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FRUITS OF *HEMITRAPA* (TRAPACEAE) FROM THE MIOCENE OF EASTERN CHINA, THEIR CORRELATION WITH *SPOROTRAPOIDITES ERDTMANII* POLLEN AND PALEOBIOGEOGRAPHIC IMPLICATIONS

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ABSTRACT—The fruits of the extinct genus *Hemitrapa* Miki (Trapaceae) are described from the Miocene Shanwang Formation, representing its first fossil record in the Cenozoic of China. Bearing a fusiform, relatively small fruit body with a very long stalk and four sub-equal, strongly ascending, horn-like arms, the Chinese fossil fruits are described as *H. shanwangensis* Q. Wang new species. Prior to this discovery, a dispersed, trapaceous pollen *Sporotrapoidites erdtmanii* (Nagy) Nagy was documented from the same formation. Recent paleobotanical and palynological studies in Europe demonstrated that *Hemitrapa* was closely related to *S. erdtmanii*, so the co-occurrence of *Hemitrapa* fruits and *S. erdtmanii* pollen at Shanwang implies that they may stem from the same parental plant population. *Hemitrapa* fruits have been widely recognized from the Miocene of mid-latitudes in France, Austria, the Czech Republic, Kazakhstan, Russia, Korea, Japan and the U.S.A. as well as from the late Oligocene–Miocene of Germany and the late Eocene of the Czech Republic. In contrast, dispersed *S. erdtmanii* pollen has been recovered from the Miocene in central Europe as well as from the late Eocene to the Pliocene of eastern Asiatic shelf basins near the Bohai Sea, Yellow Sea, East China Sea, and the Sea of Japan. Overall, the microfossil and macrofossil records demonstrate that the parental plants of *Hemitrapa* might have begun to diversify from the mid-latitudes of Eurasia since the Eocene, flourished in eastern Asia and Central Europe during the Miocene, and become extinct after the Pliocene.

INTRODUCTION

HEMITRAPA MIKI, 1941 was instituted for small, *Trapa*-like fossil fruits from the late Miocene of Japan and referred to the family Trapellaceae (F. W. Oliver) Honda and Sakisaka, 1930 (Miki, 1952a, 1952b; Gregor, 1982). *Hemitrapa* was subsequently re-classified into a monotypic family Trapaceae Dumortier, 1829 (Mai, 2001; Wójcicki and Zastawniak, 2003; Kovar-Eder et al., 2005), in which *Trapa* L., 1753 is the sole living genus. *Trapa* is allied morphologically to the Lythraceae J. Saint-Hilaire, 1805 by the partly inferior ovary, axile placentation, mature seeds without endosperm, tetramerous flowers, valvate sepals, introrse and versatile anthers, persistent floral tube, and basically opposite, simple leaves (Chen, 2007). This study recognizes the independent family Trapaceae, rather than following the APG's (2003) treatment which places Trapaceae within Lythraceae, a decision based primarily on the characteristic horn-bearing nuts (Wan, 2000; Wójcicki and Zastawniak, 2003) and crested, generally prolate-spheroidal pollen (Mohr and Gee, 1990; Zetter and Ferguson, 2001).

The fruits of *Hemitrapa*, like those of closely related extant genus *Trapa*, were usually discovered from Cenozoic lacustrine deposits in the Northern Hemisphere. About ten species of *Hemitrapa* have been described from the mid-latitude regions in France, Germany, Austria, the Czech Republic, Kazakhstan, Russia, Korea, Japan and the U.S.A. (Table 1). At higher latitudes, *H. borealis* (Heer) Miki, 1948 was reported from the middle Miocene of Port Graham (English Bay), Alaska (Miki, 1948, 1952a; Wolfe and Tanai, 1980). The fossil fruits of *Hemitrapa* and *Trapa* thus provide an important historical perspective on the early evolution, diversity, and biogeography of the Trapaceae.

Recent paleobotanical and palynological studies demonstrated that *Hemitrapa* was closely related to a dispersed trapaceous pollen *Sporotrapoidites erdtmanii* (Nagy) Nagy, 1985 (Mohr and Gee, 1990; Zetter and Ferguson, 2001; Kovar-Eder et al., 2005). Such characteristic fruits and pollen stem from the same parental plant in Trapaceae.

Sporotrapoidites erdtmanii pollen possesses three distinctive crests (i.e., exinal ridges) and a relatively thin columellate layer (Morhr, 1983; Nagy, 1985; Mohr and Gee, 1990; Song et al., 1999; Zetter and Ferguson, 2001; Kovar-Eder et al., 2005). These features are unique and easily recognized in both fossil and extant taxa of Trapaceae. Although the pollen of *Hemitrapa* and *Trapa* are very similar (i.e., rhombic obtuse in equatorial view and triangular obtuse, concave to convex in polar view), the pollen of *Hemitrapa* (i.e., *S. erdtmanii*) is clearly distinguished from other known trapaceous pollen of fossil *Trapa* (i.e., *S. illingensis* Klaus; 58.5–74.7 μm in length) and of living *Trapa natans* L. (61.2–89.3 μm in length) by its smaller size (34.3–49.4 μm in length), possibly representing the plesiomorphic form in Trapaceae (Mohr and Gee, 1990; Zetter and Ferguson, 2001).

The oldest known fruits of *Hemitrapa* were described from the late Eocene of Europe (Wójcicki and Kvaček, 2003; Wójcicki and Zastawniak, 2003). However, the microfossil record of *S. erdtmanii* in Europe was primarily recovered from the Miocene. In contrast, *Hemitrapa* fruits from Asia occurred in the Miocene while *S. erdtmanii* pollen were recognized from the late Eocene to the Pliocene of eastern Asiatic Shelf Basins near the Bohai Sea, Yellow Sea, East China Sea and the Sea of Japan (Guan, 1989; Shaw, 1995; Song et al., 1999; Yi et al., 2003; Wang, 2006; Table 2). The widespread occurrence of *S. erdtmanii* in the early Cenozoic of China implies that it should be possible to discover *Hemitrapa* fruits in the coeval deposits of China. Therefore, an overall investigation on the temporal-spatial distribution of *Hemitrapa* and *S. erdtmanii* will be very helpful to decipher the early evolution, diversity, and paleobiogeography of their parental plants.

The main purposes of this paper are to describe the newly discovered fruits of *Hemitrapa* from the Miocene Shanwang

TABLE *1*—Comparisons of *Hemitrapa* species from the Cenozoic.

Species	Fruit shape	Fruit size	Arm number	Arm orientation	Arm form	Stalk	Locality and Age	Reference
H. shanwangensis Q. Wang n. sp.	Fusiform	15–18 mm long, 6–7 mm wide	4	15–20° with the longitudinal axis of the fruit stalk	10–12 mm long, slender to medium, no barbs or a few barbs on the top	5–35 mm long	middle Miocene or late early Miocene–early middle Miocene, Shanwang, eastern China	Liu and Leopold, 1992; Deng, 2006; Wang et al., 2007, 2010; this paper
H. hokkaidoensis (Okutsu) Miki, 1948	Fusiform	25–35 mm long, 8–10 mm wide	4	~20°	10–26 mm long, slender; no barbs on the top	5–28 mm long	early Miocene–middle Miocene, Japan	Miki, 1948, 1952a; Tanai, 1961; Shikama, 1964; Gregor, 1982; Yabe, 2008
H. cf. *hokkaidoensis* (Okutsu) Miki	Fusiform	~45 mm long, 18 mm wide	4	15–20°	At least 15–28 mm long, medium; no barbs	At least 7 mm long	Miocene, Sikhote-Alin, far eastern Russia	Akhmetiev, 1978
H. trapelloidea Miki, 1941	Ovate to fusiform	15–34 mm long, 6–15 mm wide	Numerous, 4 longer and some shorter	5–40°	2–18 mm long, slender; barbs on the top of longer arms	4–10 mm long	late Miocene, Japan and Austria	Miki, 1941, 1952a, 1959, 1961; Gregor, 1982; Kovar-Eder et al., 2002
H. sachalinensis (Okutsu) Miki, 1948	Elongate fusiform	50–60 mm long, 12–15 mm wide	4	60°	8–10 mm long, robust; no barbs	At least 2 mm long	Miocene, far eastern Russia	Miki, 1948, 1952a; Gregor, 1982
H. borealis (Heer) Miki, 1948	Ovate	28 mm long, 10 mm wide	2	50–60°	6–8 mm long, robust; no barbs	At least 2 mm long	Miocene, far eastern Russia (Sikhote-Alin), Korea, Japan, Alaska U.S.A.	Miki, 1948, 1952a; Tanai and Suzuki, 1963, 1972; Huzioka, 1972; Akhmetiev, 1978; Wójcicki and Kvaček, 2003
H. yokoyamae (Nathorst) Miki, 1948	Broadly ovate	30–40 mm long, 20 mm wide	4	60–70°	4–6 mm long, robust; no barbs	At least 2 mm long	Miocene, Japan	Miki, 1948, 1952a; Tanai, 1971
Hemitrapa sp.	Broadly fusiform	~12 mm long, 7 mm wide	4	60–70°	5–6 mm long, robust; no barbs	At least 1 mm long	Miocene, Idaho, U.S.A.	*Trapa americana* Knowlton in Brown, 1935; *Trapa* sp. in Pigg and Wehr, 2002
H. heissigii Gregor, 1982	Ovate to fusiform	20–30 mm long, 16 mm wide	4	50–75°	Over 15 mm long, slender; barbs on the top	Over 8 mm long	Miocene, Germany and the Czech Republic	Gregor, 1982; Gregor and Schmid, 1983; Mai, 1985; Huckriede and Urban, 1998; Wójcicki and Kvaček, 2002
H. teumeri (Menzel) Budantsev, 1960	Ovate	21–30 mm long, 14–17 mm wide	Numerous, 2 longer	40–45°	17–26 mm long, slender; barbs on the top	At least 2–3 mm long	middle Miocene, Germany	Budantsev, 1960; Gregor, 1982; Mai, 1985, 2001
Hemitrapa sp.	Fusiform	12–18 mm long, 6–8 mm wide	2	30–60°	5–12 mm long, slender; no barbs	At least 4–8 mm long	early Miocene, Kushuka, Kazakhstan	*Trapa vassiljevii* named by Kornilova, 1960
H. praeconocarpa (Vassiljev) Budantsev, 1960	Broadly fusiform	24–28 mm long, 12–18 mm wide	2	80–90°	5–7 mm long, robust; no barbs	At least 2–3 mm long	Miocene, western Siberia, Russia	Budantsev, 1960; *Trapa* sp. by Kryshtofovich and Borsuk, 1939
H. pseudoborealis Budantsev, 1960	Obovate	38 mm long, 20 mm wide	2	85–90°	8–10 mm long, robust; no barbs	No preserved	Miocene, southeastern Baikal coast, Russia	Budantsev, 1960; Gregor, 1982
H. pomelii (Boulay) Mai, 1991	Ovate	19–22 mm long, 7–10 mm wide	4	10–15°	6–7 mm long, slender; no barbs	At least 7 mm long	early Miocene, France; late Oligocene, Germany	Mai and Walther, 1991; Wójcicki and Kvaček, 2003; Wójcicki and Zastawniak, 2003
H. cf. *pomelii* (Boulay) Mai	Ovate	~22 mm long, 12 mm wide	4?	~10°	At least 3–5 mm long, slender; no barbs	Very short preserved	late Eocene, the Czech Republic	Wójcicki and Kvaček, 2003

TABLE 2—A correlation of the temporal and spatial distribution of *Hemitrapa* and *Sporotrapoidites erdtmanii* ("—" no record).

Locality	Age	Pollen	Fruit	Reference and Note
Pfaffenzell and Entrischenbrunn of Bavaria, Germany	Miocene	*S. erdtmanii*	*H. heissigii* Gregor	Gregor, 1982; Kovar-Eder et al., 2005
Gallenbach, Germany	Middle Miocene	*S. erdtmanii*	*H. heissigii* Gregor	Gregor and Schmid, 1983, p. 64, pls. 1–3; Kovar-Eder et al., 2005
Kreuzau, Germany	Late middle Miocene	*S. erdtmanii*	*Hemitrapa sp.*	Ferguson et al., 1998, p. 162, pl. 4, figs. 4–6; Kovar-Eder et al., 2005
Großräschen, Germany	Middle Miocene	—	*H. teumeri* (Menzel) Budantsev	Gregor, 1982, p. 358, fig. 3x–3z; Mai, 1985, p. 485, fig. 11; Mai, 2001, p. 111; previously identified as *Trapa teumeri* by Menzel, 1933, p. 27, pl. 7, fig. 2a–2g
Eberstetten, Germany	Early Miocene–early middle Miocene	—	*H. heissigii* Gregor	Gregor, 1982, p. 353–354, pl. 15; Kovar-Eder et al., 2005
Lusatica and Hessen, Germany	Late Miocene	—	*H. heissigii* Gregor	Huckriede and Urban, 1998, p. 118, pl. 5, figs. 8, 9a, 9b; Mai, 2001, p. 112, pl. 24, figs. 10–13
Rott, Germany	Late Oligocene	—	*H. pomelii* (Boulay) Mai	Wójcicki and Kvaček, 2003; Wójcicki and Zastawniak, 2003
Dolní Litvínov, Most Basin, North Bohemia, the Czech Republic	Late early Miocene	—	*H. heissigii* Gregor	Wójcicki and Kvaček, 2002, p. 119, figs. 3, 4; Teodoridis and Kvaček, 2006, p. 102, 106
Kučlín, North Bohemia, the Czech Republic	Late Eocene	—	*H.* cf. *pomelii* (Boulay) Mai	Wójcicki and Kvaček, 2003, p. 167, pl. 2a–2c
Legnica, Lower Silesia, Poland	Middle Miocene	*S. erdtmanii*	—	Worobiec, 2009, p. 47, pl. 15, fig. 4
Pellendorf, Austria	Late Miocene	—	*H. trapelloidea* Miki	Kovar-Eder et al., 2002, p. 132, fig. 4, pl. 2, figs. 1–12; Harzhauser et al., 2003, p. 43
Gergovie, France	Early Miocene	—	*H. pomelii* (Boulay) Mai	Mai and Walther, 1991; Wójcicki and Kvaček, 2003, p. 170, pl. 3b–e; previously identified as *Carpolithes pomelii* by Saporta, 1878, p. 67; *Trapa pomelii* by Boulay, 1899, p. 116, pl. 9, figs. 98–100; Baranova, 1954, p. 354, pl. 164, fig. 2
Port Graham (English Bay), Kenai, Alaska, U.S.A.	Middle Miocene	*S.* cf. *erdtmanii*	*H. borealis* (Heer) Miki	Miki, 1948, p. 76; Miki, 1952a, p. 349, text-fig. f; Wolfe and Tanai, 1980, p. 39; Wójcicki and Kvaček, 2003, p. 170, pl. 3a; fruit previously named as *Trapa borealis* by Heer, 1869, p. 38, pl. 8, figs. 9–14; Schimper, 1874, p. 300, pl. 103, figs. 30, 31; Schimper and Schenk, 1890, p. 631, figs. 345, 4, 5; pollen previously identified as cf. *Trapa* by Reinink-Smith and Leopold, 2005, p. 242, pl. 15, fig. 19
Potlatch Creek and Juliaetta, Latah County, Idaho, U.S.A.	Miocene	—	*Hemitrapa sp.*	Previously identified as *Trapa americana* Knowlton by Brown, 1935, p. 581, pl. 67, fig. 17; *Trapa* sp. by Pigg and Wehr, 2002, p. 11, 12, pl. 4, fig. 44
Hatagoya, Obata, Akazu, Inzyo and Osusawa, Japan	Late Miocene	—	*H. trapelloidea* Miki	Miki, 1941, p. 289, pl. 7d, fig. 19d; Miki, 1952a, p. 349, text-fig. e; Miki, 1959, p. 291, figs. 2a, 3b; Miki, 1961, p. 114, fig. 9c; previously illustrated as *Trapa trapelloidea* (Miki) Vassiljev by Baranova, 1954, p. 354, pl. 164, figs. 3–5
Ogoya, Ishikawa Prefecture, Yokoyama, Japan	Miocene	—	*H. yokoyamae* (Nathorst) Miki	Miki, 1948, p. 76; Miki, 1952a, p. 349, text-fig. g; previously named as *Trapa yokoyamae* by Nathorst, 1888, p. 215, pl. 23, figs. 6–8; Baranova, 1954, p. 355, pl. 165, figs. 5, 6
Sakipenpetsu, Central Hokkaido, Japan	Middle Miocene	—	*H. yokoyamae* (Nathorst) Miki	Tanai, 1971, p. 166, pl. 9, figs. 4, 5
Tani-tôgé, Ishikawa Prefecture and Goshogahara, Fukui Prefecture, Japan	Late Cretaceous	—	*H. angulata* (Brown) Matsuo	Matsuo, 1970, p. 385, pl. 42, fig. 20a, pl. 43, figs. 22, 23; fruit previously named as *Trapa angulata* by Brown, 1962, p. 83, pl. 58, figs. 1–12; the present author classified it into *Palaeotrapa* Golovneva, 1991, p. 605
Oguni-machi, Yamagata Prefecture, Japan	Middle Miocene	—	*H. borealis* (Heer) Miki	Onoe, 1974, p. 56, pl. 13, fig. 5
Shichiku, Ono-mura, Ishiki-gun, Fukushima Prefecture, Japan	Middle Miocene	—	*H. borealis* (Heer) Miki	Tanai, 1961, p. 382, pl. 32, figs. 6, 7
Wakamatsu, Ogawa, Garozawa and Kanagasawa, southwestern Hokkaido, Japan	Miocene	—	*H. borealis* (Heer) Miki	Tanai and Suzuki, 1963, p. 145, pl. 10, figs. 18, 19; Tanai and Suzuki, 1972, p. 339, pl. 5, figs. 6, 7
Okushiri Island, southwestern Hokkaido, Japan	Early middle Miocene	*S. erdtmanii*	—	Previously identified as *Trapa* sp. by Yamanoi, 1992, p. 114, pl. 2, fig. 6
Kani basin, Mizunami, Central Japan	Miocene	—	*H. borealis* (Heer) Miki	Ina, 1981, pl. 38, figs. 4, 5; Ina, 1992, p. 52, pl. 3, fig. 7

TABLE 2—Continued.

Locality	Age	Pollen	Fruit	Reference and Note
Taga, Futaba and Shichiku in Jōban, Japan	Early Miocene	—	*H. borealis* (Heer) Miki	Tanai and Onoe, 1959, p. 284, pl. 4, figs. 6–9; Yabe, 2008, p. 401, figs. 3, 12, 13
Kunugidaira, Jōban, Japan	Early Miocene	—	*H. hokkaidoensis* (Okutsu) Miki	Yabe, 2008, p. 402, fig. 4, 4
Hiyoshi, Mizunami, Toki-gun, Gifu Prefecture, Japan	Middle Miocene	—	*H. hokkaidoensis* (Okutsu) Miki	Tanai, 1961, p. 383, pl. 32, fig. 2, 5, 8; Shikama, 1964, p. 202, pl. 78, fig. 20
Sakipenpetsu, Central Hokkaido, Japan	Middle Miocene	—	*H. hokkaidoensis* (Okutsu) Miki	Miki, 1948, p. 76; Miki, 1952a, p. 349, text-fig. i; Tanai, 1971, p. 165, pl. 7, figs. 3, 5, pl. 10, figs. 1, 2, 6; previously identified as *Trapa hokkaidoensis* by Okutsu, 1939, p. 329, fig. 2
Nara, Japan	Late Miocene–early Pliocene	*S. erdtmanii*	—	Previously identified as *Hemitrapa sp.* by Shimakura, 1963, p. 24, pl. 2, figs. 48–61
Tongcheon and Pohang, South Korea	Middle Miocene	*S. erdtmanii*	*H. yokoyamae* (Nathorst) Miki	Huzioka, 1972, p. 71; pollen previously identified as *Trapa sp.* by Chung and Choi, 1993, p. 148, fig. 2g; Chung and Koh, 2005, p. 6
Tonghaemyeon, Yeong'il-gun and Kyongsangbukdo, Korea	Miocene	—	*H. borealis* (Heer) Miki	Huzioka, 1972, p. 70, pl. 9, fig. 8
South Yellow Sea Basin, South Korea	Middle Miocene	*S. erdtmanii*	—	Yi et al., 2003, p. 28
Kushuka, Kazakhstan	Early Miocene	—	*Hemitrapa* sp.	Previously identified as *Trapa vassiljevii* by Kornilova, 1960, p. 67, pl. 11, figs. 1–9, pl. 28, figs. 7–10
Turgay Valley, Kazakhstan	Miocene	*S.* cf. *erdtmanii*	—	Previously identified as *Trapa sp.* by Popov, 1956, p. 454, figs. 13, 21
Irtysh River, West Siberia, Russia	Miocene	—	*H. praeconocarpa* (Vassiljev) Budantsev	Budantsev, 1960, p. 143; previously illustrated as *Trapa sp.* by Kryshtofovich and Borsuk, 1939, p. 393, pl. 4, fig. 17, pl. 6, figs. 1–3; *Trapa praeconocarpa* Vassiljev by Baranova, 1954, p. 355, pl. 165, figs. 7–9
West Siberian lowland, Russia	Late Oligocene–Miocene	*S.* cf. *erdtmanii*	—	Previously identified as *Trapa sp.* by McHedlishvili, 1953, p. 661, fig. 2a; Popov, 1956, p. 454, figs. 7–11; Merkulova, 1971, p. 128, pl. 2, fig. 45, pl. 4, fig. 35
Enissey Mountain Ridge, Russia	Miocene	*S.* cf. *erdtmanii*	—	Previously identified as *Trapa sp.* by Popov, 1956, p. 454, figs. 3–6, 15, 16, 18–20, 22–31
Southeastern Baikal coast, Russia	Miocene	—	*H. pseudoborealis* Budantsev	Budantsev, 1960, p. 143, pl. 2, fig. 13
Sakhalin, Russia	Miocene	—	*H. sachalinensis* (Okutsu) Miki	Miki, 1948, p. 76; Miki, 1952a, p. 349, text-fig. h; previously identified as *Trapa sachalinensis* by Okutsu, 1939, p. 328, fig. 1
Far East (Sikhote-Alin), Russia	Miocene	—	*H. borealis* (Heer) Miki	Akhmetiev, 1978, p. 69, pl. 2, fig. 3; previously recorded as *Trapa borealis* Heer by Kryshtofovich, 1923, p. 4; Kryshtofovich, 1937, p. 160, fig. 12; Baranova, 1954, p. 355, pl. 165, figs. 1–4; *Trapa kryshtofovichii* Vassiljev, 1949, p. 639; *H. kryshtofovichii* (Vassiljev) Budantsev, 1960, p. 143
Far East (Sikhote-Alin), Russia	Miocene	—	*H.* cf. *hokkaidoensis* (Okutsu) Miki	Akhmetiev, 1978, p. 69, pl. 2, fig. 4
Far East (Primorye), Russia	Oligocene	*S.* cf. *erdtmanii*	—	Previously identified as *Trapa sp.* by Popov, 1956, p. 454, figs. 14, 17
Fujin County, Sanjiang Basin, Heilongjiang Province, China	Early Miocene	*S. erdtmanii*	—	Zhao, 1992, p. 13, pl. 1, figs. 1–22
Shanwang, Shandong Province, China	Middle Miocene or late early Miocene–early middle Miocene	*S. erdtmanii*	*H. shanwangensis* Q. Wang n. sp.	The present paper, Figs. 1.1–1.5, 2.1–2.3; pollen previously identified as *Hemitrapapollenites medius* (Guan) Liu by Liu, 1986, p. 79, pl. 3, figs. 15, 16, 21, 22, 28; *Trapa sp.* by Wang, 1981, p. 101, pl. 3, figs. 8, 9, 11; Wang, 1988, p. 565, 566, fig. 1.27; Wang, 1991, p. 279, pl. 2, fig. 24; Wang, 1999, p. 97, 98, pl. 10, fig. 25, pl. 11, figs. 7, 8, 10; Song et al., 1999, p. 676, pl. 191, fig. 15
Xinghua County, Jiangsu Province, China	Pliocene	*S. erdtmanii*	—	Previously identified as ?*Pleurospermum* sp. 1 by Zheng et al., 1981, p. 67, pl. 10, fig. 17
Xianju County, Zhejiang Province, China	Miocene	*S. erdtmanii*	—	Previously identified as *Trapa sp.* by Zheng, 1982, p. 72, pl. 2, fig. 18
Shelf Basin of the Bohai Sea	Early Miocene–Pliocene	*S. erdtmanii*	—	Song et al., 1999, p. 676; Guan et al., 1989, p. 84, pl. 27, figs. 1–3, 5–20, pl. 29, figs. 1, 2; Wang, 2006, p. 85, fig. 7aa, 7bb, 7ff, 7gg, 7hh; previously identified as *Trapa* sp. by Yamanoi et al., 1993, p. 111, pl. 1, fig. 15

TABLE 2—Continued.

Locality	Age	Pollen	Fruit	Reference and Note
Shelf Basin of the East China Sea	Late Eocene–Pliocene	*S. erdtmanii*	—	Song et al., 1999, p. 676, pl. 191, figs. 16–20; previously identified as *Sporotrapoidites medius* Guan by Song et al., 1985, p. 120, pl. 40, figs. 1–25, pl. 42, figs. 5, 6, pl. 55, figs. 36, 37; Lei, 1989, p. 144, pl. 2, figs. 23–25; Sun et al., 1989, p. 69, pl. 21, figs. 8–13, 23; Li et al., 2003, p. 242–244, pl. 1, fig. 25, pl. 3, fig. 5; Wang, 2006, p. 85, fig. 7z, 7ee
Piling Shale and Mushan Formation, Taiwan Province, China	Early Miocene	*S. erdtmanii*	—	Shaw, 1995, p. 62, pl. 4, figs. 1–3
Na Hong Basin, Chiang Mai, Thailand	Oligocene–Miocene	*S.* cf. *erdtmanii*	—	Previously identified as *Sporotrapoidites* sp. by Songtham, 2003, p. 10; *Sporotrapoidites medius* Guan by Songtham et al., 2005, p. 23, pl. 2, figs. 3, 4.

Formation of eastern China, to correlate the temporal-spatial distribution of *Hemitrapa* fruits and closely related *S. erdtmanii* pollen from the Cenozoic in the Northern Hemisphere, and to consider their paleobiogeographic implications.

SYSTEMATIC PALEONTOLOGY

CLASS MAGNOLIOPSIDA BRONGN., 1843
ORDER MYRTALES JUSS. EX BERCHT. AND J. PRESL, 1820
FAMILY TRAPACEAE DUMORT., 1829, *NOM. CONS.*
GENUS *HEMITRAPA* MIKI, 1941
HEMITRAPA SHANWANGENSIS new species

Figures 1.1–1.5, 2.1–2.3

Diagnosis.—Fruit fusiform. Ovary half-inferior. Fruit base attenuate into a long, slim stalk. Fruit head well-defined, conical or dome-shaped, and surface finely ribbed or slightly fimbriate. Fruit frame pronounced, with two decussate pairs of strongly ascending, slender to medium, horn-like arms, inserted in approximately two thirds of the fruit body. Arms sub-equal, broadening towards the base and tapering into a pointed apex. No barbs or a few retrorse barbs, on the upper part of the arm.

Description.—Fruits are small, 15–18 mm long and 6–7 mm wide, fusiform in shape (Figs. 1.1–1.5, 2.1–2.3). The ovary is half-inferior. The fruit base is grossly attenuate in outline, bearing a very long, straight or curved stalk (Figs. 1.2, 1.3e, 2.1–2.3), at least 35 mm long and approximately 1–3 mm wide. The fruit head is well-defined (Fig. 1.3a), approximately 6–8 mm high, and tapered into a conical or dome-shaped contour, but does not form a distinctively contracted snout. The fruit head is finely ribbed or somewhat fimbriate on the surface. The frame of fruits is pronounced (Fig. 1.3c). The fruit body is somewhat quadrangular (Fig. 1.3d), bearing two decussate pairs of strongly ascending, slender to medium, horn-like arms along the fruit frame (Fig. 1.1a–d, Fig. 1.3b, Fig. 1.4a–c, Fig. 2.1–2.3). Arms are inserted approximately in two thirds of the fruit body from the fruit base, forming a very acute angle 15–20° with the longitudinal axis of the fruit stalk. The arms are delicate, vulnerable and prone to be broken at the base or apex, so only two or three complete arms are visible in each fruit. Arms are slightly curved outwardly and sub-equal in length in a given fruit, 10–12 mm long, broadening towards the base and tapering into a pointed apex. In most occasions, no barbs occur on the arms, but a few retrorse barbs have been observed on the upper part of one of the arms (Fig. 1.5), approximately 0.3–0.4 mm long.

Etymology.—From the type locality, Shanwang.

Type.—Holotype (designated here): PE-200820101021 (Fig. 1.1–1.3), a fruit compression. Paratype: PE-201010210000 (Fig. 1.4, 1.5), PE-2011042602A, B (Fig. 2.1, 2.2), and PE-2011042601 (Fig. 2.3), one fruit impression and two fruit compressions. The specimens are deposited at the Institute of Botany, the Chinese Academy of Sciences (CAS), Beijing, P. R. China (specimen numbers prefixed PE).

Occurrence.—Diatomaceous shales of the Shanwang Formation, Shanwang (N 36°54′, E 118°20′), approximately 22 km east of Linqu County, Shandong Province, P. R. China. Shanwang is a famous fossil locality with exquisitely preserved animals and plants that have been studied since the 1930s (Hu and Chaney, 1938; Yang and Yang, 1994; Sun, 1999; Yang and Sun, 2000). The Shanwang Formation has been considered to be middle Miocene (Li, 1981; Tao et al., 1999; Wang et al., 2006, 2007, 2010; Zhang and Wang, 2010) or late early Miocene to early middle Miocene in age (Liu and Leopold, 1992; Wang and Yamanoi, 1996; Deng, 2006; Strömberg et al., 2007).

Other material examined.—For comparison, the fruit impression previously described as *Beipiaoa spinosa* Dilcher, Sun and Zheng, 2001 (Sun et al., 2001) from the Late Jurassic–Early Cretaceous Yixian Formation of Beipiao, Liaoning Province in Northeast China is figured here (PE-201101100427A; Fig. 2.4). In order to correlate with the temporal-spatial distribution of the fossil fruits *Hemitrapa*, the published photographs and line-drawings of the closely related trapaceous pollen *Sporotrapoidites erdtmanii* from Shanwang and other localities were consulted (Table 2).

Remarks.—On the basis of the fusiform fruits with four, horn-like arms and a long stalk, the fossils presented here can be easily classified into an extinct trapaceous genus *Hemitrapa* (Miki, 1941, 1948, 1952a). *Hemitrapa* is superficially similar to three Mesozoic genera with uncertain affinities: *Beipiaoa* Dilcher, Sun and Zheng, 2001 from the Late Jurassic–Early Cretaceous of China (see Sun et al., 2001; Fig. 2.4), *Prototrapa* Vassiljev, 1967 from the Early Cretaceous of Australia (Vassiljev, 1967), and *Palaeotrapa* Golovneva, 1991 from the Late Cretaceous of Russia (Golovneva, 1991); but these genera appear to bear a poorly developed fruit head, a distinctive fruit body and appendages.

Hemitrapa differs from the overwhelming majority of species of *Trapa* in having a well-defined fruit head, an indistinctively contracted fruit neck, characteristically ascending arms, a longer stalk and no lower pseudo-horns (Nakano, 1913, 1964; Vassiljev, 1949; Miki, 1952a, 1952b, 1961; Gregor, 1982; Chung et al., 1987; Wójcicki and Kvaček, 2002; Wójcicki and Zastawniak, 2003; Kovar-Eder et al., 2002, 2005; Wang et al., 2006). Although the extant species *Trapa natans* has a well-defined fruit head (Chen et al., 2007), its turbinate to rhombic fruit body, horizontal, flat-triangular or broadly conic arms and a caducous stalk are obviously different from those of *Hemitrapa*. In addition, morphologically similar fruits of *Trapella* Oliver, 1887 of the unrelated family Trapellaceae noticeably differ from *Hemitrapa* in its shorter fruit head and tubular fruit body (Oliver, 1887; Glück, 1940; Miki, 1959, 1961). Based on the intermediate forms between fossil *Trapa* and *Hemitrapa*, some authors hypothesized that *Hemitrapa* may be a missing link between an ancestral stock (e.g., Lythraceae) and *Trapa* (Miki, 1952b, 1959; Mai, 1985; Mohr and Gee, 1990; Kovar-Eder et al., 2005) or that *Hemitrapa* and *Trapa* have evolved from a shared common ancestor (Wójcicki and Wilde, 2001). Recent paleobotanical and palynological studies have further reinforced the relatedness of *Hemitrapa* and *Trapa* (Zetter and Ferguson, 2001; Wójcicki and Kvaček, 2002; Kovar-Eder et al., 2002, 2005).

The fruit fossils presented here are described as a new species, i.e., *H. shanwangensis* Q. Wang n. sp., after a comparison with the other congeneric species (Table 1). Overall, *H. shanwangensis* was characterized by a combined syndrome, i.e., fusiform and relatively small fruit with a (very) long stalk, four sub-equal (in length), slender to medium, strongly ascending arms with no barbs or a few barbs, which did not simultaneously occur in any other known species in *Hemitrapa*. Of all, *H. hokkaidoensis* (Okutsu) Miki, 1948 and *H. trapelloidea* Miki, 1941from the Miocene of Japan show the most similarities to *H. shanwangensis* but these two Japanese species bear a larger fruit body and different arm morphology. Furthermore, a few retrorse barbs were observed on the upper part of an arm of *H. shanwangensis* (Fig. 1.4, 1.5), but the barbs appear to be lacking on the other arms of fruits. This implies that barbs on the arms of fruits may be caducous in the developmental and/or taphonomic processes.

DISCUSSION

Hemitrapa and its closely related fossil *Trapa* provide a historical perspective for the early evolution, diversity, and paleobiogeography of the Trapaceae. *Hemitrapa* fruits were mainly distributed in the Miocene of mid-latitudes in the Northern Hemisphere (Gregor, 1982; Table 1). Overall, central Europe and eastern Asia appear to represent two highly diversified centers of *Hemitrapa*. So far, the oldest fossil record of *Hemitrapa* was reported from the late Eocene diatomite of Kučlín, the Czech Republic (Wójcicki and Kvaček, 2003). *Hemitrapa trapelloidea* Miki, 1941 co-occurred in the late Miocene of Austria and Japan (Miki, 1941, 1948; Gregor, 1982; Kovar-Eder et al., 2002; Harzhauser et al., 2003) while *H. borealis* (Heer) Miki, 1948 co-occurred in the Miocene of far eastern Russia, Korea, Japan, and Alaskan U.S.A. (Miki, 1948, 1952a; Tanai and Onoe, 1959; Tanai, 1961; Tanai and Suzuki, 1963, 1972; Huzioka, 1972; Onoe, 1974; Akhmetiev, 1978; Wolfe and Tanai, 1980; Ina, 1981, 1992; Yabe, 2008).

Recent molecular phylogenetic analysis revealed that the Lythraceae sensu lato (including the Trapaceae) were far more likely to originate in Laurasia than Gondwana (Graham et al., 2005). Current trapaceous macrofossil evidence of *Hemitrapa* and *Trapa*, to some extent, lends credence to the molecular results regarding the biogeography of the Lythraceae. The parental plants of *Hemitrapa* may represent one of the earlier lineages in the Trapaceae, which might have begun to diversify in the mid-latitudes of the Northern Hemisphere since the early Cenozoic. Subsequently, they underwent extensive floristic exchanges among Europe, Asia, and North America during the Miocene and apparently became extinct after the Pliocene.

Palynological studies suggested that *Hemitrapa* had a very close association with dispersed trapaceous pollen species *Sporotrapoidites erdtmanii* (Mohr, 1983; Mohr and Gee, 1990; Zetter and Ferguson, 2001; Kovar-Eder et al., 2005). Hence, *Hemitrapa* fruits and *S. erdtmanii* pollen most possibly stem from the same parental plant. *Sporotrapoidites erdtmanii* has been well recognized from the Miocene in Hungary, Germany, and Poland (Nagy, 1985; Mohr and Gee, 1990; Zetter and Ferguson, 2001; Worobiec, 2009). However, the stratigraphic occurrence of *S. erdtmanii* is not entirely synchronous with that of *Hemitrapa* in Europe (Table 2). *Hemitrapa* fruits were described from the late Eocene of the Czech Republic to the Miocene of Central Europe while *S. erdtmanii* pollen mainly occurred in the Miocene of Central Europe. Contrary to the European circumstances, *S. erdtmanii* pollen had been extensively recovered from the late Eocene to the Pliocene of eastern Asiatic shelf basins near the Bohai Sea, Yellow Sea, East China Sea, and the Sea of Japan as well as from the late Oligocene to the Miocene of the mid-latitudes in Kazakhstan and Russia, but *Hemitrapa* fruits were primarily discovered in the Miocene of Asia (Table 2). Remarkably, *S. erdtmanii* pollen has been recovered from the Miocene Shanwang flora of eastern China (Table 2). This is the only well-known trapaceous pollen species from Shanwang (see Song et al., 1999, p. 676). Prior to the present study, neither *Hemitrapa* nor *Trapa* fruits were known from the Miocene of Shanwang, nor were *Hemitrapa* fruits discovered from the Cenozoic of China.

The disparity of the temporal-spatial distribution of *Hemitrapa* and *S. erdtmanii* between Central Europe and eastern Asia may reflect significant sampling biases on the fossil record of floating aquatic plants. On the basis of the current fossil record of *S. erdtmanii* from Asia, we expect to discover more *Hemitrapa* fruits from this region, especially from the Eocene to the Miocene of eastern Asia. Also, we look forward to recovering *S. erdtmanii* from the Eocene–Oligocene of Europe.

The fossil fruits, described here from the Miocene Shanwang Formation, represent the first discovery of *Hemitrapa* (Trapaceae) from the Cenozoic of China. These fruits, described as the new species *H. shanwangensis*, complement the previous recognition of the dispersed, trapaceous pollen type *Sporotrapoidites erdtmanii* that has been reported from the same formation. These co-occurring fruits and pollen most possibly represent isolated organs of the same extinct parental plant population. Overall, the microfossil and macrofossil records demonstrate that the parental plants of *Hemitrapa* might have begun to diversify from the mid-latitudes of Eurasia since the Eocene, flourished in eastern Asia and central Europe during the Miocene, and become extinct after the Pliocene.

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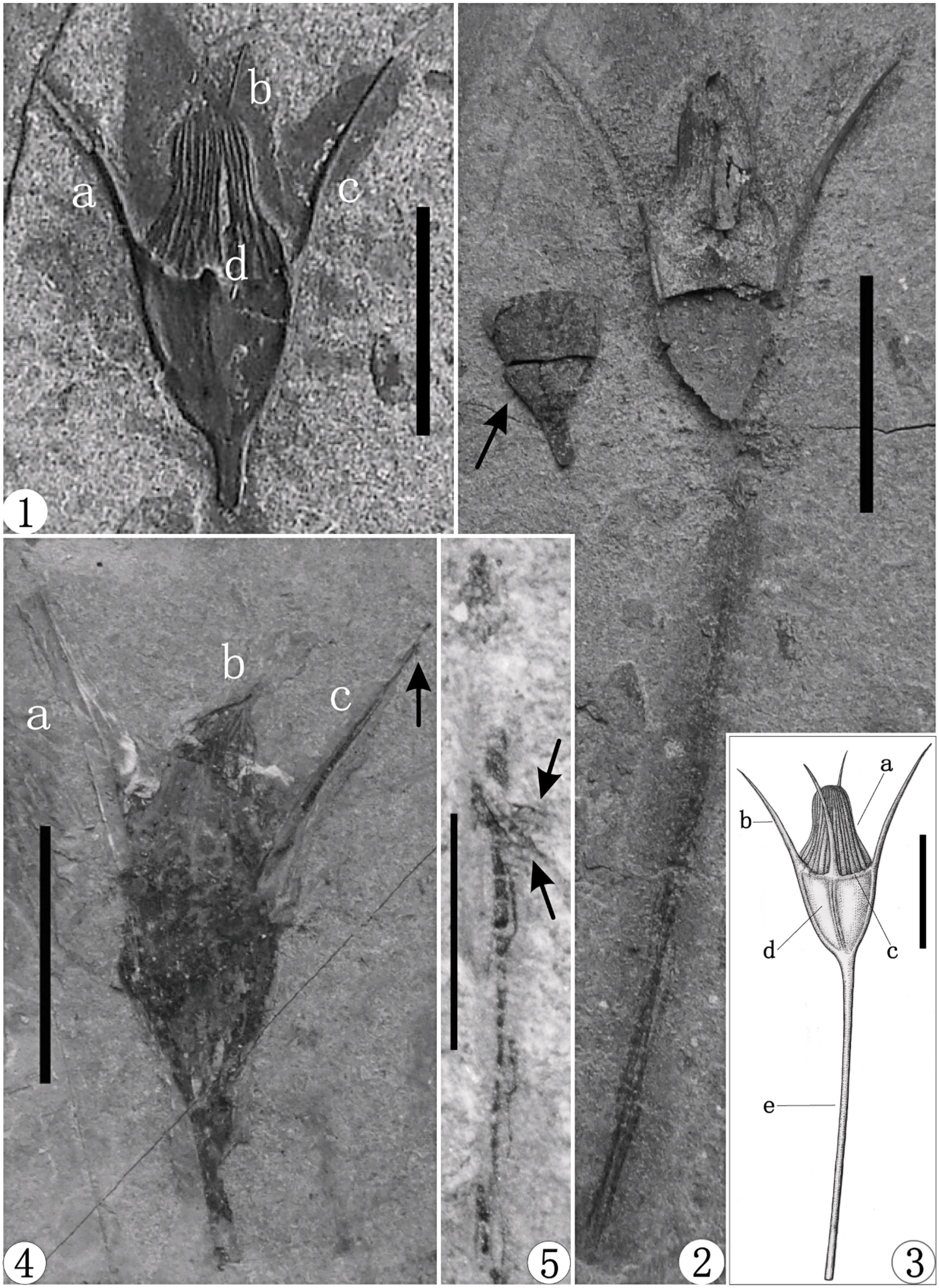

FIGURE 1—*Hemitrapa shanwangensis* Q. Wang n. sp. from the Miocene Shanwang Formation of Shandong, eastern China. *1, 2*, a fruit compression, showing the fusiform fruit with four slender horn-like arms and a very long stalk: *a–d*, arms, black arrow referring to the inner surfaces of the fruit body, holotype PE-200820101021, views *1* and *2* were photographed respectively in July 2008 and October 2010, the fruit appears to crack after drying in

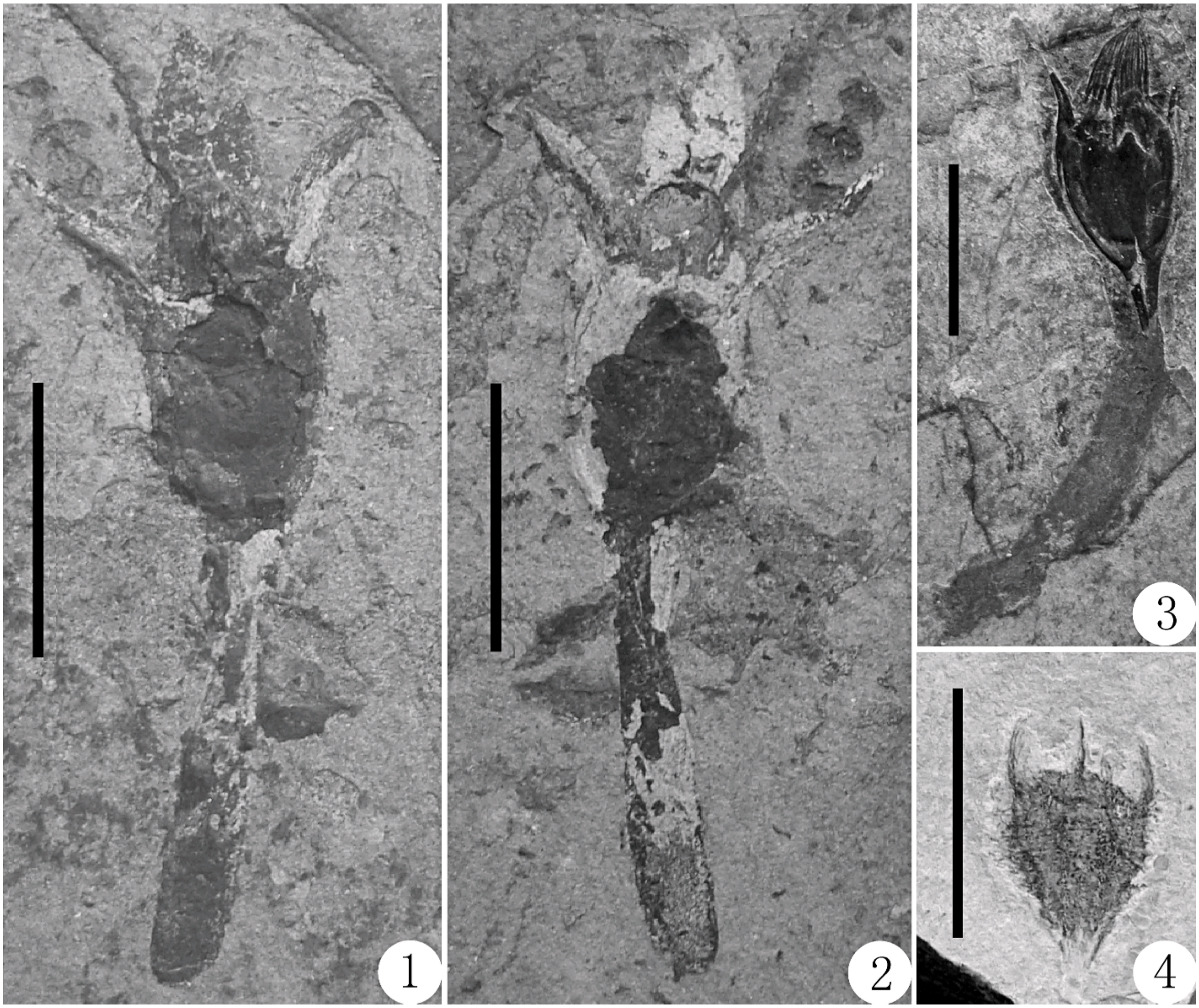

FIGURE 2—A comparison between *Hemitrapa shanwangensis* Q. Wang n. sp. and *Beipiaoa spinosa* Dilcher, Sun and Zheng, 2001. *1–2*, a fruit compression-impression of *H. shanwangensis* showing fusiform fruit with medium horn-like arms and a slightly thick long-stalk, paratype PE-2011042602A, B (part and counterpart specimens); *3*, a fruit compression of *H. shanwangensis*, showing a well-defined fruit head, three visible horn-like arms and a slightly curved stalk, paratype PE-2011042601; *4*, a fruit impression of *B. spinosa* from the late Jurassic-early Cretaceous of Beipiao, Liaoning Province, Northeast China, showing an obtriangular fruit with four horn-like arms, but no fruit head, PE-201101100427A. Scale bar=10 mm.

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storage; *3*, line-drawing of the fruit based upon the specimen in *1* and *2*: *a*, head; *b*, arm; *c*, frame; *d,* body; *e*, stalk, terminology follows Wójcicki and Kvaček (2002, p. 119); *4*, an impression specimen, showing the fusiform fruit with horn-like arms and a stalk: *a–c*, arms, black indicates the area enlarged in *5*, paratype PE-201010210000; *5*, partial enlargement of the arm *c* in *4*, which was photographed under a microscope (Nikon Eclipse E600), black arrows show retrorse barbs. Scale bar=10 mm in *1–4*; 1 mm in *5*.

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