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Asian Paleocene charophyte records demonstrate Eocene dispersals from Asia to Europe

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Abstract.—A latest Paleocene charophyte flora collected from the South Gobi area in the Junggar Basin, western China, includes the geographically widespread taxa *Peckichara torulosa* var. *varians* (Dollfus and Fritel, 1919) Sanjuan, Vicente, and Eaton, 2020, *Lychnothmanus vectensis* (Groves, 1926) Soulié-Märsche, 1989, and *Gyrogona lemani capitata* Grambast and Grambast-Fessard, 1981. *Lychnothmanus vectensis* (as *Lychnothmanus* aff. *L. vectensis*) is known from the Cretaceous–Paleocene transition in eastern China and the latest Paleocene in western China, with likely additional records from the United States (Utah). The earliest European records of *L. vectensis* are from the late Eocene to early Oligocene in Spain, France, and England. Similarly, the oldest record of *G. lemani capitata* is from the latest Paleocene in the South Gobi area, with younger records from the middle Eocene of France. These latest Paleocene gyrogonite assemblages demonstrate the origin of these charophyte lineages in Asia. The dispersal of these charophytes from Asia to Europe in the middle to late Eocene appears to have occurred before the retreat of the Turgai Strait in both the Tarim area and the Siberian Basin by the end of the late Eocene and before the "Grande Coupure" in Europe and the Mongolian Remodelling in Asia during the Eocene–Oligocene transition. We hypothesize that waterbirds may have facilitated this intercontinental dispersal, and that idea is supported by the shared occurrence of avian groups in Central Asia and Europe in the middle and late Eocene.

Introduction

Charophyte paleobiogeography has been studied widely in the past two decades. Bhatia (2006) suggested that the living Eurasian species *Lychnothamnus barbatus* (Meyen, 1827) von Leonhardi, 1863 dispersed from Western Europe (late Miocene) eastward to other parts of Europe and Central Asia in the Pliocene, with hypothesized dispersals to the Himalayas in the late Pliocene and to Australia in the Pleistocene. Martín-Closas and Wang (2008) studied the paleobiogeography of the well-documented, long-lasting fossil record of Cretaceous charophyte *Atopochara trivolvis* Peck, 1941 and concluded that the species probably originated in Eastern Europe, later achieving a global distribution. Some charophyte species have dispersed much faster than others. For example, Sanjuan and Martín-Closas (2015a) studied the Eocene–Oligocene *Nitellopsis* (*Tectochara*) *merianii* Braun and Unger in Unger, 1852 comb. Grambast and Soulié-Märsche, 1972–*Nitellopsis obtusa* (Desvaux in Loiseleur, 1810) Groves, 1919 and *Lychnothamnus stockmansii* (Grambast, 1957) Soulié-Märsche, 1989–*Lychnothamnus major* (Grambast and Paul, 1965) Soulié-Märsche, 1989 lineages, and they surmised that the *L. stockmansii*–*L. major* lineage achieved a Eurasian distribution soon after its first appearance in the late Eocene, and the *N.* (*T.*) *merianii*–*N. obtusa* lineage expanded to Eastern Europe from Spain about 10 million years after its first appearance.

From a paleogeographical perspective, Europe and Western Asia were separated from Northeastern Asia by the Turgai Straits from the Middle Jurassic (Martin and Averianov, 2004; Joyce and Rabi, 2015) to the end of the late Eocene (McKenna, 1975; Martin and Averianov, 2004; Bosboom et al., 2017). The Turgai Strait, also known as the West Siberian Sea, was a large shallow saline water body that connected the Arctic Ocean and Tethys Sea and separated the Asian and European continents. The dispersal of charophytes from Asia to Europe in the middle to late Eocene appears to have occurred before the retreat of the Turgai Strait in both the Tarim area and the Siberian Basin by the end of the late Eocene. Our recovery of late Paleocene

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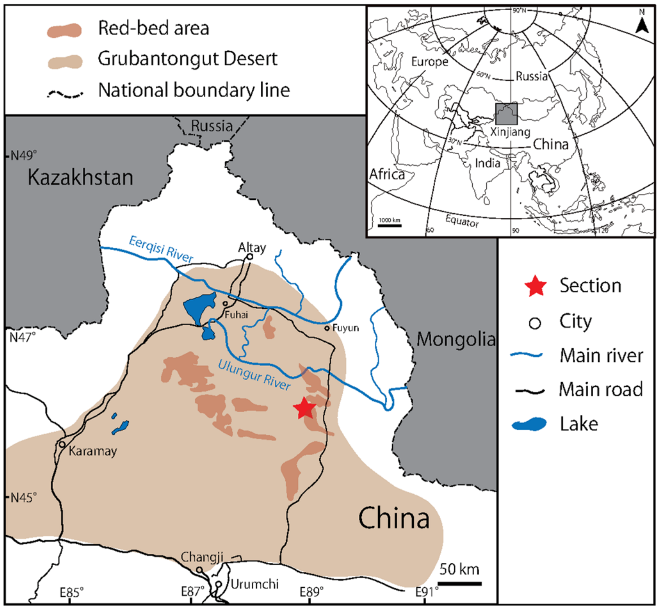

Figure 1. Geographic location. Maps showing location of the South Gobi area in the Northeastern Junggar Basin in Xinjiang, China.

charophyte fossils in Central Asia (western China) adds greatly to the paleobiogeographic story of intercontinental dispersals and distributions of charophyte taxa in the Paleogene. We use charophyte data to discuss potential agents of dispersal and paleoenvironments and to form the basis to explain the expansion and colonization of various areas by charophytes.

Geological background

The Junggar Basin is one of the largest sedimentary basins in Xinjiang, northwestern China. It is surrounded by the Zaier and Hala'alate Mountains to the northwest, the Aletay and Kelamaili Mountains to the northeast, and the Tian Shan and Bogda mountains to the south (Tang et al., 2020). The basin includes many fossiliferous horizons from the Cretaceous and Paleogene. The latest Paleocene South Gobi fossil area (46°5′19″N, 88° 11′9″E) is situated in an unnamed early Cenozoic lithological unit located in the northeastern part of the Junggar Basin in the Gurbantünggüt Desert (Fig. 1). This horizon is known primarily for its fossil vertebrate assemblage (Ni et al., 2016), but fossils of charophytes also have been discovered in this area. This fossiliferous unnamed geological unit comprises a set of sediments consisting of reddish-brown mudstones interbedded with a few grayish-green or yellowish-gray fluvial sandstone beds or lenses (Ni et al., 2016). The fossils of charophytes were recovered from the sandy mudstone unit (at the height of ∼7.5 m in Fig. 2).

The geological age of the deposit was determined through mammalian biostratigraphy (Ni et al., 2016). Mammalian fossils in the unit include species of insectivorans (*Bumbanius ningi* Missiaen and Smith, 2008 and *Asionyctia guoi* Missiaen and Smith, 2005), Glires (*Tribosphenomys minutus* Meng and Wyss, 2001 and *Neimengomys qii* Meng et al., 2007), plesiadapiforms (*Subengius mengi* Smith, Van Itterbeeck, and Missiaen, 2004), arctostylopids (*Anatolostylops* sp. aff. *Anatolostylops zhaii* Wang et al., 2008), deltatheroidan marsupials (*Gurbanodelta kara* Ni et al., 2016), and multituberculates (*Mesodmops* cf. *M. tenuis* Missiaen and Smith, 2008). Among them, seven species (all except *Anatolostylops* sp. aff. *A. zhaii*) were reported as also occurring in the well-constrained late Paleocene Subeng Fauna from the Erlian Basin of Inner Mongolia, China (Ni et al., 2016). In addition, the specimens of *Anatolostylops* sp. aff. *A. zhaii* (an arctostylopid) from the South Gobi Fauna are much larger than those of *Palaeostylops iturus* Matthew and Granger, 1925 from the late Paleocene Subeng Fauna, and they approach the size of *Anatolostylops zhaii* from the early Eocene Nomogen III Fauna of Inner Mongolia. Therefore, the mammalian fossils and the South Gobi deposit are thought to be from the latter part of the Paleocene (lacking any Eocene biostratigraphic indicators). The Paleocene–Eocene Boundary in the Erlian Basin lies within or just below the "*Gomphos*" bed, and the absence of the common *Gomphos* (Glires, Mammalia) in the South Gobi area also points to an age older than the Eocene (Ni et al., 2016 and references therein) (Fig. 2). Therefore, this latest Paleocene South Gobi Fauna (and charophyte flora) can be correlated to the late Gashatan Asian Land Mammal Age, which is roughly equivalent to the Clarkforkian North American Land Mammal Age, with the age estimate of ∼56–57 Ma (Fig. 2).

Materials and methods

Approximately 20 tons of sedimentary matrix (composing one massive sample) was collected from the latest Paleocene fossiliferous layer in Section A (Section, Fig. 1). The sample was screen washed with a minimum mesh size of 0.2 mm to maximize fossil recovery. For the semi-quantitative analyses, ∼100 gyrogonite specimens were measured for each species (e.g., *Gyrogona lemani capitata* Grambast and Grambast-Fessard, 1981). When there were fewer than 100 specimens available for a species (e.g., *Lychnothmanus vectensis* (Groves, 1926) Soulié-Märsche, 1989 and *Peckichara torulosa* var. *varians* (Dollfus and Fritel, 1919) Sanjuan, Vicente, and Eaton, 2020), all the specimens were measured. Morphometric data from specimens of *G. lemani capitata* and *L. vectensis* were compiled into statistical charts, but charts were not made for *P. torulosa* var. *varians* because there are too few specimens. The specimens were measured using the ZEN 2 system stored with a Zeiss stereomicroscope (Stemim 508) at the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences. Specimens were imaged using a Zeiss Evo MA25 scanning electron microscope at the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences, Beijing.

Repository and institutional abbreviation.—All specimens in this study are deposited in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing, China.

Systematic paleontology

Division Charophyta Migula, 1897
Class Charophyceae Smith, 1938
Order Charales Lindley, 1836

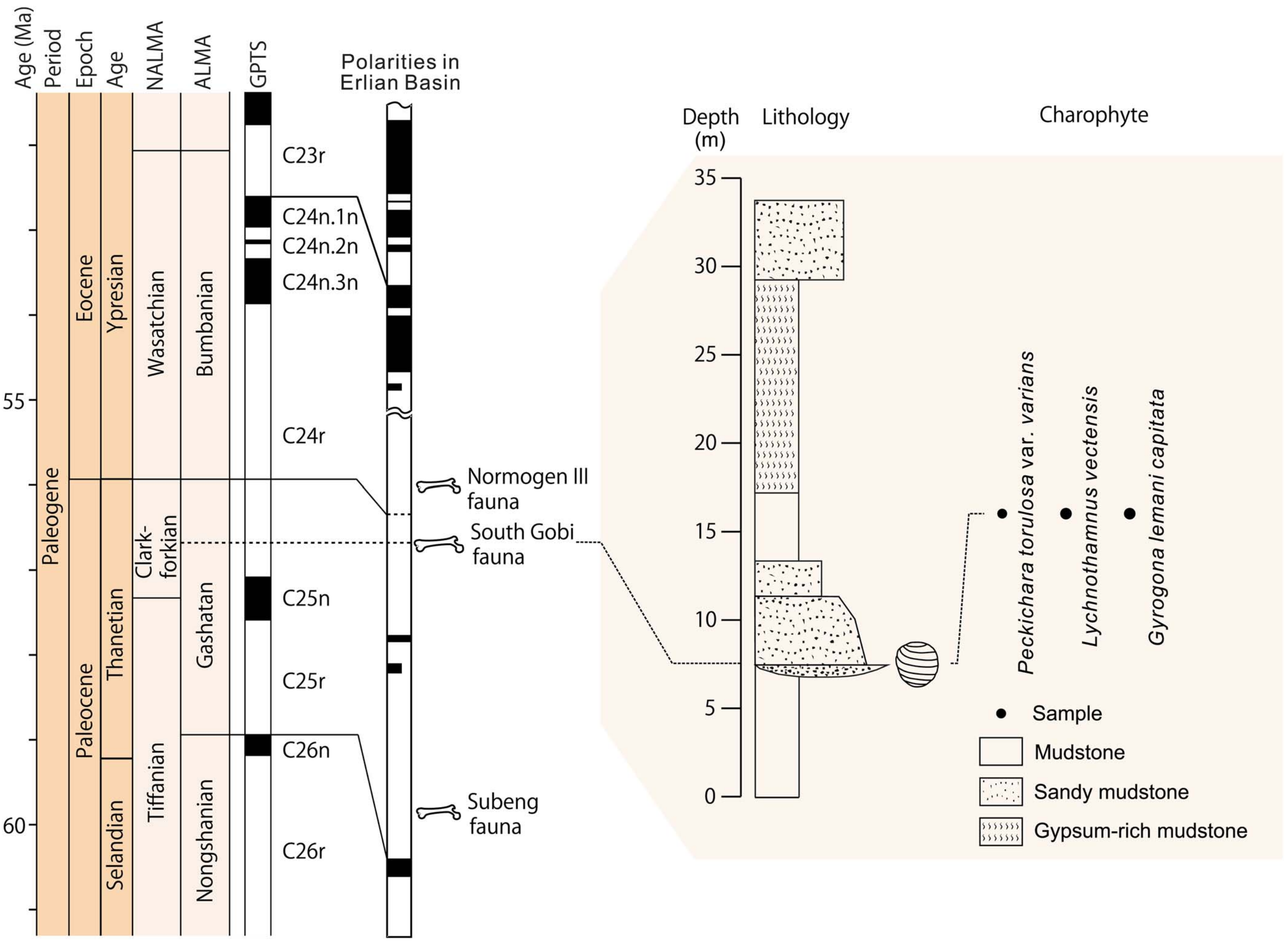

Figure 2. Correlation and age of charophyte assemblages. Charophytes and mammalian fossils from the South Gobi area are correlated with the Subeng and Nomogen III faunas from the Erlian Basin in Inner Mongolia, China. The age of the South Gobi fossil assemblage is estimated as late Gashatan Asian Land Mammal Age, roughly equivalent to the Clarkforkian North American Land Mammal Age. Modified from Ni et al. (2016).

Family Characeae Agardh, 1824
Subfamily Charoideae Braun in Migula, 1897
Genus *Peckichara* Grambast, 1957

Type species.—*Peckichara varians* Grambast, 1957 from the Paleocene to lowermost Eocene (Sparnacian local stage) of the Paris Basin, France.

Peckichara torulosa var. *varians* (Dollfus and Fritel, 1919)
Sanjuan, Vicente, and Eaton, 2020
Figure 3.1–3.7

1919 *Chara torulosa* Dollfus and Fritel, p. 249, fig. 9.
1957 *Peckichara torulosa*; Grambast, p. 15, pl. 7, figs. 1–6.
1957 *Peckichara varians*; Grambast, p. 14, pl. 8, figs. 1–8.
2020 *Peckichara torulosa* var. *varians*; Sanjuan, Vicente, and Eaton, p. 7, pl. 3, A–F.

Holotype.—Gyrogonites (with collection number not reported) from marls and lignites in Cramant (Marne), Sarron (Oise) according to Dollfus and Fritel (1919, fig. 9).

Occurrence.—*Peckichara torulosa* var. *varians* (originally as *P. varians*) is known from the Paleocene to the early Eocene of Europe and China (Li et al., 2016 and references therein).

Description.—The *P. torulosa* var. *varians* gyrogonites from the South Gobi area are medium to large; 688–770 µm high and 583–708 µm wide. Their isopolarity index ranges between 106 and 118. They are prolate spheroidal to subprolate with seven to eight convolutions in lateral view. The spiral cells are flat to convex, 90–120 µm wide, and ornamented by individualized and prominent tubercles. The tubercles are rounded or oval, usually as wide as the spiral cells, and are spaced regularly (Fig. 3.3, 3.5) or irregularly (Fig. 3.4). The surface ornamentation usually disappears near the apex. The apex is rounded to flat, with a slight to moderate thinning and narrowing of the periapical spiral cells. Sometimes well-developed apical nodules are present, and they can vary in size and shape. Some specimens display small, individualized nodules, and others exhibit thick and large nodules, forming an apical rosette. The base is rounded, with a pentagonal funnel and a pentagonal pore (50–60 µm).

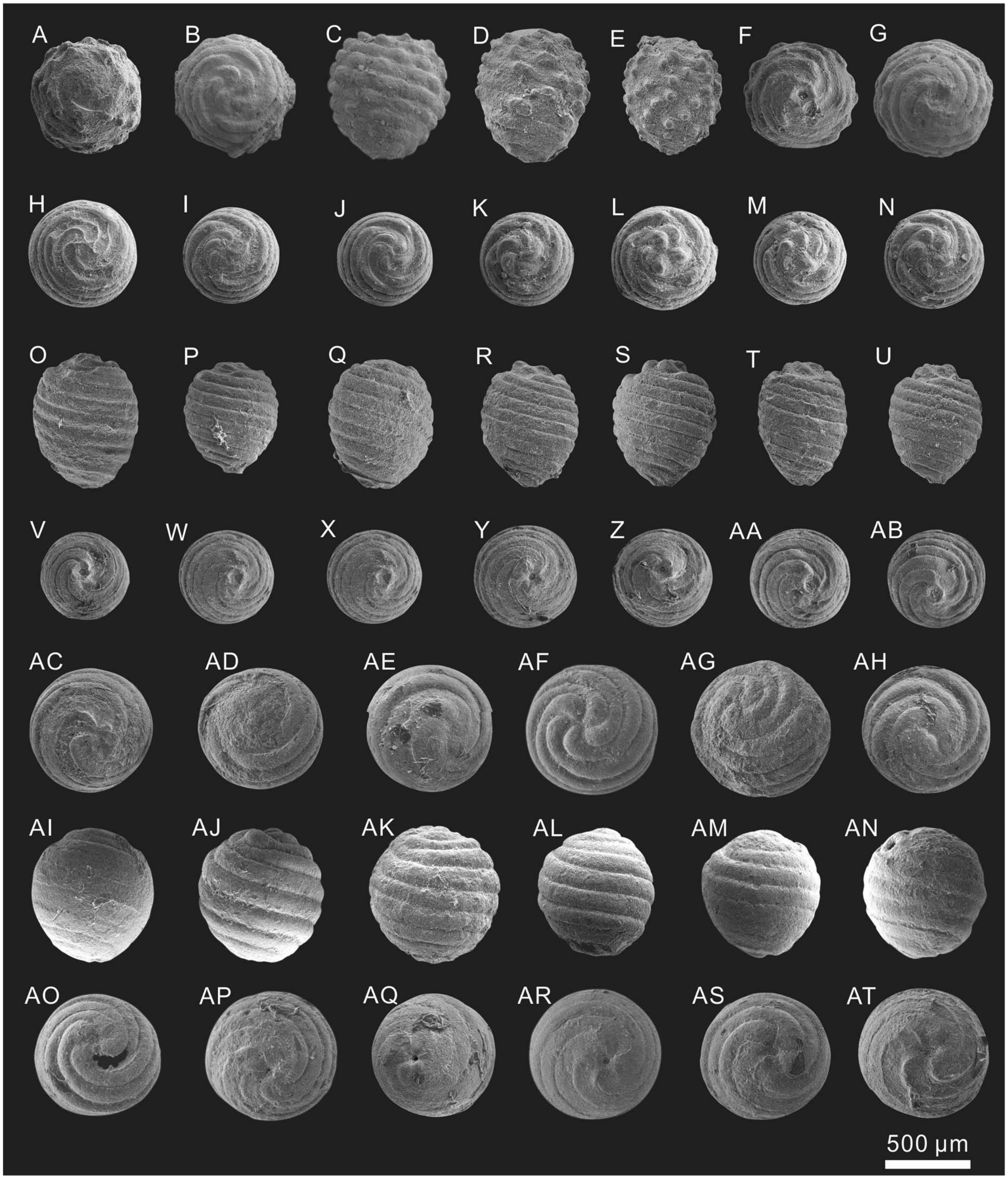

Figure 3. Scanning electron microscope images of fossil charophyte gyrogonites from the latest Paleocene South Gobi area in the Junggar Basin. (**1–7**) *P. torulosa* var. *varians*: (**1, 2**) apical view; (**3–5**) lateral view; (**6, 7**) basal view. (**8–28**) *L. vectensis*: (**8–14**) apical view; (**15–21**) lateral view; (**22–28**) basal view. (**29–46**) *G. lemani capitata*: (**29–34**) apical view; (**35–40**) lateral view; (**41–46**) basal view.

Materials.—Approximately 10 gyrogonites have been recovered from the South Gobi area.

Remarks.—Two varieties of *P. torulosa* have been proposed by Sanjuan et al. (2020). The gyrogonites that bear a mid-cellular crest and massive apical nodules have been termed *P. torulosa* var. *torulosa*, and those that exhibit isolated or irregularly connected tubercles along the spiral cells and isolated small apical nodules are called *P. torulosa* var. *varians*. The fossil population in this study is referred to *P. torulosa* var. *varians* due to the presence of individualized, prominent, irregularly rounded or elongated tubercles on the spiral cells.

Genus *Lychnothamnus* (Ruprecht, 1845) von Leonhardi, 1863 emend. Braun in Braun and Nordstedt, 1882

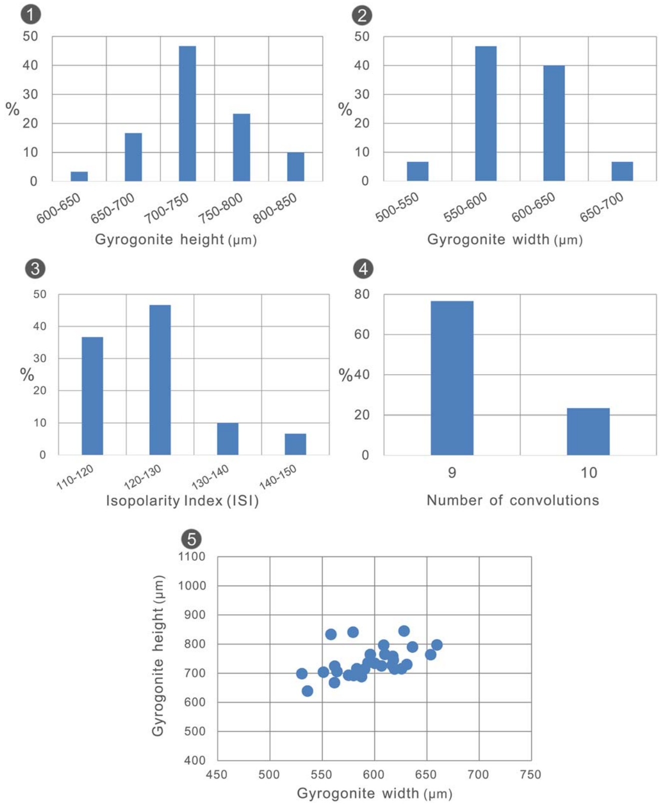

Figure 4. Morphometric data of *Lychnothmanus vectensis* (30 gyrogonites) in the South Gobi area, Junggar Basin. (**1–4**) Frequency distributions: (**1**) gyrogonite height; (**2**) gyrogonite width; (**3**) isopolarity index; (**4**) number of convolutions. (**5**) Dispersion graph of gyrogonite height/gyrogonite width.

Type species.—*Lychnothamnus barbatus* (originally as *Chara barbata*) Meyen, 1827 from the Cenozoic of "Plötzensee bei Berlin" (Germany).

Lychnothamnus vectensis (Groves, 1926) Soulié-Märsche, 1989
Figures 3.8–3.28, 4

1926 *Chara vectensis* Groves, p. 172, pl. 2, figs. 2–8.
1958 *Stephanochara vectensis*; Grambast, p. 158.
1989 *Lychnothamnus vectensis*; Soulié-Märsche, p. 160.

Holotype.—Gyrogonites (V. 18321 and V. 18355) from the Bembridge beds in Gurnard Bay on the Isle of Wight, UK (Groves, 1926, pl. 2, figs. 2–8).

Occurrence.—*Lychnothmanus vectensis* was reported first in the late Eocene Bembridge beds in Gurnard Bay on the Isle of Wight, UK (Groves, 1926). It was reported later from the late Eocene of the Paris Basin (Riveline, 1986) and the latest Priabonian to earliest Rupelian of the Ebro Basin (Sanjuan and Martín-Closas, 2014). In the United States, Vicente et al. (2020) and Sanjuan et al. (2020) reported *Lychnothamnus* sp. (probably a form with an affinity to *L. vectensis*) in the early Eocene of Utah. In China, *L. vectensis* is known from the Eocene of the Qaidam Basin on the Tibetan Plateau (Li et al., 2020), and *Lychnothamnus* aff. *L. vectensis* was reported from the Songliao Basin of China by Li et al. (2019).

Description.—The *Lychnothamnus vectensis* gyrogonites from the latest Paleocene South Gobi area are medium to large; 638–845 μm high (mean: 737 μm; standard deviation: 50) and 531–660 μm wide (mean: 596 μm; standard deviation: 32). The isopolarity index ranges from 114 to 149 (mean: 124; standard deviation: 8). They are prolate spheroidal to subprolate with 8–10 convolutions visible in lateral view. The spiral cells are generally convex, but also sometimes flat, and their width ranges between 75 and 100 μm. The apex of the periapical spiral cell is rounded and displays marked thinning. Apical nodules usually are present, and sometimes the nodules are comma or crescent shaped. The apical rosettes are usually well developed, with the apical nodules joined completely at the apical center to form a highly protruding cap. The base is rounded, with a funnel and a pentagonal basal pore ∼30–40 μm.

Materials.—Thirty gyrogonites have been recovered from the South Gobi area.

Remarks.—The size of the gyrogonites of *L. vectensis* is normal for each population measured separately (Sanjuan and Martin-Closas, 2015b). However, the gyrogonite's height range becomes extremely large if all polymorphs from different localities and different latitudes are considered together. Sanjuan and Martin-Closas (2015b) showed that the variation in size of the gyrogonites exhibits a latitudinal polarity according to the morphometric analysis carried out in three populations of *L. vectensis* from the Hampshire, Paris, and Ebro Basins in Europe. The size of the South Gobi population (current latitude: 46°5′19″N) is similar to that of the Paris Basin (current latitude: ∼48°N).

In contrast to the type *L. vectensis* population from the Isle of Wight (Groves, 1926; Sanjuan and Martín-Closas, 2015b), with more prominent apical rosette and apical nodules being separated, the apical nodules of *Lychnothamnus* aff. *L. vectensis* in the Songliao Basin population are fused. However, the ornamentation of gyrogonites may change over time, considering the evolutionary trends of other well-supported charophyte anagenetic lineages (e.g., in lineage *Peckichara pectinata* Grambast, 1971; Vicente and Martín-Closas, 2018). *Lychnothamnus* aff. *L. vectensis* probably represents an ancestor of *L. vectensis* s.s.

Genus *Gyrogona* Lamarck, 1804 ex Lamarck, 1822 emend. Grambast, 1956

Type species.—*Gyrogona medicaginula* Larmark, 1804 from the Oligocene cherts of the Paris Basin, France.

Gyrogona lemani capitata Grambast and Grambast-Fessard, 1981
Figures 3.29–3.46, 5

1822 *Chara lemani* Brongniart, p. 322, pl. 17, fig. 4.
1927 *Gyrogonites lemani*; Pia, p. 90.
1981 *Gyrogona lemani capitata*; Grambast and Grambast-Fessard, p. 12. pl. 2, figs. 8–12.

Holotype.—Gyrogonites (C121-7) from the Pont-Bernard, commune de Brény (Aisne), France (Grambast and Grambast-Fessard, 1981, p. 12. pl. 2, figs. 8–12).

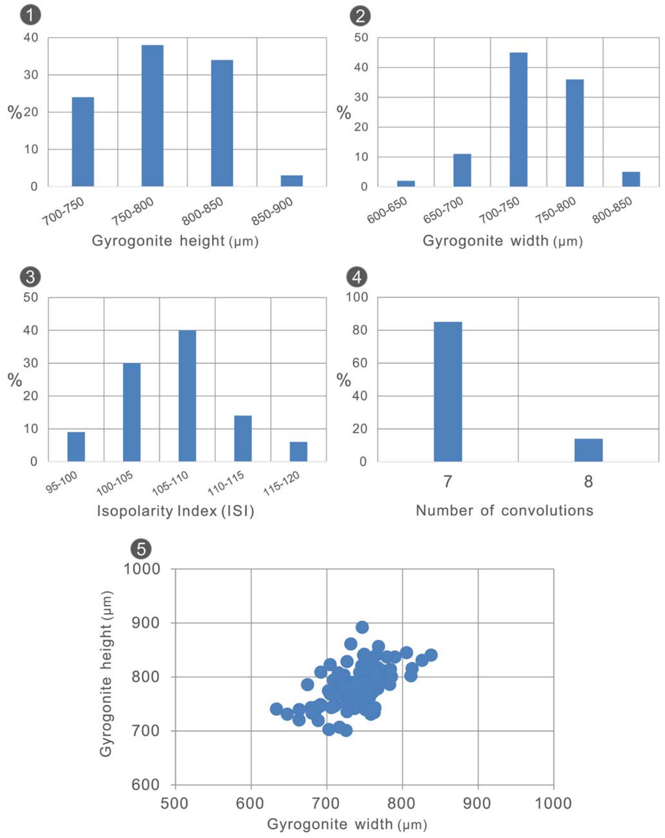

Figure 5. Morphometric data of *Gyrogona lemani capitata* (99 gyrogonites) in the South Gobi area, Junggar Basin. (**1–4**) Frequency distributions: (**1**) gyrogonite height; (**2**) gyrogonite width; (**3**) isopolarity index; (**4**) number of convolutions. (**5**) Dispersion graph of gyrogonite height/gyrogonite width.

Occurrence.—*Gyrogona lemani capitata* was reported in the Lutetian of France, including Pont-Bernard, commune de Brény (Aisne), Cuis (Marne), Pargnan, and Neuilly-Saint-Front (Grambast and Grambast-Fessard, 1981).

Description.—The *G. lemani capitata* gyrogonites are large, with a height of 701–892 µm (mean: 784 µm; standard deviation: 38) and a width of 634–838 µm (mean: 739 µm; standard deviation: 37). Their isopolarity index ranges between 96 and 119 (mean: 106; standard deviation: 5). The shape is oblate spheroidal to prolate spheroidal, with seven to eight convolutions visible in lateral view. The spiral cells are flat to convex, with a width of 115–130 µm. The apex of the gyrogonite is rounded, with moderate periapical thinning of the spiral cells, and ornamented with apical nodules on convex specimens. The base is rounded, with a pentagonal basal pore ∼30–40 µm in diameter.

Materials.—More than 100 gyrogonites have been recovered from the South Gobi area.

Remarks.—The *G. lemani capitata* population in this study is smaller in size than that from Pont-Bernard, commune de Brény (Aisne) in Grambast and Grambast-Fessard (1981), which is 950–1,250 µm high and 925–1,200 µm wide. However, the isopolarity index and number of convolutions in the two populations are similar, with an isopolarity index of 96–116 and six to eight convolutions for the French population.

Discussion

The late Paleocene fossil charophytes recorded in the South Gobi area include the oldest global record of *Gyrogona lemani capitata* and the second-oldest record for *Lychnothamnus vectensis.* The latest Paleocene *G. lemani capitata* from the South Gobi area is older than the middle Eocene record from France (Fig. 6). The oldest record of *L. vectensis* (as *Lychnothamnus* aff. *L. vectensis*) is from the Cretaceous–Paleocene transition deposits of the Songliao Basin in northeastern China (Li et al., 2019), and the oldest European record is from the late Eocene–early Oligocene transition (Fig. 6). In the United States, its oldest record is probably early Eocene (Vicente et al., 2020). These species clearly were present in Asia for some time before their dispersal to North America and Europe. The older age of the American *Lychnothamnus* aff. *L. vectensis* relative to those in Europe could suggest a pattern of dispersal from Asia to North America first. The dispersal of *L. vectensis* to Europe in the late Eocene could have occurred alongside known tetrapod dispersal events between Europe and North America or through a route (according to known mammalian dispersal patterns) from Asia to Europe (Stidham and Ni, 2014; Stidham et al., 2020). The occurrence of these widespread charophyte taxa in Asia (and North America) before their first records in Europe parallels that of a widely distributed bird group known in the middle Eocene of North America (Utah) and Central Asia (Uzbekistan) before their oldest record in the late Eocene of Western Europe (Stidham et al., 2020). For the Asia-to-Europe potential dispersal route, given physical distances and known geographic barriers (i.e., the Turgai Strait and Tethys Seaway), the charophyte lineages likely would have dispersed from Central Asia to Eastern Europe across the straits in the middle to late Eocene.

Biotic factors could have led to the intercontinental dispersal of charophytes. Birds are known to carry charophyte oospores in their stomachs and externally in mud adhering to their feet and feathers (Proctor, 1962, 1980; Proctor et al., 1967; Trabelsi et al., 2015). Through the alimentary tract of common migratory water birds, many freshwater algae probably could be carried readily between lakes 100–150 miles apart, and through the caecum, they may be carried several times this distance (Proctor, 1959). For example, oospores were found in the digestive tracts of 24% of the birds shot in the Camargue, France (including the red-crested pochard, *Netta rufina* Pallas, 1773), with charophytes, including oospores and vegetative parts, representing 21% of the stomach contents of the ducks (Allouche et al., 1988). Eurasian teal (*Anas crecca* Linnaeus, 1758) also ingested propagules of charophyte macrophytes, with 23% of the total weight ingested consisting of charophyte oospores (Tamisier, 1971). Furthermore, Proctor (1962) found that 34% of the oospores taken from mallards (*Anas platyrhynchos* Linnaeus, 1758) were able to germinate.

Our results show the direction and timing of charophyte dispersal is penecontemporaneous with the intercontinental dispersals of some extinct birds. Those bird records include a group of small-sized pangalliforms in the middle Eocene of Central Asia, Europe, and Africa, along with North America (Stidham

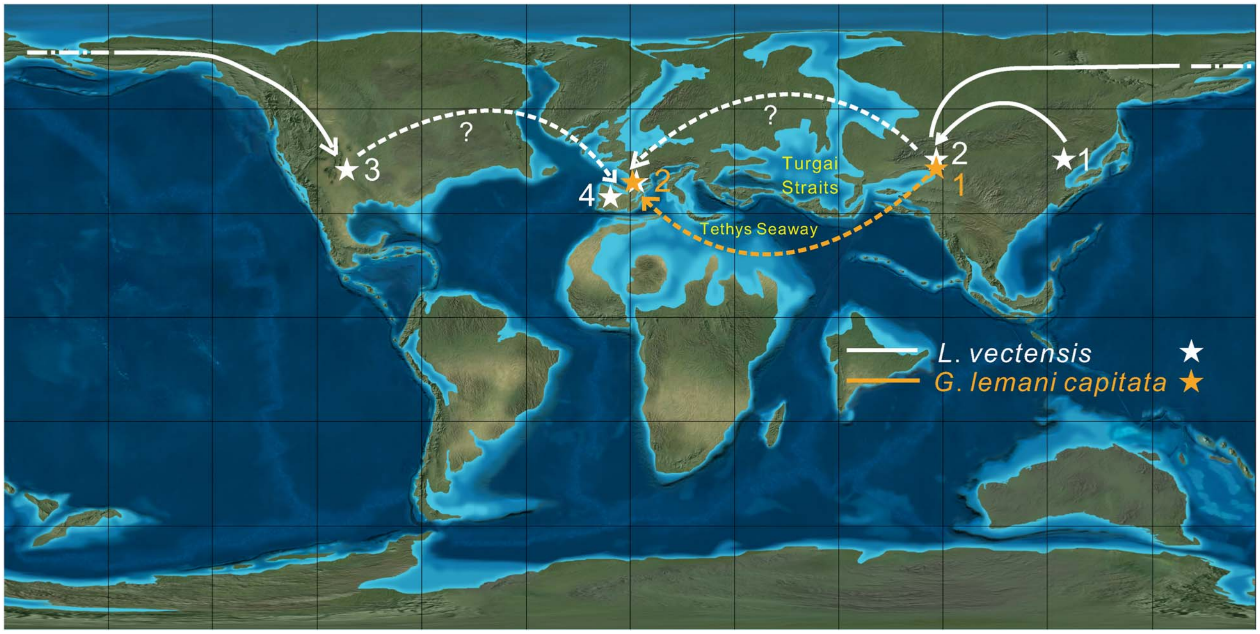

Figure 6. Potential biogeographic dispersal routes of *Lychnothmanus vectensis* and *Gyrogona lemani capitata*. *Lychnothmanus vectensis*: its earliest record is ∼300 kyr before the Cretaceous–Paleogene boundary transition, distributed in Xinjiang in the latest Paleocene, in the early Eocene of the United States, and in Spain and France in late Eocene–early Oligocene. *Gyrogona lemani capitata*: its earliest record is in the latest Paleocene in Xinjiang, then dispersed to France in the middle Eocene. The different starred localities are numbered chronologically. Paleogeographic map of the Earth at ∼60 Ma reproduced with permission from "Global Paleogeography and Tectonics in Deep Time ©2016 Colorado Plateau Geosystems Inc."

et al., 2020), ameghinornithid-like birds in the middle Eocene of Inner Mongolia, Eocene and Oligocene of Europe, and early Oligocene of Egypt (Stidham and Smith, 2015; Stidham and Wang, 2017 and references therein), and the stem anatids Romainvilliinae from the late Eocene of Xinjiang and the late Eocene and Oligocene of Europe (Stidham and Ni, 2014). The geographic distributions of those birds imply intercontinental dispersals in the Eocene across the Turgai Strait, demonstrating that the dispersal mechanism of charophytes along with birds is plausible. Furthermore, considering the hypothesized dispersals of the lineages of *Lychnothamnus stockmansii–L. major* and *Nitellopsis* (*Tectochara*) *merianii–N. obtusa* from Europe to Asia in the late Eocene (Sanjuan and Martín-Closas, 2015b), the dispersal routes of charophytes were likely bidirectional in the Eocene between Europe and Asia.

We explored the sedimentary facies of Asia, North America, and Europe to interpret the paleoenvironments of charophytes when they arrived. Proctor (1959) mentioned suitable media or environmental conditions are important for *Chara* zygotes to germinate and colonize. *Gyrogona lemani capitata* is found in sandstones and sandy mudstones attributed to deposition in intermittent riverine environments in the uppermost Paleocene of the northeastern Junggar Basin, Xinjiang (Ni et al., 2016). It was later found in middle Eocene beds of France. It occurs in marls from Pont-Bernard, commune de Brény (Aisne), Cuis (Marne), Pargnan, and Neuilly-Saint-Front of France, corresponding to sedimentation in shallow lacustrine facies (Grambast and Grambast-Fessard, 1981). Therefore, it appears that either *G. lemani capitata* shifted or varied its habitat preferences during its biogeographic history, from fluviatile environments in the South Gobi area to shallow lacustrine belts in the middle Eocene of Europe, or it occupied a wider array of habitats than previously recognized. *Lychnothmanus* aff. *L. vectensis* was reported from shallow lacustrine facies of the Songliao Basin (Li et al., 2019) and in lake delta front facies of the Jiaolai Basin, eastern China. To the west, in the northeastern Junggar Basin, Xinjiang, *Lychnothmanus* aff. *L. vectensis* is present in fluviatile sandstones and sandy mudstones. *Lychnothmanus* aff. *L. vectensis* recovered from Utah (United States) came from beds of siltstones containing mainly thin thalli, ostracods, gastropods, and trace fossils that were interpreted as representing floodplain environments. Assuming all these findings represent autochthonous populations, these data suggest the species occupied a wide range of habitats in China. When it dispersed to Europe around the Eocene–Oligocene boundary transition, *L. vectensis* appears to have become restricted in its habitats to shallow lacustrine facies. For example, *L. vectensis* is in the shallow lacustrine deposits of the Artés Formation, Ebro Basin, Catalonia (Sanjuan and Martín-Closas, 2015b) and the lacustrine bluish marls of the Argenteuil Formation in Loiret (Centre-Val de Loire) in the Paris Basin, France (Riveline, 1986). In addition, *L. vectensis* was found in the lacustrine deposits from the Bembridge Marls Member (Bouldnor Formation, Solent Group) in the Hampshire Basin on the Isle of Wight, United Kingdom (Sanjuan and Martín-Closas, 2015b and references therein).

Conclusions

We studied the taxonomy, paleoecology, and paleobiogeography of a latest Paleocene charophyte flora in the South Gobi area of Xinjiang in China, which includes the taxa *Peckichara torulosa* var. *varians*, *Lychnothmanus vectensis*, and *Gyrogona lemani capitata*. The dispersal of this flora from Asia to Europe in the middle to late Eocene probably occurred before the retreat of the Turgai Strait in both the Tarim area and the Siberian Basin by the end of the late Eocene and before the "Grande Coupure" in Europe and the "Mongolian Remodelling" event in Asia during the Eocene–Oligocene transition. Waterbirds may have played an important role in facilitating this intercontinental dispersal. In comparison with European Eocene records, it appears that *G. lemani capitata* and *Lychnothmanus* aff. *L. vectensis* had wider paleoecological tolerances in the Paleocene of China, before their migration westward.

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