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Paleogene vegetation of Eurasia: framework for mammalian faunas

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Four major categories of Paleogene vegetation are described and their general distribution in Eurasia is plotted on polar projections of paleogeographic maps. Methods and approaches for reconstructing Paleogene plants and vegetation from fossil floras are briefly outlined. Paleocene and Eocene polar, broad-leaved deciduous forests occurred in the high paleolatitudes and up to the edge of the Arctic Ocean. Relative to subsequent paratropical forests these were very low diversity forests with little habitat variation, very few climbers and more open structure. The environment was warm and equable but with up to three months of winter darkness so that most herbivorous browse and the small, dry fruits and seeds would only have been available seasonally. Late Paleocene and Eocene broad-leaved paratropical to subtropical, evergreen forests are variable in time and space. The most evergreen thermophilic forests are documented in Europe and southern China associated with the Eocene thermal maximum. These forests were highly diverse, multistratal, rich in climbers, with closed structure and would have provided many varied habitats. They would have provided year round herbivorous browse of medium to large evergreen leaves and a wide variety of fruits, including many fleshy fruits. Late Eocene and Oligocene broad-leaved mixed deciduous and evergreen forests developed as climate changed following the thermal maximum from the late Middle Eocene and through the Oligocene. These forests had lower diversity, contained fewer lianas and climbers and would have had a more open structure than the paratropical forests. They would have provided a mixture of evergreen and deciduous leaf browse and a variety of fruits but with fewer fleshy fruits and more large dry fruits. Vegetation with sclerophyllous elements was variably developed in central China, through Kazakhstan and the tethyan islands and into eastern Europe in the Eocene. In the Oligocene it was well-developed in southern Europe and also occurred in Kazakhstan. This vegetation reflects a warm humid temperate climate but with a slightly drier interval where sclerophyllous elements become significant in abundance or diversity. This would have been dominantly a forest vegetation (possibly shrubland in places) but with relatively open structure. In the most sclerophyllous belts, such as the Oligocene of southern Europe, herbivorous browse would have consisted mainly of relatively tough small leaves and the fruits and seeds would have been mainly dry with tough outer coverings. This paper paints only a very general picture of Paleogene vegetation. Paleogene floras provide the potential for detailed interpretation of vegetational, and hence biome, response to global change such as warm climate thermal maxima and tectonic events. Realising this potential requires independent dating of more fossil floras, new physiognomic analyses, rigorous re-investigation of nearest living relative assessments and integrated palynological and macrofossil studies which take account of taphonomic bias.

Keywords: Paleocene, Eocene, Oligocene, vegetation, Eurasia, paleobotany, paleoecology

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INTRODUCTION

This article is intended to provide an overview of the nature and distribution of the four major types of Paleogene vegetation in Eurasia from the perspective of the role of vegetation as mammalian habitats and food resources. Readers interested in the vegetation or flora of a particular region, zone or site, or in the variety and nature of plant communities, should consult the references cited for more specific assessments of the vegetation and species composition. The reference list is not intended to be exhaustive but to provide key examples for entry into the relevant literature. The paper also provides a brief introduction to the ways in which plants and vegetation can be reconstructed from fossils. A more wide-ranging introduction to paleobotanical techniques may be found in Jones & Rowe (1999).

RECONSTRUCTING PALEOGENE VEGETATION

Paleogene plants

A general summary of the Paleogene plant record is given in Collinson (2000b) with a more extensive review of Paleogene plant paleobiology in Collinson (1990). The Paleogene flora is dominated by flowering plants with associated ferns, conifers, *Ginkgo* and rare cycads. Among the flowering plants, the dicotyledon groups magnoliids (e.g. *Magnolia* [magnolias], Lauraceae [laurels]), hamamelids (e.g. Betulaceae [birches], Juglandaceae [walnuts, wingnuts], Platanaceae [planes], Ulmaceae [elms], Fagaceae [beeches]) and rosids (e.g. Cornales [dogwoods, mastic trees], Sapindales [soapberries], Icacinaceae [icacina lianas]) are abundant and diverse as are the monocotyledon groups alismatids (e.g. *Stratiotes* [water soldier]) and arecids [palms, aroids]). First occurrences of flowering plant families may be found in Collinson *et al*. (1993a). Details of Cenozoic ferns are given in Collinson (2001b, 2002). Information on Tertiary conifers and *Ginkgo* (maidenhair tree) is more scattered but useful sources are Mai (1995), Kunzmann (1999) and Yang & Jin (2000, for *Metasequoia* [dawn redwood]). The rare Paleogene cycads are discussed by Kvacek & Manchester (1999).

Paleogene plants are usually represented in the fossil record by various dispersed, isolated organs. Rarely, especially in the case of aquatic herbs, complete plants may be encountered. Usually 'whole' plants must be reconstructed and a variety of approaches are used (Collinson 1990, 2000b). Relatively rare fossils are able to prove conclusively the links between organs if they show organic connection, e.g. leaves and fruits attached to a woody twig or pollen within stamens of a flower. Biological connection is also valuable, e.g. if pollen survives on a persistent stigma in a fruit. Recurrent association can also be used if organs exclusively and/or repeatedly co-occur in samples at different localities. Anatomical similarity uses the presence of a distinctive character (e.g. a distinctive epidermal hair) to link organs to the same plant. Finally, it is possible to use the nearest living relative (NLR) of fossils, especially if there are multiple organs (e.g. pollen, leaves, fruits, seeds, wood and possibly flowers) all indicating the same type of plant. The philosophy applied here would follow that of Collinson (1986).

Paleogene vegetation

In situ plants, sedimentary facies and taphonomy After plants have been reconstructed they must be incorporated into reconstructed vegetation. In this task plants preserved in their position of growth are of exceptional value, including tree stumps; aquatic or marginal vegetation inundated by floods, and plants in peat-forming environments. In other circumstances the taphonomy, including sedimentary context (facies) and preservational state of the plant fossils is pivotal to judging the degree of transport and hence the relative autochthony of the assemblage. Litter mats may preserve the flora essentially in situ whereas beach deposits may contain a variety of fossils of plants, which did not originally grow together in the same vegetation. A low degree of fragmentation and abrasion, the co-occurrence of organs of different sizes and shapes but derived from the same plant, and a lack of evidence of concentration by wind or water would all indicate minimal transport. The best approach is to study plant fossils from a variety of sedimentary facies. This helps to constrain different sources and to ensure that regional (zonal), rather than only local (azonal), vegetation is being studied. Experimental (or modern) taphonomy is of considerable value in understanding plant fossil accumulations and the extent to which they reflect ancient vegetation. Approaches are summarised by Ferguson *et al*. in Jones & Rowe (1999) in which key literature on plant taphonomy is also cited.

Physiognomy The physiognomy of some plant organs, especially leaves and woods, can also contribute to reconstructing vegetation through inference of a biome type within a particular climate regime. Further discussion of the relative roles of different plant organs is given in Collinson (1990, 2000b). In particular leaf size and leaf margin, and more recently the multivariate CLAMP analysis (Wolfe & Spicer in Jones & Rowe 1999), provide evidence of climate regimes, as do the presence, absence and nature of growth rings (Creber & Francis in Jones & Rowe 1999).

Nearest living relative Inferences about ancient vegetation are often based on nearest living relatives. This approach may be very well-justified in some cases. An example would be when the fossil record reveals a suite of different fossil organs (e.g. wood, pollen, leaf, fruit) and all indicate an affinity with a particular modern group of plants all of which grow in one particular forest type (e.g. examples of the Juglandaceae, Manchester 1987). Further support would be provided if other associated fossils, from unrelated groups of plants, also indicated the same forest type on the basis of their nearest living relatives. In order for this approach to have value for reconstructing vegetation on a regional scale it is essential that a single taxonomic approach should be employed (ideally by one, or a small group) by specialists who are familiar with the floras over the entire area of study. In practice this procedure is rarely followed.

Other biota & sedimentological criteria Reconstructions of ancient vegetation can be checked for consistency against other lines of evidence such as that from other biota, primarily insects and mammals. As each of these groups is subject to varied and different taphonomic bias the approach is not straightforward. However, one factor which we have found informative, is the ecological diversity of mammalian faunas (Andrews et al. 1979, Collinson & Hooker 1987, Hooker 1998). Indeed, these provide helpful indications of spacing of plants in a vegetation (i.e. open or closed), a factor that is hard to establish directly for different kinds of ancient forest in the absence of in situ tree stumps. Relevant sedimentological criteria include coals and evaporites (Parrish et al. 1982) and paleosols (Retallack in Jones & Rowe 1999).

Independent dating Reconstructions of ancient vegetation depend on reliable independent dating of the floras. An entirely circular argument is created if the nature of the fossil flora is used to estimate its age. Such independent dating may come from absolute dates, magnetostratigraphy, from continental sequences intercalated with marine strata containing standard biostratigraphic markers and from biostratigraphy using mammalian faunas, charophytes or less ideally, palynology (when studying macrofloras).

Criteria used here Where possible the information used in this paper is drawn from recent work in primary literature, or personal observations, based on rigorous systematic studies (or revisions) of floras from independently dated sites. All approaches listed above have been employed, although not equally for all sites. The senior author (MEC) is a specialist in fruits and seeds and in western European floras and does not claim full familiarity with leaf floras or with floras in other areas. Nevertheless she has actively participated in conferences and discussions involving many of the authors whose work is cited here (see especially Boulter & Fisher 1994 section 5 on workshop discussions; and also Knobloch & Kvacek 1990, Planderova *et al*. 1993). In the cases of sites in China, Former Soviet Union, Mongolia and other sites where primary literature is not in the Roman alphabet, recent review articles in English have been used to assess vegetation in combination with illustrations and floral lists in original literature. The use of literature is no substitute for study of specimens and the senior author fully acknowledges this inadequacy. However, as this article deals only with broad vegetation categories the consequences may not be too severe. Where heavy reliance has been placed on literature an attempt has been made to use articles from a small number of authors or collaborators in order to reduce the problems of multiple taxonomic approaches. In spite of the above attempts at mitigation this paper includes: information based on floral lists with no illustrations; leaf floras which are impression floras with few diagnostic characters; floras known to require major systematic revision and floras which are not independently dated. These and other problems can only be solved by future research. Readers should check the primary literature for any particular area in which they are interested.

PALEOCENE AND EOCENE POLAR, BROAD-LEAVED, DECIDUOUS FORESTS

Floras

The floras are characterised by deciduous flowering plants (especially plants with *Trochodendroides* and *Corylites* leaf types) and taxodiaceous conifers. A representative leaf assemblage is from Atanikerdluk, Greenland (Mai 1995, fig. 131). A fern understory or forest marginal vegetation is associated with these floras (Collinson 2001b, 2002). It includes *Osmunda*, *Onoclea*, *Woodwardia* and the extinct *Coniopteris*.

In the Greenland Region (Greenland, Spitsbergen, Ellesmere Island, Scotland) the floras are typified by *Trochodendroides*, *Corylites* and *Metasequoia*. They include *Nordenskioldia* plants (Trochodendraceae) and *Nyssidium* plants (Cercidiphyllaceae), both with *Trochodendroides* leaves (*Nordenskioldia* also at Tsagayan, east Russia, Crane *et al*. 1991), *Macclintockia* (Incertae Sedis ?Urticaceae, Mai 1995), *Ushia* (?Fagaceae), Platanaceae (*Platanus* and *Platanites*, Crane *et al*. 1988); *Fagopsiphyllum* (Manchester 1999), *Palaeocarpinus* (Golovneva 2002), *Ginkgo* and relatively rare pinaceous conifers (McIver & Basinger 1999, Golovneva 2000, Boulter & Kvacek 1989, Kvacek & Manum 1993, Kvacek *et al*. 1994).

In far eastern and northern mainland Russia and Sakhalin the floras are also characterised by a *Trochodendroides*/*Corylites*/*Metasequoia* association (in Kamchatka, Rarytkin Ridge and northern Sakhalin (Boshnyakovo Formation) and in the Lena River (Budantsev 1994a, 1997; Herman 1993; Herman & Spicer 1996; Golovneva 1994, 2000). This contrasts with the *Taxodium*/*Trochodendroides* association in the Zaysan area, Kazakhstan, Tsagayan and Kivda region of Amur, Russia and Mongolia (Golovneva 1996). The aquatic plant *Quereuxia* is a distinctive element in the far eastern Russian assemblages (Golovneva 1996). This plant also appears in the North American Paleocene (e.g. in Canada at Ravenscrag Butte, Saskatchewan; McIver & Basinger 1993) and on Ellesmere Island (McIver & Basinger 1999), being one of a number of elements indicating dispersal between these areas (Manchester 1999) across Beringia.

Occasional thermophilic elements are documented in the Kamchatka floras, e.g. *Magnolia*, *Nyssa* and *Sassafras* at Snatol (Maslova 2000, Fotyanova 1995). In eastern Kazakhstan in the Zaysan Basin (Kara-Beryuk) a short-lived interval contains a *Trochodendroides*-rich polar deciduous type of flora (Golovneva 1996).

The floras from Mongolia are similar to some of those from the Zaysan Basin (Makulbekov 1987). Indeed, the flora from the Naran Member at Naran Bulak and Tsagan Khushu (Makulbekov 1988, table 4) is of very low diversity with several *Trochodendroides* leaf types, *Trochodendrocarpus* and *Nordenskioldia* fruits, *Myrica* and two other dicotyledon leaves, the endemic conifer *Gobiostrobus* Makulbekov (Makulbekov 1995) and other conifers of the Taxodiaceae. The flora from the Naran Member at Kaychin Ula I is more diverse with Taxodiaceae, many *Trochodendroides* leaf types, *Macclintockia*, Betulaceae, Ulmaceae, Myricaceae and *Viburnum*-like leaves (Badamgarav & Reshetov 1985, table 2; Makulbekov 1988, table 4). Many elements of these floras are typical of the polar deciduous forests and of the floras of eastern and western Kazakhstan (Makulbekov 1988, table 8). These floras may represent the polar deciduous forest or a taphonomically restricted, but more mixed, vegetation. The presence of Myricaceae (Makulbekov 1988, table 8) distinguishes this flora from the polar deciduous forests, as does the long narrow-leaved nature of some unidentified dicotyledon leaves mentioned by Makulbekov (1983) although these may remain indeterminate (Makulbekov 1988). For these reasons the floras have been assigned here to the mixed component of Paleocene vegetation. The Mongolian floras are referred to as a *Taxodium*/*Trochodendroides* association by Makulbekov (1983) and Golovneva 1996).

The Tsagayan flora (Ohana & Kimura 1995, Krassilov 1995, Golovneva 1996) also exhibits a predominance of *Taxodium* and *Trochodendroides* and includes many elements from the polar deciduous forest. However additional elements include Nyssa and this flora also represents a somewhat mixed assemblage. A flora of late Paleocene or early Eocene age in South Sakhalin includes thermophilic elements such as *Alchornea*, which are found in Eocene floras of Japan (Kodrul 1994).

Paleocene communities within this vegetation were interpreted by Krassilov (1995). They included a) aquatics (with e.g. *Quereuxia* in eastern Russia and the USA) b) a marginal waterside community (represented by monocotyledonous leaves); c) a swamp forest community (Taxodiaceae and *Trochodendroides*-bearing plants); and d) an upslope deciduous woodland or more open forest. (The inference of openness was based on debris flow deposits indicating erosion).

Middle Eocene communities within this vegetation included *Metasequoia* swamp forests, (with *Alnus* groves as a successional stage). Dicotyledonous angiosperms especially Betulaceae (and the fern *Osmunda*) are judged to be a significant component of the swamp forest although they are often overlooked in the litter assemblages (McIver & Basinger 1999, p. 535). Tree density in these swamp forests reached 1100/hectare comparable to modern tropical rain forests (Basinger *et al*. 1994, McIver & Basinger 1999, Vann *et al*. oral comm. 2001). Rarely, swamp leaf litters exhibit a mixture of other conifers including Pinaceae, which were evergreen. The remains of these evergreen conifers also occur in fluvial sands (channel or point bar deposits) suggesting presence of a more distant ‘upland’ mixed evergreen conifer and deciduous angiosperm forest (Basinger *et al*. 1994, Lepage 2001, McIver & Basinger 1999). The other main community was lowland broad-leaved deciduous forests (with deciduous conifers) in better-drained sites with remains deposited in overbank or fluvial deposits. In the middle Eocene a few thermophilic or evergreen elements occur in these lowland forest communities (Menispermaceae, *Nyssa*, and lobed oaks) alongside the typical deciduous elements (Basinger *et al*. 1994, McIver & Basinger 1999). Herbaceous wetlands included *Equisetum* and *Sparganium* (McIver & Basinger 1999).

Vegetation overview

These polar deciduous forests are characterised by a low to very low diversity (single sites with less than 20 leaf species, often only a few (Basinger *et al*. 1994). There would thus have been little habitat variation within the forests. That the nature of the environment was warm, equable and largely frost-free, with a long favourable growing season and a sudden shutdown of growth in winter, is documented by leaf floras, wood physiognomy and associated biota including large land tortoises, varanid lizards and alligators (Estes & Hutchison 1980, Basinger *et al*. 1994, McIver & Basinger 1999).

The plants include a number of well-understood genera, which are known from reconstructed whole plants. These include *Cercidiphyllum*-like plants such as *Nyssidium* and *Trochodendrocarpus*; *Nordenskioldia* plants, Platanaceae and Betulaceae (Crane *et al*. 1991; Crane *et al*. 1988; Boulter & Kvacek 1989; Golovneva 2000, 2002; Crane 1981, 1984; Maslova 1997; Krassilov & Fotyanova 1995; Pigg & Stockey 1991; Chen *et al*. 1999; Feng *et al*. 2000). *Metasequoia* is also known from reconstructed plants scarcely distinguishable from modern species (Basinger 1984) and is represented in the Eocene of Axel Heiberg by wood, leaves, pollen cones and seed cones (McIver & Basinger 1999). All of these plants are characterised by a colonising strategy. This is proven by Paleocene examples from the *Joffre* Bridge site in Alberta, Canada. There, the Joffrea plant (Cercidiphyllaceae), platanaceous plants and *Metasequoia*-like plants (Stockey & Crane 1983, Crane & Stockey 1985, Pigg & Stockey 1991, Falder *et al*. 1999) all have small seeds and exhibit simultaneous germination proven by fossil seedlings.

These forests have essentially no lianas or climbers. One leaf type (*Archeampelos*) in the assemblages on Axel Heiberg & Ellesmere Islands may belong to the Vitaceae and may possibly represent a vine (McIver & Basinger 1999) and a probable menispermaceous vine occurs in the middle Eocene floras of Axel Heiberg and Ellesmere Islands. One leaf from Mull may be related to Vitaceae (Boulter & Kvacek 1989). Understory, or at least marginal vegetation included a low diversity fern flora (Collinson 2001b, 2002). The trees were mainly deciduous (with a few evergreen elements in more southern 'mixed' floras) with thin, medium and large leaves. The fruits were characterised by small to very small dry seeds in woody follicles (*Cercidiphyllum*-like plants) or capsules (*Nordenskioldia*) or small nuts (Betulaceae, Juglandaceae, Ulmaceae) or small seeds in conifer cones. Only *Ginkgo* (apparently not an abundant element) would have produced a substantial-sized seed (although the outer flesh of living *Ginkgo* has an unpleasant smell which may render it rather unpalatable). These dietary resources would have been almost entirely seasonal in their availability although evergreen conifers occurred in 'uplands' at some sites (e.g. Axel Heiberg). This polar deciduous forest, a warm forest with winter darkness in a mesothermal humid climate, has no modern analogue and this biome is extinct.

LATE PALEOCENE AND EOCENE BROAD-LEAVED, PARATROPICAL TO SUBTROPICAL, EVERGREEN (RAIN) FOREST

Introduction

This vegetation is not equivalent simply to 'tropical rainforest' for several reasons. (1) Mean annual temperature (MAT) from leaf physiognomy does not usually indicate temperatures greater than 25°C, which is the lowest for tropical forest (Wolfe 1987). (2) Temperate or deciduous elements/indicators often co-occur, resulting in mixtures not found in modern tropical rain forests. (3) There is no direct analogue for the fossil forests in modern tropical forests. Although many nearest living relatives occur in Southeast Asian tropical rain forests today, key elements, especially dipterocarps and epiphytes, are rare to absent in Eocene forests. For further discussion see Collinson (1983a, 2000b, 2001a).

Late Paleocene and Paleocene/Eocene transition floras

The early late Paleocene Gelinden flora (which requires detailed systematic revision) is judged by Mai (1995) to be dominantly thermophilic and taken by him as the key Paleocene representative of this vegetation in Europe. The typical leaf assemblage is shown in Mai (1995 fig. 133). It does include a few deciduous elements e.g. *Ushia* but is dominated by evergreen Fagaceae and Lauraceae, esp. *Dryophyllum*, typical of the Eocene examples of this vegetation type. Mai (1989, 1991,1995) considered this as an evergreen laurophyllous forest or evergreen notophyllous broad-leaved forest (the latter being mesothermal rather than megathermal sensu Wolfe (1987)). Woods associated with this flora show only indistinct growth rings (Gerrienne *et al*. 1999).

The later late Paleocene floras of Eisleben and Roda, Germany, are judged by Mai (1987, 1995) to be boreotropical (i.e. thermophilic) floras but with smaller and more serrated leaves than is a typical for this vegetation. The floras from Rusava, Rusca and Dobre Sreca are judged to be thermophilic; the former two include palms but, atypically for this vegetation, lack Fagaceae and Lauraceae (Mai 1987,1995). The floras of western Kazakhstan and the Volga area (Bolytschka, Kamyshin, Ushi, Romankol and Tykbutak) are subtropical floras with many palms and evergreen Lauraceae and Fagaceae (like Gelinden, also including *Ushia*) (Shilin 2000, Makulbekov 1987).

However, in the Paleocene some western European floras also include more of the characteristic deciduous elements of the Late Paleocene/Eocene polar deciduous forests. These have been characterised as "mixed" on the vegetation map. Floras of ‘mixed’ aspect with some indicators of the paratropical to subtropical forest vegetation, (e.g. large evergreen leaves, members of the Lauraceae, fruits and seeds with living relatives in subtropical to paratropical forests) occur in western Europe at Sézanne and Menat (Mai 1995), in southern England (Collinson 2000a, Collinson & Cleal 2001a), at Vervins and in the Soissonnais (Mai 1995). The Sézanne and Menat floras, like that from Gelinden, also require major revision.

In eastern Kazakhstan in the Zaysan Basin (Kara-Beryuk) a short-lived interval contains a *Trochodendroides*-rich polar deciduous type of flora (Golovneva 1996). This is replaced by subtropical floras (e.g. at the Chakel’mes site), which may include *Dryophyllum* & *Dewalquea* (at the Tayzhuzgen site) and sometimes lack *Trochodendroides* (e.g. at Kiin-Kerish), but still retain many affinities with boreal northern Asian deciduous floras e.g. Platanaceae (Golovneva 1996, Makulbekov 1983, 1987). Mongolian floras have been discussed above under polar deciduous forests. All these floras are categorised as ‘mixed’ on the vegetation map.

The few Paleocene floras from China are reviewed in Guo (1990) and Liu *et al*. (1996) with an additional flora from Lingbao County, Henan (S. Guo pers. comm. 2001). These floras indicate a mixed vegetation of temperate deciduous broad-leaved elements with warm temperate to subtropical elements. They include *Trochodendroides* and *Cercidiphyllum*-type leaves, *Ushia*, Betulaceae, Platanaceae and Taxodiaceae, but also some more thermophilic elements.

Eocene floras

Strongly thermophilic/evergreen floras in Europe Leaf floras are dominated by evergreen Fagaceae and Lauraceae. A typical example of a leaf flora is that from Messel, Germany, illustrated in Mai (1995 p. 136). The leaf morphology (large leaves, thick leathery texture, entire margins) is indicative of evergreen habit for many leaves. Leaf physiognomy indicates megathermal to very warm mesothermal vegetation. Key elements include *Eotrigonobalanus*, *Trigonobalanopsis* (Fagaceae), *Steinhauera* (Altingiaceae), *Rhodomyrtophyllum* (Myrtaceae), and *Litsea*, *Lindera*, *Ocotea*, *Daphnogene* (Lauraceae) species (Mai 1995, Wilde 1995, Walther 1994). Sterculiaceae, Icacinaceae, Sapotaceae, Menispermaceae, Vitaceae, Nyssaceae, Apocynaceae, Arecaceae and Symplocaceae are also recorded in leaf floras (Mai 1995, Wilde 1989, 1995). Ferns such as *Lygodium* are frequent. *Doliostrobus* is a common conifer and the cycad *Eostangeria* is also present (Wilde 1989,1995, Mai 1995, Kvacek & Manchester 1999, Collinson 2001b, 2002). Juglandaceae (especially *Platycarya* and *Engelhardia* groups) are also documented from fruits and foliage (Manchester 1987, Mai 1995). Woods show little evidence of growth rings. Growth rings are absent in about 70% of twigs from the English London Clay flora (Collinson 1983a, Poole 1992, 2000). In European Eocene fruit and seed floras, taxa whose nearest living relatives occur in paratropical forests are diverse and abundant (Collinson 1983a, 2000b, Collinson & Cleal 2001b, Tiffney 1994, Mai 1970, 1989,1995). These elements include members of the Arecaceae, Anacardiaceae, Anonaceae, Burseraceae, mastixioid Cornaceae, Dilleniaceae, Icacinaceae, Lauraceae, Menispermaceae, Sabiaceae, Sapindaceae, and Vitaceae.

Although a few members of some of these taxa extend today into temperate zones, a high diversity is only found in megathermal to warm mesothermal vegetation. Diverse palms are particularly important because palm functional biology confirms warm conditions without recourse to living relatives. Collinson (2000b, 2001a) also discussed this vegetation type.

Strongly thermophilic/evergreen floras in China Floras in southern China indicate an evergreen broad-leaved forest growing in a wet and tropical climate. The leaves are leathery and some are coriaceous but these are larger than in the central Chinese region (see vegetation with sclerophyllous elements). Evergreen Fagaceae, Lauraceae and palms are significant elements (Guo 1990).

Other strongly thermophilic floras More isolated records of thermophilic floras occur in Japan and Kamchatka. The Japanese floras from the Ube coalfield, Honshu are evergreen mainly tropical floras with some deciduous elements (Huzioka & Takahashi 1970, Tanai 1995). Those from the Ishikari coalfield, Hokkaido are similar with abundant tropical elements, especially Euphorbiaceae, Icacinaceae, Menispermaceae and Sterculiacaeae, as well as palms and Musaceae (Tanai 1990) and evergreen Fagaceae (Tanai 1990, 1995). Deciduous elements also occur in these floras (Tanai 1981,1990, 1994) and become more common in the floras of the Kushiro coalfield (Tanai 1970, 1990), which is late Eocene in age (Tanai 1990) and has been assigned here to the subtropical floras (see below).

The most thermophilic flora in Kamchatka is the flora of the Chemurnaut Bay area, which is still under study (Budantsev 1994a, 1997). This flora contains 43-45% entire margined leaves, many leaves are large, and some have drip tips and there are many thermophilic elements with near living relatives in the Lauraceae, Arecaceae, Sapindaceae, Styracaceae, Symplocaceae, Apocynaceae, Sabiaceae and a high diversity of legumes etc. (Budantsev 1994a, 1997). This is not a sufficiently thermophilic flora to be considered equivalent to the European or southern Chinese floras. However, it seems to be significantly more thermophilic than, and very different floristically from, the other (Paleocene and Eocene) floras of Kamchatka (Budantsev 1994a, 1997). It has therefore been plotted as strongly thermophilic on the map to draw attention to this fact. It should also be noted that there is debate about the age of the floras. For example the floristically rich Tkapravayam Formation is argued to be middle Eocene by Budantsev (1994a, 1997) but late Paleocene by Maslova (1997), both of whom took account of marine faunal evidence. Krassilov & Fotyanova (1995) also considered the formation to be late Paleocene. Blokhina (1997, 1998) who studied woods, and found them to have distinct growth rings (as would be expected at this high paleolatitude), also commented on the disparate dating. Other Eocene floras in Kamchatka contain thermophilic elements such as the most northern occurrence of Sterculiaceae in the late Eocene Sedanka site, Napana River (Budantsev & Baranova 1995). Further study and age refinement (e.g. exploiting the foraminifera documented by Fotyanova & Serova 1994) of the Kamchatkan floras will clearly be of great significance for the understanding of high latitude Paleogene floras.

Floras designated subtropical/with temperate elements These floras are distinguished on the Eocene map as they do not seem to represent forests that are as strongly thermophilic or evergreen as those represented by the floras discussed above. The distinction is in places tenuous and is largely based on comments in the literature (see references for specific sites in Table 1) where these floras are referred to as 'subtropical' (rather than paratropical or evergreen/thermophilic) and/or where temperate elements are emphasised. The distinction is complicated by the fact that there is a temporal transition, in places starting in the late Middle Eocene, with increasing temperate deciduous (and/or sclerophyllous) elements in floras. The transition is discussed under late Eocene to Oligocene mixed deciduous and evergreen forests. The dates for some floras are not specific (e.g. Eocene) and for others the dating is based largely or entirely on the floral composition. Further research, including independent dating, physiognomic approaches, in depth re-appraisal of nearest living relatives and detailed comparisons between floras, is needed to explore the temporal and spatial distribution of the variations in the Eocene paratropical/subtropical evergreen forests.

Mangroves Further evidence of the humid thermophilic aspect of Eocene vegetation is afforded by the presence of mangroves dominated by the *Nypa* palm (represented by fruits and pollen). These ranged from north western Europe through central and eastern Europe to India, South East Asia and Australasia and into North and South America, but are not recorded from eastern Asia (given that a pollen record from Japan is questionable).

A map of the distribution of ancient *Nypa* was produced by Collinson (2000b, Fig. 16.4, p. 233). Localities with *Nypa* in the Paleogene of Eurasia are Figure 2 and Table 1 site numbers 15,19,45,52,92 and 100 (Collinson 1993, 2000b; Tralau 1964). In addition *Nypa* is recorded from Kiev, Ukraine (near site number 98) (Tralau 1964, Mai 1995, p.106); Hruby Regiel, Tatra Mountains, Poland (near site number 29) (Tralau 1964, Mai 1995, p.382); Dudar in the Dorog Basin, Hungary (near site number 86) (Tralau 1964, Mai 1995, p.382) and near Odessa, southern Ukraine (Tralau 1964). Details of localities in England, Belgium and France may be found in Collinson (1983a, 1993, 1996) and Tralau (1964). All these *Nypa* sites are associated with ancient coastlines bordering the strongly evergreen thermophilic vegetation in western and south-eastern Europe and the Ukraine. In England, members of the Rhizophoraceae (true mangroves) such as *Ceriops* (fossils of the viviparous embryos) are associated with the *Nypa*, as is an extinct plant, which produced *Wetherellia* fruit fossils (Collinson 1983a, 1993, 1996, 2000b, 2001a). Fossil pollen whose nearest living relatives are mangroves today (e.g. *Avicennia* and) suggest the presence of other mangrove taxa in association with *Nypa* at some sites (e.g. Helmstedt, site number 55, Riegel *et al*. 1999).

Vegetation overview This vegetation had very high diversity. More than 300 species are recorded in some of the fruit and seed floras of the London Clay Formation of the London and Hampshire Basins, southern England (Collinson 1983a; Collinson & Cleal 2001a,b) though these are exceptionally well-represented owing to various taphonomic and collecting factors. The Messel leaf flora, sourced only from the catchment of a relatively small lake, is at the opposite extreme, but even this has 65 species based on leaves (Wilde 1989). Additional taxa are represented in the fruit, seed and pollen floras, so that 58 families of angiosperms are represented overall at Messel (Schaal & Ziegler 1992). The middle Eocene Clarno flora, representing this vegetation in North America, has 173 species based on fruits and seeds. Pollen floras as indicators of former biodiversity in this vegetation are considered in the section on India and Southeast Asia. The high diversity would mean that these forests provided a richly varied habitat.

The plants display a wide range of ecological strategies, from colonisers to those adapted to climax forests. Leaves are medium to large, leathery and entire margined and trees were dominantly evergreen. Analogy with modern forests would suggest the presence of two canopy layers, probably with an additional emergent layer. There are numerous lianas and climbers based on nearest living relatives and leaf physiognomy (especially a high diversity of Menispermaceae and Vitaceae known from fruits and seeds, as well as from leaves with cordate shape and drip tips). Fragments of twining stem in the London Clay floras demonstrate the presence of climbers. The most strongly thermophilic of these forests would have experienced little (possibly in some cases no) seasonality. Growth rings are absent in 70% of twig woods and very rare in trunk woods in the London Clay flora (Poole 1992, 2000). Deciduous trees are rare. Increased proportions of deciduous elements in some of the floras mapped here as subtropical/with temperate elements may indicate increased seasonality, decreasing temperatures, or both. This vegetation yields a wide variety of fruits and seeds with a range of sizes. Diverse fleshy fruits are predicted from nearest living relatives of many taxa represented by fossil seeds or fruit stones. Fleshy fruits are conclusively demonstrated by exceptionally preserved specimens at Messel with leathery flesh and outer fruit pericarp (skin) preserved (Schaal & Ziegler 1992, Collinson 1999, Hooker & Collinson 2001).

LATE EOCENE AND OLIGOCENE BROAD-LEAVED MIXED DECIDUOUS AND EVERGREEN FOREST

Introduction

Areas which preserve a temporal sequence of sites e.g.: southern England (Collinson & Cleal 2001a,b,c), The Weisselster Basin, Germany (Mai & Walther 1978, 1985; Mai 1995); the Czech Republic (Mai 1995, Buzek *et al.* 1990); Kamchatka (Budantsev 1994a, 1997); Kazakhstan (Zhilin 1989, Makulbekov 1987) and Japan (Tanai 1990) all show transitional floras following those of the Eocene paratropical/subtropical evergreen forests. These may reflect an increase in temperate and deciduous elements, with vegetation changing, for example, through evergreen notophyllous forest to mixed mesophytic forest. Alternatively, they may show an increase in sclerophyllous elements (see below under vegetation with sclerophyllous elements). The changes may commence as early as the late middle Eocene in some areas and they continue through the late Eocene and into the Oligocene, the exact timing being variable and well-constrained in only a few areas. Each area is discussed below.

European floras

The transitional, continuous rather than abrupt, nature of vegetational change in Europe was outlined by Collinson (1992) and Knobloch *et al.* (1993). In Central Europe the late Eocene Stare Sedlo flora, Czech

Republic (monographed by Knobloch *et al*. 1996) is dominantly evergreen containing many elements of subtropical rain forests and referred by Mai (1995) to the same floral complex as the Zeitz flora (see below). The transition was very well illustrated for Central Europe by diagrams in Buzek *et al*. (1990) also redrawn in Mai (1995 fig. 138) and was discussed by Walther (1994). The paratropical elements do not all disappear at once, indeed some persist well into the Oligocene. Lauraceae are retained but are represented by different species e.g. of *Litsea* and *Laurophyllum*. However, incoming taxa (Betulaceae, Ulmaceae, *Acer*, *Liquidambar*, *Fagus*, *Carya*, *Craigia* [formerly *Ptelea*], Tiliaceae, *Cercidiphyllum*) include many deciduous elements and most of these first appear in the Oligocene.

In western Europe the transition is more gradual with loss of paratropical elements and incoming of deciduous elements from the late middle Eocene (Collinson 1992). Typical leaf floras of the Late Eocene have been interpreted as evergreen to semi-evergreen mesophilic e.g. Célas, France (leaf assemblage illustrated by Mai 1995, fig. 163) or as evergreen notophyllous vegetation e.g. the Zeitz Complex, Weisselster Basin, Germany (Mai 1995, leaf assemblage illustrated in Walther 2000, fig. 1).

Fruits belonging to the incoming elements include larger dry nuts e.g. of Fagaceae, *Carya* and Betulaceae. The deciduous component is floristically distinct from that of the Paleocene polar deciduous forests. For example, it generally lacks extinct plant genera, has smaller leaf sizes and includes a wider variety of fruit types, especially larger dry fruits.

The late Eocene and Oligocene mixed deciduous and evergreen forests are truly a mixed vegetation, with the proportions of different elements varying through time and in different geographic areas. One excellent example of relatively local geographic variation is the difference between the early Oligocene floras of the Czech Republic and Hungary (Kvacek 1996, Kvacek & Walther 1998), the former being mixed mesophytic forests and the latter notophyllous evergreen forest. In Hungary the deciduous temperate elements only appeared very sporadically in the early Oligocene but they became significant in the late Oligocene (Hably 1993, Kvacek 1996). Kvacek and Walther (2001) further documented provinciality in the Oligocene of Europe, showing that a southern province was distinguished by the persistence of more subtropical elements with temperate elements only appearing in the late Oligocene. Fluctuations in the proportions of leaf physiognomic types and of nearest living relatives offer great potential for more precise vegetation and climate delimitation during transitional intervals. However, great care must be taken to study regional (zonal) rather than local (azonal) vegetation and to take account of taphonomic bias and paleogeographic settings (Kvacek & Walther 1998, 2001; Kvacek 2000). Such detail is unfortunately outside the scope of this general article.

The Kundratice and Haselbach floras and floras of the Lausitz region (Mai 1994) are other examples of European Oligocene vegetation. The leaf assemblage at Haselbach is illustrated by Mai (1995, fig. 140) and the vegetation is interpreted as mixed mesophytic forest. The leaf assemblage from Kleinsaubernitz is illustrated by Walther (1999, text-fig. 16) and the assemblage interpreted to represent a mixed mesophytic forest with more than 50% evergreen and thermophilic elements. The floral assemblage from Kundratice is illustrated by (Kvacek & Walther 1998, text fig. 13). At Kundratice, (volcanic floras preserved in depressions of fault basins and maar lakes), communities include a broad-leaved deciduous forest in a humid habitat (e.g. lake margin) with rare evergreens (*Platanus neptuni* and *Daphnogene*) and a mixed mesophytic forest dominated by deciduous broad-leaved trees. Evergreen Lauraceae persist here. MAT is estimated at 9-13°C with a humid (Cfa type) climate (Kvacek & Walther 1998). Fruit and seed floras are represented in the Lausitz region in the Calau Beds (Mai 1998) and in Saxonian Lausitz (Mai 1997). The Calau flora was also interpreted as representing a mixed mesophytic forest.

Japanese floras

Deciduous elements become more common in the floras of the Kushiro coalfield (Tanai 1970, 1990), which is late Eocene in age (Tanai 1990). Floras from near Kobi City, Honshu (Tanai & Uemura 1994, Tanai 1995, Fotyanova 1997) and from the Rikubetsu and Kitami coalfields, Hokkaido (Tanai 1981, 1990, 1992, 1994, 1995; Tanai & Uemura 1994; Fotyanova 1997), are possibly of late Eocene or early Oligocene age. They are referred to as warm temperate floras.

Floras in Kamchatka

The late Eocene floras of Kamchatka have been divided into three floral stages (Budantsev 1997). The oldest two stages are considered to represent temperate mesophilic floras. They include a proportion of temperate deciduous elements and some small-leaved elements but they also retain some evergreen thermophilic elements characteristic of earlier floras. First appearances for the area of thermophilic elements such as *Firmiana* of the Sterculiaceae (Budantsev & Baranova 1995, Budantsev 1997) as well as *Magnolia* and Euphorbiaceae are also notable. The latest floral stage (Irgirninian) contains dominantly broad-leaved deciduous plants, including taxa not encountered earlier, and lacks the thermophilic elements (Budantsev 1997). Refined independent dating of these floras will be very important for understanding high latitude Paleogene floral change. As far as we can determine none of the floras in this area are considered to be Oligocene in age.

Floras in Kazakhstan

Shilin (2000) emphasised the subtropical nature of the Paleocene and Eocene floras of Kazakhstan, noting the presence of palms and evergreen dicotyledons with narrow leathery leaves including members of the Lauraceae and Fagaceae. A radical change was noted in the Oligocene with the rise of a warm temperate deciduous flora, termed the Turgai (= Turgay/Turgayan) flora or the flora of Turgai ecological type (Shilin 2000, Zhilin 2001). Further discussion of sclerophyllous elements, which are very important in these floras, is given in the section on vegetation with sclerophyllous elements.

In eastern Kazakhstan, in the Zaysan Basin floras such as Kershi and Kalmakpay are dated to middle Eocene on the basis of the associated Obayla mammal fauna and they represent subtropical forests, having large leaves, few temperate elements and lacking such groups as birches. Overlying late Eocene floras (e.g. Akkezen [same location as Kalmakpay]) retain some subtropical elements (e.g. *Lindera*) but show an increase in temperate elements, some of which are small-leaved sclerophylls (Iljinskaya 1984a,b; Makulbekov 1977, 1987). The site at Kiin-Kerish (same Eocene map location as Kershi) yields floras assigned to the late Eocene and early Oligocene, with the former containing a higher proportion of subtropical elements and the latter more temperate and sclerophyllous elements (Zhilin 1989; Makulbekov 1977, 1987). The Oligocene flora of Ashutas is also a temperate flora with sclerophyllous elements.

In northern and central Kazakhstan, floras are generally sclerophyllous earlier, even in the middle Eocene, possibly an effect of local paleogeography (Makulbekov 1987). Palms and evergreen Fagaceae and Lauraceae are characteristic of floras assigned to the middle Eocene (Karasor) and the late Eocene to early Oligocene (e.g. Zhamantuz, Akhzar, Shiderty) but the leaves are dominantly small, leathery sclerophyllous elements (Makulbekov 1972, 1977, 1987).

In western Kazakhstan, middle Eocene floras (e.g. Karakol) show slight indications of xeromorphic elements but also show similarities with earlier Paleocene floras at Tykbutak. The late Eocene (partly possibly middle

Eocene) floras including those at Baki, Zharlykap, Karashandak and Kundyzdy, are very different. They lack the dominants of the previous floras, instead being dominated by small leaved sclerophyllous elements including species of *Myrica* and oaks. Thermophilic elements have increased and include palms and narrow-leaved laurels such as *Litsea*. Late Eocene to early Oligocene transitional floras (such as Shadiniskii/Shana Graben, Romanovsk and Martuk) contain a mixture of subtropical and warm temperate elements, indicating a mosaic of thermophilic and mesophilic elements with a moderately subtropical aspect (Makulbekov 1977, 1987; Zhilin 1989). Subtropical elements persist in the early Oligocene but are lost in the late Oligocene (Zhilin 1989) a comparable situation to parts of central Europe.

Strongly thermophilic floras

Four of the sites on the Oligocene map (Fig. 3) seem to contain a rather high proportion of evergreen thermophilic elements. Two of these, Tim and Pasekovo in central Russia, previously considered as Oligocene, might be Late Eocene or Eocene/Oligocene transition (Vickulin 1999a, b) but all these ages have been inferred from the floristic composition, which is currently being revised. The other two sites are from the Caucasus and the interpretation of these has been taken from a general article (Akhmetiev 1995) where the early Oligocene of western Caucasus (Akhmetiev 1995 p. 175) was described as ‘inhabited by Lauraceae and evergreen Fagaceae’. This area has marine intercalations but specific evidence for the dating is not given. The interpretation is based partly on small floras in older literature (including woods and leaves) and partly on valuable, but small, new collections. Therefore, all four of these floras, which we have indicated as ‘strongly evergreen’, may be subject to a revised interpretation in future following further research.

Freshwater wetlands

The changes in the forest vegetation are accompanied by a change in the coastal wetland vegetation. Best documented in southern England, the mangrove is replaced by a rich herbaceous marsh, dominated by *Acrostichum* and *Typha*, including lakes with a rich aquatic flora. The vegetation is likely to have resembled the vegetation of the Florida Everglades today. Taxodiaceous trees were also part of this wetland as in the earlier polar swamps but represented now by *Taxodium* or a different extinct genus *Quasisequoia* KUNZMANN (Kunzmann 1999, formerly named *Sequoia couttsiae* Heer and common in England, Collinson & Cleal 2001b,c).

Vegetation overview

This vegetation is obviously variable because of its transitional nature. However, broadly it is based upon mixed mesophytic forest vegetation. This mixed broad-leaved deciduous and evergreen forest vegetation has medium to high diversity. The Late Eocene Weisselster Basin Zeitz Complex flora has 149 species (Mai & Walther 1985) and the Oligocene Haselbach flora is similar with 132 species (Mai & Walther 1978), both based on a combination of leaf and seed fossils. The late Eocene flora of Stare Sedlo has 135 species based on the list of leaves (Knobloch *et al.* 1996). The Oligocene flora of Kundratice has 89 species (Kvacek & Walther 1998) based mostly on leaves. This forest would therefore contain a wide variety of habitats but fewer than the multistratal, paratropical/subtropical forests.

The plants exhibit a variety of ecological strategies from colonisers to those adapted to climax forests. This vegetation contains fewer lianas and climbers and is inferred to be more open than the paratropical/subtropical forests. The leaves vary from deciduous, medium-sized and thin with serrate margins, to evergreen, larger and leathery with entire margins. Some seasonality is present, being induced either by changes in temperature or water availability or both. The plants would produce a variety of fruits and seeds but with relatively few fleshy fruits and an increase in the component of large dry nuts such as those of the Fagaceae, Juglandaceae and Betulaceae.

VEGETATION WITH SCLEROPHYLLOUS ELEMENTS

European floras

Several of the European late Eocene floras (e.g. Haring, Austria, leaf assemblage illustrated by Mai 1995, fig. 150) and a larger number of the European Oligocene floras contain elements where the leaves exhibit xeromorphy (modification to handle reduced water availability). There are distinct taxa with small and thick coriaceous leaves. In addition, representatives of typically mesomorphic taxa may exhibit enhanced xeromorphy i.e. smaller and thicker leaves compared to other occurrences (e.g. oaks, laurels, the conifer *Tetraclinis*). Characteristic elements are *Zizyphus zizyphoides*, *Comptonia schrankii* and *Myrica longifolia*, a variety of legumes and sometimes the conifer *Tetraclinis* (Mihajlovic 1992,1993; Hably & Fernandez Marron 1998; Hably *et al*. 2000; Kvacek 1996; Kvacek *et al*. 2000). The communities have been variously interpreted as: evergreen laurophyllous forest, oak/laurel/*Zizyphus* forest; mixed mesic-subhumid forest; xerophytic shrub forest; sclerophyllous subhumid vegetation or subxerophytic vegetation. Palamarev (1989) discussed the nature and origin of this vegetation, recognising Oligocene xerothermic centres on the Iberian, Apeninian and Balkan peninsulas and in some central European and French regions leading ultimately to the evolution of sclerophyllous paleomediterranean vegetation in the Neogene.

The European floras seem to exhibit a very wide variation in proportions of these sclerophyllous elements. Some floras such as those in Lausitz and Hungary have only one or two elements within an otherwise mixed mesophytic forest or notophyllous evergreen forest assemblage (Hably & Fernandez Marron 1998; Kvacek 1996; Mai 1994,1998). In contrast, some floras e.g. those at Sarreal in Spain and some sites in Romania (Mera bei Cluj, Girbou Cluj, associated with gypsum), Croatia (Mt Promina, Socka,) and Macedonia (Pcinja Basin) have many sclerophyllous elements (Mihajlovic 1990, 1992, 1993; Hably & Fernandez Marron 1998). A typical leaf flora rich in sclerophyllous elements from Ljiljanks Reka (Serbia) is illustrated by Mihajlovic (1992, fig. 1). Mihajlovic (1992, fig. 2) also illustrates the complete range of leaves of these sclerophyllous elements from the western Balkan Peninsula. The proportions of these sclerophyllous elements, and the expression of xeromorphy, seem to increase southwards in Europe.

Wilde & Frankenhauser (1999) drew attention to the risks of using nearest living relative preferences of a relict endemic taxon like *Comptonia*, a deciduous plant which inhabits poor and acid soils in eastern and central USA, as indicative of dry habitats in the past. In fact, fossil *Comptonia*-like leaves are found associated with fossil floras where all other elements indicate high humidity. Furthermore, xeromorphy is also known to be associated with nutrient poor acid soils, as with modern *Comptonia*, some mire species of *Myrica* and with the southern hemisphere family Proteaceae, all of which have a very similar leaf morphology. A few fossils with xeromorphic leaves should certainly not be used to justify reconstruction of a sclerophyllous vegetation, even if some of their nearest living relatives inhabit dry areas. Nevertheless, it is reasonable to argue that *Comptonia schrankii* is a sclerophyllous element because it characterises leaf assemblages dominated by sclerophyllous xeromorphic forms (Mihajlovic 1992, Hably & Fernandez Marron 1998).

Oligocene sites rich in sclerophyllous elements occur in the Ebro Basin in Spain (Sarreal, Cervera and Tarrega – MP21-MP23 – Hably & Fernandez Marron 1998). A sedimentological study (Anadón *et al*. 1989) showed that these floras were preserved in a series of lacustrine depositional sequences which include playas and playa lakes with evaporites and carbonates (limestones and marls) and in which the megasequences may reflect fluctuating climate or possibly Pyrenean tectonic activity. Some of the floras (Sarreal) are preserved in strata interpreted as more or less perennial stratified lakes. The Ebro Basin was landlocked since the Oligocene (Vilena *et al*. 1996a) so that loss of oceanic influence could also have affected the local climate and sedimentation. Vilena *et al*. (1996a,b) documented the presence of both large and small alluvial fans on the Iberian Margin of the Ebro Basin along with mud flats, carbonated lakes and saline lakes. They argued for dominantly tectonic controls on the alluvial fan sedimentation rather than variations between humid and arid climates but they did not exclude climate involvement in the shift from evaporitic to carbonate lacustrine sedimentation. In a study of the late Oligocene to Late Miocene lacustrine systems of the central Ebro basin Arenas & Pardo (1999) proposed a model where ephemeral rainfall on the Iberian margin resulted in playa lake settings. Laminated limestones were deposited at high water levels and nodular gypsum deposits at low water levels. Overall, sedimentological evidence tends to support the presence of intervals of water deficit in the Oligocene Ebro Basin.

Palynological evidence from the Ebro Basin was interpreted by Cavagnetto & Anadón (1996) to indicate a change, in the late Eocene, to a climate with a dry season. In the early Oligocene Sarral Formation (from which the macrofossils are derived) evidence for this included: the incoming of pollen whose nearest living relatives are herbaceous plants (e.g. grasses, Caryophyllaceae, Lamiaceae, Portulacaceae and Valerianaceae); the incoming of taxa such as Mimosaceae, *Mahonia* and *Daphne*, alongside those already present including *Ephedra* and Chenopodiaceae, whose nearest living relatives were argued to suggest drier conditions and more open vegetation; and the abundance of Cupressaceae pollen argued to be an indicator of a drier climate. Quantitative data for all taxa were not reported but it is clear that the herbaceous plants and flowering plant drier climate indicators were very rare, as the samples were dominated by bisaccate conifer pollen, Cupressaceae pollen and pteridophyte spores. Whilst some angiosperm pollen are underrepresented owing to their insect pollination strategy, grass pollen is wind dispersed and would be abundant if grass plants had been abundant. The Sarral Formation samples also included a high proportion (49%) of taxa with megathermal or mega/mesothermal affinities and many of the taxa have nearest living relatives, which are trees.

In southern England, sclerophyllous *Palibinia*-like foliage (see other areas below) occurs in the Bembridge Limestone Formation and Bembridge Marls Member (Bouldnor Formation), strata, which span the Eocene/Oligocene transition (Collinson *et al*. 1993b). The genus *Raskya* (Manchester & Hably 1997) also occurs within the Bembridge Marls in the Insect Limestone and it has recently been reported at the early Oligocene site of Céreste (Thiebaut 1999) in laminated lacustrine limestones deposited during water level fluctuations. *Raskya* also occurs at Kuclin (Czech Republic) and Obuda and Eger-Kiseged in Hungary (Thiebaut 1999). The Bembridge Marls Insect Limestone flora also contains *Zizyphus zizyphoides* but otherwise has a wide variety of wetland elements and no other sclerophyllous elements (Collinson *et al*. 1993b, Collinson in progress). The Bembridge Marls floras were interpreted as an extensive marshland (Collinson 1983b). Drier conditions were considered as one possible explanation for subtle differences between the Bembridge Marls and Bembridge Limestone floras, the Insect Limestone of the Bembridge Marls being more comparable to the latter (Collinson *et al*. 1993b). Insects from the Insect Limestone (which contains the sclerophylls mentioned) were interpreted, after taphonomic study, by McCobb *et al*. (1998) as reflecting a primary subtropical to tropical forest subject to significant seasonal rainfall. Open vegetation pollen types are rare to absent in pollen spectra, *Ephedra* type pollen is present but no grasses have been reported (Machin 1971, Collinson 1983b, Collinson *et al*. 1993b). In contrast, insects from Céreste, in particular a butterfly of the family Satyridae, (one isolated forewing) were suggested to indicate spreading of grasses in the early Oligocene of Europe (Pfretzschner 1998). The theridomyid rodent *Pseudoltinomys* from Céreste, on the basis of its gerbil-like locomotor adaptation, was suggested to indicate a semi-arid open habitat (Schmidt-Kittler & Storch 1985). Kvacek and Erdei (2001) reported the presence of xeromorphic foliage of *Berberis* (Berberidaceae) in the Oligocene of south France (including Céreste) but considered the overall vegetation to be a mesophytic forest reflecting a warm temperate to subtropical, subhumid climate.

Palynospectra from Toru Ajgyr (middle Eocene) in Kyrgyzstan (Fortuna 1979, Erfurt *et al*. 1999) are said to be dominated by xerophytes with grass pollen most frequent in all samples but they also contain many trees including subtropical elements. Xerophytic elements may be represented by chenopods, *Artemesia*, Myricaceae and *Ephedra* in the palynofloral list (percentages not stated).

Complementary sedimentological, palynological and macrofossil (especially foliar physiognomic) studies from sites with varied proportions of sclerophyllous elements across Europe are necessary to improve our understanding of this vegetation. Palynological processing and counting methods would need to be fully standardised (including quantification of grains per sediment volume) and comparable facies (including a range of facies) need to be examined for palynomorphs from all areas.

Summary Sclerophyllous elements occur rarely in southern Europe in the late Eocene. In the early Oligocene they occur rarely in northern Europe and more commonly in the south. In the south they dominate some sites (e.g. Sarreal, Spain and Macedonia) and they are important at others. Taking leaf floras, palynofloras, and sedimentological evidence into account it seems reasonable to regard the belt with common sclerophylls in southern Europe as vegetation adapted to a climate with a slightly drier interval. In view of the proportions of associated deciduous plants, the drier interval may have been in winter (Mai 1998). It should be emphasised that we are speaking of an overall humid, warm temperate climate with only slightly drier winters.

Floras of other areas

In China, Guo (1990) recognised a broad belt of distinctive vegetation with sclerophyllous elements in the central region in the Eocene. The key floral element, commonly found in every locality in this flora, is *Palibinia*. Other floral elements represent deciduous hardwoods, characterised by thick coriaceous and microphyllous leaves with serrate margins, and evergreen trees, mostly with leathery microphyllous leaves with entire margins (Guo 1990). Sedimentological indicators of drying out such as red beds, gypsum and halite are associated with the floras (Guo 1990).

Palibinia also occurs in the Bembridge Limestone and Bembridge Marls floras of England (Eocene/Oligocene transitional strata) (Tao 1965, Zhilin 1989, Collinson *et al*. 1993b); in late (?middle in earlier literature) Eocene floras at Badchyza in Turkmenistan (a flora lacking Lauraceae and palms characteristic of less sclerophyllous floras) and in the Pcinja Ovce Polje group Basin on the borders of Serbia with the former Yugoslavian Republic of Macedonia and Bulgaria (Mihajlovic 1993) also associated with other sclerophyllous elements. The genus is also very important in the early Oligocene Turgai floras of western Kazakhstan (Zhilin 1989) though it does not extend into the late Oligocene and it is apparently lacking in eastern Kazakhstan (Ashutas, Kiin-Kerish, Shiderty, Zhilin 1989, Makulbekov 1987). Mihajlovic (1993) argued that the vegetation containing *Palibinia* characterised the Tethyan archipelago, with aridification starting in the middle Eocene and reaching a maximum in the late Eocene and early Oligocene.

A thorough systematic revision of all *Palibinia* records by a single specialist, examining cuticles where possible, is badly needed. *Palibinia* has been variously compared with Proteaceae and Myricaceae. A relationship with the former seems unlikely in Europe on geographical grounds (Proteaceae being a southern hemisphere family) and other putative European Proteaceae have been reidentified to other families (e.g. Kvacek & Erdei 2001). Myricaceae may also be excluded on cuticle and hair base detail on new collections of British *Palibinia*-like specimens (Collinson *et al*. 1993b). Tao (1965) distinguished *Palibinia* as having pinnatifid coriaceous leaves, tertiary veins directed towards the sinus below, and one or two interstitial veins developed between the lateral veins. There is a strong primary vein and a secondary vein at 45-65° running straight to the apex with branching tertiary veins to the sinus below, sometimes with interstitial veins between the secondaries. Cuticle characters were not described. *Palibinia* is readily distinguished from *Comptonia*, which, in contrast, has 2-3 secondary veins leaving the main vein at angles of 60-90° (Wilde & Frankenhauser 1999, Manchester 1999).

Floras with many sclerophyllous elements (small, narrow and thick leaved oaks and laurels as well as *Myrica*) occur in northern and central Kazakhstan from the middle Eocene onwards, in western Kazakhstan in the late Eocene (?possibly middle Eocene) and in the Zaysan Basin in eastern Kazakhstan in the late Eocene. Oligocene floras of Kazakhstan also contain sclerophyllous elements including *Palibinia* as discussed earlier in this section (Zhilin 1989, Makulbekov 1987). Floras of Kazakhstan are discussed further in the section on late Eocene to Oligocene mixed deciduous and evergreen forests.

Vegetation overview

This vegetation is very variable depending on the proportion of the sclerophyllous elements. This overview is based on the sclerophyllous belt in southern Europe. The vegetation has medium to low diversity. Floras rich in sclerophyllous elements tend to contain relatively few easily determined key taxa whilst others remain unidentified, rendering even a preliminary statement about species diversity difficult. Mihajlovic (1992) figured sixty-two named categories of leaves from all the floras in the western Balkan Peninsula. One of these may include several taxa of legumes. The key taxa include *Zizyphus zizyphoides*, *Comptonia schrankii*, and *Myrica longifolia* combined with a high proportion of legume leaflets and pods and sometimes the conifer *Tetraclinis* and the enigmatic flowering plant *Palibinia*. These floras are perhaps best characterised by their physiognomic features, having large numbers of small (microphyllous or smaller), thick, coriaceous leaves with entire margins, often narrowly elongate in shape (Mihajlovic 1992, fig. 2; Hably & Fernadez Marron 1998).

This vegetation is inferred, by comparison with modern analogues rich in sclerophyllous elements, and on the basis of palynomorph evidence for some herbaceous plants, to have been more open forest or patchy forest (by comparison with the mixed mesophytic forests) ranging to shrubland. We do not know of any direct fossil evidence for the stature of the plants such as might come from study of paleosols (rooting depth or root size) or from associated wood floras (large or small diameter axes). Lianas and climbers were few or lacking in this flora. Some of the legumes may have been climbers on the basis of the habits of some living representatives. The vegetation was probably mainly evergreen. Xeromorphy would reduce water loss and enable leaves to be retained in drier intervals. The climate is suggested to have been a humid warm temperate climate with a slightly drier interval. Fruit resources would be very variable dependent on the dominant taxa. *Zizyphus* (fossil fruit stones known from Calau) probably had thin leathery flesh whilst fossils show that Myricaceae had small dry nuts and legumes had dry pods with various sizes of dry seeds. Fruit resources would be seasonal in their availability. This vegetation is therefore characterised by relatively tough coarse browse of small leaves, at least some of which was probably available at low levels, and many dry fruits/seeds with tough protective coverings.

DISTRIBUTION OF PALEOGENE VEGETATION AND COMMENTS ON ASSOCIATED MAMMALS

Introduction

Wolfe (1985) produced vegetation maps that, as he emphasised (Wolfe 1985 p. 372), provided only a partial picture and were painted with a broad brush. They showed vegetation belts on a global scale. The maps produced here plot vegetation at specific sites in Eurasia using the paleogeographic maps being developed by Paul Markwick (Markwick *et al*. 2000) as a framework and benefiting from a wide variety of recent literature (See text and references in Table 1). Occasional sites in North America are included where they are critical for vegetation reconstruction (e.g. Axel Heiberg) or to represent phytogeographic similarity. The picture is still only partial and the brush is still too broad (see 'criteria used here') but the data provide a general framework within which mammal faunas may be interpreted. The reader should refer to the individual references cited in the locality lists (Table 1) for details of the vegetation at any one site or region. More detailed location maps with additional sites may be found in Mai (1995), Tanai (1992), Takhtajan (1974, 1982), and Budantsev (1994b).

Paleocene of the northern hemisphere (Fig. 1)

Vegetation distribution The distribution map (Fig. 1) shows polar broad-leaved deciduous forest in the high northern paleolatitudes ranging from the northern-most land, at about 80° North, south to between 45 and 60° North depending on the area. Important areas and sites include Alaska; Rarytkin Ridge, Kamchatka and Sakhalin in Russia; Spitsbergen; Greenland; Axel Heiberg and Ellesmere Islands, Canada; Scotland and Ireland. Very similar floras are also known in Alberta and Saskatchewan (Canada) and in the Fort Union Formation of Wyoming (Montana and North Dakota, USA). 'Mixed' vegetation with some polar deciduous elements but also other, often thermophilic, elements is mapped in southern England and France, Sakhalin, China, Mongolia and the Zaysan Basin (east Kazakhstan). Elsewhere in western Europe and eastwards to west Kazakhstan the vegetation includes a high proportion of evergreen thermophilic elements. This thermophilic vegetation is the forerunner of the Eocene paratropical to subtropical evergreen vegetation but it also includes deciduous elements, which dominate further north. Unfortunately we are not aware of Eurasian records south of about 30° North, which would enable assessment of the wider distribution of this thermophilic vegetation in the Paleocene.

A workshop discussion, reported in Boulter & Fisher (1994 p. 391), and studies by Mai (1987, 1989, 1991, 1995) indicate paleophytogeographic subdivision into an Arctotertiary Realm and a Boreotropical Realm consistent with the polar deciduous floras and the more evergreen floras respectively. The former can be subdivided floristically into the Greenland and Beringian Regions and the latter includes the Gelinden Region and the Volgo-Mugojar Region (Mai 1991, fig. 2). The floras of China and Mongolia were not discussed by these authors but may represent another

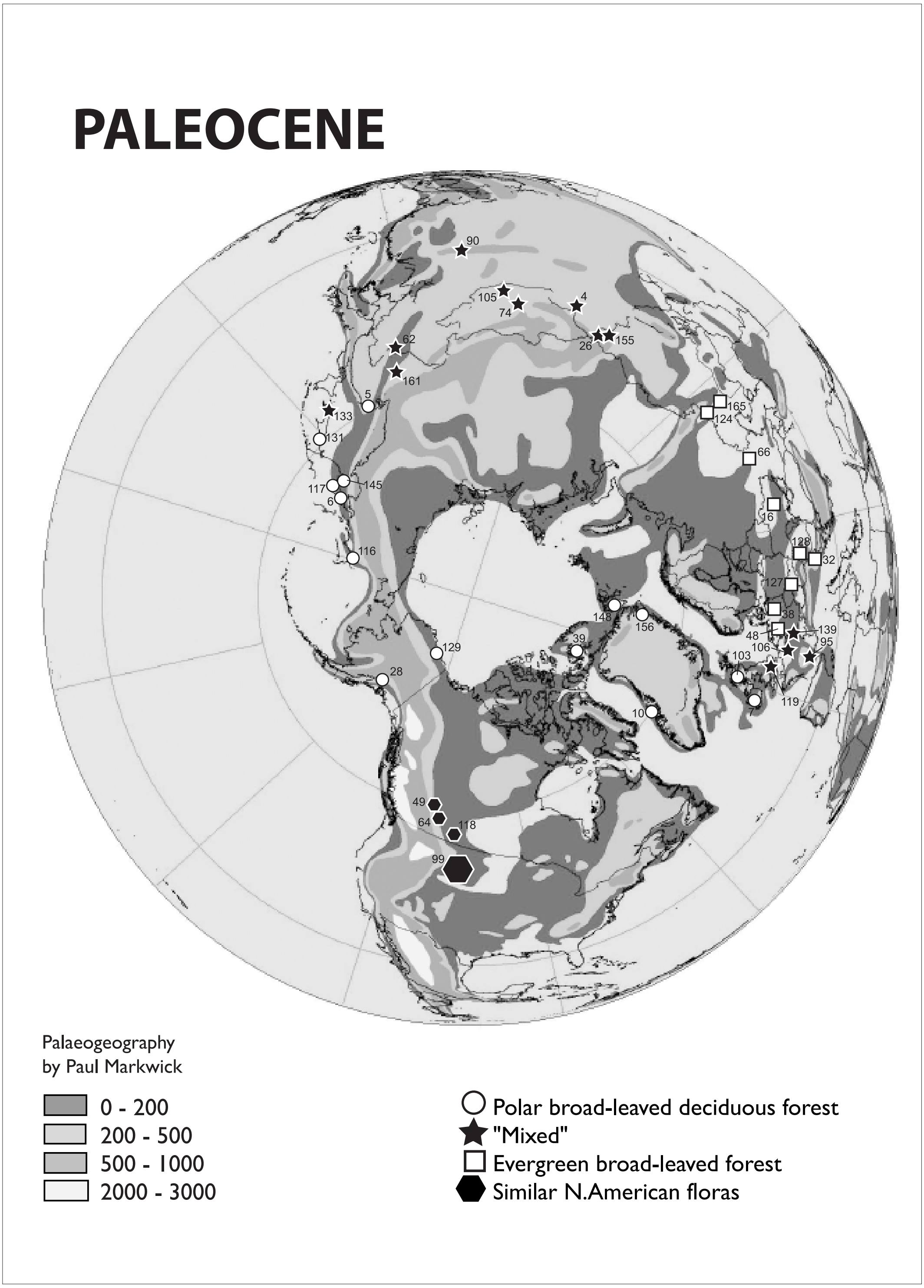

Figure 1 Distribution map of the Paleogene floras which are listed in Table 1 (Paleocene). Palaeogeography from unpublished maps being produced by Paul Markwick (see Markwick *et al*. 2000).

realm or region, where some of the floras (e.g. Mongolia) are only slightly different from those of the polar deciduous forests.

These latitudinally controlled vegetation distribution realms, with distinct floral Regions, seem to have been inherited from the late Cretaceous. Late Cretaceous palynofloral provinces show a northern *Aquilapollenites* province and a southern *Normapolles* province and also show distinctive vegetation in the European area versus the Kamchatka area (Herngreen *et al*. 1996). Latest Cretaceous leaf floras from Kamchatka and the Rarytkin Ridge and other high northern areas contain many elements also present in the Paleocene polar broad-leaved deciduous floras and reflect the same vegetation type (Herman 1993; Herman & Spicer 1996, 1997; Spicer *et al*. 1994; Golovneva 1996).

Dispersal routes Patterns of plant distribution are of three types; circumboreal, North American/Asian and North American/ European (Manchester 1999). In the Paleocene there are many circumboreal plants. Some of these distributions may have been inherited from the Cretaceous (e.g. for *Nordenskioldia* [see Crane *et al*. 1991 for map] and *Nyssidium* plants). In contrast, others, e.g. that of the tree *Palaeocarpinu*s of the Betulaceae (Crane 1981, Chen *et al*. 1*999, Golovneva 2002) and the aquatic herb Haemanthophyllum* (Golovneva 1997), seem to have been achieved in the Paleocene. In the Paleocene there are a number of taxa (at least 6 genera including small aquatic plants like *Quereuxia* and trees of the Platanaceae and other reconstructed woody plants like *Amersina* of the Cornales (Manchester *et al*. 1999)) shared between Asia and North America indicating dispersal via Beringia. There are also taxa, such as other trees of Platanaceae (*Platanites*) and trees of the Fagaceae (*Fagopsiphyllum*), which occur in North America and Europe but not in Asia, suggesting dispersal via North Atlantic land bridges (Manchester 1999).

Mammals in the Mongolian late Paleocene
The mammal faunas with the closest association with polar deciduous forests in the late Paleocene are those from Mongolia and northern China (Inner Mongolia). The relevant faunas of the Naran Member at Naran Bulak and of the Gashato and Bayan Ulan sites need to be summed to provide an adequate sized assemblage to assess their ecological diversity. Small animals dominate e.g. multituberculates, mixodontians, arctostylopids and a pseudictopid. The largest were a wolf-sized mesonychid, a pig-sized dinocerate and a cow-sized coryphodontid pantodont. Available postcranial evidence indicates that these were terrestrial (Archibald, Lucas in Janis *et al*. 1998, Flerov 1967) or, in the case of the smaller animals (not well known), probably mostly semiterrestrial (Kielan-Jaworowska & Gambaryan 1994, Li & Ting 1993, Cifelli & Schaff in Janis *et al*. 1998, Sulimski 1968). The only evidence of adaptation for tree-climbing ability belongs to the creodont *Prolimnocyon*, based on skeletal remains from North America (Gebo & Rose 1993), although Lucas (in Janis *et al*. 1998) has hinted that the small pantolambdodontoid pantodonts may have been tree-dwelling. A significant number of the mammals from this fauna, including the smaller ones, were browsing herbivores. This paucity of tree-dwellers and large numbers of herbivores somewhat resembles patterns obtained from modern semi-deciduous forests (Andrews *et al*. 1979), largely consistent with reconstructed vegetation.

Eocene of the northern hemisphere - polar broad-leaved deciduous forests (Fig. 2)

Vegetation distribution In the Eocene the polar deciduous forest is still represented at high northern latitudes including sites on Spitsbergen, Axel Heiberg and Ellesmere Islands (Kvacek *et al*. 1994, Golevneva 2000, McIver & Basinger 1999). The flora of the

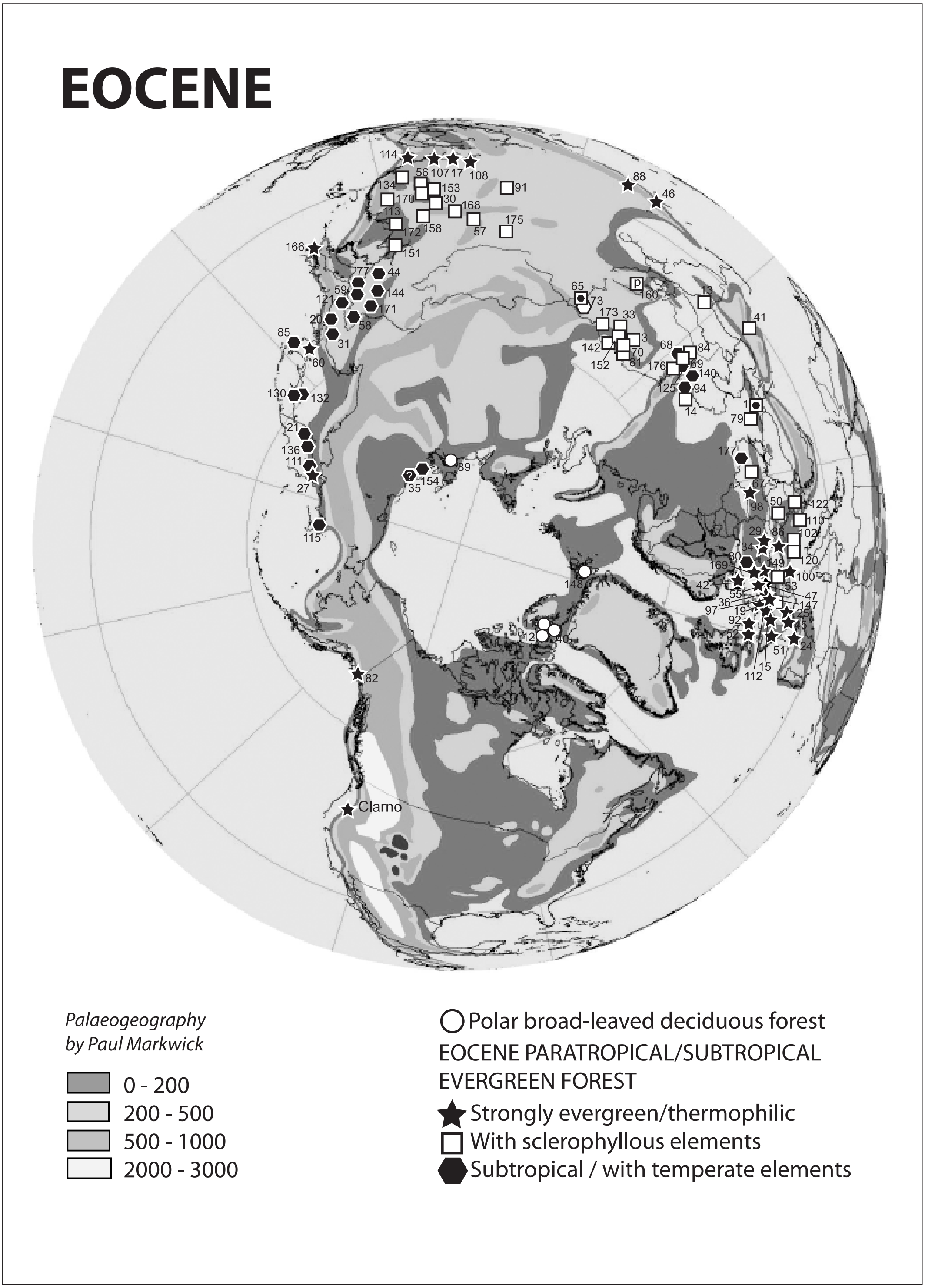

Figure 2 Distribution map of the Paleogene floras which are listed in Table 1 (Eocene). Palaeogeography from unpublished maps being produced by Paul Markwick (see Markwick *et al.* 2000).

Lena River in northern Russia (Budantsev 1994a) is similar. Rather different floras occur in the Rarytkin range at the Podbazovyi Creek on the Taljain Creek tributary in the Pravataljainskaya Formation (Akhmetiev & Samsonenko 1997) and at Tastakh (Budantsev 1994a). The extent to which these indicate different vegetation requires more detailed systematic and physiognomic comparison. The floral lists do suggest that they indicate a more thermophilic vegetation.

Mammals associated with Eocene polar broad-leaved deciduous forests In the late Early Eocene, mammal faunas are known from Ellesmere Island and one species from Axel Heiberg (West & Dawson 1977, 1978, McKenna 1980, Eberle & Storer 1999). The faunas so far published contain no truly arboreal mammals (e.g. in the form of primates). Tree-dwellers were potentially scansorial (post-cranials not known for confirmation, extrapolation based on partial skeletons, skeletal elements elsewhere of related taxa, specimens not yet described), including rodents (Szalay 1985), paromomyids and plagiomenids. The last two groups may have been gliders but this is controversial (Beard 1990, Runestad & Ruff 1995, Szalay & Lucas 1996). Scansorial mammals depend less on trees than truly arboreal mammals in that they do not need the aerial walkways (overlappping branches, lianas etc.) afforded by a closed canopy forest.

There are relatively few frugivores in the fauna. The multituberculate *Neoplagiaulax* is likely to have had a mixed diet of insects and dry fruit/seeds (Krause 1982). Paromomyids are usually attributed a mixed fruit/exudate diet (Beard 1990, McKenna 1980). The rodents would have had a mixed fruit/insect diet and the dawn horse "*Hyracotherium*"? a mixed fruit/leaf diet. On the other hand the diverse plagiomenids and the abundant *Hyrachyus* (stem rhino) and *Coryphodon* (pantodont) and probably *Lambdotherium* (brontothere) would have had a near exclusive leaf-browsing diet. It is possible that the absence of insectivores may represent a collecting bias as relatively little screenwashing was undertaken. Lower latitude faunas of equivalent age in North America have a greater diversity and abundance of frugivores, e.g. in the form of hyopsodontid condylarths and notharctid primates notable absentees from Ellesmere.

Eberle & Storer (1999) suggested that Brontotheres (perissodactyls - as hindgut fermenters) survived in the 2-3 months of winter darkness by feeding on litter (leaves fruits and seeds etc.) and bark, branches, twigs etc., being able to handle low quality food provided it is available in high quantity. The other large herbivores *Hyrachyus & Coryphodon* would also have been hindgut fermenters but have low-crowned bilophodont teeth comparable to those of modern tapirs which live in very low seasonality tropical forests, bulk feeding on leaves of evergreen trees. As there is no modern analogue for a warm dark forest (Basinger *et al*. 1994, McIver & Basinger 1999) it is difficult to predict how deciduous leaves would behave and how much nutrition would remain in the litter. Clearly, the fossiliferous levels prove that huge thicknesses of litter accumulated and persisted. The large-leaved dicotyledons in the flora might then have been fed upon from the litter by these mammals. The ‘upland’ broad-leaved deciduous forests contained evergreen conifers (McIver & Basinger 1999, Basinger *et al*. 1994) and these may have contributed to the food of herbivore browsers during the winter darkness. However, there is an issue that the large hoofed browsers would probably not have been able to reach much of the evergreen conifer browse if the ancient trees were of comparable stature to their nearest living relatives. This browse would, nevertheless, have been available to the climbing plagiomenids. Dentally, however, these seem unsuited to masticating conifer needles and hibernation might have been an alternative option for them.

Eocene of the northern hemisphere - paratropical/subtropical evergreen forest with sclerophyllous elements

Vegetation distribution There are several areas where paratropical to subtropical vegetation contains sclerophyllous elements at different times in the Eocene. The first area is in the late Eocene of southern Europe east to Ukraine and the Caucasus. These sclerophyllous elements are those which become much more common in southern Europe in the Oligocene, especially *Zizyphus zizyphoides*, *Comptonia schrankii* and other Myricaceae. The second area is in the late (or in places middle and late) Eocene of Kazakhstan, Turkmenistan, central Iran and Kyrgyzstan (the last from palynological evidence only). The third area is in the Eocene of central China where precise dates are lacking. Arguably these form a discontinuous belt between about 30-50° North. It must be emphasised that the mere presence of sclerophyllous elements in these floras may not be sufficient to justify reconstruction of a drier climate. If the climate was drier we are speaking of a slightly drier interval within an otherwise humid setting. *Palibinia*, the key sclerophyllous element in the Chinese floras, is also recorded in Turkmenistan and in Eocene/Oligocene transitional and Oligocene floras further west (see vegetation with sclerophyllous elements).

Mammals in China In China a central belt with sclerophyllous elements, and hence possibly a drier interval, is bounded to the south by evergreen paratropical rain forest and to the northeast by subtropical evergreen forest (Guo 1990). Information on Chinese Paleogene mammalian faunas is obtained from the comprehensive review by Russell & Zhai (1987). Lagomorphs are almost entirely restricted to Mongolia and northern Chinese localities, very few straying southwards (Russell & Zhai 1987, Zhang *et al*. 2001). Lagomorphs are ground dwellers and are typical of dry open habitats today. They have had relatively high-crowned teeth since their oldest undoubted records in the Eocene and this can be attributed to an abrasive herbivorous diet. The Eocene vegetation of Mongolia has not yet been studied (Makulbekov 1987). However, the middle Eocene northern Chinese lagomorph records overlap with floras indicating sclerophyllous/microphyllous forest vegetation.

In contrast, typical bunoselenodont anthracotheriid artiodactyls are almost entirely restricted in the Irdinmanhan Asian land mammal age (Lutetian) to the extreme south of China and Burma with only one record in central China. However, more reach the central and northern regions in the Sharamurunian (Bartonian) but were gone again in the late Eocene Ergilian. These are likely to have had a mixed frugivorous/herbivorous diet which might have restricted them from moving north into the central, possibly drier, region except during the slight late Middle Eocene climatic amelioration. Brontotheriid perissodactyls occur throughout the area but show a greater diversity in both the north and south than in the central region of China. Although no account here is taken of taphonomic/collecting bias, this pattern does persist through the middle and late Eocene after which extinction intervened. It is difficult to account for this but inasmuch as they became extinct at the end of Eocene the vegetation types in the Eocene (e.g. with sclerophyllous elements) that heralded those of the Oligocene may have been suboptimal for them. On the basis of the almost total absence of any primate, plesiadapiform or bat in the Eocene of the Mongolian plateau except the single early Eocene primate species *Altanius orlovi*, Meng and McKenna (1998) concluded that this implied the absence of dense forest in the region. In contrast, a diversity of primates and plesiadapiforms (all assumed tree-dwelling) are known from the central Chinese region (Wutu: Beard & Wang 1995, Yuanqu: Beard *et al*. 1996, Shanghuang fissure fillings: Beard *et al*. 1994) suggesting treed habitats consistent with the plant evidence.

Eocene of the northern hemisphere - paratropical/subtropical evergreen forests (Fig. 2)

Vegetation distribution The most strongly evergreen thermophilic category of this vegetation (Fig. 2 stars) is present in a belt through western, central and eastern Europe and extending into Ukraine. Strongly thermophilic vegetation also occurs as a belt in southern China and as more isolated records in Japan and Kamchatka. The high latitude record in Kamchatka is matched by a similar high latitude record (the Kultieth flora) in Alaska. The high latitude Tastakh flora in northern Russia contains a number of thermophilic elements (Budantsev 1994a) but the Lena River flora is warm temperate (Budantsev 1994a) and more similar to the Eocene polar deciduous forest floras and was discussed earlier. Unfortunately we have not been able to locate an original reference for the flora of Dzilon-Sise. The Rarytkin Range Podbazovyi Creek flora is described as thermophilic mesophilic conifer-broadleaved deciduous forest vegetation (Akhmetiev & Samsonenko 1997). It lacks the *Trochodendroides* leaf types characteristic of Eocene polar deciduous forests. Tanai (1992, fig. 5a) mapped mixed Coniferous forest at high northern latitudes in the middle Eocene based on the floras of Rarytkin, Tastakh and Dzilon-Sise (Tanai 1992, fig. 1 map). This does not seem to be an appropriate interpretation of the floral lists. The variations in far eastern and northern Russian high latitude floras may be due to age differences but we are not aware of independent dating for these floras. Further research is required to compare these floras more closely with one another and with the Eocene polar deciduous floras, especially from a physiognomic perspective.

The majority of the dominantly evergreen vegetation in Europe occurs around the thermal maximum in the early and early middle Eocene (evidence from independent dating). Elsewhere the dating is not so precise. Those sites where the literature uses the term ‘subtropical’ rather than paratropical, and emphasises ‘with temperate elements’, have been distinguished on the map (Fig. 2, hexagons). The extent to which these floras differ, and the precise nature of the differences, needs further detailed study. In several areas of Europe, and in Kazakhstan, Kamchatka and Japan trends during the Eocene (either through independently dated floras or superposed floras) can be recognised with an increase in the component of temperate deciduous elements (or sclerophyllous elements) with time (see Oligocene floras below). The subtropical/with temperate elements vegetation on the Eocene map, therefore, encompasses both spatial and temporal variation in Eocene vegetation, which cannot be more precisely plotted without improved independent dating and further detailed comparisons of the floras across Eurasia. Furthermore, it should be noted that the European region, with strongly evergreen thermophilic vegetation in the Early and early Middle Eocene, also contains sites with more deciduous temperate elements in the late Middle and Late Eocene. These could not all be plotted on a single map.

Dispersal routes Dispersal routes are likely to have been present via the North Atlantic and North Pacific. The Middle Eocene (44Ma) Clarno flora of western North America (Fig. 2) shares 24% genera with Europe (20% genera and 10% species with London Clay flora alone) (Manchester 1994). This clearly indicates interchange prior to the Middle Eocene. A dispersal route via Beringia is possible but would need confirmation from records in Asia. Only a very few newly appearing taxa are shared between Asia and North America (Manchester 1999) but fruit and seed floras comparable to those of Clarno and the London Clay are not known in Asia. In any case the Turgai seaway may have intervened. Exchange via the North Atlantic (via Greenland and Iceland using either the Thule or de Geer Route) is more likely (Manchester 1999, Tiffney 2000). However the high latitude floras in the North Atlantic area give little hint of the presence of thermophilic taxa at the time when dispersal should have been occurring (Manchester 1999, McIver & Basinger 1999). Indeed, more thermophilic floras seem to occur in the Beringian region (e.g. at Tastakh and at Chemurnaut Bay, Kamchatka) although these require more precise dating (see earlier).

Associated mammals in Europe The ecological diversity patterns of the mammals from Early Eocene sites in Europe match quite closely with those of evergreen forests in Borneo (Hooker 1998). The ecological diversity of mammals suggests that in the middle Eocene, after the thermal maximum, there is an increase in the number of larger mammals and of herbivore browsers (with the low crowned bilophodont tooth type found today in tapirs, Hooker 2000). By the late Lutetian there was a slight increase in hypsodonty in perissodactyls (Legendre *et al*. 1991) indicating coarser browse and a slight further increase in larger mammals suggesting slightly more open forests; however, many fruit-eaters persisted. These changes persisted. The bilophodont tooth types were lost by the end of the middle Eocene (Collinson & Hooker 1987). The late Eocene saw a further increase in hypsodonty not just in perissodactyls but especially in rodents such as theridomyids (Vianey-Liaud 1991) and a reduction in frugivorous types and specialisations for seed-eating in glirids, demonstrated by gnawed *Stratiotes* seeds (Collinson & Hooker 2000). There are also more larger mammals and fewer arboreal forms. All these changes are consistent with the gradual change from the evergreen thermophilic forests to the mixed deciduous and evergreen forests of the Oligocene.

Oligocene of the northern hemisphere - broad-leaved mixed deciduous and evergreen forests (Fig. 3)

Vegetation distribution As noted above there is a gradual trend from Eocene paratropical/subtropical evergreen forest vegetation through vegetation with an increasing proportion of temperate deciduous elements resulting in the Oligocene in establishment of broad-leaved mixed deciduous and evergreen forests across Eurasia between about paleolatitudes 55 and 40° North (Fig. 3).

Four sites in central Russia (Vickulin 1999a,b) and Caucasus (Akhmetiev 1995) may reflect more thermophilic vegetation but these require further study (see earlier). Floras in Hungary indicate retention of a strong thermophilic signal into the early Oligocene but its loss by the late Oligocene. There seems to be only one flora (Sergeya in Russia) from high northern paleolatitudes (Tanai 1992). We have not been able to locate recent literature on this site and the age is uncertain (Takhtajan 1982). Three floras in China indicate the presence of tropical/subtropical forests in the south and warm temperate deciduous broad-leaved forests in the north (Guo 1990,1993). The two Japanese sites are late Eocene to early Oligocene and are referred to as having warm temperate deciduous floras.

The European floras seem to exhibit very wide variation in the proportions of sclerophyllous elements. Some floras have only one or two sclerophyllous elements within an otherwise mixed mesophytic forest assemblage (e.g. Lausitz) or a notophyllous evergreen forest (e.g. Hungary). In contrast some floras, e.g. those at Sarreal in Spain and sites in Romania, Croatia and the former Yugoslavian Republic of Macedonia, have many sclerophyllous elements. The proportions seem to increase southwards. Evidence from leaf floras, palynology and sedimentology seems to indicate that the belt with common sclerophylls in southern Europe was, at least in places, a vegetation adapted to a humid warm temperate climate but with a slightly drier interval, probably in winter.

In Kazakhstan the floras also contain sclerophyllous elements. The sclerophyllous element *Palibinia* characterises the early

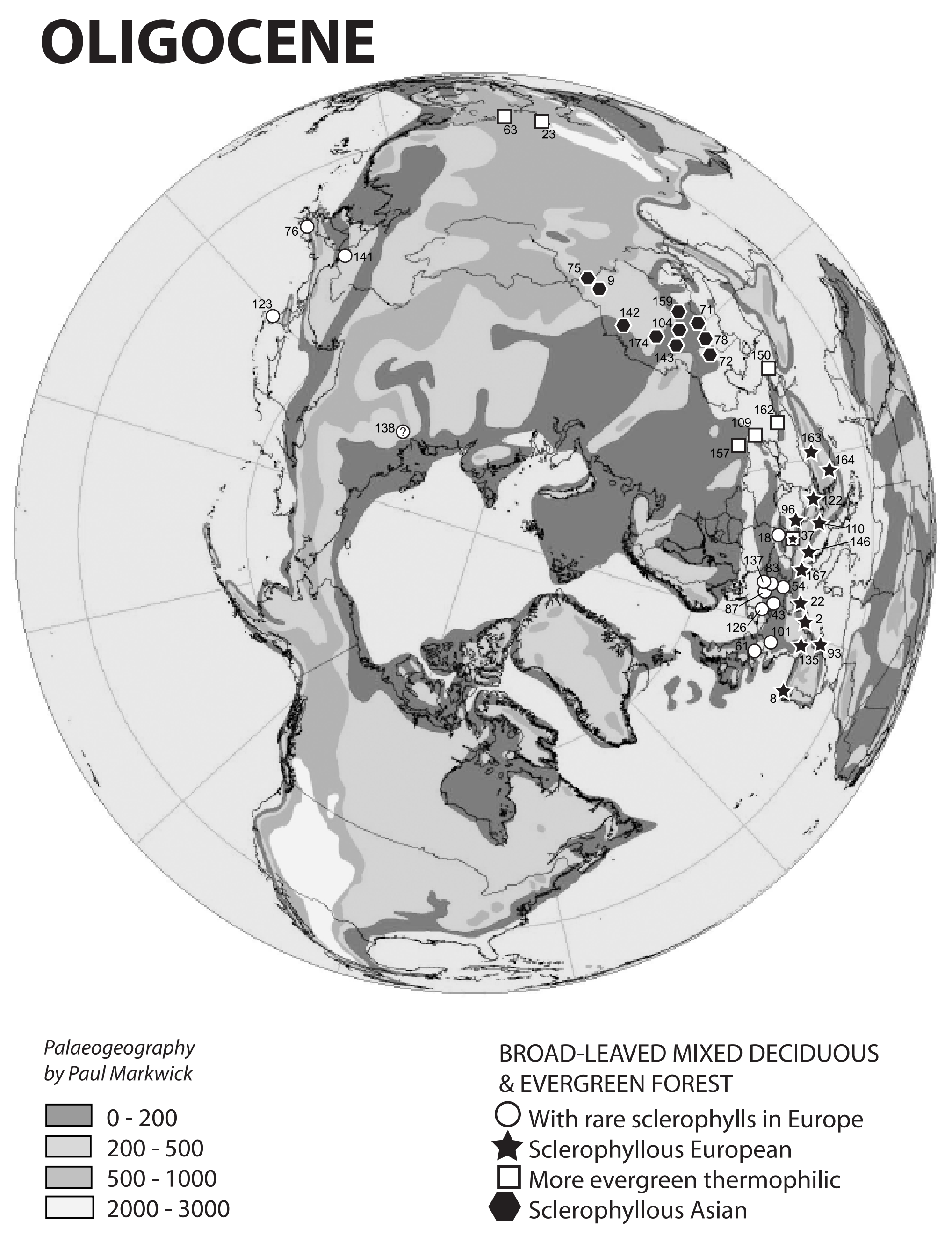

Figure 3 Distribution map of the Paleogene floras which are listed in Table 1 (Oligocene). Palaeogeography from unpublished maps being produced by Paul Markwick (see Markwick *et al.* 2000).

Oligocene floras of western Kazakhstan but it is lacking in floras further east in the Zaysan Basin. In western Kazakhstan subtropical elements persist in the early Oligocene but are lost by the late Oligocene (Zhilin 1989).

Dispersal routes A number of identical or closely related taxa are shared between Europe and North America in the Oligocene (e.g. species of the conifer *Tetraclinis* and the flowering plants *Cercidiphyllum*, *Mahonia*, *Cedrelospemum*, *Catalpa* and *Saportaspermum* (Hably *et al*. 2000). These indicate that exchange must have occurred during or prior to the Oligocene and although some e.g. *Cedrelospermum* seem to have established this range in the Eocene, others may have done so in the Oligocene (e.g. *Mahonia* and *Saportaspermum*) (Manchester 1999, Hably *et al*. 2000). In addition there are a number of circumboreal genera in the Oligocene (Hably *et al*. 2000), which may have attained this distribution prior to or during the Oligocene. Dispersal could have been via Beringia or North Atlantic Bridges, though the Turgai/west Siberian seaway intervened in the Eocene and it was not until the Oligocene that there was a full land connection between Europe and Asia. The extent to which the land bridges were available, is discussed by Tiffney (2000). The North Atlantic land bridge would seem to have been broken by the beginning of Chron C24N (early Eocene) (Hooker 1998). Further comparisons at species level using reconstructed whole plants will be necessary to establish phytogeographic similarities with more precision.

Mammals indicative of drier habitats Evidence from the paleoecology of mammals for drier more open habitats in the Oligocene has been put forward for both Europe and the Mongolian Plateau. This has involved particularly rodents, which, in both areas, undergo significant increases in molar crown height (Vianey-Liaud 1991, Meng & McKenna 1998) and several European taxa have enlarged auditory bullae and ricochetal locomotion (hopping) (Vianey-Liaud 1991). Furthermore, hindgut-fermenting perissodactyls diminish while foregut-fermenting artiodactyls increase (Meng & McKenna 1998, Janis 1989) suggesting use of high quality but rare/patchy browse rather than abundant low quality browse. These trends were beginning in the European late Eocene when mammalian ecological diversity is indicative of drier more open habitats in southern France than in southern England (Hooker 1992, Franzen 1968). Moreover, northward dispersal of certain mammalian taxa suggests northward expansion of such habitats (Hooker *et al*. 1995).

India and Southeast Asia

Vegetation distribution Indian Paleogene floras are best known from the Deccan Intertrappean series (latest Cretaceous/Paleocene transition). These floras, which are preserved in cherts, are dominated by fossil wood along with some fruits and seeds. These are hard to compare with floras from Eurasia. Some leaf floras are also known but I am not aware of any work with a thorough systematic comparison of these with Eurasian leaf floras. Study of wood and leaf physiognomy, combined with evidence from nearest living relatives of woods, leaves and palynomorphs, suggests that warm, humid tropical to subtropical, evergreen to semi-evergreen forest vegetation existed in India through the Paleogene (e.g. Kar & Sharma 2001; Morley 2000; Bande & Chandra 1990; Prakash 1960, 1973; Singh & Sarkar 1990; Kumar 1994; Awasthi & Mehrotra 1995; Guleria & Srivastava 2001). This was probably similar to wet evergreen forests in the area today (Guleria & Srivastava 2001) e.g. the western Ghats (Banda & Chandra 1990). Similar vegetation is indicated by palynological evidence from Java for the Middle Eocene (Lelono 2000) and generally in Southeast Asia (Morley 2000) and also by the rather sparse macrofossils from Southeast Asia (Bande & Prakash 1986).

The family and generic affinities (macrofossils) of the Southeast Asian Paleogene floras (Bande & Prakash 1986) differ from those of the European floras (Mai 1995). It must also be emphasised that the European thermophilic floras do not represent modern Southeast Asian rain forest (Collinson 1983a, 2000b, 2001a) although many fossils with near living relatives in these rain forests do occur in the European Paleogene. Notably, in the Paleogene of Europe, dipterocarps are represented only in the London Clay flora and only by one twig, and the rest of the wood flora (Poole 2000) differs from that of the Paleogene of India and Southeast Asia. It should, however, be noted that dominance of dipterocarps did not characterise even the Southeast Asian rainforests until the Neogene (Morley 2000). A further difference is the apparent absence of epiphytes (Collinson 2000b, 2001a) though this may be due to taphonomic factors. At least some lignites in Java have been shown to originate from palm-dominated mires based on palynological evidence (Lelono 2000, Morley 2000) and palms are abundant and diverse in the Paleogene floras of both India and Southeast Asia (references above).

Modern Southeast Asian tropical rainforests are characterised by very high diversity (e.g. Morley 2000) and it is interesting to consider the past situation. The very different nature of plant macrofossils and facies in the Southeast Asian and Indian Paleogene floras makes it impossible to compare diversity from this evidence. Palynological data offer the best opportunity for comparison but this is also severely hampered by different taxonomic approaches including different nomenclature systems in Southeast Asia and Europe for historical reasons. During the course of PhD work by Lelono (2000), Morley, Collinson and Lelono noted a number of pollen types that seem to be very similar to, if not the same as, those from the European Paleogene (see also Harley & Morley 1995). Further work is needed by an experienced palynologist making direct comparisons of material from both areas.

Lelono (2000) in his study of the Middle to Late Eocene coastal sequences of Java recorded over 300 different palynomorphs with 80 distinct taxa occurring at over 3% i.e. important in the flora. Collinson *et al*. (1981) and Boulter & Hubbard (1982) studying the Eocene coastal sequences of England, recorded 80-100 distinctive and important form genera on which they based their statistical analyses. (The total number of form species was not documented). Thiele-Pfeiffer (1988) documented 173 form species from the early Middle Eocene of Messel, Germany, whilst Nickel (1996) documented 190 from the late Middle Eocene of Eckfeld, Germany, both representing isolated lake basins. Harrington & Kemp (2001) and Harrington (2001) documented 164 form species in the Paleocene /Eocene boundary interval of the United States Gulf Coast paratropical forests whilst Wing & Harrington (2001) recorded only 93 in the comparable interval in the continental interior Bighorn Basin, Wyoming, USA. These figures tend to suggest that northern hemisphere Eocene evergreen thermophilic forests had similar levels of diversity to the Eocene Southeast Asian forests in their 'common' constituents (around 80-100 form species) whilst the overall diversity may have been lower, totalling up to 200 rather than over 300 taxa. These figures represent a very inadequate glimpse into this topic and further research by a single individual applying a uniform taxonomic approach and using samples from comparable facies (ideally several facies) is essential to provide a more meaningful comparison.

Dispersal The palynological record provides strong evidence for dispersal of plants from India into Southeast Asia by the Middle Eocene (Morley 1998, 2000, Lelono 2000). Lelono (2000) and Morley (1998, 2000) reported at least 15 distinctive palynomorphs, which first appear in the Paleocene or early Eocene of India (e.g. Frederiksen 1994, Kar & Sharma 2001), and are also found in the Middle Eocene of Southeast Asia. These include taxa whose near living relatives are several kinds of palms (pollen of *Proxapertites*, *Longapertites*, *Quillonipollenites*, and the peat-former *Palmaepollenites kutchensis*) and members of the Bombacaceae (*Lakiapollis ovatus*), Sapindaceae and possibly Proteaceae (*Beaupreadites*), Linaceae, Olacaceae, Polygalaceae and Ctenolophonaceae and one spore type. Diverse arrays of *Spinizonocolpites* (= *Nypa* pollen) species are present in the Paleocene of Indo-Pakistan but by the Eocene only one survives (Frederiksen 1994). The occurrence of only one (although variable) type (*S. echinatus*), in Southeast Asia (Morley 2000, Lelono 2000) suggests that dispersals from India did not reach Southeast Asia in the Paleocene. Frederiksen (1994) also argues that the occurrence of Normapolles pollen in the late Paleocene of Pakistan may be evidence for sporadic filtered dispersals from Eurasia to Indo-Pakistan at this time.

The paleogeography of the India and Southeast Asian areas has been studied by Hall (1998, pers comm. 2001) who argues that the Indian/Asian collision had taken place by the end of the early Eocene (50Ma) implying the earlier close proximity of land. Roger *et al*. (2000) also argue in favour of India's initial impact "well before" 48 Ma on the basis of overthrusting already in progress at that time. Rowley (1996) presented evidence for well constrained dating of the collision starting in the late Ypresian in the western Zanskar-Hazara region of the Himalayan region. Areas of land in Greater India and Greater Asia are largely speculative (Hall 1998), but supported, at least as island areas, by early Eocene mammalian faunas from Pakistan (Gingerich *et al*. 1997, Clyde & Khan 2000). India has been cited (Krause & Maas 1990) as one possible source of the mammals that spread rapidly across the northern hemisphere at the beginning of the Eocene in what is termed the Mammalian Dispersal Event. Mammalian dispersal from central Asia into the Indian subcontinent at this time has also been proposed (Maas *et al*. 2001). Plant fossil evidence (above) indicates that the mammalian dispersals would have occurred within humid thermophilic evergreen forests, although disturbance to this vegetation should be predicted as a result of tectonic activity (e.g. vulcanicity).

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Table 1 List of sites of the Paleogene floras which are plotted on Figures 1-3. In the 'Age' column * indicates age undefined within the interval stated.

Number	Site name	Location	Age	Literature
1	Achalziche	Georgia, Caucasus	late Eocene	Mai 1995, Akhmetiev 1995
2	Aix en Provence, Marseille & Céreste	South France	early Oligocene	Mai 1995, Hably et al 2000, Thiebaut 1999.
3	Akhzar	Kazakhstan	late Eocene/early Oligocene	Makulbekov 1977, 1987
4	Altai County, Wulonggu Fm	Xinjiang, S China	Paleocene	Liu et al 1996, Guo 1990, Crane et al 1991
5	Amur, Malomikhaylovskaya Fm	Amur Region, E Russia	early Paleocene	Herman & Spicer 1996, Kvacek & Manum 1993, Golovneva 1996
6	Anadyrka	Kamchatka	late Paleocene to early Eocene*	Budantsev 1994a,1997, Fotyanova 1995
7	Antrim, Ballypalady	Northern Ireland	Paleocene	Boulter & Kvaeck 1989
8	As Pontes	Spain	late Oligocene	Hably & Fernandez Marron 1998
9	Ashutas	Zaysan, E .Kazakhstan	Oligocene	Zhilin 1989, Makulbekov 1987,
10	Atanikerdluk	W. Greenland	Paleocene	Koch 1963, Boulter & Kvacek 1989
11	Axel Heiberg Is., Buchanan Lake Fm.	Axel Heiberg Island, Canada	middle Eocene	McIver & Basinger 1999
12	Axel Heiberg Is., Strand Bay, Iceberg Bay Fm	Axel Heiberg Island, Canada	early Eocene	McIver & Basinger 1999
13	Badkhyz/Badchyza (Eroylanduz)	Turkmenistan	middle or late Eocene*	Zhilin 1989, Mihajlovic 1993
14	Baki	Kazakhstan	late Eocene	Makulbekov 1977,1987
15	Belleu and Vervin, Aisne	Paris Basin, France	early Eocene	Mai 1995; Collinson 1983a 1993; Koeniguer et al 1985; Koeniguer 1988
16	Boltyschka	Volga region	Paleocene	Mai 1995
17	Bose Basin	Guangxi, S China	Eocene	Liu et al 1996, Guo 1990
18	Brezno	Central Slovakia	?mid-late Oligocene*	Sitar & Kvacek 1993, Mai 1995
19	Brussels	Belgium	early middle Eocene	Mai 1995, Collinson 1983a, Collinson 1993
20	Buyanikha & Velikaya Kema Rivers	Primorye Region, Russia	late Eocene	Fotyanova 1997, Tanai 1995
21	Bystraya & Belogolovaya Rivers	Kamchatka, Russia	late Eocene	Budantsev 1994a,1997
22	Cadibona near Savona	Liguria, Italy	Oligocene	Mai 1995
23	Cangyuan County, Manghui Fm	Yunnan, SW China	Oligocene	Guo 1990,1993
24	Castrais	South France	Eocene	Mai 1995
25	Célas, Languedoc	South France	late Eocene	Mai 1995
26	Chakel'mes,Kiin-Kerish,Kara-Beryuk	Zaysan, E Kazakhstan	Paleocene	Zhilin 1989, Golovneva 1996, Takhtajan 1974
27	Chemurnaut Bay & nearby sites	Kamchatka, Russia	?middle Eocene	Budantsev 1994a,1997; Maslova 1995, 1997; Blokhina 1997,1998; Krasilov & Fotyanova 1995, Fotyanova 1995
28	Chikaloon	Alaska	late Paleocene	Wolfe 1994
29	Chlabowka nr Zakopane	central Carpathians	Eocene	Glazek & Zastawniak 1999
30	Dangyang County, Fangjiahe Fm 1st mbr	Hubei, C China	Eocene? Paleogene*	Liu et al 1996, Guo 1990
31	Dembi & Son'e Bays	Primorye Region, Russia	late Eocene	Fotyanova 1997, Tanai 1995
32	Dobra Sreca	East Serbia	Paleocene	Mai 1987, 1995
33	Dombraly	Kazakhstan	late Eocene	Makulbekov 1977
34	Drienovec	Carpathians, Slovakia	Paleocene/Eocene*	Sitar & Kvacek 1993
35	Dzilon-Sise	N.Russia	Eocene	Budantsev 1994b, Tanai 1992 [no reference for flora seen]
36	Eckfeld	Germany	middle Eocene	Wilde & Frankenhauser 1998
37	Eger-Kiseged, Pomaz,Vértesszolos, Kissel etc.	near Budapest, Hungary	early to late Oligocene	Hably 1985,1990,1993,1994,Hably & Fernandez Marron 1998, Kvacek & Hably 1991, Kvacek 1996
38	Eisleben & Roda	eastern Germany	Paleocene	Mai 1987, 1995
39	Ellesmere, Expedition Fm	Ellesmere Island, Canada	Paleocene	McIver & Basinger 1999
40	Ellesmere, Iceberg Bay & Margaret Fms.	Ellesmere Island, Canada	late Paleocene to early Eocene*	McIver & Basinger 1999
41	Enarek (?=Anarak)	Central Iran	Eocene	Makulbekov 1984
42	Fehmarn Island	Germany	early/mid Eocene	Mai 1995, Collinson 1983a.
43	Flörsheim, Mainz Basin	Germany	Oligocene	Mai 1995
44	Fushun City, Guchengzi Fm	Liaoning, NE China	mid to late Eocene*	Liu et al 1996, Guo 1990
45	Gan	France	Eocene	Mai 1995, Collinson 1993
46	Gar County, Menshi Fm, Lr Moincer Gp.	Xizang, SW China	early Eocene	Liu et al 1996, Guo 1990, Guo 1993
47	Geiseltal	Germany	early to middle Eocene	Wilde 1989,1995,Wilde & Frankenhauser 1998, Rüffle 1976
48	Gelinden	Belgium	early Late Paleocene	Mai 1995, Gerienne et al 1999
49	Genesee, Alberta	Canada	Paleocene	Chandrasekharam 1974
50	Girbou, Cluj	Romania	middle Eocene	Mai 1995, Givulescu 1990.
51	Grès à Sabals sites, Mans, Anger	France	early /mid Eocene	Mai 1995, Collinson 1983a
52	Hampshire Basin	S.England	early to late Eocene	Collinson 1996, Collinson & Cleal 2001a,b,c.
53	Häring, Tirol	Austria	late Eocene	Mai 1995
54	Hausham	Germany	late Oligocene	Mai 1995
55	Helmstedt	Germany	early to middle Eocene	Wilde 1989,1995; Wilde & Frankenhauser 1998; Riegel et al 1999.
56	Hengyang City, Chashannao Fm	Hunan, C China	late Eocene	Liu et al 1996, Guo 1990
57	Huanxian County	Gansu, C China	middle Eocene	Liu et al 1996, Guo 1990
58	Hulin	N. China	Eocene	Guo 1990

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59	Hunchin	N. China	Eocene	Guo 1990
60	Ishikari Coalfield, Hokkaido	Japan	mid-late Eocene	Tanai 1981, 1990, 1994, 1995
61	Isle of Wight, Hamstead & Bouldnor Cliff	S.England	latest Eocene to earliest Oligocene	Collnson & Cleal 2001c
62	Jiayin County, Wuyur Fm	Heilongjiang,NE China	Paleocene	Liu et al 1996, Guo 1990, Feng et al 2000
63	Jinggu County, Caijiachong Fm.	Yunnan, SW China	Oligocene	Liu et al 1996, Guo 1990,1993
64	Joffre Bridge, Alberta	Canada	Paleocene	Hoffman & Stockey 1999
65	Kalmakpay & Akkezen	Zaysan, E. Kazakhstan	Eocene	Zhilin 1989, Makulbekov 1987,
66	Kamyshin and Ushi	Volga region	Paleocene	Mai 1995, Zhilin 1989
67	Kanev,Adzamka, west bank Dneiper River	Ukraine	mid-late Eocene	Mihajlovic 1990
68	Karakol	Kazakhstan	mid Eocene	Makulbekov 1977, 1987
69	Karashandakh/Karashandy	Kazakhstan	late Eocene	Makulbekov 1977,1987
70	Karasor	Kazakhstan	middle Eocene	Makulbekov 1977, 1987
71	Kenderle, Kara Sabdyk,Kumbulak,Butakov Bay	north of the Aral Sea, Kazakhstan	early to late Oligocene	Zhilin 1989
72	Kenkous & Chagryan plateau, n Ustyurt, Sandal	Kazakhstan	early Oligocene	Zhilin 1989
73	Kershi and Kiin-Kerish	Zaysan, E. Kazakhstan	Eocene	Zhilin 1989, Makulbekov 1977, 1987
74	Khaychin Ula I	Gobi, Mongolia	Paleocene	Makulbekov 1987,1988,1995, Badamgarav & Reshetov 1985
75	Kiin-Kerish	Zaysan, E. Kazakhstan	Oligocene	Zhilin 1989. Makulbekov 1987
76	Kobi City, Honshu	Japan	late Eocene/early Oligocene	Tanai & Uemura 1994, Tanai 1995, Fotyanova 1997.
77	Kogonvon & Kungsim	North Korea	late Eocene	Fotyanova 1997, Tanai 1995
78	Korzhindy, Kumsuat	north of the Aral Sea, Kazakhstan	early to late Oligocene	Zhilin 1989
79	Kuban near Cherkessk	Georgia, Caucasus	middle Eocene	Akhmetiev 1995
80	Kuclin near Bilina	Czech Republic	latest Eocene	Kvacek et al 1989, Mai 1995, Buzek et al 1990, Hably et al 2000, Kvacek 1996, 2000.
81	Kulboldy	Kazakhstan	late Eocene	Makulbekov 1977, Zhilin 1989
82	Kultieth	Alaska	early Eocene	Wolfe 1977,1994
83	Kundratice,Suletice,Valec,Bechlejovice, etc	Bohemia, Czech Republic	early to late Oligocene	Kvacek et al 1989, Kvacek & Walther 1998, Kvacek 2000, Walther 1999
84	Kundyzdy	Kazakhstan	late Eocene	Makulbekov 1977,1987
85	Kushiro Coalfield, Hokkaido	Japan	late Eocene	Tanai 1990, 1995
86	Labatlan & Tatabanya	Hungary	middle Eocene	Hably 1985
87	Lausitz region, Saxony, & Haselbach (WB)	Germany	early to late Oligocene	Mai 1994,1997,1998; Walther 1999 (see also Weisselster Basin (WB) site 169)
88	Lazi County, Liuqu Fm	Xizang, SW China	mid to late Eocene*	Liu et al 1996
89	Lena River	N.Russia	?early Eocene	Budantsev 1994a
90	Lingbao County	Henan, China	Paleocene	Guo pers. comm 2001
91	Litang County, Relu Fm	W.Sichuan, C China	early or late Eocene*	Liu et al 1996, Guo 1990, Guo 1993
92	London Basin	S.England	early Eocene	Collinson 1983a, Collinson & Cleal 2001a,b
93	Mallorca	Spain	middle Oligocene	Hably & Fernandez Marron 1998
94	Martuk	Kazakhstan	Eocene	Zhilin 1989
95	Menat	France	Paleocene	Mai 1995
96	Mera bei Cluj	Romania	early Oligocene	Mai 1995
97	Messel	Germany	middle Eocene	Wilde 1989,Wilde & Frankenhauser 1998, Schaa & Ziegler 1992
98	Mogilno	Ukraine	late Eocene	Mai 1968,1995
99	Montana,Wyoming,N.Dakota, Fort Union Fm	USA	Paleocene	Hickey 1980
100	Montebolca	Italy	early Eocene	Mai 1995
101	Montmorency & Fontainbleau	Paris Basin, France	early Oligocene	Grambast 1962, Mai 1995, Plaziat et al 1989.Koeniguer 1988,Koeniguer et al 1985
102	Mt Promina	Croatia	late Eocene	Mai 1995, Mihaljovic 1990, 1992
103	Mull	Scotland	latest Paleocene/earliest Eocene	Boulter & Kvacek 1989. Collinson & Cleal 2001a
104	Murunchink	Kazakhstan	early Oligocene	Zhilin 1989
105	Naran Bulak & Tsagan Khushu	Gobi, Mongolia	Paleocene	Makulbekov 1987,1988,1995, Badamgarav & Reshetov 1985
107	Ningming County, Nadu Fm	S.China	Eocene	Liu et al 1996, Guo 1990
106	Oise, le Quesnoy	Paris Basin, France	Paleocene/Eocene transition	Nel et al 1999, Hooker 1998
108	Panxian County, Shinao Basin, Shinao Fm	Guizhou, SW China	Eocene	Liu et al 1996
109	Pasekovo	Central Russia	?late Eocene or early Oligocene	Vickulin 1999a,b
110	Pcinja Basin, Poljanica-Ovce Polje Gp.	Macedonia	late Eocene & early Oligocene	Mihajlovic 1990, 1993
111	Podkagernaya Bay	Kamchatka	late Eocene	Budantsev 1994a,1997, Maslova 1995
112	Prémontré (Aisne)	Paris Basin, France	early Eocene	Mai 1995, Koeniguer 1988, Koeniguer et al 1985
113	Qingjiang County, Qingjiang Fm	Jiangxi, C China	Eocene	Liu et al 1996, Guo 1990
114	Qiongshan County, Changchang Fm	Hainan Island, S China	late Paleocene to mid Eocene*	Liu et al 1996, Guo 1990
115	Rarytkin Range, Podbazovyi Creek.	Northern Koryakia, Russia	late Eocene	Akhmetiev & Samsonenko 1997
116	Rarytkin Ridge	Koryak Upland, Russia	early Paleocene	Herman 1993, Budantsev 1994a, Herman & Spicer 1996, Golovneva 1994, 2000.
120	Rasa	Croatia	early Eocene	Mihajlovic 1990
117	Rassoshina River & Napana River	Kamchatka, Russia	late Paleocene to early Eocene*	Budantsev 1994a,1997

Table 1 List of sites of the Paleogene floras which are plotted on Figures 1-3. In the 'Age' column * indicates age undefined within the interval stated. (continued)

118 Ravenscrag Butte, Saskatchewan	Canada	Paleocene	McIver & Basinger 1993
119 Reading area and S. England sites	S. England	Paleocene/Eocene transition	Collinson 2000a, Collinson & Cleal 2001a
121 Rettikovka & Bolotnaya Rivers	Primorye Region, Russia	late Eocene	Fotyanova 1997, Tanai 1995
122 Rhodopes central floras, Hvojna Basin	S. Bulgaria	late Eocene/early Oligocene	Cernjavska et al 1988, Palamarev & Petkova 1990, Mihajlovic 1990, Hably et al 2000
123 Rikubetsu & Kitami Coalfields, Hokkaido	Japan	late Eocene/early Oligocene	Tanai, 1981,1990, 1992, 1994,1995; Tanai & Uemura 1994; Fotyanova 1997
124 Romankol	Kazakhstan	Paleocene	Mai 1968, Zhilin 1989, Shilin 2000, Makulbekov 1987
125 Romanovsk	Kazakhstan	late Eocene/early Oligocene	Makulbekov 1977, 1987
126 Rott	Germany	late Oligocene	Koenigswald 1996
127 Rusava	Czech Republic	Paleocene	Mai 1987, 1995
128 Rusca	S. Romania	Paleocene	Mai 1987, 1995
129 Sagwon, Lr Colville River, Sagavanirktok Fm.	Alaska	Paleocene	Herman & Spicer 1996, Spicer et al 1994, Golovneva 1997
130 Sakhalin, Bogataya River	E. Sakhalin, Russia	late Eocene	Fotyanova 1997
131 Sakhalin, Boshnyakovo Fm.	Sakhalin, Russia	early Paleocene	Herman & Spicer 1996, Kvacek & Manum 1993, Golovneva 1996
132 Sakhalin, Kama & Aral'skaya Rivers	W. Sakhalin, Russia	middle Eocene	Fotyanova 1997
133 Sakhalin, Krasnoyarka River	S. Sakhalin, Russia	late Paleocene or early Eocene	Kodrul 1994
134 Sanshui County, Buxin Fm	Guangdong, C. China	early to mid Eocene*	Liu et al 1996, Guo 1990
135 Sarreal,Cervera,Tarrega, Ebro Basin	Spain	early Oligocene	Hably & Fernandez Marron 1998
136 Sedanka site, Napana River,	Kamchatka, Russia	late Eocene	Budantsev 1994a, 1997, Budantsev & Baranova 1995
137 Seifhennersdorf	Germany	early Oligocene	Mai 1995, Hably et al 2000,Walther 1999
138 Sergeya	N.Russia	Oligocene-Miocene*	Takhtajan 1982 [reference on flora not seen]
139 Sézanne	Paris Basin, France	Paleocene	Mai 1987, 1995, Koeniguer et al 1985
140 Shadiniskii/Shana graben	Kazakhstan	late Eocene/early Oligocene	Makulbekov 1977,1987
141 Shanhe Town, Yanbian County	Jilin, NE China	Oligocene	Liu et al 1996, other sites mentioned by Guo 1990
142 Shiderty	Kazakhstan	late Eocene/early Oligocene	Makulbekov 1977, 1987
143 Shintuzsay	Kazakhstan	early Oligocene	Zhilin 1989
144 Shulan County, Shulan Fm	Jilin, NE China	Eocene	Liu et al 1996, Guo 1990
145 Snatol	Kamchatka, Russia	late Paleocene to early Eocene*	Budantsev 1994a,1997, Lavrenko & Fotjanova 1994; Fotyanova 1995; Maslova 2000
146 Sotzka/Socka & Divljana	Slovenia	early Oligocene	Mai 1995, Mihaljovic 1990, 1992
147 Spechbach, Alsace	France	latest Eocene	Mai 1995
148 Spitsbergen	Spitsbergen	early Paleocene to early Eocene	Boulter & Kvacek 1989, Kvacek & Manum 1993, Kvacek et al 1994, Golovneva 2000
149 Stare Sedlo Fm, Bohemia	Czech Republic	late Eocene	Knobloch et al 1996
150 Sumgait River & Ezry-Cala near Baku	Azerbaijan, Caucasus	early Oligocene	Mai 1995, Akhmetiev 1995
151 Tai'an City, Dawenkou Fm,Shahejie Fm	Shandong, C China	Eocene	Liu et al 1996, Guo 1990
152 Takyrsor	Kazakhstan	late Eocene	Makulbekov 1977, Zhilin 1989
153 Taoyan County, Yuzitang & Jianjiaxi Fms	Hunan, C China	Eocene	Guo 1990
154 Tastakh	N.Russia	middle Eocene	Takhtajan 1974, Budantsev 1994a
155 Tayzhugen	Zaysan, E Kazakhstan	Paleocene	Zhilin 1989, Makulbekov 1983, Crane et al 1991, Takhtajan 1974
156 Thyra	E. Greenland	late Paleocene or early Eocene	Boyd 1990
157 Tim	Central Russia	?late Eocene or early Oligocene	Vickulin 1999a,b
158 Tongbai County, Wulidui Fm	Henan, C China	Eocene	Liu et al 1996, Guo 1990
159 Tortmola, Turgai	Kazakstan	early Oligocene (Rupelian)	Zhilin 1989.
160 Toru Ajgyr, NW side Issyk-kul lake	Kyrgyzstan	middle Eocene (Lutetian)	Erfurt et al 1999, Fortuna 1979 [palynolgy only]
161 Tsagayan	Bureja Region, E. Russia	Paleocene	Ohana & Kimura 1995, Crane et al 1991, Golovneva 1996
162 Tsitse (Cice) & Karatsitse (Kura-Cice)	Georgia, Caucasus	early Oligocene	Mai 1995, Akhmetiev 1995
163 Turkey (area 23 in Palamarev 1989)	Turkey	Oligocene	Palamarev 1989, Mädler & Steffens 1979
164 Turkey (area 24 in Palamarev 1989)	Turkey	Oligocene	Palamarev 1989, Mädler & Steffens 1979
165 Tykbutak	Kazakhstan	Paleocene	Zhilin 1989, Makulbeko 1987
166 Ube Coalfield, Honshu	Japan	mid ?late Eocene	Huzioka & Takahashi 1970, Tanai 1995, Russell & Zhai 1987
167 Vicenza province, Chiavon-Flus nr Farra	Italy	Oligocene	Mai 1995
168 Weinan County, Bailuyan Fm	Shaanxi, C. China	late Eocene	Liu et al 1996, Guo 1990
169 Weisselster Basin (see also 87)	Germany	late Eocene to Oligocene	Kvacek et al 1989, Walther 1990, Mai 1995, Mai & Walther 1978,1985
170 Xiangxiang County, Xiawanpu Fm	Hunan, C. China	Eocene	Liu et al 1996, Guo 1990
171 Yilan County, Yilan Fm, Dalianhe Fm	Heilongjiang, NE China	early Eocene & late Eocene	Liu et al 1996, Guo 1990, He & Tao 1994, 1997
172 Yizheng County, Funing Fm	Jiangsu, C. China	Eocene	Liu et al 1996, Guo 1990
173 Zhamantuz	Kazakhstan	late Eocene/early Oligocene	Makulbekov 1977, 1987, Zhilin 1989
174 Zhamon-Kaindy, near Arkalyk	Kazakhstan	early Oligocene	Zhilin 1989
175 Zhangye County	Gansu, C. China	middle Eocene	Liu et al 1996, Guo 1990
176 Zharlykap	Kazakhstan	late Eocene	Makulbekov 1977,1987
177 Zmiev (Gotvaldou), near Kharkov	Ukraine	late Eocene	Mai 1995

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