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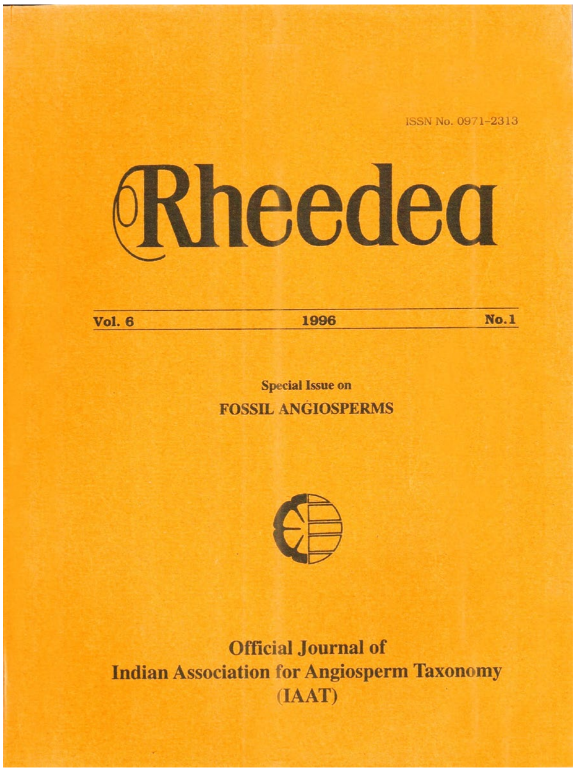

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Leaves of Urticales from the Late Cretaceous and Early Tertiary in the Northern hemisphere and their ecology

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Abstract

The so called *Viburnum* leaves of Late Cretaceous seem to belong to Hamamelidales, often associated with Platanaceae. Epidermis containing – sediments are rare in Cretaceous. Thus the closely related Urticales were confused with Rhamnaceae, which gave rise to a wrong ecological interpretation of Cretaceous climate. After Knowlton, Brown and Takhtajan the *Celtis* area was confirmed to be a Tethyan one, while *Ulmus* remained in the North.

INTRODUCTION

Nearly all the so-called *Viburnum* leaves of Late Cretaceous seem to belong to the Hamamelidaceae and related groups (Rüffle, 1980). Most of the leaves identified as *Zizyphus*, *Ceanothus* or *Paliurus* should be taken into account as members of the Urticales or their ancestors, that means immediate ancestors of Ulmaceae, Urticaceae, Moraceae or *Rhoiptelea* (Rüffle & Knappe, 1977). Particularly *Celtis* and *Trema* are confused with *Zizyphus* in paleobotanical literature, as well as in modern field work where they are misidentified sometimes because of absence of flowers and fruits. There are hardly any pollen of *Viburnum* (Caprifoliaceae) or *Zizyphus* (Rhamnaceae) in Cretaceous sediments. The present paper tries to find out if some leaf types correspond to the so-called Normapolles, *Trudopollis* Pflug in particular, and to describe their ancient morphology and distribution in the northern hemisphere.

Collinson (1989) did not take into account the above mentioned confusions concerning leaves. More over her discussion of pollen (such as *Complexiopollis* Krutzsch for *Rhoiptelea* and *Catinipollis* Krutzsch for *Dorstenia)* are insufficient. On the other hand Knobloch and Mai (1986) mentioned seeds of *Boehmeria, Debregeasia, Memorialis* and *Pilea.* Nathorst (1890) and Delevoryas (1964) referred to fruits and leaves of *Artocarpus* in the Cenomanian of Greenland and South Dakota. *Artocarpus* obviously was distributed in the western part of the Normapolles province (like *Macclintockia* or *Gleichenia)* from Late Cretaceous to Paleocene and even missing in Europe. At present *Artocarpus* exists in periodical eastside climate (monsoon) of Asia and Africa characterized by *Trudopollis.* Friis (1983) published a Senonian flower with an ancient *Trudopollis in situ.* Her reference to a juglandaceous relationship is not founded by flower morphology. It must be taken into account that modern pollen of *Ficus* and *Celtis (Trudopollis)* in a similar way are characterized by some features reminding of *Carya* as the fossil *Trudopollis (Subtriporopollenites)* does. The same problem of character combination arises in the case of *Complexiopollis (Plicapollis)* which belongs to the *Rhoiptelea.* Obviously the combination of characters seems to be a question of mosaic evolution. It is remarkable that Zaklinskaya (in Vakhrameev et al., 1970, p. 327) described a Danian – Paleocene Ural locality with plenty of leaves of *Macclintockia* (Fig. 1 A) containing *Trudopollis* only, and that she postulated an organic connection between the two genera. Heer (1866, p. 277; 1869, p. 118) first supposed that *Macclintockia* of Greenland is a member of Proteaceae, but later (1869, p. 479), as a member of Menispermaceae *(Cocculus),* and in 1883 (p. 125) as a member of Urticaceae *(Boehmeria).* Zaklinskaya (1970) agreed with Heer's (1883) opinion that *Macclintockia* belongs to Urticales with pollen of the *Trudopollis* type, and hence related to *Celtis* and *Boehmeria.* Takhtajan (1982, p. 25) adds the artificial genera *Celtidophyllum* Krasser and *Arykumia* Shilin besides *Macclintockia.* There is yet another genus *Penzhinia* Herman (1987, p. 103) from the Turonian of NW Kamtchatka which may be related to them, but with a semi-circluar leaf base it resembles more with *Celtis* or *Urtica* than with *Macclintockia. Zizyphoides kolymensis* Krysht. from the Siberian Turonian (Ogomsk) (Budantsev, 1983, p. 110, pl. 60, 61) also must be mentioned in this context. All the leaves illustrated by Herman (1987), particularly *Celastrophyllum retinerve* Herm. strikingly resembles with *Urtica exemplaris* Hollick and of *U. alaskana* Hollick (Hollick, 1930, p. 73, pl. 29, fig. 4; pl. 39, fig. 1, 2). Hollick (1930, p. 102, pl. 79) mentioned many so-called species of Rhamnaceae and *Viburnum* from the Late Cretaceous of Alaska (similar to the specimens in figure 4, A–C). He was obviously correct in determining figure 4 (A–C) as *Urtica* or as belonging to Urticaceae.

Leaf morphology and epidermis

Most modern Urticales are characterized by three basal main veins and asymmetrical leaf bases. In the contrary to Lauraceae and some Hamamelidaceae (and Liliaceae) the margin is strongly dentate, teeth are often very irregular and heterogenous (Figs. 2, 3). On the whole, the group seems easy to be recognized, eventhough many genera are not distinguishable by leaves. *Ulmus* (missing in *Celtis* floras), *Cannabis, Dorstenia, Cecropia* and *Artocarpus* seem to be exceptions; they can be identified by leaf morphology. In *Memorialis, Pouzolzia, Urtica, Ficus* and some others, five basal main veins are common (Friedrich, 1883, pl. 22; Koorders 1924, p. 457; Takhtajan 1980, p. 259). There are no rhamnaceous leaves with five basal veins. A main character of Urticales consists of pattern of tertiary venation which are rectangular or quadratic in form (Figs. 1, 2 B, 3 F). By combination of two characters, such as the veins and epidermis, the leaves of Urticales are easily recognizable. One should take

Explanation of Fig. 1: A. *Macclintockia lyallii* Heer, 1869 (Mus. Naturk. 79/2824) Atanekerdluk, Greenland, Early Paleocene; B. *Boehmeria excelsaefolia* Friedrich (1883 p. 167, pl 22, fig. 1., Mus. Naturk. Berlin Nr. 821) Eisleben, Germany, Maestrichtian; C. *Boehmeria excelsaefolia* Friedr. 125 x, stomata and silicate cells (see arrows) belonging to figure 4D, Quedlinburg, Germany, Senonian; D. *Pilea melastomoides* Wedd. (Flora Philippines, Herb. Bureau Science 16045, Botan. Mus. Berlin–Dahlem).

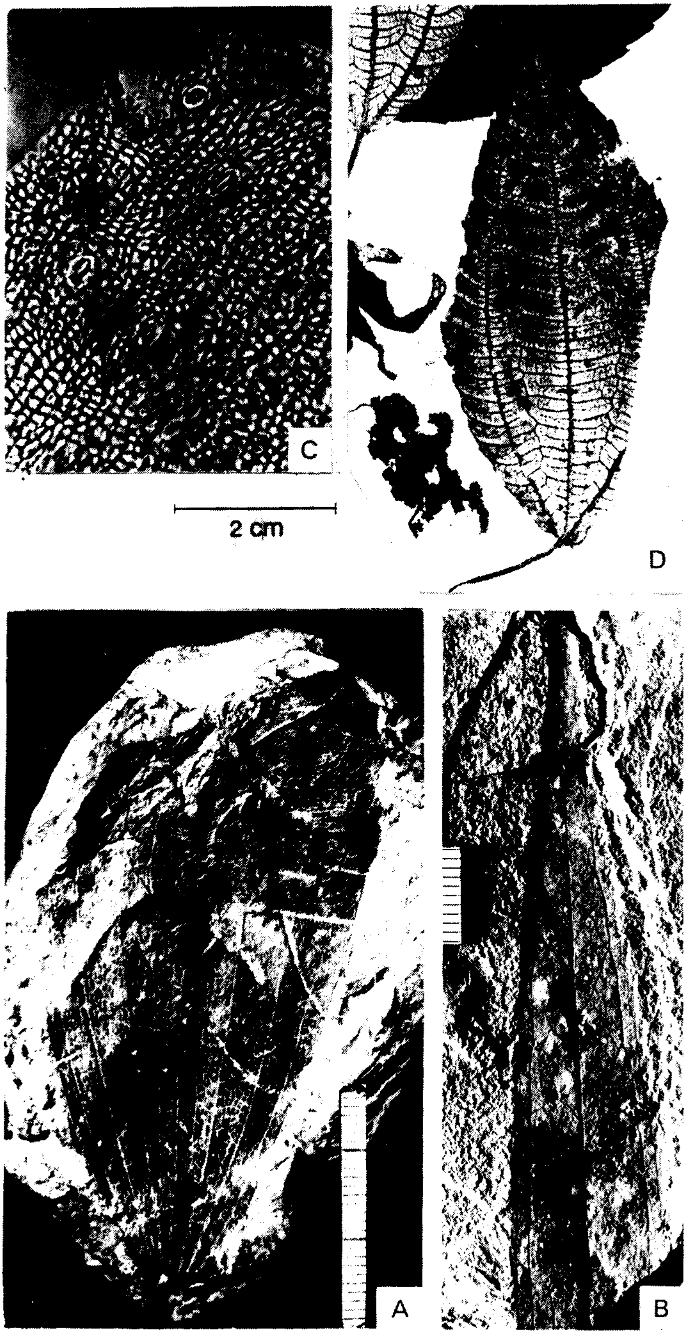

Figure 1.

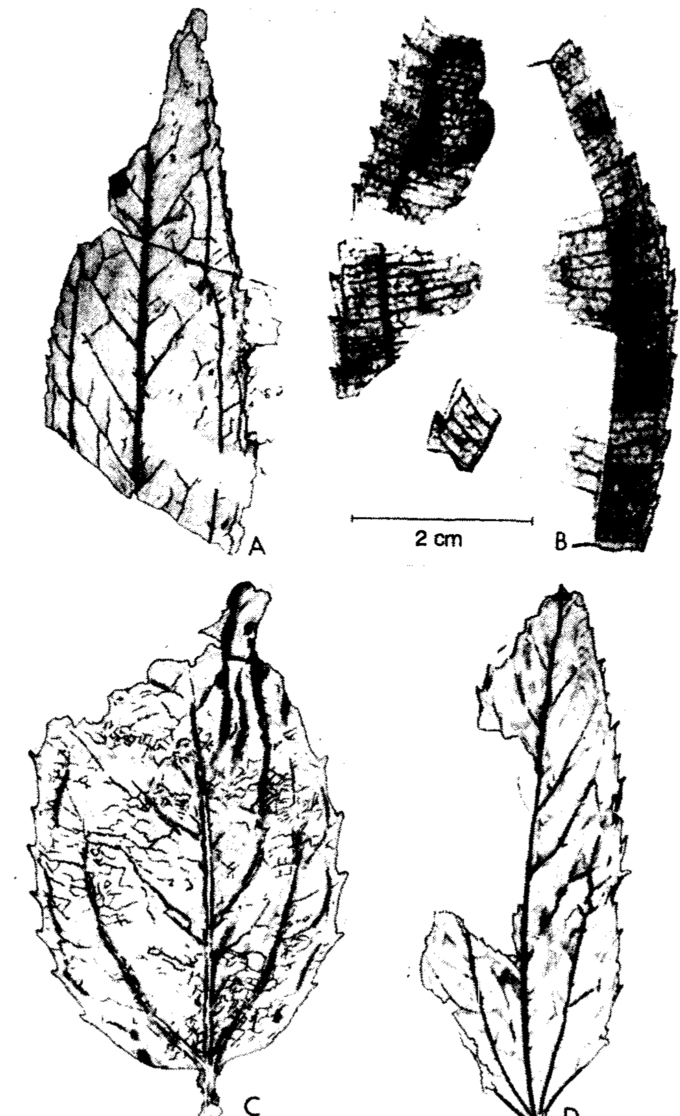

Fig. 2: A. *Boehmeria excelsaefolia* Friedrich (1883, p. 167, pl. 22, fig. 6, Mus. Naturk. Berlin Nr. 824) Eisleben, Germany, Maestrichtian; B. *Helobiaephyllum undulatum* (Ett.) Rüffle (after Laurent 1899, p. 130, pl. 13, fig. 20) Celas, France, Early Oligocene; C. *Celtis leuschneri* (Friedr.) nov. comb. (after Friedrich 1883, p. 203, pl. 25, fig. 2, Mus. Naturk. Berlin Nr. 866), Eisleben, Germany, Maestrichtian; D. *Celtis leuschneri* (Friedr.) nov. comb. (after Friedrich 1883, p. 207, pl 27, fig. 17, Mus. Naturk. Berlin Nr. 874), Eisleben, Germany, Maestrichtian.

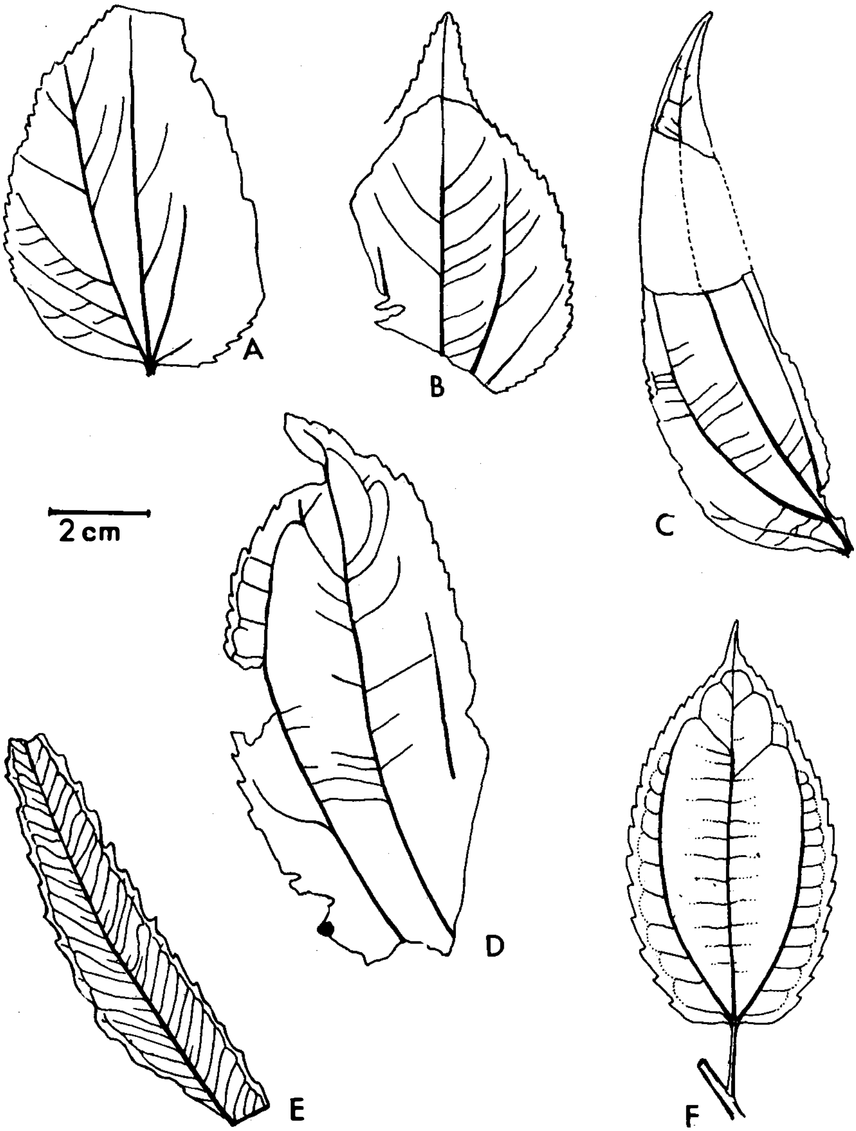

Fig. 3: A, B. *"Zizyphus" meigsii* (Lesq.) Schimper after Knowlton 1917, p. 336, pl. 99, fig. 1, 2, Raton formation, Latest Cretaceous; C. *"Zizyphus" falcatus* Berry (1916, p. 277, pl. 70, fig. 2) Wilcox formation, Early Eocene; D. *"Zizyphus" meigsii* (Lesq.) Schimper after Berry (1916, p. 278, pl. 70, fig. 5) Wilcox formation, Early Eocene; E. *"Panax" longifolium* Friedrich (1883, p. 186, pl. 24, fig. 5, Mus. Naturk. Berlin Nr. 859) Eisleben, Germany, Maestrichtian; F. *Morus (Celtis) lactea* (T. R. Sim.) Mildbr. (syn. *Morus mesozygia* Stapf), SE Africa, similar to *Sloetiopsis* Engl. (after Palgrave).

into consideration epidermis and silicate cells in particular as reported by Gangadara and Inamdar (1977). *Pilicoronicutis* Roselt & Schneider (1969, p. 79) is an artificial genus for an isolated epidermis from the Early Oligocene of Leipzig (Germany) belonging to *Ficus* and *Castilloa* and characterized by deeply sunken stomata surrounded by ring walls and accompanied by silicate cells (Figs. 1 C, 4G).

Putative Urticales in the American literature

The above mentioned combination of characters, quadratic tertiary venation in particular, seems to be common in the Potomac flora (Aptian – Albian). *Ulimphyllum brookense* Fontaine and *Ficophyllum tenuinerve* Fontaine (1899, p. 292, pl. 145) are of high significance. They seem to belong to the early angiosperms. As far as the venation is concerned some further genera *Myrtophyllum* and *Eucalyptophyllum* are remarkable. Though with entire margin the quadratic venation rather reminds of some modern species of *Ficus, Memorialis, Debregeasia* or *Procris* (see also Fig. 1, B). As shown by Rüffle and Jähnichen (1976, p. 313) the venation in question is common also in Myrtaceae. The structure of epidermis of *Eucalyptophyllum* excluding Myrtaceae was published by Upchurch (1984, p. 526, pl. 2, 3) and pointed out some confusion concerning Fontaine's (1899) determinations.

In the Cenomanian of Kansas (Dakota formation) triple – veined and flat–dentate leaves are called *Zizyphus dakotensis* Lesquereux (1892, pl. 36, figs. 4 – 7); some others named them as *Paliurus.* They are close to *Z. ripleyensis* Berry (1925, p. 69, pl. 13, figs. 4 – 6). Both are nearly identical with *Macclintockia* Heer, which Koch (1963, p. 76) and Budantsev (1983, p. 110) in accordance with Heer who compared it with *Boehmeria* and *Pilea* and their relatives (Figs. 1, 2). An undetermined serrate leaf of the Paleocene of the Rocky Mountains (Brown, 1962, p. 90, pl. 66, fig. 5) must be placed with *M. iyellii* Heer (Fig. 1, A). In this context *Celtis cretacea* Berry (1925, p. 47, pl. 7, fig. 2) of the Ripley formation is of much significance, because Berry did not consider it to be *Zizyphus.* Concerning *Zizyphys meigsii* Knowlton (1917, p. 336, pl. 99) from the Raton Formation, one should take into consideration Berry's statement (1916, p. 277, pl. 70) on the same species from the Wilcox Formation (Fig. 3) that the species passes the Cretaceous – Tertiary boundary. It reminds more of modern *Celtis;* the very long apex refers to a more or less periodical damp climate prevailed during Tertiary. The Late Cretaceous climate seemed to have been rather equalized as indicated by the distribution of *Artocarpus* in America and Greenland. (Knowlton, 1917; Brown, 1962). The herein described flora refers to a nearly humid climate as evidenced by the presence several species of *Credneria* and *Ulmus.* Assignment of the leaves in question to the rather xerotherm *Zizyphus* and *Paliurus* should be rejected. The occurrence of ancestors of the closely related Rhamnales and Celastrales is so far unknown.

Late Cretaceous in Germany

Though *Artocarpus* is missing in Europe there is no essential difference between American and European Cretaceous floras. Perhaps the Maestrichtian of Eisleben contains

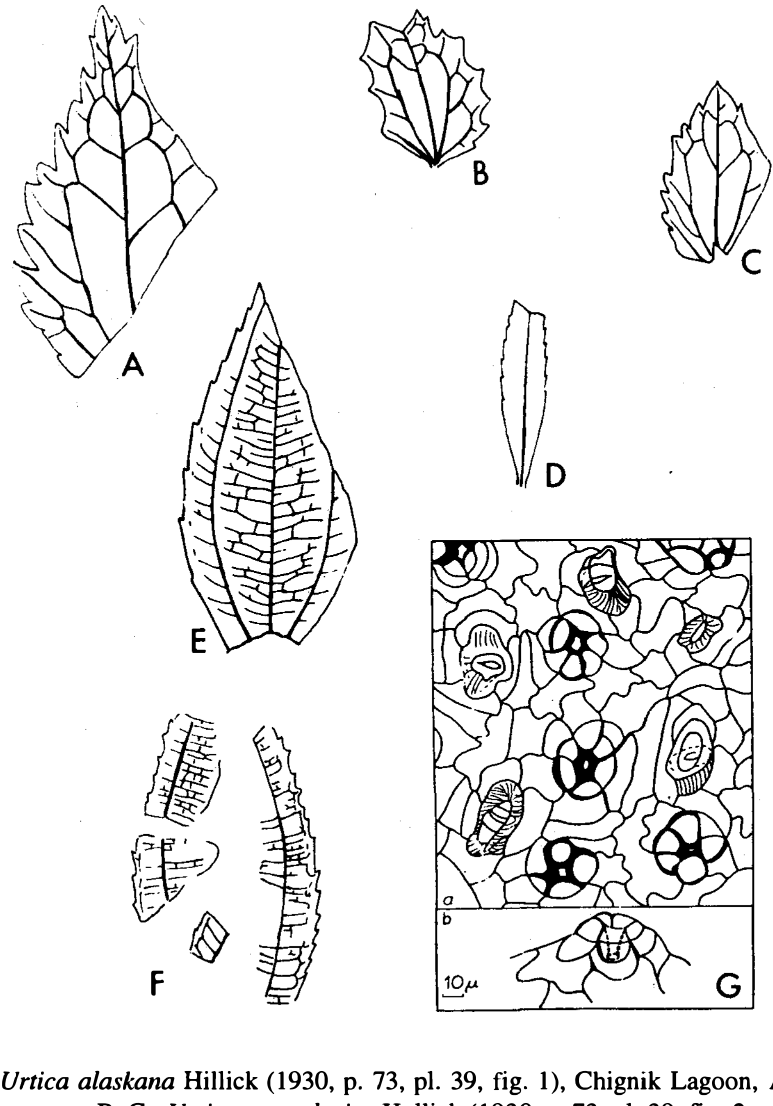

Fig. 4: A. *Urtica alaskana* Hillick (1930, p. 73, pl. 39, fig. 1), Chignik Lagoon, Alaska, Late Cretaceous; B, C. *Urtica exemplaris* Hollick (1930, p. 73, pl. 39, fig. 2, p. 29, fig. 4b; see figure 4 A.); D. *Boehmeria excelsaefolia* Friedr. belonging to figure 1 C (Mus. Naturk. Berlin Coll. Knappe 104) Quedlinburg, Germany, Senonian; E. *Helobiaephyllum undulatum* (Ett.) Ruffle (1963, p. 158, pl. 3, fig. 8), Randecker Marr, Germany, Miocene, F. *Helobiaephyllum undulatum* (Ett.) Ruffle (after Laurent 1899, p. 130, pl. 13, fig. 20) Celas, France, Early Oligocene; G. *Pilicoronicutis velamirima* Roselt & Schneider (1969, p. 79, fig. 29) Espenhain near Leipzig, Germany, Early Oligocene, Brown coal, cf. *Ficus*, cf. *Castilloa.* (Fotos by W. Harre, Graphics by J. P. Mendau, Museum fur Naturkunde, Berlin).

some peculiarities. The occurrene of *Lyonothamnus* and some other xerotherm Rosaceae are similar to the occurrence in the Miocene of Western Nevada (Axelrod, 1995; Givulescu, 1982). Recurvate secondaries are common in this locality (Fig. 1 B, 3 E), they remind some leaf types of the extant Australian savannas (Proteaceae, *Lomatites* Saporta in Rüffle, 1993, pp. 114 – 116). Similar leaves like, *Celastrus arctica* Heer (1883, p. 40, pl. 61, fig. 5– d, e), with recurvate secondaries are described by Newberry (1895, p. 98, pl. 13, fig. 8 - 18) from the Amboy Clays. Evidently identical leaves of Eisleben (Friedrich 1883, p. 197, pl. 26) are called *"Celastrus" lanceolatus*. Very small specimens of this type are also common in the Senonian of Quedlinburg (Figs. 1 C, 4 D). The Quedlinburg locality is characterized by a rather high degree of arid climate (Ruffle & Knappe, 1977, 1988). The author prefers a determination of the leaves in question as *Boehmeria excelsaefolia* Friedrich (1883, p. 167, pl. 22, fig. 1) (Fig. 1 B, 2 A). There is no substantial difference to the leaves described by Newberry (1895). *Trudopollis* is common in this sediment, whereas pollen of Rhamnaceae or Celastraceae are missing. Similarly the Eisleben collection of the Naturkunde Museum Berlin contains much more Urticales than Friedrich's determinations (Proteaceae, Araliaceae, Celastraceae) would suggest. The description of *Cannabis* is of high interest, because it indicates high diversity of Urticales at the locality (Friedrich 1883, p. 165, pl. 21, fig. 16).

"Zizyphus" leuschneri Friedrich (1883, p. 203, pl. 25, fig. 2) must be merged with *Celtis* (Fig. 2 C) (see also Fig. 2 D, Friedrich 1883, p. 207, pl. 27, fig. 17). Friedrich himself drew attention to *Celtis* in a footnote.

Cretaceous – Tertiary boundary

The character combination of Urticales as shown for *Macclintockia* occur also in *Helobiaephyllum (Zizyphus) undulatum* (Ett.) Ruffle (1963, p. 158, pl. 3, fig. 8) (Fig. 2 B, 4 E, F). This species occurs occasionaly in the younger Tertiary, the main occurrence is in the Early Tertiary. This refers to an extrazonal distribution. The leaves are very similar to many species of *Pilea* (Fig. 1 D). With respect to the periodically changing climate of the Early Tertiary, the pantropic distribution of the modern genus *Pilea* seems surprising because the genus occurs today in humid to perhumid climate. This reminds of the Cretaceous distribution of *Gleichenia.* Either the fossil species was an extrazonal member of shore vegetation within zonal aridity as ferns are in general, or the ecological amplitude was bigger as in *Dorstenia.* The pollen of *Dorstenia (Catinipollis)* appears first in the Maestrichtian of Canada and becomes common in the Eocene of America and Europe. The present distribution with about 120 species is compared by Axelrod (1970, pp. 296, 299; 1975, p. 79) with the distribution of Bombacaceae in Africa, a recent arid refugium. In view of leaf morphology *Urtica pulchella* Link, *Procris pedunculata* (Forst.) Wedd., *Boehmeria platyphylla* Don. & Hamilt., *B. hamiltoniana* Wedd., *Maoutia diversifolia* (Bl.) Wedd. and some others also should be taken into consideration (Koorders, 1922, 1924; Takhtajan, 1980). Presently, *Pilea* consisting of about 200 species and *Procris* of about 300 species are known from tropical river plain populations. Unlike *Dorstenia,* arid species of *Pilea* and *Procris* are unknown yet.

Survey of fossils which are close to *Pilea* (Fig. 1 D)

"Zizyphus" ovata Weber (1852, p. 89, pl. 6, fig. 1) in Late Tertiary brown coal of West Germany, Miocene.

"Zizyphus" raincourtii Saporta (1868, Mem. Soc. Geol. France Paris 8, p. 414, pl. 45, figs. 8 – 10) Sezanne, Paleocene.

?Potamogeton dal–lagi Squinabol (1901, p. 34, pl. 2, fig. 4) in Tertiary of Italy, Novale.

"Zizyphus" paradisiaca Heer in Laurent (1899, p. 130, pl. 13, fig. 20) Early Oligocene of France, Celas. This specimen belongs to *Helobiaephyllum undulatum* (Ett.) Rüffle (Fig. 2 B, 4 F).

"Melastomites" sp. Vassilewskaya (1957, Paper collection in memory of A. N. Kryshtofowich, Acad. Sci. Moscow Leningrad, – in Russian) p. 162, pl. 3, fig. 6) Eocene of Turkmenia (see Saporta, 1868; Makulbekov, 1977; Baikovskaya, 1984).

Helobiaephyllum undulatum (Ett.) Rüffle (1963, p. 158, pl. 2, fig. 8; see Fig. 4E) Early Miocene of Germany, the same species as in Laurent, 1899. Laurent's name is a synonym.

"Viburnum" sp. Makulbekov (1977, p. 130, pl. 35, fig. 2, 3) Late Paleocene, Early Eocene of Karakol, Kasakhstan, (close to the specimen of Vassilewskaya, 1957. Quadratic tertiary venation occurs also in *Viburnum*).

Macclintockia angustifolia Baikovskaya (1984, Paleocene flora of Romankul, S Ural, Acad. Sci. Moscow, Leningrad, – in Russian, p. 63, pl. 28, fig. 2; see Saporta, 1868; Vassilewskaya, 1957; Makulbekov, 1977).

Pilea petralifasciata Gro & Dou (1984, p. 132, pl. 4, fig. 4; see also *"Clematis"* in p. 133, pl. 1, fig. 12), Paleocene of Xinjiang, Altai. This flora is abundant in leaves as described above, sometimes reminding of *Urtica exemplaris* Hollick. Though Guo supposes a humid subtropical climate, the present author would prefer a semiarid, one close to the present day climate of this area. Obviously by there was zonal aridity as several Cupressaceae suggest.

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