

## ON *MANNIA ANDROGYNA* (AYTONIACEAE, MARCHANTIOPHYTA) IN EASTERN ASIA

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**Abstract.** The discovery of *Mannia androgyna* (L.) A. Evans in Russian Asian and Japanese localities changes the conception of the distribution patterns of the taxon, previously regarded as principally a Mediterranean species. A description and illustrations based on specimens collected in Russian Asia and Japan are provided. The history of the taxonomic understanding of *Mannia androgyna* is briefly reviewed, and features differentiating closely related species are discussed.

**Key words:** Aytoniaceae, distribution, Hepatics, phytogeography, taxonomy

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### INTRODUCTION

*Mannia androgyna* (L.) A. Evans has been regarded as a Mediterranean hepatic distributed mainly in Southern Europe (Schumacker & Vána 2005) and North Africa (Wigginton 2004), although disjunctively occurring eastward to the Arabian Peninsula (Kürschner *et al.* 2001) and as far as the Indian subcontinent (Singh & Singh 2009). Recently it was found in the Russian Far East (Borovichev & Bakalin 2013b). In addition to the latter record, the first author later revealed the species in the Altay Republic, Chelyabinsk and Sakhalin Provinces (Russian Asia) and Saitama Prefecture (Japan). These records confirm a distribution of the taxon wider than previously known.

This paper lists new localities for the species and discusses its distribution pattern in light of the new data presented, and provides a description of *Mannia androgyna* based on available specimens from the area studied.

### HISTORICAL TAXONOMIC BACKGROUND

Raddi (1818) described the genus *Grimaldia* based on the single species *G. dichotoma* Raddi. Unfortunately the generic name proved to be an illegitimate later homonym of the name used for vascular plants *Grimaldia* Schrank published in 1805 [now generally treated as *Chamaecrista* sect. *Grimaldia* (Schrank) H. S. Irwin & Barneby]. Overlooking that evidence, Corda (1829) in Opiz's *Beiträge zur Naturgeschichte* accepted the genus *Grimaldia* Raddi with two species, *G. raddii* Corda and *G. michelii* Corda (both names being illegitimate – see below), but Opiz, the editor of the book, noticed the priority of *Grimaldia* Schrank and proposed to replace *Grimaldia* Raddi for *Mannia* (in honor of Dr. Wenzeslaus B. Mann). Nevertheless, *Grimaldia* *sensu* Raddi was used for a long time until the middle of the 20<sup>th</sup> century (Gottsche *et al.* 1844–1847; Leitgeb 1881; Schiffner 1893, 1908; Stephani 1898–1924; Müller 1954). In 1934 the generic name *Mannia* was restored to the literature by Wheeler (1934) and then used by Frye and

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Clark (1937), Evans (1938), Schuster (1953, 1992) and others. Evans (1938) stressed that the name *Mannia* must be accredited to Opiz rather than to Corda (the same with the combinations *M. raddii* and *M. michelii*).

Only Müller (1954) refrained from the usage of *Mannia* in favor of *Grimaldia* Raddi. He stated that *Marchantia androgyna* L. is distinct from *Grimaldia dichotoma* Raddi. The decision was connected with the fact that *G. dichotoma* is based on two different elements: *Marchantia triandra* Scop. (Scopoli 1772) and Micheli's polynomial *Hepatica minor, angustifolia, capitulo hemisphaerico* (Micheli 1729).

After the name *Mannia* had been widely accepted, another generic name for this taxon was found: *Cyathophora* Gray, validly published in 1821, with the single species *C. angustifolia* (Gray 1821). Since *Cyathophora* is earlier than *Mannia* it ought to be adopted formally. However, to avoid further nomenclatural changes, Grolle (1981, 1983b, c) proposed to conserve *Mannia* Opiz against *Cyathophora* Gray, and the Committee for Bryophyta accepted his proposal in 1988 (Ziljstra 1989).

Publishing his *Grimaldia dichotoma*, Raddi (1818) cited the earlier and validly published name *Marchantia triandra* Scop. (Scopoli 1772) in its synonymy. So, in addition to having an illegitimate generic name, *Grimaldia dichotoma* Raddi is a superfluous name [see ICN, Art. 52.1 and 52.2(e)]. Likewise, the names *Grimaldia raddii* Corda (= *Mannia raddii* Opiz) and *Grimaldia michelii* Corda (= *Mannia michelii* Opiz) are superfluous, since *Grimaldia dichotoma* Raddi (and therefore *Marchantia triandra* Scop.) is cited as a synonym of the former, and *Marchantia angustifolia* Neck. as a synonym of the latter. In fact, *Marchantia angustifolia* Neck. is also a superfluous name, because its synonymy completely repeats that of *Marchantia androgyna* L. Similarly, *Marchantia androgyna* is cited in the synonymy of *Cyathophora angustifolia* Gray, to make the latter superfluous as well. The earliest legitimate name of the discussed taxon at the rank of species is *Marchantia androgyna* L., so its epithet ought to be used to make the correct combination. This

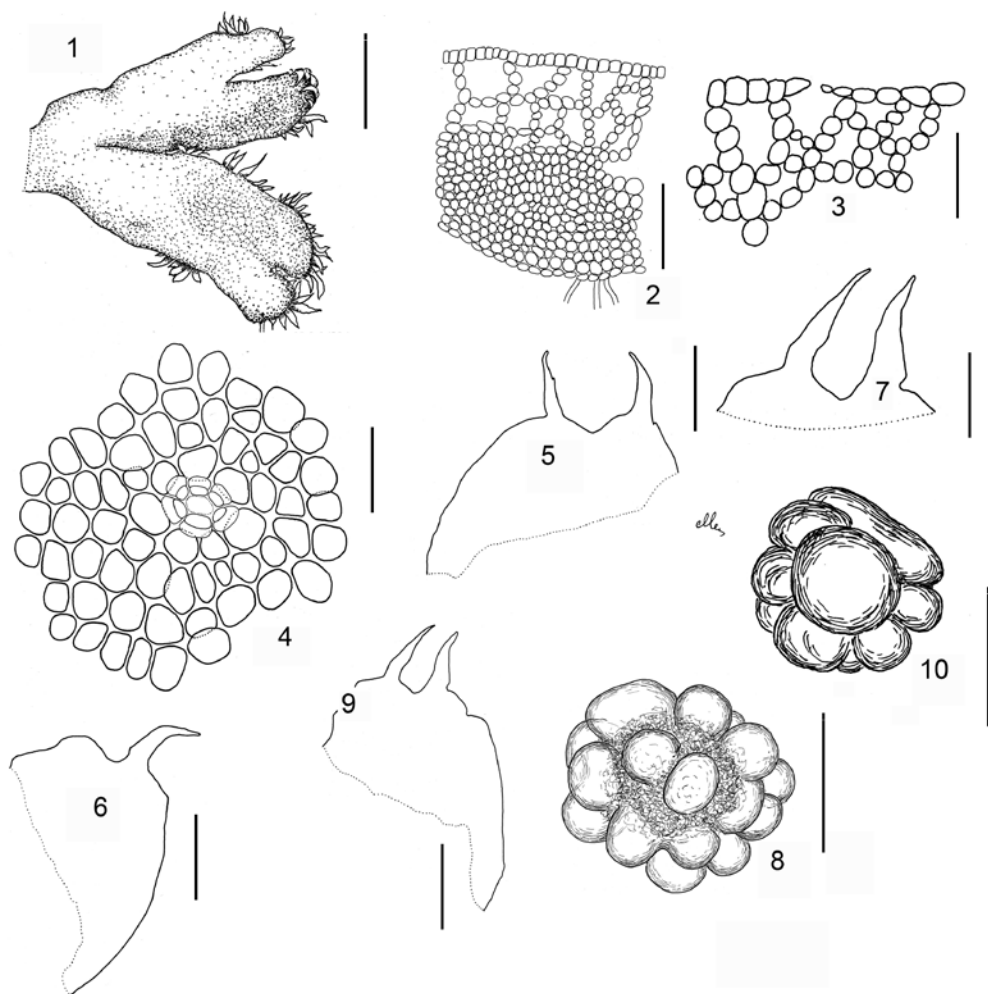
was done by Evans (1938), who published *Mannia androgyna* (L.) A. Evans.

Arnell (1961a) proposed the new combination *Mannia dichotoma* (Raddi) S. W. Arnell. Later, Udar and Chandra (1965), overlooking Arnell's valid combination (Arnell 1961a), cited his later paper (Arnell 1961b) where this name was only mentioned, and regarded Arnell's combination as 'comb. nudum'. As the result they created a superfluous combination: *Mannia dichotoma* (Raddi) Udar & Chandra. In addition, they cited *Marchantia androgyna* as a synonym of the name.

Grolle (1968) found *Mannia androgyna* and Micheli's polynomial *Hepatica minor, angustifolia, capitulo hemisphaerico* formally lectotypified by *Marchantia androgyna* L. Later Grolle suggested that the name *Grimaldia dichotoma* was a synonym of the name *Mannia triandra* and therefore proposed to consider the latter as lectotype, basing on Scopoli's specimen. That would make *Mannia triandra* a type of genus (Grolle 1975, 1983a, b). However, the ICBN Nomenclature Committee for Bryophyta (Ziljstra 1990) rejected Grolle's proposal and chose Micheli's polynomial (as the older one) as lectotype of *G. dichotoma*. Therefore the Linnaean name *Marchantia androgyna* has priority over *Grimaldia dichotoma*; *Mannia androgyna* is the type species of both *Mannia* and *Grimaldia* Raddi; the lectotype of *Mannia androgyna* is the same as the lectotype of *Grimaldia dichotoma*, and the combination proposed by Evans (1938) as *Mannia androgyna* is correct.

### *Mannia androgyna* (L.) A. Evans Figs 1 & 2

Chron. Bot. 4: 225. 1938. – *Marchantia androgyna* L., Sp. Pl.: 1138. 1753. – *Grimaldia dichotoma* Raddi, Opusc. Sci. (Bologna) 2: 356. 1818. – *Mannia dichotoma* (Raddi) S. W. Arnell, Bot. Not. 114: 179. 1961; *idem*, Svensk Bot. Tidskr. 55: 382. 1961b. *nom. inval.* – *Mannia dichotoma* (Raddi) Udar & Chandra, Canad. J. Bot. 43: 153. 1965. *nom. inval.* – *Grimaldia raddii* Corda in Opiz, Beitr. Naturgesch. 12: 646. 1829. – *Mannia raddii* (Corda) Opiz, Beitr. Naturgesch. 12: 646. 1829. – *Grimaldia michelii* Corda in Opiz, Beitr. Naturgesch. 12: 646. 1829. – *Mannia michelii* (Corda) Opiz, Beitr. Naturgesch. 12: 646. 1829. – *Marchantia angustifolia* Neck., Method. Musc.: 117. 1771. – *Cyathophora angustifolia* S. F. Gray, Nat. Arr. Brit. Pl. 1: 683.



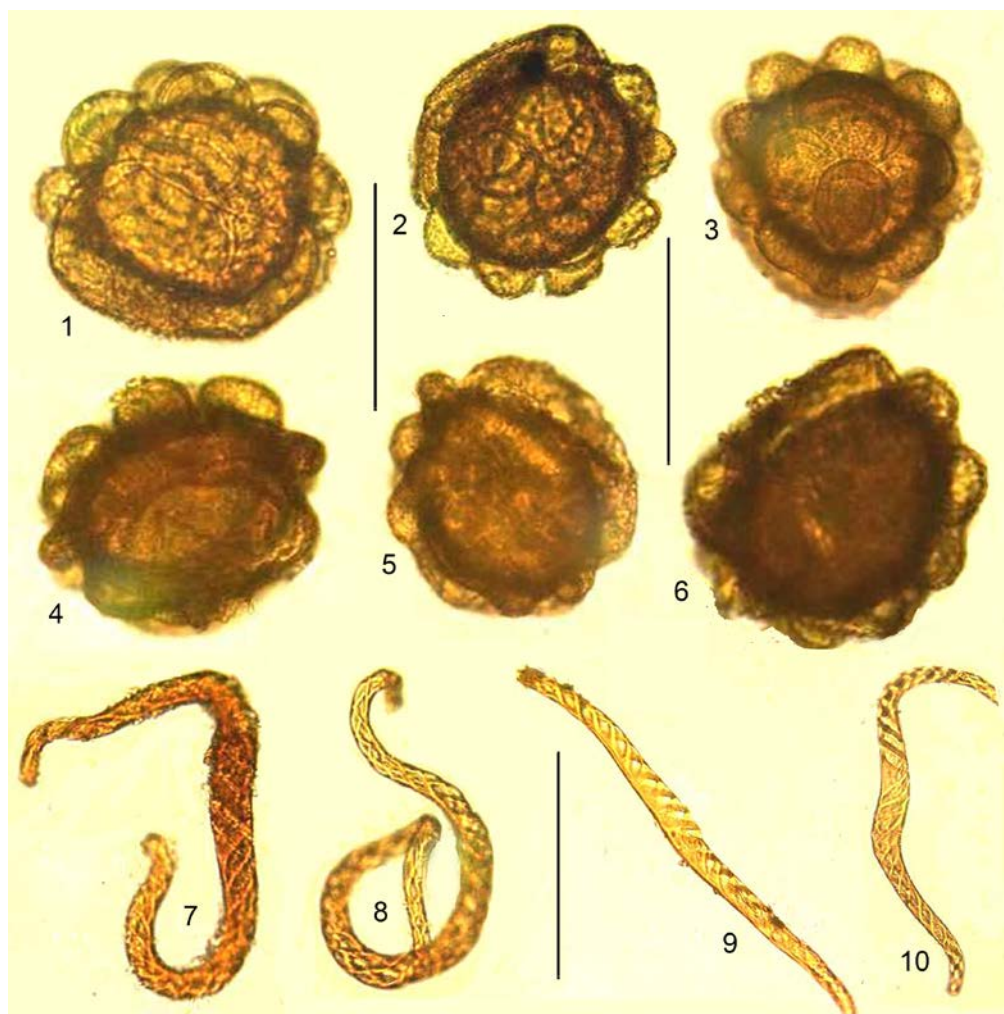
**Fig. 1.** *Mannia androgyna* (L.) A. Evans: 1 – habit of sterile plant, dorsal view; 2 & 3 – part of transverse section with air-pore; 4 – air-pore from dorsal epidermis of thallus; 5, 6 & 9 – ventral scales with appendages; 7 – appendages of ventral scale; 8 & 10 – distal face of spores. 1–7 & 9 – from Sakhalin Province, 23 July 2010, *Barckalov* (VBGI); 8 & 10 – from Altay Republic, 29 July 1991, *Ignatov & Ignatova*, (MHA). Scale bars: 1 = 3 mm; 5–7 & 9 = 600  $\mu$ m; 2 & 3 = 300  $\mu$ m; 4, 8 & 10 = 60  $\mu$ m.

1821. – *Duvalia angustifolia* Lindb., Not. Sällsk. Faun. Fl. Fenn. **9**: 285. 1868. – *Grimaldia androgyna* Lindb. Hep. Utveckl.: 26. 1877. – *Grimaldia capensis* Steph., Sp. Hepat. **1**: 90. 1898. – *Mannia capensis* (Steph.) S. W. Arnell, Mitt. Bot. Staatssamml. München **16**: 263. 1957. – *Mannia capensis* var. *pallida* S.W. Arnell, Hep. S. Africa.: 72. 1963.

ILLUSTRATIONS: Müller (1954: 345, fig. 62; 346, fig. 63 as *Grimaldia dichotoma*); Perold (1994: 10, fig. 1; 11, fig. 2 as *Mannia capensis*); Schill (2006: 111, fig. 4.2; 112, fig. 4.3); Casas *et al.* (2009: 31, fig. 3: 4–5);

Frahm (2010: 25). MAP: Müller (1954: 343, fig. 61 as *Grimaldia dichotoma*); Schill (2006: 113, fig. 4.33).

*Thalli* thick, strongly xeric habit, not fragrant, small, lobes (4–)5–12(–14) mm long, 1–3 mm wide, forming extensive,  $\pm$ pure patches, very sparingly dichotomously branched, frequently with both ventral and terminal innovations; *segments* linear-lingulate to oblong, rather leathery; *apex* rounded, ventral scale appendages mainly overlapping lobe apex; *upper surface* smooth, slightly



**Fig. 2.** *Mannia androgyna* (L.) A. Evans: 1–3, 5 & 6 – distal face of spores; 4 – proximal face of spore; 7–10 – elaters. Scale bars: 1–6 = 50  $\mu$ m; 7–10 = 70  $\mu$ m. 1–3 & 7–9 from Altay Republic, Ignatov & Ignatova, 29 July 1991 (MHA); 4–6 & 10 from Japan, Inoue, 6 July 1957 (TNS).

concave, not reticulate, pores visible with hand lens as whitish points, brownish or whitish lacunose when disintegrating, color of upper surface green, in older parts becoming brownish; *thallus margins* dark purple to slightly purple, slightly undulate, when dry slightly to strongly inrolled, tubular and black or not strongly inrolled. *Dorsal epidermis* delicate to firm, mostly colorless to rose-tinged; *cells* 12–18(–20)  $\times$  (15–)20–30  $\mu$ m, with thin to slightly thickened walls and distinct trigones; *pores* simple, only slightly elevated above

epidermis, 15–28  $\mu$ m in diameter, surrounded by 2–3 concentric rings of (5–)6–7(–8) cells in each, cell walls thin or slightly thickened. *Aerenchyma* compact, occupying ca 1/3–1/2 of thallus height in the middle; *air chambers* small, rounded to subisodiametric, 2–3-layered with few free secondary filaments or without them; *ventral tissue* occupying ca 2/3–1/2 of thallus height in the middle and absent in the wing, parenchymatous, consisting of thin-walled cells; *oil-bodies* lacking or present, pale-greyish in both aerenchyma and ventral tissue.

*Midrib thallus segment* 340–650  $\mu\text{m}$  thick in cross section,  $\pm$  well-defined. *Rhizoids* smooth and pegged, hyaline to purplish towards base, covering ventral surface of midrib of thallus. *Ventral scales* purple to reddish with sometimes pale purple margins, in two rows on each side of midrib, semicircular to broad-semicircular or lunate, sometimes with a few slime-papillae on margin; *body size* (500–)600–1200  $\mu\text{m}$  long and (250–)350–900  $\mu\text{m}$  wide; *appendages* two, subulate, hyaline or reddish, margins irregularly serrate or irregularly weakly crenulate, 150–600(–700)  $\mu\text{m}$  long and (80–)100–300  $\mu\text{m}$  wide; *appendage apex* long- to shortly acute to acuminate; *oil bodies* numerous, 10–25  $\mu\text{m}$  in diameter, present in both body and appendages. *Sexual condition* usually paroicous or terminal-autoicous, occasionally female-ventral autoicous. *Anteridia* situated on main thallus on other dichotomous bearing a female receptacle or equally long branch of a dichotomy bearing an archegoniophore (terminal-autoicous) or arising dorsally on leading thallus behind female receptacle (paroicous), but sometimes on main thallus with archegoniophore on shorter ventral branch (female-ventral autoicous); *androecial papillae* in clusters or loosely dispersed, conspicuous, purplish. *Gynoecea* in apical notch of terminal branches of thallus or borne on shorter ventral branches; *stalk of receptacle* brownish green, frequently brownish at base or below receptacle, 10–15 mm long, with single rhizoidal furrow. *Archegonial scales* hyaline to whitish, irregularly triangular-ovate or rounded. *Carpoccephalum* hemispherical, yellowish green when young, mature turning green and often purple at margins; *disc* convex, 3–4-lobed, each involucre with single sporophyte; involucre margin membranous; pseudoperianth lacking. *Capsule* large, globose, with single-layered walls; without thickenings. *Spores* yellow-brown to brownish, globose, 45–70  $\mu\text{m}$  in diameter, distal face distinctly saccate, bearing very conspicuous hemispherical papillae, mostly separated from each other, with distinct, large hemispherical exosporial cup on proximal face. Elaters yellowish brown to straw-colored, 100–210  $\mu\text{m}$  long, 8.0–9.5  $\mu\text{m}$  width at middle, trispiral.

#### DIFFERENTIATION AND VARIATION

*Mannia androgya* is characterized by pale-grayish oil-bodies in both the aerenchyma and basal tissue, the presence of paroicous- or terminal-autoicous-, rarely female-ventral autoicous inflorescences, and saccate spores with a conspicuous proximal disc. *Mannia androgya* appears to be most similar to *M. californica* and *M. fragrans*. It differs from *M. fragrans* in the following characters: (i) never aromatic when fresh, in contrast to the commonly aromatic (cedar-oil) smell of *M. fragrans*; (ii) dorsal surface green with pores visible with a hand lens as whitish points rather than dorsally bright or dark green, sometimes purplish without visible pores; (iii) even in female branches, small, deep purplish scales not forming a dense cluster at the thallus apex, unlike the bleached appendages of scales commonly forming a conspicuous cluster at the apex in *M. fragrans*, especially noticeable in female branches; and (iv) antheridia in loosely or densely aggregated clusters, vs. antheridia forming a slightly upraised disc in *M. fragrans*. *Mannia androgya* and *M. californica* are more similar morphologically and can be confused. *Mannia androgya* may be distinguished from *M. californica* by the following characters: (i) *M. androgya* has pale grayish oil-bodies in both the aerenchyma and basal tissue, vs. dark blackish oil-bodies in *M. californica*; (ii) generally paroicous or terminal-autoicous inflorescences, vs. female-ventral autoicous in *M. californica*; and (iii) saccate spores, vs. alveolate in *M. californica*.

Most authors state that *M. androgya* is usually paroicous (antheridia arising dorsally on leading thallus behind female receptacle – called terminal-autoicous by Schill 2006) or terminal-autoicous (antheridia situated on other branches of main thallus bearing a female receptacle or an equally long branch of a dichotomy bearing an archegoniophore), rarely female-ventral autoicous (female gametangia occur on ventral side branches). In contrast, *M. californica* is characterized by a uniformly autoicous inflorescence with gynoecea located on the ventral branches (e.g., Stephani 1898–1924; Huggonot & Schill 2006; Schill *et al.* 2008). Studies of abundant material

from Japan revealed that the species is able to bear both ventral and terminal autoicous inflorescences, but the latter is more common. Sometimes early-decaying thallus bases give the appearance of being dioicous, but careful examination always shows that the male and female branches originally were united in a single thallus. Similar cases of pseudodioicous inflorescences were described in *Sauteria alpina* (Nees) Nees (Cleveaceae) (Schuster 1992; Borovichev *et al.* 2012).

**ECOLOGY.** In respect of its ecology, *Mannia androgyna* is broadly similar to *Mannia fragrans* (Balb.) Frye & L. Clark, tending to occupy dry or rarely wet soil-filled crevices in rock outcrops and cliffs at open sites. The majority of records from the studied area are from coastal cliffs or open cliffs along watercourses but avoiding direct exposure to running water. Sometimes the species occurs on dry slopes under semi-xeric shrubs such as *Caragana* spp. and *Lespedeza* spp., as well as in discontinuous low grass communities on steep slopes to sea coasts, lakes and rivers (away from direct contact with water). Other species with which *Mannia androgyna* sometimes grows include *Reboulia hemisphaerica* (L.) Raddi and *Targionia hypophylla* L.

**DISTRIBUTION.** The species has a generally Mediterranean–circum-Tethian distribution, though also occurring in central Japan in areas with more or less xeric conditions. In Europe the distribution area covers Portugal (including the Azores, Madeira and Canary Islands), Italy (including Sardinia and Sicily), Spain (including the Balearic Islands), Greece (including Crete), Serbia, Bulgaria, Croatia, Montenegro, Turkey, Bosnia and Herzegovina, Albania, France (including Corsica), Austria, Switzerland (Söderström *et al.* 2002; Schumacker & Váňa 2005; Schill 2006) and Ukraine (Borovichev & Nyporko 2014). In Africa the species has been reported from Morocco, Algeria, Chad, the Cape Verde Islands, Eritrea, Ethiopia and the island of Socotra (Wigington 2004). Eastward, *M. androgyna* spreads to the Arabian Peninsula (United Arab Emirates: Kürschner *et al.* 2001) and the Indian Subcontinent (Pakistan, as *Asterella calciatii* (Gola) Kachroo

& Bapna: Long 2006; Himalayan India: Singh & Singh 2009). Within Russia the species was reported from the North Caucasus in the Republic of Adygeya (Konstantinova *et al.* 2009) and is also found in the Russian Far East: Primorsky Territory and Amurskaya Province (Borovichev & Bakalin 2013b). There is also a record by Brotherus (1892) from ‘Osetia, Lars & Kobi ad fl. Terek’ that probably relates to North Ossetia (currently a republic within Russia) or to South Ossetia. The present account provides additional data on the distribution of the taxon in the Altay Republic (South Siberia), Chelyabinsk Province and Sakhalin Province. Eastward of Russia we recorded this species from Japan in Ohtaki-mura, Chichibu Mts.

**SPECIMENS OF *MANNIA ANDROGYNA* EXAMINED** (newly reported areas asterisked): RUSSIA. \*ALTAY REPUBLIC, Altay State Nature Reserve, Schebalino District, Katun River Valley near Ust'-Sema, ~51°40'N, 85°52'E, 580 m alt., rather dry slope, on soil rich in humus, in shade of *Caragana* shrubs, with sporogonium, 29 July 1991, *M.S. Ignatov & E.A. Ignatova s.n.* (MHA); *ibidem*, rock outcrops near Katun bank, 28 July 1991, *M.S. Ignatov & E.A. Ignatova s.n.* (MHA); *ibidem*, eastern shore of Teletzkoe Lake, Chiri, xeric S-facing rocky slope, ~51°22'N, 87°50'E, 450 m alt., on dry soil among rocks, 19 July 1991, *M.S. Ignatov s.n.* (MHA); \*CHELYABINSKAYA PROVINCE, Zyuratkyul' National Park, Mal'j Moskal' Range, 54°54'41.7"N, 59°09'15.4"E, limestone cliffs along road, on soil, 22 May 2009, *I.N. Urbanavichene s.n.* (LE; as *Mannia fragrans* var. *inodora*); AMURSKAYA PROVINCE, Bureinsky District, left side of Bureya River near Cheudga Settlement, 12 July 1973, *D.I. Martynenko s.n.* (VBGI, KPABG; as *Mannia fragrans*); \*SAKHALIN PROVINCE, Kuril Islands, Schikotan Island, Bezymyannaya Bay near Nepokorniy Cape, ~43°42'N, 146°38'E, on wet rocks near stream, on wet fine-grained soil, 23 July 2010, *V.Yu. Barkalov s.n.* (VBGI, KPABG; as *Reboulia hemisphaerica*); PRIMORSKY TERRITORY, \*Ol'ginskiy District, Vatovskogo Peninsula, northern edge of Vladimir Bay near Ol'ga Settlement, 43°53'00"N, 131°30'37"E, 25 m alt., fine-grained ground in crevice of coastal cliff, 21 Sept. 2007, *V.A. Bakalin #P83-16-07* (VBGI, KPABG; as *Reboulia hemisphaerica*); Khankajsky District, Khankajsky State Reserve, Luzanovskaya Sopka cordon, 16 July 1997, *S.K. Gambaryan s.n.* (VBGI, KPABG; as *Mannia fragrans*); Ussurijsky District, neighborhood of Kamenushka Settlement, left side of Komarovka River Valley, 28 May 2008, *V.A. Bakalin #P-1-4-08* (VBGI, KPABG;

as *Athalamia nana* (Shimizu & S. Hatt.) S. Hatt. and *Targionia hypophylla* L.). \*JAPAN, OHTAKI-MURA, Chichibu, Saitama Prefecture, 50°18'N, 130°28'E, on wet fine-grained soil, with sporogonia, 6 July 1957, *H. Inoue* #8086 (TNS 142061; as *Mannia levigata* Shimizu & S. Hatt.,<sup>2</sup> 7 July 1957, *H. Inoue* #8084 & 8085 (TNS 202602, 202603 as *Mannia levigata*).

SPECIMENS OF *MANNIA CALIFORNICA* EXAMINED: PAKISTAN, Northwest Frontier Province, Dunga Gali (North of Murree), 20 August 1990, *M. Higuchi* #19773 (TNS; KPABG); *ibidem*, Kaghan Valley, Bajakot, 24 July 1990, *M. Higuchi* # 20313 (TNS; KPABG); USA, Arizona, Santa Cruz County, Santa Rita Mts, Madera Canyon, 25 March 1995, *W.B. Schofield* & *R.M. Schuster* #B158559 (TNS).

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<sup>2</sup> Japanese specimens collected by H. Inoue (##TNS 142061, 202602, 202603) near *locus classicus* of *Mannia levigata* Shimizu & S. Hatt. and identified by him as *M. levigata* are characterized by: (i) both parocious and female-ventral autoicous inflorescences; (ii) pale grayish oil-bodies in both aerenchyma and basal tissue; and (iii) yellow-brown to straw-colored saccate spores (Fig. 2). Due to those features we re-identified them as *M. androgyna*. However, this does not mean that *M. levigata* is a synonym of *M. androgyna*. The former is characterized (unlike *M. androgyna*) by (i) a delicate, pale to deep green thallus; (ii) having plants not of xeric habit; (iii) dorsal epidermal cells almost invisible; (iv) having a single ventral scales appendage; and (v) having spores distally areolate or ridged. It was discussed by Borovichev and Bakalin (2013a). Schill (2006: 124) regarded *M. levigata* as a synonym of *M. californica*; this is contrary to our previous observations discussed by Borovichev and Bakalin (2013a).

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