



Research papers

New fossil endocarps of *Sambucus* (Adoxaceae) from the upper Pliocene in SW China

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ABSTRACT

A new species of fossil endocarp is described from the Sanying Formation of the upper Pliocene at Fudong Village, Lanping County of northwestern Yunnan Province, Southwest China. The endocarps are elliptic, ovate or oblong elliptic, 2.1–2.5 mm long and 1.2–1.7 mm wide. The dorsal face is convex and the ventral is concave or more flattened. The endocarp surface is loosely, transversely or sinuously furrowed and ridged, forming a reticulate and alveolate pattern on the ridges, and the inner wall of the surface cells on the ridges is flaky and scaly. They are morphologically compared with selected extant genera of Adoxaceae and Caprifoliaceae. The interspecific comparisons show diagnostic differences of the fossil endocarps from the selected modern species and other fossil taxa, supporting their recognition as a new species: *Sambucus alveolatisemina* Huang, Liu et Zhou, sp. nov. Previous records of the reliable *Sambucus* fossils were from mid-high latitude regions in Europe, northeastern Asia and northern North America. Therefore, it is interesting to note that *S. alveolatisemina* represents a fossil record from a low latitude region. *Sambucus* apparently has existed at low latitudes in China at least since the upper Pliocene. A review of other *Sambucus* fossil occurrences indicates that plants of this genus have been living at higher latitudes in the geological past than they are at present.

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1. Introduction

Sambucus L. of Adoxaceae is a small genus of approximately 25 species of deciduous shrubs, small trees and a few perennial herbs (Eriksson and Donoghue, 1997). It is mainly distributed in temperate and subtropical regions of the Northern Hemisphere, but a few species occur in the Southern Hemisphere, restricted to parts of Australasia and South America (Hu and He, 1988; Wu et al., 1991b).

The organs of *Sambucus* plants, such as pollen, wood and endocarp, are often preserved as fossils (Table 4). *Sambucus* pollen lacks diagnostic characteristics that distinguish it from *Adoxa* and *Viburnum* in the Adoxaceae (Chen et al., 1992; Du et al., 2007; Hu and He, 1988). *Sambucus* wood provides weak evidence for identification, and therefore the reliability of genus assignment based on wood is questionable (Ogata, 1988; Zhu et al., 2004). In contrast to pollen and wood, *Sambucus* endocarps provide highly reliable diagnostic characteristics at both the generic and specific levels (Hu et al., 1996). Transverse furrows and ridges on the surface are exclusively diagnostic of *Sambucus* endocarps

(Chandler, 1961; Hu et al., 1996; Jacobs et al., 2010). Their convex dorsal face and concave or more flattened ventral face are also important characteristics used to distinguish them from the other genera in the Adoxaceae and its sister family Caprifoliaceae (Bojňanský and Fargašová, 2007; Hu et al., 1996; Jacobs et al., 2010). Therefore, endocarp remains of *Sambucus* can be identified reliably and are considered the most reliable *Sambucus* fossils. They are the best material for studying the past biodiversity and biogeography of this genus.

Sambucus endocarps have been widely reported from the Palaeocene to Holocene in Europe (e.g., Reid and Chandler, 1926; Reid and Reid, 1915), northeastern Asia (e.g., Nikitin, 1979, 2006, 2007) and northern North America (e.g., Matthews et al., 1986, 2003) (Table 4). They were all recovered from mid-high latitudes in the Northern Hemisphere. Yunnan Province is situated in Southwest China on the southeast of the Tibetan Plateau, with a latitudinal range of approximately 22°–28° N. The discovery of *Sambucus* endocarp fossils in this region constitutes the southernmost record and is therefore important for our understanding of the fossil history and biogeography of this genus. The Neogene sediments in Yunnan are well developed (Wang, 1990), and contain abundant palaeofloras (e.g., Tao, 1986; Tao et al., 2000). The upper Pliocene Fudong Flora is one of the palaeofloras in this geologically important region. It is well known for its leaf assemblage, which contains more than 120 specimens belonging to 17 species, with a clear dominance of

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Quercus sect. *Heterobalanus* (Tao, 1986). Newly recovered and well preserved fossil fruits/seeds, such as *Sambucus* endocarps from this fossil site preserve surface details that can be studied by scanning electron microscopy (SEM) for improved comparison and identification.

In this study, our purposes include the following three aspects: (1) to morphologically compare the fossil endocarps with related extant and published fossil taxa; (2) to establish the first confirmed fossil record of *Sambucus* from a low latitude region in China; and (3) to provide important evidence of the past biodiversity and biogeography of this genus.

2. Materials and methods

2.1. Fossil site

The fossil site is located at Fudong Village, 1 km southeast of Lanping County, northwestern Yunnan Province, Southwest (SW) China (26°28'N, 99°26'E; 2470 m asl; Fig. 1). The deposit belongs to the Sanying Formation based on regional stratigraphic correlations (BGMRYP, 1990; WGRSY, 1978). The geological age of the Sanying Formation is determined as upper Pliocene mainly based on regional stratigraphic correlations (BGMRYP, 1990; Ge and Li, 1999; WGRSY, 1978), floristic assemblage (Tao, 1986), and pollen assemblage (Xu et al., 2004). Recently recovered mammalian fossils, such as *Cervavitus* sp. from this formation demonstrated that the Sanying Formation belonged to the Piacenzian (upper Pliocene), and further confirmed the age assignment (Su et al., 2011). The geological setting was described in detail following the “Regional Stratigraphy of Southwest China” (WGRSY, 1978) and our field observation (Fig. 2). The sediments are 702.6 m thick and comprise 12 lithologic units, within which plant fossils occur. Three units yield abundant plant fossils, i.e., carbonaceous layers within the red claystone, claystone with fine sandstone and grey–yellow fine sandstone. These units are 16.8 m, 83.8 m and 87.5 m thick, respectively. The fossil endocarps in this

Strata	Thickness (m)	Stratigraphic column	Lithology	
Quaternary			Alluvia and eluvia	
Pliocene	Sanying Formation		Sandstone with conglomerate	
		89.6		Upper part:red claystone Lower part:coarse sandstone
		63.3		Red claystone with carbonaceous layers
		16.8		White-yellow coarse
		16.4		Siltstone with conglomerate
		27.6		Upper part:claystone with fine sandstone Lower part:black shale
		83.8		Fine sandstone
		34.1		Grey siltstone
		18.4		Grey-yellow fine sandstone with several lignite seams
		114		Conglomerate
		37.8		Upper part:grey claystone Lower part:fine sandstone
		37.2		Grey sandstone and conglomerate, with a lignite seam
87.5		Red boulder conglomerate		
Mesozoic			Red boulder conglomerate	

Plant fossil

Fig. 2. Stratigraphy of the Fudong fossil site (modified from WGRSY [1978]). Charcoalified fruits and seeds were collected from a carbonaceous layer within the red claystone.

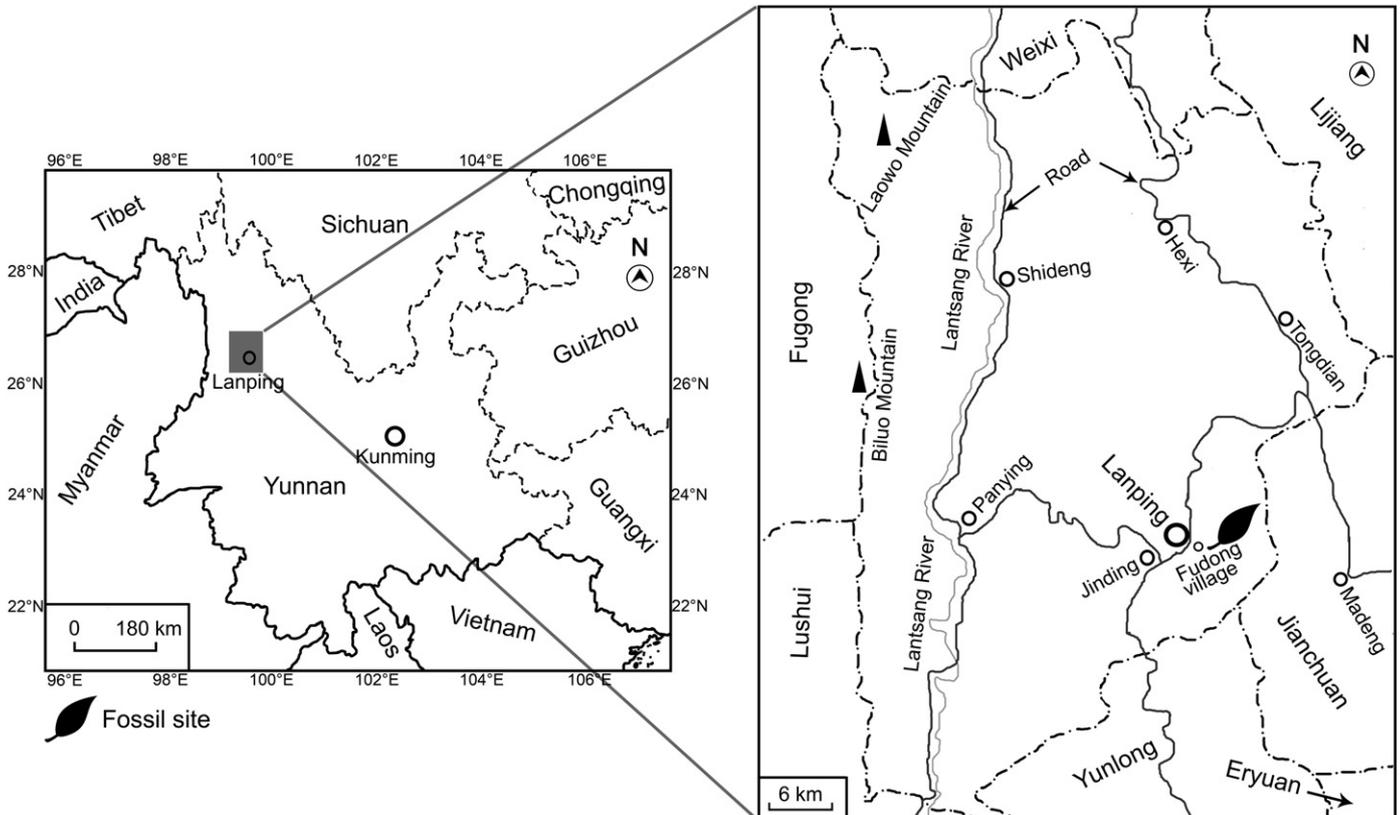


Fig. 1. Map showing the location of the fossil site in northwestern Yunnan, Southwest China. The fossil site, labelled by a black leaf, is approximately 1 km southeast of the county seat of Lanping County.

Table 1
Comparison of the present fossils with 12 selected extant genera in the Adoxaceae and Caprifoliaceae. Endocarp morphological data from 11 genera (*Adoxa*, *Sambucus*, *Viburnum*, *Diervilla*, *Kolkwitzia*, *Leycesteria*, *Linnaea*, *Lonicera*, *Symphoricarpos*, *Triosteum* and *Weigela*) were taken from Wu et al. (1991a, 1991b), Ishikawa (1994), Hu et al. (1996), Bojňanský and Fargašová (2007), Guo et al. (2009) and Jacobs et al. (2008, 2009, 2010). Endocarp morphology of *Abelia* was observed from herbarium specimens. L = length; W = width.

Taxa	Family	Shape	Surface	Size (L×W mm)
The present fossil	Adoxaceae	Elliptic, ovate or oblong elliptic, dorsal face convex, ventral face concave or more flattened	Transversely furrowed and ridged	2.1–2.5×1.2–1.7
<i>Abelia</i>	Caprifoliaceae	Fusiform	Longitudinally furrowed and ribbed	4.0–7.0×1.2–3.5
<i>Adoxa</i>	Adoxaceae	Elliptic or ovate, often laterally compressed	Finely waved	2.4–2.8×1.7–2.0
<i>Diervilla</i>	Caprifoliaceae	Elliptic or ovate, laterally compressed	Reticulate to foveolate	0.9–1.1×0.6–0.9
<i>Kolkwitzia</i>	Caprifoliaceae	Elliptic or ovate	Smooth, with a long beak	6.0–8.0×2.0–2.4
<i>Leycesteria</i>	Caprifoliaceae	Elliptic or ovate, laterally compressed	Smooth	0.9–1.2×0.5–0.9
<i>Linnaea</i>	Caprifoliaceae	Ovate, enfolded by persistent bracteoles	Often smooth	3.3–3.7×1.9–2.2
<i>Lonicera</i>	Caprifoliaceae	Elliptic or ovate, laterally flattened or compressed	Waved or smooth, sometimes tuberculate, roundly or longitudinally furrowed	2.0–6.1×1.4–4.5
<i>Sambucus</i>	Adoxaceae	Elliptic or ovate, dorsal face convex, ventral face concave or more flattened	Transversely furrowed and ridged	0.9–3.5×0.6–2.5
<i>Symphoricarpos</i>	Caprifoliaceae	Elliptic, dorsal face slightly convex, ventral face flattened	Smooth	2.2–4.7×1.8–3.2
<i>Triosteum</i>	Caprifoliaceae	Unknown	Often with 5–6 ribs	4.5–6.6×1.8–3.2
<i>Viburnum</i>	Adoxaceae	Elliptic or ovate, laterally flattened or compressed,	Waved or tuberculate, dorsal or/and ventral face longitudinally furrowed	4.0–10×3.0–6.0
<i>Weigela</i>	Caprifoliaceae	Cylindric, slanting at the apex and the inner wall, winged to some extent	Waved or reticulate or foveolate	1.3–1.7×0.7–0.9

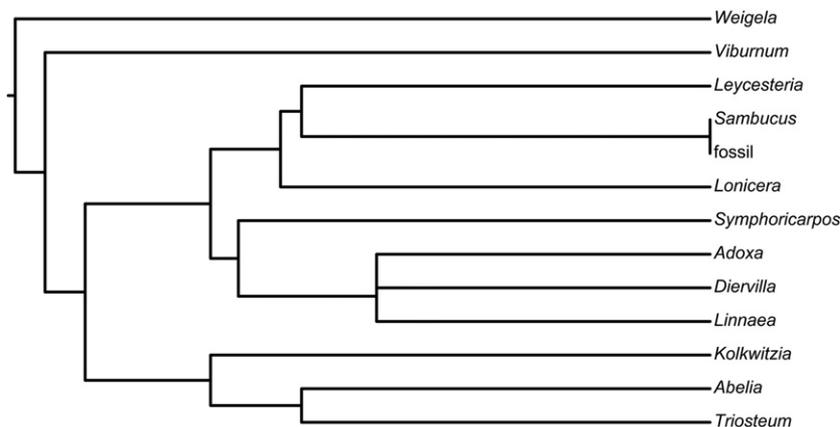


Fig. 3. Cluster analysis of the fossil taxon and 12 extant genera in Adoxaceae and Caprifoliaceae based on endocarp morphological data. The analysis shows that the present fossil taxon is much closer to the genus *Sambucus* in endocarp morphology.

study were all uncovered from one carbonaceous layer that was approximately 1–3 cm thick within the red claystone.

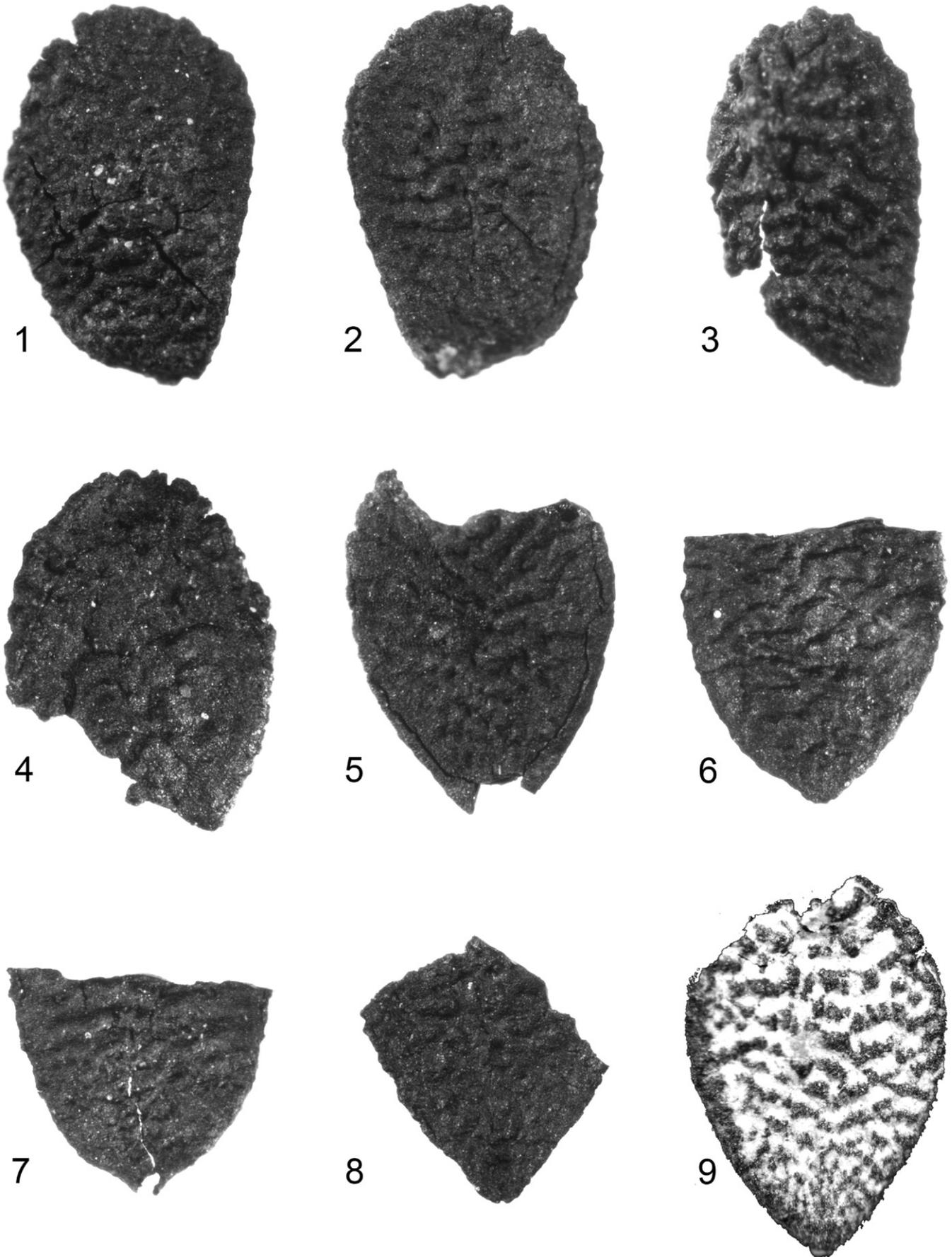
2.2. Fossil sampling and processing

One carbonaceous organic-rich layer within the red claystone was sampled for fossil material in the field. Samples of clay approximately 12 dm³ were soaked in water with a small amount of H₂O₂ (30%) until a slurry was formed. The slurry was then washed and sieved gradually in a 0.5 mm sieve to remove finer sediments from the

charcoalified plant fragments. The residues were further sieved in water using a 4 mm sieve to remove the larger fragments, and facilitate observation. Fossil fruits and seeds were then sorted out from the other organic remains under a stereomicroscope. They were carefully cleaned using an ultrasonic cleaner (UC, KO – 50 M) at a frequency of 40 kHz to remove adhering clay particles on the fossil surface. In total, more than 200 specimens of charcoalified fruits and seeds were separated. Nine specimens were identified as *Sambucus* endocarps according to their characteristic convex dorsal face, concave or more flattened ventral face, and transverse furrows and ridges on the surface.

Plate 1. Fossil endocarps of *Sambucus alveolatisemina* Huang, Liu et Zhou, sp. nov. from Fudong Village, northwestern Yunnan, Southwest China. Scale bar for all images = 1 mm.

- 1–2. Holotype FD 001.
 1. Showing the dorsal face.
 2. Showing the ventral face.
3. Paratype FD 002, showing the dorsal face.
4. Paratype FD 003, showing the roundish apex.
5. Paratype FD 004.
6. Paratype FD 005.
7. Paratype FD 006.
8. Paratype FD 007.
- 5–8. Showing that the endocarp base gradually narrows.
9. Paratype FD 008, showing the fossil specimen without treatment by the ultrasonic cleaner (UC).



2.3. Morphological observation

The general morphology of the endocarps was examined under a binocular microscope (BM, SZX16). The detailed surface characteristics were observed under a scanning electron microscope (SEM, KYKY-

1000). Virtual cross and longitudinal sections were scanned by synchrotron radiation-based X-ray tomographic microscopy (SRXTM, 2-BM).

The fossils were morphologically compared with endocarps from selected extant taxa of Adoxaceae and its sister family Caprifoliaceae. They were also compared with the previously published fossil taxa.

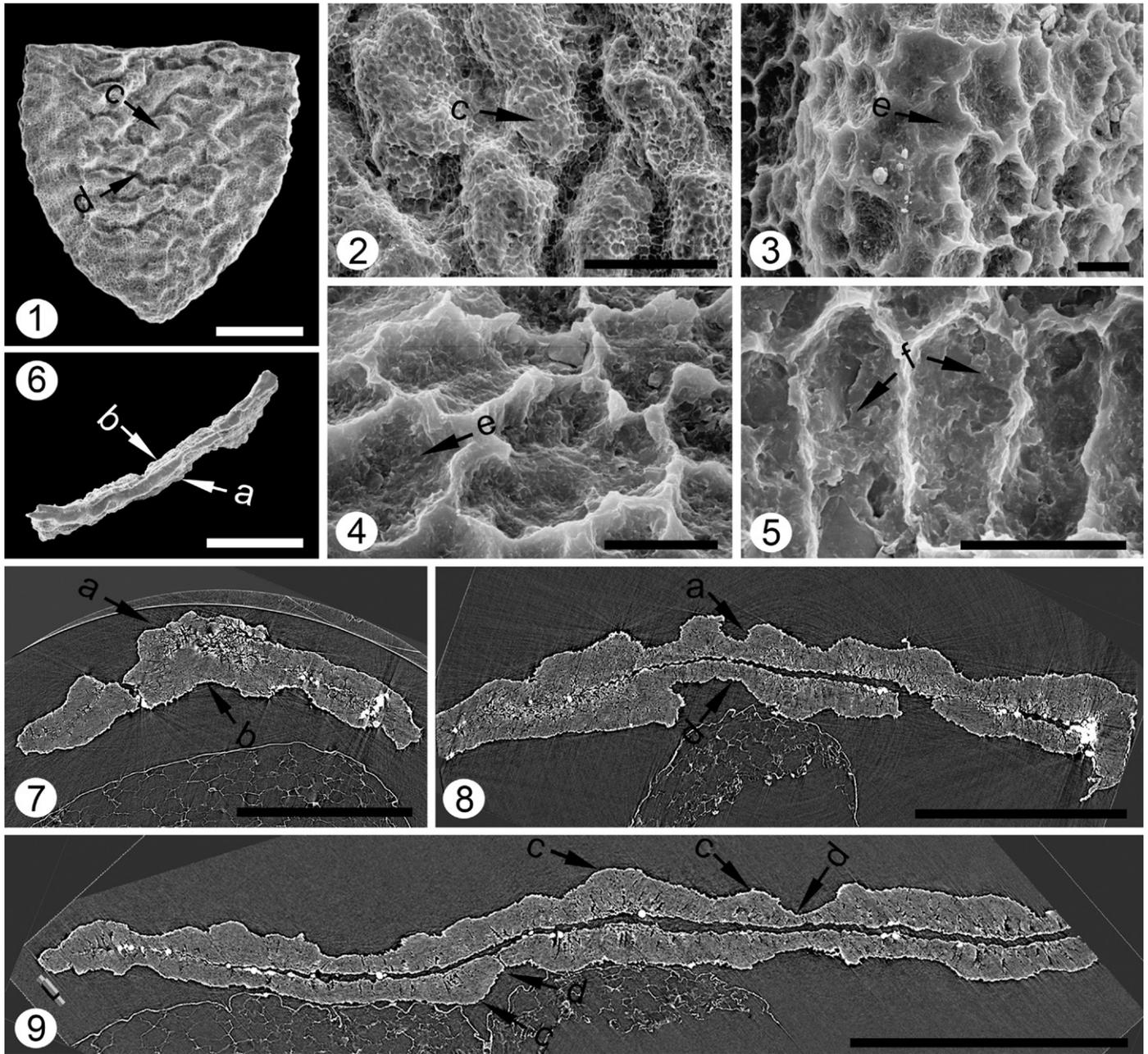


Plate II. Endocarp surface and cross/longitudinal details of *Sambucus alveolatisemina* Huang, Liu et Zhou, sp. nov. studied using SEM and X-ray microtomography. Scale bar = 0.5 mm for Plate II, 1, 6–9; 0.1 mm for Plate II, 2; 0.01 mm for Plate II, 3–5.

1. General view of the fossil endocarp. Ridges and furrows can be clearly seen.
2. Surface details. The ridge surface shown is reticulate and alveolate.
- 3–5. Surface details. The inner wall of the surface cells on the ridges is flaky and scaly.
6. Cross section studied using SEM. The dorsal face is convex, and the ventral face is concave or more flattened.
- 7–8. Cross section studied with X-ray microtomography. The dorsal face is convex, and the ventral face is concave.
9. Longitudinal section studied with X-ray microtomography. The raised point shows the ridge, and the sunken part shows the furrow.
- a. Dorsal face.
- b. Ventral face.
- c. Ridge.
- d. Furrow.
- e. A surface cell on the ridge.
- f. The inner wall of a surface cell.

Table 2

Comparison of the present fossils with 19 selected extant species of *Sambucus*. Endocarp morphological data for three species (*S. coreana*, *S. foetidissima* and *S. mandshurica*) were taken from Hu et al. (1996); data for *S. ebulus* were taken from Bojňanský and Fargašová (2007); and data for another three species (*S. australis*, *S. caerulea* and *S. canadensis*) were taken from Jacobs et al. (2010). The endocarp morphology of the other 12 species was observed from the herbarium specimens. L = length; W = width.

Species	Shape	Size (L×W mm)	L/W	Apex	Base	Number of ridges	Surface details
The present fossil	Elliptic, ovate or oblong elliptic	2.1–2.5×1.2–1.7	1.5–1.8	Roundish	Gradually narrowed	12–14	Loosely, transversely or sinuously ridged, ridge surface reticulate and alveolate
<i>S. adnata</i>	Elliptic	2.3–2.7×1.4–1.7	1.5–1.6	Roundish	Slightly roundish	8–10	Transversely ridged, ridge surface reticulate and alveolate
<i>S. australis</i>	Unknown	2.9–3.3×1.6–2.0	1.8	Unknown	Unknown	Unknown	Unknown
<i>S. bugergeriana</i>	Oblong elliptic	2.8–3.4×1.3–1.7	2.0–2.1	Roundish	Roundish, gradually narrowed	15–17	Transversely ridged, ridge surface reticulate
<i>S. caerulea</i>	Triangular	2.8–3.0×1.9–2.1	1.4	Roundish	Narrowed	13–15	Transversely ridged
<i>S. canadensis</i>	Triangular	2.6–3.0×1.4–1.8	1.7	Nearly straight	Narrowed	12–15	Loosely, transversely ridged
<i>S. chinensis</i>	Ovate, nearly roundish	1.6–1.9×1.4–1.6	1.1–1.2	Roundish	Narrowed	6–7	Transversely ridged, ridge surface reticulate and alveolate
<i>S. coreana</i>	Elliptic	1.4–1.6×0.8–1.0	1.6–1.7	Slightly roundish	Gradually narrowed	Unknown	Tuberculate
<i>S. ebulus</i>	Elliptic	3.2–3.4×1.6–1.8	1.9–2.0	Slightly roundish	Gradually narrowed	Unknown	Transversely ridged
<i>S. foetidissima</i>	Oblong elliptic, ovate	1.1–1.4×0.7–1.0	1.4–1.5	Roundish	Gradually narrowed	Unknown	Transverse and interruptive ridges
<i>S. hookeri</i>	Triangular, drop-shaped	2.5–2.8×1.6–1.8	1.5–1.6	Roundish	Narrowed and pointed	7–8	Transversely ridged, ridge surface reticulate and alveolate
<i>S. javanica</i>	Ovate, nearly roundish	2.2–2.6×1.8–2.2	1.1–1.2	Roundish	Narrowed	7–8	Transversely ridged, ridge surface tuberculate
<i>S. latipinna</i>	Oblong elliptic	2.1–2.4×1.3–1.6	1.5–1.6	Roundish	Gradually narrowed, with a protuberance	11–12	Transversely ridged, ridge surface reticulate
<i>S. mandshurica</i>	Oblong elliptic, ovate	2.0–2.5×1.3–1.5	1.5–1.7	Slightly roundish	Gradually narrowed	16–18	Transverse and interruptive ridges
<i>S. mexicana</i>	Ovate, nearly roundish	2.6–2.9×1.9–2.1	1.3–1.4	Roundish	Roundish	9–10	Transversely ridged, ridge surface weakly reticulate
<i>S. nigra</i>	Oblong elliptic	2.3–2.7×1.3–1.4	1.7–2.0	Roundish	Gradually narrowed, with a protuberance	10–11	Transversely ridged, ridge surface reticulate and alveolate
<i>S. pubens</i>	Oblong elliptic	2.0–2.4×1.2–1.4	1.6–1.7	Roundish	Slightly roundish, gradually narrowed	15–16	Transversely ridged, ridge surface tuberculate
<i>S. racemosa</i>	Elliptic	2.0–2.3×1.2–1.4	1.6–1.7	Roundish	Roundish	13–14	Transverse and weak ridges, ridge surface nearly smooth
<i>S. sieboldiana</i>	Oblong	2.7–3.0×1.4–1.6	1.8–1.9	Roundish	Gradually narrowed	17–19	Transversely ridged, ridge surface weakly reticulate
<i>S. williamsii</i>	Nearly roundish	2.6–2.9×2.2–2.5	1.1–1.2	Roundish	Roundish	11–13	Transversely ridged, ridge surface reticulate and alveolate

Morphological data were mainly retrieved from the literature (e.g., Bojňanský and Fargašová, 2007; Chandler, 1963; Jacobs et al., 2010; Nikitin, 2006). The endocarp morphology of *Abelia* and 12 extant

species of *Sambucus* was observed from herbarium specimens obtained from the Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences (KUN). To reveal the surface details of the

Table 3

Comparison of the present fossils with previously published fossil taxa of *Sambucus*. The data are from Reid and Reid (1915), Reid and Chandler (1926), Chandler (1961, 1963), Dorofeev (1963), Nikitin (2006), Velichkevich and Zastawniak (2007), Martinetto (2009) and Zyuganova (2009). L = Length; W = Width.

Fossil taxa	<i>S. alveolatisemina</i>	<i>S. pulchella</i>	<i>S. pulchella</i>	<i>S. parvula</i>	<i>S. mudensis</i>	<i>S. lucida</i>	<i>S. minor</i>	<i>S. nigra</i>	<i>S. nigra</i>
Reference	This study	Reid and Reid, 1915; Dorofeev, 1963; Nikitin, 2006	Velichkevich and Zastawniak, 2007	Reid and Chandler, 1926; Chandler, 1961	Chandler, 1963	Dorofeev, 1963; Nikitin, 2006	Nikitin, 2006	Martinetto, 2009	Zyuganova, 2009
Age	Upper Pliocene	Pliocene	Upper Pliocene	Palaeocene	Paleogene	Upper Oligocene to lower Miocene	Priabonian of upper Eocene	Middle Pleistocene	Upper Pleistocene
Locality	Northwestern Yunnan, Southwest China	Western Siberia	Southeastern Belarus	Dorset, southern England	Southern England	Tomsk, eastern Russia	Novosibirsk, Russia	Lombardy, northern Italy	Valdai Upland, northwestern Russia
Shape	Elliptic, ovate, oblong elliptic	Ovate, oblong	Elliptic, ovate	Oblong elliptic, ovate	Elliptic, oblong elliptic	Ovate, oblong elliptic	Elliptic, ovate	Ovate	Elliptic, ovate
Apex	Roundish	Roundish	Roundish	Roundish	Roundish	Roundish	Roundish	Roundish	Roundish
Base	Gradually narrowed	Narrowed, pointed	Narrowed	Gradually narrowed	Gradually narrowed	Gradually narrowed	Narrowed, pointed	Narrowed	Narrowed
Surface	Transversely or sinuously furrowed and ridged	Transversely furrowed and ridged	Transversely furrowed and ridged	Transversely furrowed and ridged	Transversely furrowed and ridged	Transversely furrowed and ridged	Transversely furrowed and ridged	Transversely furrowed and ridged	Transversely furrowed and ridged
Size (L×W mm)	2.1–2.5×1.2–1.7	1.6–3.2×0.9–1.8	2.92×1.64	0.9–1.4×0.6–0.9	2.1–2.8×1.2–1.5	1.5–2.8×0.9–1.8	1.0–1.5×0.7–0.9	1.8–3.4×0.9–1.4	4.13×2.27

comparative endocarps from the herbarium specimens for better comparisons with the fossils, some treatment was performed following Forman (1974) and Tiffney (1991).

The terminology used in this study mainly follows Jacobs et al. (2010), except for the terminology for characteristics of ridge surface details and the number of ridges. The number of ridges intercepted by a fictitious vertical line from the apex to the base of the endocarp is defined as the number of ridges. The format of the descriptions of a new plant fossil taxon mainly follows Punt (1994).

2.4. Morphological affinities

To confirm the morphological affinities of the fossil endocarps with the extant groups, we carried out a cluster analysis. We built a taxon-characteristic matrix, including 13 taxa, i.e., the newly described fossil species plus 12 genera of Adoxaceae and Caprifoliaceae, and 18 characteristics. The matrix is given as supplementary data (Appendix). The cluster analysis was carried out using the software Past (Hammer et al., 2001) and Euclidean distances.

3. Systematics

Species: Sambucus alveolatisemina Huang, Liu et Zhou, sp. nov. (Plate I, 1–9; Plate II, 1–9)

Holotype: FD 001 (Plate I, 1–2).

Paratypes: FD 002 (Plate I, 3), FD 003 (Plate I, 4), FD 004 (Plate I, 5), FD 005 (Plate I, 6; Plate II, 1–5), FD 006 (Plate I, 7; Plate II, 7), FD 007 (Plate I, 8), FD 008 (Plate I, 9), and FD 009 (Plate II, 7–9).

Repository: All specimens are housed at KUN.

Type locality: Fudong Village, 1 km southeast of Lanping County, northwestern Yunnan, Southwest China (26°28'N, 99°26'E).

Stratigraphic horizon: In the carbonaceous layer within the red claystone of the upper Pliocene Sanying Formation.

Etymology: The specific epithet *alveolatisemina* is given for the alveolate sculpture on the ridge surface of the fossil endocarps, a unique characteristic compared to the extant species of *Sambucus*. It comprises two Latin words: *alveolatum* and *semen*, meaning alveolate and seed, respectively.

Diagnosis: Endocarps elliptic, ovate or oblong elliptic; dorsal face convex and ventral face concave or more flattened; surface transversely furrowed and ridged; ridge surface reticulate and alveolate.

Description: Endocarps elliptic (Plate I, 3–5), ovate (Plate I, 1–2, 9), or oblong elliptic (Plate I, 3); apex roundish and inflated (Plate I, 1–4), base gradually narrowed (Plate I, 1–3, 6–9, Plate II, 1); dorsal face convex (Plate I, 3, Plate II, 6–8), ventral face concave (Plate II, 7–8) or more flattened (Plate II, 6); endocarp length 2.1–2.5 mm (mean = 2.4 mm, standard deviation = 0.16, n = 5), width 1.2–1.7 mm (mean = 1.5 mm, standard deviation = 0.17, n = 5), length–width ratio 1.5–1.8; endocarp surface loosely, transversely or sinuously furrowed and ridged (Plate I, 1–2, 4–5; Plate II, 1, 9); number of ridges

12 (Plate I, 3) to 14 (Plate I, 1–2) (mean = 13, standard deviation = 1, n = 2); ridge surface reticulate and alveolate (Plate II, 2); the inner wall of the cells on the ridge surface flaky and scaly (Plate II, 3–5).

4. Morphological comparisons

The present fossil endocarps are characterized by a convex dorsal face and a concave or more flattened ventral face, and transverse furrows and ridges on the surface. The combination of these characteristics demonstrates that the fossil endocarps are similar to endocarps of the genus *Sambucus*. To avoid misidentification, we gathered information on the endocarp morphology of other extant genera, based on data mainly from Bojňanský and Fargašová (2007), and identified their differences compared to the present new fossil species. Here, we particularly compare this fossil taxon with both *Sambucus* and its relatives in detail.

Sambucus was included in the Caprifoliaceae in older classifications (Cronquist, 1981; Hutchinson, 1967, 1973; Takhtajan, 1980; Thorne, 1976), but was later transferred into the Adoxaceae mainly based on morphological and embryological studies (Benko-Iseppon and Morawetz, 1993; Donoghue, 1983; Liang and Wu, 1995; Thorne, 1992; Xu, 1983). The latest phylogenetic and molecular analyses brought new evidence to support this assignment (Eriksson and Donoghue, 1997; Liu et al., 2000; Zhang et al., 2003). *Sambucus* is now widely recognized as a genus in the Adoxaceae (Donoghue et al., 2001; Jacobs et al., 2008, 2010). Adoxaceae and Caprifoliaceae are closely related and are considered as sister families (Eriksson and Donoghue, 1997; Jacobs et al., 2010). To allow a better comparison of the fossils with modern relatives, we include both families in the taxonomic discussion below.

4.1. Placement into *Sambucus*

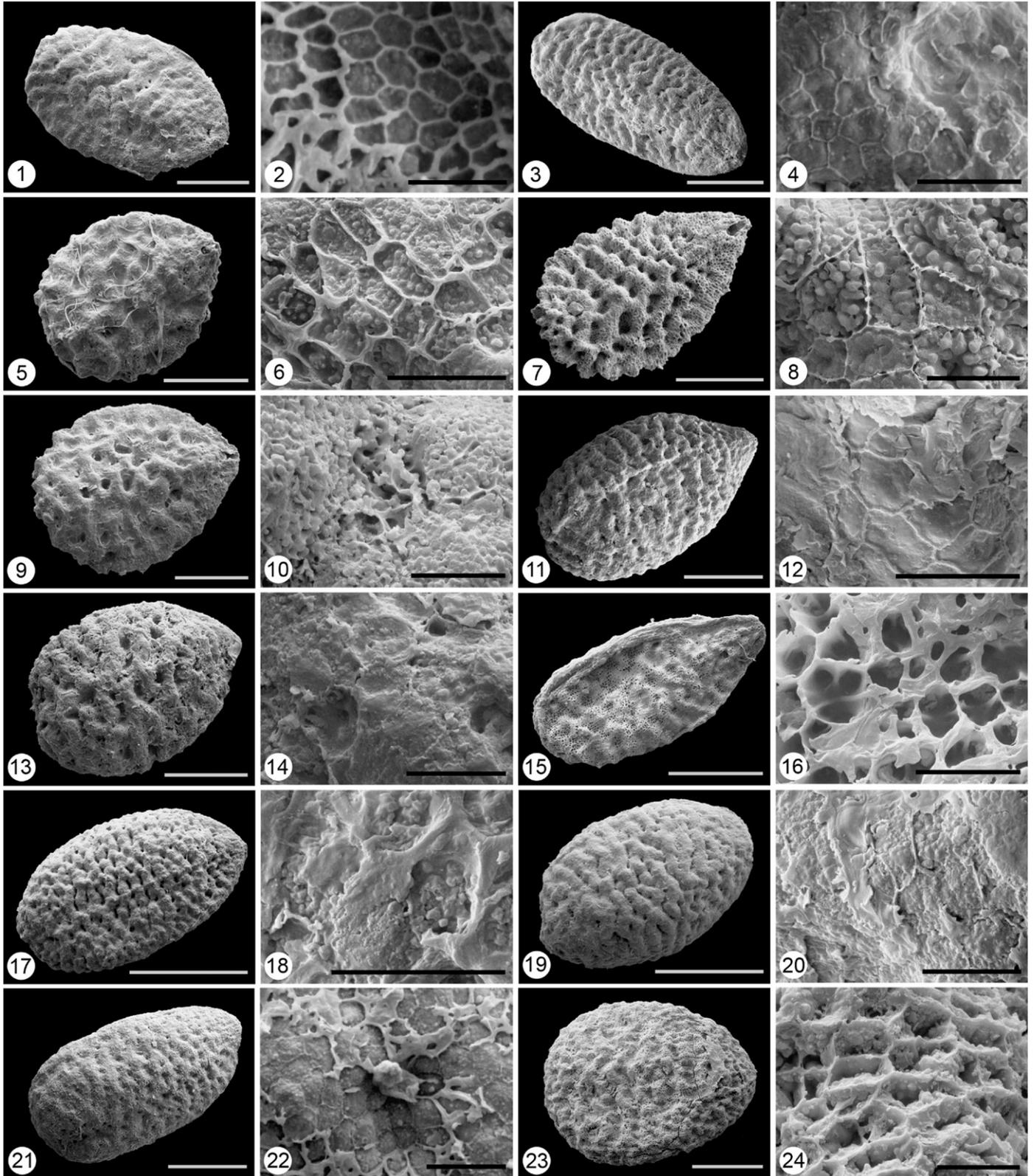
Adoxaceae and Caprifoliaceae together contain approximately 16 genera (Wu et al., 1991a, 1991b). Their endocarps exhibit high morphological diversity (Jacobs et al., 2009, 2010). We gathered endocarp morphological information of 104 species from 12 genera within the two families, representing 75% of the genera. A brief comparison was made for some important morphological features: endocarp shape, size and surface sculpture (Table 1). The most important of these features is surface sculpture, which plays a significant role in generic identification. The endocarp surfaces of four genera (*Kolkwitzia*, *Leycesteria*, *Linnaea* and *Symphoricarpos*) are smooth; the endocarp surfaces of four other genera (*Adoxa*, *Diervilla*, *Triosteum* and *Weigela*) are waved, tuberculate or reticulate-foveolate; and those of the last four genera (*Abelia*, *Lonicera*, *Viburnum* and *Sambucus*) are ribbed and furrowed. The fossil endocarps described here also have furrowed surfaces, and can therefore be compared with the latter four genera. Endocarps of *Abelia*, *Lonicera* and *Viburnum* are roundly or longitudinally ribbed and furrowed, while those of *Sambucus* are transversely

Plate III. Endocarps of extant *Sambucus* species and their surface details observed under SEM. Scale bar = 1 mm for Plate III, 1, 3, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23; 0.05 mm for Plate III, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24.

1–2.	An endocarp of <i>S. adnata</i> , showing the general view and surface details.
3–4.	<i>S. buergeriana</i> .
5–6.	<i>S. chinensis</i> .
7–8.	<i>S. hookeri</i> .
9–10.	<i>S. javanica</i> .
11–12.	<i>S. latipinna</i> .
13–14.	<i>S. mexicana</i> .
15–16.	<i>S. nigra</i> .
17–18.	<i>S. pubens</i> .
19–20.	<i>S. racemosa</i> .
21–22.	<i>S. sieboldiana</i> .
23–24.	<i>S. williamsii</i> .

furrowed. Furthermore, endocarps of *Viburnum* (4.0–10 × 3.0–6.0 mm) are obviously larger than endocarps of *Sambucus* (0.9–3.5 × 0.6–2.5 mm). The fossil endocarps also bear a convex dorsal face, a concave

or more flattened ventral face, transverse furrows and ridges on the surface, and comparable size, which together support their inclusion in the genus *Sambucus*.



The cluster analysis (Fig. 3) shows that the new fossil species is clearly grouped with *Sambucus*, and further confirms the hypothesis of a morphological affinity between the newly described fossils and *Sambucus*; and therefore justifies their inclusion in this genus.

4.2. Assignment to species

The shape, size and surface characteristics of endocarps are variable in different *Sambucus* species, and are therefore useful for infra-generic classification (Jacobs et al., 2010). Our fossil endocarps were compared with endocarps of 19 extant species of *Sambucus*, representing 76% of the species of the genus (Plate III, Table 2). They all share some common features: a convex dorsal face; a concave or more flattened ventral face; and a transversely furrowed and ridged surface. Differences can be seen in the shape, size and surface details. Endocarps of six species (*S. australis*, *S. caerulea*, *S. canadensis*, *S. hookeri*, *S. mexicana* and *S. williamsii*) are obviously larger than the fossil endocarps, whereas those of *S. coreana* and *S. foetidissima* are smaller than the fossil endocarps. The length–width ratio of the endocarps differs considerably among the remaining eleven species. Endocarps of three species (*S. bugergeliana*, *S. ebulus* and *S. sieboldiana*) are slender (length–width ratio 1.8–2.1), while those of *S. chinensis* and *S. javanica* are clearly shorter and wider (length–width ratio 1.1–1.2) than the fossils. The remaining six species (*S. adnata*, *S. latipinna*, *S. mandshurica*, *S. nigra*, *S. racemosa* and *S. pubeus*) have comparable endocarp shape and size with the fossil taxon. However, their surface ornamentation differs from that of the fossils. Although their endocarps all bear transverse ridges on the surface, the number of ridges differs. *S. adnata*, *S. mandshurica*, *S. nigra* and *S. pubeus* have 8–10, 16–18, 10–11 and 15–16 ridges, respectively, while the fossil taxon has 12–14 ridges. Therefore, the fossil taxon can be distinguished from these four species. The last two species (*S. latipinna* and *S. racemosa*) have 11–12 and 13–14 ridges, respectively, similar to that of the fossil taxon. Slight difference can be seen in the endocarp bases. The endocarp base of *S. racemosa* is roundish, and the base of *S. latipinna* has a protuberance, while that of the fossil taxon is gradually narrowed. Therefore, the fossil endocarps cannot be included in any extant species. Consequently, we have described them as a new species: *S. alveolatisemina* Huang, Liu et Zhou, sp. nov..

4.3. Comparison with other fossil taxa

More than seven taxa of *Sambucus* endocarps have been reported from the Palaeocene to Holocene in Europe, northeastern Asia and northern North America (Bůžek et al., 1985, 1996; Chandler, 1961, 1963; Dorofeev, 1963; Knobloch et al., 1996; Martinetto, 2009; Nikitin, 2006; Reid and Chandler, 1926; Reid and Reid, 1915; Velichkevich and Zastawniak, 2007; Zyuganova, 2009) (Table 4). Most of them are well documented with figures, morphological descriptions or both. We compared six fossil taxa with *S. alveolatisemina* based on certain features, such as endocarp shape, size and surface (Table 3). *S. alveolatisemina* and these six fossil taxa are quite similar in endocarp shape and surface details. They share an elliptic or ovate general shape and transverse furrows and ridges on the surface. Difference can be seen only in the endocarp size. The endocarp size of *S. alveolatisemina* (2.1–2.5 × 1.2–1.7 mm) is considerably larger than that of *S. parvula* (0.9–1.4 × 0.6–0.9 mm) and *S. minor* (1.0–1.5 × 0.7–0.9 mm), and smaller than that of *S. nigra* (4.13 × 2.27 mm) from northwestern Russia (Zyuganova, 2009). The remaining three fossil taxa (*S. pulchella*, *S. mudensis* and *S. lucida*) have endocarp sizes comparable to *S. alveolatisemina*. The endocarp sizes of *S. pulchella* from southeastern Belarus and western Siberia are 2.92 × 1.64 mm and 1.6–3.2 × 0.9–1.8 mm, respectively; the endocarps of *S. mudensis* are 2.1–2.8 × 1.2–1.5 mm; and those of *S. lucida* are 1.5–2.8 × 0.9–1.8 mm. Therefore, *S. alveolatisemina* cannot be easily distinguished

from these three fossil taxa based only on endocarp morphology. However, endocarps of *S. pulchella*, *S. mudensis* and *S. lucida* were found in southeastern Belarus and western Siberia, southern England, and southeastern Siberia, respectively. Those regions are geographically distant from Yunnan, Southwest China. Therefore, the fossils described here should not be treated as belonging to *S. pulchella*, *S. mudensis* or *S. lucida*. Further, endocarps of *S. mudensis* and *S. lucida* are Palaeogene and upper Oligocene to lower Miocene in age, respectively, which are significantly lower than that of *S. alveolatisemina*. For these reasons, we believe that the fossil newly described here should be classified as a new species.

5. Discussion

5.1. Fossil history and biogeography of *Sambucus*

Sambucus fossils have been widely reported from the Palaeocene to Holocene in the Northern Hemisphere (Table 4, Fig. 4). They are represented by different organs, i.e., pollen, wood and endocarp. Because the endocarps exhibit highly diagnostic characteristics, using their morphology in genus determination is considered more reliable and convincing (Chandler, 1961; Hu et al., 1996; Jacobs et al., 2010). Therefore, this discussion is exclusively based on the data of the fossil endocarp. The earliest known fossil endocarp of *Sambucus* was found from the Palaeocene in southern England (Chandler, 1961; Reid and Chandler, 1926). Many *Sambucus* fossil endocarps were also recovered from the Palaeocene to Holocene in western Germany, Bulgaria, southeastern Belarus, northwestern Russia and northern Italy in Europe, Siberia in northeastern Asia, and Alaska and northern Canada in northern North America. They mainly occurred in mid-high latitude regions in the Northern Hemisphere (Table 4, Fig. 4), and rarely in low latitude regions or regions from the Southern Hemisphere. *S. alveolatisemina*, however, represents the first confirmed fossil record from a low latitude region in Southwest China. It is also the southernmost fossil record of *Sambucus* and may provide new important evidence to the past geography of this genus. *Sambucus* plants might have been present at low latitudes of China at least since the upper Pliocene.

Today, *Sambucus* plants are widespread in temperate and subtropical regions of the Northern Hemisphere, and a few species exist in the Southern Hemisphere ((Hu and He, 1988; Wu et al., 1991b). They are distributed in both high and low latitude regions of North America, Asia, Europe, northern Africa, the West Indies, the east and southeast of Australia and the Andean region of South America in both hemispheres (Bollí, 1994; Hu and He, 1988) (Fig. 4). A few species even exist and survive at latitude as low as 15°N (e.g., *S. chinensis* is distributed in southern China, India, Thailand, Laos and Vietnam) (Wu et al., 1991b). However, the fossil evidence as discussed above shows their restriction to the Northern Hemisphere and narrower ranges of latitude. Fossil endocarps of *Sambucus* found in Europe, Siberia and Southwest China are within their modern distribution regions. Those from northern North America are out of their modern distribution regions; they clearly occurred at higher latitudes (Fig. 4). These distributions imply that the *Sambucus* plants might have been living at higher latitudes in the geological past than they are at present.

5.2. Palaeoenvironmental implications

The leaf assemblage uncovered at this fossil locality was dominated by *Quercus* sect. *Heterobalanus* (Tao, 1986), which indicates a sclerophyllous forest and mountain climate during the upper Pliocene in northwestern Yunnan, Southwest China. The fossil endocarps of *Sambucus* recovered from the same locality described here thus coexisted with *Quercus* sect. *Heterobalanus*. Sclerophyllous forests are now widespread in the eastern Himalayas and the Hengduan mountains. Modern *Sambucus* plants can be found in these sclerophyllous forests. This implies that the vegetation

Table 4*Sambucus* fossils reported from the Palaeocene to Holocene.

Fossil taxa	Type	Age	Latitude (N)	Locality	References
<i>Sambucus</i> sp.	Pollen	Late Glacial and Holocene	49°23'	Northern France	Bakels, 1995
<i>Sambucus</i> sp.	Pollen	Early Paleolithic	51°28'	Northwestern Altai Mountains, Russia	Bolikhovskaya et al., 2006
<i>Sambucus</i> sp.	Pollen	Upper Miocene to Pliocene	35°53'	Gansu, north-central China	Li et al., 2005
<i>Sambucus</i> sp.	Pollen	Upper Pliocene to lower Quaternary	Around 32°20'	Southwestern Tibet, China	Han et al., 2005
<i>Sambucus</i> sp.	Pollen	9870–2170 cal. BP, Holocene	30°25'–31°43'	Anhui, eastern China	Wang et al., 2008
<i>Sambucus</i> sp.	Pollen	Middle-upper Eocene	Around 40°20'	Central Anatolia, Turkey	Akkiraz et al., 2008
<i>S. colwellensis</i>	Pollen	Oligocene	49°–50°	Northern Czech Republic	Kvaček and Bůžek, 1995; Kvaček and Teodoridis, 2007
<i>Sambucus</i> sp.	Pollen	Pleistocene	30°40'	Georgia, southeastern USA	Rich, 1984
<i>S. alveolatisemina</i>	Endocarp	Sanying Formation, upper Pliocene	26°28'	Northwestern Yunnan, Southwest China	This paper
<i>S. lucida</i>	Endocarp	Upper Oligocene to lower Miocene	Unknown	Tomsk, eastern Russia	Dorofeev, 1963; Nikitin, 2006
<i>S. minor</i>	Endocarp	Priabonian of upper Eocene	Unknown	Novosibirsk, Russia	Nikitin, 2006
<i>S. mudensis</i>	Endocarp	Paleogene	Around 51°	Southern England	Chandler, 1963
<i>S. nigra</i>	Endocarp	Middle Pleistocene	45°48'	Lombardy, northern Italy	Martinetto, 2009
<i>S. nigra</i>	Endocarp	Upper Pleistocene	Around 63°	Valdai Upland, northwestern Russia	Zyuganova, 2009
<i>S. parvula</i>	Endocarp	Palaeocene	Around 51°	Dorset, southern England	Reid and Chandler, 1926; Chandler, 1961
<i>S. pulchella</i>	Endocarp	Upper Pliocene	Around 54°	Southeastern Belarus	Velichkevich and Zastawniak, 2007
<i>S. pulchella</i>	Endocarp	Pliocene	Unknown	Western Siberia	Reid and Reid, 1915; Dorofeev, 1963; Nikitin, 2006
<i>S. pulchella</i>	Endocarp	Paleogene	49°–50°	Northern Czech Republic	Bůžek et al., 1985, 1996; Knobloch et al., 1996;
<i>S. pulchella</i>	Endocarp	Vildštejn Formation, Pliocene	49°–50°	Northern Czech Republic	Kvaček and Teodoridis, 2007
<i>Sambucus</i> sp.	Endocarp	“Lower Clayey–Sandy” Formation, upper Oligocene	49°–50°	Northern Czech Republic	Kvaček and Teodoridis, 2007
<i>Sambucus</i> sp.	Endocarp	Central Paratethys Stage, upper Miocene	Around 51°	Western Germany	Kovar-Eder, 1987
<i>Sambucus</i> sp.	Endocarp	Miocene to Pliocene	60°–70°	Siberia, eastern Russia	Nikitin, 1979, 2007
<i>Sambucus</i> sp.	Endocarp	Meighen Island Beaufort Formation, upper Pliocene	65°–80°	Alaska and northern Canada	Matthews and Ovenden, 1990; Matthews et al., 2003
<i>Sambucus</i> sp.	Wood	Pliocene	Around 45°	Southern Primory'e, far east of Russia	Blokhiina and Bondarenko, 2004
<i>Sambucus</i> sp.	Unknown	Beaufort Formation, upper Pliocene	Around 80°	Banks Island, northern Canada	Matthews et al., 1986
<i>Sambucus</i> sp.	Unknown	Miocene	Around 48°	Northeastern Moldova, Rumania	Negru, 1972
<i>Sambucus</i> sp.	Unknown	6780 ± 135 cal. BP, Holocene	Around 41°	Western Iberia, Portugal	García-Amorena et al., 2007

type and climatic conditions of this region during the upper Pliocene might be, to some extent, similar to the present conditions.

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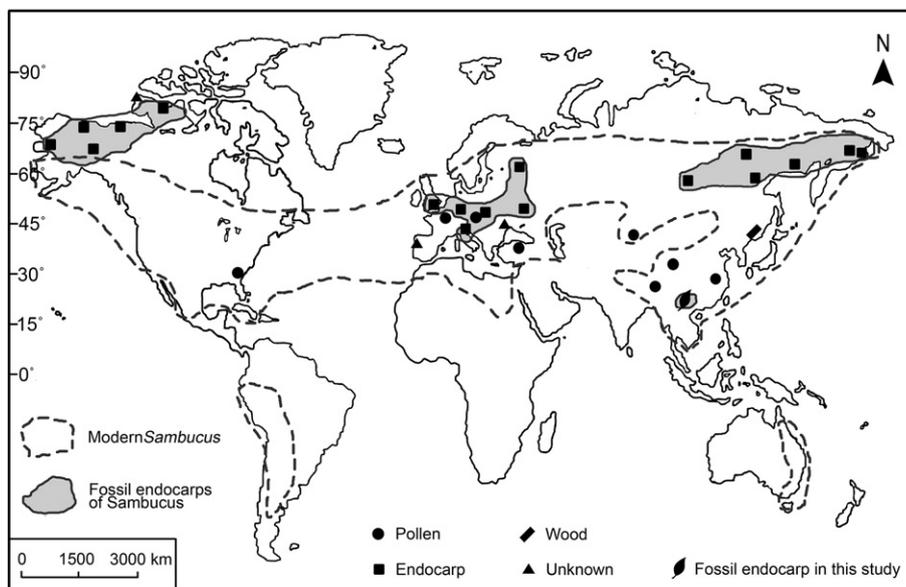


Fig. 4. Map showing the locations from which *Sambucus* fossils were recovered and the general distribution of modern *Sambucus*. The fossil newly described here constitutes the southernmost record of *Sambucus* fossils.

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References

- Akkiraz, M.S., Kayseri, M.S., Akgün, F., 2008. Palaeoecology of coal-bearing Eocene sediments in Central Anatolia (Turkey) based on quantitative palynological data. *Turkish Journal of Earth Sciences* 17, 317–360.
- Bakels, C., 1995. Late glacial and Holocene pollen records from the Aisne and Vesle Valleys, Northern France: the pollen diagrams Maizy–Cuiry and Bazoches. *Mededelingen Rijks Geologische Dienst* 52, 223–234.
- Benko-Iseppon, A.M., Morawetz, W., 1993. Cold-induced chromosome regions and karyosystems in *Sambucus* and *Viburnum*. *Botanica Acta* 106, 183–191.
- Blokhina, N.I., Bondarenko, O.V., 2004. Woody plant assemblages and palaeoenvironments in the Pliocene of Pavlovskaya depression (Southern Primorye). *Acta Palaeontologica Romaniae* 4, 23–35.
- Bojňanský, V., Fargašová, A., 2007. Atlas of Seeds and Fruits of Central and East-European Flora: the Carpathian Mountains Region. Springer, The Netherlands, pp. 505–513.
- Bolikhovskaya, N.S., Derevyanko, A.P., Shun kov, M.V., 2006. The fossil palynoflora, geological age, and climatostratigraphy of the earliest deposits of the Karama site (early Paleolithic, Altai Mountains). *Paleontological Journal* 40 (5), 558–566 (suppl.).
- Bolli, R., 1994. Revision of the genus *Sambucus*. *Dissertationes Botanicae* 223, 1–227.
- Bureau of Geology and Mineral Resources of Yunnan Province (BGMRYP), 1990. Regional Geological of Yunnan Province. Geological Publishing House, Beijing, pp. 248–268.
- Bůžek, Č., Holý, F., Kvaček, Z., 1996. Early Miocene flora of the Cyprus Shale (western Bohemia). *Acta Musei Nationalis Pragae, Series B – Historia Naturalis* 52, 1–72.
- Bůžek, Č., Kvaček, Z., Holý, F., 1985. Late Pliocene palaeoenvironment and correlation of the Vildštejn floristic complex within Central Europe. *Rozpravy ČSAV, Řada matematicko-přírodních věd* 95, 1–72.
- Chen, K.G., Du, F.G., Song, J.H., Huang, Y., 1992. A preliminary study on the pollen morphology of *Sambucus* in Jilin province. *Journal of Jilin Forestry University* 8 (2), 39–46 (in Chinese, with English Abstr.).
- Chandler, M.E.J., 1961. The Lower Tertiary Floras of Southern England I, Palaeocene Floras, London Clay Flora (suppl.). *British Museum (Natural History)*, London, pp. 230–354.
- Chandler, M.E.J., 1963. The Lower Tertiary Floras of Southern England III, Flora of the Bournemouth Beds, the Boscombe, and the Highcliff Sands. *British Museum (Natural History)*, London.
- Cronquist, A., 1981. An Integrated System of Classification of Flowering Plants. Columbia University Press, New York.
- Donoghue, M.J., 1983. A preliminary analysis of phylogenetic relationships in *Viburnum* (Caprifoliaceae). *Systematic Botany* 8, 45–58.
- Donoghue, M.J., Bell, C.D., Li, J., 2001. Phylogenetic patterns in Northern Hemisphere plant geography. *International Journal of Plant Sciences* 162, 41–52 (suppl.).
- Dorofeev, P.I., 1963. The Tertiary Floras of Western Siberia. U.S.S.R. Academy of Sciences, Komarov Botanical Institute, pp. 272–273 (in Russian).
- Du, F.G., Zhu, T.C., Zhu, J.Y., Luan, Z.H., Wang, B.Q., Ma, J.Y., Dong, Y., 2007. Sculpture type of pollen surface of *Sambucus* Linn. in China. *Journal of Beihua University (Natural Science)* 8 (3), 271–275 (in Chinese, with English Abstr.).
- Eriksson, T., Donoghue, M.J., 1997. Phylogenetic relationship of *Sambucus* and *Adoxa* (Adoxaceae) based on nuclear ribosomal ITS sequences and preliminary morphological data. *Systematic Botany* 22, 555–573.
- Forman, L.L., 1974. The endocarps of *Cocculus* (Menispermaceae). *Kew Bulletin* 29, 477–481.
- García-Amorena, I., Manzanique, F.G., Rubiales, J.M., Granja, H.M., Carvalho, G.S., Morla, C., 2007. The Late Quaternary coastal forests of western Iberia: a study of their macroremains. *Palaeogeography, Palaeoclimatology, Palaeoecology* 254, 448–461.
- Ge, H.R., Li, D.Y., 1999. Cenozoic Coal-bearing Basins and Coal-forming Regularity in West Yunnan. Yunnan Science and Technology Press, Kunming. (in Chinese).
- Guo, Q.S., Wang, Q.Y., Liu, Y., 2009. The Illustrated Seeds of Chinese Medicinal Plants. China Agriculture Press, Beijing, p. 356 (in Chinese).
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Palaeontological statistical software for education and data analysis. *Palaeontologia Electronica* 4.
- Han, J.Z., Yu, J., Meng, Q.W., Lü, R.P., Zhu, D.G., Meng, X.G., Shao, Z.G., 2005. Palynological records in the Qangzè Section of the Zanda Basin, Ngari, Tibet. *Journal of Geomechanics* 11 (4), 320–327 (in Chinese, with English Abstr.).
- Hu, C.C., He, C.X., 1988. Pollen morphology of Caprifoliaceae from China and its taxonomic significance. *Journal of Systematics and Evolution* 26 (5), 343–352 (in Chinese, with English Abstr.).
- Hu, R., Du, F.G., Jiang, B.W., 1996. A preliminary study on the seed morphology of *Sambucus* in Jilin province. *Journal of Jilin Forestry University* 12 (2), 104–108 (in Chinese, with English Abstr.).
- Hutchinson, J., 1967. The Genera of Flowering Plants. Clarendon, Oxford.
- Hutchinson, J., 1973. The Genera of Flowering Plants, 2nd ed. Oxford University Press, London.
- Ishikawa, S., 1994. Seeds / Fruits of Japan, pp. 215–218. Printed in Japan.
- Jacobs, B., Donohue, M.J., Bouman, F., Huysmans, S., Smets, E., 2008. Evolution and phylogenetic importance of endocarp and seed characters in *Viburnum* (Adoxaceae). *International Journal of Plant Sciences* 169 (3), 409–431.
- Jacobs, B., Lens, F., Smets, E., 2009. Evolution of fruit and seed characters in the *Diervilla* and *Lonicera* clades (Caprifoliaceae, Dipsacales). *Annals of Botany* 104, 253–276.
- Jacobs, B., Huysmans, S., Smets, E., 2010. Evolution and systematic value of fruit and seed characters in Adoxaceae (Dipsacales). *Taxon* 59 (3), 850–866.
- Knobloch, E., Konzalová, M., Kvaček, Z., 1996. Die Obereozäne Flora Der Staré Sedlo-Schichtenfolge in Böhmen (Mitteleuropa). *Český geologický ústav, Praha* 49, 1–260 (in German).
- Kovar-Eder, J., 1987. Pannonian (upper Miocene) vegetational character and climatic inferences in the central Paratethys area. *Annals of the Natural History Museum Vienna* 88, 117–129.
- Kvaček, Z., Bůžek, Č., 1995. Endocarps and foliage of the flowering plant family Icacinaeae from the Tertiary of Europe. *Tertiary Research* 15 (3), 121–138.
- Kvaček, Z., Teodoridis, V., 2007. Tertiary macrofloras of the Bohemian Massif: a review with correlations within Boreal and Central Europe. *Bulletin of Geosciences* 82 (4), 383–409.
- Li, J., Wang, L., Pei, Y.P., Peng, S.Z., 2005. Ecological changes during 6.2–2.4 Ma BP. revealed by palynological record from red clay deposits in the Loess Plateau and implications. *Quaternary Sciences* 25 (4), 469–473 (in Chinese, with English Abstr.).
- Liang, H.X., Wu, Z.Y., 1995. On the taxonomic system, phylogeny and distribution in Adoxaceae. *Acta Botanica Yunnanica* 17 (4), 380–390 (in Chinese, with English Abstr.).
- Liu, J.Q., Chen, Z.D., Lu, A.M., 2000. The phylogenetic relationship of an endemic genus *Sinodoxa* in the Qinghai–Xizang plateau: evidence from ITS sequence analysis. *Acta Botanica Sinica* 42 (6), 656–658.
- Martinetto, E., 2009. Palaeoenvironmental significance of plant macrofossils from Piànico Formation, middle Pleistocene of Lombardy, North Italy. *Quaternary International* 204, 20–30.
- Matthews Jr., J.V., Mott, R.J., Vincent, J.-S., 1986. Preglacial and interglacial environments of Banks Island: pollen and macrofossils from Duck Hawk Bluffs and related sites. *Géographie physique et Quaternaire* 40, 279–298.
- Matthews Jr., J.V., Ovenden, L.E., 1990. Late Tertiary plant macrofossils from localities in Arctic/Subarctic North America: a review of the data. *Arctic* 43 (4), 364–392.
- Matthews Jr., J.V., Westgate, J.A., Ovenden, L., Carter, D., Fouch, T., 2003. Stratigraphy, fossils, and age of sediments at the upper pit of the Lost Chicken gold mine: new information on the late Pliocene environment of east central Alaska. *Quaternary Research* 60, 9–18.
- Negru, A.G., 1972. Rannearmatskaia Flora Severovostoka Moldavii. Izdat, Stiinta, pp. 1–171 (in Russian).
- Nikitin, V.P., 1979. Neogene floras of North-East USSR (material of paleocarpological investigations). *Continental Tertiary Deposits of North-East Asia. Siberian Branch, Novosibirsk Nauka*, pp. 130–149.
- Nikitin, V.P., 2006. Palaeocarpology and stratigraphy of the Paleogene and the Neogene strata in Asian Russia. *Novosibirsk*, pp. 123–125 (in Russian).
- Nikitin, V.P., 2007. Paleogene and Neogene strata in Northeastern Asia: paleocarpological background. *Russian Geology and Geophysics* 48, 675–682.
- Ogata, K., 1988. Wood anatomy of the Caprifoliaceae of Japan. *IAWA Bulletin* 9 (4), 299–316.
- Punt, W., 1994. Format of descriptions of new taxa of fossil plants (genera, species). *Review of Palaeobotany and Palynology* 80, 7–8.
- Reid, C., Reid, E.M., 1915. The Pliocene Floras of the Dutch–Prussian Border. *Matinus Nijhoff, 'S-Gravenhage*, pp. 135–253.
- Reid, E.M., Chandler, M.E.J., 1926. The Bembridge Flora – catalogue of Cainozoic plants in the department of geology. *British Museum (Natural History)* London, p. 206.
- Rich, F.J., 1984. Ancient flora of the eastern Okefenokee Swamp, as determined by palynology. *The Okefenokee Swamp Wetlands Surveys. Los Alamos, NM*, pp. 410–422.
- Su, T., Jacques, F.M.B., Liu, Y.S., Xiang, J.Y., Xing, Y.W., Huang, Y.J., Zhou, Z.K., 2011. A new *Drynaria* (Polypodiaceae) from the upper Pliocene of Southwest China. *Review of Palaeobotany and Palynology* 164, 132–142.
- Takhtajan, A.L., 1980. Outline of classification of flowering plants (Magnoliophyta). *The Botanical Review* 46 (3), 225–359.
- Tao, J.R., 1986. Neogene flora of Lanping and its significance in middle watershed of Selween–Mekong–Yantze Rivers. *Hengduan Mountain Investigation Special. Science & Technology Publishing House, Beijing*, pp. 58–65 (in Chinese).
- Tao, J.R., Zhou, Z.K., Liu, Y.S., 2000. The Evolution of the Late Cretaceous–Cenozoic Floras in China. Science Press, Beijing. (in Chinese).
- Thorne, R.F., 1976. A phylogenetic classification of the Angiospermae. *Journal of Evolutionary Biology* 9, 35–106.
- Thorne, R.F., 1992. An updated classification of the flowering plants. *Aliso* 13, 365–389.
- Tiffney, B.H., 1991. The collection and study of dispersed angiosperm fruits and seeds. *Palaos* 5, 499–519.
- Velichkevich, F.Y., Zastawniak, E., 2007. The state of investigation of the upper Pliocene Dvoretz flora (SE Belarus). *Acta Palaeobotanica* 47 (1), 261–273.
- Wang, P., 1990. Neogene stratigraphy and paleoenvironments of China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 77, 315–334.
- Wang, X.Y., Zhang, G.S., Wu, L., Zhang, X.H., Zhang, E.L., Xiao, X.Y., Jian, Q.F., 2008. Environmental changes during early-middle Holocene from the sediment record of the Chaohu Lake, Anhui Province. *Chinese Science Bulletin* 53, 153–160.
- Writing Group of Regional Stratigraphy of Yunnan (WGRSY), 1978. Regional Stratigraphy of Southwest China. Geological Publishing House, Beijing, pp. 282–283 (in Chinese).

- Wu, Z.Y., Chen, J., Yuan, J.H., et al., 1991a. Flora Yunnanica (Tomus 3). Chinese Science Press, Beijing, p. 677 (in Chinese).
- Wu, Z.Y., Chen, J., Yuan, J.H., et al., 1991b. Flora Yunnanica (Tomus 5). Chinese Science Press, Beijing, pp. 352–451 (in Chinese).
- Xu, B.S., 1983. Preliminary studies on numerical taxonomy of Caprifoliaceae. *Journal of Systematics and Evolution* 21 (1), 26–31.
- Xu, J.X., Ferguson, D.K., Li, C.S., Wang, Y.F., Du, N.Q., 2004. Climatic and ecological implications of Late Pliocene Palynoflora from Longling, Yunnan, China. *Quaternary International* 117, 91–103.
- Zhang, W.H., Chen, Z.D., Li, J.H., Chen, H.B., Tang, Y.C., 2003. Phylogeny of the Dipsacales s.l. based on chloroplast *trnL-F* and *ndhF* sequences. *Molecular Phylogenetics and Evolution* 26, 176–189.
- Zhu, J.Y., Lu, J.M., Xiao, Z., 2004. The wood anatomy study on stem of *Sambucus williamsii*. *Journal of Wuhan Botanical Research* 22 (6), 561–564 (in Chinese, with English Abstr.).
- Zyuganova, I.S., 2009. Upper Pleistocene carpological assemblages from the south of the Valdai Upland. *Paleontological Journal* 43 (10), 1351–1362.