On the extinct Mastixiaceae (Cornales) in Europe

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A critical revision of fossil fruits of the Mastixiaceae from Europe has reduced the number of extinct genera to *Beckettia, Eomastixia, Mastixicarpum (=Diplopanax), Mastixiopsis, Retinomastixia* and *Tectocarya*. All the species of these genera from the Upper Cretaceous to the Late Tertiary (Pliocene) are of biostratigraphic and palaeoclimatic significance.

Key-words—Mastixiaceae, Upper Cretaceous-Pliocene, Europe.

INTRODUCTION

THE frequency and diversity of the Mastixiaceae are always surprising in the carpological investigations of the Tertiary floras of Europe. This small family of the Cornales now consists only two genera, viz., *Mastixia* Bl. (19 extant species) and *Diplopanax* Handel-Mazzetti (1 extant species). The arborescent species of these two genera are mainly distributed in the tropical rain forest of Southeast Asia. Some species are also known to occur under cooler climatic conditions in the mountain forests of Vietnam and southern China (Kirchheimer, 1943; Eyde & Xiang Qiuyun, 1990). Hence the presence of mastixiaceous fossils in the subtropical Tertiary floras of Europe is especially significant. In the European fossil floras they are most dominant exhibiting a great degree of diversity. Recognizing these facts, Kirchheimer (1938a) devoted a number of publications to the fossils of Mastixiaceae and the "Mastixioidean floras". They consist of a number of extinct genera which are distinguished by carpological features.

The history of research on the fossil Mastixiaceae in the European Tertiary began with the discovery of the fruit-stone of the genus *Mastixia* Bl. in the Oligocene Browncoal clays of Bovey Tracey in England (Reid & Reid, 1910). Chandler (1926) noticing the differences in the endocarp of two more fossils of this family and the endocarp of *Mastixia* suggested the possibility of the occurrence of some extinct genera of Mastixiaceae in the past. Consequently, she established two extinct genera *Mastixicarpum* and *Eomastixia*. Further investigations were marked by a quick multiplication of such extinct genera in the subsequent years. Reid and Chandler (1933) added the genera *Beckettia, Lanfrancia* and *Langtonia*. Kirchheimer's investigations resulted in a major splitting of the fossil remains of the Mastixiaceae into many genera and species which were not always distinguishable with certainity. Kirchheimer (1934b, 1935a, 1936a,b) described a number of new genera, viz., *Diplomastixia, Platymastixia, Tectocarya, Mastixioidea, Mastixiopsis,* and *Plexiplica*. Adding to this list three more genera, viz., *Retinomastixia, Xylomastixia* (Kirchheimer, 1938a) and *Portnallia* (Chandler, 1961a), described in subsequent years, the total number of extinct genera of Mastixiaceae thus recorded from Europe became sixteen with 40 species.

The difficulties started when the generic diagnosis for various genera was given. They were further increased because of the lack of uniformity of pattern on the basis of which new genera were differentiated from the existing ones by different workers. This practice of a free choice in instituting new genera was criticised by many workers like Kräusel (1936, 1938a, 1938b).

Continuous additions of numerous new collections in the last decade has necessitated revision of these genera and species. After a fresh investigation of all the type and original material in the previous years, and the identification of the variability of the populations by means of more than a hundred examples of most species in the new collections, have resulted the reduction in the number of genera and species of Mastixiaceae. The first critical revision of the then existing fossil genera initiated by Kirchheimer (1938a,b) who suggested that *Diplomastixia* Kirchh. and *Ganitrocera* Kirchh. are synonyms. The assignment of *Langtonia* Reid & Chandl. was also rejected. The same author doubted the generic identity of

Mastixioidea Kirchh., *Lanfrancia* Reid & Chandl. and *Xylomastixia* Kirchh. and opined that they are synonyms of *Tectocarya* Kirchh., *Beckettia* Reid & Chandl. and *Mastixicarpum* Chandl. (Kirchheimer, 1957, p. 552). But in doing so, the rules of nomenclature were not followed strictly. *Plexiplica* Kirchh. was merged with *Eomastixia* Chandl. by Chandler (1960, p 234). Mai (1964, p.44) placed *Xylomastixia* Kirchh. in *Mastixicarpum* Chandl. Holý (1975, p.138) merged *Ganitrocera* Kirchh. with *Eomastixia* Chandl. According to variation-statistical investigations *Platymastixia* Kirchh. comes under the synonymy of *Mastixicarpum* Chandl. (Mai & Walther, 1978, p.120) *Portnallia* Chandl. was recognized as a species of *Beckettia* Reid et Chandl. (Knobloch & Mai, 1986, p.107). On the basis of the fruit-pattern, the genus *Mastixicarpum* Chandl. (1926) was recognized unambiguously as congeneric with the extant Chinese genus *Diplopanax* Handel-Mazzetti (1933). It was described as an Araliacean genus, seven years after the discovery of the fossils in England (Eyde & Xiang Qiuyun, 1990, p.692). With that there remain only five genera- *Eomastixia* Chandl., *Beckettia* Reid et Chandl., *Tectocarya* Kirchh., *Mastixiopsis* Kirchh. and *Retinomastixia* Kirchh. of the many extinct genera of Mastixiaceae.

A revision of these fossil genera was desirable not only at the generic level but even more urgently for the species which were described under several genera. Such revisions were carried out by Holý (1975) for *Eomastixia* Chandl. and *Tectocarya* Kirchh. and by Gregor (1978b) for *Retinomastixia* Kirchh. Keys for the remaining species of *Beckettia* Reid et Chandl., *Eomastixia* Chandl., *Mastixicarpum* Chandl. and *Mastixiopsis* Kirchh. were prepared by Mai and Walther (1978, 1985) and Knobloch and Mai (1986). In addition, Mai (1987a, p.115) described a new species of *Tectocarya* Kirchh. A revision of the fossil fruit-stone of the genus *Mastixia* in the European Tertiary was given by Mai (1970). Holý (1982) has further described a new species of this genus. These critical revisions have resulted, on the one hand in the reduction of the number of extinct genera while on the other hand in an increase in the number of species of the fossil Mastixiaceae in Europe.

EXTINCT GENERA AND SPECIES

The characteristic features on the basis of which a carpological fossil can be assigned to the Mastixiaceae are: seed locule horse-shoeshaped, sulcus-like infold of the endocarp into this locule, dehiscence with an elliptical valve around the whole length of the endocarp, which contains the infold in the middle, infold and valve mark the dorsal side of the endocarp of the fruit. Such constructed fruit-stones of fruits may be assigned with certainty to *Mastixia*-like plants, in some cases to *Mastixia* itself. Some fossil forms show more variations than these diagnostic features, e.g., multiplication of the number of locules, the absence of an outside-furrow which corresponds to the infold into the endocarp, a woody pericarp and resin ducts in the mesocarp. The variations have established the assumption of extinct genera of the Mastixiaceae. Before accepting the usefulness of morphological and anatomical characters for generic differentiation, they must withstand a very critical test. After considering all the different combination of characters in the extinct taxa of Mastixiaceae, it was found that these taxa can be classified to six distinct groups or as six separate genera in the opinion of the earlier workers. As in case of some other Cornalean genera, e.g., *Nyssa*, *Cornus* or *Alangium*, these groups have a certain relation in their differences in morphology, histology and locule number between each other and the recent *Mastixia* Bl. In the opinion of the present author it would not be in an unusual practice to treat the extinct European genera of the Mastixiaceae as subgenera of *Mastixia* Bl. or *Diplopanax* Hand-Mazz.

Key to genera

1. Fruit-stone 2 to 4-loculed.....6
   Fruit-stone always 1-loculed.....2

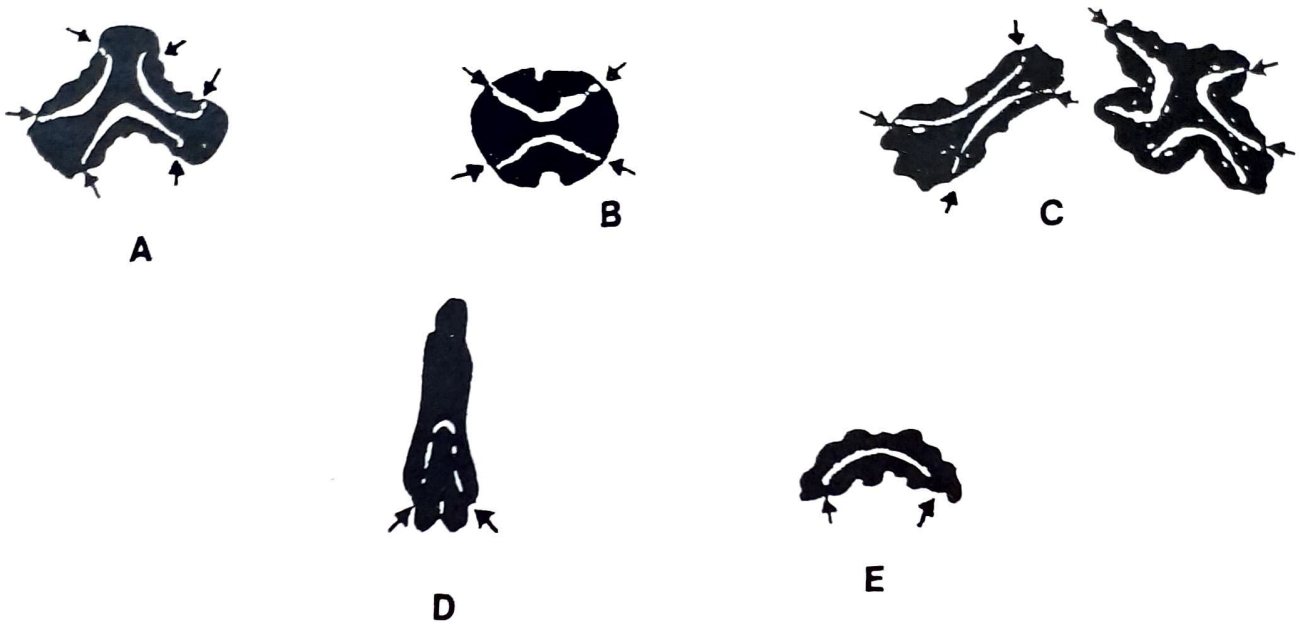
2. Endocarp and epicarp (exo-and mesocarp) more or less compactly aggregated, both ligneous.....4
   - Endocarp and epicarp slightly detached, endocarp ligneous, mesocarp fleshy, exocarp dermatous; fruit ovate to fusiform.....3

3. Dorsal sulcus shallow, the edges not contacting each other, loculum in the cross-section shallow U-shaped..... ***Mastixiopsis* Kirchh.**
   - Dorsal sulcus deep, the edges of the infolding compressed closely together or separated bow-shaped; loculum in the cross-section horseshoe-shaped.....4

4. Endocarp and mesocarp without lacunous resin tissues.....5
   - Endocarp and mesocarp with lacunous resin tissues full of retinit; edges of the infolding free; endocarp and epicarp compactly aggregated ..... ***Retinomatixia* Kirchh.**

5. Dorsal sulcus with compactly compressed or separated edges of the infolding; epicarp thick, compactly aggregated with the endocarp, sometimes with cavities..... ***Mastxicarpum* Chandl.**
   - Dorsal suclus with bow-shaped separated edges of the infolding, in the upper two third of the dehiscence valve with paired cavities, which leave a septum shaped lamellae; epicarp thin, after abrasion detached from the endocarp, otherwise aggregated with them ..... ***Tectocarya* Kirchh.**

6. Endocarp and epicarp compactly aggregated; locules shallow U-shaped, with separated edges of the infolding, not contacting each another; without resin tissues.....***Beckettia* Reid & Chandl.**
   - Endocarp and epicarp variable in thickness, the epicarp usually smaller than the endocarp, more or less slightly detached, infolding sulcus-like with the edges compressed closely together or separated, bow-shaped; lacunous resin tissues with retinit in the mesocarp and endocarp..... ***Eomastixia* Chandl.**



Text-figure 1. Schematic cross-section of the fruit-stone of the Upper Cretaceous Mastixiaceae: A. *Beckettia pyriformis* Knobl. et Mai; B. *Beckettia aamuelis* Knobl. et Mai, C. *Eomastixia rostrata* Knobl. et Mai; D. *Mastixicarpum cretaceum* Knobl. et Mai; E. *Mastixiopsis kirchheimeri* Knobl. et Mai.

Beckettia Reid et Chandl.

Genotype- *Beckettia mastixioides* Reid & Chandler, 1933, p.455-457, pl.25, figs 28-36; Sheppey (England), Lower Eocene.

Lanfrancia Reid et Chandl.

Genotype- *Lanfrancia subglobosa* Reid & Chandler, 1933, p.457-459, pl. 25, figs 37-40; Sheppey, Lower Eocene.

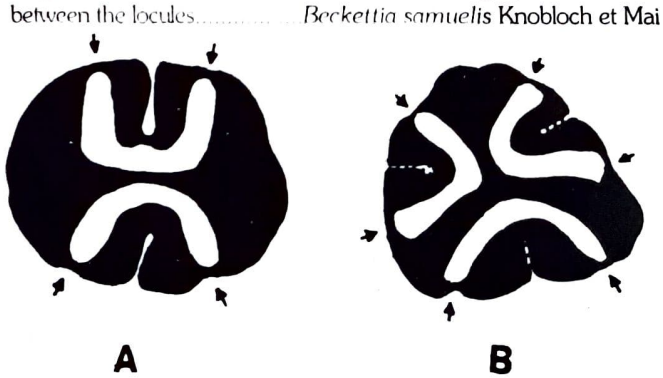
Portnallia Chandl.

Genotype- *Portnallia bognorensis* Chandler, 1961a; 285-286, pl.28, figs 39-44; Bognor (England), Lower Eocene.

In the greater number of locules (3-4) *Lanfrancia* Reid & Chandl. could be different from *Beckettia* Reid et Chandl. However, according to Kirchheimer (1936b, p.284), a 4-locular form is comparable with *Beckettia* Reid et Chandl. "The splitting in a one-locular pyrena may be based on the subsequent processes of reduction". In view of the other multilocular genera of Mastixiaceae such a combination is ingenious. In the form and size, both the species of *Portnallia* Chandler (1961a) are very similar, which also belong to *Beckettia* and probably represent one species only (Knobloch & Mai, 1986, p.107). In the possession of the shallow U-shaped locules, important sign of a differentiation from other genera, reminding one distinctly of the proportions to *Mastixiopsis* Kirchh. Kirchheimer (1936b, p.284) has further emphasized that the endocarp consists mainly of parenchyma. The form of the locule and the shallow infolding of the dehiscence valve reminds one of the conditions in the Alangiaceae.

Key to species

1. Endocarp about 10 mm long, subglobose or ovoid, dehiscence valve with only one longitudinal infolding.....*Beckettia mastixioides* Reid et Chandl.
   - Endocarp below 10 mm long, mostly smaller.....2
2. Dehiscence valve only with a shallow depression, not an infolding; fruit-stone pear shapped to obovoid, 3-loculed, valves indistinctly deducted.....*Beckettia pyriformis* Knobloch et Mai
   - Dehiscence valve with a broad longitudinal infolding, fruitstone 2- to 4-loculed, valves distinctly deducted.....3.
3. Fruit-stone subglobose to ovoid, commonly 3, rarely 2- or 4-loculed; surface wrinkled with narrow furrows between the locules..... *Beckettia bognorensis* (Chandl.) Mai
   - Fruit-stone ovoid, fusiform, 2- or 3- loculed; surface irregular longitudinal wrinkled, with ramificated tissue vestiges, without furrows between the locules..... *Beckettia samuelis* Knobloch et Mai



Text-figure 2. Schematic cross section of *Beckettia mastixioides* Reid et Chandl: A. 2- loculed fruit-stone after Reid & Chandler (1933); B. 3- loculed fruit-stone as *Lanfrancia subglobosa*" by Chandler (1961a).

Species

1. *Beckettia mastixioides* Reid et Chandler

Type- Reid & Chandler, 1933, p.455-457, pl.25, fig.28; Sheppey.

Synonym - *Lanfrancia subglobosa* Reid & Chandler, 1933, p.457-459,. pl. 25, figs 37-40; Sheppey.

2. *Beckettia pyriformis* Knobloch et Mai

Type- Knobloch & Mai, 1986, p.106-107, pl.23, figs 1-2; Walbeck, Foreland of the Harz Mts. (Germany).

3. *Beckettia bognorensis* (Chandl.) Mai

Type- *Portnallia bognorensis* Chandler, 1961a, p. 5-286, pl.28, fig. 39; Bognor (England).

Synonym- *Portnallia sheppeyensis* Chandler, 1961a, p.286, pl.28, fig.45; Sheppey (England).

4. *Beckettia samuelis* Knobloch et Mai

Type- Knobloch & Mai, 1986, p.107, pl.23, figs 7-8; Eisleben, Foreland of the Harz Mts. (Germany).

This extinct genus with its ancestral patterns occurred biostratigraphically in the Upper Cretaceous of Middle Europe (2 species Knobloch & Mai, 1986) and in the Lower Eocene (London Clay) of England (Reid & Chandler, 1933; Chandler, 1961a).

Eomastixia Chandl.

Genotype- *Eomastixia bilocularis* Chandler, 1926, p.37, pl.6, figs a-e; Hordle/Hants (England), Upper Eocene.

Diplomastixia Kirchh.

Genotype- *Diplomastixia carinata* Kirchheimer, 1934b, p.788-789, fig.17; Kausche (Welzow), Lower Lusatia (Germany), Middle Miocene.

Ganitrocera Kirchh.

Genotype- *Ganitrocera saxonica* (Menzel) Kirchheimer, 1934b, p.773, fig.12 (= *Elaeocarpus saxonicus* Menzel. Menzel, Gothan & Sapper, 1933, p.26, pl.6, fig.9); Gohra/Lower Lusatia (Germany), Middle Miocene.

Plexiplica Kirchh.

Genotype- *Plexiplica reidi* Kirchheimer, 1935b, p.293, fig. 18; Groβzössen, Weiβelster Basin (Germany), Lower Oligocene

Diplomastixia Kirchh., *Ganitrocera* Kirchh. and *Plexiplica* Kirchh. are synonyms. Kirchheimer (1936b, p.285) gave a distinct reference to the affiliation of *Diplomastixia* to *Ganitrocera*. Since then this genus was regarded as a synonym : "*Diplomastixia* Kirchh. must be inserted because the assignated remains are badly preserved fruit-stones of the *Ganitrocera* Kirchh. exclusively" (Kirchheimer, 1938c, p.642). The frame of the epicarp, more or less connected with the endocarp, the disc, the resin ducts and the histological structures are similar to those of *Eomastixia* Chandl. and *Ganitrocera* Kirchh. Therefore the different patterns of both do not justify their distinction as independent genera but can be separated as different species (Holý, 1975). Kirchheimer (1957, p.259) has established specific identity of *Plexiplica reidi* Kirchh. and *Plexiplica rugosa* (Zenker) Kirchh. Chandler (1960, p.234) undertook the identification of *Plexiplica* Kirchh. with *Eomastixia* Chandl. in agreement with Kirchheimer. The Haselbach collection (Mai & Walther, 1978, p.122) has presented the basis of the biostratigraphical investigations.

Key to species

1. Fruit-stones very small, mostly below 10 mm long, distinctly narrowed or rostral at the small apical discus.....2
   - Fruit-stones bigger, with a large discus mostly at a rounded or flattened apex 3
2. Fruit-stones urceolate, 3- to 4- loculed, with resin ducts in the sulcus of the dehiscence valve and in each septum; surface longitudinal, wrinkled to furrowed; length 6 to 13 mm..... *Eomastixia urceolata* Chandl.
   - Fruit-stone elliptical to fusiform, rostrate at the apex, (1-) 2- to 3-loculed, with resin ducts passing over into each other near the locules ; surface angular wrinkled, with tissue vestiges and single resin ducts; length 4 to 7.5 mm ....*Eomastixia rostrata* Knobloch et Mai
3. Infoldings of the dehiscence valves not separated ; fruit-stones only medium-sized, 9.5 to 20 mm long, 5.5 to 10 mm broad, 2-loculed; epicarp thin, more or less connected with the endocarp, difficult to separate from one another.....*Eomastixia bilocularis* Chandl.
   - Infoldings of the dehiscence valves separated; fruit-stones great, (1-) 2- to 3- loculed.....4
4. Ribs of the fruit-stones obtuse ; epicarp thin snuggling to the ribed surface, difficult to separate from one another 5
   - Ribs of the fruit-stones acuto-angular; epicarp thick, over the ribs forming a smooth surface; easy to separate from one another; fruit-stones very big, 26 to 55 mm. long, 25 to 40 mm broad; infoldings with a pocket-like hollow.....*Eomastixia holzapfelii* (Menzel) Mai
5. Fruit-stones in the middle 10 to 20 mm long, 7 to 15 mm broad; infoldings of the dehiscence valves slightly or not separated, ? without an apical discus ..... *Eomastixia rugosa* (Zenker) Chandl.
   - Fruit-stone in the middle 10 to 42 mm long, 8 to 30 mm broad; infoldings of the dehiscence valves within a great cavity, an apical discus existing 6
6. Fruit-stones 9 to 30 mm long, 8 to 16 mm broad, index of the length/breadth about 1.7 to 2.1; smaller and narrower than the following species.. *Eomastixia hildegardis* (Unger) Holý
   - Fruit-stones 17 to 42 mm long, 11 to 30 mm broad; index of the length/breadth about 1.3 to 1.9.....*Eomastixia saxonica* (Menzel) Holý

Species

1. *Eomastixia urceolata Chandl.*

Type- Chandler, 1962, p.126-127, pl.19, fig.8. Lake/Doset (England)

2. *Eomastixia rostrata* Knobloch & Mai

Type- Knobloch & Mai, 1986, p.108, pl.23, figs 11-12; Walbeck Foreland of the Harz Mts. (Germany)

Text-figure 3. Schematic cross-sections of *Eomastixia* species: A. *Eomastixia bilocularis* Chandl., 2-loculed fruit-stone according to Mai & Walther (1985); B. *Eomastixia urceolata* Chandl., 3- loculed fruit-stone according to Chandler (1962); C. *Eomastixia rugosa* (Zenk.) Chandl., 2- loculed fruit-stone as "*Eomastixia bilocularis*" by Chandler (1926); D. 2-loculed fruit-stone, abraded and somewhat modified, as "*Ganitrocera minima*" by Kirchheimer (1935a); E. 3-loculed fruit-stone, as *Plexiplica reidi* by Kirchheimer (1936b); F. *Eomastixia hildegardis* (Ung.) Holý 1- loculed fruit-stone with remains of the epicarp, as "*Diplomastixia arzbergiana*" by Kirchheimer (1936b); G. *Eomastixia saxonica* (Menz.) Holý, 2-loculed fruit-stone according to Kirchheimer (1936b); H. 2-loculed fruit-stone with a weakly developed loculum, as "*Ganitrocera torulosa*" by Kirchheimer (1935a); I. *Eomastixia holzapfelii* (Menz.) Mai, 1- loculed fruit-stone according to Kirchheimer (1935a); J. 2- loculed fruit-stone as "*Ganitrocera menzelii*" Kirchheimer (1935a); K. 3- loculed fruit-stone as "Ganitrocera menzelii" by Kirchheimer (1935a). Black coloured (Endocarp); black dotted (epicarp); white with black frame (resin tissue); white (locules & lysigenous cavities in all figures.

3. *Eomastixia bilocularis* Chandl.

Type- Chandler, 1926, p.37, pl.6, fig.6; Hordle/Hants (England)

4. *Eomastixia holzapfelii* (Menzel) Mai

Type- *Elaeocarpus holzapfelii* Menzel, 1913, p. 46, pl.4, figs. 31-33; Herzogenrath, Rhineland (Germany).

Synonyms

Ganitrocera holzapfelii Kirchheimer 1934b, p.771, fig.4; Herzogenrath.
Ganitrocera menzeli Kirchheimer, 1944, p.16, figs 2a-d (diagnosis in Kirchheimer, 1957, p.555); Konzendorf, Rhineland (Germany).

5. *Eomastixia rugosa* (Zenker) Chandl.

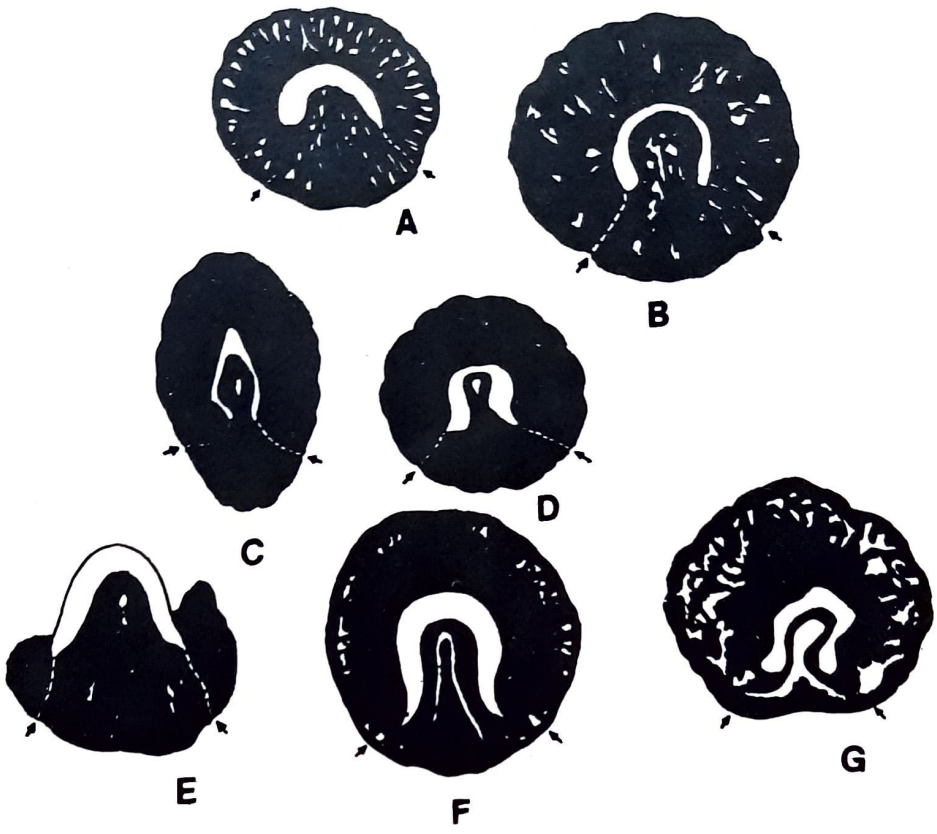
Type- *Baccites rugosus* Zenker, 1833, p.12-13, pl.1, fig.9, Altenburg, Weißelster Basin (Germany).

Synonyms

Ganitrocera ? minima Kirchheimer, 1935a, p.93-94, pl.13, figs 41a-c; Altenburg.
Plexiplica reidi Kirchheimer, 1936b, p.292, pl.8, figs 1a-d; Groß-Zössen, Weißelster Basin (Germany).
Plexiplica rugosa Kirchheimer, 1957, p.259-260, figs 47b, 161a-d; Regis, Weißelster Basin (Germany).

6. *Eomastixia hildegardis* (Unger) Holý

Type- *Amygdalus hildegardis* Unger, 1866, p.63, pl.29, fig.19 (=Unger, 1850a, p.482, nom. nudum); Starost, Cheb (Czechoslovakia).



Text-figure 4. Schematic cross-section of *Mastixicarpum* species: A. *Mastixicarpum crassum* Chandl., fruit-stone according to Chandler (1926); B. *Mastixicarpum cacaoides* (Zenk.) Mai, fruit-stone from sands with big cavities, as "*Mastixicarpum compactum*" by Kirchheimer (1936b); C. flattened fruit-stone from clays according to Mai & Walther (1978); D. fruit-stone from clays without cavities as "*Platymastixia cacaoides*" by Kirchheimer (1936b); E. *Mastixicarpum limnophilum* (Ung.) Kirchh., fragment of a fruit-stone from salt showing the dorsal part, original in the BM. Kraków (Poland); F. fruit-stone from salt according to Kirchheimer (1941); G. fruit-stone from sand with many cavities, as "*Xylomastixia lusatica*" by Kirchheimer (1938a).

Synonyms

Amygdalus persicoides Unger, 1866, p.63, pl.29, figs 16-18 (=Unger 1850a, p.483 nom. nudum; Starost.
Diplomastixia arzbergiana Kirchheimer, 1936b, p.293-294, pl.8, figs 4-5; Seussen, Arzberg (Germany).

7. *Eomastixia saxonica* (Menzel) Holý

Type- *Elaeocarpus saxonicus* Menzel. Menzel, Gothan & Sapper, 1933, p.26, pl.6, fig.9; Gohra, Lower Lusatia (Germany).

Synonyms

Ganitrocera saxonica Kirchheimer, 1935a, p.55-59, pl.4, figs 15a-q, pl.5, figs 16a-f; Gohra.
Ganitrocera juglandoides Kirchheimer, 1935a, p.61-62, pl.6, figs 21a-i; Merka -Quatitz, Upper Lusatia (Germany).
Ganitrocera torulosa Kirchheimer, 1935a, p.60, pl.5, figs 15a-d, pl.6, fig.19e; Merka-Quatitz.
Diplomastixia carinata Kirchheimer, 1935a, p.54, pl.3, figs 14a-e; Kausche, Lower Lusatia (Germany).
Ganitrocera persicoides Kirchheimer, 1957, p.179-180, figs 31b, 162a-i; Merka-Quatitz.
Eomastixia persicoides (Unger) Gregor, 1975, p.170-172; Wackerdorf, Oberpfalz (Germany).

This extinct genus extends from the Upper Cretaceous (Maastrichtian, Knobloch & Mai, 1986) through the Upper Miocene (Menzel, 1913; Kirchheimer, 1944) in the Western and Middle Europe.

***Mastixicarpum* Chandl.**

Genotype- *Mastixicarpum crassum* Chandler, 1926, p.36-37, pl.6 figs 5a-d, text-fig.18; Hordle Hants (England). Upper Eocene.

***Baccites* Zenker**

Genotype- *Baccites cacaoides* Zenker, 1833, p.10-12, pl.1, figs 4- 8+E, and 11-16; Altenburg, Weißelster Basin (Germany), Lower Oligocene

***Platymastixia* Kirchh.**

Genotype- *Baccites cacaoides* Zenker, 1833, p.8-12, pl.1, figs 4- 16+E pro parte; Altenburg, Lower Oligocene.

***Xylomastixia* Kirchh.**

Genotype- *Xylomastixia lusatica* Kirchheimer, 1938a, p.348-350, pl.7, figs 1-6; Wiesa, Upper Lusatia (Germany), Lower Miocene.

According to the generic diagnoses, *Platymastixia* Kirchh. and *Xylomastixia* Kirchh. do not differ from *Mastixicarpum* Chandl. and are recognized as different states of preservation. *Baccites* Zenker is a superfluous genus. Zenker (1833) gave explanations as the conception of a denotation of an organ and not a generic name: "...*Baccites* was derived from *Bacca*, the berry, and attached with the ending *ites* which may point out the fossil relations ...". The genus *Diplopanax* Handel-Mazzetti (1933) now occurring in Gungxi (China) is congeneric with the fossil *Mastixicarpum* Chandler (1926).

Key to species

1. Fruit-stone small, below 18 mm long 2
   - Fruit-stone large and compact, up to 45 mm long 3
2. Fruit-stone with an apical discus; epicarp and endocarp fast connected, only medium-sized thick, without lacunae.....*Mastixicarpum cretaceum* Knobloch *et* Mai
   - Fruit-stone without an apical discus; epicarp slightly abrasionable, endocarp very thick, rich in lacunae...*Mastixicarpum crassum* Chandl.
3. Fruit-stone 18 to 22 mm long, ovoid to cylindrical, edges of the sulcus in the infolding not separated; endocarp rarely with lacunae...*Mastixicarpum cacaoides* (Zenker) Mai
   - Fruit-stone 25 to 45 mm long, ellipsoidal, edges of the sulcus in the infolding separated, sometimes with a pocket-like cavity; endocarp always with lacunae.....*Mastixicarpum limnophilum* (Unger) Kirchh.

Species

1. *Mastixicarpum cretaceum* Knobloch et Mai

Type- Knobloch & Mai, 1986, p.109, pl.23, figs 15-16; Walbeck, Foreland of the Harz Mts. (Germany).

2. *Mastixicarpum crassum* Chandl.

Type- Chandler, 1926, p.36-37, pl.6, figs 5a-d; Hordle (England).

3. *Mastixicarpum cacaoides* (Zenker) Mai

Type- *Baccites cacaoides* Zenker, 1833, p.10-12, pl.1, figs 4-8+E, figs 11-16; Altenburg, Weißelster Basin (Germany).

Synonyms

Anona altenburgensis Unger, 1861, p.26, pl.10, figs 8-11; Altenburg

Anona cacaoides Schenk, 1890, p.507, fig.295; Altenburg.

Platymastixia cacaoides Kirchheimer, 1934b, p.790, fig.21; Altenburg

Mastixicarpum compactum Kirchheimer, 1935a, p.90-91, pl.13, figs 39a-k; Regis II, Groe.-Zössen, Phoenix, Weisselster Basin (Germany).

4. *Mastixicarpum limnophilum* (Unger) Kirchh.

Type- *Quercus limnophila* Unger, 1850b, p.319, pl.35, figs 1-2 (non figs 3-4); Wieliczka (Poland).

Synonyms

Raphia ungeri Stur, 1873, p.8-9; Wieliczka.

Xylomastixia lusatica Kirchheimer, 1938a, p.348-350, pl.7, figs 1-6; Wiesa, Upper Lusatia (Germany).

Mastixicarpum lusaticum Mai, 1964, p.44, fig. 8a; Wiesa.

Stratigraphically this genus with 4 species ranges from the Upper Cretaceous (Knobloch & Mai, 1986) to the Middle Miocene (Kirchheimer, 1941, p.614) in Europe. The remains are widespread regionally from England (Chandler, 1926) to Greece (Velitzelos & Gregor, 1982).

Mastixiopsis Kirchh.

Genotype- *Mastixiopsis nyssoides* Kirchheimer, 1936b, p. 291-292, pl.7, figs 5a-g; Riestedt near Sangerhausen (Germany), Lower Eocene.

In this ancestral genus of Mastixiaceae undoubtedly the differences between related genera of the Cornales become obliterated. In the shape and sculpture, the fruit-stones are nyssoid (Kirchheimer, 1936b, p.285). In the breadth of the locule and the dehiscence-valve are indicated the relationships to the fruit-stones of *Alangium* Lam. The construction of the infolding and the histological structure are still mastixioid.

Key to Species

1. Fruit-stones big, 17 to 23 mm long, externally slightly ribbed, wrinkled, with an indication of a lamella in the apical part of the sulcus..... *Mastixiopsis nyssoides* Kirchh.
   - Fruit-stones very small, only 3.5 to 7 mm long, externally ribbed, single rib interrupted, irregular, without lamella, but with transverse wrinkles in the sulcus.....*Mastixiopsis kirchheimeri* Knobloch et Mai

Species

1. *Mastixiopsis kirchheimeri* Knobloch et Mai

Type- Knobloch & Mai, 1986, p.109, pl.23, figs 20-21; Eisleben, Foreland of the Harz Mts. (Germany).

2. *Mastixiopsis nyssoides* Kirchh.

Type- Kirchheimer, 1936b, p.291-292, pl.7, figs 5a-g; Riestedt.

Synonym

? *Mastixia cantiensis* Chandler, 1962 (non-Reid & Chandl., 1933), p.122-123, pl.18, figs 1-3, Arne/Dorset (England).

This genus is temporally limited to the Upper Cretaceous (Knobloch & Mai, 1986) and the Palaeocene in Middle Europe (Mai, 1987b, p.214) and also the Lower Eocene in the Harcynian foreland (Kirchheimer, 1936b) and England (Chandler, 1962) with two species only. The fruit-stones from Arne figured by Chandler certainly belong to *Mastixiopsis*. Without the knowledge of the originals, it is not possible to decide whether this determination is also correct for the typical *Mastixia cantiensis* Reid et Chandler (1933) from the London Clay.

Retinomastixia Kirchh.

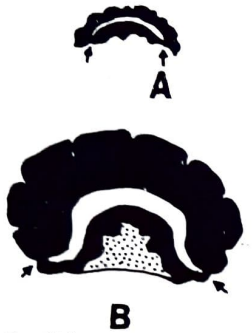
Genotype- *Retinomastixia schultei* Kirchheimer, 1938a: 350-352, pl.7, figs 7-8 (non figs 9-13); -- Nieder-

pleis, Lower Rhine (Germany) Upper Oligocene or Lower Miocene.

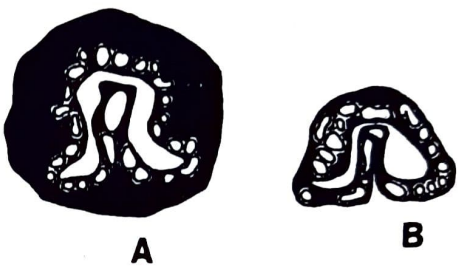
This genus is different from all the other genera of the family in the richness of resin in the lacunar resin-tissues of the fruit-stone. In this regard it is related to some species of the genus *Cornus* Linn. *sensu lato*.

Key to species (After Gregor, 1978b, p.148)

1. Fruit-stones without external furrow and remarkable dehiscence-valve but with internal infolding, 7 to 19 mm long, with 12-18 longitudinal ribs....*Retinomastixia schultei* Kirchh.
   - Fruit-stones with external furrow and internal infolding.....2
2. Resin tissues distributed near the external wall without external ribs; fruit-stones 7.7. to 13.5 mm long, dehiscence-valve indistinct .....*Retinomastixia glandulosa* (Chandl.) Mai
   -Resin tissue distributed near the internal wall, with 8-12 external longitudinal ribs; fruit-stones 8 to 22 mm long with dorsal dehiscence-valve..... *Retinomastixia oerteli* Gregor



Text-figure 5. Schematic cross-sections of *Mastixiopsis* species: A. *Mastixiopsis kirchheimeri* Knobl. et Mai., fruit-stone with shallow horeshoe-shaped loculum, according to Knobloch & Mai (1986); B. *Mastixiopsis nyssoides* Kirchh., fruit-stone with remains of the epicarp into the dorsal infolding, original in the Mfn. Berlin.



Text-figure 6. Schematic cross-sections of *Retinomastixia* species: A. *Retinomastixa oertelli* Gregor, fruit-stone according to Gregor (1978b); B. *Retinomastixia glandulosa* (Chandl.), Mai, fruit-stone as "*Mastixia glandulosa*" by Chandler (1926).

Species

1. *Retinomastixa schultei* Kirchh.

Type- Kirchheimer, 1938a, p.350-352, pl.7, figs 7-8; Niederpleis.

2. *Retinomastixia glandulosa* (Chandl.) Mai

Type- *Mastixia glandulosa* Chandler, 1961b, p.142-143, pl.29, figs 118-121; Hordle/Hants (England).

3. *Retinomastxia oerteli* Gregor

Type- Gregor, 1978a, p.64, pl.14, fig.1; Schwandorf, Oberpfalz (Germany).

This genus is known from Middle to Upper Eocene in England and the Weißelster Basin in Germany (Chandler, 1961b, 1963; Mai & Walther, 1985), and from the Middle Miocene of Germany, Czechoslovakia and Poland (Holý, 1975; Gregor, 1978b), with 3 distinctly vicariant stepping species. During uppermost Middle Miocene, from southwestern Europe it reached the Bordeaux Basin, France (Gregor, 1978b).

***Tectocarya* Kirchh.**

Genotype- *Tectocarya rhenana* Kirchheimer, 1935a, p.62, pl.7, figs 22a-n; Konzendorf, Lower Rhine (Germany), Upper Miocene.

***Mastixioidea* Kirchh.**

Genotype- *Mastixioidea tectocaryoides* Kirchheimer, 1936a, p.219-220, pl.13, figs 5a-f; Konzendorf, Upper Miocene.

The identification of *Tectocarya* Kirchh. with *Mastixioideae* Kirchh. had already been done by Kirchheimer (1936b, p.285). The certainty of this synonymy has resulted from the revision of the originals from the Konzendorf locality (Lower Rhine, Germany). A septum-like lamella as a residuum of the paired cavities in the infolding of the endocarp is present in all the species. This pattern differentiates *Tectocarya* from all the other Mastixioidean genera.

Key to species

1. Fruit-stones with verrucose sculpture which is arranged in slightly longitudinal rows; endocarp considerably thick, cylindrical- ovoid in shape ..... *Tectocarya nerchauensis* Mai
   - Fruit-stones with ridges or slightly wrinkled sculpture which is arranged distinctly longitudinally, endocarp thinner, often enveloped by mesocarp.....2
2. Fruit-stones with distinct ridges, irregularly interrupting, oblong-ovoid in shape, rarely with resin tissues; mesocarp compact and thin, fruit-stone upto 45 mm long.....*Tectocarya elliptica* (Unger) Holy
   - Fruit-stones nearly smooth to slightly longitudinally wrinkled, cylindrical in shape with resintissues; mesocarp compact and thick; fruit-stones up to 65 mm long..... *Tectocarya rhenana* Kirchh.

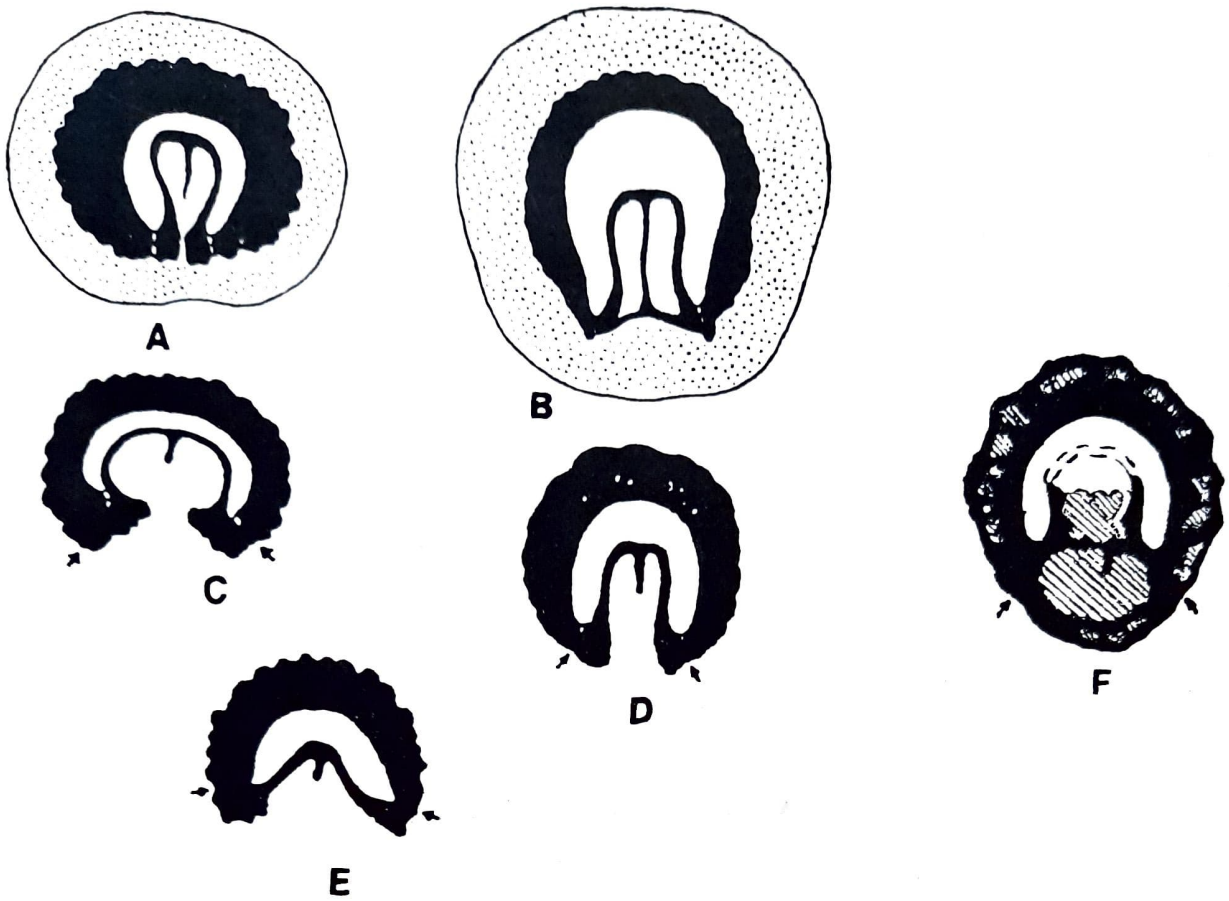
Species

1. *Tectocarya nerchauensis* Mai

Type- Mai, 1987a, p.115, pl.8, fig.1; Nerchau, northwestern Saxony (Germany).

2. *Tectocarya elliptica* (Unger) Holý

Type- *Anona elliptica* Unger, 1866, p.43, pl.14, fig.2;



Text-figure 7. Schematic cross-sections of *Tectocarya* species: A. *Tectocarya elliptica* (Ung.) Holý, fruit-stone with epicarp as "*Tectocarya elliptica*" by Mai (1987a); B. *Tectocarya rhenana* Kirchh., fruit-stone with epicarp according to Kirchheimer (1935a); C. *Tectocarya elliptica* (Ung.) Holý, fruit-stone as "*Tectocarya robusta*" by Kirchheimer (1935a); D. *Tectocarya rhenana* Kirchh., fruit-stone as "*Mastixioidea tectocaryoides*" by Kirchheimer (1936a); E. *Tectocarya nerchauensis* Mai, fruit-stone according to Mai (1987a); *Tectocarya* cf. I. *rhenana* Kirchh., fruit-stone as "*Tectocarya lusatica*" by Kolakovskij (1969).

Radoboj, Croatia (Yugoslavia) = (Unger, 1850a, p.442, nom. nud.).

Synonyms

Tectocarya lusatica Kirchh. 1935a; 65-67, pl.8, figs 23a-n (Kirchheimer, 1934b: 774, nom. nud.) : Merka and quatitz, Upper Lusatia (Germany).

Tectocarya robusta Kirchheimer, 1935a, p.67-68, pl.8, figs 24 a-f (Kirchheimer, 1934a, p.617-618, nom. nud.); Merka Quatitz.

3. *Tectocarya rhenana* Kirchh.

Type- Kirchheimer, 1935a, p.62-64, pl.7, figs 22 a-n; text figs 6-7 (Kirchheimer, 1934b, p.771 nom. nud.) .. Konzendorf, Lower Rhine (Germany).

Synonyms

Phoenix sp. Jurasky, 1930, p.443, fig.8; Konzendorf.

Mastixioidea tectocaryoides Kirchheimer, 1936a, p.219-220, pl.13, figs 5a-f (Kirchheimer, 1935b, p.291, fig.6, nom. nud.); Konzendorf.

Tectocarya lusatica Kolakovski, 1969, p.738, fig.1; Duab, Colchidia (Georgia).

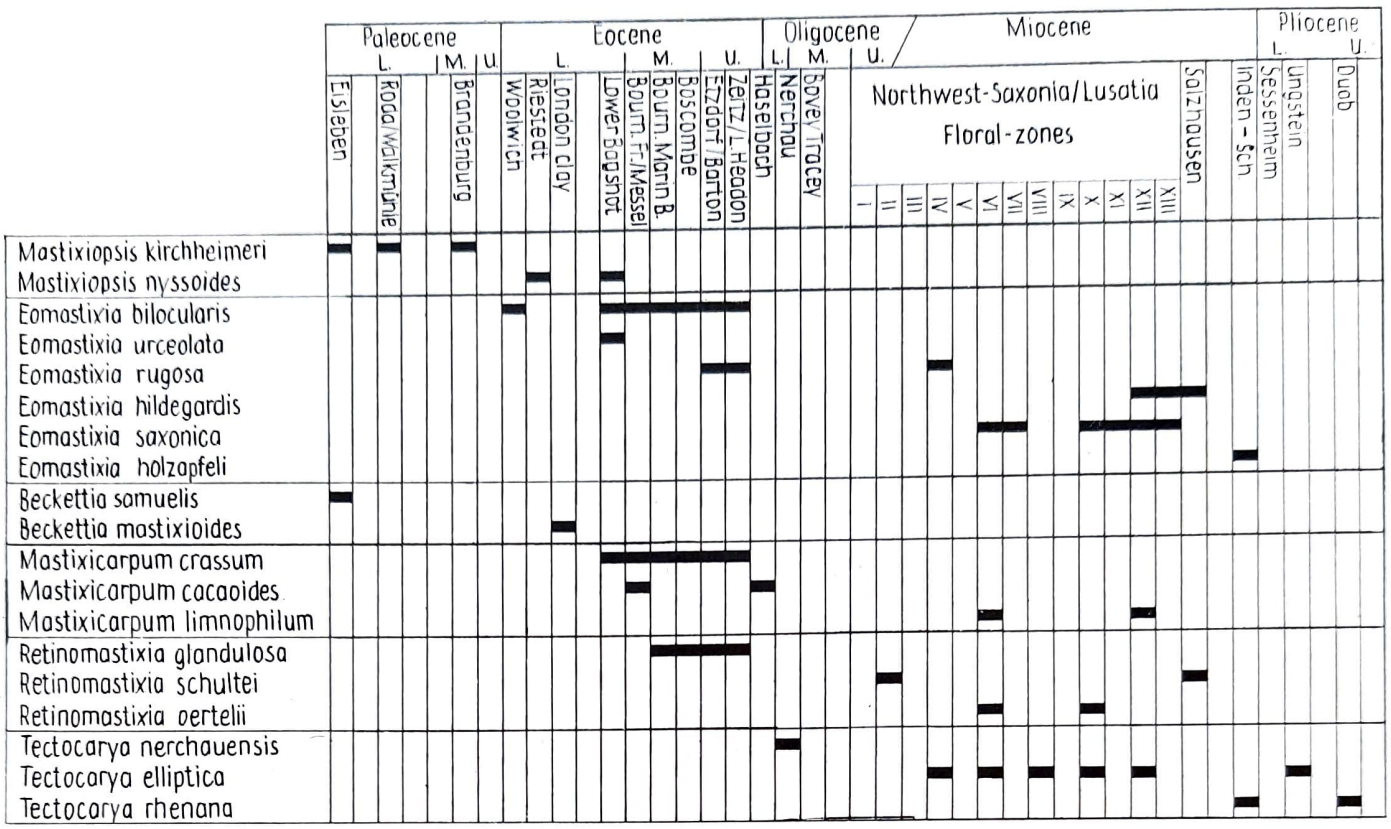
The genus *Tectocarya* Kirchh. appeared in the Middle Oligocene to the Upper Miocene time in Central Europe, mostly with the 3 well defined species occurring together. It survived until Lower Pliocene in the Rhenish refugium (*T. lusatica* Kirchh. after Gregor & Schumann, 1987, p.24) and Kimmerian stage in the Colchidian refugium (*T. lusatica* Kirchh. erroneously after Kolakovski, 1969, p.738).

BIOSTRATIGRAPHY AND PALAEOECOLOGY

In Europe, the Mastixiaceae is represented by a number of extinct genera which are different in carpological patterns. They are *Beckettia* Reid et Chandl., *Eomastixia* Chandl., *Mastixiopsis* Kirchh., *Retinomastixia* Kirchh. and *Tectocarya* Kirchh. Whereas the extant members of the family consists of only two genera, viz., *Mastixia* Bl. and *Mastixicarpum* Chandl. (=*Diplopanax* Hand-Mazz.).

In the stratigraphical interpretation of the whole remains we have followed the latest position of the geological investigations, viz., all the earlier hypotheses about pre-Miocene age of the fossil Mastixiaceae were disregarded without a detailed discussion. More serious is the occurrence of 4 of these extinct genera in the European Upper Cretaceous (Maastrichtian), which clearly

Table 1. Stratigraphic significance of the extinct Mastixiaceae in the European Tertiary



shows the origin of the "Mastixioidean flora" in Europe (Knobloch & Mai, 1986). In the Palaeogene their occurrence was optimal, Kirchheimer (1938c, p.615) regarded them as "exclusively older Tertiary elements". They share in the conduction of many subtropical elements in the laurophyllous floras of the Miocene in Europe. Beyond these the different species of most of the genera of Mastixiaceae are just good examples of a temporal vicariancy of fossil species. Mai (1970) has shown the biostratigraphic usefulness of the genus *Mastixia* Bl. The biostratigraphical table (Table 1) demontrates the same for all extinct genera. The last members of this family go out as relics in the Lower Pliocene in the Rhenish and the Kolkhidian areas are Tectocarya Kirchh. and *Mastixia* Bl.

Palaeoecologically the fossil Mastixiaceae of Europe provides some references for a deduction of wet to moist eutrophic to mesotrophic soils and humid subtropical to warm-temperate climate (Van Der Burgh, 1987). The mass-deposits observed till now of fruit-stones of *Mastixia* Bl. and the closely related extinct genera come from fluviatile sands and clays in the immediate vicinity of brown coal seams. They owe their concentration to the running water which washed them together from the surroundings of the peat layers formations. Therefore Schneider (1973), Palamarer and Rüffle (1979) have realised the "Mastixioidean floras" as not directly peat-forming but as a special phytofacies in a foot-hills zone, while Kirchheimer (1944) and Mai (1970) have observed them, in contrast, as precursors to the settlement of coal-forming bogs. This has been proved also by a very characteristic pollen type from the European brown coals (*Tricolporites edmundi* R. Potonié) which was connected recently with the genus *Mastixia* Bl. This pollen-type likewise disappeared from Europe before the end of the Pliocene (Zagwijn, 1986, p.148).

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