

***Caelestium* (Polygonaceae, Polygoneae), evidence based on morphology**

***Caelestium* (Polygonaceae, Polygoneae): морфологические основания**

O. V. Yurtseva¹, G. A. Lazkov²,
U. A. Ukrainskaja³, A. G. Deviatov¹

¹ Lomonosov Moscow State University
Faculty of Biology, Department of Higher Plants
Leninskiye Gory, 1, Bld. 12, Moscow, 119234, Russia
olgayurtseva@yandex.ru

² Institute for Biology and Pedology, National Academy of
Sciences of the Kyrgyz Republic
Laboratory of Flora
Chui Ave., 265, Bishkek, 720071, Kyrgyz Republic

³ Lomonosov Moscow State University
Faculty of Biology, Botanical Garden
Leninskiye Gory, 1, Bld. 12, Moscow, 119234, Russia

О. В. Юрцева¹, Г. А. Лазьков²,
У. А. Украинская³, А. Г. Девятков¹

¹ Московский государственный университет имени
М. В. Ломоносова
Биологический факультет, кафедра высших растений
Ленинские горы, 1, стр. 12, Москва, 119234, Россия
olgayurtseva@yandex.ru

² Биолого-почвенный институт Национальной академии наук
Кыргызской Республики, Лаборатория флоры
пр. Чуй, 265, Бишкек, 720071, Кыргызская Республика

³ Московский государственный университет имени
М. В. Ломоносова
Биологический факультет, Ботанический сад
Ленинские горы, 1, стр. 12, Москва, 119234, Россия

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Abstract. Morphological characters and fruit anatomy were analysed for distinguishing the new genus *Caelestium*, containing *C. lazkovii* (= *Bactria lazkovii*), endemic of the Central Tien Shan (Kyrgyzstan), and *C. tianschanicum* (= *Polygonum tianschanicum*), endemic of the Eastern Tien Shan (Xinjiang, China), from the genus *Bactria* in its updated circumscription, now containing only *B. ovczinnikovii*, endemic of the Pamir (Tajikistan). The genus *Caelestium* was established based on the results of molecular analyses and the details of the secondary structure of pre-rRNA of the ITS1 and ITS2 loci, but its morphology is poorly known. The morphological characteristics of *Bactria* and *Caelestium* were compared, and the anatomy of fruit was examined for these taxa and some species of *Persepolium* and *Atraphaxis*. *Caelestium lazkovii* and *C. tianschanicum* share the morphology of their leaf blades, perianth, fruits and styles, but differ in the color of annual shoots, the size of the perianth and fruits. They resemble *Bactria ovczinnikovii* in their life form, morphology of shoots, ochreas, inflorescences, and sporoderm ornamentation, but differ from the latter in the shape of leaf blades, fruits, and styles, micromorphology of tepals, and exocarp structure. SEM and LM images illustrating morphological characters are provided. The geographic ranges of the taxa are presented on the distribution map. Morphological characteristics distinguishing *Caelestium* and *Bactria* from *Atraphaxis*, *Persepolium*, and *Polygonum* are discussed.

Keywords: *Polygoneae*, *Atraphaxis*, *Bactria*, *Caelestium*, *Persepolium*, *Polygonum*, taxonomy, new genus, flower morphology, pollen, fruit anatomy.

Аннотация. Проанализированы морфологические признаки и анатомия плода для различения нового рода *Caelestium*, содержащего два локальных эндемика, *C. lazkovii* (= *Bactria lazkovii*) из Центрального Тянь-Шаня (Кыргызстан) и *C. tianschanicum* (= *Polygonum tianschanicum*) из Восточного Тянь-Шаня (Синьцзян, Китай), от рода *Bactria* в его обновленном объеме, эндемичного для Памира (Таджикистан) и в настоящее время включающего только *B. ovczinnikovii*. Род *Caelestium* был установлен на основании результатов молекулярного анализа и деталей вторичной структуры пре-рРНК локусов ITS1 и ITS2, но его морфология практически не изучена. Сопоставлены морфологические характеристики *Bactria* и *Caelestium*, исследована анатомия плода для этих таксонов и некоторых видов *Persepolium* и *Atraphaxis*. *Caelestium lazkovii* и *C. tianschanicum* имеют сходную морфологию листьев, околоцветника, плодов и стилодиев, но отличаются по окраске однолетних побегов, размеру околоцветника и плодов. Они напоминают *Bactria ovczinnikovii* своей жизненной формой, морфологией побегов, раструбов, соцветий и орнаментацией спородермы, но отличаются от последнего формой листьев, плодов и стилодиев, микроморфологией листочков околоцветника и структурой экзокарпия. Предоставлены SEM и LM изображения, иллюстрирующие морфологические признаки. Географическое распространение таксонов показано на карте. Обсуждаются морфологические особенности, отличающие *Caelestium* и *Bactria* от *Atraphaxis*, *Persepolium* и *Polygonum*.

Ключевые слова: *Polygoneae*, *Atraphaxis*, *Bactria*, *Caelestium*, *Persepolium*, *Polygonum*, систематика, новый род, морфология цветка, анатомия плода, пыльца.

The recent Maximum Likelihood and Bayesian analyses of the combined regions of the plastid genome and the ITS regions of nrDNA for 58 species of tribe *Polygoneae* (Yurtseva, Mavrodiev, 2019, in this issue) have shown a monophyly of *Bactria* Yurtseva et Mavrodiev in the plastid trees. In the ITS-based trees, the clade, which combines *Bactria lazkovii* Yurtseva et Mavrodiev (Yurtseva et al., 2016: 43) and *Polygonum tianschanicum* Chang Y. Yang (Yang, 1983: 55; 2010), showed a separate position from *Bactria ovczinnikovii* (Czuckav.) Yurtseva et Mavrodiev (Yurtseva et al., 2016: 43), and also from the rest genera of *Polygoneae*. Based on the results of molecular analyses, the details of the secondary structure of pre-rRNA of the ITS1 and ITS2 loci, fine morphological distinctions, and distributional data, the genus *Caelestium* Yurtseva et Mavrodiev was established to include *Bactria lazkovii* from the Central Tien Shan, Kyrgyzstan, and *Polygonum tianschanicum* from the Eastern Tien Shan, Xinjiang, China (Yurtseva, Mavrodiev, 2019, in this issue). The morphology of these rare endemics is, however, poorly known.

In this study we aimed to perform a detailed comparative morphological analysis of *Bactria ovczinnikovii* and two representatives of *Caelestium*, and to find morphological differences between *Bactria*, *Caelestium* and related genera of tribe *Polygoneae*.

Originally, *Polygonum ovczinnikovii* Czuckav. (Czuckavina, 1962: 64) and *P. tianschanicum*, which is the earlier name for *P. popovii* Borodina (1989: 104), were described in the genus *Polygonum* L., and in the framework of the earlier taxonomic concept, both species were once placed in *Atraphaxis* L. as *A. ovczinnikovii* (Czuckav.) Yurtseva (Yurtseva et al., 2014: 763) and *A. popovii* (Borodina) Yurtseva (Yurtseva et al., 2014: 763). Thus, we paid special attention to the differences between *Bactria*, *Caelestium*, *Polygonum*, and *Atraphaxis*.

Recent molecular phylogenetic studies of *Polygonaceae* Juss. (Schuster et al., 2011; Tavakkoli et al., 2015; Yurtseva et al., 2016) revealed the difficulties with the taxonomic delimitation and diagnostic characters of the genera *Atraphaxis* and *Polygonum* in tribe *Polygoneae*. Generally, the most significant difference between *Atraphaxis* and *Polygonum* is the morphology of the perianth, which has five equal tepals in *Polygonum*, but two or three inner tepals enlarged in fruiting in *Atraphaxis* (Jaubert, Spach, 1844–1846; Meisner, 1857; Komarov, 1936; Brandbyge, 1993; Li et al., 2003). Part of *Polygonum* species, which have five equal-sized tepals and share the habit and striate-perforate sporoderm ornamentation with *Atraphaxis* (Yurtseva et al., 2014), were nested separately among the rest species of the clade *Atraphaxis* (Yurtseva et al., 2010; Schuster et al., 2011), so these species have been included in

Atraphaxis (Schuster et al., 2011). In contrast, *Persepolium* Yurtseva et Mavrodiev (Yurtseva et al., 2017: 185), which was originally described in *Polygonum* as *P. “§” Spinescentia* Boissier (1879: 1027) and later transferred to the widely circumscribed *Atraphaxis* emend. S. Tavakkoli as *Atraphaxis* section *Polygonoides* S. Tavakkoli, Kaz. Osaloo et Mozaff. in Tavakkoli et al. (2015: 1167), was established as a new genus sister to *Atraphaxis* in all molecular and morphological analyses (Yurtseva et al., 2016, 2017; Mavrodiev, Yurtseva, 2017). Comparing the morphological characteristics of *Caelestium* and *Bactria* with those of *Atraphaxis* and *Polygonum*, we involved *Persepolium* in consideration.

Materials and methods

This morphological study is based on the nomenclatural types and other reliably identified specimens of *Bactria ovczinnikovii*, *Caelestium lazkovii*, *C. tianschanicum*, *Persepolium salicornioides*, and *Atraphaxis* species deposited in the Herbaria of the Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg, Russia (LE) and Lomonosov Moscow State University, Moscow, Russia (MW). Appendix (see the journal's website: www.binran.ru/journals/novitates/) contains information on the origin of the material used in the study.

Light microscopy (LM) images of flowers and fruits were made with a stereoscopic microscope Stemi 2000-C Carl Zeiss using a camera AxioCam-MR and a program AxioVision LE 64, free edition. For scanning electron microscopy (SEM), dry material was transferred onto aluminum stubs, coated with gold or platinum and palladium using a JFC-1100E sputter coater, and studied under a scanning electronic microscope CamScan-S2 at 15–20 kV. SEM work was performed at the Electron Microscopy Laboratory of Faculty of Biology of the Lomonosov Moscow State University.

Perianth and fruit surface is described using the terminology by L.-P. Ronse Decraene and J. R. Akeroyd (1988), S.-P. Hong et al. (1998), and Ronse Decraene et al. (2000). Pollen morphology is described as suggested by W. Punt et al. (2007) and M. Hesse et al. (2009). The terminology of E. J. H. Corner (1976), W. Barthlott (1981), T. A. Fedotova (1991), and Ronse Decraene et al. (2000) is used to describe the anatomy and surface of the fruit.

A comparison of the morphological characteristics of *Polygonum*, *Atraphaxis* and *Persepolium* was performed using observations of herbarium specimens deposited in LE and MW. In addition, comprehensive observations from the following publications on *Polygoneae* were used: Ronse Decraene, Akeroyd (1988), Ronse Decraene, E. F. Smets (1991), Hong (1995),

Hong et al. (1998, 2005), O. V. Yurtseva et al. (2010, 2012a, b, 2014, 2016) for *Polygonum* and *Atraphaxis*; H.-F. C. Jaubert, E. Spach (1844–1846), E. Boissier (1879), C. F. Meisner (1857), H. Gross (1913), V. Mozaffarian (2012), A. R. Khosravi, S. Poormahdi (2008), S. Tavakkoli et al. (2015), Yurtseva et al. (2016, 2017) for *Persepolium*. For *Caelestium tianschanicum* (= *Polygonum tianschanicum*, *P. popovii*, *Atraphaxis popovii*), *C. lazkovii*, and *Bactria ovczinnikovii*, in addition to new observations, data from A. P. Czukavina (1962, 1968), C. Y. Yang (1983), A. E. Borodina (1989), and Yurtseva et al. (2014, 2016, 2017) were compared.

For anatomical studies, mature fruits were softened in alcohol : glycerol : water (1 : 1 : 1), cut in sections 10–20 μm thick, and stained with 0.1 % cresyl violet or processed with 0.1 % phloroglucinol and concentrated HCl. Fruit structure was studied in the middle part of the side and at the ribs. The cross sections of the exocarp cells were studied with a microscope Carl Zeiss Axioplan 2 using a camera AxioCam-MR and a program AxioVision LE 64 free edition.

A distribution map was constructed using herbarium specimens (LE, MW) and all known localities of *Bactria ovczinnikovii*, *Caelestium lazkovii*, and *C. tianschanicum* (Czukavina, 1962, 1968; Borodina, 1989).

Results

Morphological comparison of *Bactria* and *Caelestium*

Life form and shoots. All three species are divaricately branched dwarf shrubs 10–30(50) cm tall (Fig. 1) with second-year shoots ca. 3–5 mm diam., and branchlets departing under 45°, all covered with a fibrously disintegrated bark. Annual shoots are finely ribbed, 5–8(12) cm long and 1 mm diam. with widely spaced nodes, or 1–3 cm long, with congested nodes. Leaves are alternate, petiolate, articulated at the base. The annual shoots and leaf blades are covered with short pointed trichomes 30–120 μm long in *Bactria ovczinnikovii*, and 30–60 μm long in *Caelestium lazkovii* and *C. tianschanicum*. The trichomes are especially dense at the ribs of the shoot and at the bases of ochreas (Figs. 2: I–J; 3: A, B; 4: A–D; 5: E, G). The annual shoots of *Bactria ovczinnikovii* (Fig. 1: A) and *Caelestium tianschanicum* (Fig. 1: C, H) are greenish-gray or creamy. The second-year shoots have a pale-gray bark and a pinkish wood. *C. lazkovii* (Fig. 1: B) differs with foxy-brown annual shoots, a gray bark and a foxy-brown wood of the second-year shoots.

Thyrses. Terminal frondose or frondulose thyrses include 5–13 cymes of 2–3 flowers in the axils of developed leaf blades gradually reducing their size towards the top of the thyrses. In all the species, the lower cymes

are spaced by internodes 10 mm long, the upper internodes are reduced to 2–3 mm. Pedicels 0.5–1 mm long are hidden in ochreolas. The fruits of *Bactria ovczinnikovii* and *Caelestium lazkovii* are pendulous with bent pedicels, breaking off easily (Fig. 1: A–B). The flowers of *C. tianschanicum* have erect pedicels in flowering and fruiting (Figs. 1: C, G; 2: J).

Leaf blades. *Bactria ovczinnikovii* has glaucous, thick, ovate or broadly ovate leaf blades 5–7 $\times$ 3–6 mm with a rounded or shortly mucronate apex and a rotundate-cuneate base suddenly narrowed into a wide petiole 0.8–1 mm (Fig. 1: A; more in Yurtseva et al., 2016). The leaf blades are finely crenulate and slightly revolute at the margins, with a conspicuous midvein and two oblique lateral veins on the low side. Stomata are more numerous on the lower side. The both sides bear pointed trichomes 30–120 $\times$ 10 μm with a longitudinal striation, and are especially dense along the midvein below (Fig. 3: A, B).

Caelestium lazkovii (Fig. 1: B) and *C. tianschanicum* (Figs. 1: C; 2: G–I) share bright-green or dark-green, leathery, oblong-elliptical, oblanceolate, or spatulate leaf blades 7–10(15) $\times$ 2.5–3(5) mm with an obtuse or acuminate apex and a cuneate base gradually narrowed to the petiole 0.6–1 mm long. The leaf blades of *C. lazkovii* are 7–10 $\times$ 2.5–3 mm, revolute at the margins. *C. tianschanicum* has leaf blades 7–15 $\times$ 3–5 mm with flat smooth margins. In both species a conspicuous midvein is dilated to the petiole on the low side. The upper side of the leaf blade is almost glabrous. Rare trichomes 30–60 $\times$ 15–20 μm cover the petiole, the edges of the leaf blade and the midvein below (Figs. 4: F–H; 5: A–D). Stomata are especially numerous on the low side (Figs. 4: I; 5: C).

Ochreas and ochreolas. In all the species the ochreas are 2–4 mm long, oblique lanceolate-tubular, herbaceous, brownish and densely minutely puberulent at the base, above membranous, semitransparent, whitish, scarcely puberulent along the keel, later split in two lanceolate lacinulas, each with a single hardly visible vein (Figs. 4: A–E; 5: E, G). In thyrses, the ochreolas are 2–3 mm long, broadly ovate, funnel-shaped or cup-shaped, inflated under the petiole, greenish-brown, herbaceous, densely minutely puberulent at the base, above membranous, semitransparent, without veins, bilacinate or bidentate, with entire or dentate-incised margins (Fig. 2: A, J).

Perianth morphology. The perianth is divided in five equal-sized tepals, with a short tube (Figs. 1: D–F; 2: B–D, K; 3: D; 4: J–L; 5: F, H, I; 6: A). In *Bactria ovczinnikovii* and *Caelestium tianschanicum* the perianth is divided to $\frac{5}{6}$ – $\frac{9}{10}$, in *C. lazkovii* – to $\frac{4}{5}$ – $\frac{5}{6}$, not enclosing the mature fruit.



Fig. 1. Type material.

A — *Bactria ovczinnikovii*, fragment of the holotype (LE 01065511); B — *Caelestium lazkovii*, fragment of the holotype (MW0595509); C–F — *Caelestium tianschanicum*, fragments of the paratype of *Polygonum popovii* (LE 01013265); G, H — *Caelestium tianschanicum*, fragment of the holotype of *Polygonum popovii* (LE 01013264).

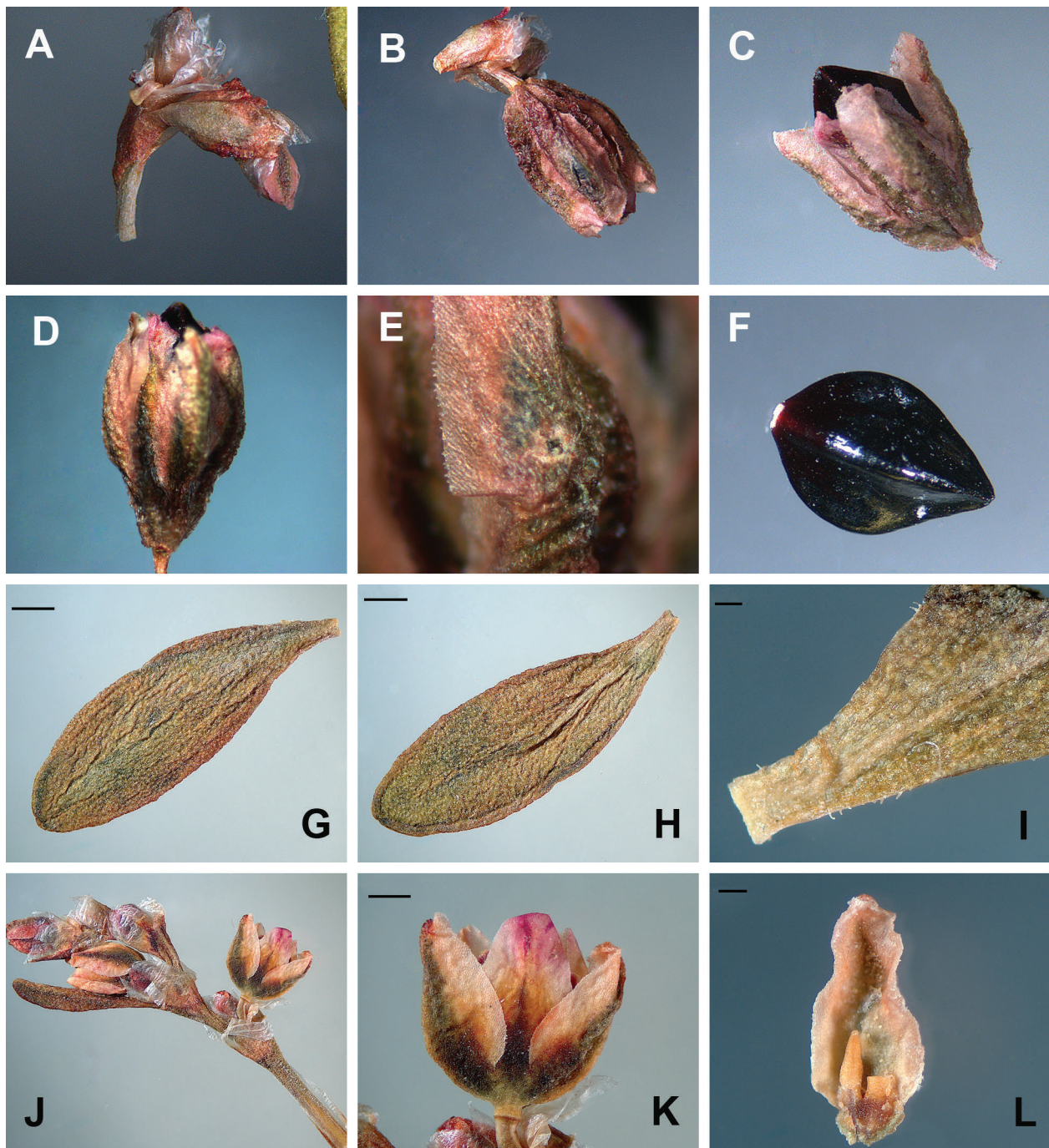


Fig. 2. Details of morphology of two species of *Caelestium*.

A–F: *Caelestium lazkovii*, holotype (MW0595509): A – axillary cyme with a pedicel and two flower buds; B–D – mature fruits in a perianth; E – fragment of the tepal with papillate edge; F – mature fruit.

G–L: *Caelestium tianschanicum*, paratype of *Polygonum popovii* (LE 01013265): G–I – leaf blade adaxially and abaxially; J – thyrses top; K – young flower; L – outer tepal with two filaments inside. Scale bars – 1 mm.

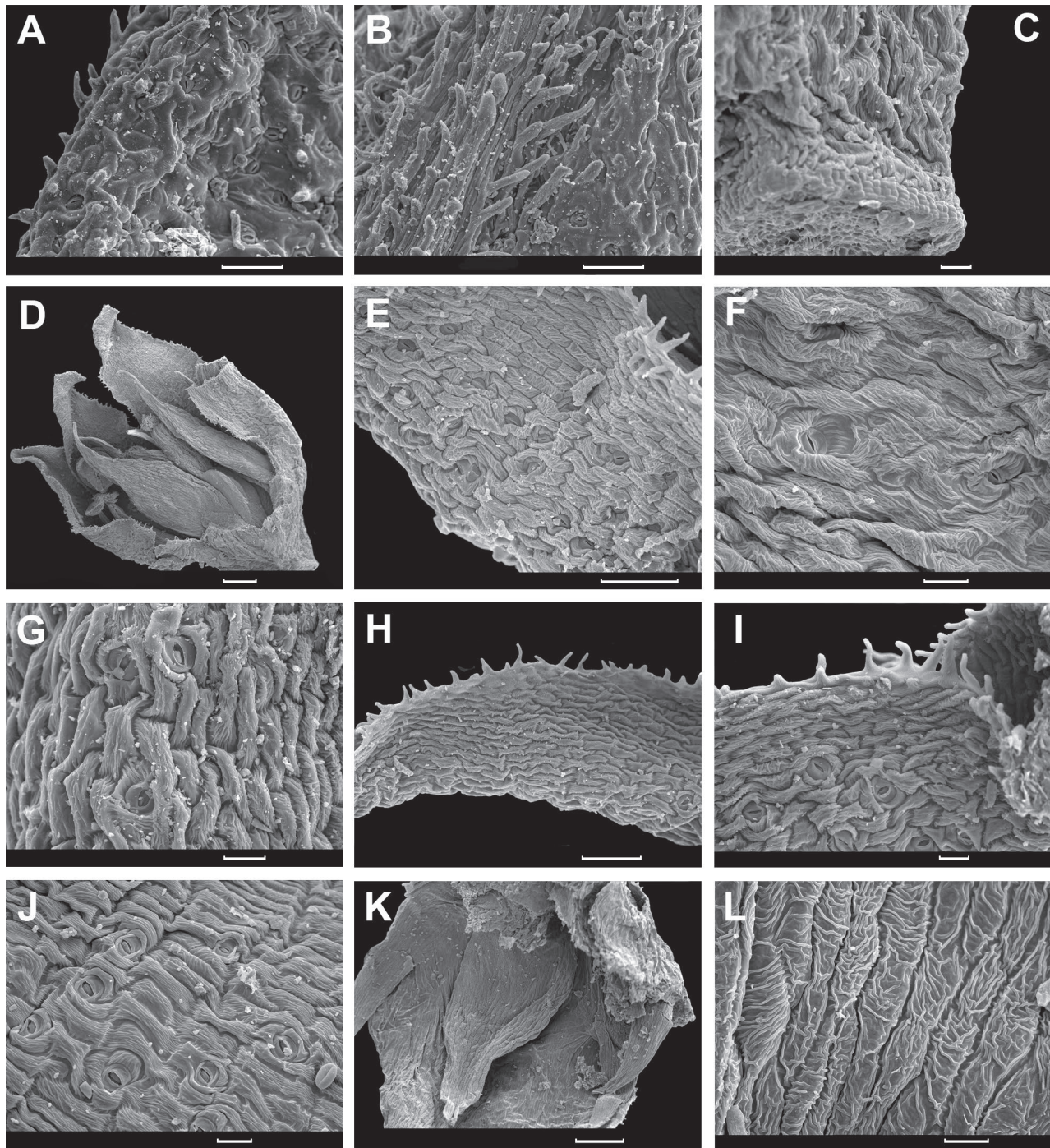


Fig. 3. SEM images of *Bactria ovczinnikovii* (Botschantzev, Egorova, № 814, LE).

A, B — leaf blade adaxially and abaxially; C — basal part of a perianth tube; D — young flower with dilated filaments inside; E, F — base of a tepal with stomata; G — a tepal from the outside; H, I — a tepal, side view; J — a tepal from inside; K — a perianth with filaments inside; L — filament surface. Scale bars: A, B, E, H — 100 µm; C, F, G, I, J, L — 30 µm; D, K — 300 µm.

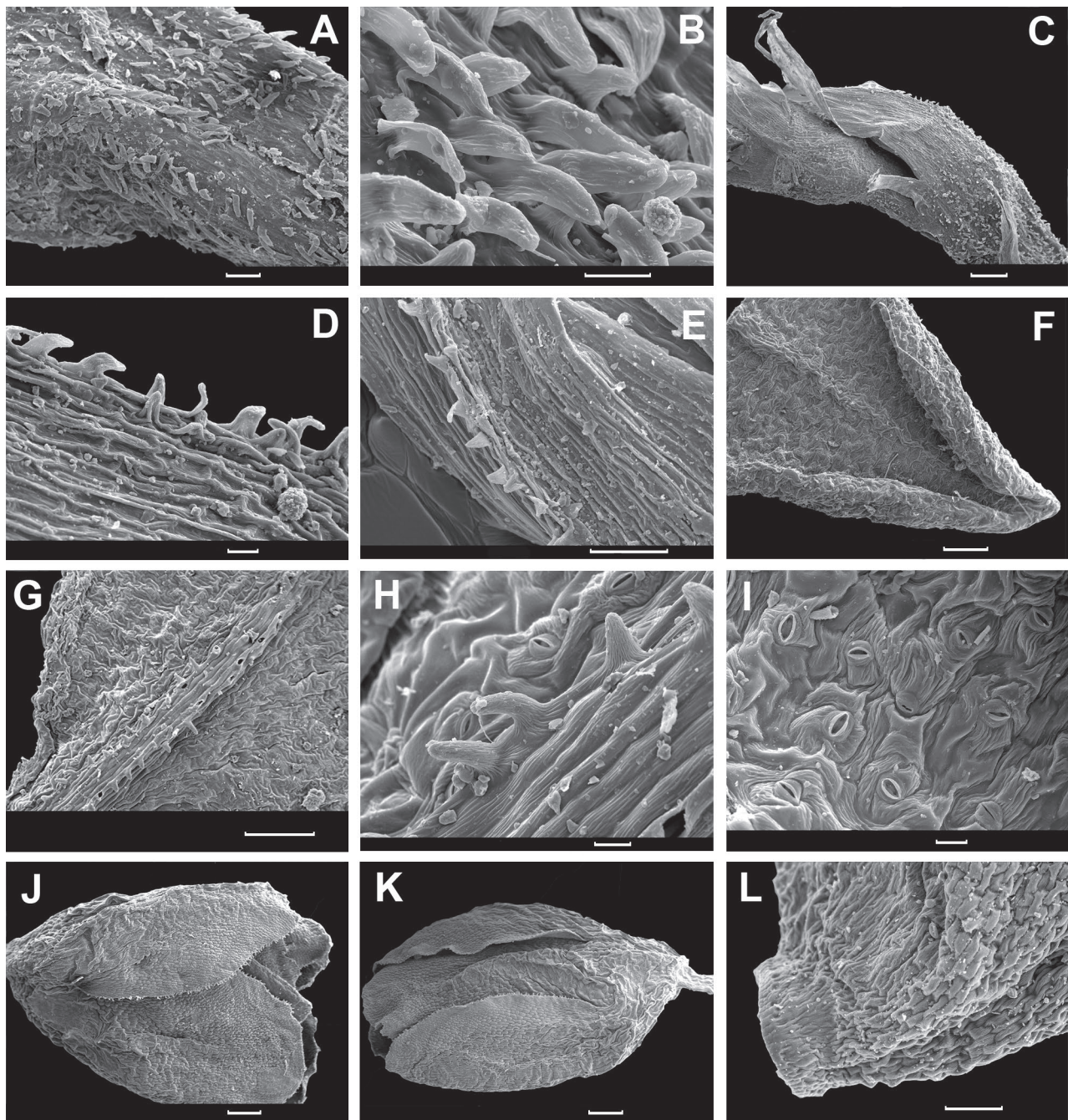


Fig. 4. SEM images of *Caelestium lazkovii* (MW0595509).

A — a puberulent annual shoot below the ochrea; B — trichomes at the ochrea base; C — a bilacerate ochrea puberulent at the base and along the keel; D, E — trichomes along the ochrea keel; F–I — fragments of abaxial leaf blade with trichomes along the midvein (G, H) and stomata (I); J–K — a young flower; L — a basal part of the perianth tube. Scale bars: A, E — 100 μm; B–D, H, I — 30 μm; C, F, G, J, K — 300 μm.

Bactria ovczinnikovii differs with lanceolate to ovate tepals $3-4 \times 1.2-1.7$ mm, all of them greenish-purple, rigid, leathery, with a narrow petaloid pinkish margin, which bear papillae inserted at the edge (Fig. 3: H, I). The outer tepals are slightly acuminate, cucullate, with narrow keels (Fig. 3: D), the inner tepals are almost flat. The tube is funnel-shaped, 0.5–0.9 mm, gradually narrowed to a filiform basal part 0.1–0.18 mm long (Fig. 3: C).

Caelestium lazkovii and *C. tianschanicum* share broadly elliptical to broadly ovate tepals $2-3.3 \times 1.2-1.7$ mm (Figs. 2: B–E, J–L; 4: J, K; 5: H, I), flat, greenish-purple along the midveins, with wide petaloid white-pinkish margins and papillate at the edges (Figs. 2: E, K; 4: J, K; 5: L; 6: C, G, H; 7: A; 8: A, B). The tepals are obtuse in *C. lazkovii*, obtuse or slightly acuminate in *C. tianschanicum*. The perianth tube is widely cup-shaped or sacciform, 0.5–0.7 mm long in *C. tianschanicum*, 0.5–0.9 mm in *Bactria lazkovii*, suddenly narrowed into a short filiform basal part 0.1–0.13 mm long.

Perianth surface. The tepals of *Bactria ovczinnikovii* are covered abaxially with elongate-rectangular epidermal cells with straight anticlinal walls and flat outer periclinal walls, the latter with a fine oblique, longitudinal, or random cuticular striation (Fig. 3: E–I). The tube is covered with rectangular or 5–6-gonal epidermal cells with straight anticlinal walls and dome-shaped or flat outer periclinal walls, the latter with deep irregular cuticular striations (Fig. 3: C). Numerous stomata are randomly scattered across the outside of the tube and the tepals, but are absent from the narrow tepal margins (Fig. 3: E–I). The adaxial surface of the tepals is lined with elongate-rectangular or irregular epidermal cells with straight anticlinal walls and flat outer periclinal walls with a prominent longitudinal striation, the pavement cells are interspersed with stomata (Fig. 3: J). The perianth is glabrous outside and inside, but the cells of the tepal edges form papillae 25×35 μ m long, $(5)8 \times 11$ μ m diam. with a tightly pressed longitudinal striation (Fig. 3: H, I). These papillae resemble the trichomes which are present on the leaf blades, but are shorter.

In *Caelestium lazkovii* and *C. tianschanicum*, the epidermal cells covering the tube and the bases of the tepals externally are elongate-rectangular or irregular, with straight anticlinal walls and flat outer periclinal walls with a longitudinal striation (Figs. 4: L; 5: J; 6: A, B, D, E). On the tepal margins, the epidermal cells become strongly sinuate or undulate in outline (Figs. 5: K; 6: C, F–H; 8: A, B), their outer periclinal walls bear a random cuticular striation. Stomata are scattered across the abaxial side of the tepals along the midveins, but are absent from the wide petaloid margins (Figs. 5: K; 6: C,

G, H; 8: A, B). In contrast to *Bactria ovczinnikovii*, the stomata are absent from the inner surface of the tepals (Figs. 5: L; 6: I). Papillae 30–35(40) μ m long and 13–20(40) μ m diam. are inserted at the tepal edges (Figs. 5: L; 6: G, H; 8: A, B).

Receptacle and stamens. All three species have a hypanthium or receptacle formed by the bases of the tepals, and eight stamens in two whorls. The flattened bases of the filaments are inserted closer to the base of the receptacle and are slightly fused to it adaxially. The filaments of the five outer stamens are lanceolate-subulate, gradually dilated to the base, 1–1.2 mm long and are half the length of the tepals (Figs. 3: D, K; 7: A). The outer stamens are inserted higher than the inner stamens at the hypanthium (Figs. 3: K; 7: A). The inner stamens are 2–4 times wider and somewhat longer, 1.4–1.9 mm long, strongly expanded at $\frac{1}{3}$ of the basal part (Figs. 2: L; 3: D, K; 7: A; 8: C).

The inner surface of the perianth tube (that could be also interpreted as a concave receptacle) is lined below and around the bases of the filaments by rounded or polygonal nectar-secreting epidermal cells with smooth convex outer periclinal walls (Figs. 3: K; 7: B; 8: D). The filaments are covered with oblong-rectangular, almost linear epidermal cells with fine longitudinal or irregular cuticular striations, resembling the epidermis covering the adaxial sides of the tepals (Figs. 3: L; 7: C, D; 8: G). Only *Caelestium lazkovii* has broadly conical papillae 40–50 μ m long and 45–50 μ m diam. inserted laterally at the filaments of the three inner stamens (Fig. 7: D) and resembling the papillae inserted at the tepal edges (Fig. 6: G, H). The filaments of *C. tianschanicum* and *Bactria ovczinnikovii* have no papillae (Figs. 3: D, K; 8: C). The bases of the filaments of *Caelestium tianschanicum* are covered with elongate-rectangular smooth nectar-secreting cells (Fig. 8: E, F). All the species have orbiculate, dark-pink anthers.

Styles. The styles are partly fused at the base and terminated with small capitate stigmas in *Bactria ovczinnikovii* and free from the base and linear throughout the length in *Caelestium lazkovii* and *C. tianschanicum* (see also Yurtseva et al., 2016: 19, fig. 5; Yurtseva et al., 2017: 172, fig. 15: K).

Fruit morphology and surface. *Bactria ovczinnikovii* bears fruits in May – June, *Caelestium lazkovii* in July, and *C. tianschanicum* in July – August. The fruits are ovoid, trigonous, slightly exserted from the perianth, with almost winged distinct ribs and concave sides in *Bactria ovczinnikovii*, with obtuse ribs and flat sides in *Caelestium lazkovii* and *C. tianschanicum*. They are larger in *Bactria ovczinnikovii* ($4-5 \times 2.5-2.8$ mm), than in *Caelestium lazkovii* ($2-3 \times 2.5-2.8$ mm) and *C. tianschanicum* ($3-4 \times 2-3$ mm). The light-brown

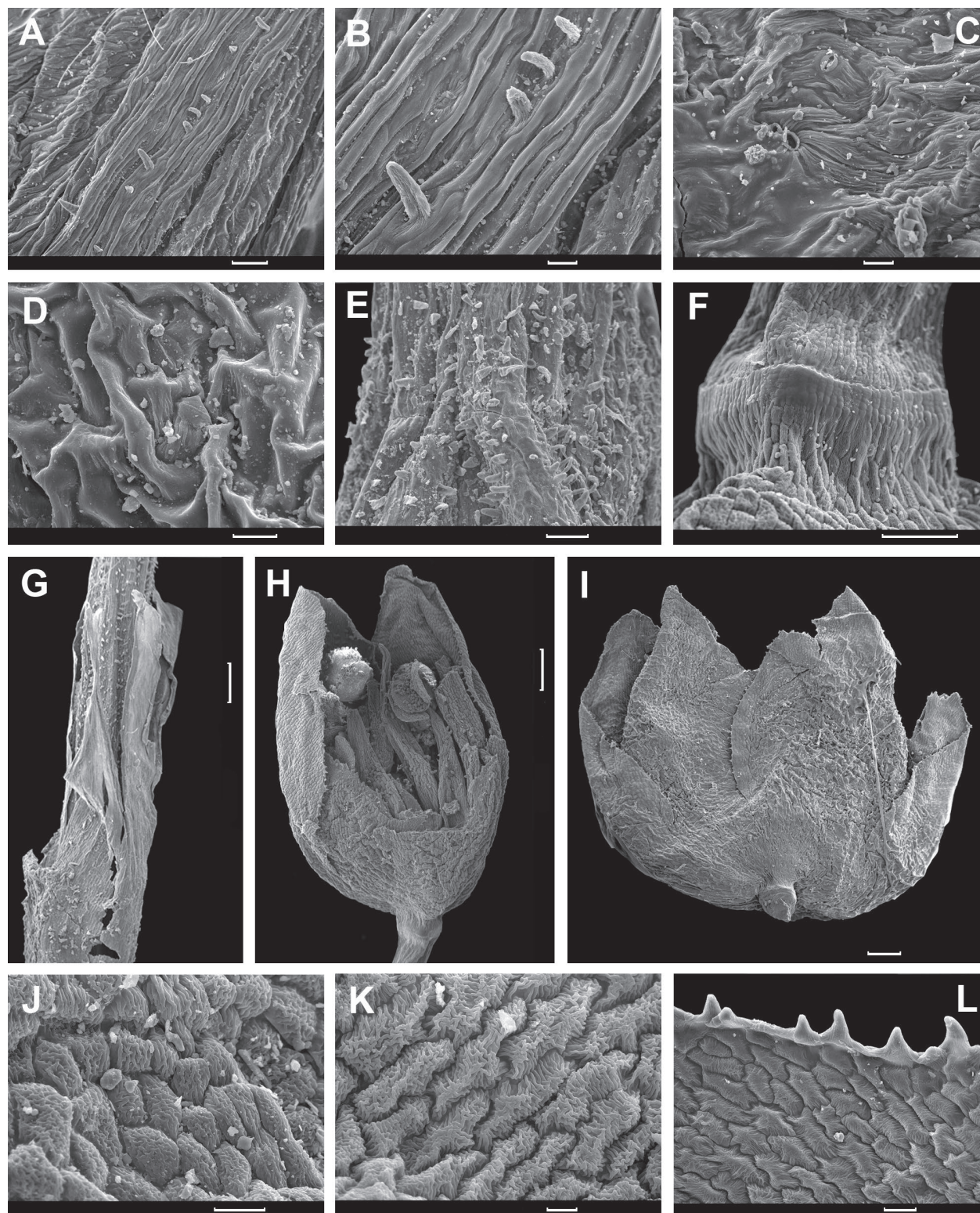


Fig. 5. SEM images of *Caelestium tianschanicum*, paratype of *Polygonum popovii* (LE 01013265).

A–C – fragment of the lower side of leaf blade with trichomes along the midvein (A–B) and stomata (C); D – fragment of the upper side of leaf blade; E – trichomes on an annual shoot; F – perianth tube jointed to a pedicel; G – tubular-bilacerate ochrea around an annual shoot; H, I – adaxial and abaxial view of the perianth; J, K – epidermis of perianth tube (J) and a tepal (K) abaxial side; L – epidermis of tepal margin on adaxial side. Scale bars: A, E, F – 100 µm; B–D, J–L – 30 µm; G–I – 300 µm.

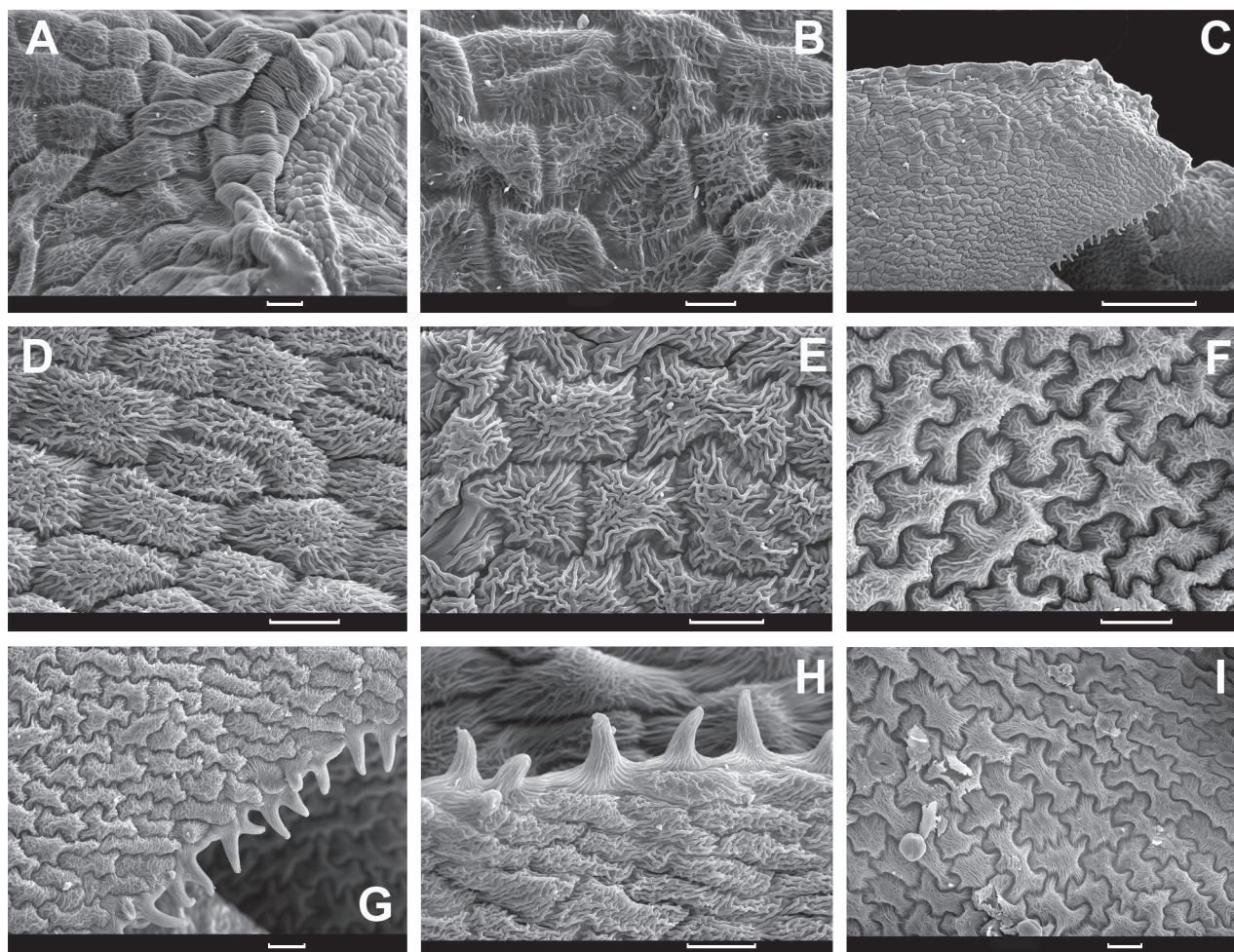


Fig. 6. SEM images of *Caelestium lazkovii* (MW0595509).

A – a perianth tube jointed to a pedicel; B, D – epidermis on the perianth tube outside; C – the top of the tepal with stomata and papillate edge, side view; E – epidermis on the tepal base outside; F – epidermis on the tepal edge outside; G, H – papillae at the tepal edge outside; I – epidermis covering the tepal inside. Scale bars: A, B, D–I – 30 μm ; C – 300 μm .

color and finely rough fruit surface of *Bactria ovczinnikovii* contrasts to the dark-brown, almost black color and smooth glossy fruit surface of the species of *Caelestium* (Figs. 2: F; 7: E, F; 8: H, I; see also Yurtseva et al., 2016: 19: fig. 5; 20: fig. 6; Yursteva et al., 2017: 172, fig. 15: K).

Pericarp anatomy. In cross section, the shape of fruits is different (Fig. 9). The fruits of *Bactria ovczinnikovii* have distinct, almost winged ribs. The pericarp consists of one-layered exocarp, several layers of parenchymatous mesocarp and 1–2 layers of endocarp, the latter is obliterated in mature fruits (Fig. 9: A–C). The ribs are formed by expanded adjacent sides, so that the inverted exocarp layers are connected by several layers of mesocarp cells. In the ribs, below the fused sides, the mesocarp includes a vascular bundle consisting of a few phloem and xylem elements with annular and helical thickening. In cross section, most

of the pericarp height is represented by exocarp cells, which are higher in the ribs (Table 1).

In surface view, the exocarp cells of *Bactria ovczinnikovii* are strongly sinuate in outline, the lobes interdigitate (Fig. 7: J), that indicates a premature fruit. In cross section, the exocarp cells have almost straight anticlinal walls gradually thickening to the periphery. The lumen is rectangular, broadened across the height and branched in the outer periclinal wall (OPW) in several channels directed into the lobes on the surface (Fig. 9: A–C). The OPW strongly undulates, forming invaginations and protrusions. The adjacent protrusions merge, providing the thickening of the OPW, which has an irregular relief, is finely pitted and covered with a cuticle 1 μm thick on the surface. Vertical channels 1.6–4.5 μm diam. between the invaginations of the OPW end blindly near the surface (Fig. 9: B, C). The walls of the exocarp cells

Table 1. Characteristics of exocarp cells in *Bactria ovczinnikovii*, *Caelestium lazkovii*, and *Persepolium salicornioides*

Characters	<i>Caelestium lazkovii</i>		<i>Bactria ovczinnikovii</i>		<i>Persepolium salicornioides</i>	
	In side	In rib	In side	In rib	In side	In rib
Pericarp height, μm	80–90	100–125	54–65	62–70	85–95	66–75
Exocarp cells height, μm	58–69	75–83	43–54	54–63	53–60	54–56
Exocarp cells width, μm	20–52	18–19	25–29	12–21	55–73	28–39
Anticlinal walls width in the middle, μm	8–17	7–9	5–6.5	2.9–3.3	8–11	8–10
Outer periclinal wall, thick, μm	18–28	17–24	6.5–13	4.1–8.2	17–21	12–17
Diameter of lumen at base, μm	17–30	17–18	16–25	8.3–12.5	46–60	17–21
Diameter of lumen before branching, μm	1.6–3.3	1.6–1.7	10–19	14–21	17–38	12–15
Diameter of channels in the OPW, μm	0.8–2	0.7–0.9	1.7–4.5	1.6–3.5	1.5–5.2	2–3.3
Cuticle thickness, μm	0.8–1	0.8–1.1	0.8–1	0.8–1	0.8–1.2	0.8–1.1
Color of exocarp walls	red-brown		colorless		colorless	
Color of lumina content	dark brown		light brown		light brown	

are colorless, the lumen is light-brown. The walls are lignified in the ribs, but not in the sides, that also characterizes a slightly premature fruit.

Caelestium lazkovii has the fruits with obtuse ribs and a thicker pericarp, but the exocarp has similar height and is higher in the ribs (Fig. 9: D–F; Table 1). In cross section, the anticlinal walls of the exocarp cells are straight, much thicker than in *Bactria ovczinnikovii*, the lumen is broaden at the base, above suddenly narrowed into a vertical channel, which is dendritically branched in the OPW into channels 0.7–2 μm diam. The OPWs are much thicker than in *B. ovczinnikovii*, the surface of the OPWs is smooth, covered with a cuticle. The walls are lignified, red-brown, the protoplast is dark-brown, that agrees with almost black color of the fruits.

The exocarp cells of *Bactria ovczinnikovii* and *Caelestium lazkovii* have similar size, but differ in the width of the anticlinal walls and OPWs, the shape and size of the lumen. These differences are due to a much stronger thickening of the anticlinal walls and OPWs of the exocarp cells in *C. lazkovii*, which leads to a significant decrease of the lumen size and its dendritic branching in the OPW in the latter.

We compared the exocarp of *Bactria ovczinnikovii* and *Caelestium lazkovii* with those of *Persepolium salicornioides* and some species of *Atraphaxis*. The fruits of *P. salicornioides* are similar to those of *Bactria ovczinnikovii* in the shape, concave sides and distinct ribs. In cross section, the exocarp cells (Fig. 9: G–I) are almost rectangular, much wider than in *Bactria* and *Caelestium*, with a vast trapezoidal lumen (Table 1). The anticlinal walls and OPWs are much thicker than in *Bactria ovczinnikovii* and comparable with those in *Caelestium*. Several channels 1.5–5.2 μm diam. go to the surface between the invaginations of the OPW, some of the chan-

nels enter the tubercles on the surface. The walls are colorless and lignified, the lumen is colored brown with phlobaphens. The cuticle is as thin as in *Caelestium* and *Bactria*.

Atraphaxis demonstrates a wide diversity of exocarp cells (in preparation) varying in: 1) the height; 2) the shape and thickness of the anticlinal walls across the height from strongly wavy to straight (Fig. 9: J–L); 3) the shape of the lumen from the trapezoidal, gradually narrowed outwards (Fig. 9: J, K), to the broadened at base and suddenly tapering into a vertical channel, dendritically branched in the OPW (Fig. 9: L); 4) in the color of the walls from colorless to intensely red-brown or purple. Some species have tubercles on the fruit surface (Fig. 9: J). Thus, the variants of exocarp cells found in *Bactria ovczinnikovii* and *Caelestium lazkovii* fall within the range of exocarp cells variability for *Atraphaxis*.

Pollen. *Bactria ovczinnikovii*, *Caelestium lazkovii*, and *C. tianschanicum* have spheroidal to oblong-spheroidal pollen grains $30\text{--}37 \times 18\text{--}23 \mu\text{m}$ (P/E = 1.2); tricolporate, elliptical, or almost circular in equatorial view, rounded-trilobed in polar view; colpi distinct, long and deep; ora distinct, lalongate or circular (Figs. 6: G, H, K; 8: J, K) (also in Yurtseva et al., 2014: 756, fig. 4: a–c, l, m, sub. *Atraphaxis ovczinnikovii* and *A. popovii*; Yurtseva et al., 2016: 34, fig. 19: A–B, K–L; Yurtseva et al., 2017: 175, fig. 17: F). Exine is tectate, ca. 1.7 μm thick. The sporoderm ornamentation is microreticulate-foveolate, foveolate, or foveolate-perforate (Figs. 6: I, L; 8: L). In *Bactria ovczinnikovii* and *Caelestium tianschanicum*, 4–6-angular pits 0.6–0.9 μm diam. are sharply outlined or gradually smooth at the edges and located at a distance 0.2–0.4 μm (Figs. 6: L; 8: L). *C. lazkovii* demonstrates a variability of sporo-

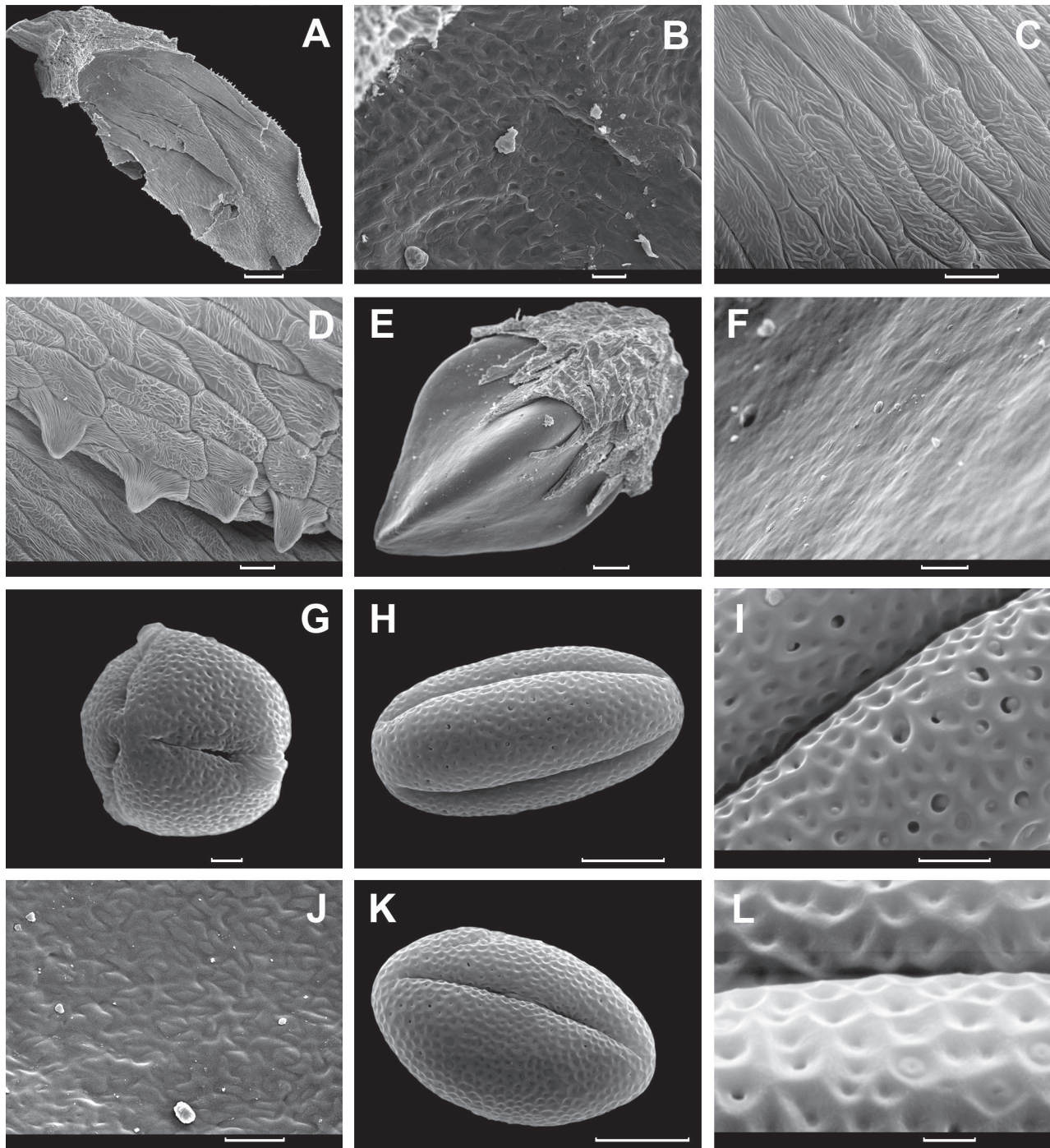


Fig. 7. SEM images of *Caelestium lazkovii* (MW0595509) (A–I) and *Bactria ovczinnikovii* (Botschantzev, Egorova, № 777, LE) (J–L).

A – fragment of the tepal adaxially with the filaments of inner and outer whorls; B – nectar-secreting zone of the receptacle; C – epidermis on the filament; D – fragment of the filament with papillae inserted laterally, against the inner tepal; E – mature fruit with the filaments; F, J – fruit surface; G, H, K – pollen grain, polar and equatorial view; I – foveolate-perforate sporoderm ornamentation; L – microreticulate-foveolate sporoderm ornamentation. Scale bars: A, E – 300 μ m; B–F, J – 30 μ m; H, K – 10 μ m; G, I – 3 μ m; L – 1 μ m.

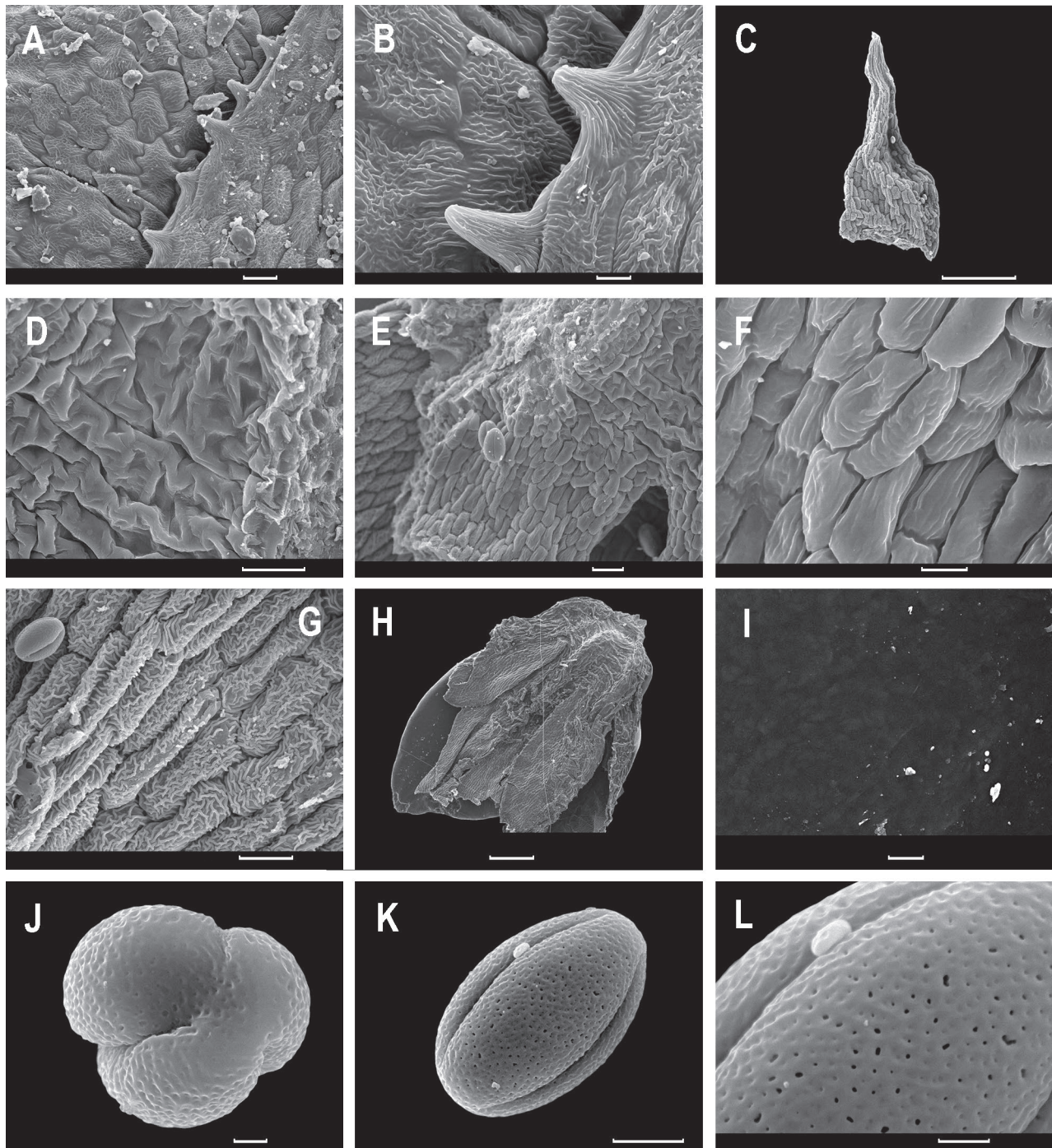


Fig. 8. SEM images of *Caelestium tianschanicum*, paratype of *Polygonum popovii* (LE 01013265).

A, B — papillae inserted in the tepal edge; C — the filament of the inner stamen; D — nectar-secreting zone of the receptacle; E, F — nectar-secreting cells covering the base of the filament; G — epidermis covering the middle part of the filament; H — fruit in the perianth; I — the fruit surface; J–L — pollen grains: polar view, equatorial view, microreticulate-foveolate sporoderm ornamentation. Scale bars: A, D, E, G — 30 μm ; B, F, K — 10 μm ; C — 300 μm ; H — 500 μm ; I — 20 μm ; J, L — 3 μm .

derm ornamentation in a single pollen sample, which varies from the microreticulate-foveolate type with the 4–6 angular pits peculiar for *Bactria ovczinnikovii* (Fig. 6: L), to the foveolate-perforate type 0.7–1.5 μm diam. (Fig. 6: I) with the rounded pits smooth at the edges and located at a distance 0.7–1.7 μm . Some pits bear perforations at the bottom. They are few and small (0.1–0.2 μm) in *B. ovczinnikovii* and *Caelestium tianschanicum*, but larger (0.1–0.8 μm) in *C. lazkovii*, single at the lumen, or rarely double.

Distribution and ecology of *Bactria* and *Caelestium*

Bactria ovczinnikovii is an endemic of the Southwestern Pamir (Tajikistan), but records from Afghanistan can be expected (Fig. 10). It grows on the right bank of the Pyandj River in the Dasti-Zhum Nature Reserve (Tajikistan, Khatlon Region, Shuroabad District), which flora contains more than 80 endemic plant species (Kasirov, 2006). This region is located at the western border of the Afgan-Tajik Depression and the Southwestern Pamir, which belongs to the Western Asian climatic region. This territory is characterized by warm semi-arid (mediterranean) climate (BSk, or cold steppe-desert climate by Köppen climate classification, in Kottek et al., 2006; Arnfield, 2016) with hot, dry summer, the lack of moisture in the soil, high evaporation and frequent winds from Afghanistan, which carry a lot of fine dust obstructing normal biological activity of plants. From March to May, the territory is sufficiently provided with water (Table 2), but plants suffer from a moisture deficit from June to October (Kasirov, 2006).

Bactria ovczinnikovii blossoms in May, bears fruits in June. It inhabits low ridges along the Pyandj River at the elevations 600–1900 m a. s. l., where it grows on the rocky and gravelly slopes, in the crevices or clefts of the rocks composed of red and gray sandstone (Fig. 11) (Czukavina, 1962, 1968). The habitats are located in the belt of forest-steppe (shibliak) formed by mesoxerophytic and xerophytic mesothermal deciduous low trees

and shrubs: *Pistacia vera* L., *Cercis griffithii* Boiss., *Rhus coriaria* L., *Calophaca grandiflora* Regel, *Acer regelia* Pax, *Ziziphus jujuba* Mill. and others, or in grass semisavannas (steppe) replacing the destroyed forest-steppe. The grass group includes ephemeric *Carex pachystylis* J. Gay, *Poa bulbosa* L., *Aegilops* sp., *Bromopsis turkestanica* (Drobow) Holub, *Elytrigia* sp. (Stanyukovich, 1982; Khalimov, Saidzoda, 2017).

Caelestium lazkovii is a local endemic of the Inner Tien Shan (Kyrgyzstan), where it was collected in a single location on the southern slopes of the Kavak-Toõ Ridge (total 4144 m), 5 km N of Sary-Bulun, at the elevation ca. 1500 m (Fig. 10). It is a petrophyte growing on the massive sheer cliffs of southern exposition, being sheltered in the crevices of granite rocks, but is absent from screes or circumdenudation mountains. The rocks are free of vegetation, except a few plants of mesophytic *Spiraea lasiocarpa* Kar. et Kir. *Caelestium lazkovii* blossoms and bears fruits in June – July.

Sary-Bulun has a moderate cold (boreal) climate (Dsb, snow climate with dry warm summer, by Köppen climate classification, in Kottek et al., 2006; Arnfield, 2016). Below 3200 m the snow cover is unstable (Table 2). According to the phytogeographical zonation by R. V. Kamelin (2002), this area belongs to the Kokomeren district of the Central Asian province, which is rich in endemic species. The Inner Tien Shan is a plateau with wide and flat valleys and elevated plains 2000–4000 m high. Up to the 1500–2000 m the dry inter-montane basin is occupied by Turan-Dzungar semi-shrub deserts and solanaceous semi-deserts, which predominate up to 2000 m and only at higher elevations (2000–2500 m) are replaced by forest-steppe and dry steppe (Murzaev, 1958).

Caelestium tianschanicum is an endemic of the southern macroslope of the Eastern Tien Shan (China, Xinjiang Uyghur Autonomous Region) (Fig. 10). It was collected on rocks and dry stony slopes in the environs of Balguntay, Korla, Karashar (Bayingholin Mongol

Table 2. Climatic characteristics of collection sites of *Bactria* and *Caelestium* (Climate-Data.org, Atlas..., 1987)

	Dasti-Zhum	Sary-Bulun	Ürümqi
Climate by Köppen classification (Kottek et al., 2006; Arnfield, 2016)	BSk, cold semi-arid steppe climate	Dsb, moderately cold (boreal)	BSk, cold semi-arid steppe climate
The average annual t°	+14 $^{\circ}\text{C}$	+7.5 $^{\circ}\text{C}$	+7 $^{\circ}\text{C}$
The average t° in January	+2.8 $^{\circ}\text{C}$	–8.2 $^{\circ}\text{C}$	–12.9 $^{\circ}\text{C}$
The average t° in July	+28.6 $^{\circ}\text{C}$	+21 $^{\circ}\text{C}$	+24.1 $^{\circ}\text{C}$
Annual precipitation	543 mm	455 mm	230 mm
Maximum precipitation	March – April	May – June	June – August
Drought period	June – August	July – September	June – September
Precipitation for summer	3 mm	91 mm	77 mm
Precipitation for the period with $t^{\circ} > 10^{\circ}\text{C}$	191 mm	254 mm	155 mm

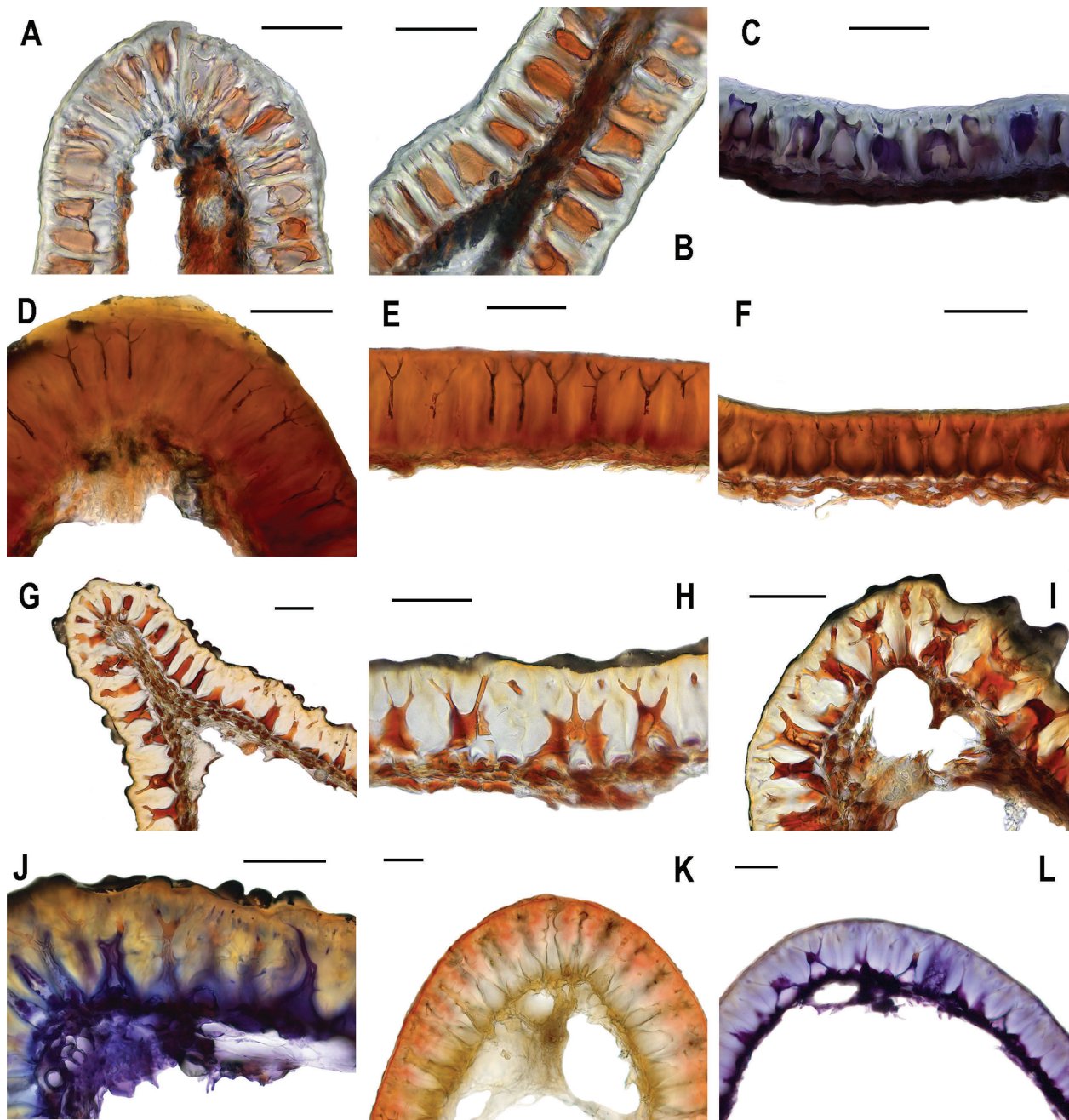


Fig. 9. Fruit anatomy of *Bactria ovczinnikovii* (A–C), *Caelestium lazkovii* (D–F), *Persepolium salicornioides* (G–I), *Atraphaxis toktogulica* (J), *A. kopetdagensis* (K), *A. pyrifolia* (L). Scale bars — 50 μm.



Fig. 10. Distribution of *Bactria ovczinnikovii* (●), *Caelestium lazkovii* (■), and *C. tianschanicum* (▲) based on material seen.

Autonomous prefecture), Kucha (Aksu prefecture), and Ürümqi (Ürümqi prefecture) at the elevations (1000)1400–2600 m (Li et al., 2003).

The Eastern Tien Shan has a semi-arid cold climate (BSk, or cold steppe climate by Köppen climate classification, in Kottek et al., 2006; Arnfield, 2016) with a very hot summer, frosty and snow-free winter. Annual precipitation totals 57 mm in Korla and Karashar, 76–117 in Kucha, 198–284 in Balguntay, 230–290 mm in Ürümqi, however, the elevated Central ridges of the Eastern Tien Shan get 400 and even 500 mm (Murzaev, 1966; Volkova, Rachkovskaya, 2009; Miao et al., 2012).

The southern macroslopes of the Eastern Tien Shan to the SW of Ürümqi at the elevations 1500–2400 m are occupied by mountain steppes with *Agropyron cristatum* (L.) Gaertn., *Koeleria cristata* (L.) Pers., *Artemisia frigida* Willd., which are the most probable habitats for *Caelestium tianschanicum*. The stony slopes at the elevations 1500–2600 m a. s. l. covered by *Caragana jubata* Poir., *Atraphaxis*, *Ephedra* L. are also suitable for it (Popov, 1931; Murzaev, 1966, Volkova, Rachkovskaya, 2009).

Discussion

Diagnostic characteristics which discriminate *Caelestium* from *Bactria*

Both species of the genus *Caelestium*, *C. lazkovii* and *C. tianschanicum*, share the morphology and micromorphology of leaf blades gradually tapering to the petiole and covered with trichomes. Both species have a perianth with five equal, broadly ovate to broadly elliptical petaloid tepals, which bear broadly conical papillae at

the tepal edges. Conical papillae inserted laterally into the filaments of the internal stamens of *C. lazkovii* resemble papillae inserted along the tepal edges, which is probably the result of the expression of the genes which are responsible for the petaloidy of tepals, in filaments (Ferrario et al., 2004; Theissen, Melzer, 2007). Similar examples of the homeotic conversion of epidermal cells along the filament edges were found in the petal-stamen intermediate organs of the AP2–5 mutants of *Arabidopsis thaliana* (L.) Heynh. (Kunst et al., 1989), or the mutant *gp* (*green petal*) of *Petunia* Juss. (Van der Krol, Chua, 1993; Van der Krol et al., 1993). Both species of *Caelestium* have broadly ovoid fruits with almost flat faces, obtuse ribs, and free linear styles.

Although both members of *Caelestium* are similar to *Bactria ovczinnikovii* in the shrubby habit, the morphology of shoots, inflorescences, ochreas, and the ornamentation of sporoderm, they differ from *Bactria* in the shape of leaf blades, the fruits with obtuse ribs and flat sides, in the structure of exocarp cells, the linear styles, the petaloid tepals bearing the papillae, which are twice wider at the base than the papillae of *Bactria*.

Bactria differs from *Caelestium* by the ovoid to broadly ovate leaf blades suddenly tapering to the petiole, the sepaloid tepals, the fruits with concave faces, distinct ribs and three styles partly fused at the base and terminated with small capitate stigmas.

Bactria ovczinnikovii grows in a semi-arid climate with warm winter, humid spring and very dry summer, while *Caelestium lazkovii* and *C. tianschanicum* grow in moderately cold semi-arid climates with cold winter and sufficient precipitation in summer. The differences in the

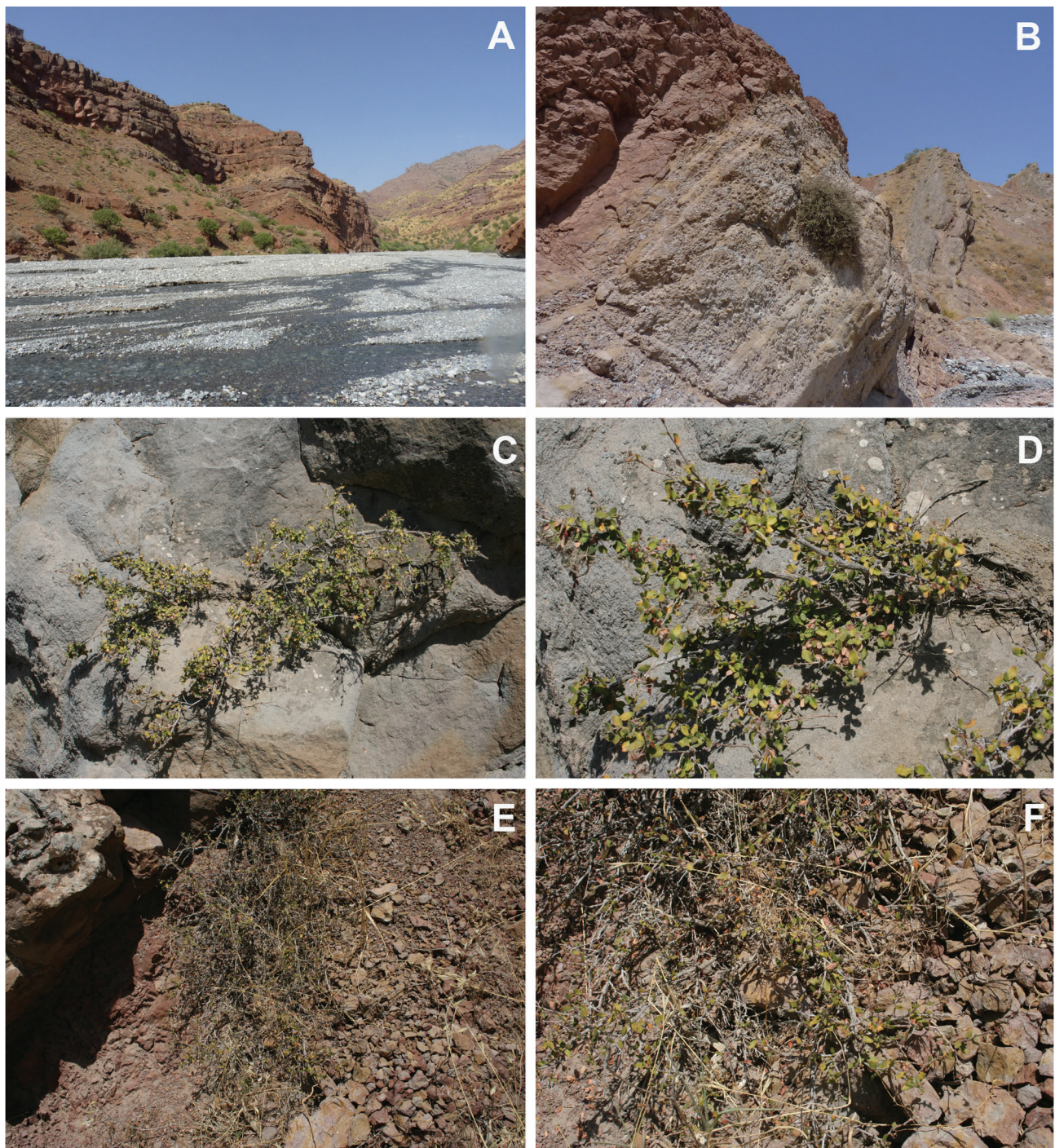


Fig. 11. Habitats and habit of *Bactria ovczinnikovii* in Tajikistan, Khatlon Region, Shuroabad District.
A — the bank of the Shpilau River near the village Bag; B — a plant on a cliff face; C, D — a plant in a cleft of gray sandstone rock;
E, F — a plant on a red sandstone gravel. Photos by U. Ukrainskaja.

Table 3. Morphological characteristics of *Caelestium* and some other taxa of *Polygoneae*

Characters	<i>Polygonum</i> s. str. (sect. <i>Polygonum</i> , sect. <i>Tephis</i> , sect. <i>Pseudomollia</i>)	<i>Caelestium</i>	<i>Bactria</i>	<i>Persopolium</i>	<i>Atraphaxis</i>
Life span/form	annual, perennial herbs, undershrubs, dwarf shrubs	dwarf stout shrubs	dwarf stout shrub	caespitose dwarf shrubs or undershrubs	dwarf or tall shrubs or undershrubs
Thyrse	frondose, frondulose, or bracteose	frondulose	frondulose	frondose to frondulose	bracteose
Compactness of thyrses	no/yes	no	no	no	yes
Ochrea length, mm	7–10	2–4	2–4	3–10	3–10
Ochrea shape	lanceolate-tubular, later fimbriate-lacinate, with (5)7–17 veins	lanceolate-tubular, later bilacinate, without veins	lanceolate-tubular, later bilacinate, without veins	truncate-tubular; lanceolate-tubular, with 0–6 veins	tubular, with two linear-lanceolate lacinas connected by serrate- incised middle part, with 2 veins
Perianth partition	$\frac{1}{2}-\frac{5}{6}$	$\frac{4}{5}-\frac{9}{10}$	$\frac{5}{6}$	$\frac{2}{3}-\frac{3}{4}$	$\frac{1}{3}-\frac{3}{4}$ ($\frac{9}{10}$ in <i>A. teretifolia</i>)
Tepals in fruiting	equal	equal	equal	equal	equal or inner accrescent
Tepal shape	oblong-elliptical, broadly ovate, or obovate	broadly ovate, broadly elliptical	lanceolate	oblong-elliptical to oblong- ovate	oblong-elliptical to rotundate and reniform
Tepal consistence	petaloid	petaloid	sepaloid	sepaloid	petaloid
Surface of tepals abaxially	glabrous or papillate across the tube	glabrous	glabrous	shortly velutinous- puberulent	glabrous or papillate across the tube
Papillae on perianth tube, µm	60–80 × 15–45	–	–	17–60 × 5–8(12)	30–50 × 20–35
Papillae on tepal edge, µm	–	30–35(40) × 13–20(40)	25–35 × (5)8–11	25–35 × 10	35 × 30
Pedicel length, mm	1.5–2	0.5–1	0.5–1	0.5–1	1–6
Perianth tube length, mm	1–1.2	0.5–0.9	0.5–0.9	1.3–2	1–7.5
Filiform base of perianth tube length, mm	–	0.1–0.13	0.1–0.18	0.1–0.3(0.5)	0.5–7
Stigmas	capitate	linear	capitate	linear	capitate
Sporoderm ornamenta- tion	psilate, micropunctate, microspinulose (<i>Aticularia</i>); psilate around the colpi, verrucate at $\frac{1}{3}$ mesocolpia and poles (<i>Pseudomollia</i>)	microreticulate-foveolate to foveolate-perforate	microreticulate-foveolate	foveolate, foveolate- perforate, microreticulate- foveolate, striate-perforate	striate-perforate, rarely reticulate-perforate (<i>A. tokogulica</i>)
Achene sides	concave to flat	flat	concave	concave	concave to convex
Achene ribs	obtuse	obtuse	sharp, winged	sharp, winged	sharp, winged to obtuse
Anticlinal walls of exo- carp cell	undulate to straight	straight	straight	straight	undulate to straight
Outer periclinal wall of exocarp cell	undulate to straight	straight	undulate	undulate	undulate to straight
Lumen of exocarp cell	rectangular, trapezoid, dendratically branched in the outer periclinal wall	dendratically branched in the outer periclinal wall	rectangular	rectangular	trapezoid, dendritically branched, triangular, low-domed

environmental conditions and rainfall times caused some differences in the flowering and fruiting times, as well in the structure of the exocarp. The differences in the shape of the perianth, fruits, styles, the micromorphology of the tepals are apparently more significant, because they are less affected by environmental conditions.

Diagnostic characteristics which discriminate *Caelestium* and *Bactria* from other genera of *Polygoneae*

Morphological characteristics that distinguish *Caelestium* and *Bactria* from *Atraphaxis*, *Persepolium*, and *Polygonum* s. str. (including the Old World sections *Polygonum*, *Pseudomollia* Boiss., and *Tephis* (Adans.) Meisn.) are summarized in Table 3. These characteristics are based on own and reference data (see Materials and methods).

Caelestium resembles some species of *Polygonum* in the morphology of perianths and fruits, but differs in the morphology of ochreas, the ornamentation of sporoderm (Hedberg, 1946; Hong et al., 2005), styles, papillae along the tepal edges, which are absent from *Polygonum* (Table 3).

Bactria resembles *Atraphaxis* in the shrubby habit and the morphology of shoots and thyrses, the shape of leaf blades, but differs in the morphology of ochreas, perianth, and the ornamentation of sporoderm. *Bactria* resembles *Persepolium* in the morphology of perianth and fruit, the ornamentation of sporoderm, the structure of exocarp cells, but has different habit and morphology of shoots, ochreas, and leaf blades, and the glabrous perianth. The morphology of leaf blades, ochreas, and the sporoderm ornamentation differentiate *Bactria* from *Polygonum*.

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Supplementary material (Appendix) to the article is available on the journal's website (www.binran.ru/journals/novitates/).

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