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Research papers

First discovery of *Cucubalus* (Caryophyllaceae) fossil, and its biogeographical and ecological implications

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ABSTRACT

A new species of *Cucubalus* is described based on two fossil seeds recovered from the upper Pliocene Sanying Formation in northwestern Yunnan Province, southwestern China. The seeds are characterized by a reniform to circular outline in shape, and sinuous and discontinuous rugulae made of rod-like elements radiating from the hilum region to the dorsal margin. The combination of these characteristics shows their close resemblance to the extant genus *Cucubalus* in the Caryophyllaceae. A morphological principal coordinates (PCO) analysis further supports the assignment to this genus. *Cucubalus* is a monotypic genus today, but the late Pliocene fossil seeds have been described as a new species, *Cucubalus prebaccifer* Huang, Liu et Zhou, sp. nov. This newly documented *Cucubalus* fossil, representing the first fossil record of this genus, implies that the genus has existed in northwestern Yunnan, southwestern China, at least since the late Pliocene. It provides important information on the past biodiversity and biogeography of both the genus *Cucubalus* and the fossil-scant family Caryophyllaceae.

1. Introduction

Caryophyllaceae, the pink family, is a species-rich family of approximately 86 genera and 2200 species of annual or perennial herbs, rarely shrubs (Wu et al., 1995; Tang et al., 1996; APG, 2009). It is principally holarctic, particularly wide spread in temperate regions in Eurasia (Wu et al., 1995; Tang et al., 1996; Fior et al., 2006). However, fossil record of this large and cosmopolitan family is poorly known, despite its flourishing so well today (Jordan and Macphail, 2003). Previously described fossil records of this family are almost exclusively of pollen grains (Muller, 1981; Fyles, 1990; Velichkevich and Zastawniak, 2007), but these have proved questionable in identification due to their high morphological similarities to many other groups (Truswell et al., 1985). Only a few records are of macrofossils, including a middle-late Eocene flower of an extinct taxon, *Caryophylloflora paleogenica*, from Tasmania, Australia (Jordan and Macphail, 2003), and some seed remains, such as *Hantsia* from the Palaeocene of southern England (Chandler, 1960, 1961), *Cerastium*, *Minuartia*, *Silene* and *Stellaria* from the Quaternary of Yukon, Canada (Zazula et al., 2005), and *Arenaria* or *Minuartia* from the late glacial of Maine, USA (Thompson et al., 2011). As yet, most genera of the Caryophyllaceae have no fossil documented. The past biodiversity and biogeography of this family is therefore far from well known. For this reason, it would be critically important if new fossils of this family are recovered, so that our understanding of its past biodiversity and biogeography could be improved.

Cucubalus, a monotypic genus in the Caryophyllaceae, contains a single species, *Cucubalus baccifer* L. (Wu et al., 1995; Tang et al., 1996). Today, *C. baccifer* is intercontinentally distributed in temperate and warm areas across Eurasia (Wu et al., 1995; Tang et al., 1996), but its fossil has never been recognized or documented. It remains unanswerable about the species diversity and distribution pattern in the geological past of this successful genus today.

The present study aims to describe two *Cucubalus* (Caryophyllaceae) seed specimens newly recovered from the upper Pliocene Sanying Formation in northwestern Yunnan Province, southwestern China, and to discuss the biogeographical and ecological implications of the new find.

2. Materials and methods

2.1. Fossil materials

The fossil materials were collected from the deposit of the Sanying Formation at Fudong Village, Lanping County, northwestern Yunnan Province, southwestern China (26°28′N, 99°26′E; 2740 m a.s.l.; Fig. 1).

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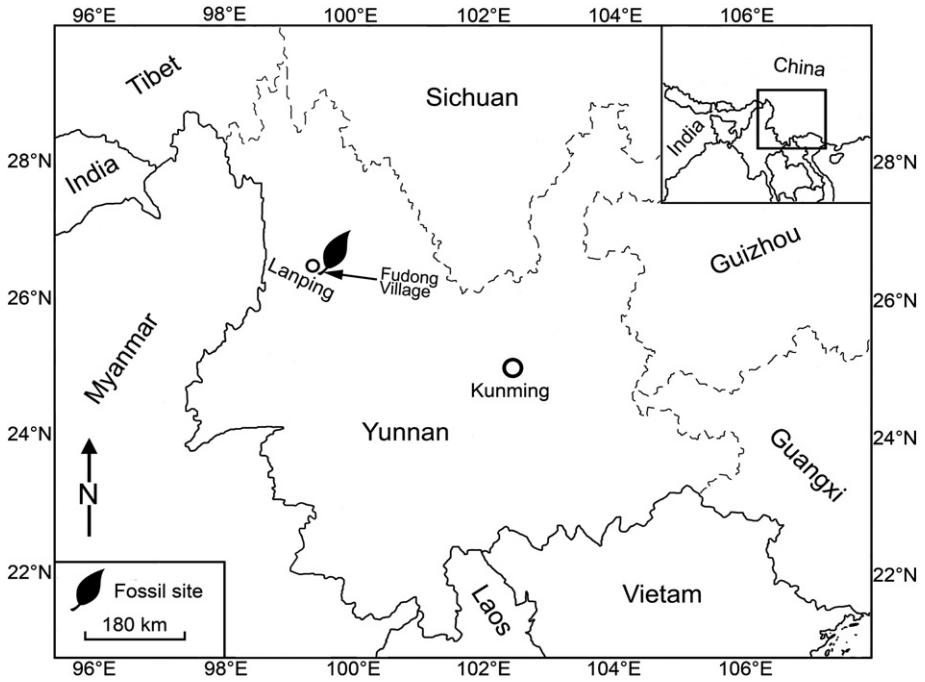


Fig. 1. Map showing the location where the *Cucubalus* fossil seeds were uncovered.

The Sanying Formation is considered to be upper Pliocene in age, mainly based on regional stratigraphic correlations (WGRSY, 1978; BGMRYP, 1990; Ge and Li, 1999) and floristic assemblages (Tao, 1986; Xu et al., 2004). The recently recovered mammalian fossils, such as *Cervavitus* sp., further confirm the age assignment of this formation (Su et al., 2011; Huang et al., 2012). The geological setting of the deposit has been previously described in detail based on regional stratigraphic correlations and field observations (WGRSY, 1978; Huang et al., 2012). A recent study shows that this deposit bears abundant charcoalified seeds and fruits (Huang et al., 2012). More than 200 seed and fruit specimens have been recovered from a carbonaceous layer within the thick red claystone, from which *Sambucus* endocarps have been recently described (Huang et al., 2012). Two of those specimens are outstanding due to their reniform to circular seed shape, and unique testa surface covered by sinuous and discontinuous rugulae made of rod-like elements radiating from the hilum to the dorsal margin. The combination of these characteristics shows a close resemblance to the extant genus *Cucubalus* in the Caryophyllaceae. They are selected for the present study.

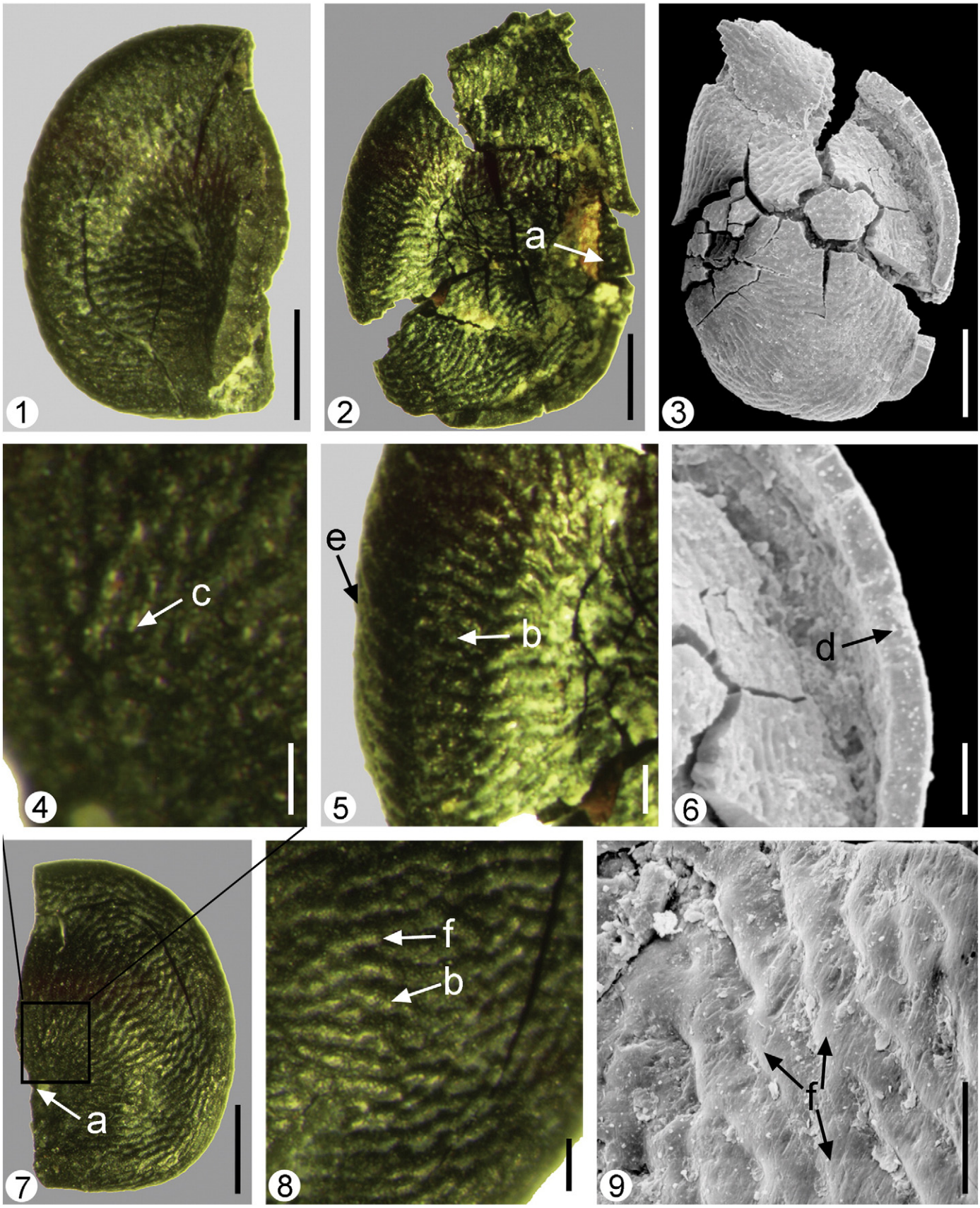
2.2. Taxonomic analysis

The general morphology of the fossil seeds and seeds of the living species, *Cucubalus baccifer* L., was observed under a binocular microscope (SZX16). Testa morphology was examined by a scanning electron microscope (SEM, KYKY-1000). Extant seed materials of *C. baccifer* were obtained from five herbarium specimens (KUN No. 0251811, No. 0251825, No. 0251827, No. 0251829 and No. 0251841) housed at the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN). Seed morphology of the Caryophyllaceae has rarely been studied, except for Bojňanský and Fargašová (2007). Seed morphological data of the Caryophyllaceae were therefore taken from Bojňanský and Fargašová (2007). Morphological comparisons were made between the fossil taxon and extant members of this family. To compare the morphology of the fossil seeds with the extant relatives, a morphological principal coordinates (PCO) analysis was carried out. The PCO analysis is a method to explore and to visualize similarities or dissimilarities of data. It is often used to find out both the genetic diversity and morphological disparity (e.g., Kloda et al., 2008; Brusatte et al., 2011), and is considered useful and reliable in visualizing individual or group differences (Brusatte et al., 2011). The PCO analysis usually starts with a symmetric distance matrix and assigns for each item a location in a low-dimensional space (Gower, 1966; Anderson, 2003). In this study, a taxon-characteristic matrix, including the fossil taxon plus 28 extant relatives in the Caryophyllaceae, and 46 characteristics (see supplementary data in the Appendix) was built and provided. The PCO analysis was carried out using the software MVSP (Kovach, 1998) and Euclidean distances after the data were standardized. The terminology used is after Bojňanský and Fargašová (2007). The format of the descriptions of a new plant fossil species is mainly after Punt (1994).

3. Systematics

Family: Caryophyllaceae Jussieu
Genus: *Cucubalus* L.
Species: *Cucubalus prebaccifer* Huang, Liu et Zhou, sp. nov.
Holotype: FD 061 (Plate 1, 1, 4, 7–8) here designated
Paratype: FD 062 (Plate 1, 2–3, 5–6, 9)
Repository: Both fossil specimens are kept at the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

Plate 1. Fossil seeds of *Cucubalus prebaccifer* Huang, Liu et Zhou, sp. nov. from the upper Pliocene in northwestern Yunnan, southwestern China.Scale bar = 0.5 mm for images 1–3, 7; 0.1 mm for images 4–6, 8–9.1, 4, 7–8. Holotype FD 061.2–3, 5–6, 9. Paratype FD 062.1–2, 7. General shape of the fossil seeds and testa surface covered by rugulae radiating from the hilum to the dorsal margin, observed under the binocular microscope.3. General shape of the fossil seeds observed under SEM.4. Surface details, showing the radially tuberculate pattern close to the hilum region.5. Showing the dorsal margin slightly wavy and rugulae almost orthogonal to the dorsal margin.6. Showing the cross section of the testa.8. Surface details observed under the binocular microscope, showing the sinuous and discontinuous rugulae made of rod-like elements. One rod-like element is pointing to a region between two adjacent "rods" in the outer concentric row.9. Surface details observed under SEM, showing the cell-like sculptures are wedged in arrangement, one "cell" aiming at the space between two adjacent "cells" ahead.a. Hilum.b. Rugula.c. Tuberculum.d. Cross section of the testa.e. Dorsal margin.f. The arrangement that one rod-like element ("cell") is aiming at the space between two adjacent "rods" ("cells") in the outer concentric row.


1
2
a
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Type locality: Fudong Village, Lanping County, northwestern Yunnan Province, southwestern China (26°28′N, 99°26′E).
Stratigraphy: Sanying Formation
Age: Upper Pliocene
Etymology: The specific epithet *prebaccifer* is given to represent the close resemblance to the only living species in *Cucubalus*, i.e., *Cucubalus baccifer* L.
Diagnosis: Seed reniform to circular in shape, curved; testa surface covered by sinuous and discontinuous rugulae made of rod-like elements, radiating from the hilum to the dorsal margin; each rod-like element pointing to a region between two adjacent "rods" in the outer concentric row.
Description: Seeds reniform to circular in general shape, curved, laterally compressed; 1.5–2.3 mm long, and 1.2–1.6 mm wide, length to width ratio 1.2–1.5; ventral side almost straight, dorsal side convex and roundish, dorsal margin slightly wavy or almost smooth; hilum located near the middle on the ventral side; testa around 83 μm thick; testa surface rather lustrous, radially tuberculate close to the hilum, and expressively striate and rugulose in other region of the surface; rugulae sinuous and discontinuous, made of rod-like elements, radiating from the hilum to the dorsal side, orthogonall to the dorsal side, but nearly parallel to the dorsal margin at the apical and basal extremities; the number of these discontinuous rugulae varying from 39 to 52; width of the rugula almost the same to that of the furrow between; the rod-like elements coaxially and radially close; each "rod" pointing to a region between two adjacent "rods" in the outer concentric row; the epidermal-cell-like sculpture on the testa surface rhomboidal and wedged in arrangement, one "cell" aiming at the space between the two adjacent "cells" ahead.

4. Morphological comparisons

The present fossil seeds are clearly curved. Many families, e.g., Caryophyllaceae, Fabaceae, Malvaceae, Papaveraceae, etc., also bear curved seeds (Bojňanský and Fargašová, 2007). However, these families evidently do not have radially sculptured seed surface, and therefore do not correspond to the fossil taxon. It appears that only the Caryophyllaceae shares similar seed morphology with the fossil taxon, based on seed and fruit morphological information of more than 9000 angiospermous taxa from herbarium specimens and the literature (Ishikawa, 1994; Bojňanský and Fargašová, 2007; Guo et al., 2009). We therefore focused seed morphological comparisons below on between the fossil taxon and the Caryophyllaceae.

Caryophyllaceae is a large family, with wide range of habitats and global ubiquity (Tang et al., 1996; Fior et al., 2006). Understanding of the classification of the family based on molecular evidence has increased in the last decade (Oxelman et al., 2001; Fior et al., 2006). Although there are also classifications based on morphological characters (e.g., Bittrich, 1993), studies based on seed morphology remain sparse. Bojňanský and Fargašová (2007) have described the seed morphology of 28 genera in the Caryophyllaceae with full figures. We therefore gathered comparative information of these 28 genera for comparisons and morphometric analysis, representing all 11 tribes in this family.

Seeds of the Caryophyllaceae are often curved, reniform, circular, elliptic or shield-shaped in outline, ventral side concave or almost straight and dorsal side convex, a few laterally winged, seed surface scattered mostly with papillae in disorder or arranged in concentric rows, and sometimes with rugulae radially extending from the hilum to the margin (Bojňanský and Fargašová, 2007). Based on seed morphological data from Bojňanský and Fargašová (2007), we grouped 18 of the 28 genera in three main seed morphotypes (Table 1). It appears that different genera grouped in the same morphotype cannot be convincingly separated from each other, merely based on seed morphology. Particularly, Morphotype 2 contains as many as 14 genera (Table 1), which have closely comparable seed morphology (Bojňanský and Fargašová, 2007). That is why the taxonomic status of the fossil seeds from southern England (Chandler, 1960, 1961) is still thought questionable (Jordan and Macphail, 2003), and the taxonomic status of the fossil seed from Maine, USA, is also uncertain (Thompson et al., 2011). However, a few other genera, such as *Cucubalus*, *Honkenya* and *Scleranthus* that bear unique combination of diagnostic characteristics, cannot be included in any of the three morphotypes. Those genera are therefore more distinguishable from other genera in the Caryophyllaceae. Seeds of the genus *Cucubalus* are evidently characterized by a reniform to circular general shape, hilum located near the middle on the ventral side, and discontinuous rugulae made of rod-like elements radiating from the hilum to the dorsal margin on the testa surface. The combination of these characteristics demonstrates that *Cucubalus* cannot be included in any of the three seed morphotypes. They are unique characteristics that can help distinguish the genus from its close relatives. The present fossils seeds are also reniform to circular in general shape, and bear sinuous and discontinuous rugulae made of rod-like elements radiating from the hilum to the dorsal margin on the testa surface, which warrant the taxonomic assignment.

To support the inclusion of the fossil taxon in the genus *Cucubalus*, a PCO analysis was carried out based on seed morphological data (Fig. 2). Result of the PCO analysis shows that the fossil taxon has a shorter distance from *Cucubalus* than any of the other 27 extant relatives in the Caryophyllaceae, which clearly demonstrates that the fossil taxon is closer to *Cucubalus* in seed morphology. Consequently, we have placed the fossil taxon in the genus *Cucubalus*.

The monotypic *Cucubalus* contains only one species, i.e., *Cucubalus baccifer* L. (Wu et al., 1995; Tang et al., 1996). It might represent the nearest living relative of the present fossil taxon. To further confirm both the genus and species affinity, detailed morphological comparisons were performed between the fossil taxon and the living *C. baccifer*, based on seed morphological features, such as general shape, seed size and testa surface sculpture (Plate 2, Table 2). Seeds of the fossil taxon and the living *C. baccifer* share several characteristics in morphology. They are both reniform to circular in general shape; ventral side is almost straight, and dorsal side is convex with a slightly wavy margin; testa surfaces are both rather lustrous (Plate 1, 2, 5; Plate 2, 1–2), sculptured by discontinuous rugulae made of rod-like elements, which start from the hilum and end at the dorsal margin; one "rod" points to a region between other two "rods" in the outer concentric row; the arrangement on the fossil seed surface that the cell-like sculpture is aiming at between two adjacent "cells" ahead is quite similar with the pattern on the extant seed that an epidermal cell aims at the space between two adjacent epidermal cells in the outer concentric row. All these morphological affinities at a specific level further support the placement of the fossil taxon into *Cucubalus*. However, some differences can also be seen between the fossil and extant seeds, particularly in some quantitative characters. The fossil seeds (1.2–1.6 × 1.5–2.3 mm) seem slightly different from the extant seeds (1.3–1.5 × 1.6–1.8 mm) in size. This seed size disparity might be largely related to taphonomic process; some deformation clearly took place in the fossil seeds caused by compression or others during the process of preservation (Plate 1, 2–3). Rugulae on the seed testa of the fossil taxon (39–52) appear more than those of *C. baccifer* (35–40), and more closely arranged. The testa of the fossil taxon is clearly much thicker than that of *C. baccifer*; the former measures around 83 μm, as compared to 46 μm of the latter. After all and in brief, the fossil is comparable with and closely related to *C. baccifer*, the only living species in *Cucubalus*. Considering the difference from *C. baccifer* in a few quantitative characters, we have herein described this late Pliocene taxon as a new species, *Cucubalus prebaccifer* Huang, Liu et Zhou, sp. nov.

Table 1
The three main seed morphotypes of the Caryophyllaceae, based on morphological data from Bojňanský and Fargašová (2007).

Mor.	Characteristics	Representatives
Mor. 1	Elliptic to circular in shape, laterally winged	*Herniaria*, *Spergula*, *Spergularia*
Mor. 2	Reniform to circular in shape, papillae in disorder or arranged in concentric rows	*Agrostemma*, *Arenaria*, *Cerastium*, *Eremogone*, *Gypsophila*, *Lychnis*, *Minuartia*, *Myosoton*, *Sagina*, *Saponaria*, *Silene*, *Spergularia*, *Stellaria*,
Mor. 3	Shield-shaped, radicle extended, hilum in the center of the seed face, rugulae radiating from the hilum to the margin	*Dianthus*, *Petrorhagia*

Mor. = morphotype.

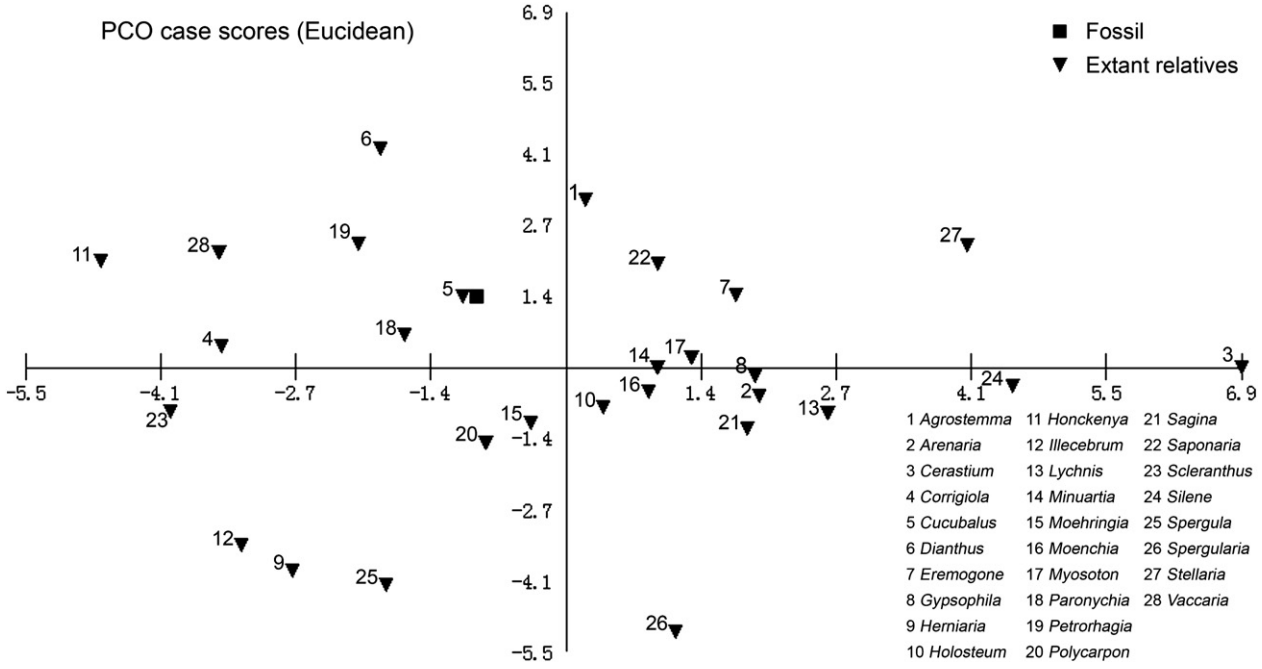

Fig. 2. The morphological principal coordinates (PCO) analysis based on seed morphological data of the fossil taxon and 28 extant genera in the Caryophyllaceae. The genus *Cucubalus* has a shorter distance from the fossil taxon than any other genus.

5. Biogeographical and ecological implications

Caryophyllaceae has rarely been found as fossils, even as microfossils, such as pollen grains (Jordan and Macphail, 2003). Until now, only a few genera, e.g., *Arenaria*, *Cerastium*, *Hantsia*, *Minuartia*, *Silene* and *Stellaria*, have been recorded from the geological time (Chandler, 1960, 1961; Zazula et al., 2005; Thompson et al., 2011). As yet, the genus *Cucubalus* in this family has no fossil record. To the best of our knowing, the present fossil taxon from the upper Pliocene in southwestern China represents the first fossil record of this genus. This provides highly important information on the past biodiversity and biogeography of both the genus *Cucubalus* and the fossil-scant family Caryophyllaceae. It suggests that *Cucubalus* plants have occurred in northwestern Yunnan, southwestern China, at least since the late Pliocene. This brings useful information to our understanding of the diversification of the Caryophyllaceae. This newly described fossil taxon can be used to calibrate the molecular clock in the phylogeny of this family.

Today, the genus *Cucubalus* is widely spread in temperate and warm areas in central Europe and Asia (Wu et al., 1995; Tang et al., 1996). In China, it is mainly distributed in the northeast, northwest and southwest of the mainland, and Taiwan (Wu et al., 1995; Tang et al., 1996). The newly described fossil taxon suggests the early occurrence of *Cucubalus* in southwestern China during the late Pliocene. It therefore might have some close correlations with the extant *Cucubalus* species living in the present southwestern China. Other fossil elements documented from the same deposit, including *Quercus* sect. *Heterobalanus* (Tao, 1986) and *Sambucus* (Huang, et al., 2012), demonstrate that all these groups have coexisted in northwestern Yunnan, southwestern China, during the late Pliocene. Interestingly, the three groups are commonly seen in this region today. This implies that the vegetation type and climatic conditions in northwestern Yunnan, southwestern China, might have little changed since the late Pliocene.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.revpalbo.2012.11.011.

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Appendix A

The taxon-characteristic matrix for PCO analysis, including 29 taxa, i.e., the fossil taxon plus 28 extant relatives in the Caryophyllaceae, and 46 characteristics. 1 means Yes; 0 means No

a. reniform; b. circular; c. ellipsoid; d. ovoid; e. fusiform; f. pyriform; g. cordiform; h. triangular; i. clavate; j. globose; k. cuneat;

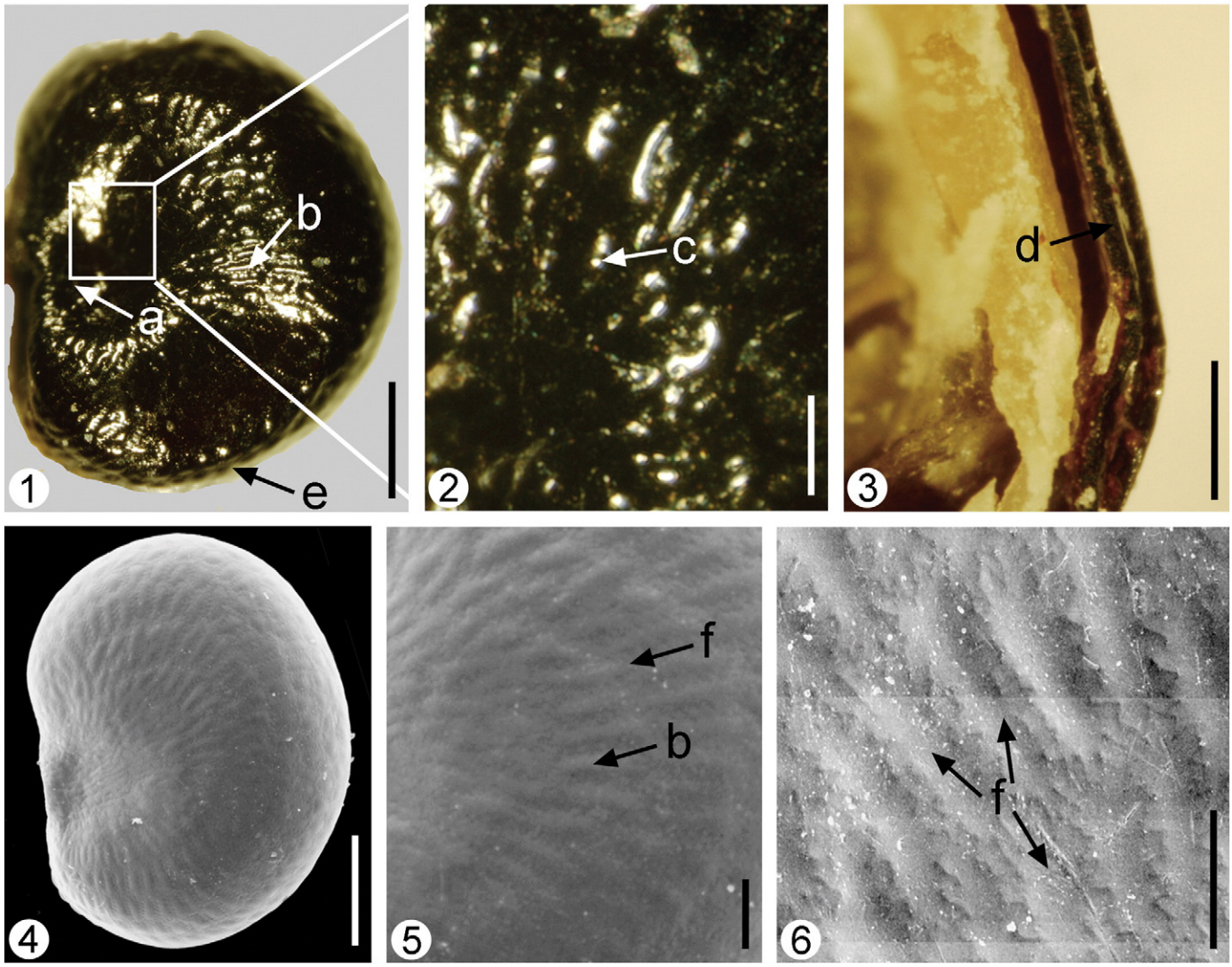

Plate 2. Extant seeds of *Cucubalus baccifer* L. observed under the binocular microscope and SEM, and their surface details. Scale bar = 0.5 mm for images 1, 4; 0.1 mm for images 2–3, 5–6. 1, 4. Showing the general shape and discontinuous rugulae made of rod-like elements radiating from the hilum to the dorsal margin, observed under the binocular microscope and SEM, respectively. 2. Surface details, showing the radially tuberculate pattern on the testa surface close to the hilum. 3. Showing the cross section of the testa. 5. Showing the discontinuous rugulae made of rod-like elements, one "rod" pointing to the space between two adjacent "rods" in the outer concentric row. 6. Surface details observed under SEM. The testa epidermal cells are clearly wedged in arrangement, one cell aiming at the space between two adjacent cells ahead. a. Hilum. b. Rugula. c. Tuberculum. d. Cross section of the testa. e. Dorsal margin. f. The arrangement that one rod-like element (epidermal cell) is aiming at the region between two adjacent "rods" (epidermal cells) in the outer concentric row.

l. shield-shaped; m. horseshoe-shaped; n. radicle extended; o. radicle longer than cotyledon; p. winged; q. wing transversely striate; r. not winged; s. hilum in the center; t. caruncula expressive; u. dorsal convex; v. dorsal straight; w. ventral convex; x. ventral concave; y. ventral straight; z. smooth; aa. furrowed; ab. reticulate; ac. tuberculate; ad. aculeate; ae. with a longitudinal suture; af. papillae in disorder; ag.

Table 2
Detailed seed morphological comparisons between the fossil taxon and the extant *Cucubalus baccifer* L.

Taxa	Fossil taxon	*Cucubalus baccifer* L.
Shape	Reniform to circular, dorsal convex and roundish, ventral almost straight, dorsal margin lightly wavy or almost smooth	Reniform to circular, dorsal convex, ventral concave, straight, or humped in the middle, dorsal margin slightly wavy
Testa surface	Lustrous and rugulose, rugulae, discontinuous and sinuous, made of rod-like elements, radiating from the hilum to the dorsal margin	Lustrous, covered by discontinuous rugulae made of rod-like elements radiating from the hilum to the dorsal margin
Rod-like element	The rod-like element as wide as the furrow between, coaxially and radially close, one "rod" aiming at the region between two adjacent "rods" in the outer concentric row	The rod-like element not as wide as the space between, coaxially and radially loose, one "rod" aiming at the region between two adjacent "rods" in the outer concentric row
Number of rugulae	39–52	35–40
Testa thickness	83 μm	46 μm
Testa epidermal "cell"	The cell-like sculpture rhomboidal and wedged in arrangement, one "cell" aiming at the space between two adjacent "cells" ahead.	Rhomboidal and wedged in arrangement, one cell aiming at the space between two adjacent cells ahead
Size (L×W)	1.2–1.6×1.5–2.3 mm	1.3–1.5×1.6–1.8 mm
L:W	1.2–1.5	1.2–1.3

L = length; W = width.

papillae in concentric rows; ah. rugulae radial; ai. pricky; aj. wavy; ak. with excresce; al. <1 mm; am. 1–2 mm; an. 2–3 mm; ao. >3 mm.

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