PALEOBOTANY

Endocarps of *Prunus* (Rosaceae: Prunoideae) from the early Eocene of Wutu, Shandong Province, China

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Abstract Endocarps of the genus *Prunus* (family Rosaceae) have been described from early Eocene clay deposits in the Wutu Coal Mine, Shandong Province, China. Endocarps are elliptical or ovoid in lateral view, with a long canal that approaches the apex of the endocarp and contains the ventral vascular bundle. Comparisons with related living and fossil species of *Prunus* indicate that these endocarps should be assigned to *Prunus wutuensis* sp. nov. The endocarps from Wutu represent the earliest record of *Prunus* in Asia. Based on the distribution of fossil *Prunus* endocarps, the palaeobiogeographic history of the genus is shown on palaeogeographic maps of the Northern Hemisphere. The fossil data suggest that the genus first appeared in the early Eocene of North America and Asia, and then extended to Europe in the middle Eocene.

Keywords China; early Eocene; endocarps; *Prunus*; Wutu

INTRODUCTION

The genus *Prunus*, established by Linnaeus in 1753, belongs to the subfamily Prunoideae Focke of Rosaceae. It is represented by shrubs and trees, which are characterized by a solitary carpel, a fleshy drupe, five sepals and five petals (Rehder, 1940). Over 200 species exist (Rehder, 1940) with some of them being especially well known for their cultivated fruits, such as cherries, plums (*prunes* in French), peaches, apricots and almonds. The most widely adopted classification of *Prunus* is the one of Rehder (1940) that divides the genus into five subgenera: *Amygdalus* L., *Cerasus* Miller, *Laurocerasus* Duhamel, *Padus* Miller and *Prunophora* Neck. (= subg. *Prunus*). The subgenera are widely distributed in the Holarctic except for subg. *Laurocerasus* which is restricted to tropical and subtropical regions (Yü & al., 1986).

The oldest records of *Prunus* were based on leaves from the Late Cretaceous of Wyoming, New Jersey and Nebraska, U.S.A. (Berry, 1916; Brown, 1933) but their identification has not yet been confirmed. The earliest record of *Prunus* endocarps was from late Paleocene of Colorado, U.S.A. (Brown, 1962). This material was reevaluated by Pigg & al. (2008) and determined to belong to Icacinaceae rather than Rosaceae. Since the Eocene, abundant endocarps were reported from the Northern Hemisphere including both mold-casts (e.g., Reid & Reid, 1910, 1915; Kirchheimer, 1936, 1942, 1957; Miki, 1936, 1938; Mädler 1939; Szafer, 1961; Tanai, 1961; Dorofeev, 1963; Mai, 1964, 1973, 1984, 1995; Geissert, 1972; Gregor, 1978) and some specimens with internal anatomical structure (Cevallos-Ferriz & Stockey, 1991; Manchester, 1994).

Leaves assignable to *Prunus* are a significant component of the latest early Eocene Okanogan Highlands floras of northeastern Washington state (Republic) and related floras of British Columbia, Canada (Wehr & Hopkins, 1994; DeVore & Pigg, 2007). Flowers of *Prunus* and *Oemleria* are currently under study from the Republic flora as well (Benedict & al., 2008).

Fossil wood referred to *Prunus* has been reported from the Eocene to Miocene of the Northern Hemisphere (Wheeler & al., 1978; Guleria & al., 1983; Suzuki, 1984; Takahashi & Suzuki, 1988; Cevallos-Ferriz & Stockey, 1990; Wheeler & Manchester, 2002). However, to data the wood of *Prunus* from the Oligocene of Japan (Suzuki, 1984) represents the first record of *Prunus* in Asia, and the earliest occurrence of endocarps in Asia was reported from the Late Miocene of Japan (Tanai & Onoe, 1961). Surprisingly, no fossils of *Prunus* were found in Asia until the Oligocene although the diversity center of extant *Prunus* is located in Eastern Asia, particularly in the Sino-Himalayan floristic region (Mai, 1984).

Here we provide evidence for the recognition of the extant genus *Prunus* in the early Eocene of East China. The new specimens are endocarps collected from the Wutu Coal Mine in the Wutu Basin of the Shandong Province. This important fossil locality, which also yielded seeds of *Nuphar* (Nymphaeaceae) (Chen & al., 2004), is mainly known for its mammal fauna that has allowed to assign an early Eocene age to the Wutu Formation (Tong & Wang, 1998). Although Beard & Dawson (1999) even proposed a late Paleocene age for the Formation based on the presence of some primitive mammals with North American affinities such as the neoplagiaulacid multituberculate *Mesodmops dawsonae* and the carpolestid plesiadapiform *Carpocristes oriens*, it is now widely accepted to be of early Eocene age. This is based on the microevolution of seed-eating carpolestid mammals (Bloch & al., 2001) and is confirmed by a diversified mammal association (51 species) mainly including derived taxa belonging to modern orders such as the hyaenodontid creodont *Preonictis youngi*, the miacid carnivoran *Zodiocyon zetesios*, the perissodactyls *Pappomoropus taishanensis*, *Chowliia laoshanensis* and *Homogalax wutuensis*, and the artiodactyl *Wutuhyus primiveris* (Tong & Wang, 2006). Moreover, the discovery of the neoplagiaulacid *Mesodmops tenuis* and the carpolestid *Subengius mengi* in the late Paleocene of Inner Mongolia has shown that the two families dispersed from North America to Asia long before the mammalian migration waves of the Paleocene/Eocene boundary (Smith & al., 2004; Missiaen & Smith, 2008) and are thus relict families in Wutu.

In the present paper, we describe endocarps of *Prunus wutuensis* sp. nov. from Wutu and compare them with fossil and extant species. The new fossils represent the earliest record of *Prunus* in Asia. Based on fossil record of *Prunus* endocarps, the distribution of the genus in time and space is shown on a series of paleobiogeographic maps of the Northern Hemisphere.

■ MATERIALS AND METHODS

The endocarps of *Prunus* described here were collected from the surface tailings of the Wutu Coal Mine near the town of Wutu, Linqu County, Shandong Province, China, in 2008 and 2009. The Wutu Formation, which is reaching about 1000 m in thickness, was established by Geological Team No. 121, Shandong Coal and Geology Exploration Bureau in 1960, and consists of several members that are from bottom to top (Zhao, 1981): the lower coal-bearing member, the oil shale member, the middle coal-bearing member (containing twelve coal beds), and the upper coal-bearing member (Fig. 1).

The fossils were embedded in black shale (Fig. 2) at the contact of coal beds 5 and 7 from the middle coal-bearing member at about 250 m below the ground (Fig. 1). The 50 specimens collected are fragile compressions, some of which are deformed (Figs. 5–7). They were exposed from the matrix by "dégagement" (Leclercq, 1960) under a Nikon SMZ1000 stereomicroscope and photographed by a Canon DS8101 camera and a FEI Quanta-200 ESEM. The terminology used to describe the endocarps follows Mai (1984) and Manchester (1994).

The palaeocoordinates were converted from extant coordinates of fossil sites using "PointTracker for Windows" software, and plotted on 5 individual palaeogeographical maps on Projections of Lambert Equal-Area Azimuthal (North Pole) by using ArcView GIS v.3.2 software. The maps cover 5 time intervals, i.e., the Paleocene/Eocene (ca. 55 Ma), the Oligocene (ca. 30 Ma), the Miocene (ca. 14 Ma) modified from Scotese (1997), Smith & al. (2004) and LePage & al. (2005), the Pliocene (ca. 3 Ma) and the Pleistocene (ca. 1 Ma) from ArcView GIS software.

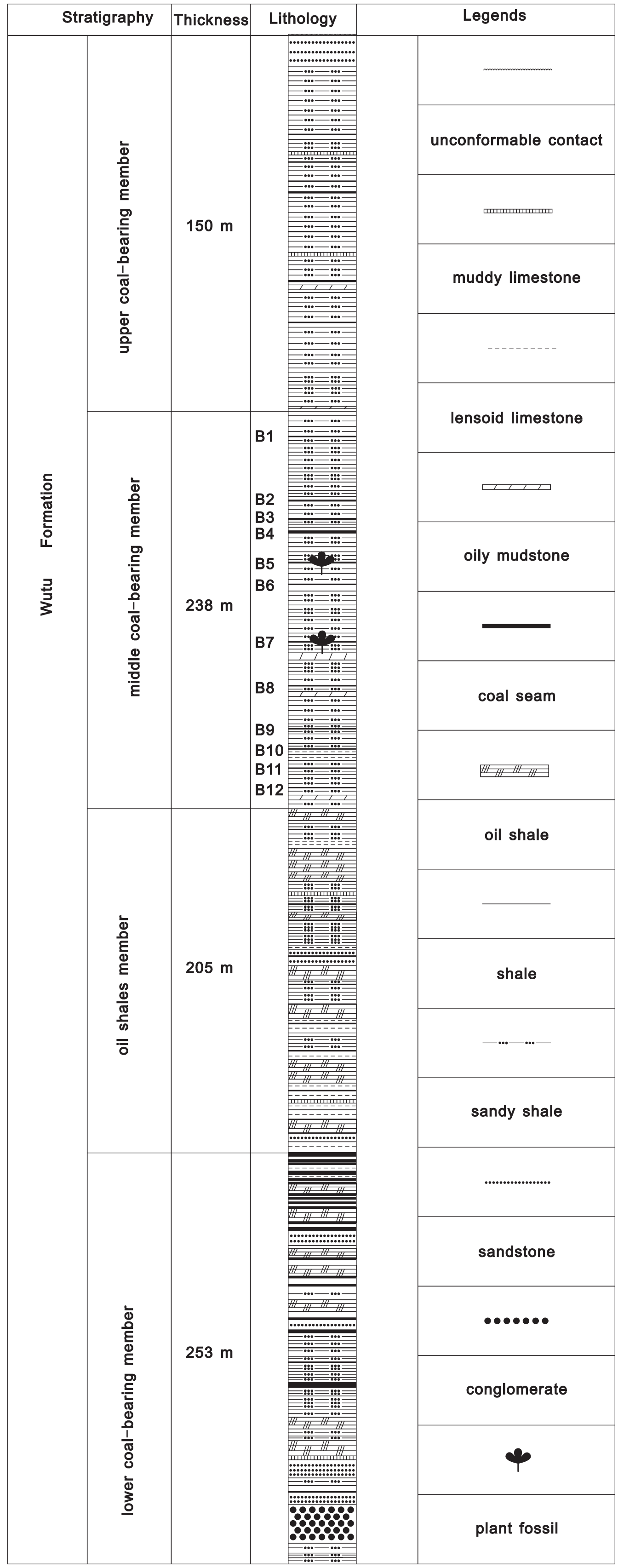


Fig. 1. A general stratigraphic column of Wutu Formation, indicating where the fossils were found. B1–B15 stand for coal seams.

■ DESCRIPTION OF THE NEW SPECIES

Order: Rosales
Family: Rosaceae
Subfamily: Prunoideae Focke
Genus: *Prunus* Linnaeus, 1753

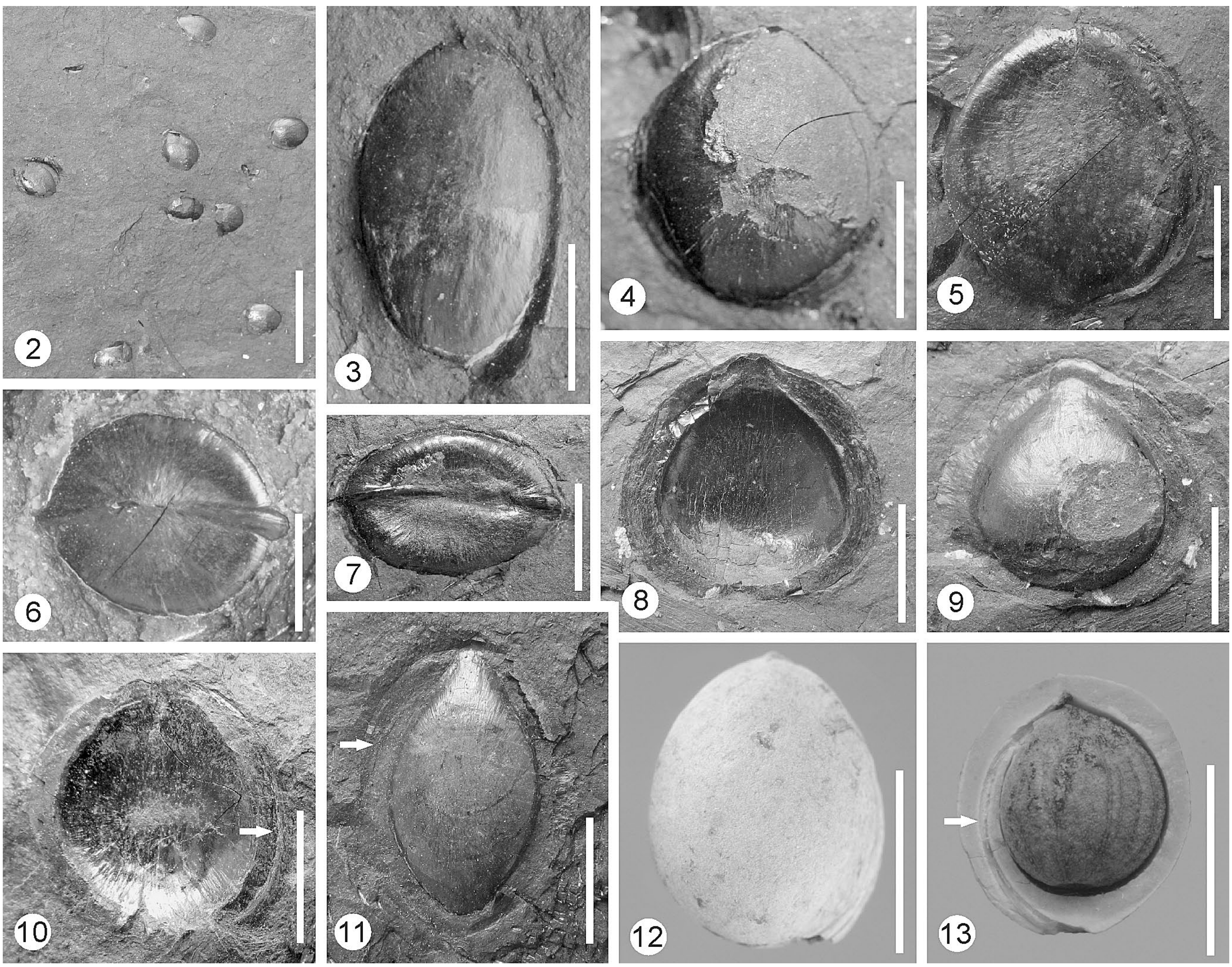
Prunus wutuensis Y. Li, T. Smith, C.J. Liu, N. Awasthi, J. Yang, Y.F. Wang & C.S. Li, **sp. nov.**

Species diagnosis. – Endocarps elliptical or ovoid, 8.5–12.0 mm long, 7.0–11.5 mm wide, and 2.5–3.0 mm thick. Each endocarp bearing a broad ventral keel, a round and obtuse apex and a round base. Endocarp surface smooth. A ventral vascular bundle approaching endocarp apex.

Type stratum. – The middle coal-bearing member of the Wutu Formation, early Eocene in age.

Type locality. – Wutu Coal Mine, Linqu County, Shandong Province, China.

Holotype. – Stratum and locality as above, *Cheng-Sen Li, Jian Yang, Ya Li, Qian-Qian Zhang & Bin Sun*, August 2009, Institute of Botany, Chinese Academy of Sciences, Beijing (IBCAS) No. 2009E002.



Figs. 2–13. Endocarps of *Prunus*. **2,** Black shale with eight *Prunus* endocarps partially exposed on the surface; specimen No. ibcas2009E001; scale bar = 2 cm. **3,** An elliptical *Prunus* endocarp in lateral view, with ventral keel to the right; specimen No. ibcas2009E002; scale bar = 5 mm. **4,** An ovoid *Prunus* endocarp in lateral view; specimen No. ibcas2009E003; scale bar = 5 mm. **5,** A laterally compressed *Prunus* endocarp; specimen No. ibcas2009E004; scale bar = 5 mm. **6,** A compressed *Prunus* endocarp in basal view, showing two ridges in the plane of symmetry; specimen No. ibcas2009E005; scale bar = 5 mm. **7,** A compressed *Prunus* endocarp in apical view, showing two ridges in the plane of symmetry; specimen No. ibcas2009E006; scale bar = 5 mm. **8–9,** A *Prunus* endocarp separated into two halves: part (Fig. 8) and counterpart with locule cast (Fig. 9); specimen No. ibcas2009E007a, b; scale bar = 5 mm. **10,** Longitudinal section of an endocarp showing the ventral vascular bundle canal (indicated by arrow); specimen No. ibcas2009E008; scale bar = 5 mm. **11,** Longitudinal section of another endocarp showing the ventral vascular bundle canal (indicated by arrow); specimen No. ibcas2009E009; scale bar = 5 mm. **12,** An extant endocarp of *Prunus avium* (L.) L. showing smooth surface and a ventral keel in the right (http://plants.usda.gov/java/largeImage?imageID=prav_002_ahp.tif); scale bar = 5 mm. **13,** Longitudinal section of an endocarp of extant *Prunus yedoensis* Matsum. showing the ventral vascular bundle canal (indicated by arrow) approaching apex and subapical placenta; scale bar = 5 mm.

Description. – The fruits are unilocular, single-seeded drupes. Endocarps are flattened, elliptical or ovoid in lateral view, bilaterally symmetrical, 8.5–12.0 mm (average 10.4 mm) long, 7.0–11.5 mm (average 9.0 mm) wide, and 2.5–3.0 mm thick in the compressions. Each of them possesses a broad ventral keel, a round and obtuse apex, as well as a round base. Endocarp outer surface is smooth (Figs. 3–4). Laterally compressed endocarps are flat (Fig. 5). Apically or basally compressed endocarps show two distinct ridges along the suture (Figs. 6 and 7). The endocarp sometimes dehisces into two equal halves along the suture (Figs. 8 and 9). Endocarp inner surface is smooth or with radial striation (Figs. 8 and 10). Locule casts are broad ovoid in lateral view, smooth or striated, with acute apex, and acute or round base, 7.3–9.3 mm long, 5.5–8.6 mm wide (Figs. 9 and 11). A curved canal originally hosting the ventral vascular bundle approaches the apex of the endocarp (Figs. 10, 11, 14 and 15).

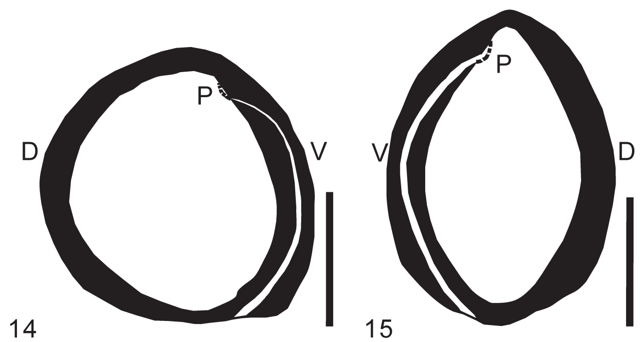


Fig. 14–15. Illustration of endocarps of *Prunus* from Wutu showing vascular bundle canals and possible placentas. D, dorsal suture; P, placenta; V, ventral suture. Scale bars = 5 mm.

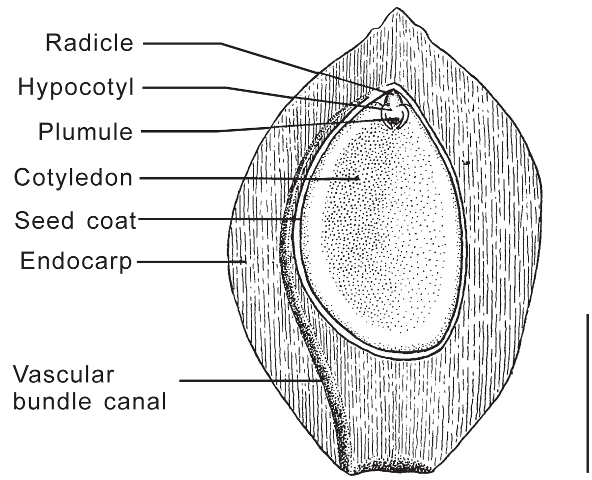
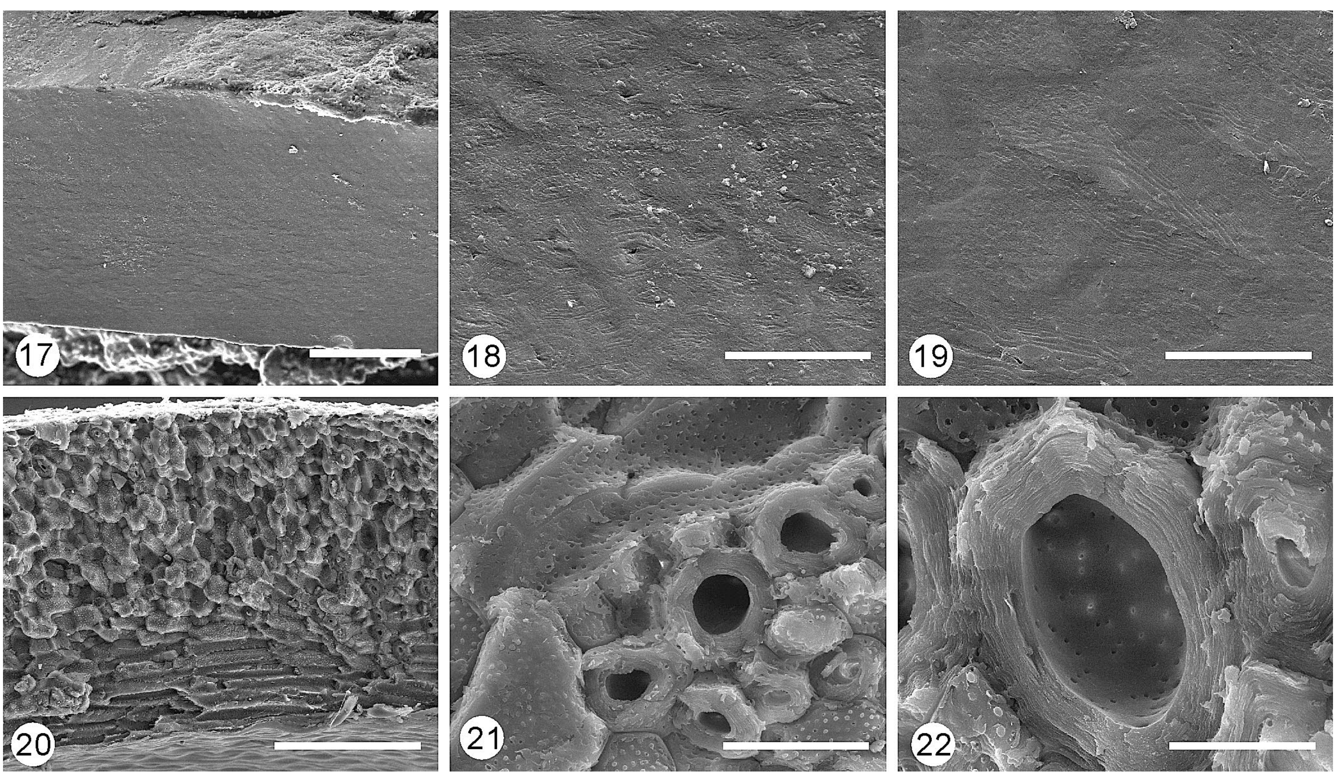


Fig. 16. *Prunus persica*, peach: longitudinal section through an endocarp showing vascular bundle canal and "hanging" seed, modified from Young & Young (1992: 279). Scale bar = 10 mm.



Figs. 17–22. The ESEM of endocarps of *Prunus*. **17,** Transverse sections of endocarps of *Prunus* from Wutu; scale bar = 200 µm. **18,** Enlargement of Fig. 17, showing details of sclereids; scale bar = 50 µm. **19,** Enlargement of Fig. 18, showing details of sclereid secondary walls; scale bar = 20 µm. **20,** Transverse sections of endocarps of *Prunus yedoensis*; scale bar = 200 µm. **21,** Enlargement of Fig. 20, showing details of sclereids; scale bar = 40 µm. **22,** Enlargement of Fig. 21, showing details of sclereid secondary walls; scale bar = 20 µm.

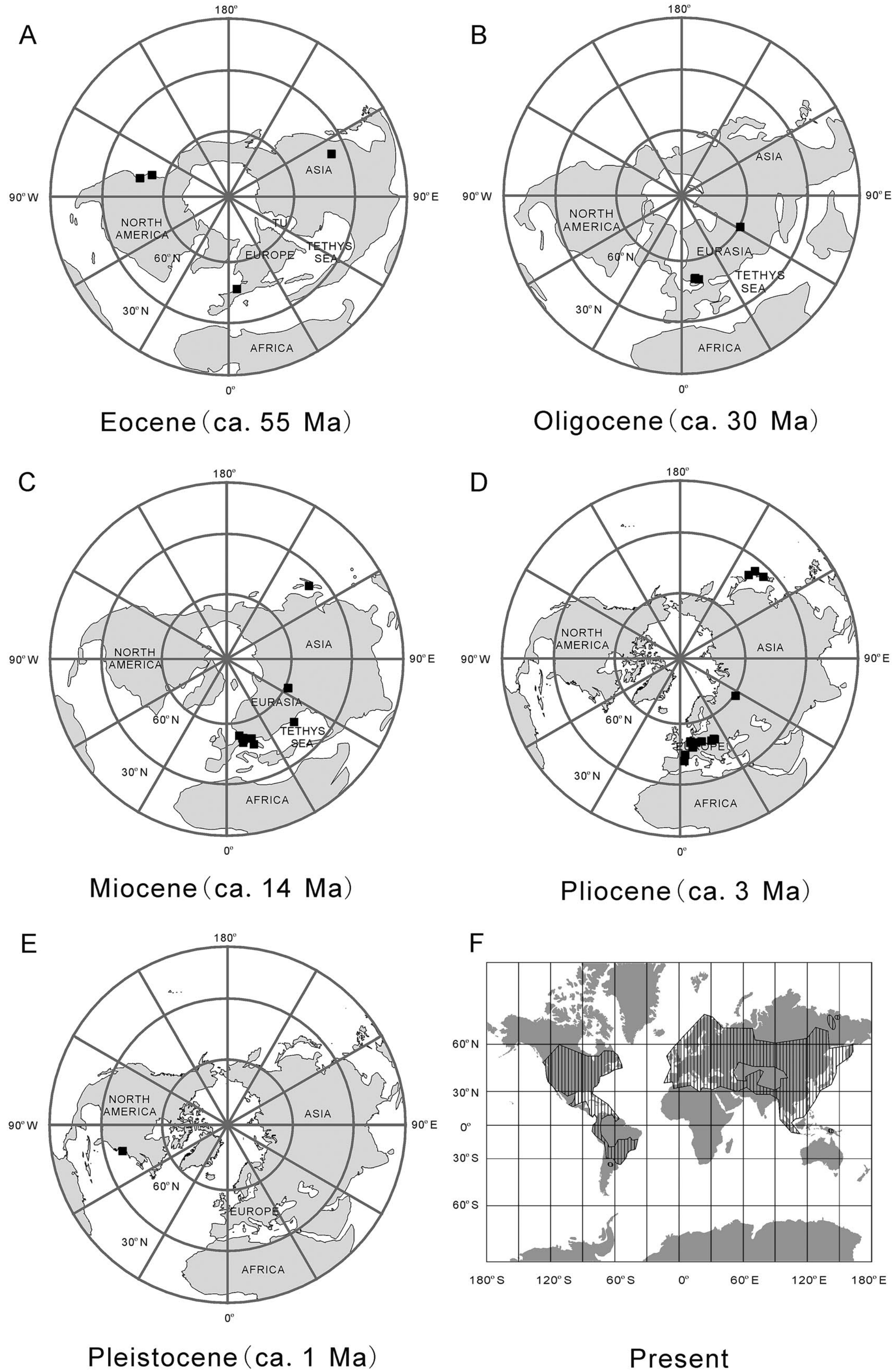


Fig. 23. Maps showing distribution of *Prunus* endocarps through the Cenozoic marked as black squares.

Table 1. Comparison of fossil species of *Prunus*.

	Prunus from Wutu	*Prunus* sp. (type 1)	*Prunus* sp. (type 2)
Endocarps:			
Apex	Obtuse, round	–	–
Base	Round	–	–
Ventral side	A broad keel	–	–
Outer surface	Smooth	Irregular	Irregular
Length (mm)	8.5–12.0	–	–
Width (mm)	7.0–11.5	12	Ca. 9
Thickness (mm)	Ca. 2.5–3.0	5	Ca. 6
Wall thickness (mm)	Ca. 0.3–1.5	–	–
Canal of vascular bundle	Present	–	–
Locality	Shandong, China	British Columbia, Canada	British Columbia, Canada
Age	Early Eocene	Middle Eocene	Middle Eocene
Reference	This article	Cevallos–Ferriz & Stockey, 1991	Cevallos–Ferriz & Stockey, 1991

	P. praecommunis	*P. nerchauensis*	*P. scharfii*
Endocarps:			
Apex	Acuminate	Acuminate, obtuse	Acute or obtuse
Base	–	Acuminate, obtuse	Round
Ventral side	A broad keel	A keel	A broad keel
Outer surface	Smooth	–	Smooth
Length (mm)	33	4–7	12–18
Width (mm)	24	3.5–5.5	8–16
Thickness (mm)	–	–	–
Wall thickness (mm)	–	–	–
Canal of vascular bundle	–	–	Present
Locality	Czech Republic	Germany	Germany
Age	Oligocene	Middle Oligocene	Oligocene to Miocene
Reference	Mai, 1984	Mai, 1984	Mai, 1984; Gregor, 1978

	P. insititia var. *pliocaenica*	*P. aviiformis*	*P. girardii*
Endocarps:			
Apex	Tapering	Obtuse	Round
Base	Tapering	Round	Tapering
Ventral side	A broad keel, grooved	A broad keel	A broad keel, grooved
Outer surface	Shallowly pitted	–	Weakly wrinkled
Length (mm)	10–20	7.5–11.5	6–10
Width (mm)	6–12	7–9.5	4.5–7.5
Thickness (mm)	6	–	–
Wall thickness (mm)	–	–	–
Canal of vascular bundle	Present	–	Present
Locality	Germany, France	Germany	France, Poland
Age	Pliocene	Pliocene	Pliocene
Reference	Mädler, 1939; Mai, 1984	Mädler, 1939	Kirchheimer, 1949; Geissert, 1972; Szafer, 1954

Prunus sp. (type 3)	*P. olsonii*	*P. weinsteinii*	*P. moselensis*	
–	Acute	Pointed	Acuminate	
–	Round to truncate	Round	Acuminate	
–	An apical keel	A broad keel	A broad keel	
Irregular	–	Rugulate	–	
–	6.6–6.8	10.4	8	
Ca. 7	5.3–5.9	8.6	6.5	
Ca. 4	4.5–5.3	6.2	4.6	
–	0.35–0.65	0.8–1.2	–	
–	–	–	Present	
British Columbia, Canada	Oregon, U.S.A.	Oregon, U.S.A.	Zwickau, Germany	
Middle Eocene	Middle Eocene	Middle Eocene	Middle Eocene	
Cevallos–Ferriz & Stockey, 1991	Manchester, 1994	Manchester, 1994	Mai, 1984	
P. stipitata	*P. leporimontana*	*P. protossiori*	*P. crassa*	
Acuminate	Acuminate	Obtuse	Obtuse	
Stipitate	Round	Cordate	Round	
A broad keel	A keel	–	A broad keel	
Wrinkled	–	Tuberculate	Smooth	
8	5–8	12.6	15.6–16.4	
5	4–7	9.3	12.8–13.4	
–	–	–	11.4	
–	–	–	–	
Present	Present	–	Present	
Germany, Russia	Germany, Poland	Japan	Germany, Poland	
Oligocene to Pliocene	Miocene	Late Miocene	Miocene to Pliocene	
Reid & Reid 1915; Dorofeev, 1963	Kirchheimer, 1942, 1957; Mai, 1964; Szafer, 1961; Gregor, 1978	Tanai & Onoe, 1961	Mai, 1973, 1984; Kirchheimer, 1936;	
P. tenerirugosa	*P.* cf. *sibirica*	*P.* cf. *triloba*	*P. haussknechti*	*P.* cf. *serrulata*
Obtuse	Acuminate or round	Acuminate or round	Round	Obtuse
Round	Acuminate	Obtuse	Round	Obtuse
A broad keel	A broad keel, grooved	A broad keel, grooved	A broad keel, grooved	A keel
Wrinkled	–	–	–	–
4–6	13.5	10–11	11.6–14.0	6.5–7.5
3.5–5.5	12	9–10	12	4.3–4.5
–	–	–	–	4
–	–	–	–	–
Present	Present	–	Present	–
France, Poland, Netherlands	Hyōgo, Japan	Hyōgo, Japan	Iwate, Japan	Tokyo, Japan
Pliocene	Pliocene	Pliocene	Pliocene	Pliocene
Reid & Reid, 1910, 1915; Mai, 1984	Miki, 1936	Miki, 1936	Miki, 1938	Miki, 1938

The endocarp wall consists of successive layers of sclereids and is compressed (Figs. 17–19), with a thickness of 1.0–1.5 mm (average 1.4 mm) along the suture and 0.4–0.6 mm in the rest. The endocarp wall at the ventral suture has the same thickness as that at the dorsal suture (Figs. 8–11). The secondary walls of sclereids are composed of parallel layers (Figs. 18 and 19).

■ DISCUSSION

Carpological comparisons. — The fossil record of prunoid endocarps has been reviewed by Mai (1984), who provided a key of carpological characteristics of the five genera of Prunoideae, based on the characters of extant and fossil endocarps. According to this key, the prunoid taxon from Wutu does not belong to the genera *Pygeum*, *Maddenia*, *Oemleria*, and *Prinsepia*, but is similar to *Prunus*.

The endocarps from Wutu are characterized by: (1) unilocular, single-seeded drupes; (2) elliptical or ovate shape; (3) development of a ventral keel; (4) a curved vascular bundle canal approaching the apex (Figs. 10, 11, 14, 15); and (5) sclereids in the endocarp wall. These characters are common to the genus *Prunus* (Figs. 12, 13, 16, 20–22).

At the subgeneric level, *Prunus* from Wutu differs from *P.* subg. *Amygdalus* in having a smooth surface of the endocarp while the latter has a wrinkled, often deeply furrowed and pitted surface of the endocarp (Mai, 1984). It also differs from *P.* subg. *Padus* in the vascular bundle canal that remains much beyond the half of endocarp length while the latter has a vascular bundle canal reaching up to the half of endocarp length (Mai, 1984).

Among extant *Prunus*, endocarps of twenty-five species have been described and figured by Bojnanský & Fargašová (2007: 279–284), and photographs of endocarps of thirty-seven species are available from the plants database of the Natural Resources Conservation Services, United States Department of Agriculture (http://plants.usda.gov/java/nameSearch). Endocarps from Wutu match those of *Prunus avium* (L.) L. (*P.* subg. *Cerasus*) (Fig. 12) in their overall shape, smooth surface and length. The secondary walls of the sclereids in the fossils consist of layers, which are similar to those found in the extant *Prunus yedoensis* Matsum (Figs. 21 and 22).

Five species of *Prunus* from the Eocene of North America (Cevallos-Ferriz & Stockey, 1991; Manchester, 1994), twenty-three (seventeen fossil species and six extant species) from the Eocene to Pleistocene of Europe (Mai, 1984), and five from the Late Miocene to Pliocene of East Asia (Miki, 1936, 1938; Tanai & Onoe, 1961) have been recorded as endocarps. Based on endocarp morphology, Mai (1984) confirmed the identification of the twenty-three species of *Prunus* from Europe and referred them to four subgenera. However, the subgeneric classification could not be confirmed with certainty by the carpological data. As mentioned above, the *Prunus* material from Wutu is different from *P.* subg. *Amygdalus* and subg. *Padus*. We therefore restricted our comparisons to the eleven fossil species of the *P.* subg. *Prunus* and subg. *Cerasus* from Europe and the ten fossil species from North America and Asia (Table 1).

Among the fossil specimens, only *Prunus* sp. from Wutu, *P. moselensis* Mai, *P. scharfii* Gregor, *P. stipitata* Reid & Reid, *P. leporimontana* Mai, *P. crassa* (Ludwig) Schimper, *P. insititia* var. *pliocaenica* Mädler, *P. girardii* Kirchheimer, *P. tenerirugosa* Mai, *P.* cf. *sibirica* Miki and *P. haussknechti* Miki show the canal in the vascular bundle which is a key character of *Prunus* (Mai, 1984). In the other species the presence of a vascular bundle canal cannot be ascertained. We therefore further restrict the comparison of the new specimen from Wutu with the fossil endocarps having a vascular bundle canal.

It appears that the endocarps from Wutu differ from *P. insititia* var. *pliocaenica*, *P. girardii*, *P.* cf. *sibirica* and *P. haussknechti* by lacking a grooved ventral side, from *P. moselensis*, *P. stipitata* and *P. leporimontana* by the apex being obtuse to rounded rather than acuminate, and from *P. tenerirugosa* by the surface being smooth rather than wrinkled. In endocarp shape and surface, our specimens are more similar to those of *P. scharfii* and *P. crassa* but the new ones are 8.5 –12 mm long, while the latter two are larger, 12–18 mm resp. 15.6 –16.4 mm in length. It thus appears that the new specimens cannot be assigned to any known fossil species of *Prunus* and are therefore described as a new species, *Prunus wutuensis*. The endocarps of *P. wutuensis* represent the oldest endocarps of the genus *Prunus* in Asia.

Phytogeographical implications. — Based on hybridization experiments, Watkins (1976) speculated that *Prunus* originated in Central Asia and dispersed later into the rest of Eurasia and the New World. The analysis of combined ITS and *trnL-trnF* indicated that *Prunus* originated in Eurasia (Bortiri & al., 2001). However, these two types of studies have not been supported by fossil evidence. The fossil record of endocarps and wood suggests that *Prunus* first appeared in the early Eocene of North America and Asia, then extended to Europe in the middle Eocene, and flourished luxuriantly during Miocene and Pliocene in Eurasia (Fig. 23; Table 1) (Wheeler & al., 1978).

According to a calibrated molecular tree, *Prunus* diverged from its sister clade Maloideae s.l. at least 44.3 Ma ago during the middle Eocene (Oh & Potter, 2005). The time of divergence may have been even earlier based on fossil endocarps and wood from the early Eocene (Wheeler & al., 1978; this paper).

Rosaceae underwent a tremendous diversification during the Eocene (Wolfe, 1987; Stockey & Wehr, 1996), once the conditions for the development of broad-leaved deciduous forests were established (Wolfe, 1987). According to the palynological data from the Wutu Formation, temperate broad-leaved deciduous plants, such as *Betula*, *Alnus*, *Ulmus*, *Quercus* dominated the vegetation, and tropical to subtropical elements like *Liquidambar*, Myrtaceae and gymnosperm were less abundant (Wang, 2003; Wang & al., 2005).

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LITERATURE CITED

Beard, K.C. & Dawson, M.R. 1999. Intercontinental dispersal of Holarctic land mammals near the Paleocene/Eocene boundary: Paleogeographic, paleoclimatic and biostratigraphic implications. *Bull. Soc. Geol. France* 170: 697–706.

Benedict, J.C., DeVore, M.L. & Pigg, K.B. 2008. Rosaceous flowers resembling *Prunus* from the Eocene Republic flora of eastern Washington State, USA. Botany 2008, Vancouver, B.C., July 2008. http://2008.botanyconference.org/engine/search/index.php?func=detail&aid=694. [Abstract]

Berry, E.W. 1916. The lower Eocene floras of southeastern North American. *Profess. Pap. U. S. Geol. Surv.* 91: 1–481.

Bloch, J.I., Fisher, D.C., Rose, K.D. & Gingerich, P.D. 2001. Stratocladistic analysis of Paleocene Carpolestidae (Mammalia, Plesiadapiformes) with description of a new late Tiffanian genus. *J. Vertebr. Paleontol.* 21: 119–131.

Bojnanský, V. & Fargašová, A. 2007. *Atlas of seeds and fruits of Central and East-European flora*. Dordrecht: Springer Netherlands.

Bortiri, E., Oh, S.H., Jiang, J.G., Baggett, S., Granger, A., Weeks, C., Buckingham, M., Potter, D. & Parfitt, D.E. 2001. Phylogeny and systematics of *Prunus* (Rosaceae) as determined by sequence analysis of ITS and the chloroplast *trnL-trnF* Spacer DNA. *Syst. Bot.* 26: 797–807.

Brown, R.W. 1933. Fossil plants from the Aspen Shale of southwestern Wyoming. *Proc. U.S. Natl. Mus.* 82: 1–10.

Brown, R.W. 1962. Paleocene flora of the Rocky Mountains and Great Plains. *Profess. Pap. U. S. Geol. Surv.* 375: 1–119.

Cevallos-Ferriz, S.R.S. & Stockey, R.A. 1990. Vegetative remains of the Rosaceae from the Princeton Chert (Middle Eocene) of British Columbia. *I.A.W.A. Bull.*, n.s.,11: 261–280.

Cevallos-Ferriz, S.R.S. & Stockey, R.A. 1991. Fruits and seeds from the Princeton Chert (Middle Eocene) of British Columbia: Rosaceae (Prunoideae). *Bot. Gaz.* 152: 369–379.

Chen, I., Manchester, S.R. & Chen, Z. 2004. Anatomically preserved seeds of *Nuphar* (Nymphaeaceae) from the early Eocene of Wutu, Shandong Province, China. *Amer. J. Bot.* 91: 1265–1272.

DeVore, M.L. & Pigg, K.B. 2007. A brief review of the fossil history of the family Rosaceae with a focus on the Eocene Okanogan Highlands of eastern Washington State, USA, and British Columbia, Canada. *Pl. Syst. Evol.* 266: 45–57.

Dorofeev, P.I. 1963. *Die tertiären Floren Westsibiriens*. Moskau, Leningrad: Akademia Nauk SSSR, Bot. Inst. V.L. Komarov.

Geissert, F. 1972. Neue Untersuchungen im Pliozän der Hagenauer Umgebung (nördliches Elsaß). *Mainzer Naturwiss. Arch., Beiheft* 11: 191–221.

Gregor, H.J. 1978. Die miozänen Frucht- und Samenfloren der Oberpfälzer Braunkohle. I. Funde aus den sandigen Zwischenmitteln. *Palaeontographica, Abt. B, Paläophytol.* 167: 8–103.

Guleria, J.S., Thakur, V.C., Virdi, N.S. & Lakhanpal, R.N. 1983. A fossil wood of *Prunus* from the Kargil (= Liyan) Formation of Ladakh. Pp. 187–193 in: Thakur, V.C. & Sharma, K.K. (eds.), *Geology of Indus Suture Zone of Ladakh*. Dehra Dun: Wadia Institute of Himalayan Geology.

Kirchheimer, F. 1936. Beiträge zur Kenntnis der Tertiärflora. *Palaeontographica, Abt. B, Paläophytol.* 82: 71–141.

Kirchheimer, F. 1942. Rosaceae. Pp. 1–259 in: Jongmans, W. (ed.), *Fossilium Catalogus II: Plantae*, part 25. s'Gravenhage: Junk.

Kirchheimer, F. 1949. Zur Kenntnis der Pliozaenflora von Soufflenheim im Elsaß. *Ber. Oberhess. Ges. Natur-Heilk. Giessen* 24: 206–230.

Kirchheimer, F. 1957. *Die Laubgewächse der Braunkohlenzeit mit einem kritischen Katalog ihrer Früchte und Samen*. Halle/Saale: Knapp.

Leclercq, S. 1960. Refendage d'une roche fossilifère et dégagement de ses fossiles sous binoculaire. *Senckenberg. Leth.* 41: 483–487.

LePage, B.A., Yang, H. & Matsumoto, M. 2005. The evolution and biogeographic history of *Metasequoia*. Pp. 3–114 in: LePage, B.A., Williams, C.J. & Yang, H. (eds.), *The geobiology and ecology of* Metasequoia. Dordrecht: Springer Press.

Linnaeus, C. 1753. *Species plantarum*. Stockholm: Impensis Laurentii Salvii.

Mädler, K. 1939. Die pliozäne Flora von Frankfurt am Main. *Abh. Senckenberg. Naturf. Ges.* 446: 1–202.

Mai, D.H. 1964. Die Mastixioideen-Floren im Tertiär der Oberlausitz. *Pälaontol. Abh., Abt. B, Paläobot.* 2: 1–192.

Mai, D.H. 1973. Die Revision der Originale von R. Ludwig 1857, ein Beitrag zur Flora des unteren Villafranchien. *Acta Palaeobot.* 14: 89–117.

Mai, D.H. 1984. Karpologische Untersuchungen der Steinkerne fossiler und rezenter Amygdalaceae (Rosales). *Feddes Repert.* 95: 299–322.

Mai, D.H. 1995. *Tertiäre Vegetationsgeschichte Europas*. Jena: Fischer.

Manchester, S.R. 1994. Fruits and seeds of the Middle Eocene Nut Beds flora, Clarno Formation, North Central Oregon. *Palaeontogr. Amer.* 58: 1–205.

Miki, S. 1936. Plant fossils from the Stegodon beds and Elephas beds near Akashi. *Jap. J. Bot.* 8: 303–341.

Miki, S. 1938. On the change of flora of Japan since the Upper Pliocene and the floral composition at the present. *Jap. J. Bot.* 9: 213–251.

Missiaen, P. & Smith, T. 2008. The Gashatan (late Paleocene) mammal fauna from Subeng, Inner Mongolia, China. *Acta Palaeontol. Polon.* 53: 357–378.

Oh, S.H. & Potter, D. 2005. Molecular phylogenetic systematics and biogeography of tribe Neillieae (Rosaceae) using DNA sequences of cpDNA, rDNA, and LEAFY. *Amer. J. Bot.* 92: 179–192.

Pigg, K.B., Manchester, S.R. & DeVore, M.L. 2008. Fruits of Icacinaceae (Tribe Iodeae) from the Late Paleocene of Western North America. *Amer. J. Bot.* 95: 824–832.

Rehder, A. 1940. *A manual of cultivated trees and shrubs hardy in North America exclusive of the subtropical and warmer temperate regions*, 2nd ed. New York: Macmillan Press.

Reid, C. & Reid, E.M. 1910. A further investigation of the Pliocene flora of Tegelen. *Proc. Kon. Ned. Akad. Wetensch., Nat. Sci.* 13: 192–201.

Reid, C. & Reid, E.M. 1915. The Pliocene floras of the Dutch-Prussian border. *Meded. Rijkskopsporing Delftstoffen* 6: 1–178.

Scotese, C.R. 1997. *Paleogeographic atlas*. PALEOMAP progress report no. 90-0497. Arlington: Department of Geology, University of Texas.

Smith, A.G., Smith, D.G. & Funnell, B.M. 2004. *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge: Cambridge University Press.

Smith, T., Van Itterbeeck, J. & Missiaen, P. 2004. Oldest Plesiadapiform (Mammalia, Proprimates) from Asia and its paleobiogeographic implications for faunal interchange with North America. *Comp. Rend. Palévol* 3: 43–52.

Stockey, R.A. & Wehr, W.C. 1996. Flowering plants around Eocene lakes of the interior. Pp. 234–247 in: Ludvigsen, R. (ed.), *Life in stone: Fossils of British Columbia*. Vancouver: University of British Columbia Press.

Suzuki, M. 1984. Some fossil woods from the Paleogene of northern Kyushu, III. *Bot. Mag. (Tokyo)* 97: 457–468.

Szafer, W. 1954. Pliocenska Flora okolic Czorsztyna i jej stosunek do Plejstocenu. *Instytut Geologiezny Prace* 11: 1–238.
Szafer, W. 1961. Miocenska Flora ze Starych Gliwic na Slasku. *Instytut Geologiezny Prace* 33: 1–205.
Tanai, T. 1961. Neogene floral change in Japan. *J. Fac. Sci. Hokkaido Univ., Ser. 4, Geol. Mineral.* 11: 119–398.
Tanai, T. & Onoe, T. 1961. A Mio-Pliocene flora from the Ningyotoge area on the border between Tottori and Okayama Prefectures, Japan. *Rep. Geol. Surv. Japan* 187: 1–62.
Takahashi, A. & Suzuki, M. 1988. Two new fossil woods of *Acer* and a new combination of *Prunus* from the Tertiary of Japan. *Bot. Mag. (Tokyo)* 101: 474–481.
Tong,Y. & Wang, J. 1998. A preliminary report on the Early Eocene mammals of the Wutu fauna, Shandong province, China. *Bull. Carnegie Mus. Nat. Hist.* 34: 186–193.
Tong, Y.S. & Wang, J.W. 2006. Fossil mammals from the Early Eocene Wutu Formation of Shandong Province. *Palaeontol. Sin.*, n.s. C, 28: 1–195. [In Chinese.]
Wang, X.M. 2003. *Palynology, paleovegetation and paleoclimate of Paleogene of Northern China*. Masters Thesis, Shandong University of Science and Technology, Shandong, China. [In Chinese with English abstract.]
Wang, X.M., Wang, M.Z. & Zhang, X.Q. 2005. Eocene palynostratigraphy of Wutu, Shandong and its stratigraphical significance. *J. Stratigr.* 29: 22–27. [In Chinese with English abstract.]
Watkins, R. 1976. Cherry, plum, peach, apricot and almond. Pp. 242–247 in: Simmonds, N.W. (ed.), *Evolution of crop plants*. London: Longman Press.
Wehr, W.C. & Hopkins, D.Q. 1994. The Eocene orchards and gardens of Republic, Washington. *Washington Geol.* 22: 27–34.
Wheeler, E.A. & Manchester, S.R. 2002. Wood of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon, USA. *I.A.W.A. J.,* Suppl. 3: 1–188.
Wheeler, E.A., Scott, R.A. & Barghoorn, E.S. 1978. Fossil dicotyledonous woods from Yellowstone National Park, part II. *J. Arnold Arbor.* 59: 1–26.
Wolfe, J.A. 1987. An overview of the origins of the modern vegetation and flora of the northern Rocky Mountains. *Ann. Missouri Bot. Gard.* 74: 785–803.
Young, J.A. & Young, C.G. 1992. *Seeds of woody plants in North America*. Oregon: Dioscorides Press.
Yü, T.T., Lu, L.T., Ku, T.C., Li, C.L., Kuan, K.C. & Chiang, W.F. 1986. *Flora of China*, vol. 38, *Rosaceae and Connaraceae*. Beijing: Science Press. [In Chinese.]
Zhao, J.S. 1981. Discussing Tertiary age problem based on microfossil and sporopollen of Wutu coal field. *Shandong Geol. Inf.* 4: 76–80 [In Chinese.]