Acta Palaeobotanica 47(1): 237–251, 2007

Podocarpium A. Braun ex Stizenberger 1851 from the middle Miocene of Eastern China, and its palaeoecology and biogeography

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Received 2 August 2006; accepted for publication 28 February 2007

ABSTRACT. Fruit and leaf impressions of the legume genus *Podocarpium* A. Braun ex Stizenberger 1851 (formerly *Podogonium* Heer 1857) from the middle Miocene Shanwang Formation of Shandong Province, eastern China were reinvestigated. The results suggest that these specimens, previously identified as *Podogonium oehningense* (Koenig) Kirchh. and *P. knorrii* (A. Braun) Heer, actually belong to the same taxon, which can be assigned to a common species *Podocarpium podocarpum* (A. Braun) Herendeen from Miocene floras of Europe. Its leaflet architecture and fruit morphology are comparable with related genera in the subfamily Caesalpinioideae of the family Leguminosae, but all the characters of *Podocarpium* do not conform to any single extant legume genus. The fruits and/or leaves of *Podocarpium* have been discovered from the early Oligocene to the Pliocene of Eurasia. Based upon the megafossil and possibly related pollen records, paleoecology and biogeography of *Podocarpium* through the Neogene of Eurasia are discussed, with special reference to the floristic regions and climatic zones in the Miocene of China. The origin of *Podocarpium* may have been in the early Paleogene of eastern Asia, then spread into non-arid middle latitudes of Eurasia during the Miocene. *Podocarpium* gradually became restricted to "East Asia" and "East, South, and Central Europe" during the latest Oligocene and early Miocene due to climate deterioration, Asian Monsoon systems, and Asian interior desertification. It may have become extinct during the Pleistocene in the eastern Mediterranean.

KEY WORDS: *Podocarpium*, Leguminosae, biogeography, palaeoecology, Miocene, Shanwang Formation, China

INTRODUCTION

The genus *Podocarpium* A. Braun ex Stizenberger 1851 (formerly *Podogonium* Heer 1857) is one of the most common legume megafossils in the Neogene of Eurasia (Herendeen 1992a,b, Liu et al. 2001, Wang et al. 2005, Wang 2006). Its characteristic fruits and leaflets are well known from some Miocene floras of Switzerland and southern Germany (Heer 1857, Hantke 1954, Kirchheimer 1957, Rüffle 1963, Gregor & Hantke 1980, Gregor 1986), Austria (Kovar-Eder et al. 2004), Czech Republic (Bůžek 1971), Poland (Zastawniak 1980), Thailand (Endo & Fujiyama 1966), Japan (Ishida 1970, Hayashi 1975, Tanai 1978) and eastern China (Hu & Chaney 1940, WGCPC 1978, Sun 1999, Wang 2006). The systematic relationship of *Podocarpium* has long been controversial and was first illustrated as an unidentified fruit (Knorr 1755), then assigned to *Cabomba* Aublet. (Koenig 1825), *Gleditschia* or *Gleditsia* L. (Braun 1845, Gregor & Hantke 1980, Gregor pers. comm.), *Dalbergia* L. (Unger 1851), *Copaifera* L. (Kováts 1856), *Podocarpium* Braun ex Stizenberger (Stizenberger 1851), and *Podogonium* Heer (Heer 1857). While Herendeen (1992b) noted similarities between *Podocarpium* and several genera in the tribes Detarieae and Amherstieae (Caesalpinioideae, Leguminosae), Liu et al. (2001) could not assign *Podocarpium* specifically to

Caesalpinioideae. A close association with the pollen species *Fupingopollenites* (*Tricolporopollenites*) *wackersdorfensis* (Mohr & Gregor 1984, Liu et al. 2001) has been postulated, however, recent palynological studies suggest that *F. wackersdorfensis* may be related to Verbenaceae from the middle Eocene to early Pleistocene of Eurasia (Song et al. 1999) or an enigmatic extinct dicotyledonous plant (Song et al. 2004, Wang & Harley 2004). Therefore, an accurate appreciation for the botanical affinities of *Podocarpium* and possibly related pollen is at present uncertain.

In China, *Podogonium* (i.e. *Podocarpium*) megafossils were first reported by Hu and Chaney (1940) from the Miocene Shanwang Formation of Shandong Province (Fig. 1), and subsequently from other numerous localities (Guo 1980, Li 1981, Li et al. 1984, 1987, Guo & Zhou 1992, Liu et al. 2001). Furthermore, *Leguminosites climensis*, described by Chaney (1933) from the Pliocene of Shanxi Province, while known as *Podogonium* (Sun 1999), should be re-assigned to *Podocarpium* (Wang 2006). Specimens deposited at the Institute of Botany (Beijing, P. R. China) from the Shanwang Formation of Shandong Province were previously identified as *Podogonium oehningense* (Koenig) Kirchh. (WGCPC 1978, Sun 1999) or *P. knorrii* (Braun) Heer (Hu & Chaney 1940). The purpose of this paper is to re-investigate the taxonomy of these specimens and to discuss the palaeoecology and biogeography of *Podocarpium* through the Neogene of Eurasia based on megafossil and possibly related pollen records.

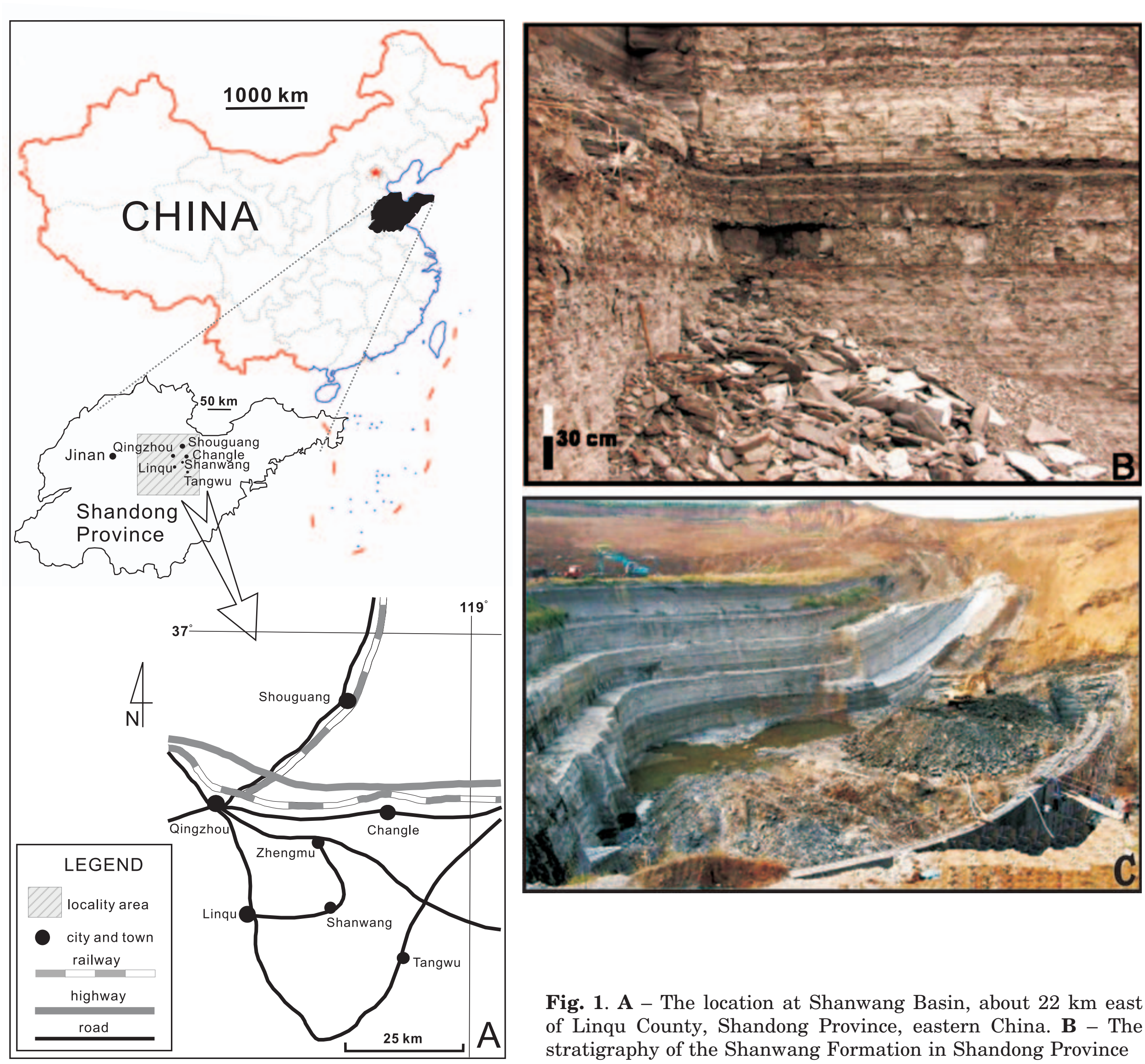

Fig. 1. **A** – The location at Shanwang Basin, about 22 km east of Linqu County, Shandong Province, eastern China. **B** – The stratigraphy of the Shanwang Formation in Shandong Province

NOMENCLATURAL NOTES

Podocarpium A. Braun ex Stizenberger 1851 used in this paper is entirely different from the other two superficially similar generic names, *Podocarpium* (Benth.) Yang & Huang 1979 and *Podocarpium* Unger 1864 (for a detailed discussion see Wang 2006). The name *Podocarpium* was once regarded as two infrageneric ranks (i.e. a section or a subgenus) within an extant legume genus *Desmodium* Desv. (Ohashi & Mill 2000), but it was recognized by Yang and Huang (1979) as an independent genus, i.e. *Podocarpium* (Benth.) Yang & Huang. Recently, Ohashi and Mill (2000) have proposed a replacement name *Hylodesmum* Ohashi & Mill for *Podocarpium* (Benth.) Yang & Huang, which is a later homonym of two earlier names, *Podocarpium* A. Braun ex Stizenberger 1851 and *Podocarpium* Unger 1864. *Podocarpium* Unger was used for a gymnospermous wood fossil in the Podocarpaceae (Unger 1864, Herendeen 1992a, b). *Podogonium* Heer 1857 was once suggested to be a conserved name for legume fossils assignable to *Podocarpium* A. Braun ex Stizenberger 1851 (Bůžek 1971, Li et al. 1987). After a thorough re-evaluation of the taxonomy of *Podogonium knorrii*, however, Herendeen (1992b) rejected this conserved name and validated *Podocarpium* A. Braun ex Stizenberger 1851.

MATERIAL AND METHODS

The *Podocarpium* fossils used in this study were collected from diatomaceous shales of the Shanwang Formation, Shandong Province in eastern China (36°54′N. Lat., 118°20′E. Long.). Shanwang is famous for exquisitely preserved fossil insects, ostracodes, spiders, fish, amphibians, reptiles, birds, mammals and plants since the 1930's onwards (Skvortzov 1937, Hu & Chaney 1940, Yang & Yang 1994, Sun 1999). The Shanwang fossil biota is considered to be middle Miocene (Li 1981, Yang & Yang 1994) or late Early to early Middle Miocene (Liu & Leopold 1992). At present, most palaeontologists and geologists have accepted a middle Miocene age for the Shanwang Formation of Shandong Province in eastern China (Sun et al. 2002, Liang et al. 2003, Wang 2006, Wang et al. 2006).

Fossil specimens were preserved as impressions of leaves, leaflets, and fruits. Photographs were taken using a digital camera (Sanyo VPC-J2EX). Figures were drawn using CorelDraw 10.0 software. Terminology used in the specimen description is from Hickey (1973), Dilcher (1974) and the Leaf Architecture Working Group (LAWG 1999).

SYSTEMATICS

In this paper, subfamily and tribe are not given for the genus *Podocarpium* A. Braun ex Stizenberger 1851 due to previous inconsistent viewpoints and lack of new evidence. The following is a systematic scheme for *Podocarpium* from the Miocene Shanwang Formation of Shandong Province in eastern China.

Leguminosae

Podocarpium A. Braun ex Stizenberger 1851

Synonym. *Podogonium* Heer, 1857

Podocarpium podocarpum
(A. Braun) Herendeen 1992

Basionym. *Gleditschia podocarpa* A. Braun 1845

Synonyms

1940 *Podogonium knorrii* (Braun) Heer; Hu & Chaney, p. 76, pl. 50, figs 4, 5, 7, 10, 11.
1978 *Podogonium oehningense* (Koenig) Kirchh.; WGCPC, p. 112, pl. 88, fig. 5, pl. 90, fig. 2, pl. 93, figs 4, 5, 7, *non* pl. 88, fig 7, pl. 89, fig 7.
1999 *Podogonium oehningense* (Koenig) Kirchh.; Sun, p. 42, 71, pl. 28, fig. 5.

Specimens examined. Leaves: 50483a (Pl. 1, fig. 1), 50483b (Pl. 1, fig. 2), 50483c (Pl. 1, fig. 4), 52463 (Pl. 1, fig. 6), 50508a (Pl. 1, fig. 8), 50489a, 50489b, and 52058c. Fruits: 2860 (Pl. 2, fig. 1), 52913 (Pl. 2, fig. 2), 51706 (Pl. 2, fig. 3), 52058a (Pl. 2, fig. 4), 201a (Pl. 2, fig. 5), 51868 (Pl. 2, fig. 6), 51989 (Pl. 2, fig. 7), 1569 (Pl. 2, fig. 8), 51721, and 50373.

Repository. Institute of Botany, the Chinese Academy of Sciences, Beijing, P. R. China.

Locality. Shanwang Basin, ca. 22 km east of Linqu County, Shandong Province, P. R. China (36°54′N. Lat., 118°20′E. Long., Fig. 1A).

Stratigraphic horizon. Diatomaceous shales of the Shanwang Formation (Fig. 1B.).

Geological age. Middle Miocene.

Description. The leaves are paripinnate with at least 5 pairs of opposite leaflets, up to 7.5 cm long. The petiole has a wrinkled pulvinus, and the rachis is 0.6–1.1 mm wide. The leaflets are sessile or short petioluled (ca.

0.5 mm), with a pulvinus, lamina lanceolate, oval to oblong-oval, 2–4.4 cm long and 0.6–1.1 cm wide, apex obtuse, rounded, emarginated to rarely mucronate, base asymmetrical, oblique, acute to obtuse, margin entire. The midvein is stout, straight or slightly curved. The leaflets have 1–2 prominent basal veins, arising from the midvein base at acute angles and extending parallel to the leaflet margin. Secondary veins are numerous, over 12 pairs, at 30–70° angles, pinnately brachidodromous, irregular, forming polygonal network, and course extends to near the leaflet margin, forming angular loops. Intersecondary veins are parallel to the secondary veins, extending to near the leaflet margin. The tertiary veins are fine, dense, irregular, and form a polygonal network. The texture is thin and membranaceous. The cuticle is unavailable. The fruits are dehiscent or indehiscent, single seeded, with a straight or slightly curved stipe, at least 2–4 cm long and about 1 mm wide. The seeds are oblong, 12–15 mm long and 8–10 mm wide. Valve venation is indistinct, the shape is elliptic, 1.8–2.8 cm long by 0.8–1.1 cm wide. Valve apex is acute, base acute or attenuate, slightly oblique, and margins not winged.

DISCUSSION

Comparison. Leaf, leaflet and fruit characters of the fossils presented here provide evidence for a relationship to the family Leguminosae. The leaf bears a prominent wrinkled pulvinus on its petiole base (Pl. 1, figs 1–3) or on its petioluled leaflet base (Pl. 1, figs 4, 5), which is one of the most important characters of the families Leguminosae and Connaraceae. However, the leaflet architecture of these fossils is similar to the Leguminosae but not found in the Connaraceae, and the tertiary venation of the Connaraceae is more prominent. The fruit consists of a single carpel dehiscent along two sutures (Pl. 2, figs 4–8), which is also characteristic of the Leguminosae. Based on leaflet architecture and fruit morphology, these fossils can be attributed to a common species, *Podocarpium podocarpum* (A. Braun) Herendeen (Herendeen 1992b), from the Miocene floras of Europe. Here, a detailed comparison between Chinese and European *Podocarpium* is presented (Tab. 1) showing few morphological differences.

Previously, fossil leaf and fruit assignable to *Podocarpium podocarpum* from Europe (Fig. 2: 1–5) were often described as various species under the generic name *Podogonium* (Heer 1857, Hantke 1954, Kirchheimer 1957, Rüffle 1963, Bůžek 1971, Zastawniak 1980). *Podocarpium* fossils presented here from the Shanwang Formation of Shandong Province in eastern China were formerly described as *Podogonium oehningense* (Koenig) Kirchh. (WGCPC 1978, Sun 1999) or *P. knorrii* (Braun) Heer (Hu & Chaney 1940). In this paper, we adopt Herendeen's (1992b) treatment *Podogonium* as a later synonym of *Podocarpium* (see Nomenclatural Notes in this paper).

The fossils from China did not show a direct association between leaves and fruits, but a similar specimen from the Miocene flora of Switzerland does indicate an organic connection (Fig. 2: 1). Thus, the fossil leaves and fruits presented here are described under a single name, i.e. *Podocarpium podocarpum* (A. Braun) Herendeen, which originated from a population in the Miocene age Shanwang flora of eastern China.

Affinity. The generic affinity of *Podocarpium*, based upon leaves, leaflets, fruits, and flowers, has previously been referred to *Gleditsia*, *Dalbergia*, *Copaifera*, the Detarieae/Amberstieae complex, or an extinct genus in the Leguminosae (Unger 1851, Kováts 1856, Gregor & Hantke 1980, Herendeen 1992a, Liu et al. 2001). We support Herendeen's (1992a,b) viewpoint that *Podocarpium* A. Braun ex Stizenberger 1851 does not conform to any single extant legume genus.

The affinity of the tricolpate pollen species *Fupingopollenites* (syn. *Tricolporopollenites*) *wackersdorfensis* from the Cenozoic of Eurasia was thought to be closely associated with the flowers of *Podocarpium podocarpum*, or to Verbenaceae, or with an unknown affinity (Mohr & Gregor 1984, Song et al. 1999, 2004 Liu et al. 2001, Wang & Harley 2004). Similar tricolpate pollen was also discovered from the Miocene Shanwang Formation, which was once identified as *Convolvulus* sp. (Convolvulaceae; Song et al. 1964, Wang 1991, Sun 1999). Based upon a comparative study of modern and Cenozoic pollen in *Convolvulus* and related

Table 1. A comparison of fruits and leaves of *Podocarpium* from China and Europe (references from Heer 1857, Herendeen 1992a. Direct observation on hand specimens herein, Pl. 1, figs 1–8, Pl. 2, figs 1–8)

Locality	Leaves							Leaflet form						
	Pattern	Form	Length	Pairs	Arrangement	Petiole	Rachis width	Petiolule	Pulvinus	Lamina				
										Size	Shape	Margin	Apex	Base
Europe	alternate	paripinnate	8.0 cm	5–10	opposite to rarely subopposite	wrinkled pulvinus	0.5–1.0 mm	sessile to short (0.5 mm)	present	1.2–4.5 cm long, 0.4–1.2 cm wide	lanceolate, oval, elliptical to oblong	entire	acute, obtuse, rounded, truncate, emarginated, or sometimes mucronate	asymmetrical, acute to obtuse
China	unknown	paripinnate	7.5 cm	>5	opposite	wrinkled pulvinus	0.6–1.1 mm	sessile to short (ca. 0.5 mm)	present	2.0–4.4 cm long, 0.6–1.1 cm wide	lanceolate, oval to oblong-oval	entire	obtuse, rounded, emarginated, rarely mucronate	asymmetrical, oblique, acute to obtuse

Locality	Leaflet venation								Fruits								
	Mid-vein	Special features	Secondary				Intersec-ondary	Tertiary	Dehis-cence	Seed			Stipe	Valves			
			Pairs	Course	Pattern	Looping	Course	Pattern		Num-ber	Shape	Size		Size	Shape	Apex	Base
Europe	straight to slightly curved	2–3 prominent basal veins, near base, acute angle, near & parallel margin	numerous	extend to near margin	irregular, forming polygonal network	angular near margin	extend to near margin	irregular, forming polygonal network	tardily dehis-cent	One	oblong	10–13 mm long, 6–8 mm wide	2.3– at least 4.1 cm long, 1 mm wide	1.5–2.9 cm long, 0.6–1.0 cm wide	elliptic	acute	acute or attenuate, slightly oblique
China	straight to slightly curved	1–2 prominent basal veins, near base, acute angle, near & parallel margin	numerous (>12 pairs)	extend to near margin	irregular, forming polygonal network	angular near margin	extend to near margin	irregular, forming polygonal network	dehiscent or indehis-cent	One	oblong	12–15 mm long, 8–10 mm wide	at least 2–4 cm long, 1 mm wide	1.8–2.8 cm long, 0.8–1.1 cm wide	ellliptic	acute	acute or attenuate, slightly oblique

Fig. 2. Sketch of leaves and fruits of *Podocarpium* A. Braun ex Stizenberger 1851 (formerly *Podogonium* Heer 1857) from the Miocene floras of Europe. Scale bars – 1 cm. **1** – Organic connection between leaves and fruits from the Miocene flora of Switzerland (from Heer 1857, Plate 134, Figure 25), **2** – leafy shoot from the Miocene flora of Switzerland (from Heer 1857, plate 135, figure 1), **3–5** – fruits from the Miocene flora of Switzerland (from Heer 1857, plate 135, figures 14, 20, 21), **6** – partial reconstruction of the parent plant of *Podogonium* (from Heer 1857, Monograph cover of „Die Tertiäre Flora der Schweiz, Flora Tertiaria Helvetiae“), **7** – leaflet architecture of *Podogonium* from the Miocene Öehningen of the Upper Freshwater Molasse sequence near the border of southern Germany and Switzerland (from Herendeen 1992a)

genera, Martin (2001) demonstrated that Convolvulaceae might have evolved in the tropical latitudes of Africa-South America by the early Eocene. Also, pollen of *Convolvulus* are larger than the tricolpate pollen found in the Shanwang flora of eastern China.

PALAEOECOLOGY AND BIOGEOGRAPHY

The climatic and edaphic conditions are the most important ecological factors for land plants. Indications or proxies of these factors can be reflected in the palynoflora and floristic assemblage, and sedimentary facies from a given fossil locality. Based on the floristic assemblage, Tao (1992) suggested a scheme for the Neogene floristic regions of China, and the fruits and/or leaves of *Podocarpium* primarily occurred in those floristic regions of eastern and southern China. Song et al. (1983) proposed three floristic regions for the Miocene floras of China, which are subdivided into five provinces based mainly upon their palynofloras (Fig. 3A). The fruits and/or leaves of *Podocarpium* have been discovered from two of these floristic regions. They occur mainly in the two provinces that have warm temperate-subtropical and tropical conditions (Fig. 3A). Therefore, the range of ecological tolerances of *Podocarpium* is moderate. Judging from their frequent occurrence and abundance in specific local floras, the parent plants of *Podocarpim* lived predominantly under temperate to subtropical climatic conditions. Recently, the palaeoenvironment and palaeoclimate of the Shanwang Formation have been studied in detail (Sun et al. 2002, Liang et al. 2003) and the climate of this flora is hypothesized to be subtropical. The parent plant of *Podocarpium* has been considered to be a thermophilous, moisture-loving plant (Rüffle 1963, Li et al. 1987) and may be one element of gallery forests (Herendeen 1992a, Liu et al. 2001) or semi-arid habitats (Kovar-Eder pers. comm.) The Miocene climatic zone of China (Fig. 3B) further demonstrates that the geographic distribution of *Podocarpium* megafossils in the Miocene of China matches well with the humid and humid / arid transitional zones. Overall, the terrestrial vegetation in the Eurasian Cenozoic underwent the replacement of evergreen subtropical forests by deciduous woodlands and, progressively in the late Miocene, more seasonal warm temperate woodlands with more open habitats or grasslands flourished (Tanai 1967, Wolfe 1975, 1985, Tao 1992, Kovar-Eder 2003). The fruits and/or leaves of *Podocarpium* have been discovered from the early Oligocene to the Pliocene in Eurasia (Fig. 3C) and are especially abundant in numerous late early and middle Miocene floras (Heer 1857, Bůžek 1971, Gregor 1986, Sun 1999, Liu et al. 2001, Kovar-Eder et al. 2004, Wang 2006). Therefore, it is possible that the parent plant of *Podocarpium* enjoyed favorable environmental circumstances in the late early and middle Miocene intervals over much of Eurasia.

Land-sea relations and global climatic circulation patterns underwent significant changes due to the Alpine-Himalayan orogeny in the Cenozoic era. Phased uplift of the Himalayan-Tibetan plateau and changes in land-sea distribution have been regarded as driving forces behind long-term Cenozoic climate deterioration (Ruddiman & Kutzbach 1991, Broccoli & Manabe 1992, Ramstein et al. 1997, An et al. 2001, Molnar 2005). The northern hemisphere Cenozoic climatic evolution included stepped global cooling events (Barron 1985, Miller et al. 1987, Zachos et al. 2001, Tiffney & Manchester 2001) and climate fluctuations (Tanai 1967, Wolfe 1971, 1978). Evolution of the Asian monsoon system (Sun & Wang 2005, Wang et al. 2005) and interior desertification (An et al. 2001) directly affected land vegetation in Eurasia. The onset of the Asian monsoon system might have occurred in the latest Oligocene (Sun & Wang 2005). The initial desertification in the Asian interior was inferred to have taken place by the early Miocene (Guo et al. 2002). Therefore, we can assume that *Podocarpium* might have extended its maximum geographic range under more favorable environmental circumstances during the Miocene, and then became geographically restricted to refugia due to tectonic and regional environmental changes during the Neogene.

The stratigraphic range of *Fupingopollenites* (*Tricolporopollenites*) *wackersdorfensis* is from the early Eocene of eastern China (Zhang & Qian 1992) to the Pleistocene of the eastern Mediterranean region (Liu et al. 2001). If we assume that partial fossil records of pollen species *F. wackersdorfensis*, and possibly related taxa represents the existence of its parent plant *Podocarpium* since the Palaeogene as Liu et al. (2001) suggested, then the first appearance of *Podocarpium* might be during the early Eocene. *Fupingopollenites wackersdorfensis* was inferred to be a mesophyte that lived under warm temperate to subtropical climatic conditions (Liu 1985, Wang & Harley 2004). Based upon leaf physiognomy, fruits, and pollen records, Kovar-Eder (2003) emphasized that the Mediterranean region constituted a warm and humid refuge suitable for subtropical taxa, which are called “Central European relicts”,

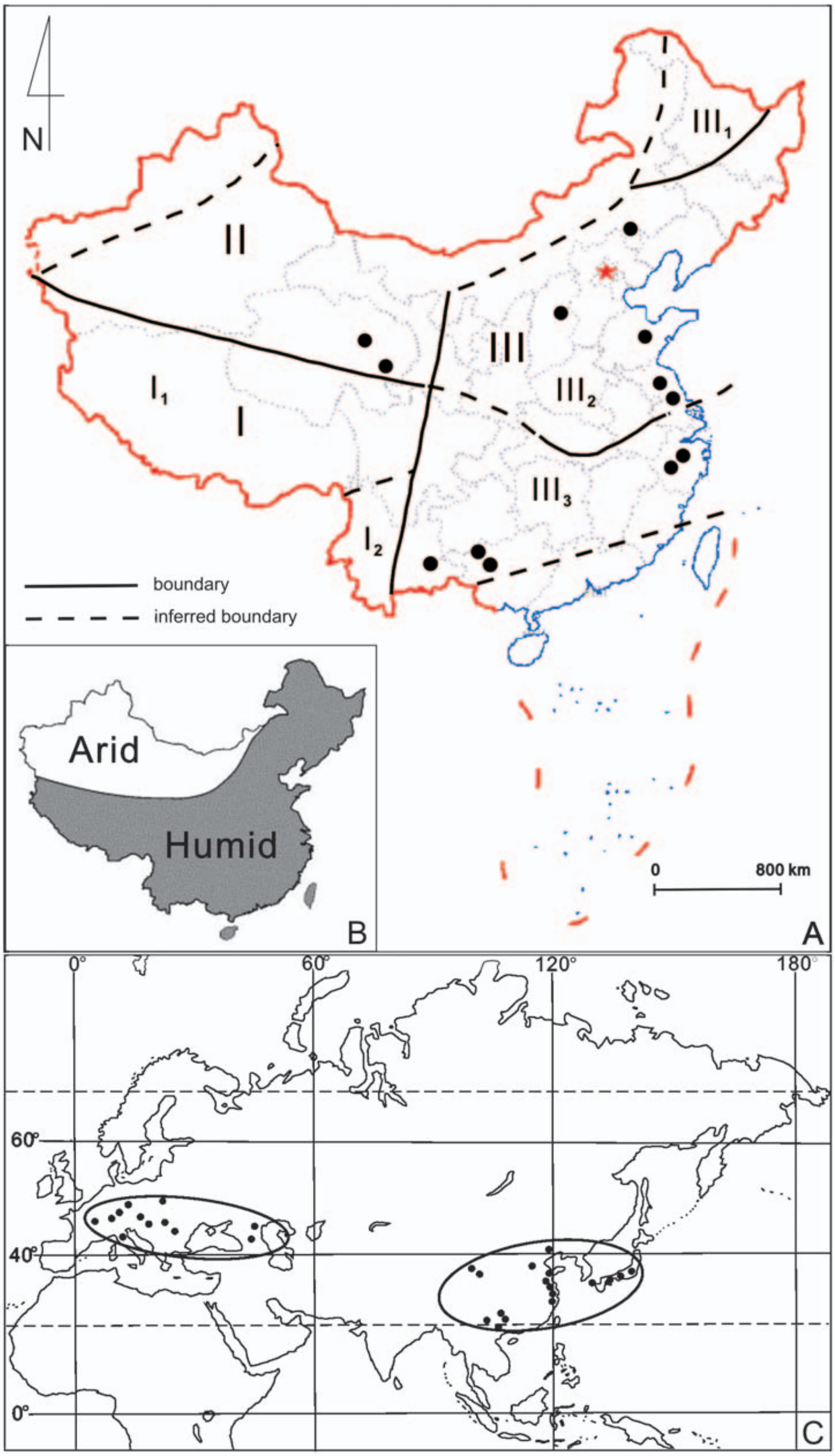

Fig. 3. **A** – the distribution of megafossils of *Podocarpium* A. Braun ex Stizenberger 1851 in the floristic regions and climatic zones in the Miocene of China (after Song et al.1983, modified); **I** – Qihai-Xizang *Quercus-Betula*-thicket floristic region. **I$_1$** – Qihai-Xizang Plateau floristic province; **I$_2$** – Hengduan Mountain floristic province; **II** – inland forest-meadow and steppe floristic region; **III** – eastern monsoon broad-leaved forest floristic region; **III$_1$** – northern temperate floristic province; **III$_2$** – Central warm temperate-subtropical floristic province; **III$_3$** – southern south-subtropical and tropical floristic province. **B** – the Miocene arid and humid zones in China (after from Sun & Wang 2005, modified). **C** – the distribution of *Podocarpium* megafossils and the Neogene of Eurasia (references from Endo & Fujiyama 1966, Ishida 1970, Hayashi 1975, Guo 1980, Zastawniak 1980, Li 1981, Li et al. 1987, Guo & Zhou 1992, Sun 1999, Tao 2000, Liu et al. 2001, Kovar-Eder et al. 2004, Wang 2006)

since the late Miocene-Pliocene onwards. This perspective may explain why *F. wackersdorfensis* persisted in the eastern Mediterranean region until the early-middle Pleistocene, although climatic deterioration had begun during the Oligocene in the northern hemisphere. An ancestral population of *Podocarpium* might have originated in the early Paleogene of eastern Asia and then spread to most of non-arid middle latitude areas in Eurasia during the Miocene, and primarily lived under warm temperate-subtropical, humid and semi-arid conditions. Later, with Asian interior desertification during the Miocene, *Podocarpium* gradually became restricted to the two disjunct regions of "East Asia" and "East, South and Central Europe", finally becoming extinct during the Pleistocene in the eastern Mediterranean.

ACKNOWLEDGEMENTS

The authors thank Dr. Hans-Joachim Gregor, Germany and Prof. Dr. Johanna Kovar-Eder, Staatliches Museum für Naturkunde, Stuttgart, Dr. Barbara Mohr, Humboldt University of Berlin, Dr. Kazuhiko Uemura, National Science Museum (Tokyo), Dr. Liu Yu-Sheng, East Tennessee State University, Dr. Xu Hong-He, Nanjing Institute of Geology and Palaeontology, and Prof. Tao Jun-Rong, Institute of Botany, the Chinese Academy of Sciences (Beijing) for helpful correspondence.

This work was partially supported by the National Natural Science Foundation of China (NSFC), Project for Young Scientists' Fund (# 40402001), the Pilot Project of the Botanical Garden and Taxonomy, the Chinese Academy of Sciences (KSCX2-YW-Z-063) to QW, and the Becker-Dilcher Research Fund and National Science Foundation Funding (INT0074295) and Deep Time grant (DEB0090283) to DLD.

This paper is the University of Florida Contribution to Paleobiology publication no. 588.

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PLATES

Plate 1

Leaves of *Podocarpium* A. Braun ex Stizenberger 1851 from the Miocene Shanwang Formation of Shandong Province in eastern China

1–2. Part and counterpart of a comparative complete leaf. Specimens: 50483a, 50483b

3. Partial enlargement of the leaf petiole in Figure 2, showing some transverse coaly impressions, which imply that there may be a wrinkled pulvinus

4. An incomplete leaflet. Specimen: 50483c

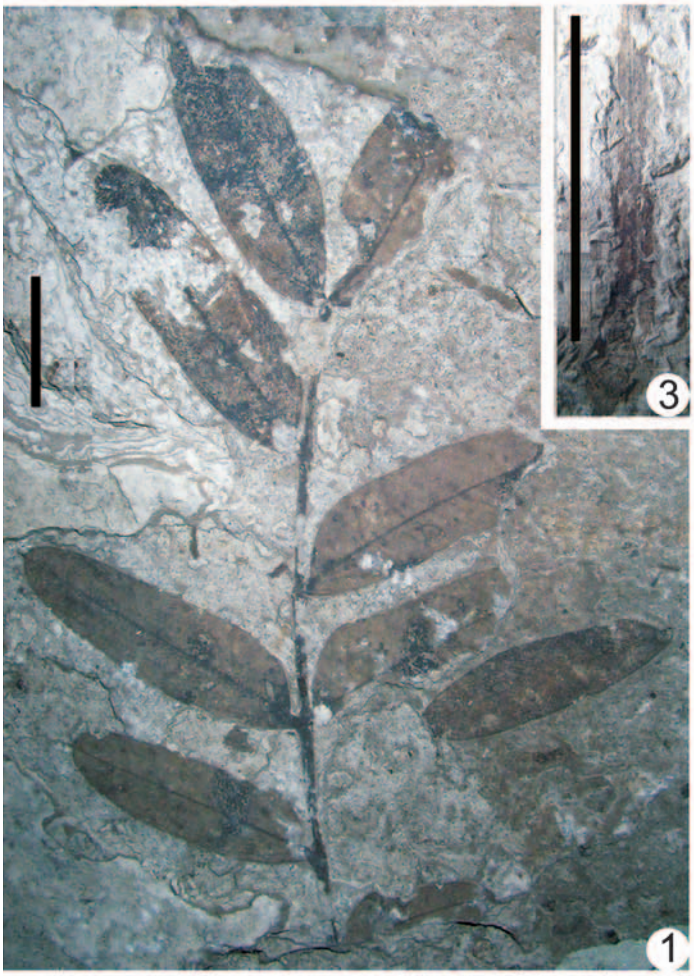
5. Partial enlargement of the leaflet basal part in Figure 4, showing a pulvinate petiolule

6. A complete leaflet with a straight midvein and a basal vein. Specimen: 52463

7. Partial enlargement of the leaflet apical part in Figure 6, showing an slightly emarginated apex

8. A complete leaflet with a curved midvein and an oblique base. Specimen: 50508a

Scale bar – 1 cm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6


8

Plate 2

Fruits of *Podocarpium* A. Braun ex Stizenberger 1851 from the Miocene Shanwang Formation of Shandong Province in eastern China

1–3. Indehiscent fruits with a straight or slightly curved stipe (incomplete). Specimens: 2860, 52913, 51706
4–7. Dehiscent fruits with an incomplete stipe. Specimens: 52058a, 201a, 51868, 51989
8. A fruit and an associated seed. Specimen: 1569

Scale bar – 1 cm


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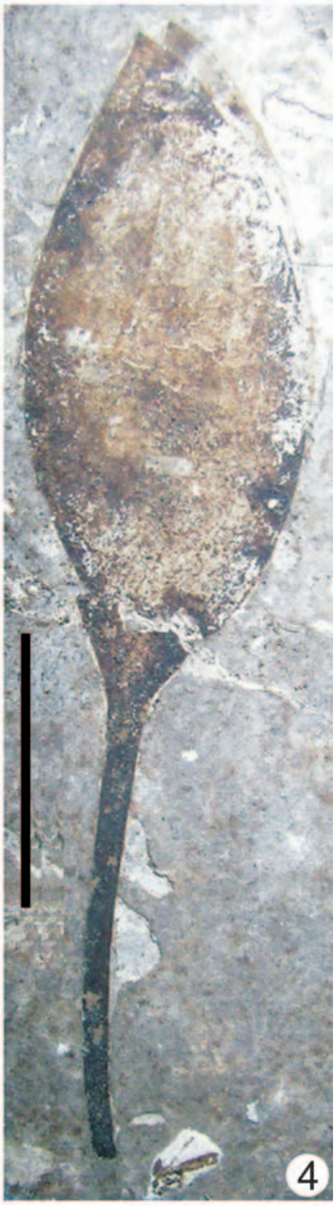
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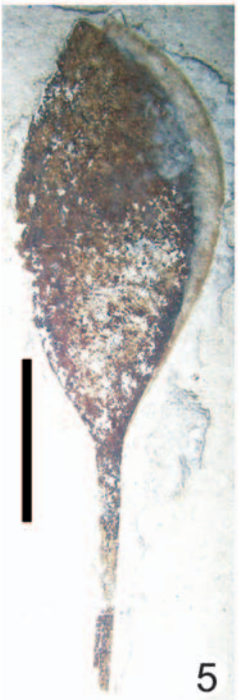
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