
Some artificial genera (Fagaceae, Platanaceae, Araliaceae) of Upper Cretaceous of the Northern Hemisphere and heterophylly in some modern hybrids

Ludwig Ruffle

Ruffle L 1995. Some artificial genera (Fagaceae, Platanaceae, Araliaceae) of Upper Cretaceous of the Northern Hemisphere and heterophylly in some modern hybrids. *Palaeobotanist* 44: 225-237.

Pedate or three - pieced leaves of Upper Cretaceous angiosperm genera of Europe and North America. *Dewalquea*, *Araliophyllum*, *Araliopsis* and *Proteophyllum* are investigated for their cuticles. Most of the European samples yielded only one epidermis type pointing to Fagaceae (*Castanopsis*, *Pasania*), which is confirmed by fine venation. Some specimens of the Czech Cenomanian seem to have belonged to Araliaceae (*Oreopanax*). In addition, the leaf morphology in question is common in several remains of Platanaceae with comparable cuticles. In view of the phylogeny, Platanaceae and Fagaceae families are closely related. Heterophylly in Lianas and some modern hybrids of Ranunculaceae, Oleaceae and Fagaceae suggests that an apparent irregular leaf-growth predominated during Cretaceous resembling pteridosperms or ferns. In modern counterparts, in the cotyledonary regions and bud scales similar patterns are seen. The apparent unusual leaf growth is caused by atavistic accelerated meristem growth at the leaf bases and the margins. It is concluded that long or dwarf shoot growth and timbers occurred during Cretaceous. It has been concluded that most of simple leaves of Tertiary and Present time must have been derived from the pedate type of Cretaceous.

Key-words—Angiosperms, Heterophylly, Fagaceae, Platanaceae, Araliaceae, Morphogenetics Cretaceous..

Ludwig Ruffle, Palaeontologisches Institut, Museum für natur-kunde, Humboldt-Universität, 10115 Berlin, Germany.

सारांश

उत्तरी गोलार्द्ध के उपरि क्रीटेशी कल्प से कुछ कृत्रिम प्रजातियाँ (फैगेसी, प्लेटेनेसी, अरेलिएसी)
तथा कुछ वर्तमान संकरों में विषमपर्ण

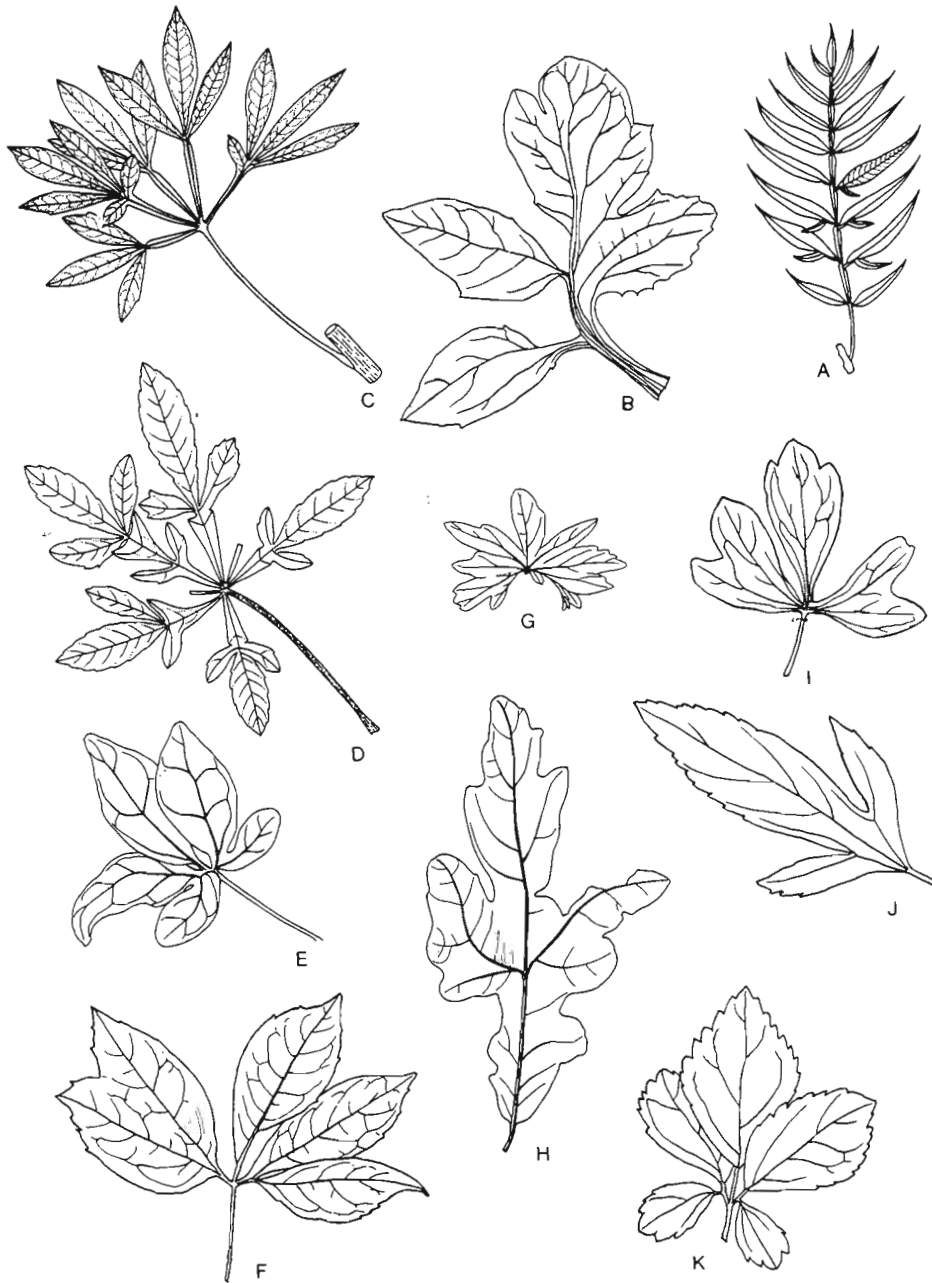
लुडविग रफ्ले

यूरोप एवं उत्तरी अमेरिका की उपरि क्रीटेशी आवृतबीजी प्रजातियों – *दीवालकुइया*, *अरेलियोफिल्लम*, *अरेलियोप्सिस* एवं *प्रोटोओफिल्लम* की त्रिपर्णकी पत्तियों की उपचर्मों का अध्ययन किया गया। यूरोपीय नमूनों में से अधिकांश से फैगेसी (*कास्टेनोप्सिस*, *पसानिया*) प्रकार की बाह्यचर्म उपलब्ध हुई हैं जिनकी बारीक शिरान्यास से पुष्टी होती है। चैक के सीनोमनियन कल्प से प्राप्त कुछ प्रादर्श अरेलिएसी (*ओरियोपेनेक्स*) से सम्बद्ध प्रतीत होते हैं। इसके अतिरिक्त पत्तियों की आकारिकी प्लेटेनेसी के कई अवशेषों से मिलती जुलती है। वैसे पत्तियों के उद्भव की दृष्टि से प्लेटेनेसी एवं फैगेसी आपस में घनिष्ठता व्यक्त करती हैं। लिआना, रेनकुलेसी, ओलिएसी एवं फैगेसी के कुछ वर्तमान संकरों में विषमपर्णता से प्रस्तावित होता है कि क्रीटेशी कल्प में टेरीडोस्पर्मों अथवा फर्नों से मिलती-जुलती अनियमित पर्ण-वृद्धि विद्यमान थी। वर्तमान प्रजातियों में बीजपत्री क्षेत्र एवं कलिका शल्क एक ही जैसे प्रतीत होते हैं।

यह निष्कर्ष निकाला गया है कि क्रीटेशी कल्प में लघु प्ररोह वृद्धि एवं काष्ठ विद्यमान थे तथा तृतीयक एवं वर्तमान कालीन सामान्य पत्तियों का विकास क्रीटेशी कालीन त्रिपर्णी-प्रकार की पत्तियों से हुआ है।

CLUES to the phylogenetic past and patterns of progress can be gathered from the heterobathmic (mosaic) mode of evolution called heterochrony of characters by Hill and Crane (1982). Melville (1960) and Hagemann (1984a) pointed out that some phylogenetically older organs and characters remain ancient in state and shape while others decrease in size and increase in quantity by partial multiplication and condensation, that is by

fractionization into different parts. These parts usually can yield, via fusion, a new organ in phylogeny. Heidenhain (1932, p. 96, 116) suggested the same mode of organization in ontogeny. His illustrations of several angiosperm leaves, particularly in *Ailanthus* as well as in some Lianas and Ranunculaceae (*Helleborus*), give insight into different heterobathmic components of meristematic growth: partially an axial one in the petiole



Text-figure 1— **A**, *Erythrophysa transvaalensis* Verdoorn (Sapindaceae) (1/8 x); **B**, *Ailanthus altissima* Swingle (Simarubaceae), bud scale with Pteridosperm venation; **C**, *Cussonia arborea* Hochst. & A. Rich. (Araliaceae) (1/5 x); **D**, *Cussonia nicholsonii* Strey (Araliaceae) (1/5 x); **E**, *Hedera helix* L. *pedata* Hibb. (Araliaceae) (1/2 x); **F**, *Parthenocissus vitacea* Hitchcock (Vitaceae) (1/2 x); **G**, *Fagus sylvatica* L. *cristata* Lodd. (Fagaceae) — (1/2 x); **H**, *Quercus robur* L. (Fagaceae) (1/2 x); **I**, *Paeonia suffruticosa* Andr. (Paeoniaceae), leaf from cotyledonary region (1/2 x); and **J-K**, *Forsythia intermedia* Zbl. (*F. suspensa* Vahl x *F. viridissima* Ldl.), heterophylly (1/2 x) (Oleaceae)

region as well as a further one at the leaf margin as common in ferns. In *Ailanthus*, the bud scales frequently contain a longitudinal meristem from leaf base to the

apex yielding normal leaflets and leaf blades but sometimes combined with ancient bud scale venation (Text-figure 1B). In the specimen pictured the midrib is



Text-figure 2 — Heterophylly in *Clematis jackmannii* Th. Moore (Ranunculaceae) (*C. lanuginosa* Ldl. x *C. viticella* L.) (1/2 x).
On the right side above: from cotyledonary region (1 x).

bifurcated, the right leaf blade contains a double venation, that is, atavism reminding of some pteridosperms. The same pattern is common in many cotyledonary regions. In *Paeonia* and *Clematis* (Text-figures 1 I, 2) this is recognizable by a basal axis containing meristem across the petiole. By accelerated meristem growth similar atavisms assert themselves in many genera and families, particularly in Sapindaceae and Bignoniaceae which contain many Lianas (Potonié, 1912a, b; Goebel,

1928, p. 460; Weberling, 1967; Rufflé, 1980a,b). In many sapindaceous leaves a dichotomous apex is common e.g., *Erythrophysa* E. Mey, *Filicium* Thw. (Text-figure 1A). *Sapindopsis* Fontaine (1889) from the Potomac Group after all seems to be related to Sapindaceae. Crane (1989) and Crane *et al.* (1983) have suggested a relationship to the Platanaceae because of some attached inflorescences. It is evident that leaves of some Platanaceae in the Potomac Group arose by pteri-



Text-figure 3 — A, *Dewalquea westerhausiana* (Richter) Rüffe & Knappe from clay, Quedlinburg (1/4 x), see Pl. 2, fig. 1; B, *Dewalquea westerhausiana* (Richter) Rüffe & Knappe from clay, Quedlinburg (1/4 x), see Pl. 2, fig. 2; C, *Araliopsis wellingtoniana* (Lesq.) Lesq. from clay, Quedlinburg (1/2 x); D, *Araliopsis wellingtoniana* (Lesq.) Lesq. from clay, Quedlinburg (1/2 x), see Pl. 2, fig. 3; E, "*Aralia*" *denticulata* Hos. & v.d. Marck, Restoration (1/2 x) (*Araliopsis wellingtoniana* ?); F-G, *Dewalquea smithii* Berry from the Tuscalosa Formation (North America) after Berry 1919 (1/2 x); H, Restoration of *Dewalquea smithii* by Berry 1914. (see also *D. pulchella* Knowlton 1917); I, *Dewalquea gelindenensis* Sa. & Mar., lower epidermis after Stockmans from the type specimen (holotype); and J, *Dewalquea gelindenensis* Sap. & Mar. from the Type Locality, Palaeocene of Gelinden, see Pl. 1, fig. 2 (1/2 x) (Museum für Paläontologie Nr. 87-348).



Text-figure 4 — *Forsythia cf. suspensa* Vahl. (Oleaceae) with peltate leaf.

dosperm-like combination of longitudinal (axial) and marginal meristem growth in leaves.

Combinations of instable partial axial meristems with marginal ones are common in some modern cultivars (Rüffle, 1992b). Heidenhain (132, pp. 124, 127) described similar leaves in *Juglans* and *Rubus*. Particularly hybrids, for instance *Clematis jackmannii* Th. Moore (*C. lanuginosa* Ldl. x *C. viticella* L. — Text-figure 2), are rich in atavisms. Since acceleration of transversal axial meristems within leaf blades can differ strongly, atavistic heterophyly becomes evident. Acceleration of growth in the main axes often recapitulates in petioles and leaf bases. Text-figure 1K, L demonstrates *Forsythia intermedia* Zbl. (*F. suspensa* Vahl. x *F. viridissima* Ldl.). In the pictured *Forsythia Quercus*, *Fagus*, *Parthenocissus* and *Hedera* (Text-figure 1 I, H, G, F, E) basiplast meristems are arranged across the petioles resembling *Helleborus* (Hagemann, 1984, p. 188; Hagemann & Kürbs, 1971). Heterobathmic patterns in the leaves as mentioned above are evident. Concerning secondary axis-like meristems within leaf blades, one must compare the homologies. In view of heterobathmy (mosaic mode of characters) compound leaves with ped-

ate or pinnate shapes as shown above are homologous to whole simple leaves as well as to any leaflet and to stipules also. Thus in respect to phylogeny and heterochrony of characters many homologies in the plant kingdom seem to be ambiguous (Rüffle, 1978, 1986, 1992a, b).

According to Heidenhain (1932, p. 116) any palmately compound (three to seven lobed) leaf in the present genera should be derived from the above mentioned pedate palinactinodromous leaf type by condensation and reduction. Meeuse (1982, p. 349) interprets simple leaves of the modern Fagaceae in a similar way by so-called apomorphy (neoteny) with respect to the Mesozoic *Dewalquea* Sap. & Mar. 1873 (Text-figure 3). Stipules seem to be rudimentary only. Svoboda (1972, 1976) pointed out that some cultivars of *Hedera* and *Fagus* are blocked up as to the midrib, the former simple leaves dissolved to pedate association of stipules (Text-figure 1G, E). Acceleration and retardation within the main axes are, in general, obvious conclusions, particularly in primary and secondary shoots, expanding spur shoots and long ones, including inflorescences (Dilcher, 1979; Rüffle, 1986, 1992a, b). In the present paper, Text-figures 1 and 2 represent the so-called *Dewalquea* type and *Araliophyllum* type of Mesozoic leaves in some modern plant families. Georgescu (1927, p. 102) obtained similar type by cutting cotyledons in *Phaseolus multiflorus*, reminding of the foliage in *Clematis jackmannii* (Text-figure 2).



Text-figure 5 — *Platanus (Mallotus) ruefflei* (Ablaev & Vassiliev) nov. comb. after Ablaev & Vassiliev 1994.

Debeya Micquel (1853, pl. 1, fig. 1), on the contrary, is an unobtrusive three-pieced leaf and should not be combined with *Dewalquea* Sap. & Mar. as Knobloch (1964, p. 147) did. Nevertheless, this leaf type is common in many genera of Bignoniaceae. In the same paper Knobloch proposed a survey of the artificial (fossil) genus *Dewalquea* and its fossil species. It seems to have been distributed through the Upper Cretaceous amphiatlantic province of the Northern Hemisphere (Europe, North America, including Greenland) in a similar area in which *Gleichenia* and some Matoniaceae were present. Meeuse (1987, pp. 164, 166) is convinced that the above mentioned morphology yields some hints to more or less ancient features of timbers, such as in Sapindaceae, many taxa of Leguminosae, and stem anatomy (spur and long shoots) in Gnetales (*Welwitschia* remaining in a cotyledon like condition?). One should compare these groups to some Pteridosperms (*Medullosa* Cotta, *Tempskya* Corda). Modern rhizomes should also be interpreted in a similar way. It is more important that one must mention the fractionized doubled and manifold vascular bundles especially xylem in Piperales, Caryophyllales, Nymphaeaceae. *Thalictrum*, *Aquilegia* and Podophyllaceae, in particular, are referred to by Hagemann (1984a, p. 185, 1984b; Heidenhain, 1932, p. 106; Rufflé, 1980a, p. 424) concerning marginal leaf meristems and monocotyl-like vessels (atectostele). Podophyllaceae and *Thalictrum* in fertile state produce pollen type *Punctioratipollis* Krutzsch. These distinct combinations of several modes of growth in main axes as well as in leaves and their intermediate stages obviously could point to a moderate paleoecology in the Late Mesozoic when distinction between summer and winter might have been balanced moderately in the mentioned palaeoprovince. In the Upper Cretaceous of the Arctic region as well as of the equatorial one, this phenomenon is missing. Condensation and reduction (neoteny?) of the pedate palinactinodromous leaf type, like *Helleborus* or *Dewalquea*, to a palmate or simple modern type might

be due to seasonal climatic changes in Tertiary and the more in the present time (Hagemann, 1984b, p. 333). Marginal meristems become more and more checked, sometimes by fractionization only. Angiosperms looked no longer like ferns or pteridosperms after having passed the boundary from Cretaceous to Tertiary. Intercalary leaf growth across the petiole (Hagemann, 1984a, p. 188; Heidenhain, 1932, p. 116) was common in the Cretaceous in several well known families. In many leaves of the Mesozoic and in Monimiaceae in particular (Rufflé, 1965; Rufflé & Knappe, 1988), marginal meristem growth of leaves is evident by an extremely extended network of tertiary veins additionally reminding of ferns or Pteridosperms.

In Schenk's 1893 Liana monograph *Piper fluminense* C. DC. is marked by several vascular bundles in the stem similar to the Sapindaceae, *Serjania clematidifolia* Camb. and *Paullinia neuroptera* Radlk. In the case of Fasciation, as usual in Lianas, peltation or ascidiation of leaves might be possible (Text-figure 4). Bignoniaceae and Centrospermae are described by Schenk. Menispermaceae are still more important. Buzek (1971, p. 88) described some leaves from the Tertiary based on heterophylly, e.g., *Diversiphyllum* (*Aristolochia aesculapi*) (Heer) nov. comb. supposing of Convolvulaceae. The present author rather would prefer to call it as *Sinomenium* (Menispermaceae). Other workers described similar leaves as *Dioscorea* or *Nymphaea*. It is evident that nearly all attempts of determination point to Liana genus.

FAGACEAE

Nearly all specimens (Plates 1-3) belong to the family Fagaceae. In Text-figure 3 marginal fine venation is striking. The secondaries bifurcate in marginal position (see Ettingshausen, 1896; Rufflé *et al.*, 1976). The lower part ends in a tooth, the upper one touches the above following secondary close to the margin. This character is referred to in several species of *Castanopsis*. In

PLATE 1

(All figures are of natural size, unless otherwise mentioned)

1. *Debeya serrate* Micquel 1853, Genotype after Micquel (1/2 x)
2. *Dewalquea gelindenensis* Sap. & Mar. from the Type Locality (Museum für Palaeontologie Nr. 87-348) see Text-fig. 3I, K.
3. *Dewalquea westerhausiana* (Richter) Rufflé & Knappe from Heidelberg Sandstein, Blankenburg, Westerhausen, Type Locality (Museum für Palaeontologie Nr. 89-91) (1/2 x)
4. *Dewalquea westerhausiana* (Richter) Rufflé & Knappe from clay, Quedlinburg (1/2 x)

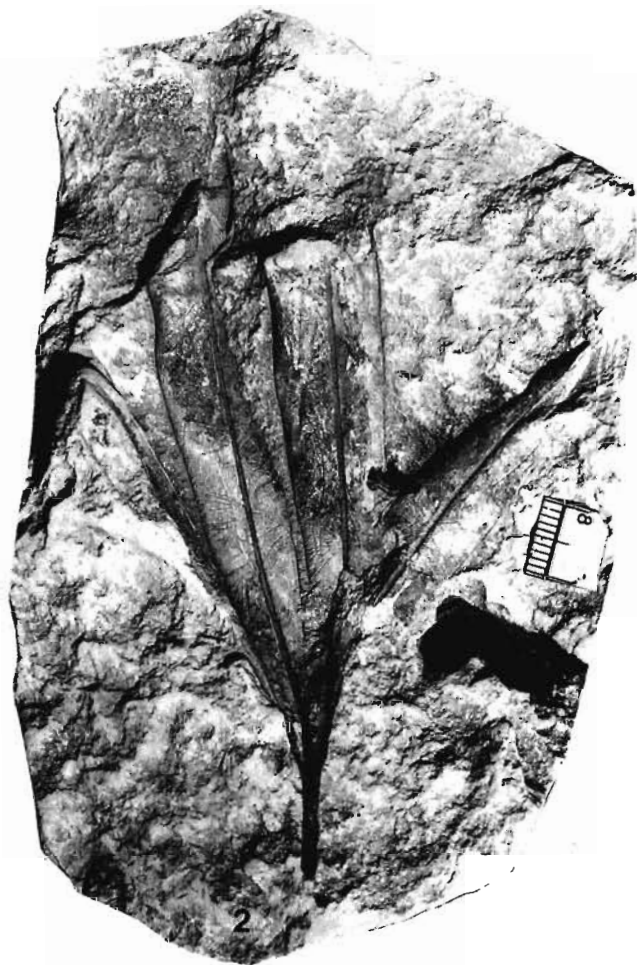
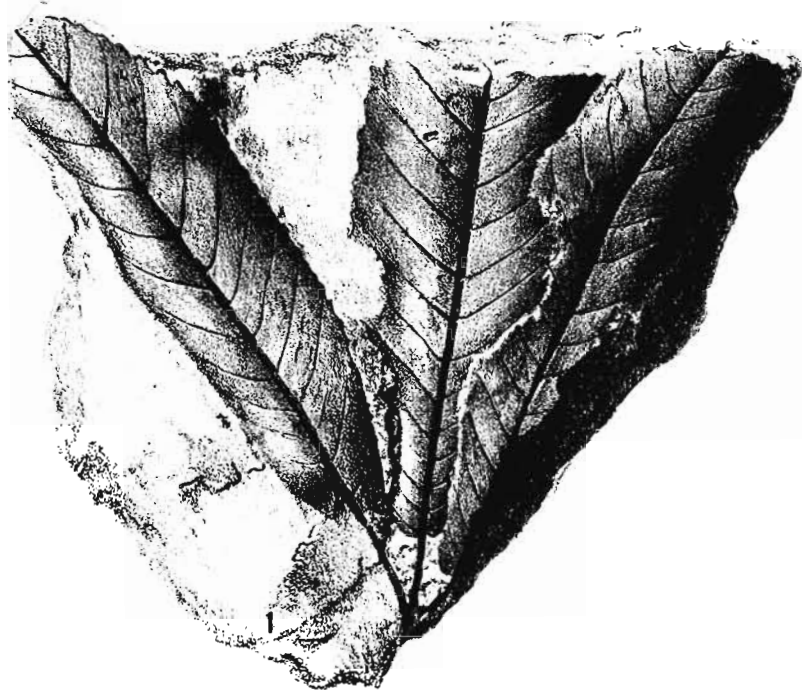


PLATE 1

Dewalquea and *Araliophyllum* (*Araliopsis*) three or five *Castanopsis*-like leaves (so-called *Dryophyllum* Debey), as it were, are arranged in the above described pedate (palinactinodrom) compound leaf type reminding one on Platanaceae. The cuticles as pictured in the present paper likewise point to *Castanopsis*. Dr Crane, has drawn my attention to the presumable connection in phylogeny of Fagaceae and Platanaceae. The above mentioned leaf type in this view might not be an accidental one within *Dewalquea*.

Knobloch (1964, pp. 147-1978) and Rufflé and Knappe (1977, pp. 279, 281) could observe that in several Cretaceous localities the leaf types *Dryophyllum* Debey, *Araliophyllum* Ett., *Araliopsis* Sap. & Mar., *Dewalquea* Sap. & Mar. must have belonged to only one natural (fossil) genus, dentate as well as with entire margin. The cuticles pictured in Plates 2 and 3 in the present paper seem to approve this (see Rufflé & Knappe, 1977; *Clematis* in Text-figure 2). In *proteophyllum* Velenovsky 1889 Knobloch (1978) observed the same heterophyllous leaf morphology but with a quite strange cuticle, being undeterminable so far. There is no indication of Fagaceae (Kvacek in Kovar-Eder, 1992).

Dalembia Herman & Lebedev 1991 is still remarkable. To the present author, this artificial genus seems similar to *Dewalquea*. About five *Quercus* leaves are compound in the same manner as shown in Text-figure 1H but beyond it is combined or attached with *Cissites formosus* Heer 1882. *Quercus* leaves with waved margins may have existed in the arctic zone of Late Cretaceous. It is important, too, that *Fagus* also seems to have existed at this time in the northern zone of Arctic: *Fagoxylon* Stopes & Fuji from the Cenomanian of Japan looks like modern *Fagus* wood (Süss, 1986).

In the present paper most of the pictured specimens come from the Senonian (Santon) of Quedlinburg (Harz). The clay sediment yielded well-preserved cuticles. Obviously, the following specimens belong to only one fossil species:

Dewalquea westerhausiana (Richter) Rufflé & Knappe 1977, syn. *Bignonia* "westerhausiana" Richter 1904, syn. *Debeya bohemica* Knobloch 1964, and syn. *Quercophyllum triangulodentatum* Knobloch 1964 (Pl. 1, figs 3,4; Pl. 2, fig. 2, (see Text-figure 3A,B); Pl. 2, fig.1).

Araliopsis wellingtoniana (Lesq.) Lesquereux 1893

syn. in Fritel, 1914; Seward, 1927; Ablaev 1974,

Pl. 2, fig. 3 (see Pl. 3, fig. 1)

The Type locality of the genus *Dewalquea* is Haldem (Westfalen), described by Saporta and Marion, 1873 and Hosius and v.d. Marck, 1880. The complete sequence consists of sandstones. The Type species is *D. haldemiana* Sap. & Mar. The specimens pictured in Plate 2 figures 4 and 5 are not the original ones but from the Type locality (Berlin Naturkunde Museum). The cuticle is not preserved (see also Roemer, 1889).

Dewalquea gelindenensis Sap. & Mar. 1973 has been recorded from the Palaeocene flora of Gelinden (Belgium). Plate 1, figure 2 also presents topotypic material. Text-figure 3 I, J is the cuticle of Saporta's and Marion's Holotype published by Stockmans (1932). This reminds of those mentioned above. It is important that Saporta and Marion (1878) proposed an artificial genus *Pasaniopsis* (Fagaceae) on the basis of isolated simple leaves. It has also been recovered from this locality. But an organic connection with *Dewalquea* seems unsure so far. On the distribution at the northern coast of the Tethys Sea, Johnson and Gilmore (1921) and Makulbekov (1977) made important comments (Atlantic - Kazakhstan).

Dewalquea insignis Hos. & v.d. Marck (1880, 1885) in Plate 3, figure 1, is wide-spread in the Senonian of Europe (see also Roemer, 1889). The cuticle in Plate 3, figure 2 originates from the Czech Senonian locality-Zliv (Nemejc & Kvacek, 1976). In Quedlinburg, there were only fragments. The pictured sample comes from

PLATE 2

1. *Dewalquea westerhausiana* (Richter) Rufflé & Knappe from clay, Quedlinburg (lower epidermis 250 x), see Text-fig. 3A.
2. The same from Text-fig. 3B.
3. *Araliopsis wellingtoniana* (Lesq.) Lesq. from clay, Quedlinburg, see Plate 3, fig. 1
- 4.-5. *Dewalquea haldemiana* Sap. & Mar. from Haldem Sandstone, Type Locality (Museum für Paläontologie Nr. 88-1)

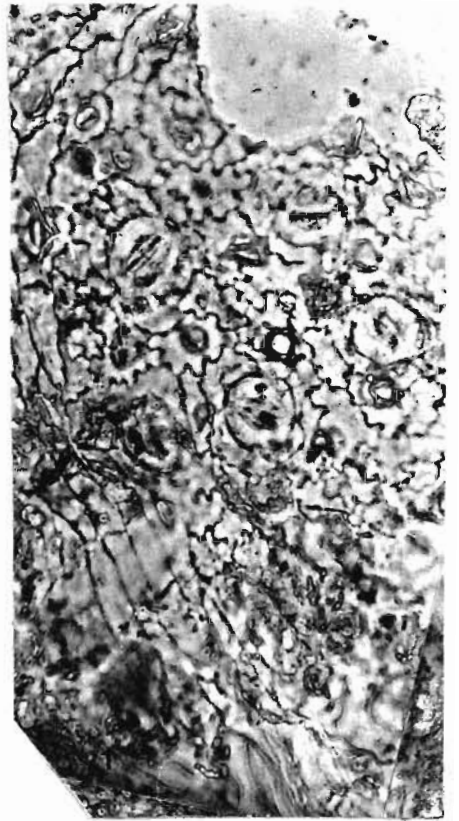


PLATE 2

the so-called Heidelberg Sandstein near Blankenburg (Harz).

There are also some American species, viz., *Dewalquea smithii* Berry (1914, 1919), from the Upper Cretaceous Tuscaloosa Formation (Text-figure 3F, H). They are quite similar to *D. westerhausiana* (Richter) Rüffle & Knappe and perhaps belong to the German species (see also *Dewalquea pulchella* Knowlton, 1917, p. 90).

ARALIACEAE

There are some more reasons to draw attention to the Araliaceae. Berry (1916, pl. 98) refers *Oreopanax oxfordensis* Berry from the Lower Eocene Wilcox Formation. His very striking pictures look like *Dewalquea*, perhaps surviving in the Eocene, but Araliaceae cannot be excluded. Likewise, Fritel (1914) and Johnson and Gilmore (1921) discussed Araliaceae. *Dewalquea groenlandica* Heer (1882, p. 87) should be combined as *Araliophyllum grönlandicum* (Heer) Fritel. Concerning this species, the present author would prefer Platanaceae relationship. The restoration of "*Aralia*" *denticulata* Hos. & v.d. Marck (Text-figure 3E) should link to *Araliopsis wellingtoniana* (see above). In Czech Cenoman there are several leaves called *Cussoniphyllum* Velenovsky 1889 looking like *Cussonia* (Text-figure 1C,D). By the described marginal meristem growth of Cretaceous leaves one should take into account many possibilities in several families. It is quite manifest that besides *Hedera helix*, *L. pedata* Hibb. (Text-figure 1E) and species of *Cussonia*, *Tetrapanax papyrifera* (Hook.) K. Koch and other Araliaceae resemble closely the pedate leaf forms in *Platanus*. But only *Dewalquea* (*Aralia*) *coriacea* (Vel.) Velenovsky from the Czech Cenoman is well known by its cuticles (Nemejc & Kvacek, 1976) resembling many modern cuticles of Araliaceae, for instance *Oreopanax*. As to the above mentioned *Proteophyllum* Vel., one should take Araliaceae in consideration.

PLATANACEAE

Dewalquea fraxinifolia and *hibernica* Johnson & Gilmore were assigned to the genus *Platanus* by Walther 1985 (see Ruffle, 1980b). The recently published *Mallotus ruefflei* Ablaeu & Vassiliev 1994 (Text-figure 5) is a peltate leaf close to those in Ruffle (1979) called *Proteophyllum pseudospermoides* Lesq., and *Platanus cuneiformis* Krasser. In 1968, the present author (Ruffle, 1968) confounded *Credneria* with *Macaranga* (Euphorbiaceae). In fact, the new species, described by the two Russian authors on the same reason should be combined with *Platanus* or *Proteophyllum* Lesq. The elongated leaves are the same as described by Potonié (1912b) in *Platanus* on the basis of accelerated leaf growth and atavisms.

Platanus ruefflei (Ablaeu & Vassiliev)
nov. comb.

This species originates from the Tertiary coast of the Japanese Sea and seems to be a relict of Cretaceous (Ablaeu, 1974; p. 102, fig. 22; Ruffle, 1980 b). Platanaceae, though principally distributed in the Arctic zone of Late Cretaceous, some genera (*Credneria*, *Platanus*) reached the Cretaceous amphiatlantic province (northern Tethys sea coast) where *Gleichenia* and some Matoniaceae and Dipteridaceae existed in association with *Dewalquea*, *Liriodendron*, and other. According to Crane (1989) one should take into account many phylogenetic relationships between Platanaceae and Fagaceae. The former exists since Mid-Cretaceous. The pollen found from the Mid-Cretaceous up to the present time are close to Fagales. Though Araliaceae and Euphorbiaceae are known, their significance in the Upper Cretaceous is so far not known.

ACKNOWLEDGEMENTS

The present author wishes to express gratitude to Dr Ablaeu, Vladivostok, and Dr Mrs. H. Kloene, Hamburg for discussion and first reading of the manuscript.

PLATE 3

1. *Araliopsis wellingtoniana* (Lesq.) — Lower epidermis (250 x) from the sample in Plate 2, figure 3.
2. *Dewalquea insignis* Hos. & v.d. Marck, lower epidermis from Zliv (Czechia) 500 x.

3. *Dewalquea insignis* Hos. & v.d. Marck from Heidelberg Sandstein near Blankenburg (Harz) (1/2 x)

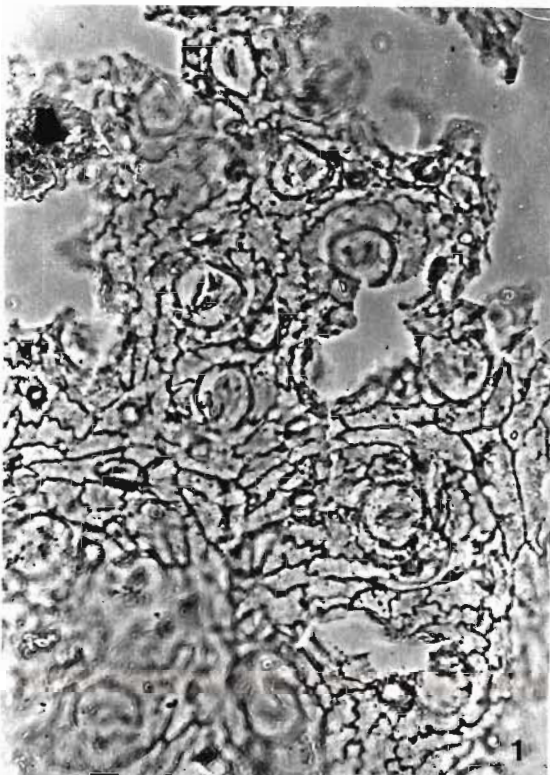
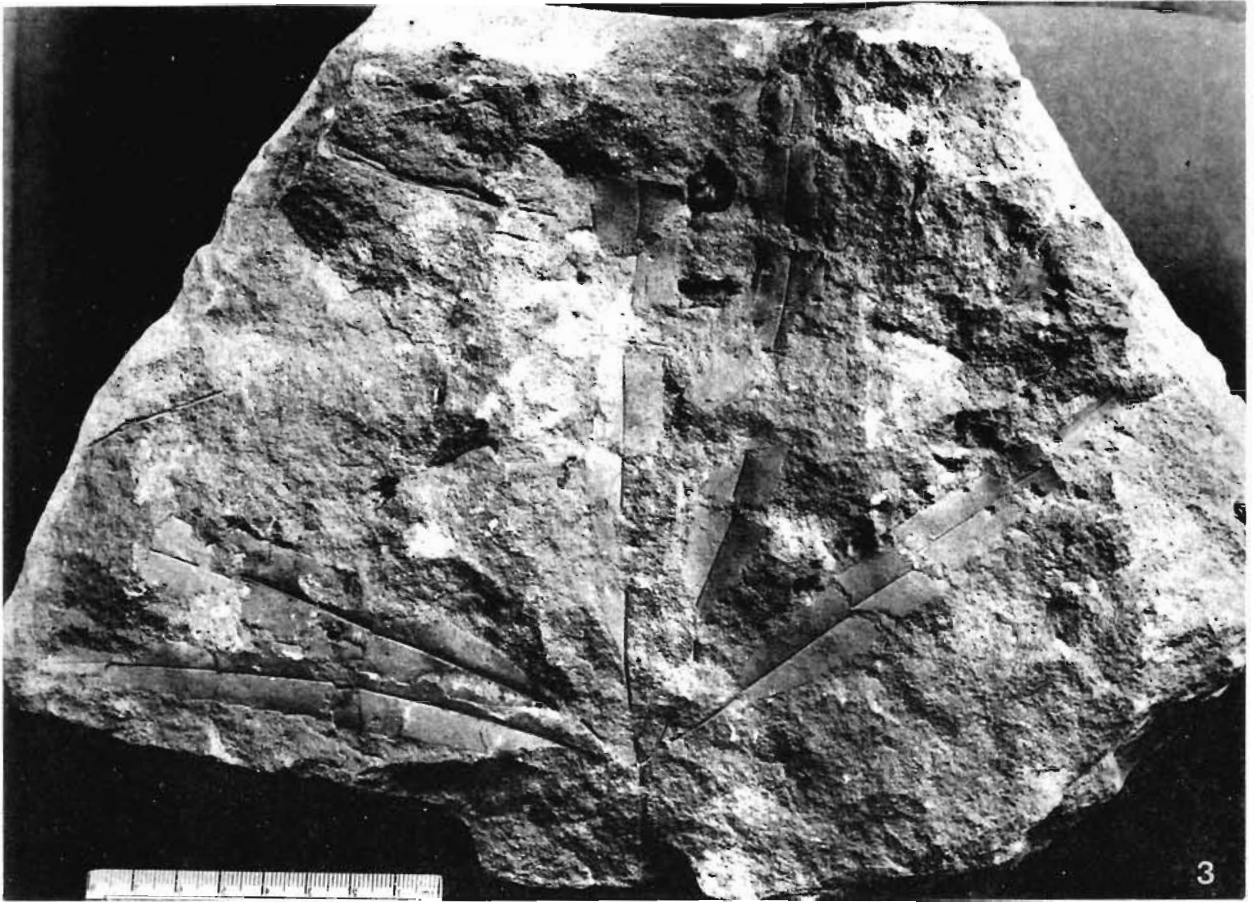


PLATE 3

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बी० मा० पु० सं०
 पुस्तकालय
 परिग्रहण सं० 54020