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Hemitrapa Miki (Lythraceae) from the earliest Oligocene of southeastern Qinghai-Tibetan Plateau and its phytogeographic implications

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ABSTRACT

Hemitrapa Miki (Lythraceae) is an extinct aquatic genus that shows the close morphological affinity to water chestnut (*Trapa*), it has rich fossil records ranging from the late Paleocene to early Pliocene of the Northern Hemisphere. Recently, we found numerous *Hemitrapa* fruit fossils and pollen grains of *Hemitrapa* from the earliest Oligocene of southeastern Qinghai-Tibetan Plateau, comprising its southmost fossil record worldwide and the earliest fossil record in Asia. We studied the morphology of fruit fossils and pollen grains of *Hemitrapa*, and compared them with previous fossil records. Two pairs of arms and parallel ridges along the main body of the fruit, as well as pollen grains with three distinctive crests and of a smaller size than living *Trapa natans*, clearly assign these fossils to *Hemitrapa*. We described here a new species, namely *Hemitrapa alpina* T. Su et Z.K. Zhou sp. nov. The finding of *H. alpina* could not only contribute to plant diversity in the geological past of the Qinghai-Tibetan Plateau, but also indicate that *Hemitrapa* grew on the plateau by the earliest Oligocene. Meanwhile, *H. alpina* greatly expands the geographic distribution of *Hemitrapa* during the Paleogene of the Northern Hemisphere, the disappearance of *Hemitrapa* might be due to dramatic paleoenvironmental changes on the plateau since the Paleogene.

1. Introduction

The Qinghai-Tibetan Plateau, the highest plateau in the world with average altitudes of greater than 4000 m, underwent dramatic tectonic activity throughout the Cenozoic, which not only shaped the topography of eastern Asia, but also had profound influence on regional and even global climate patterns (Harris, 2006; Song et al., 2010). Consequently, paleoenvironmental changes in this region greatly contributed to the diversity of plants there. Today, areas adjacent to the Qinghai-Tibetan Plateau, especially along the southeast marginal part, are one of the world's modern biodiversity hotspots (Myers et al., 2000). Molecular studies continue to debate the diversification patterns under paleoenvironmental changes on the Qinghai-Tibetan Plateau (Renner, 2016). Fossil records provide solid evidence for the biodiversity history on earth (Taylor et al., 2008). However, well-preserved fossil floras uncovered in the core areas of the Qinghai-Tibetan Plateau are still rare, preventing us from understanding the evolutionary and biogeographic histories of plants in this fascinating region.

Fossils, especially those belonging to extinct taxa, are pivotal to understand not only the biodiversity in the geological past, but also the evolutionary patterns of many living taxa (Doyle and Endress, 2010). *Hemitrapa* is an extinct aquatic genus in the family Lythraceae that was discovered through fruit fossils from the Miocene of Japan (Miki, 1941), and shows close morphological similarity to the water chestnut (*Trapa*). Fruits of both genera have one or two pairs of arms, as well as a head with parallel ridges, which are unique among taxa in angiosperms. *Hemitrapa* was formerly assigned to Trapaceae, and was moved along with *Trapa* to Lythraceae according to recent phylogenetic revision (Graham et al., 2005).

Hemitrapa in the form of fruit was once widely distributed in strata ranging from the Upper Paleocene to the Lower Pliocene of the Northern Hemisphere (Miki, 1948; Tanai, 1971; Akhmetiev, 1978; Gregor, 1982; Mai and Walther, 1991; Mai, 2001; Kovar-Eder et al., 2002; Yabe, 2008) (Fig. 1). The oldest occurrence of *Hemitrapa* is from the late Paleocene of Canada (Dawson, 1875; Graham, 2013). *Hemitrapa* later became more diversified during the Miocene of Eurasia (Miki, 1952; Tanai and Suzuki, 1963; Wójcicki and Kvaček, 2003; Wang,

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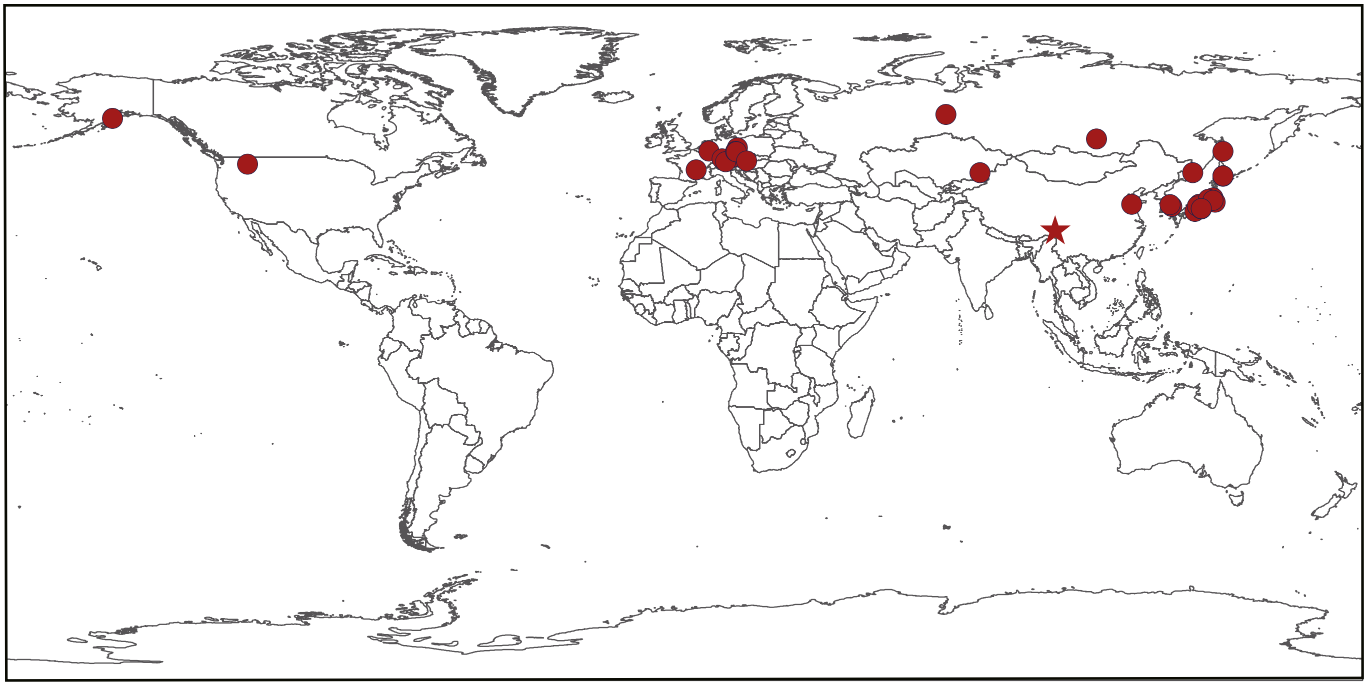

Fig. 1. Previous fruit fossil records of *Hemitrapa* (circles), and *Hemitrapa* fossils from Kajun village, Markam County, southeastern Qinghai-Tibetan Plateau in this study (star). Information on previous fruit fossil records is from Wang (2012: Table 2). Map is created using ArcGIS 9.3 (ESRI, Redlands, CA).

2012). It was not until the Pliocene that *Hemitrapa* was extinct worldwide (Graham, 2013). Meanwhile, pollen grains that showed morphological similarity to *Trapa* judging by the outline and surface ornaments, but significantly smaller size, were discovered in numerous *Hemitrapa*-bearing sediments, and were called *Sporotrapoidites* (Mohr and Gee, 1990; Zetter and Ferguson, 2001; Wang, 2012).

Even rich fossil records in middle and high altitudes of the Northern Hemisphere, there is only one megafossil record of *Hemitrapa* in China, namely *Hemitrapa shanwangensis* Q. Wang from the middle Miocene of Shangwang, Shandong Province, North China (Wang, 2012). We recently discovered numerous well-preserved *Hemitrapa* fruits and associated pollen grains from the earliest Oligocene of Markam County, southeastern Qinghai-Tibetan Plateau. This finding is the southernmost fossil record for the genus, as well as its earliest fossil record in Asia. In this paper, we first described the morphology of these fossils and reported a new species of *Hemitrapa*, followed by a discussion of its implications for biogeography.

2. Materials and methods

2.1. Geological setting

Fossils for this study were collected from the Lawula Formation in Kajun village, which is located about 16 km northwest of Gatuo Town, Markam County in southeastern Qinghai-Tibetan Plateau, China (29°45′ N, 098°26′ E; 3878 m a.s.l.; Plate I, 1). The Lawula Formation occurs widely throughout eastern Tibet (Bureau of Geology and Mineral Resources of Xizang (BGMRX), 1991). In Kajun village, the strata consist of the Lower Cretaceous Jingxing Formation at the base, followed by the fossiliferous Lawula Formation, and capped by Quaternary deposits (Su et al., 2014). The Lawula Formation measures about 1000 m in thickness and consists of volcanic rock, sandstone, and mudstone. Several layers of sandstone and mudstone in the middle and upper sections of the Lawula Formation contain an abundance of well-preserved plant fossils. Tao and Du (1987) first described the flora of the Lawula Formation in Markam, which is dominated by Betulaceae.

Recently, we found a new outcrop of the Lawula Formation that is made up of several layers of mudstone and sandstone containing numerous plant fossils, which are different in floristic components than those reported by Tao and Du (1987). Fossils in this study were found in a layer of red to brown mudstone in the upper part of the stratum that measures around 30 cm in thickness (Plate I, 2, 3), which is in higher layer than any of the taxa that had been previously recorded in the stratum, i.e., *Equisetum oppositum* (Equisetaceae) (Ma et al., 2012), *Elaeagnus tibetensis* (Elaeagnaceae) (Su et al., 2014), and *Quercus tibetensis* (Fagaceae) (Xu et al., 2016).

The geological age of the Lawula Formation was previously thought to be the late Miocene based on stratigraphic comparisons with adjacent areas (BGMRX, 1991) and paleofloristic correlations (Tao and Du, 1987). We found several layers of volcanic rock among the sediment of the Lawula Formation. One volcanic layer, which is just ~5 m below the fossil-rich layer of this study, yields a ^{40}Ar/^{39}Ar age of 33.4 Ma (Su et al., unpublished data, measured in the Ar-Ar and Noble Gas Research Laboratory of The Open University, UK), indicating that the age of the fossils in this study is the earliest Oligocene, which generally agrees with previous radiometric dating from the same formation (Zhang et al., 2005).

2.2. Morphological observation and imaging

Impressions of fossil fruits were prepared using a dissecting needle under a stereoscope (Leica EZ4) in the laboratory of Paleoecology Research Group, Xishuangbanna Tropical Botanical Garden (XTBG), to remove a layer of rock that covered some parts of the fossils. Then, photos of the gross morphology of the fruits were taken with a digital camera (Nikon D700, lens) in oblique light. During this procedure, some specimens were immersed in aviation-grade kerosene to improve the contrast, following the method of Kerp and Bomfleur (2011). A stereoscope (Zeiss Smart Zoom 5) was used to photograph the detailed morphology of the fruits at the XTBG Central Laboratory. Photos were compiled by Adobe Illustrator CS6 (Adobe Systems, San Jose, California, USA).

Pollen grains from the mudstone containing the fruit fossils were extracted using the standard procedure of Traverse (2007). The sediment sample was first ground into fine particles and then treated with 10% HCl, 5% NaOH, and 39% HF, separated by rinsing with distilled water

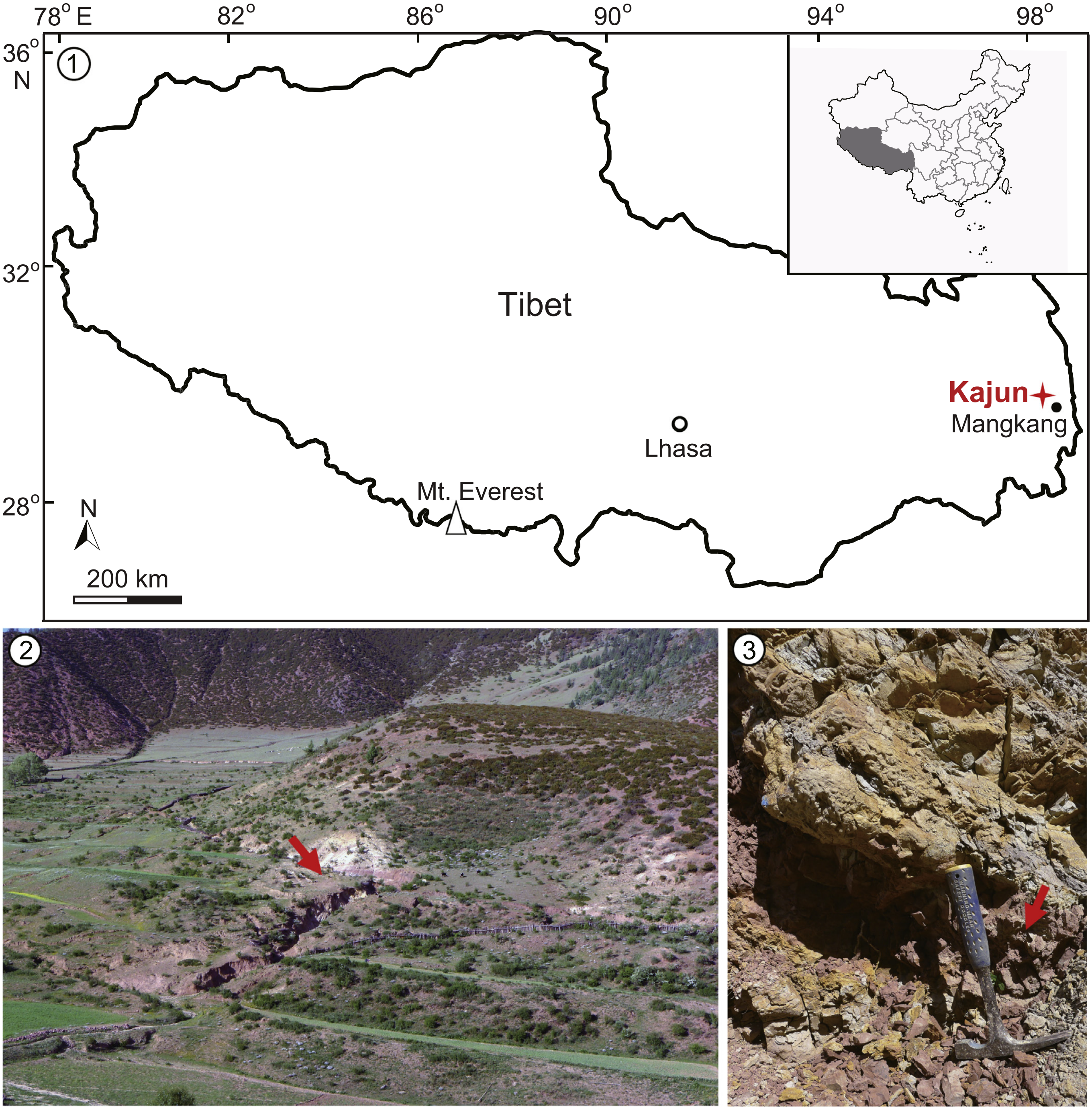

Plate I. Fossil site in this study from Kajun village, Markam County, southeastern Qinghai-Tibetan Plateau, China.
1: the location of the fossil site; 2: the view of the Lawula Formation at the fossil site; 3: the fossil-bearing layer. Arrows indicate the layer where fossils in this study were collected.

and centrifugation. An ultrasonic sieve was used to remove particles smaller than 5 μm. The remains were made smear slides and transferred to the light microscope for further examination. Photographs of the pollen grains were taken at 600× magnification using a light microscope (Leica DM750). Single pollen technique (Ferguson et al., 2007), namely moving single pollen grain from a slide to a stub, was applied to observe the pollen morphology with a scanning electron microscope (Zeiss EVO LS10).

3. Systematic description

Order: Myrtales Juss. ex Bercht. & J. Presl

Family: Lythraceae J. St.-Hil

Genus: ***Hemitrapa*** Miki

Species: *Hemitrapa alpina* T. Su et Z.K. Zhou sp. nov.

Holotype: KUNPC XZKJ4-0006 (Plate II, 6) (designated here).

Paratypes: KUNPC XZKJ4-0001-0005 (Plate II, 1–5), KUNPC XZKJ4-0007 (Plate II, 7) (designated here).

Repository: The Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN). "PC" denotes the paleobotanical collections.

Type locality: Lawula Formation, Kajun village, Markam County, southeastern Qinghai-Tibetan Plateau, China (Plate I, 1).

Age: Earliest Oligocene.

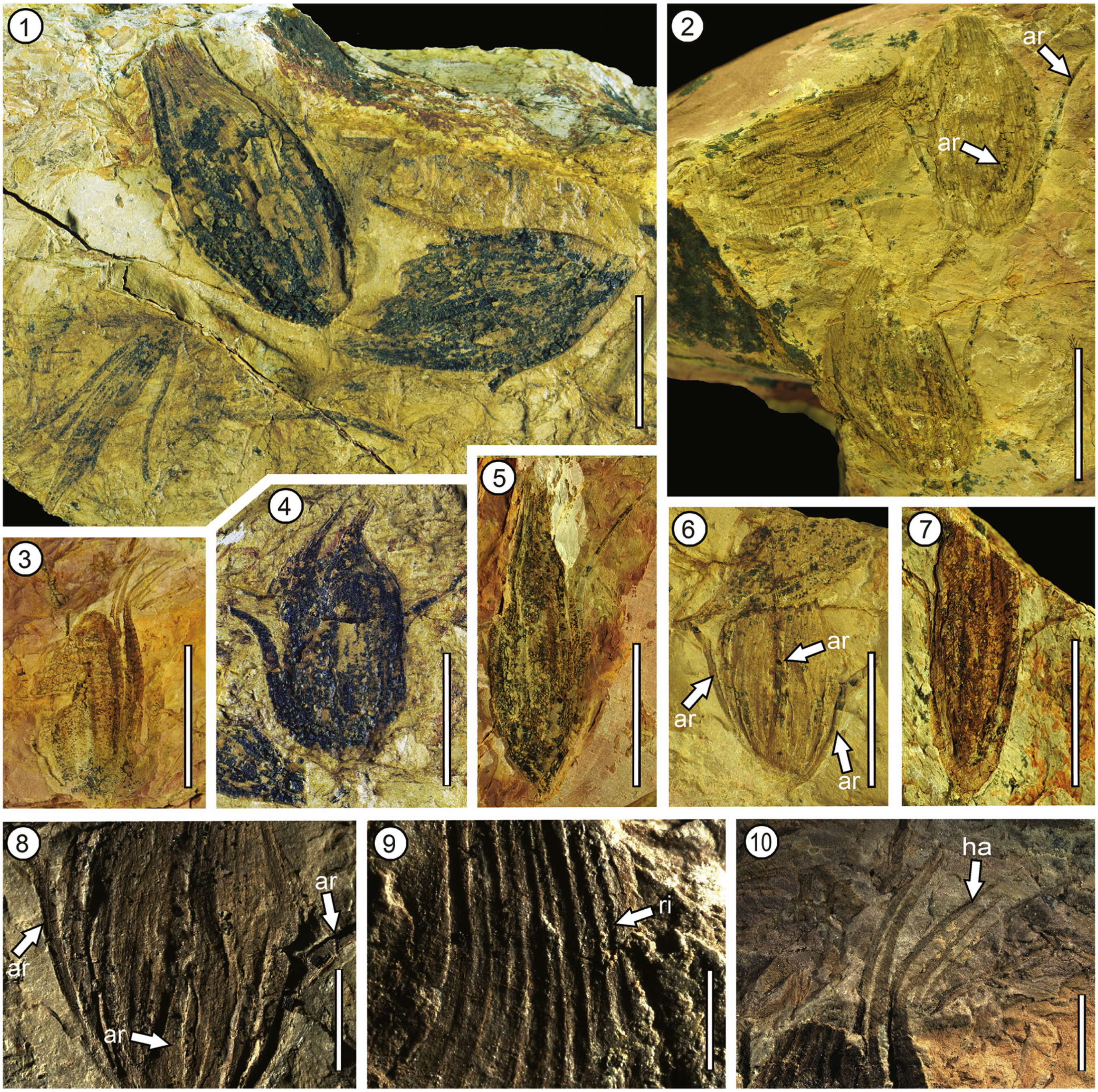

Plate II. *Hemitrapa alpina* T. Su et Z.K. Zhou sp. nov. Scale bars: 1–7 = 1 cm; 8 = 1 mm; 9, 10 = 2 mm.
Specimen numbers: 1–7. KUNPC-XZKJ4-0001-0007. Holotype: KUNPC XZKJ4-0006; paratypes: KUNPC XZKJ4-0001-0005; KUNPC XZKJ4-0007.
8: arms (ar) attaching to the fruit base. Specimen number: A, KUNPC-XZKJ4-0002 (upper part); 9: parallel ridges (ri) at the fruit head. Specimen number: KUNPC-XZKJ4-0001 (top-left); 10: hairs (ha) pointing upward at the top of fruit head. Specimen number: KUNPC-XZKJ4-0003.

Etymology: The specific epithet "*alpina*" refers to the collection site of these fossils are from a high mountain, named Mt. Lawula in Markam County, which located on southeastern Qinghai-Tibetan Plateau.

Diagnosis: Fruits elongate or fusiform in shape (Plate II, 1–7). The fruit head not well defined, with hairs at the top of the neck (Plate II, 1, 2). Longitudinal ribs along the body of the fruit (Plate II, 2). The base of the fruit rounded and sessile (Plate II, 1–7). Two pairs of arms at the base of the fruit extending upward (Plate II, 2, 6, 8); one pair of arms shorter than the other (Plate II, 2).

Description: Fruits are elongate or fusiform in shape, approximately 17–25 mm long and 7–11 mm wide (Plate II, 1–7). The broadest part of the fruit body is about 1/4 to 3/4 of the whole length above the base, and it gradually narrows toward each end of the body (Plate II, 4, 5). The head of the fruit is not well defined, and the surfaces of both the head and neck are finely ribbed (Plate II, 5, 9), while an elongated cluster of vertical hairs can be observed in some specimens at the top of the head of the fruit (Plate II, 1, 3, 4, 5, 10). There are fewer longitudinal ribs on the surface of the lower part of the fruit body, and they are evenly spaced (Plate II, 2, 5, 6). The fruit base is round in shape and sessile (Plate II, 1, 2). Two pairs of slender arms approximately 8–15 mm in length point upward (Plate II, 2–8). One pair of arms could be shorter than the other pair, joining the longer pair at the base of the fruit body (Plate II, 6). The arms are attached to the base of the fruit, the angle between one arm and the main body ranges from 30° to 55° (Plate II, 4–8) and arms gradually taper in length (Plate II, 6, 8). In most specimens, only two or three arms could be observed on each fruit fossil (Plate II, 6, 8), possibly because they are vulnerable to breaking off.

Description of trapaceous pollen grains found in the same layer—Trapaceous pollen grains, previously named *Sporotrapoides*, were obtained from the same layer (Plate III, 1–4). Each grain has three distinctive crests (Plate III, 1); the outline is obtuse; pollen grains are ~28 μm in length and ~25 μm in width; rhombic in equatorial view, and triangular obtuse; concave to convex in polar view. Pollen grains have three protruding apertures (Plate III, 1–3). The surface of the grain is slightly granulated (Plate III, 4). Generally, these pollen grains show high morphological similarity to *Trapa*, but the size of the pollen (Plate III, 1–4) is significantly smaller than that of *Trapa* (Plate III, 5–8).

4. Discussion

4.1. Morphological comparison

Fruit fossils from Markam County in southeastern Qinghai-Tibetan Plateau display unique morphological features for their systematic assignment, such as two pairs of arms, and longitudinal ribs along the surface of the fruit (Plate II). These characteristics display a close similarity to *Trapa* and *Hemitrapa* (Graham and Graham, 2014). It is not an easy task to distinguish these two genera when morphological variation of all fossil records is considered (Graham, 2013). However, our fossils are different from living species of *Trapa* by the elongate or fusiform shape of the fruit body, and quite slender arms starting from the base of the fruit body (Plate II).

Many fossil records of *Hemitrapa* have been discovered in the Eocene and Miocene sediments of the Northern Hemisphere mid-latitudes (Graham, 2013). Generally, there are two types of arms on *Hemitrapa*, namely one pair, e.g., *Hemitrapa borealis*, and *Hemitrapa praeconocarpa*, and two pairs, e.g., *Hemitrapa heissigii*, and *Hemitrapa shanwangensis* (Wang, 2012). Meanwhile, the arm positions can be divided into two types, with some species having them above the center of the fruit body, e.g., *Hemitrapa trapelloidea*, while others are inserted near the base of the fruit, e.g., *Hemitrapa pomelii* (Wang, 2012). The fossils in this study have two pairs of arms, with one pair that is longer than the other (Plate II). In addition to that, the arms of several fruits are well preserved, and are inserted near the base of the fruit. In some of our specimens, the basal part of the arm is close to the fruit, but we also observed that these arms attach to the basal part of the fruit body. One young fruit clearly shows this feature (Plate II, 1, lower left). Therefore, the arm position is stable among the Markam specimens. Both elongate and fusiform fruit shapes were found among our specimens. One young fruit (Plate II, 1, lower-left), as well as some other fruits (Plate II, 5, 7), have an elongated shape, while the sizes of these fruits are relatively smaller than the fusiform fruits. Therefore, it is plausible to infer that the elongated specimens are young fruits, whereas the fusiform specimens are mature fruits (Plate II, 1–4).

Our fossils are morphologically different from some previous fossil records because they do not have barbs on top of the arms, but barbs do exist in several fossil taxa of *Hemitrapa*, i.e., *Hemitrapa heissigii*, *Hemitrapa teumeri*, and *Hemitrapa trapelloidea*. The arms are inserted into the basal part of the fruits in our fossils (Plate II, 1, 2, 6), a characteristic that only exists in *Hemitrapa pomelii*, and *H*. cf. *pomelii*; however, the mature fruit shapes of our fossils and these two fossil species are fusiform and ovate, respectively. In addition to that, our fossil specimens do not have stalks, whereas previous fossil records have relatively long or short stalks (Wang, 2012). This may be due to the taphonomic basis or the automatic detachment of mature fruits from the stalks in our fossils. Judging by the morphological difference between our fossils and previously reported fossils, we assign these fruit fossils from southeastern Qinghai-Tibetan Plateau to be a new species, namely *Hemitrapa alpina* T. Su et Z.K. Zhou sp. nov.

In the basal rocks containing *Hemitrapa alpina*, we found plenty of pollen grains that show similar morphology to *Sporotrapoides erdtmanii*. Several unique features of the pollen grains in *Trapa*, including three distinctive crests and the thin columellate layer (Mohr and Gee, 1990), are present in our samples, except for the much smaller size of pollen grains from Markam (Plate III). In many other fossil sites that contain *Hemitrapa*, *Sporotrapoides* pollen grains were also observed in the same layer as *Hemitrapa* (Mohr and Gee, 1990; Wang, 2012; Graham, 2013). Therefore, our finding further supports the idea that fruits and pollen grains from southeastern Qinghai-Tibetan Plateau should be from the same species as previously suggested (Mohr and Gee, 1990).

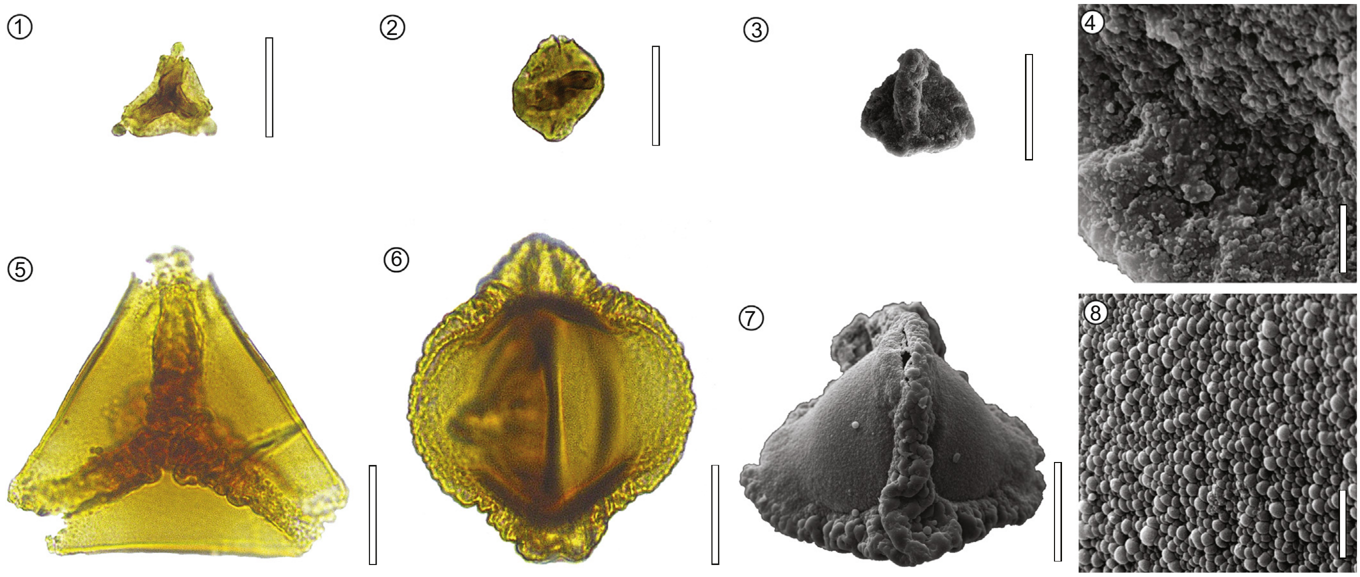

Plate III. Pollen morphologies of *Sporotrapoides* sp. (1–4) from Kajun village, Markam County and *Trapa bicornis* var. *cochinchinensis* (5–8). Scale bars: 1–3, 5–7 = 25 μm; 4, 8 = 2 μm.
1, 2, 5–6: polar and equatorial views of *Sporotrapoides* sp. and *T. bicornis* var. *cochinchinensis* pollen grain under light microscope, respectively. Please note that they use the same scale bars.
3, 7: polar view of *Sporotrapoides* sp. and *Trapa bicornis* var. *cochinchinensis* pollen grain under SEM, respectively.
4, 8: the surface of *Sporotrapoides* sp. and *T. bicornis* var. *cochinchinensis* pollen grain under SEM, respectively.

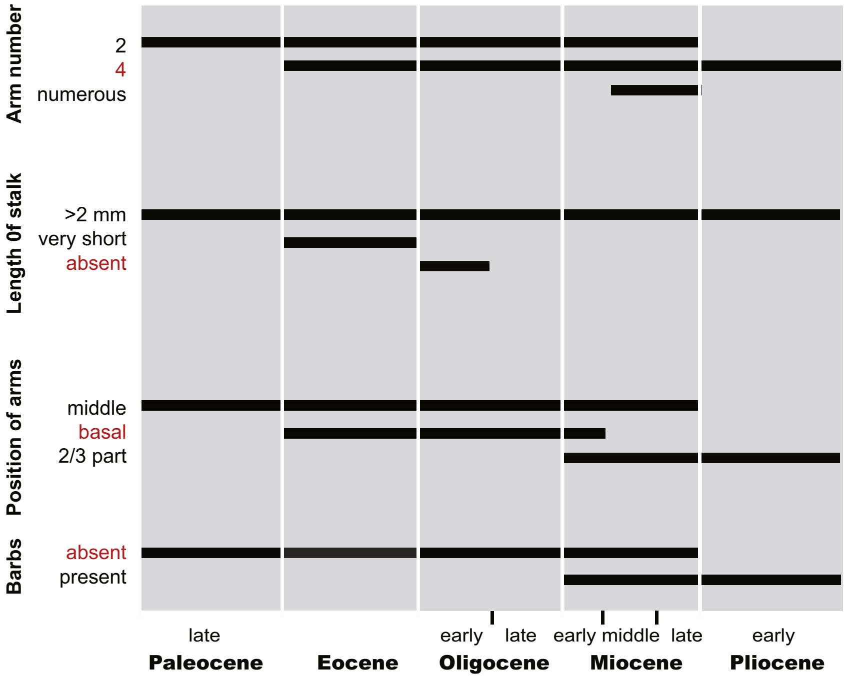

Fig. 2. The evolution of selected morphological traits in fossil records of *Hemitrapa*. Data are from Wang (2012) and this study. Morphological characters in red are observed in *H. alpina* T. Su et Z.K. Zhou sp. nov.

4.2. Evolution of morphological traits

The morphology of *Hemitrapa* is quite diverse during their occurrence from the late Paleocene to the early Pliocene (Fig. 2). Fossil records indicate that some morphological traits in *Hemitrapa* had existed as early as the late Paleogene and lasted until the late Miocene, e.g., two arms, arms inserting to the middle part of the fruit, and the absence of barbs on the top of the arms (Fig. 2), whereas some other traits emerged later, e.g., numerous arms, and the presence of barbs on the top of the arms (Fig. 2). Among all morphological traits observed, only the relatively long stalk (>2 mm) existed as long as the occurrence of *Hemitrapa* throughout the geological time (Fig. 2). However, it is too early to elucidate the trait evolution based on limited characters preserved on fossils.

Even the high morphological similarity between *Hemitrapa* and *Trapa*, the evolutionary significance for the morphological difference between *Hemitrapa* and *Trapa* is still unresolved. As the pollen grain is concerned, it is reasonable to hypothesize that the smaller pollen grain size in *Hemitrapa* would be more easily transported by wind. Meanwhile, the longer hairs are found at the tops of the fruits, compared to the shorter hairs found in *Trapa*. If this structure existed in their flowers, it could be more efficient for capturing pollen grains in the air. Therefore, *Hemitrapa* might belong to anemophilous, instead of multiple pollination patterns in *Trapa* at the present day (Wang and Chen, 1996).

4.3. Phytogeographic history of Hemitrapa

We reported on *Hemitrapa* specimens from the early Oligocene of southeastern Qinghai-Tibetan Plateau, comprising the earliest fossil record of this genus in Asia. The finding of *Hemitrapa alpina* indicates that *Hemitrapa* might be distributed on the Qinghai-Tibetan Plateau much earlier than in many other regions of the Northern Hemisphere. Moreover, *Hemitrapa alpina* is the southmost fossil record of this genus around the world to our current knowledge, which greatly expands the spatial distribution of *Hemitrapa* during the Paleogene. Together with previous fossil records worldwide, it indicates that *Hemitrapa* had been widely distributed throughout Eurasia by the Oligocene.

Lythraceae has a long fossil history that could be dated back to the late Cretaceous (Taylor et al., 2008). As *Hemitrapa* is concerned, its earliest fossil record is from the late Paleocene of Alberta and Saskatchewan in Canada (Graham, 2013). It is not until the early Miocene that *Trapa* first occurred in the Northern Hemisphere (Graham, 2013). Even *Hemitrapa* is morphologically different from *Trapa* at the genus level, it is difficult to separate *Hemitrapa* from *Trapa* using gross morphology in some cases because fossils occasionally display an intermediate morphology between these two genera (Budantsev, 1960; Graham, 2013). This morphological similarity may indicate their close evolutionary affinity, and further supports the idea that *Hemitrapa* should be an ancestor of *Trapa* (Miki, 1959; Mohr and Gee, 1990).

Some other plant fossils were discovered from the same stratum in Kajun village, e.g., *Elaeagnus tibetensis* (Elaeagnaceae) (Su et al., 2014), and *Quercus tibetensis* (Fagaceae) (Xu et al., 2016), indicating that the plant diversity in southeastern Qinghai-Tibetan Plateau during the Paleogene was much higher than in present day there. It is interesting that numerous Neogene floras have been reported from Yunnan Province, a region adjacent to southeastern Qinghai-Tibetan Plateau (Tao, 2000; Huang et al., 2016); however, fossils of *Trapa* instead of *Hemitrapa*, were found from the Pliocene of Yunnan Province (Huang et al., 2016), we could expect that *Hemitrapa* might be found from Paleogene floras in this region, because the drainage system between Qiangtang and Lhasa blocks on the Qinghai-Tibetan Plateau and north part of Yunnan had collected by the Eocene (Yan et al., 2012). As aquatic plants, *Hemitrapa* could migrate via the drainage system.

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