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New *Hannaea* Patrick (Fragilariaceae, Bacillariophyta) species from Asia, with comments on the biogeography of the genus

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ABSTRACT
Light and scanning electron microscope observations are provided on four new *Hannaea* Patrick species from Asia. The areas in Asia the new taxa are described from include Tibet, Mongolia and the Pamir mountainous region in western Asia. Both subgroups of the genus are represented, including *H. tibetiana* Q. Liu, Glushchenko, Kulikovskiy & Kociolek, sp. nov. and *H. pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov., from the group that includes the generitype and has striae composed of single rows of areolae and one rimoportula per valve. *Hannaea dorofeyukae* Kulikovskiy, Glushchenko, Q. Liu & Kociolek, sp. nov. and *H. mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. have striae composed of two rows of areolae and two rimoportulae; one at each end of the valve. The group with two rimoportulae per valve and biseriate striae is known only from Lakes Baikal, Khövsgöl and the surrounding areas in Asia. New combinations are proposed for four other species. These taxa are also known from Asia. Two of them are known from Japan, one is from China and one is from Lake Baikal in Russia. It appears that Asia is an important center of diversity for *Hannaea*.

KEY WORDS
Diatoms, morphology, biogeography, China, Tajikistan, Mongolia, new species.

RÉSUMÉ

*Description de nouvelles espèces d'*Hannaea *Patrick d'Asie et notes sur la biogéographie du genre*

Des observations au microscope optique et électronique à balayage sont fournies sur quatre nouvelles espèces de *Hannaea* Patrick en provenance d'Asie. Les nouveaux taxons décrits proviennent d'Asie, notamment du Tibet, de Mongolie et de la région montagneuse du Pamir, en Asie occidentale. Les deux sous-groupes du genre sont représentés, *H. tibetiana* Q. Liu, Glushchenko, Kulikovskiy & Kociolek, sp. nov. et *H. pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov., du groupe qui comprend le generitype et qui a des striae composées de deux rangées simples d'aréoles et d'un rimoportule par valve. *Hannaea dorofeyukae* Kulikovskiy, Glushchenko, Q. Liu & Kociolek, sp. nov. et *H. mongolica* Glushchenko, Koulikovskiy, Q. Liu & Kociolek, sp. nov. ont des stries composées de deux rangées d'aréoles et de deux rimoportules; un à chaque extrémité de la valve. Le groupe à deux rimoportulae par valve et aux striae bisériques est connu uniquement des lacs Baïkal, Khövsgöl et des régions environnantes d'Asie. De nouvelles combinaisons sont proposées pour quatre autres espèces. Ces taxons sont également connus en Asie, deux d'entre eux du Japon, un de Chine et un du lac Baïkal en Russie. Il semble que l'Asie soit un centre de diversité important pour *Hannaea*.

MOTS CLÉS
Diatoms, morphologie, biogeographie, Chine, Tadjikistan, Mongolie, nouvelles espèces.

INTRODUCTION

Central and Eastern Asia include the countries of Tajikistan, Mongolia and China. Diatoms from these countries have not been comprehensively studied. Investigation of the freshwater diatom flora of China has produced the description of a large number of new species and genera, especially over the last decade (Li *et al.* 2007, 2010 and many others). Mongolia was studied from floristic and hydrobiological perspectives (e.g. Dorofeyuk & Kulikovskiy 2012; Dorofeyuk *et al.* 2014). New taxonomic works revealed many new species and some new genera from Mongolia (Kulikovskiy *et al*. 2009, 2010, 2013; Metzeltin *et al*. 2009; Kulikovskiy & Kuznetsova 2016). There have been no modern phycological investigations of the diatoms from Tajikistan.

The diatom genus *Hannaea* Patrick is diagnosed as including araphid pennate diatoms, asymmetrical to the apical axis, usually with a small, unornamented tumid area on one side of the center of the valve (Patrick & Reimer 1966). Bixby & Jahn (2005) discussed the nomenclatural history of the genus and designated a lectotype for *H. arcus* (Ehrenberg) Patrick, the type species of the genus. Electron microscopical observations for species of the genus show taxa with uniseriate stria and a single rimoportula at one end (e.g. *H. arcus, H. superiorensis*, Bixby et al. 2005) or biseriate striae with a rimoportula at both apices (*H. baicalensis, H. hovsgolensis*, Vishnyakov et al. 2015), and several taxa have been proposed that are barely asymmetrical to the apical axis (e.g. *H. arcus* var. *hattoriana* (Meister), Ohtsuka 2002) or that have straight margins (*H. arcus* var. *subarcus* (Iwahashi), Lee in Lee *et al*. 1992).

The genus is known across the northern hemisphere, and a species was described originally by Krasske (1939), *H. chilensis* (Krasske) Kulikovskiy, from Chile, but there are no records of the genus from Africa, Australasia or Antarctica (Kociolek, Accepted). In collections we have made from Asia (Tajikistan, Mongolia and China), we have identified some species that appear to be new to science. The purpose of the present report is to formally describe these new species, document their morphologies with light and scanning electron microscopy, and discuss the biogeographic distribution of the genus.

MATERIAL AND METHODS

A sample from China was collected by Q. Liu, J. Wang and S. L. Shi in 2015. It is designated as "Sample no 201507029 – Midui Glacier, Tibet, periphyton, 13.VII.2015 (29°87.684'N, 96°29.678'E)". Water temperature was measured at about 8°C, pH was 8.81 and conductivity was recorded as 455µS/cm using a Hanna multiparameter probe (HANNA HI 98 128 meter).

Samples from Mongolia were collected by M.S. Kulikovskiy and E.S. Gusev in 2011 and 2015. Sample no 00060 was collected at Terkhiin Tsagaan Lake, Khangai Mountains, periphyton, on 13.VIII.2011 (46°42.371'N, 096°39.862'E). The water temperature was about 12°C, pH = 8.58 and conductivity 94 µS/cm. Samples no 02496, 02687, 02694 are from Khövsgöl Lake, periphyton, collected on 27.VII.2015 (50°47.215'N, 100°31.837'E). The water temperature was about 21°C, pH = 8.79 and conductivity 234 µS/cm. Samples nos 03097 and 03098 are from the Suman Gol River, benthos, collected on 06.VII.2015 (48°09.166'N, 99°57.062'E). The water temperature was about 4.5°C, pH = 9.07 and conductivity 100 µS/cm. Finally, the sample from Tajikistan, no 02547, is from the Pamir Mountains, Mountain pass Maisara (Kok-Bay), collected from an unnamed river, periphyton (37°28.269'N, 72°38.958'E). Temperature, pH and conductivity were determined for all samples using a HANNA HI 98 128 meter.

Samples were treated with 10% hydrochloric acid to remove carbonates and washed several times with deionized water for 12 h. Afterwards, samples were boiled in concentrated hydrogen peroxide (≈ 37%) to dissolve organic matter. They were washed again with deionized water four times at 12 h intervals. After decanting and filling with deionized water up to 100 ml, the suspension was spread onto coverslips and left to dry at room temperature. Permanent diatom preparations

were mounted in Naphrax®. Light microscopic (LM) observations were performed with a Zeiss Axio Scope A1 microscope equipped with an oil immersion objective (x100, n.a. 1.4, differential interference contrast [DIC]) and Axio Cam ERc 5s camera (Zeiss). Valve ultrastructure was examined by means of a JSM-6510LV scanning electron microscope (IBIW, Institute for Biology of Inland Waters RAS, Borok, Russia). For scanning electron microscopy (SEM), parts of the suspensions were fixed on aluminum stubs after air-drying. The stubs were sputter coated with 50 nm of Au.

Observations on all species described herein are based on 50 or more specimens.

The sample and slides from the Tibet collection are housed at the Freshwater Algal Herbarium (SXU) at Shanxi University, China. Samples and slides from Mongolia and Tajikistan are deposited in the collection of Maxim Kulikovskiy at the Herbarium of the Institute of Plant Physiology Russian Academy of Science, Moscow, Russia.

RESULTS

Class FRAGILARIOPHYCEAE Round (1990)
Order FRAGILARIALES P.C. Silva (1962)
Family FRAGILARIACEAE Grev. (1833)
Genus *Hannaea* Patrick (1966)

Hannaea tibetiana Q.Liu, Glushchenko, Kulikovskiy & Kociolek, sp. nov. (Figs 1-3)

HOLOTYPE. — Slide no 201507029-1; illustrated in Fig. 1H in collection at Qi Liu of the Freshwater Algal Herbarium of Shanxi University (SXU).

TYPE LOCALITY. — China, Midui Glacier, Tibet, unnamed river, periphyton, (N29°87.684', E96°29.678').

ETYMOLOGY. — The specific epithet "*tibetiana*" refers to the name of the region where this species was observed.

DISTRIBUTION. — As yet known only from the type locality.

DESCRIPTION

Valves

Asymmetrical about the apical axis, lunate to almost rectangular, with capitate to bent-capitate apices, length 22-43 µm, breadth 15-18 µm (n=45).

Central sternum

Distinct to indistinct, with striae parallel to slightly radiate, 16-18/10 µm.

Bent apices

Deflected towards the ventral margin.

The concave valve

May bear an unilaterally-positioned unornamented area on the concave margin of the valve in the center, slightly tumid to undifferentiated.

SEM, external views (Fig. 2)

The exterior of the valve can be seen to have a distinct central sternum, with heavily silicified ridges perpendicular, extending across the valve face (Fig. 2A, B). Striae uniseriate, comprised of small, rounded areolae (Fig. 2A-C), that extend onto the valve mantle (Fig. 2C, D). Areolae number 85-90 /10 µm within a stria. Cingulum comprised of numerous bands (Fig. 2E). At one apex some striae can extend the central sternum, and even be oriented along the apical axis of the valve (Fig. 2F). An elongated opening at one end of the valve is the external expression of the single rimoportula. Ocellimbi are present at each apex, positioned on the valve mantle (Fig. 2G).

SEM, internal views (Fig. 3):

The central sternum is narrow, and striae are positioned alternatively on each side (Fig. 3A, B). At one apex there is no rimoportula (Figs 3A, C), at the other a rimoportula is present (Fig. 3A, D). The rimoportula is comprised of two thickened strips of silica on either side of a slit-like opening (Fig. 3D). At the apices striae may extend across the central sternum. Small, square-shaped porelli comprise the ocellimbi on the mantle of each apex (Fig. 3C, D).

Hannaea pamirensis Glushchenko, Kulikovskiy, Q.Liu & Kociolek, sp. nov. (Figs 4-6)

HOLOTYPE. — Slide no 02547; illustrated in Fig. 4B in collection of Maxim Kulikovskiy at the Herbarium of the Institute of Plant Physiology Russian Academy of Science, Moscow, Russia.

TYPE LOCALITY. — Tajikistan, Pamir Mountains, Mountain pass Maisara (Kok-Bay), unnamed river, periphyton (37°28.269'N, 72°38.958'E).

ETYMOLOGY. — The specific epithet "*pamirensis*" refers to the name of the Mountain range where this species was observed.

DISTRIBUTION. — As yet known only from the type locality.

DESCRIPTION

Valves

Asymmetrical about the apical axis, weakly arcuate to almost linear with capitate to rostrate apices, length 42-45 µm, breadth 5.5-7.0 µm.

Axial area

Narrow, slightly expanded to the central part of valve.

Central area

Unilaterally tumid on the concave margin, large, with ghost striae. Striae parallel, 16.5-18.0 in 10 µm.

SEM, external views (Fig. 5)

Striae uniseriate, comprised of small, rounded areolae (Fig. 5B-D). Marginal spines flattened (Fig. 5). Areolae number 75-80 /10 µm within a stria.

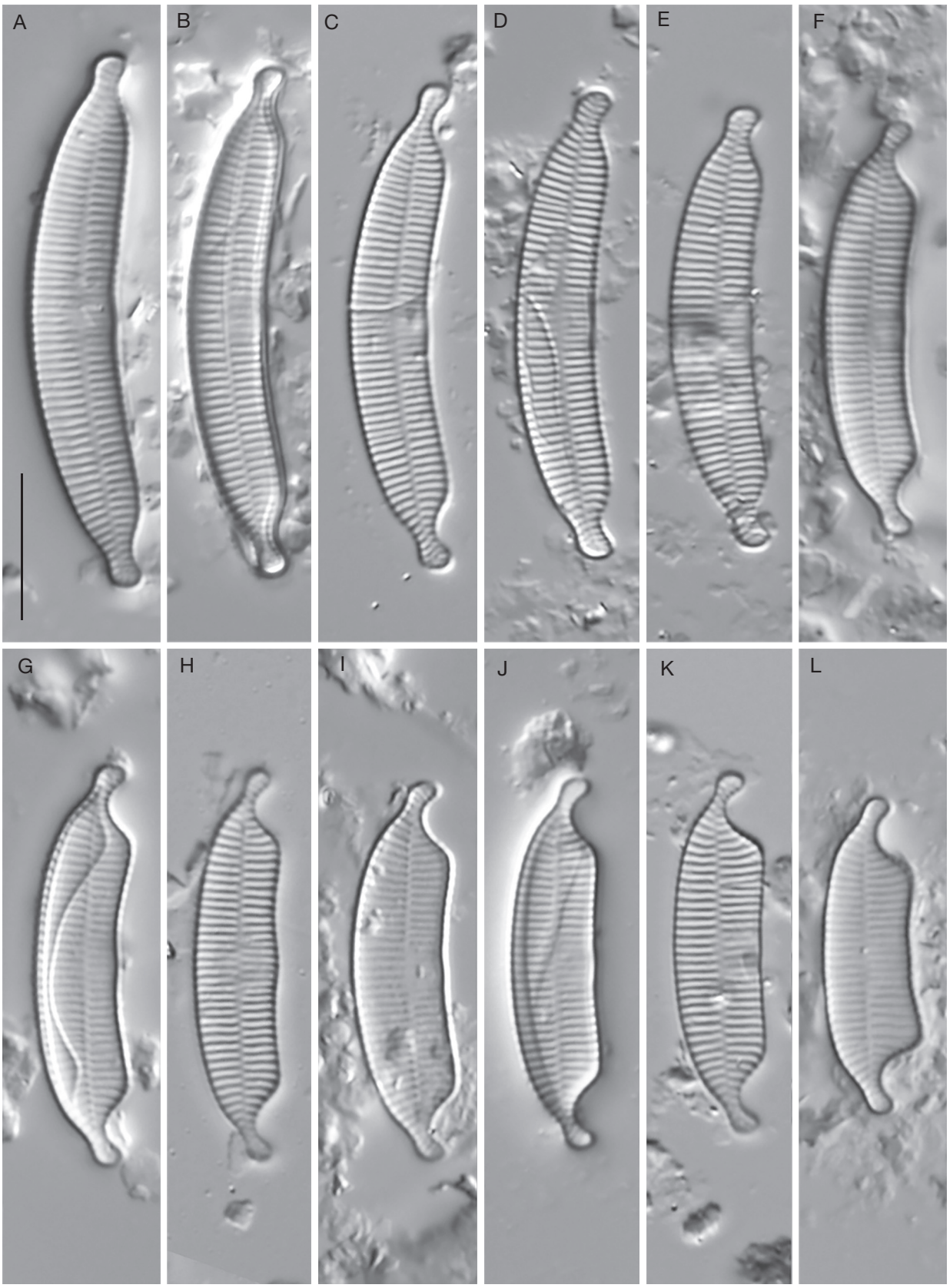

FIG. 1. — *Hannaea tibetiana* Q. Liu, Glushchenko, Kulikovskiy & Kociolek, sp. nov. LM, DIC. Valves views. Size diminution series. Type population (slide no 201507029-1). **F**, Holotype. Scale bar: 10 µm.

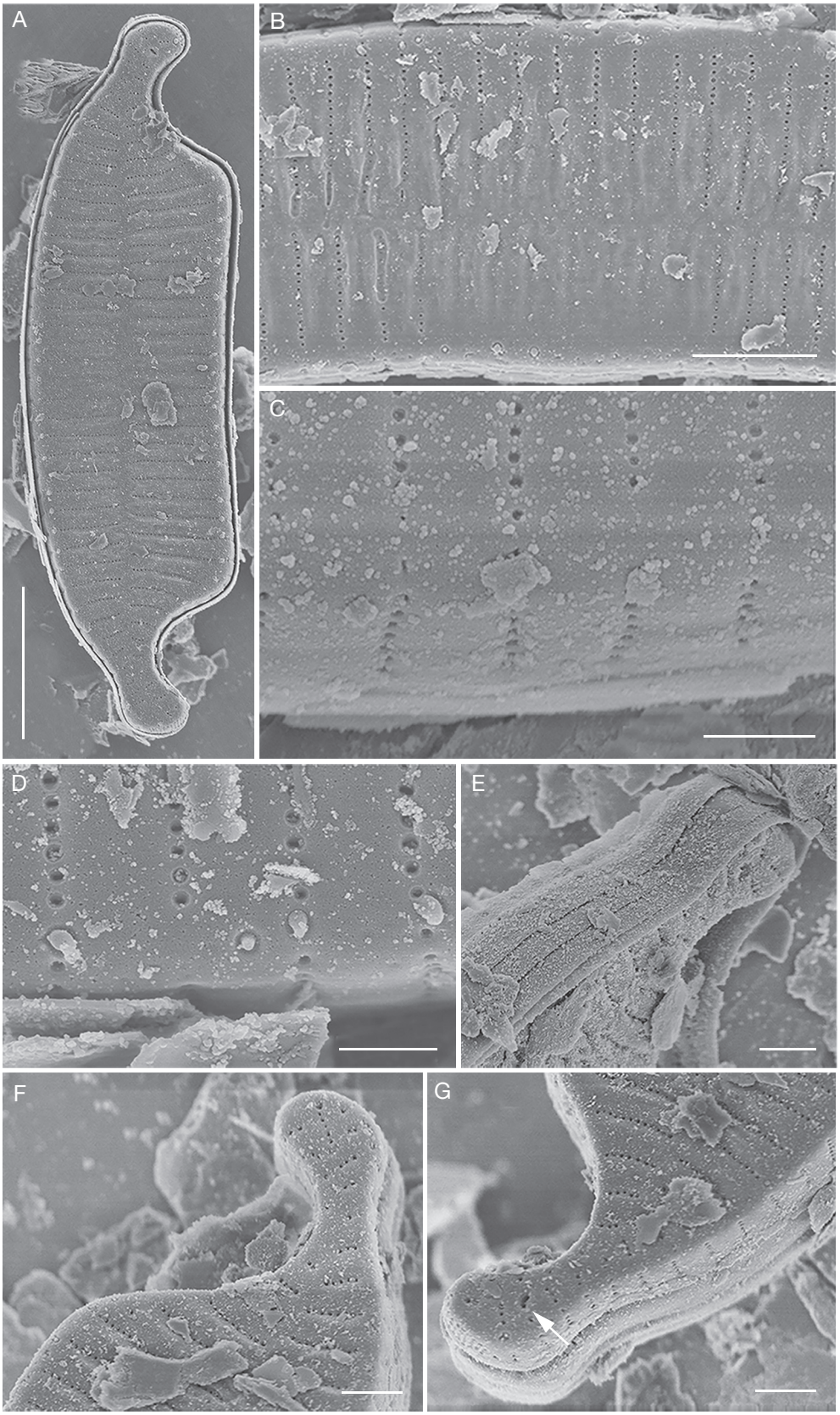

FIG. 2. — *Hannaea tibetiana* Q. Liu, Glushchenko, Kulikovskiy & Kociolek, sp. nov. SEM. External views. **White arrow** shows the opening of the rimoportulae. Scale bars: A, 5 µm; B, 2 µm; C, E-G, 1 µm; D, 0.5 µm.

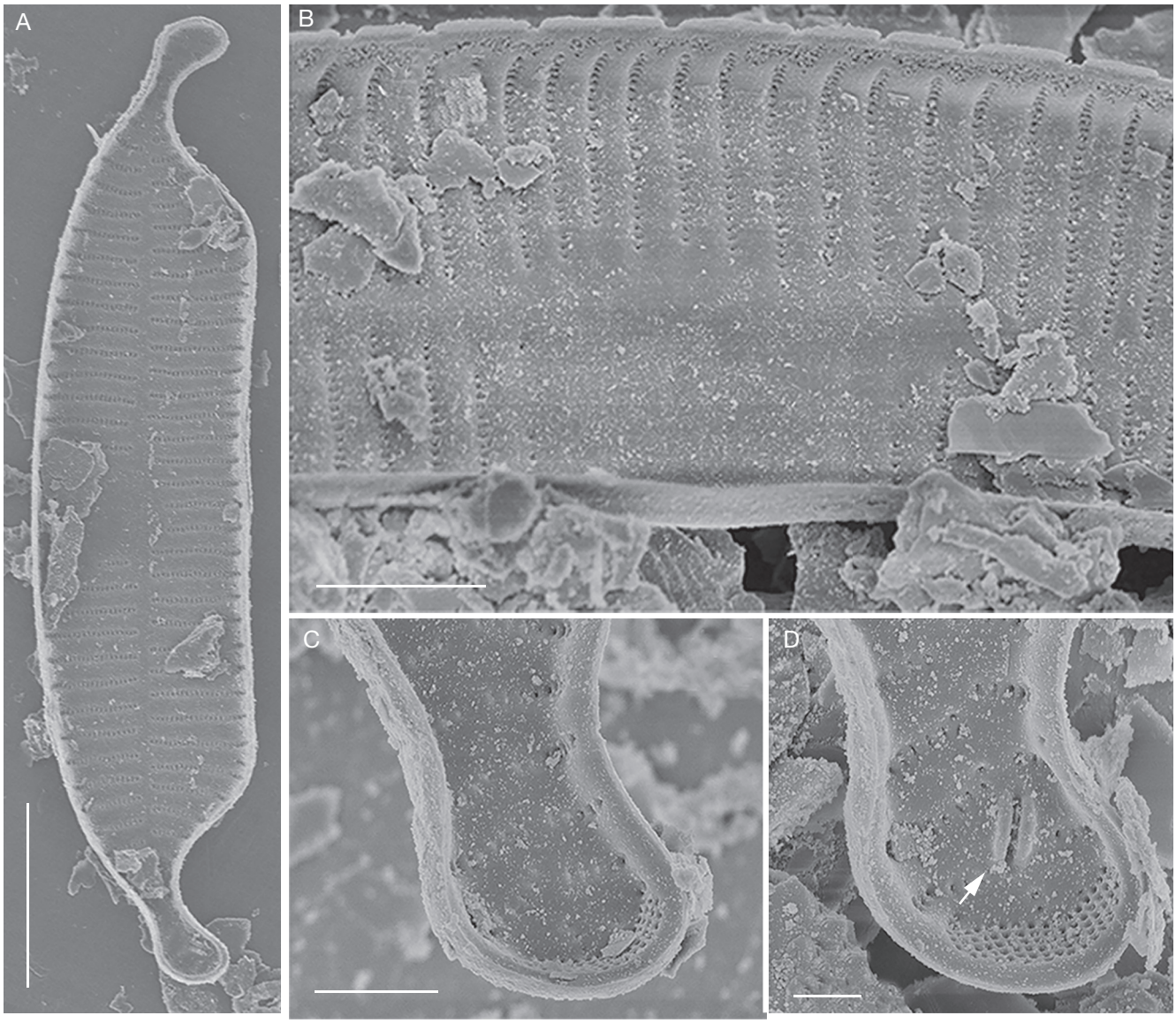

Fig. 3. — *Hannaea tibetiana* Q. Liu, Glushchenko, Kulikovskiy & Kociolek, sp. nov. SEM. Internal views. **White arrow** shows the rimoportula. Scale bars: A, 5 µm; B, 2 µm; C, 0.5 µm; D, 1 µm.

SEM, internal views (Fig. 6)

Striae are located alternatively on each side (Fig. 6). On central area there are false striae (Fig. 6B). Areolae slit-shaped (Fig. 6B-F). Ocellimbi are present on both valve ends (Figs 6C-F). A single rimoportula on one end of valve (Fig. 6A) and comprised of two thickened strips of silica on either side of a slit-like opening (Fig. 6C-E). Rimportulae are located near the ocellimbi, oriented either perpendicularlyto the striae, Fig. 6E) or laterally (oriented parallel to the striae; Fig. 6C, D).

Hannaea mongolica Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov.
(Figs 7-10)

Holotype. — Slide no 00060; illustrated in Fig. 8A, in collection of Maxim Kulikovskiy at the Herbarium of the Institute of Plant Physiology Russian Academy of Science, Moscow, Russia, leg. M.S. Kulikovskiy and E.S. Gusev.

Type locality. — Mongolia, Terkhiin Tsagaan Lake, Khangai Mountains, periphyton, 13.VIII.2011 (46°42.371'N, 096°39.862'E).

Etymology. — The specific epithet "*mongolica*" refers to the name of the country where this species was observed.

Distribution. — Type locality and slides no 02496, 02694, 003097, 03098. Mongolia: Tuul River, Herlen River (as *Hannaea* ? in Metzeltin *et al.* 2009: pl. 9, figs 1-8).

Description

Valves

Arcuate, smoothly tapering to the ends with capitate to rostrate apices, length 39.0-93.5 µm, breadth 6.5-8.0 µm.

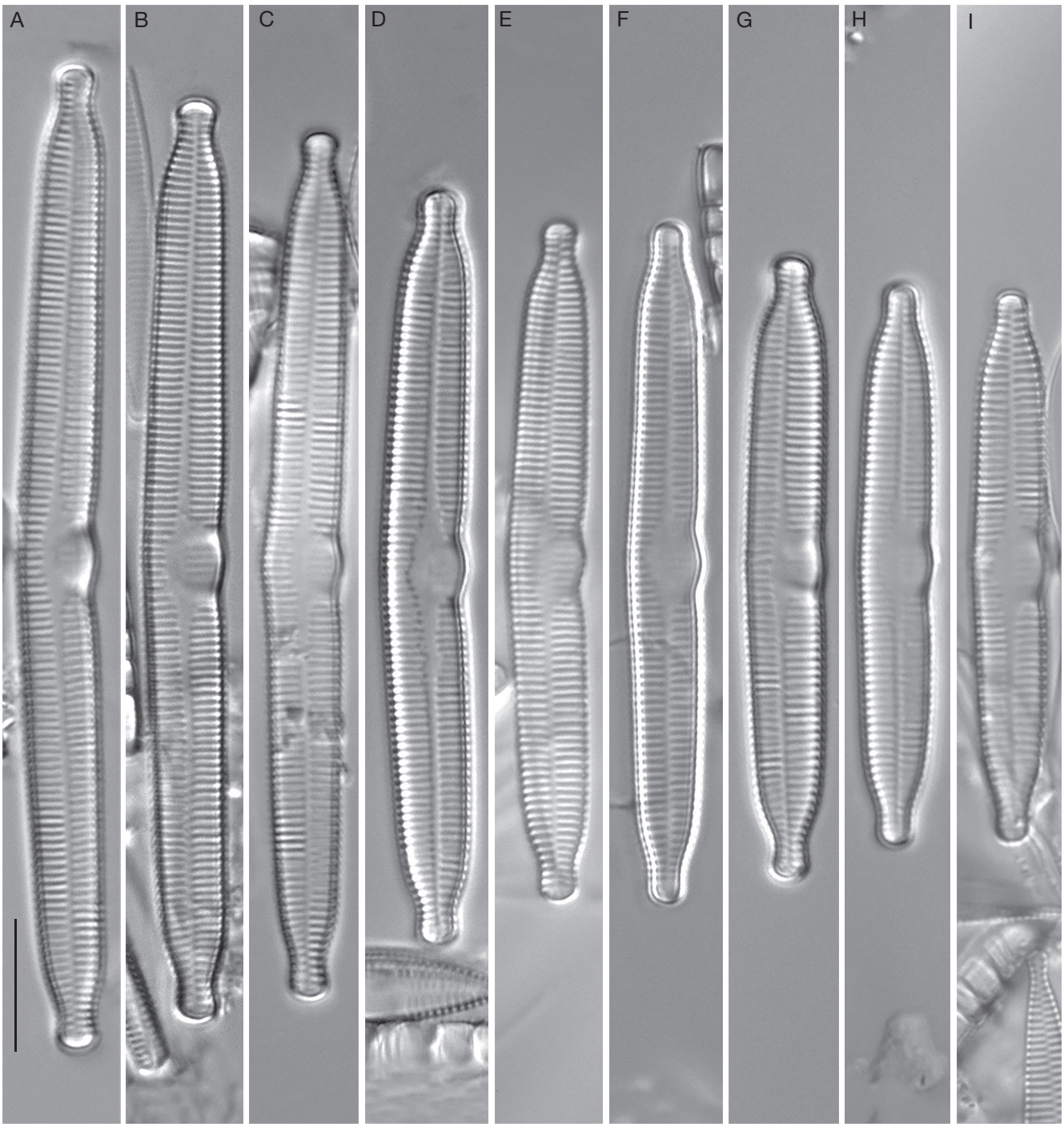

Fig. 4. — *Hannaea pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. LM, DIC. Valves views. Size diminution series. Type population (slide no 02547). **D**, Holotype. Scale bar: 10 µm.

Axial area
Narrow, linear. Central area is expanded unilaterally on the concave margin, large, with ghost striae present. Striae parallel, 17-18 in 10 µm.

SEM, external views (Fig. 9)
Valve face is flat (Fig. 9A-C). Striae biseriate going from valve face to the mantle. No silica ridge is evident between valve face and mantle. Axial area is very narrow. Central area is unilaterally expanded, large, swollen on the ventral side of the valve with evident ghost striae (Fig. 9B, C). Small circle or slit-like openings of rimoportulae are present on each valve end. Ocellimbi are present on mantle in each valve ends (Fig. 9D, E). Spines were not detected (Fig. 9A-C).

SEM, internal views (Fig. 10)
Striae biseriate, lying in depressions. Striae extend onto the mantle. Axial area is narrow. Central area is unilaterally-

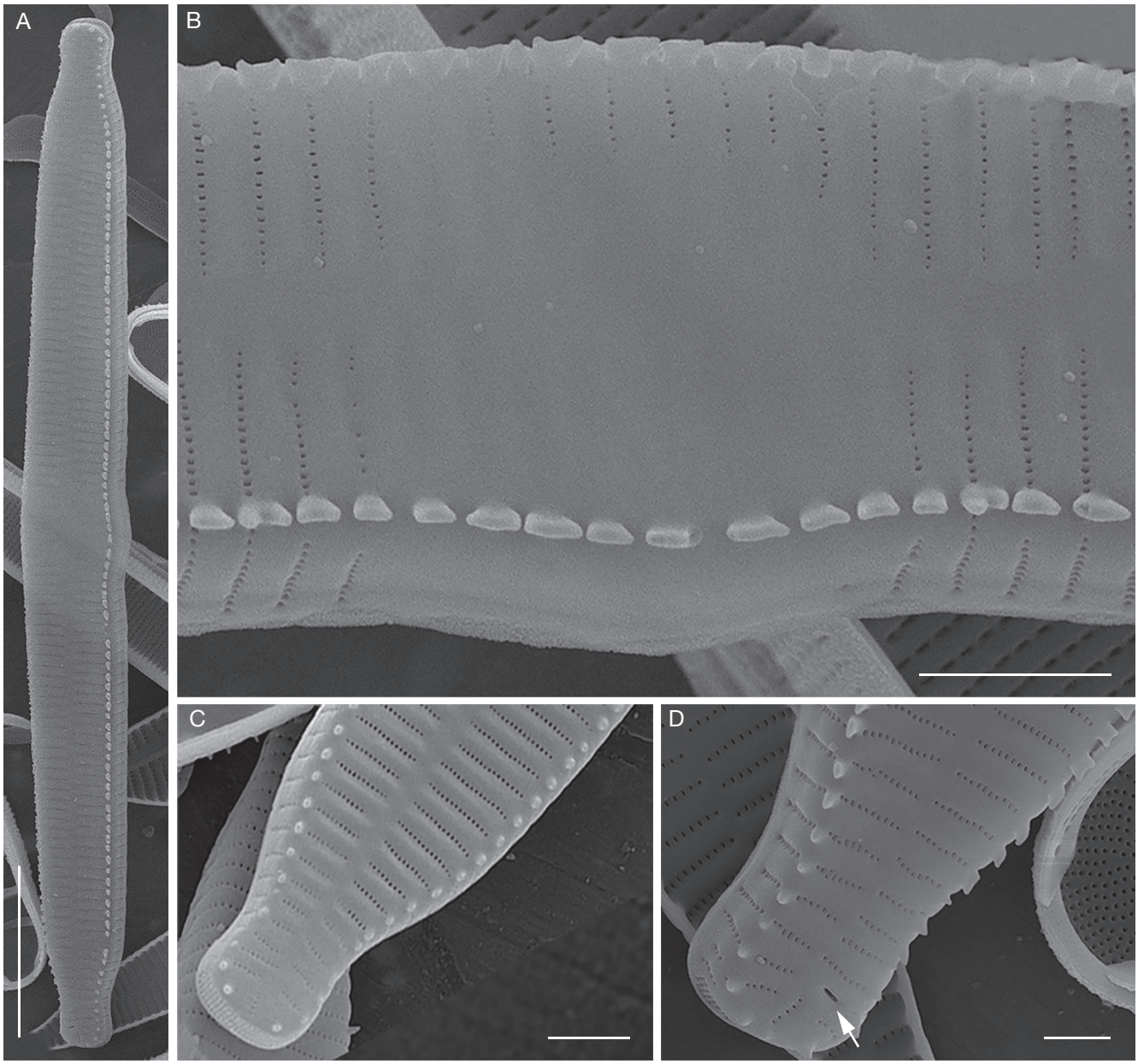

Fig. 5. — *Hannaea pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. SEM. External views. **White arrow** shows the opening of the rimoportulae. Scale bars: A, 10 µm; B, C, 2 µm; D, 1 µm.

expended, large, located on the concave side of the valve with evident ghost striae (Fig. 10A-C). One rimoportula is present at each valve apex. Ocellimbi are present at each valve end, positoned on mantle (Fig. 10D, E).

Hannaea dorofeyukae Kulikovskiy, Glushchenko, Q.Liu & Kociolek, sp. nov. (Figs 11-14)

Holotype. — Slide no 02694; illustrated in Fig. 11C in collection of Maxim Kulikovskiy at the Herbarium of the Institute of Plant Physiology Russian Academy of Science, Moscow, Russia, leg. M.S. Kulikovskiy and E.S. Gusev.

Type locality. — Mongolia. Khövsgöl Lake, periphyton, 27.VII.2015 (N50°47.215', E100°31.837').

Etymology. — Species dedicated to Nadezhda Dorofeyuk, renown Russian algologist and specialist of the Mongolian diatom flora.

Distribution. — Type locality and slides no 02687, 02694, 03097, 03098.

Description

Valves

Arcuate, smoothly tapering to the ends with capitate to rostrate apices, length 45-91 µm, breadth 6-7 µm.

Axial area

Narrow, linear, expanded at the central area.

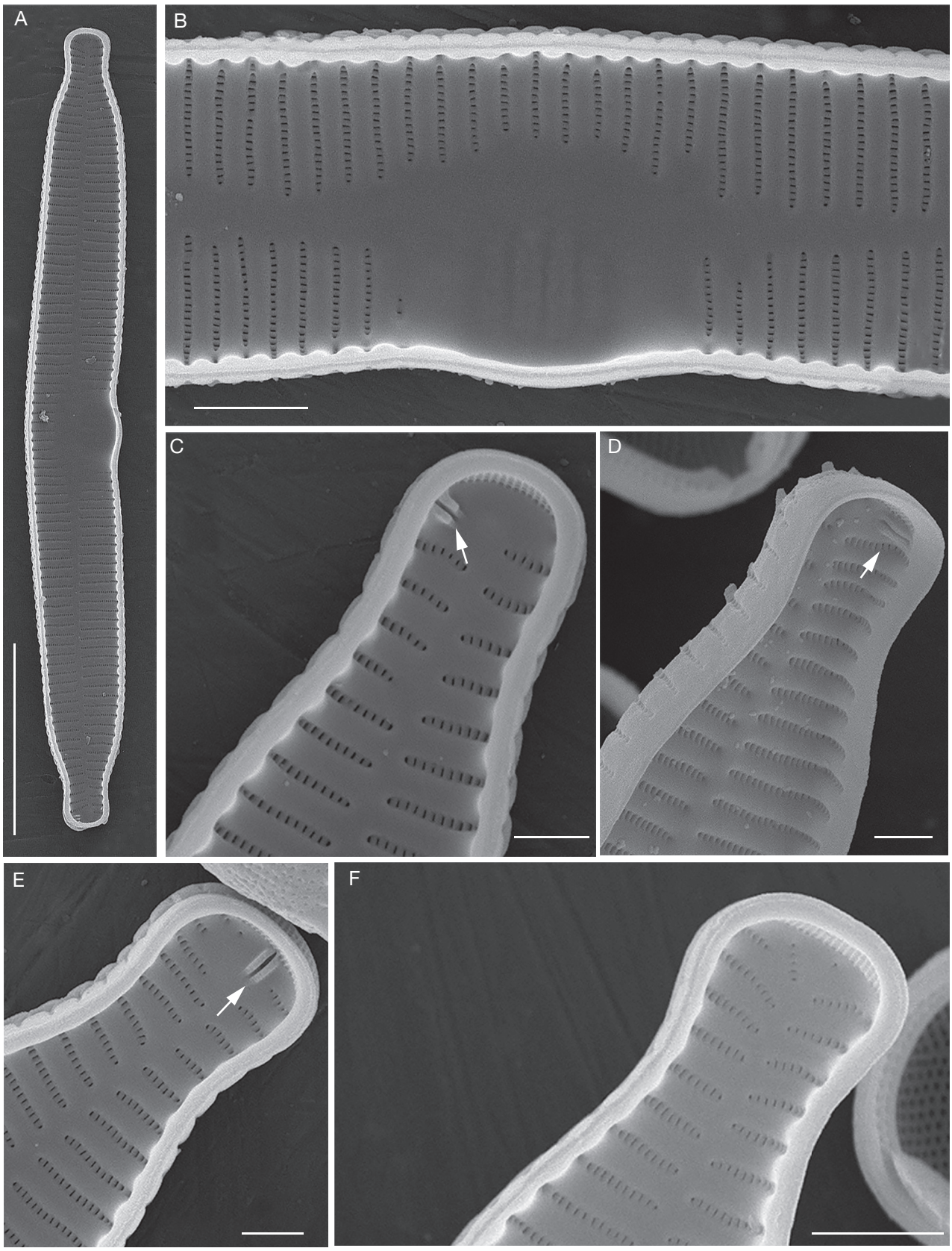

Fig. 6. — *Hannaea pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. SEM. Internal views. **White arrows** show the rimoportulae. Scale bars: A, 10 µm; B, F, 2 µm; C-E, 1 µm.

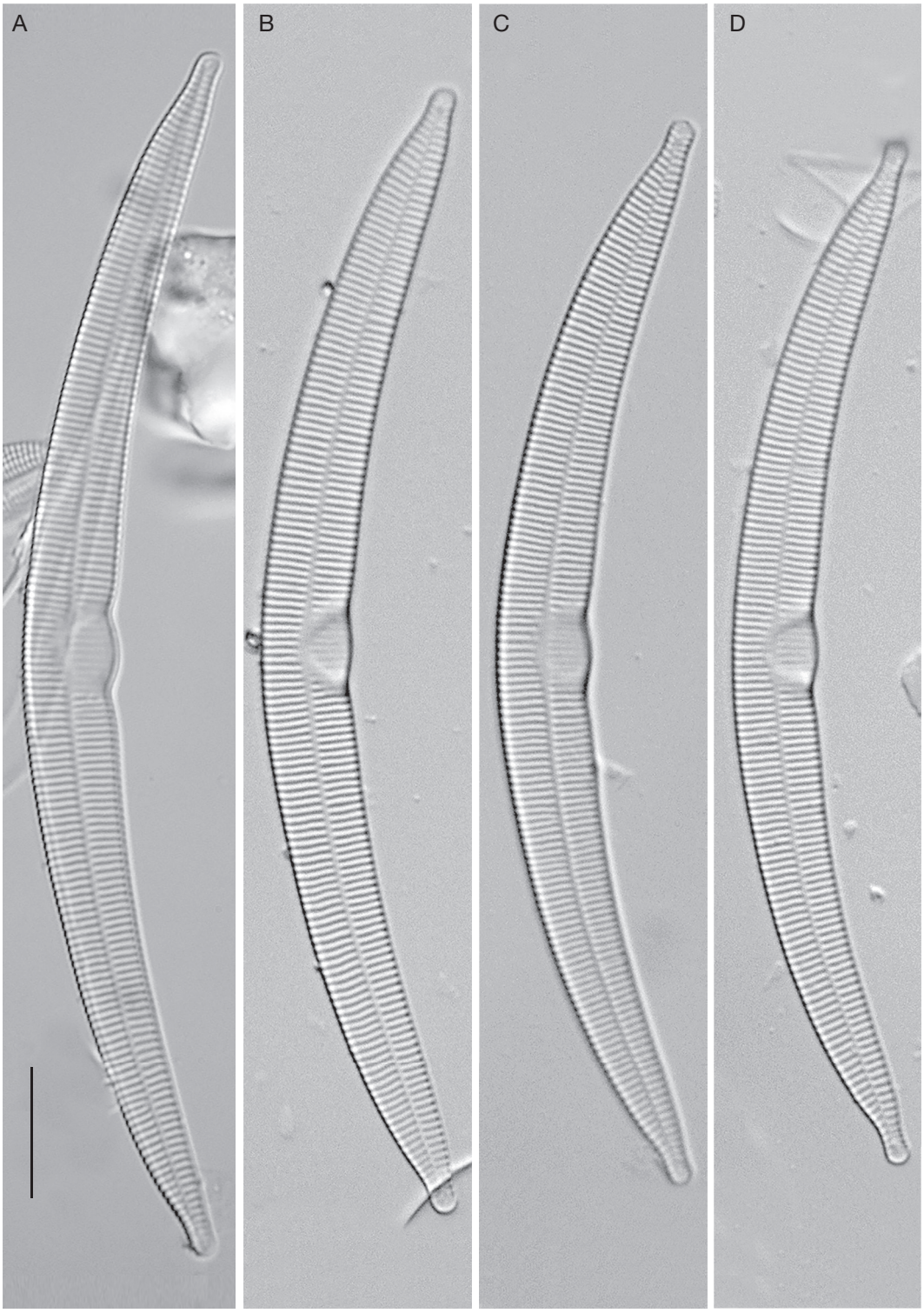

Fig. 7. — *Hannaea mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. LM, DIC. Valves views. Size diminution series. Type population (slide no 00060). Scale bar: 10 µm.

Central area
Large, unilaterally expanded and swollen on the concave margin of the valve without ghost striae. Striae parallel, 14-16 in 10 µm.

SEM, external views (Fig. 13)
Valve face is flat (Fig. 13A). Spines are present on some valves (Fig. 13B-D). Striae uniseriate or biseriate going from valve face to the mantle. Uniseriate striae present on the side opposite

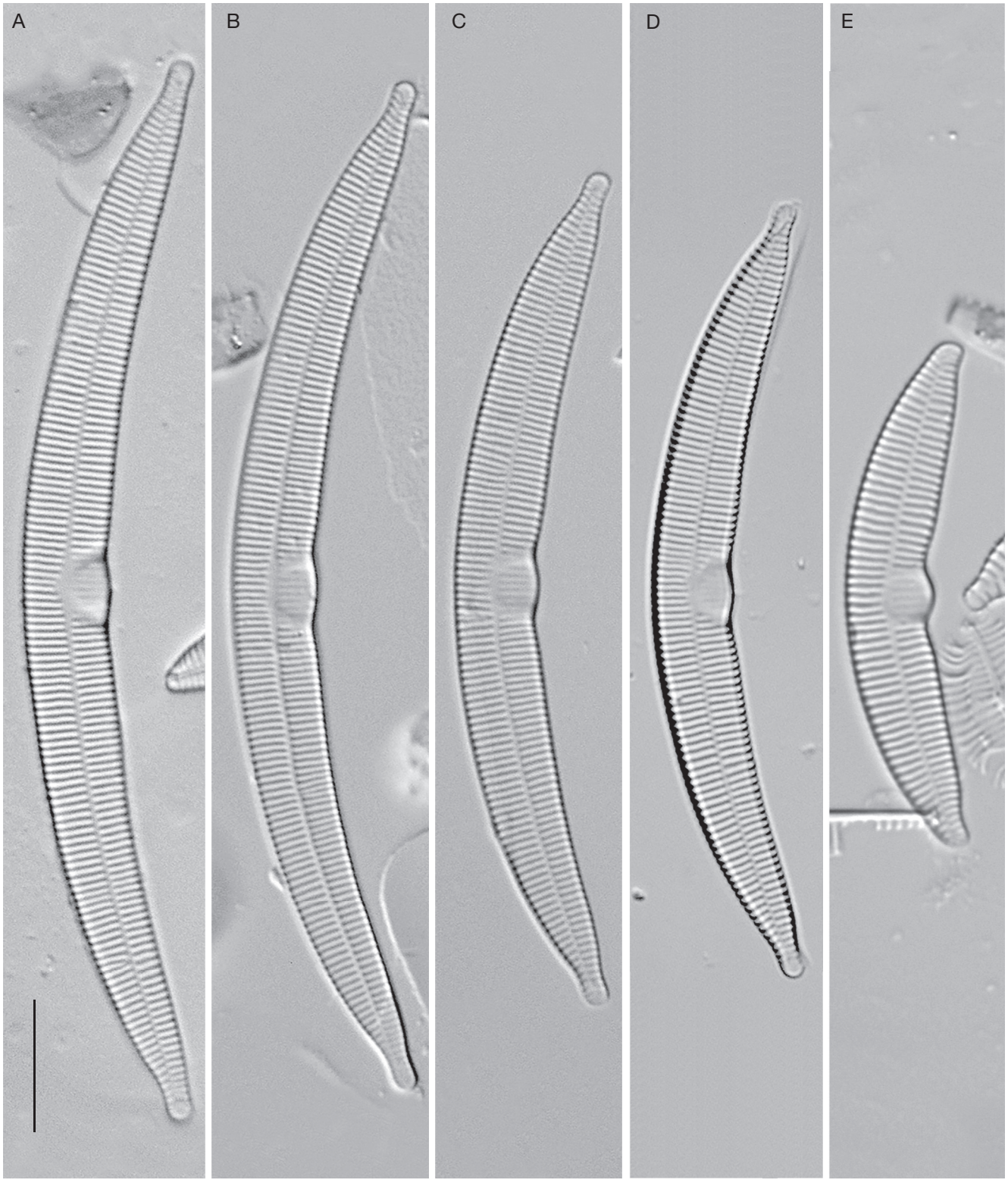

Fig. 8. — *Hannaea mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. LM, DIC. Valves views. Size diminution series. Type population (slide no 00060). **A**, Holotype. Scale bar: 10 µm.

from unilaterally-expanded central area (Fig. 13B, C). Uniseriate striae also evident in central part of valve near the central area (Fig. 13C). Axial area is narrow and evidently broader to the central area. Central area is large, unilaterally-expanded on the ventral side of the valve; ghost striae are wanting (Fig. 13A-D). Small round or slit-like openings of rimportue are present on each valve end. Ocellimbi are present on mantle on each valve apex (Fig. 13E, F).

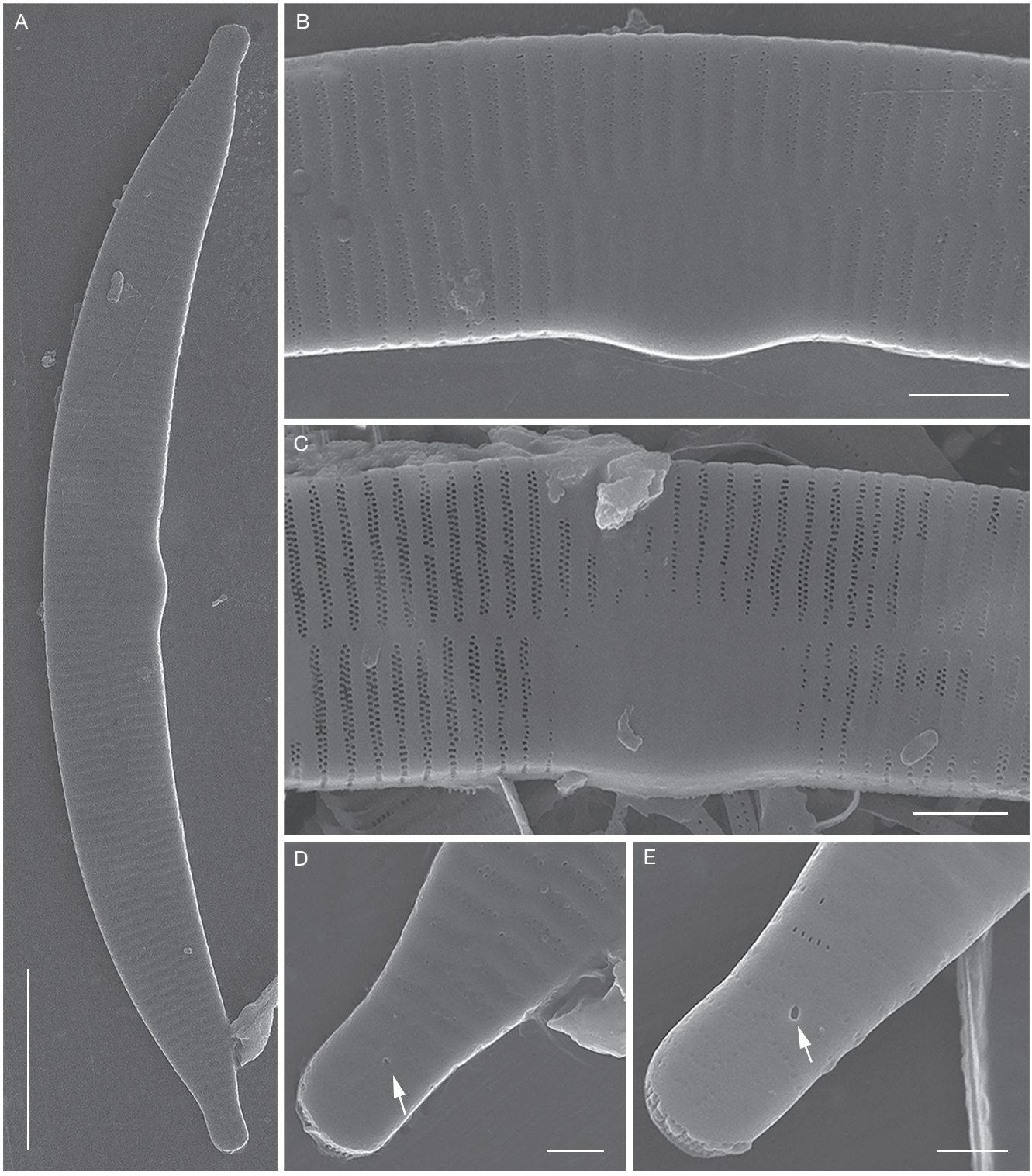

FIG. 9. — *Hannaea mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. SEM. External views. **White arrow** show the opening of the rimoportulae. Scale bars: A, 10 µm; B, C, 2 µm; D, E, 1 µm.

SEM, internal views (Fig 14)

Striae uniseriate or biseriate lying in narrow depressions (Fig. 14B-E). Uniseriate striae present especially in the central part of valve (Fig. 14B-E). Striae extend onto the mantle (Fig. 14B). Axial area is narrow and evidently broader near the central area. Central area is large, unilaterally-expanded on the ventral side, without ghost striae (Fig. 14A, B, E). One rimoportula is present at each valve apex. Ocellimbi are present on each valve ends on the mantle.

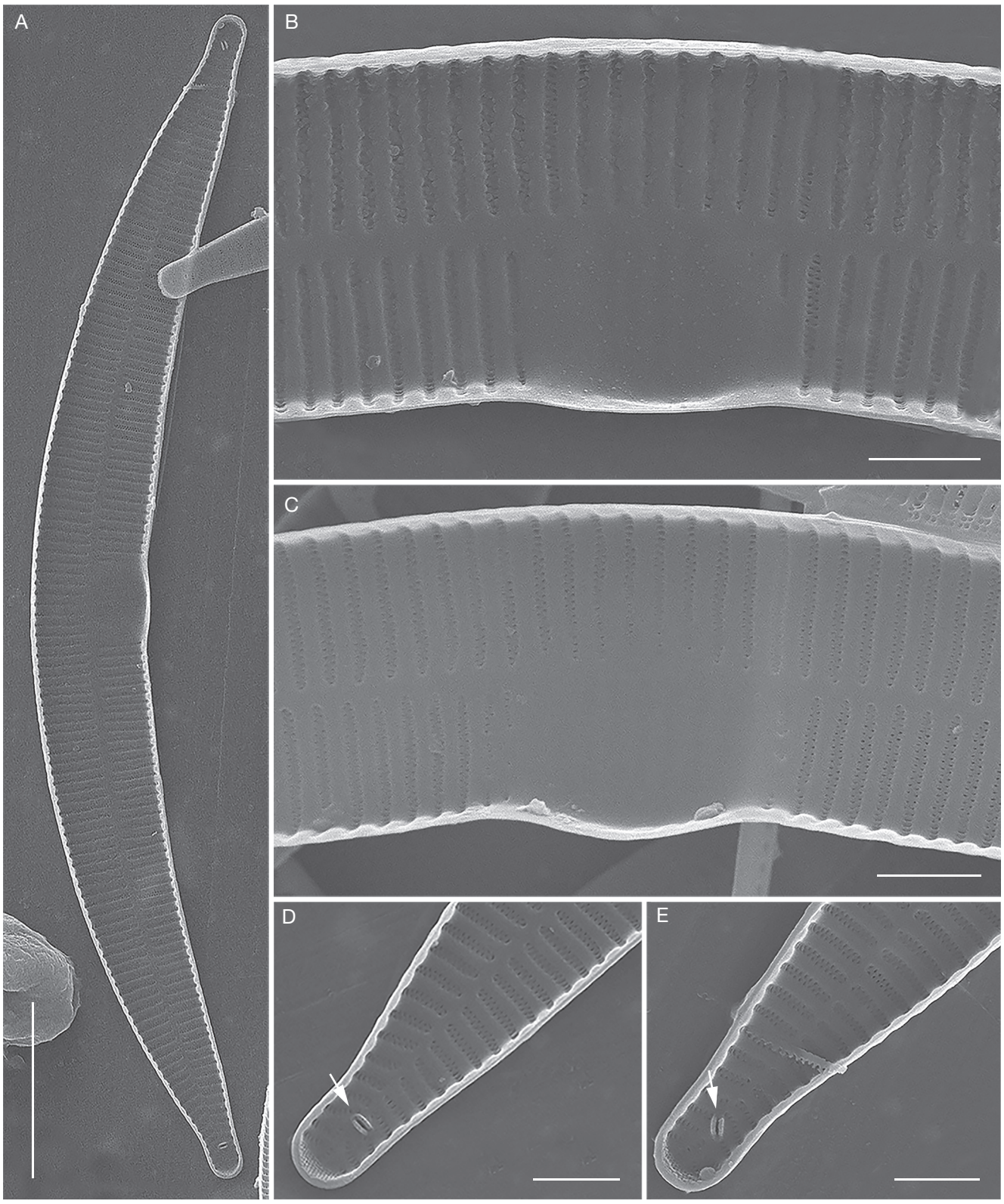

Fig. 10. — *Hannaea mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. SEM. Internal views. **White arrows** show the rimoportulae. Scale bars: A, 10 µm; B-E, 2 µm.

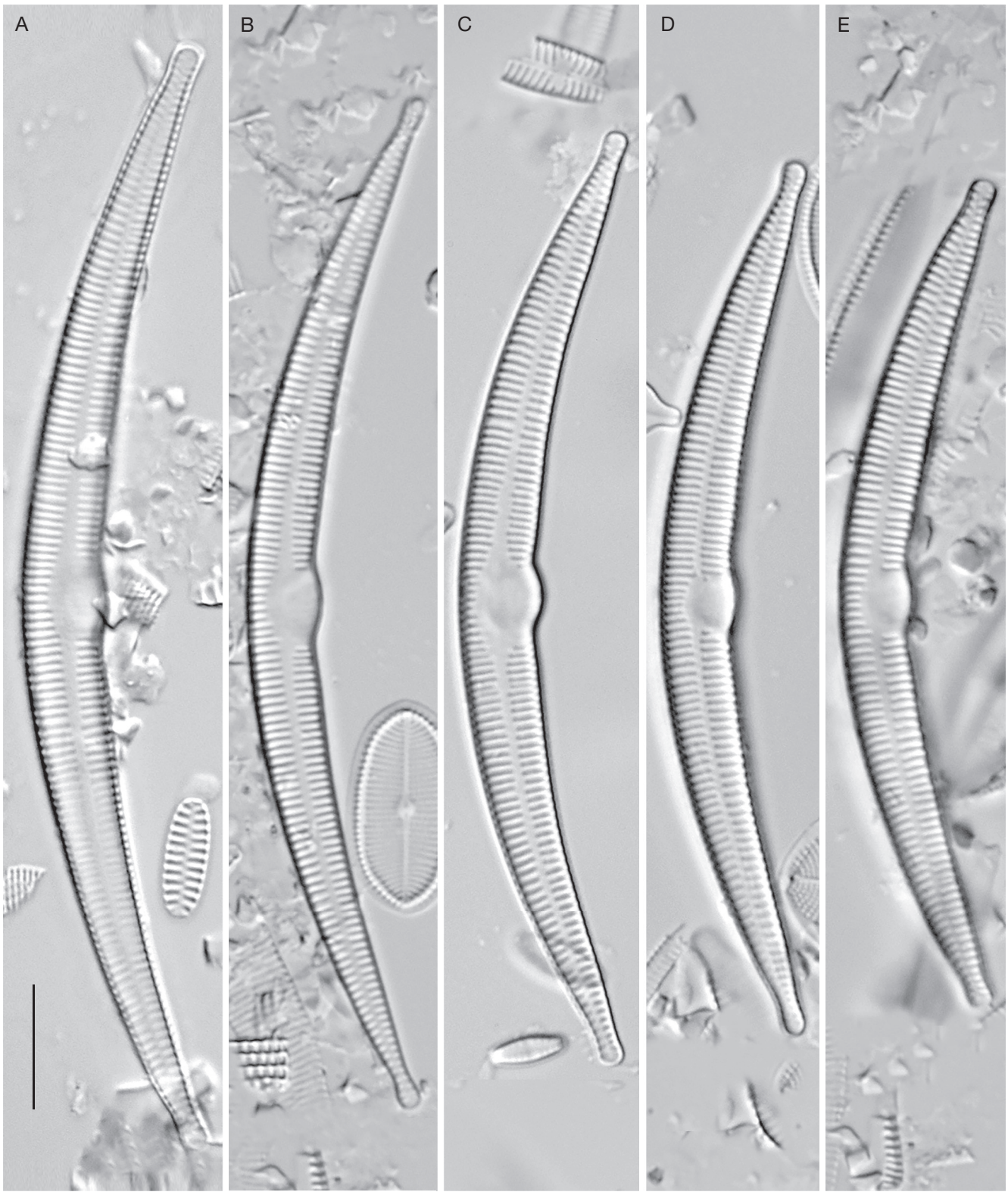

Fig. 11. — *Hannaea dorofeyukae* Kulikovskiy, Glushchenko, Q. Liu & Kociolek, sp. nov. LM, DIC. Valves views. Size diminution series. **A**, **B**, **D**, **E**, Suman Gol River (slide no 03098); **C**, Hövsgöl Lake (slide no 02694) holotype. Scale bar: 10 µm.

NEW COMBINATIONS

In addition to these four new species, there are several taxa that require formal transfer from *Ceratoneis* to *Hannaea*, or reconsideration of their status. These taxa are considered below:

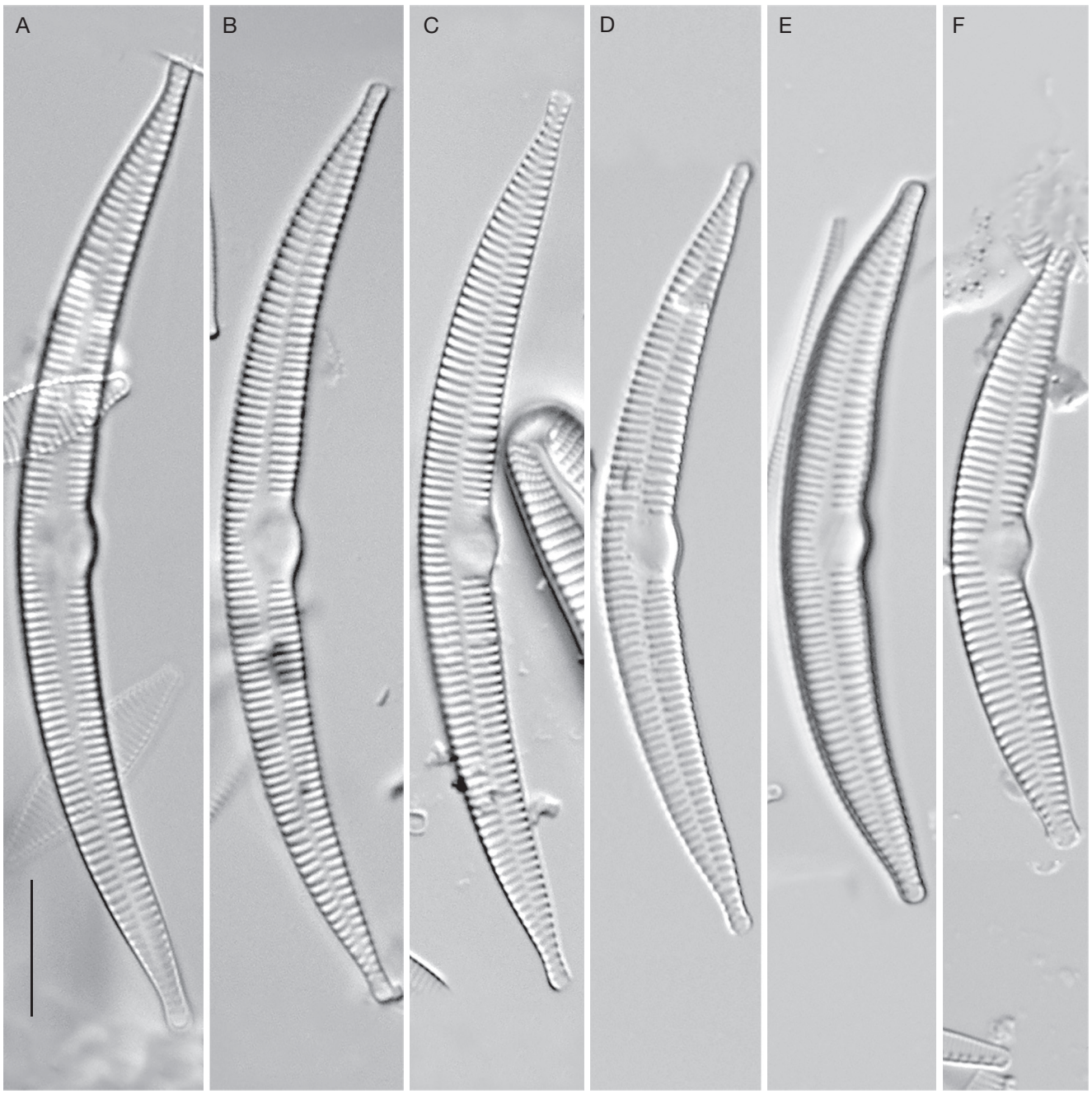

Fig. 12. — *Hannaea dorofeyukae* Kulikovskiy, Glushchenko, Q. Liu & Kociolek, sp. nov. LM, DIC. Valves views. Size diminution series. **A**-**C**, **E**, Type population (slide no 02694) **D**, Hövsgöl Lake (slide no 02687), **F**, Suman Gol River (slide no 03097). Scale bar: 10 µm.

Hannaea orientalis (Skuja) Q. Liu, Glushchenko, Kulikovskiy & Kociolek, comb. nov., stat. nov.

Ceratoneis arcus var. *orientalis* Skuja *Algae. Symbolae Sinicae. Botanische ergebnisse der Expedition der Akademie de Wissenschaften in Wien nach Südwest-China 1914/1918* 1: 50, plate 3, figures 20, 21 (1937).

Locality — Southwestern China.

Hannaea recta (Skvortzow & Meyer) Q. Liu, Glushchenko, Kulikovskiy & Kociolek, comb. nov., stat. nov.

Ceratoneis amphioxys var. *recta* Skvortzow & Meyer, *Proceedings of the Sungaree River Biological Station* 1 (5): 8; pl. 1, fig. 11 (1928). — *Ceratoneis arcus* f. *recta* (Skvortzow & Meyer) Skvortzow, *Proceedings of the Harbin Society of Natural History and Ethnography* 2:

19; pl. 2, fig. 40 (1946). — *Ceratoneis arcus* f. *recta* (Skvortzow & Meyer) Proschkina-Lavrenko in Zabelina, *Opredelitel presnovodnych vodoroslei SSSR. Gosudarstvennoe Izdatelystvo Sovetskaya Nauka* 4: 138; fig. 76, 3 (1951). — *Ceratoneis recta* (Skvortzow & Meyer) Iwahashi, *Journal of Japanese Botany* 12: 391 (1936). — *Ceratoneis arcus* f. *recta* (Skvortzow) Poretsky in Poretsky & Sheshukova, *Leningrad State University*: 145-146; fig. 3 (1953). — *Ceratoneis arcus* subsp. *recta* (Skvortzow) Skabichevskii, *Trudy Limnologicheskogo Instituta* 2: 52; fig. a, b (1963).

LOCALITY. — Lake Baikal.

Hannaea subarcus (Iwahashi) Q. Liu, Glushchenko, Kulikovskiy & Kociolek, comb. nov., stat. nov.

Ceratoneis recta f. *subarcus* Y. Iwahashi, *Journal of Japanese Botany* 12: 391, text fig. 1, d-f (1936). — *Hannaea arcus* var. *subarcus* (Iwahashi) Lee in Lee *et al. The Japanese Journal of Diatomology* 7: 50, pl. 2: fig. 34 (1992).

LOCALITY. — Western Japan.

Hannaea hattoriana (Meister) Q. Liu, Glushchenko, Kulikovskiy & Kociolek, comb. nov., stat. nov.

Ceratoneis arcus var. *hattoriana* Meister, *Archiv für Hydrobiologie und Planktonkunde, Stuttgart* 9: 226, pl. 8, fig. 1-3 (1914). — *Hannaea arcus* var. *hattoriana* (Meister) Ohtsuka, *The Japanese Journal of Diatomology*. 18: p. 35; figs. 100, 101 (2002).

LOCALITY. — Japan.

DISCUSSION

The species treated here would seem to be best placed in the genus *Hannaea*. *Hannaea tibetiana* Q. Liu, Glushchenko, Kulikovskiy & Kociolek, sp. nov. also differs from many of the more commonly-reported species by having most valves without a tumid area on the concave margin, and the small, capitate, bent apices, especially distinct in smaller cells. However, in almost all other aspects of the valve ultrastructure, this species resembles the generitype and others in the genus whose ultrastructure has been documented (Bixby & Jahn 2005).

In the case of *H. pamirensis* Glushchenko, Kulikovskiy, Q.Liu & Kociolek, sp. nov., described from the Pamir Mountains, the nearly straight valves are quite different in outline from the most commonly reported species, *H. arcus*, though there are many taxa that are straight or nearly straight from Asia (see Table 1). We found *Hannaea pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. in samples together with *H. arcus*. The straight shape of valves of *H. pamirensis* Glushchenko, Kulikovskiy, Q.Liu & Kociolek, sp. nov. is also known for such species as *H. hattoriana* comb. nov., stat. nov., *H. inaequidentata* (Lagerstedt) Genkal & Kharitonov, *H. recta* comb. nov., stat. nov. and *H. subarcus* comb. nov., stat. nov. (Table 1). *Hannaea pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. differs from *H. hattoriana* comb. nov., stat. nov. by having less cuneate valves towards to the valve ends, from *H. recta* comb. nov, stat. nov. by having more curved valves and evidently wider valves (4.2-6.0 µm in *Hannaea recta* comb. nov., stat. nov. and 5.5-7.0 µm in *Hannaea pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov.) and a higher number of striae in 10 µm (15-16 in *Hannaea recta* comb. nov., stat. nov. and 16.5-18.0 in *Hannaea pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov.).

Hannaea pamirensis Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. differs from *H. subarcus* comb. nov., stat. nov. by having a greater number of striae in 10 µm (16.5-18.0 in *Hannaea pamirensis* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. and 14 in *H. subarcus* comb. nov., stat. nov.). Our new species differs from *H. inaequidentata* by having the unornamented tumid area on one side of the center of the valve and valves that are more highly arched. In *H. inaequidentata* the tumid area is larger and, in many valves, extends to both sides of the valves.

H. mongolica Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. is similar to *H. baicalensis* and *H. hovsgolensis* on the basis of valve shape, presence of biseriate striae, and by having two rimoportula, one on each end of the valves. *H. mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. differ from two species mentioned above by shorter valves and shape. Our new species is characterized by having fewer striae in 10 µm (17-18 in *H. mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. and 16-20 in *H. hovsgolensis*). Our new species is distinguished from *H. arcus* by having biseriate striae and two rimoportulae, one on each valve end.

H. dorofeyukae Kulikovskiy, Glushchenko, Q.Liu & Kociolek, sp. nov. differs from *H. mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. by its slimmer valves, ends curved to dorsal side, and by the presence of uniseriate-biseriate striae, not strongly biseriate striae, like in *H. mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, and the absence of ghost striae in its unilaterally-expanded central area. *Hannaea dorofeyukae* Kulikovskiy, Glushchenko, Q. Liu & Kociolek, sp. nov. differs from *H. hovsgolensis* by its shorter valves and differing shape of valves.

Based on the data currently available about the genus (Kociolek *et al.* 2018; Guiry & Guiry 2018), and the treatment of the new species and new combinations proposed herein (see below), *Hannaea* is comprised of nearly 15 taxa, though there are many taxa (> 100; Kociolek *et al.* 2018) residing in the genus *Ceratoneis* Ehrenberg that may ultimately belong in *Hannaea*.

The morphological variation in the genus is interesting, and two distinct groups can be identified. One group has uniseriate striae and a single rimoportula located at one apex. This includes the generitype of the genus, *H. arcus*, (Round *et al.* 1990), as well as most other species (Bixby *et al.* 2005). The other group has biseriate striae and two rimoportula, one located at each apex (*H. baicalensis*, *H. dorofeyukae* Kulikovskiy, Glushchenko, Q.Liu & Kociolek, sp. nov., *H. hovsgolensis* and *H. mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov., see Table 1). These members of the genus are found only in Lakes Baikal and Khövsgöl as well as some smaller lakes of Mongolia. Further research might suggest

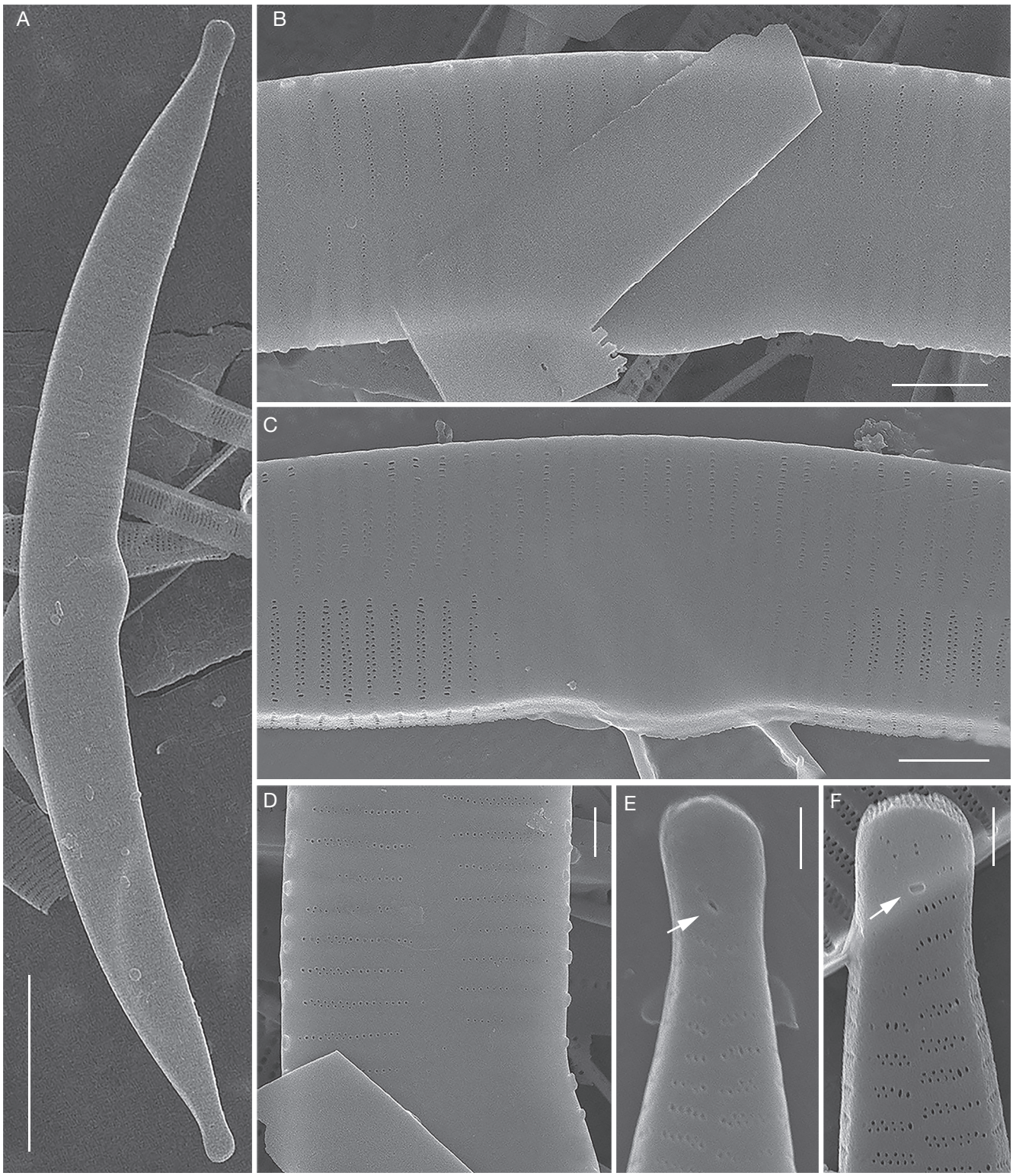

Fig. 13. — *Hannaea dorofeyukae* Kulikovskiy, Glushchenko, Q. Liu & Kociolek, sp. nov. SEM. External views. **White arrows** show the opening of the rimoportulae. Scale bars: A, 10 µm; B, C, 2 µm; D-F, 1 µm.

these morphological groups are worthy of being recognized as independent genera.

Most of discussed species, excluding *H. superiorensis*, *H. linearis*, *H. inaequidentata* and *H. arcus*, are known only from Asia (Tajikistan, China, Japan, Asian part of Russia). *Hannaea tibetiana* Q. Liu, Glushchenko, Kulikovskiy & Kociolek, sp. nov. and *H. pamirensis* Glushchenko, Kulikovskiy, Q.Liu & Kociolek, sp. nov. are known just from their type localities.

TABLE 1. — Differences between species of the genus *Hannaea*.

Species	Valve shape	Valve length (µm)	Valve width (µm)	Number of striae in 10 µm	Number of rimoportula	Distribution	References
Hannaea arcus (Ehrenberg) Patrick in Patrick & Reimer 1966 Basionym: *Navicula arcus* Ehrenberg, 1836	arcuate	15-177	4-10	12-18 uniseriate	1	Holarctic	Patrick & Reimer 1966 Bixby & Jahn 2005 Levkov *et al.* 2007 Genkal & Kharitonov 2008 Genkal *et al.* 2011 Kharitonov & Genkal 2012 Genkal *et al.* 2013 Kulikovskiy *et al.* 2016
Hannaea baicalensis Genkal, Popovskaya & Kulikovskiy, 2008	arcuate	(22) 43-182.3	(4.8) 5.8-14.7	11-18 biseriate	2	Russia: Baikal Lake Angara River Bratsk Reservoir Balan-Tamur Lake	Genkal *et al.* 2008 Vishnyakov *et al.* 2015
Hannaea chilensis (Krasske) Kulikovskiy 2008 Basionym: *Ceratoneis chilensis* Krasske, 1939 Synonym: *Fragillaria chilensis* (Krasske) Lange-Bertalot in Lange-Bertalot *et al.,* 1996	arcuate	17-21	2-3	20	No data	South Chile	Krasske 1939 Lange-Bertalot *et al.* 1996 Kulikovskiy 2008
Hannaea dorofeyukae Kulikovskiy, Glushchenko, Liu & Kociolek sp. nov.	arcuate	45-91	6-7	uniseriate, biseriate 14-16	2	Mongolia: Sum Gol River, Khövsgöl Lake	This paper
Hannaea hattoriana (Meister) Liu, Glushchenko, Kulikovskiy & Kociolek, comb. nov., stat. nov. Basionym: *Ceratoneis arcus* var. *hattoriana* Meister, 1914 Synonym: *Hannaea arcus* var. *hattoriana* (Meister) Ohtsuka, 2002	slightly arcuate to almost linear	40-85	6-7	13-14	No data	Japan	Meister 1914 Ohtsuka 2002
Hannaea hovsgolensis Vishnjakov, Kulikovskiy & Genkal in Vishnyakov *et al*., 2015	arcuate	87.3-158.5	5.9-7.6	16-20.5 biseriate, rarely uniseriate	2	Khövsgöl Lake	Vishnyakov *et al.* 2015 Kulikovskiy *et al.* 2016
Hannaea inaequidentata (Lagerstedt) Genkal & Kharitonov, 2008 Basionym: *Fragilaria aequalis* var. *inaequidentata* Lagerstedt, 1873	linear	32-128	4-8.6	12-18 uniseriate	1, rarely 2	Russia: Elgygytgyn Lake; Europe: Norway, Sweden, Finland; Asia: Mongolia	Genkal & Kharitonov 2008 Kulikovskiy *et al.* 2016
Hannaea linearis (Holmboe) Álvarez-Blanco & S. Blanco, 2013 Basionym: *Ceratoneis arcus* f. *linearis* Holmboe, 1899	arcuate	81.9-137.3	5.3-5.4	15-16 uniseriate	1	Sweden	Álvarez-Blanco & S. Blanco 2013
Hannaea mongolica Glushchenko, Kulikovskiy, Liu, Kociolek, sp. nov.	arcuate	50.5-93.5	6.5-8	17-18 biseriate	2	Mongolia: Tuul River, Herlen River (as *Hannaea* (? nov. spec. in Metzeltin et al 2009: Pl. 9, figs 1-8); Terkhiin Tsagaan Lake	This paper
Hannaea orientalis (Skuja) Liu, Glushchenko, Kulikovskiy & Kociolek, comb. nov., stat. nov. Basionym: *Ceratoneis arcus* var. *orientalis* Skuja, 1937	slightly arcuate	25-86	5.5-8	15-17	No data	Southwestern China	Skuja 1937
Hannaea recta (Skvortzow & Meyer) Liu, Glushchenko, Kulikovskiy & Kociolek, comb. nov, stat. nov. Basionym: *Ceratoneis amphioxys* var. *recta* Skvortzow & Meyer, 1928	linear	37.4-61	4.2-6	15-16	No data	Russia: Baikal Lake	Skvortzow & Meyer 1928
Hannaea subarcus (Iwahashi) Liu, Glushchenko, Kulikovskiy & Kociolek, comb. nov, stat. nov. Basionym: *Ceratoneis recta* f. *subarcus* Iwahashi, 1936	slightly arcuate to almost linear	30-74	5-8	14	No data	Western Japan	Iwahashi 1936
Hannaea superiorensis Bixby & Edlund in Bixby, Edlund & Stroemer, 2005	arcuate	111.8-170.2	4.97-8	10.3-15.1 uniseriate	1	USA: Superior Lake	Bixby *et al.* 2005
Hannaea pamirensis Glushchenko, Kulikovskiy, Liu, Kociolek, sp. nov.	linear	42-75	5.5-7	16.5-18 uniseriate	1	Tajikistan: Pamir	This paper

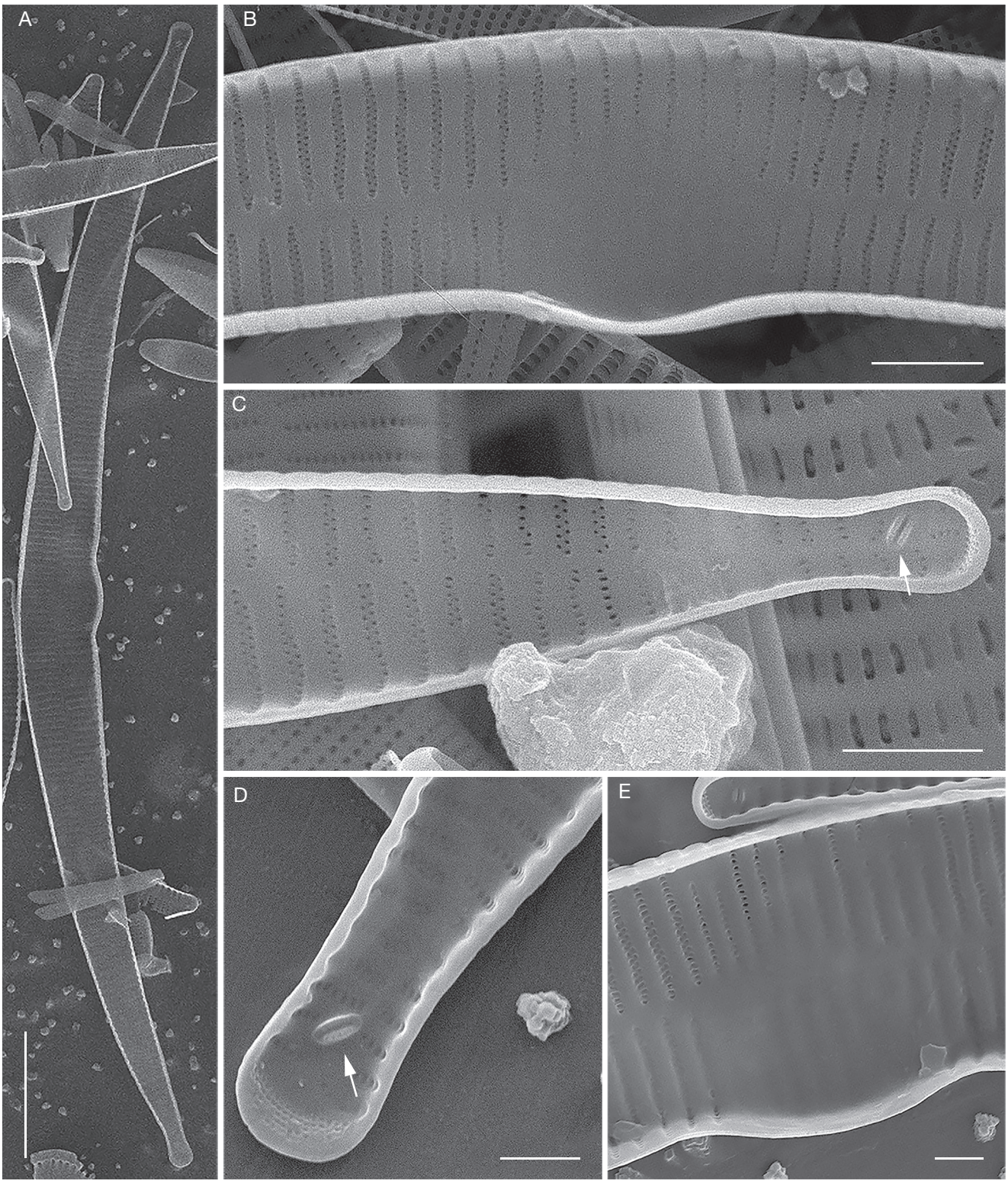

Fig. 14. — *Hannaea dorofeyukae* Kulikovskiy, Glushchenko, Q. Liu & Kociolek, sp. nov. SEM. Internal views. **White arrows** show the rimoportulae. Scale bars: A, 10 µm; B, C, 2 µm; D, E, 1 µm.

H. mongolica Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. and *H. dorofeyukae* Kulikovskiy, Glushchenko, Q.Liu & Kociolek, sp. nov. are known from some several distinct ecosystems in Mongolia. For example, *H. mongolica* Glushchenko, Kulikovskiy, Q. Liu & Kociolek, sp. nov. was identified from two rivers in Mongolia as "*Hannaea* ?nov. spec." (Metzeltin *et al.* 2009: pl. 9, figs 1-8). Many of the species of the genus are known from Asia, and one of the subgroups of the genus is only known from this continent. Asia harbors more endemic genera of freshwater diatoms

than all other continents combined (Kociolek 2019). It is possible that genera such as *Hannaea*, which collectively is known worldwide, may have its greatest diversity from Asia, reflecting the importance of this area to our knowledge of freshwater diatom phylogeny ad biogeography.

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