, Anacardiaceae, Bignoniaceae, Euphorbiaceae, Juglandaceae, Myrsinaceae, Oleaceae and Verbenaceae. However, with the exception of the Euphorbiaceae examined, these species were characterized by glands with a single basal cell. In the species of *Mallotus* (Euphorbiaceae) examined the number was 2 or more. However, these species differed from the leaf-remains in having leaves with a length/breadth ratio of 0.8 : 1–2.2 : 1, 4–7 secondary veins per side and oval stomata with long stomatal slits.

Of the material examined to date only certain members of the Myricaceae had leaves resembling the fossil in gross-morphology, the nature of the stomata and epidermal cells, and in the presence of similar glands.

While certain authors consider the Myricaceae to contain a single genus, other authors have recognized a number of separate generic entities. According to the last monographic account of the family (CHEVALIER, 1901) the family consists of three genera, *Comptonia*, *Gale* and *Myrica*. These genera can be distinguished on the basis of leaf characters. *Comptonia* (= *Myrica asplenifolia* L.) has pinnatifid leaves, while the cell walls of the upper epidermis are moderately undulate. The leaves of *Myrica* s.s. and *Gale* (= *Myrica gale* L. etc.) are rarely incised and usually have an entire or toothed margin. In both cases the cell walls of the upper epidermis are \pm straight. The leaves of *Gale* only have a thin cuticle and the accessory cells have papillae which partially mask the stomata. On the other hand, the leaves of *Myrica* s.s. have a moderately thick cuticle and accessory cells without the development of papillae. The leaf-remains in question fall into this latter category and can therefore be referred to *Myrica* sensu strictu.

While the specimens of *Myrica* examined showed slight differences in cell size and the amount of undulation of the cell walls on the lower surface of the leaves, the impression gained from the cuticles is one of uniformity. CHEVALIER (1901, p. 311) pointed out that certain characters to which a certain amount of importance was sometimes attributed e.g. form and dimension of the cells of the various leaf tissues, the thickness of the cuticle, and the dimensions and distribution of hairs and glands vary from one

individual to another, dependant on the age of the branch, environment etc. . Of the material examined by the present author, only *Myrica cordifolia* L., in which the stomata are largely confined to the area immediately underlying the glands, can be considered to have a distinctive epidermis. Differences in the outward appearance of the leaves are more marked than differences in the nature of the epidermides. However, while the gross-morphological features of the leaves of *Myrica* may aid in the determination of the species, specific determination based on the leaves alone would appear, with a few notable exceptions, to be impossible to date.

The erection of *Myrica marcodurensis* Kräusel et Weyland was partially based on supposed differences in the cuticle. Not only are such differences unlikely to be of sufficient importance to support the establishment of another taxon (see above), but the supposed differences proved to be unreliable. KRÄUSEL and WEYLAND (1950, p. 42) mention that the stomata were 27–40 microns broad i.e. broader than long. However, an examination of their Tafel 4 fig. 5 casts doubt on this statement. A re-examination of the holotype (Senckenberg Museum 6290/1) proved that the measurement of the stomata could not be carried out with any degree of accuracy, due to the poor state of preservation of the cuticle. Furthermore the size of the specimen, upon which Kräusel and Weyland placed much weight, did not prove to be exceptional in the light of the variability of material in the Utrecht collection (0.7–3.1 cm in width, as opposed to 2.4 cm in *Myrica marcodurensis*). Other differential features were lacking. There is also insufficient evidence for considering the specimen figured by WEYLAND (1934) as Tafel 2 fig. 5 as *Myrica vindobonensis* to represent a separate taxonomic entity. Although this specimen did not yield a cuticle, it resembled other material from which cuticle preparations could be obtained to such an extent as to be indistinguishable from these.

Herbarium material examined in detail:

<i>Andromeda glaucophylla</i> Link.	Coll. R. Horner 3-9-1955	(U) _____
<i>Andromeda nitida</i> Bartr.	Coll. P. O. Schallert 19620	(U) _____
<i>Ardisia affinis</i> Hemsl.	Coll. Y. Tsiang 5619	(E) det. E. H. Walker
<i>Ardisia punctata</i> Lindl.	Coll. H. H. Chung 2246	(E) det. E. H. Walker
<i>Ardisia radicans</i> Kurz.	Coll. G. Forrest 18445	(E) det. E. H. Walker
<i>Castanea seguinii</i> Dode	Coll. H. C. Cheo 44	(E) _____
<i>Catalpa fargesii</i> Bur.	Coll. G. Forrest 4679	(E) det. J. Paclt
	Coll. E. Bodinier s.n.	(E) det. L. A. Lauener
	30-3-1897	
<i>Cerothamnus pumilus</i> (Mich.) Small	Coll. P. O. Schallert 19624	(U) _____
<i>Chamaedaphne calyculata</i> (L.) Moench.	Coll. C. G. Alm 999	(E) _____
<i>Clerodendron cyrtophyllum</i> Turcz.	Coll. A. N. Steward 2630	(E) det. E. D. Merrill
<i>Dodonaea viscosa</i> Jacq.	Coll. J. L. Gressitt 1765	(E) det. E. D. Merrill
	Coll. E. G. B. Gooding	(U) det. J. Monachino
	15567	

<i>Embelia oblongifolia</i> Hemsl.	Coll. A. Henry 11394 A	(E) det. E. H. Walker
<i>Embelia rudis</i> Handel-Mazzetti	Coll. W. P. Fang 5613	(E) det. E. H. Walker
<i>Eranthemum nervosum</i> (Vahl.) R. Br.	Coll. Handel-Mazzetti 5844	(E) det. Handel-Mazzetti
<i>Fontanesia fortunei</i> Carr.	Coll. C. Y. Chiao 2464	(E) det. A. Rehder
<i>Fraxinus griffithii</i> C. B. Clarke	Coll. A. Henry 1863	(E) det. A. Lingelsheim
<i>Gmelina montana</i> W. W. Smith	Coll. G. Forrest 22081	(E) det. W. E. Evans
<i>Hicoria aquatica</i> (Mich. f.) Britton	Coll. J. K. Small 21-5-1917	(U) _____
<i>Leucothoë axillaris</i> (Lam.) D. Don	Coll. H. E. Ahles & J. A. Duke 38495	(U) _____
	Coll. H. E. Ahles & P. J. Crutchfield 56439	(E) _____
<i>Leucothoë racemosa</i> (L.) Gray	Coll. J. S. Beard 1016	(U) _____
<i>Ligustrum acutissimum</i> Koehne	Coll. A. N. Steward 2720	(E) det. E. D. Merrill
<i>Ligustrum obtusifolium</i> Sieb. et Zucc.	Coll. C. Y. Chiao 2468	(E) det. A. Rehder
<i>Lyonia ferruginea</i> (Walt.) Nutt.	Coll. J. R. Bozeman & J. D. Aspinwall 10658	(E) _____
<i>Lyonia ovalifolia</i> (Walt.) Drude	Coll. T. Sørensen, K. Larsen & B. Hansen 6603	(E) det. H. O. Sleumer
<i>Mallotus contubernalis</i> Hance	Coll. E. Bodinier 1596	(E) det. F. Pax
<i>Mallotus japonicus</i> (Thunb.) Muell.-Arg.	Coll. C. Y. Chiao 14153	(E) det. E. D. Merrill
<i>Mallotus tenuifolius</i> Pax	Coll. W. P. Fang 1086	(E) _____
<i>Mangifera indica</i> L.	Coll. P. H. Burgers 537	(U) det. A. L. Stoffers
<i>Markhamia cauda-felina</i> (Hance) Craib	Coll. S. K. Lau 573	(E) det. E. D. Merrill
<i>Myrica asplenifolia</i> L.	Coll. A. M. Keefe 15-7-1939	(U) _____
<i>Myrica californica</i> Cham. et Sch.	Coll. P. F. van Heerdt 749	(U) det. A. C. de Roon
<i>Myrica carolinensis</i> Mill.	Coll. J. G. ten Houten & A. Schoenmakers 730	(U) _____
<i>Myrica cerifera</i> L.	Coll. O. van der Maas 33	(U) det. O. van der Maas
<i>Myrica conifera</i> Burm.	Coll. A. Stolz 2215	(U) _____
<i>Myrica cordifolia</i> L.	Coll. J. Lanjouw 101	(U) det. M. R. Levyns
<i>Myrica costaricensis</i> Berg.	Coll. A. Smith 2652	(U) _____
<i>Myrica esculenta</i> Ham.	Coll. G. Forrest 7833	(E) _____
<i>Myrica faya</i> Ait.	Coll. T. C. Hunt 241	(U) _____
	Coll. L. H. Q. van Ufford 4-1908	(U) det. L. H. Q. van Ufford
<i>Myrica gale</i> L.	Coll. J. T. de Smidt 20-8-1966	(U) det. J. T. de Smidt
<i>Myrica javanica</i> Blume	Coll. A. Pulle 4191	(U) det. S. H. Koorders
<i>Myrica kilamandsiharica</i> Engler	Coll. A. Stolz 831	(U) _____

<i>Myrica mexicana</i> Willd.	Coll. T. G. Yuncker, R. F. Dawson & H. R. Youse 5911	(U) _____
<i>Myrica pensylvanica</i> Loisel.	Coll. R. F. Britt 3049	(U) _____
<i>Myrica rubra</i> Sieb. et Zucc.	Coll. R. C. Ching 22-5-1924	(E) det. J. G. Jack & A. Rehder
	Coll. G. Murata 9548	(U) _____
<i>Myrica sapida</i> Wall.	Coll. J. D. Hooker & T. Thomson	(U) _____
<i>Neopieris mariana</i> (L.) Britton	Coll. J. G. ten Houten & A. Schoenmakers 923	(U) _____
<i>Oroxylum indicum</i> (L.) Vent.	Coll. Handel-Mazzetti 5237	(E) det. Handel- Mazzetti
<i>Osmanthus suavis</i> King ex C. B. Clarke	Coll. T. T. Yü 16697	(E) det. P. S. Green
<i>Pieris japonica</i> (Thunb.) D. Don	Coll. M. Mizushima 16-5-1961	(E) det. M. Mizushima
<i>Pieris ovalifolia</i> (Wall.) D. Don	Coll. G. Forrest 19860	(E) det. W. E. Evans
	Coll. G. Forrest 26200	(E) det. W. E. Evans
<i>Premna integrifolia</i> L.	Coll. A. Henry 13205	(E) _____
<i>Premna puberula</i> Pamp.	Coll. Expt. Kwangtung- Tonkin Border 26743	(E) det. E. D. Merrill
<i>Premna scoriarum</i> W. W. Smith	Coll. G. Forrest 17897	(E) _____
<i>Radermachera bipinnata</i> (Coll. et Hemsl.) Steenis ex Chatterjee	Coll. A. Henry 13020	(E) det. C. G. G. J. van Steenis
<i>Radermachera sinica</i> (Hance) Hemsl.	Coll. J. L. Gressitt 1074	(E) det. E. D. Merrill
	Coll. Handel-Mazzetti 6285	(E) det. Handel- Mazzetti
<i>Rapanaea neriifolia</i> (Sieb. et Zucc.) Mez.	Coll. J. Gressitt 1742	(E) det. E. D. Merrill
<i>Rhododendron lutescens</i> Franch.	Coll. E. H. Wilson 1199	(E) det. A. Rehder & E. H. Wilson
<i>Rhododendron micranthum</i> Turez.	Coll. E. H. Wilson 1526	(E) det. W. B. Hemsley & E. H. Wilson
<i>Rhododendron nivale</i> Hook. f.	Coll. Ludlow, Sherriff & Elliott 13125	(E) det. J. Hutchinson & G. Taylor
<i>Rhododendron polylepis</i> Franch.	Coll. A. David	(E) det. A. Franchet CO-TYPE
<i>Sapindus mukorossii</i> Gaertn.	Coll. Y. Tsiang 2586	(E) det. E. D. Merrill
<i>Sapindus saponaria</i> L.	Coll. J. S. Beard 204	(U) det. A. C. Smith
<i>Vitex lanceolata</i> P'ei	Coll. G. Forrest 7856	(E) _____
<i>Vitex quinata</i> (Lour.) F. N. Will.	Coll. Expt. Kwangtung- Tonkin Border 26758	(E) det. E. D. Merrill
<i>Vitex yunnanensis</i> W. W. Smith	Coll. G. Forrest 10719	(E) det. W. W. Smith
<i>Xolisma ferruginea</i> (Walt.) Heller	Coll. R. M. Harper 2047	(E) _____
<i>Xolisma fruticosa</i> (Michx.) Nash	Coll. S. M. Tracy 9210	(E) _____
	Coll. G. V. Nash 700	(E) _____

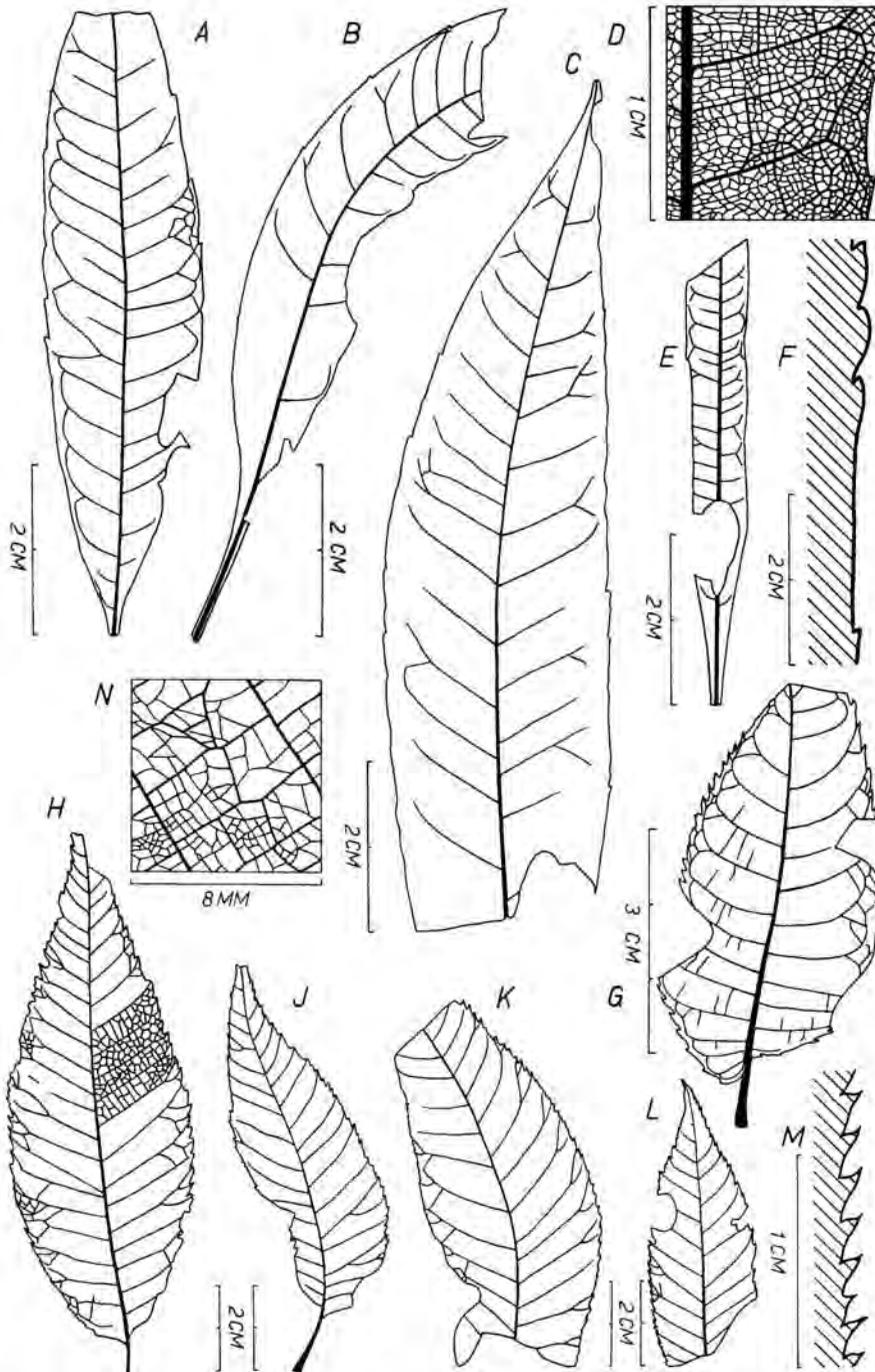


Fig. 12. A-F = VII: A = Utrecht 3423; B = Utrecht 3425; C = Utrecht 3426; D = detail showing venation; E = Utrecht 3424; F = detail showing leaf margin. G-N = VIII: G = Utrecht 3795; H = Berlin 304 (Type of *Saurauia rhenana* Weyland); J = Cologne, Coll. H. Weyland s.n.; K = Berlin s.n. (KA 17); L = Utrecht 3790; M = detail showing leaf margin; N = detail showing venation.

FAMILY JUGLANDACEAE

In his account of the Kreuzau assemblage WEYLAND (1934) described six species which he referred to the Juglandaceae. *Engelhardia brongniartii* Saporta was based on the remains of a fruit only. The remaining five species were, however, represented by leaf-remains. WEYLAND (1934) attributed three of these species to *Juglans* and one each to *Pterocarya* and *Carya*. The material referred to as *Juglans bilinica* Unger and *J. ungeri* Heer has been included with a certain amount of reservation under No. LVIII in the present account. The specimens determined as *Juglans acuminata* A. Braun represent diverse taxa (e.g. Nos. XXI, L and LXII) and are in part identical with those referred to as *Pterocarya castaneaeifolia* (Goeppert) Menzel (No. LXII). None of the above taxa can be attributed to the Juglandaceae with certainty. However, the specimens described by WEYLAND (1934) as *Carya serraefolia* (Goeppert) Kräusel would appear to warrant inclusion in this family. Nevertheless, their generic affinity is somewhat uncertain.

VIII

Synonyms: *Betula prisca* Ett.

pro parte e.g. Deutsche Akad. Wiss. Berlin s.n. (K 60), det. H. Weyland!

Carya serraefolia (Goeppert)
Kräusel

WEYLAND, 1934, p. 49!

Saurauia rhenana Weyland

WEYLAND, 1934, pp. 102-103,
Tafel 16, fig. 1!

Description:

Petiole 9-17 mm long and 0.45-1.2 mm wide at mid-point, somewhat increasing in width from 0.4-0.8 mm wide at leaf base to 1.3-1.7 mm wide at base of petiole, straight or curved, sometimes making an angle with the midvein.

Lamina ovate or elliptical, 4.8-12.3 cm long, 1.5-4.3 cm wide, the length/breadth ratio being 1.6:1-c.3.4:1, sometimes asymmetrical with regard to the midvein. Leaf apex acute or acuminate, leaf base obtuse, rounded or cordate, sometimes oblique.

Leaf margin non-entire, serrulate, with acute (apex often mucronulate) teeth 0.15-1.8 mm across, (c.20-) c.30-c.55 per side, alternating with acute, angular or rarely rounded sinuses. Teeth of one size group.

Venation craspedodromous or camptodromous, midvein straight or curved, slightly or markedly tapering along length, 0.2-0.65 (-1.2) mm wide at mid-point between base and apex of the lamina. Midvein bearing 13-30 secondary veins per side, the most proximal vein arising at 45°-90° (-140°), arising in the remaining part of the basal third of the lamina at 45°-90° (-130°), in the median third at 45°-80°, in the apical third at 45°-90°. The angle at which the veins arise (increasing-), constant or decreasing within the first few mms. The spacing of the veins either reaching

a maximum mid-way or more or less constant or somewhat irregular (figs. 11, 13). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.05–0.25 mm wide at mid-point, sometimes dichotomising at (0–) $1/2$ – $9/10$ the distance from the midvein to the leaf margin, the veins interconnected by fine extensions of secondary veins or tertiary veins. Intermediate veins 0–6 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 45° – 120° , running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to $1/6$ – $2/3$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 4–14 per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 55–120 per 10 mm² with some free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of c.850 cells per 0.1mm², the cell length/cell breadth ratio being 1 : 1–2.5 : 1. Cell wall 0.4–0.9 microns thick, unpitted or pitted, straight. Cells over veins elongate, the cell length/cell breadth ratio up to 6 : 1. Finer veins somewhat reflected in cuticle. Cells at leaf margin c.850 per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3.5 : 1, arranged in c.20 rows. Cell wall c.0.6 microns thick, largely unpitted, straight, transverse walls sometimes slanting but mostly at right angles to the lateral walls. Epidermis in stomatal condition poorly preserved, bearing glands 105–117 microns in diameter. These glands are borne on a single basal cell. Internal resinous bodies absent.

Specimens examined : 26, among which the numbered specimens:
 Deutsche Akad. Wiss. Berlin: 304(K 86), s.n. (K 54), s.n. (K 60), s.n. (K 139), s.n. (KA 17)
 Geol. Inst. Cologne: Coll. H. Weyland s.n.
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3615B, 3790, 3791, 3792, 3793A, 3794, 3795, 3796, 3797, 3798, 3799, 3800, 3801, 3802.

Discussion :

Berlin 304, the type of *Saurauia rhenana* Weyland, was found to have a somewhat different aspect from the remaining specimens included here. However, it was not found possible to distinguish this specimen from those which Weyland referred to *Carya serraeifolia* (Goepfert) Kräusel. Moreover, the presence in the Kreuzau assemblage of a genus occurring at the present day in tropical parts of America and Asia would seem unlikely (see p. 28).

Another, unnumbered, specimen in the Berlin collection, which was referred to *Betula prisca* Ett. by Weyland, would seem to belong to the present taxon. Not only did the specimen have a strongly asymmetrical lamina and markedly oblique base, but the venation in the apical part of the lamina was camptodromous and the secondary veins in the distal half

of the lamina were interconnected by extensions of the secondary veins.

Of the herbarium material examined the fossil most resembled leaf material of *Aesculus pavia* L., *Castanopsis indica* (Roxb.) A.DC., *Clethra delavayi* Franch. and various members of the Juglandaceae.

The leaves of *Aesculus pavia* (Hippocastanaceae), differ from the fossil in having a lamina which decreases rapidly in width near the apex and is attenuate at the leaf base. Moreover, the secondary veins do not show any tendency to branch near the leaf margin. No branching of the secondary veins was to be found in the leaves of *Castanopsis indica* either. In addition

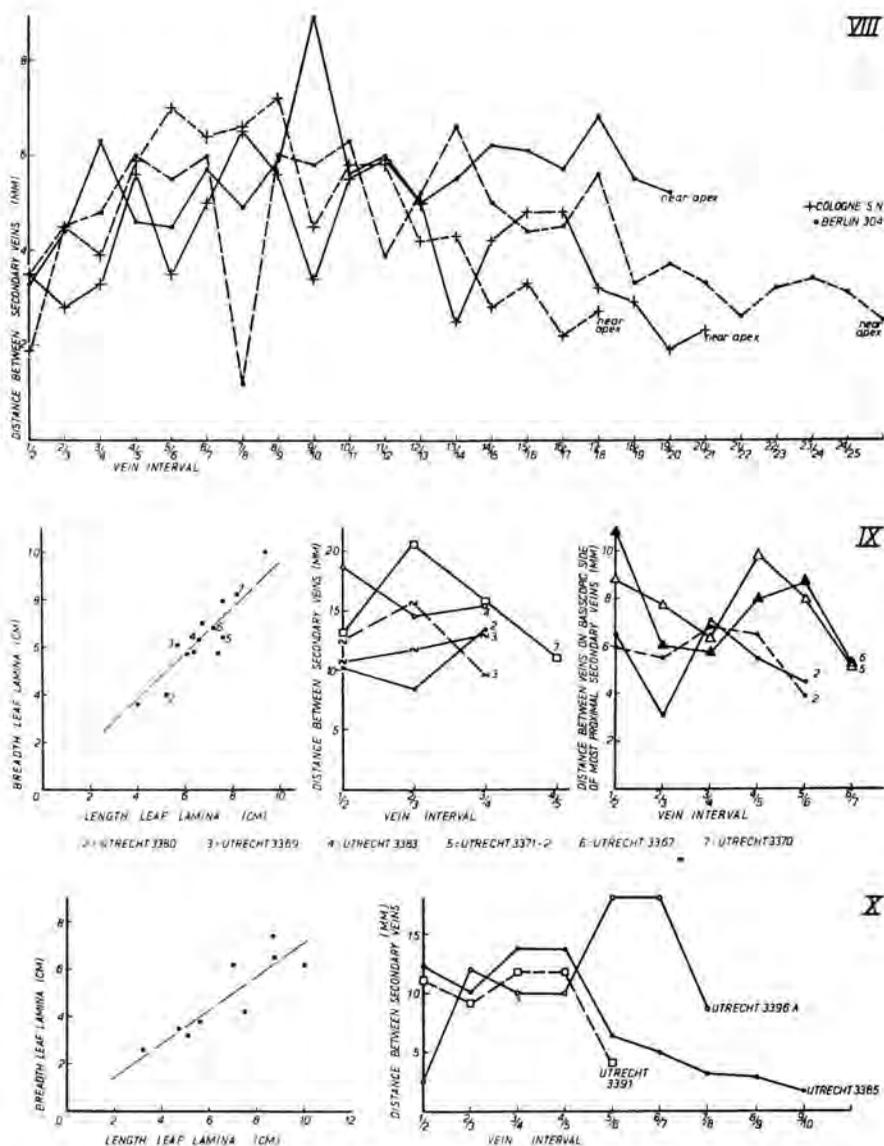


Fig. 13. Graphs VIII cont., IX and X.

this and other species of the Fagaceae never have teeth developed in that part of the leaf margin between the secondary veins. The leaves of *Clethra delavayi* (Clethraceae), although similar to the fossil in certain respects, have coarser teeth lacking mucronulate tips and secondary veins which are markedly arched throughout the length of the lamina. Such forwardly arched veins are generally restricted to the apical part of the lamina in the fossil. While in itself no proof of this, the presence of glands supported by a single basal cell adds to the cumulative evidence in support of a reference to the Juglandaceae.

Of the Juglandaceae the fossil most resembles the leaflets of members of *Carya*, *Juglans* and *Platycarya* and it was to *Carya* that WEYLAND (1934) referred some of the specimens included here. In the Juglandaceae the leaves are pinnate and while the terminal leaflet may have a long petiolule the lateral leaflets are either sessile or only have very short petiolules. If a reference to the Juglandaceae is indeed valid those leaf-remains with a well-developed petiolule would therefore appear to represent terminal leaflets. In the material of *Carya* examined such terminal leaflets have an acute base, while those of *Juglans* and *Platycarya* may be acute, obtuse, truncate or rounded. The combination of not uncommonly falcate leaflets, teeth with mucronulate apices etc. might suggest a close affinity to *Platycarya*. However, with the possible exception of one leaflet in W. P. Fang 2073, the base of the terminal leaflet in *Platycarya* would appear to be invariably symmetrical and never asymmetrical or oblique. In *Juglans*, on the other hand, the terminal leaflet may have an asymmetrical or oblique base. Nevertheless, to determine the leaf-remains as those of *Juglans* would not appear to be justified as none of the species examined were found to have a margin similar to that of the leaf-remains.

FAMILY SALICACEAE

In his revision of the Kreuzau assemblage WEYLAND (1934) recorded nine species of Salicaceae. In this account only 4 taxa are described, including one taxonomic entity new since Weyland's revision. Differences between this account and that of Professor Weyland can partly be attributed to differences in concept, brought about by a considerable increase in the amount of material available for study. In addition specimens referred to as *Populus gaudinii* Fischer-Ooster and *P. mutabilis* Heer by WEYLAND (1934, p. 43) have had to be excluded from the Salicaceae. In all fairness to Professor Weyland it ought to be pointed out that he considered their reference to *Populus*, or for that matter to the Salicaceae, as somewhat doubtful. Both species were based on a single specimen. The specimen referred to as *Populus gaudinii* appears to have been lost or misplaced, for it could not be found in the Berlin collection and was not to be found in a number of institutes contacted. On the basis of the short description and illustration (WEYLAND, 1934, Tafel 3, fig. 1) there appears to be no reason for referring this specimen to the Salicaceae. The specimen referred to as

Populus mutabilis (Deutsche Akad. Wiss. Berlin s.n. (K 154)) was available for study, but proved to have very different stomata and accessory cells from those encountered in the Salicaceae. While the Salicaceae are usually characterized by having stomata with stomatal slits almost as long as the stomata themselves, those of the specimen referred to as *Populus mutabilis* have stomatal slits only 56–63% stomatal length. The stomatal slits in the Salicaceae moreover gradually taper to a point, whereas those of the material referred to as *Populus mutabilis* have rounded poles. Furthermore, in the specimen referred to as *Populus mutabilis* the two lateral accessory cells encircle the stomata entirely, while in members of the Salicaceae lateral accessory cells meet at the poles but do not encircle the stomata.

IX *Populus* Section *Leuce* Duby.

Synonyms: *Populus attenuata* A. Braun

Populus crenata Unger

Populus grossi-dentata Heer

Populus latior A. Braun

Populus c.f. *melanaria* Heer

QUAAS, 1910, p. 984; FLIEGEL
and STOLLER, 1910, p. 243.

WEYLAND, 1934, p. 44 pro parte!

QUAAS, 1910, p. 984.

FLIEGEL and STOLLER, 1910, p.
243; WEYLAND, 1934, p. 43!

QUAAS, 1910, p. 984; FLIEGEL
and STOLLER, 1910, p. 243.

Description:

Petiole 45–71 mm long and 0.6–2.0 mm wide at mid-point, 0.5–1.3 mm wide at leaf base and 1.5–4.0 mm wide at base of petiole, straight or sometimes slightly curved, sometimes making an angle with the midvein.

Lamina ovate, 3.5–9.6 cm long, 2.5–10.2 cm wide, the length/breadth ratio being 0.93 : 1–1.8 : 1 (fig. 13). Leaf apex acute or acuminate, leaf base rounded, truncate or cordate.

Leaf margin non-entire, dentate with sharp teeth 0.4–3.0 mm across, (5–) 10–23 per side, alternating with rounded sinuses. Teeth of one size group.

Venation craspedodromous-actinodromous, midvein straight or gently curved throughout, small-scale bends generally present distally, markedly tapering along length, 0.1–1.0 mm wide at mid-point between base and apex of lamina. Midvein bearing 3–8 secondary veins per side, the most proximal vein arising at 25°–55° (–80°), arising in the remaining part of the basal third of the lamina at 30°–55°, in the median third at 40°–60°, in the apical third at 30°–90°. The angle at which the veins arise increasing, constant or rarely decreasing within the first few mms. The spacing of the veins irregular, reaching a maximum proximally or mid-way (fig. 13). Secondary veins mostly subopposite to alternately arranged, although the most proximal veins opposite. Secondary veins hardly to somewhat tapering along length, 0.05–0.40 mm wide at mid-point, sometimes dichotomising at 1/2–2/3 the distance from the midvein to the leaf margin, the veins interconnected distally by fine extensions of secondary veins or ter-

tiary veins. The most proximal secondary vein bearing basiscopically 5–7 minor veins arising at 35° – 65° , the spacing of which is somewhat irregular, reaching a maximum proximally, mid-way or distally (fig. 13). Intermediate veins 3–7(–11) per intercostal field, the veins arising from the midvein at 55° – 130° , running more or less parallel to one another or converging/diverging, the spacing between them being more or less constant, increasing distally or irregular. The veins similar in width, extending from 0 to $1/5$ – $1/2$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 3–10 per 1 cm secondary vein, generally little branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles (10–) 50–90 per 10 mm^2 , with some to many branched free vein-endings.

Epidermis in non-stomatal condition composed of 400–585 more or less polygonal cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–4 : 1. Cell wall 0.6–1.5 microns thick, largely unpitted or finely pitted, straight. Cells over veins narrow, more or less square or rectangular, the cell length/cell breadth ratio being 1 : 1–6 : 1. Finer veins somewhat reflected in cuticle. Hair bases, 7.2–10.8 microns in diameter, 7–63 per 0.1 mm^2 , grouped and especially common on veins, with up to 7 associated cells radiating away from base. Epidermis in stomatal condition composed of (255–) 420–750 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–3.5 : 1, cuticle sometimes coarsely striate next stomata. Cell wall 0.5–1.5 (–2.0) microns thick, unpitted or pitted, more or less straight or irregularly twisted. Cells over veins square, rectangular or spindle-shaped, the cell length/cell breadth ratio being 1 : 1–6 : 1 or more. Finer veins hardly reflected in cuticle. Stomata 9.0–21.6 microns long and 7.2–19.8 microns broad, breadth 75–133% length, 38–70 per 0.1 mm^2 , stomatal index 5.6–17.5 (–20)%. Stomata variously orientated, somewhat depressed, arranged in groups, apices non-retuse. Stomatal slit 47–67% (possibly more) stomatal length. Accessory cells 2(–4), symmetrical with 0(–2) polar and 2 lateral cells, somewhat smaller than the rest of the accessory cells. Hair bases, 5.4–9.0 microns in diameter, 0–35 per 0.1 mm^2 , grouped and especially common on veins, rare elsewhere, with 5–8 associated cells radiating from base.

Specimens examined: 45, among which the numbered specimens:
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3367, 3368,
3369, 3370, 3371, 3372, 3374, 3375, 3376, 3377, 3378, 3379,
3380, 3381, 3382, 3383, 3384, 3544A, 3546, 3682B.

Discussion:

While various authors have considered it possible to retain *Populus attenuata* as a separate specific entity, others have considered this taxon to be simply a variety of *Populus latior*. It is noteworthy that Alexander Braun himself changed his mind as to the exact status of this taxon.

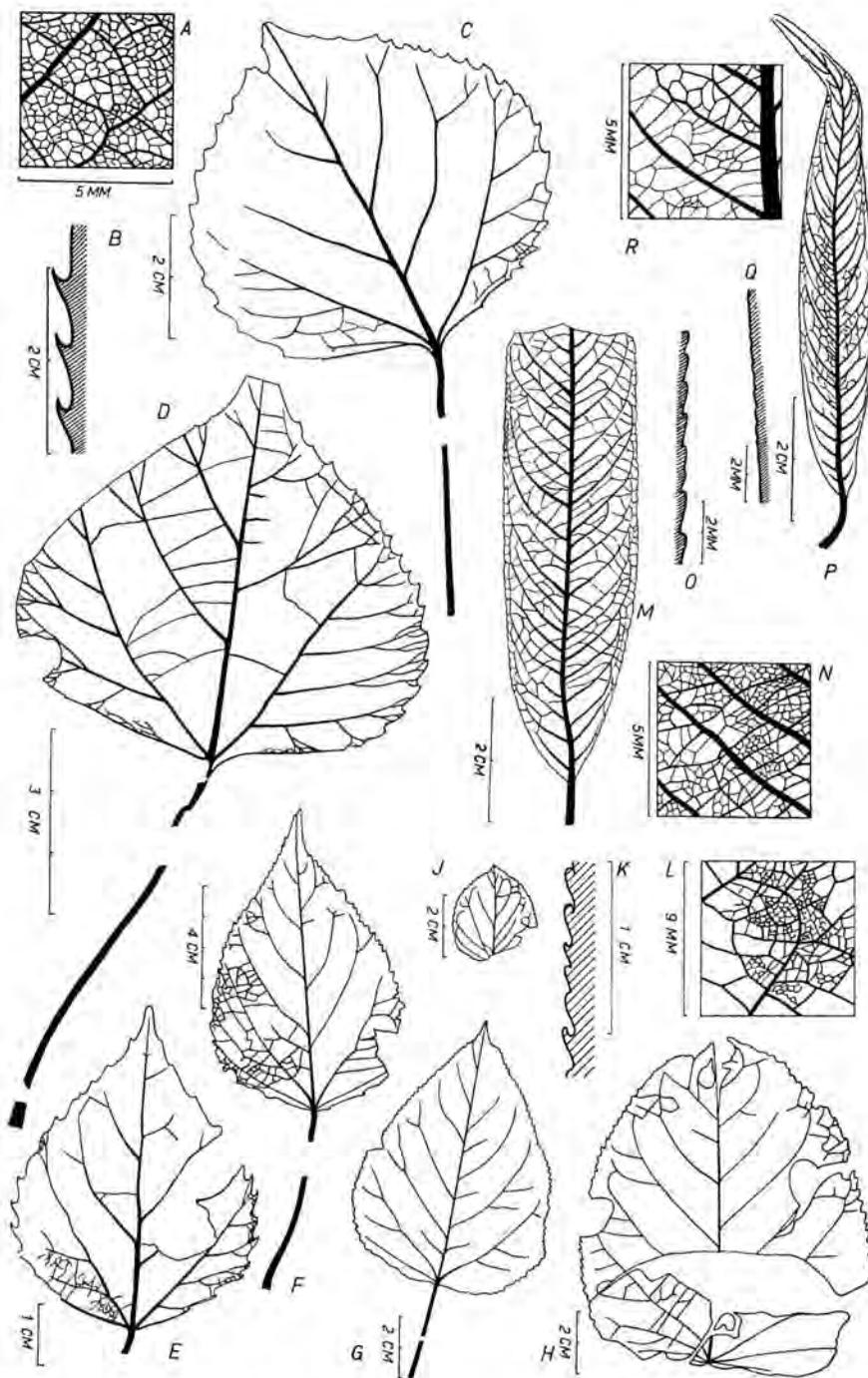


Fig. 14. A-E = IX: A = detail showing venation; B = detail showing leaf margin; C = Utrecht 3369; D = Utrecht 3367; E = Utrecht 3380. F-L = X: F = Utrecht 3393; G = Berlin s.n. (K 35), H = Utrecht 3395; J = Utrecht 3390; K = detail showing leaf margin; L = detail showing venation. M-R = XI: M = Utrecht 3516; N = Utrecht 3516, detail showing venation; O = Utrecht 3516, detail showing leaf margin; P = Utrecht 3518; Q = Utrecht 3518, detail showing leaf margin; R = Utrecht 3518, detail showing venation.

While originally considering it to have a specific rank, he referred to it as a variety in other lists of the Oeningen plant-remains (in BRUCKMANN, 1850; STIZENBERGER, 1851). No characteristic "attenuata" material was found in the Berlin collection made use of by J. Stoller in compiling his lists of the Kreuzau assemblage (QUAAS, 1910; FLIEGEL and STOLLER, 1910) and neither was material referred to *Populus attenuata* by J. Stoller met with. However, the fact that Stoller mentioned (in FLIEGEL and STOLLER, 1910, p. 243) that the leaves, and presumably the leaf base, were highly variable in shape would suggest that the material be referred to the present taxon. WEYLAND (1934) did not recognize *Populus attenuata* and did not mention *Populus grossi-dentata* either. The material referred to in QUAAS (1910, p. 984) under the title of *Populus grossi-dentata* Heer was presumably that of *Populus latior* f. *grossi-dentata* mentioned in FLIEGEL and STOLLER (1910, p. 243). Although no material referred to *Populus* cf. *melanaria* was met with in the course of the revision, a reference to the present taxon would seem most likely. HEER (1856, p. 16), in describing the taxon, emphasised its similarity to *Populus latior*. An unnumbered specimen (Coll. A. Quaas in 1903) in the Berlin collection, which was determined as *Populus crenata* by H. Weyland, was found to have a dentate leaf margin and would appear to belong to the present taxon, even though a cuticle preparation attempted proved unsuccessful.

Of the Chinese and American material investigated by the present author only 4 species had leaves resembling the fossil in external morphology. These species were *Vitis pentagona* Diels et Gilg, *Populus tremula* L., *P. grandidentata* Michx. and *P. bonatii* Lévl. The very thin cuticle of *Vitis pentagona* (Vitaceae) was difficult to prepare and was found to be covered with numerous unicellular and multicellular hairs; furthermore the cell outline was difficult to make out. Not only can one suppose that a cuticle of this nature would not withstand the process of fossilization, but the strong cell walls and the infrequent trichome bases found in the fossil would tend to suggest that the fossil had no affinity with this recent species. The only possibility as regards affinity would appear to be *Populus*. In the 12 species of *Populus* investigated by the present author marked differences in the nature of the epidermis were found to exist. Since present ideas on the taxonomy of living *Populus* species would suggest that one is dealing with a total of 20-40 species at the present-day (WILLIS, 1960; Melchior in ENGLER, 1964; AIRY SHAW, 1966), it is possible that the epidermis may be of use at an infrageneric level. *Populus tremula* has an upper epidermis composed of cells with straight to undulate cell walls, but can be ruled out of consideration on the basis of the lower epidermis. This has fine cell walls and only fine striae are to be seen next the stomata. In this respect the epidermis of *Populus bonatii* approximates more closely to that of the fossil. The lower epidermis has strong cell walls with an irregularly twisted outline as well as coarse striae next the stomata. However, the leaves of *Populus bonatii* are characterized by having domed cells on the upper

epidermis, a feature which is lacking in the fossil. The leaves of *Populus grandidentata*, which are otherwise similar to the leaf-remains in question, differ in having cells of the upper epidermis with generally undulate cell walls. It is possible that one may be dealing with an extinct species, for while the fossil fits within the generic limits of *Populus* it does not resemble any of the recent species of *Populus* investigated in its entirety. However, there remains the possibility that the fossil may be referable to a living species of *Populus*, which has not been investigated to date. Before a decision can be taken as to the specific status of the fossil, more living material requires to be investigated.

Herbarium material examined in detail:

<i>Populus adenopoda</i> Maxim.	Coll. E. H. Wilson 724	(E)	det. C. Schneider
<i>Populus angulata</i> Ait.	Coll. C. Silva & M. Silva 10-11-1942	(U)	_____
<i>Populus balsamifera</i> L.	Coll. W. J. Cody & C. C. Loan 3778	(U)	_____
	Coll. E. Roy 2477	(U)	_____
<i>Populus bonatii</i> Lévl.	Coll. E. E. Maire 1977	(E)	det. Handel- Mazzetti
	Coll. Handel-Mazzetti 8687	(E)	det. Handel- Mazzetti
<i>Populus cathayana</i> Rehder	Coll. C. O. Lee 5512	(E)	det. A. Rehder
<i>Populus deltoides</i> Marsh	Coll. Marie-Victorin, Rolland-Germain, E. Rouleau & E. Raymond 5006	(U)	_____
<i>Populus grandidentata</i> Michx.	Coll. L. M. Umbach 5143	(U)	_____
<i>Populus heterophylla</i> L.	Coll. K. U. Kramer 846	(U)	det. R. H. Mohlen- brock
<i>Populus nigra</i> L.	Coll. C. Y. Chiao 2573	(E)	det. A. Rehder
<i>Populus szechuanica</i> C. Schneider	Coll. J. F. Rock 17606	(E)	_____
<i>Populus tremula</i> L.	Coll. C. Y. Chiao 3155	(E)	det. A. Rehder
	Coll. K. U. Kramer 23-5-1951	(U)	det. K. U. Kramer
	Coll. R. W. Tienstra 211	(U)	det. R. W. Tienstra
<i>Populus yunnanensis</i> Dode	Coll. Handel-Mazzetti 1146	(E)	det. Handel- Mazzetti
<i>Vitis pentagona</i> Diels et Gilg	Coll. Handel-Mazzetti 11924	(E)	det. Handel- Mazzetti

X. *Populus* Section Aigeiros Duby

Synonyms: *Populus balsamoides* Goepfert
Populus crenata Unger

WEYLAND, 1934, p. 44!

WEYLAND, 1934, p. 44 pro parte!

Description:

Petiole up to 60 mm long and 0.65–1.30 mm wide, more or less parallel-sided, straight, sometimes making an angle with the midvein.

Lamina suborbicular or ovate, 3.2–11 cm long, 2.6–9.5 cm wide, the length/breadth ratio being 0.8: 1–1.75: 1 (fig. 13). Leaf apex acute or acuminate, leaf base rounded or slightly cordate.

Leaf margin non-entire, more or less crenulate with (acute-) rounded teeth 0.2–1.3 mm across, c.17–c.55 per side, alternating with acute, angular or rounded sinuses. Teeth of one size group.

Venation camptodromous (– actinodromous), midvein straight or apically curved, hardly or markedly tapering along length, 0.35–0.85 mm wide at mid-point between base and apex of lamina. Midvein bearing 5–10 secondary veins per side, the most proximal vein arising at 45°–60° (–110°), arising in the remaining part of the basal third of the lamina at 35°–75°, in the median third at 30°–60° (–90°), in the apical third at 35°–65°. The angle at which the veins arise increasing, constant or decreasing within the first few mms. The spacing of the veins somewhat irregular not uncommonly with two maxima, one proximally and one distally (fig. 13). Secondary veins mostly alternately arranged, although most proximal veins opposite. Secondary veins hardly to somewhat tapering along their length, 0.07–0.40 mm wide at mid-point, occasionally dichotomising at 1/2–2/3 the distance from the midvein to the leaf margin, the veins interconnected distally by fine extensions of secondary veins, or tertiary veins. Intermediate veins (0–) 3–12 per intercostal field, arising from the midvein at 45°–135°, running more or less parallel to one another or converging/diverging, the spacing between them being more or less constant, increasing distally or somewhat irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/4–5/8 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 3–7 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles (c.25–) 55–70 (–130) per 10 mm² with many free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of 440–525 cells per 0.1 mm², cuticle frequently finely striate in particular in the vicinity of the stomata, the cell length/cell breadth ratio being 1: 1–2.5: 1. Cell wall up to 0.7–1.2 microns thick, unpitted or pitted, straight. Cells over veins narrow, rectangular or spindle-shaped, the cell length/cell breadth ratio being 1: 1–6: 1, the cell wall somewhat thicker than that of the rest of the epidermal cells. Finer veins somewhat reflected in cuticle. Stomata 14.4–27.0 microns long and 9.0–21.6 microns broad, breadth 30–87.5% length, 40–57 per 0.1 mm²; stomatal index 6.6–12.5%. Stomata variously orientated, undepressed, equidistant or somewhat arranged in groups, apex non-retuse. Stomatal slit 64–88% stomatal length. Accessory cells 0 or 4–6, when present more or less symmetrical with 2 polar cells and 2–4 lateral cells, similar in size to the rest of the epidermal cells. Internal resinous bodies absent.

Specimens examined: 37, among which the numbered specimens:
Geol. Inst. Cologne: Coll. H. Weyland 1640
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3385, 3386,
3387, 3388, 3389, 3390, 3391, 3392, 3393, 3394A, 3395, 3396A,
3526C, 3543, 3545, 3548B, 3681B, 3931B.

Discussion:

While a number of older authors regarded *Populus crenata* as having specific status e.g. GOEPPERT, 1852, 1855; UNGER, 1851 this practice has found few followers e.g. KOWNAS, 1955; PÁLFALVY, 1953 in more recent times. WEYLAND (1934) attributed three specimens from the Berlin collection to this species, without further comment or description. An incomplete leaf with petiole still attached to shoot, which belongs to collection K 150, was examined by the present author. The specimen did not yield a cuticle, so that one is forced to rely simply on outward appearance. While the distal part of the lamina was missing the leaf was 2.9 cm wide and would appear to have been ovate in shape. The leaf base was rounded and the leaf margin bore numerous \pm crenulate teeth such as in the present taxon. While the more distal secondary veins would appear to have been alternate in arrangement, the two most proximal pairs would appear to have been opposite. Further details could not be made out. There would appear to be no reason to consider it as belonging to a separate species and while ENGELHARDT (1876, 1877, 1881) and PILAR (1883) referred to *Populus crenata* as a synonym for *Populus mutabilis* Heer no evidence could be found for this assumption either. A reference of this specimen to the present taxon would seem to be justified.

Leaves similar to the fossil are to be found in various *Populus* species as well as in *Callicarpa americana* L. (Verbenaceae). This latter is to be distinguished from the fossil by the presence of glands and multicellular, sometimes stellate, hairs on the leaves. In the fossil the hair bases are but small and restricted to the larger veins, whereas the hairs of *Callicarpa americana* with their large hair bases are to be found on the smaller veins as well. Furthermore, the glands present in *Callicarpa americana* are found on and between the veins and would be expected to occur in the fossil as well, if a relationship did in fact exist. On the other hand an affinity between the fossil and several *Populus* species can be demonstrated on the grounds of the cuticle in addition to the gross morphological features. None of the present specimens of the fossil yielded a cuticle free of stomata and the same is true of certain specimens investigated by KOWNAS (1955) and R. Litke (personal communication, 1967). In dicotyledonous plants the upper epidermis, when free of stomata, tends to have a thicker cuticle than that found on the lower epidermis. When dealing with fossils one can assume that, if selection during fossilization has taken place, that the thinner of the two cuticles will be rare or absent. The fact that one constantly finds cuticles indicating an epidermis with stomata would tend to suggest that one is dealing with a species belonging to the Section Aigeiros Duby.

According to REHDER (1927, p. 90) this section is characterized by being stomatiferous on both sides of the leaf lamina. In referring the fossil to this section of *Populus* it should be pointed out that the circumscription of this section is by no means entirely satisfactory. Neither specimens of *Populus balsamifera* L. examined were found to have stomata on the upper epidermis and a specimen of *Populus cathayana* Rehder, bearing stomata on both upper and lower epidermides and determined by REHDER (1931) should, according to the same author (REHDER, 1949), belong to the Section Tacamahaca Spach. Within the Section Aigeiros the characters used in the separation of the species are trivial and not infrequently lead to misidentifications. The best solution at the present time would appear to be to leave the specific identity of the fossil as uncertain.

Herbarium material examined in detail:

<i>Callicarpa americana</i> L.	Coll. J. G. ten Houten & A. Schoenmakers 1096	(U) det. T. W. J. Gadella
<i>Populus adenopoda</i> Maxim.	Coll. E. H. Wilson 724	(E) det. C. Schneider
<i>Populus angulata</i> Ait.	Coll. C. Silva & M. Silva 10-11-1942	(U) _____
<i>Populus balsamifera</i> L.	Coll. W. J. Cody & C. C. Loan 3778	(U) _____
	Coll. E. Roy 2477	(U) _____
<i>Populus cathayana</i> Rehder	Coll. C. O. Lee 5512	(E) det. A. Rehder
<i>Populus deltoides</i> Marsh	Coll. Marie-Victorin, Rolland-Germain, E. Rouleau & E. Raymond 5006	(U) _____
<i>Populus heterophylla</i> L.	Coll. K. U. Kramer 846	(U) det. R. H. Mohlenbrock
<i>Populus nigra</i> L.	Coll. C. Y. Chiao 2573	(E) det. A. Rehder
<i>Populus szechuanica</i> C. Schneider	Coll. J. F. Rock 17606	(E) _____
<i>Populus yunnanensis</i> Dode	Coll. Handel-Mazzetti 1146	(E) det. Handel-Mazzetti

XI. *Salix*

<i>Synonyms</i> : <i>Salix longa</i> A. Braun	WEYLAND, 1934, p. 41!
<i>Salix palaeopurpurea</i> Fr. Meyer	WEYLAND, 1934, pp. 41-42, Tafel 3, fig. 5!
<i>Salix varians</i> Goeppert	WEYLAND, 1934, p. 41!

Description :

Petiole 6-10 mm long and 1.0-1.5 mm wide at mid-point, more or less parallel-sided or increasing in width from leaf base to base of petiole, straight or rarely curved, sometimes making an angle with the midvein.

Lamina ovate, elliptical or oblong, 4.8-15.4 cm long, 0.55-2.30 cm wide, the length/breadth ratio being 7 : 1-8.7 : 1. Leaf apex long acute, leaf base attenuate, acute or rounded.

Leaf margin (entire-) non-entire, more or less crenulate with (acute-) rounded teeth 0.03-0.35 mm across, (0-) 35-125 per side, alternating with acute or rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein straight or curved, hardly or markedly tapering along length, 0.3–0.7 mm wide at mid-point between base and apex of lamina. Midvein bearing c.13–c.30 secondary veins per side, the most proximal vein arising at 30°–65°, arising in the remaining part of basal third of lamina at 35°–80°, in the median third at 40°–70° (–90°), in the apical third at 30°–60° (–90°). The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the secondary veins somewhat irregular, showing no particular trend (fig. 15). Secondary veins opposite or alternately arranged, hardly to somewhat tapering along their length, 0.05–0.20 mm wide at mid-point, interconnected distally by fine extensions of secondary veins, or tertiary veins. Intermediate veins 1–10 per intercostal field, rarely with somewhat twisted course, arising from midvein at 45°–130°, running more or less parallel to one another or converging/diverging, the spacing between them increasing distally. The veins more or less similar in width or increasing in width with increase in length, extending from 0 to 1/2–7/8 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary veins 5–22 per 1 cm secondary vein, little or somewhat branched, the lengths on acroscopic and basiscopical sides of secondary vein more or less similar. Areoles 7–74 per 10 mm², the number apparently varying greatly within a single leaf, with some free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of c.550–840 more or less polygonal cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2.5 : 1. Cell wall 0.5–2.0 microns thick, unpitted or pitted, straight. Cells over veins narrow, rectangular or spindle-shaped, the cell length/cell breadth ratio being 2.5 : 1–6 : 1. Finer veins somewhat reflected in cuticle. Cells at leaf margin c.1050 per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2 : 1, not distinctly arranged in rows. Cell wall slightly pitted, straight. Epidermis in stomatal condition composed of c.425–c.525 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–5 : 1. Cell wall 0.4–0.6 microns thick, largely unpitted or pitted, straight. Cells over veins unknown. Stomata 10.8–19.8 microns long and 5.4–10.8 microns wide, breadth 50–56% length, 19–56 per 0.1 mm²; stomatal index 3.6–13.0%. Stomata variously orientated, undepressed or slightly depressed, equidistant or somewhat arranged in groups, apices non-retuse. Stomatal slit 75–95% stomatal length. Accessory cells (0–) 2(–4), symmetrical with 0–2 polar cells and 0–2 lateral cells, similar in size to the rest of the epidermal cells. Internal resinous bodies rare.

Specimens examined : 53, among which the numbered specimens:

Deutsche Akad. Wiss. Berlin: 297 (K 152)

Geol. Inst. Cologne: Coll. H. Weyland 1364(K 126), 1364a (K 126, counterpart of 1364), 1364b(K 126), 1712

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3515, 3516, 3517, 3518, 3519, 3520, 3521, 3522, 3523A, 3524, 3525, 3526A, 3547B, 3548A, 3549.

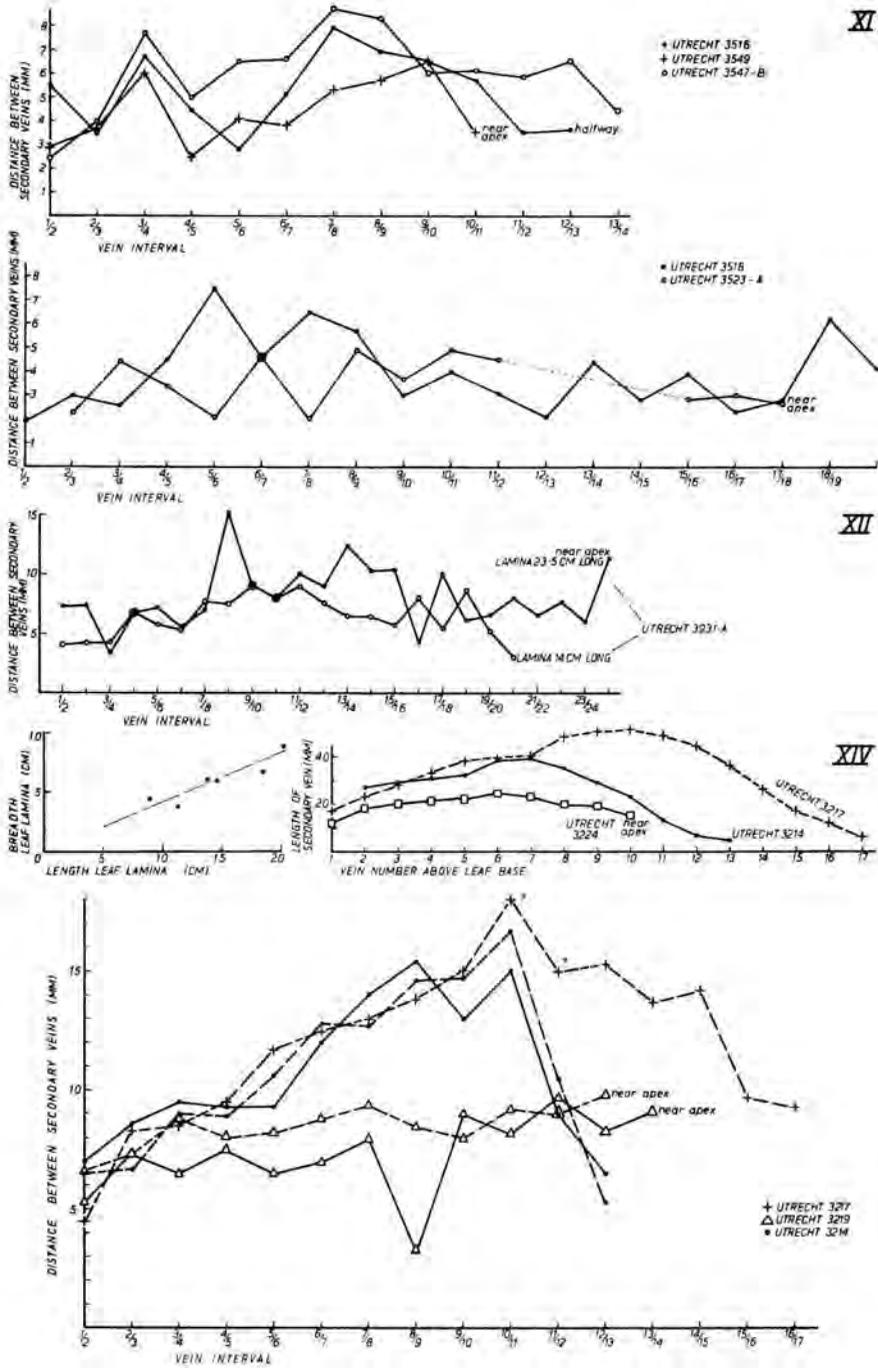


Fig. 15. Graphs XI, XII, XIV.

Discussion:

The present circumscription of this taxonomic entity differs from that employed by WEYLAND (1934) in his revision of the Kreuzau material. In this revision Weyland recognized 3 specific entities: *Salix longa* A. Braun, *S. palaeopurpurea* Fr. Meyer and *S. varians* Goepfert. No description was given of *Salix longa*, but an examination of material attributed to this species by Weyland proved that these leaf-remains fell within the range of variation encountered in material attributed to *Salix varians*. WEYLAND (1934, p. 41) described *Salix palaeopurpurea* as being obovate with a finely toothed leaf margin in the distal part of the leaf and as having a relatively wide midvein. However an examination of the only specimen figured from Kreuzau (WEYLAND, 1934, Tafel 3, fig. 5) has shown that the leaf was in all probability elliptical. Moreover, while the width of the midvein is 0.7 mm half way along its length, that of material referred to *Salix varians* was found to vary between 0.3 and 0.7 mm wide. In much the same way the nature of the leaf margin fell within the range of variation encountered in the material attributed to *Salix varians*. An apparent difference in the number of intermediate veins present in the intercostal field (*Salix varians*: 1-6; *S. palaeopurpurea*: 6-10) could not be confirmed in other material referred to *Salix palaeopurpurea* (Coll. H. Weyland 1364, 1364a, 1364b). Other differences could not be found and it seems reasonable to refer all these remains to a single taxon.

While Weyland's taxonomic concept cannot be upheld, his reference of the material to *Salix* would appear to be justified. Leaves superficially resembling those of the fossil are to be found in a number of families other than the Salicaceae e.g. Campanulaceae, Caprifoliaceae, Celastraceae, Ericaceae, Myrsinaceae, Rosaceae, Saxifragaceae, Stachyuraceae, Theaceae, and Ulmaceae, but none were found to agree with the leaf-remains in all respects. *Lobelia pyramidalis* Wall. (Campanulaceae) has leaves which are similar to the fossil as regards shape and secondary venation. However the tertiary veins run more or less at right angles to the midvein, while the leaf margin has \pm sharp teeth and large epidermal cells and stomata (stomata 33-57 microns long). In the Caprifoliaceae e.g. *Ebulum javanicum* (Reinw.) Airy Shaw, *Sambucus adnata* Wall. ex DC. and *S. sieboldiana* Blume the shape and venation of the leaves may be similar, but the leaf margin is invariably serrate and the stomata, 24-72 microns long, are surrounded by finely striate cells. In much the same way *Euonymus clivicola* W.W. Smith and *E. cornutoides* Loes. (Celastraceae) were found to have stomata with a length of 21-43 microns and to differ from the fossil in such features as undulate cell walls, papillose adaxial surface e.g. *Euonymus clivicola* and a serrulate leaf margin. The leaves of *Pieris formosa* D. Don (Ericaceae) approximate very closely to the fossil in their shape, venation and crenulate margin. However this species is characterized by having stomata, 18-37 microns long, more or less round in outline with a very short stomatal slit and strongly thickened 2-3 celled hair bases on

the upper and lower surfaces of the leaf. The leaves of *Embelia vestita* Roxb. (Myrsinaceae) also resemble the fossil very closely in their gross-morphology, but again differ as to epidermal characteristics. The epidermal cells have undulate cell walls, while the cuticle is found to bear triangular thickenings in the angles of the cells. The stomata have only a short stomatal slit and are surrounded by two narrow accessory cells. The junction of these accessory cells could not be made out in the cuticle with the result that these appear to form a ring round each stoma. Plants having leaves (leaflets) resembling the leaf-remains are found in a number of genera of the Rosaceae e.g. *Photinia lancifolia* Rehd. et Wils., *Spiraea japonica* Linn.f., and various species of *Prunus* and *Sorbus*. The leaflets of *Sorbus* would appear to differ from the leaf-remains in a number of respects. The margin of the leaflets, while often proximally entire, is serrate or serrulate rather than crenulate in a non-entire state. Moreover the leaflets lack petiolules. The stomata, while varying in length between 14 and 40 microns, have a mean length greater than that of the fossil. Between these stomata the cells are striate and sometimes papillate as well. The epidermis of *Prunus persica* (L.) Batsch. resembles those of the *Sorbus* species examined and in this case the stomata were found to be 21–43 microns long. The stomata in *Prunus perulata* Koehne are smaller (13–33 microns long) and resemble those of the fossil more closely. However *Prunus perulata* has leaves with a serrulate leaf margin and a cuticle striate on both surfaces. *Spiraea japonica* has relatively small stomata such as found in *Prunus perulata*, but unlike the fossil has epidermal cells with slightly to highly undulate cell walls, a serrate leaf margin and fewer (± 8) secondary veins. In much the same way the leaves of *Photinia lancifolia* differ from the fossil under consideration in that the leaf margin is serrulate, there are only 6–9 secondary veins present and the adaxial epidermis is characterized by having somewhat to markedly undulate cell walls. *Hydrangea aspera* D. Don (Saxifragaceae) has leaves similar to the leaf-remains as regards shape and venation, but differing in that the leaf margin bears stumpy projections and in the presence of hairs with hair bases having a large diameter on both surfaces of the lamina. The epidermal cells on the abaxial surface of the leaf are moreover papillate. In *Stachyurus salicifolius* Franch. (Stachyuraceae) the leaves have a serrulate leaf margin and moreover differ from the leaf-remains in that the loops by which the secondary veins are distally interconnected occur at c.2/3 the distance from the midvein to the leaf margin. The stomata are depressed and 14–33 microns in length. The leaves of *Eurya graffii* Merrill (Theaceae) are similar to the leaf-remains in shape and nature of the leaf margin, but like those of *Stachyurus salicifolius* differ with regard to the venation. The secondary veins which are \pm straight are looped at quite some distance from the leaf margin. Moreover the stomata, 21–31 microns in length, are oval to round in outline and with a relatively short stomatal slit. The leaves of *Trema virgata* Blume (Ulmaceae), while otherwise similar to the fossil in external appearance,

have only 5-7 secondary veins per side with the secondary vein interval reaching a maximum distally. The presence of hairs, with a hair base having a large diameter, on both surfaces of the leaf in addition to other small 2-celled hair bases on the abaxial surface, confirms the opinion that the affinities of the fossil lie elsewhere.

While the leaves of the species of *Salix* (Salicaceae) examined on this occasion differed from each other in various respects they all displayed arched secondary veins similar to those of the fossil. These secondary veins either merged with the leaf margin or were interconnected with each other by fine extensions of the secondary veins or tertiary veins close to the margin. In this respect and in the nature of the intermediate and tertiary veins these species bear a close resemblance to the leaf-remains. These species are moreover characterized by stomata with long stomatal slits and by the presence of guard cells with somewhat thickened epidermal walls, except in the polar areas where the epidermal wall is generally difficult to make out in the cuticles. While similar long stomatal slits were present in the fossil, the preservation of the cuticle of the fossil was not sufficient to confirm the latter feature. The living *Salix* species however agreed with the fossil in the presence of epidermal cells with invariably straight cell walls and in the presence in some cases of small stomata, upwards of 5 microns in length. These characters taken as a whole would tend to suggest that one is dealing with *Salix*. Within *Salix* one meets with a certain amount of variation in the size and shape of the leaves and in the nature of the leaf margin. What is perhaps less well known is that the cuticle also shows a certain amount of variation at the infrageneric level (ALEKSANDROV and MIROSLAVOV, 1962). BANCROFT (1934) has shown that the number of stomata per sq. mm may vary between one species of willow and another. Furthermore in some species the stomata may be, with few exceptions, confined to the abaxial surface of the leaf. In other species e.g. *Salix nigra* Marsh they may be as numerous on the adaxial surface as on the abaxial surface of the lamina. The size of the stomata also varies from one species to another. In *Salix chienii* Cheng the stomata were found to have a length of 7-16 microns, whereas *Salix areostachya* C. Schneider has stomata which are 18-49 microns long. However, even among the species taken into consideration on the present occasion so much convergence in leaf characters was found to exist, that any attempt at specific determination must be dismissed as impossible.

Herbarium material examined in detail:

<i>Ebulum javanicum</i>	Coll. J. Esquirol 919	(E) det. H. K. Airy Shaw
(Reinw.) Airy Shaw	7-1906	
<i>Embelia vestita</i> Roxb.	Coll. G. Forrest 27982	(E) det. E. H. Walker
<i>Euonymus clivicola</i>	Coll. G. Forrest 12690	(E) det. W. W. Smith
W. W. Smith		TYPE
<i>Euonymus cornutoides</i> Loes.	Coll. G. Forrest 3094	(E) det. T. Loesener TYPE
<i>Eurya graffii</i> Merrill	Coll. C. O. Levine	(E) det. E. D. Merrill;
	31-10-1918	L. A. Lauener

<i>Hydrangea aspera</i> D. Don	Coll. A. Henry 9208A	(E) det. E. McClintock
<i>Lobelia pyramidalis</i> Wall.	Coll. G. Forrest 215	(E) _____
<i>Photinia lancifolia</i> Rehd. et Wils.	Coll. A. Henry 12833	(E) det. A. Rehder & E. H. Wilson CO-TYPE
<i>Pieris formosa</i> D. Don	Coll. H. T. Tsai 57341	(E) det. W. P. Fang
<i>Prunus persica</i> (L.) Batsch.	Coll. T. T. Yü 5176	(E) det. T. T. Yü
<i>Prunus perulata</i> Koehne	Coll. C. Schneider 1259	(E) det. T. T. Yü
<i>Salix amphibia</i> Small	Coll. J. K. Small & J. J. Carter 1-1909	(U) _____
<i>Salix areostachya</i> C. Schneider	Coll. A. Henry 9338	(E) det. C. Schneider TYPE
<i>Salix babylonica</i> L.	Coll. E. E. Maire 2089	(E) det. Handel- Mazzetti
<i>Salix chienii</i> Cheng	Coll. C. S. Fan & Y. Y. Li 116	(E) _____
<i>Salix dictyoneura</i> von Seemen	Coll. R. C. Ching 2756	(E) det. Handel- Mazzetti
<i>Salix dunnii</i> C. Schneider	Coll. H. H. Chung 18-4-1925	(E) _____
<i>Salix elegans</i> Wall.	Coll. J. F. Duthie 22-5-1893	(E) _____
<i>Salix longipes</i> Shuttleworth	Coll. R. F. Martin 26-5-1939	(U) _____
<i>Salix marginata</i> Wimm.	Coll. P. F. van Heerdt 184	(U) _____
<i>Salix nigra</i> Marsh	Coll. F. R. Rickson 206	(U) det. F. R. Rickson
<i>Salix rosthornii</i> von Seemen	Coll. Handel-Mazzetti 11597	(E) det. Handel- Mazzetti
<i>Sambucus adnata</i> Wall. ex DC.	Coll. G. Forrest 2414	(E) _____
<i>Sambucus sieboldiana</i> Blume	Coll. W. P. Fang 25-5-1928	(E) _____
<i>Sorbus harrowiana</i> (Balf. f. et W. W. Smith) Rehder	Coll. G. Forrest 21806	(E) det. W. E. Evans
<i>Sorbus hupehensis</i> C. Schneider	Coll. Handel-Mazzetti 1625	(E) det. Handel- Mazzetti
<i>Sorbus rehderiana</i> Koehne	Coll. G. Forrest 16731	(E) det. Handel- Mazzetti
<i>Sorbus sargentiana</i> Koehne	Coll. E. H. Wilson 887	(E) det. E. Koehne
<i>Spiraea japonica</i> Linn. f.	Coll. E. H. Wilson 1570	(E) _____
<i>Stachyurus salicifolius</i> Franch.	Coll. W. P. Fang 2720	(E) _____
<i>Trema virgata</i> Blume	Coll. E. H. Wilson 2812	(E) det. C. Schneider

XII. *Salix*

Description:

Shoots bearing leaves apparently in spiral fashion.

Petiole 6.5–23 mm long and 1.5–1.9 mm wide at mid-point, gradually increasing in width from 1.1–1.6 mm wide at base of lamina to 2.0–2.2 mm wide at base of petiole, straight or curved, sometimes making an angle with the midvein.

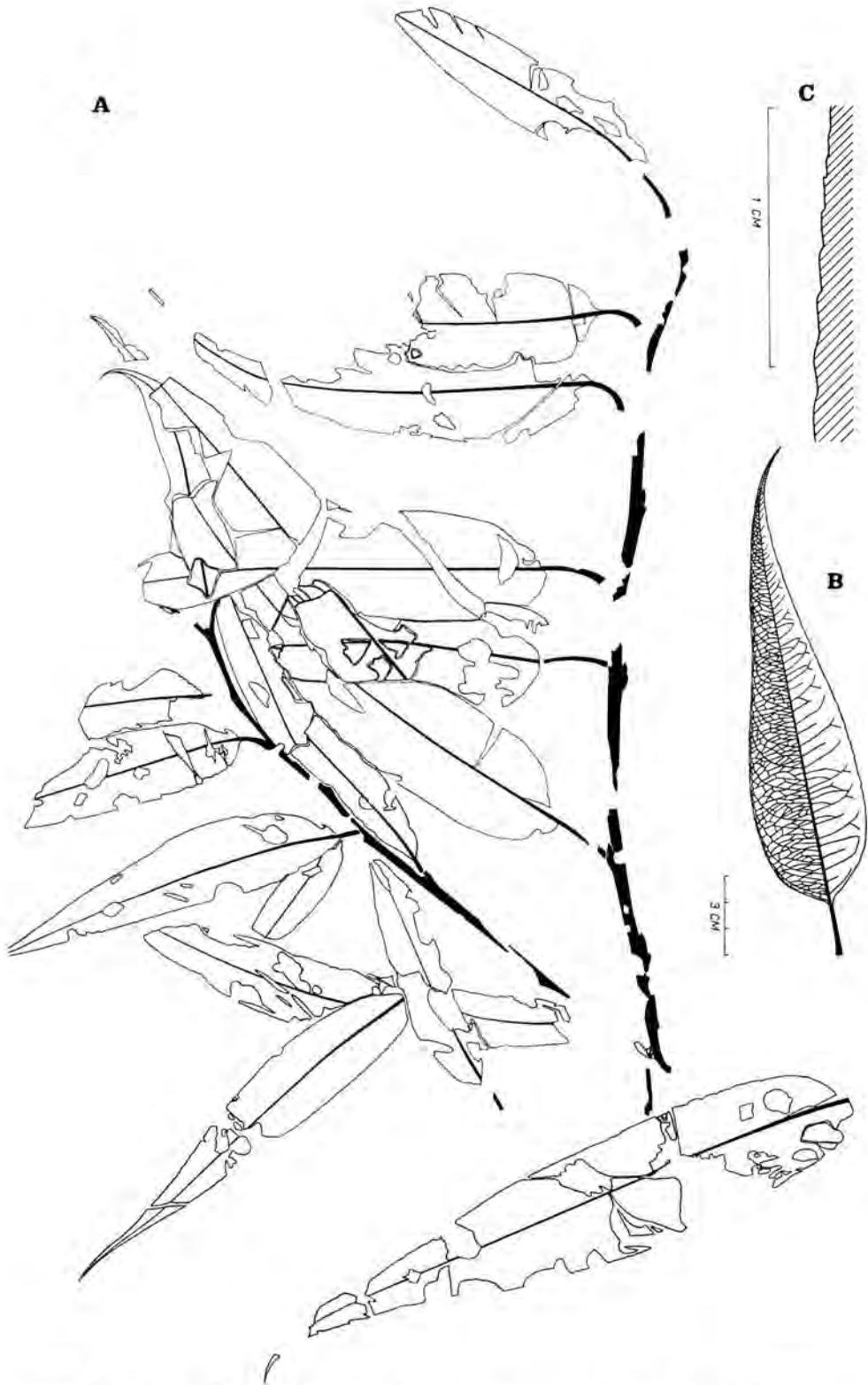


Fig. 16. A-C = XII: A = Utrecht 3931 A, branch with leaves. Note the presence of buds. B = leaf (reconstructed) showing venation; C = Utrecht 3931 A, detail showing leaf margin.

Lamina ovate or elliptical, 11.6–23.5 cm long, 2.40–4.65 cm wide, the length/breadth ratio being 4.9 : 1–8.5 : 1. Leaf apex long acute, leaf base rounded.

Leaf margin non-entire, crenulate with rounded teeth up to 0.2 mm across, c.45–c.115 per side, alternating with angular or rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein straight or curved, markedly tapering along length, 0.3–0.7 mm wide at mid-point between base and apex of lamina. Midvein bearing (14–) 21–30 secondary veins per side, the number being more or less connected with the length of lamina, the most proximal vein arising at 40°–70°, arising in the remaining part of the basal third of the lamina at (40°–) 60°–80°, in the median third at 60°–90°, in the apical third at c.60°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the veins somewhat irregular, showing no obvious trend (fig. 15). Secondary veins mostly alternately arranged, although sometimes opposite or sub-opposite, hardly to somewhat tapering along their length, 0.05–0.20 mm wide at mid-point, interconnected distally by fine extensions of secondary veins. Intermediate veins (0–) 2–8 per intercostal field, some having a somewhat twisted course, arising from the midvein at (35°–) 70°–110°, running more or less parallel to one another or converging/diverging, the spacing between them more or less constant or increasing distally. The veins similar in width, extending from 0 to 1/2–7/8 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mostly distally. Tertiary veins 4–14 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. The nature of areoles and free vein-endings unknown.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of c.440 (?) more or less polygonal cells, the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall 0.35–1.50 microns thick, largely unpitted, straight. Cuticle over veins finely striate, cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–7 : 1. Finer veins reflected in cuticle. Stomata 8.0–30.6 microns long and 8.1–18.0 microns broad, breadth 35–125% length, 45–50 per 0.1 mm²; stomatal index uncertain. Stomata variously orientated, undepressed, equidistant, with well-developed epidermal wall except in polar areas, apices non-retuse. Stomatal slit c.90% stomatal length. Accessory cells 2–4, symmetrical with 0–2 polar and 2 lateral cells, more or less similar in size to the rest of the epidermal cells. Internal resinous bodies absent.

Specimens examined : Bot. Mus. & Herb. Utrecht, Div. of Palaeobot. : 3857, 3858, 3931A.

Discussion :

Various taxa belonging to the Araliaceae, Magnoliaceae, Rutaceae and Salicaceae have leaves resembling the fossil in form and venation. Of

these taxa *Schefflera hypoleuca* Harms (Araliaceae) and *Alcimandra cathcartii* (Hook.f. et Thoms.) Dandy (Magnoliaceae) differ from the fossil on the basis of the epidermis and the entire margin to the lamina. Leaves of *Zanthoxylum* (Rutaceae) and *Salix* (Salicaceae) may, however, resemble each other fairly closely. The epidermides of certain species of *Zanthoxylum* are characterized by the presence of glands but these are not always present. In the fossil the epidermal wall of the guard cells is somewhat thickened with the exception of the polar areas. This feature is not found in *Zanthoxylum*, while constant for all the *Salix* species investigated. Moreover, while *Salix* species are known to have stomata ranging in size from 5 to more than 40 microns in length, the *Zanthoxylum* species investigated had stomata which were never smaller than 14.5 microns in length. The presence in the fossil of stomata only 8 microns long would tend to suggest that one is dealing with *Salix*. The number of *Salix* species known to have leaves of the order of size of the fossil is limited. The ratio of the length of the petiole to the length of the lamina reduces the number of possibilities somewhat, but specific determination would not appear to be possible.

While it is true that only size differences can be made use of as key characters in the separation of this taxon from that described immediately prior to the present taxon, such characters are sometimes used in separating living species of *Salix* from one another. However it would be wrong to regard this key character as being the only difference between these two taxa. The present taxon would appear to differ in that the leaves are more frequently ovate, have a lamina tapering to a finer apex and possibly differing in having stomata in equal numbers on both surfaces of the lamina. These features tend to give the leaf-remains at present under consideration a different aspect.

Herbarium material examined in detail:

<i>Alcimandra cathcartii</i> (Hook. f. et Thoms.) Dandy	Coll. J. D. Hooker	(E) det. J. Dandy
<i>Salix amphibia</i> Small	Coll. J. K. Small & J. J. Carter 1-1909	(U) _____
<i>Salix areostachya</i> C. Schneider	Coll. A. Henry 9338	(E) det. C. Schneider TYPE
<i>Salix babylonica</i> L.	Coll. E. E. Maire 2089	(E) det. Handel-Mazzetti
<i>Salix chienii</i> Cheng	Coll. C. S. Fan & Y. Y. Li 116	(E) _____
<i>Salix dietyoneura</i> von Seemen	Coll. R. C. Ching 2756	(E) det. Handel-Mazzetti
<i>Salix dunnii</i> C. Schneider	Coll. H. H. Chung 18-4-1925	(E) _____
<i>Salix elegans</i> Wall.	Coll. J. F. Duthie 22-5-1893	(E) _____
<i>Salix longipes</i> Shuttleworth	Coll. R. F. Martin 26-5-1939	(U) _____

<i>Salix marginata</i> Wimm.	Coll. P. F. van Heerdt 184	(U)	_____
<i>Salix nigra</i> Marsh	Coll. F. R. Rickson 206	(U)	det. F. R. Rickson
<i>Salix rosthornii</i> von Seemen	Coll. Handel-Mazzetti 11597	(E)	det. Handel-Mazzetti
<i>Schefflera hypoleuca</i> Harms	Coll. G. Forrest 29370	(E)	det. S. C. Sun
<i>Zanthoxylum ailanthoides</i> Sieb. et Zucc.	Coll. U. Faurie 467	(E)	det. L. A. Lauener
<i>Zanthoxylum avicennae</i> DC.	Coll. Y. Tsiang 1645	(E)	det. C. C. Huang
<i>Zanthoxylum bungeanum</i> Maxim.	Coll. W. P. Fang 2183	(E)	det. C. C. Huang
<i>Zanthoxylum cuspidatum</i> Champ.	Coll. W. Y. Chun 5952	(E)	det. C. C. Huang
<i>Zanthoxylum esquirolii</i> Lévl.	Coll. W. P. Fang 2037	(E)	det. C. C. Huang
<i>Zanthoxylum planispinum</i> Sieb. et Zucc.	Coll. G. Forrest 7535	(E)	det. C. C. Huang
<i>Zanthoxylum rhesoides</i> Drabe	Coll. J. Cavalerie 1771	(E)	det. C. C. Huang
<i>Zanthoxylum simulans</i> Hance	Coll. R. C. Ching 2725	(E)	det. C. C. Huang

FAMILY FAGACEAE

WEYLAND (1934) considered that six species in the Kreuzau deposit belonged to the Fagaceae. Five of these species were referred to the genus *Quercus* and one to *Castanea*. The large number of *Quercus* species immediately arouses suspicion as to the accuracy of the determinations. The material described as *Quercus platania* Heer was later transferred to *Alnus palaeojaponica* Weyland (WEYLAND, 1943). In the present account this material is included in No. LVIII. Furthermore, the leaf-remains determined as *Quercus neriifolia* A. Braun and *Q. pseudocastanea* Goepfert are now to be attributed to the Myricaceae. The affinity of the material referred to as *Quercus drymeia* Unger is somewhat uncertain. On the other hand, it would appear to be justified to refer the specimens described as *Castanea atavia* Unger and *Quercus furcinervis* (Rossmässler) Heer to the Fagaceae. This material has been united into a single taxon. In addition another taxon has been recognized on the basis of a specimen present in the Utrecht collection.

XIII

Description:

Petiole unknown.

Lamina oblong, c. 9 cm long, 3.0 cm wide, the length/breadth ratio being c. 3:1. Leaf apex acute, leaf base unknown.

Leaf margin non-entire, \pm denticulate, with stump-like teeth 0.4–1.3 mm across, (0–) 1 per secondary vein and 0 per intercostal field, equivalent to c. 10 per side, alternating with rounded sinuses. Teeth of one size group.

Venation craspedodromous, midvein more or less straight, only tapering at very apex of the leaf, 0.5 mm wide at mid-point between base and apex

of the lamina. Midvein bearing 12–13 secondary veins per side, the angle at which the most proximal vein arises unknown, arising in the remaining part of the basal third of the lamina at 55° – 65° , in the median third at 50° – 55° , in the apical third at 50° – 60° (-90°). The angle at which the veins arise constant or increasing within the first few mms. The spacing of the veins slightly greater in the middle of the lamina or more or less constant throughout. Secondary veins opposite or sub-opposite in the proximal half of the lamina, sub-opposite or alternate in the distal half, hardly tapering along their length, 0.1–0.2 mm wide at mid-point, interconnected distally by tertiary veins or vein network. The nature of the intermediate veins unknown. Tertiary veins 7–9 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. The nature of the areoles and free vein-endings unknown.

Cuticle poorly preserved. Finer veins somewhat reflected in cuticle. Cells at leaf margin elongate, arranged in c.8 rows.

Specimen examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3856.

Discussion:

This specimen, although closely resembling the following taxon, would appear to differ in a number of points, of which the most obvious are the size of the lamina and the presence of small stump-like teeth.

Leaves resembling the fossil are to be found in living species of *Castanea* and *Fagus*. Various characters were made use of in an attempt to distinguish between these two genera on the basis of their leaves. With the exception of certain somewhat anomalous pinnatifid forms, the *Fagus* species investigated by the present author did not have a leaf lamina with a length/breadth ratio exceeding 2.7 : 1. In *Castanea*, on the other hand, the lamina not infrequently exceeds a ratio of 3 : 1 and in this respect more closely resembles the fossil. Furthermore, the oblong leaf form as such is not met with in *Fagus*, although present in certain species of *Castanea*. However, the leaves of *Castanea* would appear to differ from the fossil in a number of respects. In the first place, the leaf margin is either markedly dentate or provided with bristle-like, but not stump-like teeth. Secondly, the secondary veins are almost without exception markedly arched near the apex of the lamina. In these respects the fossil resembles the leaves of *Fagus* more closely. In this genus the presence of stump-like teeth is not uncommon and the course followed by the secondary veins seems to be little affected by the narrowing of the lamina towards the apex. Furthermore, *Castanea* leaves tend to be coarser in texture and show a more strongly developed vein reticulum than those of *Fagus*. The fact that the finer venation was poorly developed in the fossil may be significant in this connection. However, for reasons given above, it is not possible to refer the fossil with certainty to *Fagus*. In the absence of further information it seems reasonable to resist an allocation of the fossil to either *Castanea* or *Fagus*.

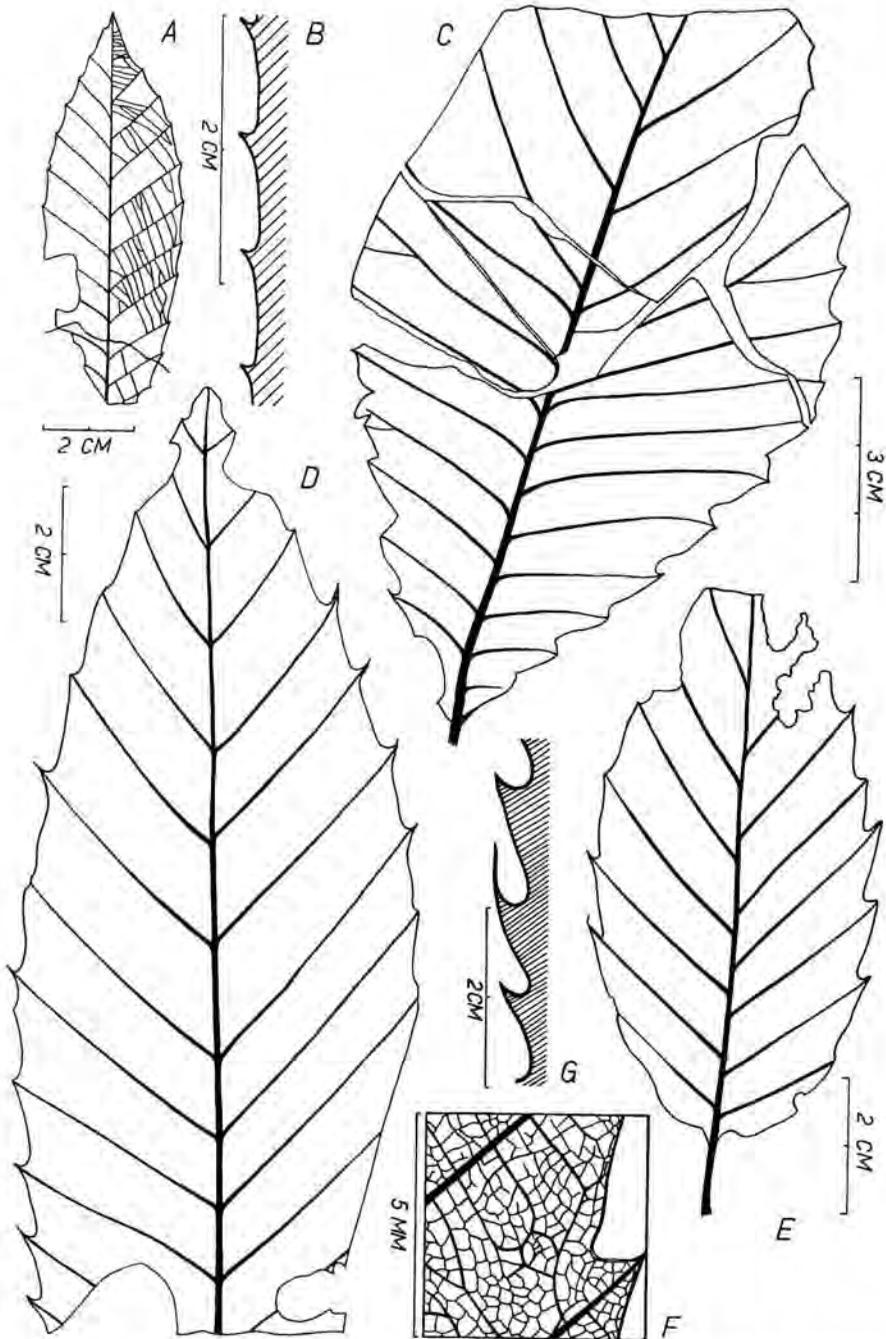


Fig. 17. A-B = XIII: A = Utrecht 3856; B = Utrecht 3856, detail showing leaf margin. C-G = XIV: C = Utrecht 3219; D = Utrecht 3215; E = Utrecht 3804; F = detail showing venation; G = detail showing leaf margin.

Herbarium material examined in detail:

<i>Castanea crenata</i> Sieb. et Zucc.	Coll. E. P. St. John, R. P. St. John & J. K. Small 2-12-1936	(U) _____
<i>Castanea dentata</i> (Marshall) Borkh.	Coll. J. R. Bozeman, N. L. Pence & B. L. King 7948	(U) _____
	Coll. F. R. Rickson 216	(U) det. F. R. Rickson
	Coll. J. G. ten Houten & A. Schoenmakers 129	(U) det. K. Willemssen
<i>Castanea henryi</i> Rehd. et Wils.	Coll. C. Y. Chiao 14227	(E) det. E. D. Merrill
<i>Castanea mollissima</i> Blume	Coll. J. Ewan 24-5-1961	(U) _____
	Coll. W. P. Fang 22-8-1928	(E) _____
<i>Castanea ozarkensis</i> Ashe	Coll. D. M. Moore 1-6-1954	(U) _____
<i>Castanea pumila</i> (L.) Mill.	Coll. H. E. Ahles & R. S. Leisner 14869	(U) det. H. R. Trotten
	Coll. L. Melvin 18-6-1953	(U) _____
	Coll. J. R. Bozeman & J. F. Logue 11356	(U) _____
	Coll. E. A. Bartholomew 13-6-1952	(U) _____
<i>Castanea sativa</i> Mill.	Coll. W. J. J. Colaris 1610	(U) det. W. J. J. Colaris
	Coll. J. J. Swart 15-7-1943	(U) det. J. J. Swart
<i>Castanea seguinii</i> Dode	Coll. H. C. Cheo 44	(E) _____
<i>Castanea vesca</i> Gaertn.	Coll. M. Buysman 348	(U) _____
	Coll. Stud. biol. Rheno-Trai in itinere 13-7-1922	(U) det. J. P. Karthuis
<i>Fagus crenata</i> Blume	Coll. M. Hotta 24758	(U) _____
	Coll. M. Hotta & N. Fukuoka 243	(U) _____
<i>Fagus grandifolia</i> Ehrh.	Coll. D. Demaree 48209	(U) _____
	Coll. J. H. Soper 2053	(U) _____
	Coll. D. M. Moore 480426	(U) _____
	Coll. A. E. Radford 37274	(U) det. H. R. Trotten
	Coll. E. A. Bartholomew 29-9-1952	(U) _____
<i>Fagus japonica</i> Maxim.	Coll. G. Murata 7038	(U) _____
	Coll. M. Tagawa 573	(U) _____
	Coll. M. Tagawa 574	(U) _____
	Coll. M. Tagawa 1652	(U) _____
<i>Fagus orientalis</i> Lipsky	Coll. M. J. A. de Koster, I. J. van de Wall Repelaer, H. W. E. Croockewit & H. P. Maas Geesteranus 10-5-1951	(U) det. H. P. Maas Geesteranus
<i>Fagus sinensis</i> Oliv.	Coll. Handel-Mazzetti 11112	(E) det. A. Rehder

XIV

Synonyms: *Castanea atavia* Unger

Quercus furcinervis (Rossmässler) Heer

WEYLAND, 1934, p. 54!

WEYLAND, 1934, p. 58.

Description:

Petiole 10–29 mm long and 1.0–1.6 mm wide at mid-point, more or less parallel-sided for the greater part of its length but increasing in width at very base, straight or slightly curved, making no angle with the midvein.

Lamina ovate, elliptical or obovate, 8.9–21.5 cm long, 3.8–9.0 cm wide, the length/breadth ratio being 2 : 1–3 : 1 (fig. 15). Leaf apex acute, leaf base obtuse or rounded.

Leaf margin non-entire, dentate, with teeth 1–7 mm across, 1 per secondary vein and 0 per secondary vein interval, alternating with rounded sinuses. Teeth of one size group.

Venation craspedodromous, midvein straight or curved, markedly tapering along length, 0.4–1.5 mm wide at mid-point between base and apex of lamina. Midvein bearing 8–17 secondary veins per side, the most proximal vein arising at 40°–60°, arising in the remaining part of the basal third of the lamina at 35°–60°, in the median third at 40°–60°, in the apical third at 35°–50°. The angle at which the veins arise mostly constant, but occasionally slightly increasing or decreasing, within the first few mms. The spacing of the veins either initially increasing and thereafter more or less constant or increasing somewhat irregularly up to a maximum mid-way or more commonly apically (fig. 15). The length of the veins reaching a maximum proximally or mid-way (fig. 15). Secondary veins opposite or alternately arranged, hardly tapering along their length, (0.1–) 0.2–0.3 (–0.4) mm wide at mid-point, occasionally dichotomising at more than 2/3 the distance from the midvein to the leaf margin, the veins interconnected distally by tertiary veins. Intermediate veins 4–8 per intercostal field, arising from the midvein at 60°–130°, running more or less parallel to one another, the spacing between them constant. The veins similar in width, extending from 0 to 3/4 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary veins 3–10 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 18–30 per 10 mm² with some unbranched free vein-endings.

Epidermis in non-stomatal condition composed of 120–750 cells per 0.1 mm², the number varying considerably within a single leaf, the cell length/cell breadth ratio being 1 : 1–4 : 1. Cell wall 0.6–2.0 microns thick, largely unpitted, straight or very occasionally undulate, the depth from the tips of the lobes to the bottoms of the sinuses up to 6 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–8 : 1. Hair bases with traces of the attachment of 6–9 hairs radiating from the point of attachment present, 0–14 per 0.1 mm². Epidermis in stomatal condition composed of 520–1020 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–7 : 1. Cell wall 0.3–2.0 microns thick, unpitted or somewhat pitted, straight or rarely undulate, 0–7 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 3.5 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–7 : 1. Stomata

16.2–25.2 microns long and 14.4–19.8 microns broad, breadth 64–100 % length, (4–) 20–50 per 0.1 mm²; stomatal index (1–) 4–10 %. Stomata variously orientated, undepressed, somewhat arranged in groups, apices rarely slightly retuse. Stomatal slit 38.5–70 % stomatal length. Accessory cells absent or poorly differentiated, cells in immediate proximity to the stomata 4–7 in number, similar in size to the rest of the epidermal cells. Hair bases with traces of the attachment of 6–14 hairs radiating from the point of attachment present, 0–25 per 0.1 mm².

Specimens examined: 59, among which the numbered specimens:

Geol. Inst. Cologne: Coll. H. Weyland 1411(K 41), 1412(K 41)
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3210, 3211,
 3212, 3213, 3214, 3215, 3217, 3218, 3219, 3220, 3221, 3222,
 3223, 3224, 3803, 3804.

Discussion:

Though the specimen referred to *Quercus furcinervis* (Rossmässler) Heer (= *Castanopsis furcinervis* (Rossmässler) Kräusel et Weyland) by WEYLAND (1934) was not available for examination, it seems likely that it can be referred to the present taxon. Cuticle analysis (KRÄUSEL and WEYLAND, 1950; JÄHNICHEN, 1956) has proved that other leaves referred to under this name had an epidermis similar, if not identical, to those obtainable from leaves referred to as *Castanea atavia* Unger.

In gross-morphology the leaf-remains resemble the leaves of plants belonging to the Fagaceae (*Castanea* p.p., *Quercus* p.p.), but also those of *Dillenia pentagyna* Roxb. (Dilleniaceae). The leaves of *Dillenia pentagyna* are, however, to be distinguished from the fossil by the lack of trichomes and the presence of large stomata and long stomatal slits (stomatal slits 15–25 microns long), accompanied by finely striate accessory cells. The *Castanea* and *Quercus* species considered were typified by small, oblong, stomata and the small size of the remaining epidermal cells, such as one finds in the fossil as well. These living species are furthermore characterized by the presence of trichomes. In certain *Castanea* species e.g. *Castanea sequinii* Dode, these are in the form of glands but in other species they are in the form of unicellular hairs arranged in stellate fashion. When shed these hairs leave traces as to their former point of attachment on the leaf. Similar traces are to be found in the fossil. An examination of the leaves of certain species of *Castanea* and *Quercus* demonstrated that a choice between these two genera could not be made on the basis of the gross-morphology and the epidermal characters of the leaves.

Herbarium material examined in detail:

<i>Castanea mollissima</i> Blume	Coll. W. P. Fang 22-8-1928	(E) _____
<i>Castanea pumila</i> (L.) Mill.	Coll. H. E. Ahles & R. S. Leisner 14869	(U) det. H. R. Trotten
<i>Castanea sequinii</i> Dode	Coll. H. C. Cheo 44	(E) _____

<i>Dillenia pentagyna</i> Roxb.	Coll. C. Ritchie	(E) det. R. D. Hoogland
<i>Quercus acutissima</i> Carruthers	Coll. S. K. Lau 93	(E) det. E. D. Merrill
<i>Quercus oxyodon</i> Miq.	Coll. G. Forrest 19776	(E) det. Handel-Mazzetti
<i>Quercus variabilis</i> Blume	Coll. W. R. Carles 9-7-1882	(E) —————

FAMILY ULMACEAE

In his account of the Kreuzau assemblage WEYLAND (1934) attributed 4 taxa to the Ulmaceae. He described three species of *Ulmus* and one species of *Zelkova*. Two of the three species of *Ulmus* have been retained within this genus, while the material described by WEYLAND (1934, p. 61) as *Ulmus longifolia* (No. LXVII) is here considered to be of uncertain affinity. Other material resembling the leaves of *Zelkova* have been retained within this genus, although this opinion may have to be revised at some future date.

SUBFAMILY ULMOIDEAE

XV. *Ulmus*

Synonym: *Ulmus carpinoides* Goepfert WEYLAND, 1934, p. 61!

Description:

Petiole 6.5–15 mm long and 0.25–2.60 mm wide at mid-point, parallel-sided or gradually increasing in width from leaf base to base of petiole, straight, sometimes making somewhat of an angle with the midvein.

Lamina ovate or elliptical, 2.1–8.3 cm long, 1.0–3.4 cm wide, the length/breadth ratio being 1.75:1–2.75:1 (fig. 18), sometimes asymmetrical about midvein. Leaf apex acute, leaf base rounded to angular obtuse or very slightly cordate, sometimes oblique.

Leaf margin non-entire, serrate, bearing acute to somewhat rounded teeth 0.2–2.5 mm across, c.15–c.35 per side, alternating with acute, angular or rarely rounded sinuses. Teeth fall into two size groups, the larger being served by secondary veins and the smaller ones (0–3 per intercostal field) by branches of the secondary veins.

Venation craspedodromous, midvein straight or curved, hardly or markedly tapering along length, 0.15–0.60 mm wide at mid-point between base and apex of lamina. Midvein bearing c.8–c.17 secondary veins per side, the most proximal vein arising at 55°–110°, arising in the remaining part of the basal third of the lamina at 45°–70°, in the median third at 30°–70°, in the apical third at 30°–70°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the veins somewhat irregular, reaching a maximum mid-way or apically (fig. 18). The length of the veins reaching a maximum roughly mid-way (fig. 18). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.08–0.30 mm wide at mid-point, sometimes dichotomising at 1/4–3/4 the distance from the midvein to the leaf margin, the

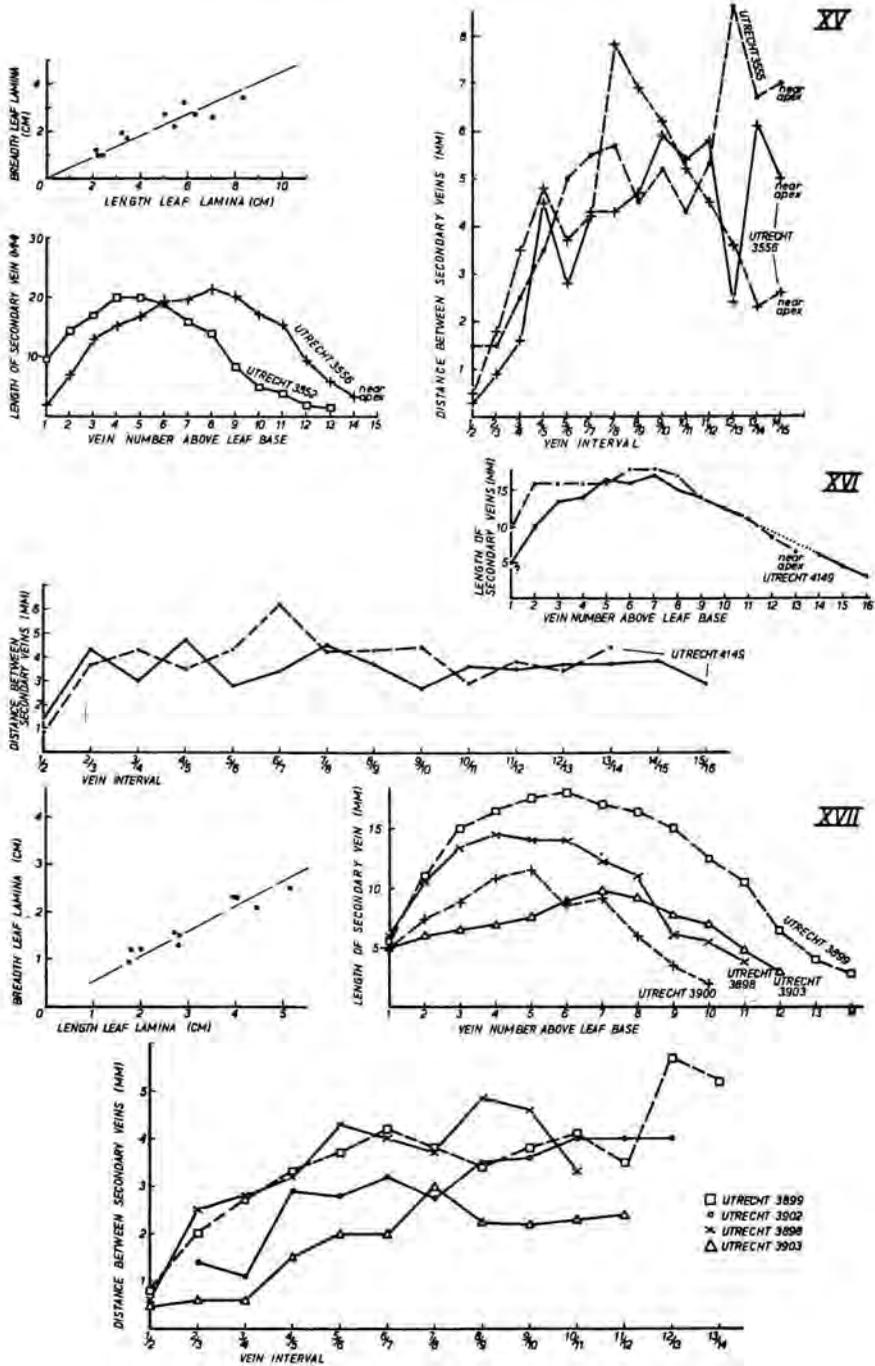


Fig. 18. Graphs XV, XVI, XVII.

veins interconnected distally by tertiary veins or vein network. Intermediate veins 1–6 per intercostal field, occasionally having a somewhat twisted course, arising from midvein at 45° – 120° , running more or less parallel to one another or converging/diverging, the spacing between them more or less constant or increasing distally. The veins similar in width or rarely increasing in width with increase in length, extending from 0 to $1/5$ – $1/4$ ($-1/2$) the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field midway or distally. Tertiary veins 4–18 per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 40–95 per 10 mm^2 with some to many free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of c.300 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–3.3 : 1. Cell wall 0.35–0.70 microns thick, largely unpitted, undulating with (0–) 1–8 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 14.4 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–5 : 1, cell wall straight, no thicker than that of the rest of the epidermal cells. Finer veins reflected in cuticle. Epidermis in stomatal condition composed of c.470 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–2.6 : 1. Cell wall 0.4–1.0 microns thick, largely unpitted or finely pitted, somewhat undulate with (0–) 1–6 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells over veins elongate, the cell length/cell breadth ratio being up to 8.6 : 1, cell wall straight, no thicker than that of the rest of the epidermal cells. Finer veins reflected in cuticle. Stomata 18.0–23.4 microns long and 9.9–25.2 microns broad, breadth 50–110 % length, c.39 per 0.1 mm^2 ; stomatal index c.8 %. Stomata variously orientated, undepressed, slightly arranged in groups, apices non-retuse. Stomatal slit 46–64 % stomatal length. Accessory cells 4–5, symmetrical with 2 polar and 2–3 lateral cells, similar in size to the rest of the epidermal cells. Internal resinous bodies absent.

Specimens examined : 17, among which the numbered specimens:
Geol. Inst. Cologne: Coll. H. Weyland 1388 (K48)
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3551, 3552,
3553, 3554, 3555, 3556, 3620C, 3907, 3908, 3909, 3910A,
3910B, 4147.

Discussion :

In the closely set dichotomising secondary veins, the biserrate leaf margin and the sometimes oblique leaf base, the fossil showed the greatest resemblance to the leaves of certain *Ulmus* species. Size and shape of lamina, the nature of the leaf apex and leaf base, the spacing of the secondary veins and the amount of pubescence are characters showing a certain amount of variation within *Ulmus*. Some species e.g. *Ulmus americana*

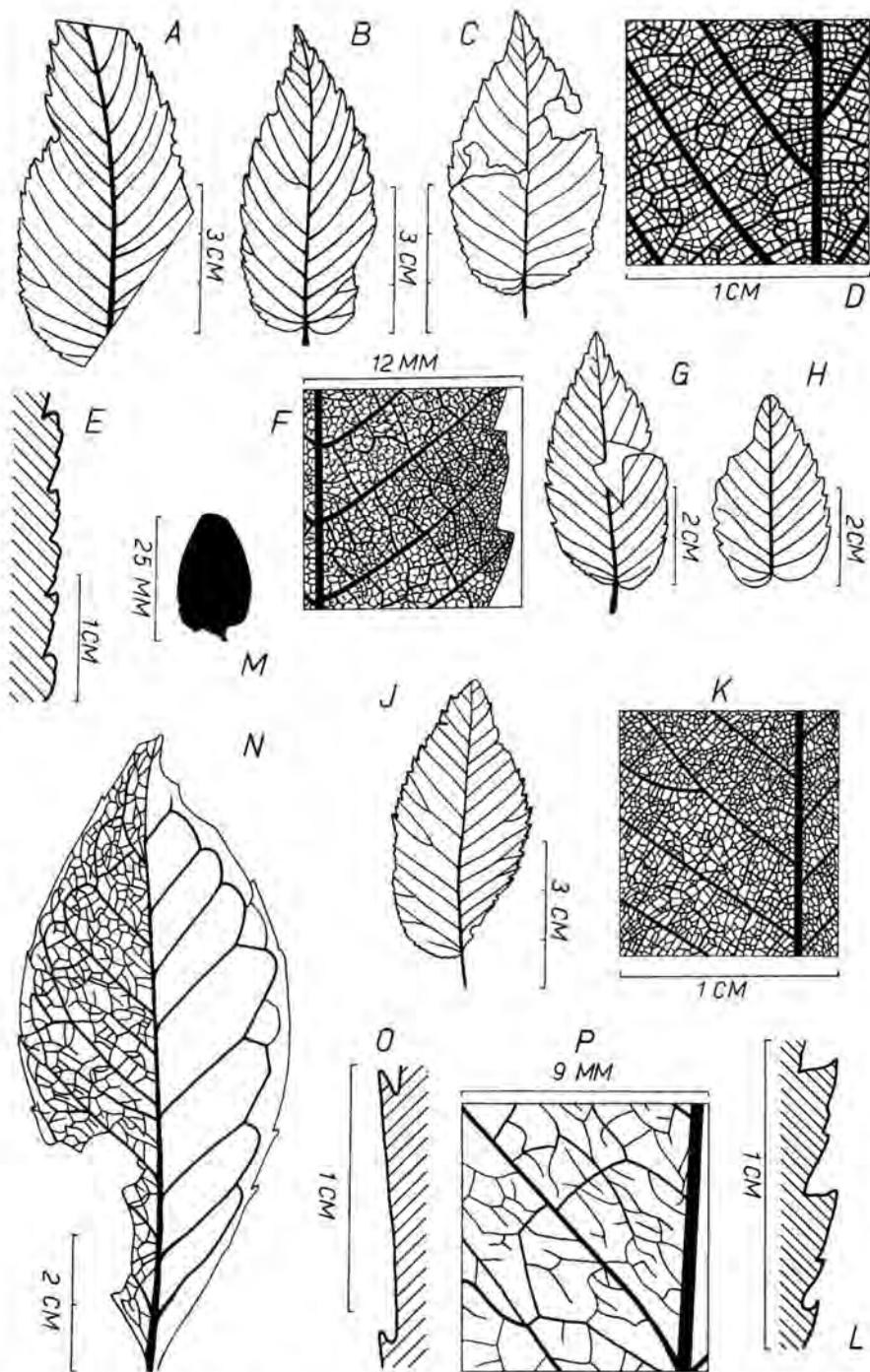


Fig. 19. A-E = XV: A = Utrecht 3555; B = Utrecht 3556; C = Utrecht 3552; D = detail showing venation; E = detail showing leaf margin. F-H = XVII: F = detail showing venation; G = Utrecht 3899; H = Utrecht 3898. J-L = XVI: J = Utrecht 4149; K = Utrecht 4149, detail showing venation; L = Utrecht 4149, detail showing leaf margin. M = XVIII: Cologne, Coll. H. Weyland 1698. N-P = XIX: N = Berlin 283 (Type of *Kadsura breddinii* Weyland); O = Berlin 283, detail showing leaf margin; P = Berlin 283, detail showing venation. Note large areoles with many free vein-endings.

L. have a markedly asymmetrical leaf base, while other species may have a symmetrical or only slightly asymmetrical leaf base. The fossil falls into this latter group. A comparison was made with the leaves of *Ulmus bergmanniana* C. Schneider, *U. davidiana* Planch. (= *U. japonica* Sargent non Sieb.), *U. glabra* Huds. (= *U. scabra* Mill.), *U. glaucescens* Franch., *U. parvifolia* Jacq., *U. pumila* L., *U. racemosa* Thomas (= *U. thomasi* Sargent) and *U. wilsoniana* C. Schneider. Although certain differences in venation etc. were noticed between these species, the material proved to be too limited for a decision as to the constancy of the differences. Since it is by no means certain whether species can be recognized on the basis of the leaves alone, a reference of the fossil to a specific entity was considered somewhat premature.

Herbarium material examined in detail:

<i>Ulmus bergmanniana</i> C. Schneider	Coll. E. H. Wilson 2805	(E) det. C. Schneider
<i>Ulmus davidiana</i> Planch.	Coll. W. Purdom 262	(E) det. C. Schneider
	Coll. T. Makino 8-1929 (Makino Herb. 19601)	(E) det. K. Hiyama
	Coll. T. Makino 9-1935 (Makino Herb. 19580)	(E) det. K. Hiyama
	Coll. T. Makino 25-4-1937 (Makino Herb. 19589)	(E) det. K. Hiyama
<i>Ulmus glabra</i> Huds.	Cultivated	(U) det. E. A. Mennega
<i>Ulmus glaucescens</i> Franch.	Coll. R. C. Ching 140	(E) _____
<i>Ulmus japonica</i> Sargent	Coll. W. Purdom 983	(E) _____
	Coll. H. Takeda 3-10-1908	(E) _____
	Coll. H. Takeda 17-10-1908	(E) _____
<i>Ulmus parvifolia</i> Jacq.	Coll. C. Y. Chiao 2772	(E) det. A. Rehder
	Coll. M. Azuma 26-4-1955	(U) det. M. Azuma
	Coll. M. Hotta 16791	(U) _____
<i>Ulmus pumila</i> L.	Coll. W. Purdom 96	(E) _____
	Coll. W. Purdom 357	(E) _____
	Coll. C. Y. Chiao 3150	(E) det. A. Rehder
	Coll. J. F. Rock 13324	(E) _____
<i>Ulmus scabra</i> Mill.	Coll. A. Palmgren 28-6-1912	(U) _____
<i>Ulmus thomasi</i> Sargent	Coll. C. R. Janssen 8	(U) det. C. R. Janssen
<i>Ulmus wilsoniana</i> C. Schneider	Coll. G. Forrest 21139	(E) det. Handel-Mazzetti
	Coll. C. Schneider 1113	(E) det. C. Schneider
	Coll. E. H. Wilson 2803	(E) det. C. Schneider

XVI. *Ulmus*

Synonym: *Ulmus braunii* Heer

WEYLAND, 1934, p. 61, Tafel 7,
fig. 3.

Description:

Petiole > 7 mm long and 0.8 mm wide, parallel-sided, straight, making no angle with the midvein.

Lamina elliptical, c.6 cm long (Weyland: 6.5–9.0 cm), 2.8 cm wide (Weyland: 3.0–3.5 cm), asymmetrical about midvein. Leaf apex acute or acuminate, leaf base asymmetrical, on one side acute and on the other side slightly cordate.

Leaf margin non-entire, serrate, bearing acute teeth 0.2–1.3 mm across, c.35–c.40 per side, alternating with acute sinuses. Teeth fall into two size groups, the larger being served by secondary veins and the smaller ones ((0–) 1 (–2) per intercostal field) by branches of the secondary veins.

Venation craspedodromous, midvein slightly curved, markedly tapering along length, 0.4 mm wide at mid-point between base and apex of lamina. Midvein bearing 12–15 secondary veins per side, the most proximal vein arising at 40°–70°, arising in the remaining part of the basal third of the lamina at 40°–50°, in the median third at 45°–50°, in the apical third at 45°–60°. The angle at which the veins arise mostly constant (occasionally increasing or decreasing) within the first few mms. The spacing of the veins somewhat irregular without any noticeable trend (fig. 18). The length of the veins reaching a maximum roughly mid-way (fig. 18). Secondary veins mostly alternately arranged, occasionally opposite, hardly tapering along their length, 0.07–0.15 mm wide at mid-point, sometimes dichotomising at 1/2–3/4 the distance from the midvein to the leaf margin, the veins interconnected distally by tertiary veins or vein network. Intermediate veins 0–5 per intercostal field, arising from midvein at 60°–120°, running more or less parallel to one another or converging/diverging, the spacing between them more or less constant or increasing distally. The veins similar in width, extending from 0 to 1/4–1/3 (–4/5) the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary veins 7–13 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 70–110 per 10 mm² with some free vein-endings, these being unbranched and branched.

Cuticle unknown.

Specimen examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 4149.

Discussion:

Although material referred to *Ulmus braunii* Heer by WEYLAND (1934) was not available to the present author, Weyland's Tafel 7, fig. 3 showed such a close resemblance to the present material as to suggest identity of the remains. Both leaf-remains were characterized by a markedly asymmetrical leaf base and secondary veins spaced at irregular intervals. The markedly asymmetrical leaf base, in combination with characters such as the dichotomy of some of the secondary veins and the nature of the leaf margin would suggest that the fossil should be referred to the genus *Ulmus*. Leaves with a markedly asymmetrical leaf base are characteristic of a number of *Ulmus* species. A comparison of the fossil with leaves of *Ulmus*

americana L. and *U. carpinifolia* Gled. (= *U. campestris* L. p.p.) was sufficient to indicate that specific determination was, however, impossible.

Herbarium material examined in detail:

<i>Ulmus americana</i> L.	Coll. K. K. Mackenzie	(E)	_____
	1173		
	Coll. A. Ruth 1225	(E)	_____
	Coll. L. Jenkins 5493	(U)	_____
	Coll. H. Rhodes & K. Mills 1616	(U)	det. H. Rhodes
<i>Ulmus campestris</i> L.	Coll. J. H. Soper & R. P. Burcher 2064	(U)	_____
	Coll. L. S. Rodrigues Lopes 40	(U)	det. L. S. Rodrigues Lopes
	Coll. M. Buysman 423	(U)	_____
	Coll. Stud. biol. Rheno-Trai. in itinere 63-3747	(U)	det. F. van Dommelen
<i>Ulmus carpinifolia</i> Gled.	Coll. Stud. biol. Rheno-Trai. in itinere 63-3614	(U)	det. J. Frings

SUBFAMILY CELTIDOIDEAE

XVII. *Zelkova*

Synonym: *Zelkova ungeri* Kováts

WEYLAND, 1934, p. 61; GOTHAN and WEYLAND, 1964, p. 415, Abb. 289.

Description:

Petiole 3.0–6.5 mm long and 0.5–0.9 mm wide at mid-point, parallel-sided or gradually increasing in width from leaf base to base of petiole, straight or curved, making a slight angle with the midvein.

Lamina ovate or elliptical, 1.75–5.25 cm long, 0.95–2.50 cm wide, the length/breadth ratio being 1.7 : 1–2.1 : 1 (fig. 18). Leaf apex generally acute, although the leaf margins sometimes meeting at a right angle, leaf base rounded or slightly cordate, sometimes asymmetrical.

Leaf margin non-entire, serrate, bearing acute or somewhat rounded teeth 0.4–1.5 mm across, alternating with acute or somewhat rounded sinuses. Teeth of one size group.

Venation craspedodromous, midvein straight or curved, hardly or markedly tapering along length, 0.1–0.4 mm wide at mid-point between base and apex of lamina. Midvein bearing 8–15 secondary veins per side, the most proximal vein arising at 60°–110°, arising in the remaining part of the basal third of the lamina at 45°–75°, in the median third at 35°–65°, in the apical third at 35°–55°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the veins more or less regular, reaching a maximum (mid-way –) apically (fig. 18). The length of the veins reaching a maximum roughly mid-way (fig. 18). Secondary veins opposite or alternately arranged, the most proximal veins

frequently opposite, the more distal veins generally alternately arranged, hardly tapering along their length, 0.05–0.20 mm wide at mid-point, interconnected distally by tertiary veins or vein network. Intermediate veins 0–5 per intercostal field, not infrequently having a somewhat twisted course, arising from the midvein at 45°–120°, running more or less parallel to one another or converging/diverging, the spacing between them being more or less constant, increasing distally or irregular. The veins similar in width, extending from 0 to 1/4–1/3 (– 1/2) the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way, distally or remaining roughly the same length throughout. Tertiary veins 9–20 per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 35–70 per 10 mm², with few to many free vein-endings, these being unbranched and/or branched.

Epidermis unknown.

Specimens examined: 17, among which the numbered specimens:

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3894, 3895,
3896, 3897A, 3898, 3899, 3900, 3901, 3902, 3903, 3904, 3905,
3906, 4151B.

Discussion:

Superficially this fossil resembles the leaves of a number of taxa belonging to the Fagaceae and Ulmaceae.

Lithocarpus cornea (Lour.) Rehder (Fagaceae) sometimes has leaves similar to the leaf-remains. This recent species, however, has a leaf base which is attenuate to obtuse. While *Quercus schottkyana* Rehd. et Wils. has leaves resembling the fossil, they differ in the presence of an acute or obtuse leaf base. Moreover, the leaves possess tertiary veins which are closely spaced and but little branched.

While certain species of *Ulmus*, e.g., *U. pumila* L. may have a simply serrate leaf margin, members of the genus *Zelkova* have leaves resembling the fossil more closely. It would appear to be possible to refer the leaf-remains to this genus. Within *Zelkova*, species can be differentiated to a certain extent by means of a number of leaf characters. However, not only are shape of lamina, nature of leaf margin and number of secondary veins important for specific determination in *Zelkova*, but characters such as hairiness of the leaves and size, shape and ornamentation of the nutlets as well (CZEREPAŃOV, 1957). Thus in the absence of all the characters necessary for specific determination the affinity of the leaf-remains must remain somewhat uncertain (c.f. TRALAU, 1963).

Herbarium material examined in detail:

<i>Lithocarpus cornea</i> (Lour.)	Coll. S. K. Lau 411	(E) det. E. D. Merrill
Rehder		
<i>Quercus schottkyana</i> Rehd.	Coll. G. Forrest 20616	(E) det. A. Camus
et Wils.		

Ulmus pumila L.	Coll. W. Purdom 96	(E)	_____
	Coll. W. Purdom 357	(E)	_____
	Coll. C. Y. Chiao 3150	(E)	det. A. Rehder
	Coll. J. F. Rock 13324	(E)	_____
Zelkova abelicea (Lam.) Boiss.	Coll. W. Greuter 7712	(E)	_____
Zelkova carpinifolia (Pall.) K. Koch	Coll. A. E. Bobrov & N. N. Tsvelev 740	(E)	_____
	Coll. P. Wendelbo 513	(E)	_____
Zelkova crenata Spach	Coll. A. D. G. Agnew 29	(E)	_____
	Coll. P. H. Davis 45013	(E)	_____
Zelkova serrata (Thunb.) Makino	Coll. C. Y. Chiao 2453	(E)	det. A. Rehder
	Coll. C. Y. Chiao 2514	(E)	_____
	Coll. G. Murata & N. Fukuoka 72	(U)	_____
	Coll. M. Togashi in 1952 (Nat. Sci. Mus. Tokyo 590)	(E)	_____
	Coll. M. Togashi 11-10-1965	(E, U)	_____
	Coll. T. Makino 8-1904 (Makino Herb. 19679)	(E)	det. K. Hiyama
	Coll. T. Makino in 1928 (Makino Herb. 19721)	(E)	det. K. Hiyama
	Coll. T. Makino in 1935 (Makino Herb. 19678)	(E)	det. K. Hiyama
Zelkova sinica C. Schneider	Coll. Y. Tsiang 7190	(E)	det. Handel-Mazzetti
	Coll. E. H. Wilson 2699	(E)	_____
	Coll. W. P. Fang 4405	(E)	_____
	Coll. W. P. Fang 5543	(E)	_____

FAMILY LORANTHACEAE

XVIII.

Description:

Petiole unknown.

Lamina elliptical or obovate, c.3 cm long, 1.45 cm wide. Leaf apex rounded, leaf base unknown.

Leaf margin entire.

Venation not visible.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of 25-35 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1-3:1. Cell wall 0.5-2.0 microns thick, largely unpitted, straight. Stomata 68.4-86.4 microns long, breadth uncertain as boundary between guard cells and accessory cells indistinct, 2-3 per 0.1 mm²; stomatal index 7.7-8.6 %. Stomata variously orientated, undepressed, more or less equidistant, apices occasionally retuse. Stomatal slit 52-70 % stomatal length. Accessory cells 2, symmetrical with 0 polar cells and 2 lateral cells, similar in size to the rest of the epidermal cells but generally distinguished from these in being finely striate.

Specimen examined: Geol. Inst. Cologne: Coll. H. Weyland 1968

Discussion:

Leaves with very large epidermal cells and stomata, such as encountered in the fossil would appear to be characteristic of the Loranthaceae s.l. Taken as a whole the epidermides of the Loranthaceae are fairly uniform, so that use must be made of characters such as leaf form and venation in an attempt to determine the affinity of the fossil more closely. Leaves characterized by the presence of a rounded leaf apex, as in the fossil, were only found in a limited number of taxa available to and examined by the author. Of the North American and Chinese material examined only *Phoradendron eatonii* Trelease, *P. flavescens* (Pursh) Nuttall and *Viscum album* L. had leaves bearing a close resemblance to the fossil. The leaves of *Phoradendron flavescens* are to be distinguished from those of *P. eatonii* and *Viscum album* in the presence of unicellular hairs. In overall appearance the fossil therefore resembles the leaves of *Phoradendron eatonii* and *Viscum album* more closely. However, on the basis of the present material it was not found possible to distinguish between the leaves of these two genera. As pointed out by TRELEASE (1916, p. 8) leaf shape is a somewhat unreliable character, as it may vary in the same species or even on the same branch. In the absence of more comparative material a reference of the fossil to a particular genus within the Loranthaceae would not appear to be justified.

Herbarium material examined in detail:

Phoradendron eatonii	Coll. P. F. van Heerdt	(U) det. H. J.
Trelease	157	Ketellapper
Phoradendron flavescens	Coll. Langenberg 115	(U) det. L. Y. T.
(Pursh) Nuttall		Westra
Viscum album L.	Coll. G. Forrest 25388	(E) det. B. H. Danser

FAMILY SCHISANDRACEAE

XIX. *Kadsura*

Synonym: *Kadsura breddinii* Weyland

WEYLAND, 1934, p. 68, Tafel 11, fig. 2;
 WEYLAND, 1941, Tafel 19, Abb. 2;
 KRÄUSEL and WEYLAND, 1950, pp. 48-50, Abb. 13, Tafel 9, figs. 1-2;
 GOTHAN and WEYLAND, 1964, p. 426, Abb. 297c!

Description:

Petiole > 2.5 mm long and 1.5 mm wide, straight, making no angle with the midvein.

Lamina obovate, 8.7 cm long, 3.6 cm wide, the length/breadth ratio being 2.4:1. Leaf apex acuminate, leaf base acute.

Leaf margin non-entire, serrulate-denticulate, with acute or occasionally rounded teeth 0.15-0.80 mm across, 8-9 per side, alternating with acute, angular or rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein very slightly sinuous, markedly tapering along length, 0.55 mm wide at mid-point between base and apex of the lamina. Midvein bearing 8 secondary veins per side, the most proximal vein arising at 30° , arising in the remaining part of the basal third of the lamina at 40° – 45° , in the median third at 40° – 50° , in the apical third at (20° –) 35° – 50° . The angle at which the veins arise constant or increasing within the first few mms. The spacing of the veins rather irregular and showing no distinct trend (fig. 20). Secondary veins opposite or alternately arranged, slightly tapering along their length, 0.07–0.35 mm wide at mid-point, interconnected distally by fine extensions of secondary veins. Intermediate veins 0–5 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 45° – 120° , converging/diverging from one another, the spacing between them increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to $1/4$ – $2/3$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field midway or distally. Tertiary veins 2–6 (–9) per 1 cm secondary vein, somewhat branched, the lengths on the acroscopic and basiscopical sides of secondary vein more or less similar. Areoles 1–6 per 10 mm^2 , with many free vein-endings, these being sometimes unbranched but more commonly branched.

Epidermis in non-stomatal condition composed of c.390–c.500 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–2 : 1 (–3 : 1). Cell wall 2.0–2.4 microns thick, largely unpitted, somewhat undulating with 0–5 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells over veins arranged in rows, the cell length/cell breadth ratio being 1 : 1–3.5 : 1, the cell walls undulating. Cells at leaf margin composed of 150–300 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 0.4 : 1–3 : 1, arranged in at least 40 rows. Cell wall c.3.5 microns thick, largely unpitted, straight, the transverse walls sometimes slanting but usually occurring at right angles to the lateral walls. Epidermis in stomatal condition composed of 320–340 frequently strongly striate cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–2 : 1 (–3 : 1). Cell wall 0.4–1.5 microns thick, largely unpitted, straight, or slightly undulating with 0–5 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells over veins arranged in rows, secondary cell walls sometimes developed, the cell length/cell breadth ratio being 0.5 : 1–4.3 : 1, cell wall more or less straight or slightly undulate, the transverse walls slanting or at right angles to the lateral walls. Stomata 17.1–44.1 microns long and 11.7–38.7 microns broad (fig. 20), breadth 50–130 % length, 34–37 per 0.1 mm^2 ; stomatal index 10.7–12.5 %. Stomata variously orientated, mostly depressed, more or less equidistant or somewhat arranged in groups, apices non-retuse. Guard cells generally covered by a ring of cutin. Stomatal slit 40–70 % stomatal length. Accessory cells 2–4, symmetrical with 0–2 polar cells and 2 lateral

cells, or radially arranged. Accessory cells similar in size or smaller than the rest of the epidermal cells.

Specimens examined : Deutsche Akad. Wiss. Berlin : 283(K 71)

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 4150

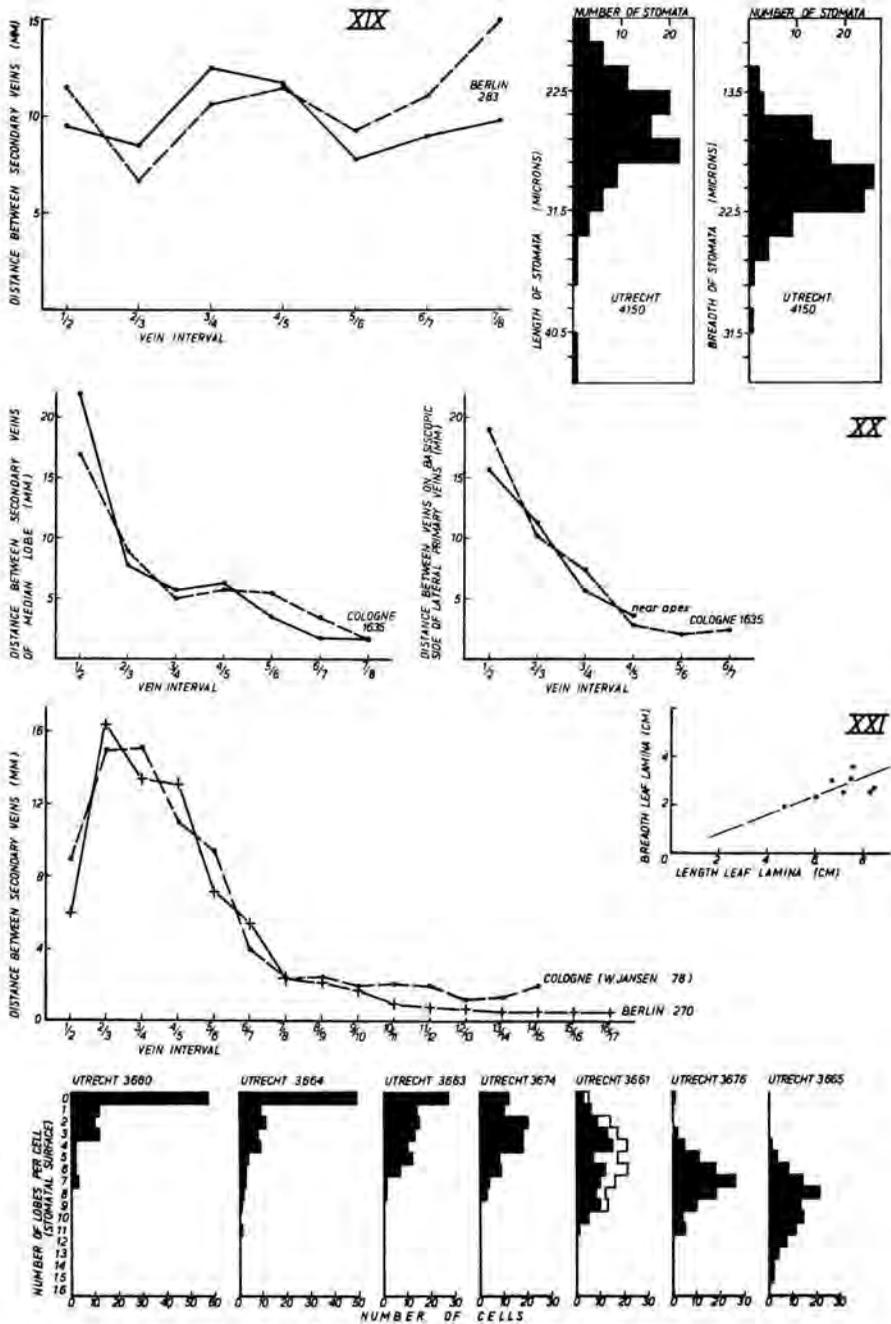


Fig. 20. Graphs and histograms XIX, XX, XXI p.p.

Discussion:

The affinities of this taxon have been discussed by WEYLAND (1934, 1941) and KRÄUSEL and WEYLAND (1950). These authors pointed out that the fossil most resembled the leaves of *Kadsura* (Schisandraceae). The presence of large areoles with numerous, branched, free vein-endings would tend to support a reference to the Schisandraceae. This family consists of two genera, *Kadsura* and *Schisandra*. No absolute boundary can be drawn between these genera on the basis of the cuticles and gross-morphology of the leaves. However, the well developed ring of cutin covering the guard cells would not appear to be developed in *Schisandra*, while present in certain species of *Kadsura*. A reference of the fossil to *Kadsura* would therefore seem to be justified. *Kadsura* is a genus estimated as having 8-22 species at the present day (WILLIS, 1960; Buchheim in ENGLER, 1964). The leaves of four species have been examined by the present author. This is, however, an insufficient basis on which to confirm or reject the application of the new binomial, *Kadsura breddinii*, proposed by WEYLAND (1934) for the taxon under consideration.

Herbarium material examined in detail:

<i>Kadsura coccinea</i> (Lem.) A. C. Smith	Coll. E. Bodinier 1214	(E) det. L. A. Lauener
<i>Kadsura interior</i> (A. C. Smith)	Coll. T. T. Yü 17320	(E) det. A. C. Smith
<i>Kadsura longepedunculata</i> Finet, et Gagnep.	Coll. H. H. Chung 2903	(E) det. A. C. Smith
<i>Kadsura polysperma</i> Yang	Coll. W. P. Fang 2683	(E) det. A. C. Smith
<i>Schisandra glaucescens</i> Diels	Coll. E. H. Wilson 164	(E) det. A. Rehder & E. H. Wilson
<i>Schisandra grandiflora</i> (Wall.) Hook. f. et Thoms.	Coll. O. Polunin, W. R. Sykes & L. H. J. Williams 2123	(E) _____
<i>Schisandra henryi</i> Clarke	Coll. W. P. Fang 1121	(E) det. A. C. Smith
<i>Schisandra lanifolia</i> (Rehd. et Wils.) A. C. Smith	Coll. McLaren's collectors L. 106A	(E) det. A. C. Smith
<i>Schisandra neglecta</i> A. C. Smith	Coll. T. T. Yü 16148	(E) det. A. C. Smith
<i>Schisandra propinqua</i> (Blume) Hook. f. et Thoms.	Coll. T. T. Yü 16315	(E) det. A. C. Smith
<i>Schisandra rubriflora</i> Rehd. et Wils.	Coll. T. T. Yü 10319	(E) det. A. C. Smith
<i>Schisandra sphaerandra</i> Stapf.	Coll. G. Forrest 4797	(E) det. A. C. Smith
<i>Schisandra sphenanthera</i> Rehd. et Wils.	Coll. H. C. Chow 689	(E) det. A. C. Smith
<i>Schisandra viridis</i> A. C. Smith	Coll. R. C. Ching 3166	(E) det. A. C. Smith

FAMILY LAURACEAE

Our knowledge of the presence and distribution of the Lauraceae in the past is based on wood-, fruit- and leaf-remains, since the pollen of this family does not prove to be resistant to fossilization.

In his revision WEYLAND (1934) referred a fair percentage of the Kreuzau leaf-remains to the Lauraceae. Cuticle analysis has confirmed a reference to the Lauraceae in most cases. Only material which Weyland referred to as *Persea speciosa* Heer could be proved to belong to another family. On the other hand some of the material described by Weyland under the name of *Ficus arcinervis* (Rossmässler) Heer is here referred to the Lauraceae on the basis of its epidermis. Other differences between the present account and that of WEYLAND (1934) include both the addition of a number of taxa, new since Weyland's revision, and changes in the circumscription of the taxa.

In his revision of the Kreuzau assemblage WEYLAND (1934) made use of binomials proposed by Braun, Heer, Unger, Von Ettingshausen, Weber etc. in the middle of the 19th Century. While Weyland realized that the generic reference of certain of these fossils was questionable or even blatantly wrong he considered it wiser, for the sake of stability, to continue to use these binomials. This opinion is arguable. One might have expected that the use of cuticle analysis would have aided a reference of the leaf-remains to particular generic entities. However, while a fair range of variation is encountered in the cuticles of the Lauraceae, the differences do not run parallel to the generic units made use of in present-day taxonomic works. With the exception of certain highly characteristic forms e.g. *Sassafras* a reference of the fossils to particular genera, such as one finds in the work of BANDULSKA (1926, 1928), would not appear to be feasible. An alternative is to refer the fossils to organ-genera. However the use of organ-genera such as *Laurophyllum*, *Laurophyllites*, *Daphnogene* and *Cinnamomophyllum* is not to be recommended either. Not only are the boundaries between these organ-genera poorly defined, but the usage of these categories leads to a very arbitrary grouping of the fossil material. The use of these organ-genera has acted as little more than a spring-board for the description of new specific entities. This practice is not followed in the present account.

XX. *Sassafras*

Synonym: *Sassafras ferretianum* Massalongo Coll. H. Weyland 1635, det.
H. Weyland!

Description:

Petiole unknown.

Lamina palmate, 3-lobed, 5.8 cm long, 4.8 cm wide, the length/breadth ratio being 1.2 : 1. Leaf apices acute, leaf base acute. Lamina dissected round primary veins to a depth of 44 %, sinuses rounded, the distance from the origin of the lateral primary veins to the sinus 2.6–2.7 cm. The distance from the central apex to the lateral apices 2.0–c.3.2 cm. The angle formed by joining the apex of the central lobe via a primary sinus to the apex of one of the lateral lobes 50°–85°.

Leaf margin entire.

Venation actinodromous, primary veins 3. Lateral primary veins arising at 30° from the central primary vein 7 mm above the junction of the lamina and petiole; these lateral primary veins 0.2–0.3 mm wide at mid-point, 80 % the length of the central primary vein. The percentage of the lamina on the basiscopic side of the lateral primary veins c.50 %. Lateral primary veins bearing c.8 secondary veins on their acroscopic side, arising at 60° – 90° . The angle at which the veins arise constant or decreasing within the first few mms, hardly tapering along their length, 0.03–0.05 mm wide at mid-point. Lateral primary veins bearing 7 or more secondary veins on their basiscopic side, the most proximal vein (the only vein arising in the basal third) arising at 40° – 45° , arising in the median third at 60° – 80° , in the apical third at 65° – 90° . The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins successively decreasing from base to apex (fig. 20). Secondary veins slightly tapering along their length, 0.03–0.25 mm wide at mid-point. Central primary vein curved throughout, markedly tapering along length, 0.35 mm wide at mid-point. Central primary vein bearing 7 secondary veins per side, arising in the median third of the lobe at 50° – 80° , in the apical third at 55° – 80° . The angle at which the veins arise constant within the first few mms. The spacing of the veins decreasing successively from base to apex (fig. 20). Secondary veins alternately arranged, hardly to somewhat tapering along their length, 0.05–0.20 mm wide at mid-point, interconnected distally by fine extensions of the secondary veins, or tertiary veins. Intermediate veins 2–5 per intercostal field, arising from the central primary vein at 65° – 90° (-120°), running more or less parallel to one another, the spacing between them constant or increasing distally. The veins similar in width, extending from 0 to $1/2$ –1 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally or rarely mid-way. Tertiary veins 5(–11) per 1 cm secondary vein, little branched. Areoles c.25 (?) per 10 mm², the nature of the free vein-endings unknown.

Epidermis unknown.

Specimen examined: Geol. Inst. Cologne: Coll. H. Weyland 1635

Discussion:

The only possibility as regards affinity would appear to be with the living *Sassafras* species. These plants have simple to palmate leaves and when palmate in form the central lobe is seen to be markedly expanded half way along its length. This characteristic in combination with the entire leaf margin, the acute leaf base and the origin of the lateral primary veins well above the leaf base go to make up an unusual and easily identified leaf. At the present day this genus is represented by 2–3 species, which resemble each other very closely in leaf form and venation. *Sassafras*

tzumu (Hemsl.) Hemsl., however, has lobes with more pointed apices than *Sassafras albidum* (Nuttall) Nees and *S. randaiensis* (Hayata) Rehder. The ratio of the distance between the origin of the lateral primary veins and the base of the leaf against the total length of the leaf, which varies somewhat among the species, was not found to be diagnostic. Similarly the ratio of the distance between the apices of the lateral lobes against the point where a line joining the lateral apices intersects the central primary vein and the base of the lamina, while showing a certain amount of variation, did not prove to be completely diagnostic. In *Sassafras albidum* and *S. randaiensis* (figures for the latter based on LI, 1963, fig. 84) the percentage ratio is rarely less than 75% (65%–115%), while in *Sassafras tzumu* the equivalent figure is 50–84(–125)%. In respect of the nature of the lobes and the above-mentioned ratio the fossil agrees more closely with *Sassafras albidum* and *S. randaiensis*. On the present evidence it does not appear feasible to refer the fossil to a separate specific entity, *Sassafras ferretianum*.

Only one specimen could be attributed with certainty to the genus *Sassafras*, but because this genus shows marked heterophylly leaf-remains, ovate or elliptical in shape and displaying acrodromous venation, may belong here. The epidermal structure of both *Sassafras* species available to the author were compared with that of No. XXVI. However, while the stomata were similar, the leaves of both *Sassafras* species were glabrous (only the young leaves tend to be hairy), while hair bases were very common in No. XXVI.

Herbarium material examined in detail:

<i>Sassafras albidum</i> (Nuttall)	Coll. J. F. Logue 2048	(U) _____
Nees		
	Coll. N. C. Fassett & J. T. Curtis 160	(U) _____
	Coll. O. Harbin 132	(U) _____
	Coll. J. H. Soper, R. P. Burcher & L. O. Gaiser 2204	(U) det. Imchanitokaya
	Coll. J. G. ten Houten & A. Schoenmakers 1117	(U) det. Imchanitokaya
	Coll. L. B., D. L., C. B., C. C. Smith & E. Rouleau 12-8-1945	(E, U) _____
	Coll. H. E. Ahles & J. Haesloop 53584	(E) _____
	Coll. R. F. Britt 1876	(E) _____
	Coll. Rugel 7-1840	(E) _____
	Coll. G. Watson 5-1845	(E) _____
	Coll. C. K. Dodge 21-7-1896	(E) _____
	Coll. F. T. Aschman 5-6-1887	(E) _____
	Coll. W. J. Cody 991	(E) det. H. L. Mitchell

	Coll. E. S. Steele & Mrs. Steele 29-8-1898	(E) _____
	Coll. E. S. Steele 25-10-1896	(E) _____
	Coll. E. S. Steele 22-7-1897	(E) _____
	Coll. T. H. Kearney Jr. 216	(E) _____
<i>Sassafras tzumu</i> (Hemsl.) Hemsl.	Coll. C. S. Fan & Y. Y. Li 119	(E) _____
	Coll. C. Y. Chiao 14254	(E) det. E. D. Merrill
	Coll. E. H. Wilson 710	(E) det. J. S. Gamble
	Coll. E. H. Wilson s.n. 8-1907	(E) _____
	Coll. Handel-Mazzetti 11828	(E) det. A. Rehder

XXI

<i>Synonyms</i> : <i>Benzoin antiquum</i> Heer	WEYLAND, 1934, p. 84 pro parte e.g. Tafel 16, fig. 8!
<i>Ficus arcinervis</i> (Rossmässler) Heer	WEYLAND, 1934, pp. 62-63 pro parte e.g. Tafel 9, fig. 3!, fig. 4!; WEYLAND, 1943, p. 106, Tafel 18, Abb. 5!, Tafel 19, fig. 1!
<i>Juglans acuminata</i> A. Braun	WEYLAND, 1934, p. 48 pro parte!
<i>Laurus grandifolia</i> Ett.	WEYLAND, 1934, p. 75, Tafel 13, fig. 6!
<i>Laurus obovata</i> Weber	WEYLAND, 1934, pp. 75-76, Tafel 12, fig. 4!
<i>Laurus styracifolia</i> Weber	WEYLAND, 1934, pp. 77-78, Tafel 12, fig. 2!; Tafel 19, fig. 1!

Description :

Petiole 7-8 mm long and 1.2-1.4 mm wide at mid-point, curved in all known cases, more or less parallel-sided, making an angle with the midvein.

Lamina elliptical, 3.5-c.15 cm long, 1.3-4.2 cm wide, the length/breadth ratio being 2.1:1-c.3.8:1 (fig. 20). Lamina sometimes somewhat asymmetrical about midvein. Leaf apex acuminate, leaf base acute, obtuse or rounded.

Leaf margin entire.

Venation camptodromous, midvein straight, apically curved or gently curved throughout length, hardly to markedly tapering along length, 0.27-0.80 mm wide at mid-point between base and apex of lamina. Midvein bearing 4-8 secondary veins per side, excluding small veins in acuminate tip, the most proximal vein arising at 40°-65°, arising in the remaining part of the basal third of the lamina at 40°-60°, in the median third at 45°-80° and in the apical third at 45°-110°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the secondary veins at a maximum proximally or mid-way (fig. 20). Secondary veins opposite or alternately arranged, slightly to

markedly tapering along their length, 0.03–0.30 mm wide at mid-point, interconnected distally by strong or fine extensions of the secondary veins. Intermediate veins 4–13 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 60°–120°, running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/2–7/8 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 3–9 per 1 cm secondary vein, somewhat or much branched, the lengths on acropic and basipic sides of secondary vein more or less similar. Areoles (12–) 40–60(–110) per 10 mm² with some free vein-endings, these being unbranched and less commonly branched.

Epidermis in non-stomatal condition composed of 200–510 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2.5 : 1(–5 : 1). Cell wall 0.4–3.0 microns thick, unpitted or pitted with elongate or hemispherical projections, straight or undulate with 0–8 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells over veins somewhat smaller than the rest of the epidermal cells, the cell length/cell breadth ratio being 1 : 1–5 : 1. Finer veins not reflected in cuticle. Epidermis in stomatal condition composed of 180–360 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–4.2 : 1. Cell wall 0.4–2.0 microns thick, unpitted or pitted with elongate or hemispherical projections, straight or undulate with 0–15 lobes per cell (fig. 20), the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells over veins narrower than the rest of the epidermal cells, the cell length/cell breadth ratio being 1 : 1–14 : 1. Cell wall never undulate in the case of major veins in which case cell wall sometimes reaching 5.5 microns thick. Finer veins reflected in cuticle. Stomata 13.5–35.1 microns long (fig. 21) and (8.4–)12.6–47.7 microns broad (fig. 21), breadth 67–127 % length, 16–48 per 0.1 mm²; stomatal index 6.25–19.50 %. Stomata variously orientated, undepressed or somewhat depressed, more or less equidistant, apices non-retuse. Stomatal slit 37.5–73.0 % stomatal length and bordered by strongly developed stomatal ledges. Accessory cells 2,4–9(–11), mostly symmetrical with 0–4 polar and 2–4 lateral cells, although when 9–11 cells present a radial arrangement results. Accessory cells somewhat larger, similar to or somewhat smaller than the rest of the epidermal cells.

Specimens examined : Deutsche Akad. Wiss. Berlin: 269(K 155), 270(K 107), 271(K 117), 286(K 120), 294(K 68), 339(K 92), 356(K 120), s.n.(K 83).
 Geol. Inst. Cologne: Coll. W. Jansen 78, Coll. H. Weyland 1396(K 107)
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3657, 3658, 3659, 3660, 3661, 3662, 3663, 3664, 3665, 3666, 3667, 3668, 3669, 3670, 3671, 3672, 3673, 3674, 3675, 3676, 3897B.

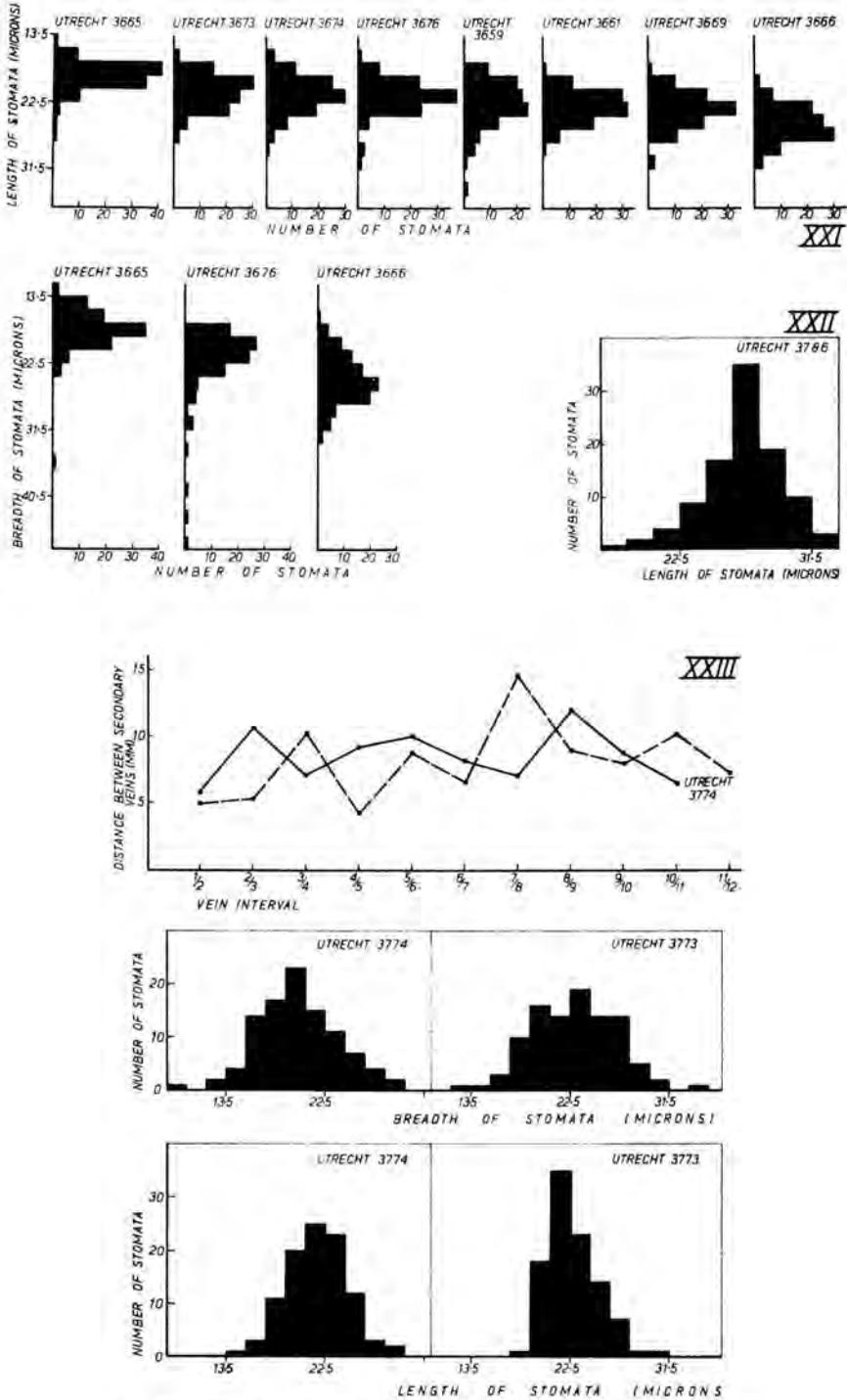


Fig. 21: Graph and histograms XXI cont., XXII, XXIII.

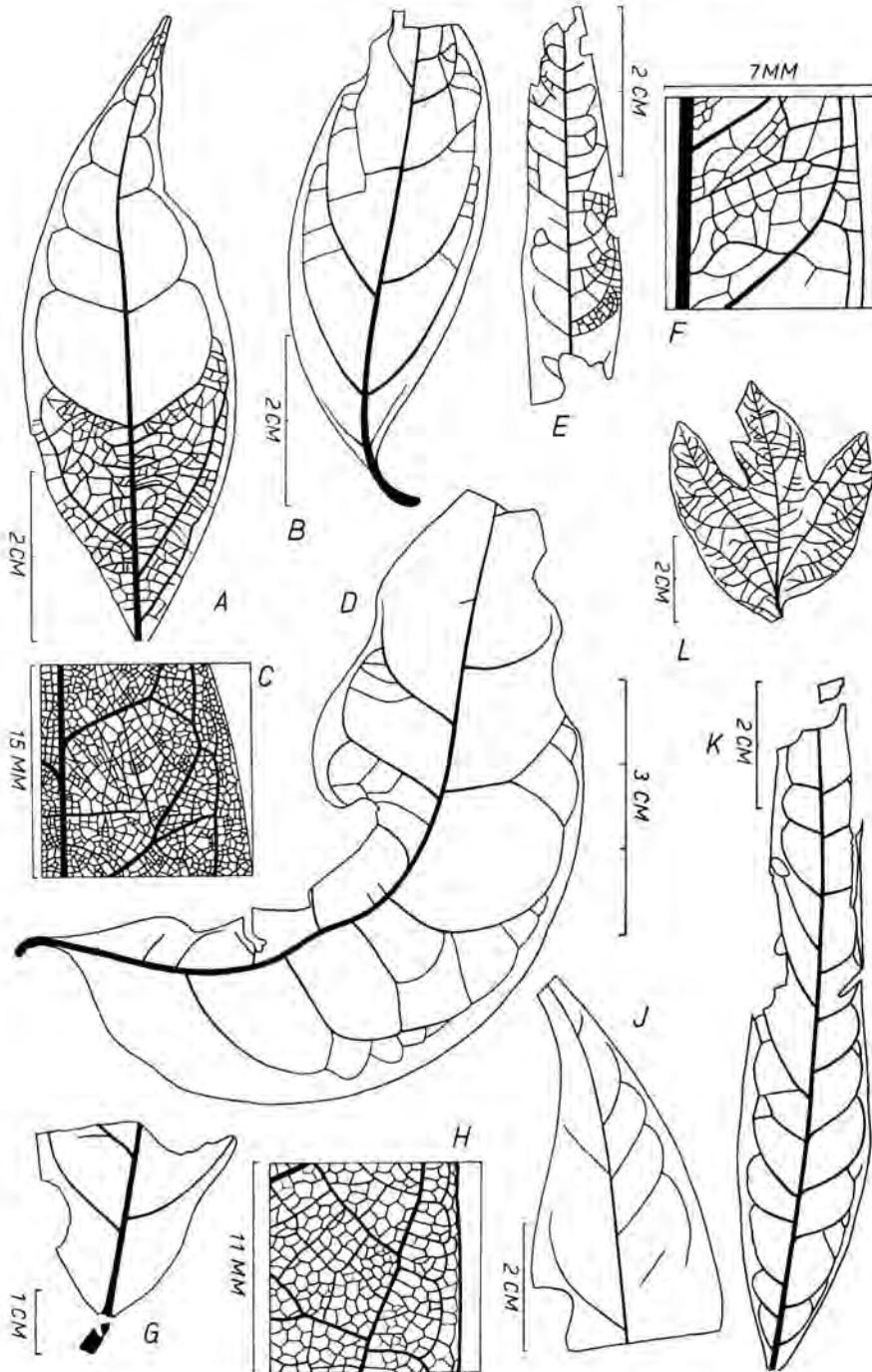


Fig. 22. A-D = XXI: A = Berlin 270; B = Utrecht 3663; C = detail showing venation and leaf margin; D = Utrecht 3659. E-F = XXII: E = Utrecht 3786; F = Utrecht 3786, detail showing venation and leaf margin. G-K = XXIII: G = Utrecht 3773; H = detail showing venation and leaf margin; J = Utrecht 3772; K = Utrecht 3774. L = XX: Cologne, Coll. H. Weyland 1635.

Discussion:

This taxon is typified by a very characteristic epidermal structure. The presence of hemispherical or elongate projections on the cell walls and the presence of stomata with stomatal ledges in combination with the other characters go to make up a distinctive entity.

The specimens referred to by WEYLAND (1934) as *Laurus grandifolia*, *L. obovata* and *L. styracifolia* and a specimen referred to *Juglans acuminata* yielded cuticles reflecting the characteristic stomata and cell walls, while the specimens of *Ficus arcinervis* and *Benzoin antiquum* referred to in the synonymy, although only yielding cuticles reflecting the epidermis in a non-stomatal condition, were considered suitably characteristic to be referred to the same taxonomic entity. All these specimens furthermore agreed in gross-morphology with those specimens already examined in the Utrecht collection.

The variability encountered within the taxon throws a certain amount of light on the species concept currently held by certain authors. In 1963 WEYLAND and KILPPER described as new the taxa *Laurophyllum pseudo-princeps* and *L. undulatum*. These taxa were separated roughly as follows: *Laurophyllum pseudo-princeps* with straight epidermal cell walls, *Laurophyllum undulatum* with strongly undulating cell walls. However, the large percentage of intermediate forms encountered in the present investigation (fig. 20) would suggest that one is dealing with one, rather than two, entities. There again, *Laurophyllum macrostoma* Weyland et Kilpper 1963, very briefly described by the authors, was typified by stomata up to 35 microns long, hence the specific name. However, in the absence of further information this entity might fall within the present circumscription as well.

WEYLAND's (1934) reference of the material to *Ficus* and *Laurus* was based on a comparison with the older literature in which a good proportion of the leaf-remains were referred to these two genera. A comparison of the epidermides of *Ficus* and *Laurus* with that of the leaf-remains leaves no room for doubt that the affinities of the fossil leaves lie elsewhere. Most of the available *Ficus* species proved to have leaves with thin cuticles, which stand little chance of being found in large strips in the fossil state. In contrast, of all the leaf-remains from Kreuzau the present taxon possesses the most easily won cuticle. Moreover, in *Ficus* the epidermal cell walls on the upper and lower surfaces of the leaf are straight, or only occasionally undulate on the lower surface, and without the hemispherical or elongate projections so characteristic of the fossil. Furthermore, the cuticle in *Ficus* is commonly traversed by fine striae and the stomata are without stomatal ledges.

The leaves of *Laurus* are characterized by an epidermis with strongly undulate cell walls, more so than in the fossil. These cell walls are, moreover, without hemispherical or elongate projections. The stomata, unlike those of the leaf-remains, are frequently rhombic in shape and free from stomatal ledges.

A reference of the present taxon to *Benzoin* would appear to be incorrect as well. This genus is often referred to *Lindera* (e.g. Buchheim in ENGLER, 1964, p. 126), but *Lindera* s.l. does not have an epidermis resembling that of the fossil in question. While certain species of *Lindera* may have an upper epidermis with undulate cell walls, combined in some cases with hemispherical projections, the lower epidermides of such species differ from that of the leaf-remains. Stomatal ledges never appear to be present in *Lindera* s.l. (see SHAKRAL, 1965).

A reference of the leaf-remains to *Juglans* could also be ruled out as the leaves of this genus are characterized by glands having a single basal cell. Moreover, the epidermal cell walls are \pm straight and the stomata have a long stomatal slit and no stomatal ledges.

While a reference to *Laurus* or *Benzoin* would appear to be incorrect, the overall similarity and in particular the presence of stomatal ledges on the guard cells tended to indicate a Lauraceous affinity for the fossil. While the presence of stomatal ledges is by no means confined to the Lauraceae they are to be found within a number of genera of this family e.g. *Aniba*, *Cryptocarya*, *Nectandra* and *Ocotea*. Certain members of the Santalaceae e.g. *Osyris wightiana* Wight and *O. lanceolata* Hochst. et Steud. were found to have stomatal ledges as well. However, while the nature of the stomata and accessory cells in these species approximate very closely to those of the leaf-remains, stomata are present in equal numbers on both surfaces of the lamina and few, if any, of the veins beside the midvein are reflected in the cuticle. Moreover, the cell walls are apparently without exception straight and unpitted.

Of the herbarium material from Eastern North America and China investigated by the author, that of *Nectandra coriacea* (Sw.) Griseb. had leaves approximating most closely to the fossil taxon. The investigation was extended to include other species of *Nectandra* in order to assess the range of variation encountered within the genus. The upper epidermis of *Nectandra* consists of polygonal, invariably straight-walled cells. The epidermal cells of the lower surface may be more or less polygonal or, as in *N. cuspidata*, more elongate. The epidermal cell walls are straight or only slightly undulate, while the stomata usually possess stomatal ledges, although these are absent in *Nectandra rubra*. Elongate projections from the cell wall, such as found in the fossil, are present in some leaves of *Nectandra coriacea*, which also resembles the fossil closely in gross-morphology. *Nectandra coriacea* is, moreover, the only *Nectandra* species occurring in the climatic zone indicated by the fossil assemblage (see fig. 4). However, in none of the *Nectandra* species available were highly undulate cell walls encountered. Such undulate cell walls in combination with other characters exhibited by the fossil cuticle are displayed by the cuticles of other Lauraceous genera e.g. *Aniba canellila* (H.B.K.) Mez and various species of *Ocotea* (SHAKRAL, 1965). The fact that the genus *Ocotea* is sometimes taken to include *Nectandra* e.g. Buchheim (in ENGLER,

1964, p. 125), while C. K. Allen, one of the specialists in the Lauraceae, considers *Nectandra* as a separate genus indicates the state of confusion which exists as to the generic limits within the family. Under such circumstances it was considered better to avoid assigning the leaf-remains to one of the possible genera. More work on the recent members of this family may make it possible to assign the fossil to a generic entity at some future date.

Herbarium material examined in detail:

Benzoin obtusilobum (Blume) O. Kuntz	Coll. C. Y. Chiao 2820	(E) det. A. Rehder
Benzoin touyunense (Lévl.) Rehder	Coll. R. C. Ching 3129	(E) det. A. Rehder
<i>Ficus baileyi</i> Hutch.	Herb. Univ. Nanking 14213	(E) det. E. D. Merrill
<i>Ficus benjamina</i> L.	Coll. F. C. How & N. K. Chun 70010	(E) det. E. J. H. Corner
<i>Ficus chincha</i> Roxb.	Coll. G. Forrest 8007	(E) det. E. J. H. Corner
<i>Ficus erecta</i> Thunb.	Coll. E. Taquet 4423	(E) det. E. J. H. Corner
<i>Ficus esquirolii</i> Lévl. et Vant.	Coll. Y. Tsiang 1471	(E) det. E. J. H. Corner
<i>Ficus filicauda</i> Handel- Mazzetti	Coll. T. T. Yü 20002	(E) det. E. J. H. Corner
<i>Ficus formosana</i> Maxim.	Coll. W. Y. Chun 5160	(E) det. E. J. H. Corner
<i>Ficus houberi</i> Miq.	Coll. T. T. Yü 17818	(E) det. E. J. H. Corner
<i>Ficus lacor</i> Ham.	Coll. S. Ten 114	(E) det. E. J. H. Corner
<i>Ficus laducea</i> Roxb.	Coll. W. P. Fang 3751	(E) det. E. J. H. Corner
<i>Ficus macropodocarpa</i> Lévl. et Vant.	Coll. J. Cavalerie s.n.	(E) det. E. J. H. Corner
<i>Ficus nemoralis</i> Wall.	Coll. G. Forrest 26648	(E) det. E. J. H. Corner
<i>Ficus pyriformis</i> Hook. et Arn.	Coll. 17-4-1898 Herb. H. Lévillé	(E) det. E. J. H. Corner
<i>Ficus retusa</i> L.	Coll. H. H. Chung 23-9-1922	(E) det. E. J. H. Corner
<i>Ficus scandens</i> Roxb.	Coll. N. K. Chun & C. L. Tso 43555	(E) det. E. J. H. Corner
<i>Ficus stenophylla</i> Hemsl.	Coll. A. N. Steward, C. Y. Chiao & H. C. Cheo 877	(E) det. E. J. H. Corner
<i>Ficus subpyriformis</i> Miq.	Coll. A. Henry 9531	(E) det. E. J. H. Corner
<i>Ficus superba</i> Miq.	Coll. H. H. Chung 3461	(E) det. E. J. H. Corner
<i>Ficus tinctoria</i> Forst.	Herb. H. Lévillé	(E) det. E. J. H. Corner
<i>Ficus trivia</i> Corner	Coll. 5-1910 Herb. H. Lévillé	(E) det. E. J. H. Corner
<i>Ficus tuphapensis</i> Drabe	Coll. A. Henry 9908	(E) det. E. J. H. Corner
<i>Juglans californica</i> Wats.	Coll. E. K. Balls 8368	(E) _____
<i>Juglans cathayensis</i> Dode	Coll. H. C. Chow 29-6-1934	(E) _____
<i>Juglans cinerea</i> L.	Coll. E. S. Steele 30-5-1899	(E) _____
	Coll. E. J. Palmer 4615	(E) _____
<i>Juglans major</i> (Torrey) Heller	Coll. L. N. Goodding 166	(E) _____
<i>Juglans rupestris</i> Engelm.	Coll. D. T. MacDougal 271	(E) _____
	Coll. E. O. Wootton 362	(E) _____

<i>Laurus nobilis</i> L.	Coll. W. H. A. Hekking 372	(U) det. W. H. A. Hekking
<i>Lindera benzoin</i> (L.) Blume	Coll. K. U. Kramer 241	(U) det. J. Haeck
<i>Lindera bifaria</i> (Nees) Benth.	Coll. Handel-Mazzetti 867	(E) det. Handel- Mazzetti
<i>Lindera cercidifolia</i> Hemsl.	Coll. G. Forrest 29087	(E) _____
<i>Lindera citriodora</i> (Sieb. et Zucc.) Hemsl.	Coll. A. N. Steward 2725	(E) det. E. D. Merrill
<i>Lindera kariensis</i> W. W. Smith	Coll. G. Forrest 13877	(E) det. W. W. Smith TYPE
<i>Lindera megaphylla</i> Hemsl.	Coll. S. S. Chien 5033	(E) det. S. S. Chien
<i>Lindera reflexa</i> Hemsl.	Herb. Univ. Nanking 14318	(E) det. E. D. Merrill
<i>Lindera umbellata</i> Thunb.	Coll. J. L. Gressitt 1450	(E) det. E. D. Merrill
<i>Nectandra ambigua</i> Meissn.	Coll. R. Schomburgk 29	(U) det. C. K. Allen ISOTYPE
<i>Nectandra coriacea</i> (Sw.) Griseb.	Coll. J. K. Small, J. J. Carter & G. K. Small 2-1911	(U) _____
<i>Nectandra cuspidata</i> (Martius ex Nees) Nees	Coll. R. Schomburgk 69	(U) det. C. K. Allen
	Coll. J. J. Wurdack & L. S. Adderley 43578	(U) det. C. K. Allen
<i>Nectandra kaburiensis</i> Kostermans	Coll. B. W. Arbor 649	(U) det. A. Kostermans
<i>Nectandra oligoneura</i> Urban	Coll. H. von Türkheim 6-1910	(U) det. C. K. Allen
<i>Nectandra pisi</i> Miq.	Coll. B. W. 3209	(U) det. A. Kostermans
<i>Nectandra rubra</i> (Mez) Allen	Coll. G. T. Prance & T. D. Pennington 1696	(U) det. C. K. Allen
<i>Nectandra sanguinea</i> Rottb.	Coll. Schiede s.n.	(U) det. A. Kostermans
<i>Nectandra savannara</i> (Standley et Steyermark) Allen	Coll. P. H. Gentle 3488	(U) det. C. K. Allen
<i>Nectandra smithii</i> Allen	Coll. P. H. Allen 3534	(U) det. C. K. Allen
<i>Osyris lanceolata</i> Hochst. et Steud.	Coll. T. T. Yü 17971	(E) det. H. U. Stauffer
<i>Osyris wightiana</i> Wight	Coll. A. Henry 9906	(E) det. C. Schneider

XXII

Description:

Petiole unknown.

Lamina probably elliptical c.7.5–8.0 cm long, 1.2 cm wide. Leaf apex and leaf base unknown.

Leaf margin entire.

Venation camptodromous, midvein straight, slightly tapering along length, 0.45 mm wide at mid-point between base and apex of lamina. Midvein bearing numerous secondary veins per side, arising in the median third of the lamina at 45°–60°. The angle at which the veins arise constant within the first few mms. Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.06–0.15 mm wide at mid-point,

interconnected distally by fine extensions of the secondary veins. Intermediate veins up to 4 per intercostal field, arising from midvein at 50° – 80° , running more or less parallel to one another, the spacing between them being more or less constant. The veins more or less similar in width, extending from 0 to $1/4$ – $2/3$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way. Tertiary veins 8–11 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. The nature of the areoles and free vein-endings unknown.

Epidermis in non-stomatal condition composed of 375–565 more or less polygonal cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall 0.6–4.0 microns thick, somewhat pitted, straight. Cells over veins but little elongate, the cell length/cell breadth ratio being 1 : 1–2 : 1. Epidermis in stomatal condition composed of 280–320 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–5 : 1. Cell wall 0.7–1.2 microns thick, largely unpitted, straight. Cells over veins unknown. Stomata 19.8–32.4 microns long (fig. 21) and 14.4 microns or more broad, the actual size limits difficult to estimate as the boundary between the guard cells and the accessory cells often vague. Stomata 18–27 per 0.1 mm^2 ; stomatal index 9.50–11.25 %. Stomata variously orientated, undepressed, more or less equidistant, apices non-retuse. Stomatal slit 37.5–60 % stomatal length and bordered by moderately strongly developed stomatal ledges. Accessory cells 2,4–10, mostly symmetrical, although radial arrangement may result when 8–10 cells present. Accessory cells similar in size to the rest of the epidermal cells.

Specimen examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3786

Discussion:

With regard to its epidermis this taxon approximates very closely to XXI. However, it differs strikingly in the length/breadth ratio of the lamina and in the number of secondary veins present per side. There would seem to be no reason for uniting the two taxa at this stage.

XXIII

Description:

Petiole 7.0 mm long and 2.4 mm wide at mid-point, increasing from 1.25 mm wide at base of lamina to 3.2 mm wide at base of petiole, straight, making a slight angle with the midvein.

Lamina ovate or elliptical, 12 cm or more long, 2.8–3.4 cm or more wide. Leaf apex long acute or acuminate, leaf base acute or obtuse.

Leaf margin entire.

Venation camptodromous, midvein straight or gently curved, hardly or markedly tapering along length, 0.6–0.9 mm wide at mid-point between base and apex of lamina. Midvein bearing c.10–c.15 secondary veins per

side, the most proximal vein arising at 45° – 60° , arising in the remaining part of the basal third of the lamina at 45° – 65° (– 90°), in the median third at 45° – 70° , in the apical third at 60° – 70° . The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the secondary veins somewhat irregular and showing no trend (fig. 21). Secondary veins alternately arranged, rarely opposite or subopposite, hardly to somewhat tapering along their length, 0.15–0.40 mm wide at mid-point, interconnected distally by strong or fine extensions of secondary veins. Intermediate veins 1–7(–14) per intercostal field and occasionally having a somewhat twisted course, arising from the midvein at 60° – 140° , running more or less parallel to one another or converging/diverging, the spacing between them more or less similar or increasing distally. The veins more or less similar in width or increasing in width with increase in length, extending from 0 to $1/2$ – $3/4$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 2–8 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopical sides of secondary vein more or less similar. Areoles 42–65 per 10 mm², free vein-endings few and unbranched.

Epidermis in non-stomatal condition composed of 190–375 rarely slightly striate cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3.5 : 1. Cell wall 0.35–0.90 microns thick, unpitted or pitted, undulating with (0)–4–14 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 12.6 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–3 : 1, the primary cells often subdivided by secondary cell walls, the cell walls but slightly undulate or even straight. Finer veins somewhat reflected in cuticle. Cells at leaf margin 575–770 per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–4 : 1 arranged in c.20 rows, cell wall 0.5–2.0(–4.0) microns thick, hardly pitted, more or less straight. *Epidermis* in stomatal condition composed of 200–425 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–5 : 1. Cell wall 0.45–0.90(–2.0) microns thick, unpitted or pitted, undulating with (0)–2–14 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 12.6 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–10 : 1, the primary cells sometimes subdivided by secondary cell walls, the cell wall undulate over small veins and on the lateral parts of large veins, which otherwise have straight cell walls. Finer veins somewhat reflected in cuticle. Stomata frequently rhombic in shape 12.6–35.1 microns long and 8.1–35.1 microns broad (fig. 21), breadth 41–170 % length, 15–47 per 0.1 mm²; stomatal index 7–20 %. Stomata variously orientated, undepressed or slightly depressed, more or less equidistant or somewhat arranged in groups, apices rarely retuse. Stomatal slit 25–77 % stomatal length. Accessory cells 4–6(–9), mostly symmetrical with 2–4 polar and 2–3 lateral cells, although when 7 or 9 cells present a radial arrangement results. Accessory

cells more or less similar in size to the rest of the epidermal cells. Internal resinous bodies rare.

Specimens examined: 4, among which the numbered specimens:

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3772, 3773,
3774

Discussion:

This taxon was not described by WEYLAND (1934) and nor could any material available to Weyland be referred to it. The taxon possesses none the less a very characteristic epidermis. The stomata are frequently rhombic in form and the epidermal cell wall is intensely undulate. Of the herbarium material available to the author such rhombic stomata were found to be restricted to the Lauraceae, with the exception of *Magnolia denudata* Desr. (Magnoliaceae). The leaves of this living species are distinguishable from the fossil, however, in that the lamina is broad ovate and the upper epidermis is covered by numerous hairs with strongly thickened hair bases. Such hair bases are present on the veins of the lower epidermis and the lower epidermis is, moreover, characterized by straight-walled cells and accessory cells more or less spirally arranged round the stomata. At least one of these accessory cells is U-shaped as a result.

Epidermal structures resembling that of the fossil to some extent are to be found within a number of genera of the Lauraceae e.g. *Actinodaphne*, *Apollonias*, *Laurus*, *Lindera*, *Litsea*. Differences such as the presence of hairs e.g. *Actinodaphne cupularis* (Hemsl.) Gamble, *Lindera fragrans* Oliv., *Litsea greenmaniana* Allen, straight or only slightly undulate cell walls e.g. *Actinodaphne trichocarpa* Allen, *Litsea greenmaniana* Allen, or the fact that even very fine veins are sometimes reflected in the cuticle of the lower epidermis e.g. *Actinodaphne cupularis* (Hemsl.) Gamble, *Litsea greenmaniana* Allen would tend to indicate that all but *Apollonias* and *Laurus* can be excluded from further consideration. Of all the members submitted to a detailed examination in this context only the epidermides of *Apollonias* and *Laurus* displayed the intensely undulate cell walls so characteristic of the cuticle of the fossil taxon. Apparent differences between the leaves of *Apollonias* and *Laurus* and the leaf-remains, such as the length/breadth ratio (1.7:1–3.5:1 in the herbarium material available) and the size of the stomata (mean of stomatal length greater in recent species) may prove to be of importance in this connection.

The taxon at present under discussion agreed with *Laurophyllum abchasicum* Kolakovskiy et Shakral as to its cuticle. The cuticle of a paratype was made available to the present author through the kindness of Dr. L. Ruffle (Berlin). The description of the gross-morphological features of this species (KOLAKOVSKIY and SHAKRAL, 1958) moreover agreed closely with that of the present taxon. The authors considered that their taxon resembled *Laurus nobilis* L. to a certain extent. However,

as SHAKHAL (1965, p. 41) pointed out, the authors considered it more appropriate to refer the species to the organ-genus *Laurphyllum* in the absence of any work on the construction of the stomata and variability of the epidermides. LITKE (1966) has described what would appear to be the same taxon as cf. *Apollonias canariensis* (Willd.) Nees. He compared the size and shape of the stomata of *Laurus canariensis* Webb., *L. nobilis* L. and *Apollonias canariensis* (Willd.) Nees with those of the fossil and came to the conclusion that the fossil showed the greatest resemblance to *Apollonias*. While pointing out the difficulty of separating *Laurus* from *Apollonias* on the basis of their cuticles he considered that the gross-morphology of the fossil leaves, when these are not too fragmentary, might solve the problem as to the generic affinity of the fossil. However, while features such as the spacing of the secondary veins did differ somewhat, it did not prove possible to separate material referred to *Laurus canariensis* Webb. from *Apollonias canariensis* (Willd.) Nees satisfactorily on the basis of vegetative features alone. In *Apollonias canariensis* the largest intercostal field tended to be situated \pm mid-way along the lamina, while the distance between the secondary veins diminished rapidly in both proximal and distal directions. In *Laurus canariensis* on the other hand the spacing of the secondary veins tended to be more or less constant over a greater part of the lamina. However, while this trend could be recognized by an analysis of a number of leaves from a given specimen, the variability encountered in individual leaves was such as to render this character of little use for determining isolated leaf-remains.

Herbarium material examined in detail:

<i>Actinodaphne cupularis</i> (Hemsl.) Gamble	Coll. W. P. Fang 5663	(E)	det. C. K. Allen
<i>Actinodaphne lancifolia</i> (Sieb. et Zucc.) Meisener	Coll. S. Chen 37	(E)	det. C. K. Allen
<i>Actinodaphne trichocarpa</i> Allen	Coll. W. P. Fang 3100	(E)	det. C. K. Allen
<i>Apollonias canariensis</i> (Willd.) Nees	Coll. E. Bourgeau 140	(AWH)	det. H. van Heurck
	Coll. N. H. Mason in 1856	(AWH)	det. H. van Heurck
	Coll. G. Mandon 218	(AWH)	det. H. van Heurck
<i>Laurus canariensis</i> Webb.	Coll. N. H. Mason in 1856	(AWH)	det. A. Kostermans
	Coll. G. Mandon 219	(AWH)	det. H. van Heurck
	Coll. T. C. Hunt 226	(AWH)	det. H. van Heurck
	Coll. E. Bourgeau 182	(AWH)	det. H. van Heurck
<i>Laurus nobilis</i> L.	Coll. W. H. A. Hekking 372	(U)	det. W. H. A. Hekking
<i>Lindera fragrans</i> Oliv.	Coll. A. Henry 3295	(E)	_____
<i>Litsea greenmaniana</i> Allen	Coll. J. L. Gressitt 1687	(E)	det. C. K. Allen
<i>Magnolia denudata</i> Desr.	Coll. C. Y. Chiao 2825	(E)	det. A. Rehder

XXIV

Synonym: *Laurus primigenia* Unger

WEYLAND, 1934, p. 71, Tafel 12,
fig. 11; Tafel 13, fig. 5!

Description:

Petiole 7->14 mm long and c.1.2 mm wide at mid-point, increasing from 0.6-0.8 mm at leaf base to c.1.5 mm wide at or near base of petiole. Petiole straight or curved, sometimes making an angle with the central primary vein.

Lamina ovate, elliptical or obovate, 4.1-7.6 cm or more long, 1.4-2.75 cm wide, the length/breadth ratio being 1.85:1-5.5:1. Leaf apex acuminate, leaf base acute, obtuse or rounded.

Leaf margin entire.

Venation acrodromous (-camptodromous), primary veins 1-3. Lateral primary veins (or most proximal secondary veins) opposite or alternate, arising from central primary vein at 30°-50°, 0.07-0.25 mm wide at mid-point along their length, extending for 44-68 % the length of the lamina. Central primary vein straight or curved, hardly or somewhat tapering along length, c.0.25-0.50 mm wide at mid-point between the base and apex of the lamina. Central primary vein bearing 3-6(-8) secondary veins per side, arising in the basal third of the lamina at 40°-60°, in the median third at (30°-)40°-65°(-75°), in the apical third at 45°-65°(-100°). The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins at a maximum proximally (fig. 24). Secondary veins mostly alternately arranged, hardly to somewhat tapering along their length, 0.05-0.20(-0.30) mm wide at mid-point, interconnected distally by extensions of the secondary veins. Intermediate veins (0-)2-20 per intercostal field, occasionally having a somewhat twisted course, arising from the central primary vein at (40°-)55°-125°, running more or less parallel to one another or converging/diverging, the spacing between them being constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/2-9/10 the distance from the central primary vein to the leaf margin, reaching their greatest length in intercostal field (mid-way-) distally. Tertiary veins 4-11 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 80-100 per 10 mm², with some unbranched and branched free vein-endings.

Epidermis in non-stomatal condition composed of 245-350(-625) more or less polygonal cells per 0.1 mm², the cell length/cell breadth ratio being 1:1-3:1(-4:1). Cell wall 0.4-1.6 microns thick, largely unpitted, straight. Cells over veins narrow rectangular or spindle-shaped, the cell length/cell breadth ratio being 1:1-6:1, transverse cell walls slanting or at right angles to lateral walls. Finer veins reflected in cuticle. Cells at leaf margin (c.280-)575-875 per 0.1 mm², the cell length/cell breadth

ratio being 1:1-3:1, arranged in 15-30 rows, cell wall 1.0-2.5 microns thick, unpitted, straight, transverse walls slanting or at right angles to lateral walls. Epidermis in stomatal condition composed of (130-) 230-390 hardly to markedly domed cells per 0.1 mm², the cell length/cell breadth ratio being 1:1-3.5:1. Cell wall 0.6-2.0(-3.0) microns thick, unpitted or pitted, straight. Cells over veins elongate, the cell length/cell breadth ratio being 1.5:1-12:1, transverse cell walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Stomata 12.6-28.0 microns long and 12.6-30.0 microns broad, breadth 50-170 % length, 17-60 per 0.1 mm²; stomatal index 7-20 %. Stomata variously orientated, depressed, equidistant or somewhat arranged in groups, apices non-retuse. Stomatal slit 32-72 % stomatal length. Accessory cells (2-) 4-5(-6), mostly symmetrical with 0-3 polar and 2 lateral cells, although when 3 or 6 cells present a radial arrangement results. Accessory cells similar in size or somewhat smaller than the rest of the epidermal cells. Internal resinous bodies not uncommon.

Specimens examined: 12: Deutsche Akad. Wiss. Berlin: 346(K 156), 361(K 99)
 Geol. Inst. Cologne: Coll. H. Weyland 1405(K 99),
 reverse side of 1450, 1669b
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3823,
 3824, 3825, 3826, 3827, 3838, 3829.

Discussion:

KRÄUSEL and WEYLAND (1950, p. 58) considered it probable that material described as *Laurus primigenia* had a similar epidermal structure to that of the leaf-remains they described as *Laurophyllum princeps* (Heer) Kräusel et Weyland [later redescribed as *Laurophyllum pseudoprinceps* Weyland et Kilpper (WEYLAND and KILPPER, 1963), following remarks by HANTKE (1953)]. While JÄHNICHEN (1955) found that material from Preschen referred to *Laurus primigenia* had indeed an epidermis similar to that of *Laurophyllum pseudoprinceps*, RÜFFLE (1963) found material which he referred to *Laurus primigenia* to have a different epidermal structure. The cuticles of the material from the Randecker Maar, although poorly preserved, closely resembled that of the Kreuzau material referred to *Laurus primigenia* by WEYLAND (1934).

WEYLAND (1934, p. 71) was one of a number of authors to point out the rather heterogeneous nature of material referred to *Laurus primigenia*, and emphasised the need to refer back to the diagnosis of Unger's type material from Sotzka (UNGER, 1850, p. 423; 1851, p. 168). This material was diagnosed as follows: *L. foliis subcoriaceis late lanceolatis acuminatis integerrimis penninerviis, nervo primario valido, nervis secundariis tenuibus subrectis simplicibus sparsis subangulo acuto egredientibus*. A comparison of the illustrations given by UNGER (1851, Tafel 19, figs. 1-4) and the material figured by WEYLAND (1934, Tafel 12, figs. 1 and 3, Tafel 13, figs. 2 and 5) indicates that the number and spacing of the lateral

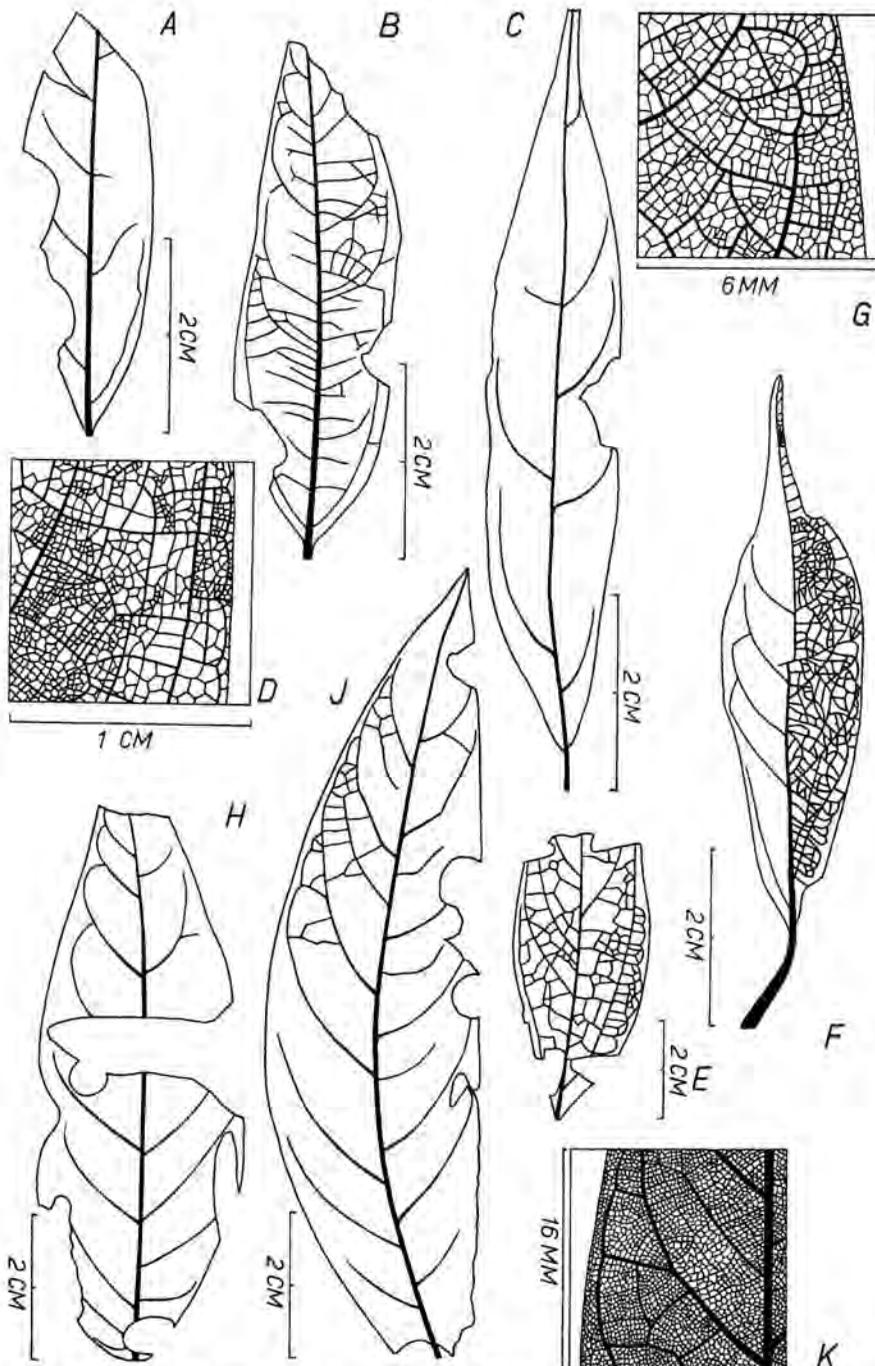


Fig. 23. A-G = XXIV: A = Utrecht 3829; B = Cologne, Coll. H. Weyland 1405; C = Utrecht 3827; D = Utrecht 3823, detail showing venation and leaf margin; E = Utrecht 3826; F = Berlin 346; G = Berlin 346, detail showing venation and leaf margin. H-K = XXV: H = Utrecht 3821; J = Utrecht 3822 (drawing based on specimen and its counterpart); K = Utrecht 3822, detail showing venation and leaf margin.

veins was similar in both cases. However, while Weyland's material had a length/breadth ratio of only 3.5:1-4.0:1 the type material had a length/breadth ratio of c.5:1-c.7:1. Nevertheless, the great amount of variability encountered in the length/breadth ratio of material collected since Weyland's revision would tend to suggest that the material from Kreuzau was similar, if not identical, to that from Sotzka. No details of the cuticle of the Sotzka material are known.

The material referred to *Laurus primigenia* by WEYLAND (1934) is fairly uniform, with the exception of Berlin 336, figured by WEYLAND (1934, Tafel 12, fig. 3). This specimen differs from the remaining specimens in that the spacing of the lateral veins reaches a maximum mid-way, rather than proximally. While Berlin 346 and 361 yielded cuticles reflecting the characteristic domed cells of the epidermis, Berlin 336 lacked any trace of a cuticle. The status of this specimen must therefore remain in doubt.

WEYLAND (1934, p. 71) considered the present taxonomic entity to be referable to *Laurus* on the basis of the course of the secondary veins. In expressing this opinion Weyland does not seem to have taken the length/breadth ratio of the leaves (usually 1.2:1-3.8:1 in living material of *Laurus*), or the number and spacing of the lateral veins into consideration. Compared with the fossil, lateral veins are more numerous in the leaves of *Laurus* and tend to reach a maximum spacing mid-way along the lamina, and never proximally. Cuticle analysis also refutes the reference of the material to *Laurus*. Leaves of *Laurus* are characterized by having an upper and lower epidermis with highly undulate cell walls, and stomata which are frequently rhombic in shape. While a reference of the fossil to *Laurus* proved incorrect, a reference to the Lauraceae would appear to be substantiated by cuticle analysis. Of all the American and Chinese material submitted to examination by the present author, certain species of Lauraceae approximated most closely to the fossil in overall appearance, and more particularly in the presence and nature of the domed cells. Domed cells are found in species belonging to families other than the Lauraceae e.g. *Acer cinnamomifolium* Hayata (Aceraceae), *Amorpha crenulata* Rydb. (Leguminosae), *Rhodoleia parvipetala* Tong (Hamamelidaceae), *Cyclea sutchuenensis* Gagnep. (Menispermaceae), *Actinidia melanandra* Franch. (Actinidiaceae), *Euptelea pleiosperma* Hook. f. et Thoms. (Trochodendraceae). However, these species were found to differ from the fossil when given a close scrutiny.

The leaves of *Acer cinnamomifolium*, while closely resembling the fossil in venation, have an epidermis differing in a number of respects from that of the fossil. The doming of the cells is restricted to the epidermal cells over the veins and the form of the guard cells cannot be made out clearly in the cuticle.

In the same way *Amorpha crenulata* has domed cells restricted to those parts of the epidermis over the veins. Moreover, the leaflets of *Amorpha*

crenulata differ from the leaf-remains in several other respects as well. The leaflets have a rounded apex and camptodromous venation in which the secondary veins are straight for the greater part of their length.

Although *Rhodoleia parvipetala* has domed cells over the entire leaf surface, it differs in that the venation pattern is camptodromous and the finer veins are not reflected in the cuticle. Furthermore, the presence of large hair bases and guard cells with a markedly thickened poral wall constitute differences of a sufficient magnitude to distinguish this species and the fossil without difficulty.

In *Cyclea sutchuenensis* domed cells are present on and between the veins on the lower surface of the leaf but the upper epidermis, unlike that of the fossil, is characterized by markedly undulate cell walls. The leaves of *Cyclea sutchuenensis* moreover differ markedly in outward appearance from the leaf-remains in question. The lamina is broad ovate with a markedly cordate leaf base, while the venation is more or less actinodromous.

While the leaf-remains have an entire leaf margin *Actinidia melanandra* has leaves with a non-entire margin and need not be considered further.

In *Euptelea pleiosperma* the leaves sometimes have an entire margin but more commonly is the leaf margin characterized by the presence of strongly serrate teeth, with each tooth ending in a mucronulate tip. The venation is furthermore camptodromous and the cuticle very thin.

Leaves with an epidermis similar to that encountered in the fossil are found in a number of genera of the Lauraceae e.g. *Machilus ichangensis* Rehd. et Wils., *Neolitsea zeylanica* (Nees) Merrill and various species of *Lindera* and *Litsea*. WILLIS (1960, p. 401) quotes *Machilus* as having 20 species in all. CHUNG (1924) mentions 15 species as occurring in China. Of these fifteen the present author has been able to examine 7 species. All these species were characterized by leaves having camptodromous venation with 8-23 secondary veins per side. This would seem to leave only *Lindera*, *Litsea* and *Neolitsea* as possibilities. In members of these genera cuticles very similar to or identical with the type displayed by the fossil are found e.g. *Lindera cercidifolia* Hemsl., *L. citriodora* (Sieb. et Zucc.) Hemsl., *Litsea eubeba* (Lour.) Pers., *L. ichangensis* Gamble and *Neolitsea zeylanica* (Nees) Merrill. These five species show differences in gross-morphology. While the leaves of *Lindera citriodora* and *Litsea eubeba* have camptodromous venation, those of *Lindera cercidifolia*, *Litsea ichangensis* and *Neolitsea zeylanica* have more or less acrodromous venation. The leaves of *Litsea ichangensis* and *Neolitsea zeylanica* resemble the fossil more closely than those of *Lindera cercidifolia*. While *Lindera cercidifolia* has leaves with a broad ovate lamina and a truncate base, *Litsea ichangensis* has leaves with an elliptical or obovate lamina and an acute leaf base, and *Neolitsea zeylanica* ovate to elliptical leaves with an obtuse or rounded leaf base. However, it should be remembered that *Lindera*, *Litsea* and *Neolitsea* are large genera. *Lindera* (inclusive of

Benzoin) tells 80–100 species and *Litsea* 180–400 species, while *Neolitsea* is estimated to have 80 species (WILLIS, 1960; Buchheim in ENGLER, 1964). All three genera have a number of species with acrodromous venation, so that a choice between these genera would not appear to be feasible at this stage.

Herbarium material examined in detail:

<i>Acer cinnamomifolium</i> Hayata	Coll. R. C. Ching 1983	(E) det. W. P. Fang
<i>Actinidia melanandra</i> Franch.	Coll. W. P. Fang 2364	(E) det. H. L. Li
<i>Amorpha crenulata</i> Rydb.	Coll. J. K. Small 3-5-1923	(U) _____
<i>Cyclea sutchuenensis</i> Gagnep.	Coll. G. Forrest 9829	(E) det. W. E. Evans
<i>Euptelea pleiosperma</i> Hook. f. et Thoms.	Coll. G. Forrest 19639	(E) det. W. E. Evans
<i>Lindera cercidifolia</i> Hemsl.	Coll. G. Forrest 29087	(E) _____
<i>Lindera citriodora</i> (Sieb. et Zucc.) Hemsl.	Coll. A. N. Steward 2725	(E) det. E. D. Merrill
<i>Litsea eubeba</i> (Lour.) Pers.	Coll. A. Henry 11395	(E) det. C. K. Allen
<i>Litsea ichangensis</i> Gamble	Coll. E. H. Wilson 34	(E) det. C. K. Allen SYNTYPE
<i>Machilus grijsii</i> Hance	Coll. T. M. Tsui 127	(E) det. F. P. Metcalf
<i>Machilus ichangensis</i> Rehd. et Wils.	Coll. Handel-Mazzetti 7778	(E) det. Handel- Mazzetti
<i>Machilus rehderi</i> Allen	Coll. 8-6-1905, Herb. H. Léveillé	(E) det. C. K. Allen PARATYPE
<i>Machilus shweliensis</i> W. W. Smith	Coll. G. Forrest 9624	(E) det. W. W. Smith TYPE
<i>Machilus thunbergii</i> Sieb. et Zucc.	Coll. C. Y. Chiao 2908	(E) det. A. Rehder
<i>Machilus velutina</i> Champ.	Coll. Y. Tsiang 1543	(E) det. E. D. Merrill
<i>Machilus viridis</i> Handel- Mazzetti	Coll. J. F. Rock 8920	(E) det. H. Liou
<i>Neolitsea zeylanica</i> (Nees) Merrill	Coll. W. P. Fang 5775	(E) det. C. K. Allen
<i>Rhodoleia parvipetala</i> Tong	Coll. A. Henry 11425	(E) det. A. W. Exell

XXV

Synonym: *Ficus lanceolata* Heer? Coll. H. Weyland 1663, det. H. Weyland!

Description:

Petiole > 9–11.5 mm long and 1.8–2.1 mm wide, more or less parallel-sided, straight, sometimes making a slight angle with the midvein.

Lamina elliptical, c. 8.2–10.6 cm long, 2.4–3.7 cm wide, the length/breadth ratio being 2.8:1–3.6:1 (–c. 4:1). Leaf apex acute, leaf base acute, obtuse or rarely rounded.

Leaf margin entire.

Venation camptodromous, midvein straight or curved, hardly or markedly tapering along length, 0.40–0.45 mm wide at mid-point between

base and apex of lamina. Midvein bearing 7-c.12 secondary veins per side, the most proximal vein arising at 30°-65°, arising in the remaining part of the basal third of the lamina at 35°-80°, in the median third at 40°-65°, in the apical third at 45°-70°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the veins somewhat irregular reaching maximum mid-way or apically (fig. 24). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.05-0.25 mm wide at mid-point, interconnected distally by fine extensions of secondary veins. Intermediate

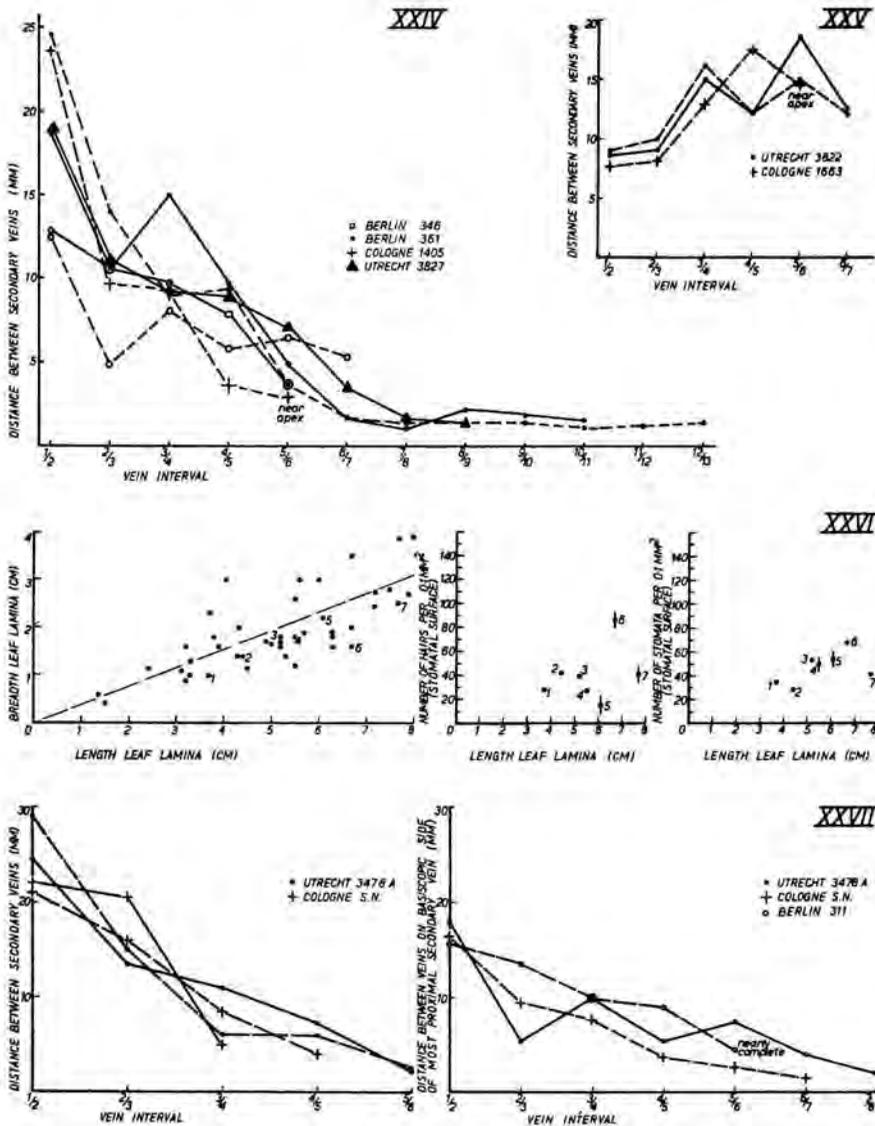


Fig. 24. Graphs XXIV, XXV, XXVI, XXVII.

veins 1-7 per intercostal field, occasionally having somewhat twisted course, arising from the midvein at 55° - 120° , running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to $1/2$ - $7/8$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 5-12 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 60-115 per 10 mm^2 , surrounded by broad veinlets with only a few, unbranched, free vein-endings.

Epidermis in non-stomatal condition composed of 220-440 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1-2.5:1. Cell wall 0.5-3.0 microns thick, largely unpitted, straight or occasionally somewhat undulate, 0-6 lobes per cell, depth from the tips of the lobes to the bottoms of the sinuses up to 7.2 microns. Cells over veins elongate, more or less rectangular and smaller than the rest of the epidermal cells, the cell length/cell breadth ratio being 1:1-3:1. Finer veins only sometimes reflected in cuticle. Cells at leaf margin c.400 per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1-3.5:1, unspecialised or arranged in c.30 rows, cell wall 1.0-1.5 microns thick, hardly pitted, straight. Epidermis in stomatal condition composed of 280-630 somewhat domed cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1-5:1. Cell wall 0.35-1.50 microns thick, largely unpitted, straight. Cells over veins elongate, the cell length/cell breadth ratio being 1:1-5.5:1. Finer veins somewhat reflected in cuticle. Stomata 16.2-27.0 microns long and 12.6-21.6 microns broad, breadth 64-133 % length, 0-15 per 0.1 mm^2 ; stomatal index 0-4 %. Stomata variously orientated, slightly depressed, somewhat arranged in groups, apices non-retuse. Stomatal slit 50-77 % stomatal length. Accessory cells 2, 4-5, symmetrical with 0-3 polar and 2-3 lateral cells, more or less similar in size or somewhat larger than the rest of the epidermal cells. Hair bases present, 6.3-12.6 microns in diameter, over and between the veins, 0-14 per 0.1 mm^2 , those between the veins with 5-9 associated cells radiating out from the base, sometimes with somewhat thickened cell walls. Internal resinous bodies apparently absent.

Specimens examined: Geol. Inst. Cologne: Coll. H. Weyland 1663, 1717
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3820, 3821,
3822.

Discussion:

Closely resembling No. XXIV; the taxa, however, differ in the number of secondary veins per side, the spacing of the secondary veins and the stomatal index. Leaves similar in gross-morphology and having a similar epidermis are to be found in a number of genera of the Lauraceae e.g. *Lindera*, *Litsea* and *Machilus*. However, no decision as to the generic

affinity of the leaf-remains could be made on the basis of the comparative material available to the author.

XXVI

<i>Synonyms</i> : <i>Cinnamomum buchii</i> Heer	QUAAS, 1910, p. 984; FLIEGEL and STOLLER, 1910, p. 246!
<i>Cinnamomum</i> c.f. <i>buchii</i> Heer	QUAAS, 1910, p. 984; FLIEGEL and STOLLER, 1910, p. 246
<i>Cinnamomum lanceolatum</i> (Unger) Heer	QUAAS, 1910, p. 984; FLIEGEL and STOLLER, 1910, p. 246!
<i>Cinnamomum polymorphum</i> (A. Braun) Heer	WEYLAND, 1934, p. 81!
<i>Cinnamomum</i> c.f. <i>polymorphum</i> (A. Braun) Heer	QUAAS, 1910, p. 984
<i>Cinnamomum scheuchzeri</i> Heer	QUAAS, 1910, p. 984; FLIEGEL and STOLLER, 1910, pp. 245-246; WEYLAND, 1934, p. 81!
<i>Cinnamomum sezannense</i> Watelet	FLIEGEL and STOLLER, 1910, p. 246
<i>Cinnamomum spectabile</i> Heer	WEYLAND, 1934, pp. 81-83, Tafel 14, fig. 7; GOTHAN and WEYLAND, 1964, p. 428, Abb. 298f!
<i>Litsea</i> sp.	Coll. H. Weyland 1670, det. H. Weyland!
<i>Ziziphus integrifolia</i> Heer	FLIEGEL and STOLLER, 1910, p. 245

Description :

Petiole (4-)12-17 mm long and 0.8-1.8 mm wide at mid-point, more or less parallel-sided or increasing in width away from leaf base, straight or somewhat curved near the base of the lamina, making no angle with the central primary vein.

Lamina (ovate-)elliptical(-obovate), 1.3-c.11 cm long, 0.57-4.5 cm wide, the length/breadth ratio being 1.9 : 1-4.25 : 1 (fig. 24). Leaf apex acute or acuminate, leaf base acute or rounded and sometimes somewhat oblique.

Leaf margin entire.

Venation acrodromous or rarely camptodromous, primary veins (1-)3. Lateral primary veins opposite or alternately arranged, arising at 25°-45° from the central primary vein 0-20 mm above leaf base; these lateral veins 0.05-0.2(-0.4) mm wide at mid-point, extending for 50-75 % length of lamina. The lateral primary veins bearing 5-20 veins of a higher order on their basisopic side. Central primary vein straight, apically curved or gently curved throughout length, slightly or markedly tapering along length, 0.15-0.60 mm wide at mid-point between base and apex of the lamina. Central primary vein bearing 1-3(-7) secondary veins per side, arising from the central primary vein at 40°-70°, the angle at which the veins arise slightly decreasing within the first few mms. Secondary veins mostly alternately arranged, hardly to slightly tapering along their length, (0.05-) 0.10-0.25 mm wide at mid-point, interconnected distally by fine

extensions of the secondary veins, or tertiary veins. Intermediate veins 2–18 per intercostal field, minor ones having a somewhat twisted course, arising from the central primary vein at 50° – 110° , running more or less parallel to one another, the spacing between them constant, increasing distally or occasionally somewhat irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to $1/2$ – $2/3$ the distance from the central primary vein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary veins 3–10 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basisopic sides of secondary vein more or less similar. Areoles, 120–240 per 10 mm^2 , with none to many free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of 300–680 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–2 : 1(–4 : 1). Cell wall (0.5–) 0.9–2.0(–5.5) microns thick, largely unpitted, sometimes with hemispherical projections, straight or slightly undulate with 0–8 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells over veins somewhat more rectangular than in the areas between, the cell length/cell breadth ratio being 1 : 1–4 : 1. Finer veins not reflected in cuticle. Hair bases 6.3–16.2 microns in diameter sometimes present, 0–10 per 0.1 mm^2 , with 4–7 associated cells arranged in a radiating or rarely spiral pattern. Cell walls unthickened next hair bases. Cells at leaf margin c.750 per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–3 : 1, not arranged in rows. Cell wall 1–2 microns thick, unpitted, \pm straight. Epidermis in stomatal condition composed of 305–635 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–3 : 1. Cell wall 0.6–1.0 microns thick, rarely or somewhat pitted, sometimes with hemispherical or elongate projections, straight or slightly undulate with 0–10 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 6 microns. Cells over veins square or rectangular, the cell length/cell breadth ratio being 1 : 1–12.5 : 1, the cell wall somewhat undulate in the case of the fine veins and straight in the case of wide veins, cell wall 0.6–3.0 microns thick. Finer veins reflected in cuticle. Stomata 8.4–25.2 microns long and 7.0–24.0 microns broad, sometimes asymmetrical or angular in outline, breadth 50–171 % length, (10–)20–55(–85) per 0.1 mm^2 , the number showing little correlation with the length of the lamina (fig. 24); stomatal index 8–25 %. Stomata variously orientated, undepressed or slightly depressed, somewhat arranged in groups, apices rarely retuse. Stomatal slit 37.3–75.0 % stomatal length, the cuticle over the guard cells thin-walled and easily destroyed. Accessory cells (3–)4–7, mostly symmetrical with 2–4 polar and 2–4 lateral cells, although when only 3 cells present a radial arrangement results. Accessory cells similar in size to the rest of the epidermal cells. Hair bases 4.5–11.2 microns in diameter present, (0–)23–93 per 0.1 mm^2 (fig. 24) with, when not occurring over a vein, 4–7 associated cells arranged radially. Cuticle

somewhat thicker, up to 6 microns in thickness, in close proximity to the hair bases. Internal resinous bodies sometimes present.

Specimens examined: 298, among which the numbered specimens:

Deutsche Akad. Wiss. Berlin: 357(K 27), 360(K 27)
 Geol. Inst. Cologne: Coll. H. Weyland 1397(K 36), 1399(K 6),
 1400(K 36), 1401(K 6), 1402(K 36), 1403(K 6), 1404a(K 6),
 1404b(K 6), 1404c(K 6), 1404d(K 6), 1670
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3238A, 3248,
 3249, 3250, 3251, 3252, 3253, 3254, 3255, 3256A, 3257, 3258,
 3259, 3260, 3261, 3262, 3263, 3264, 3265, 3266, 3267A, 3268,
 3269, 3270, 3271, 3272, 3273, 3274, 3275, 3276, 3277, 3278A,
 3278B, 3279, 3280, 3281, 3282A, 3283, 3284, 3285, 3286, 3287,
 3288, 3289, 3290, 3291, 3292, 3293, 3294, 3295A-J, 3296A-N,
 3297A-J, 3410B, 3542B, 3845, 3846A, 3913B, 3931C.

Discussion:

Leaf-remains with acrodromous venation have been the source of taxonomic confusion for some time. While authors in the middle of last century described such leaf-remains under a host of different binomials, there has been a general tendency to a reduction in the number of binomials in current use.

In his provisional list of the Kreuzau assemblage J. Stoller (in FLIEGEL and STOLLER, 1910, p. 246) mentioned the presence of *Cinnamomum sezannense* Watelet (= *Daphnogene sezannense* (Watelet) Saporta), which he apparently considered to be synonymous with *Cinnamomum lanceolatum* (Unger) Heer (= *Daphnogene lanceolata* Unger). However, PIMENOVA (1939) has recorded *Daphnogene sezannense* as occurring alongside *Cinnamomum lanceolatum* in an assemblage from the Ukraine, while FISCHER (1950) considered the former taxon to have the rank of species as well. Nevertheless, a comparison of *Cinnamomum lanceolatum* with the drawing of the type material of *Cinnamomum sezannense* (WATELET, 1865-6, Planche 50, fig. 2) in no way contradicts Stoller's opinion. The specific status of *Cinnamomum lanceolatum* itself has come to be questioned. While the majority of authors publishing during the course of last century and the beginning of the present century considered *Cinnamomum lanceolatum* to be a recognizable specific entity, there has been a trend to combine *Cinnamomum lanceolatum* (Unger) Heer and *C. scheuchzeri* Heer in a single taxon e.g. SCHEID (1929), GILLET (1954), KNOBLOCH (1962) and WALTHER (1964). Recent exceptions are MILAKOVICÁ (1955) and PALAMAREV (1961, 1964), who consider *Cinnamomum scheuchzeri* and *C. lanceolatum* to represent two separate taxa. CAVARA (1886, p. 751) was one of the earliest authors to suggest that *Cinnamomum lanceolatum* was probably only a variety of *Cinnamomum scheuchzeri* or *Cinnamomum polymorphum* (A. Braun) Heer. While retaining *Cinnamomum scheuchzeri* and *C. lanceolatum* as two separate taxa, J. Stoller (in FLIEGEL and STOLLER, 1910, p. 246) noted that all possible transitions existed between

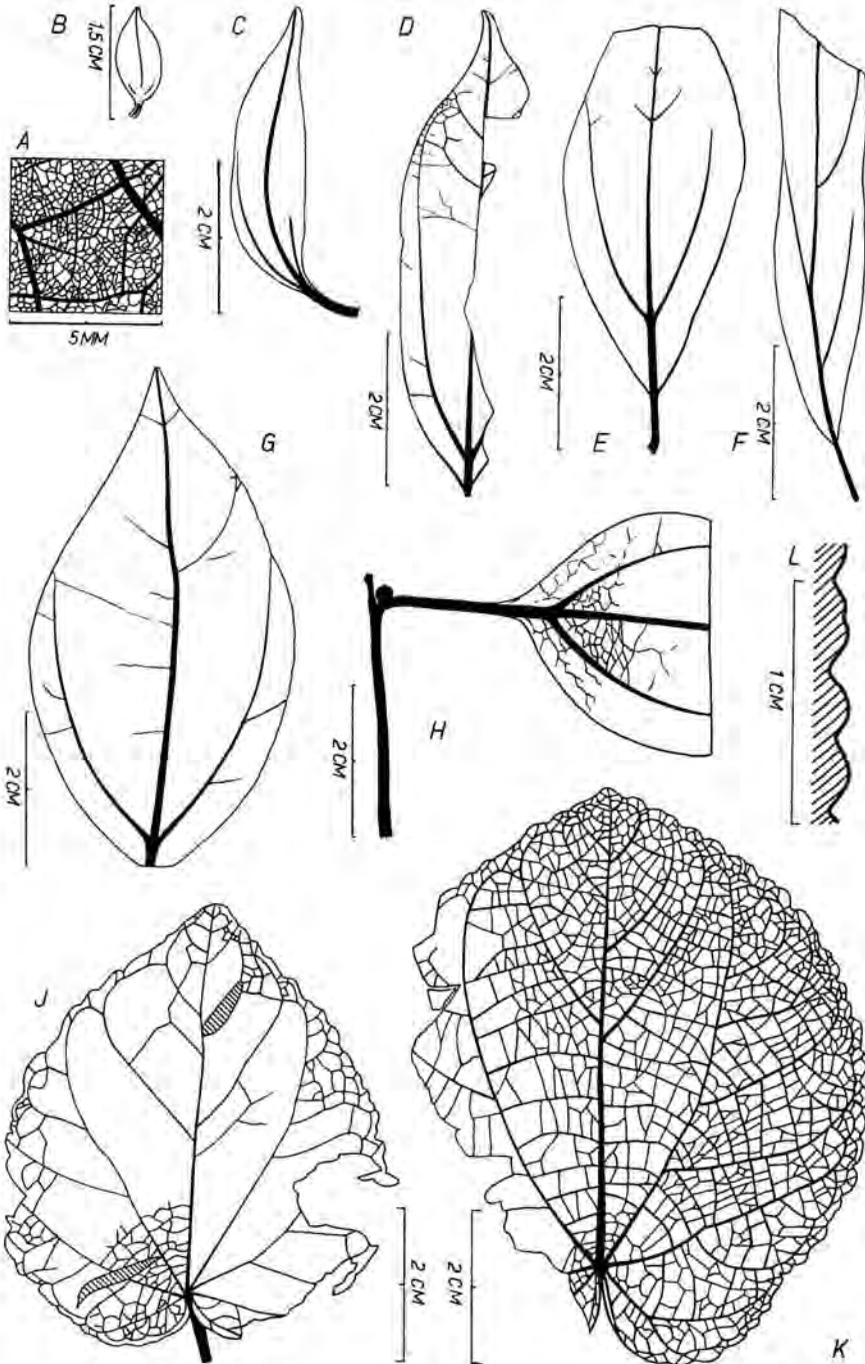


Fig. 25. A-H = XXVI: A = detail showing venation; B = Utrecht 3288; C = Utrecht 3261; D = Utrecht 3266; E = Utrecht 3257; F = Utrecht 3279; G = Utrecht 3270; H = Utrecht 3260. J-L = XXVII: J = Cologne, Coll. H. Weyland s.n.; K = Utrecht 3478 A; L = Utrecht 3478 A, detail showing leaf margin.

specimens from Kreuzau referred to one or other species. WEYLAND (1934, p. 81) considered *Cinnamomum lanceolatum* a synonym for *C. scheuchzeri*. The submerging of these two species in a single taxon has tended to be upheld by cuticle analysis. Although only fragmentary, the epidermis of the material referred to by REID and CHANDLER (1926) as *Cinnamomum lanceolatum* would appear to have been the same as that obtainable from Kreuzau specimens attributed to *Cinnamomum scheuchzeri* by Professor Weyland.

While the material from Kreuzau determined as *Cinnamomum lanceolatum* and *C. scheuchzeri* can be united, the material of *Cinnamomum buchii* Heer from Kreuzau as determined by J. Stoller appeared to be the same as H. Weyland's *Cinnamomum polymorphum*. WEYLAND (1934) made no mention of *Cinnamomum buchii* in his discussion of *Cinnamomum polymorphum*, but SCHEID (1929) and HADŽIEV and PALAMAREV (1962) referred to *Cinnamomum buchii* and *C. polymorphum* as being synonymous.

The species referred to by WEYLAND (1934) as *Cinnamomum polymorphum* was originally referred to as *Ceanothus polymorphus* by Alexander Braun. VON ETTINGSHAUSEN (1852) renamed this species *Daphnogene polymorpha* (A. Braun) Ett., while Oswald Heer referred to it as either *Camphora polymorphum* or *Cinnamomum polymorphum*. KRÄUSEL and WEYLAND (1950) and later authors referred to it as *Cinnamomophyllum polymorphum*.

In proposing the new specific entity, *Cinnamomum scheuchzeri*, HEER (1856, p. 88) pointed out that it could be differentiated from *Cinnamomum polymorphum* on the basis of three characters: 1) Mostly shorter petiole, 2) Lateral veins close to and running parallel to the leaf margin, 3) No "abgesetzte" leaf apex. However, while *Cinnamomum polymorphum* and *C. scheuchzeri* Heer (= *Cinnamomophyllum scheuchzeri* (Heer) Kräusel et Weyland) are universally accepted taxa, commonly mentioned as occurring together in a given fossil assemblage, a glance at the synonymy will indicate the state of confusion which exists as to the circumscription of these taxa. HEER (1856), ENGELHARDT (1881), STAUB (1882, 1887) and MESCHINELLI and SQUINABOL (1893) considered *Ceanothus polymorphus* A. Braun as being equivalent to *Cinnamomum scheuchzeri* in part. Those specimens referred to *Ceanothus polymorphus* by UNGER (1847, Tab. 49, figs. 12, 13) were referred to *Cinnamomum scheuchzeri* by HEER (1856) and PILAR (1883). While PILAR (1883) and STAUB (1887) considered the specimens figured from Swoszowice by UNGER (1849, Tab. 14, figs. 17-18) to be *Cinnamomum polymorphum*, IL'INSKAYA (1964) in her revision of the Swoszowice assemblage considered only Unger's Tab. 14, fig. 18 to be *Cinnamomum polymorphum* and referred Tab. 14, fig. 17 to *Viburnum swoszowicianum* n. sp. Material referred to *Cinnamomum scheuchzeri* in a provisional list of the Swoszowice assemblage (MCHEDLISHVILI, 1956, p. 97) was replaced in *Cinnamomum polymorphum* by Il'inskaya. VON ETTINGSHAUSEN (1855) described some leaf-remains from Monte Promina

as *Daphnogene polymorpha*. PILAR (1883) considered some of the material (Tab. 6, figs. 3-5; Tab. 7, fig. 2) to be that of *Cinnamomum polymorphum*, but referred Tab. 7, figs. 3-6 to *Cinnamomum lanceolatum* (see also STAUB, 1887). In much the same way STAUB (1887) considered a specimen referred to as *Cinnamomum polymorphum* by VON ETTINGSHAUSEN (1872b, Tab. 10, fig. 1) to be *Cinnamomum lanceolatum*.

Although he was aware that R. Kräusel had encountered all possible transitions between *Cinnamomum scheuchzeri* and *C. polymorphum* in his (Schossnitz) material, WEYLAND (1934, p. 81) considered it possible to distinguish between these taxa on the basis of the Kreuzau material available to him. This opinion, based simply on the external appearance of the leaf-remains, was upheld by Professor Weyland in later work (KRÄUSEL and WEYLAND, 1950) in which the epidermal structure was also dealt with. A comparison of their descriptions, drawings and photographs of material from a number of localities would appear to indicate a certain difference between these two taxa. While the leaves attributed to *Cinnamomophyllum scheuchzeri* were leathery in texture and had numerous hairs on both surfaces of the lamina, the leaves attributed to *Cinnamomophyllum polymorphum* had a less xeromorphic texture and hair bases could not be recognized as such. The possibility that hairs may have been present in *Cinnamomophyllum polymorphum*, in conjunction with the great amount of variation encountered in typical "scheuchzeri" material (fig. 24) examined by the present author, has indicated that too much weight should not be placed on this character. KRÄUSEL and WEYLAND (1950) do not seem to have placed much weight on the hairiness of the leaves either, for they considered *Cinnamomum wonnacottii* BANDULSKA as a possible synonym for *Cinnamomophyllum scheuchzeri*. BANDULSKA (1928, p. 139) made a point of emphasising the fact that no hair bases were present on the epidermis of *Cinnamomum wonnacottii*. A re-examination of the cuticle preparation of *Cinnamomum wonnacottii* (V 20439a), figured by BANDULSKA (1928, Plate 8, fig. 8) and deposited in the British Museum (Natural History), has confirmed Bandulska's statement. Furthermore, while it is true that extreme forms referred to as *Cinnamomum polymorphum* do have a less resistant cuticle, this may simply have been the result of certain environmental factors. Leaves with a more mesomorphic texture and fewer hairs are to be expected of shade-leaves or of plants growing in a more humid environment. It therefore seems reasonable to combine the material referred to *Cinnamomum scheuchzeri* and *C. polymorphum* (WEYLAND, 1934) in a single taxon. These results agree with those of HANTKE (1954) who, on the basis of statistical work carried out on these forms, was forced to reunite these two taxa. This viewpoint has been accepted by WEYLAND and KILPPER (1963).

Neither of the specimens referred to by WEYLAND (1934, p. 81) as *Cinnamomum spectabile* Heer yielded more than a fragmentary cuticle indicating the presence of straight to undulate cell walls and a number

of internal resinous bodies. While *Cinnamomum spectabile* is generally considered a distinct entity the specimen figured as Tafel 14, fig. 7 by WEYLAND (1934) resembled the remaining specimens in outward appearance to such an extent that, in the absence of any contrary evidence, it was felt possible to include this specimen here. Only differences of a quantitative nature could be demonstrated between this and the remaining specimens. The lamina was larger, being 4.5 cm wide as opposed to 0.57–4.2 cm for the remaining material and this character went paired with wider lateral primary veins (0.4 mm mid-way along length, as opposed to 0.05–0.2 mm) and stronger secondary veins, with a width of 0.2–0.25 mm as opposed to 0.05–0.2 mm half-way along their length. No other differences could be recognized. The affinity of the other specimen referred to *Cinnamomum spectabile* by WEYLAND (1934, Tafel 14, fig. 6) is less certain. While the exact differences are difficult to pin down, the venation is \pm camptodromous. The texture of the leaf is moreover coarse, with the higher order veins prominent, while in the remaining material the higher order veins are difficult to make out. This and the fact that only 45–90 areoles were present per 10 mm² might suggest another affinity for the fossil. However, in the absence of an adequate cuticle preparation the exact status of this specimen will have to remain uncertain.

A glance at the synonymy of the present taxon should be enough to show how convinced the earlier authors were as to the generic affinity of the fossil. However, J. Stoller (in FLIEGEL and STOLLER, 1910) in referring some material to *Ziziphus* appears to have been aware that possibilities other than *Cinnamomum* existed and the same can be said of Professor Weyland's unpublished reference of Weyland 1670 to *Litsea*. In the years following his revision of the Kreuzau material Professor Weyland's opinion changed with regard to the leaf-remains he previously referred to *Cinnamomum*. Together with the late Professor R. Kräusel (KRÄUSEL and WEYLAND, 1950) he pointed out the difficulties involved in determining the affinities of such leaf-remains. Leaves with an acrodromous pattern of venation are to be found at the present day in a number of angiospermous families e.g. Ranunculaceae, Coriariaceae, Loganiaceae, Menispermaceae, Caprifoliaceae, Ericaceae, Compositae, Melastomataceae, Myrtaceae, Oleaceae, Leguminosae, Ulmaceae, Rhamnaceae and Lauraceae. While a detail survey of these families is not possible at present, a few comments would seem in place.

Leaves with acrodromous venation, although originating from very different angiosperm families may show a remarkable similarity to one another in gross-morphology. This would make it difficult to ascertain the affinity of the leaf-remains were it not for differences displayed by the epidermides of these taxa.

While a certain number of Monocotyledons may have leaves with an acrodromous venation pattern the majority of plants with such leaves belong to the Dicotyledons.

Of the Ranunculaceae certain species of *Clematis* e.g. *C. finetiana* Lév. et Vant. and *C. uncinata* Champ. have leaves with acrodromous venation. While the epidermal cell walls may be straight or undulating such as in the fossil, the adaxial epidermis is characterized by being large-celled. Furthermore, no hairs are present on the epidermis and the finer veins are not reflected in the cuticle.

Much the same can be said of the members of the Coriariaceae examined. Leaves of both *Coriaria nepalensis* Wall. and *C. sinica* Maxim. had large epidermal cells and an epidermis free of hairs. The stomata are moreover narrow.

Of the Loganiaceae leaves of certain species of *Strychnos* bore an outward resemblance to the leaf-remains. However, in neither species for which cuticle preparations were available were the finer veins reflected in the cuticle and neither bore hairs.

The external appearance of at least some *Cocculus* species (Menispermaceae) has confused taxonomists working on recent plants and specimens of this genus have not infrequently been referred to *Cinnamomum* (see KRÄUSEL and WEYLAND, 1950, p. 67). The material of *Cocculus laurifolius* DC. made use of here was originally described as a new species of *Cinnamomum* (*C. esquirolii*) by Hector Léveillé (see LAUENER, 1962, p. 73). The epidermides of the two species examined differed markedly from each other and from material examined by KRÄUSEL and WEYLAND (1950, pp. 66-67). The leaves of *Cocculus heterophyllus* Hemsl. et Wils. have straight epidermal cell walls and stomata which are symmetrical and with a somewhat thickened poral wall to the guard cells. The epidermal wall of the guard cells is moderately well developed. Adjoining the stomata are 4-8 accessory cells. The leaf material of *Cocculus laurifolius* DC. examined on the present occasion had epidermides with highly undulate cell walls, those of the upper surface having hemispherical projections. The stomata resemble those of *Cocculus heterophyllus*. However, the boundary between the guard cells and the accessory cells, two in number, was vague in the cuticle preparation, as was the junction between these accessory cells. This gives an impression that the stomata are separated from the rest of the epidermal cells by a structureless ring. On the leaves of this species, as in *Cocculus heterophyllus*, no hairs were present and the finer veins were, at most, only somewhat reflected in the cuticle.

One finds stomata with accessory cells similar to those found in *Cocculus laurifolius* in certain members of the Caprifoliaceae having leaves with an acrodromous venation pattern e.g. *Viburnum cinnamomifolium* Rehder, *V. davidii* Franch. and *V. propinquum* Hemsl. The accessory cells are separated from the remaining epidermal cells by a thickened cell wall. Furthermore, only very few hair bases were encountered on the epidermides of these three species.

Like the Caprifoliaceae, members of the Ericaceae having leaves with acrodromous venation e.g. *Gaultheria dumicola* W. W. Smith, *Thibaudia*

costaricensis Hoer., *T. floribunda* H.B.K. have straight or undulate epidermal cell walls which sometimes show a development of hemispherical projections. Certain resemblance to the leaf-remains is to be found in the nature of the stomata, stomatal slit and accessory cells. However, while trichome bases are sometimes present, small hair bases such as encountered in the leaf-remains are not present and the finer venation is not reflected in the cuticles of either surface of the lamina.

Certain members of the Compositae e.g. *Vernonia henryi* Dunn have leaves displaying an acrodromous venation pattern. Glands are present on the leaves of *Vernonia henryi* which, moreover, has stomata which are symmetrical and oval to round in outline. While hair bases are present in *Vernonia henryi* these are not of the type encountered in the leaf-remains.

In leaves of *Myrtus melastomoides* Muell. (Myrtaceae) trichomes are present as well. However the hair bases, present over the veins, are much larger than those encountered in the fossil, being some 28–43 microns in diameter. The stomata, oval or round in outline and sometimes with retuse apices, are always symmetrical.

In the Oleaceae hair bases may be present over the entire lower surface of the lamina or confined to the leaf margin. However, when present on the abaxial epidermis e.g. in *Jasminum urophyllum* Hemsl. these were found to be larger than those encountered in the fossil i.e. 14–70 microns in diameter. In this species the cuticle over the accessory cells was unlike that of the leaf-remains in being striate and showing no sign of cell walls between the individual accessory cells. However, while this is not true of another species having leaves with acrodromous venation (*Jasminum humile* L.) the stomata were oval to round in outline and symmetrical in both cases.

Various species of *Bauhinia* (Leguminosae) not only resemble the fossil in having leaves displaying acrodromous venation, but have epidermides showing a remarkable resemblance to that of the leaf-remains. The epidermides of *Bauhinia finlaysoniana* Srah. and *B. kockiana* Korth. resemble that of the fossil very closely in cell shape, nature of the cell wall, arrangement of the accessory cells and in the nature of the guard cells. Like those of the fossil material the guard cells are characterized by having a thin poral wall. In the two species of *Bauhinia* examined hairs are also present on the abaxial surface of the leaves. However, the hair bases of these species differ from those of the leaf-remains in being larger (diameter 11.4–28.6 microns) and being more highly thickened.

Various species of *Celtis* (Ulmaceae) have leaves with acrodromous venation and while many of these species have a non-entire leaf margin this is not invariably the case. The epidermis on both surfaces of the lamina has straight or slightly undulate cell walls and hair bases which are sometimes large e.g. *Celtis pallida* Torr., but more commonly similar to those of the fossil in size. While the stomata may have guard cells

with somewhat thickened poral walls, the poral walls may be as thin as in the fossil material under comparison. However, the four species of *Celtis* submitted to detailed examination had stomata which were invariably symmetrical, while the finer veins were not found to be reflected in the cuticle.

Members of the Rhamnaceae having leaves with acrodromous venation examined in the present connection had epidermides similar to those encountered in *Celtis*. The epidermides were not unlike that of the fossil in many respects. The epidermal cells had straight or undulate cell walls and the finer veins are reflected in the cuticle on the abaxial surface of the lamina. While hairs are not invariably present on the abaxial surface of the lamina they may be so numerous as to render the other features impossible to observe. A few hairs may be present on the adaxial surfaces of the leaves as well. These hairs have hair bases with a similar diameter to those of the leaf-remains. The stomata may have guard cells with thin poral walls, such as encountered in the leaf-remains, but it is worth pointing out that while the fossil not infrequently has asymmetrical stomata or stomata with an angular outline these were invariably symmetrical and oval to round in outline in the species of *Paliurus* and *Ziziphus* examined. Until evidence to the contrary is forthcoming, J. Stoller's reference of some of the fossil material to *Ziziphus* cannot be accepted.

As pointed out by KRÄUSEL and WEYLAND (1950) leaf-remains such as those under consideration would appear to be referable to the Lauraceae on grounds of the great similarity between the overall appearance of the fossils and the leaves of certain members of the Lauraceae. Representatives of this family not infrequently display stomata angular in outline and asymmetrical in form and without a thickening of the poral walls of the guard cells, so typical of most of the above-mentioned families. An arrangement of the accessory cells similar to that of the leaf-remains is to be found in the Lauraceae as well. However, a reference of the leaf-remains to one of the possible genera has proved to be a difficult, if not impossible, task. KRÄUSEL and WEYLAND (1950) considered that the taxon in question might be referable to *Cinnamomum*. The upper and lower epidermides of *Cinnamomum* have mostly unpitted cell walls which are either straight, slightly undulate or markedly undulate. Hairs may or may not be present. The finer veins are, at most, but slightly reflected in the cuticle on the adaxial surface of the lamina; the finer veins are mostly reflected in that on the abaxial surface. Like those of the leaf-remains the accessory cells are mostly arranged symmetrically round the stomata, with 2-4 polar and 2-4 lateral cells. Internal resinous bodies are mostly present. However, the stomata of *Cinnamomum* are rarely asymmetrical in form or angular in outline and the guard cells either bear stomatal ledges e.g. *Cinnamomum pedunculatum* (Thunb.) Nees or display a somewhat thickened poral wall. Of the American and Chinese material

examined by the present author the epidermides of *Neolitsea homilantha* Allen, *Lindera fragrans* Oliv., but more particularly that of *Lindera strychnifolia* Hemsl. showed a not uncertain affinity to that of the leaf-remains.

However, the leaves of none of these species showed complete agreement with the fossil. In the material of *Lindera strychnifolia* and *L. fragrans* the lateral primary veins invariably arose at the very base of the lamina. Moreover, in *Lindera strychnifolia* the cell wall of the upper epidermis was markedly pitted and the finer veins were not reflected in the cuticle of the lower surface of the leaves. In *Lindera fragrans* no hairs were present on the upper surface of the leaf and the finer veins were only somewhat reflected in the abaxial cuticle. In the leaves of *Neolitsea homilantha* the poral wall of the guard cells was mostly somewhat thickened. A reference of the fossil leaves to one of the possible genera is not warranted at this stage.

Herbarium material examined in detail:

Bauhinia finlaysoniana Srah.	Coll. Scortehini s.n.	(U) _____
Bauhinia kockiana Korth.	Coll. H. H. Bartlett 7581	(U) det. E. D. Merrill
Celtis cinnamomea Lindl.	Herb. Hortus Bot. Utrecht 044048	(U) det. J. Amshoff
Celtis integerrima Merrill	Coll. S. K. Lau 66	(E) det. E. D. Merrill ISOTYPE
Celtis pallida Torr.	Coll. L. C. Hinckley 3376	(U) _____
Celtis philippensis Blanco	Coll. F. A. McClure 8926	(E) det. E. D. Merrill
	Coll. A. D. E. Elmer 18138	(U) _____
Celtis wightii Pl.	Coll. S. K. Lau 271	(E) det. E. D. Merrill
Cinnamomum burmanii (Nees) Blume	Coll. A. Henry 3466	(E) det. C. K. Allen
	Coll. Winckel 1735B	(U) det. H. Cammerloher
Cinnamomum camphorum Nees et Eberm.	Coll. C. Y. Chiao 14576	(E) det. E. D. Merrill
	Coll. M. Buysman 225	(U) _____
Cinnamomum inunctum Meisn.	Coll. S. S. Chien 5305	(E) det. S. S. Chien
Cinnamomum japonicum Sieb.	Coll. G. Murata 20-12-1961	(U) _____
Cinnamomum pedunculatum (Thunb.) Nees	Coll. Tso & Tsiang 2042	(E) det. E. D. Merrill
Clematis finetiana Lévl. et Vant.	Herb. H. Lèveillé	(E) det. L. A. Lauener
Clematis uncinata Champ.	Coll. C. Y. Chiao 14648	(E) det. E. D. Merrill
Cocculus heterophyllus Hemsl. et Wils.	Coll. unknown	(E) det. L. Diels
Cocculus laurifolius DC.	Coll. J. Esquirol 3586	(E) det. A. Rehder; det. L. A. Lauener
Coriaria nepalensis Wall.	Coll. G. Forrest 7553	(E) _____
Coriaria sinica Maxim.	Coll. S. S. Chien 5415	(E) det. S. S. Chien
Gaultheria dumicola W. W. Smith	Coll. G. Forrest 18832	(E) det. H. K. Airy- Shaw

<i>Jasminum humile</i> L.	Coll. G. Forrest 29005	(E) det. P. S. Green
<i>Jasminum urophyllum</i> Hemsl.	Coll. W. P. Fang 2196	(E) det. C. E. Kobuski
<i>Lindera fragrans</i> Oliv.	Coll. A. Henry 3295	(E) det. D. Oliyer SYNTYPE
<i>Lindera strychnifolia</i> Hemsl.	Coll. J. L. Gressitt 1564	(E) det. E. D. Merrill
<i>Litsea javanica</i> Blume	Coll. S. H. Koorders 3330B	(U) det. S. H. Koorders
<i>Myrtus melastomoides</i> Muell.	Herb. Bot. Mus. Utrecht 66144B	(U) _____
<i>Neolitsea aciculata</i> (Blume) Koidz.	Coll. G. Murata 15881	(U) _____
<i>Neolitsea aurata</i> (Hayata) Merrill	Coll. T. K. Peng, T. W. Tak, T. U. Kin 5-7-1924	(E) det. C. K. Allen
<i>Neolitsea homilantha</i> Allen	Coll. G. Forrest 9524	(E) det. C. K. Allen TYPE
<i>Paliurus aculeatus</i> Lam.	Herb. W. Behrendsen	(U) _____
<i>Paliurus spini-christi</i> Mill.	Stud. biol. Rheno-Trai in itinere 20-5-1960	(U) det. A. C. de Roon
<i>Strychnos aculeata</i> Solered.	Coll. A. J. M. Leeuwenberg 3196	(U) det. A. J. M. Leeuwenberg
<i>Strychnos axillaris</i> Colebr.	Coll. C. A. Backer 2630I	(U) det. P. W. Leenhouts
<i>Thibaudia costaricensis</i> Hoer.	Coll. P. H. Allen 4808	(U) det. A. C. Smith
<i>Thibaudia floribunda</i> H.B.K.	Coll. A. H. G. Alston 8103	(U) det. H. Sleumer
<i>Vernonia henryi</i> Dunn.	Coll. A. Henry 13343	(E) _____
<i>Viburnum cinnamomifolium</i> Rehder	Coll. W. K. Hu 8874	(E) det. T. R. Dudley
<i>Viburnum davidii</i> Franch.	Coll. K. L. Chu 2650	(E) det. T. R. Dudley
<i>Viburnum propinquum</i> Hemsl.	Coll. H. C. Chow 704	(E) det. T. R. Dudley
<i>Ziziphus borneensis</i> Merrill	Coll. A. D. E. Elmer 20149	(U) det. E. D. Merrill
<i>Ziziphus jujuba</i> Mill.	Coll. Stud. biol. Rheno- Trai in itinere 62-577	(U) det. R. C. J. van den Boom
<i>Ziziphus lota</i> (L.) Lam.	Coll. A. Palmomy 19-7-1939	(U) _____
<i>Ziziphus mauritiana</i> Lam.	Coll. A. L. Stoffers 4512	(U) det. A. L. Stoffers
<i>Ziziphus mucronata</i> Willd.	Coll. J. Lanjouw 1144	(U) det. A. M. E. Verhoef
<i>Ziziphus rignonii</i> Delp.	Coll. R. J. Wagner 630	(U) _____
<i>Ziziphus suluensis</i> Merrill	Coll. A. D. E. Elmer 21895	(U) _____

FAMILY CERCIDIPHYLLACEAE

XXVII. *Cercidiphyllum*

Synonym: *Grewia crenata* (Unger) Heer Weyland, 1934, p. 100, Tafel 22, fig. 7!

Description:

Petiole > 33 mm long and 1.9 mm wide at mid-point, more or less straight, making no angle with the midvein.

Lamina ovate or suborbicular, 5.7–7.5 cm long, 5.0–9.1 cm wide, the length/breadth ratio being 0.9 : 1–1.2 : 1. Leaf apex representing an angle of 90° or obtuse, leaf base cordate.

Leaf margin non-entire, sinuate with rounded teeth 0.2–1.5 mm across, alternating with acute or rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein straight, slightly tapering along length, 0.3–0.5 mm wide at mid-point between base and apex of lamina. Midvein bearing 4–6 secondary veins per side, arising in the basal third of the lamina at 35°–45°, in the median third at 35°–60°, in the apical third at 50°–80°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing and length of the secondary veins decreases away from the proximal end of the lamina (fig. 24). Secondary veins mostly subopposite or alternately arranged, although most proximal veins opposite, veins hardly to markedly tapering along their length, 0.15–0.55 mm wide at mid-point, interconnected distally by fine extensions of the secondary veins. Most proximal secondary veins give rise basiscopically to 6–c.8 higher order veins, the spacing and length of which decreases from proximal to distal end of the secondary vein (fig. 24). The most proximal of these veins gives rise to another series of 5–6 veins on its basiscopic side. Intermediate veins 1–7 per intercostal field, arising from the midvein at 60°–120°, running more or less parallel to one another or converging/diverging, the spacing being constant or increasing distally. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/2 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary veins 4–9 per 1 cm secondary vein, somewhat branched, the lengths on acrosopic and basiscopic sides of secondary vein more or less similar. Areoles 1–11 per 10 mm², with some to many free vein-endings, these being unbranched and branched.

Epidermis fragmentary, c.680–c.765 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–7 : 1. Cell wall 0.4–1.5 microns thick, largely unpitted, straight. Hair bases or stomata present, surrounded by 6–8 associated, radiating, cells. Internal resinous bodies absent.

Specimens examined : Deutsche Akad. Wiss. Berlin : 311(K 127)
Geol. Inst. Cologne : Coll. H. Weyland s.n.
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot. : 3477, 3478A

Discussion :

WEYLAND (1934) referred the material to *Grewia crenata* (Unger) Heer. This species, originally described as *Dombeyopsis crenata* Unger (UNGER, 1850, p. 448), was later transferred by the same author to *Ficus crenata* (Unger) Unger (UNGER, 1861, p. 14). HEER (1859, p. 42) transferred the species to *Grewia crenata* (Unger) Heer under which name it was widely known until BROWN (1939) reassigned it to *Cercidiphyllum crenatum* (Unger) Brown.

None of the leaf material of *Ficus* available to the present author was found to resemble the fossil under consideration, although the leaf-remains do show a certain similarity to the leaves of *Morus cathayana* Hemsl. However in *Morus cathayana* the successive distance between the secondary veins is more or less uniform or only decreasing gradually, while the leaf margin has teeth which are generally broad and sharp. Moreover, the leaf apex of *Morus cathayana* is acute or acuminate and the leaf base generally truncate or only slightly cordate.

Grewia (Tiliaceae), although more typical of the tropics, does occur in sub-tropical areas. An examination of the available material of the genus from the Middle East and China, which was housed in the Edinburgh Herbarium (E) proved that of all the species the leaves of certain specimens of *Grewia abutilifolia* Vent ex Juss. approximated most closely to the fossil. However, the leaf base in this species is rounded, truncate or only slightly cordate and the teeth of the leaf margin are not infrequently knob-like in appearance.

The leaves of *Celtis cercidifolia* C. Schneider and *Lantana involucrata* L. showed a certain resemblance to the leaf-remains.

In *Celtis cercidifolia* (Ulmaceae), however, the leaf apex is acute, the leaf base rounded and the teeth, which only occur on the distal part of the leaf margin, are not rounded. Furthermore, the distance between the successive secondary veins does not show the marked decrease met with in the leaf-remains.

In *Lantana involucrata* (Verbenaceae) the venation is similar to that encountered in the fossil, but is indistinct due to the hairiness of the leaves. The leaf margin is such as one finds in the leaf-remains, but unlike the fossil the leaf apex is rounded and the leaf base obtuse or almost truncate, but never cordate.

As indicated by BROWN (1939) and other authors the fossil displays a marked resemblance to the leaves of *Cercidiphyllum* borne on the short shoots. These leaves have a leaf base which is frequently cordate and a leaf apex which is more or less obtuse. Furthermore, the distance between the successive secondary veins shows a marked decrease in a distal direction. The obscurely sinuate leaf margin of *Cercidiphyllum* is yet another point of similarity. The fossil may be attributed to *Cercidiphyllum* with a fair degree of certainty. Although AIRY-SHAW (1966, p. 221) states that *Cercidiphyllum* is represented by one species only, most authors would appear to recognize two species, *Cercidiphyllum japonicum* Sieb. et Zucc. and *C. magnificum* (Nakai) Nakai. OHWI (1965, p. 439) states that the leaves on the short shoots of *Cercidiphyllum magnificum* are broadly orbicular and have a distinctly cordate leaf base. He described the leaves of *Cercidiphyllum japonicum* as being slightly narrowed distally and having a shallowly cordate or nearly truncate leaf base. However, these differences did not hold for the herbarium material available to the present author and an examination of SWAMY and BAILEY (1949, p. 188,

fig. 1g) indicates that the leaves of *Cercidiphyllum japonicum* may be orbicular as well. While not contesting the distinctness of these two species, it was found impossible to separate these species from each other or from the fossil on the basis of the leaf-material available. A reference of the leaf-remains to a separate specific entity would not appear to be justified.

Herbarium material examined in detail:

<i>Celtis cercidifolia</i> C. Schneider	Herb. H. Léveillé	(E) det. Handel-Mazzetti
<i>Cercidiphyllum japonicum</i> Sieb. et Zucc.	Coll. J. Bisset 1401	(E) _____
	Coll. J. Bisset 1402	(E) _____
	Coll. M. Hotta 16753	(E,U) _____
	Coll. H. C. Chow 354	(E) _____
<i>Cercidiphyllum magnificum</i> (Nakai) Nakai	Coll. J. Ohwi 15-8-1951 (Nat. Sci. Mus. Tokyo 283)	(E) _____
	Coll. S. Kitamura & G. Murata 19-8-1952	(U) _____
	<i>Grewia abutilifolia</i> Vent ex Juss.	Coll. F. A. McClure 18-4-1922
<i>Lantana involucrata</i> L.	Coll. T. T. Yü 17567	(E) det. L. A. Lauener
	Coll. A. Henry 9887A	(E) det. M. Burret
	Coll. A. Henry 9887D	(E) det. M. Burret
<i>Morus cathayana</i> Hemsl.	Coll. O. Lakela 27504	(U) _____
	Coll. Handel-Mazzetti 12106	(E) det. A. Rehder

FAMILY PLATANACEAE

XXVIII. *Platanus platanifolia* (Ett.) Knobloch

Synonym: *Platanus aceroides* Goepfert Weyland, 1934, p. 85!

Description:

Petiole (19-) 42-60 mm long and 1.0-2.2(-5.0) mm wide at mid-point, more or less parallel-sided for the greater part of its length but increasing in width at the very base of the petiole, which has the form of a candle-snuff. Petiole straight or slightly curved, making no angle with the central primary vein.

Lamina (simple-)palmate, 6.1-c.40 cm long, 3.9-c.36 cm wide, the length/breadth ratio being 1.05:1-1.57:1 (fig. 27). Leaf apices acute (-acuminate), leaf base obtuse, rounded or cordate. Lamina dissected round primary veins to a depth of (0-) 21-47%, sinuses rounded, the distance from the origin of the lateral primary veins to the sinus 3.5-9.5 cm, the distance being related to the length of the lamina (fig. 27). The distance from the central apex to the lateral apices 3.7-9.7 cm, the distance being related to the width of the lamina (fig. 27). The angle formed by joining the apex of the central lobe via a primary sinus to the apex of

one of the lateral lobes (45° - 72° - 101° , the angle being somewhat related to the width of the lamina.

Leaf margin non-entire, dentate, with acute teeth 0.45-4.0 mm across, projecting apically, (0-) 1 per secondary vein and 0(-1) per intercostal field, alternating with rounded sinuses. Teeth of one size group.

Venation actinodromous, primary veins 3. Lateral primary veins arising at 30° - 46° from the central primary vein 0-4 mm above the junction of the lamina and petiole; these lateral veins 0.2-0.7 mm wide at mid-point, 74-93 % the length of the central primary vein (fig. 27). The percentage of the lamina on the basiscopic side of the lateral primary veins c.25-40 % total. Lateral primary veins bearing 0-6 secondary veins on their acroscopic side, arising at 45° - 80° . The angle at which the veins arise constant or decreasing within the first few mms, hardly or somewhat tapering along their length, 0.05-0.25 mm wide at mid-point. Lateral primary veins bearing (6-)10-16 secondary veins on their basiscopic side, the most proximal vein arising at 45° - 65° , arising in the remaining part of the basal third of the lobe at 35° - 70° , in the median third at 40° - 80° , in the apical third at 45° - 80° . The angle at which the veins arise constant or decreasing within the first few mms. The spacing between the veins reaches a maximum mid-way (fig. 27). Secondary veins hardly to somewhat tapering along their length, 0.05-0.40 mm wide at mid-point, sometimes branched. Central primary vein straight or curved, markedly tapering along length, 0.25-1.20 mm wide at mid-point between base and apex of lobe. Central primary vein bearing 6-13 secondary veins per side, arising in the basal third of the lobe at 40° - 60° , in the median third at 40° - 70° , in the apical third at 45° - 70° . The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins decreases from base to apex of the lamina (fig. 27), the distance between the point of origin of the lateral primary veins and that of the first secondary vein in the central lobe showing little correlation with the length of the lamina. Secondary veins opposite or alternately arranged, hardly to somewhat tapering along their length, 0.1-0.4(-0.6) mm wide at mid-point, interconnected distally by tertiary veins or vein network. Intermediate veins 0-10 per intercostal field, some having a somewhat twisted course, arising from the central primary vein at 45° - 120° , running more or less parallel to one another or converging/diverging, the spacing between them constant or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/2-2/3 the distance from the central primary vein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 1-5(-9) per 1 cm secondary vein, somewhat to much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 30-70 per 10 mm², with some free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of 100-400 cells per

0.1 mm², the cell length/cell breadth ratio being 1 : 1-2 : 1. Cell wall 0.6-2.0 microns thick, unpitted or finely pitted, straight or undulate with 0-7 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 14 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1-5 : 1, transverse walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Hair bases round to oval, (1.5-) 7.2-25.2 microns in diameter, over and between the veins, 0-3 per 0.1 mm². Cells at leaf margin c.500 per 0.1 mm², the cell length/cell breadth ratio being 1 : 1-5 : 1, arranged in 6-10 rows. Cell wall 1-4 microns thick, largely unpitted, straight, transverse walls slanting or at right angles to the lateral walls. Epidermis in stomatal condition composed of 180-400 generally finely striate cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1-4 : 1. Cell wall 0.4-1.5 microns thick, unpitted or pitted, straight or slightly undulate with 0-6 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 12.6 microns. Cells over veins narrow elongate. Stomata 19.6-39.6 microns long and 12.6-36.0 microns broad, breadth 55-143 % length, (12-) 35-55 per 0.1 mm²; stomatal index 20-23 %. Stomata variously orientated, undepressed, more or less equidistant to somewhat arranged in groups, apices non-retuse. Stomatal slit 55-75(-88) % stomatal length. Accessory cells poorly differentiated 6-8 in number, symmetrical with 2-4 polar and 2-4 lateral cells. Accessory cells similar in size to the rest of the epidermal cells. Hair bases round to oval 9.0-21.6 microns in diameter, over and to a lesser extent between the veins, (0-) 6-15 per 0.1 mm², with 7-10 associated cells between veins, these cells frequently radiating from hair base. Hairs fragmentary, in the form of unicellular papillae 29->45 microns long with a cell wall 0.5-0.6 microns thick. Internal resinous bodies absent.

Specimens examined : 53, among which the numbered specimens :
 Geol. Inst. Cologne: Coll. H. Weyland 1432
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3203, 3204,
 3205, 3206, 3207, 3208, 3209, 3503, 3504, 3505, 3506, 3507,
 3508, 3509, 3510, 3511, 3512, 3513, 3514, 3536, 3608B, 3838C.

Discussion :

In the light of present knowledge there would only appear to be one possibility as regards the systematic affinity of the fossil under consideration. Of all the genera submitted to examination only the leaves of *Platanus* were found to agree with the fossil in the particular combination of characters displayed. The shape and dentation of the fossil is similar to that encountered in the leaves of certain species of *Platanus*. Moreover, both the leaf-remains and the leaves of *Platanus* are characterized by an enlarged, hollow, petiole base in the form of a candle-snuff. In *Platanus* species the cavity at the base of the petiole is filled by the buds for the coming year. Stellate hairs are present on the leaves of *Platanus* species. These hairs are frequently jointed and when shed all that remains is a

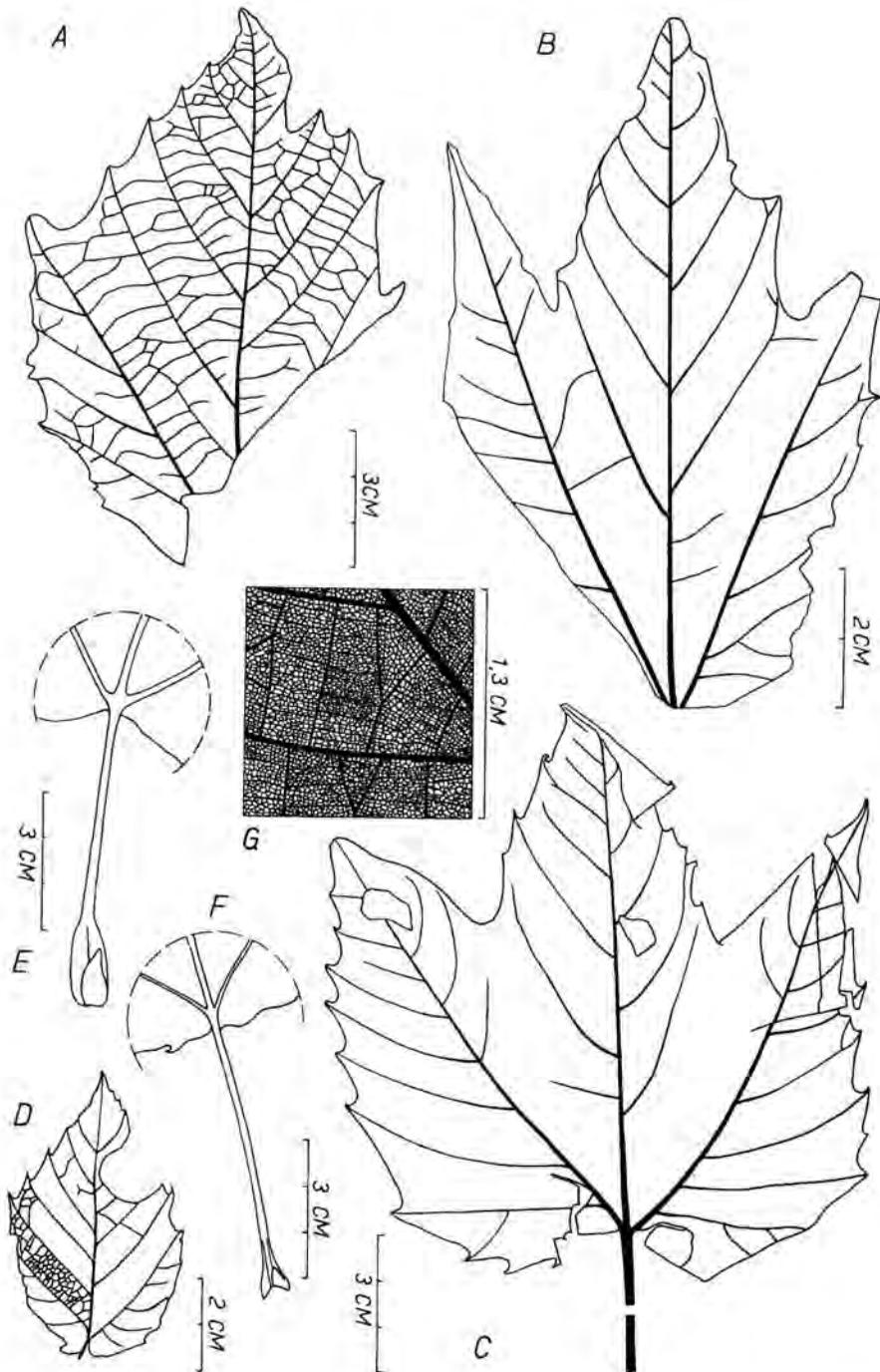


Fig. 26. A-G = XXVIII: A = Berlin s.n.; B = Utrecht 3536; C = Utrecht 3514; D = Utrecht 3373; E = Utrecht 3203, petiole with base in the form of a candle-snuff; F = Utrecht 3206, petiole; G = detail showing venation.

papillate stump. Similar structures were encountered in the fossil. The nature of the stomata and other features displayed by the cuticles of both the fossil, and living species of *Platanus* confirms the relationship. A reference of the fossil to *Platanus* would therefore seem acceptable.

In *Platanus* the epidermis is more or less identical in all species. For specific identification of detached leaves one must turn to features of shape and dentation. In *Platanus occidentalis* L., for instance, the leaves are only shallowly lobed, these lobes being mostly broader than long. In *Platanus orientalis* L., *P. racemosa* Nuttall and *P. wrightii* Wats., on the other hand, the leaves are deeply lobed. The leaves of *Platanus racemosa* and *P. wrightii*, however, either have an entire margin or are only remotely dentate, and the same applies to the specimens of *Platanus glabrata* Fernald (= *P. occidentalis* var. *glabrata* of some authors) and *P. lindeniana* Mart. et Gal. available. In contrast the fossil has a leaf margin, which is generally markedly dentate. While *Platanus orientalis* might be considered similar to the fossil in this respect it has leaves which are 5-7 lobed, with lateral primary veins arising at some distance above the leaf base. With regard to these characters the fossil resembles *Platanus occidentalis*, with leaves having 3(-5) lobes and lateral primary veins arising at or near the leaf base, more closely. While it has been suggested (JOHNSON, 1933) that one is possibly dealing with the cross between *Platanus orientalis* and *Platanus occidentalis* (= *P. X acerifolia* Willd.) this would seem to be unlikely. In the absence of leaves attributable to *Platanus orientalis* and *P. occidentalis* it seems more likely that one is dealing with a forerunner of the present-day *Platanus* species, in which the combinations of characters were not fully evolved. The amount of variation in the ratio length/breadth of the lobes might be taken as an indication of this. The use of another (fossil) specific name for this taxon would seem to be justified.

Of the leaf-remains described in the literature the present leaf-remains show a great similarity to those described as *Platanus aceroides* Goepfert. It was to this species that WEYLAND (1934, p. 85) referred the present leaf-remains. This species, although listed in 1852, was first described in 1855 (GOEPPERT, 1855, p. 21). Similar leaf-remains, while most commonly referred to this species have been referred to as *Platanus deperdita* (Massalongo) Sordelli by a number of Italian authors e.g. MESCHINELLI and SQUINABOL (1893), SORDELLI (1896), PEOLA (1899), PRINCIPI (1914, 1922). This combination made in 1874 was based on a specimen described by MASSALONGO (1853, fig. 7) from Forli as *Acerites deperditum*. The diagnosis of this specimen is as follows: Foliis petiolatis, basi cuneato-attenuatis, palmato-trilobis, inciso-dentatis (duplicato-serratis), acuminatis, lobo medio productissimo, lobis lateralibus valde minoribus, sinibus acutis. Costa valida, nervis alternis ramosis arcuatis, venis flexuosis laxis. However, the fact that this species had a cuneate to attenuate leaf base and a doubly serrate leaf margin, while the material from Kreuzau had an obtuse, rounded or cordate leaf base and simply serrate leaf margin would

tend to suggest that one is dealing with two separate taxonomic entities. On the other hand, another specimen from Forlì figured by MASSALONGO (1853, fig. 6) as *Acerites? incerta* Massalongo, while only fragmentary, would appear to be identical to the species under consideration. While included in the synonymy of *Platanus aceroides* (STAUB, 1887) or *Platanus deperdita* (MESCHINELLI and SQUINABOL, 1893; SORDELLI, 1896) this species would appear to be a *nomen nudum*.

VIVIANI (1833, p. 131) described a fossil from the Tertiary gypsum beds of Stadella as *Acerites ficifolia*. Professor Viviani gave the following diagnosis: *Acerites* foliis ambitu cordato-ovatis tri vel triplinerviis; lobis obtusis sinuato-dentatis; dentibus, rotundatis, lobo medio productiore subtrilobo. This diagnosis would suggest that one is dealing with a leaf similar to those of the present taxon. This is borne out by an examination of Viviani's Planche A (= Planche IX), fig. 5. However, while the specimen agrees as to shape and venation, the leaf margin was so poorly preserved that an exact similarity could not be proven. The same can be said of *Platanus pannonica* Ett. (VON ETTINGSHAUSEN, 1852) considered by STAUB (1887) as identical to *Platanus aceroides* Goeppert.

A leaf described as *Cissus platanifolia* by VON ETTINGSHAUSEN (1851, p. 20, Tab. 4, fig. 1) from Tertiary sediments near Vienna also deserves attention. The diagnosis of this species was given as follows: *C. foliis* (circ. 10 centm. long. et 11 centm. lat.) cordato subrotundis, lobatis, lobis acutiusculis, angulato-repandis et remote sinuato-dentatis, sinubus obtusis; nervo primario debili versus apicem sensim evanescente; nerviis secundariis sub angulo 35-60° orientibus, 12-15 m.m. distantibus; nerviis tertiariis obsoletis. As VON ETTINGSHAUSEN (1851, p. 20) pointed out, the generic determination was questionable and he mentioned a number of other genera, including *Platanus*, as possible alternatives. In a compilation of the fossils referable to *Cissus* (VON ETTINGSHAUSEN, 1861) this species was notably absent. Although cuticle analysis of the Vienna material has proved to be fruitless (BERGER, 1953), an examination of the diagnosis and illustration would tend to indicate identity of the Kreuzau material and that from Vienna. *Cissus platanifolia* would appear to be the earliest validly published name for the present taxonomic entity. The transfer of *Cissus platanifolia* to *Platanus* was made by KNOBLOCH (1964, p. 601).

Herbarium material examined in detail:

<i>Platanus glabrata</i> Fernald	Coll. S. S. White 1703	(U) det. Johnston
<i>Platanus lindeniana</i> Mart. et Gal.	Coll. R. M. Rosas 371	(U) _____
<i>Platanus mexicana</i> Moric.	Coll. H. H. Bartlett 10025	(U) _____
<i>Platanus occidentalis</i> L.	Coll. J. H. Soper & R. P. Burcher 2271	(U) _____
	Coll. F. R. Rickson 202	(U) det. F. R. Rickson
<i>Platanus orientalis</i> L.	Coll. J. T. de Smidt 276	(U) det. J. T. de Smidt
	Coll. J. J. C. Piket 272	(U) det. J. T. de Smidt

<i>Platanus racemosa</i> Nuttall	Coll. F. M. Muller 19-10-1930	(U) det. F. M. Muller
<i>Platanus wrightii</i> Wats.	Coll. J. C. Blumer 10-1906 Coll. S. S. White 4413	(U) _____ (U) _____

FAMILY HAMAMELIDACEAE

SUBFAMILY HAMAMELIDOIDEAE

Tribe Distylieae

XXIX

Description:

Petiole 2.8 mm or more long and 1.0 mm wide, more or less parallel-sided, straight, making no angle with the midvein.

Lamina suborbicular, ovate or elliptical, c.4–c.7.5 cm long and 1.3–c.3.0 cm wide, the length/breadth ratio being c.1.3 : 1–3.0 : 1, sometimes asymmetrical about midvein. Leaf apex acute or acuminate, leaf base acute or obtuse, oblique.

Leaf margin entire.

Venation camptodromous, midvein gently curved, hardly or markedly tapering along length, 0.1–0.4 mm wide at mid-point between base and apex of the lamina. Midvein bearing (5–) 7–12 secondary veins per side, the most proximal vein arising at 45°–70°(–90°), arising in the remaining part of the basal third of the lamina at 55°–90°, in the median third at 40°–90°, in the apical third at (30°–) 60°–90°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the secondary veins reaches a maximum in the middle of the lamina in general, although the trend is sometimes slightly irregular (fig. 27). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.03–0.25 mm wide at mid-point, interconnected distally by strong or fine extensions of the secondary veins. Intermediate veins 2–10 per intercostal field, arising from the midvein at 45°–130°, running more or less parallel to one another or converging/diverging, the spacing between them being constant, increasing distally or irregular. The veins either similar in width or increasing in width with increase in length, extending from 0 to 1/4–3/4 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field proximally, midway or distally. Tertiary veins 5–12 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 13–26 per 10 mm², the nature of the free vein-endings being unknown.

Epidermis in non-stomatal condition composed of 100–200 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3 : 1. Cell wall 0.45–1.3(–2.3) microns thick, largely unpitted or finely pitted, rarely straight and more usually highly undulate with 1–9 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 14.4

microns. Cells over major veins elongate, the cell length/cell breadth ratio being 2:1-4:1, cell wall straight or only slightly undulate. Finer veins not reflected in cuticle. Compound hair bases with a cell wall 5.5-14 microns thick surrounding a 4-7 sided central area 9-30 microns across are present, 0-2 per 0.1 mm². The epidermal cells tend to radiate away from these hair bases. Cells at leaf margin not specialized, being similar in number to those on other parts of leaf surface, not arranged in rows parallel to leaf margin, somewhat less undulate than remaining epidermal

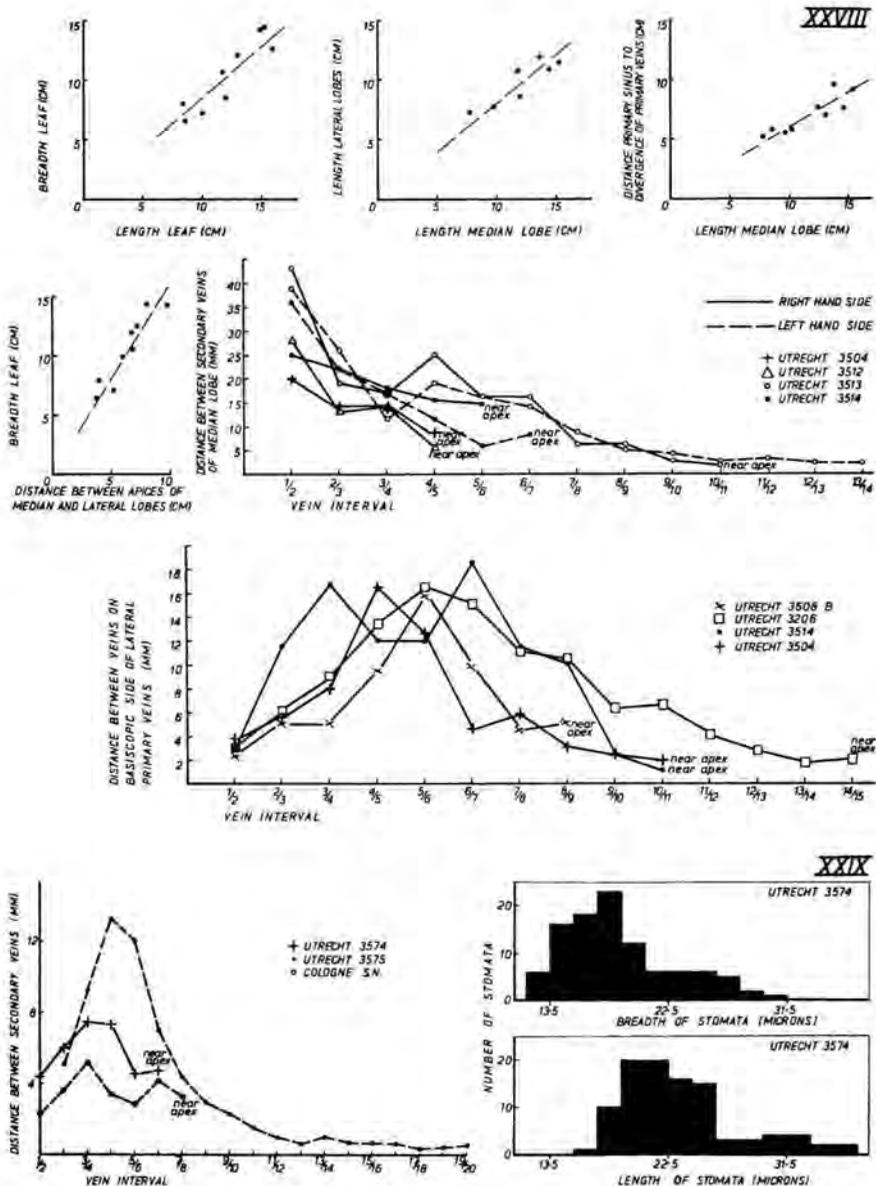


Fig. 27. Graphs and histograms XXVIII, XXIX.

cells. Epidermis in stomatal condition composed of 100–230 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–3 : 1. Cell wall 0.4–3.0 microns thick, largely unpitted, undulate with 3–11 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 12.6 microns. Cells over major veins elongate, the cell length/cell breadth ratio being 1 : 1–5 : 1, the cell wall tending to be less undulate than otherwise over the central part of the vein. Finer veins not reflected in cuticle. Stomata 15.3–36.9 microns long and 11.7–31.5 microns broad (fig. 27), breadth 53–118 % length, 0–23 per 0.1 mm^2 ; stomatal index 0–11.5 %. Stomata variously orientated, somewhat depressed, arranged in groups or equidistant, apices non-retuse. Stomatal slit 25–64 % stomatal length. Accessory cells 0–2(–4?), symmetrical with 0(–2?) polar and 0–2 lateral cells, narrower than the rest of the epidermal cells. Compound hair bases with a cell wall 6–20 microns thick surrounding a 3–7 sided, oval or somewhat irregularly-shaped central area 9–34 microns across are present, 0–4 per 0.1 mm^2 . The epidermal cells, often somewhat striate, tend to radiate away from these hair bases. Internal resinous bodies apparently absent.

Specimens examined: Geol. Inst. Cologne: s.n.

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3573, 3574, 3575.

Discussion:

This taxonomic entity was not recognized by WEYLAND (1934) as such and neither of the two specimens in the Cologne collection that can be referred to this taxon are numbered. The taxon is typified by the presence of large hair bases. Such hair bases are only found in a limited number of angiosperm families at the present day, which fact facilitates the identification of the leaf-remains in question. Hair bases similar to those of the fossil are found in the Caprifoliaceae, Fagaceae, Hamamelidaceae and Oleaceae.

The leaves of certain species of *Viburnum* (Caprifoliaceae) e.g. *Viburnum odoratissimum* Ker., *V. punctatum* Ham. resemble the fossil ones in the presence of such leaf bases. The epidermis of *Viburnum odoratissimum* only differs from that of the leaf-remains on a few points, such as a more highly undulate cell wall on the upper surface of the leaf and in the presence of fine striae on the lower surface of the leaf. These differences may be considered insignificant, but *Viburnum odoratissimum* differs moreover in the presence of tertiary veins running more or less at right angles to the midvein and in having a leaf apex which is often, but not always, rounded. The epidermis of *Viburnum punctatum* resembles that of the fossil to a lesser extent and the hair bases are much smaller than those of the fossil. Furthermore, while the leaf apex is acute and sometimes tapered, the nature of the secondary venation differs strongly from that of the fossil. The secondary veins are not only arched but each extends over a great

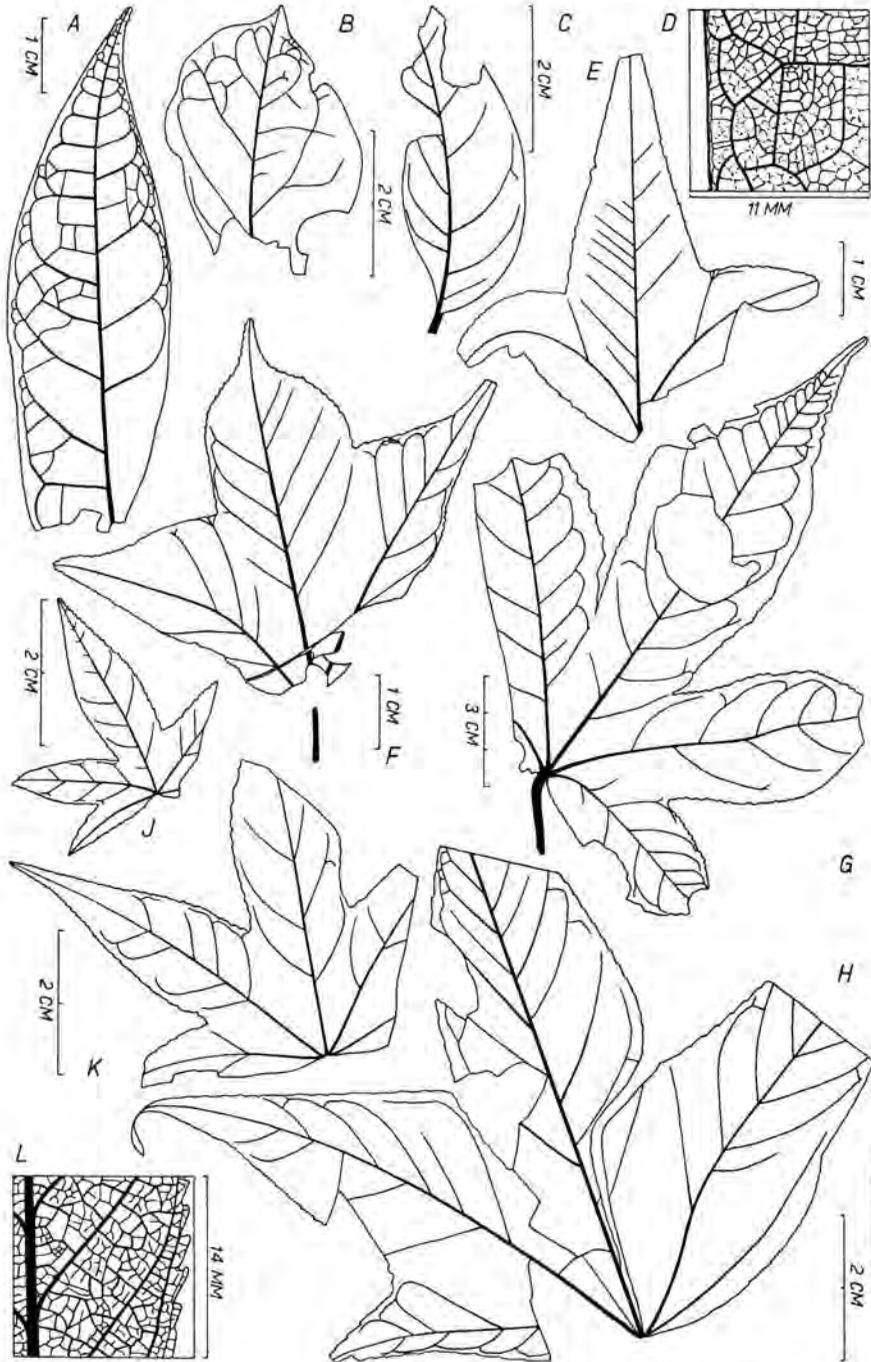


Fig. 28. A-D = XXIX: A = Utrecht 3575; B = Cologne s.n.; C = Utrecht 3574; D = Utrecht 3575, detail showing venation and leaf margin. E-L = XXX: E = Utrecht 3246; F = Utrecht 3240; G = Cologne, Coll. H. Weyland 1442; H = Utrecht 3245; J = Utrecht 3228; K = Utrecht 3247; L = detail showing venation and leaf margin.

part of the lamina. It is therefore not possible on the basis of the present information to attribute the leaf-remains to *Viburnum*.

Hair bases similar to those of the fossil are also to be found on the leaves of various species of *Quercus* (Fagaceae) e.g. *Quercus baronii* Skan., *Q. myrtifolia* Willd. and *Q. virginiana* Mill. *Quercus myrtifolia* and *Quercus virginiana*, however, differ from the fossil in having straight epidermal cell walls on the upper (non-stomatal) surface of the leaf, in having the finer veins reflected in the cuticle and a lamina in which the leaf apex is obtuse or rounded. *Quercus baronii* has an epidermis approximating more closely to that of the fossil (undulate cell walls on the upper surface of the leaf; finer veins hardly reflected in the cuticle) but differs in gross-morphology. The leaves are lanceolate with craspedodromous venation and each secondary vein in the distal half of the lamina ends in a well-developed tooth.

The members of the Oleaceae found to have leaves with similar hair bases (*Osmanthus marginatum* (Champ. ex Benth.) Hemsl., *Ligustrum compactum* Hook. f. et Thoms., *L. delavayanum* Harriot, *L. lucidum* Ait. and *L. quihoui* Carr.) while often resembling the leaf-remains in general appearance were found to differ from these, when submitted to detailed examination. With the exception of *Ligustrum quihoui*, which has moderately strongly unulate epidermal cell walls on the upper surface of the leaf, the above-mentioned species were all characterized by \pm straight cell walls (In *Ligustrum quihoui* the lower surface of the leaf has straight-walled cells). Moreover, the cells are small and the stomatal index is high as compared with that of the fossil. Not only this, but these species differ from the fossil in having secondary veins which are almost straight except for the marginal loop interconnecting these veins distally.

The only other possibility known to the present author was the Hamamelidaceae. Leaves of various members of this family have hair bases similar to those of the fossil and certain genera e.g. *Distylium*, *Sycopsis* were found to show a very close resemblance to the fossil in other respects as well. The resemblance is so close that an affinity between these genera and the fossil seems fairly certain. Schulze-Menz (in ENGLER, 1964) has followed others in placing *Distylium* and *Sycopsis* in the Tribe Distylieae, belonging to the Subfamily Hamamelidoideae. By way of checking whether it was possible to refer the fossil to the Tribe Distylieae or even the Subfamily Hamamelidoideae on the basis of leaf characters an examination was undertaken of the family as a whole.

According to Schulze-Menz the family is divisible into 5 Subfamilies: Disanthoideae, Rhodoleioideae, Symingtonioideae (Bucklandioideae), Liquidambaroideae and Hamamelidoideae.

The Subfamily Disanthoideae is represented by a single species, *Disanthus cercidifolius* Maxim. The leaves are broad ovate in shape and often have a cordate base. The margin of the leaves is entire. The cuticle is thin and no hair bases such as developed in the fossil are present. Moreover, the finer veins are reflected in the cuticle.

The Subfamily Rhodoleioideae is represented by one or more species of *Rhodoleia*. The leaves are elliptical or ovate-elliptical with an apex varying from slightly acuminate to rounded and a base varying from acute, obtuse to rounded or subcordate; leaf margin entire. With few exceptions e.g. Holotype of *Rhodoleia forrestii* (G. Forrest 26589) in EXELL (1933, Plate 26), the secondary veins are almost straight except for a marginal loop by which these veins are interconnected distally. Furthermore, the ratio of the distance from the midvein to the apex of the loop as against the distance between successive secondary veins is generally greater than that for the leaf-remains in question.

Hair bases similar to those of the fossil are present and, as in the fossil, the finer veins are not reflected in the cuticle. The epidermal cell walls, however, differ in being straight, while those of the fossil are almost invariably markedly undulate.

The leaves of the Subfamily Symingtonioideae are palmate with an entire margin. Hair bases are rare, and when present poorly developed. The stomata are, moreover, characterized by having guard cells with a markedly thickened poral wall.

The following Subfamily, the Liquidambaroideae (sometimes considered a separate family), also differs markedly from the leaf-remains in question. The leaves, which are either simple or palmate, usually have a toothed margin. The cuticle is but thin and the hair bases are absent or only poorly developed. The finer veins may or may not be reflected in the cuticle.

The remaining Subfamily, the Hamamelidoideae, contains more species than the rest of the subfamilies put together. It is possible to divide this subfamily into 5 tribes: Corylopsideae, Fothergilleae, Eustigmataeae, Hamamelideae and Distylieae.

Members of the Tribe Corylopsideae (here considered to include *Corylopsis*, *Fortunearia*, and *Sinowilsonia*) have ovate, elliptical or obovate leaves with a leaf apex which is acute or short acuminate, rarely obtuse, and a leaf base which is rounded, truncate or subcordate. The leaf margin may be either entire or more commonly denticulate with mucronulate apices to the teeth. The venation is craspedodromous with the secondary veins arising at a slight angle, while the most proximal secondary vein bears numerous higher order veins on its basiscopic side. The cuticle is thin and while hair bases are present these are sometimes only weakly developed. Members of this tribe seem to bear little affinity with the leaf-remains under consideration.

The same applies to the next tribe, the Fothergilleae (incorporating *Fothergilla*, *Parrotia*, *Parrotiopsis*).

Members of the Tribe Fothergilleae have ovate, elliptical or obovate leaves with a leaf apex which is acute or obtuse, and a leaf base which is rounded or subcordate. The leaf margin may be almost entire or alternatively crenate-dentate or sinuate-dentate or denticulate, but without

mucronulate apices to the teeth. The venation, as in the Corylopsideae, is craspedodromous and in this respect differs from that of the fossil. Moreover, the cuticle is thin and although hair bases are present, the finer veins are reflected in the cuticle of the upper and lower surfaces of the leaves.

Gross-morphologically the leaves of the Tribe Eustigmateae (only 1 genus: *Eustigma*) resemble those of the fossil. The leaves are elliptical with acute or acuminate leaf apices and leaf bases which are acute. The leaf margin is either entire or with a few small blunt teeth in the distal half of the lamina. The venation is furthermore camptodromous. However, the cells reflected in the cuticle have straight or only somewhat undulate cell walls. No hair bases are present and the stomata have guard cells with markedly thickened poral walls. The epidermal cells and stomata are, moreover, considerably larger than those of the fossil.

The leaves of the following tribe, the Hamamelideae, show a considerable amount of variation. This tribe consists of *Dicoryphe*, *Hamamelis* and *Trichocladus*. The leaves are ovate, elliptical or obovate, with an acute or obtuse leaf apex and a leaf base which is acute, obtuse, rounded or subcordate and sometimes oblique. The leaf margin is either entire e.g. *Trichocladus* or wavytoothed or occasionally with short mucronulate teeth (*Hamamelis*). The venation is either craspedodromous (*Hamamelis*) or camptodromous (e.g. *Trichocladus*). The cells reflected in the cuticle on the adaxial surface of the leaf have straight or but slightly undulate cell walls. Hair bases are present. The finer veins are generally reflected in the cuticles of *Hamamelis*, while only sometimes reflected in those of *Trichocladus*.

Dicoryphe and *Trichocladus* are to be found in Madagascar and tropical Southern and Eastern Africa respectively and as such are hardly to be expected in the Upper Tertiary flora of Europe. The remaining member of the Hamamelideae, *Hamamelis*, differs from the fossil in so many respects (leaf margin, venation etc.) that this tribe can also be ruled out of consideration. This leaves the Tribe Distylieae as the only possibility within the Hamamelidaceae with regard to the affinity of the leaf-remains.

The leaves of the Distylieae (*Distylium*, *Loropetalum*, *Matudaea* and *Sycopsis*) are ovate, elliptical or obovate and have an obtuse, acute or acuminate leaf apex and a leaf base which is acute, obtuse, rounded or subcordate. The leaf base is sometimes oblique and/or asymmetrical as in the leaf-remains. The leaf margin may be entire, with a somewhat wavy margin or with a few teeth in the distal half of the lamina. The venation is either acrodromous (*Matudaea*) or camptodromous (*Distylium*, *Loropetalum* and *Sycopsis*) with forwardly arched secondary veins. The ratio of the distance from the midvein to the apex of the loop, through which the secondary veins are distally interconnected, as against the distance between successive secondary veins is similar to that of the leaf-remains. The cells reflected in the cuticle, like those of the fossil, generally

have highly undulate cell walls. Furthermore, hair bases such as encountered in the leaf-remains are well developed and numerous with the exception of *Matudaea* in which they are rare and but poorly developed. This and the fact that the leaves of *Matudaea* display acrodromous venation would tend to rule out this genus as a possibility as regards the affinity of the fossil. The choice rests on the three remaining genera. In his provisional revision of *Distylium* and *Sycopsis* WALKER (1944) made considerable use of leaf characters for completing a separation of the individual species. His key to the genera was, however, based on differences in floral structure.

An examination of the limited amount of material available to the present author has shown that while none of the species of *Distylium* have a striate cuticle, the cuticles of *Loropetalum* and *Sycopsis* are striate on the abaxial (stomatal) surface of the leaf. In *Loropetalum* the striae are fine, while those of *Sycopsis* are thick, occasionally branching and having a coarse-grained appearance. Because of differences such the above-mentioned striae, stomata with markedly thickened poral walls to the guard cells, and the small number of secondary veins (4-6) the monotypic *Loropetalum* need not be considered further. The choice is between *Distylium* and *Sycopsis*. Like *Loropetalum*, the material of *Sycopsis* examined had stomata in which the poral walls of the guard cells were considerably thickened. In the fossil and certain species of *Distylium* the poral wall of the guard cells is thickened to a lesser extent. However, in *Distylium* the development of the poral walls of the guard cells varies from one species (or specimen) to another. The possibility exists that the same is true of *Sycopsis*, so that a reference of the fossil to *Distylium* is not warranted at this stage. The lack of comparative material, rather than the nature of the tribe, is therefore the prime factor preventing a more exact determination.

Herbarium material examined in detail:

<i>Altingia gracilipes</i> Hemsl.	Coll. R. C. Ching 2199	(E) _____
<i>Bucklandia populnea</i> R. Br. ex Griff.	Coll. W. Y. Chun 5852	(E) _____
<i>Bucklandia tricuspis</i> Hallier f.	Coll. ?	(U) det. Hallier f. TYPE
<i>Corylopsis himalayana</i> Griff.	Coll. G. Forrest 29810	(E) det. J. M. Chao
<i>Corylopsis multiflora</i> Hance	Coll. W. Y. Chun 5820	(E) det. J. M. Chao
<i>Corylopsis pauciflora</i> Sieb. et Zucc.	Coll. G. Murata 19245	(U) _____
<i>Corylopsis platypetala</i> Rehd. et Wils.	Coll. G. Forrest 17174	(E) det. J. M. Chao
<i>Corylopsis sinensis</i> Hemsl.	Coll. E. H. Wilson 173	(E) det. J. M. Chao
<i>Corylopsis willmottiae</i> Rehd. et Wils.	Coll. G. Forrest 28154	(E) det. J. M. Chao
<i>Corylopsis yui</i> Hu et Cheng	Coll. T. T. Yü 19509	(E) det. J. M. Chao
<i>Corylopsis yunnanensis</i> Diels	Coll. G. Forrest 23588	(U) _____
<i>Disanthus cercidifolius</i> Maxim.	Coll. G. Murata & M. Togashi 173	(U) _____

<i>Distylium buxifolium</i> (Hance) Merrill	Coll. A. Henry 3314	(E) det. E. H. Walker
<i>Distylium hondurense</i> Standley apud Walker	Coll. T. G. Yunker, R. F. Dawson & H. R. Youse 6377	(U) det. E. H. Walker
<i>Distylium myricoides</i> Hemsl.	Coll. R. C. Ching 3026	(E) det. E. H. Walker
<i>Distylium racemosum</i> Sieb. et Zucc.	Coll. C. Y. Chiao 5-2-1928	(E) det. E. H. Walker
<i>Distylium stellare</i> O. Ktze.	Coll. W. Zwart 6580	(U) det. J. G. B. Beumée
<i>Eustigma oblongifolium</i> G. et C.	Coll. J. L. Gressitt 204	(U) _____
<i>Fothergilla major</i> (Sims.) Lodd.	Coll. A. E. Radford 45392	(U) _____
<i>Fothergilla monticola</i> Ash.	Cultivated	(U) det. F. A. Stafleu & P. A. Florschütz
<i>Hamamelis japonica</i> Sieb. et Zucc.	Coll. G. Murata & S. Kitamura 1569	(U) _____
<i>Hamamelis mollis</i> Oliv.	Coll. Handel-Mazzetti 11199	(E) det. A. Rehder
<i>Hamamelis vernalis</i> Sarg.	Coll. K. U. Kramer 546	(U) _____
<i>Hamamelis virginiana</i> L.	Coll. C. R. Bell 4415	(U) det. A. E. Radford
<i>Ligustrum compactum</i> Hook. f. et Thoms.	Coll. C. Schneider 1649	(E) det. R. Mansfeld
<i>Ligustrum delavayanum</i> Hariat	Coll. C. Schneider 1689	(E) det. R. Mansfeld
<i>Ligustrum lucidum</i> Ait.	Coll. S. Ten 188	(E) det. R. Mansfeld
<i>Ligustrum quihoui</i> Carr.	Coll. A. Henry 3973	(E) det. A. Rehder & E. H. Wilson; det. R. Mansfeld
<i>Liquidambar formosana</i> Hance	Coll. Shimizu & Chuang (Plantae Taiwanianae 20448)	(E) _____
	Coll. C. Y. Chiao 14238	(E) det. C. Y. Chiao; det. E. D. Merrill
<i>Liquidambar styraciflua</i> L.	Coll. F. G. Meyer & D. J. Rogers 24	(U) _____
	Coll. F. R. Rickson 242	(U) det. F. R. Rickson
<i>Loropetalum chinense</i> (R. Br.) Oliv.	Coll. Handel-Mazzetti 11593	(E) det. A. Rehder
<i>Matudaea trinervia</i> Lundell	Coll. G. B. Hinton 6163	(U) _____
<i>Osmanthus marginatum</i> (Champ. ex Benth.) Hemsl.	Coll. C. Wang 34465	(E) det. P. S. Green
<i>Parrotia persica</i> C. A. Mey.	Cultivated	(U) det. P. A. Florschütz
<i>Parrotiopsis jacquemontiana</i> (Decne.) Rehder	Coll. T. A. Rao 9188	(U) _____
<i>Quercus baronii</i> Skan.	Coll. J. F. Rock 14995	(E) _____
<i>Quercus myrtifolia</i> Willd.	Coll. G. V. Nash 8-1894	(U) det. J. K. Small
<i>Quercus virginiana</i> Mill.	Coll. J. K. Small, G. K. Small & C. A. Mosier 7000	(U) _____
<i>Rhodoleia forrestii</i> Chun ex Exell	Coll. G. Forrest 25671	(E) det. A. W. Exell

Rhodoleia teysmannii Miq.	Coll. Boschproefstation 9068	(U) det. J. G. B. Beumée
Sycopsis sinensis Oliv.	Coll. E. H. Wilson 1825	(E) det. E. H. Walker
Trichocladus ellipticus Eickl. et Zeyh.	Coll. A. Stolz 2101	(U) _____
Trichocladus goetzei Engler	Coll. A. Stolz 1065	(U) _____
Viburnum odoratissimum Ker.	Coll. W. Y. Chun 6209	(E) det. T. Dudley
Viburnum punctatum Ham.	Coll. McLaren's collectors AA 160	(E) det. T. Dudley

SUBFAMILY LIQUIDAMBAROIDEAE

XXX

Liquidambar

Synonym: *Liquidambar europaea* A. Braun QUAAS, 1910, p. 984; WEYLAND,
1934, p. 85!

Description:

Petiole up to more than 40 mm long, 0.7–2.6 mm wide at mid-point, more or less parallel-sided, straight, sometimes making a marked angle with the central primary vein.

Lamina palmate, 3–7 lobed, 1.4–16 cm long, 2.4–c.19 cm wide, the length/breadth ratio being 0.58:1–1.0:1 (fig. 29). Leaf apex acute or acuminate, leaf base obtuse, rounded or cordate. Lamina dissected round primary veins to a depth of 20–62.5 %, sinuses acute or angular, the distance from the origin of the lateral primary veins to the sinus 0.55–4.2 cm, the distance being related to the length of the lamina (fig. 29). The distance from the central apex to the neighbouring lateral apices 1.35–10.1 cm, the distance being related to the width of the lamina (fig. 29). The angle formed by joining the apex of the central lobe via a primary sinus to the apex of one of the neighbouring lateral lobes 60°–82° in 5-lobed forms and c.80°–133° in 3-lobed forms, the angle being unrelated to the width of the lamina.

Leaf margin non-entire, crenulate with rounded teeth 0.2–0.8 mm across projecting apically, alternating with acute sinuses. Teeth of one size group.

Venation actinodromous, primary veins 3–5. Lateral primary veins arising at 28°–50°(–60°) from the central primary vein 0–1 mm above the junction of the lamina and petiole; these lateral primary veins 0.1–0.6 mm wide at mid-point, 50–102 % the length of the central primary vein (fig. 29). The percentage of the lamina on the basisopic side of the major lateral primary veins c.20–33 % in the case of 3-lobed forms, 40–c.45 % in the case of 5-lobed forms. Lateral primary veins bearing 3–6(–7?) secondary veins on their acroscopic side, arising at 45°–75°. The angle at which the veins arise constant or decreasing within the first few mms, hardly tapering along their length, 0.05–0.22 mm wide at mid-point.

Lateral primary veins bearing up to 10-18 secondary veins on their basiscopic side, the most proximal vein arising at 40°-50°, arising in the remaining part of the basal third of the lamina at 40°-50°, in the median third at 45°-55°, in the apical third at 45°-60°. The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins either initially increasing and thereafter gradually decreasing,

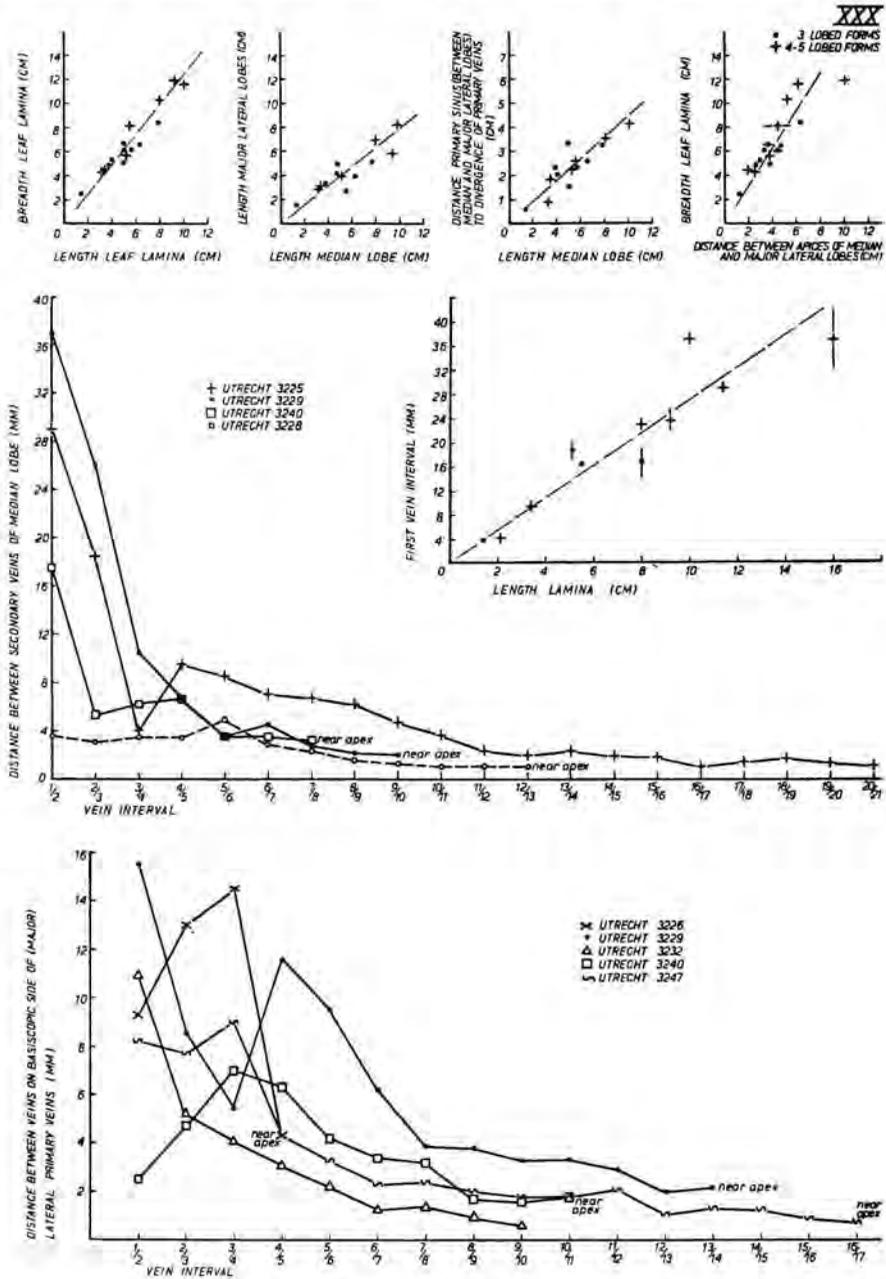


Fig. 29. Graphs XXX.

or successively decreasing from base to apex (fig. 29). Veins hardly or somewhat tapering along their length, 0.05–0.20 mm wide at mid-point, sometimes branched. Central primary vein straight, hardly to markedly tapering along length, 0.2–0.6 mm wide at mid-point. Central primary vein bearing 10–20 secondary veins per side, those near the apex very short and fine, arising in the basal third of the lobe at 40° – 45° , in the median third at 40° – 45° , in the apical third at 40° – 55° . The angle at which the veins arise increasing, constant or decreasing within the first few mms. The spacing of the veins initially great but rapidly decreasing in general, the distance between the secondary veins near the apex being but small (fig. 29). The distance between the point of origin of the lateral primary veins and that of the first secondary vein in the central lobe roughly correlated with the length of the lamina (fig. 29). Secondary veins mostly alternately arranged, hardly or somewhat tapering along their length, 0.1–0.2 mm wide at mid-point, interconnected distally by extensions of secondary veins. Intermediate veins 0–5 per intercostal field, some having a somewhat twisted course, arising at 60° – 120° , converging/diverging, the spacing between them constant or irregular. The veins similar in width or increasing in width with increase in length, extending up to $3/4$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 3–20 per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 10–50 per 10 mm², with some or many free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of c.95–400 more or less polygonal cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–2:1. Cell wall 1.4–2.0(–3.5) microns thick, unpitted or occasionally pitted, straight. Cells over veins elongate, the transverse walls either slanting or at right angles to the lateral walls. Finer veins somewhat reflected in cuticle. Cells at leaf margin c.300 per 0.1 mm², the cell length/cell breadth ratio being 1:1–10:1, arranged in 8–10 rows. Cell wall 0.7–0.8 microns thick, largely unpitted, straight; transverse walls slanting or at right angles to the lateral walls. Epidermis in stomatal condition composed of 90–400 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–5:1. Cell wall 0.5–1.0 microns thick, unpitted or pitted, straight or somewhat undulate with 0–6 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1:1–6:1 or more. Finer veins reflected in cuticle. Stomata 18.0–30.6 microns long and 10.8–25.2 microns broad, breadth 53–100 % length, c.12–14 per 0.1 mm²; stomatal index 3.3–9.0 %. Stomata variously orientated, undepressed, more or less equidistant or somewhat arranged in groups, apices rarely retuse. Stomatal slit 47–82 % stomatal length. Accessory cells 2,4–6, symmetrical with 0–2 polar and 2–4 lateral cells, similar in size

or somewhat smaller than the rest of the epidermal cells. Internal resinous bodies absent.

Specimens examined: 90, among which the numbered specimens:

Geol. Inst. Cologne: Coll. H. Weyland 1440, 1442, 1469, 1469a, 1469b, 1538, 1539.

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3225, 3226, 3227, 3228, 3229, 3230, 3231, 3232, 3233, 3234, 3237, 3238, 3239, 3240, 3241, 3242, 3243, 3244, 3245, 3246, 3247, 3396D.

Discussion:

In gross morphology the leaf-remains were found to resemble leaves of *Acanthopanax septemlobum* (Thunb.) Koidz., *Kalopanax pictus* (Thunb.) Nakai, *Passiflora incarnata* L. and those of certain species of *Acer* and *Liquidambar*. Differences involving the nature of the free vein-endings were to be seen in herbarium material, but unfortunately the preservation of the leaf-remains is not sufficient to enable one to make definite use of this character. However, the leaves of *Acanthopanax septemlobum* (Araliaceae) and all species of *Acer* (Aceraceae) resembling the leaf-remains are characterized by a sharply toothed leaf margin. *Passiflora incarnata* (Passifloraceae), *Liquidambar* (Hamamelidaceae) and *Kalopanax pictus* (Araliaceae) like the fossil have a crenulate leaf margin, albeit with an occasional sharp tooth.

The leaves of *Passiflora incarnata* differ from the fossil ones and those of the two remaining genera in having a markedly narrowed base to the middle of its 3 lobes and in the presence of markedly rounded sinuses between the central and lateral lobes. Thus *Kalopanax* and *Liquidambar* are the most likely possibilities.

In gross morphology the leaves of *Kalopanax pictus* and *Liquidambar* resemble each other very closely. However, the lower epidermis in these two genera does show certain features which enable one to separate the leaf forms. *Kalopanax pictus* is characterized by much narrower stomata (breadth only 33-61 % of length) than are to be found in *Liquidambar* (breadth 47-117 % of length). Furthermore, in *Kalopanax pictus* the stomatal slit is long and may sometimes extend the whole length of the stoma, a feature which is not to be found in *Liquidambar*. On the basis of these features the fossil leaves may be taken to belong to *Liquidambar*.

Differences in the nature of the leaves characterize the three species of *Liquidambar* available to the author at the present time. *Liquidambar formosana* Hance is characterized by leaves with 3(-5) lobes and numerous stomata with short stomatal slits. *Liquidambar styraciflua* L. and *L. orientalis* Mill. on the other hand have leaves with (3-) 5(-7) lobes and fewer stomata with long stomatal slits. Among other things, the fact that the 3-lobed form is fairly common (23 % total) in the assemblage, while the stomatal index is fairly low in the leaf-remains might suggest that the leaf-remains represent an ancestral form in which the particular

combinations of characters characteristic of recent *Liquidambar* species were not yet differentiated. A decision as to the taxonomic status of the leaf-remains cannot, however, be made until herbarium material of the other *Liquidambar* species has been investigated.

Herbarium material examined in detail:

<i>Acanthopanax septemlobum</i> (Thunb.) Koidz.	Coll. Godshalk 17130	(U) det. J. Monachino
<i>Acer erianthum</i> Schwerin	Coll. W. P. Fang 4208	(E) det. W. P. Fang
<i>Acer flabellatum</i> Rehder	Coll. W. P. Fang 7784	(E) det. W. P. Fang
<i>Acer oliverianum</i> Pax	Coll. R. C. Ching 2799	(E) det. W. P. Fang
<i>Acer robustum</i> Pax	Coll. W. P. Fang 10362	(E) det. W. P. Fang
<i>Acer sinense</i> Pax	Coll. R. C. Ching 2963	(E) det. W. P. Fang
<i>Kalopanax pictus</i> (Thunb.) Nakai	Coll. C. Y. Chiao 2783	(E) det. H. L. Li
<i>Liquidambar formosana</i> Hance	Coll. Shimizu & Chuang (Plantae Taiwanianae 20448)	(E) _____
	Coll. C. S. Fan & Y. Y. Li 75	(E) _____
	Coll. H. C. Cheo 274	(E) _____
	Coll. C. Y. Chiao 14238	(E) det. C. Y. Chiao; det. E. D. Merrill
	Coll. J. Esquirol 845	(E) _____
	Coll. R. C. Ching 1578	(E) _____
<i>Liquidambar orientalis</i> Mill.	Coll. P. H. Davis 13474	(E) _____
	Coll. P. H. Davis 15484	(E) _____
	Coll. P. H. Davis 41281	(E) _____
	Coll. T. R. Dudley 35402	(E) _____
	Coll. M. R. K. Lambert & T. K. Thorp 626	(E) _____
<i>Liquidambar styraciflua</i> L.	Coll. F. G. Meyer & D. J. Rogers 24	(U) _____
	Coll. F. R. Rickson 242	(U) det. F. R. Rickson
	Coll. C. R. Bell 14332	(E) _____
	Coll. R. M. Harper 1-7-1902	(E) _____
<i>Passiflora incarnata</i> L.	Coll. K. U. Kramer 876	(U) _____

FAMILY ROSACEAE

Due to convergence in leaf form, this family is one which is generally difficult to recognize simply on the basis of isolated leaves or leaflets. Thus, while the four species WEYLAND (1934) referred to the Rosaceae could not be excluded from this family with certainty, no absolute proof could be found that the leaf-remains actually originated from members of the Rosaceae. In the present account only two taxa have been recognized.

XXXI. *Rosa*

Synonym: *Xanthoxylum serratum* Heer

WEYLAND, 1934, p. 91 pro parte
e.g. Tafel 14, fig. 4!

Description :

Shoots 29.5- > 38.0 mm long and 0.45-1.2 mm wide bearing forwardly or backwardly arched prickles, projecting 0.4-0.7 mm laterally and 0.6-1.3 mm long (measured from tip to middle of base) and, moreover, numerous capitate glands. The globose glands are borne on a stalk 0.04-0.20 mm long, and have a diameter of 0.05-0.13 mm. Stipule hastate, > 10 mm long, 5-6 mm wide, with entire margin. Leaf arrangement compound with 5 leaflets.

Leaflets ovate (-elliptical), 1.0-c.3.2 cm long, 0.5-1.6 cm wide, the length/breadth ratio being c. 1.7: 1-c.2: 1. Apices acute, base slightly cordate in the case of the apical leaflet, rounded in the more distal pair, and obtuse or rounded in the more proximal pair of leaflets. Margin of the leaflets non-entire, serrulate, with acute teeth 0.05-0.9 mm across, 7-c.25 per side, alternating with acute sinuses. Teeth of one size group.

Venation craspedodromous, midvein straight or curved, hardly or markedly tapering along their length, 0.06-0.26 mm wide at mid-point between base and apex of the lamina. Midvein bearing 4-c.10 (?) secondary veins per side, the most proximal vein arising at 45°-60°, arising in the remaining part of the basal third of the lamina at 45°-60°, in the median third at 45°-65°, in the apical third at 30°-60°. The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins reaching a maximum mid-way or remaining more or less constant. Secondary veins alternately arranged, hardly tapering along their length, 0.05-0.15 mm wide at mid-point, interconnected distally by tertiary veins or vein network. The nature of the intermediate veins, tertiary veins, areoles and free vein-endings unknown.

Epidermis unknown.

Specimens examined : Deutsche Akad. Wiss. Berlin: 345(K 161)
Geol. Inst. Cologne: Coll. H. Weyland 1433(K 161), 1434(K 161), s.n.
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3538

Discussion :

Although isolated leaflets are difficult to identify, the arrangement of the leaflets on the shoots and the presence and nature of the stipules show a sufficiently close agreement with those of *Rosa* to warrant a reference of these remains to that genus. *Rubus*, although closely resembling *Rosa* in these vegetative characters, would never appear to have such broadly winged stipules.

Within *Rosa* a certain amount of variation exists as regards the number of leaflets, their form, size, and extent to which the tertiary and finer veins are developed. In certain species the tertiary and finer veins are comparatively thick and project markedly above the areoles on the lower surface of the leaflets; in other species the tertiary and finer veins may be almost indistinguishable from the rest of the leaf substance. The leaf-remains would appear to belong to the latter category. Furthermore,

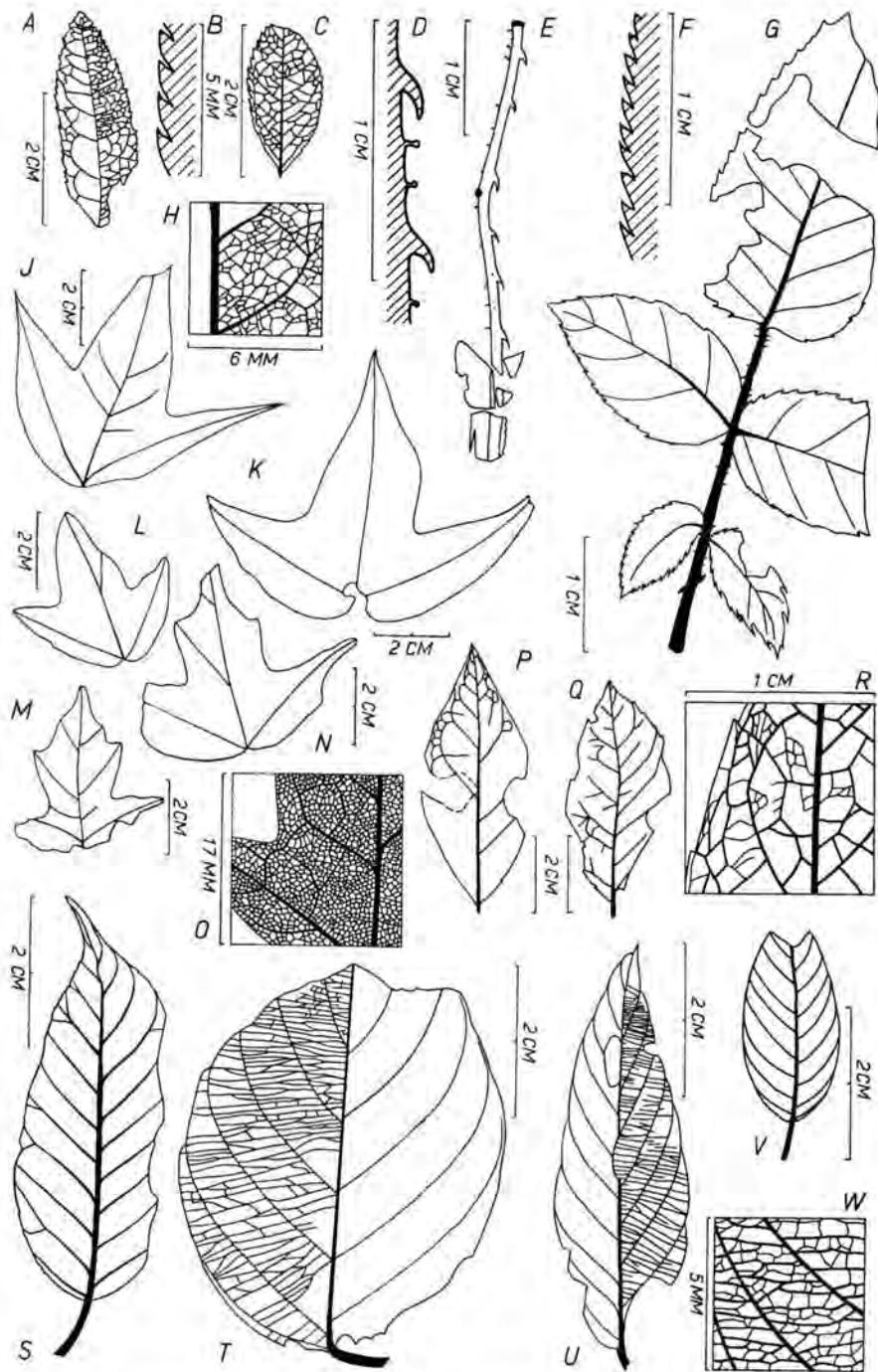


Fig. 30. A-C, H = XXXII: A = Cologne, Coll. H. Weyland 1648; B = detail showing leaf margin; C = Utrecht 3874; H = detail showing venation. D-G = XXXI: D = Utrecht 3538, detail showing capitate glands and prickles; E = Utrecht 3538. Note shape of stipule. F = Cologne s.n., detail showing leaf margin; G = Cologne s.n. J-O = XXXIII: J = Utrecht 3491; K = Utrecht 3492; L = Utrecht 3479 A; M = Utrecht 3489; N = Utrecht 3493; O = detail showing venation and leaf margin. P-R = XXXIV: P = Utrecht 3880; Q = Cologne, Coll. H. Weyland 1457; R = Utrecht 3880, detail showing venation and leaf margin. S-W = XXXV: S = Utrecht 3531; T = Cologne, Coll. H. Weyland 1547; U = Cologne, Coll. H. Weyland 1736; V = Utrecht 3527; W = Utrecht 3531, detail showing venation.

while certain species may be without any trichomes or prickles, other *Rosa* species are characterized by their presence. When present, prickles may be either straight or somewhat bent. This character would appear to have a certain taxonomic value. Stalked glands may or may not be present on the shoots, stipules and leaves. The presence of such glands in the fossil and the somewhat bent prickles, in conjunction with the size, shape and venation of the leaflets should act as a guide to the more exact affinity of the leaf-remains.

None of the leaf material from the living species of *Rosa* examined was found to agree with the fossil in all respects. While this might be considered sufficient grounds for applying another specific name to the leaf-remains it should be pointed out that the present author has only been able to cover little more than 10 % of all living species of *Rosa*. Moreover, of the species covered the one herbarium sheet examined is unlikely to reflect the complete range of variability within a given species.

Herbarium material examined in detail:

<i>Rosa banksiae</i> R. Br.	Coll. E. E. Maire s.n.	(E) det. P. Herring
<i>Rosa banksiopsis</i> Baker	Coll. E. H. Wilson 1045	(E) det. C. E. Kobuski
<i>Rosa bracteata</i> Wendl.	Coll. C. Y. Chiao 14077	(E) det. E. D. Merrill
<i>Rosa brunonii</i> Lindl.	Coll. Mombeig 94	(E) det. C. E. Kobuski
<i>Rosa chinensis</i> Jacq.	Coll. G. Forrest 16391	(E) det. P. Herring
<i>Rosa gentiliana</i> Lévl.	Coll. E. H. Wilson 2722A	(E) det. C. E. Kobuski
<i>Rosa glomerata</i> Rehd. et Wils.	Coll. G. Forrest 20998	(E) det. A. Rehder
<i>Rosa graciliflora</i> Rehd. et Wils.	Coll. E. H. Wilson 3583	(E) det. A. Rehder & E. H. Wilson TYPE
<i>Rosa helenae</i> Rehd. et Wils.	Coll. G. Forrest 10220	(E) det. A. Rehder
<i>Rosa laevigata</i> Michx.	Coll. J. L. Gressitt 1212	(E) det. E. D. Merrill
<i>Rosa longicuspis</i> Bertoloni	Coll. Ducloux 28-4-1909	(E) det. C. E. Kobuski
<i>Rosa microcarpa</i> Lindl.	Coll. A. K. Schindler 301	(E) det. C. E. Kobuski
<i>Rosa multibracteata</i> Hemsl. et Wils.	Coll. Mombeig 95	(E) det. C. E. Kobuski
<i>Rosa multiflora</i> Thunb.	Coll. G. Forrest 25724	(E) det. C. E. Kobuski; P. Herring
<i>Rosa omeiensis</i> Rolfe	Coll. C. Schneider 3521	(E) det. C. E. Kobuski
<i>Rosa roxburghii</i> Trattinick	Coll. Handel-Mazzetti 27-4-1914	(E) det. Handel-Mazzetti
<i>Rosa sericea</i> Lindl.	Coll. G. Forrest 17595	(E) det. W. E. Evans; P. Herring
<i>Rosa sertata</i> Rolfe	Coll. G. Forrest 22527	(E) det. A. Rehder
<i>Rosa souliana</i> Crépin	Coll. G. Forrest 19403	(E) det. P. Herring

XXXII

Synonym: *Pterocarya* c.f. *castaneaeifolia* (Goepfert) Menzel Coll. H. Weyland 1648, det. H. Weyland!

Description:

Petiole 0.8 mm long and 0.45 mm wide at mid-point, constricted in middle and reaching 0.8 mm wide at base of petiole, straight, making no angle with the midvein.

Lamina oblong or elliptical, 2.0–c.4.0 cm long, 1.0–1.3 cm wide, the length/breadth ratio being 2 : 1–3 : 1. Leaf apex acute, leaf base obtuse.

Leaf margin non-entire, serrulate, with acute triangular teeth 0.15–0.9 mm across, c.20–c.35 per side, alternating with acute sinuses. Teeth of one size group.

Venation camptodromous, frequently dictyodromous, midvein straight or curved, hardly tapering along length, c.0.1–0.2 mm wide at mid-point between base and apex of the lamina. Midvein bearing c.9 or more secondary veins per side, the most proximal vein arising at 40°–70°, arising in the remaining part of the basal third of the lamina at 45°–80°, in the median third at 45°–90°, in the apical third at 50°–90°. The angle at which the veins arise initially constant. The spacing of the veins reaching maximum proximally or mid-way (fig. 31). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.025–0.10 mm wide at mid-point, interconnected distally by fine extensions of secondary veins or tertiary veins. Intermediate veins 1–6 per intercostal field, many having a somewhat twisted course, arising from the midvein at 45°–120°(–135°), running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width, extending from 0 to 2/3–9/10 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally, rarely of approximately equal length throughout. Tertiary veins 7–11 per 1 cm secondary vein, much branched, sometimes hardly distinguishable from vein network. Areoles up to 100 per 10 mm², the nature of the free vein-endings uncertain.

Epidermis unknown.

Specimens examined : 7, among which the numbered specimens:

Geol. Inst. Cologne: Coll. H. Weyland 1648

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3871, 3872 (counterpart 3871), 3873, 3874.

Discussion :

Although two specimens in the Cologne collection (Coll. H. Weyland 1648) were labelled *Pterocarya* c.f. *castaneaefolia* the fossil differs from the leaflets of *Pterocarya* in a number of respects e.g. in the presence of fewer teeth, which are moderately large in relation to the size of the lamina. Foliar organs similar to the fossil are to be found in certain species of *Rosa* and *Sorbus* Section Aucuparia. Although a reference to the Rosaceae would appear to be acceptable, a reference to one of the possible genera is impossible on the basis of the present evidence.

Herbarium material examined in detail:

<i>Pterocarya hupehensis</i> Skan.	Coll. K. L. Chu 4105	(E) det. W. E. Manning
<i>Pterocarya rhoifolia</i> Sieb. et Zucc.	Coll. M. Tamura 3417	(E) det. M. Tamura
	Coll. N. Fukuoka 6845	(E) —————

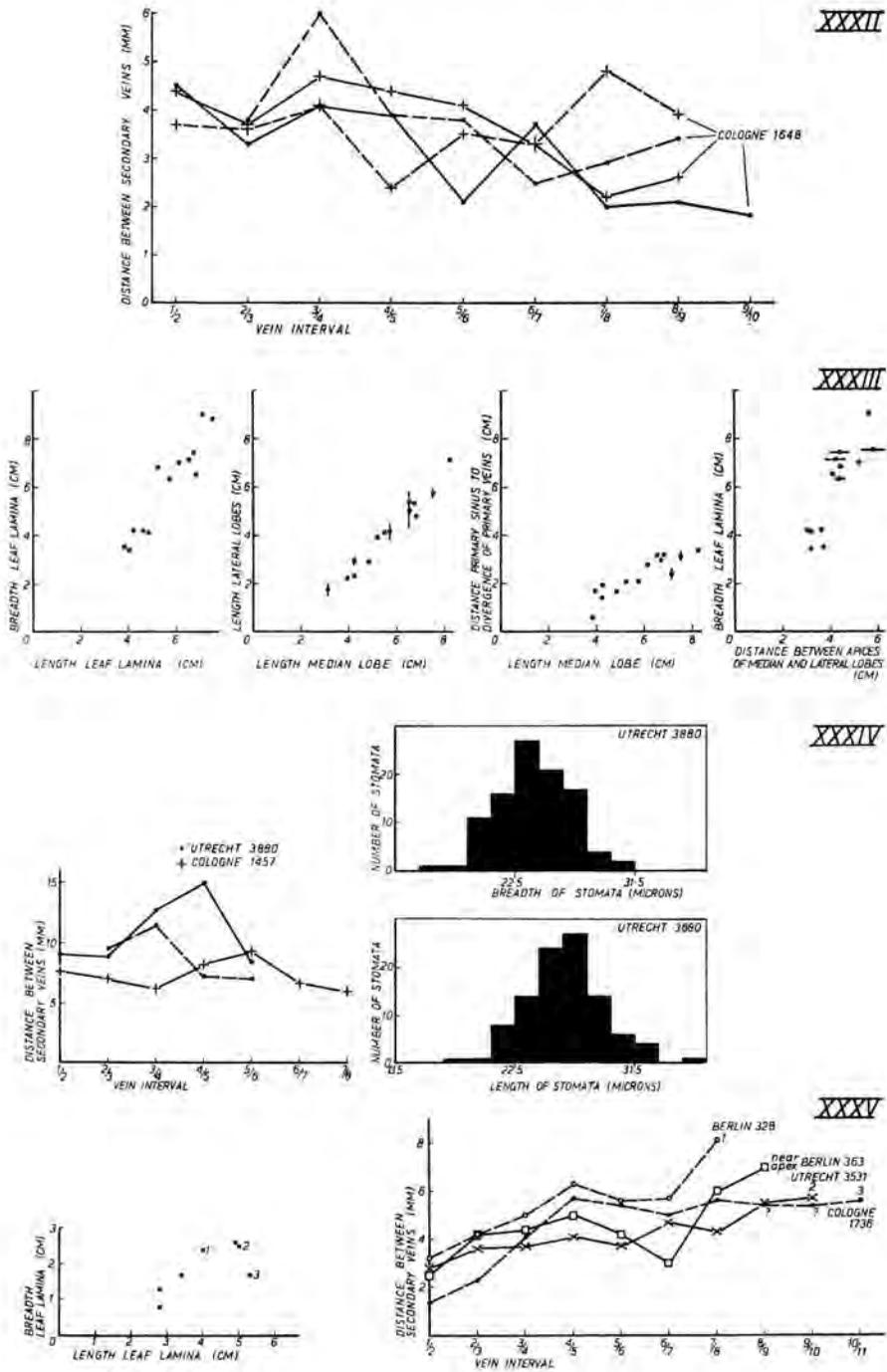


Fig. 31. Graphs and histograms XXXII, XXXIII, XXXIV, XXXV.

Pterocarya stenoptera C. DC.	Coll. J. Esquirol 2457	(E)	det. W. E. Manning
Pterocarya sp.	Coll. P. H. Davis & M. J. E. Coode D 37450	(E)	_____
	Coll. P. H. Davis & M. J. E. Coode D 37497	(E)	_____
	Coll. P. H. Davis & M. J. E. Coode D 39099	(E)	_____
Rosa banksiae R. Br.	Coll. E. E. Maire s.n.	(E)	det. P. Herring
Rosa microcarpa Lindl.	Coll. A. K. Schindler 301	(E)	det. C. E. Kobuski
Rosa omeiensis Rolfe	Coll. C. Schneider 3521	(E)	det. C. E. Kobuski
Sorbus aucuparia L.	Coll. J. van der Burgh 8-9-1967	(U)	det. J. van der Burgh
Sorbus commixta Hedl.	Coll. T. Shimizu 23-6-1964	(U)	_____
Sorbus foliolosa Spach	Coll. M. A. Rau 15-6-1961	(U)	_____
Sorbus matsumurana Koehne	Coll. S. Kitamura & G. Murata 470	(U)	_____
Sorbus prattii Koehne	Coll. G. Forrest 19583	(E)	det. Handel-Mazzetti
Sorbus pteridophylla Handel-Mazzetti	Coll. G. Forrest 14919	(E)	det. T. T. Yü
Sorbus rehderiana Koehne	Coll. G. Forrest 28712	(U)	_____
Sorbus sambucifolia Roen.	Coll. M. Azuma 25-7-1957	(U)	_____

FAMILY ACERACEAE

WEYLAND (1934) described four species of *Acer* as being present in the Kreuzau deposit. None of the leaf material referred to *Acer trilobatum* by H. Weyland was available to the present author in the course of his revision. However, a photograph of a specimen on loan to Dr. H. Walther (Dresden) was made available to the present author. Nevertheless, in the absence of a more detailed examination, the affinity of this specimen (Plate 53B) must remain somewhat uncertain. The remaining three species are here united into a single taxon and attributed to the genus *Acer*.

Although only one taxon could be referred to the Aceraceae with certainty, one should not overlook the possibility that other taxa e.g. No. XXXVII, No. XXXIX and No. XL may belong to this family. However, due to the poor state of preservation of these leaf-remains, no decision could be taken as to their proper affinity.

XXXIII. *Acer* Section Platanoidea Pax

<i>Synonyms</i> : <i>Acer crenatifolium</i> Ett.	WEYLAND, 1934, p. 94, Tafel 17, fig. 1!
<i>Acer integrilobum</i> Weber	WEYLAND, 1934, pp. 94-95, Tafel 18, figs. 1-3!
<i>Acer subcampestre</i> Goeppert	WEYLAND, 1934, p. 94!

Description:

Petiole 21-→46 mm long and 0.3-1.5 mm wide at mid-point, more or less parallel-sided, straight or curved, sometimes making an angle with the central primary vein.

Lamina palmate, 2.5–8.2 cm long, 3.4–12.0 cm wide, the length/breadth ratio being 0.76:1–1.18:1 (fig. 31). Leaf apices acute or acuminate, leaf base obtuse, rounded or cordate. Lamina dissected round primary veins to a depth of 28–62 %, sinuses acute or rounded, the distance from the origin of the lateral primary veins to the sinuses 1.45–3.60 cm, the distance being related to the leaf length (fig. 31). The distance from the central apex to the lateral apices 2.9–8.2 cm, the distance being related to the width of the lamina (fig. 31). The angle formed by joining the apex of the central lobe via a primary sinus to the apex of one of the lateral lobes 80°–130°, the angle being unrelated to the width of the lamina.

Leaf margin entire or having an occasional lobe, lobes acute or rounded, sinuses acute or rounded.

Venation actinodromous, primary veins 3. Lateral primary veins arising at 35°–60°(–80°) from the central primary vein at the junction of the lamina and petiole; these lateral veins 0.15–0.40 mm wide at mid-point, 48–90 % the length of the central primary vein (fig. 31). The percentage of the lamina on the basiscopic side of the lateral primary veins 20–31 %. Lateral primary veins bearing 2–7 secondary veins on their acroscopic side, arising at 45°–90°. The angle at which the veins arise constant or decreasing within the first few mms, hardly tapering along their length, 0.05–0.15 mm wide at mid-point. Lateral primary veins bearing 3–9 secondary veins on their basiscopic side, the most proximal vein arising at 30°–55°, arising in the remaining part of the basal third of the lobe at 50°–80°, in the median third at 50°–80°, in the apical third at 50°–100°. The angle at which the veins arise constant or decreasing within the first few mms. Secondary veins hardly tapering along their length, 0.03–0.15 mm wide at mid-point. Central primary vein straight or curved, hardly or markedly tapering along length, 0.1–0.4 mm wide at mid-point. Central primary vein bearing 3–11 secondary veins per side, arising in the basal third of lobe at 55°–65°, in the median third at 40°–60°, in the apical third at 40°–60°(–90°). The angle at which the veins arise constant or decreasing within the first few mms. Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.03–0.20 mm wide at mid-point, interconnected distally by fine extensions of secondary veins or tertiary veins. Intermediate veins 0–7 per intercostal field, occasionally having a somewhat twisted course, arising from the central primary vein at 55°–110°, running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins mostly similar in width, extending from 0 to 1/2–3/4 the distance from the central primary vein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 3–9 (rarely more) per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 30–90 per 10 mm², with some or many free vein-endings, these being unbranched and to a lesser extent branched.

Epidermis in non-stomatal condition composed of 200–550 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–3:1. Cell wall 0.4–1.8 microns thick, unpitted or pitted, straight. Cells over veins narrow elongate, the transverse walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Cells at leaf margin c.350 per 0.1 mm², the cell length/cell breadth ratio being 1:1–6:1, arranged in c.10 rows. Cell wall 0.5–1.5 microns thick, somewhat pitted, straight, the transverse walls slanting or at right angles to the lateral walls. Epidermis in stomatal condition composed of c.350–c.560 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–2:1. Cell wall 0.5–1.0 microns thick, unpitted or finely pitted, straight. Cells over veins narrow elongate, the cell length/cell breadth ratio being 1:1–3.5:1, the transverse walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Stomata 12.6–28.8 microns long and 10.8–18.2 microns broad, breadth 50–90 % length, c.40 (?)–c.50 (?) stomata per 0.1 mm²; stomatal index uncertain. Stomata variously orientated, undepressed, equidistant or somewhat arranged in groups, apices non-retuse. Stomatal slit 37.5–60 % stomatal length. The nature of the accessory cells, if any, uncertain. Appendage bases, round or oval, 12–24 microns in diameter, sometimes present over veins, 0–2 per 0.1 mm² with 6–8 associated cells, cell wall generally thickened. Internal resinous bodies absent.

Specimens examined: 77, among which the numbered specimens:

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3479A, 3480, 3481, 3482, 3483, 3484, 3485, 3486, 3487, 3488, 3489, 3490, 3491, 3492, 3493, 3494, 3495, 3496, 3497, 3498, 3499, 3500, 3501, 3502.

Discussion:

Although possibly resulting in a somewhat heterogeneous collection of leaf-forms, leaf-remains referable to *Acer integrilobum* on the one hand and *Acer crenatifolium* and *A. subcampestre* on the other have been united in a single taxon. The only definable difference found between these forms was the presence or absence of an additional lobe on the central lobe of the leaf.

Plants having a leaf-form similar to that of the fossil are to be found in a number of dicotyledonous families e.g. Aceraceae (various *Acer* species), Araliaceae (e.g. *Hedera*), Bignoniaceae (e.g. *Oroxylum indicum*), Caprifoliaceae (some *Viburnum* species), Cucurbitaceae (e.g. *Feuillea trilobata*), Malvaceae (species of *Thespesia* and *Gossypium*), Menispermaceae (e.g. *Cocculus carolinus*) and Passifloraceae (e.g. *Passiflora pallens*). In outward appearance the leaves of these species may be almost indistinguishable. However, the cuticles of the various species act as a guide to the separation of these taxa from one another. In the leaf-remains under consideration the finer veins are reflected in the cuticle and the epidermal cells are relatively small. Of the taxa mentioned above only the cuticles of *Acer* agree with the fossil in these respects.

Species of *Acer* having leaves resembling those of the fossil in outward appearance are referred to various sections in the classification of this genus (e.g. PAX, 1902; POJARKOVA, 1933; FANG, 1939). Within these sections a certain amount of variation is encountered in the nature of the cuticles. This can be made use of in attempting to ascertain the affinity of the fossil. The nature of the cell walls on the upper surface of the leaves would appear to have a certain taxonomic value. Furthermore, the amount of variation encountered in the lower epidermis can be made use of in classification at an infrageneric level. The cells of the lower epidermis may be domed in certain cases e.g. *Acer albopurpurascens* Hayata, *A. cinnamomifolium* Hayata, *A. buergerianum* Miq., *A. hyrcanum* Fisch. et Meyer, *A. monspessulanum* L., *A. oblongum* Wall. and *A. oliverianum* Pax. The presence or absence of hairs (unicellular or multicellular), while no doubt somewhat related to the age of the leaf, may be of some use in determination. The presence and frequency of glands can also be made use of.

The cuticle preparations obtained from the leaf-remains would suggest that the leaves had straight-walled cells and only few trichomes. Of the species of *Acer* having leaves similar in gross-morphology only a few had a similar epidermis to that of the fossil e.g. *Acer amplum* Rehder, *A. bodinieri* Lév., *A. mono* Maxim. and *A. wilsonii* Rehder. These species were all referred to Section Platanoidea by FANG (1939). However, none of these species show the lobing characteristic of certain extreme forms of the taxon as circumscribed here. In outward appearance these extreme forms resemble the leaves of *Acer campestre* L. (including *A. austriacum* Tratt. and *A. orthopteron* Masner.) and *A. miyabei* Maxim. While there exists the possibility that the leaves of these extreme forms may be found to have a different epidermal structure, it should be pointed out that species such as *Acer campestre* are also placed in the Section Platanoidea in modern treatments of the genus (compare, e.g. WALTERS, 1968). Thus, while a reference to a specific entity would appear to be impossible on the basis of the leaf-remains alone, their attribution to the Section Platanoidea would appear to be fully warranted.

Herbarium material examined in detail:

<i>Acer albopurpurascens</i> Hayata	Coll. T. Shimizu & M. T. Kao 23-4-1961	(E) _____
<i>Acer amplum</i> Rehder	Coll. R. C. Ching 1466	(E) det. W. P. Fang
	Coll. C. N. Chen 3849	(E) det. W. P. Fang
<i>Acer austriacum</i> Tratt.	Coll. A. Lang 163	(U) _____
<i>Acer bodinieri</i> Lév.	Coll. G. Forrest 17908	(E) det. W. P. Fang
	Coll. G. Forrest 24394	(E) det. W. P. Fang
<i>Acer buergerianum</i> Miq.	Coll. C. N. Chen 3704	(E) det. W. P. Fang
	Coll. C. Y. Chiao 2463	(E) det. A. Rehder; det. W. P. Fang
<i>Acer campestre</i> L.	Coll. A. Callier 568	(E) det. F. Pax
	Coll. Stud. biol. Rheno- Trai. in itinere 20-7-1967	(U) det. J. van der Burgh

	Coll. J. C. Lindeman & A. C. de Roon 3-6-1958	(U) det. J. C. Lindeman & A. C. de Roon
<i>Acer cappadocicum</i> Gundelsheim ex Gled.	Coll. W. Koelz 16723	(E) det. A. Pojarkova
	Coll. F. Kingdon Ward 4113	(E) det. W. P. Fang
	Coll. G. Forrest 19856	(E) det. W. P. Fang
<i>Acer cinnamomifolium</i> Hayata	Coll. R. C. Ching 1983	(E) det. W. P. Fang
<i>Acer creticum</i> L.	Coll. T. G. Orphanides 51	(E) _____
	Coll. Heldreich 23-7-1886	(E) _____
<i>Acer divergens</i> Pax	Coll. N. Busch, B. B. Marcowicz & G. N. Woronov 268	(E) det. E. Murray
<i>Acer floridanum</i> (Chapm.) Pax	Coll. A. H. Curtiss 5874	(E) _____
	Coll. G. V. Nash 10, 11-8-1895	(E) _____
<i>Acer grandidentatum</i> Nutt.	Coll. L. C. Hincley 2733	(U) _____
	Coll. S. M. Tracy & F. S. Earle 253	(E) _____
<i>Acer hyrcanum</i> Fisch. et Meyer	Coll. K. Maly 4855	(E) _____
<i>Acer leucoderme</i> Small	Coll. W. B. Fox & R. K. Godfrey 7-5-1948	(U) _____
	Coll. A. H. Curtiss 6465	(E) _____
<i>Acer miyabei</i> Maxim.	Coll. M. Togasi 27-8-1954 (Nat. Sci. Mus. Tokyo 1069)	(E) _____
	Coll. H. Koyama & K. Iwatsuki 24-8-1965	(E) _____
<i>Acer mono</i> Maxim.	Coll. N. Fukuoka 6800	(E) _____
	Coll. R. C. Ching 2788	(E) _____
<i>Acer monspessulanum</i> L.	Coll. E. Reverchon 481	(E) _____
	Coll. S. Demirci 2147	(E) det. E. Murray
	Coll. T. G. Orphanides 808	(E) _____
	Coll. P. H. Davis & O. Polunin D 23846	(E) det. F. Yaltirik
<i>Acer oblongum</i> Wall.	Coll. G. Forrest 10769	(E) det. W. P. Fang
<i>Acer oliverianum</i> Pax	Coll. R. C. Ching 2799	(E) det. W. P. Fang
<i>Acer orientale</i> L.	Coll. W. Greuter 7523	(E) _____
	Coll. H. Kayacik & F. Yaltirik 3380	(E) det. F. Yaltirik
<i>Acer orthopteron</i> Masner.	Coll. anon. ante annum 1840	(U) _____
<i>Acer saccharum</i> Marsh	Coll. R. M. Kriebel 849	(E) _____
	Coll. K. K. MacKenzie 15	(E) _____
	Coll. K. K. MacKenzie 1877	(E) _____
	Coll. K. U. Kramer 551	(U) det. K. U. Kramer
<i>Acer syriacum</i> Boiss. et Gaillardot	Coll. Y. I. Barkoudah 262	(U) det. Y. I. Barkoudah
	Coll. P. H. Davis 4748	(E) det. A. Pojarkova
	Coll. T. Kotschy 829	(E) det. A. Pojarkova

<i>Acer wilsonii</i> Rehder	Coll. Handel-Mazzetti 12074	(E) det. A. Rehder; det. W. P. Fang
	Coll. Canton Christian College Herb. 12516	(E) det. W. P. Fang
<i>Cocculus carolinus</i> (L.) DC.	Coll. K. U. Kramer 866	(U) det. K. U. Kramer
<i>Feuillea trilobata</i> L.	Coll. Y. Mexia 5459	(U) det. P. C. Standley
<i>Gossypium acuminatum</i> Roxb.	Coll. A. D. E. Elmer 15545	(U) det. J. van Borssum Waalkes
<i>Gossypium arboreum</i> L.	Coll. R. Zimmermann 131	(U) _____
<i>Gossypium barbadense</i> L.	Coll. E. Heldring-Talma in 1947	(U) det. A. E. Stolck
<i>Gossypium hirsutum</i> L.	Coll. F. C. Craighead 28-11-1962	(U) _____
<i>Hedera rhombea</i> Sieb. et Zucc.	Coll. G. Murata 13827	(U) _____
<i>Passiflora pallens</i> Poepp.	Coll. J. K. Small 7799	(U) _____
<i>Thespesia lampas</i> Dalz. et Gibs.	Coll. C. A. Backer 4-1904	(U) det. C. A. Backer
<i>Viburnum sargentii</i> Koehne	Coll. R. C. Ching 1034	(E) det. D. R. Egolf

FAMILY AQUIFOLIACEAE

XXXIV. *Ilex*

Synonym: *Benzoin antiquum* Heer pro parte e.g. Coll. H. Weyland 1457, det. H. Weyland!

Description:

Petiole 4.0–4.5 mm long and c.0.7–1.5 mm wide at mid-point, straight, making no angle with the midvein.

Lamina elliptical, 5.7–6.5 cm long, 2.65–2.9 cm wide, the length/breadth ratio being 2.15 : 1–2.24 : 1. Leaf apex acute, leaf base acute.

Leaf margin non-entire, serrulate or denticulate, with acute teeth 0.05–0.30 mm across, 10–14 per side, alternating with acute or rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein straight, hardly or markedly tapering along length, 0.4 mm wide at mid-point between base and apex of the lamina. Midvein bearing 6–8 secondary veins per side, the most proximal vein arising at 40°–45°, arising in the remaining part of the basal third of the lamina at 45°–50°, in the median third at 40°–60°, in the apical third at 40°–50°. The angle at which the veins arise constant within the first few mms. The spacing of the veins reaching a maximum in the apical half of the lamina (fig. 31). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.05–0.20 mm wide at mid-point, interconnected distally by strong extensions of secondary veins. Intermediate veins 3–5 per intercostal field, arising from the midvein at 45°–120°, converging/diverging from one another, the spacing between them being constant or increasing distally. The veins similar in width, extending from 0 to 3/4–5/6 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary

veins 4–10 per 1 cm secondary vein, somewhat branched. The nature of the areoles and free vein-endings unknown.

Epidermis in non-stomatal condition composed of 145–280 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–2:1. Cell wall 0.35–0.60 microns thick, largely unpitted, rarely straight and more commonly undulating with 0–8 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 14.4 microns. Cells over veins similar to the rest of the epidermal cells. Cells at leaf margin c.120 per 0.1 mm², the cell length/cell breadth ratio being 1:1–4.2:1, arranged in c.10 rows. Cell wall 0.35–0.60 microns thick, largely unpitted, straight, the transverse walls slanting or at right angles to lateral walls. Epidermis in stomatal condition composed of 120–140 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–3:1. Cell wall 0.35–0.60 microns thick, largely unpitted, rarely straight and more commonly undulating with 0–10 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 12.6 microns. Cells over veins similar to the rest of the epidermal cells. Stomata 17.1–36.9 microns long and 15.3–31.5 microns broad (fig. 31), breadth 60–130 % length, 0–20 per 0.1 mm²; stomatal index 0–15.4 %. Stomata variously orientated, undepressed, markedly arranged in groups, apices non-retuse. Stomatal slit 33–58 % stomatal length. Accessory cells 3–5, symmetrically or spirally arranged. Accessory cells narrower than the rest of the epidermal cells. Hair bases 8.5–12 microns in diameter present, 0–1 per 0.1 mm², cells in immediate proximity have a less highly undulate cell wall.

Specimens examined: Geol. Inst. Cologne: Coll. H. Weyland 1457
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3880

Discussion:

While the leaf-remains under consideration have a non-entire margin, members of the Lauraceae are very rarely found to have anything other than entire leaves. Furthermore, the stomata and accessory cells in the fossil differ from those encountered in the Lauraceae. Thus, while H. Weyland referred H. Weyland 1457 to *Benzoin antiquum* Heer, this cannot be supported in the light of the present evidence.

Of all the cuticle preparations examined the greatest resemblance was found between those of the fossil and certain species of *Ilex* e.g. *I. hanceana* Maxim. In this species the same variation in size and arrangement of the accessory cells was to be found. The great variation in stomatal index encountered in the leaf-remains under consideration reflects a marked grouping of the stomata. Grouping of the stomata to such an extent is, in the author's experience, a relatively rare feature among the dicotyledons. However, a grouping of the stomata such as found in the fossil is displayed by certain species of *Ilex* e.g. *I. formosana* Maxim. While more herbarium material requires to be examined before a decision as to the infrageneric

status of the fossil can be taken, a reference to the genus *Ilex* would appear to be fairly well founded.

Herbarium material examined in detail:

<i>Ilex cassine</i> L.	Coll. J. R. Bozeman, A. E. Radford & E. C. Leonard 11520	(U) _____
<i>Ilex coriacea</i> (Pursh) Chapman	Coll. H. E. Ahles & J. A. Duke 44630	(U) _____
<i>Ilex edicostata</i> Hu et Tang	Coll. A. N. Steward, C. Y. Chiao & H. C. Cheo s.n.	(E) det. S. Y. Hu
<i>Ilex excelsa</i> (Wall.) Hook. f.	Coll. Wang & Liu 85048	(E) det. S. Y. Hu
<i>Ilex formosana</i> Maxim.	Herb. H. Lévêillé	(E) det. S. Y. Hu
<i>Ilex glabra</i> (L.) Gray	Coll. J. K. Small, G. K. Small & C. A. Mosier 6770	(U) _____
<i>Ilex hanceana</i> Maxim.	Coll. J. L. Gressitt 1534	(E) det. E. D. Merrill
<i>Ilex krugiana</i> Loes.	Coll. J. K. Small & C. A. Mosier 5507	(U) _____
<i>Ilex latifolia</i> Thunb.	Coll. A. N. Steward 9-8-1924 (Herb. Univ. Nanking 7140)	(E) det. A. Rehder
<i>Ilex rotunda</i> Thunb.	Coll. J. M. Dalziel s.n.	(E) det. S. Y. Hu
<i>Ilex wilsonii</i> Loes.	Coll. Handel-Mazzetti 12063	(E) det. T. Loesener TYPE

FAMILY RHAMNACEAE

WEYLAND (1934) described four species from Kreuzau as belonging to this family. The material originally determined as *Rhamnus gaudinii* Heer was later referred to as *Alnus palaeojaponica* Weyland (WEYLAND, 1943). In the present account this material is described under No. LVIII. The other three species described by WEYLAND (1934) are here combined in a single taxon (No. L). This taxon has an epidermis unlike those of members of the Rhamnaceae examined. However, while none of the material referred to the Rhamnaceae by WEYLAND (1934) would appear to be referable to this family, other material described as that of *Cornus* (WEYLAND, 1934; GOTHAN and WEYLAND, 1964) should be transferred to this family.

XXXV. *Berchemia*

<i>Synonyms</i> : <i>Cornus rhamnifolia</i> Heer non Weber	WEYLAND, 1934, pp. 108-109, Tafel 21, fig. 6! GOTHAN and WEYLAND, 1964, Tafel 28, fig. 4!
<i>Cornus studeri</i> Heer	WEYLAND, 1934, p. 109, Tafel 21, fig. 4!

Description:

Petiole 5.0-9.8 mm long and 0.65-1.3 mm wide at mid-point, more or less parallel-sided or gradually increasing in width away from leaf base, straight or curved, making an angle with the midvein.

Lamina ovate, c.2.75–c.7.6 cm long, 1.25–4.25 cm wide, the length/breadth ratio being c.1.5 : 1–3.1 : 1 (fig. 31). Leaf apex acute or acuminate, leaf base rounded.

Leaf margin entire or sub-entire, lamina constricted above termination of each secondary vein.

Venation craspedodromous, midvein straight or curved, somewhat tapering along length, 0.2–0.5 mm wide at mid-point between base and apex of the lamina. Midvein bearing 6–12 secondary veins per side, the most proximal vein arising at 40°–60°(–90°), arising in the remaining part of the basal third of the lamina at 40°–60°(–70°), in the median third at 35°–60°, in the apical third at 30°–50°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the veins more or less constant or somewhat irregular, not infrequently with two maxima, one mid-way and another apically (fig. 31). Secondary veins opposite or alternately arranged, hardly tapering along length, 0.08–0.25 mm wide at mid-point, interconnected distally by fine extensions of secondary veins or tertiary veins. Intermediate veins 2–11 (–16) per intercostal field, arising from the midvein at 60°–120°, running more or less parallel to one another, the spacing between them more or less constant. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/3–1/2 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary veins 9–26 per 1 cm secondary vein, arranged more or less at right angles to the midvein, little branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles (30–) 50–100 per 10 mm², some free vein-endings apparently present, these being unbranched and branched.

Epidermis poorly preserved, composed of c.600 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall c.0.45 microns thick, largely unpitted, straight. Cells over veins elongate, the cell length/cell breadth ratio up to 4 : 1 or more. Finer veins reflected in cuticle. Cells at leaf margin with a cell length/cell breadth ratio of 1 : 1–3 : 1, arranged in up to 20 rows. Cell wall c.1 micron thick, unpitted, straight.

Specimens examined: Deutsche Akad. Wiss. Berlin: 328(K 132), 363(K 100)
 Geol. Inst. Cologne: Coll. H. Weyland 1547, 1736
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3527, 3528,
 3529, 3530A, 3531, 3532, 3533, 3534, 3550.

Discussion:

While Cologne 1547 and Berlin 328 were determined as *Cornus rhamnifolia* by Weyland, Weyland referred Cologne 1736 and Berlin 363 to *Cornus studeri*. WEYLAND (1934) gave no indication of the characters he employed in separating these taxa. The only difference which could be found by the present author between these two taxa was the length/breadth ratio. In *Cornus studeri* this was c.2.3 : 1–3.1 : 1, while the leaf-

remains referred to *Cornus rhamnifolia* had a length/breadth ratio of c.1.5:1–1.65:1. However, material in the Utrecht collection was found to have a length/breadth ratio of 1.9:1–2.2:1. This would seem to warrant the inclusion of the material determined as *Cornus studeri* and *C. rhamnifolia* in a single taxon.

Of the leaf material of the *Cornus* species available only that of *Cornus hemsleyi* and *C. stolonifera* resembled the fossil in the presence of closely set tertiary veins running at right angles to the midvein. However, unlike the fossil, the leaves of *Cornus hemsleyi* and *C. stolonifera* have secondary veins arising from the midvein at increasingly greater intervals distally. In the fossil the spacing of the secondary veins is either irregular or more or less constant throughout the length of the lamina. Dr. I. K. Ferguson (personal communication, 1969) has confirmed that the leaf-remains do not resemble the leaves of any American species of *Cornus* known to him.

Of the Chinese and American material examined only the leaves of *Berchemia* were found to resemble the fossil as regards shape, leaf margin, distance between successive secondary veins and the pattern formed by the tertiary veins. Species of *Berchemia* tend to have a sub-entire leaf margin in which the lamina is constricted above the termination of each secondary vein. This feature is to be seen in certain specimens of the fossil as well. All species of *Berchemia* examined had a more or less mucronate leaf apex. Unfortunately, the apex of none of the fossil leaves was sufficiently complete to be able to confirm this feature. While the leaves of this genus are very distinctive, leaf characters are of little use in distinguishing the various species of *Berchemia*. In extreme cases the size of the lamina may aid in the separation of one species from another. However, a great range of intermediate sizes exists, so that it is not possible in the present case to suggest a specific affinity for the fossil.

Herbarium material examined in detail:

<i>Berchemia floribunda</i> (Wall.) Brongn.	Coll. F. A. McClure 9568	(E) det. E. D. Merrill
<i>Berchemia giraldiana</i> C. Schneider	Coll. E. E. Maire s.n. 7-1913	(E) det. L. A. Lauener; det. M. C. Johnston
<i>Berchemia hypochrysa</i> C. Schneider	Coll. E. H. Wilson 3382	(E) det. C. Schneider
<i>Berchemia kulingensis</i> C. Schneider	Coll. A. N. Steward 2414	(E) det. E. D. Merrill
<i>Berchemia polyphylla</i> Wall.	Coll. J. Esquirol 3250	(E) det. L. A. Lauener; det. M. C. Johnston
<i>Berchemia scandens</i> (Hill) Trelease	Coll. J. K. Small & C. A. Mosier 5952	(U) _____
<i>Berchemia sinica</i> C. Schneider	Coll. E. H. Wilson 3386	(E) det. C. Schneider TYPE
<i>Cornus brachypoda</i> Meyer	Coll. E. H. Wilson 1152	(E) det. W. Wangerin
<i>Cornus controversa</i> Hemsl.	Coll. A. Henry 10747 A.	(E) det. A. Rehder
<i>Cornus florida</i> L.	Coll. H. E. Ahles & P. Crutchfield 53260	(U) _____

<i>Cornus hemsleyi</i>	Coll. W. Purdom 1085	(E) _____
C. Schneider et Wang		
<i>Cornus hupehensis</i> Fang	Coll. H. C. Chow 606	(E) det. W. P. Fang
<i>Cornus kousa</i> Hance	Coll. Farges s.n.	(E) det. W. P. Fang
<i>Cornus rehderiana</i> Fang	Coll. E. H. Wilson 1849	(E) det. W. P. Fang
<i>Cornus stolonifera</i> Michx.	Coll. F. G. Meyer & D. J. Rogers 2912	(E) _____
<i>Cornus stricta</i> Lam.	Coll. J. R. Bozeman, G. S. Ramsour & A. E. Radford 45136	(U) _____
<i>Cornus walteri</i> Wangerin	Coll. C. Y. Chiao 2833	(E) det. A. Rehder

DICOTYLEDONEAE INCERTAE SEDES

XXXVI

Description:

Petiole unknown.

Lamina palmate, 4.5 cm and more long, 6.0–c.10 cm wide. Leaf apices acute, leaf base cordate. Lamina dissected round primary veins to a depth of c.65 %, sinuses rounded, the distance from the origin of the lateral primary veins to the sinuses 1.3–1.7 cm.

Leaf margin entire.

Venation actinodromous, primary veins 3. Lateral primary veins arising at 65° from the central primary vein at the junction of the lamina and petiole; these lateral veins 0.1–0.2 mm wide at mid-point, c.87 % the length of the central primary vein. The percentage of the lamina on the basiscopic side of the lateral primary veins c.20–c.25 %. Lateral primary veins bearing a number of secondary veins on their acroscopic side, arising from the lateral primary vein at 60°–65°. The angle at which the veins arise constant or decreasing within the first few mms, hardly tapering along their length, 0.05–0.15 mm wide at mid-point. Lateral primary veins bearing a number of secondary veins on their basiscopic side, the most proximal vein arising at c.45°, arising in the remaining part of the basal third of the lobe at c.45°, in the median third at 45°–70°, the angle in the apical third being unknown. The angle at which the veins arise constant or decreasing within the first few mms. Secondary veins hardly tapering along their length, 0.05–0.15 mm wide at mid-point. Central primary vein straight, hardly tapering along length, 0.25–0.50 mm wide at mid-point between base and apex of lobe. Central primary vein bearing a number of secondary veins per side, arising in the median third of the lamina at 40°–90°, and in the apical third at 60°–80°. The angle at which the veins arise constant or decreasing within the first few mms. Secondary veins mostly alternately arranged, hardly tapering along their length, 0.05–0.20 mm wide at mid-point, interconnected distally by fine extensions of secondary veins. Intermediate veins 0–10 per intercostal field, some having a somewhat twisted course, arising from the central primary vein at 70°–120°, running more or less parallel to one another or converging/

diverging, the spacing between them constant or increasing distally. The veins similar in width or increasing in width with increase in length, extending from 0 to 2/3 the distance from the central primary vein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 3-4 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopical sides of secondary vein more or less similar. Areoles c.30 per 10 mm², with some free vein-endings, these being unbranched and branched.

Cuticle fragmentary, the epidermal cells having a length/breadth ratio of 1:1-3:1(-4:1). Cell wall 0.6-1.8 microns thick, largely unpitted, straight. Cells over veins elongate. Finer veins reflected in cuticle. Cells at leaf margin 290-375 per 0.1 mm², the cell length/cell breadth ratio being 1:1-3:1, sometimes arranged in up to 6 rows, cell wall 0.6-1.8 microns thick, unpitted, straight.

Specimens examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3882, 4151A.

XXXVII

Synonym: c.f. *Hedera* sp.

WEYLAND, 1934, p. 108, Tafel 20, fig. 5!

Description:

Petiole 13->40 mm long and 0.4-1.1 mm wide at mid-point, more or less parallel-sided for the greater part of the length but expanded sometimes sharply at base of petiole, straight or curved, sometimes making an angle with the midvein.

Lamina triangular or palmate (3- or 5-lobed), 3.4-8.8 cm long, 2.1-8.0 cm wide, the length/breadth ratio being 1.0:1-c.1.7:1. Leaf apices acute, leaf base rounded or cordate. Lamina dissected round primary veins to a depth of up to 23 %, sinuses rounded, the distance from the origin of the lateral primary veins (or most proximal secondary veins) to the sinuses 3.4-5.9 cm. The distance from the central apex to the lateral apices, when present, 4.0-4.6 cm or more. The angle formed by joining the apex of the central lobe via a primary sinus to the apex of one of the neighbouring lateral lobes 84°-120°.

Leaf margin entire.

Venation camptodromous or actinodromous, when actinodromous primary veins 3. Lateral primary veins (or most proximal secondary veins) arising at 35°-55° from the central primary vein 0-0.5 mm above the junction of the lamina and petiole; these lateral veins 0.1-0.4 mm wide at mid-point, 57-65 % the length of the central primary vein (or midvein). The percentage of the lamina on the basiscopical side of the lateral primary veins c.30-c.40 % total. Lateral primary veins bearing 0-2 higher order veins on their acroscopic side, arising at c.50°. The angle at which the veins arise initially decreasing, somewhat tapering along their length, 0.04-0.06 mm wide at mid-point. Lateral primary veins (or most proximal secondary veins) bearing 6-9 higher order veins on their basiscopical side,

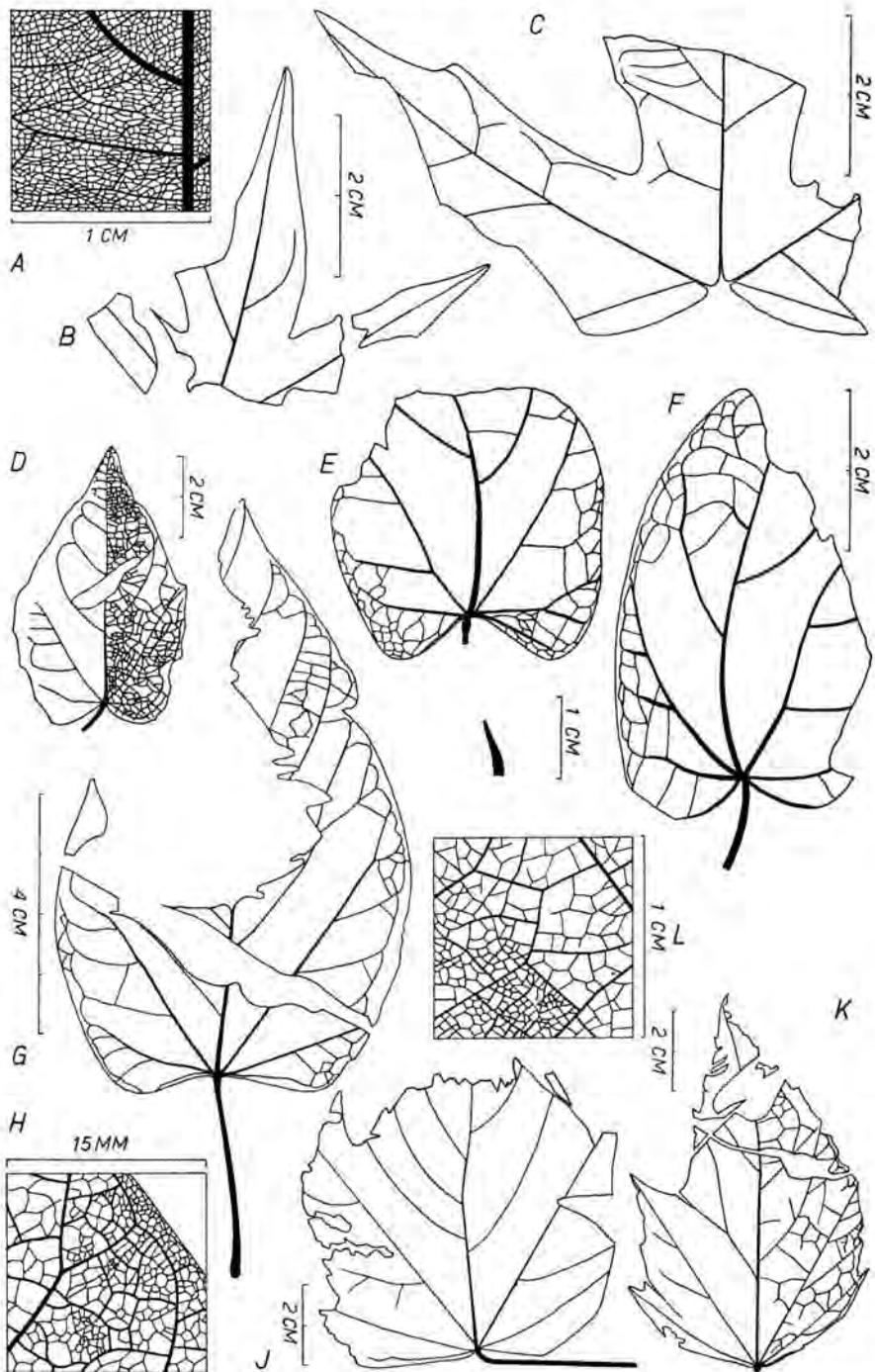


Fig. 32. A-C = XXXVI: A = Utrecht 3882, detail showing venation; B = Utrecht 4151 A; C = Utrecht 3882. D-L = XXXVII: D = Berlin 366; E = Utrecht 3734; F = Utrecht 3737; G = Utrecht 3744; H = Utrecht 3744, detail showing venation and leaf margin; J = Utrecht 3931 D; K = Utrecht 3740; L = detail showing venation.

the most proximal vein arising at 30° – 50° , arising in the remaining part of the proximal third at 30° – 65° , in the median third at 45° – 65° , in the apical third at 55° – 90° . The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins decreasing distally (fig. 34). Veins somewhat tapering along their length, 0.05–0.20 mm wide at mid-point. Central primary vein (or midvein) straight or curved, hardly or markedly tapering along length, 0.2–0.45 mm wide at mid-point. Central primary vein bearing 3–7 secondary veins per side, arising in the basal third of the lamina at (30° –) 45° – 65° , in the median third at 50° – 70° , in the apical third at 50° – 80° (-100°). The angle at which the veins arise constant or decreasing, rarely increasing within the first few mms. The spacing of the veins decreasing towards the apex (fig. 34). Secondary veins opposite or alternately arranged, slightly tapering along their length, 0.02–0.20 mm wide at mid-point, interconnected distally by fine extensions of secondary veins, or tertiary veins. Intermediate veins (0–) 3–12 per intercostal field, occasionally having a somewhat twisted course, arising from the central primary vein at 55° – 130° , more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to $1/5$ – $1/2$ –($3/4$) the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 2–7–(13) per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 40–100 per 10 mm^2 , with some or many free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of unknown number of finely striate cells. Cells over veins elongate, the cell length/cell breadth ratio being 2 : 1–4 : 1 or more, transverse walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Cells at leaf margin c.500 per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–4 : 1, arranged in 8–10 rows. Cell wall 0.3–1.5 microns thick, largely unpitted, straight, transverse walls slanting or at right angles to the lateral walls. *Epidermis* in stomatal condition composed of uncertain number of finely striate cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–2.5 : 1. Cell wall poorly demarcated, 0.3–0.7 microns thick, largely unpitted or pitted, generally straight. Cells over veins elongate. Finer veins reflected in cuticle. Stomata 18.0–28.8 microns long and 14.4–18.0 microns broad, breadth 56–85 % length, c.20–c.50 per 0.1 mm^2 ; stomatal index unknown. Stomata variously orientated, undepressed, more or less equidistant, apices non-retuse. Stomatal slit 46–56 % stomatal length. The nature of the accessory cells, if any, unknown. Internal resinous bodies rare.

Specimens examined : Deutsche Akad. Wiss. Berlin: 366(K 165)
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3734, 3735,
3736, 3737, 3738, 3739, 3740, 3741, 3742, 3743A, 3744A, 3931D.

XXXVIII

- Synonyms* : *Bombax dechenii* (Weber) Friedrich WEYLAND, 1934, p. 100, Tafel 22, fig. 1!
Ficus tiliaefolia (A. Braun) Heer WEYLAND, 1934, pp. 64-65, Tafel 8, fig. 2!; Tafel 9, fig. 1!
WALTHER, 1964, Tafel 27, fig. 3!
Ficus c.f. tiliaefolia (A. Braun) Heer QUAAS, 1910, p. 984; FLIEGEL and STOLLER, 1910, p. 245!

Description :

Petiole 3.5 (?) - > 60 mm long and c.1.6-5.0 mm wide, more or less parallel-sided for the greater part of the length but expanded at base of petiole, straight or curved, sometimes making an angle with the central primary vein.

Lamina sub-orbicular or palmate (3-lobed), c.8.5-c.18.5 cm and more long, 6.9-c.30 cm wide, the length/breadth ratio being 1.1:1-1.35:1. Leaf apices acute or acuminate, leaf base obtuse or cordate. Lamina dissected round primary veins to a depth of up to 28 %, sinuses rounded, the distance from the origin of the lateral primary veins to the sinuses 6.5-7.0 cm or more. The distance from the central apex to the lateral apices, when present, 5.7-7.5 cm or more. The angle formed by joining the apex of the central lobe via a primary sinus to the apex of one of the neighbouring lateral lobes 75°-110°.

Leaf margin entire.

Venation actinodromous, primary veins 3. Lateral primary veins arising at 30°-45° (-70°) from the central primary vein 0-2 mm above the junction of the lamina and petiole; these lateral veins 0.2-1.0 mm wide at mid-point, c.70-87 % the length of the central primary vein. The percentage of the lamina on the basiscopic side of the lateral primary veins c.30-c.47 % total. Lateral primary veins bearing 0-6 secondary veins on their acroscopic side, arising at 45°-60°. The angle at which the veins arise decreasing within the first few mms, hardly or somewhat tapering along their length, 0.10-0.15 mm wide at mid-point. Lateral primary veins bearing 6-9 secondary veins on their basiscopic side, the most proximal vein arising at 30°-55°, arising in the remaining part of the proximal third at 45°-75°, in the median third at 45°-50°, in the apical third at 40°-55°. The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins decreasing distally (fig. 34). Veins somewhat tapering along their length, 0.1-0.8 mm wide at mid-point. Central primary vein straight or curved, hardly or markedly tapering along length, c.0.3-c.1.4 mm wide at mid-point. Central primary vein bearing 4-9 secondary veins per side, arising in the basal third of the lamina at 35°-60°, in the median third at 45°-70°, in the apical third at 45°-70° (-100° at very apex). The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins decreases towards the apex (fig. 34). Secondary veins opposite or alternately ar-

ranged, hardly tapering along their length, 0.07–0.5 mm wide at mid-point, interconnected distally by fine extensions of secondary veins or tertiary veins. Intermediate veins 3–12 per intercostal field, occasionally having a somewhat twisted course, arising from the central primary vein at 55°–125°, running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/3–2/3 the distance from the central primary vein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 1–8 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 30–55(–100) per 10 mm² with some free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of 150–250 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3 : 1. Cell wall 0.5–3.0 microns thick, hardly pitted, straight. Cells over veins elongate, the cell length/cell breadth ratio being 1.5 : 1–5 : 1, the transverse walls slanting or at right angles to the lateral walls. Finer veins sometimes reflected in cuticle. Cells at leaf margin c.400 per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–4 : 1, arranged in c.20 rows. Cell wall 1.5–3.0 microns thick, hardly pitted, straight. Epidermis in stomatal condition unknown. Internal resinous bodies apparently absent.

Specimens examined: Deutsche Akad. Wiss. Berlin: 295(K 52), 305(K 128), 476(K 153), s.n.
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3927, 3928, 3929, 3930.

Discussion:

While WEYLAND (1934, p. 100) considered Berlin 305, which he described as *Bombax dechenii* (Weber) Friedrich (= *Dombeyopsis dechenii* Weber), to differ from the material he referred to *Ficus tiliaefolia* (A. Braun) Heer the present author is of the opinion that these leaf-remains can be referred to the same taxon.

The affinity of the leaf-remains described as *Ficus tiliaefolia* (A. Braun) Heer 1856 [= *Cordia tiliaefolia* A. Braun 1845, *Dombeyopsis tiliaefolia* (A. Braun) Unger 1850, *Buettneria tiliaefolia* (A. Braun) Depape 1922, *Alangium tiliaefolium* (A. Braun) Krishtofovich et Borsuk 1939, *Byttneriophyllum tiliaefolium* (A. Braun) Knobloch et Kvaček 1965] has been the subject of much discussion in the last few years (compare, e.g., GIVULESCU, 1959; TAKAHASHI and OBATA, 1962; KNOBLOCH and KVAČEK, 1965a, 1965b). However, due to the convergence of leaf-forms, the leaf-remains can be compared with a fair number of living taxa. Since the stomata and other features of the lower epidermis are not known from the present material, a detailed comparison with the numerous possibilities was not undertaken.

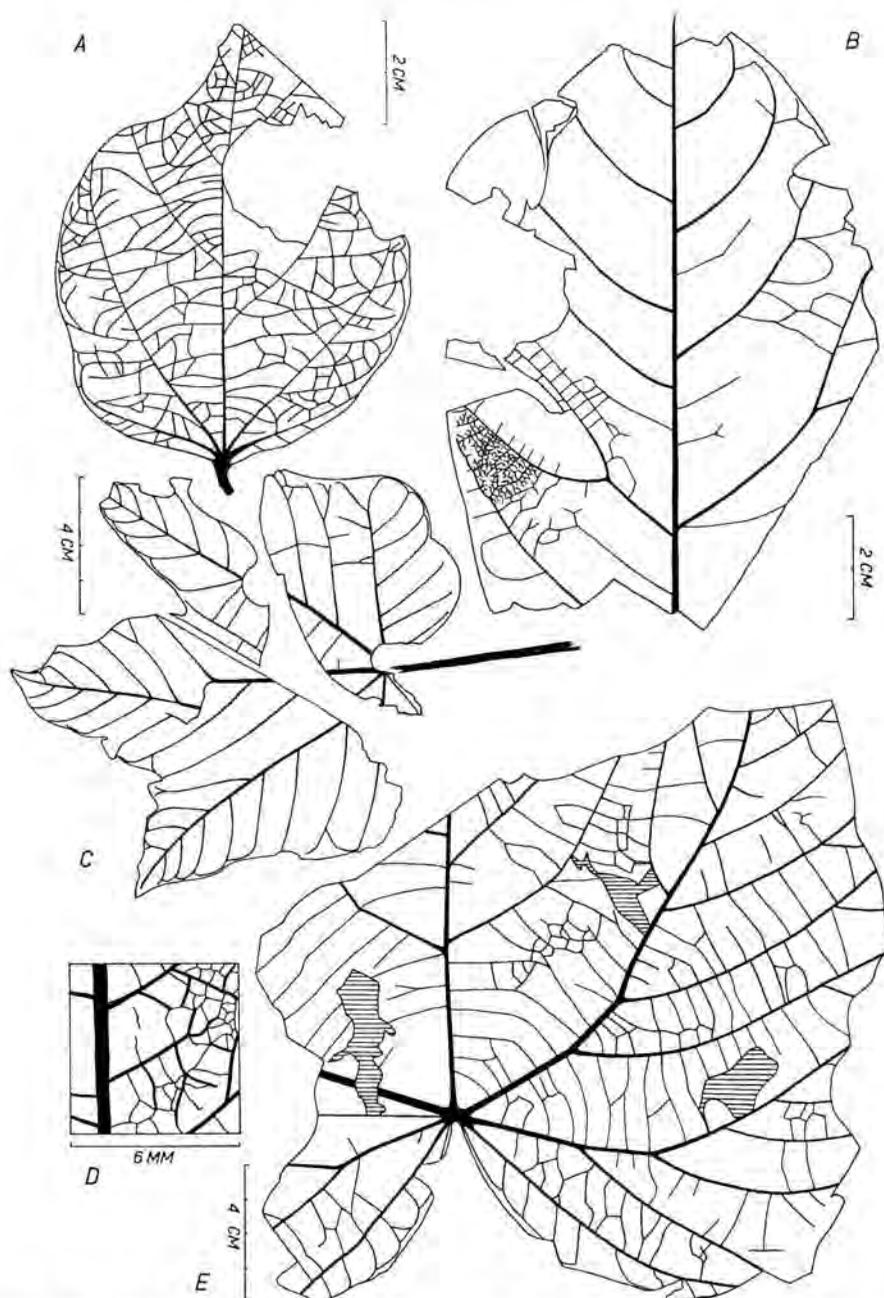


Fig. 33. A-E = XXXVIII: A = Berlin 476; B = Utrecht 3927; C = Utrecht 3928; D = Utrecht 3927, detail showing venation; E = Berlin s.n. (drawing based on specimen and its counterpart).

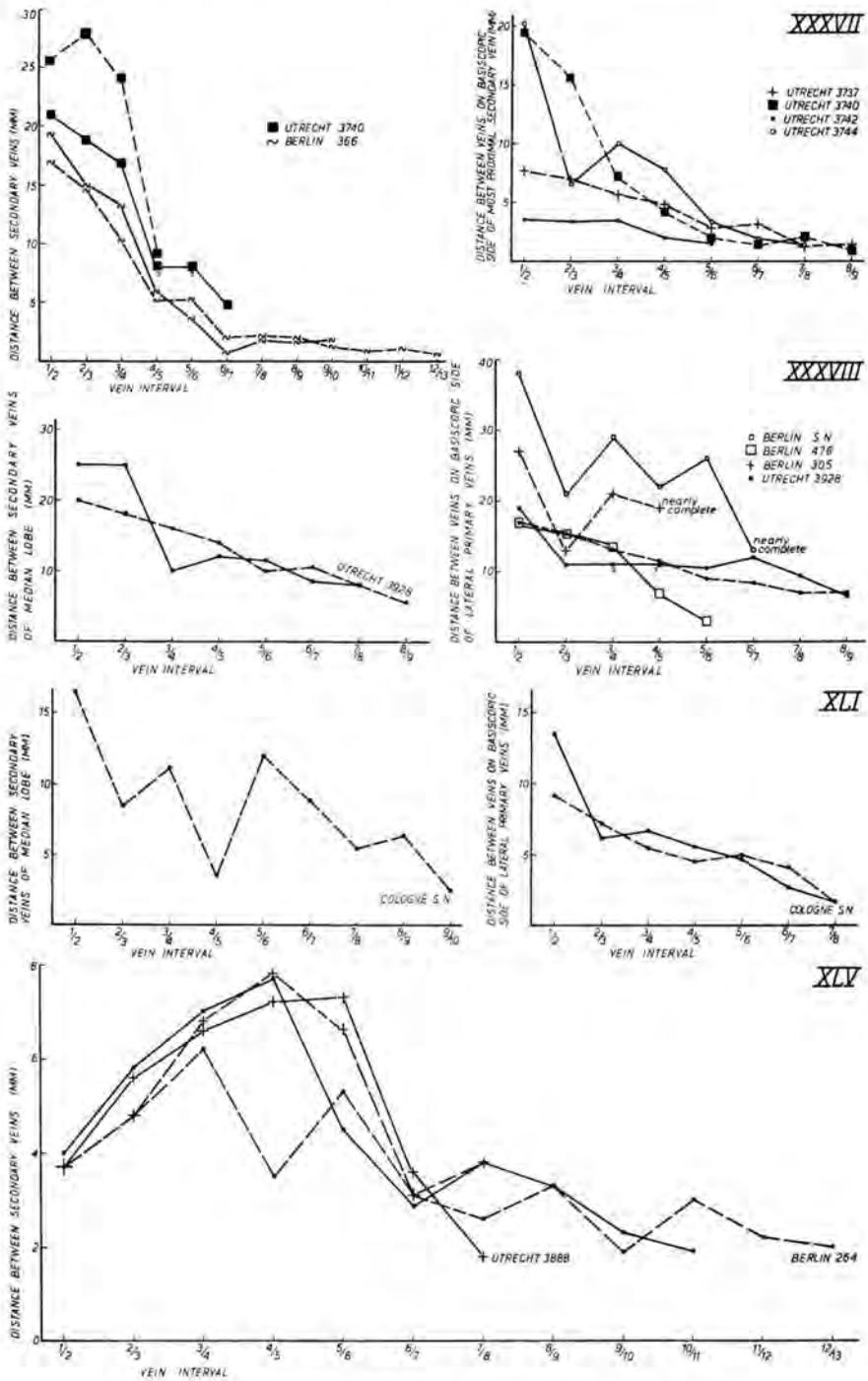


Fig. 34. Graphs XXXVII, XXXVIII, XLI, XLV.

XXXIX

Description:

Petiole up to >22 mm long and 1.0–1.3 mm wide at mid-point, more or less parallel-sided, straight, making no angle with the central primary vein.

Lamina palmate, c.7–c.9 cm long, c.7–9.8 cm wide, the length/breadth ratio being 0.9 : 1. Leaf apices acute, leaf base obtuse. Lamina dissected round primary veins to a depth of 33.5–52.0 %, sinuses acute or rounded, the distance from the origin of the lateral primary veins to the sinuses 2.7–4.5 cm. The distance from the central apex to the lateral apices 4.2–5.0 cm, the distance being related to the width of the lamina. The angle formed by joining the central lobe via a primary sinus to the apex of one of the lateral lobes 63°–80°.

Leaf margin non-entire, serrate-crenate, with acute or rounded teeth 0.5–8.0 mm across, 1 per secondary vein and 0–7 per intercostal field, alternating with acute sinuses. Teeth fall into two size groups.

Venation actinodromous, primary veins 3. Lateral primary veins arising at 30°–40° from the central primary vein at the junction of the lamina and petiole; these lateral veins 0.20–0.35 mm wide at mid-point, c.72–97 % the length of the central primary vein. The percentage of the lamina on the basiscopic side of the lateral primary veins 25–33 % total. Lateral primary veins bearing 4–c.12 secondary veins on their acroscopic side, arising at 50°–70° (–90° at apex). The angle at which the veins arise constant or decreasing within the first few mms, hardly tapering along their length, 0.03–0.13 mm wide at mid-point. Lateral primary veins bearing 7–12 secondary veins on their basiscopic side, the most proximal vein arising at 30°, arising in the remaining part of the basal third of the lobe at 45°–50°, in the median third at 45°–65°, in the apical third at 45°–80°. The angle at which the veins arise constant or decreasing within the first few mms. Secondary veins hardly to somewhat tapering along their length, 0.04–0.25 mm wide at mid-point. Central primary vein straight or curved, markedly tapering along length, 0.35–0.75 mm wide at mid-point between base and apex of the lamina. Central primary vein bearing up to 6 secondary veins per side, arising in the basal third of the lobe at 45°, in the median third at 45°–50°, in the apical third at 40°–60°. The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins decreasing towards the apex. Secondary veins opposite or alternately arranged, somewhat tapering along their length, 0.1–0.2 mm wide at mid-point, interconnected by tertiary veins or vein network. Intermediate veins 3–8 per intercostal field, some having a twisted course, arising from the central primary vein at 55°–110°, running more or less parallel to one another or converging/diverging, the spacing between them constant or increasing distally. The veins similar in width, extending from 0 to 1/2–2/3 the distance from the central primary vein to the leaf margin, reaching their greatest length in intercostal field

mid-way or distally. Tertiary veins 4–7 per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 9–32 per 10 mm², with many free vein-endings, these being unbranched and branched.

Cuticle poorly preserved. Finer veins reflected in cuticle. Internal resinous bodies absent.

Specimens examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3785B, 3876.

XL

Description:

Petiole unknown.

Lamina palmate, c.6.0–6.5 cm long, c.5.5–6.0 cm wide, the length/breadth ratio being 1.1 : 1. Leaf apices acute or obtuse, leaf base unknown. Lamina dissected round primary veins to a depth of c.40–c.50 %, sinuses acute, the distance from the origin of the lateral primary veins to sinus 2.2–c.3 cm. The distance from the central apex to the lateral apices 3.5–c.4.3 cm. The angle formed by joining the apex of the central lobe via a primary sinus to the apex of one of the lateral lobes 63°–c.85°.

Leaf margin non-entire, ± crenate, with acute or rounded teeth 0.3–3.5 mm across, 0–1 per secondary vein and 0 per intercostal field, alternating with acute or rounded sinuses.

Venation actinodromous, primary veins 3. Lateral primary veins arising at c.35° from the central primary vein, these lateral veins 0.3–0.4 mm wide at mid-point, c.66–c.85 % the length of the central primary vein. The percentage of the lamina on the basiscopic side of the lateral primary veins c.25–c.35 % total. Lateral primary veins bearing c.8 secondary veins on their acroscopic side, arising at 45°–90°. The angle at which the veins arise constant within the first few mms, somewhat tapering along their length, 0.07–0.12 mm wide at mid-point. Lateral primary veins bearing 8–10 secondary veins on their basiscopic side, the most proximal vein arising at c.45°, arising in the remaining part of the basal third of the lobe at 40°–50°, in the median third at 45°–60°, in the apical third at c.50°. The angle at which the veins arise constant within the first few mms. The spacing of the veins reaching a maximum mid-way. Secondary veins somewhat tapering along their length, 0.07–0.20 mm wide at mid-point. Central primary vein straight, somewhat or markedly tapering along length, 0.4–0.5 mm wide at mid-point between base and apex of lobe. Midvein bearing 6–7 secondary veins per side, arising in the median third of the lobe at 40°–60° and in the apical third at 45°–80°. The angle at which the veins arise constant within the first few mms. Secondary veins opposite or alternately arranged, somewhat tapering along their length, 0.1–0.2 mm wide at mid-point, interconnected distally by tertiary veins or vein network. Intermediate veins 3–5 per intercostal field, arising from the central primary vein at 45°–115°, running more or less parallel to

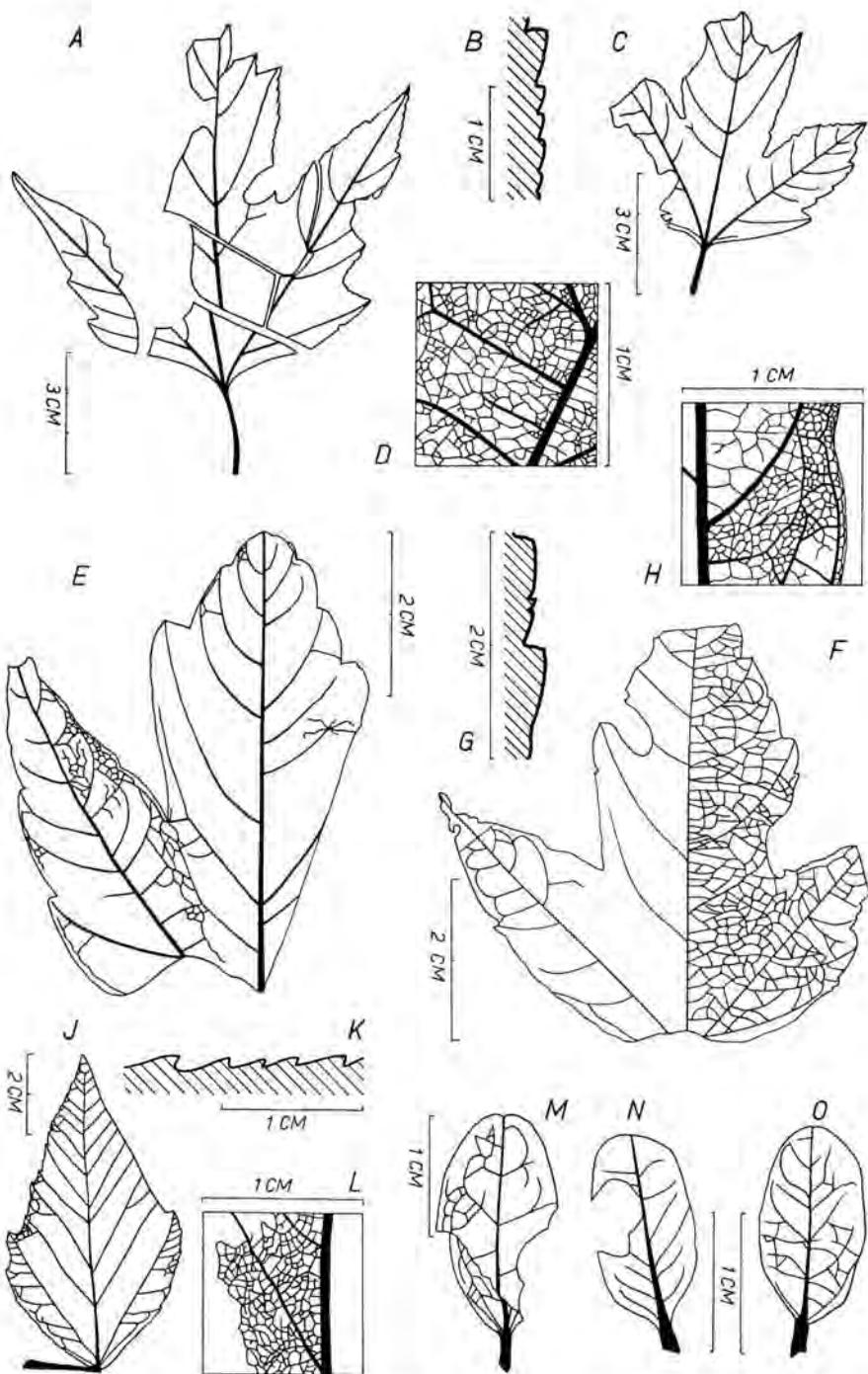


Fig. 35. A-D = XXXIX; A = Utrecht 3785 B; B = detail showing leaf margin; C = Utrecht 3876; D = detail showing venation. E-H = XL: E = Utrecht 3775 A (drawing based on specimen and its counterpart); F = Cologne, Coll. H. Weyland s.n.; G = Utrecht 3775 A, detail showing leaf margin; H = Utrecht 3775 A, detail showing venation and leaf margin. J-L = XLI: J = Cologne, Coll. H. Weyland s.n.; K = Cologne, Coll. H. Weyland s.n., detail showing leaf margin; L = Cologne, Coll. H. Weyland s.n., detail showing venation. M-O = XLII: M = Utrecht 3853; N = Berlin 351; O = Cologne, Coll. H. Weyland 1408.

one another or converging/diverging, the spacing between them constant or irregular. The veins similar in width, extending from 0 to 1/2 to the whole distance from the central primary vein to the leaf margin. Tertiary veins 5-7 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles (5-) 15-30 per 10 mm², with some free vein-endings, these being unbranched and branched.

Cuticle poorly preserved. Finer veins reflected in cuticle. Internal resinous bodies absent.

Specimens examined: Geol. Inst. Cologne: Coll. H. Weyland s.n.

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3775A.

Discussion:

Professor Weyland has referred to the specimen in the Cologne collection as a leaf of *Ficus* sp.?, *Rhus* or *Acer*? In certain respects it also resembles the leaves of *Ribes*. However, a reference of the fossil to one of possible genera did not prove to be possible.

XLI

Description:

Petiole 18 mm long and 1.2 mm wide at mid-point, parallel-sided, straight, making a marked angle with the central primary vein.

Lamina palmate, 3-lobed, 7.8 cm long, 4.3 cm wide, the length/breadth ratio being 1.8:1. Leaf apices acute, leaf margins meeting at 90° at leaf base. Lamina dissected round primary veins to a depth of 10.5%, sinuses angular to rounded, the distance from the origin of the lateral primary veins to the sinus 3.9-4.1 cm. The distance from the central apex to the lateral apices 4.6-4.9 cm. The angle formed by joining the apex of the central lobe via a primary sinus to the apex of one of the lateral lobes 110°-115°.

Leaf margin non-entire, serrulate-denticulate, with acute teeth 0.2-0.8 mm across, (0-)1 per secondary vein and 0-1 per intercostal field, equivalent to c.20 per side, alternating with acute or rounded sinuses. Teeth of one size group.

Venation actinodromous, primary veins 3. Lateral primary veins arising at 30° from the central primary vein at the junction of the lamina and petiole; these lateral veins 0.25-0.30 mm wide at mid-point, 50-52.5% the length of the central primary vein. The percentage of the lamina on the basiscopic side of the lateral primary veins c.15%. Lateral primary veins bearing 1 secondary vein on their acroscopic side, arising at 65°-75°. The secondary vein hardly tapering along its length, 0.04-0.07 mm wide at mid-point. Lateral primary veins bearing 8 secondary veins on their basiscopic side, the most proximal vein arising at 25°-45°, arising in the remaining part of the basal third of the lobe at 45°, in the median third at 45°-60°, in the apical third at 50°-80°. The angle at which the veins

arise initially increasing or constant. The spacing of the veins with the exception of slight irregularities, successively decreasing from base to apex (fig. 34). Secondary veins hardly tapering along their length, 0.05–0.15 mm wide at mid-point. Central primary vein more or less straight, slightly tapering along length, 0.35 mm wide at mid-point. Central primary vein bearing 10–11 secondary veins per side, arising in the basal third of the lamina at 30°–45°, in the median third at 35°–50°, in the apical third at 45°–90°. The angle at which the veins arise constant within the first few mms. The spacing of the secondary veins initially decreasing, thereafter highly irregular and showing no recognizable trend (fig. 34). Secondary veins sub-opposite or alternately arranged, hardly tapering along their length, 0.07–0.20 mm wide at mid-point, interconnected distally by tertiary veins or vein network or at very apex by fine extensions of the secondary veins. Intermediate veins (2–) 4–10 per intercostal field, the finer ones in particular having a somewhat twisted course, arising from the central primary vein at 60°–120°, running more or less parallel to one another or converging/diverging, the spacing between them constant or increasing distally. The veins increasing in width with increase in length, extending from 0 to (1/2–) 9/10–1 the distance from the central primary vein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 5–10 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 50–60 per 10 mm², with some free vein-endings, these being unbranched and branched.

Epidermis unknown.

Specimen examined: Geol. Inst. Cologne: Coll. H. Weyland s.n.

XLII

Synonym: *Pimelea crassipes* Heer

WEYLAND, 1934, pp. 103–104,
Tafel 21, fig. 5!

Description:

Petiole 1.3–3.0 mm or more long and 0.6–1.1 mm wide at mid-point, more or less parallel-sided, straight, sometimes making a slight angle with the midvein.

Lamina oblong, 0.88–1.8 cm long, 0.4–1.0 cm wide, the length/breadth ratio being 1.6:1–2.2:1. Leaf apex rounded, possibly mucronate, leaf base obtuse.

Leaf margin entire.

V*enation* hypodromous (uninervia) to craspedodromous or camptodromous, midvein straight or curved, hardly or markedly tapering along length, c.0.1–0.2 mm wide at mid-point between base and apex of the lamina. Midvein sometimes seen to bear 5–7 secondary veins per side, arising in the basal third of the lamina at 30°–55°(–90°), in the median third at 30°–60°, in the apical third at 50°–90°. The angle at which the

veins arise initially more or less constant. Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.03–0.08 mm wide at mid-point, interconnected distally by extensions of the secondary veins. The nature of the intermediate veins and tertiary veins unknown. Areoles c.45 per 10 mm², the nature of the free vein-endings unknown.

Cuticle poorly preserved. Finer veins reflected in the cuticle. Cells at leaf margin elongate, arranged in c.6 rows, cell wall straight. Internal resinous bodies apparently absent.

Specimens examined: Deutsche Akad. Wiss. Berlin: 351(K 80)
Geol. Inst. Cologne: Coll. H. Weyland 1408(K 80)
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3853

Discussion:

Weyland's reference of the fossil to *Pimelea* was simply based on the resemblance of the Kreuzau material to leaf-remains described by HEER (1856) as *Pimelea crassipes* (Thymelaeaceae). As pointed out by GOTHAN and WEYLAND (1964, p. 457) plant-remains referred to *Pimelea* are of uncertain affinity.

XLIII

Synonym: *Sophora europaea* Unger

WEYLAND, 1934, p. 89 pro parte:
Tafel 15, fig. 12!

Description:

Petiole >2.5 mm long and 0.6 mm wide, more or less parallel-sided, straight, making no angle with the midvein.

Lamina oblong, 2.1 cm long, 1.4 cm wide, the length/breadth ratio being 1.5:1. Leaf apex rounded with mucronate tip, leaf base rounded.

Leaf margin entire.

Venation camptodromous, midvein straight, markedly tapering, c.0.3 mm wide at mid-point between base and apex of the lamina. Midvein bearing 6–8 secondary veins per side, the most proximal vein arising at 90°, arising in the remaining part of the basal third of the lamina at 60°–85°, in the median third at 55°–60°, in the apical third at 40°–65°. The angle at which the veins arise initially constant. The spacing of the veins may reach a maximum mid-way, although sometimes prone to irregularities. Secondary veins sub-opposite or alternately arranged, hardly tapering along their length, 0.07–0.15 mm wide at mid-point, interconnected by strong or fine extensions of the secondary veins. Intermediate veins 2–5 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 60°–105°, converging/diverging from one another, the spacing between them being constant or irregular. The veins similar in width, extending from 0 to 1/2–3/4 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 6–8 per 1 cm secondary

vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 30–55 per 10 mm², some unbranched free vein-endings apparently present.

Epidermis unknown.

Specimen examined: Deutsche Akad. Wiss. Berlin: 330(K 103)

Discussion:

The number, spacing and angle of origin of the secondary veins were sufficiently different in the two specimens figured by WEYLAND (1934) as *Sophora europaea* Unger that these can be considered as two separate taxa. The fossil is similar to the leaves or leaflets of a number of living taxa, so that a reference to *Sophora* (Leguminosae) must be considered insufficiently grounded.

XLIV

Synonym: *Sophora europaea* Unger

WEYLAND, 1934, p. 89 pro parte:
Tafel 15, fig. 9!

Description:

Petiole 5.5 mm long and 1.2 mm wide at mid-point, slightly increasing in width away from the base of the lamina, straight, making an angle with the midvein.

Lamina suborbicular, 3.2 cm long, 2.2 cm wide, the length/breadth ratio being 1.45:1. Leaf apex rounded, leaf base rounded.

Leaf margin entire.

Venation camptodromous, midvein slightly curved, markedly tapering along length, 0.4 mm wide at mid-point between base and apex of the lamina. Midvein bearing 3 secondary veins per side, arising at 40°–60°. The angle at which the secondary veins arise initially constant. The spacing of the veins decreasing away from leaf base. Secondary veins opposite or alternately arranged, slightly tapering along their length, 0.05–0.10 mm wide at mid-point, interconnected distally by fine extensions of the secondary veins. Intermediate veins 4–6 per intercostal field, many having a somewhat twisted course, arising from the midvein at 55°–120°, converging/diverging from one another, the spacing between them increasing distally. The veins increasing in width with increase in length, extending from 0 to 1/2–3/4 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 4–6 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles c.40 per 10 mm², the nature of the free vein-endings unknown.

Epidermis unknown.

Specimen examined: Geol. Inst. Cologne: Coll. W. Jansen 84

XLV

Synonym: *Porana oeningensis* Heer WEYLAND, 1934, p. 111, Tafel 21, fig. 3!

Description:

Petiole 4.0–6.0 mm long and 0.9–1.05 mm wide at mid-point, parallel-sided, curved, making no angle with the midvein.

Lamina ovate, 4.0–4.5 cm long, 2.2–2.3 cm wide, the length/breadth ratio being 1.8:1–2.0:1. Leaf apex acute (very apex sometimes rounded), leaf base acute or obtuse.

Leaf margin sub-entire, shallowly sinuolate, undulations with an amplitude of 0.3–1.0 mm, 2–7 per side.

Venation camptodromous, midvein straight although sometimes curved at very apex, markedly tapering along length, 0.40–0.45 mm wide at mid-point between base and apex of the lamina. Midvein bearing 9–13 secondary veins per side, the most proximal vein arising at 35°–45°, arising in the remaining part of the basal third of the lamina at 45°–65°, in the median third at 45°–60°, in the apical third at 40°–80°. The angle at which the veins arise (increasing-) constant (-decreasing) within the first few mms. The spacing of the veins reaches a maximum \pm mid-way (fig. 34). Secondary veins sub-opposite or alternately arranged, hardly tapering along their length, 0.07–0.15 mm wide at mid-point, interconnected distally by fine extensions of secondary veins or occasionally tertiary veins. Intermediate veins 2–10 per intercostal field, sometimes having a somewhat twisted course, arising from the midvein at 60°–110°, somewhat converging/diverging from one another, the spacing between them increasing distally or irregular. The veins similar in width, extending from 0 to 1/2–5/6 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 5–9 per 1 cm secondary vein, many of which running at right angles to the midvein, somewhat branched, the lengths on acroscopic and basiscopical sides of secondary vein more or less similar. The nature of the areoles and free vein-endings unknown.

Epidermis unknown.

Specimens examined: Deutsche Akad. Wiss. Berlin: 264(K 85)
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3888

Discussion:

WEYLAND (1934, p. 111) mentioned the different opinions which have existed as to the affinity of the fossil. He pointed out that his determination of the fossil as *Porana oeningensis* Heer (Convolvulaceae) was simply provisional. However, the use of a binomial for leaf-remains of such uncertain affinity is questionable.

XLVI

Description:

Petiole 11 mm long and 1.6–2.3 mm wide at mid-point, straight or curved, sometimes making a slight angle with the midvein.

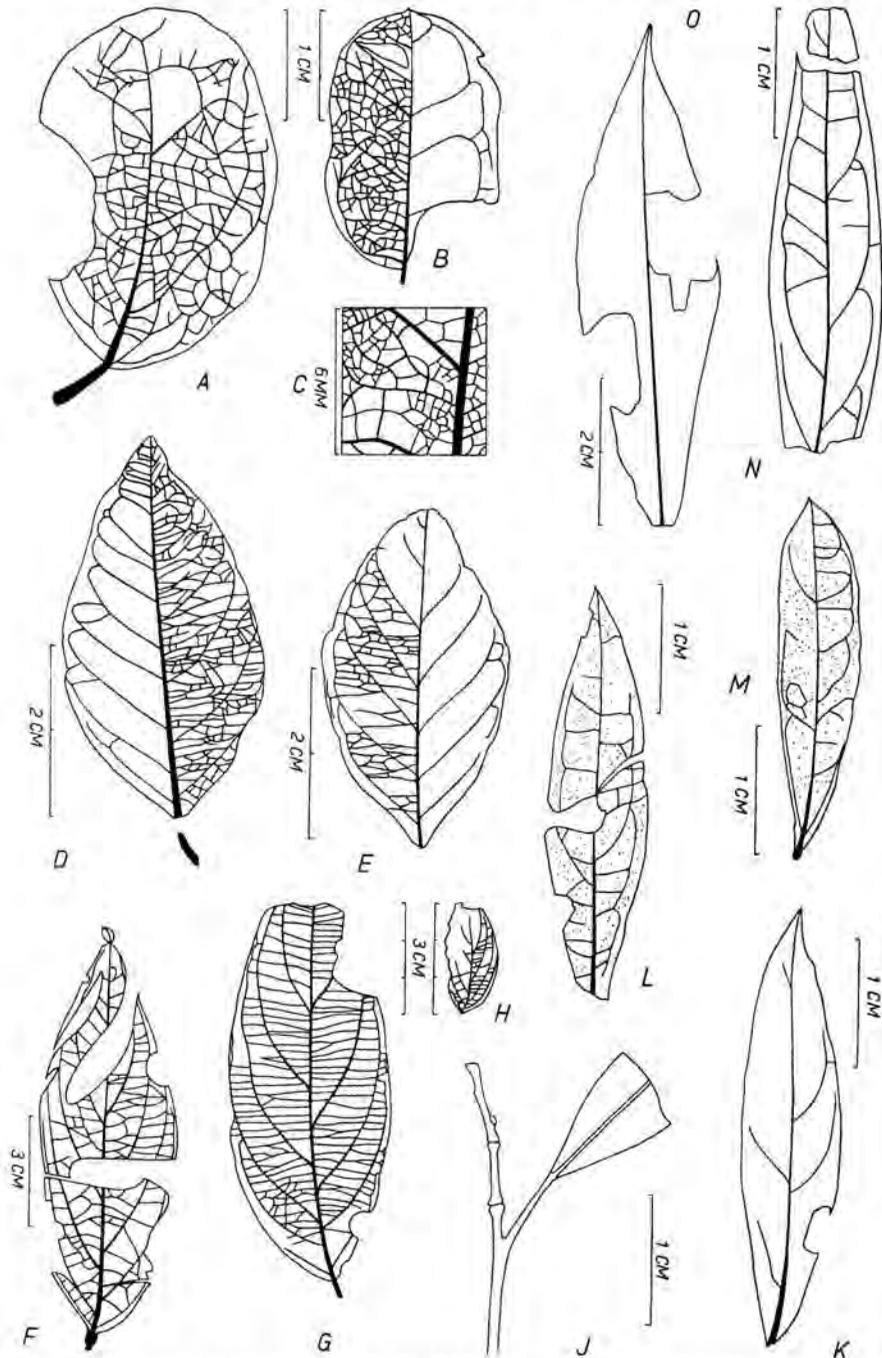


Fig. 36. A = XLIV: Cologne, Coll. W. Jansen 84. B-C = XLIII: B = Berlin 330; C = Berlin 330, detail showing venation. D-E = XLV: D = Berlin 264; E = Utrecht 3888. F-H = XLVI: F = Utrecht 3785 A; G = Utrecht 3784; H = Cologne s.n. J-N = XLVII: J = Cologne, reverse side of Coll. H. Weyland 1450; K = Cologne, Coll. H. Weyland 1406; L = Berlin 262; M = Berlin 324; N = Berlin s.n. (K 149). O = XLVIII: Utrecht 3830.

Lamina elliptical c.3.2–c.12.5 cm long, 1.4–4.1 cm wide, the length/breadth ratio being c.2.3 : 1–3.0 : 1. Leaf apex acute, leaf base obtuse or rounded.

Leaf margin entire.

Venation camptodromous, midvein slightly curved, slightly or markedly tapering along length, 0.2–0.55 mm wide at mid-point between base and apex of the lamina. Midvein bearing 4–7 secondary veins per side, the most proximal vein arising at 35°–50°, arising in the remaining part of the basal third of the lamina at 35°–60°, in the median third at 45°–55°, in the apical third at 45°–60°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the veins reaching a maximum distally. Secondary veins alternately arranged, hardly or somewhat tapering along their length, 0.05–0.35 mm wide at mid-point, interconnected distally by fine extensions of secondary veins, or tertiary veins. Intermediate veins 3–20 per intercostal field, arising from midvein at 60°–120°, running more or less parallel to one another or converging/diverging, the spacing between them constant or increasing distally. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/2–3/4 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary veins 3–8 per 1 cm secondary vein, arranged more or less at right angles to the midvein, little branched. The nature of the areoles and free vein-endings unknown.

Epidermis unknown.

Specimens examined: Geol. Inst. Cologne: s.n.

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3783, 3784, 3785A.

XLVII

Synonyms: *Acacia philippii* Weyland

WEYLAND, 1934, p. 87, Tafel 15, fig. 11!; Tafel 16, fig. 9!

Eugenia haeringiana Unger

WEYLAND, 1934, p. 105!

Description:

Finer branches pseudo-articulated.

Petiole 4–7 mm long and 0.5–0.8 mm wide, parallel-sided, somewhat curved, making no angle with the midvein.

Lamina elliptical or obovate, c.2.2–c.4.5 cm long, 0.57–0.85(–1.3) cm wide, the length/breadth ratio being (2.8 : 1–) 4.2 : 1–c.5.3 : 1. Leaf apex acute, sometimes slightly mucronate, leaf base attenuate.

Leaf margin entire.

Venation camptodromous (almost hypodromous), midvein straight or curved, hardly or somewhat tapering along length, 0.10–0.35 mm wide at mid-point between base and apex of lamina. Midvein bearing a number of poorly visible secondary veins, the most proximal vein arising at

20°–45°, arising in the remaining part of the basal third of the lamina at 30°–65°, in the median third at 35°–70°, in the apical third at 45°–55°. The angle at which the veins arise initially constant. The spacing of the secondary veins reaching a maximum mid-way or somewhat irregular. Secondary veins alternately arranged, hardly tapering along their length, 0.04–0.09 mm wide at mid-point, interconnected distally by marginal vein, strong or fine extensions of the secondary veins. Intermediate veins rarely visible, 3–7 per intercostal field, arising from the midvein at 45°–140°, markedly converging/diverging from one another, the spacing between them irregular. The veins similar in width, extending from 0 to 2/3–5/6 the distance from the midvein to the leaf margin, usually reaching their greatest length in intercostal field distally. The nature of the tertiary veins, areoles and free vein-endings unknown.

Epidermis unknown, although surface of leaf generally characterized by the presence of numerous small resinous bodies (glands?), 0.02–0.06 (–0.10) mm in diameter, or when these are no longer preserved, by small ± round depressions.

Specimens examined: 13, among which the numbered specimens:
 Deutsche Akad. Wiss. Berlin: 324(K 78), 362(K 78), s.n. (K 149)
 Geol. Inst. Cologne: Coll. H. Weyland 1406(K 78), reverse side of 1450
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3703, 3704, 3807, 3808.

Discussion:

The leaflets of four species of *Acacia* examined by the present author were all characterized by a markedly asymmetrical leaf base and a lamina, which was asymmetrical with regard to the midvein. This would appear to cast doubt on a reference of the leaf-remains to *Acacia*. In much the same way Weyland's reference of a specimen to *Eugenia* (Myrtaceae) would appear to be negated. While the leaves of *Eugenia* material examined are, like the fossil, dotted with glands and marked by the presence of a marginal vein, they differ from the fossil in the presence of numerous closely spaced secondary veins (compare, e.g. *Eugenia bullockii* Hance, *E. cuminii* (L.) Druce and *E. microphylla* Abel.).

Taxa with small, gland-dotted, leaves are known from a number of angiosperm families. Of the material examined to date, only that of *Hypericum* (incl. *Ascyrum*) was found to display a pseudo-articulation of its finer branches. However, *Hypericum* (Guttiferae) is characterized by having an opposite or whorled arrangement of the leaves on the stem, while the fossil displays an alternate arrangement. The exact affinity of the leaf-remains must be considered to be uncertain.

XLVIII

Description:

Petiole unknown.

Lamina elliptical, 6.9 cm long, 1.95 cm wide, the length/breadth ratio being 3.5:1. Leaf apex acuminate, leaf base acute.

Leaf margin entire.

Venation hypohdromous (uninervia), midvein \pm straight, hardly tapering along length, 0.45 mm wide at mid-point between base and apex of the lamina.

Epidermis in non-stomatal condition composed of 275–325 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–2:1. Cell wall 1.2–3.5 microns thick, largely unpitted, straight or rarely undulate, 0(–1) lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 5.4 microns. Epidermis in stomatal condition composed of 280–500 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–6:1. Cell wall 0.9–3.0 microns thick, largely unpitted, straight or slightly undulate with 0–8 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 10.8 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1:1–6:1. Stomata 15.3–27.0 microns long and 12.0–20.7 microns broad, breadth 50–128 % length, (10–) 14–33(–38) per 0.1 mm²; stomatal index 3.3–10 %. Stomata variously orientated, undepressed, somewhat arranged in groups, apices non-retuse. Stomatal slit 42–53 % stomatal length. Accessory cells 2–5, symmetrical with 0–2 polar and 2–3 lateral cells, covered by only a thin layer of cuticle. The epidermal cells surrounding the accessory cells not infrequently concentrically orientated round stomata. Hair bases, c.15 microns in diameter, sometimes present over veins.

Specimen examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3830.

XLIX

Synonym: *Illicium fliegelii* Weyland

WEYLAND, 1934, pp. 67–68,

Tafel 11, fig. 1!

KRÄUSEL and WEYLAND, 1950,

Tafel 9, fig. 4!

Description:

Petiole alate, c.18 mm long and 2.0–3.2 mm wide at mid-point, parallel-sided, straight, making no angle with the midvein.

Lamina elliptical, 10.8–c.12.5 cm long, 3.2–4.3 cm wide, the length/breadth ratio being c.3:1–3.4:1. Leaf apex rounded (always?), leaf base attenuate.

Leaf margin entire.

Venation camptodromous, midvein straight or curved, markedly tapering along length, 0.6–1.0 mm wide at mid-point between base and apex of the lamina. Midvein bearing 15–20 secondary veins per side, the most proximal vein arising at 30°–65°, arising in the remaining part of the basal third of the lamina at 40°–80°, in the median third at 45°–75°, in the apical third at 45°–80°. The angle at which the veins arise constant

within the first few mms. The spacing of the veins somewhat irregular and without any trend or reaching a maximum roughly mid-way (fig. 38). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.10–0.25 mm wide at mid-point, interconnected distally by strong or fine extensions of secondary veins. Intermediate veins 0–8 per intercostal field, some or many having a somewhat twisted course, arising from the midvein at 45°–120°, running more or less parallel to one another or converging/diverging, the spacing between them constant or increasing distally. The veins similar in width, extending from 0 to 5/12–7/8 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 4–9 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 55–90 per 10 mm², with a few unbranched free vein-endings.

Epidermis in non-stomatal condition unknown. Cells at leaf margin c.600 per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3 : 1, arranged in 35–40 rows. Cell wall 2–6 microns thick, largely unpitted, straight, the transverse walls slanting or at right angles to lateral walls. Epidermis in stomatal condition composed of 280 (?) cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall 0.6–0.9 microns thick, largely unpitted, undulating with 4–11 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 7 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–3 : 1, lateral walls straight or only slightly undulate, transverse walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Stomata 16.2–25.2 microns long and 14.4–28.8 microns broad, breadth 88–140 % length, 35–40 per 0.1 mm²; stomatal index c.14 % (?). Stomata variously orientated, undepressed, ± equidistant, apices non-retuse. Stomatal slit 38–40 % stomatal length. Accessory cells 0–2 or more, when present symmetrically or spirally arranged. Accessory cells narrower than the rest of the epidermal cells. Internal resinous bodies very numerous.

Specimens examined : Deutsche Akad. Wiss. Berlin: 282(K 116)

Geol. Inst. Cologne: Coll. H. Weyland 1458(K 116), 2020
Bot. Mus.- & Herb. Utrecht, Div. of Palaeobot.: 3813

Discussion :

While having an epidermis fairly similar to that of No. L, a marked difference in gross-morphology was to be observed between these two taxa. In gross-morphology the leaf-remains under consideration resemble the leaves of *Illicium* (Illiciaceae) and it was on the basis of this outward similarity that WEYLAND (1934) established a new species, *Illicium fliegelii*. Cuticle analysis, however, negates a reference of the leaf-remains to *Illicium*. This genus has stomata sunken beneath the leaf surface and surrounded by a ring of cutin. Moreover, the cuticle is thickened at both stomatal poles. This thickening may either resemble a *Papaver* fruit in

silhouette, or may be echinate or bulbous in shape. Furthermore, in *Illicium* the stomata are accompanied by large accessory cells. While this cannot be stated with certainty as yet, of all the possibilities a reference to the Ericaceae would appear to be the most likely.

L

<i>Synonyms: Andromeda vacciniifolia</i> Unger	WEYLAND, 1934, p. 109, Tafel 22, figs. 3-5!
<i>Castanopsis dechenii</i> (Weber) Kräusel et Weyland	KRÄUSEL and WEYLAND, 1954, pp. 137-138, p. 136 Abb. 14, Tafel 17, figs. 6-8, Tafel 30, fig. 1
? <i>Juglans acuminata</i> A. Braun	WEYLAND, 1934, p. 48 pro parte!
<i>Persea speciosa</i> Heer	WEYLAND, 1934, pp. 78-80, Tafel 12, figs. 7-8!
<i>Rhamnus acuminatifolia</i> Weber	WEYLAND, 1934, p. 99, Tafel 19, figs. 5-6, Tafel 20, fig. 1!
<i>Rhamnus dechenii</i> Weber	WEYLAND, 1934, p. 98, Tafel 19, figs. 3-4! Tafel 20, figs. 1 & 4!; WEYLAND, 1943, Tafel 23, figs. 11-15!
<i>Rhamnus rectinervis</i> Heer	WEYLAND, 1934, p. 98!

Description:

Petiole 2.5-10.0 mm long and 0.55-2.2 mm wide at mid-point, more or less parallel-sided but having a swollen base, petiole straight or curved, sometimes making an angle with the midvein.

Lamina (ovate-)elliptical (-obovate), 2.0-12.5 cm long, 0.9-5.7 cm wide, the length/breadth ratio being 1.75:1-3.3:1 (fig. 38). Leaf apex acute or acuminate, leaf base acute, obtuse or rounded.

Leaf margin entire.

Venation camptodromous, midvein straight or curved, hardly or markedly tapering along length, 0.1-0.6 mm wide at mid-point between base and apex of the lamina. Midvein bearing 5-13 secondary veins per side, the most proximal vein arising at 45°-60°(-100°), arising in the remaining part of the basal third of the lamina at 40°-70°(-90°), in the median third at 30°-65°, in the apical third at (30°-) 45°-65°(-90°). The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins generally reaches a maximum (proximally-) mid-way, but is sometimes somewhat irregular and without an obvious trend (fig. 38). Secondary veins opposite or alternately arranged, hardly or somewhat tapering along their length, 0.03-0.30 mm wide at mid-point, interconnected distally by fine extensions of secondary veins, or tertiary veins. Intermediate veins 1-7 per intercostal field, some having a somewhat twisted course, arising from the midvein at 50°-120°, running more or less parallel to one another or converging/diverging, the spacing between them being constant or increasing distally. The veins similar in width,

extending from 0 to $1/3$ – $2/3$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 4–15 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basisopic sides of secondary vein more or less similar. Areoles (33–) 50–70(–130) per 10 mm^2 , with few or many free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of 380–700 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–3.5 : 1. Cell wall 0.5–2.0 microns thick, somewhat pitted and sometimes bearing hemispherical projections. Cell wall straight or undulating with 0–7 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 5.4 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–6 : 1, the cell wall up to 3.5 microns thick. Hair bases 12.6–16.2 microns in diameter present, 0–6(–24) per 0.1 mm^2 . Cells at leaf margin c.2000(?) per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–3 : 1, arranged in c.20 rows. Cell wall c.1 micron thick, largely unpitted, straight, the transverse walls slanting or at right angles to the lateral walls. Epidermis in stomatal condition composed of 280–760 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–5 : 1. Cell wall 0.6–2.0 microns thick, somewhat pitted, straight or undulate with 0–10 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 7.2 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–12 : 1, the transverse walls slanting or at right angles to the lateral walls. Finer veins somewhat reflected in cuticle. Stomata 13.6–29.7 microns long and 10.0–29.7 microns broad, breadth 73–133 % length, (18–) 24–50(–66) per 0.1 mm^2 , the number being somewhat connected with the length of the lamina (fig. 38); stomatal index 6–14 %. Stomata variously orientated, somewhat depressed, equidistant or somewhat arranged in groups, apices non-retuse. Stomatal slit 25–50 (–67) % stomatal length. Accessory cells 4–8 in number, narrower than the rest of the epidermal cells and covered by a somewhat thicker layer of cutin than the other epidermal cells. Hair bases 11.2–18.0 microns in diameter invariably present, 0–20 per 0.1 mm^2 . Internal resinous bodies absent.

Specimens examined : 589, among which the numbered specimens
 Deutsche Akad. Wiss. Berlin: 303(K 73), 309(K 73), 319(K 110), 320(K 110), 323(K 146), 325(K 146), 358(K 67)
 Geol. Inst. Cologne: Coll. H. Weyland 1393(K 67), 1394(K 67)
 counterpart of Berlin 358, 1415(K 146), 1417(K 146), 1419(K 73), 1420, 1421, 1422, 1423, 1682, 1705A, 1705B (counterpart of 1705A), 1705C
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3267B, 3298, 3299, 3300, 3301, 3302, 3303, 3304, 3305, 3306, 3307, 3308, 3309, 3310, 3311, 3312, 3313, 3314, 3315, 3316, 3317, 3318, 3319, 3320, 3321, 3322, 3323, 3324, 3325, 3326, 3327, 3328, 3329, 3330, 3331, 3332, 3333, 3334, 3335, 3336, 3337, 3338, 3339, 3340, 3341, 3342, 3343, 3344, 3345, 3346, 3347, 3348,

3349, 3350, 3351, 3352, 3353, 3354, 3355, 3356, 3357, 3358, 3359, 3360, 3361, 3362, 3363, 3364, 3365, 3366, 3396B, 3396C, 3414B, 3463B, 3475B, 3526B, 3535B, 3586B, 3592B, 3607B, 3620B, 3705, 3706, 3707, 3708A, 3709, 3710, 3711, 3712, 3713, 3714, 3775B, 3886B, 3913C, 3931E.

Discussion:

The taxon as circumscribed here includes several entities described by WEYLAND (1934) as belonging to a number of different taxa. The commonest of these was a taxon called *Rhamnus dechenii* Weber (Rhamnaceae) and subsequently referred to as *Castanopsis dechenii* (Weber) Kräusel et Weyland (Fagaceae). Not only has the circumscription of this "species" proved a matter of some difficulty, but its proper affinity is still a matter for debate.

In the present account the taxon is taken to incorporate material referred to as *Castanopsis toscana* (Bandulska) Kräusel et Weyland (= *Tristania toscana* Bandulska). According to KRÄUSEL and WEYLAND (1954) this taxon has smaller leaves with a less pronounced drip-point and more numerous hair bases than *Castanopsis dechenii*. However, KILPPER (1968, p. 177) pointed out that it is questionable whether the retention of these two taxa as separate entities is warranted. This opinion would appear to be supported by the transitions encountered in the Kreuzau material.

In his account of the Kreuzau assemblage WEYLAND (1934) described *Rhamnus dechenii* Weber, *R. rectinervis* Heer and *R. acuminatifolia* Weber as being very similar to one another. A specimen (Coll. A. Quaas s.n. in 1902) in the Berlin collection, which was determined by H. Weyland as *Rhamnus rectinervis*, has secondary veins running in an almost straight course towards the leaf margin. This represents a deviation from the arched camptodromous venation of material described as *Rhamnus dechenii*. However, not only was this the only authentic specimen of *Rhamnus rectinervis* available to the present author, but the specimen did not yield a cuticle preparation and was not found to differ in any other respects from leaf-remains determined by H. Weyland as *Rhamnus dechenii*. It was therefore considered preferable to unite these two taxa. This would also appear to be the best solution in the case of *Rhamnus acuminatifolia* and *R. dechenii*. WEYLAND (1934, p. 99) described the lamina of *Rhamnus acuminatifolia* as being broader than that of *Rhamnus dechenii* and as having a more pronounced drip-point. An examination of a large number of specimens proved that complete transitions existed between the two entities.

KRÄUSEL and WEYLAND (1954, p. 138) considered that specimens referred to as *Persea speciosa* Heer (Lauraceae) might belong here. However, they state that, while the secondary veins are looped at the leaf margin in the present case, those of "Persea" specimens are looped at some distance from the leaf margin. Nevertheless, this does not apply to the Kreuzau material illustrated by WEYLAND (1934, Tafel 12, figs.

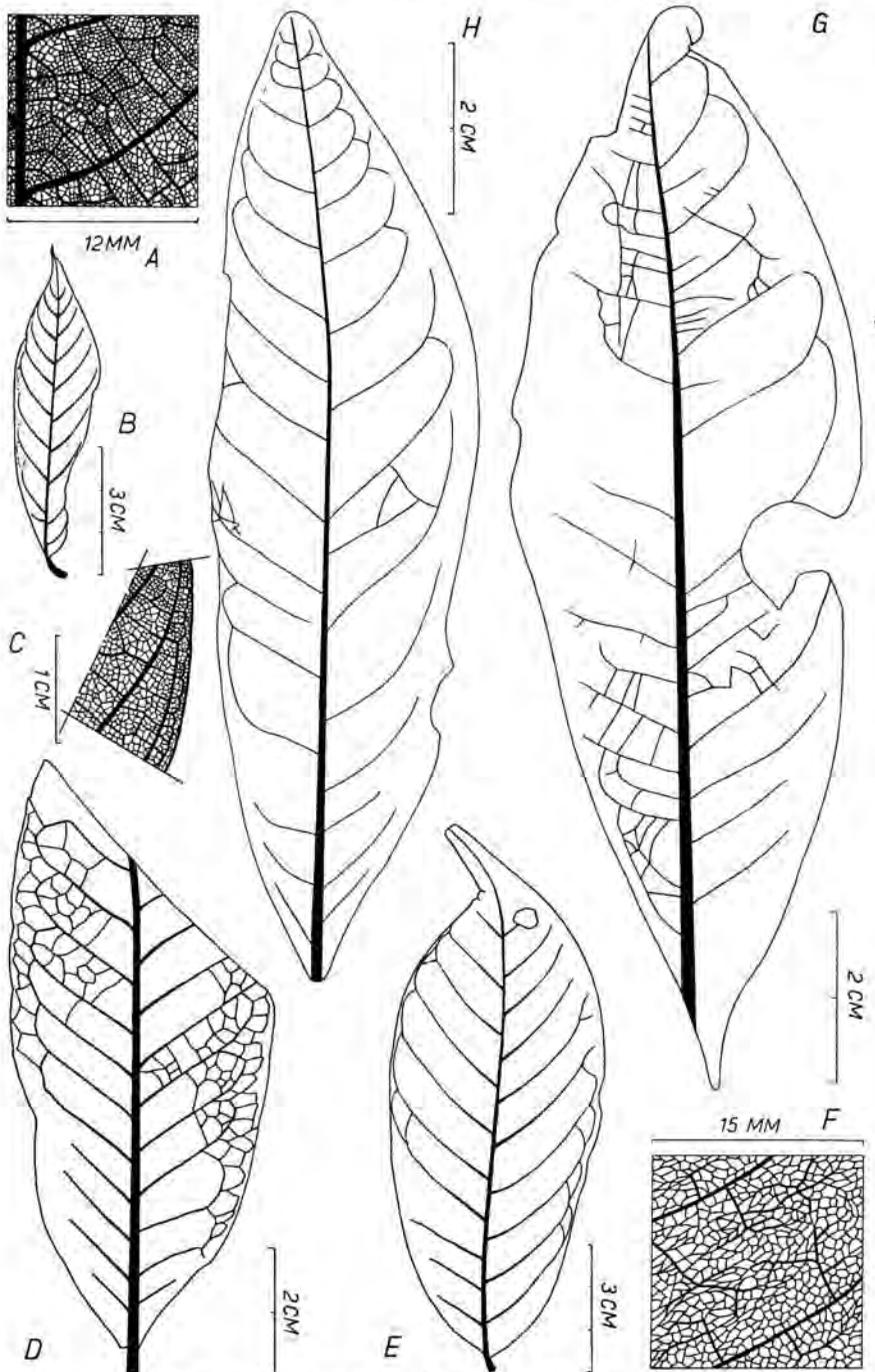


Fig. 37. A-C, E = L: A = detail showing venation; B = Utrecht 3352 (drawing based on specimen and its counterpart); C = detail showing venation and leaf margin; E = Utrecht 3351 (drawing based on specimen and its counterpart). D, F-H = XLIX: D = Utrecht 3813; F = Berlin 282, detail showing venation; G = Cologne, Coll. H. Weyland 1458; H = Berlin 282 (Type of *Illicium fliegelii* Weyland).

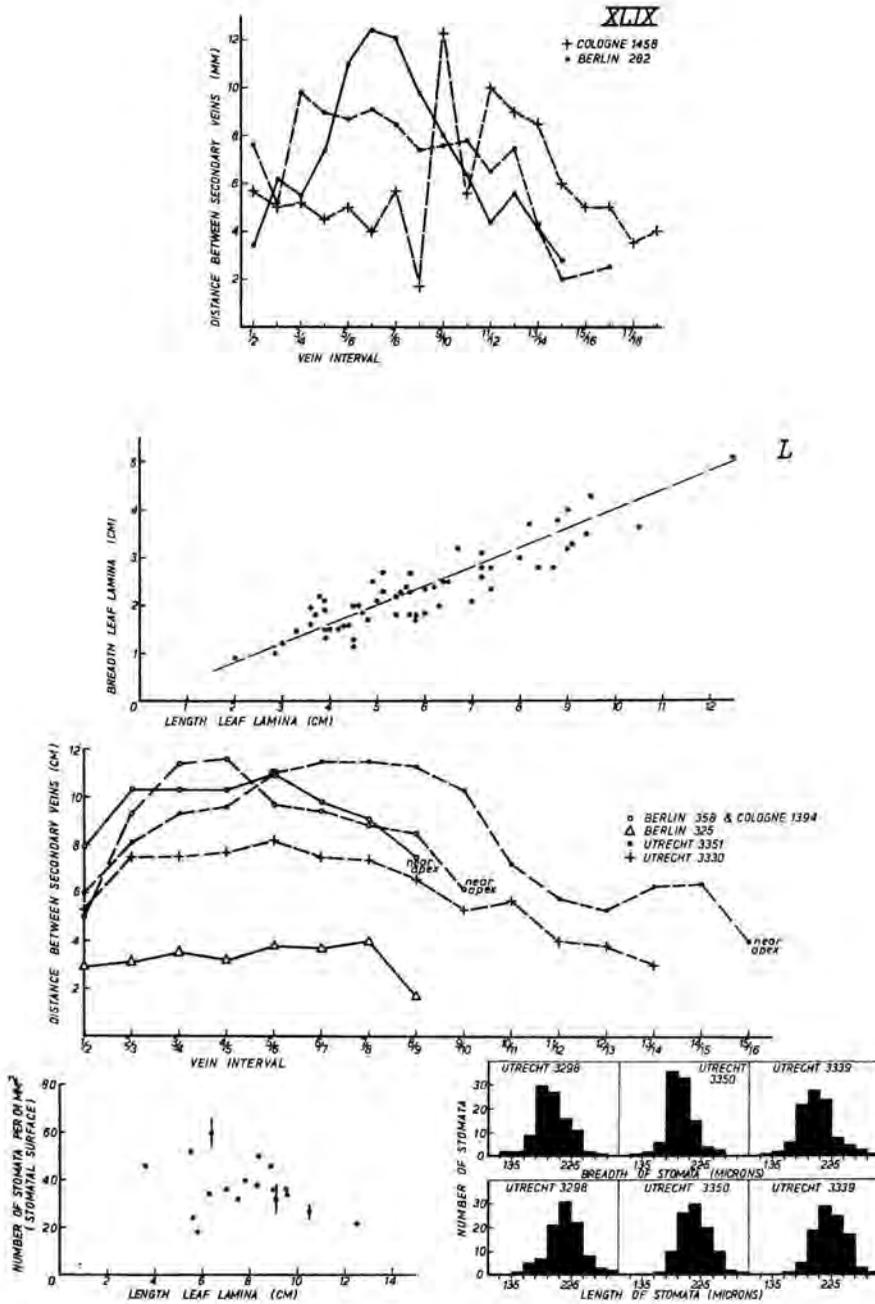


Fig. 38. Graphs and histograms XLIX, L.

7-8). This material yielded a cuticle preparation representing an epidermis indistinguishable from that of the present taxon. Neither could differences in gross-morphology be ascertained.

The leaf-remains referred to *Andromeda vaccinifolia* Unger (Ericaceae) by WEYLAND (1934), while smaller than those he determined as *Rhamnus dechenii*, were not found to differ from the latter in any essential features. A cuticle preparation made from Berlin 323, which WEYLAND (1934) figured as Tafel 22, fig. 4, supports the claim that these two taxa should be united. On the other hand, the reference of a specimen (Berlin s.n. (K 83)) determined by H. Weyland as *Juglans acuminata* A. Braun (Juglandaceae) to the present taxonomic entity must remain somewhat uncertain in the absence of a cuticle preparation. However, the description of this specimen was found to agree with that of the present taxon.

None of the generic names which have been proposed for the taxon under consideration would appear to be justified. In the material of *Juglans*, *Persea* (incl. *Machilus*), *Rhamnus* and *Tristania* (Myrtaceae) which has been examined the accessory cells were much the same size as the remaining epidermal cells. The cuticle was not thickened over the accessory cells and the accessory cells were not separated from the rest of the epidermal cells by an undulate cell wall. Moreover, in *Juglans* and *Persea* the stomatal slit tends to be rather long. There again in the leaves of the *Tristania* species examined the secondary veins are more numerous than in the leaf-remains and tend to be recurved rather than forwardly arched. While KRÄUSEL and WEYLAND (1954) considered that cuticle preparations made from the leaf-remains resembled those of *Castanopsis*, KILPPER (1968, p. 177) has pointed out that a reference to this genus is by no means certain. The lower epidermis of the leaves of *Castanopsis* species examined by the present author resembled that of the leaf-remains to some extent e.g. in the presence of relatively small epidermal cells and the numerous stomata and hair bases. The cuticle immediately surrounding the stomata is sometimes thicker than over the rest of the epidermis, and results in a halo such as found in the fossil. However, unlike the fossil, the outer margin of this halo never shows more than a slight tendency (e.g. H. C. Cheo 167) to be finely undulate. The same is true of other members of the Fagaceae e.g. *Lithocarpus* species, which have an epidermis similar to that of *Castanopsis*. Moreover, while the upper epidermal cells and those epidermal cells over the finer veins on the lower surface of the leaves of *Castanopsis* may have slightly undulate cell walls, the cells occurring amongst the stomata are invariably straight-walled.

Within *Andromeda* sensu latissimo species having leaves with an epidermis somewhat similar to that of the fossil are to be found e.g. *Pieris formosa* (Wall.) D. Don (= *Andromeda formosa* Wall.) and *Pieris japonica* (Thunb.) D. Don (= *Andromeda japonica* Thunb.). These species were found to have stomata and accessory cells similar to those of the fossil.

However, the leaves of these species bear glands resting on a thickened 2-cell base and do not resemble the fossil in outward appearance.

The comparison was extended to cover other taxonomic entities, but without success. Although the lower epidermis of the leaf-remains was very characteristic, none of the cuticle preparations in the author's collection reflected an epidermis sufficiently similar to warrant the reference of the leaf-remains to a given taxon.

Herbarium material examined in detail:

<i>Castanopsis caudata</i> Franch.	Coll. H. C. Cheo 167	(E) _____
<i>Castanopsis concolor</i> Rehd. et Wils.	Coll. G. Forrest s.n. 10-1903	(E) det. Handel- Mazzetti
<i>Castanopsis cuspidata</i> Schottky	Coll. R. C. Ching 2599	(E) det. J. G. Jack & A. Rehder
<i>Castanopsis echidnocarpa</i> A. DC.	Coll. A. N. Steward, C. Y. Chiao & H. C. Cheo 884	(E) det. Luong Toan
<i>Castanopsis eyrei</i> (Camp) Tutch.	Coll. W. T. Tsang 20282	(E) det. F. P. Metcalf
<i>Castanopsis fargesii</i> Franch. ?	Coll. J. Cavalerie	(E) det. Luong Toan
<i>Castanopsis indica</i> (Roxb.) A. DC.	Coll. S. K. Lau 378	(E) det. Luong Toan
<i>Castanopsis wattii</i> Camus	Coll. W. Y. Chun 5641	(E) det. Luong Toan
<i>Juglans californica</i> Wats.	Coll. E. K. Balls 8368	(E) _____
<i>Juglans cathayensis</i> Dode	Coll. H. C. Chow 29-6-1934	(E) _____
<i>Juglans cinerea</i> L.	Coll. E. S. Steele 30-5-1899	(E) _____
<i>Juglans major</i> (Torrey) Heller	Coll. E. J. Palmer 4615	(E) _____
<i>Juglans rupestris</i> Engelm.	Coll. L. N. Goodding 166	(E) _____
	Coll. D. T. MacDougal 271	(E) _____
	Coll. E. O. Wooton 362	(E) _____
<i>Machilus ichangensis</i> Rehd. et Wils.	Coll. Handel-Mazzetti 7778	(E) det. Handel- Mazzetti
<i>Machilus rehderi</i> Allen	Herb. H. Léveillé	(E) det. C. K. Allen PARATYPE
<i>Machilus shweliensis</i> W. W. Smith	Coll. G. Forrest 9624	(E) det. W. W. Smith TYPE
<i>Machilus thunbergii</i> Sieb. et Zucc.	Coll. C. Y. Chiao 2908	(E) det. A. Rehder
<i>Machilus viridis</i> Handel-Mazzetti	Coll. J. F. Rock 8920	(E) det. H. Liou
<i>Persea borbonia</i> (L.) Spreng.	Coll. O. Lakela & D. Laker 29142	(U) _____
<i>Pieris formosa</i> (Wall.) D. Don	Coll. H. T. Tsai 57341	(E) det. W. P. Fang
<i>Pieris japonica</i> (Thunb.) D. Don	Coll. M. Mizushima 16-5-1961	(E) det. M. Mizushima
<i>Rhamnus caroliniana</i> Walter	Coll. A. E. Radford 45405A	(U) _____
<i>Rhamnus crenata</i> Sieb. et Zucc.	Coll. J. L. Gressitt 1547	(E) det. E. D. Merrill

Rhamnus esquirolii Lév.	Coll. Handel-Mazzetti 10747	(E) det. Handel- Mazzetti
Rhamnus hemsleyana C. Schneider	Coll. G. Forrest 7391	(E) det. W. E. Evans
Rhamnus nigricans Handel-Mazzetti	Coll. Handel-Mazzetti 6311	(E) det. Handel- Mazzetti
Rhamnus sargentiana C. Schneider	Coll. E. H. Wilson 862	(E) det. C. Schneider TYPE
Rhamnus velutina Anth.	Coll. F. Kingdon Ward 5059	(E) det. J. Anthony TYPE
Tristania callobuxa Ndzu.	Coll. C. McMillan 5141	(E) det. A. Guillaumin
Tristania elliptica Stapf	Coll. J. Sinclair, K. bin Tassim & K. bin Sisiron 9094	(E) det. J. Sinclair
Tristania exiliflora F. v. M.	Coll. S. F. Kajewski 1394	(E) _____
Tristania glauca Brong. et Gris.	Coll. C. McMillan 5125	(E) det. A. Guillaumin
Tristania obovata Benn.	Coll. J. Sinclair & K. bin Tassim 10312	(E) _____
Tristania paniculata Kurz.	Coll. J. W. Helfer in 1838	(E) det. K. Biswas
Tristania rufescens Hance	Coll. K. Bunchuai 1547	(E) det. T. Smitinand
Tristania whiteana Griff.	Coll. J. Sinclair 11-4-1953	(E) det. J. Sinclair

LI

<i>Synonyms</i> : <i>Ficus arcinervis</i> (Rossmässler) Heer	WEYLAND, 1934, pro parte e.g. p. 62, Abb. 3!
? <i>Persea</i> c.f. <i>braunii</i> Heer	WEYLAND, 1934, p. 80, Tafel 15. fig. 6!

Description:

Petiole 11.5–21 mm long and 0.8–2.1 mm wide at mid-point, more or less parallel-sided but increasing in width at the base of the petiole, straight or curved, making no angle with the midvein.

Lamina elliptical, c.9–c.14.5 cm long, 2.05–4.30 cm wide, the length/breadth ratio being c.2.4 : 1–4.9 : 1. Leaf apex acute or acuminate, leaf base attenuate.

Leaf margin entire.

Venation camptodromous, midvein straight or curved, hardly to markedly tapering along length, 0.35–0.75 mm wide at mid-point between base and apex of the lamina. Midvein bearing (3–) 5–9 secondary veins per side, the most proximal vein arising at 40°–45°, arising in the remaining part of the basal third of the lamina at 45°–70°, in the median third at 45°–70°, in the apical third at (50°–) 60°–90°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing of the veins reaching a maximum proximally or mid-way (fig. 41). Secondary veins opposite or alternately arranged, hardly or somewhat tapering along their length, 0.1–0.4 mm wide at mid-point, interconnected distally by fine extensions of secondary veins. Intermediate veins (1–) 4–13(–24) per intercostal field, rarely having a somewhat twisted

course, arising from the midvein at 60° – 120° , running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to $1/4$ – $7/8$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 5–12 per 1 cm secondary vein, somewhat branched. Areoles 40–100 or more per 10 mm^2 , the nature of the free vein-endings being unknown.

Epidermis in non-stomatal condition composed of c.300–420 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1–3:1. Cell wall 0.35–0.8(–2.0) microns thick, largely unpitted, straight or undulate with 0–11 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 12.6 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1:1–6:1, transverse walls slanting or at right angles to the lateral walls. Finer veins somewhat reflected in the cuticle. Cells at leaf margin c.240–680 cells per 0.1 mm^2 , the length/breadth ratio being 1:1–2.5:1, arranged in c.15–c.20 rows. Cell wall 1.0–2.0(–4.0) microns thick, largely unpitted, straight. Epidermis in stomatal condition composed of 225–425 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1–5:1. Cell wall 0.35–1.0 microns thick, largely unpitted, rarely having hemispherical projections, straight or undulate with 0–13 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 4 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1:1–11:1, transverse walls slanting or at right angles to the lateral walls. Finer veins somewhat reflected in cuticle. Stomata 14.4–30.6 microns long and 10.8–25.2 microns broad, breadth 58–133 % length, 24–56 per 0.1 mm^2 ; stomatal index 10–20 %. Stomata variously orientated, undepressed or slightly depressed, equidistant or somewhat arranged in groups, apices occasionally retuse. Stomatal slit 40–75 % stomatal length. Accessory cells 2–6, mostly symmetrical with 0–4 polar and 2–4 lateral cells, although when 3 cells present a radial arrangement results. Accessory cells similar in size or somewhat smaller than the rest of the epidermal cells. Hair bases 2.0–12.6 microns in cross-section rarely present, 0(–1) per 0.1 mm^2 , with c.7 associated cells arranged round the hair base in radial fashion. The cell wall may be somewhat thicker in close proximity to the hair bases. Internal resinous bodies common.

Specimens examined: Deutsche Akad. Wiss. Berlin: 269(K 155), 367(K 69)
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3814, 3815,
3817, 3818.

Discussion:

Berlin 269, determined as *Ficus arcinervis* by H. Weyland, proved to have an epidermis unlike those of other specimens referred to *Ficus arcinervis*. The epidermis, although fragmentary, was similar to that of the present taxon. This specimen furthermore agrees in gross-morphology.

Berlin 367 (*Persea* c.f. *braunii*), although not yielding a cuticle, closely resembled Utrecht 3817 and was only found to differ from the present taxon in the presence of 110–120 areoles per 10 mm².

Leaf-remains having a lower epidermis resembling that of the taxon under consideration have been described as *Litsea edwardsii* Bandulska (BANDULSKA, 1926) or *Cinnamomophyllum edwardsii* (Bandulska) Weyland et Kilpper (WEYLAND and KILPPER, 1963). The specimen figured by H. Bandulska as Plate 13, fig. 45 was a leaf having a camptodromous venation pattern. The leaf-remains figured by WEYLAND and KILPPER (1963, p. 105, Abb. 11–12), on the other hand, had a \pm acrodromous venation pattern. While the presence of numerous resinous bodies in the mesophyll of the fossil might suggest an affinity with the Lauraceae (see KRÄUSEL and WEYLAND, 1950) other possibilities cannot be ruled out at this stage. An examination of preparations of *Litsea edwardsii* Bandulska in the British Museum (V 17215, V 19419) proved to be inconclusive.

LII

Description:

Petiole >3.5 mm long and 1.5 mm wide, straight, making a slight angle with the midvein.

Lamina elliptical, 7 cm long, 2.5 cm wide, the length/breadth ratio being 2.8:1. Leaf apex acute or acuminate, leaf base acute.

Leaf margin entire.

Venation camptodromous, midvein slightly curved, markedly tapering along length, c.0.3 mm wide at mid-point between base and apex of the lamina. Midvein probably bearing c.7 secondary veins per side, the most proximal vein arising at 60°, the angle at which the veins arise in the remaining part of the basal third and median third of the lamina unknown, arising in the apical third at 65°. The angle at which the veins arise constant within the first few mms. Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.1–0.2 mm wide at mid-point, interconnected distally by fine extensions of secondary veins. The nature of the intermediate veins, tertiary veins, areoles and free vein-endings unknown.

Epidermis in non-stomatal condition composed of 180–280 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–2:1. Cell wall 0.9–1.5 microns thick, unpitted or finely pitted, \pm straight. The nature of the cells over veins unknown. Epidermis in stomatal condition composed of c.280 cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–3.5:1. Cell wall 0.2–0.45 microns thick, somewhat pitted, straight. The nature of the cells over veins unknown. Stomata 16.2–30.6 microns long and 18.0–25.2 microns broad, breadth 73–108 % length, c.35–c.55 per 0.1 mm²; stomatal index uncertain. Stomata variously orientated, undepressed, somewhat arranged in groups, apices non-retuse. Accessory

cells 4-5 in number possibly present although in shape and size the cells in the immediate proximity to the stomata resemble the other epidermal cells. Compound hair bases composed of 5-7 hair bases 3-7 per 0.1 mm^2 , cell wall 0.5-1.5 microns thick.

Specimen examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3840

Discussion:

The fossil was found to resemble the leaves of certain species of *Elaeagnus* (Elaeagnaceae) and *Styrax* (Styracaceae), but no more exact determination was considered possible.

LIII

Description:

Petiole 11 mm long and 1.8-2.1 mm wide at mid-point, straight, more or less parallel-sided, sometimes making an angle with the midvein.

Lamina elliptical, c.5-7.8 cm long, 2.7-3.1 cm wide, the length/breadth ratio being c.2:1-2.5:1. Leaf apex acuminate, leaf base obtuse.

Leaf margin entire.

Venation camptodromous, midvein apically curved, somewhat or markedly tapering along length, 0.5-0.9 mm wide at mid-point between base and apex of lamina. Midvein bearing c.11 secondary veins per side, the most proximal vein arising at 50° - 55° , arising in the remaining part of the basal third of lamina at 55° - 70° , in the median third at 55° - 65° , in the apical third at 50° - 60° . The angle at which the veins arise constant or rarely increasing within the first few mms. The spacing of the veins more or less constant. Secondary veins rarely opposite mostly alternately arranged, hardly tapering along length, 0.15-0.20 mm wide at mid-point, interconnected distally by fine extensions of secondary veins. Intermediate veins 3-10 per intercostal field, arising from midvein at 60° - 120° , converging/diverging from one another, the spacing between them constant. The veins similar in width, extending from 0 to $3/4$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or rarely distally. Tertiary veins 5-14 per 1 cm secondary vein, somewhat branched. Areoles 63-80 per 10 mm^2 , the nature of the free vein-endings unknown.

Epidermis in non-stomatal condition composed of c.340 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1-3:1. Cell wall 0.5-1.2 microns thick, finely pitted, straight or slightly undulate, 0-4 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells at leaf margin c.260 per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1-3:1, arranged in c.15 rows, cell wall 1.0-4.5 microns thick, somewhat pitted, straight. Epidermis in stomatal condition composed of 190-360 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1-2.5:1(-4:1). Cell wall 0.4-2.0 microns thick, finely pitted,

straight or slightly undulate, 0-5 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 14 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1:1-6.5:1, transverse walls slanting or at right angles to the lateral walls. Finer veins somewhat reflected in cuticle. Stomata 16.2-32.4 microns long and 16.2-30.6 microns broad, breadth 67-117 % length, 8-24 per 0.1 mm²; stomatal index 2.2-8.6 %. Stomata variously orientated, undepressed or very slightly depressed, somewhat arranged in groups, apices non-retuse. Stomatal slit 43-70 % stomatal length. Accessory cells 4-8, mostly symmetrical with 2-4 polar and 2-4 lateral cells, although arrangement occasionally radial. Accessory cells similar in size or somewhat smaller than the rest of the epidermal cells. Hair bases, c.11 microns in diameter, occasionally present, 0 (-1) per 0.1 mm². Internal resinous bodies rare or absent.

Specimens examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3859, 3860

LIV

Synonym: *Xanthoxylum braunii* Weber Weyland, 1934, p. 90, Tafel 16, fig. 3!

Description:

Petiole 9-14 mm long and 1.3-2.0 mm wide at mid-point, increasing from 0.9-1.7 mm wide at leaf base to 2.1 mm or more wide at base of petiole, straight, sometimes making a slight angle with the midvein.

Lamina oblong to elliptical, 7.4- > 8.5 cm long, 3.1-4.9 cm wide, the length/breadth ratio being c.2.4:1-2.6:1. Leaf apex unknown, leaf base ± obtuse or rounded, although a narrow band of lamina persists for some distance resulting in a somewhat attenuate appearance. Leaf base sometimes slightly oblique.

Leaf margin entire.

Venation camptodromous, midvein slightly curved throughout length, somewhat tapering along length, 0.45-0.60 mm wide at mid-point between base and apex of the lamina. Midvein bearing c.9-c.15 secondary veins per side, the most proximal vein arising at c.45°-75°, arising in the remaining part of the basal third of the lamina at 40°-75°, in the median third at 45°-80°, in the apical third at 45°-65°. The angle at which the veins arise constant or increasing within the first few mms. The spacing of the veins irregular and showing no trend (fig. 41). Secondary veins opposite to alternately arranged, hardly or markedly tapering along their length, 0.03-0.20 mm wide at mid-point, interconnected distally by moderate or fine extensions of secondary veins, rarely by tertiary veins. Intermediate veins 1-8 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 50°-120°, running more or less parallel to one another or converging/diverging, the spacing between them constant or increasing distally. The veins similar in width or increasing in

width with increase in length, extending from 0 to $(1/5 -) 1/2-11/12$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 3-7 per 1 cm secondary vein, somewhat or much branched. The nature of the areoles and free vein-endings unknown.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of c.500 (?) frequently finely striate cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1-3 : 1. Cell wall 0.4-0.9 microns thick, largely unpitted, more or less straight. Cells over veins elongate, the cell length/cell breadth ratio up to 5 : 1, the transverse walls slanting or at right angles to lateral walls. Finer veins somewhat reflected in cuticle. Stomata 14.4-25.2 microns long and 10.8-21.6 microns broad, breadth 58-122 % length, up to 18 per 0.1 mm^2 ; stomatal index uncertain. Stomata variously orientated, undepressed, more or less equidistant or somewhat grouped, apices non-retuse. Stomatal slit 37.5-77 % stomatal length. The nature of the accessory cells, if any, uncertain. Internal resinous bodies sometimes present.

Specimens examined: Deutsche Akad. Wiss. Berlin: 341(K 114)
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3810, 3811A,
3812.

Discussion:

Since similar leaves are found in taxa belonging to a number of families of dicotyledons, a reference to *Zanthoxylum* (= *Xanthoxylum*) (Rutaceae) must be considered as unproven.

LV

Description:

Petiole > 5.4 mm long and > 2.3 mm wide at mid-point, constantly increasing in width from 1.5 mm at leaf base to 3.0 mm at exposed base, straight, making no angle with the midvein.

Lamina oblong, c.9.5-c.10.5 cm long, 3.0-4.0 cm wide, the length/breadth ratio being c.2.6 : 1 or more. Leaf apex unknown, leaf base acute, obtuse or rounded.

Leaf margin entire.

Venation camptodromous, midvein straight or curved, markedly tapering along length, 0.40-0.65 mm wide at mid-point between base and apex of the lamina. Midvein bearing 9-c.11 secondary veins per side, the most proximal vein arising at 50° , arising in the remaining part of the basal third of the lamina at $30^\circ-50^\circ$, in the median third at $30^\circ-60^\circ$, in the apical third at $45^\circ-50^\circ$. The angle at which the veins arise increasing, constant or occasionally decreasing within the first few mms. The spacing of the veins more or less constant or somewhat irregular with a tendency to increase away from leaf base. Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.08-0.20 mm wide at mid-

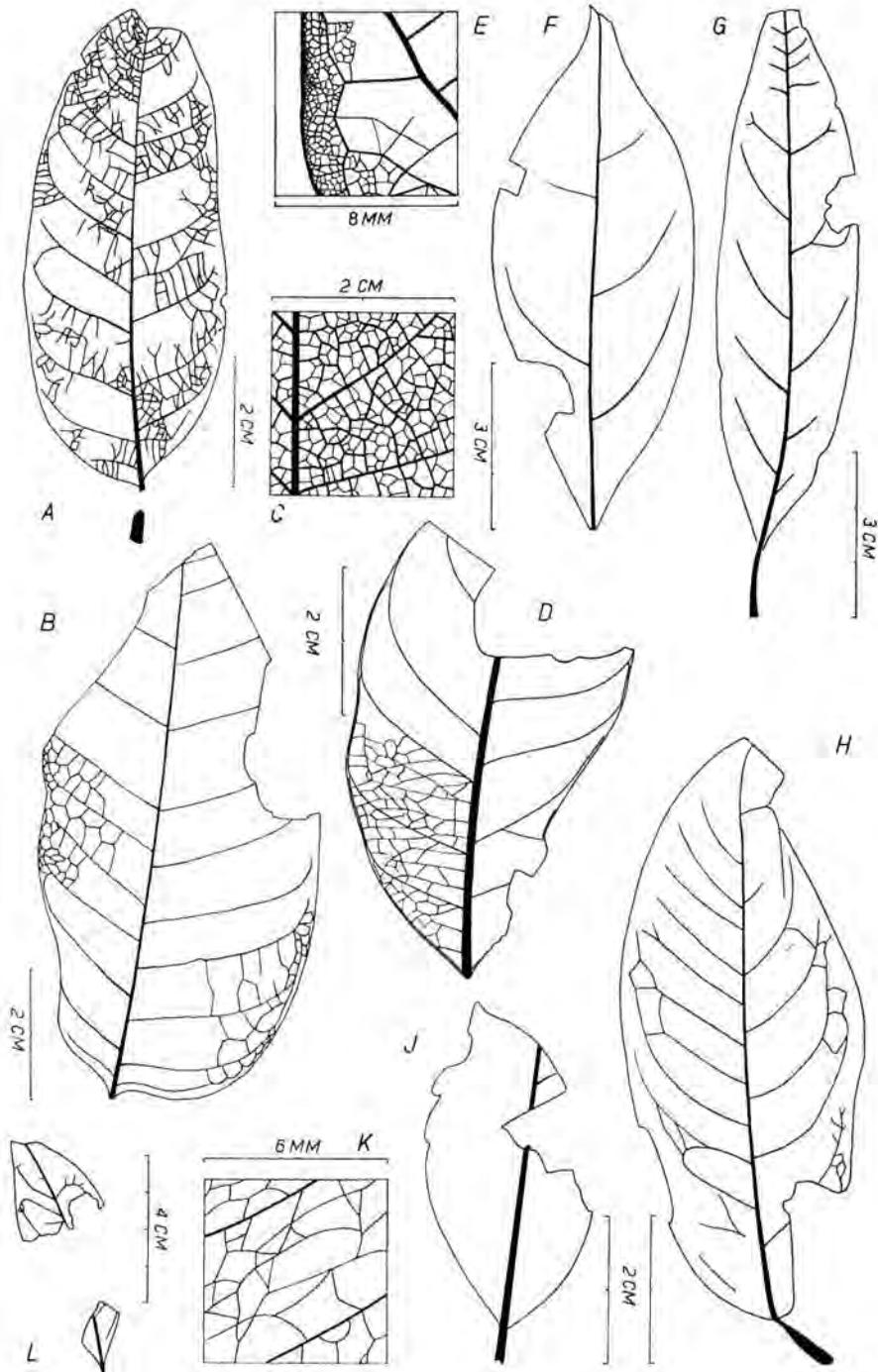


Fig. 39. A-D = LIV: A = Berlin 341; B = Utrecht 3810; C = detail showing venation; D = Utrecht 3812. E-G = LI: E = detail showing venation; F = Berlin 269; G = Utrecht 3818. H-K = LIII: H = Utrecht 3859; J = Utrecht 3860; K = Utrecht 3859, detail showing venation. L = LII: Utrecht 3840.

point, interconnected distally by fine extensions of the secondary veins. Intermediate veins 1-5 per intercostal field, arising from the midvein at 60° - 110° , running more or less parallel to one another, the spacing between them being constant. The veins more or less similar in width, extending from 0 to $1/3$ - $1/2$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 2-9 per 1 cm secondary vein, little or somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles c.30 per 10 mm^2 , the nature of the free vein-endings being unknown.

Epidermis in non-stomatal condition composed of 115-160 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1-3 : 1. Cell wall 2.0-6.3 microns thick, largely unpitted, straight or somewhat undulate with 0-6 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 16 microns. Cells over veins showing certain tendency to be arranged in rows, the cell length/cell breadth ratio being 1 : 1-2 : 1. Finer veins not reflected in cuticle. Cells at leaf margin 100-110 per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1-2.5 : 1, arranged in 25-30 rows, cell wall 2.0-4.5 microns thick, hardly pitted, straight. Epidermis in stomatal condition composed of 110-230 coarsely striate cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1-2.5 : 1. Cell wall 0.5-4.0 microns thick, largely unpitted, straight or slightly undulate with 0-8 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 14.5 microns. Cells over veins somewhat elongate, the cell length/cell breadth ratio being 1.5 : 1-4.6 : 1. Finer veins not reflected in cuticle. Stomata 16.2-39.6 microns long and 10.8-27.0 microns broad, breadth 50-100 % length, 3-10 per 0.1 mm^2 ; stomatal index 2-c.9 %. Stomata variously orientated, although those situated close to the leaf margin show a tendency to align themselves parallel to it. Stomata depressed, equidistant or somewhat arranged in groups and sometimes forming centres from which the epidermal cells radiate, apices non-retuse. Stomatal slit 50-70 % stomatal length, epidermal wall of guard cells thickened. Accessory cells 2-4 (-8), symmetrical with 0-2 (-4) polar and 2 (-4) lateral cells, slightly smaller than the rest of the epidermal cells. Internal resinous bodies rare.

Specimens examined : Bot. Mus. & Herb. Utrecht. Div. of Palaeobot. : 3891, 3892, 3893.

LVI

Synonym : *Populus mutabilis* Heer

WEYLAND, 1934, p. 43!

Description :

Petiole 25 mm long and 1.8 mm wide at mid-point, more or less parallel-sided, slightly curved, making a marked angle with the midvein.

Lamina ovate or elliptical, 7.8 cm long, 3.4 cm wide, the length/breadth ratio being 2.3 : 1. Leaf apex acuminate, leaf base obtuse.

Leaf margin entire.

Venation camptodromous, midvein very slightly sinuous, markedly tapering along length, 0.5 mm wide at mid-point between base and apex of the lamina. Midvein bearing 6 secondary veins per side, the most proximal vein arising at 35° – 45° , arising in the remaining part of the basal third of the lamina at 40° – 45° , in the median third at 40° – 45° , in the apical third at 55° – 60° . The angle at which the veins arise constant within the first few mms. The spacing of the veins irregular (fig. 41). Secondary veins occasionally opposite, mostly alternately arranged, hardly tapering along their length, 0.08–0.20 mm wide at mid-point, interconnected distally by strong or fine extensions of secondary veins. Intermediate veins 6–10 (and possibly fewer) per intercostal field, arising from the midvein at 45° – 100° , running more or less parallel to one another, the spacing between them constant or increasing distally. The veins similar in width, extending from 0 to $3/4$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. The nature of the tertiary veins, areoles and free vein-endings unknown.

Epidermis in non-stomatal condition composed of c.270 finely striate cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall c.2 microns thick, largely unpitted, straight or somewhat undulating, 0–7 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 11 microns. The nature of the cells over veins unknown. Cells at leaf margin c.400 per 0.1 mm^2 , the cell length/cell breadth ratio being 0.5 : 1–1.5 : 1, arranged in c.20–c.45 rows. Cell wall c.2.0–3.5 microns thick, somewhat pitted, straight. Epidermis in stomatal condition composed of an uncertain number of cells, cell outline obscure. Cuticle much striate on a fine scale. The nature of the cells over veins unknown. Stomata 28.8–32.4 microns long and 19.8–27.0 microns broad, breadth 61–94 % length, 15–25 per 0.1 mm^2 ; stomatal index unknown. Stomata variously orientated, somewhat depressed, equidistant or somewhat arranged in groups, apices non-retuse. Stomatal slit 56–63 % stomatal length. Accessory cells probably 2 in number, encircling the stomata completely, narrower than the rest of the epidermal cells. Trichome base with up to 3 cells and up to 43 microns in diameter present, 0–1 per 0.1 mm^2 , cell wall thicker than that of the surrounding epidermal cells. Internal resinous bodies apparently absent.

Specimen examined: Deutsche Akad. Wiss. Berlin: s.n. (K 154)

Discussion:

While closely resembling the leaf-remains described by O. Heer as *Populus mutabilis* in shape and venation, the Kreuzau specimen proved to have a cuticle unlike those of species of *Populus* (Salicaceae). However, as yet, it has not proved possible to suggest the proper affinity of the fossil.

It is possible that Weyland 1711 (Geol. Inst. Cologne) may belong here, for the cuticle preparations indicate a similar or identical epidermis to

that of the present taxon. However, Weyland 1711 differs from Berlin s.n. in having a leaf apex which is rounded obtuse and has, among other things, a surface marked by elongate pits 0.4–1.7 mm in cross-section. The cuticle follows the outline of these pits, which may therefore mark the position of internal channels.

LVII

Synonym: *Cassia* c.f. *hyperborea* Unger

Coll H. Weyland 1674, det. H. Weyland!

Description:

Petiole > 3 mm long and 1.1 mm wide, making no angle with the midvein.

Lamina elliptical, 6.6–c.12 cm long, 1.55–4.4 cm wide, the length/breadth ratio being c.2.7 : 1–4.2 : 1. Leaf apex acute or acuminate, leaf base attenuate or acute.

Leaf margin entire.

Venation camptodromous, midvein straight or curved, hardly or markedly tapering along length, 0.25–0.60 mm wide at mid-point between base and apex of the lamina. Midvein bearing c.16–c.30 secondary veins per side, the most proximal vein arising at 45°–50°, arising in the remaining part of the basal third of the lamina at 40°–80°, in the median third at 35°–65° (–80°), in the apical third at 45°–70° (–90°). The angle at which the veins arise increasing, constant or decreasing within the first few mms. The spacing of the veins more or less constant or slightly irregular. Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.05–0.20 mm wide at mid-point, sometimes dichotomising at 1/10–1/3 the distance from the midvein to the leaf margin, the veins interconnected distally by a marginal vein. Intermediate veins 0–4 (–7) per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 35°–125°, running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width, extending from 0 to 1/2–11/12 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 4–c.15 per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. The nature of the areoles and free vein-endings unknown.

Epidermis in non-stomatal condition composed of c.300 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall 1.0–1.5 microns thick, largely unpitted, somewhat or markedly undulate with 0–9 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 10 microns. Cells over veins not clear. Finer veins not reflected in cuticle. Cells at leaf margin c.250 per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2.5 : 1, arranged in c.25 rows. Cell wall 1.0–1.5 microns thick, largely unpitted, straight. Epidermis in stomatal condition composed of c.300 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2 : 1.

Cell wall 0.6–0.9 microns thick, largely unpitted, straight or somewhat undulate, the extent to which the cell walls are undulate being uncertain. Cells over midvein elongate, the cell length/cell breadth ratio being 1 : 1–3.5 : 1, lateral walls straight, transverse walls slanting or at right angles to lateral walls. Finer veins not reflected in cuticle. Stomata 19.8–41.4 microns long and 18–36 microns broad, breadth 56–100 % length, 25–40 per 0.1 mm²; stomatal index c.8–c.13 %. Stomata mostly orientated roughly parallel to the midvein, depressed, somewhat arranged in groups, apices non-retuse. Stomatal slit 50 – almost 100 % stomatal length, epidermal wall of guard cells 2–4 microns thick. Accessory cells 2, symmetrical with 0 polar and 2 lateral cells. Accessory cells narrow, smaller than the rest of the epidermal cells.

Specimens examined: Geol. Inst. Cologne: Coll. H. Weyland 1674
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3809A, 4148

Discussion:

Species with leaves having a similar venation pattern to that of the fossil are to be found in a number of families of angiospermous plants living at the present day. Representatives are to be found, for instance, in the Anacardiaceae, Apocynaceae, Asclepiadaceae, Moraceae, Myrsinaceae, Myrtaceae, Rhizophoraceae, Rutaceae, Sapotaceae and Simaroubaceae. Convergence is sometimes so strong that it is impossible to tell the leaves of different taxa apart, if such leaves are only examined as to their gross-morphology. An examination of the cuticles may prove to be rewarding. The fossil is typified by having sunken stomata, bounded on the outside by a marked thickening of the epidermal wall. Of the species examined by the author and having a similar venation pattern to that of the fossil only *Ficus benjamina* L. and *F. retusa* L. (Moraceae) displayed this thickening of the cuticle. These two species are referred to *Ficus* Subgenus *Urostigma* Section *Conosycea* (CORNER, 1965).¹ However, of the 21 species of *Ficus* examined by the present author none were found to have an upper epidermis with undulate cell walls such as displayed by the fossil.²

LVIII

Synonyms: *Alnus phocaeensis* Saporta

WEYLAND, 1934, pp. 51–52,
Tafel 4, fig. 5!

¹) Professor E. J. H. Corner (personal communication, 1969) states that most species of the Subgenus *Urostigma* have sunken stomata.

²) Professor Corner's work on *Ficus* would confirm these observations, since, according to him, all species with coriaceous leaves and all with a hypodermis have subrectangular epidermal cells. Species with thinner leaves, while often having a lower epidermis with \pm undulate cell walls, rarely display any undulations in the cell walls of the upper epidermis.

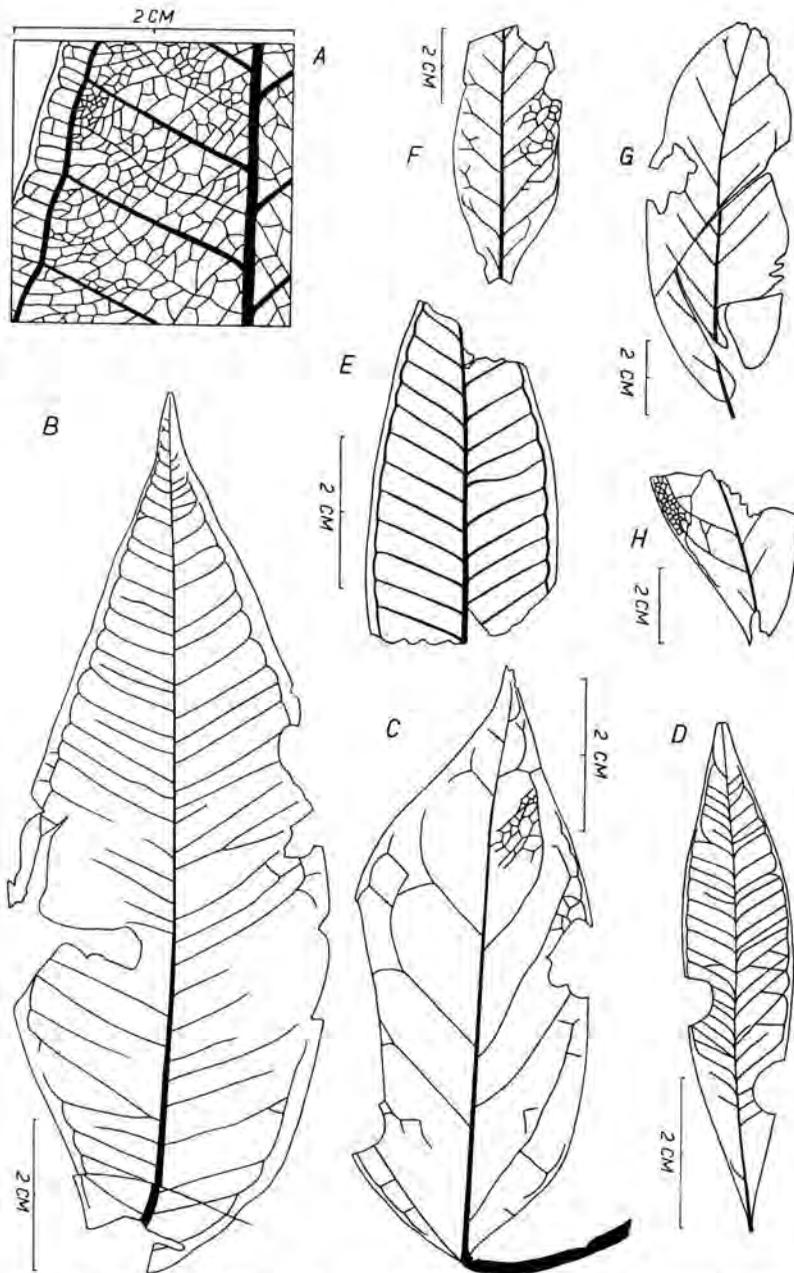


Fig. 40. A-B, D-E = LVII: A = Utrecht 3809 A, detail showing venation; B = Cologne, Coll. H. Weyland 1674; D = Utrecht 4148; E = Utrecht 3809 A. C = LVI: Berlin s.n. (K 154). F-H = LV: F = Utrecht 3892; G = Utrecht 3893; H = Utrecht 3891.

<i>Alnus palaeojaponica</i> Weyland	WEYLAND, 1943, pp. 103–104, Tafel 17, Abb. 9–10; Tafel 18, Abb. 1–4! (under <i>Alnus pseudojaponica</i> in Explanation of Plates)
<i>Ampelopsis denticulata</i> Menzel	WEYLAND, 1934, p. 97, Tafel 19, fig. 2!; Tafel 20, fig. 6!
c.f. <i>Artocarpidium olmediaefolium</i> Unger	WEYLAND, 1934, p. 62, Tafel 8, figs. 3–4!
<i>Betula macrophylla</i> (Goepfert) Heer	WEYLAND, 1934, p. 50 pro parte e.g. Coll. H. Weyland 1543!
<i>Carpinus grandis</i> Unger	WEYLAND, 1934, p. 52 pro parte e.g. Coll. H. Weyland 1654, 1655!
<i>Celastrus persei</i> Unger	WEYLAND, 1934, p. 92, Tafel 17, fig. 3!
<i>Commersonia rhenana</i> Weyland	WEYLAND, 1934, p. 102, Tafel 21, fig. 2! (on p. 20 as <i>Commersonia grandifolia</i>)
<i>Euonymus kurtzii</i> Weyland	WEYLAND, 1934, p. 93, Tafel 16, fig. 2! (as <i>Euonymus kreuzauensis</i> in MS.)
<i>Juglans bilinica</i> Unger	WEYLAND, 1934, p. 49!
? <i>Juglans ungeri</i> Heer	WEYLAND, 1934, p. 49, Tafel 3, fig. 2!
<i>Quercus platania</i> Heer	WEYLAND, 1934, pp. 55–58, Tafel 5, fig. 2; Tafel 7, figs. 1–2
<i>Rhamnus gaudinii</i> Heer	WEYLAND, 1934, pp. 99–100, Tafel 19, figs. 7–8!
<i>Xanthoxylum serratum</i> Heer	WEYLAND, 1934, p. 91 pro parte e.g. Coll. H. Weyland 1676!

Description:

Petiole 4.2–27.0 mm long and (0.55–) 0.85–2.2(–2.5) mm wide at mid-point, more or less parallel-sided and somewhat expanded at base or gradually increasing from (0.5–) 0.75–1.30(–1.80) mm wide at leaf base to 1.4–3.0 mm wide at base of petiole, straight or curved, making little or no angle with the midvein.

Lamina ovate or elliptical, 1.0–21 cm or more long, 0.55–9.0 cm wide, the length/breadth ratio being (1.1 : 1–) 1.75 : 1–3.2 : 1(–4.4 : 1) (fig. 41). Leaf apex acute or acuminate, rarely emarginate, leaf base obtuse, rounded or slightly cordate, rarely acute, sometimes slightly oblique.

Leaf margin entire or non-entire, sometimes bearing acute or occasionally rounded teeth 0.05–1.3(–1.8) mm across, 0–45 per side, alternating with acute, angular or rounded sinuses. Teeth of one size group or falling into two size groups, the larger ones being served by secondary veins and the smaller ones by branches of secondary veins.

Venation camptodromous or craspedodromous, midvein straight or curved, hardly or markedly tapering along length, 0.17–1.1 mm wide at mid-point between base and apex of the lamina. Midvein bearing 5–13 secondary veins per side, the most proximal vein arising at 30°–105°.

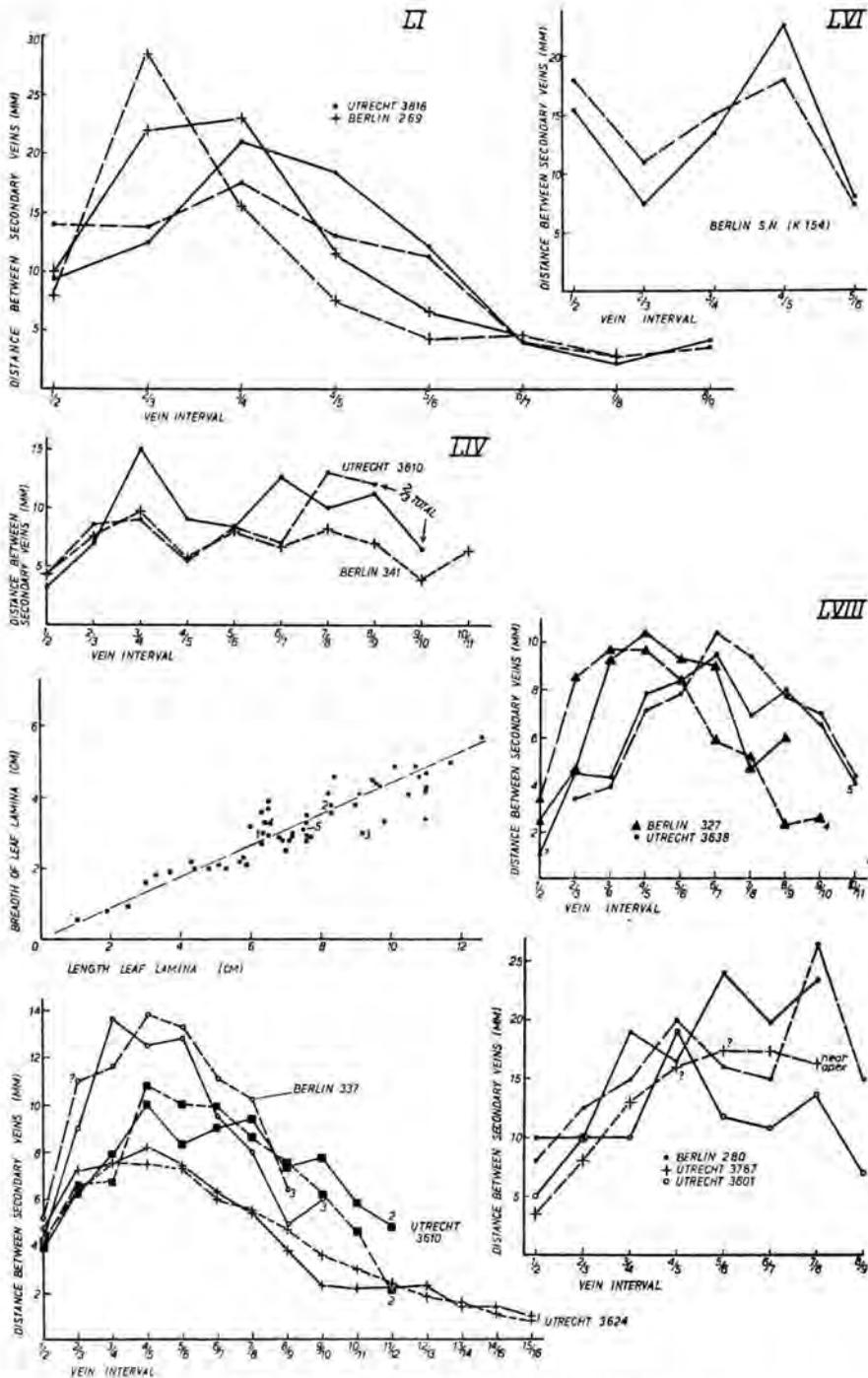


Fig. 41. Graphs LI, LIV, LVI, LVIII.

arising in the remaining part of the basal third of the lamina at 35° – 75° , in the median third at 35° – 70° , in the apical third at 40° – 70° (-90°). The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins reaching a maximum roughly mid-way or rarely apically (fig. 41). Secondary veins opposite or alternately arranged, hardly or somewhat tapering along their length, 0.05–0.50 mm wide at mid-point, occasionally dichotomising in any part of the lamina at $1/2$ – $3/4$ the distance from the midvein to the leaf margin, the veins interconnected distally by fine extensions of secondary veins, or tertiary veins. Intermediate veins (0–)2–12 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 60° – 135° , running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, the veins extending from 0 to $1/4$ – $9/10$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Tertiary veins 2–13 per 1 cm secondary vein, sometimes arranged at right angles to the midvein, little or much branched, the lengths on acroscopic and basiscopic sides of secondary veins more or less similar. Areoles 25–60 (-110) per 10 mm^2 , with some free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition composed of 170–525 more or less polygonal cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–3 : 1. Cell wall 0.45–0.60 microns thick, largely unpitted or very finely pitted, straight. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–6 : 1, cell wall up to 0.8 microns thick, transverse walls slanting or at right angles to the lateral walls. Cells at leaf margin c.700 per 0.1 mm^2 , the cell length/cell breadth ratio being 1.5 : 1–4 : 1, arranged in 15–20 rows. Cell wall 1.0–1.5 microns thick, unpitted or finely pitted, straight, transverse walls slanting or at right angles to the lateral walls. *Epidermis* in stomatal condition composed of 390–720 more or less polygonal cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1 : 1–4 : 1. Cell wall 0.3–1.2 microns thick, largely unpitted or very finely pitted, straight. Cuticle over veins sometimes finely striate, cells over veins elongate, the cell length/cell breadth ratio being 1 : 1–8 : 1, cell wall up to 2 microns thick. Finer veins reflected in cuticle. Stomata 14.4–36.0 microns long and 10.8–30.6 microns broad, breadth 52–122 % length, 10–36 per 0.1 mm^2 ; stomatal index 2.3–5.0 %. Stomata variously orientated, undepressed or somewhat depressed, more or less equidistant or somewhat arranged in groups, apices non-retuse. Stomatal slit 41–81 % stomatal length, epidermal wall of guard cells often obscure in cuticle. Accessory cells (2–) 4–6, symmetrical with (0–)2(–4) polar and 2–4 lateral cells. Accessory cells sometimes \pm same size as, but generally narrower than, the remaining epidermal cells. Hair bases c.11 microns in diameter rarely present over veins, 0(–1) per 0.1 mm^2 . Internal resinous bodies absent.

Specimens examined: 451, among which the numbered specimens:
 Deutsche Akad. Wiss. Berlin: 263(K 148), 273(K 61), 280(KA 11), 310(K 46), 314(K 75), 327(K 133), 337(K 134), 349(K 75), 364(K 148)
 Geol. Inst. Cologne: Coll. H. Weyland 1398(K 61), 1418(K 61), 1424(K 46), 1425(K 46), 1426(K 46), 1427(K 46), 1428(K 46), 1430(K 46), 1448(K 134), 1449(K 134), 1450, 1451(K 133), 1452(K 133), 1454(K 34), 1459(K 108), 1460(K 75), 1461(K 75), 1462(K 75), 1536(KA 11) counterpart of Berlin 280, 1543, 1651, 1654, 1655, 1667(K 148), 1676, 1681, 1734
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3216, 3256B, 3394B, 3464B, 3523B, 3530B, 3535C, 3542C, 3576, 3577, 3578, 3579, 3580, 3581A, 3582, 3583, 3584, 3585, 3586A, 3587, 3588, 3589, 3590, 3591, 3592A, 3593, 3594, 3595, 3596, 3597, 3598, 3599, 3600, 3601, 3602, 3603A, 3603B, 3604, 3605, 3606, 3607A, 3608A, 3609A, 3610, 3611, 3612, 3613, 3614, 3615A, 3616, 3617, 3618, 3619, 3620A, 3621, 3622, 3623, 3624, 3625, 3626, 3627, 3628, 3629, 3630, 3631, 3632, 3633, 3634, 3635, 3636, 3637, 3638, 3639, 3640A, 3690B, 3708B, 3727B, 3744B, 3771B, 3787, 3788A, 3789, 3875, 3877, 3914C.

Discussion:

A reference of certain of the leaf-remains from Kreuzau to *Rhamnus gaudinii* Heer (WEYLAND, 1934) was later questioned by WEYLAND (1943). Professor H. Weyland therefore proposed a new binomial, *Alnus palaeo-japonica* Weyland (Betulaceae) to cover these fossils. In this taxon he included material from Kreuzau, which he had referred to in 1934 as *Quercus platania* Heer (Fagaceae). A re-examination of this and other material described by WEYLAND (1934) as separate entities proved that the latter could not be satisfactorily distinguished from the former on the basis of the characters made use of in the present account. While none of this material yielded anything more than poorly preserved cuticles, certain of the material in the Utrecht collection was sufficiently well preserved to enable cuticle preparations to be made. An examination of the preparations proved that material somewhat variable in outward appearance had a uniform epidermal structure. Since transitions between one form and another were to be observed, any subdivision of this taxon would appear to be arbitrary. However, since leaves resembling the fossil macroscopically and microscopically are to be found in a number of dicotyledonous families, there is a strong possibility that the present taxon may not represent a natural entity. Thus a definite assignation to a particular group of living plants would not appear to be feasible.

LIX

Synonyms: *Elaeodendron helveticum* Heer

WEYLAND, 1934, p. 93, Tafel 17,
fig. 7!

Rhus pyrrhae Unger

WEYLAND, 1934, p. 92, Tafel 16,
figs. 4-5!

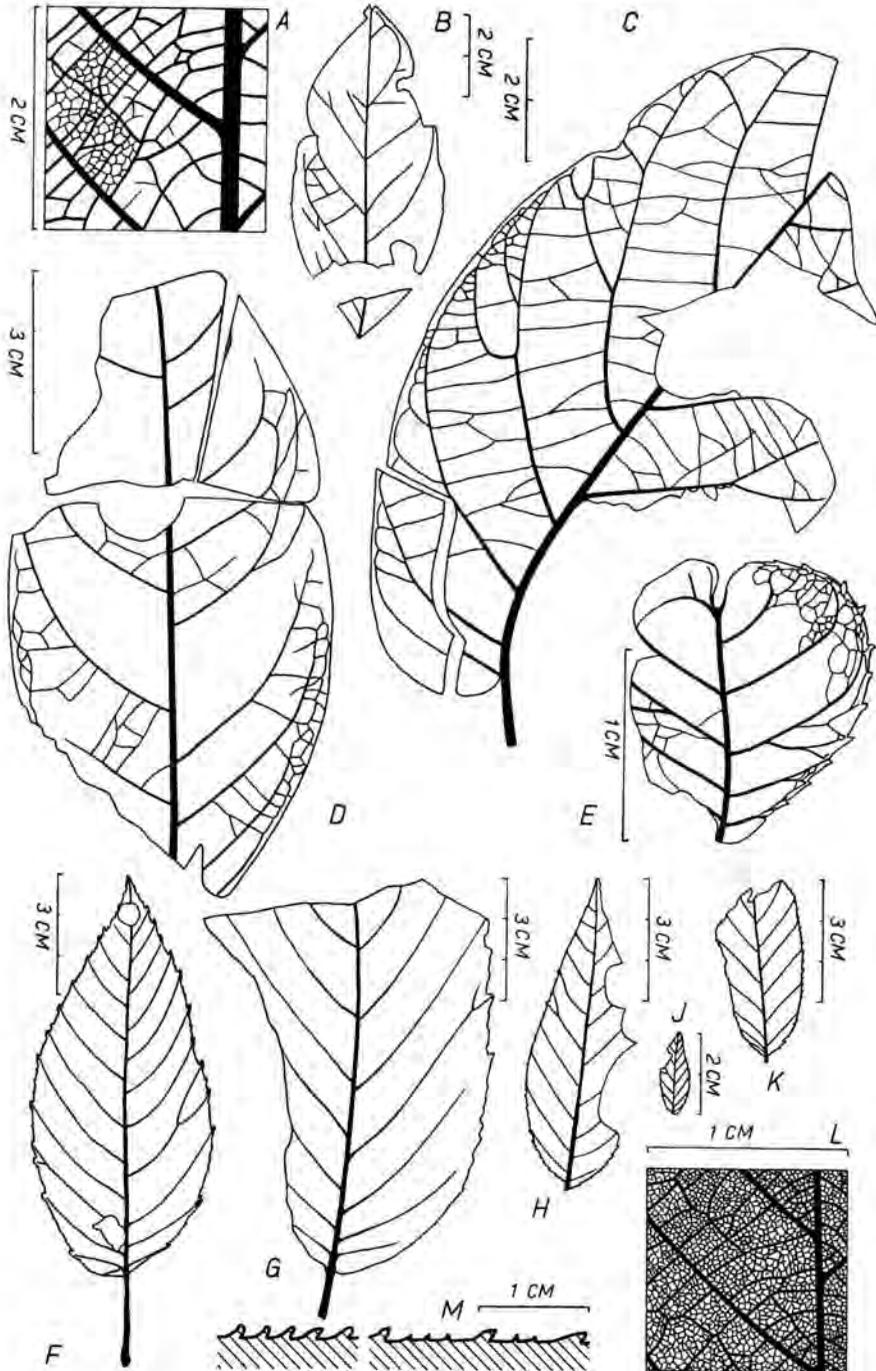


Fig. 42. A-M = LVIII: A = Utrecht 3620 A, detail showing venation; B = Utrecht 3875; C = Utrecht 3620 A; D = Utrecht 3601; E = Utrecht 3877; F = Utrecht 3625; G = Utrecht 3613; H = Utrecht 3631; J = Utrecht 3611; K = Utrecht 3627; L = detail showing venation; M = detail showing types of leaf margin developed.

Description:

Petiole 3–12 mm or more long and 0.7–2.6 mm wide, more or less parallel-sided or increasing in width from 0.7–1.5 mm at leaf base to 1.0–2.6 mm or more at base of petiole, straight, sometimes making a slight angle with the midvein.

Lamina ovate or elliptical, c.3–11.3 cm long, 2.1–6.1 cm wide, the length/breadth ratio being 1.3 : 1–1.85 : 1, sometimes asymmetrical round midvein. Leaf apex acute or acuminate, leaf base slightly to markedly attenuate.

Leaf margin non-entire, \pm serrate, with acute or rounded teeth 1.2–4.0 mm across, 0–1 per secondary vein and 0 (–1) per intercostal field, equivalent to 3–7 per side, only occasionally present in proximal half of lamina. These teeth alternating with acute, angular or rounded sinuses. Teeth of one size group.

Venation craspedodromous, midvein straight or curved, hardly or somewhat tapering along length, 0.15–0.60 mm wide at mid-point. Midvein bearing 5–11 secondary veins per side, the most proximal vein arising at 35°–65° (rarely more), arising in the remaining part of the basal third of the lamina at 40°–55° (–90°), in the median third at 50°–70°, in the apical third at 45°–80°. The angle at which the veins arise increasing, constant, or slightly decreasing within the first few mms. The spacing of the veins initially increasing, thereafter remaining more or less constant or decreasing (fig. 44). Secondary veins mostly alternately arranged, although the most proximal pair may be opposite, somewhat tapering along their length, 0.1–0.2 mm wide at mid-point, interconnected distally by tertiary veins or vein network, less commonly by fine extensions of secondary veins. Intermediate veins 0–10 per intercostal field, some having a twisted course, arising from the midvein at 60°–120°, running more or less parallel to one another or converging/diverging, the spacing between them more or less constant, decreasing distally or irregular. The veins more or less similar in width, extending from 0 to $(1/7 -) 1/3 - 3/4$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field sometimes mid-way or more commonly distally. Tertiary veins 3–7 per 1 cm secondary vein, somewhat branched. Areoles c.8 per 10 mm², possibly with some unbranched free vein-endings.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of an unknown number of striate cells per 0.1 mm². Cell wall 0.5–1.0 microns thick, largely unpitted, somewhat undulate, the depth from the tips of the lobes to the bottoms of the sinuses up to 10 microns. Cells over veins elongate. Finer veins reflected in cuticle. Stomata 23.4–37.8 microns long and 14.4–21.6 microns broad, breadth 42–70 % length, 5–8 per 0.1 mm²; stomatal index unknown. Stomata variously orientated, undepressed, more or less equidistant, apices non-retuse. Stomatal slit 70–90 % stomatal length. Accessory cells 2, symmetrical with 0 polar and 2 lateral cells. Internal resinous bodies absent.

Specimens examined: 13, among which the numbered specimens:
 Deutsche Akad. Wiss. Berlin: 267(K 157), 288(K 98), 315(K 98)
 Geol. Inst. Cologne: Coll. H. Weyland 1470(K 98), 1471(K 98)
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3414C, 3767,
 3768, 3769, 3770, 3771A.

Discussion:

The material from Kreuzau referred to *Elaeodendron helveticum* Heer and *Rhus pyrrhae* Unger by Weyland proved to be inseparable and must therefore be considered as belonging to a single taxon.

No satisfactory comparison could be made with the leaf material of woody species studied by the present author. While the number of secondary veins present in the leaflets of living species of *Rhus* is generally 10-25 per side, certain species e.g. *Rhus aromatica* Ait. and *R. diversiloba* Torrey et Gray have leaflets resembling the fossil in shape and number of secondary veins. However, in both these species the lower epidermis is characterized by the presence of fairly numerous large hair bases bearing unicellular hairs and smaller hair bases bearing multicellular hairs. While a striate cuticle similar to that found in the fossil is present in *Rhus succedanea* L., the cuticle from the lower surfaces of the leaflets of *Rhus aromatica* Ait. and *R. diversiloba* Torrey et Gray are at most only weakly striate. At this stage a reference of the fossil to *Rhus* (Anacardiaceae) cannot be substantiated.

A reference of the fossil to *Elaeodendron* (Celastraceae) could not be substantiated either. Not only is this a genus found at the present-day in tropical parts of Asia, Australia, Africa, the New Hebrides, West Indies and Central America, but the epidermis of none of the species examined was found to resemble that of the fossil. The epidermis is composed of straight-walled and at most but slightly striate cells and the stomata are sunken with a short stomatal slit.

Epidermides similar to that of the fossil were observed in certain members of the Annonaceae, Araliaceae, Asclepiadaceae, Caprifoliaceae, Meliaceae, Oleaceae, Rutaceae and Simaroubaceae. However, none of this material was found to have leaves resembling the fossil in gross-morphology.

Herbarium material examined in detail:

<i>Elaeodendron australe</i>	Coll. J. Staer 12-1911	(E) _____
F. v. M.		
<i>Elaeodendron dioicum</i>	Coll. W. Harris 5125	(E) _____
Griseb.		
<i>Elaeodendron melanocarpum</i>	Coll. N. Michael 1182	(E) _____
F. v. M.		
<i>Elaeodendron stuhlmannii</i>	Coll. J. R. Dale 624	(E) _____
Loes.		
<i>Elaeodendron subtrotundum</i>	Coll. J. Sinclair 5-2-1950	(E) det. J. Sinclair
King		

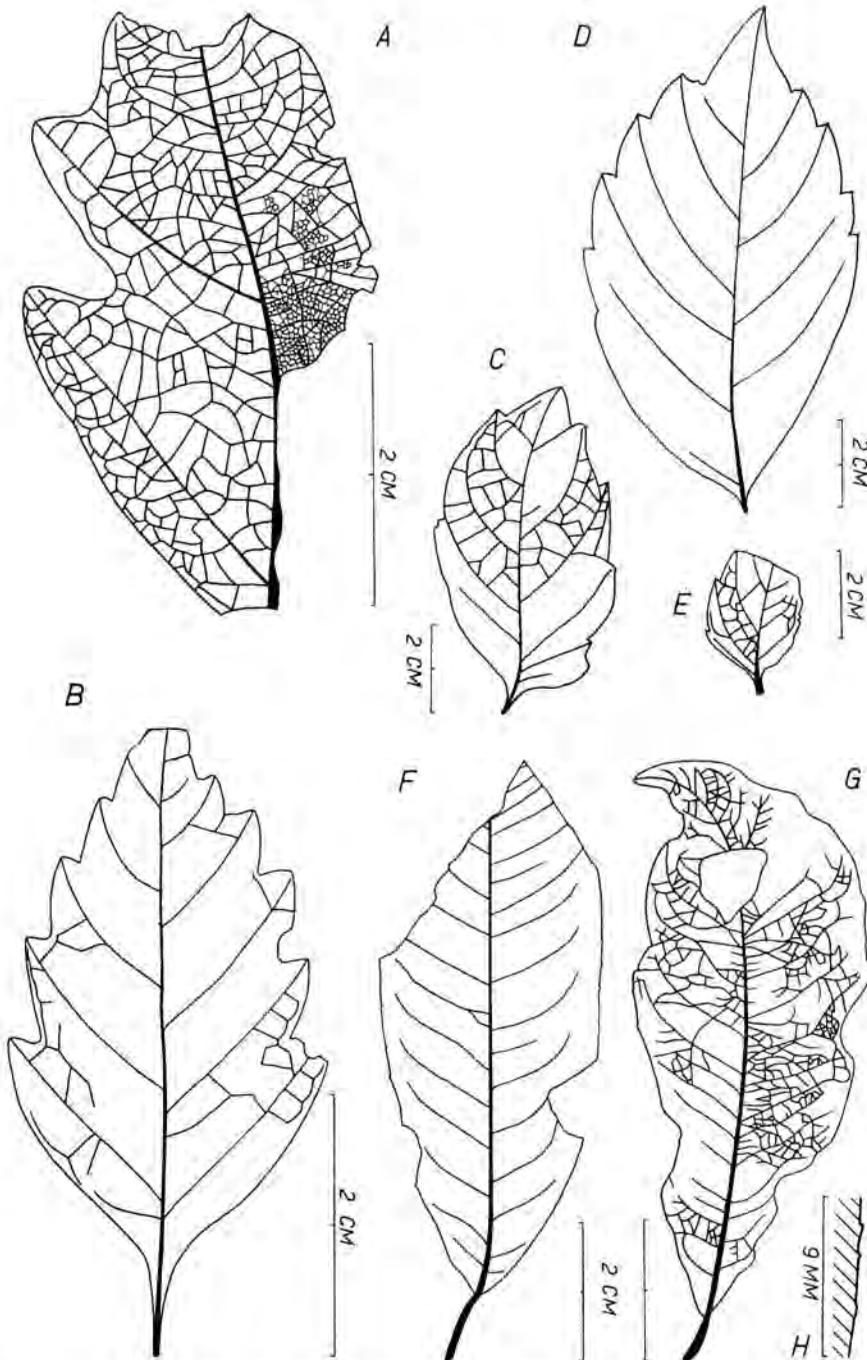


Fig. 43. A-B = LX: A = Berlin 343; B = Berlin s.n. C-E = LIX: C = Berlin 315; D = Utrecht 3768; E = Utrecht 3770. F-H = LXI: F = Utrecht 3839; G = Berlin 296 (Type of *Myrica kreuzauensis* Weyland); H = Utrecht 3839, detail showing leaf margin.

Elaeodendron xylocarpum DC.	Coll. A. E. Rickseck 323	(E)	_____
Rhus aromatica Ait.	Coll. W. A. Matthews 4714	(E)	_____
	Coll. G. L. Fischer 3-7-1911	(E)	_____
	Coll. A. Ruth 1429	(E)	_____
Rhus delavayi Franch.	Coll. Handel-Mazzetti 1958	(E)	det. Handel- Mazzetti
Rhus diversiloba Torrey et Gray	Coll. L. R. Abrams & E. A. McGregor 46	(E)	_____
Rhus potaninii Maxim.	Coll. S. S. Chien 5280	(E)	det. S. S. Chien
Rhus punjabensis Stewart	Coll. J. F. Rock 16122	(E)	_____
Rhus semialata Thunb.	Coll. C. Y. Chiao 2806	(E)	det. A. Rehder
Rhus succeedanea L.	Coll. S. K. Lau 55	(E)	det. E. D. Merrill
Rhus sylvestris Sieb. et Zucc.	Coll. E. Taquet 4173	(E)	det. A. Rehder & E. H. Wilson
Rhus trichocarpa Miq.	Coll. Handel-Mazzetti 11757	(E)	det. Handel- Mazzetti
Rhus verniciflua Stokes	Coll. C. Y. Chiao 2578	(E)	det. A. Rehder

LX

Synonyms: *Quercus* c.f. *pseudocastanea*
Goepfert
Rhus quercifolia Goepfert

Deutsche Akad. Wiss. Berlin s.n.,
det. H. Weyland!
WEYLAND, 1934, p. 91, Tafel 17,
fig. 10!

Description:

Petiole c.6.5 mm long and 0.3–0.4 mm wide, straight, making no angle with the midvein.

Lamina pinnatifid, with sometimes acute but generally rounded lobes 1.5–6.0 mm long, (0–)1 per secondary vein and 0 per intercostal field, equivalent to 2–7 per side, alternating with acute or rounded sinuses. The nature of the dissection simple. Lamina ovate, 4.2–c.5.5 cm long, 2.5–4.0 cm wide, the length/breadth ratio being 1.4:1–1.7:1. Leaf apex acute, leaf base attenuate.

Leaf margin entire.

Venation craspedodromous, midvein straight or curved, slightly tapering along length, 0.1–0.3 mm wide at mid-point between base and apex of the lamina. Midvein bearing 3–7 secondary veins per side, the most proximal vein arising at 40°–55°, other veins if present in the basal third of the lamina arising at 55°–60°, in the median third at 45°–60°, in the apical third at 60°–65°. The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the secondary veins more or less constant, sometimes somewhat irregular. Secondary veins opposite or alternately arranged, somewhat tapering along their length, 0.02–0.20 mm wide at mid-point, interconnected distally by tertiary veins or vein network. Intermediate veins 3–c.15 per intercostal field, arising from the midvein at 55°–120°, more or less parallel to one another or converging/

diverging, the spacing between them constant or increasing distally, the veins similar in width, extending from 0 to $1/2-9/10$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 4-5 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopical sides of secondary vein more or less similar. Areoles c.80 per 10 mm², with apparently many free vein-endings, these being unbranched and sometimes branched.

Cuticle poorly preserved. Finer veins reflected in cuticle. Internal resinous bodies uncommon.

Specimens examined: Deutsche Akad. Wiss. Berlin; 343(K 131), s.n. (reverse side of K 154).

Discussion:

While Weyland referred both Berlin 338 and 343 to the same taxon (*Rhus quercifolia* Goeppert), no leaf base was present in Berlin 338 (see WEYLAND, 1934, Tafel 17, fig. 9). This means that the possibility cannot be ruled out that this specimen was a fragmentary leaf referable to No. XXXIII.

Berlin 343, which resembled the specimen determined by Weyland as *Quercus* c.f. *pseudocastanea* in shape, was found to differ from the latter in certain respects related to the venation. In Berlin 343 the number of secondary veins was smaller (3 as opposed to 6-7) and the number of intermediate veins larger (c.8-c.15 as opposed to 3-5). Furthermore, the midvein and secondary veins were better developed in Berlin 343. The midvein was 0.3 mm wide mid-way along its length, as opposed to 0.1 mm, and the secondary veins had a width of 0.1-0.2 mm at mid-point, whereas those of "*Quercus* c.f. *pseudocastanea*" were only 0.02-0.06 mm wide. It is questionable whether the last mentioned differences have any significance, for two separate readings can be obtained in living plants by measuring the width of the veins on the upper and lower surfaces of the same leaf. The remaining differences were not thought to be of great significance and the two specimens were therefore considered as belonging to the same taxon. This taxon, and in particular the specimen determined by H. Weyland as *Quercus* c.f. *pseudocastanea*, resembles No. LIX. However, in the absence of cuticles in the present specimens it was felt wiser to avoid uniting these taxa at this stage.

While none of the herbarium material of *Quercus* (Fagaceae) examined by the present author had leaves resembling the leaf-remains, these were found to resemble leaflets of *Rhus aromatica* Ait., *R. diversiloba* Torrey et Gray, *R. trilobata* Nutt. and *Toxicodendron quercifolium* (Michx.) Green (Anacardiaceae) as well as leaves of *Acer griseum* (Franch.) Pax and *A. cissifolium* K. Koch (Aceraceae). However, in the absence of further evidence e.g. cuticle preparations it did not prove possible to assign the leaf-remains to one of the possible genera.

LXI

Synonym: *Myrica kreuzauensis* Weyland

WEYLAND, 1934, pp. 45-46,

Tafel 2, fig. 2!

Description:

Petiole 12 mm long and 0.9-c.1.5 mm wide at mid-point, parallel-sided, curved, sometimes making a slight angle with the midvein.

Lamina elliptical or obovate, c.8-8.3 cm long, 3.2-3.55 cm wide. Leaf apex acute, leaf base acute or obtuse.

Leaf margin non-entire, crenulate to serrulate, with acute or rounded teeth, 0.2-0.8 mm across, 10-20 per side, only sporadic in the basal third of the lamina, alternating with acute or rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein straight or curved, hardly tapering along length, 0.7-1.0 mm wide at mid-point between base and apex of the lamina. Midvein bearing c.16-20 secondary veins per side, the most proximal vein arising at 80°-85°, arising in the remaining part of the basal third of the lamina at 50°-85°, in the median third at 45°-85°, in the apical third at 40°-60°. The angle at which the veins arise constant or occasionally increasing within the first few mms. The spacing of the veins reaching a maximum roughly mid-way along lamina or rather irregular (fig. 44). Secondary veins mostly alternately arranged sometimes opposite, more particularly proximally, hardly tapering along their length, 0.05-0.30 mm wide at mid-point, interconnected distally by fine extensions of secondary veins, or tertiary veins. Intermediate veins 1-8 per intercostal field, some having a twisted course, arising from the midvein at 60°-120°, running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/2-7/8 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 5-11 per 1 cm secondary vein, somewhat branched, the lengths on acropic and basiscopic sides of secondary vein more or less similar. Areoles c.140 (?) per 10 mm², the nature of the free vein-endings unknown.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of c.500 (?) cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1-2 : 1. Cell wall c.0.45 microns thick, straight or somewhat undulate, the depth from the tips of the lobes to the bottoms of the sinuses up to 6 microns. Cells over veins elongate, the cell length/cell breadth ratio being 1 : 1-9 : 1, the transverse walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Stomata 14.4-27.0 microns long and 16.2-21.6 microns broad, breadth 67-125 % length, up to 15 (?) per 0.1 mm²; stomatal index uncertain. Stomata variously orientated, undepressed, somewhat arranged in groups, apices non-retuse. Stomatal slit 28.5-62.5 % stomatal length. Accessory cells 6-12 in number possibly present, although in shape and size the cells in immediate proxi-

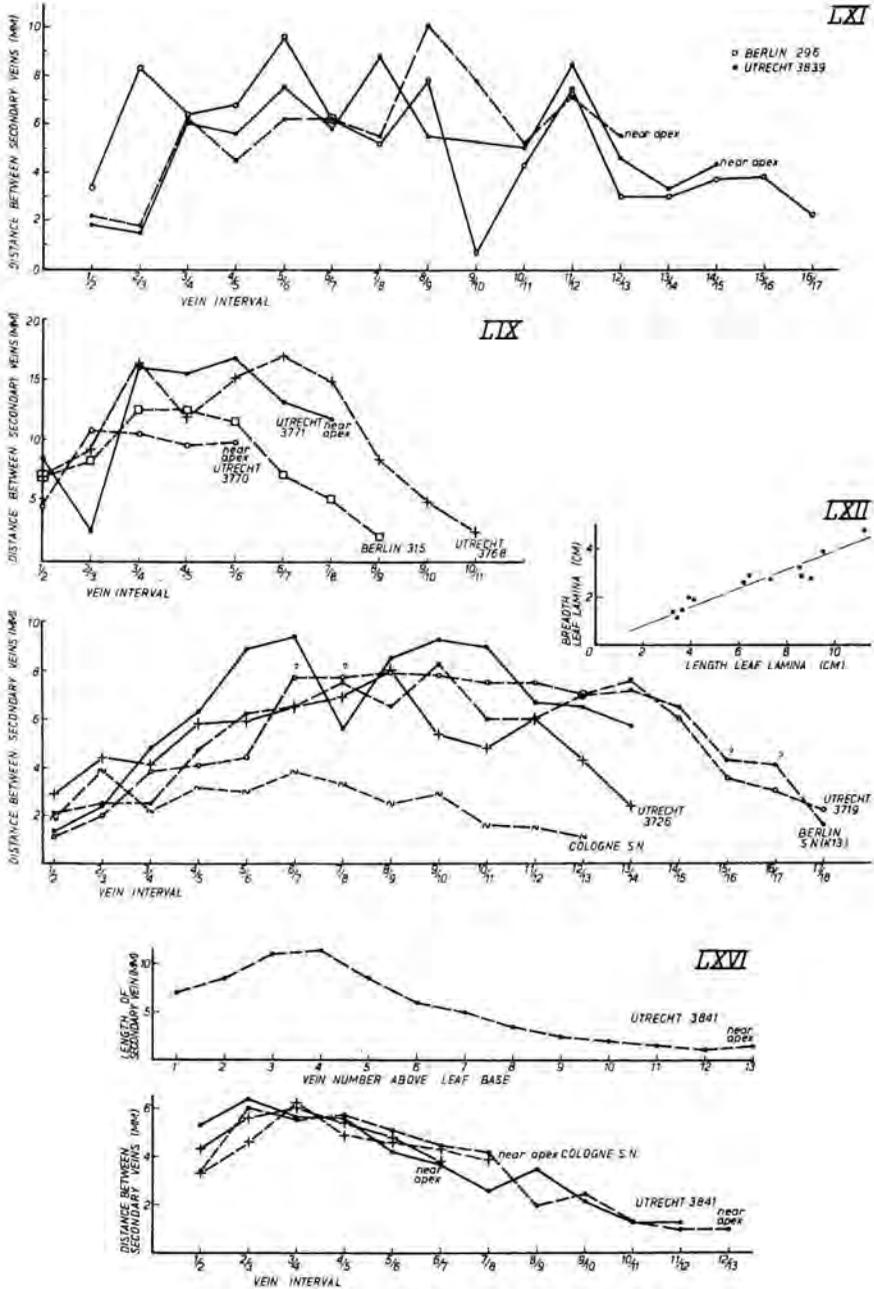


Fig. 44. Graphs LIX, LXI, LXII, LXVI.

mity to the stomata resemble the other epidermal cells. Internal resinous bodies rare.

Specimens examined: Deutsche Akad. Wiss. Berlin: 296(K 151)
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3839

Discussion:

Weyland only had a single specimen available for examination. An attempt to make a cuticle preparation from this specimen proved to be fruitless. However, a second specimen (Utrecht 3839) only differing from the former specimen in a few quantitative aspects e.g. the more numerous tertiary veins per 1 cm secondary vein (Utrecht 3839: 6–11; Berlin 296: 5–7) yielded a cuticle. Although Weyland referred Berlin 296 to *Myrica* (Myricaceae) none of the 16 species of *Myrica* examined by the present author had a gross-morphology in close agreement with the fossil. Moreover, the cuticle was not found to bear glands such as would be expected should the fossil be referable to the Myricaceae. Such glands generally prove to be fairly resistant to fossilization.

An alternative name for Weyland's taxon did not prove possible. Taxa with leaves having epidermides resembling that of the fossil are found in a large number of families of the dicotyledons at the present day.

LXII

<i>Synonyms</i> : <i>Ficus</i> sp.	WEYLAND, 1934, p. 65, Tafel 7, fig. 4!
<i>Juglans acuminata</i> A. Braun f. <i>acuminata</i>	GOTHAN and WEYLAND, 1964, p. 408, Abb. 281b!
<i>Prunus sambucifolia</i> Menzel	WEYLAND, 1934, p. 86, Tafel 15, fig. 5!
<i>Pterocarya castaneaefolia</i> (Goeppert) Menzel	WEYLAND, 1934, p. 49!
<i>Terminalia radoboensis</i> Unger	WEYLAND, 1934, pp. 104–105, Tafel 18, fig. 5; WEYLAND, 1943, pp. 115–116, Tafel 20, Abb. 7!
<i>Xanthoxylum serratum</i> Heer	WEYLAND, 1934, p. 91 pro parte e.g. Tafel 14, fig. 5!

Description:

Petiole up to 10 mm long and 1.1 mm wide at mid-point, straight, making no angle with the midvein.

Lamina (ovate-) oblong, elliptical or occasionally obovate, 3.25–c.12 cm long, 1.15–5.0 cm wide, the length/breadth ratio being 2.0:1–3.3:1 (fig. 44). Leaf apex acute or acuminate, leaf base acute, rounded or cordate, frequently asymmetrical and sometimes oblique.

Leaf margin non-entire, ± serrulate, with acute or somewhat rounded triangular or step-like teeth 0.05–1.1 mm across, c.20–c.70 per side, alternating with acute, angular or sometimes rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein straight or curved, hardly or markedly tapering along length, (0.1 -) 0.3-0.6(-1.0) mm wide at mid-point between base and apex of the lamina. Midvein bearing 10-c.22 secondary veins per side, the most proximal vein arising at (45° -) 70°-120°, arising in the remaining part of the basal third of the lamina at 50°-105°, in the median third at 40°-90°, in the apical third at 50°-100°. The angle at which the veins arise constant or slightly increasing or slightly decreasing within the first few mms. The spacing of the veins reaching a maximum roughly mid-way (fig. 44). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.03-0.30 mm wide at mid-point, interconnected distally by strong or fine extensions of the secondary veins. Intermediate veins 0-10 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 50°-135°, running more or less parallel to one another or converging/diverging, the spacing between them constant or increasing distally. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/5-7/8 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally, rarely of equivalent length throughout. Tertiary veins 4-21 per 1 cm secondary vein, slightly to much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles (25 -) 40-100 per 10 mm² with some or many free vein-endings, these being unbranched and branched.

Cuticle poorly preserved. Finer veins reflected to some extent in the cuticle. Internal resinous bodies apparently absent.

Specimens examined: 45, among which the numbered specimens:
 Deutsche Akad. Wiss. Berlin: 322(K 161), 342(K 109),
 350(K 142), 354(K 72).
 Geol. Inst. Cologne: Coll. H. Weyland 1362(K 13), 1431(K 13),
 reverse side of 1432, 1542(K 12).
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3715, 3716,
 3717, 3718, 3719, 3720, 3721, 3722, 3723, 3724, 3725, 3726,
 3727A, 3728, 3729A, 3730, 3731, 3732, 3733, 3867.

Discussion:

Not all the specimens determined by WEYLAND (1934) as *Prunus sambucifolia* Menzel (Rosaceae) were available to the present author. However, the specimen illustrated by WEYLAND (1934, Tafel 15, fig. 5) proved to fall within the circumscription of the present taxon. The above specimen resembled Berlin 354(K 72) and Berlin 342(K 109) referred to respectively as *Ficus* sp. (Moraceae) and *Terminalia radoboensis* Unger (Combretaceae) (WEYLAND, 1934, 1943). No characters validating the retention of these specimens as separate taxonomic entities were found. WEYLAND (1934, p. 104) stated that Berlin 342 had an entire leaf margin. However, a close examination of this specimen proved that numerous fine teeth, 0.1-0.2 mm across, did in fact exist. The specimen illustrated by GOTHAN and WEYLAND (1964, p. 408, Abb. 281b) and referred to *Juglans acuminata* A. Braun

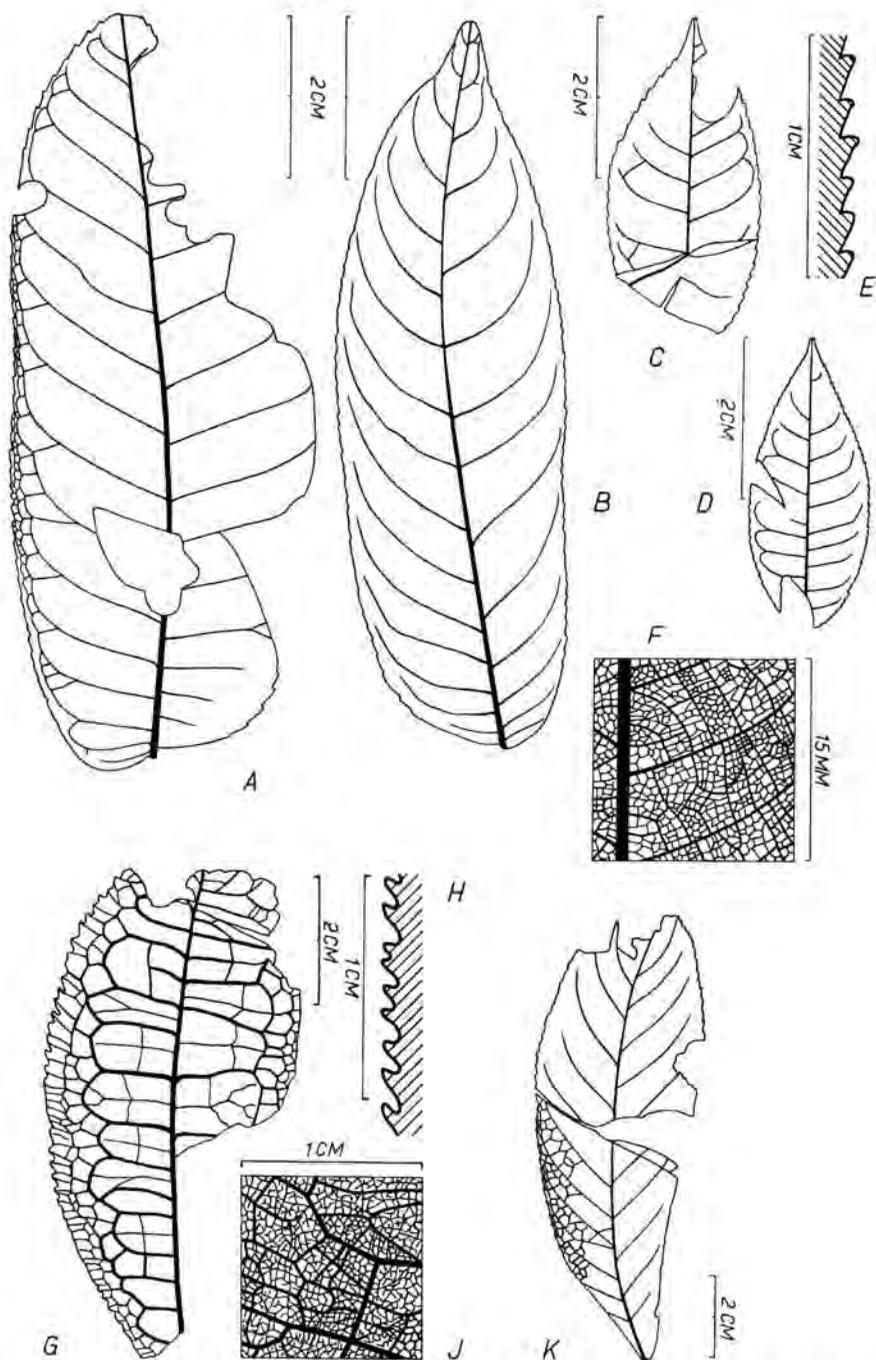


Fig. 45. A-F, K = LXII: A = Utrecht 3719; B = Berlin s.n. (K 13); C = Utrecht 3715; D = Utrecht 3724; E = detail showing leaf margin; F = detail showing venation; K = Utrecht 3716. G-J = LXIII: G = Utrecht 2057; H = Utrecht 2057, detail showing leaf margin; J = Utrecht 2057, detail showing venation.

f. *acuminata* was originally determined by WEYLAND (1934) as *Pterocarya castaneaefolia* (Goeppert) Menzel. This would appear to indicate some uncertainty as to the actual affinity of the leaf-remains. While these resemble the leaflets of certain species of *Juglans* and *Pterocarya* (Juglandaceae), one should not overlook the possibility that the leaf-remains could be derived from a taxon or taxa belonging to a family other than the Juglandaceae. Leaves or leaflets similar to the taxon under consideration are to be found in a number of families of dicotyledons e.g. *Aesculus wilsonii* Rehder (Hippocastanaceae), *Garuga pinnata* Roxb. (Burseraceae) and *Zanthoxylum ailanthoides* Sieb. et Zucc. (Rutaceae). Since the fossil did not yield any sufficiently well-preserved cuticles to enable a comparison to be made, no decision as to the affinity of the leaf-remains could be taken.

LXIII

Description:

Petiole unknown.

Lamina obovate, c.8.5 cm long, 4.7 cm wide. Leaf apex unknown, leaf base unknown.

Leaf margin non-entire, sinuolate, with rounded teeth 0.6–1.5 mm across, c.50 per side, alternating with rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein slightly curved, hardly tapering along length, c.0.7 mm wide at mid-point between base and apex of the lamina. Midvein bearing c.15 secondary veins per side, arising in the basal third of the lamina at 75°–90°, in the median third at 70°–100°, in the apical third at 80°–100°. The angle at which the veins arise sometimes constant but more commonly increasing within the first few mms. The spacing of the veins somewhat irregular. Secondary veins sub-opposite or opposite, hardly tapering along their length, 0.2–0.3 mm wide at mid-point, interconnected distally by strong or fine extension of the secondary veins. Secondary veins inclusive of their arched interconnection not extending for more than 58–75 (–82) % of the distance from the midvein to the leaf margin, the more marginal parts being served by finer veins arising more or less radially from the arched interconnections. These veins may in turn be joined by an arched interconnection and bear similar off-shoots. Intermediate veins (0–)1–4 per intercostal field, sometimes having a somewhat twisted course, arising from the midvein at 60°–100°, running more or less parallel to one another, the spacing between them constant. The veins similar in width, extending from 0 to 1/3–2/3 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way. Tertiary veins 3–4 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 23–30 per 10 mm², with many free vein-endings, these being unbranched but more commonly branched.

Epidermis unknown.

Specimen examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 2057

Discussion:

Although this taxon has a very distinctive appearance, it was not found to resemble the leaves of any of the woody species examined. However, it does show a certain resemblance to leaves of some species of herbaceous plants e.g. *Dipsacus sylvestris* Huds. (Dipsacaceae) and various species of *Rumex* (Polygonaceae). Since no attempt has been made to examine the leaves of herbaceous plants systematically, a more exact determination cannot be given at the present time.

LXIV

Description:

Petiole 1.5 mm long and 0.6 mm wide at mid-point, increasing in width from 0.4 mm wide at leaf base to 0.75 mm wide at base of petiole, straight, making no angle with the midvein.

Lamina elliptical, 3.0–3.05 cm long, 1.1–1.17 cm wide, the length/breadth ratio being 2.6 : 1–2.7 : 1. Leaf apex acute or somewhat rounded, leaf base attenuate, obtuse or rounded, slightly oblique.

Leaf margin non-entire, serrulate-denticulate, with acute teeth 0.10–0.35 mm across, 11–c.20 per side, alternating with acute or rounded sinuses. Teeth of one size group.

Venation camptodromous, midvein curved, hardly tapering along length, 0.2–0.3 mm wide at mid-point between base and apex of lamina. Midvein bearing c.6–9 secondary veins per side, the most proximal vein arising at 50°–65°, arising in the remaining part of the basal third of the lamina at 50°–65°, in the median third at 50°–65°, in the apical third at 45°–70°. The angle at which the veins arise initially constant. Secondary veins sub-opposite or alternately arranged, hardly or somewhat tapering along their length, 0.05–0.10 mm wide at mid-point, interconnected distally by fine extensions of secondary veins or tertiary veins. Intermediate veins 2–c.5 per intercostal field, arising from the midvein at 70°–135°, running more or less parallel to one another, the spacing between them constant or increasing distally. The veins similar in width, extending from 0 to 1/2–3/4 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. The nature of the tertiary veins, areoles and free vein-endings unknown.

Epidermis unknown.

Specimens examined: Geol. Inst. Cologne s.n.

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot. 3883

LXV

Synonym: *Dryandroides angustifolia* Unger WEYLAND, 1934, pp. 47–48,
Tafel 3, fig. 4!

Description:

Petiole 0.5–1.5 mm long and 0.5 mm wide at mid-point, increasing in width from 0.25 mm wide at leaf base to 0.7 mm wide at base of petiole, straight, making no angle with midvein.

Lamina ovate or elliptical, 2.65–8.0 cm long, 0.5–1.2 cm wide, the length/breadth ratio being 5.3 : 1–7.4 : 1. Leaf apex acute, leaf base obtuse or rounded.

Leaf margin non-entire, serrulate, with acute teeth 0.3–1.5 mm across, 4–14 per side, alternating with acute or angular sinuses. Teeth of one size group.

Venation camptodromous-craspedodromous, midvein straight or curved, hardly or markedly tapering along length, 0.1–0.4 mm wide at mid-point between base and apex of the lamina. Midvein bearing 10–27 secondary veins per side, arising in the basal third of the lamina at 45°–65°, in the median third at 40°–65°, in the apical third at 40°–60° (–90°). The angle at which the veins arise initially constant. The spacing of the veins varies between 1–3 mm throughout. Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.03–c.0.05 mm wide at mid-point, generally interconnected distally by strong extensions of secondary veins. Intermediate veins 1–4 (–5) per intercostal field, some (particularly the finer ones) having a somewhat twisted course, arising at 45°–60°, running more or less parallel to one another, the spacing between them being more or less constant. The veins similar in width or increasing in width with increase in length, extending from 0 to 7/8 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way. Tertiary veins 10–21 per 1 cm secondary vein, much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 80–155 per 10 mm², with some unbranched free vein-endings.

Epidermis in non-stomatal condition unknown. Cells at leaf margin 1500 per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–4 : 1, arranged in 6–10 rows. Cell wall 0.5–2.0 microns thick, somewhat pitted, straight, the transverse walls slanting or at right angles to the lateral walls. Epidermis in stomatal condition composed of c.1100 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall 0.3–0.6 microns thick, finely pitted, straight. Cells over veins elongate, sometimes finely striate. Finer veins reflected in cuticle. Stomata 12–24 microns long and 12–24 microns broad, breadth 60–125 % length, the number per 0.1 mm² and stomatal index uncertain. Stomata variously orientated, un-depressed, apices sometimes retuse. Stomatal slit 50–62.5 % stomatal length. The nature of the accessory cells, if any, unknown. Glands 84–140 microns in diameter, resting on single basal cell 6–16 microns in diameter present, 7–16 per 0.1 mm². Internal resinous bodies rare.

Specimens examined: Deutsche Akad. Wiss. Berlin: 290(K 112)
Geol. Inst. Cologne: Coll. H. Weyland 1644, 1732, 1733
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3776, 3777,
3778, 3779, 3780, 3781, 3782.

Discussion:

Although the generic name *Dryandroides* might suggest an affinity with *Dryandra* (Proteaceae), this genus tends to be referred to the Myricaceae

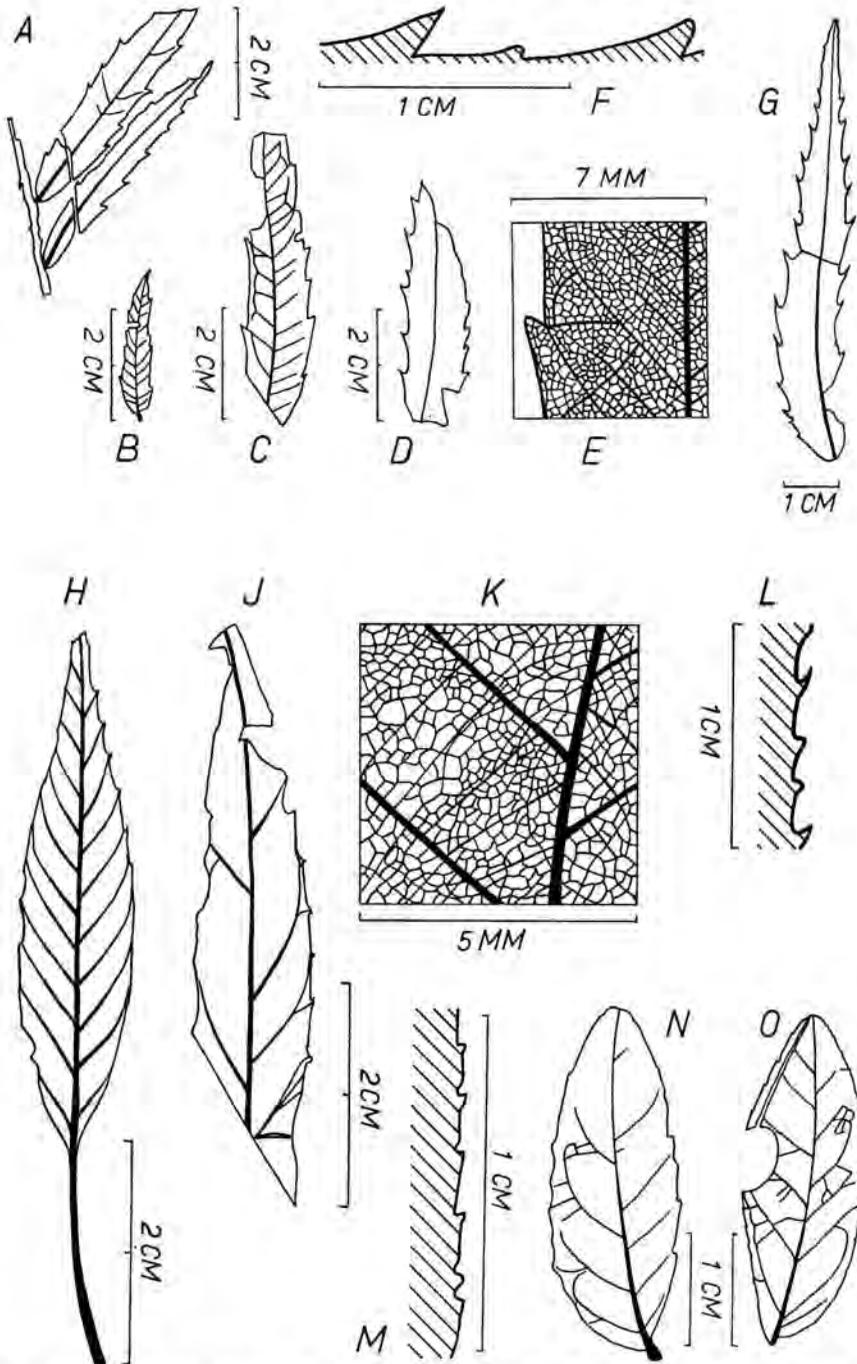


Fig. 46. A-G = LXV: A = Cologne, Coll. H. Weyland 1733; B = Cologne, Coll. H. Weyland 1732; C = Utrecht 3776; D = Utrecht 3780; E = detail showing venation and leaf margin; F = detail showing leaf margin; G = Utrecht 3779. H-L = LXVI: H = Utrecht 3841; J = Utrecht 3842; K = detail showing venation; L = detail showing leaf margin. M-O = LXIV: M = Utrecht 3883, detail showing leaf margin; N = Cologne s.n.; O = Utrecht 3883.

in recent palaeobotanical literature. WEYLAND (1934, p. 48) even went as far as to suggest that the material he referred to *Myrica lignitum* and the material of *Dryandroides* might represent a single taxonomic entity. Cuticle analysis has however proved that this is not the case. While the Myricaceae are characterized by the presence of glands superimposed on a 2(-3) celled base, those of the fossil are characterized by having a single basal cell. Leaves with glands having a single basal cell are found in a number of families of woody plants e.g. Acanthaceae, Anacardiaceae, Bignoniaceae, Euphorbiaceae, Fagaceae, Juglandaceae, Myrsinaceae, Oleaceae and Verbenaceae. Of the material examined the fossil most closely resembled the leaflets of *Tecoma stans* (L.) Juss. (Bignoniaceae). However, while the leaflets of *Tecoma stans* resembled the fossil in shape and nature of the leaf margin, the venation was arched camptodromous, rather than the brochidodromous venation pattern encountered in the fossil. Furthermore, the glands of *Tecoma stans* and other members of the Bignoniaceae examined were smaller than those encountered in the fossil. In *Tecoma stans* the glands had a diameter of 36-70 microns.

LXVI

Synonym: *Quercus drymeia* Unger

WEYLAND, 1934, pp. 58-59,
Tafel 3, fig. 3!

Description:

Petiole 17.5 mm long and 0.5 mm wide at mid-point, more or less parallel-sided, slightly curved, making no angle with the midvein.

Lamina elliptical, 4.1-c.8 cm long, 1.0-1.5 cm wide, the length/breadth ratio being 4.1:1-c.5:1. Leaf apex acuminate, leaf base acute.

Leaf margin mostly entire proximally, distally non-entire with acute (- rounded) teeth 0.3-0.6 mm across, 1 per secondary vein in distal half of the lamina and 0 (-1) per intercostal field, alternating with acute or rounded sinuses. Teeth of one size group.

Venation craspedodromous, midvein straight or curved, hardly tapering along length, 0.3-0.4 mm wide at mid-point between base and apex of the lamina. Midvein bearing 9 or more secondary veins per side, the most proximal vein arising at c.30°-45°, arising in the remaining part of the basal third of the lamina at c.30°, in the median third at 30°-45°, in the apical third at 30°-65°. The angle at which the veins arise constant or decreasing within the first few mms. The spacing of the veins reaching a maximum proximally (fig. 44). The length of the veins reaching a maximum proximally (fig. 44). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.1-0.2 mm wide at mid-point, interconnected distally by tertiary veins. Intermediate veins 7-10 per intercostal field, arising from the midvein at 70°-120°, running more or less parallel to one another, the spacing between them mostly constant. The veins similar in width, extending from 0 to 2/3 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field distally. Ter-

tiary veins c.13–20 per 1 cm secondary vein, somewhat branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles c.80 (?) per 10 mm², the nature of the free vein-endings being unknown.

Cuticle poorly preserved. Finer veins reflected in cuticle. Internal resinous bodies apparently absent.

Specimens examined: Deutsche Akad. Wiss. Berlin: 274(K 122)
Geol. Inst. Cologne: s.n.
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3841, 3842.

Discussion:

WEYLAND (1934, pp. 58–59) referred the only specimen of this taxon available to him to *Quercus* (Fagaceae) on the basis of a comparison with leaf-remains attributed to *Quercus* by F. Unger and O. Heer. The leaf-remains are certainly not unlike the leaves of a number of *Quercus* species e.g. *Q. acrodonta* Von Seemen, *Q. baronii* Skan., *Q. cocciferoides* Handel-Mazzetti, *Q. glauca* Thunb. and *Q. handeliana* Camus. However, in the absence of well-preserved cuticle preparations, which might confirm the generic affinity of the fossil, a reference to *Quercus* would appear to be somewhat premature.

LXVII

<i>Synonyms</i> : <i>Carpinus pyramidalis</i> (Goeppert)	QUAAS, 1910, p. 983
Heer	
<i>Ulmus longifolia</i> Unger	WEYLAND, 1934, p. 61, Tafel 8, fig. 1!

Description:

Petiole 5–15 mm long and 0.9–2.0 mm wide at mid-point, straight or curved throughout length, sometimes making a slight angle with the midvein.

Lamina ovate, 5.2–13.0 (– > 17) cm long, 1.8–4.0 (– 6.2) cm wide, the length/breadth ratio being 2.75 : 1–4.4 : 1 (fig. 48). Leaf apex acute, leaf base rounded or slightly cordate, sometimes asymmetrical.

Leaf margin non-entire, serrulate, with acute or somewhat rounded teeth, 0.1–1.4 mm across, 1 per secondary vein and 0–4 per intercostal field, equivalent to c.30–c.55 per side, alternating with acute sinuses. Teeth falling into two size groups.

Venation craspedodromous, midvein straight or curved, slightly or markedly tapering along length, 0.3–0.6 mm wide at mid-point between base and apex of the lamina. Midvein bearing 14–27 secondary veins per side, the most proximal vein arising at 45°–110°, arising in the remaining part of the basal third of the lamina at 40°–70°, in the median third at 30°–55°, in the apical third at 20°–55°. The angle at which the veins arise constant or somewhat decreasing within the first few mms. The spacing

of the veins somewhat irregular, reaching maximum mid-way or apically (fig. 48). The length of the veins reaching a maximum proximally or mid-way (fig. 48). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.10–0.25 mm wide at mid-point, sometimes dichotomising at $(1/2 -) 2/3 - 3/4$ the distance from the midvein to the leaf margin, the veins interconnected distally by tertiary veins. Intermediate veins 0–5 per intercostal field, arising from the midvein at $50^\circ - 120^\circ$, running more or less parallel to one another or converging/diverging, the spacing between them constant or increasing distally. The veins similar in width, extending from 0 to $1/4 (- 1/2)$ the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins $(4 -) 10 - 16$ per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopical sides of secondary vein more or less similar. Areoles 95–160 per 10 mm^2 , with some or many free vein-endings, these being unbranched and branched.

Cuticle poorly preserved. Finer veins reflected in cuticle. Internal resinous bodies absent.

Specimens examined: 59, among which the numbered specimens:
 Deutsche Akad. Wiss. Berlin: 293(K 31)
 Geol. Inst. Cologne: Coll. H. Weyland 1385(K 14), reverse side of 1537(KA 35), 1660
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3478B, 3640B, 3677, 3678, 3679, 3680, 3681A, 3682A, 3683, 3684, 3685, 3686, 3687, 3688, 3689, 3690A, 3805A, 3809B, 3911, 3912.

Discussion:

The leaf-remains under consideration were referred to *Carpinus pyramidalis* (Goeppert) Heer (= *Ulmus pyramidalis* Goeppert) by J. Stoller (in QUAAAS, 1910). This binomial is considered to be a synonym for *Ulmus longifolia* Unger (see, e.g. HANTKE, 1953). The generic affinity of the specimens is by no means certain. While not unlike the leaves of some *Ulmus* species in certain respects, a search through the Utrecht herbarium (U) yielded few specimens of *Ulmus* having such an elongate leaf form and none having the large number of secondary veins displayed by the fossil. Dr. R. Melville (personal communication, 1969) is also of the opinion that a reference of the fossil to *Ulmus* is highly unlikely. Closer agreement is to be found with the leaflets of *Rubus illecebrosus* Focke, *Sorbaria arborea* C. Schneider, *S. sorbifolia* (L.) A.Br. and *S. tomentosa* (Lindl.) Rehder (Rosaceae). Not only do the leaflets of these species agree with the fossil in having numerous secondary veins and a similar margin, but also in the presence of a sometimes asymmetrical base. However, the secondary veins of these species very rarely dichotomise (in *Sorbaria* occasionally seen e.g. U. Faurie 577, T.T. Yü 7821) and the leaflets, with the possible exception of the terminal leaflets, are sessile. Thus agreement sufficient to warrant the reference of the fossil to a particular taxon was not met with.

LXVIII

<i>Synonyms</i> : <i>Betula prisca</i> Ett.	WEYLAND, 1934, p. 50 excl. Deutsche Akad. Wiss. Berlin s.n. (K 60)!
<i>Betula subpubescens</i> Goepfert	WEYLAND, 1934, p. 50!
<i>Carpinus grandis</i> Unger	WEYLAND, 1934, p. 52 excl. Coll. H. Weyland 1654, 1655!
<i>Crataegus prunoides</i> Menzel	WEYLAND, 1934, p. 86, Tafel 15, fig. 3!
<i>Sorbus alnoidea</i> Menzel	WEYLAND, 1934, p. 86, Tafel 15, fig. 1!

Description :

Petiole 6–17 mm or more long and 0.4–1.5 mm wide at mid-point, more or less parallel-sided or increasing in width from 0.4–1.2 mm at leaf base to 0.6–2.0 mm wide at base of petiole. Petiole straight or curved, sometimes making a slight angle with the midvein.

Lamina ovate or elliptical, 2.5–8.3 cm long, 1.4–3.7 cm wide, the length/breadth ratio being 1.4 : 1–2.7 : 1 (fig. 48). Leaf apex acute or acuminate, leaf base rarely acute, mostly obtuse, rounded or cordate.

Leaf margin non-entire, serrulate, with acute teeth 0.15–1.6 mm across, 1 per secondary vein and 0–8 per intercostal field, equivalent to c.20–c.65 per side, alternating with acute sinuses. Teeth of one size group or falling into two size groups, the larger teeth being served by secondary veins and the smaller teeth by branches of the secondary veins.

Venation craspedodromous, midvein straight or curved, hardly or markedly tapering along their length, 0.15–0.40 mm wide at mid-point between base and apex of lamina. Midvein bearing 7–14 secondary veins per side, the most proximal vein arising at 30°–120°, arising in the remaining part of the basal third of the lamina at 35°–70°, in the median third at 30°–50°, in the apical third at 35°–60°. The angle at which the veins arise constant or slightly increasing or decreasing within the first few mms. The spacing of the veins reaching a maximum proximally or mid-way (figs. 48–49). The length of the veins reaches a maximum proximally (figs. 48–49). Secondary veins frequently opposite but also alternately arranged in particular in the apical part of the leaf, hardly tapering along their length, 0.035–0.30 mm wide at mid-point, interconnected distally by tertiary veins, or occasionally at the very apex of the lamina by fine extensions of secondary veins. Intermediate veins 0–8 per intercostal field, some or many having a somewhat twisted course, arising from the midvein at 50°–140° (mostly at an obtuse angle), running more or less parallel to one another or converging/diverging, the spacing between them constant or increasing distally. The veins similar in width or increasing in width with increase in length, extending from 0 to 1/10–1/2 (– 2/3 at apex) the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins (3–) 5–17 per 1 cm secondary vein, somewhat or much branched, the

lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 40–140 per 10 mm², with none or few free vein-endings, those which are present being unbranched or less commonly branched.

Epidermis in non-stomatal condition composed of 175 (?) – 340 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3.5 : 1. Cell wall 0.45–1.2 microns thick, finely pitted, straight. Cells over veins elongate, the cell length/cell breadth ratio being up to 6 : 1. Finer veins reflected in cuticle. Epidermis in stomatal condition composed of uncertain number of cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3 : 1. Cell wall 0.2–0.45 microns thick, finely pitted, straight. Cells over veins elongate, the cell length/cell breadth ratio being 2 : 1–6 : 1, cell wall reaching a thickness of 2 microns in the case of larger veins, transverse walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Stomata 12.6–30.6 microns long and 7.2–21.6 (–25.2) microns broad, breadth 44–100 % length, 15–48 per 0.1 mm²; stomatal index unknown. Stomata variously orientated, undepressed, equidistant or somewhat arranged in groups, apices non-retuse. Stomatal slit 41–75 % stomatal length. Accessory cells absent or poorly differentiated, cells in immediate proximity to the stomata up to 6–7 in number, more or less similar in size to or narrower than the rest of the epidermal cells. Internal resinous bodies very rare.

Specimens examined : 102, among which the numbered specimens:
 Deutsche Akad. Wiss. Berlin : 359(K 136), 365(K 137)
 Geol. Inst. Cologne: Coll. H. Weyland 1386(K 32), 1387, 1446
 (K 137), 1465
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot. : 3544B, 3557,
 3558, 3559, 3560, 3561, 3562, 3563, 3564, 3565, 3566, 3567,
 3568, 3569, 3570, 3571, 3572, 3691, 3692, 3693, 3694, 3695,
 3696, 3697, 3698, 3699, 3700, 3701, 3702, 3861, 3862, 3863,
 3864, 3865, 3866, 3868, 3916.

Discussion :

Most of the specimens included here were referred to by H. Weyland as either *Carpinus grandis* Unger or *Betula subpubescens* Goeppert. However, differences in size and length/breadth ratio between these two entities were found to break down and no other distinguishing features were to be noted. The same applies to other specimens referred to various other taxonomic entities. Berlin 365(K 137) described and figured (WEYLAND, 1934, Tafel 15, fig. 1) as *Sorbus alnoidea* Menzel was found to differ from specimens determined as *Carpinus grandis* in having an acute leaf base and teeth of one size group only. Another specimen (Coll. H. Weyland 1446) also proved to be similar, but had a rounded leaf base. Thus both specimens available to the present author had teeth of one size group only. However, a single character difference cannot be considered as a reliable basis on which to uphold this as a separate taxon. Moreover, at the time of his revision WEYLAND (1934) had access to certain material no longer available.

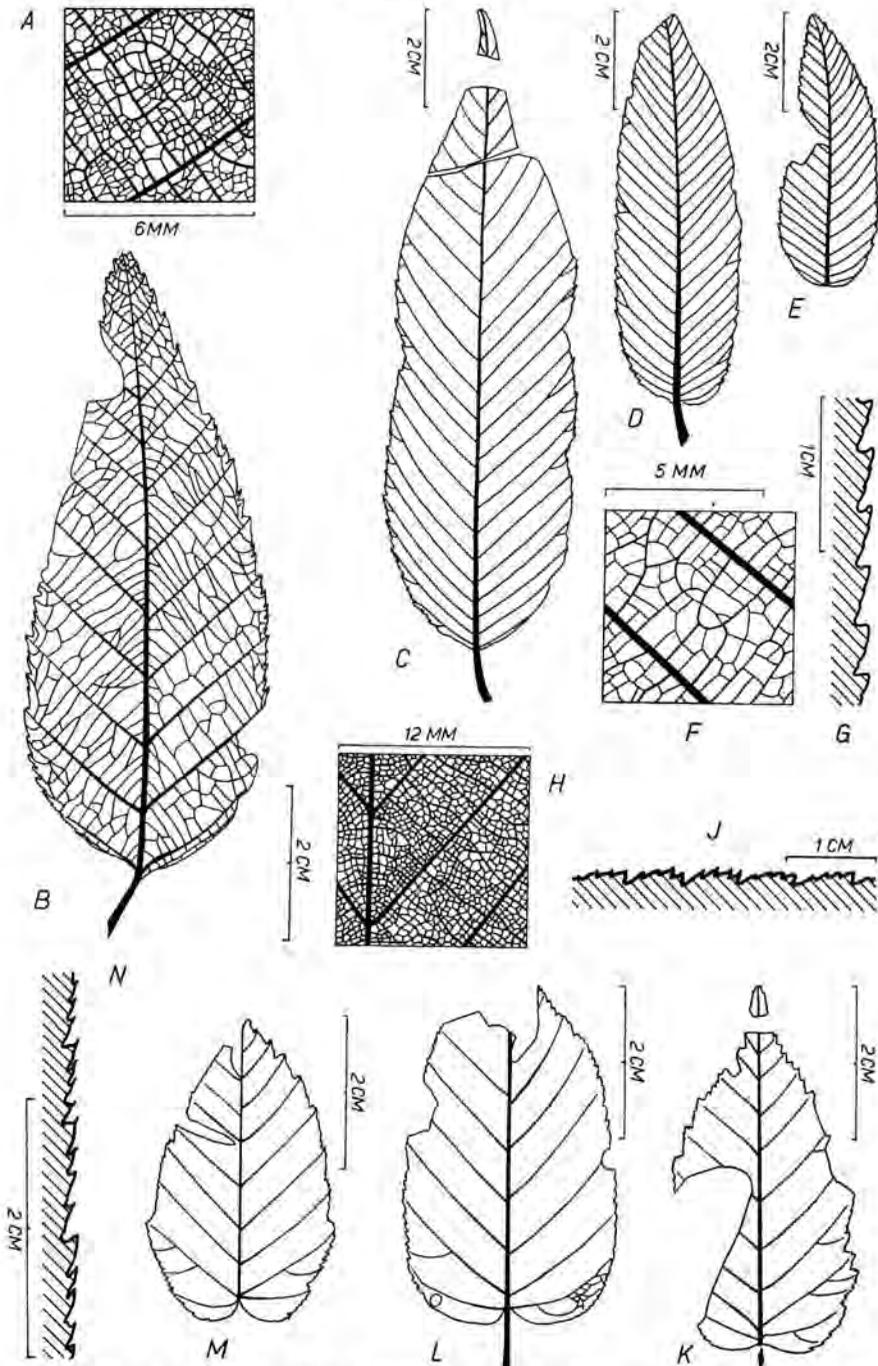
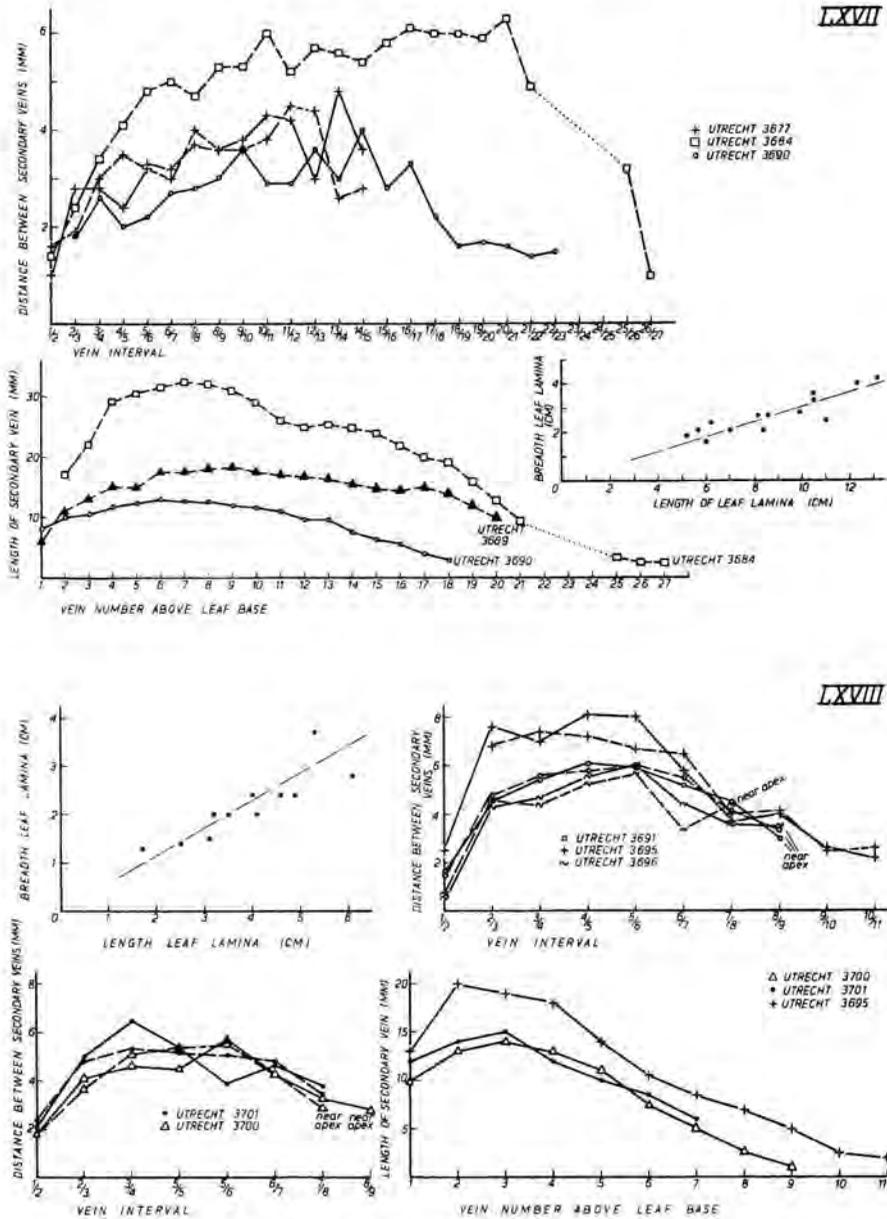


Fig. 47. A-B, H-N = LXVIII: A = Utrecht 3563, detail showing venation; B = Utrecht 3563; H = Utrecht 3696, detail showing venation; J = Utrecht 3696, detail showing leaf margin; K = Utrecht 3691; L = Utrecht 3694; M = Utrecht 3696; N = Utrecht 3563, detail showing leaf margin. C-G = LXVII: C = Utrecht 3684; D = Utrecht 3689; E = Utrecht 3690; F = detail showing venation; G = detail showing leaf margin.

This material would appear to have had teeth falling into two size groups, for WEYLAND (1934, p. 86) described *Sorbus alnoidea* as "doppelt kleingezähnt".

WEYLAND (1934) determined three specimens present in the Berlin collection as *Crataegus prunoides* Menzel. Two of these specimens were seen by the present author. One of these specimens (Berlin s.n. (K 136)) was so poorly preserved that a reference to any of the possible taxa could not be



expected. The other specimen (Berlin 359), which was figured by WEYLAND (1934, Tafel 15, fig. 3) was found to resemble material determined as *Carpinus grandis* Unger. However, this specimen differed from the material referred to *Carpinus grandis* in having a petiole increasing from 1.2 mm wide at the leaf base to 2.0 mm wide at its base. In the other material included here the petiole was 0.4–0.8 mm wide at the leaf base and 0.6–1.4 mm wide at its base. A difference of this nature is of uncertain taxonomic importance, but since it was not paired with any other recognizable difference(s) it was considered better to include the specimen in the present taxonomic entity.

As suggested by the binomials applied by WEYLAND (1934), the leaf-remains most closely resemble leaves or leaflets of members of the Betu-

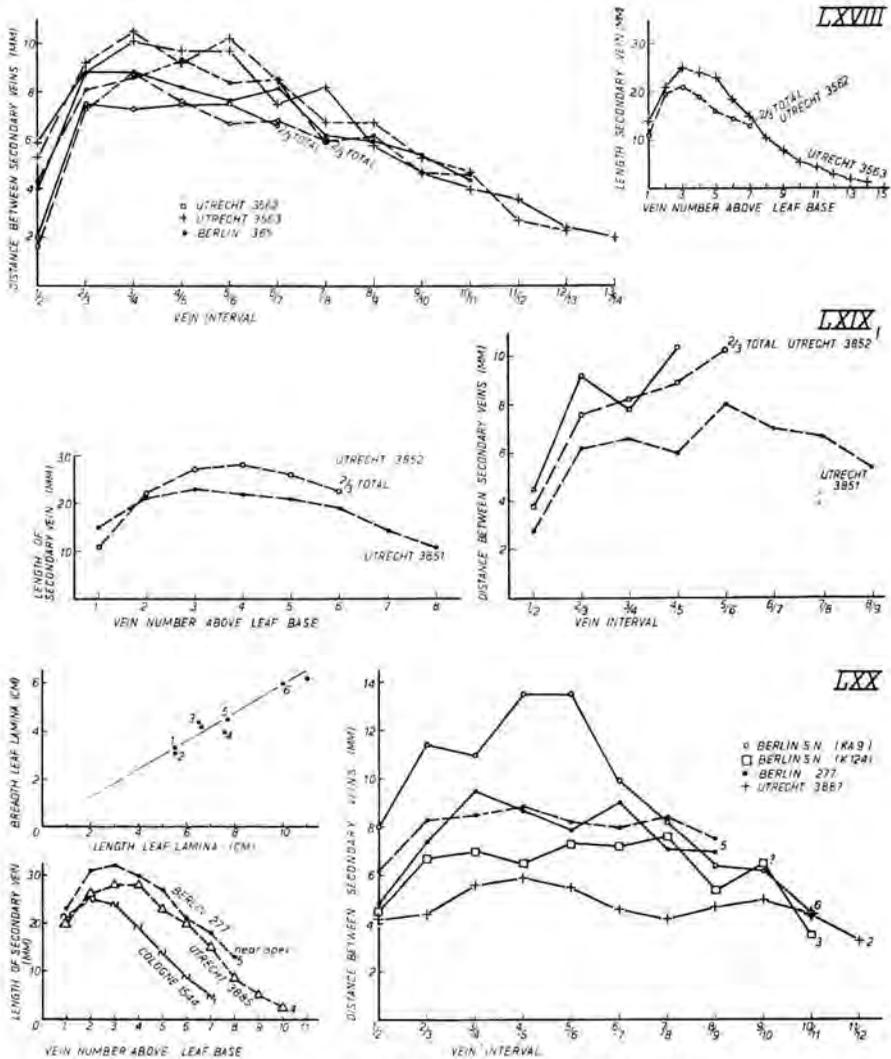


Fig. 49. Graphs LXVIII cont., LXIX, LXX.

laceae and Rosaceae. Certain species of *Acer* (Aceraceae), while having leaves not unlike the leaf-remains in form and venation, were found to be characterized by the presence of numerous free vein-endings.

Of the Betulaceae the leaf-remains most closely resembled the leaves of species belonging to *Betula*, *Carpinus* and *Ostrya*. However, a reference to *Betula* could not be substantiated for a number of reasons. In the first place, the leaves of *Betula* rarely have a cordate leaf base (MEYERHOFF, 1952). Secondly, a complex pattern of vein endings, such as characterizes the leaves of *Betula* (MEYERHOFF, 1952), could not be demonstrated. Finally, whereas certain of the leaf-remains were found to have stomata as small as 12.6 microns long, those of the *Betula* species examined were (20 -) 23-52 microns in length. While a reference to *Betula* had to be ruled out, any possible affinity between *Ostrya* and the leaf-remains under consideration had to be dismissed as well. The leaves of *Ostrya* species are characterized by a strong development of "external veins" (MEYERHOFF, 1952) i.e. veins arising from the secondary veins and curving to join the leaf margin. While such "external veins" may be present in the leaves of certain species of *Carpinus* as well, other *Carpinus* species have only a few poorly developed "external veins". In this respect and in the presence of simple free vein-endings *Carpinus* leaves show a greater affinity to the leaf-remains than any other members of the Betulaceae.

However, although a resemblance to *Carpinus* can be demonstrated, a reference of the leaf-remains to this genus cannot be accepted with absolute certainty. Members of the Rosaceae e.g. various *Crataegus*, *Rubus*, and *Sorbus* species have leaves or leaflets, which are very similar to the leaf-remains. In the absence of a detailed study dealing with the occurrence and nature of such leaves and leaflets within the Rosaceae, a possible reference of the leaf-remains to this family must be borne in mind.

Herbarium material examined in detail:

<i>Acer carpiniifolium</i> Sieb. et Zucc.	Coll. K. Okamoto 18-6-1951 (Nat. Sci. Mus. Tokyo 272)	(E) _____
	Coll. U. Faurie 3854	(E) _____
<i>Acer davidii</i> Franch.	Coll. G. Forrest 10045	(E) det. W. P. Fang
	Coll. W. P. Fang 2369	(E) det. W. P. Fang
<i>Acer forrestii</i> Diels	Coll. G. Forrest 11226	(E) det. W. P. Fang
<i>Acer ginnalum</i> Maxim.	Coll. C. Y. Chiao 2948	(E) det. W. P. Fang
	Coll. C. S. Fan & Y. Y. Li 111	(E) _____
<i>Acer hookeri</i> Miq.	Coll. F. Ludlow, G. Sherriff & G. Taylor 7007	(E) _____
<i>Acer laxiflorum</i> Pax	Coll. W. C. Cheng 1496	(E) det. W. P. Fang
<i>Acer morifolium</i> Koidzumi	Coll. M. Tagawa & F. Konta 12	(E) _____
<i>Acer stachyophyllum</i> Hieron.	Coll. W. P. Fang 4514	(E) det. W. P. Fang

<i>Acer tataricum</i> L.	Coll. V. Střibrný 17-6-1899	(E) _____
	Coll. P. H. Davis & I. C. Hedge D 32859	(E) det. A. Pojarkova
	Coll. F. C. Crawford 7	(E) _____
<i>Acer tetramerum</i> Pax	Coll. W. P. Fang 10017	(E) det. W. P. Fang
	Coll. W. Purdom 793	(E) det. W. P. Fang
	Coll. G. Forrest 30462	(E) det. W. P. Fang
<i>Betula alnoides</i> Ham.	Coll. G. Forrest 29410	(E) _____
<i>Betula chinensis</i> Maxim.	Coll. E. H. Wilson 8677	(E) _____
<i>Betula delavayi</i> Franch.	Coll. G. Forrest 28728	(E) _____
<i>Betula insignis</i> Franch.	Coll. W. C. Cheng 1745	(E) _____
<i>Betula luminifera</i> Winkl.	Coll. G. Forrest 28691	(E) _____
<i>Betula nigra</i> L.	Coll. H. E. Ahles & J. McNeely 53348	(U) _____
<i>Betula utilis</i> D. Don	Coll. G. Forrest 19505	(E) det. W. E. Evans
<i>Carpinus austrosinensis</i> Hu	Coll. Y. Tsiang 7470	(E) det. H. H. Hu
<i>Carpinus cordata</i> Blume	Coll. E. H. Wilson 508	(E) _____
<i>Carpinus fangiana</i> Hu	Coll. W. P. Fang 1935	(E) _____
<i>Carpinus handelii</i> Rehder	Coll. Handel-Mazzetti 20-5-1918	(E) det. A. Rehder
<i>Carpinus henryi</i> Winkl.	Coll. E. H. Wilson 645	(E) _____
<i>Carpinus kweichowensis</i> Hu	Coll. Y. Tsiang 4638	(E) det. H. H. Hu
<i>Carpinus kweitingensis</i> Hu	Coll. A. N. Steward, C. Y. Chiao & H. C. Cheo 71	(E) _____
<i>Carpinus londoniana</i> Winkl.	Coll. G. Forrest 26622	(E) _____
<i>Carpinus mollis</i> Rehder	Coll. W. P. Fang 4245	(E) _____
<i>Carpinus monbeigiana</i> Handel-Mazzetti	Coll. Handel-Mazzetti 3431	(E) det. Handel-Mazzetti
<i>Carpinus polyneura</i> Franch.	Coll. S. S. Chien 5671	(E) _____
<i>Carpinus seemeniana</i> Diels	Coll. H. C. Chow 1486	(E) _____
<i>Carpinus tschonoskii</i> Maxim.	Coll. R. C. Ching 3219	(E) _____
<i>Carpinus tsiangiana</i> Hu	Coll. Y. Tsiang 8610	(E) det. H. H. Hu
<i>Carpinus tungtzensis</i> Hu	Coll. Y. Tsiang 5440	(E) det. H. H. Hu
<i>Carpinus turezaninowii</i> Hance	Coll. C. Y. Chiao 3071	(E) det. A. Rehder
<i>Carpinus viminea</i> Wall.	Coll. Handel-Mazzetti 7876	(E) det. Handel-Mazzetti
<i>Rubus acuminatus</i> Sm.	Coll. G. Forrest 15976	(E) det. Handel-Mazzetti
<i>Rubus corchorifolius</i> Linn. f.	Coll. G. Forrest 7613	(E) det. W. E. Evans
<i>Rubus macilentus</i> Cambess.	Coll. G. Forrest 11927	(E) det. Handel-Mazzetti
<i>Rubus thunbergii</i> Sieb. et Zucc.	Herb. H. Lèveillé	(E) det. A. Rehder
<i>Sorbus caloneura</i> (Stapf) Rehder	Coll. Handel-Mazzetti 11226	(E) det. Handel-Mazzetti
	Coll. Handel-Mazzetti 11227	(E) det. Handel-Mazzetti
	Coll. K. L. Chu 2910	(E) _____
	Coll. K. L. Chu 3201	(E) _____
	Coll. E. H. Wilson 348	(E) _____
<i>Sorbus zahlbruckneri</i> C. Schneider	Coll. E. H. Wilson 1980	(E) _____

LXIX

Description:

Petiole unknown.

Lamina elliptical, c.5.5–6.5 cm long, 3.2–4.0 cm wide. Leaf apex unknown, leaf base rounded or slightly cordate, sometimes asymmetrical.

Leaf margin non-entire, biserrulate, with acute teeth 0.3–1.5 mm across, c.35–c.50 per side, alternating with acute sinuses.

Venation craspedodromous, midvein straight or curved, somewhat tapering along length, 0.15–0.25 mm wide at mid-point between base and apex of the lamina. Midvein bearing c.8–c.10 secondary veins per side, the most proximal vein arising at 50°–60°, arising in the remaining part of the basal third of the lamina at 45°–60°, in the median third at 45°–60°, in the apical third at 45°–50°. The angle at which the veins arise generally constant, although occasionally increasing or decreasing within the first few mms. The spacing of the veins reaches a maximum mid-way or in the apical half of the lamina (fig. 49). The length of the veins greatest proximally or mid-way along the lamina (fig. 49). Secondary veins opposite or alternately arranged, hardly tapering along their length, 0.07–0.20 mm wide at mid-point, interconnected distally by tertiary veins. Intermediate veins 1–9 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 80°–135°, running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width, extending from 0 to 1/5–1/3 the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 7–14 per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 85–100 per 10 mm², with none or few free vein-endings.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of c.650 (?) cells per 0.1 mm², the cell length/cell breadth ratio being 1:1–2:1. Cell wall 0.3–0.45 microns thick, largely unpitted, more or less straight. Cells over veins elongate. Finer veins reflected in cuticle. Stomata 12.6–19.8 microns long and 9–18 microns broad, breadth 50–114 % length, apparently < 5 per 0.1 mm²; stomatal index unknown. Stomata variously orientated, undepressed, apices non-retuse. Stomatal slit 60–93 % stomatal length. Accessory cells apparently absent. Internal resinous bodies absent.

Specimens examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3851, 3852

LXX

Synonyms: *Betula brongniartii* Ett.

WEYLAND, 1934, p. 50, Tafel 5, fig. 3;

GOTHAN and WEYLAND, 1964,

p. 410, Abb. 283k!

Betula macrophylla (Goepfert) Heer

WEYLAND, 1934, p. 50 pro parte!

Stephanandra rhenana Weyland

WEYLAND, 1934, p. 85, Tafel 15,

fig. 2!

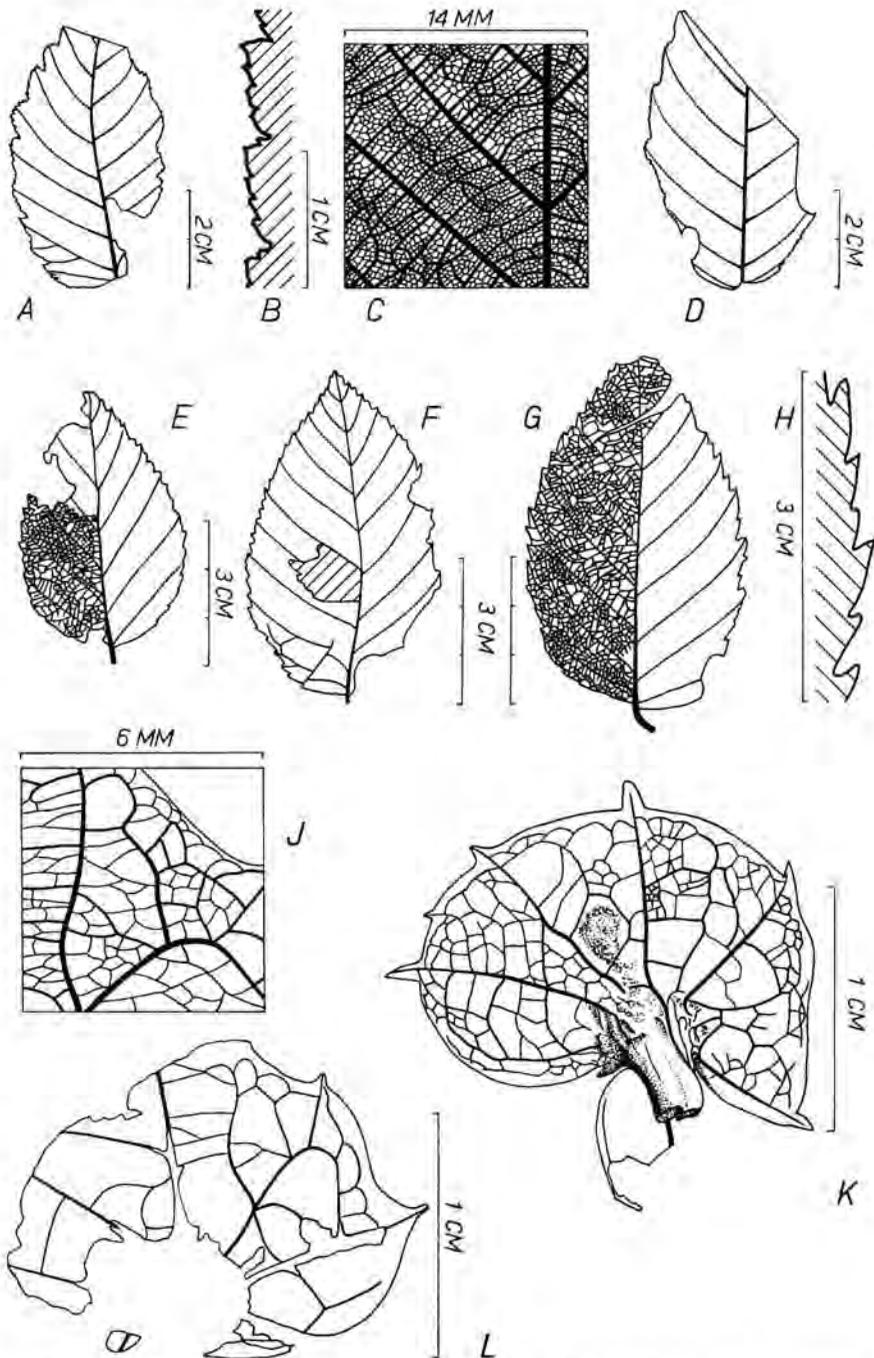


Fig. 50. A-D = LXIX: A = Utrecht 3851; B = detail showing leaf margin; C = detail showing venation; D = Utrecht 3852. E-H = LXX: E = Cologne, Coll. H. Weyland 1544; F = Cologne, Coll. H. Weyland 1375; G = Berlin 277; H = detail showing leaf margin. J-L = LXXI: J = Utrecht 3843, detail showing venation; K = Utrecht 3844; L = Utrecht 3843.

Description :

Petiole > 4–16 mm long and 0.8–1.4 mm wide at mid-point, gradually increasing in width throughout length or parallel-sided and markedly expanded near base of petiole, where the width is 1.3–2.5 mm. Petiole straight or markedly curved, sometimes making an angle with the midvein.

Lamina ovate, 5.5–c.11 cm long, 3.1–6.2 cm wide, the length/breadth ratio being 1.4:1–1.8:1 (fig. 49), sometimes asymmetrical. Leaf apex acute, leaf base obtuse or rounded, sometimes oblique.

Leaf margin non-entire, \pm serrulate, with acute (rarely rounded) teeth 0.2–1.9 mm across, 1 per secondary vein and 0–4 (–5) per intercostal field, equivalent to 25–55 per side, alternating with acute or angular (rarely rounded) sinuses. Teeth fall into two size groups, the larger triangular-shaped teeth served by secondary veins and the smaller triangular or step-like ones by branches of the secondary veins.

Venation craspedodromous, midvein straight or curved, hardly or markedly tapering along length, 0.25–0.65 mm wide at mid-point between base and apex of the lamina. Midvein bearing 7–12 secondary veins per side, the most proximal vein arising at 45° – 70° , arising in the remaining part of the basal third of the lamina at 40° – 65° , in the median third at 35° – 60° , in the apical third at 35° – 60° . The angle at which the veins arise sometimes increasing in proximal part of the lamina but generally constant or slightly decreasing within the first few mms. The spacing of the secondary veins more or less constant or reaching a maximum mid-way (fig. 49). The length of the veins reaching a maximum proximally to mid-way (fig. 49). Secondary veins opposite or alternately arranged, hardly or slightly tapering along their length, 0.08–0.40 mm wide at mid-point, occasionally dichotomising in the median third of the lamina mid-way between the midvein and the leaf margin, the veins interconnected distally by tertiary veins or vein network. Intermediate veins 1–8 per intercostal field, occasionally having a somewhat twisted course, arising from the midvein at 50° – 135° , running more or less parallel to one another or converging/diverging, the spacing between them constant, increasing distally or irregular. The veins similar in width, extending from 0 to $1/6$ – $1/2$ (rarely $1/2$ – $3/4$ near apex) the distance from the midvein to the leaf margin, reaching their greatest length in intercostal field mid-way or distally. Tertiary veins 3–9 per 1 cm secondary vein, somewhat or much branched, the lengths on acroscopic and basiscopic sides of secondary vein more or less similar. Areoles 20–c.90 per 10 mm^2 with none or some free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of 270–300 cells per 0.1 mm^2 , the cell length/cell breadth ratio being 1:1–3.5:1. Cell wall 1.0–1.5 microns thick, largely unpitted, straight. Cells over veins elongate, the cell length/cell breadth ratio being 1:1–7:1, the transverse walls slanting or at right angles to the lateral walls. Finer veins reflected in cuticle. Stomata 19.6–25.2

microns long and 15.4–22.4 microns broad, breadth 78–88 % length, < 10 per 0.1 mm²; stomatal index uncertain. Stomata variously orientated, undepressed. Stomatal slit 57–78 % stomatal length. Accessory cells apparently absent. Internal resinous bodies apparently absent.

Specimens examined: 15, among which the numbered specimens:
Deutsche Akad. Wiss. Berlin: 277(K 124), s.n.
Geol. Inst. Cologne: Coll. H. Weyland 1375(K 124), 1544(KA 9), 1657
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3884, 3885, 3886A, 3887

Discussion:

A re-examination of the holotype of *Stephanandra rhenana* Weyland and material referred to *Betula brongniartii* Ett. and *B. macrophylla* (Goepfert) Heer by H. Weyland, proved that these were incapable of being separated from one another on the basis of the characters made use of in the present study.

While WEYLAND (1934, p. 85) considered one of the specimens included in the present description (Berlin s.n.) to resemble the leaf of a *Stephanandra*, a reference of this or other specimens to *Stephanandra* would seem unlikely. *Stephanandra* (Rosaceae) is a genus with 3–4 living species (WILLIS, 1960; Schulze-Menz in ENGLER, 1964). The leaves of three species have been examined by the present author. While the leaves of *Stephanandra chinensis* Hance and *S. incisa* (Thunb.) Zabel often have a simple outline, the leaves of *Stephanandra tanakae* Franch. et Sav. are invariably palmate in form. The leaf margin in all species is doubly serrate and in this respect resembles that of the fossil leaf. However, the major teeth terminating each secondary vein are either recurved or when minor teeth are developed on the acroscopic side of these teeth such minor teeth do not project apically, as in the fossil, but converge on the major teeth.

While no evidence could be found for a reference to *Stephanandra*, a fairly close resemblance exists between the leaf-remains and leaves of certain *Betula* species. Both have a midvein which is frequently crooked and a non-cordate leaf base sometimes running parallel to the most proximal secondary vein (see MEYERHOFF, 1952). None the less a reference to *Betula* (Betulaceae) could not be ratified, as the leaf-remains also proved to be similar to the leaves of a number of taxa belonging to the Rosaceae. The leaves of certain specimens of *Rhodotypus kerrioides* and the leaflets of a number of species of *Rubus* resemble the fossil fairly closely. However, of all the taxa of the Rosaceae examined the closest resemblance would appear to be with the leaves of certain specimens of *Sorbus folqneri* (C. Schneider) Rehder. While the lower epidermis of this and other species belonging to the Rosaceae are distinguishable from that of *Betula*, the only cuticle preparation obtained from the leaf-remains was insufficiently preserved to permit identification.

Herbarium material examined in detail:

Betula alnoides Ham.	Coll. G. Forrest 29410	(E)	_____
Betula chinensis Maxim.	Coll. E. H. Wilson 8677	(E)	_____
Betula delavayi Franch.	Coll. G. Forrest 28728	(E)	_____
Betula insignis Franch.	Coll. W. C. Cheng 1745	(E)	_____
Betula luminifera Winkl.	Coll. G. Forrest 28691	(E)	_____
Betula nigra L.	Coll. H. E. Ahles & J. McNeely 53348	(U)	_____
Betula utilis D. Don	Coll. G. Forrest 19505	(E)	det. W. E. Evans
Rhodotypos kerrioides	Coll. E. H. Wilson 1797	(E)	_____
Sieb. et Zucc.	Coll. E. H. Wilson 3345	(E)	_____
Rubus corchorifolius Linn. f.	Coll. G. Forrest 7613	(E)	det. W. E. Evans
Rubus macilentus Cambess.	Coll. G. Forrest 11927	(E)	det. Handel- Mazzetti
Rubus thunbergii Sieb. et Zucc.	Herb. H. Léveillé	(E)	det. A. Rehder
Sorbus folgeneri (C. Schneider) Rehder	Coll. N. K. Ip 25-6-1922 (Herb. Univ. Nanking 1808)	(E)	det. E. D. Merrill
Stephanandra chinensis Hance	Coll. W. P. Fang 2177	(E)	_____
	Coll. E. H. Wilson 1724	(E)	det. A. Rehder
	Coll. R. C. Ching 1655	(E)	_____
	Coll. C. S. Fan & Y. Y. Li 30	(E)	_____
	Coll. A. N. Steward 7-7-1922 (Herb. Univ. Nanking 2445)	(E)	det. E. D. Merrill
Stephanandra incisa (Thunb.) Zabel	Coll. C. Y. Chiao 2644	(E)	det. A. Rehder
	Coll. R. Moran 4271	(E)	det. E. H. Walker
	Coll. E. H. Wilson 8607	(E)	_____
	Coll. U. Faurie 320	(E)	_____
	Coll. U. Faurie 1564	(E)	_____
	Coll. E. Taquet 1457	(E)	_____
	Coll. E. Taquet 2805	(E)	_____
	Coll. S. Kobayashi 28-6-1959 (Makino Herb. 16329)	(E)	det. M. Mizushima
	Coll. T. Matsuoka 6-7-1951 (Nat. Sci. Mus. Tokyo 359)	(E)	_____
	Coll. H. Kubota 10-5-1953 (Nat. Sci. Mus. Tokyo 678)	(E)	_____
Stephanandra tanakae Franch. et Sav.	Coll. N. Fukuoka 6741	(E)	_____
	Coll. M. Togasi 24-6-1951 (Nat. Sci. Mus. Tokyo 366)	(E)	_____
	Coll. P. H. Dorsett & W. J. Morse 802	(E)	det. E. H. Walker
	Coll. H. Sakurai 19-1-1911	(E)	_____

LXXI

Description:

Stipule kidney-shaped, 1.2–1.3 cm long, 1.7–1.8 cm wide, the length/breadth ratio being 0.7 : 1. Veins, 5 in number, radiating from point of

attachment, these veins straight, slightly curved or somewhat sinuous, somewhat tapering along length, 0.07–0.20 mm wide mid-way along length, ending in apiculate projections, 0.2–1.6 mm long. Cuticle unknown, obscured by a thick layer of mesophyll. Internal resinous bodies absent.

Specimens examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3843, 3844

CLASS MONOCOTYLEDONEAE

In his account of the Kreuzau assemblage WEYLAND (1934) referred 4 taxa to the Monocotyledoneae. One of the taxa he mentioned, *Cyperites* sp. has had to be excluded in the present account, since no specimens were available and no description given. The material which H. Weyland referred to as *Typha latissima* A. Braun and *Phragmites oeningensis* A. Braun is here united into a single taxon. Another specimen described as *Smilax grandifolia* is relegated to the *Incertae Sedes*, while material originally referred to the Dicotyledoneae, *Melastomites menzelii* Weyland, is considered to be a member of the Liliaceae. Two additional taxa are described in the present account.

FAMILY LILIACEAE

SUBFAMILY SMILACOIDEAE

LXXII

Description:

Petiole unknown.

Lamina ovate, > 6 cm long, 5.8 cm wide. Leaf apex unknown, leaf base truncate.

Leaf margin entire.

Venation acrodromous or campylodromous, primary veins 3. Lateral primary veins arising at c.45° from the central primary vein at the leaf base; these lateral primary veins 0.15 mm wide at mid-point along their length. The lateral primary veins give rise on their basiscopic side to higher order veins. Central primary vein gently curved throughout length, somewhat tapering along length, 0.5 mm wide at mid-point between base and apex of the lamina. Secondary veins may be present distally, but their presence could not be proven. Higher order veins present between the central primary and the lateral primary veins numerous, arising from the central primary vein at 45°–90°. The nature of the areoles and free vein-endings unknown.

Epidermis in non-stomatal condition composed of 50–60 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall 1.0–3.0 microns thick, more or less unpitted, strongly undulating with 6–12 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses 3–20 microns. Cells over veins elongate with a cell length/cell breadth ratio of 3 : 1–4 : 1 and only slightly undulating. Finer veins not reflected in cuticle. Cells at leaf margin up to 170 per 0.1 mm², the cell length/cell

breadth ratio being 1.5 : 1–5.0 : 1, sometimes arranged in up to 10 rows, cell wall 1.5–2.0 microns thick, hardly pitted, more or less straight. Epidermis in stomatal condition composed of c.55 cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–2 : 1. Cell wall 0.8–2.2 microns thick, slightly pitted, strongly undulating with 6–8 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses 6–31 microns. Cells over the veins elongate, less undulate than the surrounding cells. Finer veins not reflected in cuticle. Stomata 14.4–21.6 microns long and 9.9–21.6 microns broad, breadth 61–109 % length, 0–4 per 0.1 mm²; stomatal index 8 % and less. Stomata variously orientated, undepressed, more or less equidistant, with thickened epidermal wall to the guard cells, apices non-retuse. Stomatal slit 50–83 % stomatal length, poral wall of the guard cells unthickened. Accessory cells 0 (–4), when present symmetrical with 2 polar cells and 2 lateral cells, similar in size to the rest of the epidermal cells.

Specimen examined: Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3535A

Discussion:

Similar leaves with large, markedly undulate, epidermal cells, having stomata without any specialized accessory cells, in combination with an acrodromous or campylodromous venation pattern, and higher order veins between the central primary and the lateral primary veins arising at an acute angle are to be found in species of *Smilax* growing at the present day. While the epidermal features would appear to be fairly uniform within the genus, *Smilax laurifolia* L. with its coarse striae, *S. pumila* Walt. with its multicellular hairs and *S. glauca* Walt. which has papillose cells, were found to differ from the rest of the species examined. In their work on *Smilax* PENNELL (1916), APT (1922), KOYAMA (1960), MORTON (1962) and MANGALY (1968) have made use of vegetative characters in delineating species. Characters such as the shape of the leaf, the number of primary veins, the presence or absence of pubescence, the nature of the leaf apex and leaf base, and the relative length of the petiole and lamina have been used to differentiate species. However as PENNELL (1916) and MANGALY (1968) pointed out, such characters are ecologically plastic and characters made use of in studies simply based on herbarium material may be found to break down when the species are examined in the field. Leaf shape has been found to vary not only on different individuals of the same species, but on the same plant, depending on its location on the plant, and also among plants of different ages. Thus in the absence of more comparative material it was not considered possible to refer the fossil to a specific entity. In addition, while the limited material of *Heterosmilax* available to the author (2 of the 5–15 species) did not resemble the fossil in gross-morphology, it was considered wiser to resist a reference to *Smilax* in the light of the variability encountered in the leaves of *Smilax* species and probably species of *Heterosmilax* as well. These two genera could not be distinguished on the basis of their epidermides.

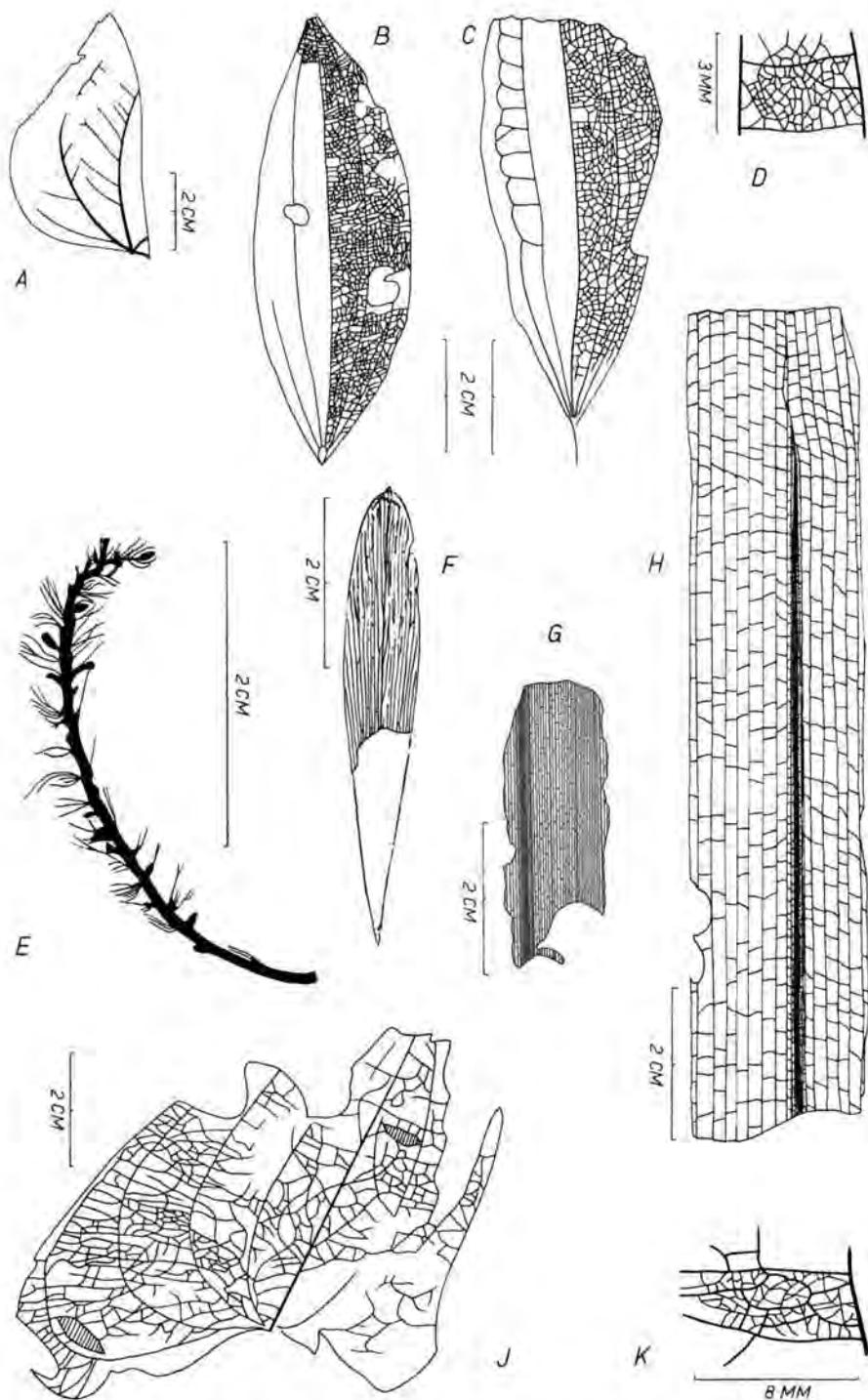


Fig. 51. A = LXXII: Utrecht 3535 A (drawing based on specimen and its counterpart). B-D = LXXIII: B = Berlin 278 (Type of *Melastomites menzelii* Weyland); C = Cologne, Coll. H. Weyland 2021; D = Berlin 278, detail showing venation. E = LXXVII: Cologne s.n. (drawing based on specimen and its counterpart). F = LXXV: Cologne s.n. G-H = LXXVI: G = Utrecht 3755; H = Utrecht 3746 A. J-K = LXXIV: J = Berlin 495; K = Berlin 495, detail showing venation.

Herbarium material examined in detail:

Heterosmilax chinensis Wang	Coll. Wang & Tang 22855	(E)	det. F. T. Wang HOLOTYPE
Heterosmilax gaudichan- diana (Kunth) Rehder	Coll. E. Bodinier 731	(E)	det. A. Rehder
Smilax china L.	Coll. E. Taquet 3306	(E)	det. Wang & Tang
Smilax discotis Warb.	Coll. J. F. Rock 4718	(E)	det. W. E. Evans
Smilax ferox Wall.	Coll. G. Forrest 3099	(E)	det. Wang & Tang
Smilax flaccida C. H. Wright	Coll. A. Henry 3630B	(E)	_____
Smilax glauca Walt.	Coll. H. E. Ahles 34411	(U)	_____
Smilax glauca-china Warb.	Coll. C. Y. Chiao 14064	(E)	det. E. D. Merrill
Smilax havanensis Jacq.	Coll. J. K. Small 7460	(U)	_____
Smilax herbacea L.	Coll. J. R. Bozeman, A. E. Radford & D. Culwell 10676	(U)	_____
Smilax hispida Muhl.	Coll. J. R. Bozeman 9166	(U)	_____
Smilax laurifolia L.	Coll. A. E. Radford 15576	(U)	det. H. E. Ahles
Smilax mairei Lévl.	Coll. E. E. Maire s.n.	(E)	det. H. Lévillé TYPE
Smilax ovalifolia Roxb.	Coll. H. Fung 20128	(E)	det. E. D. Merrill
Smilax pumila Walt.	Coll. H. E. Ahles & J. G. Haesloop 53100	(U)	_____
Smilax rigida Wall.	Coll. G. Forrest 20247	(E)	det. W. E. Evans
Smilax rotundifolia L.	Coll. H. E. Ahles & C. R. Bell 16780	(U)	_____
Smilax smallii Morong.	Coll. H. E. Ahles & J. G. Haesloop 53099	(U)	_____
Smilax vaginata Decne.	Coll. Handel-Mazzetti 1601	(E)	det. Handel- Mazzetti

LXXIII

<i>Synonyms</i> : <i>Maianthemophyllum petiolatum</i> Weber	WEYLAND, 1948, Tafel 18, Abb. 6!
<i>Melastomites menzelii</i> Weyland	WEYLAND, 1934, pp. 105-107, Abb. 8!

Description :

Petiole > 8 mm long and 0.7 mm wide, straight, making no angle with the central primary vein.

Lamina elliptical, 8.0-c.10 cm long, 2.4-3.1 cm wide, the length/breadth ratio being 2.9 : 1 or more. Leaf apex acute, leaf base acute.

Leaf margin entire.

Venation campylodromous, primary veins 5. Primary veins arising simultaneously at leaf base from rounded extremity, 1.5 mm in diameter, of petiole, each vein making an angle of 15° with the neighbouring vein(s). Central primary vein more or less straight, slightly tapering along length, 0.15-0.25 mm wide at leaf base, 0.10-0.15 mm wide at mid-point between base and apex of lamina. Lateral primary veins immediately adjoining the central primary vein extend over the entire length of the leaf and are 0.10-0.20 mm wide at leaf base and 0.05-0.15 mm wide at mid-point be-

tween base and apex of the lamina. The outer pair of primary veins, which extend for 30–60 % of the length of the leaf before becoming somewhat irregular (outwardly arched) in course are 0.05–0.10 mm wide at leaf base and 0.025 mm wide at mid-point between base and apex of the lamina. Higher order veins present between the primary veins, 4–7 per 1 cm primary vein. Areoles 5–13 per 10 mm², with some unbranched free vein-endings.

Epidermis poorly preserved. Cells at leaf margin c. 600 (?) per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–5 : 1, arranged in 10–15 rows. Cell wall 1–2 microns thick, largely unpitted, straight.

Specimens examined : Deutsche Akad. Wiss. Berlin: 278

Geol. Inst. Cologne: Coll. H. Weyland 2021

Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3475A, 3476

Discussion :

In its gross-morphology the fossil resembles the leaves of a number of dicotyledonous and monocotyledonous taxa.

The first of the leaf-remains to be included here was found just prior to the publication of Weyland's revision of the Kreuzau assemblage. WEYLAND (1934, pp. 105–107) referred the specimen to a new species of *Melastomites*, *M. menzelii*. While he pointed out that the inclusion of the fossil within this genus does not automatically infer the presence of a member of the Melastomataceae, he considered the leaves of certain members of the Melastomataceae to show the closest resemblance to the fossil. A few comments and a discussion of possible alternatives would seem to be in place.

Members of the Melastomataceae often have ovate or elliptical leaves, an acute leaf base and the development of a reticulum between the primary veins. Of the woody species of the Melastomataceae from Florida and China seen by the author the leaves of *Osbeckia crinita* Bentham, *O. stellata* Buch.-Ham. ex D. Don, *Blastus cochinchinensis* Lour. and *Plagiopetalum serratum* Diels most closely resembled the leaf-remains. In *Osbeckia crinita* and *O. stellata*, however, hairs are present on both surfaces of the lamina and the leaf margin is sometimes markedly ciliate. Furthermore, in forms bearing five or more primary veins the outer primary veins are not outwardly arched between the successive higher order veins, interconnecting the primary veins in the distal half of the lamina. The same applies to the leaves of *Blastus cochinchinensis*. In the leaves of *Plagiopetalum serratum* bearing 5 primary veins this outward arching of the outer pair of primary veins may be moderately well developed. However, the leaf margin in this species is non-entire and slightly ciliate.

Saururus chinensis (Lour.) Baill. (Saururaceae) has leaves similar to the fossil ones in the nature of their venation. The leaves have 3–7 primary veins, show well-developed arching of the outer pair of primary veins and the presence of a vein reticulum. However, this species can be dismissed as a possibility, since the leaves have a truncate or cordate leaf base.

WEYLAND (1934, p. 106) briefly mentioned the fact that leaves similar to the present taxon are to be found in the Monocotyledons. He mentioned the leaves of *Potamogeton* (Potamogetonaceae) as an example, but dismissed these on the basis of their often numerous primary veins and the fact that the higher order veins, present between the primary veins, are unbranched.

Leaves resembling the leaf-remains to some extent are to be found in members of the Stemonaceae, Hydrocharitaceae, Dioscoreaceae and Liliaceae.

Although otherwise similar to the fossil the leaves of *Stemona vagula* W. W. Smith (Stemonaceae) did not display a vein reticulum as a result of the presence, between the primary veins, of closely spaced higher order veins.

In the leaves of *Ottelia polygonifolia* (Gagnep.) Dandy (Hydrocharitaceae) the vein reticulum is only poorly developed and when 5 primary veins are present no development of the arching of the outer pair of primary veins, so characteristic of the fossil, is to be observed.

While the leaves of many species of *Dioscorea* (Dioscoreaceae) are heart-shaped, those of *Dioscorea benthamii* Pr. et Burk. are lanceolate. The leaves of this species have only 3-5 primary veins. When 5 primary veins are developed, the outer pair show no tendency to be arched.

Of the Liliaceae examined the leaves of *Heterosmilax chinensis* Wang and *Smilax flaccida* C. H. Wright were found to resemble the fossil most closely. While the material of *Heterosmilax chinensis* had only 3 primary veins, it is possible that the number of primary veins may vary, as is the case in certain *Smilax* species (see PENNELL, 1916). Those leaves of *Smilax flaccida* examined were ovate and with an obtuse leaf base. The lamina was traversed by 5 primary veins of which the outermost pair showed a marked tendency to be arched. Of the material examined these leaves approximated most closely to the leaf-remains under consideration. While WEYLAND (1934, p. 106) dismissed *Smilax* and other members of the Liliaceae from consideration, on the grounds of their poorly developed fine venation, an examination of the photograph of the specimen he referred to *Melastomites menzelii* proves that the fine venation is by no means strongly impressed. Material collected later on (Coll. H. Weyland 2021) and referred to *Maianthemophyllum petiolatum* Weber was only found to differ from the type material of *Melastomites menzelii* (Deutsche Akad. Wiss. Berlin 278) in its larger lamina (3.1 cm wide as opposed to 2.8 cm). The difference in degree to which the vein reticulum was developed in these two specimens was found to be insignificant. *Maianthemophyllum* was a generic name proposed in 1851 by WEBER (1851-2, p. 156) for leaf-remains similar to the leaves of *Smilax* and related taxa ("Folia petiolata ovata plurinervia foliis Smilacinarum similis"). *Maianthemophyllum petiolatum* Weber, the type species, was diagnosed as follows: "M. foliis petiolatis ovatis integerrimis crassiusculis, nervis primariis quinque strictis parallelis, nervulis

transversis scalaribus inter se conjunctis ad apicem convergentibus (?).” The diagnosis of *Melastomites menzelii* given by WEYLAND (1934, p. 107) was the following: “Blätter lanzettlich-oval, beiderseits zugespitzt, ganzrandig; mit sieben von der Basis ausgehenden geraden, unverzweigten Hauptnerven, von denen die beiden äusseren Paare die Blattspitze nicht erreichen, sondern sich in den äusseren Bogen von Sekundärnerven der inneren Hauptnerven fortsetzen; mit mehr oder weniger zum Hauptnerven senkrechten, dicht stehenden und sich weiter verästelnden Queranastomosen.” Apparent differences in the number and longitudinal extension of the primary veins existing in these diagnoses proved to be insignificant. The outermost pair of veins mentioned by Weyland as present in *Melastomites menzelii* hardly seem worth considering as primary veins as these only extend for a very short distance before petering out. On the other hand, although Weber considered that the five primary veins of *Maianthemophyllum petiolatum* all extended over the entire length of the lamina (see his reconstruction on Tafel 18, fig. 5b), his drawing of the type material (Tafel 18, fig. 5a) indicates that the distal half of the lamina was missing. Moreover, the leaf, contrary to what is stated in the diagnosis, was in all probability elliptical. *Maianthemophyllum petiolatum* Weber and *Melastomites menzelii* Weyland can therefore be considered as being synonymous. While no sufficiently well-preserved cuticles could be won from the present material, cuticles of material referable to *Maianthemophyllum petiolatum* have proved that the epidermis was similar to those of *Heterosmilax* and *Smilax* (see WEYLAND, 1957). The new combination proposed for this taxon, *Smilax petiolata* (Weber) Weyland (WEYLAND, 1957, p. 60) would, however, appear to be somewhat premature.

Herbarium material examined in detail:

Blastus cochinchinensis Lour.	Coll. J. M. Dalziel 5-9-1899	(E) det. L. Diels
Dioscorea benthamii Pr. et Burk.	Coll. C. Y. Chiao 11-8-1927 (Herb. Univ. Nanking 14609)	(E) det. E. D. Merrill
	Coll. Y. Tsiang 681	(E) _____
Heterosmilax chinensis Wang	Coll. Wang & Tang 22855	(E) det. F. T. Wang HOLOTYPE
Osbeckia crinita Bentham	Coll. J. F. Rock 6366	(E) det. W. E. Evans
Osbeckia stellata Buch.- Ham. ex D. Don	Coll. Stainton, Sykes & Williams 6701	(E) _____
Ottelia polygonifolia (Gagnep.) Dandy	Coll. G. Forrest 8442	(E) det. J. E. Dandy
	Coll. G. Forrest 8784	(E) det. J. E. Dandy
Plagiopetalum serratum Diels	Coll. Y. Tsiang 9344	(E) det. L. Diels
Saururus chinensis (Lour.) Baill.	Coll. Y. Tsiang 479	(E) _____
Smilax flaccida C. H. Wright	Coll. A. Henry 3630B	(E) _____
	Coll. H. C. Chow 739	(E) _____

Stemona vagula W. W. Smith	Coll. G. Forrest 10711	(E) det. W. W. Smith TYPE
	Coll. G. Forrest 12534	(E) det. W. E. Evans
	Coll. G. Forrest s.n.	(E) det. W. W. Smith
	Coll. Handel-Mazzetti 7589	(E) det. Handel- Mazzetti
	Coll. E. E. Maire s.n.	(E) det. W. E. Evans

MONOCOTYLEDONEAE INCERTAE SEDES

LXXIV

Synonym: *Smilax grandifolia* (Unger) Heer Weyland, 1934, p. 41, Tafel 1, fig. 7!

Description:

Petiole unknown.

Lamina ovate, > 8.2 cm long, c.8.8 cm wide. Leaf apex unknown, leaf base markedly cordate.

Leaf margin entire.

Venation campylodromous, primary veins 9. Primary veins arising simultaneously at leaf base, each vein making an angle of c.45° with the neighbouring vein(s). Primary veins more or less similar in width, slightly tapering along length, 0.25 mm wide at mid-point between base and apex of lamina. Lateral primary veins adjoining the central primary vein appear to extend for much if not all of the way from the leaf base to the apex of the lamina. The lateral primary veins immediately adjoining these veins extend for at least 2/3 of the length of the lamina and the outer two pairs of primary veins for at least 1/2 the length of the lamina. Higher order veins present between the primary veins, 4–7 per 1 cm primary vein. Areoles 20–40 per 10 mm², with some free vein-endings, these being unbranched and branched.

Epidermis in non-stomatal condition unknown. Epidermis in stomatal condition composed of 200(?) – 350(?) cells per 0.1 mm², the cell length/cell breadth ratio being 1 : 1–3 : 1. Cell wall 0.5–1.0 microns thick, unpitted, straight or markedly undulate with 0–6 lobes per cell, the depth from the tips of the lobes to the bottoms of the sinuses up to 9 microns. Cells over veins elongate. Finer veins not reflected in cuticle. Stomata 18.0–32.4 microns long and c.20 microns broad, the actual size limits difficult to estimate as the boundary between the guard cells and accessory cells often vague. Stomata 20–30 per 0.1 mm², either orientated largely parallel to one another or randomly orientated, undepressed, more or less equidistant, apices non-retuse. Stomatal slit 43–67 % stomatal length. Accessory cells 2, symmetrical with 0 polar cells and 2 lateral cells, similar in size or slightly larger than the rest of the epidermal cells. Internal resinous bodies very rare.

Specimen examined: Deutsche Akad. Wiss. Berlin: 495(K 51)

Discussion:

WEYLAND (1934, p. 41) originally described this form as *Smilax grandifolia* (Unger) Heer (= *Smilacites grandifolia* Unger). At a later date, however, he considered the possibility that he was dealing with a *Saururus*, as he explained in a letter to Professor Remy dated the 5th of January 1960. Having attempted to make cuticle preparations from this specimen he had to admit that not only was he unable to confirm that the specimen was a *Saururus*, but doubted an affinity with *Smilax* on the grounds of the fossil's thin cuticle. Professor Weyland compared the fossil with *Saururus cernuus* from Florida. However, the leaves of *Saururus chinensis* (Lour.) Baill. with their large stomata and long stomatal slits (16–29 microns long) were also found to differ from the fossil, in which the stomatal slit was only 7–12.5 microns in length. In gross-morphology the fossil was found to resemble the leaves of *Dioscorea belophylloides* Pr. et Burk., *D. collettii* Hemsl., *D. floridana* Bart., *D. opposita* Thunb. and *D. villosa* L. (Dioscoreaceae), *Bauhinia championii* Bentham (Leguminosae), *Rubia cordifolia* L. (Rubiaceae), *Ottelia esquirolii* (Lévl. et Vant.) Dandy (Hydrocharitaceae), *Clematis loureiriana* DC. and *C. meyeniana* Walp. (Ranunculaceae), *Heterosmilax gaudichandiana* (Kunth) Maxim., *Smilax china* L., *S. glauca* Walt., *S. herbacea* L. and *S. rotundifolia* L. (Liliaceae).

On grounds of form and venation the fossil most closely resembles the leaves of certain species of *Dioscorea*, with their broad heart-shaped leaves and higher order veins, present between the primary veins, running more or less at right angles to the central primary vein. However, the leaves of *Dioscorea* differ from the fossil in having large epidermal cells and large stomata (10–20 per 0.1 mm²) with a stomatal slit generally ranging in length from 11–36 microns. The epidermal cells in the fossil are much smaller with 20–30 stomata present per 0.1 mm², while the stomatal slit only reaches a length of 7–12.5 microns. The only *Dioscorea* approaching the fossil in these respects was found to be *Dioscorea benthamii* Pr. et Burk., but the leaves of this species are lanceolate. The epidermis of *Dioscorea* is characterized by the presence of multicellular club-shaped trichomes. In the *Dioscorea* species investigated on the present occasion these trichome bases were found to be sparsely distributed. Although not ruling out the possibility that the fossil was indeed related to *Dioscorea*, the vain search for similar structures in the fossil means that the affinity of the fossil must be considered open. Not only was it found impossible on the basis of the present material to attribute the fossil to *Dioscorea*, but none of the other apparent possibilities exhibited complete agreement with the fossil either.

The epidermis of leaves of *Bauhinia championii* is characterized by the presence of very narrow stomata, the breadth being only 20–55% of the length.

The leaves of *Rubia cordifolia*, although outwardly similar to the fossil, have very large epidermal cells with strongly undulate cell walls and stomata with a stomatal slit 23–36 microns in length.

Ottelia esquirolii has an auriculate leaf base, a feature not found in the fossil, and large polygonal cells.

The leaves of both species of *Clematis* investigated resembled each other closely in the presence of large epidermal cells. Moreover, the stomata had a length of 36–49 microns (stomatal slit 21–33 microns long) and could therefore be distinguished from those of the fossil.

The leaves of the species of *Smilax* and *Heterosmilax* examined had large epidermal cells. This and the fact that the higher order veins present between the primary veins make an angle of less than 90° with the central primary vein enables one to distinguish between the leaves of these genera and the fossil in question.

Herbarium material examined in detail:

Bauhinia championii	Bentham Coll. W. Y. Chun 7709	(E) det. W. Y. Chun
Clematis loureiriana	DC. Coll. J. Cavalerie 3578	(E) det. L. A. Lauener
Clematis meyeniana	Walp. Coll. S. K. Lau 396	(E) det. E. D. Merrill
Dioscorea belophylloides	Coll. C. Y. Chiao 14346	(E) det. E. D. Merrill
Pr. et Burk.		
Dioscorea benthamii	Pr. et Coll. Y. Tsiang 681	(E) _____
Burk.	Coll. C. Y. Chiao	(E) det. E. D. Merrill
	11-8-1927 (Herb. Univ. Nanking 14609)	
Dioscorea collettii	Hemsl. Coll. C. Y. Chiao 14331	(E) det. E. D. Merrill
Dioscorea floridana	Bart. Coll. P. O. Schallert 20835	(U) _____
Dioscorea opposita	Thunb. Coll. C. Y. Chiao 14075	(E) det. E. D. Merrill
Dioscorea villosa	L. Coll. J. R. Bozeman, A. E. Radford & D. Culwell 10687	(U) _____
Heterosmilax gaudichandiana	(Kunth) Maxim. Coll. E. Bodinier 731	(E) det. A. Rehder
	Coll. E. Bodinier 22-8-1894	(E) det. A. Rehder
	Coll. H. H. Chung 620	(E) _____
	Coll. E. H. Wilson 674	(E) _____
Ottelia esquirolii	(Lévl. et Vant.) Dandy Coll. J. Esquirol 732	(E) _____
Rubia cordifolia	L. Coll. A. Henry 2226	(E) _____
Saururus chinensis	(Lour.) Baill. Coll. Y. Tsiang 479	(E) _____
Smilax china	L. Coll. E. Taquet 3306	(E) det. Wang & Tang
Smilax glauca	Walt. Coll. H. E. Ahles 34411	(U) _____
Smilax herbacea	L. Coll. J. R. Bozeman, A. E. Radford & D. Culwell 10676	(U) _____
Smilax rotundifolia	L. Coll. H. E. Ahles & C. R. Bell 16780	(U) _____

LXXXV

Description:

Lamina elliptical or obovate, 4.5–c.8 cm long, 0.60–0.82 cm wide, the length/breadth ratio being 6 : 1–7.5 : 1 or more. Leaf apex acute or rounded with a mucronate tip, leaf base attenuate.

Venation parallelodromous, midvein 0.075–0.10 mm wide, c.6–c.12 veins, more or less uniform in size or divisible into larger and smaller veins, present on either side of and roughly parallel to the midvein. These veins are spaced at intervals of 0.03–0.06 mm. Transverse commissures, 3–25 per 10 mm², present connecting these veins.

Epidermis composed of uncertain number of rectangular cells per 0.1 mm², arranged in rows, the cell length/cell breadth ratio being 1 : 1–2.5 : 1. Cell wall 0.5 microns thick, largely unpitted, straight. Stomata unknown.

Specimens examined: Geol. Inst. Cologne: s.n.
Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3831, 3834,
3835, 3836, 3837

Discussion:

Leaf-remains such as these, when only fragmentary, might well be referred to the grasses. However in complete specimens the attenuate leaf base can be observed. While it would not seem advisable (due to the lack of comparative material) to attribute the leaf-remains to this genus, these show a marked similarity to the leaves of certain *Potamogeton* species e.g. *P. compressus* L. Species of *Potamogeton* (*Potamogetonaceae*) with lanceolate leaves have an attenuate leaf base and an acute or rounded (sometimes mucronate) leaf apex. While the lateral veins may converge at the leaf apex, the larger of these not infrequently bend inwards to meet the midvein at some distance from the leaf apex. Although the preservation of the leaf-remains does not allow one to state this with certainty, something of a similar nature would appear to be present in the fossil.

LXXXVI

Synonyms: *Phragmites oeningensis* A. Braun WEYLAND, 1934, p. 40!
Typha latissima A. Braun WEYLAND, 1934, p. 40!

Description:

Lamina linear, reaching a length of more than 21.5 cm, 1.0–3.3 cm wide. Leaf apex and leaf base unknown. Lamina hollow, divided into long compartments by longitudinal septa, 0.1–0.3 (–0.6) mm wide, 7–23 per leaf blade, spaced at a distance of 0.4–4.2 mm. These long compartments broken up into smaller compartments by transverse septa, as wide as the longitudinal septa or somewhat thinner. Transverse septa 2–80 per 10 mm². Surface of lamina longitudinally striate, striae uniform in size or divisible into larger and smaller striae. Smaller striae, when present, alternating with or grading into larger striae, which are spaced at intervals of 0.05–0.60 mm. Transverse commissures may be present joining the larger striae.

Cuticle thin, epidermis composed of 150–500 rectangular cells per 0.1 mm², arranged in rows, the cell length/cell breadth ratio being 1 : 1–6 : 1. Cell wall 0.5–1.5 microns thick, unpitted or pitted, straight. Stomata unknown.

Specimens examined: 128, among which the numbered specimens:
 Bot. Mus. & Herb. Utrecht, Div. of Palaeobot.: 3620D, 3745,
 3746A, 3747, 3748, 3749, 3750, 3751, 3752, 3753, 3754, 3755,
 3756, 3757, 3758, 3759, 3760, 3761, 3762, 3763, 3764, 3765,
 3766

Discussion:

At the time of H. Weyland's revision the Berlin collection had 5 specimens referable to the present taxon. WEYLAND (1934) attributed two of these specimens to *Typha latissima* (Typhaceae) and three to *Phragmites oeningensis* (Gramineae). Only one specimen attributed to *Typha latissima* and one specimen determined as *Phragmites oeningensis* could be found when the present author examined this collection in 1967. These two specimens did not appear to differ in any respect. Both displayed the characteristic transverse and longitudinal septa. While the absence or at least infrequent occurrence of stomata and the presence of hollow compartments, such as is also found in the leaves of *Sparganium* (Sparganiaceae), might suggest that the plant was a hydrophyte, it would not appear to be possible to determine the fossil more accurately.

PLANT-REMAIN OF UNCERTAIN AFFINITY

LXXVII

Description:

Shoot or rhizome c.35 mm long, curved, with an axis 0.35–0.45 mm wide with bundles of 3–7 unbranched hair-like structures, 1.0–3.8 mm long and 0.04–0.05 mm wide, often borne on a short lateral projection. Elliptical bodies, 1.1–1.6 mm long and 0.25–0.50 mm wide present at very apex.

Specimen examined: Geol. Inst. Cologne: s.n.

Discussion:

H. Weyland determined this specimen as that of a water plant and suggested an affinity with *Myriophyllum*, *Utricularia* or *Ceratophyllum*. Plant-remains similar to the fossil have been described by DE VISIANI (1858) as *Myriophyllites*(?) *radiciformis*. De Visiani recognized that his material could in fact be that of a root or rhizome. The plant-remain under consideration differed from *Myriophyllum* in that in place of filiform leaves the shoot or rhizome is covered by whorls of hair-like structures. A reference to *Utricularia* or *Ceratophyllum* would also seem unlikely on morphological grounds.

Herbarium material examined in detail:

Ceratophyllum demersum L.	Coll. M. S. Clemens 1795	(E)	_____
Myriophyllum propinquum	Coll. E. E. Maire 1925	(E)	det. R. van der Meijden
A. Cunn.			
Myriophyllum spicatum L.	Coll. E. E. Maire 324	(E)	det. R. van der Meijden

<i>Utricularia aurea</i> L.	Coll. Handel-Mazzetti 11350	(E) det. Handel-Mazzetti
<i>Utricularia multicaulis</i> Oliv.	Coll. Handel-Mazzetti 9887	(E) det. Handel-Mazzetti

LEAF-REMAINS OMITTED FOR VARIOUS REASONS

This category consists of taxa recognized by WEYLAND (1934), which are now considered better omitted from consideration, and those whose affinity must remain uncertain, as they were not available to the author at the time of the revision. The specimens designated by WEYLAND (1934) as *Cassia ambigua* Unger, *C. berenices* Unger, *Diospyros brachysepala* A. Braun and *Ficus rueminiana* Heer fall into the former category. Other specimens referred to as *Acer trilobatum* (Sternberg) A. Braun, *Cassia hyperborea* Unger, *Cyperites* sp., c.f. *Oreopanax* sp., and *Populus gaudinii* Fischer-Ooster make up the latter category. The material of *Acer trilobatum* and c.f. *Oreopanax* sp. was on loan to Dr. H. Walther (Dresden) from Berlin. Photographs of both these specimens were made available to the present author by Dr. Walther. Enquiries addressed to Professor H. Weyland (Wuppertal), the Institute of Geology and Palaeontology in Bonn, the Technical University in Aachen and the Geological Survey of the D.D.R. as to the whereabouts of the remaining material proved to be fruitless.

Acer trilobatum (Sternberg) A. Braun WEYLAND, 1934, p. 93

As pointed out by WALTHER (1968) *Acer trilobatum* (Sternberg) A. Braun is a later homonym for *Acer trilobatum* Lamarek and should be replaced by the binomial *Acer tricuspdatum* Bronn. However, while the specimen from Kreuzau may well represent a good taxonomic entity, the generic and specific status of this fossil is still unproven.

Cassia ambigua Unger WEYLAND, 1934, p. 88, Tafel 15, fig. 10!

Specimen examined: Deutsche Akad. Wiss. Berlin: 347(K 104)

The specimen illustrated by H. Weyland was examined by the present author. It could possibly be referred to No. L, the only distinction being that the intermediate veins extend from 3/4–5/6 the distance from the midvein to the leaf margin in the specimen under consideration. However, in the absence of a cuticle preparation no definite decision was considered to be warranted.

Cassia berenices Unger WEYLAND, 1934, p. 88, Tafel 15, figs. 4, 13!

Specimens examined: Deutsche Akad. Wiss. Berlin: 334(K 102), 344(K 102)
Geol. Inst. Cologne: Coll. H. Weyland 1407–1407a

Of the six specimens mentioned in Weyland's account, only three were available to the present author. None of these specimens yielded a cuticle and in the lack of any diagnostic characters by which to recognize the

taxon it was felt better to omit the entity. Furthermore, it is by no means certain whether the specimens show sufficient agreement to be referred to a single taxon. Although agreeing in being small, 3.5–c.4.5 cm long and 2.0–2.5 cm wide, they display a certain amount of variation with regard to leaf shape, leaf base and venation.

Cassia hyperborea Unger WEYLAND, 1934, p. 88, Tafel 15, fig. 8

It is possible to state with certainty that this specimen is distinct from that described as *Cassia* c.f. *hyperborea* (see No. LVII). However, in the absence of evidence as to its epidermal structure, a reference of this entity to one of the taxa described in the present account can neither be supported nor negated. The specimen was in the possession of Mr. W. Jansen (Cologne) at the time of H. Weyland's revision (WEYLAND, 1934). This collection has since been dispersed. Certain of the specimens have been commercially distributed by Dr. F. Krantz (Bonn) and it is possible that this specimen was one of them.

Cyperites sp. WEYLAND, 1934, p. 40

This taxon was listed by H. Weyland in his account of the Kreuzau assemblage. WEYLAND (1934, p. 18) mentioned that 6 specimens were present in the Berlin collection at the time of his revision. However, no specimens from Kreuzau labelled as *Cyperites* sp. were found in the course of the present revision.

Diospyros brachysepala A. Braun WEYLAND, 1934, p. 110, Tafel 20, fig. 3!

Specimen examined: Deutsche Akad. Wiss. Berlin: 340(K 101)

WEYLAND (1934, p. 110) referred a small number of specimens to this taxon. However, only that specimen which he illustrated in his account of the Kreuzau assemblage was available for examination. This specimen did not yield a cuticle preparation and the nature of the venation was not sufficiently diagnostic to prove identity to any of the taxa with entire leaf margin mentioned in the present account.

Ficus rueminiana Heer WEYLAND, 1934, pp. 63–64, Tafel 9, fig. 2!

Specimen examined: Deutsche Akad. Wiss. Berlin: 265(K 70)

While WEYLAND (1934, p. 64) considered Berlin 265 to be "very probably" a *Ficus* leaf, an examination of this specimen proved that this statement was based on very uncertain evidence. The specimen did not yield a cuticle preparation and did not have a distinctive venation pattern. This not only renders a comparison with other Kreuzau taxa with an entire leaf margin an all but impossible task, but rules out any hope of determination.

c.f. *Oreopanax* sp. WEYLAND, 1934, p. 108, Tafel 20, fig. 2

This specimen may well represent a taxonomic entity distinct from

those taxa described in the present account. However, in the absence of a detailed examination, this cannot be stated with certainty.

Populus gaudinii Fischer-Ooster WEYLAND, 1934, p. 43, Tafel 3, fig. 1

This specimen, present in the Berlin collection before the Second World War, was considered by WEYLAND (1934, p. 43) to be possibly referable to the same taxon as Berlin s.n. (K 154), determined as *Populus mutabilis* Heer (see No. LVI). The specimen was not seen by the present author.

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PLATES 1-53

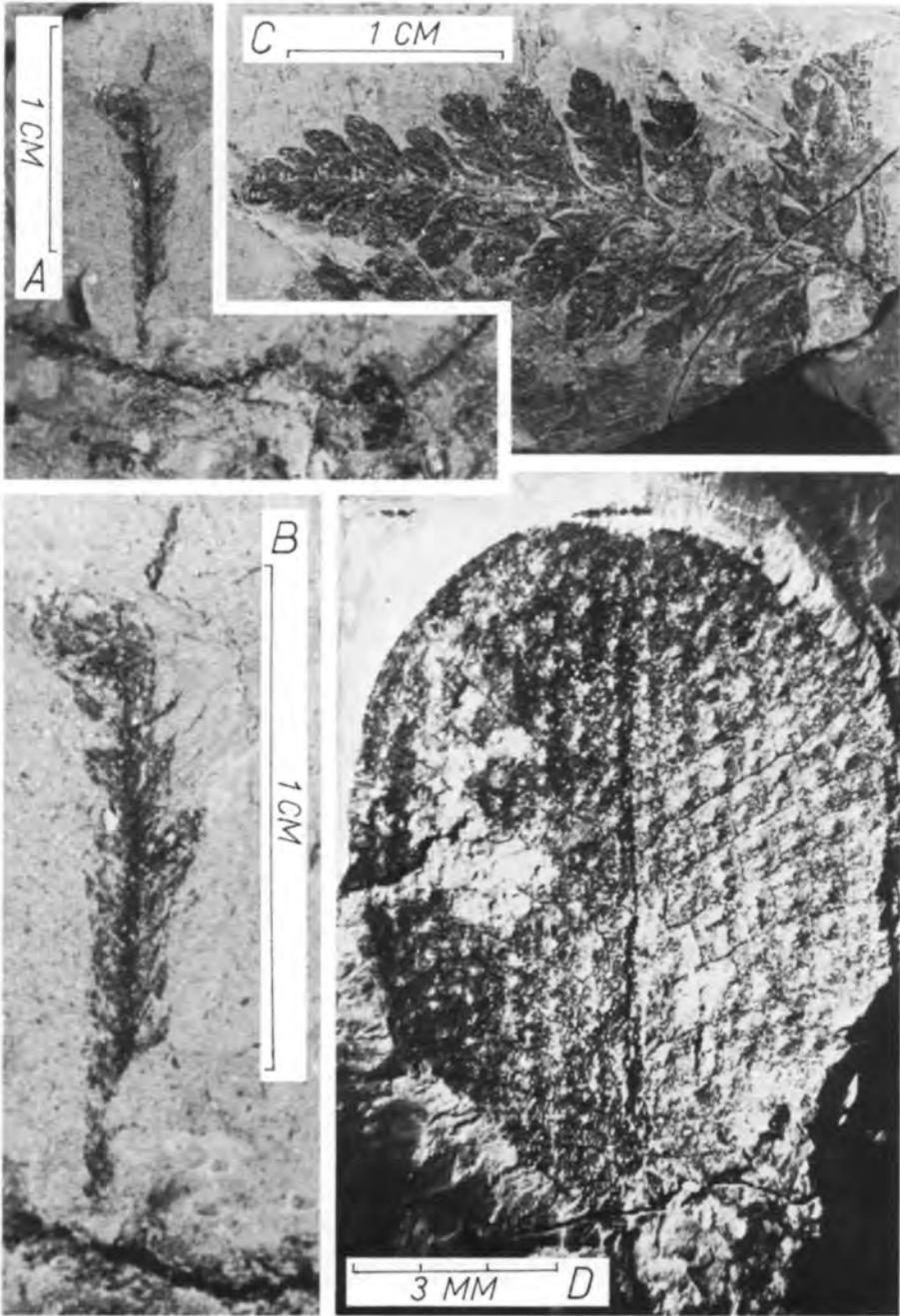


PLATE 1

A-B = I: Utrecht 3854. C = II: Cologne s.n. D = III: Utrecht 3848.

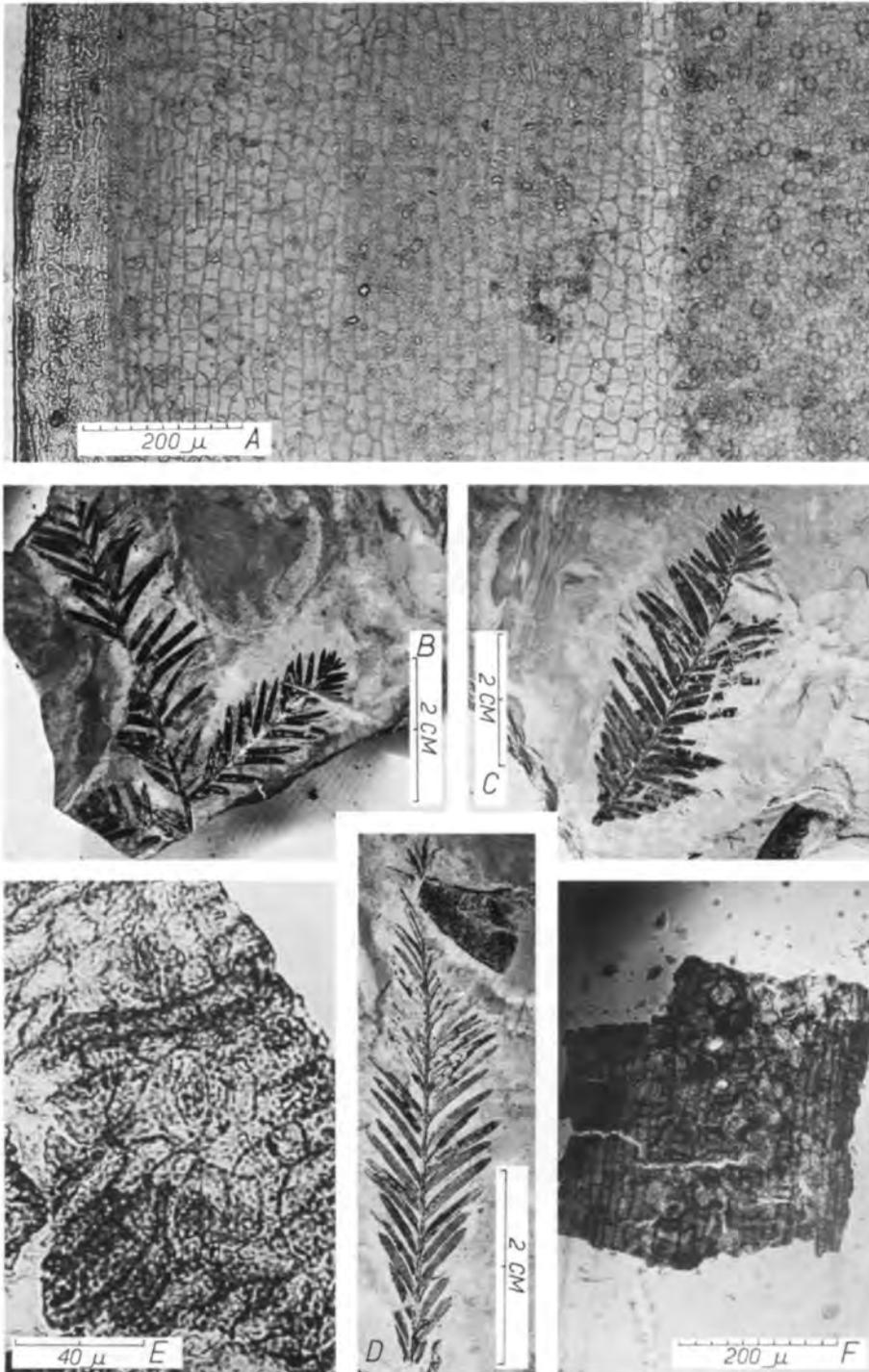


PLATE 2

A = V: Utrecht 3471, epidermal cell structure of part of the lower surface of a leaf (continued on Plate 3). B-F = IV: B = Utrecht 3435; C = Utrecht 3397; D = Utrecht 3410 A; E-F = cuticle of Utrecht 3401.

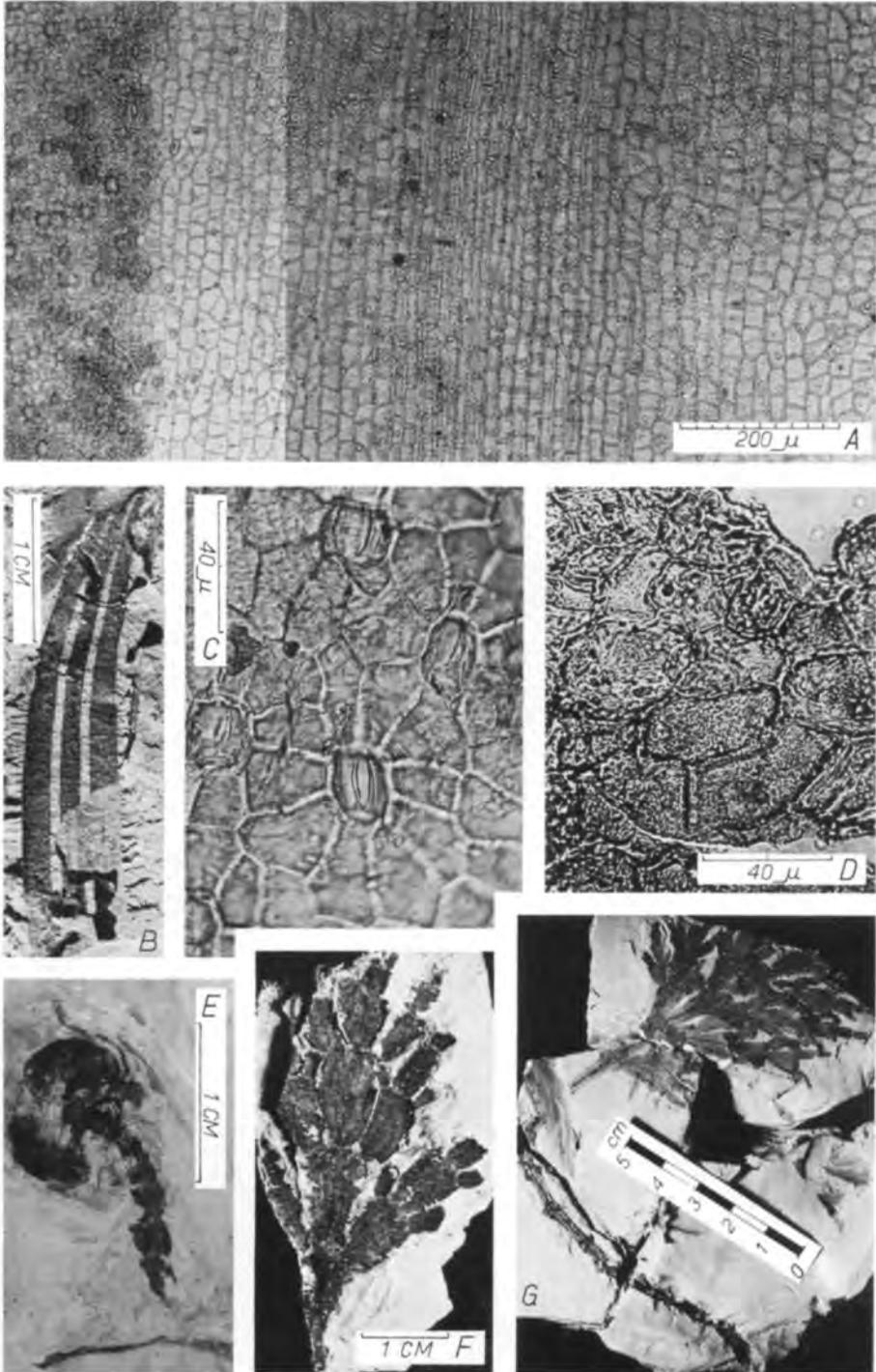


PLATE 3

A-C = V: A = Utrecht 3471, epidermal cell structure of part of the lower surface of a leaf (continued from Plate 2). Note the narrow cells over the midvein. B = Utrecht 3474; C = Utrecht 3471, detail of part of the stomatal band to show the stomata surrounded by numerous accessory cells. D-G = VI: D = Utrecht 2055, cuticle of cone-scale displaying in top right hand corner the presence of a stoma; E = Utrecht 2055, cone; F = Utrecht 3646; G = Utrecht 3652.

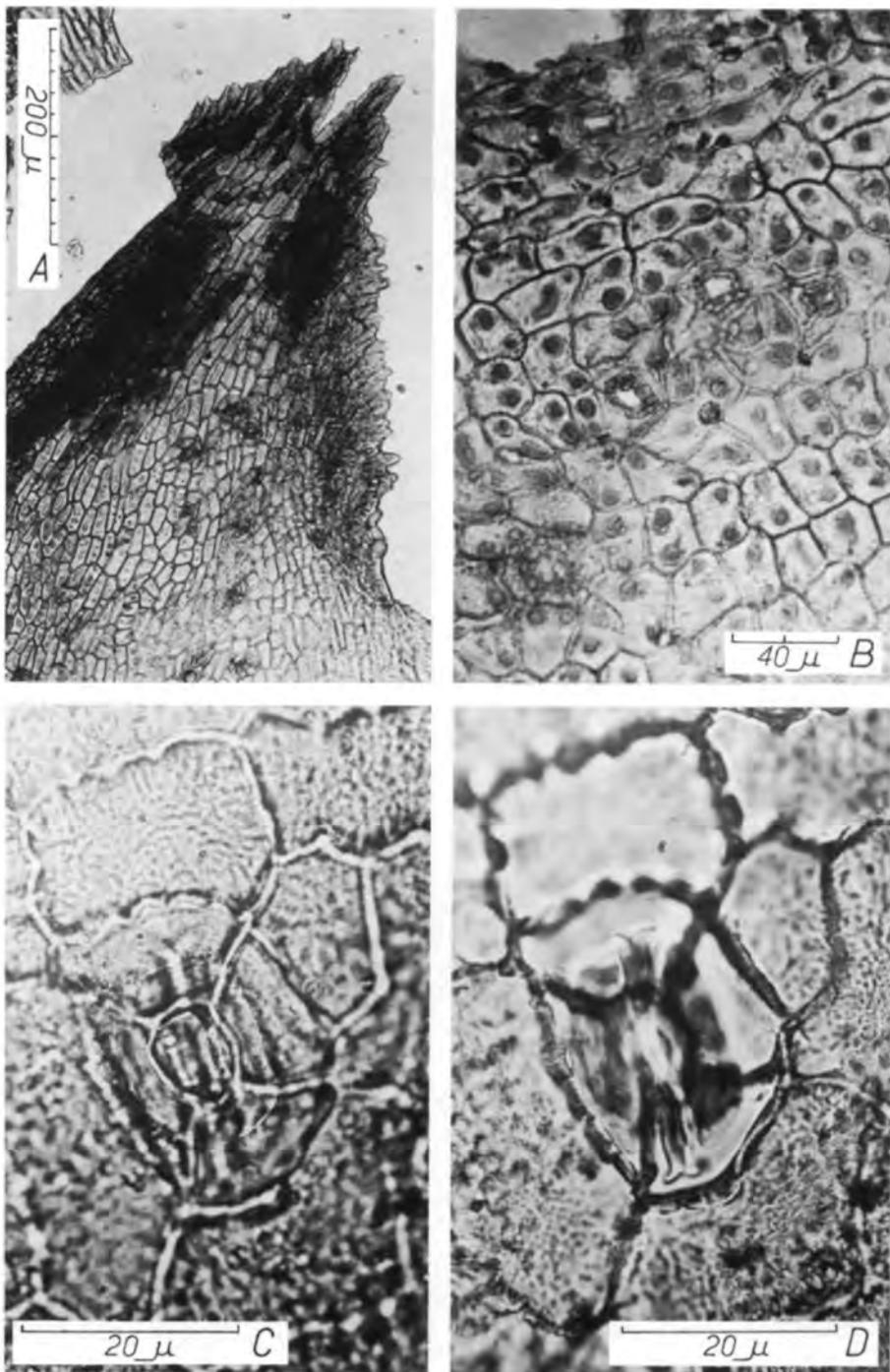


PLATE 4

A-D = VI: A = Utrecht 3654, apex of marginal leaf showing papillation of the leaf margin; B = Utrecht 3654, facial leaf showing papillation of cells; C = Utrecht 3654, stoma, external view with ring of cutin; D = Utrecht 3654, internal view of same stoma showing guard cells separated by T-shaped piece.

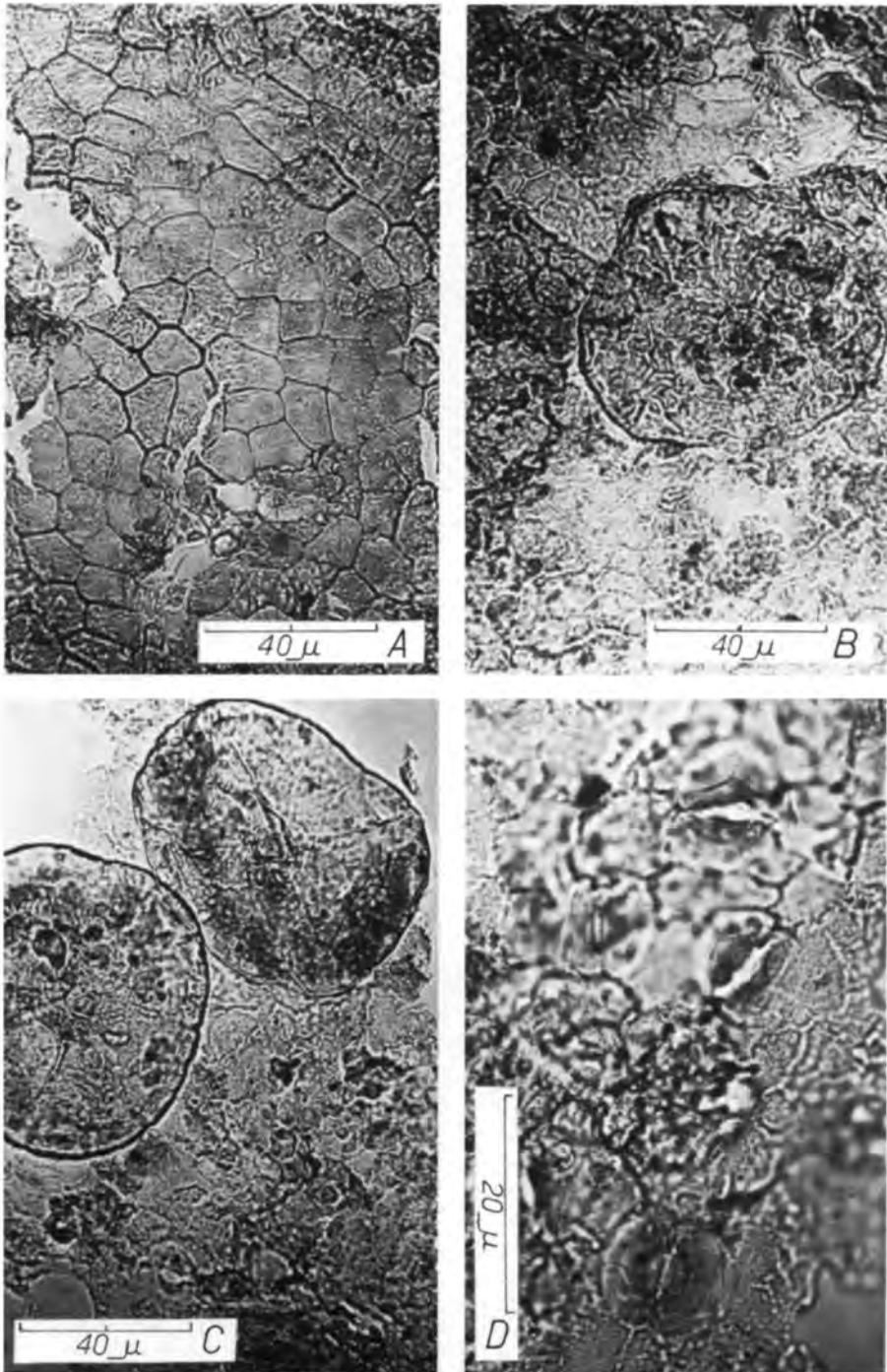


PLATE 5

A-D = VII: A = Utrecht 3451, cuticle showing epidermal cell structure in non-stomatal condition; B = Utrecht 3465, cuticle showing epidermal cell structure in non-stomatal condition and the presence of a gland; C = Utrecht 3441, cuticle showing epidermal cell structure in stomatal condition and the presence of two glands; D = Utrecht 3465, cuticle showing epidermal cell structure in stomatal condition.

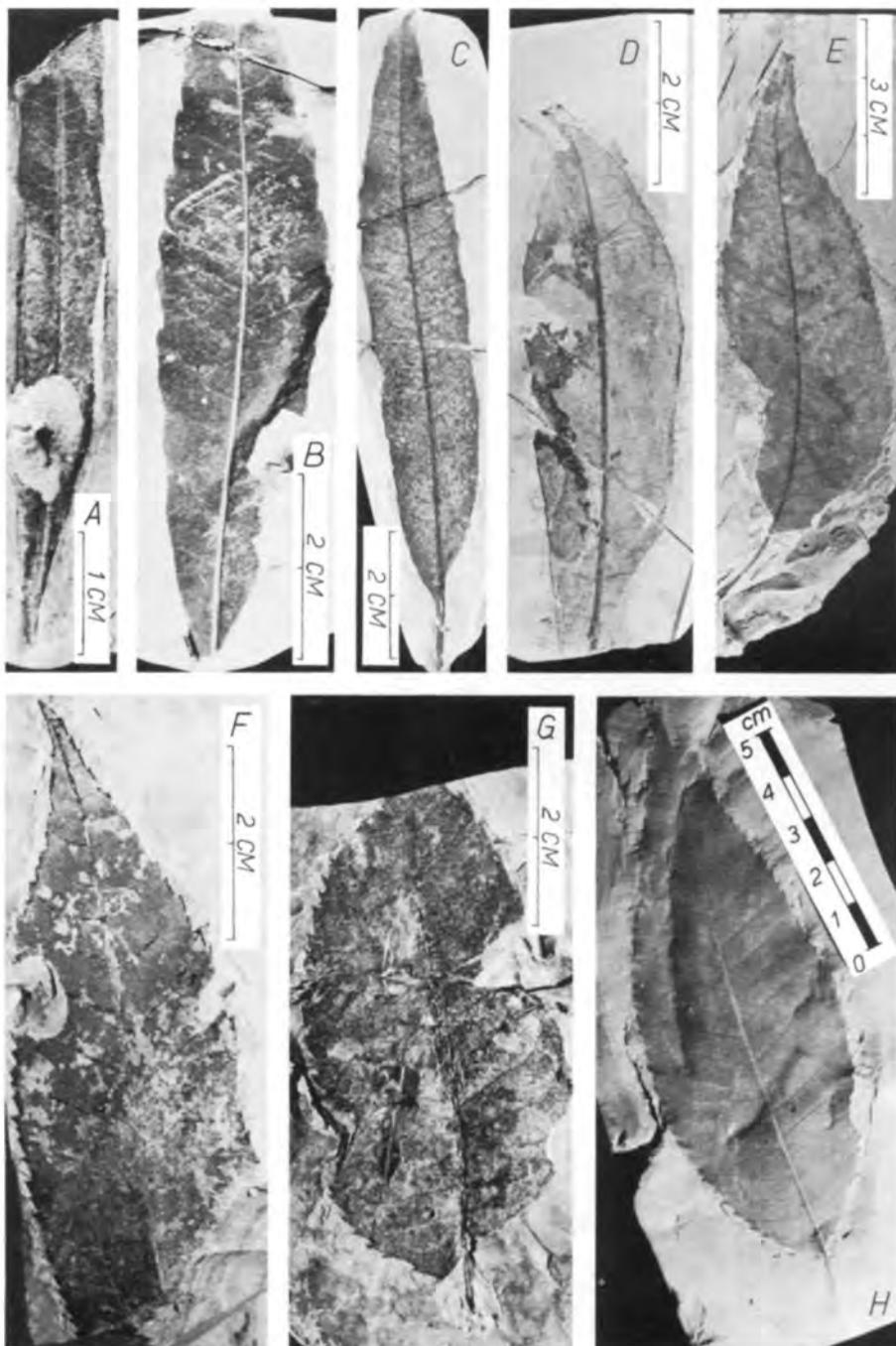


PLATE 6

A-D = VII: A = Utrecht 3424; B = Utrecht 3423; C = Berlin 285; D = Cologne, Coll. H. Weyland 1665. E-H = VIII: E = Cologne, Coll. H. Weyland s.n.; F = Utrecht 3790; G = Utrecht 3795; H = Berlin 304 (Type of *Saurauia rhenana* Weyland).

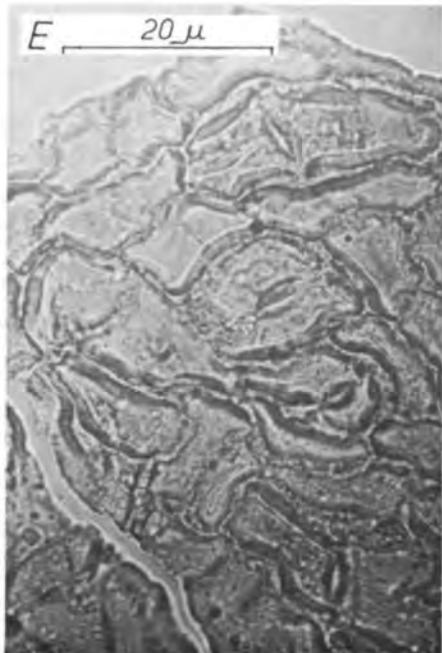
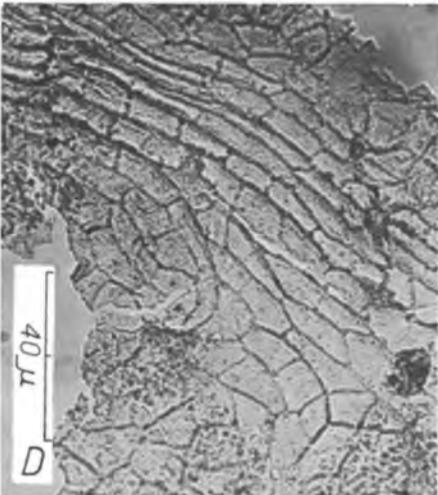
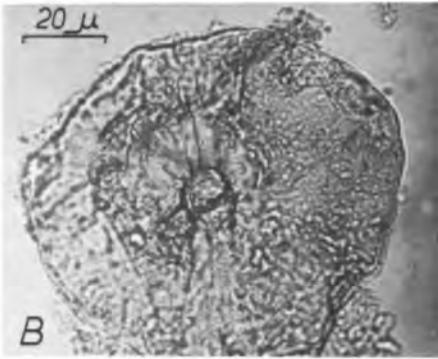
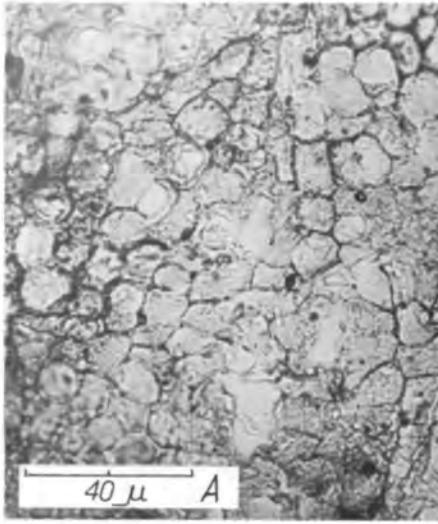


PLATE 7

A-B = VIII: A = Utrecht 3798, cuticle showing epidermal cell structure in non-stomatal condition; B = Utrecht 3798, gland. C-E = IX: C = Utrecht 3369; D = Utrecht 3381, cuticle showing epidermal cell structure in non-stomatal condition. Note hair bases over vein. E = Utrecht 3375, cuticle showing epidermal cell structure in stomatal condition.

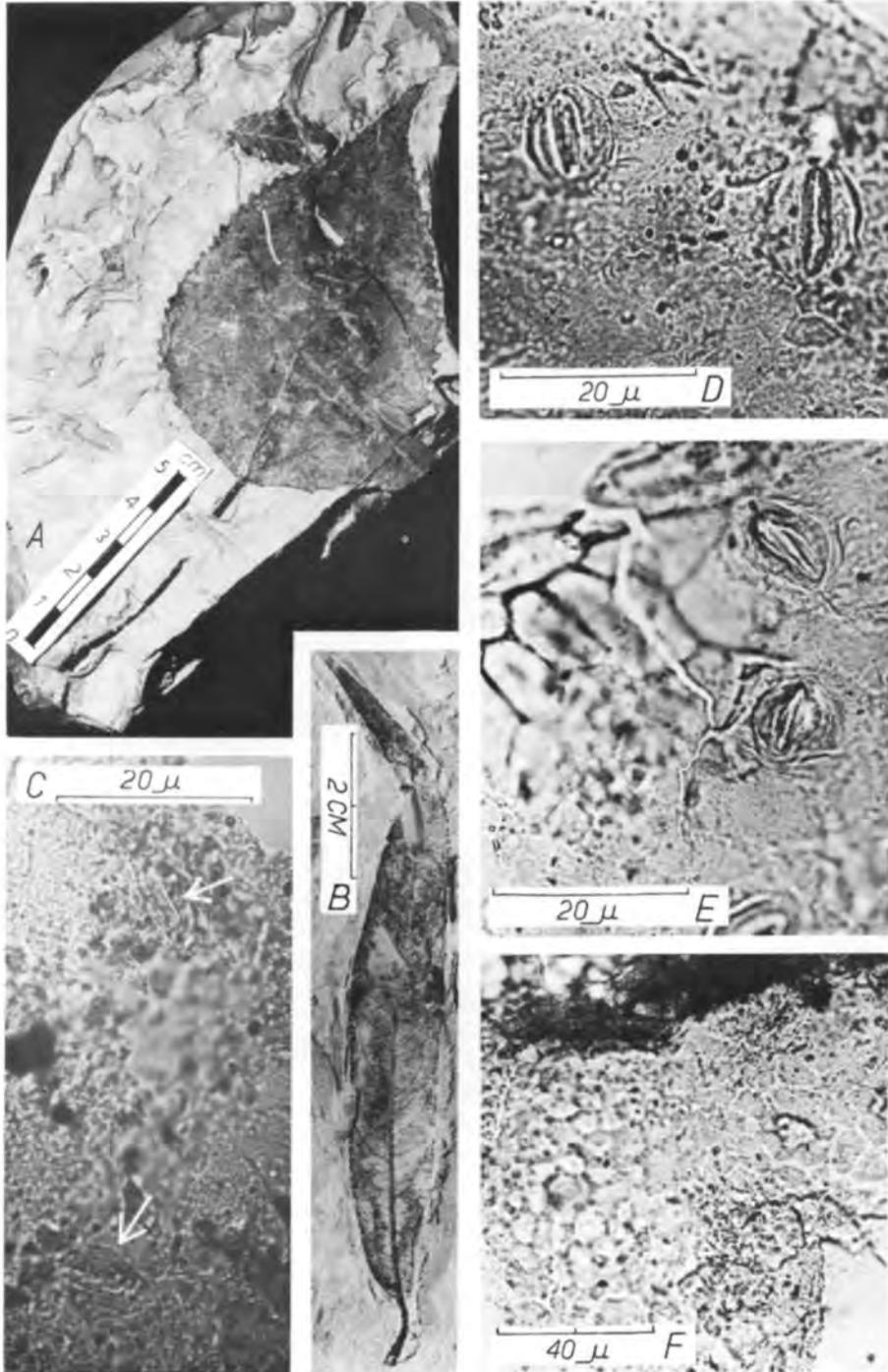


PLATE 8

A, D, E = X: A = Utrecht 3393; D = Utrecht 3388, two stomata. Note fine striation next stoma on right hand side of photograph. E = Utrecht 3388, cuticle showing epidermal cell structure and stomata. B, C, F = XI: B = Utrecht 3518; C = Utrecht 3549, cuticle reflecting the presence of two stomata (position of stomata indicated by arrows); F = Utrecht 3525, cuticle showing epidermal cell structure in non-stomatal condition.



PLATE 9

XII: Utrecht 3931 A, branch with leaves.

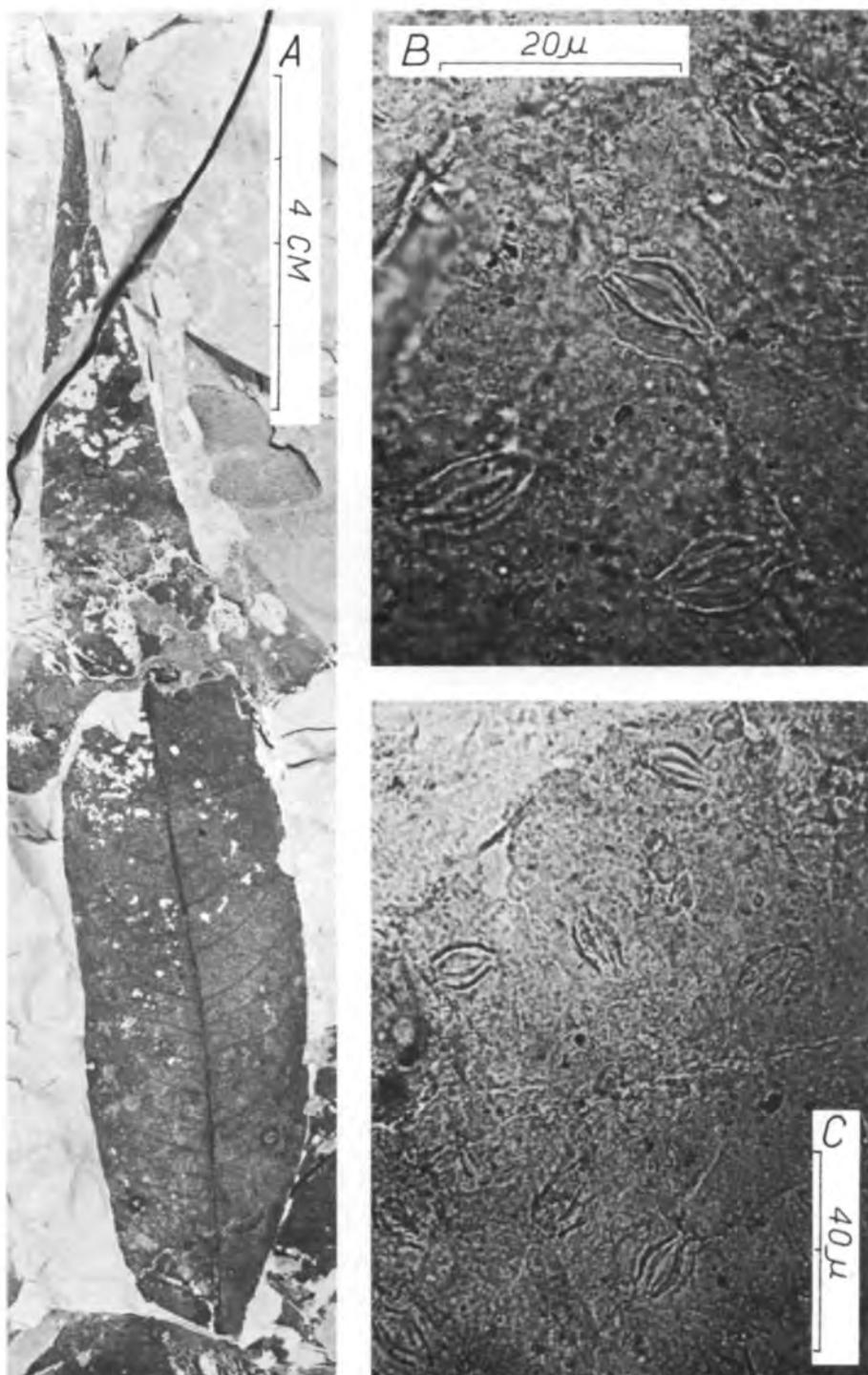


PLATE 10

A-C = XII: A = Utrecht 3931 A, detail of one of the leaves; B = Utrecht 3931 A, detail of stomata. Note long stomatal slits. C = Utrecht 3931 A, general view of cuticle reflecting the presence of stomata.

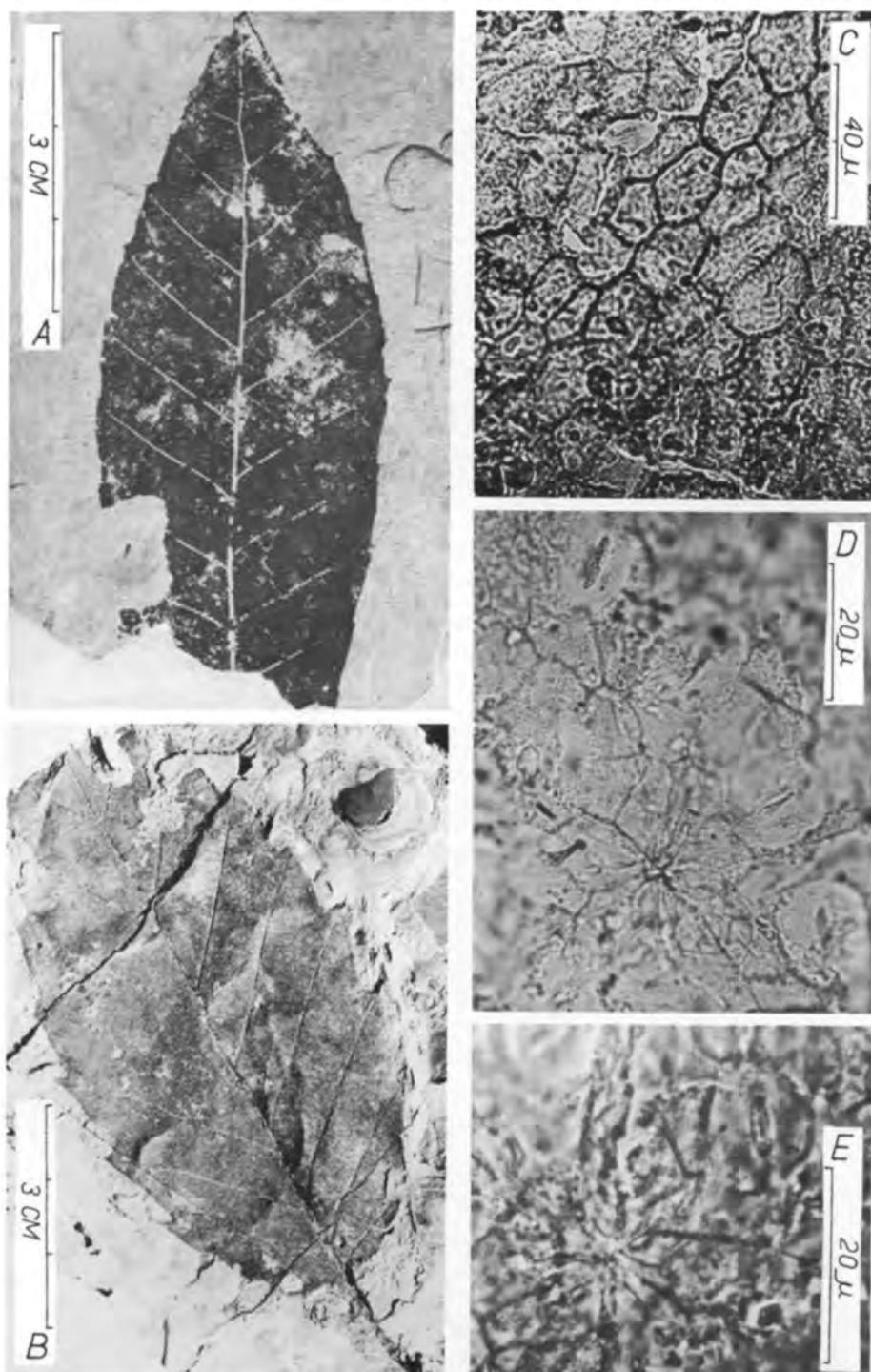


PLATE 11

A = XIII: Utrecht 3856. B-E = XIV: B = Utrecht 3804; C = Utrecht 3218, cuticle showing epidermal cell structure in non-stomatal condition; D = Utrecht 3222, cuticle showing epidermal cell structure in stomatal condition. Note hair base to the left of the stomata in the lower half of the photograph. E = Utrecht 3222, hair base and a single stoma photographed under phase contrast.

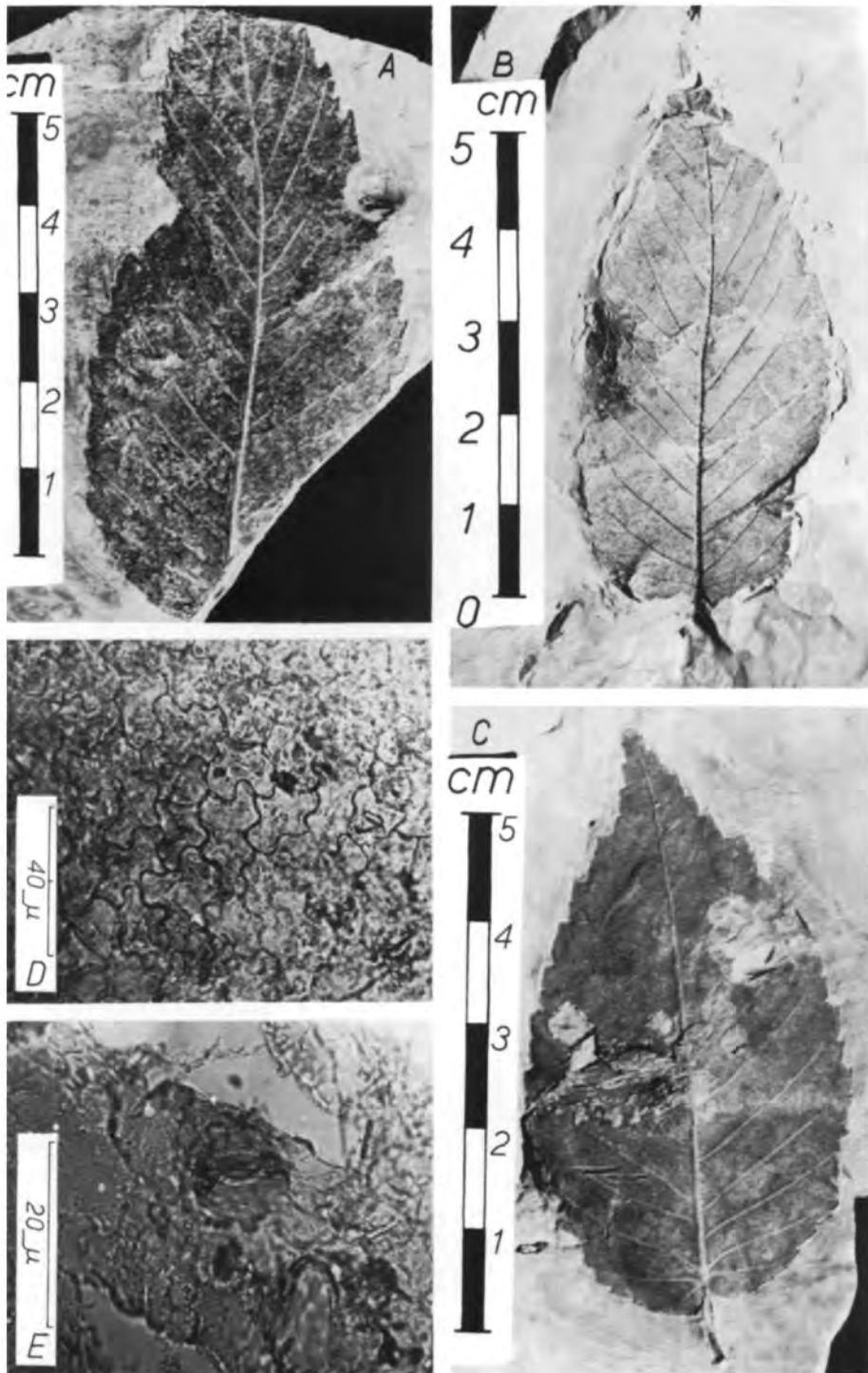


PLATE 12

A-E = XV: A = Utrecht 3555; B = Utrecht 3556; C = Utrecht 3552; D = Utrecht 4147, cuticle showing epidermal cell structure in non-stomatal condition; E = Utrecht 4147, cuticle showing epidermal cell structure in stomatal condition.

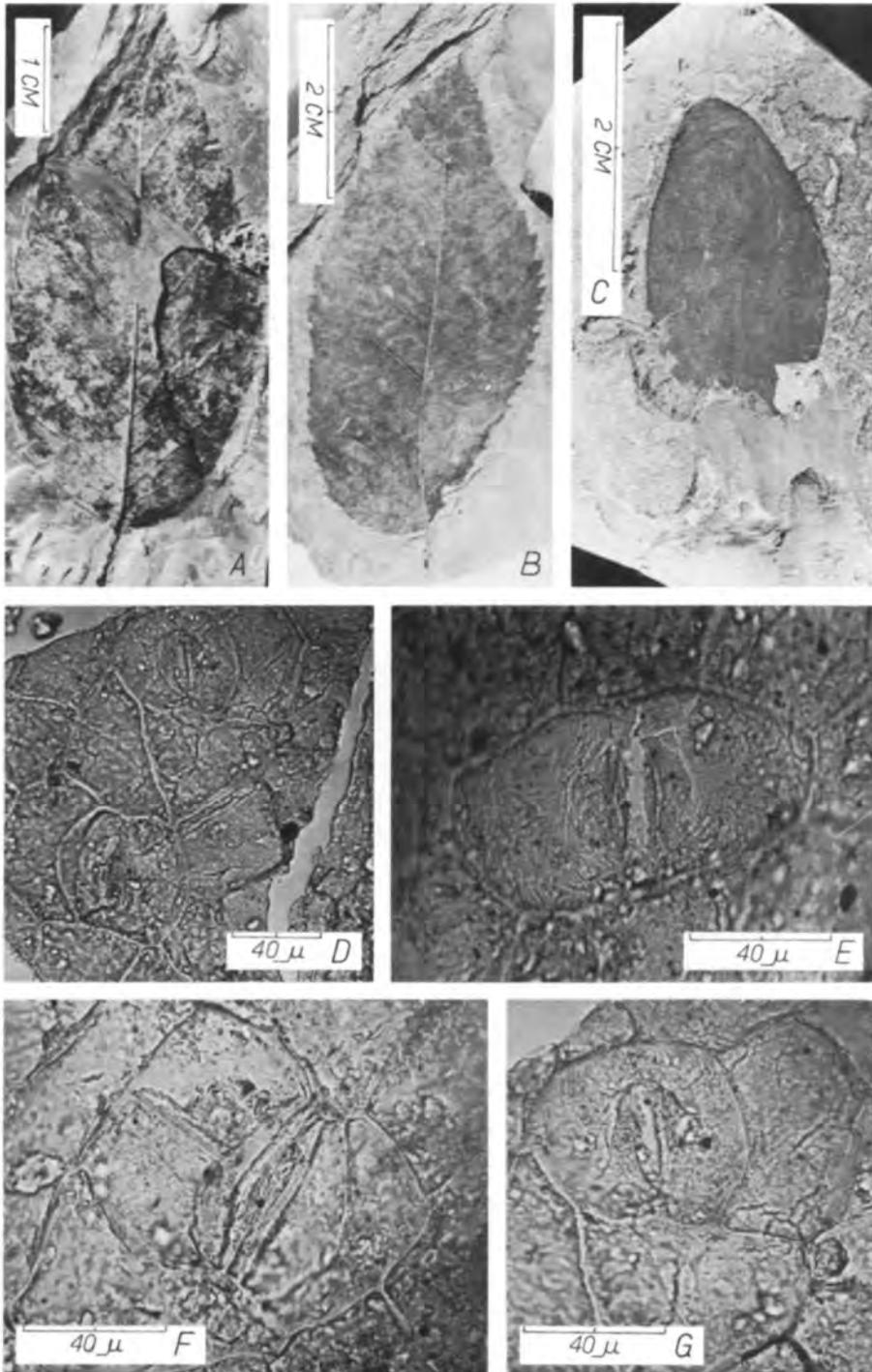


PLATE 13

A = XVII: Utrecht 3899. B = XVI: Utrecht 4149. C-G = XVIII: C = Cologne, Coll. H. Weyland 1698; D = Cologne, Coll. H. Weyland 1698, cuticle showing epidermal cell structure and stomata; E-G = Cologne, Coll. H. Weyland 1698, stomata. Note the large size and variable shape of the stomata.

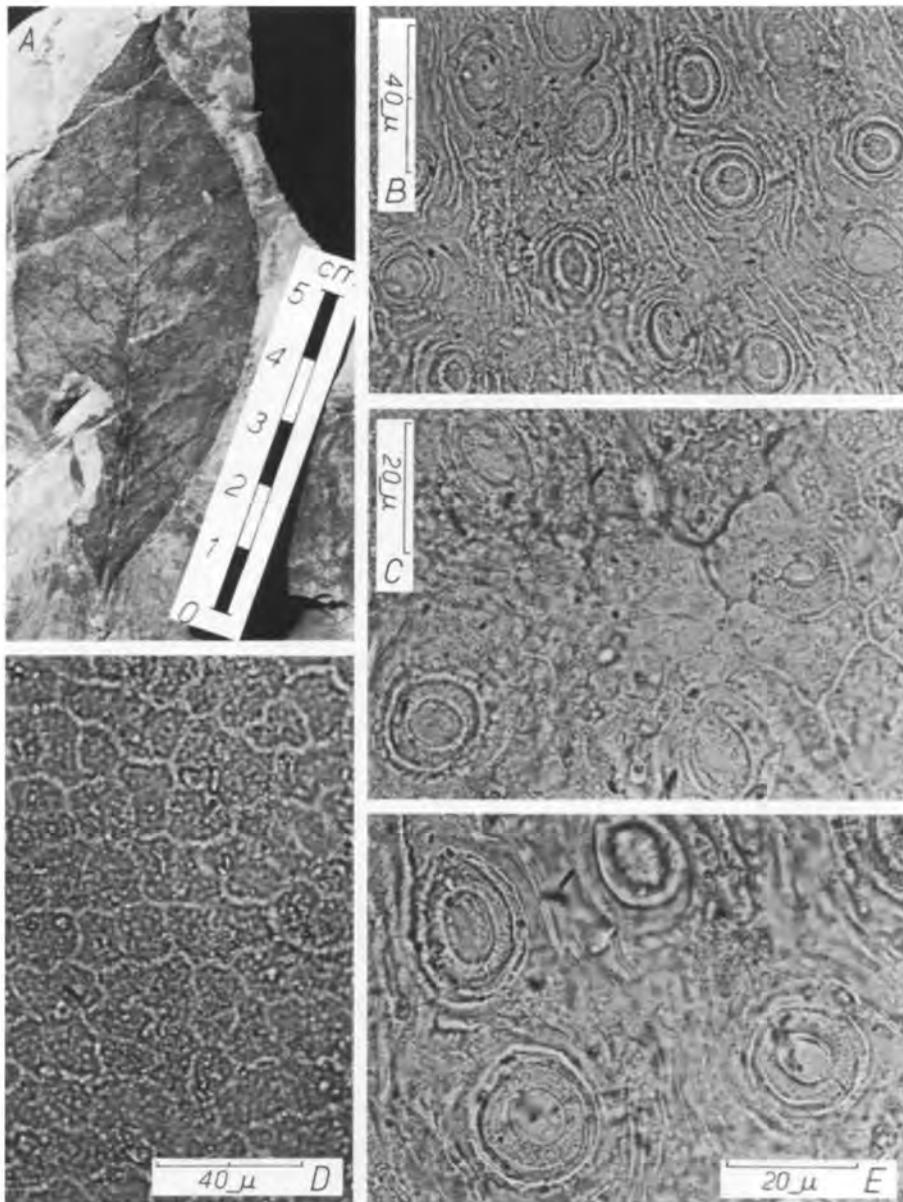


PLATE 14

A-E = XIX: A = Berlin 283 (Type of *Kadsura breddinii* Weyland); B = Utrecht 4150, cuticle showing epidermal cell structure in stomatal condition; C = Utrecht 4150, detail of stomata. Note arrangement of accessory cells round stoma on right hand side of photograph. D = Utrecht 4150, cuticle showing epidermal cell structure in non-stomatal condition; E = Utrecht 4150, detail of stomata. Note the presence of a ring of cutin over stomata.

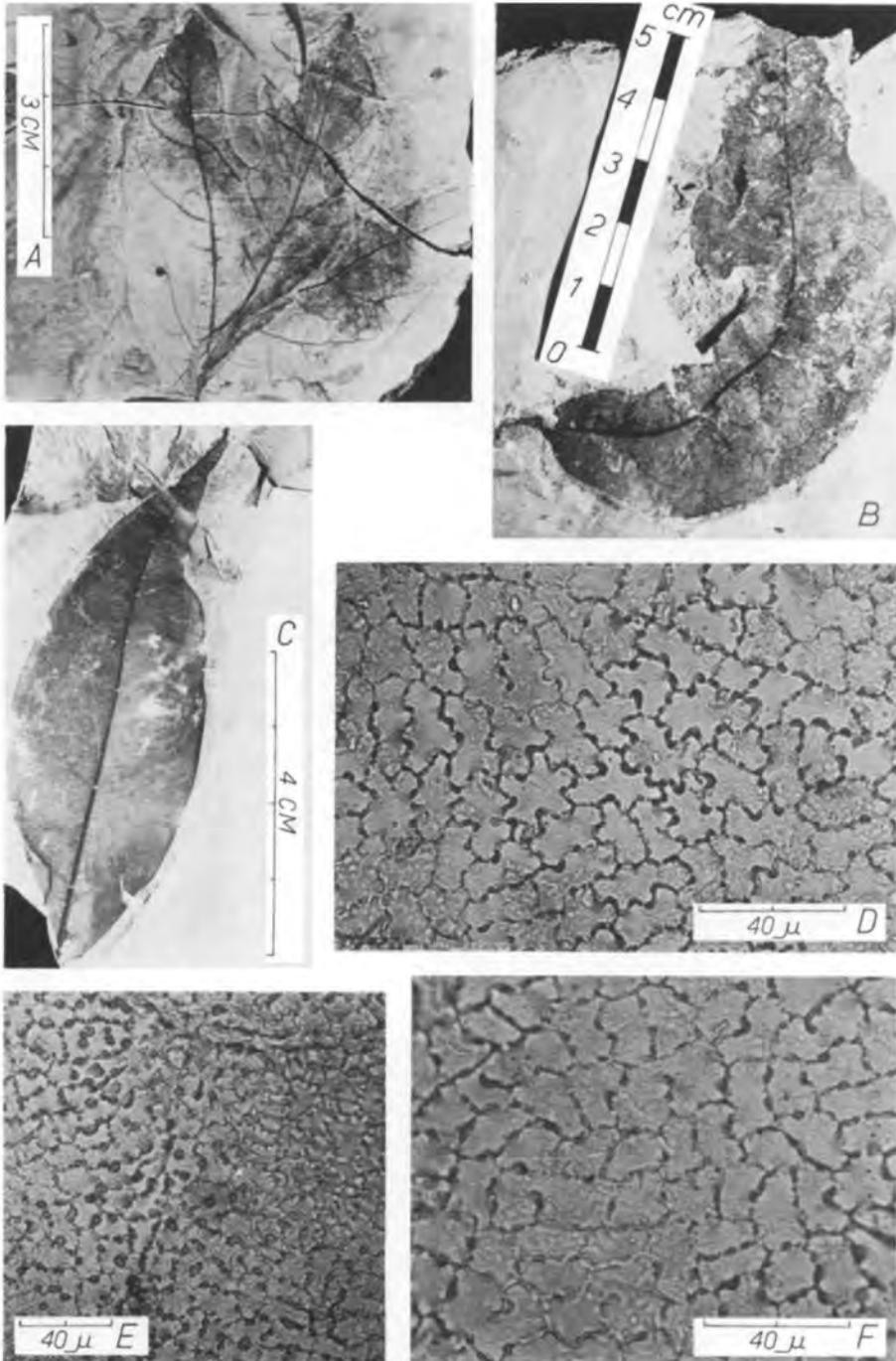


PLATE 15

A = XX: Cologne, Coll. H. Weyland 1635. B-F = XXI: B = Utrecht 3659; C = Berlin 270; D = Utrecht 3665, cuticle showing epidermal cell structure in non-stomatal condition; E = Utrecht 3669, cuticle showing epidermal cell structure in non-stomatal condition. Note strong development of hemispherical projections. F = Utrecht 3668, cuticle showing epidermal cell structure in non-stomatal condition.

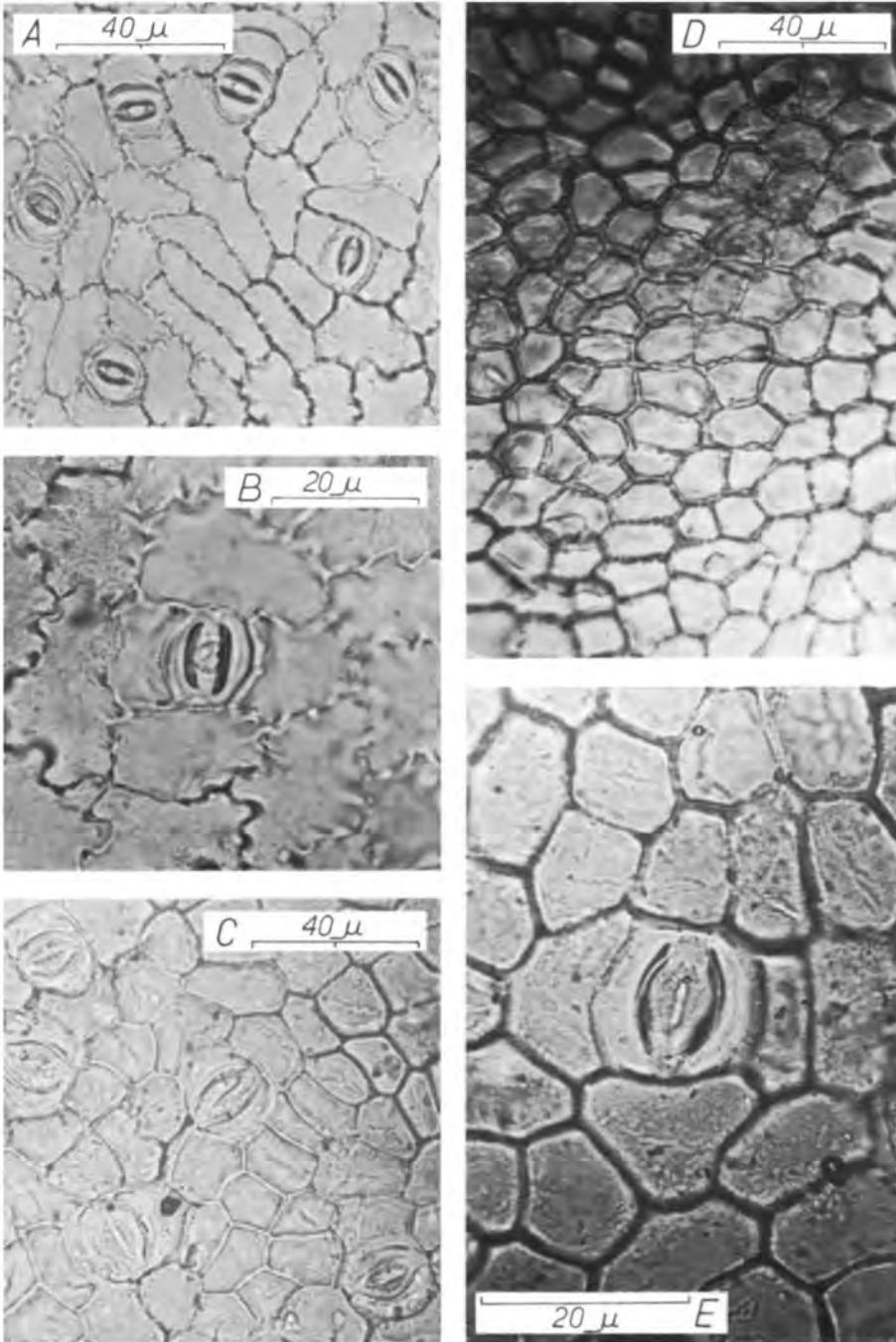


PLATE 16

A-B = XXI: A = Utrecht 3668, cuticle showing epidermal cell structure in stomatal condition; B = Utrecht 3665, cuticle showing epidermal cell structure in stomatal condition. Note well-developed stomatal ledges on guard cells. C-E = XXII: C = Utrecht 3786, cuticle showing epidermal cell structure in stomatal condition; D = Utrecht 3786, cuticle showing epidermal cell structure in non-stomatal condition. Note pitted cell walls. E = Utrecht 3786, cuticle showing epidermal cell structure in stomatal condition. Detail of stoma displaying stomatal ledges.

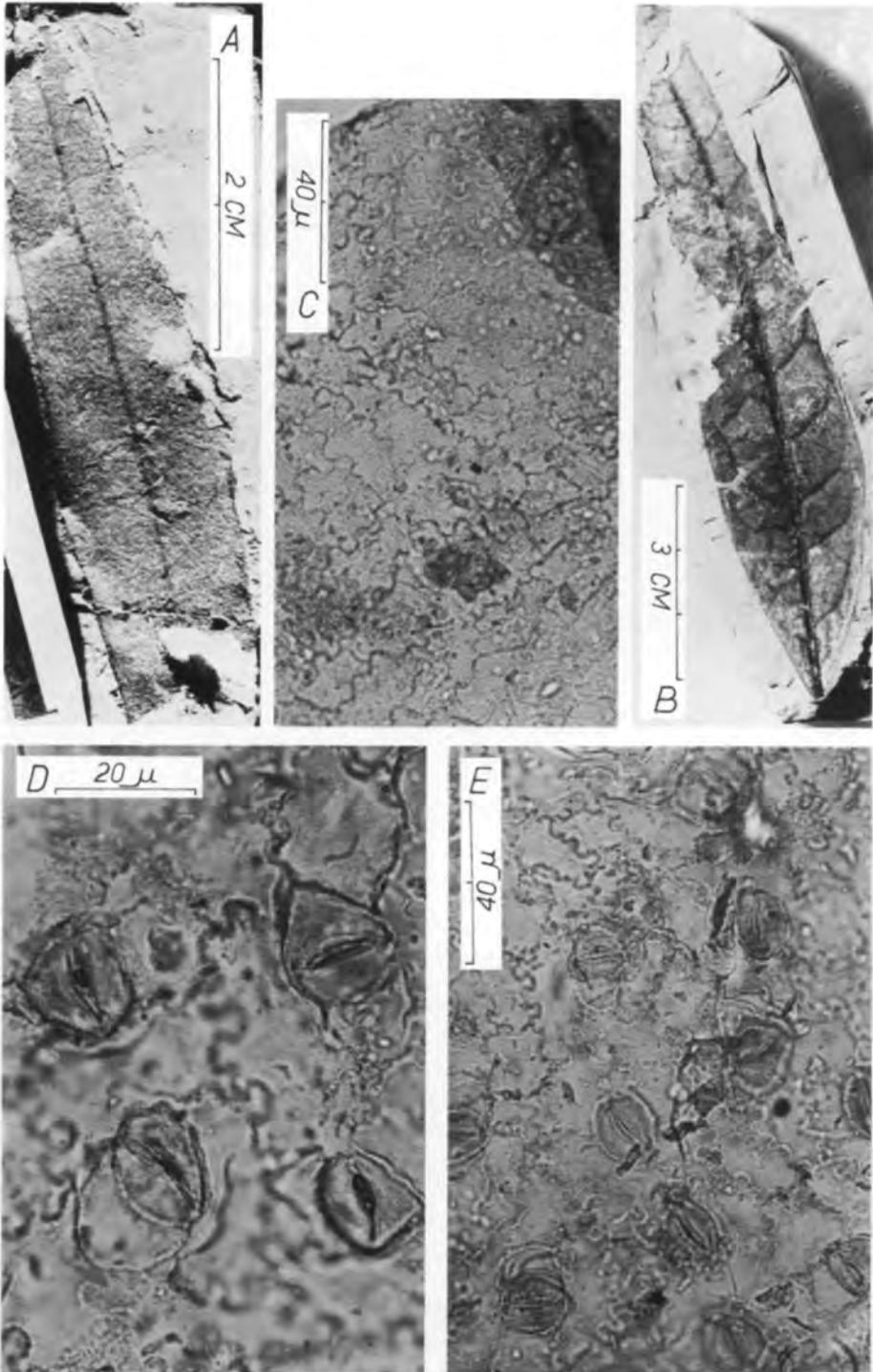


PLATE 17

A = XXII: Utrecht 3786. B-E = XXIII: B = Utrecht 3774; C = Utrecht 3774, cuticle showing epidermal cell structure in non-stomatal condition; D = Utrecht 3773, detail of cuticle showing epidermal cell structure in stomatal condition. Note highly undulate cell walls and rhombic stomata. E = Utrecht 3773, general view of cuticle showing epidermal cell structure in stomatal condition.

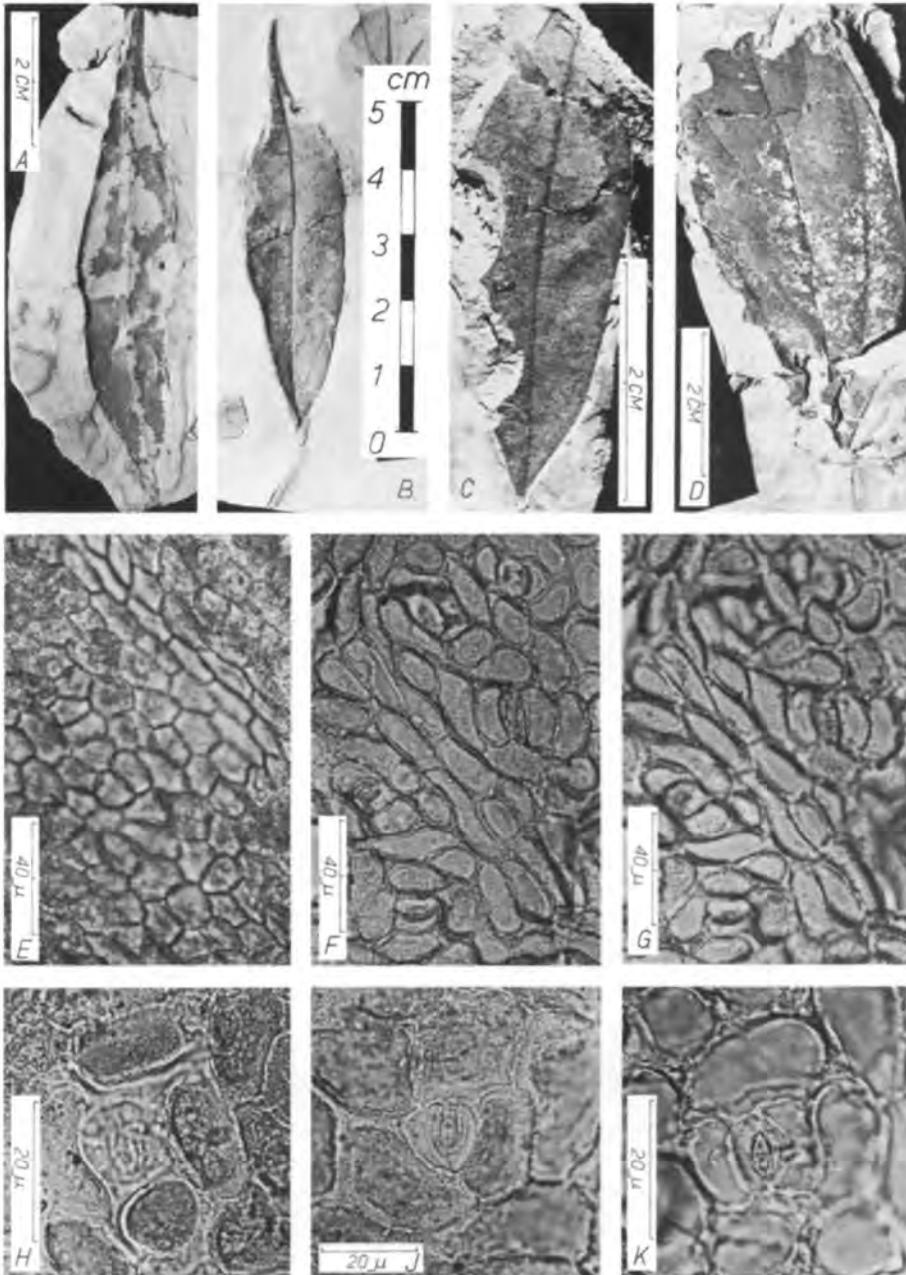


PLATE 18

A-K = XXIV: A = Utrecht 3827; B = Berlin 346; C = Utrecht 3829; D = Utrecht 3826; E = Utrecht 3827, cuticle showing epidermal cell structure in non-stomatal condition; F = Utrecht 3827, cuticle showing epidermal cell structure in stomatal condition, low focus; G = Utrecht 3827, same field as F, but high focus. Note the domed nature of the cells. H = Utrecht 3827, stoma with accessory cells. Note sunken stoma and domed accessory cells. J = Utrecht 3826, stoma with accessory cells; K = Utrecht 3827, stoma and accessory cells, low focus.

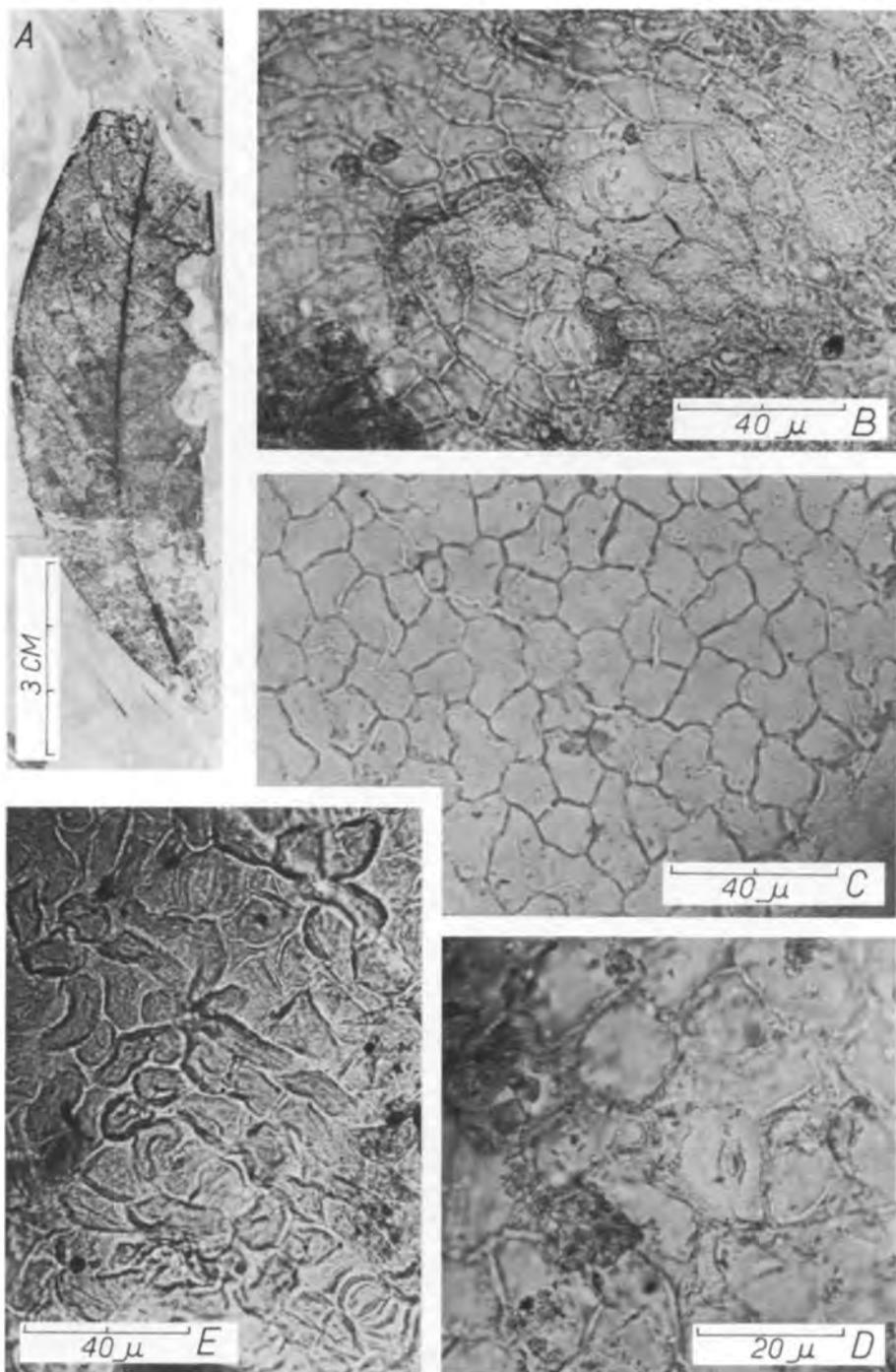


PLATE 19

A-E = XXV: A = Utrecht 3822; B = Utrecht 3822, cuticle showing epidermal cell structure in stomatal condition; C = Utrecht 3820, cuticle showing epidermal cell structure in non-stomatal condition; D = Utrecht 3822, detail showing stoma and associated cells; E = Utrecht 3820, general view of epidermal cell structure in stomatal condition. Note the domed cells.

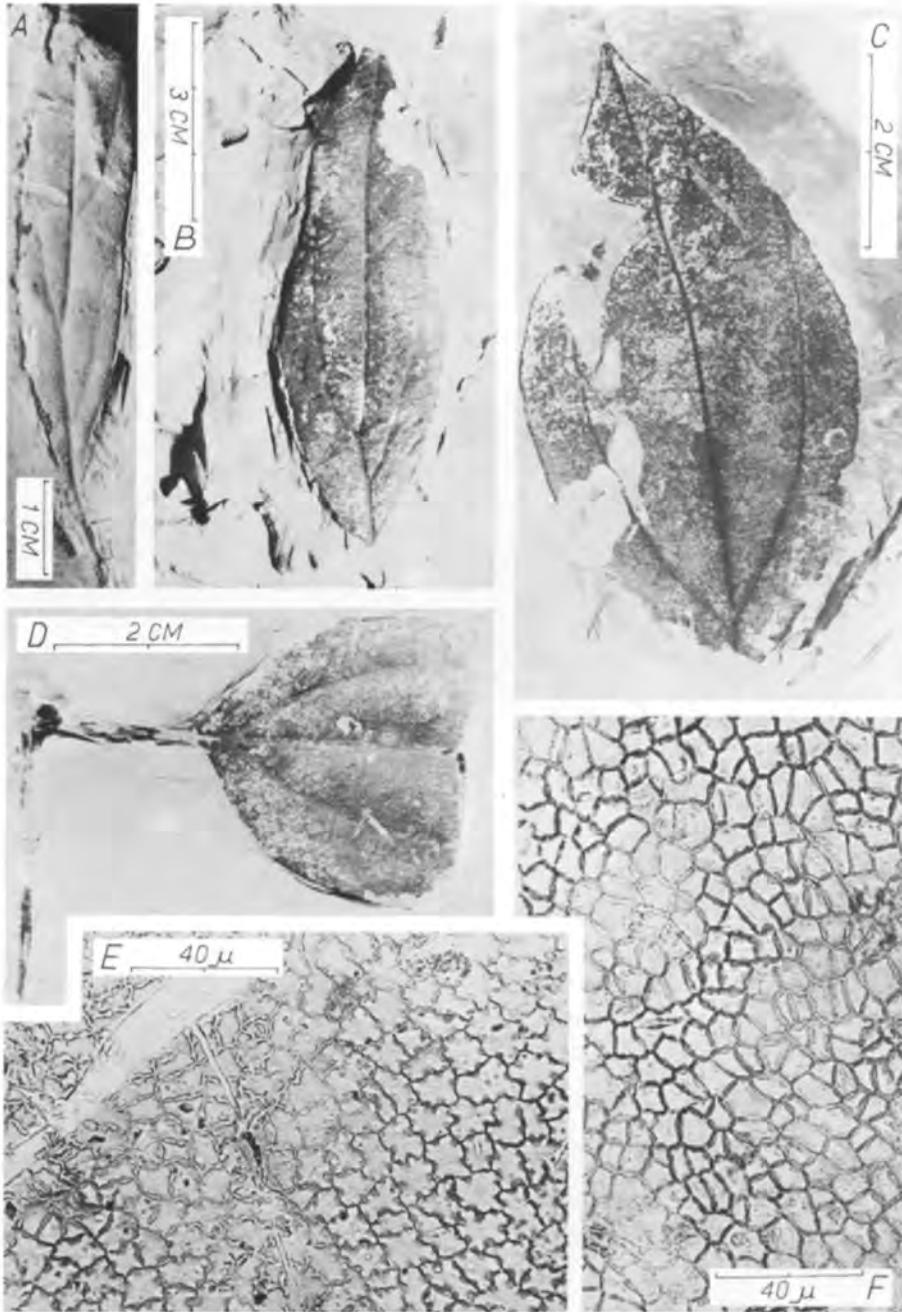


PLATE 20

A-F = XXVI: A = Utrecht 3279; B = Utrecht 3262; C = Utrecht 3270; D = Utrecht 3260; E = Utrecht 3285, cuticle showing epidermal cell structure in non-stomatal condition. Note the undulate cell walls and the presence of hemispherical projections; F = Utrecht 3282 A, cuticle showing epidermal cell structure in non-stomatal condition. Note straight-walled cells and odd stoma.

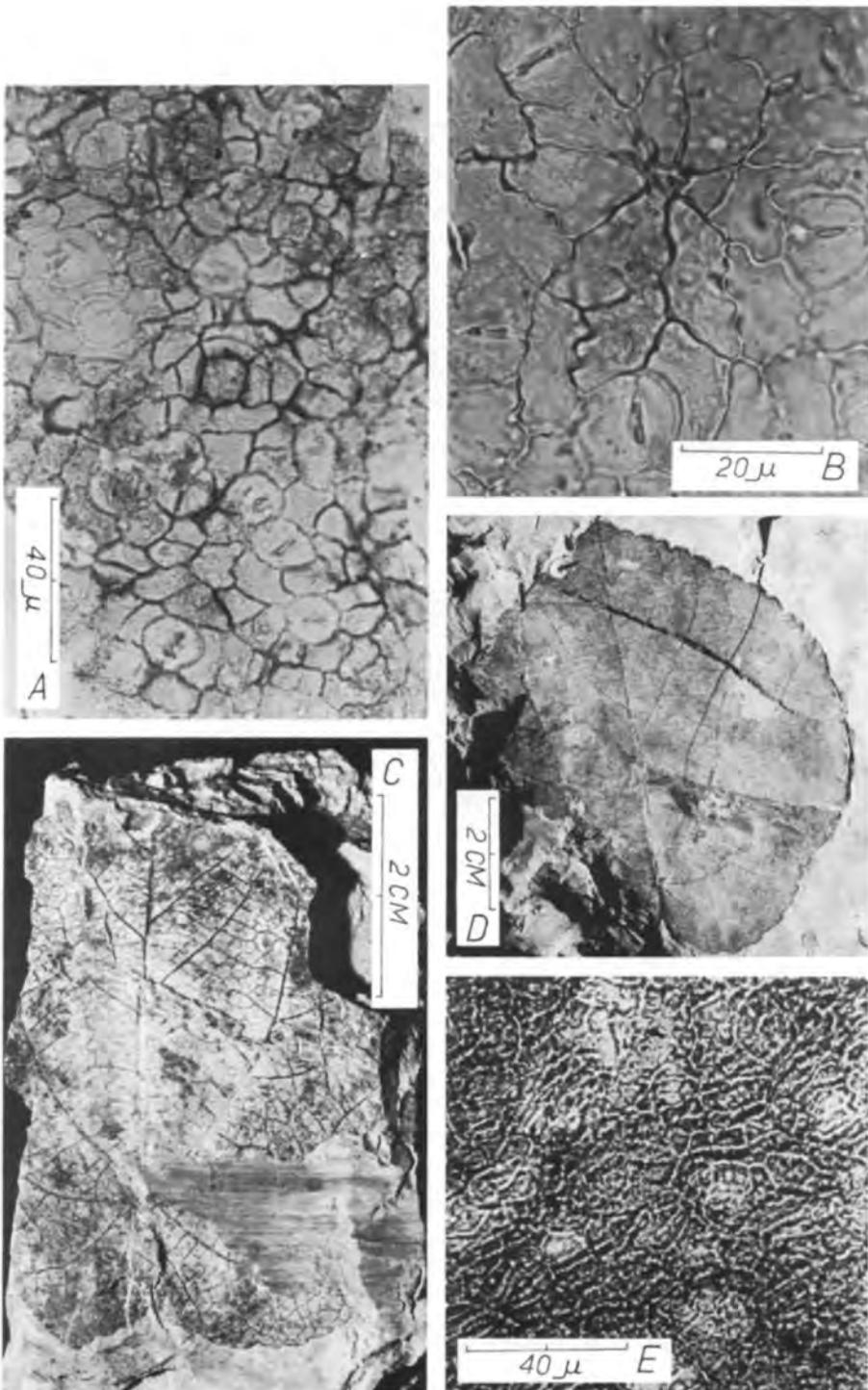


PLATE 21

A-B = XXVI: A = Utrecht 3286, general view of epidermal cell structure in stomatal condition; B = Utrecht 3269, detail of stomata and a hair base. Note asymmetrical shape of some of the stomata. C-E = XXVII: C = Utrecht 3477; D = Utrecht 3478 A; E = Utrecht 3478 A, cuticle showing epidermal cell structure. Lighter areas either represent stomata or hair bases.

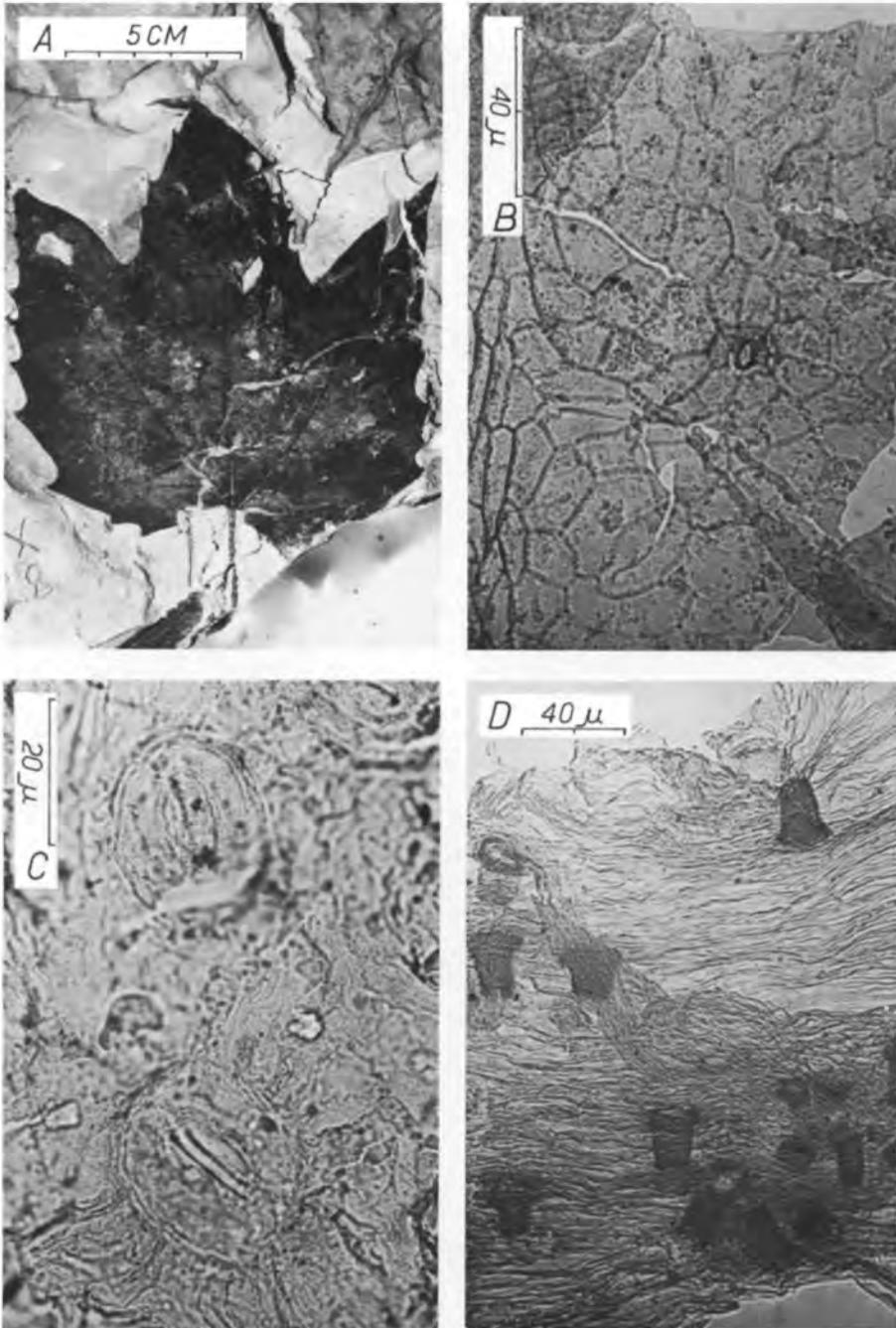


PLATE 22

A-D = XXVIII: A = Utrecht 3514; B = Utrecht 3509, cuticle showing epidermal cell structure in non-stomatal condition. Note the presence of a hair base. C = Utrecht 3509, cuticle showing epidermal cell structure in stomatal condition. Note fine striations. D = Utrecht 3509, detail over vein showing the presence of stump-like hair bases.

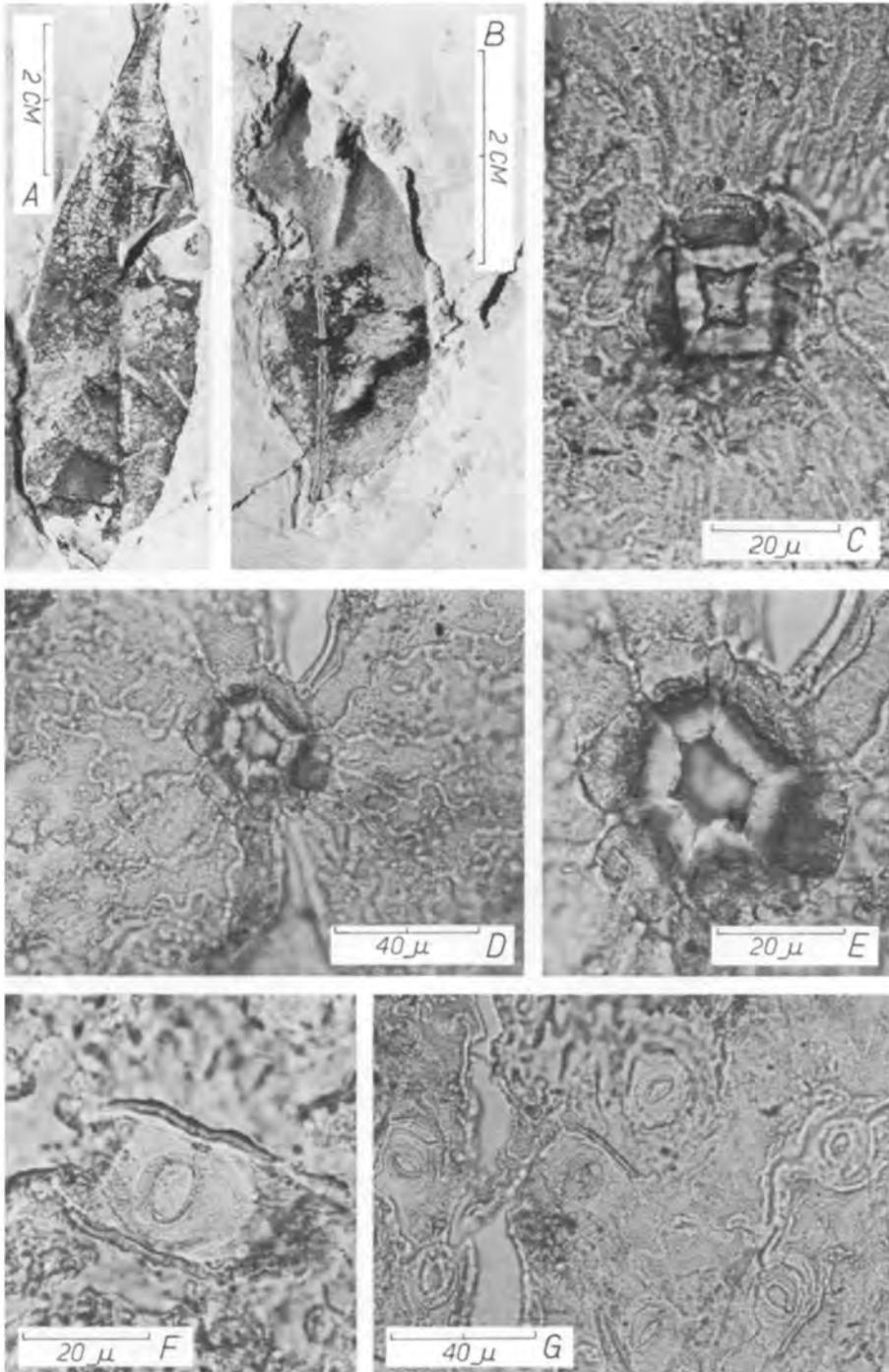


PLATE 23

A-G = XXIX: A = Utrecht 3575; B = Utrecht 3574; C = Utrecht 3574, detail of 4-sided hair base; D = Utrecht 3574, cuticle showing epidermal cell structure in non-stomatal condition; E = Utrecht 3574, detail of 6-sided hair base; F = Utrecht 3574, detail of stoma; G = Utrecht 3574, cuticle showing epidermal cell structure in stomatal condition.

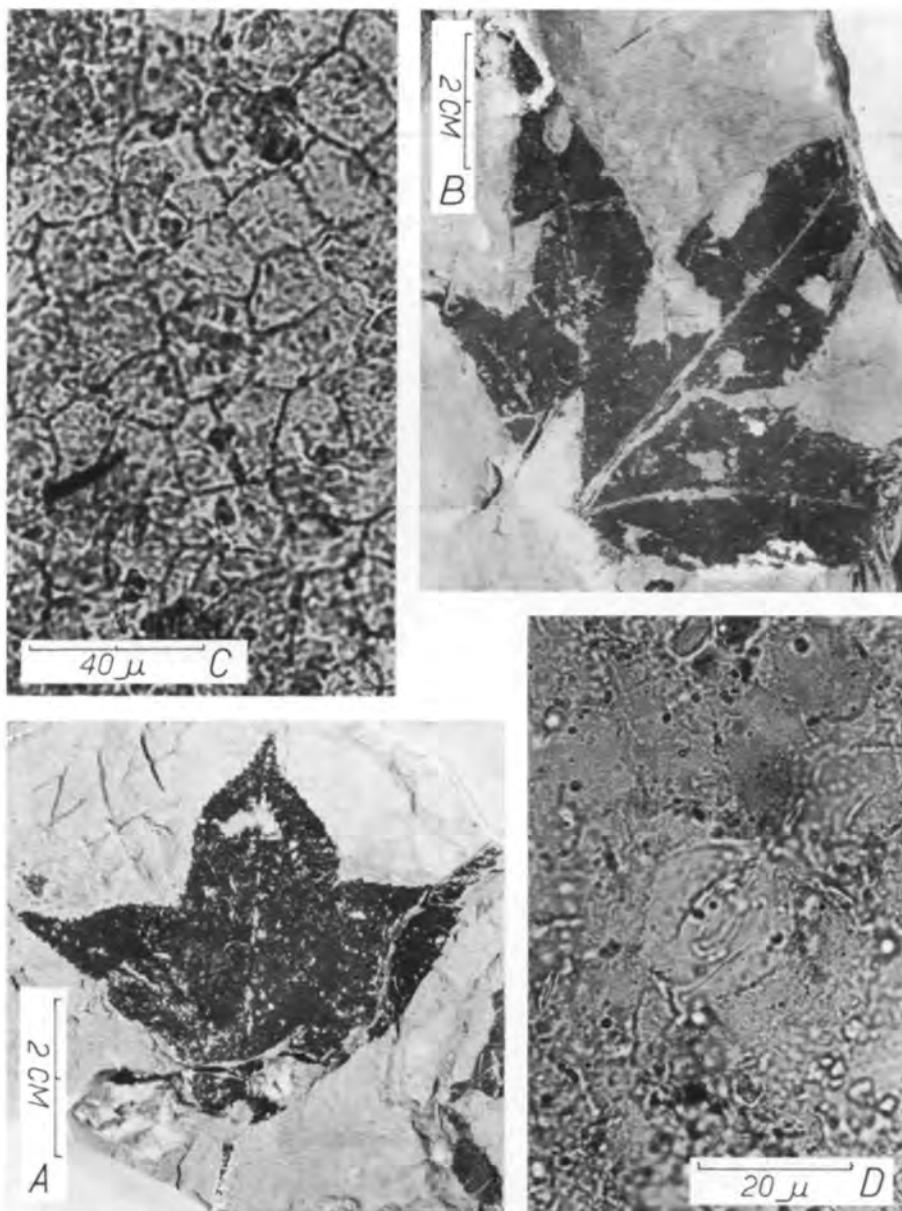


PLATE 24

A-D = XXX: A = Utrecht 3240, 3-lobed form; B = Utrecht 3245, 4-lobed form; C = Utrecht 3243, cuticle showing epidermal cell structure in non-stomatal condition; D = Utrecht 3234, cuticle showing epidermal cell structure in stomatal condition.

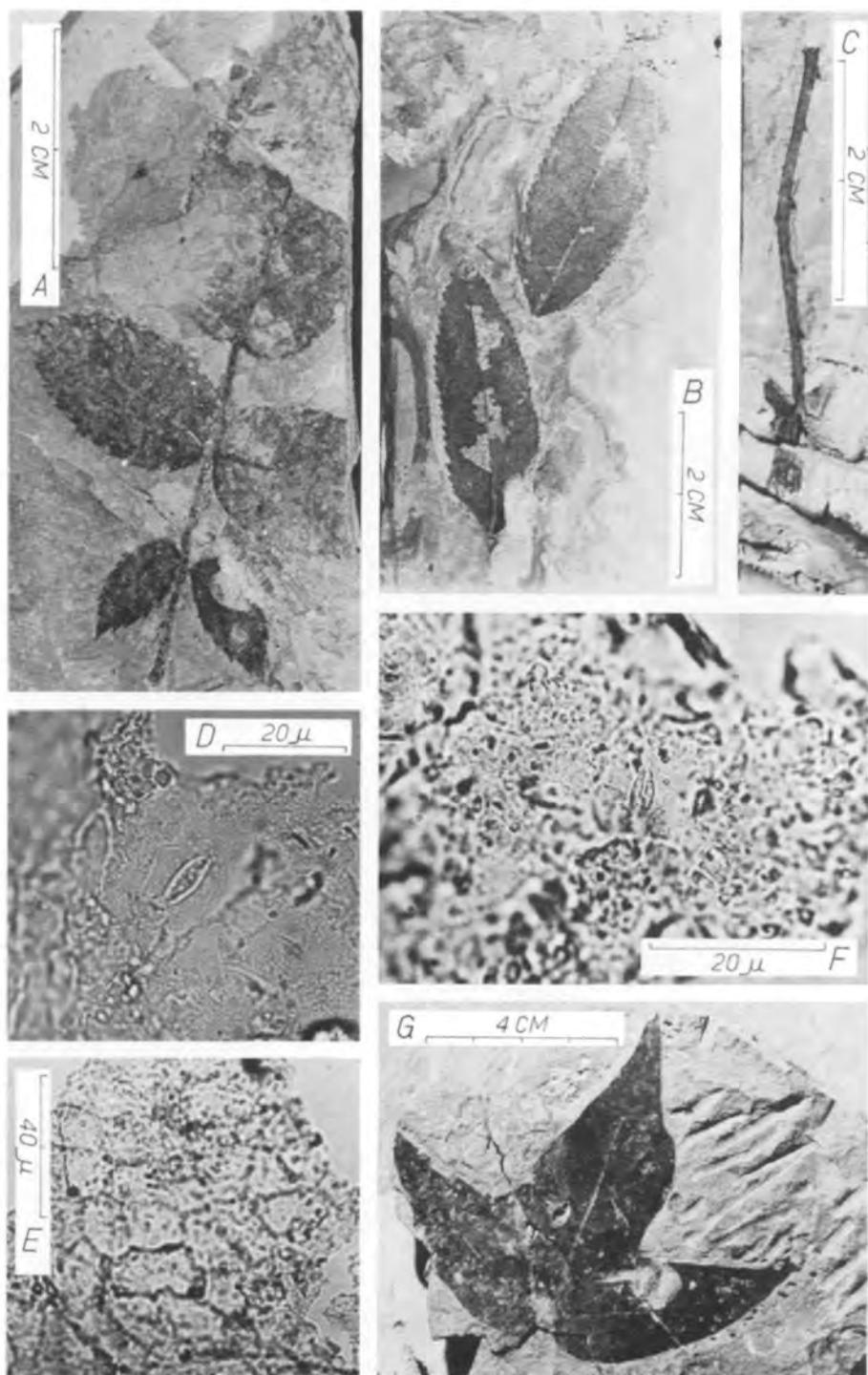


PLATE 25

A, C = XXXI: A = Cologne s.n.; C = Utrecht 3538. Note form of stipule. B = XXXII: Cologne, Coll. H. Weyland 1648. D-G = XXXIII: D = Utrecht s.n. (F 18), detail of stoma; E = Utrecht s.n. (F 18), cuticle showing epidermal cell structure in non-stomatal condition; F = Utrecht 3491, detail of stoma; G = Utrecht 3492.

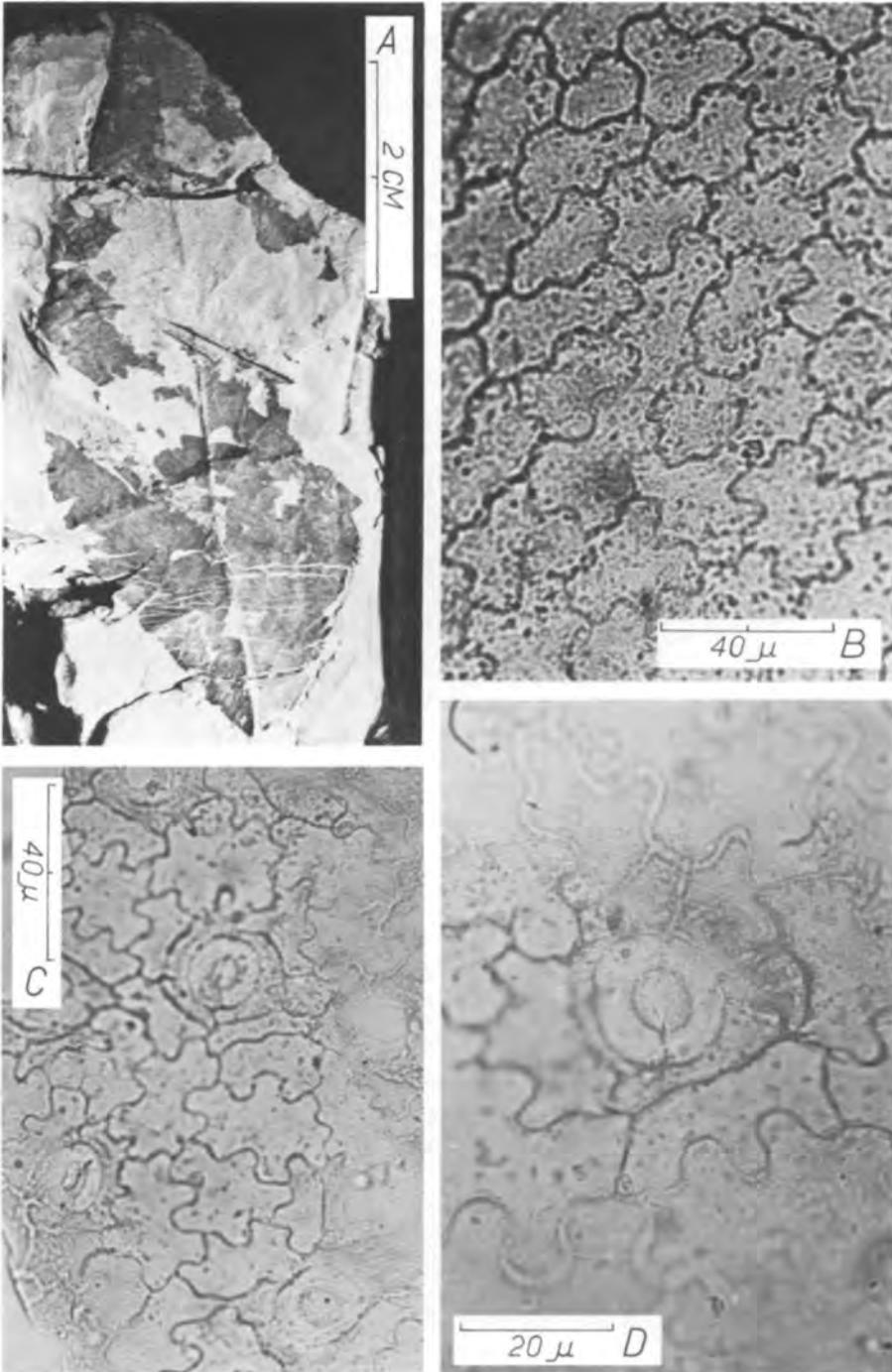


PLATE 26

A-D = XXXIV: A = Utrecht 3880; B = Utrecht 3880, cuticle showing epidermal cell structure in non-stomatal condition; C = Utrecht 3880, cuticle showing epidermal cell structure in stomatal condition; D = Utrecht 3880, detail of stoma and accessory cells.

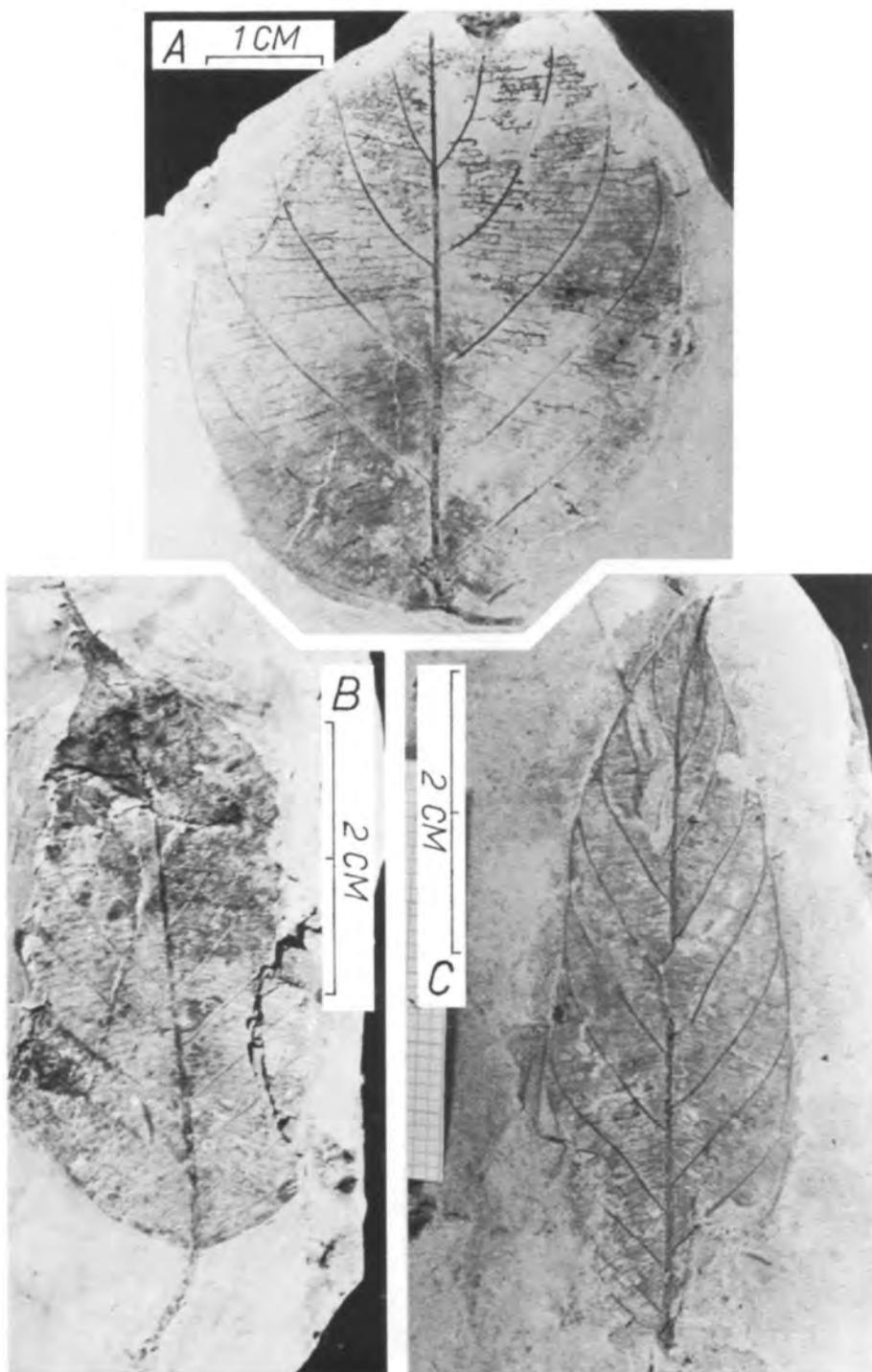


PLATE 27

A-C = XXXV: A = Cologne, Coll. H. Weyland 1547; B = Utrecht 3531; C = Cologne, Coll. H. Weyland 1736.

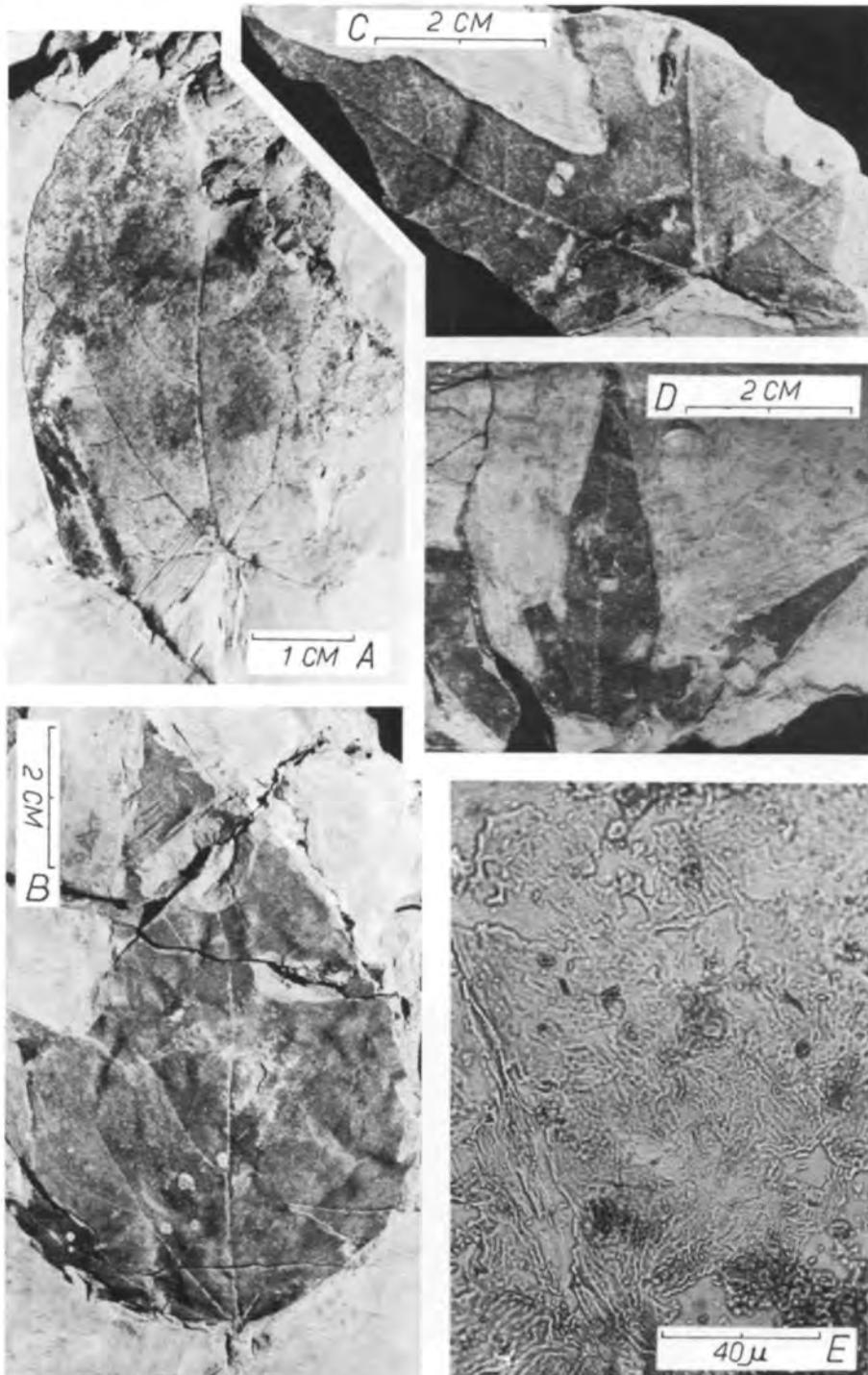


PLATE 28

A-B, E = XXXVII: A = Utrecht 3737; B = Utrecht 3740; E = Utrecht 3738,
 cuticle from non-stomatal surface of the leaf. C-D = XXXVI: C = Utrecht 3882;
 D = Utrecht 4151 A.

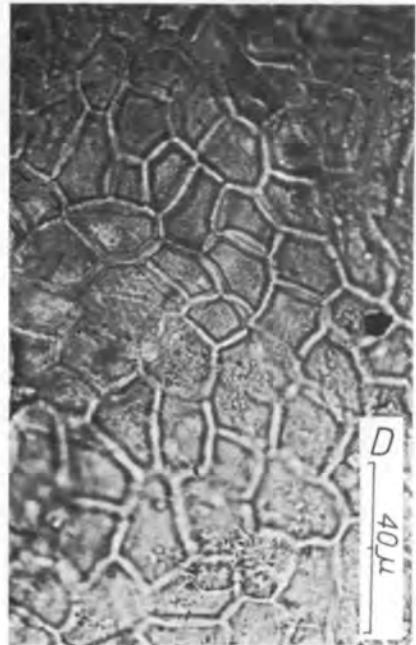
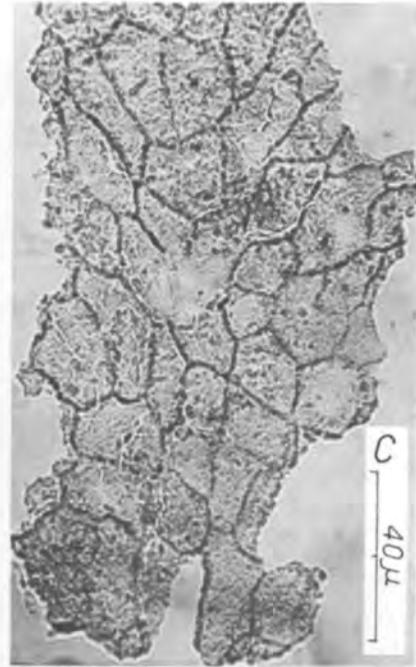
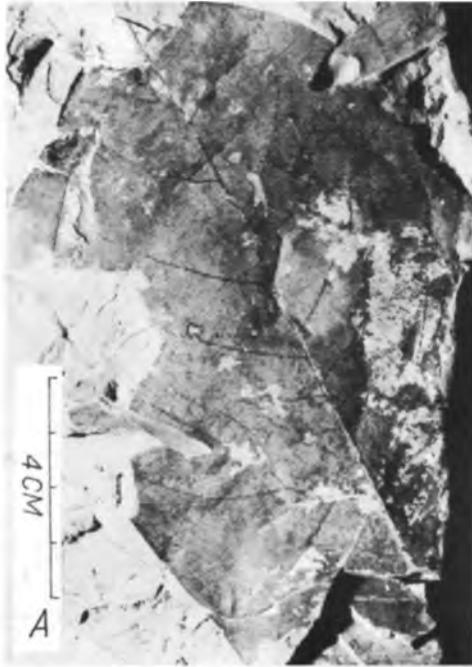


PLATE 29

A-D = XXXVIII: A = Utrecht 3927; B = Berlin 476; C = Utrecht 3928, cuticle showing epidermal cell structure in non-stomatal condition; D = Utrecht 3927, cuticle showing epidermal cell structure in non-stomatal condition.

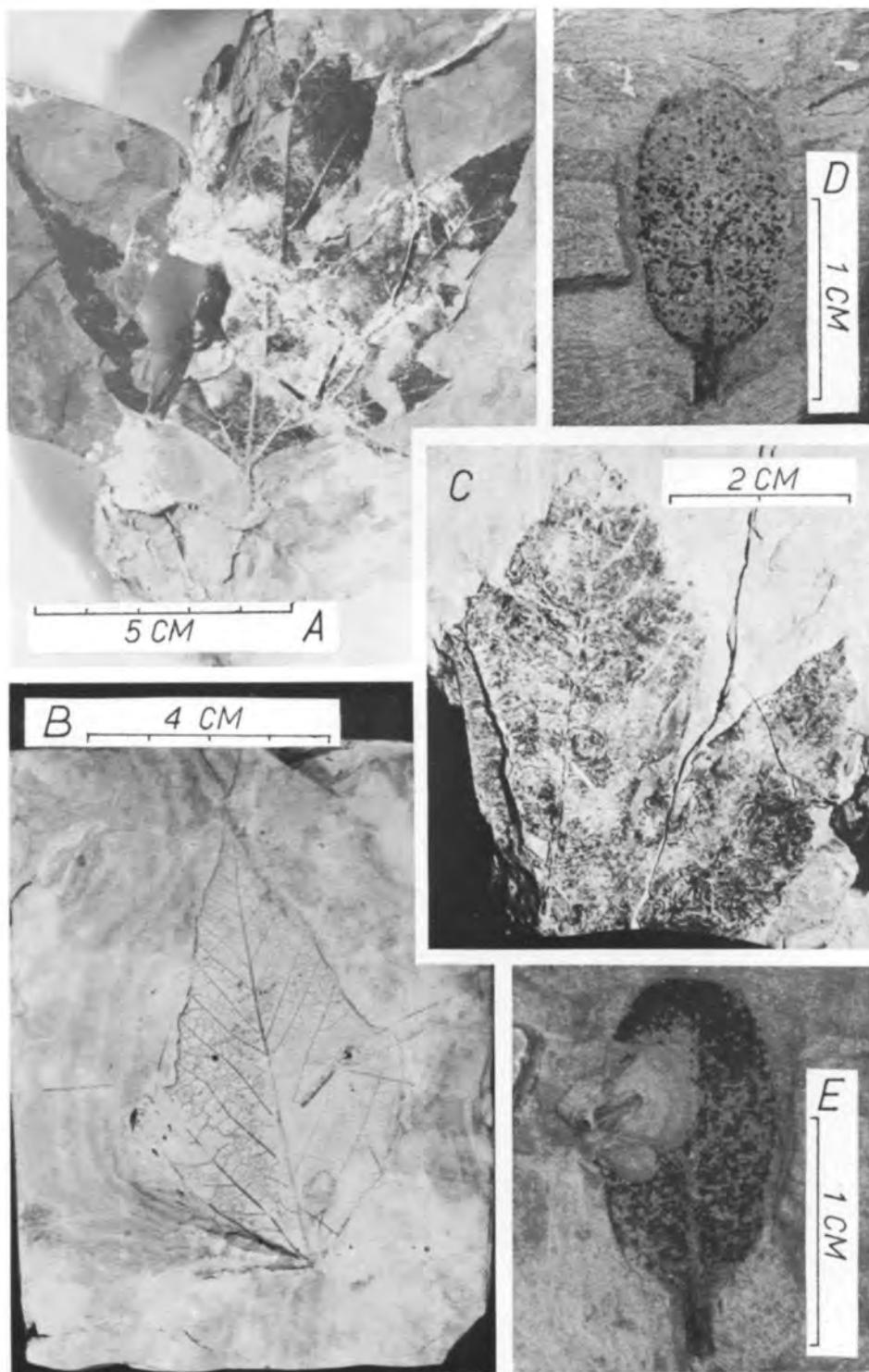


PLATE 30

A = XXXIX: Utrecht 3785 B. B = XLI: Cologne, Coll. H. Weyland s.n. C = XL:
 Utrecht 3775 A. D-E = XLII: D = Cologne, Coll. H. Weyland 1408; E = Berlin
 351.

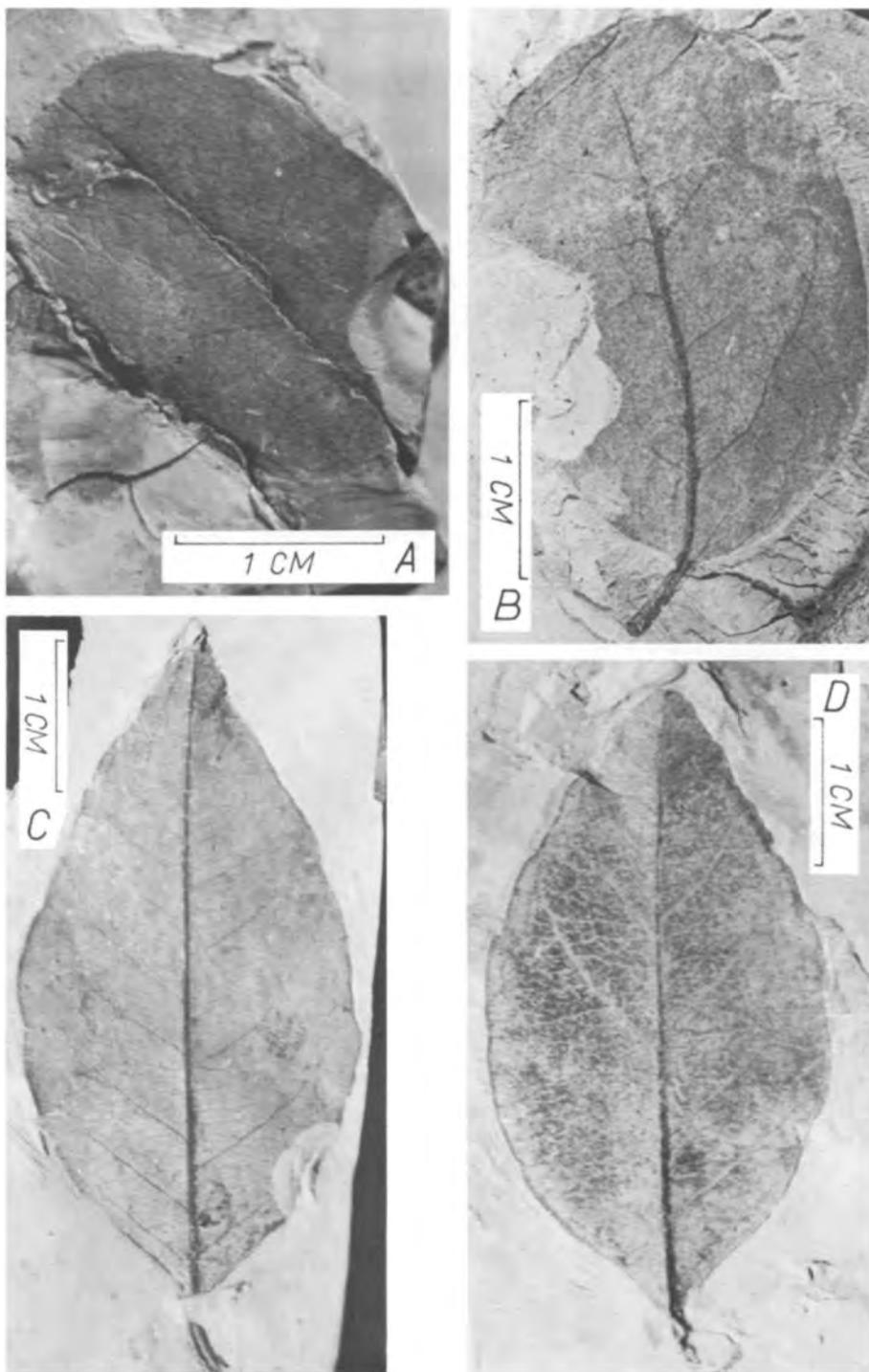


PLATE 31

A = XLIII: Berlin 330. B = XLIV: Cologne, Coll. W. Jansen 84. C-D = XLV:
C = Berlin 264; D = Utrecht 3888.

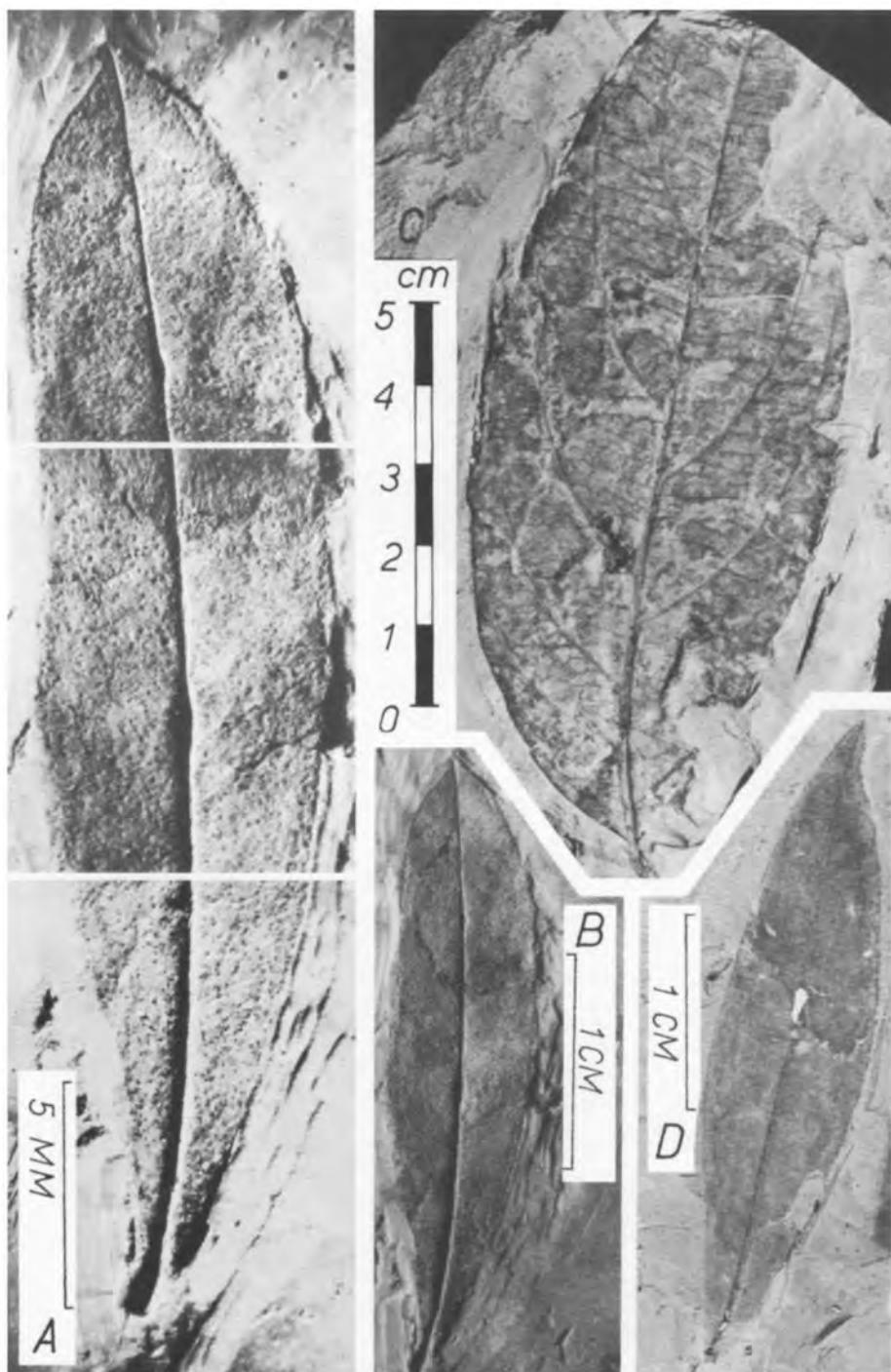


PLATE 32

A-B, D = XLVII: A = Berlin 324. Note the presence of rounded pits scattered over leaf surface; B = Berlin 324; D = Cologne, Coll. H. Weyland 1406; C = XLVI: Utrecht 3784.

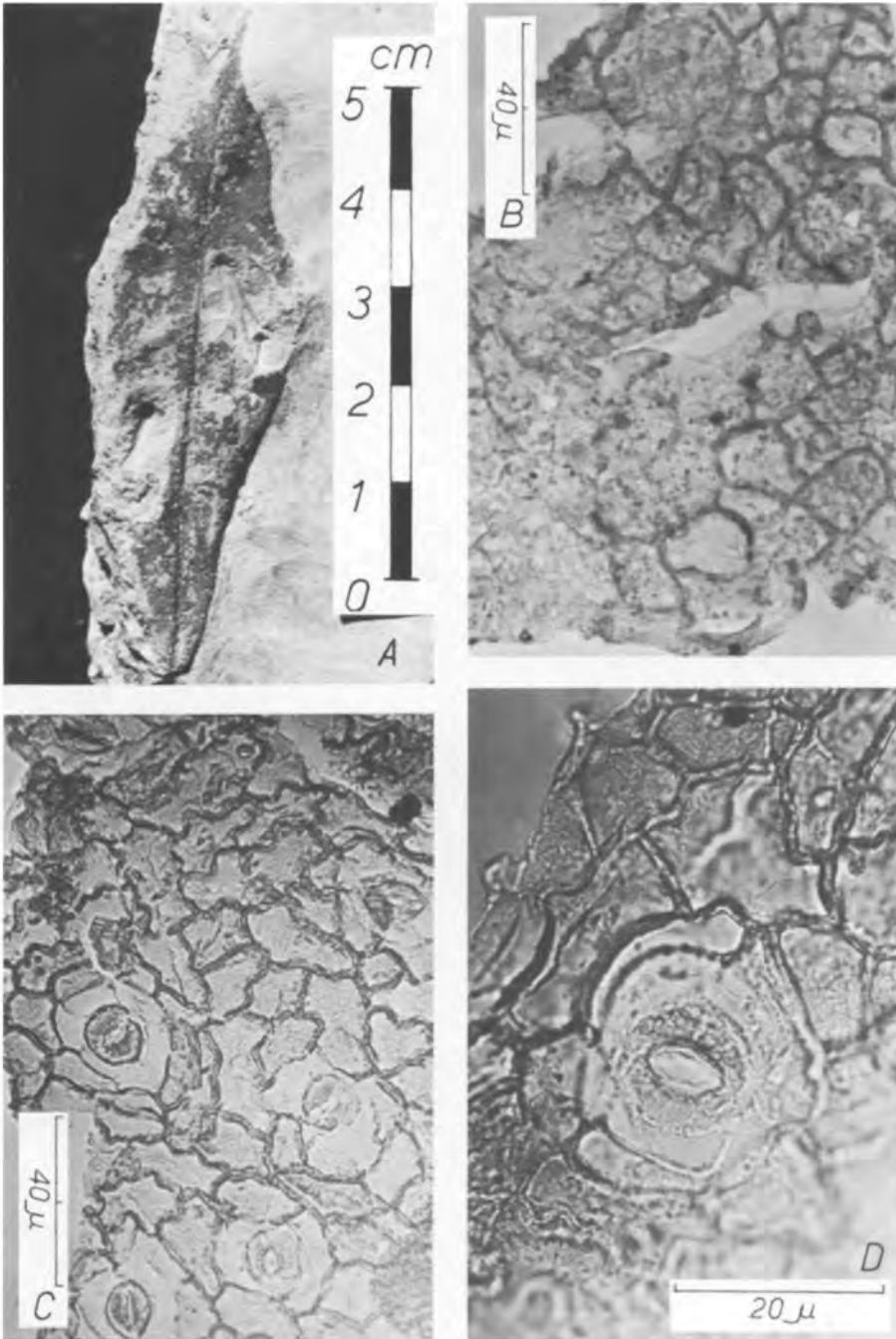


PLATE 33

A-D = XLVIII: A = Utrecht 3830; B = Utrecht 3830, cuticle showing epidermal cell structure in non-stomatal condition; C = Utrecht 3830, cuticle showing epidermal cell structure in stomatal condition; D = Utrecht 3830, detail of stoma and accessory cells.

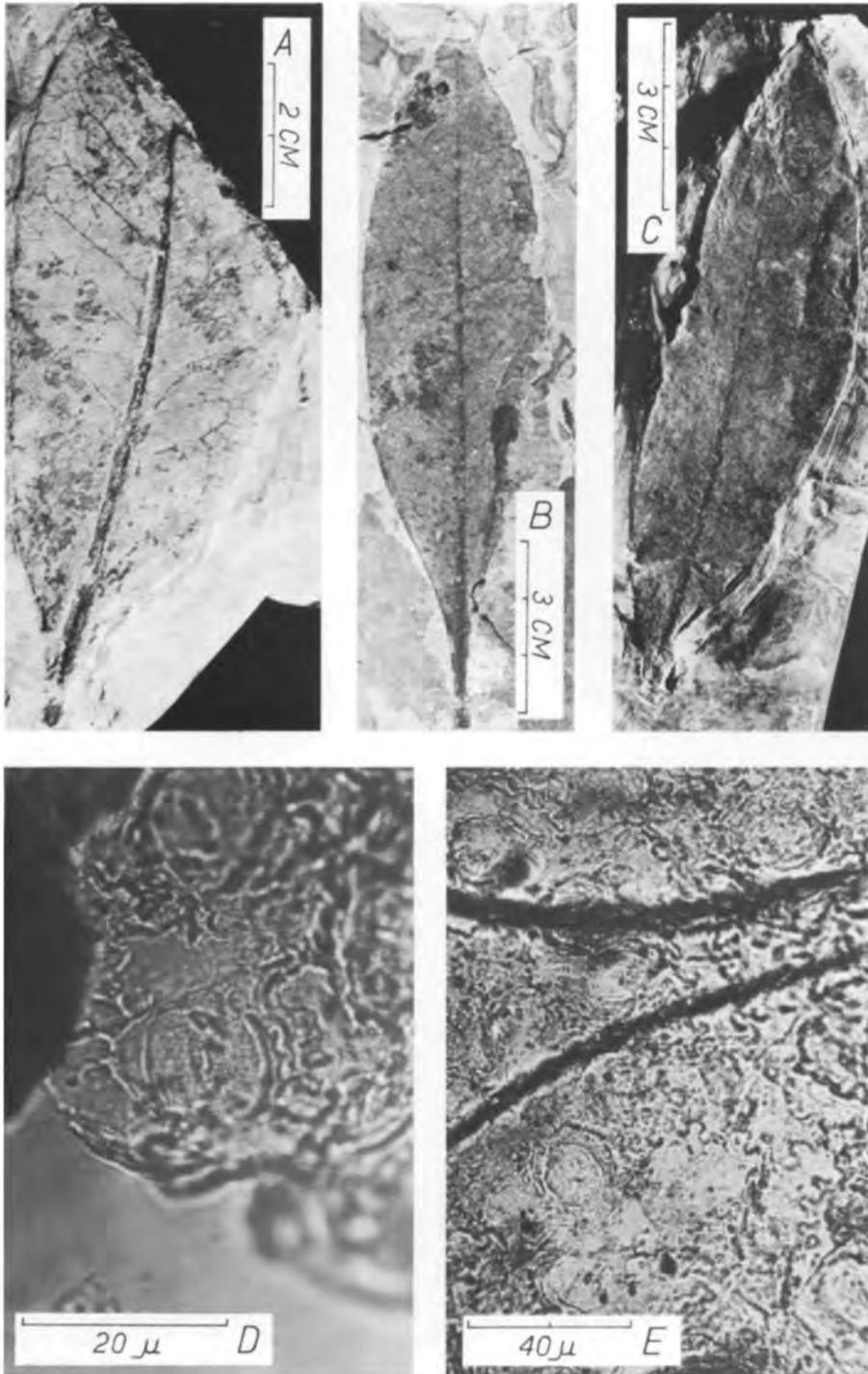


PLATE 34

A-E = XLIX: A = Utrecht 3813; B = Cologne, Coll. H. Weyland 2020; C = Berlin 282 (Type of *Illicium fliegeli* Weyland); D = Cologne, Coll. H. Weyland 1458, detail of stoma; E = Cologne, Coll. H. Weyland 1458, cuticle showing epidermal cell structure in stomatal condition.

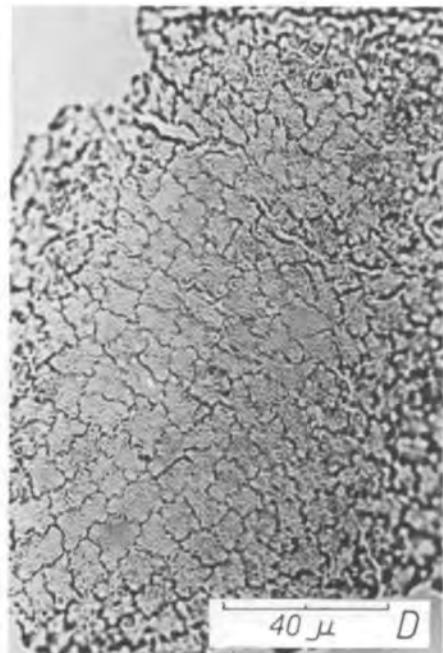
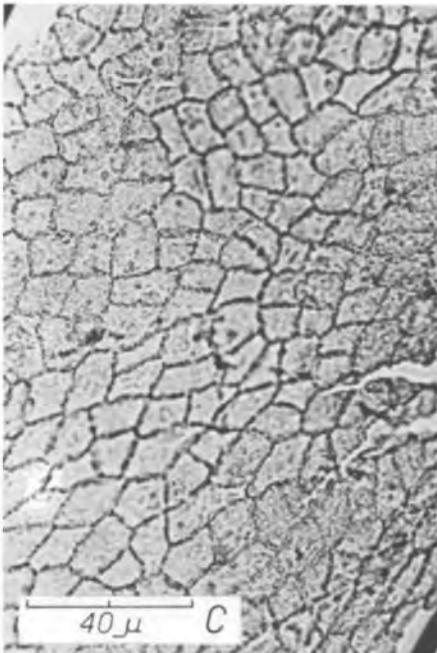


PLATE 35

A-D = L: A = Utrecht 3351; B = Utrecht 3352; C = Utrecht 3352, cuticle showing epidermal cell structure in non-stomatal condition; D = Utrecht 3302, cuticle showing epidermal cell structure in non-stomatal condition.

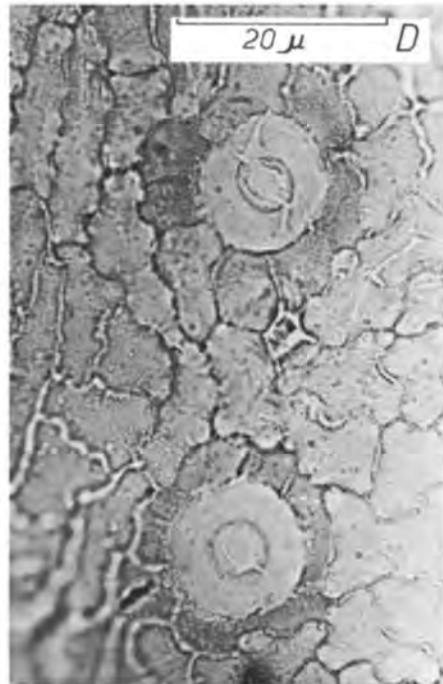
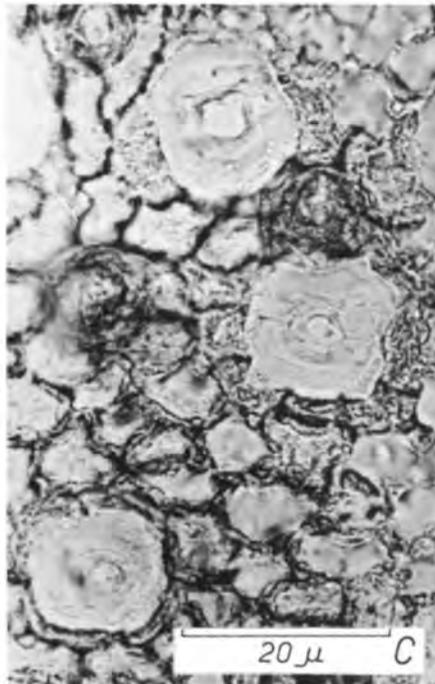
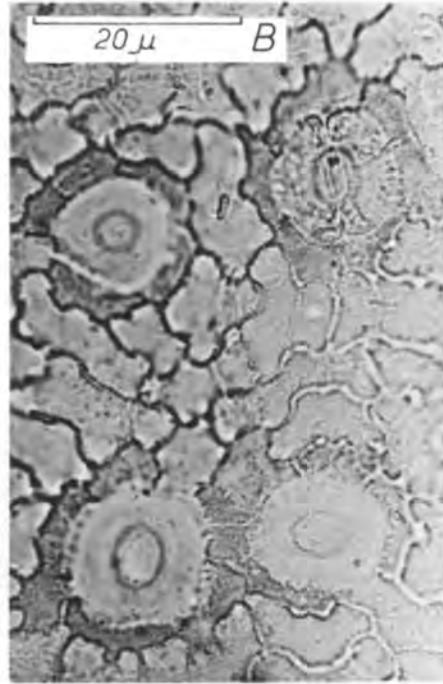
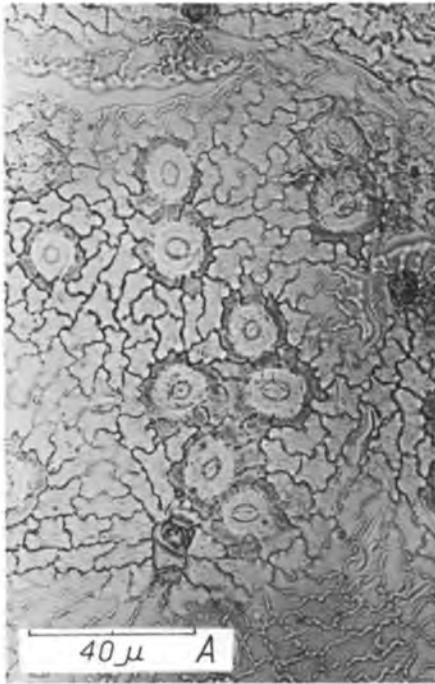


PLATE 36

A-D = L: A = Utrecht 3320, cuticle showing epidermal cell structure in stomatal condition. Note tendency of stomata to be grouped and the presence of a number of hair bases. B = Utrecht 3320, detail of stomata showing the presence of small accessory cells. Cuticle over accessory cells thickened. Note that cells with undulate walls are present between the stomata. C = Utrecht 3337, detail of stomata and hair bases; D = Utrecht 3320, detail of stomata with up to 8 accessory cells.

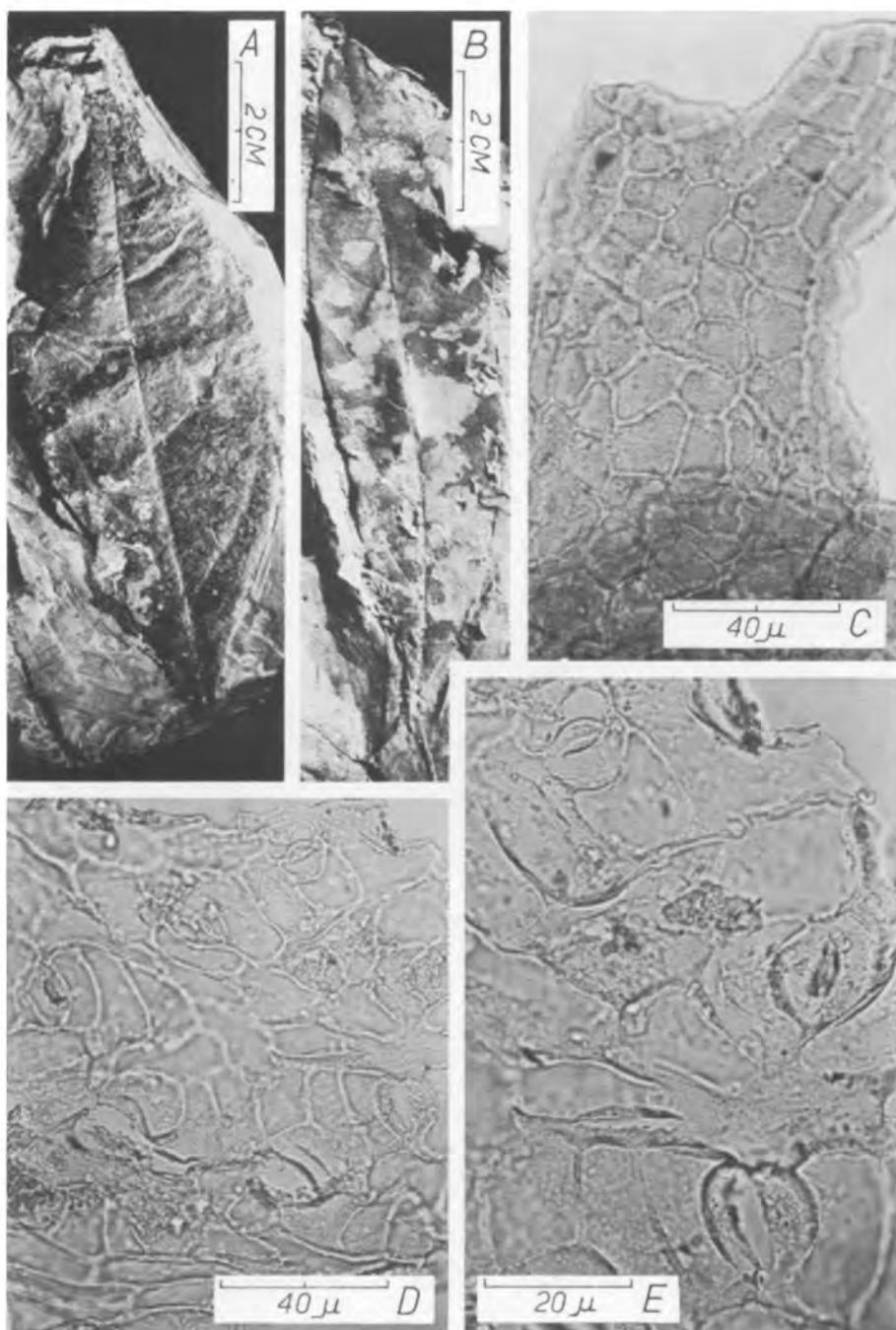


PLATE 37

A-E = LI: A = Berlin 269; B = Utrecht 3818; C = Utrecht 3819, cuticle showing epidermal cell structure in non-stomatal condition; D = Utrecht 3819, cuticle showing epidermal cell structure in stomatal condition; E = Utrecht 3819, detail of stomata and accessory cells.

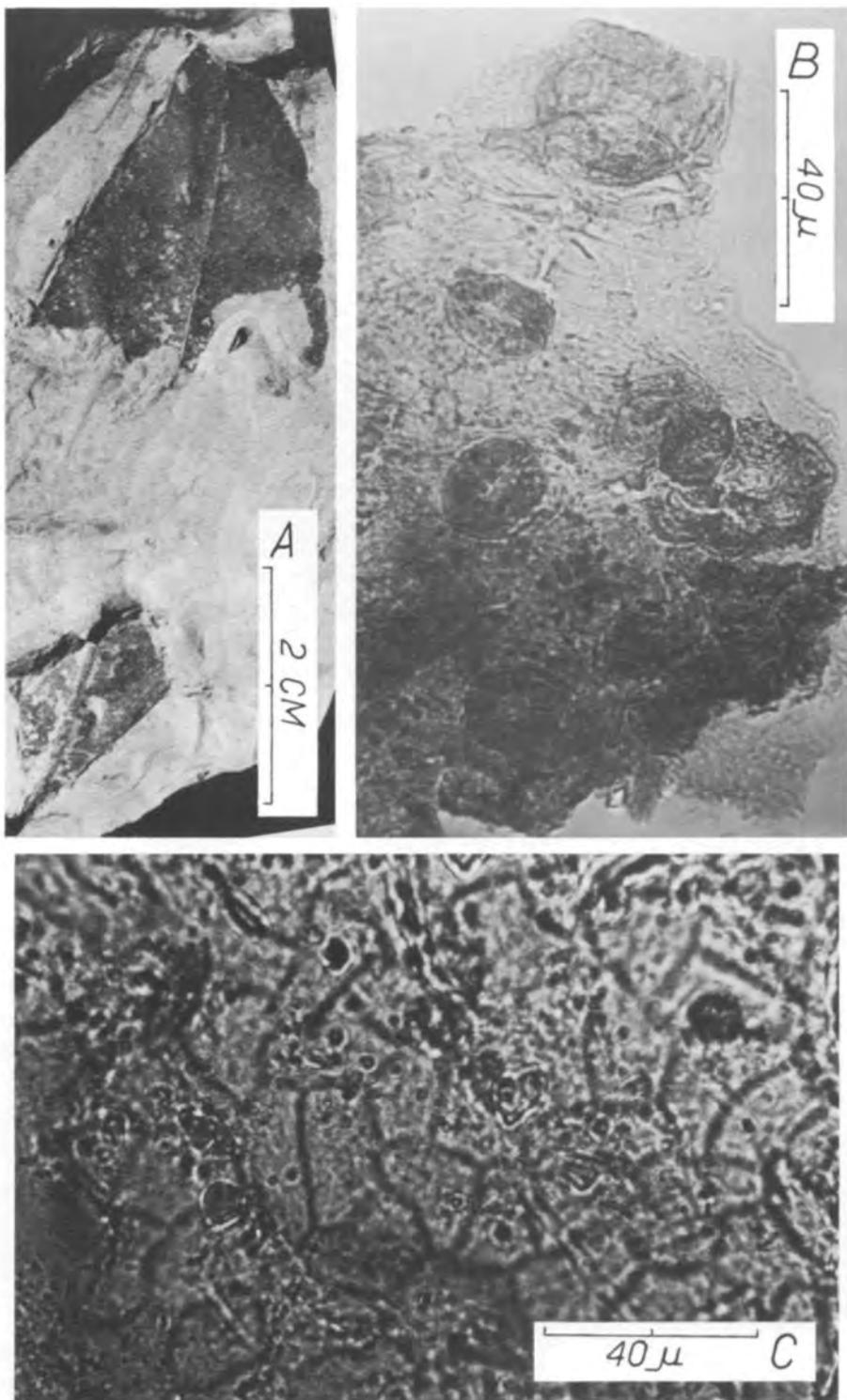


PLATE 38

A-C = LII: A = Utrecht 3840; B = Utrecht 3840, cuticle showing epidermal cell structure in stomatal condition. Note the presence of two hair bases. C = Utrecht 3840, cuticle showing epidermal cell structure in non-stomatal condition.

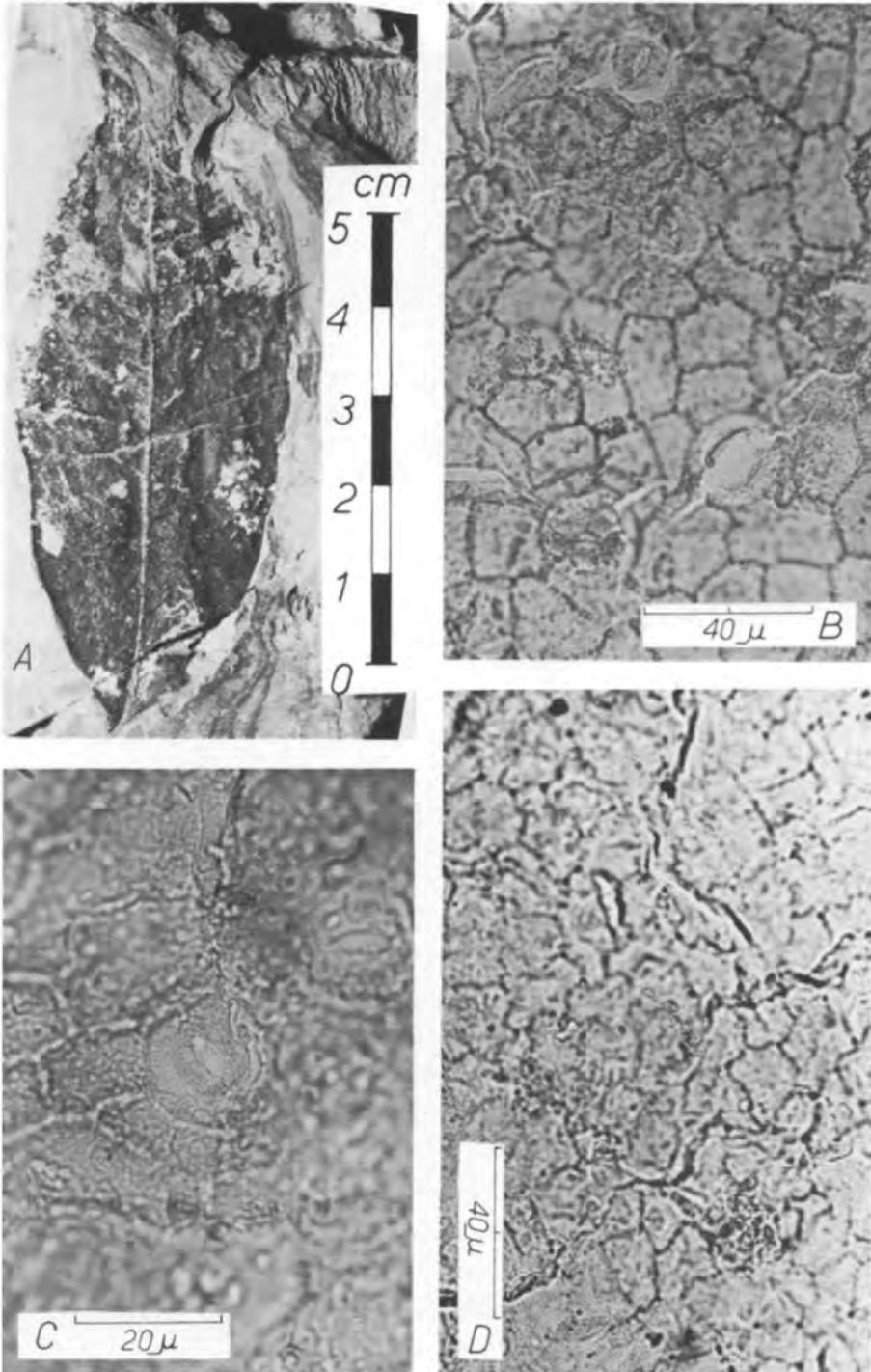


PLATE 39

A-D = LIII: A = Utrecht 3859; B = Utrecht 3860, cuticle showing epidermal cell structure in stomatal condition; C = Utrecht 3859, detail of stomata; D = Utrecht 3859, cuticle showing epidermal cell structure in non-stomatal condition.

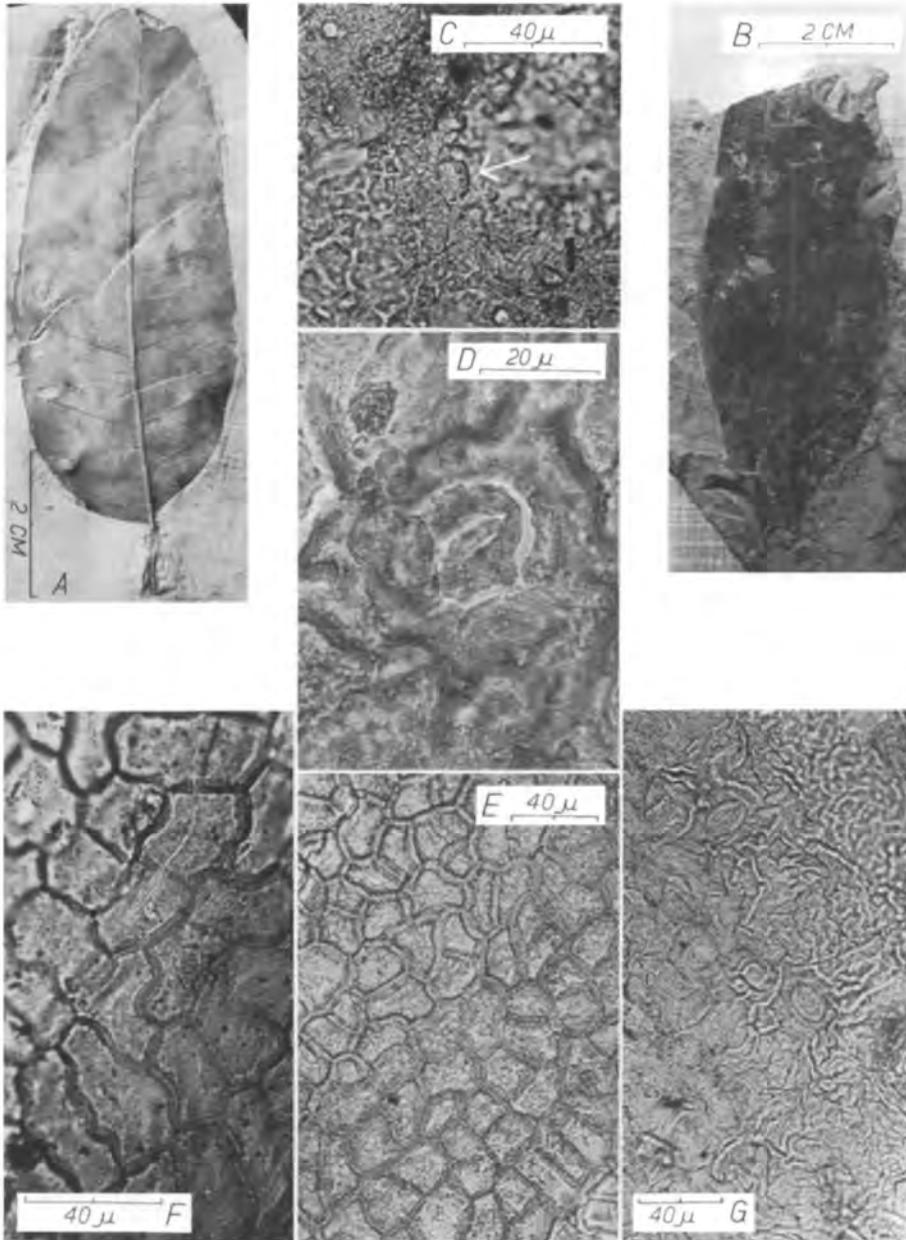


PLATE 40

A, C = LIV: A = Berlin 341; C = Utrecht 3811, cuticle showing epidermal cell structure in stomatal condition (position of a stoma indicated by arrow). B, D-G = LV: B = Utrecht 3892; D = Utrecht 3893, detail of stoma; E = Utrecht 3891, cuticle showing epidermal cell structure in non-stomatal condition; F = Utrecht 3891, detail of epidermal cell structure in non-stomatal condition; G = Utrecht 3893, cuticle showing epidermal cell structure in stomatal condition. Note coarse striae.

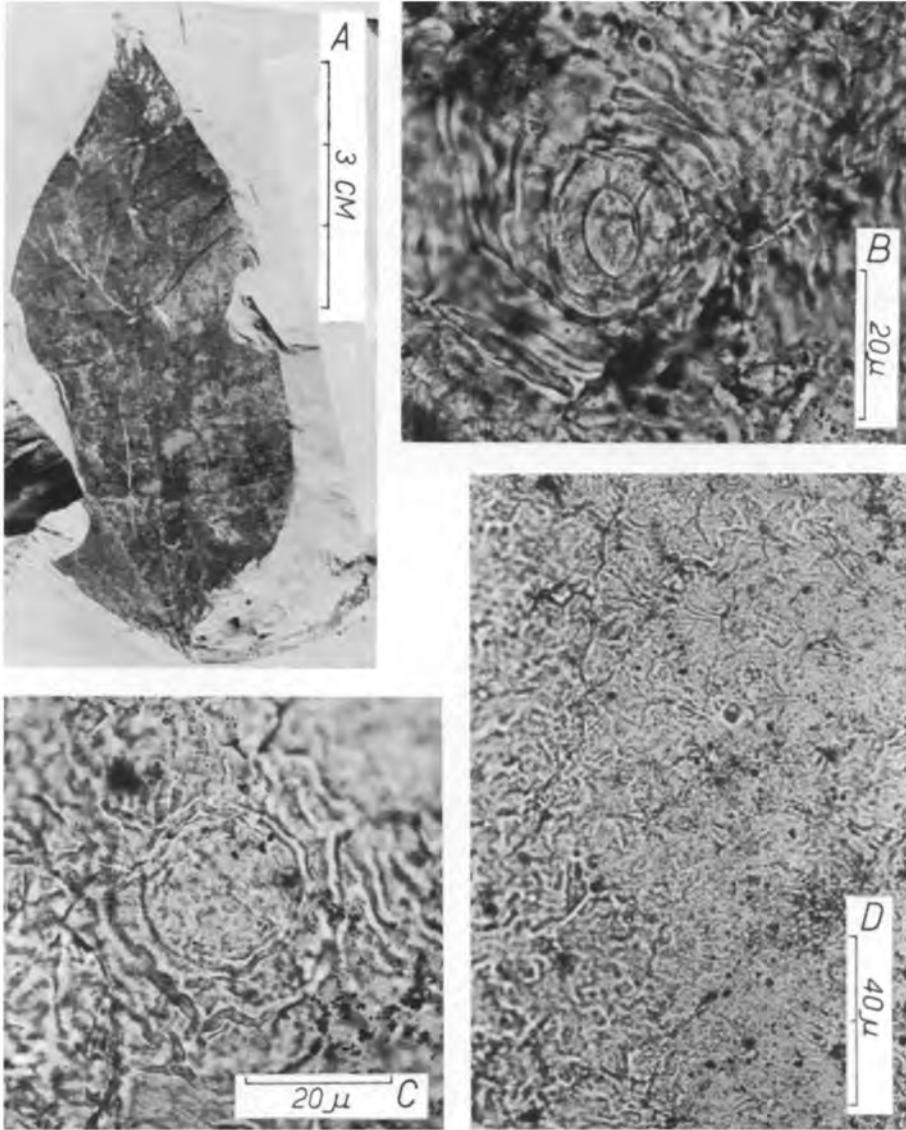


PLATE 41

A-D = LVI: A = Berlin s.n. (K 154); B = Berlin s.n. (K 154), detail of stoma. Note the presence of numerous striae. C = Berlin s.n. (K 154), trichome base; D = Berlin s.n. (K 154), cuticle showing epidermal cell structure in non-stomatal condition. Note the presence of fine striae.

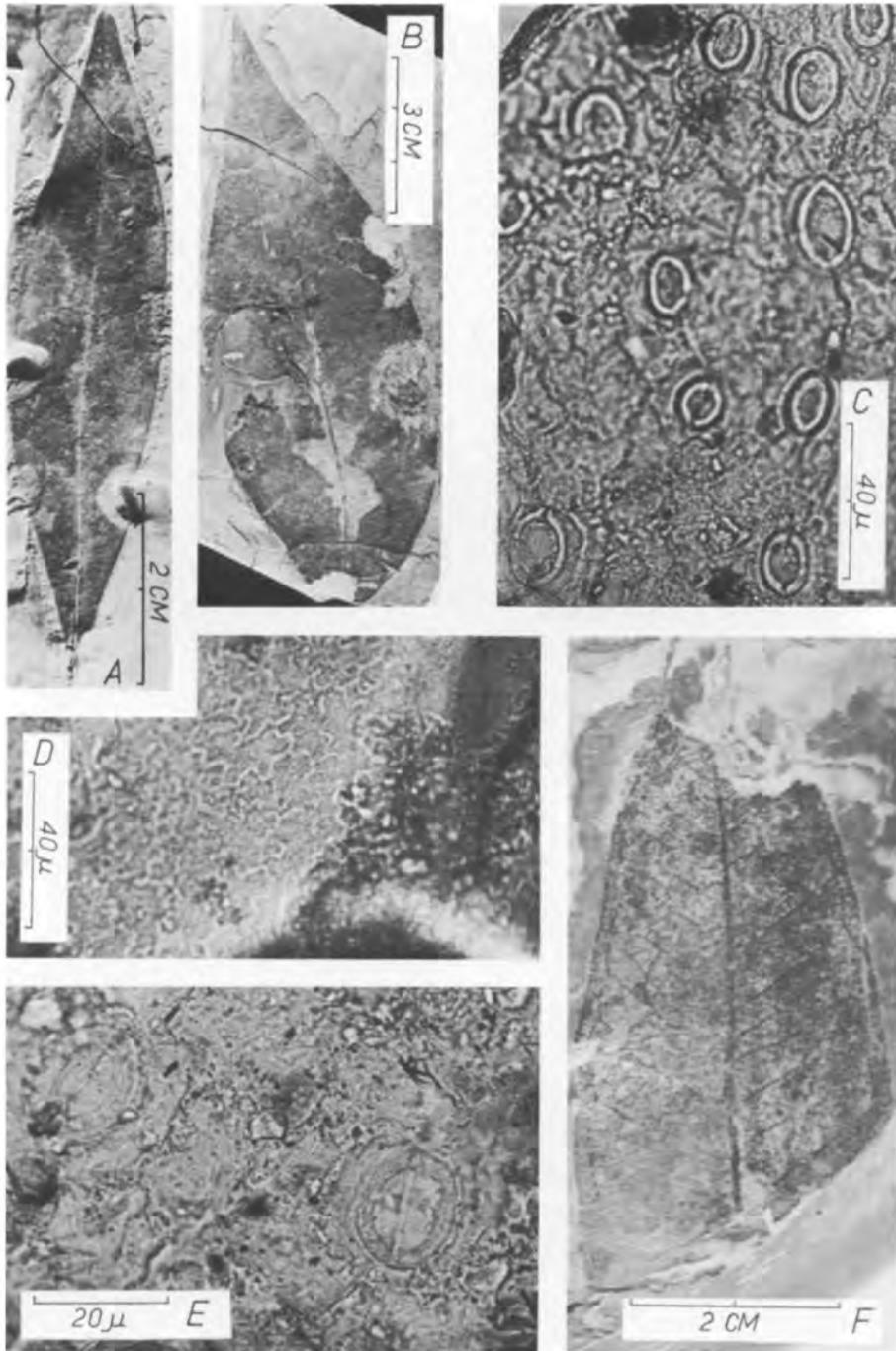


PLATE 42

A-F = LVII: A = Utrecht 4148; B = Cologne, Coll. H. Weyland 1674; C = Utrecht 4148, cuticle showing epidermal cell structure in stomatal condition. Note that most of the stomata are orientated with their length parallel to the midvein. D = Utrecht 4148, cuticle showing epidermal cell structure in non-stomatal condition; E = Utrecht 4148; detail of two stomata. Note ring of cutin. F = Utrecht 3809 A.

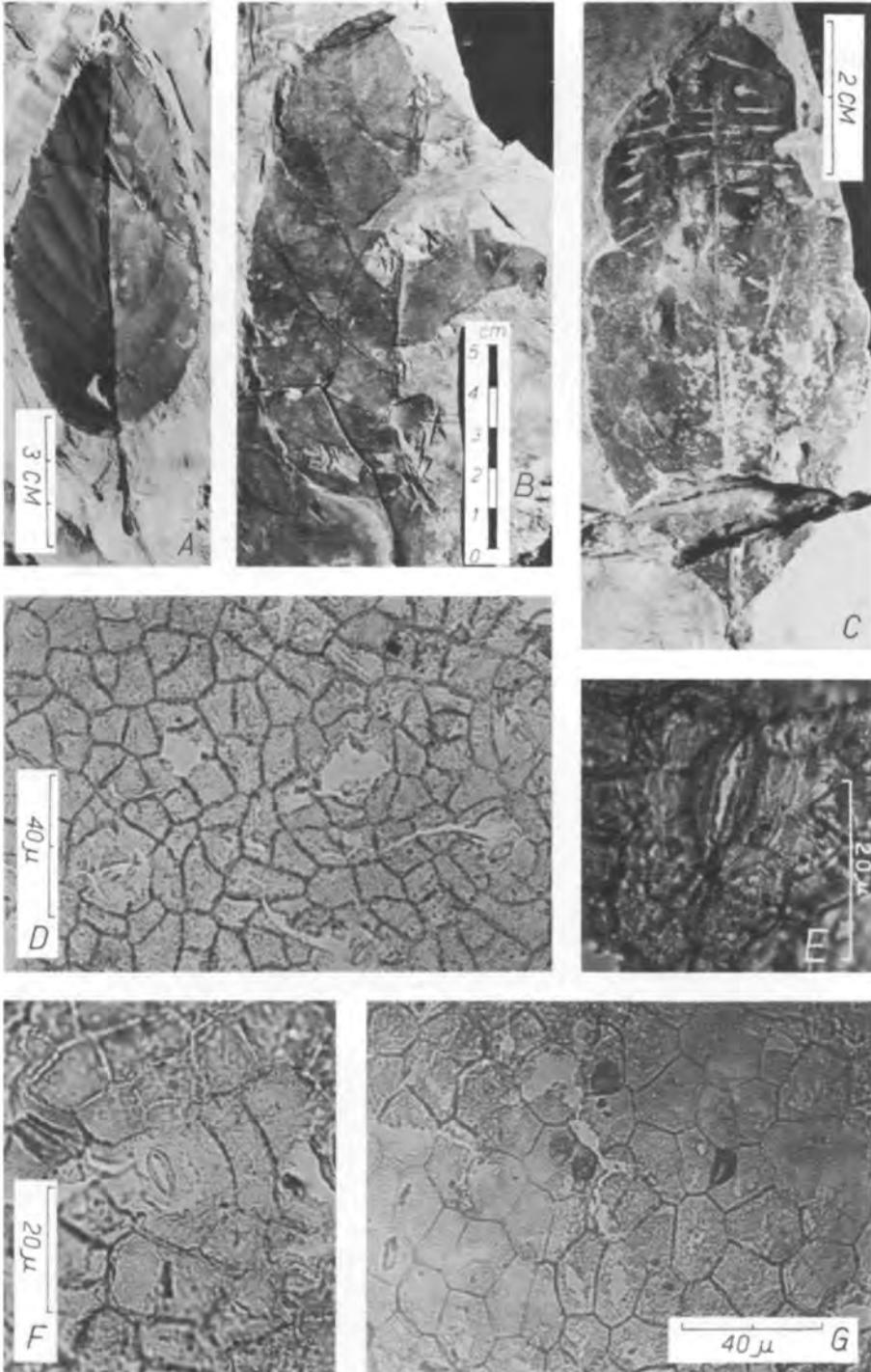


PLATE 43

A-G = LVIII: A = Utrecht 3625; B = Utrecht 3620 A; C = Utrecht 3875; D = Utrecht 3875, cuticle showing epidermal cell structure in stomatal condition; E = Utrecht 3620 A, detail of stoma; F = Utrecht 3875, detail of stoma; G = Utrecht 3636, cuticle showing epidermal cell structure in non-stomatal condition.

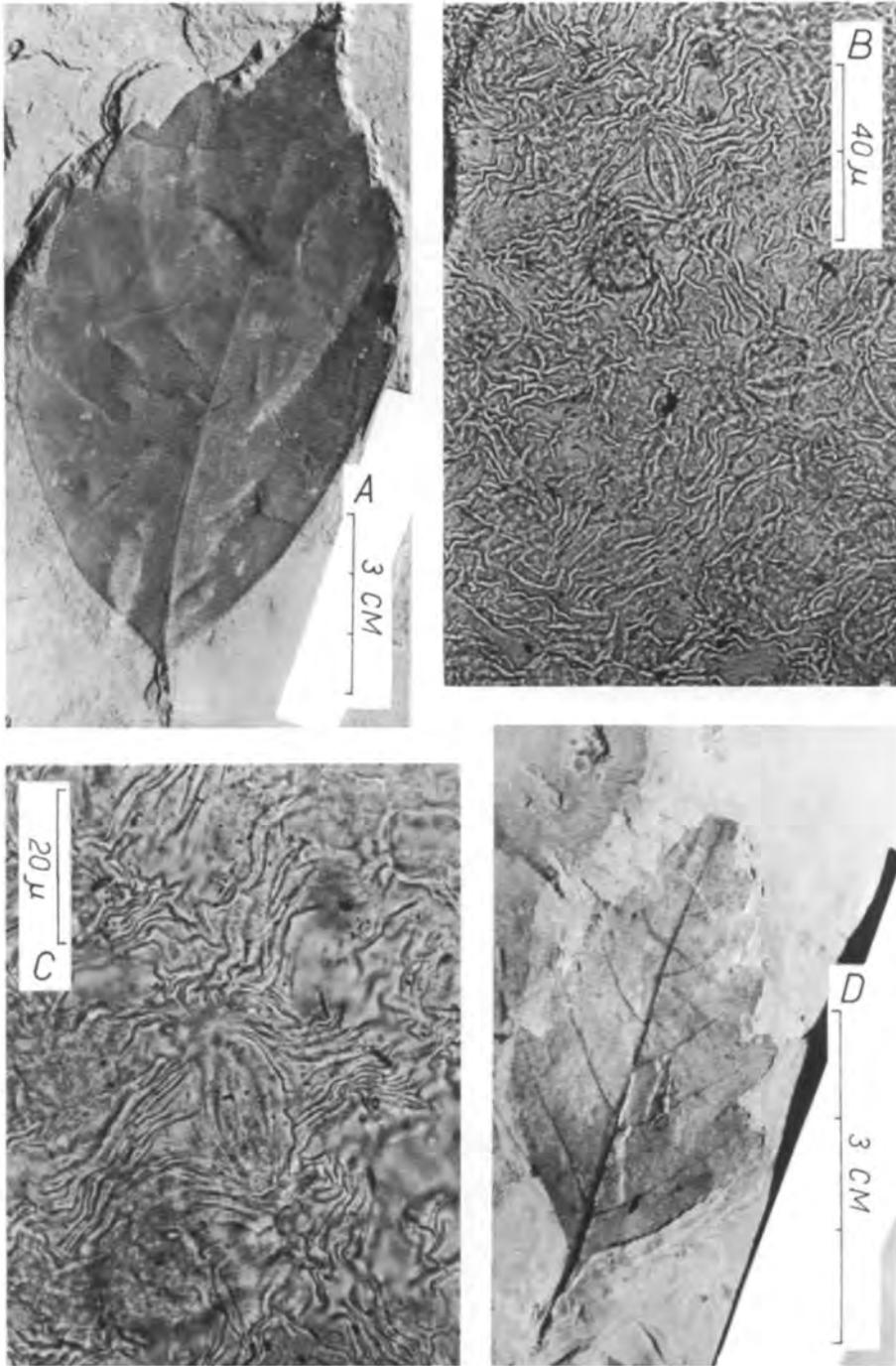


PLATE 44

A-C = LIX: A = Utrecht 3768; B = Utrecht 3770, cuticle showing epidermal cell structure in stomatal condition ; C = Utrecht 3770, detail of stoma; D = LX: Berlin s.n.

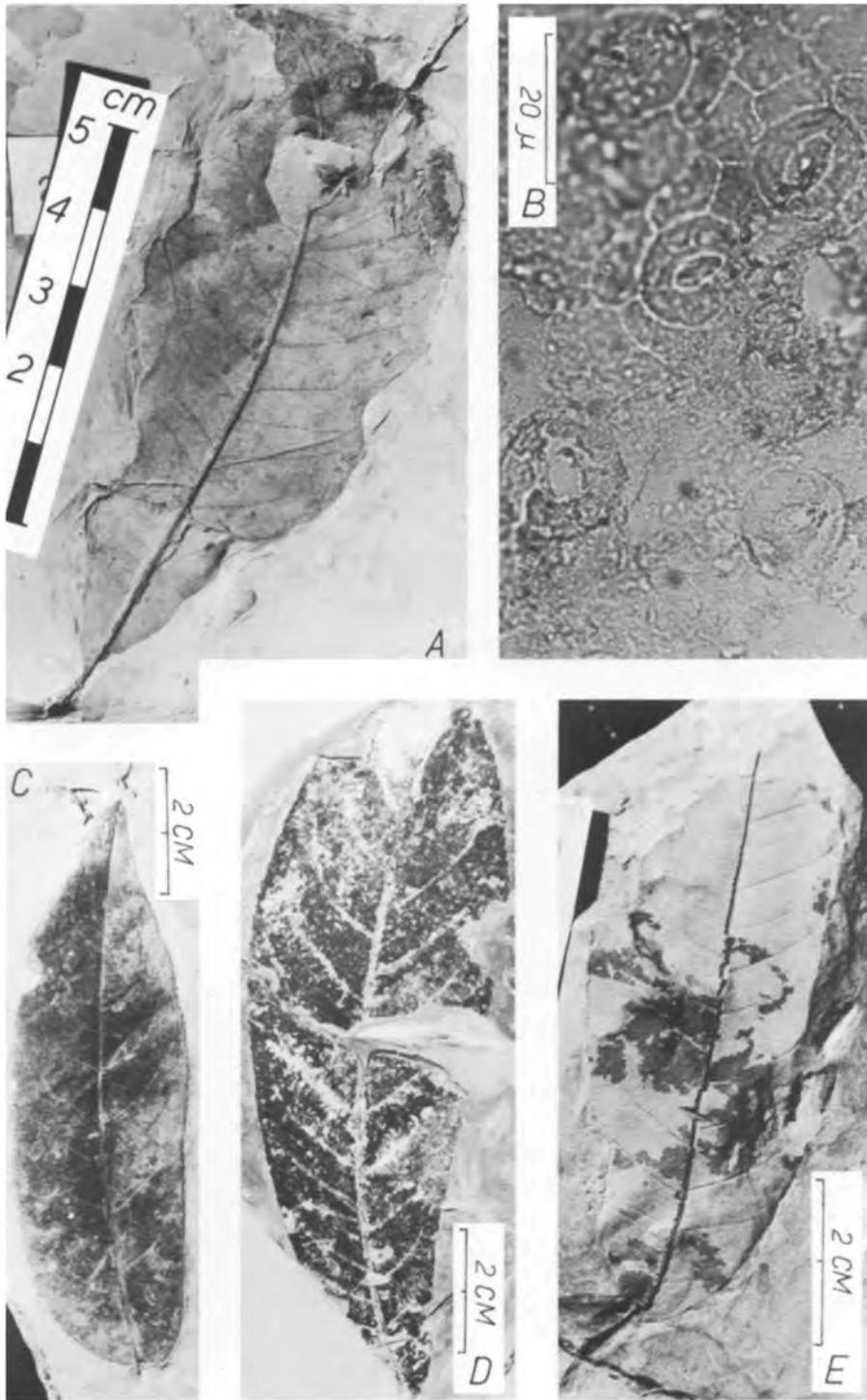


PLATE 45

A-B, E = LXI: A = Berlin 296 (Type of *Myrica kreuzauensis* Weyland); B = Utrecht 3839, cuticle showing epidermal cell structure in stomatal condition;
 E = Utrecht 3839. C-D = LXII: C = Berlin s.n. (K 13); D = Utrecht 3716.

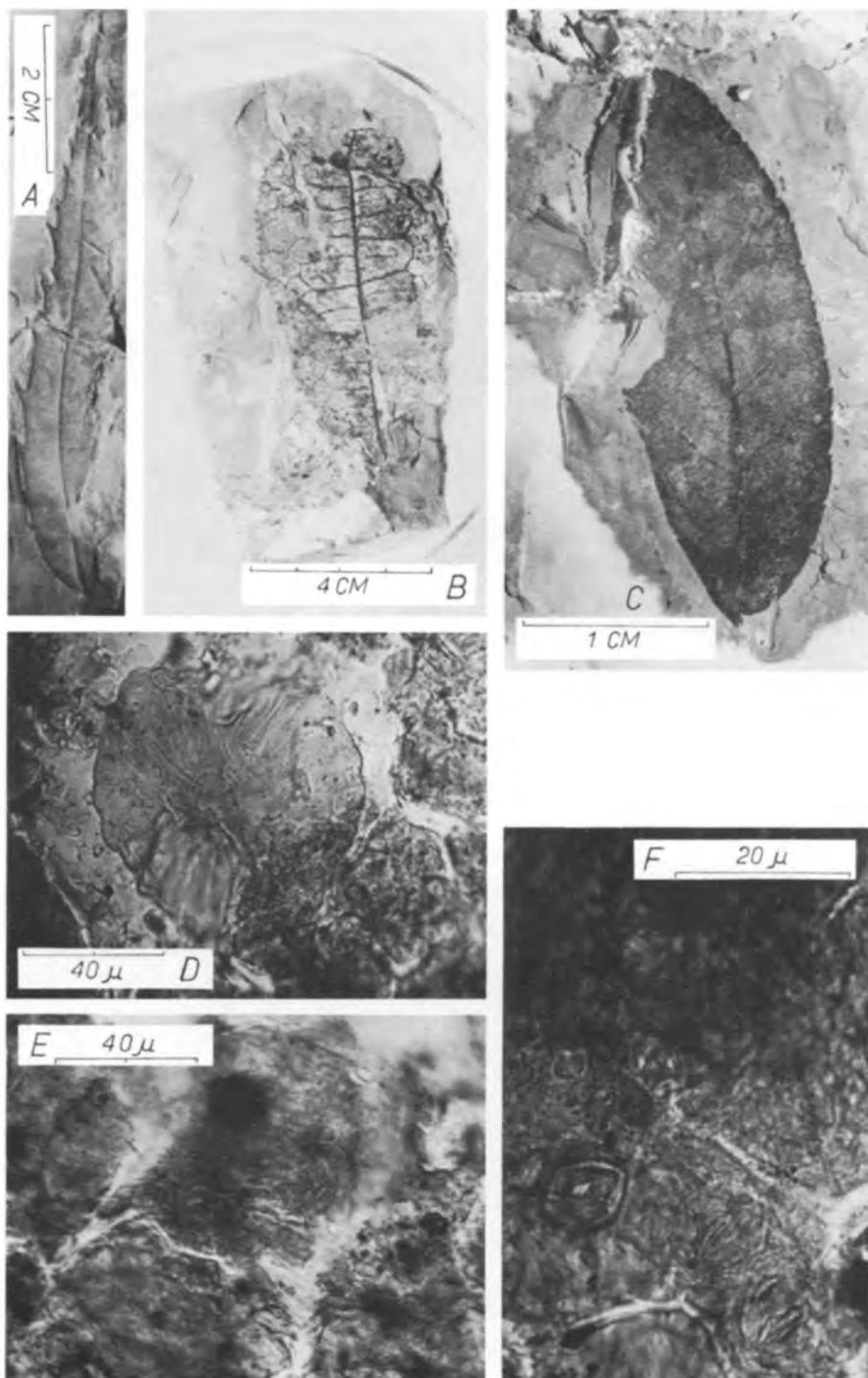


PLATE 46

A, D-F = LXV: A = Utrecht 3779; D = Utrecht 3782, gland; E = Utrecht 3782, gland. Note single basal cell. F = Utrecht 3782, detail showing two stomata (lower right hand corner) and a single trichome base. B = LXIII: Utrecht 2057. C = LXIV: Utrecht 3883.

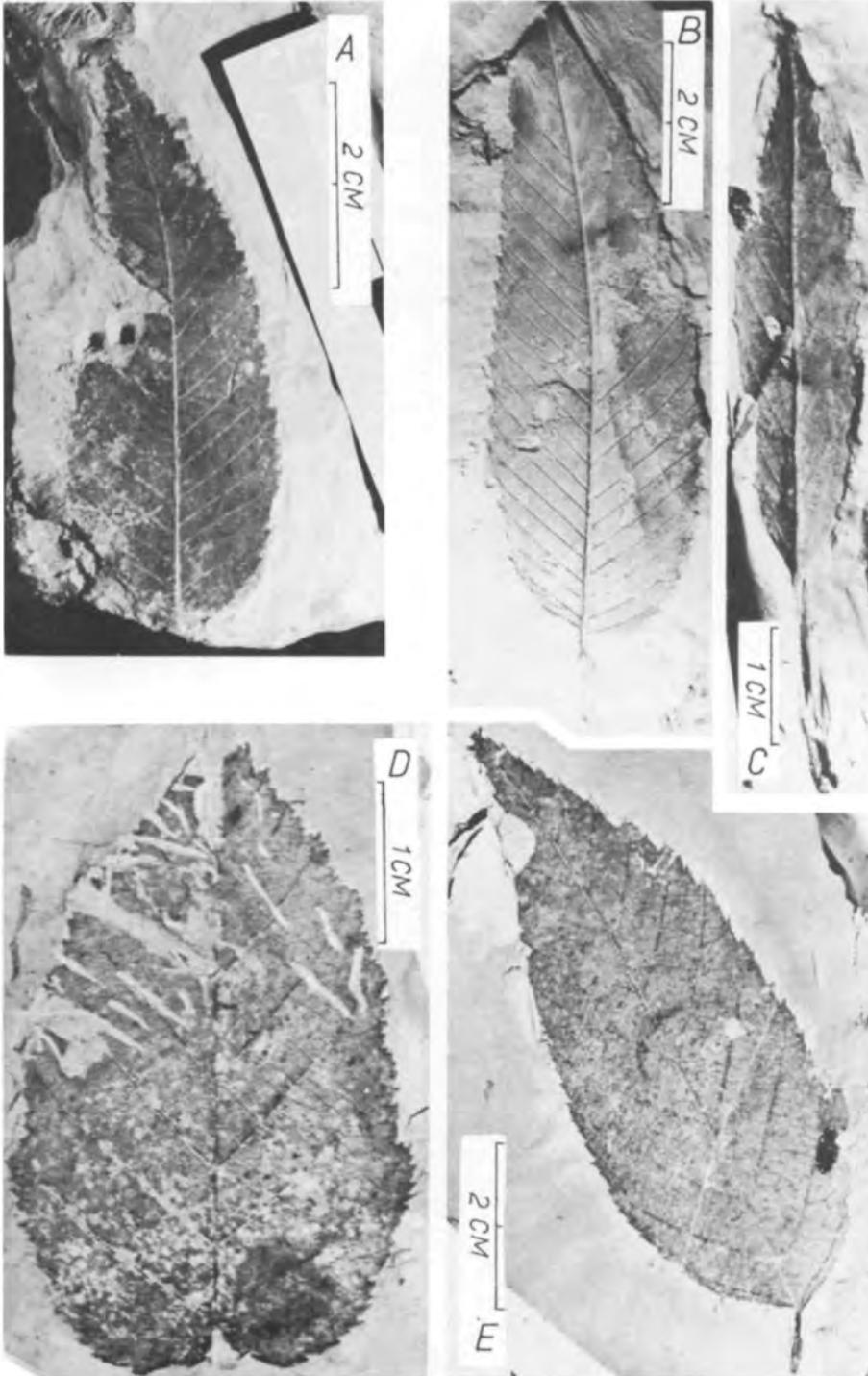


PLATE 47

A-B = LXVII: A = Utrecht 3690; B = Utrecht 3689. C = LXVI: Utrecht 3841.
 D-E = LXVIII: D = Utrecht 3696; E = Utrecht 3563.

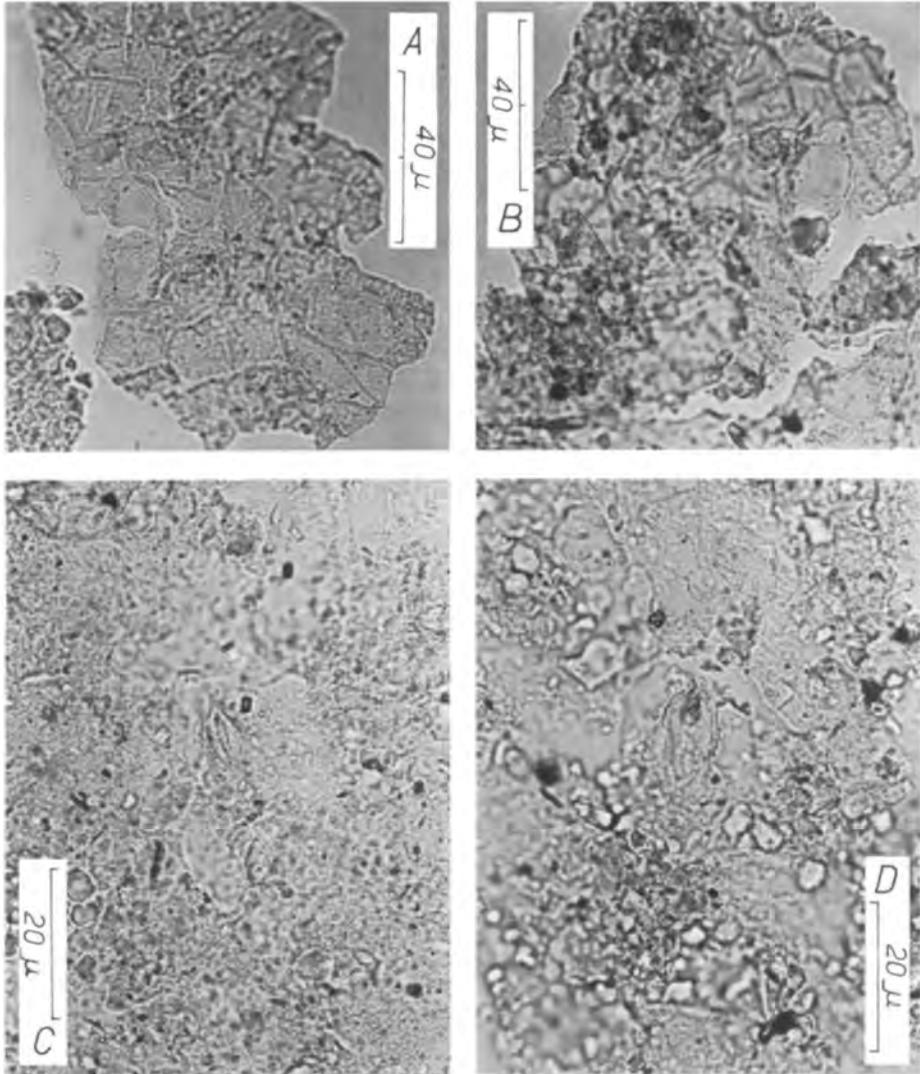


PLATE 48

A-D = LXVIII: A = Utrecht 3700, cuticle showing epidermal cell structure in non-stomatal condition; B = Utrecht 3861, cuticle showing epidermal cell structure in non-stomatal condition; C = Utrecht 3861, detail of stoma as reflected in cuticle from stomatal surface; D = Utrecht 3692, detail of stoma as reflected in cuticle from stomatal surface.

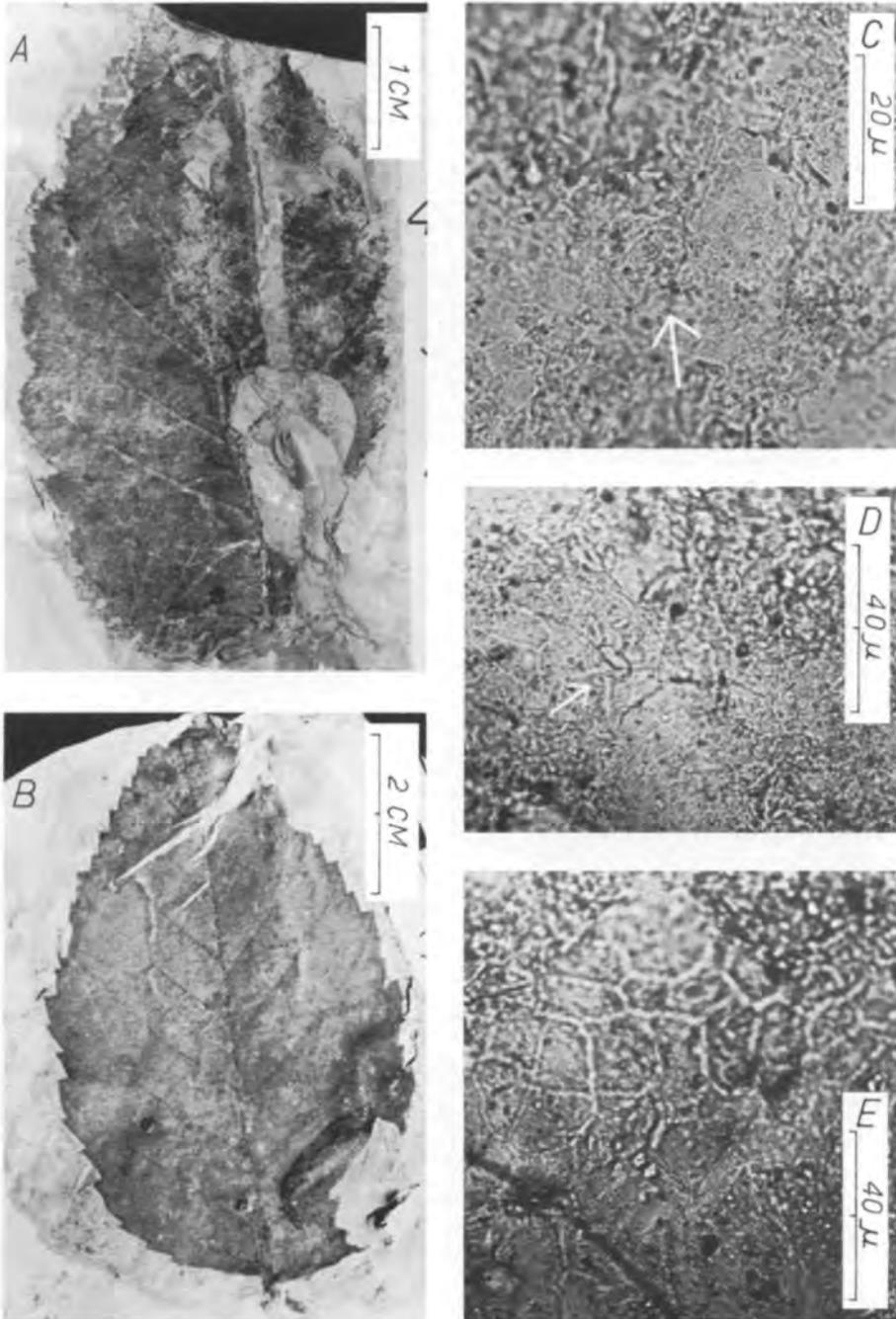


PLATE 49

A, C = LXIX: A = Utrecht 3851; C = Utrecht 3851, detail of stoma as reflected in cuticle from stomatal surface (position of stoma indicated by arrow). B, D-E = LXX: B = Berlin 277; D = Berlin s.n. (K 124), cuticle showing epidermal cell structure in stomatal condition (position of stoma indicated by arrow); E = Berlin s.n. (K 124), epidermal cells as reflected in the cuticle.

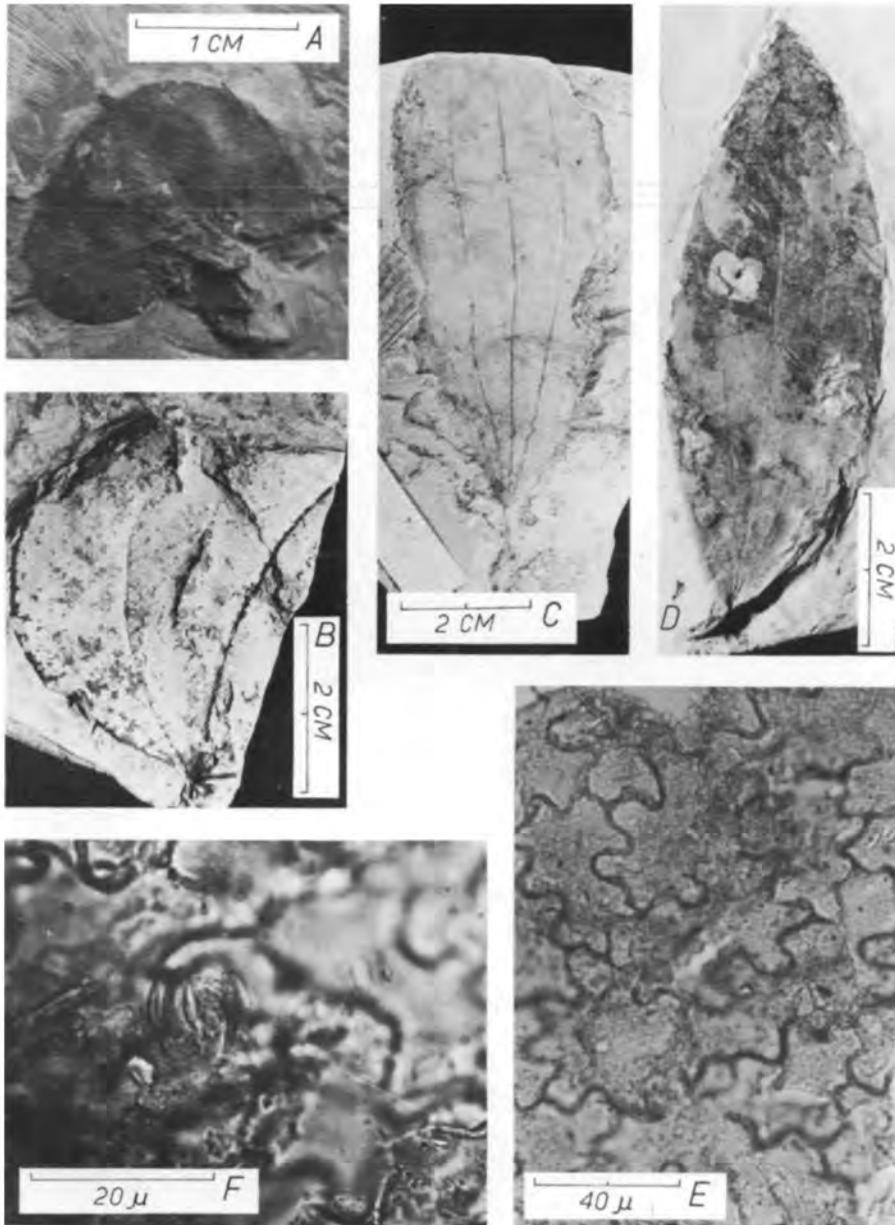


PLATE 50

A = LXXI: Utrecht 3844. B, E-F = LXXII: B = Utrecht 3535 A; E = Utrecht 3535 A, cuticle showing epidermal cell structure in non-stomatal condition. Note large epidermal cells. F = Utrecht 3535 A, cuticle showing epidermal cell structure in stomatal condition. C-D = LXXIII: C = Cologne, Coll. H. Weyland 2021; D = Berlin 278 (Type of *Melastomites menzelii* Weyland).

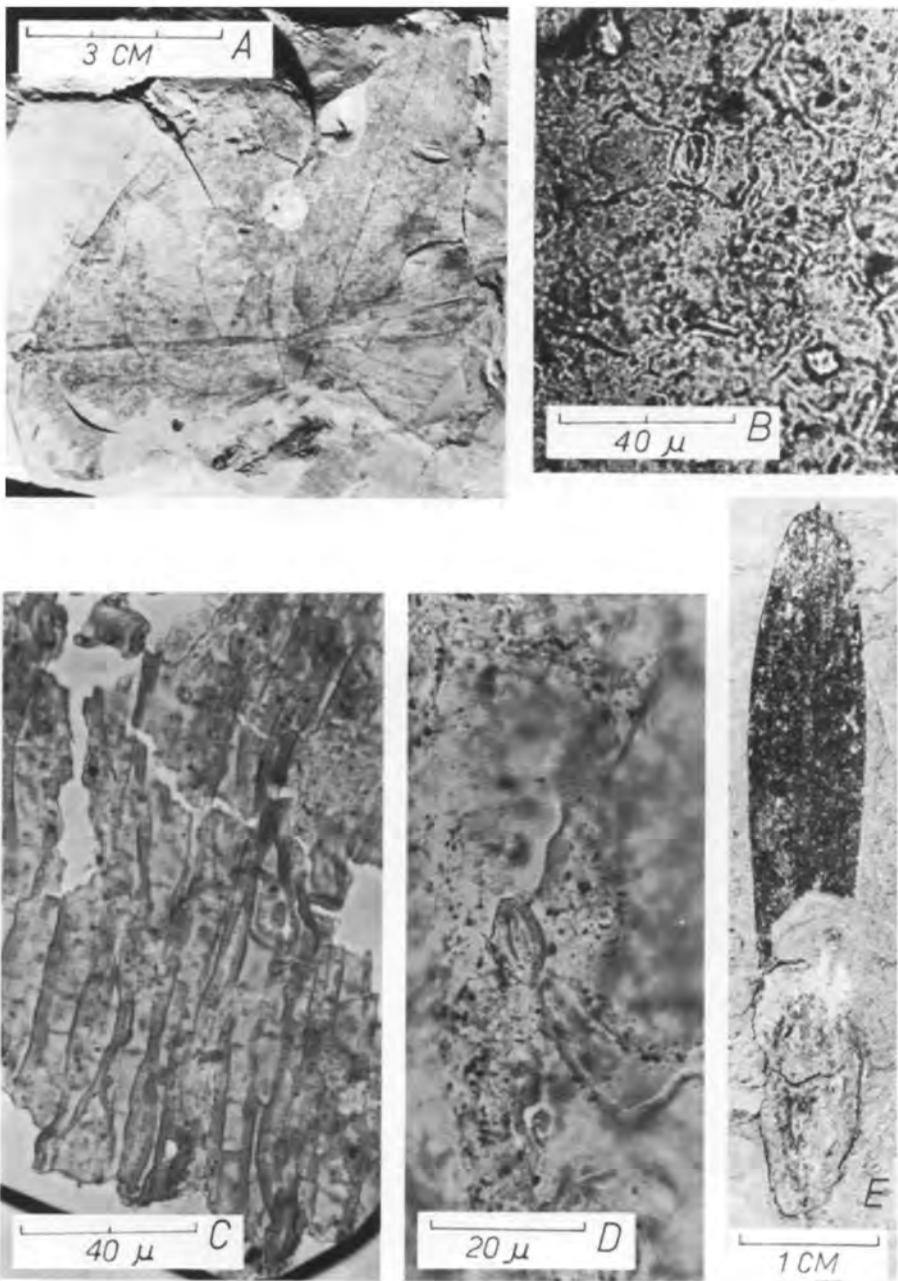


PLATE 51

A-B, D = LXXIV: A = Berlin 495; B = Berlin 495, cuticle showing epidermal cell structure in stomatal condition. Note the two accessory cells. D = Berlin 495, detail showing a single stoma. C, E = LXXV: C = Utrecht 3835, cuticle showing epidermal cell structure; E = Cologne s.n.

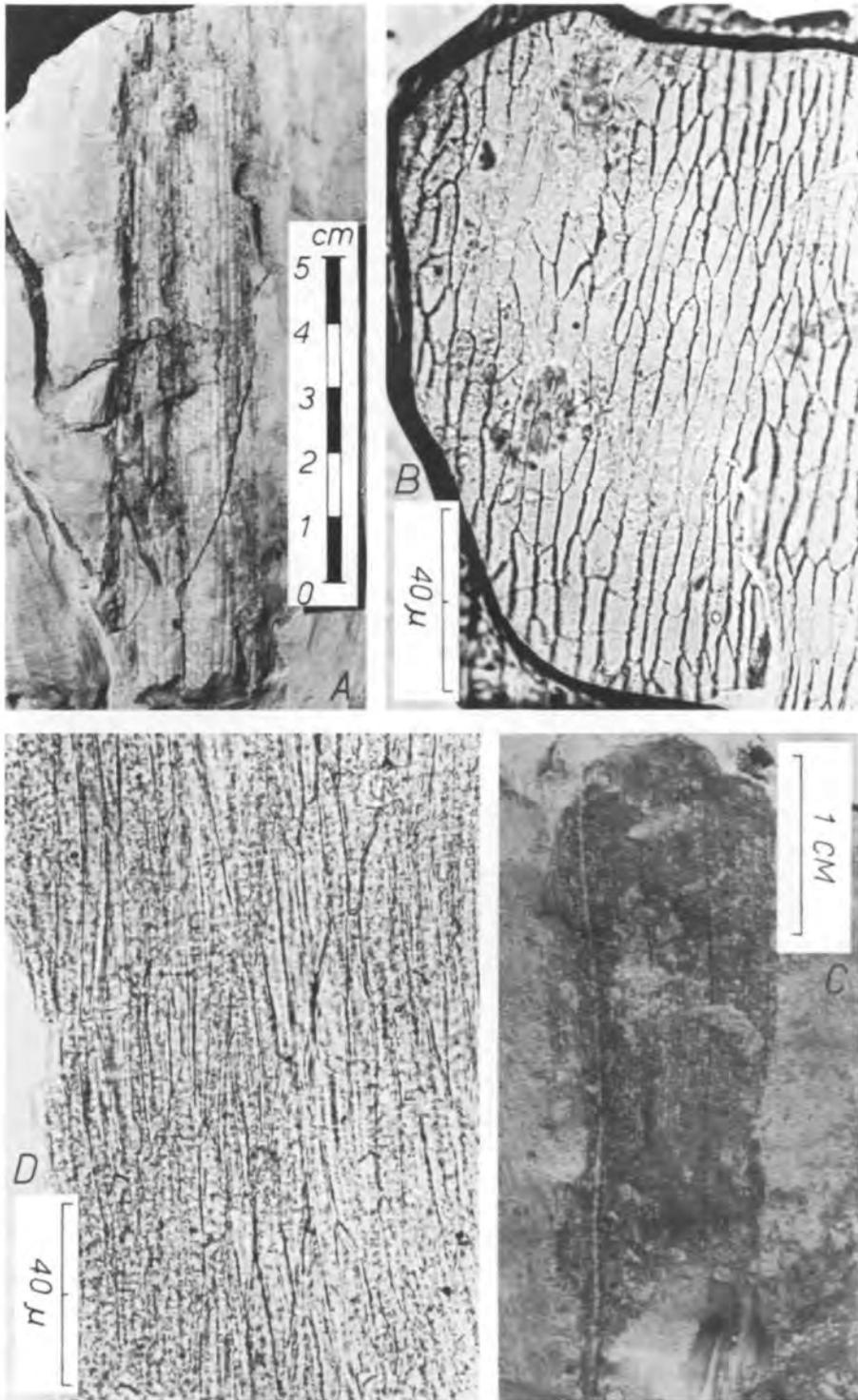


PLATE 52

A-D = LXXVI: A = Utrecht 3746 A; B = Utrecht 3745, cuticle showing epidermal cell structure; C = Utrecht 3755; D = Utrecht 3756, cuticle showing epidermal cell structure.

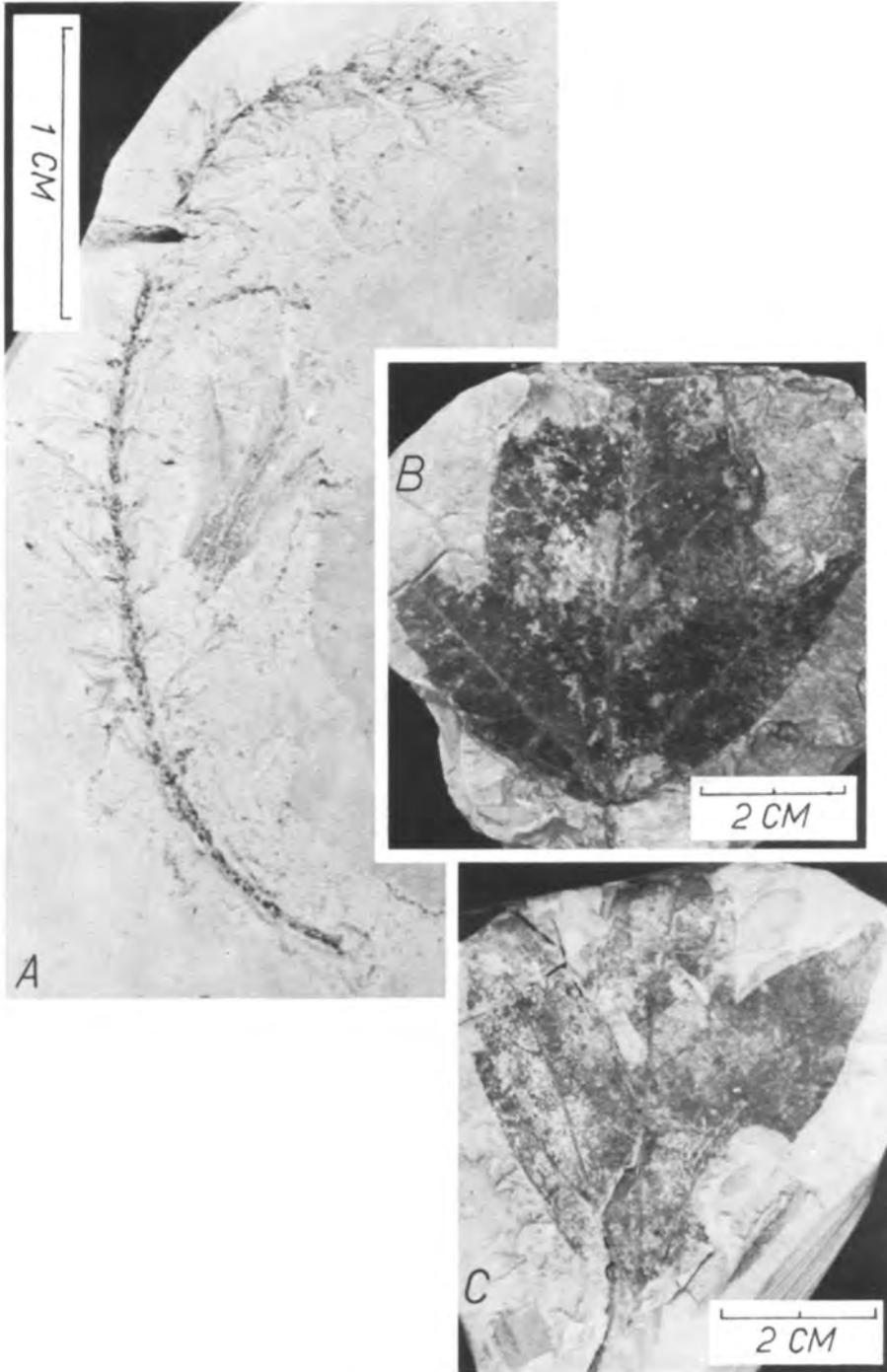


PLATE 53

A = LXXVII: Cologne s.n. B = "*Acer trilobatum*", Berlin. C = "*c.f. Oreopanax sp.*", Berlin.