Fossil endocarps of *Aralia* (Araliaceae) from the upper Pliocene of Yunnan in southwest China, and their biogeographical implications

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Abstract: *Aralia stratosa* H. Zhu, Y.J. Huang et Z.K. Zhou sp. nov. is described based on fossil endocarps from the upper Pliocene of northwest Yunnan in southwest China. The endocarps are characterized by a semicircular to elliptic outline in the lateral view, an apical beak-like structure bending towards the ventral side, and a transversely wrinkled surface, collectively indicating taxonomical inclusion in the genus *Aralia*

(Araliaceae). The new fossil taxon is compared with nine extant species of *Aralia* based on endocarp morphology and anatomy, showing the carpological resemblance to *A. echinocaulis*. *Aralia stratosa* sp. nov. represents the first confirmed fossil record from lower latitudes in the Northern Hemisphere. This implies a southerly biogeographical range for this genus than was previously interpreted. The fossil records of *Aralia* suggest a Cretaceous origin in North America and an Eocene dispersal to eastern Asia, likely via the Bering land bridge, followed by Miocene establishment in Europe. The genus likely began to inhabit lower latitudes in eastern Asia no later than the late Pliocene, which is in line with results from molecular analyses. All these may suggest a southward distributional change probably associated with the global cooling and northern aridification.

Key words: *Aralia*; endocarp; late Pliocene; Sanying Formation; southwest China; eastern Asia

1. Introduction

The genus *Aralia* Linnaeus (Araliaceae) is composed of 71 living species of perennial herbs, shrubs, lianas or deciduous trees (Wen, 1993, 2011). It is distributed in northern temperate to tropical regions, showing a classical intercontinental disjunction between eastern Asia and the Americas (Li, 1952; Wu, 1983; Wen et al., 1998; Xiang et al., 1998; Wen, 2011). Eastern Asia, home to 57 species, represents the modern biodiversity centre of this genus (Wen et al., 1998; Wen, 2011).

Aralia has an excellent fossil record extensively documented from the Cretaceous to Pleistocene in the northern boreal areas (e.g., Tanai, 1961, 1970; Bell,

1963; Dorofeev, 1963, 1988; Gregor, 1978; Mai and Walther, 1988; Geissert et al., 1990; Mai, 1997, 2001; Kovar-Eder and Meller, 2001; Nikitin, 2006; Ghiotto, 2010). *Aralia* fossils are particularly abundant in Europe (e.g., Szafer, 1954; Gregor, 1978; Łańcucka-Środoniowa, 1979; Mai and Walther, 1988; Geissert et al., 1990; Mai, 1997, 2001; Martinetto et al., 1997; Ghiotto, 2010), north-central Asia (e.g., Dorofeev, 1963, 1988; Nikitin, 2006) and northeast Asia (e.g., Fedotov, 1977; Nikitin, 2006), in contrast to its modern absence from these regions. In eastern Asia, *Aralia* fossils are relatively uncommon (e.g., Tanai, 1961, 1970), although the region today exhibits the highest biodiversity of the genus (Wen, 2011). For this reason, the historical biogeography and biodiversity of *Aralia* in eastern Asia remain poorly understood. Furthermore, previous fossils have been documented mainly from the middle to high latitudes of the Northern Hemisphere, while modern *Aralia* is distributed primarily in much lower latitudes of eastern Asia. The difference in distribution seems to imply an overall southward movement of the genus throughout the Cenozoic, which is probably associated with the overall global cooling and northern aridification trends throughout the Cenozoic (Zachos et al., 2001; Mosbrugger et al., 2005; Eronen et al., 2010, 2012). Molecular evidence suggests that *Aralia* might have reached the low latitudes of eastern Asia during the Miocene or earlier times (Wen et al., 1998; Wen, 2000). This hypothesis, however, has not been supported by fossil evidence. Hence new fossil finds from the lower latitude regions are particularly informative for understanding the historical biogeographical changes of the genus from the higher to lower latitudes in the Northern Hemisphere.

Here, we describe a new species of *Aralia* based on fossil endocarps from the late Pliocene of northwest Yunnan in southwest China. We examine the fossil endocarps morphologically and anatomically, and then compare them with members of Araliaceae at both the generic and specific levels. Finally, we summarize the megafossil record of *Aralia*, on which we base our discussion of palaeophytogeography of the genus.

2. Material and methods

2.1. Fossil materials and examinations

The fossil endocarps were collected at Fudong Village, Lanping County in northwest Yunnan Province, southwest China (26°27'32" N, 99°25'56" E; Fig. 1). The deposits of the fossil site belong to the Sanying Formation based on regional lithostratigraphic and biostratigraphic correlations (WGRSY, 1978; BGMRY, 1990; Ge and Li, 1999). The Sanying Formation is dated as being from the late Pliocene by regional stratigraphic correlations (WGRSY, 1978; BGMRY, 1990; Ge and Li, 1999), floristic correlations (Tao and Kong, 1973; Tao, 1986; Ge and Li, 1999; Xu et al., 2004), mammalian fossils (Su et al., 2011), and magnetostratigraphic data (3.6 Ma, Li et al., 2013). The geological settings of the fossil site have been previously described in detail (WGRSY, 1978; Tao, 1986; Huang et al., 2012).

The Fudong fossil site was first known for its leaf fossils (Tao, 1986) and regained attention due to abundant fossil seeds and fruits in recent years (Huang et al., 2012, 2013). Numerous anatomically preserved seeds and fruits have been collected during several field trips. In total, 17 endocarp specimens of *Aralia* were singled out

from the fossil collection under a binocular microscope (Nikon, SZX16). To facilitate observation, the clay particles adhering to the endocarp surface were removed with an ultrasonic cleaner (UC, KO-50M) at a frequency of 40 KHz for 5–10 seconds. The fossils were then observed under the Nikon binocular microscope, and pictures were taken. One fossil specimen was dissected by using a blade to get the anatomical details. The exterior surface and interior structures of the fossils were examined under a scanning electron microscope (SEM, Zeiss EVO LS10) and pictures were captured. Longitudinal sections were scanned by the SEM and a synchrotron radiation-based X-ray tomographic microscope at 2-BM beamline of Advanced Photon Source. All of the fossil specimens are housed at the Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences.

2.2. Extant materials and examinations

We compared the present fossil taxon with 23 extant species belonging to 14 genera in the Araliaceae, representing more than half of the Chinese genera of the Araliaceae and one third of the total genera of the family (Xiang and Lowry II, 2004). The endocarp morphology of extant Araliaceae was based primarily on our observations from the herbarium specimens at the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN), and partly obtained from published sources (Ishikawa, 1994; Bojňanský and Fargašová, 2007; Guo et al., 2009). To expose the endocarps, the fruit materials obtained from the KUN were treated by following the method described by Tiffney (1990). The endocarps of nine *Aralia*

species were studied morphologically and anatomically with the SEM.

3. Systematics

Family: Araliaceae Jussieu

Genus: *Aralia* Linnaeus

Species: *Aralia stratosa* H. Zhu, Y.J. Huang et Z.K. Zhou sp. nov.

Holotype: FD 010 (Plate I, 1)

Paratype: FD 011 (Plate I, 3), FD 012 (Plate I, 7), FD 013 (Plate I, 6), FD 060 (Plate II, 3–6), FD 070 (Plate I, 8), FD 071 (Plate I, 4), FD 072 (Plate I, 5), FD 073 (Plate I, 2; Plate II, 1–2; Plate IV, 1)

Repository: All fossil specimens are kept at the Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences.

Type locality: Fudong Village, Lanping County, northwest Yunnan Province, southwest China (26°27'32" N, 99°25'56" E)

Stratigraphic horizon: Sanying Formation of the upper Pliocene

Etymology: The epithet *stratosa* is from the Latin *stratosus*, in reference to the stratose structure in the longitudinal section of the fossil endocarp.

Diagnosis: Endocarp laterally compressed, generally lunate or semicircular, a few elliptic in lateral view; dorsal side convex, ventral side almost straight or slightly convex; apex having a beak-like structure, bending toward the ventral side; both exterior and interior surfaces transversely wrinkled.

Description: Endocarps are laterally compressed, lunate, elliptic to prolonged

elliptic in lateral view (Plate I). They are 2.4–3.1 mm in length (mean = 2.8 mm, standard deviation = 0.27, n = 12) and 1.5–2.0 mm in width (mean = 1.7 mm, standard deviation = 0.14, n = 12), with a length–width ratio of 1.2–1.9. The dorsal side is convex, and the ventral side is almost straight (Plate I, 3, 6) to slightly convex (Plate I, 1–2, 4–5, 7–8). The base is generally rounded, and the apex is rounded (Plate I, 1–2) to moderately acute (Plate I, 3–8), with a beak-like structure bending toward the ventral side. On the lateral surface is a longitudinal rib which is only weakly developed (Plate I, 2, 8). The exterior surface of the endocarps is finely transversely wrinkled and in some cases the wrinkles are weakly curved (Plate II, 1–2). The transverse wrinkles or rugulae diverge from the ventral margin to dorsal margin; they are discontinuous and almost parallel with each other at intervals of about 2–6 μm (Plate II, 1–2). The wrinkles are densely located close to the ventral side and relatively sparse near the dorsal side; those on the upper (lower) parts of the endocarp slightly incline upward (downward) (Plate I, 2, 3; Plate IV, 1). These transverse wrinkles are the outward extension of stratose elements, which likely represent the elongation of the exterior sclerenchyma cells of the endocarp. The stratose elements seen from the longitudinal section are nearly vertical to both the exterior and interior surfaces, and are arranged more densely near the interior surface (Plate II, 6–7). The interior surface of the endocarps is transversely and finely rugose spaced about 1–3.5 μm apart (Plate II, 3–4), and in some areas the transverse wrinkles are connected by weakly developed wrinkles (Plate II, 5).

4. Comparisons

4.1. Placement in *Aralia*

The present fossil endocarps display a lunate, semicircular to elliptic outline in lateral view, a convex dorsal side, an almost straight to slightly convex ventral side, and an apical beak-like structure bending toward the ventral side (Plate I), and transversely wrinkled surface. The combination of these morphological characteristics shows a resemblance to endocarps of *Aralia* in the Araliaceae. To confirm the generic determination, we also compared our fossils with endocarps of 13 other genera of the family that exist in southwest China today (Table 1). Extant endocarps of the Araliaceae show significant intrafamilial variation in morphology (Plate III). The fossils are comparable to the endocarps of *Aralia*, *Eleutherococcus* Maxim., *Fatsia* Decne. & Planch., *Kalopanax* Miq., *Metapanax* J. Wen & Frodin, *Polyscias* J.R. Forst. & G. Forst., and *Schefflera* J.R. Forst. & G. Forst. by sharing a lunate to semicircular outline. The fossils are therefore compared with the endocarps of these seven genera. Surface sculpture plays an important role in distinguishing these genera. The endocarp surface of *Polyscias* is reticulate-alveolate and that of *Metapanax* is pusticulate and alveolate, or random-alveolate, while that of the other five genera (*Aralia*, *Eleutherococcus*, *Fatsia*, *Kalopanax*, and *Schefflera*) shows a wrinkled pattern. However, the endocarp surface of *Eleutherococcus* is usually longitudinally furrowed, different from our fossils. The endocarp surface of the remaining four genera (*Aralia*, *Fatsia*, *Kalopanax*, and *Schefflera*) has transverse wrinkles, as is also the case in our fossils. Nonetheless, our fossils ($2.4\text{--}3.1 \times 1.5\text{--}2.0$ mm) are smaller than *Fatsia* ($3.8\text{--}4.4 \times 2.4\text{--}2.6$), *Kalopanax* ($3.3\text{--}3.6 \times 2.3\text{--}2.5$ mm), and *Schefflera* ($3.1\text{--}3.9 \times$

2.0–2.6), but are more comparable in size to those of *Aralia* ($2.1\text{--}3.9 \times 1.3\text{--}1.9$ mm).

In addition, the fossils resemble *Aralia* endocarps in the interior surface which is sculptured by transverse wrinkles (Plate IV, Plate V). Based on these comparisons, we believe that the present fossil endocarps can be confidently placed in the genus *Aralia*.

4.2. Species designation

Eastern Asia has the highest species diversity of *Aralia*; 57 species occur there (Wen, 2011). In China, there are currently approximately 40 species of the genus (Wen, 2011). Based primarily on our observations and partially on published data (Ishikawa, 1994; Bojňanský and Fargašová, 2007), the endocarps of *Aralia* are infragenerically uniform in morphology (Plate IV; Plate V). In an attempt to improve species circumscription, we compared our fossils with the endocarps of nine Chinese species of *Aralia* morphologically and anatomically (Table 2). The fossil and extant endocarps are similar in general morphology (Plate IV, Plate V). However, some differences between them can still be observed. The dorsal margins of *A. searelliana* and *A. thomsonii* endocarps are undulate and their ventral margins prolong to form a sheet structure different from our fossils. The endocarp surface of *A. dasyphylloides* has two distinctive longitudinal ribs near the dorsal side and that of *A. elata* is tuberculate near the dorsal side, while only a weakly longitudinal rib can be seen in our fossils (Plate I, 2, 8). Endocarps of *A. searelliana* ($3.9\text{--}4.1 \times 1.9\text{--}2.1$ mm) are larger, and those of *A. cordata* ($2.3\text{--}2.4 \times 1.4\text{--}1.5$ mm), *A. elata* ($2.2\text{--}2.3 \times 1.1\text{--}1.3$ mm) and *A. undulata* ($2.0\text{--}2.3 \times 1.3\text{--}1.5$ mm) are smaller than our fossils ($2.4\text{--}3.1 \times 1.5\text{--}2.0$ mm). The interior surface sculptures of the fossil and extant endocarps are

similar in appearance, i.e., they are transversely and finely wrinkled, but the exterior surface sculptures differ. The exterior surfaces of our fossils are transversely finely wrinkled, similar to that of these five species: *A. echinocaulis*, *A. chinensis*, *A. dasyphyloides*, *A. elata* and *A. gintungensis*, while the transverse wrinkles of the remaining three species (*A. cordata*, *A. searelliana*, *A. thomsonii*) originate from the transverse arrangement of the prolonged cells. In addition, the longitudinal sections of the endocarps of most *Aralia* species, i.e., *A. chinensis*, *A. dasyphyloides*, *A. elata*, *A. gintungensis*, *A. searelliana*, *A. thomsonii* and *A. undulata*, are sculptured by circular to elliptic lumina that are arranged in three to five lines; and that of *A. cordata* is reticulate and furrowed, characteristics not observed in the fossil endocarps. The longitudinal sections of the fossils are sculptured by stratostructure that is densely arranged close to the interior surface and perpendicular to both the exterior and interior surfaces. The presence and arrangement of the stratostructure are similar only to the endocarps of *A. echinocaulis*. Generally, the endocarp morphology and anatomy show that the new fossil taxon carpologically resembles *A. echinocaulis*. The difference between the fossil and modern taxa is that the stratostructure elements on the longitudinal section of the fossils are more densely arranged than *A. echinocaulis*. Furthermore, the transverse wrinkles on the interior surfaces of the fossils are partly crossed by a few longitudinal wrinkles, which are not prominent in *A. echinocaulis*. Therefore, it is appropriate to designate the fossils to a new fossil species, *Aralia stratosa* sp. nov.

5. Biogeographical implications

Modern *Aralia* is widely distributed in low latitude regions in eastern Asia and the Americas (Li, 1952; Wen, 2001, 2011), in contrast to its past distributional ranges which were mainly in boreal areas as revealed by fossil records (e.g., Drofeev, 1963, 1988; Mai and Walther, 1988; Geissert et al., 1990; Mai, 1997, 2001; Kovar-Eder and Meller, 2001; Nikitin, 2006). This suggests an overall southward movement or shrinkage of its geographical distribution since the Paleogene. The newly described fossil taxon, *Aralia stratosa* sp. nov., was recovered from the upper Pliocene of southwest China. It represents the first confirmed fossil record from a much lower latitude region. This new find implies that an *Aralia* population was already established in relatively low latitudes at least in the late Pliocene. This is in line with the assumption based on molecular analysis that *Aralia* might have populated the low latitudes of eastern Asia during the Miocene or earlier (Wen et al., 1998; Wen, 2000). *Aralia stratosa* also represents one of the few fossil records of *Aralia* in eastern Asia. This therefore provides new important information to better frame the distributional pattern and species diversity of the genus in the Asian Cenozoic. It suggests a wider biogeographical distribution of the genus in the geological time than we previously thought.

Aralia was represented by pollen, leaves and seeds (endocarps) in previous records. As the pollen of *Aralia* resembles that of its closest relatives, such as *Panax* (Wen and Nowicke, 1999; Wen, 2001, 2011; Wen et al., 2001), pollen fossils of the genus may not be readily recognized. This is perhaps the key reason why only a few pollen fossil records of this genus have ever been reported (e.g., Portniagina, 1971).

243 Megafossils of the genus, including leaves and endocarps, however, have more stable
244 taxonomy owing to their diagnostic morphologies. For this reason, the discussion here
245 is based only on megafossil records. The earliest *Aralia* fossils were represented by
246 the early Cretaceous leaves from Canada (Mellon et al., 1963) and the United States
247 (Fontaine, 1889; Berry, 1922), suggesting a North American origin of the genus as
248 early as the Cretaceous. *Aralia* fossils from this continent were also represented by
249 leaves from other periods, such as the middle Eocene (e.g., Knowlton, 1899). In
250 Eurasia, the first fossil record of *Aralia* is represented by Eocene leaves from eastern
251 Russia (Fedotov, 1977) and Eocene seeds from central Russia (Nikitin, 2006). This
252 suggests that *Aralia* might have dispersed from North America to eastern Asia most
253 likely via the Bering land bridge, which functioned as a corridor for biotic
254 connections between North America and eastern Asia from the middle Cretaceous to
255 Pliocene (Wen and Jasen, 1995). The genus probably entered Europe during the
256 Miocene, as the Turgai Strait completely closed by the Oligocene, removing a
257 biogeographical barrier (Tiffney, 1985; Wen, 1999; Scotese, 2004). Based on the
258 abundant *Aralia* fossil records from the European Neogene (e.g., Szafer, 1954; Gregor,
259 1978; Łańcucka-Środoniowa, 1979; Mai and Walther, 1988; Geissert et al., 1990;
260 Martinetto et al., 1997; Mai, 1997, 2001; Fig. 2), we presume that *Aralia* might have
261 already broadly flourished on the continent at that time. The genus likely began to
262 diminish in Europe since the Pleistocene, as revealed by the decreasing and lacking
263 fossil records, and eventually became extinct there (Fig. 2). Hence, the
264 intercontinental disjunction of the genus between eastern Asia and the Americas

might have been established no earlier than the Pleistocene. In eastern Asia, *Aralia* probably underwent biogeographical expansion and southward dispersal after its first appearance in the Eocene. The genus likely started to colonize lower latitude regions no later than the Pliocene, as was demonstrated by the newly described fossils and previous molecular data (Wen et al., 1998; Wen, 2000). This southward distributional extension might have been driven mainly by the global cooling and northern aridification (Zachos et al., 2001; Mosbrugger et al., 2005; Eronen et al., 2010, 2012).

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Table 1. Comparison of the fossils with endocarps of 14 genera of Araliaceae. Endocarp morphological data of two genera (*Hedera* and *Tetrapanax*) were obtained from published data (Bojňanský and Fargašová, 2007; Guo et al., 2009), while those of the remaining 12 genera were based on our observations from herbarium specimens.

Table 2. Carpological comparisons between *Aralia stratosa* sp. nov. and nine extant species of *Aralia*.

Fig. 1. Map showing the fossil site where the *Aralia* fossil endocarps were collected.

Fig. 2. Map showing the megafossil records and modern distribution ranges of *Aralia*.

Plate I. *Aralia stratosa* sp. nov., lateral view of the fossil endocarps. Scale bar = 0.5 mm for all images.

Plate II. *Aralia stratosa* sp. nov., surface microstructures, and longitudinal sections of the fossil endocarps with the SEM and X-ray tomographic microscope. Scale bar = 25 μ m for 2; 0.01 mm for 4–5; 50 μ m for 3 and 6; 0.1 mm for 1; and 0.5 mm for 7.

1–2. Exterior surface, showing the transverse, discontinuous wrinkles nearly parallel with each other.

3–5. Interior surface, showing the transverse wrinkles with a parallel arrangement that are partially crossed by a few indistinctive wrinkles.

6. Longitudinal section under the SEM, showing stratose elements vertical to both the exterior and interior surfaces that are arranged loosely near the exterior surface but densely near the interior surface.

7. Longitudinal section under the X-ray tomographic microscope, showing stratose elements vertical to both the exterior and interior surfaces.

a. Wrinkles. b. Stratose elements.

Plate III. Endocarps of 11 extant representatives belonging to 11 genera of the Araliaceae. Scale bar = 2 mm for all images. 1. *Eleutherococcus cissifolius*. 2. *Fatsia polycarpa*. 3. *Gamblea ciliata*. 4. *Dendropanax chevalieri*. 5. *Kalopanax pictus*. 6.

466 *Merrilliopanax listeri*. 7. *Metapanax davidii*. 8. *Panax japonicus*. 9. *Polyscias*
467 *delavayi*. 10. *Schefflera brevipedicellata*. 11. *Macropanax undulatus*.

468 **Plate IV.** Endocarps of *Aralia stratos* sp. nov. and extant *Aralia* species observed
469 under the SEM. Scale bar = 0.5 mm for images 1, 5, 9, 13 and 17; 50 μ m for images
470 2–4, 6–8, 10–12, 14–16 and 18–20. 1–4. *A. stratos*. 5–8. *A. echinocaulis*. 9–12. *A.*
471 *chinensis*. 13–26. *A. cordata*. 17–20. *A. dasyphyloides*. 1, 5, 9, 13 and 17. General
472 shape. 2, 6, 10, 14 and 18. Exterior surface. 3, 7, 11, 15 and 19. Interior surface. 4, 8,
473 12, 16 and 20. Longitudinal section.

474 **Plate V.** Endocarps of extant *Aralia* species observed under the SEM. Scale bar = 0.5
475 mm for images 1, 5, 9, 13 and 17; 0.05 mm for images 2–4, 6–8, 10–12, 14–16 and
476 18–20. 1–4. *A. elata*. 5–8. *A. gintungensis*. 9–12. *A. searelliana*. 13–26. *A. thomsonii*.
477 17–20. *A. elata*. 1–4. *A. gintungensis*. 9–12. *A. searelliana*. 13–26. *A. thomsonii*.
478 17–20. *A. undulata*.

479 1, 5, 9, 13 and 17. General shape.
480 2, 6, 10, 14 and 18. Exterior surface.
481 3, 7, 11, 15 and 19. Interior surface.
482 4, 8, 12, 16 and 20. Longitudinal section.

Fig. 1

Fig. 2

Table 1

Taxa	Shape	Surface details	Size (length × width mm)
The present fossils	Compressed, lunate, semicircular, or elliptic	Transversely wrinkled	2.4–3.1 × 1.5–2.0
<i>Aralia</i>	Compressed, lunate, semicircular, elliptic, or obovate	Transversely wrinkled, or oblong cells transversely and continuously arranged	2.1–3.9 × 1.3–1.9
<i>Dendropanax</i>	Compressed, prolonged elliptic	Longitudinally ribbed (2–3 ribs)	8.2–8.4 × 3.0–3.4
<i>Eleutherococcus</i>	Sectoroid or compressed (lunate, (prolonged) elliptic or obovate)	Randomly or reticulate foveate, or longitudinally wrinkled	3.8–7.9 × 2.2–3.6
<i>Fatsia</i>	Compressed, ovate, elliptic or semicircular	Transversely and finely wrinkled	3.8–4.4 × 2.4–2.6
<i>Gamblea</i>	Planoconvex	Ventral face transversely furrowed, dorsal face longitudinally and weakly ribbed	4.8–5.0 × 3.2–3.4
<i>Hedera</i>	Ellipsoid to obovoid, sectorial, planoconvex	Strongly ruminant	4.2–5.0 × 3.0–3.6
<i>Kalopanax</i>	Compressed, elliptic or obovate	Pusticulate and transversely wrinkled	3.3–3.6 × 2.3–2.5
<i>Macropanax</i>	Concavo-convex	Ventral face finely wrinkled, dorsal face longitudinally ribbed near the margins and transversely and finely wrinkled	6.8–7.2 × 3.2–3.5
<i>Merrilliopanax</i>	Concavo-convex	Ventral face transversely and finely wrinkled, dorsal face randomly wrinkled	4.3–4.4 × 2.8–2.9
<i>Metapanax</i>	Compressed, elliptic or semicircular	Pusticulate and alveolate, or random-alveolate	3.2–4.4 × 1.9–2.8
<i>Panax</i>	Spherical	Dorsal face pusticulate and transversely furrowed	3.6–3.7 × 3.1–3.2
<i>Polyscias</i>	Compressed, lunate or elliptic	Reticulate-alveolate	3.5–4.0 × 2.2–2.5
<i>Schefflera</i>	Compressed, ovate or lunate	Transversely or longitudinally and finely furrowed	3.1–3.9 × 2.0–2.6
<i>Tetrapanax</i>	Planoconvex	Longitudinally ribbed and foveate	About 1.8 × 1.1

Table 2

Taxa	Shape	Size (length × width mm)	L/W	Ventral side	Dorsal side	Exterior surface	Interior surface	Longitudinal section
<i>Aralia rugosa</i> sp. nov.	Lunate, semicircular, elliptic	2.4–3.1 × 1.5–2.0	1.2–1.9	Straight or slightly convex	Convex	Transversely wrinkled	Transversely finely wrinkled	Stratose and vertical to both exterior and interior surfaces
<i>A. echinocaulis</i>	Broad elliptic or obovate	2.2–2.5 × 1.5–1.7	1.3–1.5	Slightly convex	Convex	Transversely wrinkled	Transversely finely wrinkled	Stratose and vertical to both exterior and interior surfaces
<i>A. chinensis</i>	Elliptic	2.6–2.7 × 1.5–1.7	1.6–1.7	Slightly convex	Convex	Transversely wrinkled	Transversely finely wrinkled	Tiny lumina arranged in lines
<i>A. cordata</i>	Broad elliptic	2.3–2.4 × 1.4–1.5	1.5–1.7	Straight or slightly convex	Convex	Prolonged cells transversely and continuously arranged	Transversely finely wrinkled	Reticulate furrowed
<i>A. dasyphylloides</i>	Prolonged elliptic or lunate	2.4–2.6 × 1.3–1.5	1.7–1.9	Straight or slightly convex	Convex	Loosely, transversely wrinkled	Transversely finely wrinkled	Tiny lumina arranged in lines
<i>A. elata</i>	Elliptic	2.2–2.3 × 1.1–1.3	1.8–2.0	Straight or slightly convex	Convex	Loosely, transversely wrinkled	Transversely finely wrinkled	Tiny lumina arranged in lines
<i>A. gantungensis</i>	Broad elliptic	2.2–2.6 × 1.5–1.7	1.4–1.5	Slightly convex	Convex	Loosely, transversely wrinkled	Transversely finely wrinkled	Tiny lumina arranged in lines
<i>A. searelliana</i>	Prolonged elliptic or lunate	3.9–4.1 × 1.9–2.1	1.8–2.1	Straight or slightly convex, with a prolonged sheet structure	Convex	Prolonged cells transversely and continuously arranged	Transversely finely wrinkled	Tiny lumina arranged in lines
<i>A. thomsonii</i>	Broad elliptic	2.7–2.9 × 1.6–1.8	1.5–1.7	Straight or slightly convex, with a prolonged sheet structure	Convex	Prolonged cells transversely and continuously arranged	Transversely finely wrinkled	Tiny lumina arranged in lines
<i>A. undulata</i>	Broad elliptic	2.0–2.3 × 1.3–1.5	1.4–1.6	Slightly convex	Convex	Transversely wrinkled	Transversely finely wrinkled	Tiny lumina arranged in lines