

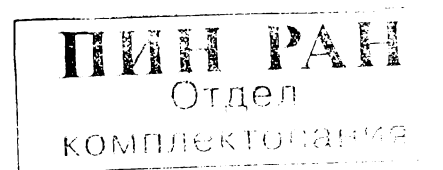
Extinct and Extant Platanaceae and Hamamelidaceae: Morphology, Systematics, and Phylogeny

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Abstract—The geological history of the families Platanaceae and Hamamelidaceae is studied on the basis of original fossil material and available literature. The evolutionary stages of morphological and taxonomic diversity are revealed. The trends in vegetative and reproductive evolution are traced. On the basis of chronological relationships and finds of transitional forms (links), the phylogeny of the Platanaceae and Hamamelidaceae is reconstructed, and different evolutionary patterns in these families of early angiosperms are shown.

Key words: Early angiosperms, Platanaceae, Hamamelidaceae, Cretaceous, Tertiary, plant morphology, plant phylogeny.

INTRODUCTION

The order Hamamelidales Wettstein is intermediate between the angiosperm groups placed at the base of the phylogenetic tree and the relatively advanced orders of the Amentiferae. The order Hamamelidales displays a wide range of primitive morphological and anatomical characters as well as certain features commonly considered to be advanced characters (Hallir, 1903, 1912; Takhtajan, 1960, 1966, 1970, 1987; Hutchinson, 1969; Cronquist, 1981).

In modern systematics, the creation of classification systems on the basis of relevant data on the phylogeny of particular groups and macroevolutionary patterns is a high priority. Of particular interest therefore is the order Hamamelidales, which occupies a key position in the angiosperm macrosystem.

To date, a great amount of data concerning the morphology and anatomy of leaves and reproductive structures of living members of the Hamamelidales have been obtained. However, the systematization of the extant material is far from complete. The problem is partially accounted for by a significant morphological reduction of hamamelid floral structures hampering their unequivocal homologization. Additional problems arise in the study of fossil material. At the same time, the homology can be established only by tracing structural development over the evolutionary history of the group as documented in the fossil record. In the case of the Hamamelidales, this problem is especially interesting, since the initial morphotypes have been considerably changed in the course of evolution.

Paleobotanical data are important for the understanding of phylogenetic relationships between the orders of lower and higher hamamelids as well as between the taxa within the Hamamelidales.

Fossil members of the order have been studied for more than a century. The first paleobotanical records of the Hamamelidales were leaf remains of a characteristic morphology, which were described as extant genera (Newberry, 1868; Lesquereux, 1892; and others). Subsequent studies significantly extended the taxonomic content of the Hamamelidales. However, for a long time, these studies were based exclusively on the leaf

macromorphology and, to a lesser degree, on reproductive structures. In effect, many fossil genera and species lack precise morphological characteristics; this hampers their classification. Until recently, the systematics of fossil members of the families Platanaceae Dumortier and Hamamelidaceae R. Brown had mostly been based on the morphology of leaf remains. However, the extremely high variability, parallelism, and overlapping ranges of variation substantially decrease the significance of fossil leaves for taxonomic and evolutionary studies at the macromorphological level.

In the 1970s, paleobotanists began to use modern facilities (the scanning electron microscope (SEM) and, somewhat later, the transmission electron microscope, TEM); this brought paleobotanical investigations to a radically higher level and provided a means for a revision of available material on extinct angiosperms with the application of all macromorphological and microstructural characters of vegetative and generative organs.

Previous paleobotanical studies showed that the currently monotypic family Platanaceae was an extensive group in the geological past and played an important role and often even dominated in the vegetation of the Northern Hemisphere in the Cretaceous and Cenozoic (Bůžek *et al.*, 1967; Kvaček, 1970; Krassilov, 1976; Vakhrameev, 1976; Hickey and Doyle, 1977; Manchester, 1986; Crane *et al.*, 1988; Friis *et al.*, 1988; Pigg and Stockey, 1991; and others). Geological precursors of the presently diverse Hamamelidaceae are little known. This is especially true for the Cretaceous finds, whereas the Tertiary remains of leaves, wood, seeds, pollen, inflorescences, and infructescences are more representative (Hu and Chaney, 1940; Brown, 1946; Mai, 1968; Wolfe, 1973; Knobloch and Kvaček, 1976; Tanai, 1976; Mai and Walter, 1978; Tiffney, 1986; Ferguson, 1989; Wang, 1992). Only in the last decade, have new hamamelid taxa been described, contributing to the hamamelid diversity in the geological past (Endress and Friis, 1991; Manchester, 1994; Magallón-Puebla *et al.*, 1996, 2001; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou *et al.*, 2001).

The reproductive structures of the lower hamamelids are of great importance for the understanding of

phylogenetic relationships in early angiosperms. To date, capitate inflorescences and infructescences of the Platanaceae and some members of the Hamamelidaceae are best studied. However, macromorphologically, such structures can be fairly similar in different members of the Hamamelidaceae. Detailed micromorphological studies are especially needed for the identification of genera (sometimes, even families) of paleobotanical finds. The microstructural technique is rather useful for the differentiation of convergently similar capitate inflorescences and infructescences in some Platanaceae and Hamamelidaceae and for the establishment of the morphological diversity of fossil members of these families (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b).

CHAPTER 1. MATERIALS AND METHODS

The present study is focused on fossil members of the Platanaceae and Hamamelidaceae from the Cretaceous and Cenozoic deposits of the Far East and Siberia. Published data on fossil members of these families from North American and European localities are used for comparison.

The fossil remains of the Hamamelidales described below were partly collected by the author in the Paleogene of the Kamchatka Peninsula and Sakhalin Island; however, the bulk of the material was kindly provided by L.I. Fotyayeva (Moscow, Paleontological Institute of the Russian Academy of Sciences, PIN), M.A. Akhmetiev and T.M. Kodrul (Moscow, Geological Institute of the Russian Academy of Sciences, GIN), V.A. Krassilov (Moscow, PIN), L.B. Golovneva (St. Petersburg, Komarov Botanical Institute of the Russian Academy of Sciences, BIN) from the Cretaceous and Paleogene of the Kamchatka Peninsula, Sakhalin Island, Primorye, Amur Region, and Eastern Siberia. The material examined comes from 22 localities and comprises 345 leaf impressions of different preservation (not to mention small fragments) and more than 20 capitate inflorescences.

The methods include the selection and preparation of leaf and reproductive remains with a binocular microscope MBS-9. Measurements, photodocumentation, and macromorphological drawings were performed with the aid of a microscope CYTOVAL. Chemical treatment of compressions and their separation from the host rock were performed with fluoric acid. The bulk maceration of the rock matrix for the extraction of dispersed microfossils and the microstructural study of compressions and subcrustations (inner mineral films: see Krassilov and Makulbekov, 1996) were performed with a CAMSCAN SEM and a light microscope Axioplane (LM). The maceration of the cuticle followed the generally accepted technique with the preparation of slides for LM and SEM. Pollen grains were extracted from pollen organs and subsequently studied under LM and SEM.

The taxonomic diversity and morphological evolution were analyzed on the basis of available published data and the original material from the Cretaceous and Paleogene localities of Northern Asia.

The morphological analysis involved the key reproductive characters and their correlation with leaf characters. In the macromorphological and epidermal study of leaves of the Hamamelidales, the herbarium materials from the Botanical Garden of Sukhumi as well as the East Asian and North American herbaria housed at the BIN and the Main Botanical Garden of the Russian Academy of Sciences (Moscow) were used for comparison. The assessment of the relative development of floral structures (perianth, androecium, and gynoecium) and their homologization were based on detailed examination of extant material (Bogle, 1970, 1986; Endress, 1989b) and on the original data. The method for quantitative assessment of characters of different evolutionary significance was applied for the analysis of morphological diversity and disparity. In phylogenetic analysis, the chronological relationships and the presence of intermediate or transitional forms (fossil links) were used as the main criteria. The methodological approach to the analysis of morphological patterns and evolution of characteristics was based on theoretical models of homologous variation and evolutionary parallelism developed by Vavilov (1921), Krassilov (1977, 1989), and Meyen (1987).

CHAPTER 2. SYSTEMATICS OF THE HAMAMELIDALES: PRESENT STATE AND UNRESOLVED PROBLEMS

Notwithstanding a long history of investigation, opinions still differ on the taxonomic composition of the order Hamamelidales. Hallier (1912) included in this order only two families, the Hamamelidaceae (including the genera *Trochodendron* Sieb. et Zucc., *Tetracentron* Oliv., *Euptelea* Sieb. et Zucc., *Cercidiphyllum* Sieb. et Zucc., and *Eucommia* Oliv.) and the Coriariaceae A.P. Decandolle.

Hutchinson (1967) assigned to this order the families Tetracentraceae van Tieghem, Platanaceae, Stachyuraceae J.G. Agardh, Buxaceae Dumortier, Daphniphyllaceae Müller Argau, and Bruniaceae A.P. Decandolle.

Takhtajan has repeatedly revised the order content. In 1966, he included in the Hamamelidales four families, the Hamamelidaceae, Altingiaceae Lindley, Platanaceae, and the Myrothamnaceae Niedenzu. Later, he divided the order into three families, the Hamamelidaceae (including Altingiaceae, Disanthaceae Nakai, and Rhodoleiaceae Nakai), Platanaceae, and the Myrothamnaceae (Takhtajan, 1970). His latest review (Takhtajan, 1987) treated the Hamamelidales as composed of the Hamamelidaceae, Rhodoleiaceae, Altingiaceae, and Platanaceae; the family Myrothamnaceae was ranked after Nakai (1943) as a separate order

Myrothamniales Nakai. Cronquist (1981) placed five families in the Hamamelidales, the Cercidiphyllaceae Engler, Eupteleaceae Wilhelm, Platanaceae, Hamamelidaceae, and the Myrothamnaceae.

To date, the latter two are the most widely accepted systems among the researchers of systematics and phylogeny of angiosperms. New data on extant and fossil members of the order Hamamelidales evoke a lengthy discussion of the composition of the families within this order and their phylogeny (Bogle, 1970, 1986; Goldblatt and Endress, 1977; Wisniewski and Bogle, 1982; Endress, 1989a, 1989b; Schwarzwaldner and Dilcher, 1991; Zhang and Lu, 1995).

The unresolved problems of the fossil Hamamelidales taxonomy include (1) the assignment of the platanoid form genera to the family Platanaceae; (2) the justification of the generic assignment of Cretaceous leaves to the genus *Platanus* L.; and (3) the status of the genera *Altingia* Nor., *Liquidambar* L., and *Semiliquidambar* Chang, which should be assigned to either a separate family, Altingiaceae, or the subfamily Altingioideae of the family Hamamelidaceae.

This paper is devoted to fossil members of two families of the order Hamamelidales, the Platanaceae and Hamamelidaceae. The composition of these families (including their extant and extinct members) and their classification are briefly discussed below.

FAMILY PLATANACEAE

The extant family Platanaceae includes the sole genus *Platanus* composed of the subgenera *Platanus* Leroy and *Castaneophyllum* Leroy (Leroy, 1982). The species of the subgenus *Platanus* have typical lobed leaves and compound inflorescences, including a shortened axis and one to five sessile heads (*P. occidentalis* L., *P. orientalis* L., *P. mexicana* Moricaud, and *P. wrightii* S. Watson). This subgenus is also characterized by vessels with predominantly simple perforations and pollen grains 18–22 µm in polar diameter.

The subgenus *Castaneophyllum* includes the sole species *Platanus kerri* Gagnepain characterized by simple elliptical leaves and compound inflorescences of an elongated axis and at least 12 heads. In contrast to the vessels of the subgenus *Platanus*, those of *P. kerri* have mostly scalariform perforations and smaller pollen grains (the polar diameter is 16–18 µm).

Kvaček *et al.* (2001) have introduced the third subgenus *Glandulosa* composed of only fossil members of the genus (*Platanus bella* (Heer) Kvaček, Manchester *et al.*, *P. fraxinifolia* (Johnson *et al.* Gilmore) Walter, and *P. neptunii* (Ettings.) Bůžek, Holý *et al.* Kvaček). This subgenus is distinguished by the presence of both simple and compound (with three to five leaflets) leaves with alternate semicraspedodromous or camptodromous venation, large peltate trichomes, and a well-pronounced scar on the pedicle of the solitary infructescence.

The sole extant member of the Platanaceae, the genus *Platanus*, is a remnant of the previously extensive polymorphic group, which played a significant (sometimes, dominant) role in plant communities over vast territories in the Northern Hemisphere (Krassilov, 1976; Vakhrameev, 1976; Herman, 1994). To date, the microstructural study of reproductive organs of extinct platanoids has uncovered their significant morphological diversity. The leaf morphotypes of the ancient platanoids are also rather diverse. The geological history of the family Platanaceae is apparently one of the most comprehensively studied among the lower hamamelids.

An unresolved problem of the systematics of the Platanaceae is the taxonomic position of the group composed of predominantly Late Cretaceous leaf genera, which are common in continental deposits of the Northern Hemisphere.

Inferring from similarities in leaf macromorphology between these remains and living *Platanus*, a number of researchers place them in the Platanaceae (Krishtofovich and Baikovskaya, 1960; *Osnony paleontologii...*, 1963; *Iskopaemye tsvetkovye...*, 1974; Budantsev, 1975). Other paleobotanists consider these genera to be closely related to the Platanaceae and indicate that epidermal analysis gives rather contradictory data (Krassilov, 1976; Herman, 1984; Herman and Golovneva, 1988). In his early study, Vakhrameev (1952) included some of these genera in the Platanaceae; however, subsequently, he proposed to assign them to a separate group, taking into consideration their epidermal features (Vakhrameev, 1976). He noticed an extremely high superficial similarity of these leaves and proposed their close phylogenetic relationships.

Platanoids include the leaf genera *Protophyllum* Lesq., *Pseudoprotophyllum* Hollick, *Aspidiophyllum* Lesq., *Credneria* Zenker, *Paraprotophyllum* Herman, *Arthollia* Golovneva *et al.* Herman, etc. Some of them presently comprise about two dozens species established exclusively on characters of leaf macromorphology. The generic diagnoses are far from precise, scarcely taking into consideration the variability of morphological characters. In addition, many characters ascribed to a particular leaf genus and indicated as diagnostic characters sporadically occur in other genera. The morphological distinctness of leaf genera is thereby lost, and the increasing number of species additionally complicates the problem.

In view of the morphological overlaps between the platanoid genera, identification of such form genera is extremely complicated; therefore, the platanoid system should be substantially revised (Herman and Golovneva, 1988). These researchers indicate that the main direction of the study of fossil platanoids is the discovery of the variability of particular morphological characteristics on the basis of extensive samples of platanoid fossils from the same locality.

In my opinion, additional data on the leaf microstructure would be of certain significance for a better

taxonomic differentiation of platanoid genera. Currently available data on this topic are rather fragmentary. For example, Ruffle (1968) allied Cenomanian *Platanus (Credneria) cuneifolia* (Bronn) Jarmol. to the family Menispermaceae on the basis of epidermal micromorphology. Krassilov (1973) studied epidermal characteristics of Late Cretaceous *Protophyllum ignatianum* Krysh. et Baik. and revealed that they are similar to those of *Liquidambar* from the family Hamamelidaceae. On the basis of their cuticular structure, I have confirmed the assignment of the genus *Arthollia* to the family Platanaceae. The Eocene species *Arthollia anadyrensis* sp. nov. shows the leaf epidermal microstructure that is characteristic of living plane trees and some extinct members of the Platanaceae.

These examples show a controversial situation in the taxonomy of these form genera, which becomes even more ambiguous with the inclusion of the form genera not assigned to the Platanaceae but closely similar to them in leaf macromorphology, such as *Grewiopsis* Saporta, *Populites* Viviani, and *Pterospermites* Heer.

A detailed revision of extinct platanoid form genera deserves a special investigation, which is beyond the scope of the present study. However, it is evident that the system of Cretaceous platanoids should be revised with due respect to the variability of leaf macromorphological characters on the basis of extensive monotypic samples and microstructural analysis.

The presence of the genus *Platanus* in the Cretaceous is also a matter of discussion. For more than a hundred years, this generic name was uncritically applied to the fossil leaf remains. A large number of fossil *Platanus* species are reported, while remains of reproductive organs are relatively scarce. For a long time, simple and variously lobed leaves, which are common in the Upper Cretaceous floras, were mostly assigned to the extant genus *Platanus*. The determination of this extant genus on the basis of leaf remains in the Cretaceous has already been questioned (Wolfe, 1973; Krassilov, 1976, 1979); however, microstructural methods have been only sporadically used in paleobotany. Nonetheless, many researchers traditionally continue to assign leaves of this morphotype to the genus *Platanus* and introduce more and more species. Moreover, with the accumulation of data on microstructural diversity of superficially identical capitata inflorescences of the Platanaceae, it has become evident that the assignment of superficially similar fossil heads to the extant genus *Platanus* is rather questionable.

Available information on the diversity of reproductive structures associated with the leaves of a typically platanoid appearance indicates that the presence of plane in the Cretaceous should be radically revised (Maslova, 1997, 2001a, 2002a, 2002b).

As is shown below, not all the assignments of fossil leaves to the genus *Platanus*, plausible at first sight, would stand in the face of additional data on the epider-

mal structure and reproductive organs. Typically platanoid leaf morphotypes are recorded from the Cretaceous; however, the presence of this genus has not yet been proved by critical evidence provided by reproductive organs. At the same time, the microstructurally studied reproductive structures of early platanoids significantly enlarge the content of the family. Such finds have been reported from the Cretaceous (Krassilov, 1973, 1976; Knobloch and May, 1986; Friis *et al.*, 1988; Crane *et al.*, 1993; Pedersen *et al.*, 1994; Krassilov and Shilin, 1995; Magallón-Puebla *et al.*, 1997), Paleocene (Crane *et al.*, 1988; Pigg and Stockey, 1991; Maslova, 1997, 2002; Kvaček *et al.*, 2001; Maslova and Krassilov, 2002; Maslova and Kodrul, 2003), Eocene (Manchester, 1986, 1994), and the Oligocene–Miocene (Bůžek *et al.*, 1967; Kvaček, 1970).

FAMILY HAMAMELIDACEAE

According to different estimates, the family Hamamelidaceae comprises from 24 to 30 extant species (Bogle, 1970; Skvortsova, 1975; Endress, 1989a; Zhang and Lu, 1995).

There were several attempts to subdivide the hamamelid genera into subfamilies. Thus, on the basis of the ovule number per ovary, Niedenzu (1891) introduced two subfamilies, the Hamamelidoideae (one ovule) and the Bucklandioideae (numerous ovules). However, many genera of the Hamamelidoideae are known to have two ovules (Baillon, 1871; Schoemaker, 1905; Bogle, 1970; Kapil and Kaul, 1972). It is evident that a solitary character is insufficient for an objective classification of the family.

A comprehensive supergeneric classification of the Hamamelidaceae has been developed by Harms (1930), who recognized the following five subfamilies within the family: the Disanthoideae Harms, Hamamelidoideae Reinsch, Rhodoleioideae Harms, Bucklandioideae Reinsch, and Liquidambaroideae Harms. The name Liquidambaroideae was traditionally used after Harms; however, this subfamily would more properly be named Altingioideae Reinsch, according to the priority principle (Reinsch, 1890).

The system proposed by Harms was long accepted. However, new data on various members of the family and the discovery of such new genera as *Semiliquidambar* (Chang, 1962), *Molinadendron* Endress (Endress, 1969), *Distyliopsis* Endress (Endress, 1970), and *Noahdendron* Endress, Hyland et Tracey (Endress *et al.*, 1985) necessitated the revision of the supergeneric system. The genus *Chunia* Chang and the unknown (during Harms's time) genus *Mytilaria* Lecomte were clustered in the subfamily Mytilarioideae Chang (1973).

Endress (1989b) revised the subfamilial classification and proposed a new system of the Hamamelidaceae. The most diverse is the subfamily Hamamelidoideae containing 22 genera. Three genera are included in the subfamily Altingioideae; two genera are

in the Mytilarioideae; and the subfamilies Disanthoideae, Rhodoleioideae, and Exbucklandioideae are monotypic. Endress noticed that the morphological distances between the genera belonging to three small subfamilies Exbucklandioideae, Mytilarioideae, and Disanthoideae are not greater than those within the subfamily Hamamelidoideae. The alliance of the genera *Disanthus* Maxim. and *Exbucklandia* R. Brown was previously suggested by Reinsch (1890). Endress (1989a) interpreted *Mytilaria* and *Chunia* as transitional forms between *Exbucklandia* and *Disanthus*. On the basis of the similar leaf and reproductive morphologies and identical chromosome numbers, Endress clustered these genera in the subfamily Exbucklandioideae. As a result of the revision performed by Endress, the family Hamamelidaceae currently includes four subfamilies: the Hamamelidoideae (tribes Hamamelideae, Fothergilleae, Eustigmateae, and Corylopsideae), Rhodoleioideae, Exbucklandioideae, and the Altingioideae. The chromosome numbers for the hamamelid genera agree with this classification (Goldblatt and Endress, 1977).

The position of the genera *Altingia*, *Liquidambar*, and *Semiliquidambar* is one of the main points of discussion. Lindley (1853) noticed a similarity between *Altingia* and *Liquidambar* and proposed to assign them to a separate family, the Altingiaceae. De Candolle (1864) assigned *Altingia* and *Liquidambar* to the Platanaceae.

The familial rank of the Altingiaceae is based on the anatomy of the seeds and conducting system, pollen morphology, and chromosome numbers (Lindley, 1853; Andersen and Sax, 1935; Skvortsova, 1960a; Chang, 1964; Takhtajan, 1966, 1987; Melikyan, 1971, 1973a; Rao, 1974; Rao and Bhupal, 1974; Dahlgren, 1975). On the other hand, a number of morphological, anatomical, and developmental features suggest the subfamilial status of this group within the Hamamelidaceae (Harms, 1930; Makarova, 1957; Schmitt, 1965; Thorne, 1968; Hutchinson, 1969; Meeuse, 1975; Goldblatt and Endress, 1977; Cronquist, 1981; Wisniewski and Bogle, 1982; Uemura, 1983; Bogle, 1986; Goldberg, 1986; Tiffney, 1986; Endress, 1989a, 1989b; Hoey and Parks, 1991, 1994; Zhang and Lu, 1995). Some researchers consider the genera *Altingia* and *Liquidambar* to be primitive members of the family (Makarova, 1957; Schmitt, 1965; Meeuse, 1975), while others believe that they are the most advanced forms (Schulze-Menz, 1964).

The taxonomic affinity of *Altingia* and *Liquidambar* is also disputable. For instance, De Candolle (1864) and Leroy (1982) assigned them to the same genus *Liquidambar* exclusively on the basis of the leaf and infructescence morphology. However, the superficial similarity of the infructescence morphology is not substantiated by the anatomy, since alongside with the evident similarity of the main structures, there are also certain differences, which prove the validity of each genus

(Bogle, 1986). A significant distinctive feature is different leaf morphotypes. *Altingia* has simple leaves with pinnate venation, while *Liquidambar* is characterized by lobed leaves with palmate venation. Both morphological types occur in the genus *Semiliquidambar*.

The author of the genus *Semiliquidambar* considered it as an intermediate link between *Altingia* and *Liquidambar* (Chang, 1962, 1973). Of interest is the range of this genus, embracing the vast territory of southeastern China and Hainan Island (Chang, 1962). This region is situated exactly between the modern ranges of *Altingia* and *Liquidambar*. Bogle (1986) proposed that *Semiliquidambar* is a hybrid between *Altingia* and *Liquidambar*. The interfertility of three species of *Liquidambar* was proved experimentally (Santamour, 1972). However, analogous data concerning *Altingia* and possible *Altingia* × *Liquidambar* hybridization are absent.

In summary, *Altingia* and *Liquidambar* share the following characteristic features: (1) resin channels associated with the vascular bundles in the stem, leaves, and inflorescences; (2) compound bisexual inflorescences; (3) compact capitate infructescences; (4) naked functionally unisexual flowers; (5) the presence of sterile structures (intrafloral phyllomes and staminodes) surrounding the ovary of pistillate flowers; (6) multiporate pollen; (7) numerous ovules; and (8) small winged seeds. Such a combination of characters opposes these genera to other hamamelids. However, resin channels, compound inflorescences, sterile structures in pistillate flowers, and multiporate pollen are also observed in other subfamilies of the Hamamelidaceae. These are not unique characters of the genera *Altingia* and *Liquidambar*.

Because of this, and taking into account the original paleobotanical data (see below), I believe that it is better to assign these genera and the related *Semiliquidambar* to the subfamily Altingioideae of the family Hamamelidaceae.

The paleobotanical data on the Hamamelidaceae are rather scarce. Only the genus *Liquidambar* is a common component of the Cenozoic floras of the Northern Hemisphere and is comprehensively represented in paleobotanical literature. It is easily recognized by its characteristic leaf features. Nevertheless, the species composition of this genus has been differently interpreted (Harms, 1930; Makarova, 1957; Uemura, 1983; Bogle, 1986; Maslova, 1995a). It should be noted that nearly all reported fossil *Liquidambar* are leaf remains. Few records of reproductive organs of the genus are based on superficial morphological descriptions.

The majority of anatomically-studied reproductive organs of fossil hamamelids resemble those of extant members of the subfamily Hamamelidoideae (Endress and Friis, 1991; Manchester, 1994; Magallón-Puebla *et al.*, 1996, 2001). Some finds are allied to the Altingioideae (Mai, 1968; Krassilov, 1976; Friis and Crane, 1989; Maslova and Krassilov, 1997; Maslova and

Golovneva, 2000b; Zhou *et al.*, 2001). The recently described genus *Viltyungia* N. Maslova from the Cenomanian of Eastern Siberia combines the characters typical of the subfamilies Exbucklandioideae, Altingioideae, and Hamamelidoideae (Maslova and Golovneva, 2000b).

On the basis of published data and taking into consideration the paleobotanical material under study, the following Hamamelidales system is accepted.

Order Hamamelidales Wettstein

Family Platanaceae Dumortier

Genus *Platanus* L.

Subgenus *Platanus* Leroy

Subgenus *Castaneophyllum* Leroy

Family Hamamelidaceae R. Brown

Subfamily Altingioideae Reinsch

Genus *Altingia* Nor.

Genus *Liquidambar* L.

Genus *Semiliquidambar* Chang

Subfamily Exbucklandioideae Reinsch

Genus *Chunia* Chang

Genus *Disanthus* Maxim.

Genus *Exbucklandia* R. Brown

Genus *Mytilaria* Lecomte

Subfamily Hamamelidoideae Reinsch

Tribe Hamamelideae A. DC.

Genus *Dicoryphe* Du Petit-Thouars

Genus *Embolanthera* Merr.

Genus *Hamamelis* L.

Genus *Loropetalum* R. Brown ex Reich.

Genus *Maingaya* Oliv.

Genus *Neostrearia* L.S. Smith

Genus *Noahdendron* Endress, Hyland et Tracey

Genus *Ostrearia* Baill.

Genus *Tetrathyrium* Benth.

Genus *Trichocladus* Pers.

Tribe Corylopsideae Harms

Genus *Corylopsis* Sieb. et Zucc.

Tribe Eustigmateae Harms

Genus *Eustigma* Gardn. et Champ.

Genus *Fortunearia* Rehd. et Wils.

Genus *Sinowilsonia* Hemsl.

Tribe Fothergilleae A. DC.

Genus *Distyliopsis* Endress

Genus *Distylium* Sieb. et Zucc.

Genus *Fothergilla* Murray

Genus *Matudaea* Lundell

Genus *Molinadendron* Endress

Genus *Parrotia* C.A. Mey

Genus *Parrotiopsis* Schneider

Genus *Sycopsis* Oliv.

Genus *Shaniodendron* (Chang) Deng, Wei et Wang

Subfamily Rhodoleioideae Harms

Genus *Rhodoleia* Champ. ex Hook

CHAPTER 3. GEOGRAPHICAL DISTRIBUTION AND BIOLOGICAL FEATURES OF EXTANT HAMAMELIDALES

FAMILY PLATANACEAE

The modern family Platanaceae comprises the single genus *Platanus* with the type species *P. orientalis*. The species composition of *Platanus* is variously treated by different researchers and ranges from five to 11 species (Ward, 1888; Berry, 1914; Oishi and Huzioka, 1943; *Derev'ya i kustarniki SSSR*, 1954; Endo, 1963; *Zhizn' rastenii*, 1980). Depape (1966) adheres to the extreme point of view admitting the presence of only two species, *P. orientalis* and *P. occidentalis*, in the modern flora.

It is most likely that the extant flora includes seven species, several varieties, and hybrids (*Derev'ya i kustarniki SSSR*, 1954). Nowadays, the generic range embraces North America from Mexico to Canada (eight species), the Balkan Peninsula, islands of the Aegean Sea, Crete, western Asia (*P. orientalis*), and Indochina (*P. kerrii*). The origin of the Platanaceae vegetating in the forests of Armenia, Azerbaijan, and Central Asia is a matter of discussion. Some plane forests of these territories could be of natural origin (Safarov, 1984), which is substantiated by the similar ecological conditions and floristic compositions of the communities (woody and shrubby strata).

In North America, there are *P. occidentalis* and a morphologically isolated group of plane trees, including *P. wrightii*, *P. racemosa* Nutt., *P. glabrata* Fernald, *P. mexicana*, and *P. lindeniana* Mart. et Gal. These species usually have lobed entire-margined leaves. A characteristic feature of this group is the frequently observed peltate base of the leaf blade. Among extant plane trees, only this group displays this feature. Many researchers consider these species as conspecific or propose clustering them in one or two species with several ecological varieties. Thus, MacGinitie (1937, 1941) noticed a high resemblance between *P. racemosa* and *P. wrightii*. MacGinitie believed that *P. glabrata* displays a series of transitional forms to *P. mexicana*, while *P. lindeniana* is most distant from these species but similar in several features to *P. occidentalis*. This researcher believes that, in regard to a number of characters, *P. lindeniana* is closer to Eocene species than any living form.

The genus *Platanus* includes large deciduous trees with a broad crown. The optimal conditions for the vegetation of plane trees are restricted to banks and valleys

of rivers and lakes. Less commonly, plane trees occur in mountain forests. In natural conditions, the plane prefers rich and mellow alluvial soils (Pshenichnyi, 1960; Safarov, 1984). Due to their high requirement for light, plane trees never form a closed forest stand (*Derev'ya i kustarniki SSSR*, 1954). The trees are very long-lived, individuals are known to be up to 2000 years old.

Planes are typical anemophilous and anemochorous plants. Numerous fruits, nutlets, are arranged in compact capitate infructescences. After germination, they remain on the tree during winter. In spring, the infructescences disintegrate into separate fruits, which are spread by wind due to the presence of bristles at the fruit bases.

FAMILY HAMAMELIDACEAE

The modern family Hamamelidaceae consists of 30 genera and 144 species (Zhang and Lu, 1995), including the latest data provided by Endress *et al.* (1985) and Deng *et al.* (1992a). About a half of the genera are monotypic. The largest genus *Corylopsis* comprises 33 species (Morley and Chao, 1977). When analyzing the modern geographical distribution of the genera of the Hamamelidaceae, Zhang and Lu (1995) established two main types of distribution. The first, tropical, type embraces 18 genera vegetating in tropical regions of Asia (*Exbucklandia*, *Rhodoleia*, *Mytilaria*, *Chunia*, *Altingia*, *Tetrathirium*, *Maingaya*, *Embolanthera*, *Eustigma*, *Sycopsis*, and *Distylium*), central America (*Molinedendron* and *Matudea*), Africa (*Dicoryphe* and *Trichocladus*), and Australia (*Ostrearia*, *Neostrearia*, and *Noahdendron*).

The second, temperate, type includes 12 genera, represented in Asia (*Disanthus*, *Semiliquidambar*, *Loropetalum*, *Corylopsis*, *Fortunearia*, *Sinowilsonia*, and *Shaniodendron*), western Asia (*Parrotia* and *Parrotiopsis*), western and southern Asia and North America (*Liquidambar*), and North America (*Fothergilla*). Thus, the family is currently distributed in western, eastern, and southeastern Asia, eastern and southern Africa, northeastern Australia, Central America, and southeastern North America. The family Hamamelidaceae is absent from Europe and South America. Of certain interest is a high number of endemic species of the Hamamelidaceae (121 species that comprise 84% of the total number of species). In particular, 19 genera (102 species) occur in the southern part of eastern Asia and northern Indochina (63 and 70% of the total numbers of the genera and species, respectively) (Zhang and Lu, 1995).

The family is represented by both evergreen (*Rhodoleia*, *Exbucklandia*, *Tetrathirium*, *Trichocladus*, *Sycopsis*, *Dicoryphe*, *Altingia*, and others) and deciduous (*Hamamelis*, *Parrotia*, *Parrotiopsis*, *Corylopsis*, *Disanthus*, *Liquidambar*, and others) trees and shrubs. These plants considerably contribute to forest vegetation, composing mostly the subcanopy layer. Usually, they do not form pure stands, although they occasio-

nally dominate in mountain forests (e.g., *Altingia excelsa* Nor., Java Island). Members of the family prefer mountain habitats (up to 3000 m above sea level). Some of them grow predominantly on rocky mountain slopes (*Disanthus*), hills (*Sinowilsonia*), and in relatively thin forests only along southern mountain slopes (*Rhodoleia*). *Hamamelis* prefers rocky river banks and forest borders (Skvortsova, 1975).

Members of the family vary from giant trees up to 60 m high, such as *Altingia excelsa*, to low shrubs at most 1 m high (North American *Fothergilla gardenii*). Some lowland plants of the monotypic genus *Parrotia* are represented by shrubs with multiple interwinning and coalescent trunks, which form an impenetrable thicket. When vegetating over 300-m in altitude, parrotias become well-developed trees with a straight trunk and well-formed crown (*Zhizn' rastenii*, 1980).

The pollination patterns of the Hamamelidaceae are highly diverse. Some members of the family are pollinated by insects or birds and have various pollinator attractants: numerous stamens with bright filaments and heavy pollen production (food of bees and bumblebees) in *Fothergilla*, bright bracts supporting the inflorescence (*Parrotiopsis*), purple awned petals of the corolla with nectaries at their bases (*Disanthus*), and massive elongated petals and well-developed nectaries (*Corylopsis*, *Hamamelis*, and *Maingaya*) (*Zhizn' rastenii*, 1980; Li *et al.*, 1997).

Several genera (*Sycopsis*, *Parrotia*, *Distylium*, and *Matudaea*) combine entomophily and anemophily (Endress, 1977). The genera *Altingia* and *Liquidambar* are typically anemophilous (Bogle, 1986).

Fruits of the Hamamelidaceae, woody capsules, are arranged in more or less compact infructescences (spike, raceme, or head). Seed dispersion of the Hamamelidaceae is variable. For instance, ballistic ejection of seeds by pressing on the fruit wall as a result of desiccation is known in *Hamamelis* and *Parrotia* (Tiffney, 1986). The genera *Altingia* and *Liquidambar* produce very small winged seeds. Mature seeds of *Altingia* attract birds and monkeys (Vink, 1957). *Exbucklandia* is characterized by large winged seeds. The small discoid seeds of *Rhodoleia* are easily spread for a long distance by wind.

CHAPTER 4. MORPHOLOGY OF LEAVES AND REPRODUCTIVE STRUCTURES AS THE BASIS FOR THE SYSTEMATICS OF EXTANT AND EXTINCT HAMAMELIDALES

ON THE MOST SIGNIFICANT MORPHOLOGICAL CHARACTERS OF LEAVES

As compared with modern plant studies, paleobotany is often restricted to the purely morphological approach to its objects. New taxa are often described on the basis of material showing only insignificant morphological differences from previously known forms.

Therefore, the number of poorly substantiated taxa increases, scarcely reflecting actual taxonomic diversity. In addition, the limited material available for paleobotanical study prevents a comprehensive analysis of individual, age-related, seasonal, ecological, and geographical variability. Because of limitations of paleobotanical objects, it is difficult to delineate the variation range of fossil taxa and differentiate between them. Therefore, whenever possible, paleobotanical studies should take into account the data of modern botany, which is able to scrutinize the limits of variability of particular characteristics.

The extent to which a certain parameter varies and the range of variation at different ontogenetic stages or under various ecological conditions are very important for the estimation of the taxonomic significance of a parameter. Such studies help to reveal the degree of genetic determination of a parameter. The knowledge of the variation range of a parameter in one species allows one to foresee the variation range of the same parameter in a related extinct species.

This approach decreases the number of dubious species and, sometimes, higher taxa are established because of the overestimated significance of certain intraspecific variants. This particularly concerns paleobotanical studies, where the material is often limited and insufficiently preserved. Moreover, paleobotanists usually deal with isolated plant organs.

Nevertheless, it is possible to perform such investigations using fossil material. For instance, an extensive leaf sample of Maastrichtian "*Platanus*" *raynoldsii* Newberry emend. Brown from a monotypic locality allowed us to reconstruct three leaf morphotypes and the shoot of this species (Moiseeva, 2003).

A significant variability in leaf morphology makes modern planes promising objects of such studies. A number of studies were devoted to leaf variability in extant species of *Platanus*. Henry and Flood (1919) analyzed the leaf morphology of *Platanus* and pointed out a number of widely variable features (base, apex, leaf blade margin, and serration). They considered the depth of sinuses between the lobes as the stablest characters. Suzuki (1958) also considered this feature to be rather constant in planes. However, MacGinitie (1937) believed that the lobe depth depends on the illumination and temperature. This researcher noticed that planes with deeply lobed leaves (*P. orientalis*, *P. racemosa*, and *P. wrightii*) grow on the banks of open river beds, in well-insolated and relatively dry sites, whereas *P. occidentalis* with less differentiated lobes prefers wet and shady sites.

Shkarlet (1979) showed the taxonomic significance of individual morphological features of plane leaves. Using abundant leaf samples of extant *P. orientalis* from the Crimea and Tajikistan, this researcher applied mathematical statistics to the study of 11 characters of the leaf blade. Four features (lobe number, length to width ratio of the leaf blade, the angle between the mid-

vein and basisopic veins, and the angle between the midvein and secondary veins) are shown to vary at a very low (Tajikistan) and low (Crimea) level; the level of variability is about 7 and 15%, respectively. Shkarlet concluded that these parameters are of particular taxonomic importance.

Unfortunately, similar studies of taxonomically important features of leaf morphology and the degree of their variability have not been performed for the Hamamelidaceae.

The main morphological and microstructural features of extant and extinct members of the Platanaceae and Hamamelidaceae are considered below.

FAMILY PLATANACEAE

Leaf Morphology of the Genus *Platanus*

The leaf blade shape of representatives of this genus widely varies. In extant planes, lobed leaf blades predominate, ranging from weakly to deeply lobed. *P. kerrii* is the sole extant species characterized by entire leaves. Its leaves principally differ from the leaf blades of other species of the genus. The generic identification of such leaf morphotypes could be performed only in association with reproductive structures (the morphology of the flower, infructescence, and seed). Among fossil planes, species with lobed leaves (*P. basicordata* Budants., *P. acutiloba* Borsuk, etc.) are more common; the species having narrow entire castanoid leaves (*P. neptunii* (Ettings.) Bůžek, Holy et Kvaček) are relatively rare. However, many Cretaceous platanoids had broad entire or weakly lobed leaf blades. Leaves of the living Platanaceae vary in the morphology of the leaf base, which is highly variable even within the same species. Subcordate, cuneiform, and decurrent leaf bases are most frequent. Cordate, truncate, and asymmetric bases occur more rarely. Similar variability in the outline of the leaf base is also present in early plane species.

Vakhrameev (1976) considers the more or less decurrent leaf base as a distinctive feature of Cretaceous planes. According to Vakhrameev, this feature allows one to differentiate *Platanus* from morphologically similar members of the family. Among living planes, the group of North American species (*P. lindneriana*, *P. mexicana*, and *P. racemosa*) occasionally have a peltate base. However, the proportion of such leaves is relatively small in these species. Occasionally, this feature is observed in *P. occidentalis* (Ward, 1890). The peltate base is characteristic of many Cretaceous platanoids. In Paleocene *Platanus*, this base shape occurs substantially less frequently, while in the Neogene *Platanus*, the peltate leaf base has not been registered.

The leaf blade margin is an important diagnostic feature of the genus *Platanus*. Among Cretaceous platanoids, almost entire-margined leaves and leaves with an undulate margin occur relatively often. The overwhelming majority of Cenozoic and modern planes

have a serrate margin; as a rule, its teeth have the characteristic concave–concave outline. This feature, in combination with other characters, is a reliable distinguishing feature of the genus.

Some plane species are distinguished by the tooth density along the leaf margin, tooth measurements, height, etc. Species characterized by the predominantly whole leaf blade often show leaves with one or several teeth. Lobed entire-margined leaves occasionally have a small serration in the upper region of the lobes. These teeth are usually small and are represented by naked vein endings (setae). It was shown on the basis of extensive herbarium material that serration in extant *Platanus* changes depending on the leaf age. The low teeth of juvenile leaves often have characteristic papilla-like thickenings. The completely formed plane leaves have typical concave–concave teeth.

Leaf Morphology of Other Members of the Platanaceae

The leaf morphology of the fossil Platanaceae is extremely diverse. In addition to the typical variously lobed leaves of *Platanus* (section *Platanus*) and the genus *Macginitiea* Wolfe et Wehr, entire pinnate leaves of *Platanus* (section *Castanephyllum*) also existed.

The morphological variation of leaf structures is significantly extended by the Cretaceous platanoid form genera. The difficulties in generic and species diagnostics, caused by loose diagnoses and insufficient information (in particular, the lack of epidermal data), were discussed above. Thus, *Protophyllum* has entire and broadly elliptical or ovate leaves with pinnate (more rarely, palmate–pinnate) venation, secondary veins, attaining the maximal length in the central leaf region and becoming shorter toward the base and apex, the peltate base, and the entire or undulate margin (Lesquereux, 1874; Budantsev, 1975; Vakhrameev, 1976). *Pseudoprotophyllum* is distinguished by the palmate–pinnate venation, the peltate base, and the characteristic serration similar to that of extant *Platanus* (Hollick, 1930; Budantsev, 1975; Vakhrameev, 1976). The genus *Paraprotophyllum* (Herman, 1984) has a different base shape, ranging from truncate to pseudopeltate.

The genus *Aspidiophyllum*, described from the Cretaceous deposits of the Dakota Formation (Lesquereux, 1883), is characterized by trilobate leaves, palmate–pinnate venation, the camptodromous secondary veins, a peltate base, rounded lobe apices, and an entire or weakly undulate margin.

The genus *Credneria* from the Cretaceous deposits of Hartz, Germany (Zenker, 1833), is characterized by entire ovate leaves, a rounded or truncated base, and a nearly entire leaf margin (widely spaced small teeth are occasionally present only in the upper part of the blade). One pair of secondary veins is more developed than other secondaries and has basisopic branches, and the infrabasal veins are well developed. The se-

condary veins are usually camptodromously terminated; in the case where teeth are present in the upper part of the leaf blade, some secondary veins terminate in these teeth. *Credneria* from the Upper Cretaceous deposits of Alaska has a slightly different morphology: the leaf margin is nearly completely dentate, the teeth are characteristically incised, and the venation is craspedodromous (Hollick, 1930).

Leaves of the genus *Arthollia* are entire, broadly elliptical to ovate, and, occasionally, subrhomboidal (Herman and Golovneva, 1988). The well-pronounced basal veins deviate suprabasally. The leaf base is truncated, broadly rounded, occasionally broadly cuneate, and lacks pelta. The marginal teeth are triangular or broadly triangular and often have an apical gland.

Summarizing available data concerning platanoid leaf macromorphology, one can conclude that leaf characteristics of many genera are highly polymorphous, and the variation ranges of related genera often overlap; this often results in poorly pronounced taxonomic differences.

The findings of compound leaves of the Late Maas-trichtian *Erlingdorffia* Johnson (Johnson, 1986) and the Paleocene *Platanites hebridicus* Forbes (Crane *et al.*, 1988) have considerably extended information concerning leaf morphology of the Platanaceae. Leaves of *Platanites* Forbes and *Erlingdorffia* consist of a trilobate terminal leaflet of typically platanoid appearance, resembling the leaf of *Platanus* (section *Platanus*), and two simple more or less asymmetrical lateral leaflets. The pistillate and staminate structures associated with leaves of *Platanites hebridicus* also show characteristic features of the Platanaceae, supporting the assignment of these leaves to this family.

Compound leaves are unknown in extant planes. However, many species have well-developed stipules. Crane *et al.* (1988) proposed that the stipules of *Platanus* could have been homologous to the leaflets of *Platanites*. Ward (1888) hypothesized the homology between the stipules of extant planes and the excessively developed basal lobes or peltate base (fused basal lobes) of extinct and extant members of the genus.

The diversity of the leaf morphotypes of the Platanaceae is supplemented by the compound pinnate or pinnatifid leaves of the Early Cretaceous genus *Sapindopsis* Fontaine. The study of the *Sapindopsis* cuticle (Upchurch, 1984) and associated pistillate and staminate heads (Crane *et al.*, 1993) supported the earlier assumption (Hickey and Doyle, 1977; Crane, 1989) about the close relationship of this genus to the Platanaceae. Leaves of *Sapindopsis* vary in the morphology of leaf blades and margin (Fontaine, 1889; Hickey and Doyle, 1977). Some morphotypes (pinnately compound leaves) have trilobate terminal leaflets, which resemble typical leaves of *Platanus* (Hickey and Doyle, 1977).

Epidermal Characters of the Platanaceae

Leaves of extant *Platanus* were described as hypostomatic (Baas, 1969). The upper epidermis consists of polygonal cells with straight or slightly undulating walls and scattered hairs. Cuticular folds radiate from the hair bases.

Ordinary epidermal cells of the lower leaf surface are identical in outline to those of the upper surface, but smaller. The lower leaf surface bears variously oriented stomata and round hair bases.

The epidermal study of extant *Platanus occidentalis* shows irregularly disposed stomata on the upper surface (less numerous than those on the lower surface); hair bases and stellate hairs, which often persist in mature leaves and tend to be restricted to the vein areas; and glands. Thus, extant *Platanus* has both hypostomatic and amphistomatic leaves.

The stomata of *Platanus* are described as anomocytic (Metcalf and Chalk, 1950). Krassilov (1973) also determined the stomata of planes as anomocytic; however, he indicated that a pair of narrow paracytic subsidiary cells is occasionally observed in *Platanus*. Fryns-Claessens and Van Cotthem (1973) assigned the stomata of *Platanus kerrii* described by Baas (1969) to the cyclocytic type. Brett (1979) described the stomata of extant *P. orientalis* as pleioparacytic and indicated that five to six, or, more rarely, eight subsidiary cells are the most characteristic number for the genus. Van Horn and Dilcher (1975) remarked that guard cells of *Platanus* are slightly elevated above two to four subsidiary cells.

The stomata of extant *P. occidentalis* are anomocytic, having five to six subsidiary cells. Guard cells are raised above the surface of the epidermis to form cylindrical thickenings (Maslova, 1997).

Upchurch (1984) showed that the epidermal features characteristic of the family had already been formed in the Albian. The cuticles studied of leaves of platanoid appearance and leaves of *Sapindopsis* demonstrated features characteristic of the Platanaceae (trichome pattern, cuticular folds radiating from the stomata and hair bases, and glands).

Reproductive Structures of the Platanaceae

The data on reproductive structures of the Cretaceous and Paleogene members of the Platanaceae are shown in Tables 1, 2.

Inflorescence type. The reproductive sphere of the genus *Platanus* and fossil members of the family comprises compound inflorescences, consisting of the central axis and sessile or pedicellate unisexual heads. Rudiments of the opposite sexual structures are occasionally present (staminodes in pistillate flowers and rudimentary pistils in staminate flowers).

The number of heads on the axis allows one to identify species of extant planes. Thus, *P. occidentalis* has a single head on a short axis; other species of the subgenus

Platanus have two to five heads (usually, two heads in *P. acerifolia*, three or four in *P. racemosa*, and four or five heads in *P. orientalis*). The heads are sessile or have a short pedicel. *P. kerrii* (subgenus *Castaneophyllum*) has an elongate axis bearing up to 12 sessile heads.

Inflorescences of the extinct Platanaceae are usually spheroid. The majority of them lack pedicels. They differ in dimensions of the head. The smallest heads are characteristic of *Platanocarpus marylandensis* Friis, Crane et Pedersen (3–4 mm) and *P. carolinensis* Friis, Crane et Pedersen (4.3–6.1 mm). In *Platanites hybridicus*, *Macginicarpa manchesteri* Pigg et Stockey, and *Platanus laevis* Velen., heads are larger, 10–17, 10–16, and 20 mm, respectively.

Oreocarpa N. Maslova et Krassilov and *Tanyoplatanus* Manchester stand conspicuously apart with reference to inflorescence morphology. *Oreocarpa* has very small heads, consisting of several underdeveloped carpellodia and a single ripening fruit. *Tanyoplatanus* is characterized by an elongated cylindrical inflorescence with a straight central axis surrounded by numerous densely packed flowers. The inflorescence reaches 30 mm in length and 11 mm in width.

Heads of the extant plane do not shed in the autumn, persisting on the tree during the winter period. Next spring, they disintegrate into detached fruits and are spread by wind. The Paleocene genus *Archaranthus* Maslova et Kodrul is known to have a staminate inflorescence, which are broken into individual flowers and stamens after maturation (Maslova and Kodrul, 2003).

Perianth. In the heads of *Platanus*, numerous tightly pressed flowers radiate from a relatively conspicuous receptacle. For a long time, the floral morphology of *Platanus* has been a matter of discussion. The main discrepancies concerned the presence of perianth. Beginning with Clark (1858), the perianth of the plane was interpreted as a double perianth, including distinct calyx and corolla. Griggs (1909) proved the absence of corolla in pistillate flowers of *P. occidentalis*. Bretzler (1924) believed that the perianth of *Platanus* is substantially reduced and the flower is nearly naked. Boothroyd (1930) recognized the calyx and corolla in the flower of plane; however, the characters distinguishing these elements remained uncertain. At the same time, Boothroyd indicated that the corolla is often absent. The vascular elements were not recognized in these structures. Manchester (1986) indicated that the perianth of *Platanus* is extremely small and did not find it possible to distinguish between the calyx and corolla in the perianth. The thin, membranous, and free (or, occasionally, fused into a tubule) elements of the perianth are at most one-fifth of the flower length.

In contrast to extant *Platanus*, extinct members of the Platanaceae had well-developed perianths (*Platanocarpus* Friis, Crane et Pedersen; *Macginicarpa* Manchester; *Platananthus* Manchester; *Quadriplatanus* Magallón-Puebla, Herendeen et Crane; *Hamatia* Pedersen, Crane et Drinnan; *Tanyoplatanus*; and

Table 1. Morphological characters of Cretaceous and Paleogene pistillate inflorescences of the Platanaceae: (1) after Crane *et al.*, 1993; (2, 6) Friis *et al.*, 1988; (3) Pedersen *et al.*, 1994; (4) Magallón-Puebla *et al.*, 1997; (5) Knobloch and May, 1986; (7) Pigg and Stockey, 1991; (8) Maslova, 1997; (9) Crane *et al.*, 1988; (10) Maslova and Krassilov, 2002; (11) Manchester, 1986; (12, 13) Manchester, 1994; and (14) Bůžek *et al.*, 1967

No.	Taxon	Age	Infructescence type	Head diameter, mm	Perianth	Number of carpels per flower	Pubescence	Carpel shape	Stylode
1	<i>Platanocarpus brookensis</i>	Early–Middle Albian	Sessile head	5–6	Well-developed, two circles	5	–	Triangular	–
2	<i>Platanocarpus marylandensis</i>	Late Albian	Sessile head	3–4	Well-developed	5	–	Narrow triangular	Weakly developed
3	<i>Platanocarpus elkneckensis</i>	Late Albian	Sessile head	6	Well-developed	5	–	Triangular	–
4	<i>Quadriplatanus georgianus</i>	Coniacian–Santonian	Sessile head	1.14–2.39	Well-developed, two circles	4	–	Triangular	–
5	<i>Platanus richteri</i>	Santonian	Head with very short pedicel	7	?	?	Hairy carpels	Broadly elliptical	Very short
6	<i>Platanocarpus carolinensis</i>	Santonian–Campanian	Sessile head	4.3–6.1	Well-developed	5	–	Triangular	–
7	<i>Macginicarpa manchesteri</i>	Paleocene	Pedicellate head	1.0–1.6	–	5(?)	–	From elliptical to ovate	Elongate, slightly curved
8	<i>Platanus stenocarpa</i>	Late Paleocene–Early Eocene	Head, attachment?	13	Absent	?	+	Narrowly ovate	?
9	<i>Platanites hybridicus</i>	Paleocene	Head, attachment?	10–17	Reduced	?	?	?	Elongate curved
10	<i>Oreocarpa bureica</i>	Early Paleocene	Head with solitary fruit	4	Absent	1	Fruit	Elliptical, with three longitudinal ribs	Short
11	<i>Macginicarpa glabra</i>	Middle Eocene	Pedicellate head	10–15	Well-developed	5	–	From elliptical to ovate	Elongate, slightly curved
12	<i>Tanyoplatanus cranei</i>	Middle Eocene	Cylindrical	30 × 5–11	Well-developed	3–4	+	Oval	Elongate
13	<i>Platanus hirticarpa</i>	Middle Eocene	Head, attachment?	8.0	Reduced	4	+	Oval or triangular	Elongate
14	<i>Platanus nep-tuni</i>	Miocene	Pedicellate head	20	Absent	4–8	Hairy carpels	Oval	Elongate

Archaranthus). The presence of the nondifferentiated perianth was reported in Middle Eocene *Platanus hirticarpa* Manchester (Manchester, 1993). *Sarbaya radiata* Krassilov et Shilin from the Cenomanian–Turonian deposits of Kazakhstan has a weakly developed perianth, which is less than, or equal to, one-third of the stamen length (Krassilov et Shilin, 1995). Paleocene *Platanites hybridicus* (Boulter and Kvaček, 1989; Crane *et al.*, 1998) and *Platanus stenocarpa* N. Maslova (Maslova, 1997) display extremely reduced perianths.

Androecium. Staminate flowers of extant *Platanus* have three to five stamens consisting of a short filament and elongated tetrasporangiate anthers. The

underdeveloped carpels are occasionally present in the staminate flowers. The stamen number varies even within one head (Boothroyd, 1930). Stamen filaments can be so short that anthers seem sessile. Each anther consists of two thecae with two pollen sacs each. The thecae are connected by the connective, which is apically peltate. The anthers are asymmetric because of uneven development of the thecae and vary in size within the same stamen (Hufford and Endress, 1989). Each theca bursts open into two valves (Endress, 1989b).

Staminate inflorescences of extinct platanoid genera are considerably diverse. The common feature of all

Table 2. Morphological characters of Cretaceous and Paleogene staminate inflorescences of the Platanaceae: (1) after Crane *et al.*, 1993; (2, 7, 8) Friis *et al.*, 1988; (3) Pedersen *et al.*, 1994; (4) Krassilov and Shilin, 1995; (5) Magallón-Puebla *et al.*, 1997; (6) Knobloch and May, 1986; (9) Maslova and Kodrul, 2003; (10) Krassilov, 1973; (11) Pigg and Stockey, 1991; (12) Crane *et al.*, 1988; (13) Maslova, 2002a; (14) Manchester, 1986; (15) Manchester, 1994; and (16) Bůžek *et al.*, 1967

No.	Taxon	Age	Inflorescence type	Inflorescence diameter, mm	Perianth	Number of stamens per flower
1	2	3	4	5	6	7
1	<i>Aquia brookensis</i>	Early–Middle Albian	Head, attachment?	2.5	+	?
2	<i>Platananthus potamacensis</i>	Late Albian	?	?	+	5
3	<i>Hamatia elknekensis</i>	Late Albian	Sessile head	3–4	+	5?
4	<i>Sarbaya radiata</i>	Cenomanian–Turonian	Sessile head	5	–	4
5	<i>Quadriplatanus georgianus</i>	Coniacian–Santonian	Sessile head	0.89–2.55	+	4
6	<i>Platanus richteri</i>	Santonian	Head with short pedicel	7	?	?
7	<i>Platananthus hueberi</i>	Santonian–Campanian	Sessile head	1.9–3.6	+	5
8	<i>Platananthus scanicus</i>	Santonian–Campanian	Pedicellate head	4.9–5.8	+	5
9	<i>Archaranthus krassilovii</i>	Maastrichtian–Early Paleocene	Pedicellate head	5	+	4
10	<i>Tricolpopollianthus bureensis</i>	Early Paleocene	Head with short pedicel	7–8	–?	?
11	<i>Platananthus speirsae</i>	Paleocene	Pedicellate head	7–9	–?	?
12	<i>Platanites hebridicus</i>	Paleocene	Pedicellate head	6–11	+	?
13	<i>Chemurnautia staminosa</i>	Late Paleocene–Early Eocene	Sessile head	4	–	?
14	<i>Platananthus synandrus</i>	Eocene	Sessile head	3–10	+	5
15	<i>Macginistemon mikanoides</i>	Middle Eocene	?	?	?	5
16	<i>Platanus neptuni</i>	Miocene	Head sessile, Pedicellate?	–	Reduced	6–7?

No.	Taxon	Stamen length, mm	Shape of extension of connective	Pubescence	Pollen size, μm	Exinal structure	Anther filament
1	2	8	9	10	11	12	13
1	<i>Aquia brookensis</i>	1.2–2.0	Conical	–	10–12	Alveolate–reticulate	Long
2	<i>Platananthus potamacensis</i>	0.5–0.6	Peltate	–	8.5–12	Reticulate with isodiametric alveolae	Short
3	<i>Hamatia elknekensis</i>	0.4–0.6	Cuneate	–	10–12	Reticulate	Short
4	<i>Sarbaya radiata</i>	1.8	?	–	13.5–16.5	Reticulate, polygonal meshes	Short
5	<i>Quadriplatanus georgianus</i>	0.86–1.34	Cuneate, triangular	–	11–16.9	Reticulate with identical meshes	Short
6	<i>Platanus richteri</i>	?	Peltate	–	16–19	Reticulate	Short
7	<i>Platananthus hueberi</i>	0.6–0.9	Peltate	+	13–15	Reticulate, polygonal meshes	Short
8	<i>Platananthus scanicus</i>	1.2–2.8	Triangular	–	15–16.5	Finely reticulate	Short
9	<i>Archaranthus krassilovii</i>	1.2	Conical	+	16.8–13.3	Reticulate	Short
10	<i>Tricolpopollianthus bureensis</i>	3.0	Widened, triangular	–	18	Reticulate	Short
11	<i>Platananthus speirsae</i>	2.2–2.5	Conical	?	16–18	Reticulate	Short
12	<i>Platanites hebridicus</i>	?	Widened	?	16–20	Finely reticulate	Short
13	<i>Chemurnautia staminosa</i>	0.9	Undeveloped	–	11–13	Reticulate	Short
14	<i>Platananthus synandrus</i>	?	Conical, peltate	+	12–16	Reticulate with small meshes	Short
15	<i>Macginistemon mikanoides</i>	2.5	Conical	+	20–25	Reticulate	Short
16	<i>Platanus neptuni</i>	?	Peltate	? extension of the connective	?	?	Short

fossil members of the Platanaceae is the shape of the capitate inflorescence and the number of stamens per flower (usually five), which is constant within an inflorescence. The main differences concern stamen morphology. Massive anthers on shortened filaments are characteristic of Cretaceous *Sarbaya radiata* (Krassilov and Shilin, 1995), *Quadriplatanus georgianus* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla *et al.*, 1997), *Platananthus hueberi* Friis, Crane et Pedersen, *Platananthus scanicus* Friis, Crane et Pedersen (Friis *et al.*, 1988), and *Hamatia elkneckensis* Pedersen, Friis, Crane et Drinnan (Pedersen *et al.*, 1994); Paleocene *Platananthus speirsae* Pigg et Stockey (Pigg and Stockey, 1991) and *Archaranthus krassilovii* (Maslova and Kodrul, 2003); and Eocene *Platananthus synandrus* Manchester (Manchester, 1986).

Early Cretaceous *Aquia brookensis* Crane, Pedersen, Friis et Drinnan is remarkable among fossil staminate inflorescences (Crane *et al.*, 1993). This species is characterized by well-developed stamen filaments, which are twice as large as the anthers.

There are differences in the morphology of connectives in the extinct Platanaceae. The connectives are developed to a greater or lesser extent; the apical extension can be poorly pronounced (*Aquia brookensis*); the outline of the apical part is conical (*Platananthus synandrus* and *P. speirsae*), triangular (*P. scanicus*), flattened (*P. hueberi*), or peltate (*Platanus richteri* and *Platananthus potomacensis* Friis, Crane et Pedersen). Hairs on the connectives are present in *Platananthus hueberi*, *P. synandrus*, *Platanus neptuni*, *Aquia brookensis*, stamen assemblages of *Macginistemon mikaneides* (MacGinitie) Manchester and *Archaranthus krassilovii*, while in *P. potomacensis*, *P. scanicus*, *P. speirsae*, and *Platanus richteri* they are absent. The connective epidermis of *Aquia brookensis* has numerous stomata and stomata-like secretory glands, that of *Archaranthus krassilovii* has an anomocytic stomata.

Gynoecium. The apocarpous gynoecium of extant *Platanus* consists of 5–8 (occasionally, 3–9) carpels, arranged in two or three circles and having long stylodes. The distinguishing feature of plane is the incomplete fusion between the edges of the carpel even at maturity (Sporne, 1974). The stigma is decurrent along the ventral suture of the style. The ovule is usually solitary, crassinucellate, and orthotropous.

The female sphere of extinct members of the Platanaceae is distinguished by the constant number of carpels per flower. *Platanocarpus brookensis* Crane, Friis et Drinnan, *P. marylandensis*, *P. elkneckensis* Pedersen, Friis, Crane et Drinnan, *P. carolinensis*, *Macginicarpa manchesteri*, and *M. glabra* have five carpels per flower. *Quadriplatanus georgianus* has clearly tetramerous flowers. Four (or, possibly, more) carpels were apparently present in *Platanus hirticarpa*; three or four carpels were present in *Tanyoplatanus cranei* Manchester.

The carpel shape changed from narrow triangular (in *Platanocarpus marylandensis*, *P. brookensis*, and *P. carolinensis*) to narrow elliptical (*Platanocarpus* sp., Friis *et al.*, 1988), broadly elliptical (*Platanus richteri*), ovate–elliptical (*Macginicarpa glabra*), narrow elliptical (*Platanus stenocarpa*), obovate to triangular (*P. hirticarpa*), and ovate to obovate (*Tanyoplatanus cranei*). *Oreocarpa* remarkably stands out in fruit morphology. The fruit of this genus is elongated and exceeds the head in size. It has a short stylode, basal locule, and a winged distal part with three longitudinal ribs.

The absence of disperse hairs in pistillate flowers is a characteristic feature of extinct members of the Platanaceae. The exceptional Eocene genus *Tanyoplatanus* has numerous relatively large hairs at the fruit base. The presence of disperse hairs in pistillate flowers is one of the generic characters of *Platanus*. Extinct species of this genus had hairs on the carpel surface (*Platanus laevis*, *P. richteri*, *P. stenocarpa*, and *P. neptuni*). In the extinct Platanaceae studied, one ovule per carpel is a constant condition.

Characteristic Features of Pollen Grains of the Platanaceae

The pollen of *Platanus* is tricolpate, or, very rarely, tricolporate; spheroid or slightly elongate in equatorial view; and rounded or angular in polar view. The polar diameter is 19–24 μm , the equatorial diameter is 17–22 μm . The colpi are lenticular or oval, with indistinct margins. The exinal sculpture is reticulate (Hesse, 1978; Pacltova, 1982; Zavada and Dilcher, 1986).

The pollen of extinct members of the Platanaceae is rather uniform. In general, it is smaller than that of living *Platanus* (e.g., 8.5–12 μm in *Platananthus potomacensis*, 13–15 μm in *P. hueberi*, and 16–20 μm in *Platanites hybridicus*). The most important structural differences are found in *Aquia brookensis* and *Archaranthus krassilovii*. The pollen grains of the former species have alveolate–reticulate exine, unlike the typically reticulate exine of other extinct platanoids (Crane *et al.*, 1993). Some pollen grains of the latter species have additional colpi.

FAMILY HAMAMELIDACEAE

Leaf Morphology of the Hamamelidaceae

The morphology of leaves in the family Hamamelidaceae is rather diverse (Skvortsova, 1960; Li and Hickey, 1988). The majority of genera have alternate leaf arrangements, except for *Dicoryphe* and *Trichocladus*, whose leaves show an opposite arrangement. Various developed stipules are present in all genera of the family. The presence of stipules in *Rhodoleia* has been disputed for a long time. Mature leaves of this genus do not exhibit stipules (Vink, 1957; Tardieu-Blot, 1965; Hutchinson, 1967). However, a developmental

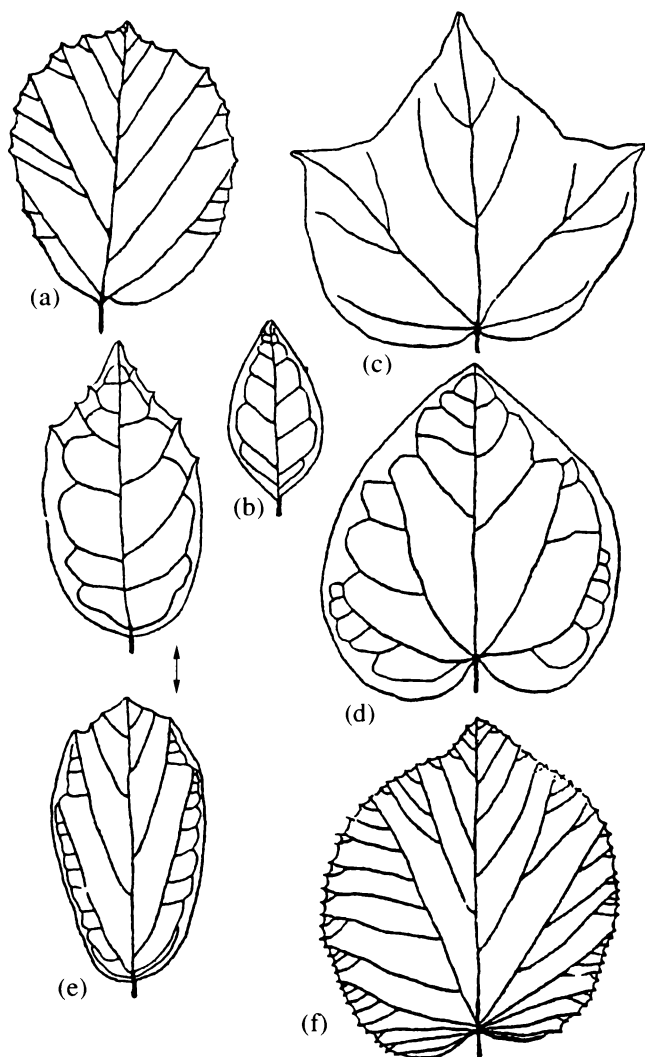


Fig. 1. Venation types in the family Hamamelidaceae (after Skvortsova, 1960): (a) pinnate-craspedodromous, (b) pinnate-brochidodromous, (c) palmate-craspedodromous, (d) palmate-brochidodromous, (e) pinnate-brochidodromous-craspedodromous, and (f) palmate-pinnate-craspedodromous.

study revealed the presence of peculiar stipules in foliar organs, intermediate between bud scales and mature leaves (Endress, 1978). Such stipules develop asymmetrically. One of them is represented by a small scale, another is a narrow elongate structure. The stipules persist on the shoot for a short time and are shed together with the bud scales.

Nearly all genera of the Hamamelidaceae have entire leaf blades, except for *Mytilaria*, which is characterized by trilobate entire-margined leaves, and *Exbucklandia*, which often displays large lobelike teeth at the ends of one or both basal veins.

Skvortsova (1960) studied venation patterns in living members of the family and recognized six types of venation (Figs. 1a–1f); four of them are widespread among angiosperms, one is apparently confined to the

Hamamelidaceae, and one type subsequently got a new interpretation on the basis of anatomical studies.

The pinnate–craspedodromous venation is characteristic of species of the genera *Hamamelis*, *Parrotia*, *Parrotiopsis*, *Fortunearia*, and *Sinowilsonia* (Fig. 1a). In this type, the basal veins are usually distinctly pronounced and naked to a greater or lesser extent at the leaf base (especially in the genus *Parrotiopsis*).

The pinnate–brochidodromous venation occurs in *Loropetalum*, *Trichocladus*, *Maingaya*, *Embolanthera*, *Dicoryphe*, *Sycopsis*, *Rhodoleia*, and *Ostrearia* (Fig. 1b). In the leaves of these genera, the secondary veins terminate short of reaching the leaf blade margin, and loop to form a contact with the upper veins. The secondary and tertiary venation is developed to a various extent.

The palmate–craspedodromous venation is observed in the leaves of *Mytilaria* (Fig. 1c). The palmate–brochidodromous venation occurs in *Disanthus* and *Exbucklandia* (Fig. 1d).

Skvortsova considers the pinnate–brochidodromous–craspedodromous venation (Fig. 1e) to be the most interesting type, representing a transition between the craspedodromous and brochidodromous variants. This type occurs in *Fothergilla*, *Sycopsis*, *Distylium*, *Eustigma*, and *Tetrathirium*. Several pairs of veins in the lower part of the leaf typically loop, while the secondary veins in the upper part terminate in marginal teeth. The proportions of the brochidodromous and craspedodromous veins differ in different genera. Thus, in *Fothergilla*, only the lower pair of veins loops to form contact with the next pair, while other secondary veins terminate in teeth. In *Sycopsis*, *Distylium*, and *Eustigma*, only one to three pairs of secondary veins in the upper leaf region are directed to the teeth, while the majority of the secondary veins are looping. According to Skvortsova, only the Hamamelidaceae display this type of venation. Such venation patterns have been registered in Paleocene *Ushia* Kolak., which is closely similar to the Tertiary and living *Nothofagus* (Krassilov *et al.*, 1996).

The palmate–pinnate–craspedodromous venation is characteristic of the genus *Corylopsis* (Fig. 1f). Macroscopically, the leaves of this genus show a well-developed pair of repeatedly branching basal veins. However, a more detailed study of the venation in the basal leaf region has shown that the apparent branches of the basal veins are in actual fact separate veins, deviating from the midvein at a certain distance from each other. Serial sections in the region of vein deviation corroborate this point, i.e., the conducting bundles diverge from the vascular cylinder of the petiole at different levels. Thus, the pinnate veins in the lower leaf region appear as palmate–radiate because of the extremely closely positioned nodes and short internodes.

The above listed venation patterns, which are characteristic of the Hamamelidaceae (Skvortsova, 1960), are convenient morphological criteria for the identifica-

tion of genera within the family considered, especially in combination with other features of leaf morphology. When studying venation of the higher orders, Skvortsova did not find any taxonomically significant characters. The tertiary venation in leaves of the Hamamelidaceae is uniformly represented by a series of parallel veins with perpendicular or oblique anastomoses in the middle of their course. Veins of the higher orders occasionally form areoles of various shapes and dimensions.

A more detailed study of the venation of the higher orders and the venation in the marginal region of the leaf blade in extant representatives of the Hamamelidaceae apparently may provide important data on generic distinctions in the Hamamelidaceae.

It should be noted that Skvortsova excluded the genera *Altingia* and *Liquidambar* from the Hamamelidaceae. *Semiliquidambar* was unknown at that time. Therefore, describing the venation patterns of the family, she did not consider these three genera.

Altingia has evergreen, more or less elliptical, elongated leaves with the pinnate venation. *Liquidambar* has deciduous lobed leaves. My study of the herbarium material of the Botanical Institute of the Russian Academy of Sciences (genera *Altingia* and *Liquidambar*) and species of *Liquidambar* cultivated in the Botanical Garden of Sukhumi substantiated that the leaf blades of these genera show insignificant variations within an individual. In contrast, generic and specific differences are relatively well pronounced.

Judging from the significant variability of the leaf shape in the living *Liquidambar formosana* Hense, Makarova (1957) assumed similar leaf variability in fossil members of the genus. In addition to trilobate leaves typical of this species, several transition forms to the *Altingia* leaf have been registered, i.e., entire leaves with underdeveloped lobes, one asymmetrical lobe, and, eventually, entire leaves typical of *Altingia* (Makarova, 1957, pl. II). This diversity was revealed in the herbarium specimens of *Liquidambar formosana* from the Quangdung Province of China. Chang (1962, 1973) described from the Recent flora of southeastern China the genus *Semiliquidambar*, which is probably of a hybrid origin. This genus is characterized by polymorphous leaves; i.e., entire, single-lobed, and typically lobed leaves are present on one and the same shoot. The polymorphism of the leaf blades of *Liquidambar formosana* described by Makarova in actual fact concerns the genus *Semiliquidambar*, which was unknown at the time of her work. Recall that the herbarium specimens of *Liquidambar formosana* described by Makarova as polymorphous come from China.

Epidermal Characters of the Hamamelidaceae

The leaf epidermal morphology in extant members of the Hamamelidaceae was studied by Harms (1930),

Metcalf and Chalk (1950), Skvortsova (1960b, 1975), and Pan *et al.* (1990).

Leaves of all genera of the Hamamelidaceae are hypostomatic. According to Skvortsova (1960), the number of stomata per unit of leaf surface can be used as a diagnostic character of the genera. The differences in the number of cells and the thickness of cell walls of the upper epidermis are significant. The size of the stomata is a relatively constant character. In the majority of genera, the stomata are 27–30 μm long. Only several genera have the stomata 22–25 μm long or 36–40 μm long.

The morphology of the upper and lower epidermis allowed Skvortsova (1960b, 1975) to divide the family into five groups. The epidermis of the first group (*Hamamelis*, *Parrotia*, and *Fortunearia*) consists of large and thin-walled cells with an undulating sinuous outline and a relatively small number of anomocytic stomata. The second group embraces the genera *Trichocladus*, *Rhodoleia*, *Distylium*, and *Sycopsis*, whose epidermis consists of relatively small polygonal cells with moderately thickened walls and paracytic stomata, which are more numerous than in the first group. The third group (*Exbucklandia*, *Mytilaria*, and *Disanthus*) is distinguished by the relatively large, thick-walled, polygonal cells rectilinear in outlines. The stomata are paracytic or encyclocytic. The fourth group (*Fothergilla* and *Tetrathyrum*) is transitional between the first and the second. This group is similar to the first group in cell size, cell wall thickness, and their weakly sinuous outline; it is similar to the second in its stomatal type. The fifth group contains a single genus, *Corylopsis*, with thin-walled epidermal cells of rectilinear outlines and with paracytic stomata.

Epidermal data on fossil members of the Hamamelidaceae are absent.

Reproductive Structures of the Hamamelidaceae

The generative sphere of extant members of the family is very diverse and is considerably well studied (Shoemaker, 1905; Schmitt, 1965; Mizushima, 1968; Bogle, 1970, 1984, 1986, 1987; Kapil and Kaul, 1972; Kaul and Kapil, 1974; Wisniewski and Bogle, 1982; Endress, 1989b; Hufford and Endress, 1989). In recent years, paleobotany has supplemented the data on the diversity of the reproductive organs of the Hamamelidaceae (Endress and Friis, 1991; Crepet *et al.*, 1992; Manchester, 1993; Magallón-Puebla *et al.*, 1996, 2001; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou *et al.*, 2001).

The major characters of reproductive structures in Cretaceous and Paleogene members of the family Hamamelidaceae are shown in Table 3.

Inflorescence type. Simple or compound spike is the main inflorescence type of the family (Endress, 1977). Some genera have simple or compound and more or less compact racemes, or, more

Table 3. Morphological characters of Cretaceous and Paleogene reproductive structures of the Hamamelidaceae: (1) after Maslova and Golovneva, 2000a; (2) Zhou *et al.*, 2001; (3) Maslova and Golovneva, 2000b; (4) Magallón-Puebla *et al.*, 2001; (5) Endress and Friis, 1991; (6) Magallón-Puebla *et al.*, 1996; (7) Maslova and Krassilov, 1997; and (8, 9) Manchester, 1994

No.	Taxon	Age	Inflorescence type	Inflorescence diameter, mm	Unisexual flowers	Bisexual flowers	Perianth	Number of carpels	Carpel shape
1	2	3	4	5	6	7	8	9	10
1	<i>Viltyungia eclecta</i>	Cenomanian	Sessile head	10–11	–	+	Well-developed	2	Broadly cuneate
2	<i>Microaltingia apocarpela</i>	Late Turonian	Pedicellate head	7	+	–	–	2	?
3	<i>Lindacarpa pubescens</i>	Coniacian	Head, attachment?	19	+	–	Double	?	Broadly cuneate
4	<i>Androdecidua endressii</i>	Late Santonian	Flowers, inflorescence structure?	?	–?	+?	Five petals	–	–
5	<i>Archamamelis bivalvis</i>	Santonian–Campanian	Flowers, inflorescence structure?	?	–	+	Double	2?–3	?
6	<i>Allonia decandra</i>	Campanian	Flowers, inflorescence structure?	?	+	–	Narrow petals	–	–
7	<i>Evacarpa polysperma</i>	Paleocene	Pedicellate head	4–5	+	–	–	2	Narrowly elliptical
8	<i>Fortunearites endressii</i>	Middle Eocene	Cylindrical	2.4 in diameter and 53 in length	+	–	?	2	Elliptical
9	Male inflorescences associated with <i>F. endressii</i>	Middle Eocene	Head	7	+	–	Double	–	–

No.	Taxon	Number of ovules	Pubescence	Sterile structures	Number of stamens per flower	Anther stalk	Shape of extension of connective	Tetrasporangiate anther
1	2	11	12	13	14	15	16	17
1	<i>Viltyungia eclecta</i>	At least 7	Carpels, stamens, perianth	Staminodes	?6	Short	–	+
2	<i>Microaltingia apocarpela</i>	ca. 10	–	Phyllomes	–	–	–	–
3	<i>Lindacarpa pubescens</i>	?	Carpels, perianth	?–	–	–	–	–
4	<i>Androdecidua endressii</i>	–	–	–	10	Broad, massive, parallel-margined	Elongate	+
5	<i>Archamamelis bivalvis</i>	2?	–	Staminodes? 7	6–7	Short, 0.2 mm	?	–
6	<i>Allonia decandra</i>	–	–	Nectaries	5	Short	Elongate	+
7	<i>Evacarpa polysperma</i>	Numerous	–	Staminodes and phyllomes	–	–	–	–
8	<i>Fortunearites endressii</i>	1	?	–	–	–	–	–
9	Male inflorescences associated with <i>F. endressii</i>	–	Perianth	Underdeveloped carpels, staminodes	10	?	?	?

Table 3. (Contd.)

No.	Taxon	Bisporangiate anthers	Anther opens by valves	Anther opens by longitudinal slit	Pollen size, μm	Exine structure and number of colpi
1	2	18	19	20	21	22
1	<i>Viltyungia eclectic</i>	–	–	+	16–19	Reticulate exine, 3 meridional and 3 additional colpi
2	<i>Microaltingia apocarpela</i>	–	–	–	3.1–10	Reticulate exine, 3 colpi
3	<i>Lindacarpa pubescens</i>	–	–	–	–	–
4	<i>Androdecidua endressii</i>	+	+	–	13.2–13.9	Coarsely reticulate exine, 3 colpi
5	<i>Archamamelis bivalvis</i>	+	+	–	13–15	Reticulate exine, 3 colpi
6	<i>Allonia decandra</i>	–	+	–	20.8–26	Reticulate exine, 3 colpi
7	<i>Evacarpa polysperma</i>	–	–	–	–	–
8	<i>Fortunearites endressii</i>	–	–	–	–	–
9	Male inflorescences associated with <i>F. endressii</i>	?	?	?	?	Reticulate exine, 3 colpi

rarely, heads. Three extant genera (*Altingia*, *Liquidambar*, and *Semiliquidambar*) of the subfamily Altingioideae have heads, which are similar to those of the Platanaceae. The microstructure of reproductive organs in the Hamamelidaceae has been comprehensively studied (Flint, 1959; Schmitt, 1965; Wisniewski and Bogle, 1982; Bogle, 1986). Some members of the subfamilies Hamamelidoideae and Exbucklandioideae have extremely compact inflorescences, simulating heads. However, in spite of a superficial similarity, their floral morphology is different. There are both unisexual and bisexual flowers, with or without perianth.

Bogle (1970) showed an interesting case of the formation of the pseudanthium in some members of the Hamamelidaceae. The researcher believes that the species of *Distylium* represent an early stage of pseudanthium development. In this genus, the inflorescence axes are compressed and the bracts and staminate flowers aggregate around the pistillate flower to form a false flower. The inflorescence of *Rhodoleia* consists of five to eight flowers forming the pseudanthium, pollinated by birds (Bogle, 1987).

Among fossil hamamelids, the capitate inflorescence is known in *Evacarpa* N. Maslova et Krassilov (Maslova and Krassilov, 1997), *Lindacarpa* N. Maslova (Maslova and Golovneva, 2000a), and *Microaltingia* Zhou, Crepet et Nixon (Zhou et al., 2001) from the subfamily Altingioideae, and in *Viltyungia* (Maslova and Golovneva, 2000b), showing a combination of microstructural characters typical of the subfamilies Exbucklandioideae, Altingioideae, and Hamamelidoideae. The genus *Steinhauera* Presl., which is considered to be

similar to *Liquidambar*, has morphologically similar heads (Kirchheimer, 1943, 1957; Tiffney, 1986; Krassilov, 1989, 1997; Ferguson, 1989).

Of particular interest is the find of staminate and pistillate heads, which display both platanoid and hamamelid features, in the Turonian of the Raritan Formation of New Jersey (Crepet et al., 1992). Crepet and coauthors consider these heads to be generally similar to the extant Hamamelidaceae. However, the description suggests that the heads show hamamelid characteristics different from those of the Altingioideae.

Manchester (1994) described staminate heads associated with the racemose infructescences *Fortunearites endressii* Manchester and containing in situ pollen grains. This researcher cast doubt on the assignment of these reproductive structures to one and the same plant, because the infructescences are similar to the extant genera *Fortunearia* and *Sinowilsonia*, while the staminate heads with in situ pollen are more similar to *Hamamelis* and *Corylopsis*.

Fossil reproductive structures of the Hamamelidaceae, namely, *Archamamelis* Endress et Friis (Endress and Friis, 1991), *Allonia* Magallón-Puebla, Herendeen et Endress (Magallón-Puebla et al., 1996), and *Androdecidua* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 2001), are solitary flowers. No data on their arrangement in inflorescences have been discovered.

F l o w e r. The extant Hamamelidaceae include both the taxa possessing unisexual (Altingioideae) and bisexual (Exbucklandioideae and Hamamelidoideae)

flowers. Flowers of the Altingioideae are functionally unisexual, although staminodes producing nonfertile pollen are observed (Bogle, 1986). In the genus *Hamamelis*, the development of ovary is retarded to the moment of pollen discharge (Shoemaker, 1905; Endress, 1977; Mione and Bogle, 1990). Rudimentary pistils occur in the functionally staminate flowers of some members of the Hamamelidoideae, i.e., in the tribes Fothergilleae and Eustigmataeae (Endress, 1989a, 1989b).

The extinct genus *Archamamelis* apparently had bisexual and, possibly, functionally unisexual flowers. In *Androdecidua*, the flower is pentamerous, actinomorphic, with a well-developed androecium. Although the gynoecium is not preserved, Magallón-Puebla (2000) proposed on the basis of comparison with earlier findings that these flowers might be bisexual. The genus *Allonia* was established on the basis of flowers at an early developmental stage where the petals are well formed and open, while the fertile organs are incompletely developed, which hampers the recognition of female structures, although the presence of male structures is evident. The flowers of *Viltingia* are bisexual. *Lindacarpa* is a pistillate inflorescence containing carpels at different stages of maturation. The flowers of *Microaltingia* are unisexual. The pistillate flower of *Evacarpa* contains sterile structures resembling staminodes.

Perianth. Several lineages of the lower dicots, including various genera of the Hamamelidaceae, have a double perianth differentiated into the calyx and corolla (Endress, 1989b; Drinnan *et al.*, 1994). The Hamamelidaceae are usually characterized by a double perianth where the calyx and corolla are developed to a various extent. The perianth is tetramerous or pentamerous; more rarely, it lacks petals. The perianth lobes are free or more or less fused into a tube; occasionally, they are partially adnate to the ovary. In some extant members of the Hamamelidoideae, the perianth lobes are basally fused with the stamens to form the hypanthium (*Parrotia* and *Fothergilla*), which is supposedly accompanied by a decrease in the stamen number (*Parrotiopsis*, *Molinadendron*, and *Sycopsis sinensis* Oliv.), and partial fusion of the floral tube and the ovary (*Parrotiopsis* and *Fothergilla*) (Bogle, 1970).

In the hamamelidacean genera having a differentiated corolla, the petals are variable in shape. They are usually ribbon-shaped, narrow, with parallel margins; however, petals in the genera *Neostrearia* and *Trichocladus* are slightly constricted at the base; in *Dicoryphe* (Magallón-Puebla *et al.*, 1996), they are spatulate; in *Disanthus*, they are broadly triangular; and in *Corylopsis*, they range from elongated to rounded (Morley and Chao, 1977).

The genera with ribbon-shaped perianth elements show a coiling of these elements at the bud. This feature is typical for the tribes Hamamelideae and Disanthoideae, while in the Rhodoleioideae and, possibly, Exbucklandioideae, the perianth elements are erect in

the bud. The fleshy petals of the genus *Noahdendron* remain coiled for a long time, but their apical parts are often shed with maturation (Endress *et al.*, 1985).

The presence of the perianth in the Altingioideae has long been debated. It is clearly absent from staminate flowers. However, opinions differ as to the presence or absence of perianth in the pistillate flowers. Bogle (1986) proposed that the reports concerning the presence of the perianth in pistillate flowers were a result of misinterpretation. In particular, the intrafloral phylomes (Hooker and Thomson, 1858; Clarke, 1858; Oliver, 1867), a stiff sclerenchymatous ring surrounding flowers in a mature head (Sargent, 1922), and a circle of sterile stamens (Horne, 1914) were taken for the corolla. Endress (1977) indicated that the perianth is absent nearly everywhere. Many researchers believe the flowers of the modern Altingioideae to be naked (Wilson, 1905; Tong, 1930; Vink, 1957; Schulze-Menz, 1964; Bogle, 1986). In this group, the perianth elements are absent even at early ontogenetic stages (Wisniewski and Bogle, 1982).

Many genera of other subfamilies composing the Hamamelidaceae have both naked and dichlamydeous or monochlamydeous flowers. Thus, in the subfamily Hamamelidoideae, the flowers of *Distylium* and *Sycopsis dunnei* Hemsl. are naked, and the perianth of *Parrotiopsis* is substantially reduced (Bogle, 1970). *Sycopsis sinensis* and *S. griffithiana* Oliv. have a perianth composed of four to seven sepals (Endress and Anliker, 1968). *Parrotia* has six to ten perianth elements, which vary in shape and measurements (Bogle, 1970). In the subfamily Exbucklandioideae, *Chunia* has naked flowers, *Exbucklandia* exhibits a separate calyx only at early ontogenetic stages, and *Mytilaria* and *Disanthus* have distinctly dichlamydeous flowers (Bogle, 1986). In *Matudaea*, the fused bracts on the floral axis simulate a calyx (Endress, 1989b).

Bogle (1986) assumed the existence in the geological past of ancestral hamamelids with a well-developed perianth. Actually, the genus *Allonia* has a well-differentiated corolla with narrow and parallel-margined petals and irregularly developed sepals. In the flowers of *Androdecidua*, the calyx members are absent. The petals are fusiform, constricted at both the base and the apex, and partially fused with the stamens of the outer circle of the androecium. The differentiated perianth of *Archamamelis* most likely has six or seven members. The triangular, basally expanded, petals are similar to those of extant *Disanthus*. *Viltingia* has a well-developed perianth. The inner members of the perianth are relatively narrow, while the outer members are wide and hairy. The pubescent perianth is known in extant *Parrotia* (Bogle, 1970). The genus *Lindacarpa* has a well-developed perianth, which is attached slightly above the base of the gynoecium and almost entirely embraces the flower lengthwise. The flowers of the genus *Evacarpa* are naked.

The findings of early fossil hamamelids having well-developed perianths suggest that, in the course of evolution, this structure was reduced. Thus, the naked flower of extant *Liquidambar* and *Altingia* is a derived character.

Androecium. The morphology of the male sphere of extant hamamelids has been comprehensively studied (Endress, 1989b; Hufford and Endress, 1989). Nearly all hamamelids have tetrasporangiate anthers. The thecae with a solitary locule occur only in the genera *Hamamelis* and *Exbucklandia* (Shoemaker, 1905; Kaul and Kapil, 1975).

Endress (1989b) recognized the main types of the anther dehiscence in members of the subclass Hamamelididae. In his classification, the lower hamamelids *Euptelea* (Eupteleaceae), *Cercidiphyllum* (Cercidiphyllaceae), and *Myrothamnus* (Myrothamnaceae) and the hamamelids *Parrotia*, *Sycopsis*, *Distyliopsis*, *Distylium*, *Disanthus*, and, possibly, *Liquidambar* occupy an isolated position. In these genera, anthers open by a longitudinal slit. This feature is characteristic of the higher hamamelids and is associated with anemophily. The majority of genera of the Hamamelidaceae have anthers that open into two valves.

An expanded apex of the connective and the basally attached anthers are characteristic features of the lower hamamelids. The extension of the connective that exceeds the thecae in length is typical for many lower hamamelids. This character is especially well-pronounced in the tribe Hamamelideae of the family Hamamelidaceae (*Loropetalum*, *Tetrathirium*, *Maingaya*, and *Embolanthera*), where the extensions of connectives are hornlike.

Among the extinct Hamamelidaceae, the genus *Allonia* has anthers with a well-defined hornlike extension of the connective; this is a distinctive feature of the extant subtribe Loropetalinae.

The androecium of *Androdecidua* consists of ten stamens, arranged into two circles. The stamen filaments are thick, broad, parallel-margined, and fused at the base. The stamen bases of the external circle are fused with the petal bases. The extensions of the connectives are distinct. They are directed toward the center of the flower, where they unite to form an acuminate tip. A distinctive feature of *Androdecidua* is the difference in morphology between the outer and inner stamen circles. The outer stamens have bisporangiate anthers consisting of two thecae. Each theca lacks an adaxial pollen sac. The anther dehisces by a single valve. The inner stamens have tetrasporangiate anthers composed of two thecae and dehiscing by two valves.

The above-mentioned extinct hamamelids *Archamamelis*, *Allonia*, and the Turonian staminate heads have valved anthers. The anther of *Viltyungia* opens by a longitudinal slit. It is noteworthy that the anther shape in this Cretaceous genus (which has a strongly convex dorsal face) is identical to that of living

Disanthus (Endress, 1989a, 1989b; Endress and Hufford, 1989).

Viltyungia is the sole currently known extinct hamamelid whose anthers open by a longitudinal slit.

Sterile structures of flower. The intrafloral phyllomes (sterile structures other than staminodes in the pistillate flowers) are difficult to interpret. They have been discovered in genera belonging to different subfamilies (*Altingia* and *Liquidambar* in the Altingioideae; *Exbucklandia* in the Exbucklandioideae; and *Rhodoleia* in the Rhodoleioideae). Needle-like, obtuse, ribbonlike, and spheroid phyllomes have been registered.

The position of phyllomes between the stamen circle and the ovary of the flower suggests their origin from rudimentary floral structures (Vink, 1957). Some researchers considered them to be calycate elements (see above), bracts supporting flowers (Guillaumin, 1920), underdeveloped styles of sterile flowers occurring among normal flowers (Harms, 1930), staminodes (Tong, 1930), papillae (Schmitt, 1965), or nectaries (Leeuwen, 1938). Croizat (1947) believed that the phyllomes are located at the periphery of the flowers, growing directly on the receptacle. However, these structures proved to have vessels from the same bundles as vessels of stamens and carpels; therefore, there is no convincing evidence for the extrafloral origin of phyllomes (Bogle, 1986).

Bogle (1986) indicated that the phyllomes of *Liquidambar* are similar to abortive pistils, indicating their possible homology, as was proposed by Harms (1930). However, no trace of stigma or ovule have been found (Bogle, 1986). Moreover, the pistillate origin of phyllomes contradicts their branching vascular bundles, which are dissimilar to those of the carpels, and the later appearance of phyllomes in their ontogeny (Wisniewski and Bogle, 1982). No evidence of a staminate nature of phyllomes has been obtained. The function of the phyllomes is still uncertain, although, in *Rhodoleia*, they are possibly glandular. The phyllomes of *Rhodoleia* and *Liquidambar* are very similar in morphology and anatomy (Bogle, 1989).

Krassilov (1989) considered the intrafloral phyllomes to be the primary sterile structures of proangiospermous preflowers (containing such structures in the bennettites and gnetophytes). He interpreted their superficial resemblance to perianth members, stamens, and carpels as secondary features, which appeared in connection with the adaptation for entomophily.

Another type of sterile structure observed in flowers of some hamamelids (e.g., in the Altingioideae) are staminodes. Tong (1930) does not differentiate between staminodes and phyllomes, considering both as sterile structures of the flower. The staminodes (which are reduced stamens) are able to produce a large amount of nonfertile pollen. As a rule, such pollen grains are considerably smaller than the fertile grains.

Fossil sterile floral structures have been extremely rarely reported. They are known in the genus *Evacarpa*, which has two types of such structures, differing in size and shape. The smaller and narrower structures were interpreted as phyllomes, the broader and more massive are considered to be staminodes. The latter apparently did not produce pollen.

The genus *Viltyungia* apparently had staminodes with considerable pollen production. Pollen masses (constituted by underdeveloped and bound together pollen grains, which are smaller than the fertile pollen) were found attached to the cuticle of the gynoecium.

The flowers of *Microaltingia* have two or three circles of rounded phyllomes, located on the margin of the hypanthium.

The debatable nature of such structures even in the extant members of the Hamamelidaceae explains the difficulties in interpretation of these structures in fossil forms.

Gynoecium. The syncarpous semi-inferior ovary of two carpels is a key character for all hamamelids. Nevertheless, in some genera, the number of carpels is variable. For instance, one to five carpels are found along with the more typical bicarpellate gynoecia in *Exbucklandia* (Kaul and Kapil, 1974). The flowers of *Parrotiopsis* contain one to three carpels (Kapil and Kaul, 1972).

Free, usually, elongate, and filiform styles tend to persist on the fruit. The stigmata are papillate and decurrent.

Some hamamelids have pubescent gynoecia. This feature is observed in various genera of the Hamamelidoideae (Bogle, 1970; Kapil and Kaul, 1972). Within the subfamily Altingioideae, *Liquidambar* shows naked carpels, and *Altingia* has a pubescent distal part of the ovary (*Altingia excelsa*; Bogle, 1986).

The number of ovules per ovary significantly varies in the Hamamelidaceae. The solitary ovule is observed in all members of the subfamily Hamamelidoideae. The occurrence of ovaries with one and two ovules is known in *Parrotiopsis jacquemontiana* (Decne.) Rehd. (Kapil and Kaul, 1972). The genera of other subfamilies have 5–8 (*Disanthus*, *Exbucklandia*, *Mytilaria*, and *Chunia*), 10–20 (*Rhodoleia*), 20–30 (*Liquidambar*), and 28–47 (*Altingia*) ovules (Endress, 1989b).

The majority of hamamelids have anatropous ovules. The orthotropous ovules are characteristic of the subfamily Altingioideae. The placentation is axial or (more rarely) parietal.

Melikyan (1971, 1972, 1973a, 1973b) and Zhang and Wen (1996) performed comprehensive studies of the seed anatomy of the family.

Characteristic Features of Pollen Grains of the Hamamelidaceae

A number of publications are devoted to the palynomorphology of the Hamamelidaceae. Early works deal with individual members of the family (Sears, 1930; Simpson, 1936; Erdtman, 1946; Ikuse, 1956; Chang, 1958; Chang, 1959, 1964; Lee, 1969; Eramyan and Melikyan, 1975; Hesse, 1978; Ananova, 1982). The most comprehensive review for that time by Chang (1964) included descriptions of pollen morphotypes in 21 genera and 57 species of hamamelids. Note that the researcher considered the genera *Altingia* and *Liquidambar* as members of the separate family Altingiaceae.

The above cited studies were conducted with the aid of a light microscope only. In recent decades, SEM and TEM have considerably extended our knowledge of the pollen ultrastructure. The illustrated review by Bogle and Philbrick (1980) contains detailed descriptions of pollen grains in 28 extant hamamelid genera, supplemented by SEM microphotographs. Only two genera of the family, *Semiliquidambar* and *Shaniodendron* (Chang) Deng, Wei et Wang, were not included in the review. The researchers considered the former genus as a hybrid between *Altingia* and *Liquidambar* and noticed its isolated position. *Shaniodendron* was described by Deng *et al.* (1992a) after publication of the review. The data on the pollen morphology of *Shaniodendron* are provided by Deng *et al.* (1992b). Zavada and Dilcher (1986) accomplished a comparative palynomorphological investigation of 20 families of the subclass Hamamelidae.

In the majority of extant genera of the Hamamelidaceae, pollen grains are typically tricolpate and reticulate. However, the genera of the subfamily Altingioideae are characterized by periporate pollen, whereas in *Chunia* (subfamily Exbucklandioideae), pollen grains have six rugae. The subfamily Hamamelidoideae displays several pollen morphotypes: typically tricolpate (in *Maingaya*, *Ostrearia*, *Hamamelis*, *Loropetalum*, *Corylopsis*, *Parrotiopsis*, and others), tetracolpate to ten-rugate (*Distylium*), tetracolpate to 12-rugate (*Matudaea*), and periporate (*Sycopsis*) (Bogle and Philbrick, 1980).

The typically tricolpate pollen grains of the Hamamelidaceae vary in the configuration of the colpi (in *Rhodoleia*, *Exbucklandia*, *Eustigma*, *Loropetalum*, and *Fothergilla*, the colpi closely approach the poles, while the colpi of *Forthunearia*, *Chunia*, and *Molinadendron* are somewhat shorter); the width of the apocolpia; and the dimensions, outline, and number of reticular meshes. Among hamamelids, there is a group of genera with peculiar pollen grains bearing various additional apertures (of the diffused colpate pollen type). Thus, in the subfamily Hamamelidoideae, pollen grains of *Distylium* in addition to the short colpi with rounded ends also show up to 10 rugae or pores. In *Matudaea*, pollen grains range from tetracolpate to 12-rugate. The

apertures in the genus *Sycopsis* vary from more or less elongated rugae to rounded pores. An interesting case of aberrant appearance of the additional colpus in extant *Platanus occidentalis* was presented by Zavada and Dilcher (1986, p. 352, text-fig. 9).

The genus *Chunia* is a remarkable case where both tricolpate pollen grains and those having four and six rugae have been described (Bogle and Philbrick, 1980). Chang (1964) reported the presence of a small proportion of polyporate pollen grains in this genus.

Extinct hamamelids include the genera characterized by tricolpate pollen grains with a finely reticulate exine, i.e., *Archamamelis*, *Allonia*, and staminate inflorescences associated with *Forthunearites endressii*. The pollen grains of *Androdecidua* are tricolpate, distinguished by a coarser exinal reticulum. The pollen grains having three meridional and three additional colpi are typical of *Viltyungia*. The Late Turonian genus *Microaltingia* is of interest, since, based on inflorescence morphology, it fits in the subfamily Altingioideae, but differs in its palynomorphology. In this genus, pollen grains are tricolpate (rather than periporate, as is typical of the subfamily) and have a coarser exinal reticulum.

CHAPTER 5. LOCALITIES OF THE FOSSIL PLATANACEAE AND HAMAMELIDACEAE STUDIED IN THIS WORK

Information concerning the localities yielding material for the present study is given below. Table 4 displays the occurrence of the Hamamelidales taxa in these localities.

(1) Eastern Siberia, Lena–Vilyui Depression, Tyung River; Timerdyakhskaya Formation, Cenomanian; collection BIN, no. 1181.

The Timerdyakhskaya Formation is at least 700 m thick. The formation consists of whitish gray inequigranular obliquely laminated sands and loose sandstones. The presence of interlayers of brownish fallow ferruginous sandstones is a distinctive feature of the formation. Plant remains are dominated by *Trochodendroides arctica* (Heer) Berry and cones of *Sequoia*. *Ginkgo adiantoides* Unger, *Trochodendroides smilacifolia* (Newb.) Krysh., and *Platanus* sp. are also present.

Data on the section and age of the formation are provided by Vakhrameev (1958).

(2) Eastern Siberia, Lena–Vilyui Depression, Linda River; Chirimyiskaya Formation, Coniacian; collection BIN, no. 1196.

The deposits of the Chirimyiskaya Formation consist of light gray, in places ferruginous, weakly cemented predominantly alluvial sandstones and clays. The deposits contain numerous plant remains, including *Ginkgo adiantoides*, *Macclintockia trinervis* Heer, two species of *Sequoia*, two species of *Trochodendroi-*

des Berry, *Platanus cuneiformis* Krassil., *Protophyllum leconteanum* Lesq., and *Credneria inordinata* Hollick.

The data on the geological section and age are provided by Vakhrameev (1958).

(3) Amur Region, southeast of the village of Arkhara; Tsagayan Formation, upper part of the middle subformation, Maastrichtian–Danian; collection GIN, no. 4867.

The reproductive structures described below were found on the northern side of the Arkhara-Boguchanskoe locality, in the light gray clays of the upper part of the Middle Tsagayan Subformation, between the coaly seams *Nizhnii* and *Dvoynoi*. The assemblage includes abundant remains of ferns, conifers of the families Tadoxidiaceae and Cupressaceae, and diverse angiosperms.

Data on the section and age are provided by Akhmetiev *et al.* (2002).

(4) Amur Region, right bank of the Bureya River, below the mouth of its right tributary, the Darmakan River, Bureinskii Tsagayan locality; Tsagayan Formation, Lower Paleocene; collections GIN, nos. AB and BG.

The interlayers of gray medium-grained sandstones and yellowish clayey fine-grained sandstones with debris are dominated by *Tiliaephyllum tsagajanicum* (Krysh. et Baik.) Krassilov, *Trochodendroides arctica*, and “*Platanus*” *raynoldsii*.

Data on the section and age are provided by Krassilov (1976).

(5) Northwestern Kamchatka Peninsula, Chemurnaut Bay; collection PIN, no. 3736.

(a) Upper part of the Kamchik Formation–lower part of the Tkaprovyayam Formation, Upper Paleocene–Lower Eocene.

The Kamchik Formation is composed of fine-grained and coarse-grained sandstones, which are in places obliquely bedded. The plant remains occur in the upper part of the formation.

The lower part of the Tkaprovyayam Formation is composed of alternating sandstones, siltstones, clays, gritstones, and conglomerates. The entire section of the exposed Tkaprovyayam Formation contains plant remains.

The section is dominated by the genera *Trochodendroides*, *Platanus*, and *Aesculus*. The genera *Juglans* L., *Carya* Nutt., *Pterocarya* Kunth., *Engelhardia* Lechen ex Blume (Juglandaceae), and *Myrica* L. (Myricaceae). *Ulmus* L. are common. Less frequent members of the assemblage are “*Acer*” *arcticum* Heer, *Alnus*?, *Quercus* L., and *Alangium* Lamarck.

In the lower part of the Tkaprovyayam Formation, individual specimens of thermophilic taxa (*Magnolia amurensis* Imch., genera *Lindera* Thunb., and *Nyssa* L.) are present.

Data on age and section are provided by Serova *et al.* (1989).

Table 4. Occurrence of platanoid and hamamelid fossil remains studied: (h) heads and (l) leaves

Eastern Siberia, Lena–Vilyui Depression, Tyung River; Timerdyakhskaya Formation, Cenomanian	<i>Vilyungia eclecta</i> (h)
Eastern Siberia, Lena–Vilyui Depression, Linda River; Chirimyskaya Formation, Coniacian	<i>Lindacarpa pubescens</i> (h)
Amur Region, southeast of the village of Arkhara; Tsagayan Formation, upper part of the middle subformation, Maastrichtian–Lower Paleocene	<i>Archaranthus krassilovii</i> (h)
Amur Region, right bank of the Bureya River, downstream from the mouth of its right tributary, the Darmakan River, Bureinskii Tsagayan locality; Tsagayan Formation, Lower Paleocene	<i>Oreocarpa bureica</i> (h)
Northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkprovayam Formation, Upper Paleocene–Lower Eocene	<i>Platanus acutiloba</i> (l) <i>Platanus basicordata</i> (l) <i>Platanus stenocarpa</i> (h) <i>Platanus asymmetrica</i> (l) <i>Platimeliphyllum palanense</i> (l) <i>Chemurnautia staminosa</i> (h) <i>Macginitiea latiloba</i> (l) <i>Sycopsiphyllum kamchaticum</i> (l) <i>Liquidambar miosinica</i> (l) <i>Parrotiopsis shimanskiana</i> (l)
Northwestern Kamchatka Peninsula, section between the capes Rebro and Getkilnin; Tkprovayam Formation, Upper Paleocene–Lower Eocene	<i>Platanus integrifolia</i> (l) <i>Platanus basicordata</i> (l) <i>Platimeliphyllum palanense</i> (l) <i>Macginitiea latiloba</i> (l) <i>Evacarpa polysperma</i> (h) <i>Evaphyllum kamchaticum</i> (l)
Western Kamchatka Peninsula, Evravayam River; Tkprovayam Formation, Upper Paleocene–Lower Eocene	<i>Platanus acutiloba</i> (l) <i>Platimeliphyllum palanense</i> (l) <i>Chemurnautia staminosa</i> (h)
Western Kamchatka Peninsula, Snatol River: 1. upper part of the Khulginskaya Formation, Lower Paleocene 2. Napana Formation, Upper Paleocene	<i>Platanus integrifolia</i> (l) <i>Platanus iljinskajae</i> (l) <i>Platimeliphyllum snatolense</i> (l) <i>Parrotiopsis shimanskiana</i> (l)
Western Kamchatka, Anadyrka River; Tigil Group, Middle? Eocene	<i>Platanus integrifolia</i> (l) <i>Platanus acutiloba</i> (l) <i>Platimeliphyllum palanense</i> (l) <i>Arthollia anadyrensis</i> (l)
Sakhalin Island, Onor River, isolated block of coal-bearing deposits; Middle? Eocene	<i>Platanus mabutii</i> (l) <i>Altingiophyllum onorensis</i> (l)
Southern Sakhalin Island, Krasnoyarka River Basin; Naiba Formation, Middle Eocene	<i>Platanus acutiloba</i> (l) <i>Platimeliphyllum denticulatum</i> (l) <i>Liquidambar miosinica</i> (l)
Southern Sakhalin Island, Naiba River; Naiba Formation, Middle Eocene	<i>Platanus mabutii</i> (l) <i>Liquidambar miosinica</i> (l)
Western Sakhalin Island, Snezhinka, Kama, and Aral'skaya rivers; Snezhinka Formation, Middle Eocene	<i>Liquidambar miosinica</i> (l)
Eastern Sakhalin, Bogataya River; Lyukama Formation, Upper Eocene	<i>Platanus mabutii</i> (l) <i>Liquidambar pachyphylla</i> (l)
Western Kamchatka Peninsula, Utkholokskii Peninsula; Zubchatyi Cape Formation, Upper Eocene	<i>Platanus asymmetrica</i> (l) <i>Hamamelis certa</i> (l)
Northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgirinskaya Formation, Upper Eocene	<i>Platanus basicordata</i> (l) <i>Platanus mabutii</i> (l) <i>Hamamelordia ochotensis</i> (l) <i>Parrotia kamchatica</i> (l) <i>Liquidambar miosinica</i> (l)
Eastern Sakhalin, Makarovskii Region, Korallovka River, Verkhneduiskaya Formation, Lower Miocene	<i>Liquidambar miosinica</i> (l) <i>Parrotia pristina</i> (l)

(b) Cape Chemryl; upper part of the Tkaprovayam Formation, Lower Eocene.

The floristic assemblage of this section remarkably differs from the above described assemblages from Chemurnaut Bay. *Myrica* is abundant, the family Fabaceae is diverse, the lauraceous *Lindera*, *Cinnamomophyllum* Kraus. et Weyl., and *Laurophyllum* Goepf. are rather common. *Magnolia* L. and *Anacardites* Sap. are abundant. *Trochodendroides*, *Juglans*, *Carya*, *Aesculus*, *Platanus*, and *Vitis* L. are subordinate members of the assemblage.

Data on the geological section and age are provided by Fotyanova (1989).

(6) Northwestern Kamchatka Peninsula, section between the capes Rebro and Getkilnin; Tkaprovayam Formation, Upper Paleocene–Lower Eocene; collection PIN, no. 4257.

The Tkaprovayam Formation is formed by heterogeneous sandstones, both horizontally laminate and obliquely bedded, interbedded by aleurolites, argillites, gritstones, conglomerates, and thin lens-shaped coaly seams. Plant impressions are abundant throughout the section. The plant assemblage resembles that from Chemurnaut Bay, although the Fabaceae are more prominent. Palms are known from the middle part of the section (Budantsev, 1983).

Data on the section and age are provided by Serova *et al.* (1989).

(7) Western Kamchatka Peninsula, Evravavayam River; Tkaprovayam Formation, Upper Paleocene–Lower Eocene; collection PIN, no. 4778.

Along the Evravavayam River, the Tkaprovayam Formation crops out with alternating conglomerates, sandstones, and siltstones. Plant remains come from greenish gray, coarse-grained and medium-grained platy sandstones. *Dyospiros* L., *Magnolia*, *Platanus*, *Macginitiea*, and "*Acer*" *arcticum* have been recorded.

Data on the section and plant assemblage are provided by Gladenkov *et al.* (1997), the age determination is after Serova *et al.* (1989).

(8) Western Kamchatka Peninsula, Snatol River; collection PIN, no. 4256.

(a) Upper part of the Khulgunskaya Formation, Lower Paleocene.

Light yellow coarse-grained sandstones contain *Equisetum* sp., *Metasequoia occidentalis* (Newb.) Chaney, *Trochodendroides arctica*, *Platanus integrifolia* N. Maslova, *Alnites shimanskii* Lavrenko et Fotyanova, *Myrica beringiana* Budants., and *Aesculus* sp.

Data on the section are provided by Fotyanova (personal communication) and the geological age is after Lavrenko and Fotyanova (1994).

(b) Napana Formation, Upper Paleocene.

The plant-bearing strata are composed of gray coarse-grained sandstones with abundant plant debris, containing fossil wood and concretions, with gray

(light brown on the weathering surface) and hard siliceous fine-grained sandstones with well-preserved plant remains.

The reference section outcropping along the Snatol River north of the mouth of Tatiana Creek contains a plant assemblage dominated by impressions of *Trochodendroides speciosa* (Ward) Berry, "*Acer*" *arcticum*, *Aesculus magnifica* (Newb.) Iljinskaja, and *Platanus* sp. The flora is peculiar in having thermophilic elements *Magnolia basicordata* Fotyanova et Lavrenko, *Nyssa budantsevii* Fotyanova, *Parrotiopsis shimanskiana* N. Maslova, *Sassafras* sp., and *Rhus* sp.

Data on the section are provided by Fotyanova (personal communication), the age was determined by Lavrenko and Fotyanova (1994).

(9) Western Kamchatka Peninsula, Anadyrka River; Tigil'skaya Group, Middle? Eocene; collection PIN, no. 3858.

The section in the mouth of the Anadyrka River is composed of greenish gray medium and coarse-grained sandstones with interlayers of laminated aleurolites and silicified sandstones with abundant plant remains, which include *Metasequoia occidentalis*, *Trochodendroides arctica*, *Pterocarya*, *Platanus*, *Glyptostrobus*, and genera of the Juglandaceae.

Data on the section and plant assemblage are provided by Fotyanova (personal communication), the age was determined by Serova (1969) and Serova and Fotyanova (1992).

(10) Sakhalin Island, Onor River, isolated block of coal-bearing deposits; Middle? Eocene; collection PIN, no. 4251.

A relatively poor plant assemblage was collected in the Onor River Basin, in an isolated block of coal-bearing deposits. The assemblage is conspicuously different from that of the Onor River (Verkhneduisckaya Formation). The deposits were preliminary dated as the Middle? Eocene (Fotyanova, personal communication).

(11) Southern Sakhalin Island, Krasnoyarka River Basin; Naiba Formation, Middle Eocene; collection PIN, no. 4252.

The formation is predominantly composed of fine-grained deposits: aleurolites and argillites, containing interlayers and lenses of fine-grained sandstones, coaly argillites, and coals.

The formation is characterized by widespread predominantly carbonaceous concretions. Small (less than 3–4 cm) rounded or flattened concretions prevail. They often compose extended lenses or chainlike interlayers up to 0.5 m thick. The deposits of the Naiba Formation (including concretions) abound in plant debris.

The plant assemblage includes *Equisetum arcticum* Heer, *Trochodendroides arctica*, *Metasequoia occidentalis*, *Taxodium dubium* (Sternb.) Heer, *Alnus kushiroensis* Tanai, *Platanus* sp., *Aesculus magnificum*, and *Cercidiphyllum palaeojaponicum* Endo.

Data on the section and age are provided by Kodrul (1999).

(12) Southern Sakhalin Island, Naiba River; Naiba Formation, Middle Eocene; collection PIN, no. 4253.

Along the right bank of the Naiba River, there is an outcropping of gray nonhard fine-grained sandstones with numerous concretions of silicified ferruginous sandstones. The plant assemblage is dominated by "*Acer*" *arcticum*, *Metasequoia*, *Platanus*, and *Trochodendroides*.

The data on the section and floristic assemblage are provided by Fotyanova (personal communication). The age assignment is after Kodrul (1999).

(13, 14, 15) Western Sakhalin Island, Snezhinka, Kama, and Aral'skaya rivers; Snezhinka Formation, Middle Eocene; collections PIN, nos. 4856, 4857, 4854, respectively.

The Snezhinka Formation is lithologically divided into three subformations. The lower subformation is composed mostly of aleurolites, argillites, and coaly argillites with coal-bearing interbeds. Sandstones, gritstones, and conglomerates are less prominent. The middle subformation is formed predominantly of heterogeneous sandstones with siliceous pebbles, gritstones with rare interlayers of aleurolites and argillites and isolated coal-bearing beds. The upper subformation includes mostly sandstones, grading upward into thin interbedding argillites, aleurolites, and sandstones.

Kodrul (1999) described in detail the stratotypic section and plant assemblages of the Snezhinka Formation. She correlated the subformations of the Snezhinka section with analogous deposits of the Kama and Aral'skaya rivers on the basis of lithology and flora.

The lower subformation is dated as the Early?–Middle Eocene, the middle and upper subformations are assigned to the Middle Eocene. The fossil material studied in the present paper came from the middle and upper subformations of the Snezhinka Formation.

Data on the section and age are provided by Kodrul (1999).

(16) Eastern Sakhalin Island, Bogataya River; Lyukama Formation, Upper Eocene; collection PIN, no. 4129.

In the middle course of the Bogataya River, there are outcrops of thin laminated argillites with interlayers of gray calcareous sandstones containing a rich flora. The plant assemblage contains *Castanea* Miller, *Quercus*, *Platanus*, *Ginkgo* L., *Pterocarya*, *Acer* L., *Cercidiphyllum*, and others.

Data on the section and plant assemblage are provided by Fotyanova (personal communication). Fotyanova (personal communication) has dated this formation as the Late Eocene, the earlier assignment was to the Eocene (Mitrofanova *et al.*, 1991).

(17, 18) Western Kamchatka Peninsula, Utkholokskii Peninsula; Zubchatyi Cape Formation, Upper Eocene; collection PIN, no. 4395.

(a) Coastal section between Yuznyi Cape and the mouth of the Utkholok River.

The coastal section is 418 m thick. It includes four plant assemblages. Three come from thin-laminated light brown sandstones with interlayers of cherty brick-red sandstones. One locality comes from a lens of dark gray, nearly black argillites, exposed in the tidal zone at low tides. Fotyanova *et al.* (1996) analyzed these assemblages and established two ecological types of vegetation. The first type reflects an intrazonal lowland vegetation. It is dominated by *Platanus* (*P. asymmetrica* N. Maslova), *Trochodendroides*, *Cercidiphyllum*, *Pterocarya*, *Populus*, and "*Acer*" *arcticum*. This assemblage shows a low generic and species diversity.

The second type corresponds to upland vegetation. It is specific in representing diverse modern genera of angiosperms dominated by *Quercus moiseevii* Fotyan. *et N. Maslova* and a small-leaved species of the genus *Betula*. *Hamamelis* (*H. certa* N. Maslova), *Broussonetia*, *Castanea*, *Fagopsis*, *Ulmus*, *Tilia*?, *Celtis*, *Rhus*, and others are rather common. The conifers *Metasequoia*, *Glyptostrobus*, and *Pinus* are abundant. Plants of the intrazonal type, *Platanus*, *Trochodendroides*, and "*Acer*" *arcticum*, are represented by isolated specimens.

(b) Bay south of the Zubchatyi Cape.

The coastal section 378 m thick is formed by alternating sandstones, aleurolites, argillites, and coaly aleurolites. The plant assemblage includes *Ginkgo* ex gr. *adiantoides*, *Metasequoia occidentalis*, *Trochodendroides arctica*, *Hamamelis certa*, *Platanus asymmetrica*, *Platanus mabutii* Oishi *et Huzioka*, species of the genus *Alnus* L., and *Mallotus orbiculatus* Tanai.

Data on the sections and age are provided by Fotyanova *et al.* (1996).

(19) Northwestern Kamchatka Peninsula, Podkagermaya Bay; Irgirinskaya Formation, Upper Eocene; collection PIN, no. 3862.

The Irgirinskaya Formation is exposed in a coastal outcrop near the Bozhedomova Cape about 9 or 10 km downstream of the mouth of the tributary Podkagermaya River.

The impressions of *Metasequoia occidentalis*, *Ginkgo* ex gr. *adiantoides*, *Trochodendroides speciosa*, *Zizyphus* sp., *Alnus kushiroensis*, *Pterocarya kamtschatica* (Krysht.) Cheled., *Carya ezoensis* Tanai, *Acer* sp., and *Alangium kryshtofovichii* Baik. were collected in the lower part of greenish gray, mostly coarse-grained loose sandstones with interlayers of brownish gray aleurolites.

Dryopteris sp. and *Sequoia* sp. are found in the lenses of siliceous aleurolites in the tidal zone. *Nelumbo nipponica* Endo, *Trochodendroides speciosa*, *Cercidiphyllum eojaponicum*, *Quercus furuhjelmi* Heer, *Parrotia kamchatica* N. Maslova sp. nov., *Ulmus* sp., *Zelkova* sp., *Castanea* sp., *Carpinus* sp., *Alnus* sp., *Pterocarya kamtschatica* (Krysht.) Cheb., *Carya ezoen-*

sis Tanai, *Cyclocarya* sp., and *Cercis* sp. are present in the upper layers of the section.

Data on the section and age are provided by Fotyano and Serova (1983).

(20) Western Sakhalin Island, Uglegorskii District, town of Shakhtersk; Verkhneduiskaya Formation, Lower Miocene; collection PIN, no. 3572.

Plant remains are nonuniformly distributed in the section. They are mostly restricted to the roof and bottom of the coal-bearing beds. The genus *Hamamelis* was found at the base of Bed no. 51 and was accompanied by *Ulmus* (*U. drepanodonta* Grub., *U. rarinervia* Fotjan., *U. speciosa* Newb.), *Alnus* (*A. duensis* (Baik.) Iljinskaya, *A. harneyana* Chaney et Axelrod, *A. schmalhauseni* Grub.), *Castanea tanaii* Huzioka, *Pterocarya duensis* Fotjan., *Populus kabagashii* K. Suzuki, *Spirea longifolia* Fotjan., and *Alangium tiliifolium* (A. Br.) Krysh.

The deposits enclosing this flora are mostly gray or dark gray aleurolites (massive to thinly laminated), with several beds of fine-grained sandstones and interlayers of dark gray or brownish gray mostly nonlaminated argillites.

Data on the section and age are provided by Fotyano (1988).

(21) Southern Sakhalin Island, Korsakovskii District, village of Novikovo; Verkhneduiskaya Formation, Lower Miocene; collection PIN, no. 3861.

The plant remains came from the middle coal-bearing subformation of the Verkhneduiskaya Formation, composed mostly of aleurolites and argillites. Sandstones and breccias appear in the upper part of the section. The subformation contains two coal-bearing seams.

Among angiosperms, genera of the family Fagaceae (*Fagus* and *Castanea*) and *Acer* predominate. Two conifer genera, *Glyptostrobus* and *Metasequoia*, are also abundant.

Data on the section and age are provided by Fotyano (1988).

(22) Eastern Sakhalin Island, Makarovskii District, Korallovka River; Verkhneduiskaya Formation, Lower Miocene; collection PIN, no. 3782.

In this region, the coal-bearing subformation of the Verkhneduiskaya Formation is only somewhat exposed. Plant remains were collected from homogeneous gray fine-grained laminated or lenticular ferruginous sandstones. The plant assemblage is specific in the presence of the genera *Parrotia*, *Liquidambar*, *Fagus*, *Castanea*, *Platycarya*, and *Pterocarya*.

Data on the section and age are provided by Fotyano (1988).

(23) Eastern Sakhalin Island, Shakhtnaya River, tributary of the Gornaya River; Verkhneduiskaya Formation, Lower Miocene; collection PIN, no. 4855.

The plant assemblage is similar to that from the Korallovka River locality (Eastern Sakhalin). The age is given after Fotyano (1988).

CHAPTER 6. SYSTEMATIC PALEOBOTANY

FAMILY PLATANACEAE DUMORTIER

Taxa Established on the Basis of Reproductive Structures

Genus *Archaranthus* N. Maslova et Kodrul

Type species. *Archaranthus krassilovii* N. Maslova et Kodrul.

Species composition. Type species.

Comparison. Although pedicellate heads are present in many platanoids, *Archaranthus* differs from the latter in the smaller number of flowers per inflorescence and in the disintegration of the mature head into separate flowers and stamens. Among members of the family Platanaceae, flowers with four stamens are known in the Cretaceous genera *Sarbaya* (Krassilov and Shilin, 1995) and *Quadriplatanus* (Magallón-Puebla *et al.*, 1997). *Archaranthus* is distinguished from *Sarbaya* by the well-developed perianth, the presence of stomata in the epidermis of the connective, and smaller exinal meshes. *Archaranthus* differs from the genus *Quadriplatanus* in the extension of the connective that is less developed and devoid of stomata and in the pollen grains that are less variable in size and shape and have a finer exinal reticulum.

Archaranthus krassilovii N. Maslova et Kodrul

Archaranthus krassilovii: Maslova and Kodrul, 2003, p. 93, pl. V, figs. 1–4; pl. VI, figs. 1–5; text-figs. 1a–1d.

Description (Figs. 2a–2d, 3a–3d, 4a, 4b). The material consists of a staminate head that is attached by a 4-mm-long pedicel to a 1-mm-thick fragmentary axis of the first order (Fig. 2a). The inflorescence (about 5 mm in diameter) consists of a rounded receptacle (2 mm in diameter) and radiating flowers.

After maturation the inflorescence disintegrates into separate flowers and stamens (Figs. 2a, 2b). Under a light microscope, rounded scars (lift by the shedding of flowers) and partially preserved perianth members are seen on the receptacle surface. There are seven or eight scars on the visible hemispherical surface of the head; therefore, the total number of flowers per head should be approximately 15.

SEM revealed the microstructure of the flowers. A separate flower comprises four stamens and a well-developed perianth. Since the mature inflorescence disintegrated into individual flowers and stamens, the elements of the perianth either have survived as fragments attached to the receptacle or are present only in some flowers. The epidermis of the outer members of the perianth is composed of elongate cells arranged in rows. Their long walls are slightly sinuous and well cutinized, the transverse wall are nearly indistinguish-

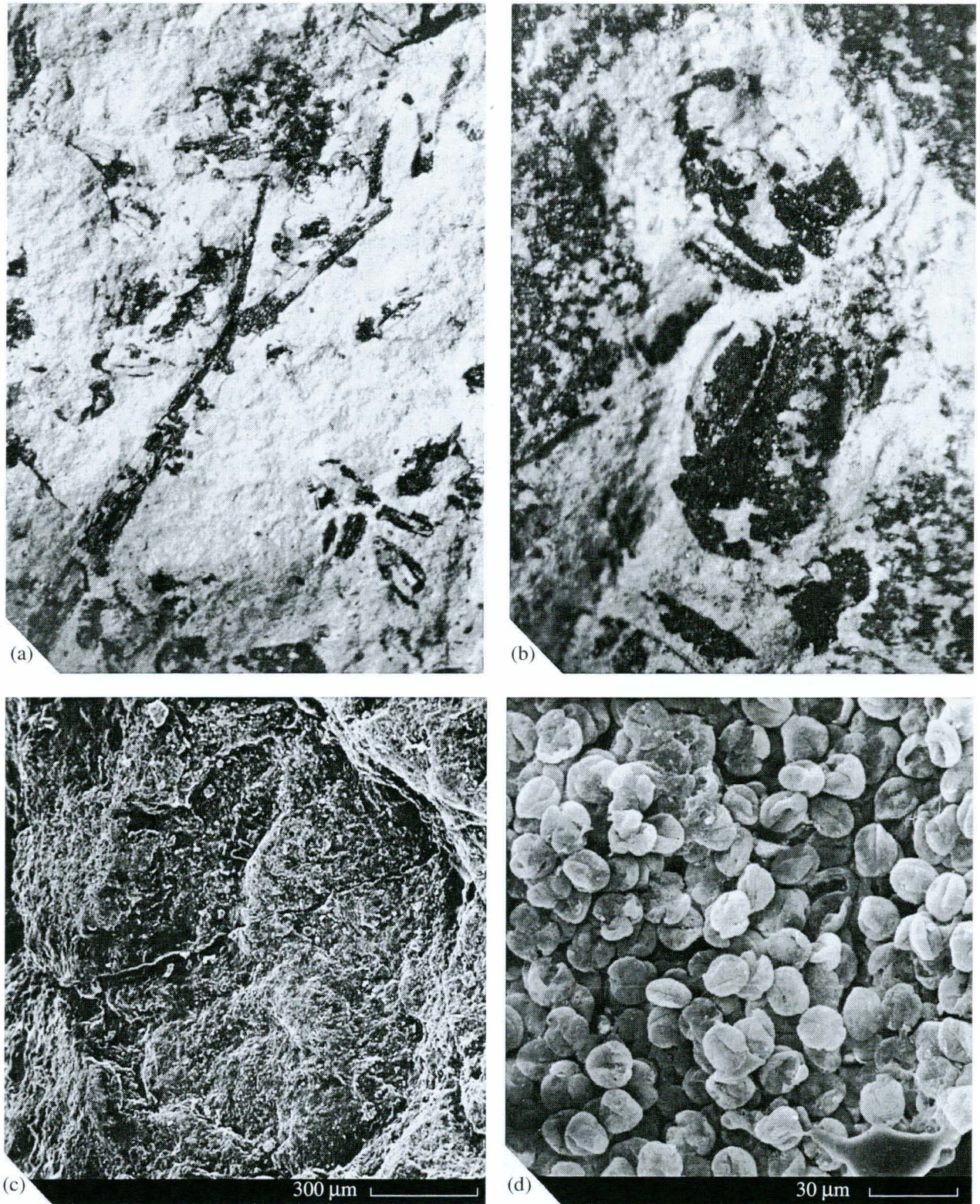


Fig. 2. *Archaranthus krassilovii* N. Maslova et Kodrul, holotype GIN, no. AB3-81: (a) capitate inflorescence attached to the axis of a compound inflorescence with a pedicel, isolated stamens are seen around, $\times 7$; (b) two stamens, $\times 20$; (c) isolated flower with four stamens, upper view, SEM; and (d) pollen mass from an anther, SEM. Amur Region, southeast of the village of Arkhara; Tsagayan Formation, upper part of the middle subformation, Maastrichtian–Lower Paleocene.

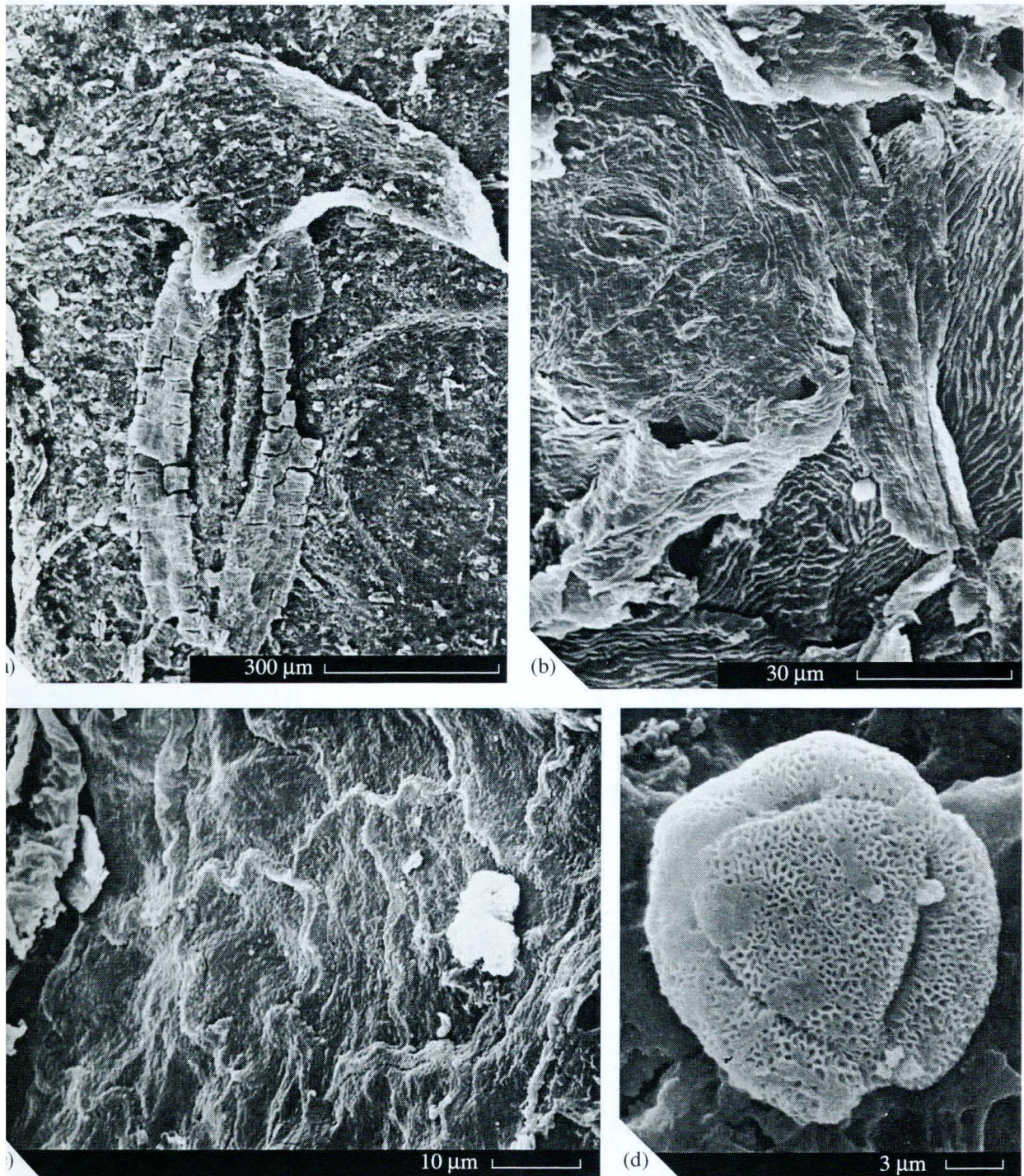


Fig. 3. *Archaranthus krassilovii* N. Maslova et Kodrul, SEM, GIN, no. AB3-81: (a) stamen, note triangular extension of the connective; (b) epidermis of external perianth members (elongate cells) and epidermis of the extension of the connective (stomata are absent); (c) epidermis of the inner perianth members; and (d) pollen grain in polar view, note additional colpi. Amur Region, southeast of the village of Arkhara; Tsagayan Formation, upper part of the middle subformation, Maastrichtian–Lower Paleocene.

(Fig. 3b). The inner members of the perianth are covered with an epidermis composed of nearly isodiametric cells with well-defined sinuous walls (Fig. 3c). Epidermal cells on the abaxial side of the petal are cutinized and, therefore, more distinctly sinuous.

No hair bases or stomata have been found in perianth elements.

The androecium comprises four stamens (Fig. 3c). The stamen filament is short, the anthers are tetrasporangiate, the thecae are joined by a connective that runs

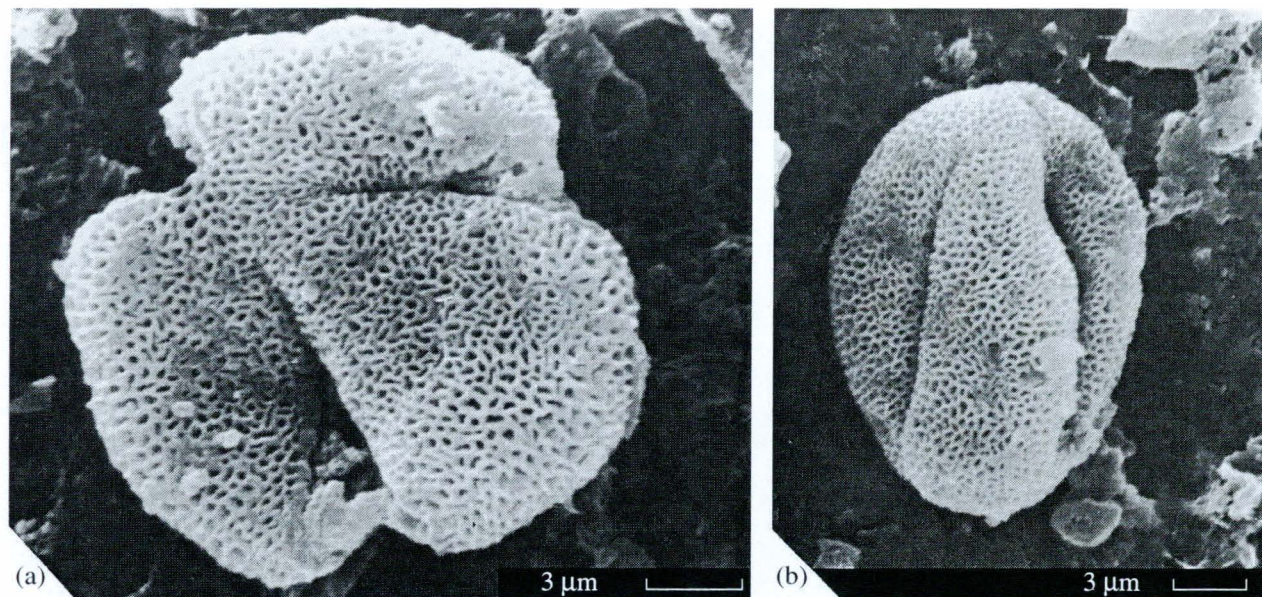


Fig. 4. *Archaranthus krassilovii* N. Maslova et Kodrul, SEM, GIN, no. AB3-81: (a) pollen grain in polar view, colpi closely approach the pole; (b) pollen grain in equatorial view. Amur Region, southeast of the village of Arkhara; Tsagayan Formation, upper part of the middle subformation, Maastrichtian–Lower Paleocene.

along the total length of the anther. The connective is basically narrow and slightly widens apically. The connective epidermis is composed of isodiametric cells and bears anomocytic stomata, slightly varying in size (Fig. 3b), and rounded hair bases. The maximal stoma length is 25 μm ; the minimal, 15 μm ; the maximal width is 18 μm ; and the minimal, 14 μm . The extension of the connective is conical triangular, in plan (Fig. 3a). The epidermis of the extension of the connective consists of isodiametric cells and is devoid of stomata; hair bases are occasionally present.

A separate mature stamen is approximately 1200 μm long. Its width in the central region reaches about 900 μm . The pollen sacs are oval and slightly widen distally. The inner epidermis of the pollen sacs is composed of longitudinal rows of elongated cells.

The pollen grains are elliptical and tricolpate. The equatorial diameter of a mature pollen grain is 13.3–15.3 μm , the polar diameter is 16.0–16.8 μm . The colpi almost reach the poles (Fig. 4a). The maximal width of apocolpium is 4.5–4.8 μm , that of mesocolpium is 7.5–11.0 μm . The exine is reticulate. The meshes vary in outline (rounded to elongate) and dimensions. There are 2–3 meshes per 1 μm . The margin of a colpus is distinct, formed by a sporopolliniferous thread. The meshes situated near the colpus margin and in the central part of the mesocolpium are identical.

Some pollen grains have additional colpi (Fig. 3d). They are situated in the polar region and are short, superficial, and virtually devoid of apocolpium and distinct margins.

Remarks. The number of heads on the axis of the compound inflorescence of *Archaranthus* is unknown.

There apparently were at least two heads, since the preserved fragment of the axis of the first order bears a pedicellate head and a fragmentary pedicel of one more head (Fig. 2a). The number of flowers per inflorescence (about 15) sets apart *Archaranthus* from other platanoids. The extant *Platanus* has staminate heads comprising up to 300 flowers. There are 50 to 100 flowers in the Cretaceous *Platananthus*. The preservation of many fossil platanoid inflorescences is insufficient for revealing the exact number of flowers and, in consequence, not all paleobotanists take notice of this quantitative character. Nevertheless, available illustrations show considerably more than 15 flowers per head.

The disintegration of mature inflorescence into detached flowers and stamens is only known in *Archaranthus*. Describing Paleocene staminate inflorescences associated with *Platanites hebridicus*, Crane *et al.* (1988, text-figs. 3b, 3c) presented a picture of a head with fragmentary preserved perianth members and stamens. Since these authors have reported no information on the finds of detached flowers or stamens near such heads, it is unclear whether this picture represents a disintegrated mature head or is a result of destruction during fossilization.

After the flowers have been shed during head maturation, some perianth members remain on the receptacle and others at the flower bases. The number of perianth members in the flowers of *Archaranthus* remains unknown. However, this genus has two distinct types of perianth members with different epidermal features (Figs. 3b, 3c). The flowers of *Archaranthus krassilovii* are tetramerous. Four stamens per flower are also observed in *Sarbaya* and *Quadriplatanus*. Members of the genus *Platananthus* and, supposedly, *Hamatia* are

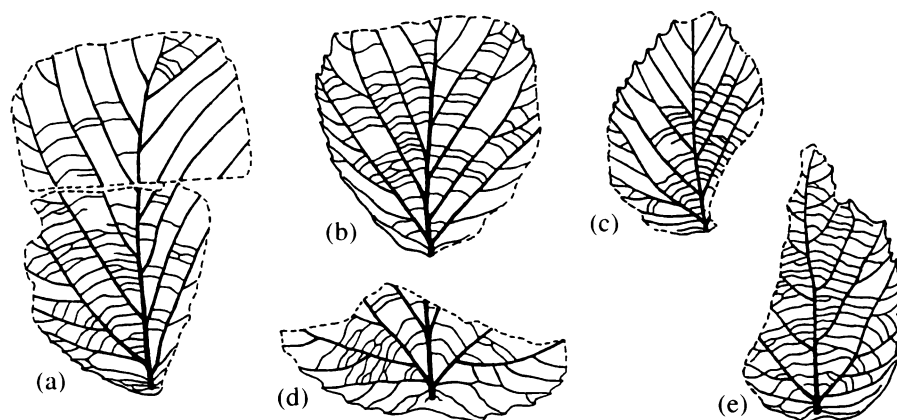


Fig. 6. Leaves associated with inflorescences of *Archaranthus krassilovii* N. Maslova et Kodrul, $\times 0.5$: (a) GIN, no. AB2-2; (b) GIN, no. AB3-7; (c) GIN, no. AB2-29; (d) GIN, no. AB3-66; and (e) GIN, no. AB3-44. Amur Region, southeast of the village of Arkhara; Tsagayan Formation, upper part of the middle subformation, Maastrichtian–Lower Paleocene.

Of interest is the presence in the anthers of *Archaranthus krassilovii* of pollen grains with additional polar colpi (Fig. 3d). Such a diffuse-colpate type of pollen grain is characteristic of members of the family Hamamelidaceae (*Distylium*, *Matudaea*, and *Sycopsis* of the subfamily Hamamelidoideae and *Chunia* of the subfamily Exbucklandioideae; Bogle and Philbrick, 1980). An aberrant additional colpus in the extant *Platanus occidentalis* has been illustrated by Zavada and Dilcher (1986, p. 352, text-fig. 9).

The inflorescences assigned to the genus *Archaranthus* are associated with the foliage of the typically *Platanus* morphotype (Figs. 5, 6). Although none of these fossils have been met in organic connection, there are strong grounds to suppose that they come from one plant. They cooccur within one bed, even within the same piece of rock. Any other leaves referable to platanoids are absent in the fossil plant assemblage. Moreover, pollen grains identical to those extracted from the anthers of *Archaranthus* were found to be attached to the surface of these leaves (Fig. 5d).

Leaves associated with the inflorescences under description have entire or weakly lobed blades with peltate bases, palmate–pinnate craspedodromous venation, well-developed infrabasal veins, and repeatedly branching basal veins (Fig. 6).

The cooccurrence of leaves of a platanoid appearance and reproductive structures different from those of the genus *Platanus* and assigned to the genus *Archaranthus* on the basis of microstructural data is an additional reason for the revision of the traditional concept of the presence of *Platanus* in the Cretaceous.

Material. One impression (with counterpart) of an inflorescence on the axis and numerous detached stamens from the type locality.

Genus *Oreocarpa* N. Maslova et Krassilov

Type species. *Oreocarpa bureica* N. Maslova et Krassilov.

Species composition. Type species.

Comparison. The genus differs from capitate infructescences of the Platanaceae and other members of the Hamamelidales in having very small heads and few seed organs, only one of which ripens and exceeds the head in size. The differentiation of the fruit into a locule and winged appendage with three ribs is a distinctive feature unknown in other members of the Platanaceae. The fruits most likely dehiscent to disseminate seeds. However, this (unusual for Platanaceae) dissemination remains hypothetical and has not been included in the generic diagnosis.

Oreocarpa bureica N. Maslova et Krassilov

Oreocarpa bureica: Maslova and Krassilov, 2002, p. 107, pl. V, figs. 1–4, text-figs. 1a–1j.

Description (Figs. 7a–7e). The inflorescences are pistillate heads with a single ripe fruit. Underdeveloped carpellodia are preserved near the fruit base (Figs. 7a, 7b).

The spherical head (4 mm in diameter) is placed on a short longitudinally striate pedicel (1 mm long). There are about ten densely appressed and partly overlapping carpellodia on the impression surface. The carpellodia have peltate apophyses about 1 mm in diameter. Short downcurved stylodes are preserved only in the lower carpellodia (Fig. 7b).

The single ripening fruit completely covers the head with its base, which is level with the locule. The elongated distal appendage of the fruit rises about 6 mm above the head and ends with a short stylode (0.8 mm long). The locule is rounded-ovate, oriented a little obliquely relative to the midline of the fruit, and is bordered on the surface by a broad arched fold. Three longitudinal ribs, which most likely correspond to vascular bundles, are distinguishable distally (Fig. 7a). The midrib extends from the locule apex to the stylode base; two other ribs embrace the locule laterally. The stylode is situated in the apical depression of the fruit. The sty-

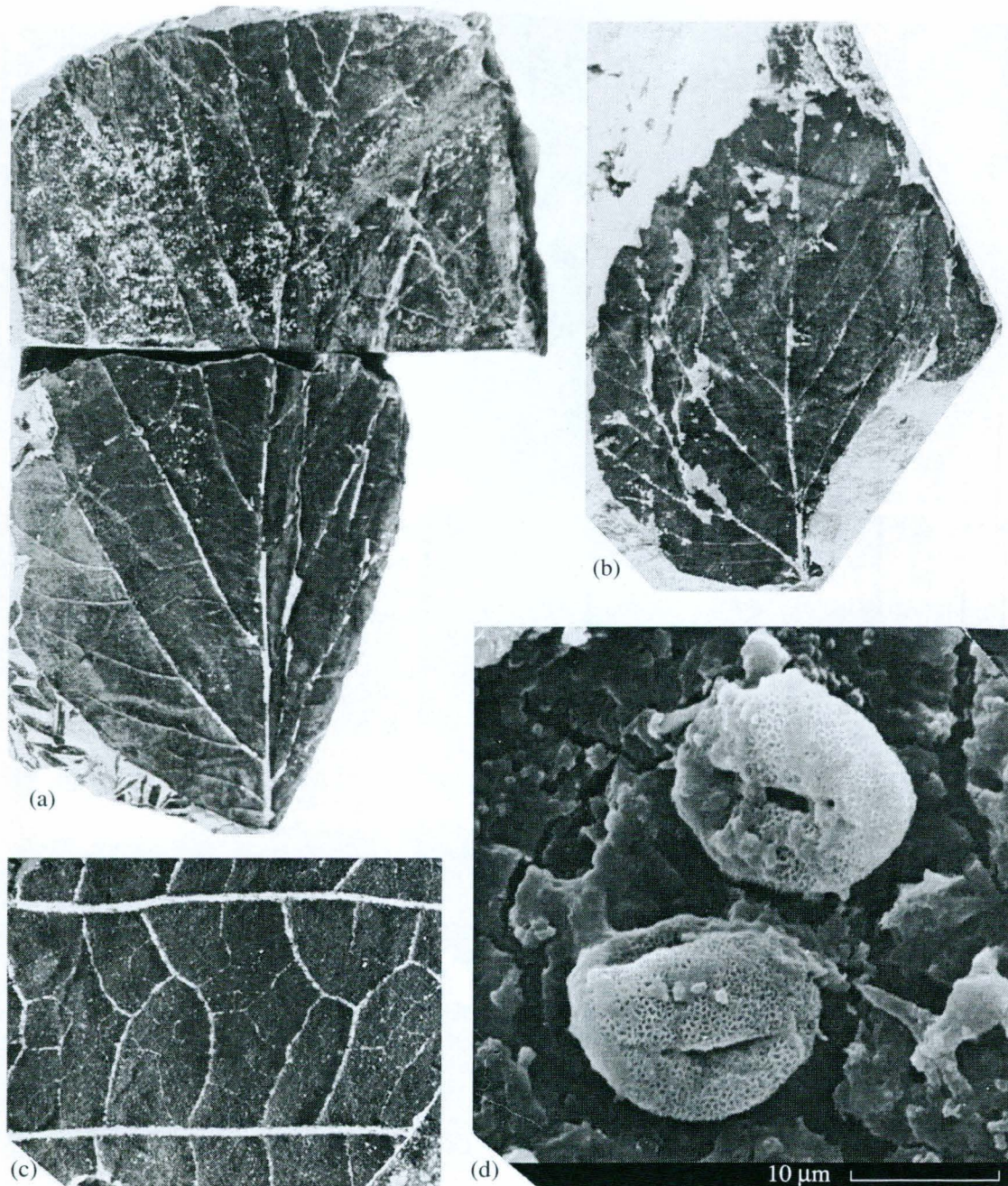


Fig. 5. Leaves associated with inflorescences of *Archaranthus krassilovii* N. Maslova et Kodrul (a–c): (a) GIN, no. AB2-2, $\times 1$; (b) GIN, no. AB2-29, $\times 1$; (c) GIN, no. AB3-66, tertiary venation, $\times 8$; and (d) pollen grains found on the surface of leaves associated with inflorescences of *Archaranthus krassilovii* N. Maslova et Kodrul. SEM. Amur Region, southeast of the village of Arkhara; Tsagan Formation, upper part of the middle subformation, Maastrichtian–Lower Paleocene.

characterized by strictly pentamerous flowers. The number of floral elements in a head of the extant *Platanus* varies (Boothroyd, 1930).

The stamens of *Archaranthus* exhibit a typically platanoid morphology. There are differences in the epidermal morphology of the connective and its extension. In *Archaranthus krassilovii* the connective epidermis is composed of isodiametric cells, there are numerous anomocytic stomata and occasional rounded hair bases.

The epidermis of the connective extension bears rare hair bases and is devoid of stomata. Among fossil platanoids, *Platananthus hueberi*, *P. synandrus*, *Platanus neptuni*, *Aquia brookensis*, and dispersed stamen groups of *Macginistemon mikaneides* have hairy connectives. Stomata on connective extensions are observed only in *Aquia brookensis*, *Quadriplatanus georgianus*, and dispersed platanoid stamens from Santonian–Campanian deposits of Sweden (Friis *et al.*, 1988).

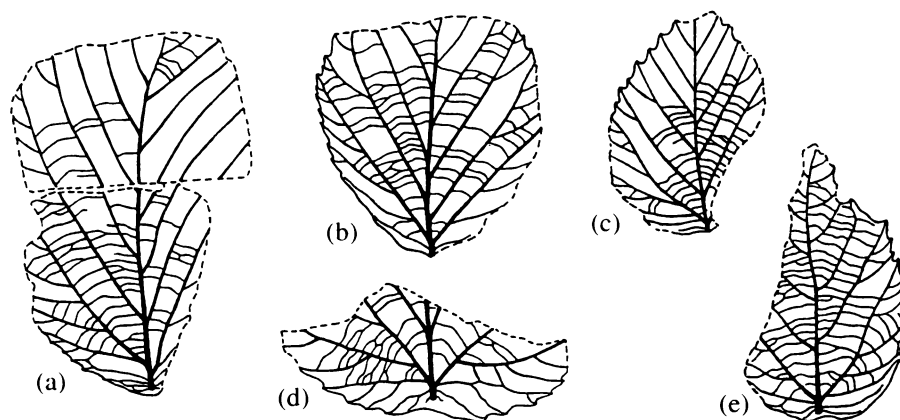


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Type species. *Oreocarpa bureica* N. Maslova et Krassilov.

Species composition. Type species.

Comparison. The genus differs from capitate infructescences of the Platanaceae and other members of the Hamamelidales in having very small heads and few seed organs, only one of which ripens and exceeds the head in size. The differentiation of the fruit into a locule and winged appendage with three ribs is a distinctive feature unknown in other members of the Platanaceae. The fruits most likely dehisced to disseminate seeds. However, this (unusual for Platanaceae) dissemination remains hypothetical and has not been included in the generic diagnosis.

Oreocarpa bureica N. Maslova et Krassilov

Oreocarpa bureica: Maslova and Krassilov, 2002, p. 107, pl. V, figs. 1–4, text-figs. 1a–1j.

Description (Figs. 7a–7e). The inflorescences are pistillate heads with a single ripe fruit. Underdeveloped carpellodia are preserved near the fruit base (Figs. 7a, 7b).

The spherical head (4 mm in diameter) is placed on a short longitudinally striate pedicel (1 mm long). There are about ten densely appressed and partly overlapping carpellodia on the impression surface. The carpellodia have peltate apophyses about 1 mm in diameter. Short downcurved stylodes are preserved only in the lower carpellodia (Fig. 7b).

The single ripening fruit completely covers the head with its base, which is level with the locule. The elongated distal appendage of the fruit rises about 6 mm above the head and ends with a short stylode (0.8 mm long). The locule is rounded-ovate, oriented a little obliquely relative to the midline of the fruit, and is bordered on the surface by a broad arched fold. Three longitudinal ribs, which most likely correspond to vascular bundles, are distinguishable distally (Fig. 7a). The midrib extends from the locule apex to the stylode base; two other ribs embrace the locule laterally. The stylode is situated in the apical depression of the fruit. The sty-

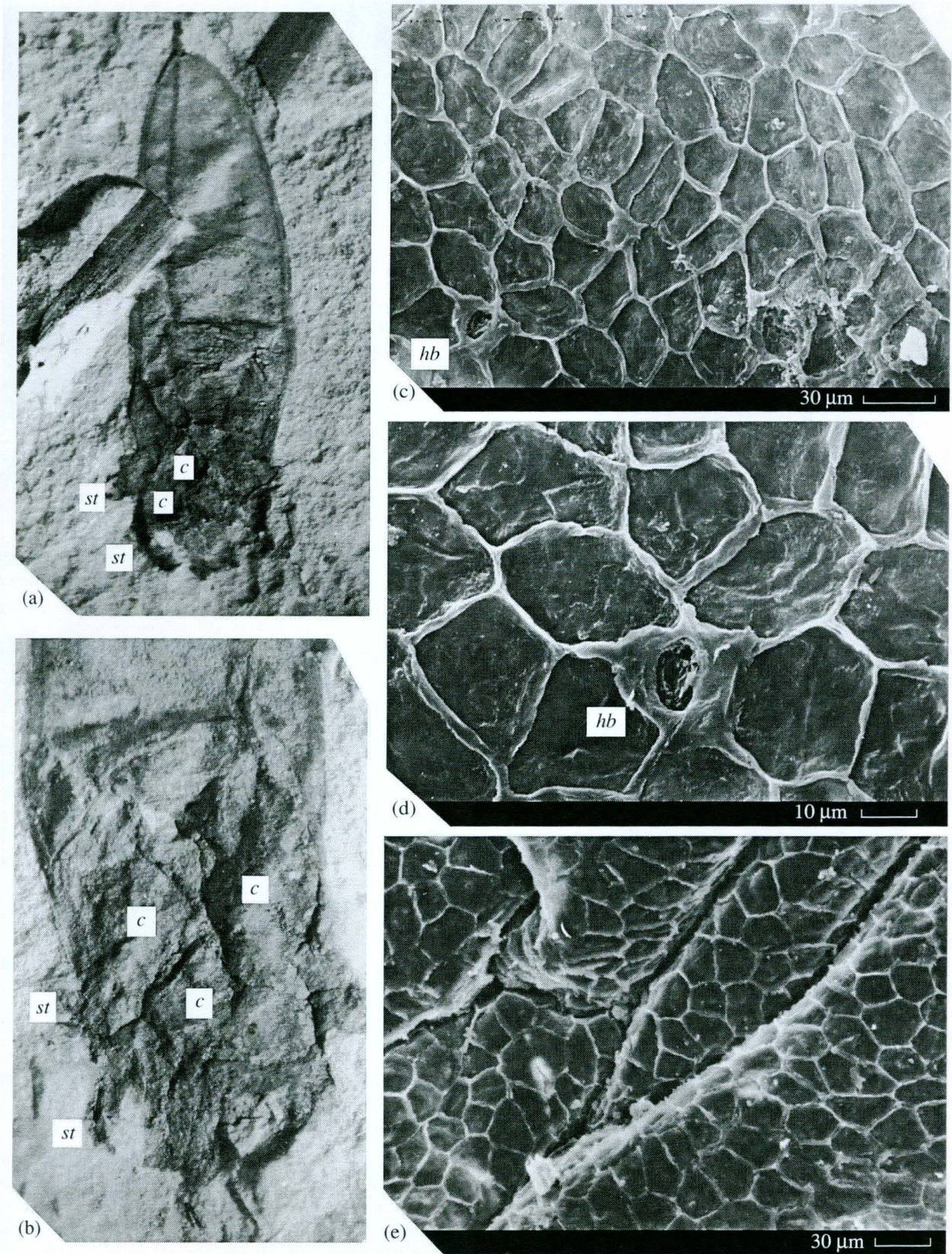


Fig. 7. *Oreocarpa bureica* N. Maslova et Krassilov, GIN, no. BG-42, holotype: (a) head with a solitary well-developed fruit, peltate apices of carpellodia (c) and curved apices of stylodes (st) are seen. $\times 10$; (b) head with the lower part of the fruit. $\times 17$; (c) cuticle of the apex of a carpellodia with hair bases (hb), SEM; (d) hair base (hb), SEM; and (e) boundaries between carpellodia at the head base, SEM. Amur Region, right bank of the Bureya River, below the mouth of its right tributary Darmakan River; Tsagayan Formation, Lower Paleocene.

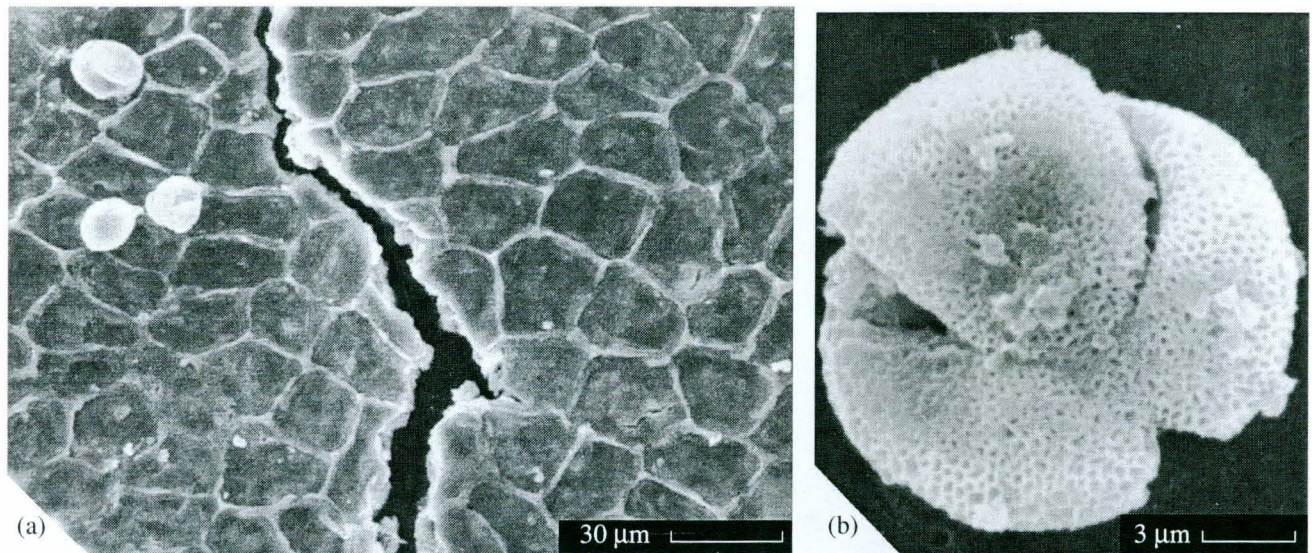


Fig. 8. Pollen stuck to the carpellodia of *Oreocarpa bureica* N. Maslova et Krassilov. SEM: (a) three pollen grains on the surface of the carpellodium and (b) pollen grain in polar view. Amur Region, right bank of the Bureya River, below the mouth of its right tributary, Darmakan River; Tsagayan Formation. Lower Paleocene.

lode is straight and has pointed pits on its surface, obviously corresponding to the hair bases.

The material is preserved as a ferruginous incrustation with small fragments of a phytollemma. The cuticle has been macerated from these fragments. The epidermis of the ripened fruit and carpellodia consists of irregularly polygonal cells, which have thick slightly sinuous anticlinal walls. The cells are randomly arranged but occasionally form short longitudinal rows. The cells of these rows are irregularly quadrilateral, relatively narrow, and elongated across the row (Fig. 7c). The hair bases, which are scattered over the entire surface, are elliptical and have a thick cuticular rim (Figs. 7d, 7e). The cells surrounding trichomes are almost isodiametric, are arranged radially, and form an irregular ring of five to six cells (Fig. 7d).

Pollen grains, supposedly remaining attached after pollination, are found on the cuticle of the carpellodia (Figs. 8a, 8b). The pollen grains are elliptical and tricolpate, their equatorial diameter is 15.5–16.0 µm, their polar diameter is 18.0–19.0 µm. The colpi nearly reach the poles. The exine is reticulate. The meshes of the reticulum vary in size and shape (rounded to elongate). There are 2–3 meshes per 1 µm. The margin of the colpus is distinct, formed by a thin sporopollenin thread.

Remarks. Additional material collected by Akhmetiev and Kodrul after the publication of *Oreocarpa bureica* contained tricolpate reticulate pollen attached to carpellodia. A few pollen grains were observed on the cuticle of carpellodia in several heads. This find evidently suggests that the pollen grains were attached to the carpellodia after pollination and, therefore, were produced by the staminate organs of the plant that had pistillate inflorescences of the *Oreocarpa* type. The

pollen is similar to that of *Tricolpopollianthus burejensis* Krassilov (Krassilov, 1976) in its main characters.

In the first description of *Carinalaspermum bureicum* Krassilov, the lot of specimens includes, in addition to detached winged seeds, fruits in which carpellodia preserved at their bases (Krassilov, 1976, pl. 33, figs. 3, 4). These specimens should be excluded from this species and transferred to *Oreocarpa bureica*. The structure of epidermis in the fruit and carpellodia from the additional material provides supportive evidence for Krassilov's opinion that these seed organs belong to a plant with leaves of the "*Platanus*" *raynoldsii* type since both of these organs show virtually the same morphology in the cells of hair bases and in the adjacent cells.

The heads of *Oreocarpa* associate with polymorphous leaves of "*Platanus*" *raynoldsii*.

Material. Holotype and its counterpart and eight impressions of heads from the type locality.

Genus *Chemurnautia* N. Maslova

Type species. *Chemurnautia staminosa* N. Maslova.

Species composition. Type species.

Comparison. Several traits of *Chemurnautia* are similar to those of the modern plane tree. These are capitate inflorescences, short stamen filaments, narrow fusiform parallel-margined sporangia, well-developed endothecium, and tricolpate reticulate pollen. The genus differs from *Platanus* in the significantly smaller inflorescences, the anther that is devoid of an extension of the connective and differs from the anthers of the plane tree and other Hamamelidales in the radial

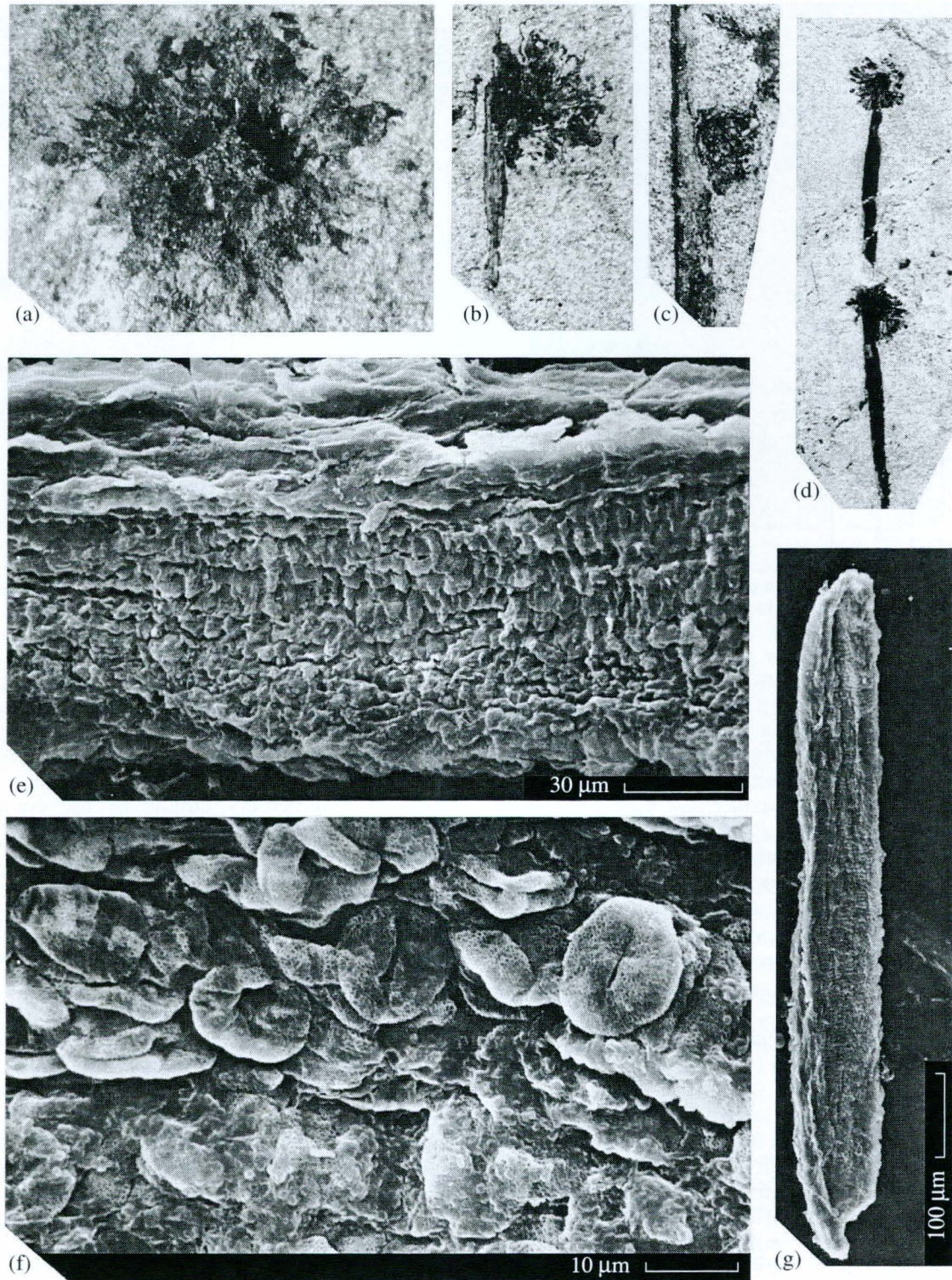


Fig. 9. *Chemurnautia staminosa* N. Maslova (a, c, e–g) and staminate inflorescences associated with the leaves of *Platimeliphyllum snatolense* N. Maslova (b, d): (a) PIN, no. 3736/45, holotype, $\times 12$; (b) PIN, no. 4256/36, $\times 5$; (c) PIN, no. 4778/274, $\times 5$; (d) PIN, no. 4256/14, $\times 3$; (e) PIN, 3736/45, fragmentary sporangium, thickened cells of the endothecium are seen. SEM; (f) PIN, 3736/45, pollen mass in the sporangium, SEM; and (g) PIN, 3736/45, detached sporangium, SEM; (a, e, f) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; (b, d) western Kamchatka, Snatol River; Napana Formation, Upper Paleocene; (c) western Kamchatka, Evravavayam River; Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

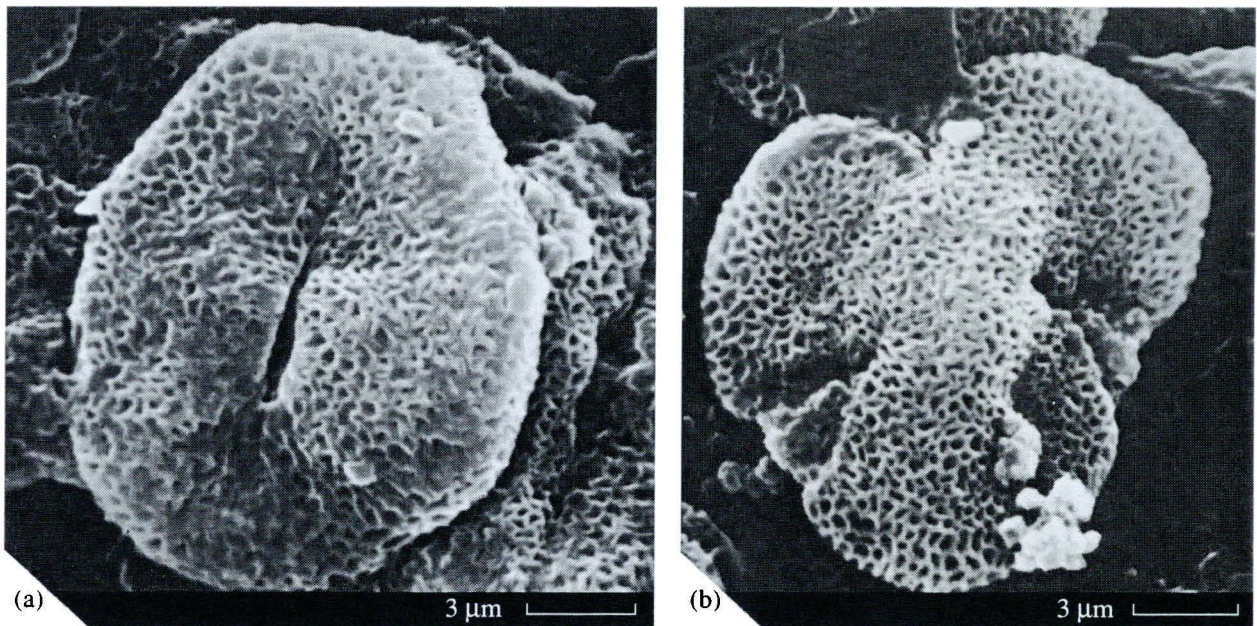


Fig. 10. Pollen grains of *Chemurnautia staminosa* N. Maslova, SEM, PIN, 3736/45: (a) pollen grain in equatorial view; (b) pollen grain in polar view, finely granulate apocolpium is distinct. Northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation. Upper Paleocene–Lower Eocene.

arrangement of extremely narrow (nearly linear) sporangia that are only slightly or not at all fused with each other and form no distinct synangia (thecae), the absence of hairs on the connective epidermis, and the finer pollen with wide colpi and a well-developed apocolpium. Among extinct platanoids, Upper Cretaceous *Platananthus scanicus* and *P. hueberi* have pollen with a well-defined finely granulate apocolpium; however, they are significantly different in other characters of male reproductive morphology (Friis *et al.*, 1988).

Chemurnautia staminosa N. Maslova

Chemurnautia staminosa: Maslova, 2002a, p. 98, pl. IX, figs. 5 and 6, text-figs. 2c–2i, 5a–5d.

Description (Figs. 9a–9g, 10a, 10b). The staminate capitate inflorescences are sessile. There are a few heads on an axis 1.5 mm in diameter. The maximal observed number of heads per axial fragment is three. The maximal diameter of a head is 4 mm. The flowers are closely appressed to each other and radiate from the central core. The length of an individual flower reaches 1.5 mm. The flowers are variously deformed; thus, it is impossible to reveal the number of flowers per head. Perianth members are indistinguishable.

The fragments of a head that have been transmitted to a varnish film are an aggregation of stamens. The length of the mature stamen is about 900 µm on average. It comprises a short filament and a relatively large elongate anther. The anther includes four narrow fusiform sporangia. The sporangia are unequal, dehiscing by a longitudinal slit along the entire length. They are radially arranged, partially fused basally (occasionally also in the apical region) or free, deviating in the middle

part. The sporangial cuticle is composed of elongate cells devoid of stomata and hairs. An individual sporangium is 700–900 µm length, 80–100 µm wide, elongate, parallel-margined, and has a pointed apex (Fig. 9g). Extensions of the connectives are not developed. A fragmentary cuticle of the connective is formed by polygonal cells with weakly distinct margins of individual cells, without stomata or hairs.

A subepidermal cellular layer, endothecium, is observed in several fragments of the sporangial cuticle (Fig. 9e). The cells of the endothecium are arranged in regular rows, their walls are thickened. The locule cuticle consists of distinct rows of rectangular cells.

The pollen grains are numerous (Fig. 9f). They are elliptical and tricolpate. The equatorial diameter of the mature pollen is 11–13 µm, the polar diameter is 13–16 µm. As a rule, the colpi nearly reach the pollen pole (Fig. 10b), some colpi are shorter and reach about a half of the polar diameter. The apocolpium is well developed, about 3 µm wide, finely granulate (Fig. 10b). The exine is reticulate. The meshes vary in size and shape (circular, rectangular, or polygonal). The margins of the colpi are indistinct, the reticulum of the mesocolpium and that of the margins are identical.

Remarks. The heads from the Evravavayam locality are slightly smaller than those from Chemurnaut Bay. Microstructural differences have not been revealed. The Evravavayam finds apparently represent not completely mature inflorescences. They are characterized by the smaller measurements of heads (2.5 mm), individual pollen sacs (about 450 µm long and 40–50 µm wide), and pollen grains (7–8 µm in equatorial diameter and 10–11 µm in polar diameter).

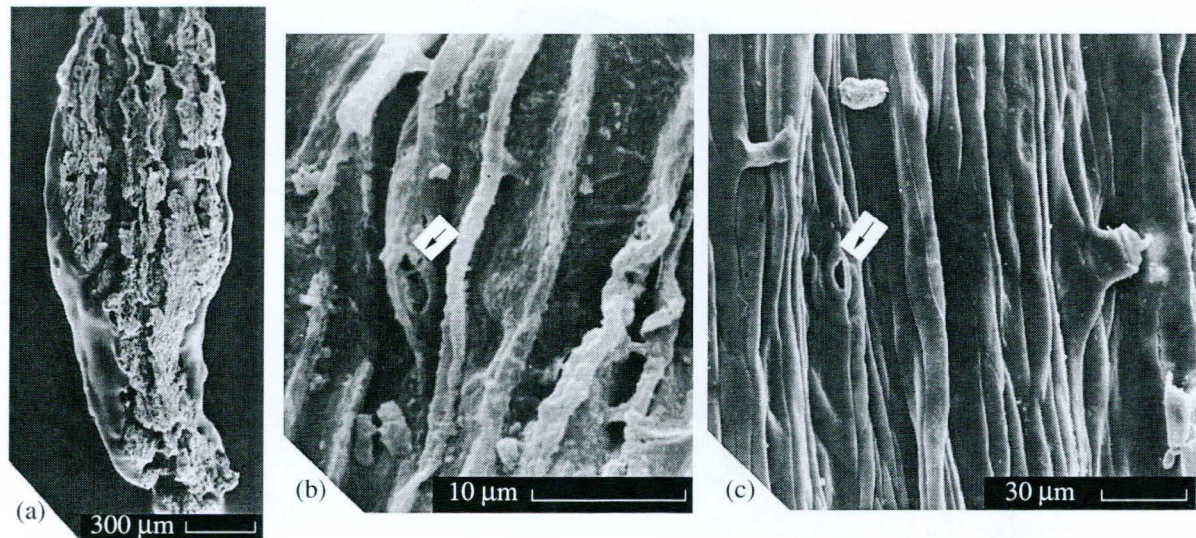


Fig. 11. *Platanus stenocarpa* N. Maslova, SEM, PIN, 3736/57: (a) carpel; (b) epidermis of the carpel bearing hair bases (arrow). *Platanus occidentalis* L., SEM: (c) herbarium specimen, the surface of a carpel with hair bases (arrow); (a, b) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

The exinal reticulum is weakly defined. The apocolpium is poorly developed.

The impressions of the inflorescences from the Snatol River locality are devoid of phytollems that prevented the obtainment of microstructural information. Their macromorphology is identical to that of the above-described inflorescences.

The inflorescences of *Chemurnautia staminosa* associate with the leaves of *Platimeliphyllum palanense* (Budants.) N. Maslova, which have been assigned to the Platanaceae on the basis of their macromorphological and epidermal characteristics.

Occurrence. Northwestern Kamchatka Peninsula: Chemurnaut Bay, upper part of the Kamchik–lower part of the Tkaprovayam formations, Upper Paleocene–Lower Eocene; Evravavayam River, Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

Material. Four inflorescences from the Chemurnaut Bay locality, four inflorescences from the Evravavayam River locality, and five inflorescences from the Snatol River locality.

Genus *Platanus* L.

Platanus stenocarpa N. Maslova

Platanus stenocarpa: Maslova, 1997, p. 92, pl. X, figs. 1–5.

Description (Figs. 11a, 11b, 22b, 22c). A single pistillate head is 13 mm in diameter. Since the head is detached from the axis, it is not known whether the inflorescences were simple or compound. Through a light microscope, the head shows a globular receptacle 5 mm in diameter and numerous, dense, radially spreading carpels. The latter are of approximately the same size.

Individual flowers are indistinct. The perianths are strongly reduced, leaving scarcely discernible scars at the base of the carpels. The morphology of a separate carpel was studied with SEM. The carpel is spindle-shaped, about 2.2 mm long, and 0.6 mm wide. The stylole is not preserved (Fig. 11a). The lower part of the carpel surface is irregularly pitted with hair bases. The epidermal cells are narrow elongate and form longitudinal rows. The hair bases are elliptical, about 4 µm wide (Fig. 11b). The seed apparently filled the locule, since its cuticle is appressed to the wall of the carpel. The seed coat cuticle shows polygonal cells with distinct, slightly sinuous anticlinal walls. The cells are about 18.8 µm in length and 12.5 µm in width.

Comparison. The infructescence shows characteristic features of the genus *Platanus*. Typical of the genus are the simultaneous maturation of carpels in the head, reduced perianths, variable number of floral members per head (even within the same head), and pubescent achenes.

The material studied provides no evidence of the number of heads, the mode of their attachment, and details of individual flowers. The uniform dimensions of the carpels suggest their identical maturation. The epidermal patterns of elongate cells and the hair bases are as in the extant species (Fig. 11c).

Epidermal structures similar in cell shape have been described in *Platanocarpus* sp. from the Late Cretaceous of Sweden (Friis *et al.*, 1988). However, that specimen lacks hair bases on the surface of the carpel. The seed coat epidermal structure of *P. stenocarpa* is also as in the extant *Platanus*. Thus, on the basis of morphological and epidermal evidence, the infructescence is assignable to the genus *Platanus* and differs

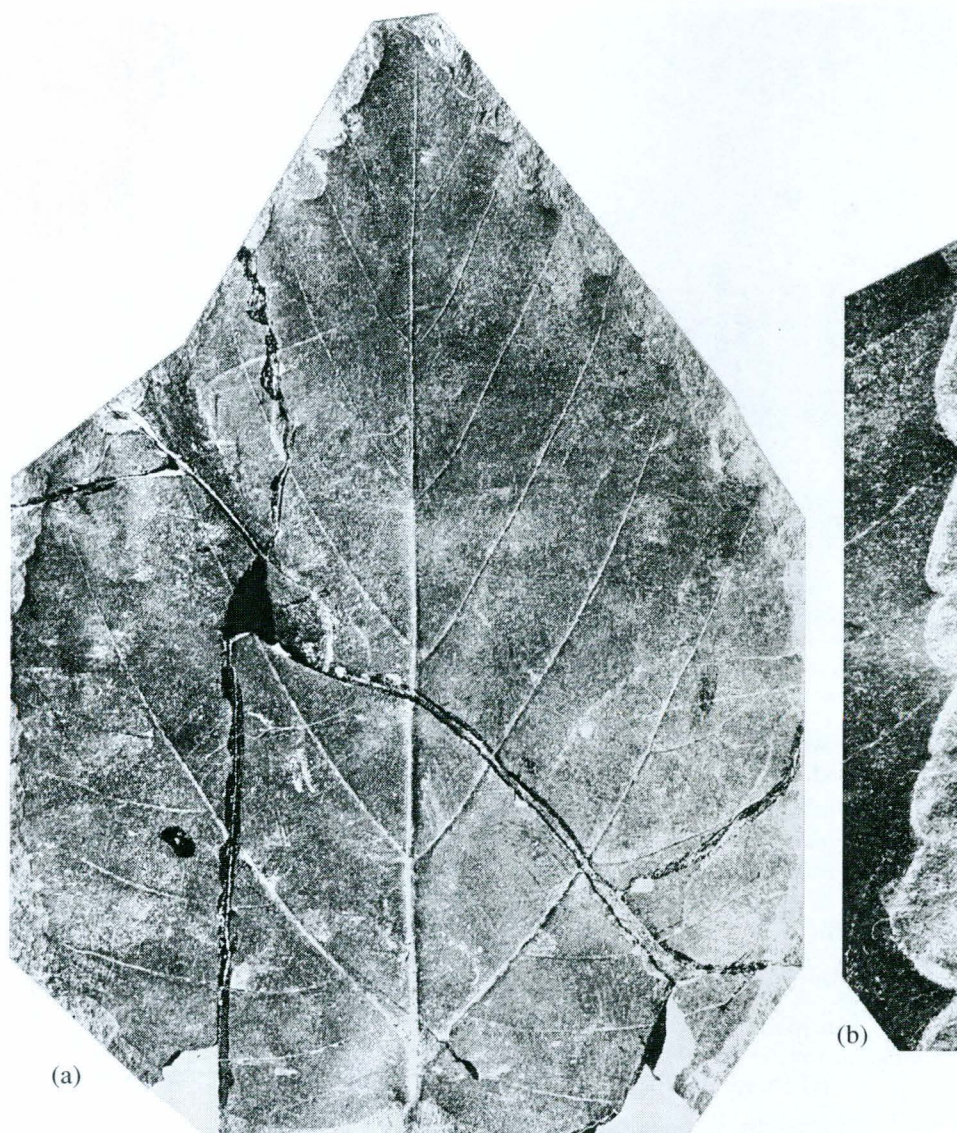


Fig. 12. *Platanus integrifolia* N. Maslova: (a) PIN, no. 4257/30, holotype, $\times 1$; (b) PIN, no. 4257/30, holotype, marginal teeth, $\times 2$; northwestern Kamchatka Peninsula, a section between the capes Rebro and Getkilnin; Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

from the presently known fossil platanoid genera in the extremely reduced perianths and pubescent carpels.

Remarks. The infructescence of *Platanus stenocarpa* was found in association with leaf remains of *Platanus basicordata*. All the platanoid leaves and reproductive organs that have been found in association from the Paleocene significantly differ from our finds. *Platanites hybridicus* from the Paleocene of Mull, northwestern Scotland, has compound leaves atypical of *Platanus* and the majority of other platanoid genera and pistillate flowers in (Crane *et al.*, 1988), which the number of elements is unknown and the carpels are glabrous. The “Joffre plane tree” from the Paleocene of western Canada has trilobed dentate leaves with basal veins arising from the base of the leaf blade and the

infructescences showing carpels at different developmental stages and lacking epidermal hairs (Pigg and Stockey, 1991).

Material. Holotype.

Taxa Established on the Basis of Leaf Remains

Genus *Platanus* L.

Platanus integrifolia N. Maslova

Platanus integrifolia: Maslova and Fotyanova, 1990, p. 704, pl. II, figs. 2–4, text-figs. 1, 10–14; Maslova and Fotyanova, 1991, text-figs. 2, 14–17; Gladenkov *et al.*, 1997, p. 144, p. p., text-fig. 53, fig. 2; text-fig. 75, fig. 1; text-fig. 76, figs. 2–7.

Description (Figs. 12a, 12b, 13a, 14a–14e). The leaves are predominantly entire (Fig. 14a) or with weakly defined lateral lobes (Fig. 14e). The leaf blade



Fig. 13. *Platanus integrifolia* N. Maslova, PIN, no. 3858/26, $\times 1$; western Kamchatka Peninsula, Anadyrka River; Tigil Group, Middle? Eocene.

is rounded-ovate (length/width ratio is 1.0–1.2) to pointed elliptical (length/width ratio is 1.5–2.0). The base of the leaf blade is truncated to cuneate, the apex is acute. The leaf margin is regularly serrate. The teeth are low, acute, concave–concave, there are one or two

teeth per 1 cm of leaf margin (Fig. 12b). The basal and apical sides of the tooth are approximately equal.

The midvein is straight or weakly sinuous in the upper leaf part. The basal veins deviate suprabasally at

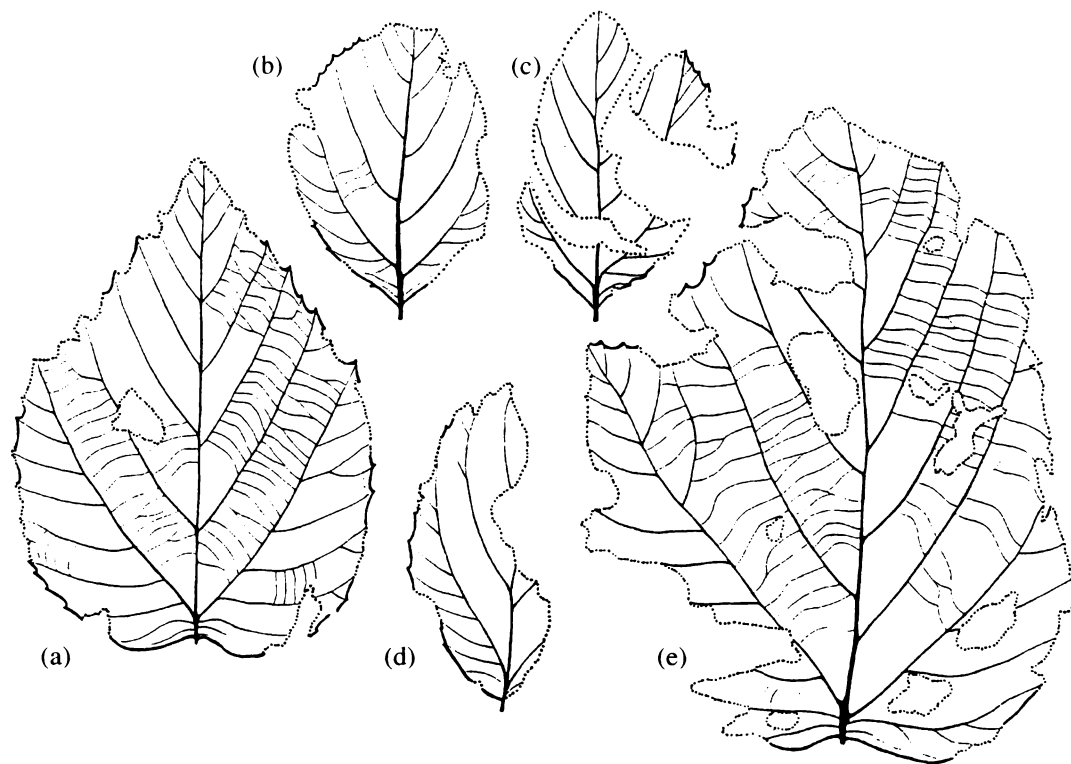


Fig. 14. *Platanus integrifolia* N. Maslova, $\times 0.5$: (a) PIN, no. 4257/30, holotype; (b) PIN, no. 4256/78; (c) PIN, no. 4256/77; (d) PIN, no. 4256/81; and (e) PIN, no. 3858/26; (a) northwestern Kamchatka Peninsula, a section between the capes Rebro and Getkilnin; Tkaprovayam Formation, Upper Paleocene–Lower Eocene; (b–d) western Kamchatka Peninsula, Snatol River; upper part of the Khulginskaya Formation, Lower Paleocene; (e) western Kamchatka, Anadyrka River, Tigil Group, Middle? Eocene.

an angle of 35° – 50° . They are approximately as thick as the secondary veins. There are up to eight basicopic veins, they are thin, arched, occasionally have up to three deviations. The leaves with weakly defined lobes occasionally have two or three acroscopic veins, but more often these veins are lacking. Below the point of the basal vein deviation, weak infrabasal veins are often observed. They end blindly or are brochidodromously connected with each other. There are six to eight pairs of secondaries. They are thin and straight, two or three lower pairs are branching. The angle of deviation of the secondaries is 35° – 50° . The tertiaries are branching or nonbranching, distinct, with repeated anastomoses, deviate at an angle of 120° – 125° .

Comparison and remarks. These fossil finds are assigned to the genus *Platanus* on the basis of the leaf morphology typical of this genus. Equivalents of *P. integrifolia* are absent among extant species of the genus. Fossil *P. asymmetrica* and *P. mabutii* have predominantly entire leaf blades; however, they differ in a range of other characters.

Occurrence. Western Kamchatka Peninsula: Snatol River, upper part of the Khulginskaya Formation, Lower Paleocene; section between the capes Rebro and Getkilnin, Tkaprovayam Formation, Upper Paleocene–Lower Eocene; Anadyrka River, Tigil Group, Middle? Eocene.

Material. Thirteen specimens from the Snatol River locality, five specimens from the section between the capes Rebro and Getkilnin, and four specimens from the Anadyrka River locality (Kamchatka Peninsula).

Platanus iljinskajae N. Maslova

Platanus iljinskajae: Maslova and Fotyanova, 1991, p. 182, pl. I, figs. 1–3, text-figs. 2, 12, and 13.

Description (Figs. 15a–15d, 16a–16d, 17a–17d). The leaf blade is distinctly trilobate, the length/width ratio is 1.0–1.1. The central lobe is short, basally broad, and abruptly narrowing toward the apex. The apices of the lobes are only fragmentarily preserved; supposedly, they were slightly elongated and acute. The base is emarginate. The leaf blade margin is toothed. The teeth are acute, there are three to five teeth per 1 cm of the leaf margin (Figs. 15a, 15b). The basal side of each tooth is considerably longer than the apical side (Fig. 15d). The regions between the lobes are toothed (Fig. 16b).

The basal veins are slightly arched, approximately as thick as the midvein, and deviate suprabasally at an angle of 40° – 50° . There are eight or nine arch-shaped basicopic veins. Not rarely they branch two or three times, the lower vein gives up to eight or ten deviations. There are two or three thin, occasionally branching



Fig. 15. *Platanus iljinskajae* N. Maslova: (a) PIN, no. 4256/605, holotype, $\times 1$; (b) PIN, no. 4256/605, holotype, marginal serration, $\times 3$; (c) PIN, no. 4256/603, $\times 1$; (d) PIN, no. 4256/603, marginal serration, $\times 5$; western Kamchatka Peninsula, Snatol River; Napana Formation, Upper Paleocene.

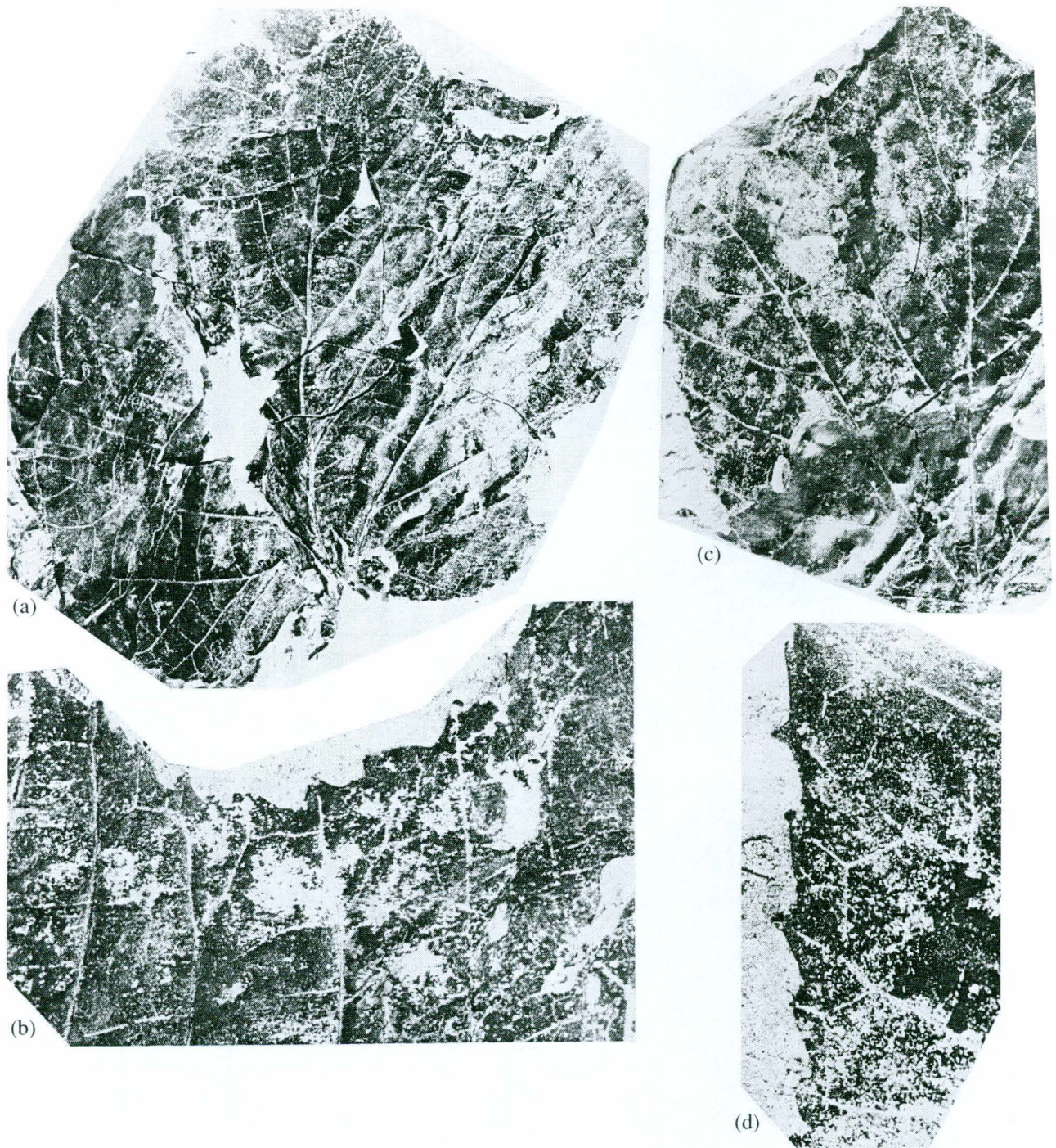


Fig. 16. *Platanus iljinskajae* N. Maslova: (a) PIN, no. 3736/86, $\times 1$; (b) PIN, no. 3736/86, serration in sinus, $\times 3$; (c) PIN, no. 3736/87, $\times 1$; and (d) PIN, no. 3736/87, marginal serration, $\times 3$; northwestern Kamchatka Peninsula, Chemurnaut Bay, Chemryl Cape; upper part of the Tkaprovayam Formation, Lower Eocene.

infrabasal veins situated below the point of deviation of the basal veins. There are seven or eighth pairs of secondary veins, which are straight or slightly arch-shaped and, occasionally, branch one or two times. The angle between the midvein and secondaries is 40° – 50° . The tertiary veins are branching or nonbranching. There are three or four tertiaries per 1 cm of secondary

vein. The angle between the midvein and tertiaries is about 130° in the lower part of the leaf and diminishes to 90° in the upper region.

Comparison. Being similar to *P. acutiloba* Bor-suk, it differs from the latter in the more numerous secondary and basiscopic veins, lobe shape, and teeth morphology.

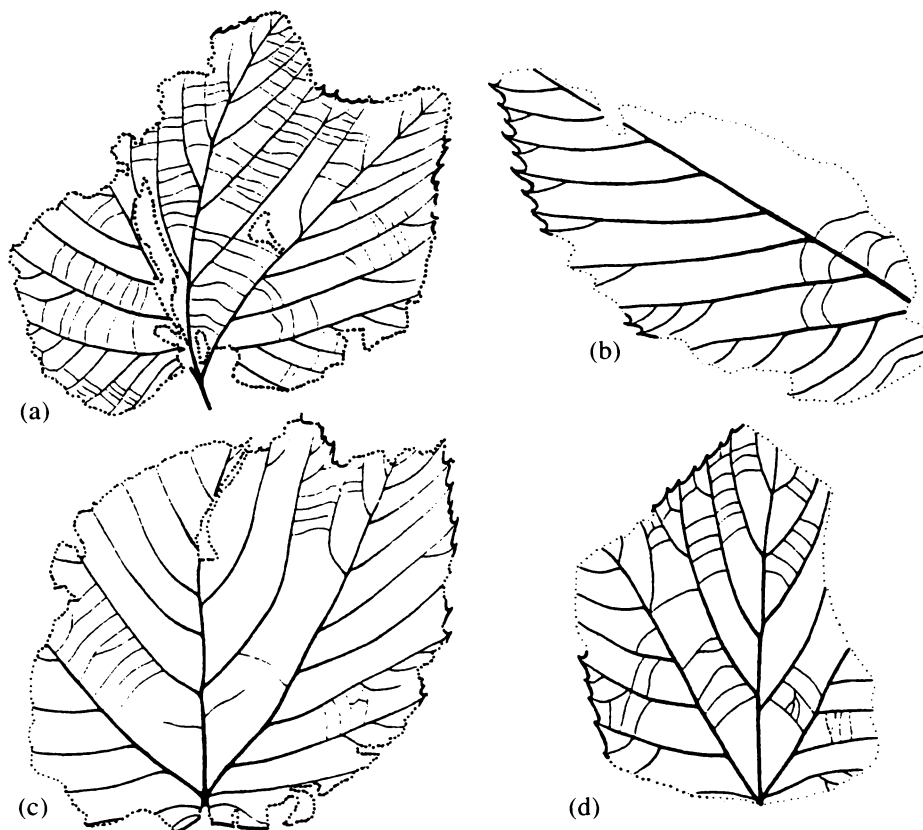


Fig. 17. *Platanus iljinskajae* N. Maslova, $\times 0.5$: (a) PIN, no. 3736/86; (b) PIN, no. 4256/603; (c) PIN, no. 4256/605; and (d) PIN, no. 3736/87; (a, d) northwestern Kamchatka, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkprovayam Formation, Upper Paleocene–Lower Eocene; (b, c) western Kamchatka, Snatol River; Napana Formation, Upper Paleocene.

Occurrence. Western Kamchatka Peninsula: Snatol River, Napana Formation, Upper Paleocene; Chemurnaut Bay, Chemryl Cape, upper part of the Tkprovayam Formation, Lower Eocene.

Material. Three specimens from the Snatol River locality and two specimens from the Chemurnaut Bay locality, Chemryl Cape (Kamchatka Peninsula).

***Platanus acutiloba* Borsuk**

Platanus acutiloba: Borsuk, 1956, p. 59, text-figs. 7 and 8; pl. 13, figs. 1 and 3; Medyulyanov, 1975, p. 29, p. p., pl. 5, figs. 2 and 3; Sycheva, 1977, p. 26, p. p., pl. 10, fig. 4; *Iskopaemye...* 1974, p. 142, pl. 65, figs. 3 and 4; Maslova and Fotyanova, 1991, p. 181, text-figs. 2 and 11.

Description (Figs. 18a–18e, 19a–19f). The leaves are trilobate, the lobes are short, triangular, and abruptly narrowing. The base of the leaf blade is cordate, more or less decurrent. The lobe apices are pointed.

The midvein is straight, slightly undulate at the apex of the central lobe. There are four to six pairs of secondary veins. They are slightly arched and deviate at an angle of 30° – 40° . The basal veins are as thick as the midvein, arch-shaped, deviate at an angle of 25° – 40° , and reach four-fifths of the leaf blade length. There are

up to seven (usually five) basiscopic deviations of the basal veins. They are arch-shaped and branch one or, occasionally, two times. The lower pair of basiscopic veins gives up to five deviations, which end in teeth. There are two or three acrosopic deviations of the basal veins. They are distinct and arch-shaped. The lower acrosopic vein is directed at the sinus, where it branches and forms anastomoses with tertiaries. Other acrosopic veins end in teeth.

The leaf blade margin is dentate. The teeth are numerous, up to three or four per 1 cm of the leaf margin. Larger teeth develop at the endings of secondary veins. The tooth shape varies from the typically concave–concave with a longer basal and shorter apical sides and acute apex to nearly triangular with an apical gland.

Comparison. The author of this species notices the similarity between the leaves of *P. acutiloba* and *P. aceroides* Goepf. *P. acutiloba* differs in the relatively small leaves, crowded secondary veins, and small frequent teeth.

Occurrence. Sakhalin Island: Soldatskaya ravine, Nizhneduiskaya Formation, Lower–Middle Eocene; Krasnoyarka River Basin, Naiba Formation, Middle Eocene; Uglegorka River, Snezhinka Forma-

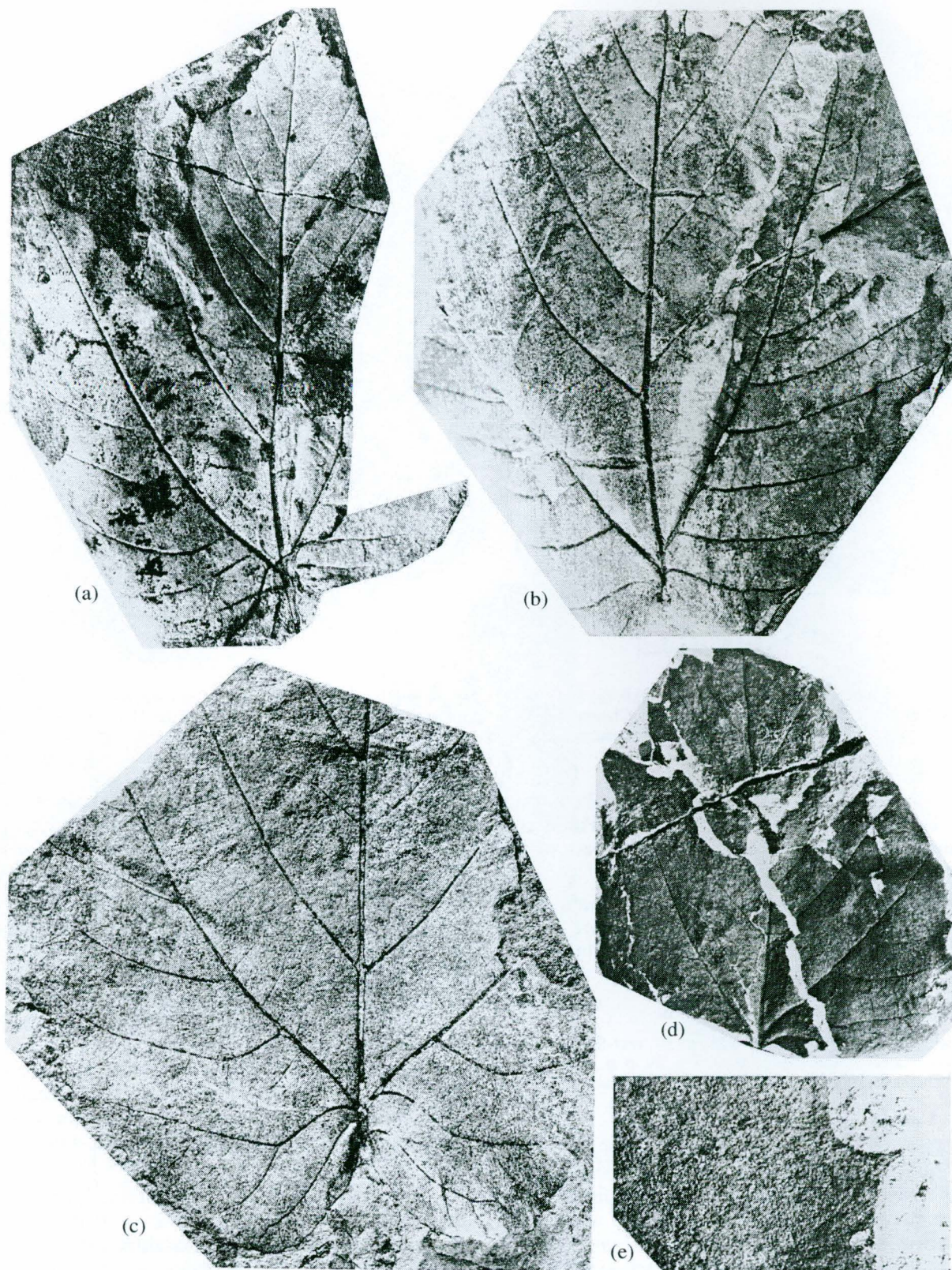


Fig. 18. *Platanus acutiloba* Borsuk: (a) PIN, no. 4778/289, $\times 1$; (b) PIN, no. 3736/88, $\times 1$; (c) PIN, no. 3858/20, $\times 1$; (d) PIN, no. 4252/46, $\times 1$; and (e) PIN, no. 4252/46, marginal tooth, $\times 5$; (a) western Kamchatka Peninsula, Evravavayam River; Tkaprovayam Formation, Upper Paleocene–Lower Eocene; (b) northwestern Kamchatka, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; (c) western Kamchatka, Anadyrka River, Tigil Group, Middle? Eocene; and (d, e) southern Sakhalin Island, Krasnoyarka River Basin; Naiba Formation, Middle Eocene.

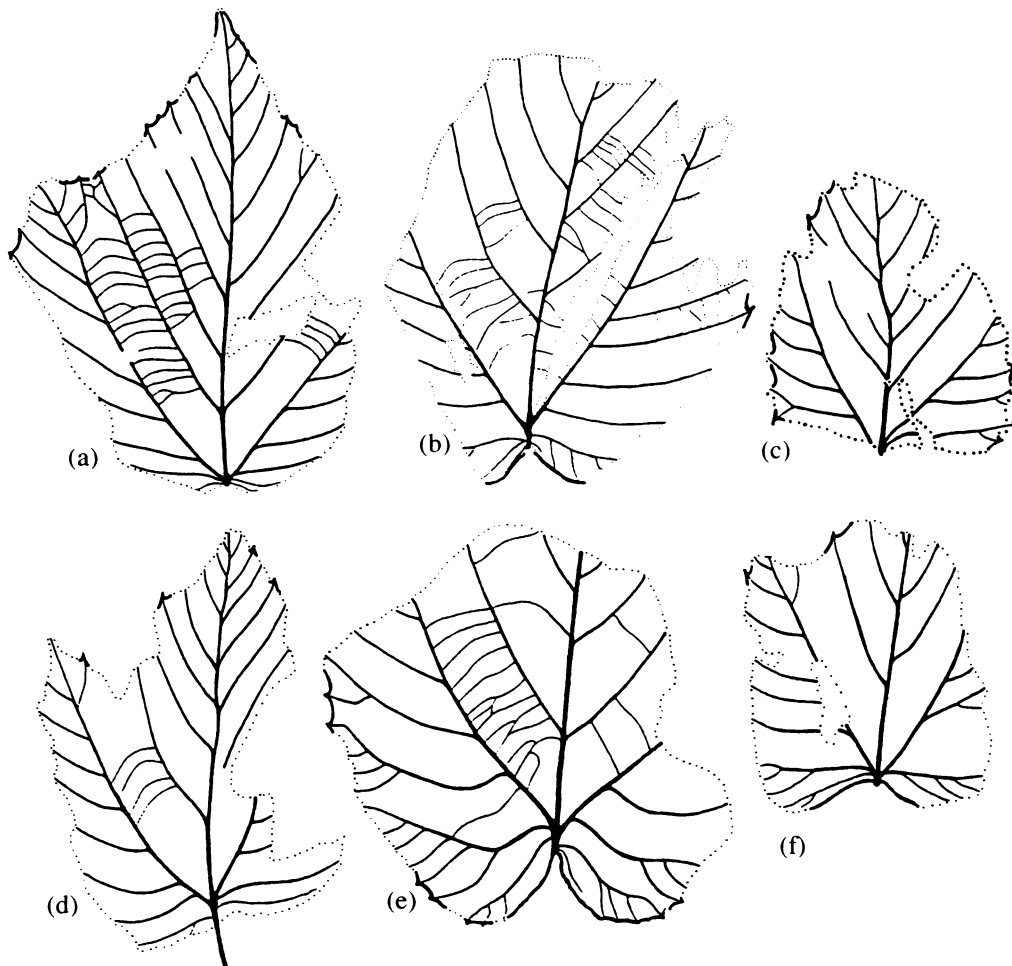


Fig. 19. *Platanus acutiloba* Borsuk, $\times 0.5$: (a) PIN, no. 4253/10; (b) PIN, no. 3736/88; (c) PIN, no. 4256/46; (d) PIN, no. 4778/289; (e) PIN, no. 3858/20; and (f) PIN, no. 4252/51; (a) Sakhalin Island, Naiba River; Naiba Formation, Middle Eocene; (b) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; (c) western Kamchatka, Snatol River; Napana Formation, Upper Paleocene; (d) western Kamchatka Peninsula, Evravavayam River; Tkaprovayam Formation, Paleocene; (e) western Kamchatka Peninsula, Anadyrka River; Tigil Group, Middle? Eocene; and (f) Sakhalin Island, Krasnoyarka River Basin; Naiba Formation, Middle Eocene.

tion, Middle Eocene. Western Kamchatka Peninsula: Chemurnaut Bay, upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; Evravavayam River, Tkaprovayam Formation, Upper Paleocene–Lower Eocene; Anadyrka River, Tigil Group, Middle? Eocene.

Material. Five specimens from the Krasnoyarka River locality (Sakhalin Island); eight specimens from the Chemurnaut Bay locality, four specimens from the Evravavayam River locality, and five specimens from the Anadyrka River locality (Kamchatka Peninsula).

Platanus mabutii Oishi et Huzioka

Platanus mabutii: Oishi and Huzioka, 1943, p. 113, p.p., tab. 19, fig. 1; tab. 20, fig. 1; Medyulyanov, 1975, p. 33, p.p., pl. 6, fig. 7; Maslova and Fotyanova, 1990, p. 701, pl. I, figs. 6 and 7; pl. II, fig. 1, text-figs. 1, 1–6, text-figs. 3 (3); Maslova and Fotyanova, 1991, text-figs. 2, 21–24.

Description (Figs. 20a–20e, 21a–21g). The leaf blade is entire (occasional specimens with a well-developed acroscopic vein are weakly lobed), nearly rounded or slightly transversely elongated, the length/width ratio is 0.8–0.9. The leaf blade base is truncate, emarginate, rarely slightly cordate, often peltate (Figs. 20c–20e, 21a, 21e–21g). The apex is not completely preserved; however, the available fragments suggest its acute shape. The leaf blade margin is toothed. The teeth are low, predominantly concave–concave, one to three teeth per 1 cm of the leaf margin (Fig. 20b). The basal side of the tooth is as long as the apical side or slightly longer.

The basal veins are straight, occasionally slightly arch-shaped, and deviate suprabasally (more rarely basally) at an angle of 35° – 55° to the midvein. Basally, the basal veins are as thick as the midvein or slightly thinner. There are six to nine basisopic veins, they are



Fig. 20. *Platanus mabutii* Oishi et Huzioka: (a) PIN, no. 4253/1, $\times 1$; (b) PIN, no. 4253/1, marginal serration, $\times 3$; (c) PIN, no. 3862/583, $\times 1$; (d) PIN, no. 4129/517, $\times 2$; and (e) PIN, no. 4251/5, $\times 1$; (a, b) Sakhalin Island, Naiba River; Naiba Formation, Middle Eocene; (c) northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgiminskaya Formation, Upper Eocene; (d) eastern Sakhalin Island, Bogataya River; Lyukama Formation, Upper Eocene; and (e) Sakhalin Island, Onor River, isolated block of coal-bearing deposits; Middle? Eocene.

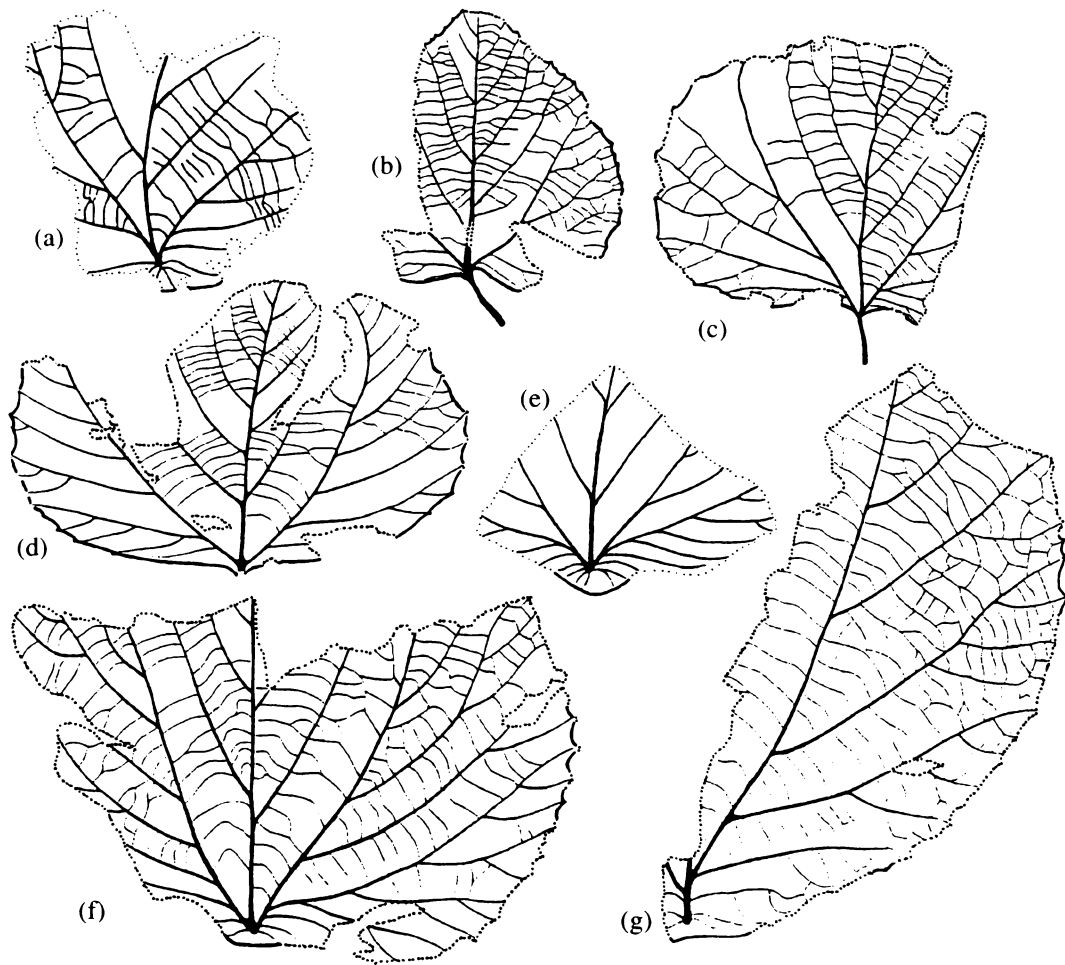


Fig. 21. *Platanus mabutii* Oishi et Huzioka, $\times 0.5$: (a) PIN, no. 4129/517; (b) PIN, no. 4129/521; (c) PIN, no. 4129/522; (d) PIN, no. 4253/1; (e) PIN, no. 4129/526; (f) PIN, no. 4251/4; and (g) PIN, no. 4251/5; (a–c, e) eastern Sakhalin Island, Bogataya River; Lyukama Formation, Upper Eocene; (d) Sakhalin Island, Naiba River; Naiba Formation, Middle Eocene; and (f, g) Sakhalin Island, Onor River, isolated block of coal-bearing deposits; Middle? Eocene.

straight or arch-shaped, become greatly thinner near the leaf blade margin, occasionally form two to five deviations, and end in teeth. There are four to six thin, usually straight secondaries, directed at an angle of 40° – 50° . The density of tertiary veins is two to four per 1 cm of secondary vein. They are branching or nonbranching, distinct, often with anastomoses. The angle between the tertiary veins and the midvein is 95° – 110° .

Comparison. The species resembles Late Cretaceous *P. affinis* Lesq. (British Columbia, Nanaimo group, Vancouver Island; Bell, 1957). However, *P. mabutii* is distinguished by the smaller angle of basal vein deviation and by the peltate base. Unlike *P. affinis*, *P. mabutii* is characterized by the presence of two to five deviations of the basiscopic vein and by teeth beginning at a low part of the leaf.

Occurrence. Sakhalin Island: Naiba River, upper part of the Naiba Formation, Eocene; Onor River,

isolated block of coal-bearing deposits, Middle? Eocene; Bogataya River, Lyukama Formation, Upper Eocene. Northwestern Kamchatka Peninsula: Podkagernaya Bay, Irgirinskaya Formation, Upper Eocene. Primorye, Khasan Formation, Upper Eocene. Hokkaido, Sakubetsu Formation, Upper Eocene.

Material. Five specimens from the Naiba River locality, two specimens from the Onor River locality, 15 specimens from the Bogataya River locality (Sakhalin Island); and seven specimens from the Podkagernaya Bay locality (Kamchatka Peninsula).

***Platanus basicordata* Budantsev**

Platanus basicordata: Budantsev, 1983, p. 135, pl. 24; Maslova and Fotyanova, 1991, p. 181, text-figs. 2, 26, and 27; Maslova, 1997, p. 89, text-figs. 1a, 2b, and 2d.

Description (Figs. 22a, 23a–23d, 24a–24c). The leaf blade is trilobate, about 12–14 cm long and

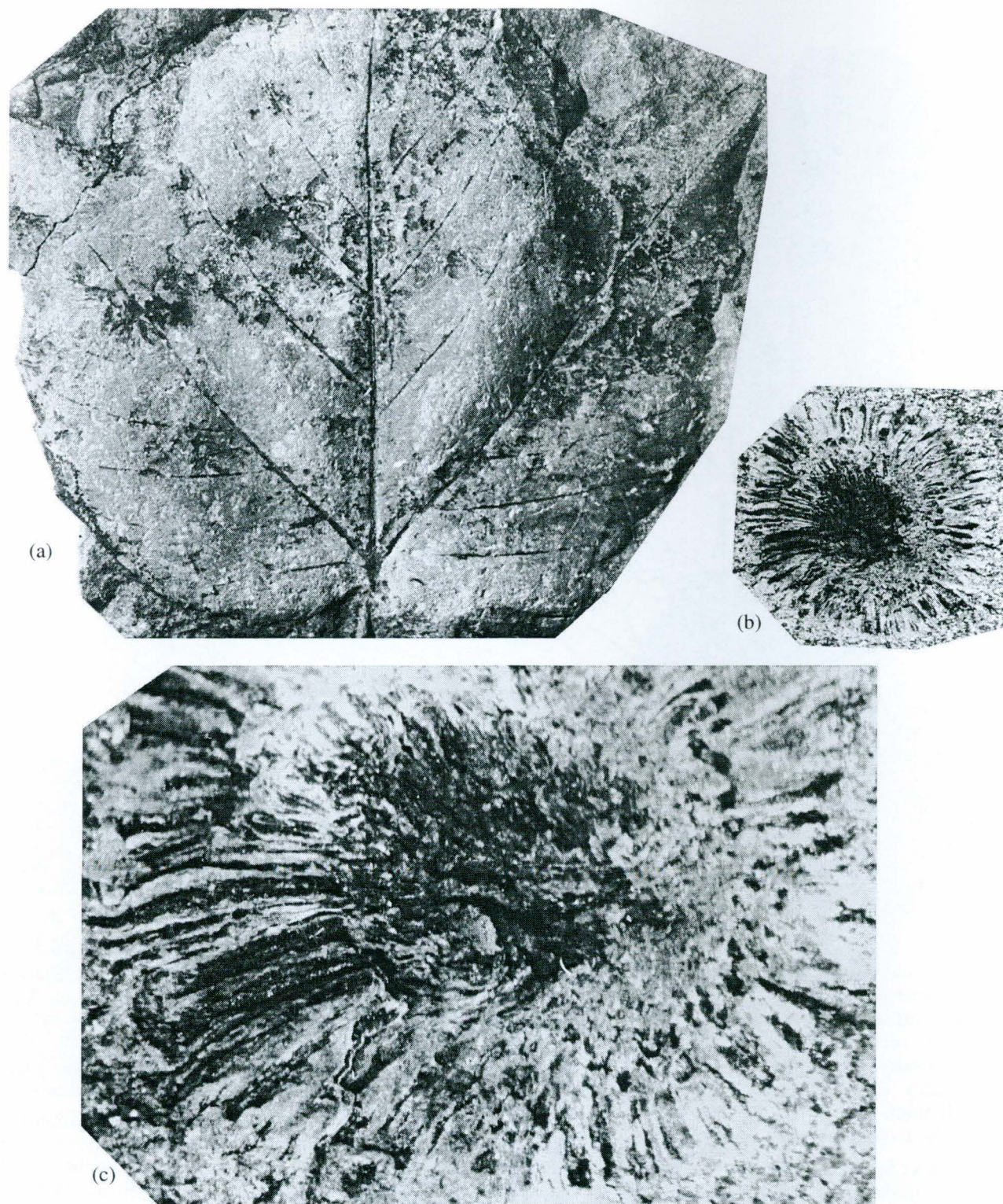


Fig. 22. *Platanus basicordata* Budantsev: (a) PIN, no. 3736/6, $\times 1$; *Platanus stenocarpa* N. Maslova: (b, c) PIN, no. 3736/57, holotype: (b) $\times 3$ and (c) $\times 10$; northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkrovayam Formation, Upper Paleocene–Lower Eocene.

11–13 cm wide on average. The central lobe is triangular, basally broad. Sinuses of the lobes are symmetrical, dissecting the leaf blade approximately at one-third of

its length. The apices of the lateral lobes are pointed. The base of the leaf blade is cordate, slightly decurrent. The leaf margin is entire in the basal region and in the

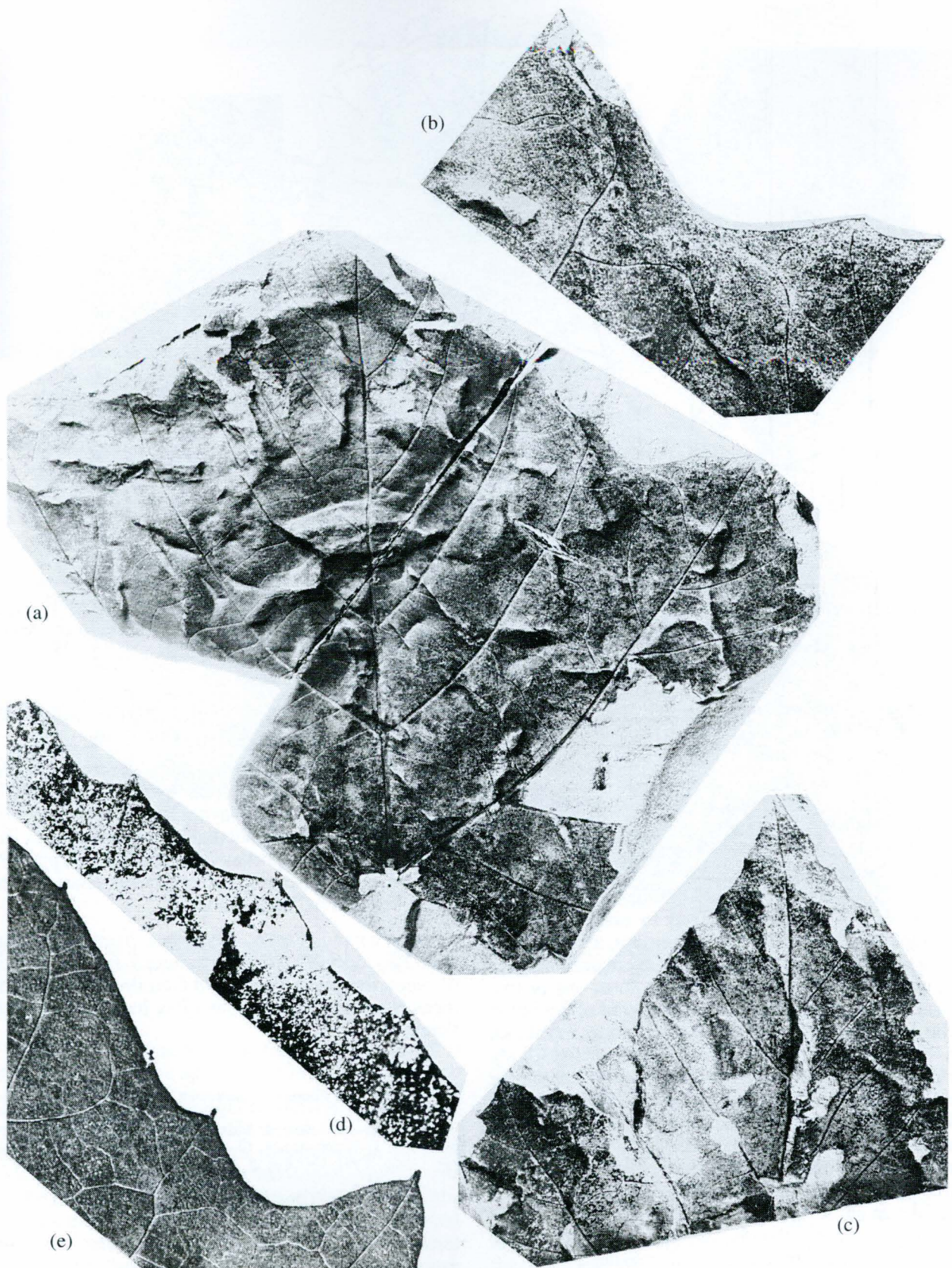


Fig. 23. *Platanus basicordata* Budantsev: (a, b) PIN, no. 3862/580: (a) $\times 1$ and (b) venation in sinus, $\times 2$; (c, d) PIN, no. 3862/575: (c) $\times 1$ and (d) marginal serration, $\times 3$. *Platanus orientalis* L.: (e) extant species, compare marginal serration, $\times 3$; (a–d) northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgirinskaya Formation, Upper Eocene.

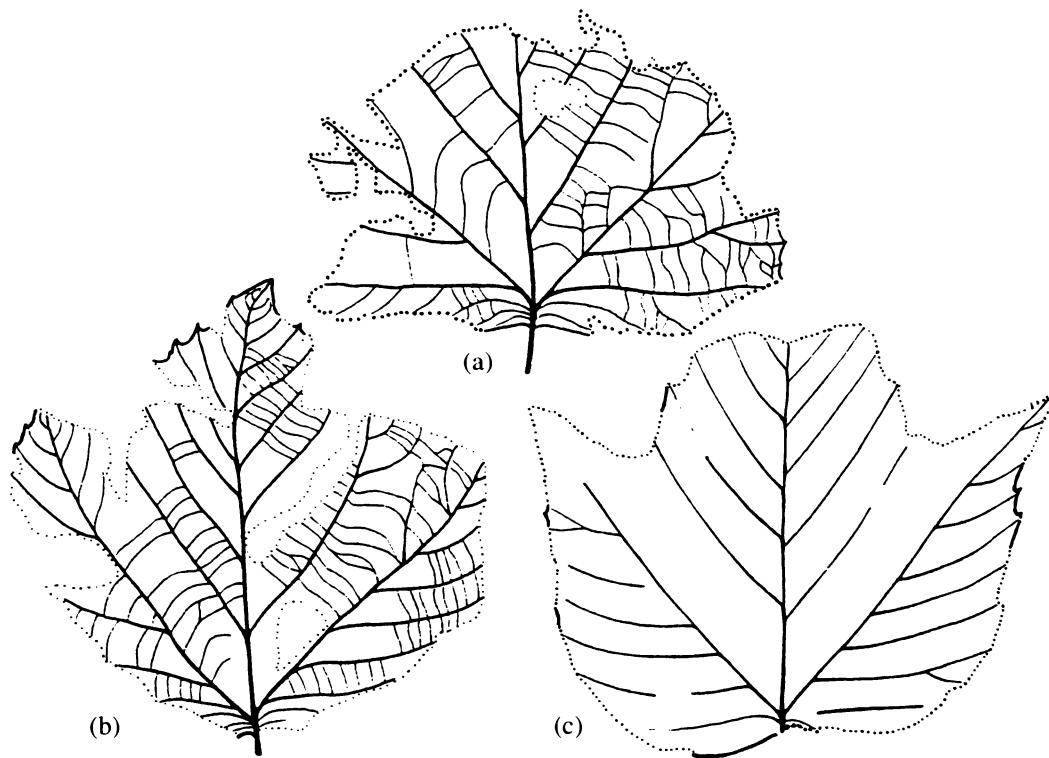


Fig. 24. *Platanus basicordata* Budantsev, $\times 0.5$: (a) PIN, no. 3862/576; (b) PIN, no. 3862/581; and (c) PIN, no. 3736/6; (a, b) northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgiminskaya Formation, Upper Eocene; (c) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

lobe sinuses, in other regions it is toothed. The teeth are small, pointed, devoid of glands, one or two per 1 cm of the leaf margin, the apical margin is concave, the basal margin is convex (Figs. 23b, 23d).

The midvein is straight, weakly sinuous near the leaf apex, becomes gradually thinner from the base toward the apex for the thickness of the deviating secondary vein. Basally, the basal veins are as thick as the midvein. They are straight and deviate suprabasally at an angle of 40° . There are seven to nine basicopic deviations of the basal veins. They are arch-shaped, usually nonbranching. One or two of them occasionally form weak branches. The basal veins form one or two weak acroscopic branches. Below the point of deviation of the basal veins there are two or three infrabasal veins. The secondary veins are arranged in five or six pairs. They are slightly arch-shaped, two or three lower pairs form one or two basicopic deviations. The angle between the midvein and secondary veins is 40° – 30° . The tertiary veins are distinct, alternate or branching, there are up to four tertiaries per 1 cm of a secondary vein. The tertiaries are perpendicular to the secondaries and make an angle of 110° – 130° with the midvein. The venation of higher orders is fine, reticulate, and forms orthogonal (more often pentagonal) meshes.

Comparison. The species is similar to *P. rectinervis* Hollick from the Tertiary deposits of Alaska (Hollick, 1936).

Remarks. The leaves of *P. basicordata* associate with the infructescences of *P. stenocarpa*.

Occurrence. Northwestern Kamchatka Peninsula: Chemurnaut Bay, upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; section between the capes Rebro and Getkilnin, Tkaprovayam Formation, Upper Paleocene–Lower Eocene; Podkagernaya Bay, Irgiminskaya Formation, Upper Eocene.

Material. Seven specimens from the Chemurnaut Bay locality, three specimens from the section between the capes Rebro and Getkilnin, and six specimens from the Podkagernaya Bay locality (Kamchatka Peninsula).

Platanus asymmetrica N. Maslova

Platanus asymmetrica: Maslova and Fotyanova, 1990, p. 702, pl. 1, figs. 1–5, text-figs. 1, (7–9), text-figs. 3, (1, 2); Maslova and Fotyanova, 1991, text-figs. 2, 29–32.

Description (Figs. 25a–25d, 26a–26d). The leaf blade is entire to trilobate with weakly defined lateral lobes, small, and asymmetrical. The length/width ratio is 1.4–1.7. The apex is pointed and attenuated. The base is cordate, with unequal sides. The leaf blade margin is toothed. The teeth are acute, concave–convex, occasionally with a straighten basal side, three or four

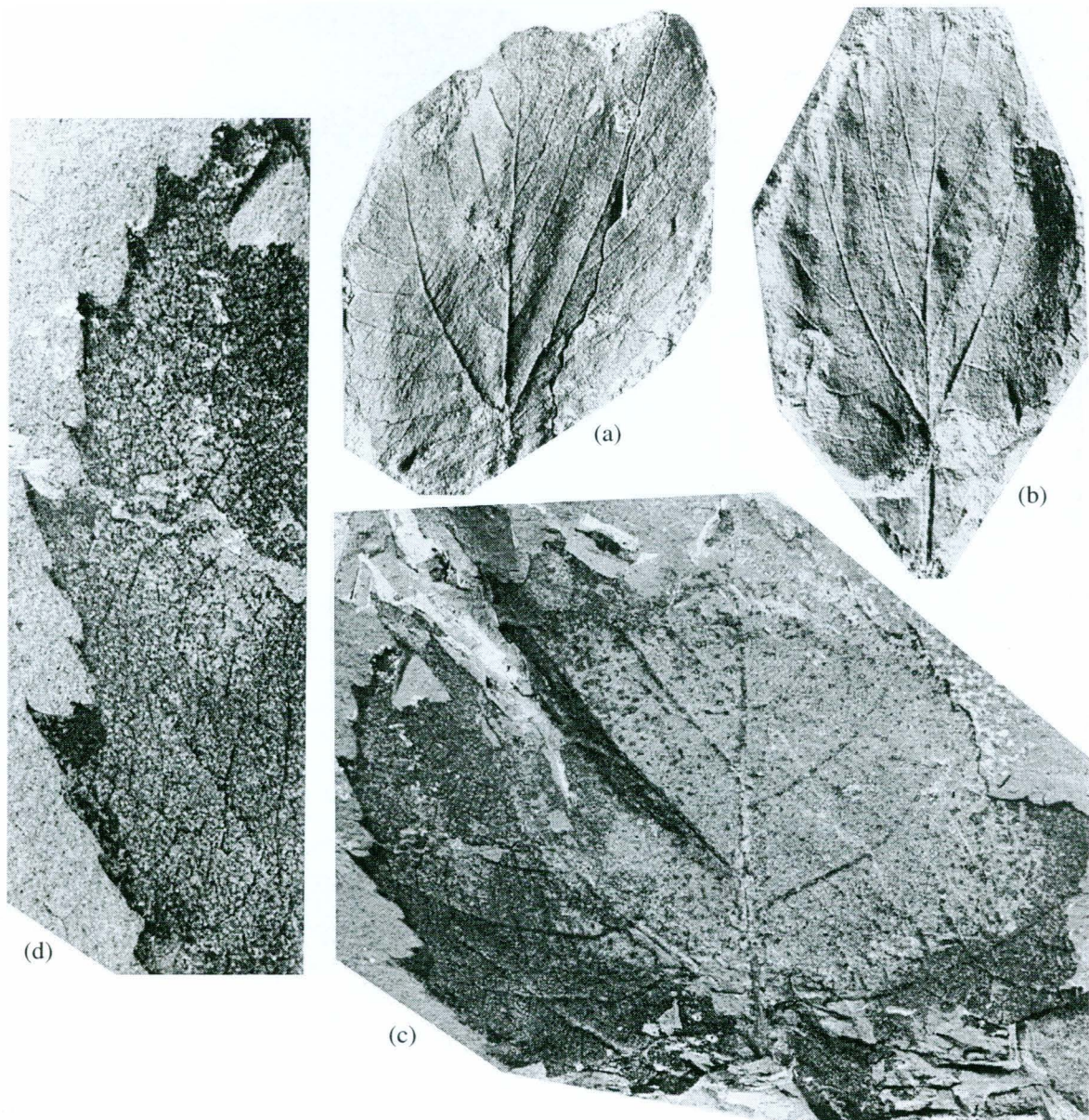


Fig. 25. *Platanus asymmetrica* N. Maslova: (a) PIN, no. 4395/606, $\times 1$; (b) PIN, no. 4395/604, holotype, $\times 1$; (c, d) PIN, no. 4395/15: (c) $\times 1$ and (d) marginal serration, $\times 2$; northwestern Kamchatka Peninsula, Utkholokskii Peninsula; Zubchatyi Cape Formation, Upper Eocene.

per 1 cm of the leaf margin. The basal side of a tooth is usually longer than the apical side (Fig. 25d).

The basal veins are straight or slightly arch-shaped, deviate suprabasally or basally, are nearly as thick as the midvein in the basal region, directed at an angle of 30° – 50° . There are up to eight basisopic veins. They are thin, arch-shaped, occasionally slightly broken, the nearest to the base vein form up to seven deviations. Below the point of deviation of basal veins (in case of suprabasal venation), there are one to three short weak veins. The secondary veins are arranged in six to nine pairs. They are straight or slightly arch-shaped and run at an angle of 25° – 30° . This angle occasionally

becomes greater (up to 40° – 45°) in one half of the leaf, thus increasing the asymmetry of the leaf blade. The tertiary veins are nonbranching or branching, distinct, frequent, up to six tertiaries occur per 1 cm of secondary vein. The angle between the midvein and tertiaries is about 130° – 140° .

Comparison. The species does not display a great similarity to any known extinct species of plane trees. It only vaguely resembles *P. dissecta* Lesq. from the Miocene of the Columbia Plateau (Chaney and Axelrod, 1959). This similarity includes the acute angle of deviation of basal and secondary veins, comparable number of secondary and basisopic veins, and the

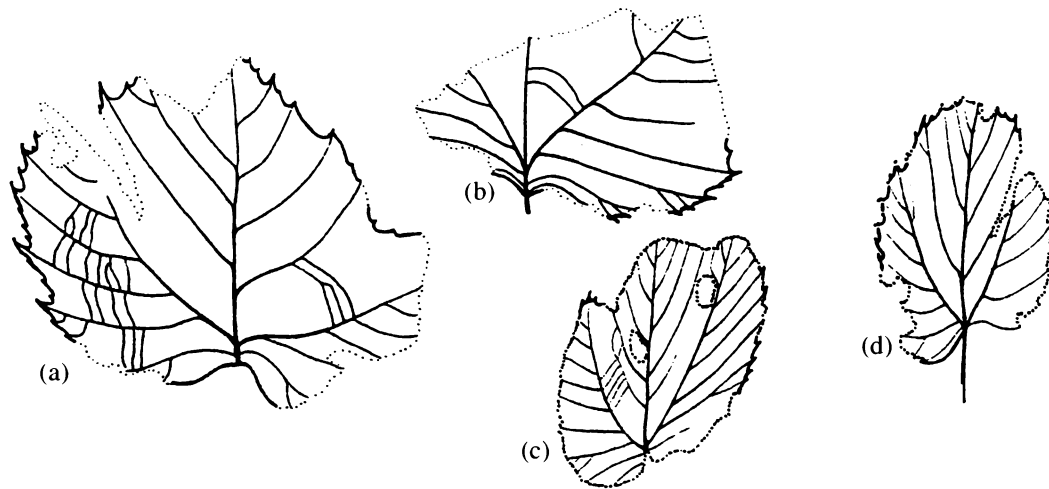


Fig. 26. *Platanus asymmetrica* N. Maslova, $\times 0.5$: (a) PIN, no. 4395/15; (b) PIN, no. 4395/14; (c) PIN, no. 4395/606; and (d) PIN, no. 4395/604, holotype; western Kamchatka Peninsula, Utkholokskii Peninsula; Zubchatyi Cape Formation, Upper Eocene.

teeth morphology. *P. dissecta* significantly differs in its parallel-margined elongate central lobe and distinct narrow lateral lobes.

Remarks. The species resembles the extant species *P. occidentalis* in teeth morphology but differs in the denser arrangement of teeth and weakly defined lobes.

Occurrence. Western Kamchatka Peninsula: Chemurnaut Bay, upper part of the Kamchik Formation—lower part of the Tkaprovayam Formation, Upper Paleocene—Lower Eocene; Utkholokskii Peninsula, Zubchatyi Cape Formation, Upper Eocene.

Material. Three specimens from the Chemurnaut Bay locality and 19 specimens from the Utkholokskii Peninsula locality (Kamchatka Peninsula).

Genus *Macginitiea* Wolfe et Wehr in Manchester, 1986

Macginitiea latiloba Budantsev

Macginitiea latiloba: Budantsev, 1996, p. 70, pl. I, fig. 1, pl. II, figs. 1–3.

Macginitiea kamtschatica: Gladenkov *et al.*, 1997, p. 146, text-fig. 75, fig. 2; text-fig. 77; text-fig. 78, figs. 1 and 2; text-fig. 79, figs. 1–6; text-fig. 80.

Platanus nobilis: Maslova and Fotyano, 1991, p. 181, text-fig. 2.

Description (Figs. 27a, 27b, 28a). There are two specimens in the collection. The large leaf blade (up to 25 cm long) has five lobes. The central and two inner lateral lobes are larger, shorter, triangular, basally broad, the apices are not preserved. Two lower lobes are considerably smaller than the central lobes. The sinuses between the lobes are broad and rounded. The leaf is entire-margined along the total length. The leaf base is weakly cordate.

The venation is palynactinodromous. Three veins of equal thickness deviate from the base of the leaf blade. The midvein is straight, two basal veins are slightly curved, at a distance of about 2 cm from the point of

deviation they form thinner short veins, which end in lateral lobes. The secondary veins are densely spaced and meet to form loops. The angle of deviation of the secondary veins is about 50° in the upper part of the lobes and 90° in the lower part. In the lower region of the leaf blade, the secondary veins are weaker. They are distinctly thin and meet the equivalent veins of the adjacent lobes to form weak chevrons. The chevrons occupy more than two-thirds of the leaf blade length. Tertiary venation has not been found.

Comparison. The author of the species considers the presence of leaves with three and seven lobes and the absence of a toothed leaf margin to be the distinguishing features of *Macginitiea kamtschatica* Cheleb. (Gladenkov *et al.*, 1997). However, the number of lobes has been shown to vary in *Macginitiea*. This genus includes species with varying numbers of leaf blade lobes; e.g., *M. angustiloba* (Lesq.) Manchester (Manchester, 1986) and *M. whitneyi* (Lesq.) Manchester (Manchester, 1986). In the description of *M. latiloba*, the author of the species noticed the presence of both entire-margined leaves and leaves with occasional small teeth (Budantsev, 1996). The same combination of variants with the distinctly dominating entire margin occurs also in *M. angustiloba*. Other characters are identical in *M. latiloba* and *M. kamtschatica*.

Remarks. These fossil finds were first erroneously assigned to *Platanus nobilis* Newb. (Maslova and Fotyano, 1991). *Macginitiea* and *Platanus nobilis* show extremely similar leaf morphotypes. The holotype of *Platanus nobilis* is a leaf with five lobes (three larger central lobes and two smaller lateral lobes), with chevrons not exceeding the lower third of the leaf blade, and with a toothed margin (Newberry, 1898). The genus *Macginitiea* was described from Eocene deposits of North America (Wolfe and Wehr, 1987). However, a year before Manchester (1986) substantiated the validity of this genus by referring to his earlier

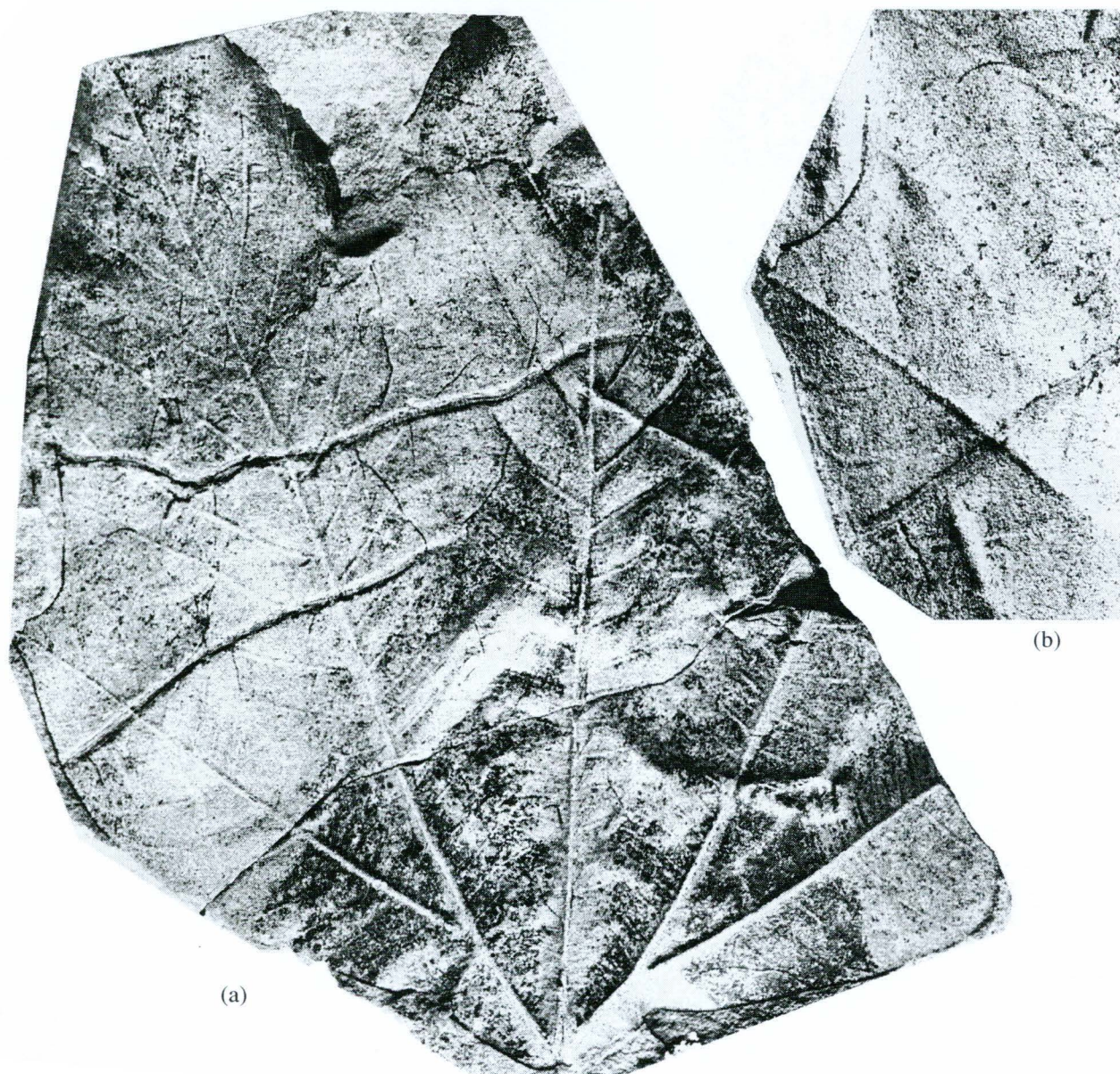


Fig. 27. *Macginitiea latiloba* Budantsev, PIN, no. 3736/76: (a) $\times 1$ and (b) lower lobe, looping secondaries, $\times 2$; northwestern Kamchatka Peninsula, section between the capes Rebro and Getkilnin; Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

but still unpublished paper. Manchester studied reproductive organs that associate with the leaves of *Macginitiea* to reconstruct the plant and prove its affinity to the family Platanaceae. A detailed analysis of the genus with a review of finds from the Kamchatka Peninsula was done by Budantsev (1996). The similarities and differences between *Macginitiea* and *Platanus nobilis* s. str. were discussed in Pigg and Stockey (1991).

None of the macromorphological leaf characters can serve as the only decisive criterion for the assignment of leaf remains to the genus *Macginitiea* or *Platanus*. The finds under description differ from *P. nobilis* s. str. by several characters. These are (1) predominantly entire-margined morphotypes, (2) insignificant sinuses

between lobes, and (3) chevrons occupying nearly the entire length of the leaf blade.

Analyzing the characters, Pigg and Stockey (1991) supposed *P. nobilis* to be a transition between *Macginitiea* and the extant *Platanus*. This hypothesis is substantiated by the presence of chevrons at the leaf base in extant *P. orientalis* (Manchester, 1986) and *P. wrightii* (Pigg and Stockey, 1991).

Occurrence. Northwestern Kamchatka: Chemurnaut Bay, upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; section between the capes Rebro and Getkilnin, Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

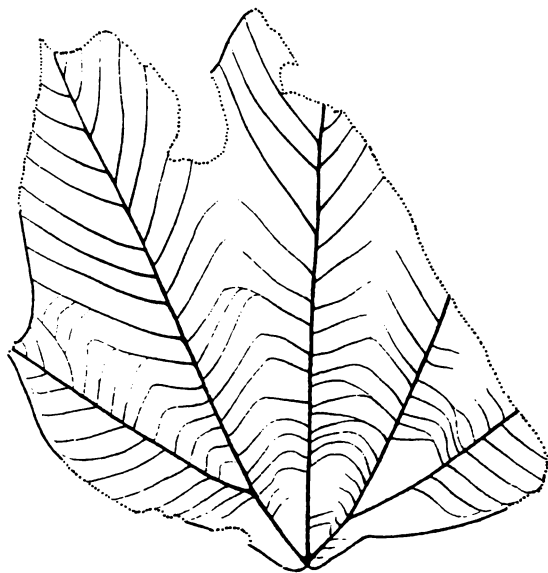


Fig. 28. *Macginitiea latiloba* Budantsev, PIN. no. 3736/76, $\times 0.5$; northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

Material. One specimen from the Chemurnaut Bay locality and one specimen from the section between the capes Rebro and Getkilnin (Kamchatka Peninsula).

Genus *Platimeliphyllum* N. Maslova

Type species. *Hamamelites palanensis* Budantsev, 1983.

Species composition. *Platimeliphyllum palanense* (Budants.) N. Maslova, *Platimeliphyllum snatolense* N. Maslova and *Platimeliphyllum denticulatum* N. Maslova.

Comparison. The species of the genus *Platimeliphyllum* combine hamamelid and platanoid characters. This polymorphous genus has symmetrical and asymmetrical leaves with typically platanoid concave-concave teeth or rounded typically hamamelid teeth. Apart from the macromorphological characters of these two families, the leaves of *Platimeliphyllum* show epidermal characters typical of the family Platanaceae. The reproductive structures that associate with *Platimeliphyllum* foliage also suggest their platanoid affinity.

It should be noted that the new genus is similar to *Platimelis* Golovneva, a common member of northern temperate floras of the Upper Cretaceous–Paleocene. The latter genus was established on the basis of macromorphological analysis of leaf remains. The main distinguishing character is the shape of leaf margin teeth. *Platimelis* has rare broadly triangular teeth with a rounded apex. Epidermal information concerning this genus is lacking. The author of the genus believes that *Platimelis* combines platanoid and hamamelid characters with a greater portion of the latter.

The genus *Davidoidea* (especially *D. hebridica* Johnson from the Paleocene deposits of the Isle of Mull; Boulter and Kvaček, 1989) is very close in leaf morphology to *Platimeliphyllum*. However, leaves of *D. hebridica* have a greater number of straight frequently forked secondary veins and better developed pomes.

Remarks. Leaves of this morphotype from the Paleocene deposits of the Kamchatka Peninsula were earlier described as *Hamamelites* Saporta (Budantsev, 1983, 1997). This formal genus was introduced to describe fossil leaves morphologically identical to leaves of the extant *Hamamelis* (Saporta, 1868).

As more and more fossil leaves of this morphotype were studied by paleobotanists, the morphological boundaries of this genus significantly changed. Leaves that show macromorphological characters of many extant hamamelids but cannot be reliably assigned to any of them have been included in this genus.

The representative fossil material studied has shown that the leaves previously assigned to *Hamamelites palanensis* have both a complex of macromorphological characters of several hamamelid genera and the typically platanoid epidermal morphology. Moreover, the highly diverse morphology of these leaves allows both comparison of some morphotypes (from one and the same species, locality, and bed) with hamamelids on the basis of macromorphological characters such as general symmetry of the leaf blade and its base, weakly defined basal veins, a camptodromous connection of basisopic veins, and low obtuse teeth and a comparison of other morphotypes with platanoids (typical suprabaasal deviation of well-defined basal veins with craspedodromously ending basisopic branches, well-developed infrabaasal veins, and concave–concave teeth with a longer basal side). In fact, particular leaf morphotypes of this genus morphologically resemble various extant genera of the Hamamelidaceae (e.g., *Corylopsis*, *Hamamelis*, and *Parrotia*).

The assignment of such leaves to the family Platanaceae is additionally supported by their evident association at least in three localities (northwestern Kamchatka Peninsula: Chemurnaut Bay, Snatol River, and Evravavayam River) of these polymorphous leaves with heads of *Chemurnautia* demonstrating a platanoid microstructure.

Taking into account the cooccurrence in three Early Paleogene fossil plant assemblages of leaves of the genus *Platimeliphyllum* and staminate inflorescences of *Chemurnautia*, I believe that they belong to one and the same plant.

Platimeliphyllum palanense (Budants.) N. Maslova

Hamamelites palanensis: Budantsev, 1983, p. 134, p. p., pl. 25, figs. 2 and 3, pl. 26, fig. 1, pl. 27, fig. 6.

Hamamelites kinkilensis: Budantsev, 1997, p. 62, p. p., pl. 22, fig. 6, pl. 24, fig. 3.

Platimeliphyllum palanense: Maslova, 2002a, p. 92, pl. IV, figs. 3 and 4, text-figs. 1a–1k, 2a, and 2b.

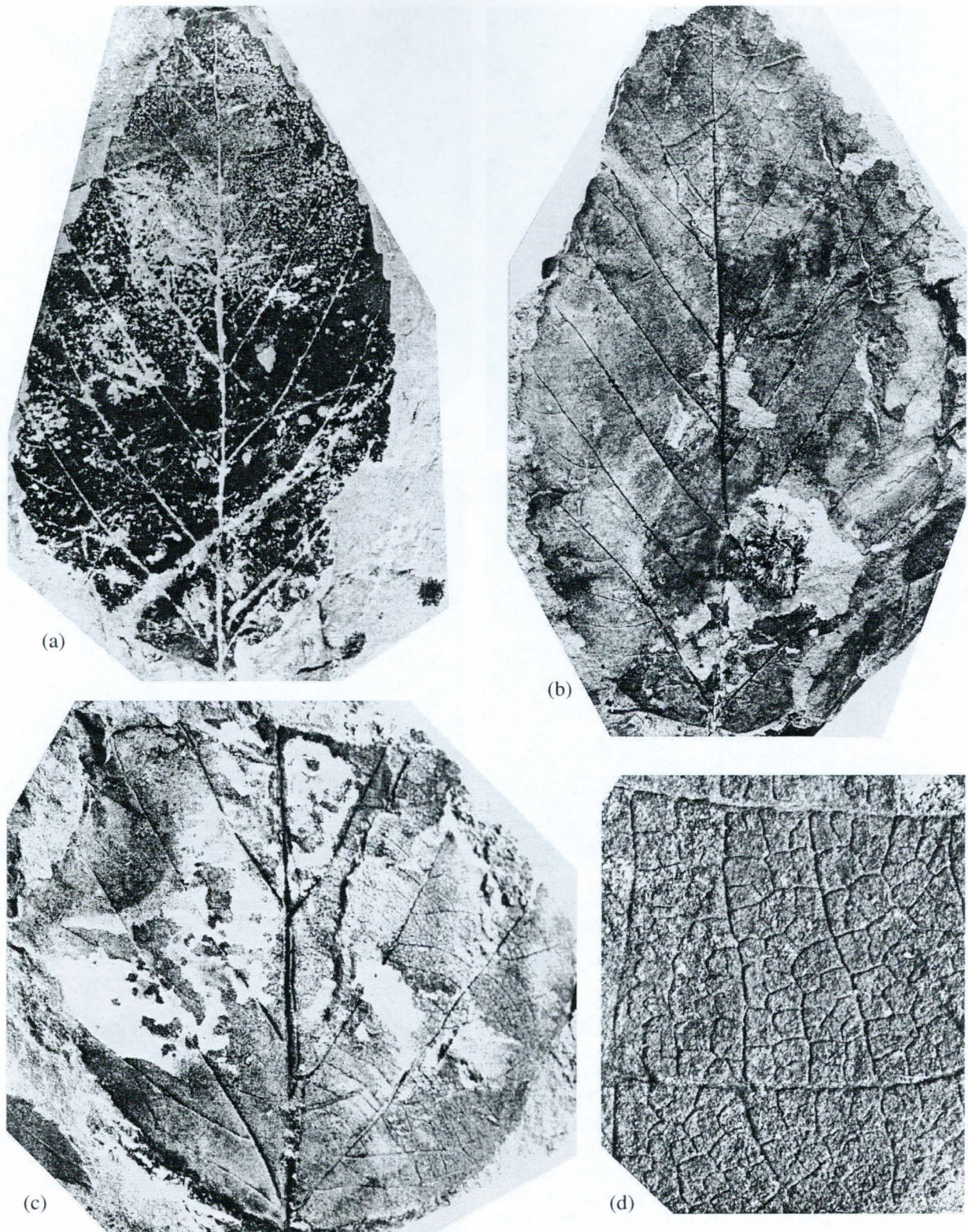


Fig. 29. *Platimeliphyllum palanense* (Budants.) N. Maslova: (a) PIN, no. 3736/54, two heads of *Chemurnautia staminosa* N. Maslova are seen on the right, $\times 1$; (b) PIN, no. 4778/243, $\times 1$; and (c, d) PIN, no. 4778/281: (c) $\times 1$ and (d) tertiary venation, $\times 5$; (a) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; and (b–d) western Kamchatka, Evravayam River; Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

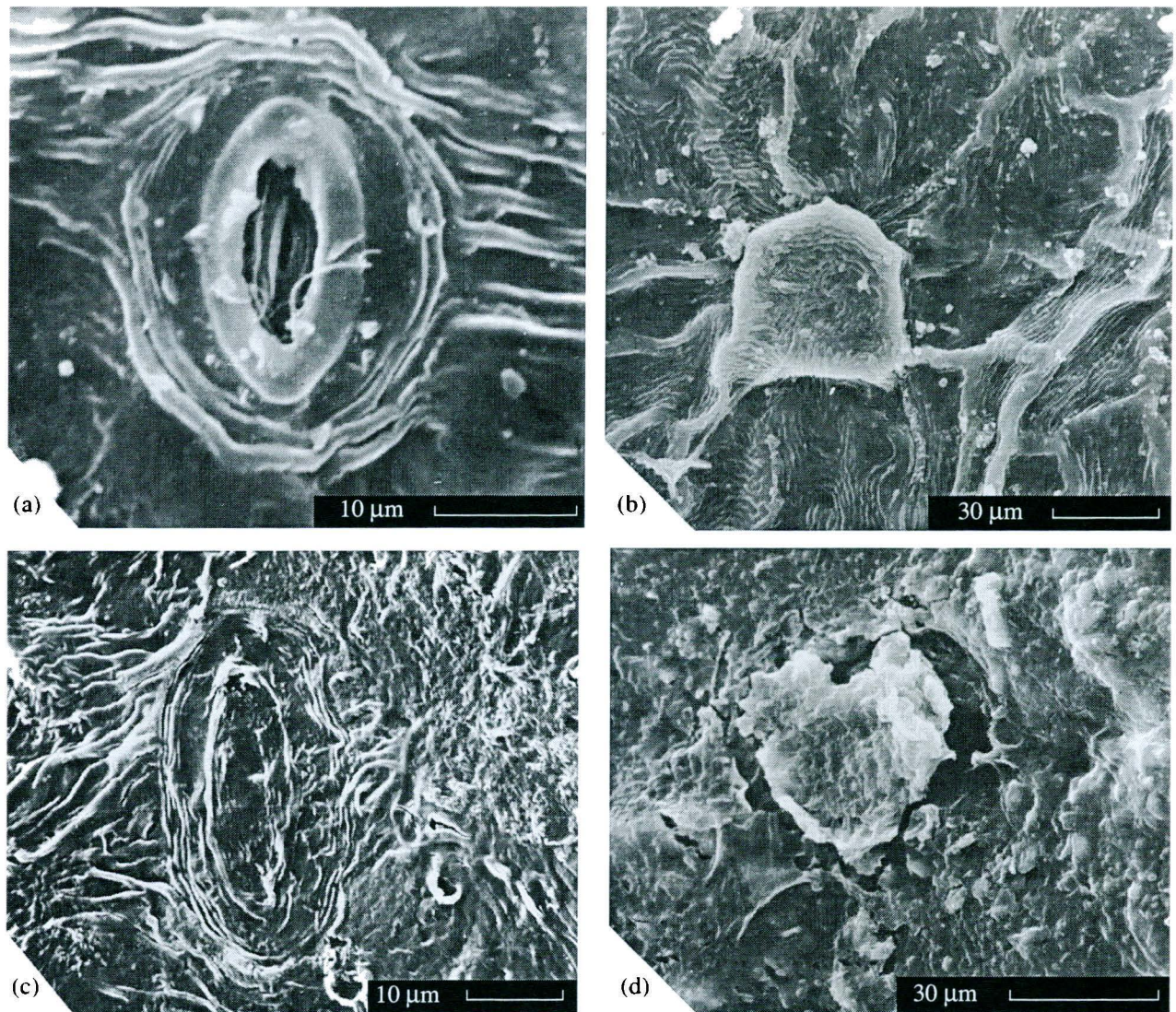


Fig. 30. Herbarium specimen of extant *Platanus occidentalis* L. for comparison, SEM: (a) stoma, radiating cuticular folds are visible; (b) upper leaf epidermis, gland. *Platimeliphyllum palanense* (Budants.) N. Maslova, PIN. no. 3736/54, SEM: (c) stoma, folded cuticle is seen; (d) gland; (c, d) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkprovoyam Formation, Upper Paleocene–Lower Eocene.

Description (Figs. 29a–29d, 30a–30d, 31a–31m, 32a–32m). The leaves are simple, entire, and petiolate. The leaf blade is oval, often asymmetrical, the maximal width is situated in its central part. The length of the largest specimens is 15 cm, the width is 12 cm. The length/width ratio of the leaf blade is 1.2–1.4, rarely 1.6. The base is asymmetric, predominantly rounded; truncated and cuneate bases also occur. The leaf apex tapers off to a point. Above the base of the leaf blade, the leaf margin is toothed. The first teeth (one or two per 1 cm of the leaf margin) appear on the endings of basicopic branches of basal veins. If these branches loop, the teeth appear at a height of approximately one-third of the leaf blade, on the endings of basal veins. The shape of the teeth varies. The typically concave-concave teeth with the shorter apical side and longer

basal side that end with a spine predominate. Rounded teeth occur more rarely.

The venation is pinnate. The midvein is straight, occasionally sinuous in the upper part of the leaf blade. The basal veins are arch-shaped, as thick as the first pair of secondary veins, deviate from the leaf blade base or slightly above it with a certain shift relative to each other, and reach at least one-third of the leaf blade length. Some leaves have naked bases of the basal veins. There are six or seven basicopic deviations of the basal veins. They are thin, arch-shaped, the lower deviations form loops, while the upper deviations end in teeth. Occasionally, the basal vein is not directed at a tooth but loops with the first secondary vein. Five to seven pairs of the secondary veins are mostly alternate, thin, arch-shaped, and fork one or two times. The ter-

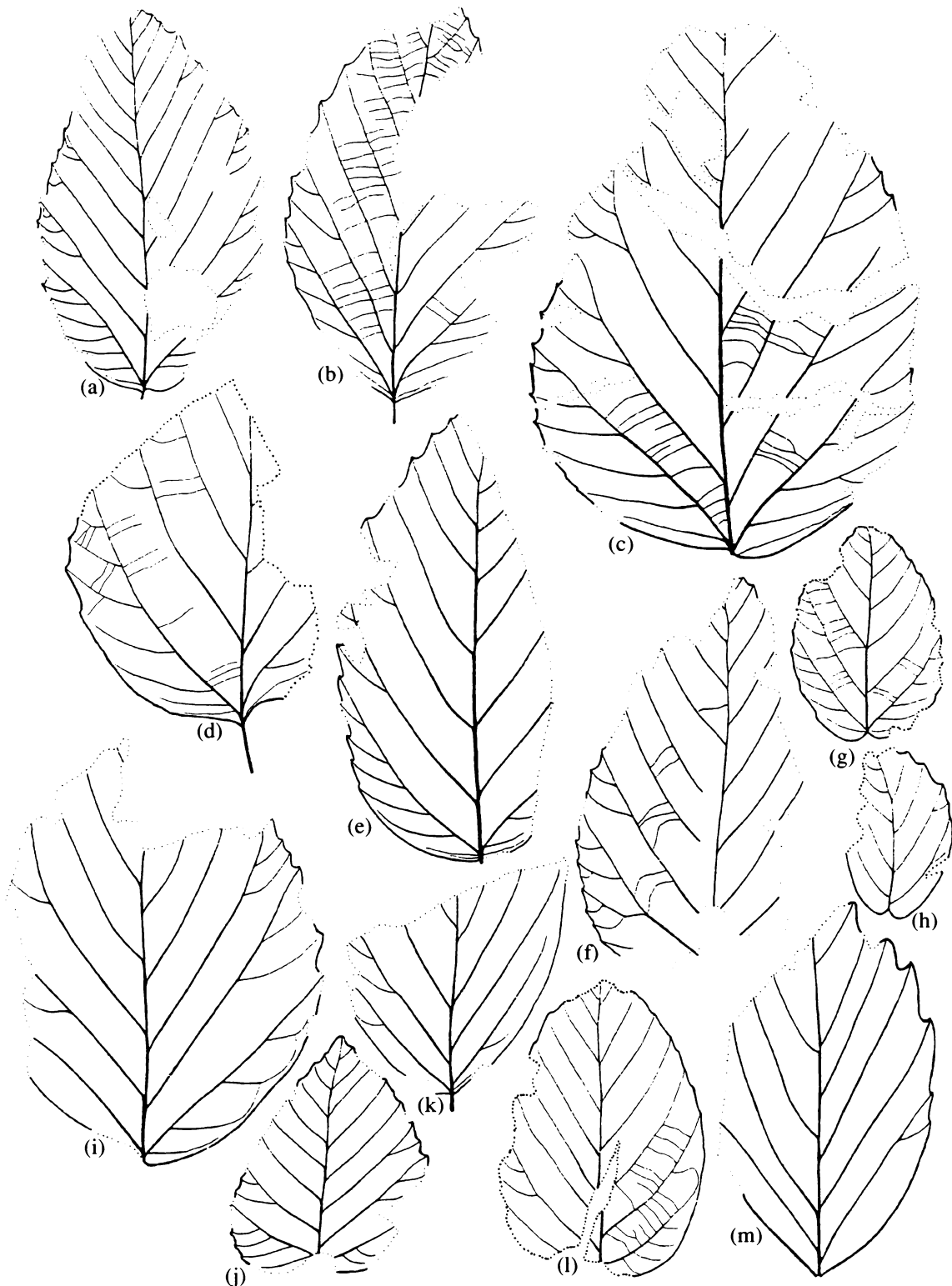


Fig. 31. *Platimeliphyllum palanense* (Budants.) N. Maslova, $\times 0.5$: (a) PIN, no. 4778/243; (b) PIN, no. 4778/261; (c) PIN, no. 4778/249; (d) PIN, no. 4778/296; (e) based on PIN, no. 4257/11 and its counterpart PIN, no. 4257/23; (f) PIN, no. 4778/248; (g) PIN, no. 3736/92; (h) PIN, no. 3736/22; (i) PIN, no. 3736/40; (j) PIN, no. 4257/6; (k) PIN, no. 3236/7; (l) PIN, no. 3736/50; and (m) PIN, no. 4257/2; (a–d, f) western Kamchatka, Evravayam River; Tkprovayam Formation, Upper Paleocene–Lower Eocene; (e, j, m) northwestern Kamchatka Peninsula, section between the capes Rebro and Getkilnin; Tkprovayam Formation, Upper Paleocene–Lower Eocene; (g–i, k, l) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkprovayam Formation, Upper Paleocene–Lower Eocene.

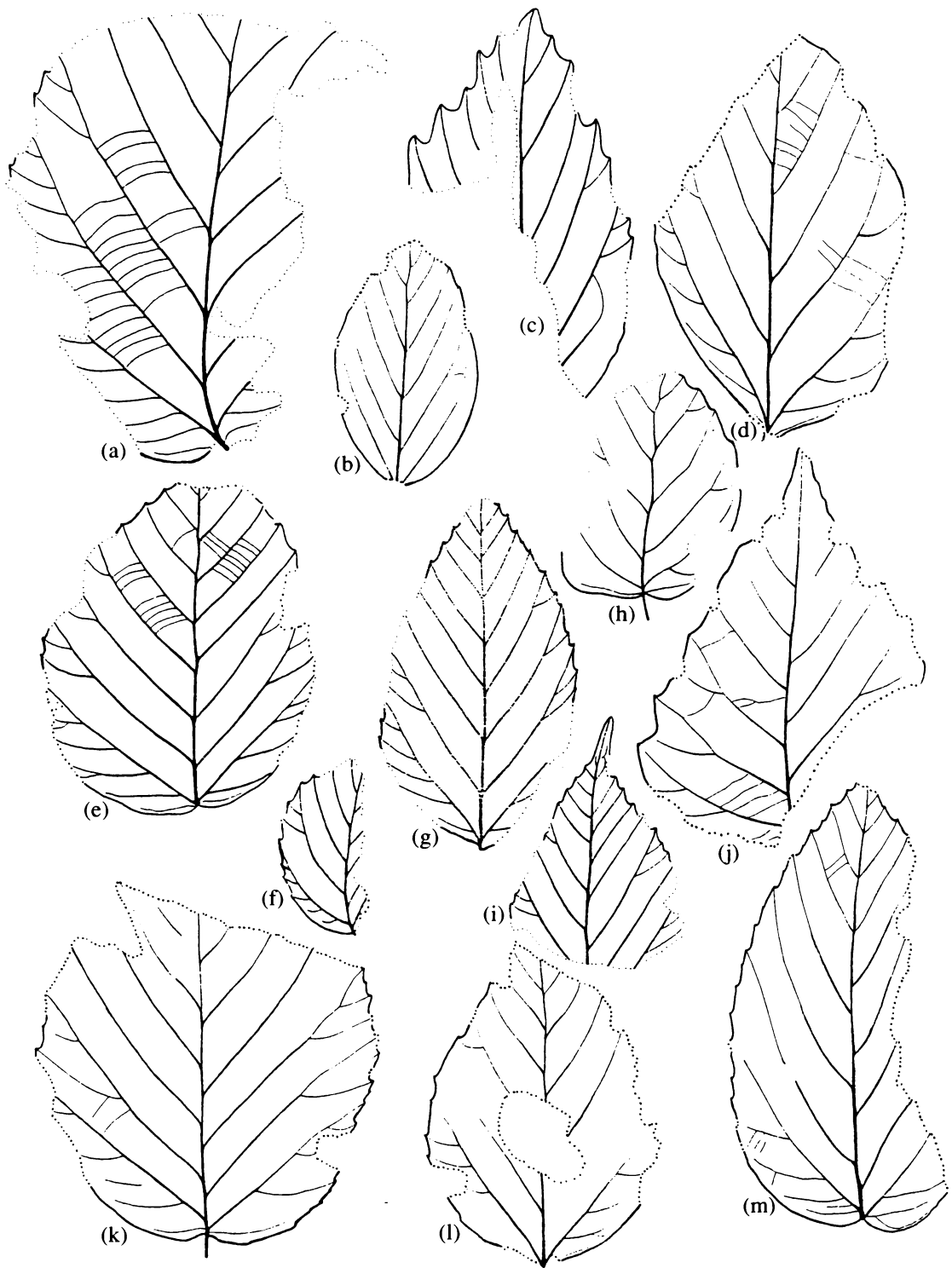


Fig. 32. *Platimeliphyllum palanense* (Budants.) N. Maslova, $\times 0.5$: (a) PIN, no. 3736/42; (b) PIN, no. 4257/10; (c) PIN, no. 4257/1; (d) PIN, no. 3736/25; (e) PIN, no. 3736/47; (f) PIN, no. 3736/85; (g) PIN, no. 3736/54; (h) PIN, no. 3736/23; (i) PIN, no. 3736/26; (j) PIN, no. 4257/27; (k) PIN, no. 3736/86; (l) PIN, no. 3736/13; and (m) PIN, no. 3736/2; (a, d–i, k–m) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; (b, c, j) northwestern Kamchatka Peninsula, section between the capes Rebro and Getkilnin; Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

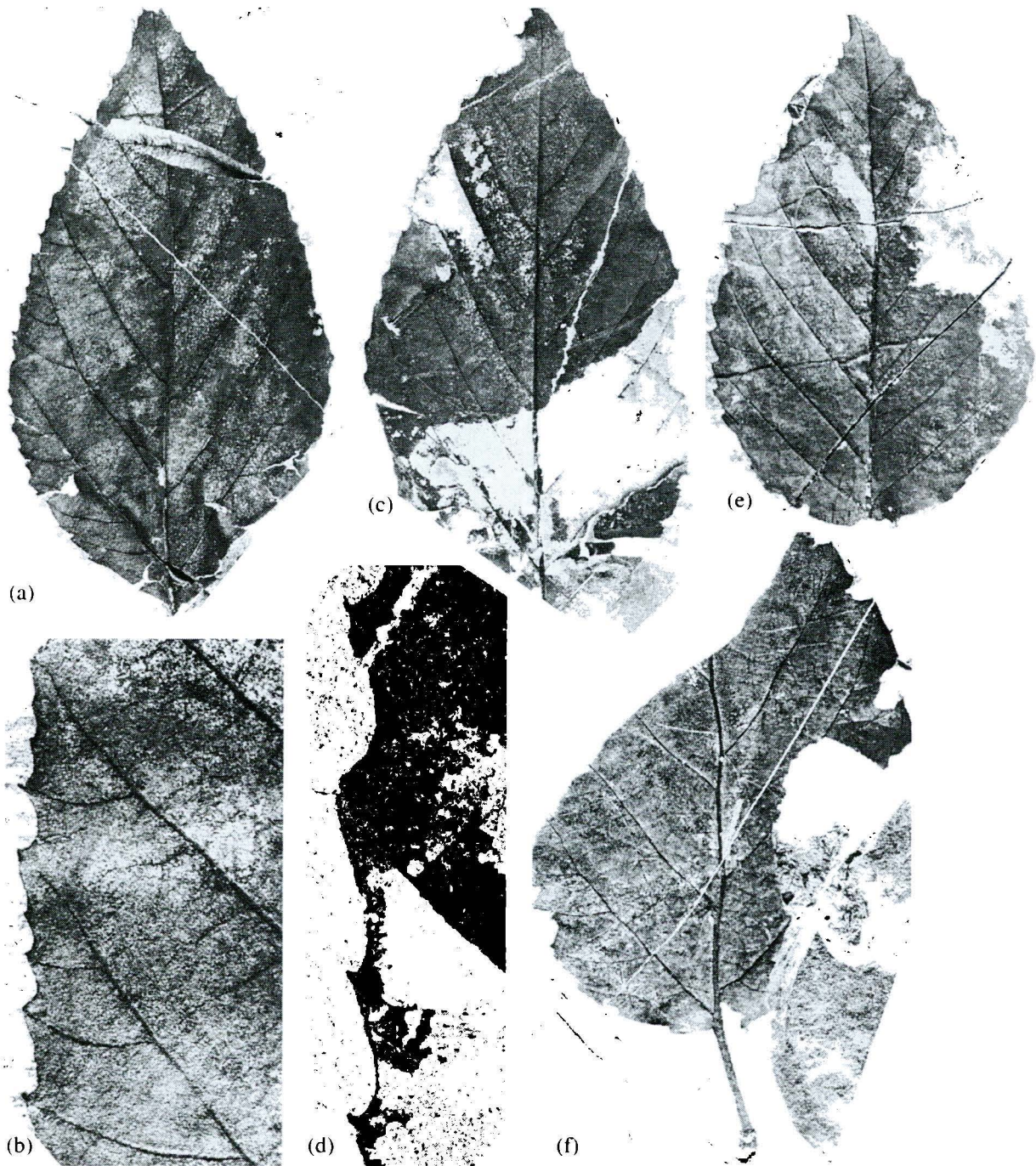


Fig. 33. *Platimeliphyllum snatolense* N. Maslova: (a, b) PIN, no. 4256/350: (a) $\times 1$ and (b) marginal serration, $\times 5$; (c, d) PIN, no. 4256/66: (c) $\times 1$ and (d) marginal serration, $\times 6$; (e) PIN, no. 4256/55, holotype, $\times 1$; and (f) PIN, no. 4256/68, $\times 1$; western Kamchatka, Snatol River; Napana Formation, Upper Paleocene.

tiary veins are very thin, alternate, three or four per 1 cm of the secondary vein length. Venation of higher orders is not defined.

The cuticle is folded, the folds radiate from stomata (Fig. 30c). The stomata are anomocytic, with five or six subsidiary cells. The upper leaf surface bears rounded glands (Fig. 30d).

Comparison. The species *Platimeliphyllum palanense* differs from other species of this genus described below by the presence of leaves with naked bases of basal veins, the better defined asymmetry of the base and leaf blade, and the teeth varying in shape and size.

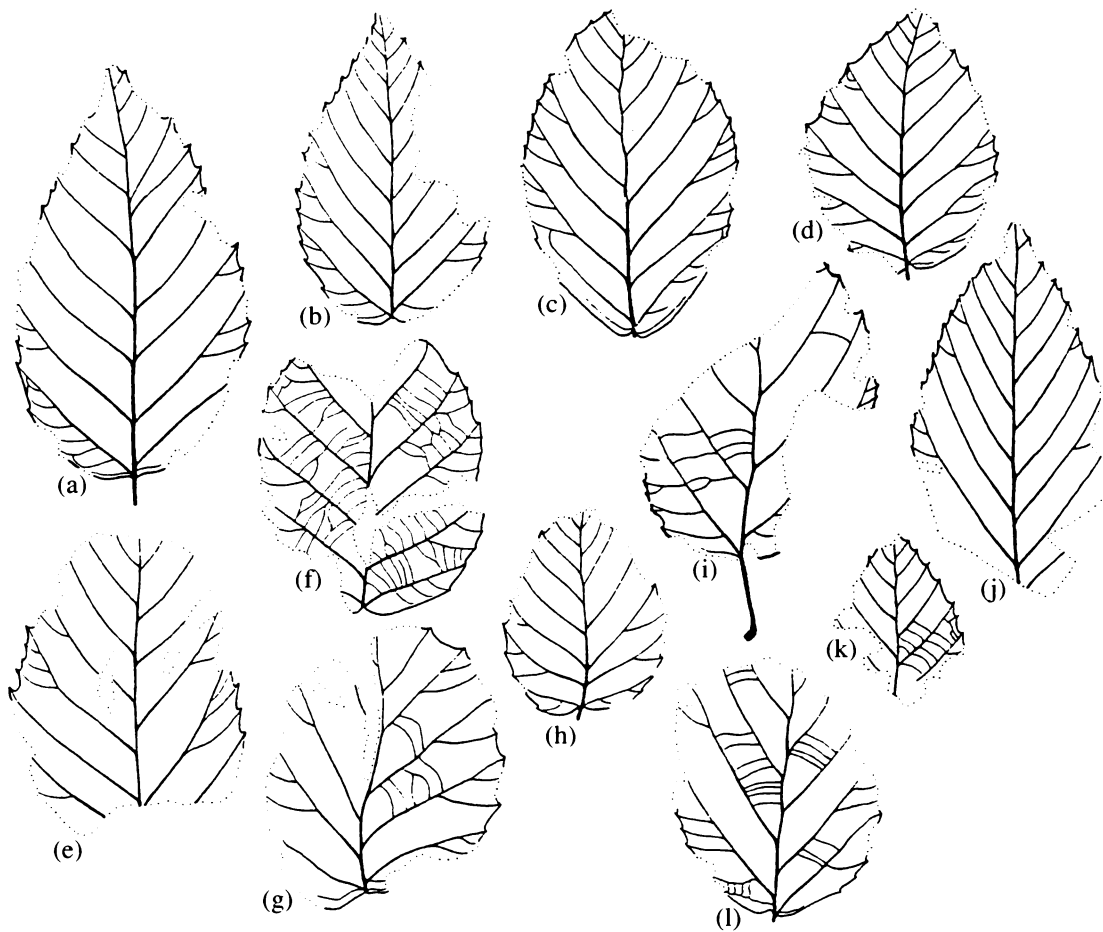


Fig. 34. *Platimeliphyllum snatolense* N. Maslova, $\times 0.5$: (a) PIN, no. 4256/23; (b) PIN, no. 4256/55, holotype; (c) PIN, no. 4256/62; (d) PIN, no. 4256/10; (e) PIN, no. 4256/15; (f) PIN, no. 4256/65; (g) PIN, no. 4256/27; (h) PIN, no. 4256/82; (i) PIN, no. 4256/68; (j) PIN, no. 4256/66; (k) PIN, no. 4256/49; and (l) PIN, no. 4256/24; western Kamchatka, Snatol River; Napana Formation, Upper Paleocene.

Remarks. The leaves from the Chemurnaut Bay and Evravavayam River localities associate with the reproductive structures of *Chemurnautia staminosa*.

Occurrence. Western Kamchatka Peninsula: Chemurnaut Bay, upper part of the Kamchik–lower part of the Tkaprovyayam Formation, Upper Paleocene–Lower Eocene; section between the capes Rebro and Getkilnin, Tkaprovyayam Formation, Upper Paleocene–Lower Eocene; Evravavayam River, Tkaprovyayam Formation, Upper Paleocene–Lower Eocene.

Material. Seventy-one specimens from the section between the capes Rebro and Getkilnin and the Evravavayam River in the Kamchatka Peninsula.

Platimeliphyllum snatolense N. Maslova

Platimeliphyllum snatolense: Maslova, 2002a, p. 95, text-figs. 2i, 3a–3h.

Description (Figs. 33a–33e, 34a–34l). The leaves are simple, entire, and petiolate. The petiole is up to 2 cm long and widens basally. The leaf blade is oval,

the maximal length is 12 cm, the width is 8 cm. The length/width ratio of the leaf blade is 1.5–1.6. The base is rounded, occasionally slightly asymmetrical, the apex is acuminate. The leaf margin is toothed. The teeth are small, acute, concave-concave, four teeth occur per 1 cm of leaf margin.

The venation is pinnate. The midvein is straight, occasionally sinuous in the upper part of the leaf. The basal veins are as thick as the first pair of secondary veins, deviate above the leaf blade base, more often they are opposite and reach one-third (or less) of the leaf blade length. There are up to seven basisopic deviations. They are thin, end in marginal teeth or thin and disappear near the leaf margin. The basal vein occasionally connects with the nearest secondary vein (Fig. 34c). Below the point of basal vein deviation, there are one or two thin infrabasal veins. The secondary veins form up to seven pairs. They are thin, arch-shaped, the lower pair has up to four thin basisopic branches, the subsequent veins also branch two or three



Fig. 35. *Platimeliphyllum denticulatum* N. Maslova, $\times 1$: (a) PIN, no. 3858/12; (b) PIN, no. 4252/26; (c) PIN, no. 3858/1; (d) PIN, no. 4252/7; and (e) PIN, no. 4252/16; (a, c) western Kamchatka Peninsula, Anadyrka River; Tigil Group, Middle? Eocene; (b, d, e) southern Sakhalin Island, Krasnoyarka River Basin; Naiba Formation, Middle Eocene.

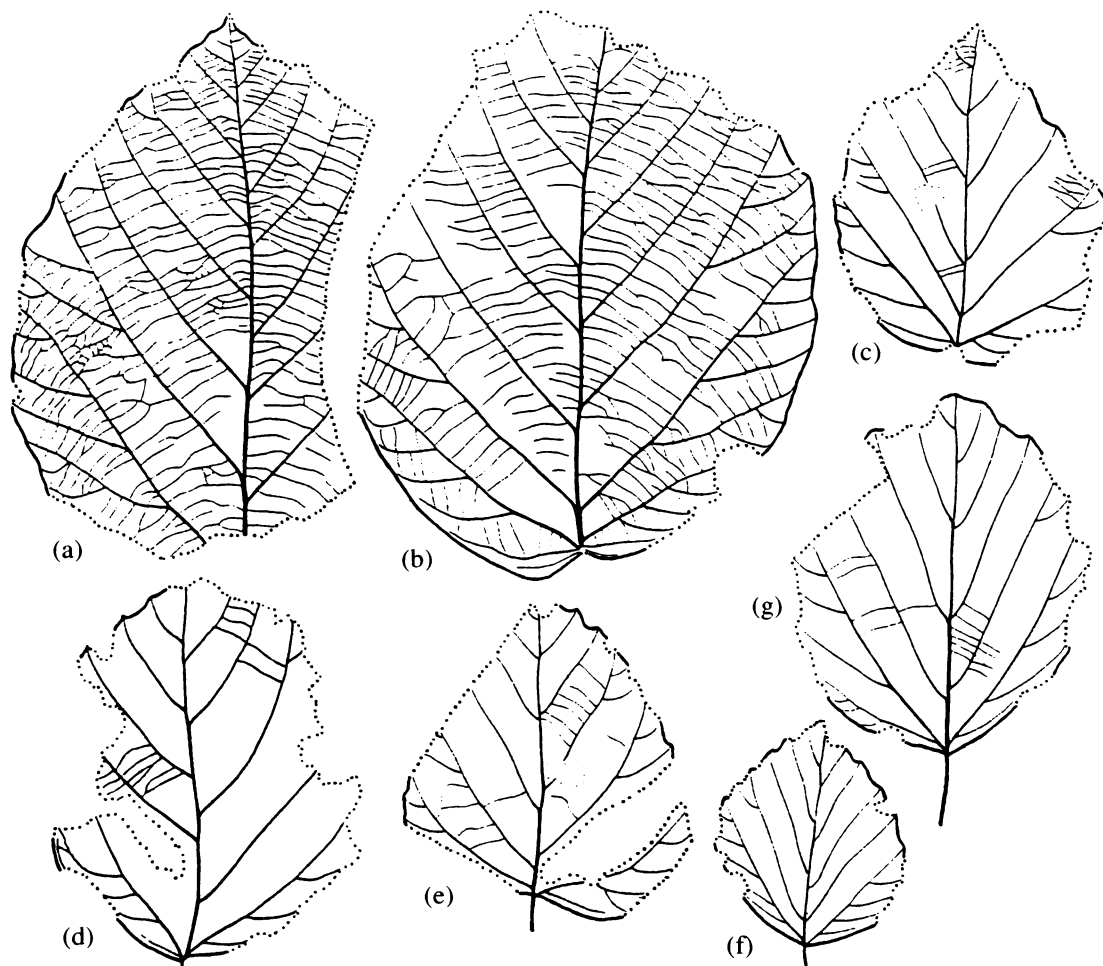


Fig. 36. *Platimeliphyllum denticulatum* N. Maslova, $\times 0.5$: (a) PIN, no. 3858/4; (b) PIN, no. 3858/15b; (c) PIN, no. 4252/18; (d) PIN, no. 3858/19; (e) PIN, no. 4252/49; (f) PIN, no. 4252/7; and (g) PIN, no. 4252/26; (a, b, d) western Kamchatka Peninsula, Anadyrka River; Tigil Group, Middle? Eocene; (c, e, f, g) southern Sakhalin Island, Krasnoyarka River Basin; Naiba Formation, Middle Eocene.

times. The tertiary veins are thin, branching or alternate. The venation of higher orders is a reticulum of polygonal meshes, in which forked endings disappear.

Comparison. The species differs from other species of the genus in the smaller, predominantly symmetrical leaves, the maximal length/width ratio of the leaf blade, the shorter distance reached by basal veins, and the denser teeth.

Material. Thirty specimens from the type locality.

Platimeliphyllum denticulatum N. Maslova

Platimeliphyllum denticulatum: Maslova, 2002a, p. 96, text-figs. 2j, 4a–4h.

Description (Figs. 35a–35e, 36a–36g). The leaves are simple, entire, and petiolate. The length of the petiole reaches 2.5 cm. The leaf blade is oval with a length/width ratio equal to 1.1–1.3 (rarely up to 1.5). The maximal length and width of the leaf blade is 16 and 12 cm, respectively. The base of the leaf blade is

rounded, truncated, occasionally asymmetrical. The apex is slightly acuminate. The leaf margin is toothed in the upper part of the leaf and entire or slightly undulate in its lower part. The teeth are low, triangular, and end with a prominent vein.

The venation is pinnate. The midvein is straight or slightly sinuous, with a maximal thickness in the lower third of the leaf. The basal veins exceed one-third of the leaf blade length. They are arch-shaped, thin, opposite, form up to six basisopic branches. Occasionally, uneven development of the basal veins is observed. One of them is shorter, only approaches the height of the second basal vein and forms a loop with the first secondary vein (Fig. 35a). In this case, the secondary vein is better developed than its pair vein and gives rise to numerous (up to six) basisopic deviations. There are five pairs (more rarely up to seven pairs) of secondary veins. They are thin and arch-shaped, only the first pair forms up to three branches, the other veins do not branch or occasionally form a single weak branchlet.

The tertiary venation is dense, there are up to five (more often three or four) veins per 1 cm of secondary vein. The tertiaries are alternate, occasionally branching. They are connected by numerous anastomoses.

Comparison. This species is distinguished from other species of this genus by having the smallest length/width ratio of the leaf blade, rare low triangular spiny teeth, and more distinct tertiaries.

Occurrence. Western Kamchatka Peninsula: Anadyrka River, Tigil Group, Middle? Eocene. Southern Sakhalin Island: Krasnoyarka River Basin, Naiba Formation, Middle Eocene.

Material. Seventeen specimens from the Anadyrka River locality (Kamchatka Peninsula) and 11 specimens from the Krasnoyarka River locality (Sakhalin Island).

Genus *Arthollia* Golovneva et Herman

Arthollia anadyrensis N. Maslova, sp. nov.

Etymology. From the Anadyrka River.

Holotype. PIN, no. 3858/30, impression of the lower leaf part; northwestern Kamchatka Peninsula, Anadyrka River, Tigil Group, Middle? Eocene; Figs. 37e and 40e.

Diagnosis. Entire leaves with prominent petiole. Leaf blade broadly oval maximally thick in lower third. Apex acuminate, base truncate with naked veins to cordate. Leaf margin toothed. Teeth small, frequent, concave-concave, ending with gland. Basal veins form seven to nine basispic deviations, some of them with one or two branches ending in teeth. Secondary veins in seven to nine pairs with four or five lower pairs branching. Tertiary veins alternate, branching near leaf margin, and ending in teeth.

Description (Figs. 37b–37e, 38a–38d, 39a–39b, 40a–40e). The leaves are entire and broadly oval (to nearly triangular). The maximal thickness of the leaf blade is situated in its lower half. The pedicel is prominent, more than 4 cm long in large specimens. The leaf base is truncate with naked veins to deeply cordate. The apex is abruptly narrowing, acuminate. The leaf margin is toothed. The leaf base is virtually devoid of teeth, the first teeth in the basal region are more widely spaced. They develop on the endings of branching infrabasal veins or on the lower basispic branch of the basal vein. The teeth are densely spaced in the middle leaf region. The teeth are small, varying from typically concave-concave with a longer basal side to low triangular. The teeth apices are acute or rounded, ending with a gland.

The midvein remains as thick as the petiole from the leaf base to the point of deviation of the second pairs of secondary veins, subsequently it quickly thins, especially in the apical region. The midvein shows some undulations in the upper leaf part, being straight elsewhere. The basal veins are arch-shaped and deviate

suprabasally, within a limited distance from the leaf blade base, or basally (in this case the basal veins are slightly naked at their beginning). They do not exceed one-third of the leaf blade length and give rise to seven to nine basispic deviations, which in turn branch one or two times and end in teeth. Where the basispic branches fork, the basal veins appear broken. There are one or two thin sinuous infrabasal veins.

There are seven to nine pairs of secondary veins. They are arch-shaped, the lower pair of the secondary veins are opposite, the majority of subsequent veins are also opposite. The distance between the point of basal vein deviation and the first lower pair of secondary veins is shorter than the subsequent interspaces between the secondary veins. In the upper third of the leaf blade, the secondary veins do not branch. In the lower and central parts they branch two or three times. There are three or four tertiaries per 1 cm of secondary vein. They are alternate, slightly curve centrally, occasionally branching. Near the leaf margin the tertiaries can form perpendicular deviations entering a tooth.

The cuticle has been prepared to show epidermal features. The cuticle is relatively thick and folded, the folds radiate from stomata, boundaries between cells are weakly defined. The stomata are $40 \times 20 \mu\text{m}$ in size, surrounded by five subsidiary cells. The stomatal aperture is elliptical, the subapertural ring is thickened (Fig. 38d).

The epidermis of the petiole is composed of elongate cells up to $60 \mu\text{m}$ long and about $10 \mu\text{m}$ wide, the angles of the cells are acute. Stomata are absent. The hair bases are numerous and rounded, their diameter is $7\text{--}10 \mu\text{m}$ on average (Fig. 38c).

Comparison. The species resembles the Late Cretaceous *Arthollia pacifica* Herman (Herman and Golovneva, 1988). It differs in the smaller length/width ratio of the leaf blade, in the slightly smaller distance from the leaf base to the point of basal vein deviation in the case of suprabasal venation, and the more prominent petiole in the lower part of the midvein.

Remarks. The type species *A. pacifica* comes from the middle and upper parts of the Valizhgenskaya Formation of the Konglomeratovyi Cape (northwestern Kamchatka Peninsula) and the Elistratov Peninsula (western coast of the Penzhinskaya Bay) of the Turonian–Coniacian age. *A. anadyrensis* sp. nov. exhibits a distinct similarity with the type species. The authors of the genus discussed the possible affinity of *Arthollia* to the family Platanaceae but finally placed the genus within a conventional group, platanaceous plants, because of the absence of microstructural information. The epidermal morphology of the new species displays characters of the modern plane tree and some extinct members of the Platanaceae. These data as well as available information on leaf macromorphology provide strong evidence for the assignment of the genus *Arthollia* to the Platanaceae.

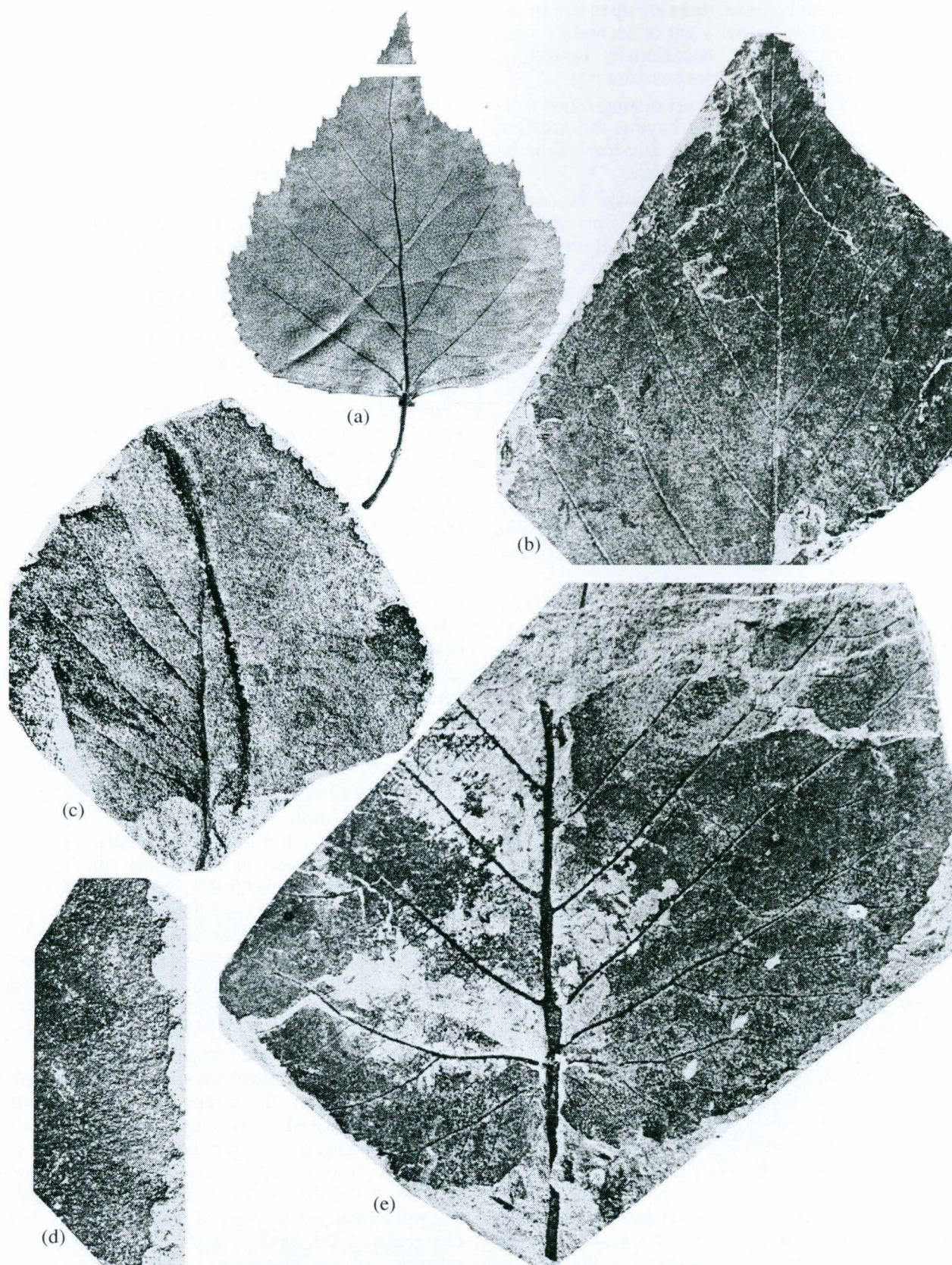


Fig. 37. (a) *Betula platyphylla* Sukacz. extant species for comparison, $\times 1$; (b–e) *Arthollia anadyrensis* N. Maslova, sp. nov.: (b) PIN, no. 3858/28, $\times 1$; (c, d) PIN, no. 3858/17: (c) $\times 1$ and (d) marginal serration, $\times 2$; and (e) PIN, no. 3858/30, holotype, $\times 1$; (b–e) western Kamchatka Peninsula, Anadyrka River; Tigil Group, Middle? Eocene.

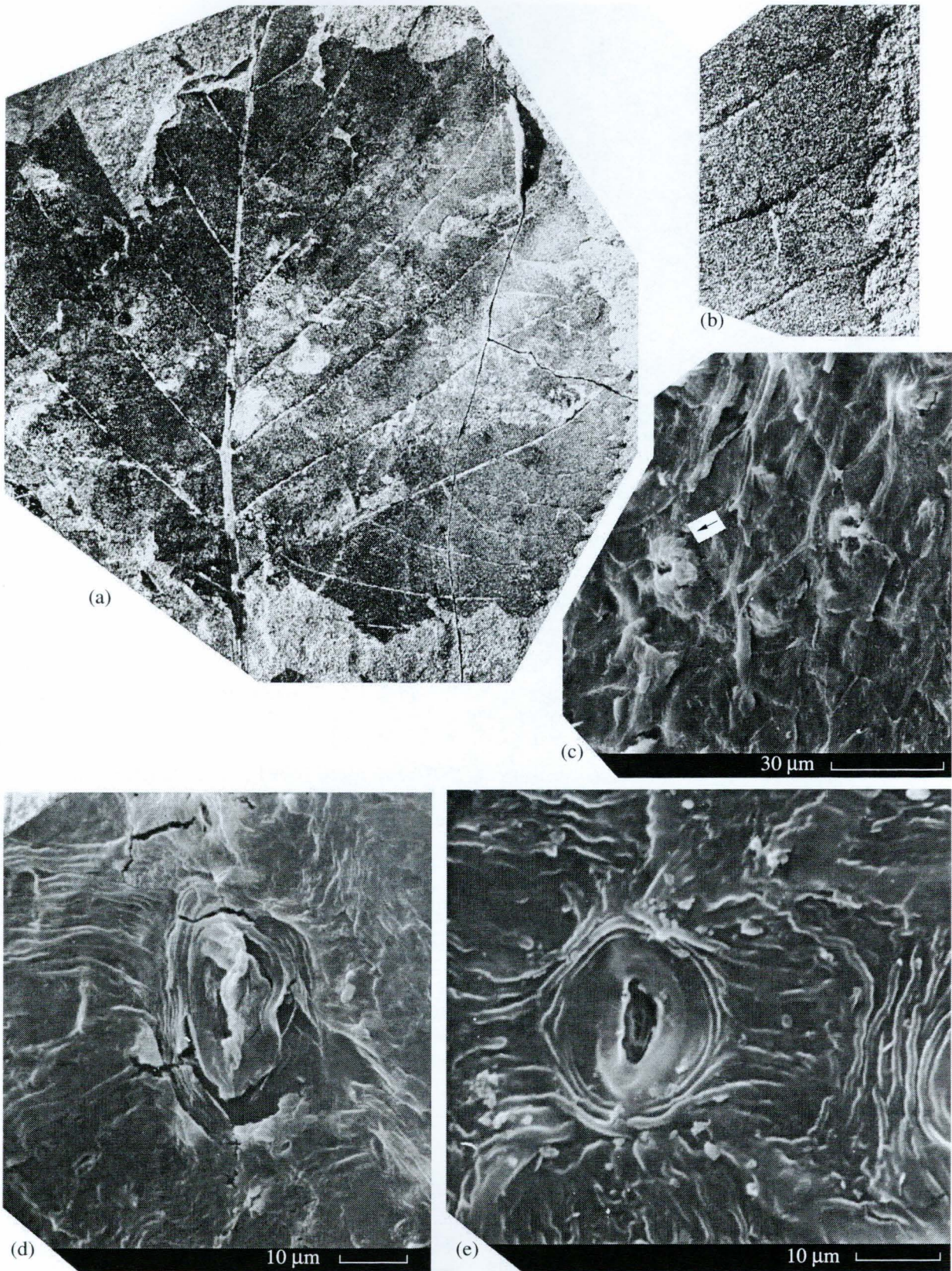


Fig. 38. *Arthollia anadyrensis* N. Maslova, sp. nov.: (a, b) PIN, no. 3858/7: (a) $\times 1$ and (b) marginal serration, $\times 2$; (c, d) PIN, no. 3858/30: (c) epidermis of petiole, note hair bases (arrow), SEM and (d) stoma, cuticular folds are seen, SEM; and (e) *Platanus occidentalis* L., extant species, stoma for comparison, SEM; (a–d) western Kamchatka Peninsula, Anadyrka River; Tigil Group, Middle? Eocene.



Fig. 39. *Arthollia anadyrensis* N. Maslova, sp. nov., PIN, no. 3858/31: (a) $\times 1$ and (b) marginal venation, $\times 3$; western Kamchatka Peninsula, Anadyrka River; Tigil Group, Middle? Eocene.

Of interest is the morphological similarity between leaves of *Arthollia* and those of some members of the Betulaceae. *A. anadyrensis* sp. nov. resembles modern *Betula platyphylla* Sukacz. in the leaf blade shape (Fig. 37a). The similarity with this species also includes the truncate leaf base and teeth morphology. Naked bases of basal veins are observed in *Betula maximovieziana* Rgl. Branches of tertiary veins ending in marginal teeth are a distinctive character of the genus *Alnus* and are also observed in *Arthollia anadyrensis* sp. nov.

Material. Five specimens of different preservation from the type locality.

FAMILY HAMAMELIDACEAE R. BROWN

Taxa Established on the Basis of Reproductive Structures

Genus *Viltyungia* N. Maslova

Type species. *Viltyungia eclecta* N. Maslova.

Species composition. Type species.

Comparison. Unlike *Viltyungia*, the Late Cretaceous genus *Archamamelis* (Endress and Friis, 1991) has bisporangiate anthers, dehiscing inside by two valves, well-developed rounded extension of the connective, and typically tricolpate pollen with a distinct reticulum. *Allonia* from the Campanian of the United

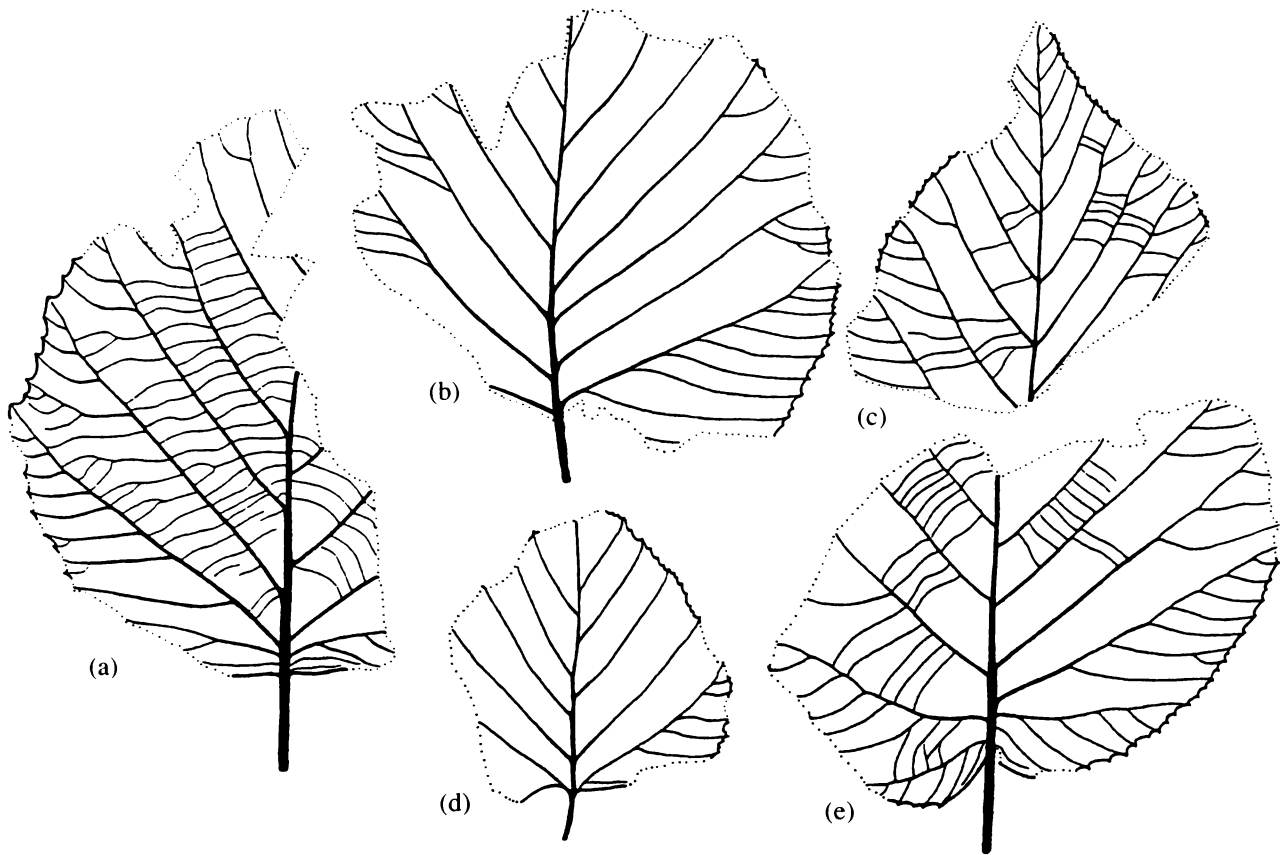


Fig. 40. *Arthollia anadyrensis* N. Maslova, sp. nov., $\times 0.5$: (a) PIN, no. 3858/31; (b) PIN, no. 3858/7; (c) PIN, no. 3858/28; (d) PIN, no. 3858/17; and (e) PIN, no. 3858/30, holotype; western Kamchatka Peninsula, Anadyrka River; Tigil Group, Middle? Eocene.

States (Magallón-Puebla *et al.*, 1996) has tetrasporangiate anthers opening outside with two valves, massive hornlike extension of the connective, pollen with short colpi, and a coarse reticulum. The male heads described from the Turonian (Raritan Formation, New Jersey, Crepet *et al.*, 1992) are characterized by anthers dehiscing by valves and elongate pollen grains with apertures nearly reaching the poles. The male capitate inflorescences from the Clarno Formation of the Eocene of Oregon have flowers with an abortive gynoecium, ten stamens and staminodes, and a differentiated perianth of five narrow petals and five sepals the external epidermis of which is covered by stellate hairs (Manchester, 1994).

Vilyungia eclectic N. Maslova

Vilyungia eclectic: Maslova and Golovneva, 2000b, p. 41, pl. 6, figs. 1–6; text-figs. 1–3.

Description (Figs. 41a–41g, 42a–42d, 43a–43d). The preserved part of the inflorescence is a stout axis 37 mm long, 2 mm thick, bearing two complete heads and fragments of two poorly preserved heads. The heads are spherical, 10–11 mm in diameter, sessile, at a distance of 4 mm from each other.

The head consists of a central receptacle that is 3–4 mm in diameter and bears radially disposed, variously compressed deformed flowers (Figs. 41b, 41c). The receptacle is covered with rounded scars of shed flowers, about 0.5 mm in diameter. The flowers are 4 mm long, some of them show protruding slender styloides visible through a binocular microscope.

The total number of flowers per head is difficult to establish; the surface of the impression shows six or seven flowers, the most probable value is 12. In compressed heads the boundaries of individual flowers are indistinct, thus preventing the determination of the number of floral members. Each flower contains a massive gynoecium and several stamens and staminodes (Fig. 42a). The stamens are partly preserved as stumps of broken filaments concentrically disposed around the gynoecium; there are three stamens on the visible side of the flower, the most probable total number of stamens is six. The perianth members are preserved as small pads of tissue between the flowers. The morphology of the floral members was studied in macerated fragments of the compression transferred to a varnish film.

The microstructure of individual floral members was studied with SEM. The perianth members are broadly elliptical, at least 330 μm long, 470–500 μm wide, and densely covered with hairs, which are 20–25 μm long (Figs. 41d, 41g).

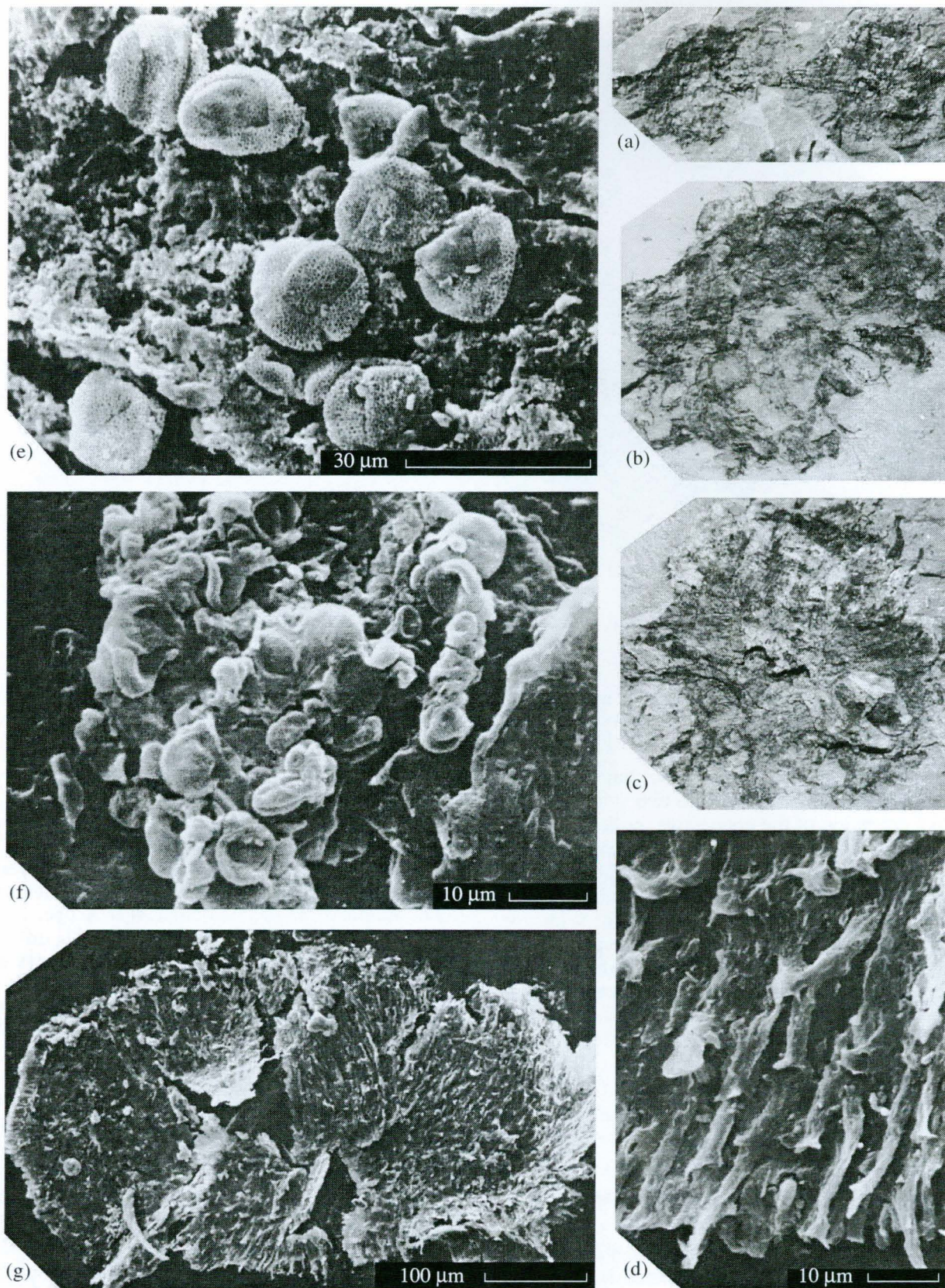


Fig. 41. *Vilyungia eclectic* N. Maslova, BIN, no. 1181-3-585, holotype: (a) $\times 1$; (b, c) $\times 2.5$; (d) hairs of perianth member, SEM; (e) aggregation of fertile pollen, SEM; (f) aggregation of pollen from staminodes; and (g) perianth member, SEM; eastern Siberia, Lena-Vilyui Depression, Tyung River; Timerdyakhskaya Formation, Cenomanian.

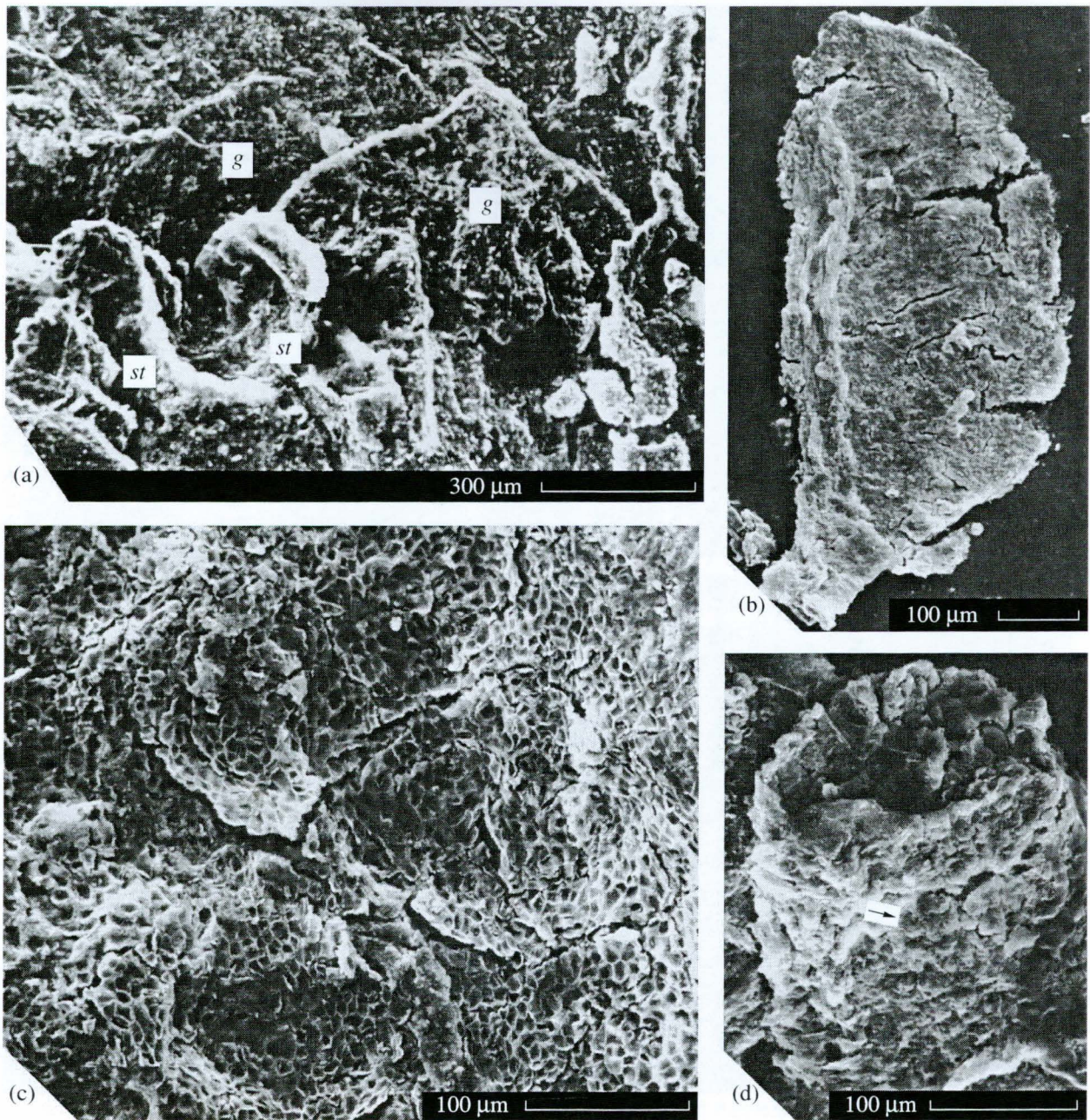


Fig. 42. *Viltyungia eclectic* N. Maslova, SEM, BIN, no. 1181-3-585, holotype: (a) floral members, note (g) bicarpellate gynoecium and (st) stamens; (b) anther; (c) inner epidermis of carpel, vestiges of developing ovules are seen; and (d) fragmentary stylode, papillae are seen (arrow); Eastern Siberia, Lena–Vilyui Depression, Tyung River; Timerdyakhskaya Formation, Cenomanian.

The stamens surround a more massive gynoecium, some of them were removed from the inflorescences. The stamen filament is short, about 100 µm long and 80 µm thick. The anthers are tetrasporangiate, two thecae are connected by a well-defined connective extending along the entire length of the anther but devoid of an extension. The anther is 600–650 µm long and 200–230 µm wide in the central part and crescent-shaped. Dorsally, the theca is convex, showing a slightly curved dehiscence line (Fig. 42b).

The anther opens through a longitudinal slit. The inner surface of the dehiscid anther is covered with small epidermal cells (approximately 5×10 µm), arranged in transverse rows. A longitudinal strand of cells situated along the central axis of the anther locule supposedly marks the position of the median septa that was dissolved before dehiscence. The dehiscid anther and the surface of closed thecae bear both individual pollen grains and pollen masses in the ventral region.

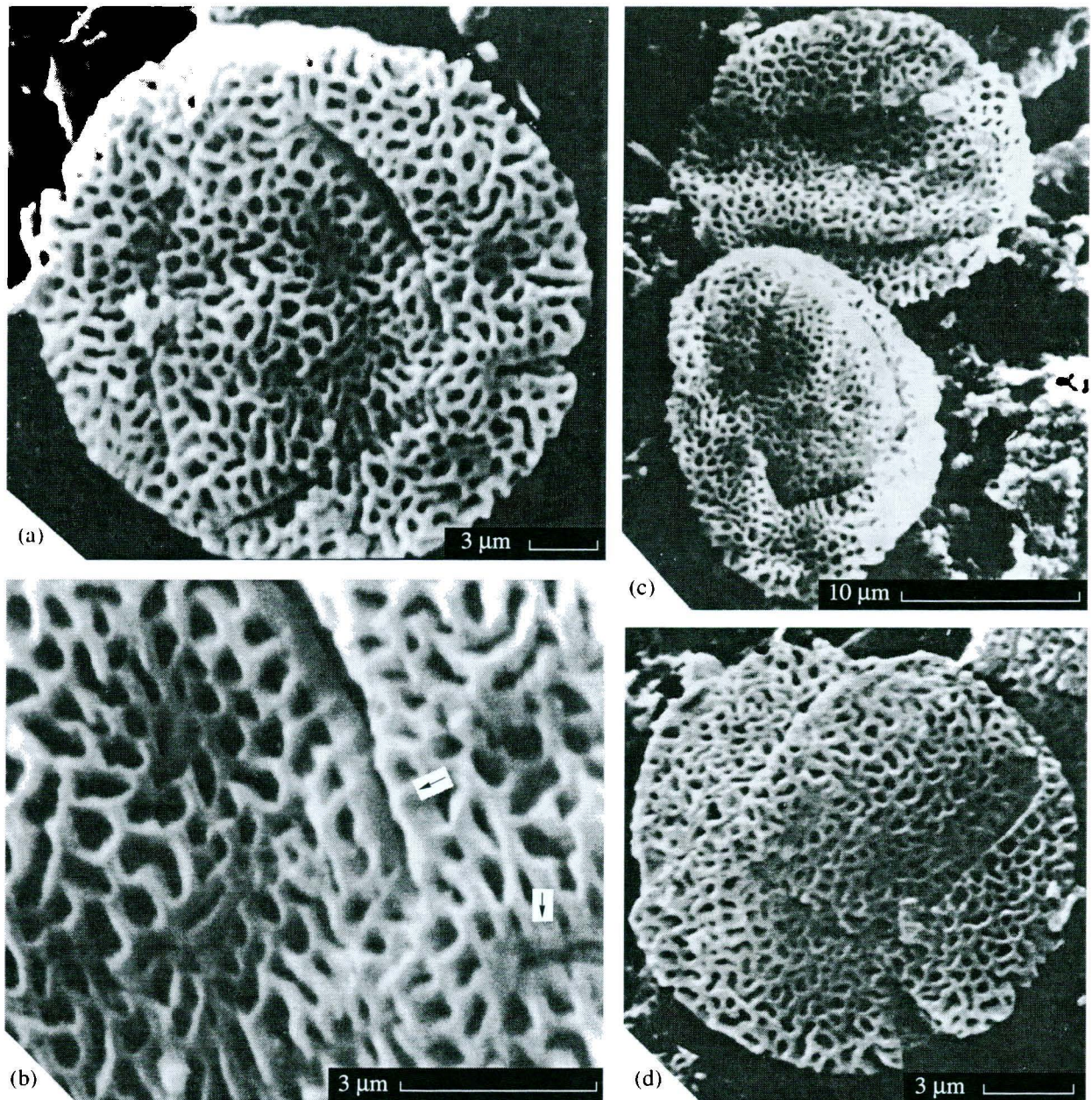


Fig. 43. *Vilyungia eclecta* N. Maslova, SEM, BIN, no. 1181-3-585, holotype: (a, c, d) morphology of pollen grains; (b) reticulate exine of the pollen grain (Fig. 43a), various meshes and distinct margins of colpi are seen: Eastern Siberia, Lena-Vilyui Depression, Tyung River; Timerdyakhskaya Formation, Cenomanian.

The pollen grains are predominantly solitary, some of them form tetrads in which one grain is slightly smaller than the other three. Typically, pollen grains are nearly circular in the polar view and elliptical in equatorial view, $16 \times 19 \mu\text{m}$. The three meridian colpi are about $3 \mu\text{m}$, occasionally up to $5 \mu\text{m}$ wide, gradually tapering toward the poles, wedging out before the poles (Fig. 43d). The apocolpium is finely granulate. The margin of the colpus is distinct, formed by a well-defined thread, which is surrounded by smaller meshes (Fig. 43b). The mesocolpium is $10\text{--}12 \mu\text{m}$ wide. The

exine is reticulate. The meshes of the reticulum vary from rounded (not more than $0.5 \mu\text{m}$ in diameter) and elongate (0.5×1.0 ($1.5 \mu\text{m}$ in size) to falcate or S-shaped (Fig. 43b).

In the polar region there are additional rugae oriented parallel to the equator (Figs. 43a, 43c). Usually they are three, their margins are close to each other, sometimes the margins join to form a close triangular contour. The rugae are superficial, the apocolpium is virtually lacking. Their margins are distinct and identical to those of main colpi.

In addition to the stamens with typical pollen grains, some staminate structures contain relatively small pollen grains with an indistinct reticulum. Such pollen occurs as dense masses rather than individual grains (Fig. 41f). These structures may be interpreted as staminodes.

The gynoecium consists of two carpels and can be seen in longitudinal sections. The external cuticle consists of randomly arranged cells of different shapes, which vary from nearly isometric polygonal to elongate, nearly rectangular. The mean length is 8–10 μm ; the maximal length is 15 μm . Oval, occasionally rounded, hair bases (12 \times 8 μm) are distinguishable in the epidermis structure.

The inner cuticle of the carpel is composed of rectangular to square cells 5 \times 10 μm to 5 \times 5 μm , respectively. The inner walls of the ovary show vestiges of growing ovules (Fig. 42c). These are at least seven elliptical bodies 100 \times 120 μm in size, alternately disposed in two rows. As in many primitive angiosperms, the growing ovules were obviously appressed upon the locule, thus leaving marks on the inner cuticle.

Remarks. The reproductive structures of *Viltyungia* are most similar to those of the genera *Chunia*, *Exbucklandia*, and *Disanthus* (Exbucklandioideae). *Viltyungia* resembles *Exbucklandia* in having capitate inflorescences of 8 to 13 bisexual flowers with a well-developed perianth (Chang, 1948; Kaul and Kapil, 1974). The number of ovules per ovary in these four genera of the Exbucklandioideae is five to eight and is comparable with that of *Viltyungia*. In the shape and dehiscence of the anthers, *Viltyungia* most closely resembles *Disanthus*. The palynomorphology of *Viltyungia* is closer to that of the genus *Chunia*.

Viltyungia closely resembles the Altingioideae in the inflorescence shape, number of flowers per head, hairs of the ovary, presence of staminodes, and numerous ovules; however, the genera of this subfamily are characterized by heads with functionally unisexual naked flowers and polyporate pollen.

Such characters as bisexual flowers with a well-developed perianth (hairy perianths are known only in the subfamily Hamamelidoideae of extant hamamelids; Bogle, 1970, 1986; Endress, 1989b), anthers dehiscing through a longitudinal slit (*Parrotia*, *Sycopsis*, *Distyliopsis*, *Distylium*; Endress 1989b), and additional apertures in pollen grains (*Sycopsis* and *Distylium*) make *Viltyungia* closer to members of the Hamamelidoideae.

Material. Holotype and its counterpart.

Genus *Lindacarpa* N. Maslova

Type species. *Lindacarpa pubescens* N. Maslova.

Species composition. Type species.

Comparison. This genus differs from the macromorphologically similar capitate inflorescences of the extant *Platanus* and fossil platanoids in the gynoecial

structure of two carpels that form a syncarpous semi-inferior ovary. It differs from altingioid fructifications in having a perianth. In particular, *Evacarpa* (Maslova and Krassilov, 1997) shows typically altingioid characters: the perianth is lacking, while the intrafloral phyllomes and staminodes are relatively well preserved. The capitate inflorescences from the Turonian (Raritan Formation) of New Jersey (Crepet *et al.*, 1992) are much smaller (male heads 1–2 mm, female heads up to 2.7 mm) and the perianth is relatively weakly developed. *Microaltingia apocarpela* differs in the well-developed rounded phyllomes arranged in three circles along the hypanthium margin and in the small tricolpate pollen (Zhou *et al.*, 2001).

Lindacarpa pubescens N. Maslova

Lindacarpa pubescens: Maslova and Golovneva, 2000a, p. 103, pl. XII, figs. 1–6, text-fig. 2.

Description (Figs. 44a–44f, 45a–45d). A detached pistillate head is preserved as an impression with a fragmentary phytollemma. The head is 19 mm in diameter, with a massive receptacle 5.5 mm in diameter that bears crowded, radially disposed floral units at different developmental stages, some perhaps at the fruiting stage, with persistent perianths (Fig. 44a). The boundaries between individual flowers can only occasionally be seen in a light microscope. There are about 30 flowers in total. The rounded scars of the receptacle have been left by shed flowers.

SEM examination has revealed details of microstructure. The isolated fruits are broadly cuneate, 7 mm long, distally up to 2 mm broad, with a conspicuous conical base. They are enveloped in perianth members that are attached at a height of about 0.8 mm above the base (Fig. 44d). The outer perianth members are connate almost over their entire length, thus forming a distally lobed tube. The thinner inner members of the perianth are seen inside the tube (Fig. 44f). They differ from the outer members in their epidermal structure.

The gynoecium is seen in longitudinal splits of perianths and in transverse cuts of flowers. In lateral view (Fig. 44c) the carpels diverge about 1.7 mm above the base. The ovary is syncarpous along about one-fourth of its length. Free parts of carpels are adnate for some distance and flare only near the very apex. An ovary transversely cut near the base (Fig. 44e) shows locules that are elongate-rhomboid or elliptical and vary in width. Stylodes are lacking.

The epidermis of the carpels consists of irregularly arranged isodiametric cells of irregular shapes, about 10–15 μm wide. Along the contact surface of the carpels the walls of epidermal cells are folded. The hair bases are irregularly scattered all over the surface, occasionally forming fascicles of three hairs (Fig. 45a).

The external epidermis of the outer perianth members consists of isodiametric tabloid cells 10–15 μm wide, with a pitted periclinal wall, disposed in distinct longitudinal rows (Fig. 45b). The abaxial cuticle of the

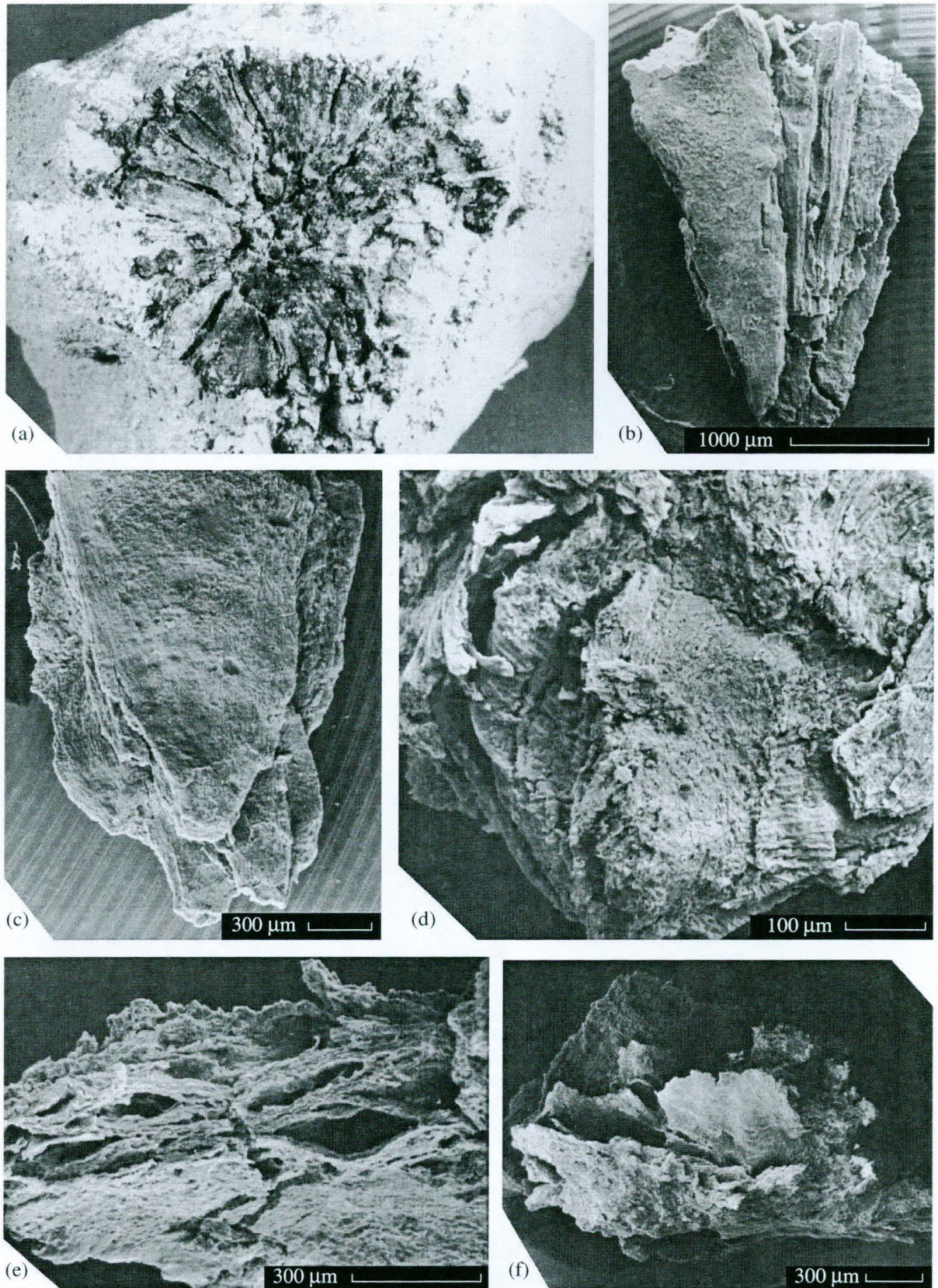


Fig. 44. *Lindacarpa pubescens* N. Maslova, BIN, no. 1196-20-62: (a) $\times 4$; (b) individual flower with a longitudinally split floral tube, gynoecium is seen, SEM; (c) several flowers with protruding bases of ovaries, SEM; (d) ovary base with attached perianth members, underside view, SEM; (e) transverse section of the bicarpellate gynoecium surrounded by perianth members, SEM; and (f) fragment of perianth, inner members are seen, SEM; Eastern Siberia, Lena–Vilyui Depression, Linda River; Chirimyskaya Formation, Coniacian.

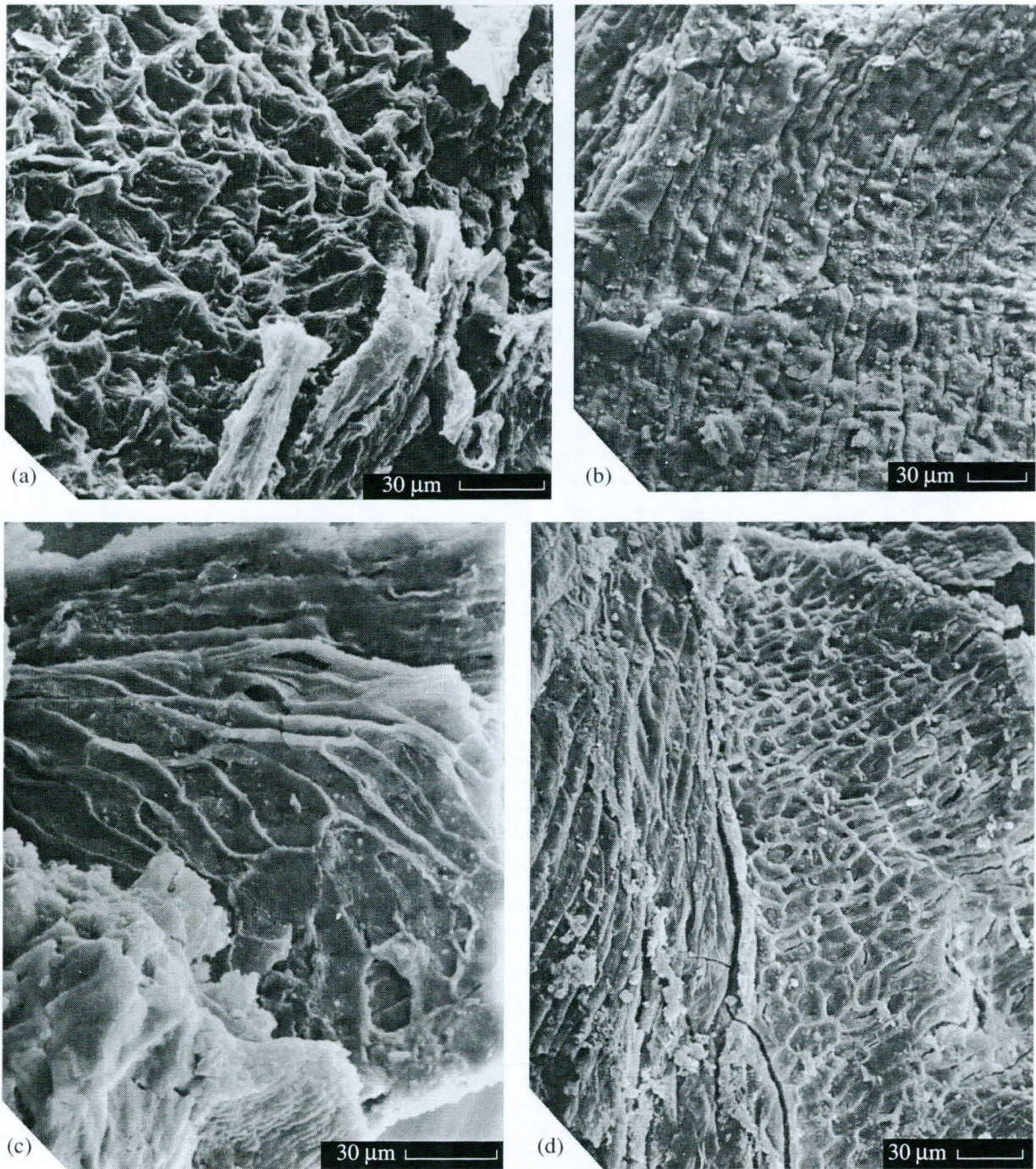


Fig. 45. *Lindacarpa pubescens* N. Maslova, SEM, BIN, no. 1196-20-62: (a) carpel epidermis with preserved hairs; (b) upper epidermis of external perianth members; (c) adaxial epidermis of members of the inner perianth circle; and (d) abaxial epidermis of members of the inner perianth circle; Eastern Siberia, Lena–Vilyui Depression, Linda River; Chirimyiskaya Formation, Coniacian.

inner tepals is composed of irregular polygonal cells, which are 20–30 μm long, 10–15 μm wide, and form no distinct rows (Fig. 45d). Their adaxial epidermis consists of larger polygonal cells of variable dimensions, 40–80 μm long, 5–30 μm wide. The isolated relatively small rounded-elliptical cells apparently represent remains of hair bases (Fig. 45c).

Remarks. The inflorescences of the Altingioideae are characterized by naked flowers with paired carpels that are fused in the lower part and variously apocarpous in the upper part; diachronous maturation of fruits (completely mature fruits and carpels at early developmental stages occur in one and the same head); presence in pistillate flowers of sterile structures (stamino-

des and intrafloral phyllomes) that were attached in a circle to the base of the apocarpous part of the carpels (semi-inferior ovary); numerous ovules; and shedding stylodes (*Altingia*).

The genus *Lindacarpa* is similar to the extant *Altingia* and *Liquidambar* in the number of flowers per head (which are much more numerous in the Platanaceae) and to the Late Cretaceous *Microaltingia apocarpela*, which has about ten flowers. The variable dimensions of the fruits indicate their diachronous maturation. The gynoeceum of *Lindacarpa* consists of two carpels forming a semi-inferior ovary (perianth members attached above the base of the ovary). These characters are typical of hamamelids.

At the same time, *Lindacarpa* resembles the extant *Platanus* in having a pubescent gynoeceum and is similar to Cretaceous members of the Platanaceae in the well-developed perianth. In contrast, the Altingioideae (with the sole exception of *Altingia excelsa*) lack gynoeceal hairs (Bogle, 1986).

However, the hairy gynoeceum of *Lindacarpa* indicates the early appearance and subsequent extinction of this character in altingioids. The paired carpels of *Lindacarpa* are fully enveloped in a tube of connate tepals of supposed bracteate origin. The inner tepals are morphologically different from the outer tepals. Their epidermal characters are consistent with both a petaloid and bracteate origin. More material is needed to elucidate their development.

The presence in the flowers of *Lindacarpa* of sterile structures (staminodes or phyllomes), which are characteristic of Altingioideae, also remains uncertain. However, even in the extant genera their interpretation is the subject of debate (see Chang, 1962, 1973; Schmitt, 1965; Endress, 1977; Wiśniewski and Bogle, 1982; Bogle, 1986).

Flowers of the extant *Liquidambar* have been shown to be naked. Dichlamideous flowers, as well as flowers with variously reduced perianths, also occur in other hamamelid subfamilies.

The find of a *Lindacarpa* inflorescence suggests the presence of well-developed perianths in early hamamelids and subsequent reduction of this character within this evolutionary line. Thus, the naked flowers of extant *Liquidambar* and *Altingia* appeared secondarily.

Material. Holotype.

Genus *Evacarpa* N. Maslova et Krassilov

Type species. *Evacarpa polysperma* N. Maslova et Krassilov.

Species composition. Type species.

Comparison. Morphologically similar inflorescences occur both in extant and fossil platanoid and hamamelid genera. As a rule, *Liquidambar* and *Altingia* (Altingioideae) have compound bisexual inflorescences, one female head is situated at the base of the main axis bearing several male inflorescences. How-

ever, purely female inflorescences have been observed both in these two genera (Bogle, 1986) and in *Evacarpa*.

The material studied contains only female inflorescences, pollen grains have not been detected on their surface. The absence of pollen is obviously explained by distanced male inflorescences. The staminodes that were present in the head supposedly did not produce pollen. Staminodes as well as intrafloral phyllomes are common in the extant *Altingia* and *Liquidambar*.

The number of flowers per inflorescence makes *Evacarpa* closer to *Altingia*, since *Platanus* and platanoid genera have a greater number of flowers per head. Naked flowers are characteristic of the extant *Altingia* and *Liquidambar* and, apparently, of *Macginicarpa manchesteri* (Pigg and Stockey, 1991), while other fossil platanoids have a variously developed perianth. The gynoeceum of *Evacarpa* shows typically altingioid characters like paired carpels fused in the basal part up to a half of the length, free in the upper part, and having numerous ovules. *Platanus* has a gynoeceum with more numerous (three to nine, more often five to eight) free carpels with one (extremely rarely, two) ovules. Fossil members of the Platanaceae had a constant number of carpels (usually five).

In *Evacarpa*, stylodes shed after the fruit maturation; thus showing an affinity of the genus to *Altingia*. *Liquidambar* and *Platanus* have persisted stylodes in maturing heads.

Evacarpa polysperma N. Maslova et Krassilov

Evacarpa polysperma: Maslova and Krassilov, 1997, p. 70, pls. I–V.

Description (Figs. 46a–46c, 47a–47d). There are several detached capitate inflorescences and one fragment of a main axis with a head attached. The main axis is 1.5 mm thick, has a wide longitudinal scar, and becomes slightly wider near the node. The heads are opposite, with a pedicel 5–7 mm long and 0.5 mm wide, disposed at an angle of 30°–60° to the main axis. The solitary fragment with a preserved axis shows a small opposite bract in a node (Fig. 46a).

The heads are spheroid, 4–5 mm in diameter, with a 1-mm-wide central receptacle, which can be readily seen through a light microscope. The receptacle is surrounded by radial overposing flowers. Individual flowers are not distinguishable in impressions. After maceration, SEM reveals that the heads are either completely mature infructescences or combine mature fruits and variously maturing carpels. The flowers constituting the heads are either easily distinguishable, separated with shallow grooves, or adpressed and indistinct. One hemisphere of the head is composed of eight flowers; thus, the total number of flowers per infructescence is equal to 16.

An individual flower consists of a relatively massive gynoeceum of paired carpels and small scalelike struc-

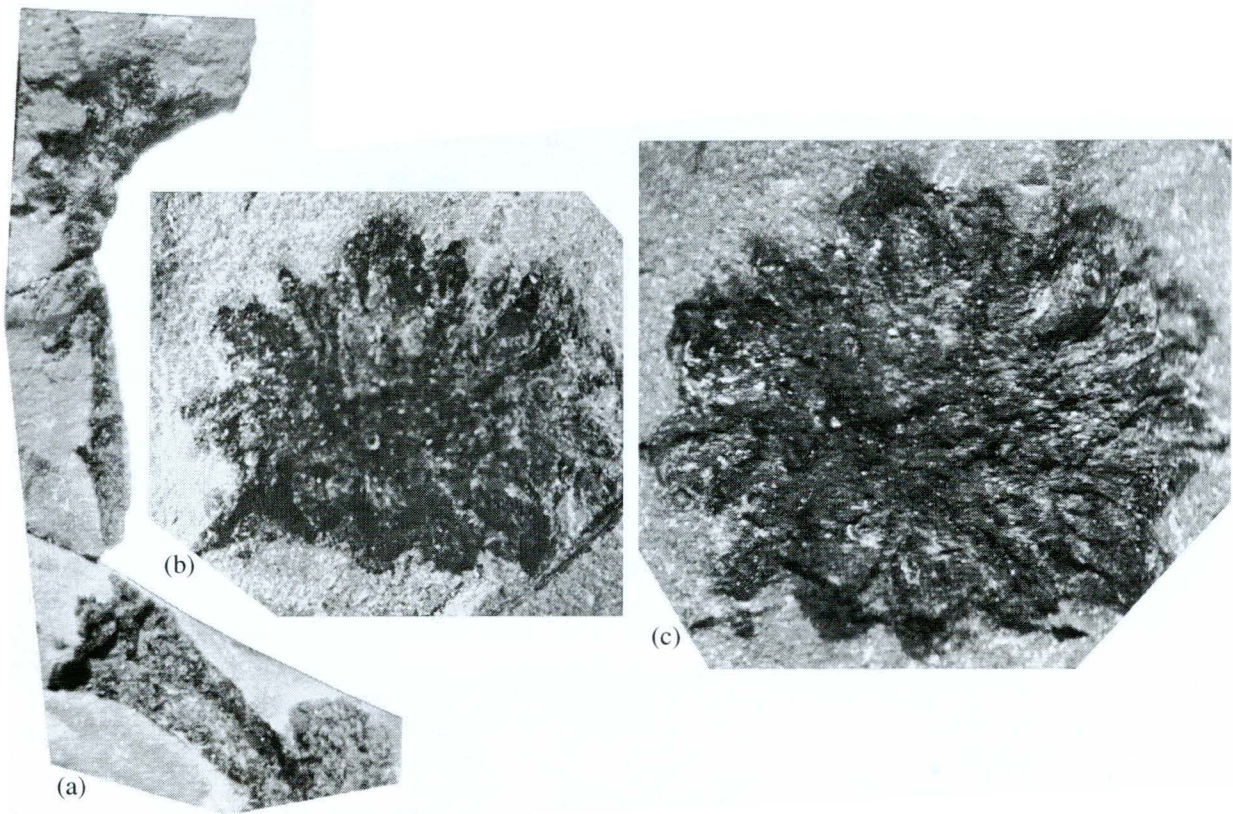


Fig. 46. *Evacarpa polysperma* N. Maslova et Krassilov: (a) PIN, no. 4257/43, inflorescence axis with pedicellate head, $\times 7$; (b) PIN, no. 4257/14, $\times 10$; and (c) PIN, no. 4257/44, holotype, $\times 15$; northwestern Kamchatka Peninsula, section between the capes Rebro and Getkilnin; Tkaprovayam Formation. Upper Paleocene–Lower Eocene.

tures surrounding the gynoecium (Fig. 47a). Some of them are larger than others, 0.6 mm long and 0.3 mm wide in a widened region, acute, with a thickened central core and convex lobes. I believe that these structures are staminodes. Inside of them there are smaller (about 0.4 mm long and 0.2 mm wide) membranous structures with slightly curved margins. Adaxially, the middle groove is only slightly distinguishable. Abaxially, the surface of these structures seems to be ribbed. In mature infructescences these membranous structures adnate to the fruit wall (Fig. 47d). These structures are interpreted here as intrafloral phyllomes.

The gynoecium consists of two carpels fused proximally along one-third or a half of their length. A wide scar of fusion with partially preserved septae is seen in a detached carpel. Different stages of maturation are well distinguishable in the carpels. The underdeveloped fruit is narrow elliptical, with acute apices, dehiscing distally. The ovules are numerous, arranged in a row along the entire curved margin of the carpel (Fig. 47c). The ovules are rounded elliptical, about 1 mm long.

The mature fruits are oval, 0.7–0.9 mm long, slightly appressed laterally. One of a pair of carpels is usually slightly longer than the other. The epidermis of the mature fruit is composed of rectangular, longitudi-

nally oriented cells. Stomata or hairs are lacking. The stylodes have been shed, leaving an elliptical scar with ribs radiating from a central slitlike pore (Fig. 47b).

Material. Five nearly complete inflorescences and several fragments of inflorescences from the type locality.

Taxa Established on the Basis of Leaf Remains

Genus *Parrotiopsis* (Niedz.) Schneid.

Parrotiopsis shimanskiana N. Maslova

Parrotiopsis shimanskiana: Maslova, 1995b, p. 161, pl. 1, figs. 2–6; 2, text-figs. 2b–2d, 3.

Description (Figs. 48c–48g; 49c–49f). The leaf blade is rounded to elliptical. The leaf base is cordate and variously asymmetrical. The leaf apex is slightly acuminate.

In the lower region of the leaf, the midvein is straight; in the upper region, it is sinuous. It gradually becomes thinner at the expense of the deviating secondaries. The basal veins are naked basally (up to 3–4 mm), they are almost as thick as the lower pair of the secondary veins and reach about the half way point of the leaf blade. The angle of deviation is 40° – 50° . Two or three

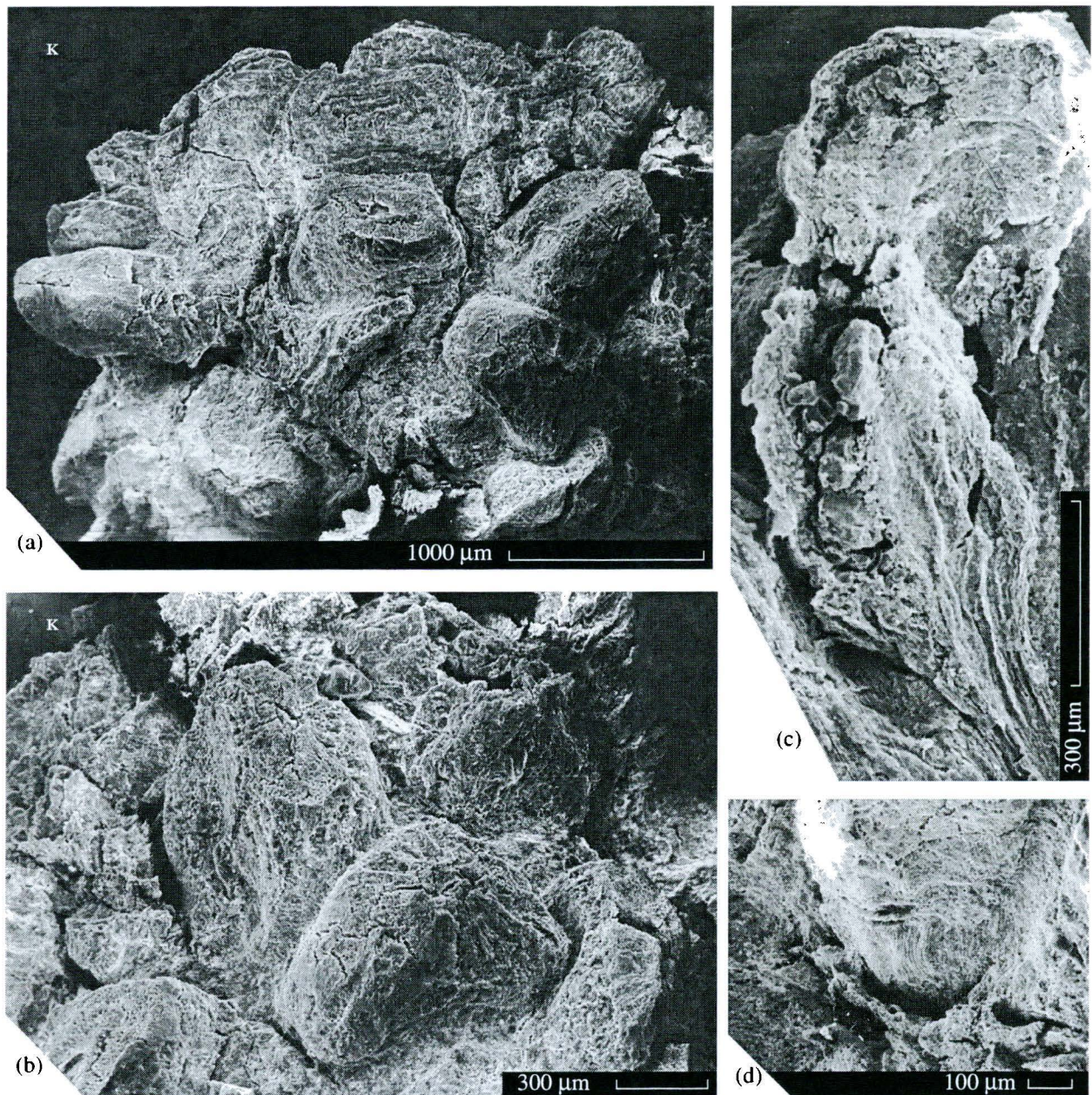


Fig. 47. *Evacarpa polysperma* N. Maslova et Krassilov, SEM, PIN, no. 4257/44: (a, b) mature head, paired carpels, staminodes, and intrafloral phyllomes are seen; (c) longitudinal section of a carpel, ovules are seen; and (d) phyllome fused with the carpel base; northwestern Kamchatka Peninsula, section between the capes Rebro and Getkilnin; Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

basiscopic deviations of the basal veins, the nearest to the base, are looping, while the others end in teeth.

There are four or five pairs of secondary veins. The first pair has up to three basiscopic deviations. One or two of the subsequent pairs also branch one time. The angle of deviation of secondaries diminishes from the leaf base toward the apex, from 40° to 20° . The first pair of secondary veins runs basally parallel to the basal veins, then gradually curves upward, thereby making the distance between the basal vein and the first sec-

dary vein at the point of their deviation considerably shorter than the distance between their ends at the leaf margin. The first pair of secondary veins (after basal veins) reaches at least two-thirds of the total length of the leaf blade. The tertiary veins are straight or branching. There are three or four tertiaries per 1 cm of secondary vein.

The leaf margin is toothed. The teeth appear slightly above the leaf base. The teeth are small, low, varying from obtuse triangular to acuminate concave–concave

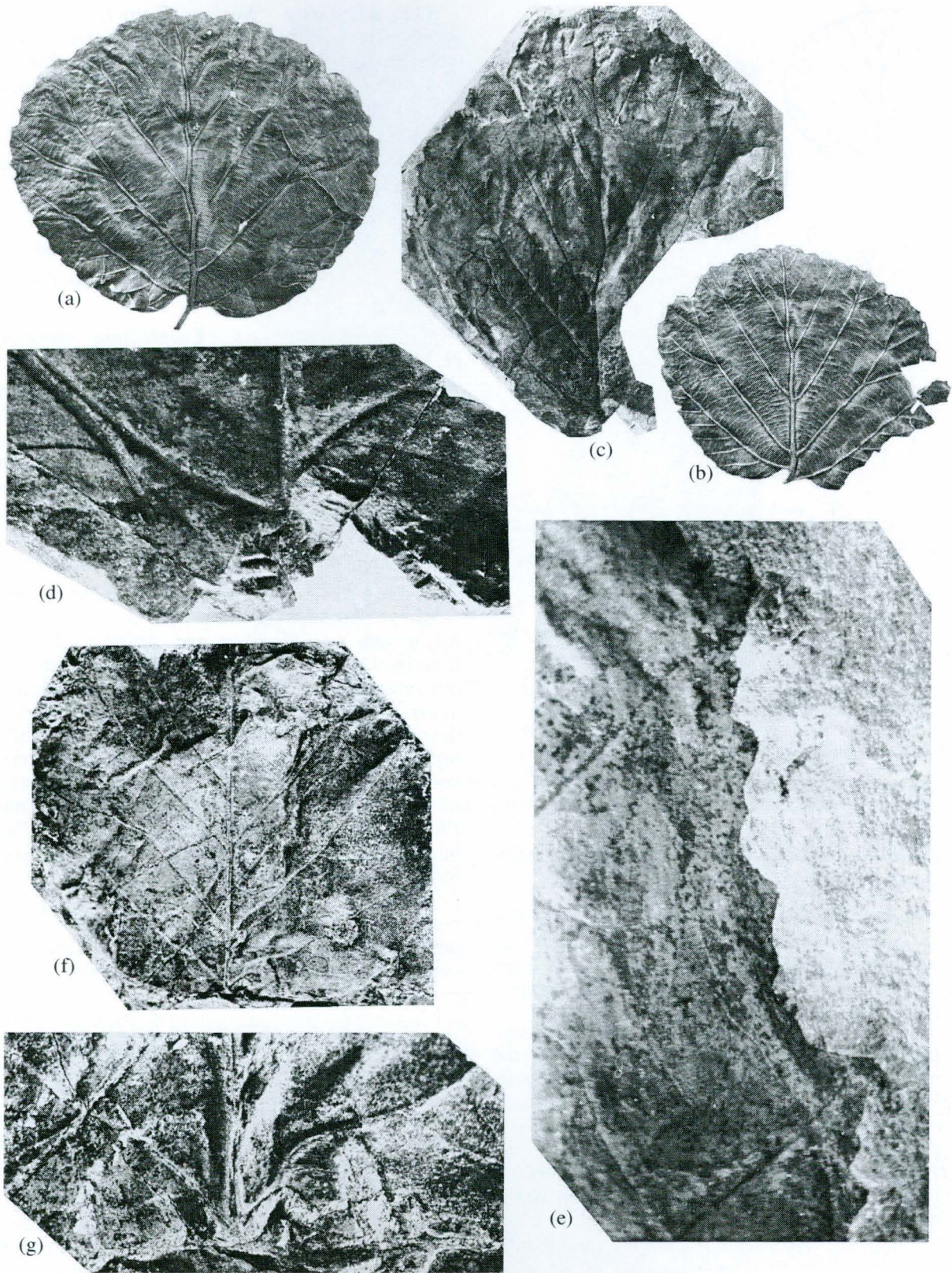


Fig. 48. *Parrotiopsis jacquemontiana* (Decne.) Rehd.: (a, b) extant species for comparison, $\times 1$; (c–g) *Parrotiopsis shimanskiana* N. Maslova: (c–e) PIN, no. 4256/84, holotype: (c) $\times 1$; (d) leaf blade base, $\times 3$; and (e) marginal serration, $\times 7$; (f, g) PIN, no. 3736/63: (f) $\times 1$ and (g) leaf blade base, $\times 3$; (c–e) western Kamchatka, Snatol River; Napana Formation, Upper Paleocene; (f, g) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

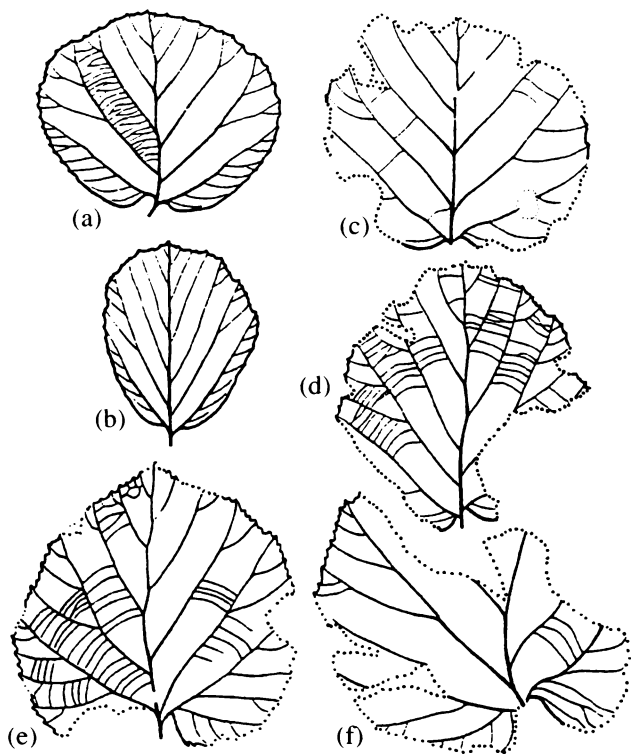


Fig. 49. *Parrotiopsis jacquemontiana* (Decne.) Rehd.: (a, b) extant species for comparison, $\times 0.5$; *Parrotiopsis shimanskiana* N. Maslova, $\times 0.5$: (c) GIN, no. 3736/63; (d) PIN, no. 4256/84, holotype; (e) PIN, no. 4256/600; and (f) PIN, no. 4256/598; (c) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik-lower part of the Tkprovayam Formation, Upper Paleocene-Lower Eocene; (d-f) western Kamchatka, Snatol River; Napana Formation, Upper Paleocene.

of the platanoid appearance. The larger teeth occasionally bear small teeth.

Comparison. The only modern species of this genus, *P. jacquemontiana*, has a limited range, embracing northeastern Afghanistan (Nuristan), northern Pakistan, and northwestern India (Kashmir) (*Zhizn' rastenii*, 1981).

As the herbarium of the Botanical Institute of the Russian Academy of Sciences shows, leaves of the solitary extant species *P. jacquemontiana* vary only slightly. There are only minor differences in leaf blade shape (length/width ratio) between leaves from one shoot (Figs. 49a, 49b). The other leaf blade characters (the morphology of leaf apex, leaf base with naked veins, undulate midvein, pattern of venation, and leaf margin outline) are very stable. *P. shimanskiana* greatly resembles the extant *P. jacquemontiana* in all main characters (Figs. 48a, 48b, 49a, 49b). An interesting feature of both species is the fact that veins of all orders are distinct on the lower leaf surface, whereas on the upper surface they are sunken in the mesophyll and appear as grooves.

Occurrence. Western Kamchatka Peninsula: Snatol River, Napana Formation, Upper Paleocene; Chemurnaut Bay, upper part of the Kamchik Formation-lower part of the Tkprovayam Formation, Upper Paleocene-Lower Eocene.

Material. Nine specimens from the Snatol River and one specimen from Chemurnaut Bay, Kamchatka Peninsula.

Genus *Evaphyllum* N. Maslova, gen. nov.

Etymology. From the name Eva and Greek *phylum* (leaf).

Type species. *Evaphyllum kamchaticum* N. Maslova.

Diagnosis. Leaves entire, elliptical. Basal and secondary veins as thick as midvein. Basal veins higher than half of leaf blade length, having six or seven pairs of basicopic branches, weakly looping and separating short veins with ends in sinuses. Secondary veins looping, short branches deviate in teeth or in sinuses. Leaf margin toothed. Teeth small, rare.

Species composition. Type species.

Comparison. Leaves of such an appearance combine characters of the genus *Platanus* and those of the genera *Liquidambar* and *Altingia*. The species described resembles *Platanus* in leaf blade shape (most of Cretaceous and Early Paleogene platanoids and *Platanus* had entire and weakly lobed leaf blades), the deviation of basal veins above the leaf base, well-developed basicopic branches dichotomizing from basal veins and resulting in a weakly sinuous (broken) aspect of the basal vein (a character of ancient members of *Platanus*, while *Liquidambar* and modern *Platanus* have straight basal veins), and tertiary venation. The following characters of the genus are present also in *Liquidambar*: the brochidodromous connection of secondary veins and basicopic deviations of basal veins, deviation from the latter of short branchlets ending in sinuses or in teeth, and characteristic teeth.

***Evaphyllum kamchaticum* N. Maslova, sp. nov.**

Etymology. From the Kamchatka Peninsula.

Holotype. PIN, no. 4257/16, Moscow, nearly complete leaf impression; northwestern Kamchatka Peninsula, section between the Rebro and Getkilnin capes, Tkprovayam Formation, Upper Paleocene-Lower Eocene; Figs. 50a-50c.

Diagnosis. As for the genus.

Description (Figs. 50a-50c). The leaf blade is elliptical. The base and apex have not been preserved. The midvein in the lower half of the leaf is straight. The basal veins are approximately as thick as the midvein and secondary veins and reach at least a half of the leaf blade length. The angle of the basal vein deviation is 25° - 30° . Six or seven basicopic branches of the basal

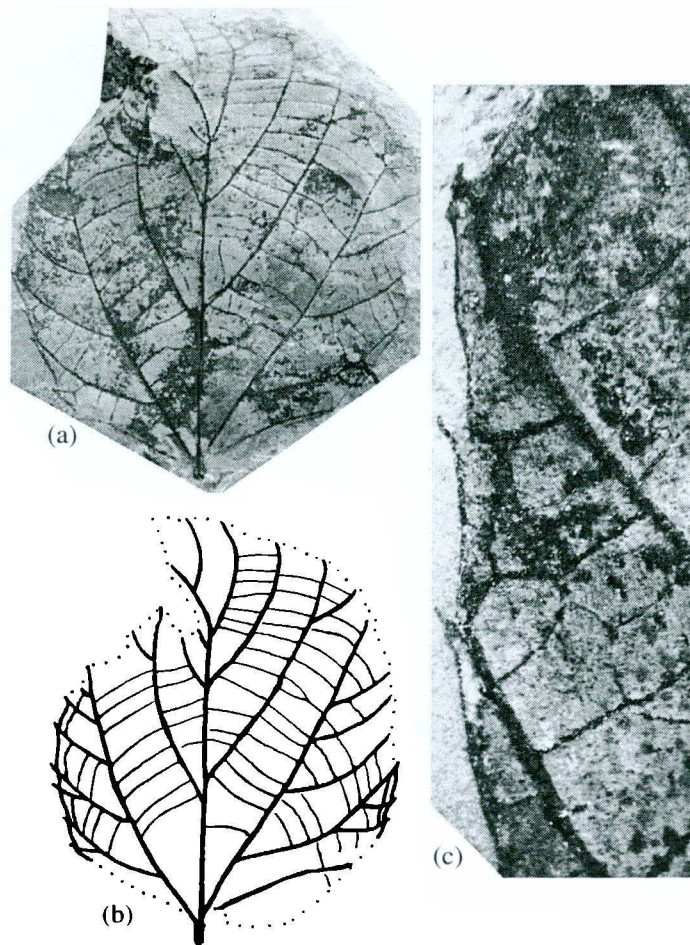


Fig. 50. *Evaphyllum kamchaticum* N. Maslova, gen. et sp. nov., PIN, no. 4257/16: (a) $\times 1$; (b) drawing, $\times 1$; and (c) marginal serration of the leaf blade, $\times 6$; northwestern Kamchatka Peninsula, section between the capes Rebro and Getkilnin; Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

veins fork, weakly loop, and send short branchlets to the sinuses.

There are five pairs of secondary looping veins. The lower two pairs form one or two basispic branches, which also loop. The short weak branchlets deviate from the loops and end in marginal teeth or sinuses. The angle of deviation of the secondary veins is equal to 20° – 30° . The tertiary veins are straight, occasionally branching, with up to five veins per 1 cm of secondary vein. The leaf blade margin is toothed. The teeth are small, rare (three teeth per 1 cm of leaf margin).

Remarks. The leaves of *Evaphyllum kamchaticum* N. Maslova sp. nov. associate with the capitate inflorescences of *Evacarpa polysperma*. This material comes from one and the same locality (Rebro Cape). In this locality leaf remains belong to a single genus, *Myrica*, which has radically different reproductive organs. Although these fossil leaves and inflorescences were not in organic connection, their affinity to one plant is highly probable because they demonstrate common hamamelid characters.

Material. Holotype with a counterpart and some more leaf fragments from the type locality.

Genus *Sycopsiphyllum* N. Maslova, gen. nov.

Etymology. From the extant genus *Sycopsis* and the Greek *phyllum* (leaf).

Type species. *Sycopsiphyllum kamchaticum* N. Maslova, sp. nov.

Diagnosis. Leaves entire, asymmetrical, with short petiole. Leaf blade base asymmetrical, apex attenuate, pointed. Leaf blade margin entire or with occasional small teeth near leaf apex. Teeth low, triangular, with prominent spine of secondary vein. Midvein straight, abruptly thinning from leaf base toward its apex. Secondary veins thin, brochidodromous. Distance between secondary veins near leaf base is shorter than between subsequent veins.

Species composition. Type species.

Comparison. Leaves of *Sycopsiphyllum* gen. nov. resemble those of the extant genus *Sycopsis*



Fig. 51. (a–e) *Sycopsiphyllum kamchaticum* N. Maslova, gen. et sp. nov.: (a, b) PIN, no. 3736/62, holotype: (a) $\times 1$ and (b) marginal tooth in the upper region of the leaf, $\times 3$; (c) PIN, no. 3736/69, $\times 1$; (d) PIN, no. 3736/61, $\times 1$; (e) PIN, no. 3736/68, $\times 1$, northwestern Kamchatka, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; (f–h) *Sycopsis sinensis* Oliv., extant species for comparison: (f) $\times 1$, (g) $\times 1$, and (h) $\times 5$; *Sycopsis dunnii* Hemsl., extant species for comparison: (i) $\times 1$.

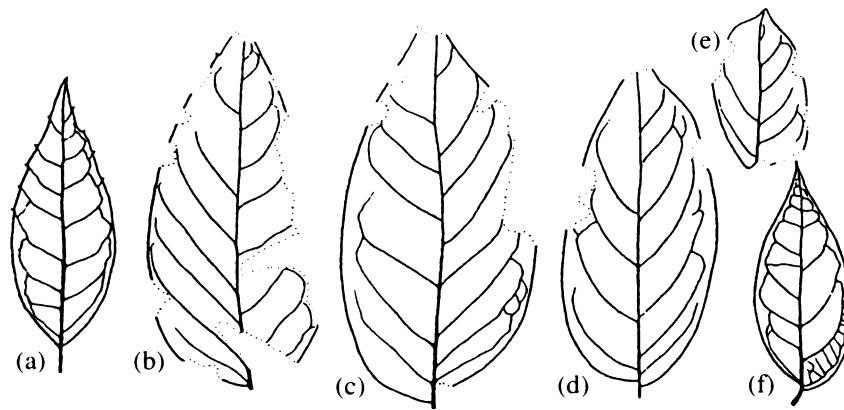


Fig. 52. (a, f) *Sycopsis sinensis* Oliv., $\times 0.5$, extant species for comparison; (b–e) *Sycopsiphillum kamchaticum* N. Maslova, gen. et sp. nov.: (b) PIN, no. 3736/62, holotype; (c) PIN, no. 3736/68; (d) PIN, no. 3736/61; and (e) PIN, no. 3736/68; (b–e) northwestern Kamchatka, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

(Hamamelidaceae) but differ from them in the larger size and more numerous secondary veins.

Sycopsiphillum kamchaticum N. Maslova, sp. nov.

E t y m o l o g y. From the Kamchatka Peninsula.

H o l o t y p e. PIN, no. 3736/62, Moscow; nearly complete leaf impression; northwestern Kamchatka, Chemurnaut Bay, upper part of the Kamchik Formation–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene; Figs. 51a, 51b, and 52b.

D i a g n o s i s. As for the genus.

D e s c r i p t i o n (Figs. 51a–51e, 52b–52e). The leaves are simple, entire, asymmetrical, and shortly petiolate. The leaf blade base is asymmetrical, the apex is attenuate pointed. The leaf blade margin is predominantly entire; however, occasional apical teeth were observed in some specimens. The tooth is triangular, with a prominent spine being a continuation of a secondary vein.

The venation is pinnate, brochidodromous. The midvein is straight; being thicker in the lower part of the leaf blade, it greatly thins in the apical region. The secondary veins are thin, arch-shaped, connected to each other by a series of broken loops. In the presence of a marginal tooth, the secondary vein ends craspedodromously. The maximum distances between secondary veins occur in the middle leaf region. Basally, these veins are crowded, whereas in the apical part they are extremely thin and hardly distinguishable. The tertiary veins are very thin and are connected by numerous anastomoses.

R e m a r k s. The new species is similar to the extant species *Sycopsis sinensis* and *S. dunnei*. *S. sinensis* has asymmetrical leaves displaying both entire-margined (Fig. 51f) and toothed (Fig. 51g) morphotypes. In *S. dunnei* the secondary veins approach each other basally, the maximal distances between secondaries

occur in the central leaf region, the secondary veins are weakly defined in the apical region (Fig. 51i). Both species have tertiary venation similar to that of *Sycopsiphillum kamchaticum* sp. nov. Denser secondary veins than in *Sycopsis* and larger leaf blades are macromorphological distinguishing characters of the new species.

The closely related Middle Miocene *Sycopsis chaneyi* Ishida differs in having asymmetrical leaf blades with more prominent apical teeth (Ishida, 1970).

In spite of the obvious similarity, the assignment of the fossil material in question to the extant genus *Sycopsis* seems to be premature. Confident identification of such leaves is difficult, since macromorphologically they also demonstrate a certain degree of similarity to leaves of other hamamelid genera (e.g., *Loropetalum*, *Distylium*, etc.) as well as to genera of other families. Identification of an extant genus with leaves of such a morphotype in the Paleocene flora should be additionally substantiated by finds of reproductive organs and microstructural data. Unfortunately, our material is represented by leaf impressions, which cannot be studied microstructurally.

M a t e r i a l. Four nearly complete specimens and numerous leaf fragments from the type locality.

Genus *Liquidambar* L.

Liquidambar miosinica Hu et Chaney

Liquidambar miosinica: Hu and Chaney, 1940, p. 46, pl.; Tanai and Suzuki, 1965, p. 28, pl. 21, fig. 9; Ishida, 1970, p. 85, pl. 13, fig. 7; Onoe, 1974, p. 44, pl. 9, fig. 8; Fotyayanova, 1988, p. 80, pl. 3, fig. 12, text-figs. 30, 7; 31, 7; Ozaki, 1991, p. 139, pl. 7, fig. 9, pl. 8, fig. 2; Maslova, 1995a, p. 149, figs. 1–9.

D e s c r i p t i o n (Figs. 53a–53f, 54a–54d, 55a–55g). The leaves are asymmetrical and lobed. There are three to five lobes, which are triangular basally and pointed apically. The central lobe is larger than the lateral ones, sinuses between the lobes are acute or rectan-

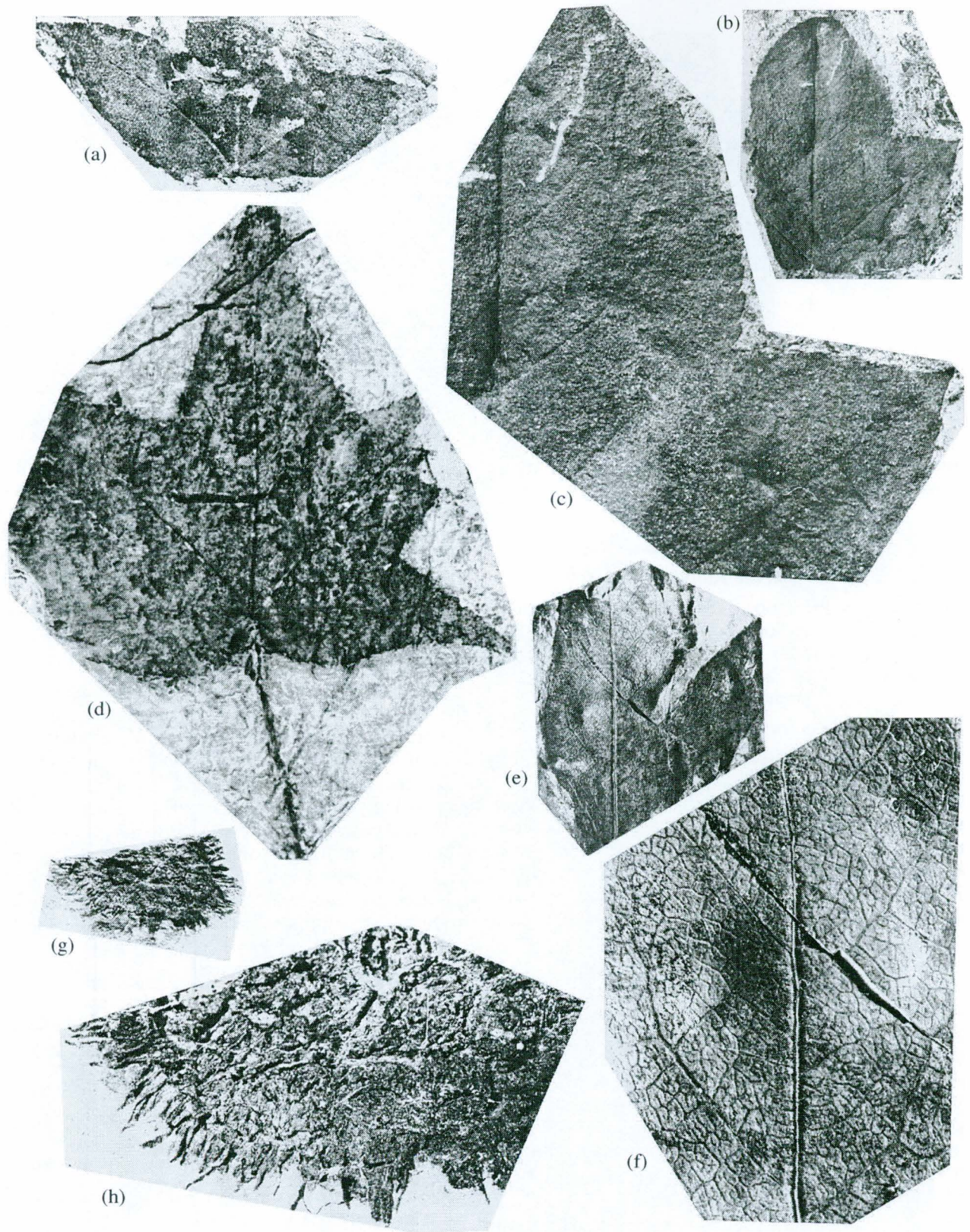


Fig. 53. (a–f) *Liquidambar miosinica* Hu et Chaney: (a) PIN, no. 4253/40, $\times 1$; (b) PIN, no. 3862/286, $\times 1$; (c) PIN, no. 3862/286, $\times 3$; (d) PIN, no. 4855/9, $\times 1$; (e) PIN, no. 3862/485, $\times 1$; and (f) PIN, no. 3862/485, venation patterns of higher orders, $\times 3$; (g, h) *Liquidambar* sp., PIN, no. 4395/283: (g) infructescence, $\times 1$ and (h) $\times 3$; (a) Sakhalin Island, Naiba River; Naiba Formation, Middle Eocene; (b, c, e–h) northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgirinskaya Formation, Upper Eocene; (d) eastern Sakhalin Island, Shakhtnaya River, tributary of the Gornaya River; Verkhneduiskaya Formation, Lower Miocene.

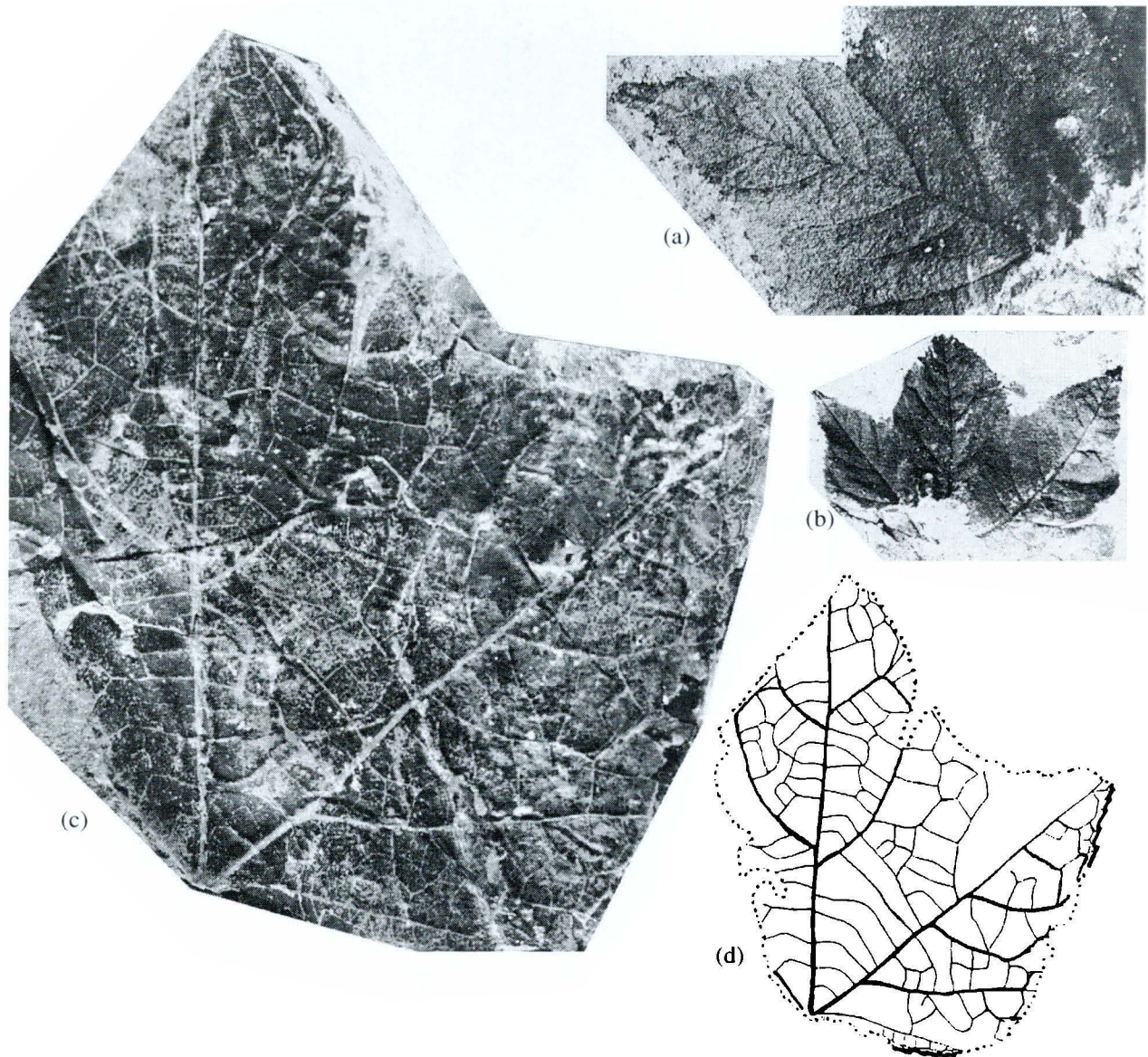


Fig. 54. *Liquidambar miosinica* Hu et Chaney: (a, b) PIN, no. 4252/40: (a) leaf lobe, $\times 3$ and (b) $\times 1$; (c, d) GIN, no. 3736/27: (c) $\times 2$ and (d) drawing, $\times 1$; (a, b) southern Sakhalin Island, Krasnoyarka River Basin; Naiba Formation, Middle Eocene; (c, d) northwestern Kamchatka Peninsula, Chemurnaut Bay; upper part of the Kamchik–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene.

gular. The leaf blade base is broadly rounded, occasionally slightly cordate.

The midvein is straight, a groove running along the total length of the vein is clearly seen from the upper leaf side. The basal veins are mostly curved. The secondary veins are thin, number at least six pairs, and loop along the leaf margin. The last-order deviations of the loops end in sinuses. The teeth appear from the leaf base. They are thin and end with a gland.

Comparison. *L. miosinica* have highly variable leaves. Hu and Chaney (1940) first described only trilobate leaves but later leaves with five lobes were also

included in the species. The typical leaf morphotype of *L. miosinica* resembles that of the extant *L. formosana*.

Remarks. A solitary leaf impression of *Liquidambar* from the Late Paleocene of the Chemurnaut Bay merits special consideration (Figs. 54c, 54d).

The specimen is distinctive because of a completely straight midvein and angular loops formed by secondary veins. Unfortunately, inadequate preservation of the material has prevented microstructural studies. The limited material hampers a detailed study of this find, thus, it is unreasonable to establish a new species. Supposedly, this find is the most ancient fossil remains of the genus in the Far East.

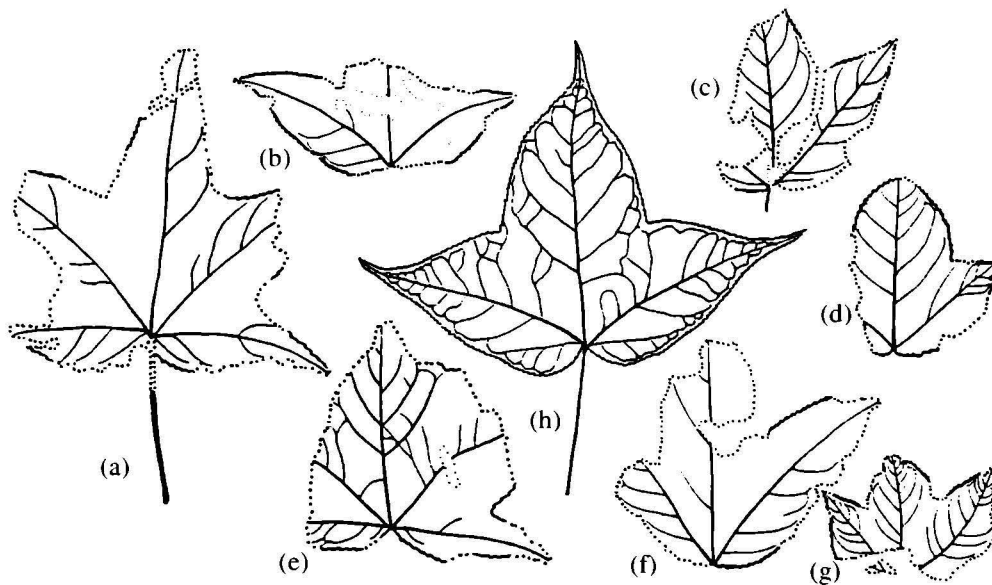


Fig. 55. (a–g) *Liquidambar miosinica* Hu et Chaney., $\times 0.5$: (a) PIN, no. 4855/9; (b) PIN, no. 4253/5; (c) PIN, no. 3862/275; (d) PIN, no. 3862/286; (e) PIN, no. 3782/11; (f) PIN, no. 4857/5; and (g) PIN, no. 4252/40; (h) *Liquidambar formosana* L., $\times 0.5$, extant species for comparison: (a) eastern Sakhalin, Shakhtnaya River, tributary of the Gornaya River; Verkhneduiskaya Formation, Lower Miocene; (b) Sakhalin Island, Naiba River; Naiba Formation, Middle Eocene; (c, d) northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgiminskaya Formation, Upper Eocene; (e) eastern Sakhalin, Korollovka River; Verkhneduiskaya Formation, Lower Miocene; (f) western Sakhalin, Kama River; Snezhinka Formation, Middle Eocene; and (g) southern Sakhalin, Krasnoyarka River Basin; Naiba Formation, Middle Eocene.

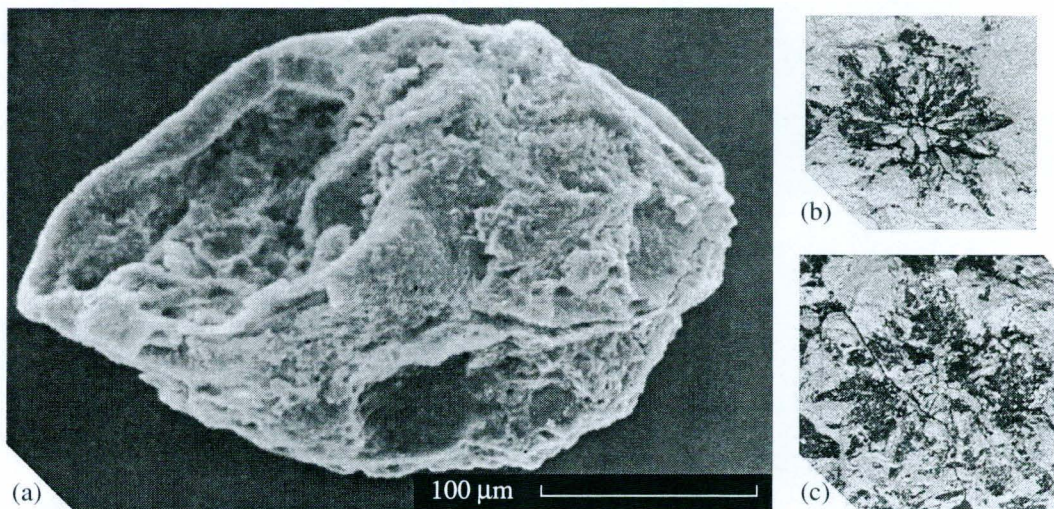


Fig. 56. *Liquidambar* sp.: (a) seed, PIN, no. 4855/4, SEM; (b) infructescence, PIN, no. 4855/2, $\times 1$; and (c) infructescence, PIN, no. 4855/3, $\times 1$; eastern Sakhalin, Shakhtnaya River, tributary of the Gornaya River; Verkhneduiskaya Formation, Lower Miocene.

In the locality of the Shakhtnaya River, a tributary of the Gornaya River (eastern Sakhalin Island, Verkhneduiskaya Formation, Lower Miocene), leaves of *L. miosinica* associate with capitate infructescences (Figs. 56b, 56c) containing seeds (Fig. 56a). The seed is oval, 0.25 mm long. The chalazal extremity is obtuse, the micropylar one is pointed and has a narrow winged bordering. The cuticle of the seed cover is composed of irregularly tetragonal (more rarely polygonal) cells, arranged in indistinct rows.

Occurrence. Sakhalin Island: Snezhinka, Kama, and Aral'skaya rivers, Snezhinka Formation, Middle Eocene; Krasnoyarka River Basin and Naiba River Basin, Naiba Formation, Middle Eocene; Korollovka River, Verkhneduiskaya Formation, Lower Miocene; Shakhtnaya River, a tributary of the Gornaya River, Verkhneduiskaya Formation, Lower Miocene. Northwestern Kamchatka: Podkagernaya Bay, Irgiminskaya Formation, Upper Eocene. Northeastern China,

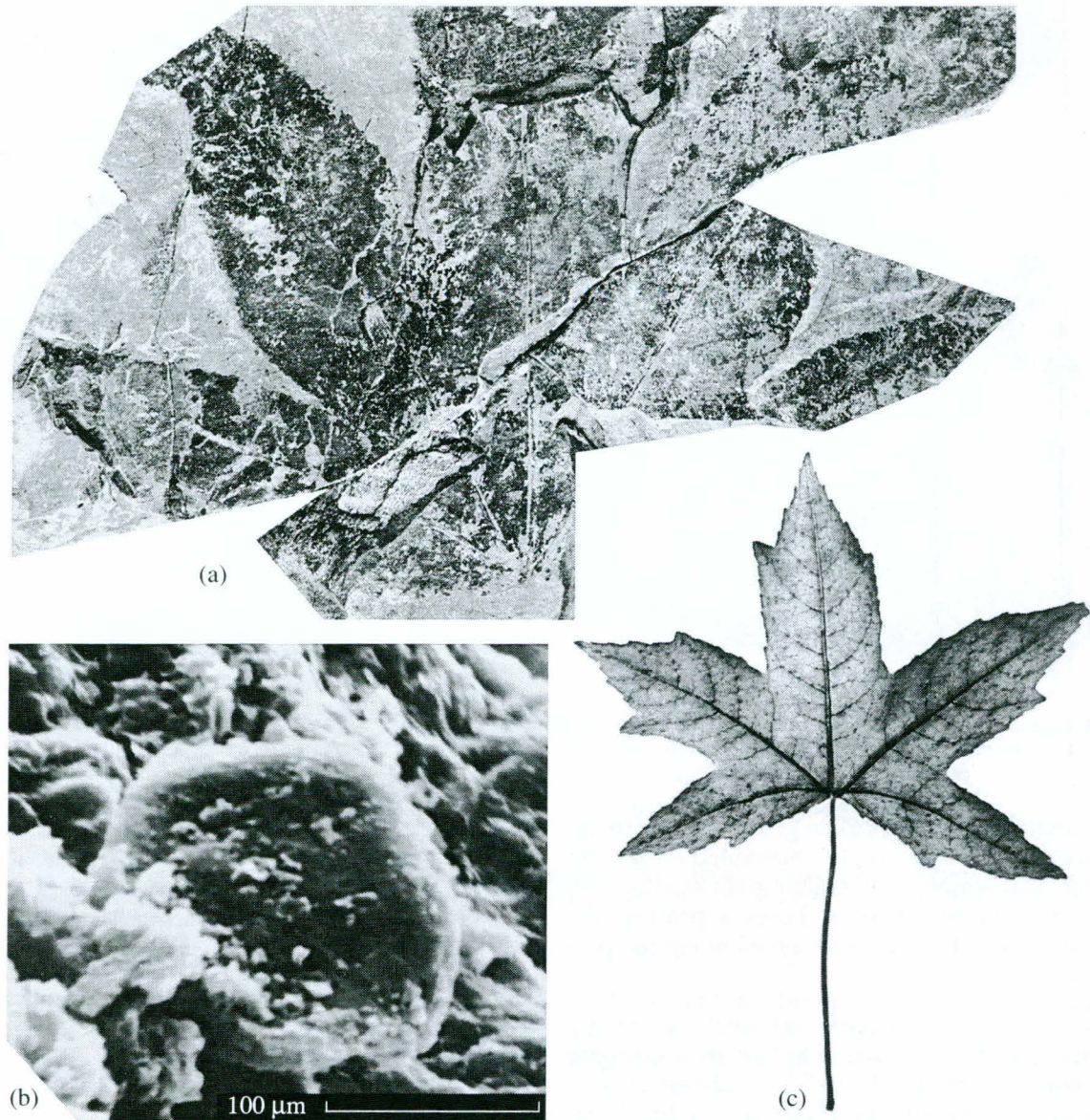


Fig. 57. (a, b) *Liquidambar pachyphylla* Knowlton: (a) PIN, no. 4129/155, $\times 1$; (b) pollen grain attached to the leaf of *Liquidambar pachyphylla* Knowlton, SEM; eastern Sakhalin, Bogataya River; Lyukama Formation, Upper Eocene; (c) *Liquidambar orientalis* L., extant species for comparison, $\times 1$.

Shandong Province, Shanwang Group, diatom member; Upper Miocene.

Material. More than 40 leaves of different preservation from the localities of the Snezhinka, Kama, Aral'skaya, Krasnoyarka, Naiba, Korollovka, and Shakhtnaya rivers (Sakhalin) and the Podkagernaya Bay locality (Kamchatka).

***Liquidambar pachyphylla* Knowlton**

Liquidambar pachyphylla: Knowlton, 1902, p. 63, pl. 9, fig. 1; Maslova, 1995a, p. 151, pl. 1.

Description (Figs. 57a, 58a, 58b, 59b–59e). The leaves are different in size, symmetrical, and typically pentalobate. The lobes are ovate, ovate–lanceolate,

and elongate. The lobes are mostly parallel-margined, narrowing apically. The sinuses between the lobes are acute. The leaf base is rounded, slightly cordate.

The midvein is straight, the basal veins are as thick as the midvein. The secondary veins number up to ten pairs, are thin, and loop near the leaf margin. The short branch that deviates from the loop of the last order ends in a sinus. The teeth are regularly arranged along the margin of the leaf blade. The size and shape of the teeth slightly vary with their position: in the central region of the lobes, the teeth are slightly larger and hook-shaped, whereas in the apical and basal parts, the teeth are small and of typically *Liquidambar* shape.

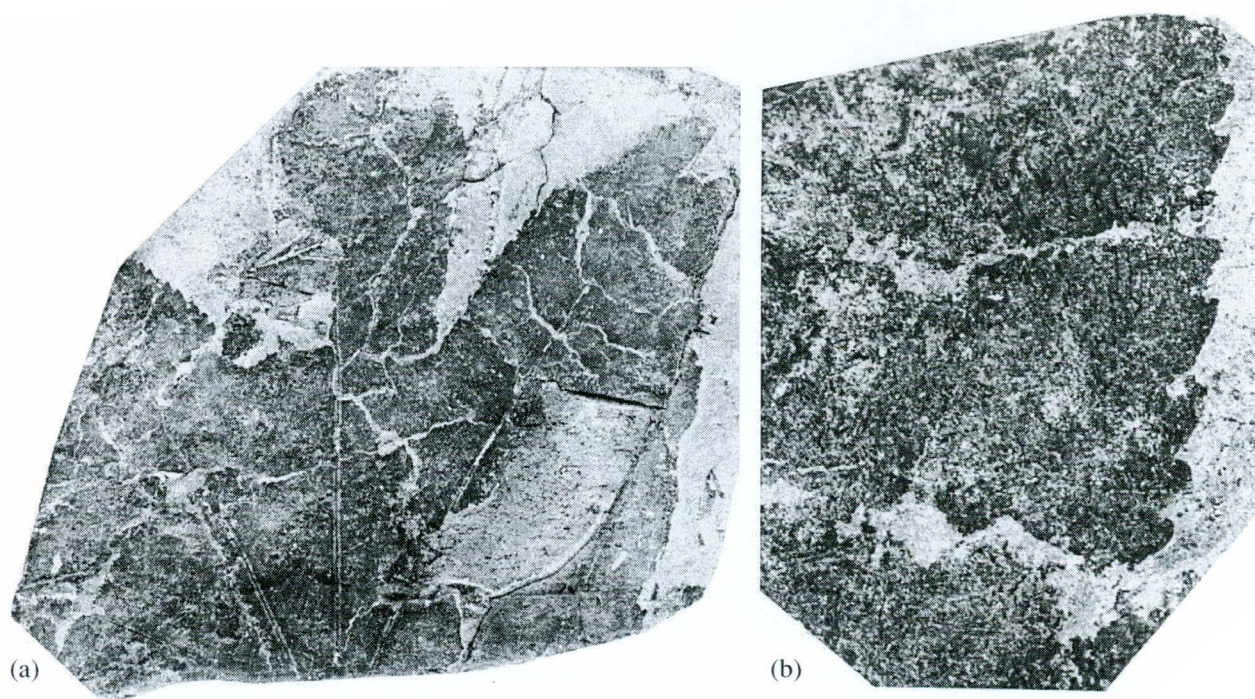


Fig. 58. *Liquidambar pachyphylla* Knowlton: (a) PIN, no. 4129/512, $\times 1$, (b) PIN, no. 4129/512, marginal serration, $\times 4$; eastern Sakhalin, Bogataya River; Lyukama Formation, Upper Eocene.

Poor preservation of the pollen grain attached to the leaf surface of *L. pachyphylla* has prevented its generic assignment. Equatorially, the pollen grain is elliptical, $18.0\ \mu\text{m}$ long and $14\ \mu\text{m}$ wide. Pores appearing like hardly distinguishable pits are observed along the pollen periphery (Fig. 57b).

Comparison. *L. pachyphylla* is characterized by predominantly pentalobate leaves with narrow elongate mostly parallel-margined lobes. This character distinctly differentiates the species from all described fossil species of *Liquidambar*. The larger hook-shaped teeth in the central part of the lobes are a characteristic feature of *L. pachyphylla* (Fig. 58b). The shape of the leaf blade makes this species closer to the Japanese *L. protojaponica* and *L. yabei*. Among extant liquidambar, *L. orientalis* shows the most similar external morphology (Fig. 57c).

The epidermis of the fossil species under description is similar to that of *L. styraciflua* in the arrangement of stomata and the distinctive features of subsidiary cells. Among extant liquidambar, *L. styraciflua* is transitional in the density of the stomata arrangement: in *L. orientalis* the stomata are arranged almost two times more densely, while in *L. formosana* they are markedly more widely spaced than in *L. styraciflua*.

Occurrence. Eastern Sakhalin Island: Bogataya River, Lyukama Formation, Upper Eocene. North America: Oregon, John Day Basin, Middle Eocene.

Material. Four nearly complete specimens and nine fragmentary leaf remains from the Bogataya River locality (Sakhalin Island).

Genus *Altingiophyllum* N. Maslova, gen. nov.

Etymology. From the extant genus *Altingia* and Greek *phyllum* (leaf).

Type species. *Altingiophyllum onorense* N. Maslova, sp. nov.

Diagnosis. Upper part of leaf blade elliptical and parallel-margined. Apex attenuated and pointed. Marginal teeth of leaf blade frequent, small, hook-shaped, with apical gland. Leaf apex without teeth. Secondary veins camptodromous. Loops broken, indistinct. Branches of loops of the last order end in sinuses.

Species composition. Type species.

Comparison. *Altingiophyllum* gen. nov. resembles the extant genus *Altingia*. It differs in the more elongated leaf blade that has parallel margins along most of its length, the less prominent venation of the secondary and higher orders, and less distinct looping of the secondary veins.

***Altingiophyllum onorense* N. Maslova, sp. nov.**

Etymology. From the Onor River.

Holotype. PIN, no. 4251/2, Moscow; leaf impression devoid of the base; western Kamchatka

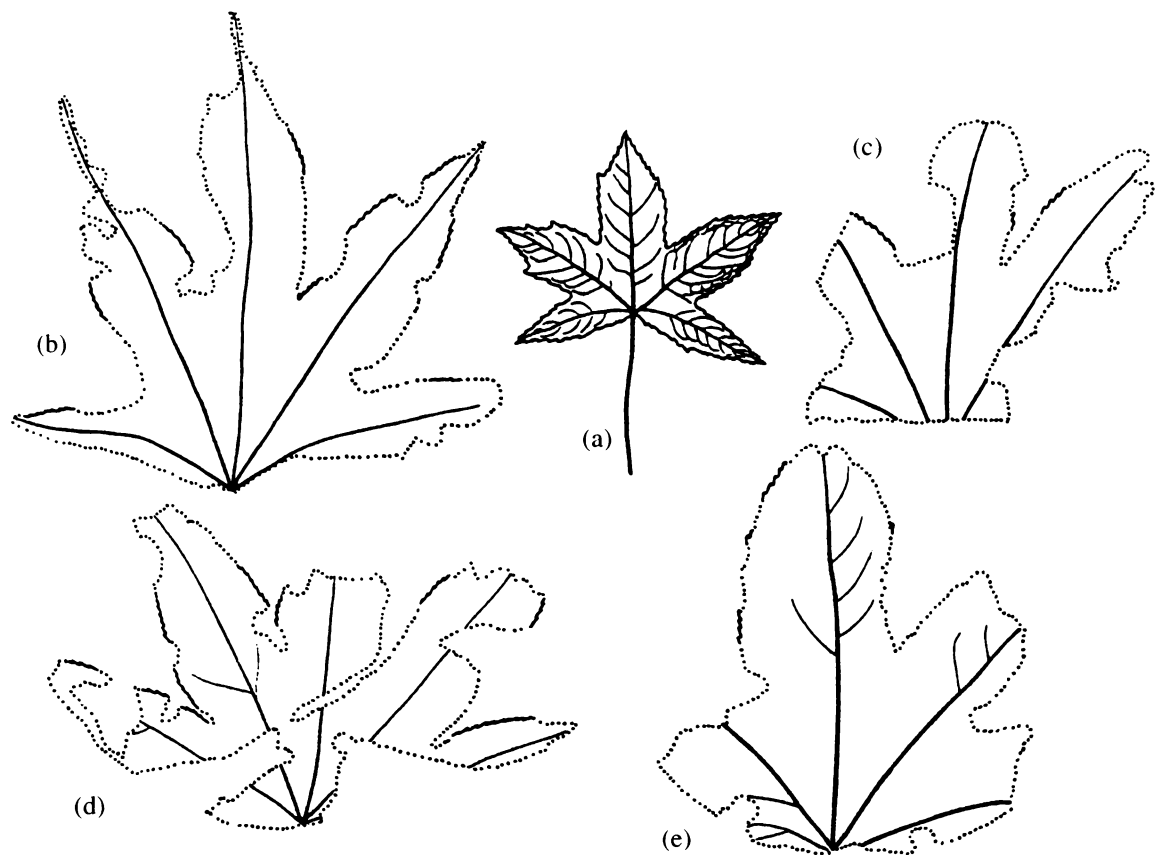


Fig. 59. (a) *Liquidambar orientalis* L., extant species for comparison, $\times 0.5$; (b–e) *Liquidambar pachyphylla* Knowlton, $\times 0.5$: (b) PIN, no. 4129/158; (c) PIN, no. 4129/512; (d) PIN, no. 4129/155; and (e) PIN, no. 4129/515; (b–e) eastern Sakhalin, Bogataya River; Lyukama Formation, Upper Eocene.

Peninsula, Onor River, isolated block of coal-bearing deposits, Middle? Eocene; Figs. 60a–60c.

Diagnosis. As for the genus.

Description (Figs. 60a–60c). The shape of the leaf blade is supposedly narrow elliptical, mostly parallel-margined. The morphology of the base is unknown. The apex is weakly attenuate, pointed. The leaf blade margin is toothed. The teeth are small, closely spaced, four teeth occur per 1 cm of leaf margin, their differences in size and shape result in a slightly curved line of the leaf margin. The teeth are mostly hook-shaped, with a longer concave basal side and short apical side ending with a gland. Apically, the teeth become more widely spaced, the margin of the attenuate part of the leaf blade is entire.

The venation is pinnate, camptodromous. The midvein is straight. The secondary veins are thin and alternate and deviate at unequal distances from each other. Near the leaf margin the secondaries are broken and are connected by a series of indistinct loops. The loops of the last order shoot thin branchlets into the sinuses. The veins of the tertiary order form a net of unequal polygonal meshes.

Remarks. The new species is described on the basis of a solitary impression of an incomplete leaf with a counterpart. Macromorphologically, the leaf of *Altingiophyllum onorense* sp. nov. resembles species of the extant *Altingia*. Thus, the new species is similar to *Altingia chinensis* (Champ.) Oliv. in the shape of the parallel-margined leaf blade and attenuate apex devoid of teeth. In *A. excelsa*, the loops formed by secondary veins are broken and less distinct than in other extant species.

The absent leaf blade base prevents confident assignment of the material to the genus *Altingia*. A similar external morphology is also observed in the lobes of *Liquidambar*. However, in the latter genus the patterns of secondary veins in lobes on different sides of the midvein are different, while in *Altingiophyllum* gen. nov. the patterns of secondary veins are identical in the visible region of the leaf blade. The teeth of the leaf margins represent an additional difference: in *Liquidambar* they have an equal size and shape, being regularly disposed along the leaf blade margin, including the apices of lobes. The polymorphous genus *Semiliquidambar*, a supposed hybrid of *Altingia* \times *Liquidambar*, also has similar morphotypes.

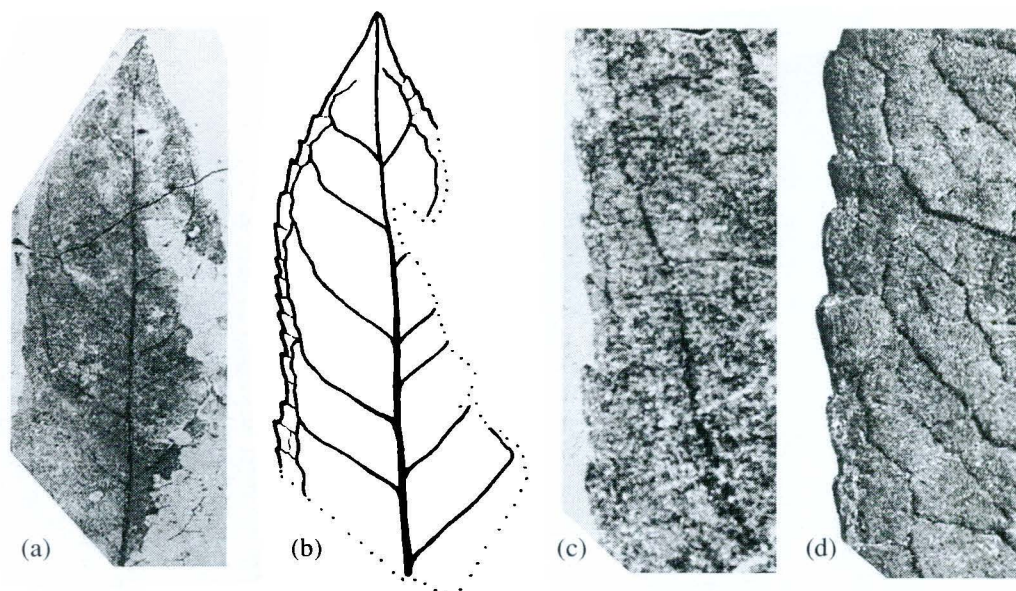


Fig. 60. (a–c) *Altingiophyllum onorense* N. Maslova gen. et sp. nov.: (a) PIN, no. 4251/2, holotype, $\times 1$; (b) PIN, no. 4251/2, drawing, $\times 1$; and (c) PIN, no. 4251/2, venation pattern and marginal serration, $\times 4$; Sakhalin Island, Onor River, isolated block of coal-bearing deposits: Middle? Eocene; (d) *Altingia excelsa* Nor., extant species for comparison, marginal venation and serration, $\times 3$.

Although the fossil finds clearly resemble the modern *Altingia*, *Liquidambar*, and *Semiliquidambar*, their poor preservation and scarcity prevent their assignment to any of these genera; therefore, the description of these leaves as a formal genus *Altingiophyllum* gen. nov. appears to be more reasonable.

Material. Holotype with a counterpart from the type locality and several leaf fragments.

Genus *Hamamelis* L.

Hamamelis certa N. Maslova

Hamamelis certa: Fotyanova *et al.*, 1996, p. 43, pl. 1, figs. 1, 2, and 5.

Description (Figs. 61b–61e). The leaf blade is asymmetrical, rhomboidal-elliptical or rhomboidal-oval, the base has unequal sides, the apex is obtuse. The petiole has not been preserved.

The midvein is undulate in the apical region. The basal veins are well defined, unequal in length, one of them can reach more than a half of the leaf blade length. These veins are as thick as the secondary veins and form four or five (more rarely up to seven) basisopic deviations, which end craspedodromously. The angle of deviation varies from 35° to 60° . There are four or five pairs of secondary veins, which are usually arch-shaped, more rarely some lower secondary veins can be straight basally and deviate at an angle of 25° – 40° . The first two pairs of secondary veins form up to two basisopic deviations.

The leaf margin is undulated-toothed, the teeth appear higher than one-third of the leaf length. The

teeth are large, low, rounded, some of them end with a short spine representing a vein ending.

Comparison. The species differs from *H. protojaponica* Tanai et N. Suzuki, described from the Late Miocene of Japan (Tanai and Suzuki, 1965) and the Middle Miocene of Korea (Huzioka, 1972), in the distinct basal veins giving use to basisopic deviations ending in the leaf margin.

The species is closest to *H. miomollis* Hu et Chaney, which was originally described from the Miocene of the Shandong Province (northeastern China; Hu and Chaney, 1940). It differs in the curved midvein, the smaller angle of deviation of the secondary veins, less numerous basisopic deviations of basal veins, and larger teeth.

It is distinguished from the Late Eocene *H. ochotensis* Cheleb. (Gladenkov *et al.*, 1991) by the sharp asymmetry of the leaf, arched secondary veins, and the absence from deviations of the lower basisopic vein.

Remarks. *H. certa* shows the main generic characters of the extant *Hamamelis*. These are an asymmetric, rhomboid leaf blade; asymmetric leaf base; undulate midvein; arch-shaped secondary veins; and undulate-toothed leaf margin. The only significant difference is the fact that the regions of the leaf blade limited by basal veins are developed better than in most extant *Hamamelis*. This character is also present in some other fossil members of *Hamamelis*. *H. certa* exhibits maximal similarity to the extant *H. mollis* Oliv. and *H. virginiana* L.

Material. Four leaves of different preservation and about ten small leaf fragments from the Utkholokskii Peninsula locality (Kamchatka Peninsula).

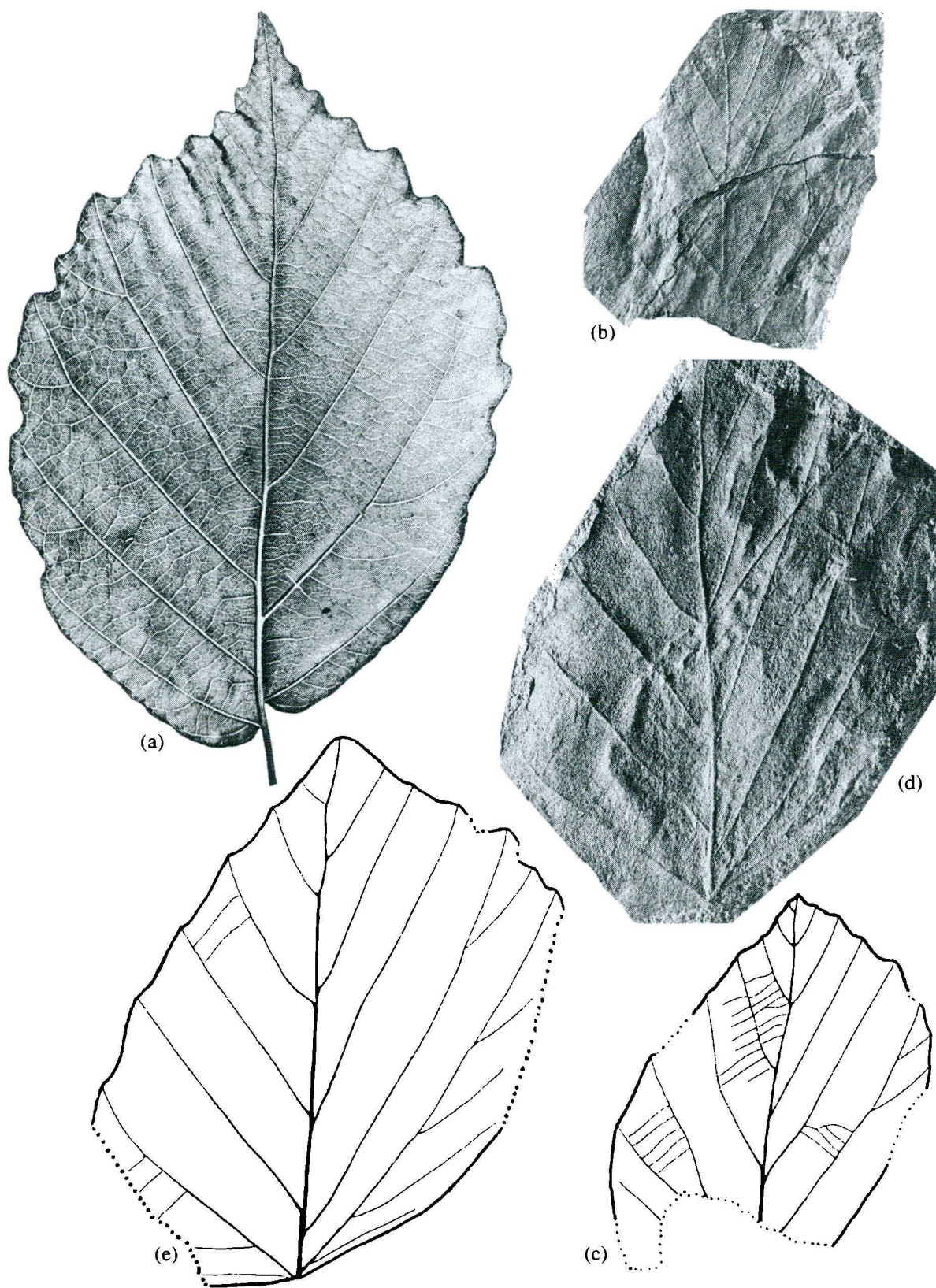


Fig. 61. (a) *Hamamelis virginiana* L., extant species for comparison, $\times 1$; (b–e) *Hamamelis certa* N. Maslova, $\times 1$: (b, c) PIN, no. 4395/463: (c) drawing; (d, e) PIN, no. 4395/522, holotype: (e) drawing; (b, c) western Kamchatka Peninsula, Utkholokskii Peninsula, coastal section between Yuznyi Cape and the mouth of the Utkholok River; Zubchatyi Cape Formation, Upper Eocene; (d, e) western Kamchatka Peninsula, Utkholokskii Peninsula, south of Zubchatyi Cape; Zubchatyi Cape Formation, Upper Eocene.

Genus *Hamamelordia* N. Maslova, gen. nov.

Etymology. From the family Hamamelidaceae and the genus *Cordia*.

Type species. *Hamamelordia ochotensis* (Cheleb.) N. Maslova comb. nov.

Diagnosis. Leaves entire, petiolate. Leaf blade ovate, with cuneate, rounded, often asymmetrical base and obtuse, occasionally attenuate apex. Leaf margin toothed. Teeth large, with rounded apex, with their basal side longer than their apical side. Basal veins deviate above leaf blade base, not reaching lower one-third of leaf length. Weak infrabasal veins perpendicular to midvein and camptodromous. Vascular elements with numerous scalariform thickenings.

Species composition. *Hamamelordia ochotensis* (Cheleb.) N. Maslova.

Comparison. The new genus is macromorphologically similar to the extant hamamelid genera *Hamamelis* and *Parrotia*. It differs in such characters lacking in hamamelids as the midvein that is straight along its entire length, basal veins deviating above the base of the leaf blade, infrabasal veins, and the decurrent base of the leaf blade. The genus differs from the genus *Cordia* (family Boraginaceae A.L. de Jussieu) in the secondary veins closely spaced basally, less prominent venation (especially tertiary venation), thick petiole significantly exceeding the midvein in thickness, and the scalariform thickenings of walls of vascular elements.

Remarks. Leaves of this type were originally described by Chelebaeva (1984) from the Upper Eocene deposits of the Irgirinskaya Formation (western Kamchatka Peninsula) as *Cordia ochotensis* Cheleb. She also described *C. kamtschatica* Cheleb. from the Irgirinskaya, Shamankinskaya, and Kamchik formations of the Kamchatka Peninsula and proposed two new combinations *Cordia platanifolia* (Ward) Cheleb. and *Cordia congerminalis* (Hollick) Cheleb. for the leaves previously assigned to the formal genus *Grewiopsis* (Eocene of Montana, Ward, 1887; Paleocene of Alaska, Hollick, 1936; Maastrichtian of Tsagayan, Kryshfovich and Baikovskaya, 1966).

The systematic assignment of these fossils to the genus *Cordia* was questioned by Budantsev (1997). This paleobotanist supposed their affinity to one of the extinct lines of the family Hamamelidaceae. However, for lack of convincing evidence he made no changes in the nomenclature of the species except for the quotation marks.

The modern genus *Cordia* includes greatly various leaf morphotypes. Several species (*C. myxa* L., *C. alba* Roem. et Schult., and *C. grandis* Roxb.) exhibit a vague similarity to this fossil material. However, within the limits of these species the morphology of the leaf blade varies.

Among the characters typical of *Cordia* (few secondary veins, deviation of basal veins from one point or

with an insignificant shift above the leaf base, brochidromous basicopic veins deviating from basal veins, and the presence of infrabasal veins), *Hamamelordia ochotensis* comb. nov. has several distinctive features that are not characteristic of *Cordia*. First of all, these are large teeth developed on the endings of secondary veins. A group of extant species, used for comparison, has leaves with low concave-concave notched teeth, which are present both on secondary and basicopic veins. If the basicopic veins loop instead of end in teeth, they show no such distinct loops as in *Hamamelordia ochotensis* comb. nov. The midvein with a variously sinuous upper part, which is observed in the majority of specimens, is not characteristic of *Cordia*. Slightly decurrent leaf bases occasionally occur in extant species of *Cordia*; however, among specimens of *Hamamelordia ochotensis* comb. nov. there are those with a well-defined cuneate leaf base, lacking in *Cordia*.

Reviewing the distinctions between fossil members of "*Cordia*" and species of *Hamamelis*, Chelebaeva (1984) pointed out that ovate leaf blades and teeth appearing in the upper leaf region are not characteristic of *Hamamelis*. However, herbarium studies have revealed the presence of such forms among extant members of *Hamamelis* (pl. 59, fig. 6). Of some interest is a convergent similarity to the Pliocene *Hamamelis kachetica* Kolak., which is depicted in *Iskopaemye...* (1974, vol. 1, p. 130, text-fig. 81).

The most essential morphological differences between *Hamamelordia ochotensis* comb. nov. and the extant hamamelid genera taken for comparison are a cuneate leaf base and basal veins deviating above the leaf base. Extant members of *Hamamelis* usually have a sinuous midvein, although leaves with a straight midvein also occur. Morphotypes with a straight midvein are more typical of *Hamamelordia ochotensis* comb. nov., although midveins that are weakly sinuous in the upper leaf region have been observed in some specimens.

After the paper by Chelebaeva (1984), Wang and Li (2000) analyzed the morphological variability of a recently discovered genus, *Shaniodendron* (Hamamelidaceae). These researchers studied three leaf groups in *Shaniodendron*: (1) juvenile, (2) mature, and (3) leaves of reproductive shoots. The genera *Parrotia*, *Parrotiopsis*, *Fothergilla*, and *Hamamelis* were used for comparison. The leaf blades from the first group are ovate, with a rounded base, basal veins reaching one-third of the leaf blade length, and large teeth at the ends of secondary veins (Wang and Li, 2000; text-figs. 1a, 1b, pl. I, figs. 1–5). Leaves of this morphotype (Figs. 65a, 65b) resemble leaves of *Hamamelordia ochotensis* comb. nov. but differ from them in the small sizes and more pointed teeth. Leaves of the third group (Wang and Li, 2000; text-fig. 1d, pl. I, figs. 9–14) are similar to entire- or wavy margined specimens of *Hamamelordia* gen. nov. (Fig. 63d).

In spite of the similarity between the leaves under description and those of *Cordia*, the leaf macromor-

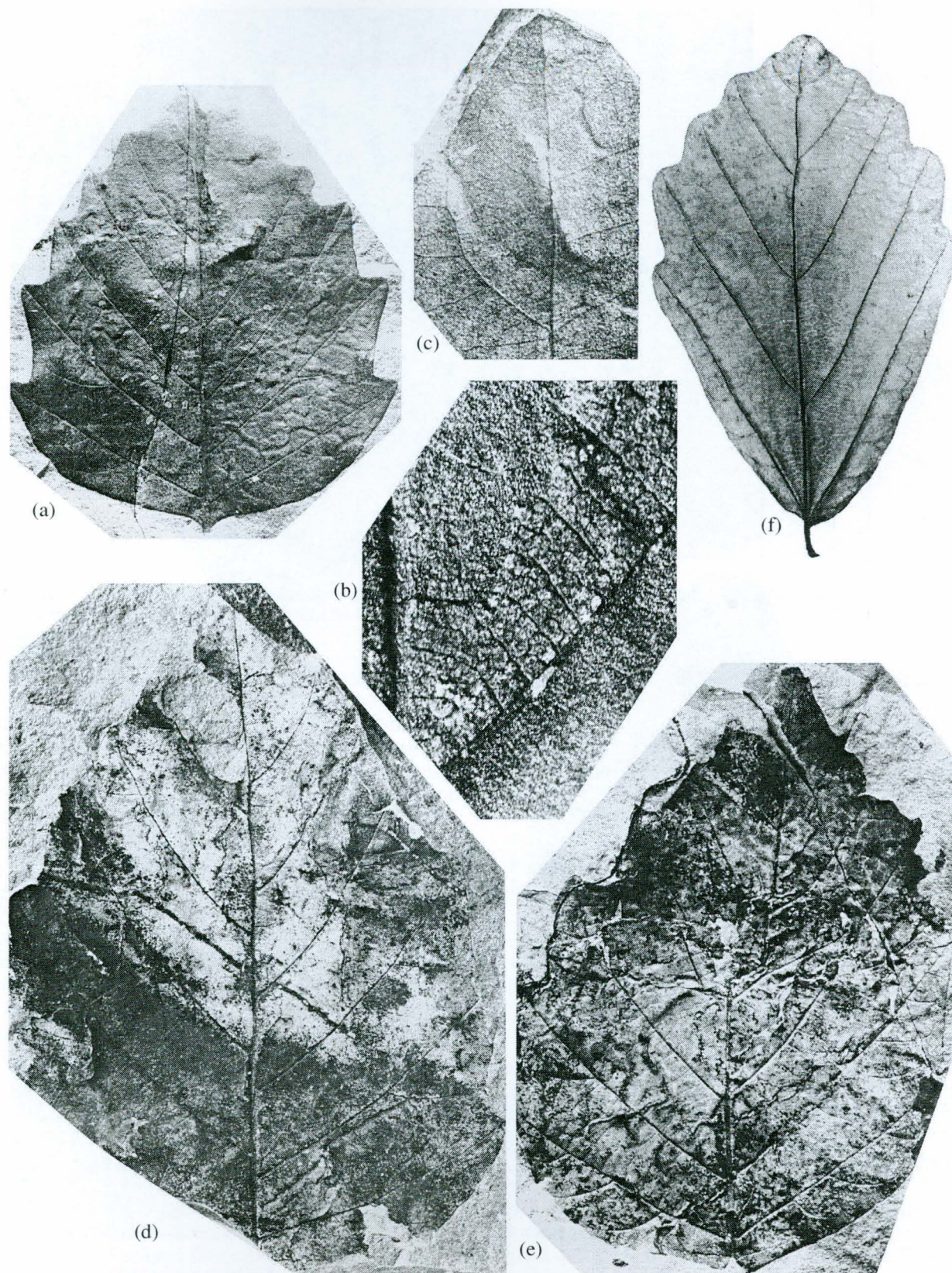


Fig. 62. *Hamamelordia ochotensis* (Chelebaeva) N. Maslova, comb. nov.: (a) PIN, no. 3862/242, $\times 1$; (b) PIN, no. 3862/532, counterpart of PIN, no. 3862/242, tertiary venation, $\times 5$; (c) PIN, no. 3862/532, venation pattern in tooth, $\times 2$; (d) PIN, no. 3862/526, $\times 1$; and (e) PIN, no. 3862/245, $\times 1$; northwestern Kamchatka Peninsula, Podkagernaya Bay; Irginskaya Formation, Upper Eocene; (f) *Hamamelis virginiana* L., extant species for comparison, $\times 1$.

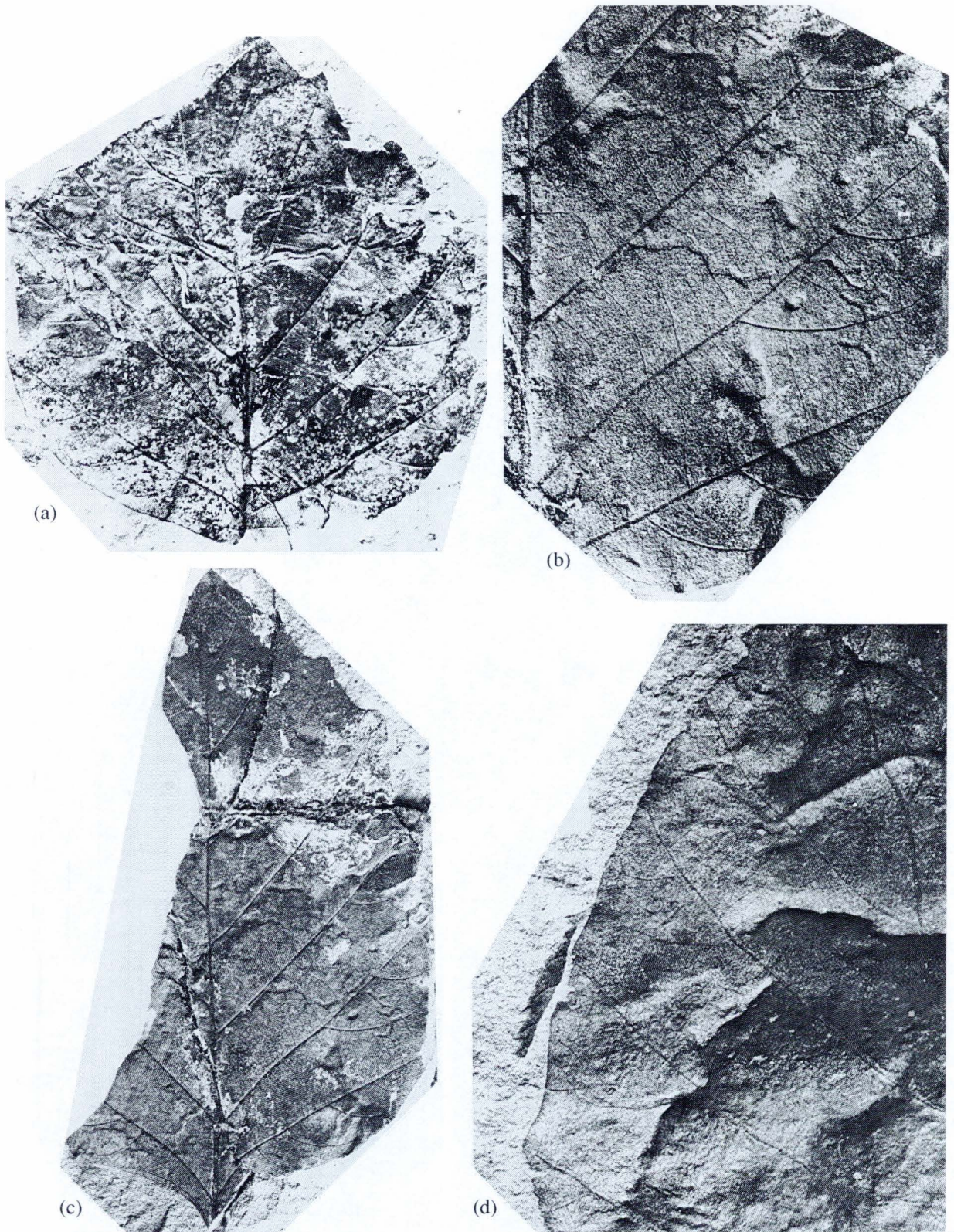


Fig. 63. *Hamamelordia ochotensis* (Chelebaeva) N. Maslova, comb. nov.: (a–c) PIN, no. 3862/243: (a) $\times 1$, (b) $\times 2$, and (c) PIN, no. 3862/537, $\times 1$; (d) PIN, no. 3862/517, $\times 2$; northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgirinskaya Formation, Upper Eocene.

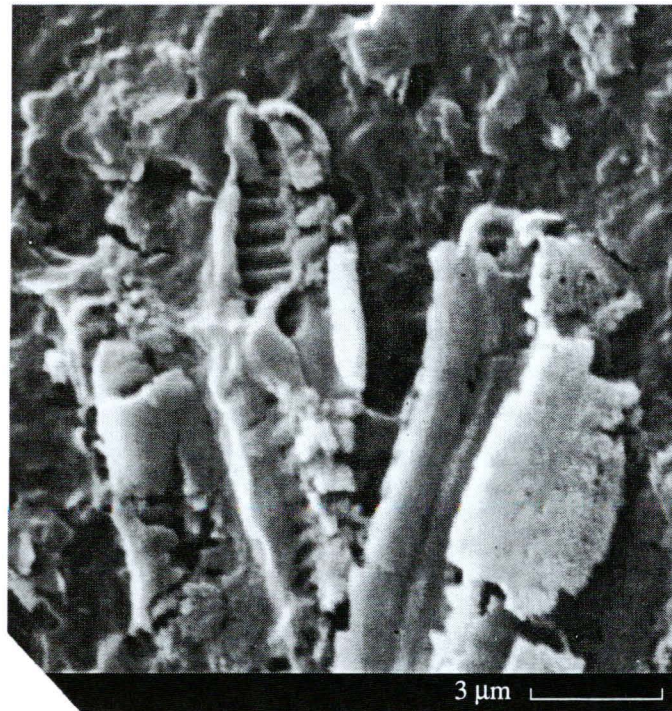


Fig. 64. *Hamamelordia ochotensis* (Chelebaeva) N. Maslova, comb. nov.: PIN, no. 3862/243. tracheal elements with scalariform thickenings of walls; northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgiminskaya Formation, Upper Eocene.

phology instead suggests the assignment of *Hamamelordia ochotensis* comb. nov. to the family *Hamamelidaceae*. This is additionally confirmed by the structure of vascular elements. Scalariform thickenings of vessel walls with numerous partitions are typical of the *Hamamelidaceae*, while members of the family *Boraginaceae* have vessels with pores (Goldberg, 1986).

Presently, other species of *Cordia* described by Chelebaeva are difficult to estimate. As is shown above, several genera, including *Grewiopsis*, constitute a polymorphous group supposedly related to the *Hamamelidales*. Hence, confident taxonomic assignment of the combinations proposed by Chelebaeva needs a comprehensive study of the type material. In my opinion, *Cordia kamtschatica* represents a heterogeneous group of taxa, some of which supposedly belong to the *Platanaceae*.

***Hamamelordia ochotensis* (Chelebaeva) N. Maslova, comb. nov.**

Cordia ochotensis: Chelebaeva, 1984, p. 609, figs. 4, 1–4; fig. 5; fig. 6.

"*Cordia*" *ochotensis*: Budantsev, 1997, p. 98, pl. 73, fig. 1; pl. 74, figs. 1–3; pl. 75, figs. 1–3; pl. 76, figs. 1–3; pl. 77, figs. 1 and 2.

Holotype. Institute of Volcanic Geology and Geochemistry, Far East Division, Russian Academy of Sciences, no. 8101:46, petiolate leaf impression, western Kamchatka Peninsula, coast of the Tobizin Peninsula, 2 km west of the Podkagernaya River mouth, Irgiminskaya Formation, Upper Eocene; Chelebaeva, 1984, p. 609, figs. 4, 1; 6, 1.

Diagnosis. Leaves entire and petiolate. Leaf blade ovate, with rounded, often unequal, variously decurrent base and obtuse, occasionally attenuated apex. Leaf margin toothed, more rarely entire. Teeth large, with rounded apex and basal side larger than apical side. Teeth located at endings of secondary veins, basiscopic veins ending camptodromously. Basal veins deviating above leaf blade base, not higher than lower one-third of leaf length. Weak infrabasal veins camptodromous and perpendicular to midvein.

Description (Figs. 62a–62e, 63a–63d; 64, 65c–65g). The leaves are entire and petiolate. The petiole is prominent, up to 5 cm long. The leaf blade is ovate with an obtuse, occasionally slightly attenuated, apex and rounded base, which is usually decurrent and, occasionally, cuneate.

The leaf margin is toothed, occasionally undulate or entire. The teeth are large, with an obtuse or (more rarely) acute apex, the basal (convex) side of the tooth is considerably larger than the apical (concave) side.

The leaf base is always entire-margined. The largest teeth occur in the middle region of the leaf. The midvein is prominent, in the upper part becoming greatly thinner and occasionally sinuous. The basal veins deviate above the leaf base at an angle of 50°–65°. They are as thick as secondary veins and give rise to five basiscopic deviations, which end camptodromously. Acroscopic branches are absent. As a rule, there is a pair of thin infrabasal veins, which are perpendicular to the midvein and end blindly. The secondary veins are

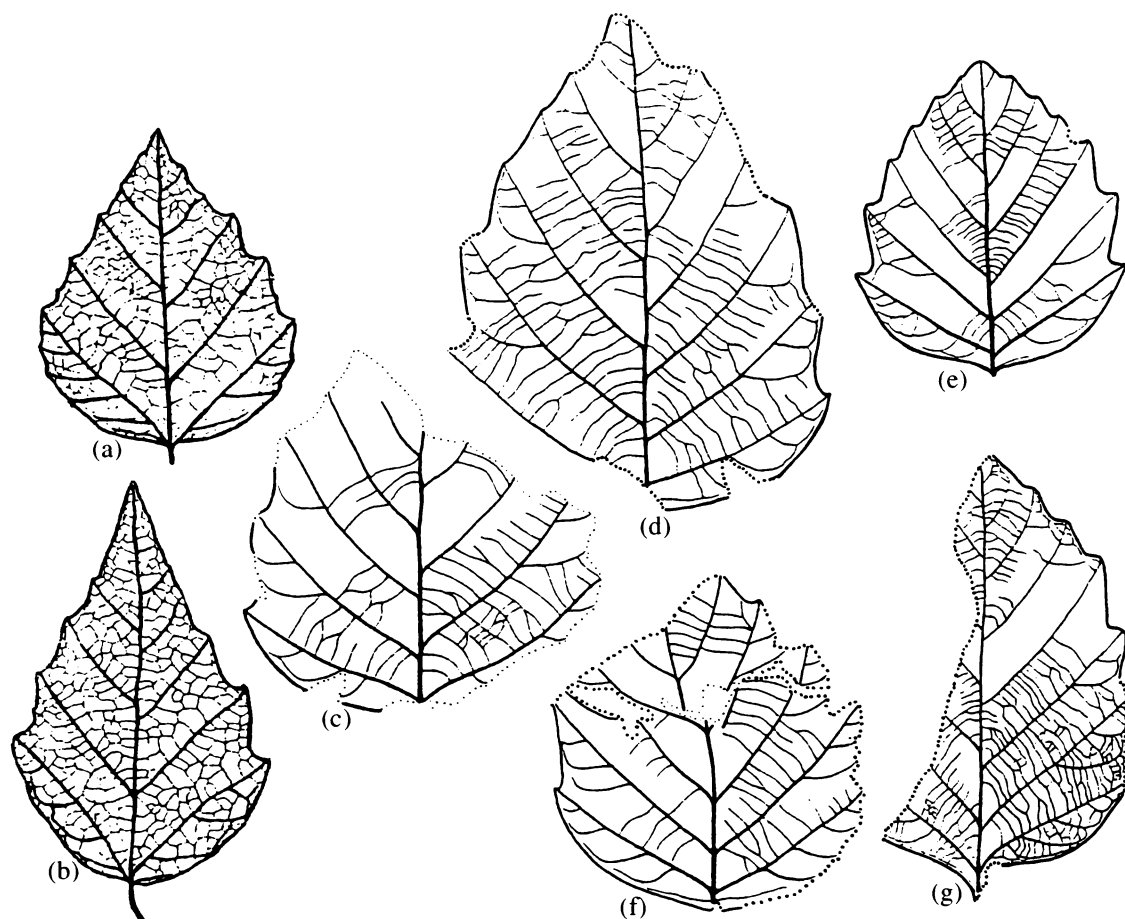


Fig. 65. (a, b) *Shaniodendron subaequale* Deng, Wei et Wang, extant species for comparison, after Wang and Li (2000), $\times 0.5$; (c–g) *Hamamelordia ochotensis* (Chelebaeva) N. Maslova, comb. nov., $\times 0.5$: (c) PIN, no. 3862/239; (d) PIN, no. 3862/526; (e) PIN, no. 3862/242; (f) PIN, no. 3862/243; and (g) PIN, no. 3862/537; (c–g) northwestern Kamchatka Peninsula, Podkagernaya Bay; Irgirinskaya Formation, Upper Eocene.

straight in the lower leaf part and slightly arch-shaped in the upper part. They constitute five to eight pairs and deviate at an angle of 35° – 50° , the lower two to four veins branch two or three times, camptodromously connecting with each other. In the upper leaf part the midvein can form one or two weak veins ending camptodromously. The tertiary veins are branching or non-branching. There are three or four tertiaries per 1 cm of secondary vein. They often form anastomoses. The angle between the midvein and tertiaries is about 120° – 130° in the lower leaf part and 90° – 110° in the upper leaf part.

After maceration vascular elements show numerous scalariform thickenings (Fig. 64).

Material. Eleven leaf specimens of different preservation from the Chemurnaut Bay locality (Kamchatka Peninsula).

Genus *Parrotia* C.A. Meyer

Parrotia kamchatica N. Maslova, sp. nov.

Etymology. From the Kamchatka Peninsula.

Holotype. PIN, no. 3862/179, Moscow; leaf impression devoid of apex; northwestern Kamchatka Peninsula, Podkagernaya Bay, Irgirinskaya Formation; Upper Eocene; Figs. 66a–66c, 67d.

Diagnosis. Leaf blade obovate, with rounded, often slightly asymmetrical base and obtuse apex. Leaf toothed in its upper half and entire-margined in lower part. Large, obtuse teeth develop at endings of secondary veins. Basicopic veins end camptodromously. Basal veins naked basally (up to 2–3 mm), as thick as lower pair of secondary veins, reach about one half of leaf blade. Secondary veins in points of their attachment to the midvein form characteristic thickenings.

Description (Figs. 66a–66f, 67b–67e). The leaves are obovate and slightly asymmetrical. The petiole is up to 5 mm long. The base of the leaf blade is rounded, rounded-cuneate, and asymmetrical. The leaf apex is obtuse. The lower leaf part is entire-margined, the upper margin is undulate or weakly toothed. The teeth are low and obtuse.

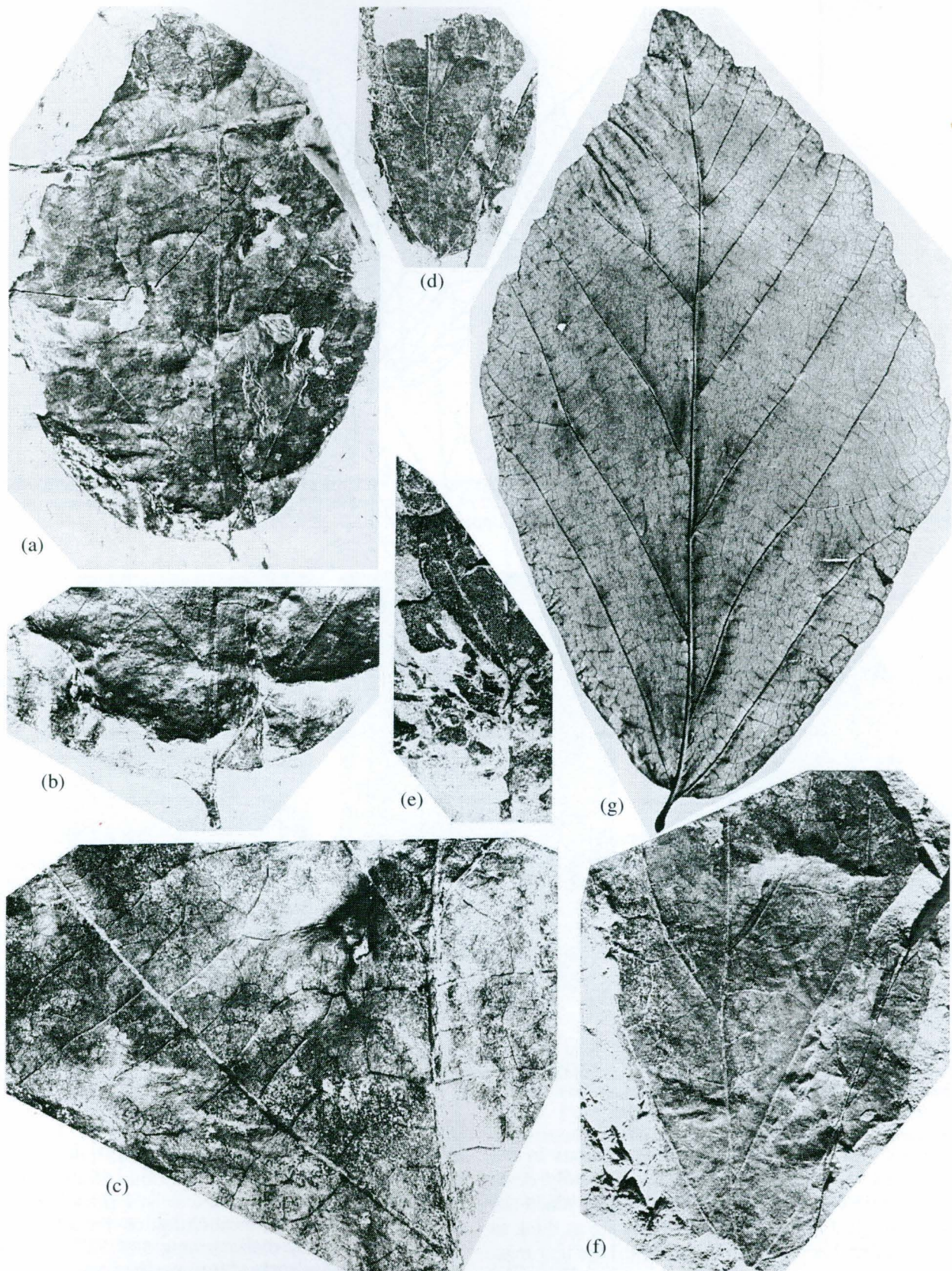


Fig. 66. (a–f) *Parrotia kamchatica* N. Maslova, sp. nov.: (a–c) PIN, no. 3862/179, holotype: (a) $\times 1$; (b) leaf base, $\times 2$; and (c) tertiary venation, $\times 3$; (d) PIN, no. 3862/175, $\times 1$; (e) PIN, no. 3862/174, $\times 1$; and (f) PIN, no. 3862/175, $\times 2$; northwestern Kamchatka Peninsula, Podkagernaya Bay; Irginskaya Formation, Upper Eocene; (g) *Parrotia persica* C.A. Meyer, extant species for comparison, $\times 1$.

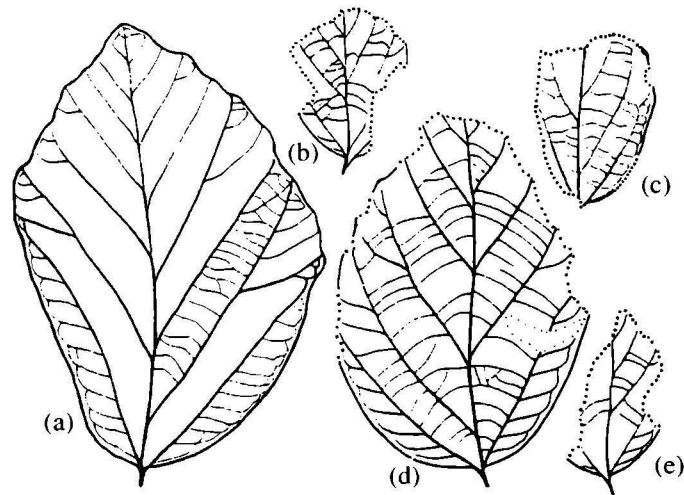


Fig. 67. (a) *Parrotia persica* C.A. Meyer, extant species for comparison, $\times 0.5$; (b–e) *Parrotia kamchatica* N. Maslova, $\times 0.5$: (b) PIN, no. 3862/288; (c) PIN, no. 3862/175; (d) PIN, no. 3862/179, holotype; and (e) PIN, no. 3862/291; (b–e) northwestern Kamchatka Peninsula, Podkagemaya Bay; Irginskaya Formation, Upper Eocene.

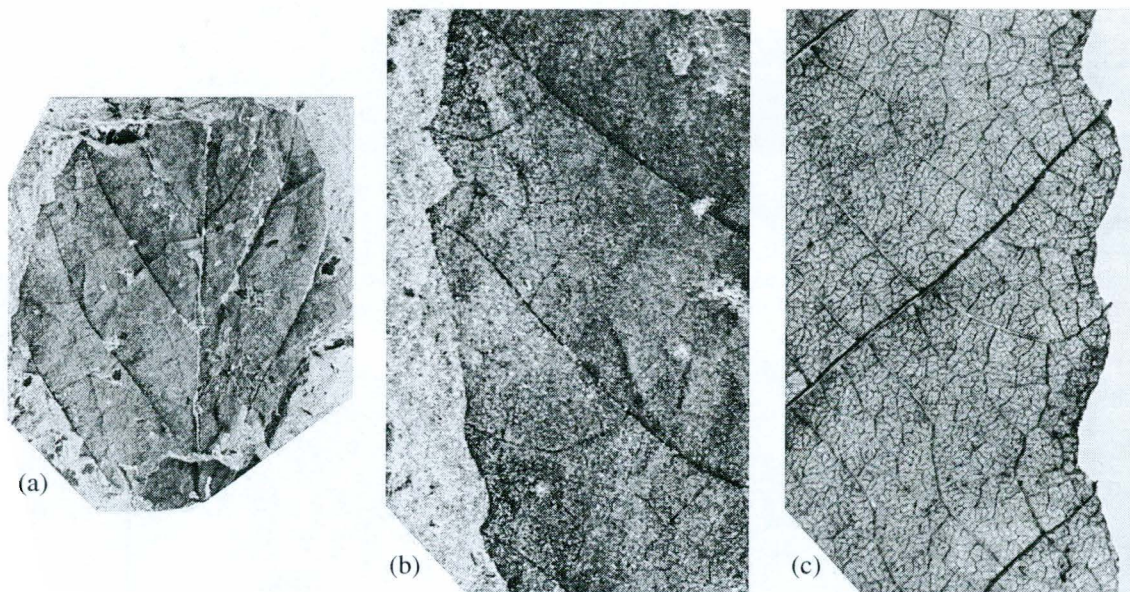


Fig. 68. (a, b) *Parrotia pristina* (Ettingsh.) Stur., PIN, no. 4855/15: (a) $\times 1$ and (b) leaf blade margin, $\times 3$; eastern Sakhalin. Shakhtnaya River, tributary of the Gornaya River; Verkhneduisкая Formation, Lower Miocene; (c) *Parrotia persica* C.A. Meyer, extant species for comparison, tertiary venation and marginal serration, $\times 3$.

The midvein is straight or slightly sinuous in the upper leaf part. The basal veins are naked basally, deviate at an angle of about 30° – 40° , and nearly reach the middle of the leaf blade. The basal veins are as thick as the secondaries, becoming thinner toward the leaf margin and disappearing among tertiary veins. From the lower side the basal veins send up to eight weak veins, which connect brochidodromously between each other. The secondary veins are thin, arched, number at least

six pairs, deviate at an angle of 30° – 45° , and form one or two basiscopic branches. In points of attachment to the midvein they form characteristic thickenings. The tertiary veins are nonbranching or branching, with anastomoses. They make an angle of 120° – 130° relative to the midvein. In the upper leaf part, this angle becomes 100° – 110° .

Comparison. The species resembles *P. fagifolia* (Goepf) Heer described by Tanai and Suzuki (1965)

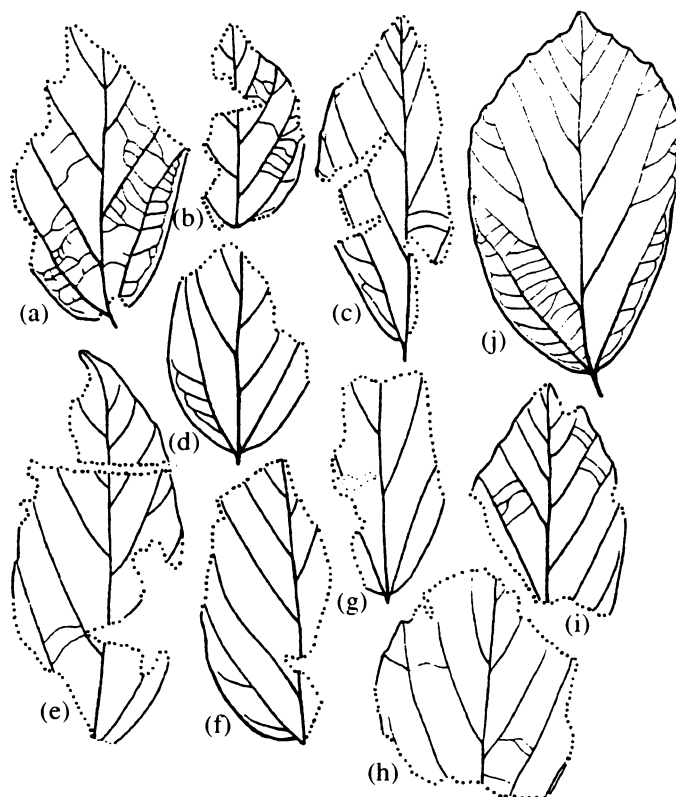


Fig. 69. *Parrotia pristina* (Ettingsh.) Stur., $\times 0.5$: (a) PIN, no. 3782/16; (b) PIN, no. 3782/17; (c) PIN, no. 3782/9; (d) PIN, no. 3782/19; (e) PIN, no. 3782/20; (f) PIN, no. 3782/18; (g) PIN, no. 3782/7; (h) PIN, no. 4855/16; and (i) PIN, no. 3782/21; (a–g, i) eastern Sakhalin, Korallovka River; Verkhneduiskaya Formation, Lower Miocene; (h) eastern Sakhalin, Shakhtnaya River, tributary of the Gornaya River; Verkhneduiskaya Formation, Lower Miocene; (j) *Parrotia persica* C.A. Meyer, extant species for comparison, $\times 0.5$.

from the Miocene Yosioka Formation of Japan. The new species differs in the more elongate leaf blade (the length/width ratio in the new species is 1.5–2.0 times that in *P. fagifolia*) and the greater number of secondaries.

Material. Four incomplete leaf impressions, two of which (with counterpart), come from the type locality.

Parrotia pristina (Ettingsh.) Stur

Parrotia pristina: Stur, 1867, p. 192, pl. 5, figs. 2 and 3; Fotyanova, 1988, p. 79, pl. 3, fig. 11; pl. 4, figs. 2 and 3; text-figs. 31, 2, 4, 5, and 9.

Description (Figs. 68a, 68b, 69a–69i). The leaf blade is oval, its length/width ratio is 1.8–2.3. The leaf base is rounded, the apex is gradually narrowing, pointed. The lower half of the leaf blade is devoid of teeth. In the upper leaf part there are low teeth, occasionally with a prominent ending of a secondary vein (Fig. 68b). The teeth are often poorly defined and the leaf margin appears to be undulate.

The midvein is straight, the basal veins are as thick as the secondaries, reach a half or more of the leaf

length, and become thinner and disappear near the margin or loop with the lower secondary vein. The bases of the basal veins are naked (Figs. 69c, 69f). The basispic deviations of basal veins are numerous (up to ten), weak, connecting by broken loops. There are four to six pairs of secondary veins, which arch and end in teeth. The tertiary veins are indistinct, usually branching.

Comparison. The species is similar to the extant *P. persica*, especially to those morphotypes that have symmetrical leaf blades and a length/width ratio approximating 2.0 (Fig. 69k). Typical leaves of the extant *Parrotia* have asymmetrical leaf blades with numerous secondaries and their basispic deviations.

Remarks. Some of the material is described under the same specific name in Fotyanova (1988).

Occurrence. Austria, plant-bearing beds, Miocene. Eastern Sakhalin Island, Korallovka River, Verkhneduiskaya Formation, Lower Miocene.

Material. About 20 specimens from the Korallovka River locality, Sakhalin Island.

CHAPTER 7. ANALYSIS
OF TAXONOMIC
AND MORPHOLOGICAL DIVERSITY
OF THE PLATANACEAE
AND HAMAMELIDACEAE

On the basis of both the original material and published data on fossil and extant hamamelids, I tried to estimate their taxonomic and morphological diversity during specific intervals of geological time. Here the diversity is assessed at the generic level as numbers of genera per geological epoch.

Any quantitative estimation of the diversity depends on several factors such as the completeness of the geological record, ecological differences, taphonomy, evolutionary transformations, errors in dating, and the unequal duration of stratigraphic units.

Recently, Alekseev *et al.* (2001) showed that interpretations of the geological distribution of taxa strongly depend on the time scale chosen. Thus, the summation of taxa that existed during a relatively long time interval (over a geological age) may result in distortion of the real diversity. However, distortion is inevitably present even using the time scale of geological ages let alone their unequal durations. Age assignments down to ages/stages of the International geochronological scale are available for most Cretaceous records, but not for Tertiary records. Because of this, the geological epoch rather than age is here used as an operational time unit. Anyway, the taxonomic (generic) richness is only one aspect of morphological diversity.

Since as taxa are established on the basis of macro- and micromorphology, taxonomic diversity reflects the morphological diversity. Yet taxonomic ranking is not an adequate representation of morphological distances between the taxa. Taxonomic diversity increases with the multiplication of species or genera that are only slightly morphologically different from each other. On

the other hand, the appearance of a deviant morphology in a single genus (such as *Oreocarpa*; Maslova and Krassilov, 2002) has a slight effect on the total taxonomic diversity but significantly increases the morphological disparity. In this respect, it seems expedient to assess the morphological disparity independently of the taxonomic diversity, but with due attention to the evolutionary significance of morphological features.

Such a study of the Hamamelidales was made for the first time and, thus, is only preliminary. The latter concerns predominantly the family Hamamelidaceae, in which a limited number of fossil taxa are presently known. However, the extant members of this family constitute a relatively diverse group of 30 genera and over 140 species, representing various combinations of vegetative and generative characters.

The most ancient find of the Hamamelidaceae is dated to the Cenomanian (*Viltyungia eclectic*). The genus *Viltyungia* is characterized by a distinctive combination of floral characters, which presently occur in representatives of three subfamilies, Altingioideae, Exbucklandioideae, and Hamamelidoideae. It definitely belongs to the so-called synthetic type, a source of morphological differentiation giving rise to a considerable taxonomic diversity later on. Although the range of morphological disparity might have been nearly the same as in present day hamamelidaceans, they were represented by fewer genera. In contrast, the diversity of extinct platanoids was considerable, with the present day *Platanus* representing only an insignificant part of it.

Therefore, the evolutionary histories of the Hamamelidaceae and Platanaceae were entirely different and they represent alternative evolutionary trends in early angiosperms. The available chronology of innovative evolutionary events and the first appearances and extinctions of morphological traits are shown in Tables 5–8 and are discussed later in the chapter.

Table 5. Stratigraphic range of the platanoid genera, established on leaf remains: (1) after Maslova, 2001; (2) Hickey and Doyle, 1977; (3, 4) Budantsev, 1975; Vakhrameev, 1976; (5) *Osnovy paleontologii...*, 1963; Vakhrameev, 1976; (6) Herman, 1984; (7) Herman and Golovneva, 1988; (8) Johnson, 1996; (9) Manchester, 1986; Wolfe and Wehr, 1987; (10) Crane *et al.*, 1988; (11) Maslova, 2002a; and (12) MacGinitie, 1941

Genus	K ₁	K ₂	P ₁	P ₂	P ₃	N	Q
1. <i>Platanus</i>			—————				
2. <i>Sapindopsis</i>	—						
3. <i>Protophyllum</i>		—————					
4. <i>Pseudoprotophyllum</i>		—————					
5. <i>Credneria</i>		—————					
6. <i>Paraprotophyllum</i>		—————					
7. <i>Arthollia</i>			—————				
8. <i>Erlingdorfia</i>			—				
9. <i>Macginitiea</i>				—————			
10. <i>Platanites</i>			—————				
11. <i>Platimeliphyllum</i>				—————			
12. <i>Platanophyllum</i>					—————		

Table 6. Stratigraphic range of the platanoid genera, established on the basis of reproductive structures: (1) Crane *et al.*, 1993; (2) Pedersen *et al.*, 1994; (3) Manchester, 1986; Friis *et al.*, 1988; (4) Friis *et al.*, 1988; (5) Krassilov and Shilin, 1995; (6) Magallón-Puebla *et al.*, 1997; (7) Maslova and Kodrul, 2003; (8) Krassilov, 1973; (9) Maslova and Krassilov, 2002; (10) Krassilov, 1976; (11) Crane *et al.*, 1988; (12) Maslova, 2002a; (13) Manchester, 1986; (14) Maslova, 1997; Kvaček *et al.*, 2001

Genus	K ₁	K ₂	P ₁	P ₂	P ₃	N	Q
1. <i>Aquia</i>	—						
2. <i>Hamatia</i>	—						
3. <i>Platananthus</i>	—	—	—	—	—	—	—
4. <i>Platanocarpus</i>	—	—					
5. <i>Sarbaya</i>		—					
6. <i>Quadriplatanus</i>			—				
7. <i>Archaranthus</i>			—				
8. <i>Tricolpopollianthus</i>			—				
9. <i>Oreocarpa</i>			—				
10. <i>Carinalaspermum</i>			—				
11. <i>Platanites</i>			—				
12. <i>Chemurnautia</i>				—			
13. <i>Macginicarpa</i>				—			
14. <i>Platanus</i>				—			

FOSSIL FINDS OF THE FAMILY PLATANACEAE

While analyzing the literature, I selected those fossil taxa that seem to be most reliably identified. These are taxa established on the basis of (a) reproductive structures, (b) associations of different organs, (c) leaves studied by both macromorphological and microstructural methods, and (d) a combination of characters unique for the genus. The analysis ignores the taxa that are only listed or described without illustrations (or inadequately illustrated) or with questionable generic affinity. I discuss the taxa that were only tentatively assigned to or compared with certain families of the Hamamelidales by their authors only if I accept the assignment supported by those authors.

The first reports on fossil members of the Platanaceae belong to Lesquereux, Newberry, Velenovsky, Heer, and other European and American paleobotanists of the 19th century. Lobed leaves were usually assigned to the modern genus *Platanus*, thus supporting its early appearance in the geological record. Entire or weakly lobed leaves were assigned to the genera *Credneria*, *Protophyllum*, and *Pseudoprotophyllum* (Zenker, 1833; Lesquereux, 1874; Hollick, 1930). Generic names of fossil plants with the suffix "ites" implied close taxonomic affinity to extant genera. For example, the genus *Hamamelites* included fossil leaves supposedly belonging to an extinct species of *Hamamelis* (Saporta, 1868). The name *Platanites* meant leaves of fossil plane trees (Forbes, 1851). This approach to naming fossil genera had been widely used until the 1960s. It was shown later that leaves of *Platanites* are compound, comprising a terminal leaflet of typically platanoid appearance and two asymmetrical lateral leaflets

(Crane *et al.*, 1988; Boulter and Kvaček, 1989; McIver and Basinger, 1993; Johnson, 1996), a morphology no longer existing in the Platanaceae.

Later, such taxa were partly emended on the basis of their type species morphology (Krassilov, 1979), or they were abandoned as taxonomically ill-defined. The descriptions of the Cretaceous and Paleogene platanoids of the Far East, Siberia, and Kazakhstan are based on the traditional classification (Vakhrameev, 1952; Kryshtofovich and Baikovskaya, 1966; Shilin, 1986). Budantsev (1975) and Herman and Golovneva (1988) were the first to introduce leaf genera with definite morphological characteristics. However, abundant leaf material has not yet been taxonomically revised with an application of microstructural analysis. Consequently, the validity and content of some platanoid genera have remained controversial.

For instance, *Osnovy...* (1963), *Iskopaemye...* (1974), and Krassilov (1979) interpret *Protophyllum* and *Pseudoprotophyllum* as taxonomically synonymous with vague differences between them. Other researchers accept these genera as taxonomically valid (Budantsev, 1975; Vakhrameev, 1976; Herman, 1984). The genus *Protophyllum* presently seems heterogeneous. Fragmentary epidermal data on the leaves of *Protophyllum* morphotype from the Cretaceous of Sakhalin Island show a greater resemblance to the Hamamelidaceae than to the Platanaceae (Krassilov, 1973). However, this conclusion should not be extended to species of *Protophyllum* from other localities. Only a detailed study of the type material can determine the systematic position of *Protophyllum* and other morphological genera.

A different base shape (truncate to pseudopeltate) allowed Herman (1984) to separate some leaf remains in the genus *Paraprotophyllum* previously assigned to *Protophyllum* (Kryshstofovich and Baikovskaya, 1960).

The leaves assigned to *Protophyllum* and *Arthollia* combined platanoid and hamamelid macromorphological characters. *Arthollia anadyrensis* sp. nov. shows the platanoid epidermal structures. Similar leaves with large marginal glands are found in association with staminate heads of the extinct platanoid genus *Sarbaya* (Krassilov and Shilin, 1995).

The material that is assigned to the genus *Credneria* (Zenker, 1833) is awaiting a detailed analysis. There are two groups of species within this genus that different in major morphological characters and ranges. The genus was originally described from the Cretaceous of the Hartz Mountains, Germany (Zenker, 1833). Later, Hollick (1930) described under this generic name leaves from the Late Cretaceous of Alaska. Members of *Credneria* were recorded from the Cretaceous of the Russian Far East and northeastern Russia (Kryshstofovich and Baikovskaya, 1960; Ablav, 1974). The European and Pacific groups of species supposedly belong to different genera (*Osnovy...*, 1963; Vakhrameev, 1976). Some of the Cretaceous leaf remains described as *Credneria* even macromorphologically should be assigned to hamamelids rather than to platanoids. For example, *Credneria grewiopsioides* Hollick from the Cretaceous of Sakhalin Island (Kryshstofovich and Baikovskaya, 1960) differs from the type material in its distinctly asymmetrical leaf blade and a lower deviation of unequal basal veins. These characters associating with such features as low, wide, widely set marginal teeth, sinuous secondary veins, and weak tertiaries are typical of the Hamamelidaceae.

The first finds of the leaf morphotype assigned to *Platanus* are dated to the Late Cretaceous. However, the presence of the genus *Platanus* in the Cretaceous has not been substantiated by reproductive structures. The appearance of this genus in the northern Asian floras was interpreted in two different ways. A common opinion holds this genus to appear in the Late Cretaceous contemporaneously with other platanoid genera that developed in parallel later on (Budantsev, 1975; Herman, 1994). Alternatively, it might have appeared only in the Paleogene implying that Cretaceous records based on leaves are highly doubtful (Wolfe, 1973; Krassilov, 1976, 1979; Maslova, 2001, 2002b).

Several cases of cooccurrence of typically platanoid leaves and reproductive structures that radically differ from those of the modern plane tree have recently been recorded. For instance, "*Platanus*" *raynoldsii*, described by Krassilov (1976) on the basis of the leaf remains from the Tsagayan deposits of the Amur region, associates with specific reproductive structures (pistillate heads of *Oreocarpa bureica*, seeds of *Carnalasperrum bureicum*, and staminate heads of *Tricolpopollianthus burejensis* Krassilov), which exhibit

characteristic features of the family Platanaceae, differing, however, from those of the modern plane (Maslova and Krassilov, 2002). The leaves of "*Platanus*" *raynoldsii* are also highly polymorphous. Macromorphologically, their extreme variants are even referable to genera of other families. The most typical morphotype was traditionally assigned to the genus *Platanus*; however, this is not the case for the Tsagayan finds. It is obvious that the Tsagayan plant had, in addition to morphotypes typical of *Platanus*, other morphotypes and other reproductive organs.

Leaves of platanoid appearance were found in association with the staminate heads of *Archaranthus krassilovii*. The assemblage of microstructural characters sets these heads far apart from the modern plane tree (Maslova and Kodrul, 2003). It would have been rewarding to look for platanoids among the leaves assigned to *Acer*, *Vitis*, etc. Microstructural analysis may facilitate their recognition.

Not all species of the genus have lobed leaves. The extant *Platanus kerrii* and the Miocene *P. neptunii* are characterized by entire elliptical leaves with pinnate venation, whereas their reproductive morphology fits the generic diagnosis.

Moreover, the leaves of extinct Platanaceae are rather similar to those of extant hamamelids. Thus, the leaves of *Platimelis* (Golovneva, 1994), *Platimeliphyl- lum* (Maslova, 2002a), as well as some Cretaceous leaves assigned to *Platanus*, have morphological characteristics of both families. Some of these leaves supposedly belong to extinct genera of the Hamamelidaceae, the geological history of which (especially of leaf remains) is presently insufficiently documented. Likewise, the reproductive structures of some hamamelidaceans convergently resemble those of the Platanaceae. They can be distinguished only with the application of microstructural analysis (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b).

In my view the leaves of *Platanus prisca* Herman from the Coniacian deposits of the northwestern Kamchatka Peninsula (Herman, 1989) are comparable with *Hamamelis*. Herman described the leaf blade in this species as symmetric. However, the illustrations show a distinctly asymmetrical leaf with basal veins unequal in length and in height over the leaf blade base. The illustration showing a fragmentary leaf base also suggests its asymmetric shape. The teeth are large, widely set, with slightly convex sides. The basal veins are as thick as the midvein and as the next (after the basal veins) pair of secondary veins. The tertiary network is fine. These characters suggest that the leaves are closer to the Hamamelidaceae than to the genus *Platanus*. At the same time, *P. prisca* differs from *Hamamelis* in the presence of marginal glands, which are absent in this latter genus, although they are common in some other hamamelids. In addition, the leaves of *Platanus prisca* resemble the juvenile leaves of extant *Shaniodendron* (Figs. 64a, 64b).

The hamamelidaceous affinity of the Late Albian–Early Cenomanian *Platanus louravetlanica* Herman et Shchepetov (Herman, 1994) is also a possibility supported by the asymmetry of the leaf blade, the unequal development of basal veins differing in length and thickness, and by the distinctive features of tertiary venation (predominantly orthogonal-reticulate). These characters relate *P. louravetlanica* to the adult leaves of *Shaniodendron* (Wang and Li, 2000, text-figs. c, d). An essential difference from the Hamamelidaceae, however, is the suprabasal deviation of basal veins and distinct infrabasal veins.

Of certain interest in this respect is the problem of differentiation between leaves of *Macginitiea* and *Platanus nobilis*. Such leaves are macromorphologically similar (see the analysis under *Macginitiea latiloba*). Leaves of *Macginitiea* associate with the reproductive structures of *Macginicarpa* and *Platananthus* (Manchester, 1986), which are different from those of *Platanus*. Pigg and Stockey (1991) described the Paleocene leaves of *Platanus nobilis* s. str. found in association with reproductive structures of *Macginicarpa* and *Platananthus*. This find allows one to question the assignment of such leaf remains to *Platanus*. Similar leaves from the Paleocene of the Takhobe River (Primorye), which were assigned to *Platanus nobilis* (Borsuk, 1952), differ in the closely set prominent tertiaries; however, they are identical to those of *P. nobilis* in all other macromorphological features. Nevertheless, the association of such leaves with reproductive structures differing from those of the plane tree (Pigg and Stockey, 1991) makes their assignment to *Platanus* unjustified. In the future, the "*Platanus nobilis*" morphotype should probably constitute a new genus of the Platanaceae.

Thus, recent studies have shown that the solitary extant genus *Platanus*, embracing a limited number of species, represents an insignificant part of the once diverse group of platanoids, known since the Early Cretaceous (Crane *et al.*, 1988, 1993; Friis *et al.*, 1988; Pigg and Stockey, 1991; Manchester, 1994; Pedersen *et al.*, 1994, 1997; Krassilov and Shilin, 1995; Magallón-Puebla *et al.*, 1997; Maslova, 1997, 2002; Maslova and Krassilov, 2002). Comprehensive morphological data on leaves and the reproductive structures of fossil platanoids indicate the existence in the geological past of plants showing a combination of lobed leaves typical of the plane tree and reproductive structures that are completely different from those of the plane tree. The finds of the earliest fossil reproductive structures of *Platanus* are restricted to the Paleocene (Maslova, 1997; Kvaček *et al.*, 2001).

The differences between numerous Cretaceous species of "plane trees" are often obscure. The shape of the leaf blade, the shape of the base and its expressivity, and the nature of the leaf margin morphology are sometimes used as distinctive characters of a species. Thus, Kryshstovovich and Baikovskaya (1966) have used the

general leaf outline as a distinguishing feature between *P. schmidtii* Kryshst. et Baik. and the related *P. haydenii* Newb. and *P. platanifolia* var. *latifolia*. A high range of variability of these macromorphological features in the genus *Platanus* makes their application as specific criteria unreasonable. A repeated cooccurrence in one locality of several "species" of "plane trees" and other platanoid genera suggests that they belong to a single or few polymorphic species.

Revision of Cretaceous platanoid genera should be based on morphological considerations. Namely: (1) The modern plane tree has both lobed (*Platanus* of the section *Platanus*) and entire castanoid leaves (*Platanus* of the section *Castaneophyllum*). Entire leaves have been described in the fossil *Platanus neptunii*, but most of them apparently remain unidentified. (2) In addition to simple leaves, fossil members of Platanaceae also had compound leaves. Within the latter group, the genus *Sapindopsis* greatly differs from other platanoids in leaflet morphology. *Platanites*, some morphotypes of *Erlingdorfia*, and several species of *Sapindopsis* have apical leaflets similar to the simple leaves of the plane tree, whereas the lateral leaflets have a different morphology. Found detached, such leaflets are assignable to different genera. At least some of the so-called Cretaceous plane trees possibly are apical leaflets of compound leaves of the *Platanites*, *Erlingdorfia*, and *Sapindopsis* types. Lateral leaflets are described as *Viburnum*, *Alnites*, *Grewiopsis*, and other genera (e.g., *Grewiopsis amurensis* Kryshst. et Baik., *Viburnum antiquum* (Newb.) Hollick; Kryshstovovich and Baikovskaya, 1966). Repeated cooccurrence in several localities suggests that these "genera" belong to one and the same plant. However, in each case the taxonomic decision should be based on a detailed study of macromorphological variation in large monotypic samples and with the application of microstructural methods. (3) The leaves macromorphologically referable to the Hamamelidaceae (*Platimeliphyllum*) associate with platanoid inflorescences (*Chemurnautia*). These examples show that in many cases researchers failed to differentiate the families Platanaceae and Hamamelidaceae on the basis of leaves. The role of platanoids is probably overestimated at the expense of the Hamamelidaceae.

Therefore, I believe that the Cretaceous leaf remains should not be described under the traditional name *Platanus* in spite of its wide use in many paleobotanical monographs. The leaf macromorphology is insufficient to prove the identity with modern plane trees at the generic level. Moreover, the Cretaceous finds of reproductive structures do not support the existence of plane trees at that time.

The application of the generic name *Platanus* to Cretaceous leaf remains is justified only if it is confirmed by the microstructural study of associated reproductive organs. Numerous Cretaceous species of plane trees that have been established solely on leaf remains

await a thorough revision that will probably change their generic assignment. For this purpose, the morphological variability of such leaves should be studied in representative samples and accompanied by a detailed epidermal analysis. It is quite possible that in the future Cretaceous platanoid leaves will be described under a new formal generic name. For the present they should be better described under “*Platanus*” (e.g., Krassilov, 1976).

The Cenozoic plane trees are also problematic. Specific differences often appear insignificant, within the limits of variations of previously described species (e.g., *P. nigra* Cheleb., *P. pseudoraynoldsii* Cheleb., *P. snatolana* Cheleb.; Gladenkov *et al.* 1991, 1997; etc.).

FOSSIL FINDS OF THE FAMILY HAMAMELIDACEAE

Among modern genera of the Hamamelidaceae, *Liquidambar* is most often described in a fossil state. This genus was important in the Tertiary floras of the northern hemisphere as an obligate member of broad-leaved Arcto-Tertiary forests. Its species composition

(both current and ancient) is a matter of discussion. Thus, Depape (1966) considered the modern genus as monotypic, with a single polymorphous species *L. styraciflua*, whereas Uemura (1983) suspects the presence of at least four (perhaps more) species.

Considering the high leaf polymorphism in *Liquidambar*, the establishment of a great number of fossil species based on subtle morphological distinctions is scarcely justifiable. The analysis of ancient members of the genus on the basis of both the original and published data allows classification of all extinct species of *Liquidambar* into two groups. The first group, “*Liquidambar miosinica*,” consists of the species *L. miosinica*, *L. mioformosana*, *L. mioformosana* var. *cordata*, and *L. cordata* (K. Suzuki) Uemura. The second group, “*Liquidambar pachyphylla*,” comprises *L. pachyphylla*, *L. protopalmata* (K. Suzuki) Uemura, and *L. yabei*. The groups differ in the lobe shape (short, triangular, widest at the base in the first group; narrow, elongate, and parallel-margined in the second), number of secondary veins (about six to eight pairs in the first

Table 7. Stratigraphic range of the hamamelidaceous genera, established on leaf remains: (1, 2) Golovneva, 1994b; (3) Golovneva, 1994a, 1994b; (4) Matsuo, 1967; (5, 10) Budantsev, 1983; (6) Saporta, 1868; (7) Maslova, 1995a; (8) Maslova, 1995b; (9, 11, 15, 19) Maslova, this study; (12) Wolfe and Wehr, 1987; (13) Tanai and Suzuki, 1965; Fotyanova *et al.*, 1996; (14) Budantsev, 1997; (16) Wang and Li, 2000; (17) Ozaki, 1991; (18) Huzioka and Takahasi, 1970; (20) Knobloch *et al.*, 1996; (21) Ishida, 1970; and (22) Onoe, 1974

Genus	K ₁	K ₂	P ₁	P ₂	P ₃	N	Q
							30 genera
1. <i>Renea</i>		—					
2. <i>Dizanthophyllum</i>		—					
3. <i>Platimelis</i>		—————					
4. <i>Disanthus</i>			—————				
5. <i>Corylopsis</i>			—————				
6. <i>Hamamelites</i>			—————				
7. <i>Liquidambar</i>			—————				
8. <i>Parrotiopsis</i>				—————			
9. <i>Evaphyllum</i>				—			
10. <i>Corylopsiphyllum</i>			—————				
11. <i>Sycopsiphyllum</i>				—			
12. <i>Langeria</i>				—————			
13. <i>Hamamelis</i>					—————		
14. <i>Pylgavayamia</i>					—		
15. <i>Hamamelordia</i>					—		
16. <i>Shaniodendron</i>						—————	
17. <i>Fortunearia</i>						—————	
18. <i>Distylium</i>						—————	
19. <i>Parrotia</i>						—————	
20. <i>Matudaea</i>							—————
21. <i>Sycopsis</i>							—————
22. <i>Eustigma</i>							—————

group and about eight to ten pairs in the second group), and marginal teeth (larger, hook-shaped teeth in the second group). Further information on reproductive structures and leaf epidermal micromorphology will show whether we are dealing with two groups of several closely related species or just with two species, *L. miosinica* and *L. pachyphylla*.

As noted above, the modern family Hamamelidaceae includes taxa widely divergent in their vegetative and reproductive macromorphology. Several genera (*Parrotia*, *Parrotiopsis*, *Hamamelis*, *Corylopsis*, and others) show a distinctive combination of leaf macromorphological characters allowing their relatively confident assignment to modern genera in the case of well-preserved fossils. Thus, the generic affinity of *Corylopsis orientalis* Borsuk from the Nizhneduiskaya Formation of Sakhalin Island is beyond reasonable doubt (Borsuk, 1956). In contrast, the reports on these genera made on the basis of fragmentary remains are scarcely reliable (e.g., Miocene *Hamamelis protojaponica* Tanai et Suzuki; Ablaev, 1978).

The genus *Shaniodendron*, recently discovered in the modern flora of China (Deng *et al.*, 1992a), has clarified the enigmatic presence of the genus *Fothergilla* in the Miocene Shanwang flora of China (Wang and Li, 2000). Nowadays, this genus occurs exceptionally in North America, whereas all other genera of this flora are of eastern Asiatic affinities. Wang and Li have revised hamamelid genera from the Shanwang flora, previously studied by Hu and Chaney (1940), and have shown the fossil material previously described as *Fothergilla* and *Hamamelis* to fit the limits of variation in *Shaniodendron*. They established a new combination, *Shaniodendron viburnifolium* (Hu et Chaney) Wang et Li.

Generic assignments are problematic for the hamamelidaceous leaves of a less distinctive morphology, such as simple entire-margined (or occasionally serrate near the apex) leaves with variously expressed brochidodromous venation (e.g., *Rhodoleia*, *Loropetalum*, *Distylium*, *Sycopsis*, etc.). Such finds can be easily confused with similar leaves of unrelated angiosperm families and vice versa. Hopefully the situation can be improved with an increase in the number of characters, in particular those of epidermal micromorphology, involved in taxonomic analysis.

The presence of modern taxa in Cretaceous floras is often substantiated by finds of dispersed fruits and seeds comparable to those of modern genera of the Platanaceae and Hamamelidaceae. Thus, fruits comparable with those of *Platanus* and of a reliable platanoid affinity are reported from the Cretaceous of Siberia. They, however, differ from those of the modern plane tree in the absence of basal tufts of hairs (Fig. 70). Cretaceous seeds determined as *Hamamelis*, *Disanthus*, and *Rhodoleia* also show several significant differences from the respective modern taxa (Knobloch and May, 1986). Such finds in the Cretaceous deposits are



Fig. 70. Detached fruit of the Platanaceae. SEM; eastern Siberia, Lena–Vilyui Depression, Tyung River; Timerdyakhskaya Formation, Cenomanian.

extremely important as evidence of evolutionary lines leading to modern taxa. However, their conventional assignment to the latter may result in misjudgment of the rates of evolutionary advancement.

The assignment of seeds from Late Cenozoic floras to modern hamamelidaceous genera seems to be more reliable. The finds of *Fortunearia cf. sinensis* Rehder et Wilson and *Corylopsis cf. pauciflora* Sieb. et Zucc. in the Oligocene of Siberia (Dorofeev, 1963) appear fairly modern, differing from extant species in their smaller size alone.

TAXONOMIC DIVERSITY OF THE PLATANACEAE

Figure 71 shows the changes in the total number of genera of platanoid angiosperms (on the basis of leaves and remains of reproductive structures). During the Early Cretaceous, the taxonomic diversity of the family was relatively high; all finds are assigned to extinct genera. A significant (more than twofold) increase of generic numbers occurred in the Late Cretaceous and continued in the Paleogene. This period is characterized by the maximal taxonomic diversity of the Platanaceae.

Reproductive remains of the genus *Platanus* are known starting with the Paleocene (Maslova, 1997; Kvaček *et al.*, 2001). The specific diversity of this genus increased through the Cenozoic. This was accompanied by an increase in abundance of plane remains. Obviously, the Paleocene and the beginning of

Table 8. Stratigraphic range of the hamamelidaceous genera, established on the basis of reproductive structures: (1) Maslova and Golovneva, 2000a; (2) Zhou *et al.*, 2001; (3) Maslova and Golovneva, 2000b; (4) Magallón-Puebla *et al.*, 2001; (5) Endress and Friis, 1991; (6) Magallón-Puebla *et al.*, 1996; (7) Knobloch, 1960; Krassilov, 1976; (8) Maslova and Krassilov, 1997; (9) Krassilov and Fotyaynova, 1995; (10) Manchester, 1994; (11, 16, 17, 19) Kirchheimer, 1957; (12) Gregor, 1978; Knobloch and Mai, 1984; (13) Knobloch and Mai, 1984, 1986; (14) Knobloch and Mai, 1986; (15) Friis, 1985; and (18) Miki, 1941

Genus	K ₁	K ₂	P ₁	P ₂	P ₃	N	Q
Inflorescences							30 genera
1. <i>Viltyungia</i>		—					
2. <i>Microaltingia</i>		—					
3. <i>Lindacarpa</i>		—					
4. <i>Androdecidua</i>		—					
5. <i>Archamamelis</i>		—					
6. <i>Allonia</i>		—					
7. <i>Steinhauera</i>			—				
8. <i>Evacarpa</i>				—			
9. <i>Itelantha</i>				—			
10. <i>Fortunearites</i>					—		
11. <i>Hamamelidanthium</i>					—		
Seeds							
12. <i>Disanthus</i>			—	—	—	—	—
13. <i>Rhodoleia</i>			—	—	—	—	—
14. <i>Klikovispermum</i>		—					
15. <i>Liquidambar</i>				—	—	—	—
16. <i>Hamamelidoidea</i>					—		
17. <i>Corylopsis</i>					—	—	—
18. <i>Fortunearia</i>					—	—	—
19. <i>Hamamelis</i>						—	—

the Eocene can be considered as a time of the maximal species diversity of this genus.

With the start of the Eocene the taxonomic diversity of the family gradually declines. During this epoch the number of genera virtually returned to the initial level

of the Early Cretaceous. Since the Oligocene the family has been represented by a single genus, *Platanus*.

Figure 72a displays the dynamics of the generic diversity of platanoids on the basis of their leaf remains. The picture is virtually the same for the genera estab-

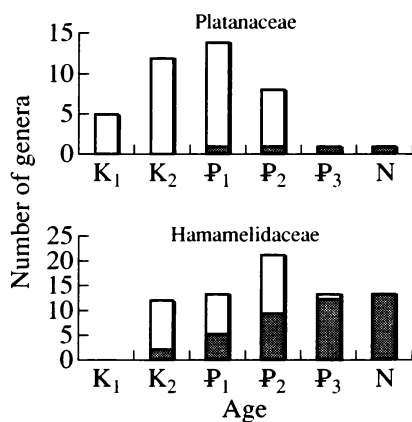


Fig. 71. Evolution of the generic diversity of the Platanaceae and Hamamelidaceae (white columns are extinct genera, gray columns are extant genera).

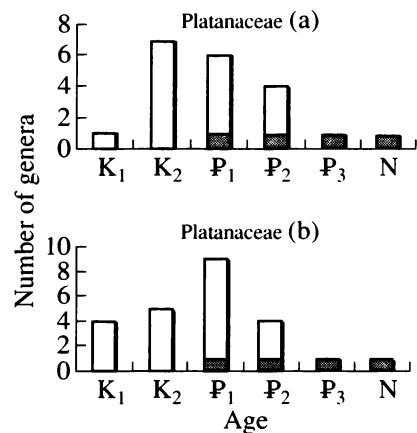


Fig. 72. Evolution of the generic diversity of the Platanaceae on the basis of (a) leaf remains and (b) reproductive structures (white columns are extinct genera, gray columns are extant genera).

lished through the joint consideration of leaves and reproductive organs (Fig. 71). The initial Early Cretaceous diversity increased significantly during the Late Cretaceous, declined during the Paleocene, persisting through the Oligocene and Miocene as a single genus until the present. The modern leaf morphotype of *Platanus* is recorded since the Late Cretaceous.

The dynamics of the taxonomic diversity of the Platanaceae reconstructed on the basis of reproductive structures are shown in Fig. 72b. Here the increase from the Early to Late Cretaceous is also prominent. However, the curves for leaves and reproductive structures are different, in particular for the Paleocene. While the leaf genera decreased in number, the diversity of genera based on reproductive structures was maximal during this period. This discrepancy in the number of taxa established on different organs can be due to either taphonomic bias or the conservative nature of the leaves and their slower evolution rates relative to reproductive structures or both. New genera appeared both as new combinations of characters present in their precursory genera and owing to morphological innovations. The diversity of taxa established on reproductive structures declined to the initial Early Cretaceous level in the Eocene and has been restricted to a single genus since the Oligocene.

Our data show two events of adaptive radiation that are confined to the post-crisis phases of evolutionary history (the Albian–Cenomanian and Maastrichtian–Paleocene).

TAXONOMIC DIVERSITY OF THE HAMAMELIDACEAE

Figure 73 represents the changes in the diversity of hamamelid taxa (established on the basis of leaves and reproductive structures). No reliable hamamelid finds have been reported from the Early Cretaceous. A large number of taxa have been recorded from the Late Cretaceous. Even for that time the existence of modern taxa has been established on the basis of seed remains (*Disanthus* and *Rhodoleia*; Knobloch and May, 1986). The taxonomic diversity insignificantly increased in the Paleocene and then, explosively, in the Eocene. The Oligocene and Miocene records suggest a lower taxonomic diversity relative to the Eocene. Alongside the rapid change in the total number of taxa, a steady growth of the number of modern taxa is occurred from Late Cretaceous to the Miocene.

This tendency toward an increase of modern taxa from epoch to epoch remains distinct both for taxa established on the basis of leaves (Fig. 73a) and reproductive organs (Fig. 73b). The number of hamamelid leaf genera was low through the Late Cretaceous, increased threefold in the Paleocene, and reached its maximum in the Eocene. This latter epoch also had the maximal number of extinct genera. Since the Oligocene, exclusively modern taxa have been recorded among the hamamelid leaf remains.

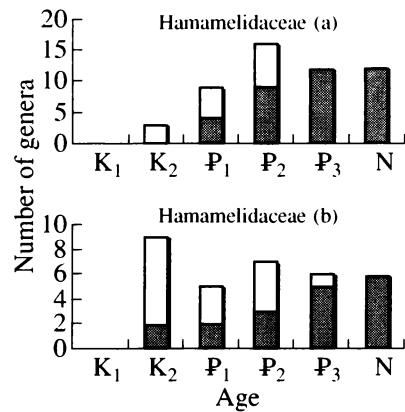


Fig. 73. Evolution of the generic diversity of the Hamamelidaceae on the basis of (a) leaf remains and (b) reproductive structures (white columns are extinct genera, gray columns are extant genera).

According to the selective criteria (see above), not all of the published descriptions of leaf genera have been included in the taxonomic analysis of the Hamamelidaceae. Their actual diversity might have been underestimated owing to recognition problems noted above.

The hamamelid taxonomic diversity curves are slightly different for the leaf genera and those based on reproductive organs. The maximal number of the latter genera is known from the Late Cretaceous, most of them are extinct. The Paleocene is marked by a decrease in diversity of fructification morphotypes. During the Eocene, this component of taxonomic diversity only slightly increased. Later fluctuations during the Oligocene and Miocene are quantitatively insignificant.

Fossil finds of extant hamamelid genera are usually represented by seeds. Until recently, the floral structures were poorly known. However, the available information suggests a considerable diversity of extinct types among them. With the accumulation of data, the general diversity of the family will be studied in more detail.

Thus, some preliminary conclusions regarding the dynamics of the taxonomic diversity of Platanaceae and Hamamelidaceae can be made; however, the difference between the degrees of understanding of the geologic history of these families should be remembered. Platanaceae are known to appear in the Early Cretaceous and reached the maximal number of genera in the Late Cretaceous and Paleocene. The subsequent gradual decline ended in the Oligocene with only one surviving genus *Platanus*. Hamamelids appeared in the Late Cretaceous as a relatively distinct group, comprising predominantly extinct genera. The number of modern genera has gradually increased since then. In the Eocene, there was a considerable diversity of archaic genera that disappeared at the end of the epoch.

MORPHOLOGICAL DIVERSITY OF THE PLATANACEAE AND HAMAMELIDACEAE

The morphological diversity of the Hamamelidales is discussed on the basis of reproductive features.

Table 9. Stratigraphic range of characters and index of morphological diversity of the Platanaceae

Character	K ₁	K ₂	P ₁	P ₂	P ₃	N	Q	Index of characters
Capitate inflorescences	_____							1
Sessile heads	_____							1
Pedicellate heads	_____							1
Monocarpous head		—						8
Oligocarpous head	_____							1
Well-developed perianth	_____							4
Reduced perianth		_____						6
Constant number of floral members	_____							4
Varying number of floral members				_____				6
Dispersal hairs				_____				6
Hairy carpels	_____							1
Well-developed stylodes		_____						6
Well-developed extension of connective	_____							1
Hairy stamens	_____							1
Long anther filaments	—							4
Short anther filament	_____							1
Reticulate exine	_____							1
Alveolate--reticulate exine	—							4
Presence of endoapertures	—							4
Orthotropous ovules	_____							1
Nonorthotropous ovules		—						8
Index of diversity	27	32	38	42	34	34	34	

Leaves are excluded from the analysis because their macromorphological characters are highly polymorphic, while microstructural studies are still inadequately known. In platanoids, the definition of discrete leaf morphotypes is hampered by the characters that overlap even in closely related genera. It is also impossible to consider sets of leaf characters since only a small part of Hamamelidales can be identified on the basis of these sets.

In contrast, the reproductive structures of both extant and fossil hamamelids are fairly well studied and they play a key role in the taxonomy of the group. The changes in their morphological diversity through time are summarized in Tables 9 and 10. Here the characters are given arbitrary numerical values reflecting their different evolutionary histories. The characters are clustered into four groups.

It should be emphasized that these numerical values lack particular information. I use them to reflect qualitative information for visual comparison.

The first members of the Platanaceae are known from the Albian; the earliest find of hamamelids is dated to the Cenomanian. As noted above, in studying taxonomic and morphological diversity I use a time

scale equivalent to an epoch. Therefore, the appearance of the first members of the families (Early Cretaceous for the Platanaceae; Late Cretaceous for the Hamamelidaceae) was assumed as a starting point for the comparison of all subsequent changes of morphological characteristics.

The first group includes characters that appeared in the Cretaceous and have persisted until the present. These conservative characters did not change qualitatively during geological history and they do not affect the dynamics of morphological diversity. The value of this group of characters is minimal (index value 1).

The second group is composed of characters that also appeared in the Cretaceous but have not persisted to the present. Such extinct characters reflect a decrease in morphological diversity (index value 4).

The third group embraces post-Cretaceous characters that persisted to the present, thus contributing to morphological diversity (index value 6).

The fourth group comprises post-Cretaceous characters that disappeared later, being restricted to relatively short time intervals. These are aberrations maximally increasing the variance (index value 8).

Table 10. Stratigraphic range of characters and index of morphological diversity of the Hamamelidaceae

Character	K ₁	K ₂	P ₁	P ₂	P ₃	N	Q
Capitate inflorescences							
Sessile heads							
Pedicellate heads							
Bisexual flowers							
Unisexual flowers							
Well-developed perianth							
Reduced perianth							
Paired carpels							
Staminodes in bisexual flowers							
Staminodes in female flowers							
Phyllomes							
Hairy carpels							
Hairy stamens							
Shedding stylodes							
Well-developed extension of connective							
Reticulate exine							
Long anther filament							
Short anther filament							
Tricolpate pollen							
Additional colpi							
Pollen with pores							
Bisporangiate anthers							
Tetrasporangiate anthers							
Anthers open in valves							
Anthers open by longitudinal slit							
Hairy perianth							
Cluster inflorescence							
Locule with solitary seed							
Locule with many seeds							
Massive testa							
Thin testa							
Index of diversity	0	23	53	59	65	71	71

For a semiquantitative analysis of the dynamics of morphological diversity, an index of diversity has been calculated for each epoch by summing up the indices for each group of characters (Fig. 74).

In the Late Cretaceous, the platanoids show a decrease in morphological diversity relative to the initial burst in the Early Cretaceous (Fig. 74a). The index of morphological diversity reaches its maximum in the Paleocene, decreasing later on. Since the Oligocene, the level of platanoid morphological diversity has remained constant.

In platanoids, the morphological and diversities showed opposite trends through the Cenozoic (compare Figs. 72b, 74a). Against a significant increase in the number of genera in the Cenozoic, there was a decrease in the index of morphological diversity relative to its initial value. At the same time, a large number of new genera originated due to the recombination of available characters rather than morphological innovation. This process was accompanied by the appearance of inadaptive variants, which appeared during the initial burst of diversification in the Albian. Since the Cenozoic, the declining trends of taxonomic and

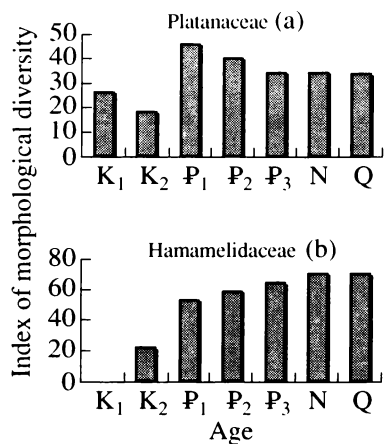


Fig. 74. Evolution of the morphological diversity of the Platanaceae and Hamamelidaceae.

logical diversities coincide. Of certain interest is the Paleocene/Eocene transition. An insignificant decrease in the index of morphological diversity in the Eocene correlates with a rapid (up to initial level) fall in the number of platanoid taxa. This is due to the appearance of a small number of taxa with innovative morphological features.

The dynamics of the hamamelidacean morphological diversity (Fig. 74b) differs from that of platanoids. Since the Late Cretaceous, when the family appeared for the first time in the geological record, being represented by a relatively diverse group of taxa, the index of their morphological diversity steadily increased from epoch to epoch. This trend generally coincides with the trend toward an increase in the number of extant taxa during these epochs.

Against this background, the change in the generic number of Hamamelidaceae is particularly interesting (Fig. 73b). A low index of morphological diversity in the Late Cretaceous is accompanied by the large number of genera. In this case new taxa originated through recombination of then available characters. A decreasing generic number in the Paleocene, accompanied by a more than twofold increase in the index of morphological diversity, reflects the extinction of those genera that combined various conservative features and their replacement by genera that significantly enriched the morphological diversity with their innovative characters. Later, in the Eocene, the recombination of characters (including the innovative characters) resulted in an insignificant peak of the number of taxa, which correlated with an insignificant change in the morphological diversity index. In the Oligocene, *Hamamelidoidea* was the only archaic genus that did not survive into the Neogene. Since the Miocene, only modern genera of the family have been recorded. New genera originated through morphological innovations as well as recombination of existing characters. This is reflected in an insignificant increase in the index of morphological diversity from epoch to epoch.

CHAPTER 8. GENERAL EVOLUTIONARY TRENDS AND PHYLOGENETIC RELATIONSHIPS OF THE PLATANACEAE AND HAMAMELIDACEAE

The development of the classification systems and phylogenetic models based on the paleobotanical record is essential for the advance of plant sciences. The available classifications are to be significantly improved with the application of data on the historical development of particular groups. Of certain interest in this respect is the order Hamamelidales maintaining a key position in the angiosperm system. Revealing evolutionary trends for particular characters of the order, as well as evolutionary stages for the families and genera within this order are, therefore, of considerable interest.

EVOLUTIONARY TRENDS IN THE DEVELOPMENT OF REPRODUCTIVE AND VEGETATIVE CHARACTERS IN THE PLATANACEAE AND HAMAMELIDACEAE

Here the platanoid and hamamelid diversities are analyzed in respect to the general evolutionary trends and those of particular characters.

Diverse in the Cretaceous and Paleocene and reduced to a solitary genus *Platanus* since the Oligocene, the members of the Platanaceae show the following evolutionary sequence in the development of reproductive structures:

- (1) Appearance of both sessile and pedicellate inflorescences;
- (2) Increase in the number of flowers per inflorescence;
- (3) Increase in the inflorescence diameter;
- (4) Reduction of perianth;
- (5) Increase in the numerical diversity of floral elements;
- (6) Elongation of stamen;
- (7) Increase in pollen sizes; and
- (8) Appearance at the fruit base of hairy gynoeceum and tufts of hairs serving for dispersal. These trends appeared in parallel in lineages with five (*Platananthus*) and four (*Quadriplatanus*) stamens. Androeceum enclosed in a perianth tube is known in the ancient members of the family; the latest records of this character are known from the Paleocene. This condition correlates with another primitive trait: the stomata on peltate extensions of the connectives.

Endress (1989b) noted a correlation between the perianth differentiation and constancy of floral members in lower hamamelids. As a rule, a well-developed perianth is accompanied by a constant number (four or five) of stamens and carpels. Actually, in extinct members of the Platanaceae the perianths were well developed and the number of floral structures was constant, whereas the extant plane tree has naked flowers with a varying number of members.

The phylogenetic scheme of the Platanaceae proposed in Maslova (2001b) was based on the morphological diversity of reproductive characters, transitional forms, and their geological age.

The evolutionary trends in the leaf characters of the Platanaceae are more controversial. As noted above, the classification of several highly polymorphous leaf genera are ambiguous and even their familial assignments are problematic. This primarily concerns the leaves of platanoids, but opinions differ also in respect to *Platanus* itself. Consequently, trends in the development of leaf characters within the family are difficult to confidently depict, since nonplatanoid taxa are possibly included in the analysis.

More carefully selected macromorphological and epidermal characters, as well as whole-plant reconstructions on the basis of leaf and reproductive remains show the following evolutionary trends in leaf characters:

(1) Evolution of leaf blades from the compound pinnatifid of the *Sapindopsis* type through the compound with a terminal typically platanoid leaflet of *Platanites* and *Erlingdorfia* to the variously lobed simple blade of *Platanus*. Basal lobes of *P. basilobata* Ward (Ward, 1888), variously developed peltate leaf bases (platanoid genera and *Platanus*), and stipules in the extant *Platanus* can be considered as derived, resulting from an aggregation of compound and pinnatifid leaves. Within the limits of *Platanus* (subgenus *Platanus*), the leaf blade evolved from an entire or weakly lobed blade (Paleocene species) to a strongly lobed blade (extant species);

(2) From the leaf blades with basal and suprabasal venation to leaf blades with dominating suprabasal venation with well-developed basal and infrabasal veins;

(3) Evolution of the leaf blade margin from weakly undulate or ones possessing low obtuse teeth to serrate concave–concave teeth with a longer basal side; and

(4) Epidermal characters originated in the Early Cretaceous (striate cuticular folds radiating from stomata and hair bases, hairs with rounded and strongly cutinized bases, glands) and have persisted in some younger platanoids (*Platimeliphyllum* and *Arthollia*) as well as in the extant *Platanus*.

These hypothetical evolutionary trends of leaf characters in the platanoids will no doubt be studied at length as more paleobotanical data appear.

As to the Platanaceae, information concerning the geological precursors of the Hamamelidaceae is significantly less comprehensive. Presently, there are 30 hamamelidaceous genera and 144 species of four subfamilies (Endress, 1989a; Zhang and Lu, 1995). A great amount of monotypic extant genera in this family suggests the existence of a more extensive group in the geological past. The available evidence shows the relative advancement of certain reproductive characters within the subfamilies.

The earliest find of exbucklandioid reproductive morphologies is dated by the Cenomanian (Maslova and Golovneva, 2000b). Later, this subfamily experienced the following changes:

(1) Substitution of compact heads by looser paniculate inflorescences;

(2) Decrease in the number of flowers per inflorescence;

(3) Reduction of perianth to the monochlamidous (*Exbucklandia*) and, finally, to a naked flower (*Chunia*);

(4) Loss of hairs on floral structures;

(5) Replacement of anthers dehiscing through a longitudinal slit by those opening in two valves;

(6) Appearance of typically tricolpate pollen in addition to diffuse-colpate palynotype; and

(7) Increase in pollen sizes.

Altingioid morphotypes are known as early as the Cenomanian. The earliest find assigned to this subfamily is reported from the late Turonian (Zhou *et al.*, 2001). Trends in the reproductive evolution of the Altingioideae include:

(1) Reduction of perianth members with their possible transformation into sclerotized tissue, separating flowers in pistillate heads;

(2) Loss of hairs on carpels;

(3) Occurrence of sterile structures (staminodes and phyllomes) in pistillate flowers. This characteristic feature of the subfamily is observed in the Altingioideae since the Paleocene;

(4) Replacement of the initial tricolpate reticulate palynotype by the periporate palynotype;

(5) Substitution of elongate pollen grains by spheroidal palynotype; and

(6) Increase in pollen sizes.

The Hamamelidoideae is the largest subfamily among the Hamamelidaceae. It includes genera greatly divergent in reproductive morphology. At present, however, a limited number of fossil finds (relative to the diversity of extant genera) makes reconstruction of evolutionary trends problematic. On the basis of the floral morphology of extant hamamelids, Bogle (1970) reconstructed an archetype of floral structures that could potentially give rise to the total diversity of hamamelid reproductive morphologies. This is a bisexual flower having a perianth with an inconstant number of nondifferentiated members, numerous stamens, and a superior ovary of two or three carpels. Such a flower could lead to morphological types with perianth elements basally fused to stamens resulting in a hypanthium (*Parrotia* and *Fothergilla*), with a possible decrease in the number of stamens (*Molinadendron* and *Sycopsis sinensis*) and subsequent fusion of the hypanthium to the ovary (*Tetrathirium* and *Parrotiopsis*). The development of hypanthium can be accompanied by a reduction of perianth (*Sycopsis dunnii*) and a suppressed development of gynoecium either in lateral

flowers (*Sycopsis dunnii*) or in all flowers of the inflorescence (*Sycopsis sinensis*). This trend might have finally resulted in inflorescences combining staminate and bisexual flowers.

The pseudanthia in *Distylium* are a supposed result of another trend: from a bisexual flower through the reduction of perianth and gynoecium (in case of lateral staminate flowers) or perianth and androecium (in case of terminal pistillate flowers) with a further shortening of inflorescence axes and aggregation of bracts (Bogle, 1970).

Although the history of the Hamamelidoideae is as yet insufficiently studied, the analogy with other subfamilies (see above) suggests a reduction of perianth and the appearance of unisexual inflorescences in this subfamily. However, the hypanthium appeared at early evolutionary stages of hamamelids (*Microaltingia*, Late Turonian), thus scarcely representing an innovation in the Hamamelidoideae.

PHYLOGENETIC RELATIONSHIPS OF THE PLATANACEAE AND HAMAMELIDACEAE

Morphology, anatomy, and biochemistry appear to support a relatedness between the families Platanaceae and Hamamelidaceae (Tippo, 1938; Takhtajan, 1966; Jay, 1968; Hickey and Wolfe, 1975; Cronquist, 1981; Zavada and Dilcher, 1986; Krassilov, 1989; Schwarzwald and Dilcher, 1991). However, the primitive or advanced state of these families remains a matter of discussion. It is arguable how close phylogenetically these families are.

For example, Bretzler (1924) considered the Platanaceae to be a more advanced family and positioned it after the Hamamelidaceae in the phylogenetic system. Brouwer (1924) argued for an isolated position of the platanoids among angiosperms. Anatomical data (i.e., wood anatomy) allowed Tippo (1938) to consider the Platanaceae as a more advanced family relative to the Hamamelidaceae, Myrothamnaceae, and the Buxaceae. Hickey and Wolfe (1975) noticed an early appearance of leaf morphotypes of the platanoid-type aspect in the geological record and considered platanoids as the first members of the lower hamamelids. Cronquist (1981) believed platanoids and hamamelids to be closely related and derived from a common stock with the former as a more primitive and earlier separated family.

Opinions differ in respect to the position of the genera *Altingia*, *Liquidambar*, and *Semiliquidambar* (see above). The data obtained support the affinity of these genera to the subfamily Altingioideae (Hamamelidaceae), as this group exhibits the main diagnostic features of the Hamamelidaceae and the variations of characters do not exceed the range of variations in other subfamilies. There is not a single vegetative or reproductive morphological character in this group of genera which is lacking in other hamamelids and this is the case for both extant and fossil members. Moreover, the Cretaceous genera *Viltyungia* (Maslova and Golovneva,

2000b), *Microaltingia* (Zhou *et al.*, 2001), *Lindacarpa* (Maslova and Golovneva, 2000a), and the Paleocene *Evacarpa* (Maslova and Krassilov, 1997) have microstructural characters that occur not only in the Altingioideae but also in other subfamilies of the Hamamelidaceae and even in some extinct platanoids.

The maximal macro- and micromorphological similarity of vegetative and generative structures is observed between the extant *Platanus* and members of the Altingioideae (Maslova, 1998). Leaf morphotypes of *Platanus* resembling those of *Liquidambar* and *Semiliquidambar* suggest a structural parallelism in the development of the Platanaceae and Altingioideae. Macromorphologically, the lobed leaves typical of the nominative subgenus *Platanus* are comparable with the lobed leaves of *Liquidambar*. The entire leaves with pinnate venation of *Platanus kerrii* (subgenus *Castaneophyllum*) correspond to those of *Altingia*. Of certain interest is the presence of both leaf morphotypes (lobed and entire) in one plant (and even in one and the same shoot) in the genus *Semiliquidambar*. Transitions from entire leaf blades (stump sprouts) to weakly lobed and distinctly tri- and pentalobate blades are observed in the extant *Platanus acerifolia*.

The reproductive morphologies of these genera also have much in common. Both platanoids and altingioids have compact capitate functionally unisexual inflorescences. The perianths are lacking, staminodes occur in pistillate flowers. These characters are also present in some other hamamelid subfamilies. In particular, heads are known in *Chunia* and *Exbucklandia* (Exbucklandioideae). The flowers of *Distylium* and *Sycopsis dunnii* (Hamamelidoideae, Bogle, 1970) are devoid of perianth. Staminodes may occur in the flowers of *Rhodoleia* (Rhodoleioideae, Bogle, 1987), etc.

However, such floral features as the apocarpous gynoecium of three to five carpels and solitary ovules in *Platanus*, on the one hand, and the paired, basally connate carpels with numerous ovules and intrafloral phylomes in *Altingia* and *Liquidambar*, on the other, introduce a significant morphological distance between the extant members of these groups.

Recent paleobotanical studies have confirmed the phylogenetic relatedness between the Platanaceae and Hamamelidaceae and their deviation from a common ancestor. Several taxa combining characters of both families have been discovered.

The pistillate inflorescences from the Turonian (Raritan Formation of New Jersey, Crepet *et al.*, 1992) showing hamamelid characters (bicarpellate syncarpous ovary, well-developed perianth, and the presence of staminodes with nectaries in the flowers) associate with staminate heads having platanoid characters (capitate unisexual inflorescences, compact arrangement of stamens in the flower, broadly triangular apical extension of the connective, and reticulate tricolpate pollen).

The genus *Quadriplatanus* from the Coniacian–Santonian Eutaw Formation (Magallón-Puebla *et al.*,

1997) is assigned to the family Platanaceae, but it also shows certain hamamelid characters. A stamen tube is observed in *Quadriplatanus* but is as yet unknown in other platanoids. However, Magallón-Puebla *et al.*, (1997) compare the stamen tube with the adnate bases of stamen filaments and petals in *Embolanthera* and *Dicoryphe* (Hamamelidaceae).

The systematic position of some other fossils is also problematic. This primarily pertains to the reproductive structures (capitate inflorescences and infructescences), which are fairly different in extant members of the families at the macromorphological level but not always distinguishable at the generic or even familial level in the fossil state (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b).

The genera *Viltyungia* and *Lindacarpa* from the Late Cretaceous and the Paleocene *Evacarpa* (Maslova and Krassilov, 1997) are assigned to the Hamamelidaceae, although superficially their reproductive structures are scarcely distinguishable from those of the Platanaceae. Microstructural study allowed a more precise generic and familial allocation of these reproductive organs. A combination of characters of three subfamilies of the Hamamelidaceae is reflected in the specific epithet of *Viltyungia eclectic*. In addition to the typically hamamelid morphology, this plant also shows certain platanoid microstructural characters. These are the well-developed double hairy perianth comparable to that of some extinct members of the Platanaceae; the weakly developed connective, similar to that of the extant plane tree; the diffuse-colpate pollen present in few hamamelids and atypical of platanoids, but observed as an aberration in the Maastrichtian–Paleocene *Archaranthus* (Maslova and Kodrul, 2003) and the extant *Platanus occidentalis* (Zavada and Dilcher, 1986).

Although *Lindacarpa pubescens* is allied to the subfamily Altingioideae, it shows both typically hamamelid characters and microstructural features, similar to those of the Platanaceae, for example, the differentiated perianth. The carpels are hairy as in *Platanus*, but unlike the extinct platanoids. The extant members of the Altingioideae have naked carpels except in *Altingia excelsa*, showing a hairy apocarpous portion of the gynoecium (Bogle, 1986). The presence of hairs on carpels of *Lindacarpa* suggests an early appearance and subsequent loss of this character in the Altingioideae.

In *Evacarpa polysperma*, the floral micromorphology is typical of Altingioideae. However, the presence of staminodes in the pistillate flowers makes *Evacarpa* comparable with *Platanus*. Moreover, the leaves of *Evaphyllum kamchaticum* sp. nov. associated with *Evacarpa* combine characters of *Platanus*, *Altingia*, and *Liquidambar*.

Such leaf genera of the Hamamelidales as *Platimelis* Golovneva (1994a) are morphologically transitional between the platanoids and hamamelids. Species of the genus *Platimeliphyllum* also combine hamamelid and

platanoid characters (Maslova, 2002a). This polymorphous genus has symmetrical and asymmetrical leaves either with concave-concave teeth of a typically platanoid appearance or rounded teeth typical of hamamelids. Such finds substantiate a close relationship between these families.

The supposed relatedness of ancient platanoids to rosids is paleobotanically substantiated (Crane, 1989; Crane *et al.*, 1993; Pedersen *et al.*, 1994; Krassilov and Shilin, 1995). Hufford and Crane (1989) have remarked a certain similarity between members of the Hamamelidaceae and those of the Rosidae in their perianth differentiated into calyx and corolla as well as the bicarpellate gynoecium.

The existence in the geological past of a common polymorphous ancestral group is highly probable. This group gave rise to diverging phylogenetic lines leading to the extant families Platanaceae and Hamamelidaceae. Additional finds of fossil morphotypes showing a combination of platanoid and hamamelid characters can be expected at early evolutionary stages. However, the isomorphous polymorphism in several vegetative and reproductive characters between the extant *Platanus* and the altingioid genera also includes late appearing characters, which can be interpreted as a result of evolutionary parallelism.

PRIMITIVE AND ADVANCED CHARACTERS OF THE PLATANACEAE AND HAMAMELIDACEAE AND APPROACHES TO PHYLOGENETIC RECONSTRUCTION

Paleontological data contribute significantly to the problem of primitive (the least specialized) vs. advanced (specialized) character states. In actual botany, the problem is resolved on the basis of morphological correlations as well as the commonly accepted evolutionary concepts for a particular group. With this approach, the hypotheses of structural complication or reduction lack factual justification. It is impossible to rank morphological characters as primitive or advanced without due concern to their chronological succession. Such ranking will remain controversial until the reliable chronological information becomes available.

Only paleontological evidence gives us an idea of evolutionary advancement. The morphological character state in the earliest members of a group should be considered as the most primitive, and they provide a starting point for morphological lineages (morphoclines). For example, the earliest hamamelid genus *Viltyungia* (Cenomanian) had small flowers arranged in a compact capitate inflorescence. Therefore, such inflorescences have to be placed at the base of the morphocline of this character plotted for the family Hamamelidaceae.

Recent paleobotanical data have shown that most of the earliest (since Albian time) finds of angiospermous reproductive organs are clusterlike, paniculate or capitate inflorescences consisting of inconspicuous small

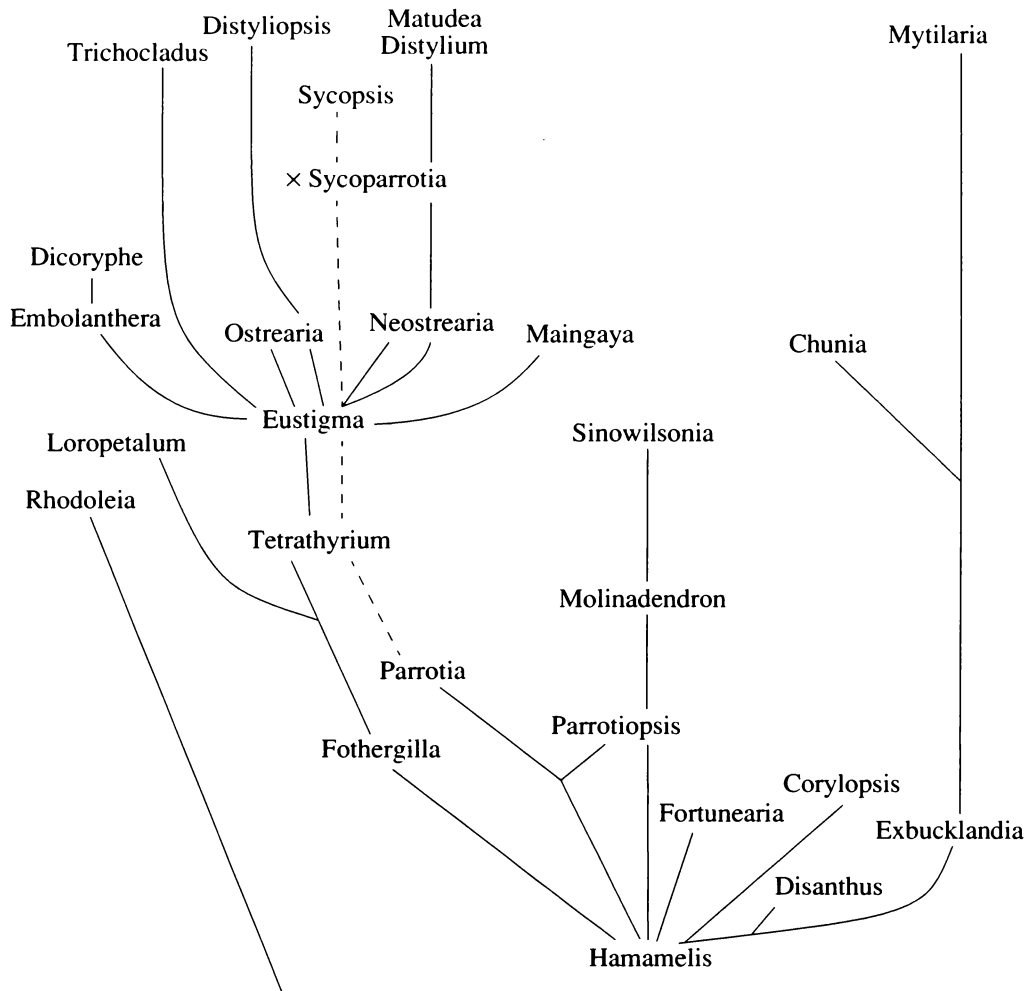


Fig. 75. Phylogenetic relationships of the genera of the Hamamelidaceae (after Skvortsova, 1975).

flowers with variously reduced floral parts. Hence, the concept of primitive solitary flowers with many parts (Takhtajan, 1960) has to be revised.

The assumed basal positions in morphoclines for critical characters allowed one to reconstruct archetypes as combinations of all the most primitive character states. However, such primitive morphologies were never found in the fossil record. Taxa preceding others in the succession of first appearances are characterized by combinations of both primitive and the most advanced characters. For example, *Vilyungia* has anthers dehiscing by a longitudinal slit, a trait that is characteristic of the relatively advanced amentiferous genera. The diffuse-colpate type of pollen grains, occurring in *Vilyungia*, is considered as a derivative from tricolpate morphotypes (Walker and Doyle, 1975). Mosaic evolution is also observed in other representatives of geologically ancient groups. Accordingly, the definition of a character on the basis of a correlation with other characters conventionally consi-

dered as primitive or advanced (a usual practice in plant morphology) is scarcely justifiable.

Phylogenetic schemes constructed solely on the basis of extant morphotypes often contradict paleontological data and appear artificial. For instance, a phylogenetic model for the Hamamelidaceae based on vegetative morphology (leaves and wood) of extant representatives (Skvortsova, 1975; this researcher considered *Altingia* and *Liquidambar* within the separate family Altingiaceae) places *Hamamelis* at the base of the sequence (Fig. 75). However, the criteria of primitiveness are not indicated. *Disanthus*, which is often considered as the most primitive genus among the extant hamamelids (Takhtajan, 1966, 1987; Cronquist, 1981), is also positioned by Skvortsova near the base of the phylogenetic tree but as a member directly derived from *Hamamelis*. According to Endress (1989a, 1989b), these genera belong to different subfamilies (Exbucklandioideae and Hamamelidoideae) and are markedly dissimilar in their vegetative and especially reproductive morphology.

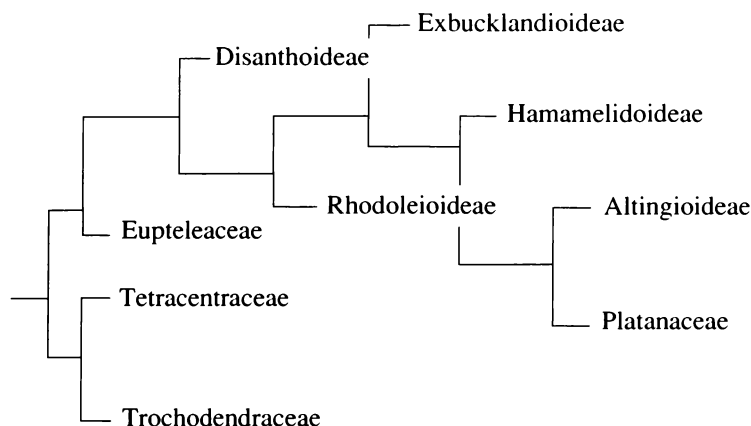


Fig. 76. Cladogram of lower hamamelids with the families Tetracentraceae and Trochodendraceae as outgroup (after Schwarzwaldler and Dilcher, 1991).

The fossil genus *Viltyungia* combining floral characters of three hamamelid subfamilies (Altingioideae, Exbucklandioideae, and Hamamelidoideae) suggests the origin of the genera *Hamamelis* and *Disanthus* from a common ancestral group rather than directly from each other. Moreover, characteristic features of these subfamilies already appeared in the Cenomanian, with exbucklandioid characters dominating the “synthetic” morphology. There are also some controversial points in the upper part of the phylogenetic tree worked out by Skvortsova, especially when the data on floral structures (Bogle, 1970) are taken into account.

Goldblatt and Endress (1977) established two lines within the family Hamamelidaceae on the basis of cytological data. They also hypothesized phylogenetic relationships between the genera based on chromosome numbers. One of the lines, including the Hamamelidoideae and Rhodoleioideae, has basal chromosomes number 12, another comprises the subfamilies Altingioideae and Exbucklandioideae with $n = 8, 16, \text{ or } 32$. *Disanthus* ($n = 8$) is considered ancestral for several hamamelid lineages. The extant members of the subfamilies are shown to be basically related, deviating from a common ancestral group.

Studying leaf trichomes, Fang and Fan (1993) have reconstructed possible phylogenetic relationships within the Hamamelidaceae. They established two evolutionary lines, Disanthoideae–Exbucklandioideae–Liquidambaroideae (genera *Disanthus* and *Exbucklandia* are considered in separate subfamilies) and Rhodoleioideae–Hamamelidoideae. Fang and Fan believe *Corylopsis* to be the most primitive genus among the Hamamelidoideae.

However, the search for ancestors among extant taxa is apparently doomed to fail. Horizontal relations between taxa could serve as a basis for classification systems showing morphological distances rather than the sequence of descent, their transformation into phylogenetic (vertical) relations being questionable.

Takhtajan (1987, p. 12) wrote that in spite of the great success of angiosperm paleobotany, fossil material is of use primarily for reconstruction of flora and vegetation rather than phylogeny. At the same time, he agreed that without sufficient knowledge of fossils the morphological relations lack a temporal dimension (Takhtajan, 1987, p. 13). As more data on fossil plant groups appear, paleobotanical contribution gains in importance for particular groups within the Magnoliophyta. This is the case for the Hamamelidales, in which paleobotanical evidence serves as a source of reliable information concerning the geological age of particular characters and their evolutionary trends. Phylogenetic schemes based on fossil evidence admittedly depend on the completeness of the geological record, as well as on the precision of age determination and morphological interpretations. It should be underscored that phylogenetic schemes are not strictly genealogical but rather reflect general evolutionary trends.

In recent years, cladistic analysis was sometimes used as a substitute for paleontological sequencing. A cladogram based on supposedly uniquely derived (apomorphic) characters reveals the potential sister groups yet fails to discover the vertical, or paternal relations that are more readily recognizable on the basis of plesiomorphic characters that are excluded from analysis. No wonder then, that cladistic schemes do not conform to paleobotanical data. For example, in the cladistic scheme for the lower hamamelids (Schwarzwaldler and Dilcher, 1991) the families Tetracentraceae and Trochodendraceae were chosen as an outgroup and the family Platanaceae was placed within the Hamamelidaceae s. l. as a sister group of the subfamily Altingioideae. According to this scheme (Fig. 76), the family Platanaceae derived from a common stock as one of the upper branches, after several dichotomies giving rise to subfamilies of the Hamamelidaceae. However, the Albian finds of platanoids contradict this assumption. The following chronological sequence was proposed for the hamamelid subfamilies: Disanthoideae, Rhodo-

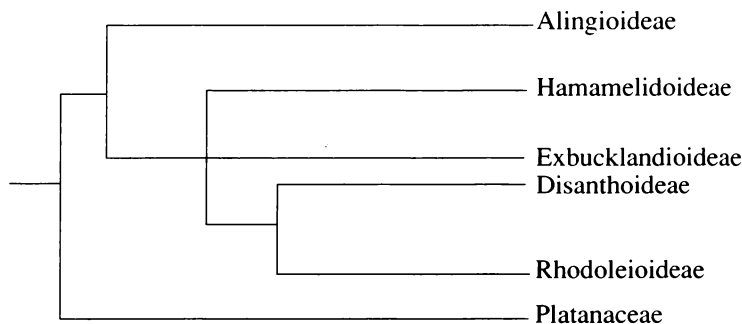


Fig. 77. Cladogram of the Hamamelidales with the family Platanaceae as outgroup (after Schwarzwaldner and Dilcher, 1991).

leioideae, Exbucklandioideae, Hamamelidoideae, and Altingioideae (these authors consider the Disanthoideae and Exbucklandioideae as separate subfamilies), whereas the paleobotanical evidence locates the Altingioideae among the most ancient hamamelids.

Schwarzwaldner and Dilcher (1991) also worked out an alternative scheme choosing the Platanaceae as an outgroup (Fig. 77) with the following chronological sequence for the hamamelid subfamilies: Altingioideae and Exbucklandioideae, Hamamelidoideae, Disanthoideae, and Rhodoleioideae. This scheme agrees with paleobotanical evidence for the early appearance of the Platanaceae. However, the position of the Disanthoideae and Rhodoleioideae as the recently derived groups contradicts the fossil record for these subfamilies.

Below, phylogenetic relationships within the families Platanaceae and Hamamelidaceae are reconstructed on the basis of transitional characters in reproductive organs and taking into account the geological age of the critical morphotypes.

PHYLOGENETIC RELATIONSHIPS WITHIN THE FAMILY PLATANACEAE

Chronologically, at the base of the phylogenetic scheme for the platanoids (Fig. 78), there is a group of Early Cretaceous (Albian) morphotypes of staminate (*Hamatia*, *Aquia*, and *Platananthus*) and pistillate (*Platanocarpus*) inflorescences. The genus *Aquia* is distinguished by stamens with long filaments exceeding the anthers two times, weakly developed connectives, and alveolate-reticulate pollen grains. The genus *Hamatia* has stamens with short filaments, tetrasporangiate anthers, a conspicuous hornlike extension of the connective, and tricolporate pollen. *Hamatia* and *Aquia* are monotypic genera, restricted to the Albian. Their reproductive structures suggest a relationship between the lower hamamelids and rosids (Crane, 1989; Crane *et al.*, 1993; Pedersen *et al.*, 1994). Krassilov has inferred a phylogenetic link between the platanoids and Rosidae on the basis of palynomorphology of tricolporate cingulate pollen grains in the Cenomanian genus *Sarbaya* (Krassilov and Shilin, 1995).

The obligatory pentamerous flowers with well-developed perianths, short stamen filaments, elongate anthers, peltate extensions of the connectives, and tricolporate reticulate pollen are diagnostic of the genus *Platananthus*. The genus includes five species known from the Late Albian to Middle Eocene. In spite of significant differences in the morphology of staminate inflorescences, the genera *Hamatia*, *Aquia*, and *Platananthus* associate in the Early Cretaceous with pistillate inflorescences of one and the same *Platanocarpus* morphotype.

Hence, the late Albian was a time of rapid diversification of staminate structures combined with a relatively conservatism in associated pistillate structures. The genera *Hamatia* and *Aquia* do not extend into the Late Cretaceous representing blind branches of the initial radiation. The genus *Platananthus* persisted until the Middle Eocene giving rise to a new round of generic diversification in the Paleocene. The latest record of *Platanocarpus* is dated to the Santonian–Campanian.

During the Cretaceous, a group of genera with tetramerous flowers, *Sarbaya* and *Quadriplatanus*, diverged from the main stock.

In the Paleocene, there was a second burst of adaptive radiation in the Platanaceae. At the base of it we find *Archaranthus*, *Oreocarpa*, *Tricolpopollianthus*, *Platanites*, and *Chemurnautia* apparently derived from the persisting *Platananthus*–*Platanocarpus* lineage. While the Early Cretaceous staminate flowers of the *Platananthus* type cooccurred with the pistillate inflorescences of the *Platanocarpus* type, the Paleocene species of the same staminate morphotype associate with the pistillate heads of *Macginicarpa*. The distinguishing features of *Archaranthus* are the smaller (relative to other platanoids) numbers of flowers per inflorescence, disintegration of a mature head into separate flowers, well-developed, differentiated perianths, stomata on the connectives, and finely reticulate pollen grains.

Staminate flowers of *Chemurnautia* are devoid of perianth. The stamens consist of a short filament and elongate anthers of narrowly fusiform, parallel-margined, unequal sporangia with insignificant extensions of the connectives. The genus *Oreocarpa* includes pis-

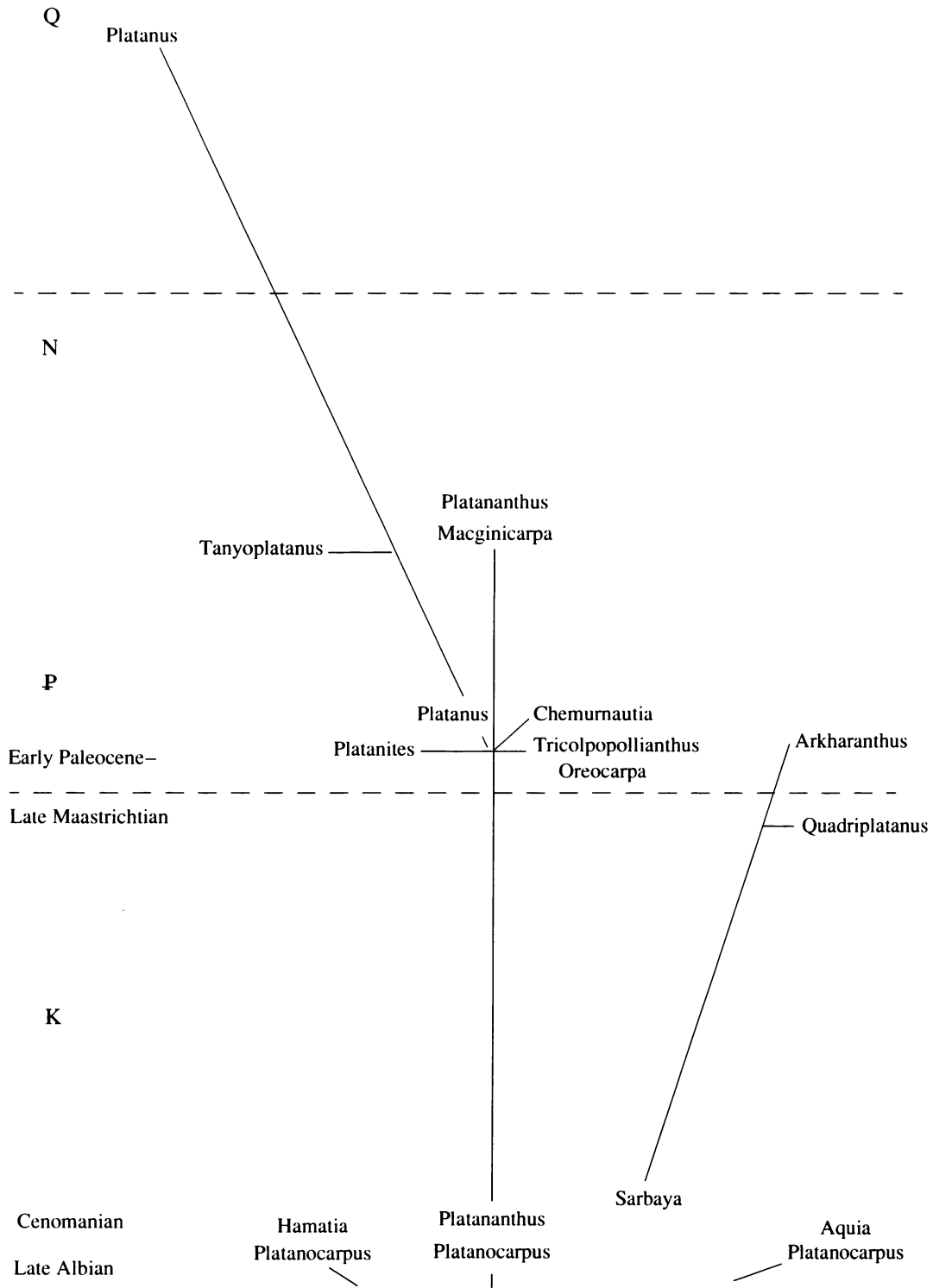


Fig. 78. Phylogeny of the family Platanaceae.

tillate heads with a solitary maturing fruit, exceeding the head in size. A similar domination of few fruits within the head is observed in *Macginicarpa glabra* Manchester (Manchester, 1986). These pistillate heads associate with the staminate inflorescences of the *Tri-*

colpopollianthus type. The genera *Chemurnautia*, *Oreocarpa*, and *Tricolpopollianthus* are blind evolutionary lines of the Paleocene radiation.

The solitary extant genus, *Platanus*, obviously originated from forms related to the genus *Platanites*. The

PHYLOGENETIC RELATIONSHIPS
WITHIN THE FAMILY HAMAMELIDACEAE

latter was established on the basis of leaves and staminate as well as pistillate inflorescences. The staminate flowers of *Platanites* had weakly developed perianths, stamens with short filaments and long anthers, and with a short apical extension of the connective. The pistillate flowers are characterized by persisting stylodes, narrow elliptical apparently naked carpels (although the authors of the genus do not completely exclude the presence of hairs on the carpels).

The earliest find of reproductive structures of *Platanus* is dated to the Paleocene. At that time the main diagnostic characters of the genus were established. However, one of the distinguishing characters of the Paleocene species of *Platanus* is narrow elliptical carpels (in the extant species the carpels are more distinctly ovate). This shape of the carpels is shared with *Platanites*. There is also a range of common characters in the morphology of staminate inflorescences (heads comparable to those of *Platanus* in size, short stamen filaments, elongate anthers, and a relatively short apical extension of the connectives).

Tanyoplatanus might have deviated from the *Platanites*–*Platanus* line in the Middle Eocene. The genus is peculiar in having cylindrical inflorescence, a well-developed perianth, persistent stylodes, and distinct hairs at the fruit base obviously serving for dispersal. The latter character is diagnostic of *Platanus* and is not observed in any extinct platanoids.

As noted above, the staminate inflorescences of *Platananthus* were associated with the pistillate inflorescences of *Platanocarpus* in the Cretaceous and with *Macginicarpa* in the Paleocene. *Platanocarpus* and *Macginicarpa* are similar in inflorescence shape, the definite number (five) of carpels per flower, and a non-differentiated perianth, the main difference between them being the long persistent stylodes in the latter genus.

Thus, there were two distinct stages in the evolution of the Platanaceae: in the Albian–Cenomanian and the Late Maastrichtian–Paleocene. The first stage is marked by a rapid diversification of staminate structures and of the pollen morphology. The female structures remained relatively conservative. The compound pinnate leaves, supposedly similar to the ancestral morphological type of the family, were prominent among the leaf records. At this stage a range of short-living forms appeared. Only a single lineage with the *Platananthus* stamen morphotype continues to be involved in the second round of morphological radiation into the Paleocene. The evolutionary style is different at the second stage, giving rise to new types of pistillate structures. Among these, the short-living aberrant forms appeared. Some of them (*Oreocarpa*) show archaic characters, such as folliculate fruits. The compound pinnate leaves persisted in the lineage that supposedly gave rise to the modern plane. Various lobed leaves, as in the modern plane, were associated with fructifications both typical and atypical of *Platanus* (Maslova, 1997; Maslova and Kodrul, 2003).

The earliest find of hamamelids is dated to the Cenomanian. The genus *Viltyungia* at the base of the phylogenetic tree (Fig. 79), combines characters of three hamamelid subfamilies, Exbucklandioideae, Hamamelidoideae, and Altingioideae, with a greater dominance of exbucklandioid characters. To date, no other fossil reproductive structures of exbucklandioid morphology were found.

The first appearance of altingioid morphotypes is dated to the late Turonian (Zhou *et al.*, 2001). The genus *Microaltingia* had unisexual flowers with bicarpellate gynoecium, hypanthium, and phyllomes arranged in consecutive circles, and numerous ovules. These are typical of the Altingioideae. Yet, the small elongate tricolpate reticulate pollen grains are distinct from the pollen morphologies characteristic of this group.

The genus *Lindacarpa* is characterized by asynchronous maturation of fruits in the head, a bicarpellate gynoecium, and a semi-inferior ovary. This genus differs from the typical altingioids in the well-developed differentiated perianth and the absence of sterile floral structures (staminodes or phyllomes). The phylogenetic line *Viltyungia*–*Microaltingia*–*Lindacarpa* might have led to the Paleocene genus *Evacarpa*, characterized by naked flowers with bicarpellate gynoecium, staminodes, and intrafloral phyllomes.

Information concerning the supposed geological precursors of the most numerous and diverse extant subfamily Hamamelidoideae is limited to four fossil genera. The earliest find (*Androdecidua*) comes from the Late Santonian. This genus has pentamerous actinomorphic flowers, perianth members are basally fused to the stamens that arise in two cycles and are dimorphic. The stamens consist of massive, broad, parallel-margined filaments and relatively short anthers with long apical extensions. In the inner cycle, the anthers are bithecate tetrasporangiate, opening by two valves, whereas in the outer circle they are bisporangiate lacking adaxial sporangia. On account of the typical hamamelidaceous morphology, the authors of the genus do not exclude the bisexuality of *Androdecidua* although the gynoecium is not preserved.

The genus *Archamamelis* from the Santonian–Campanian has bisexual flowers with well-developed perianth, bisporangiate anthers dehiscing by a single valve, staminodes, and dimerious, or supposedly trimerous, gynoecium. Several characters place this genus close to *Hamamelis*. Its main distinction is the trimerous gynoecium.

The Campanian genus *Allonia* is assigned by its authors to the tribe Hamamelideae (subtribe Loropetalinae). It has pentamerous flowers with a perianth, tetrasporangiate anthers, and thecae dehiscing in two valves. *Allonia* differs from extant members of the tribe Hamamelideae in having two circles of functional sta-

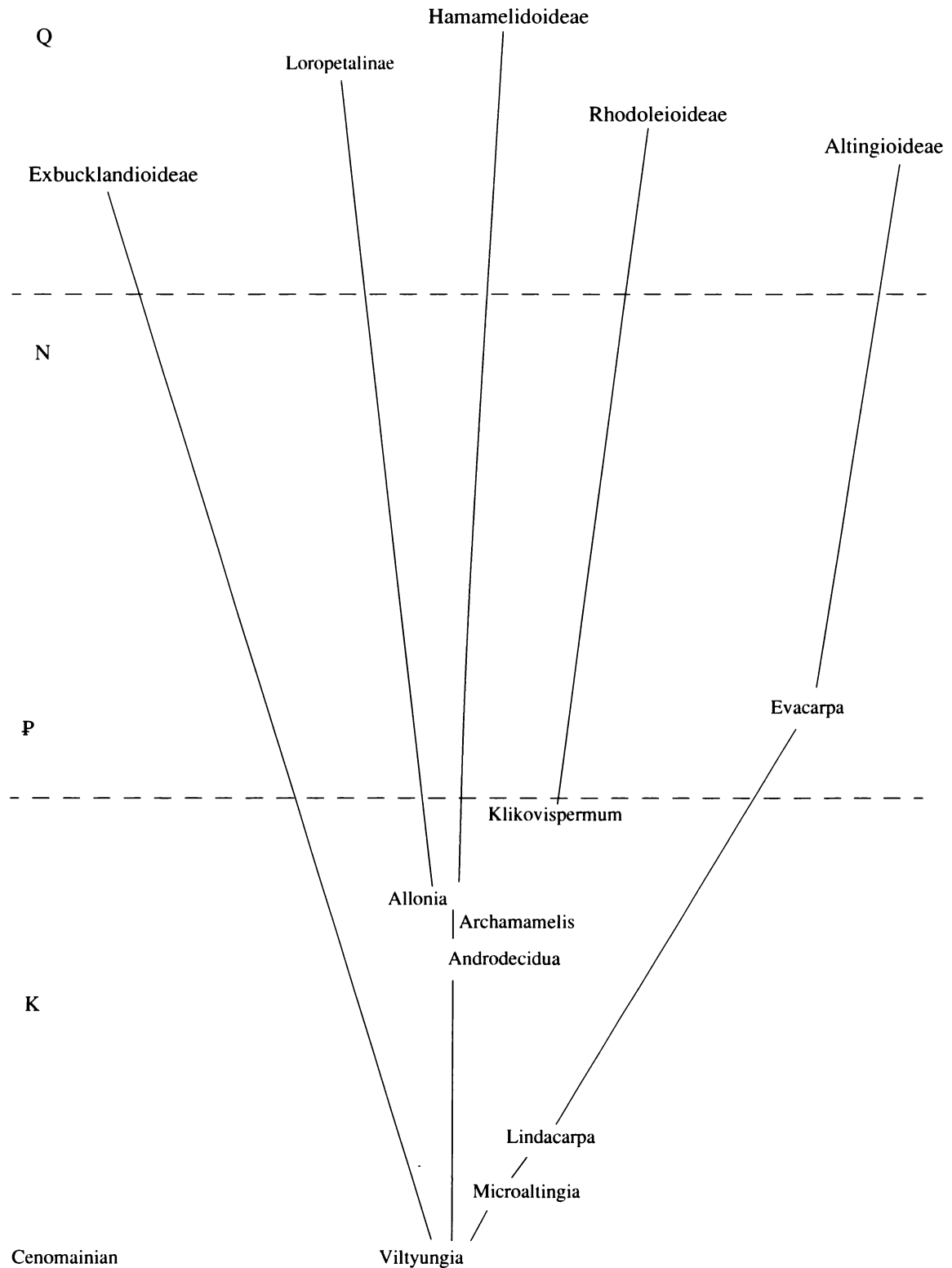


Fig. 79. Phylogeny of the family Hamamelidaceae.

mens (however, additional circles of stamens are also known in the subfamily Hamamelidoideae, Endress, 1989c).

The Middle Eocene genus *Fortunearites* is represented by a spikelike infructescence consisting of a massive axis and densely packed fruits developed from

a bicarpellate gynoecium. This genus is reminiscent of extant *Fortunearia* and *Sinowilsonia*. However, the staminate inflorescences associating with *Fortunearites* are close to those of extant *Corylopsis* and *Hamamelis*.

The subfamily Rhodoleioideae appeared in the Late Cretaceous with the genera *Klikovispermum* and *Rhodoleia* represented by seed remains. To this day, the morphology of other reproductive organs has remained unknown.

Accordingly, the preliminary phylogenetic reconstruction for the family Hamamelidaceae accomplished on the basis of the available paleobotanical data shows the synthetic genus *Vilryungia* at the basal node of morphological radiation. The characters of the three main subfamilies were distinguishable even in the Cenomanian. The evolutionary line of the Altingioideae, with the transitional forms *Microaltingia*, *Lindacarpa*, and *Evacarpa* is sufficiently documented. Leaf morphotypes typical of the extant *Liquidambar* appeared significantly earlier than its reproductive structures and could actually belong to one of the transitional forms. The same is the case for the *Parrotia* and *Parrotiopsis*-type leaves. The limited number of hamamelid leaf genera would probably increase at the expense of some morphotypes presently assigned to the Platanaceae and other families.

In other hamamelid subfamilies, the characters of extant genera, mainly the seed characters, appeared at the end of the Cretaceous (*Klikovispermum*, *Rhodoleia*, and *Hamamelis*). All the Cretaceous members of the lineages ascending to extant genera show unequal rates of evolutionary advancement (mosaic evolution) of their critical characters. Topologically, the phylogenetic scheme of the Hamamelidaceae significantly differs from that of the Platanaceae (compare Figs. 78, 79) representing an alternate mode of evolutionary development in the basal angiosperms.

CONCLUSIONS

(1) On the basis of the original fossil material and the relevant published data on fossil and extant platanoids and hamamelids, the evolutionary stages of their taxonomic and morphological diversities have been revealed. The taxonomic diversity is estimated as the numbers of genera per geological epoch, the morphological diversity is assessed as the numbers of vegetative and generative characters, the evolutionary significance of which is determined by their appearance/disappearance subsequences and the duration of their persistence in the geological record.

The geological history of the Platanaceae was begun in the Early Cretaceous (Albian). The maximal taxonomic diversity of the family was attained in the Late Cretaceous–Paleocene. The first stage of adaptive radiation of the family is marked by the appearance of short-living genera (blind evolutionary branches).

From the Paleocene to the Oligocene, the generic content of the family gradually decreased. Since the Oligocene, the family has been represented by the solitary genus *Platanus*. In the Cretaceous, numerous finds of *Platanus*-like leaf morphotypes were accompanied by reproductive structures different from those of the modern plane, necessitating a revision of the traditional concept of its wide distribution in the Cretaceous. The maximal morphological diversity of platanoids is recorded in the Paleocene.

Fossil precursors of the family Hamamelidaceae, which appeared in the Late Cretaceous and currently comprise up to 30 genera, are insufficiently known. In this family, the maximal taxonomic diversity is recorded in the Eocene. Since the Late Cretaceous, the extant taxa have steadily increased in number.

(2) The chronology of the appearance and development of vegetative and reproductive characters shows a correlation between taxonomic and morphological diversities. However, the numbers of genera do not correlate with morphological distances, and the evolution of morphological disparity, studied on the basis of reproductive characters, appears as an independent variable of considerable evolutionary significance.

The morphological diversity of the Platanaceae changed discontinuously from the Early Cretaceous to the Oligocene, being constant during the later periods. A slight increase in the number of genera in the Late Cretaceous is accompanied by a significant decrease in morphological diversity. At this stage, the generic diversification mostly reflects a recombination of previously existing characters. The maximal index of morphological diversity is obtained for the Paleocene representatives of the family. In the Eocene, an insignificant decrease of morphological diversity is accompanied by a rapid reduction in the number of platanoid taxa. In the Early Cretaceous, Paleocene, and Eocene, the limits of morphological variation extended on account of deviating morphologies of a limited stratigraphic range (the pistillate structures of *Oreocarpa*, *Tanyoplatanus*, etc.).

Since the Late Cretaceous, the morphological diversity of the Hamamelidaceae has increased over consecutive epochs. This trend generally coincides with the increase in the ratio of extant hamamelid genera.

The differences in taxonomic and morphological diversity between the Platanaceae and Hamamelidaceae relate to their contrasting evolutionary modes. Thus, in the Platanaceae, the bursts of new taxa are mostly related to morphological innovation (the appearance of closed perianthous calyptres, monopistillate heads, etc.). In contrast, the increase of hamamelid taxonomic diversity was primarily achieved through recombination of characters that appeared at the initial stage of their evolution.

(3) The phylogenies of the Platanaceae and Hamamelidaceae are reconstructed on the basis of chronological relationships and the finds of intermediate links. The emerging patterns of evolutionary development are profoundly different in these ancient angiosperm families. In the Platanaceae, there were two bursts of adaptive radiations, in the Albian–Cenomanian and the Maastrichtian–Paleocene, respectively, linked by the persistent *Platananthus*–*Platanocarpus* lineage, in which the staminate structures remained more conservative, whereas the pistillate structures underwent a morphological innovation and new leaf morphotypes appeared (*Macginitiea*). The perianth reduction obviously took place in parallel, but at different rates, in the evolutionary lines, which appeared in the Paleogene (*Tanyoplatanus*, *Tricolpopollianthus*, and *Platanus*). At the first stage, an evolutionary line with tetrastaminate flowers diverged from the main stock, disappearing in the Paleocene.

In the family Hamamelidaceae, several extinct Cretaceous taxa combined characters of two or more subfamilies serving as intermediate links between them (e.g., *Viltyungia* showing typical characters of the Exbucklandioideae, Altingioideae, and Hamamelidoideae; *Lindacarpa* combining characters of the subfamilies Altingioideae and Hamamelidoideae). Differentiation of the extant subfamilies Altingioideae, Exbucklandioideae, and Hamamelidoideae took place in the mid-Cretaceous, while the rhodoleioid characters appeared later (in seed genus *Klikovispermum*). The main adaptive radiation of the family obviously occurred during the Late Cretaceous. Later, diversification at lower taxonomic levels took place. The extant hamamelid genera first appeared in the terminal Cretaceous (seed remains), whereas the latest appearance of extinct genera is recorded in the Eocene.

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