

**FRUITS OF *KOELREUTERIA* (SAPINDACEAE) FROM THE CENOZOIC  
THROUGHOUT THE NORTHERN HEMISPHERE: THEIR ECOLOGICAL,  
EVOLUTIONARY, AND BIOGEOGRAPHIC IMPLICATIONS<sup>1</sup>**

QI WANG<sup>2,5</sup>, STEVEN R. MANCHESTER<sup>3</sup>, HANS-JOACHIM GREGOR<sup>4</sup>, SI SHEN<sup>2</sup>, AND ZHEN-YU LI<sup>2,5</sup>

<sup>2</sup>State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, P.R. China; <sup>3</sup>Florida Museum of Natural History, the University of Florida, Gainesville, Florida 32611-7800 USA; and <sup>4</sup>Palaeo-Bavarian Geological Survey, Daxerstrasse 21, Olching, Germany 82140

- *Premise of the study:* *Koelreuteria* (Sapindaceae) has four extant deciduous tree species, disjunctly distributed in eastern Asia and the Fiji Islands. While *K. paniculata* is widely cultivated, the biogeographic origin and evolutionary history of *Koelreuteria* remain unclear.
- *Methods:* Fruits, pollen, wood, and leaves of closely related extant taxa were examined in comparison with fossil remains to evaluate the fossil record and biogeographic history of *Koelreuteria*.
- *Key results:* Overall, characters of capsular fruits are more diagnostic than other organs for this genus. We describe two new species of fruit remains from the Eocene, *K. taoana* sp. nov. (northeastern China and far eastern Russia) and *K. dilcheri* sp. nov. (western United States), and give emended descriptions of three species: *K. allenii* (Lesq.) W. N. Edwards (early–late Eocene of the United States), *K. macroptera* (Kováts) W. N. Edwards (late Oligocene–early Pliocene of Europe), and *K. miointegrifoliola* Hu et R. W. Chaney (Miocene of eastern Asia).
- *Conclusions:* Reliable fossil records of capsules and ring-porous wood indicate that *Koelreuteria* may have originated in North Pacific-Rim area of the northern hemisphere by the early Eocene, representing an early temperate lineage in Sapindaceae adapted for wind dispersal. The fossils herein place a minimum age (ca. 52 Ma) for the divergence of *Koelreuteria* from tropical genera that appear more basal in the molecular phylogeny of Sapindaceae. Regional extinctions after the Eocene in North America and the Pliocene in Europe, reduced the range of *Koelreuteria* to eastern Asia, where three species occur today. The present distribution of another species in the Southern Pacific may be explained by long-distance dispersal.

**Key words:** biogeography; Cenozoic; ecology; Eocene; evolution; fruits; *Koelreuteria*; Miocene; paleobotany; Sapindaceae.

<sup>1</sup>Manuscript received 8 August 2012; revision accepted 27 November 2012.

The authors thank the associate editor and two anonymous reviewers for their invaluable suggestions; A. Roth-Nebelsick (Staatliche Museum für Naturkunde, Stuttgart), B. Erdei (Hungarian Natural History Museum, Budapest), H. S. Wang (Florida Museum of Natural History, Gainesville), M. Pika-Biolzi (Geological Institute, ETH, Zürich); D. J. Yuan, S. X. Guo, G. L. Shi, L. M. Mao, and F. M. B. Jacques (Nanjing Institute of Geology and Palaeontology, CAS, Nanjing); and X. J. Yang (Institute of Botany, CAS, Beijing) for access to specimen collections; Y. B. Sun, Institute of Botany, CAS for line drawings; and A. Pavlova (National Institute of Carpology, Moscow) and S. Snigirevsky (St. Petersburg State University) for linguistic assistance in Russian. The authors also thank D. L. Dilcher (Indiana University, Bloomington), S. A. Rood (editor of *Journal of the Washington Academy of Sciences*), E. B. Leopold (University of Washington), A. Yabe (National Museum of Nature and Science, Tsukuba), B. I. Pavlyutkin (Far Eastern Geological Institute, Vladivostok), T. Denk (Swedish Museum of Natural History, Stockholm), Z. Kvaček and J. Sakala (Charles University, Prague), J. Klein (Natural History Museum, Rotterdam), J. H. Jin (Sun Yat-sen University, Guangzhou), S. S. Ying (National Taiwan University, Taipei), J. Y. Guo (Claremont Colleges), C. H. Xiong (Peking University, Beijing), Y. W. Xing (Xishuangbanna Tropical Botanical Garden, CAS, Menglun), and H. Jiang (Yunnan Academy of Forestry, Kunming) for important help. The study was supported by the National Natural Science Foundation of China (no. 40830209, 40972015) and the State Key Laboratory of Systematic and Evolutionary Botany (no. 56176G1044) to Q.W. and Z.Y.L.

<sup>5</sup>Authors for correspondence (e-mail: happyking@ibcas.ac.cn; lizy@ibcas.ac.cn)

doi:10.3732/ajb.1200415

*Koelreuteria* Laxm. of the soapberry family (Sapindaceae Juss.) comprises four extant deciduous tree species, disjunctly distributed in eastern Asia (China, Korea, and Japan) and on the Fiji Islands in the South Pacific (Smith, 1985; Wu et al., 2007; Acevedo-Rodríguez et al., 2011; Ying and Chen, 2011) (Table 1). In eastern Asia, distributions of *K. paniculata* Laxm. to the north and *K. bipinnata* Franch. to the south converge at approximately 32° north latitude (Xia and Luo, 1995). In the Pacific, two species *K. elegans* A. C. Sm. (Smith, 1951, 1952, 1955, 1985) and *K. henryi* Dümmer (= *K. formosana* Hayata) (Dümmer, 1912; Hayata, 1913; Kanehira, 1936; Li, 1963, 1977; Chen, 1993; Ying and Chen, 2011) are distributed in Taiwan (China) and Fiji, respectively, with a discontinuity of ca. 7000 km. Alternatively, they are treated as two subspecies, *K. elegans* subsp. *formosana* (Hayata) F. G. Mey. and *K. elegans* subsp. *elegans* A. C. Sm. (Meyer, 1976; Luo and Chen, 1985; Xia and Luo, 1995; Xia and Gadek, 2007). Considering their morphological variation (e.g., pollen and petiolules, see Table 1) and long-distance disjunct distributions, we here did not adopt such sub-specific ranks of *K. elegans*.

*Koelreuteria* has been used as an official memorial tree cultivated on the tombs of scholars since the Chou Dynasty (1122–240 BC) and was introduced into Europe in 1763 (Li, 1996; Dosmann et al., 2006). Based upon the cultivated tree at St. Petersburg, Finnish naturalist Erik Laxmann (1772) named *Koelreuteria* after a German botanist Joseph Gottlieb Kölreuter (1733–1806) at Karlsruhe, with the type species *K. paniculata*

TABLE 1. Pollen, capsules, leaves, distribution and ecology of four living species in *Koelreuteria*.

Taxa	Pollen				Capsule				Leaf			Distribution and ecology	
	Form	Size	Exine	Ektexine	Form	Valve form	Valve size	Valve Septum	Form	Leaflet margin	Leaflet apex		Petiolule
<i>K. paniculata</i> Laxm. <sup>1, 8-9, 15-16</sup>	Subprolate to spheroidal	24–28.2 × 21–33.8 μm	1.5–2 μm thick	More or less longitudinally striate	Trigonous-ovoidal	Ovate, tapering to apex, acute	2.2–7.2 × 2–4 cm	1/3 of valve length	Pinnate, rarely bipinnate	Coarsely crenate-serrate to pinnatisect and lobulate	Abruptly to narrowly acuminate, often apiculate	1–2 mm long	North, Northeast, East, and Southwest China <sup>8, 11, 15</sup> ; Korea and Japan <sup>12, 14</sup> ; (0)–300–3,800 m. elevations in river courses, open forest areas, rocky mountain slopes, and valleys
<i>K. bipinnata</i> Franch. (= <i>K. integrifolia</i> Merr.) <sup>4, 8-9, 15-16</sup>	Oblate-spheroidal	22–28.2 × 23–31 μm	2–2.4 μm	Finely striate	Ellipsoidal, ovoidal-globose	Elliptic to round, apex short acuminate, mucronate	3.7–6.6 × 3–5 cm	Over 1/3 to 1/2 of valve length, or occasionally complete when suture being straight	Bipinnate	Entire or uniformly serrate, lower leaflets never pinnatisect	Acute to short acuminate	Sessile to 3 mm long	South and Southwest China <sup>8, 11, 15</sup> ; (100)–250–(1,500)–2,600 m. elevations in open fields, hillside forests, light woods, thickets, and roadsides
<i>K. henryi</i> Dümmer [= <i>K. formosana</i> Hayata; <i>K. elegans</i> subsp. <i>formosana</i> (Hayata) F. G. Mey.] <sup>2, 3, 5, 7, 8, 10, 13, 15-16</sup>	Mostly spheroidal	20–23 × 21–23 μm	1.5 μm	Striate	Subglobose	Suborbicular, apex short acuminate, mucronate	4–5 × 3–4.5 cm	1/2 of valve length	Bipinnate	Entire or irregularly crenate-serrate, lower leaflets sometimes pinnatisect	Long acuminate, sometimes caudate	1–3 mm long	Taiwan of China; at low elevations (less than 1,000 m.) in broad-leaved forests and light woods
<i>K. elegans</i> (Seem.) A. C. Sm.[= <i>K. elegans</i> subsp. <i>elegans</i> A. C. Sm.] <sup>6, 8, 15-16</sup>	Mostly spheroidal	24–26 × 24–26 μm	1.5 μm	Irregularly striate-reticulate	Subglobose	Suborbicular, apex short acuminate, mucronate	3.4–5 × 3.1–4.6 cm	1/2 of valve length	Bipinnate	Entire or irregularly crenate-serrate, sparsely, lower leaflets sometimes pinnatisect	Long acuminate, sometimes caudate	4–5 mm long	Vanua Levu and Viti Levu of Fiji; 50–(350)–825–(900) m. elevations in dense or open forest or on its edges

References: <sup>1</sup> Laxmann, 1772; <sup>2</sup> Dümmer, 1912; <sup>3</sup> Hayata, 1913; <sup>4</sup> Merrill, 1922; <sup>5</sup> Kanehira, 1936; <sup>6</sup> Smith, 1952, 1985; <sup>7</sup> Li, 1963, 1977; <sup>8</sup> Meyer, 1976; <sup>9</sup> Wang and Chien, 1956; <sup>10</sup> Chen, 1993; <sup>11</sup> Xia and Luo, 1995; <sup>12</sup> Dosmann et al., 2006; <sup>13</sup> Luo and Chen, 1985; <sup>14</sup> Sasaki and Ohashi, 2007; <sup>15</sup> Xia and Gadek, 2007; <sup>16</sup> Direct observations on the cultivated plants and the herbaria kept at the Chinese National Herbarium (PE), the Missouri Botanical Garden Herbarium (MO), and Arnold Arboretum Herbarium, Harvard University (A).

being better known as the golden-rain tree. *Koelreuteria henryi*, native in Taiwan, was introduced to the United States in 1915 and Australia around 2000, and subsequently became naturalized in southern Florida and Hawaii in the United States (Meyer, 1976; Frohlich and Lau, 2010) and in New South Wales (Hosking et al., 2003). The wood of *Koelreuteria* can be used for making furniture. *Koelreuteria* is popularly cultivated as an ornamental around the world because of the aesthetic appeal of its spreading canopy, imparipinnate and bipinnate leaves, large yellow thyrses, and colorful, membranous, inflated capsules. However, the early evolution and biogeographic spread of *Koelreuteria* through the geological ages remain unclear.

*Koelreuteria*, along with *Stocksia* Benth. in Afghanistan, Iran, and Pakistan (Abdulia, 1973) and *Erythrophysa* E. Mey. ex Arn. from Ethiopia, South Africa, and Madagascar (Verdcourt, 1962; Capuron, 1969; Palmer and Pitman, 1972), were traditionally classified into the tribe Koelreuterieae of the subfamily Dodonoideae in Sapindaceae on the basis of their imparipinnate leaves, convolute cotyledons, zygomorphic flowers and inflated capsules (Radlkofer, 1931) (Figs. 1–7, 9–12), and simply structured tricolporate pollen (i.e., type-A pollen, sensu Muller and Leenhouts, 1976) (Fig. 8). Koelreuterieae was thought to be derived from the most basal sapindaceous tribe Dodonoideae, represented by *Dodonaea* L. mainly from Australia and New Caledonia (Xia and Gadek, 2007; Harrington, 2008; Acevedo-Rodríguez et al., 2011). Recent molecular phylogenetic studies have suggested that *Koelreuteria* is closely related to some subtropical and tropical genera from Asia, Australasia, and Africa, e.g., *Stadmania* Lam. (fruits not membranous), *Allophylus* L. (fruits not capsular), *Smelophyllum* Radlk. (fruits chartaceous or fleshy), *Cupaniopsis* Radlk. (fruits fleshy), and *Harpullia* Roxb. (fruits chartaceous to woody) (Harrington et al., 2005; Muellner et al., 2007; Buerki et al., 2009, 2010). Hence, the evolutionary origin and phylogenetic relationships of *Koelreuteria* are likely to be rooted in subtropical and tropical lineages. The fossil record of *Koelreuteria* may provide temporal and paleogeographic data relevant to the evolutionary and biogeographic history of these genera.

The main objectives of this paper are to (1) review the morphology and taxonomy of living *Koelreuteria* with particular reference to fruit morphology and some subsidiary references to pollen, leaf, and wood anatomical characters, all of which can be used to identify the fossil remains of the genus; (2) reinvestigate the previously reported fossil species in *Koelreuteria* and provide a reliable fruit fossil record of the genus; and (3) consider their ecological, evolutionary, and biogeographic implications.

## MATERIALS AND METHODS

**Nomenclature**—Fossils of *Koelreuteria* are preserved as isolated parts (e.g., dispersed leafy shoots, leaves, leaflets, wood, capsules, capsular valves, seeds, and pollen). Some of the previously reported fossil species were established on the basis of the hypothesized combination of both leaves and capsular valves occurring together at the same localities, but there was no direct proof in the form of organic connections (e.g., Massalongo, 1852; Hu and Chaney, 1938; Brown, 1946; Becker, 1961). Such taxonomic practice may be problematic because two or more unrelated elements were prone to be involved in the original description. On the basis of reliable fruit remains, we here reconsider the nomenclature and taxonomy of fossil *Koelreuteria*.

**Macrofossils**—The macrofossils used in this study (see Appendix 1) were collected from the following localities in approximate order according to geological age. (1) Green River Formation, USA. Capsules from the Green River Formation of Colorado, Utah, and Wyoming are deposited at USNM (National Museum

of Natural History, Smithsonian Institution, Washington, D.C., USA), UCM (University of Colorado Museum of Natural History, Boulder, CO, USA), UCMP (University of California Museum of Paleontology, Berkeley, CA, USA), FMNH (Field Museum, Chicago, IL, USA), and YPM (Peabody Museum of Natural History, Yale University, New Haven, CT, USA). The geological age of these Green River Formation localities is early Eocene (ca. 52 Ma) to middle Eocene on the basis of radiometric dating as well as mammalian biostratigraphy (Smith et al., 2008). (2) Republic, Washington, USA. A few capsular valves were collected from Republic, Washington, northwestern USA. The specimens (prefixed “UWBM”) are deposited at the Burke Museum of Natural History, the University of Washington, Seattle. The age of the Republic flora is early–middle Eocene (Wolfe et al., 1998; Greenwood et al., 2005; DeVore and Pigg, 2010). (3) Independence Hill, California, USA. One capsular valve was collected from Independence Hill near Colfax, California and deposited at USNM. The geological age of the Chalk Bluffs flora of Independence Hill is early–middle Eocene (Brown, 1946; Edwards, 2004). (4) Huadian, Jilin Province, China. One capsular valve (part and counterpart) was collected from siltstone beds of the Huadian Formation at the Gonglangtuo Mine No. 3, Huadian County, Jilin Province in northeastern China (42°59′54″N, 126°51′58″E). The specimens (prefixed “PE”) are deposited at the Chinese National Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing. The geological age of the Huadian flora has been accepted as middle Eocene on the basis of co-occurring vertebrate fossils (Smith et al., 2011). (5) Teater Road, Oregon, USA. Capsular valves were collected from the John Day Formation of Teater Road, Oregon and deposited at UF (Florida Museum of Natural History, Gainesville). The geological age of this John Day Formation locality is late Eocene (Manchester and McIntosh, 2007). (6) Florissant, Colorado, USA. Numerous capsular valves were collected from the Florissant lake beds of Florissant, Colorado. The specimens are deposited at YPM and USNM. The geological age of the Florissant flora is latest Eocene on the basis of radiometric dating and mammal correlations (Meyer and Smith, 2008). (7) Randecker Maar, Germany. Ten capsular valves were observed from Randecker Maar in collections at the Staatliche Museum für Naturkunde (Stuttgart) (specimens prefixed “SMNS”) and the Nature Museum Augsburg (prefixed NMA). The age of the Randecker Maar flora is early Miocene (Gregor, 1982; Krautter and Schweigert, 1991). (8) Shanwang, Shandong Province, China. Twelve capsular ovules were collected from Shanwang (36°54′N, 118°20′E) at Linqu County, Shandong Province, eastern China. The specimens are deposited at UF, PE, and Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing (prefixed “PB”). The geological age for plant-bearing diatomaceous shales of the Shanwang Formation is Middle Miocene (Li, 1981; Tao et al., 1999; Wang et al., 2010) or late Early Miocene to early Middle Miocene (Liu and Leopold, 1992; Deng, 2006; Wang, 2012). (9) Tállya, Hungary. One capsular valve was examined from Gomboska of Tállya, Hungary. The specimen (prefixed “BP”) is deposited at the Hungarian Natural History Museum, Budapest. The age of the Tállya flora is Middle Miocene (Hably, 2006). (10) Abaujzántó, Hungary. One capsular valve was collected from Abaujzántó, Hungary, which is deposited at BP. The age of the Abaujzántó flora is Middle Miocene (Hably, 2006). (11) Bavaria, Germany. Capsular valves were collected from Derching, Burtenbach, Derndorf, and Geisenhausen, sediments of the Upper Freshwater Molasse of Bavaria, southern Germany. The specimens are deposited at NMA. The ages of these Bavarian floras are from the Lower Middle Miocene of Burtenbach to the middle part of the Middle Miocene of Derching as well as to the Middle–Upper Miocene of Geisenhausen and Derndorf (Gregor, 1982; Gregor et al., 1992; Seehuber, 2009).

**Herbaria**—The extant voucher specimens examined for this study (see Appendix 1) are housed at the following herbaria: Chinese National Herbarium (PE), Missouri Botanical Garden Herbarium (MO), and Arnold Arboretum Herbarium, Harvard University (A). Capsules and leaves of *K. paniculata*, *K. bipinnata* and *K. henryi* cultivated at the Institute of Botany, Chinese Academy of Sciences (Beijing), Yunnan Academy of Forestry (Kunming), and the University of Florida (Gainesville) were collected to compare with the fossils presented here.

Cleared leaflets and capsular valves of *Koelreuteria* were made by soaking fresh samples in 40% sodium hydroxide (NaOH) solution for about 3 d, then neutralizing in running water, and mounting with Canada balsam in glass slides. Data regarding fossil and extant capsules, pollen, leaflets, and wood of *Koelreuteria* were tabulated (Tables 1, 2), and comparisons of *Koelreuteria* with other taxa bearing similar fruits were made (Table 3). Terminology used in the specimen descriptions for seeds, pollen, fruits, and leaves follows Corner (1976), Müller and Leenhouts (1976), and Ellis et al. (2009). The author citation of plant names is applied by Brummitt and Powell (1992).

Online databases were consulted including those of (1) National Museum of Natural History, Smithsonian Institution, Washington, D.C. (<http://collections.nmnh.si.edu/search/paleo/>), (2) University of California Museum of Paleontology,

Berkeley (<http://bscit.berkeley.edu/cgi/ucmp/>), (3) Peabody Museum of Natural History, Yale University, New Haven (<http://peabody.yale.edu/collections/paleobotany/>), (4) Museum of Natural History, the University of Colorado, Boulder (<http://cumuseum.colorado.edu/Exhibits/StoneLace/specimens2.html>), (5) Burke Museum of Natural History and Culture, the University of Washington (<http://www.burkemuseum.org/paleontology/collections/>), (6) The Staatliche Museum für Naturkunde (Stuttgart) (<http://www.dbsmns.naturkundemuseum-bw.de/>), (7) The Inside Wood (<http://insidewood.lib.ncsu.edu/search/>), and (8) eFloras (<http://www.efloras.org>).

**Figures**—Photographs of hand specimens were taken with digital cameras (Panasonic DMC-FZ30, Nikon D90, CoolPix S230, and Canon PowerShot A630). Images of capsular valve and leaflet clearings were made on a flatbed scanner (Epson Perfection 2580 Photo). Micrographs of pollen grains were taken with a Scanning Electron Microscope (SEM) (Hitachi S-4800). Line drawings of previously published figures of fossil *Koelreuteria* were drawn when the original specimens were not available for photography. The International Stratigraphic Chart (Gradstein et al., 2004) was used for time calibration. Figures were prepared with Adobe Photoshop 6.0 (San Jose, California, USA) and CorelDRAW 10.0 (Corel, Ottawa, Ontario, Canada) programs.

## RESULTS

The taxonomy of living *Koelreuteria* is primarily based upon growth habit, vegetative shoot, leaf, inflorescence, flower, fruit, seed and seedling, pollen, and chromosome characters (Meyer, 1976; Xia and Gadek, 2007) (Table 1), but paleobotanists usually have to identify *Koelreuteria* fossils in the light of dispersed leaves, leaflets, wood, capsules, capsular valves, seeds, and pollen (Table 2).

**Fruits of extant *Koelreuteria***—Fruits of *Koelreuteria* are three-valved, loculicidal capsules, which open completely along the three dorsal sutures; each valve consists of two halves of adjoining carpels (Figs. 1–7). Overall, the capsules of *Koelreuteria* are trigonous-conoidal, ellipsoidal, ovoidal-globose or subglobose and measure 2.2–7.2 cm long by 2–5 cm wide (Table 1); the carpels are membranous and bladder-like, and each valve bears two seeds oppositely or suboppositely along the two sides of the lower or middle part of the placental suture (Fig. 2); the seed is globose, about 5–9 mm in diameter, with sclerenchymatous testa, and contains a large embryo, with two coiled or convoluted cotyledons and a radicle that protrudes into a pocket of the seed coat (Corner, 1976); the placentation (or axile partition) above the suture where seeds are attached is usually incomplete, or occasionally complete when the placental suture is straight, forming a septum accounting for 1/3 to all of the valve length from the base (Figs. 5, 6). The distally incomplete septum is developed from the septal slits occurring within the style (Ronse Decraene et al., 2000). Although *K. bipinnata* occasionally has a nearly complete septum in capsules, the distal, slim septal slits above the seed-bearing placental suture are still visible.

The capsules of *Koelreuteria* can be easily subdivided into two types: *K. paniculata*-type (Fig. 1) and *K. bipinnata*-type (Figs. 3, 4). *Koelreuteria paniculata*-type represented only by the type-species *K. paniculata* bears ovate capsular valves with an acute apex and a basal septum approximately 1/3 of the valve length (Figs. 2, 5). In contrast, *K. bipinnata*-type, including the other three species *K. bipinnata*, *K. henryi*, and *K. elegans*, typically possesses elliptical, ovate-elliptical or suborbicular capsular valves with an obtuse apex and a longer septum accounting for more than 1/3 to all of the valve length. Overall, the capsular valves of *K. bipinnata* are the most variable, ranging from elliptical, ovate-elliptical to suborbicular.

Comparisons have been made between *Koelreuteria* and other genera of the Sapindaceae including *Arfeuillea* Pierre ex Radlk., *Boniodendron* Gagnep. (= *Sinoradlkofera* F. G. Mey.), *Stocksia* Benth., *Erythrophysa* E. Mey. ex Arn. (Meyer, 1977; Bůžek et al., 1989; Manchester, 1999; Buijsen et al., 2003; Manchester and O’Leary, 2010). *Koelreuteria* fruits also superficially resemble genera with membranous or papery fruits in several other families, including tilioid Malvaceae Juss. [*Craigia* A. C. Sm. et W. E. Evans (= *Pteleaearpum* Weyland)], Rutaceae Juss. (*Ptelea* L.), and the Nyctaginaceae Juss. (*Abronia* Juss.) (Kvaček et al., 1991, 2005; Manchester and O’Leary, 2010) (Table 3). However, *Koelreuteria* is distinguished from these other genera by several characters: incomplete septum with two seeds at a single level within each ovate, elliptical to suborbicular, polygonally elongated reticulate, membranous valve that is greater than 2 cm long (ca. 4 cm long on average). Occasionally, a nearly complete septum occurs in *K. bipinnata* when the placental suture appears straight, in which case the distinction of *Koelreuteria* from other genera may be less secure.

The morphology of capsular valves is helpful in distinguishing taxa. Some small-sized (around 2 cm long) valve fossils with a “central body” (i.e., locular area) formerly attributed to *Koelreuteria* belong to either a living tilioid malvaceous genus *Craigia* or probably another extant sapindaceous genus *Boniodendron* (Kvaček et al., 1991, 2005; Manchester et al., 2009) (Table 2). These misidentified species should be excluded from the fossil record of *Koelreuteria*, including *K. eointegrifolia* S. Endō, *K. eocenica* S. Endō, *K. oregonensis* C. A. Arnold, and *K. microcarpa* H. M. Li (Endō, 1942, 1968; Arnold, 1952; WGCP, 1978; Zhang, 1980). Fossils belonging to *Craigia* usually have serial seed attachments and/or complete septa within the valves, forming a fusiform or elliptical central body. The small capsular valves called *Koelreuteria arnoldii* H. F. Becker from the early middle Eocene to Oligocene of the United States and Canada (Becker, 1961, 1969; Wolfe and Wehr, 1987; Dillhoff et al., 2005) may represent *Boniodendron*, whose capsules are about half the size of those in living *Koelreuteria* (Manchester et al., 2009) (Table 3). Furthermore, pedicels of *Boniodendron*, when preserved at the base of such smaller valves, have no persistent sepals (Table 3); *K. annosa* Brown was described for the capsular valve and leaflet from the Paleocene of the United States (Brown, 1956, 1962), but its valve appears to bear an elongated, central locular area and a long pedicel. Numerous specimens of this species in the UF collections all lack seeds, so the placentation remains unclear. Hence, this species is also rejected from *Koelreuteria*.

Although the trilobular capsules with incomplete septa are also produced sporadically in two other living sapindaceous species *Euphorianthus euneurus* (Miq.) Leenh. (velvety and fleshy capsules), possibly *Erythrophysa paniculata* Capuron (pilose and membranous-papery capsules) and the fossil species *Sapindaceacarpum koelreuterioides* Vaudois-Miéja et Lejal-Nicol (glabrous and membranous capsules), their capsular valves are not reticulate (Capuron, 1969; Vaudois-Miéja and Lejal-Nicol, 1988; Acevedo-Rodríguez et al., 2011) (Table 3). Hence, well-preserved capsular valves are easily recognizable in the fossil record and can provide a reliable proxy for deciphering the biogeographic history of *Koelreuteria*.

**Pollen, leaves, and woods of *Koelreuteria***—Pollen grains of extant *Koelreuteria* are primarily spheroidal, oblate-spheroidal or rarely prolate-spheroidal, 20–28.2 × 21–33.8 μm in size (Table 1). The polar axis is triangular and the grains are tricolporate.

TABLE 2. Previously described fossils assignable or similar to *Koelreuteria* in approximately stratigraphic order.

Published name	Locality	Organ	Cited figure	Geological age	Age reference	Identification
<i>Talispites megorites</i> Z. C. Song et M. Y. Li	Gongju County of Changdou, Qiabulin and Cuojiangding of Zhongba County, Xizang (Tibet), China	Pollen (simply structured tricolporate pollen, i.e., type-A pollen)	Song and Li, 1982, p. 20, pl. 4, figs. 8, 9; Song et al., 1999, p. 591, pl. 149, figs. 22, 23, 27; Li et al., 2008, p. 297, fig. 3, G, fig. 4, H	Santonian–Maastrichtian, Late Cretaceous to the Eocene	Song et al., 1999, 2004; Li et al., 2008	Similar to living <i>K. bipinnata</i> Franch.
<i>Senipites striatus</i> Z. C. Song	Subei Basin, Taizhou Formation, Jiangsu Province, China	Pollen (type-A)	Song et al., 1999, p. 590, pl. 152, figs. 9–12, 19	Senonian (Coniacian–Maastrichtian), Late Cretaceous	Song et al., 1999, 2004	Similar to living <i>K. paniculata</i> Laxm. and <i>K. bipinnata</i> Doubtful
<i>K. prenitigricans</i> W. A. Bell	Vancouver Island, British Columbia, Canada	Leaves and leaflets	Bell, 1957, p. 61, pl. 51, fig. 1, pl. 14, fig. 2, pl. 15, figs. 1, 4, 7	Paleocene	Bell, 1957	Capsules bear a complete septum, so it was rejected from <i>Koelreuteria</i> herein
<i>K. annosa</i> R. W. Br.	Little Powder River, near Biddle, Montana and Point of Rocks, Wyoming, USA	Capsular valve (2.7 × 1.8 cm, elliptic) and leaflets	Brown, 1956, p. 107, p. 76, pl. 59, figs. 8, 9	Paleocene	Brown, 1962	Doubtful
<i>K. eakini</i> Hollick	Yukon River, Alaska, USA	Leaf	Hollick, 1936, p. 137, pl. 81, fig. 1	Paleocene	Wolfe, 1972	Showing the pattern of convoluted cotyledons, tongue-like radicle, and thin seed coat
<i>Palaeoallophylus rotundatus</i> E. Reid et M. Chandler	Sheppey, southern London, UK	Seeds (11–13 mm in diameter, embryo with large coiled cotyledons; globose)	Reid and Chandler, 1933, p. 362, pl. 17, fig. 8–12, text fig. 9d	Early Eocene	Collinson and Cleal, 2001	Characteristic of seeds of living <i>Koelreuteria</i> and <i>Allophylus</i> L.
<i>K. viridifluminis</i> (Hollick) R. W. Br.	Green River, Colorado, Wyoming and Utah, USA	Capsular valve (4.2 × 2.1 cm, obovoid-elliptic) and leaflets	Lesquereux, 1878b, p. 132, pl. 17, figs. 9–12; Brown, 1934, p. 62, pl. 10, fig. 10; Brown, 1943, p. 863, fig. 1N; MacGinitie, 1969, p. 120, pl. 21, fig. 3	Early to middle Eocene	Smith et al., 2008	Reliable for the capsular valves, which were reclassified as <i>K. allenii</i> herein; some of the leaflets doubtful
<i>K. mixta</i> (Lesq.) R. W. Br.	You Bet and Independence Hill, California; Republic, Washington, USA	Capsular valve (3.5–5.8 × 2.8–3.6 cm, elliptic, oblong or oblong-elliptic) and leaflet	Lesquereux, 1878a, p. 30, pl. 9, fig. 13; Brown, 1946, p. 351, figs. 1, 2, this paper, Figs. 17–21	Early to middle Eocene	Brown, 1946; Wolfe et al., 1998; Edwards, 2004; Greenwood et al., 2005; DeVore and Pigg, 2010	Reliable for the capsular valve, which was reclassified as <i>K. dlicheri</i> sp. nov. in this paper; leaflets doubtful
<i>Koelreuteria</i> sp.	Gonglangou Mine No. 3, Huadian, Jilin Province, China	Capsular valves (2.5 × 1.6 cm, elliptic)	Manchester et al., 2005, p. 10, pl. 4, figs. 8–10; this paper, Figs. 13–15	Middle Eocene	Smith et al., 2011	Reliable; reclassified as <i>K. taoana</i> sp. nov. herein
<i>Koelreuteria</i> sp. or <i>Koelreuteria</i> cf. <i>mitointegrifolia</i> Hu et R. W. Chaney	Uglovsky (Uglovskaya) Basin, South Primorye, Russia	Capsular valve (2.4 × 1.7 cm, ovoid-elliptic)	Ablaev, 1978, p. 170, pl. 10, fig. 5; Ablaev, 2000, p. 53, pl. 15, figs. 6, 7; this paper, Fig. 16	Middle Eocene	Pavlyutkin and Petrenko, 2010	Reliable; reclassified as <i>K. taoana</i> sp. nov. in this paper
<i>Palaeoallophylus globosa</i> Manchester	Clarno, north-central Oregon, USA	Seeds (3.6–6.0 × 3.7–5.2 mm, globose)	Manchester, 1994, p. 86, pl. 38, figs. 9–10	Middle Eocene	Manchester, 1994	Similar to seeds of <i>Koelreuteria</i> and <i>Allophylus</i> ; smaller than seeds of <i>Palaeoallophylus rotundatus</i> E. Reid et M. Chandler from early Eocene London Clay flora
<i>K. kamschatnica</i> Budantsev	Kingy Cape and Napana River, far eastern Russia	Leaf and leaflet	Budantsev, 1997, p. 86, pl. 54, figs. 1, 2; Budantsev, 2006, p. 118, pl. 133, fig. 5	Middle to late Eocene	Budantsev, 1997, 2006	Doubtful; superficially resembling the leaves of living <i>K. paniculata</i>
Cf. <i>Koelreuteria</i> sp.	Florissant, Colorado, USA	Wood (ring porous)	Wheeler, 2001, p. 193, pl. 3, A–F	Late Eocene	Meyer and Smith, 2008	Reliable
<i>Koelreuteria</i> sp.	Florissant, Colorado, USA	Pollen (type-A)	Leopold and Clay-Poole, 2001, p. 35, pl. 7, fig. 1; Leopold et al., 2008, p. 56, tab. 1	Late Eocene	Meyer and Smith, 2008	Doubtful

TABLE 2. Continued.

Published name	Locality	Organ	Cited figure	Geological age	Age reference	Identification
<i>K. allenii</i> (Lesq.) W. N. Edwards	Florissant, Colorado, USA	Leaves, leaflets, and capsular valves (2.3–3.8 × 1.6–2.2 cm, obovate, obovoid-elliptic)	Lesquereux, 1878b, p. 65, pl. 5, fig. 11; Holltick, 1923, p. 207, pl. 10, figs. 1, 3, 6–11, pl. 11, figs. 1–3; Holltick, 1929, pl. 2, fig. 3; MacGinitie, 1953, p. 145, pl. 55, figs. 1–4, 7, pl. 75, fig. 1; this paper, Figs. 22–29	Late Eocene	Meyer and Smith, 2008	Reliable for capsular valves, which were classified into <i>K. allenii</i> herein; resembling those of living <i>K. paniculata</i>
<i>K. eocenica</i> S. Endō	Ishikari Coal-field, Hokkaido, Japan	Capsular valves (2.4 × 1.2 cm, elliptic, with a central body)	Endō, 1968, p. 437, pl. 14, figs. 4–6, pl. 25, fig. 6	Late Eocene	Endō, 1968	<i>Pteleacarpum bronniei</i> (Unger) Weyland by Bůžek et al., 1989; reassigned to the genus <i>Craigia</i> A. C. Sm. et W. E. Evans as <i>C. bronniei</i> (Unger) Kvaček et al. herein
<i>K. borealis</i> Heer	Renardodden, Spitzbergen, Norway	Leaflet	Heer, 1876, p. 89, pl. 25, fig. 5; Budantsev and Golovneva, 2009, p. 40, pl. 94, figs. 4, 5	Late Eocene	Kvaček et al., 1994; Budantsev and Golovneva, 2009	Rejected by Tralau, 1963
<i>Koelreuteria</i> sp.	West Primorye, far eastern Russia	Capsular valve (1.5 × 1.1 cm, elliptic, with a central body)	Tashchi et al., 1996, p. 131, pl. 15, figs. 3, 4	Eocene	Tashchi et al., 1996	Reassigned to <i>Craigia bronniei</i> by Kvaček et al., 2005 and herein
<i>K. maffei</i> ana A. Massal.	Monte Bolca, Italy	Leaf	Massalongo, 1852, p. 19, pl. 4, fig. 14	Eocene	Edwards and Wonnacott, 1928	Doubtful or unidentifiable
<i>K. eoinTEGRIFOLIA</i> S. Endō	Fushun Coal-field, Liaoning Province, China	Capsular valve (1.5 × 1.1 cm, elliptic, with a central body)	Endō, 1942, p. 42, pl. 17, fig. 13	Eocene	Endō, 1942; WGCPC, 1978	Reassigned to <i>Craigia bronniei</i> herein
<i>K. arnoldii</i> H. F. Becker	Upper Ruby River and Beaverhead Basins, southwestern Montana; Okanagan Highlands, Republic and McAbee, northeastern Washington (USA) and southern British Columbia (Canada)	Leaves and capsular valves (1.4–1.8 × 1.2–1.4 cm, elliptic or suborbicular)	Becker, 1961, p. 83, pl. 27, figs. 1–6; Becker, 1969, p. 115, pl. 36, figs. 20, 21; Wolfe and Wehr, 1987, p. 21, pl. 12, figs. 8, 10; Wehr, 1995, p. 9, pl. 3, fig. 9; Dillhoff et al., 2005, p. 160, pl. 3, fig. F	Early to middle Eocene–Oligocene	Becker, 1969; Wolfe and Wehr, 1987; Greenwood et al., 2005; Manchester et al., 2009	Probably belonging to <i>Bonitodendron</i> Gagnep. (= <i>Sinoradiolofera</i> F. G. Mey.); leaves resembling those of living species <i>K. paniculata</i>
<i>K. microcarpa</i> H. M. Li	Fushun, Liaoning Province, China	Leaflets and capsular valves (1.5–2.3 × 0.9–1.5 cm, oblong or suborbicular)	WGCPC, 1978, p. 131, pl. 111, fig. 4, pl. 115, fig. 4, pl. 117, figs. 3–6; Zhang, 1980, p. 333, pl. 209, figs. 2, 6, pl. 210, fig. 6; Guo, 1990, p. 33	Late Eocene to early Oligocene	Bůžek et al., 1989; Guo, 1990	Doubtful for leaflet identification. Capsular valves reclassified as <i>Craigia bronniei</i> by Kvaček et al., 1991, 2005
<i>K. oregonensis</i> C. A. Arnold	Wheeler County, Oregon, USA	Capsular valves (1.5–3 × 1.2–3.3 cm, elliptic or obovate)	Arnold, 1952, p. 77, pl. 1, figs. 1–3, text-fig. 1; Bůžek et al., 1989, p. 485, figs. 36–44	Early Oligocene	Bůžek et al., 1989	Reclassified as <i>Craigia oregonensis</i> (C. A. Arnold) Kvaček et al. by Kvaček et al., 1991, 2005
<i>Phyllites</i> sp.	Indzhachaj River, Azarbadžan	Leaf (ca. 8–10 cm long, brochidodromous)	Kasumova, 1966, p. 51, pl. 12, fig. 5	Middle Oligocene	Kasumova, 1966	Identified as a capsular valve of <i>Koelreuteria</i> sp. by Bůžek, 1971; reject herein
<i>Koelreuteria</i> sp.	Rott, Germany	Capsular valve (ca. 4.2 × 2.4 cm, ovate)	Weyland, 1937, p. 88, text-fig. 17, pl. 11, fig. 2; Kirchner, 1957, p. 206; Winterscheid, 2006, p. 159, pl. 16, fig. 4; in this paper, Fig. 38	Late Oligocene	Kirchner, 1957; Winterscheid, 2006	Reliable; reclassified as <i>Koelreuteria macroptera</i> (Kováts) W. N. Edwards herein
<i>K. reticulata</i> (Ettingsh.) W. N. Edwards	Holedeč, Most Basin, the Czech Republic	Capsular valves (2–3.2 × 1.2–2 cm, oblong-ovate)	Brabeneč, 1904, p. 2, fig. 1; Teodoridis, 2002, p. 122, pl. 7, fig. 9	Late Oligocene	Teodoridis, 2002	Reliable; synonymous with <i>K. macroptera</i> (Kováts) W. N. Edwards herein

TABLE 2. Continued.

Published name	Locality	Organ	Cited figure	Geological age	Age reference	Identification
<i>Sapindaceacarpum koelreuterioides</i> Vaudois-Miéja et Lejal-Nicol	South-West of Khartoum, Sudan	Capsules (incomplete septum, but no veins)	Vaudois-Miéja and Lejal-Nicol, 1988, p. 855, pl. 1, figs. 1–6, pl. 2, figs. 1–6	Most possibly Oligocene	Prasad et al., 1986	Similar to extant <i>Koelreuteria</i> Laxm., but lacking reticulate venation in valves. Probably belonging to <i>Erythrophyssa</i> E. Mey. ex Arn. Doubtful
<i>K. miointegrifoliola</i> Hu et R. W. Chaney	Sakito, northwestern Kyushu Prefecture, Japan	Leaflets	Matsuo, 1970, p. 33, pl. 9, figs. 3–5, pl. 11, fig. 1	Oligocene	Matsuo, 1970	Doubtful
<i>K. jilinensis</i> S. X. Guo (nom. nud.)	Sanhe, Longjing County, Jilin Province, China	Capsular valve (1.4 × 1.3 cm, suborbicular)	Guo, 1990, p. 35; Guo and Zhang, 2002, p. 203, pl. 3, figs. 8, 11	Oligocene	Guo, 1990; Guo and Yang, 1997; Guo and Zhang, 2002	Reclassified as <i>Craigia oregonensis</i> by Guo and Zhang, 2002
<i>K. rhombifolia</i> S. X. Guo	Sanhe, Yanji County, Jilin Province, China	Leaflet and capsular valve (1.4 × 1.3 cm, suborbicular)	Guo, 1992, p. 578, pl. 269, figs. 1, 1a, 6	Oligocene	Guo and Yang, 1997; Guo and Zhang, 2002	Capular valve reclassified as <i>Craigia oregonensis</i> herein; leaflet doubtful
<i>Koelreuteria</i> sp.	Sanhe, Longjing County, Jilin Province, China	Leaflets	Guo and Zhang, 2002, p. 202, pl. 2, figs. 7, 9	Oligocene	Guo and Yang, 1997; Guo and Zhang, 2002	Doubtful
<i>K. bettitiana</i> A. Massal.	Chiavon, Italy	Leaflet	Massalongo, 1852, p. 18, pl. 4, fig. 13; Principi, 1926, p. 76, pl. 6, fig. 22	Oligocene	Principi, 1926; Edwards and Wonnacott, 1928	Doubtful; resembling the leaflet of <i>Rhus</i> L.
<i>K. prisca</i> A. Massal.	Chiavon, Salcedo, Italy	Leaf, leaflet and capsular valve	Massalongo, 1852, p. 17, pl. 3, figs. 10–12; Principi, 1926, p. 76, pl. 8, fig. 16	Oligocene	Principi, 1926; Edwards and Wonnacott, 1928	Doubtful; assigned to <i>Planera ungeri</i> by Eitingshausen, 1867; resembling the leaflet of <i>Zelkova</i> Spach
<i>K. bipinnatoides</i> H. F. Becker	Metzel Ranch, Upper Ruby River Basin, southwestern Montana, USA	Leaflets	Becker, 1972, p. 45, pl. 12, figs. 3–10	Oligocene	Becker, 1972	Doubtful; resembling the leaflet of living <i>K. bipinnata</i>
<i>K. reticulata</i> (Eitingsh.) W. N. Edwards	Tállya and Tokay, Hungary; St. Galler Findlinge (Kunkler), Germany; Pétipsy Area and Biflora (Most Basin), North Bohemia, the Czech Republic	Capsular valves (3.5–4.0 × 2.5–2.8 cm, oblong-ovate or ovate)	Eitingshausen, 1854, p. 813, pl. 4, fig. 5; Heer, 1857, p. 156, pl. 145, fig. 16; Hollick, 1923, p. 212, pl. 10, figs. 4, 5; Rásky, 1958, p. 184, pl. 17, fig. 9; Bůžek, 1971, p. 84, pl. 31, figs. 22, 23; Kvaček et al., 2004b, p. 94, figs. d, e	Early to middle Miocene	Kirchheimer, 1957; Rásky, 1958; Bůžek, 1971; Kvaček et al., 2004a, b; Hably, 2006	Reliable; synonymous with <i>K. macroptera</i> (Kováts) W. N. Edwards herein
<i>Sapindaceacarpum lunulatum</i> Andreánszky	Déflő, Hungary	Capsular valve (3.8 × 3.2 cm, ovate)	Andreánszky, 1959, p. 156, pl. 47, fig. 5, text-fig. 183;	Early Miocene	Andreánszky, 1959; Hably, 2006	Reclassified as <i>Koelreuteria macroptera</i> (Kováts) W. N. Edwards by Gregor, 1982 and herein
<i>Koelreuteria</i> sp.	Pingzhuang Basin, Chifeng, Inner Mongolia, China	Unknown	Shang et al., 2001, p. 109, not figured	Early Miocene	Shang et al., 2001	Doubtful
<i>K. macroptera</i> (Kováts) W. N. Edwards	Gomboska of Tállya, Abatujszántó and Szántó, Hungary; Randecker Maar, Bavaria and Kreuzau, Germany; Bohemia, the Czech Republic; Chiuzbaia, Romania; Klepariv of L'viv City, Ukraine	Capsular valves (3.4–5 × 2.5–4 cm, ovate or oblong-ovate, with two seeds)	Kováts, 1856, p. 51, pl. 1, fig. 2; Unger, 1870, p. 14, pl. 5, fig. 1; Kirchheimer, 1943, p. 404, text-fig. 11; Weyland, 1948, p. 133, pl. 21, fig. 6; Kirchheimer, 1957, p. 206, pl. 33, fig. 143a, b; Rásky, 1958, p. 184, pl. 17, figs. 10, 11; Rufflé, 1963, p. 237, pl. 12, figs. 28–31, pl. 13, figs. 1–5, pl. 27, fig. 9; Gregor, 1982, p. 113, pl. 7, fig. 14; Shvareva, 1983, p. 135, pl. 79, fig. 6, text-fig. 33, 3; Gregor et al., 1992, p. 21, pl. 3, fig. 2; Hably et al., 2001, p. 73, 83, 106, pl. 101, fig. 1, pl. 122, fig. 3; this paper, Figs. 30–37	Early to middle Miocene	Gregor, 1982; Krautter and Schweigert, 1991; Gregor et al., 1992; Ferguson et al., 1998; Hably, 2006; Sechuber, 2009	Reliable. Basionym: <i>Ptelea macroptera</i> Kováts, 1856; synonym: <i>Koelreuteria</i> sp. in Weyland, 1948

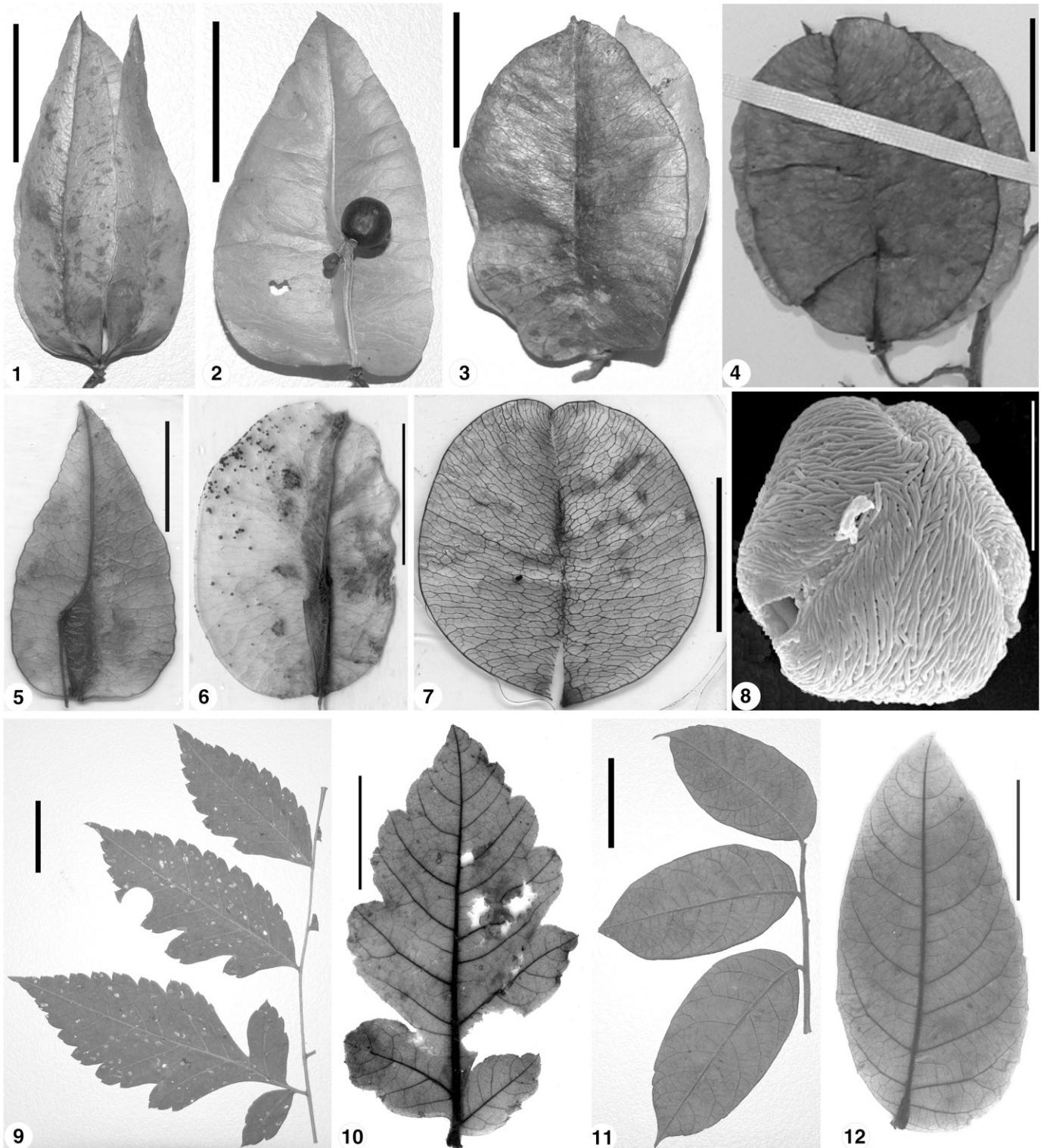
TABLE 2. Continued.

Published name	Locality	Organ	Cited figure	Geological age	Age reference	Identification
<i>K. macrocarpa</i> J. R. Tao	Shanwang Basin, Linqiu County, Shandong Province, China	Leaflet and capsular valve (3.8 × 2.9 cm, elliptic)	WGPC, 1978, p. 130, pl. 116, fig. 8, text-fig. 65; Tao et al., 1999, p. 46, 75, pl. 43, fig. 2	Early to middle Miocene	Li, 1981; Liu and Leopold, 1992; Deng, 2006; Wang et al., 2010; Wang, 2012	Capsular valve referred to <i>K. miointegrifoliola</i> Herein; leaflet similar to <i>K. bipinnata</i>
<i>Koelreuteria</i> sp.	Shanwang Basin, Linqiu County, Shandong Province, China	Capsular valve (4.5 × 3.5, ovate)	Sze, 1954, p. 80, pl. 68, fig. 5	Early to middle Miocene	Li, 1981; Liu and Leopold, 1992; Deng, 2006; Wang et al., 2010; Wang, 2012	Reliable; referred to <i>K. miointegrifoliola</i> herein
<i>Koelreuteria</i> sp.	Shanwang Basin, Linqiu County, Shandong Province, China	Leaflet	Tao et al., 1999, pl. 14, fig. 4	Early to middle Miocene	Li, 1981; Liu and Leopold, 1992; Deng, 2006; Wang et al., 2010	Doubtful
<i>K. crenulata</i> Pavlyutkin	Novokachalinsk, Khanka Area, Primorye, far eastern Russia	Leaflets	Pavlyutkin, 2005, p. 124, pl. 36, fig. 9, pl. 37, fig. 1	Middle Miocene	Pavlyutkin, 2005	Doubtful
<i>Koelreuteria</i> sp.	Shimo-tokusan, Tatsunokuchi-machi, Kaga, Ishikawa Prefecture, Japan	Leaflets	Fuji and Kitataka, 1988, p. 138, fig. 3, 4; Kitataka and Fuji, 1988, p. 112, fig. 17.	Middle Miocene	Fuji and Kitataka, 1988; Kitataka and Fuji, 1988	Doubtful
<i>K. oeningensis</i> Heer	Oeningen, Baden, southern Germany	Leaflets	Heer, 1857, p. 63, pl. 121, figs. 18–20, pl. 127, fig. 39a; Engelhardt, 1873, p. 31, pl. 12, fig. 12; Schimper and Schenk, 1890, p. 553, fig. 314, 3	Middle Miocene	Edwards and Wonnacott, 1928; Rufflé, 1963	Doubtful
<i>K. vetusta</i> Heer	Oeningen, southern Germany	Leaflet	Heer, 1857, p. 63, pl. 127, fig. 39a	Middle Miocene	Edwards and Wonnacott, 1928; Rufflé, 1963	Assigned to a rosaceous species <i>Crataegus longepetiolata</i> Heer by Hantke, 1954
<i>K. miointegrifoliola</i> Hu et R. W. Chaney	Shanwang Basin, Linqiu County, Shandong Province, China; Osudo, Niigata Prefecture, Oguni-machi, Chōjōbaru, Iki Island, Shimomoseki, Tottori Prefecture, Southwest Honshu, Kabutoiwa, border of Gumma and Nagano prefectures, Central Honshu, Japan	Leaflets and capsular valves (3.2–5.2 × 3.0–4.2, ovate, oblong, elliptic or suborbicular)	Hu and Chaney, 1938, p. 64, pl. 38, figs. 1, 3, pl. 39, fig. 3; Takahashi and Naito, 1952, p. 71, fig. 2; Huzioka and Takahashi, 1973, p. 141, pl. 4, figs. 2, 3; Onoe, 1974, p. 52, pl. 12, figs. 2, 4; Hayashi, 1975, p. 26, pl. 21, fig. 3, pl. 22, figs. 2, 4, 6, 8; Kamoi et al., 1978, p. 18; Ozaki, 1980, p. 4, fig. 1; Ozaki, 1991, p. 159, pl. 17, fig. 9; Tao et al., 1999, p. 46, 76, pl. 35, fig. 1, pl. 43, fig. 3; this paper, Figs. 39–47	Miocene	Ishida et al., 1970; Ozaki, 1980; Li, 1981; Liu and Leopold, 1992; Deng, 2006; Wang et al., 2010; Wang, 2012; this paper	Reliable for the capsule valves; some leaflets belonging to <i>Juglans</i> L., the others excluded from <i>K. miointegrifoliola</i> by Brown, 1946 and herein
<i>K. caucasica</i> Palib.	Leninakan, Armenia	Leaf	Palibin, 1939, p. 623, not figured; Kolakovsky, 1973, p. 135	Miocene	Kolakovsky, 1973	Rejected by Iljinskaja, 1963
<i>K. ulmifolia</i> A. Massal.	Sinigaglia, Italy	Leaflets	Massalongo, 1858, p. 80, pl. 1, pl. 17, pl. 36, fig. 8	Miocene	Meschinelli and Squinabol, 1892	Doubtful; combined into <i>Cissus ulmifolia</i> by Massalongo, 1858
<i>K. ? serrata</i> Heer	Sakhalin, far eastern Russia	Leaflet	Heer, 1878, p. 52, pl. 14, fig. 10	Miocene	Edwards and Wonnacott, 1928	Unidentifiable
<i>Koelreuteria</i> sp.	Khanka, West Primorye, far eastern Russia	Leaflet	Ablaev et al., 1994, p. 129, pl. 15, figs. 4, 5	Miocene	Ablaev et al., 1994	Doubtful
<i>K. cf. reticulata</i> (Eitingsh.) W. N. Edwards	Chiuzbaia, Romania	Capsular valves (2.3 × 2.1 cm, elliptic, with a central body)	Givulescu, 1984, p. 83, pl. 1, figs. 1–2; Givulescu, 1990, p. 120, pl. 34, figs. 4–5	Late Miocene	Givulescu, 1990	Reclassified as <i>Craigia bromii</i> herein
<i>Koelreuteria</i> sp.	Bangmai and Mengtuo, Lincang, Yunnan Province, China	Leaflet and valves (3.1–3.7 × 2.3–2.6 cm, elliptic)	Tao and Chen, 1983, p. 88, pl. 19, figs. 6, 13; Tao et al., 2000, p. 275, pl. 71, fig. 8; Guo, 2011, p. 359, pl. 9, figs. 6, 7, 11	Late Miocene	Ge and Li, 1999; Tao et al., 2000; Guo, 2011	Doubtful; leaflet incomplete; valves were reclassified as <i>Salvinia paralleloneura</i> S. X. Guo by Guo, 2011



TABLE 2. Continued.

Published name	Locality	Organ	Cited figure	Geological age	Age reference	Identification
<i>K. margaritifera</i> (R. Ludw.) Mai	Rhön Mountains, Salzhausen, Lettengraben, Salzhausen, Wackersdorf, Germany; Styria, Austria; Wieliczka, Poland; Tanaro Basin, Ca' Viettone and San Miniato, Italy	Seeds (3.4–6.5 mm in diameter, originally globose. Surface very smooth, without furrows or ridges. Hilum scar larger)	Kirchheimer, 1936, p. 89, pl. 9, fig. 1a–f; Gregor, 1982, p. 32, pl. 10, figs. 1–6, 8; Mai and Walthier, 1991, p. 108, pl. 13, fig. 17; Cavallo and Martinetto, 1996, p. 22, pl. 6, fig. 3; Łańcucka-Srodoniowa and Zastawniak, 1997, p. 18, pl. 3, fig. 3; Martinetto, 2001, p. 309, pl. 1, figs. 26a, b; Kovar-Eder and Meller, 2001, p. 86, pl. 6, fig. 1; Gumbel and Mai, 2006, p. 21, pl. 4, figs. 4–6	Early to middle Miocene–early to middle Pliocene	Gregor, 1982; Cavallo and Martinetto, 1996; Łańcucka-Srodoniowa and Zastawniak, 1997; Martinetto, 2001; Kovar-Eder and Meller, 2001; Gumbel and Mai, 2006	Generally smaller than seeds of <i>Koelreuteria</i> (5–9 mm in diameter), with a very smooth surface and larger hilum scar that further differs from <i>Koelreuteria</i> ; classified into <i>Sapindoidaea</i> <i>margaritifera</i> (R. Ludw.) Kirchh. by Gregor, 1978, 1980, 1982; Cavallo and Martinetto, 1996; Martinetto, 2001 and this paper
<i>Koelreuteria</i> cf. <i>oeningensis</i> Heer <i>Phyllites</i> cf.	Imola, Italy	Leaflet	Sangiorgi, 1916, p. 293, pl. 15, fig. 19	Miocene–Pliocene	Sangiorgi, 1916	Doubtful
<i>K. bipinnata</i> Franch. <i>Koelreuteria</i> sp. aff. <i>K.</i> <i>integrifolia</i> Merr.	Toutang, Mengzi County, Yunnan Province, China Brusturilor-Bach and Valea Neagră Bezirk Crisana, Romania	Leaflets Capsular valve (3.4 × 2.6 cm, ovate)	Colani, 1920, p. 227, pl. 9, figs. 4, 8 Givulescu, 1961, p. 103, fig. 8; Givulescu, 1962, p. 160, pl. 37, fig. 263 Cao and Cui, 1989, p. 371, not figured Cheng et al., 2012, p. 302, fig. 1	Miocene–Pliocene Early Pliocene	Edwards and Womacott, 1928; WGCP, 1978 Givulescu, 1967	Doubtful Reliable; reclassified as <i>Koelreuteria macroptera</i> herein
<i>Koelreuteria</i> cf. <i>integrifolia</i> Merr.	Zhangcun, Yushe Basin, Shanxi Province, China	Unknown		Late Pliocene	Shi et al., 1993	Doubtful
<i>K. yunnanensis</i> Cheng, Yin, Mehrotra et Li	Hutiaotan Earth Forest (Lower Yuanmou Formation), Yuanmou Basin, Yunnan Province, China	Wood (ring porous)		Pliocene	Qian, 1991; Cheng et al., 2012	Reliable



Figs. 1–12. Morphology of extant species in *Koelreuteria* Laxm. **1.** Capsule and **2.** capsular valve of *K. paniculata* Laxm. from cultivated tree at the Institute of Botany, Chinese Academy of Sciences, Beijing. **3.** Capsule of *K. bipinnata* Franch. from cultivated tree at Yunnan Academy of Forestry, Kunming. **4.** Capsule of *K. elegans* (Seem.) A. C. Sm. from Tailevu, Viti Levu of Fiji. Voucher: A 1213, B. E. Parham. **5.** Cleared capsular valve of *K. paniculata*, showing a basal septum equivalent to ca. 1/3 of valve length. **6.** Cleared capsular valve of *K. bipinnata*, showing a straight placental suture. **7.** Cleared capsular valve of *K. henryi* Dümmer from cultivated tree at the University of Florida, Gainesville, showing polygonal, transversely elongated nets. UF Slide no.: 20100203. **8.** Polar view of pollen grain of *K. paniculata* under SEM, showing a type of longitudinally striated tectexine. **9, 10.** Partial leaf and cleared leaflet of *K. paniculata*, showing deeply lobed margins. **11, 12.** Partial leaf and cleared leaflet of *K. bipinnata*, showing almost entire margins. Bars = 2 cm, except in Fig. 8, which is 10  $\mu$ m.

The exine is about 1.5–2.4  $\mu\text{m}$  thick, and the ornamentation of the extexine is, more or less, longitudinally striate, finely striate, or irregularly striate-reticulate (Wang and Chien, 1956; Meyer, 1976; Acevedo-Rodríguez et al., 2011) (Fig. 8). On the basis of the ectoaperture and pollen grain shape, Muller and Leenhouts (1976) recognized 12 pollen types in Sapindaceae and placed *Koelreuteria* in their type A, characterized by colporate spheroidal pollen grains of the kind found in most genera of the family, which they considered to be basic (Buerki et al., 2009) and possibly plesiomorphic. Pollen fossil records, such as the recently reported *Talisiipites megorites* Z. C. Song et M. Y. Li, *Senipites striatus* Z. C. Song (Song and Li, 1982; Song et al., 1999, 2004; Li et al., 2008), and *Koelreuteria* sp. (Leopold and Clay-Poole, 2001; Leopold et al., 2008) closely resemble this extant genus and date from the Late Cretaceous to the Eocene of southern China and western United States. The paleogeographic pattern of sapindaceous pollen may be important for correlation with the *Koelreuteria* fruit fossils.

Leaves of *Koelreuteria* are alternate, imparipinnate, bipinnate, and estipulate (Figs. 9–12; Table 1). The leaflets are sessile or shortly petiolulate. The blades are ovate, obliquely ovate, wide ovate to oblong-ovate or ovate-lanceolate. The bases are slightly or extremely oblique, wide cuneate, rounded or subtruncate. The apices are obtuse, acute, short or long acuminate to caudate. The margins vary among different species, from entire (e.g., *K. bipinnata*, see Figs. 11, 12) to variously lobed, with irregularly obtuse or incurved serrations (e.g., *K. paniculata*, see Figs. 9, 10), belonging to the rosoid tooth type (sensu Hickey and Wolfe, 1975). The rosoid tooth type is thought to stem from the base of core eudicots (Doyle, 2007), but appears to be apomorphic in *Koelreuteria* and closely related taxa. *Koelreuteria* bears polygonal leaf epidermal cells and anomocytic stomatal apparatus, both of which also occur in other sapindaceous genera such as *Allophylus* L., *Boniiodendron* Gagnep., *Erioglossum* Blume, *Delavaya* Franch., *Eurycorymbus* Hand-Mazz., *Handelioidendron* Rehder, *Paranephelium* Miq., and *Xanthoceras* Bunge (Cao and Xia, 2008). The bipinnate leaves bearing the leaflets with rosoid teeth assigned to *Koelreuteria allenii* (Lesq.) W. N. Edwards from the late Eocene Florissant Formation of Colorado (see MacGinitie, 1953: pl. 55, figs. 1–4; pl. 75, fig. 1) appear to be a reliable fossil representative of *Koelreuteria*. The name *K. allenii* is originally based on fruits; the hypothesis that associated leaves may represent the same species is reasonable, but not proven by specimens showing these organs in attachment. Overall, the leaflet morphology of *Koelreuteria* shows considerable similarities to that of other sapindalean genera, which often places fossil investigators in a predicament. The majority of species of the previously published leaf and leaflet fossils of *Koelreuteria* are questionable (Table 2) because they present suites of characters that are not unique to extant *Koelreuteria*. Some of them are too poorly preserved to be amenable to investigation of higher order venation and epidermal anatomy.

The woods of *Koelreuteria* have distinct growth rings, marked by radial flattened latewood fibers and much larger vessels in the earlywood and marginal parenchyma (Li et al., 1995; Klaassen, 1999). The wood is ring porous. Vessels in the earlywood are mainly solitary (*K. bipinnata* and *K. elegans*) or in irregular clusters of 2 or 3 (*K. paniculata*). More anatomical details of *Koelreuteria* are available (<http://insidewood.lib.ncsu.edu/search>). Fossil woods of *Koelreuteria* have been described from the latest Eocene Florissant Formation of Colorado, western United States (Wheeler, 2001) and the Pliocene Lower Yuanmou Formation of Yunnan, southwestern China (Cheng et al., 2012). Remarkably, ring to

semiring porosity in Sapindaceae is known only in three genera, *Sapindus* L., *Xanthoceras*, and *Koelreuteria* (including *K. elegans* in Fiji as well as the temperate species, see Li et al., 1995; Klaassen, 1999), whereas the usual condition is diffuse, or semiring porous. Hence, the paleogeographic pattern of sapindaceous wood fossils is helpful to correlate with that of *Koelreuteria* fruit fossils.

**Systematics of capsular fossils in *Koelreuteria***—About 30 fossil species under the name *Koelreuteria* have been documented from the Late Cretaceous to the Cenozoic of Eurasia and North America (Table 2). Overall, the fruit capsule and capsular valves are more reliably diagnostic than the pollen, leaflet, and wood for secure identification of the genus. The fruit taxa can be distinguished by the following taxonomic key:

**Key to species—**

1. Capsular valves obovate or obovoid-elliptic, with a cuneate or decurrent base.....*K. allenii* (Lesq.)  
W. N. Edwards
1. Capsular valves ovate, elliptic, oblong, ovoid-elliptic, oblong-elliptic, or suborbicular, without a cuneate or decurrent base..... 2
2. Capsular valves elliptic, oblong, ovoid-elliptic, oblong-elliptic, with a rounded or slightly truncate base and a rounded apex..... 3
2. Capsular valves ovate, oblong-ovate, oblong, elliptic or suborbicular, with a rounded or slightly cordate base and a convex, acute, short acuminate, or slightly emarginated apex..... 4
3. Capsular valves smaller, 2.4–2.5 cm long.....*K. taoana* sp. nov.
3. Capsular valves larger, 3.5–5.8 cm long.....*K. dilcheri* sp. nov.
4. Capsular valves ovate, or oblong-ovate, with a septum accounting for approximately 1/3 or slightly more than 1/3 of the valve length from the base.....*K. macroptera* (Kováts) W. N. Edwards
4. Capsular valves ovate, oblong, elliptic or suborbicular, with a septum accounting for approximately half of the valve length from the base.....*K. miointegrifoliola* Hu et R. W. Chaney

SYSTEMATIC PALEOBOTANY

**Family—**

Sapindaceae Juss.

**Subfamily—**

Dodonoideae Hook.

**Tribe—**

Koelreuterieae Radlk.

**Genus—**

*Koelreuteria* Laxm.

**Species—***Koelreuteria taoana* Qi Wang, Manchester, H.-J. Gregor, S. Shen et Z. Y. Li, sp. nov. (Figs. 13–16).

TABLE 3. Comparisons between *Koelreuteria* species and other taxa with similar fruits.

Species (Family)	Fruit				Valve				Seed	
	Shape	Length (cm)	Texture	Dehiscence	Central body	Shape	Septum	Sepal		Position
<i>Abronia fragrans</i> Nutt. ex Hook. <sup>5,14</sup> (Nyctaginaceae Juss.)	4-5-winged or not winged, fusiform, arrowhead shaped	0.5-1.2	Papery or coriaceous	No	Absent	Triangular or rhombic	No	Caducous	One level	1 (Oblong)
<i>Abronia macrocarpa</i> L. A. Galloway <sup>5</sup> (N.)	5-winged, broadly turbinate or cordate	0.8-1.5	Papery, scarious	No	Absent	Triangular	No	Caducous	One level	1 (Obovoid)
<i>Craigia kwangsiensis</i> H. H. Hsue <sup>5</sup> (Malvaceae Juss.)	5-locular, winged, 5-angled	2.5-3	Membranous	Loculicidal or septicidal	Present	Elliptic to oblong	Complete	Caducous	Biserial	4 (Ovoid-oblong)
<i>C. yunnanensis</i> A. C. Sm. et W. E. Evans <sup>5,23</sup> (M.)	5-locular, winged, 5-angled	Ca. 3.5	Membranous	Loculicidal or septicidal	Present	Suborbicular to elliptic	Complete	Caducous	Biserial	1, 2 or 4 (Oblong)
<i>C. bromii</i> (Unger) Kvaček et al. [= <i>Ptelea carpinum</i> bromii (Unger) Weyland] <sup>1,6</sup> (M.)	5-locular, winged	0.9-2.4	Membranous	Loculicidal or septicidal	Present	Elliptic, obovate or suborbicular	Complete	Caducous	Biserial	2-3 (Obovoid)
<i>C. oregonensis</i> (C. A. Arnold) Kvaček et al. [= <i>P. oregonensis</i> (C. A. Arnold) Manchester] <sup>1,6</sup> (M.)	5-locular, winged	1.5-3	Membranous	Loculicidal or septicidal	Present	Elliptic or obovate	Complete	Caducous	Biserial	2-4 (Obovoid)
<i>Ptelea enervosa</i> H. V. Sm. <sup>14,22</sup> (Rutaceae Juss.)	2-3-Locular, winged, flattened, suborbicular	1.6-1.8	Papery	No	present	Suborbicular	No	Persistent	One level	1 (Reniform)
<i>Afraillea arborescens</i> Pierre. <sup>1,19</sup> (Sapindaceae Juss.)	3-Locular, winged, inflated	2-4	Papery	Loculicidal	Absent	Wide elliptic or suborbicular	Complete	Caducous	One level	1 (Globose)
<i>Boniodendron minus</i> (Hemsl.) T. C. Chen [= <i>Sinoradlkofera minor</i> (Hemsl.) F. G. Mey.] <sup>-4,14,19,23</sup> (S.)	3-locular, winged, subglobose	1.8-2.3	Membranous	Loculicidal	Absent	Suborbicular or obcordate	Complete	Caducous	One level	1 (Globose)
<i>Bridgesia boyayensis</i> Manchester et O'Leary <sup>14</sup> (S.)	At least 2-locular, winged, inflated	1.5-1.6	Membranous	Loculicidal	Absent	Wide elliptic	Complete	Caducous	One level	1 (Globose)
<i>B. incisifolia</i> Bertero ex Cambess. <sup>3,14,23</sup> (S.)	3-Locular, winged, inflated	Ca. 1.5	Papery	Loculicidal	Absent	Wide elliptic	Complete	Caducous	One level	1 (Globose)
<i>Cardiospermum halicacabum</i> L. <sup>2,3,15,16</sup> (S.)	3-Locular, inflated, turbinate, obtriangular or ellipsoid	1.5-3	Membranous or papery	Septifragal or marginicidal	Absent	Obtriangular or elliptic	Complete	Persistent	One level	1 (Globose)
<i>Conchopetalum brachysepalum</i> Capuron <sup>3,5,16,19</sup> (S.)	3-Locular, more or less compressed	2.5-6.0	Membranous or papery	Loculicidal	Absent	Elliptic	Complete	Persistent	One level	2 (Globose)
<i>Cupaniopsis anacardioides</i> (A. Rich.) Radlk. <sup>3,5</sup> (S.)	3-Locular, 3-4-sided, pyriform or subglobose	2-2.3	Woody, crustaceous	Loculicidal	Absent	Suborbicular	Complete	Persistent	One level	1 (Oblong)
<i>Dodonaea viscosa</i> (L.) Jacq. <sup>2,3,5,7,14,16,21,25</sup> (S.)	2-6-Locular, winged, obcordate or compressed globose	1.5-2.2	Membranous or papery	Septifragal or septicidal	present	Suborbicular or wide obovate	Complete	Caducous	One level	1-2 (Lenslike)
<i>Erythrophylla alata</i> (Eckl. et Zeyher) Hutch. <sup>3,8,21</sup> (S.)	3-Locular, inflated, trigonous, obovoid	4-7	Membranous	Loculicidal	Absent	Ovate	Complete	Caducous	One level	2 (Globose)
<i>E. paniculata</i> Capuron <sup>3,16</sup> (S.)	3-Locular, inflated, trigonous, obovoid	3.5-4	Membranous-papery (pilose)	Loculicidal	Absent	Obovate	Possibly incomplete	Persistent	One level	2 (Globose)

TABLE 3. Continued.

Species (Family)	Fruit				Valve				Seed	
	Shape	Length (cm)	Texture	Dehiscence	Central body	Shape	Septum	Sepal	Position	No./valve (Shape)
<i>E. septentrionalis</i> Verdc. <sup>3, 8</sup> (S.)	3-Locular, inflated, subglobose	3.5	Membranous	Loculicidal	Absent	Suborbicular	Complete	Caducous	One level	2 (Globose)
<i>E. transvaalensis</i> L. Verd. <sup>3, 8, 21</sup> (S.)	3-Locular, 3-ridged, inflated, obovoid or subglobose	8	Membranous	Loculicidal	Absent	Obovate or suborbicular	Complete	Caducous	One level	1-2 (Globose)
<i>Euphoranthus euneurus</i> (Miq.) Leenh. <sup>3, 9</sup> (S.)	3-Locular, inflated, globose	0.8-1	Velvety or fleshy	Loculicidal	Absent	Suborbicular	Incomplete	Persistent	One level	1 (Obovoid)
<i>Koeltreuteria paniculata</i> Laxm. <sup>1-5, 10, 23</sup> (S.)	3-Locular, inflated, not winged, trigonous-conoidal	2.2-7.2	Membranous (glabrous)	Loculicidal	Absent	Ovate	Incomplete	Persistent	One level	2 (Globose)
<i>K. bipinnata</i> Franch. <sup>1-5, 10, 14, 23</sup> (S.)	3-Locular, inflated, 3-ridged, not winged, ellipsoid or subglobose	4-7	Membranous (glabrous)	Loculicidal	Absent	Elliptic, suborbicular	Incomplete or rarely complete with septal slits	Persistent	One level	2 (Globose)
<i>K. henryi</i> Dümmer (= <i>K. formosana</i> Hayata) <sup>1-5, 10-12, 23</sup> (S.)	3-Locular, inflated, 3-ridged, not winged, subglobose	4-5	Membranous (glabrous)	Loculicidal	Absent	Suborbicular	Incomplete	Persistent	One level	2 (Globose)
<i>K. elegans</i> (Seem.) A. C. Sm. <sup>1-5, 13, 23</sup> (S.)	3-Locular, inflated, 3-ridged, not winged, subglobose	3.4-5	Membranous (glabrous)	Loculicidal	Absent	Suborbicular	Incomplete	Persistent	One level	2 (Globose)
<i>Majidea zanguebarica</i> J. Kirk ex Oliv. <sup>3, 5, 16, 19</sup> (S.)	3-Locular, inflated, not winged, subglobose	Ca. 3	Crustaceous	Loculicidal, deeply lobed	Absent	Suborbicular	Complete	Persistent	One level	2 (Obovoid-oblong)
<i>Paullinia hispida</i> Jacq. <sup>3, 14</sup> (S.)	3-Locular, winged, obovoid	1.2-1.5	Coriaceous	Septifragal	Absent	Obovate	Complete	Caducous	One level	1 (Ovoid)
<i>P. dasystachya</i> Radlk. <sup>3, 15</sup> (S.)	3-Locular, winged, obovoid	1.8-2.2	Crustaceous	Septifragal	Absent	Obovate	Complete	Persistent	One level	1 (Ellipsoid)
<i>Sapindaceacarpum koeltreuterioides</i> Vaudois-Miçija et Lejal-Nicol <sup>17</sup> (S.)	3-Locular, inflated, not winged, subglobose	2.0-2.2	Membranous (glabrous, not reticulate)	Loculicidal	Absent	Suborbicular	Incomplete	Persistent	One level	1-2 (Globose)
<i>Serjania altissima</i> (Poepp.) Radlk. <sup>3, 15</sup> (S.)	3-Locular, winged, inflated, ovoid to oblong	Up to 3	Membranous or papery	Septifragal	Absent	Ovate	Complete	Persistent	One level	1 (Ellipsoid)
<i>S. polyphylla</i> (L.) Radlk. <sup>3</sup> (S.)	3-Locular, winged, inflated	3.3	Membranous	Septifragal	Absent	Ovate	Complete	Persistent	One level	1 (Globose)
<i>Smelephyllum capense</i> (Sond.) Radlk. <sup>3, 20, 21</sup> (S.)	2-3-Locular, inflated, globose	1.3	Chartaceous or fleshy	Loculicidal, usually two-lobed	Absent	Orbicular	Complete	Caducous	One level	1 (Globose)
<i>Stocksia brahuica</i> Benth. <sup>3, 14, 18</sup> (S.)	3-Locular, winged, inflated, subglobose	2.5-3	Membranous	Loculicidal	Absent	Suborbicular or wide ovate	Complete	Caducous	One level	1-2 (Subglobose)
<i>Urvillea filipes</i> Radlk. <sup>3, 14</sup> (S.)	3-Locular, inflated, marginally winged	Ca. 2.0	Membranous	Septifragal	Absent	Suborbicular	Complete	Caducous	One level	1 (Globose)
<i>U. chacoensis</i> Hunz. <sup>3, 14, 23</sup> (S.)	3-Locular, inflated, marginally winged	Ca. 2.2	Membranous	Septifragal	Absent	Obovate	Complete	Persistent	One level	1 (Globose)
<i>U. ulmacea</i> Kunth <sup>3, 15</sup> (S.)	3-Locular, inflated, marginally winged, ellipsoid	3.2-4	Membranous or papery	Septifragal	Absent	Elliptic to obovate	Complete	Persistent	One level	1 (Globose)

Reference notes: <sup>1</sup> Bůžek et al., 1989; <sup>2</sup> Xia and Gadek, 2007; <sup>3</sup> Acevedo-Rodríguez et al., 2011; <sup>4</sup> Meyer, 1976, 1977; <sup>5</sup> see <http://www.efloras.org>; <sup>6</sup> Kvaček et al., 2005; <sup>7</sup> Paoli and Sarti, 2008; <sup>8</sup> Verdcourt, 1962; <sup>9</sup> Leenhouts, 1988; <sup>10</sup> Luo and Chen, 1985; <sup>11</sup> Li, 1963, 1977; <sup>12</sup> Chen, 1993; <sup>13</sup> Smith, 1952, 1985; <sup>14</sup> Manchester and O'Leary, 2010; <sup>15</sup> Weckerle and Rutishauser, 2005; <sup>16</sup> Capuron, 1969; <sup>17</sup> Vaudois-Miçija and Lejal-Nicol, 1988; <sup>18</sup> Abdullia, 1973; <sup>19</sup> Buijssen et al., 2003; <sup>20</sup> Schönland, 1913; <sup>21</sup> Palmer and Pitman, 1972; <sup>22</sup> Call and Dilcher, 1995; <sup>23</sup> Direct observations on the cultivated plants and the herbaria kept at the Chinese National Botanical Garden Herbarium (PE), the Missouri Botanical Garden Herbarium (MO), and Arnold Arboretum Herbarium, Harvard University (A).

*Synonym*—*Koelreuteria* cf. *miointegrifolia* Hu et R. W. Chaney in Ablaeuv (1978), 187, pl. 10, fig. 5; *Koelreuteria* sp. in Ablaeuv (2000), 53, pl. 15, figs. 6, 7 (Fig. 16 herein); *Koelreuteria* sp. in Manchester et al. (2005), 10, pl. 4, figs. 8–10 (Figs. 13–15 herein).

*Diagnosis*—Capsular valves, entire-margined, elliptic or ovoid-elliptic with a longitudinal, middle carpellary suture, over 2 cm long. Apex rounded. Base rounded or slightly truncate. Septum present along the lower part of the carpellary suture. Lateral veins on both sides of the suture sinuous, reaching margin. Thinner veins between lateral veins consisting of irregular, transversely elongated reticulum.

*Etymology*—The specific epithet is dedicated to Prof. Tao Junrong (Institute of Botany, CAS, Beijing) for her important contributions to Cenozoic paleobotany.

*Holotype*—PE 054018a, b, c (Figs. 13, 14) (part and counterpart specimens, designated here; Huadian County, Jilin Province, Middle Eocene Huadian Formation of northeastern China; first illustrated by Manchester et al. (2005: pl. 4, figs. 8–10)).

*Description*—Fossils are preserved as individual capsular valve impressions. Capsular valves are entire-margined, elliptic (Figs. 13–15) or ovoid-elliptic (Fig. 16), 2.4–2.5 cm long and 1.6–1.7 cm wide. The valve apex is rounded, and the base is rounded or slightly truncate. A longitudinal, middle carpellary suture is prominent and thicker in the lower part than the upper one. Along the lower part of the carpellary suture, the valve is involutely fused, forming a septum (Figs. 14, 15). The septum extends approximately half of the valve length from the base and is about 3 mm high, terminating in a prominent placental suture. Seeds are not preserved. On both sides of the carpellary suture, lateral veins diverge at 30°–90° (or even 120° at the base) and arrive at the margin. Numerous thinner veins between lateral veins anastomose, forming a polygonal reticulum with areoles that are mostly irregular and transversely elongated in outline (Figs. 15, 16). The texture of valves is membranous.

*Comments*—In comparison with the length range observed in extant *Koelreuteria* capsules (2.2–7.2 cm long; see Table 1), the valves of this fossil species are relatively small. The small number of fossil capsular valves from the localities may limit our knowledge of the full range of variation, and larger capsular valves might be found from these Asian localities in the future. *K. taoana* was distributed along the North-West Pacific-Rim areas in the middle Eocene of northeastern China and far eastern Russia (Fig. 48).

*Species*—*Koelreuteria dilcheri* Qi Wang, Manchester, H.-J. Gregor, S. Shen et Z. Y. Li, sp. nov. (Figs. 17–21).

*Synonym*—*Koelreuteria mixta* (Lesq.) R. W. Br., Brown (1946), pro parte, 351, fig. 1 (non fig. 2) (Figs. 17, 18 herein).

*Diagnosis*—Capsular valves, entire-margined, oblong or oblong-elliptic with a longitudinal, middle carpellary suture, more than 3 cm long. Apex rounded. Base rounded. Septum occurring along the lower part of the carpellary suture. Lateral veins on both sides of the suture sinuous, reaching the margin.

*Etymology*—The specific epithet is dedicated to Prof. David Dilcher (Indiana University), who has made important contributions to Cenozoic paleobotany.

*Holotype*—USNM P42363 (Figs. 17, 18) (designated here; Independence Hill near Colfax, California, United States, middle Eocene Chalk Bluffs flora; first illustrated by Brown [1946: fig. 1]).

*Paratypes*—UWBM PB94575 (Fig. 19), 1695 and 1696 (Figs. 20, 21) (part and counterpart specimens; Republic, Washington, United States, early to middle Eocene Republic flora).

*Description*—Fossils are preserved as individual capsular valve impressions. Capsular valves are entire-margined, elliptic (Figs. 17, 18), oblong or oblong-elliptic (Figs. 19–21), 3.5–5.8 cm long and 2.8–3.6 cm wide. Both apex and base are rounded. A longitudinal, middle carpellary suture is prominent and thicker in the lower half-part than the upper one (Fig. 19), implying an incomplete septum in the valves. Seeds are not preserved. On both sides of the carpellary suture, lateral veins diverge at 30°–110° and arrive at the margin. Between lateral veins, thinner veins anastomose, forming a polygonal reticulum with areoles that are mostly irregular and transversely elongated in outline (Figs. 18, 20–21). The texture of valves is membranous.

*Comments*—Brown (1946) first described this capsular valve and associated leaflet fossils under the name *Koelreuteria mixta* from middle Eocene Chalk Bluffs flora of Independence Hill near Colfax, California, but its basionym *Rhus mixta* Lesq. (Lesquereux, 1878a) was only used for leaflet fossils. Hence, we separate the capsular valve fossil from *K. mixta* and reclassify it into *K. dilcheri* sp. nov. This new species is very similar to the above described *K. taoana* from northeastern Asia, but these two species show a certain degree of discontinuity in valve size. *Koelreuteria dilcheri* was distributed along the North-East Pacific-Rim areas in the early to middle Eocene of western United States (Fig. 48).

*Species*—*Koelreuteria allenii* (Lesq.) W. N. Edwards (Figs. 22–29).

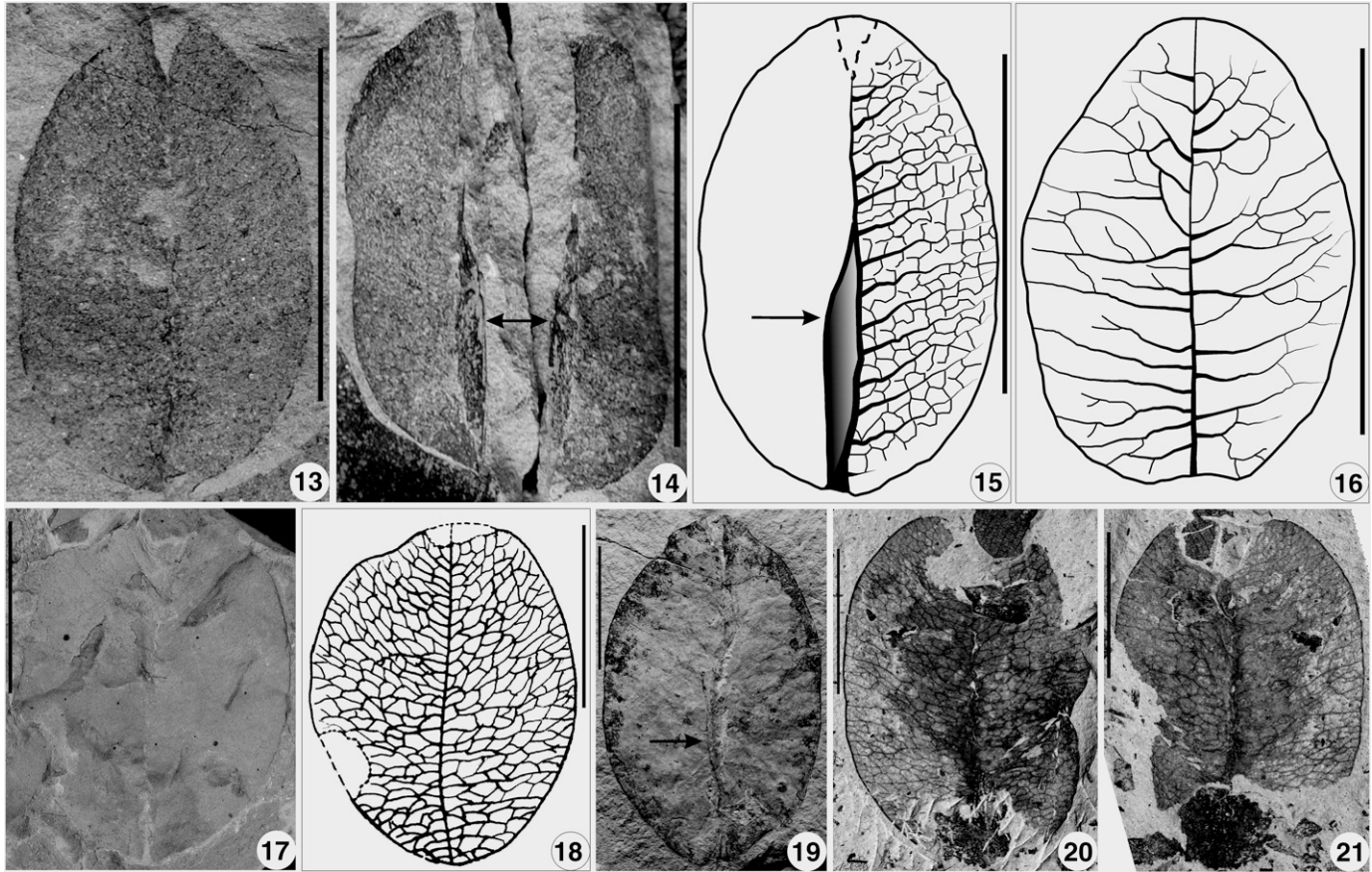
*Koelreuteria alleni* (Lesq.) W. N. Edwards (1927), 110; MacGinitie (1953), pro parte, 145, pl. 55, fig. 7 (non pl. 55, figs. 1–4 nec pl. 75, fig. 1).

*Basionym*—*Ophioglossum alleni* Lesq., Lesquereux (1873) in *Lignitic Formation and Fossil Flora*, 371.

*Synonym*—*Salvinia alleni* (Lesq.) Lesq., Lesquereux (1878b), 65, pl. 5, fig. 11; Lesquereux (1883), 136, pl. 21, figs. 10–11; *Tmesipteris alleni* (Lesq.) Hollick (1894), 256, pl. 205, fig. 12; *Carpolithes alleni* (Lesq.) Cockerell (1913), 500; Hollick (1923), 211, pl. 10, figs. 1–3, 6–11, pl. 11, figs. 1–3; *Phyllites alleni* (Lesq.) Florin (1919), 254; *Staphylea viridifluminis* Hollick (1929), 96, pl. 2, fig. 3; *Koelreuteria viridifluminis* (Hollick) R. W. Br., 62, pl. 10, fig. 10. 1934; *K. nigricans* (Lesq.) R. W. Br. in Manchester (1999), 493, fig. 11A.

*Holotype*—USNM P1617 (Florissant, Colorado, United States; latest Eocene Florissant Formation; collected by Mr. S. A. Allen and first illustrated by Lesquereux [1878b: pl. 5, fig. 11]).

*Other specimens examined*—USNM P36692 (Fig. 22), P36691 (Fig. 23), P36695 (Fig. 24), P36688, P36689, P36690, P36693, P36694, and P36695a (Florissant Formation, Florissant,



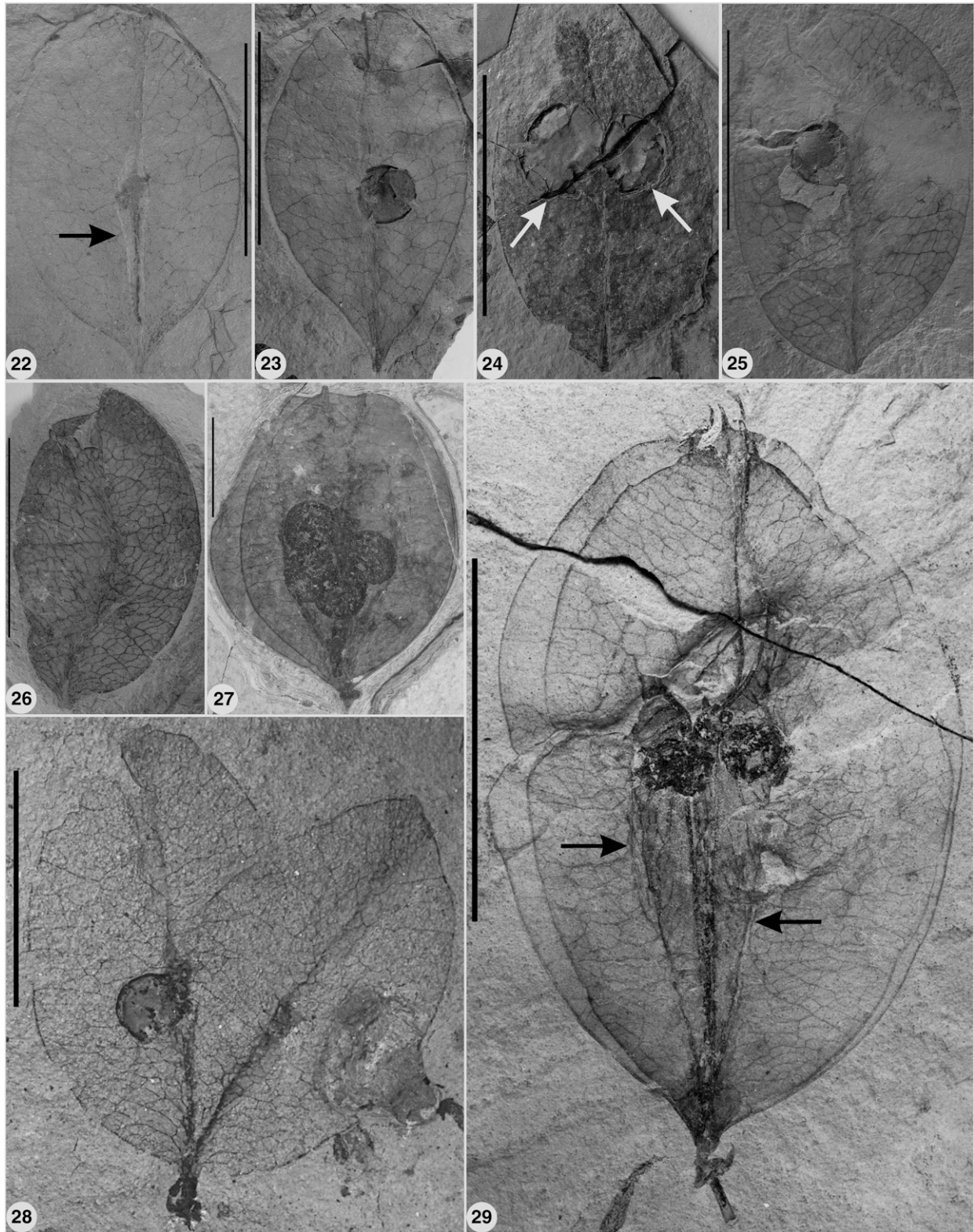
Figs. 13–21. *Koelreuteria taoana* sp. nov. and *K. dilcheri* sp. nov. from the Eocene of far eastern Russia, northeastern China, and western United States. Figs. 13–16. *K. taoana*. 13–15. An elliptic capsular valve from the middle Eocene Huadian Formation of Jilin Province in northeastern China. Arrows refer to a septum only in the lower part. The line drawing shows irregularly polygonal and transversely elongated nets. Arrow indicates a proximal septum. Holotype: PE 054018a, b, c. 16. Line drawing of ovoid-elliptic capsular valve from the middle Eocene Uglovskaya Formation of South Primorye, Russia (based on Ablaev, 1978: pl. 10, fig. 5). Figs. 17–21. *K. dilcheri*. 17–18. Elliptic capsular valve (and its line drawing, based on Brown, 1946: fig. 1 and republished with permission of the Washington Academy of Sciences) from the middle Eocene of Independence Hill near Colfax, California. Holotype: USNM P42363. 19–21. Larger, oblong capsular valves from the early to middle Eocene of Republic, Washington. UWBM PB94575, PB1695, and PB1696. Arrow refers to a lower, thicker carpellary suture. Bars = 2 cm.

Colorado); UF 256-20740 (Fig. 25), 256-20745 (Fig. 26) (John Day Formation, Teater Road, Oregon); FMNH PP55094 (Fig. 27) (Green River Formation, Wyoming); YPM PB158849 (Fig. 28) (Florissant Formation, Florissant, Colorado) and PB020681 (Fig. 29) (Green River Formation, De Beque, Colorado).

**Emended description**—Fossils are preserved as individual (Figs. 22–26), two connected capsular valves (Fig. 28), or complete capsules (Figs. 27, 29), about 3–5.5 cm long and 1.8–2.4 cm wide. Capsules appear to be inflated in contour, with a short pedicel and an acuminate style (fused when the capsule is indehiscent) (Fig. 29). Pedicels are ca. 3–4 mm long and bear perianth scars (Figs. 27–29), implying that the flower of its parent plant is hypogynous. Placentation is axile, with 2–4 seeds at a single level of placental sutures in each capsule (Figs. 27, 29). Seeds are globose (Figs. 23–25, 27–29), ca. 4–6 mm in diameter. The seed surface appears to be smooth (Fig. 25), irregularly furrowed or ridged (Figs. 23, 24, 27–29). Capsules are three-valved and loculicidal, with a septum in the proximal position of each valve (Fig. 29). The septum extends approximately half or slightly more than 1/2 of the valve length from the base, about 3 mm high (Figs. 22, 29). Individual capsular valves are

slightly asymmetrical, obovate or obovoid-elliptic, with a prominent, entire margin. The apex is rounded or slightly emarginate, or mucronate, representing a partial style. The base is narrowly cuneate or decurrent, and slightly asymmetrical (Figs. 22–26). A longitudinal, middle carpellary suture is prominent and appears to be thicker in the lower part than the upper one (Fig. 28). Lateral veins are sinuous and diverge at about 30°–90° and extend directly to join a fimbrial vein at the margin. The veins are branched and connected into polygonal areoles that are irregular and transversely elongated in outline (Figs. 22, 23, 25, 26, 28, 29). The texture of valves is membranous.

**Comments**—*Koelreuteria allenii* was originally instituted for an isolated capsular valve fossil under the name *Ophioglossum allenii* by Lesquereux (1873) from the latest Eocene Florissant Formation, Colorado, but was subsequently used for detached leafy shoots, leaves, leaflets, and capsular valves (MacGinitie, 1953). These leafy shoot fossils are preserved fairly well, which may allow us to make a detailed comparison with those of living *K. paniculata*, both of which bear extremely similar odd-pinnate leaves and dissected leaflets. However, these leaves and capsular valves do not show any organic



Figs. 22–29. *Koelreuteria allenii* (Lesq.) W. N. Edwards from the Eocene of western USA. 22–24. Obovoid-elliptic capsular valves from the late Eocene Florissant Formation of Colorado. Black arrow in Fig. 22 refers to a lower-half septum. White arrows in Fig. 24 refer to two globose seeds, showing some irregular ridges on the surface. USNM P36692, P36691 and P36695. 25–26. Obovoid-elliptic capsular valves from late Eocene John Day Formation of Teater Road, Oregon. UF 256-20740 and 256-20745. 27. Complete capsule from early Eocene Fossil Butte Member of the Green River Formation of Wyoming. FMNH PP55094. 28. Two united capsular valves from the late Eocene Florissant Formation of Colorado. YPM PB158849. 29. Complete capsule from the middle Eocene Green River Formation near De Beque, Colorado. Arrows refer to proximal septa. YPM PB020681. Bars = 2 cm.



connections, so we here use *K. allenii* only for reliable fruit remains. Associated leaves and leaflets may require another name, perhaps using the epithet *hilliae* from Lesquereux (1883) who described the foliage as *Rhus hilliae* Lesq. *Koelreuteria allenii* occurred in the Rocky Mountain region, ranging from the Early Eocene (ca. 52 Ma) of the Fossil Butte Member, through the Middle Eocene Parachute Creek Member of the Green River Formation, Utah and Colorado, to the latest Eocene (ca. 34 Ma) Florissant Formation, Colorado. It was also discovered in the late Eocene John Day Formation of Teater Road, Oregon. Overall, *K. allenii* appears to have existed during an interval of about 18 Ma in the Eocene of western USA (Fig. 48).

**Species**—*Koelreuteria macroptera* (Kováts) W. N. Edwards (Figs. 30–38).

*Koelreuteria macroptera* (Kováts) W. N. Edwards (1927), 112; Kirchheimer (1943), 404, text-fig. 11; Kirchheimer (1957), 206, pl. 33, fig. 143a, b; Rásky (1958), 184, pl. 17, figs. 10, 11; Ruffle (1963), 237, pl. 12, figs. 28–31, pl. 13, figs. 1–5, pl. 27, fig. 9; Schmidt (1976), 54; Schmidt (1980), 15; Shvareva (1983), 135, pl. 79, fig. 6, text-fig. 33.3; Csaki and Urlichs (1985), 31; Gregor (1982), 113, pl. 7, fig. 14; Gregor (1986), 11; Gregor et al. (1992), 21, pl. 3, fig. 2; Seehuber (2009), 239.

**Basionym**—*Ptelea macroptera* Kováts (1856) in *Arbeiten der Geologischen Gesellschaft für Ungarn* 1: 51, pl. 1, fig. 2.

**Synonym**—*Dalbergia reticulata* Ettingsh., Ettingshausen (1854), pro parte, 813, pl. 4, fig. 5 (non fig. 6); *Salvinia reticulata* (Ettingsh.) Heer (1857), 156, pl. 145, fig. 16; Brabeneč (1904), 2, fig. 1, a–b; *Phyllites reticulata* (Ettingsh.) Florin (1919), 255; *Koelreuteria ? reticulata* (Ettingsh.) W. N. Edwards in Edwards and Wonnacott (1928), 39; *Abronia bronni* (Unger) L. Laurent in Weyland (1937), pro parte, 88, pl. 11, fig. 2, text-fig. 17 (non fig. 3, text-figs. 18, 19); *K. reticulata* (Ettingsh.) R. W. Br., Brown (1946) 350; *Koelreuteria* sp. in Weyland (1948), 133, pl. 21, fig. 6; Kirchheimer (1957), 206; *Sapondaceacarpum lunulatum* Andreánszky (1959), 156, pl. 47, fig. 5, text-fig. 183; *K. reticulata* (Ettingsh.) W. N. Edwards in Rásky (1958), 184, pl. 17, fig. 9; Bůžek (1971), 84, pl. 31, figs. 22, 23; Teodoridis (2002), 122, pl. 7, fig. 9; Kvaček et al. (2004b), 94, figs. d, e (non figs. b, c); Winterscheid (2006), 159, pl. 16, fig. 4; *Koelreuteria* sp. aff. *K. integrifolia* Franch. in Givulescu (1961), 103, fig. 8; Givulescu (1962), 160, pl. 37, fig. 263.

**Holotype**—BP 58.2.1 (Fig. 30) (Gomboska of Tállya, Hungary; middle Miocene; part and counterpart specimens first illustrated by Kováts [1856: pl. 1, fig. 2] and Rásky [1958: pl. 17, fig. 11], respectively).

**Other specimens examined**—BP 60.815.1 (Fig. 31) (Abaújszántó, Hungary); SMNS P1224/509 (Fig. 32), P1224/506 (Fig. 33), P1224/511 (Fig. 34), P1224/515 (Fig. 35), P1224/508 (Fig. 36), P1224/507, P1224/510 and P1224/512 (Randecker Maar, Germany); NMA 92-15/413, 92-17/413 (Fig. 37) (Randecker Maar, Germany), 91-2048/800 (Burtenbach, Germany), and 91-2518/403 (Geisenhausen, Germany).

**Emended description**—Fossils are preserved as individual capsular valve impressions. Capsular valves are entire-margined, oblong-ovate (Figs. 30, 31, 33), wide or narrow ovate (Figs. 32, 34–38), about 3.4–5 cm long and 2.5–4 cm wide. The base is rounded, slightly truncate, cordate or concave-convex

(Figs. 33–37). The apex is rounded, acute, slightly emarginate, or mucronate, representing a partial style. A longitudinal, middle carpellary suture is prominent, with a septum in the proximal position of valves (Figs. 32, 34, 36). The septum extends approximately 1/3 or slightly more than 1/3 of the valve length from the base, about 5 mm high. There are two seeds attached at a single level near the upper part of the placental suture on the septum (Figs. 30, 31, 33). The seeds are globose, ca. 5–7 mm in diameter. The seed surface appears to have some irregular furrows (Fig. 30). Lateral veins are straight or sinuous and diverge at about 30°–90° (or even 110° at the base) and arrive at the margin. The veins are branched and connected into polygonal areoles that are irregular and transversely elongated in outline (Figs. 36, 38). The texture of valves is membranous.

**Comments**—Some of the specimens presented here from Central Europe were previously described as *Koelreuteria reticulata* (Ettingsh.) W. N. Edwards (Rásky, 1958; Bůžek, 1971; Teodoridis, 2002; Kvaček et al., 2004b), but its basionym *Dalbergia reticulata* Ettingsh. (Ettingshausen, 1854) was based on two heterogeneous specimens. One was actually a legume fruit fossil (Kováts, 1856; Bůžek, 1971), and the other was a capsular valve fossil, both of which are missing. Also, *Dalbergia reticulata* Ettingsh. is a senior homonym of an extant legume species name *Dalbergia reticulata* Merr. (Merrill, 1915), so *D. reticulata* Merr., unless conserved, is illegitimate (McNeill et al., 2012; Wang, 2013). Considering similar characters (in illustrations and specimens) and geographic distribution, we here treat the name *K. reticulata*, previously used for those isolated capsular valves, as a synonym of *K. macroptera* (Kováts) W. N. Edwards. Moreover, we exclude one specimen formerly placed under the name *Phyllites* sp. (Kasumova, 1966: pl. 12, fig. 5) from the middle Oligocene of Indžačaj River, Azarbaijdžan, which was assigned to *Koelreuteria* by Bůžek (1971) because of its larger size (ca. 8–10 cm long) and brochidodromous venation, which are inconsistent with *Koelreuteria*. Overall, *K. macroptera* was distributed in the late Oligocene to early Pliocene of Germany, Hungary, the Czech Republic, Romania, and Ukraine (Fig. 48).

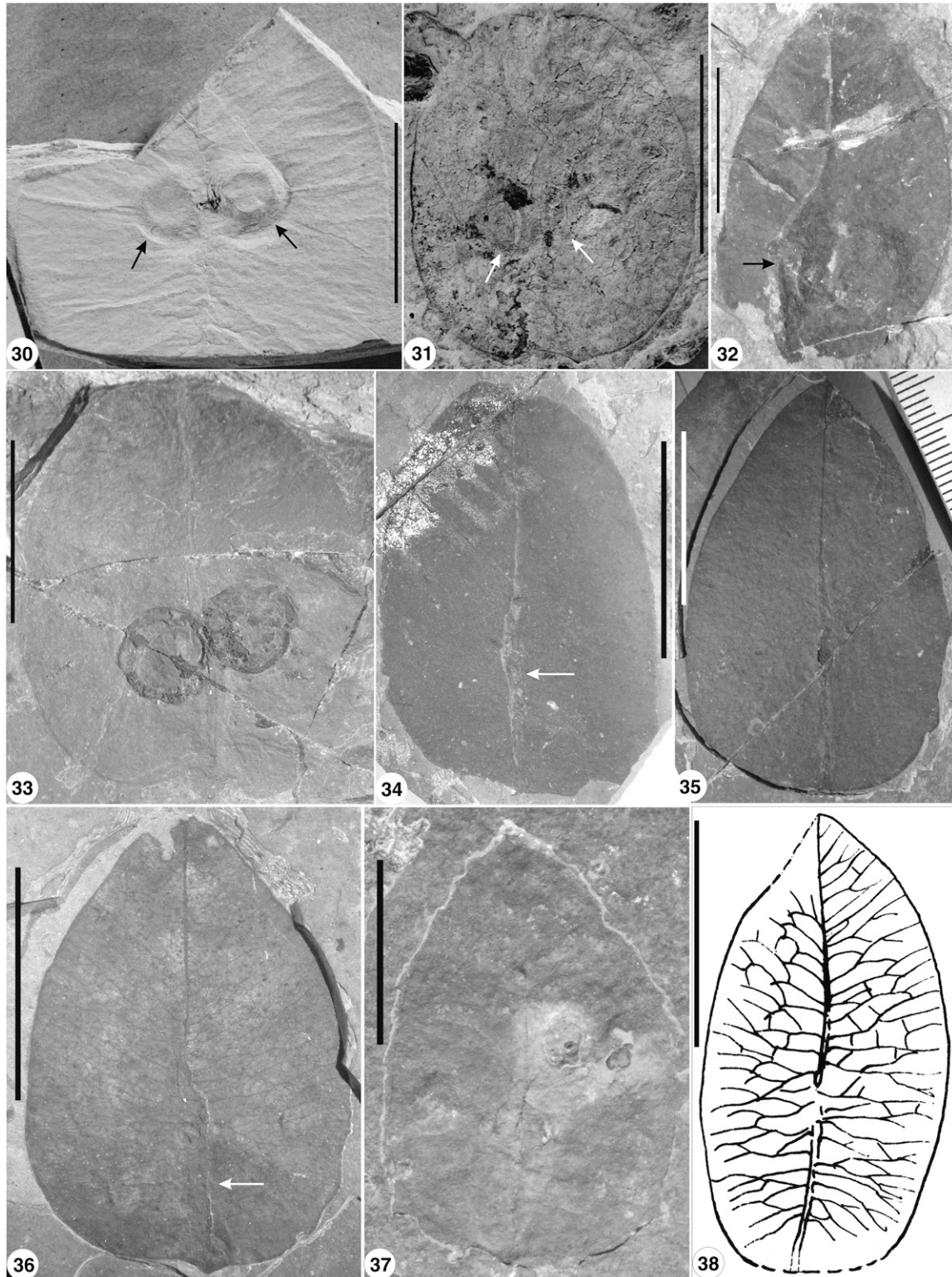
**Species**—*Koelreuteria miointegrifoliola* Hu et R. W. Chaney emend. (Figs. 39–47).

*Koelreuteria miointegrifoliola* Hu et R. W. Chaney, Hu and Chaney (1938), pro parte, 64, pl. 38, fig. 1 (non pl. 38, fig. 3 nec pl. 39, fig. 3) (the epithet ‘*miointegrifolia*’ corrected by Hu and Chaney, who suggested this fossil species similar to a living species *K. integrifoliola* Merr., 1922); Huzioka and Takahashi (1973), 141, pl. 4, figs. 2, 3; Onoe (1974), 52, pl. 12, fig. 2 (non fig. 4); Hayashi (1975), 26, pl. 21, fig. 3, pl. 22, figs. 2, 4 (non pl. 22, figs. 6, 8); WGCP (1978), 131, pl. 116, figs. 5, 6 (non pl. 117, fig. 2); Ozaki (1980), 24, pl. 4, fig. 1 (non pl. 4, figs. 2, 7); Tao et al. (1999), 46, 76, non pl. 35, fig. 1 nec pl. 43, fig. 3.

**Synonym**—*Koelreuteria* sp. in Sze (1954), 80, pl. 68, fig. 5; *K. macrocarpa* J. R. Tao in Tao et al. (1999), 46, 75, pl. 43, fig. 2.

**Lectotype**—PB No. 58 (H) (Figs. 45, 46) [designated here; Shanwang, Shandong Province, the Miocene Shanwang Formation of eastern China; first illustrated by Hu and Chaney (1938: pl. 38, fig. 1)].

**Other specimens examined**—UF 15839-56774, 15839-56774' (part and counterpart specimens, Figs. 39–42), and 15839-56775 (Fig. 44) (Shanwang, China); PE 50384 (Fig. 43),



Figs. 30–38. *Koelreuteria macroptera* (Kováts) W. N. Edwards from the Oligocene–Miocene of Hungary and Germany. **30.** Incomplete capsule valve from the Miocene of Gomboska at Tállya, Hungary. Arrows indicate two seeds attached on either side of the suture at a single level. Holotype: BP 58.2.1. **31.** Ovate capsular valve from the Miocene of Abaújszántó, Hungary. Arrows indicate two seeds, with some irregular furrows on the surface. BP 60.815.1. **32.** Ovate capsular valve from the Miocene of Randecker Maar, Germany. Arrow refers to a proximal septum. SMNS P1224/509. **33.** Wide ovate capsular valve from the Miocene of Randecker Maar, showing two globose seeds. SMNS P1224/506. **34–37.** Ovate capsular valves from the Miocene of Randecker Maar, showing a proximal septum (arrows). SMNS P1224/511, P1224/515, P1224/508 and NMA 92-17/413. **38.** Line drawing of ovate capsular valve from the late Oligocene of Rott, Germany (based on Weyland, 1937: pl. 11, fig. 2). Bars = 2 cm.

50567, 52440, 50455 (Fig. 47), 20111117, 20111118A, B, and 20080916 (Shanwang, China).

**Emended description**—Fossils are preserved as individual capsular valve impressions. Capsular valves are entire-margined, wide ovate, oblong, elliptic or suborbicular (Figs. 39, 40, 43–47), 3.2–5.2 cm long and 3.0–4.2 cm wide. The base is rounded, slightly truncate or cordate, with a short pedicel (Figs. 39, 43), about 2–3 mm long. The apex is rounded, slightly emarginated, or mucronate, representing a partial style. A longitudinal, middle carpellary suture is prominent and appears to be thicker in the lower part than in the upper part. The septum is proximal and incomplete above the placental suture attached seeds, extending from the base to approximately half of the valve length, about 4 mm high (Figs. 39–42). Two seeds are suboppositely attached at a single level on both sides of approximately the middle part of the longitudinal central placental suture in each valve. Seeds are grossly globose, ca. 4–9 mm in diameter, with a short funiculus (Fig. 41), ca. 2 mm long. The seed surface appears to have some irregular furrows (Figs. 41, 44). The placental suture is curved slightly and diverges into numerous, lateral sinuous veins at 30°–150° through the carpellary suture, arriving at the margin (Figs. 42–47). The lateral veins are branched and connected into polygonal areoles, which are irregular and transversely elongated in outline. Areoles are moderately developed, with branched freely ending veinlets (Fig. 42). The texture of valves is membranous.

**Comments**—*Koelreuteria miointegrioliola* Hu et R. W. Chaney, as a sapindaceous fossil, was originally based on three specimens, which Hu and Chaney (1938) designated as “co-types” (i.e., syntypes) (PB No. 58 [H] and No. 56 [H], referring to a capsular valve and a leaflet, respectively) and the “paratype” (PB No. 57 [H], referring to a leaflet), from the Miocene Shanwang Formation of Shandong Province, eastern China. The two leaflets were subsequently reidentified as the species of *Juglans* L. in the Juglandaceae A. Rich. ex Kunth (Brown, 1946; Sze, 1951; Rufflé, 1963; WGCP, 1978). Although additional leaflets from Shanwang and some Japanese localities (Table 2) continued to be described as *K. miointegrioliola* (Onoe, 1974; Hayashi, 1975; WGCP, 1978; Ozaki, 1980, 1991) or *K. macrocarpa* J. R. Tao (Tao et al., 1999), there is no evidence of an organic connection between leaflets and capsular valves, nor is there a detailed leaf architectural analysis to reliably assign the leaflets to *Koelreuteria*. Thus, we here use *K. miointegrioliola* only for the sapindaceous capsular valves, which were distributed in the Miocene of eastern China and Japan (Fig. 48).

## DISCUSSION

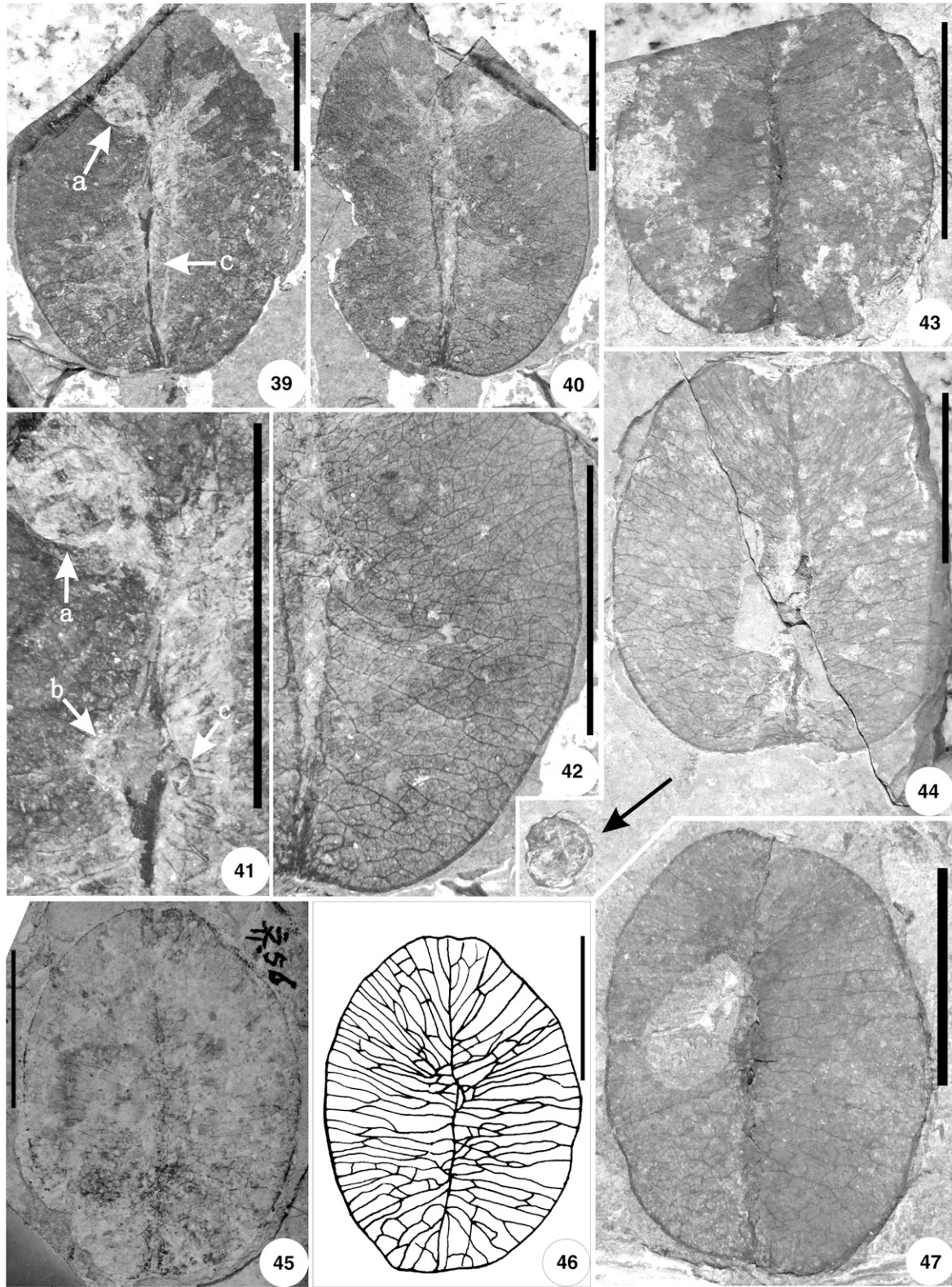
**Hypotheses on the origins of the Sapindaceae**—The Sapindaceae is a pantropical angiosperm family of trees, shrubs, lianas, and rarely herbaceous climbers comprising 142 genera and ca. 1900 species (Buerki et al., 2009, 2010; Acevedo-Rodríguez et al., 2011). This family, as currently defined by molecular systematics, encompasses both Aceraceae Juss. and Hippocastanaceae Rich. and is widely distributed in tropical and subtropical regions and is especially well represented in tropical Southeast Asia, but a few genera (e.g., *Acer* L., *Dodonaea*, and *Koelreuteria*) have species adapted to temperate regions (Xia and Luo, 1995; Harrington et al., 2005; Xia and Gadek, 2007; Buerki et al., 2009, 2010).

Recent biogeographic analysis inferred that Sapindaceae originated in Eurasia around the Early Cretaceous (Buerki et al., 2011). However, paleopalynological evidence seems to support that Sapindaceae made their debut in the Late Cretaceous (Coniacian–Santonian) of the paleotropics (i.e., an African–Indian origin, see Muller, 1981; Taylor, 1990; Song et al., 1999, 2004). The earliest fossils bearing finely wrinkled or longitudinally striated exteine ornamentations similar to the simply structured tricolporate pollen (i.e., type-A pollen, sensu Muller and Leenhouts 1976) (Fig. 8) of extant *Koelreuteria* have been reported from the Late Cretaceous to the Eocene of southern Laurasian margin (Tibet) (Song and Li, 1982; Li et al., 2008), South China (Song et al., 1999, 2004) (Table 2; Fig. 48). Therefore, microfossil evidence seems to support a southern Laurasian origin for *Koelreuteria*.

**Early differentiation of sapindaceous wood with ring porosity**—The wood anatomical literature indicates that the earliest fossil record of Sapindaceae as *Sapindoxylon* Kräusel is reported from the Late Cretaceous Deccan Intertrappean Beds, India (Dayal, 1965; Chitale and Shallom, 1969; Friis et al., 2011). *Sapindoxylon* lacks growth rings and has been reported from numerous tropical localities in the Tertiary of Africa, India, and Southeast Asia (Kräusel, 1922; Bande and Prakash, 1986; Dupéron-Laudoueneix and Dupéron, 1995) (Fig. 48) and in the Eocene of southern England (Wilkinson, 1988) and western United States (Wheeler and Manchester, 2002). By the latest Eocene, ring porous woods of *Koelreuteria* have been described from the Florissant Formation of Colorado, western United States (Wheeler, 2001). Ring porosity in woody angiosperms is a derived character in response to the climatic conditions characteristic of the North Temperate Zone (Gilbert, 1940) and may be considered a reliable ecological marker after the early Tertiary (Wheeler and Baas, 1993; Baas et al., 2003). Hence, anatomical evidence supports the suggestion that the sapindaceous plants bearing *Koelreuteria*-type wood with ring porosity appear to have begun to differentiate in the northern hemisphere since the latest Eocene.

**Ecological implications for the fruits and seeds of Koelreuteria**—Many sapindaceous genera bear schizocarpous, winged fruits such as *Acer* and *Dipteronia* Oliv., which are ecological adaptations for wind dispersal in the North Temperate Zone (Manchester and O’Leary, 2010), and are thus functionally similar to the bladder-like capsules of *Koelreuteria*. *Acer* and *Dipteronia* have been reported from North America since the Paleocene (Manchester, 1999; McClain and Manchester, 2001), reflecting ecologically adaptive radiations and deep phylogenetic splits between the temperate (e.g., mixed mesophytic forest) and tropical (e.g., evergreen broad-leaved forest) biomes or lineages that occupy temperate or tropical regions. In contrast with the more ovoid seeds found in some of the other sapindaceous genera (Table 3), the perfectly globose seeds of *Koelreuteria* are blown from the high trees and still contained in their light, membranous, bladder-like capsules, so they are dispersed by wind or sometimes by water. Furthermore, such small, shiny, nutrition-rich seeds of *Koelreuteria* have attracted animal dispersants including birds (Lin et al., 2011). Hence, birds may also play a key role in long-distance seed dispersal of *Koelreuteria*.

**Evolutionary and biogeographic implications for the fruits of Koelreuteria**—The reliable fossil distribution of *Koelreuteria*



Figs. 39–47. *Koelreuteria miointegrifoliola* Hu et R. W. Chaney from the Miocene of Shanwang, Shandong Province, eastern China. **39, 40.** An oblong capsular valve (part and counterpart), showing a detached seed (a), a placental suture (b) and a carpillary suture (c). UF 15839-56774 and 15839-56774'. **41, 42.** Partial enlargements of specimens in Figs. 39 and 40, indicating a detached globose seed, with some irregular ridges on the surface (a), two short funiculi (b and c). **43.** A suborbicular capsular valve. PE 50384. **44.** Wide ovate capsular valve. Arrow indicates a detached seed with some irregular ridges or furrows on the surface. UF 15839-56775. **45–46.** Elliptic capsular valve and its line drawing. Lectotype: PB No. 58 (H). **47.** Elliptic capsular valve. PE 50455. Bars = 2 cm.

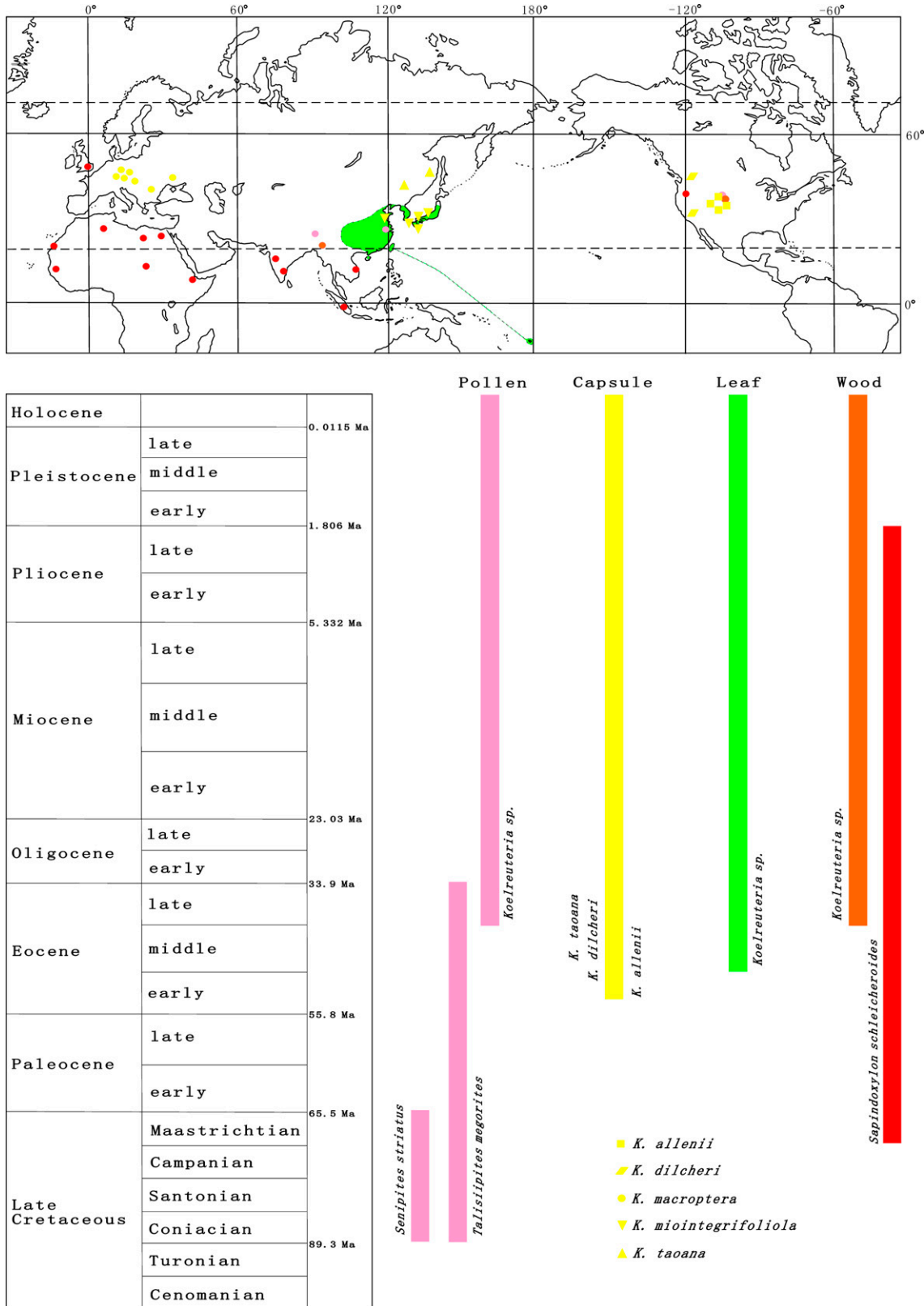


Fig. 48. Map and stratigraphic chart showing the diversity and distribution of *Koelreuteria* Laxm., with references to Tables 1 and 2. Red dots refer to *Sapindoxylon*-type wood fossil localities (Kräusel, 1922; Dayal, 1965; Chitale and Shallom, 1969; Bande and Prakash, 1986; Wilkinson, 1988; Poole and Wilkinson, 1992; Dupéron-Laudoueneix and Dupéron, 1995; Wheeler and Manchester, 2002). Orange dots refer to *Koelreuteria*-type wood fossil localities (Wheeler, 2001; Cheng et al., 2012). Pink dots refer to *Koelreuteria*-like pollen fossil localities (Song and Li, 1982; Song et al., 1999; Leopold and Clay-Poole, 2001; Li et al., 2008).

capsules shows three areas of concentration: eastern Asia, Central Europe, and western North America (Fig. 48). The oldest known specimen of a capsular valve of *Koelreuteria* is *K. allenii* from the early Eocene Fossil Butte Member of the Green River Formation, Wyoming, which places a minimum age (ca. 52 Ma) for the divergence of *Koelreuteria* from presumably tropical genera that occupy more basal positions in molecular phylogenetic trees of Sapindaceae. *Koelreuteria allenii* persisted from the middle Eocene Parachute Creek Member of Green River Formation, Utah and Colorado to the late Eocene (ca. 34 Ma) Florissant Formation, Colorado in the Rocky Mountain region and the John Day Formation of Teater Road, Oregon.

It is remarkable that *K. allenii*, *K. taoana*, and *K. dilcheri* have occurred in Eocene mid-latitudes (ca. 40°–45°) of far eastern Russia, northeastern China, and western United States. Except for valve size, both *K. taoana* and *K. dilcheri* are typically elliptic and have occurred around the North Pacific Rim areas—an indication of Eocene floral links between eastern Asia and western North America via the Bering land bridge (Tiffney and Manchester, 2001; Milne and Abbott, 2002) and/or Aleutian land bridge (Lindroth, 1963). *Koelreuteria*, as well as the Aceraceae, Betulaceae Gray, Menispermaceae Juss., Vitaceae Juss., and Pinaceae Lindl., which are common in western North American Eocene localities, are noticeably absent from the coeval localities in southeastern North America. Such floristic differences may have resulted from the dispersal barrier represented by the Cannonball Epeiric Sea, that traversed some parts of the Midcontinent in the Paleocene (Leopold et al., 2008) and environmental heterogeneity (Manchester, 1999). Moreover, the Eocene biotas of East Asia show closer relationships to those of North America than to Europe (Budantsev, 1992; Manchester et al., 2005). On the basis of the differences in capsular valve morphology, either there may be an exchange and rapid diversification into different types or there seems to have been no exchange between *Koelreuteria* species in western North America and Europe via the North Atlantic land bridge (Tiffney and Manchester, 2001; Milne and Abbott, 2002). *Koelreuteria* may have become regionally extinct in western North America after the Eocene or the early Oligocene. The fossil record of *Koelreuteria* in the late Oligocene of Germany (Weyland, 1937; Kirchheimer, 1957; Winterscheid, 2006) (Fig. 38) and the Czech Republic (Teodoridis, 2002) implies that populations in North America before extinctions invaded Europe via the North Atlantic land bridge, while a direct floristic exchange between the northern central regions of Asia and Europe may have been impeded by the West Siberian Sea and Turgai Strait (Akhmetiev and Beniamovski, 2009) during the early Paleogene. Alternatively, populations of *Koelreuteria* in northeastern Asia migrated westward into Europe with the closure of the Turgai Strait during the Oligocene. By the Miocene, *Koelreuteria* had been restricted gradually to the middle latitudes of Eurasia.

Among the four extant species of *Koelreuteria* now restricted to eastern Asia and Fiji, fruit characters and pollen morphology as well as karyotype analyses (Urdampilleta et al., 2005; Zhang and Wang, 2009) suggest that *K. bipinnata* and *K. henryi* are more closely related to each other than either is to *K. paniculata*. The capsular valve fossils (*K. allenii*, *K. taoana*, *K. dilcheri*, and *K. miointegrioliola*) from the Eocene to Miocene of eastern Asia and western North America appear to belong to the *K. bipinnata*-type, which usually bears a septum extending 1/3 to half of the valve length from the base. In contrast, the

capsular valve fossils (*K. macroptera*) from the late Oligocene to early Pliocene of Europe are the *K. paniculata*-type, bearing a proximal septum only about 1/3 of the valve length. This distribution suggests that a derivative of *K. macroptera* may have migrated eastward into eastern Asia in the Miocene, evolving into the extant *K. paniculata*. Extant *K. bipinnata* and *K. henryi* may stem from a vicariance event involving the separation of Taiwan from eastern Asian continent after the Miocene. Overall, the fruit fossil record of *Koelreuteria* indicates that this genus may have had a biogeographic origin and rapid spread in the northern hemisphere and around the North Pacific Rim areas during the Eocene. With the regional extirpations after the Eocene in North America and the Pliocene in Europe, *Koelreuteria* became restricted gradually to eastern Asia. Therefore, eastern Asia is a living museum for *Koelreuteria*.

On the basis of *Koelreuteria* shared by eastern Asia and Fiji, Wu et al. (2007) suggested that Fiji was linked with Laurasia. Proximal to the Australian–Pacific Plate boundary, the Fiji Platform has been active since at least the late Eocene, during which the oldest island-arc volcanic rocks were formed in Fiji (Stratford and Rodda, 2000; Neall and Trewick, 2008) and the earliest populations of *Koelreuteria* were developed around the North Pacific Rim areas. So far, neither fossil nor extant wild populations of *Koelreuteria* have been discovered on the tropical islands between eastern Asia and the Fiji Islands (Smith, 1978, 1985; Bande and Prakash, 1986). Hence, the present distribution of *K. elegans* in South Pacific Oceania might have been derived from an ancient chance dissemination (“waif introduction” from the west) as some authors have hypothesized (Smith, 1978; Heads, 2006) or resulted from a historical long-distance dispersal by migrating birds (e.g., Carlquist, 1967; Proctor, 1968; Higgins et al., 2003) between eastern Asia and the Fiji Islands, which appears to have failed to succeed in dispersing to intervening land areas.

#### LITERATURE CITED

- ABDULIA, P. 1973. Sapindaceae. Flora of West Pakistan, vol. 39, 1–10. University of Karachi, Karachi, Pakistan.
- ABLAEV, A. G. 1978. Geology and floral history in coastal region of the Sea of Japan (Late Cretaceous and Tertiary age), 1–192. Nauka, Moscow, Russia.
- ABLAEV, A. G. 2000. Paleogene biostratigraphy of the coastal region in South Primorye, 1–117. Dalnauka, Vladivostok, Russia.
- ABLAEV, A. G., S. M. TASHCHI, AND I. V. VASSILIEV. 1994. Miocene Khanka Depression of the West Primorye, 1–168. Dalnauka, Vladivostok, Russia.
- ACEVEDO-RODRÍGUEZ, P., P. C. VAN WELZEN, F. ADEMA, AND R. W. J. M. VAN DER HAM. 2011. Sapindaceae. In K. Kubitzki [ed.], The families and genera of vascular plants, vol. 10, Flowering plants, Eudicots: Sapindales, Cucurbitales, Myrtaceae, 357–407. Springer, Berlin, Germany.
- AKHMETIEV, M. A., AND V. N. BENIAMOVSKI. 2009. Paleogene floral assemblages around epicontinental seas and straits in Northern Central Eurasia: Proxies for climatic and paleogeographic evolution. *Geologica Acta* 7: 297–309.
- ANDREÁNSZKY, G. 1959. Die Flora der Sarmatischen Stufe in Ungarn, 1–360. Akadémiai Kiadó, Budapest, Hungary.
- ARNOLD, C. A. 1952. Tertiary plants from North America 2. Fossil capsule valves of *Koelreuteria* from the John Day Series of Oregon. *Palaeobotanist* 1: 74–78.
- BAAS, P., S. JANSEN, E. SMETS, AND E. A. WHEELER. 2003. Ecological adaptations and deep phylogenetic splits—Evidence and questions from the secondary xylem. In T. F. Stuessy, V. Mayer, and E. Hörandl [eds.], Deep morphology: Towards a renaissance of morphology in

- plant systematics. *Regnum Vegetabile* vol. 141, 221–239. A.R.G. Gantner, Ruggell, Liechtenstein.
- BANDE, M. B., AND U. PRAKASH. 1986. The Tertiary flora of Southeast Asia with remarks on its palaeoenvironment and phytogeography of the Indo-Malayan region. *Review of Palaeobotany and Palynology* 49: 203–233.
- BECKER, H. F. 1961. Oligocene plants from the Upper Ruby River Basin, southwestern Montana. *Memoir of the Geological Society of America* 82: 1–127.
- BECKER, H. F. 1969. Fossil plants of the Tertiary Beaverhead Basins in southwestern Montana. *Palaeontographica Abteilung B* 127: 1–142.
- BECKER, H. F. 1972. The Metzler Ranch flora of the Upper Ruby River Basin, southwestern Montana. *Palaeontographica Abteilung B* 141: 1–61.
- BELL, W. A. 1957. Flora of the Upper Cretaceous Nanaimo Group of Vancouver Island, British Columbia. *Memoir of the Geological Survey of Canada* 293: 1–84.
- BRABENEC, B. 1904. O novém nalezišti třetihorních rostlin ve spodním pásmu vrstev žateckých. *Rozpravy České Akademie Věd a Umění, Třída 2 (Mathematicko-Přírodnická)* 13: 1–25.
- BROWN, R. W. 1934. The recognizable species of the Green River flora. *U.S. Geological Survey Professional Paper* 185-C: 45–77.
- BROWN, R. W. 1943. Some prehistoric trees of the United States. *Journal of Forestry* 41: 861–868.
- BROWN, R. W. 1946. Alterations in some fossil and living floras. *Journal of the Washington Academy of Sciences* 36: 344–355.
- BROWN, R. W. 1956. New items in Cretaceous and Tertiary floras of the western United States. *Journal of the Washington Academy of Sciences* 46: 104–108.
- BROWN, R. W. 1962. Paleocene flora of the Rocky Mountains and Great Plains. *U.S. Geological Survey Professional Paper* 375: 1–119.
- BRUMMITT, R. K., AND C. E. POWELL. 1992. Authors of plant names, 1–732. Royal Botanic Gardens, Kew, UK.
- BUDANTSEV, L. Y. 1992. Early stages of formation and dispersal of the temperate flora in the Boreal Region. *Botanical Review* 58: 1–48.
- BUDANTSEV, L. Y. 1997. Late Eocene flora of western Kamchatka. *Proceedings of Komarov Botanical Institute of the Russian Academy of Science* 19: 3–115.
- BUDANTSEV, L. Y. 2006. Early Paleogene flora of western Kamchatka. *Proceedings of the Komarov Botanical Institute of the Russian Academy of Sciences* 22: 1–160.
- BUDANTSEV, L. Y., AND L. B. GOLOVNEVA. 2009. Fossil flora of Arctic 2. Paleogene flora of Spitsbergen. Russian Academy of Sciences, Komarov Botanical Institute, 1–400. Marafon, St. Petersburg, Russia.
- BUERKI, S., F. FOREST, P. ACEVEDO-RODRÍGUEZ, M. W. CALLMANDER, J. A. A. NYLANDER, M. HARRINGTON, I. SANMARTÍN, P. KÜPFER, AND N. ALVAREZ. 2009. Plastid and nuclear DNA markers reveal intricate relationships at subfamilial and tribal levels in the soapberry family (Sapindaceae). *Molecular Phylogenetics and Evolution* 51: 238–258.
- BUERKI, S., F. FOREST, N. ALVAREZ, J. A. A. NYLANDER, N. ARRIGO, AND I. SANMARTÍN. 2011. An evaluation of new parsimony-based versus parametric inference methods in biogeography: A case study using the globally distributed plant family Sapindaceae. *Journal of Biogeography* 38: 531–550.
- BUERKI, S., P. P. LOWRY II, N. ALVAREZ, S. G. RAZAFIMANDIMBISON, P. KÜPFER, AND M. W. CALLMANDER. 2010. Phylogeny and circumscription of Sapindaceae revisited: Molecular sequence data, morphology and biogeography support recognition of a new family, Xanthoeraceae. *Plant Ecology and Evolution* 143: 148–159.
- BUIJSEN, J. R. M., P. C. VAN WELZEN, AND R. W. J. M. VAN DER HAM. 2003. A phylogenetic analysis of *Harpullia* (Sapindaceae) with notes on historical biogeography. *Systematic Botany* 28: 106–117.
- BŮŽEK, Č. 1971. Tertiary flora from the northern part of the Pětipsy area (North Bohemian Basin). *Rozpravy Ústředního Ústavu Geologického* 36: 1–118.
- BŮŽEK, Č., Z. KVAČEK, AND S. R. MANCHESTER. 1989. Sapindaceous affinities of the *Ptelea carpum* fruits from the Tertiary of Eurasia and North America. *Botanical Gazette* 150: 477–489.
- CALL, V. B., AND D. L. DILCHER. 1995. Fossil *Ptelea* samaras (Rutaceae) in North America. *American Journal of Botany* 82: 1069–1073.
- CAO, J. X., AND H. T. CUI. 1989. Research of Pliocene flora and palaeoenvironment of Yushe Basin on Shanxi Plateau, China. *Scientia Geologica Sinica* 4: 369–375.
- CAO, L. M., AND N. H. XIA. 2008. Structural characters of leaf epidermis and their systematic significance in Sapindaceae from China. *Acta Botanica Yunnanica* 30: 405–421.
- CAPURON, R. 1969. Revision des Sapindacees de Madagascar et des Comores. *Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série, Série B Botanique* 19: 7–189.
- CARLQUIST, S. 1967. The biota of long-distance dispersal. 5. Plant dispersal to Pacific islands. *Bulletin of the Torrey Botanical Club* 94: 129–162.
- CAVALLO, O., AND E. MARTINETTO. 1996. Flore Plioceniche del bacino del Tanaro. *Alba Pompeia* 17: 5–31.
- CHEN, C. H. 1993. Sapindaceae. In T. C. Huang [ed.], *Flora of Taiwan*, 2nd ed., vol. 3, 599–608. Editorial Committee of the Flora of Taiwan, Second Edition, Taipei, China.
- CHENG, Y. M., Y. F. YIN, R. C. MEHROTRA, AND C. S. LI. 2012. A new fossil wood of *Koelreuteria* (Sapindaceae) from the Pliocene of China and remarks on the phytogeographic history of *Koelreuteria*. *International Association of Wood Anatomists Journal* 33: 301–307.
- CHITALEY, S. D., AND L. J. SHALLOM. 1969. *Sapindoxylon chhindwarensis* sp. nov., a new fossil dicot wood from the Deccan Intertrappean beds of Madhya Pradesh. *Journal of the Indian Botanical Society* 48: 38–43.
- COCKERELL, T. D. A. 1913. The fauna of the Florissant (Colorado) shales. *American Journal of Science, series 4* 36: 498–500.
- COLANI, M. 1920. Études sur les flores tertiaires de quelques gisements de lignite de l'Indochina et du Yunnan. *Bulletin du Service Géologique de l'Indochine* 8: 1–526.
- COLLINSON, M. E., AND C. J. CLEAL. 2001. Early and early-middle Eocene (Ypresian-Lutetian) palaeobotany of Great Britain. In C. J. Cleal, B. A. Thomas, D. J. Batten, and M. E. Collinson [eds.], *Mesozoic and Tertiary palaeobotany of Great Britain*. Geological Conservation Review Series, No. 22, 185–226. Joint Nature Conservation Committee, Peterborough, UK.
- CORNER, E. J. H. 1976. The seeds of dicotyledons, vol. 1, 1–311. Cambridge University Press, Cambridge, UK.
- CSAKI, C., AND M. URLICHS. 1985. Types and originals in the Staatliches Museum für Naturkunde Stuttgart—Palaeobotany. *Stuttgarter Beiträge zur Naturkunde. Serie B, Geologie und Palaontologie* 114: 1–52.
- DAYAL, R. 1965. *Sapindoxylon schleicheroides* sp. nov., a fossil dicotyledonous wood from the Deccan Intertrappean beds of Madhya Pradesh. *Palaeobotanist* 13: 163–167.
- DENG, T. 2006. Chinese Neogene mammal biochronology. *Vertebrata Palasiatica* 44: 143–163.
- DEVORE, M. L., AND K. PIGG. 2010. Floristic composition and comparison of middle Eocene to late Eocene and Oligocene floras in North America. *Bulletin of Geosciences* 85: 111–134.
- DILLHOFF, R. M., E. B. LEOPOLD, AND S. R. MANCHESTER. 2005. The McAbee flora of British Columbia and its relation to the Early-Middle Eocene Okanagan Highlands flora of the Pacific Northwest. *Canadian Journal of Earth Sciences* 42: 151–166.
- DOSMANN, M. S., T. H. WHITLOW, AND H. D. KANG. 2006. The (un) natural and cultural history of Korean goldenrain tree. *Arnoldia* 64: 16–30.
- DOYLE, J. A. 2007. Systematic value and evolution of leaf architecture across the angiosperms in light of molecular phylogenetic analyses. *Courier Forschungs-Institut Senckenberg* 258: 21–37.
- DÜMMER, R. A. 1912. New or noteworthy plants—*Koelreuteria henryi* Dümmer sp. nov. *Gardeners' Chronicle, 3rd series* 52: 148.
- DUPÉRON-LAUDOUENEIX, M., AND J. DUPÉRON. 1995. Inventory of Mesozoic and Cenozoic woods from Equatorial and North Equatorial Africa. *Review of Palaeobotany and Palynology* 84: 439–480.
- EDWARDS, S. W. 2004. Paleobotany of California. *The Four Seasons: Journal of the Regional Parks Botanic Garden* 12: 3–75.
- EDWARDS, W. N. 1927. The occurrence of *Koelreuteria* (Sapindaceae) in Tertiary rocks. *Annals and Magazine of Natural History, Series 9* 20: 109–112.
- EDWARDS, W. N., AND F. M. WONNACOTT. 1928. Sapindaceae. In W. Jongmans [ed.], *Fossilium catalogus 2, Plantae, pars 14*, 1–84. W. Junk, Berlin, Germany.
- ELLIS, B., D. C. DALY, L. J. HICKEY, K. R. JOHNSON, J. D. MITCHELL, P. WILF, AND S. L. WING. 2009. *Manual of leaf architecture*, 1–190. Cornell University Press, Ithaca, New York, USA.

- ENDŐ, S. 1942. On the fossil flora from the Shulan Coal-field, Kirin Province and the Fushun Coal-field, Fengtien Province. *Bulletin of the Central National Museum of Manchoukuo* 3: 33–43.
- ENDŐ, S. 1968. The flora from the Eocene Woodwardia Formation, Ishikari Coal field, Hokkaido, Japan. *Bulletin of the National Science Museum* 11: 411–449.
- ENGELHARDT, H. 1873. Die Tertiärflora von Göhren. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum* 36: 1–42.
- ETTINGSHAUSEN, C. 1854. Beiträge zur Kenntniss der fossilen Flora von Tokay. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 11: 779–816.
- ETTINGSHAUSEN, C. 1867. Die fossile Flora des Tertiärbeckens von Bilin I. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse* 26: 79–176.
- FERGUSON, D. K., M. PINGEN, R. ZETTER, AND C.-C. HUFMANN. 1998. Advances in our knowledge of the Miocene plant assemblage from Kreuzau, Germany. *Review of Palaeobotany and Palynology* 101: 147–177.
- FLORIN, R. 1919. Eine Übersicht der fossilen *Salvinia*-arten mit besonderer Berücksichtigung eines Fundes von *Salvinia Formosa* Heer im Tertiär Japans. *Bulletin of the Geological Institutions of the University of Uppsala* 16: 243–260.
- FRIIS, E. M., P. R. CRANE, AND K. R. PEDERSEN. 2011. Early flowers and angiosperm evolution, 1–585. Cambridge University Press, Cambridge, UK.
- FROHLICH, D., AND A. LAU. 2010. New plant records from O'ahu for 2008. *Bishop Museum Occasional Papers* 107: 3–18.
- FUJI, N., AND T. KITANAKA. 1988. Discovery of fossil plants from the Miocene series in the Nomi Hill, Ishikawa Prefecture. *Journal of the Geological Society of Japan* 94: 137–140.
- GE, H. R., AND D. Y. LI. 1999. Cenozoic coal-bearing basins and coal, forming regularity in West Yunnan, 1–104. Yunnan Science and Technology Press, Kunming, China.
- GILBERT, S. G. 1940. Evolutionary significance of ring porosity in woody angiosperms. *Botanical Gazette* 102: 105–120.
- GIVULESCU, R. 1961. Beiträge zur Kenntnis der Pannonischen Flora Rumäniens. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, Jahrgang* 2: 98–104.
- GIVULESCU, R. 1962. Die Fossile Flora von Valea Neagră Bezirk Crisana, Rumänien. *Palaeontographica Abteilung B* 110: 128–187.
- GIVULESCU, R. 1967. Einige Betrachtungen über Entwicklung und Aussagewert der Tertiärflora in Rumänien. *Abhandlungen des Zentralen Geologischen Instituts, Berlin* 10: 155–164.
- GIVULESCU, R. 1984. Die fossile Flora des Fundortes Chiuzbaia "H" (Kreis Maramureș, Rumänien). *Dări de Seamă ale sedințelor, Institutul de Geologie și Geofizică* 69: 69–93.
- GIVULESCU, R. 1990. Fossil flora of higher Miocene in Chiuzbaia (Maramureș county), 1–238. Editura Academiei Române, București, Romania.
- GRADSTEIN, F. M., J. G. OGG, A. G. SMITH, W. BLEEKER, AND L. J. LOURENS. 2004. A new geologic time scale, with special reference to Precambrian and Neogene. *Episodes* 27: 83–100.
- GREENWOOD, D. R., S. B. ARCHIBALD, R. W. MATHEWES, AND P. T. MOSS. 2005. Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: Climates and ecosystems across an Eocene landscape. *Canadian Journal of Earth Sciences* 42: 167–185.
- GREGOR, H.-J. 1978. Die miozänen Frucht- und Samen-Floren der Oberpfälzer Braunkohle 1. Funde aus den sandigen Zwischenmitteln. *Palaeontographica Abteilung B* 167: 8–103.
- GREGOR, H.-J. 1980. Die Miozänen Frucht- und Samen-Floren der Oberpfälzer Braunkohle 2. Funde aus den Kohlen und tonigen Zwischenmitteln. *Palaeontographica Abteilung B* 174: 7–94.
- GREGOR, H.-J. 1982. Die jungtertiären Floren Süddeutschlands. Paläokarologie, Phytostratigraphie, Paläoökologie, Paläoklimatologie, 1–278. Ferdinand Enke, Stuttgart, Germany.
- GREGOR, H.-J. 1986. On the flora of the Randecker Maar (Miocene, Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde, Serie B, Geologie und Paläontologie* 122: 1–29.
- GREGOR, H.-J., E. KNOBLOCH, M. SCHÖTZ, AND H. J. UNGER. 1992. Geisenhausen-eine neue Blattfundstelle aus der Oberen Süßwassermollasse Bayerns. *Documenta Naturae* 71: 13–26.
- GÜMBEL, F., AND D. H. MAI. 2006. Neue Pflanzenfunde aus dem Tertiär der Rhön—Die Miozäne Flora vom Lettengraben. *Beiträge zur Naturkunde in Ostthessen* 42: 3–46.
- GUO, S. X. 1990. A brief review on megafloora successions and climatic changes of the Cretaceous and early Tertiary in China. In E. Knobloch and Z. Kvaček [eds.], Proceedings of symposium "Palaeofloristic and palaeoclimatic changes in the Cretaceous and Tertiary", 23–38, 1989, Prague. Geological Survey Publisher, Prague, Czech Republic.
- GUO, S. X. 1992. The Cenozoic plants. In Bureau of Geology and Mineral Resources of Jilin Province [eds.], Paleontological atlas of Jilin, China, 563–580. Jilin Science and Technology Publishing House, Changchun, China.
- GUO, S. X. 2011. The late Miocene Bangmai flora from Lincang County of Yunnan, southwestern China. *Acta Palaeontologica Sinica* 50: 353–408.
- GUO, S. X., AND X. L. YANG. 1997. Age of the "Hunchun Formation" in Jilin, Northeast China. *Journal of Stratigraphy* 21: 307–311, 320.
- GUO, S. X., AND G. F. ZHANG. 2002. Oligocene Sanhe flora in Longjing County of Jilin, Northeast China. *Acta Palaeontologica Sinica* 41: 193–210.
- HABLY, L. 2006. Catalogue of the Hungarian Cenozoic leaf, fruit and seed floras from 1856 to 2005. *Studia Botanica Hungarica* 37: 41–129.
- HABLY, L., B. ERDEL, AND Z. KVAČEK. 2001. 19<sup>th</sup> Century's palaeobotanical types and originals of the Hungarian Natural History Museum, 1–235. Hungarian Natural History Museum, Budapest, Hungary.
- HANTKE, R. 1954. Die fossile Flora der obermiozänen Oehninger-Fundstelle Schrotzburg (Schienerberg, Süd-Baden). *Denkschriften der Schweizerischen Naturforschenden Gesellschaft* 80 (Mémoires 2): 31–118.
- HARRINGTON, M. G. 2008. Phylogeny and evolutionary history of Sapindaceae and *Dodonaea*, 1–185. Ph.D. dissertation, James Cook University, Townsville, Australia.
- HARRINGTON, M. G., K. J. EDWARDS, S. A. JOHNSON, M. W. CHASE, AND P. A. GADEK. 2005. Phylogenetic inference in Sapindaceae *sensu lato* using plastid *matK* and *rbcL* DNA sequences. *Systematic Botany* 30: 366–382.
- HAYASHI, T. 1975. Fossils from Chōjōbaru, Iki Island, Japan, 1–120. Shima-no-Kagaku Kenkyusho, Ishida-cho, Nagasaki, Japan.
- HAYATA, B. 1913. Icones plantarum formosanarum, nec non et contributiones ad floram formosanam, vol. 3, 1–222. Bureau of Productive Industry, Government of Formosa, Taihoku, Japan.
- HEADS, M. 2006. Seed plants of Fiji: An ecological analysis. *Biological Journal of the Linnean Society* 89: 407–431.
- HEER, O. 1857. Die Tertiäre Flora der Schweiz. *Flora Tertiaria Helvetiae* 3: 1–200. Verlag der lithographischen Anstalt von Wurster & Comp, Winterthur, Switzerland.
- HEER, O. 1876. Beiträge zur fossilen Flora Spitzbergens. *Kongl Svenska Vetenskaps-Akademiens Handlingar* 14: 1–141.
- HEER, O. 1878. Miocene Flora der Insel Sachalin. *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, Série VII* 25: 1–61.
- HICKEY, L. J., AND J. A. WOLFE. 1975. The bases of angiosperm phylogeny: Vegetative morphology. *Annals of the Missouri Botanical Garden* 62: 538–589.
- HIGGINS, S. J., R. NATHAN, AND M. L. CAIN. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* 84: 1945–1956.
- HOLLIICK, A. 1894. Fossil salvinias, including description of a new species. *Bulletin of the Torrey Botanical Club* 21: 253–257.
- HOLLIICK, A. 1923. The taxonomic and morphologic status of *Ophioglossum allenii* Lesquereux. *Bulletin of the Torrey Botanical Club* 50: 207–213.
- HOLLIICK, A. 1929. New species of fossil plants from the Tertiary shales near De Beque, Colorado. *Bulletin of the Torrey Botanical Club* 56: 93–96.
- HOLLIICK, A. 1936. The Tertiary flora of Alaska. *U.S. Geological Survey Professional Paper* 182: 1–185.
- HOSKING, J. R., B. J. CONN, AND B. J. LEPSCHI. 2003. Plant species first recognised as naturalised for New South Wales over the period 2000–2001. *Cunninghamia* 8: 175–187.
- HU, H. H., AND R. W. CHANEY. 1938. A Miocene flora from Shantung Province, China. Part 1. Introduction and systematic considerations. *Carnegie Institution of Washington Publication* 507: 1–82.



- HUZIOKA, K., AND E. TAKAHASHI. 1973. The Miocene flora of Shimonoseki, Southwest Honshu, Japan. *Bulletin of the National Science Museum* 16: 115–148.
- ILJINSKAJA, I. A. 1963. Sapindaceae A. L. De Jussieu, 1789. *Osnovy Paleontologii* 15: 565–566. Gosgeoltekhizda, Moscow, Russia.
- ISHIDA, S., I. FUJIYAMA, T. HAYASHI, Y. NOGUCHI, AND Y. TOMODA. 1970. Geology and paleontology of the Chojaburu Diatomite, Iki, Japan. *Memoirs of the National Science Museum* 3: 49–63.
- KAMOI, Y., I. KOBAYASHI, AND K. SUZUKI. 1978. The middle Miocene Ōsuda fossil flora in the northern part of Niigata Prefecture. *Journal of the Geological Society of Japan* 84: 15–21.
- KANEHIRA, R. 1936. Formosan trees indigenous to the island (revised), 1–754. Department of Forestry, Government Research Institute, Formosa, China.
- KASUMOVA, G. M. 1966. Flora Oligocenovykh Otloženij Severo-Vostočnykh Predgorij Malogo Kavkaza (Azarbadžan) I Jeje Stratigrafičeskoje, 1–59. Izdatel'stvo Akademii Nauk Azerbajdžanskoj SSR, Baku, Azerbaijan.
- KIRCHHEIMER, F. 1936. Beiträge zur Kenntnis der Tertiärflora, Früchte und Samen aus dem Deutschen Tertiär. *Palaeontographica Abteilung B* 82: 73–141.
- KIRCHHEIMER, F. 1943. Bemerkenswerte Frucht- und Samenreste, besonders aus den Braunkohlenschichten der Lausitz. *Botanisches Archiv* 44: 362–430.
- KIRCHHEIMER, F. 1957. Die Laubgewächse der Braunkohlenzeit, 1–783. Veb Wilhelm Knapp Verlag, Halle (Saale), Germany.
- KITANAKA, T., AND N. FUJI. 1988. Neogene Daijima-type "Tatsunokuchi Fossil Flora" in Kaga, Ishikawa Prefecture, Central Japan. *Bulletin of the Faculty of Education, Kanazawa University, Natural Science* 37: 97–117.
- KLAASSEN, R. K. W. M. 1999. Wood anatomy of Sapindaceae. *International Association of Wood Anatomists Journal* 2 (Supplement): 1–214.
- KOLAKOVSKY, A. A. 1973. Catalogue of the fossil plants of the Caucasus, 1–315. Metsniereba, Tbilisi, Georgian Republic.
- KOVAR-EDER, J., AND B. MELLER. 2001. Plant assemblages from the hanging wall sequence of the opencast mine Oberdorf N Voitsberg, Styria (Austria, Early Miocene, Otnangian). *Palaeontographica Abteilung B* 259: 65–112.
- KOVÁTS, J. 1856. Fossile flora von Tálya. *Arbeiten der Geologischen Gesellschaft für Ungarn* 1: 39–52.
- KRÄUSEL, R. 1922. Fossile Hölzer aus dem Tertiär von Südsumatra. *Verhandlungen der Geologie en Mijnbouw Genootschap voor Nederland en Kolonien. Geologie Serie* 5: 231–287.
- KRAUTER, M., AND G. SCHWEIGERT. 1991. Remarks on the sedimentation, flora and the paleoclimate of the Randecker Maar (Lower/Middle Miocene, Swabian Alb). *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* 1991: 505–514.
- KVAČEK, Z., M. BÖHME, Z. DVOŘÁK, M. KONZALOVÁ, K. MACH, J. PROKOP, AND M. RAJCHL. 2004a. Early Miocene freshwater and swamp eco-systems of the Most Basin (northern Bohemia) with particular reference to the Bílina Mine section. *Journal of the Czech Geological Society* 49: 1–40.
- KVAČEK, Z., Č. BUŽEK, AND S. R. MANCHESTER. 1991. Fossil fruits of *Pteleacarpum* Weyland—Tiliaceous, not Sapindaceous. *Botanical Gazette* 152: 522–523.
- KVAČEK, Z., Z. DVOŘÁK, K. MACH, AND J. SAKALA. 2004b. Třetihorní rostliny severočeské hnědouhelné pánve (Tertiary plants of the North-Bohemian brown-coal basin), 1–160. Severočeské doly and Granit, Chomutov and Praha, Czech Republic.
- KVAČEK, Z., S. R. MANCHESTER, AND M. A. AKHMETIEV. 2005. Review of the fossil history of *Craigia* (Malvaceae s. l.) in the Northern Hemisphere based on fruits and co-occurring foliage. In M. A. Akhmetiev and A. B. Herman [eds.], *Modern problems of palaeofloristics, palaeophytogeography and phytostatigraphy*. Transactions of the International Palaeobotanical Conference, vol. 1, 114–140, Moscow, Russia, 2005. GEOS, Moscow, Russia.
- KVAČEK, Z., S. B. MANUM, AND M. C. BOULTER. 1994. Angiosperms from the Palaeogene of Spitsbergen, including an unfinished work by A. G. Nathorst. *Palaeontographica Abteilung B* 232: 103–128.
- ŁAŃCUCKA-ŚRODONIOWA, M., AND E. ZASTAWIAK. 1997. The middle-Miocene flora of Wieliczka—Revision of Jan Zabłocki's collection. *Acta Palaeobotanica* 37: 17–49.
- LAXMANN, E. 1772. *Koelreuteria paniculata* novum plantarum genus. *Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae* 16: 561–564.
- LEENHOUTS, P. W. 1988. Notes on some genera of the Sapindaceae—Cupanieae. *Blumea* 33: 197–213.
- LEOPOLD, E. B., AND S. T. CLAY-POOLE. 2001. Florissant leaf and pollen floras of Colorado compared: Climatic implications. *Proceedings of Denver Museum Nature & Science, Series 4* 1 17–70.
- LEOPOLD, E. B., S. R. MANCHESTER, AND H. W. MEYER. 2008. Phytogeography of the late Eocene Florissant flora reconsidered. *Geological Society of America Special Paper* 435: 53–70.
- LESQUEREUX, L. 1873. Lignitic formation and fossil flora. In F. V. Hayden [ed.], *Sixth Annual Report of the United States Geological Survey of the Territories*, 317–427. Government Printing Office, Washington D.C., USA.
- LESQUEREUX, L. 1878a. Report of the fossil plants of the auriferous gravel deposits of the Sierra Nevada. *Memoirs of the Museum of Comparative Zoölogy at Harvard College* 6: 1–62.
- LESQUEREUX, L. 1878b. The Tertiary flora. *Report of the United States Geological Survey of the Territories* 7: 1–366.
- LESQUEREUX, L. 1883. The Cretaceous and Tertiary floras. *Report of the United States Geological Survey of the Territories* 8: 1–283.
- LI, B. Z., B. J. H. TER WELLE, AND R. K. W. M. KLAASSEN. 1995. Wood anatomy of trees and shrubs from China 7. Sapindaceae. *International Association of Wood Anatomists Journal* 16: 191–215.
- LI, H. L. 1963. Woody flora of Taiwan, 1–974. Livingston Publishing, Narberth, Pennsylvania, USA.
- LI, H. L. 1977. Sapindaceae. In H. L. Li, T. S. Liu, T. C. Huang, T. Koyama, and C. E. DeVol [eds.], *Flora of Taiwan*, 1st ed., vol. 3, 583–592. Epoch Publishing, Taipei, China.
- LI, H. L. 1996. Shade and ornamental trees: Their origin and history, 1–282. University of Pennsylvania Press, Philadelphia, Pennsylvania, USA.
- LI, H. M. 1981. The geological age of Shanwang flora. In *Palaeontological Society of China [ed.], Selected papers of the 12th Annual Meeting of the Palaeontological Society of China*, 158–162. Science Press, Beijing, China.
- LI, J. G., D. J. BATTEN, AND Y. Y. ZHANG. 2008. Late Cretaceous palynofloras from the southern Laurasian margin in the Xigaze Region, Xizang (Tibet). *Cretaceous Research* 29: 294–300.
- LIN, Y. C., P. J. LIN, H. H. WANG, AND I. F. SUN. 2011. Seed distribution of eleven tree species in a tropical forest in Taiwan. *Botanical Studies (Taipei, Taiwan)* 52: 327–336.
- LINDROTH, C. H. 1963. The Aleutian Islands as a route for dispersal across the North Pacific. In J. L. Gressitt [ed.], *Pacific Basin biogeography*, 121–131. Bishop Museum Press, Honolulu, Hawaii, USA.
- LIU, G. W., AND E. B. LEOPOLD. 1992. Paleocology of a Miocene flora from the Shanwang Formation, Shandong Province, northern East China. *Palynology* 16: 187–212.
- LUO, X. R., AND D. Z. CHEN. 1985. Sapindaceae Juss. *Flora Reipublicae Popularis Sinicae* vol. 47, 4–72. Science Press, Beijing, China.
- MACGINNIE, H. D. 1953. Fossil plants of the Florissant Beds of Colorado. *Carnegie Institution of Washington Publication* 599: 1–198.
- MACGINNIE, H. D. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. *University of California Publications in Geological Sciences* 83: 1–140.
- MAI, D. H., AND H. WALTHER. 1991. Die Oligozänen und untermiocänen Floren Nordwest-Sachsens und des Bitterfelder Raumes. *Abhandlungen des Staatlichen Museum für Mineralogie und Geologie zu Dresden* 38: 1–230.
- MANCHESTER, S. R. 1994. Fruits and seeds of the Middle Eocene Nut Beds flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58: 1–205.
- MANCHESTER, S. R. 1999. Biogeographical relationships of North American Tertiary floras. *Annals of the Missouri Botanical Garden* 86: 472–522.
- MANCHESTER, S. R., Z. D. CHEN, B. Y. GENG, AND J. R. TAO. 2005. Middle Eocene flora of Huadian, Jilin Province, northeastern China. *Acta Palaeobotanica* 45: 3–26.
- MANCHESTER, S. R., Z. D. CHEN, A. M. LU, AND K. UEMURA. 2009. Eastern Asian endemic seed plant genera and their palaeogeographic history throughout the Northern Hemisphere. *Journal of Systematics and Evolution* 47: 1–42.

- MANCHESTER, S. R., AND W. C. MCINTOSH. 2007. Late Eocene silicified fruits and seeds from the John Day Formation near Post, Oregon. *PaleoBios* 27: 7–17.
- MANCHESTER, S. R., AND E. O'LEARY. 2010. Phylogenetic distribution and identification of fin-winged fruits. *Botanical Review* 76: 1–82.
- MARTINETTO, E. 2001. The role of central Italy as a centre of refuge for thermophilous plants in the late Cenozoic. *Acta Palaeobotanica* 41: 299–319.
- MASSALONGO, A. B. 1852. Sapindacearum fossilium monographia, 1–22. Typis Ramanzinianis, Verona, Italy.
- MASSALONGO, A. B. 1858. Synopsis florae fossilis senogalliensis, 1–136. Apud A. Merlo, Verona, Italy.
- MATSUO, H. 1970. Palaeogene floras of northwestern Kyushu, part 2: The Sakito flora. *Annals of Science, College of Liberal Arts, Kanazawa University* 7: 13–62.
- MCCLAINE, A. M., AND S. R. MANCHESTER. 2001. *Dipteronia* (Sapindaceae) from the Tertiary of North America and implications for the phyto-geographic history of the Aceroidae. *American Journal of Botany* 88: 1316–1325.
- MCNEILL, J., F. R. BARRIE, W. R. BUCK, V. DEMOULIN, W. GREUTER, D. L. HAWKSWORTH, P. S. HERENDEEN, ET AL. 2012. International code of nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress, Melbourne, Australia, 2011. *Regnum Vegetabile* vol. 154, 1–208. Koeltz Scientific Books, Königstein, Germany.
- MERRILL, E. D. 1915. New or worthy Philippine plant, XI. *Philippine Journal of Science, Section C: Botany* 10: 1–84.
- MERRILL, E. D. 1922. Notes on the flora of southeastern China. *Philippine Journal of Science* 21: 491–514.
- MESCHINELLI, A., AND X. SQUINABOL. 1892. Flora Tertiaria italica, 1–575. Sumptibus Auctorum Typis Seminarii, Patavii, Italy.
- MEYER, F. G. 1976. A revision of the genus *Koelreuteria* (Sapindaceae). *Journal of the Arnold Arboretum* 57: 129–166.
- MEYER, F. G. 1977. *Sinoradlkofera*: A new genus of Sapindaceae. *Journal of the Arnold Arboretum* 58: 182–188.
- MEYER, H. W., AND D. M. SMITH. 2008. Paleontology of the Upper Eocene Florissant Formation, Colorado. *Geological Society of America Special Paper* 435: 1–177.
- MILNE, R. I., AND R. J. ABBOTT. 2002. The origin and evolution of Tertiary relict floras. *Advances in Botanical Research* 38: 281–314.
- MUELLNER, A. N., D. D. VASSILIADIS, AND S. S. RENNER. 2007. Placing Biebersteiniaceae, a herbaceous clade of Sapindales, in a temporal and geographic context. *Plant Systematics and Evolution* 266: 233–252.
- MULLER, J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review* 47: 1–142.
- MULLER, J., AND P. W. LEENHOUTS. 1976. A general survey of pollen types in Sapindaceae in relation to taxonomy. In I. K. Ferguson, and J. Muller [eds.], *The evolutionary significance of the exine*. Linnean Society Symposium Series 1, 407–445. Academic Press, London, UK.
- NEALL, V. E., AND S. A. TREWICK. 2008. The age and origin of the Pacific islands: A geological overview. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 363: 3293–3308.
- ONOE, T. 1974. A middle Miocene flora from Ogumi-machi, Yamagata Prefecture, Japan. *Report of the Geological Survey of Japan* 253: 1–64.
- OZAKI, K. 1980. Late Miocene Tatsumitoge flora of Tottori Prefecture, Southwest Honshu, Japan (3). *Science Reports of the Yokohama National University, Section 2* 27: 19–45.
- OZAKI, K. 1991. Late Miocene and Pliocene floras in Central Honshu, Japan. *Bulletin of Kanagawa Prefectural Museum Natural Science Special Issue*, 1–244. Kanagawa Prefectural Museum, Yokohama, Japan.
- PALIBIN, J. W. 1939. Materialy k tretichnoi flore Armenii. A volume dedicated to president of Academy of Sciences of the USSR Academician V. L. Komarov at the time of his 70<sup>th</sup> anniversary, 607–639. Academy of Sciences of the USSR, Leningrad & Moscow, Russia.
- PALMER, E., AND N. PITMAN. 1972. *Trees of southern Africa*, vol. 2, 705–1497. A. A. Balkema, Cape Town, South Africa.
- PAOLI, A. A. S., AND J. SARTI. 2008. Morphology and anatomy of the fruits and seeds in *Dodonea viscosa* (L.) Jacquin (Sapindaceae). *Revista Brasileira de Sementes* 30: 33–42.
- PAVLYUTKIN, B. I. 2005. The Mid-Miocene Khanka flora of the Primorye, 1–216. Dalnauka, Vladivostok, Russia.
- PAVLYUTKIN, B. I., AND T. I. PETRENKO. 2010. Stratigraphy of Palaeogene-Neogene sediments in Primorye, 1–164. Dalnauka, Vladivostok, Russia.
- POOLE, I., AND H. P. WILKINSON. 1992. Two sapindaceous woods from the London Clay (Eocene) of Southeast England. *Review of Palaeobotany and Palynology* 75: 65–75.
- PRASAD, G., A. LEJAL-NICOL, AND N. VAUDOIS-MIÉJA. 1986. A Tertiary age for upper Nubian Sandstone Formation, Central Sudan. *AAPG Bulletin* 70: 138–142.
- PRINCIPI, P. 1926. La flora Oligocenica di Chiavon e Salcedo. *Memorie Per Servire Alla Descrizione Della Carta Geologica D'Italia* 10: 1–130.
- PROCTOR, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. *Science* 160: 321–322.
- QIAN, F. 1991. Paleobotany. In F. Qian and G. X. Zhou [eds.], *Stratigraphy and paleontology of the Yuanmou Basin, Yunnan Province, China*, 107–116. Science Press, Beijing, China.
- RADLKOFER, L. 1931. Sapindaceae 1 (Bogen 1–20). In A. Engler [ed.], *Das Pflanzenreich*, vol. IV, 165, Heft 98a, 1–320. Verlag von Wilhelm Engelmann, Leipzig, Germany.
- RÁSKY, K. 1958. Die obermiozäne Flora von Tállya (Ober-Ungarn). *Paläontologische Zeitschrift* 32: 181–189.
- REID, E. M., AND M. E. J. CHANDLER. 1933. The London Clay flora, 1–561. British Museum (Natural History), London, UK.
- RONSE DE CRAENE, L. P., E. SMETS, AND D. CLINCKEMAILLIE. 2000. Floral ontogeny and anatomy in *Koelreuteria* with special emphasis on monosymmetry and septal cavities. *Plant Systematics and Evolution* 223: 91–107.
- RÜFFLE, L. 1963. Die Obermiozäne (Sarmatische) Flora vom Randecker Maar. *Paläontologische Abhandlungen* 1: 139–298.
- SANGIORGI, D. 1916. Flora fossile dell'imoiese. *Bollettino della Società Geologica Italiana* 35: 279–302.
- SASAKI, Y., AND H. OHASHI. 2007. Natural distribution and habit of *Koelreuteria paniculata* Laxm. (Sapindaceae) in Japan and its new form. *Journal of Japanese Botany* 82: 160–174.
- SCHIMPER, W., AND A. SCHENK. 1890. Palaeophytologie. In K. A. Zittel [ed.], *Handbuch der Palaeontologie* 2, 1–958. Druck und Verlag von R. Oldenbourg, München & Leipzig, Germany.
- SCHMIDT, C. 1976. Obermiozäne Flora von Derching bei Augsburg. *Bericht des Naturwissenschaftlichen Vereins für Schwaben* e. 80: 53–56.
- SCHMIDT, C. 1980. Ein Profil von pflanzenführenden Schichten der Sandgrube Derching. *Berichte des Naturwissenschaftlichen Vereins für Schwaben* e. 84: 13–15.
- SCHÖNLAND, S. 1913. On *Smelophyllum capense*, Radlk. *Records of the Albany Museum* 2: 459–461.
- SEEHUBER, U. 2009. Litho- und biostratigraphische Untersuchungen in der Oberen Süßwassermolasse in der Umgebung von Kirchheim in Schwaben. *Documenta Naturae* 175: 1–355.
- SHANG, P., J. H. JIN, D. J. SUN, AND J. MU. 2001. Early Miocene flora from Pingzhuang Basin of Inner Mongolia and its palaeoenvironment. *Acta Scientiarum Naturalium Universitatis Sunyatseni* 40: 108–112.
- SHI, N., J. X. CAO, AND L.-K. KÖNIGSSON. 1993. Late Cenozoic vegetational history and the Pliocene–Pleistocene boundary in the Yushe Basin, S. E. Shanxi, China. *Grana* 32: 260–271.
- SHVAREVA, N. J. 1983. Miocene flora of Precarpathians, 1–160. Naukova Dumka, Kiev, Ukraine.
- SMITH, A. C. 1951. The vegetation and flora of Fiji. *Scientific Monthly* 73: 3–15.
- SMITH, A. C. 1952. Studies of Pacific Island plants, 10 The Meliaceae of Fiji, Samoa and Tonga. *Contributions from the United States National Herbarium* 30: 469–522.
- SMITH, A. C. 1955. Phanerogam genera with distributions terminating in Fuji. *Journal of the Arnold Arboretum* 36: 273–292.
- SMITH, A. C. 1978. A precursor to a new flora of Fiji. *Allertonia* 1: 331–414.
- SMITH, A. C. 1985. Flora vitiensis nova: A new flora of Fiji (spermatophytes only), vol. 3, 1–758. Pacific Tropical Botanical Garden, Lawai, Kauai & Hawaii, USA.
- SMITH, K. T., S. F. K. SCHAAL, W. SUN, AND C. T. LI. 2011. Acrodont iguanians (squamata) from the middle Eocene of the Huadian Basin

- of Jilin Province, China, with a critique of the taxon "*Tinosaurus*". *Vertebrata Palasiatica* 49: 69–84.
- SMITH, M. E., A. R. CARROLL, AND B. S. SINGER. 2008. Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. *Geological Society of America Bulletin* 120: 54–84.
- SONG, Z. C., AND M. Y. LI. 1982. Eocene palynological assemblages from the Gonjo Formation in eastern Xizang. In Regional Geological Surveying Team of Sichuan Geological Bureau, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences [eds.], Stratigraphy and palaeontology in West Sichuan and East Xizang, China, part 2, 7–28. Sichuan People's Publishing House, Chengdu, China.
- SONG, Z. C., W. M. WANG, AND F. WANG. 2004. Fossil pollen records of extant angiosperms in China. *Botanical Review* 70: 425–458.
- SONG, Z. C., Y. H. ZHENG, M. Y. LI, Y. Y. ZHANG, W. M. WANG, D. N. WANG, C. B. ZHAO, ET AL. 1999. Fossil spore and pollen of China, vol. 1. The Late Cretaceous and Tertiary spore and pollen, 1–910. Science Press, Beijing, China.
- STRATFORD, J. M. C., AND P. RODDA. 2000. Late Miocene to Pliocene palaeogeography of Viti Levu, Fiji Islands. *Palaeogeography, Palaeoclimatology, Palaeoecology* 162: 137–153.
- SZE, H. C. 1951. Review of H. H. Hu and R. W. Chaney's "A Miocene Flora from Shantung Province, China". *Scientia Sinica* 2: 245–252.
- SZE, H. C. 1954. Cenozoic plants. In H. C. Sze and J. Hsü [eds.], Chinese index fossils: Plants, 68–83. Geological Publishing House, Beijing, China.
- TAKAHASHI, E., AND G. NAITO. 1952. Tertiary plants from Shimonoseki. *Journal of the Geological Society of Japan* 58: 71–72.
- TAO, J. R., AND M. H. CHEN. 1983. Neogene flora of south part of the watershed of Salween-Mekong-Yangtze Rivers (the Lincang region) Yunnan. Special Issue of Hengduan Mountains Scientific Expedition 1, 74–89. Yunnan People's Press, Kunming, China.
- TAO, J. R., B. SUN, AND H. YANG. 1999. Plant megafossils of the Shanwang Formation. In B. Sun [ed.], Shanwang plant fossils, 13–89. Shandong Science and Technology, Ji'nan, China.
- TAO, J. R., Z. K. ZHOU, AND Y. S. LIU. 2000. The evolution of the Late Cretaceous-Cenozoic floras in China, 1–282. Science Press, Beijing, China.
- TASHCHI, S. M., A. G. ABLAEV, AND N. G. MELNIKOV. 1996. Cenozoic basin of the West Primorye and adjacent territories of China and Korea, 1–168. Dalnauka, Vladivostok, Russia.
- TAYLOR, D. W. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and Early Tertiary of the North American area. *Botanical Review* 56: 279–417.
- TEODORIDIS, V. 2002. Tertiary flora and vegetation of the Hlavačov gravel and sand and the surroundings of Holedeč in the Most Basin (Czech Republic). *Acta Musei Nationalis Pragae, Series B, Historia Naturalis* 57: 103–140.
- TIFFNEY, B. H., AND S. R. MANCHESTER. 2001. The use of geological and paleontological evidence in evaluating plant phytogeographic hypotheses in the Northern Hemisphere Tertiary. *International Journal of Plant Sciences* 162: S3–S17.
- TRALAU, H. 1963. Asiatic dicotyledonous affinities in the Cainozoic flora of Europe. *Kungliga Svenska Vetenskapsakademiens Handlingar, Fjärde Serien* 9: 1–87.
- UNGER, F. 1870. Die Fossile Flora von Szánó in Ungarn. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 30: 1–20.
- URDAMPILLETA, J. D., M. S. FERRUCCI, AND A. L. L. VANZELA. 2005. Karyotype differentiation between *Koelreuteria bipinnata* and *K. elegans* ssp. *formosana* (Sapindaceae) based on chromosome banding patterns. *Botanical Journal of the Linnean Society* 149: 451–455.
- VAUDOIS-MIÉJA, N., AND A. LEJAL-NICOL. 1988. African paleocarpology: *Sapindaceacarpum koelreuterioides* n. sp., a new fruit from Upper Nubian of East Africa. *Comptes Rendus de l'Académie des Sciences, Série 2* 307: 855–862.
- VERDCOURT, B. 1962. A new species of *Erythrophysa* E. Mey. ex Arn. (Sapindaceae) from Ethiopia. *Journal of the Linnean Society of London* 58: 185–205.
- WANG, F. X., AND N. F. CHIEN. 1956. A contribution to the pollen morphology of Sapindaceae. *Acta Botanica Sinica* 5: 327–338.
- WANG, Q. 2012. Fruits of *Hemitrapa* (Trapaceae) from the Miocene of eastern China, their correlation with *Sporotrapoidites erdtmanii* pollen and paleobiogeographic implications. *Journal of Paleontology* 86: 156–166.
- WANG, Q. 2013. (2125) Proposal to conserve the name *Dalbergia reticulata* Merr. (Recent Leguminosae) against *D. reticulata* Ettingsh. (fossil Leguminosae). *Taxon* 62: in press.
- WANG, Q., S. R. MANCHESTER, AND D. L. DILCHER. 2010. Fruits and foliage of *Pueraria* (Leguminosae, Papilionoideae) from the Neogene of Eurasia, and their biogeographic implications. *American Journal of Botany* 97: 1982–1998.
- WECKERLE, C. S., AND R. RUTISHAUSER. 2005. Gynoecium, fruit and seed structure of Paullinieae (Sapindaceae). *Botanical Journal of the Linnean Society* 147: 159–189.
- WEHR, W. C. 1995. Early Tertiary flowers, fruits, and seeds of Washington State and adjacent areas. *Washington Geology* 23: 3–16.
- WEYLAND, H. 1937. Beiträge zur Kenntnis der Rheinischen Tertiärflora 2. Erste Ergänzungen und Berichtigungen zur Flora der Blätterkohle und des Polierschiefers von Rott im Siebengebirge. *Palaeontographica Abteilung B* 83: 67–122.
- WEYLAND, H. 1948. Beiträge zur Kenntnis der Rheinischen Tertiärflora 7. Fünfte Ergänzungen und Berichtigungen zur Flora der Blätterkohle und des Polierschiefers von Rott im Siebengebirge. *Palaeontographica Abteilung B* 88: 113–188.
- WGCP [Writing Group of "Cenozoic Plants from China", Institute of Botany and Nanjing Institute of Geology and Palaeontology, Academia Sinica]. 1978. Fossil plants of China, vol. 3. Cenozoic plants from China, 1–232. Science Press, Beijing, China.
- WHEELER, E. A. 2001. Fossil dicotyledonous woods from Florissant fossil beds National Monument, Colorado. *Proceedings of Denver Museum Nature & Science, Series 4*: 187–204.
- WHEELER, E. A., AND P. BAAS. 1993. The potentials and limitations of dicotyledonous wood anatomy for climatic reconstructions. *Paleobiology* 19: 487–498.
- WHEELER, E. A., AND S. R. MANCHESTER. 2002. Woods of the Eocene Nut Beds flora, Clarno Formation, Oregon, USA. *International Association of Wood Anatomists Journal, Supplement* 3: 1–188.
- WILKINSON, H. P. 1988. Sapindaceous pyritised twigs from the Eocene of Sheppey, England. *Tertiary Research* 9: 81–86.
- WINTERSCHIED, H. 2006. Die oligozänen und untermiozänen Floren in der Umgebung des Siebengebirges (südliche Niederrheinische Bucht) (2 Teile). *Documenta Naturae* 158: 1–485.
- WOLFE, J. A. 1972. An interpretation of Alaskan Tertiary floras. In A. Graham [ed.], Floristics and Paleofloristics of Asia and eastern North America, 201–233. Elsevier Publishing Company, Amsterdam, Netherlands.
- WOLFE, J. A., C. E. FOREST, AND P. MOLNAR. 1998. Paleobotanical evidence of Eocene and Oligocene paleoaltitudes in midlatitude western North America. *Geological Society of America Bulletin* 110: 664–678.
- WOLFE, J. A., AND W. WEHR. 1987. Middle Eocene dicotyledonous plants from Republic, northeastern Washington. *U.S. Geological Survey Bulletin* 1597: 1–25.
- WU, Z. Y., H. SUN, Z. K. ZHOU, H. PENG, AND D. Z. LI. 2007. Origin and differentiation of endemism in the flora of China. *Frontiers of Biology in China* 2: 125–143.
- XIA, N. H., AND P. A. GADEK. 2007. Sapindaceae. In Z. Y. Wu, P. H. Raven, and D. Y. Hong [eds.], Flora of China, vol. 12 (Hippocastanaceae through Theaceae), 5–24. Science Press, Beijing, China & Missouri Botanical Garden Press, St. Louis, USA.
- XIA, N. H., AND X. R. LUO. 1995. Geographical distribution of Sapindaceae in China. *Journal of Tropical and Subtropical Botany* 3: 13–28.
- YING, T. S., AND M. L. CHEN. 2011. Plant geography of China, 1–598. Shanghai Scientific & Technical Publishers, Shanghai, China.
- ZHANG, L., AND Y. F. WANG. 2009. The karyotype analysis of *Koelreuteria paniculata* Laxm. *Journal of Shandong Forestry Science and Technology* 6: 55–56, 88.
- ZHANG, Z. C. 1980. Subphylum Angiospermae. In Shenyang Institute of Geology and Mineral Resources [ed.], Paleontological atlas of Northeast China, 2. Mesozoic and Cenozoic volume, 308–339. Geological Publishing House, Beijing, China.

## APPENDIX 1. Information on the specimens used in this study.

Taxon	Number	Preservation	Locality	Age	Repository
<i>Boniodendron minus</i> (Hemsl.) T. C. Chen	1111426, 0923579	Herbarium	Ruyuan, Guangdong, China	Recent	PE
	1000957	Herbarium	Douan, Guangxi, China	Recent	PE
<i>Bridgesia incisifolia</i> Bertero ex Cambess.	909993	Herbarium	Coquimbo, Chile	Recent	MO
<i>Craigia yunnanensis</i> A. C. Sm. et W. E. Evans	02157045	Herbarium	Tengchong, Yunnan, China	Recent	PE
	02145497	Herbarium	Malipo, Yunnan, China	Recent	PE
<i>Dodoniaea viscosa</i> (L.) Jacq.	1886617, 1234058	Herbarium	Yongsheng, Yunnan, China	Recent	PE
	02174471, 02174472	Herbarium	Haikang, Guangdong, China	Recent	PE
	Grierson & Long 4187	Herbarium	Tongsa District, Bhutan	Recent	A
<i>Koelreuteria allenii</i> (Lesq.) W. N. Edwards	P1617, P36692, P36691, P36695, P36688, P36689, P36690, P36693, P36694, P36695a	Impression	Florissant, Colorado, USA	Latest Eocene	USNM
	256-20740, 256-20745	Impression	Teater Road, Oregon, USA	Late Eocene	UF
	PP55094	Impression	Wyoming, USA	Early Eocene	FMNH
	PB158849	Impression	Florissant, Colorado, USA	Latest Eocene	YPM
	PB020681	Impression	De Beque, Colorado, USA	Middle Eocene	YPM
<i>Koelreuteria bipinnata</i> Franch.	0991406, 0991407	Herbarium	Shangyou, Jiangxi, China	Recent	PE
	02174429, 297889	Herbarium	Hengshan, Hunan, China	Recent	PE
<i>Koelreuteria dilcheri</i> sp. nov.	P42363	Impression	Independence Hill near Colfax, California, USA	Middle Eocene	USNM
	PB94575, 1695, 1696	Impression	Republic, Washington, USA	Early to middle Eocene	UWBM
<i>Koelreuteria elegans</i> (Seem.) A. C. Sm.	1213, B. E. Parham	Herbarium	Tailevu, Viti Levu, Fiji	Recent	A
<i>Koelreuteria henryi</i> Dümmer	1516597, 1583132	Herbarium	Hualian and Taoyuan, Taiwan, China	Recent	PE
	20100203	Slide	University of Florida, Gainesville, USA	Recent	UF
<i>Koelreuteria macroptera</i> (Kováts) W. N. Edwards	58.2.1	Impression	Gomboska of Tállya, Hungary	Middle Miocene	BP
	60.815.1	Impression	Abaújszántó, Hungary	Middle Miocene	BP
	P1224/509, P1224/506, P1224/511, P1224/515, P1224/508, P1224/507, P1224/510, P1224/512	Impression	Randecker Maar, Germany	Early Miocene	SMNS
	92-15/413, 92-17/413	Impression	Randecker Maar, Germany	Early Miocene	NMA
	91-2048/800, 91-2518/403	Impression	Burtenbach and Geisenhausen, Bavaria, Germany	Middle to late Miocene	NMA
<i>Koelreuteria miointegrifoliola</i> Hu et R. W. Chaney	No. 58 (H)	Impression	Shanwang, Shandong, China	Early to middle Miocene	PB
	50384, 50567, 52440, 50455, 20111117, 20111118A, 20111118B, 20080916	Impression	Shanwang, Linqu, Shandong, China	Early to middle Miocene	PE
	15839-56774, 15839-56774', 15839-56775	Impression	Shanwang, Linqu, Shandong, China	Early to middle Miocene	UF
<i>Koelreuteria paniculata</i> Laxm.	0894897	Herbarium	Yuxian, Henan, China	Recent	PE
	0872783, 02234144	Herbarium	Taian, Shandong, China	Recent	PE
<i>Koelreuteria taoana</i> sp. nov.	054018a, b, c	Impression	Huadian, Jilin, China	Middle Eocene	PE
<i>Urvillea chacoensis</i> Hunz.	T. Meyer 8829	Herbarium	Argentina	Recent	A

Notes: A: Arnold Arboretum Herbarium, Harvard University; BP: Hungarian Natural History Museum, Budapest; FMNH: Field Museum, Chicago; MO: Missouri Botanical Garden Herbarium; NMA: Nature Museum Augsburg, Augsburg; PB: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing; PE: Chinese National Herbarium, Beijing; SMNS: Staatliche Museum für Naturkunde, Stuttgart; UF: Florida Museum of Natural History, Gainesville; USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UWBM: Burke Museum of Natural History, the University of Washington, Seattle; YPM: Peabody Museum of Natural History, Yale University, New Haven.