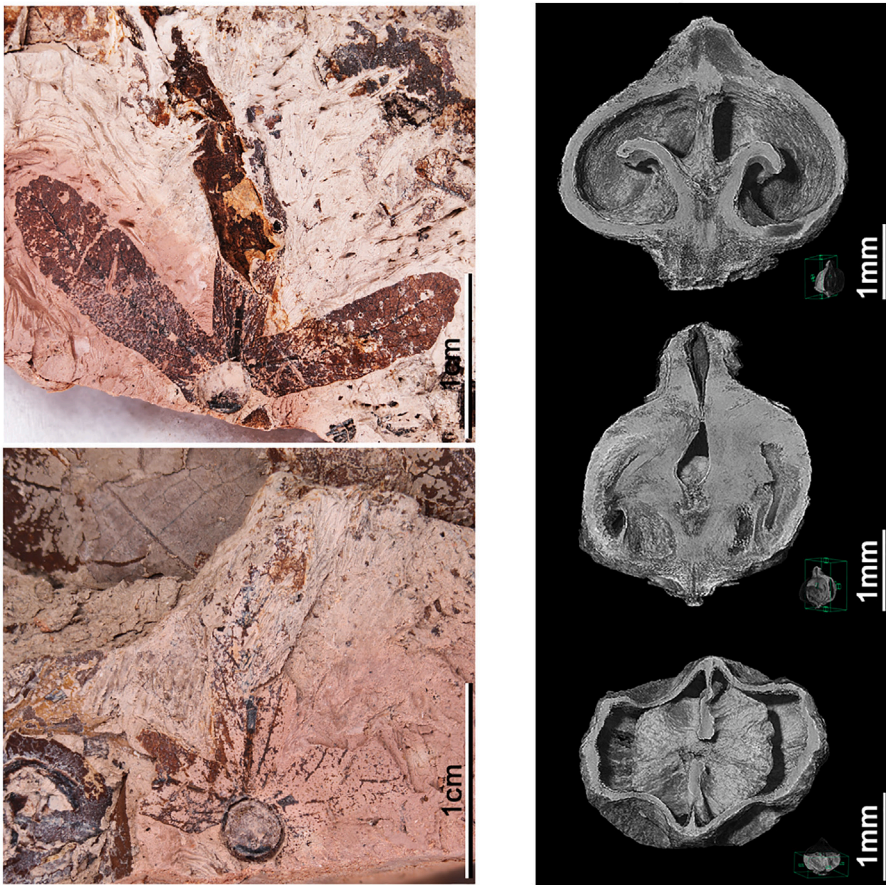


## Article

First reliable Miocene fossil winged fruits record of *Engelhardia* in Asia through anatomical investigation***Engelhardia guipingensis* sp. nov.**  
from the Miocene of Guangxi, South China

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**Highlights**

First detailed anatomical  
study of *Engelhardia*  
winged fruits in East Asia

New fossils clearly  
attributed to the genus  
*Engelhardia*

*Engelhardia* species  
reached its modern  
distribution during the  
Miocene

Miocene climate of the  
Guiping Basin resembled  
present-day Asian tropics  
and subtropics

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## Article

First reliable Miocene fossil winged fruits record of *Engelhardia* in Asia through anatomical investigationHanzhang Song,<sup>1</sup> Luliang Huang,<sup>2,3,\*</sup> Helanlin Xiang,<sup>1</sup> Cheng Quan,<sup>4,\*</sup> and Jianhua Jin<sup>1,3,5,\*</sup>

## SUMMARY

**Fossil genera with similar features to the winged fruits of the living *Engelhardia* Lesch. ex Blume (e.g., *Palaeocarya* G. Saporta) have been widely reported in Cenozoic fossil floras of the Northern Hemisphere. However, fossil winged fruits of *Engelhardia* with detailed anatomical structures have only been found in the upper Eocene of North America. This study reports the first *Engelhardia* fossil winged fruits with detailed anatomical structures in East Asia from the Miocene Erzitan Formation of Guangxi, South China. The anatomical and morphological features of the new fossils, including the unique structure of secondary septa, clearly distinguish them from other fossil genera and show unambiguously their attribution to the genus *Engelhardia*. This discovery suggests that *Engelhardia* had reached its modern distribution during the Miocene and the climate of the Guiping Basin in Guangxi during the Miocene was similar to that of present-day tropical and subtropical regions in Asia.**

## INTRODUCTION

In the Angiosperm Phylogeny Group (APG) IV classification, Juglandaceae belongs within the order Fagales and contains three subfamilies, Rhoipteleoideae, Engelhardioideae, and Juglandoideae.<sup>1</sup> Engelhardioideae consists of three genera, *Engelhardia* Lesch. ex Blume, *Oreomunnea* Oerst., and *Alfaroa* Standl.<sup>2–7</sup> It has also been suggested that Engelhardioideae should contain four genera and that in addition to the three genera mentioned above, the monotypic genus *Alfaropsis* Iljinsk. should be included. *Alfaropsis* is supposedly separate from *Engelhardia* and contains only one species *Alfaropsis roxburghiana* (Wall.) Iljinsk.<sup>8–12</sup> Considering the controversial classification of *Alfaropsis* and its rejection as a monophyletic genus based on both morphological and molecular analyses,<sup>6</sup> we conservatively consider *A. roxburghiana* as a synonym of *Engelhardia roxburghiana* Wall. in this study. *Engelhardia* is distributed in Southeast Asia and the tropical and subtropical regions of East Asia, and the exact number of species it contains is questionable, with *Oreomunnea* and *Alfaroa* being distributed in tropical Central America and containing about 3 and 5 species, respectively.<sup>3,6,13–18</sup>

Although an abundance of fossils with similar features to those of *Engelhardia* have been reported, most of them are assigned to fossil forms, and only a few of them can be confidently assigned to extant *Engelhardia*. One reason for this is that the internal structure of *Engelhardia* fruits, knowledge of which is crucial for identification, is often poorly preserved in fossils. To date, the only fossil record of *Engelhardia* featuring comprehensive anatomical structures is *Engelhardia trinitiensis* Huegele et Manchester from the upper Eocene of east Texas, USA.<sup>19</sup> Additionally, fossil winged fruits morphologically similar to those of living *Engelhardia* have been widely reported from Cenozoic strata of the Northern Hemisphere. From the nineteenth century to the mid-twentieth century, a substantial number of engelhardioid winged fruit fossils were discovered in the Cenozoic of North America, East Asia and Europe, with many initially attributed to *Engelhardia*.<sup>20–32</sup> At the end of the twentieth century, Manchester<sup>3</sup> conducted a thorough investigation on these fossils, leading to a revision of their classification into the fossil genera *Palaeocarya* G. Saporta, *Paraengelhardia* Berry and *Paleooreomunnea* Dilcher, Potter et Crepet. Subsequently, the majority of discovered engelhardioid winged fruit fossils have been assigned to the fossil genera *Palaeocarya*.<sup>33–44</sup> Despite this, some engelhardioid winged fruit fossils have still been assigned to *Engelhardia*, for example, *Engelhardia macroptera* (Brongniart) Unger discovered in the Cenozoic of Europe.<sup>45–50</sup> However, it is more

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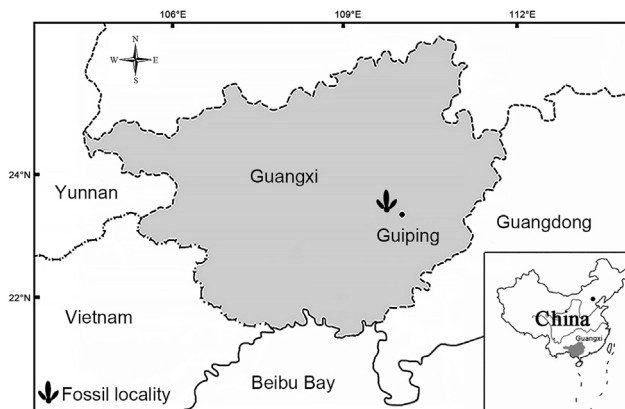
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**Figure 1. The geographical location of the Guiping Basin, Guangxi, China**  
Modified from Wu et al.<sup>51</sup>

appropriate to attribute these fossils to *Palaeocarya* rather than *Engelhardia*, because these fossils do not possess further characteristics beyond the revision by Manchester.<sup>3</sup>

In this paper, the new *Engelhardia* fossil winged fruits collected from the Miocene Erzitang Formation of Guangxi, South China (Figure 1), are described in detail after a thorough anatomical investigation, which provides new fossil evidence for the paleogeography and paleoecology of this genus.

## RESULTS

### Systematic paleontology

#### Family

Juglandaceae DC. ex Perleb 1818<sup>52</sup>

#### Subfamily

Engelhardioideae Iljinsk. 1990<sup>53</sup>

#### Genus

*Engelhardia* Lesch. ex Blume 1825<sup>54</sup>

#### Species

*Engelhardia guipingensis* H.-Z. Song et J.-H. Jin sp. nov.

#### Holotype

GP-608a, b, Figures 2A and 2C.

#### Paratypes

GP-613 and GP-642, Figures 3A–3P.

#### Type locality

Xunwang Town, Guiping City, Guangxi, China.

#### Stratigraphic horizon and age

Erzitang Formation, Miocene.

#### Etymology

Species name is derived from the fossil locality "Guiping".

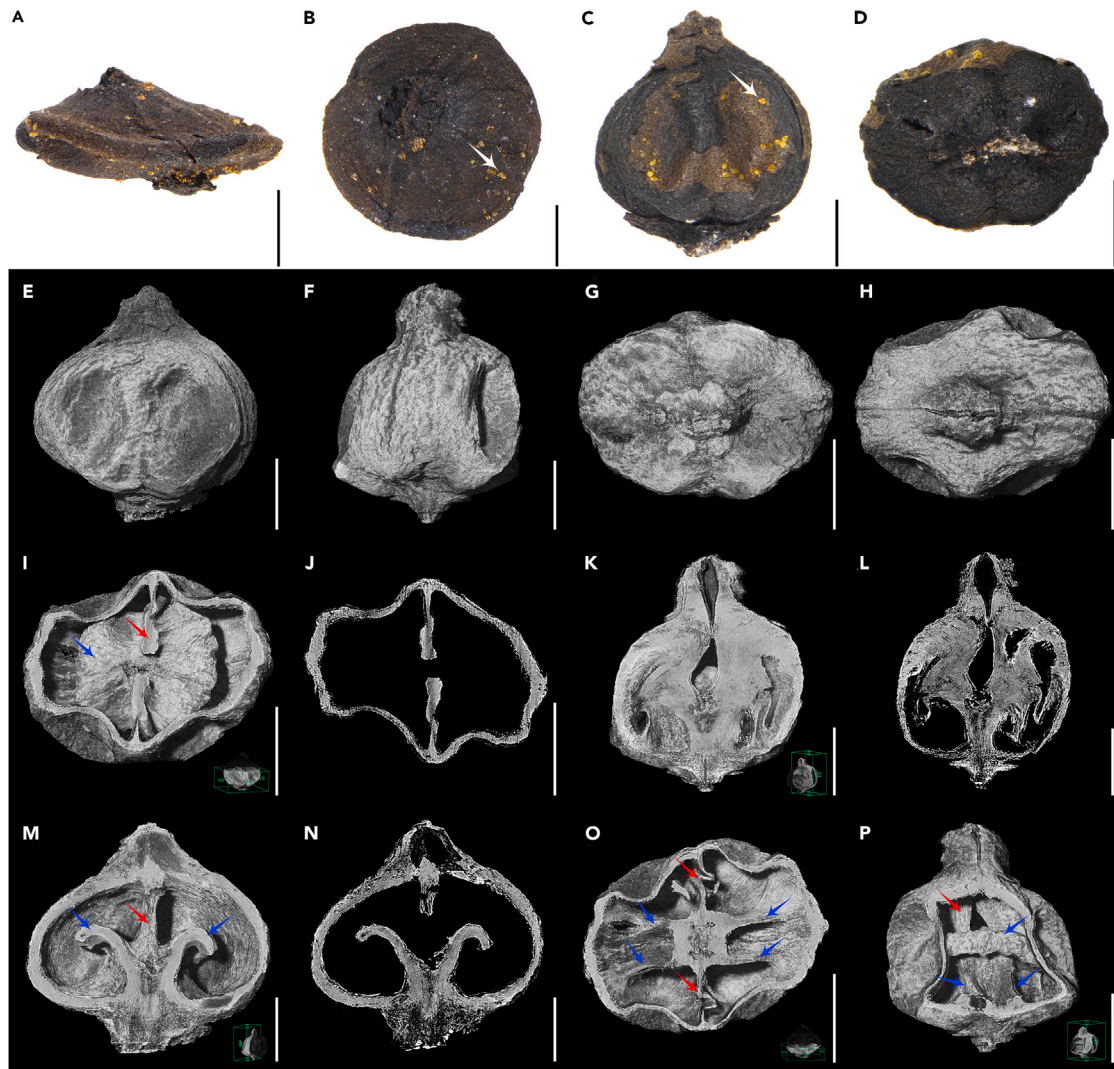


**Figure 2. General morphology of *Engelhardia guipingensis* H.-Z. Song et J.-H. Jin sp. nov.**

- (A) General morphology of the holotype GP-608a.  
 (B) Interpretative line-tracing of A.  
 (C) General morphology of the holotype GP-608b.  
 (D) Interpretative line-tracing of C.  
 (E) Partial enlargement of A, showing the venation at the base of the median lobe.  
 (F) Partial enlargement of A, showing the terminal venation of lateral lobe.  
 (G) Partial enlargement of A, showing the thick and straight midvein and the loops forming by the adjacent secondary veins.  
 (H) Partial enlargement of C, showing the nutlet, white arrows indicate the sepals. Scale bars = 1 cm (A–D), 1 mm (E–H).

### Diagnosis

Trilobate-winged fruit; lateral lobes long obovate, diverging from the median lobe at 45–55°; lobe venation generally pinnate, midvein strong and straight, divided in the terminal region; secondary veins departing from midvein at 20–70°, forming loops with adjacent veins; in the median lobe, a pair of the basal secondary veins diverge from the base of the midvein at a small angle; tertiary veins irregularly reticulate, forming loops; prophyllum absent; nut rounded, retaining four sepals at the apex; exocarp membranous, covered with yellow peltate scales; endocarp woody, surface smooth; locule partitioned into two compartments by primary septum; secondary septa symmetrical on each side of the primary septum, in the equatorial section secondary septa extend from the primary septum and are curved, in the basal quarter of the locule two secondary septa extend from the primary septum in each side, perpendicular to the primary septum and the equatorial section.



**Figure 3. The outlet of *Engelhardia guipingensis* H.-Z. Song et J.-H. Jin sp. nov.**

(A and B) Paratype GP-613: A, front view; B, bottom view.

(C and D) Paratype GP-642: C, front view; D, bottom view.

(E–P) The micro-computed tomography scans of paratype GP-642: E, front view; F, lateral view; G, bottom view; H, top view; I and J, equatorial sections; K–N, longitudinal sections; O, cross section, basal quarter of the locule; P, tangential section. Scale bars = 1 mm, white arrows indicate yellow peltate scales, red arrows indicate the primary septum, blue arrows indicate secondary septum.

### Description

The fruit wing is trilobate. The median lobe is approximately oblanceolate, but the specimen is missing the top portion. The remaining part of the median lobe is 15.8 mm long and 3.2–4.9 mm wide (Figures 2A–2D). The lateral lobes are obovate, 14.0–15.9 mm long and 3.8–4.9 mm wide, diverging from the median lobe at 45–55° (Figures 2A–2D). The apex of the lateral lobes is rounded to obtuse. The lobe veins are generally pinnate, and a pair of the basal secondary veins diverge from the base of the midvein at a small angle in the median lobe, extending along the margin (Figure 2E). However, the exact extension to the lobe is unclear due to the missing portion of the mid lobe. The midvein is thick and straight and does not reach the lobe apex directly but divides two or three times (Figure 2F). The angle between the midvein and the lateral veins gradually increases from the base to the apex from about 20° near the base to 70° near the apex. The lateral veins extend to the margin and are connected to the adjacent lateral veins to form a closed loop (Figures 2F and 2G). The tertiary veins are irregularly reticulate and connected, forming loops

(Figures 2F and 2G). A prophyllum is absent and a pedicel is not observed. The nutlet is located at the junction of the lobes, with four sepals at the apex (Figure 2H). The nutlet is generally spherical, but some specimens show that the nutlet is squeezed from different directions into an ellipsoidal or disc shape (Figures 3A–3H). The exocarp of the nutlet is membranous, covered with yellow peltate scales, and the endocarp is woody with a smooth surface (Figures 3A–3H). The locule is partitioned into two compartments by a primary septum (Figures 3I–3L). Secondary septa are symmetrical on each side of the primary septum, and in the equatorial section, the secondary septa extend from the primary septum and are curved, but do not reach the edge to form more compartments (Figures 3I, 3M, and 3N). In the basal quarter of the locule, two secondary septa extend outward from the primary septum in each compartment, which are perpendicular to the primary septum and the equatorial section (Figures 3O and 3P).

## DISCUSSION

### Comparison with extant and fossil species

Engelhardioideae members belong to the Juglandaceae and can be grouped into three genera, *Engelhardia* Lesch. ex Blume, *Oreomunnea* Oerst., and *Alfaroa* Standl. The fruits of these three genera are morphologically distinct and can be easily distinguished.<sup>3</sup> The fruit of *Alfaroa* is wingless and larger than those of *Oreomunnea* and *Engelhardia*.<sup>3,55</sup> The fruit of *Oreomunnea* and *Engelhardia* both have trilobed wings, but differ clearly in wing venation, prophyllum features, and nut characters. The fruits of *Oreomunnea* have tri-veined wing venation with a large prophyllum and a hairless nut, while the fruits of *Engelhardia* have pinnate wing venation with a reduced or absent prophyllum, and the nut is usually hairy.<sup>3,55</sup> In addition, the septa and compartments inside the nut are also key features that distinguish *Engelhardia* from *Oreomunnea* and *Alfaroa*. The nutlet of *Engelhardia* is usually partitioned into two or four compartments by primary and secondary septa, while *Oreomunnea* and *Alfaroa* have eight compartments partitioned by primary, secondary, and tertiary septa.<sup>3,39,41,55,56</sup> The current fossil represents a trilobate-winged fruit, wing venation is generally pinnate, and the nutlet is partitioned into two compartments by the primary septum.

The exact number of extant species of *Engelhardia* is questionable, and there are 4–6 species distributed in China.<sup>3,6,13–18</sup> The current fossil is clearly distinguishable from the winged fruits of the extant species *Engelhardia danumensis* E.J.F.Campb., *Engelhardia kinabaluensis* E.J.F.Campb., *Engelhardia mendalomensis* E.J.F.Campb., *Engelhardia hainanensis* P.Y.Chen, *Engelhardia rigida* Blume, *Engelhardia serrata* Blume, and *Engelhardia spicata* Lesch. ex Blume (Figures 4A–4G). The midvein of the lobes of the above seven extant species all extend to the apex, do not divide, and these seven species have large prophyllum with hairy nutlets (Figures 4A–4G), while the present fossil does not display these characteristics. The wing venation of the present fossil is similar to that of the extant *Engelhardia mersingensis* E.J.F.Campb., *Engelhardia colebrookiana* Lindl., and *Engelhardia mollis* Hu, all of which are pinnate, and in these species secondary veins form loops with adjacent veins (Figures 4H–4J). However, the median lobe of *E. mersingensis* is ovate and the nutlet has short hairs on the surface (Figure 4H), and *E. colebrookiana* and *E. mollis* both have hairy nutlets and larger prophylla (Figures 4G and 4J). The current fossil can be distinguished from these three species based on these characteristics. The current fossil shares similar characteristics to the living species *E. roxburghiana*. These include divided apices of midveins and a hairless nutlet covered with peltate scales. (Figures 4K and 4L). However, the lobe shape and the wing venation of *E. roxburghiana* are highly variable. Some specimens of *E. roxburghiana* are significantly different from the current fossil, exhibiting a long ovate median lobe and separated lateral veins (Figure 4K), while some specimens have an oblanceolate median lobe and obovate lateral lobes, similar to those of the current fossil (Figure 4L). In addition, the nutlet of *E. roxburghiana* is generally rounded (Figures 5A–5D), the nutlet surface is covered with yellow peltate scales (Figures 5A and 5B), four sepals are visible at the apex (Figures 5A–5D), the nutlet is divided into two compartments by the primary septum (Figures 5E–5H), and the secondary septa formed by the extension of the primary septum are curved, surrounded by seeds (Figures 5I and 5J). The above features of *E. roxburghiana* are similar to those of the current fossil. However, the current fossil is different from the extant *E. roxburghiana* in the structure of the septum. That is to say, in the basal quarter of the locule, within each compartment of the extant *E. roxburghiana* nutlet, only one thick secondary septum extends perpendicularly from the primary septum (Figures 5K and 5L), while in each compartment of the fossil nutlet described here, two secondary septa extend from the primary septum.

To date, the only fossil record of *Engelhardia* featuring comprehensive and definitive anatomical structures is *E. trinitensis* Huegele et Manchester from the upper Eocene of east Texas, USA.<sup>19</sup> *E. trinitensis* is only



**Figure 4. Extant winged fruits of genus *Engelhardia* Lesch. ex Blume**

(A) Isotype of *E. danumensis* E.J.F.Campb., Herbarium of the Arnold Arboretum (A), barcode A00076168.

(B) Isotype of *E. kinabaluensis* E.J.F.Campb., Herbarium of the Arnold Arboretum (A), barcode A00076169.

(C) *E. mendalomensis* E.J.F.Campb., US National Herbarium, Department of Botany, National Museum of Natural History (NMNH), Smithsonian Institution, barcode 03390390.

(D) *E. hainanensis* P.Y.Chen, the Herbarium of South China Botanical Garden (IBSC), No. 369893, barcode 0002222.

(E) Isotype of *E. rigida* Blume, Missouri Botanical Garden (MO), barcode MO277411.

(F) Isotype of *E. serrata* Blume, Missouri Botanical Garden (MO), barcode MO1766824.

(G) *E. spicata* Lesch. ex Blume, the Herbarium of South China Botanical Garden (IBSC), No. 273038, barcode 0418358.

(H) Type of *E. mersingensis* E.J.F.Campb., National Herbarium of Victoria (MEL), barcode MEL2422587.

(I) *E. colebrookiana* Lindl., the Herbarium of South China Botanical Garden (IBSC), No. 343929, barcode 0417740.

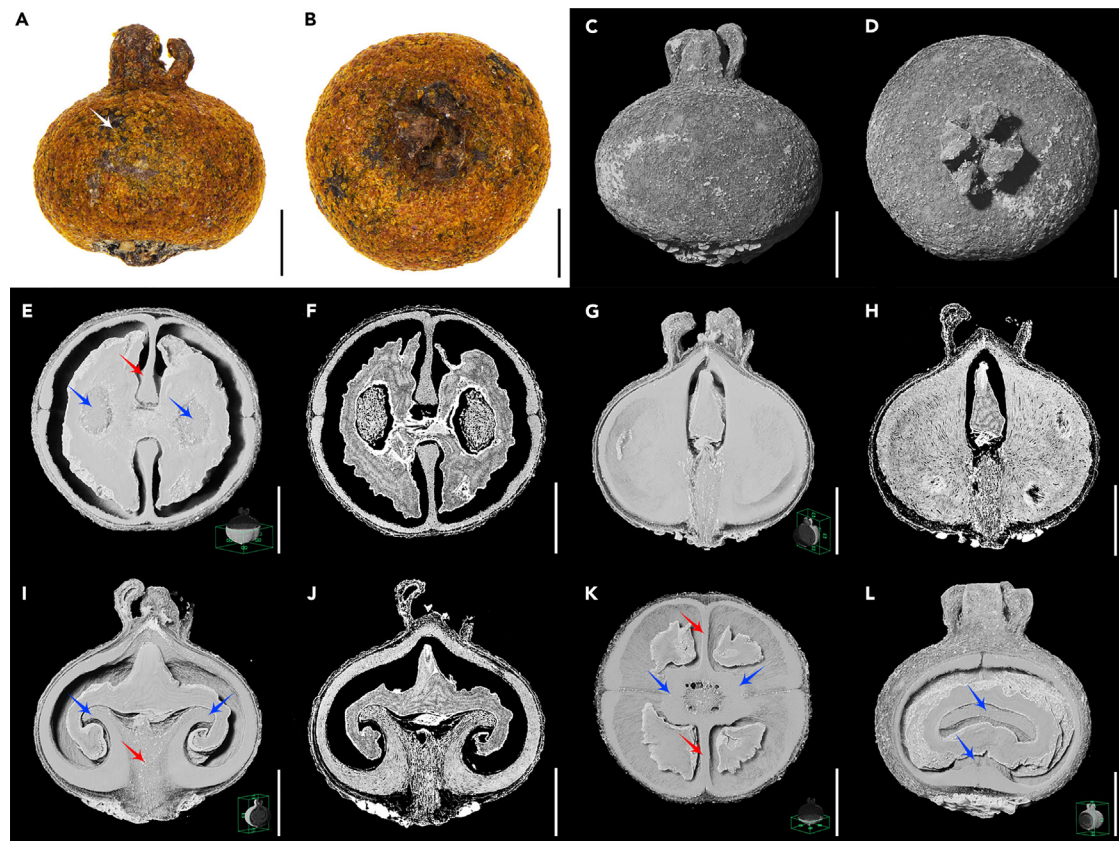
(J) Isotype of *E. mollis* Hu, Herbarium of the Arnold Arboretum (A), barcode A00033617.

(K) *E. roxburghiana* Wall. (= *E. chrysolepis* Hance), the Herbarium of South China Botanical Garden (IBSC), No. 6983, barcode 0002216.

(L) *E. roxburghiana* Wall., the Herbarium of South China Botanical Garden (IBSC), No. 18165, barcode 0418029. Scale bars = 1 cm.

preserved as a nutlet, without wings. The nutlet of *E. trinitiensis* is subglobose, with a high primary septum and a lower secondary septum, and basally the locules are four-lobed with two lobes on either side of the primary septum.<sup>19</sup> In contrast, the current fossil is preserved with both wings and a rounded nutlet, and the locule is separated into two compartments by the primary septum, and as such is significantly different from *E. trinitiensis*.

Almost all winged fruit fossils similar to modern *Engelhardia* are assigned to the fossil genus *Palaeocarya* Saporta, and only a few of them have been observed with septal structures within the nutlets, including *Palaeocarya macroptera* (Brongniart) Jählich, *Palaeocarya olsoni* (Brown) Manchester, *Palaeocarya hispida* H. H. Meng et Z. K. Zhou, and *Palaeocarya indica* Hazra, Hazra M. et Khan.<sup>3,27,39,43,57</sup> *P. macroptera* has been found extensively in Eocene to Pliocene sediments in Europe.<sup>3,57</sup> The nutlets of *P. macroptera* possess narrow secondary septa, with 2 or basal 4 chambers and a hook-shaped bulging appendage in the middle of the compartment.<sup>57</sup> To some extent, similar characteristics can be observed in both the nutlets of *P. macroptera* and those of the current fossils, although differences in the features of the secondary



**Figure 5. The nutlet of extant *Engelhardia roxburghiana* Wall.**

(Specimen number: SYS-BYS-202008-001).

(A and B) The nutlet of *E. roxburghiana*: A, front view; B, top view.

(C–L) Micro-computed tomography scans of the nutlet of *E. roxburghiana*: C, front view; D, top view; E and F, equatorial sections; G–J, longitudinal sections; K, cross section, basal quarter of the locule; L, tangential section. Scale bars = 1 mm, white arrow indicates yellow peltate scale, red arrows indicate the primary septum, blue arrows indicate the secondary septum.

septa are evident. Furthermore, the tri-veined median lobe and large prophyllum of *P. macroptera* are significantly distinct from those observed in the current fossils.

*P. olsoni* was found in the Oligocene of Oregon and Alaska and the Miocene of Idaho,<sup>3,27</sup> all in the United States. The nutlet of *P. olsoni* has a thick septum located centrally, which Manchester<sup>3</sup> considered as a median secondary septum. Combined with the characteristics of venation, it seems that *P. olsoni* is more closely related to the extant *Oreomunnea*.<sup>3</sup>

*P. hispida* was found in the late Miocene of southeastern Yunnan, China.<sup>39</sup> Its nutlet is subdivided by a septum into two compartments but lacks specific information about the number of septa and compartments inside the nutlets.<sup>39</sup>

*P. indica* was found in the Pliocene of eastern India and its nutlet is hispid, subdivided by a septum into two compartments.<sup>43</sup> Hazra et al.<sup>43</sup> believed that *P. indica* is most similar to the extant *E. spicata*. Although the septal structures of nutlets can be observed in *P. olsoni*, *P. hispida*, and *P. indica*, compared to the fossils described here they do not preserve more detailed internal anatomical structures, such as the structure of the primary and secondary septa or the exact number of compartments.

Another species commonly found in the Neogene of Asia is *Palaeocarya koreanica*, a species that has been reported from the Oligocene of China and Russia, the Miocene of China, Korea, and Japan, as well as the Pliocene of China.<sup>3,23,28,29,32,34,37,38,44</sup> *P. koreanica* displays morphological similarities to the fossils reported



here, notably in terms of the venation of each lobe, which consists of a midvein with pinnate secondary veins and a pair of fine lateral veins situated on either side of the midvein, ascending along the margin.<sup>3,32</sup> However, there are notable differences between the two in that the median vein terminates near the lobe apex. Specifically, in *P. koreanica*, the midvein remains unbranched all the way to the distal tip, with a potential mucro at the apex,<sup>3,32</sup> while in our fossils, midvein does not reach the lobe apex directly but instead divides two or three times. In addition, the detailed internal structural features of nutlets are not preserved in *P. koreanica* when compared to the current fossil, and some fossil records lack preserved nutlets. These observations indicate that *P. koreanica* may represent a distinct species related to the fossil described here.

In summary, our fossil specimen shows strong similarities to the extant species *E. roxburghiana*, but still with discernible differences in septal characteristics. In addition, comparisons were made between the other similar fossil species, revealing distinctions in wing venation or internal nutlet structures. Based on a comprehensive examination of the fossil's external morphology, including its venation, prophyllum, and sepals, as well as the internal anatomy of the nutlet, particularly the primary and secondary septa, and in consideration of its comparison with extant *Engelhardia* and similar fossil species, we propose the classification of the specimen as a new fossil species, *E. guipingensis* sp. nov..

### Paleogeographical and paleoecological implications

Currently, only one fossil record of *Engelhardia* that features relatively detailed internal structure has been reported, and that is from the upper Eocene of east Texas, USA.<sup>19</sup> The features of the compartments and septa inside the nutlets were imaged using micro-computed tomography X-ray scanning technology, thereby enabling a more detailed description of its internal structure.<sup>19</sup> From the 19th century to the mid-20th century, a large number of engelhardioid winged fruit fossils were reported from the Cenozoic of North America, East Asia and Europe.<sup>20–32</sup> Subsequently, after *Oreomunnea* was recognized as an independent genus separated from *Engelhardia*,<sup>13,58</sup> Manchester<sup>3</sup> suggested that the morphology of some of these fossil fruits lies between that of *Engelhardia* and *Oreomunnea*, i.e., the wing venation of some of the fossils is similar to those of the extant *Oreomunnea*, but the nutlet and style characters are similar to those of extant *Engelhardia*. Thus, the fossil genus *Palaeocarya* G. Saporta was revised, and all fruit fossils with morphological features of the *Engelhardia*–*Oreomunnea* complex were included in *Palaeocarya*.<sup>3</sup> Since then, almost all engelhardioid winged fruit fossils have been assigned to *Palaeocarya*.<sup>33–44</sup> Apart from that, a small number of engelhardioid fruit fossils have been attributed to the fossil genus *Paraengelhardtia* Berry and *Paleooreomunnea* Dilcher, Potter et Crepet.<sup>3,22,30</sup> In addition, it should be noted that some engelhardioid winged fruit fossils have still been assigned to *Engelhardia*, for example, *E. macroptera* (Brongniart) Unger discovered in the Cenozoic of Europe.<sup>45–50</sup> However, the descriptions of these fossils are similar to those provided by Jähnichen et al.<sup>57</sup> and Manchester,<sup>3</sup> and no additional information on nutlet anatomy is currently available. As a result, it may be more appropriate to assign these fossils to *Palaeocarya* rather than *Engelhardia*.

*Engelhardia* species are deciduous, semi-evergreen, or evergreen trees. *Engelhardia* is endemic to South-east Asia and the tropical and subtropical regions of East Asia, specifically distributed in parts of Nepal, southern Xizang (Tibet) and south of the Yangtse River in China, the Indochina Peninsula, the Malay Peninsula, Borneo, Sulawesi, the Indonesian Archipelagoes, the Philippines, and Papua New Guinea.<sup>5,6,14–16,39</sup> Today there are about 4–6 species of *Engelhardia* occurring naturally in China, mainly in mountainous areas, and less commonly in lowlands and plains.<sup>6,14,15</sup> The most similar extant species to the fossil described here, *E. roxburghiana*, grows mainly in mixed broad-leaved or evergreen forests at elevations of about 200–1500 m and is widely distributed within subtropical areas of China to Indonesia.<sup>6,15</sup>

The discovery of fossil winged fruits, *E. guipingensis*, from the Guiping Basin of Guangxi suggests that *Engelhardia* species were already present within the modern distribution of the genus during the Miocene. Based on the growth environment of *E. roxburghiana*, the most similar living species of *E. guipingensis*, we suggest that during the Miocene the climatic conditions of the Guiping Basin are similar to those of the tropical and subtropical regions of Asia today.

### Limitations of the study

The majority of paleobotanical research is subject to some limitations related to the objects of study. The first limitation is the preservation quality of plant megafossils. The second limitation concerns the representativeness of the data. Both of these factors may influence taxonomic identification of plant fossils, the

assessment of morphological variability of different plant organs, the possibility of whole-plant reconstructions, and, eventually, paleogeographical and paleoecological reconstructions.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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## ACKNOWLEDGMENTS

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## AUTHOR CONTRIBUTIONS

J. J., H. S., and C. Q. conceived and designed the project and photographed material. J. J., C. Q., and L. H. organized field work and led the data acquisition. H. S. and H. X. prepared and imaged fossil and modern specimens. H. S. and J. J. contributed to initial manuscript preparation. All authors discussed results, read, and approved the final manuscript.

## DECLARATION OF INTERESTS

The authors declare no conflict of interest.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
<i>Biological samples</i>		
<i>Engelhardia guipingensis</i> fossil specimens	Museum of Biology, Sun Yat-sen University, Guangzhou	GP-608a, b; from GP-613 to GP-642
<i>E. danumensis</i>	Herbarium of the Arnold Arboretum (A)	A00076168
<i>E. kinabaluensis</i>	Herbarium of the Arnold Arboretum (A)	A00076169
<i>E. mendalomensis</i>	US National Herbarium, Department of Botany, National Museum of Natural History (NMNH), Smithsonian Institution	03390390
<i>E. hainanensis</i>	the Herbarium of South China Botanical Garden (IBSC)	No. 369893, barcode 0002222
<i>E. rigida</i>	Missouri Botanical Garden (MO)	MO277411
<i>E. serrata</i>	Missouri Botanical Garden (MO)	MO1766824
<i>E. spicata</i>	the Herbarium of South China Botanical Garden (IBSC)	No. 273038, barcode 0418358
<i>E. mersingensis</i>	National Herbarium of Victoria (MEL)	MEL2422587
<i>E. colebrookiana</i>	the Herbarium of South China Botanical Garden (IBSC)	No. 343929, barcode 0417740
<i>E. mollis</i>	Herbarium of the Arnold Arboretum (A)	A00033617
<i>E. roxburghiana</i>	the Herbarium of South China Botanical Garden (IBSC)	No.6983, barcode 0002216; No.18165, barcode 0418029

### RESOURCE AVAILABILITY

#### Lead contact

Further questions should be directed to the lead contact, Jianhua Jin ([jsjhh@mail.sysu.edu.cn](mailto:jsjhh@mail.sysu.edu.cn)).

#### Materials availability

Specimens GP-608a, b, GP-613 to GP-642 are deposited in the Museum of Biology, Sun Yat-sen University, Guangzhou, China.

#### Data and code availability

- All data reported in this paper will be shared by the [lead contact](#) upon request.
- No novel code was used in this study.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

#### Plants

All specimens used here were obtained as herbarium specimen from the source organizations listed in the key resources table.

### METHODS DETAILS

#### Geological setting

The *Engelhardia* fossil fruits described here were recovered from the Miocene Erzitang Formation of Guiping Basin, located near Xunwang Town, Guiping City, Guangxi, China (23°23'09.67" N, 110°09'55.21" E; [Figure 1](#)). The Erzitang Formation comprises greyish yellow conglomerates and greyish black mudstone deposited in lacustrine and swamp environments, and the age of the Erzitang Formation is considered to be Miocene based on the mammal fossil *Prolipotes yujiangensis* Zhou, Zhou et Zhao.<sup>59,60</sup> A large number of plant fossils have been found in Guiping Basin, including those previously reported as *Quercus* L., *Canarium* L., *Elaeocarpus* L. and *Dacrycarpus* (Endl.) de Laub.<sup>51,60–62</sup>

### Specimen preparation

A total of thirty-one fossils were studied, including one well-preserved fossil winged fruit (with number GP-608a, b) and thirty fossil nuts without wings (with number from GP-613 to GP-642). For the well-preserved fossil winged fruit tweezers and brushes were used to clean the surface, and the fossil nuts were cleaned using an ultrasonic cleaner (JP-020S, 120W; Jiemeng, Shenzhen, China) and then air dried. Macroscopic photographs of specimens were taken with a Canon digital camera (Canon EOS 500D) and a stereo microscope (Zeiss Stereo Discovery V20 stereomicroscope AxioCam HRC; Carl Zeiss, Göttingen, Germany) at the Museum of Biology, Sun Yat-sen University, Guangzhou, China. Photographs of the 3D internal structure of the nuts were taken using a Zeiss 520 Versa 3-D X-ray tomography microscope at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS). The morphological terms used of the winged fruit are those of Manchester.<sup>3</sup>

### QUANTIFICATION AND STATISTICAL ANALYSIS

No statistical analysis is included in this study.