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Late Eocene landscape, ecosystems and climate in northern Bohemia with particular reference to the locality of Kučlín near Bílina

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Abstract. A new interpretation of the Late Eocene landscape in northern Bohemia is offered. Late Eocene age has been proven by palaeontological records and radiometric dating of volcanogenic strata representing the earliest surface products of volcanic activity in the České středohoří Mountains (the lowermost part of the Středohoří Complex, Ústí Formation p.p.). Most of them, the sites of Kučlín, Kostomlaty – Mrtvý vrch and Roudný, and the lower parts of the sections at Lbín (core Lb 1), Hlinná (core Úc 9), and Kundratice (core KU 1) line the southern periphery from Bílina to Litoměřice. These deposits, which comprise diatomites, marlstones to limestones, tuffitic claystones or coarser volcaniclastics, represent a volcanic facies coeval with the Staré Sedlo Formation, which is composed of quartzites, sandstones and sands of fluvial settings. Although the floras of either lithostratigraphic unit differ in some respect, this is due to the synecology of vegetation and environmental differences (aquatic to upland communities on fertile volcanogenic soils versus riparian forests along rivers on oligotrophic sandy soils). A volcanogenic lake system apparently existed in the southern part of the České středohoří Mountains at that time, which was drained across northern Bohemia and Saxony towards the North Sea, as corroborated by fish fauna (*Morone*). The Kučlín diatomite and the other mentioned sites at the base of the Ústí Fm. reveal mainly a mesophytic forest vegetation suggesting a warm, (paratropical) subtropical seasonal climate without frosts and with slightly deficient (? summer) precipitation. Plant assemblages of the Staré Sedlo Fm. reflect azonal, predominantly woody vegetation along riverbanks (riverine gallery forests). This type of vegetation, supplied by groundwater, was also (paratropical) subtropical and seasonal but perhumid in aspect. Such differences between plant assemblages connected with the basinal/fluvial versus volcanogenic environment can be found elsewhere during the Paleogene (the Middle Eocene sites of Messel, Eckfeld and Geiseltal or the Early Oligocene sites of the České středohoří Mountains and the Haselbach Floral Assemblage in Saxony). At Kučlín and the other listed localities of the earliest effusive activity, no distinct hiatus (sedimentation gap) towards the Staré Sedlo Formation existed. The Late Eocene landscape of northern Bohemia, in contrast to the hitherto accepted interpretation, was a peneplain with lowland rivers, lakes, maars and moderate volcanic uplands.

Key words: Late Eocene, landscape, ecosystems, northern Bohemia, volcanic complex

Introduction

The neo-volcanic area of the České středohoří Mountains offers a rare opportunity to follow the landscape and ecosystem development for a longer period during late Paleogene times. The site of Kučlín near Bílina has been known since the pioneering studies in geology and palaeontology in northern Bohemia. This section and other sections of the České středohoří Mountains, which are studied in detail in the present account, i.e. marlstones and limestones of Mrtvý vrch and Roudný Hills near Kostomlaty, diatomaceous claystones near Kundratice (core KU 1– lower level), Hlinná (core Úc 9), and Lbín (outcrops and core Lb 1), are situated in the lowermost part of the Paleogene stratigraphical column in northern Bohemia and are dated to the Late Eocene by the ancient fish fauna (Obrhelová and Obrhel 1987), the extinct conifer *Doliostrobus* (Bůžek et al. 1968, 1978), palynology (Konzalová 1981) and radiometric data (Bellon et al. 1998). Of particular interest is the newly suggested migration route of sea perch (*Morone*, Moronidae), a new member of the Kučlín ichthyofauna (Micklich and Böhme 1997). This marine fish can penetrate hundreds of kilometres inland via river systems and withstand freshwater environment. Micklich and Böhme (1997) suggested a connection between the Kučlín Lake and the Eocene "North Sea" by drainage across northern Bohemia (Staré Sedlo Fm.) and Saxony (Lower Borna Fm.). Therefore, the quartzitized sandstone at Skalice and Žitenice was also included in our correlation.

The present account is focused on more general characteristics of the environment and ecosystems (vegetation, fauna, climate, relief, substrate) derived from new palaeontological data. Some possible explanations are offered, which would help to elucidate problems of the palaeogeography and stratigraphy of Late Eocene deposits in northern Bohemia.

Material and methods

New taxonomical treatments of the previously collected material as well as new specimens obtained recently by extensive field activities of amateur palaeontologists and collectors are presented herein in an abbreviated form. The following collections of fossil plant material have been studied:

– Lobkowitz collection, the Hungarian Natural History Museum, Budapest – BP
– Geologische Bundesanstalt, Wien – GBW
– Naturhistorisches Museum, Wien – NHMW
– Staatliche Naturhistorische Sammlungen, Museum für Mineralogie und Geologie, Dresden – MMG
– Czech Geological Survey, Praha – ČGS
– Department of Palaeontology, National Museum, Praha – NM

– Regional Museum, Teplice – RMT
– Z. Dvořák's collection, Bílina Mine – DB
– Private collection of J. Valíček, Most.

Additional data on the vertebrate and insect fauna is included, based on previous publications and new preliminary studies (fishes – N. Micklich, Darmstadt, M. Böhme, München, B. Ekert, Praha; insects – J. Prokop, Praha). The respective specimens are scattered in the above mentioned institutions and the Hessisches Landesmuseum, Darmstadt, the Forschungsinstitut Senckenberg, Frankfurt am Main, and the Institut für Geophysik und Geologie der Universität Leipzig.

Comparative studies carried out on the Eocene sites of Messel, Eckfeld and in the Weisselster Basin in co-operation with V. Wilde, Frankfurt am Main, H. Frankenhäuser, Mainz, and H. Walther, Dresden, as well as earlier studies of plant collections from the Eocene of England (British Natural History Museum, London) and Oligocene plants from Hungary (in collaboration with L. Hably, Budapest) contributed to a better understanding of the Eocene flora in northern Bohemia.

The Late Eocene plant fossils from northern Bohemia are mostly preserved as impressions. Only the cores near Lbín, Hlinná and Kundratice yielded coalified compressions, suitable for cuticular studies. Plant fossils from Germany are mostly preserved as compressions, in oil shales or clays, and allow studies of epidermal anatomy as well (Sturm 1971, Mai and Walther 1985, Wilde 1989). A routine procedure of cuticle preparations (Schulze solution, KOH) was applied (for details see Knobloch et al. 1996).

Geology

Since the first incomplete information on the position and structure of basal deposits of the northern Bohemian Tertiary (Reuss 1840, 1844, Reuss and Meyer 1852, Kafka 1908, 1911, Hibsch 1905, 1908, 1924, 1926, Hibsch and Seemann 1913), our knowledge has been greatly improved thanks to detailed mapping (Kopecký ed. 1990), geological investigations (Horáčková ed. 1967) and other field activities (Krutský 1997, Váně 1999, 2001, Radoň 2001), as well as petrological, geochemical and stratigraphical research (e.g. Shrbený in Klomínský 1994, Bellon et al. 1998, Cajz et al. 1999, Cajz 2000, Ulrych et al. 2001). Unfortunately, an optimistic mood fades away if we focus our interest on selected sections. Much more work is needed, particularly in the lithological research of volcanogenic sediments and sedimentology in general, because mainly magmatic bodies have been studied in detail. The following review is based on various sources. Besides published accounts, also manuscript reports on preliminary field studies were excerpted, some data were obtained from consultations of experts in geology and palaeontology of northern Bohemia and the author's own observations.

The Tertiary of the České středohoří Mts. has traditionally been divided into two lithostratigraphic units – the Staré Sedlo Formation (including the quartzitized sandstones at Skalice, Žitenice and Volfartice) of Late Eocene age and the Středohoří Complex (alkali volcanic and pyroclastic rocks) ranging from the Late Eocene to earliest Miocene age (Shrbený in Klomínský 1994). In a recent study, Cajz (2000) attempted to divide the latter into three formations according to the lithology and geochemical characteristics as well as an overall geological structure. As it follows from the characteristics, which are given below for the respective sites of the České středohoří Mts. of Late Eocene age, the lowermost part of the former Středohoří Complex does not fit well into this new lithostratigraphic subdivision (see also Ulrych et al. 2001). New dating provides evidence for their correlation and facies differentiation (Fig. 1).

Kučlín – Trupelník Hill (Trippelberg at Kutschlin)

The Paleogene section of Trupelník Hill at Kučlín forms an erosional remnant of volcanogenic material and sediments near Bílina (Hibsch 1924, Kopecký ed. 1990). It is the best known site of Late Eocene age in the České středohoří Mts. Its structure and lithology have been reported in many accounts, starting with Reuss (1840). Several cores (Mrázek and Procházka 1953, Horáčková ed. 1967) are available to date to follow the section in detail. Core V 2 situated 50 m NE off the summit (356.5 m a.s.l.) did not reach the Upper Cretaceous, and was petrologically characterised in detail (Kafka and Holá in Horáčková ed. 1967). Cores V 2 (depth 33.5 m) and V 3 (depth 19.8 m and 28.6 m) yielded darker organogenic sediments, from which palynological data were obtained (Mazancová in Horáčková ed. 1967).

Paleogene rocks at Kučlín overlie directly the Upper Cretaceous sediments. Their thickness is variable due to tectonics and geomorphology. According to Mrázek and Procházka (1953) the lowermost interval of the Tertiary starts with pyroclastics. The quartzite bed is absent. The lower part of the section is formed by marlstone about 15 m thick. This thick interval is composed of re-deposited material from the Upper Cretaceous at the base, and organogenic lacustrine marlstone to limestone of various character: breccia, sandy-silty marlstone recalling diatomite, often thinly bedded and laminated, rarely massive limestone (Kafka in Horáčková ed. 1967). Volcaniclastic admixtures and darker coaly clay beds are rarer and thinner. The rest of the sedimentary body comprises various kinds of diatomite with thin volcaniclastic intercalations. Fossiliferous diatomite is whitish pale, well oxidised, and represents a variety of technological sorts (Holá in Horáčková ed. 1967). It is partly cemented by silica, partly soft, mostly thinly bedded, passing into diatomite marl in the lower positions. A thicker body of the basanite tuff overlies the diatomite, and partly laterally replaces the upper portion of the diatomite, which is exposed on Trupelník Hill. Two kinds of magmatic bodies occur adjacent to the sedimentary fill. A thin basaltic sheet, partly disintegrated, partly transformed by weathering (hydrothermal

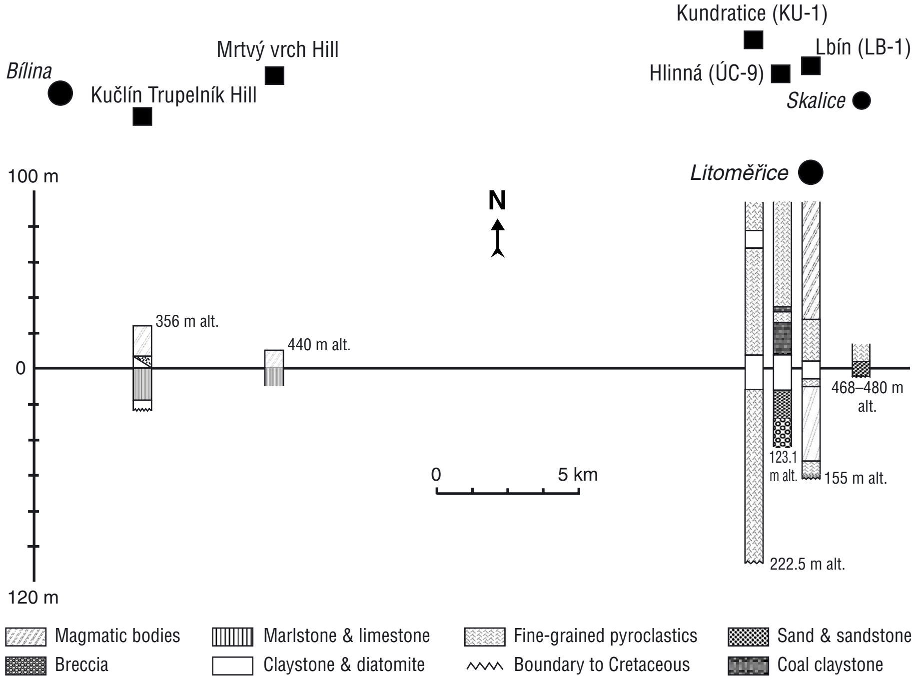

Fig. 1. Geographic situation of the studied sites between Bílina and Litoměřice (above) and their geological sections levelled on the Late Eocene landscape surface (below).

alteration?) processes covers the top of the sedimentary body. Tephrite flow sampled from large loose rock slabs on the top of the hill yielded radiometric age of 38.3 ± 0.9 Ma (Bellon et al. 1998). Another tephrite occurrence on the slope yielded a slightly younger age (33.5 ± 1.5 Ma; Ulrych et al. 2001). The most popular palaeontological collecting site from the 19th century was at an old mill below the hill (Ettingshausen 1869). Due to an extensive landslide, this diatomite block, which has been fully exploited, lies much lower than the rest of the diatomite. The main section is much higher, at about 335 m a.s.l., as documented by core Kč 1 (Kopecký ed. 1990). We suspect that Kafka (1908, 1911) was unaware of this landslide when performing four test pits on Trupelník Hill. Therefore, his description of the sedimentary content of the Kučlín site is obviously misleading (his sections I–III repeat in the upper section IV). Within the main diatomite body, a fault-induced subsidence by 12–15 m of its northern part is observed.

These sediments are interpreted as the fill of a freshwater lake, which was formed in a calmer period of volcanic activity in response to the first large-scale movements of the Ohře Rift, and was (partly) supplied by mineral springs (Obrhelová and Obrhel 1987). The radiometric data (Bellon et al. 1998) and palynology (Konzalová 1981) suggest its Late Eocene age.

Kostomlaty pod Milešovkou (Kostenblatt), Mrtvý vrch Hill (Todten Berg) and Roudný Hill (Raudnay)

Late Eocene deposits are developed at two sites near Kostomlaty. A small remnant of freshwater sediments occurs about 4 km NE of Trupelník Hill below a cover of the magmatic body of Mrtvý vrch Hill. The sediment rests on the Upper Cretaceous sediments again, with no sign of quartzite beds at the base. After Reuss (1840) had reported these outcrops, the position of the site was fixed by geological mapping (Hibsch 1905, 1926, Müller 1963). The sediment is brownish, silicified, unevenly thinly bedded marlstone to limestone of unknown total thickness (content of $CaCO_3$ 59.6%; Radoň 2001).

The second site of the limestone has been known since Reuss's (1840) time from Roudný Hill north of Kostomlaty. This limestone forms irregular lenses, which were used in the 19th century for making lime, and only very limited information is available about its structure. Reuss (1840) reported a short gallery and published a section showing the limestone intercalated by volcanic rock (see Radoň 2001).

The marlstone of Mrtvý vrch Hill undoubtedly corresponds to the lower part of the section of Kučlín, as is apparent from the geological documentation of core V 2. The limestone of Roudný Hill may be at least partly coeval with the Mrtvý vrch section, as anticipated by Hibsch (1905, 1926). The corresponding age of the sites of Kučlín, Mrtvý vrch and Roudný Hills is corroborated by the macroflora (*Doliostrobus*) and ichthyofauna (*Thaumaturus* and *Amia/Cyclurus*). As suggested by the present study, Kučlín Lake must have extended several kilometres to the east and its sedimentary fill was later separated by erosion. No radiometric data for the magmatic bodies of Mrtvý vrch and Roudný Hills are available to test the age of the sediments.

Kundratice (Kundratitz) north of Litoměřice

A surface outcrop in diatomite and bituminous shale at the beginning of the Rytina Creek ("Jesuitengraben"), Early Oligocene in age, is usually referred to under this geographical name. Late Eocene plant and fish assemblages were recovered in the lower diatomite in core KU 1 (depth of about 160 m) situated near the road north of Kundratice (Bůžek et al. 1978, Kvaček and Walther 1998; Fig. 1). This section lies about 2 km NW of the Lbín area. Upper Cretaceous sediments were reached by this core at the depth of about 223 m. The boundary interval with the Palaeogene does not show any sign of silicification. The lower portion of volcanogenic strata consists of finer volcaniclastics intercalated with thin coarse-grained bodies. Depths of about 200 m are dominated by pelitic sediments including marl intercalations. The lower fossiliferous diatomite was reached at the depth between 167.3 and 159.0 m. The dating is based on the flora (Eocene Lauraceae – present paper) and ichthyofauna (*Bilinia*, Obrhelová 1976, 1979). The upper diatomite bed (84.4–95.0 m) contains another plant assemblage dated by the overlying lava flow to a minimum of 32.7 ± 0.8 Ma (Early Oligocene) and is considered equivalent to the outcrop in the "Jesuitengraben" (Bellon et al. 1998). No exposures of the lower diatomite were found in the surrounding area.

Lbín (Welbine)

A group of sites designated as Lbín include surface outcrops (test pits) and core Lb 1 near the village. Late Eocene fossiliferous deposits were reached in the lowermost position of the core (depth 89 to 97 m). Equivalent strata were documented in core Úc 9 at Hlinná about 1 km further west. In core Lb 1 the Palaeogene section starts with a clayey coal bed overlain by coarse-grained volcaniclastics. Above, a thick basanite (30.7 ± 0.7 and 28.4 ± 0.7 Ma; Bellon et al. 1998) is wedged between the basal deposits and sandy-silty clays including the fossiliferous diatomite. This basanite is obviously a younger intrusion, because the coal on the upper contact (depth 101.5 m) is charred. A small florula including lauroid leaves and a small twig of *Doliostrobus* (Bůžek 1958: 292; author's own study of material in ČGU) was found in a test pit made by Procházka and Mrázek (1955) in the landslide area at Lbín. It must be the same diatomite claystone that differs from the black greyish claystone in the core in its brownish colour (oxidised surface outcrop). Other diatomite beds are exposed near Mentaurov and Poustevny north of Skalice. They are called the "Lbín diatomite", and are younger and form an extension of the diatomite of Skalice (Radoň 2001). The coal seams, once worked near Lbín and Hlinná, have not been characterised palaeontologically. The sedimentary body at Lbín is covered by a lava flow of alkaline basalt (29.6 ± 0.6 and 30.1 ± 0.7 Ma; Bellon et al. 1998) coeval with the basanite intrusion below the diatomite.

Core Úc 9 starts with coarse pyroclastic rocks and breccias (depth below 107 m), which may be interpreted as a diatreme fill. The section continues with a sedimentary complex several tens of metres in thickness including claystones of volcanic origin, tuffitic intercalations, diatomites and coal seamlets. The rest of the section is formed by ash deposits or volcaniclastics about 50 m thick. The fossiliferous claystone at the depth of 86 to 71 m and overlying the coal seams can be interpreted as a maar lake deposit. The extent of the supposed maar is unknown; no gravity survey has been undertaken. Nevertheless, in some features it reminds of similar maar deposits from the periphery of the Vogelsberg, Westerwald Mountains and elsewhere in the Bitburg-Kassel area in Germany (Pirrung 1998, Pirrung et al. 2001).

The dating of the strata at Lbín and Hlinná is based on the macroflora dominated by *Doliostrobus* and on palynological data (Konzalová 1980, 1981). The younger fish fauna of *Protothymallus* (Gaudant in Bellon et al. 1998; Laube 1901 – as *Leuciscus fritschii*; Obrhelová 1969, 1970 – as *Varhostichthys*), which is labelled as coming from Lbín (coll. anonymus in 1865, NM), is present in thinly bedded diatomite of the Skalice type. The obvious collection site were the outcrops near Mentaurov, which coincide with the Skalice diatomite.

Skalice (Skalitz)

The name of this village 2 km north of Litoměřice has been used for two palaeontological sites (Hibsch and Seemann 1913). One site is represented by diatomaceous shale of Oligocene age that yielded fish fauna with *Protothymallus* (syn. *Varhostichthys*) and florula with modern Arcto-Tertiary elements (Laube 1901, Obrhelová 1969, 1970, Procházka 1955, Bůžek 1963). The second site, which is treated in this paper, shows quartzitized sandstone exposed north of Skalice above the Upper Cretaceous sands (see Radoň 2001 and Váně 2001 for details on local geography). Although the extent of the sandstone is much larger, reaching to the Lbín area, only the beds containing a typical macroflora of the Staré Sedlo type (also loose blocks slid downhill at the site of Žitenice, Farský háj – Engelhardt 1876) can be safely dated to the Late Eocene. The dating is based on the occurrence of *Doliostrobus* and the correlation of the flora with the Cheb, Sokolov and Weisselster basins (Knobloch et al. 1996, Mai and Walther 2000). The thickness of the sandstone bed is about 2 m. According to Macák (1966) and Shrbený ed. (1967), the cementation by silica also penetrates to the underlying Cretaceous sediments, which means that the lithology itself may be independent of the age of the sediment (see also Hibsch 1935). The bed is overlain by variegated volcaniclastics without fossils. The sediments were deposited in a river valley and later uplifted to the altitude of 476–480 m by young tectonic movements.

Important and new Late Eocene land plants of northern Bohemia

The macroflora of Kučlín was first described by Ettingshausen (1866, 1868, and 1869) with small additions by Sieber (1879, 1881) and Menzel (1901). New studies (e.g. Bůžek et al. 1967, 1968, 1990, Březinová et al. 1994, Kvaček and Bůžek 1995, Manchester and Hably 1997, Mai 1999, Kvaček et al. 2001, Wilde et al. in press) explained the systematic position of many components. Some other are added for the first time (in co-operation with S. R. Manchester) in the present account. Previous taxonomic lists (e.g. Kafka 1908, 1911) include many misidentifications and fictions. Even now, many of the recovered plant fossils cannot be unambiguously assigned into the natural system. Ettingshausen (1866, 1868, and 1869) and Sieber (1881) also treated plant remains from Kostomlaty. New data about the Kostomlaty floras were acquired from the collections of NM, GBA and DB. Some plants from the sites near Lbín, Hlinná and Kundratice were published by Bůžek et al. (1968, 1978), and additional taxa have been identified by recent cuticular studies. The flora of the Staré Sedlo Fm. (including Skalice and Žitenice) was treated by Knobloch et al. (1996), additions were reported by Radoň (2001). The following review gives the most up-to-date information on selected important plant elements of the sites studied.

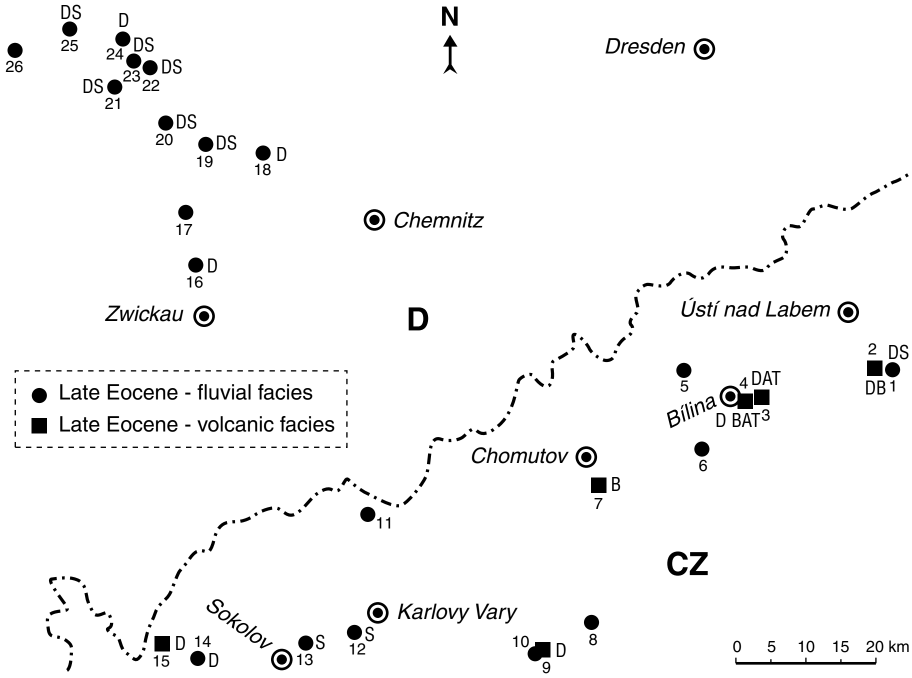

Fig. 2. Palaeogeography of the Late Eocene sites of fluvial (dot) and volcanic (square) facies across Saxony and northern Bohemia. (Macropalaeontological dating indicated, if available: D – *Doliostrobus*, S – *Steinhauera*, A – *Amia*, B – *Bilinia*, T – *Thaumaturus*.) 1 – Skalice – quartzite, 2 – Lbín area (cores Lb 1, Úc 9, KU 1), 3 – Kostomlaty – Mrtvý vrch and Roudný Hills, 4 – Kučlín, Trupelník Hill, 5 – Horní Litvínov, 6 – Břvany, Sedlec, 7 – Březno-Libouš, 8 – Podbořany, 9 – Valeč – limestone, 10 – Valeč – quartzite, 11 – Boží Dar-Rýžovna, 12 – Český Chloumek, 13 – Staré Sedlo, Jehličná, 14 – Nový Kostel, 15 – Velký Luh, 16 – Mosel, 17 – Meerane, 18 – Frohnsdorf, 19 – Klausa, 20 – Knau, 21 – Phoenix-Nord, 22 – Haselbach, 23 – Schleenhain, 24 – Peres, 25 – Profen, 26 – Deuben.

Pteridophytes

Osmunda lignitum (Giebel) Stur

Fragments of pinnae, showing characteristic free venation of this typical Palaeogene European fern (Barthel 1976), were recovered from Kučlín only (Pl. 1, fig. 10).

Pronephrium stiriacum (Unger) Knobloch et Z. Kvaček
(? Syn. *Aspidium fischeri* Heer *sensu* Ettinsghausen 1866:17, pl. 3, figs 9–12)

Leaf fragments of this common Tertiary swamp fern, showing a goniopterid venation (Pl. 4, fig. 7), are also known from Kučlín only.

? *Blechnum dentatum* (Göppert) Heer
(Syn. *Lomariopsis bilinica* Ettinsghausen 1866:13, pl. 3, fig. 13)

Because of its larger width, Ettingshausen (1866) believed this single pinna from Kučlín (refigured in Pl. 4, fig. 1) to be comparable with lomaroid and even acrostichoid ferns. Hably (in Hably et al. 2001) transferred this record into synonymy with *Blechnum dentatum.* Indeed, larger pinnae of *Blechnum dentatum* (see, e.g. Kvaček and Hably 1991, pl. 2, fig. 3) are indistinguishable from the Kučlín specimen, but also *Cyclopeltis jani* Barthel (1976) from the Upper Eocene of Geiseltal shows the same type of venation and morphology. Such sterile fern foliage with free secondary veins is hardly determinable to a genus.

Acrostichum lanzeanum (Visiani) Chandler

Bůžek et al. (1990, fig. 3) mentioned the occurrence of this fern with anastomosing venation from Kučlín. The recovered specimens (Pl. 4, fig. 9) are of those, which do not show anastomoses very distinctly (cf. Gardner and Ettingshausen 1879–1882, pl. 1). A similar but not so well preserved specimen as those from Kučlín has been recovered from the Skalice quartzite recently (Radoň 200, p. 213, as fern foliage – refigured in Pl. 3, fig. 8). *Acrostichum* was found in a number of other Eocene floras in Europe (e.g. Eckfeld, Geiseltal, Célas, Bembridge) and rarely survived into the Oligocene (e.g. at Eger-Kiseged, Hungary; Andreánszky 1954). It differs from its nearest living relative *A. aureum* in the form of the pinna base (see Frankenhäuser and Wilde 1993, as *Acrostichum* sp.).

Conifers

Doliostrobus taxiformis (Sternberg) Z. Kvaček var. *sternbergii* Mai et Walther
(Syn. *Doliostrobus certus* Bůžek, Holý et Z. Kvaček)

This extinct conifer, which shares some features with araucarians (pollen morphology, a single seed per scale), is a common element of the Eocene vegetation of Germany (Mai and Walther 1985, Kunzmann 1999). With its variety *hungaricus* Hably et Z. Kvaček (1998) it survived to the Early Oligocene in Hungary and Rumania. A silicified trunk, which was described from Kučlín as *Podocarpoxylon helmstaedtianum* by Březinová et al. (1994), may belong to the same plant, although its structure does not correspond to the branch wood of *Doliostrobus* (see Kvaček, in press; according to H. Falcon-Lang, Halifax, personal communication, the wood structure corresponds to *Cupressinoxylon*). Konzalová reported tentatively on the araucarioid pollen from the Kučlín cores V 2 and V 3 (Mazancová in Horáčková ed. 1967), and from Lbín and Hlinná (Konzalová 1981), which may be assigned to *Doliostrobus* as well. Cone scales and twigs of *Doliostrobus* occur at Kučlín (Pl. 1, fig. 6), Mrtvý vrch (Pl. 2, fig. 7), and the cores at Hlinná (Pl. 3, fig. 6) and Lbín. Only sterile twigs are available from Kostomlaty-Roudný (Pl. 2, fig. 9), Lbín test pits and the Skalice quartzite (Pl. 2, fig. 8). *Doliostrobus* is rarely represented in the Staré Sedlo Fm. (Cheb Basin) and is typical of the Zeitz flora except for the youngest part above the Weisselster coal seam III (Mai and Walther 2000).

Tetraclinis salicornioides (Unger) Z. Kvaček

Its cladode-like twigs and seeds occur extremely rarely in the Kučlín diatomite (Ettingshausen 1866, a seed in DB). This conifer became more wide-spread only in younger strata of the České středohoří Mountains and was widely distributed in the European Oligocene and Neogene (Kvaček 1989). This conifer is, contrary to its extant and fossil subxerophytic relatives *T. verticillata* and *T. brachyodon*, a humid subtropical element avoiding riverine vegetation. Its earliest record was documented from the Middle Eocene (Eckfeld maar – Wilde and Frankenhäuser 1998, as *Libocedrites*) in Europe and from the Oligocene in North America (Kvaček et al. 2000). Its last remnants are known from the Pliocene of Germany, Italy and the Caucasus Mts. area (Mai 1995 – as *Tetraclinis brachyodon*).

Angiosperms

Nymphaeaceae gen.

Seeds of nymphaeacean affinity are common fossils at Kučlín and Mrtvý vrch Hills. Their exact determination would require a study of anatomical details of the testa. Associated fragmentary leaves (Pl. 1, fig. 2) and petiole scars (Pl. 4, fig. 2) usually identified as *Nymphaea gypsorum* Saporta or *N. polyrrhiza* Saporta (Ettingshausen 1869) certainly belong to the same group. Because the seeds occur in several forms of different sizes, several representatives of these aquatic plants may have co-occurred. They suggest a moderate depth of the Kučlín Lake. The Nymphaeaceae have not been recovered at other studied Late Eocene localities in northern Bohemia.

Daphnogene cinnamomifolia (Brongniart) Unger
(Syn. *Daphnogene kutschlinica* Ettingshausen 1868, pl. 34, fig. 12)

Cinnamomoid leaves belong to the commonest among the woody elements of the Kučlín flora and are known from the sites at Kostomlaty-Roudný Hill, Lbín and Hlinná as well as from the Staré Sedlo Fm. at Skalice (Pl. 3, fig. 2). Broader leaf forms prevail in the fluvial facies of the latter site. This difference is most probably due to ecological influence of higher groundwater supply. Hence, *Daphnogene cinnamomea* (Rossm.) Knobloch can be better interpreted as an ecotype of *Daphnogene cinnamomifolia*, which is common in mesophytic sites of the Oligocene as well as in the Late Eocene (Mai and Walther 1985). Not all triveined leaves are assigned to this unit (see below).

"*Litsea*" *tertiaria* (Engelhardt) Sturm
(Syn. *Lauraceoderma alatum* Sturm 1971, *Laurophyllum alatum* (Sturm) Wilde 1989, *Litsea cinnamomifolia* Bandulska 1926, *Cinnamomum wonnacotii* Bandulska 1928).

This cinnamomoid foliage was documented only in core KU 1 at the depth of 159.5 m (as *Dicotylophyllum* sp. *sensu* Bůžek et al. 1978 on pl. 4, fig. 2). A very similar cuticular structure was described from leaf fragments of the Staré Sedlo Fm. from the Cheb Basin (Knobloch et al. 1996 – as cf. *Litsea tertiaria*) and from triveined leaves of the Middle Eocene of England (Bandulska 1926, as *Litsea cinnamomifolia*; 1928, as *Cinnamomum wonnacottii*) and Messel (Sturm 1971, as *Litsea tertiaria*). The generic affinity to *Litsea* needs to be verified by further comparative studies.

Laurophyllum syncarpifolium (Friedrich) Wilde

This Eocene element has been documented in core Úc 9 (Bůžek et al. 1978, pl. 2, fig. 3, pl. 4, fig. 2 – as cf. *Litsea glaphyre* Sturm) and in the Staré Sedlo Fm. of the Cheb and Sokolov basins (Knobloch et al. 1996, pl. 17). Mere leaf impressions of this species without epidermal structure are not recognisable. To date, *Laurophyllum syncarpifolium* has been known from the Eocene of Germany, Great Britain and the Czech Republic.

Laurophyllum streble (Sturm) Wilde

This rare lauraceous element was described from the type locality of Messel (Sturm 1971, as *Litsea streble*). The same epidermis structure has been documented for fragmentary leaves from core Úc 9.

? *Matudaea* sp.

Wide ovate, triveined leaves do not always belong to the Lauraceae. Hably and Kvaček (1998) interpreted such leaf forms from the Lower Oligocene of Eger-Kiseged as representatives of Hamamelidaceae (*Matudaea*). Similar leaves occur also at Kučlín (Pl. 1, fig. 3) and Staré Sedlo Fm. (*Daphnogene pseudopolymorpha* Knobloch et Z. Kvaček in Knobloch et al. 1996). A study of epidermal anatomy is necessary to prove their affinities to the Hamamelidaceae unambiguously (see Walther 1980).

Platanus neptuni (Ettingshausen) Bůžek, Holý et Z. Kvaček

Kučlín is the type locality of this unusual plane with oblanceolate leaves (Pl. 3, fig. 7) common in the Eocene to Miocene of Europe (Walther 1985). It is a successor of a still more ancient compound-leaved *P. bella* (Heer) Z. Kvaček, Manchester and Guo (2001) known from the Paleocene-Eocene of North America, Greenland and East Asia. *P. neptuni* was documented by its typical cuticular structure also from core Úc 9 (Pl. 3, fig. 1) and the Staré Sedlo Fm. in the Cheb Basin. In the Zeitz floras, it is known more often in the trifoliolate–quinquefoliolate form (Mai and Walther 1985, as *Platanus fraxinifolia*). This ancient plane thrived abundantly on fertile volcanic soils (Markvartice, Ipolytarnóc) and mostly avoided fluvial environment, contrary to the extant plane trees growing often along streams.

Eotrigonobalanus furcinervis (Rossmässler) Walther et Z. Kvaček

Leaves of this extinct fagaceous element are common in the Late Eocene fluvial sandstones of the Staré Sedlo Fm. and other sites of this kind in Germany, Ukraine and elsewhere in Europe (Kvaček and Walther 1989), being often accompanied by *Doliostrobus* and *Steinhauera*. Only one or two leaves have been recovered from Kučlín (Pl. 2, fig. 4), while they occur in masses at Skalice. *Eotrigonobalanus furcinervis* was spread also in the Oligocene, usually as an entire-margined form (*E. furcinervis* f. *haselbachensis* Walther et Z. Kvaček), known also from the Staré Sedlo Fm. in the Sokolov Basin (*E. furcinervis* ssp. *flagelliformis* (Rossm.) Knobloch et Z. Kvaček). This tree preferred oligotrophic acidic soils of peat-forming basins and avoided volcanogenic terrains. It was common in coal-forming associations (e.g. Geiseltal) but scarce or absent in mesophytic "volcanic" assemblages (e.g. Eckfeld).

Hooleya hermis (Unger) E.M. Reid et Chandler

This extinct member of the Juglandaceae was described from the Late Eocene Bembridge Marl and from other localities of the European Eocene (e.g. Eckfeld – Frankenhäuser and Wilde 1994, Messel – Manchester et al. 1994), rarely in Early Oligocene (Manchester 1987a). Although the whole plant is not known, typical slender, fine-toothed leaflets and complete leaves accompany these pterocarioid fruits at Eckfeld (Wilde and Frankenhäuser 1998). Also at Kučlín, these fruits (Pl. 1, fig. 6) co-occur with juglandaceous foliage of this kind. Similar leaflets can be met also in the limestone at Kostomlaty – Roudný (Pl. 1, fig. 9) and the diatomite claystone in the area of Lbín and Hlinná (Pl. 3, fig. 3, Pl. 4, fig. 4).

Engelhardia macroptera (Brongniart) Unger
Engelhardia orsbergensis (Weber) Jähnichen, Mai et Walther

Fruits of *Engelhardia macroptera,* a thermophilic extinct member of the Juglandaceae, are accompanied by typical leaves and isolated leaflets at Kučlín (*Engelhardia orsbergensis*), much like at many other sites (e.g. Holý Kluk, Suletice–Berand). The leaflets occur rarely also at Kostomlaty – Roudný (*Hakea bohemica* Ettingshausen 1868). This plant is indicative of a warm climate but has no value for stratigraphical purposes because it occurrs in Europe from the Eocene to Pliocene (Manchester 1987a, as *Palaeocarya*).

Cedrelospermum leptospermos (Ettingshausen) Manchester

This extinct representative of the Ulmaceae is recognisable by winged samaras with an asymmetrically positioned stigmatic cleft (Manchester 1987b). The foliage twigs with attached fruits from the Eocene of North America (Manchester 1989) and Messel (V. Wilde, pers. comm.) prove that narrow ulmoid leaves in the association can be interpreted as belonging to the same plant. This is the case in *Quercus tenerrima* Weber (i.e. *Tremophyllum tenerrimum* (Weber) Rüffle) from the Oligocene of Rott, and also in *Callicoma microphylla* Ettingshausen (1869) from Kučlín. Although the fruits (Pl. 2, fig. 10) are very rare at Kučlín, the leaves (Pl. 2, fig. 3) are more frequent and have also been found at Mrtvý vrch and Roudný Hills near Kostomlaty. *Cedrelospermum* was distributed in Europe from Eocene to Miocene, usually in assemblages of sub-humid aspect. The European populations formed a homogeneous complex with trends towards larger fruits in the Oligocene and Miocene (Thiébaut 2001, Hably and Thiébaut in press).

Palaeohosiea bilinica (Etingshausen) Z. Kvaček et Bůžek

Endocarps of this paratropical liana of the Icacinaceae, closely related to *Iodes* (Manchester 1999) were rarely encountered at Kučlín. Fruits of *Palaeohosiea suleticensis* Z. Kvaček (Bůžek, which may belong to the same species, occur in the Oligocene of Suletice and Holý Kluk (Kvaček and Bůžek 1995, Radoň et al. in press). Similar fruits have been described from the Paleocene and Eocene of England and from the Oligocene of Germany (Kvaček and Bůžek 1995).

Sloanea nimrodi (Ettingshausen) Z. Kvaček et Hably

The leaves of *S. nimrodi* (Pl. 2, fig. 11) were misinterpreted for the Icacinaceae foliage at first (Kvaček and Bůžek 1995). A more detailed study of comparative material and particularly the co-occurrence of very characteristic spiny fruits (capsules) allowed to re-assign these plant remains to *Sloanea* (Elaeocarpaceae), a tree widely spread in tropical to subtropical forests throughout the world (Kvaček et al. 2001). The only fruit remain found in the association at Kučlín (Pl. 4, fig. 8) reveals further differences between this Eocene small-leaved representative, whose capsules bear longer and coarser spines, and the Oligocene *S. artocarpites* (Ettingsh.) Z. Kvaček et Hably, accompanied by finely and shortly spiny fruits. *S. elliptica* (Andreánszky) Z. Kvaček et Hably from the Hungarian Oligocene is another species with robust, variable foliage and very large fruits covered with long spines.

S. nimrodi was found, besides Kučlín, also in core Úc 9, and is common also in the Late Eocene Zeitz Floral Assemblage of the Weisselster Basin (Mai and Walther 1985 – as *Dicotylophyllum sparsidentatum*; Mai and Walther 2000, pl. 5, fig. 6 – as *Icaciniphyllum artocarpites*), but missing in the Staré Sedlo Fm. It obviously preferred mesophytic conditions, like its extant relatives, but occasionally appeared also in riverine and swamp forests (in the Haselbach Mine and the Klausa sand pit in the fluvial facies, in the Profen Mine in the coal facies – Mai and Walther 2000). *S. nimrodi* was replaced by large-leaved *S. artocarpites* in the Oligocene (Kvaček et al. 2001).

Ailanthus cf. *confucii* Unger

A single incomplete fruit of *Ailanthus* was recovered from the Kučlín diatomite (Pl. 2, fig. 6). In its shape and position of the seed part it matches that from the Upper Eocene of Célas (Laurent 1899). Similar fruits have been also reported from the Middle Eocene of Messel (Collinson 1988) and many other Tertiary localities. The fruits known from the Early Oligocene Tard Clay of Hungary are much bigger and will be separated as an independent species (Hably, pers. comm.).

Hydrangea microcalyx Sieber

Tetramerous petaloid calyces of this hydrangea (Pl. 2, fig. 12) occur very rarely at Kučlín (type locality, the oldest record of the genus in Europe) and more frequently in the Oligocene (Mai 1985). Hydrangeas differ markedly in their broader form and venation pattern from the extinct genus *Raskya*, co-occurring at Kučlín (see below).

"Acer" sotzkianum Unger

Affinities of these maple-like fruits described under the above taxon are controversial. These samaras occur rarely at Kučlín (Pl. 2, fig. 1), and elsewhere, e.g., in the Oligocene of Holý Kluk (Radoň, Kvaček and Walther in press) and at the type locality of Socka of Oligocene (? Eocene) age (Mai 1999). The narrowed base of the seed part suggests that the fruits represent rather individual samaras, unlike the typical double samaras of maple. Mai (1999) believes that the fruits of *Acer* subgen. *Negundo* are most similar, but the *Negundo*-like foliage never co-occurs with the mentioned fruits.

Sterculia crassinervia (Ettingshausen) Procházka et Bůžek

Leaves recalling maples from Kučlín (Ettingshausen 1869) were re-investigated by Procházka (in Procházka and Bůžek 1975) and transferred to the genus *Sterculia* (Malvaceae *sensu lato*) on the basis of the venation. Indeed, the malvalean affinities are more probable, even though the direct placement in *Sterculia* may not be appropriate. The leaves of this kind are morphologically variable. They are known either as lobed, i.e. *Acer crassinervium* Ettingsh. (Pl. 2, fig. 13), or in a simple, non-lobed form, called *Ficus reussii* Ettingsh. Both forms are not rare at Kučlín and occasionally occur also at Mrtvý vrch and Kostomlaty – Roudný (Pl. 1, fig. 8). More information about the leaf anatomy is needed to resolve the true affinities and species boundaries within this form complex. Laurent (1899) assigned much larger but in principle similar foliage from the Upper Eocene of Célas, France (the type locality of *Doliostrobus*) to various fig species.

Sterculia labrusca (Unger) Unger

These trilobate (to quinquelobate) leaves with slender, almost parallel-sided lobes were rarely recovered from Kučlín (Ettingshausen 1869 – refigured in Pl. 4, fig. 10). This species varies in the leaf size and the lobes. Most of the specimens from the Staré Sedlo Fm. (Knobloch et al. 1996) are smaller, but the leaf described by Engelhardt (1876, pl. 27, fig. 17) from the Žitenice quartzite matches well that from Kučlín.

The affinity of *Sterculia labrusca* has not been fully clarified (Knobloch et al. 1996) and the often suggested analogue, *Brachychiton* (Sterculiaceae), is unlikely because of its modern distribution in Australia.

Pungiphyllum cf. *waltheri* Frankenhäuser et Wilde

Spiny-lobed leaves usually referred to "*Quercus*" *cruciata* A. Br., which are spread in the European Tertiary, differ in the type of stomata from the Fagaceae (Kvaček and Walther 1981). Individual populations of this enigmatic plant vary in the leaf shape and size during the Tertiary. Small and often shallow-lobed forms from the Middle Eocene of Eckfeld were described as an independent species *Pungiphyllum waltheri* Frankenhäuser et Wilde (1995). Only few similar, slightly larger leaves of this kind were recovered from Kučlín (Pl. 2, fig. 5).

Raskya vetusta (Ettingshausen) Manchester et Hably

Four-winged propeller-like fruits (calyces) are typically developed in several fossil plants. Their distinction depends on the structure of the fruit itself. Those described as *Raskya* Manchester et Hably (2000) bear a long elongate-fusiform body in the centre, in contrast to the similar *Cruciptera* Manchester (1991), *Tetrapterys harpyarum* Unger emend. Hably et Manchester (2000), or *Asterocarpinus* Manchester et Crane (1987) with a central globose fruit. Kučlín is the type locality of *Raskya* (Pl. 1, fig. 5, Pl. 3, fig. 5). Its fruits are distributed only in the Eocene (Bembridge, Kučlín) and Oligocene (Eger-Kiseged, Óbuda) of Europe (Manchester and Hably 1997). The exact affinities and corresponding foliage are still doubtful. The previous interpretation as the fruits of *Abelia* (Reid and Chandler 1926) is erroneous because the calyx of *Abelia*, in contrast to *Raskya*, is epigynous. All occurrences of *Raskya* outside Bohemia are connected with marginal marine facies.

Apocynospermum striatum E.M. Reid et Chandler

These detached spindle-shaped seeds with a long terminal coma were recognised as belonging to Apocynaceae–Asclepiadaceae by Reid and Chandler (1926). The specimens are scattered, solitary and quite rare. Neither the fruit bodies, which contained the seeds, nor the corresponding foliage are known. Cases where two seeds adhere to each other (Pl. 2, fig. 2) are exceptional. The occurrences of *Apocynospermum* in Europe range from the Eocene to the Miocene (*Echitonium* Unger by earlier authors). In northern Bohemia, similar forms have been reported from Kučlín, Mrtvý vrch Hill and also from the Oligocene sites, like Kundratice (Kvaček and Walther 1998).

Saportaspermum sp. div.

Winged seeds, originally described as belonging to the same group as *Cedrelospermum* by Saporta (1889), differ in the seed form and wing venation (Meyer and Manchester 1997). They were distributed in Europe during the Eocene to Miocene times and in North America during the

Oligocene only. Various distinct forms (morpho-species) of different sizes and shapes occur at Kučlín (Pl. 1, fig. 4) and Mrtvý Vrch. Their affinities are enigmatic.

Nitophyllites bohemicus Wilde, Z. Kvaček et Bogner

A large incomplete leaf, which was found at Kučlín (Pl. 1, fig. 1), documents helophytic araceous plants typical of warm climate today. Other occurrences of this kind are extremely rare, in the Eocene of North America, and in the Paleocene-Eocene of Kazakhstan and Far East. Araceous foliage is abundant at the Middle Eocene site of Messel in Germany, but represented by different morphotaxa (Wilde et al. in press).

? *Dioscorea* sp.

A lunate shaped seed was recovered from Kučlín (Pl. 4, fig. 5) and recognised by S. R. Manchester (pers. comm.) as possibly belonging to the Dioscoreaceae. More complete fruits of this plant group were recovered at the Hungarian Early Oligocene site of Eger-Kiseged (Andreánzsky 1959, as *Dioscoreocarpum*).

Ecosystems, environment and palaeoclimate

The studied sites in northern Bohemia, which are dated as Late Eocene, include more or less different fossil assemblages. The differences may partly result from two factors. First, the possibilities of collecting vary from site to site (Kučlín vs. Mrtvý vrch vs. cores at Lbín). Secondly, different environmental conditions may bias the composition of coeval floras (mesophytic vegetation on fertile volcanogenic soils vs. azonal vegetation in alluvial settings). Similar phenomenon can be noticed in the Middle Eocene of Germany, when comparing plant assemblages of the lignite basin of the Geiseltal and the maar fills of Eckfeld and Messel (Wilde 1995). The same applies to the Early Oligocene vegetation of Haselbach, representing a coal-forming and alluvial vegetation compared to “volcanic” plant assemblages in the České středohoří Mountains (Kvaček and Walther 2001).

The flora of Kučlín was explored for the longest period and its plant assemblages are the most diversified. Aquatic and helophytic plants (Nymphaeaceae, Araceae and other monocots) were confined to shallow water of the lake. Deep swamps were not developed along the lake, at least in such an extent to produce thick lignite beds. The only hygrophilic conifer, *Doliostrobus*, was present, but in medium frequency. The other trees common in the basins and alluvial sandy facies (oligotrophic substrates), notably *Eotrigonobalanus*, *Steinhauera*, *Sabal*, were either rare or absent. The most common plant fossils in the Kučlín diatomite are the seeds of Nymphaeaceae, which may belong to the same plants as co-occurring rhizomes of *Nymphaea polyrrhiza*. Other herbaceous elements (ferns, monocots) are rare. It can be reasonably assumed that also the araceous *Nitophyllites bohemicus*, represented by a single fragment, belonged to helophytic vegetation, which bordered the volcanic lake. Rare remains of *Sabal*, Zingiberales-like (*Musa bilinica*) and strap-like monocot foliage are the other elements of this community. Heavy infructescenses and whole branches of *Platanus neptuni* may indicate that even this tree grew partly on the shores of the lake. The Kučlín flora is typically heterogeneous, and includes also mesophytic elements, which were blown into the lake by wind (winged fruits or seeds of *Raskya venusta*, *“Acer” sotzkianum, Engelhardia macroptera, Hooleya hermis, Apocynospermum*).

The overall character of the vegetation of Kučlín fits best to a flatland with surrounding moderate uplands. Most of the recovered woody plants including lianas are mesophytic, like Lauraceae (narrow-leaved *Daphnogene*, *Laurophyllum*), Juglandaceae (*Engelhardia, Hooleya*), Icacinaceae (*Palaeohosiea*), Elaeocarpaceae (*Sloanea*), and even subxerophytic (*Cedrelospermum*, *Ziziphus, Mimosites*). Affinities of many plants from Kučlín have not been clarified yet (cf. Pl. 3, fig. 4) but none of them can be interpreted as a modern Arcto-Tertiary element in the sense of Kvaček (1994), i.e. an Oligocene immigrant from Asia. *Tetraclinis salicornioides, Platanus neptuni*, *Sterculia labrusca*, *Raskya vetusta* and other species accompanied evergreen forests elsewhere in Europe, mainly in the Late Eocene. Physiognomy of the vegetation of Kučlín was similar to that of the Middle Eocene sites of Messel and Eckfeld (Wilde 1989, Wilde and Frankenhäuser 1998) and the Oligocene sites of Suletice–Berand and Holý Kluk (Kvaček and Walther 1995, Radoň et al. in press). These floras, however, are of different age and include partly different species spectra.

The Kučlín Lake was obviously a freshwater reservoir as documented by diatoms (Řeháková 1967, in Malkovský ed. 1985). Facultative halophytes, like *Acrostichum*, cannot provide unequivocal evidence of salt marshes, because today this fern is spread also outside mangroves (see Frankenhäuser and Wilde 1993). Fish fauna includes the only marine representative, *Morone* (Pl. 5, figs 1–3), that penetrated inland into the freshwater environment via rivers (Micklich and Böhme 1997). Nevertheless, descendants of another member of fish fauna – a percoid *Bilinia* (Obrhelová 1969, 1976) – also live in marine environments today. Therefore, Obrhelová and Obrhel (1987) supposed a higher mineral content in the lake due to mineral springs. The remaining *Thaumaturus* and *Amia* (treated recently as *Cyclurus* by Gaudant 1977, 1996, Bellon et al. 1998) are obligate freshwater dwellers, like other aquatic animals – *Diplocynodon* (Kafka 1911), *Trionyx* (Laube 1882), small crayfish (Meyer 1852, Frič 1872) and a newly recovered frog (coll. DB). Algal taphocoenoses are dominated by freshwater diatoms *Melosira distans*, *Fragilaria* and *Synedra.* Řeháková (in Malkovský ed. 1985) listed 19 species of pennate diatoms and a stenothermic *Eunotia clevei* typical of cold waters. She recognized the Kučlín assemblage as the most ancient among diatomite occurrences.

The land around the Kučlín Lake was lying well above the ground water table, where evergreen forests were developed with rare ferns on the ground. Even low slopes can be expected due to the presence of subxerophytic plants like *Cedrelospermum* with extremely narrow leaves and *Ziziphus*. Palynological data (Mazancová in Horáčková ed. 1967, Konzalová 1981) provided additional information on the surrounding vegetation. The pollen spectra from the marl underlying the diatomite yielded bituminous alga *Botryococcus*, which is typical of stagnant eutrophic waters, and microsporangia of aquatic ferns. Among leptosporangiate ferns, a thermophilic climber (*Lygodium*), Gleicheniaceae and some more exotic spores of unknown affinities were noted. Conifers are represented by the cupressaceous *hiatus-dubius* group, but also by the araucarioid pollen probably corresponding to *Doliostrobus*. Various bisaccate forms document the Pinaceae including the *haploxylon* type, today partly referred to *Cathaya*. Pollen of *Carya, Engelhardia* and *Myrica* occurred among the Juglandaceae – Myricaceae group. Tilioid pollen documents some extinct members of the Malvales. Various forms of tricolpoporoid pollen have usually been interpreted as Fagaceae, Leguminosae, Nyssaceae, Aquifoliaceae and Araliaceae, tetracolpoporoid forms as Sapotaceae and Meliaceae. Noteworthy are stratigraphically significant sporomorphs – the *rhizophorus* type (comparable with lianas *Iodes* ~ *Palaeohosiea*, Icacinaceae) and *Cupaneidites* (Myrtaceae vel Sapindaceae). Among monocots, rare pollen of *Sparganium* and palms has been identified. Beetles inhabiting dry land dominate by 90% among the insects (Prokop in press). The Curculionoidea forms one-half of the respective taphocoenosis, two other groups – Elateridae and Buprestidae – are also abundant, while only a single aquatic element, *Anisops heidenii* Deichm., is present. In composition and aspect, the Kučlín insect fauna matches those of the Middle Eocene sites of Eckfeld and Messel. Large forms, whose extent analogues are most diversified in modern tropical and subtropical areas (Dascillidae, Buprestidae and Trogositidae), suggest a very thermophilic character.

The locality of Kostomlaty – Mrtvý vrch Hill shares all plants so far recovered from this florula with Kučlín. *Doliostrobus* is represented by cone scales and twigs, together with additional Nymphaeaceae seeds, *Magnolia longipetiolata, Engelhardia orsbergensis, Platanus neptuni, Sterculia crassinervia, Cedrelospermum* foliage, *Apocynospermum,* and *Saportaspermum*. According to Obrhelová and Obrhel (1987) the ichthyofauna includes *Thaumaturus* and *Amia.* A fish scale identified by Micklich as *Amia* vel *Cyclurus* (Pl. 4, fig. 6) also corroborates the correlation and dating to the Late Eocene. The diatom assemblage belongs to the older type (Kučlín type) *sensu* Řeháková (in Malkovský et al.1985). It is obvious that the Mrtvý Vrch marlstone represents a deposit of the same large lake as that underlying the diatomite of Kučlín, extending over a distance of at least 3 km (Fig. 1).

The locality of Kostomlaty – Roudný Hill differs in the type of the fossiliferous sediment – bedded and massive limestone containing only rare plant fossils. The plant assemblage is only partly similar to those of Kučlín and Mrtvý vrch Hill. The microphyllous *Mimosites,* Juglandaceae including *Engelhardia* (as *Hakea bohemica* Ettingshausen, 1868, pl. 35, fig. 3), *Cedrelospermum* and narrow, entire-margined *Apocynophyllum*-like leaves prevail over solitary larger leaf fossils determined as *Sterculia*, Ulmaceae (Pl. 1, fig. 7, Pl. 4, fig. 3), *Ficus* and *Laurophyllum* (coll. NM, NHMW, GBA). Besides *Doliostrobus* twigs, also one matching *Chamaecyparites* or *Taxodium* (determined as *Sequoia langsdorfii* by Ettingshausen 1866) was encountered. The burial of plant fossils probably took place far from the shore in these places. In view of differences in the flora and plant taphonomy, the limestone of Roudný Hill can be interpreted as a deposit of the deeper part of the Kučlín Lake. The fish fauna includes *Amia* and *Thaumaturus* and matches that of Kučlín (Obrhelová 1979, Obrhelová and Obrhel 1987). The limestone levels may not all be contemporaneous, because their plant content differs.

The outcrops at Lbín and the corresponding level in cores Lb 1, Úc 9 and Ku 1 (Bůžek et al. 1978) correlate with the earliest volcanogenic strata elsewhere. This correlation is based on the common occurrence of *Doliostrobus,* the Eocene Lauraceae and an ancient percoid fish *Bilinia* (in core Ku 1; Obrhelová 1979). Fossiliferous beds are composed of diatomaceous or coaly tuffitic claystones between magmatic bodies and pyroclastics. *Doliostrobus* remains are the most frequent at Lbín and Hlinná, suggesting swampy conditions around the depositional sites. Lignite seamlets were formed in periods of shallow mire development, although no palaeobotanical data are available directly from the coal. The diatomaceous claystone of the Lbín and Hlinná cores yielded pollen spectra similar to those from Kučlín in many respects (Konzalová 1981). These levels also contain exotic fern spores, araucaroid pollen, the *rhizophorus* type, *Carya, Engelhardia* and *Ilex* pollen. A rare type of exotic Lecythidaceae pollen was encountered in the Lbín core (Konzalová 1980). All the hitherto recognised broad-leaved trees, partly identified on the basis of epidermal characteristics, are shared with Kučlín *(Platanus neptuni, Sloanea nimrodi*), Kostomlaty (*Apocynophyllum*) or with the Staré Sedlo Formation (*Laurophyllum syncarpifolium*, *"Litsea" tertiaria*). The sedimentary setting and the surrounding vegetation may have corresponded to the conditions expected for flat large maar lakes (see Pirrung et al. 2001).

The quartzite of Skalice includes a plant assemblage dominated by *Eotrigonobalanus* and broad-leaved *Daphnogene* (Knobloch et al. 1996, Radoň 2001). This combination is typical of azonal riverine gallery forests, known also in the Cheb, Sokolov and Weisselster basins (Knobloch et al. 1996; Mai and Walther 1985, 2000). Recent collections of Radoň in 1999 added elements new to this site – *Acrostichum* and *Doliostrobus*, represented by unique, poorly preserved specimens. Both plants occur also at Kučlín. A more diversified plant assemblage from Žitenice (Engelhardt 1876), which comes from the equivalent fossiliferous level (Radoň 2001, Váně 2001), added some more riparian trees like *Steinhauera*. *Sterculia labrusca* belongs to mesophytic elements shared with Kučlín.

Pinus ornata and Pinaceae needles refer to pine stands near the alluvial plain. Pines rarely grew directly in volcanogenic areas, but are documented by bisaccate pollen in the spectra of Kučlín, Hlinná and Lbín (Konzalová 1981). Principally, these fluvial deposits were approximately contemporaneous with those of the Kučlín Lake and the Lbín maar. Floristic and vegetational differences among all quoted localities were apparently due to different environment. Unfortunately, no other arguments are available for such a correlation, because acidic quartzite deposition prevented the preservation of vertebrate fossils, pollen and leaf cuticles.

On the whole, both azonal (Skalice, Žitenice) and zonal vegetation types (Kučlín, Hlinná, Lbín) feature evergreen forests now limited to paratropical to subtropical climatic conditions (Cwa type, mean annual temperature around 20 °C). The presence of palms and other tropical to subtropical elements (*Sloanea,* cf. *Iodes*, *Engelhardia*) shared with other Eocene localities in Europe indicate a mean coldest month temperature of 6–13 °C, which is the limiting factor for the listed frost-sensitive taxa. The mean warmest month temperature of at least 23 °C may have caused a short period of humidity deficit, suggested by the semihumid *Cedrelospermum,* narrow-leaved Leguminosae (*Mimosites* at Kučlín, Kostomlaty, Hlinná) and shrubby *Ziziphus*. Narrow earlywood of growth rings and regular-sized tracheids in latewood of *Podocarpoxylon helmstedtianum* (Březinová et al. 1994) may also be considered an influence of long equable and humid growing seasons with short periods of drought, although this indication must be considered with caution (Creber 1977). In general, the climatic regime was humid, well over 1500 mm of annual precipitation. Slightly higher estimates were made for the Middle Eocene of Messel (Wilde 1989), also based on the zonal vegetation. The discrepancy of the climatic signal given by land plants and cold-water diatoms in the Kučlín diatomite (Řeháková 1967, in Malkovský ed. 1985) can be explained by changes in the autecology of this group of algae during the Tertiary. The immigration of deciduous woody plants (modern Arcto-Tertiary elements) signalling climatic deterioration took place in northern Bohemia later, at the Eocene/Oligocene boundary (Kvaček 1994, Walther 1994, Kvaček and Walther 2001). The earliest flora of the Středohoří Complex dominated by deciduous arboreal elements at Roudníky is dated to 35.4 ± 0.9 Ma (Bellon et al. 1998).

Palaeogeographic considerations

The record of marine fish *Morone* in the diatomite of Kučlín (Micklich and Böhme 1997) made us think about its migration route from the Late Eocene "North Sea" to northern Bohemia. Most of the deposits in between are not suitable for the preservation of vertebrate fossils. At Kučlín, the fish association *Morone-Amia-Thaumaturus-Bilinia* co-occurs with *Doliostrobus*, a typical conifer of the Late Eocene Zeitz Floral Assemblage of the Weisselster Basin. It can be expected that this flora can suggest contemporaneous deposition indicating pathways for the migration of *Morone*.

Late Eocene marine sediments are in contact with freshwater sediments of the Weisselster Basin at few localities only. According to Mai and Walther (2000) this contact is traceable mainly near Schortau. Freshwater deposits with the Zeitz flora in Saxony include coal seams I–III and adjacent sand deposits. They belong to the Lower Borna Formation and extend over a large area towards northern Bohemia. The last remnants of the quartzite containing *Doliostrobus* were identified near Mosel and Zwickau some 50 km from the border between Bohemia and Saxony (Fig. 2). Because of the uplift of the Krušné hory (Erzgebirge) Mountains during the late Cenozoic, most of the sediments were eroded there. Micklich and Böhme (1997) expected a connection with the sedimentary basins in northwestern Bohemia via the Jáchymov Fault, however, yet other possibilities were certainly available for the Late Eocene river system to reach the Weisselster Basin from northern Bohemia. The equivalent Staré Sedlo Fm. stretches from the west (Cheb Basin) to the north (Litoměřice), as indicated by its typical flora (Knobloch et al. 1996). The facies development includes mostly quartzites, sandstones, rarely sands (Cheb Basin, Podbořany Sand in the Most Basin) with clay lenses.

At Valeč, the occurrence of *Doliostrobus* is connected with the limestone of the Doupov Volcanic Complex (Bůžek et al. 1968). This occurrence is exceptional because most other limestone lenses and tuffitic beds of the Doupovské hory Mountains are younger. They yielded plant assemblages with modern Arcto-Tertiary elements and were deposited during Early Oligocene. Adjacent tuffitic beds are also of Early Oligocene age, as documented by the mammal fauna at Dětaň (Fejfar 1987). The typical flora of the Staré Sedlo Fm. was found beneath the Doupov Volcanic Complex also at Valeč (Engelhardt 1880). The continuation towards the Most Basin – the Podbořany Sand ("Krásný Dvůr Formation" *sensu* Křelina) – is almost free of fossils. At some places, the sand facies interfingers with volcanogenic rocks (Cílek 1966, Kodymová in Malkovský ed.1985: 123, fig. 13). This may suggest that at least the upper part of the Podbořany Sand was coeval with the volcanic activity. Neither the quartzites in the southern part of the Most Basin (Váně 1999) nor the occurrences on the Krušné hory Mts. near Boží Dar (Lomozová and Mrňa 1967) have been dated. Only a secondary occurrence of *Steinhauera* in a quartzite boulder found at Horní Litvínov (Knobloch et al. 1996) may prove that the Staré Sedlo Formation did extend between the Doupovské hory and České středohoří Mountains. Late Eocene deposits were also found in the volcanogenic facies in the Most Basin, such as the maar fill at Libouš dated by palynology (Konzalová 1977, 1981) and ichthyofauna (Obrhelová 1990). However, the exact connection between the easternmost occurrences of the Staré Sedlo Formation at Skalice north of Litoměřice and the Weisselster Basin remains enigmatic.

Thus, a connection between Kučlín and the North Sea was possible, because volcanogenic lakes and river/basin systems existed at the same time in northern Bohemia and Saxony, allowing migration of fish fauna. This landscape was surely different from the today's one because the mountain range of the Krušné hory Mountains did not exist. The general idea viewing the Bohemian Massif as a peneplain with lowland rivers (Domácí in Malkovský ed. 1985) must be now amended by adding the volcanic products. Lakes, maars and moderate volcanic upland made the relief of the landscape slightly uneven at that time. Lakes were extensive and partly supplied by mineral springs, as supposed by Obrhelová and Obrhel (1987). Similar conditions are common in many modern volcanic areas. The Yellowstone National Park in Wyoming, USA, where the Yellowstone Lake extends over more than 30 km and is drained by the Yellowstone River, offers a good model to compare. Adjacent hot springs on the Geyser Plateau and the mighty Mammoth Hot Springs have produced masses of marlstone/limestone deposits. At the same time, the river valley is associated with the fluvial, psammitic/psephitic facies.

As the Staré Sedlo Formation and coeval volcanogenic deposits generally follow the direction of the Litoměřice Fault in their extent, their origin is obviously connected to early development stages of the Ohře Rift.

Conclusions

Similarities of the land flora and the fish fauna suggest a correlation between the Palaeogene lacustrine deposits at Kučlín, Kostomlaty and wider surroundings of Lbín. The Late Eocene age of these deposits has been proven by biostratigraphy and radiometric dating. This lowermost part of the volcanic complex of the České středohoří Mts. (Ústí Fm. *pro parte*) overlaps the Staré Sedlo Fm. in time. These two formations are in part to be interpreted as two heteropic facies from the same period, at some places without any hiatus. Macroclimatic conditions in northern Bohemia during the Late Eocene were (paratropical) subtropical with variable humidity, as reflected by the flora and vegetation on volcanic uplands. A perhumid aspect of the azonal riverine gallery forests bound to the fluvial facies (Staré Sedlo Fm.) was mainly due to the groundwater supply. Similar differentiation of the plant cover has been reported from other Middle Eocene and Oligocene landscapes of Central Europe.

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Explanation of plates

Plate I ⇒ ⇒ ⇒ ⇒ ⇒

1 – *Nitophyllites bohemicus* Wilde, Z. Kvaček et Bogner, Kučlín, leaf fragment, coll. NM G 7778, holotype, × 0.5; 2 – Nymphaeaceae gen., Kučlín, leaf fragment, coll. DB, × 0.5; 3 – ? *Matudaea* sp., Kučlín, leaf impression, coll. DB, × 1; 4 – *Saportaspermum* sp., Kučlín, seed, coll. DB, × 2.5; 5 – *Raskya vetusta* (Ettingsh.) Manchester et Hably, Kučlín, calyx, coll. NM G 7567b, neotype, × 2; 6 – above *Hooleya hermis* (Ung.) E.M. Reid et Chandler, fruit, below *Doliostrobus taxiformis* (Sternb.) Z. Kvaček var. *sternbergii* Mai et Walther, Kučlín, twig, coll. NM G 3724, × 2; 7 – Ulmaceae gen., Kostomlaty – Roudný Hill, leaf impression, coll. NM G 7786, × 1; 8 – "*Ficus*" *reussii* Ettingsh., Kostomlaty, leaf impresion, coll. NM G 4782, × 1.5; 9 – Juglandaceae gen., Kostomlaty – Roudný Hill, leaflet impression, coll. NM 7779, × 2; 10 – *Osmunda lignitum* (Giebel) Stur, Kučlín, pinna, coll. NM 7896a, × 2;

Photos Z. Kvaček

Plate II ⇒ ⇒ ⇒ ⇒ ⇒

1 – "*Acer*" *sotzkianum* Ung., Kučlín, samara, coll. NM 7893a, × 2; 2 – *Apocynospermum* sp., Kučlín, two adhering seeds with coma, coll. DB, × 1.5; 3 – *Cedrelospermum* sp., Kučlín, leaf impression, coll. NM 7897a, × 1.5; 4 – *Eotrigonobalanus furcinervis* (Rossm.) Walther et Z. Kvaček, Kučlín, leaf impression, coll. DB, × 1; 5 – *Pungiphyllum* cf. *waltheri* Frankenhäuser et Wilde, Kučlín, leaf impression, coll. DB, × 1; 6 – *Ailanthus* cf. *confucii* Ung., Kučlín, samara, coll. NM G 7898a, × 1.5; 7 – *Doliostrobus taxiformis* (Sternb.) Z. Kvaček var. *sternbergii* Mai et Walther, Mrtvý Vrch, cone scale, coll. DB, × 2; 8 – *Doliostrobus taxiformis* (Sternb.) Z. Kvaček var. *sternbergii* Mai et Walther, Skalice – quartzite, twig, coll. RMT, 9 – *Doliostrobus taxiformis* (Sternb.) Z. Kvaček var. *sternbergii* Mai et Walther, Kostomlaty – Roudný Hill, twig, coll. NM G 7792, × 1.6; 10 – *Cedrelospermum leptospermos* (Ettinsgh.) Manchester, Kučlín, fruit, coll. NM G 7894, × 20; 11 – *Sloanea nimrodi* (Ettingsh.) Z. Kvaček et Hably, Kučlín, leaf impression, coll. NM G 7899a, × 1.5; 12 – *Hydrangea microcalyx* Sieber, Kučlín, calyx, coll. NM G 7892, × 1.2; 13 – *Sterculia crassinervia* (Ettingsh.) Procházka et Bůžek, Kučlín, leaf impression, coll. DB, × 0.75;

Photos Z. Kvaček

Plate III ⇒ ⇒ ⇒ ⇒ ⇒

1 – *Platanus neptuni* (Ettingsh.) Bůžek, Holý et Z. Kvaček, core Úc 9, Hlinná, leaf compression, coll. ČGS, × 2; 2 – *Daphnogene cinnamomifolia* (Brongn.) Ung., Skalice – quartzite, leaf impression, coll. RMT, × 1.5; 3 – Juglandaceae gen., core Úc 9, Hlinná, leaf compression, coll. ČGS, × 2.7; 4 – indetermined fruits, Kučlín, coll. DB, × 2.5; 5 – *Raskya venusta* (Ettingsh.) Manchester et Hably, Kučlín, calyx with fruit, coll. DB, × 2.5; 6 – *Doliostrobus taxiformis* (Sternb.) Z. Kvaček var. *sternbergii* Mai et Walther, core Úc 9, Hlinná, cone scale with a seed, holotype of *Doliostrobus certus* Bůžek, Holý et Z. Kvaček, coll. ČGS, × 5; 7 – *Platanus neptuni* (Ettingsh.) Bůžek, Holý et Z. Kvaček, Kučlín, twig, coll. Valíček, × 0.5; 8 – *Acrostichum lanzeanum* (Visiani) Chandler, Skalice – quartzite, pinna, coll. RMT, × 1;

Photos Z. Kvaček

Plate IV ⇒ ⇒ ⇒ ⇒ ⇒

1 – *? Blechnum dentatum* (Goepp.) Heer, Kučlín, pinna fragment, holotype of *Lomariopsis bilinica* Ettinsgh., coll. BP 55.2489.1, × 0.8; 2 – *Nymphaea polyrrhiza* Sap., Kučlín, petiole and root scars, coll. NHMW, × 1; 3 – Ulmaceae gen., Kostomlaty – Roudný Hill, leaf impression, holotype of *Weinmannia rectinervis* Ettingsh., coll. NHMW 1864/40/956, × 2; 4 – Juglandaceae gen., core Úc 9, Hlinná, leaflet compression, coll. ČGS, × 2; 5 – ? *Dioscorea* sp., Kučlín, seed, coll. NM G 7900a, × 1.5; 6 – *Amia* vel *Cyclurus*, Mrtvý Vrch, fish scale, coll. DB, × 5; 7 – *Pronephrium stiriacum* (Ung.) Knobloch et Z. Kvaček, Kučlín, pinna, coll. DB, × 2.5; 8 – *Sloanea* sp., Kučlín, fruit, coll. NM G 7895, × 2; 9 – *Acrostichum lanzeanum* (Visiani) Chandler, Kučlín, pinna, coll. ČGS, × 4; 10 – *Sterculia labrusca* (Ung.) Ung., Kučlín, leaf impression, refigured orig. Ettingshausen (1869, pl. 43, fig. 5), coll. NHMW 1864/40/844, × 1;

Photos Z. Kvaček

Plate V ⇒ ⇒ ⇒ ⇒ ⇒

Morone sp., Kučlín, NM G Pc 2850. 1 – almost entire skeleton, × 0.5; 2 – ctenoid scales behind the head, × 5; 3 – detail of the head (arrow – praeoperculum with a low outer crista), × 2;

Photos Z. Kvaček

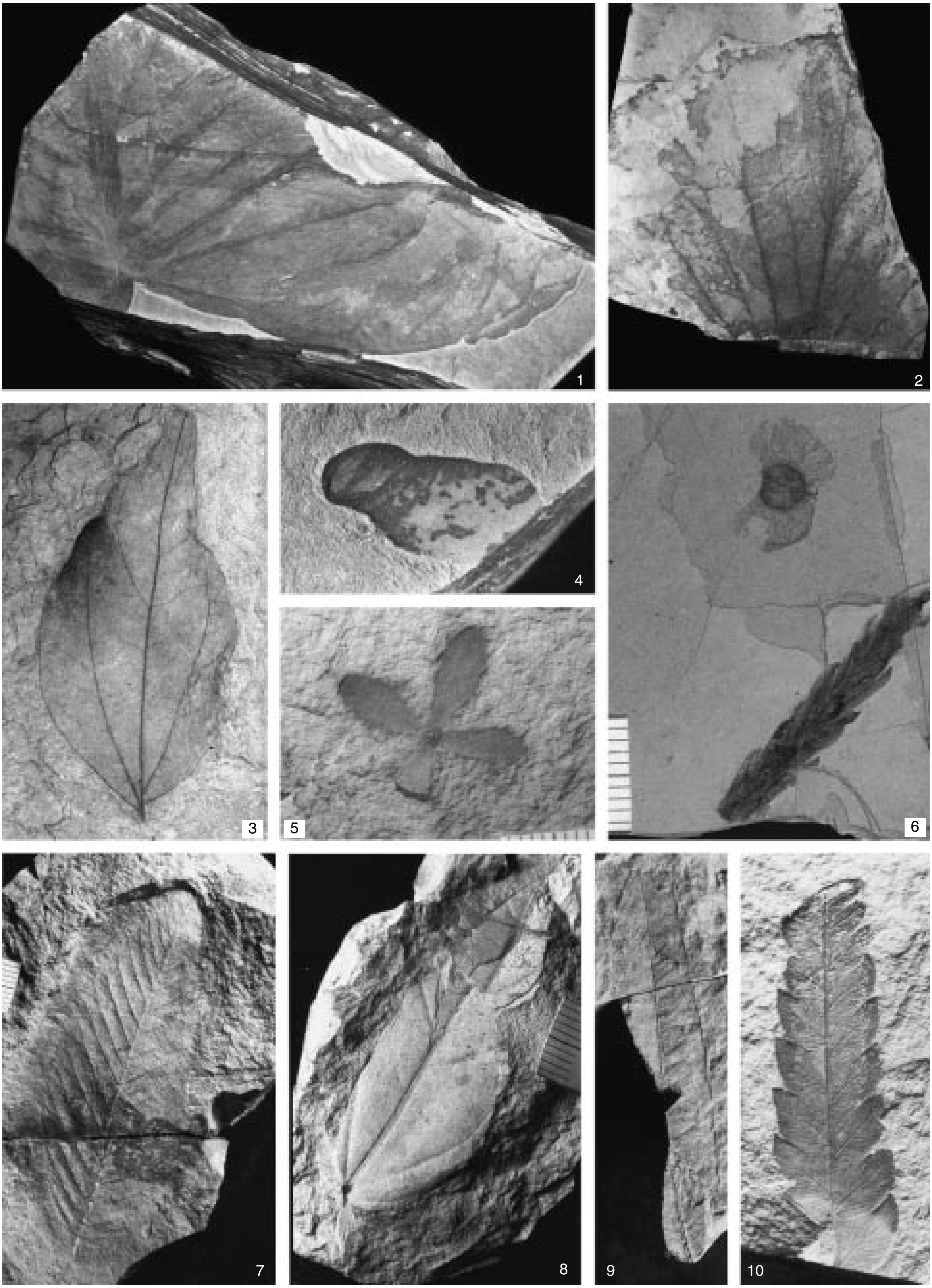


Plate I

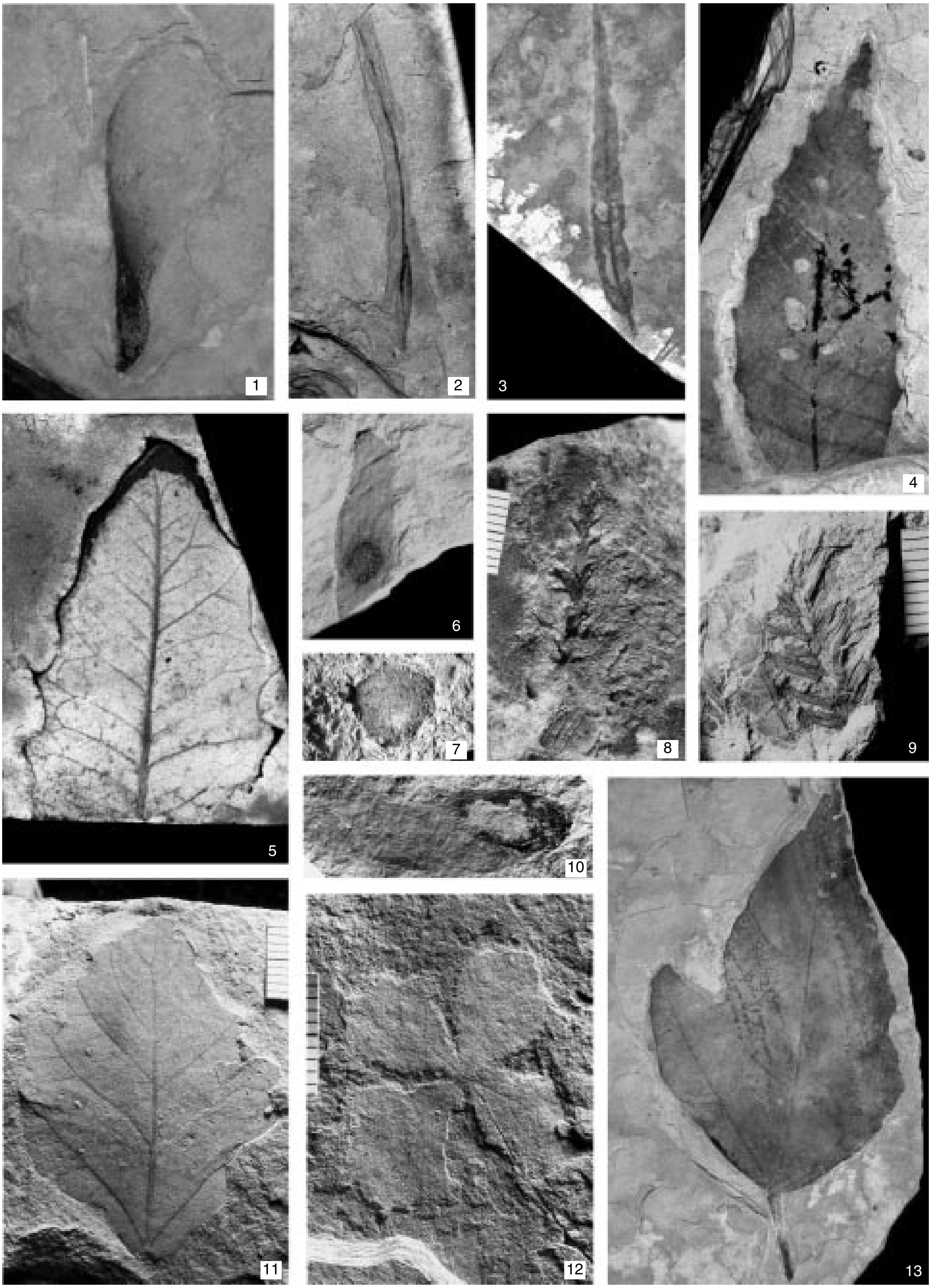
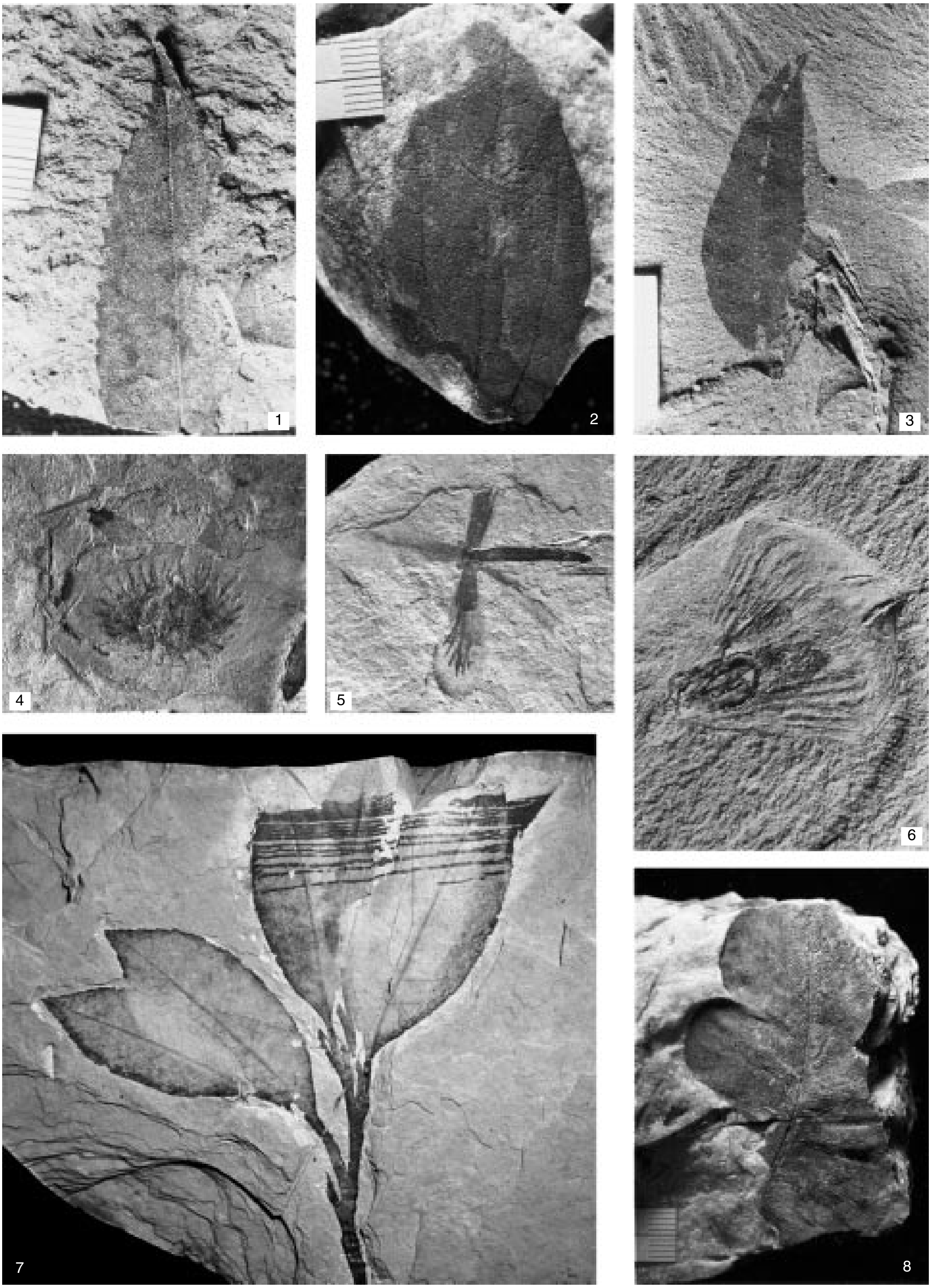


Plate II



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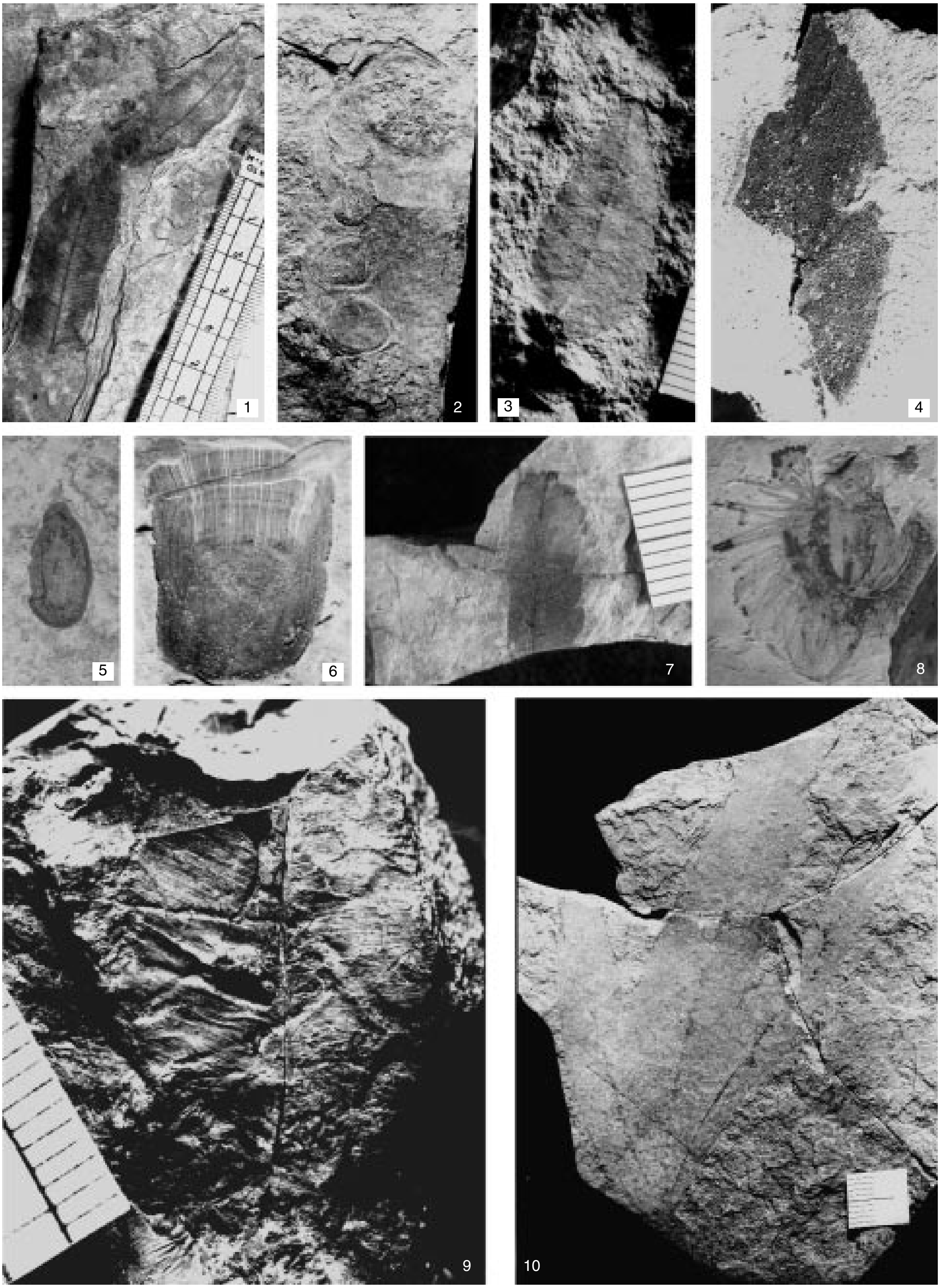

Plate IV

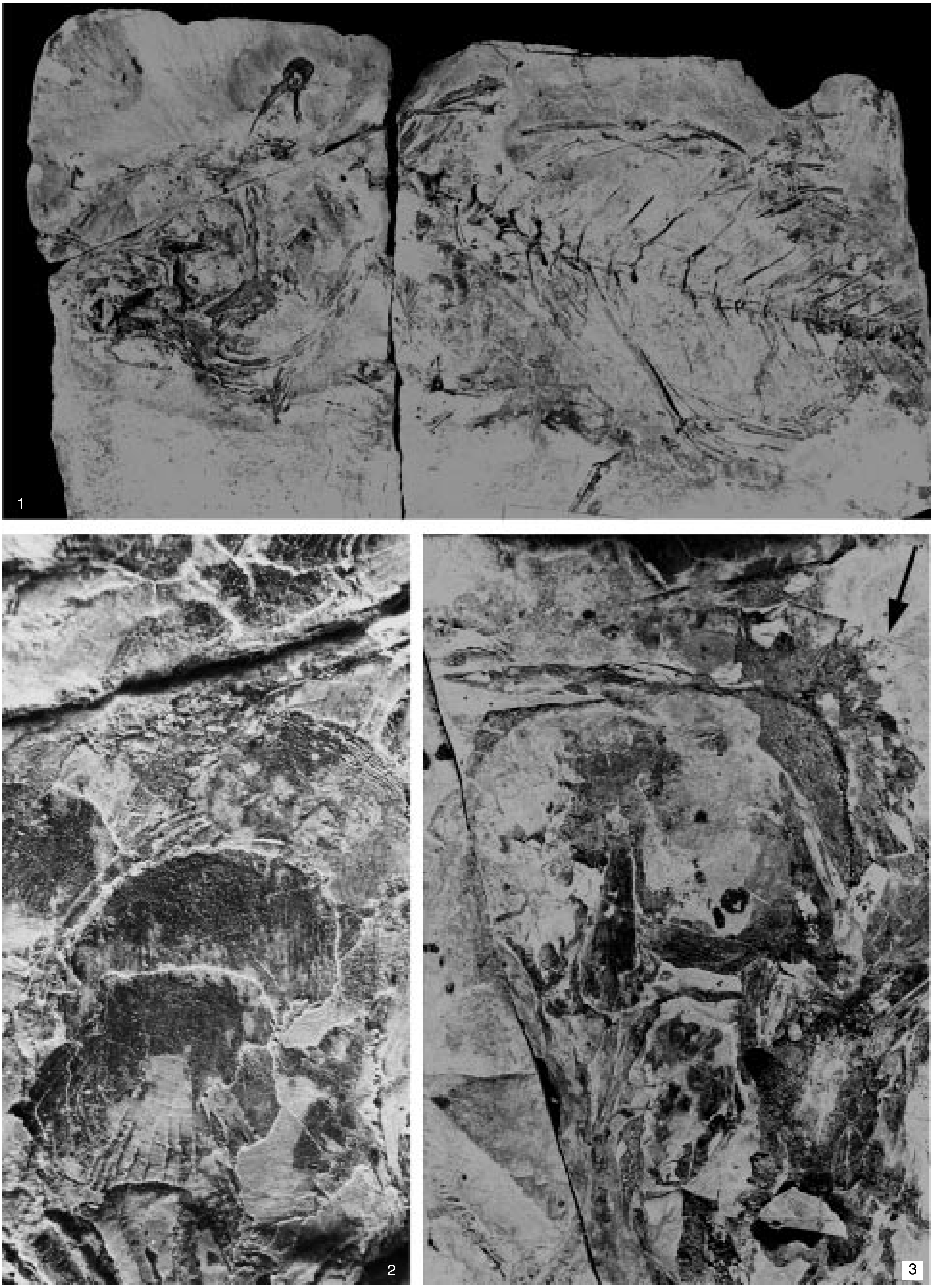

Plate V