

# Forest flora and vegetation of the European early Palaeogene – a review

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An attempt is made to follow the extent of forest types during the Palaeocene and Eocene in time and space over Europe. Problems that hinder producing more detailed maps of potential Eocene vegetation are the different palaeogeographic configuration of land and sea and changing relief due to orogeny, the variation in global climate, atmospheric circulation and the world ocean. The early Palaeogene palaeofloristic sites in Europe are widely spaced and the data so far obtained are of varying quality from one site to another. The differences between zonal, intrazonal (azonal) and extrazonal formations and impact of precipitation must be considered. Objective definitions of units based on diversity percentages of components are still to be elaborated. The macropalaeobotanical data thus far available allow us to distinguish intuitively three zonal vegetation types: 1) Broad-leaved evergreen/semi-evergreen quasi-paratropical forest with a high diversity of woody angiosperms related to tropical families, ferns and a low diversity of conifers (mostly *Doliosstobus*), 2) Broad-leaved nothophyllous evergreen forest with evergreen Fagaceae, Lauraceae, Altingiaceae, Myrtaceae and some conifers (*Pinus*, *Doliosstobus*, *Cephalotaxus*) and 3) Polar deciduous to mixed mesophytic forest with well diversified angiosperms predominantly deciduous and moderate representation of *Ginkgo*, conifers and ferns. Intrazonal (azonal) formations include riparian gallery forests, coal-forming swamp forests, and poorly developed mangroves with marginal freshwater wetland/aquatic vegetation. The Eocene extrazonal vegetation is less distinct in Europe, consisting probably of pine forests in high mountains and lowland sclerophyllous scrub on specific substrates. • Key words: Palaeocene, Eocene, Europe, flora, vegetation, phytogeography.

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This account is an extended contribution to the symposium on Palaeogene floras and global change events held at the 7<sup>th</sup> European Palaeobotany and Palynology Conference in Prague 2006. It revises and expands on the general overview of Eurasian floras by Collinson & Hooker (2003) by providing significant detailed and up-to-date information and preliminary vegetation reconstructions for the European Palaeogene. The paper is based entirely on the macrofossil record and does not consider palynological data. It is rather incomplete because early Palaeogene paleobotanical sites in Europe are rather widely spaced and their floras not always properly worked out. The review of the floras follows the updated system of Floral Assemblages (= “Florenkomplexe”) published by Mai (1995) with additional references on recent advances in systematic studies, notably of woody plant elements. Reconstructions of ancient forest vegetation are based on approaches considering both foliage physiognomy and the floristic composition.

To assess more objectively the differences between various types of vegetation, a new statistical approach has

been suggested for the Neogene plant assemblages. This approach evaluates proportions of different components, in particular broad-leaved mesophytic dicots in connection with their leaf physiognomy (Kovar-Eder *et al.* 2008). The present attempt is a start for future potential application of a similar approach for the Eocene. It is certainly very incomplete because full analyses of plant assemblages at various sites are mostly hindered due to preservation and the state of taxonomic revisions. Also the role and palaeoecological properties of many early Palaeogene plant elements are uncertain, because they are much more distant from their modern analogues than in the Neogene.

Opinions on climatic proxies during the Palaeocene-Eocene differ according to various authors as well as do views of plant composition at different sites (Golovneva 2000, Uhl *et al.* 2007). Therefore, many of vegetation reconstructions suggested below are oversimplified in this assessment and must be considered only tentative.

## RESULTS

### Floristic analysis and the “Florenkomplex” concept

The European Palaeocene-Eocene flora was reviewed and subdivided according to the bio-provinces by Mai (1995). He suggested a new grouping according to the concept of a “Florenkomplex”, or “Florenbild”, or “Floral Assemblage” introduced by Mai & Walther (1978, p. 168), which is based on floristic properties as well as the stratigraphic position of related floras independent of the environment/vegetation type (hence the term “Komplex”). The present overview follows in general the same concept detailed in Mai & Walther (2000) but stresses the necessity to replace the system of the “Florenkomplex” groups by a more appropriate system in the future. The term “Florenkomplex” uses a pre-occupied term “complex” that is also employed in lithostratigraphy. (Therefore it is replaced by “unit” in the following text). However, revision of the “Florenkomplex” would require a re-definition and re-naming of Mai and Walther’s units. The extent of these units in time and space would need to be updated and more stress should be laid upon more critical re-appraisal of plant elements. Such a revision is beyond the scope of the present paper. The present “state-of-the-art” is summarized in Table 1.

### Atlantic Boreal Province

*European Arctic.* – Mai’s system of “Florenkomplexe” (Mai 1995, pp. 340–342) starts with the northern part of the Atlantic-Boreal bioprovince called also the Greenland Region *sensu* Seward (1931) or the Thule Province *p.p. sensu* Budantsev (1983). This region also includes the Brito-Arctic Igneous Province *sensu* Boulter & Manum (1989) and extends as far southwards as to northern France in the Palaeocene. During the period from the early Palaeocene to the Eocene/Oligocene transition, three units have been recognized in the European Arctic.

The oldest is called “Atanikerdluk”, and is Danian in age. It is represented first of all by well known floras occurring at several sites in western Greenland (Heer 1868, 1869, 1874, 1883; Koch 1963). The assemblage has been called “*Macclintockia-Metasequoia-Cercidiphyllum*” (Koch 1963), the latter element representing obviously the extinct forms also known as the *Trochodendroides-Nyssidium* plant. Additional noteworthy dicots have been recognized as extinct “*Lauraceaephyllum stenolobatus*” with affinities to *Sassafras* (Koch 1963), the *Nordenskioldia-Ziziphoides* plant, *Fagopsiphyllum groenlandicum* (Manchester 1999), *Ushia olafsenii* (Boulter & Kvaček 1989) probably synonymous with *Rarytkinia quercifolia* (Golovneva 2000), *Platanus bella* (Kvaček *et al.* 2001), and *Sloanea ungeri*

(Manchester 1999, Manchester & Kvaček 2009). Among gymnosperms *Ginkgo* and various ancient Cupressaceae (*Metasequoia*, *Mesocyparis*) and Pinaceae (*Pseudolarix*) occur. The other sites of approximately the same age are known also in the Spitsbergen Firkanten Formation (Budantsev 1983, Kvaček *et al.* 1994, Golovneva 2000), and share some endemic elements (*e.g.*, “*Quercus juglandina*”), but differ by the presence of *Torreliia* (Ginkgoaceae) and the lack of *Macclintockia dentata* and *Platanus bella*.

The next unit is called “Antrim” and is dated to the Late Palaeocene. A most representative flora belonging here is that of Isle of Mull (Boulter & Kvaček 1989). It includes the noteworthy *Onoclea* among ferns, new gymnosperms, namely *Amentotaxus*, *Cephalotaxus*(?), *Elatocladus*, and also new angiosperms like *Platanites hebridicus*, *Camptodromites major*, *Davidoidea* and *Calycites ardtunensis* (Crane 1988, Crane *et al.* 1988, Boulter & Kvaček 1989), but differs from the Atanikerdluk unit in scarcity of *Metasequoia*. A few florulas in Ballypallady and Glenarm, Ireland, have several typical conifers, like *Glyptostrobus dunoyeri*, *Cupressoconus machenryii* and *Pinus plutonis* (Boulter & Kvaček 1989). Some others in the Isle of Skye (Poulter *et al.* 2009), Faeroes (Rasmussen & Koch 1963) and elsewhere (Mai 1995) are again rich in *Metasequoia*.

The Eocene floral unit called “Bröggerhalvøya” (Mai 1995) is mainly represented in Spitsbergen (Heer 1870, 1876; Storvola taphoflora *sensu* Budantsev 1983; Golovneva 2000) and includes the Aspelintoppen and Renardodden formations (Schloemer-Jäger 1958; Kvaček & Manum 1993, 1997; Kvaček *et al.* 1994; Uhl *et al.* 2007). Floristic differences from the two older units are not very pronounced (Mai 1995), particularly expressed mainly among angiosperms, where new elements appeared: the *Craigia bronniil/Dombeyopsis* plant (Kvaček *et al.* 2005), *Aesculus longipedunculus*, *Ulmus* (or *Ulmites*), *Platimelis* and *Haemanthophyllum* (Golovneva 2000; Uhl *et al.* 2007). The Renardodden Fm. yielded a new conifer *Taiwania schaeferi* (Schloemer-Jäger 1958). The fern *Coniopteris blomstrandii* (Kvaček & Manum 1993) is also a characteristic element. A similar but poorer late Danian flora is known in north Greenland as the Thyra Ø flora (Boyd 1990). The Eocene Ifsorisok flora of West Greenland belongs also to the unit Bröggerhalvøya, where *Aesculus* and *Ulmus* are lacking (Golovneva 2000) but this flora requires taxonomic revision.

*Western and Central Europe.* – Most west-central European sites of early Palaeogene floras have been grouped (Mai 1995, Mai & Walther 2000) into three Palaeocene units, called Eisleben-Roda, Gelinden and Menat and mostly six Eocene units stretching into late Palaeocene and earliest Oligocene: Reading-Vervins, Belleu-Sheppey, Messel-Selsey, Scheiplitz, Hordle-Zeititz and Bembridge-Spechbach. The oldest unit includes the Eisleben Basin in

**Table 1.** Updated overview of Palaeocene and Eocene Floral Assemblages (“Florenkomplexes” *sensu* Mai & Walther 1978) in Europe. Fm. = Formation.

System	PALAEOGENE					
Series	PALAEOCENE		EOCENE		OLIGOCENE	
Stages	Early (Danian)	Late	Early	Middle	Late	Early
BIOPROVINCE						
1. ATLANTIC BOREAL						
-European Arctic	Atanikerdluk Western Greenland Spitzbergen Firkanten	Antrim Isle of Mull Ballypallady Glenarm Isle of Skye Faeroe Spitzbergen	Ifsorisok	Bröggerhalvøya Aspelintoppen Fm. Renardodden Fm.		
-Western & Central Europe	Eisleben-Roda, Gelinden Ménat	Reading	Belleu-Sheppey	Messel, Eckfeld Geiseltal Helmstedt Scheiplitz	Henigsbury Head Hordle-Zeitz Spechbach-le-Bas Grès à Sabal Brunstatt Staré Sedlo Kučlín	Bembridge Marls
2. TRANSEUROPEAN PARATETHYS	Rusca Montană Dobra Sreća Rusava (Maastrichtian-Danian)			Lábatlan	Girboa-Häring	
3. EASTERN EUROPE		Kamyschin	Volhynian		Amber – “Blaue Erde”	
4. MEDITERRANEAN TETHYS			Montebolca		Célas	

Germany, where several enigmatic leaf morphotypes are known besides perhaps more accurately recognizable *Comptonia*, *Myrica*, *Boehmeria* and Araliaceae (Friedrich 1883). Much more reliable are taxa based on fruits and seeds (Knobloch & Mai 1986, Mai 1995), which belong to Theaceae (*Eurya*, *Palaeoschima*, *Protovisnea*), Hamamelidaceae (*Exbucklandia*, *Klikovispermum*), *Saurauia*, *Mastixiopsis*, *Iodes*, Juglandaceae (*Caryanthus*, *Platycarya*); some ancient elements survived from the Cretaceous (*e.g.*, *Walbeckia*, *Barclayopsis*, *Laramisemen*). The florulas from Roda, and adjacent Schwarze Mina are similar. The dating relies on the pollen zones (Kruttsch 1967).

The famous but yet unrevised Gelinden flora (Saporta & Marion 1873, 1878) is mostly known as a foliage assemblage dominated by extinct Fagaceae of the *Ushia* and *Dryophyllum*-type, Platanaceae (*Dewalquea* – Kvaček *et al.* 2001) and extinct *Macclintockia* that connects this site with the Arctic. Many broad-leaved morphotypes remain enigmatic. Palms and a few conifers (*Pinus*, Cupressaceae) have been indicated.

The Ménat unit includes the type locality, Ménat,

France (Laurent 1912, Piton 1940), which is noteworthy by an association of *Platanus schimperii* – *Quercus subfalcata*, and the extinct *Palaeocarpinus-Craspedodromophyllum* plant (Betulaceae; Crane 1981, 1989). Juglandaceae – *Casholdia* (Crane & Manchester 1982) and a *Sassafras*-like morphotype are known. Similar plant assemblages occur at Sézanne (France), Gonna-Walkmühle (Germany) as well as the Herne Bay and Woolwich beds (England) typical of a mixture of temperate extinct elements (Ulmaceae, deciduous *Quercus*, Cercidiphyllaceae, Juglandaceae) and palaeotropical elements (Icacinaeae, Symplocaceae, Theaceae, Lauraceae, *Steinhauera*, *etc.* – see Mai 1995).

The latest Palaeocene Reading flora in southern England (for dating see Collinson *et al.* 2003) shares similar aspects with Ménat and also many elements, *e.g.* *Platanus schimperii*, *Sassafras* – like “*Lauraceaephyllum stenobatus*”, *Nyssidium-Trochodendroides* (Crane 1978), *Palaeocarpinus-Craspedodromophyllum* (Crane 1981), *Casholdia* (Crane & Manchester 1982). Many elements from the Reading and Woolwich formations have been based on

carpological material as summarized by Chandler (1961a, 1964), where Lauraceae, Icacinaceae, Mastixiaceae and Theaceae are well documented. Collinson & Crane (1978) added *Rhododendron*. Floras from the Riestedt and Bornstedt basins in Germany, where new elements appear (*Carya*, *Dryophyllum sprengelii*, *Actinodaphne germari* – Friedrich 1883, Walther in Mai & Walther 1985, Mai 1995) are also assigned to the same unit.

The Early Eocene London Clay flora has been assigned to the unit Belleu-Sheppey (Mai 1995). It is the richest Palaeogene assemblage in Europe (Reid & Chandler 1933; Chandler 1961a, 1964, 1978; Collinson 1983) comparable only with the Middle Eocene Nut Beds flora in Oregon (Manchester 1994). Most elements are based on pyritized fruits and seeds collected at several sites along the southern coast of England. The flora is poor in conifers (*Quasisequoia*, and some other extinct Cupressaceae, *Doliosstrobos*, Cephalotaxaceae, *Pinus*) but extremely rich in angiosperms. Only a smaller part of elements can be assigned to modern genera. Collinson (1983) analyzed the present status of the flora and issued floral lists of individual sites – Sheppey, Bognor, Herne Bay and a few others.

Representatives of over 150 genera are treated by her and assigned to mostly subtropical and tropical families, such as Anacardiaceae, Annonaceae, Arecaceae, Burseraceae, Cornaceae, Dilleniaceae, Euphorbiaceae, Flacourtiaceae, Icacinaceae, Lauraceae, Lythraceae, Magnoliaceae, Menispermaceae, Nyssaceae, Ranunculaceae (Pigg & DeVore 2005), Rhizophoraceae, Rutaceae, Sabiaceae, Sapindaceae, Sapotaceae and Vitaceae. A few elements, such as Cupressaceae, Cercidiphyllaceae, Platanaceae and Fagaceae are documented by permineralized wood (Collinson 1983). Many genera are extinct but some are still extant, e.g. South African *Curtisia* (Manchester *et al.* 2007b). There is almost no information about fossil angiosperm foliage for floras of this age. Slightly younger sites in Alum Bay (leaf beds with mostly leaf impressions) provided only limited taxonomic information (Crane 1977).

The Belleu flora in France (Watelet 1866, Frittel 1924) is preserved also as leaf impressions and requires taxonomic revision. According to the illustrations, besides conifers (*Doliosstrobos*?), only *Comptonia*, large-leaved probably evergreen Fagaceae, Lauraceae and some more enigmatic morphotypes can be recognized.

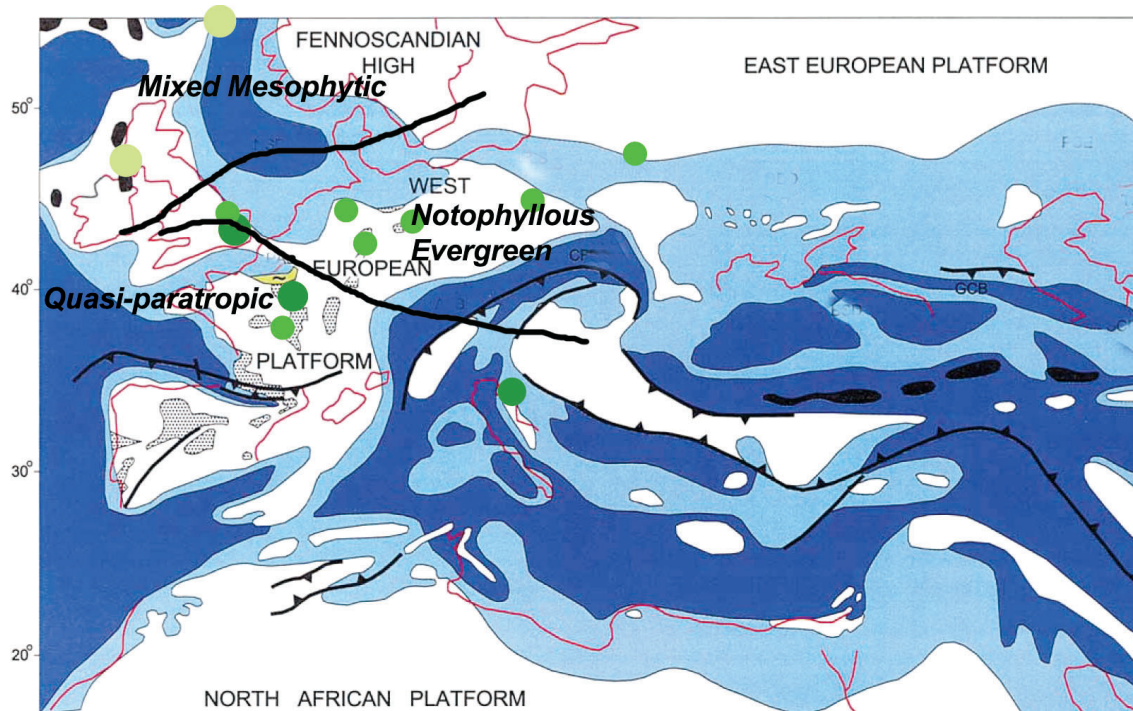
The Middle Eocene unit Messel-Selsey (Mai 1995) is typified by two floras – Selsey in England and Messel in Germany and includes also the sites at the Alum Bay, Boscombe and Bournemouth in England, floras in the Paris Basin and Geiseltal, Eckfeld and Helmstedt in Germany. The late Early-Middle Eocene Selsey flora (Chandler 1961b) and other assemblages from Bracklesham Bay in England are prevailingly herbaceous including *Nypa*,

*Limnocarpus*, *Selseycarpus* (Collinson 1996) and *Cyclanthus* (Smith *et al.* 2008). Woody elements are rare – *Doliosstrobos* (*Araucarites selseyensis* – Chandler 1961b), extremely rare cones of *Pinus*, Menispermaceae, Rutaceae, mastixioids and Theaceae (Collinson 1996). More diverse elements are represented by the carpological material from the Lower Bagshot flora of Dorset (Chandler 1962) and the Bournemouth – Boscombe floras in the Hampshire Basin (Chandler 1963). Besides macrofossils of conifers (*Araucarites sensu* Chandler = *Doliosstrobos* – Bůžek *et al.* 1968, *Cupressistrobos sensu* Chandler = *Chamaecyparites* – Kvaček 1971, *Sequoia sensu* Chandler = *Quasisequoia* – Kunzmann 1999) and palms a great variety of subtropical-tropical woody dicots of the families Moraceae, Menispermaceae, Altingiaceae (*Protoaltingia sensu* Chandler = *Steinhauera* – Mai 1968), Magnoliaceae, Annonaceae, Lauraceae, Icacinaceae (*Natsiatum sensu* Chandler = *Palaeohosiea* – Kvaček & Bůžek 1995), Theaceae, Flacourtiaceae, Nyssaceae, Cornaceae, Clethraceae, Symplocaceae and others have been indicated.

The Alum Bay and Bournemouth leaf assemblages, which yielded compressions with preserved cuticles, are still not fully known in respect of taxonomical composition (Crane 1977, 1978) because fossils leaves of uniform morphology have rarely preserved epidermal features and even then their affinities remain obscure. The pioneer studies by Bandulska (1923, 1924, 1926, 1928, 1931) were complemented by new information (Crane 1978) and revised by subsequent epidermal studies in other Eocene floras (Rüffle 1976, Rüffle *et al.* 1976, Rüffle & Jähnichen 1976, Mai & Walther 1985, Wilde 1989, Knobloch *et al.* 1996, *etc.*). Important index fossils were identified by Bandulska, like *Doliosstrobos* (*Araucarites goeppertii sensu* Bandulska), *Rhodomyrtophyllum* (*Rhodomyrtus sinuata sensu* Bandulska), *Dicotylophyllum spiculatum* (?*Stemonurus*), “*Nothofagus*” *stopesae*, *Laurophyllum hirsutum*, *L. syncarpifolium* (*Litsea bournensis* Bandulska and *Cinnamomum wonnacottii* Bandulska) and others.

The Middle Eocene site Messel in Hesse (Collinson 1982, 1986, 1988; Wilde 1989, 2004, 2005; Collinson *et al.* 2010) is by far the most promising, the material is well preserved, but unfortunately still not entirely documented. The flora includes a few conifers (e.g., *Doliosstrobos*, *Cephalotaxus*), various dicots with predominant Lauraceae and abundant *Palmae*. Taxonomic studies of the Messel assemblage have recently progressed considerably and include studies of Rutaceae (Collinson & Gregor 1988), Juglandaceae (Manchester *et al.* 1994), *Cedrelospermum* (Ulmaceae, Wilde & Manchester 2003), Araceae (Wilde *et al.* 2005), Anacardiaceae (Manchester 1994) including *Anacardium* (Manchester *et al.* 2007a), *Cyclanthus* (Cyclanthaceae, Smith *et al.* 2008), and additional groups (Collinson *et al.* 2010). A similar but less diversified flora is preserved in the same sedimentary setting of a maar lake





**Figure 1.** Phytogeographical map of the European Early-Middle Eocene indicating boundaries between polar deciduous, subtropical evergreen and quasi-paratropical forests.

deposit at Eckfeld (Wilde & Frankenhäuser 1998). It shares the ferns *Osmunda*, *Lygodium*, *Acrostichum*, and “*Rumohra*”, as well as Juglandaceae (e.g., *Hooleya*, Frankenhäuser & Wilde 1994) with Messel but differs by the abundance of *Comptonia* (Wilde & Frankenhäuser 1999), the enigmatic spiny leaves of *Pungiphyllum* (Frankenhäuser & Wilde 1995), and *Canarium*, the rare occurrence of conifers (*Tetraclinis*) and Lauraceae, and the lack of *Doliodendron*, *Fagaceae*, *Rhodomyrtophyllum* and others.

The Middle Eocene part of the Geiseltal section in Germany including the coal seams (Barthel 1976, Mai 1976, Rüffle 1976, Rüffle & Jähnichen 1976, Rüffle *et al.* 1976) is now separated into the Scheiplitz unit (Mai & Walther 1983, 2000) together with the type localities Scheiplitz and Dörstewitz. The fern-like cycad *Eostangeria* (Barthel 1976) is important, occurring with its vicarious relative in the Eocene of North America (Kvaček & Manchester 1999), the earliest occurrence of *Eotrigonobalanus* (Kvaček & Walther 1989) associated with other extinct *Fagaceae* of the *Dryophyllum*-type, various Lauraceae, Theaceae (*Gordonia*, *Schima*, *Ternstroemites*), Myricaceae and Myrtaceae (*Rhodomyrtophyllum*) as well as various *Palmae* (Mai & Walther 2000).

The Helmstedt brown-coal flora was first reported by Wilde (1989). The macrofossil spectrum includes common *Doliodendron*, typical Eocene plants including *Laurophyllum syncarpifolium*, ?*Stemonurus*, *Apocynophyllum echitiforme*, cf. *Dryophyllum album* and *Sterculia labrusca*.

In the periphery of the Weissester Basin, two floras – Dörstewitz and Scheiplitz typify the Floral Assemblage Scheiplitz (Mai & Walther 2000), which deviates from the previous one by predominantly xeromorphic narrow and small-leaved Lauraceae, *Fagaceae* besides *Pinus*, *Doliodendron*, *Comptonia* and palms.

The Middle Eocene sites near and within Paris (Trocadero, Puteau, Mont Rouge – Saporta 1879, Watelet 1866) are noteworthy by the occurrence of the xeromorphic *Tetraclinis brachyodon* and *Comptonia schrankii* (syn. *C. dryandriifolia*). The flora is so far very inadequately known (*Ottelia parisiensis* Saporta, 1879, *Nerium parisiense* Saporta, 1879) and requires a new revision. *Sabalites*, *Nypa*, *Sterculia labrusca*, and various enigmatic Lauraceae and evergreen *Fagaceae* are present.

The late Middle to Late Eocene unit Hordle-Zeitz reflects a lowering of diversity and the proportion of subtropical-tropical elements (Collinson & Hooker 1987, Mai 1995) due to climatic deterioration. The unit comprises besides type sites Hordle in England and Zeitz in Germany also many others, such as Hengistbury Head, Mudeford in the Hampshire Basin (Chandler 1963, 1964), several sites in the Loire Basin, the so-called “Grès à *Sabal*” (Frittel 1922), Staré Sedlo flora in NW Bohemia (Knobloch *et al.* 1996) and a number of individual sites in the Weissester Basin and its periphery (Mai & Walther 1985, 2000).

Mai & Walther (2000, p. 45) characterize this unit as evergreen notophyllous vegetation type with some

members of the tropical families and a few predominant elements, like *Quasisequoia coutsiae*, *Doliosobus taxiformis*, *Rhodomyrtophyllum reticulosum*, *Eotrigonobalanus furcinervis*, *Symplocos kirstei*, *Retinomastix glandulosa*, *Sterculia labrusca* and *Epacridicarpum* sp. div. Further characteristic elements of this unit, partly new immigrants are: *Actinodaphne pseudogermari*, *Becktonia hantonensis*, *Eomastixia bilocularis*, *Ficus lucida*, *Gordonia saxonica*, *G. minima*, *Laurophyllum syncarpifolium*, *L. hirsutum*, *Mastixicarpum crassum*, *Nyssa oviformis*, *Platanus neptuni* forma *fraxinifolia*, *Saurauia crassisperma*, *Steinhauera subglobosa*, *Sterculia subovoidea*, *S. labrusca*, *Ternstroemia bartonensis*. Newly recognized are *Taxodium*, *Glyptostrobos* and some partly deciduous dicots – *Ampelopsis*, *Carya*, *Cephalanthus*, *Pentapanax*, *Sambucus*, *Trigonobalanopsis* and others (Mai & Walther 2000). Dating is based mainly on pollen phytostратigraphy – Pg zones 17 and 18 *sensu* Krutzsch *et al.* (1992).

The Bembridge-Spechbach unit includes sites at or near the Eocene-Oligocene boundary. The most prominent floras of this time interval are undoubtedly those of the Bembridge Marls (including the Insect Limestone) and the immediately underlying Bembridge Limestone (Reid & Chandler 1926; Collinson 1983, 1992; Collinson *et al.* 2010). The Insect Limestone is dated to the very latest Eocene (Hooker *et al.* 2007, 2009; Collinson *et al.* 2010). The floristic content is predominantly aquatic herbaceous (*Typha-Acrostichum* association *sensu* Collinson 1983). Yet noteworthy arboreal elements are preserved in the Insect Limestone – *Doliosobus*, *Hooleya*, *Engelhardia* (*Palaeocarya*), *Apocynospermum*, and *Raskya* (Manchester & Hably 1997) besides Lauraceae, *Ziziphus*, *Palibinia* and some more obviously woody dicots (Mai 1995).

The sites Spechbach-le-Bas, Brunstatt and other floras in Alsace belong to the same units according to Mai (1995). He also maintains the same position for a classical site Kučlín in North Bohemia (Ettingshausen 1866, 1868, 1869). The latter flora is much more diversified and shares several elements with that of Bembridge (*Doliosobus*, *Apocynospermum*, *Hooleya*, *Engelhardia*, *Ziziphus*) but differs in a number of elements common to the previous units including *Eotrigonobalanus*, *Palaeohosia*, *Platanus neptuni*, *Cedrelospermum*, *Sloanea* and others of the Eocene-Early Oligocene floras in the Paratethys province – *Ailanthus*, “*Acer*” *sotzkianum* (Kvaček 2002b).

### Transeuropean Paratethys Bioprovince

Early Palaeogene sites are in this area very scanty. Only three units have been recognized: one Palaeocene called Rusca Montana – Rusava and two Eocene: Lábatlan and Gîrbou – Häring. The site Rusca Montana in Transylvania has not been revisited since the last account by Petrescu &

Duša (1980). It has been assigned to the Danian by some authors (Baikovskaya 1965; Givulescu 1966, 1968; Mai 1995) but to the Maastrichtian by others (Petrescu & Dusa 1970, 1980; J. Kvaček & Herman 2004). The flora has been the focus of interest of several palaeobotanists (Tuzson 1913, 1914; Baikovskaya 1965; Givulescu 1966, 1968) because it shares some noteworthy plants with the late Cretaceous flora of Grünbach, namely *Sabalites longirachis* and *Pandanites trinervis* (J. Kvaček & Herman 2004). Gleichenoid ferns and platanoid dicots stress also the connection with the floras of Grünbach and South Bohemian Upper Cretaceous (Herman & J. Kvaček 2007). The peculiar morphotype assigned to *Proteophyllum decorum* connects the flora with the Cenomanian of the Czech Republic. Another site Dobra Sreća, eastern Serbia (Pantić & Nikolić 1955) belongs according to Mai (1995) to the same unit because of its ancient flora (*Aenigmatophyllum*, *Dryophyllum*, *Dewalquea*, *Myrtophyllum*, *Credneria* a.o.).

The carpological assemblage of Rusava, Solán Formation in the flysch of South Moravia (Knobloch & Mai 1986) dated into Maastrichtian to Danian is rich in ancient extinct elements documented by *Klikovispermum* (Hamamelidaceae), *Valvaecarpus* (Cyrillaceae), *Caryanthus* (Juglandaceae), *Protovisnea*, *Palaeoschima* (Theaceae) and rare modern genera (*e.g.* *Boehmeria*, *Eurya*).

The Middle Eocene unit Lábatlan is developed mainly in Hungary. The type locality Lábatlan in the Dorod-Tata basin (Kovács 1961) shares a few elements with Messel, namely *Phoenicites*, a *Pterospermum*-like Malvaceae (“*Byttneria*” *apiculata* or *Byttneriophyllum sensu* Wilde) and a legume (“*Eucalyptus*” *sensu* Kovács), but affinities of most of the leaf fossils remain doubtful. Poorly preserved cuticles suggest occurrence of Juglandaceae foliage instead of Fagaceae (Knobloch *et al.* 1996) and the affinity is corroborated by a co-occurring *Carya*-like fruit (Z. Kvaček, personal observation). Much more diversified floras are in the Tatabánya brown-coal basin. Most of the elements are widely distributed elsewhere in Europe, including *Eotrigonobalanus*, various *Palmae* including *Nypa*, *Engelhardia* (*Palaeocarya*), and *Ziziphus*. A new site Csordakút (Erdei & Rákosi 2009) includes *Daphnogene*, cf. *Eotrigonobalanus*, *Cedrelospermum*, *Myrica* and *Comptonia*, legumes, *Ziziphus*, *Sloanea* and *Smilax*. The revision of several other preliminarily studied floras (Andreánszky 1955, Kovács 1968) is needed (see Hably 1985, 2006). The nearest relations are probably with the next unit Gîrbou – Häring (Erdei & Rákosi 2009) and Selsey-Messel (Mai 1995, p. 383).

The Late Eocene (to earliest Oligocene) unit Gîrbou – Häring is rather heterogenous and not well characterized. Mai (1995) stresses its subxerophilous aspect valid at least for some sites. The leaf impression flora of Gîrbou in Transylvania, Roumania (Petrescu *et al.* 1976, Petrescu & Givulescu 1987) is dominated by legumes including a large-leaved *Dolichites* (= *Dioclea sensu* Petrescu *et al.*),

evergreen Fagaceae (?*Eotrigonobalanus*, ?*Trigonobalanopsis*), Lauraceae and includes also *Acrostichum*, *Ziziphus*, *Comptonia schrankii* and ?*Pungiphyllum* (“*Ilex*” *praeaquifolium* Petrescu *et al.*, 1976). The lack of cuticles prevents a more exact characterisation, though a domination of sclerophyllous and subhumid elements is obvious.

The classic site Håring in Tyrol, Austria (Ettingshausen 1853, Butzmann & Gregor 2002) bears partly sub-xerophilous character as well, expressed by *Tetraclinis brachyodon*, a variety of legumes (incl. *Mimosites haeringianus*) and various partly small-leaved so far enigmatic dicot morphotypes. Conifers (*Doliosobus*, *Chamaecyparites*, *Pinus*) and palms are common. Identifiable dicots belong to *Engelhardia* (*Palaeocarya*), *Comptonia schrankii*, *Myrica longifolia*, *Ziziphus*, *Daphnogene*, *Cedrelospermum*, and *Ailanthus*, many morphotypes should be still taxonomically resolved. In my opinion recently indicated *Taxodium balticum*, *Buxus egeriana*, *Nyssa altenburgensis*, and *Apocynophyllum helveticum* (Butzmann & Gregor 2002) are misidentifications. Besides the assemblage from the bituminous limestone Ettingshausen (1853) illustrated a few large-leaved morphotypes (Lauraceae, *Eotrigonobalanus*) collected in another layer close to the coal seam. The two different aspects of the Håring flora are easily explained by a different habitat and substrate.

Several other sites with a similar aspect have been described from Bulgaria at Mesta Graben (Palamarev *et al.* 1999), in the Rhodopes (Palamarev & Petkova 1975, Černjavská *et al.* 1988), Serbia (Pantić & Mihajlović 1985, Mihajlović 1985), and Macedonia (Mihajlović & Ljubotenski 1994). According to Palamarev (1973) a carpo-flora from Rudnik near Burgas has clear relations to the Eocene of Geiseltal and England because of noteworthy elements *Palaeonymphaea*, *Becktonia*, *Stephania*, *Gironiera*, *Zanthoxylon*, *Iodes* and *Burtonella* besides various evergreen Lauraceae and Fagaceae. New biostratigraphic data (R.F. Sachsenhofer, personal communication) assigned also the Socka Beds at least partly to the Late Eocene, namely the classic site, from where the famous Socka flora was described (Unger 1850). Recent revisions indicate the presence of *Doliosobus* (Kunzmann 1999), *Tetrapteris* (Hably & Manchester 2000), and *Sloanea* (Hably & Kvaček 2008) but the flora requires a full revision. There are more elements in common with the Early Oligocene Tard Clay floras in Hungary (*e.g.* Hably 1979, Kvaček & Hably 1998) and also the latest Eocene floras in the Boreal province (“*Acer*” *sotzkianum* at Kučlín).

## Eastern Europe

As stated by Mai (1995), sites with macrofloras in the East European early Tertiary are scanty and afford a small addition to the floral evolution, although they were used to in-

crease the resolution of transcontinental floral development in general [Kryštofovich (1955 – for discussion on the Poltava type flora see Zhilin (1989)]. For the late Palaeocene-Middle Eocene, the Kamyshin type flora [or *Ushia* unit *sensu* Zhilin (1986)] is important and can be characterised by variable foliage of *Ushia*, Lauraceae and *Dewalquea gelindensis*. Noteworthy is an endemic plant *Oxycarpia bifaria* interpreted as *Nothofagus*-like cupules (Krassilov *et al.* 1996). The Eocene Volhynian (Drevlyany) unit in Ukraine contains *Doliosobus*, *Pinus*, *Macclintockia*, *Eotrigonobalanus*, *Comptonia schrankii*, palms including *Nypa* and is hardly differentiated from the contemporaneous floras in Western Europe (Mai 1995). The Late Eocene-Early Oligocene Baltic unit represents the famous “Amber Flora” from the Baltic “Blaue Erde”. More than 700 plant species have been described (*e.g.* Conwentz 1886, 1890; Czecczott 1961) but a full interpretation is still not available. The source of amber could be a conifer, but putative “*Pinus succinifera*” recently has been rejected (Mai & Schneider 1988). Fagaceae and palms are commonly reported besides a number of other angiosperm families based on flowers. The main collection was destroyed during the Second World War.

## Mediterranean Tethys Bioprovince

In the South European area Mai (1995) recognized only two units – the Early-Middle Eocene Montebolca unit and the latest Eocene Célas unit. Leaf epidermal studies have not been carried out at any of the sites and most of the floristic data are based on leaf impressions.

The unit Montebolca is typified by the Ypresian site of Monte Bolca (Mons Bubulca), north of Verona in Italy. This site is a world “Lagerstätte” known particularly for fish fauna (Bellwood 1996), large fossils of palms and large-leaved dicot morphotypes the affinities of which are still equivocal. Mai (1995) lists presence of palms, legumes and probable representatives of Myrtaceae, Bombacaceae, Sterculiaceae, Moraceae, Myricaceae, among identifiable elements also *Doliosobus*, *Ziziphus*, *Dombeyopsis* and various lauroids, partly scattered in other sites in northern Italy near Verona. The second site of this unit is Monte Promina (today Siverič) in Croatia (Ettingshausen 1855), from where a similar plant assemblage with *Doliosobus*, *Daphnogene*, *Comptonia schrankii*, *Myrica longifolia*, *Ziziphuis ziziphoides*, *Sterculia labrusca* and other, mostly unidentifiable, morphotypes are known. Noteworthy is the occurrence of *Nelumbo* and various ferns. Mihajlović (1990) considers this type of subxerophyllous floras to be generally distributed in the Tethys phytogeographical province during the Eocene-Early Oligocene. The unit Célas is typified by impression flora of Célas in the Alés Basin in southern France (Laurent 1899). The dominant el-



ement is a variable large-leaved malvalean morphotype assigned as a rule to *Ficus* (“*Ficus*” *marionii*) or some other genera. Other elements typical of Late Eocene-Early Oligocene floras in southern Europe are present – *Comptonia schrankii*, *Ziziphus ziziphoides*, *Ailanthus*, *Engelhardia* (*Palaeocarya*), legumes and other partly enigmatic morphotypes (“*Ilex*” *pachynervis*, “*Dodonea*” *saportana*). Célas is the type locality of *Doliosobus*, *Doliosobaceae* (Kvaček 2002a), which is a very typical conifer rarely crossing the Eocene-Oligocene boundary (e.g. Tard Clay in Hungary, Mera in Roumania), being replaced in the terminal Eocene by other conifers elsewhere (e.g. by *Juniperus* at Čermníky in North Bohemia – Kvaček 2002c). Mai (1995) maintains that the flora of Sarreal/Tarragona in Spain (Fernandez-Marron 1973a, b; Hably & Fernandez-Marron 1998) belongs to the same unit and possesses similar significance.

## Vegetation reconstructions

### Zonal vegetation

*Polar deciduous to mixed mesophytic forest.* – The coldest assemblages correspond to the polar deciduous to mixed mesophytic forest, as exemplified by the Eocene assemblages of Spitsbergen and Isle of Mull within the Brito-Arctic Igneous Province. This formation is characterized by a dominant broad-leaved deciduous component, usually with a large size of the leaf lamina, with rare *Ginkgo* and mesophytic conifers – *Amentotaxus* and extinct cupressoids.

The Isle of Mull assemblages (Boulter & Kvaček 1989) are dated on the boundary between Palaeocene and Eocene. Two of them are partly mesophytic. That from Ardtun comes from the massive lowermost bed of fossiliferous limestone (basal leaf bed *sensu* Gardner 1887). According to Boulter & Kvaček (1989), in this assemblage *Corylites* (probable foliage of *Palaeocarpinus*) and *Trochodendroides* (probable foliage of *Nyssidium*), both deciduous, predominate. Also additional components are mostly deciduous (e.g., *Davidoidea*, *Camptodromites*, *Juglandiphyllites*, and *Fagopsiphyllum*). Some probably belonged to the riparian intrazonal plants, e.g., *Platanites*, *Vitiphyllum*). Gymnosperms are represented by deciduous *Ginkgo* and evergreen *Amentotaxus* and others, all much less frequent than deciduous woody eudicots. The latter are mostly of doubtful affinities and over 90% of the components are hardly assignable to the modern genera form. Another more or less mesophytic plant assemblage comes from Ballypalady, Ireland. It is dominated by conifers, particularly Pinaceae and cupressoids. Among arborescent dicots, the deciduous component prevails: cf. *Platanus* (*Glandulosa* *neptuni*, *Ushia* and *Camptodromites* (Boulter & Kvaček 1989, p. 126).

The Spitsbergen assemblages (Schweitzer 1974; Buidantsev 1983; Kvaček & Manum 1993, 1997; Golovneva 2000, 2002 *etc.*) are of early Palaeocene to late Eocene age. Those from the Sturvola (= Aspelintoppen) Formation are Early Eocene in age and are included here. Several local sites are assigned to this formation (Kvaček *et al.* 1994, table 2) and in general composition they are similar each other. The more or less mesophytic component of the plant assemblages includes *Ginkgo*, *Ushia*, *Corylites*, *Craspedodromophyllum* and *Aesculus*, to name the most characteristic plants, while *Metasequoia*, trochodendroids and ulmoids belong to the intrazonal part. The components are prevailingly broad-leaved deciduous and mostly show distant or quite unknown affinities to modern genera with rare exceptions.

*Mid-latitude notophyllous broad-leaved evergreen forest.* – This forest type is best documented at Hordle, England (late Eocene), Eckfeld in Germany (Middle Eocene), less completely at Lábatlan in Hungary (Middle Eocene) and Kučlín in north Bohemia (late Eocene). It is characterized by dominating Lauraceae, common Juglandaceae, Ulmaceae (*Cedrelospermum*), Malvaceae (“*Ficus*” *daphnogenes*, “*Byttneria*” *apiculata*), Leguminosae, rare conifers (*Tetraclinis*, partly azonal *Doliosobus*, *Cephalotaxus*) and various accessory exotic and extinct elements (e.g., *Pungiphyllum*, *Ailanthus*, *Sloanea*, Icacinaceae, Menispermaceae, Vitaceae). The foliage size category is noto- to microphyllous.

The late Eocene diatomite Kučlín in North Bohemia (Kvaček 2002a) differs in new immigration of *Platanus* (*Glandulosa* *neptuni* (Kvaček & Manchester 2004), *Raskya* (Manchester & Hably 1997) but sharing with Messel a number of extinct plants (e.g., *Doliosobus*, *Hooleya*, “*Ficus*” *daphnogenes*). The drawback of this classical site is poor preservation of leaf fossils representing impressions without cuticles. Zonal parts of the Zeitz flora (Mai & Walther 1985, 2000), rich in mastixioids, undoubtedly belong to this formation, although it may be that many elements are riparian (see below).

*Mid-latitude quasi-paratropic rain forest.* – The best documented vegetation of this type is known from the Early Eocene London Clay fruit and seed flora (Collinson 1983). The considerable part of this highly allochthonous assemblage can serve for mesophytic components. The forest can be characterized, as suggested by Collinson (1983) by polydominating families Annonaceae, Cornaceae, Icacinaceae, Lauraceae, Menispermaceae, Palmae, Rutaceae, Vitaceae *etc.* Conifers are rare – *Tetraclinis*?, *Doliosobus*?, *Quasisequoia*?, various mesophytic components, mostly with tropical affinities are present: Annonaceae, Lauraceae, Cornaceae, Flacourtiaceae, Icacinaceae, Menispermaceae, Vitaceae and some Palmae.



Mai (1995) and Wilde (2005) also considered the Mes-sel flora to be paratropical due to floristic composition (abundant Araceae, palms). However, the notophyllous size category prevails among partly evergreen (most Lauraceae, Myrtaceae) and partly deciduous woody dicots (Ulmaceae, Araliaceae), contrary to the comparable paratropical vegetation, *e.g.* in Hainan and elsewhere in South-east Asia, today.

Probably a paratropical kind of vegetation is reflected in the large-leaved Early Eocene Belleu assemblage from Paris environs (Watelet 1866), which is unfortunately little documented taxonomically. Foliage size category is macrophyllous to notophyllous.

Whether or not the Early Eocene assemblage of Montebolca (Mai 1995) belongs to this category is doubtful, although quite logical. The collections from this site require revisions.

## Eocene Intrazonal vegetation

*Polar coal-forming and riparian deciduous forest.* – This is particularly known from Spitsbergen (Aspelintoppen Fm. and Renardodden), also a part of the Mull assemblage consists of intrazonal elements. Swamp conifers – *Metasequoia*, Taxodiaceae and some broad-leaved deciduous obviously intrazonal angiosperms (*e.g.*, *Trochodendroides-Nyssidium* and *Zizyphoides-Nordenskiöldia*), characterize the forests.

In the Mull assemblage, coal-forming elements are represented by a taxodioid conifer *Elatocladus*, broad-leaved platanoids, trochodendroids and probably also Vitaceae. In Spitsbergen, the dominating conifer is *Metasequoia* in combination with trochodendroids and probably Ulmaceae and *Acer arcticum*.

*Broad-leaved evergreen riparian gallery forest with palms.* – The intrazonal Eocene forest of the subtropical zone in mid-latitude Europe belongs to this type. Such plant assemblages are mainly connected with the sandy facies. They are widely distributed in the Late Eocene from Loire (Grès à *Sabal*), to Germany (Zeitz, upper part of the Geiseltal section), Bohemian Massif (Staré Sedlo Formation) to Eastern Europe (Mogilno, Pasekovo *etc.*).

The forest is characterized by dominating evergreen Fagaceae (*Eotrigonobalanus* and others) and Lauraceae (*Daphnogene cinnamomea* and others). Common are Altingiaceae (*Steinhauera*), Theaceae (*Gordonia*), *Rhodomyrtophyllum*, *Populus*, sabaloid and calamoid palms. Conifers belong mostly to the taxodioid and sequoioid Cupressaceae, partly to Doliostrobaceae (*Doliostrobos*). Characteristic examples of this type of intrazonal riparian forests belong to the Zeitz unit (Mai & Walther 1985, 2000) and extend from north Bohemia to Saxony.

In Bohemia, it is distributed in the Sokolov and Cheb Basins and is well known as the Staré sedlo type (Knobloch *et al.* 1996). The plant-bearing layers contain abundant impressions of *Eotrigonobalanus*, *Daphnogene*, infructescences of *Steinhauera*, sabaloid and calamoid palms. Additional rare accessory elements include tree ferns, broad-leaved *Gordonia*, *Populus*, *Majanthemophyllum* *etc.*

*Mixed Doliostrobos (and/or Quasisequoia) and broad-leaved evergreen swamp forest.* – Another type of intrazonal coal-forming vegetation is well known from Germany (Mai & Walther 1985). The assemblages connected directly with coal swamps are first of all well known from Helmstedt, Scheiplitz, Profen (Middle Eocene). This type of coal-forming vegetation is characterized by giant *Doliostrobos* and *Quasisequoia* as main coal-forming trees and subordinate evergreen Lauraceae, Fagaceae, Myricaceae, Ericaceae, sabaloid palms and other swamp plants (Mai & Walther 1985, 2000; Wilde 1989).

*Mixed pine and broad-leaved evergreen swamp forest.* – This is a special kind of coal-forming vegetation, which is known from the Geiseltal “black” coal (Middle Eocene) and can be characterized as open stands of *Pinus* as main coal-forming trees and admixture of common evergreen Lauraceae, Fagaceae, Rutaceae, Ericaceae, Sapotaceae, diverse palms, ferns and other swamp plants including aquatic angiosperms (Mai 1976). Interesting is the occurrence of a rare cycad *Eostangeria* (Barthel 1976).

*Mangrove.* – This is the final intrazonal forest vegetation type to be mentioned. It is well documented in the London Clay and slightly younger Bracklesham Bay flora (Collinson 1983, 1996), but also by many other occurrences of mangrove palm *Nypa* elsewhere in Europe (Gee 2009). It is reconstructed as stands of *Nypa*, with locally common *Cerriops* and *Palaeobruquiera*. Additional notable associated elements are enigmatic *Wetherellia*, probably related to extant *Hypomane* (Mazer & Tiffney 1982). A newly recovered Neotropical monocot *Cyclanthus* (formerly “*Scirpus*” *lakensis* – Smith *et al.* 2008) may have accompanied freshwater inland margins of mangroves in many Early-Middle Eocene sites.

## Extrazonal vegetation

The Eocene extrazonal vegetation in Europe is poorly known and doubtful. One kind of such forests can be deciphered from the pollen spectra that include documentation of plants not represented in the macrofossil record. Another example of extrazonal vegetation is due to substrate.

*Mountain coniferous forest.* – The vegetation cover of mountains can be traced in the pollen spectra from Spitsbergen (Early Eocene), Messel (Middle Eocene), Staré Sedlo (Late Eocene) to name most striking examples. This part of the spectra includes dominating Pinaceae (*Pinus*, *Cathaya*, *Abies*, *Tsuga* etc. – see *a.o.* Konzalová in Knobloch *et al.* 1996). In warmer areas conifers are less diverse, with notable proportion of evergreen Fagaceae. There is no direct evidence of palaeoaltitudinal differentiation in the European Eocene and the above vegetation type is only inferred from an analogous altitudinal differentiation, which is particularly known in mountains of southeast China today.

*Xerophytic scrub.* – (Sub)xerophytic vegetation probably due to a specific substrate is known from Arcuei, Calcaire Grossier (Early Eocene). It is documented by *Tetraclinis brachyodon*, sclerophyllous *Comptonia schrankii* and narrow-leaved dicots with dubious affinities (Watelet 1866). Similar setting can be expected for the site Häring (Austria) on the Eocene-Oligocene transition sharing *Tetraclinis brachyodon* and *Comptonia schrankii* but differing in abundant *Doliosstrobilus*, and also for a part of the Bembridge Marls flora (*Dicotylophyllum pinnatifidum* = *Palibinia*), where xerophytes may have grown on a specific substrate. An important probably shrubby element *Ziziphus ziziphoides* may also belong here.

## Conclusions

To summarize the distribution of various individual vegetation types, a rough phytogeographical map of the European Early-Middle Eocene (Fig. 1) may indicate boundaries between polar deciduous, mid-latitude notophyllous evergreen and quasi-paratropical forests. The boundaries shifted during the Eocene northwards and typical quasi-paratropical forests did not exist within Europe towards the Eocene-Oligocene boundary. The palaeoclimatic deterioration in the latest Eocene was expressed variously depending on the latitude/palaeogeography: either within the Nothophyllous Broad-leaved Evergreen Forest (Hungary, England) or in transition from the Nothophyllous Broad-leaved Evergreen Forest to the Mixed Mesophytic Forest (North Bohemia, Saxony).

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