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Evolution of Middle and Upper Cretaceous Floras in Central and Western Europe

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With 1 Text-Figure, 4 Tables and 4 Plates

Paleobotany
Cenomanian
Maestrichtian
Fruits
Seeds
Evolution
Paleofloristic Periods

Contents

Evolution von Mittel- und Oberkreidefloren in Zentral- und Westeuropa

Zusammenfassung

Die Arbeit gibt eine Zusammenfassung über inkohlte Samen und Früchte aus der mitteren und oberen Kreide von West- und Mitteleuropa. Zahlreiche rezente paläotropische Gattungen und Familien wurden nachgewiesen: manche Gattungen sind vollkommen ausgestorben. In der Mittel- und Oberkreide werden 4 Entwicklungsabschnitte der Flora unterschieden: 1. Cenoman, 2. Ober-Turon–Santon, 3. Santon–Campan, 4. Maastricht.

Abstract

A summary is presented of carbonized seeds and fruits from the Middle and Upper Cretaceous of Western and Middle Europe. Numerous living paleotropical genera and families are mentioned. Some of the genera studied are totally extinct. Four evolutionary intervals could be recognized among the Middle and Upper Cretaceous floras: 1. Cenomanian, 2. Upper Turonian–Santonian, 3. Santonian–Campanian, 4. Maestrichtian.

1. Introduction

During the years 1975–1983, we studied rich collections of carbonized diaspores from the Middle and Upper Cretaceous of Western and Middle Europe. Geographically speaking, we investigated localities in Czechoslovakia, Germany, Austria, Hungary, Poland and the Netherlands. The fruits and seeds were mainly sieved out from greyish clays and silts. They are known from freshwater and marine sediments.

In many cases, we are able to clarify the systematic position of the plant fossils. In this way, it is possible to document the presence of many genera and families in the Cretaceous for the first time and to provide new information on the origin of the angiosperms.

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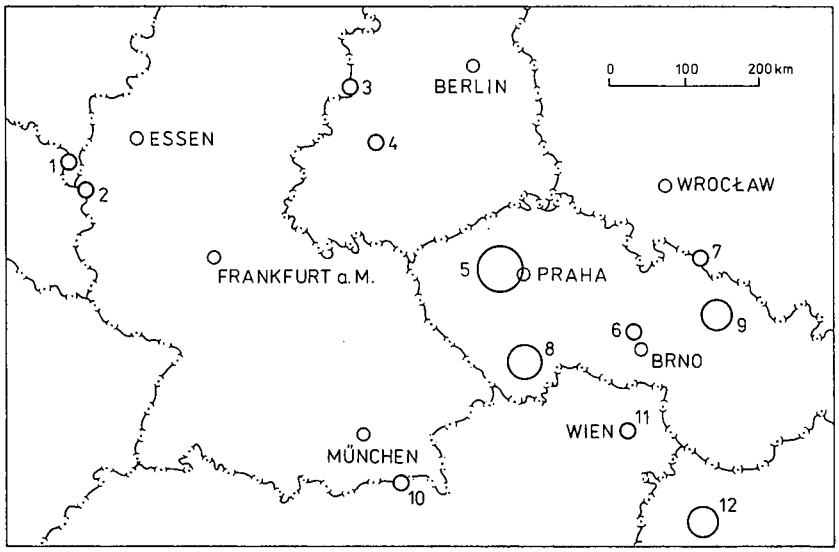

Text-Fig. 1:
The most important localities, formations and regions with Cretaceous fruits and seeds in Central and Western Europe.
1 = South-Limburg, Aachen Formation, Upper Santonian-?Lower Campanian, The Netherlands; 2 = Aachen, Aachen Formation, Upper Santonian or ?Lower Campanian, Germany; 3 = Walbeck, Maestrichtian, Germany; 4 = Eisleben, Maastrichtian, Germany; 5 = Cenomanian of West and Central Bohemia, Peruc Member, Czechoslovakia; 6 = Cenomanian of Moravia, Peruc Member, Czechoslovakia; 7 = Slezské Pavlovice, borehole OS-5, Upper Turonian-Lower Coniacian, Czechoslovakia; 8 = Klikov Formation, Upper Turonian-Upper Santonian, South Bohemia, Czechoslovakia; 9 = Flysh in the Moravian-Silesian Bezkydy Mts., Campanian-Maestrichtian, Czechoslovakia; 10 = Kössen, Niederndorf, Gosau Formation, Maestrichtian, Austria; 11 = Vienna, Flysh, Sievering Formation, Campanian-Maestrichtian, Austria; 12 = Bakony Mts., Ajka Formation, Upper Santonian - Lower Campanian, Hungary.

The study of angiosperm fruits and seeds from the Middle to Upper Cretaceous (Cenomanian–Maestrichtian) of Europe has resulted in the recognition of 270 species and 24 families and has established the existence in the Cretaceous of

1) many modern genera,
2) many extinct genera referable to Recent families and
3) extinct genera that cannot be referred to any existing family.

2. Documentation of Modern Genera and Families in the Middle and Upper Cretaceous

The Magnoliaceae are represented by fruits with 1–2 seeds (*Liriodendron* – Pl. 2, Fig. 7, *Liriodendroidea*) as well as fruits with more seeds (*Padragkutia* – Pl. 3, Fig. 7; *Manglietia*). *Padragkutia* has up to 17 seeds per locule. *Liriodendron* is documented by seeds for the first time in the Senonian of southern Bohemia and this indicates that many leaf fossils previously assigned to the genus may be correctly identified.

The new genus *Prototinomiscium* (Pl. 3, Fig. 1) demonstrates that extinct members of the Menispermaceae are not confined only to the British Lower Tertiary , but that they also occurred in the Senonian of continental Europe. The same is the case for *Typha* (Typhaceae) and *Spirematospermum* (Zingiberaceae).

The Hamamelidaceae were rather abundant during the Cretaceous and are represented in the Maestrichtian by the modern genera *Disanthus* and *Rhodoleia* (Pl. 4, Fig. 14) and in the Cenomanian to Maestrichtian by the extinct genus *Klikovispermum* (Pl. 1, Figs. 8 and 14, Pl. 2, Fig. 11) which includes 17 species. *Klikovispermum* is closely related to *Rhodoleia* and has 12–16 anatropous and semicircular seeds per locule.

The Platanaceae, which are of widespread occurrence in Cretaceous floras of the northern hemisphere, are mainly represented by leaves, fruiting organs being uncommon.

The Urticaceae are also very abundant and have been demonstrated with certainty in the Cretaceous; nutlets assigned to the genus *Boehmeria* (Pl. 1, Figs. 13 and 16, Pl. 2, Fig. 9) which today is mainly restricted to tropical areas, occur as early as the Cenomanian. The genus is represented by 9 species among the Mid- to Upper Cretaceous floras of Europe. In addition to *Boehmeria*, the Cretaceous Urticaceae include species assigned to the modern genera *Debregeasia* and *Memorialis* (Pl. 2, Fig. 1, Pl. 3, Fig. 16) and to the extinct genus *Urticoidea* (Pl. 3, Fig. 6).

Three extinct genera possibly related to the Juglandaceae are *Calathiocarpus* (Pl. 2, Fig. 13, Pl. 3, Fig. 11), *Caryanthus* (Pl. 2, Figs. 3 and 10) and *Manningia*. They are mostly characterized by the presence of a distinct hypanthium. *Caryanthus triasseris* (KNOBL.) KNOBL. et MAI is the most common fossil in the Cretaceous of Europe.

The Theaceae, which by the Tertiary are represented by numerous genera and species, appear to have had a maximum evolution in the Cretaceous. Thus, the modern genus *Eurya* (Pl. 3, Fig. 9) is represented by 3 species and *Visnea* by 1 species. The extinct genus *Palaeoschima* (Pl. 4, Fig. 9), which is closely related to the modern genus *Schima*, also exhibits some characteristics related to the Ericaceae – Andromedae, and the extinct genus *Protovisnea* (Pl. 2, Figs. 4 and 8, Pl. 3, Fig. 4), that is closely related to the modern genus *Visnea*, also exhibits many features characteristic of other families.

In the uppermost Cretaceous (Maestrichtian) the Pentaphylacaceae are documented by fruits assigned to the extinct genus *Allericarpus* and the modern genus *Pentaphylax* (Pl. 4, Fig. 11).

The Ulmaceae family is represented by the genera *Aphananthe* (Pl. 4, Fig. 3) and *Gironniera*, and the Saurauiaceae family by two species of the genus *Saurauia* (Pl. 3, Fig. 15).

Many of the extinct genera from the Cretaceous that we have recognized show relationships to various genera and families, rather than to a single taxon. This is also the case for the extinct genus *Discoclethra* (Pl. 3, Fig. 3, which shows many characteristics in common with the Clethraceae (i.e. placentation, deshicence, deeply 5-lobed and persistant calyx and seed shape) but also exhibits many characteristics related to other families, e.g. Celastraceae (discus, valves),

Hamamelidaceae (style), Cunoniaceae (discus, style) and Ericaceae (seed wall).

Several kinds of capsular fruits document the presence in the Cretaceous of Ericaceae (*Leucothoe* – Pl. 4, Fig. 5, *Viticocarpum*) and Cyrillaceae (*Diplycosiopsis*) and related taxa (*Epacridicarpum, Purdiaeopsis* – Pl. 4, Fig. 2 and *Valvaecarpus* – Pl. 3, Fig. 12, Pl. 4, Fig. 6).

Seeds from the Upper Cretaceous of southern Bohemia show a close relationship with the modern *Aldrovanda* (Pl. 2, Fig. 5) and thus indicate the presence of the Droseraceae in the Cretaceous.

The two well-known extinct Rutaceous genera from the Lower Tertiary of England, *Rutaspermum* and *Shrubsolea*, have also been documented in the Cretaceous, and the Sapindaceae are represented therein by the extinct genus *Sapindospermum* (Pl. 2, Fig. 6).

While the genera *Sabia* (Pl. 3, Fig. 14; Pl. 4, Fig. 8) and *Meliosma* (Sabiaceae) are alredy known from the Tertiary, we have now described (see KNOBLOCH & MAI, 1984, 1986) a new genus from the Cretaceous, *Insitiocarpus*, with 4 species, that extends the fossil record of the family back to the Cenomanian.

The Mastixiaceae, that are well represented by many genera in the Tertiary, are known only from the uppermost Cretaceous (Maestrichtian) by the genera *Beckettia* (Pl. 4, Fig. 12), *Mastixicarpum* (Pl. 4, Fig. 1), *Eomastixia* and *Mastixiopsis*. The same is the case for the Araliaceae (*Aralia, Acanthopanax* – Pl. 4, Fig. 7) that have been suggested, based on leaf fossils (Potomac Formation, USA), as early as the Lower Cretaceous, and also the Icacinaceae (*Icacinicarya, Iodes* – Pl. 4, Fig. 4) and the Aquifoliaceae (*Ilex*).

In addition to the Cretaceous fossils referable to Recent genera and families and to extinct genera related to Recent families, we have described (KNOBLOCH & MAI, 1984) 26 genera that cannot so far be attributed to any modern family. This could be explained by incomplete knowledge of modern carpology or by the fact that they belonged to families that are now extinct. A large number of species have been accomodated into these extinct genera. Some of them, with their characteristics, are listed below: *Bicameria* (Pl. 3, Fig. 8): fruits bilocular with a median septum (5 species); *Discosemen* (Pl. 1, Fig. 12): seed anatropous, disk-shaped and with several cell-layers of the seed wall (6 species); *Laramisemen* (Pl. 1, Fig. 17, Pl. 2, Fig. 2, Pl. 3, Fig. 13): seed anatropous, raphe forming an edge starting below hilum (30 species); *Spirellea* (Pl. 1, Figs. 1–4 and 9): seed with longitudinal ridges (18 species); *Waldbeckia* (Pl. 3, Figs. 5 and 10): one-loculed, oval two-valved fruit (10 species); *Eislebenia* (Pl. 4, Fig. 13): 1 seed with a prominent tegmen (2 species).

3. Evolutionary Paleofloristic Periods from the Cenomanian to the Maestrichtian

Fossil seeds and fruits are not rare in the Cretaceous of Middle and Western Europe. They were recorded at 176 localites (mostly boreholes). The richest layers are known from the Klikov Formation (South Bohemia), Walbeck and Eisleben (Germany) and from the Aachen Formation (Germany, The Netherlands).

A great part of the plant fossils could be assigned to living genera and families. 46 new genera were defined by the authors (KNOBLOCH & MAI, 1984, 1986). 26 genera are totally extinct and 20 show some affinities to recent families. Some of the extinct genera are also known from the Cretaceous to the Paleocene (i.e. *Barclayopsis, Klikovispermum, Valvaecarpus, Mastixiopsis, Spirellea, Normacarpus, Laramisemen, Rusavia, Walbeckia* – MAI, 1987). The number of extinct genera decreases from the Cenomanian to the Paleocene.

Up to now, four periods could be recognized in the evolution of Cretaceous floras:

1) Cenomanian
2) Upper Turonian–Santonian
3) Santonian–Campanian
4) Maestrichtian.

These 4 intervals include only some basic evolutionary tendencies. Even though the number of species studied is sufficient, our knowledge is still limited. We do not know of any rich plant collections from the Turonian, Campanian or Lower Maestrichtian; we do not know precisely if the Klikov Formation belongs to the whole stratigraphic range Upper Turonian–Upper Santonian (KNOBLOCH, 1985) or whether the Aachen Formation belongs only to the Upper Santonian or to the Lower Campanian (ALBERS & FELDER, 1979). The stratigraphic positions of some localities from the flysh of Moravia are not clear. The stratigraphic position of the Eisleben locality in Germany was ranged to the Maestrichtian, but probably belongs to the Paleocene. The stratigraphic range of some species during the Cretaceous is not known up to now.

3.1. Cenomanian

(Table 1, Plate 1)

In the Cenomanian the angiosperms show a significant worldwide „explosion" in their evolution. Leaves of angiosperms are predominant in most Bohemian fossils sites from the Cenomanian. Only 24 species of fossil fruits and seeds have been recorded in the Cenomanian sediments of Bohemia and Moravia.

Contrary to the younger floras, the flora from the Cenomanian documented by seeds and fruits shows a

Table 1.
Angiospermous seeds and fruits from the Cenomanian (Peruc Member, Czechoslovakia)

Hamamelidaceae	*Klikovispermum micromalechii* KNOBL. et MAI *Klikovispermum pragense* KNOBL. et MAI *Klikovispermum semicirculare* KNOBL. et MAI *Klikovispermum verrucosum* KNOBL. et MAI
Platanaceae	*Platanus laevis* (VEL) VEL.
Urticaceae	*Boehmeria cenomanica* KNOBL. et MAI
?Juglandaceae	*Caryanthus triasseris* (KNOBL.) KNOBL. et MAI
Sabiaceae	*Insitiocarpus moravicus* KNOBL. et MAI
Magnoliophyta fam. indet.	*Brnikia ovalis* KNOBL. et MAI *Carpolithus nyssiformis* KNOBL. et MAI *Carpolithus ovalis* KNOBL. et MAI *Carpolithus pecinovensis* KNOBL. et MAI *Curvospermum marketense* KNOBL. et MAI *Discosemen faveolatum* KNOBL. et MAI *Laramisemen hypericoides* KNOBL. et MAI *Laramisemen minor* KNOBL. et MAI
Stemonaceae	*Spirellea margaritifera* KNOBL. et MAI *Spirellea minutissima* KNOBL. et MAI *Spirellea pragensis* KNOBL. et MAI *Viniklaria bohemica* KNOBL. et MAI

Table 2.
Important species from the Upper Turonian – Santonian and their distribution in younger formations.
OS-5 = Slezské Pavlovice borehole in southern Silesia, Upper Turonian – Lower Coniacian, Czechoslovakia; Klikov Formation = Upper Turonian – Santonian, Czechoslovakia; Aachen Formation = Upper Santonian or ?Lower Campanian; Flysch in northern Moravia and Vienna = Campanian, Maestrichtian, Austria, Czechoslovakia; Eisleben = Maestrichtian, Germany.
Specimens in one sample: A = 1, B = 2–15, C = 16–100, D = more than 100.

		OS-5	Klivov Fm.	Aachen Fm.	Flysh	Eisleben
Magnoliaceae	*Liriodendron papilliformis* KNOBL. et MAI		A			
Sapindaceae	*Sapindospermum nitidum* KNOBL. et MAI		A			
?Juglandaceae	*Caryanthus deltoides* (KNOBL.) KNOBL. et MAI	A	A–C	B	?A	
	Caryanthus trebecensis KNOBL. et MAI	A–B	A–D	B		
Hamamelidaceae	*Klikovispermum malechii* (KNOBL.) KNOBL. et MAI	A	A–C	B		
	Klikovispermum bohemicum KNOBL. et MAI	A	A			
Urticaceae	*Boehmeria ctyrokyi* (KNOBL.) KNOBL. et MAI	A	A–D	?A	B	B
?Juglandaceae	*Calathiocarpus minimus* KNOBL. et MAI		A–C	A–B		
Magnoliophyta fam. indet.	*Laramisemen microcanaliculatum* KNOBL. et MAI	A	A–B			
	Laramisemen moravicum KNOBL. et MAI	A				
Stemonaceae	*Spirellea multistriata* (VANG) KNOBL. et MAI		A	B		C
	Spirellea multistriatiformis KNOBL. et MAI	A		B		
Theaceae	*Protovisnea zahajensis* KNOBL. et MAI		A–B			
	Protovisnea reticulata KNOBL. et MAI		A–C			
Urticaceae	*Memorialis verrucosa* KNOBL. et MAI		A–B			
?Juglandaceae	*Caryanthus communis* KNOBL. et MAI		A–D			
Cyrillaceae	*Epacridicarpum cretaceum* (JUNG) KNOBL. et MAI		A–C		B	
Droseraceae	*Palaeoaldrovanda splendens* KNOBL. et MAI		A–B			
Magnoliophyta fam. indet.	*Bicameria holyi* KNOBL. et MAI		A–D	? A		
	Budvaricarpus serialis KNOBL. et MAI		A–D			
	Vangerovia tricornuta (KNOBL). KNOBL. et MAI		A–B			B

most isolated and archaic character. A number of extinct genera dominate. Only the genera *Platanus* and *Boehmeria* are still living.

The gymnosperms (Taxodiaceae, Cupressaceae and Pinaceae) are characteristic for the Cenomanian of the Bohemian Massif. They are lacking

Table 3.
The most important species from the Santonian – Campanian and their distribution in older and younger formations.
Klikov Formation = Upper Turonian – Santonian, Czechoslovakia; Aachen Formation = Upper Santonian – ?Lower Campanian, Germany, The Netherlands; Ajka Formation = Upper Santonian – Lower Campanian, Hungary; Flysh of Czechoslovakia and Austria = Campanian, Maestrichtian; Walbeck, Eisleben = Maestrichtian in Germany.
Specimens in one sample: A = 1, B = 2–15, C = 16–100, D = more than 100.

		Klikov Fm.	Aachen Fm.	Ajka Fm.	Flysh	Walbeck Eisleben
Menispermaceae	*Prototinomiscium vangerowii* KNOBL. et MAI	A	C			
Magnoliaceae	*Padragkutia haasii* KNOBL. et MAI	B		C		
Urticaceae	*Memorialis rhenana* KNOBL. et MAI		B			
	Urticoidea cucurbitoides (VANG.) KNOBL. et MAI	A	B			
	Urticoidea pedicellata KNOBL. et MAI	B	A			
?Juglandaceae	*Calathiocarpus hollandicus* KNOBL. et MAI		B			
Theaceae	*Protovisnea cancellata* (VANG.) KNOBL. et MAI		B		?,B	
Saurauiaceae	*Saurauia alenae* KNOBL. et MAI	A	A			A
Clethraceae	*Discoclethra maxima* KNOBL. et MAI		C			
	Discoclethra polysperma KNOBL. et MAI	A	C			
Cyrillaceae	*Epacridicarpum cretaceum* (JUNG) KNOBL. et MAI	C			B	B
	Valvaecarpus debeyi KNOBL. et MAI	B	C			
Magnoliophyta fam. indet.	*Bicameria orbicularis* (KNOBL.) KNOBL. et MAI	C	B			
	Eislebenia goczanii KNOBL. et MAI		?,B	A–C		
	Laramisemen faboides (VANG.) KNOBL. et MAI	A	B			
	Operculispermum padragkutense KNOBL. et MAI			C		
	Walbeckia ajkoensis KNOBL. et MAI			B		
	Quedlinburgia hungarica KNOBL. et MAI			A		
Sabiaceae	*Sabia menispermioides* KNOBL. et MAI		A			
Theaceae	*Eurya crassitesta* KNOBL.				A–B	C
Magnoliophyta fam. indet.	*Walbeckia aquisgranensis* KNOBL. et MAI		B–C			

in the younger sediments (Turonian–Senonian). Many angiosperms represent monotypic and endemic genera.

The floristic characterization of this interval is made after the finds from the Peruc Member in Bohemia and Moravia (Czechoslovakia).

3.2. Upper Turonian–Santonian

(Table 2, Plate 2)

An increasing number of new extinct genera, but also a number of living genera are characteristic for the Upper Turonian and Santonian. As opposed to the Cenomanian, different species are known. Numerous species were hitherto endemic, as they were known only from the Klikov Formation.

The fruits and seeds from this interval are represented by many genera with ancient features. They belong to the following systematic units:

- **Juglandales**
  ?Budvaricarpus, Calathiocarpus, Caryanthus, Manningia
- **Hamamelidales**
  Klikovispermum
- **Urticales**
  Moroidea, Urticoidea
- Magnoliales
  Padragkutia
- **Theales – Ericales**
  Epacridicarpum, Discoclethra, Protovisena, Valvaecaropus
- **Celastrales**
  Icacinicarya
- **Droserales**
  Palaeoaldrovanda

The number of modern genera increases: *Eurya, Liriodendron, Memorialis, Rhoiptelea, Sabia, Saurauia.*

Some of the fossil genera became extinct between the Santonian and the Campanian.

The floristic characterization of this intervals was made mainly after the finds in the Klikov Formation in southern Bohemia (Upper Turonian–Santonian), the Merboltice Formation in northern Bohemia (Coniacian–Lower Santonian), the floristic remnants from Quedlingburg (Germany, Santonian) and the Slezské Pavlovice OS-5 borehole in southern Silesia (Upper Turonian–Lower Coniacian).

3.3. Santonian–Campanian

(Table 3, Plate 3)

This interval remains problematic. We know of no rich collections from Campanian sediments. This interval is defined accordig to the finds in the Aachen Formation (Upper Santonian or ?Lower Campanian), The Ajka Formation in the Bakony Mts. in Hungary (Upper Santonian–Lower Campanian) and some finds from the flysh of Moravia (Czechoslovakia) and Vienna (Austria). There are some common features between the Santonian–Campanian and the Uper Turonian–Santonian

Table 4.
Important species from the Maestrichtian (Walbeck, Eisleben) and their distribution in the flysh and Gosau Formation of Moravia and Austria (Campanian, Maestrichtian). The species mentioned are lacking in the Klikov and Aachen Formations. Specimens in one sample: A = 1, B = 2–15, C = 16–100, D = more than 100.

		Walbeck, Eisleben	Flysh, Gosau
Zingiberaceae	*Spirematospermum friedrichii* KNOBL. et MAI	B	
Magnoliaceae	*Manglietia hercynica* MAI	B	
	Prototinomiscium testudinarum KNOBL. et MAI	B	
Hamamelidaceae	*Rhodoleia cretacea* KNOBL. et MAI	B	
Ulmaceae	*Aphananthe cretacea* KNOBL. et MAI	B	
Urticaceae	*Boehmeria krutzschii* KNOBL. et MAI	C	
Theaceae	*Palaeoschima becvensis* (KNOBL.) KNOBL. et MAI	C	A–C
Cyrillaceae	*Valvaecarpus pterocaryaeformis* (KNOBL.) KNOBL. et MAI	C	A–D
Sabiaceae	*Sabia praeovalis* KNOBL. et MAI	C	
Magnoliophyta fam. indet.	*Eislebenia naviculaeformis* KNOBL. et MAI	B–C	
	Normacarpus calyciferus KNOBL. et MAI	C	
	Rusavia clavata (KNOBL.) KNOBL. et MAI		A–B
Stenomaceae	*Spirellea cerebrata* KNOBL. et MAI	B	
	Spirellea ellipsioides KNOBL. et MAI	B	
Mastixiaceae	*Mastixicarpum cretaceum* KNOBL. et MAI	B	
	Becketia samuelis KNOBL. et MAI	C	
	Becketia pyriformis KNOBL. et MAI	C	
	Eomastixia rostrata KNOBL. et MAI	B	
Araliaceae	*Acanthopanax gigantocarpus* KNOBL. et MAI	D	
Cyrillaceae	*Purdiaeopsis campanulatus* KNOBL. et MAI	B	
Pentaphylacaceae	*Pentaphylax protogaea* KNOBL. et MAI	B	
	Allericarpus pentaphylacoides KNOBL. et MAI	C	
Theaceae	*Visnea minima* KNOBL. et MAI	B	
Sabiaceae	*Insitiocarpus compressus* KNOBL. et MAI	B	
Ericaceae	*Leucothoe praecox* KNOBL. et MAI	C	
Icacinaceae	*Iodes germanica* KNOBL. et MAI	B	

and some differences to the Maestrichtian. The features common with the Upper Turonian–Santonian are connected with the coincident species from the Aachen and Klikov Formations, the differences from the floras of the Maestrichtian are connected with the first appearances of numerous living genera during the Maestrichtian.

3.4. Maestrichtian

(Table 4, Plate 4)

Contrary to the Santonian–Campanian in the Maestrichtian many living genera appeared and a great number of extinct genera are missing. 33 genera appear for the first time and 15 of them represent living plants. Among them numerous evergreen elements of the paleotropic geoflora are present:

- **Mastixiaceae**
  Becketia, Eomastixia, Mastixicarpum, Mastixiopsis
- **Theaceae**
  Palaeoschima, Visnea
- **Ericaceae**
  Diplycosiopsis, Leucothoe, Viticocarpum
- Pentaphylacaceae
  Allericarpus, Pentaphylax
- **Magnoliaceae**
  Liriodendroidea, Manglietia
- **Hamamelidaceae**
  Disanthus, Rhodoleia
- **Ulmaceae**
  Aphananthe, Gironniera
- **Aquifoliaceae**
  Ixex
- **Icacinaceae**
  Iodes
- **Zingiberaceae**
  Spirematospermum

The essential features of the Maestrichtian floras are quite different with respect to the older floras.

The floristic characterization of this interval is given by the rich flora from Walbeck in Germany. Some species from Walbeck are known also from the flysch and the Gosau Formaiton in Czechoslovakia and Austria.

4. Conclusions

Fossil fruits and seeds contribute significantly to our understanding of evolutionary trends in Upper Cretaceous angiosperms. The morphological features of the Upper Cretaceous fruits and seeds demonstrate that the angiosperms had then reached the organization level of those of the present day. The majority of families from the Central-European Cretaceous are of Laurasian origin. The assemblage corresponds to evergreen, subtropical and temperate vegetations in the northern hemisphere today. The origin of some families is questionable since they show affinity with both Laurasian and west Gondwana regions.

Plate 1 — Seeds and fruits from the Cenomanian

Figs. 1,2: ***Spirellea pragensis*** **KNOBL. et MAI (Stenomaceae).**
Praha-Břevnov, Radimova street, Peruc Member, Central Bohemia.
Fig. 1: ×36.
Fig. 2: ×17.

Figs. 3,4: ***Spirellea minutissima*** **KNOBL. et MAI (Stenomaceae).**
Praha-Břevnov, St. Margaret convent, Peruc Member, Central Bohemia.
Fig. 3: ×60.
Fig. 4: ×80.

Fig. 5: ***Carpolithus pecinovensis*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Pecínov, Peruc Member, West Bohemia, ×14.

Fig. 6: ***Viniklaria bohemica*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Vyšehořovice, Peruc Member, Central Bohemia, ×67.

Fig. 7: ***Brnikia ovalis*** **KNOBL. et MAI (Magnoliophyt** fam. indet.).
Brník, Peruc Member, Central Bohemia, ×10.

Fig. 8: ***Klikovispermum pragense*** **KNOBL. et MAI (Hamamelidaceae).**
Praha-Břevnov, V-26, 23.5 m, Peruc Member, Central Bohemia, ×44.

Fig. 9: ***Spirellea margaritifera*** **KNOBL. et MAI (Stemonaceae).**
Kněževes PV-2, 25.4 m, Peruc Member, Central Bohemia, ×40.

Figs. 10–11: ***Carpolithus nyssiformis*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Fig. 10: Pecínov, Peruc Member, West Bohemia, ×10.
Fig. 11: Vyšehořovice, Peruc Member, Central Bohemia, ×16.

Fig. 12: ***Discosemen faveolatum*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Březinka, Peruc Member, Moravia, ×10.

Fig. 13: ***Boehmeria cenomanica*** **KNOBL. et MAI (Urticaceae).**
Zeměchy, 201–53, 19.5 m, Peruc Member, West Bohemia, ×17.

Fig. 14: ***Klikovispermum verrucosum*** **KNOBL. et MAI (Hamamelidaceae).**
Slaný SA-15, 49.5 m, Peruc Member, West Bohemia, ×70.

Fig. 15: ***Carpolithus ovalis*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Pecínov, Peruc Member, West Bohemia, ×42.

Fig. 16: ***Boehmeria cenomanica*** **KNOBL. et MAI (Urticaceae).**
Zeměchy, 201–53, 19.5 m, Peruc Member, West Bohemia, ×36.

Fig. 17: ***Laramisemen hypericoides*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Praha-Břevnov, St. Margaret convent, V-26, 23.5 m, Peruc Member, Central Bohemia, ×40.

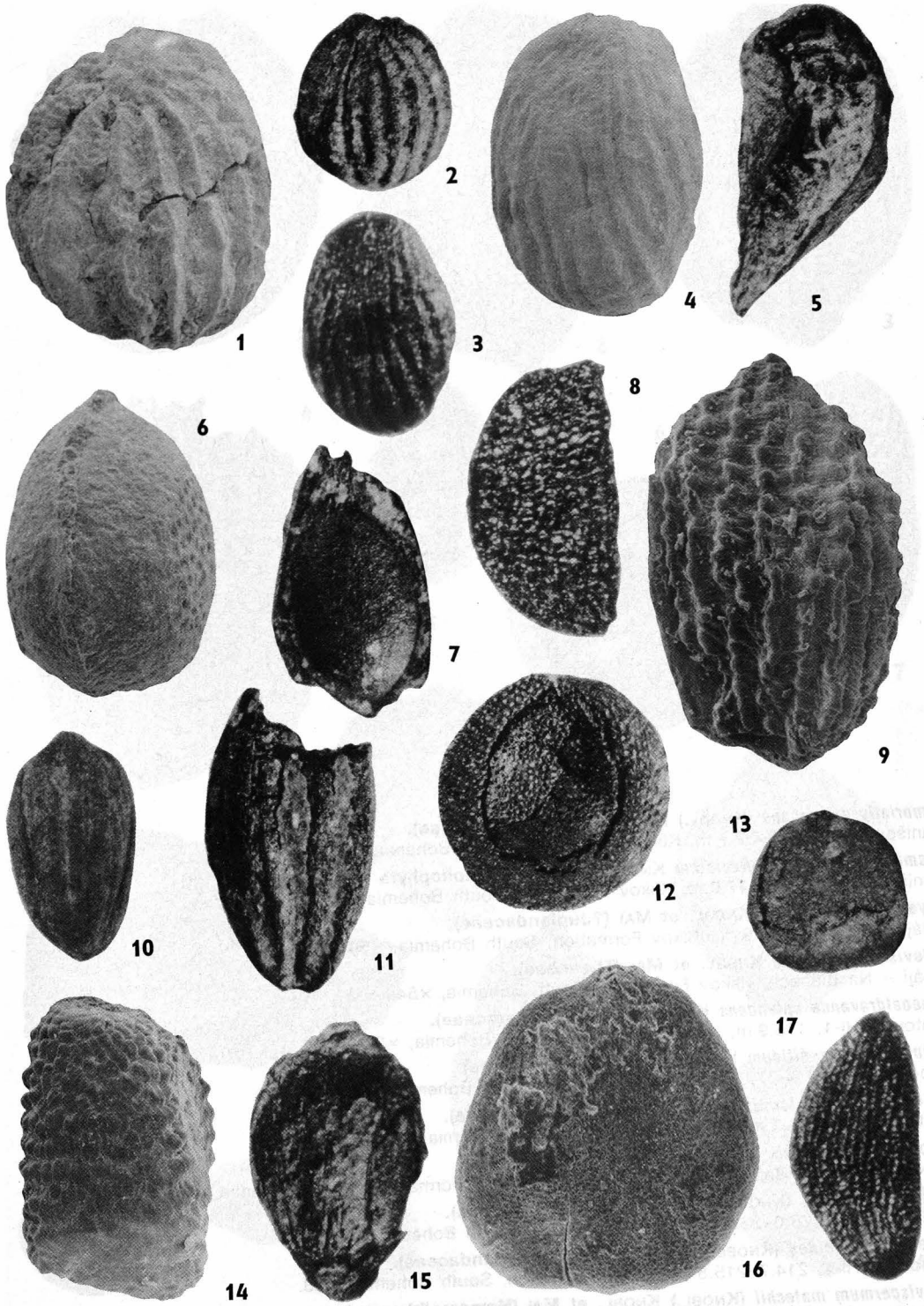
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Plate 2

Seeds and fruits from the Upper Turonian–Santonian

Fig. 1: ***Memorialis verrucosus*** **(KNOBL.) KNOBL. et MAI (Urticaceae).**
Branišov GB-3, 32.6–32.7 m, Klikov Formation, South Bohemia, ×100.

Fig. 2: ***Laramisemen microcanaliculatum*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Branišov, Br-21, 16.7–17.0 m, Klikov Formation, South Bohemia, ×100.

Fig. 3: ***Caryanthus trebecensis*** **KNOBL. et MAI (?Juglandaceae).**
Zahájí, Za-2, 17.6–18.9 m, Klikov Formation, South Bohemia, ×50.

Fig. 4: ***Protovisnea reticulata*** **KNOBL. et MAI (Theaceae).**
Zahájí – Na Blanech, Klikov Formation, South Bohemia, ×54.

Fig. 5: ***Palaeoaldrovanda splendens*** **KNOBL. et MAI (Droseraceae).**
Opatovice Hl-1, 175.9 m, Klikov Formation, South Bohemia, ×22.

Fig. 6: ***Sapindospermum nitidum*** **KNOBL. et MAI (Sapindaceae).**
Třebeč Tj-4a, 76.0–77.0 m, Klikov Formation, South Bohemia, ×25.

Fig. 7: ***Liriodendron papilliformis*** **KNOBL. et MAI (Magnoliaceae).**
Opatovice Hl-1, 66.7 m, Klikov Formation, South Bohemia, ×25.

Fig. 8: ***Protovisnea zahajensis*** **KNOBL. et MAI (Theaceae).**
České Budějovice–Rožnov ČB-3, 62.8–63.1 m, Klikov Formation, South Bohemia, ×70.

Fig. 9: ***Boehmeria ctyrokyi*** **(KNOBL.) KNOBL. et MAI (Urticaceae).**
Branišov Br 21, 23.0–23.5 m, Klikov Formation, South Bohemia, ×50.

Fig. 10: ***Caryanthus deltoides*** **(KNOBL.) KNOBL. et MAI (?Juglandaceae).**
Opatovice, Hl-1, 214.7–215.8 m, Klikov Formation, South Bohemia, ×38.

Fig. 11: ***Klikovispermum malechii*** **(KNOBL.) KNOBL. et MAI (Hamamelidaceae).**
Opatovice, Hl-1, 237.8–238.5 m, Klikov Formation, South Bohemia, ×21.

Fig. 12: ***Vangerovia tricornuta*** **(KNOBL.) KNOBL. et MAI (Magnoliophyta fam. indet.).**
České Budějovice–Vrato, TSv-7, 40.0–41.1 m, Klikov Formation, South Bohemia, ×50.

Fig. 13: ***Calathiocarpus minimus*** **KNOBL. et MAI (?Juglandaceae).**
Záblatí 65/23, 43.2 m, Klikov Formation, South Bohemia, ×70.

Fig. 14: ***Budvaricarpus serialis*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Branišov Br 21, 60.5–60.8 m, Klikov Formation, South Bohemia, ×22.

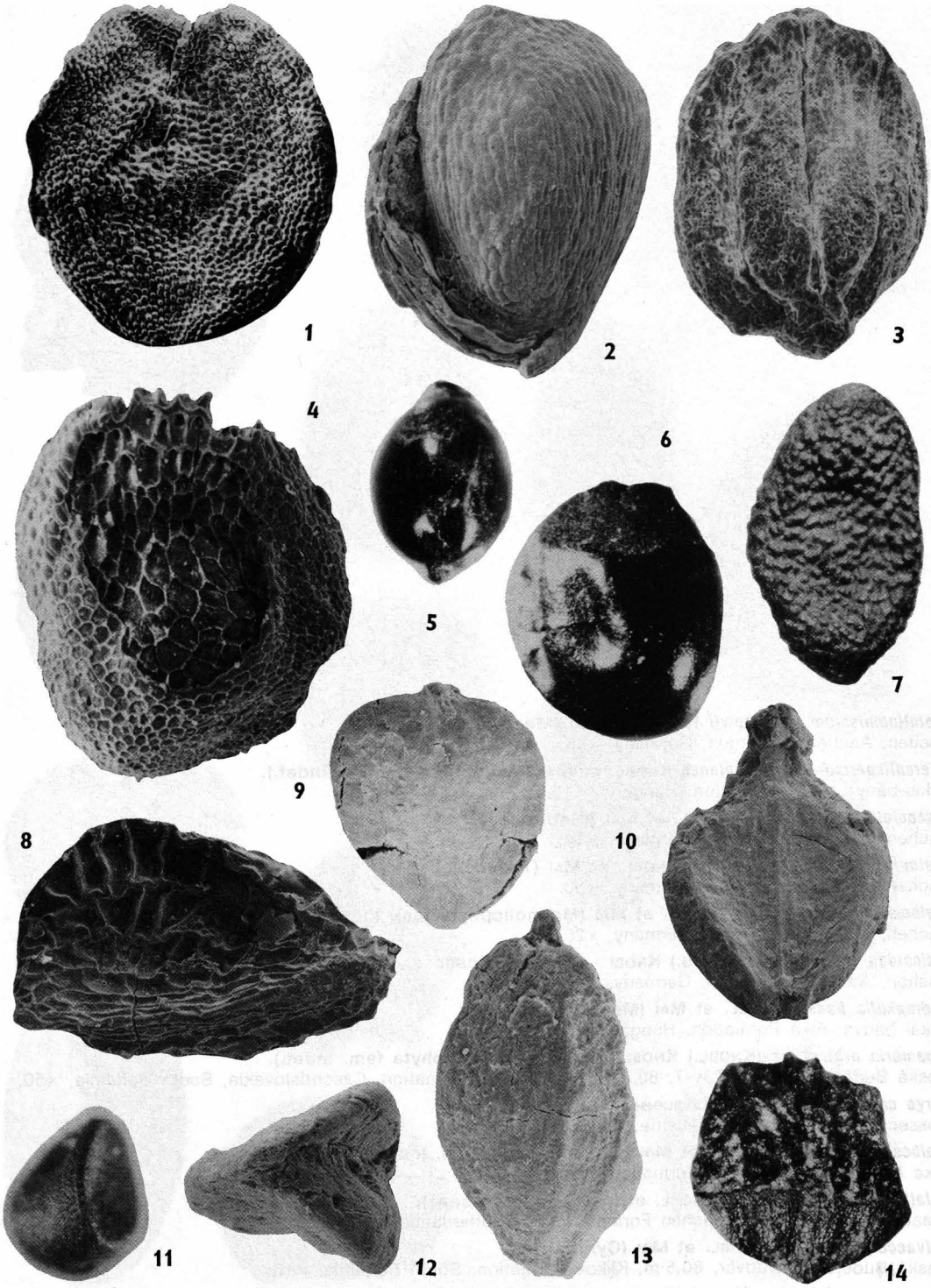
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Plate 3

Seeds and fruits from the Santonian–Campanian

Fig. 1: ***Prototinomiscium vangerowii*** **KNOBL. et MAI (Menispermaceae).**
Aachen, Aachen Formation, Germany, ×45.

Fig. 2: ***Operculispermum padragkutense*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Jokai-bánya, Ajka Formation, Hungary, × 16.

Fig. 3: ***Discoclethra polysperma*** **KNOBL. et MAI (Clethraceae).**
Aachen, Aachen Formation, Germany, ×14.

Fig. 4: ***Protovisnea cancellata*** **(VANG.) KNOBL. et MAI (Theaceae).**
Aachen, Aachen Formation, Germany, ×50.

Fig. 5: ***Walbeckia aquisgranensis*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Aachen, Aachen Formation, Germany, ×25.

Fig. 6: ***Urticoidea cucurbitoides*** **((VANG.) KNOBL. et MAI (Urticaceae).**
Aachen, Aachen Formation, Germany, ×40.

Fig. 7: ***Padragkutia haasii*** **KNOBL. et MAI (Magnoliaceae).**
Jokai bánya, Ajka Formation, Hungary, ×30.

Fig. 8: ***Bicameria orbicularis*** **(KNOBL.) KNOBL. et MAI (Magnoliophyta fam. indet.).**
České Budějovice-Vráto TSv-7, 80.3–80.8 m, Klikov Formation, Czechoslovakia, South Bohemia, ×50.

Fig. 9: ***Eurya crassitesta*** **KNOBL. (Theaceae).**
Kössen, Gosau Formation, Austria, ×30.

Fig. 10: ***Walbeckia ajkoensis*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Ajka Aj-167, 103.0 m, Ajka Formation, Hungary, ×37.

Fig. 11: ***Calathiocarpus hollandicus*** **KNOBL. et MAI (?Juglandaceae).**
Staatsmijn Maurits 554, Aachen Formation, The Netherlands, ×22.

Fig. 12: ***Valvaecarpus debeyi*** **KNOBL. et MAI (Cyrillaceae).**
České Budějovice-Budvar, 80.5 m, Klikov Formation, South Bohemia, ×15.

Fig. 13: ***Laramisemen faboides*** **(VANG.) KNOBL. et MAI (Magnoliophyta fam. indet.).**
Epen 44, 3.5–6.0 m, Aachen Formation, The Netherlands, ×120.

Fig. 14: ***Sabia menispermioides*** **KNOBL. et MAI (Sabiaceae).**
České Budějovice-Budvar, 148.5 m, Klikov Formation, Czechoslovakia, ×15.

Fig. 15: ***Saurauia alenae*** **KNOBL. et MAI (Saurauiaceae).**
Branná Sch-2, 116.1 m, Klikov Formation, Czechoslovakia, ×38.

Fig. 16: ***Memorialis rhenana*** **KNOBL. et MAI (Urticaceae).**
Aachen, Aachen Formation, Germany, × 40.

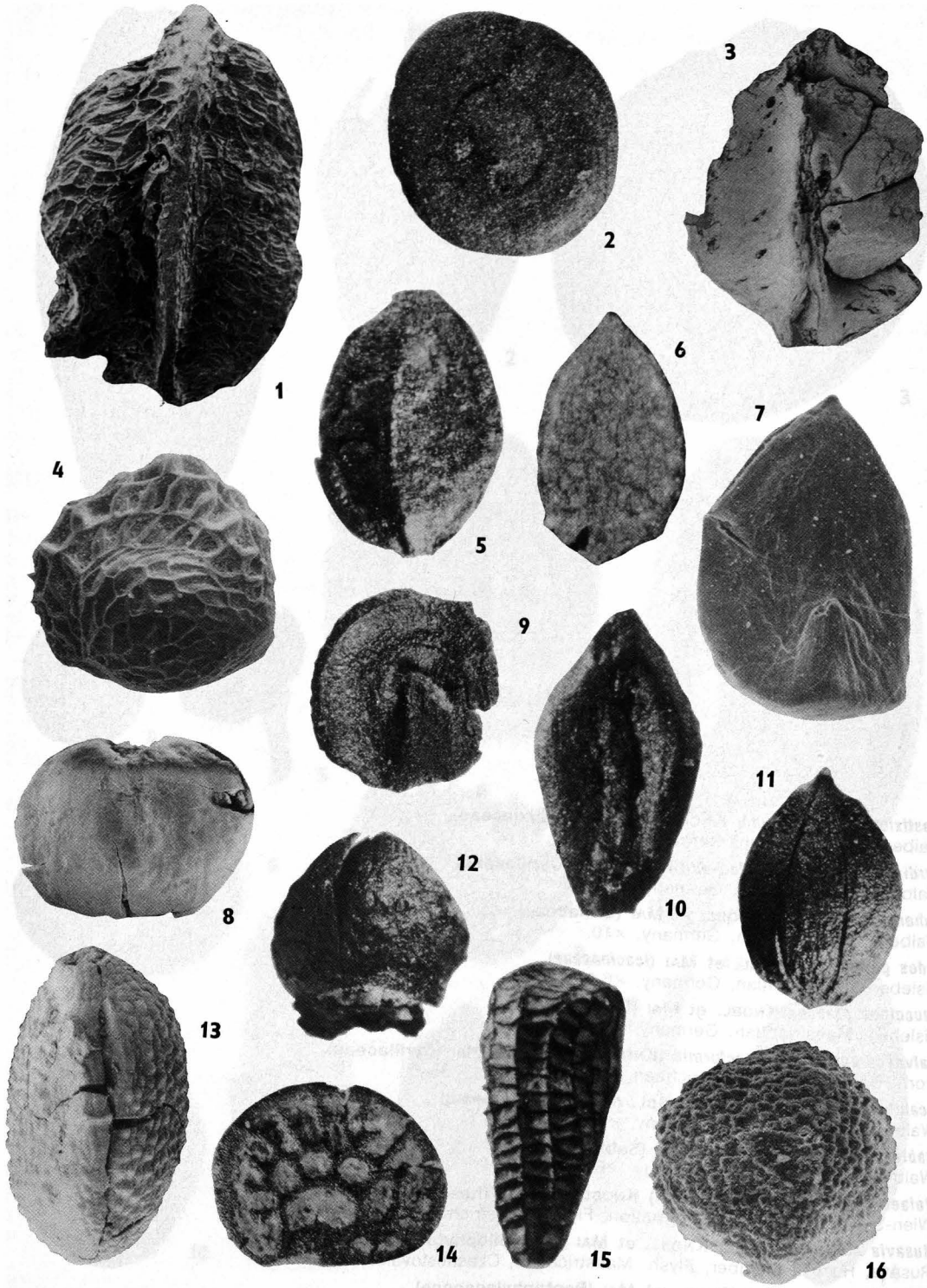
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Plate 4

Seeds and fruits from the Maestrichtian

Fig. 1: ***Mastixicarpum cretaceum*** **KNOBL. et MAI (Mastixiaceae).**
Walbeck, Maestrichtian, Germany, ×6.5.

Fig. 2: ***Purdiaeopsis campanulatus*** **KNOBL. et MAI (Cyrillaceae).**
Walbeck, Maestrichtian, Germany, ×20.

Fig. 3: ***Aphananthe cretacea*** **KNOBL. et MAI (Ulmaceae).**
Walbeck, Maestrichtian, Germany, ×10.

Fig. 4: ***Iodes germanica*** **KNOBL. et MAI (*Icacinaceae*).**
Eisleben, Maestrichtian, Germany, ×6.5.

Fig. 5: ***Leucothoe praecox*** **KNOBL. et MAI (Ericaceae).**
Eisleben, Maestrichtian, Germany, ×12

Fig. 6: ***Valvaecarpus pterocaryaeformis*** **(KNOBL.) KNOBL. et MAI (Cyrillaceae).**
Horní Bečva, Flysh, Maestrichtian, Czechsolovakia, × 35.

Fig. 7: ***Acanthopanax gigantocarpus*** **KNOBL. et MAI (Araliaceae).**
Walbeck, Maestrichtian, Germany, × 6.5.

Fig. 8: ***Sabia praeovalis*** **KNOBL. et MAI (Sabiaceae).**
Walbeck, Maestrichtian, Germany, ×6.5.

Fig. 9: ***Palaeoschima becvensis*** **(KNOBL.) KNOBL. et MAI (Theaceae).**
Wien-Sievering, Sievering Formation, Flysh, Maestrichtian, Austria, ×30.

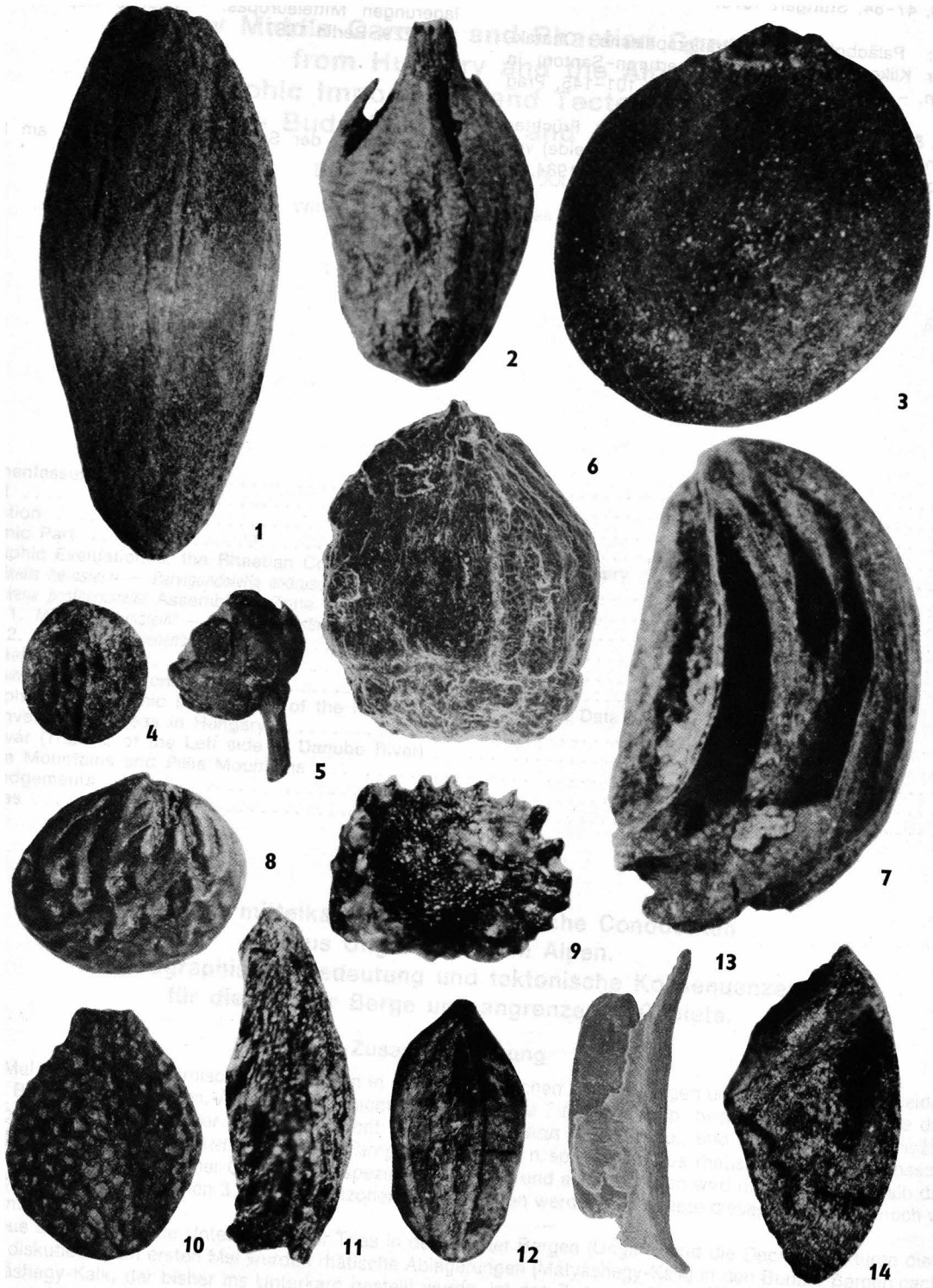
Fig. 10: ***Rusavia clavata*** **(KNOBL.) KNOBL. et MAI (Magnoliophyta fam. indet.).**
Rusava, Rusava Member, Flysh, Maestrichtian, Czechoslovakia, ×30.

Fig. 11: ***Pentaphylax protogaea*** **KNOBL. et MAI (Pentaphylacaceae).**
Walbeck, Maestrichtian, Germany, ×30.

Fig. 12: ***Beckettia samuelis*** **KNOBL. et MAI (Mastixiaceae).**
Eisleben, Maestrichtian, Germany, ×6.5.

Fig. 13: ***Eislebenia naviculaeformis*** **KNOBL. et MAI (Magnoliophyta fam. indet.).**
Eisleben, Maestrichtian, Germany, ×10.

Fig. 14: ***Rhodoleia cretacea*** **KNOBL. et MAI (Hamamelidaceae).**
Walbeck, Maestrichtian, Germany, ×25.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