

FURTHER COMMENTS ON THE GENUS *HEDWIGIA* (HEDWIGIACEAE, BRYOPHYTA)  
IN RUSSIA

К ТАКСОНОМИИ РОДА *HEDWIGIA* (HEDWIGIACEAE, BRYOPHYTA) В РОССИИ

ELENA A. IGNATOVA<sup>1</sup>, OXANA I. KUZNETSOVA<sup>2</sup> & MICHAEL S. IGNATOV<sup>1,2</sup>

ЕЛЕНА А. ИГНАТОВА<sup>1</sup>, ОКСАНА И. КУЗНЕЦОВА<sup>2</sup>, МИХАИЛ С. ИГНАТОВ<sup>1,2</sup>

Abstract

A new species from Asian Russia, *Hedwigia kuzenevae* sp. nova, is described based on integrative molecular and morphological study. It is similar to the recently described *H. czernyadjevae* in plant habit, highly recurved leaf margins and hair-point structure, but differs in multipapillose leaf cells. The latter character, as well as leaf margins recurved to the hair-point, correspond to *H. ciliata*; however, its hair-points are shorter, less strongly papillose, especially in distal part, and leaves are falcate-secund, contrary to the straight leaves of *H. kuzenevae*. Distribution area of *H. kuzenevae* includes Transbaikalia and Tukuringra Range in Amurskyaya Province; it is also known from few localities in Yakutia and Krasnoyarsk Territory. It often grows in areas with calcareous bedrocks. Another taxon, *H. emodica* var. *echinata* var. nova, is described from Asian Russia. It differs from the type variety in falcate-secund leaves and slightly shorter hair-points with sharply dentate margins and dorsal surface of hair-points covered with high, dense, branched spinulae. These morphological differences make these taxa quite distinct, though they are not separated from each other by nuclear ITS1-2 DNA marker, contrary to other taxa within *Hedwigia*. According to the DNA sequence data, *Hedwigia mollis* is also closely related to *H. emodica*, but it is better separated and likely deserves species status. It shares some morphological features with both varieties of *H. emodica*, but differs from both of them by shorter hair-points with slightly papillose distal portion. *Hedwigia emodica* var. *emodica* has a widest distribution area throughout Russia, while *H. mollis* is mainly European species and distribution of *H. emodica* var. *echinata* is restricted to the south of Russian Far East and Transbaikalia.

Резюме

На основе интегративного молекулярного и морфологического анализа из азиатской России описан новый вид, *Hedwigia kuzenevae* sp. nova. Он похож на недавно описанный вид *H. czernyadjevae* по облику растений, высоко отогнутым краям листа и длинным, сильно шероховатым гиалиновым волоскам, но отличается от него клетками с несколькими папиллами. Клетки с несколькими папиллами и высоко отогнутые края листа свойственны также *H. ciliata*, но у этого вида гиалиновые волоски менее сильно папиллозные, а листья односторонне обращенные. *Hedwigia kuzenevae* встречается в Забайкалье и Амурской области; единичные местонахождения известны из Якутии и Красноярского края. Вид растет в районах распространения карбонатных пород. Еще один таксон, *H. emodica* var. *echinata* var. nova, описан с юго-востока Азиатской России. От типовой разновидности он отличается односторонне обращенными листьями и гиалиновыми волосками с остро пильчатыми краями и с длинными, густыми шипиками на дорсальной поверхности. По морфологическим признакам эти разновидности четко различаются, но они не отделяются друг от друга по изученному молекулярному маркеру ITS1-2. Согласно данным по этому маркеру, *Hedwigia mollis* также близка к *H. emodica*, но лучше от нее отграничена и скорее заслуживает видовой статус. Она отличается от обеих разновидностей *H. emodica* более короткими гиалиновыми волосками с редкими и низкими папиллами в верхней половине. *Hedwigia emodica* var. *emodica* распространена по всей территории России, *H. mollis* встречается в европейской части и на Алтае, а *H. emodica* var. *echinata* известна только с юга российского Дальнего Востока и из Забайкалья.

KEYWORDS: mosses, taxonomy, new species, molecular phylogenetics, ITS

<sup>1</sup> – Lomonosov Moscow State University, Biological Faculty, Geobotany Dept., Leninskie Gory Str. 1-12, Moscow 119234 Russia – Россия, 119234, Москва, Ленинские Горы, д. 1 стр. 12, Московский государственный университет, биологический факультет, кафедра геоботаники. E-mails: arctoa@list.ru & misha\_ignatov@list.ru

<sup>2</sup> – Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow 127276 Russia – Россия 127276 Москва, Ботаническая 4, ГБС РАН. E-mail: oikuznets@gmail.com

## INTRODUCTION

*Hedwigia* P. Beauv. is a taxonomically difficult genus with still poorly resolved taxonomy. A number of species and intraspecific taxa were described within it during 19th century, but they were considered as synonyms of *H. ciliata* (Hedw.) P. Beauv. since Brotherus (1925). The genus was revisited in the last decade of the 20<sup>th</sup> century by Hedenäs (1994) and Buck and Norris (1996); it resulted in description of one new species from Europe, *H. stellata* Hedenäs, and raising of Californian endemic *H. ciliata* var. *detonsa* (M. Howe) Paris to a species rank. Later Biasuso (2007) described *H. brevipilifera* Biasuso from Argentina; she also recognized *H. ciliata* var. *nivalis* (Müll. Hal.) Hampe in addition to the most widespread in Argentina type variety, *H. ciliata*. *Hedwigia* was also revised by Dalton *et al.* (2013) for Sino-Himalaya, who listed three species for this region, *i.e.*, *H. ciliata*, *H. stellata* and *H. emodica* Hampe ex Müll. Hal. (= *H. ciliata* var. *leucophaea* Bruch, Schimp. & W. Gümbel).

The first molecular-phylogenetic analysis of *Hedwigia* based on mitochondrial *nad-5*, plastid *trnL-trnF* and nuclear ITS1&2 markers (Buchbender *et al.*, 2014) confirmed a separate status of *H. stellata* and *H. ciliata* var. *striata* (Wilson) Bruch & Schimp., so the latter taxon was raised to the species rank. However, it was shown that *H. ciliata* var. *leucophaea* Bruch & Schimp. cannot be maintained in its current morphological circumscription because some specimens with morphological characters of this taxon are likely of hybrid origin; it was supposed that “the distinguishing characters can obviously be developed independently in some taxa of the *Hedwigia ciliata* complex”. One cryptic species separated by molecular data but lacking the distinctive morphological characters was also mentioned.

An integrative molecular and morphological study of the genus *Hedwigia* in Russia (Ignatova *et al.*, 2016) resulted in recognizing five species in its territory. The same DNA regions as in the analysis of Buchbender *et al.* (2014) were used. It was shown that *H. ciliata* s. str. has rather restricted distribution in western part of European Russia, but it is totally absent in the Caucasus, Urals and Asian part of the country. Specimens from Asian Russia previously referred to *H. stellata* due to a single papilla per cell (Ignatov *et al.*, 2000, 2006) turned to be unrelated to the European specimens of this species by molecular data; some distinctive morphological characters were also found. This taxon described under the name *H. czernyadjevae* Ignatova, Fedosov & Ignatov was revealed in Transbaikalia, Khabarovsk Territory and Yakutia. Two other groups of specimens formed well-supported clades in the analysis of combined alignment of three DNA regions. First of them represented a species with a southern distribution in Russia (Black Sea coastal areas of the Caucasus, Zabaikalsky and Primorsky Territories);

it was also found in collections from eastern regions of the U.S.A. Combination of a small size of plants and falcate-secund leaves with short hair-points constituted its morphological distinction. The second group of specimens, mainly from European Russia, alpine areas of the Caucasus and also from Altai Mts, was described as *H. mollis* Ignatova, Fedosov & Ignatov. It was found to be distinct from *H. ciliata* s. str. both by molecular data and morphology; however, its distinction from another taxon recognized in this study, *H. emodica*, appeared to be more problematic. Both *H. mollis* and *H. emodica* differ from *H. ciliata* in only shortly recurved margins at leaf base, leaf papillae with short, round at tips branches and smaller spores; the difference between each other referred mainly to hair-point length and density of papillae. In addition, some specimens from the Russian Far East closely related to *H. emodica*-group were discussed, but their taxonomic status remained unresolved due to insufficient data.

At the same time, other specimens with unknown character combination were revealed in Asian Russia in the course of preparing of taxonomic treatment of the genus *Hedwigia* for the “Moss flora of Russia”. So, the present study aims to outline taxonomic status of these specimens and to clarify taxonomy in *Hedwigia emodica*-group.

## MATERIAL AND METHODS

All collections from LE, MHA, MW, SAS, and some specimens from other herbaria were studied for their morphology. Selection of specimens for DNA studies was addressed mainly to the problems remained from the previous study for the eastern part of Russia, where some plants were left as *Hedwigia* sp. (Ignatova *et al.*, 2016), and also to other plants from that area. Eight sequences of three taxa were newly obtained.

The nuclear ITS region was used in the present analysis alone as it provided the main phylogenetic signal in the previous studies (Buchbender *et al.*, 2014; Ignatova *et al.*, 2016). DNA extraction and amplification were done according to the laboratory protocols described in Gardiner *et al.* (2005). The newly obtained data were supplemented by sequences available in GenBank. *Braunia alopecura* (Brid.) Limpr. was used as outgroup. Totally 61 specimens were involved into the analysis. Vouchers of newly sequenced specimens and GenBank accession numbers are compiled in Appendix 1. Sequences were aligned using BioEdit (Hall, 1999). Bayesian analysis was conducted in MrBayes 3.1.2 (Ronquist *et al.*, 2012) using the GTR+G model, for 50,000,000 generations with sampling every 1000 generations. Three simultaneous runs were used. The first 25% of sampled trees were discarded for the burn-in. Maximum parsimony analysis was completed with Nona (Goloboff, 1994) within the Winclada shell (Nixon, 1999a, b), with bootstrap calculation with 2000 replications.

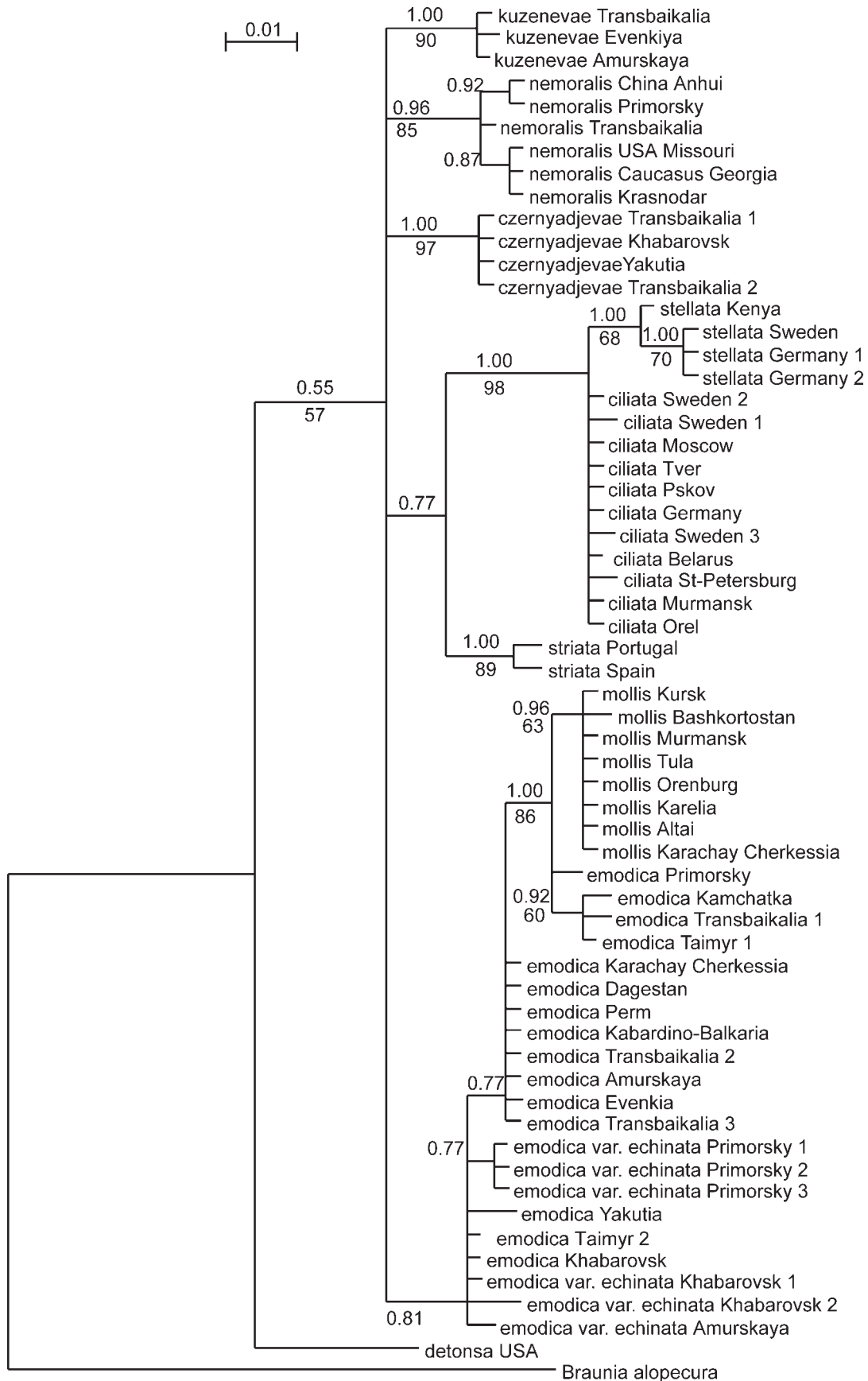


Fig. 1. Bayesian tree obtained from nuclear ITS1-2 sequences. Posterior probabilities (>0.6) and Bootstrap supports (>50) are indicated above and below branches.

## RESULTS

Phylogenetic tree from the Bayesian analysis of 60 specimens of *Hedwigia* rooted on one species of *Braunia* is shown in Fig. 1, where Bayesian posterior probabilities above 0.6 are shown and supplemented also by bootstrap support values from MP analysis, which has a similar topology with somewhat poorer resolution. American *H. detonsa* is sister to all other species of the genus in this phylogeny, where most groups are comprised in a wide polytomy of five smaller clades, the tree being monospecific and three formed of three taxa.

All three monospecific clades were found maximally or otherwise highly supported in Bayesian analysis and rather highly supported in MP analysis: *H. czernyadjevae* (PP=1, BS=97), *H. nemoralis* (PP=0.96, BS=85), and a new species described below, *H. kuzenevae* (PP=1, BS=90). The *H. nemoralis* clade comprises some geographic patterning: its subclades, albeit only moderately supported, represent (a) Caucasus + eastern North American subclade, and (b) Russian Far East + East China subclade, and Transbaikalian specimen of *H. nemoralis* is in a tritomy with these two subclades.

The *H. ciliata* + *H. stellata* + *H. striata* clade has only moderate support (PP=0.77), while two its subclades are highly supported: *H. striata* (PP=1, BS=89) is sister to the clade formed by two other species (PP=1, BS=98). *Hedwigia ciliata* forms a broad polytomy with nested clade formed by *H. stellata* and one specimen of *H. ciliata* from East Africa (PP=1, BS=68), the latter being sister to terminal clade of *H. stellata* (PP=1, BS=70).

The remaining specimens belong to the clade with moderate support of (PP=0.81), which includes a grade of *H. emodica* terminated with *H. mollis* (PP=0.96, BS=63). The basal part of this grade includes six specimens deviated in morphology and segregated below in a variety *H. emodica* var. *echinata*. In addition to morphology, both *H. mollis* and *H. emodica* var. *echinata* have a specific distribution, as the former occurs in the western part of Eurasia, whereas *H. emodica* var. *echinata* has a Far Eastern distribution.

## DISCUSSION

Three specimens from Asian Russia (Amurskaya Province, Zabaikalsky and Krasnoyarsk Territories) are described below as *H. kuzenevae* sp. nova. They form a maximally supported clade without a definite relationship. Habitually, these plants are very similar to *H. czernyadjevae* by recurved leaf margins up to hair-point and long, slightly flexuose, densely spinulose on dorsal surface hair-points. However, their leaf laminae have several branched papillae per cell, contrary to single peltate papilla in each cell in *H. czernyadjevae*. Character combination of *H. kuzenevae* is similar to *H. ciliata*, but these two species do not show definite relationship in the molecular-phylogenetic analysis. Different ornamentation of hair-point dorsal surface constitutes their morphological distinction: in *H. ciliata*, hair-points are only sparsely

and lowly papillose and follow a curvature of falcate-secund leaves, contrary to densely and highly spinulose, straight and slightly flexuose hair-points of *H. kuzenevae*. Also, *H. ciliata* has spores more than 30 µm in diameter, whereas in *H. kuzenevae* it is 22–25 µm.

The nested position of *Hedwigia mollis*-clade and a clade of Far Eastern specimens in question within *H. emodica* grade agree with their morphology. All of them are separated from all other species known in Russia by leaf margins narrowly recurved only in the lowermost leaf portion and flat in distal 4/5–2/3. *Hedwigia emodica* is also characterized by straight leaves and straight, long hair-points constituting (26–)32–47% of leaf length; hair-point margins are subentire or weakly denticulate and dorsal surface is covered by papillae and moderately dense simple and branched spinulae. Both *H. mollis* and Far Eastern specimens differ from it in having regular sharp teeth along hair-point margins; such teeth are very rarely observed in *H. emodica* (seen in two specimens from the Caucasus). *Hedwigia mollis* and Far Eastern specimens represent different trends in leaf and hair-point morphology. In *H. mollis*, leaves mainly remain straight, but hair-points are often slightly recurved; rarely leaves are slightly secund (observed in specimens from Altai and Caucasus). Hair-points are shorter than in *H. emodica*, being (11–)16–33% of leaf length. In addition, sculpture of hair-point dorsal surface changes from lower portion, covered with papillae and dense, moderately high, simple and branched spinulae, to the upper 1/2–1/3, which is sparsely and lowly papillose; in case of forms with shorter hair-points, the latter are weakly papillose throughout. At the same time, Far Eastern specimens in question are immediately separated from both *H. emodica* and *H. mollis* by strongly falcate-secund leaves. Their hair-points follow leaf curvature; they are comparable or slightly shorter than in *H. emodica* (20–41% of leaf length) and are covered with longer, strongly branched, dense spinulae, also making hair-point margins ciliate in addition to sharp, narrow, sometimes hooked teeth.

Summing up, the “typical” plants of *H. emodica*, *H. mollis* and Far Eastern specimens are easily recognized by morphology. *H. emodica* seems to be rather uniform in morphology, though it is somewhat variable in studied DNA regions, being represented by an unresolved grade and two subclades within it. Two other taxa demonstrate some variability in particular morphological characters, causing some difficulty in identification of morphologically deviating specimens. The obtained topology suggests a possibility to recognize *H. emodica* s.l. and three varieties within it; it is also possible to recognize three separate species. In our opinion, total merging of all taxa within *H. emodica* is inappropriate, because it contains three entities with different, though occasionally overlapping morphology, different ecology and geography. At the same time, specimens of *H. mollis* form a moderately supported clade within *H. emodica*, while

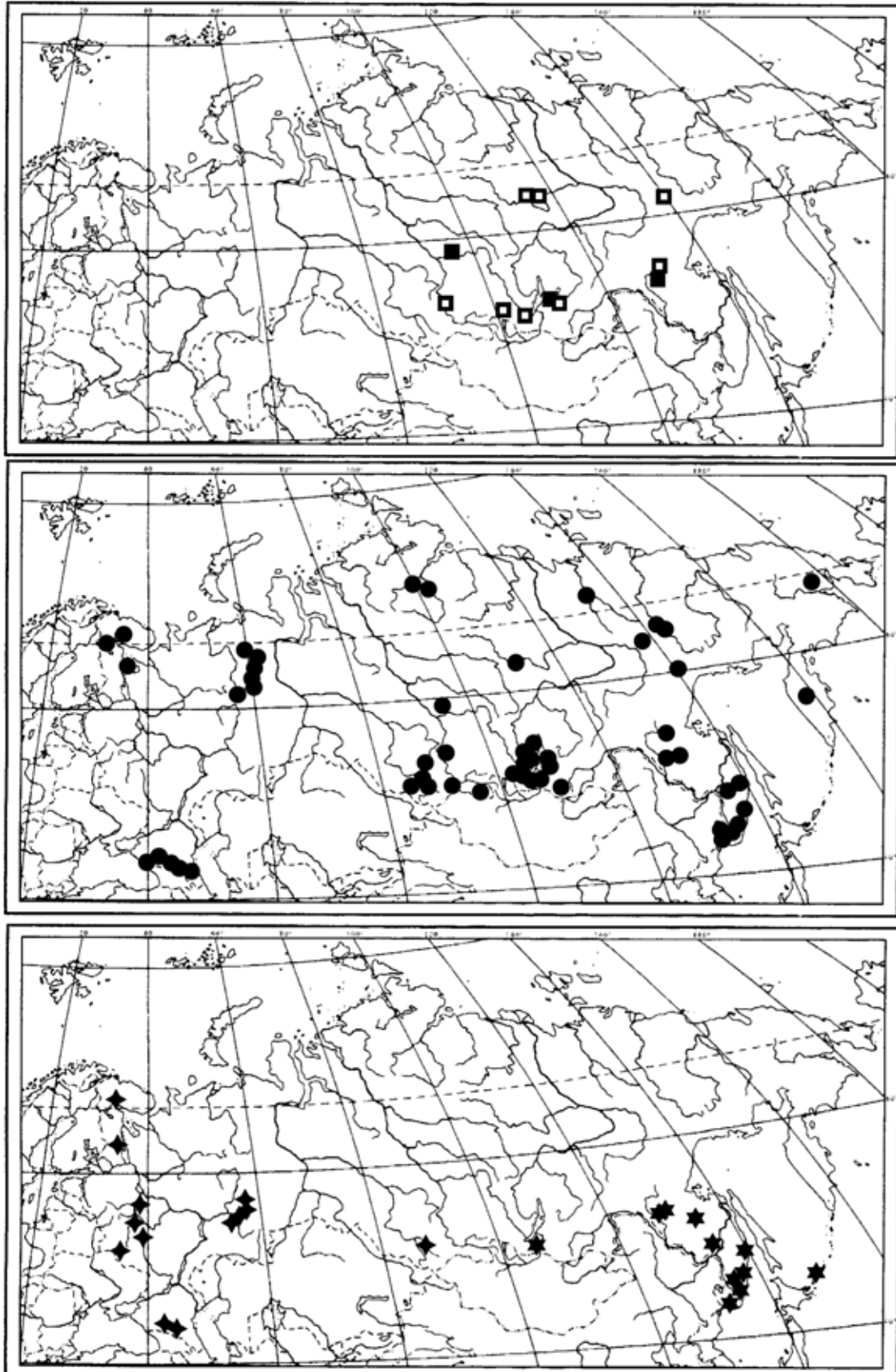


Fig. 2. Distribution of the species of *Hedwigia* in Russia and adjacent countries. *Hedwigia kuzenevae*: solid squares – sequenced specimens, hollow squares – other specimens; *H. emodica*: circles; *H. mollis*: four-pointed stars; *H. emodica* var. *echinata*: six-pointed stars.

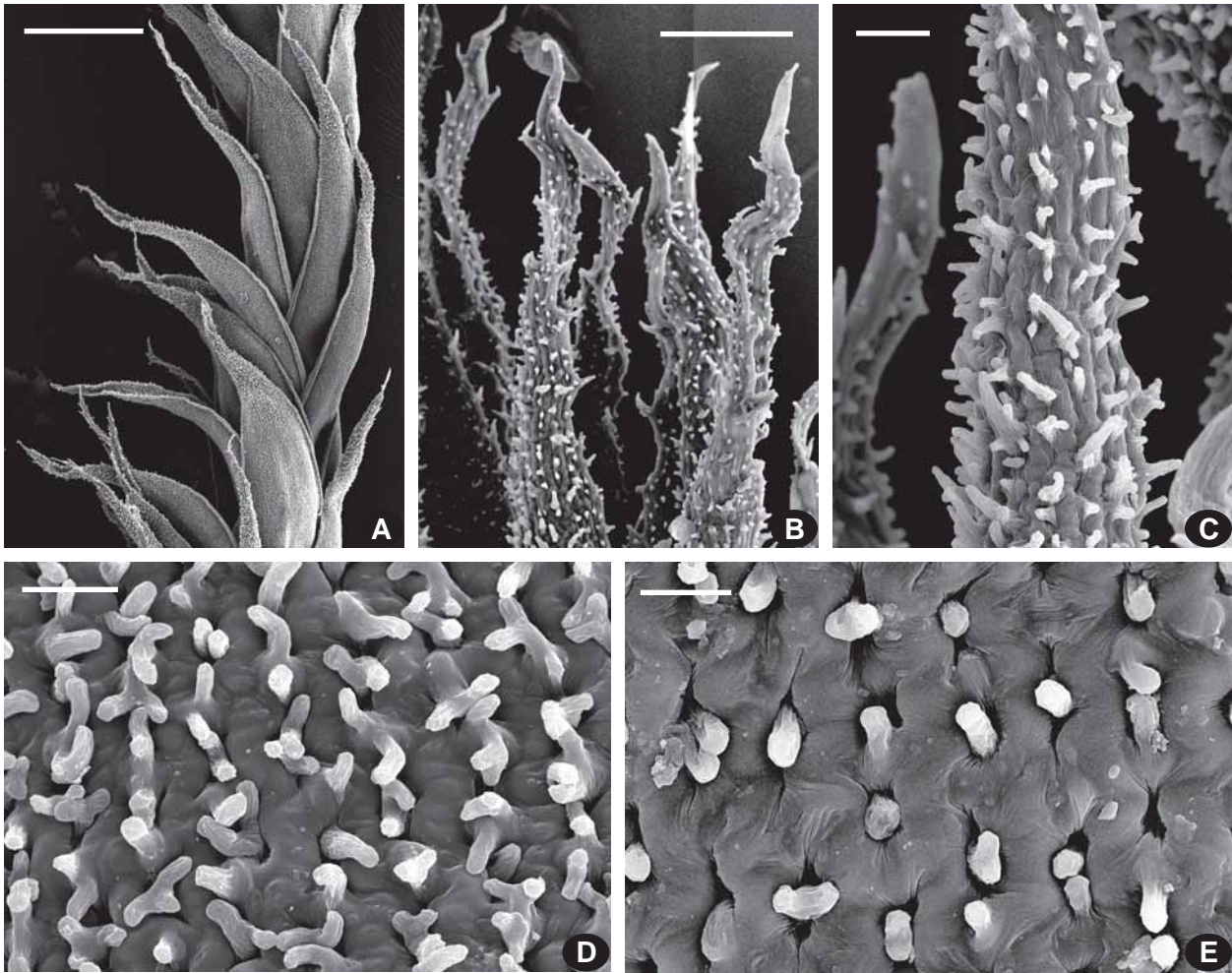


Fig. 3. *Hedwigia kuzenevae* (from: Krasnoyarsk Territory, Evenkia, 27.VI.1992, *Shcherbina 121*, MW). A–E (SEM). A–B: apical parts of leaves; C: dorsal surface of hair-point; D: papillae in mid-leaf on abaxial leaf surface; E: papillae in mid-leaf on adaxial leaf surface. Scale bars: 0.5 mm for A, 100  $\mu$ m for B; 20  $\mu$ m for C; 10  $\mu$ m for D, E.

Far Eastern specimens are less separated genetically and its clade has no support. We prefer to recognize *H. mollis* as a separate species and *H. emodica* with two varieties, var. *emodica* and var. *echinata* var. nova (described below). However, further study of expanded specimen set from other geographical regions is needed for better understanding of the taxonomy in this group.

#### TAXONOMY

##### *Hedwigia kuzenevae* Ignatova & Ignatov sp. nova

Type: Russia, Siberia, Zabaikalsky Territory, Chita District, Daursky Mt. Range, Aratsa Creek – a tributary of Ingoda River, 51°54'50"N, 114°25'06"E, 970 m alt., rock outcrops in larch forest, on rock; 13.VII.2012, Czernyadjeva 2-12 (Holotype LE, isotypes MHA and MW).

**Diagnosis.** The new species is most similar to *Hedwigia czernyadjevae* in straight leaves with leaf margins recurved up to hair-point and long, slightly flexuose, strongly papillose and spinulose on dorsal surface hair-points; their main distinctive character is multipapillose vs. unipapillose laminal cells. The distinction of *H.*

*kuzenevae* from *H. ciliata* includes straight vs. falcate-secund leaves and densely spinulose throughout vs. distantly and lowly papillose in distal portion dorsal surface of hair-points.

**Etymology.** The species name is given in honour of Olga I. Kuzeneva (1887–1978), Russian botanist, who studied vascular flora, but also collected bryophytes, particularly in Amurskaya Province, including numerous specimens of the species being described.

**Description.** Plants greyish-green or brownish-green in distal part, greyish-brown proximally, in loose, easily disintegrated tufts. Stems up to 5 cm long, irregularly branched. Leaves erect, appressed when dry, widely spread when wet, 1.6–1.8×0.7–0.8 mm, with width/length ratio 0.44–0.46, ovate and gradually narrowing to the apex or attenuate, concave; margins recurved in proximal 3/4 or up to the hair-point base; hair-points 0.5–0.7 mm long, constituting 35–42% of leaf length; margins of hair-points with long, sharp teeth, on dorsal surface with dense simple papillae and dense branched spinulae; apical cell moderately long, pointed, smooth or low-

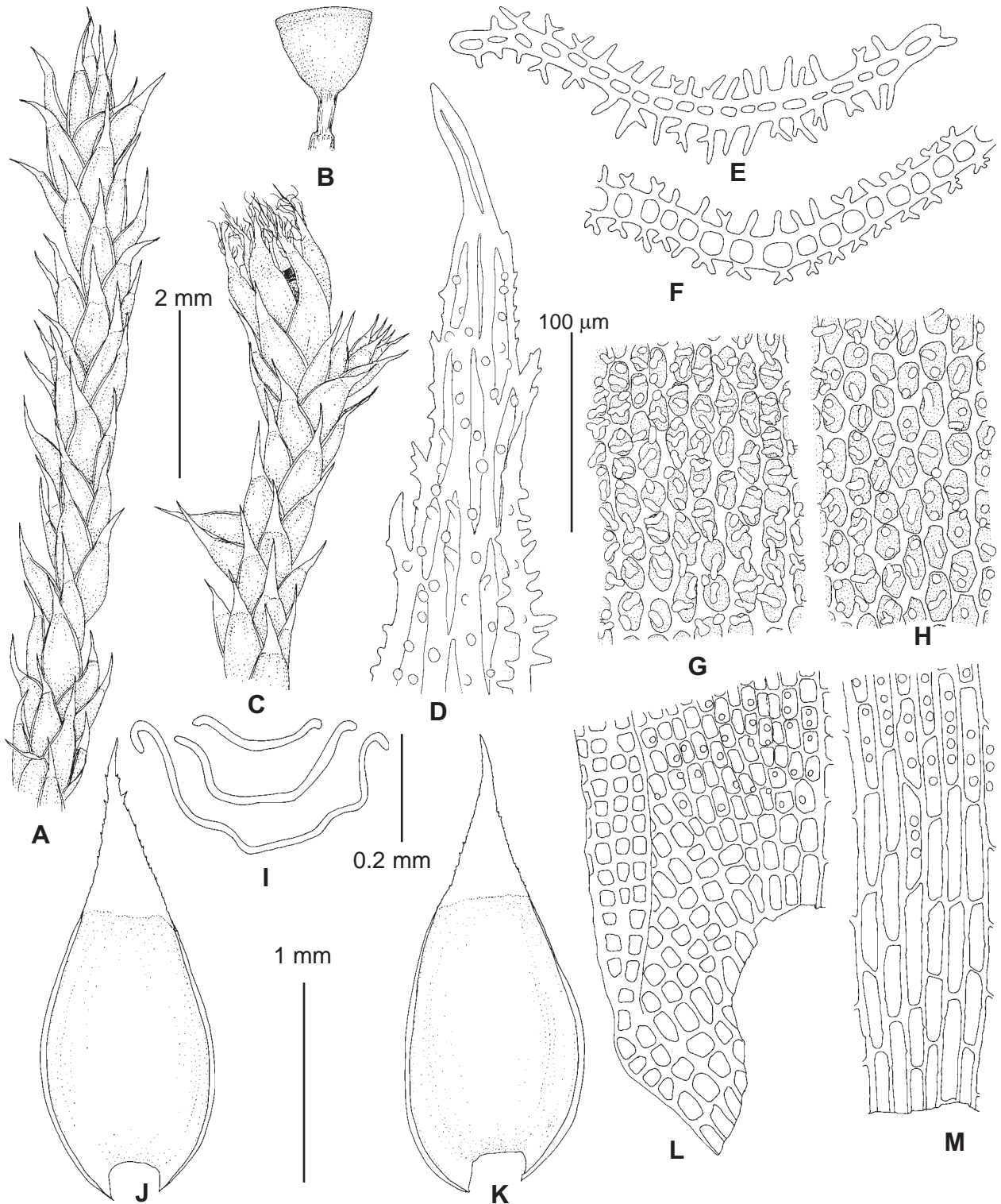


Fig. 4. *Hedwigia kuzenevae* (from holotype). A, C: habit, dry; B: capsule; D: hair-point; E-F, I – leaf transverse sections; G: median laminal cells on abaxial surface; H: median laminal cells on adaxial surface; J-K: leaves; L: basal marginal cells; M: basal cells in the middle of leaf base. Scale bars: 2 mm for A-C; 1 mm for J-K; 0.2 mm for I; 100  $\mu\text{m}$  for E-H, L-M.

ly papillose; median laminal cells (10–)12–20 $\times$ 10–12  $\mu\text{m}$ , with thick, sinuose longitudinal walls with few pores, on abaxial surface with 2–4 high branched papillae per cell, on adaxial surface with 2–4 high, simple and branched papillae per cell; cells in the middle of leaf base linear,

30–60 $\times$ 12–14  $\mu\text{m}$ , porose, orange-brown, lowermost cells smooth, then gradually becoming papillose upwards, with several simple papillae per cell, gradually transiting into median leaf cells with branched papillae; basal marginal cells quadrate and short-rectangular, with non-porose

transverse walls. *Perichaetial leaves* oblong, ca. 2.5×0.8 mm, hyaline hair-point ca. 0.5 mm, with long cilia. *Capsules* cup-like, 0.9–1.1×0.9–1.1 mm, widest at the mouth; exothecial cells in the middle part of urn rectangular or short-rectangular, at urn mouth smaller in several rows. *Operculum* lowly conical, with low central mammilla. *Spores* 22–25 µm, on distal surface with vermicular ridges. *Calyptrae* hairy in lower portion.

**Distribution and ecology.** Most numerous collections of *Hedwigia kuzenevae* are known from Tukuringra Mt. Range in Amurskaya Province (including territory of Zeya State Reserve) and between Zeya and Toko Lake in southern Yakutia. In Zabaikalsky Territory it was found, apart of the type locality in Chita District, in Nerchinsk surroundings. There is one specimen from Irkutsk Province, bear SW shore of Baikal Lake (Slyudyanka District). West of Baikal Lake, it was collected in Buryatia, in Tunka Depression (old collections of early 20th century). There are also few collections from Yenisey River basin: near Krasnoyarsk City (“Krasnoyarsk Pillars” area) and along Podkamennaya Tunguska River and its tributary. In Yakutia, this species was found in Suntar District (Vilyui River basin) and in Sette Daban Mt. Range. Grows at 340–1400 m a.s.l., on rocks in larch and birch forests, rarely in mountain tundra, on rock-fields and on dry cliffs along creeks.

**Specimens examined:** ASIAN RUSSIA: **Krasnoyarsk Territory:** Krasnoyarsk City surroundings, “Krasnoyarsk Pillars” area, 24.VI.1935, *Vereshchagin s.n.* (LE); Evenkia, Baikit District: Podkamennaya Tunguska at ca. 90 km upstream its mouth, ca. 61°30'N, 91°20'E, “Shcheki” area, 8.VII.1994, *Shcherbina 274* (MW); Stolbovaya Creek 1 km upstream its mouth, ca. 62°9'N, 91°9'E, “Pillars” area, 27.VI.1992, *Shcherbina 121* (MW). **Republic of Sakha/Yakutia:** Suntar District, Vilyui River 253 km downstream Ulakhan-Vava, 17.VIII.1958, *Kildyushevsky 112/521* (LE); Tomponsky District, Verkhojansky Mountain System, Sette Daban Range, valley of Vostochnaya Khandyga River, ca. 63°04.3'N, 137°46.3'E, 18.VII.2015, *Ignatov & Ignatova 15-680* (MW, MHA). **Zabaikalsky Territory:** Nerchinsk District, Shivki Settlement, “Shivki Pillars” area, 14.VI.1957, *Filin s.n.* (MW). **Republic of Buryatia:** Sayan Mts, Tunka District, V.1902, *Elenkin s.n.* (LE); Tunka Depression, 13.VIII.1926, *Smirnov s.n.* (LE). **Irkutsk Province:** Slyudyanka District, Utulik Railway Station, 1953, anonym (LE). **Amurskaya Province:** Orochen path from Vozdvizhenskaya to Toko Lake, Tokongro Creek, 31.VII.1911, *Prokhorov & Kuzeneva 178* (LE); Tukuringra Mt. Ridge, between Gilyui and Rakindra Rivers, 23.VII.1915, *Prokhorov & Kuzeneva 124* (LE); Tukuringra Mt. Ridge, 16.VIII.1909, *Prokhorov & Kuzeneva 365* (LE); between Byasa and Seledmdzha Rivers, Taldui Mt., 15.IX.1927, *Kuzeneva 133* (LE); Zeya State Reserve: Shirokaya Creek mouth, 8.IX.1979, *Petelin 132* (MW); Motovaya Creek, 1979, *Petelin 23* (MW); Gilyui River near Kamrai Creek mouth, 5.IX.1979, *Petelin 129* (MW); Gilyui River 0.5 km downstream of Motovaya Creek mouth, 26.VII.1977, *Petelin 17* (MW); right slope of Gilyui River valley, 54.2668°N, 126°8531'E, 26.VII.2012, *Dudov Br\_12\_009* (MW).

**Differentiation.** Habitually, *H. kuzenevae* is most similar to *H. czernyadjevae*: both species have straight leaves

with long, straight or slightly flexuose, densely spinulose hair-points and recurved margins from leaf base to hair-point base. The latter character immediately separates them from *H. emodica* and *H. mollis*, which have only shortly recurved margin at leaf base and flat at the rest part of leaf; at the same time, *H. ciliata* is similar to *H. kuzenevae* and *H. czernyadjevae* in this respect. The distinction between *H. kuzenevae* and *H. czernyadjevae* is in papillae arrangement: the former species has several branched papillae in each cell, while cells of the latter one are unipapillose. *H. ciliata* with similar multipapillose cells differs from *H. kuzenevae* in often falcate-secund leaves and shorter hair-points (15–25 vs. 35–42% of leaf length) with less strongly ornamented dorsal surface; moreover, their distribution is contrastingly different.

***Hedwigia emodica* var. *echinata*** Ignatova & Ignatov, *Arctoa* 26: 000. 2017.

Type: Russia, Khabarovsk Territory, Sovgavan District, Botchinsky State Reserve, ca. 48°18'N, 139°35'E, 362 m a.s.l., between Solonchakovy Creek and Mulpa River, 1 km N of cordon Teplyi Klyuch, rock outcrops in spruce & fir forest, on inclined rock surface, 23.VIII.2013, Ignatov & Ignatova 13-1128 (Holotype MHA, isotypes MW, LE).

**Diagnosis.** The new variety shares with *H. emodica* var. *emodica* the following characters: leaf margins narrowly recurved only in basal 1/5–1/4 of leaf and flat in distal part; hair-points long; and papillae on adaxial leaf surface 3–4 per cell, branched; their distinctive characters include: (1) falcate-secund leaves with hair-points following leaf curvature in var. *echinata* vs. always straight leaves with straight hair-points in var. *emodica*; (2) hair-points narrower and slightly shorter, constituting 30–35% vs. 30–53% of leaf length; (3) margins of hair-points with narrow, sharp teeth vs. usually subentire or with few blunt teeth (in rare cases sharp); and (4) dorsal surface of hair-points covered with simple papillae and long, dense, branched spinulae protruding also at hair-point margins vs. with moderately high papillae and spinulae.

**Etymology.** Name of the new variety corresponds to strongly ornamented surface of hair-points, covered with high and dense spinulae, that makes them “echinate”.

**Description.** *Plants* in loose or dense tufts, greyish-green distally, brownish below. *Stems* 3–5 cm long, moderately branched. *Leaves* falcate-secund, rarely almost straight appressed when dry, widely spreading when wet, 1.5–1.8×0.6–0.7 mm, with width/length ratio 0.35–0.41, ovate, gradually tapered to the apex, concave; margins narrowly recurved at proximal 1/4–1/3; hyaline hair-points 0.5–0.8 mm long, constituting 30–35% of leaf length; margins of hair-points with narrow, sharp, sometimes hooked teeth and protruding spinulae; both surfaces of hair-points covered with simple papillae and long, densely arranged, simple and strongly branched spinulae; apical cell short, finely papillose, truncate, crowned



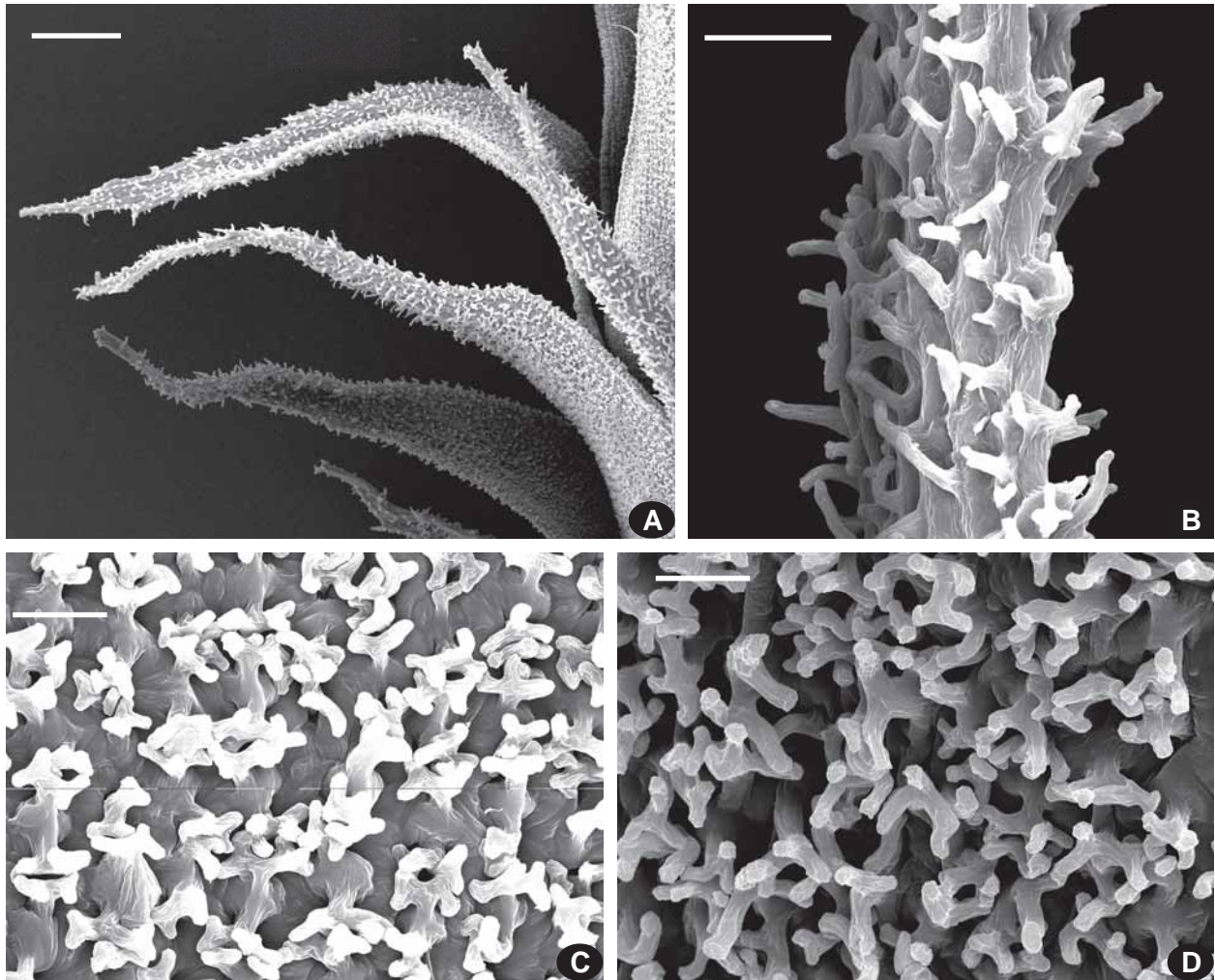


Fig. 5. *Hedwigia emodica* var. *echinata* (from holotype). A–D (SEM). A: apical parts of leaves; B: dorsal surface of hair-point, distal portion; C: papillae in mid-leaf on abaxial leaf surface; D: dorsal surface of hair-point, proximal portion. Scale bars: 100 µm for A; 20 µm for B; 10 µm for C. D.

by several sharp papillae; median laminal cells 13–30×11–14 µm, with thick, sinuose and slightly porose walls, on abaxial surface with 2–3(–4) large, branched papillae per cell, on adaxial surface with 2–3 similar, but smaller papillae per cell; cells in the middle of leaf base linear, 40–80×11–14 µm, porose, orange-brown, lowermost cells smooth, then gradually becoming papillose upwards, with several simple papillae per cell, rather abruptly transiting into median leaf cells with branched papillae; basal marginal cells quadrate and transversely rectangular, with thin longitudinal and thick and porose transverse walls. *Perichaetial leaves* oblong, ca. 3×0.8 mm, hyaline hair-points 0.8–1.0 mm, cilia long, numerous. *Capsules* cup-like or turbinate, 1–1.1×0.8–1.0 mm, widest at the mouth; exothecial cells in the middle part of urn rectangular or short-rectangular, at urn mouth smaller in several rows. *Operculum* lowly conical, with low central mammilla. *Spores* 20–25 µm, with vermicular ridges on distal surface. *Calyptrae* hairy in lower portion.

**Distribution and ecology.** Contrary to the widespread distribution of the type variety, var. *emodica* is restricted

to the southern part of Russian Far East, including Primorsky and Khabarovsk Territory and Amurskaya Province; its westernmost locality is in Buryatia (Bichura River); it was also once collected on Kunashir Island. It grows in forest zone in mountains, up to 1400 m a.s.l., on dry rocks and cliffs, both shady and exposed, occasionally in places with calcareous bedrocks.

**Specimens examined:** ASIAN RUSSIA: **Primorsky Territory:** Shkotovo District, Litovka (Khualaza) Mt., 16.VI.2006, *Kononova s.n.* (MHA); Partizansk District, Olkhovaya Peak, 43°21'N, 133°39'E, 1600 m a.s.l., 3.IX.2006, *Ignatov, Ignatova & Cherdantseva 06-2710, 06-2690* and 1200 m a.s.l., 06-2857 (MHA, MW); Lazo District: Sudzukhinsky [Lazovsky] State Reserve, 1300 m a.s.l., 4.X.1940, *Zhudova s.n.* (MHA); Elomovsky Creek, Benevskie Waterfalls, 44°14'45"N, 133°43'2"E, 630 m a.s.l., 6.IX.2013, *Ignatov & Ignatova 13-1353* (MHA); Chuguevka District, upper course of Berezovy Creek, 43°41'N, 134°10'E, 1000 m a.s.l., 19.VIII.2007, *Ignatov 07-235* (MHA); Dalnegorsk District, SW of Krasnorechensky Settlement, near the top of Sedaya Mt., 44°35'33.1"N, 135°18'35"E, 1340 m a.s.l., 1.IX.2013, *Ignatov, Ignatova & Malashkina 13-1613* (MHA). **Khabarovsk Territory:** Sovga-

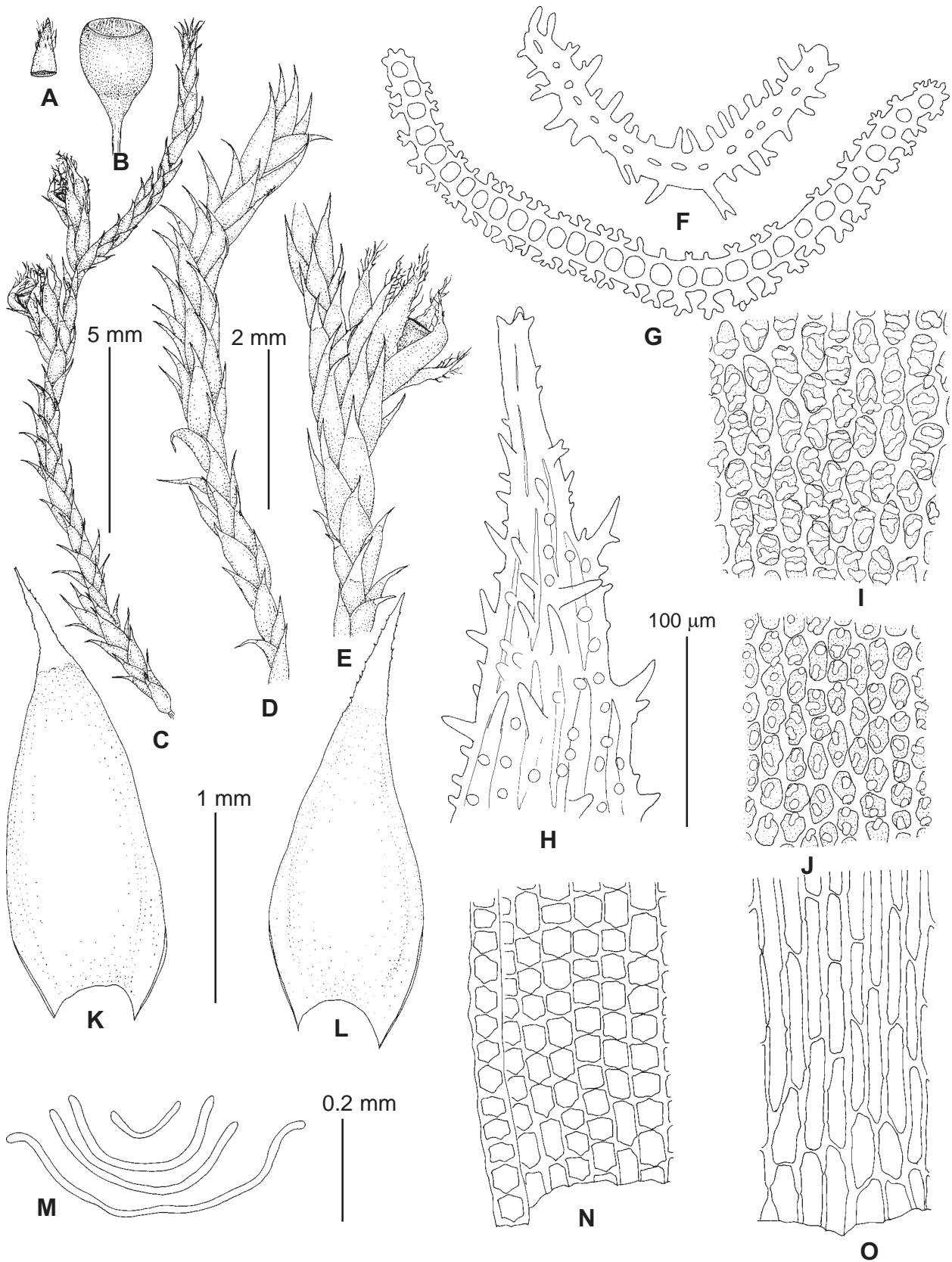


Fig. 6. *Hedwigia emodica* var. *echinata* (from holotype). A: calyptra; B: capsule; C-E: habit, dry; F-G, M – leaf transverse sections; H: hair-point; I: median laminal cells on abaxial surface; J: median laminal cells on adaxial surface; K-L: leaves; N: basal marginal cells; O: basal cells in the middle of leaf base. Scale bars: 5 mm for C; 2 mm for A-B, D-E; 1 mm for K-L; 0.2 mm for M; 100 µm for F-J, N-O.

van District, Botchinsky State Reserve, ca. 48°18'N, 139°36'E, 380 m a.s.l., 22.VIII.2013, *Ignatov & Ignatova 13-1054, 13-878, 13-759, 13-351* (MHA); Khabarovsk District, Bolshehekhtsirsky State Reserve, Sosninsky Creek, 15.VII.1975, *Gambaryan s.n.* (MHA); Verkhnebureinsk District, Bureinsky State Reserve, Pravaya Bureya River, 51°43'N, 134°18'E, 580 m a.s.l., 27.VIII.1997, *Iwatsuki 60698* (MHA); Levaya Bureya River, 51°40'N, 134°22'E, 590 m a.s.l., 16.VIII.1989, *Grigorjeva 89-M-204* (MHA). **Sakhalinskaya Province:** Kunashir Island, Ruruj Mt., 44°28'N, 146°6'E, 400 m a.s.l., 30.VIII.2006, *Ignatov 06-1119* (MHA). **Amurskaya Province:** Zeya District, Zeisky State Reserve: Tukuringra Mt. Ridge, slope to Teply Creek, 24.VIN, 127°II.1977, *Gubanov s.n.* (MHA); Shaman Creek, 54.0694 N, 127.0742°E, 579 m a.s.l., 2.VIII.2012, *Dudov Br\_12\_044* (MW); Teply Creek, 53°52'N, 127°19'E, 400 m a.s.l., 11.VIII.1980, *L.I. Abramova 107* (MHA); Smirnovsky Creek, 53°59'N, 127°24'E, 350 m a.s.l., 9.VIII.1980, *L.I. Abramova 36* (MW). **Republic of Buryatia:** Bichura District, Bichura River, *Afonina 01907* (LE).

**Differentiation.** For the distinctive characters between var. *echinata* and var. *emodica* see the *diagnosis*. There is some similarity between specimens of *H. mollis* (especially from Altai and Caucasus) and *H. emodica* var. *echinata*; some specimens from Baikal Lake area are also difficult to identify due to variability in hair-point length and leaf arrangement. However, in *H. mollis* leaves are only rarely secund, while in var. *echinata* leaves are conspicuously falcate-secund; hair-points is longer in var. *echinata* than in *H. mollis* (30–35% vs. (17–)23–27(–29)% of leaf length; in var. *echinata* surface of hair-points is covered with papillae and high, dense, branched spinulae almost throughout, excepting apical cell and few adjacent cells, while in *H. mollis* only lower half of hair-points is densely spinulose and their distal portions bear only sparse, low papillae.

#### KEY TO IDENTIFICATION OF *HEDWIGIA* SPECIES IN RUSSIA

1. Median laminal cells on abaxial side mainly with a single, branched, peltate papilla over each cell .... 2
- Median laminal cells on abaxial side with 2–4 branched, usually not peltate papillae over each cell .. 3
2. Leaf apices straight; median laminal cells strongly incrassate and porose ..... *H. czernyadjevae*
- Leaf apices reflexed; median laminal cells slightly incrassate, not porose ..... [*H. stellata*]
3. Plants small; leaves shortly acuminate, secund, with apices following leaf curvature; hyaline hair-points short, usually constituting less than 10% of leaf length ..... *P. nemoralis*
- Plants of medium size; leaves gradually narrowed to the apex or rather long acuminate, straight or secund; hyaline hair-points short to very long, usually constituting more than 10% of leaf length ..... 4
4. Leaf margins narrowly recurved in lower 1/4–1/2 of leaf ..... 5
- Leaf margins ±widely recurved in lower 2/3–3/4 of leaf ..... 7
5. Leaves straight; hyaline hair-points long, constituting 30–55% of leaf length, with subentire or bluntly denticulate margins; papillae dense, with thick, round at tips branches, obscuring cell walls .....  
..... *H. emodica* var. *emodica*
- Leaves straight or secund; hyaline hair-points usually shorter, constituting (15–)23–35% of leaf length, with narrow, sharp teeth at margins; papillae with narrow branches, irregularly arranged or forming longitudinal rows, not obscuring cell walls ..... 6
6. Leaves straight, rarely slightly secund; hyaline hair-points spreading, moderately papillose, with more or less dense papillae and spinulae in proximal portion and sparse, low papillae in distal part; mid-leaf laminal cells with compact papillae, often forming longitudinal rows; European Russia and west of Southern Siberia ..... *H. mollis*
- Leaves falcate-secund, hyaline hair-points following leaf curvature, with papillae and high, dense spinulae throughout; mid-leaf laminal cells with irregularly situated papillae; Far East .....  
..... *H. emodica* var. *echinata*
7. Leaves straight or secund; hyaline hair-points moderately papillose; spores (27.5–)30–35(–37.5) µm; European Russia ..... *H. ciliata*
- Leaves usually straight; hyaline hair-points with dense papillae and spinulae; spores 23–27.5 µm; eastern regions of Asian Russia ..... *H. kuzenevae*

#### ACKNOWLEDGEMENTS

The work on SEM was performed partially at User Facilities Center of M. V. Lomonosov Moscow State University under financial support of Ministry of Education and Science of Russian Federation. We also thank the curators of herbaria LE and VBGJ who made their collections available to us. The study of Ignatova was partially supported by RFBR grant #16-04-01156, of Kuznetsova by #15-29-02647, and of Ignatov by the Program of Bioresource Collection Support by FASO RF.

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APPENDIX 1. GenBank accession numbers (newly generated sequences are boldfaced and include specimen voucher data).

*Braunia alopecurica* LN714249; *Hedwigia ciliata* Belarus KY358099; *H. ciliata* Germany LN714255; *H. ciliata* Moscow KY358105; *H. ciliata* Murmansk KY358096; *H. ciliata* Orel KY358095; *H. ciliata* Pskov KY358113; *H. ciliata* St Petersburg KY358097; *H. ciliata* Sweden 1 LN714262; *H. ciliata* Sweden 2 LN714263; *H. ciliata* Sweden 3 LN714264; *H. ciliata* Tver KY358108; *H. czernyadjevae* Khabarovsk KY358117; *H. czernyadjevae* Yakutia KY358116; *H. czernyadjevae* Transbaikalia 1 KY358118; *H. czernyadjevae* Transbaikalia 2 KY358115; *H. detonsa* USA LN714254; *H. emodica* var. *echinata* Amurskaya KY358133 (sub. *H. sp.*); *H. emodica* var. *echinata* Khabarovsk 1 KY358131 (sub. *H. sp.*); ***H. emodica* var. *echinata* Russia, Khabarovsk Bureya, Ignatov 97-538 (MHA) OK1772 MG701917**; *H. emodica* var. *echinata* Primorsky 1 KY358129 (sub. *H. sp.*); *H. emodica* var. *echinata* Primorsky 2 KY358132 (sub. *H. sp.*); ***H. emodica* var. *echinata*, Russia, Primorsky, Benevskie Waterfalls, Ignatov and Ignatova 13-1353 (MHA), OK1588 MG701916**; *H. emodica* Amurskaya KY358089; *H. emodica* Dagestan KY358104; *H. emodica* Evenkia 1402 KY358101; *H. emodica* Kabardino Balkaria KY358125; *H. emodica* Kamchatka KY358124; *H. emodica* Karachay Cherkessiya KY358122; *H. emodica* Khabarovsk Botchi KY358126; *H. emodica* Perm KY358111; *H. emodica* Primorsky KY358127; *H. emodica* Taimyr 1 KY358088; *H. emodica* Taimyr 2 KY358103; ***H. emodica* Russia, Transbaikalia 1, 14-8-2011 Afonina # 27-11 (MHA ex LE) OK1589 MG701914**; ***H. emodica* Russia, Transbaikalia 2, Bichura, Afonina 01907 (MHA ex LE) OK 1604 MG701915**; *H. emodica* Transbaikalia 3 KY358080; *H. emodica* Yakutia KY358123; ***H. kuzenevae* Amurskaya Russia, Amurskaya Province, Zeya, Dudov #Br-12-109 (MW) OK 1590 MG701918**; ***H. kuzenevae* Russia, Evenkiya, Shcherbina s.n., 27.06.1992, (MW9042885) OK1600 MG701919**; ***H. kuzenevae* Russia, Zabaikalsky, 13 July 2012 Czernyadjeva # 2-12 (MHA ex LE) OK 1761 MG701920**; *H. kuzenevae* Amurskaya 1590 XXXXXX; *H. kuzenevae* Evenkiya 1600 XXXXXX; *H. kuzenevae* Transbaikalia 1761 XXXXXX; *H. mollis* Altai KY358083; *H. mollis* Bashkortostan KY358102; *H. mollis* Karachay Cherkessiya KY358082; *H. mollis* Karelia KY358081; *H. mollis* Kursk KY358110; *H. mollis* Murmansk KY358091; *H. mollis* Orenburg KY358079; *H. mollis* Tula KY358090; ***H. nemoralis* China Anhui China Anhui, Ignatov 05-4019 (MHA) OK1601 MG701913**; *H. nemoralis* Georgia KY358093; *H. nemoralis* Krasnodar KY358084; *H. nemoralis* Primorsky 1320 KY358087; *H. nemoralis* Transbaikalia KY358086; *H. nemoralis* USA Missouri KY358109; *H. stellata* Germany 1 LN714267; *H. stellata* Germany 2 LN714268; *H. stellata* Sweden LN714269; *H. stellata* Kenya LN714240 (sub *H. ciliata*); *H. striata* Portugal LN714266; *H. striata* Spain LN714265.