

Fruit with perianth remains of *Chaneya* Wang & Manchester (extinct Rutaceae) in the Upper Miocene of Sośnica, Poland

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ABSTRACT. Reproductive structures corresponding to the extinct sapindalean genus *Chaneya* Wang & Manchester are recognized based on perianths with attached fruiting bodies from the late Miocene Sośnica flora of western Poland. Like other members of the genus, known from the Eocene of western North America, the Eocene to Miocene of Asia and Oligocene to Miocene of Europe, *Chaneya membranosa* (Goepf). Manchester & Zastawniak comb. n. has a showy, persistent perianth and a central disk supporting five free ovaries, but it is distinguished by the larger size of its perianth compared with other fossils attributed to the genus.

KEY WORDS: *Chaneya*, fossil fruits, Rutaceae, Sapindales, Upper Miocene, Sośnica, Poland

INTRODUCTION

In the many leaf floras from the Neogene of Europe, plant impressions interpreted as fossil flowers with a 5-lobed perianth have been known for a long time (e.g. Al. Braun 1845, Unger 1847, 1850). Fossil remains of this type from the Miocene of Öhningen were identified by Heer (1859), as “fruit corollas” of the extant genus *Porana* (Convolvulaceae). Recently, many of these structures have been carefully reevaluated and interpreted as persistent corollas and fruits of the extinct sapindalean genus, *Chaneya* (Teodoridis & Kvaček 2005).

Similar, but larger, corollas have long been known from the Upper Miocene flora of Sośnica in western Poland but are still in need of systematic revision. These five-petaled flowers were assigned by Göppert (1855) to the genus *Getonia* Roxb. (syn. *Calycopteris* Lam, Combretaceae). Referring to the Sośnica fossils, Schimper (1870–1872) transferred *Getonia membranosa* Goepf. to *Porana* Burm. f. (Convolvulaceae) and indicated that the specimen

previously treated as *Getonia truncata* Goepf. should be transferred to *Diospyros brachysepala* Al.Br. In a later partial revision of the Sośnica flora, Schlechtendal (1897) merged these species, along with the impression previously named *Carpinus involvens* Goepf., under the name *Porana membranosa* (Goepf.) Schimper. More recently, all of these remains were reassigned by Mai (1985) to *Hydrangea*. However, *Hydrangea* has a single ovary per flower, whereas closer inspection of the Sośnica specimens reveals a central disk that supported five free ovaries.

In this paper, we reevaluate the affinities of *Getonia membranosa* Göppert (1855). We show that these fossils represent *Chaneya* Wang & Manchester, an extinct genus recognized previously from the Eocene of western North America, the Eocene and Miocene of eastern Asia (Wang & Manchester 2000), and from the Oligocene and Miocene of Europe (Teodoridis & Kvaček 2005).

This investigation is part in a series dealing with revision of the late Miocene (Pannonian) flora of Sośnica which played an important role in early paleobotanical works (Göppert 1855). A detailed description of Pannonian flora from the Sośnica locality was given by Collinson et al. (2001), along with a revision of aquatic ferns and angiosperms; as well as the characteristic of fossil plant communities. Collinson et al. (op. cit.) also provide a complete review of prior publications connected with this locality. Other recent revisions include Betulaceae (Zastawniak & Walther 1998) and *Acer* (Walther & Zastawniak 2005), and analyses of pollen grains *in situ* from some flowers and inflorescences (Kohlman-Adamska et al. 2004).

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MATERIAL

For this investigation, we focused on specimens from the Sośnica flora in order to reevaluate the affinities of the flowers first studied about 150 years ago. Göppert (1855) described two species of flower from this flora: *Getonia mebranosa* Goepp. (Göppert op. cit., pl. 25, fig. 12) and *Getonia truncata* Goepp. (Göppert op. cit. pl. 25 fig. 11). The original specimen of *G. mebranosa* was examined in the collection of the Geological Museum of the University of Wrocław (MGUWr 966p/l). The two remaining specimens (*G. truncata* Goepp. and *Carpinus involvens* Goepp.) have been lost. Another specimen (MGUWr 965p), has survived but in very damaged condition, broken into two parts, with original inscription: *Porana mebranosa* Goepp. on the opposite side. It was illustrated in the paper of Schlechtendal (1897, pl. 5, fig. 6a). Additional impressions from the Sośnica flora examined for this study include specimens housed in the Geological Museum of the Wrocław University (MGUWr), in the Museum of the Earth, Polish Academy of Sciences in Warsaw (MZ) and in the Palaeobotanical Museum of the W. Szafer Institute of Botany, Polish Academy of Sciences in Kraków (KRAM-P). For comparative work, we examined *Chaneya* specimens from other European, Asian and North American floras as cited in Wang and Manchester (2000).

Specimens were studied by reflected light microscopy to reveal details of perianth structure and venation and to document the morphology of the gynoecium and/or fruit. Attempts at isolation of pollen grains from the fruit perianth yielded negative results. These studies were carried out by A. Kohlman-Adamska and M. Ziemińska-Tworzydło in the Museum of the Earth, Polish Academy of Sciences in Warsaw.

TAXONOMICAL DESCRIPTION

Order Sapindales

Family Rutaceae

Genus *Chaneya* Wang & Manchester

Chaneya membranosa (Goepp). Manchester & Zastawniak **comb. n.**

Figs 1, 2

Basionym. *Getonia membranosa* Göppert, 1855, Die tertiäre Flora von Schosnitz in Schlesien, p. 38, pl. 25, fig. 11

Material. Ten impressions of fruit perianths, two with counterpart impressions: MGUWr Nos 69lp (two flowers), 738p/l (with counterpart 738p/2), 811p (with counterpart 966p/l) 965p, 2405p/2, 2474p, 2514p, MZ VII-53/390.

Lectotype. We here designate MGUWr 966p/l (Fig. 1; 1, la, b) and its counterpart impression, 811p (Fig. 1: 3, 3a), as the lectotype. The counterpart impression was originally illustrated by Göppert (1855, pl. 25, fig. 12).

Synonyms

- 1855? (non vidi) *Getonia truncata* Goepp.; Göppert, p. 37, pl. 25, fig. 11.
- 1855 *Carpinus involvens* Goepp.; Göppert, p. 20, pl. 5, fig. 8.
- 1870–1872 *Porana membranosa* (Goepp) Schimper; Schimper, p. 913.
- 1870–1872 *Diospyros brachysepala* Al.Br.; Schimper, p. 950.
- 1897 *Porana membranosa* (Goepp) Schimper; Schlechtendal, p. 25, pl. 5, figs 5a, 5b, 6a, 6b, pl. 6, figs 9, 10.
- 1985 *Hydrangea membranosa* (Goepp.) Mai; Mai, p. 83, fig. 7.
- 2005 *Chaneya oeningensis* (Unger) Teodoridis & Z. Kvaček; pl. 1, figs 12, 13 (only).

Emended diagnosis. Perianth pentamerous, petals free, elliptic to almost orbicular, with rounded apices, unequal in size, imbricate. Petal venation consisting of about five subparallel, longitudinal veins craspedodromous to camptodromous. Central disk circular to pentagonal, with bearing five distinct orbicular ovaries or fruit bodies.

Description. Impressions of the pentamerous perianth to ca. 2.5 cm in diameter; petals free, unequal in size, imbricate. Petals elliptic

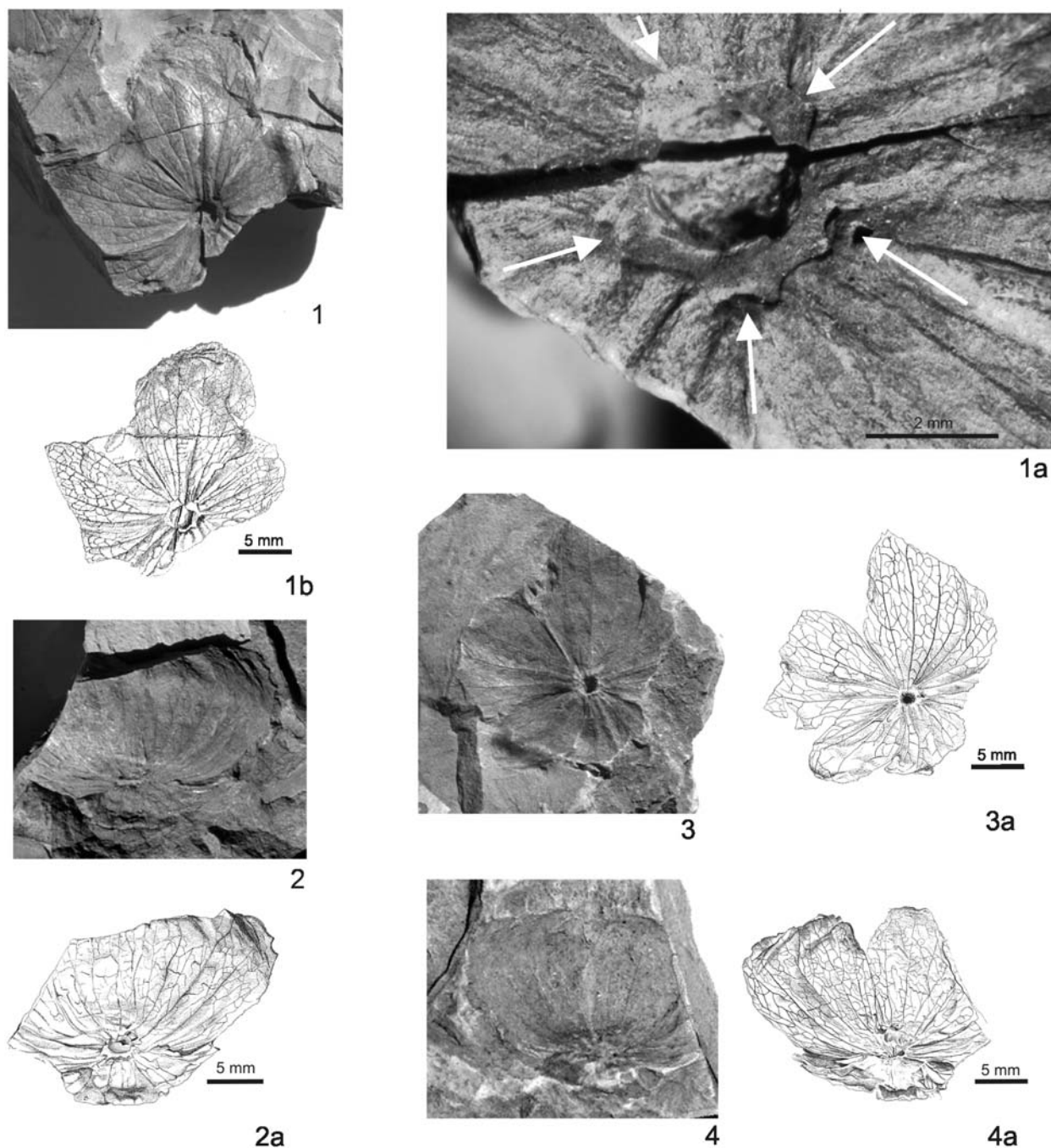


Fig. 1. *Chaneya membranosa* (Goep.) Manchester & Zastawniak comb. n. **1, 1b** – lectotype, a transversely compressed with perianth showing five veins in each lobe and a central disk. Originally figured by Göppert (1855, pl. 25, fig. 12) as *Getonia membranosa* Goep. Specimen MGUWrNo 966p/I. **1a** – enlargement showing five-lobed central disk. A separate fruit body is inferred to have been seated on each lobe of the disk (arrows). **2, 2a** – specimen MGUWrNo 738p/I, counterpart of specimen in fig. 4, 4a. **3, 3a** – counterpart impression of the lectotype in fig. 1, 1a, b. Originally published as *Getonia truncata* Goep. (Göppert 1855, pl. 25, fig. 11). Specimen MGUWr No 811p. **4, 4a** – laterally compressed with perianth showing venation radiating from the base. Specimen MGUWrNo 738p/2; counterpart of specimen in fig. 2, 2a

to almost orbicular, apices rounded; margin entire. Length of petals 8, 9, 11, 14, 15, 15, 15, 17, 20, 21 mm; width 6, 7, 9, 9, 11, 11, 13, 14 mm. Petal venation consisting of about five subparallel, longitudinal veins, which arise from the base and vary from craspedodromous to camptodromous. Secondary veins numerous, originating at right or acute angles, joining

each other and with veins of the next higher order to form polygonal areoles. Orbicular dots (resin bodies or glands) are faintly over the surface of the perianth. Pedicel up to 2.7 cm long (according to the drawing of *Carpinus involvens* by A. Assmann in Göppert 1855, pl. 5, fig. 8). On some specimens are preserved a pentagonal disk on the margin of which five

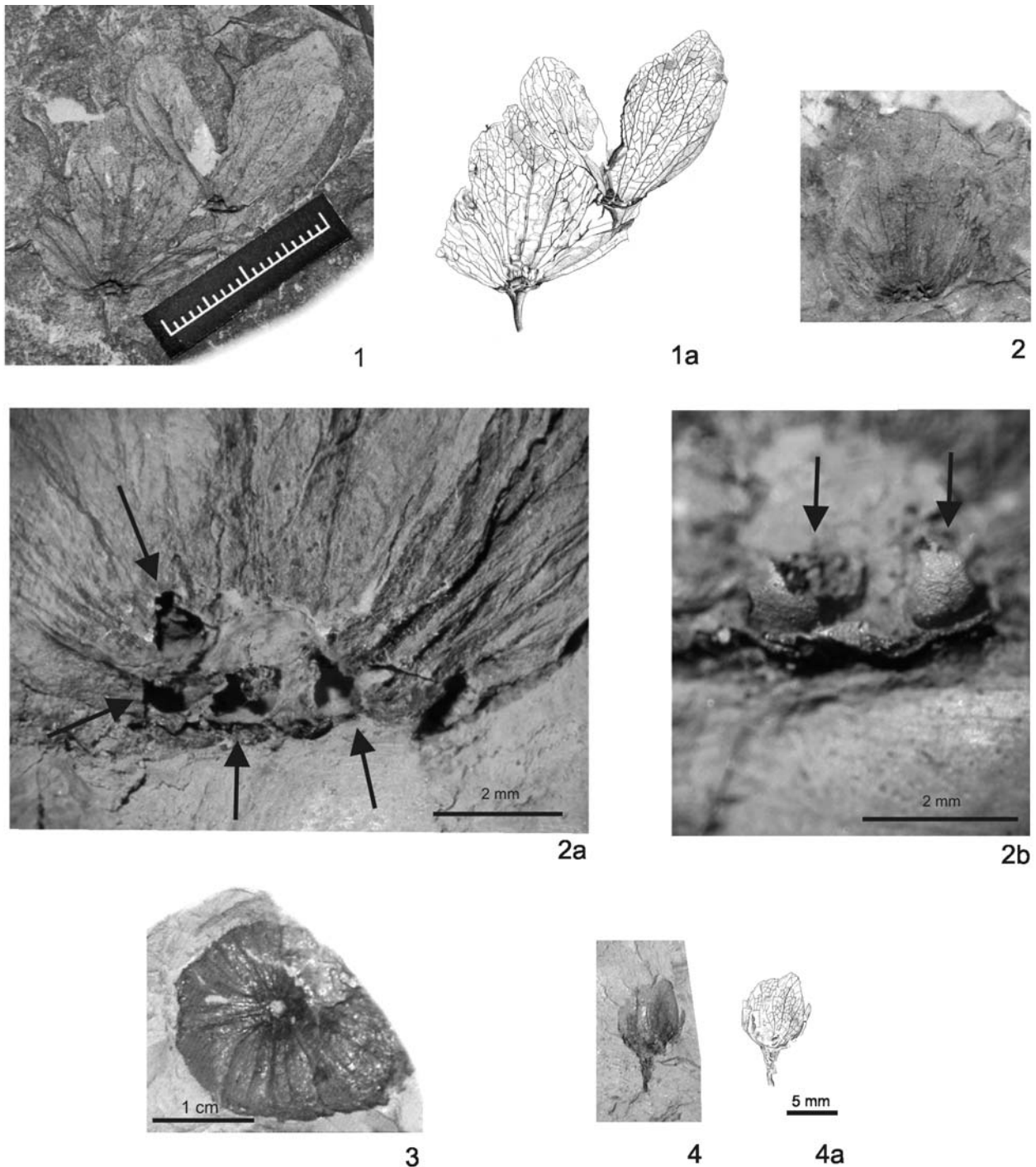


Fig. 2. *Chaneya membranosa* (Goepf.) Manchester & Zastawniak comb. n. **1, 1a** – two laterally compressed fruit with perianth with incomplete peduncles, probably parts of the same inflorescence. Specimen MGUWr No 691 p; scale bar – 2 cm. **2** – laterally compressed corolla with disk at base. Specimen MGUWr No 2474. **2a** – enlargement, showing the cavities from four orbicular fruit bodies (arrows); a fifth body is inferred from symmetry to have been in the same whorl to the upper right. **2b** – further enlargement, with lighting readjusted to show the smooth rounded surface of the fruit bodies. Note also small dark dots interpreted as glands. **3** – fruit with perianth with orbicular central disk. Specimen MZ VII 53/390. **4, 4a** – laterally compressed small fruit with perianth on pedicel. Specimen MGUWr No 2405p/2/I

small fruit bodies are attached (Fig. 1: 1a). The cuticle is not preserved.

The specimens are visible in various orientations and with fractures in different places that reveal additional features of morphology. Often the perianths are preserved in trans-

verse orientation, showing the saucer-shaped outline but with five rounded lobes at the periphery (Fig. 1: 1, 1a,b, 3, 3a, Fig. 2: 3). In the middle of the perianth a small round hole is visible which is interpreted as the pedicel scar, surrounded by a circular to pentagonal

disk, on which the whorl of ovaries was borne (Fig. 1: 1, 1a,b). Some specimens are compressed, showing the cup-like lateral outline of the flower and its attachment on the pedicel (Fig. 2: 1, 1a, 2, 2a,b, 4, 4a).

COMPARATIVE MORPHOLOGY

The venation and shape of the perianth are somewhat reminiscent of the accrescent corolla of *Hydrangea*, and on this basis, Mai (1985) transferred Göppert's species to *Hydrangea membranosa* (Goepp.) Mai. However, flowers of this fossil species are typically 5-lobed rather than 4-lobed, and the gynoecium is apocarpous, in contrast with the syncarpic bi- or tricarpellate capsule of extant *Hydrangea*. The showy perianths of *Hydrangea* inflorescences often occur on sterile outer flowers, whereas the perianths of *Chaneya* occur on fertile flowers. The Sośnica flowers show a central disk to which free fruit bodies were attached. In the arrangement of fruit bodies, and morphology of the perianth, these structures correspond closely to the extinct genus *Chaneya*, which was recently described from the Eocene of western North America and the Eocene to Miocene of eastern Asia (Wang & Manchester 2000) and from the early to middle Miocene of Europe (Teodoridis & Kvaček 2005).

An important feature shared by the European, Asian, and North American species of *Chaneya* is the central disk that bears five free fruit bodies, of which usually just one or two is found in fully enlarged state. Sometimes all five bodies are seen around the disk that did not enlarge (Fig. 2: 2a, 2b), indicating either an immature stage of fruiting or possibly flowers with merely abortive fruits. This indicates an apocarpous condition which distinguishes these flowers and fruits from genera in many other families having otherwise similar corollas or calyces, e.g. *Porana*, *Monotes*, *Astronium*, and *Florissantia*, as demonstrated by Wang and Manchester (2000). These authors treated *Chaneya* as an extinct genus with possible affinities to the extant simaroubaceous genus, *Picrasma*. *Picrasma* also bears a cycle of five free fruit bodies and has a persistent perianth, but the texture and venation of the perianth differs. Teodoridis and Kvaček (2005) recognized *Chaneya* as a common element of early and middle Miocene floras of Europe. Although

Wang and Manchester (op. cit.) considered the perianth of these fruiting specimens to be the persistent calyx, Teodoridis and Kvaček (op. cit.) interpreted them to represent corolla rather than calyx, based on their observation of what appear to be sepal remnants below the enlarged whorl in some specimens of *Chaneya*. We have adopted the same terminology here although we were unable to confirm a lower whorl of sepals in the Sośnica material.

Although the genus *Chaneya* was widely distributed in the Tertiary of western North America, Europe and eastern Asia, only one species has previously been recognized in the European Tertiary, i.e. *Chaneya oeningensis* (Unger) Teodoridis & Z. Kvaček. In their review of numerous specimens from the Öhningen locality, including Heer's original type specimens, Teodoridis and Kvaček (2005) concluded that the observed variation in width and form of perianth was insufficient, in the absence of other differentiating characters, to discriminate multiple species. Accordingly, they placed *Porana macrantha* Heer and *Porana inaequiloba* Heer in synonymy under *Chaneya oeningensis* (Unger) Teodoridis & Z. Kvaček. *Chaneya oeningensis* ranges from the late Oligocene (Rott, near Bonn, Germany) through the Miocene in the Europe. Our recognition of *Ch. membranosa* extends the genus into the late Miocene of Central Europe.

We believe that the late Miocene Sośnica specimens differ sufficiently in perianth size and morphology to be treated separately from *Chaneya oeningensis*. Teodoridis and Kvaček (2005, fig. 1) graphed the ranges in petal length and width for previously recognized North American, Asian, and European populations of *Chaneya* and were thus able to demonstrate the utility of perianth dimensions in distinguishing some of them. In comparison, the petals of *Ch. membranosa* are usually 9 to 21 (avg. 15.1) mm in length, whereas those of *Ch. oeningensis* from Öhningen fall within the range of 5.3 to 11.7 (avg. 9.6) mm long. *Ch. membranosa* petals are also larger than those of the Eocene Asian and western North American species, *Ch. tenuis* (petal length 8–16 mm). Although the length of *Ch. membranosa* petals fall within the range of the middle Miocene East Asian species, *Ch. kokangensis* (14–21 mm), the former has broader petals: 7 to 14 (avg. 10.6) mm vs. 4 to 9 (avg. 7) mm. Also, the corolla of *Ch. membranosa* appears to be

thinner in texture than in other species and more strongly convex, saucer-shaped in form. Judging from the large size and membranous texture, we suggest that one of the specimens illustrated from the Miocene of Břešťany, North Bohemia (pl. 1 figs 12 and 13 in Teodoridis & Kvaček 2005) also corresponds to *Ch. membranosa*. Although each of the specimens is fragmentary, combined information from the suite of several specimens provides the basis for reconstructing a complete flower as it may have appeared in life (Fig. 3). We have not observed stamens in this material; if *Chaneya membranosa* flowers were hermaphroditic, the androecial parts evidently were shed prior to deposition of these flowers.

Teodoridis and Kvaček (2005) provided some corrections of morphological interpretation and a revised assessment of systematic affinity of this extinct genus following the treatment of Wang and Manchester (2000). The cuticle attributed to the *Porana kokangensis* by Wang and Manchester (2000) was apparently that of a gymnosperm (now acknowledged by S. Manchester as a laboratory blunder). Whereas Wang and Manchester (op. cit.) interpreted the single preserved perianth whorl to represent persistent calyx Teodoridis and Kvaček (2005) interpreted it to represent the corolla. Wang and Manchester (2005) observed in some specimens an outer whorl of 5 ovoid structures somewhat smaller than the inner whorl, with tapered apices which they interpreted as a second whorl of ovaries, however Teodoridis and Kvaček (op. cit.) disputed that interpretation and suggested that the outer whorl may represent stamens or staminodes, which is more consistent with morphology observed in extant Simaroubaceae and Rutaceae. We have not observed these structures in *Chaneya membranosa*.



Fig. 3. Reconstruction of fruit with perianth of *Chaneya membranosa* (Goepf.) Manchester & Zastawniak comb. n. (drawn by J. Wieser)

SYSTEMATIC POSITION OF *CHANEYA*

Wang and Manchester (2000) concluded that the affinities of *Chaneya* might be close to the Simaroubaceae based on similarities to the extant genus *Picrasma*, which also bears a disk with five ovaries and perianth persisting in fruit, but noted differences that distinguish them as distinct genera. Teodoridis and Kvaček (2005) favored affinities with the adjacent family Rutaceae, because the corollas of the fossils also show orbicular dots interpreted as glands characteristic of that family that are not found in Simaroubaceae. These orbicular dots are also visible in *Chaneya membranosa*. Molecular analyses indicate that both of these families are closely adjacent along with Meliaceae in the order Sapindales (Soltis et al. 2005). It is noteworthy that the phytogeographic history of *Chaneya* in the Northern Hemisphere is similar to that of the simaroubaceous genus *Ailanthus* (Hably 2001, Corbett & Manchester 2004); however, whereas *Ailanthus* was distributed in Europe as well as North America and Asia in the Eocene, *Chaneya* has not been recovered in European strata earlier than late Oligocene. Possibly the European populations arrived from Asia as the Turgai seaway receded (Teodoridis & Kvaček 2005).

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