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TAXONOMY OF *MANNIA CONTROVERSA* (*MARCHANTIIDAE*, *AYTONIACEAE*) INCLUDING A NEW SUBSPECIES FROM EAST ASIA

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Mannia controversa (Meyl.) Schill *comb. nov*. (*Marchantiidae*, *Aytoniaceae*), a long-forgotten European taxon, is fully redescribed and a lectotype selected. It is reported from its original localities in the Swiss Alps and new sites in the Austrian and French Alps. A series of specimens from eastern Asia are closely related and are described as *Mannia controversa* subsp. *asiatica* Schill & D.G.Long. For the species, differences with other *Mannia* species are summarised and for its two subspecies, descriptions, illustrations (including SEM images) and a key are provided along with notes on ecology and distribution maps.

Keywords. *Aytoniaceae*, liverworts, *Mannia controversa*, *Marchantiidae*, spore SEM, taxonomy.

Introduction

Grimaldia controversa was originally described by C. Meylan in 1924 but has been largely overlooked since that time, probably because Müller (1954) reduced it to a synonym of *Grimaldia fragrans* (Balb.) Corda ex Nees [= *Mannia fragrans* (Balb.) Frye & L.Clark]. The original description by Meylan is based on 10 specimens from the Swiss Alps which were mostly collected by himself, H. Gams and H. Gilomen. Meylan did not designate a type specimen in his protologue so a lectotype is needed from the original material he used in preparing the description. Meylan characterised his new species by its thin-walled epidermal cells, bearded receptacle and presence of many scales around the base of the receptacle stalk; the spores he described as dark brownish yellow in colour, 50–65 μm across, with 7–8 areolae across. In his key to the Swiss species of *Grimaldia* he stressed the absence of strongly enlarged, whitish scales at the thallus apices as the main difference with *G. fragrans*. He also noted the restriction of the new species to the alpine zone and discussed the similarity of its thallus to that of *Grimaldia dichotoma* Raddi *nom. illeg*. [= *Mannia androgyna* (L.) A.Evans] and of its sporophyte to *G. sibirica* (Müll.Frib.) Müll.Frib. [= *M. sibirica* (Müll.Frib.) Frye & L.Clark].

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During preparation of a world revision of *Mannia* by the first author (Schill, 2006) it was not possible to borrow the original material of *Grimaldia controversa* for study and this name was therefore left as a doubtful species. In that work a number of specimens from Qinghai Province of China collected by the second author were studied and were considered to represent a distinctive new taxon, given the manuscript name *Mannia asiatica*, which was not formally published. Thanks to Michelle Price (Geneva) we have now been able to borrow the original material of *Grimaldia controversa* for study and its significance immediately becomes clear as follows: (1) it appears that the synonymy of *G. controversa* under *Mannia fragrans* is erroneous, (2) several recent specimens collected from Austria by H. Köckinger and R. Düll, and from France by G. Een and L. Castelli represent the same taxon, and (3) the material from East Asia treated provisionally as *Mannia asiatica* is closely allied to European *G. controversa*.

The present study therefore addresses in detail the status of these European and Asiatic specimens and results in the conclusion detailed below that they are best treated as a single distinct species of *Mannia*, *M. controversa*, which comprises two disjunct subspecies, subsp. *controversa* and a new subsp. *asiatica*. Subspecific rank has been adopted for these on account of their small but significant differences, particularly in spore ornamentation, and their large disjunction. A full redescription of *Mannia controversa* is therefore given below followed by treatment of its two constituent subspecies.

Revised Description of *Mannia controversa*

Mannia controversa (Meyl.) Schill, **comb. nov. Figs 1–6.**

Grimaldia controversa Meyl., Les hépatiques de la Suisse. Beiträge zur Kryptogamenflora der Schweiz. Band VI. Heft 1: 87 (1924). – Type: [Switzerland, Vaud] Près du Glacier des Martinets, 2200 m, ix 1918, *Ch. Meylan* s.n. (lecto LAU, selected here). Syntype citations: 'Localités suisse: Vaud: Alpes d'Alesse, 2200 m (Gams); Près du Glacier des Martinets, 2200 m (Meylan); Berne: Col du Rawyl, 2400 m (Gilomen); Grisons: Piz Fuorn, 2400 m; Piz Nair, 2600 m; Forcletta del Val del Botsch, 2500 m; Val Ftur, 2600 m; Mount la Scherra, 2500 m; Val Tavrü, 2300 m; Schambrina près Scarl, 2300 m (Meylan)'.

Thalli spreading and forming extensive patches, small, linear and narrow, rather leathery, thin, dorsally light green to brownish green or sometimes purplish, areolae sometimes visible, brownish or whitish lacunose, in older parts becoming brownish or whitish when disintegrating, xeromorphic, not fragrant; vegetative branches of terminal dichotomies, occasionally with terminal innovations; lobes (1.6–)4–19.5(–28) mm long, (0.4–)0.6–4.8(–8.3) mm wide, margins dark purple or only slightly purple, margins sometimes slightly undulate; ventrally purple; when dry, margins slightly to strongly inrolled, tubular and black or not strongly inrolled; *lobe apex* rounded and middle often grooved; *thallus* in transverse section (t.s.) (0.1–)0.2–0.9(–1) mm thick, shape

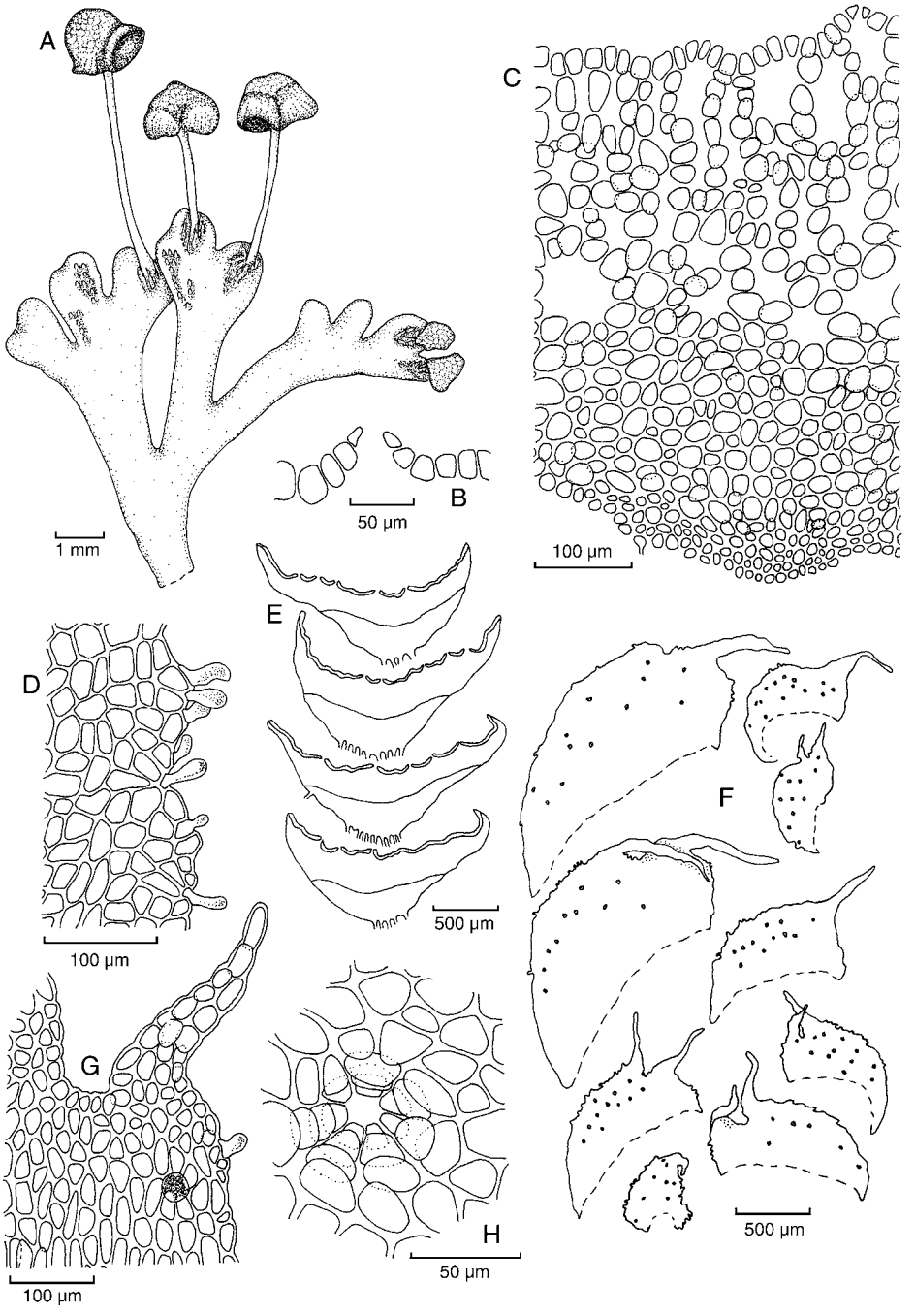


FIG. 1. *Mannia controversa* (Meyl.) Schill subsp. *controversa*. A, thallus showing androecia and archegoniophores; B, simple air pore of dorsal epidermis, side view; C, E, transverse section of thallus; D, ventral scale, margin; F, ventral scales; G, ventral scale appendage; H, air pore of dorsal epidermis. A, D, F, H, *Köckinger* 11451 (E); B, C, E, *Een* s.n. (S); G, *Castelli* 7 (S). Drawn by D. B. Schill.

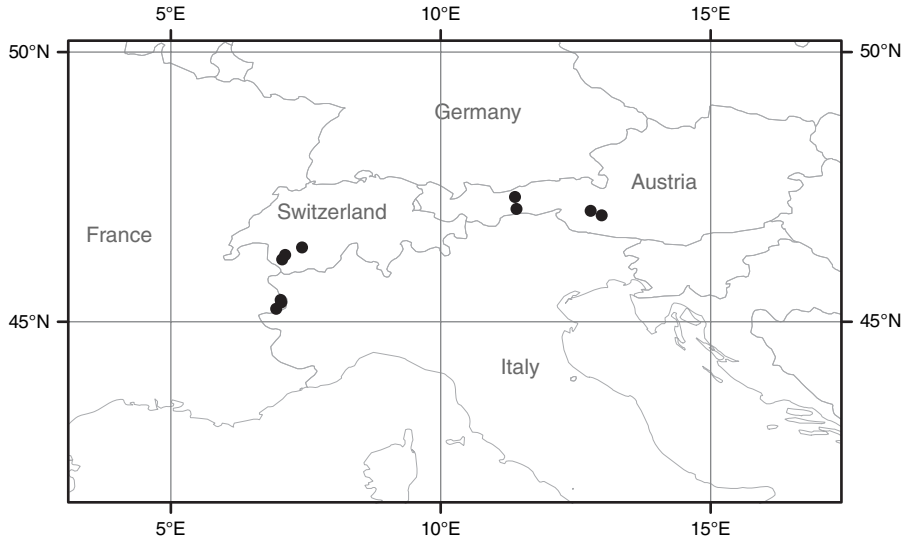


FIG. 2. Distribution of *Mannia controversa* subsp. *controversa* in Europe based on specimens studied.

usually flat, concave to broadly concave or triangular in section; *dorsal epidermis cells* (11.6–)14.5–32(–34.8) μm long, (7.2–)8.7–29(–32) μm broad, cell walls of dorsal epidermis rather thick-walled, often showing big corner thickenings (trigones) when focusing; *air pores* (11.6–)14.5–31.9(–43.5) μm in diameter, with 2–3 concentric rings of cells, outer ring of (5–)6–8(–10) cells, cells (10.1–)14.5–26.1(–29) μm long, (10.1–)11.6–34.8(–39.2) μm wide, inner ring of 6–7(–8) cells, (8.7–)10.1–20.3(–23.2) μm long, (5.8–)8.7–20.3(–26.1) μm wide, pores visible with hand-lens, of whitish colour; *assimilation tissue* rather loose to sometimes slightly compact, (92–)115–460(–506) μm high in t.s., as thick as or up to 2 times the size of basal tissue, 3–4 somewhat rounded small or big air chambers or sometimes with one upper row of vertical orientated air chambers and smaller rounded air chambers below (2–3 layers); *basal tissue* (80.5–)103.5–460(–495) μm high in t.s. with inconspicuous yellowish or dark brownish oil cells (*Köckinger* 99-1645, *Köckinger* 11451) in assimilation and storage tissue. *Rhizoids* arising from ventral epidermis, smooth and pegged, hyaline or purplish/brownish towards base. *Ventral scales* in two rows, overlapping each other and midline of thallus, purple with sometimes paler margins or light purple, (0.4–)0.5–1.5(–1.8) mm long, (0.2–)0.3–1.1(–1.3) mm broad, semicircular to oblong or broad semicircular, small slime papillae present on margin, *oil cells* 5–22(–33), marginal and central, occasionally also present in appendages; *appendages* 1–2(–3) unlobed or occasionally unequally bifid, sometimes light or bleached, (0.1–)0.2–0.8(–0.9) mm long, (0.06)0.08–0.4 mm broad at base, subulate, margins irregularly serrate or irregularly weakly crenulate, gradually narrowing into acute tip, overlapping mainly lobe apex and only rarely lobe margin and folding upwards over edge of thallus.

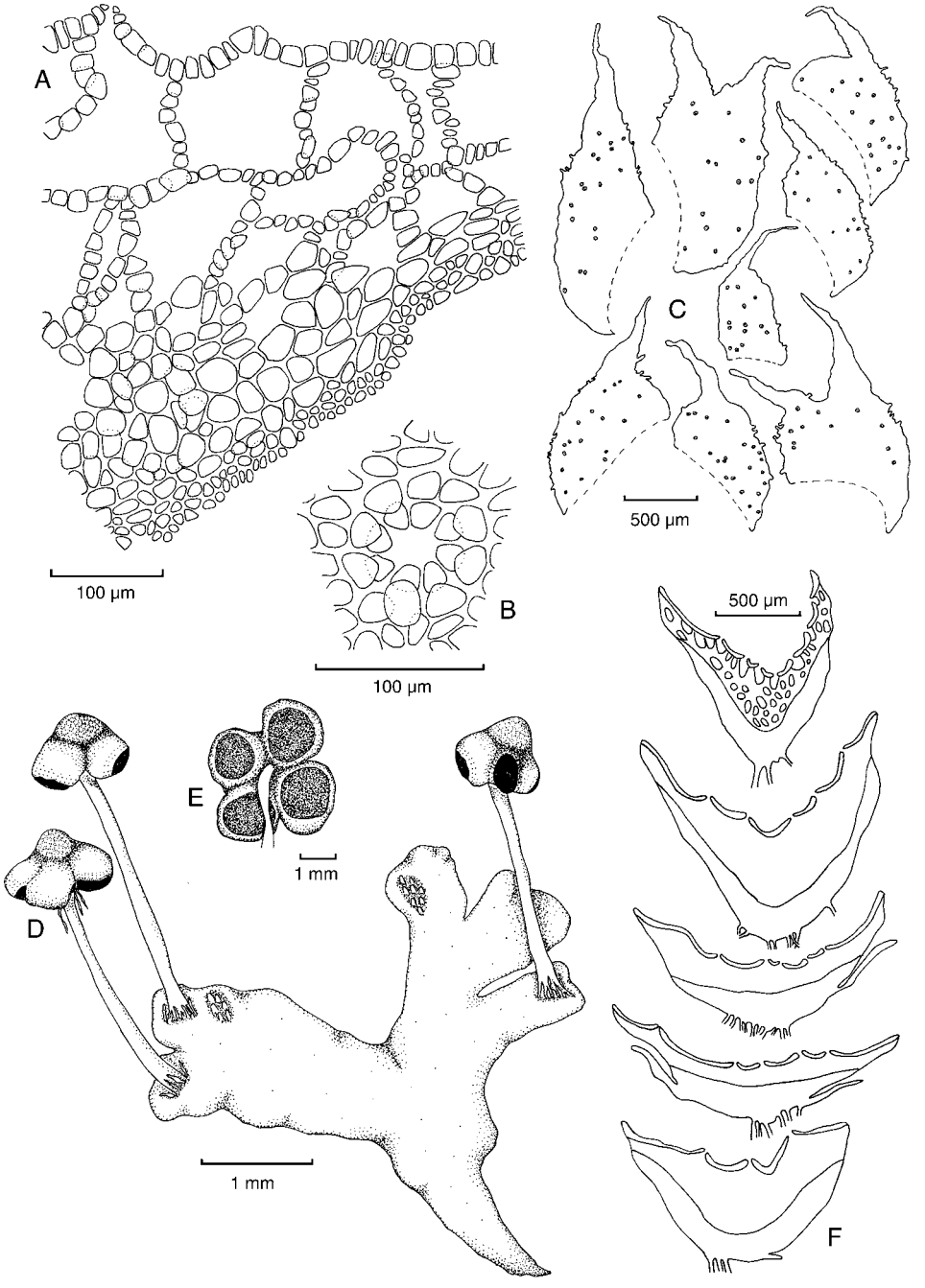


FIG. 3. *Mannia controversa* (Meyl.) Schill subsp. *asiatica* Schill & D.G.Long. A, transverse section of thallus; B, air pores of dorsal epidermis; C, ventral scales with appendages; D, thallus showing androecia and archegoniophores; E, receptacle from below; F, transverse section of thallus. A–C, F, *Long* 27016 (E); D, E, *Long* 26952-b (E). Drawn by D. B. Schill.

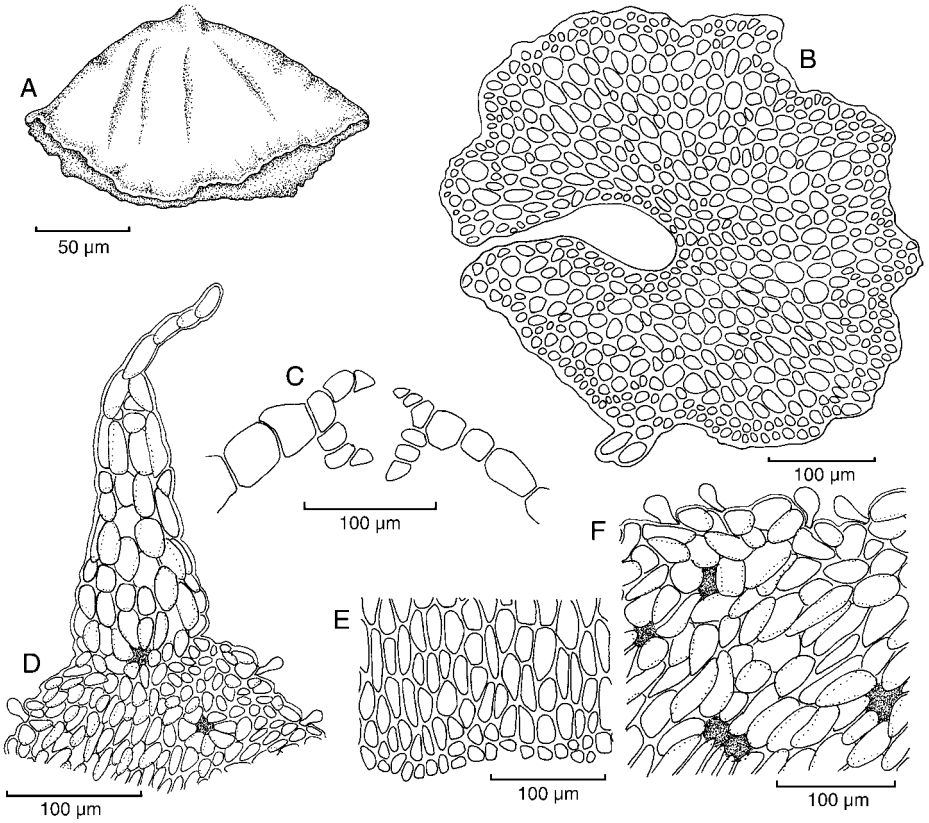


FIG. 4. *Mannia controversa* subsp. *asiatica*. A, side view of empty capsule; B, transverse section of stalk; C, compound pores of receptacle; D, ventral scale appendage; E, part of capsule margin; F, ventral scale, margin. A, E, *Long* 27270 (E); B–D, F, *Long* 27016 (E). Drawn by D. B. Schill.

Sexual condition terminal-autoicous[1] with androecia borne on shorter or equally long branch of a dichotomy, of which the other branch often bears an archegoniophore, or androecia borne terminally without associated gynoecia; sometimes *dorsal-autoicous* with androecia on the main thallus. *Androecia* inconspicuous or forming a poorly defined, slightly upraised rounded cushion or terminal slight depression or notch with purplish ostioles, usually several, often in terminal position but sometimes also dorsal along midline of thallus; ostioles ± conical, purplish, often in clusters or loosely aggregated when dorsal, surrounding thallus surface sometimes of purplish colour. *Gynoecia* with archegoniophores deriving from terminal notch of mid-thallus, surrounded by whitish scales; *receptacle* hemispherical, nodular/warty,

[1] Note: Definition of sexual condition follows Schill (in prep.).

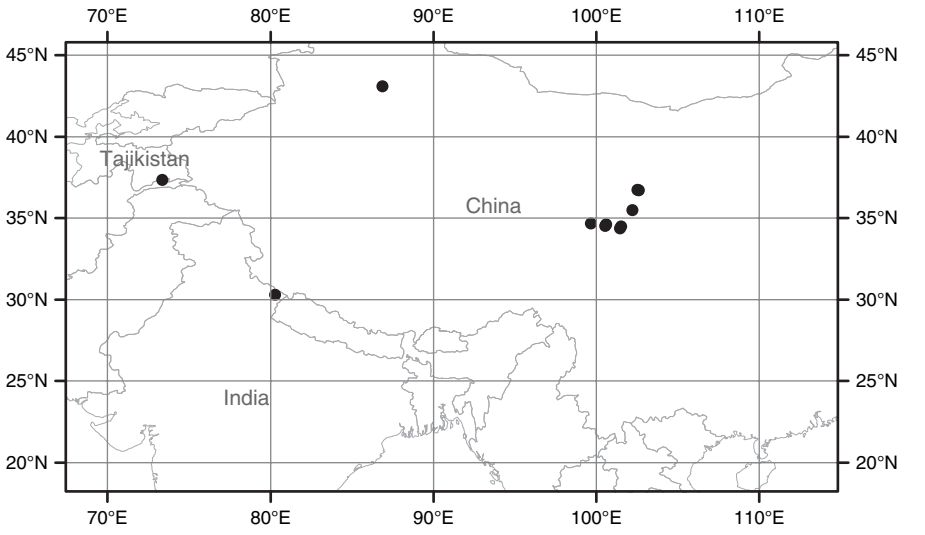


FIG. 5. Distribution of *Mannia controversa* subsp. *asiatica* in Asia based on specimens studied.

usually naked to sometimes slightly bearded, yellowish-green when young, mature turning into green and often tarnishing purple at margins; *stalk* brownish green, sometimes brownish at base or below receptacle, often with hyaline scales, 0.2–0.8 mm in diameter, irregularly triangular-ovate or rounded, ridged when dry, variable in length, (0.9–)1.2–22.4(–25) mm long, with single rhizoidal furrow, in t.s. 1–2 outer brown smaller strongly incrassate thick-walled cell rows and inner cells thin-walled, bigger, colourless, incrassate with minute to convex trigones; *receptacle* bearing 1–4(–5) capsules; *capsules* black when mature, yellow when young, cells yellowish brown, irregularly hexagonal, incrassate with minute trigones; lid irregularly rounded, (0.6–)0.7–1.7 mm in diameter, annular thickenings absent, cells incrassate, irregular hexagonal or rounded to rectangular, often strongly overlapping each other. *Spores* yellow to yellowish brown, (43.5–)46.4–78.3(–84.1) μm in diameter (light microscope), (43.6–)51–72(–74.4) μm in diameter (SEM); weakly trilete; with similar sculpturing on proximal and distal surfaces; distally either incompletely areolate with deep areolae or regularly to incompletely areolate with areolae quite shallow, (5–)6–10 areolae across, on surface minutely papillate with pits; on proximal side irregularly areolate or regularly to incompletely areolate; proximal disc absent, equatorial apertures conspicuous to sometimes only inconspicuous, usually 3; equatorial rim inconspicuous. *Elaters* yellow to brownish yellow, surface slightly minutely roughened, (150.8–)159.5–324.8(–402) μm long, (8.7–)10.1–17.4(–20.3) μm broad at middle, (2.9–)5.8–8.7(–10.2) μm broad at tip, 2–3(–4)-spiral.

Chromosome number unknown.

Taxonomic note

Although Meylan (1924) defined *Grimaldia controversa* in part by the presence of a beard below the receptacle, the beard is variably developed and completely absent in some specimens.

Relationships of *Mannia controversa* to Other *Mannia* Species

Mannia controversa is a distinctive species based on a range of morphological characters, in particular spore ornamentation and sexual condition. As stated above, Meylan (1924) compared *Grimaldia controversa* with both *G. dichotoma* [= *Mannia androgyna*] and *G. sibirica* [= *M. sibirica*]. However, in our opinion it is closest to *M. fragrans* and should be classified in subgenus *Mannia* (Schill, in prep.). It could, however, be confused with all six other species of the genus, which are all found in Europe and Asia. The differences are given below. Spores of all species are illustrated by Schill (2006, and in prep.).

(a) *Mannia sibirica* (Müll.Frib.) Frye & L.Clark.

In spores of *Mannia controversa* a proximal disc is always absent whereas it is present in *M. sibirica*. Spores are generally larger in *Mannia controversa* than in *M. sibirica* although this is not always reliable as there is sometimes an overlap. Sterile specimens can be very difficult to distinguish, though most specimens studied were fertile.

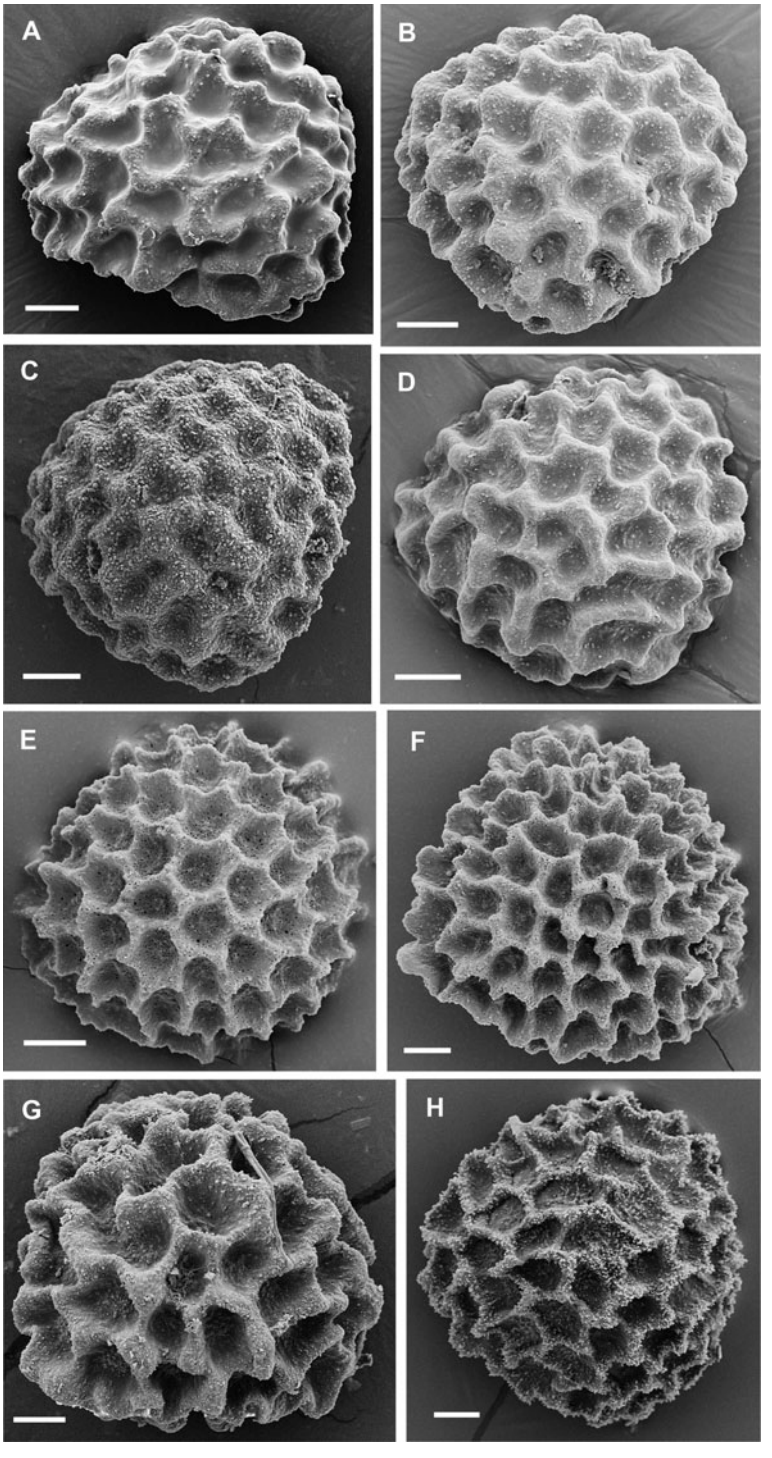
(b) *Mannia androgyna* (L.) A.Evans.

In *Mannia androgyna* the sexual condition is usually dorsal-autoicous (occasionally female-ventral autoicous); terminal-autoicy is the common condition in *M. controversa* although subsp. *controversa* sometimes can also be dorsal-autoicous. Spore ornamentation is an excellent character for diagnosis when plants are fertile: spores in *Mannia androgyna* are saccate with a conspicuous proximal disc whereas in *M. controversa* spores are areolate without a proximal disc.

(c) *Mannia fragrans* (Balb.) Frye & L.Clark.

Mannia fragrans is dioicous whereas *M. controversa* is monoicous; antheridial ostioles in *M. fragrans* are very conspicuous and arranged in a well-defined usually triangular disc in a terminal position on the thallus whereas such a disc-like structure cannot be observed in *M. controversa*. A bearded thallus apex is absent in *Mannia controversa* as is the strong cedar-oil smell of *M. fragrans*.

Fig. 6. *Mannia controversa* subsp. *controversa* (A–D) and *Mannia controversa* subsp. *asiatica* (E–H) spore from distal view. A, lectotype of *Grimaldia controversa*, Switzerland, *Meylan* s.n. (LAU); B, France, *Een* s.n. (S); C, Austria, *Köckinger* 99-1645 (E); D, Austria, *Düll* s.n. (E); E, holotype, China, *Long* 27032 (E); F, China, *Long* 26951-b (E); G, India, *Duthie* 3757 (BM); H, Tajikistan, *Boboradzchabov* 802 (JE). All scale bars 10 μm.


A
B
C
D
E
F
G
H

(d) *Mannia californica* (Gottsche ex Underw.) L.C.Wheeler.

The occurrence of dark brown oil cells is a common feature of *Mannia californica* (Hugonnot & Schill, 2006) but they are usually of pale colour in *M. controversa*. Regarding spore characters *Mannia californica* has a proximal disc, which is absent in *M. controversa*.

(e) *Mannia pilosa* (Hornem.) Frye & L.Clark.

Mannia pilosa is typically male-ventral autoicous. Spore ornamentation in *Mannia pilosa* is very different from that of *M. controversa*: the fine distal ornamentation in *M. pilosa* is spongy whereas in *M. controversa* it is minutely papillate.

(f) *Mannia triandra* (Scop.) Grolle.

Mannia controversa has a more hemispheric receptacle, whereas in *M. triandra* the receptacle is globose. In its spore ornamentation *Mannia controversa* is also easy to distinguish from *M. triandra*, the latter having a spongy spore surface.

Key to subspecies of Mannia controversa

1a. Distal ornamentation of spores regularly to incompletely areolate, areolae shallow, (5–)6–8 across the distal surface; antheridia borne terminally or dorsally on thallus; storage and assimilation tissue with yellowish or rarely dark brown oil cells _____ **M. controversa** subsp. **controversa**

1b. Distal ornamentation of spores incompletely areolate, areolae deep, (6–)7–10 across the distal surface; antheridia borne terminally on thallus; storage and assimilation tissue with pale yellowish oil cells _____ **M. controversa** subsp. **asiatica**

Subspecies Descriptions

Mannia controversa (Meyl.) Schill subsp. **controversa. Figs 1, 6A–D.**

Assimilation tissue sometimes with one upper layer of vertical orientated air chambers and smaller rounded air chambers below (2–3 layers) in cross section, with dark brownish oil cells or inconspicuous yellowish oil cells in assimilation and storage tissue; *sexual condition* terminal-autoicous or sometimes dorsal-autoicous; *spores* with distal ornamentation regularly to incompletely areolate, (5–)6–8 areolae across, areolae not deep and sometimes very shallow, muri low, usually broadly rounded in t.s.

Distribution. *Mannia controversa* subsp. *controversa* is known only from the Swiss, Austrian and French Alps, where it is largely confined to the inner, continental ranges from the Rhone (Savoy) Alps in the west to the Hohe Tauern in the east (Fig. 2).

Ecology. This rare liverwort occurs on sunny, mainly south-facing slopes of the alpine belt (c.2100–2700 m), dominated by rock-interspersed alpine meadows. It is

strictly confined to calcareous substrates, according to Meylan (1924) growing on soil (e.g. in meadow niches), at boulder bases or in rock fissures. The bedrock in the Swiss localities is mainly dolomite; in Austria and France, however, it is predominantly calcareous schist and only rarely limestone. A more detailed investigation of the habitat of *Mannia controversa* subsp. *controversa* was made only at one of the Austrian localities (Butzentörl). There it grows creeping on a south-facing, inclined rock ledge of calcareous schist, mainly on a thin layer of rock detritus but marginally also on the rock itself. This site is characterised by long snow-cover, at least until the beginning of July. After the melting of snow, however, the fully insolated site commonly gets dry in late summer and autumn. An associated species is *Asterella lindenbergiana* (Corda ex Nees) Arnell, a characteristic constituent of calcareous snow-bed communities. Other associates, including *Syntrichia norvegica* F.Weber, *Pseudoleskea incurvata* (Hedw.) Loeske and *Athalamia hyalina* (Sommerf.) S.Hatt., tolerate long snow-protection but also periodical desiccation. The last species, growing in base- and nutrient-rich habitats, was given by Meylan (1924) and Gams (1938) as the most frequent accompanying species in the Swiss localities.

In the Alps spores mature from July to September.

Specimens studied. SWITZERLAND. Val Laulesmygge?, 2600 m, viii 1930, *C. Meylan* s.n. (B74595) (S); [**Vaud**]: Près du Glacier du Martinets, 2200 m, ix 1918, *C. Meylan* s.n. (LAU, lectotype); [**Berne**]: Col du Rawyl, 2450 m, 12 iv 1922, *H. Gilomen* s.n. (LAU). **Valais**: Wallis, Kalkschutt auf Haut d'Alesses, 2230 m, 9 viii 1915, *H. Gams* s.n. (B74592) (LAU, S).

AUSTRIA. **Carinthia**: Kärnten, Hohe Tauern, Goldberggruppe, S Butzentörl am Stellkopf, c.2650 m, länger schneebedeckte Felsbank aus Kalkglimmerschiefer in S-Exposition, 16 viii 2006, *H. Köckinger* 11451 (E); same locality, 24 ix 1999, *H. Köckinger* 99-1645 (E); Kärnten, E Großglockner, 0.5 km unterhalb des Glocknerhauses, c.2100 m, 2001, *R. Düll* s.n. (E). **Tyrol**: Tirol, Matrei, Auf Kalkboden eines begrasten Abhanges auf dem Blaser in einer Höhe von 6500 Fuss, 24 viii 1871, *Arnold* 517 (NY, S); Tirol, Matrei, viii 1871, *Arnold* s.n. (E); Tirol, Hafelekarspitz bei Innsbruck, 2243 m, 17 xi 1895, *Stolz* s.n. (B74593) (S).

FRANCE. [**Rhône-Alpes**]: Savoie, Massif du Mont-Cenis, Plan de la Madeleine, valley on the S side of Lac du Mont Cenis, 27 vii 1965, *G. Een* s.n. (B58895) (S); Savoie, Col de l'Iseran, Vallon de la Lenta, alt. 2431–2500 m, Refuge du Pied Montet (loc. 22), 24 vii 1965, *G. Een* s.n. (B61314) (S); Savoie, Bessans, vallée de la Lombarde, 2250 m, sur la terre sèche (schistés lustrés), 18 vii 1952, *L. Castelli* 8 (B74588) (S); Savoie, Bessans, sur la terre au bord d'un ruisseau à sec, 2650 m, 17 viii 1952, *L. Castelli* 7 (B74591) (S).

Mannia controversa (Meyl.) Schill subsp. **asiatica** Schill & D.G.Long, **subsp. nov. Figs 3, 4, 6E–H.**

Mannia controversa subsp. *controversae* similis sed differt textura assimilanti in sectione transversali cum cavernularum stratis 3–4 modice rotundis parvis usque magnis, in textura assimilanti et penaria cellulis oleosis inconspicuis flavescentibus; conditio sexualis terminali-autoica; sporae deco distali profunde et imperfecte areolato, tranversim cum (6–)7–10 areolis, muri alti, plerumque angusti et in sectione transversali protracti. – Type: China, Qinghai Prov., Henan County, Dousong Xiang, Zhilong, 34°23′47″N, 101°28′10″E, c.3830 m, limestone hillside, soil clefts at foot of limestone cliff, 15 vii 1997, *D.G. Long* 27032 (holo E; iso NY, PE).

Similar to subsp. *controversa* but assimilation tissue with 3–4 layers of somewhat rounded small to large air chambers in cross section, with inconspicuous yellowish oil cells in assimilation and storage tissue; sexual condition terminal-autoicous; spores with distal ornamentation deeply and incompletely areolate, (6–)7–10 areolae across, muri high, usually narrow and tapering in t.s.

Distribution. It grows in the high mountains around the fringes of the Tibetan plateau and is known from China, India and Tajikistan (Fig. 5).

Ecology. It can be found on steep slopes or hillsides below cliffs, on ledges, on banks near streams and is sometimes associated with *Picea*/*Juniperus* and *Betula*/*Juniperus* woodland or with *Salix*. It grows on soil and rock (often limestone) mostly in sites with S or NW exposure. Its altitudinal range is 2735–4200 m. Associated bryophytes are *Conocephalum conicum* (L.) Dumort., *Asterella grollei* D.G.Long, *Reboulia hemisphaerica* (L.) Raddi, *Preissia quadrata* (Scop.) Nees and *Rhytidium rugosum* (Hedw.) Kindb. The spores ripen from July to August.

Specimens studied. INDIA. [**Uttaranchal**]: NW-India, Kumaun, Ralan Valley, 13,000–14,000′, 24 viii 1884, *Duthie* 311 (G), *Duthie* 3757 (BM).

CHINA. **Qinghai Province**: Henan County: Xiawate, Zhihoumao Xiang S of Henan, 34°31′20″N, 101°31′13″E, c.3800 m, steep slopes below limestone cliffs, on soil ledges, 15 vii 1997, *D.G. Long* 27016 (E); Dousong Xiang, Zhilong, 34°23′47″N, 101°28′10″E, c.3830 m, limestone hillside, soil clefts at foot of limestone cliff, 15 vii 1997, *D.G. Long* 27032 (E). Huzhu County: near Nanzhangzhagon Village, upper Zhalonggou Valley, 36°46′17″N, 102°32′44″E, c.2735 m, *Betula*/*Juniperus* woodland on limestone, on shady NW-facing banks, 24 vii 1997, *D.G. Long* 27217 (E); Jiading Xiang, Gangzigou Valley, 36°45′05″N, 102°37′49″E, c.2820 m, *Juniperus*/*Betula* woodland, on bank of stream on limestone, 25 vii 1997, *D.G. Long* 27260 (E). Maqin County: Yangkao, 34°42′58″N, 99°40′34″E, c.3835 m, steep limestone side valley, on bank under *Salix*, 9 vii 1997, *D.G. Long* 26924 (E); Jungun Naichong, between Dawu and Huang He, 34°38′50″N, 100°36′41″E, c.3585 m, valley with *Picea* and *Juniperus* woodland, on S-facing soil on limestone bank under *Juniperus*, 9 vii 1997, *D.G. Long* 26964-b (E); North of Jungun Naichong, 34°33′48″N, 100°33′28″E, c.3570 m, damp rocky side gully in dry valley, on damp soil on N-facing rocks, 10 vii 1997, *D.G. Long* 26951-b (E). Tongren County: Shuangpenxi Xiang, Kuohelongwa Valley, 35°31′42″N, 102°14′32″E, c.3200 m, degraded scrubby *Picea* woodland, on shady bank, 19 vii 1997, *D.G. Long* 27126 (E). [**Xinjiang Uyghur Autonomous Region, Tianshan District**]: Xinjiang, Kunlun-Aksai Chin, Tienshan, Urumqi valley between upper Glaciological Station and Shengli Daban, 3400–3850 m, 43°07′N, 86°52′E, subalpine and alpine forb-rich steppe and alpine Cyperaceae mats/mat fragments and cushion vegetation in the upper alpine belt, vegetation record no.: 92-9060.1, 3 vi/16 vii 1992, *G. & S. Miehe* s.n. (E).

TAJIKISTAN. S-Aschger Mountain, Zorkul Lake, along stream, 4200 m, 13 viii 1970, *Boboradzchabov* 802 (JE).

CONCLUSIONS

Mannia controversa is a distinctive species related to *M. fragrans*, consisting of two disjunct subspecies in Europe and Asia. However, it remains very poorly known in Asia and has not been seen since 1930 in Switzerland. Further field work is needed to assess its current status, full distribution and more detailed ecology. The disjunction

of its two constituent subspecies raises many questions about their evolutionary history and could provide an interesting molecular study using genetic markers such as microsatellite DNA to assess the genetic variation within and between the two populations. Potentially this could give insight into the age of the disjunction and the direction of past migration and isolation.

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