Taxonomy and phylogeny of the liverwort genus *Mannia* (Aytoniaceae, Marchantiales)

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Declaration

I hereby declare that the work contained within this thesis is my own, unless otherwise acknowledged and cited, and that this thesis is my own composition. This thesis has not in whole or part been previously presented for any other degree.

Daniela B. Schill

Abstract

The genus *Mannia* (Aytoniaceae, Marchantiales) was first described by Opiz in 1829 and it is still not clear how many species it comprises worldwide. The generic and subgeneric division of *Mannia* has long been confused and several attempts have been made to subdivide it into smaller genera. Morphologically it is typically characterised by a small, rather narrow thallus, cup-shaped involucres and the lack of a pseudoperianth. It includes both xeromorphic and mesomorphic species, which are all drought-tolerant. *Mannia* occurs almost exclusively in the northern hemisphere with exceptions in Africa and South America. It is found on rock, rocky soil or rock crevices in arctic – alpine and mediterranean climates.

A worldwide revision of the genus has not been previously attempted, and earlier treatments focused on thallus morphology and limited geographic regions.

This study comprises the first worldwide revision of *Mannia* and about 1600 specimens were studied, including all available type specimens, from both dried and fresh material collected on several field trips. The monographic work is based on reviewed morphological and anatomical characters using dissecting, compound and scanning electron microscopy. Surface ornamentation of spores has been studied and with their relatively large spores reaching up to about 90 μm diameter, the species within *Mannia* show striking spore ornamentation patterns, which are found to be species-specific and have proved to be a very valuable tool in identification and synonymy. Most spore characters are constant with only size showing large variations though this can nevertheless be diagnostic. The species status of *M. sibirica* is confirmed and its close relationship to *M. californica* is contrary to former assumptions.

A total of seven species are recognised from 22 formerly described names: (1) *M. androgyna* (L.) A. Evans, (2) *Mannia sibirica* (Müll.Frib.) Frye & L.Clark, (3) *Mannia californica* (Gottsche ex Underw.) L.C.Wheeler, (4) *Mannia fragrans* (Balbis) Frye & L.Clark, (5) newly described *Mannia asiatica* Schill & D.G. Long, (6) *Mannia triandra* (Scop.) Grolle and (7) *Mannia pilosa* (Hornem.) Frye & L.Clark. Eleven excluded or doubtful taxa are listed. Vegetative, generative and spore keys have been developed and for each species descriptions, illustrations and distribution maps are given along with ecological, taxonomic and nomenclatural notes.

Most species have a wide distribution range except for *M. androgyna*, which is restricted to areas with a meditereanean climate and *M. asiatica*, which only occurs in high mountains of the Himalayas along the fringes of the Tibetan plateau. The distribution of *M. californica* is extended from North America into Europe, Asia, India and Africa. *M. fragrans* is reported new to India and *M. californica* new to Austria, although the latter specimen shows some atypical morphological features. Some formerly assumed local endemic species are shown to be conspecific with more widespread taxa.

A parsimony analysis based on morphological characters including all *Mannia* species and 16 other taxa is inconclusive. A study of character evolution showed that homoplasious characters were a common feature in *Mannia* and related genera.

Reconstructions of phylogenetic relationships using chloroplast *trn*L-F and nuclear ribosomal LSU were based on 35 samples. Only five out of the seven accepted *Mannia* species could be included in the molecular study. Some species are represented multiple times but from different countries. *Targionia hypophylla* and *Athalamia hyalina* were used as outgroup taxa.

Maximum Parsimony and Bayesian analyses were conducted on individual and combined datasets. All phylogenetic tree topologies showed polytomies but suggest that *Mannia* has evolved from within its sister genus *Asterella* and that the genus falls into two main clades. *Mannia* is paraphyletic with *Asterella gracilis* a close relative to *M. triandra* and *M. pilosa*. Because of incongruent tree topologies morphological and molecular data sets were not combined.

Based on mainly spore characters in combination with molecular results a new infrageneric classification of *Mannia* is presented.

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Chapter 1: Introduction

1.1 General introduction

The liverworts are generally grouped with the mosses and hornworts under the term bryophyte. They are thought to have between 6000 and 8000 species worldwide (CRANDALL-STOTLER & STOTLER 2000, SCHOFIELD 1985) and include three life forms: leafy, simple thalloid and complex thalloid. The latter two forms do not have leaves but are characterised by a dorsiventrally flattened gametophyte, the so-called thallus.

The class Marchantiopsida consists of two subclasses, Jungermaniidae and Marchantiidae, the latter subdivided into three orders: Marchantiales, Sphaerocarpales and Monocleales (BISCHLER-CAUSSE ET AL. 2005). Recent molecular studies have shown that the latter two orders are nested within the Marchantiales (WHEELER 2000, BOISSELIER ET AL. 2002, LONG ET AL. 2005, HE-NYGRÉN ET AL. 2006).

A new classification of liverworts was presented by HEINRICHS ET AL. (2005) and HE-NYGRÉN ET AL. (2006). It was based on morphological and molecular evidence that suggested several clades. Both studies propose three liverwort classes: Haplomitriopsida (= Treubiopsida in HE-NYGRÉN ET AL. 2006), Marchantiopsida and Jungermanniopsida. The class Marchantiopsida consists of the two subclasses Blasiidae and Marchantiidae, the latter subdivided into Sphaerocarpales and Marchantiales (HE-NYGRÉN ET AL. 2006).

The order Marchantiales (sometimes also called the 'chambered liverworts' or 'complex thalloids') comprises 14 families with 28 included genera and about 355 species; its genera are regarded as being *"separated by sharp morphological discontinuities"* and with *"each genus [is] unambiguously defined by a number of morphological features"* (BISCHLER 1998). The classification of the order is shown in Table 1.1.

The genus *Mannia* belongs to the family Aytoniaceae within the Marchantiales. The name *Mannia* was given to the genus by Opiz in honour of his friend Dr. med. W. Mann, who was a *"diligent"* botanist and lichenologist (CORDA 1829, SCHOFIELD 2002). The first description of the genus was made by Opiz in CORDA

(1829) over 170 years ago, yet until today it has not been entirely clear how many species it comprises worldwide. According to ENGEL (1990) there are six species, according to BISCHLER (1998) 15 and according to SCHUSTER (1992b) there are around 18 species. The *Index Hepaticarum* listed 22 species and two varieties (GEISSLER & BISCHLER 1985).

A worldwide revision of the genus has never before been attempted.

Mannia has striking spore ornamentation patterns which appear to be species-specific (LONG 1999). Some of the taxa are also highly aromatic. *Mannia* includes both xeromorphic and mesomorphic species, all drought-tolerant with often fragmented ranges with a *"nearly worldwide distribution, up to the Arctic, but not recorded from tropical east Asia, Central America and Australasia"* (BISCHLER 1998). Its distribution is restricted to the northern hemisphere with exceptions in Africa and South America. The genus grows on rock or rocky soil in arctic-alpine and mediterranean climates.

There have been major gaps in our knowledge of *Mannia*. Large areas such as India, China, SE Asia and SW Asia have either not been reviewed or revisions are incomplete. Furthermore, an overview and linking of existing treatments as well as a global synthesis of the taxonomy of the genus *Mannia* has been lacking.

There have been unresolved nomenclatural and taxonomic problems of related species in different continents, for example *M. androgyna* and *M. capensis* (the latter exclusively in Africa) might be conspecific (GROLLE, pers. comm.) but have not before been critically compared. PEROLD (1994a) in her treatment of *M. capensis* in South Africa found it *"difficult to come to a definite decision"* because *M. androgyna* could not be examined more closely. She remarked that only a *"few authentically named specimens of M. androgyna* [could be] *examined"*.

Furthermore the existence of local endemics from India (*M. indica, M. perssonii* and *M. foreaui*), Japan (*M. levigata*), Peru (*M. hegewaldii*) and North America (*M. paradoxa*) may be genuine or these described species may belong to more widespread taxa. There has been a need to study these more closely and compare them to all related species worldwide. However, most of these are described from very limited material, and often with inadequate descriptions.

Table 1.1. Classification of the order Marchantiales based on morphological and molecular evidence (Bischler-Causse et al. 2005, Bischler 1998, Schuster 1984, Grolle 1983b)

Class	Subclass	Order	Suborder	Family	Genera
Marchantiopsida	Marchantiidae	Marchantiales	Monocarpineae	Monocarpaceae	*Monocarpus*
			Ricciineae	Oxymitraceae	*Oxymitra*
				Ricciaceae	*Riccia*
					Ricciocarpos
			Corsiniineae	Corsiniaceae	*Corsinia*
					Cronisia
			Targioniineae	Cyathodiaceae	*Cyathodium*
				Targioniceae	*Targionia*
			Marchantiineae	Exormothecaceae	*Aitchisoniella*
					Exormotheca
					Stephensoniella
				Cleveaceae	*Athalamia*
					Peltolepis
					Sauteria
				Monosoleniaceae	*Monosolenium*
				Aytoniaceae	*Asterella*
					Cryptomitrium
					Mannia
					Plagiochasma
					Reboulia
				Wiesnerellaceae	*Wiesnerella*
				Conocephalaceae	*Conocephalum*
				Lunulariaceae	*Lunularia*
				Marchantiaceae	*Bucegia*
					Dumortiera
					Marchantia
					Neohodgsonia
					Preissia
		Sphaerocarpales	Spharocarpineae	Sphaerocarpaceae	*Sphaerocarpos*
					Geothallus
			Riellineae	Riellaeceae	*Riella*
		Monocleales		Monocleales	*Monoclea*

The classification of *Mannia* at the subgeneric level is still uncertain, as has been the evolutionary relationship of *Mannia* to *Asterella* and other related genera. It has not even been clear whether *Mannia* is a monophyletic genus or not.

Therefore a great deal has remained to be done to clarify the taxonomy, classification, evolution and phytogeography of *Mannia*. Even the traditional alpha-taxonomic morphological studies on the genus have been far from complete.

Over the past decades several new techniques in systematics have become available, which have not before been applied to these problems in *Mannia*, and these have made significant progress possible.

Clearly two major tasks are a priority:

a) to complete a taxonomic study on the genus worldwide
b) to use modern tools to attempt to elucidate the evolutionary relationships within the genus and with related genera

Looking at the genus on a broader scale and with a combination of morphological and molecular methods it is hoped to disentangle the past taxonomic confusion and achieve a well-supported classification.

1.2 Aims and objectives

In order to complete these tasks the present study is based on the following objectives:

1) to give a general introduction to the genus *Mannia* and related genera, review its taxonomic and nomenclatural history, the species concept used and the evolutionary age of the genus (Chapter 1)
2) to review the morphological characters available within the genus that can be used for a taxonomic treatment (Chapter 2)
3) to present a survey of spores with the scanning electron microscope (SEM) to study spore ornamentation patterns and their potential use in taxonomy and identification of *Mannia* species (Chapter 3)
4) to produce an alpha-taxonomic revision of *Mannia*, using herbarium collections and fresh material from field trips, for a world monograph of the

genus, providing keys, revised infrageneric classification, species descriptions, drawings, synonymy, notes on morphology, taxonomic and nomenclatural problems, ecology, a map of distribution and a list of specimens studied for each accepted species (Chapter 4)

5) to attempt to reconstruct the phylogeny of *Mannia* and related genera using both morphological and molecular analyses to gain better insights into the genus and its character evolution, and to contribute to constructing a stable infrageneric classification of the genus. (Chapter 5)

1.3 The family Aytoniaceae

The name Aytoniaceae was first recognised by CAVERS (1911) and its type genus is *Plagiochasma* Lehm. et Lindenb.. This genus was formerly named *Aytonia* or *Aitonia* by J. R. et G. Forst. in 1775 (GROLLE 1983b) and according to UNDERWOOD (1884) the name *Aitonia* Forst. was given by Forster in honour of William Aiton, a Scottish botanist who lived from 1731 to 1793. The family is clearly defined by the dehiscence of the sporophyte capsule by a lid or operculum (as opposed to valves in other Marchantiales) and by the simple air pores in the thallus and compound pores in the receptacle. The family was first established by LEITGEB (1881) under the name 'Operculatae' based on the existence of a capsule lid as he describes *"Ich würde also im Sinne dieser Auseinandersetzungen es für zweckmässiger halten [...] die Gattungen Plagiochasma, Reboulia, Grimmaldia, Duvalia und Fimbriaria, deren Kapseln sämmtlich die Eigenthümlichkeit zeigen, dass der obere Theil der Kapselwand theils in einem Stücke (also deckelfartig) abgeworfen wird, theils in unregelmässige Platten zerfällt, wo aber in jedem Falle der untere Theil als Ganzes (Urne) erhalten bleibt, in eine Gruppe (Marchantieae operculatae) zusammenfassen"*.

Aytoniaceae has a wide distribution in the northern hemisphere but less so in the southern hemisphere (SCHOFIELD 2002). Many species are drought-tolerant (DAMSHOLT 2002) and often occur on rock crevices and rock outcrops, *Mannia* occurs additionally on rocky soil (BISCHLER 1998).

The delimitation of the genera within Aytoniaceae is much less clear cut and the genera are distinguishable from each other by a combination of morphological characters (LONG 2000). There are five genera (GROLLE 1983a): *Asterella*, *Cryptomitrium*, *Mannia*, *Plagiochasma* and *Reboulia*. A genera comparison of selected characters is presented in Table 1.2. and photographs of *Mannia* species and its sister genera are presented in Figures 1.1 to 1.4.

Mannia is generally distinguished from the other genera of Aytoniaceae by cup-shaped involucres and a small and rather narrow thallus. In sterile condition the identification can be problematic as it shows close resemblance to some *Asterella* species.

The main difference to *Asterella* is the absence of a pseudoperianth, which is a cage-like structure surrounding the capsule. This character is unique to the genus *Asterella*. Furthermore, *Asterella* species often have a fishy smell whereas the odour of *Mannia* is aromatic. The shape of the receptacle in *Mannia* is different to the discoid receptacle shape in *Cryptomitrium*, the more star-like shape in *Reboulia* or the subspherical shape in *Plagiochasma*. In the latter genus diagnostic features such as the dorsal stalk position on the thallus and the lack of a rhizoidal furrow is a further difference from *Mannia*.

The number of species belonging to the different genera in the family Aytoniaceae varies (Table 1.3). *Asterella* is the largest genus followed by *Plagiochasma* and *Mannia*. Both *Cryptomitrium* and *Reboulia* have only a few species.

Asterella has 16 recognised species in Eurasia (LONG 1999) and approximately 45 to 48 species worldwide (LONG 2006), which are often drought- and/or cold-tolerant with a worldwide distribution from the tropics to the Arctic (BISCHLER 1998).

Cryptomitrium has three species with a disjunct distribution in western North America, Central America, southern South America, south-east Africa and the Sino-Himalaya (BISCHLER 1998).

Plagiochasma has 16 species with a worldwide distribution in warm-temperate areas with Mediterranean-type climates and semi-arid areas. It is absent from humid tropical regions and from continental areas with low winter temperatures (BISCHLER 1998).

Reboulia is interpreted as either monospecific (*Reboulia hemisphaerica*) or as comprising two to three species. It inhabits warmer areas and so is frequent in the Mediterranean but is absent from continental areas with long, cold winters and also from humid tropical regions (BISCHLER 1998, DAMSHOLT 2002).

Table 1.2. Selected characters showing differences between the genera of Aytoniaceae based on BISCHLER (1998) and LONG (2000)

Morphological characters	***Asterella***	***Cryptomitrium***	***Mannia***	***Reboulia***	***Plagiochasma***
Odour	fishy	aromatic	aromatic	aromatic	aromatic
Thallus	small, or large and broad	rather large and broad	small and narrow	large and broad	large and broad
Sexual condition	monoicous or dioicous	monoicous	monoicous or dioicous	monoicous	monoicous
Rhizoidal furrow	one	one	one	one	none
Shape of receptacle	hemispherical or discoid	discoid, hardly lobed	hemispherical or globose	hemispherical, deeply lobed	subspherical
Position of stalk	terminal or ventral	terminal	terminal or ventral	terminal	dorsal
Air chambers in stalk	absent or present	absent	absent	absent or present	absent
Involucres	entire or bilobed flap	bivalved	cup-shaped	bivalved	bivalved
Pseudoperianth	present	absent	absent	absent	absent

Table 1.3. Number of species in genera of Aytoniaceae according to Bischler (1998)

	Asterella	*Cryptomitrium*	*Mannia*	*Plagiochasma*	*Reboulia*
Number of species	80	3	15	16	1-3

1.4 Historical review of genus

1.4.1 The genus *Mannia*

Mannia Opiz was first published by Opiz in CORDA (1829) as a replacement for the illegitimate *Grimaldia* Raddi (1818). The genus *Grimaldia* was based on a single species *G. dichotoma* (= *M. androgyna*), which was described by RADDI in 1818. The name *Grimaldia* chosen by Raddi, though, is a later homonym because there is an earlier *Grimaldia* Schrank, published in 1805 (WHEELER 1934, EVANS 1938). EVANS points out that there was always the *"attempt to justify its use by claiming that Grimaldia Schrank had long been included as a synonym under the genus Cassia Tourn."* which is a member of the angiosperm family Leguminosae. But in 1930 *Grimaldia* Schrank was revived when a new legume species from South America was described under it by Britton & Rose in BAILEY (1930), who recognized its validity.

NEES VON ESENBECK (1818) published *Duvalia* as a monotypic genus based on a single species *Duvalia rupestris.* LINDBERG (1868) used the orthographic variation *'Düvalia'* and in CORDA (1829) '*Duvallia'* is used. However, HAWORTH (1812) had already given the name *Duvalia* to a plant in the angiosperm family Asclepiadaceae so *Duvalia* is a later homonym as well. Borbás described a new genus *Duvaliella* for *Duvalia rupestris* Nees in 1893 but this name had already been used a year earlier by Heim for a genus of Dipterocarpaceae according to GROLLE (1983b) and is therefore illegitimate.

SCHIFFNER (1893) introduced the name *Neesiella* for *Neesiella rupestris* (now *Mannia triandra*) but WHEELER (1934) pointed out that the name *Mannia* is the *"next earliest tenable equivalent for Grimaldia Raddi"* and should therefore replace *Grimaldia.*

However, the separation of *Mannia* species into two different genera *Grimaldia* and *Neesiella* or *Duvalia* was adhered to by many authors (MASSALONGO 1914, BERGDOLT 1926) based on morphological characters such as assimilation tissue or the thallus being leathery or not.

CORDA (1829) described a new genus *Sindonisce* for *Sindonisce fragrans*. But EVANS (1938) pointed out that it was considered that *S. fragrans* is conspecific with *Grimaldia dichotoma* Raddi, so *Sindonisce* would be a substitute for *Grimaldia* Raddi and therefore a homonym as well. However, *S. fragrans* was based on Balbis's much earlier description of *Marchantia fragrans* (CORDA 1829, BALBIS 1804) and is therefore *Mannia fragrans*.

Neesia was published in 1825 by Leman based on the species *Duvalia rupestris* Nees but is an illegitimate name because Sprengel had previously described a genus of Asteraceae under that name according to GROLLE (1983b).

The name *Pleurochiton* Corda ex Nees is based on *Pleurochiton balbisianum* Corda and was synonymised by NEES (1838) under *Grimaldia fragrans*. It is an invalid name according to GROLLE (1983b).

The genus name *Arnelliella* was introduced by MASSALONGO (1914) for *Grimaldia pilosa* var. *sibirica* Müll.Frib. based on a rather intermediate type of assimilation tissue amongst other morphological characters in comparison to the two genera *Grimaldia* (compact assimilation tissue) and *Neesiella* (loose assimilation tissue).

An older legitimate name for the genus *Mannia* is actually *Cyathophora* Gray, which is described from a specimen that was collected by the author in Britain and described in 1821. The species was named *Cyathophora angustifolia* but included the synonym *Marchantia androgyna* L.. However, Gray's specimen was actually *Preissia quadrata* (Scop.) Nees based on his description according to GROLLE (1981). Furthermore GROLLE pointed out that Gray's interpretation of the Linnaean species was wrong and also that the Linnaean species is actually a mixture of two distinct genera (*Marchantia androgyna* and *Marchantia chenopoda*). *Marchantia androgyna*, now *Mannia androgyna*, was described in 1753 and is therefore older than *C. angustifolia*, the latter therefore automatically becoming a synonym.

Hence GROLLE (1983a, 1983c) proposed to conserve *Mannia* Opiz 1829 against the name *Cyathophora* Gray 1821 because the latter from the start *"has been* *defective (...) through taxonomic and nomenclatural mistakes"* as explained by him already in an earlier publication (GROLLE 1981) and *"has never been used in the sense of Mannia"*. In 1988 conservation of *Mannia* Opiz against *Cyathophora* Gray was accepted by the Committee for Bryophyta (ZIJLSTRA 1989, NICOLSON 1993, GREUTER ET AL. 2000).

1.4.2 Infrageneric classification of *Mannia*

The generic and subgeneric division of *Mannia* has long been confused and several attempts have been made to subdivide it into smaller genera. The genus was subdivided into two genera, *Grimaldia* and *Neesiella* by MÜLLER (1905–1916) and BERGDOLT (1926) following SCHIFFNER (1893) and also into *Grimaldia* and *Duvalia* by NEES VON ESENBECK (1838). Three genera were accepted by MASSALONGO (1914): *Grimaldia*, *Neesiella* and *Arnelliella*, all containing species that are now placed within *Mannia*.

A total of four infrageneric classifications have been proposed, which are shown in Table 1.4.. The first infrageneric classification of *Mannia* was published by SHIMIZU & HATTORI (1954). In this treatment the genus *Cryptomitrium* was included as a second subgenus under *Mannia*, which contradicts later taxonomic treatments.

SHIMIZU AND HATTORI (1954) subdivided *Mannia* into two subgenera: *Mannia* and *Cryptomitrium*. The subgenus *Cryptomitrium* was based on a range of morphological characters such as the assimilation tissue being either loose or compact, plants xerophytic or not, epidermal cells thin-or thick-walled, receptacle lobes and shape of involucres.

The subgenus *Cryptomitrium* was divided into the two sections *Cryptomitium* and *Neesiella* based on receptacle shape, involucre shape and position of the antheridia.

The authors suggested that the characters dividing *Mannia* from the genus *Cryptomitrium* were not strong enough for accepting *Cryptomitrium* as a separate genus, so they regarded it as a subgenus of *Mannia* with the species *M. triandra*, *M. pilosa* and *M. longiseta* (Section *Neesiella*) closer related to *Cryptomitrium* (Section *Cryptomitrium*) than the other species of *Mannia*.

There have been three further attempts at a classification of *Mannia* by GROLLE (1976, 1983b), and recently by GROLLE & LONG (2000).

Table 1.4. Past and present subgeneric classifications of Mannia by different authors

Author	**Year**	**Subgenus**	**Section**	**Species**
Shimizu & Hattori	1954	Mannia		*M. fragrans, M. dichotoma, M. sibirica, M. californica, M. indica, M. brachypoda, M. levigata*
		Cryptomitrium	Neesiella	*M. rupestris, M. pilosa, M. longiseta*
			Cryptomitrium	*M. tenerum, M. himalayense*
Grolle	1976	Mannia	Mannia	*M. californica, M. capensis, M. androgyna, M. atlantica*
			Sindonisce	*M. fragans, M. indica*
		Arnelliella		*M. pilosa, M. triandra, M. sibirica*
Grolle	1983b	Mannia		*M. pilosa, M. triandra, M. sibirica*
		Xeromannia	Xeromannia	*M. androgyna*
			Sindonisce	*M. fragrans*
Grolle & Long	2000	Mannia	Mannia	*M. androgyna*
			Sindonisce	*M. fragrans*
		Arnelliella		*M. pilosa, M. triandra, M. sibirica*
Schill	2006	Mannia	Mannia	*M. androgyna*
			Arnelliella	*M. sibirica, M. californica*
			Sindonisce	*M. fragrans*
			Asiaticae	*M. asiatica*
		Neesiella		*M. triandra, M. pilosa*

At subgeneric level Grolle divided *Mannia* at first into the subgenera *Mannia* and *Arnelliella* though it is not clear on which morphological characters that was done (GROLLE 1976). Later GROLLE (1983b) subdivided the genus into two subgenera (*Mannia* and *Xeromannia*), distinguished mainly by the structure of the assimilatory layer of the thallus and the areolation of the upper surface of the thallus. The species in *Xeromannia* have a compact assimilatory layer and only weak areolation dorsally. This was sharply criticised and not accepted by SCHUSTER (1992a). From his point of view the two sections of the subgenus *Xeromannia* *"are equally useless"* and he considered a classification based on the used characters to be in vain. He considered *M. fragrans* and *M. californica* *"as closely allied"* and should in his opinion be in the same section as *M. androgyna*. He then suggested that the position of the androecia should be adopted as *"the most fundamental feature"* for a classification but admitted a *"considerable variation in the three species (M. androgyna, M. californica and M. fragrans)"* and actually did not propose any alternative classification to Grolle's.

Most authors providing regional descriptions of *Mannia* such as SCHUSTER (1992b) and DAMSHOLT (2002) followed these later classifications and treated *Cryptomitrium* as a separate genus.

The new infrageneric classification proposed in this study (Table 4.3) is based on a combination of morphological, particularly spore, characters and molecular results as discussed in Chapter 3 (see 3.6.4) and 5 (see 5.7.3.7).

1.5 *Mannia* species and the species concept

With the introduction of a binary system for plant names by Linnaeus in 1753 the base for plant nomenclature was founded and is still in use today. In his two-volume work *'Species Plantarum'* he based his classification of liverworts on earlier work by Micheli, a botanist from Florence (MÜLLER 1954). In his work the first *Mannia* species to be described was *Mannia androgyna*, then *Marchantia androgyna*, which was then placed in the genus 'Hepatica' together with *Reboulia* and *Conocephalum* according to MÜLLER (1954). Since then many more species have been described under *Mannia*, first under the name *Marchantia* but also under *Duvalia* and *Grimaldia*. A table of *Mannia* species described worldwide in chronological order can be seen in Table 1.5.

Table 1.5. Taxa of *Mannia* described worldwide. A chronological list of names belonging to *Mannia* described in *Duvalia, Grimaldia, Mannia, Marchantia* and *Neesiella.*

Name	Publication Date	Type Locality
Marchantia androgyna L.	1753	Italy
Marchantia triandra Scop.	1772	Slovenia
Marchantia fragrans Balbis	1804	Italy
Marchantia pilosa Hornem.	1810	Norway
Marchantia ludwigii Schwägr.	1814	Helvetia?, Germania
Duvalia rupestris Nees	1818	Austria
Marchantia fasciata Myrin ex Hartm.	1832	Norway
Grimaldia barbifrons Bisch.	1835	Germany
Mannia fragrans var. *convoluta* Nees	1838	unknown
Mannia fragrans var. *fimbriata* Nees	1838	Schlesien, Tyrol, Prag, Dahurien
Grimaldia inodora Wallr.	1840	Germany
Grimaldia carnica C.Massal.	1886	Italy
Grimaldia californica Gottsche ex Underw.	1888	California
Duvalia longiseta Steph.	1897	Japan
Grimaldia capensis Steph.	1898	South Africa
Grimaldia fragrans var. *brevipes* Kaal.	1898	Norway
Grimaldia pilosa var. *sibirica* Müll.Frib.	1907	Siberia
Grimaldia indica Steph.	1916	N.W. India
Grimaldia japonica Steph.	1917	Japan
Mannia controversa Meylan	1924	Switzerland
Mannia fragrans var. *alpina* Meylan	1924	Switzerland
Grimaldia subpilosa Horik.	1934	Taiwan
Grimaldia atlantica Trab.	1942	Atlas mountains
Mannia fragrans var. *inodorata* S.Hatt.	1944	Japan
Mannia barbifrons Shimizu & S.Hatt.	1953	Japan
Mannia brachypoda Shimizu & S.Hatt.	1953	Japan
Mannia levigata Shimizu & S.Hatt.	1953	Japan
Mannia capensis var. *pallida* S.W.Arnell	1963	South Africa
Mannia foreaui Udar & Chandra	1964	South India
Mannia perssonii Udar & Chandra	1965	North India
Mannia paradoxa R.M.Schust.	1985	New Mexico
Mannia hegewaldii Bischl.	2005	Peru
Mannia asiatica Schill & D.G.Long	2006	China

According to RIDLEY (2004) *"a species is the basic unit in classification and in the study of evolution"*. There are many concepts of how to define a species. One of the earliest concepts in use was probably the typological species concept. It defines a species by morphological characters and distinguishes between species by their appearance, their character differences. Most systematists find this concept weak as it cannot detect cryptic speciation, however it is claimed that *"all taxonomists, when classifying the diversity of nature into species, follow the typological method and distinguish 'archetypes'"* (MAYR 1957).

The biological species concept has the widest acceptance (RIDLEY 2004). In it a species is defined as *"groups of interbreeding natural populations that are reproductively isolated from other such groups"* (MAYR 1969).

The difficulties with this approach of defining species is that reproduction can sometimes be asexual or partly asexual and that many closely related species may no longer be in close proximity to each other (BAKER 1970). The latter author also pointed out the practical difficulties of inbreeding experiments that can be undertaken, as there are only a limited number of plants than can be cultivated and hybridized.

In a phylogenetic species concept, species are classified *"according to how recently they share a common ancestor"* (RIDLEY 2004). Identification of species is based on molecular sequences and their divergence. This approach is claimed by some authors to raise the number of accepted species in comparison to species accepted under a biological species concept (ISAAC ET AL. 2004), and is claimed to be sometimes misleading (CLARKE ET AL. 1996) and raises the question of what to do with paraphyletic genera that form otherwise morphological distinct groups (BRUMMITT 2002, NORDAL & STEDJE 2004). It was summarised by LEVIN (2000) that *"any attempt to neatly fit biological diversity into any single species concept is likely to be futile"*. RUSE (1998) suggested not looking at just a single approach to characterize species but to make a *"virtue out of pluralisms"* and incorporate many aspects such as morphology, breeding systems, ecology and molecular data etc. into a classification. MANN (1999) in looking for a species concept in diatoms also supports a multidisciplinary approach, the so-called 'Waltonian species concept' that tries to gather all information available in order to see a broader picture and look for a general consensus.

In reviewing species concepts used by former workers on liverworts, many are based on morphology, such as treatments by NEES (1838) or MÜLLER (1954). However he considered that cytological differences in chromosome numbers can sometimes be an important character in distinguishing between species. He rejected descriptions of new species made purely on the basis of geographical parameters. This was also the approach of BISCHLER (1998) who argued that in the lack of morphological and sometimes even genetic differences many species can show a large distribution range and are known from several continents. HEINRICHS (2002), working on the leafy liverwort genus *Plagiochila* (Plagiochilaceae) explained that in his taxonomic treatment an attempt was made to include both morphology and molecular data in his species concept: *"Species are distinguished by their morphology and understood as a group of individuals which represent a continuous spectrum of phenotypes"* and that *"species should represent monophyletic lineages in the phylogenetic analyses of the molecular data".*

BISCHLER (1989) based her revision of the thalloid liverwort genus *Marchantia* (Marchantiaceae) on morphological differences and also tried to incorporate ecology. However, she added: *"Most of the described species are probably comprised of several genetically different components. [...] Structural variations are not the same, but by no means can these different kinds of populations be distinguished on a structural basis. Further subdivision of the taxa as defined here, is not thought likely to contribute to a better understanding of these plants. [...] With these considerations in mind, a broad species concept has been adopted".* This concept was again used by BISCHLER (1984) in her revision of *Marchantia* taxa of the New World: *"They [species] have to be morphologically recognisable, even if their structure might be genetically heterogeneous".*

The species concept used in the present study is based on a combination of morphological (particularly in regard to spore characters) and molecular evidence. It is hoped that the species are easily distinguishable in the field by their morphological appearance. By no means as complete a picture of the genus *Mannia* has been achieved in this study as was advocated by RUSE (1998) or MANN (1999), but all available information has been used to make decisions on species delimitation. Further work on *Mannia* is needed and other aspects such as breeding system or developmental studies should be added as they might give additional insights into species delimitation in *Mannia.*

1.6 Evolutionary age of *Mannia*

Spores that date back to the mid-Ordovician are the earliest fossil evidence for plant colonisation of land. It has been considered that these spores were possibly produced by early relatives of bryophytes as the spore ultrastructure shows liverwort affinities, although this is controversial (WELLMAN ET AL. 2003). The earliest definite fossils of land plants can be attributed to vascular plants amongst other unidentified plants (QIU ET AL. 1998). Therefore definite bryophyte fossils postdate the earliest fossils attributed to vascular plants. However, bryophytes are said to be the first plants to colonise the land based on phylogenetic studies (KENRICK & CRANE 1997, KODNER & GRAHAM 2001).
There are different hypotheses about bryophyte evolution. Whereas a few molecular studies suggest the three bryophyte lineages form a monophyletic clade (NISHIYAMA ET AL. 2004, GOREMYKIN & HELLWIG 2005), sister to the vascular plants, others suggest that they are a paraphyletic group with the liverworts forming a sister group to the hornworts, mosses and higher plants (e.g. KENRICK & CRANE 1997, QIU ET AL. 2006).
Fossil remains of liverworts were first noted from the Devonian and Lower Carboniferous periods (BISCHLER 1998). It was hypothesized by QIU ET AL. (1998, 2006) that within the bryophytes, liverworts are the earliest land plants; this view is supported by the lack of some mitochondrial introns which are present in virtually all mosses, hornworts, ferns and vascular plants.
It is said that fossil records of bryophytes such as from the order Marchantiales are generally rare because spores or tissue do not preserve well (HECKMANN ET AL. 2001, BISCHLER 1998). This is due to the absence of lignified tissues and the often delicate thallus, particularly in liverworts and hornworts (KODNER & GRAHAM 2001). Another reason could be that fossil extraction techniques may result in the loss of fragments (MILLER 1984). However, GRAHAM ET AL. (2004) considered that liverwort fossilization in thalloid liverworts such as *Marchantia polymorpha* and *Conocephalum conicum* could be underestimated and that in their experiments gametophyte tissue in these species showed resistance to

degradation and high-temperature acid treatment. They suspect that some fossils identified as belonging to the extinct group of nematophytes are possibly the remains of early marchantoid liverworts.

It is therefore difficult to put a date on the origin of Marchantiales. Their diversification and radiation time is unknown (BISCHLER 1998). Fossil records are mainly found from the Mesozoic Era about 248 to 65 million years ago. The earliest fossils of Marchantiales are known from the Triassic (KRASSILOV & SCHUSTER 1984). According to Frahm (2001), the earliest Marchantiales from the Triassic is *Marchantites cyathoides* from Natal (South Africa). There are early remains of Marchantialean gametophytes with epidermal pores, air chambers and scales reported from the Jurassic and early Cretaceous with a wider range of Marchantioid fossils known from the Cretaceous (OOSTENDORP 1987, KRASSILOV AND SCHUSTER 1984). Therefore it is assumed that genera of the Marchantiales such as *Mannia* appeared before or during the Cretaceous about 144 to 65 million years ago (KRASSILOV AND SCHUSTER 1984). However, the latter authors regret a *"lack of adequate fossil data from the Mesozoic"* and a fossil record for *Mannia* is absent.

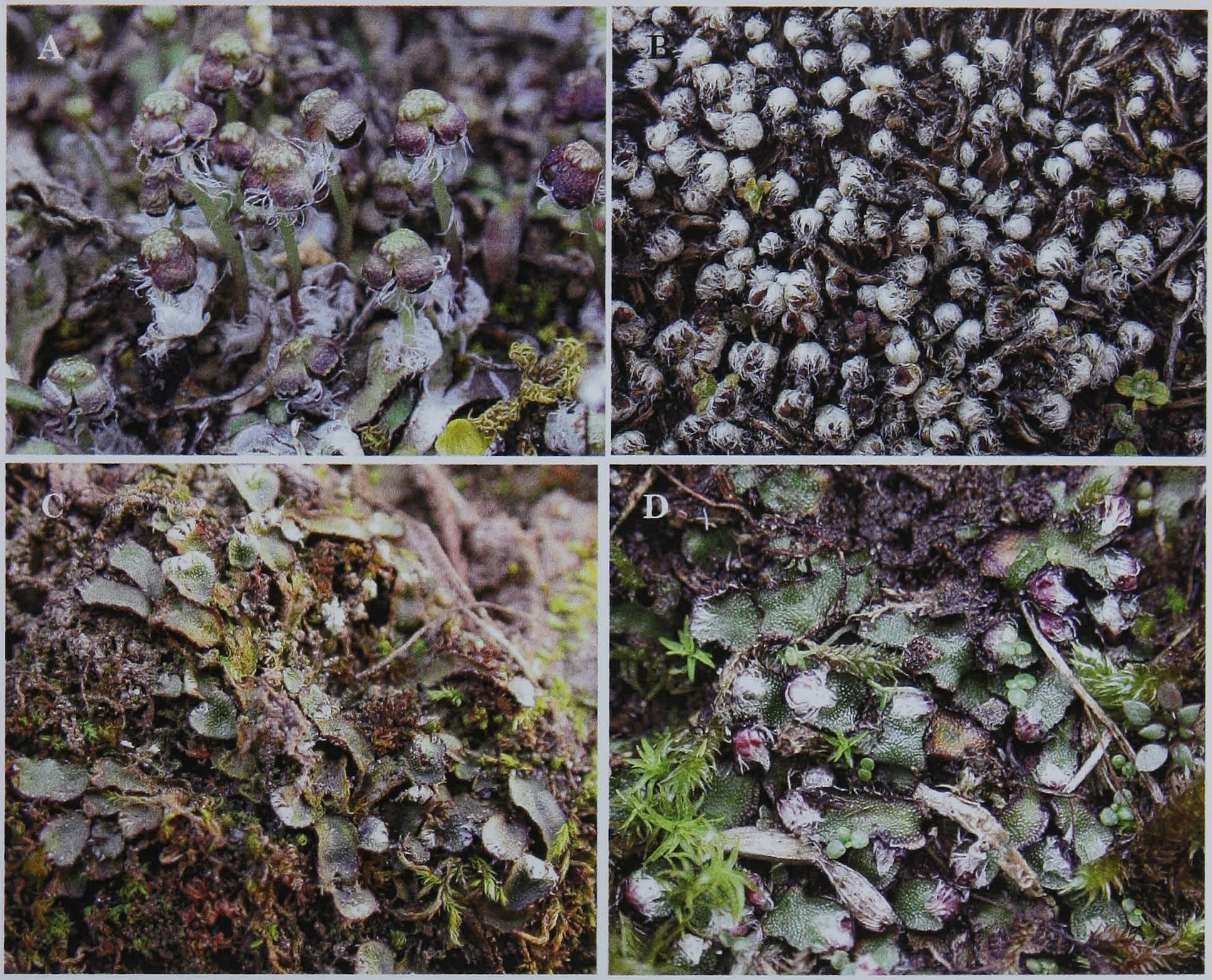


Fig. 1.1. Pictures of *Mannia* species (1). A *M. fragrans* with archegoniophores (*Schill et al. 51*, Switzerland); B *M. fragrans* in dry condition with inrolled thalli showing bearded thallus apices (Switzerland), C *M. fragrans* showing bleached appendages (*Schill & Clarke 162*, North India); D *M. fragrans* with antheridia on terminal discs (*Schill & Zündorf 3*, Germany).

Fig. 1.2. Pictures of *Mannia* species (2). A *M. californica* with archegoniophores and antheridia (*Schill & Clarke 144*, South India); B *M. californica* with antheridia (*Long 34281*, Yunnan); C *M. californica* with antheridia (*Schill & Clarke 101*, California); D *M. californica* with young archegoniophores and antheridia (*Schill & Clarke 165*, North India); E *M. californica* with antheridia (*Schill & Clarke 133*, Namibia); F *M. androgyna* with young archegoniophores and antheridia (*Schill & Clarke 121*, Namibia).

Fig. 1.3. Pictures of *Mannia* species (3). A *M. pilosa* with archegoniophores (*Schill et al. 83*, Austria); B *M. triandra* with archegoniophores (*Schill et al. 79*, Austria); C *M. triandra*, sterile thallus (*Schill et al. 81*, Austria); D *M. androgyna* with archegoniophores (*Schill & Lobo 34*, Madeira); E *M. androgyna* with young archegoniophores and antheridia (*Schill & Lobo 31*, Madeira).

Fig. 1.4. Pictures of other genera of Aytoniaceae. A *Asterella saccata* (*Schill et al. 43*), Switzerland; B *Asterella wallichiana* (*Schill & Clarke 167*), North India; C *Reboulia hemisphaerica* (*Schill et al. 46*), Switzerland; D *Plagiochasma rupestre* (*Schill 6*), Madeira; E *Cryptomitrium* spec. (*Schill 180*), Peru; F *Plagiochasma rupestre* (*Schill 191*), Peru.

Chapter 2: Taxonomic characters

2.1 Introduction

In *Mannia*, as in all of the Marchantiales, the gametophyte is highly elaborate showing a considerable number of different characters in sharp contrast to the sporophyte, which is highly reduced. This contrasts with the mosses and to a lesser extent with the leafy liverworts where the sporophyte shows greater elaboration.

Hence in the complex thalloids such as *Mannia* there is a rich selection of gametophytic characters available for taxonomic use but the sporophyte offers few characters. However, spore characters have proven to be of immense value in species identification and delimitation. The spore survey is presented in Chapter 3. For methods used in photography and morphological study see Chapters 3 and 4.

2.2 Morphological and anatomical characters in *Mannia*

The characters used in this study are grouped into vegetative and reproductive feature of the gametophyte and sporophyte characters. A summary table of selected characters is also presented. For a formal description of the genus see Chapter 4.

2.2.1 Vegetative features of gametophyte

Thallus *Mannia* species are characterized by small and rather narrow thalli, which sometimes broaden considerably towards the thallus apex. In general the thallus is either thick and leathery or rather thin and delicate; however, in some cases, the appearance can be rather intermediate. The plants usually grow intermingled in mats, or spreading and forming loose mats, which can then develop into quite extensive patches. All species have a pleasant aroma, though it is often not very strong. *M. fragrans* can have a strong cedar oil smell in the field that persists well over many years and is still present when dried specimens are remoistened. In dry field conditions the species is said to have only a faint smell and this is hard to detect (HUNECK ET AL. 1988). Sometimes *M. androgyna* shows a strong aroma unlike that of *M. fragrans*. It disappears once the plants are dried and cannot be detected when remoistened. The thallus is in general of bright green colour above although in some *M. triandra* specimens it can appear bluish green. The thalli usually have thin dark purple margins. This pigmentation is chemically not fully understood but the pigments are said to be '*localized in cell walls and not dissolved in vacuoles*', as is the case in higher plants (CRUM 2001).

When plants get older the thalli sometimes starts to disintegrate and become lacunose above. This is most evident in *M. pilosa*, where the thallus gets a whitish colour, but can also be seen in *M. triandra* and *M. fragrans*, though then the thallus colour is rather brownish. In dry conditions the thalli curl up from the margins inwards and appear like blackish threads, which are hard to see in the field. The dark colour of the thallus underside protects the thalli from high light intensities (SCHUSTER 1992b).

Vegetative branching There are several different ways by which *Mannia* thalli branch. In all species the most common branching pattern is terminal dichotomous. The thallus divides at the apex into two branches. These terminal dichotomies are either symmetrical or asymmetrical. In the asymmetrical case the shorter part of the dichotomy often bears the male part of the plant (androecia, which contain antheridia).

Vegetative branches can also be produced by ventral and terminal innovations. Ventral innovations develop from the ventral side of the thallus along the midline. They can be remote from the thallus apex or very close to it. The base of these branches is stipitate; the branches are usually linear or obovate. The branches of terminal innovations are sometimes obdeltoid with the apex somewhat truncate and tapering to the base (e.g. in *M. fragrans*). In *M. fragrans*, *M. californica* and *M. androgyna* the dichotomous branches are usually readily identifiable and continue their growth for a time before they branch again. In other species, in particular *M. triandra*, dichotomous branches at the thallus apex cannot always be clearly seen, and the apex sometimes gives the impression of being undulate because secondary dichotomies happen quite soon after the initial ones.

Dorsal epidermis A recognizable midrib is absent in *Mannia* and along the midline of the thallus, the so-called growing zone '*Wachstumszone*' (MÜLLER 1954), there is no colouring visible. Species with more leathery thalli like *M. fragrans* or *M. androgyna* do not show reticulation dorsally whereas species with more delicate thalli such as *M. triandra* or *M. pilosa* usually show a distinctly reticulate dorsal surface (Fig. 2.2 A, B).

The dorsal surface often has a purple pigment, particularly at the margins or sometimes in the area around the antheridial ostioles. The purple colouring is said to become lost in herbarium specimens (WHITTEMORE 1991). This could sometimes be observed, but often purple colouring was still present.

The dorsal epidermis consists of one layer of thin- or thick-walled cells with small or big, often convex trigones at the angles. Cell wall thickness is quite variable and can be seen as varying from thin- to thick-walled even when observing only a small part of the epidermal surface on a single specimen. This is most often the case in *M. triandra* and *M. pilosa*. Other species seem to have rather consistently thick-walled epidermal cells. SCHUSTER (1992b) suggested that the cell wall thickening might be environmentally induced.

In *M. fragrans* DAMSHOLT (2002) linked thick-walled epidermal cells to plants from xerophytic habitats and thin-walled epidermal cells to plants from more humid surroundings. The method of study used by different authors for examining cell wall thickness is sometimes unclear, as there are two ways. One is by studying the epidermis in surface view and the other is to examine transverse sections of the thallus. In the latter it is sometimes hard to decide if the cell walls are thin or thick and conclusions can therefore be ambiguous. However, the thickness of the epidermal cell walls has often been seen as a significant character by authors in former studies on *Mannia*. The genus was formerly subdivided into two different genera, *Neesiella* and *Grimaldia*, using this as one of several key characters. *Neesiella* (containing *M. pilosa* and *M. triandra*) was considered to have thin-walled epidermal cells whereas those in *Grimaldia* (*M. androgyna* and *M. fragrans*) were thick-walled (SCHIFFNER 1908). In his treatment of European species MÜLLER (1954) united these genera under

Grimaldia but also described *M. pilosa* and *M. triandra* as thin-walled. He actually used epidermal cell wall thickness as the first character in his key to distinguish between *M. fragrans* (thick-walled) and *M. androgyna* (thin-walled). In a later treatment SCHUSTER (1992b) described *M. pilosa* and *M. triandra* as having thin-walled epidermal cells, but that these species could also become thick-walled in some cases.

A new variety '*Mannia fragrans* var. *alpina*' was described by MEYLAN (1924) based on the very thick-walled epidermal cells of a plant found at high altitudes.

Air pores *Mannia* is characterised by simple epidermal air pores in the thallus (Fig. 2.3 A). Air pores connect the underlying air chamber with the surrounding atmosphere. Usually each air chamber has one air pore (Fig. 2.2 C). The pores can be inconspicuous or distinct, and are slightly to strongly upraised above each air chamber. In surface view they usually have two to three, occasionally four, concentric cell rings (Fig. 2.2 E, F, Fig. 2.6 C, D, E, F). These rings are usually found to overlap each other at least in part. The radial cell walls are thin or thick. The walls of the innermost ring cells are sometimes found to be collapsed (Fig. 2.2 E). In cultivation experiments on *Clevea* (now *Athalamia* in Cleveaceae) it has been shown that in wet environments the walls become thin whereas in dry environments they are thick (MÜLLER 1954).

Assimilation tissue The assimilation tissue appears as a 'green zone' in the thallus and is the main photosynthetic tissue. It is situated between the dorsal epidermis and the basal tissue (Fig. 2.3 B). The proportion of assimilation tissue to basal tissue varies considerably between and within species. The cells contain many chloroplasts responsible for photosynthesis. The assimilation tissue can be either spongy with small densely packed air chambers (*M. androgyna*, *M. californica*) or loose with large air chambers (*M. fragrans*, *M. pilosa* and *M. triandra*) (Fig. 2.7 A, B). The air chambers form an irregular layered group and even in cases where the assimilation tissue is thin, there is always more than one layer of chambers, at least in the middle part of the thallus.

In *M. fragrans* the assimilation tissue often contains one upper band of tall vertical air chambers and smaller more rounded air chambers below. The differences between spongy and loose assimilation tissue can sometimes be rather unclear as in *M. sibirica* and *M. asiatica*. The air chambers sometimes contain free filaments, for example below air pores. Oil cells may be present or absent.

Air chambers are said to develop schizogenously (BARNES & LAND 1907, EVANS 1918, CRUM 2001). The simple divisions take place just below the growing point of the thallus (CRUM 2001). This contradicts LEITGEB's (1881) earlier assertion that air chambers in the Marchantiales develop through sinking of the surface cells followed by parts of the surface becoming overgrown by more rapid growth of neighbouring tissues.

Basal tissue The basal tissue in *Mannia* is colourless and made up of rounded to oblong thin-walled cells. It is situated between the assimilation tissue and the ventral epidermis. It can form a thinner layer than the assimilation tissue, be the same thickness or sometimes even thicker (Fig. 2.6 B). The cells of the basal tissue contain no or only a few chloroplasts. Oil cells are usually present but scattered and are sometimes inconspicuous. In most species the single oil body is bright yellowish or occasionally greyish. In *M. californica* they are a good diagnostic taxonomic character being of a conspicuous dark brown colour, in contrast to all other *Mannia* species (Fig. 2.3 C, D, E, F). The oil cells contain one large oil body and no other organelles such as chloroplasts. They are said to be generally smaller than other cells (CRUM 2001). However, in the present study the oil cells were found to be as big as other cells. The actual oil body contains and stores terpenoids and other aromatic compounds - these essential oils are probably responsible for the aromatic nature of many liverworts (SUIRE ET AL. 2000, FIGUEIREDO ET AL. 2002). Oil bodies could possibly support the survival of the plant in dry conditions or offer protection against predators. Their function has been reviewed by SUIRE ET AL. (2000) in a study on the complex thalloid liverwort *Marchantia polymorpha* (Marchantiaceae). They suggest that oil bodies are not only useful for storage but also important in the cell metabolism cycle as they contain enzymes that are also found in plastids or the cytosol. There are some studies on aromatic compounds in Marchantiales, which include some *Mannia* species, e.g. HUNECK ET AL. (1988) (*M. fragrans*) or SCHIER (1974) (*M. fragrans, M. androgyna* and *M. capensis*).

Ventral epidermis The ventral epidermis in *Mannia* is not well differentiated. In general the cells are smaller than those of the basal tissue and of darker brownish or purple colour than the latter. Some ventral epidermal cells grow into rhizoids (MÜLLER 1954). In other Marchantiales it is has been shown that the ventral epidermal cells are not able to absorb water (MCCONAHA 1939).

Rhizoids As is the case in most Marchantiales, rhizoids in *Mannia* are dimorphic (Fig. 2.4 D, F). There are two types of rhizoids present: pegged and smooth. The internally pegged rhizoids are said to have some function in conducting water whereas the smooth rhizoids attach the thallus to the substrate (CRUM 2001, MÜLLER 1954). Another function of the smooth rhizoids is to give endophytic fungi access to the thallus cells as has been demonstrated in some Marchantiales (KACHROO 1954, POCOCK & DUCKETT 1985, LIGRONE & LOPES 1989, DUCKETT ET AL. 2000). The entirely intracellular fungal hyphae are thought to be absent from sporophytes as well as the reproductive structures of the gametophyte (POCOCK & DUCKETT 1985). The fungi in Marchantiales appear morphologically very close to fungi present in vesicular arbuscular mycorrhizas, notably from the family Endogonaceae (Zygomycota) (POCOCK & DUCKETT 1984, DUCKETT 1986) which now belong to the Glomeromycota (SCHÜßLER ET AL. 2001).

CRUM (2001) noted that, in general, smooth rhizoids emerge from the thallus midline and pegged ones from underneath the ventral scales. He also drew attention to their different orientation, the smooth ones being vertical and the pegged ones being horizontal. Rhizoids grow from their tip and can grow to over one cm long and therefore are the longest single cells known in liverworts (MÜLLER 1954). In studies on *Conocephalum* (Conocephalaceae) it has been found that the average length of pegged rhizoids is more than twice as long as that of the smooth rhizoids (MCCONAHA 1939). Large numbers of rhizoids can be found on a single thallus. In *Mannia indica*, KACHROO (1954) measured 700 pegged and 1150 smooth rhizoids per cm of thallus length.

Dehydration and in particular long periods of desiccation seem to influence the functioning of smooth rhizoids more than that of pegged ones. Cryo-Scanning Electron Microscopic studies on rhizoids showed that smooth rhizoids remain flattened after dehydration and do not regain their structure whereas pegged rhizoids revive and regain their function (DUCKETT ET AL. 2000).

Ventral scales Ventral scales in *Mannia* are situated in two rows along each side of the thallus midline and often overlap each other (Fig. 2.6 A). They also commonly overlap the lobe apex to protect the growing point (CRUM 2001). In *Mannia* each ventral scale comprises a scale body and apical appendages. The scale body is asymmetrical with a semicircular to broadly elongate or oblong-semicircular shape. Its thallus insertion is lunate and decurrently curved. The scales are just one cell thick. They are of purple colour with sometimes paler margins, reflect the light and hence protect the rolled up and dry thalli from desiccation. Along their margins small slime papillae are usually present (Fig. 2.4 C), which sometimes break off easily (*M. androgyna*) and are hard to find in older specimens.

There is usually one, two or occasionally three apical appendages on each ventral scale in *Mannia* and these are purple or bleached as in *M. fragrans*. They are subulate to broadly subulate or lingulate and they gradually narrow into an acute tip. Their base is not constricted. They catch moisture out of the air through capillary action.

The ventral scales usually contain oil cells, which are isodiametric (Fig. 2.4 A, B). An exception to this is *M. pilosa*, where oil cells are commonly absent or only few. They are usually found near the margins of the ventral scale body, sometimes also in their middle (*M. asiatica*) or at the base of the appendages. MCCONAHA (1939) demonstrated with dye experiments on *Conocephalum conicum* that the ventral scale appendages together with the rhizoids are solely responsible for water absorption. It was shown that the dye could not enter via the ventral epidermal cells of the thallus. Hence ventral scales play an important role in water uptake and regulation. Together with the rhizoids they build a complex capillary system on the ventral side of the thallus.

The evolutionary origin of ventral scales is not known and there is some controversy about their ancestry. SCHUSTER (1992b, c) suggested that ventral scales originated from slime papillae that had evolved into a '*leaflike form*', following GOEBEL (1905), who stated that the scales may have arisen from mucilage hairs or papillae. However, EVANS (1939) suggested that scales from the leaves of leafy liverworts and would therefore be homologous with leaves. This is contradicted by recent molecular research, which suggests that the complex thalloid liverworts arose before the leafy liverworts and mosses.

Vegetative propagules Vegetative propagules such as gemmae are absent in all *Mannia* species. Thallus fragments, though, can grow into new plants once distributed by water or wind. This could apply to the vegetative branches that developed from the ventral side of the thallus mid-line. They have a stalk-like insertion and could break off easily. It can be demonstrated experimentally that thallus fragments of other Marchantiales like *Marchantia* and *Lunularia* can regenerate and continue their growth in this way (MÜLLER 1954).

2.2.2 Reproductive features of gametophyte

Cytology In FRITSCH's (1991) 'Index to bryophyte chromosome counts', chromosome numbers for six *Mannia* species (*M. barbifrons, M. brachypoda, M. fragrans, M. levigata, M. pilosa* and *M. triandra*) are listed. All *Mannia* species are reported to have nine chromosomes. This was also confirmed by BISCHLER (1998). In distinguishing between different species, chromosome numbers seem to be of little value. For this reason no cytological studies have been undertaken on fresh material of *Mannia*.

Sexual condition The sexual condition of most species of *Mannia* is monoicous. In monoicous plants both antheridia and archegonia are found on one plant. The only dioicous species of *Mannia* is *M. fragrans*. Here the antheridia and archegonia are always found on separate plants but plants of both sexes are often found intermingled. *Mannia* species are usually fertile once a year for about one to two months. The fertility time of year depends on the region and often altitude, and is different for each species.

The different types of monoicy that can occur are dorsal-autoicous, male- or female- ventral-autoicous, terminal- autoicous and par-autoicous (Fig. 2.1).

In *Mannia* the androecia can be borne dorsally on the main thallus (dorsal-autoicous) with archegoniophore either on reduced ventral branches (female-ventral-autoicous) (*M. californica*), or archegoniophore on the same thallus or on a dichotomous furcation of the same thallus (*M. androgyna*). The antheridia can also be borne on reduced ventral branches of the main, often archegoniophore-bearing thallus (male-ventral-autoicous) as it is typical in *M. pilosa*. They are sometimes found on shorter or equally long branches of a dichotomous furcation (terminal-autoicous) (*M. sibirica, M. triandra, M. asiatica*) of which the other branch can bear an archegoniophore, or rarely close to the base of the archegoniophore (par-autoicous) (*M. triandra*).

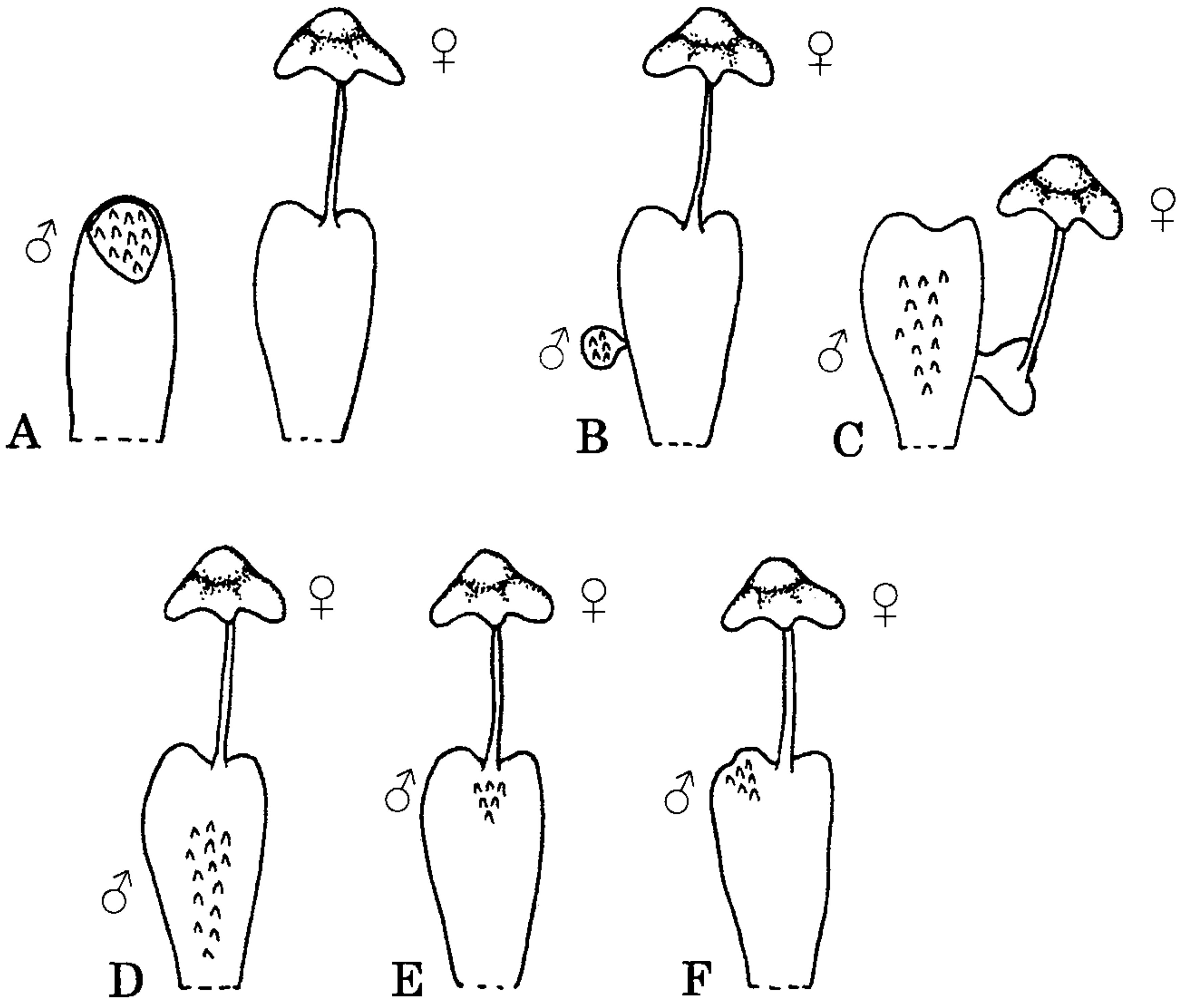


Fig. 2.1. Sexual conditions in *Mannia*. A dioicous; B male-ventral-autoicous; C female-ventral-autoicous; D dorsal-autoicous; E par-autoicous; F terminal-autoicous.

The sexual condition has been found in this study to be a good and reliable character for each *Mannia* species. In former revisions (SCHUSTER 1992b, DAMSHOLT 2002) the sexual condition of some *Mannia* species has sometimes been confused (see Chapter 4.4.3.2: Taxonomic Notes for *M. sibirica*).
LONG (1999, 2000) introduced new terms to distinguish between types of monoicy for the Marchantiales because WYATT & ANDERSON's (1984) sexual terminology did not cover the complexity of sexual conditions in this group of liverworts (Table 2.1). So the terms par-autoicous, terminal-autoicous and

ventral-autoicous follow LONG's (1999, 2000) earlier definition. In addition to that the term dorsal-autoicous has been introduced in the present treatment and ventral-autoicous has been further subdivided into male-ventral-autoicous, indicating that only male branches are found on reduced ventral branches and female-ventral-autoicous for plants that bear only archegoniophores on reduced ventral branches (Table 2.2).

Table 2.1. Definitions for monoicous conditions in *Mannia* (from LONG 1999, 2000), and the new term dorsal-autoicous

Types of monoicy	Definition
Par-autoicous	androecia borne on the main thallus immediately proximal to the base of the archegoniophore
Terminal-autoicous	androecia borne on terminally produced branches of the same thallus that bears an archegoniophore
Ventral-autoicous	androecia and/or archegoniophore borne on a ventrally derived, often reduced, branch of thallus
Dorsal-autoicous	androecia borne dorsally on main thallus, which can also bear an archegoniophore

Table 2.2. Additionally introduced terms for a further subdivision of ventral-autoicous

Types of ventral-autoicous	Definition
Female-ventral-autoicous	only archegoniophore borne on reduced ventral side branches
Male-ventral-autoicous	only androecia borne on reduced ventral side branches

Androecia In *Mannia* the androecia are sessile (Fig. 2.7 E). The antheridia are embedded in the thallus within the antheridial cavities (Fig. 2.4 E, Fig. 2.7

D) opening to the outside with a pore. The antheridia are said to have bicellular paraphyses (BISCHLER 1998). The development of antheridia does not inhibit the further vegetative growth of the male thallus although in *M. pilosa* the ventral male branches rarely seem to extend their growth.

Usually several antheridia are developed. They have their openings on the thallus surface by conical shaped and raised ostioles, which have a green colour when young but often turn purple when mature (Fig. 2.7 C, E). The surrounding epidermal tissue also often becomes crimson or purple.

The antheridia are found dorsally scattered along the midline of the thallus or in strongly or weakly upraised clusters dorsally or terminally (*M. californica, M. androgyna*).

They can also be in terminal poorly defined clusters in slight depressions or slightly upraised (*M. sibirica, M. triandra* and *M. asiatica*) or in terminal triangular, elliptic or rounded discs (*M. fragrans*). In *M. pilosa* they are found on reduced ventral branches, which have a stipitate base.

In observed *Mannia* specimens studied, the marginal scales around the antheridia where absent when mature but small purple scales were sometimes present at the start of antheridial development and then presumably later became fugacious. This is confirmed by BISCHLER (1998) who states that scales are minute or absent.

In the thalloid liverwort *Conocephalum conicum* it is reported that one antheridium can contain about 250, 000 spermatozoids (BOLLETER 1905). It is stated by KACHROO (1958) that many *Mannia* species are protandrous and release their spermatozoids before the maturation of the archegoniophore on the same plant.

Archegoniophore The archegoniophore is a highly modified branch of the thallus consisting of a stalk and a head, the so-called receptacle. In *Mannia* the archegoniophore is said to develop near the thallus apex, just above the growing point (CRUM 2001, MÜLLER 1954). It derives from the terminal notch of the thallus or is borne on a reduced ventral side branch of the thallus and inhibits further growth of the thallus apex.

Fertilization of the archegonia takes place before the stalk elongates and elevates the receptacle upwards for spore maturation (BISCHLER 1998). With the maturation of the sporophyte it has been noted that the stalk ceases its growth (KACHROO 1956).

Stalk The stalk is of greenish or yellowish colour, sometimes purple at the base or higher up. It is very variable in length. The stalk is either naked or sometimes has scales along its length, which are just one cell layer thick and a few cells across. The scales are of lanceolate to linear shape and occasionally have slime papillae or very rarely oil cells. Scales are often also present at the base of the stalk, though these are occasionally inconspicuous.

In cross section the stalk has a circular to irregularly triangular-ovate shape and is slightly ridged (Fig. 2.5 A). It has a single rhizoidal furrow suggesting evolution from a thallus and demonstrating a branch modification. In all *Mannia* species studied, air chambers could not be observed in the stalk opposite the rhizoidal furrow, though rhizoids were usually present in the rhizoidal furrow. These rhizoids are part of the capillary conduction system. The outer brownish and small epidermal cells are usually in just one layer (Fig. 2.5 B). The yellowish medulla has bigger rounded cells, which are sometimes incrassate with corners quite thickened. No stalk differences could be made out between the individual species of *Mannia*.

Receptacle The receptacle in *Mannia* is usually strongly warted/dimpled and the air chambers of the receptacle are often visible on its dorsal surface (Fig. 2.2 D) with the naked eye or a hand lens. On the ventral side rhizoids and scales can sometimes be found. As is characteristic for the family Aytoniaceae, the air pores of the receptacle are compound (Fig. 2.5 C, D) in contrast to the simple pores present at the dorsal surface of the thallus. The shape of the receptacle is subglobose in *M. triandra* and *M. pilosa* but usually hemispherical in all other species.

Some species in *Mannia* are often bearded with a tuft of white scales at the base of the receptacle. This is usually the case in *M. fragrans*, *M. pilosa* and *M. sibirica* although in some specimens the beard is not very distinctive. In other species the receptacle is usually naked as in *M. androgyna* and *M. californica*, but occasionally specimens have a few scales below the receptacle. Although *M. triandra* has a predominantly naked receptacle, in some specimens the receptacle was found to be bearded. *M. asiatica*, usually characterised by a naked receptacle, sometimes appears slightly bearded. This indicates that there is some plasticity in this character although it usually gives a good indication in distinguishing between individual species.

The receptacle is yellowish green when young and turns green and often tarnishing purple when matured. Each receptacle was found to bear between two and four, sometimes five sporophytes. The lobes of the receptacles result from forked branching, the number of lobes depending on the number of divisions of the growing point (KACHROO ET AL. 1977, CRUM 2001). In *Mannia* a double forking is assumed (KACHROO 1958, CRUM 2001), which produces four lobes, and if an archegonium in each lobe gets fertilized this would result in the development of four sporophytes. BISCHLER (1998) suggests twice- to thrice-dichotomous branching, which would on average result in the development of six sporophytes. This can be confirmed as in some cases in *Mannia* specimens five sporophytes have been counted with the remaining one archegonium unfertilized.

Involucre An important character to distinguish *Mannia* from other genera is the presence of cup-shaped involucres (BISCHLER 1998). They form the end of each receptacle lobe and surround the capsule (Fig. 2.2 D). The involucre is usually two cell layers thick and rather delicate.

Calyptra Each developing sporophyte is at first protected by a calyptra. In *Mannia* the calyptra is inconspicuous, small, thin and delicate. It is said to be two to three layered after fertilization (BISCHLER 1998). It is rounded shallowly bowl- or cup-shaped and situated at the bottom of each receptacle lobe underneath the capsule. In mature specimens it can only be seen once the capsule is removed. The presence of the calyptra could be observed in all *Mannia* species.

2.2.3 Features of sporophyte

Capsule Each receptacle lobe can have many archegonia but in general only one archegonium in each lobe is fertilised and develops into a sporophyte.

Usually one to four or sometimes five sporophytes develop on a single archegoniophore. They consist of a capsule and a much reduced short seta, which does not elongate. The capsule is globose and of yellow colour when young (Fig. 2.2 D); it turns brown or black when mature. The capsule wall is just one cell layer thick without any wall thickenings (Fig. 2.4 G). The capsule opens with a lid, sometimes also called an operculum, when spores are mature. The lid cells are rounded to rectangular and can have small corner thickenings. The capsule contains spores and elaters in a ratio of four to one (BISCHLER 1998).

Spores Spores are relatively large in *Mannia* (Fig. 2.5 E). They develop only once a year in the Marchantiales (BISCHLER & JOVET-AST 1981). The spore diameter in *Mannia* species is between about 40 and 95 µm. Although the spore size can be variable within individual species, they are generally smaller in *M. sibirica* than in other species and are therefore a good diagnostic character for this species. Within the capsule, spores are produced in tetrads, being first attached to each other at the proximal side, where they show a trilete mark once they break off. However, the trilete mark is sometimes inconspicuous. In general the number of spores per capsule varies with spore size but it is reported that *Mannia* species have about 1000 (BISCHLER 1998) or 2000 to 3000 spores in each capsule (BISCHLER ET AL. 2005). The colour is yellow, brown, yellowish brown to reddish brown or greyish brown. In *M. androgyna* and *M. californica* they can be either brown or yellow; one spore colour often dominates but both spore colours could sometimes be observed on the same specimen. All *Mannia* spores show elaborate ornamentation, distally saccate, areolate or ridged with papillae and with pits present or absent. The proximal side can possess a disc-like structure and along its equatorial rim, apertures can be present. The ornamentation on distal and proximal sides of the spore can be similar or dissimilar.

In dioicous species two spores in each spore tetrad grow into female plants, the other two into male plants (CRUM 2001). In germination experiments on *M. indica* it has been shown that spores do not require a rest period to trigger germination, which occurred after 9 days on a medium containing Knop's solution (MEHRA & KACHROO 1951). It has also been observed in this study that *M. indica* germinating spores at first become swollen, gaining a greenish colour before a rupturing of the proximal side of the spore takes place and the rhizoid and germ tube break through at the trilete mark. BISCHLER & JOVET-AST (1981) stated that spores in Marchantiales can still germinate after one to several years.

Elaters Elaters are of yellowish or brownish colour. They generally have 2 to 3 helical bands (Fig. 2.5 F). The ends of the elaters are mostly 2-spiral and the middle 3-spiral. Occasionally some elaters appear branched. This has been observed in *M. sibirica* and is often the case in *M. triandra* and *M. pilosa*. This is due to some spirals breaking through the elater wall and appearing as a pseudo-branch. In general the function of elaters is thought to help in releasing the spores once the capsule is open; they act as little springs. However, BISCHLER & JOVET-AST (1981) consider their function in *'loosening the spore mass, allowing better maturation of the spores'* within the capsule. The surface of the elaters is smooth or sometimes minutely roughened although this character varies within single species.

2.2.4 Summary Table of selected morphological characters in *Mannia*

Table 2.3. Summary Table of selected characters for all *Mannia* species

Species Characters	*M. androgyna*	*M. sibirica*	*M. californica*	*M. fragrans*	*M. asiatica*	*M. triandra*	*M. pilosa*
Growth form	dense mat	loose mat	dense mat	dense mat	loose mat	loose mat	loose mat
Ecological tolerance	xeromorph	xeromorph	xeromorph	xeromorph	xeromorph	mesomorph	xeromorph
Odour	inconspicuous to sometimes strongly aromatic	inconspicuous	inconspicuous	often conspicuously aromatic (cedar oil)	not observed on fresh material	inconspicuous	inconspicuous
Thallus structure	leathery	leathery to delicate	leathery	leathery	rather leathery	delicate to leathery	leathery to delicate
Thallus reticulation	absent	usually absent	absent	absent	usually absent	usually present	present
Branching type	terminal dichotomous, terminal and ventral innovations	terminal, dichotomous, terminal and ventral innovations	terminal dichotomous, ventral innovations (usually female)	terminal dichotomous, ventral and terminal innovations	terminal dichotomous, terminal innovations	terminal, dichotomous, terminal innovations	terminal dichotomous, terminal or ventral innovations
Assimilation tissue	compact	rather loose to compact	compact	loose	rather loose to compact	loose	loose
Air chambers	small	small to large	small	large	small to large	large	large
No of cell rings of epidermal air pores	2(–3)	2(3)	2–3	2–3	2–3	2–3	2
Colour of oil bodies	bright yellowish	yellowish grey to brownish	dark brown	bright yellowish	yellowish	yellowish brown	greyish brown to yellowish brown

Table 2.3. Summary Table of selected characters for all *Mannia* species, continued (1)

............Species Characters	*M. androgyna*	*M. sibirica*	*M. californica*	*M. fragrans*	*M. asiatica*	*M. triandra*	*M. pilosa*
Size of ventral scales	(0.6)0.8–1.2(1.3)mm long, (0.4)0.5–0.9(1.1)mm broad	(0.6)0.7–1.6(1.8)mm long, (0.08)0.4–1.0(1.2)mm broad	(0.8)0.9–1.6(1.8) mm long, (0.5)0.6–1.2(1.4) mm broad	(0.4)0.5–1.2(1.4)mm long, (0.4)0.5–1.1(1.2)mm broad	(0.5)0.7–1.5(1.8)mm long, 0.4–1.1(1.3)mm broad	(0.4)0.5–1.1(1.8)mm long, (0.2)0.3–0.9(1)mm broad	(0.6)0.7–1.4(1.7)mm long, (0.2)0.4–1(1.1)mm broad
No. of oil-bodies per ventral scale	7–34	(3)6–16(22)	6–22	12– 52	6–22(33)	1–19	usually absent, 0–2 (4)
No. of appendages	1–2(3)	1(–2)	1 –2	(1)2(3)	1–2(3)	1–2	1(–2)
Bleached appendages	absent	absent	absent	present	occasionally present	absent	absent
Sexual condition	dorsal autoicuous, female-ventral-autoicous	terminal-autoicous	dorsal autoicous, female-ventral-autoicous	dioicous; male and female often intermixed	terminal autoicous	terminal-autoicous and occasionally par-autoicous	typically male-ventral-autoicous and rarely terminal-autoicous
Position of antheridia	dorsal or terminal along thallus midline, sometimes bifurcate	terminal	dorsal or terminal along thallus midline	terminal	terminal	terminal or behind archegonio-phore	reduced ventral branches
Antheridia organisation	clusters or loose aggregations	poorly defined rounded cushions	clusters or loose aggregations	on triangular (rounded or elliptic) discs	poorly defined rounded cushions	poorly defined rounded clusters	poorly defined rounded clusters

Table 2.3. Summary Table of selected characters for all *Mannia* species, continued (2)

Species **Characters**	***M. androgyna***	***M. sibirica***	***M. californica***	***M. fragrans***	***M. asiatica***	***M. triandra***	***M. pilosa***
Position of archegoniophore	usually terminal but also on reduced ventral branches	terminal	usually ventral but also terminal	terminal and ventral	terminal	terminal	usually terminal, rarely on ventral lateral branch
Base of receptacle	naked	bearded	naked	bearded	usually naked	usually naked, sometimes bearded	bearded
Shape of receptacle	hemispherical	hemispherical	hemispherical	hemispherical	hemispherical	subglobose	subglobose
Stalk length	(4.1)5.5–22.5(24)mm	(4.6)7.3–17.9(21.4) mm	(4.3)5.6–10.9(11.5) mm	(5.8)6–14.2(16) mm	(0.9)1.9–18.9(20.8) mm	(0.9)2.2–17.9(19.8) mm	(4)5.7–26(31) mm
Stalk diameter	(517.5)540–724(748)µm	(310.5)333.5–495(563.5) µm	(517.5)609.5–862.5(908.5) µm	(290)330–495(530) µm	(207)276–517.5(529) µm	(207)253–701.5(910) µm	(310.5)333–506(529) µm
Elaters	rough	smooth	rough	smooth	smooth to rough	smooth	smooth
Spore diameter	(60)63–86.1(87.2) µm	43.1–56.2(62) µm	(52.5)58–73.8(76) µm	(54)57–74.3(76.3) µm	(54.5)60–71.7(74.4) µm	(45.6)55.2–75(77.7) µm	(63)66.6–81.5(85.7) µm
Spore colour	yellow or brown	yellow to yellowish brown	yellow or brown	yellow	yellow	yellow or greyish brown	yellow to brownish yellow
Spore type (see Chapter 3)	I	II	II	III	IV	V	V

2.3 Cultivation of living plants in a growth cabinet

There are several cultivation methods for bryophytes available in the literature such as by DUCKETT ET AL. (2004). Cultivation of living material from collected plants was undertaken in a growth cabinet for morphological study. This has been very useful in the case when sporophytes where not fully mature or in order to see if archegoniophores would develop from sterile material. Thalli were placed on sterile sand in labelled plastic containers with a lid as described by FRAHM & NORDHORN-RICHTER (1984). The containers were kept closed and the plants were occasionally watered with cold tap water or de-ionised sterile water. The temperature setting in the growth cabinet was 12°C with the light permanently on.

The cultivation of living material was successful in the sense that in many cases young immature archegoniophores could be cultivated until the spores matured. Longer cultivation (more than 6 months) often resulted in strong algal overgrowth, which in the end damaged the plants.

In all living specimens it could be observed that the natural appearance of the thallus changed in time as plants etiolated. This has also been observed by LONG (2000). In no instance did sterile material develop antheridia or archegoniophores during the cultivation phase. *Mannia* species with delicate thalli, notably *M. triandra* and *M. pilosa* did not survive the growth cabinet conditions as well as species with more leathery thalli such as *M. androgyna* and *M. fragrans*. All plants were cultivated from fresh material and most *Mannia* species were cultivated. Fresh specimens of *M. asiatica* and *M. sibirica* were unfortunately not available.

It also can be noted that in a sterile *Mannia fragrans* specimen the common cedar oil smell appeared and disappeared so that there were days when the plant smelt characteristically and days when it did not.

2.4 Discussion and conclusions

The characters employed in taxonomy for distinguishing between different species should ideally be reliable characters, independent from whether they are continuous or discontinuous, and not showing a phenotypic plasticity and therefore too much variation.

In *Mannia* there is a great diversity of gametophytic characters but a more limited range of sporophyte features that can be used for characterising the different species. The sporophyte generation is much reduced and well protected by gametophytic tissue so it is generally assumed that the gametophyte in the Marchantiales is more affected by the environment and therefore evolving more quickly than the more protected sporophyte (BISCHLER 1998).

Despite the fact that there are a great number of morphological characters available in *Mannia*, many of these characters are unreliable. Some characters show a considerable amount of variation (e.g. thallus width or size of ventral scales) or even in the case of continuous characters (e.g. bearded receptacle), they can sometimes be either present or absent. The difficulties in finding clear differences between *Mannia* species has often resulted in long keys to distinguish between species as the characters used have probably not been regarded as highly reliable (e.g. SCHUSTER 1992b, DAMSHOLT 2002). In other cases characters have been misinterpreted and regarded as variable when they are not or *vice versa*. So in studying the range of characters available in *Mannia* an attempt has been made to categorise characters as follows: key characters that are diagnostic for species identification, characters that may be variable but useful and characters that are not of great use for identification (Tab. 2.4).

Table 2.4. Summary table for key characters, variable but useful characters and variable characters of little use in *Mannia* identification

Key characters	Useful characters	Variable characters
Spore ornamentation Sexual condition	Structure of assimilation tissue Thallus reticulation Thallus colour when disintegrating Thallus apex bearded Colour of oil-bodies in thallus Number of oil-cells in ventral scales Bleached appendages Receptacle bearded/naked Receptacle shape	Thallus length/width Epidermal cell wall thickening Width of assimilation tissue Width of compact tissue Size of ventral scales Number of concentric rings of epidermal pores Stalk length and cross section Elaters smooth/rough Spore colour

Key characters for distinguishing between different species were found to be spore ornamentation pattern and sexual condition. As spore ornamentation patterns are sometimes difficult to observe with a light microscope, former keys and revisions of *Mannia* have not emphasised spore characters. However, authors like MÜLLER (1954), SCHUSTER (1992b) or DAMSHOLT (2002) used spore ornamentation in descriptions and keys but often not as a main character to distinguish between species. MÜLLER (1954) used distal ornamentation in his key to separate *M. fragrans* and *M. androgyna.* In species with more similar spore ornamentation patterns, e.g. *M. pilosa* and *M. triandra* a clear separation is more difficult since observations under the compound microscopes can often not be interpreted unambiguously. Though the spore size is quite variable in most species, it is a diagnostic feature for *M. sibirica,* which has in general smaller spores than all the other species. In a revision on *Mannia* in Southern Africa PEROLD (1994a) gave a much more detailed account of spore ornamentation in *M. capensis* as she used the scanning electron microscope to make observations.

The sexual condition of *Mannia* species has been regarded by many authors as a good character although the terms to describe it were inadequate. The terms monoicous, dioicous, polyoicous and more recently in some cases autoicous were used by many authors (NEES VON ESENBECK 1838, STEPHANI 1917, MÜLLER 1954, BISCHLER 1998, DAMSHOLT 2002, SCHUSTER 1992b, BISCHLER ET AL. 2005, PEROLD 1994a, 1999, UDAR & CHANDRA 1965). These terms were not found to be sufficient enough to describe the different types of monoicy in Marchantiales (LONG 1999) so the terms introduced by LONG (1999, 2000) have been used in this study to describe the different types of monoicy in *Mannia* and extended where necessary.

In some *Mannia* species, the sexual condition has occasionally been misinterpreted. *M. fragrans* has often been seen as a polyoicous plant being sometimes dioicous and sometimes monoicous (e.g. SCHUSTER 1992b). This cannot be confirmed since if male and female plants of *M. fragrans* occur intermixed the antheridia and archegonia have never been found on the same thallus in specimens observed, so the term polyoicous cannot be applied. This conclusion also applies to *M. californica*, which has been described as polyoicous by the same author. PEROLD (1994a, 1999) understands *M. capensis* (a synonym of *M. androgyna*) as being '*dioicous (rarely monoicous, but gametangia on different branches)*'. This contrasts with the first description by STEPHANI (1917) and ARNELL's (1963) treatment. Both described *M. capensis* as a monoicous species. This agrees with the present treatment of *M. androgyna* though the gametangia were not always found to be borne on the same thalli.

The position of gametangia on the thallus is a good character for identification. In most *Mannia* species the archegoniophore is usually borne on the main thallus in a terminal position. Exceptions to this are *M. californica* and *M. androgyna*, where the archegoniophore can be borne on reduced ventral side branches; this is more often the case in *M. californica* and has also been noted before for this species by BISCHLER ET AL. (2005) and SCHUSTER (1992b). The position and organisation of the antheridia is also useful for diagnosis. In *M. pilosa* they are typically found on reduced ventral branches and only very rarely in a terminal position. The latter was only seen twice in specimens observed. If antheridia were found terminally though, male ventral branches also occurred at the same time. This does not agree with SCHUSTER's (1992b) idea of this species. He finds it very variable in that '*androecia either on short lateroventral branches (...) or at apices of the shorter fork of a dichotomy (...) or similarly situated on short, obcordate branches arising as ventral, terminal innovation from the main thallus*'. In *M. triandra* the antheridia can be found either terminally or very occasionally close behind the archegoniophore. The latter has not been noted for this species by other authors (MÜLLER 1954, SCHUSTER 1992b).

Although observations on spore characters and sexual condition of *Mannia* species have usually been included in descriptions by former authors, limitations in the methods of studying them or misinterpretations have influenced the outcome and disguised their value.

Besides these two key characters there are some other characters, which are useful for identification though they occasionally might show some variations. With regards to gametophytic characters the thallus structure can be either leathery and rather thick or delicate and rather thin. In general, species such as *M. triandra* and *M. pilosa* belong to latter category but more leathery specimens of *M. triandra* from high altitude have been seen. The division of compact or loose assimilation tissue with air chambers small or big works quite well although it has been noted that *M. fragrans* specimens from xeromorphic habitats have thinner assimilation tissue than plants from more humid habitats (DAMSHOLT 2002), which would have influences on the appearance of the assimilation tissue. Therefore environmental factors seem to play in important role in some features of the gametophyte, notably the thallus. Furthermore regarding structure of thallus and assimilation tissue, some species are found to be rather intermediate such as *M. sibirica* and *M. asiatica*; this has also been noted by LONG (2000) for some species of *Asterella*.

The thallus reticulation of *Mannia* has been long regarded as a good feature for the characterisation of *M. pilosa* and *M. triandra*, e.g. in treatments of MÜLLER (1954) or in the identification key by SCHUMACKER & VÁŇA (2000), where it was seen as an important character. In former classifications where *Mannia* was still subdivided into the genera *Grimaldia* and *Neesiella* the areolation of the thallus has been regarded as one distinctive character amongst others for their separation (SCHIFFNER 1908).

The disintegration of the thallus is a frequent feature but in none of the species is it as apparent as in *M. pilosa*, where the thallus becomes strongly lacunose and of whitish colour, starting along the usually purple edges.

The colour of the oil bodies in the oil cells of the assimilation and mainly storage tissue has so far been overlooked as a character for species identification in

Mannia although oil bodies are taxonomically important in other liverworts such as *Plagiochila* (HEINRICHS 2002), where they can be characteristic for classifying species into sections. In the present study the dark brown oil bodies were found to be a good diagnostic feature for *M. californica*. There were only two cases observed where dark brown oil bodies were also found in *M. androgyna*.

The number of oil cells present in ventral scales is variable for most species and does not help in distinguishing between them, however it is a good diagnostic feature for *M. pilosa*. In this species, oil cells are usually absent from the ventral scales and only occasionally a few oil cells can be found. This has been reported by many authors (e. g. MÜLLER 1954, SCHUSTER & DAMSHOLT 1974, SCHUSTER 1992) and used in species delimitation. It has been found as a constant character for *M. pilosa* collections from Scandinavia and Greenland in a study by SCHUSTER & DAMSHOLT (1974).

The presence of conspicuously bleached appendages, which often result in a bearded thallus apex in *M. fragrans* is a unique feature for this species, making it easily recognisable from all other related *Mannia* species. Occasionally bleached appendages are also found in *M. asiatica* though they are never very prominent and the thallus apex is never found to be bearded.

The occurrence of scales at the base of the receptacle is a common feature for some *Mannia* species. In general this is a quite reliable character though in some usually bearded *M. pilosa* specimens the scales are sometimes rather scarce. In *M. triandra* the expected absence of scales can sometimes be deceptive since in a considerable number of specimens observed the receptacle has been found to be bearded. This has not been noted for this species before although SCHUSTER (1992b) reported *'a few bractlets at stalk apex'* in his description of *M. triandra*.

The shape of the receptacle being hemispherical (most *Mannia* species) or subglobose (only *M. pilosa* and *M. triandra*) was also found to be beneficial for distinguishing between two groups within *Mannia*. Although this character can sometimes be difficult to observe in dried herbarium specimens it is quite apparent on fresh plants in the field.

There are many characters that are of little value for distinguishing between different *Mannia* species. Measurements such as length and width of lobes, as well as other measurements, showed a considerable amount of variation even within each individual species. This is also the case for the thickness of the ventral tissue or the assimilation tissue. Their proportions can vary notably. This has been previously used in keys for example by MÜLLER (1954), SCHUSTER (1992b) and DAMSHOLT (2002).

The comparison of these variable characters amongst species often shows an overlap, resulting in not very clear species boundaries. This current study finds them to be of little use for species identification.

The size of the ventral scales is also not regarded as a good character in the present study. This is in contrast to earlier work on *Mannia* where *M. triandra* was said to have small ventral scales in comparison to e.g. *Mannia pilosa* as stated by SCHIFFNER (1908), MÜLLER (1954) or SCHUMACKER & VÁŇA (2000). The scale measurements of these species considerably overlap so that there is no clear distinction between sizes. The number of the appendages on the ventral scales did not prove to be distinct for each of the observed species either.

In the past many authors have emphasised epidermal cell wall thickness. In the present study this character is considered too variable and unreliable. This has also been noted before by DAMSHOLT (2002) for *M. fragrans* (see under 'Dorsal epidermis') though he and other authors used this character in keys (e.g. SCHUMACKER & VÁŇA 2000).

Another character previously thought to be of taxonomic value is the number of concentric rings of the epidermal air pores (SCHUSTER 1992b, DAMSHOLT 2002). In all observations little difference was apparent as regards their number. Each species had usually two to occasionally three rings. This was also confirmed by MÜLLER (1954).

Measurements of stalk cross sections did not show any significant differences between individual species. The stalk length is very variable, ranging from less than one mm to two cm within a single species and is therefore not a stable character. A variation of *M. fragrans* based exclusively on stalk length by KAALAAS (1889) is therefore considered untenable.

The surface of the elaters being smooth or minutely roughened varies within species so it is not considered a useful character. In general elaters associated with yellow spores seemed to be rather smooth whereas elaters associated to darker coloured spores were found to be minutely roughened. SCHUSTER (1992b) has observed rough elaters for *M. californica.*

Yellow and brown are the typical colours for *Mannia* spores, although variations can occur. A single colour is normally typical for a species but in some (*M. californica* and *M. androgyna*) both colours occur.

It can be concluded that species identification in *Mannia* is best undertaken with a combination of characters. Using key characters in combination with other useful characters, species identification can usually be achieved. However, in the absence of reproductive features of the gametophyte, species identification is difficult, because sterile *Mannia* species have a close resemblance to other species within the Aytoniaceae, notably *Asterella.*

BISCHLER & JOVET-AST (1981) see the morphological diversity in Marchantiales as '*an expression of their genetic richness and of a long evolutionary history*'. Unfortunately many of these characters are not of particular value for identification purposes.

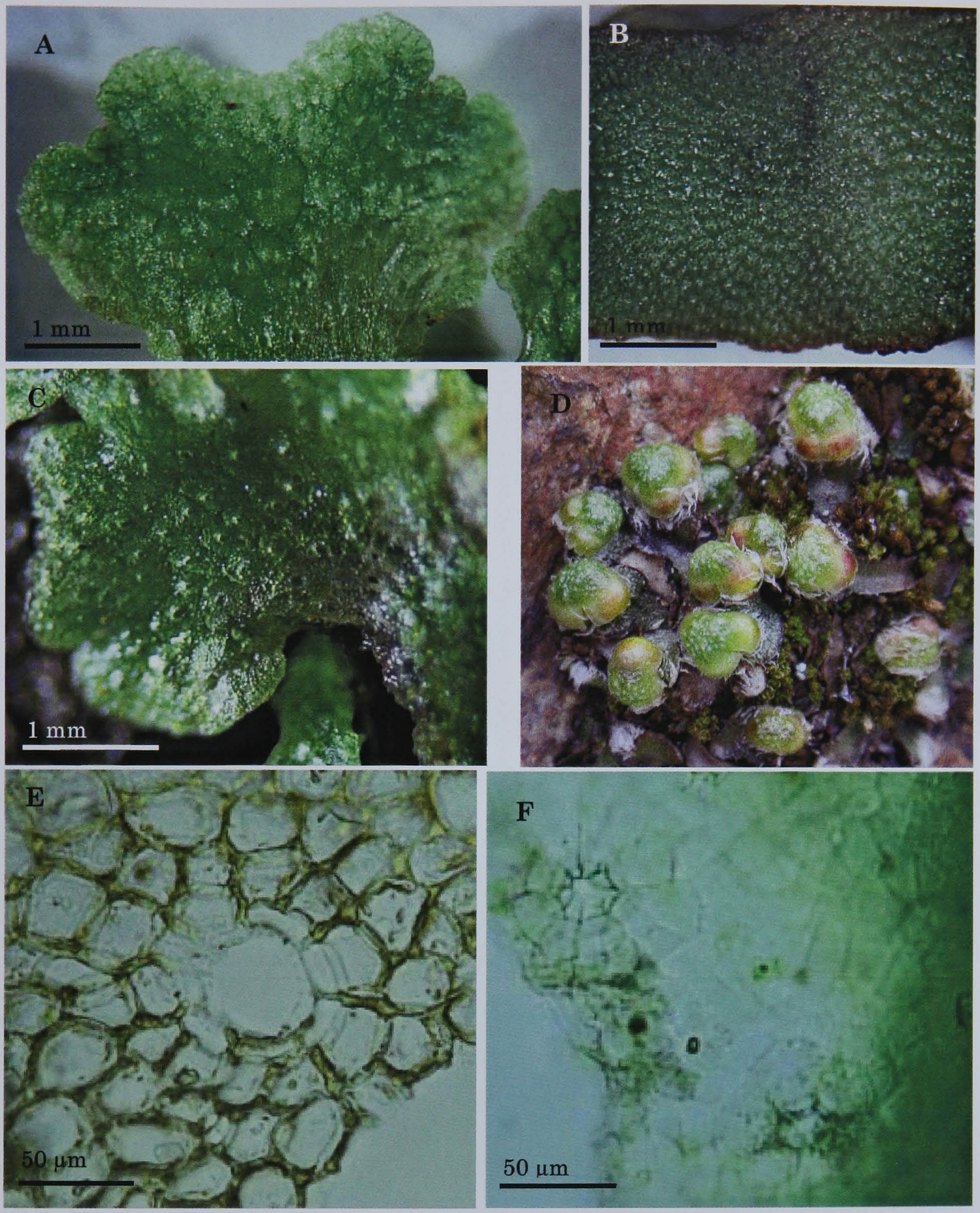


Fig. 2.2. Features of *Mannia* under LM (1). A areolate thallus surface; B non-areolate thallus surface; C epidermal air pores; D young plant showing archegoniophores with young, still yellow capsules and involucres; E epidermal air pores from inside with collapsed inner concentric ring; F epidermal air pores. A, C, E *M. triandra* (*Inoue*, Japan); B *M. androgyna* (*Schill & Clarke 122*, Namibia); D *M. fragrans* (*Schill et al. 40*, Switzerland); F *M. californica* (*Schill & Clarke 102*, California).

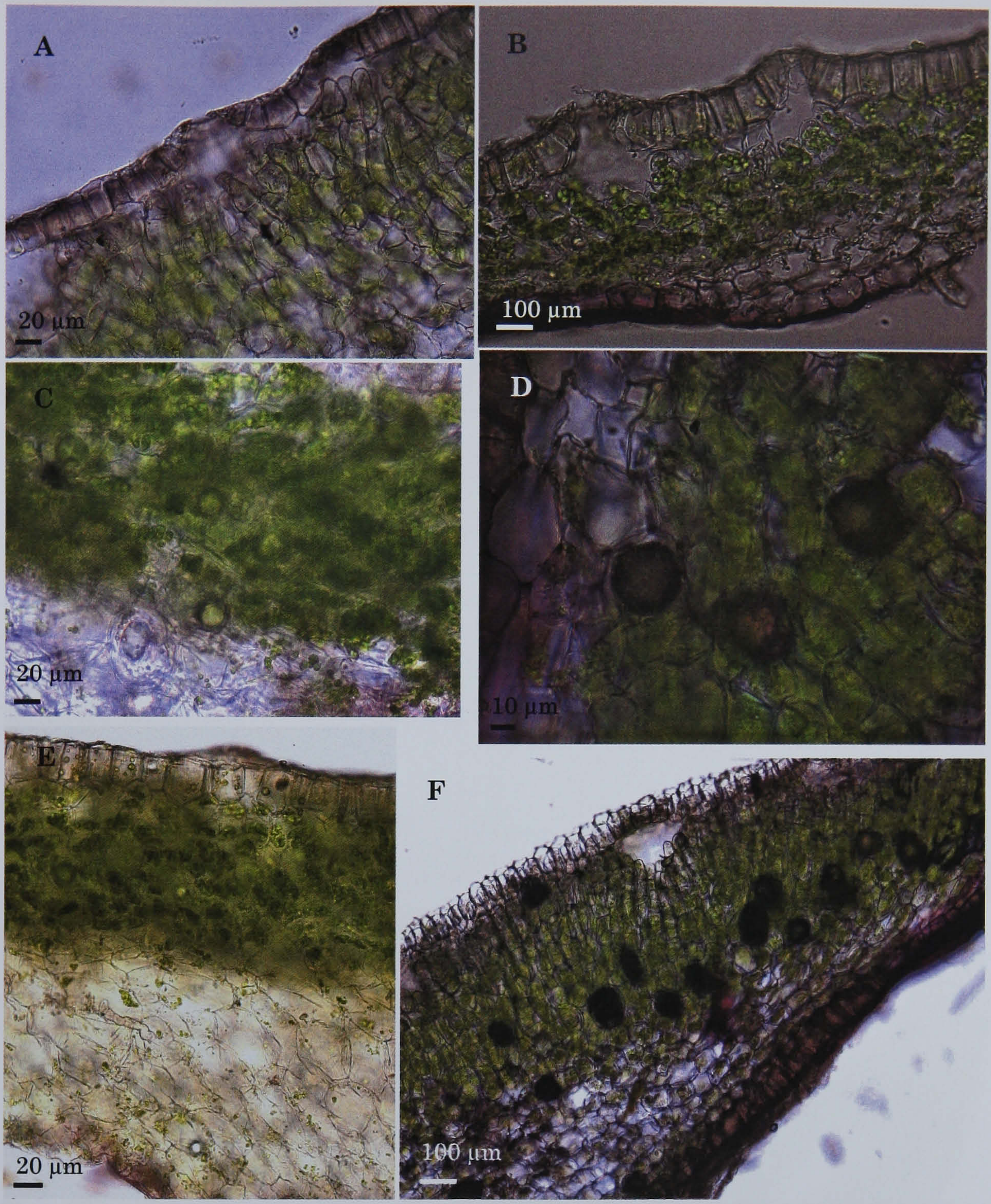


Fig. 2.3. Features of *Mannia* under LM (2). A epidermal pores in t.s.; B thallus t.s.; C, E bright coloured oil bodies in thallus t.s.; D, F dark coloured oil bodies in thallus t.s. A, D, F *M. californica* (*Long 35035*, California); B, C, E *M. androgyna* (*Schill & Lobo 34*, Madeira).

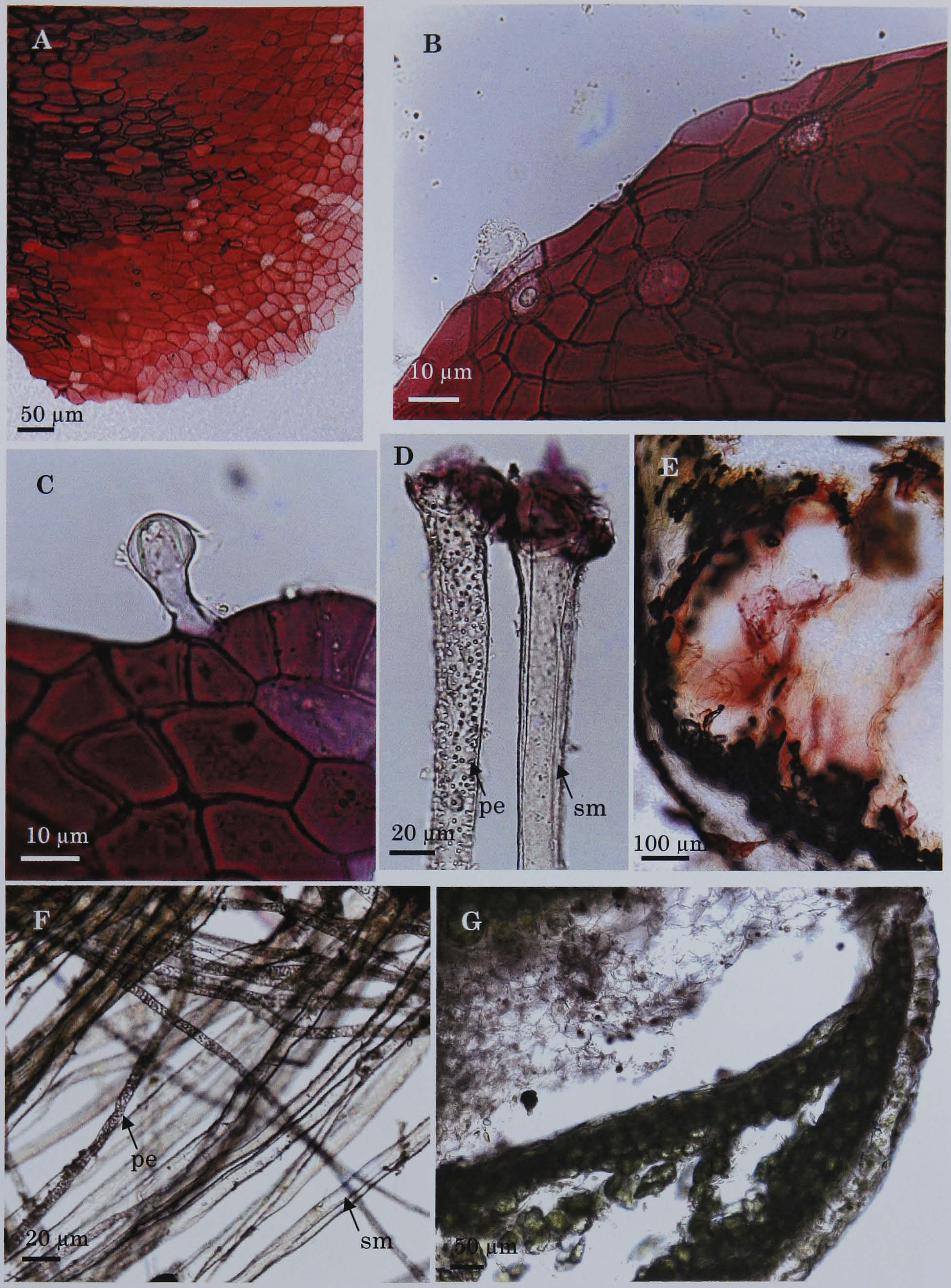


Fig. 2.4. Features of *Mannia* under LM (3). A, B part of ventral scale sections showing oil cells; C slime papilla; D, F dimorphic rhizoids, sm smooth rhizoid, pe pegged rhizoid; E antheridia t.s. showing antheridial chambers; G capsule t.s. showing young spores and elaters. A *M. fragrans* (*Schill et al. 60*, Switzerland); B, C *M. androgyna* (*Schill & Lobo 34*, Madeira); D, F *M. californica* (*Schill & Clarke 164*, North India); E *M. fragrans* (*Schill et al. 51*, Switzerland); G *M. asiatica* (*Long 25016*, China).

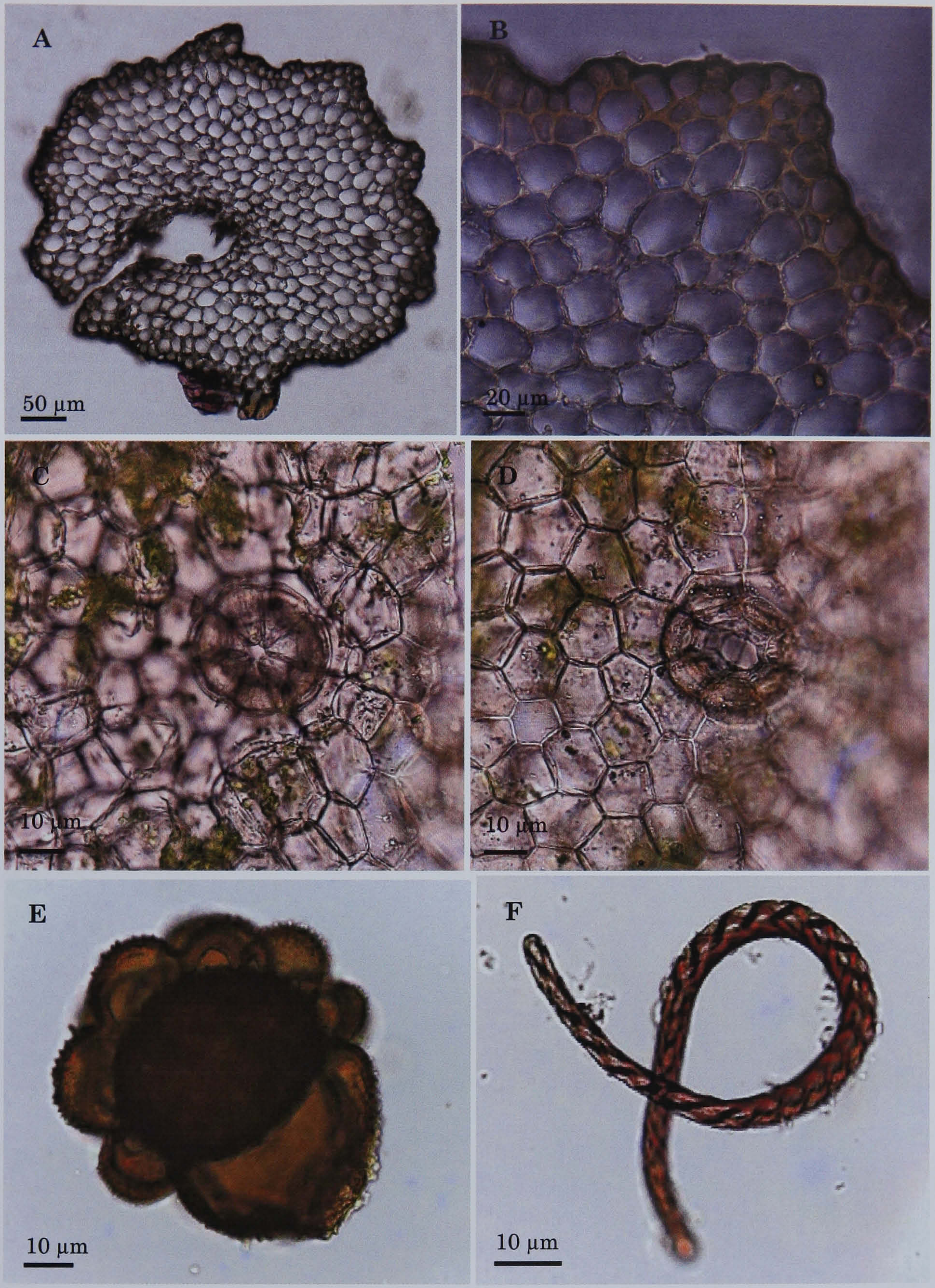


Fig. 2.5. Features of *Mannia* under LM (4). A stalk t.s. showing single rhizoidal furrow; B stalk cells in t.s.; C, D compound pores of carpocephalum in different focusing; E spore with saccate ornamentation; F elater. A, B *M. asiatica* (*Long 25016*, China); C, D, E, F *M. androgyna* (*Schill & Lobo 34*, Madeira).

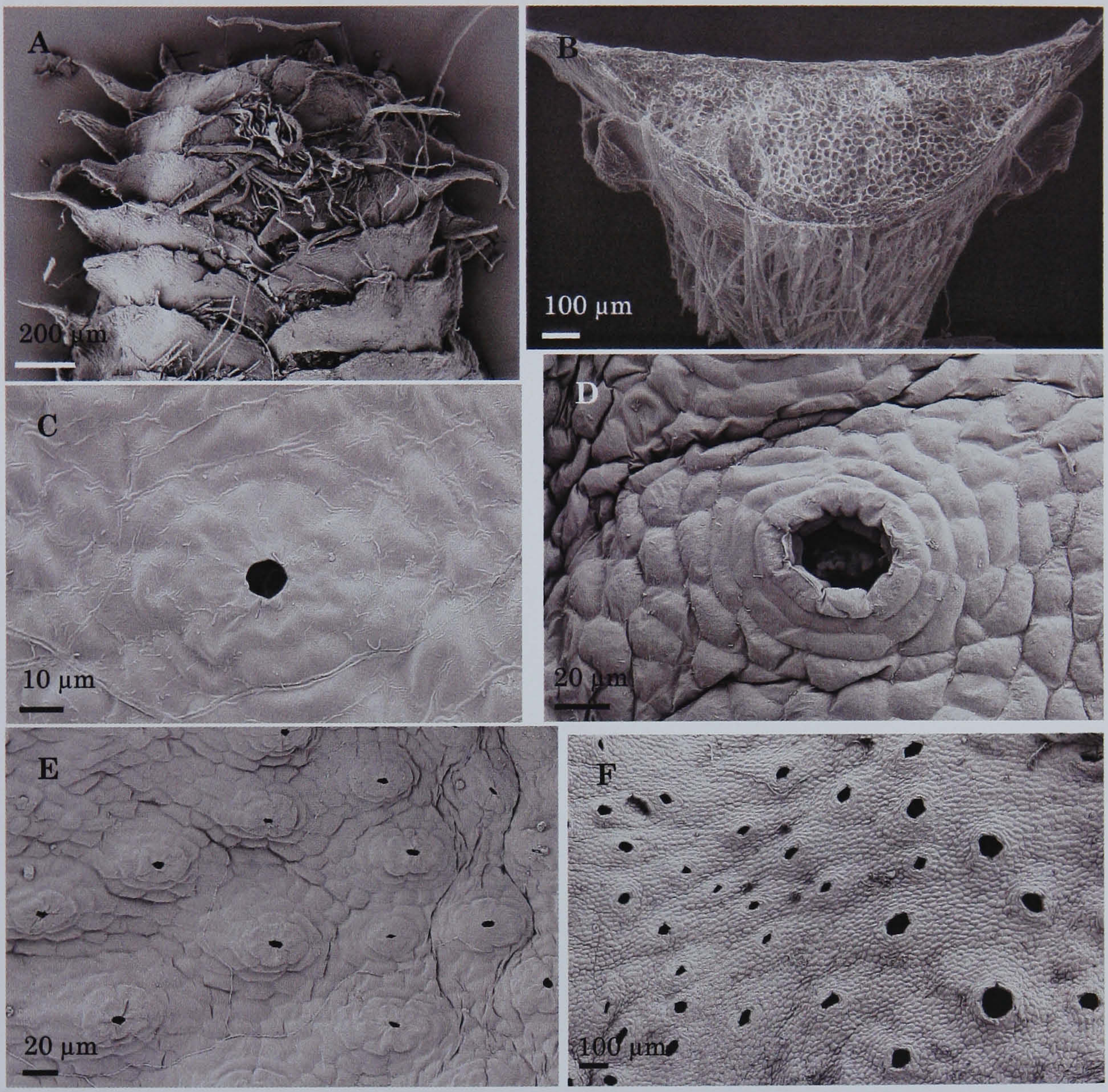


Fig. 2.6. Features of *Mannia* under SEM (1). A ventral view of thallus showing ventral scales in two rows and rhizoids; B thallus t.s.; C, D epidermal air pores from surface view, close up; E, F dorsal epidermis showing air pores. A, B, C, E *M. androgyna* (*Schill & Clarke 125*, Namibia); D, F *M. triandra* (*Inoue s.n.*, Japan).

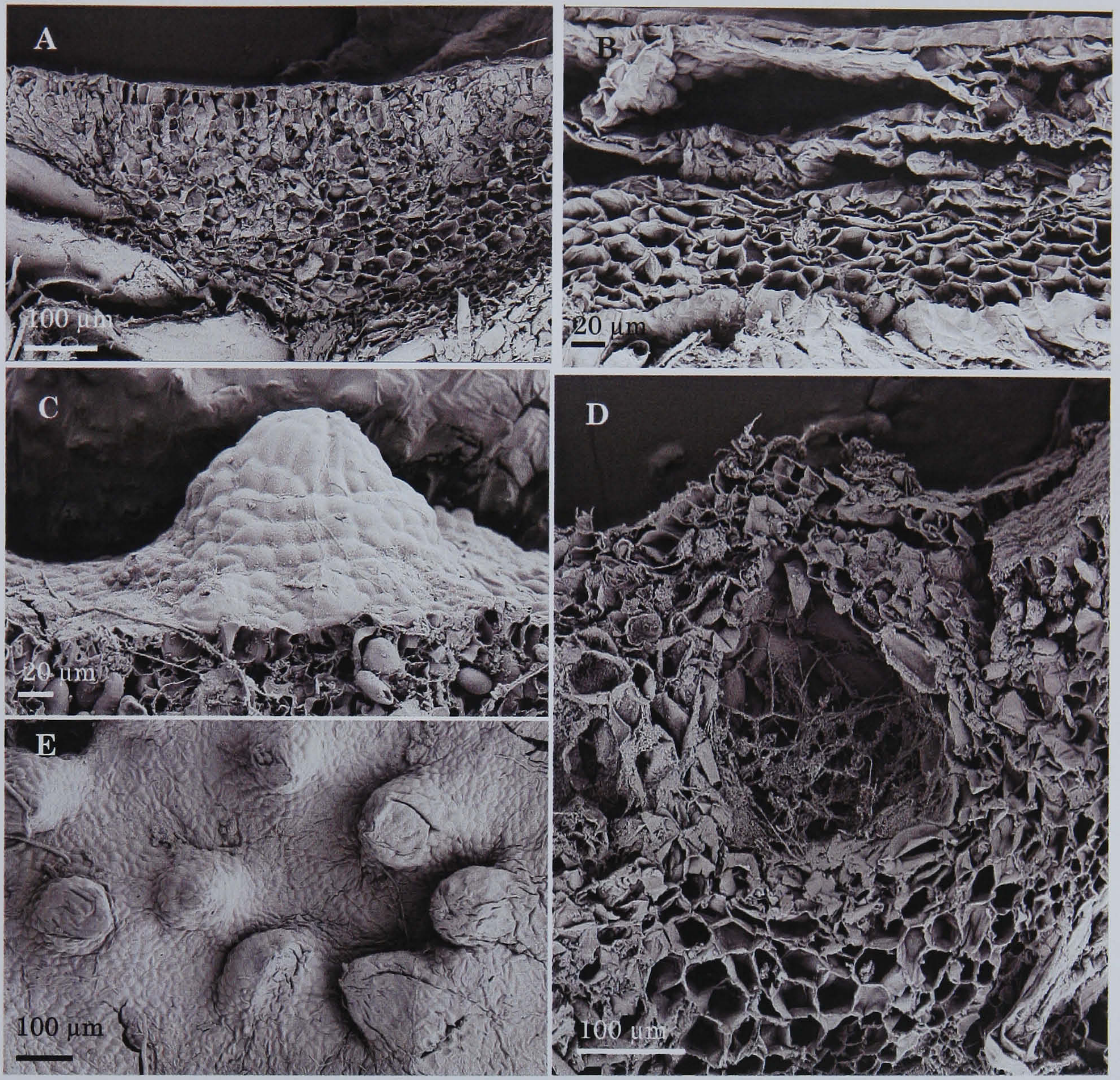


Fig. 2.7. Features of *Mannia* under SEM (2). A thallus t.s. showing compact assimilation tissue; B thallus t.s. showing loose assimilation tissue; C ostiole of antheridium in side view; D cross section through antheridium showing antheridial chamber; E ostioles of antheridia in surface view. A, C, D, E *M. androgyna* (*Schill & Clarke 125*, Namibia); B *M. triandra* (*Inoue s.n.*, Japan).

CHAPTER 3: Survey of *Mannia* spores with a scanning electron microscope

3.1 Introduction

Many works on bryophytes have included detailed descriptions of spores and their potential value in taxonomic studies and spore morphology has always been considered an important aspect in bryophyte taxonomy. Spores in liverworts are said to show less phenotypic plasticity than the gametophyte and are therefore more reliable for taxonomic studies (CLARKE 1979).

Early spore observations were usually based on light microscopy (LM). Authors such as ROTH (1904–1905) and MÜLLER (1905–1916) gave good accounts of moss or liverwort spores based on their observations with LM. Some bryophyte species were distinguished from each other purely on the basis of spore characters. A classic example is the genus *Fossombronia*, where species are separable only by a combination of spore characters. Spores are also of taxonomic importance in *Sphaerocarpos*, where species are separated by spore colour, and in *Riella* species, where spore size, amongst other characters, is a diagnostic feature (MÜLLER 1954).

An early paper on spore germination and development in Marchantiales was written by INOUE (1960). He suggested that spore sculpturing *"may characterize the species or genera"* in the Marchantiales. Later other authors (UDAR 1964, ERDTMAN 1965, MIYOSHI 1966) made a more comprehensive study of spore sculpturing and tried to classify spores into groups. All pointed out the large number of spore characters and their possible use for distinguishing species and genera. MIYOSHI (1966) considered spore characters useful in phylogenetic studies and grouped species based on spore characters in an extensive study. For many later authors MIYOSHI's work has been regarded as a landmark paper (LONG 2000).

Since the introduction of scanning electron microscopy in the 1960s, it has proven to be an important scientific tool, being applied to many areas of biology (WATT 1985, POSTEK ET AL. 1980). The use of SEM for taxonomic studies has major advantages over the compound microscope as it gives a more accurate view of morphological surface features. It has been frequently used in higher plant taxonomic studies to examine pollen sculpturing (e.g. VEZEY ET AL. 1991, SCOTLAND 1993) and has given insights into taxonomic relationships of flowering plants (CLARKE 1979). The SEM has also been applied to studies on bryophyte spores, elucidating relationships at generic and species level (DUCKETT 1986).

But whereas spores are species-specific for genera of Marchantiales (TAYLOR ET AL. 1974), in some leafy liverwort genera, such as *Anastrophyllum*, they are not considered useful in distinguishing between different species within the Sino-Himalaya (SCHILL 2002).

Some authors studied liverwort spores under the SEM from a broad range of taxa (UDAR & SRIVASTAVA 1983, UDAR & SRIVASTAVA 1984, NATH & ASTHANA 1992, BOROS ET AL. 1993) others concentrated on a genus level. TAYLOR ET AL. (1974) considered that thorough SEM spore examination of individual liverwort genera would provide valuable information for taxonomic studies.

In a SEM study on spores of the moss *Polytrichum*, the British species could be distinguished by spore characters (DICKSON 1969). In Marchantiales the earliest comprehensive studies focusing on species within one genus were done by PEROLD (1989, 1994b, 1995) on *Riccia*, *Cryptomitrium* and *Plagiochasma*, and BISCHLER (1977, 1978, 1979a,b, 1984) and BISCHLER-CAUSSE (1989) the latter author working on *Marchantia* and *Plagiochasma*. The most recent monographic work which utilized spore ornamentation as a diagnostic feature for taxonomic studies, was on the genus *Asterella* (LONG 1998, 1999, 2000). Spore characters in *Asterella* were shown to be constant and species-specific. Hence species were grouped based on spore characters and the groups used for an infrageneric classification of the genus.

There are only a few publications which included SEM micrographs of *Mannia* species: *M. androgyna* (LONG 2000, BISCHLER 1998), *M. capensis* (PEROLD 1994a) and *M. fragrans* (Bischler 1989, YU ET AL. 1999). Although the range of species is limited, the images show that the spores are very different from each other, which suggests that *Mannia*, like closely related genera such as *Asterella*, might have species-specific spores. This was also proposed by LONG (pers. com.)

and could give new insights into species delimitation and the troubled infrageneric classification of *Mannia.*

Whereas SEM examines the surface ornamentation of spores, the transmission electron microscope (TEM) can be utilised to study the organisation of cells. It could therefore provide insight into cell function and developmental processes (DUCKETT 1986).
A TEM study comparing the cell wall layers in spores was not done in present study due to time constraints and the large number of specimens. There is also a known difficulty in embedding the thick-walled Marchantiales spores in resin for a TEM study (LONG 2000). It should be however noted that similar spore ornamentations might have different developmental origins and their apparent similarity should be therefore interpreted with caution (DUCKETT 1986). He pointed out that SEM and TEM study should be combined when possible.
In bryophytes TEM has been applied mostly in studies on spore wall layering, e.g. by HECKMAN (1970) on a study on Jungermanniales, or by THAITHONG (1982) on species of *Riccia.* A combination of SEM and TEM studies on individual liverwort species such as *Plagiochasma rupestre*, *Athalamia spathysii* and some *Fossombronia* species was done by GAMBARDELLA (1986, 1987a,b) and on *M. androgyna* by GAMBARDELLA & DE LUCIA SPOSITO (1984).

3.2 Objectives

The main objectives of the SEM survey of spores were

1. to assess if spore ornamentation patterns are species-specific and therefore useful for species delimitation and synonymy in *Mannia*
2. to evaluate which spore characters are constant and which are variable
3. to develop a key to *Mannia* species based on spore characters
4. to group spores for an infrageneric classification of *Mannia*
5. to compare this classification with former *Mannia* classifications

A discussion of the infrageneric classification in comparison to the molecular evidence is presented in Chapter 5.

3.3 Material

Dried herbarium material was used to study spores with the scanning electron microscope (SEM). A survey of about 280 specimens, including some type specimens, was undertaken following the methodology for preparation of spores by LONG (1998, 2000). All species that are accepted in the taxonomic treatment were included in the SEM survey and are listed in Appendix I. The specimens were first examined under a stereo microscope for mature capsules with ripe spore material. Spores were only used when capsules were already dehisced. In some cases where no capsules remained a few spores could be found mixed with soil or debris.

3.4 Scanning electron microscopy methods

3.4.1 Specimen preparation

Using the stereo microscope spores of all *Mannia* species were selected and transferred by fine forceps and a fine moistened brush to 12 mm carbon discs mounted on 12.5 mm aluminium pin stubs to study the surface ornamentation and wall structure of spores. Spore colour was noted for each specimen observed.

3.4.2 Critical Point Drying

Critical point drying of fresh specimens was carried out according to COHEN (1979) to remove any water that would cause heat damage to the specimens. With this method specimens can be dried whilst avoiding the damaging effects of surface tensions.

3.4.3 Specimen coating and scanning

After placing the stubs in the chamber of a K575x sputter coater (Emitech), the chamber was vacuumed. After 3 min 'High Vacuum Status' was reached upon which argon gas was delivered at approximately 2 x 10^{-2} mbar for 20 seconds to evacuate the chamber.

The specimens were coated with gold palladium at a deposition of approximately 12 nm and at a rate of 25 mA for one minute and then studied under a LEO supra 55VP digital scanning electron microscope. Stubs were first scanned at low magnification to select suitable spores. The working distance was between 5 and 9 mm and the scanning voltage (EHT) set to 5 kV. Aperture alignment and correction of astigmatism had to be checked at higher magnifications because of difficulties in focusing the small spores.

Scanning was done at 1024x768 resolution with 'pixel average noise reduction'. Selected images of spores, elaters and capsule valves were than saved at different magnifications (between about 1.8 KX and 13.4 KX). Images were printed out for spore measurements and edited for size, brightness, contrast and sharpness in Adobe Photoshop 7.0.1 (ADOBE SYSTEMS INCORPORATED 2003).

3.4.4 Character selection

The spore characters used in earlier work on *Mannia* were limited to those observed by LM observations. Early authors (NEES VON ESENBECK 1838, SCHIFFNER 1908) used basic characters such as spore colour and size (spore diameter), and only very rarely ornamentation to describe *Mannia* spores. MÜLLER (1954) and UDAR & CHANDRA (1965) added ornamentation and the equatorial rim as characters. SHIMIZU & HATTORI (1953a, b) distinguished between distal and proximal sides with the latter showing a trilete mark and SCHUSTER (1992) made observations on fine ornamentation of spores such as granules. MIYOSHI (1966) gave the most detailed spore descriptions within LM studies and separated the distal and proximal side of spores.

Based on SEM studies BISCHLER (1998, 2005) also distinguished between distal and proximal faces of spores. PEROLD (1994a) used a wide range of *Mannia* spore characters: size, colour, shape, distal and proximal ornamentation and their similarity, fine ornamentation, presence of a wing, presence of equatorial pores and formation of a trilete mark. This extended range of characters was also adopted by LONG (1999, 2000) in a study on the sister genus *Asterella*.

The choice of characters used for the present study was guided by previous SEM work on Marchantiales by the authors mentioned above. The spore terminology follows LONG (1999, 2000). A picture of a spore and the characters used is presented in Fig. 3.1.

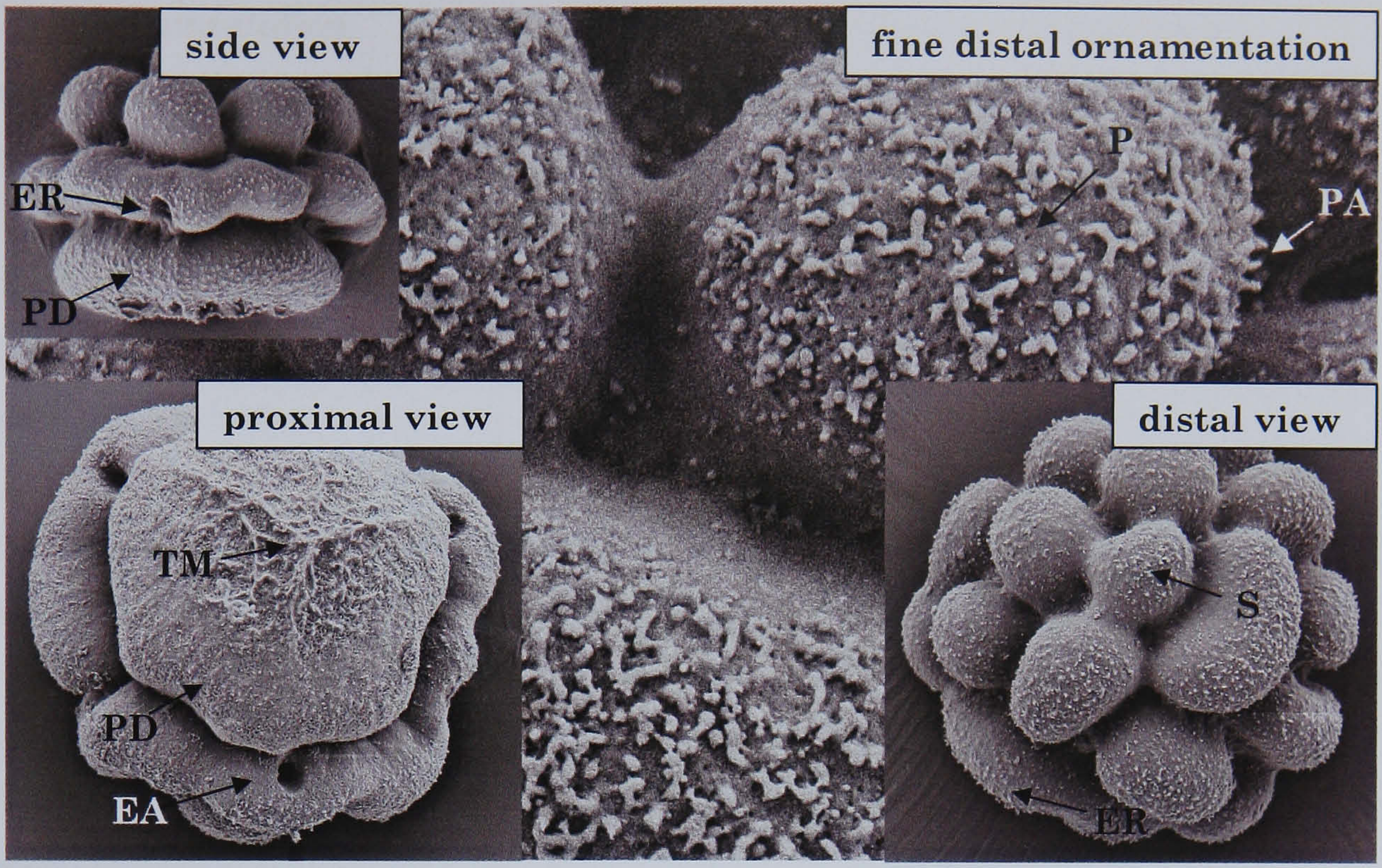


Fig. 3.1. Spore characters in *Mannia*. EA = equatorial aperture; ER = equatorial rim; Pi = pit; PA = papilla; PD = proximal disc; S = sac; TM = trilete mark.

Colour The colour of spores was observed under light microscope and grouped into mainly brown and yellow.

Size The equatorial diameter of spores was measured with the LM and SEM viewing the spore from the distal side. At least 50 measurements were taken from different specimens. For spore measurements using SEM, print-outs of pictures taken were used and the spores were measured with a small ruler using the scale bar from the image.

Shape Spore shape is a direct result of spore development in the capsule during meiosis. *Mannia* spores, as is typical for all Marchantiales, form tetrads and break apart just before they reach maturity (BISCHLER 1998). Their shape is rounded triangular to globular. Distal and proximal sides are readily distinguishable. The proximal side usually has a trilete mark, which is only weakly developed in some species; this mark is where the spores were formerly attached to each other in the tetrad during their development.

Spore ornamentation *Mannia* spores show elaborate ornamentations, which can be classified into primary and fine ornamentation. No secondary ornamentations are present in *Mannia*. Primary ornamentations are obvious features e.g. areolae or sacs, whereas fine ornamentation regards the structure of the wall surface, e.g. small papillae or pits (Fig. 3.1). A secondary ornamentation would be the presence of small areolae within one areola for example. Secondary ornamentations can be found in some species of *Asterella* (LONG 2000).

The proximal and distal ornamentation of spores can either be similar or dissimilar. Dissimilarity in *Mannia* is due to the presence of a proximal disc.

Proximal disc A proximal disc can be either present or absent in *Mannia*. It is a large triangular, rounded or more undulate to crenate structure that can be found on the proximal side of spores (Fig. 3.1).

Equatorial rim The equatorial rim or wing (Fig. 3.1) is located between the proximal and distal spore side and *"represents a slightly thickened junction between the proximal and distal surfaces"* (LONG 2000). When conspicuous it can easily be seen with a light microscope. It can often bear the equatorial apertures.

Equatorial apertures Equatorial apertures or pores in liverwort spores are said to be less complex and show less variation than apertures in pollen of higher plants (MIYOSHI 1966). They are situated between the proximal and distal spore side along the equator and if an equatorial rim exists, the apertures are found on, or just underneath it (Fig. 3.1). They are usually only visible when viewing the spore from the proximal side or in side view. It is said that they are regularly found in liverwort spores but that *"their role is still unclear"* (GAMBARDELLA & DE LUCIA SPOSITO 1984).

3.5 Results

3.5.1 Spore characters

The results for spore colour and spore size were presented in Chapter 2 and are also summarised in Table 3.1.

Shape All *Mannia* species have either a triangular or globose spore shape with a weak to strong trilete mark. The trilete mark is generally more distinctive when a proximal disc is present, e.g. in *M. androgyna*, *M. californica* and *M. sibirica* (Fig. 3.3, 3.6, 3.8-3.9).

Spore ornamentation Spores in *Mannia* are either saccate (*M. androgyna*) (Fig. 3.2), ridged (*M. californica, M. sibirica*) or areolate (*M. californica, M. sibirica* and remaining species). *M. californica* and *M. sibirica* spores can be either ridged or areolate (Fig. 3.5, 3.7-3.8). In *M. sibirica* the ridges are rather short, whereas in *M. californica* they can be quite long and wavy. The spores of *M. triandra* and *M. pilosa* can look very similar (Fig.3.14, 3.17); as regards fine ornamentation both species have a spongy interwoven surface but in *M. triandra* the surface is usually smoother and denser than in *M. pilosa* (Fig.3.16, 3.18). The fine ornamentation in all other species is minutely papillate (e.g. 3.11). Pits on the surface are lacking in *M. californica* and *M. sibirica* (Fig. 3.6, 3.9).
The distal and proximal spore ornamentation pattern is dissimilar in *M. androgyna*, *M. californica* and *M. sibirica*; it is similar in the remaining four species (e.g. Fig. 3.10, 3.11, 3.12, 3.13).

Proximal disc In species where a proximal disc is present (*M. androgyna, M. californica* and *M. sibirica*), the shape is usually rounded triangular with straight to weakly undulating margins. In *M. androgyna* the proximal disc can sometimes be strongly undulate to sinuate, e.g. in specimens from Cyprus, Turkey and Italy. In other specimens (e.g. Switzerland, Canary Islands, Madeira, Tanzania and Namibia) the disc margin is only weakly undulate (Fig. 3.3).

Equatorial rim The equatorial rim is most conspicuous in *M. androgyna*, where it can often be broad and swollen and sometimes irregularly interrupted (Fig. 3.3, 3.4). In *M. sibirica* and *M. californica* the rim is generally less swollen but usually present (Fig. 3.6, 3.8-3.9). In the remaining species the rim is inconspicuous.

Equatorial apertures Readily noticeable apertures or pores are present in *M. androgyna*, *M. californica*, *M. sibirica* and *M. fragrans*. Usually each spore has three apertures roughly equidistant from each other. Occasionally two apertures can occur close to each other or apertures are found in between two equidistant apertures (Fig. 3.3). In some spores of *M. asiatica* and *M. triandra* the apertures are hardly noticeable, this is more often the case in *M. triandra* (Fig. 3.13, 3.15). Apertures can rarely be seen in *M. pilosa* (Fig. 3.18).

A summary table comparing the different spore characters in all *Mannia* species is presented in Table 3.1.

Based on the observed spore characters in *Mannia* a classification into five different spore types can be made (Table 3.2).

Table 3.1. Summary table of spore characters and spore types of *Mannia* species

Species **Spore Characters**	***M. androgyna***	***M. sibirica***	***M. californica***	***M. fragrans***	***M. asiatica***	***M. triandra***	***M. pilosa***
Spore colour	yellow or brown	yellow	yellow or brown	yellow	yellow	yellow	yellow
Spore diameter	(60)63–86.1(87.2) µm	43.1–56.2(62) µm	(52.5)58–77.5(80) µm	(54)57–74.3(76.3) µm	(54.5)60–71.7(74.4) µm	(45.6)55.2–75(77.7) µm	(63)66.6–81.5(85.7) µm
Distal / proximal surface ornamentation affinity	dissimilar	dissimilar	dissimilar	similar	similar	similar	similar
Primary distal ornamentation	saccate	irregular short ridges/ irregular areolae	irregular short or long wavy ridges to irregular areolae	regular shallow areolae	irregular deep areolae	incomplete to regular areolae	incomplete areolae
Fine distal ornamentation	minutely papillate and pits	minutely papillate	minutely papillate	minutely papillate and pits	minutely papillate with pits	spongy, smoother and sometimes less pits	spongy, many pits
Proximal ornamentation	small areolae	small areolae	small areolae	regular areolae	irregular areolae	incomplete areolae	incomplete areolae
Proximal disc	present	present	present	absent	absent	absent	absent
Equatorial apertures	conspicuous	conspicuous	conspicuous	inconspicuous	inconspicuous	inconspicuous to sometimes conspicuous	inconspicuous
Equatorial rim	conspicuous	conspicuous	conspicuous	inconspicuous	inconspicuous	inconspicuous	inconspicuous
Spore Type	I	II	II	III	IV	V	V

Table 3.2. Spore types in *Mannia*

Spore type	Primary ornamentation	Fine ornamentation	Distal/proximal ornamentation affinity	Proximal disc	Equatorial Pores	Species
I	saccate	papillate, pits	dissimilar	present	conspicuous	*M. androgyna*
II	ridges or irregular areolae	papillate	dissimilar	present	conspicuous	*M. sibirica* *M. californica*
III	regular shallow areolae	papillate, pits	similar	absent	conspicuous	*M. fragrans*
IV	irregular deep areolae	papillate, pits	similar	absent	inconspicuous	*M. asiatica*
V	incomplete to regular areolae	spongy, pits	similar	absent	inconspicuous	*M. triandra* *M. pilosa*

3.5.2 Key to *Mannia* species based on spore characters

1 Spores with similar sculpturing on distal and proximal side, proximal disc absent; equatorial rim inconspicuous 2
1* Spores with dissimilar sculpturing on distal and proximal sides, proximal disc present; equatorial rim conspicuous 5

2 Fine distal ornamentation minutely papillate.. 3
2* Fine distal ornamentation spongy 4

3 Distal ornamentation regularly areolate (6 to 8 areolae across), muri of areolae not deep; equatorial apertures conspicuous.................................. .... Spore type III .... ***M. fragrans***
3* Distal ornamentation often deeply incompletely areolate ((6)7–10 areolae across); muri of areolae deep; equatorial apertures conspicuous to sometimes inconspicuous.......Spore type IV ....***M. asiatica***

4 Areolae irregular, distal surface with many pits, equatorial apertures inconspicuous.....................Spore type V.................................***M. pilosa***
4* Areolae rather regular, distal surface smoother with sometimes less pits, equatorial apertures inconspicuous to sometimes conspicuous .... Spore type V...***M. triandra***

5 Primary distal ornamentation saccate, pits present but not spongy ....Spore type I.......................................***M. androgyna***
5* Primary distal ornamentation irregularly long ridges, short wavy ridges or areolate..5

6 Spores large, (52)58–77(80) µm in diameter; distally with irregularly long wavy ridges or areolate......Spore type II .... ***M. californica***
6* Spores small, 43–56(62) µm in diameter; distally areolate..........................Spore type II .... ***M. sibirica***

3.5.3 Spore micrographs of species

The spore micrographs of species are presented in Figure 3.2 to 3.18.

Scale bars of spores in distal, proximal and side view are 10 μm; scale bars showing fine distal ornamentation of spores are 2 μm unless otherwise stated.

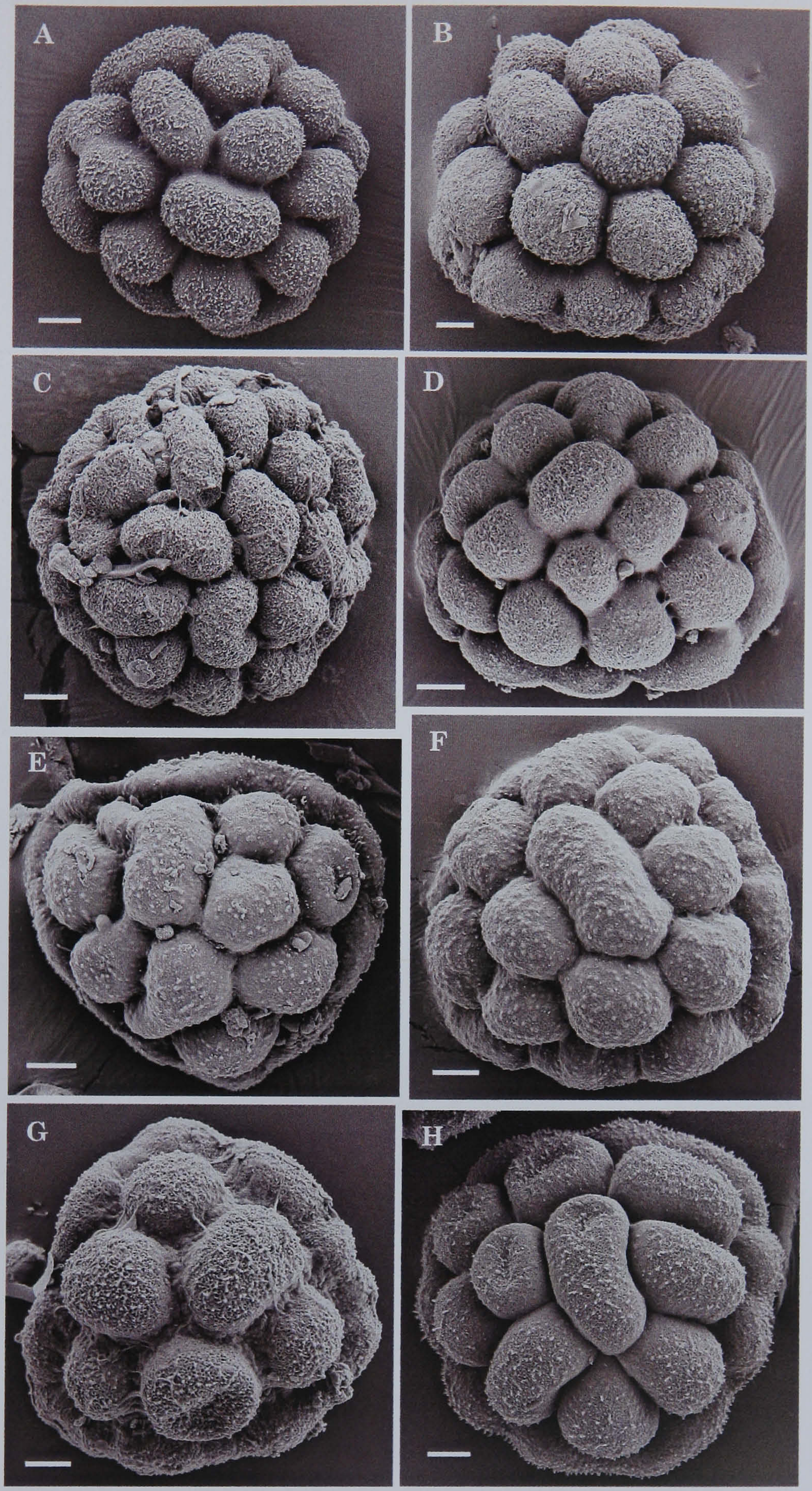


Fig. 3.2. *Mannia androgyna* spores from distal view. A Portugal, Madeira, *Schill & Lobo 32* (E); B Turkey, *Nyholm 300* (JE); C Isotype, Italy, *Raddi s.n.* (E); D Pretoria, *Bosman 199* (NY); E South Africa, *Arnell 795* (BOL); F Namibia, *Schill & Clarke 127* (E); G Tanzania, *Pocs 6902* (JE); H Cyprus, *Blockeel s.n.* (E).

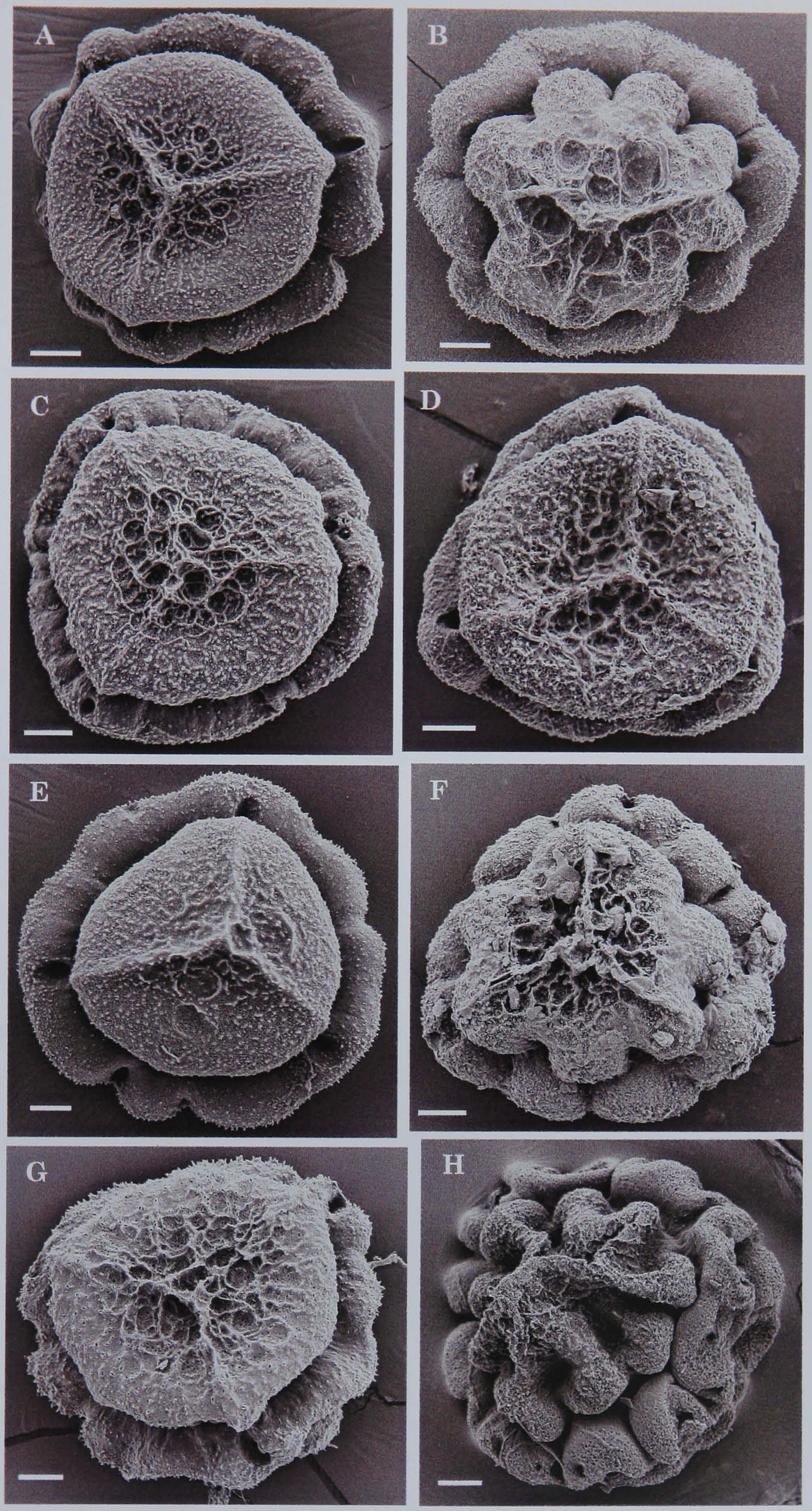


Fig. 3.3. *Mannia androgyna* spores from proximal view. A Portugal, Madeira, *Schill & Lobo 32* (E); B Cyprus, *Blockeel s.n.* (E); C Namibia, *Schill & Clarke 124* (E); D Tanzania, *Pocs 6902* (JE); E Portugal, Madeira, *Schill & Lobo 34* (E); F Turkey, *Nyholm 300* (JE); G Switzerland, Ticino, *Vautier 620* (JE); H Isotype, Italy, *Raddi s.n.* (E).

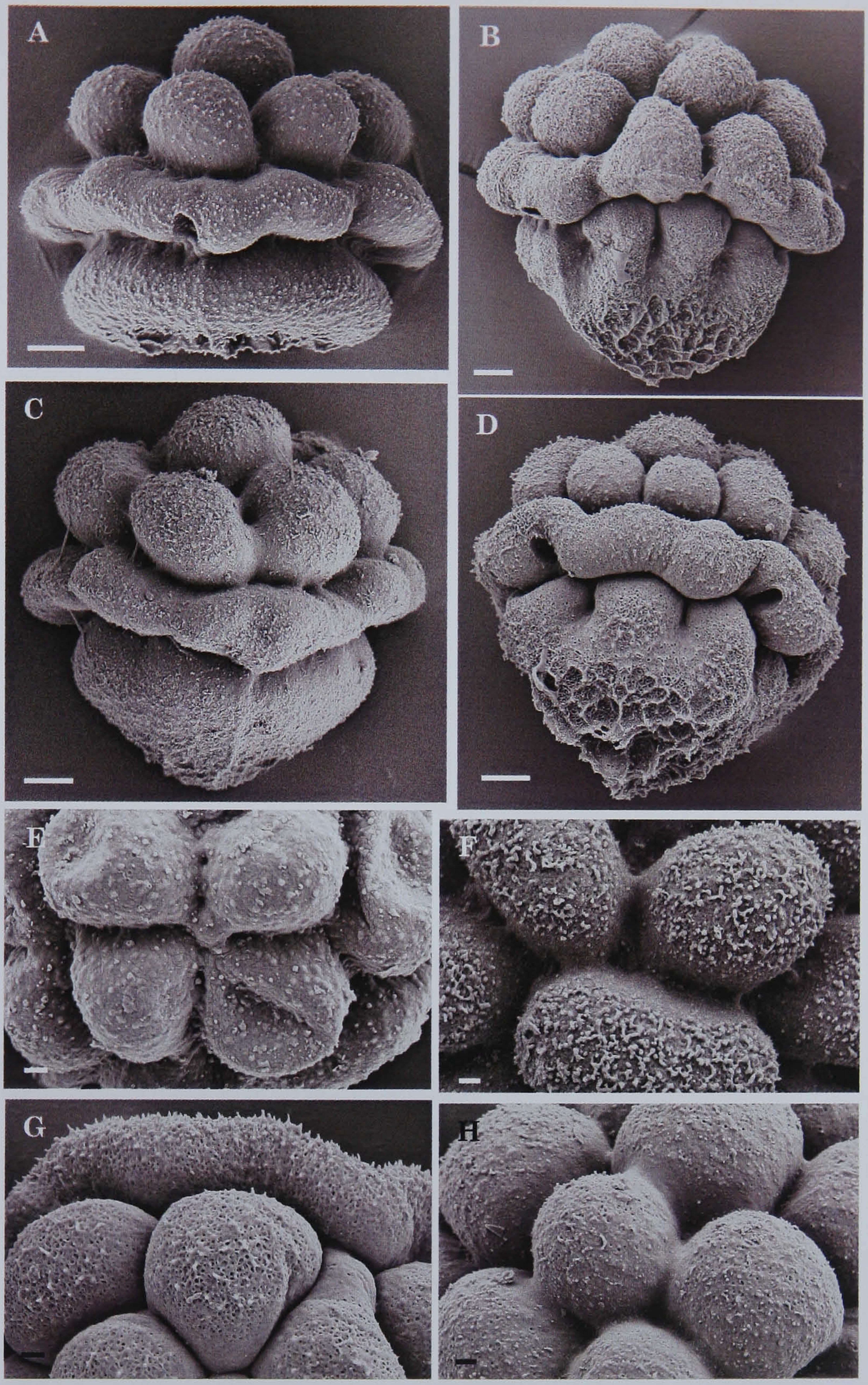


Fig. 3.4. ***Mannia androgyna*** **spores from side view (A-D) and showing fine distal ornamentation (E-H).** A, F Portugal, Madeira, *Schill & Lobo 32* (E); B Turkey, *Nyholm 300* (JE); C, H Portugal, Madeira, *Schill & Lobo 35* (E); D, G Cyprus, *Blockeel s.n.* (E); E Namibia, *Volk WIN77* (JE).

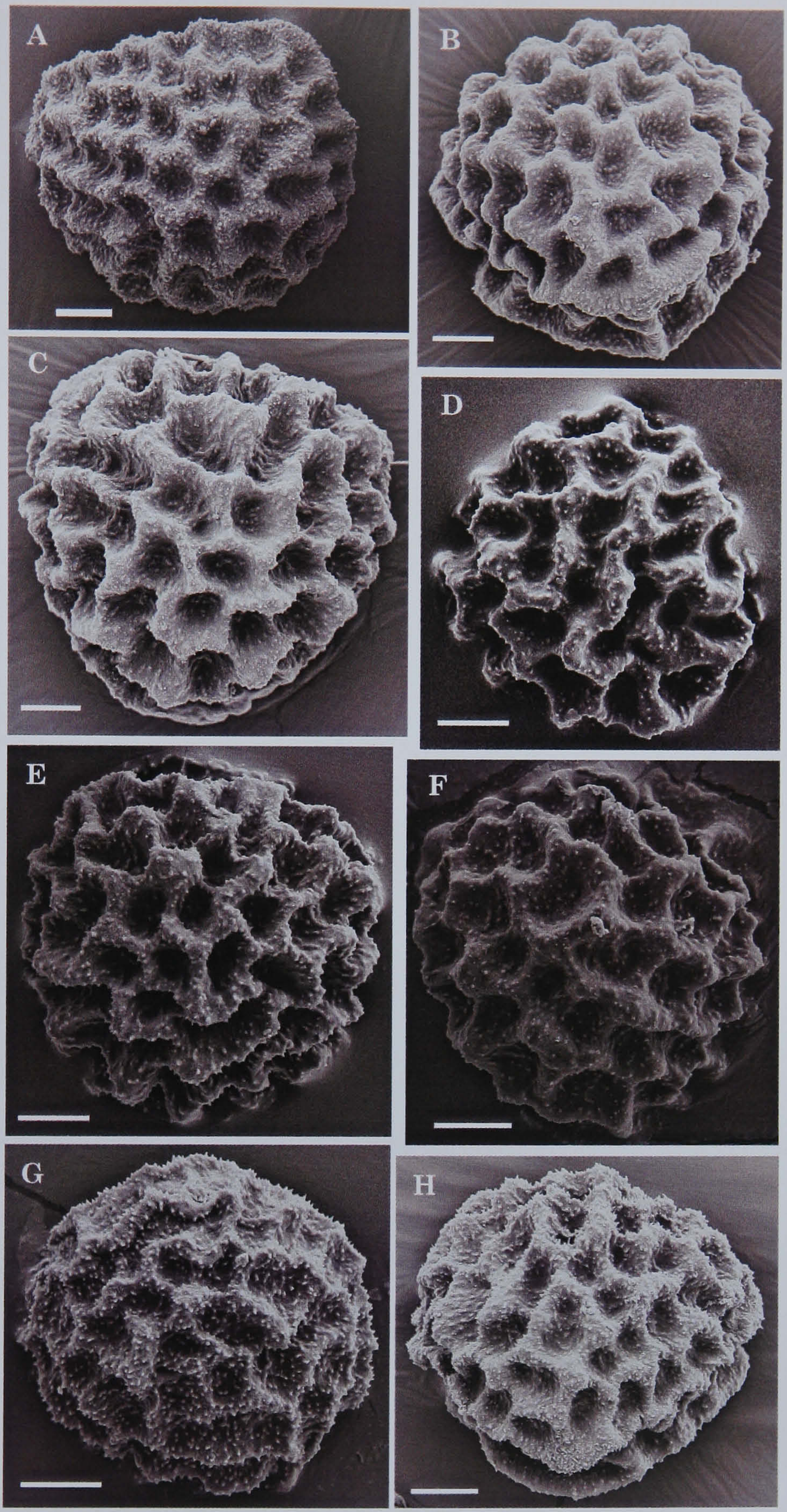


Fig. 3.5. *Mannia sibirica* spores from distal view. A Minnesota, *Schuster 14227* (F); B Canada, *Conklin 2554* (F); C Finland, *Laine s.n.* (S- B74863); D Holotype of *Grimaldia pilosa* var. *sibirica*, Siberia, *Arnell s.n.* (S-B24528); E Minnesota, *Schuster 18009* (JE); F Isotype of *M. pilosa* var. *sibirica*, Siberia, *Arnell s.n.* (JE-H1306); G Minnesota, *Schuster 14315* (F); H Alaska, *Steere & Iwatsuki 74-29* (JE).

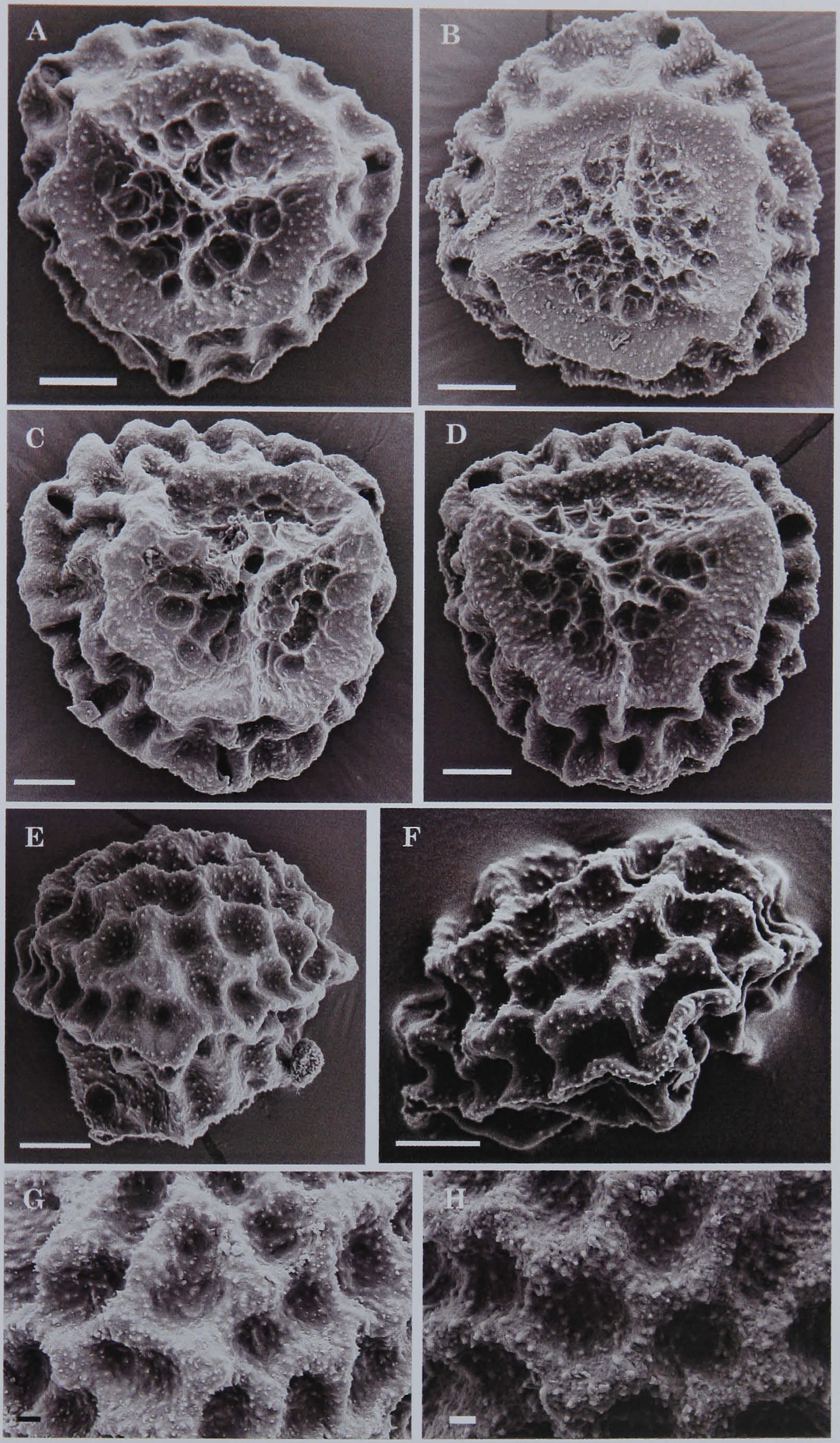


Fig. 3.6. *Mannia sibirica* spores from proximal view (A-D), side view (E-F) and showing fine distal ornamentation (G-H). A, H Minnesota, *Schuster14227* (F); B Alaska, *Steere & Iwatsuki 74-25* (NY); C Canada, *Conklin 2554* (F); D Minnesota, *Schuster s.n.* (F-1133340); E Minnesota, *Schuster 18009b* (F); F Holotype of *Grimaldia pilosa* var. *sibirica*, Siberia, *Arnell s.n.* (S-B24528); G Alaska, *Steere & Iwatsuki 74-29* (JE).

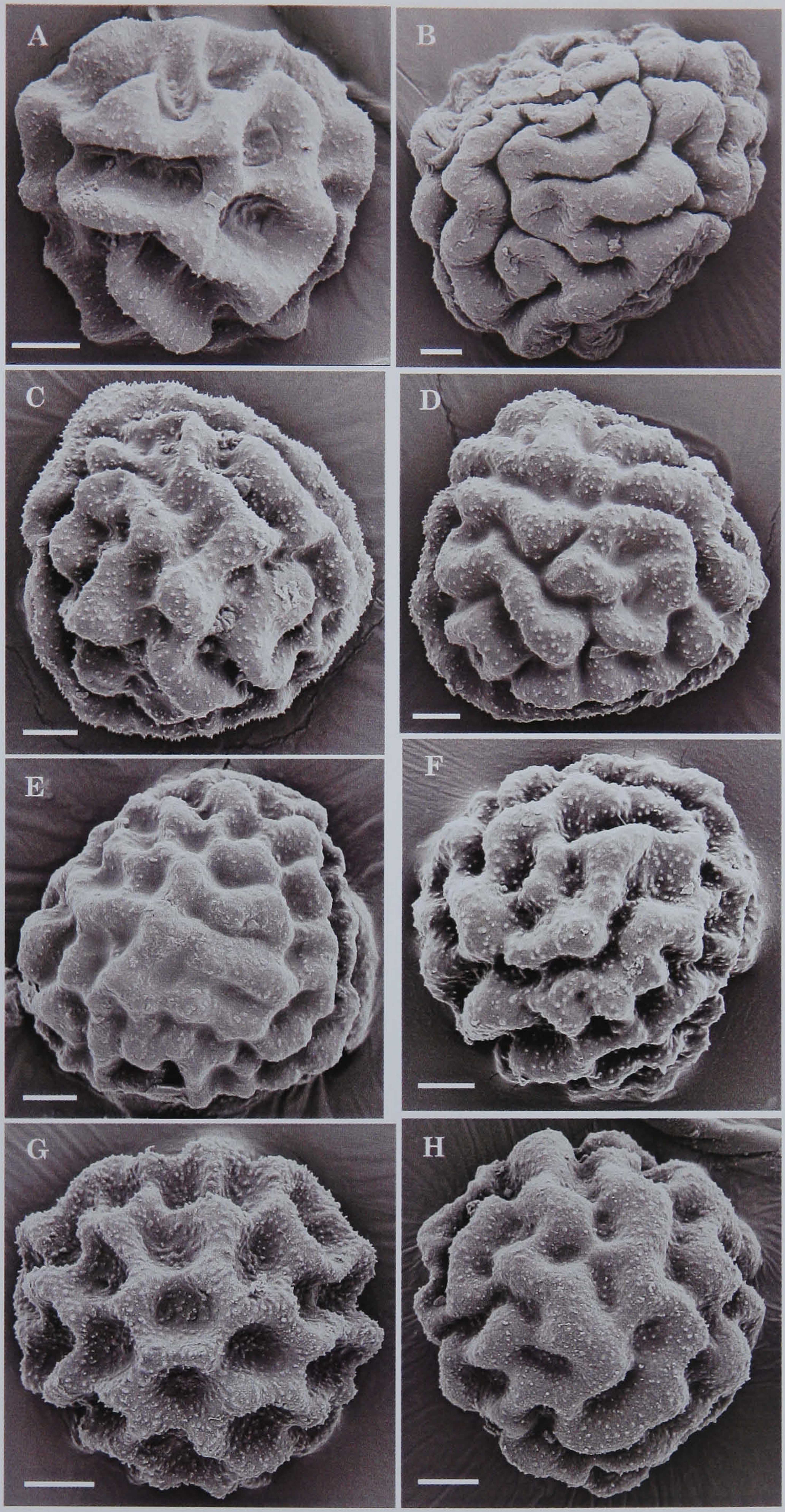


Fig. 3.7. *Mannia californica* spores from distal view. A China, Yunnan, *Shevock 24912* (E); B Lebanon, *Davis 5247* (E); C Tanzania, *Pocs 6561/q* (JE); D Isotype of *Grimaldia californica*, California, *Bolander s.n.* (NY-575647); E Canada, *Underwood Herbarium s.n.* (NY-268874); F Lesotho, *Duckett & Matcham 5149a* (E); G, H India, Uttaranchal, *Schill & Clarke 165* (E).

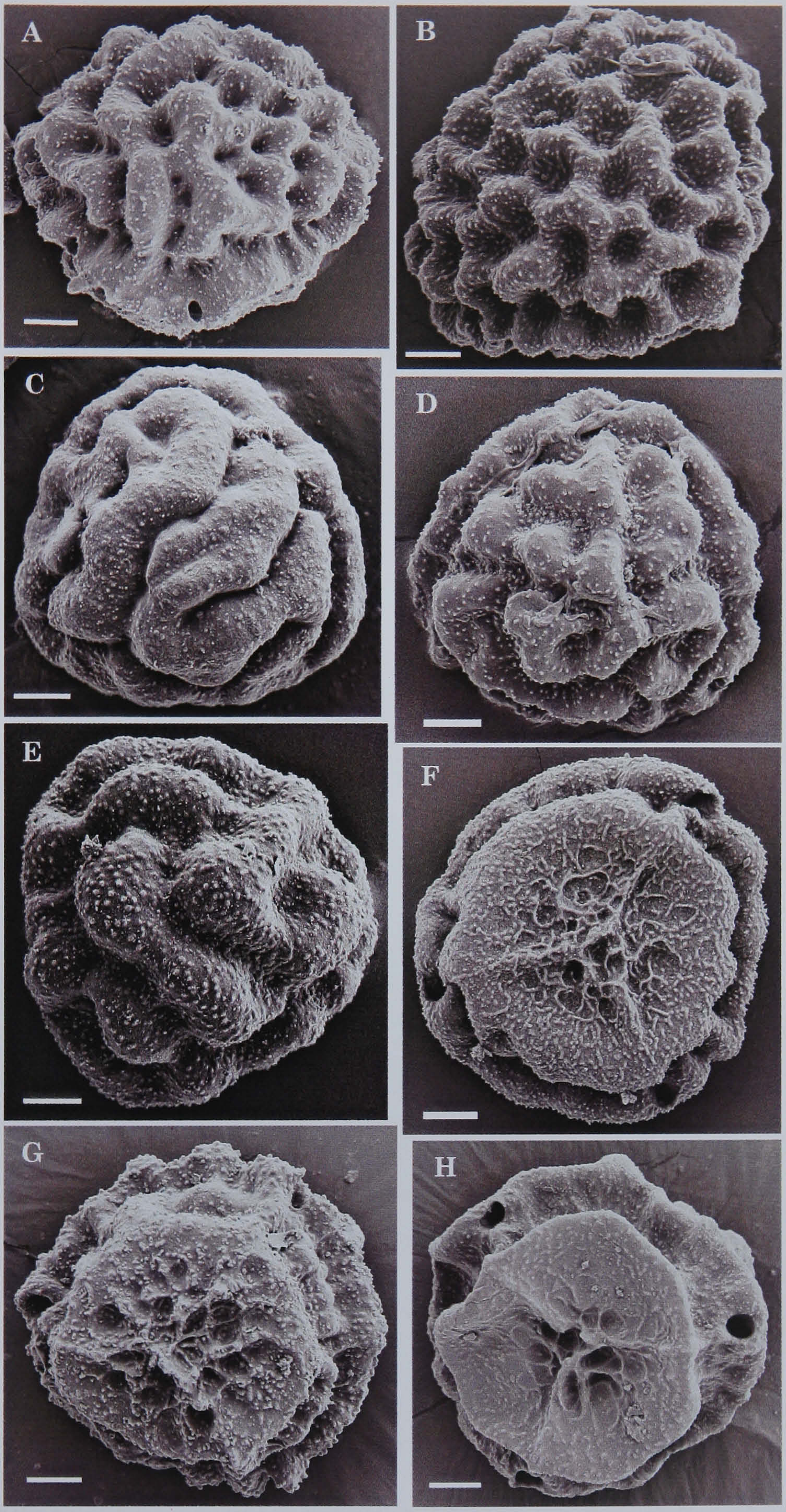


Fig. 3.8. ***Mannia californica*** **spores from distal (A-E) and proximal view (F-H).** A India, Tamil Nadu, *Schill & Clarke 146* (E); B France, *Hugonnot s.n.* (E); C Holotype of *M. levigata*, Japan, *Shimizu 52818* (NICH); D Tennessee, *Sharp & Robinson 563* (JE); E Austria, *Köckinger s.n.* (private herbarium); F California, *Doyle 2744* (NY); G Holotype of *Grimaldia californica*, California, *Bolander s.n.* (NY-575639); H China, Yunnan, *Shevock 24925* (E).

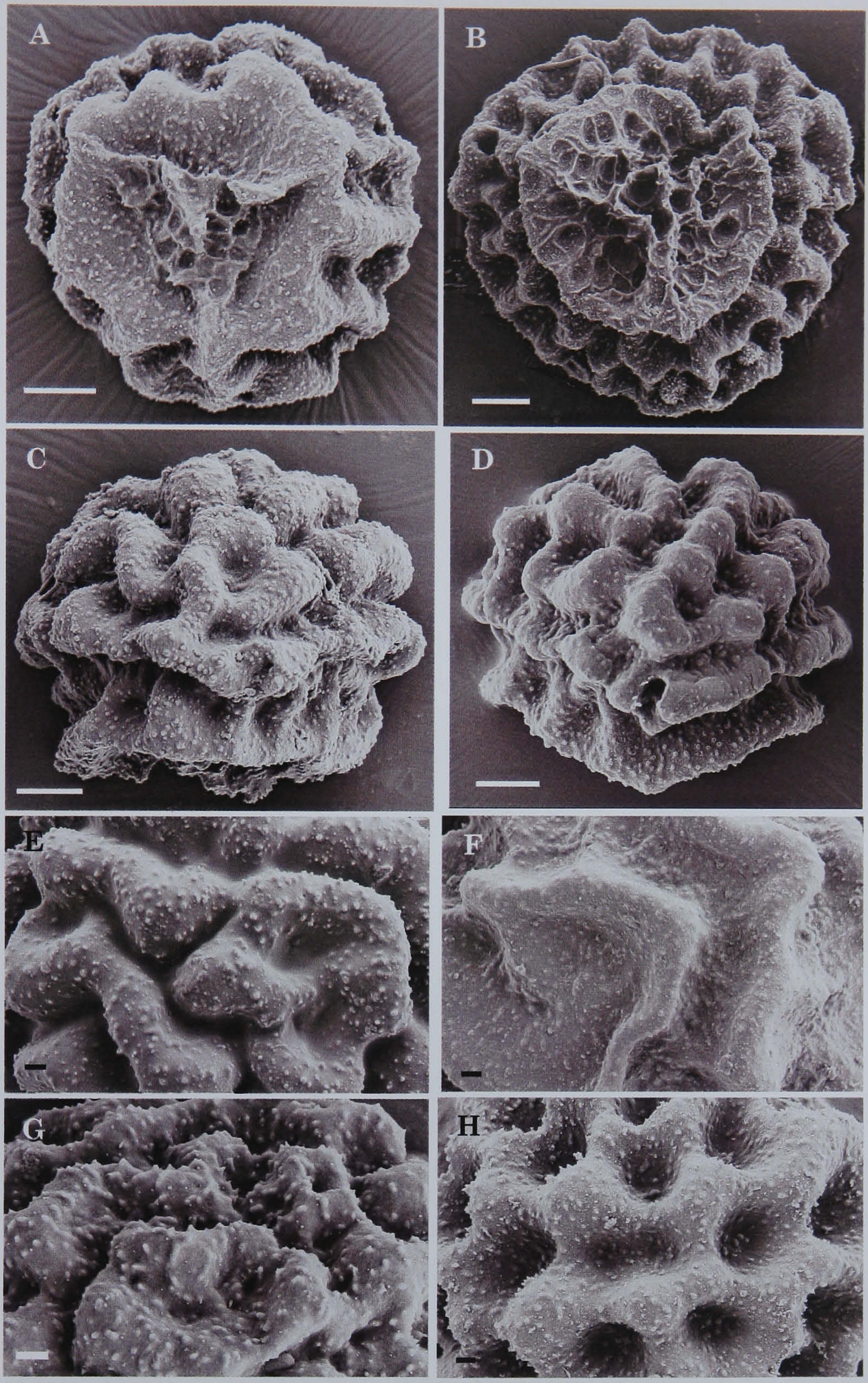


Fig. 3.9. ***Mannia californica*** **spores from proximal view (A-B), side view (C-D) and showing fine distal ornamentation (E-H).** A, H India, Uttaranchal, *Schill & Clarke 165* (E); B France, *Hugonnot s.n.* (E); C Holotype of *Grimaldia californica*, California, *Bolander s.n.* (NY-575639); D Lesotho, *Duckett & Matcham 5149a* (E); E Isotype of *Grimaldia californica*, California, *Bolander s.n.* (NY-575647); F China, Yunnan, *Shevock 24925* (E); G Arizona, *Little 4507* (JE).

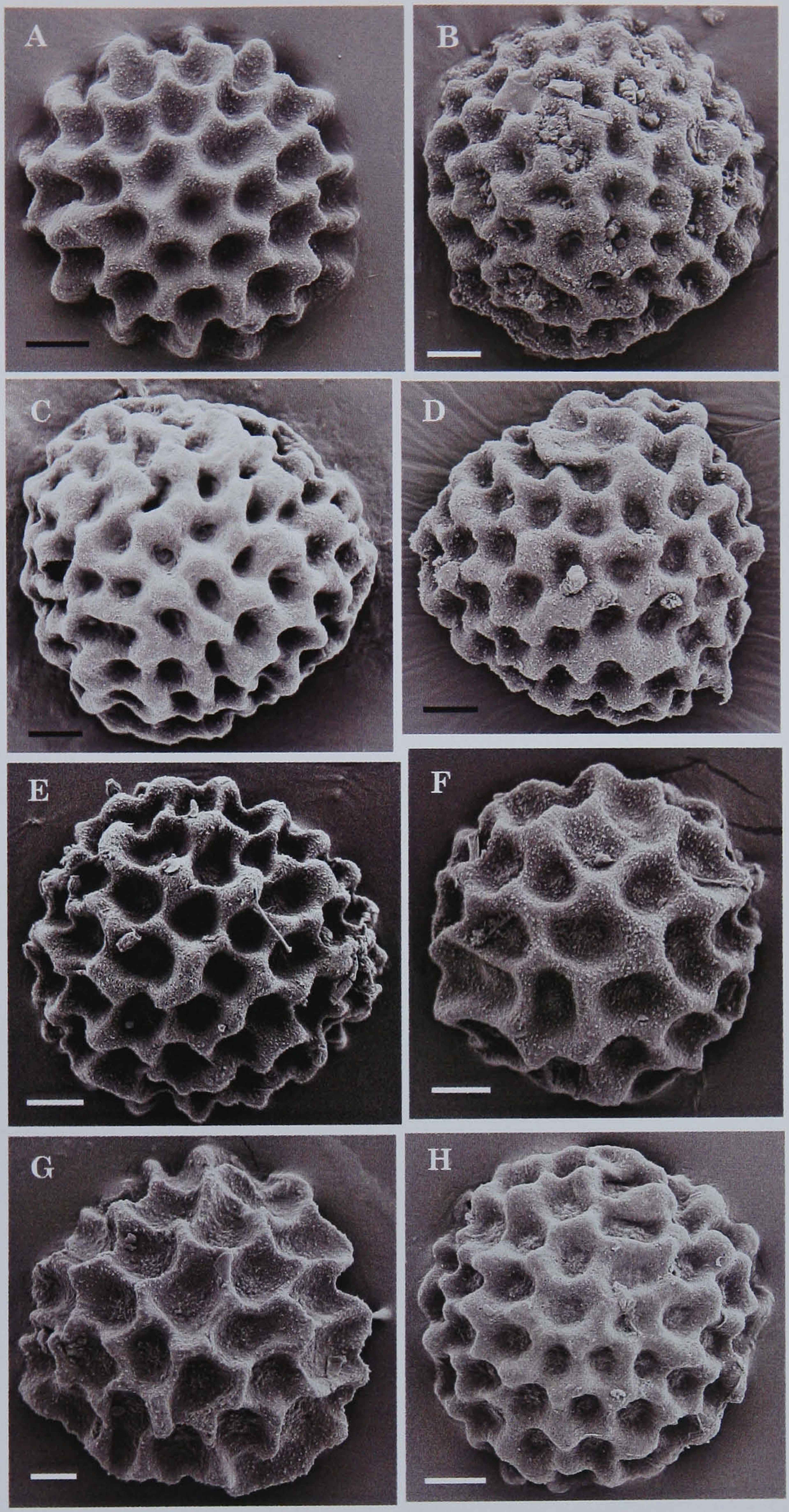


Fig. 3.10. *Mannia fragrans* spores from distal view. A Switzerland, *Schill et al. 47* (E); B Type of *M. fragrans* var. *inodorata*, Japan, *Hattori 6202* (TNS); C Type of *M. brachypoda*, Japan, *Shimizu 6202* (NICH); D China, *Rev. Jos. Giraldi s.n.* (det. Massalongo 148) (BM); E Type of *M. barbifrons*, Japan, *Shimizu 52809* (NICH); F Siberia, *Arnell s.n.* (JE-H4337); G Kansas, *McGregor 5331* (NY); H Hungary, *Pócs s.n.* (JE-H1433).

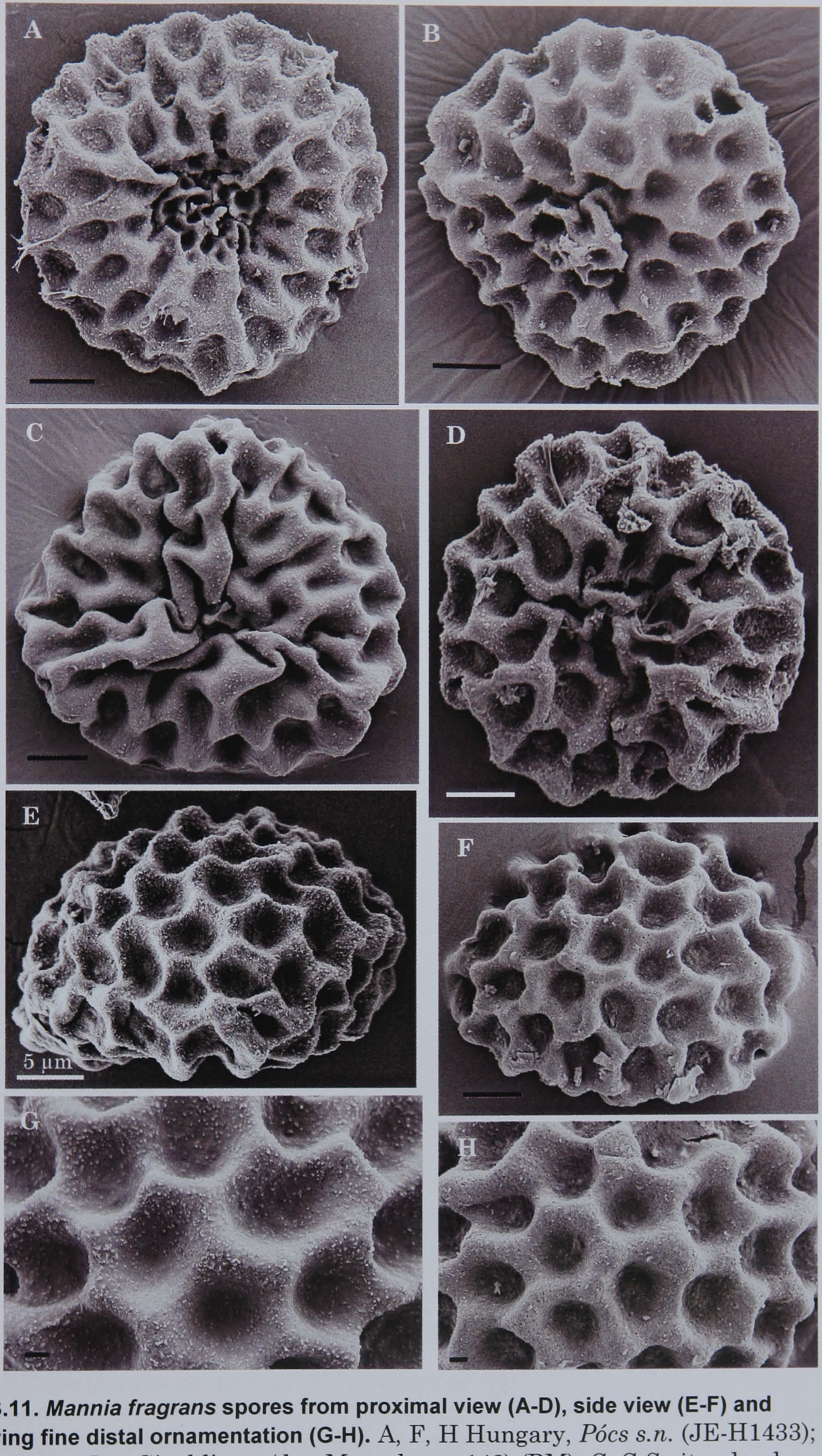


Fig. 3.11. ***Mannia fragrans*** **spores from proximal view (A-D), side view (E-F) and showing fine distal ornamentation (G-H).** A, F, H Hungary, *Pócs s.n.* (JE-H1433); B China, *Rev. Jos. Giraldi s.n.* (det. Massalongo 148) (BM); C, G Switzerland, *Schill et. al 47* (E); D Siberia, *Arnell s.n.* (JE-H4337); E Norway, *Kaalaas 1189* (NY).

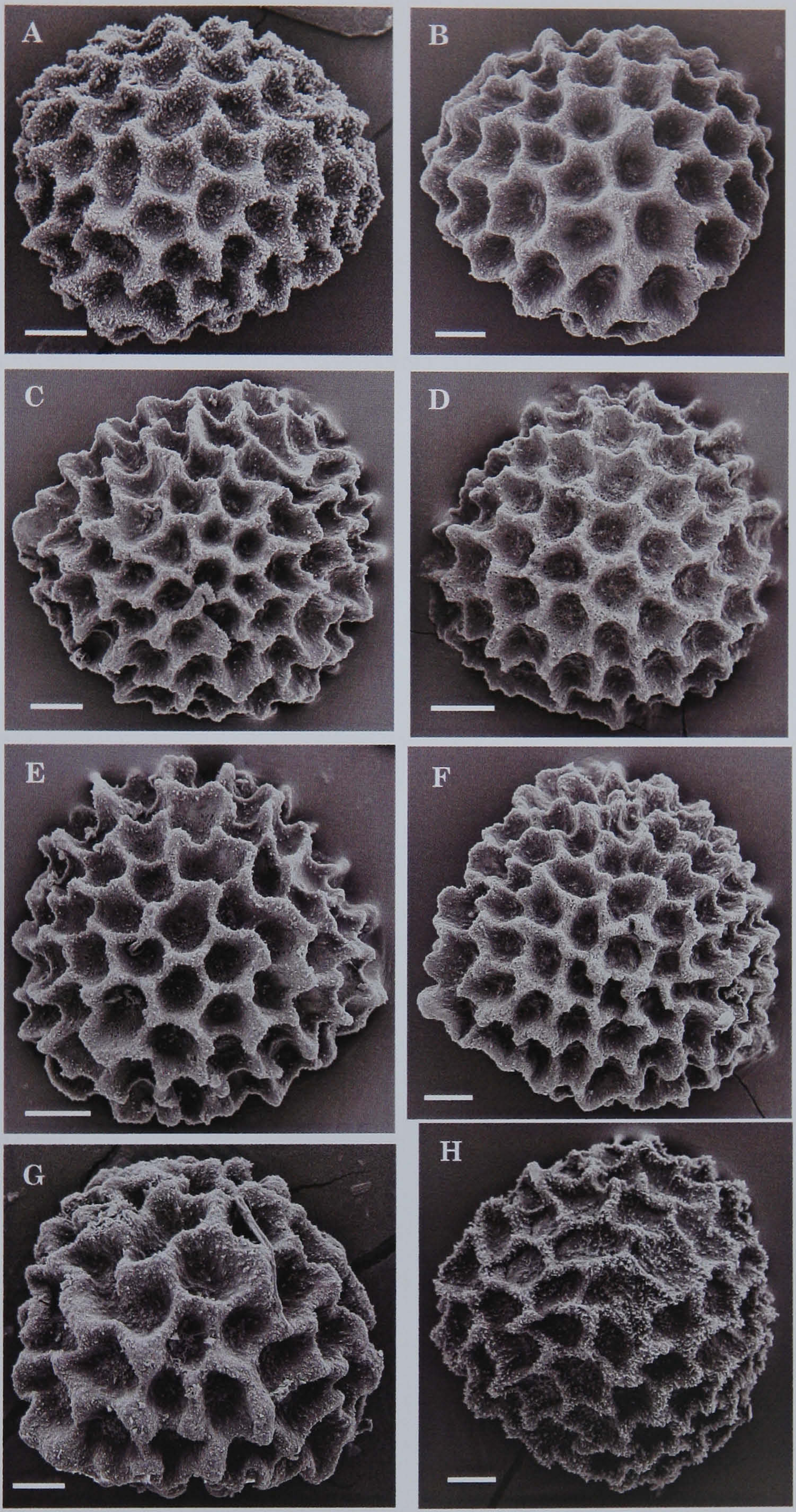


Fig. 3.12. *Mannia asiatica* spores from distal view. A-F Qinghai Province, China; G Uttaranchal, India; H Tajikistan. A *Long 27016* (E); B *Long 27260* (E); C *Long 26924* (E); D Holotype, *Long 27032* (E); E *Long 26964b* (E); F *Long 26951b* (E); G *Duthie 3757* (BM); H *Boboradzchabov 802* (JE).

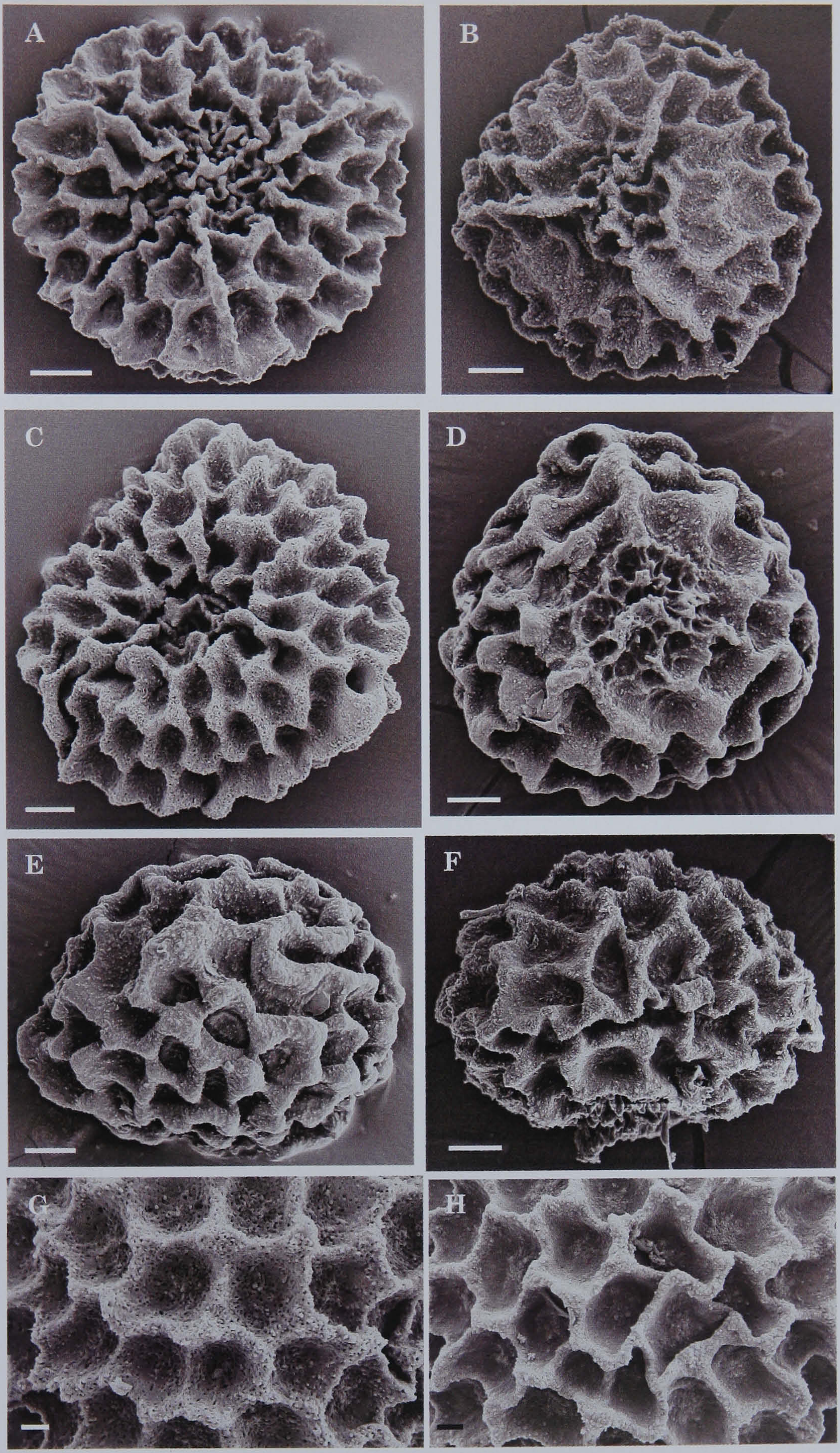


Fig. 3.13. *Mannia asiatica* spores from proximal view (A-D), side view (E-F) and showing fine distal ornamentation (G-H). A-C, G-H Qinghai Province, China; D-F Uttaranchal, India. A, G Holotype, *Long 27032* (E); B *Long 27217* (E); C *Long 26951b* (E); D-E *Duthie 311* (G); F *Duthie 3757* (BM); H *Long 27260* (E).

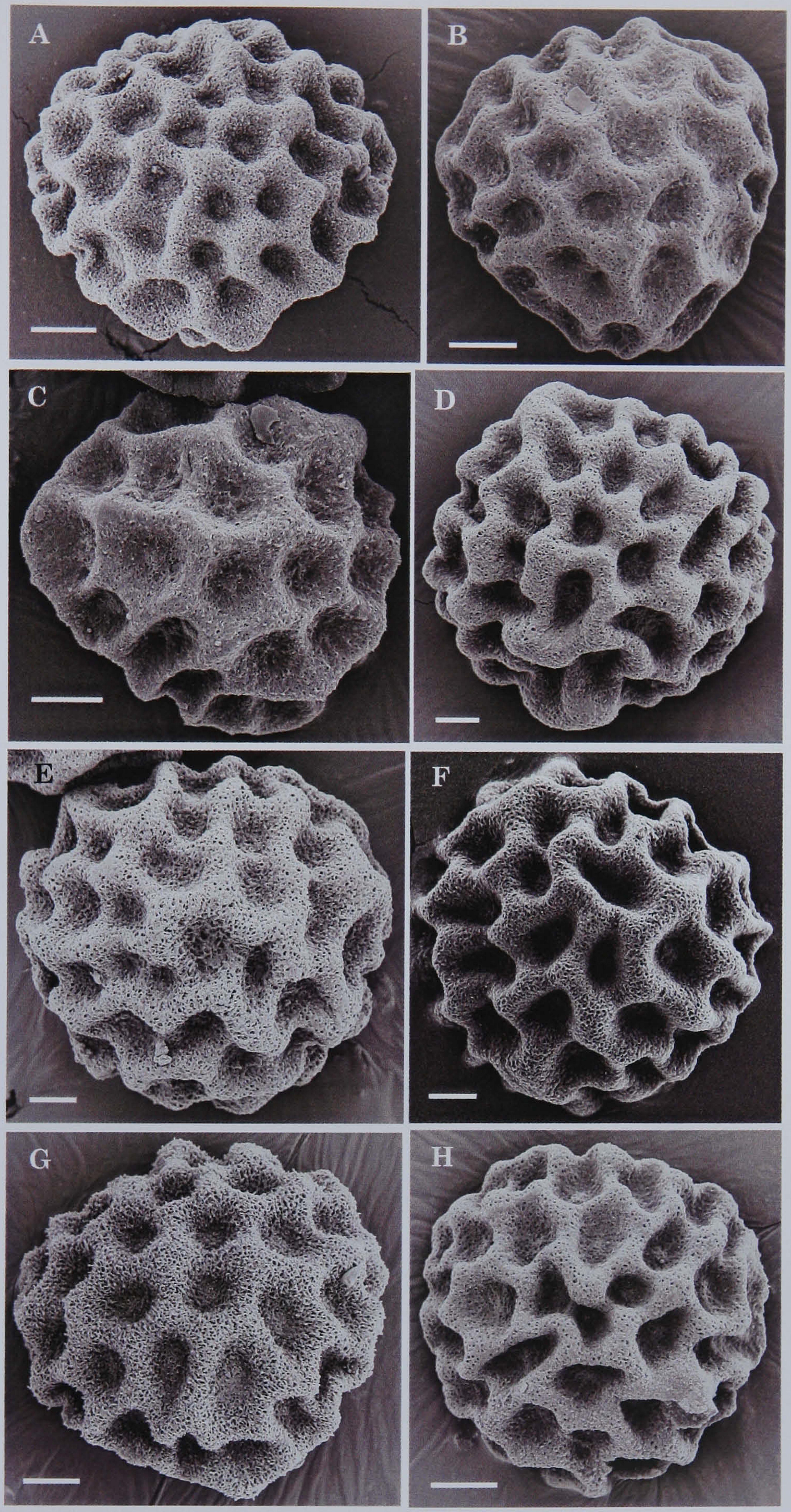


Fig. 3.14. ***Mannia triandra*** **spores from distal view**. A Austria, *Schill et al. 79* (E); B Siberia, *Andrejewa s.n.* (JE); C Japan, *Inoue s.n.* (E); D Austria, *Loitlesberger 1192* (JE); E Iowa, *Conard 7-166* (NY); F Slovenia, *Deschmann 1138* (G); G Germany, *Stephani s.n.* (BM-669301); H Japan, *Sasaki & Kudo 932* (F).

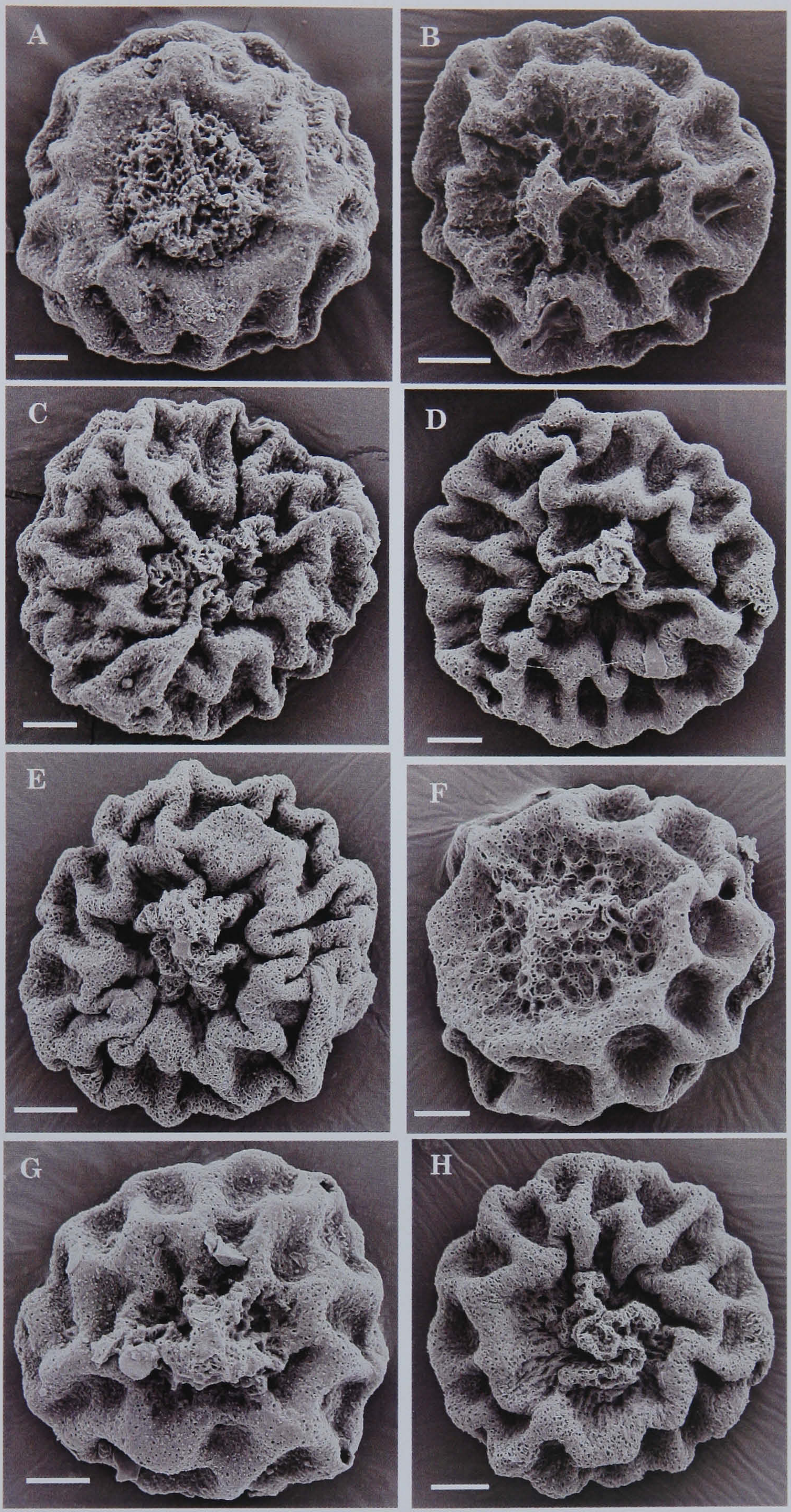


Fig. 3.15. ***Mannia triandra*** **spores from proximal view**. A Illinois, *Harper s.n.* (JE-H1296); B Japan, *Inoue* s.n. (E); C unclear locality, 12 Aug. 56, *Molander* s.n. (JE); D Austria, *Loitlesberger 1192* (JE); E Riesengebirge, *Futschig s.n.* (S-B74794); F Japan, *Kobayashi s.n.* (S-B74813); G Japan, *Sasaki & Kudo 932* (F); H Germany, *Stephani s.n.* (BM-669301).

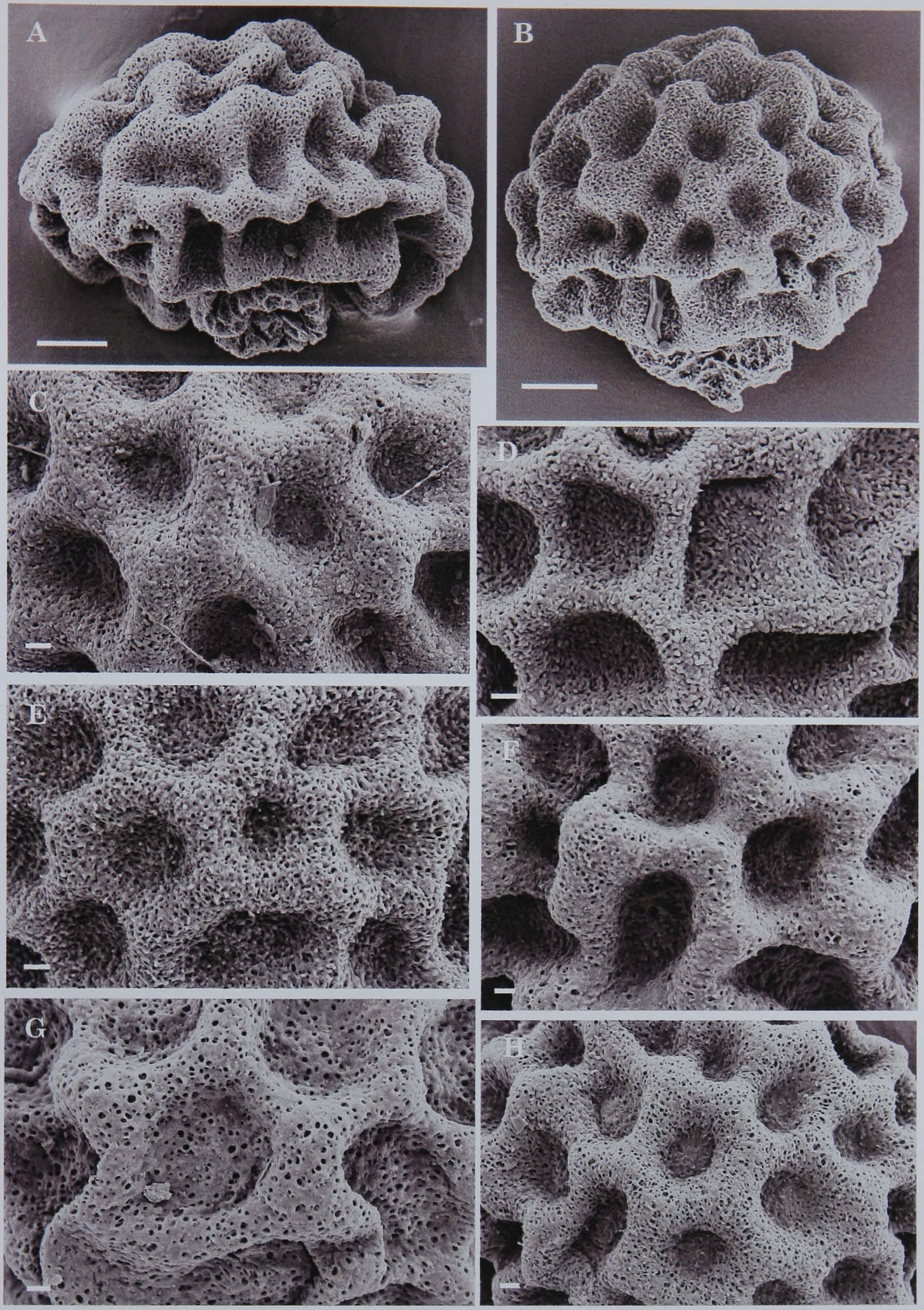


Fig. 3.16. *Mannia triandra* spores from side view (A-B) and showing fine distal ornamentation (C-H). A, F Austria, *Loitlesberger 1192* (JE); B Austria, *Schill et al. 79* (E); C Germany, *Meinunger 7108* (JE); D Siberia, *Andrejewa 144* (JE); E unclear locality, 12 Aug. 56, *Molander s.n.* (JE); G Japan, *Kobayashi s.n.* (S-B74813); H Germany, *Stephani s.n.* (BM-669301).

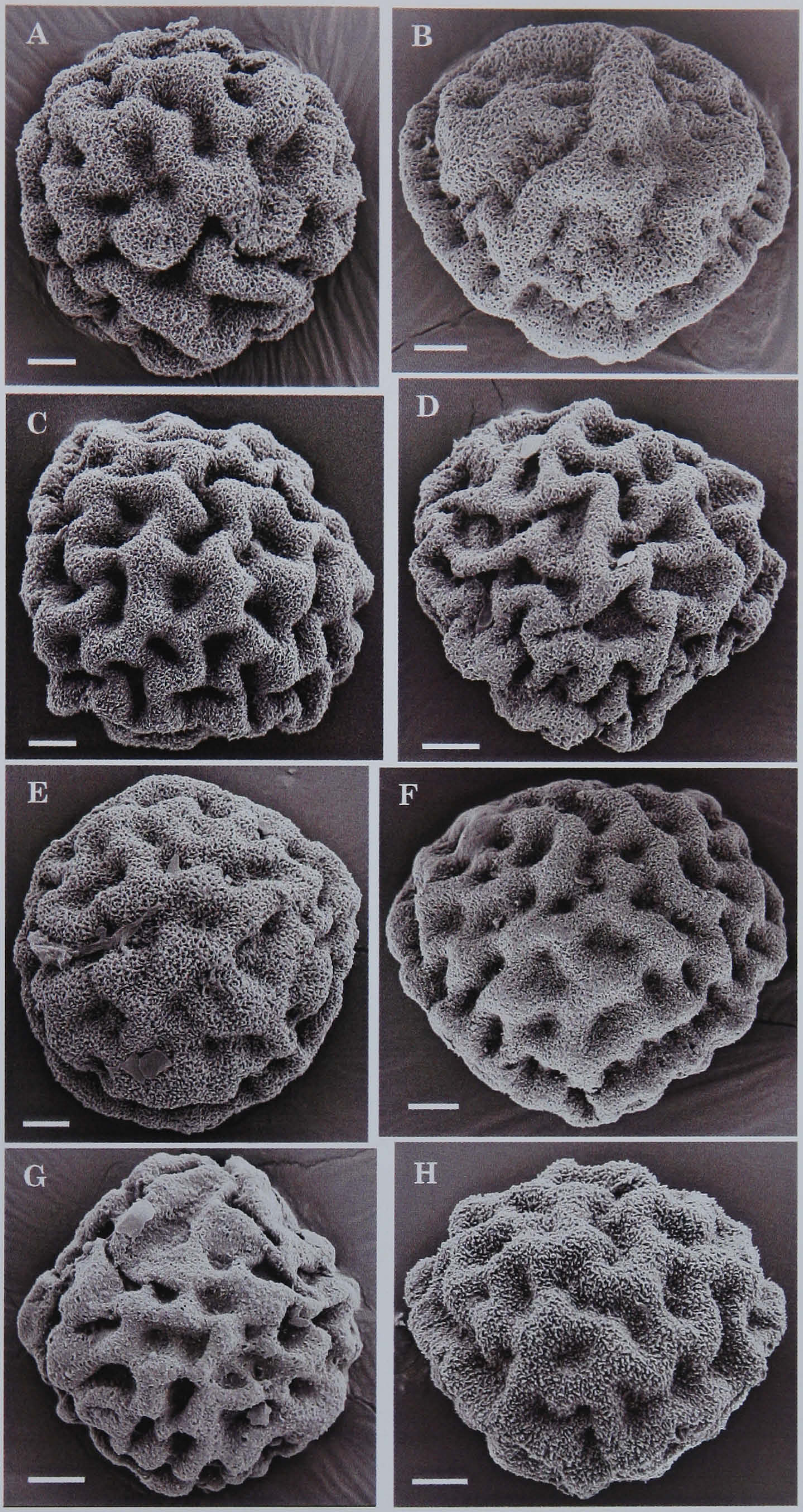


Fig. 3.17. ***Mannia pilosa*** **spores from distal view**. A Sweden, Öland, *Hülphers* s.n. (S-B74880); B Sweden, 21 v 1944, *Arnell & Persson s.n.* (S-B74890); C Austria, *Schill et al. 83* (E); D unclear locality, *Quelle s.n.* (JE); E Switzerland, *Müller s.n.* (JE-H1307); F Germany, *D.V. s.n.* (JE); G Siberia, *Arnell s.n.* (JE-H1301); H *Neesiella carnica*, Slowakia, *I. Györffy s.n.* (BM-000725087).

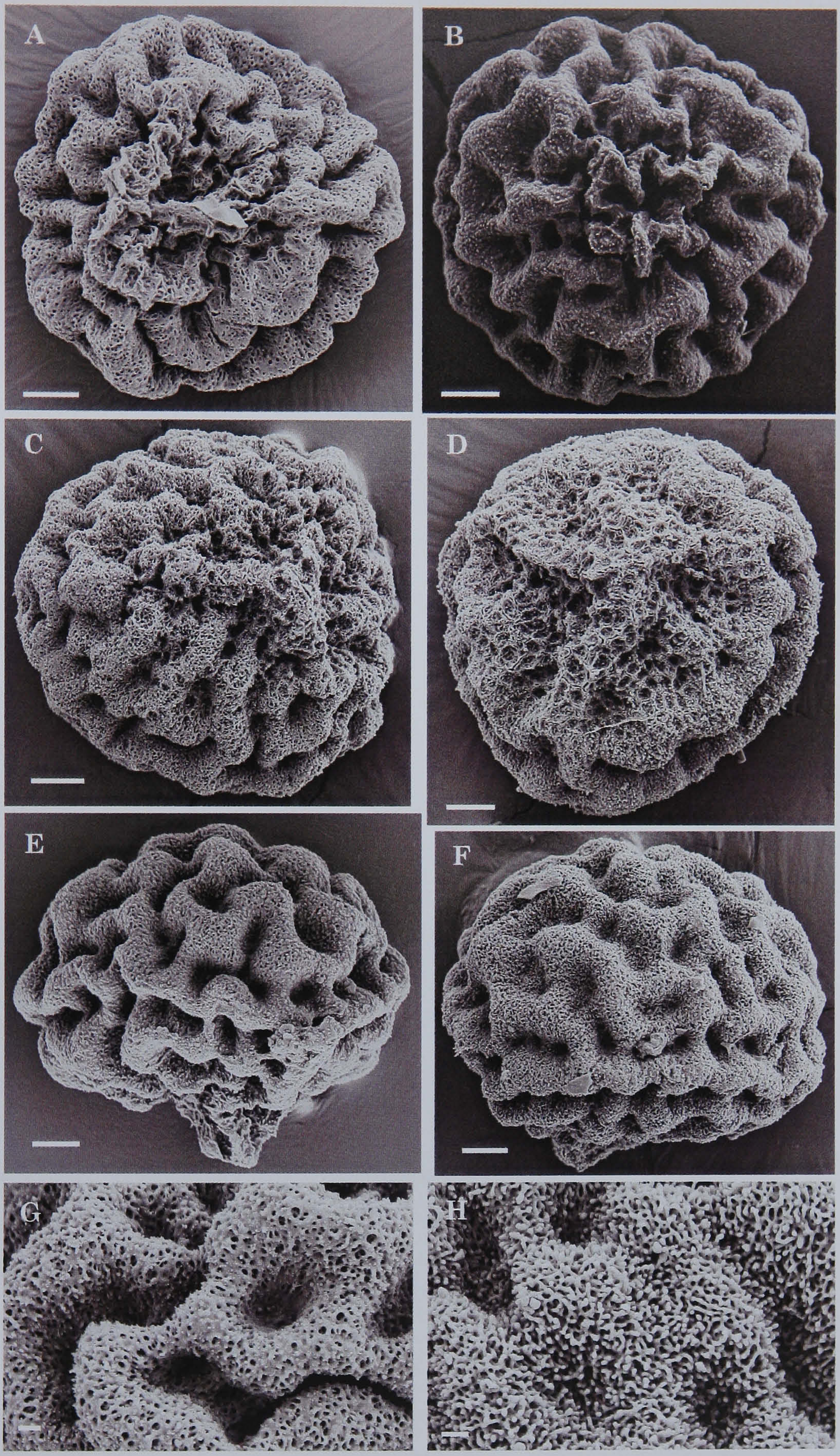


Fig. 3.18. ***Mannia pilosa*** **spores from proximal view (A-D), side view (E-F) and showing fine distal ornamentation (G-H).** A Sweden, *Samuelsson s.n.* (S-B74900); B, E Austria, *Schill et al. 83* (E); C, F Germany, *D.V. s.n.* (JE); D, H Sweden, *Hülphers s.n.* (JE-H1302); G Sweden, *Uggla s.n.* (JE-H1304).

3.6 Discussion and Conclusion

3.6.1 Species delimitation based on spore characters

Spore characters were found to have an important role and are useful for species identification and taxonomy in *Mannia*. This has also been concluded in a SEM study for the sister genus *Asterella* by LONG (1998, 2000). The ornamentation patterns were found to be constant and species-specific for each species. However, in some species there are small variations present. The primary ornamentation pattern in *M. californica* is in some specimens more ridged and in others rather areolate (Fig. 3.7-3.8). The specimen *Schill 165* from North India, which was put in the growth cabinet for spore maturation, had both ridged and areolate spores (Fig. 3.7 G,H) . The spores of a ripe receptacle were observed with the SEM and they showed a ridged ornamentation in December 2004, whereas in February 2005 a different receptacle showed areolate spores. This could suggest a certain plasticity in ornamentation patterns of *M. californica*. In general the North Indian and French *M. californica* specimens studied had more areolate ornamentations whereas spores in the North American, South Indian, Chinese and Japanese specimens observed were more ridged. In the Chinese specimens there were fewer ridges with less denser spacing. The ornamentation of some spores appears halfway between ridges and areolae (Fig. 3.7 A). However, all plants grouped under the name *M. californica* show close morphological affinities even though their spore distal ornamentation shows slight variations (see also taxonomic notes in Chapter 4.4.3.2 under this species).

For *M. androgyna* development of the proximal disc can vary (Fig. 3.3). In some specimens the margin is strongly undulate to crenate. This is not correlated with distinct geographical entities though.

The spores of *M. pilosa* and *M. triandra* can sometimes look very similar. In general *M. triandra* shows regular areolae in distal ornamentation (Fig. 3.14) whereas the areolae in *M. pilosa* are incomplete and often sunken or collapsed (Fig. 3.17). The two species however can clearly be separated by other morphological characters e.g. sexual condition.

Mannia sibirica is undoubtedly accepted as a species. It was formerly suspected by some authors to be conspecific with (MÅRTENSSON 1955, SCHUSTER 1953) or closely similar to *M. pilosa* (MÜLLER 1954, SCHUSTER & DAMSHOLT 1974, DAMSHOLT 2002). However, this can be ruled out; the spores show *M. sibirica* is quite distinct from *M. pilosa*, the spores having unexpected close affinities with the spores of *M. californica*.

Out of all spore characters, colour and size were the most variable. Most species have yellow spores or have brown and also yellow spores. This contrasts with a spore study by LONG (1998) that found spore colour to be of taxonomic value for *Asterella* species.

The spore size in individual *Mannia* species varies considerably. Spore size is not a good character for species identification, with the exception of *M. sibirica*, which generally has smaller spores than all other *Mannia* species. LONG (2000) dismissed spore size in a *Asterella* classification and pointed out the difference of spore size measurements using SEM in comparison to the LM, the latter giving larger measurements. This can also be confirmed in the present study. Spore measurements with the compound microscope were often slightly higher than with the scanning electron microscope (up to about 11%) although in some cases SEM measurements were between about 2–10% higher than LM measurements. LONG (2000) also pointed out that spore size increases with rehydration time. A 16% increase in spore diameter was measured over 90 minutes using a light microscope.

3.6.2 Synonymy

SEM is a useful tool in examining old or only fragmentary specimens and helped in establishing correct synonymy. From a former total of 22 *Mannia* names, spore ornamentation, amongst other morphological characters, was used to reduce the list of names to seven. Accepted species names can be found in Chapter 4.4.3.2.

M. capensis, a species that was believed to be endemic to Africa, consists of two taxa: one is conspecific with *M. androgyna* and one is *M. californica*. This is clearly demonstrated in the SEM survey.

M. levigata, a Japanese endemic, *M. foreaui* and *M. indica*, both Indian endemics, can all be synonymised under *M. californica* (Fig. 3.7-3.8). Spores of *Mannia brachypoda*, *M. barbifrons* and *Grimaldia inodora* are similar to *M.*

fragrans spores and are also congruent in other morphological key features (Fig. 3.10). These species sink into *M. fragans*.

A new *Mannia* species, *M. asiatica*, is described, its distinctness being based on spore ornamentation amongst other characters.

Duvalia longiseta, a species described from Japan by STEPHANI (1897) and later put into *Mannia* is found to be a synonym of *M. triandra*.

No type specimen of *M. controversa* has been seen, which was described by MEYLAN (1924) but spores from specimens examined under this name from Austria and France show a clear similarity to *M. fragrans* spores. Yet other morphological characters such as sexual condition indicate clear differences between the two. Because there was only a very limited amount of material available for study, an extended spore survey and morphological study is desirable.

The Peruvian endemic *M. hegewaldii* shows close affinities to *M. triandra*. Only two specimens were observed for this species and collections were only made from two localities in total (BISCHLER-CAUSSE ET AL. 2005). The spore ornamentation of *M. hegewaldii* is areolate but with fewer areolae, which also appear slightly bigger than in typical *M. triandra* specimens. It is possible that the spores are immature or fall into a normal range variation of *M. triandra* spores. It was observed that a specimen of *M. triandra* from Japan showed striking similarities to the spores of *M. hegewaldii*.

3.6.3 Distribution

The distribution range of most species could be confirmed through the SEM survey of spores. Most *Mannia* species show a wide distribution and are present in many continents.

A range extension could be noted for *M. androgyna*, which was mostly known from countries with Mediterranean climate (BISCHLER 2004) and now extends into the African continent. It is absent though from America and most parts of Asia. The most easterly part of its range based on observed herbarium specimens is in Turkey, Cyprus and Albania. However, in comparison to the other *Mannia* species, *M. androgyna* has the most limited and localised distribution range.

One of the most dramatic distribution changes is demonstrated for *M. californica*. This species was formerly thought to be endemic to the United States. Its distribution can now be extended into France (HUGONNOT & SCHILL 2006), Austria, Africa, India, China and Japan.

3.6.4 Classification based on spore types

It is assumed that the gametophyte in the Marchantiales is more subject to selection pressure by the environment and therefore has evolved faster than the more protected sporophyte (BISCHLER 1998); this suggests spore characters are more conserved and display a strong phylogenetic signal. So spore ornamentation could provide insights into evolutionary relationships in *Mannia* and could be used in creating a stable infrageneric classification of *Mannia*, former classifications being in conflict (SHIMIZU & HATTORI 1954, GROLLE 1976, 1983b, GROLLE & LONG 2000). Recent classifications were mainly based on thallus characters but this was strongly criticised by SCHUSTER (1992a).

For an infrageneric classification in *Asterella*, LONG (1998, 2000) used spore characters and also showed that they correlate well with molecular evidence (LONG ET AL. 2000).

Following LONG (2000) *Mannia* spores were grouped into spore types, which were used for a new infrageneric classification. In Chapter 5 (see 5.7.3.7) it is shown that these spore types are also partly reflected in the molecular results based on two markers. Both spore characters and molecular evidence were used for a new infrageneric classification of *Mannia*. The classification is presented in Chapter 4 (see 4.4.2). In contrast to all recent classifications is the position of *M. sibirica* close to *M. californica*. *M. sibirica* has always been previously considered to be a close relative to *M. pilosa* and *M. triandra*.

3.7 Conclusions

As has been the case with other Marchantiales, spore characters were found to have an important role for species identification and taxonomy in *Mannia*.

The spore ornamentation patterns were found to be species specific and constant for each species. However, there were some variations in the primary ornamentation of *M. californica* and in the proximal disc of *M. androgyna*. From all characters observed spore size was the most variable and spore colour showed little difference for individual species.

SEM has proven to be of great value in establishing correct synonymy in the genus.

A classification into five different spore types was undertaken and provided new insights.

The spore patterns of *M. sibirica* showed close affinities to *M. californica* and both were grouped together in spore type II. The position of *M. sibirica* is contrary to all recent classifications, in which it was assumed to be closely related to *M. pilosa* and *M. triandra*. The latter two species show strong spore similarities and were grouped in spore type V. The spore ornamentation of *M. fragrans*, *M. androgyna* and *M. asiatica* are so different from each other and from groups II and III that each remains in its own separate spore groups.

Chapter 4: Taxonomic Revision

4.1 Introduction

An alpha-taxonomic revision of the genus *Mannia* on a worldwide scale has been undertaken, the first attempted for this genus. Former taxonomic studies on the genus have focused on narrower geographic regions. Examples of theses are shown in Table 4.1.

Table 4.1. Earlier Revisions of *Mannia* in different geographic regions with number of species treated

Author (Year)	**Geographic Region**	**Number of species treated**
SHIMIZU & HATTORI (1953a, b)	Japan	2–3
HATTORI (1954)	Japan	1
MÜLLER (1954)	Europe	5
UDAR & CHANDRA (1965)	India	4
SCHUSTER (1992b)	North America	6
PEROLD (1994a)	Southern Africa	1
IWATSUKI (2001)	Japan	1
DAMSHOLT (2002)	Nordic	3
BISCHLER-CAUSSE ET AL. (2005)	Neotropics	2

There are 22 published names for *Mannia* in the *Index Hepaticarum* (GEISSLER & BISCHLER 1985), of which some are now treated as synonyms of other *Mannia* species or species in other genera. Some *Mannia* species have been formerly included in other genera such as *Neesiella* (6 species), *Grimaldia* (33 species), *Duvalia* (5 species), *Arnelliella* (1 species), *Sindonisce* (1 species) and *Cyathophora* (1 species) (BONNER 1965, 1966, GEISSLER & BISCHLER 1985, 1989, 1990). In other literature fifteen species of *Mannia* are given by BISCHLER (1998). In general, the numbers found in the literature vary between six (ENGEL 1990) and eighteen species (SCHUSTER 1992b, DAMSHOLT 2002) worldwide.

In the present treatment seven *Mannia* species are accepted, of which one species is new. But because type material of some species could not be located and material of some described species has not been available this treatment could still undergo further changes in the future. Furthermore as will be later discussed in Chapter 5 *Mannia* is not a monophyletic genus but has evolved from within the related genus *Asterella*, which could have further consequences for its classification.

The worldwide distribution of *Mannia* based on herbarium material studied is shown in Fig. 4.1.

Fig. 4.1. Worldwide distribution of *Mannia* based on studied herbarium material

4.2 Objectives

The main objectives of this study were to revise the genus *Mannia* on a worldwide scale based on morphological and anatomical characters, with particular emphasis on spore characters observed with the Scanning Electron Microscope (Chapter 3) as well as consideration of molecular evidence (Chapter 5). Keys to subgenera, sections and species along with species descriptions, species lists, synonyms, drawings, maps of distribution, general, ecological and taxonomic notes have been made as part of this study. Two keys are presented, one including characters from fertile plants with ripe spore material, the second based on vegetative characters in combination with sexual condition. New and old synonyms of the treated species have been listed and lectotypification has been undertaken when possible. The new classification of the genus presented here will be discussed and compared with treatments published in the past.

4.3 Material and Methods

4.3.1 Herbarium material

Mannia specimens from fourteen herbaria were requested on loan (see Table 4.2). Visits to the herbaria in G (Geneva) and Lucknow University Herbarium (LWU) were made and material selected for loan. All (about 1320 in total) specimens borrowed from herbaria have been examined.

Table 4.2. Number of specimens and *Mannia* types on loan from different herbaria

Herbarium	No. of specimens	*Mannia* types
NY (New York Botanical Garden)	400	3
BM (British Museum)	201	5
JE (Jena)	184	2
F (Field Museum Chicago)	160	-
S (Stockholm)	107	7
E (Edinburgh)	197	1
G* (Herbarium Geneva)	36	4
BOL (Bolus Herbarium South Africa)	17	1
NICH (Hattori Botanical Laboratory Japan)	7	3
BG (Bergen Herbarium)	6	1
MO (Herbarium of the Missouri Botanical Garden)	2	1
PRE (Pretoria National Herbarium)	1	-
TNS (Herbarium National Science Museum Tokyo)	1	1
H (Helsinki)	1	1

*includes collections in the herbarium of Patricia Geissler

Material requested from the herbaria of HIRO (Hiroshima University), MPU (Montpellier), LAU (Lausanne) and LWU (Lucknow University) has unfortunately never been received.

Type specimens of some taxa could either not be located or specimens were not available on loan. This resulted in the exclusion of these taxa or their listing as doubtful species.

Types which have not been seen or could not be located are cited as *'n.v.'*(non vidi), *'I have not seen'*(STEARN 2005).

4.3.2 Herbarium methods

The study of all the herbarium specimens on loan helped to get a much clearer picture of species delimitation and contributed to the species descriptions. Study of the specimens also helped in determining species variability. Many specimens have been studied for each species, ranging from ten for *M. asiatica* to about 360 for *M. fragrans*. For the other species the number of specimens was between 32 and about 200. All available types were studied with great care and were observed for key characters, particularly spore characters, where possible. FRAHM (2001) recommends the use of water-soluble embedding media for the making of permanent slides for bryophyte study. So fresh water-mounted slides and semi-permanent slides using Hoyer's Fluid (ANDERSON, 1954) was used for parts of specimens to be studied and drawn later. The latter method is described as an excellent mounting medium for hepatics even though SCHOFIELD (1985) mentions that it can distort the leaves of some bryophytes. A side effect is that it also works as a clearing agent because the chloral hydrate in the solution also causes bleaching of the cell contents. This was found to be disadvantageous for the delicate epidermal tissue of the thallus and receptacle and was therefore not used for mounting these. The permanent slides were stored flat in slide folders. Pencil drawings were made using a camera lucida attached to a compound microscope or done freehand. A microscope slide scale was used for exact measurements. After inking and shading on tracing paper, drawings were scanned digitally for editing in Adobe Photoshop CS Version 8 (ADOBE SYSTEMS INCORPORATED 2003).

Morphological Study Potential useful morphological features were initially assessed using available literature on Marchantiales, particularly by LONG (2000) and BISCHLER (1998) and plants were examined closely for these characters. However, other potentially useful characters were assessed, particularly those of value in distinguishing between species. Initially, at least six different collections of each species were used for detailed dissection, measurement and description (quantitative characters scored as minima and maxima). Species descriptions are based on these observations and measurements.

Specimens were moistened with water for at least half an hour before dissection to allow the thalli to unroll and regain their natural shape. This was problematic with older specimens because the thalli often did not unroll properly and were very brittle. Dissections were carried out under a Stereo microscope using fine forceps and a needle.

Transverse sections of thallus, stalk and receptacle were made freehand under the Stereo microscope on a slide using a razor blade and a needle. They were held in place with a needle, which was slowly rolled backwards allowing a cut of thin sections. Epidermal tissue was pulled away with a needle and fine forceps to view air pores and epidermal wall thickenings. Scales underneath the receptacle, along and on base of the stalk were pulled away with forceps and the ventral scales were pulled away along the whole length of the ventral side of the thallus using fine forceps.

4.3.3 Living material

Eight field trips have been made to places within Europe and other continents to collect living and dried material of *Mannia* species and related genera. Plants were collected for morphological and anatomical observations, spore studies (Chapter 3) and molecular work (Chapter 5). The possibility of studying and photographing living *Mannia* species in the field has been extremely valuable because during drying, herbarium specimens can change quite a lot: some do not regain their natural shape when moistened particularly if they are very old and brittle, and others are sometimes too fragmentary to study. So detailed study, including dissection, was undertaken preferentially on my own freshly-collected specimens.

The species previously reported from Europe (*M. androgyna, M. fragrans, M. pilosa* and *M. triandra*) were targeted on field trips to Germany (Saxony-Anhalt), Switzerland (Valais), Sweden (Gotland), Austria (Styria, Carinthia) and Portugal (Madeira). The so-called endemic species (*M. californica, M. paradoxa, M.capensis, M. indica, M. foreaui, M. perssonii* and *M. hegewaldii*) were searched for in the U.S. (California, Arizona, New Mexico), Namibia, North- and South-India (Uttaranchal, Tamil Nadu) and Northern Peru (La Libertad).

Due to this extensive field work, most of the species were seen in the living condition except for *Mannia sibirica* and *M. asiatica*. Some taxa unfortunately could not been found in the field such as *M. paradoxa*, *M. perssonii* and *M. hegewaldii*. In some cases where *Mannia* species could only be collected with immature archegoniophores these specimens were cultivated in a growth cabinet until spore maturity.

Requests for living material resulted in receipt of several different *Mannia* specimens from colleagues in Japan, Czech Republic, Sweden, Finland, France, Germany and Austria. The specimens included in the study are listed in Appendix I.

4.3.4 Field methods

Specimen labels of herbarium loans and literature reports of species gave a good indication as to which countries and localities and which season to visit in order to collect the desired species, particularly with regard to collecting specimens with sporophytes and ripe spore material for the SEM survey (Chapter 3). Contacts were sought beforehand wherever possible but many field trips were made without local help. Usually collecting and export permits had to be applied for a few month before the field trip took place and after completion of the field work reports were written up.

For specimens collected, notes were made directly in the field on smell, morphological appearance such as colour and texture, reproduction and shape of receptacle. Measurements of thallus width, thallus length and stalk length were partly made in the field using a small ruler. Specimens were collected with a knife. Soil was removed as much as possible before specimens were placed in prepared paper packets (dry soil in the packet can easily damage the specimen). Packets were given temporary reference numbers in the field. Data was recorded using a portable Garmin 12XL Global Positioning System navigator (GPS) for altitude, longitude and latitude. Detailed notes on locality were made as well as notes on substrate, ecology and vegetation.

Observations in the field and collection of fresh material is particularly useful as after drying some features of specimens can be lost and old herbarium specimen are often too fragmentary or small for detailed study. Cultivation of living material from collected plants was undertaken in a growth cabinet for morphological study, especially for specimens with immature sporophytes to see if archegoniophores would develop from sterile material (see Chapter 2.3). Photographic images of plants and habitats were taken with a Nikon COOLPIX4500 Digital Camera on a small field tripod or were hand-held. Images were then edited in Adobe Photoshop CS Version 8 (ADOBE SYSTEMS INCORPORATED 2003).

4.3.5 Maps of distribution

Maps of species distribution were created starting from a base map of countries and regions of the world. In this base map, large countries such as Russia, USA, Canada and China are represented by their smaller administrative regions (e.g. USA states). This helps to avoid single species records for large countries being over-emphasised in the maps. To create the maps, a tabular list of countries and regions were made for each species, and then matched to the base map using GIS software. So each filled region on the map corresponds to one or more records within that region. This method of map production was preferred to the alternative of representing each record by a point on the map because of the large number of individual records and the difficulty of placing the point on the map with any degree of confidence. Records can be more reliably assigned to a geographic region than have their latitude and longitude determined.

4.4 Taxonomic account

4.4.1 The genus *Mannia*

Mannia Opiz, Beiträge zur Naturgeschichte 12: 646. Prag. 1829. *nom. cons.* for *Grimaldia* Raddi 1818 *nom. illeg.* non Schrank 1805

Lectotype:	*M. michelii* Opiz, *nom. illeg.* (= *Grimaldia dichotoma* Raddi, *nom. illeg.*, *Marchantia androgyna* L., *Mannia androgyna* (L.) A.Evans (ZIJLSTRA 1990))
Synonyms:	*Duvalia* Nees, Gesellschaft naturforschender Freunde Berlin Magazin für die neuesten Entdeckungen in der gesamten Naturkunde 8: 269. 1818, *nom. illeg.*, non *Duvalia* Haworth 1812 (GROLLE 1983b), Type: *Duvalia rupestris* Nees (= *Mannia triandra* (Scop.) Grolle).
	Grimaldia Raddi, Opuscoli Scientifici Bologna 2: 356. 1818. *nom. illeg.*, non Schrank 1805 (GROLLE 1983b), Type: *G. dichotoma* Raddi, *nom. illeg.* (= *Mannia androgyna* (L.) A.Evans).
	Cyathophora Gray, A Natural Arrangement of British Plants 1: 683. 1821. *nom. rej.* Type: *Cyathophora angustifolia* Gray (GROLLE 1981, 1983b, ZIJLSTRA 1990) (= *Mannia androgyna* (L.) A.Evans).
	Neesia Leman, Dictionaire des sciences naturelles 34: 337, 1825, *nom. illeg.*, non Spreng 1818 (GROLLE 1983b), Type: *Duvalia rupestris* Nees (= *Mannia triandra* (Scop.) Grolle)
	Sindonisce Corda, in: Opiz (ed.) Beiträge zur Naturgeschichte 12: 648, 1829, Type: *Sindonisce fragrans* (Balb.) Corda, 1804. (GROLLE 1983b) (= *Mannia fragrans* (Balbis) Frye & L.Clark).

Pleurochiton Corda ex Nees, Naturgeschichte der Europäischen Lebermoose 4: 225, 1838. *nom. inval.* (GROLLE 1983b), Type: *Pleurochiton balbisianum* Corda ex Nees (= *Mannia fragrans* (Balbis) Frye & L.Clark).

Duvaliella Borbás, Pallas Nagy Lexikona 5: 632. 1893, *nom. illeg.*, non F.Heim 1892 (GROLLE 1983b), Type: *Duvalia rupestris* Nees. (= *Mannia triandra* (Scop.) Grolle).

Neesiella Schiffn., in Engler & Prantl, Die Natürlichen Pflanzenfamilien 1(3): 32, 1893. Type: *N. rupestris* (Nees) Schiffn. (GROLLE 1983b) (= *Mannia triandra* (Scop.) Grolle) .

Arnelliella C.Massal., Atti del reale instituto veneto di scienze, lettere ed arti Venice 73(2): 927. 1914. Type: *Arnelliella sibirica* (K. Müll.) C.Massal. (*Grimaldia pilosa var. sibirica* Müll.Frib.) (GROLLE 1983b) (= *Mannia sibirica* (Müll.Frib.) Frye & L.Clark)

Description

Plants xeromorphic or mesomorphic; aromatic and sometimes strongly fragrant (cedar smell in *M. fragrans* or aromatic smell in some specimens of *M. androgyna*); *thalli* small, growing intermingled in mats or spreading and forming loose mats (extensive patches), linear and leathery or broadening towards thallus apex and rather flat and more delicate, sometimes with slightly wavy margins; *midrib* not defined dorsally; *vegetative branches* dorsally bright green, becoming brown or whitish (*M. pilosa, M. triandra*) in older parts, sometimes strongly lacunose when disintegrating; vegetative branching in terminal symmetrical or asymmetrical dichotomies or with ventral or terminal innovations; margins dark purple or blackish, occasionally white (*M. pilosa*); ventrally purplish-black; when dry, thallus margins usually completely inrolled, tubular and black or sometimes only weakly inrolled (*M. pilosa, M. triandra, M. sibirica, M. californica*); surface areolate or not areolate; *lobe apex* rounded and middle often notched where archegoniophores develop; *thallus* in t.s. usually broadly concave or triangular, occasionally almost flat, divided into an upper epidermis with air pores, photosynthetic assimilation tissue, storage tissue and poorly differentiated lower epidermis; *dorsal epidermis* unistratose with thin-or thick-walled cells with convex trigones; *air pores* inconspicuous to distinct, simple, sometimes slightly to strongly upraised above each chamber, in surface view with 2–3(4) concentric rings of cells, rings usually partly overlapping each other, radial cell walls of innermost ring sometimes collapsed, outer ring of 5–10 cells, inner ring of 5–9 cells, radial cell walls thin or thick; *assimilation tissue* green, either spongy with small densely packed air chambers or loose with big air chambers in an irregular layered arrangement, sometimes with one upper band of tall vertical air chambers and smaller more rounded air chambers below (2–4 above each other), occasionally rather intermediate, air chambers sometimes with free filaments, oil cells present or absent; *basal tissue* colourless; cells rounded to oblong; with scattered bright to dark brown coloured oil cells and often mycorrhizal, (sometimes assimilation tissue more extensive, sometimes storage tissue).

Rhizoids hyaline and occasionally purplish or brownish towards base, arising from ventral epidermis along the midline of the thallus, of two types, smooth and pegged with peg-like wall thickenings.

Ventral scales in two rows on each side of thallus midline, sometimes overlapping each other and midline of thallus, usually overlapping lobe apex and sometimes lobe margin, purple with sometimes paler margins, or colourless, asymmetric, unistratose, semicircular to broadly elongate or oblong-semicircular, lunate and curved decurrent at insertion, small slime papillae present on margins, often abundant, sometimes easily breaking off (*M. androgyna*), *oil cells* usually present and several, in some species only a few or absent (*M. pilosa*), isodiametric, usually marginal but occasionally also found in middle of ventral scales or in appendages; *appendages* 1–2(3), usually purple or bleached (*M. fragrans*), base not constricted, subulate to broadly subulate or lingulate, gradually narrowing into acute tip.

Specialised asexual reproduction absent.

Androecia and gynoecia usually borne on different thalli of the same plant (monoicous) or on separate plants (dioicous).

Sexual condition dorsal-autoicous, male- or female-ventral-autoicous, terminal-autoicous, par-autoicous, or dioicous. Androecia borne dorsally on main thallus (dorsal- autoicous) with archegoniophore either on reduced ventral branches (female-ventral-autoicous), or archegoniophore on the same thallus or on a dichotomous furcation of the same thallus, on reduced ventral branches of the main, often archegoniophore-bearing thallus (male-ventral-autoicous), or androecia on shorter or equally long branch of a dichotomous furcation (terminal-autoicous) of which the other branch can bear an archegoniophore, or close to base of archegoniophore (par-autoicous) or plants dioicous with androecia and gynoecia always borne on different thalli but plants of both sexes often intermingled.
Androecia sessile, usually several, ostioles ±conical and raised, scattered along midline of thallus or in strongly or weakly upraised clusters, or in terminal poorly defined clusters in slight depressions or slightly upraised, without marginal scales when mature but scales sometimes present at start of antheridial development but later fugacious, green when young, gradually becoming purplish-black when mature and with sometimes purplish coloured surrounding epidermal tissue; male branches continuing vegetative growth.

Gynoecia in form of archegoniophores deriving from terminal notch of the main vegetative thallus as a modified continuation of the branch and inhibiting further growth of thallus or borne on a reduced ventral branch, surrounded by scales; archegoniophore consisting of a stalk (peduncle) and receptacle; *stalk* greenish or yellowish, sometimes purple at base or higher up, variable in length, usually with scales around its base, naked or with scales along its length, scales lanceolate to linear, with slime papillae, stalk t. s. circular to irregularly triangular-ovate, with single rhizoidal furrow, without air chambers, in t. s. with low ridges when dry, epidermal cells in one layer, brownish, small, medullar cells of rounded bigger cells, incrassate with corners quite thickened, yellowish or brownish.
Receptacle warted, with compound pores on the upper surface, hemispherical or subglobose, yellowish-green when young, maturing green and often tarnishing purple, bearded below or naked; *calyptra* inconspicuous, small and rounded shallowly bowl- or cup-shaped, thin-layered and delicate, situated at the base of

each receptacle lobe underneath the capsule; *pseudoperianth* absent; *involucres* forming the end of each receptacle lobe surrounding the capsule, cup-shaped, narrow to broad, usually bistratose and thin; receptacle bearing (1)2–4(5) *sporophytes* each with very short reduced seta; capsule rounded, yellow when young and turning brown or black when mature, wall unistratose, annular thickenings absent; lid brown, irregularly rounded to circular, shed complete and not fragmenting, lid cells rounded to rectangular, with small corner thickenings, cells often overlapping each other.

Spores yellow, brown, yellowish brown to reddish brown or greyish brown (LM), with elaborate ornamentations, distally saccate, areolate or ridged with papillae and pits, proximal side sometimes with proximal disc, weak to strong trilete mark, equatorial apertures inconspicuous or conspicuous.

Elaters yellowish or brownish, with 2–3-spiral thickenings, middle often 3-spiral and ends 2-spiral.

Chromosome number *not known* or mostly n = 9.

Distribution

Mannia is a relatively small genus with about 7 accepted species worldwide. It has a nearly worldwide distribution north to the Arctic but is not recorded from tropical East Asia, Central America and Australasia (BISCHLER 1998). Its main distribution lies in the northern hemisphere but it is also found on the African and South American continents. The worldwide distribution based on herbarium specimens studied can be seen above in Fig. 4.1.

Ecology

The genus comprises both xeromorphic and mesomorphic taxa, all drought-tolerant with often fragmented ranges (BISCHLER 1998) growing on rocky soil or rock crevices in arctic –alpine to Mediterranean climates.

Taxonomic Notes

The delimitation of *Mannia* from related genera is not clearly defined. It is characterized by a small narrow thallus and cup-shaped involucres. The lack of a pseudoperianth is the main difference from *Asterella*. Besides, it has an aromatic smell whereas many *Asterella* species are characterised by a fishy smell. The position of archegonia and antheridia as well as the shape of the receptacle differs from *Reboulia*, *Cryptomitrium* and *Plagiochasma* together with the smaller size, the colour and texture of the thallus. An important characteristic in species-level taxonomy is the spore ornamentation pattern.

Nomenclatural Notes

Mannia was published by OPIZ in 1829 as a new name (nom. nov.) for the illegitimate *Grimaldia* Raddi 1818.

According to the International Code of Botanical Nomenclature (ICBN) *Mannia* must be typified by the type of *Grimaldia*. *Grimaldia* when published by Raddi had one constituent species *Grimaldia dichotoma*. However, *G. dichotoma* Raddi was based on two different elements, which are a) *Marchantia triandra* Scop. 1772 and b) a Micheli (1729) polynomial.

In 1983b, c GROLLE proposed that *Marchantia triandra* Scop. (= *Mannia triandra* (Scop.) Grolle) be the lectotype of *Grimaldia dichotoma* Raddi but the Nomenclature Committee (ZILJSTRA 1990) rejected this and chose the Micheli element (as the older one) as lectotype of *G. dichotoma*. The Micheli element is well established as being *Mannia androgyna* (L.) Evans and was formally lectotypified by Grolle in 1968. Therefore *Grimaldia dichotoma* Raddi is a synonym of *Mannia androgyna* and is the type of both the genera *Mannia* Opiz and *Grimaldia* Raddi and not *Mannia triandra* as GROLLE (1983b,c) had earlier proposed.

4.4.2 Infrageneric subdivision

The following classification (summary in Table 4.3) is based on morphological evidence, the spore survey using SEM and also on the molecular phylogenetic data based on two molecular markers (chloroplast and nuclear) as discussed in 1.4.2, 3.6.4 and 5.7.3.7. As a result it is concluded that two subgenera, *Neesiella* and *Mannia* should be recognized, and within subg. *Mannia*, four sections are recognized, sect. *Mannia*, Sect. *Arnelliella*, sect. *Sindonisce* and sect. *Asiaticae*. Keys to subgenera and sections are given below; descriptions and nomenclatural details are given in the taxonomic account (see 4.4.3).

Table 4.3. Synopsis of infrageneric classification of *Mannia*

Subgenus	Section	Species
Mannia	*Mannia*	*Mannia androgyna*
	Arnelliella	*Mannia sibirica* *Mannia californica*
	Sindonisce	*Mannia fragrans*
	Asiaticae	*Mannia asiatica*
Neesiella		*Mannia triandra* *Mannia pilosa*

4.4.2.1 Key to *Mannia* subgenera and sections

1 Spores spongy in fine distal ornamentation, with minute pits; with similar sculpturing on proximal and distal surfaces; distally incompletely areolate; proximal disc absent; equatorial pores inconspicuous; receptacle subglobose .... **subgenus *Neesiella*** (page 150)

1* Spores not spongy in fine distal ornamentation, minutely papillate, with or without minute pits; with similar or dissimilar sculpturing on proximal and distal surfaces; distally saccate, regularly or irregularly areolate or ridged; proximal disc present or absent; equatorial pores conspicuous; receptacle hemispherical..**subgenus *Mannia*** (page 107)..2

2 Spores with proximal disc 3

2* Spores without proximal disc 4

3 Spores saccate .... **section *Mannia*** (page 107)

3* Spores areolate or ridged .... **section *Arnelliella*** (page 117)

4 Plants dioicous; spores regularly areolate; antheridia rather conspicuous, borne terminally on separate (not archegoniophore-bearing) thallus, forming a defined triangular (sometimes rounded or elliptic), sometimes slightly upraised disc; thallus apex bearded; ventral scale appendages bleached; receptacle usually bearded ....
.... **section *Sindonisce*** (page 132)

4* Plants monoicous; spores deeply areolate; antheridia inconspicuous, forming a poorly defined, slightly upraised rounded cushion or terminal slight depression or notch; thallus apex not bearded; ventral scale appendages not bleached; receptacle usually naked ....
.... **section *Asiaticae*** (page 143)

4.4.3 Species accounts

4.4.3.1 Keys to *Mannia* species without and with ripe spore material

Key to *Mannia* species without ripe spore material

1 Plants dioicous; antheridia borne terminally on separate (not archegoniophore-bearing) thallus, forming a defined triangular (sometimes elliptic or rounded) disc; thallus apex bearded with conspicuous ventral scales; ventral scale appendages bleached; receptacle bearded; thallus leathery; usually aromatic (cedar oil smell)... .... **4. *M. fragrans*** (page 132)

1* Plants dorsal-autoicous, terminal-autoicous, ventral-autoicous or par-autoicous; antheridia often on same thallus as archegoniophore or on separate thalli; thallus apex not bearded with conspicuous ventral scales; ventral scale appendages not bleached; receptacle bearded or naked; thallus leathery or delicate; aromatic or not **2**

2 Plants male-ventral-autoicous (antheridia borne on reduced ventral branches); oil cells in ventral scales often absent or only a few (0–2(4)); receptacle bearded; upper surface of thallus whitish when disintegrating, strongly lacunose........................... **7. *M. pilosa*** (page 156)

2* Plants dorsal-autoicous, terminal-autoicous or par-autoicous; oil cells in ventral scales several; receptacle bearded or naked; upper surface of thallus brownish when disintegrating, weakly lacunose **3**

3 Antheridia borne dorsally on thallus, in loosely or densely aggregated clusters, sometimes upraised; assimilation tissue compact with small air chambers; thallus thick and leathery, upper surface not reticulate; receptacle naked.. **4**

3* Antheridia borne terminally on main thallus or close to base of archegoniophore; assimilation tissue rather loose with large air chambers; thallus rather thin and delicate or leathery, upper surface reticulate or not; receptacle bearded or naked **5**

4 Archegoniophores predominantly borne on main thallus; storage and

assimilation tissue with pale-coloured oil-bodies; male and female gametangia sometimes borne on the same thallus.. 1. *M. androgyna* (page 108)

4* Archegoniophores predominantly borne on reduced ventral branches; storage and assimilation tissue with several dark brown oil-bodies; male and female gametangia not borne on the same thallus...3. *M. californica* (page 123)

5 Receptacle subglobose, usually naked; thallus usually rather delicate or sometimes leathery .... 6. *M. triandra** (page 150)

5* Receptacle hemispherical, bearded or naked; thallus rather leathery 6

6 Receptacle usually bearded; antheridia often on equally long branch of a dichotomy of which the other branch bears an archegoniophore..2. *M. sibirica**(page 118)

6* Receptacle usually naked; antheridia often on shorter branch of a dichotomy of which the other branch bears an archegoniophore.. 5. *M. asiatica** (page 144)

**M. triandra*, and particularly *M. sibirica* and *M. asiatica* can only be identified for sure with ripe spore material

Key to *Mannia* species with ripe spore material

1 Antheridia borne on reduced ventral branches; ventral scales with 0–2(4) oil cells; receptacle bearded; upper surface of thallus whitish when disintegrating, strongly lacunose ....7. *M. pilosa* (page 156)

1* Antheridia not borne on reduced ventral branches; ventral scales with usually several (up to 52) oil cells; receptacle bearded or not bearded; upper surface of thallus brownish when disintegrating, not strongly lacunose...2

2 Thallus apex bearded with conspicuous ventral scales; ventral scale appendages bleached; antheridia borne terminally on separate (not archegoniophore-bearing) thallus, forming a defined triangular

(sometimes elliptic or rounded) disc; plants dioicous, usually aromatic (cedar oil smell); thallus leathery........................4. *M. fragrans* (page 132)

2* Thallus apex not bearded with conspicuous ventral scales; ventral scale appendages not bleached; antheridia often on same thallus as archegoniophore or on separate thalli; plants monoicous, aromatic or not; thallus leathery or delicate..3

3 Antheridia borne terminally on main thallus or close to base of archegoniophore; assimilation tissue rather loose with large air chambers; thallus rather thin and delicate, upper surface reticulate; receptacle bearded or naked...4

3* Antheridia borne dorsally on thallus, in loosely or densely aggregated clusters, sometimes upraised; assimilation tissue compact with small air chambers; thallus thick and leathery, upper surface not reticulate; receptacle naked...6

4 Spores small, 43–56(62) μm, with dissimilar sculpturing on proximal and distal surfaces, with proximal disc; receptacle bearded and hemispherical; thallus rather leathery....................................... 2. *M. sibirica* (page 118)

4* Spores large, (45.6)55–75(77.7) μm, with similar sculpturing on proximal and distal surfaces, without proximal disc; receptacle usually naked, hemispherical or subglobose; thallus rather delicate or leathery............5

5 Spore surface minutely papillate, with 6–10 areolae across distal surface, equatorial apertures rather conspicuous; receptacle hemispherical; thallus leathery...5. *M. asiatica* (page 144)

5* Spore surface spongy, with 4–7 areolae across distal surface, equatorial apertures rather inconspicuous; receptacle subglobose; thallus rather delicate..6. *M. triandra* (page 150)

6 Spores distally saccate; archegoniophores usually borne on main thallus; storage and assimilation tissue with pale-coloured oil-bodies; male and female gametangia sometimes borne on the same thallus........................

.... 1. ***M. androgyna*** (page 108)

6* Spores distally areolate or ridged; archegoniophores usually borne on reduced ventral branches; storage and assimilation tissue with several dark brown oil-bodies; male and female gametangia not borne on the same thallus.. 3. ***M. californica*** (page 123)

4.4.3.2 Descriptions of subgenera, sections and species

Subgenus *Mannia*

Type: as for *Mannia* Opiz

Synonym: subgenus *Xeromannia* Grolle, Journal of Bryology 12: 405. 1983. Type: *Mannia androgyna* (L.) A.Evans

Description

Receptacle hemispherical; s*pores* with similar or dissimilar sculpturing on proximal and distal surface; distally saccate, regularly areolate, irregularly areolate or ridged; on surface minutely papillate with or without pits, not spongy; proximal disc present or absent; equatorial pores conspicuous.

Nomenclatural note

The type of subg. *Mannia* and sect. *Mannia* automatically has to follow the typification of the generic name, which has changed over the years (GROLLE 1976, 1983b,c, ZILJSTRA 1990, GROLLE 2000). It is now *Mannia androgyna* (L.) Evans as discussed in 4.4.1 under Nomenclatural Notes.

Section *Mannia*

Type as for *Mannia* Opiz

Description

Thallus apex not bearded; *sexual condition* dorsal-autoicous; *antheridia* conspicuous, scattered dorsally along midline of thallus or in terminal position, sometimes bifurcate with lobes sometimes almost parallel, often in clusters and slightly to strongly upraised along the midline of thallus or loosely scattered, sometimes found on the same thallus as the female archegoniophore; *receptacle* naked; s*pores* saccate; proximal disc present.

Type: *Mannia androgyna* (L.) Evans

1. ***Mannia androgyna*** (L.) A. Evans, Chronica Botanica 4: 225. 1938

Basionym: *Marchantia androgyna* L. Species Plantarum ed. 1: 1138. 1753. Type citation: [Italy, Florence] 'Florentia non procul'; Type specimen: FI (herb. Micheli, n.v.) (Grolle 1968).

Synonym: *Cyathophora angustifolia* Gray. A Natural Arrangement of British Plants 1: 683. 1821. Type citation: [British Isles] 'on damp places'; Type specimen: n.v. (Grolle 1981,1983b).

Synonym: *Grimaldia dichotoma* Raddi nom. illeg. (GROLLE 1968, 1976) (Isotype E-11693).

Synonym: *Grimaldia capensis* Steph., Species Hepaticarum 1: 90. 1898. **syn. nov.** Type citation: 'Transvaal, Bloemfontein (Rehmann)'; Type specimen: [South Africa] Bloemfontein, s.d., *Rehmann* 144 (G, holotype, fide Perold (1994a), n.v.). **syn. nov.**

Synonym: *Mannia capensis* (Steph.) S. W. Arnell, Mitteilungen der Botanischen Staatssammlung München 16: 263. 1957.

Synonym: *Mannia capensis* var. *pallida* S. W. Arnell, Hepaticae of South Africa: 72. 1963. Type citation: 'Montagu, Cogmans Kloof'; Type specimen: [South Africa] Cogmans Kloof, 19.9.1951, *Arnell* 798 (BOL, lectotype selected here) **syn. nov.**

Description

Thalli forming large and closely intermingled patches, small, linear and narrow, leathery, dorsally bright green, becoming yellowish-brown or brown in older parts, strongly xeromorphic, sometimes fragrant; vegetative branches usually terminal, often dichotomous, with terminal or ventral innovations; lobes (1.6)3.2–14.4(15.1)mm long, (1.1)1.6–3.8(5.8)mm wide, if bearing archegoniophore then often becoming broader towards apex, margins dark purple or blackish, ventrally purplish-black when dry, margins usually completely inrolled, tubular and black; *lobe apex* rounded and middle often grooved; *thallus* in t.s. (0.2)0.3–0.5(0.6)mm thick, shape usually broadly concave, occasionally almost flat in section; *dorsal epidermis cells* (29)31.9–40.6(46.4)µm long, (11.6)13–29(33.4)µm broad, cell walls of dorsal epidermis rather thick-walled, showing corner thickenings (trigones) when focusing; *air pores* slightly raised, (8.7)11.6–24.7(29)µm in diameter, with 2(–3) concentric rings of cells, outer ring of (6)7–8 cells, cells (11.6)17.4–37.7(43.5)µm long, (8.7)10.15–20.3(23.2)µm wide, inner ring of 6–7 cells, (11.6)14.4–26.1(34.5)µm long, (5.8)8.7–14.5(17.4)µm wide, pore visible with hand-lens, of whitish colour; *assimilation tissue* spongy, irregular, (37.7)57.5–150(184)µm high in t.s., with small air chambers, in several layers (can be as thick as basal tissue); *basal tissue* (149.5)180–300(322)µm high in t.s., with many to only a few bright-coloured oil-bodies (very rarely a few dark-coloured oil-bodies) mainly in centre of basal tissue.

Rhizoids arising from ventral epidermis, smooth or pegged.

Ventral scales in two rows, overlapping each other and midline of thallus, purple, overlapping lobe apex and lobe margin and folding slightly upwards over edge of thallus, purple with sometimes paler margins, (0.6)0.8–1.2(1.3)mm long, (0.4)0.5–0.9(1.1)mm broad, elongate-semicircular, small slime papillae present, which easily break off, *oil cells* from base upwards, occasionally in appendages, only marginal, 7–34, in t.s. (14.5)17–38(47)µm; *appendages* 1–2(3), purple, (0.13)0.31–0.66(0.84)µm long, (0.06)0.07–0.2(0.26)µm broad, subulate or sometimes lingulate, gradually narrowing in acute tip.

Sexual condition dorsal-autoicous with androecia borne on main, sometimes also archegoniophore-bearing thallus, and occasionally *female-ventral-autoicous* with androecia situated on main thallus with archegoniophore on ventral side branch.

Androecia sessile, usually several, dorsal along midline of thallus or in terminal position, sometimes bifurcate with lobes sometimes almost parallel; ostioles ±conical, often in clusters and slightly to strongly upraised along the mid-line of thallus or loosely aggregated (scattered), green when young, gradually becoming purplish-black when mature.

Gynoecia with archegoniophores usually borne terminal, sometimes borne on reduced ventral heart-shaped branches or on a terminal innovation, surrounded by scales; *receptacle* hemispherical, warty, yellowish-green when young, mature turning into green and often tarnishing purple at margins, *stalk* brownish green, sometimes purple at base or higher up, 0.5–0.7(0.8)mm in diameter, irregularly triangular-ovate in t. s., low ridged when dry, very variable in length, (4.1)5.5–22.5(24)mm long, with single rhizoidal furrow, in t.s. with one outer row of brown smaller cells and inner cells bigger, yellowish, incrassate with corners quite thickened; *receptacle* bearing 3–4 sporophytes; *capsule* black when mature, yellow when young, lid irregularly rounded, 0.7–1.1mm in diameter, annular thickenings absent, cells (14.5)20–58(64)µm long, (11.6)20.3–37.7(40.6)µm broad, rounded to rectangular, with corner thickenings, overlapping each other.

Spores type I, yellow or brown to reddish-brown, (55.1)60.9–95.7(97.75)µm in diameter (LM), (60)63–86.1(87.2)µm in diameter (SEM); trilete; with dissimilar sculpturing on proximal and distal surface; distally saccate (with 8–13 sacs; and 3–6 sacs across); sacs large, rounded or ellipsoid, on surface minutely papillate with pits; on proximal side with small areolae in centre of disc; proximal disc present, triangular or flowerlike shape; equatorial apertures conspicuous, typically three or sometimes some doubled up to six; equatorial rim conspicuous, margins triangular or undulate to sinuate.

Elaters yellowish-brownish, smooth or rough, (182)237.8–281.3(319)µm long, (7.25)8.7–11.6(14.5)µm broad at middle, 5.8–7.25(8.7)µm broad at tip, 2–3-spiral.

Chromosome number *not known.*

Illustrations (Fig. 4.2, 4.3)

Distribution (Fig. 4.4)

The distribution of *Mannia androgyna* is based on confirmed herbarium specimens from Italy, Portugal, Spain, Austria, Switzerland, Madeira, Canary Islands, Azores, Cape Verde Islands, France, Croatia, Montenegro, Greece, Turkey, Cyprus, Albania, Algeria, Tanzania, Namibia, South Africa and Zimbabwe. It is a Mediterranean and African species.

Based on literature reports it is additionally reported from Bulgaria (PETROV 1975); former Yugoslavia (PAVLETIĆ 1955); Corsica, Sardinia, Sicily, former Yugoslavia, Lebanon, Israel, Egypt, Tunisia, Morocco (BISCHLER & JOVET-AST 1973); Tunisia (BISCHLER & JOVET-AST 1971); India (West Himalaya, Punjab),

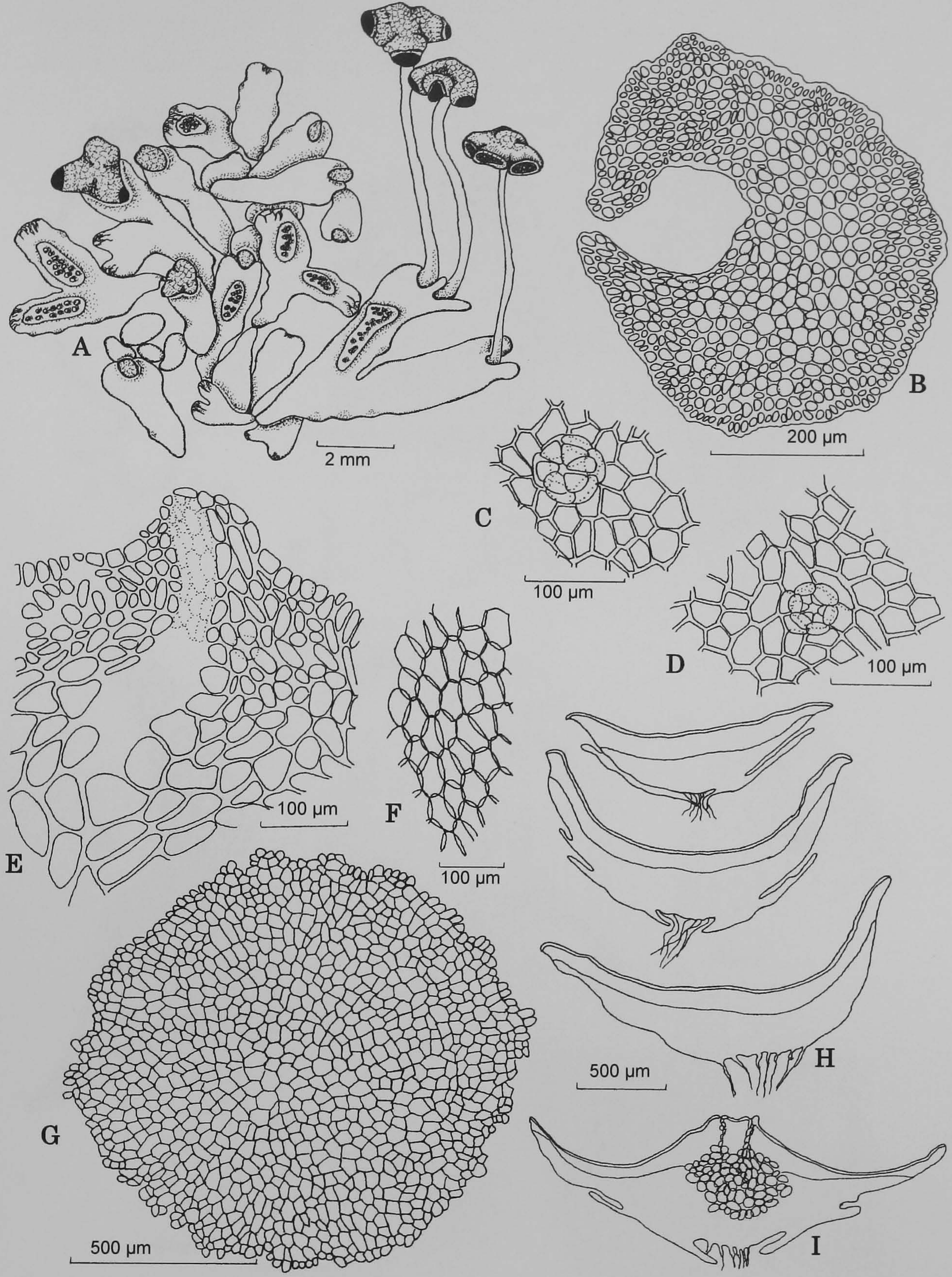


Fig. 4.2. *Mannia androgyna* (1). A thallus showing androecium and archegoniophore; B transverse section of stalk; C air pore of receptacle, dorsal view; D air pore of receptacle, ventral view; E transverse section of antheridium; F cells of capsule wall; G capsule lid; H transverse section of thallus; I transverse section of thallus showing androecium. A–I Portugal, *Schill & Lobo 36* (E).

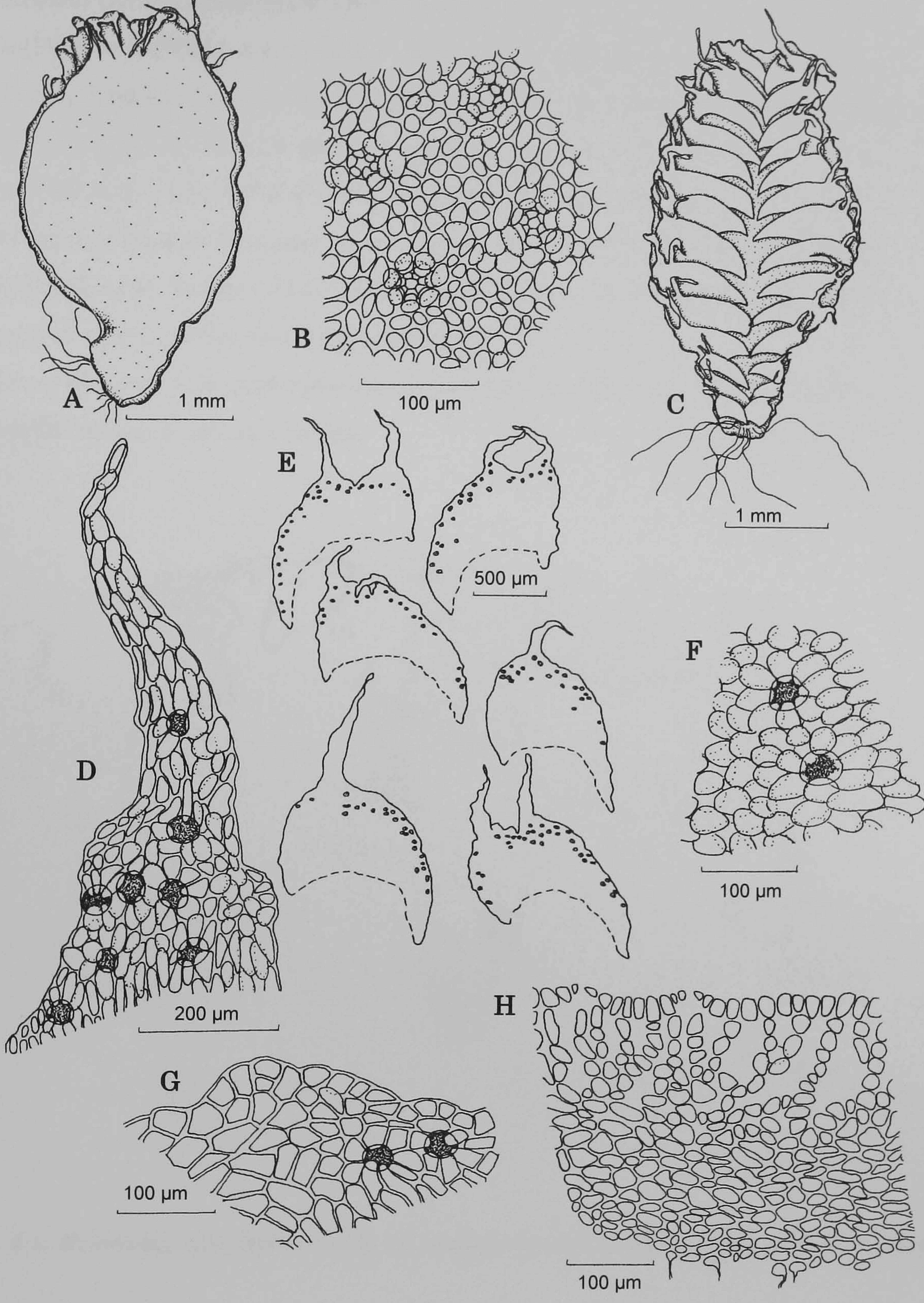


Fig. 4.3. *Mannia androgyna* (2). A thallus, dorsal view; B air pores from ventral epidermis of thallus; C thallus, ventral view; D ventral scale appendage; E, F ventral scales showing oil cells; G ventral scale, margin; H transverse section of thallus. A–H Portugal, *Schill & Lobos 36* (E).

Pakistan, Germany, Ethiopia, Caucasus (KACHROO, BAPNA & DHAR 1977); Arabian Peninsula and Socotra (Saudi-Arabia, Yemen Republic, United Arab Emirates) (KÜRSCHNER 2000, 2001); Yemen (AL-GIFRI & KÜRSCHNER 1996); Israel (FREY & KÜRSCHNER 1991); Austria (GAMS1938); Baleares, Corsica, Sardinia, Yugoslovia, Bosnia, Romania, Bulgaria, N Africa, NE Tropical Africa, Transcaucasus, W Asia, Arabian Peninsula, Indian subcontinent (SÖDERSTRÖM,URMI & VÁÑA 2002); Balearic Islands, Bulgaria, Caucasus (Russian part only), Romania, Sardinia, Sicily (SCHUMACKER & VÁÑA 2000, 2005); Ethiopia, Eritrea (GOLA 1914, WIGGINGTON 2004); Chad, Cape Verde Islands (ARNELL 1961, WIGGINGTON 2004).

Former records of *M. androgyna* from the Arabian Peninsula (LONG 1987) actually belong to *M. californica*.

Fig. 4.4. Worldwide distribution of *M. androgyna* based on herbarium material studied

Ecology

Mannia androgyna is a strongly xeromorphic species and well adapted to dry conditions and is hence found in more exposed sites. It likes mediterranean to temperate climates (BISCHLER 2004). It is found on cliffs, rocky slopes (sometimes near the sea), valley slopes, earthy ledges, stream banks, old dry walls, cultivation terraces and sometimes in open pine forests. It grows on soil and soil-covered rock (limestone and granite).

It has a typical S- or SW-exposure and is rarely N-exposed.

Altitude: c. 20– 1400m in Europe and Macaronesia, (457)1407–1910m in Southern Africa.

Taxonomic Notes

Mannia androgyna has a thick and leathery thallus very similar to that of *M. fragrans* and *M. californica*. In cross section it has compact assimilation tissue with only small air chambers in comparison to the loose assimilation tissue of *M. fragrans* with big air chambers. The sexual condition in *M. fragrans* is dioicous whereas *M. androgyna* is dorsal-autoicous.

It further differs from *M. fragrans* in having a naked receptacle and purple ventral scale appendages. A few appendages often overlap the lobe apex but the lobe apex is not bearded as in *M. fragrans.* The slime papillae in *M. androgyna* are more delicate than in *M. fragrans* and fall off quite easily.

When sterile, *M. androgyna* is quite difficult to distinguish from *M. californica.* The colour of the oil-bodies in assimilation and storage tissues is a quite reliable character for distinguishing these two species. In *M. androgyna* the oil-bodies usually have a pale colour whereas in *M. californica* there are several dark-brown oil-bodies present. Of about 300 observed herbarium specimens only two specimens of *Mannia androgyna* (Canary Islands, C.C. Townsend 78/188 (E) and France, Frere Heribaud-Joseph, (BM-72508)) had a few dark coloured oil-bodies while the spores of these specimens were clearly saccate. Both species are dorsal autoicous with antheridial chambers situated in clusters, which can be slightly to strongly upraised or more scattered along the midline of the thallus.

Mannia androgyna usually has the archegoniophores in a terminal position and in *M. californica* they are usually found on reduced heart-shaped ventro-lateral branches, although in both species both positions can be found.

Occasionally in *Mannia androgyna* the antheridia are positioned on the same thallus as the archegoniophores; this has not been observed in *M. californica.*

In the fertile condition the spores are a reliable character for diagnosis- they can be observed under a light microscope with high magnification. The spores in *M.*

androgyna are saccate whereas in *M. californica* they are ridged to areolate. However, if spores are immature or collapsed, diagnosis can be difficult.

A specimen from Madeira (*Schill* 11, E) was found to be fragrant but with a smell unlike that of *M. fragrans*. There are also notes indicating an aromatic smell for some specimens collected in Namibia by Volk, *'duftend'* (*Volk* 685, JE) and *'wohlriechend'* (*Volk* 862, JE).

Spores can be either of yellow or brownish colour and both colours can often be found together in one single collection though one colour is often dominant. The Madeiran specimens are predominantly found to be yellow whereas the spores in the African specimens are of brownish colour.

The proximal disc of the spores can sometimes show variations. It has either a triangular rounded shape as observed on some specimens from Switzerland, Canary Islands, Madeira, Tanzania and Namibia or a flower-like shape (Turkey, Italy or Cyprus).

Spores are ripe in Macaronesia in January, in Africa from March to June, in Europe from February to June.

Nomenclatural Notes

Southern Africa was formerly assumed to have only one (endemic) *Mannia* species, *Mannia capensis* (PEROLD 1994a, ARNELL 1963). In North Africa *Mannia* records were mainly accredited to *M. androgyna* (BISCHLER & JOVET-AST 1971, SÖDERSTRÖM, URMI & VÁŇA 2002). In Zimbabwe, collected *Mannia* specimens were identified as cf. *capensis* (BEST 1990) or in Ethiopia and Eritrea as *Grimaldia dichotoma* (a synonym of *M. androgyna*) (GOLA 1914).

Through study of herbarium material it became apparent that African specimens could be clearly divided into two distinct species based on morphology, particularly spore ornamentation:

A) *Mannia capensis* which is conspecific with *Mannia androgyna*, and

B) African collections identified as *Mannia capensis* clearly consist of two distinct species, *M. androgyna* and *M. californica*.

In the literature possible synonymy of *M. capensis* with *M. androgyna* has already been discussed by PEROLD (1994a) following a personal comment from Grolle that they might be identical. However, she found it *'difficult to come to a*

definite decision' about it because of the only very limited number of *M. androgyna* specimens she had available for study.
PEROLD (1994a) considers *M. capensis* as dioicous and only rarely monoicous, which is in contrast to the present treatment. A reason for this could be that in the specimens of *M. capensis* she observed the antheridia disappear before maturation of the archegoniophores. However, in the specimen collected by *Volk* 828 (JE) (listed by her under *M. capensis* specimens examined) a dichotomous thallus could be observed which bears antheridia and an archegoniophore at the same time.

ARNELL (1963) described a variety of *M. capensis* from Cogmans Kloof based on spore colour. He called the variety *pallida*, with reference to the pale yellow colour of the spores (*'sulphuric yellow'*). PEROLD (1994a) did not accept it as a variety in her treatment of Southern African *Mannia* and attributed it in her SEM study to the fact that the spores were only immature. She also emphasised a note by Garside (*Arnell* 798, BOL-54675), who saw Arnell's preparation and stated that the spores were immature. In some cases the yellow spore colour might be attributed to immaturity but in some specimens a mixture of brown and yellow spores can sometimes be found together. The specimen *Bosman 199* from Pretoria (NY) has yellow spores, which under the SEM looked mature. In the African specimens the brown spore colour dominates but in European specimens the yellow spore colour is found more frequently. This could be due to the generally higher altitude of the African localities in comparison to the European and Macaronesian localities, and hence be an adaptation to higher light intensity.

ARNELL (1963) did not designate a type for his new variety *'pallida'*. In the 'Hepaticae of South Africa' he refered to the locality 'Montagu, Cogmans Kloof' but did not give any information on date or on which specimen he based his new variety. His own collections deposited in the Bolus Herbarium (BOL) and the Pretoria National Herbarium (PRE), both in South Africa, were therefore borrowed in order to select a lectotype.
The specimen *Arnell* 798 (BOL-54675 and BOL-54727), here chosen as lectotype, had a note on the packet saying 'spec.nov.'. S. Garside notes in the packet:

'This is not a "new species" Dr S. Arnell, thought it'll be so because spores are bright yellow, but they proved to be merely immature. The bullae of the spore coat were also open at apex- perhaps by mounting in glycerine, they have burst. I saw Dr Arnell's preparation (at Sea Point where he stayed). S.G.'
The specimens show immature archegoniophores but no spores could be found. The specimen BOL-54675 is mostly *Exormotheca pustulosa* as noted by S. Perold on the packet and the duplicate BOL- 54727 is also intermixed with *Targionia hypophylla.*

The type specimen of *Marchantia androgyna* was not available for study; however it was studied by GROLLE (1968) who cited it as 'lectotype'.

Section *Arnelliella* (C. Massal.) Schill **stat. nov.**

Basionym: *Arnelliella* C. Massal., Atti del Reale Veneto di Scienze, Lettere ed Arti 73(2): 927. 1914. Type: *Arnellilla sibirica* Müll.Frib.
Synonym: *Neesiella* subgenus *Arnelliella* (C. Massal.) C. Massal., Atti del Reale Veneto di Scienze, Lettere ed Arti 73(2): 927. 1914. **nom. inval.** (Art. 34, 2) (Grolle 1976).
Mannia subgenus *Arnelliella* (C.Massal.) Grolle, Feddes Repertorium 87(3–4): 245. 1976.
Mannia subgenus *Mannia* sensu Grolle, Journal of Bryology 12: 405. 1983.
Type: *Mannia sibirica* (K. Müll.) Frye & L.Clark

Description

Thallus apex bearded or not bearded; *sexual condition* dorsal-autoicous or terminal-autoicous; *antheridia* conspicuous, scattered dorsally along midline of main thallus or in clusters, which can be slightly or strongly upraised or inconspicuous, forming a poorly defined, slightly upraised rounded cushion or terminal slight depression or notch; receptacle bearded or naked; s*pores* regularly areolate or ridged; proximal disc present.

2. ***Mannia sibirica*** (Müll.Frib.) Frye & L.Clark, *University of Washington Publications in Biology* 6: 66. 1937.

Basionym: *Grimaldia pilosa* var. *sibirica* Müll.Frib., Rabenhorsts Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, Auflage 2, 6(1): 265. 1907. Type citation: ‚Sibirien, Zwischen Krasnojarsk und Jeniseik beim Dorfe Makokovo (1876 Arnell)! Original!'; Type specimen: Sibirien, Jenisei, inter Krasnojarsk, Jenisseisk prope pagum Makokovo, 18.6.1876, H. W. Arnell; (S, Holotype (B24528) and isotypes (B24526, B24527); JE, isotype (H1306)).

Synonym: *Grimaldia sibirica* (Müll.Frib.) Müll.Frib., Rabenhorsts Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, Auflage 2, 6: 721. 1916.

Synonym: *Neesiella sibirica* (Müll.Frib.) C.Massal., Atti del Reale Veneto di Scienze, Lettere ed Arti 73: 928. 1914.

Synonym: *Arnelliella sibirica* (Müll.Frib.) C.Massal., Atti del Reale Veneto di Scienze, Lettere ed Arti 73(2): 927. 1914.

Description

Thalli spreading and forming extensive patches, small, narrow and flat, rather leathery, thin to delicate, dorsally green, occasionally purplish, areolae usually not visible, in older parts becoming brown when disintegrating, xeromorphic; vegetative branches of terminal dichotomies or with terminal and occasionally ventral innovations; lobes (2.4)3.5– 12.6(14.7)mm long, (0.4)1.1– 2.1(3.9)mm wide, margins dark purple or green, sometimes undulate; ventrally green or purple, when dry, margins slightly to strongly inrolled, tubular and black or not strongly inrolled; *lobe apex* rounded and middle often grooved;
thallus in t.s. (127.5)322–586.5(690)µm thick, shape usually flat or concave to triangular in section; *dorsal epidermis cells* (17.4)20.3–31.9(34.8)µm long, (11.6)13.05–26.1(31.9)µm broad, cell walls of dorsal epidermis rather thick-walled, showing corner thickenings (trigones) when focusing; *air pores* (8.7)11.6–23.2(29)µm in diameter, with 2(3) concentric rings of cells, outer ring of (5)6–7(8) cells, cells (14.5)17.4–31.9(40.6)µm long, (11.6)14.5–20.3 (29)µm wide, inner ring of 6–7(8) cells, (8.7)11.6–17.4(23.2)µm long, (8.7)11.6–14.5(17.4)µm wide, pores

visible with hand-lens, of whitish colour; *assimilation tissue* rather loose to sometimes slightly compact, as big as or up to 2 times the size of those of basal tissue, air chambers 2–3(4) in t.s., somewhat rounded, often subdivided, (126.5)149–276(403)µm high in t. s.; *basal tissue* (126.5)172–310.5(380) µm high in t. s., with inconspicuous yellowish grey or occasionally brownish oil cells in assimilation and storage tissue.

Rhizoids arising from ventral epidermis, smooth or pegged, hyaline or purplish/brownish towards base.

Ventral scales in two rows, sometimes only sparse, overlapping each other and midline of thallus, purple with sometimes paler margins, (0.6)0.7–1.6(1.8)mm long, (0.08)0.4–1.0(1.2)mm broad, oblong semicircular, small slime papillae present on margin, *oil cells* (3)6–16(22), often marginal, not present in appendages; *appendages* 1(–2), occasionally unequally bifid, (0.1)0.2–0.5(0.7)mm long, (0.01)0.05–0.2(0.3)mm, subulate, margins irregularly serrate, gradually narrowing into acute tip, overlapping mainly lobe apex and only rarely lobe margin and folding upwards over edge of thallus.

Sexual condition terminal-autoicous with androecia and gynoecia often borne on equally long or shorter dichotomous branch of a thallus or androecia situated on sometimes shorter branch of a dichotomy, of which the other dichotomous branch bears an archegoniophore; most fertile branches bearing both sexes or occasionally only one.

Androecia inconspicuous or forming a poorly defined, slightly upraised rounded cushion or terminal slight depression or notch with purplish ostioles, usually several ostioles per cushion.

Gynoecia with archegoniophores deriving from terminal notch of mid-thallus or occasionally ventral branch of thallus, surrounded by whitish bleached scales; *receptacle* hemispherical, nodular/warty, usually conspicuously bearded, sometimes only inconspicuously (e. g. *Schuster* 18009), yellowish-green when young, when mature turning green and often tarnishing purple at margins; *stalk* brownish green, sometimes brownish at base or below receptacle, 0.3–0.5(0.6) mm in diameter, irregularly triangular-ovate, ridged when dry, variable in length, (4.6)7.3–17.9(21.4) mm long, with single rhizoidal furrow, in t.s. one outer brown smaller strongly incrassate thick-walled cell row and inner cells thin-walled, bigger, colourless, incrassate with minute to convex trigones; *receptacle* bearing mostly (1)2–3 capsules; *sporophytes/capsules*, capsule black when mature, yellow when young, cells yellowish brown, irregularly hexagonal, incrassate with minute trigones; lid irregularly rounded, (0.7)0.8–1(1.2) mm in diameter annular thickenings absent, cells incrassate, irregular hexagonal or rounded to rectangular, often strongly overlapping each other.

Spores type II, yellow to yellowish brown, (34.5)37.7–55.1(58) μm in diameter (LM), 43.1–56.5(62) μm in diameter (SEM); trilete; with dissimilar sculpturing on proximal and distal surfaces; distally irregularly areolate sometimes with short ridges, 6–9 areolae across, on surface minutely papillate; on proximal side with small areolae in centre of disc; proximal disc present, equatorial apertures conspicuous, usually three; equatorial rim conspicuous.

Elaters yellow to brownish yellow, (255)284–365.4(411.8) μm long, 8.7–11.6(14.5) μm broad at middle, 5.8–8.7 μm broad at tip, 2–3-spiral.

Chromosome number unknown.

Illustrations (Fig. 4.5)

Distribution (Fig. 4.6)

The distribution of *Mannia sibirica* based on confirmed herbarium specimens is S-Norway, Finland, Russia (Siberia), U.S. (Iowa, Minnesota, Michigan, Arctic Alaska), Canada.

Based on literature it is also reported from N-Norway (SCHUSTER 1958); Greenland (SJÖDIN 1980); China (GAO & ZHANG 1981); Intramongolia (XUELIANG & ZUNTIAN 1996); Turkey, China, Subarctic America (SÖDERSTRÖM, URMI & VÁÑA 2002); Russian Arctic (KONSTANTINOVA, N. A. & A. D. POTEMKIN 1996) and Estonia (INGERPUU & VELLAK 2000a, b).

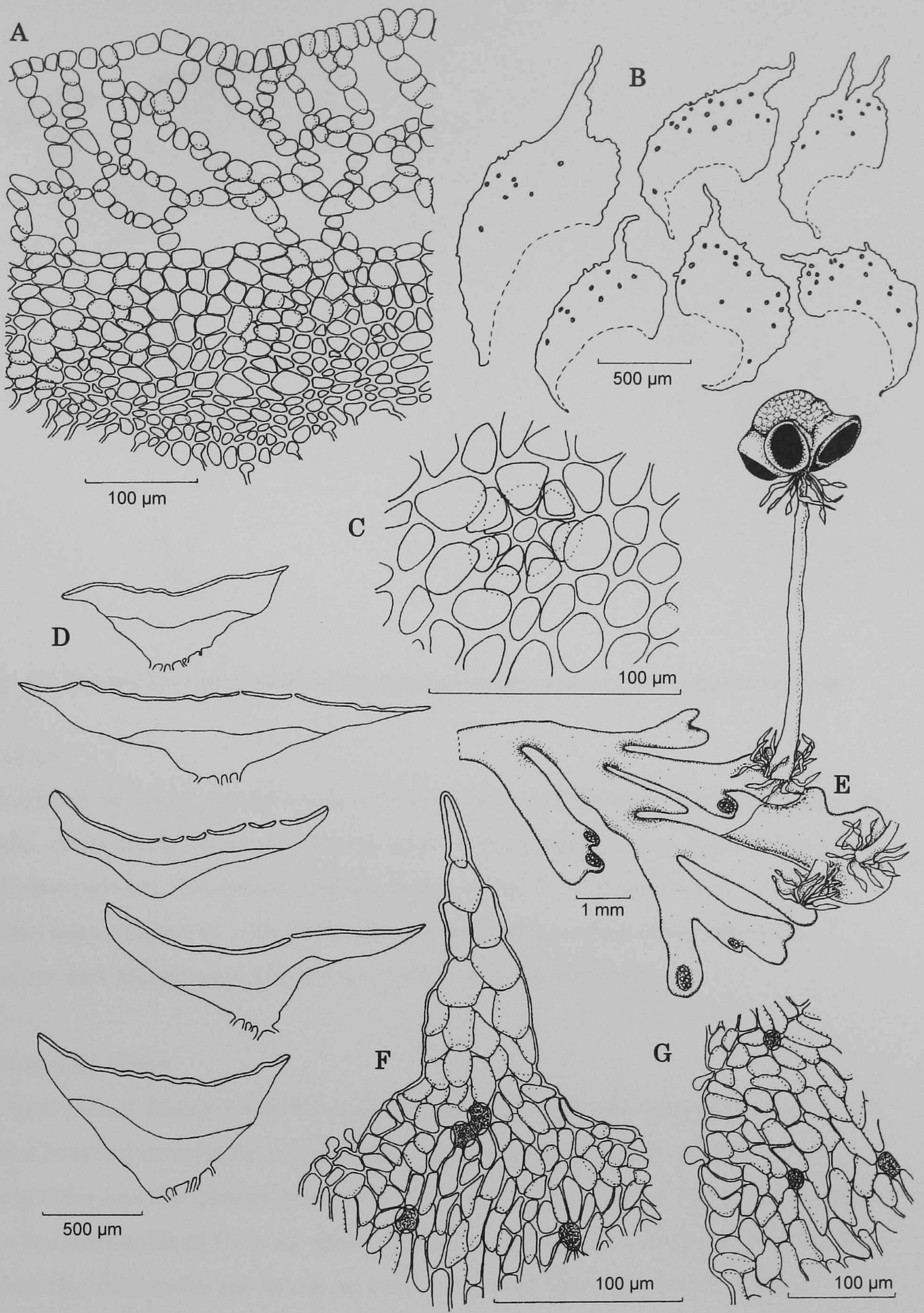


Fig. 4.5. ***Mannia sibirica***. A, D transverse section of thallus; B ventral scales showing oil cells; C air pores from ventral epidermis of thallus; E thallus showing androecium and archegoniophore; F ventral scale appendage; G ventral scale, margin. A, C–E Minnesota, *Schuster* 18009 (NY); B, F, G Minnesota, *Schuster* 18136 (F).

Fig. 4.6. Worldwide distribution of *M. sibirica* based on herbarium material studied

Ecology

M. sibirica is found in calcareous rock crevices and ledges, on cliffs and bluffs, on walls, often along rivers and occasionally in wet tundra where it grows on soil or soil-covered rock (limestone and sandstone) with E- or S-exposure.
It has been classed as a probably threatened species of unknown status in Europe and Macaronesia (SCHUMACKER & VÁŇA 2000, 2005).

Taxonomic Notes

At first glance *Mannia sibirica* could be confused with *Mannia pilosa*, which also has a bearded receptacle. They can be easily separated by the position of the antheridia and the generally smaller spore size in *M. sibirica*. In fact *M. sibirica* can be distinguished from all other *Mannia* species by its smaller spores. In *M. pilosa* the antheridia are borne on reduced heart-shaped ventral branches whereas in *M. sibirica* the antheridia are borne terminally on the main thallus. The thalli in *M. sibirica* do not get strongly lacunose and white with spore maturity, the assimilation tissue does not consist of big air-chambers and is rather intermediate. Furthermore the ventral scales in *M. sibirica* contain several oil-bodies whereas in *M. pilosa* oil-bodies are usually absent or sparse. For differentiation from *M. triandra* see Taxonomic Notes under that species. In Canada and Arctic Alaska the spores mature in June and July; in other parts of the U.S., Finland, Norway and Siberia spores mature in May and June.

Mannia sibirica was first described by K. Müller as a variety of *Mannia pilosa*. Its taxonomic status has often been regarded as doubtful and MÅRTENSSON (1955) and SCHUSTER (1953) considered it to be conspecific with *M. pilosa* whereas other authors only pointed out a close resemblance between the two species (MÜLLER 1954, SCHUSTER & DAMSHOLT 1974, DAMSHOLT 2002). According to SCHUSTER & DAMSHOLT (1974) *'there is no absolute way in which we can separate M. sibirica from M. pilosa in the field'.* In fact both authors confused *M. sibirica* in separate later publications with either *M. pilosa* or *M. fragrans*. In his book 'The hepaticae and anthocerotae of North America' SCHUSTER (1992b) shows on page 216 an illustration of *M. pilosa*, which is in fact *M. sibirica* clearly identifiable from the shown sexual condition, the antheridia being in a terminal position on the main thallus typical for *M. sibirica*. Schuster does not specify which specimen has been used for the illustration but only says *'from plants from Lake City, Minnesota, May 14, 1947'.*

In the book on 'The illustrated flora of Nordic liverworts and hornworts' by DAMSHOLT (2002) *M. sibirica* was mistaken for *M. fragrans*. Illustrating *'M. fragrans'*, the thallus, receptacle and spores of *M. sibirica* are shown. The specimen observed has been cited from Finland, collected by T. Laine. The morphological characters, in particular the sexual condition in combination with the spore ornamentation pattern clearly identify the illustrations as *M. sibirica*. The extensive morphological study on these two species in combination with results from the SEM, leave no doubt about the valid status of *M. sibirica*.

3. ***Mannia californica*** (Gottsche ex Underw.) L.C.Wheeler, Bryologist 37: 88. "1934" 1935.

Basionym: *Grimaldia californica* Gottsche ex Underw., Botanical Gazette 13: 114. 1888. Type citation: 'Yosemite valley, California, on rocks in the spray of Bridal Veil Fall, June, 1866, Bolander'; Type specimen: Yosemite

Valley, Cal., vi 1866, H.N. Bolander (Holotype, NY-575639 with slide 575641, isotypes, NY- 575640, NY- 575648, NY-575647 with slides 575642 to 575646).

Synonym: *Grimaldia indica* Steph. ex Kashyap, Journal Bombay Natural History Society 24(2): 345. 1916. Type citation: 'occurs in Mussoorie, Pathankote, rarely in Lahore in winter along the river bank'; Type specimen: n.v.. **syn. nov.**

Synonym: *Mannia indica* Kachroo, Journal of the Hattori Botanical Laboratory 12: 34. 1954. **nom. inval.** (Art. 33.2)

Synonym: *Mannia levigata* Shimizu & S.Hatt., Journal of the Hattori Botanical Laboratory 10: 49. 1953. Type citation: 'Rock crevices in exposed places, 750 m alt., Kaminakao, Chichibu, Saitama Prefecture, September 2, 1952, coll. D. Shimizu'; Type specimen: Japan, Saitama Prefecture: Chichibu Ootakimula, Kamimakao, ca. 750 m, 2 ix 1952, D. Shimizu 52818 (holotype in NICH). **syn. nov.**

Synonym: *Mannia foreaui* Udar & Chandra, Bryologist 67: 55, 1964. **nom. inval.** (Art. 36.1) ex Udar & Chandra, Canadian Journal of Botany 43: 148. 1965. Type citation: [South India] 'on slopes and rocks in xerophytic habitat in Kodaikanal; Beruliar: Coll. Vinod Chandra and Satish Chandra. September, 1962'; Type specimen: South India, Railway track, near Beruliar Rl. St. [Railway Station], 1.9.62, S. & V. Chandra (holotype B5745 and isotypes B5746–B5748, LWG). **syn. nov.**

Description

Thalli forming large and closely interwoven patches/mats, small, linear and narrow, leathery, dorsally bright green to purplish, becoming purplish brown or greyish in older parts, strongly xeromorphic; vegetative branches mostly terminal dichotomous and sometimes ventrally; lobes (4.1)5.1–14.7(17.9) mm long, (1.1)1.6–3.2(4) mm wide, margins wide, dark purple to blackish; ventrally purplish-black, when dry, margins usually completely inrolled, tubular and black or slightly inrolled with thallus surface visible; *lobe apex* rounded or middle often grooved; *thallus* in t.s. (0.4)0.5–0.8 (0.9) µm thick, shape usually concave to triangular in section; *dorsal epidermis cells* (17.4)20.3–34.8(37.7)µm long, (8.7)11.6–20.3(23.2)µm broad, cell wall of dorsal epidermis rather thick-walled, showing corner thickenings (trigones) when focusing, *air pores* slightly raised, (8.7)11.6–23.2(32) µm in diameter, with 2–3 concentric rings of cells, outer ring of (6)7–9 cells, cells (11.6)17.4–26.1(34.8) µm long, (8.7)11.6–20.3(34.8) µm wide, inner ring of (6)7(8) cells, 11.6–17.4(20.3) µm long, (5.8)8.7–11.6 µm wide, pore visible with hand-lens, of whitish colour, *assimilation tissue* spongy, irregular, 0.1–0.4(0.5) mm high in t.s., generally smaller than basal tissue, with small air chambers, in several layers; *basal tissue* 0.2–0.6(0.7) mm high in t.s., usually with several dark brown oil-bodies.

Rhizoids arising from ventral epidermis, smooth and pegged.

Ventral scales in two rows, overlapping each other and midline of thallus, purple with sometimes paler margins, (0.8)0.9–1.6(1.8) mm long, (0.5)0.6–1.2(1.4) mm broad, semicircular to oblong semicircular, small slime papillae present on margins, *oil cells* abundant, 6–22, from base up to tip, predominantly marginal but also in middle and at base of appendage; *appendages* 1 –2, (0.1)0.2–0.7(0.9)mm long, (0.08)0.1–0.4mm broad, broadly subulate with irregularly sinuate margins, with broad to very broad base, overlapping mainly lobe apex.

Sexual condition female-ventral-autoicous with androecia commonly situated dorsally on main thallus and archegoniophore usually on heart-shaped or rounded reduced ventral branches, arising from narrow stipitate base from ventral side of thallus or rarely *dorsal-autoicous* with androecia on main thallus bearing archegoniophore.

Androecia sessile, usually several, scattered dorsally along midline of main thallus or in clusters, which can be slightly or strongly upraised, sometimes found terminally (Indian specimen); ostioles ±conical, green when young, gradually becoming purplish-black when mature, 218.5–345 µm high, surrounding thallus surface sometimes of purplish colour.

Gynoecia with archegoniophores deriving from terminal notch of main thallus or more often from typically small, heart-shaped ventral branch of often androecia bearing main thallus, surrounded by a few or tufts of long brownish or purplish scales; *receptacle* hemispherical, nodular/warty, yellowish-green when young, mature turning green and often tarnishing purple, naked or with only a few hyaline scales below; *stalk* brownish green, sometimes purple at base or higher up, with very few long hyaline scales, (0.5)0.6–0.9(1.0) mm in diameter, irregularly triangular-ovate, in t. s. low ridged when dry, (4.3)5.6–10.9(11.5) mm long, with single rhizoidal furrow, in t.s. one outer brown smaller cell row and inner cells bigger, yellowish-brownish, incrassate with corners quite thickened, receptacle bearing 1–4 *sporophytes,* capsule brown to brownish black when mature, yellow when young, cells yellowish brown, irregularly hexagonal, incrassate with minute trigones, lid irregularly rounded, 1.1–1.6(1.7) mm diameter, annular thickenings absent, cells rounded to rectangular, with corner thickenings, overlapping each other.

Spores type II, yellowish brown and reddish-brown (but predominantly brown (specimen Long 27577 has the two types on the same receptacle, (58)60.9–75.4(78.3) µm in diameter (LM), (52.5)58–73.8(76) µm in diameter (SEM); trilete; with dissimilar sculpturing on proximal and distal surfaces; distally with long irregularly joined, wavy ridges or more regularly ridged to sometimes areolate (Indian specimens), (3)5–6 ridges across, 5–8 areolae across, minutely papillate; on proximal side with small areolae; proximal disc present; equatorial apertures conspicuous, usually three; equatorial rim conspicuous.

Elaters yellowish to brownish, (156.5)220.4–322(365.9) µm long, 8.7–14.5 µm broad at middle, (4.3)5.8–8.7 µm broad at tip, 2–3-spiral, rough (with little granules or longish granules on surface) in yellow spores not as rough as in brown spores.

Chromosome number n=9 (for *M. levigata*) (FRITSCH 1991).

Illustrations (Fig. 4.7)

Distribution (Fig. 4.8)

The distribution of *Mannia californica* based on confirmed herbarium specimens from France, Austria, Namibia, Uganda, South Africa, Lesotho, India, Pakistan, Yemen, Lebanon, Japan, China, U.S.A. (Tennessee, Arizona, California, North Carolina, Texas).

Based on literature it has also been reported from Arkansas (SCHUSTER 1992b) and Utah (FLOWERS 1961). Former records of *M. androgyna* from the Arabian Peninsula (LONG 1987) actually belong to *M. californica.*

Mannia californica was formerly considered to be an endemic species restricted to the U.S.A. but has recently been found in France (HUGONNOT & SCHILL 2006).

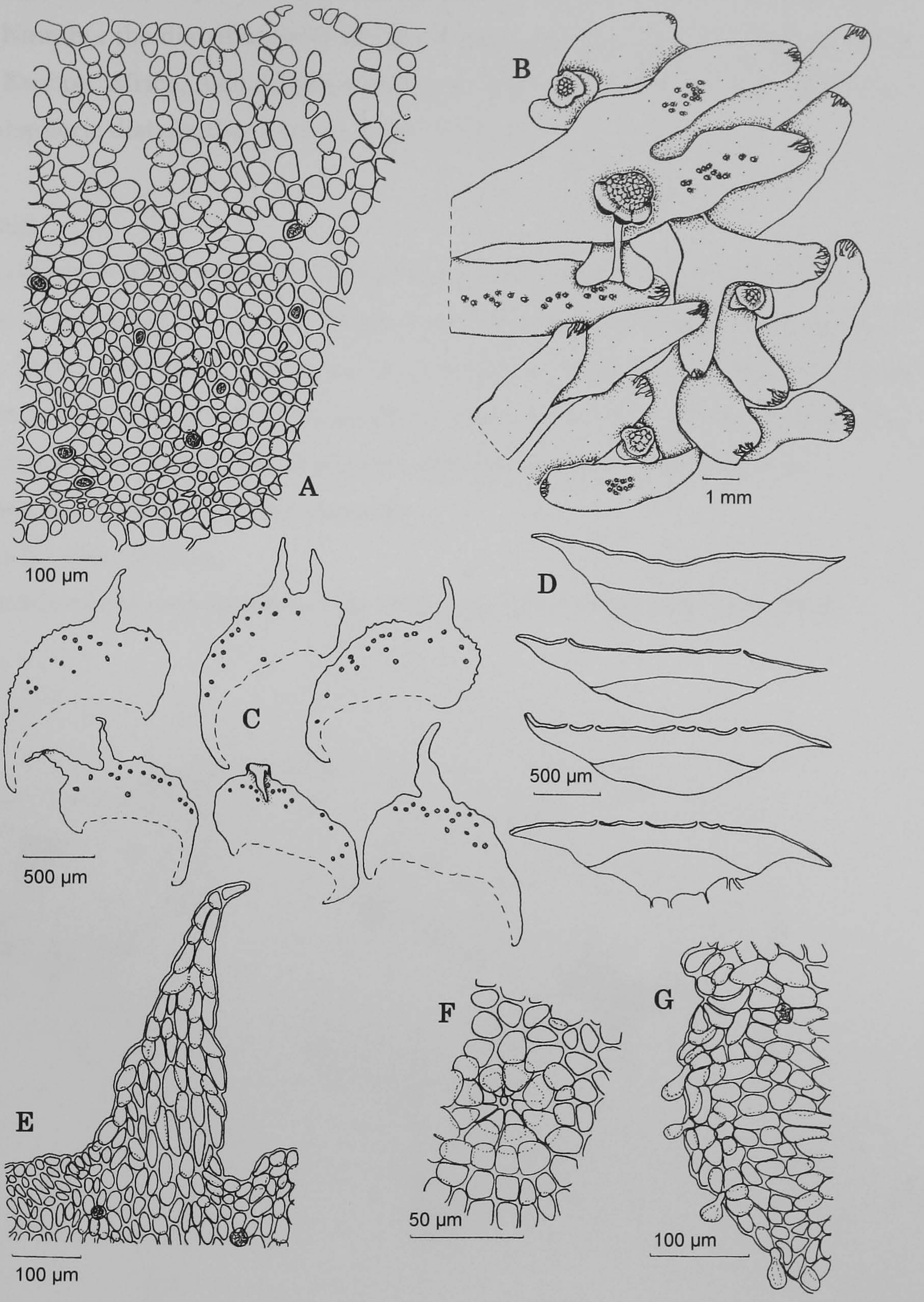


Fig. 4.7. *Mannia californica*. A, D transverse section of thallus; B thallus showing androecium and young archegoniophore; C ventral scales showing oil cells; E ventral scale appendage; F air pores from ventral epidermis of thallus; G ventral scale, margin. A, D–F California, *Schill & Clarke 102* (E); B, C, G California, *Long 27577* (E).

Through extensive spore ornamentation survey and field trips to Austria, India and Namibia the distribution of the plant has now been consideratelу expanded into Europe, Africa, Asia, China and Japan. The species has a mainly Northern Hemispheric distribution with outliers in Africa.

Ecology

M. californica is found either in moist and partly shaded places or strongly exposed and sunny localities, though having enough water supply during the year. This xeromorphic species is found on banks or ledges in valleys, often near rivers or waterfalls, in crevices, on cliffs and occasionally in gullies. It grows on both calcareous (sandstone, quartzite) and siliceous rock and rocky soil.

It often has an E or W facing exposure.

Altitude: 150– 3335 m.

M. californica is considered as rare in Europe (HUGONNOT & SCHILL 2006).

Fig. 4.8. Worldwide distribution of *M. californica* based on herbarium material studied

Taxonomic Notes

In the fertile condition, *Mannia californica* is easily identified by the position of the archegoniophores, which are typically and predominantly found on small heart-shaped side thalli deriving from the main (often male) thallus. The receptacle is not bearded but can sometimes have a few scales. The antheridial chambers in American material are found to be either dorsally scattered or in slightly to strongly prominent clusters. In the Indian specimen observed the antheridial chambers are more often found in slightly upraised clusters but also scattered antheridial chambers (particularly if only a few) are present. The appearance of the antheridial clusters might be dependent on environmental conditions such as the light intensity of the thallus or the number and proximity of the ostioles. Both conditions can sometimes be found on the same specimen.

In North America *Mannia californica* could be confused with the similar looking *Asterella bolanderi* when immature and without developed pseudoperianths, which also has the archegoniophores on ventral heart-shaped side branches. In *A. bolanderi* the antheridia are also found on small ventral side branches and not on the main thallus as is typical for *M. californica*. In the sterile condition *A. bolanderi* has a fishy smell and a paler green leathery thallus.

M. californica has a more pleasant aromatic smell and a very narrow and leathery bright green thallus. The large zone of storage tissue usually contains a high number of dark oil-bodies and the assimilation tissue is irregular, spongy and in several layers.

In the similar-looking *M. androgyna* (see under that species) the archegoniophores and antheridia are typically found together on the main thallus and there are only very few light oil-bodies in the thallus cross section. Through spores the two species can be easily kept apart. The spore colour in *M. californica* can be either yellowish or brownish, with sometimes both colours on a single specimen. Usually a brownish spore colour is found to predominate.

In the present revision a broad species concept has been adopted for *Mannia californica*. *M. californica* is probably a group of cryptic species, showing high sequence divergences in the molecular analysis without clear geographic entities (Chapter 5.7.3.5). However, different groups cannot be reliably distinguished from each other by morphological characters, so a further subdivision is not likely to contribute to an easier identification.

The synonyms do not show any notable morphological differences relating to the key characters such as the position of antheridia and gynoecia, naked receptacles, compact assimilation tissue and dark oil-bodies in thallus cross section.

There is however a variation in the distal ornamentation of the spores, which is more areolate in some Indian specimens (formerly *M. indica*) and French material than in the North American, Austrian, Japanese (formerly *M. levigata*) and S-Indian (formerly *M. foreaui*) material, which show ridges distally. The distal ridges in the Chinese specimens however shows intergradations to the former as well. They are fewer with a less denser spacing.

The Austrian specimen shows morphological variations from the other specimens but has distal ridges. Unfortunately only rather immature material from a single locality could be observed. In this specimen, both gynoecia and androecia were borne on the main thallus with sometimes the male branch extending its growth so the archegoniophore is situated on a shorter furcation of the thallus. Only one mature archegoniophore was seen, which had a bearded receptacle. In thallus cross section dark coloured oil bodies were present though.

In November 2004, recently-collected Indian material with immature archegoniophores was cultivated in a growth cabinet. The spores were observed under the SEM and it could be noted that the distal spore ornamentation in *Schill* 165 appeared rather ridged in December 2004 whereas in February 2005 the same sample had spores with areolate ornamentations. Hence a division based on one character, that seems to vary with maturity is not considered very useful.

Based on morphology no clear differences could be found between *M. californica* and the former *M. foreaui* and *M. indica*, nor the Chinese specimens.

Further morphological and molecular study using isozyme analyses or microsatellites and more widespread detailed sampling of populations would be necessary to elucidate the scale of cryptic speciation in *M. californica* and consider its possible separation into sibling species.

Nomenclatural Notes

The name *Grimaldia californica* was coined by Gottsche who sent a manuscript description in Latin to Underwood who published it in a footnote under his own new English description. It is however not a direct translation of Gottsche's. Therefore Underwood's description is considered to be the validating one and the author citation is Gottsche ex Underw.. The holotype in Underwood's herbarium (NY) is annotated *'comm. Dr. C. Gottsche July 1887'.* This species is localised *'Yosemite Valley, leg. Bolander, June 1866'.* A number of other specimens and preserved slides lack detail but are presumably isotypes.

Although Stephani coined the name *'Grimaldia indica'* there is no evidence that he wrote the validating description. This was almost certainly written by Kashyap. The specimen of this species studied and annotated by Stephani were from the herbarium of E.Levier. These were not cited by Kashyap and cannot be considered as types (as wrongly annotated by Grolle in 1972). Kashyap specimens have not been studied and a lectotype cannot therefore be selected. However the existence of specimens from Cawnpore and Saharanpur determined as *Grimaldia indica* by Stephani which match *Mannia californica* is good evidence that these can be treated as synonyms. Unfortunately no Kashyap specimen appears to have been deposited in Stephani's herbarium in G.

M. indica, *M. foreaui* and *M. levigata* are now considered synonyms of *Mannia californica*. The last is the oldest published in 1935 ('1934').

In literature R.M. Schuster considered *M. levigata* to be *'almost surely identical'* with *M. californica* (SCHUSTER 1992b) based on the drawing by SHIMIZU & HATTORI (1953b: plate VIII). He considered the spore ornamentation similar, pointed out that both species have rough elaters and considered that the thallus, ventral scales and archegoniophores were very similar.

The type locality of *M. foreaui* as given in the protologe is confusing in the sense that it actually cites two different localities in South India: Kodaikanal and Beruliar, which are hundreds of kilometres apart from each other. However, on the packet containing the holotype in the herbarium at Lucknow University it is only noted 'Beruliar' so that it can be concluded that 'Beruliar' and not 'Kodaikanal' is the type locality.

On a visit to the type locality in South India it became apparent that the place name has now changed to 'Barliaru' and that the former station has been closed down. Nevertheless when walking along the railway line three populations were refound.

Section *Sindonisce* (Corda) Grolle, Feddes Repertorium 87, Heft 3–4: 245. 1976.

<u>Basionym:</u> *Sindonisce* Corda in Opiz (ed.) Beiträge zur Naturgeschichte 12: 648. 1829.

<u>Type:</u> *Mannia fragrans* (Balbis) Frye & L.Clark

Description

Thallus apex bearded; *sexual condition* terminal- autoicous; *antheridia* rather conspicuous, borne terminally on separate (not archegoniophore-bearing) thallus, forming a defined triangular (sometimes rounded or elliptic) sometimes slightly upraised disc; *receptacle* bearded; *spores* regularly areolate; proximal disc absent.

4. *Mannia fragrans* (Balbis) Frye & L.Clark, University of Washington Publications in Biology 6: 62. 1937.

<u>Basionym</u>: *Marchantia fragrans* Balbis, Mémoires de l'Académie des Sciences Littérature et Beaux-arts de Turin. Sciences Physiques et Mathématiques 7: 76. "ann. 12". 1804. <u>Type citation</u>: 'Molineri l'avait déjà observée à Aoste dans une masure près de roche taillée'; <u>Type specimen:</u> Italien, det. Balbis (isotype in S-B36643).

<u>Synonym:</u> *Fimbriaria fragrans* (Balbis) Nees; Horae Physicae Berolinenses 45. 1820.

<u>Synonym:</u> *Sindonisce fragrans* Corda; In: Opiz (ed.) Beiträge zur Naturgeschichte 12: 648. 1829.

<u>Synonym:</u> *Grimaldia fragrans* (Balbis) Corda ex Nees; Naturgeschichte Europäischer Lebermoose 4: 225. 1838.

Synonym: *Duvalia fragrans* (Balbis) Lindb.; Notiser Sällskapets pro Fauna et Flora Fennica 9: 285. 1868.

Synonym: *Grimaldia barbifrons* Bisch.; Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum 17: 1028. 1835. Type citation: 'Habitat in regionibus montanis ad terram et super saxa; certo in Germaniae mediae pluribus locis occurrit. In ditione florae Heidelbergensis primo prope Schriesheim in valle Ludwigsthal ab amiciss. Al. Braun me comite autumno a. 1826 absque fructibus detecta, dein ab illo prope Weinheim in valle Birkenauer-Thal, serius a me quoque in valle urbis nostrae ad ripam Nicri dextram capitulis fructiferis onusta super rupes graniticas reperta, quibus omnibus locis in deiectu meridiem spectante crescit.'; Type specimen: n.v.

Synonym: *Pleurochiton balbisianum* Corda ex Nees, Naturgeschichte Europäischer Lebermoose 4: 225. 1838. Type citation: [patria ignota] 'fide iconis ad specimen Herbarii Brideliani, ab ipso Balbisio nomine Marchantiae fragrantis inscriptum, factae'; Type specimen: n.v..

Synonym: *Grimaldia inodora* Wallr., Linnaea 14: 686. 1840. Type citation: [Germany] 'An schroff abgedachten Bänken eines Gypshügels am südlichen Harze stellenweise sehr häufig'; Type specimen: n.v. **syn. nov.** Synonym: *Mannia fragrans* var. *inodora* (Wallr.) Hampe; Flora Hercynica, Halle: 373. 1873.

Synonym: *Mannia brachypoda* Shimizu & S.Hatt.; Journal of the Hattori Botanical Laboratory 9: 32. 1953. Type citation: 'on rock crevices, stone walls and on soil, 700–800 m alt., Tochimoto, Chichibu Mts., Saitama Prefecture, Sept. 9, 1952, D.Shimizu, cultured'; Type specimen: Hab. Japan, Saitama Prefecture: Chichibu Mts., Tochimoto, ca. 700–800m, Sept. 9, 1952, coll. D. Shimizu 52808 (NICH, holotype). **syn. nov.**

Synonym: *Mannia barbifrons* Shimizu & S.Hatt.; Journal of the Hattori Botanical Laboratory 10: 49. 1953. Type citation: 'Rock crevices in exposed places, 780 m alt., Tochimoto, Saitama Prefecture, August 27, 1952, D.Shimizu'; Type specimen: [Japan] Hab. Rock crevices in exposed places, 780 m alt., Tochimoto, Chichibu, Saitama Prefecture, August 27, 1952, D. Shimizu 52809 (NICH, holotype). **syn.nov.**

Synonym: *Mannia fragrans* var. *convoluta* Nees; Naturgeschichte Europäischer Lebermoose 4: 226. 1838. Type citation: ?. Type specimen: n.v.. **syn. nov.**

Synonym: *Mannia fragrans* var. *fimbriata* Nees; Naturgeschichte Europäischer Lebermoose 4: 226. 1838. Type citation: 'Schlesien, Mosig s.n.; Felsen bei Kals und Martell in Tyrol; Funck s.n.; Podbarla bei Prag, Corda s.n.; Dahurien, von Fischer s.n.'; Type specimen: ?, n.v. (type in ?). **syn. nov.**

Synonym: *Grimaldia fragrans* var. *brevipes* Kaal., Videnskabsselskabets Skrifter Christiana. I. Mathematisk-Naturvitenskapelig Klasse (9): 3. 1898. Type citation: An mehreren Orten auf der Insel Hovedöen bei Cristiana aud dürren, sonnigen Hügeln dicht am Meeresufer, April 1892; Type specimen: Norwegen, Hovedö bei Christiana, an sonnigen Abhängen, steht am Fjörufer, 24.4.1892, leg. *Kaalaas* s.n. (BG, lectotype (selected here); BG, 2 syntypes. **syn. nov.**

Synonym: *Mannia fragrans* var. *brevipes* (Kaal.) Damsholt; Illustrated Flora of Nordic Liverworts and Hornworts: 717. 2002.

Synonym: *Mannia fragrans* var. *alpina* Meyl., Beiträge zur Kryptogamenflora der Schweiz VI, Heft 1: 86. 1924. Type citation: 'Valais, Col du Jorat, 2300 m, en plein soleil sur la terre humifère décalcifiée, devant un petit rocher, Gams et Meylan'; Type specimen: [Switzerland] Col du Jorat, Valais, 2300 m, Juin 1917, f. Gams et Meylan s.n. (S B24523, isotype fide Grolle 1972 *in sched.*). **syn. nov.**

Synonym: *Mannia fragrans* var. *inodorata* S.Hatt., Botanical Magazine (Tokyo) 58: 42. 1944. Type citation: 'Tokyo: Kaisikawa-ku, Hakusangoten-mati, Nov. 1940, S.Hattori, no. 6202'; Type specimen: [Japan] Koishikawa, in Hort. Bot. Univ. Imp.Tokyo, Japan, S.Hattori no.6202 (TNS No.2248, holotype). **syn. nov.**

Synonym: *Mannia fragrans* var. *orientalis* R.M.Schust.; Hepaticae and Anthocerotae of North America VI: 201. 1992. *nom. nov.* for *Mannia barbifrons* Shimizu & S.Hatt. **syn. nov.**

Description

Thalli forming large and closely intermingled patches or mats, small, linear and narrow, leathery, dorsally bright or dark green, sometimes purplish; becoming brownish or greyish in older parts, strongly xeromorphic, when fresh usually aromatic (cedar oil); vegetative branches terminal dichotomous and occasionally ventral, often with terminal innovations on thallus bearing male gametangia, branches broadening towards apex; lobes (3.5)4.4–15.5(18)mm long, (0.8)0.9–2.3(2.9)mm wide, margins dark purple to blackish, ventrally purplish-black; when dry, margins usually strongly inrolled with thallus becoming tubular and black with conspicuous whitish ventral scale appendages; *thallus apex* bearded, rounded and middle often grooved; *thallus* in t.s. (0.4)0.5–0.9 (1.2)mm thick, shape usually concave to triangular in section, *dorsal epidermis cells* (17)20.3–29(32)μm long, (8.7)11.6–17.4(20.3)μm broad, cell walls of dorsal epidermis rather thick-walled, with small to large trigones; *air pores* slightly raised, (7.5)8.7–17.4(20.3)μm in diameter, with 2–3 concentric rings of cells, outer ring of (5)6–7(10) cells, cells (10.1)11.6–20.3(26.1)μm long, (13)20.3–32(34.8)μm wide, inner ring of (5)6–7(9) cells, (10.1)11.6–17.4(23.2) μm long, (5.8)10–14.5(17.4)μm wide, pores visible with hand lens, of whitish colour, *assimilation tissue* loose, with one upper row of big vertical orientated air chambers and smaller more rounded air chambers below (1-2 layers), (138)149–334(552)μm high in t.s., *basal tissue* (205)280–440(483) μm high in t.s., with bright oil bodies in assimilation and storage tissue.

Rhizoids arising from ventral epidermis, smooth and pegged.

Ventral scales in two rows, overlapping each other and mid-line of thallus, purple with sometimes paler margins, (0.4)0.5–1.2(1.4)mm long, (0.4)0.5–1.1(1.2)mm broad (largest towards apex), semicircular, small slime papillae present on margins, *oil cells* several, 12– 52, predominantly along margin; *appendages* (1)2(3), bleached, (0.2)0.3–1.5(1.9)μm long, (0.05)0.1–0.3(0.6)mm broad, subulate, gradually narrowing into acute tip, tip often of a single row of cells, margins irregularly serrate, folding upwards over edge of thallus and overlapping lobe apex in tufts.

Sexual condition dioicous with male and female plants often growing intermixed or in separate patches, vegetatively dissimilar with apex of archegoniophore-bearing thallus bearded with conspicuous ventral scales. *Androecia* sessile, usually several, borne terminally on separate (not archegoniophore-bearing) thallus, forming a defined triangular (sometimes rounded or elliptic) disc, disc sometimes slightly upraised and often of purplish colour, occasionally some antheridia are found scattered below disc; ostioles ±conical, green when young, gradually becoming purplish-black when mature.

Gynoecia with archegoniophores deriving from terminal notch of thallus or from long ventral side branch of main thallus, base of stalk surrounded by tufts of long bleached scales; *receptacle* hemispherical, warty, strongly bearded, yellowish-green when young, mature turning green and often tarnishing purple, bearing 3–4 sporophytes; *stalk* brownish green, sometimes purplish at base or below receptacle, in t. s. rounded to ovate, weakly ridged when dry, variable in length, (5.8)6–14.2(16) mm long, with single rhizoidal furrow, in t.s. one outer brown smaller cell row and inner cells yellowish, bigger, incrassate with corners quite thickened, involucres cup-shaped, cells yellowish-brown with slightly overlapping cell walls, with long bleached single appendages, (0.2)0.3–0.5(0.6) mm in diameter, *capsule* black when mature, yellow when young, lid irregularly rounded, (0.6)0.7–1.3(1.5) mm in diameter, annular thickenings absent, cells rounded to rectangular, with corner thickenings, overlapping each other.

Spores type III, yellow, (46.4)55.1–66.7(70) µm in diameter (LM), (54)57–74.3(76.3) µm in diameter (SEM); weakly trilete; with similar sculpturing on proximal and distal surfaces; distally regularly areolate (6 to 8 areolae across), areolae shallow, minutely papillate with pits; on proximal side regularly areolate; proximal disc absent; equatorial apertures conspicuous, usually three; equatorial rim inconspicuous.

Elaters yellowish brown, (150)165–220(260) µm long, (7.2)8.7–11.6(14.5) µm broad at middle, 5.8–8.7 µm broad at tip, 3-spiral.

Chromosome number n=9 or n=8+m (FRITSCH 1991).

Illustrations (Fig. 4.9)

Distribution (Fig. 4.10)

The distribution of *Mannia fragrans* based on confirmed herbarium specimens is Switzerland, Germany, Austria, Hungary, France, Italy, Romania, Czechoslowakia, Poland, Finland, Norway, Sweden, Russia, China, Japan, U.S.A., Arctic Alaska, Greenland, Canada and India.

Based on literature it is also reported from Czech Republic, Slovakia, Estonia, Sicily, Slovenia, Croatia, Bosnia, Macedonia, Bulgaria, Ukraine, Crimia, Madeira, Siberia, Middle Asia, Transcaucasus, Western Asia, Mongolia, Eastern Asia, Indian Subcontinent (SÖDERSTRÖM, URMI & VÁÑA 2002); Bulgaria, Caucasus, Czech Republic, Slovakia, Spain, Jugoslavia, Madeira, Crimea (to Ukraine), northern part of European Russia (excl. Novaya Zemlya), central part of European Russia (incl. Estonia, Latvia, Lithuania, Belarus, the main part of Ukraine, Moldavia and the European part of Kazakhstan), Sicily (SCHUMACKER & VÁÑA 2000, 2005); former Jugoslavia (PAVLETIĆ 1955); Czech Repulic (DUDA & VÁÑA 1974a,b); Yemen (AL-GIFRI & KÜRSCHNER 1996); Nepal (CHOPRA 1943, GROLLE 1966); Asia, Himalaya, Baltic (PETTERSSON 1946); North Africa (SJÖDIN 1980); Intramongolicae (XUELIANG & ZUNTIAN 1996); SE Siberia (VÁÑA & IGNATOV 1995); S Siberia (KONSTANTINOVA & VASILJEV 1994); and the Russian Arctic (KONSTANTINOVA & POTEMKIN 1996).

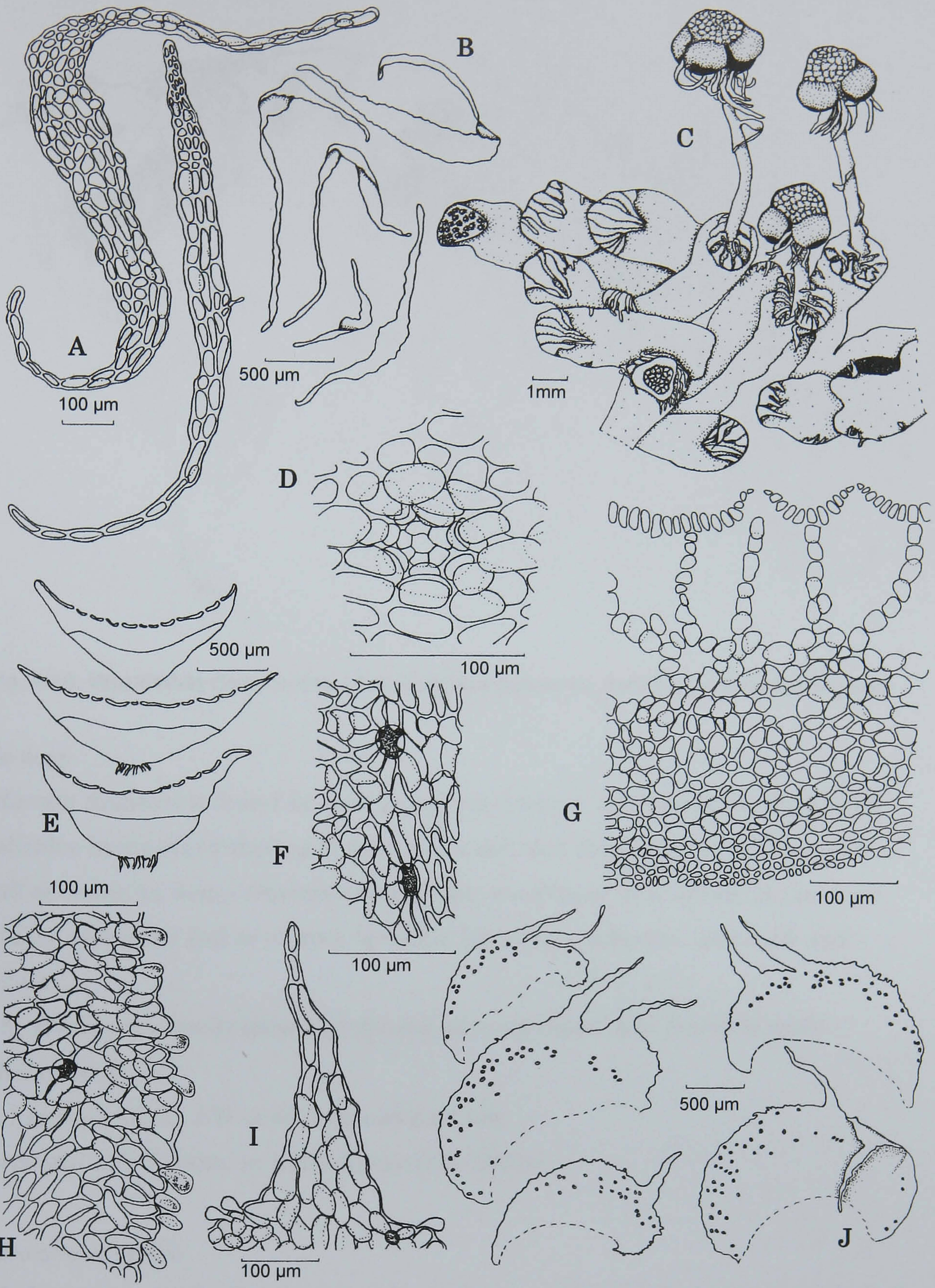


Fig. 4.9. *Mannia fragrans*. A, B scales from stalk, one showing slime papilla; C thallus showing androecium and archegoniophore; D air pores from ventral epidermis of thallus; E, G transverse section of thallus; F ventral scale, middle; H ventral scale margin with slime papillae; I ventral scale appendage; J ventral scales showing oil cells. A, B Switzerland, *Schill et al.* 51; C, E,G Switzerland, *Schill et al.* 55; D Switzerland, *Schill et al.* 60; F, H–J Switzerland, *Schill et al.* 48 (E).

Fig. 4.10. Worldwide distribution of *M. fragrans* based on herbarium material studied

Ecology

Mannia fragrans is found in open grassland, steppes or prairies, on slopes and hillsides in vineyard regions or openly wooded and then often associated with oak or cedar, in damp crevices or on banks, sometimes near rivers. It grows on grassy and rocky soil or on rock (granite, limestone, dolomite, quartzite and schist).

The species is usually growing exposed but sometimes also found in more shaded locations.

It has typically S, SW or SE exposed position.

Altitude: 100–2200m, in India from 3200–3330m.

Taxonomic Notes

M. fragrans is easily distinguished from all other *Mannia* species by its bleached ventral scale appendages and bearded thallus apex. It also is the only dioicous species within the genus *Mannia*. Male and female gametangia are always borne on separate thalli. In previous literature *M. fragrans* has often been described as polyoicous. In the present study male and female plants were predominantly found to grow intermixed but sometimes also in separate patches. The antheridia are borne terminally, typically forming a defined triangular (sometimes elliptic or rounded) disc. Gynoecia are found on the main thallus or on long ventral branches and the receptacle is bearded. When fresh, *Mannia fragrans* usually has a characteristic intense smell of cedar oil, which in some cases even remains in old herbarium specimens. Sometimes, however it is found to lack the characteristic smell in the field.

Mannia fragrans could be confused with the very similar looking *Asterella saccata*. In the fertile condition *A. saccata* is easily distinguished by its pseudoperianth, although this could be mistaken for a bearded receptacle. Additionally *A. saccata* has a faint fishy smell or is found to be not aromatic. A good character for differentiating between the two species is the position of the antheridia. *A. saccata* is par-autoicous or terminal-autoicous while in *M. fragrans* the antheridia are never found on an archegoniophore-bearing thallus. In *M. fragans* the antheridia are also borne terminally but are situated on a triangular (sometimes rounded or elliptic) disc while in *A. saccata* the antheridia form a *'weakly defined elliptic to elongate cushion with the antheridia often widely spaced'* (LONG 2000).

The spores of *M. fragrans* are ripe in April and May in central Europe and the U.S.A., in July in Russia (*Abramov 71* (E, S)) and in August and September in Japan.

EVANS (1920) noted that *Grimaldia fragrans* can sometimes lack the typical cedar oil smell. Specimens without smell in the field have often been considered as an odourless and hence chemotaxonomical variety. The chemical compounds responsible for the smell might though just be present in a pre-stage or their structure undergoes syntheses or decomposition while the plant does not show the characteristic smell. This might have seasonal reasons or be to do with the natural life cycle of the plants. That would explain an observation made on an odourless *Mannia fragrans* specimen put into a growth cabinet. A distinct smell of cedar oil became apparent after a few days and consequently disappeared and appeared again a few times.

When observing dried herbarium specimens, NEES VON ESENBECK (1838) mentioned that after soaking the specimens repeatedly the smell would be lost

and that the water would gain yellowish colour. He also noticed that dried specimens usually keep their characteristic smell. This is even the case in some very old herbarium specimen, in which the cedar oil smell is still noticable after sprinkling the specimen with water.
Sometimes a smell or only faint smell could be noticed in apparently odourless specimens after sprinkling with water.

Nomenclatural notes

In 1804 BALBIS used the name *Marchantia fragrans* to describe a plant he found in northern Italy. Unfortunately later the same name was applied again to a different plant collected by Schleicher in Switzerland, which is now known as *Asterella saccata* (LONG 2000). For the latter NEES VON ESENBECK (1820) proposed the new name *Fimbriaria fragrans*, which he based on the Swiss specimens (LONG 2000). In his publication though, he unfortunately assumed *Marchantia fragrans* to be a synonym of *Fimbriaria fragrans*. The name *Fimbriaria fragrans* has then been subsequently applied to two different taxa, sometimes *Asterella saccata* and sometimes *Mannia fragrans*. For more than 100 years this has caused confusion, not least not because the two plants share some distinctive morphological features and look very much alike in sterile condition. EVANS (1920) showed that *Fimbriaria fragans* could be interpreted as a synonym for *Mannia fragrans* but it took as long as 1976 until this was generally accepted through a publication by GROLLE (1976).

SHIMIZU & HATTORI (1953b) described a new synonym from Japan under the name *Mannia barbifrons*. This seemed to be done independently and without any reference to the earlier *Grimaldia barbifrons* described by BISCHOFF (1835). The authors probably were not aware of this earlier publication and applied the same name to the Japanes plant. As morphological differences they noted their plant being odourless amongst others in differentiation to *M. fragrans*.

Notes on variation within *Mannia fragrans*

In the past many varieties have been described for *Mannia fragrans* based on different morphological features, which are not accepted in the present revision. The characters used for the described varieties are considered to be variable and deviations lie within a natural range, often depending on environmental or habitat conditions or directly resulting from them. In many cases they also cannot unambiguously be applied to a single specimen as even a single population will show natural variations.

KAALAAS (1898) did not designate a type for his new variety of *M. fragrans* he described as *Grimaldia fragrans* var. *brevipes* in 'Beiträge zur Lebermoosflora Norwegens' in 1898. He attributed the type locality to several places along the seashore on the Norwegian Island of Hovedöen near Christiana (Oslo). His own herbarium is located in the herbarium in Bergen (BG) (STAFLEU & COWAN 1979). The specimen M5823 (BG) has been selected as a lectotype because it is material from his private herbarium, has been collected on the day mentioned in the literature and has the most information on the packet relating to the type locality that is mentioned in the literature. The specimen M5828 (BG) and M5829 (BG) are both syntypes.

The lectotype and the syntypes actually have immature archegoniophores but specimens collected by Kaalaas a month later in May show the characteristic short stalk Kaalaas refers to in literature. As many *Mannia fragrans* specimens show variations in stalk length even within a single specimen, the variety is not accepted in the present revision since specimens cannot be clearly assigned to the variety or the normal form.

The var. *alpina* was described by MEYLAN (1924) and it is characterised by airpores that are only surrounded by one or two concentric rings and thicker epidermal cell walls with an irregular starlike lumen. An isotype specimen of this variety was seen in this study.

According to NEES VON ESENBECK (1838) the var. *convoluta* is dorsally of brownish colour, the thallus smaller and strongly keeled, and the thallus margins have less overlapping scales.

The described var. *fimbriata* has strongly overlapping scales at the thallus margin and apex but a relatively weakly bearded receptacle (NEES VON ESENBECK 1838).

These described characters are all within the normal range of *M. fragrans* and are not very distinct variations. In general the thallus is known to show a certain variability depending to its locality and environmental conditions. A brownish colour instead of the usually greenish one could just indicate an adaptation of the plant to a higher light intensity.

Nees von Esenbeck did not designate a type in 1838 for either two of these new varieties. Unfortunately lectotypification could not be made because the specimens, on which he based his descriptions on could not be located. Hence a future lectotypification is desirable.

Three varieties have been described relating to the absence of the typical cedar oil smell in *Mannia fragrans.* The described variety '*inodora*' was based on WALLROTH's earlier description of the species *Grimaldia inodora* in 1840. He did not mention there its differences from *Grimaldia barbifrons* Bisch. or that the plant is odourless, though the name does not leave any doubt.

HAMPE (1873) retained the name as a variety of *Mannia fragrans* and applied it to a specimen without smell he collected in the Harz mountains in Germany. Lindberg in LINDBERG & ARNELL (1889) used the same name for a non-fragrant *Mannia fragrans* he collected in Siberia.

HATTORI (1944) described a new variety *inodorata* for a Japanese *Mannia fragrans* plant without smell. The herbarium specimen on loan however showed a faint smell of cedar oil when moistened with water.

Section *Asiaticae* Schill **sect. nov.**

Type: *Mannia asiatica* Schill & D.G.Long

Description

Thallus apex not bearded; *sexual condition* terminal-autoicous; *antheridia* inconspicuous, forming a poorly defined, slightly upraised rounded cushion or terminal slight depression or notch; *receptacle* usually naked; s*pores* deeply irregularly areolate; proximal disc absent.

5. ***Mannia asiatica*** Schill & D.G. Long **spec. nov.**

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. (E holotype; NY, PE, isotypes).

Description

Thalli spreading and forming extensive patches, small, narrow and flat, rather leathery, thin, dorsally green to brownish green or sometimes purplish, areolae sometimes visible, brownish or whitish lacunose, in older parts becoming brownish when disintegrating, xeromorphic; vegetative branches of terminal dichotomies or with terminal innovations; lobes (3.8)4.2– 19.5(25.9)mm long, (1.1)1.2– 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; l*obe apex* rounded and middle often grooved; *thallus* in t.s. (0.1)0.2–0.6(0.7)mm thick, shape usually flat or concave to triangular in section; *dorsal epidermis cells* (20.3)23.2–32(34.8)µm long, (11.6)13.05–23.2(26.1)µm broad, cell walls of dorsal epidermis rather thick-walled, showing usually 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 6–8(10) cells, cells 17.4–26.1(29)µm long, 11.6–20.3 (23.2)µm wide, inner of 6–7 cells, (11.6)13.05–17.4(20.3)µm long, (5.8)8.7–14.5(26.1)µm wide, pores visible with hand-lens, of whitish colour; *assimilation tissue* rather loose to sometimes slightly compact, (103.5)115–437(471.5)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; *basal tissue* (80.5)103.5–299(345) µm high in t. s. with inconspicuous yellowish oil cells 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, (0.5)0.7–1.5(1.8)mm long, 0.4–1.1(1.3)mm broad, oblong semicircular to broad semicircular, small slime papillae present on margin, *oil cells* 6–22(33), marginal and central, occasionally also present in appendages; *appendages* 1–2(3) unlobed or occasionally unequally bifid, sometimes bleached, 0.2–0.8(0.9)mm long, (0.07)0.09–3.0(3.2)mm broad at base, subulate, margins irregularly weakly crenulate, gradually narrowing into acute tip, overlapping mainly lobe apex and only rarely lobe margin and folding upwards over edge of thallus.

Sexual condition terminal-autoicous with androecia often borne on shorter branch of a dichotomy, of which the other branch often bears an archegoniophore, or androecia borne terminally without associated gynoecia. *Androecia* inconspicuous or forming a poorly defined, slightly upraised rounded cushion or terminal slight depression or notch with purplish ostioles, usually several.

Gynoecia with archegoniophores deriving from terminal notch of mid-thallus, surrounded by whitish scales; *receptacle* hemispherical, nodular/warty, 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, 0.2–5.1(5.3) mm in diameter, irregularly triangular-ovate, ridged when dry, variable in length, (0.9)1.9–18.9(20.8) mm long, with single rhizoidal furrow, in t.s. one outer brown smaller strongly incrassate thick-walled cell row and inner cells thin-walled, bigger, colourless, incrassate with minute to convex trigones; *receptacle* bearing 1–4 capsules; *sporophytes/capsules*, capsule black when mature, yellow when young, cells yellowish brown, irregularly hexagonal, incrassate with minute trigones; lid irregularly rounded, 1.2–1.7mm in diameter annular thickenings absent, cells incrassate, irregular hexagonal or rounded to rectangular, often strongly overlapping each other.

Spores type IV, yellow (43.5)46.4–78.3(84.1) μm in diameter (LM), (54.5)60–71.7(74.4) μm in diameter (SEM); weakly trilete; with similar sculpturing on proximal and distal surfaces; distally often deeply incompletely areolate, (6)7–10 areolae across, on surface minutely papillate with pits; on proximal side deeply irregularly areolate; proximal disc absent, equatorial apertures conspicuous to sometimes only inconspicuous, usually three; inconspicuous equatorial rim.

Elaters yellowish brown, surface slightly minutely roughened, (156.6)200–324.8(402) µm long, (8.7)10.15– 13.05(14.5) µm broad at middle, (2.9)5.8–8.7(10.2) µm broad at tip, 2–3-spiral.

Chromosome number unknown.

Illustrations (Fig. 4.12, 4.13)

Distribution (Fig. 4.11)

Based on confirmed herbarium specimens:

China, India, Tajikistan

Fig. 4.11. Worldwide distribution of *M. asiatica* based on herbarium material studied

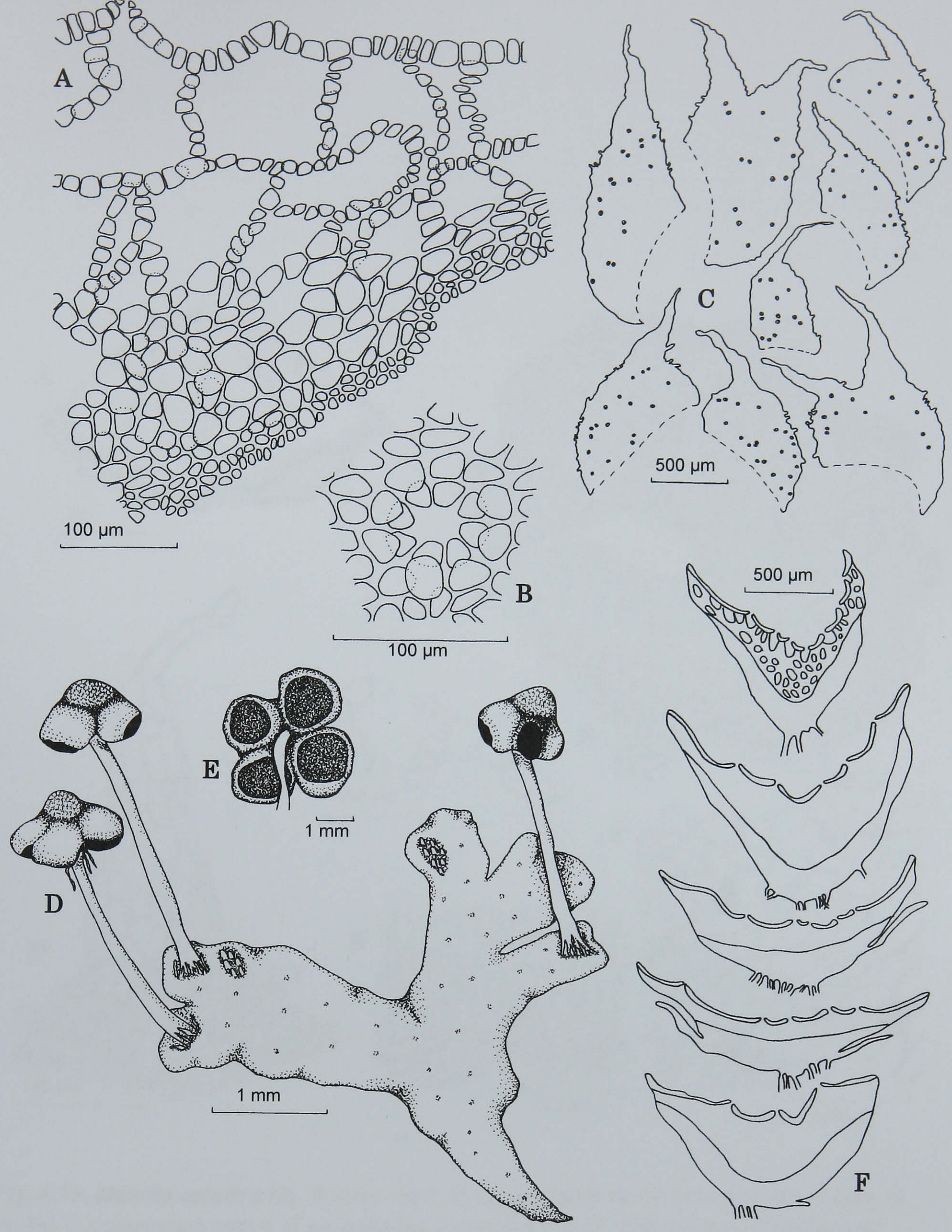


Fig. 4.12. *Mannia asiatica* (1). A transverse cection of thallus; B air pores of dorsal epidermis; C ventral scale appendage; D thallus showing androecium and archegoniophores; E receptacle from below, F transverse section of thallus. A–C, F China, *Long 27016* (E); D, E China, *Long 26952-b* (E).

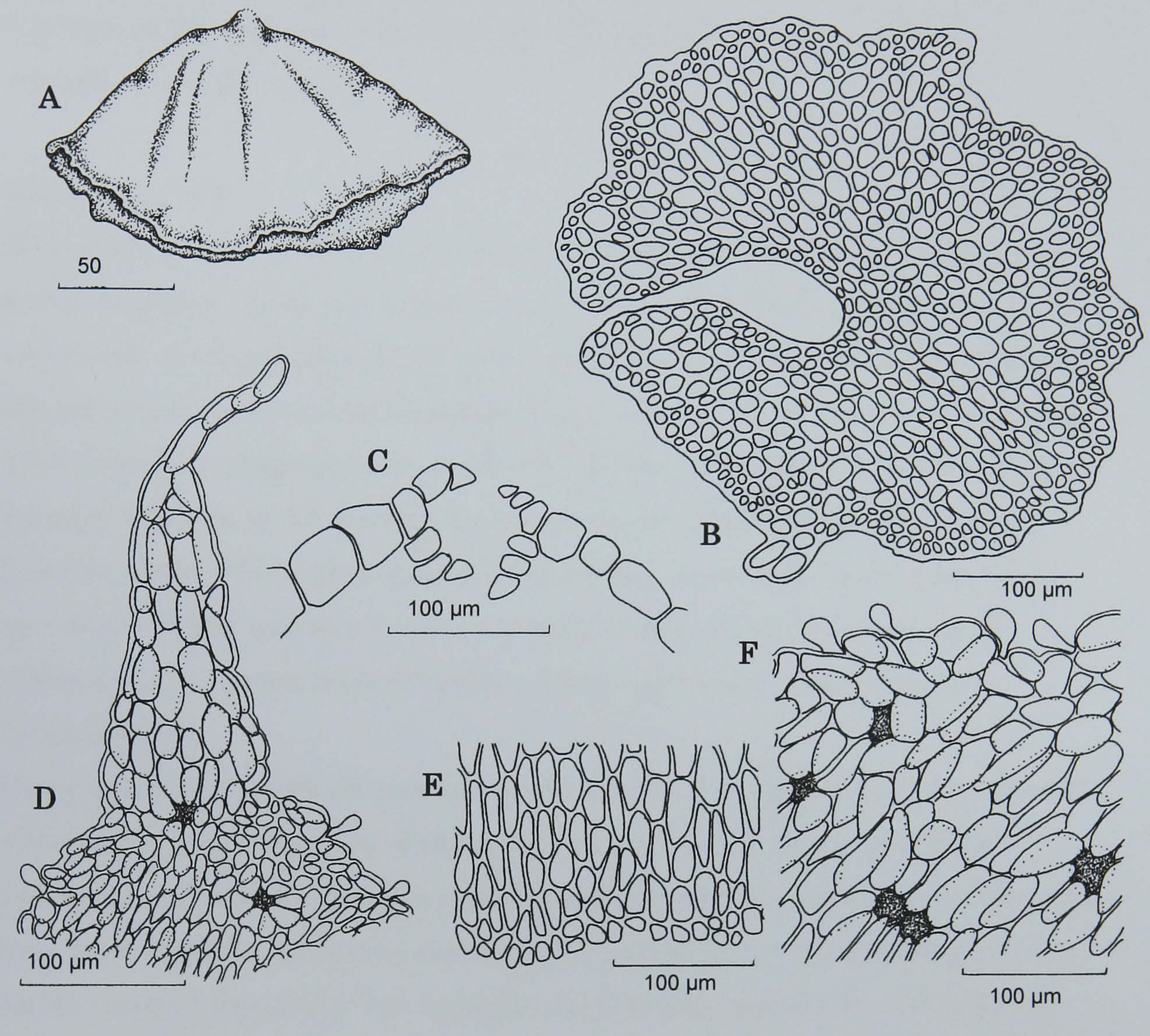


Fig. 4.13. *Mannia asiatica* (2). A side view of empty capsule; B transverse section of stalk; C compound pores of receptacle; D ventral scale appendage; E section of capsule margin, F ventral scale, margin. A, E China, *Long 27270* (E); B–D, F China, *Long 27016* (E).

Ecology

Mannia asiatica grows in the high mountains around the fringes of the Tibetan plateau, Himalayas. It is possibly endemic to the Kunlun mountain range, one of the longest mountain chains in Asia, extending more than 3000 km from east to west. 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) and has S or NW exposure.
Altitude: ca. 2735–4200m

Taxonomic Notes

M. asiatica can be confused with *M. sibirica* because of thallus similarity and sexual condition. Both are terminal-autoicous though in *M. asiatica* the antheridia are more often found on the shorter branch of a dichotomy of which the other branch bears an archegoniophore, whereas in *M. sibirica* the thallus often branches symmetrically. In *M. sibirica* the receptacle is usually strongly bearded whereas in *M. asiatica* the receptacle is naked or only very slightly bearded. Spores have quite good distinguishing characters- in *M. asiatica* the spores are bigger and do not have a proximal disc, which is present in *M. sibirica*- this can even be seen under a stereo light microscope with x50 magnification.
Using spore characters *M. asiatica* is also easy to distinguish from *M. triandra*, which has a spongy surface of the spore, rather inconspicuous equatorial apertures and only 4–7 areolae across the distal surface, the areolae being quite flat. In *M. asiatica* the spores are minutely papillate, the equatorial apertures rather conspicuous and it has typically more areolae across the distal face (6–10), the areolae being much deeper. *M. asiatica* has a more leathery thallus than *M. triandra* and a hemispherical shaped receptacle, whereas in *M. triandra* the receptacle is globose.
In China the spores are ripe in July, in India and Tajikistan in August.

Subgenus *Neesiella* (Schiffn.) Schill **stat. nov.**

Basionym: *Neesiella* Schiffn., in Engler und Prantl, Natürliche Pflanzenfamilien 1(3): 32. 1893.

Synonym: *Mannia* Subgenus *Cryptomitrium* Section *Neesiella* (Schiffn.) Shimizu & Hattori, Journal of the Hattori Botanical Laboratory 12: 71–73. 1954.

Type: *Mannia triandra* (Scop.) Grolle

Description

Receptacle globose; spores with similar sculpturing on proximal and distal surface; distally incompletely areolate, spongy in fine distal ornamentations with pits; proximal disc absent; equatorial pores inconspicuous.

6. *Mannia triandra* (Scop.) Grolle, *Journal of Bryology* 8: 487. 1975.

Basionym: *Marchantia triandra* Scop., Flora Carniolica ed. 2. 2: 354. no. 1356. tab. 63. 1772. Type citation: 'Habitat in humo, fub radicibus arborum, inter Idriam fuper. et inferiorem.'; Type specimen: [Slovenia] Carniolia, in rupestribus prope Zwischenwassern et Idria, solo calc., 328m, s.m., Deschmann 1138 (FH, Neotype designated by GROLLE (1976) n.v.; G-17010, NY, BM-725021, BM-669305, isoneotypes; BM-725002 isosyntype; S-B22547 and S-B22546 probably isosyntypes fide Grolle 1972 *in sched.*).

Synonym: *Duvalia rupestris* Nees, Berlinisches Magazin 8: 271. 1818. Type citation: 'Detegi hanc plantulam Mense Julio 1810 ad rupes arenoso-calcareos der Riesenburg prope Muggendorf, capsules jam effoetis. Tum alia vidi specimina ab Amicissimo Funckio jam pridem in Alpibus salisburgensibus lecta, quae fructus omni numero perfectissimos ferebant, quibus generic fundamenta superstrui possent'; Type specimen: by [bei] Pottenstein nächst Muggendorf, by [bei] Salzburg fand ich sie 1793 in den Höhlungen der Stadtwand. Funck. (BM725002, S-B22546, S-B22547 Isosyntypes).

Synonym: *Grimaldia rupestris* (Nees) Lindenberg, Nova Acta Academiae

Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum 14 (suppl.): 108. 1829.

Synonym: *Neesiella rupestris* (Nees) Schiffn., in Engler & Prantl, Die Natürlichen Pflanzenfamilien 1(3): 33. 1893.

Synonym: *Marchantia ludwigii* Schwägr., Historiae Muscorum Hepaticarum Prodromus 33, 1814. Type citation: 'Helvetia?, Germania, Hb. Kaulf.[uss]'; Type specimen: in Sudeticis legit et mihi communicavit, L-910, 287-188 (Lectotype selected by GROLLE (1975: 487)).

Synonym: *Asterella ludwigii* (Schwägr.) Underw. ex A. Evans, Bulletin of the Torrey Botanical Club 46: 469. 1919.

Synonym: *Fimbriaria ludwigii* (Schwägr.) Limpr. ex Müll.Frib. in Rabenhorsts Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, Auflage 2, 6: 243. 1940.

Synonym: *Duvalia longiseta* Steph., Bulletin de l'Herbier Boissier 5: 88. 1897. Type citation: 'Nemuro, Faurie 5552'; Type specimen: Japan, Yézo, forêts de Nemuro, 8.7.1820, *Faurie* 5552. (Holotype in G-17152, Isotype in BM-669266) **syn.nov.**

Synonym: *Neesiella longiseta* (Steph.) Steph., Bulletin de l'Herbier Boissier 6: 798. 1898.

Synonym: *Mannia longiseta* (Steph.) Horik., Hikobia 1: 85.1951.

Description

Thalli forming loose patches, small and rather thin, delicate, dorsally green or of greyish-blueish colour, mesomorphic; edges purplish; areolae visible, in older parts becoming brown and lacunose; vegetative branches arising as terminal dichotomies, sometimes with terminal innovations or arising from ventral surface of thallus, branches broadening towards apex; dichotomously branched; lobes (2)3.2– 13.5(16.7)mm long, (0.3)0.9– 2.8(4.9)mm wide, margins sometimes weakly crispate and hyaline with age, purple or green; ventrally green, sometimes purple when dry, margins still broad and not strongly inrolled or slightly to strongly inrolled, tubular and black; *lobe apex* rounded and middle often grooved; *thallus* in t.s. (0.2)0.3–0.6(0.8)mm thick, shape usually flat or slightly concave to triangular in section; *dorsal epidermis cells* (17.4)20.3–34.8(37.7)µm long, (11.6)16.1–34.8(40.6)µm broad, cell walls of dorsal epidermis thin- or thick-walled, showing corner thickenings (trigones) when focusing; *air pores* variable in size, (8.7)11.6–34.8(46.4)µm in diameter, with 2–3 concentric rings of cells, outer ring of 6– 8 cells, cells (14.5)17.4–37.7(46.5)µm long, (8.7)11.6–17.4(23.2)µm wide, inner ring of (6)7–8 cells, (11.6)14.5–20.3 (26.1)µm long, 8.7–14.5 (17.4)µm wide, thickening of radial walls rather thin; *assimilation tissue* loose, with big air chambers (2–3 layers), (116)172.5–495(541)µm high in t. s., up to 2 times the height of basal tissue; *basal tissue* (92)115–356(403) µm high in t. s., with inconspicuous yellowish brown oil bodies in assimilation and storage tissue.

Rhizoids arising from ventral epidermis, smooth and pegged, hyaline and often purplish or brownish towards base.

Ventral scales in two rows, sometimes only sparse or absent, overlapping each other and midline of thallus, purple with sometimes paler margins, (0.4)0.5–1.1(1.8)mm long, (0.2)0.3–0.9(1)mm broad, semicircular to oblong semicircular, small slime papillae present on margin, abundant, *oil cells* 1–19, marginal and middle, not present in appendages; *appendages* 1–2, (161)184–380(495)µm long, (17.2)23–103(126.5)µm broad, subulate, margins irregularly serrate, on base sometimes fimbriate, overlapping lobe apex and only rarely lobe margin and folding upwards over edge of thallus.

Sexual condition terminal-autoicous and par-autoicous with androecia terminal on short or equally long dichotomous branch, sometimes par-autoicous with androecia close to base of archegoniophore.

Androecia sessile, usually several, slightly upraised in poorly defined slightly raised rounded clusters or depressions; ostioles ± conical, green when young, gradually becoming purplish-black when mature.

Gynoecia with archegoniophores deriving from terminal notch of mid-thallus, surrounded by few hyaline scales; *receptacle* subglobose, nodular/warty, yellowish-green when young, mature green and often tarnishing purple at margins, *stalk* brownish green, sometimes brownish at base or below receptacle, 0.2–0.8(1)mm in diameter, irregularly triangular-ovate, in t. s low ridged when dry, variable in length, (0.9)2.2–17.9(19.8)mm long, with single rhizoidal furrow, in t.s. one outer brown smaller cell row and inner cells bigger, colourless or yellowish, incrassate with minute to convex trigones, white scales bearing slime papillae on stalk, usually not bearded though occasionally found a little to conspicuously strongly bearded, receptacle bearing (1)2–3(up to 5) *sporophytes/capsules*, capsule black when mature, yellow when young, cells irregularly hexagonal, incrassate with minute trigones, lid irregularly rounded, 0.7–1(1.2)mm in diameter, annular thickenings absent, cells rounded to rectangular, with corner thickenings, overlapping each other.

Spores type V, yellow, sometimes greyish brown (*Harper* Je-H1296), (52.2)55.1–70(78.3)µm in diameter (LM), (45.6)55.2–75(77.7)µm in diameter (SEM); trilete; with similar sculpturing on proximal and distal surfaces, distally incompletely to regularly areolate, 4–7 areolae across, surface densely spongy with pits, often smooth; on proximal side incompletely areolate; proximal disc absent; equatorial apertures rather inconspicuous, usually three; equatorial rim inconspicuous.

Elaters yellowish brownish, (49)98.6–282(319)µm long, (5.8)8.7–11.6(14.5)µm broad at middle, (2.9)4.3–7.3(11.6)µm broad at tip, 2–4-spiral.

Chromosome number n=9 (FRITSCH 1991).

Illustrations (Fig. 4.14)

Distribution (Fig. 4.15)

The distribution of *Mannia triandra* based on confirmed herbarium specimens is Sweden, Austria, Slovenia, Slovakia, Germany, France, Switzerland, Italy, Croatia, Poland, Russia, U.S., Canada, China and Japan.

Based on literature it is also reported from Hungary (SILLER 1979); Czech Republic (HRADILEK 2001); Intramongolicae (XUELIANG & ZUNTIAN 1996); Czech Republic, Hungary, Bosnia, Macedonia, Romania, Bulgaria, Albania, Ukraine, Siberia, Russian Far East, Middle Asia (SÖDERSTRÖM, URMI & VÁŇA 2002); Albania, Bulgaria, Czech Republic, Algeria, Hungary, Romania, central part of European Russia (SCHUMACKER & VÁŇA 2000, 2005); Russian Arctic (KONSTANTINOVA, N. A. & A. D. POTEMKIN 1996); Bulgaria (PETROV 1975); Czech Republic (SJÖDIN 1980) and Colorado, (HERMANN 1987).

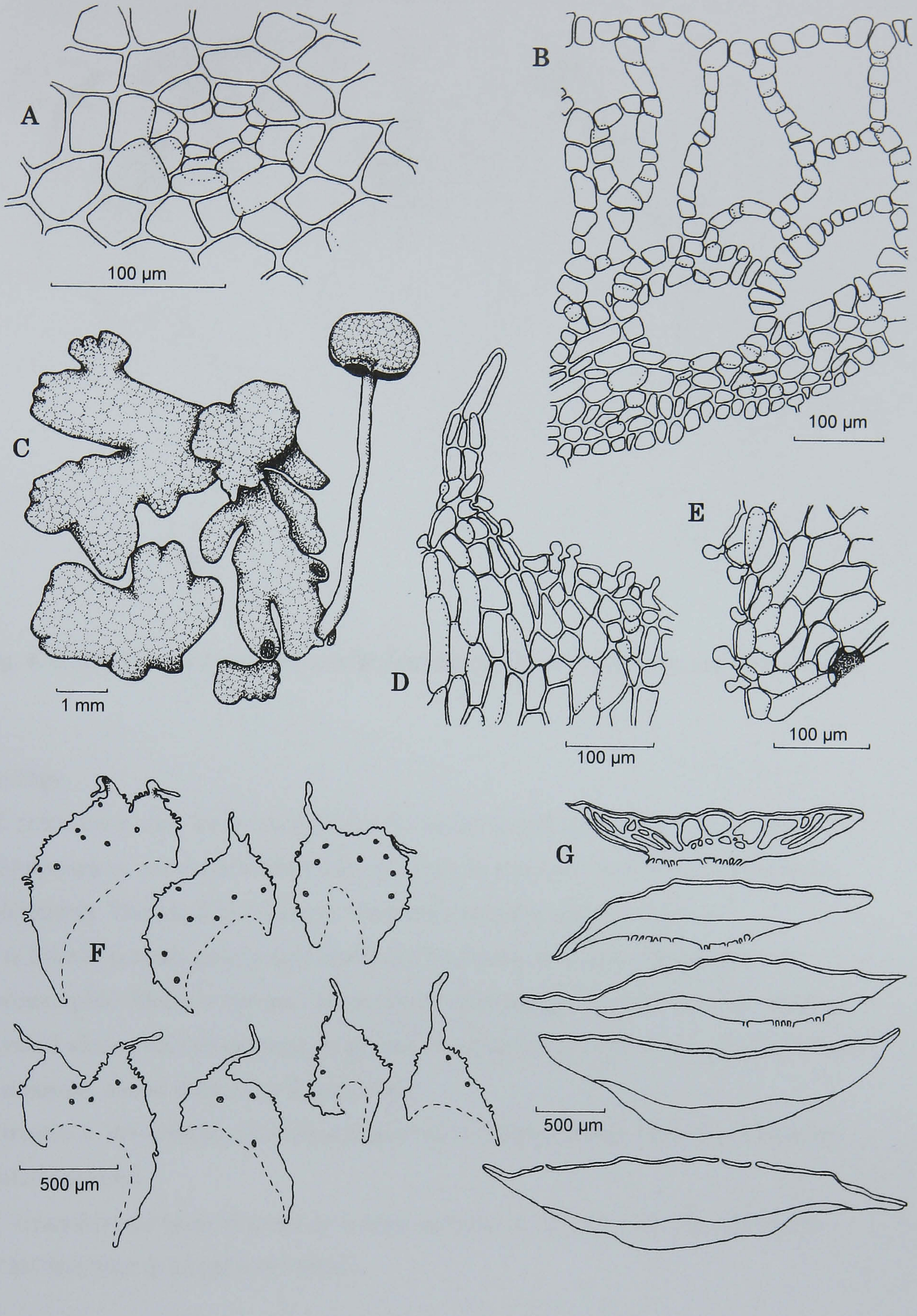


Fig. 4.14. ***Mannia triandra***. **A** air pores from ventral epidermis of thallus; **B, G** transverse section of thallus; **C** thallus showing androiceum and archegoniophore; **D** ventral scale appendage; **E** ventral scale, margin; **F** ventral scales showing oil cells. **A, D, E** Austria, *Schill et al.* 87 (E); **B** Italy, Gardasee, *Mihs?* s.n. (JE); **C** Austria, *Schill et al.* 79 (E); **F, G** Austria, *Schill et al.* 81 (E).

Fig. 4.15. Worldwide distribution of *M. triandra* based on herbarium material studied

Ecology

M. triandra seems to be an ephemeral (short-lived) plant and sometimes disappears in some habitats from one year to the next depending on climatic conditions. The thallus seems to disintegrate with spore maturity.

It is found in more shady and sheltered habitats than the other more xeromorphic *Mannia* species. It occurs on damp ledges, rock crevices, open or wooded slopes and in ravines. It grows on open, rocky soil or on rock (limestone, sandstone, slate) with N or E exposure.

Altitude: c. 40–2200m, in China found up to 3450m (where the thalli become quite leathery).

M. triandra has been classed as a rare species in Europe and Macaronesia (SCHUMACKER & MARTIGNY 1995).

Taxonomic Notes

M. triandra has rather thin and delicate thalli in contrast to the other more xeromorphic *Mannia* species and is often described as mesomorphic. It has big air chambers similar to those of *M. pilosa* and *M. fragrans*. The assimilation tissue can reach up to two times the height of storage tissue, and is often found to collapse in sectioning. Thalli start to disintegrate with spore maturity and become brown and lacunose but not as strongly or as whitish as in *M. pilosa*. For differentiation with *M. pilosa* see that species.

It can be distinguished from *M. sibirica* by the usually naked receptacle (although occasionally *M. triandra* is found to be bearded) and the usually more delicate thalli though this is also variable. In some *M. triandra* specimens from higher altitudes, e. g. from China, the thallus is somewhat leathery. The spore ornamentation and spore size are good characters to distinguish between the two species. In *M. triandra* spores are usually much bigger than in *M. sibirica*. Furthermore, spores of *M. triandra* lack a proximal disc, which is present in *M. sibirica*.

In Europe, Japan, China, Canada and the U.S.A. spores are mature from May to July, in Siberia from July to September.

Mannia triandra specimens with bearded receptacles:
(For full localities of bearded or slightly bearded *M. triandra* specimens see specimens marked with * in Appendix I)

Japan: *Sasaki & Kudo* 10524 (NICH), *Takida* 569 (NICH), *Kobayashi* s.n. (S), *Sasaki* 932 (S), *Sasaki & Kudo* 932 (F, G), *Kobayashi* s.n. (S) B74813. **Austria:** *Breidler* s.n. (S) B74805, *Breidler* s.n. (S) B74802. **Switzerland:** *Winter* s.n. (b) (BM) BM-669298, *Stephani* s.n. (BM) BM-669299. **Germany:** *Gauckler* s.n. (S) B74791. **Russia:** *E.N.Andrejeva* 144 (JE). **U.S.A.:** *Brewer* s.n. (NY) NY-268816. **Unknown locality:** *Molander* s.n. (JE), *Futschig* s.n. (S) B74794.

7. ***Mannia pilosa*** (Hornem.) Frye & L.Clark, University of Washington Publications in Biology 6: 64. 1937.

Basionym: *Marchantia pilosa* Hornem., Flora Danica 8: 7. tab. 1426. 1810.

Type citation: [Norwegen, Telemarken] 'in fissuris rupium prope Stuedalen in Tyedalen Norvegiae reperi'; Type specimen: *Duvalia pilosa* Hornemann, Norvegia, leg. Hornemann (ex Herb. Schraderi) 'specimen authenticum' (H-SOL, Isotype-2293012)

Synonym: *Neesiella pilosa* (Hornem.) Schiffn., Hedwigia 47: 314. 1810.

Synonym: *Duvalia pilosa* (Hornem.) Lindb., Notiser Sällskapets pro Fauna et Flora Fennica 9: 280. 1868.

Synonym: *Grimaldia pilosa* (Hornem.) Lindb., Musci Scandinavici, Upsala: 1. 1879.

Synonym: *Grimaldia carnica* C.Massal., Annuario del Istituto Botanico di Roma 2: 150 & 162 (54 & 66). 1886. Type citation: [Italy] 'declivi muscosi del mt. Pelmo nella regione alpine fra la Sauteria alpine, nella prov. di Belluno, C. Massalongo.' Type specimen: Italien, Mt. Pelmo, prov. Belluno, C. Massalongo. (Isotype in S B24386)

Synonym: *Neesiella carnica* (C.Massal.) Schiffn., Hedwigia 47: 314. 1908.

Synonym: *Marchantia fasciata* Myrin ex Hartm., Handbok i Skandinaviens Flora Ed. 2, 366. 1832. Type citation: [Norway] 'Lpl.- N. Nordl.'; Type specimen: Ad cataractam Baroafosfen in Malangerdalen Nordlandia Norwegiae, Lacta mecho Junis 1831, leg. Dr.A.F.Regnell. BM-725065, G (n.v.) fide Grolle ms. (Long 2000)

Synonym: *Reboulia fasciata* (Myrin ex C.Hartm.) Ångstr., Summa Vegetabilium Scandinaviae 102. 1845.

Synonym: *Asterella fasciata* (Myrin ex C.Hartm.) Trevis, Memoire del'Instituto Lombardo di Scienze e Lettere 4: 439. 1877.

Description

Thalli forming loose patches, small, narrow or broad, sometimes broadening towards apex, rather leathery thin, or sometimes more delicate, dorsally green with purple margins when young, sometimes shiny, occasionally purplish, areolate, in older parts becoming typically white when disintegrating and weakly to usually strongly lacunose with collapsing air chambers, xeromorphic; vegetative branches often dichotomous or in terminal or ventral innovations; lobes (1.6)2.5– 8.8(12.6)mm long, (0.6)0.8– 3.2(4.2)mm wide, margins purple or green or often white edged; ventrally green or purplish; when dry, margins slightly to strongly inrolled, tubular and black or still broad and not strongly inrolled; *Lobe apex* rounded and middle often grooved; *thallus* in t.s. 0.3–

1(1.2)µm thick, shape usually flat or concave to triangular in section; *dorsal epidermis cells* (14.5)17.4–29(34.8)µm long, (14.5)17.4–34.8(43.5)µm broad, cell walls of dorsal epidermis thin- or thick-walled, showing small to big corner thickenings (trigones) when focusing; *air pores* 16.5–14.5(17.4)µm in diameter, with 2 concentric rings of cells, outer ring of (6)7– 8 cells, cells (14.5)17.4–23.2(26.1)µm long, (8.7)11.6–17.4(20.3)µm wide, inner ring of 6–7 cells, 11.6–14.5(17.4)µm long, (5.8)7.2–11.6(14.5)µm wide, pores visible with hand-lens, of whitish colour; *assimilation tissue* loose, divided in one row of upper bigger vertical orientated air chambers and smaller more rounded air chambers below, in 2-4 layers, (170)230–702(760)µm high in t. s., up to 2 times the height of basal tissue; *basal tissue* (135)160–460(752) µm high in t. s., with only a few rather inconspicuous greyish brown to yellowish brown oil-bodies in assimilation and storage tissue.

Rhizoids arising from ventral epidermis, smooth and pegged, hyaline or purplish/brownish towards base.

Ventral scales in two rows, sometimes only sparse, overlapping each other and midline of thallus, purple with sometimes paler margins, (0.6)0.7–1.4(1.7)mm long, (0.2)0.4–1(1.1)mm broad, semicircular, small slime papillae present on margin, *oil cells* often absent or 0–3 (4), often marginal, seen in appendages; *appendages* 1(–2), 0.1–0.5mm long, 0.04–0.2mm broad, subulate, irregularly serrate margins, gradually narrowing into acute tip, overlapping lobe apex, only rarely folding upwards over edge of thallus.

Sexual condition typically *male-ventral-autoicous* and very rarely *terminal-autoicous* and then found together on same plant.

Androecia typically borne on reduced ventral branches of main thallus, arising from narrow stipitate base, situated on little slightly heart-shaped or more often rounded thalli that occasionally extend and grow longer (originating often lateral-ventrally or sometimes apical-ventrally from underside of thallus) or rarely situated on the shorter branch of a dichotomous furcation (terminal-autoicous) (looking like a pseudo-ventral branch of the main thallus as the longer branch of the dichotomous furcation can again be dichotomously branched). Most fertile branches bearing both sexes or occasionally only male or only female.

Androecia rather inconspicuous, forming a rounded slightly upraised or slightly depressed ill-defined cluster with inconspicuous or rather conspicuous greenish to purplish ostioles, usually several, if on a length extended ventral branch they can appear in rows of one or two.

Gynoecia with archegoniophores deriving from terminal notch of mid-thallus and inhibiting further growth or very rarely from ventral side branch of main thallus, typically bearded with hyaline scales; *receptacle* subglobose, nodular/warty, yellowish-green when young, mature turning green and often tarnishing purple at margins, with numerous hyaline scales below; *stalk* brownish green, sometimes brownish at base or below receptacle, 0.3–0.6 mm in diameter, irregularly triangular-ovate, in t. s. low ridged when dry, variable in length, (4)5.7–26(31) mm long, with single rhizoidal furrow, in t.s. one outer brown smaller cell row and inner cells bigger, colourless or yellowish, incrassate with minute to convex trigones, receptacle bearing (1)2–3(up to 5) *sporophytes/capsules*, capsule yellow when young, turning black when mature, cells yellowish brown, irregularly hexagonal, incrassate with minute trigones, lid irregularly rounded, (0.6)1.0–1.5(1.6)mm in diameter, annular thickenings absent, cells incrassate with minute to convex trigones, irregular hexagonal or rounded to rectangular, often strongly overlapping each other.

Spores type V, yellow to brownish yellow, (63.8)65.2–84.1(87)μm in diameter (LM), (63)66.6–81.5(85.7)μm in diameter (SEM); weakly trilete; with similar sculpturing on proximal and distal surfaces; distally incompletely areolate, 5–8 areolae across, surface forming a loose spongy interwoven network with pits; on proximal side incompletely areolate; proximal disc absent; equatorial apertures inconspicuous, usually three; inconspicuous equatorial rim; spore.

Elaters yellowish to brownish, (165)174–339.5(377)μm long, (10.1)11.6–14.5(16)μm broad at middle, 5.8–8.7(11.6)μm broad at tip, 2–3-spiral.

Chromosome number n=9 (FRITSCH 1991).

Illustrations (Fig. 4.16)

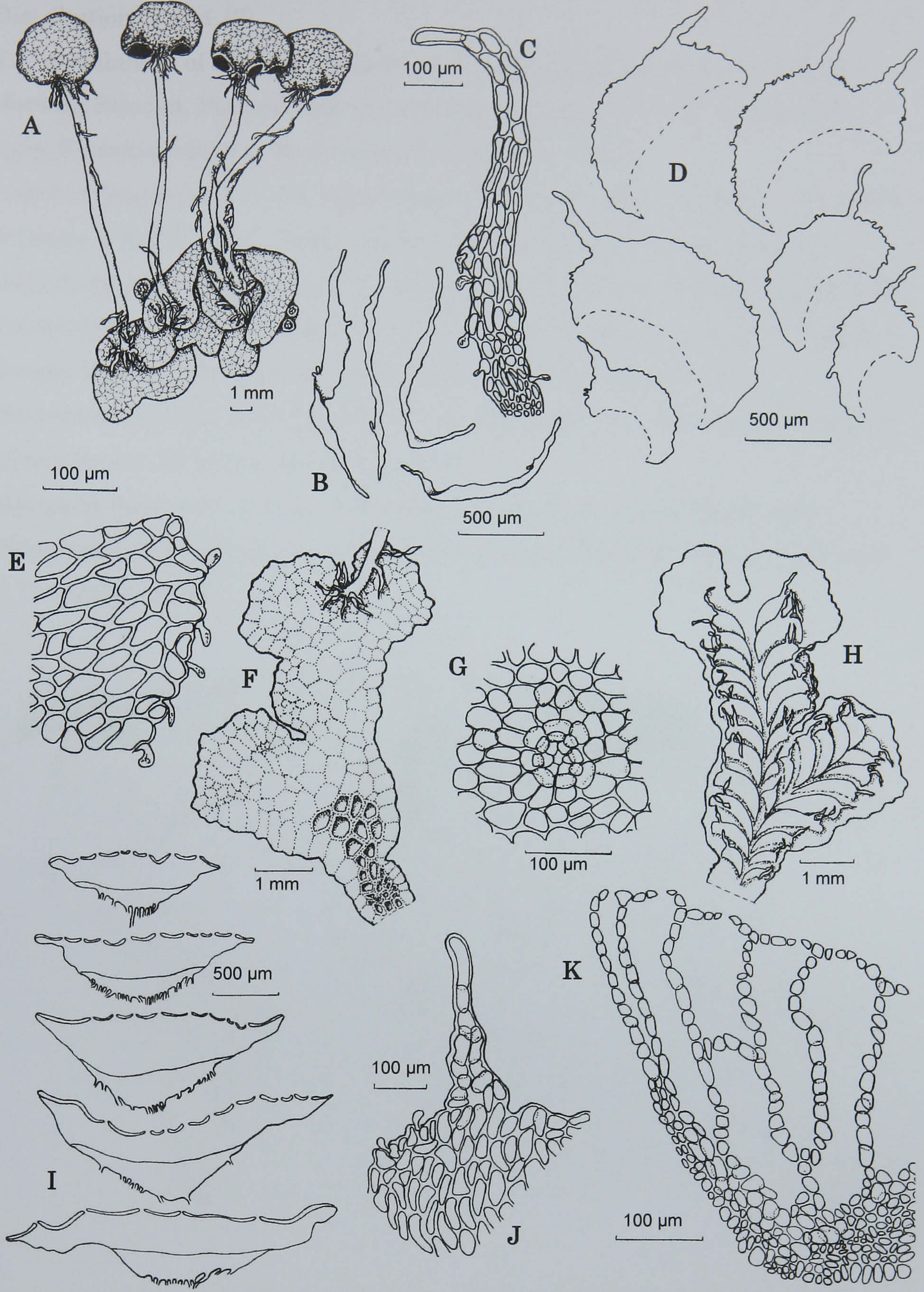


Fig. 4.16. ***Mannia pilosa***. A thallus showing androecium and archegoniophore; B, C scales of stalk with slime papillae; D ventral scales; E ventral scale, margin; F thallus, dorsal view; G air pores from ventral epidermis of thallus; H thallus, ventral view; I, K transverse section of thallus; J ventral scale appendage. A Austria, *Schill et al.* 83; B, C, I Austria, *Schill et al.* 85 (E); D, J Greenland, *Schuster* F66-045 (F); E Sweden, *Albertson* B74869 (S); F-H, K Austria, *Schill et al.* 84 (E).

Distribution (Fig. 4.17)

The distribution of *Mannia pilosa* based on confirmed herbarium specimens is Norway, Sweden, Finland, Estonia, Germany, Austria, France, Switzerland, Italy, Slovakia, Siberia, West Greenland, Alaska, Canada.

Based on literature it is also reported from Czechoslovakia (DUDA & VÁÑA 1967); Bulgaria (PETROV 1975); Poland (SZWEYKOWSKI 1958); Ellesmere Island (SCHUSTER 1958); North America, Czechoslowakia, W Asia (SJÖDIN 1980); Ural, Tatra (GAMS 1938); Slowakia, Slovenia, Romania, Bulgaria, Ukraine, N and E Russia, Russian Far East, Mongolia, N central and N eastern USA (SÖDERSTRÖM, URMI & VÁÑA 2002); Czech Republic, Slovakia, Jugoslavia in its former extent, Romania, northern part of

European Russia (excl. Novaya Zemlya), central part of European Russia (SCHUMACKER & VÁÑA 2000, 2005); Russian Arctic (KONSTANTINOVA, N. A. & A. D. POTEMKIN 1996).

Fig. 4.17. Worldwide distribution of *M. pilosa* based on herbarium material studied

Ecology

The species occurs on mountain ridges, on stony, grassy slopes, in tundras and on peaty or silt banks. It grows on rocky soil and rock (limestone, dolomite). It often has N, W or S exposure.

Altitude: 140–2900m.

Taxonomic Notes

M. pilosa is the only species of *Mannia* that has antheridia borne on reduced and usually rounded, ventral branches. The ostioles can be quite inconspicuous. The thallus has large air chambers similar to those of *M. fragrans* but lacks the bearded thallus apex. Assimilation tissue can be up to two times the thickness of the storage tissue. The thallus edges are often found to be whitish. On spore maturity the thalli typically start to disintegrate and air chambers collapse, the thallus surface becoming strongly lacunose and whitish. The receptacle is bearded with white scales also around stalk and base of stalk. The bearded receptacle differentiates this species from *M. triandra* in which the receptacle is usually naked although *M. triandra* can occasionally be bearded as well. A better difference of *M. pilosa* with *M. triandra* and *M. sibirica* is the position of the antheridia: both are terminal: autoicous or par-autoicous in those species. The thallus in *M. pilosa* is areolate and rather leathery. Thalli often considerably broaden towards the apex and are rather flat and thin. Ventral scales do not overlap the margins of the thallus, but are visible at the tip where they are reflexed. Oil-bodies in ventral scales are either absent or very sparse, whereas in both *M. triandra* and *M. sibirica*, oil-bodies are several.

In Europe, Siberia and the U.S.A. the spores are usually ripe in July and August.

Nomenclatural Notes

GROLLE (1976) points out that in older literature, *M. pilosa*, then known under the name *Marchantia pilosa* Hornem., was often misidentified for the similar looking *Asterella gracilis*. This, Grolle assumes, is partly based on Hornemann himself. The latter identified a specimen (deposited in G-15260) as *Marchantia pilosa*, which in fact is *Asterella gracilis* according to Grolle.

4.4.4 Excluded and doubtful species

1. ***Mannia subpilosa*** (Horik.) Horik., Hikobia 1: 85. 1951.

Basionym: *Grimaldia subpilosa* Horik., Monographia Hepaticarum Australi-Japonicarum. Journal of Science of the Hiroshima University 2. Series B. Div. 2. Art.2: 112–113. 1934. Type citation: 'Mt. Morrison (Taikwan-Tonbo), prov. Taichû (Y. Horikawa), no. 9251-Typus, Aug. 1932'; Type specimen: n.v. (Holotype in Herbarium of Hiroshima University (HIRO) and since 1994 on loan to Komarov Botanical Institute with Elena N. Andrejeva)

This is likely to be a synonym of *Cryptomitrium himalayense* from the illustration shown in HORIKAWA (1951). The receptacle is flat and not hemispherical or globose as it is typical for *Mannia*. The spores have a conspicuous and broad equatorial rim. The type material has not been seen. However, *Cryptomitrium himalayense* has not been recorded from Taiwan (PIIPPO 1990).

2. ***Mannia paradoxa*** R.M. Schust., Phytologia 57 (6): 408–414. 1985.

Type citation: 'Carlsbad Caverns National Park, New Mexico RMS 82-201'. Type specimen: n.v. (Holotype in private herbarium of R.M.Schuster)

This species is likely to be either *M. californica* or *Reboulia hemisphaerica*. Unfortunately SCHUSTER's description (1985, 1992b) is based on young plants with immature archegoniophores. He mentions that the antheridia are also quite young and hardly defined. They are situated on the same thallus as the archegoniophore, which is sometimes the case with *M. californica*, though not commonly. No specimens of *M. paradoxa* were available for study and on a field trip to New Mexico the plant could not been found.

3. ***Mannia hegewaldii*** Bischl., Flora Neotropica Monograph 97: 182–187. 2005.

Type citation: 'Peru, La Libertad: Otuzco, Huancamarca, Quebrada Hornillo, Hegewald 5168'; Type specimen: [Peru] Depto. La Libertad, Prov. Otuzco, Huancamarca, Quebrada Hornillo, Fels, 2690 m, 20.4.1973, leg. P. & E. Hegewald 5168 (holotype MO-5142197, isotype JE).

With regards to morphology and spore characters this species is very close to *M. triandra*. It has only been collected in two localities in Peru so there is little material available for study. On a field trip to Peru the plant could unfortunately not be refound in the two known localities. It is uncertain if the species is significantly different from *M. triandra*. According to BISCHLER-CAUSSE ET AL. (2005) the thallus in *M. hegewaldii* shows no areolation and the thallus margins are purplish and not hyaline as in *M. triandra*. She further notes that *M. hegewaldii* has a broader base in the appendages of the ventral scales and the spores have smaller and less areolae across with fine and not coarsely tuberculate distal ornamentation. With regards to thallus areolation the Peruvian material seems to differ from the majority of specimens observed, though the Chinese material of *M. triandra* shows a quite leathery thallus with less areolation as well. However in the available material studied purplish thallus margins are found to be common in *M. triandra* and the base of the appendages often show variations relating to its width. *M. hegewaldii* is weakly bearded below the receptacle, which can also be observed in some *M. triandra* specimens. Observations with the SEM have shown that in general spores of *M. triandra* have smaller and more numerous areolae than the two specimens of *M. hegewaldii* observed, though one *M. triandra* specimen from Japan (*Inoue* s.n.) showed a similar areolation to the spores seen in *M. hegewaldii*. However, spores of *M. hegewaldii* are possibly immature as can be seen in BISCHLER-CAUSSE (2005), Fig 160A.

Further collections and observations on living material are needed to elucidate its status.

4. *Mannia atlantica* (Trab.) Jelenc, 1955, Muscinées de l'Afrique du Nord: 39. **nom inval.** (Art. 36.1).

Basionym: *Grimaldia atlantica* Trab., Revue Bryologique et Lichénologique 12: 6.1942, *nom. nud.* (without latin diagnosis). Type citation: 'Atlas, Fort National'; Type specimen: n.v. (Isotype, MPU (fide Jovet-Ast in literature) (Grolle 1976)).

This is possibly a synonym of *M. androgyna* or *M. californica*. There are records from JOVET-AST & BISCHLER (1971) for *M. androgyna* in Tunisia and they also note Algeria amongst other localities in this paper. The two specimens on loan collected by Trabut in Algeria were determined as *M. androgyna*.

5. ***Mannia japonica*** (Steph.) Horik. 1951. Hikobia 1: 85

Basionym: *Grimaldia japonica* Steph., Species Hepaticarum 6 (Complément au Bulletin de l'Herbier Boissier): 10. 1917. Type citation: 'Hab. Japonia, Morioka. (Sawada legit.); Japan, Morioka, 19 v 1907, K. Sawada 30'; Type specimen: Morioka, May 19, 1907, K.Sawada 30 (Holotype in G-17019). **syn. nov.**

This is a new synonym for *Reboulia hemisphaerica* (L.) Raddi.

6. ***Mannia perssonii*** Udar & Chandra, Canadian Journal of Botany 43: 150. 1965.

Type citation: 'On moist shady rocks in Gangotri, Western Himalayas, October 1960, R. Udar'; Type specimen: [India] Western Himalayas (Gangotri), 9000 ft, coll. Ram Udar (holotype B5741 and isotypes B5742–B5744 in LWU).

This is possibly a synonym of *Mannia sibirica*. The spores belong to spore type II. The antheridial position is similar to *M. sibirica*, though the spores seem to be more ridged.

7. ***Asterella calciatii*** (Gola) Pandé et al. [Journal of the Hattori Botanical Laboratory 11:9, 1954, comb. inval. Art.33.2] ex Kachroo & Bapna, in Kachroo, Bapna & Dhar, Journal of the Indian Botanical Society 56: 74, 1977.

Basionym: *Fimbriaria calciatii* Gola, Atti dell'Accademia della Scienze Torino 49: 758, 1914. Type citation: [Pakistan] 'Kashmir: Valle Sind, prima catena a partire da Srinagar: Gund-Sonamarg: 21 v 1913 m. 2100–2600 sm, L. Borelli No. 3'; Type specimen: as above, Sped. Piacenza, Borelli 3 as 'Fimbriaria kashmirensis n. sp., G. Gola det. (Type in TO, n.v.) (LONG 2000)

Fide Grolle in LONG (2000) *Asterella calciatii* is noted as a synonym for *Mannia androgyna*. Because *M. androgyna* has its distribution range in Africa and Mediterranean Europe this is thought to be unlikely. This species is probably either a synonym of *M. californica* or *M. asiatica*.

8. ***Mannia controversa*** Meyl., Beiträge zur Kryptogamenflora der Schweiz VI, Heft 1: 87. 1924.

Type citation: 'Suisse, Vaud: Alpes d'Alesse, 2200m. (Gams). Près du Glacier des Martinets, 2200m. (Meylan). Berne: Col du Rawyl, 2400m. (Gilomen).Grisons: Piz Fuorn, 2400m.; Piz Nair, 2600m.; Forcletta del Val del Botsch, 2500m.; Val Ftur, 2600m.; Mount la Scherra, 2500m.; Val Tavrü, 2300m.; Schambrina près Scarl, 2300m. (Meylan).'; Type specimen: n.v.

Meylan did not designate a type specimen in his description and the original material was not availbale for study from Lausanne. Meylan characterises this species by its thin-walled epidermal cells, bearded receptacle and with many scales around base of stalk. The spores are of dark brownish yellow colour, 50–65µm across, 7–8 areoloae across and the species is found exclusively in the alpine zone. It shows thallus similarity to *M. androgyna* and sporophyte similarity to *M. sibirica*.

9. ***Grimaldia debilis*** Bisch., Synopsis Hepaticarum 552. 1846.

Type citation: Habitat ad terram in pascuis locis glareosis in Monte la Leona in Chili, ubi Sept. Mense a. 1828 a Bertero sub n. 354 lecta est.; Type specimen: Chili, herb. Bischoff, 1848, No. 4 (isotypes in S-B24521 and B24522)

This is a synonym of *Sauteria berteroana* Mont. fide GROLLE 1972 *in sched.*.

10. *Grimaldia chilensis* Lindenb. ex Mont., in Orbigny, Voyage Amérique Méridionale 7(2): 53. 1839.

Type citation: ad terram locis humidis prope Quillota, praesertim loco Cerro de Mallaca dicto exeunte Septembri legit Bertero, misitque sub no. 1129; Type specimen: n.v. (Isotypes in BM, G, STR fide Grolle 1975)

This is a synonym of *Sauteria berteroana* Mont. according to GROLLE (1975).

11. *Grimaldia stellaris* Müll.Frib., Feddes Repertorium 58: 61. 1955.

Type citation: 'Argentina, prov. Jujuy, Dep. Tilcara, arriba de San Gregorio, ca. 4050 m (27.12.52, H. Sleumer Nr. 3596)'; Type specimen: Prov. Jujuy, Dep. Tilcara, loc. Tilcara: arriba de San Gregorio, ca. 4050 m, 27.12.52, haud raro inter rupestr., H. Sleumer 3596 (Lectotype S-B24529 fide Grolle 1972 *in sched.*)

This is a synonym of *Targionia stellaris* (Müll.Frib.) Hässel fide Grolle 1972 *in sched.* He also notes on the packet (S-B24529): '*stellata in sched. wurde durch stellaris in der Veröffentlichung ersetzt*'.

4.5 Ecology

According to LONGTON (1997) the life history model of thalloid liverworts comes closest to the long-lived shuttle strategists. It is characterised by large spores, medium reproductive effort and relatively long-lived gametophytes. A further characteristic is that the capsule is raised on an archegoniophore in the absence of gemmae.

The genus *Mannia* is mainly found on rock, rocky soil or in rock crevices, often calcareous, gypsum or limestone. BISCHLER (2004) describes the soil type for *M. androgyna* and *M. triandra* as clay, sandy clay or sand. The species are mostly xeromorphic and hence well adapted to direct sunlight and long periods of desiccation, though between periods of drought, water supply is usually plentiful. They are dependent on water for their sexual reproduction and in particular fertilisation, which makes *Mannia* species *'temporary hygrophytes'* (BISCHLER & JOVET-AST 1981)

In general they show a leathery thallus, though *M. triandra* is sometimes found to be more delicate and rather mesomorphic in its moisture requirements. *M. triandra* is in general found in more shady or protected places that are not likely to undergo prolonged periods of desiccation. BISCHLER (2004) points out that it is often found in more *'humid zones'*. Sometimes the thallus in *M. triandra* can indeed become quite leathery. This could be observed for specimens found in higher altitudes in China.

Both *M. californica* and *M. androgyna* have similar habitat requirements and are typically found in more exposed places. BISCHLER (2004) considers the ecological tolerance of *M. androgyna* between pH 4–8 and *M. californica* is known from both calcareous and acidic sites (SCHUSTER 1992b, HUGONNOT & SCHILL 2006). They have in common a rather spongy assimilation tissue of the thallus. The other species have rather loose assimilation tissues but often also grow in exposed places (e.g. *M. fragrans*) or are found in more protected localities such as crevices or ledges underneath rock outcrops (*M. pilosa, M. triandra*). *M. fragrans* is said to be found in both siliceous and calcareous habitats (SUZA 1938, SCHUSTER 1992b).

Whereas there exist many accounts on ecology for most *Mannia* species (MÜLLER 1954, SCHUSTER 1992b, DIERßEN 2001, DAMSHOLT 2002, BISCHLER 2004) not much is yet known for *M. asiatica*. It can be noted though, that it often occurs in similar habitats to the other *Mannia* species and is found on limestone on banks along streams or on ledges.

4.6 Distribution and Phytogeography

Mannia has a mainly northern-hemispheric distribution with exceptions in South America and Africa (BISCHLER 1998). BISCHLER also remarks its absence from tropical East Asia and Australasia. This is likely to be a genuine absence as collections of Marchantiales, and in particular collections of the closely related genus *Asterella*, have been well sampled in these areas and any *Mannia* populations would have therefore not likely gone unnoticed (LONG, pers. com.). The scattered distribution of the genus that can be seen on some maps in the literature might reflect either a true picture but could also be possibly due to undercollecting, particularly in remoter parts of Asia.

The distribution pattern of *Mannia* could be explained by either ancient vicariance or recent dispersal events and requires future study.

However, MCDANIEL & SHAW (2005) noted that many recent floristic and molecular studies on mosses suggest that a broad distribution of species might arise through dispersal rather than ancient vicariance. In a molecular study on the simple thalloid liverwort *Jensenia* (Pallaviciniaceae) by FORREST ET AL. (2005) it was concluded that although the genus shows a *"classic Godwanan distribution"* its distribution pattern is more likely caused by recent dispersal than long geographical isolation. VANDERPOORTEN & LONG (2006) hypothesized that a big proportion of the endemic Macaronesian bryophytes might not be a relict *"from tertiary periods but involves fairly recent long-distance dispersal"*. In a phylogenetic study on the biogeography of the liverwort *Plagiochila* (Plagiochilaceae) HEINRICHS ET AL (2006) came to the conclusion that the present-day distribution of the genus could only be explained by a mixture of dispersal events (short and long distance), extinction and reestablishment based on climatic changes over time.

All *Mannia* species prefer either an arctic-alpine or temperate to mediterranean environment (BISCHLER 2004). The arctic-alpine species are found usually in the high mountainous areas above the forest line (such as *M. pilosa*, *M. asiatica*) whereas the Mediterranean species (e.g. *M. androgyna*, *M. californica*) prefer mild, moist winters and hot, dry summers. *M. androgyna* is according to FREY & KÜRSCHNER (1988) a circum-tethyan element including *'xerothermic regions of the Holarctic and the arid Northern American region'*. *M. triandra* is found in more sheltered and humid parts in temperate to Mediterranean climate (Bischler 2004). *M. fragrans* has a circumpolar but rather southern continental distribution (FRAHM & FREY 1992). *M. sibirica* has a northerly distribution pattern; it is found in Siberia, Finland, Norway, Canada, Arctic Alaska and the U.S.A., where it is collected in the north eastern States. SCHUSTER (1992b) describes *M. sibirica* as an *'amphizonal'* species whereas MÜLLER (1954) just describes it as *'nordic'*. Most species are found in a wider range of altitudes and are not restricted to altitudinal zonation. They usually occur from not much above sea level to higher elevations. *M. triandra* has a range from ca. 40–2200 m but can grow up to an altitude of 3450 m in China, *M. pilosa* ranges from 140–2900 m and *M. californica* from 150–3335 m. *M. androgyna* is found from 20–1400 m in Europe and the Mediterranean, though in Africa the altitude rises to 1407–1910 m. *M. fragrans* is found at higher elevations in the Indian Himalaya (3200–3330 m) than in the other continents (100–2200 m) though in literature it is said to occur in the Alps at 3000 m (MÜLLER 1954). *M. asiatica* seems to be restricted to even higher altitudes (2735–4200 m). For *M. sibirica* no information was available on the altitude from the herbarium specimen labels or in literature.

Eight local endemic species have previously been described, notably from North- and South-India (*M. indica, M. perssonii, M. foreaui*) but also from Japan (*M. levigata*), Africa (*M. capensis*), the United States (*M. californica, M. paradoxa*) and South America (*M. hegewaldii*). These so-called endemics were either found to belong to already known taxa and then reduced to synonyms or are considered doubtful (*M. perssonii, M. paradoxa, M. hegewaldii*).

M. capensis is conspecific with *M. androgyna*. This has already been suspected by GROLLE (per. com.) and by PEROLD (1994a). But because of the only limited amount of *M. androgyna* material available, she found it *'difficult to come to a definite decision about this'*. In fact the African material of *M. capensis* consists of two species (*M. androgyna* and *M. californica*), which have been formerly confused on the African continent as well as possibly in India. Records of *M. androgyna* from India by UDAR & CHANDRA (1965) are likely to be misidentifications of *M. californica.*

M. androgyna has a distribution comprising Africa, Macaronesia and Mediterranean Europe. The most northerly point of occurrence is southern Switzerland and Italy (Meran), the most easterly point Turkey and Cyprus. The species is well adapted to dry mediterranean-to-temperate climates (BISCHLER 2004).

M. californica, formerly thought to be endemic to the North American continent, with records only from the United States (CRUM & STEERE 1959, FLOWERS 1961, SCHUSTER 1992b), Canada (HICKS 1992) and Mexico (BISCHLER-CAUSSE ET AL. 2005), is much more widespread than formerly assumed. Its distribution extends into the European, African and Asian continents. It has only recently been discovered in Europe (HUGONNOT & SCHILL 2006) and has also been newly found in Austria and China. The SEM survey on spores showed that the species is a widespread but highly localised species in warm temperate and tropical regions of the Northern hemisphere and can also be found in Japan, India and Africa. The former narrow distribution pattern of this species is due to both undersampling and misidentification and the lack of a global evaluation and comparison of this plant. *M. californica* could possibly consist of several cryptic species (see Chapter 5).

Within the seven treated *Mannia* species, one is described as a new species. All plants have a more or less wide ranging distribution, usually found at least in two continents except for the newly described endemic.
Of the wider distributed species one is only found in Europe, Africa and Asia (*M. androgyna*), one in North-America, Europe, Africa and Asia (*M. californica*) and four in North-America, Europe and Asia (*Mannia fragrans, M. pilosa, M. sibirica* and *M. triandra*). Due to field work *Mannia fragrans* can be recorded new to India.

The assumed endemic species (*M. asiatica*) is so far only found in the high Kunlun mountain ranges in Asia, where it has been collected on the Tibetan plateau, the Indian Himalayas in Uttaranchal and the Aschger mountain in Tajikistan and grows in an arctic-alpine environment.

All species except for *M. californica* and *M. androgyna* (both occurring in Africa) have their main distribution in the Northern hemisphere.

4.7 Dispersal

Dispersal in bryophytes can occur via spores, asexual propagules, such as gemmae or via gametophyte fragments (LONGTON 1997).

Mannia dispersal is mainly driven by spores. In some cases thalli might break off from established populations after disturbances by wind and rain but because of the heavier weight of the thallus relative to a spore, this is considered to have only minor effects on distribution patterns on a wider scale.

The spores in *Mannia*, as is common for other Marchantiales, are quite big with elaborate wall ornamentations. They are yellow, brown, reddish brown or grey and their size in this study ranged between 43–86 µm in diameter. This agrees with BISCHLER (1998), who gives a range between 50–90 µm. She also states that there are 2000–3000 spores found in one capsule. The spore diameter in *Mannia* and other Marchantiales is considerably larger than in leafy liverworts or mosses, which are 7–40 µm in diameter (FRAHM & FREY 1992).

SHAW (2000a) suggests most spores get dispersed within one or two metres of the capsule.

In dispersal experiments on *Riccia*, which has relatively big spores (BISCHLER 1998: 40–200 µm), BERRIE (1975) collected some spores in a Petri dish, which had been placed 50 cm away and 10 cm above a colony, after a night of heavy rainfall.

There is a general assumption that spores exceeding 60 µm in diameter are not suited for long-distance dispersal and this would only be possible for spores under 30 µm (FRAHM & FREY 1992). In VAN ZANTEN & GRADSTEIN (1988) spores below 25 µm are considered best for dispersal over long distances by wind. VAN ZANTEN (1984) also suggests that Marchantiales spores are too large for transport over long distances.

This would indicate that *Mannia* with its relatively large spores would not likely be dispersed over long distances driven by wind. Larger spores are said to be more successful in stepwise dispersal *'although the possibility of their transport over longer distances is not excluded'* (VAN ZANTEN & GRADSTEIN 1988). The latter authors suggest that they would disperse through moist air currents in lower altitudes because their findings indicate that dispersal at higher altitudes is rather unlikely due to strong UV-exposure, which bryophyte spores would not survive. This was tested on experimental studies by attaching spores to an airplane across the Atlantic at jet stream altitudes (VAN ZANTEN & GRADSTEIN 1988).

BERRIE (1975) also suggests that dispersal in *Riccia* is most likely to take place over short land distances during periods of rainfall.

FRAHM & FREY (1992) however, consider that very strong winds would be able to lift up even big sized spores and point out that dust storms in the Sahara can reach Europe or the Caribbean Islands. They also consider that even if happening only on very rare occasions (once in several thousand years) establishment could be possible. MUÑOZ (pers.com.) agrees with this as he does not see spore size as a constraint for long-distance dispersal and points out that sand and dust particles can be carried over wide distances.
Most *Mannia* species are monoicous and could establish themselves with one single spore if they self-fertilize, but in the case of the dioicous *M. fragrans* two spores, one male and one female, would be needed for a successful establishment and sexual reproduction. They would possibly need to land within short distance of each other. Experiments on measuring distances from the sporophyte to the nearest male plant in mosses indicated between 2.5 cm to about 3.6 metres (LONGTON 1976, 1997). In studies on antherozoid movements he has also shown that sperm can swim about one to two metres (LONGTON 1997). This makes an establishment by rare long-distance dispersal events for this particular species more unlikely. Although *M. fragrans* is sometimes described as being polyoicous with either male or female colonies present (DAMSHOLT 2002, SCHUSTER 1992b), in the many *M. fragrans* herbarium specimens observed both male and female plants were often found in a single collection.

Elaborate spore ornamentations such as in Marchantiales seem to be of disadvantage for dispersal over long distances according to VAN ZANTEN & GRADSTEIN (1988) as verrucose and smooth spores may be *'more effectively suspended in air'*. They indicate that an elaborate spore sculpturing might play an important role for short distance dispersal over land in periods of heavy rainfall.

Spores in Marchantiales can survive long periods of desiccation. This is due to the large size of the spores, which contain a high content of food reserves to retain viability (CRUM 2001) and the spore sculpturing (BISCHLER & JOVET-AST

1981). Germination experiments showed that spores of Marchantiales such as *Mannia* are still 100% viable after drying for six months (INOUE 1960). The germination rate decreases after twelve months to 76% and spores were no longer germinating after eighteen months. VAN ZANTEN (1984) suggested that spores of thalloid liverworts were *'probably in general resistant to desiccation for periods of two years and more'*, BISCHLER & JOVET-AST (1981) consider *'one to several years'*. SUSSMAN & HALVORSON (1966) give a longevity of 20 to 25 years in some bryophyte spores. Furthermore, the spore colour in *Mannia*, which is usually yellow or brown, seems to be of advantage for wind dispersal as MUÑOZ ET. AL. (2004) state that spores that are not green show a higher viability and are more tolerant to travel in wind currents than green spores.

DALEN & SÖDERSTRÖM (1999) performed experiments on moss dispersal along streams and rivers. Their results indicated that in general the germination frequency of water-borne spores decreases over time but some species, such as the aquatic moss *Schistidium rivulare*, have spores with longer viability in water. They point out its short seta might be an adaptation to its dispersal mechanism and suggest that species with long setae might be adapted to dispersal by wind.

Only a few *Mannia* species occur occasionally along banks of streams, so a common dispersal via streams does not seem to be very likely. In general the stalks in *Mannia* species are quite long, which would indicate wind-dispersal, though occasionally the stalk is found to be short. BISCHLER & JOVET-AST (1981) consider the thick exine coat of spores good for dispersal by flowing water.

There is not much known about the possibility of spore dispersal via animals such as small insects or birds in *Mannia*. In dung mosses e. g. *Splachnum*, small sticky spores attach well to insect hairs. Though the spores in *Mannia* show elaborate sculpturing, it does not seem to be of special advantage in spore attachment other than the thick coating shows a good *'resistance against injury and desiccation'* (BISCHLER & JOVET-AST 1981). Spore dispersal via moving animals would so be possible.

Dispersal via human influence is assumed by INGERPUU & VELLAK (2000b). They suggest that diaspores of *M. sibirica* have recently been introduced to Estonia from Russia by Russian military vehicles *'during the Soviet time'.* As its main distribution area is seen to be in North America and Siberia (SCHUSTER 1992b) they consider the Estonian locality to remote and isolated. As *M. sibirica* is also recorded from Norway and Finland though, their theory seems less plausible. In fact the known Finnish locality is on an undisturbed and uninhabited small island. The Norwegian record is from 1881 and the plant has not been found since, either due to difficulties in identification or quite likely habitat change over time through human disturbances or intervention. In addition many liverworts are known to have disjunct distributions.

There exist many different hypotheses about spore dispersal in bryophytes and though there are many papers investigating dispersal mechanisms (SHAW ET. AL. 2003, HEINRICHS ET. AL. 2004) little is known about the dispersal of the spores in *Mannia*, what function the elaborate ornamentation has and an explanation for *Mannia's* distribution pattern.

A range fragmentation or a disjunctive distribution pattern could as well be due to undercollection (BISCHLER & JOVET-AST 1981, BISCHLER 1998) in the case of *Mannia*, particularly in parts of Asia and Africa.

BISCHLER & JOVET-AST (1981) conclude that flowing water plays a major role in spore dispersal in Marchantiales together with animal trampling and maybe sometimes wind.

Stepwise spore dispersal over short-distances via low altitude winds in combination with rainfalls seems to be the most likely process unless one argues the old evolutionary age of liverworts indicates ancient vicariance.

Further study on a population level like that one done by SQUIRRELL ET AL. (in prep.) using molecular markers such as microsatellites or isozyme analyses would be desirable and necessary for a better understanding of dispersal patterns in *Mannia* species. In addition a broader and more complete sampling of species from different parts of the world for a molecular analysis would be elementary.

It might then be possible to predict if in the genus *Mannia* long-distance dispersal events, stepwise dispersal over land or ancient vicariance and its resulting in a range reduction over time, were the reason for its distribution pattern and how the spores got around.

4.8 Discussion and conclusion

Seven taxa of *Mannia*, of the formerly twenty-two published species (GEISSLER & BISCHLER 1985), have been accepted, of which one is a new species. The other names are considered to be synonyms or listed under doubtful species. Many herbarium specimens have been studied for each species so a good geographical overview of each species could be seen and variations within each taxon could be assessed.

In the present treatment the genus is divided into two subgenera based on morphological characters, in particular spore ornamentation characters (Chapter 3); this was later tested by molecular methods (Chapter 5). One of the subgenera has four sections, of which one is new. Three of the sections are monotypic containing only one species. The justification for monotypic sections is possibly best explained by the evolutionary age of the genus. LONG (pers. com.) thinks that the taxa left are only relicts of a formerly more representative group with many of its members having gone extinct. The Marchantiales are known to contain many monotypic genera (BISCHLER & JOVET-AST 1981, CRUM 2001).

A worldwide revision of *Mannia* considering all species within the genus has been of advantage as the species delimitation is now more precise since all described species belonging to the genus have been observed in one study. Former regional studies have not included close relatives of the species being revised since the relatives might occur in different geographical areas. Consequently these studies have in some cases resulted in the formation of several confusing geographically localised taxa. Several described endemics were found to belong to more widespread taxa and hence synonymised. Furthermore, variations within species are now defined more clearly and key characters and differences have been clarified to distinguish between different species as previously many species have been confused with each other in literature and field identification.

It also became apparent that due to the past taxonomic uncertainties about 17 % of the examined herbarium specimens were either misidentified for another species of *Mannia* or mistaken for a species within a related genus such as *Asterella, Reboulia, Plagiochasma, Targionia, Athalamia, Riccia* or *Marchantia.*

As mentioned before, it is understood that some *Mannia* species can show distinct genetic differentiation when morphologically they are not distinct. In this case a broad species concept has been followed as a further subdivision is of no advantage in contributing to a better identification of these species. Morphological variations, which are believed to vary within taxa depending on habitat or environmental conditions, are not considered to be good characters for a further subdivision of species or justifying the formation of new species. These structural variations are considered to fall within a natural range.

It is now thought that many gametophytic characters are quite plastic. In particular the assimilation tissue of the thallus can appear quite different dependent on environmental conditions (LONG 2000). Therefore the present classification was initially based on spore ornamentation characters, which are thought to be more conserved (LONG pers. com.) and backed up by the molecular data (a chloroplast and a nuclear marker). The inclusion of spore characters in classifications of the Marchantiales has only been adopted in recent years, mainly by LONG (1998, 2000), LONG ET AL. (2000), BISCHLER (1989) and BISCHLER-CAUSSE (1989). For the sister genus *Asterella*, in the recent revision by LONG (2000) the classification was based on spore characters and was later also confirmed by a molecular analysis of two chloroplast markers (LONG ET AL. 2000).

Because not every species could be included in the molecular study in Chapter 5, some of the subgenera or sections may need to be amended but it is believed any resulting change to the main structure will be minor.

During the course of the taxonomic revision most morphological characters were found to be too variable and conflicting to take into account; an infrageneric classification of the genus based on morphological characters would have only been weak. The spore ornamentation was regarded as most useful to distinguish units.

Chapter 5: Phylogenetic Reconstruction

5.1 Introduction

Between the years 1985 and 2000 GOFFINET & HAX (2001) listed ninety molecular studies on bryophytes though the majority of these were on mosses. In recent years phylogenetic studies on liverworts have dramatically increased (e.g. DAVIS 2004, HE-NYGRÉN ET AL. 2004, 2006, FORREST & CRANDALL-STOTLER 2004, WILSON ET AL. 2004, SCHILL ET AL. 2004) and have brought much more insight as to how the different groups of liverworts are related to each other. In general molecular work is nowadays much more integrated into studies on bryophytes. Molecular studies on the phylogeny of complex thalloid liverworts, though, have been rare but were addressed at first by BOISSELIER-DUBAYLE ET AL. (1997) in a combined molecular and morphological study on Marchantiales and in the quite comprehensive study by WHEELER (2000) on the marchantioid liverwort radiation. Only recently phylogenetic relationships of the complex thalloid liverworts at the species level were addressed by LONG ET AL. (2005). Recent molecular work on Marchantiales, though, included only one to two species of *Mannia* in their analysis. LONG ET AL. (2000) included two *Mannia* species, *M. capensis* and *M. californica* in their study on the sister genus *Asterella*. In a study on the subclass Marchantiidae, BOISSELIER-DUBAYLE ET AL. (2002) included *M. fragrans* and LONG ET AL. (2005) have made a more extensive study on a wide range of complex thalloid liverworts (class Marchantiopsida) containing *M. fragrans* and *M. androgyna*.

Although the smaller scale study elucidated that *Mannia* has evolved from within its sister genus *Asterella* (LONG ET AL. 2000), this and the above mentioned phylogenetic studies gave only very limited information as to whether *Mannia* is a monophyletic genus because the sampling was very restricted. It is also not clear how the different species within *Mannia* have evolved and relate to each other. Hence a more detailed study including all *Mannia* species is necessary to elucidate phylogenetic relationships within the genus.

In the past there has been a lot of controversy about *Mannia* classification on a subgeneric and sectional level, which has so far only been tackled on a traditional morphological basis resulting in three different classifications of *Mannia* (e.g. SHIMIZU & HATTORI 1954, GROLLE 1976, GROLLE 1983b, GROLLE & LONG 2000). In even earlier treatments the species now belonging to the genus *Mannia* were assigned to two or three different genera, for example in classifications by
MASSALONGO (1914), SCHIFFNER (1893) and MÜLLER (1954), before there were united under *Mannia*.
These different *Mannia* classifications based on traditional morphological characters have never been tested by a molecular approach. Molecular tools such as DNA sequencing offer a new source of characters for testing hypotheses that previously could be inferred only from analyses of morphological characters. They provide, therefore, a different base to deal with former classification issues as it is known that morphological characters can show much phenotypic plasticity in the Marchantiales as the gametophyte is assumed to be greatly affected by the environment (BISCHLER 1998). This is often reflected by strongly incongruent tree topologies from morphological and molecular datasets (e.g. BOISSELIER-DUBAYLE ET AL. 1997).

A phylogenetic study based on morphological characters aimed to increase the understanding of character evolution in *Mannia*, to compare the morphological results with phylogenetic hypotheses resulting from molecular data and if possible combine them to see if the resulting trees are congruent.
The *Mannia* classification based on spore types from Chapter 4.4.2 can also be tested. A correlation of spore types with clades derived from molecular tree topologies have been successfully demonstrated in *Asterella* by LONG ET AL. (2000).

As such *Mannia* is also critical to an understanding of relationships within the Aytoniaceae. Former molecular studies (LONG ET AL. 2000, LONG ET AL. 2005) implied that *Asterella* is a paraphyletic genus and its sister genera *Mannia*, *Reboulia*, *Plagiochasma* and *Cryptomitrium* are nested within *Asterella*.

This raises the possible scenario of sinking *Mannia* and its sister genera into *Asterella*, from which they all derived or a change in the current generic delimitation within the Aytoniaceae.

A combination of morphological characters, in particular spore ornamentation characters together with the molecular study should contribute to a more stable classification of *Mannia* and elucidate its evolution from within *Asterella*.

Morphological characters were scored for a phylogenetic reconstruction and the tracing of character evolution in the genus. Molecular techniques were used to reconstruct phylogenetic relationships within *Mannia* and related genera of the Aytoniaceae. A non-coding region of the chloroplast DNA, the *trn*L-F region and partial nuclear ribosomal 26S were isolated. Phylogenetic analyses were performed for single and combined data sets using Parsimony Analysis and Bayesian Analysis and the results compared with the morphological tree.

5.2 Material and sampling methods

5.2.1 Taxon sampling

Plant material for DNA analysis was either collected on field trips to Germany, Portugal (Madeira), Austria, Sweden (Gotland), North America, Namibia, India and Peru by myself, and on field trips by D.G. Long to Nepal, China and Mexico or kindly provided by international collectors from the U.S.A., Austria, France and Japan. The plant material used was dried and stored in silica gel for later molecular study. All plant specimens used for the molecular analysis are listed in Appendix III. A total of thirty-six specimens were included in the molecular study, including twenty-two species from seven genera. The collection of plant material for DNA extraction in silica gel is a commonly used method for field preservation of plant samples (CHASE & HILLIS 1991). A voucher specimen for each DNA sample is kept in the Herbarium in Edinburgh (E).

5.2.2 Outgroup and Ingroup taxa

Outgroup selection followed the most recent molecular study on the Marchantiales by LONG ET AL. (2005) and therefore two taxa, *Targionia hypophylla* and *Athalamia hyalina* were chosen us outgroup taxa. A total of three outgroup samples were included: *A. hyalina* (1) and two samples of *T. hypophylla* from different countries. *T. hypophylla* has also been previously used as outgroup taxon in a molecular study on the sister genus *Asterella* by LONG ET AL. (2000). The trees were rooted on *A. hyalina* and *T. hypophylla.*

The ingroup taxa consisted of selected species within the family Aytoniaceae: *Asterella* (8), *Plagiochasma* (3), *Reboulia* (1), *Cryptomitrium* (3) and all available *Mannia* species (5). A total of 32 samples for 20 species were included in the ingroup, some species are represented by multiple samples but were from different countries. As became apparent from LONG ET AL. (2000) all genera of Aytoniaceae should be treated as ingroup because *Asterella* is a paraphyletic genus and its sister genera were found to be nested within it. Five out of seven *Mannia* species could be included in the molecular study as well as an unidentified *Mannia* specimen from North India and the dubious *M. controversa.* No material was available for *M. sibirica* and *M. asiatica.* The total number of included samples was 35.

5.3 Morphological methods

The morphological matrix was compiled using mostly the same taxa as in the molecular analysis. A total of 23 taxa were included. Additionally *Mannia sibirica* and *M. asiatica* were included, of which no fresh material was available for the molecular study. A total of twenty four morphological characters were coded for twenty three species. These characters comprised seven vegetative and nine reproductive characters of the gametophyte and eight sporophyte characters, which were discussed in Chapter 2.2. The coding for all *Mannia* species was based on own observations whereas the data for the other taxa was obtained from literature (e.g. ABRAMS 1899, HOWE 1899, KASHYAP 1915, HAUPT 1942, SHIMIZU & HATTORI 1954, KACHROO & KAUL 1971, MEHRA & SOKHI 1977, SCHUSTER 1992b, PEROLD 1994b, BISCHLER 1998, LONG 1998, 1999, 2000, PATON 1999, BISCHLER-CAUSSE ET AL. 2005).

The spore characters for *Cryptomitrium tenerum*, *C. oreades*, *Plagiochasma rupestre* and *P. wrightii* are based on my own observations from the SEM study. For coding, qualitative characters were given favour over quantitative characters as the latter show often an overlap and cannot be scored unambiguously. When quantitative characters were used (e.g. character 5: Scale appendage number and 12: Number of rhizoidal furrows) they were subdivided at stated intervals and arranged in groups to make scoring possible. Characters were either coded with absence/presence (binary coding) or were multistate characters. Certain characters of taxa occasionally show polymorphism. In this case the taxon was given both character states e.g. '1; 2'. Unknown character states were coded as '?'. All morphological characters used in the analysis, their states and the complete character matrix are given in Appendix II. Character mapping was done on a single most parsimonious tree based on a weighted molecular parsimony analysis of combined *trn*L-F and 26S sequences with the inclusion of the gap character matrix.

5.4 Molecular Methods

5.4.1 Molecular markers

The choice of markers for this study was guided by previous molecular studies on Marchantiales (LONG ET AL. 2000, BOISSELIER-DUBAYLE ET AL. 1998). In both studies the chosen markers provided phylogenetic resolution at lower taxonomic levels and provided insights into evolutionary processes.

Therefore sequence data was generated for the chloroplast region *trn*L-F and for part of the nuclear ribosomal LSU (Large Subunit), a segment of the 26S gene. The *trn*L-F consists of a non-coding intron in the *trn*L gene and an intergenic spacer between the *trn*L and *trn*F genes. The intron is one of the most commonly used markers in bryophyte phylogenetic studies (QUANDT & STECH 2005). The size of the intron ranges from 350–600 base pairs (bp) and the spacer from about 120–350 bp in higher plants (SOLTIS & SOLTIS 1992), while in leafy liverworts the intron size ranged between 305–372 bp (SCHILL ET AL. 2004). The intron is considered to be an ancient region, which became immobilized in the course of time (WHEELER 2000). It belongs to the group I introns and is distinguished by the possession of catalytic activities and by the formation of secondary structures and for these reasons the intron is expected to be less variable than the spacer (KUHSEL ET AL. 1990). It is evolving about two times slower than the spacer in Gesneriaceae (MOELLER, pers. com.).

The 26S is a coding region of about 3300-3500 bp and consists of the large ribosomal subunit (SOLTIS & SOLTIS 1992, HERSHKOVITZ ET AL. 1999). The entire 26S region is hence relatively large and is composed of conserved regions, which are interspersed by twelve variable regions, known as expansion segments or divergent domains (ca.1 kb) (KUZOFF et al. 1998, SOLTIS & SOLTIS 1992, HERSHKOVITZ ET AL. 1999).

5.4.2 DNA Extraction

Fresh plant material, collected in the field, was preliminarily cleaned using forceps to remove soil contamination before being placed in silica gel filled bags. Once in the lab, samples were cleaned more thoroughly using a Stereo microscope. Samples were then stored in silica gel until required for DNA extraction.

DNA from liverwort tissues was either extracted using a modification of the CTAB (cetyl-triethyl-ammonium-bromide) method of DOYLE and DOYLE (1990) or using a DNeasy Plant Mini Kit (Qiagen Ltd., Crawley, West Sussex, UK) following the manufactures protocol, except that elution was performed in 35 µl buffer AE only.

DNA Extraction Protocol (modified from DOYLE & DOYLE (1990)):

A small amount (ca. 6 thalli) of silica dried liverwort material was placed in a 1.5 ml eppendorf tube with one spatula each of sand and PVP (polyvinylpyrollidine). The tissue was ground to a fine powder using either a Mixer mill (1 minute at 30/sec frequency), or the tube was immersed in liquid nitrogen for a few seconds and the thallus tissue ground using a glass pestle. 700 µl of 65°C preheated CTAB buffer (2 % CTAB, 20 mM EDTA, 100 mM tris-HCl pH 8.0, 1.4 M NaCl and 0.2 % mercaptoethanol) was added to each sample and incubated at 65°C for 30 minutes. During incubation the tubes were agitated, for about three times. After incubation the tubes were cooled to ambient temperature.

700 µl of chloroform isomyl alcohol (24:1) was added to each sample and mixed on an orbital shaker for 15 minutes at medium speed.

Samples were centrifuged for 15 minutes at 13 000 revolutions per minute (rpm) to separate into two phases. Ca. 600 µl of the supernatant (aqueous upper layer) was removed to a clean 1.5 ml eppendorf tube. The chloroform extraction was repeated. Finally ca. 500 µl of the supernatant was transferred to another clean 1.5 ml eppendorf tube and the DNA precipitated by adding 350 µl of cold isopropanol (about 2/3 volume) and mixed gently.

The samples were left overnight at -20°C to allow maximal DNA precipitation.

The tubes were then centrifuged at 13 000 rpm (5 min) to pellet the DNA. The supernatant was discarded and the resultant DNA pellet was washed in 70 % cold ethanol.

The samples were then centrifuged again for 5 minutes at 13 000 rpm and the supernatant removed. Resulant pellets were dried, using a vacuum centrifuge for 3 to 5 minutes at a medium or low dry rate. The DNA was finally resuspended in 30 to 40 µl of distilled, sterile water.

5.4.3 PCR amplification

5.4.3.1 Primers

The following primers were used to amplify the 26S and *trn*L-F regions. Details are given in Table 5.1.

Table 5.1. Primers used in PCR and sequencing reactions

Region	Primer	Direction	Sequence	Reference
*trn*L-F	*trn*L-c	forward	5’-CGA AAT TGG TAG ACG CTG CG-3’	Frey et al. 1999
	*trn*L-cAyto	forward	5’-AT TGG TAG ACG CTG CG GAC TT-3’	Schill (designed for this study)
	*trn*L-d	reverse	5’-GGG GGT AGA GGG ACT TGA AC-3’	Frey et al. 1999
	*trn*L-f	reverse	5’-ATT TGA ACT GGT GAC ACG AG-3’	Taberlet et al. 1991
26S	0F	forward	5’-ACC CGC TGT TTA AGC ATA T-3’	Shaw 2000b
	12R	reverse	5’-ATC GCC AGT TCT GCT TAC CA-3’	Shaw 2000b
	316F	forward	5’-AAG TAC CGC GAG GGA AAG AT-‘3	Long et al. 2005
	920R	reverse	5’-AGT ATC GCT ACG AGC CTC CA-‘3	Long et al. 2005

5.4.3.2 Reaction conditions

Polymerase Chain Reaction (PCR) was used to amplify the chloroplast region *trn*L-F and 26S ribosomal DNA region.

Polymerase chain reaction (PCR) protocol for *trn*L-F

PCR reactions were performed in 25 µl using the following reagents:

Reagents	Quantity
10x Reaction buffer (10x: 160mM (NH4)2SO4, 670mM Tris-HCL (pH 8.8 at 25 °C) 0.1 % Tween-20) (Bioline, London, UK)	2.5 µl
MgCl2 (50 mM) (Bioline, London, UK)	1.25 µl
dNTPs (0.2 mM) (Sigma Chemicals, Pool, Dorset, UK)	1.25 µl
forward primer: trnL-c (10mM) (MWG-Biotech AG, UK)	2 µl
reverse primer: trnL-f (10mM) (MWG-Biotech AG, UK)	2 µl
sterile, distilled water	7.9–15.6µl
DNA polymerase (5U/µl) (Bioline, London, UK)	0.125 µl
DNA	0.25–8 µl

The PCR cycling conditions used to amplify the region were:

Temperature	Time	Number of cycles
94°C	3 min	x1
94°C	1 min	
52°C	1 min	x40
72°C	2 min	
72°C	2 min	x1

PCR amplification was assessed using 1% agarose gels. Resultant products were purified using either Qiaquick MinElute PCR purification kit (Qiagen Ltd., Crawley, West Sussex, UK) or GFX PCR DNA and Gel Band Purification Kit (Amersham Biosciences, UK).

The purified products were assessed again on a 1 % agarose gel.

Compounds of 1% Agarose gel:

Reagents	Quantity
Agarose	0.4 g
TBE (1%)	40 ml
Ethydiumbromide	1 µl

Polymerase chain reaction (PCR) protocol for 26S

PCR reactions were performed in 25 µl using the following reagents:

Reagents	Quantity
10x Reaction buffer (10x: 160mM $(NH_4)_2SO_4$, 670mM Tris-HCL (pH 8.8 at 25 °C) 0.1 % Tween-20) (Bioline, London, UK)	2.5 µl
$MgCl_2$ (50 mM) (Bioline, London, UK)	1.25 µl
dNTPs (0.2 mM) (Sigma Chemicals, Poole, Dorset, UK)	1.25 µl
forward primer: 0F (10mM) (MWG-Biotech AG, UK)	2 µl
reverse primer: 12R (10mM) (MWG-Biotech AG, UK)	2 µl
DMSO (Dimethyl Sulfoxide) (>99.9%) (Sigma-Aldrich Chemie GmbH, Germany)	2.5 µl
sterile, distilled water	5.4–9.4µl
DNA polymerase (5U/µl) (Bioline, London, UK)	0.125 µl
DNA	0.25–4 µl

The PCR cycling conditions used to amplify the region were:

Temperature	Time	Number of cycles
94°C	4 min	x1
93°C	1 min	
52°C	1 min	x35
72°C	3 min	
72°C	10 min	x1

5.4.4 Cloning techniques

PCR product reactions for some 26S and *trn*L-F were cloned because sequencing reactions had repeatedly failed. From subsequent sequence analyses it became clear that fungal contamination was the problem.

PCR products were cloned using the TOPO-TA cloning kit (Invitrogen, UK) using the bacterial plasmid vector system pCR4-TOPO and the host strain *E. coli* TOP10. The manufacturer's protocol was followed using 1 µl fresh PCR product for the TOPO cloning reaction. The bacterial colonies were grown on agar plates (25 g Luria-Bertani (LB) mix and 15 g agar per litre) containing the antibiotic ampicillin at 37°C overnight. The clones were screened for insert using PCR (following the same protocol as in 5.4.3.2). Eight to 24 positve colonies per species were transferred and cultured in a glass tube containing 2 ml LB broth and 50µg/ml of ampicillin at 37°C in an orbital shaker overnight.

Plasmids were purified, before sequencing, using the QIAprep Spin Miniprep Kit (QiagenLtd., Crawley, West Sussex) following the manufacturer's protocol.

5.4.5 Sequencing

Sequencing PCRs were performed and purified following the sequencing protocol in 5.4.5.1. For the 26 S the primer pair from before, as well as two internal primers 316F and 920R (LONG ET AL. 2005) were used for the sequencing PCR because there was often no overlap with the external primers and editing ambiguities could also be avoided. For *trn*L-F, both the forward primer developed by FREY ET AL. (1999) and the universal reverse primer *trn*L-f (TABERLET ET AL. 1991) were not specific enough for sequencing and a new forward primer was developed for this study (*trn*L-cAyto). The internal reverse primer *trn*L-d (FREY ET AL. 1999) was used to cover the intron in reverse but the short spacer sequence was obtained with forward primer *trn*L-cAyto only.

5.4.5.1 Sequencing Protocol for *trn*L-F and 26S

The sequencing reactions were performed using the purified PCR products and were carried out in 10 µl reactions.

Reagents	**Quantity (*trn*L-F)**	**Quantity (26S)**
Distilled sterile water	0.5–5.25	0.5–3.25
Betaine (99%) (Sigma-Aldrich Chemie GmbH, Germany)	-	2 µl
DNA template	0.25–5 µl	0.25–3 µl
Primer (10mM)	1 µl	1 µl
CEQ buffer*	1.5 µl	1.5 µl
DTCS Quickstart mix* (Dye Terminator Cycle Sequencing)	2 µl	2 µl

*CEQ reagents from Beckmann Coulter Ltd., U.S., primers *trn*L-cAyto, 316F and 920R from TAGN Ltd., Gateshead, UK, other primers from MWG-Biotech AG, UK.

Sequence amplifications were achieved using a Perkin Elmer Thermocycler PTC-200 PCR machine using the following conditions:

Temperature	**Time**	**Number of cycles**
96°C	2 min	
50°C	20 sec	35x
60°C	4 min	

5.4.5.2 Sequence reaction purification

The sequence reactions were purified as follows:

Reactions were made up to 20 µl with dH_2O and transferred to a fresh 0.5 ml microfuge tube. To each tube 5 µl of stop solution (stock B) (see below) and 60 µl of 100 % ice cold ethanol were added.

Stock B	**Volume per reaction**
0.5M EDTA (Beckmann Coulter Ltd., UK)	0.4 µl
Sigma water (Beckmann Coulter Ltd., UK)	1.6 µl
3M NaOAc pH 5.2 (Beckmann Coulter Ltd., UK)	2 µl
Glycogen (Beckmann Coulter Ltd., UK)	1 µl

The samples were mixed using a vortex mixer and centrifuged for 15 minutes at 4°C at 14 000 rpm. The supernatant was carefully removed and discarded. 200 µl of 70 % ice cold ethanol was added and the samples centrifuged at 4°C at 14 000 rpm. The supernatant was carefully removed again and discarded. The last step was repeated and the supernatant was removed and discarded again. The remaining pellet was vacuum dried on a low drying rate for 2 to 5 minutes until no trace of ethanol remained. Each pellet was then resuspended in 40 µl of sample loading solution (SLS) (Beckmann Coulter Ltd., UK) and mixed using a vortex mixer. Samples were stored at -20°C for storage and analysed using a Beckmann Coulter CEQ™ 8000 Analysis System DNA Sequencer (Beckmann Coulter Ltd., UK) by staff at RBGE.

Analysed sequences were edited using CEQ™ 8000 Genetic Analysis System Version 7.0 Software (Beckmann Coulter Ltd., US) and aligned in Sequencher™ Version 4.5 (Gene Codes Corporation, Ann Arbor, Michigan, US). The contig sequences were exported as text files for phylogenetic analysis. Sequences obtained from the cloning analysis were BLAST (Basic Local Alignment Search Tool) searched in GenBank (National Centre of Biotechnology Information (NCBI)). Results indicated that some obtained sequences were from fungal contaminants, mostly the filamentous fungi species *Phoma herbarum* Westendorp (family Pleosporaceae).

Additional 26S sequences were carried out by Michelle Hollingsworth, RBGE (*M. fragans, M. androgyna, A. africana, A. grollei, A. wallichiana, C. himalayense, P. rupestre, P. wrightii*).

5.4.6 Sequence alignment and gap coding

The alignment of both datasets, *trn*L intron and adjacent spacer and 26S was initially performed using ClustalW (European Bioinformatics Institute, UK). Alignments were achieved using the default settings and were later manually adjusted by eye. Some hypervariable or ambiguous regions were excluded from both datasets as they could not be aligned unambiguously (Appendix III). Regions with incomplete sequences (the beginnings and ends of sequenced regions) were also excluded from further analyses. The start (11 to 16 base pairs (bp) for *trn*L-F/26S) and the end (29 to 42 bp for *trn*L-F/26S) were left out. Nine gaps were coded from the *trn*L-F matrix using simple indel coding and the multistate gap region method (SIMMONS & OCHOTERENA 2000, SIMMONS ET AL. 2001, FREUDENSTEIN & CHASE 2001). The gaps present in the 26S matrix were considered too variable for indel coding. Separate analyses for both the *trn*L-F and 26S region, and a combined analysis were performed. The influence of the gap coding was investigated for both the *trn*L-F and combined data matrices through exclusion and inclusion of coded gap characters in both Parsimony and Bayesian analyses.

5.4.7 Phylogenetic analyses

For the phylogenetic reconstruction two different types of analyses were performed: Maximum Parsimony (MP) and Bayesian Analysis (BA). They were run on each of the three data sets with and without the inclusion of the gap matrix.

The MP method is based on the assumption that evolution takes place by the simplest way (CRAWFORD 1990). In MP the most parsimonious tree(s) is the tree that requires the minimum number of evolutionary changes to explain the data. But assumptions of minimal evolution are disputed by many cladists as it could underestimate the true number of changes. In MP it is assumed that a character state shared by two taxa is more likely to have been inherited from a common ancestor than that this character state has evolved more than once due to homoplasy (due to reversals, convergences, parallelisms) (HALL 2004).

BA tries to find the most probable tree(s) given the sequence data and the model of evolution (HALL 2004). BA considers that characters could have evolved more than once due to homoplasy and can allow for such changes. It compensates for these and is therefore considered to be superior in calculating distances compared to MP. It is a Likelihood method based on the concept of posterior probabilities. A tree search will look for the best set of trees and the same tree will often be considered several times during that process. In a BA it is possible to include information about evolutionary processes by different evolutionary models.

5.4.7.1 Parsimony analysis

Reconstruction of phylogenetic relationships based on the Maximum Parsimony Method (FELSENSTEIN 1983) was done in PAUP version 4.0b10 (SWOFFORD 2002). Phylogenetic trees were generated as phylograms, strict consensus and majority rule consensus trees.

Descriptive tree statistics were given by the consistency index (CI), homoplasy index (HI), retention index (RI) and rescaled consistency index (RC) (FARRIS 1989).

All trees were obtained from unweighted, unordered characters. Multistate characters were interpreted as uncertain and gaps were treated as missing. In the *trn*L-F matrix nine indels events were coded as additional characters.

For character optimisation the option 'accelerated transformation (ACCTRAN)' was used, which favours reversals. Starting trees were obtained via stepwise addition. Heuristic searches were performed for all analyses with 10 000 RANDOM addition sequence replicates using TBR with MULTREES on, STEEPEST DESCENT off and branches collapse if minimum branch length is zero.

For the morphological dataset multistate taxa were interpreted as polymorphism and 'delayed transformation (DELTRAN)' was used for character optimisation, which favours parallelisms. With these exceptions the analyses were done with the same settings as above.

Branch support analyses were carried out using Bootstrap (FELSENSTEIN 1985) and Decay Indices (BREMER 1988). Bootstrap values were calculated on 10 000 replicates with the same settings as above except with only 1 RANDOM addition replicate.

Sequence characteristics and tree statistics (see Appendix III) were calculated using PAUP and McClade version 4.06 OS X (MADDISON & MADDISON 1992).

Decay Index was calculated with default settings in AutoDecay v4.0 (ERIKSSON 1999).

To test combinability of datasets the Partition Homogeneity Test was performed in PAUP on 10000 replicates of 1 RANDOM addition sequence replicate using the same heuristic search settings as for the molecular analyses before.

5.4.7.2 Bayesian Analysis

Parameters and the evolutionary model used in the BA were selected using the program Modeltest 3.6 (POSADA & CRANDALL 1998) and are based on the Akaike Information Criterion (AIC). The AIC selects not only the evolutionary model that fits the data set best like the hierarchical Likelihood Ratio Tests (hLRTs) does. It also tries to measure the information, which is lost when a model is used to full reality in taking an increasing number of parameters into account and estimating their variation (POSADA & BUCKLEY 2004, POSADA & CRANDALL 2001). It is therefore said to have *"important advantages"* over hLRTs (POSADA & BUCKLEY 2004). However, both AIC and hLRTs analyses have been carried out. Parameters utilized for the BA are shown in Appendix III. The AIC selected model for the *trn*L-F dataset was TVM+I+G (Transversional Model) and for the 26S dataset TrN+I+G (TAMURA & NEI 1993 Model). The hLRTs selected the model F81+G (FELSENSTEIN 1981) for the *trn*L-F dataset and for the 26S data the same model as in AIC was selected. For the analyses four independent Monte Carlo Markov Chains (MCMC) were run simultaneously for 5 Mio generations, starting with a random tree and with one tree saved every 100 generations. The analyses were done with the inclusion of the gap matrix. Each dataset (26S, *trn*L-F, gap matrix) was treated as separate partition in the combined and the *trn*L-F analyses. For the 26S data set the MCMC temperature setting for the three heated chains was lowered from the default setting of 0.2 to 0.05 in a second run to observe the effect on the cold chain. The burn-in for each run was determined by plotting the log likelihood of the cold chain versus the number of generations in Microsoft Excel and the first 5000 trees were discarded. A majority rule consensus tree for the remaining trees was generated using PAUP. For each clade a confidence measure is given as a clade credibility or posterior probability value, which is the proportion of trees in which this clade is present.

5.5 Results from the molecular phylogenetic reconstruction

5.5.1 Sequence alignment

The aligned *trn*L-F matrix was of much shorter length (684 bp) than the 26S sequences (1229 bp). The aligned length of the combined dataset had a total of 1913 bp with an addition of nine gap characters when included.

Although the tree topologies from both analyses (exclusion and inclusion of gaps) were fully congruent, the analysis with the inclusion of gap characters was preferred as it allowed the inclusion of informative sites resulting in more highly resolved tree topologies and in some cases slightly higher branch support. This was particularly the case for the single analysis of *trn*L-F.

All statistical results are based on analyses with exclusion of gap characters. The characteristic features of the matrix (matrix and tree statistics) are summarised in Appendix III.

5.5.2 *trn*L-F

5.5.2.1 Sequence characteristics

The total length of the individual sequences ranged between 516 and 606 base pairs for the included 35 samples. Due to indel events (insertions/deletions) several gaps had to be inserted in the matrix and ambiguous parts were also excluded from the analysis. A gap matrix of nine additional characters was added to the alignment. Of the included 581 unambiguously aligned sites, 68% were constant. Of 32% variable sites, 13% were autapomorphies and therefore parsimony uninformative and 19% were informative characters. The transition to transversion ratio is 0.75 clarifying that transversion events are more frequent than transition, which is generally assumed. Sequence divergences in pairwise comparison were between 0 (e.g. *Mannia californica* (France) and *M. californica* (China)) and 10.5% (*Asterella lateralis* and *A. grollei*) among the Aytoniaceae; 0 (e.g. *M. californica* (North India) and *M. californica* (France)) and 6.5% (*M. pilosa* and *M. californica* France/India 104/India 105) among *Mannia*; 0 (e.g. *M. californica* 104 (North India) and *M. californica* 105 (North India)) and

3.9 % (Austria and France/North India 104/North India 105) among included *M. californica* species.

5.5.2.2 Tree topology (Fig. 5.1-5.4)

Maximum Parsimony

The parsimony analysis resulted in two most parsimonious trees of 386 steps if gap characters were included. The exclusion of nine gap characters resulted in nine trees (386 steps). The CI including uninformative characters was 0.69, the RI 0.78 and RC 0.53. The values are relatively low indicating that many characters were homoplastic. Branch support values were between one and 24 steps for the decay index and 53 to 100% for bootstrap values. The strict consensus tree is not fully resolved but shows better resolution when gap characters were included in the analysis (Fig. 5.1). Some branch support values also increased as a result. In the strict consensus tree of the two most parsimonious trees the ingroup consists of two main clades: clade A and clade B. Clade A consists of *Asterella grollei* and all *Cryptomitrium* species (bootstrap 60, d = 1). Clade B has high support (bootstrap 82, d = 3). Within it three supported remaining clades (B1-B3) fall on a polytomy sister to *A. californica*. However, when gaps are excluded *A. californica*, Clade B1, B2 and B3 rest on a polytomy. Clades B1, B2 and B3 do not have high or any branch support values and all rest on a polytomy. Clade B1 consists of *Reboulia hemisphaerica* as sister to all *Plagiochasma* species (bootstrap 63, d = 1), clade B2 is not supported and contains exclusively *Asterella* species (bootstrap < 50%, d = 1) and clade B3 consists of all included *Mannia* species and *Asterella gracilis* (bootstrap 67%, d = 2). *Asterella* is thus polyphyletic with its sister genera *Reboulia, Cryptomitrium, Plagiochasma* and *Mannia* nesting within it; the monophyly of the ingroup (Aytoniaceae) is supported by high branch support values (bootstrap 96%, d = 8). There is moderate support for monophyly of the included *Mannia* samples and *A. gracilis* (bootstrap 67%, d = 2).

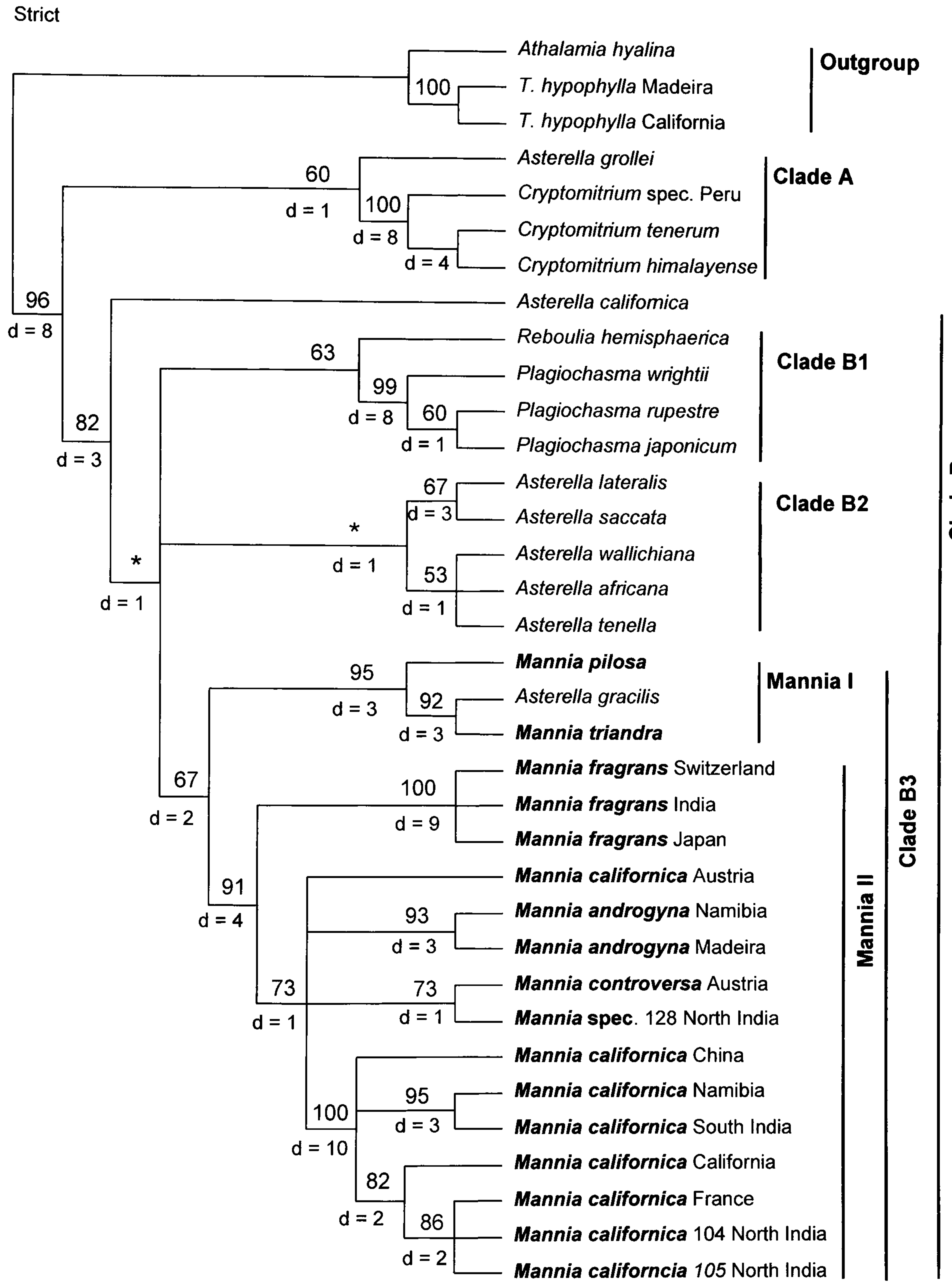


Fig. 5.1. Strict consensus tree of two trees based on *trn*L-F sequences with a heuristic search including gap characters using unweighted maximum parsimony analysis *trn*L-F data. (Tree length = 386 steps; CI = 0.69; RI = 0.78; RC = 0.53). Numbers above branches indicate bootstrap support; *asterisk indicate bootstrap < 50%; numbers below branches indicate decay indices.

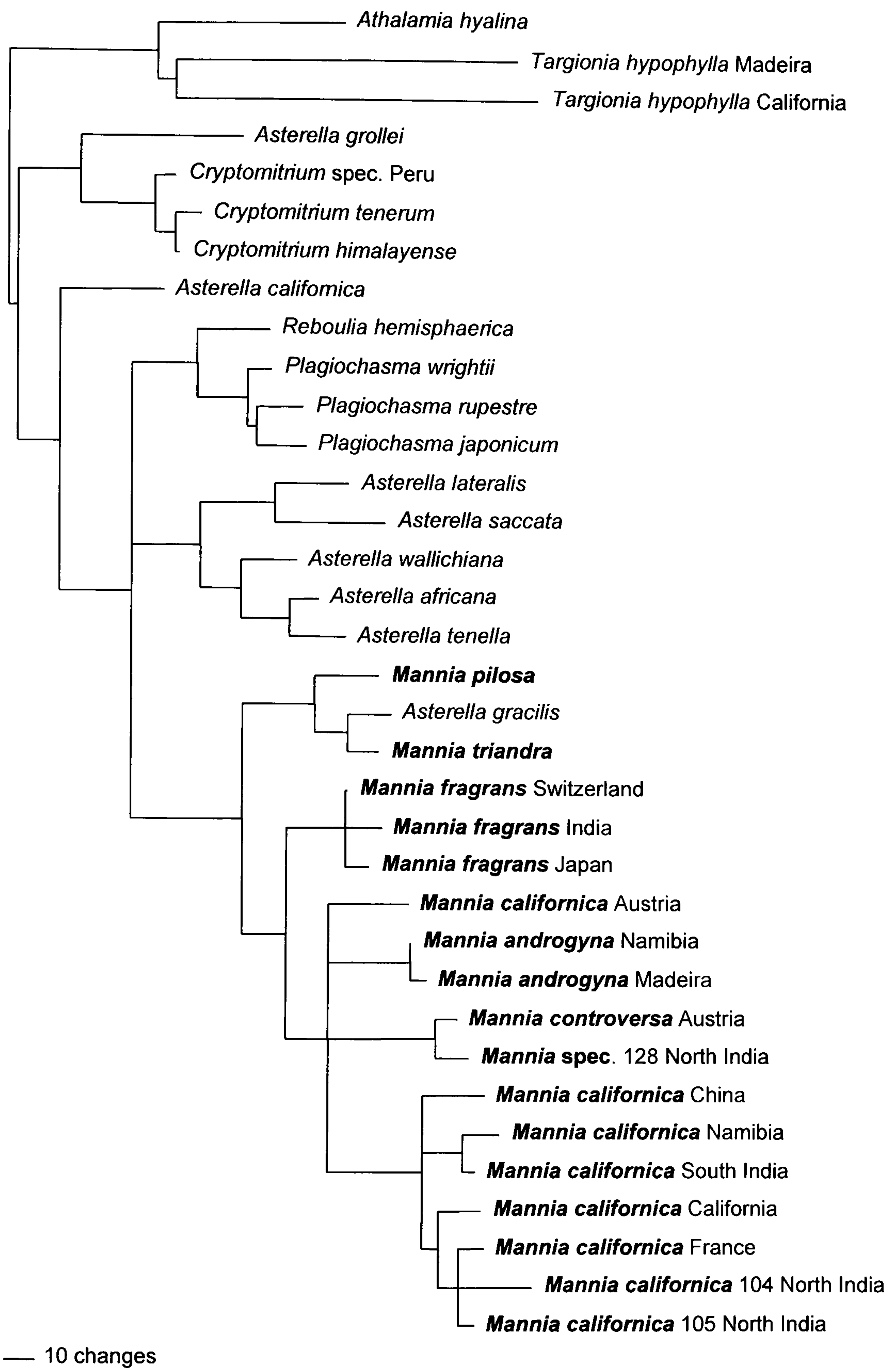


Fig. 5.2. Tree one of two trees based on *trn*L-F sequences with a heuristic search including gap characters using unweighted maximum parsimony analysis. (Tree length = 386 steps; CI = 0.69; RI = 0.78; RC = 0.53).

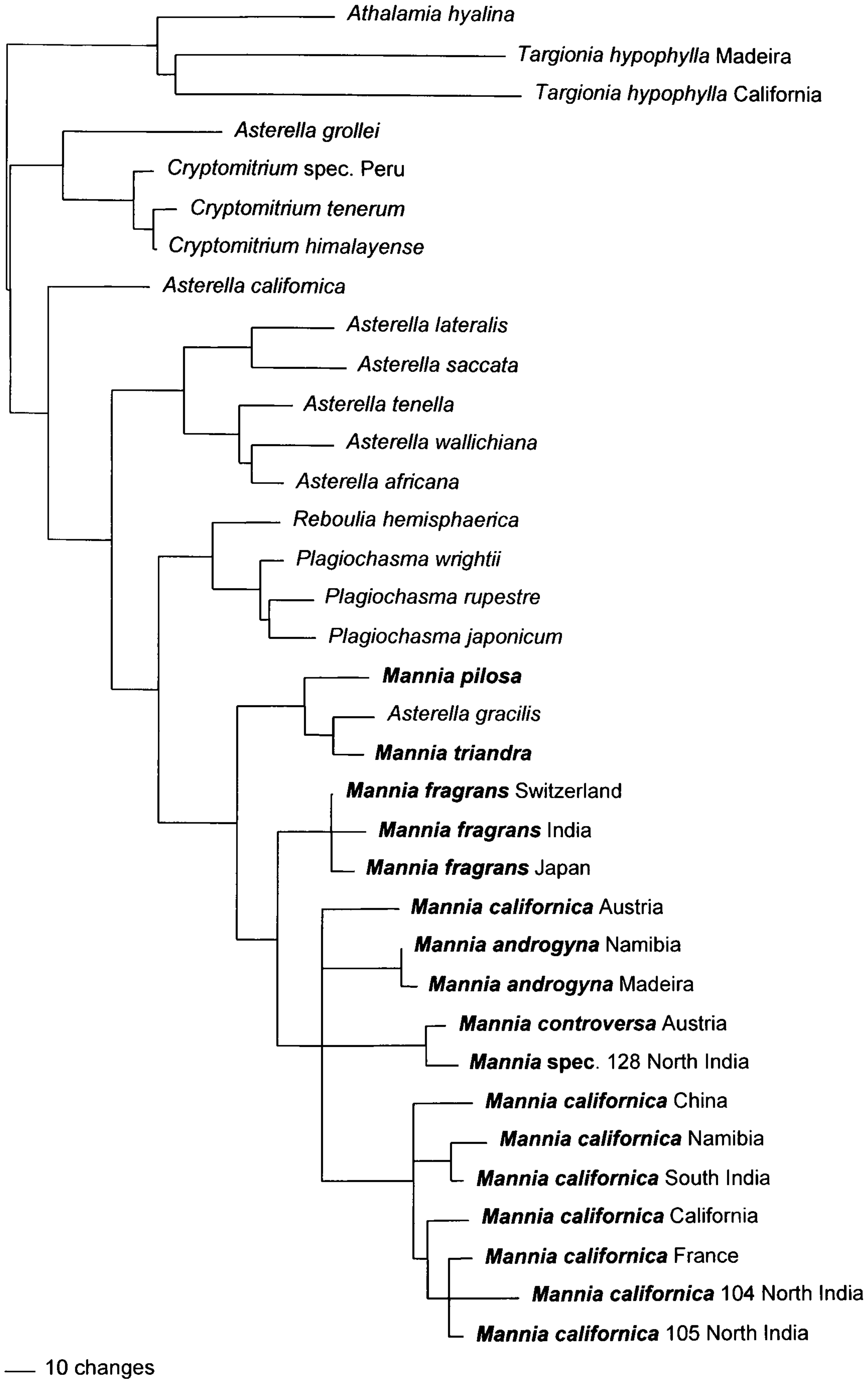


Fig. 5.3. Tree two of two trees based on *trn*L-F sequences with a heuristic search including gap characters using unweighted maximum parsimony analysis. (Tree length = 386 steps; CI = 0.69; RI = 0.78; RC = 0.53).

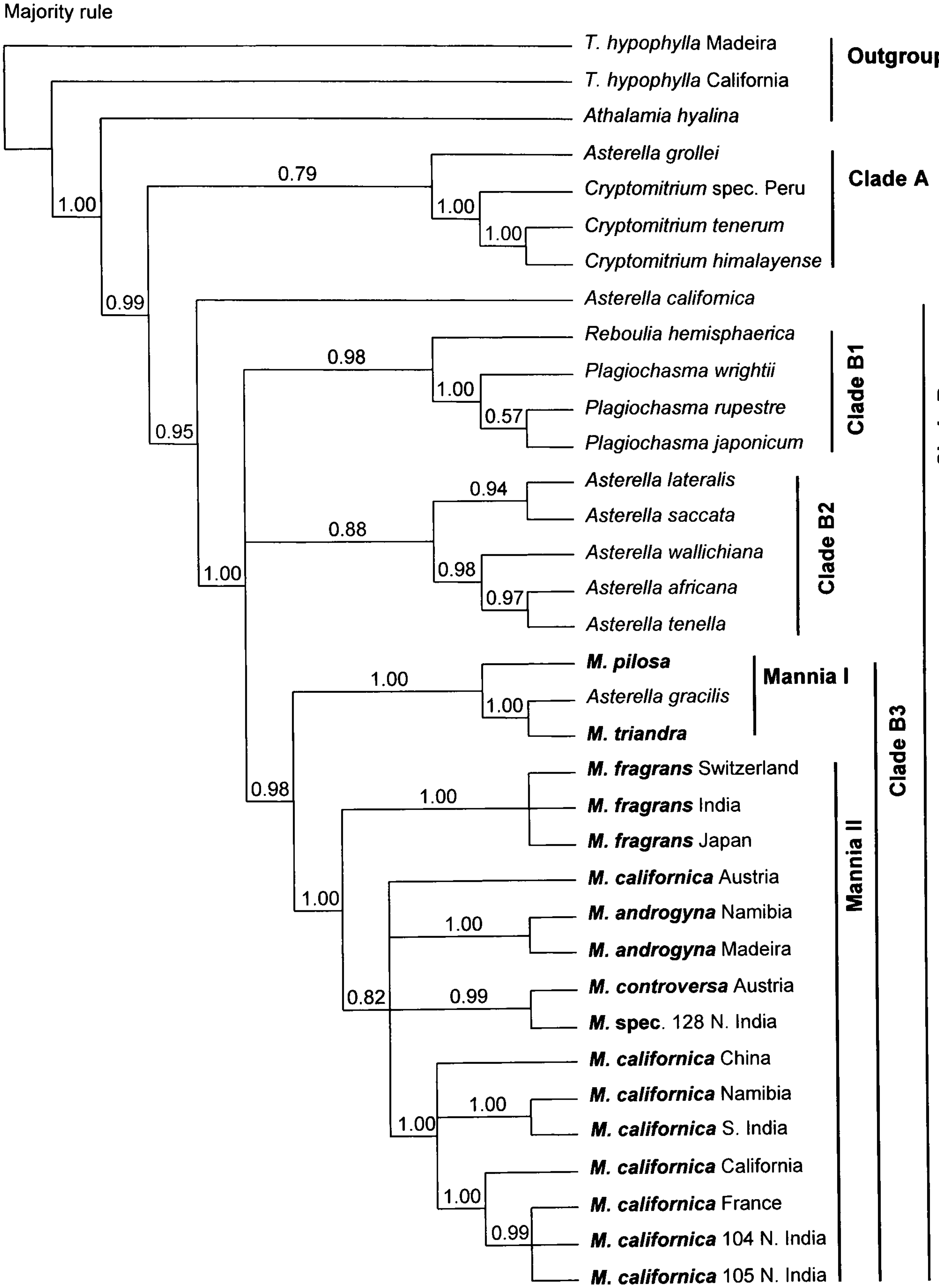


Fig. 5.4. Bayesian majority rule consensus tree obtained from a *trn*L-F data matrix with the inclusion of gap characters. Figures above branches are estimated posterior probability values.

There is high support for the genus *Mannia* falling into two main clades (bootstrap 95%, d = 3 and 91%, d = 4). One *Mannia* clade (Mannia I) contains *M. pilosa* as sister to *M. triandra* and *A. gracilis*, which shows high branch support (bootstrap 95%, d = 3) suggesting paraphyly of *Mannia*. The second *Mannia* clade (Mannia II) (bootstrap 91, d = 4) is a 'pure' *Mannia* clade containing *M. fragrans* species (bootstrap 100%, d = 9) as sister to the remaining *Mannia* species (bootstrap 73, d = 1).

The remaining *Mannia* species are on a polytomy, *M. androgyna* Madeira/Namibia (bootstrap 93, d = 3), *Mannia controversa/M. spec.* Austria/North India (bootstrap 73, d = 1) and one strongly supported clade with all *M. californica* specimens (bootstrap100 %, d = 10) with the exception of the Austrian *M. californica*, which remains on the polytomy.

Bayesian analysis

The topology of the Bayesian AIC majority rule consensus tree (Fig. 5.4) resulting from an analysis with inclusion of gaps was almost identical to the MP analysis. It showed a fully resolved clade B2 unlike the MP strict consensus tree. The posterior probability values (pp) for different clades were generally higher than the bootstrap or decay supports. It ranged from 0.57-1.00. The tree topology based on hLRTs was fully congruent with similar pp values.

5.5.3 26S

5.5.3.1 Sequence characteristics

The total length of the individual sequences was between 1059 and 1136 bp. Several gaps were inserted in the matrix and ambiguous regions were excluded from the analysis. The mean G + C content of 57. 75% is higher than the chloroplast data set which is common for nuclear regions.

The aligned region included 1076 unambiguous characters of which 87% were constant. Of 13% variable sites, 5% were uninformative and 8% were informative characters. The relation of transitions to transversions was 0.8 and so only slightly higher than in the *trn*L-F dataset.

Sequence divergence in pairwise comparison was between 0 (*Mannia californica* 105 India and *M. californica* France/ *M. californica* South India) and 4.3% (*M.*

californica 104 North India and *Asterella africana*) among the Aytoniaceae and 0 (*Mannia californica* 105 India and *M. californica* France/ *M. californica* South India) and 3.1% (*M. californica* 104 North India and *M. californica* Austria) among *Mannia*. The latter figures also apply to the sequence divergences among *M. californica* specimens.

5.5.3.2 Tree topology (Fig. 5.5-5.7)

Maximum Parsimony

The analysis resulted in 33 most parsimonious trees with a tree length of 315 steps. CI including uninformative characters was 0.58, RI 0.74 and RC 0.43 and therefore all lower than in the *trn*L-F analysis. The decay indices for clades ranged between 1 and 26 steps; the bootstrap values were between 53 and 100%. The strict consensus tree of the 26S data set (Fig. 5.5) is also not fully resolved but shows a similar topology to the *trn*L-F strict consensus with a few exceptions. The branch support values are generally lower than in the *trn*L-F analysis.

Clade A fell on a polytomy which also contains *A. californica*. Within clade A *A. grollei* is no longer sister to the clade of all *Cryptomitrium* species. The *Cryptomitrium* clade has strong branch support as in the *trn*L-F analysis (bootstrap 99, d = 6). *R. hemisphaerica* is no longer within Clade B1. The *Plagiochasma* species are now sister to Mannia I and Mannia II though this is not supported (bootstrap < 50%, d = 1).

Branch support values for the monophyly of *Mannia* and *A. gracilis* is higher than in the *trn*L-F analysis (bootstrap 84%, d = 5). Mannia II is highly supported (bootstrap 87, d = 4). In Mannia II the *M. fragrans* group is no longer at the base of the clade but rests on a polytomy with the *M. controversa*/*M. spec.* species pair and a clade bearing the other *Mannia* species. This was well supported in the *trn*L-F analysis, but not with 26S. All *M. californica* specimens are now clustering together (bootstrap 73%, d = 1) with the Austrian specimen being sister to the other *M. californica* specimens, which form a well supported clade (bootstrap 98%, d = 5).

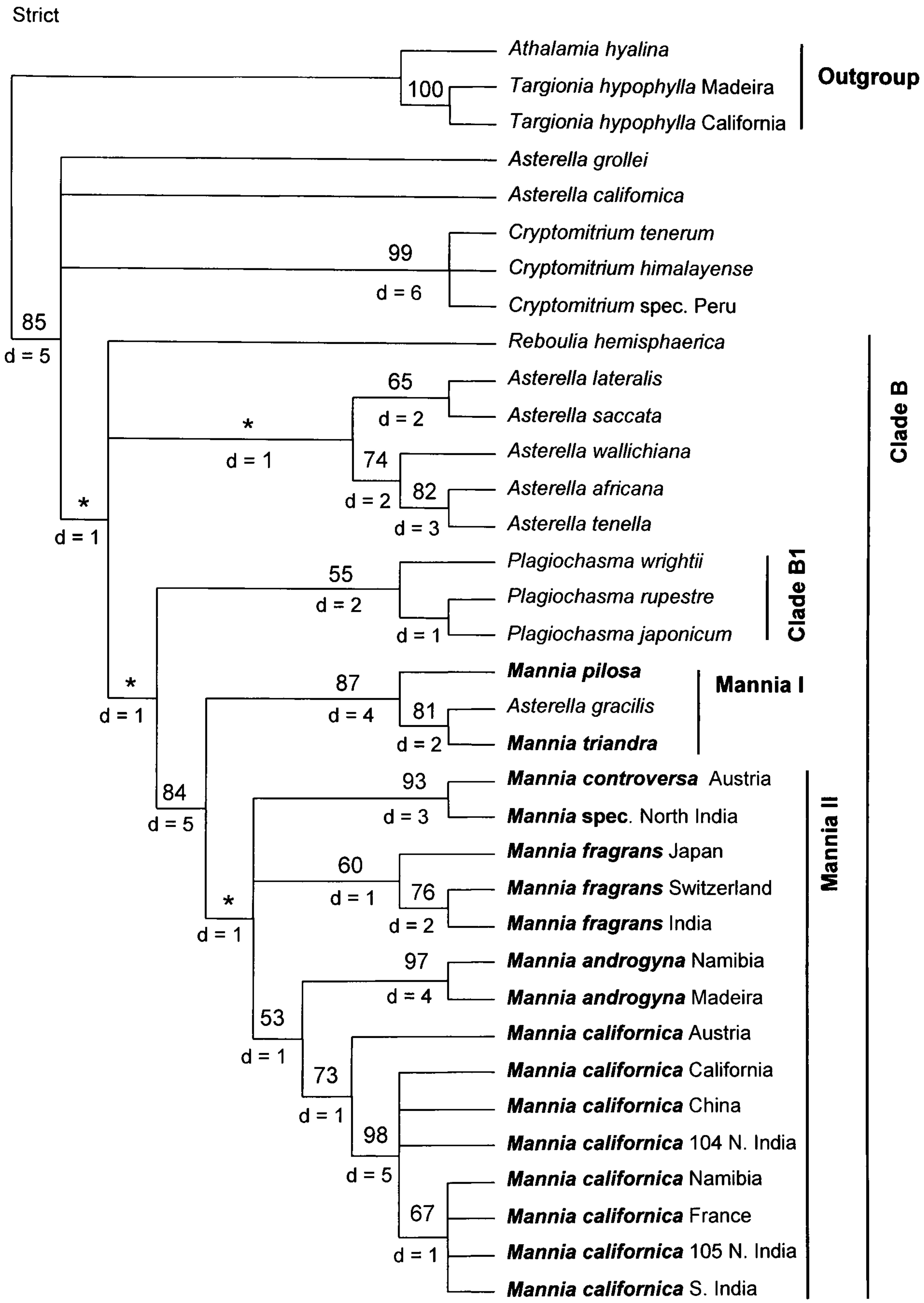


Fig. 5.5. Strict consensus tree of 33 trees based on 26S sequences with a heuristic search using unweighted maximum parsimony analysis. (Tree length = 315 steps; CI = 0.58; RI = 0.74; RC = 0.43). Numbers above branches indicate bootstrap support; *asterisk indicate bootstrap support < 50%; numbers below branches indicate decay indices.

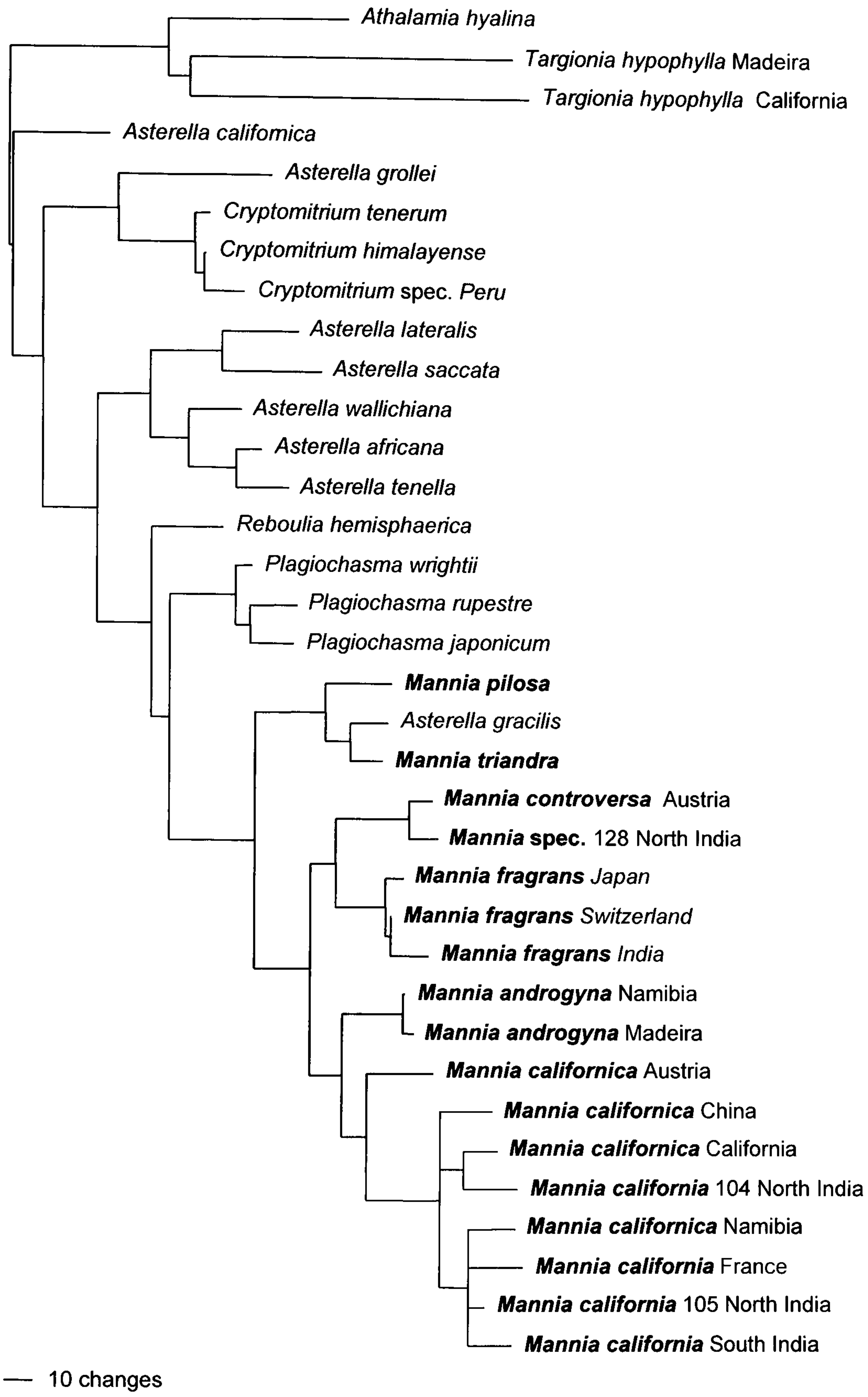
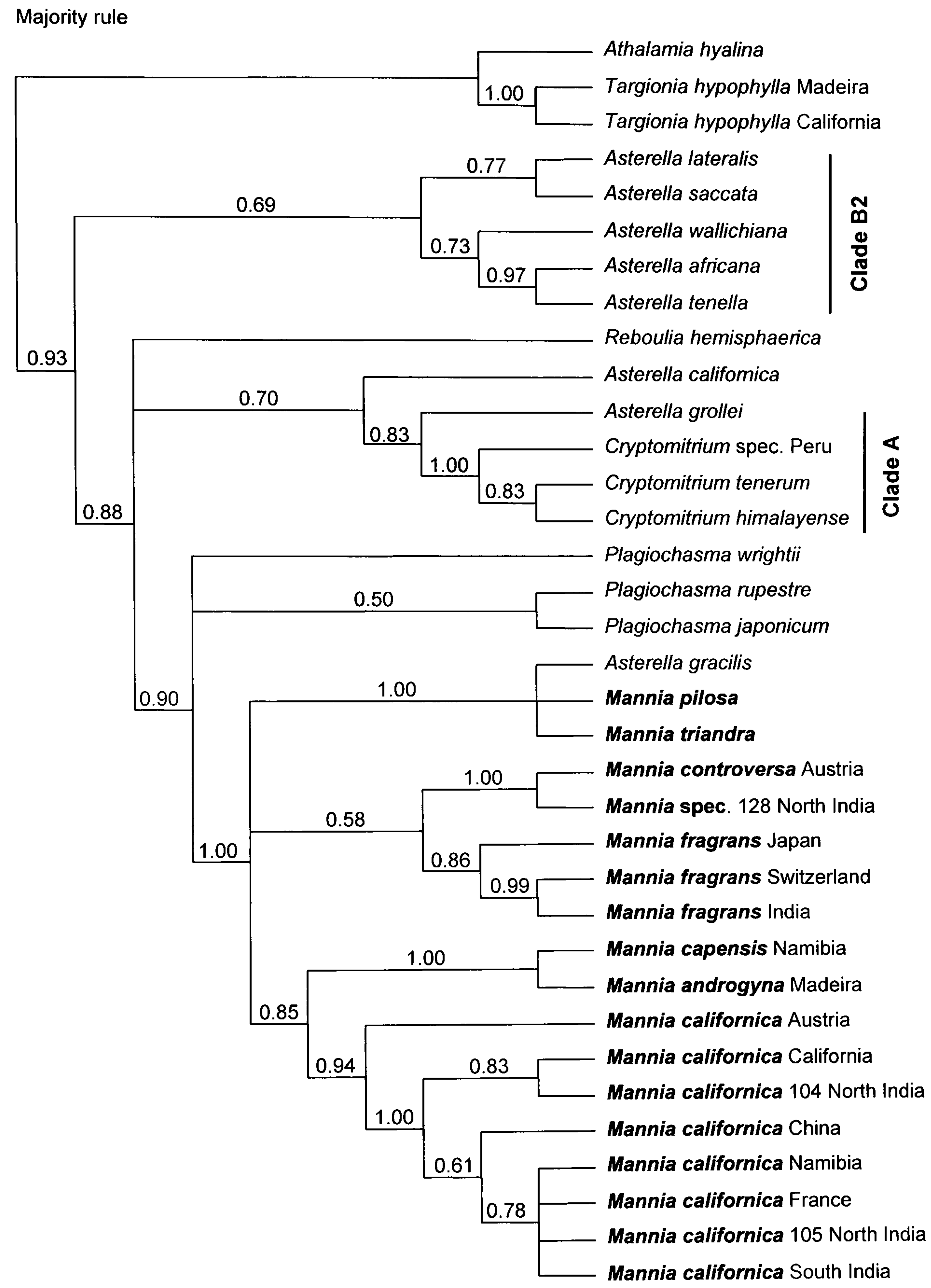


Fig. 5.6. Tree one of 33 most parsimonious trees based on 26S sequences with a heuristic search using unweighted maximum parsimony analysis of 26S data. (Tree length = 315 steps; CI = 0.58; RI = 0.74; RC = 0.43).



Fig, 5.7. Bayesian majority rule consensus tree obtained from a 26S data matrix. Temp= 0.05. Figures above branches are estimated posterior probability values.

Bayesian Analysis

The topology of the majority rule consensus tree of the BA (Fig. 5.7) was in parts not fully congruent to the MP strict consensus tree. The main difference was that clade B2 and clade A swapped places (pp 0.69, pp 0.88). Clade B2 was now found sister to the rest of the ingroup. In the latter *A. californica* is now sister to *A. grollei* and the *Cryptomitrium* clade. The position of *A. californica*, *A. grollei* and the *Cryptomitrium* clade was formerly unresolved and they were on a polytomy with clade B.

The relation between the three *Cryptomitrium* species is here fully resolved as well. In Mannia I *Asterella gracilis*, *M. triandra* and *M. pilosa* form a well supported clade (pp 1.00). The *M. fragrans* clade is here sister to the *M. controversa*/*M. spec.* clade though this is only weakly supported (pp 0.58). Within *M. californica* the Californian and North Indian specimen form a species pair and are sister to a weakly supported clade (pp 0.61), in which the Chinese specimen is now sister to the remaining *M. californica* specimens, which are resting on a polytomy as before in the MP strict consensus tree. The tree topology based on hLRTs was fully congruent with similar pp values.

5.5.3.3 Note on Bayesian search settings

In the first run of the 26S data set in the BA it became apparent that the cold chain did not change column position any more after the first 1000 generations and got stuck in one of the columns. The Metropolis coupling is said to be inefficient if the heated chains do not successfully swap states with the cold chain during the search. In that case RONQUIST ET AL. (2005) suggested lowering the temperature difference between the chains resulting in an increase of swapping states. A second run with a lowered temperature parameter was therefore conducted but the same thing could be observed though the proportion of successful exchanges was twice as high. The tree topologies and posterior probabilities were compared and found to be congruent with insignificantly higher posterior probability values for the default setting. A possible reason for the unchanging position of the cold chain could lie in the not very variable 26S data matrix.

5.5.4 Combined analysis

The Partition Homogeneity Test showed no significant incongruence between the two molecular data sets (0.447), so the *trn*L-F and 26S dataset could be combined. However, the combined molecular dataset was incongruent with the morphological data (0.001) so molecular and morphological datasets were not combined.

5.5.4.1 Sequence characteristics

The aligned length of the combined dataset was 1922 characters with nine gap characters included. The total length of the individual sequences was 1582 to 1712 basepairs.

After exclusion of ambiguous sites the aligned region included 1657 characters (excl. gap characters), 80% were constant characters. Of 20% variable sites, 8% were uninformative and 12% informative sites. The transition/transversion ratio in the combined analysis was with 0.81 only slightly higher than in the single analyses.

Sequence divergence in pairwise comparison was between 0 (*M. californica* 105 North India and *M. californica* France) and 5.7% (*Asterella grollei* and *M. pilosa*/*M. californica* 104 North India) among the Aytoniaceae and 0 (*M. californica* 105 North India and *M. californica* France) and 4.3% (*M. californica* 104 North India and *M. pilosa*) among *Mannia*; sequence divergences among *M. californica* species were between 0 (*M. californica* 105 North India and *M. californica* France) and 2.9% (*M. californica* Namibia and *M. californica* Austria).

5.5.4.2 Tree topology (Fig. 5.8-5.10)

Maximum Parsimony

The combined analysis resulted in 20 most parsimonious trees of 697 steps if gap characters were excluded. Their inclusion resulted in 40 trees of 709 steps. For the latter the CI was 0.63, RI 0.75 and RC 0.48. Branch support values were between 59 and 100% and the decay indices ranged between 1 and 50 steps for different clades. They were slightly higher when gaps were included in the analysis.

The strict consensus tree of the combined analysis is not fully resolved. Both consensus trees were fully congruent with the exception that there is better resolution of Mannia II when gap characters were excluded (data not shown). This has only weak support though (d =1, bootstrap < 50%). The strict consensus of the combined analysis (Fig. 5.8) shows a more similar topology to the consensus of the *trn*L-F analysis. An exception to this is that *R. hemisphaerica* is no longer sister to the *Plagiochasma* species in clade B1 from the *trn*L-F analysis but rests on a polytomy. The genus *Asterella* is polyphyletic with its sister genera nesting within them. Both *Plagiochasma* and *Cryptomitrium* form well-supported clades with high branch support values. However, the relationship of *Reboulia hemisphaerica* to the other samples is not clear and it resides on a large polytomy.

As before, *Mannia* separated into two main clades (Mannia I and Mannia II) with *Asterella gracilis* nesting in *Mannia* I (bootstrap 100 %, d = 6). In Mannia II the *M. fragrans* group is no longer sister to the rest of the *Mannia* species. It forms a well-supported clade (100% bootstrap, d = 9) but rests on a polytomy together with a well-supported species pair *M. spec./M. controversa* (99% bootstrap, d = 5) and a clade containing the rest of the *Mannia* species (75% bootstrap, d = 2).

The topology in the remaining clade is similar to the 26S MP tree but has higher branch support values. All *M. californica* species are found together in one clade (79% bootstrap, d = 1) as before in the 26S tree topology but their positions vary slightly. The Austrian specimen is still sister to the rest of the specimens. This clade forms a polytomy though. It contains the Chinese specimen, the well-supported species pair from Namibia/South India (bootstrap 96, d = 3) and a weakly-supported clade with the rest of the specimens forming a polytomy.

Bayesian analysis

The Bayesian majority rule consensus tree (Fig. 5.10) resulting from an analysis with the inclusion of gaps was fully congruent to the strict consensus tree of the combined analysis with two exceptions. The position of *Reboulia hemisphaerica* as sister to the *Plagiochasma* clade has high clade credibility values (pp 0.99) in the BA. The deeper nodes of some *M. californica* specimens,

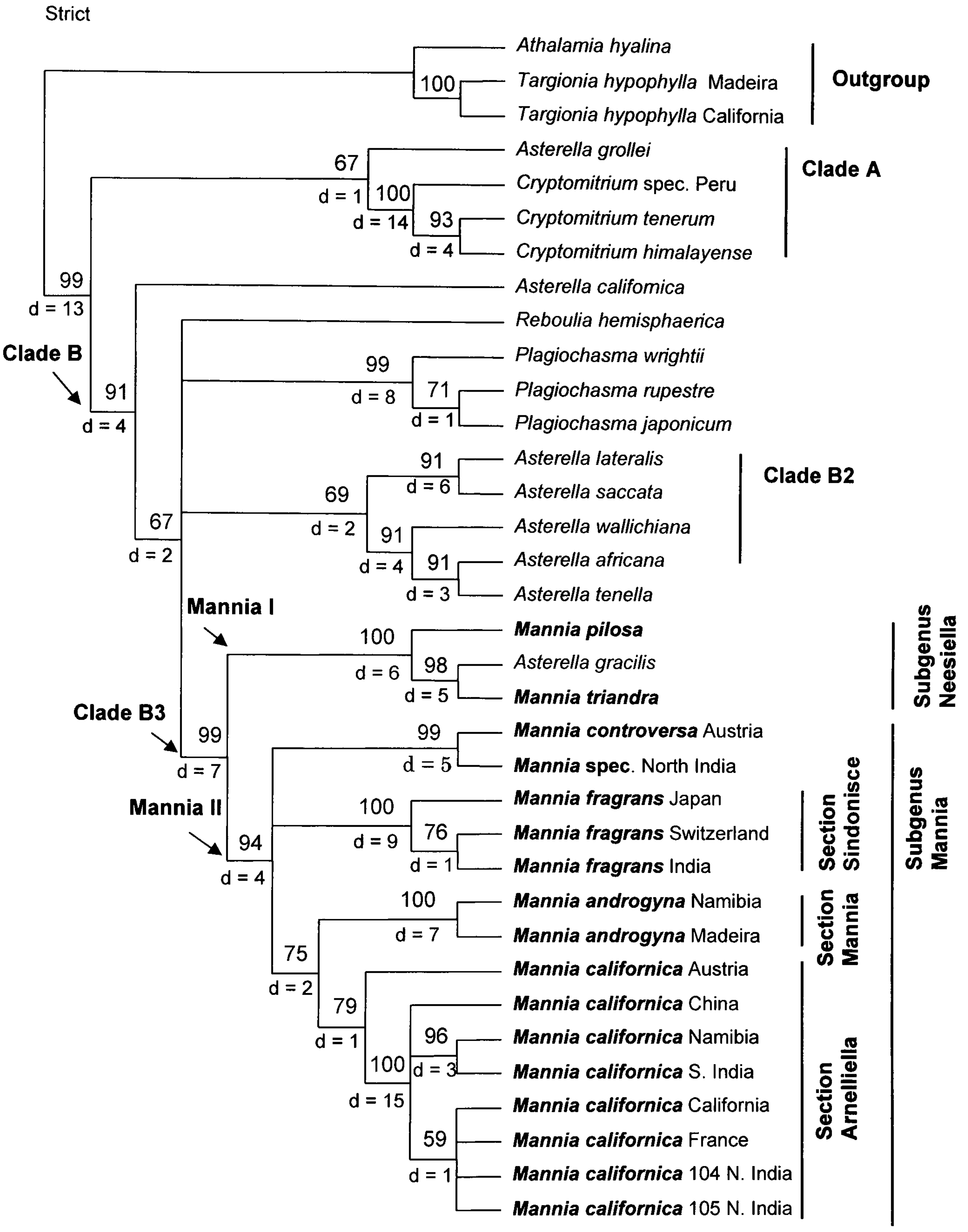


Fig. 5.8. Strict consensus tree of 40 trees based on a combined analysis including gap characters using unweighted maximum parsimony analysis of *trn*L-F and 26S data. (Tree length = 709 steps; CI = 0.63; RI = 0.75; RC = 0.48). Numbers above branches indicate bootstrap support; numbers below branches indicate decay indices.

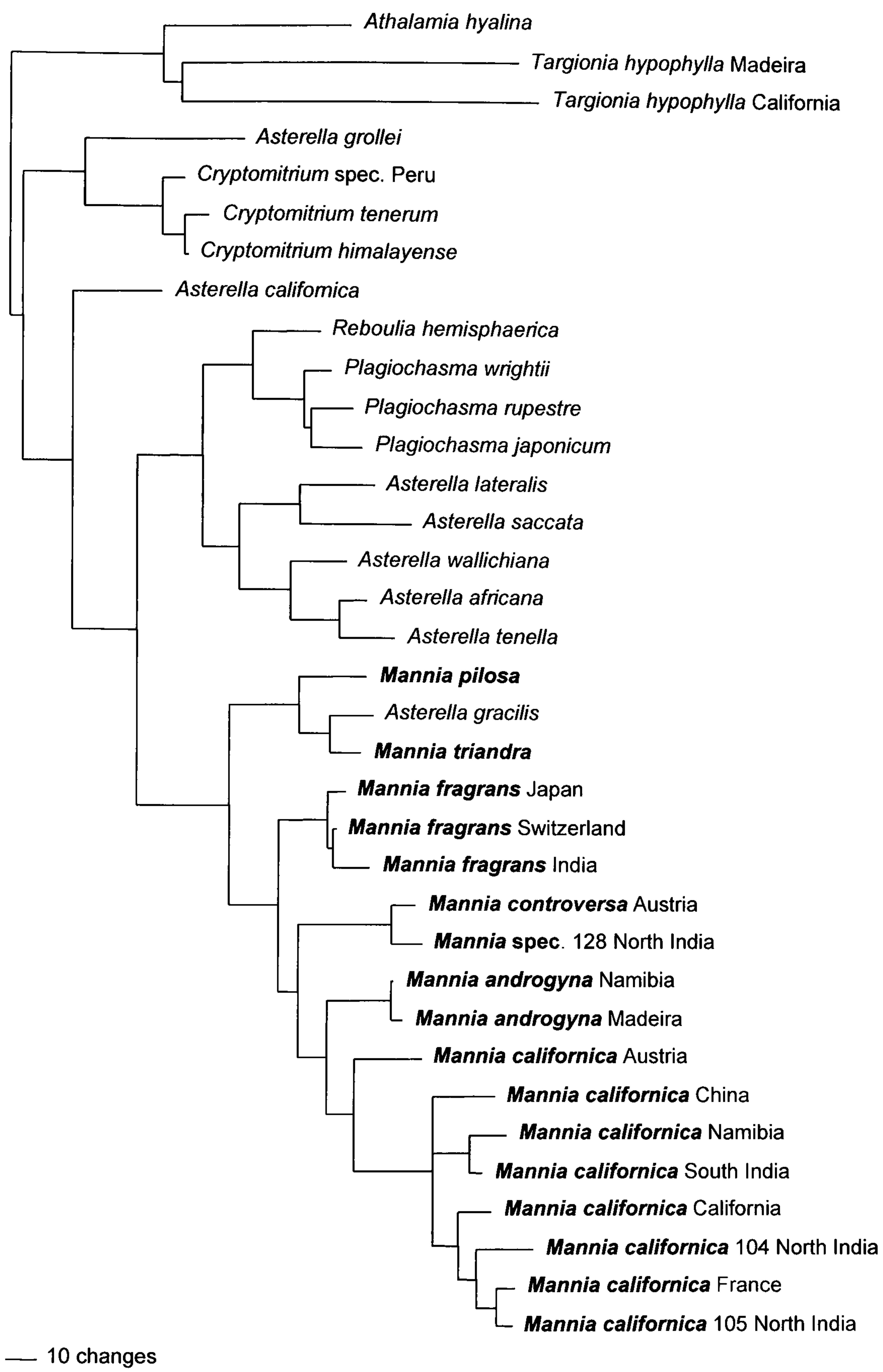


Fig. 5.9. Tree one of 40 trees based on a combined analysis including gap characters using unweighted maximum parsimony analysis of *trn*L-F and 26S data (Tree length = 709 steps; CI = 0.63; RI = 0.75; RC = 0.48).

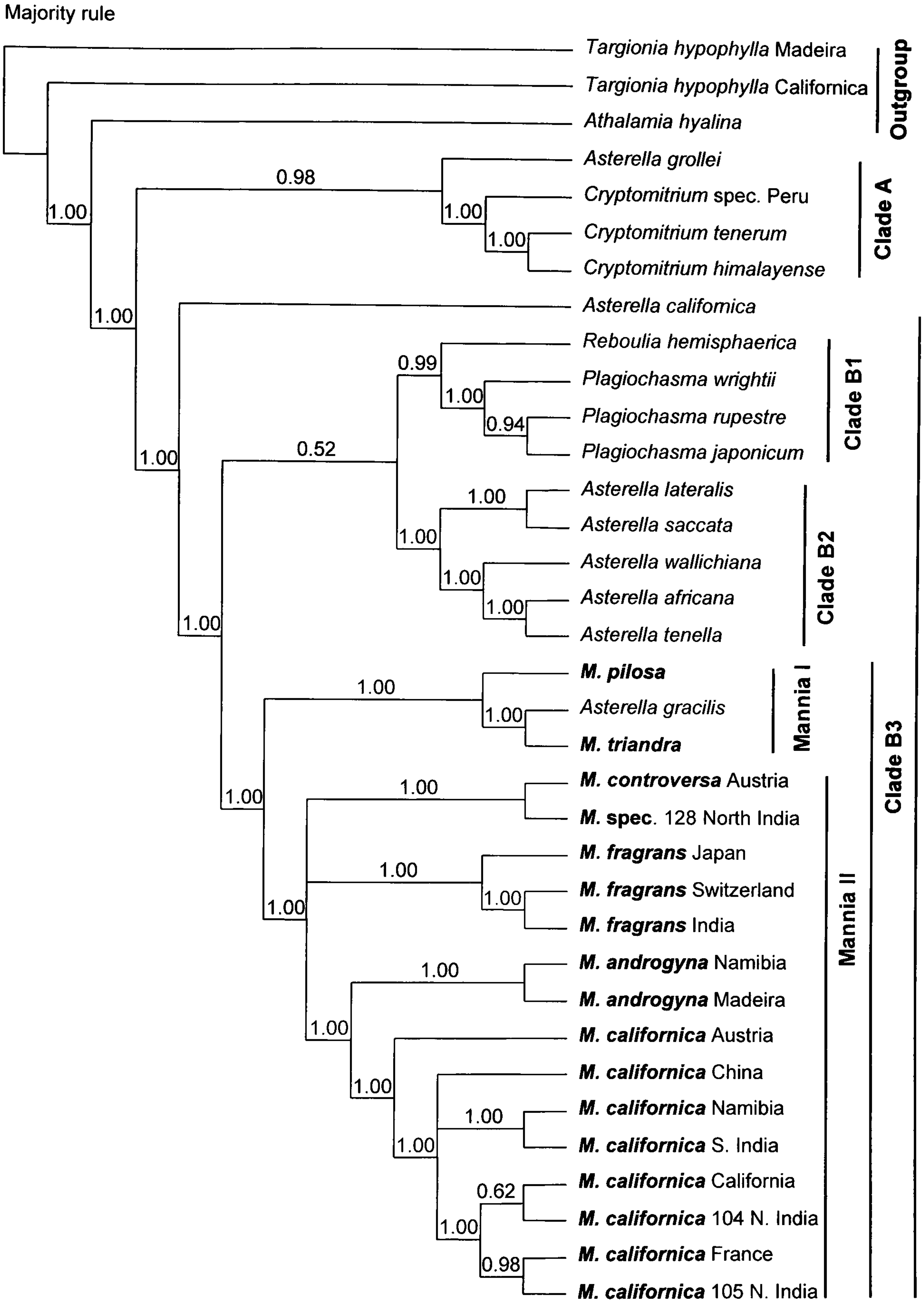


Fig. 5.10. Bayesian majority rule consensus tree obtained from a combined *trn*L-F and 26S data matrix with the inclusion of gap characters. Figures above branches are estimated posterior probability values.

which were formerly resting on a polytomy with low branch support (bootstrap 59, d = 1) in the MP have high clade credibility values in the BA (pp 1.00). The two species pairs (California/ North India 104 with pp 0.62 and France/North India 105 with pp 0.98) are forming sister clades with low to high clade credibility values. The clade probability values in BA were generally higher than the MP branch support values, ranging between 0.52 and 1.00.

5.5.5 Molecular phylogenetics versus spore types

The classification of *Mannia* based on different spore types as presented in Chapter 3 is reflected in the molecular results. However, *M. sibirica* and *M. asiatica* are not included in the molecular analysis, which may influence the molecular phylogeny. Nevertheless, at present there is no conflict between the molecular results and the classification based on spore characters.

5.6 Results of the morphological reconstruction

5.6.1 Morphological phylogeny

5.6.1.1 Tree topology (Fig. 5.11-5.14)

A heuristic search was performed with 23 taxa using *Targionia hypophylla* and *Athalamia hyalina* as outgroup taxa. The analysis resulted in 76 most parsimonious trees. The length of the trees was 142 steps. All 24 characters were parsimony informative. The Consistency Index (CI) was 0.54, Homoplasy Index (HI) 0.62, Retention Index (RI) 0.61 and the Rescaled Consistency Index (RC) was 0.33. The bootstrap values ranged between 55 and 96 %, decay index between 1 and 2.

The strict consensus tree (Fig. 5.11) of the morphological analysis is not well resolved with most of the ingroup taxa resting on a large polytomy. Although *A. hyalina* was defined as an outgroup taxon it is also found nesting in the ingroup. Two ingroup taxa (*A. africana* and *A. lateralis*) are situated outside the main group at the base of the tree. Most ingroup taxa are resting on a large polytomy of a weakly supported clade (bootstrap 55%, d = 1). Within this clade two species pairs (*Cryptomitrium himalayense* and *C. tenerum*; *Mannia pilosa* and *M. triandra*) are building separate clades with good branch support (96% and 82% respectively, both d = 2).

In the majority rule consensus tree (Fig. 5.12) most ingroup taxa are still resting on a polytomy sister to *Asterella lateralis* but form four clades (A-D). *M. asiatica* and *M. fragrans* remain on the polytomy. Clade A consists of *M. pilosa* and *M. triandra*, B has *Reboulia hemisphaerica* sister to the *Plagiochasma* species and C has *M. sibirica* sister to a *M. androgyna/M. californica* clade. Clade D consists of three clades (D1-D3): the species pair *A. californica* and *A. wallichiana* (D1), *A. hyalina* sister to the *Cryptomitrium* species (D2) and in the third clade *A. grollei* is sister to *A. palmeri* and *A. tenella* (D3).

In indivual phylograms (Tree one and tree eight) the seven included *Mannia* species are either monophyletic or paraphyletic (Fig. 5.13 and Fig. 5.14).

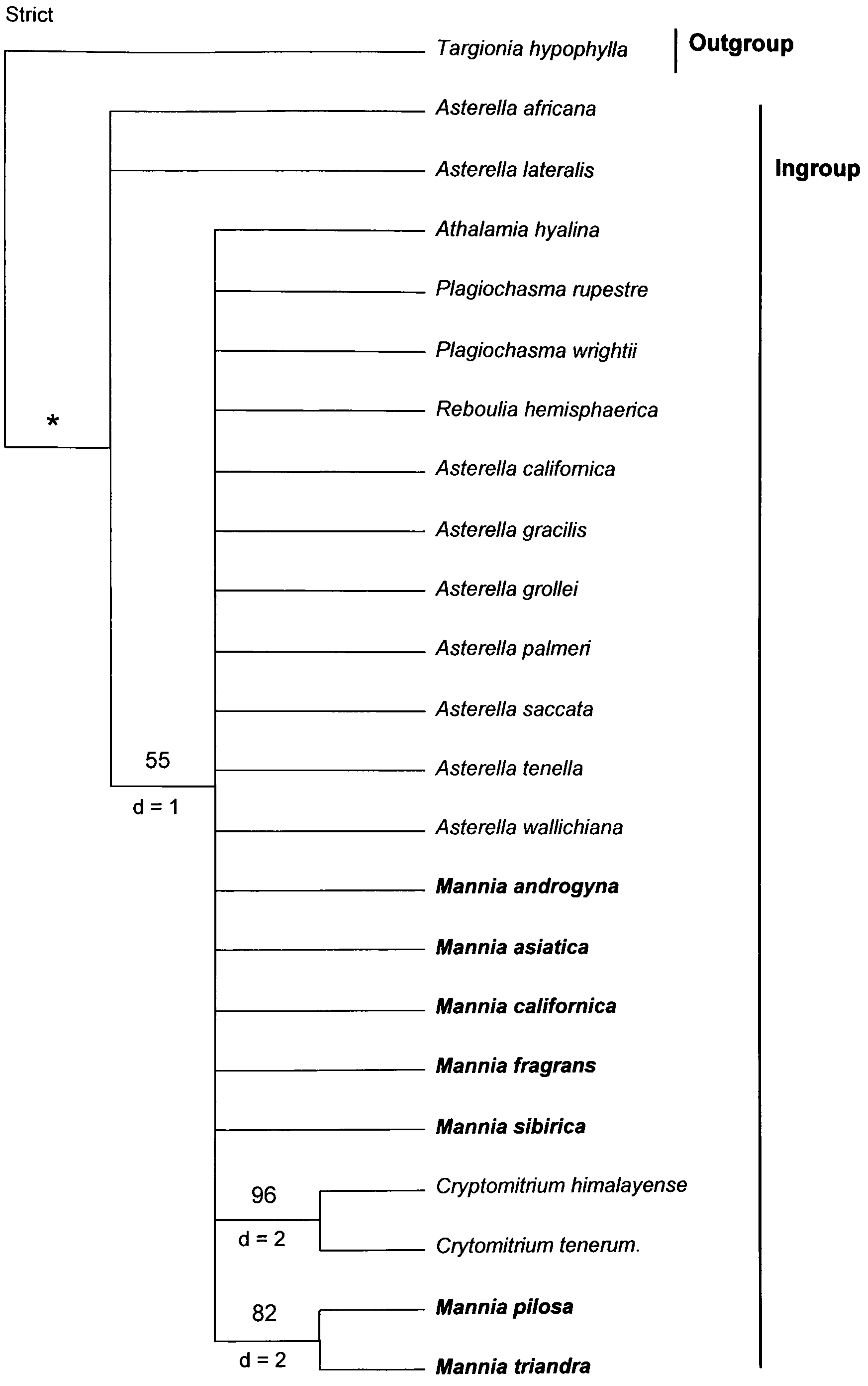


Fig. 5.11. Strict consensus tree of 76 most parsimonious trees (tree length = 142, CI = 0.53; RI = 0.61; RC = 0.33) based on 24 morphological characters for 23 taxa with an exhaustive search using unweighted parsimony. Numbers above branches indicate bootstrap support; *asterisk indicate bootstrap support < 50%, numbers below branches indicate decay indices.

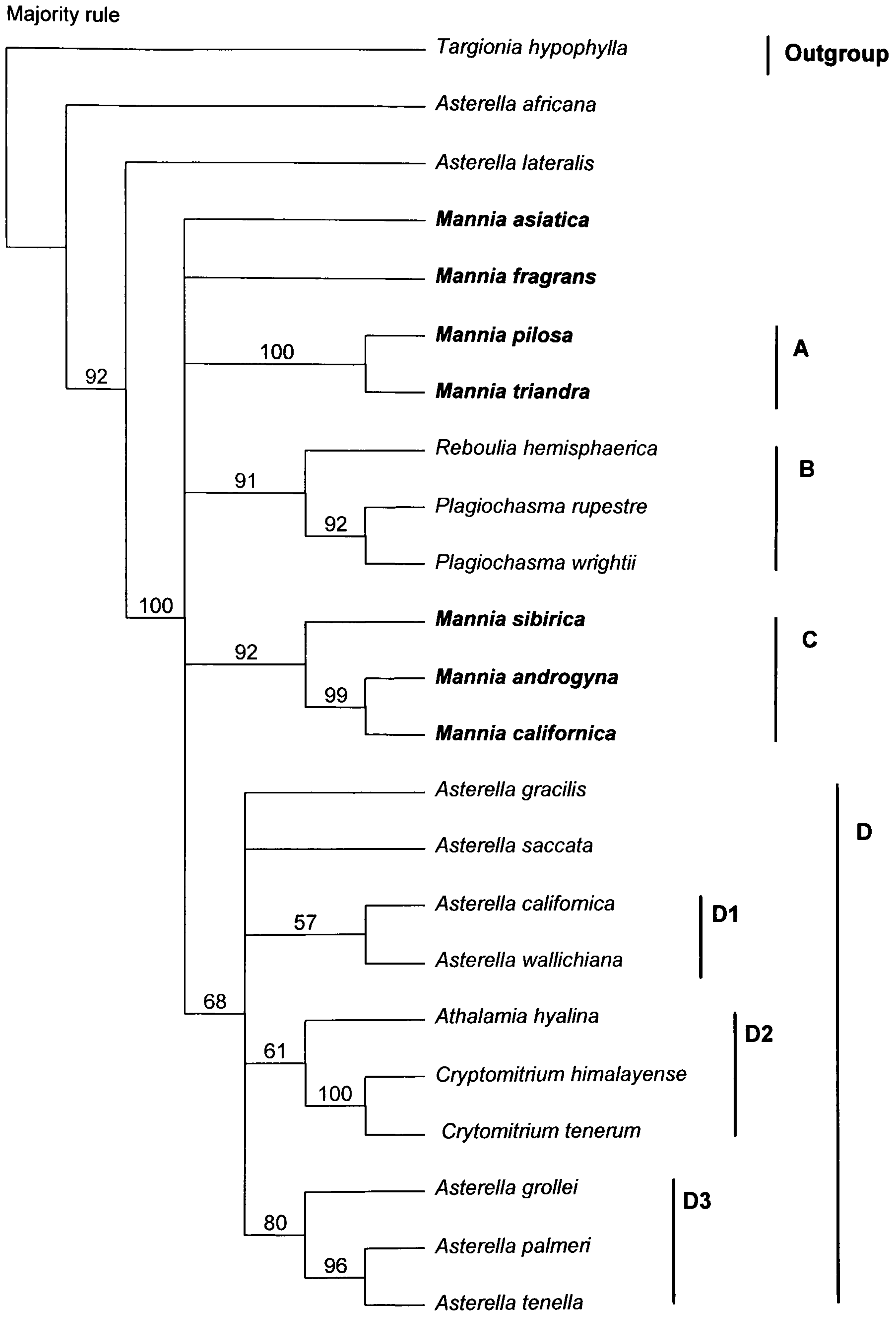


Fig. 5.12. Majority rule consensus tree of 76 most parsimonious trees (tree length = 142, CI = 0.53; RI = 0.61; RC = 0.33) based on 24 morphological characters for 23 taxa with an exhaustive search using unweighted parsimony. Figures above branches indicate percentage of trees in which branch occurs.

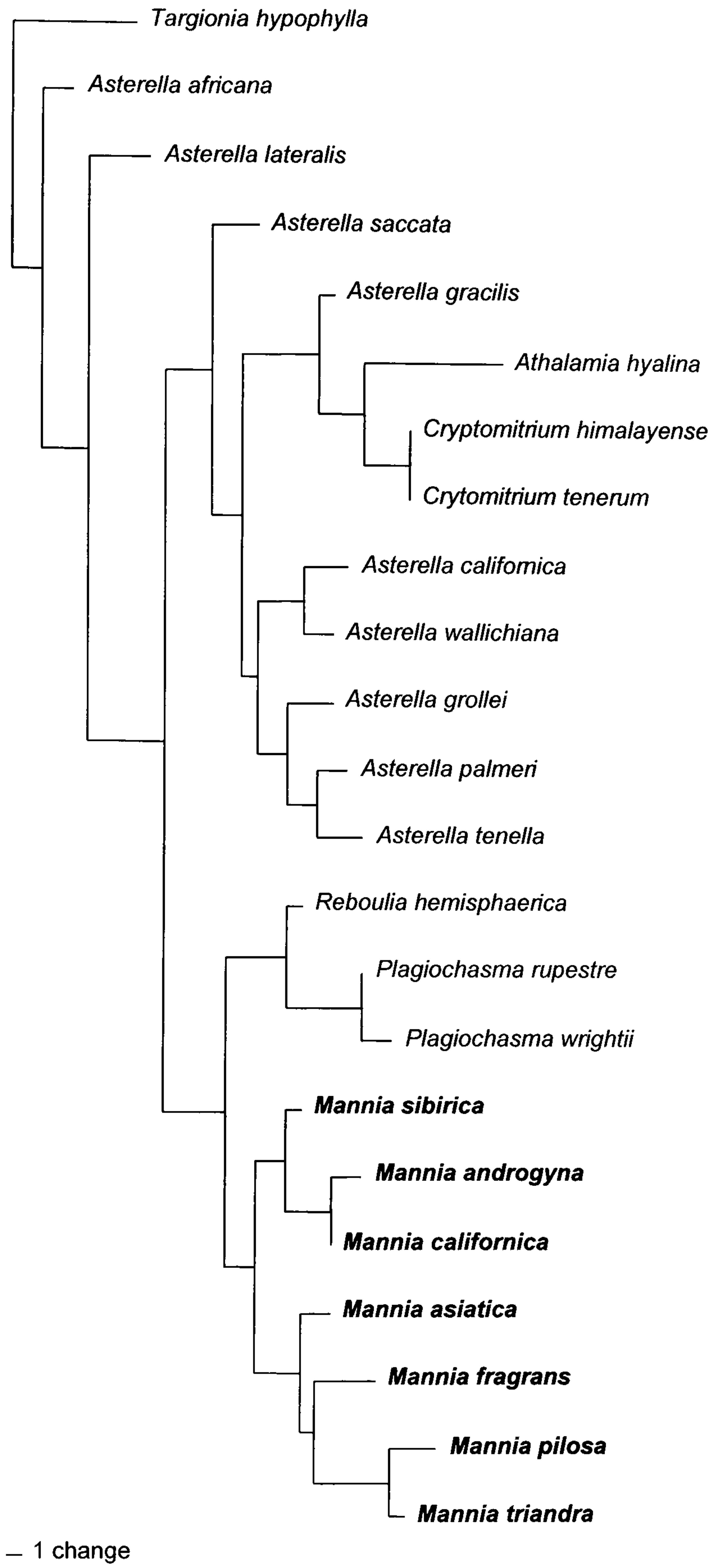


Fig. 5.13. Tree one of 76 most parsimonious trees (tree length = 142, CI = 0.53; RI = 0.61; RC = 0.33) based on 24 morphological characters for 23 taxa with an exhaustive search using unweighted parsimony

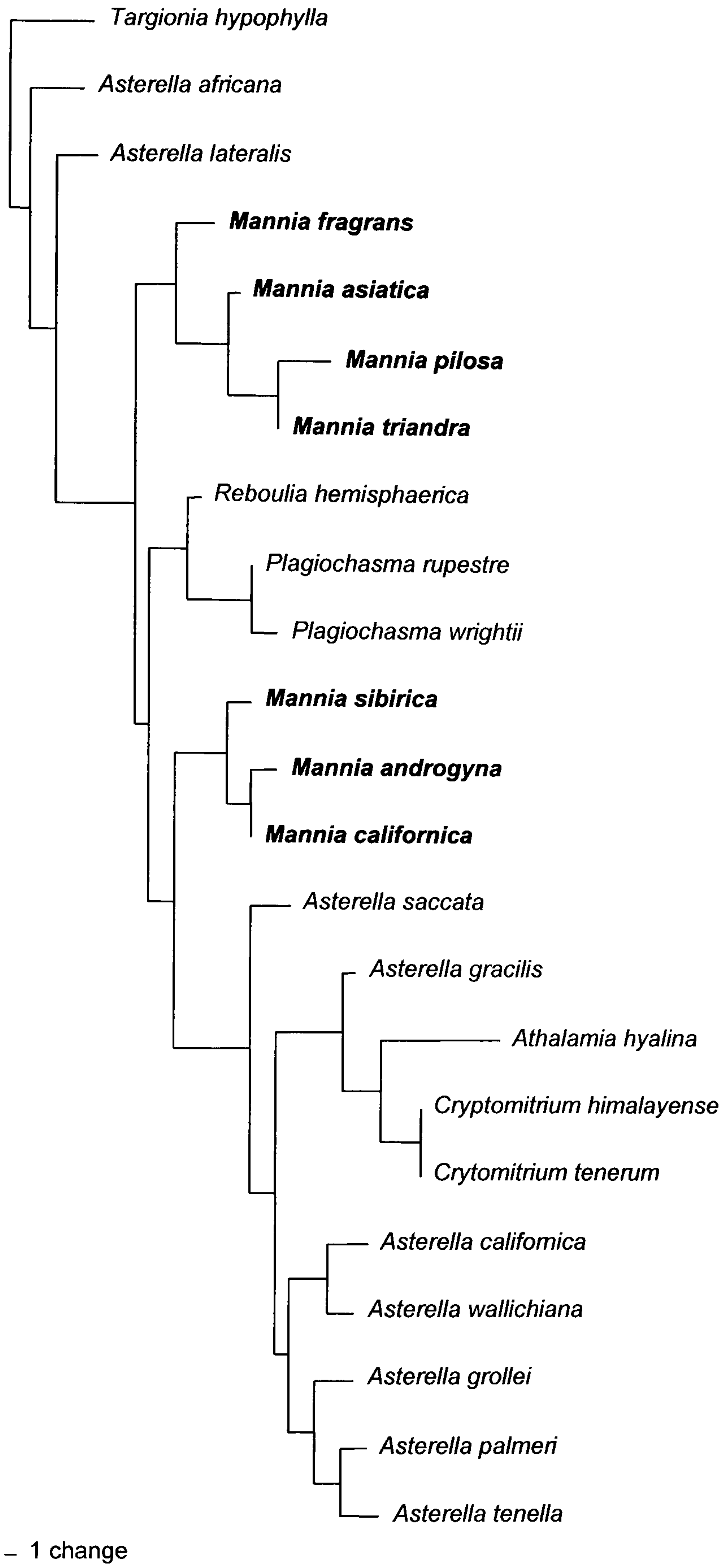


Fig. 5.14. Tree eight of 76 most parsimonious trees (tree length = 142, CI = 0.53; RI = 0.61; RC = 0.33) based on 24 morphological characters for 23 taxa with an exhaustive search using unweighted parsimony

5.6.1.2 Character evolution

In all trees the shown morphological characters appear predominantly homoplasious. They are mostly shared over a wide range of ingroup and outgroup taxa and most are not found to be a unique feature for just one clade. All results for the tracing of state changes of the 24 morphological characters can be found in Appendix II. The evolution of characters 3, 9, 15, 23 and 24 is presented in Fig. 5.15 to 5.19.

Assimilation tissue was found to be a homoplasious character (character 3) (Fig. 5.15). Loose assimilation tissue is the ancestral state in *Mannia* and the Aytoniaceae. A state change to compact assimilation tissue can be noted for the clade containing *M. androgyna* and *M. californica* and for the *Plagiochasma* clade, *R. hemisphaerica*, *A. africana* and *A. lateralis*.

Only in two cases, clades of the molecular reweighted combined tree could be defined by a synapomorphy. This was the case for the androecium type (character 9) of *Mannia fragrans* (Fig.5.16). Having antheridia in weak cushions or clusters on the thallus is the plesiomorphic state in character 9 (androecium type) for the included taxa. Defined cushions have evolved from weak cushions or clusters three times in parallel. This was the case in the *Plagiochasma* clade with *R. hemisphaerica*, *A. wallichiana* and *A. californica*. Diffuse or scattered antheridia have evolved in parallel three times in *Athalamia*, *A. gracilis* and the clade *C. tenerum* and *C. himalayense*. The *M. fragrans* clade shows a unique synapomorphy in having antheridia organised on a disc-like structure. This is not shared by any other species included in this analysis.

A unique feature of the genus *Mannia* is the cup-shaped involucres (character 15) (Fig. 5.17). All included *Mannia* species share this character which supports the *Mannia* clade in the tree (except *A. gracilis*). Having involucres as an entire flap appears to be the ancestral state for the included taxa, which has the subsequently been lost in some *Asterella* species.

The fine distal ornamentation of spores (character 23, state2: spongy) is shared only by *M. pilosa* and *M. triandra* (Fig. 5.18). In some *Asterella gracilis* specimen spores are found to be spongy but sometimes they can also be smooth, making this character polymorphic. Smooth spores are characteristic for *C. himalayense* and *C. tenerum*. Most *Mannia* spores have spores papillate in fine distal ornamentation, which have evolved from an areolate or alveolate origin.

The ancestral state of primary distal spore ornamentation (character 24) in *Mannia* and the family Aytoniaceae is not clear (Fig. 5.19). The *M. fragrans* clade has regularly areolate spores as is also the case for the included *Targionia hypophylla.* The presence of saccate spores is a synapomorphy for the two samples of the *M. androgyna* clade and has only evolved once, therefore a unique feature for this species. Because of the different distal spore ornamentation patterns occurring in *M. californica,* the character tracing for this species clade as well as for *P. wrightii* became uncertain. Further uncertainty in *M. spec.* and *M. controversa* is a result of missing data for these two species. The same is valid for *C.* spec. and *P. japonicum.* The occurrence of incompletely areolate spores has evolved three times in parallel in *Athalamia, A. tenella* and the clade out of *A. gracilis, M. triandra* and *M. pilosa.* Lamellate spores have evolved only once in the species pair *C. tenerum* and *C. himalayense.*

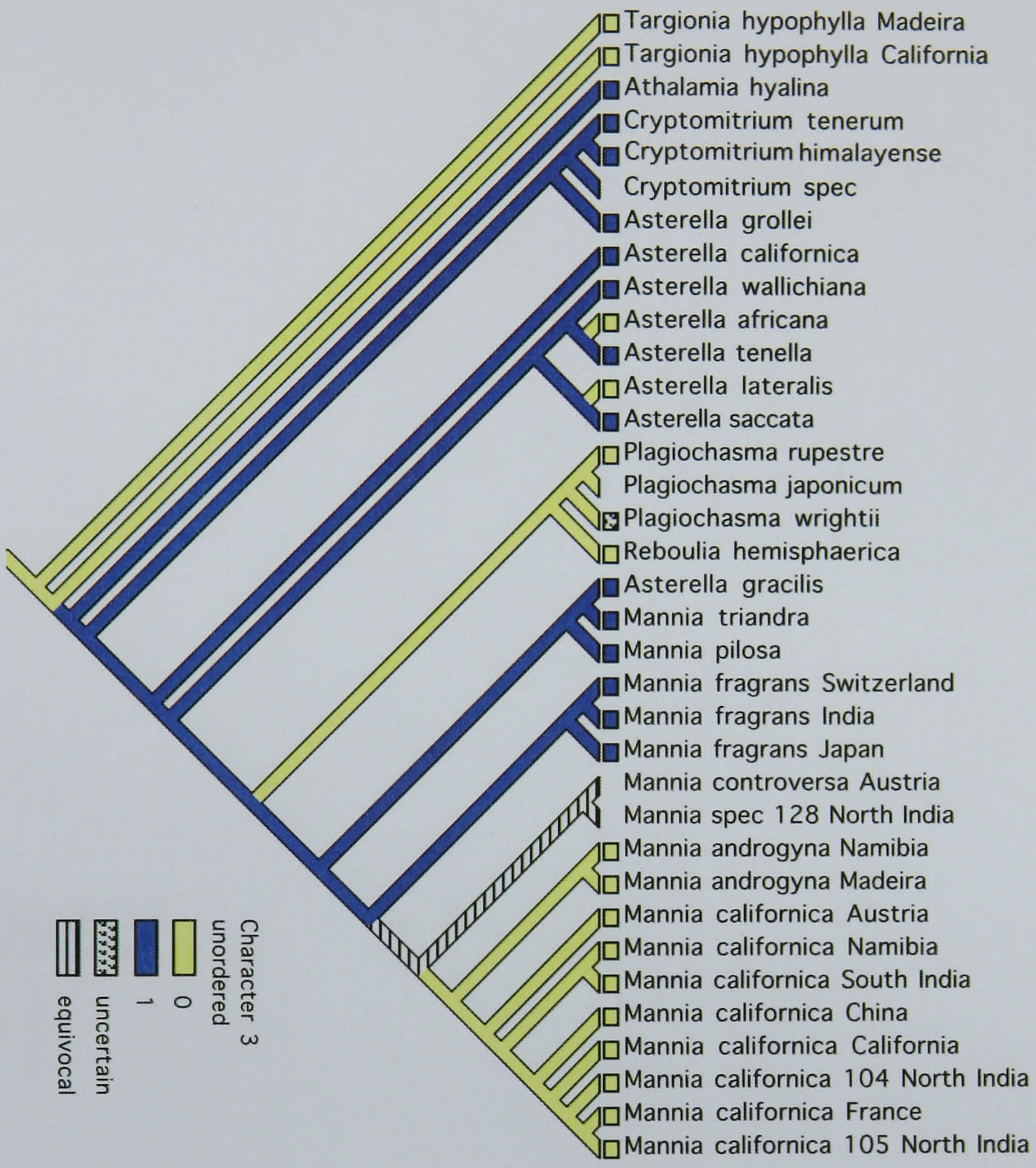


Fig. 5.15. Evolution of character 3: Assimilation tissue, mapped onto a single most parsimonious tree from the combined *trn*L and 26S molecular analysis based on a weighted Maximum Parsimony. 0 = compact; 1 = loose.

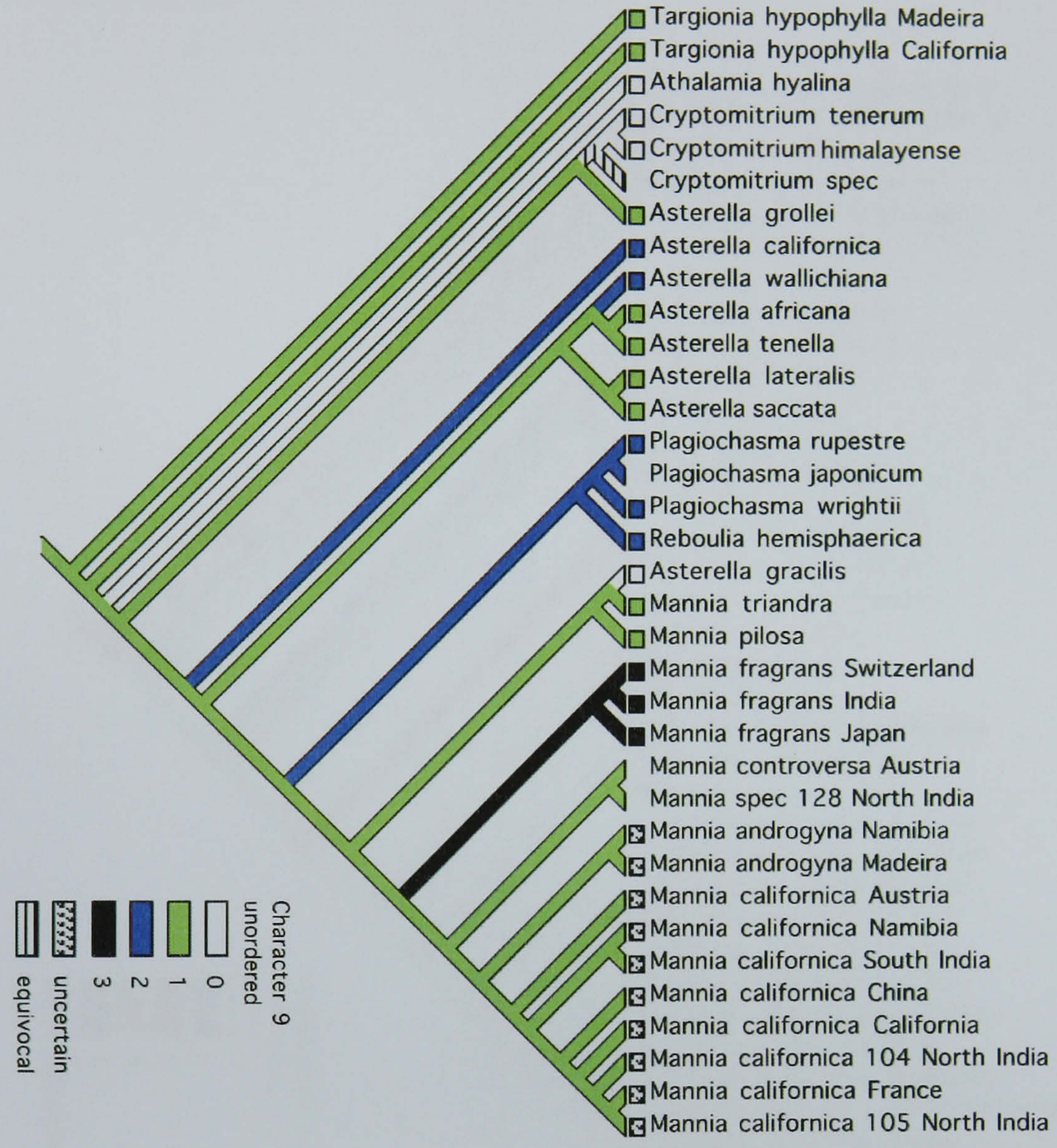


Fig. 5.16. Evolution of character 9: Androecium type, mapped onto a single most parsimonious tree from the combined *trn*L and 26S molecular analysis based on weighted Maximum Parsimony. 0 = diffuse, scattered; 1 = weak cushion or cluster; 2 = defined cushion; 3 = disc.

Fig. 5.17. Evolution of character 15: Involucre, mapped onto a single most parsimonious tree from the combined *trn*L and 26S molecular analysis based on weighted Maximum Parsimony. 0 = cup-shaped; 1 = flap; 2 = entire flap; 3 = bilabiate or bivalved; 4 = tubular.

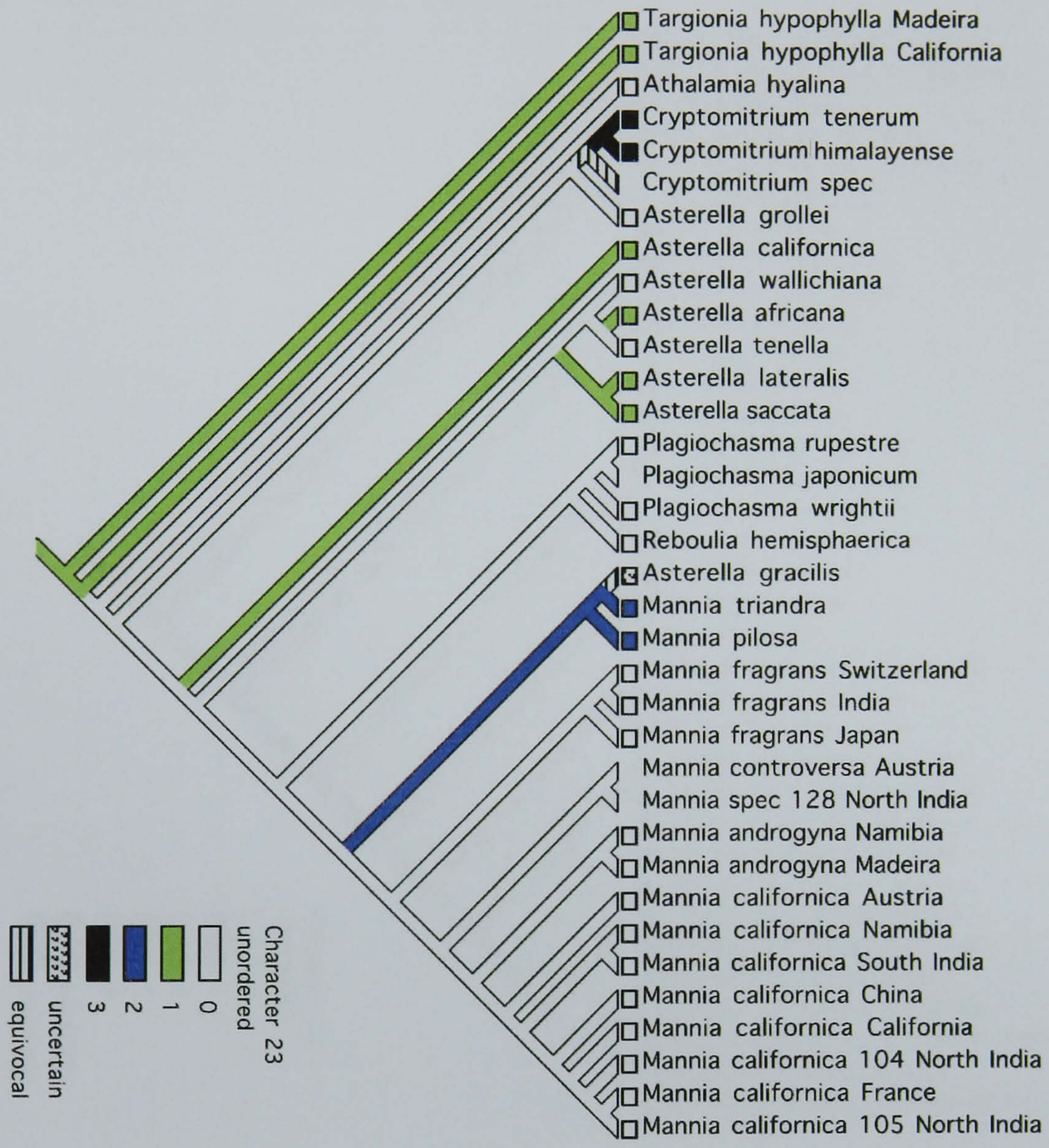


Fig. 5.18. Evolution of character 23: Fine distal ornamentation of spores, mapped onto a single most parsimonious tree from the combined *trn*L and 26S molecular analysis based on weighted Maximum Parsimony. 0 = papillate; 1 = areolate/alveolate; 2 = spongy; 3 = smooth.

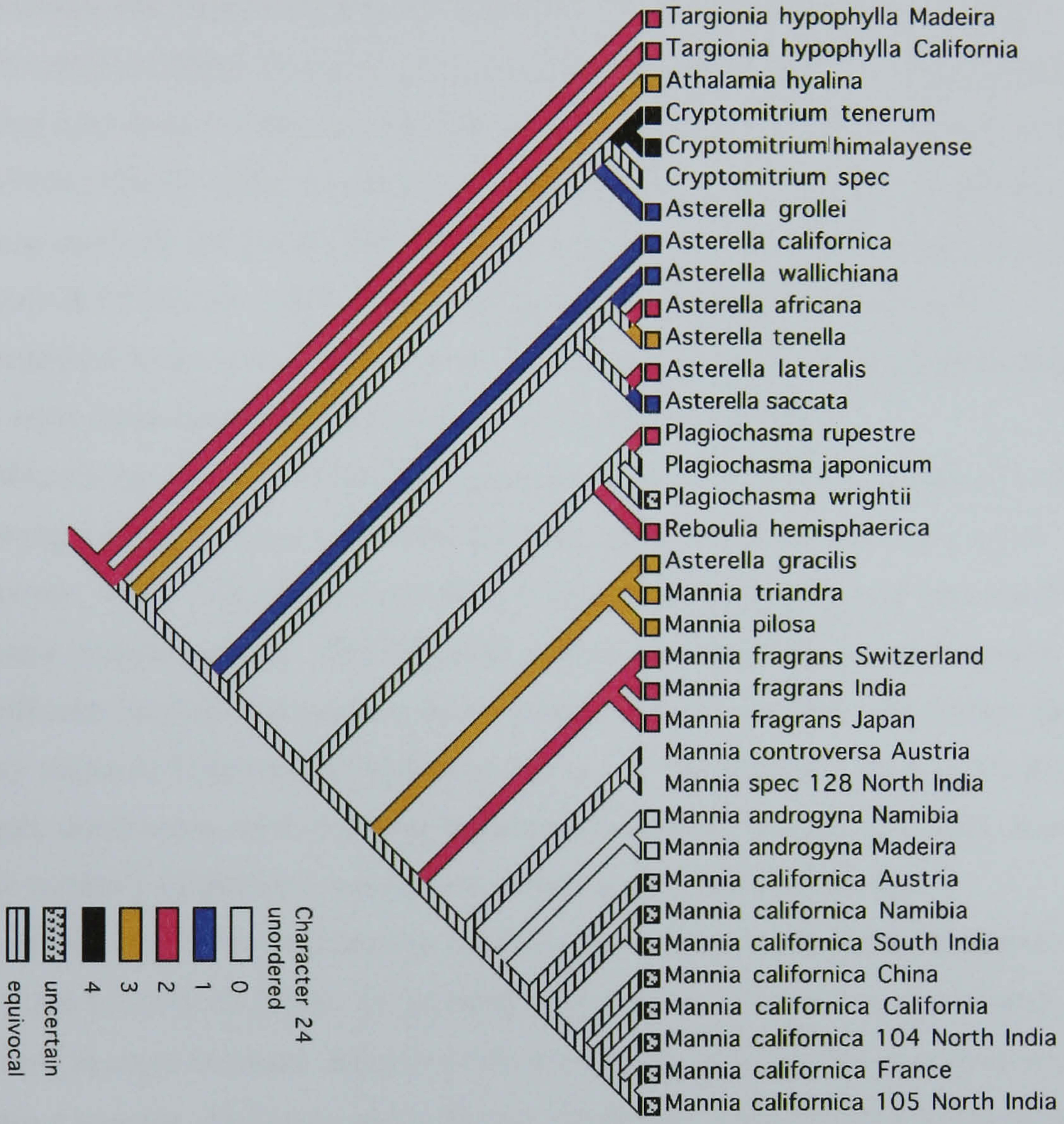


Fig. 5.19. Evolution of character 24: Primary distal ornamentation of spores, mapped onto a single most parsimonious tree from the combined *trn*L and 26S molecular analysis based on weighted Maximum Parsimony. 0 = saccate, 1 = ridges; 2 = regularly areolate; 3 = incompletely areolate; 4 = lamellate; 5 = papillate.

5.7 Discussion

5.7.1 Morphological Phylogeny

5.7.1.1 Character selection and coding

In phylogenetic studies using DNA sequence data as characters, the delimitation between the different states is easy to determine as these characters are "different, discrete and there exist no intermediate states" (PENNINGTON 2000). However, in using morphological data *"different methods of coding may lead to different phylogenetic conclusions"* according to FOREY & KITCHING (2000). This has been demonstrated on a combination of different coding methods for multistate characters in combination with binary characters (FOREY & KITCHING 2000). Therefore morphological results have to be interpreted with caution as the way of coding characters can be quite subjective and adds more interpretation to any phylogenetic estimate.

In *Mannia* as it is typical for Marchantiales, the gametophyte is highly elaborate showing a large number of characters that can be observed and measured. However, a lot of characters are often of quantitative nature and hence difficult to score unambiguously. The different measurements show in most cases a significant overlap and no clear discontinuities between different states. Hence many measured characters had to be left out of the analysis, such as thallus length, stalk cross section or the number of oil bodies in ventral scales. However, some authors subdivided quantitative characters into states where discontinuities between intervals could be seen (BISCHLER 1998, CRANDALL-STOTLER & STOTLER 2000). In general, quantitative characters were found difficult to score because there is often an overlap or they vary to a large extent within a species. Although quantitative characters were therefore generally left out of the present study, in one case the character could be subdivided into states and the most frequent case for this species has been applied (character 5: scale appendage number).

Furthermore, some characters were excluded as they might be dependent on each other and would therefore represent groupings disproportionately and consequently receiving too much weight in an analysis (e.g. thallus width might depend on thallus length, width and length of ventral scales).

Additionally only a limited number of characters could be found that were present in in- and outgroup taxa. The presence in both, in- and outgroup, is though necessary to determine character polarity by outgroup comparison (LONG 2000).

When two different states of one character were present in one species and equally observed, it was assumed to be polymorphic and both character states were scored e.g. the position of androecium in *Mannia triandra* can be either at the base of the stalk or terminal.

Problems in coding characters unambiguously resulted in a reduced number of morphological characters that could be used for the analysis. The number of characters that should be included in an analysis is a controversial issue. Whereas some authors think that a large number of characters is of advantage others say that an increasing number of characters did not necessarily contribute to a clearer phylogenetic picture and actually also correlated with an increase of ambiguous or problematic characters (SCOTLAND ET AL. 2003). The latter authors suggest that the quality of the data is the most important and the integration of fewer but critically observed morphological characters into a molecular dataset for better resolution and accuracy is of more advantage for a phylogenetic estimate.

Hence only a limited number of characters were scored, and their selection and way of coding may have had an effect on the parsimony analysis and the results should therefore be interpreted with caution.

5.7.1.2 Morphological phylogeny based on parsimony

In general the branch support values in the present morphological study are very low with a weakly supported ingroup clade and only two moderately to well-supported species pairs in the ingroup. Low branch support is a common feature of morphological studies where the number of characters is low. Bootstrap values commonly increase with the number of characters used in the morphological study (BREMER ET AL. 1999).

The strict consensus tree topology resulting from the morphological phylogenetic analysis based on Maximum Parsimony is inconclusive. It is difficult to come to any conclusion about the phylogenetic relationships within *Mannia*. It is not clear whether the genus is monophyletic or paraphyletic and the positions of

Mannia species were different in individual phylograms (Fig. 5.13 and Fig. 5.14).

Its affinity to related sister genera is also uncertain. Based on morphology, two species pairs, *Mannia triandra*/*M. pilosa* and *Cryptomitrium himalayense*/*C. tenerum* are found closely related, which can also be confirmed by molecular work. Though the latter species pair is possibly conspecific and has identical features in the morphological analysis, this is probably due to the limited number of available characters or their way of coding.

Athalamia hyalina, originally selected as an outgroup taxon, is found nested within the ingroup, indicating that its position based on the selected morphological characters is closer to the rest of the ingroup than *Targionia hypophylla*. However, it has a very long terminal branch showing its difference. The nesting of *Athalamia* in the ingroup is unexpected as molecular work clearly indicated that its phylogenetic position is outside the Aytoniaceae (LONG ET AL. 2005). However, it is said that tree topologies from morphological and molecular data are often incongruent (BOISSELIER-DUBAYLE ET AL. 1997). The reason for the close ingroup affinity of *Athalamia* lays in the large number of shared characters with others members of the ingroup. The selection of characters used or their coding therefore has a big influence.

Asterella africana and *A. lateralis*, considered to be part of the ingroup, are found outside the big ingroup clade close to *T. hypophylla*. In a study by LONG (2000) *A. africana* and a few other *Asterella* species which are not included in present study, were sister to *A. wallichiana* in a majority rule consensus tree, though this has only been the case in 69% of all 52 most parsimonious trees and can not be confirmed in the majority rule consensus tree here (Fig. 5.12). In the majority rule consensus tree of LONG (2000) *M. androgyna* and *A. gracilis* formed a sister pair in 96% of all most parsimonious trees. This is also not reflected in the present study where *A. gracilis* is found in 68% of 76 most parsimonious trees in clade D on a polytomy with *A. saccata*, other *Asterella* species (clade D1 and D3) and clade D2 with *Athalamia* sister to the two *Cryptomitrium* species. The position of *Reboulia hemisphaerica* was in both majority rule consensus trees close to *Plagiochasma* species.

5.7.2 Character evolution

The evolution of the studied characters used for character tracing in *Mannia* and related genera is generally marked by homoplasy. Homoplasious characters were found to be a common feature in the studied species. They are defined as similar characters shared by species, which do not share a common ancestor, but have developed independently either by parallel or convergent evolution or a secondary loss (PAGE & HOLMES 1998). The presence of many homoplasious characters was also the reason for the difficulties in the above morphological phylogenetic reconstruction and point to the hidden homoplasies in the phylogenetic analysis.

Because of the presence of homoplasy, clades could only be defined in a few cases by apomorphies, which then were diagnostic for species groups or species. In general the traced characters did contribute to a better understanding of the changes over time of key characters and made clear that clades are best defined by a combination of characters. The occurrence of mostly homoplasious characters in character tracing was also reported in a morphological study on the sister genus *Asterella* by LONG (2000). In this study no major clades could be defined by unique apomorphies but only through a combination of different characters.

A well established fact for the genus delimitation in *Mannia* is the presence of cup-shaped involucres, which are typical for all *Mannia* species (BISCHLER 1998). This is reflected in character 15 (Fig. 5.17) where *Mannia* stands out from related species as a group through this unique feature.

However, character tracing was sometimes uncertain because of missing data for some of the taxa. The reason for this was the application of a tree from the molecular combined analysis onto the morphological data set, in which taxa such as *M. controversa, M. spec., Plagiochasma japonicum* or *Cryptomitrium* spec. were not coded and therefore resulted in uncertainties that influenced the character tracing. Another reason was that the character state was unknown for a species.

Future work should concentrate on finding additional informative characters and a wider range of ingroup sampling would be of advantage.

5.7.3 Molecular Phylogeny

5.7.3.1 Suitability of *trn*L-F and 26S

The suitability of the chloroplast region *trn*L-F and the nuclear region 26S has already been successfully tested in a range of other studies on bryophyte phylogeny (BOISSELIER-DUBAYLE 1997, LONG ET AL. 2000, SHAW 2000b, WHEELER 2000). In these studies both regions have been proven to show a good resolution of phylogenetic relationships down to species level. However, in both data sets ambiguous regions were present that were therefore excluded before the analysis. The single 26S analysis resulted in several hypotheses of possible tree topologies, which did not elucidate phylogenetic relationships very well. The single *trn*L-F resulted in only a few trees but still showed two unresolved polytomies.

The 26S matrix showed a lower number of informative characters in comparison to the *trn*L-F despite its longer length. The number of informative sites was twice as high in the *trn*L-F dataset (16.4%) than in the 26S data set (8.1%) and therefore indicating a higher rate of evolution in the former.

Sequence divergences for the *trn*L-F were generally higher than for the 26S region.

The amount of phylogenetic signal in the analyses is reflected by descriptive tree statistics. CI indices were generally lower in the 26S data set, indicating therefore a higher amount of homoplasy than in the *trn*L-F region.

A better resolution of tree topologies and the present polytomies could possibly be achieved by increasing the number of markers and combining multiple regions (WORTLEY ET AL. 2005).

5.7.3.2 Branch support and posterior probability values

The branch support values in tree topologies of Maximum Parsimony are found to be generally lower for the same clades than the posterior probabilities in the BA. This was also frequently observed for other studies (SIMMONS ET AL. 2004, RANDLE ET AL. 2005).

The bootstrap test is a widely used statistical method to test how well branches in phylogenetic trees are supported (LI & ZHARKIKH 1994). It randomly resamples the data to build up a new data set, which is identical in size to the original set. In this process characters may get used once, several times or not at all. Therefore bootstrap values are calculated on the basis of a resampled data set. Posterior probabilities values in BA reflect the percentage in which a clade occurs in all the trees sampled based on prior calculated parameters. The clade credibility values are hence based on the actual sampled trees.

There is no broad consensus about how posterior probabilities should be interpreted in relation to bootstrap values (ALFARO ET AL. 2003). A study by SUZUKI ET AL. (2002) indicated that bootstrap values are a more reliable measure to assess the reliability of clades in phylogenetic trees than posterior probabilities. There is also the concern that Bayesian support measures are more likely to strongly support false phylogenetic hypotheses and give higher support values particularly for short internodes, that are in other analyses not well supported (DOUADY ET AL. 2003, ALFARO ET AL. 2003). It has been suggested that posterior probability values overestimate support and *"should not be interpreted as probabilities that clades are correctly resolved"* as their information is based on prior parameters and that they mainly show how well a phylogenetic model-based tree is supported by the data (CUMMINGS ET AL. 2003, SIMMONS ET AL. 2004, ALFARO ET AL. 2003).

However, DOUADY ET AL. (2003) conclude that bootstrap and Bayesian support values *"cannot directly be compared"* and suggest treating them as lower and upper limits for the reliability of individual nodes.

5.7.3.3 Sampling

The molecular results presented here can only give a preliminary idea about the molecular relationships in *Mannia* and its relationship to other genera. This is due to the limited number of samples that were included in the molecular study. For the two remaining *Mannia* species no material was unfortunately available. From a total of seven accepted *Mannia* species only five could be included and there was also only a limited number of other Aytoniaceae that could be incorporated, leaving gaps in the resulting tree topologies. Therefore the limited species selection might result in a biased picture of *Mannia* phylogeny and be influenced by the gaps in sampling. Therefore the molecular results should be seen against this background and interpreted with caution. A denser sampling strategy from a very broad range of Aytoniaceae would be highly desirable with the inclusion of the remaining *Mannia* species.

5.7.3.4 Paraphyly of *Mannia*

The results from the combined analysis have shown that *Mannia* is not a monophyletic but a paraphyletic genus due to the nesting of *Asterella gracilis* within it. There are two main clades present in *Mannia*, which are well supported by branch support values from the Parsimony analysis and posterior probability values from the Bayesian analysis.

One clade (Mannia I) is represented by *M. pilosa* and *M. triandra. Asterella gracilis* is nested within this clade showing close affinities to *M. triandra.* It has already been noted by LONG (2000) and LONG ET AL. (2000) that within the genus *Asterella, A. gracilis* is most similar to *Mannia* based on spore characters and molecular observations. This can be confirmed in the present study as *A. gracilis* is the only *Asterella* species included in this study that is found nesting within *Mannia.*

The second clade (Mannia II) contains only *Mannia* species but it is not entirely clear how the different species of this clade relate to each other as a large part of Mannia II is forming a polytomy.

5.7.3.5 Intraspecific relationships within *Mannia californica*

Eight different specimens of *M. californica* were used to study sequence variation on a worldwide scale. The distribution of *M. californica* is mainly in the Northern hemisphere with exceptions in Africa. Specimens from California, France, Austria, Africa, India and China were included. This range and number of specimens is limited as *M. californica* also occurs in other places in the world (e.g. Japan, Pakistan, Yemen, Lebanon, Canada based on herbarium specimens), with some populations only recently discovered in Europe (HUGONNOT & SCHILL 2006), China by J. Shevock and D.G. Long and on a field trip to Africa. Several described 'endemic' species e.g. from India or Japan, were synonymised under this name based on spore characters and other morphological evidence (see Chapter 3.6.2 and Chapter 4.4.3.2 under *M. californica*). The distribution of *M. californica* is in need of a worldwide reassessment and presently known and possible localities should be targeted by intense sampling strategies. Therefore the sample density of the *M. californica* specimens in the present study only allows a very limited insight into relationships within this species and the results might be biased by gaps in the sampling.

As the *M. californica* clade is not well resolved but contains a polytomy, the relationships between specimens from different geographical regions remain rather unclear. However, the position of the Austrian specimen is somewhat surprising. It has the most distant position to the rest of the *M. californica* specimens and is not closely related to the other European specimen from France, which shows closer affinities to a North Indian specimen. In the *trn*L analysis the sequence divergence between these two specimens from Austria and France is, amongst others, highest with 3.9%. They differed in 18 substitutions. Morphologically the Austrian specimen shows some differences to the typical *M. californica* morphology but also shares some key features such as spore ornamentation pattern or the presence of dark-coloured oil-bodies in thallus cross section. Based on the present morphological evidence the Austrian specimen was therefore included in this group. However, this is somewhat contrasting with the molecular results as genetically the Austrian specimen is quite different from the other *M. californica* specimens, maybe representing a relict from an early ancestor split.

In the analysis of the combined dataset a divide can be observed in the included Indian specimens with the South Indian specimen being closer to the Namibian and the North Indian specimens closer to specimens from France and California. Based on molecular evidence, no clear geographical boundaries can be found to explain the position of the different *M. californica* specimens to each other. The included specimens do not assemble in a distinct phylogeographic orientation, which might possibly be due to several dispersal events. A more intensive sampling is desirable and could shed more light on the molecular affinities of geographical different specimens.

As the branch lengths of the different *M. californica* specimens are only short, the explanation that different populations have been isolated from each other for a long time and have evolved since without any evident morphological differences is not very likely. Therefore it is concluded that different populations within *M. californica* are more likely to have dispersed recently rather than individual populations being of old age. As the spores are rather big a stepwise dispersal over short-distances via low altitude winds in combination with rainfalls seems to be the most likely explanation.

More intensive sampling of *M. californica* specimens around the world might shed more light on the phylogeography of this species. Furthermore the distribution patterns and dispersal mechanism of *M. californica* could be targeted in a study at the population level to find out if these dispersal events were recent or if the distribution is due to ancient vicariance, which is considered unlikely based on present (though only limited) study.

The observed sequence divergence in *M. californica* is higher (0-3.9% in *trn*L-F) than within the species *Asterella wallichiana* (1.2-1.4 %) though only three specimens have been included in that study by LONG ET AL. (2000).

However, all divergences were higher than within *M. androgyna* and *M. fragrans*. Two *M. androgyna* specimens from Madeira and Namibia differed only by 0.2 % (3 bp) from each other and in the three *M. fragrans* specimens (Switzerland, Japan, India) a sequence divergence of 0.3-0.6 % (4-9 bp) was observed. As to what level of genetic diversity can be expected to be found within individual species is unclear (HARRIS & FROUFE 2005). A high molecular divergence within a species generally indicates genetic differentiation over a long period of time without any speciation events taking place (FERGUSON 2002). Therefore despite the presence of a high number of molecular changes, the morphological appearance can remain the same. BATEMAN (1999) described morphological evolution as long periods of stasis followed by short periods of morphological change.

The *M. californica* specimens included in this study show a lower sequence divergence if the Austrian specimen is excluded (0-2% in the *trn*L-F analysis). However, they then still show a higher sequence divergence than within other *Mannia* species based on included samples. AVISE ET AL. (1998) noted in a study of vertebrate species that sequence divergence between separated populations can be higher than those between different species.

M. californica is therefore understood to consist of several cryptic species which show variable sequences but similar morphological characters. Based on spore morphology and other morphological characters the Austrian specimen is included in the *M. californica* group despite its genetic isolated position and some morphological differences (see 4.4.3.2 under *M. californica*).

Cryptic speciation has been observed before in both mosses and liverworts (SHAW 2001). There have also been studies on thalloid Marchantiales (ODRZYKOSKI & SZWEYKOWSKI 1991, BOISSELIER-DUBAYLE ET. AL. 1998) showing the occurrence of cryptic speciation. ODRZYKOSKI & SZWEYKOWSKI (1991) are the opinion that they might be of common occurrence in the Marchantiales as *'morphologically defined species often have very wide, cosmopolitan distributions'.*

Further morphological and molecular study using isozyme analyses or microsatellites and more widespread detailed sampling of populations particularly in Austria and other countries would be necessary to elucidate the scale of cryptic speciation in *M. californica* and consider its possible separation into sibling species.

5.7.3.6 Relationships between *Mannia* and its sister genera

The molecular results of Maximum Parsimony and Bayesian analyses showed that *Mannia* as well as the sister genera *Cryptomitrium, Reboulia* and *Plagiochasma* are nested within *Asterella* and have evolved from within it in independent evolutionary events. This has already been stated by LONG ET AL. (2000, 2005) in earlier molecular work.

The traditional division of the two subfamilies Aytonioideae (*Plagiochasma*) and Reboulioideae (*Reboulia, Asterella, Mannia, Cryptomitrium*) based on classifications by GROLLE (1976, 1983b) and GROLLE & LONG (2000) can also not be supported. This is in agreement to a molecular study by LONG ET AL. (2000).

A close relationship between *Asterella gracilis* and *Mannia* was only weakly supported in previous studies by LONG ET AL. (2000). However, the present study showed well supported branch and high posterior probability values in both Maximum Parsimony and Bayesian analyses. This could be due to a broader sampling of *Mannia* species in the present study and the inclusion of *M. triandra* and *M. pilosa*, which are close relatives of *A. gracilis.*

The results from the molecular study indicate that the pseudoperianth, typical for the genus *Asterella* and probably a plesiomorphic feature for the whole of the Aytoniaceae (LONG ET AL. 2000) has been lost in *Mannia* and its sister genera but subsequently regained again in *Asterella gracilis.*

5.7.3.7 Classification of *Mannia*

The species sampling was not fully comprehensive as from a total of seven *Mannia* species only five were included in the molecular analysis. Therefore molecular results have to be interpreted with caution.

However, former subgeneric classifications of *Mannia* were only based on morphological characters such as thallus structure and have been the subject to criticism in the past (SCHUSTER 1992b). A classification of SHIMIZU & HATTORI (1954) treated *Mannia* as a subgenus under *Cryptomitrium*. This cannot be supported by present molecular study. A classification of *Mannia* based on molecular data with the *Mannia* samples included would clearly suggest two subgenera of *Mannia* based on the presence of two well supported clades: Mannia and Neesiella. One of these clades (subgenus Neesiella) is actually the former subgenus Arnelliella (C.Massal.) Grolle (GROLLE 1976, GROLLE & LONG 2000) or Mannia respectively (Grolle 1983b) represented by *M. pilosa* and *M. triandra* but with the exclusion of *M. sibirica*.

The second *Mannia* clade (subgenus Mannia) rests on a polytomy so the relationship of the different species is not clear. However, the individual species pairs are well supported and the second clade was subdivided into the Sections Mannia (*M. androgyna*), Arnelliella (*M. californica*) and Sindonisce (*M. fragrans*) based on spore characters.

M. androgyna and *M. californica* have been formerly treated in the same section Mannia (GROLLE 1976, GROLLE & LONG 2000) or Xeromannia (GROLLE 1983b). However, their monophyly is only moderately supported in the combined strict consensus tree of the PA (bootstrap 75, d = 2) and their spore characters proved to be very different. Therefore they were subdivided into individual sections in the present treatment: sect. Arnelliella (*M. sibirica* and *M. californica*) and sect. Mannia (*M. androgyna*).

The main difference with former classifications of *Mannia* is the position of *M. sibirica*.

Its relationship could unfortunately not be tested in the molecular study but the spore ornamentation strongly indicated close affinities to *M. californica* rather than *M. pilosa* and *M. triandra*. This could be possibly due to parallelism but spore types and their correlation to molecular phylogenetic analysis were successfully tested before by LONG ET AL. (2000) in *Asterella*. Therefore spore characters might also give also a good indication of phylogenetic relationships and classification within *Mannia.*

The present classification of *Mannia* based on spore ornamentation patterns remains not in conflict with the molecular study. The division into two subgenera is well supported by the molecular data based on the included *Mannia* samples. A future inclusion of *M. sibirica* into the dataset would be highly desirable to test if its close spore affinity to *M. californica* is supported by the molecular data, therefore establishing if their position in section Arnelliella is justifiable or if it is possibly due to parallelisms.

The presence of a well-supported clade containing *M. controversa* and *M. spec.* indicate that the status of *M. controversa* has to be reconsidered and needs further careful morphological and molecular study. The Indian unidentified specimen shows close affinities to it and a wider sampling in that area would be desirable to evaluate its status and relationship. The newly described species *M. asiatica* could also not be tested by molecular analysis. Its spore patterns are similar to *M. fragrans*, but because of some spore characteristics and the sexual condition, *M. asiatica* was placed in its own Section Asiaticae.

5.7.3.8 Taxonomic implications

The traditional classification of the family Aytoniaceae into five different genera based on formerly used morphological characters is in contrast to recent molecular work on Aytoniaceae (LONG ET AL. 2000, LONG 2005) and is also reflected in the present molecular study. With *Asterella* being a paraphyletic genus and its sister genera nested within it, the concept that phylogenetic classification systems consist of monophyletic genera is not expressed. The delimitation of *Mannia* and *Asterella* is not clear cut, with *Asterella gracilis* nesting in *Mannia* and the latter therefore also becoming paraphyletic. The inclusion of *A. gracilis* into *Mannia* would achieve monophyly of the genus. However, this would conflict with the traditional understanding since *Mannia* differs from *Asterella* by the absence of a pseudoperianth. Further the presence of a pseudoperianth as a character diagnostic to *Asterella* would become meaningless. Therefore a change in the generic boundaries of *Mannia* has implications for generic delimitation in *Asterella* and can therefore not be considered in isolation.

Whereas many people believe that classification should be based on phylogeny and comprise monophyletic entities (POTTER & FREUDENSTEIN 2005), others argue that paraphyletic genera should be accepted because phylogenetic analysis and taxonomy should not necessarily be linked (NORDAL & STEDJE 2005, BRUMMITT 2002). BRUMMITT (2002) thinks that about 20-30% of recognised taxa might be paraphyletic. Therefore a case by case evaluation is desirable. Although *Plagiochasma* and *Cryptomitrium* come out on separate well supported clades this could also be due to the limited amount of sampling in these genera and an increase in sampling might give a different picture. The genus *Plagiochasma* has about 16 species worldwide (BISCHLER 1998) and is only represented by three species in the present molecular analyses. There is also the need for a taxonomic revision of *Cryptomitrium*.

Although the molecular evidence clearly shows *Mannia* to be paraphyletic, on the basis of the samples included, the genus is morphologically distinct by the lack of a pseudoperianth and its cup-shaped involucres. Although these are only a few characters they work well for genus delimitation and are reliable. However, based on the present molecular evidence *Asterella gracilis* should be included in the genus *Mannia*. It is more closely related to *M. triandra* and *M. pilosa* than to any *Asterella* species based on present molecular study. This change would also make *Mannia* a monophyletic group. There would however be a consequence for the genus *Asterella*, which is defined by the presence of a pseudoperianth.

A possible sinking of *Mannia* into *Asterella* could be considered on the basis of molecular evidence. However, a wider sampling of the remaining taxa in *Mannia* and other Aytoniaceae, particularly *Asterella* would be necessary in order to assess the situation more thoroughly and possibly to define clear groups based on morphological characters, which have support from molecular data. Although the molecular results clearly indicate that *A. gracilis* belongs to *Mannia*, the delimitation of *Mannia* is linked with the generic delimitation of *Asterella* and the other remaining genera within Aytoniaceae. Therefore the generic limits of *Mannia* should be re-examined in the near future.

Chapter 6: Conclusion

The genus *Mannia* has never before been the subject of a worldwide taxonomic revision so a monograph with evaluation of all species was badly needed. The extensive study of herbarium material and literature showed that many species were misidentified or misunderstood and therefore further study of more herbarium specimens would be desirable.

Based on the observed material most species of *Mannia* have a widespread distribution with some taxa such as *M. californica* extending much more than their previously assumed distribution range. Several formerly assumed endemic taxa were synonymised as they belong to more widespread taxa. More field work is necessary to get a clearer picture of the distribution range of individual taxa as some taxa has only been recently discovered in both well surveyed places (such as *M. californica* in Europe) and poorly known places (such as *M. fragrans* in India). Future field work would also be desirable to find out if the here newly described species *M. asiatica* is endemic to Asia or more widespread.

Some excluded taxa such as *M. controversa* and *M. hegewaldii* should undergo further research to resolve their status. A careful study of the type specimen of *M. controversa* is needed as this long-forgotten taxon might have a valid status. There is also the need to study fresh material of *M. hegewaldii* and include it in a molecular study.

The spore survey using SEM has contributed a great deal towards species delimitation and a new infrageneric classification of *Mannia* and has shown the importance of spore characters in the genus. The position of *M. sibirica* close to *M. californica* in the infrageneric classification as indicated by spore characters is in contradiction to all recent classifications on *Mannia*. Further molecular phylogenetic work should include this species and test if it shows close molecular affinity to *M. californica.*

Phylogenetic reconstruction based on morphology was inconclusive and character evolution in the genus and related genera was characterised by homoplasy. Future work could concentrate on a wider sampling of taxa and on finding more characters.

The molecular phylogenetic reconstruction of *Mannia* is incomplete in that some species such as *M. sibirica* and *M. asiatica* could not be included. Therefore molecular results of this study should only be seen as preliminary. All phylogenetic tree topologies from Maximum Parsimony and Bayesian analysis of individual and combined data sets showed polytomies so further molecular work is needed to resolve relationships.

To confirm paraphyly of the genus a broader sampling and sequencing of all species of the genus and closely related ones is necessary. Future field work should concentrate on sampling these taxa so they can be included in the phylogenetic analysis. Future molecular study might suggest some modification of the results gained here or lend stronger support to them.

In general the combination of alpha taxonomic work, spore survey with the SEM and morphological and molecular phylogenetic construction worked well in addressing different problems in *Mannia* and contributed to a new approach for an infrageneric classification of the genus. However, further work is needed to fill gaps and other aspects such as breeding systems or spore dispersal should be subjected in future research.

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Appendix I. *Mannia* specimens studied

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

ALBANIA, **[Gjirokastër County]**, Mali I Murzines, kleine Schlucht an der Strasse (Tal) zwischen Gjirokaster und Delvinë, 19 vi 1959, *F.K.Meyer* 2978 (JE). **[Tiranë County]**, Tirana, 15km sued-oestlich, c. 350m, Felsen an der Burg Petrele, 3 vii 1959, *F.K.Meyer* 3429 (JE).

BOSNIA-HERZEGOVINA, [Herzegovina-Neretva Canton], Herzegowinia, Ravno, lem Tunnelberg gegen Zavala, 10 iii 1912, *Latzel* 611 (S).

CROATIA, [Dubrovnik-Neretva County], Dalmatica, Ragusa, Lapad, in fissures murorum, 60m, terra calc., 16 ii 1908, *A.Latzel* s.n. (JE); Dalmatica, Ragusa, Lapad, in fissures murorum, 60m, terra calc., 10 ii 1908, *A.Latzel* s.n. (JE); Dalmatia, Ragusa, Lapad, ca. 40m, 11 ii 1910, *Latzel* 531 (S); Dalmatia, Ragusa, Laprona, in fisouris murorum, 60m, terra calc., 11 ii 1908, *Latzel* s.n. (S); Dalmatia, Insel Meleda, südlich Babino Polje, ca. 100m, 16 ii 1908, *Latzel* 518 (S).

FRANCE, Dep. Pyrenées, Bachboeschung oberhalb Peyrefite,c. 150m, 19 iv 1965, *Duell* II B (JE). **[Auvergne]**, Balur du chemin de St Vieillerie (Cantal), 28 iv 1897, *Heribaud* s.n. (BM). **[Languedoc-Roussillon]**, Pyren. Orient., Banyuls, 150–200m, nahe Grotte de Pouade, 1969, *van Zanten & During* 5152 (JE); Somène (Gard), 18 ii 83, *Heribaud* s.n. (BM); Südfrankreich, Béziers, kultiviert im Botanischen Garten in München, *K. Grebel* s.n. (B74446) (S). **[Provence-Alpes-Côte d'Azur]**, Riviera, bei Biot auf Erde an einem Rinnsal in einer Macchie, iv 1998, *Huneck* s.n. (JE); Marseille, *Favreau* s.n. (BM); Alpes Maritimes, env. de Grasse, petit vallon au Nord d'Auribeau, 100m, 26 iii 1951, *Vautier* 565 (S);Petit vallon au nord d'Auribeau environs de Grasse, Alpes maritime, 100m, sur murets d'oliveraie, 26 iii 1951, *Vautier* 566 (F, NY, S).

[Rhône-Alpes], Vals, Ardêche, France orientale, 21 x 1879, *Philibert* s.n. (S); Ardéche, iv 1878, *Philibert* s.n. (S).

GREECE, [Attica], Athen, *v. Heldreich* (BM). **Crete**, Rethimnon, Ida-Gebirge (Oros Idi), 1km oberhalb Anogia in der montanen Dornpolsterstufe, Kalk, c. 850m, auf Erde and an Felsen, 3 iv 1972, *Duell* 104 (JE); Pigaidhari in insula Creta, 29 iii 1921, *Samuelsson* s.n. (S); Lakki, 7 iv 1921, *Samuelsson* s.n. (S); Lakki, 7 iv 1921, *Samuelsson* s.n. (S); Lakki, 7 iv 1921, *Samuelsson* s.n. (S); NE von Khonos, 6 iv 1921, *Samuelsson* s.n. (S).

ITALY, *Raddi* s.n. (BM); *Wikström* s.n. (S); Herbarium Castromi, *Raddi* s.n. (B74437) (S); *Garovaglis* s.n. (B74425) (S); Italia, Nemi I Latium, 18 iii 1948, *Uggla* s.n. (S). **Campania**, Napoli, *Boccarini* s.n. (669104) (BM); Neapel, *Nyman* s.n. (B74415) (S); South Italy, Amalfi, limestone rocks, iv 1910, *Nicholson* s.n. (BM); On banks, road from Sarrento to Analfio, Italy, iii 1895, *A. W.E.* s.n. (NY). **Liguria**, sulla terra al margine dei campi ad Albissola marina, iii 1865, *A. Piccone* 368 (JE, NY, BM, S); Sulla terra, ad Albissola marina, i 1865, *Piccone* 218 (1218) (BM); Liguria genuensis, Arenzana, i 1953, *Sbarbaro* s.n. (F). **Lombardy**, Alfi Lepontine, *Rossi* s.n. (S); Oberitalien, Provinz Como, Sartirana (Brianza), an Felsmauern, 6 i 1899, *Artaria* s.n. (JE); Prov. Comensis, Lammago, volta presso Como, 8 xii 1898, *F.A.Artaria* s.n. (E); Provinz Como, Lipomo bei Como, an erdbedeckten Mauern, 26 xii 1899, *F.A.Artaria* 11 (JE, BM, S, E, NY);Prov. Comensis, Camnago-Valda pres Come, hauts des champs?, 24 ii 1898, *Artaria* s.n. (NY); Prov. Comensis, Cammago valda pr. Comum, 24 xi 1898, *Artaria* s.n. (S); Commago-Volta, prope Comum, ca. 350m, 8 xii 1898, *Artaria* s.n. (S); Como, 7 xii 1898, *Artaria* s.n. (S); Comenses, iv 1908, *Müller* s.n. (S); Prov. Como, Sardirana, an Felsmauern, 381m, 6 i 1899, *Artaria* s.n. (S). **Piedmont**, Vercellis, *Cesati* 65 (BM, NY); *Thomas* s.n. (669092) (BM). **Sardinia**, *Giaconini* s.n. (JE). **Sicily**, Ätna, *de Notaris* s.n. (S) Pantellaria, south of Sicily, auf Erde an einer steinigen Nord-exponierten Böschung, 200 m, 18 iii 2003, *K.-F. Günther* s.n. (H4397) (E); Pantellaria, south of Sicily, auf Nord-exponierten Fels-Podesten, 20 iii 2003, *K.-F. Günther* s.n. (H4398) (E). **Trentino-South Tyrol**, Meran, *Milde* s.n. (JE); Meran, *Bamberger* s.n. (BM); Meran, Tirol, 28 viii 1909, *Glowacki* s.n. (S). **Tuscany**, Italia media, ad terram in Trancitauorum salter prope Tetulas Tiesole, 28 ii 1876, s.n. (NY); Etraria, Pozzolatico ad emenid Florentiae, 16 I 1888, *Bacci* s.n. (NY); Florence, Italy, *Raddi* s.n. (E); Florence, *Levier* s.n. (669103) (BM); In colle Fiscole ad setentr. Florentiae jupta coenobium Franciscanorum, 29 xii 1888, *Levier* s.n. (BM); Villa Pozzolatico ad merid. Florentiae, 14 i 1888, *Levier* s.n. (BM); Toscana, suedlich von Florenz (locus classicus!) bei der Villa Pozzolatico auf blosser Erde und auf alten Mauern, 14 i 1888, *E. Levier* 12 (JE, BM, NY); Florenz, in muro pr. Villam Pozzolatus, ad merid. Florentiac, 16 i 1888, *Levier* s.n. (S); Florenz, Fiesole, neben dem Fransiskanerkloster Belvedere, 10 iii 1906, *Levier* s.n. (S); Toscana, Etrurien, juxta villam Pozzolatico, ad merid. Florentiae in murorum fissures, 14 i 1888, *Levier* s.n. (H4333) (JE); Juxto villam Pozzolatico, ad merid. Florentiae, 14 i 1888, *Levier* s.n. (B74445) (S); Etrusia, juxto villam Pozzolatico ad merid. Florentia, 14 i 1888, *Levier* s.n. (B74436) (S); Toscana, com Korstik, Herb. H.Schmidt Freiburg, s.n. (JE). **Veneto**, in rimis rupium cum *Opuntia nana*, supra Montegrotto e collibus Euganeis, 20 ii 1879, *Massalongo* 97 (BM, F, NY); Montegrotto, *Massalongo* s.n. (BM); ad rupes in collibus Euganeis supra pagum Montegretto, ii 1879, *Massalongo* s.n. (S); ad terram muscosam in Euganeis circum Padova, Vere 1876, *Massalongo* 9 (BM, NY).

MONTENEGRO, Dalmatia, Borche-Baošie, Mauer oberhalb des Mogilicafalles, 31 xii 1916, *Latzel* 438 (S); Dalmatia, Borche- Baošie, bei einer Quelle, oberhalb Sa. Nicola, 6 viii 1916, *Latzel* 443 (S); Dalmatien, Borche- Baošie, Stützmauer oberhalb des Mogilicafalles, 31 xii 1916, *Latzel* 445 (S); Dalmatia, Borche-Baošie, Stützmauer nächst des Mogilicafalles, 31 xii 1916, *Latzel* 201 (S); Dalmatia, Paštrovići, Bachmauer bei Rafailović, 19 iv 1911, *Latzel* 439 (S). **[Herceg Novi Region]**, Sued-Dalmatien, Bocche di Cattaro, Gartenmauer laengs der Kueste zwischen Castelnuovo und Savina, Ende iii 1904, *K.Loitlesberger* 1186 (NY, S, E); Dalmatia, ad vinearum muros prope Castelnuovo ditionis "Bocche di Cattaro", iv (1830?), *C.Loitlesberger* 1261 (JE, BM, NY); Dalmatia, Borche-Castelonova, ca. 50m, Terrassenmauer in Savina, 21 xi 1916, *Latzel* 446 (S); Dalmatia, Borche-Castelonova, Südhang des Podi-Zalanika-Rückens, ca. 150m, 15 ii 1915, *Latzel* 442 (S); Dalmatia, Borche-Castelnova, nächst dem Celabach bei Podi, ca. 200m, 4 iv 1915, *Latzel* 122 (S); Dalmatia, Borche-Kumbur, Hohlweg nächst der serb. Kirche, 11 iv 1915, *Latzel* 202 (S); Dalmatia, Borche-Kumbur, Stützmauer oberhalb der Kirche, 1 ii 1915, *Latzel* 206 (S); Dalmatia, Borche-Kumbur, an einer Terrasse oberhalb K., 8 i 1917, *Latzel* 208 (S); Dalmatia, Borche-Kumbur, Hohlwegrandes oberhalb K., 25 xii 1916, *Latzel* 440 (S); Dalmatia, Borche-Kumbur, Waldplatz oberhalb der Kirche, 1 ii 1915, *Latzel* 444 (S); Dalmatia, Borche-Kumbur, Mauer oberhalb der Kirche, 1 ii 1915, *Latzel* 437 (S); Dalmatia, Borche-Zelanika, beim Wasserfall jenseits der Schiessstätte im Kutital, ca. 200m, 15 xii 1914, *Latzel* 153 (S); Dalmatia, Borche-Zelenika, Katikal zwischen Sa. Fure und Rotplattestal?, ca. 140m, 4 i 1915, *Latzel* 441 (S); Dalmatia, Borche-Zelenika, bei Wasserfall oberhalb der Schiessstätte, ca. 200m, 25 xii 1914, *Latzel* 209 (S).

PORTUGAL, **Algarve**, Rocha de Pena, W of Salir, c. 300m, stony limestone slope on old cultivation terraces, 28 iii 1989, *Long* 16008 (E); Caldas de Monchique, wooded valley below town, c. 230m, on crumbling rocky sunny bank, 27 iii 1989, *Long* 15958 (E); Caldas de Monchique, village square, c. 270m, on wall overlooking square, 27 iii 1989, *Long* 15940 (E); Monchique, fissures terreuses des murettes en blocs siliceux (syénite), ca. 470m, *Allorge* 131 (F); Caldas de Monchique, on rocks by the stream from Monchique, 28 iii 1954, *A. C. Crundwell* 184 (E); Monchique, on side of wall, 25 iii 1954, *A. C. Crundwell* 67 (E). **Azores**, San Jorge, Urzelina, 220 ft., on rocky ground, 27 vii 65, *Smookler* 2 (BM). **[Centro Region]**, Coimbra, *Moller* s.n. (BM). **Madeira**, Rosario, above Sao Vincente, c. 360m, open valley slopes; on damp vertical rock face by road, 22 i 1994, *Long* 25170 (E); Serra de Agua, c. 520m, valley with open pine forest; on damp cutting by road, 22 i 1994, *Long* 25151 (E); Between Serra de Agua and Vinhaticos, below Pousada dos Vinhaticos, just below sight-seeing spot by road, c. 630m, 32°43'52.9"N, 17°01'32.7"W, on damp rock cutting, 24 i 2003, *D.B.Schill & C.Lobo 34* (E); 3.5km above Ribeira Brava, steep rocky river valley, c. 140m, on shady volcanic cliffs by road, 22 i 1994, *Long* 25144 (E); Miradouro da Ribeira Brava, 109m, 32°40'10.2"N, 17°03'47.2"W, on soil on exposed rock, 24 i 2003, *D.B.Schill & C.Lobo 30* (E); Miradouro da Ribeira Brava, 112m, 32°40'12.4"N, 17°03'43.9"W, on soil next boulder, very exposed with hardly vegetation cover, 24 i 2003, *D.B.Schill & C.Lobo 31* (E).; Ca. 3km above Ribeira Brava, steep rocky river valley, next to road, opposite waterfall and big supermarket, 121m, 32°41'39.2"N, 17°02'47.6"W, on steep vertical volcanic rock, 24 i 2003, *D.B.Schill*

& C.Lobo 32 (E); Between Ribeiro Frio and Faial, 1km below Faja turn-off of road cutting open pine forest on steep rocky slope, c. 400m, on soil covered rocks, 20 i 1994, *Long* 25074 (E); Ribeira do Porto Novo above Rochao, terraced cultivated valley, c. 750m, on rocks by road, 23 i 1994, *Long* 25182 (E); Pico de Facho, next to path on way up, 324m, 32°43'26.6"N, 16°45'32.6"W, on soil on exposed rock with *Globularia salicina* and *Opuntia tuna*, S-exposure, 22 i 2003, *D.B.Schill & C.Lobo 7* (E); Pico de Facho, 333m, 32°43'27.1"N, 16°45'31.7"W, on soil on exposed rock, South facing, 22 i 2003, *D.B.Schill & C.Lobo 11* (E); Porto Santo I., Pico de Facho, 19 I 1954, *Nóbrega* s.n. (S); Encumerada, below Restaurant of Encumerada to Jardim da Serre, just above car turning place by road, c. 990m, on shady steep rock cutting, 24 i 2003, *D.B.Schill & C.Lobo 35* (E); Between Encumerada and Pousada do Vinhages, above hotel in road turning, c. 860m, on steep rock cutting, 24 i 2003, *D.B.Schill & C.Lobo 36* (E); Ponta do Sol, Miradouro do Madaleno do Mar, 374m, 32°42'23.1"N, 17°08'24.3"W, on dry wall, S-exposed, 24 i 2003, *D.B.Schill & C.Lobo 37* (E); Ponta do Sol, Moledos, Miradouro do Madalena do Mar, 377m, 32°42'25.4"N, 17°08'21.2"W, on exposed rocks, S-exposure, 24 i 2003, *D.B.Schill & C.Lobo 38* (E); Camara de Lobos, Cabo Girão, 100m away from Miradouro by road, open Eucalyptus/Pine/Mimosa-forest, 629m, 32°39'31.6"N, 17°00'16.0"W, on soil on large S-facing boulder, 24 i 2003, *D.B.Schill & C.Lobo 39* (E); Bäckravin mellan Fonte och Choupana ovanför Funchal, 26 iv 1952, *Gillis* 44 (S). [**Norte Region**], Lusitania, Oporto, 1880, *Newton* s.n. (S); Caminha, Minho, murettes en blocs granitiques, ca. 25m, *Allorge* 151B (F) ; Lusitamia, Oporto, 1880, *Newton* s.n. (BM).

SPAIN, [**Andalucia**], Malaga, Artola, bäckravin, 3 v 1960, *Arnell* s.n. (S); Granada, on damp rocks in the Genil? Valley, towards the Sierra Nevada Hotel, 12 v 1926, *Ellman & Sandwith* 832 (BM); Granada, Maitena, ca. 1000m, 6 v 1960, *Arnell* s.n. (S); By road, Berchiules to Mecina Bombaron, s. side Sierra Nevada, Prov. Granada, 20 v 1977, *Wallace* s.n. (BM). **Canary Islands, Gran Canaria**, La Calzada, el barranco, 1 iii 1959, *Arnell* s.n. (S); Cruz de Tejeda, 1400m, 10 iii 1959, *S.Arnell* s.n. (H4335) (JE); Vega San Matteo, 13 iii 1959, *Arnell* s.n. (S); Vega San Matteo, ca. 1000m, 13 iii 1959, *Arnell* s.n. (S); Tafira Alta, Montaxna de Tafira, berghäll, ca. 450m, 20 iii 1959, *Arnell* s.n. (S); Tafira Alta, bergvägg vid Los Frailes, 20 iii 1959, *Arnell* s.n. (S); Tafira Alta, Los

Frailes, 12 iii 1959, *Arnell* s.n. (S); Montana de Tafira, 4 iii 1959, *Arnell* s.n. (S); Montana, de Tafira, 5 iii 1959, *Arnell* s.n. (S); Lagunetas, 10 iii 1959, *Arnell* s.n. (B74505) (S). **Canary Islands, La Palma**, Roadside 2km SW of Los Sauces, c. 250m, on soil on sloping rocks, 30 xi 1978, *Long* 7256 (E); Santa Cruz, Brena Alta road, c. 20m, shaded soil on roadside rocks, 29 xi 1978, *Long* 7227 (E); Side of track 2 km north of El Granel, 410 m, 13 xi 1990, *A. C. Crundwell* 1257 (E). **Canary Islands, Tenerife,** *Krause* s. n. (669264) (BM); Laguna, ad rupes, xii 1844, *Bourgeau* 295 (BM); *Bougeaux* c (BM); Aguamansa, Oratora valley, c. 1000m, dry rock crevices in barranco by village, 31 iii 1977, *Long* 5698 (E); Above Los Organos, Aguamonsa, Barranco, in pine forest, c. 1100m, on rock face, 6 iv 1977, *Long* 5890 (JE); Laguna, ad rupes, *Bourgeau* 299 (NY); Adeje, Boco del Infierno, 23 iii 1962, *Stork* s.n. (S); Mercedes, 27 iii 1958, *Arnell* s.n. (S); El bosque de Mercedes, 18 iii 1958, *Arnell* s.n. (S); Div. Buenavista del Norte, Montana del Taco, 2 km E of Buenavista, on soil on N rim of crater, c. 340 m, GR. c.323398, 6 iv 1978, *C.C. Townsend* 78/577 (E); 2km E of Puerto de la Cruz, c. 30m, dry rock crevices in small barranco, 3 iv 1977, *Long* 5808 (E); Prov. Santa Cruz, on dry, friable-surfaced rocks by the road to Bailadero just outside San Andres, 7 km NE of Santa Cruz, c. 50 m, 27 iii 1978, *C.C. Townsend* 78/188 (E); Div.Puerto de la Cruz, on dry soil beneath a rock, Barranco de la Arena, just E of Puerto de la Cruz, GR. c.510443, 1 iii 1978, *C.C. Townsend* 78/331 (E). **Catalonia**, Serria Barrimona, iv 1873, *Bolós* s.n. (S). **Extremadura**, In anpeatribus? de serra de Monsanto Extrema. Hepertissima?, iii 1840, *Welwitsch* 22 (NY); Inter prommenosis aharmagne plantarum cuspitas in montveis aficois, prope Malhache Extremadura, *Welwitsch* 23 (NY).

SWITZERLAND, Ticino, Locarno, auf Mauern, 1857, s.n. (BM); Locarno, in mur., 1818, Herbarium Hampe, s.n. (669097) (BM); Ad Verbanum p. Locarno, *Duthy* s.n. (NY); Route Morcote-Melide, de Preabella a la bifurcation pour Vicomorcote, 290m, 1951, *S. Vautier* 620 (JE, S); Route Morcote-Melide, entre Morcote et la ville Ersilia, 290m, 11 iv 1951, *Vautier* 602 (S, F).

TURKEY, Adana Province, dist. Bahçe (N. Amanus), Dumanli Dağ above Haruniye, c. 800m, moist bank, 19 iv 1957, *Davis & Hedge* 26822 (E). **Antalya Province**, in rock-crevice near the sea at Kaş, 11 iv 1972, *Crundwell, Nyholm &*

Saenger 718a/72 (S). **Giresun Province**, on moist rock cave on hill in the town Giresun, ca. 100m, 4 xi 1974, *Engelmark & Nyholm* L54, 634/74 (S). **Izmir Province**, earthy bank 10 km west of Ödemis, 50 m, 7 iv 1971, *E. Nyholm & A. C. Crundwell* 622 (E); East side of Mt Yamanlar, c. 50m, moist soil among *Proterium spinosum*, 21 iv 1970, *Elsa Nyholm* 300 (JE); Lydia, Sinus, Smyrnaeus supra Thomaso, 1 v 1906, *Bornmüller* s.n. (S); Lydia, Smyrna, prope pagum Thomaso, 1 v 1906, *J.Bornmueller* 9973 (E, JE, BM, S).

ALGERIA, *Trabut* s.n. (Herbarium Stephani) (725092) (BM);1848, *Montague* 3 (B74432) (S). [**Blida Province**], Blida c., 26 iii 1908, *Trabut* s.n. (S).

CAPE VERDE, Santo Antao Island, inside Cova, ca. 1200m, 4 xi 1958, *Byström* H35 (S); Santo Antao Island, insideCova, ca. 1200m, 1958, *Byström* H26 (S).

NAMIBIA, 1963, *Leippert* 5349/WIN85 (JE); 1957, *Volk* WIN77 (JE); Nevdamm, Glimmerschieferüberhänge, schattig, pH7.8, Carpophore bis 25mm lang, in Rasen, 14 iv 1974, *Volk* 948/WIN 63 (JE, BM); SW-Afrika, am Rivier bei Nevdamm, Glimmerschiefer-Ueberhaenge, (duftend), 11 xii 1973, *Volk* 685 (JE); SW-Afrika, an Rivier Nevdamm, Glimmerschiefer-Ueberhang, 11 xii 1973, *Volk* 686 (JE); Frauenstein, Glimmerschiefer-Ueberhang, Ufer, schattig, wohlriechend, 3 iii 1974, *Volk* 862 (JE). **Hardap Region**, near Rehoboth, next to road C24, 1475 m, 23°21'18.8"S, 17°4'4.7"E, on rock, 21 iii 2004, *D.B.Schill & J.Clarke* 138 (E). **Khomas Region**, South-West Africa, Windhoek 77, 23 ix 1957, *Volk* 11400 (BOL); South Africa, Windhoek, 1 xi 1971, *Volk* 00554 (BM); South-West Africa, Windhoek 68, 14 iv 1974, *O.H. Volk* 00948 (BOL); Matchless Mine, Khomas, Glimmerschiefer-Felsrippe, haeufig, 30 xi 1973, *Volk* 677 (JE); Windhoek, on road to Matchless Mine, little river valley, on banks, 1910 m, 22°40'31.7"S, 16°51'4.8"E, on soil under big boulder, 10 iii 2004, *D.B.Schill & J.Clarke* 118 (E); Windhoek, on road to Matchless Mine, little river valley, on banks, 1889 m, 22°40'37.3"S, 16°51'3.7"E, S-facing, in crevice by stream bed, 10 iii 2004, *D.B.Schill & J.Clarke* 121 (E); Windhoek, on road to Matchless Mine, little river valley, on banks, 1889 m, 22°40'37.4"S, 16°51'3.3"E, on soil, 10 iii 2004, *D.B.Schill & J.Clarke* 122 (E). [**Omaheke Region**], 10km östl. Windhoek, Tälchen an der Strasse nach Gobabis, schattige Glimmerschiefer- Überhänge und –Treppen, Boden sehr humos, dunkel, Staubboden, 1974, *Volk* 905 (JE); **Otjozondjupa Region**, auf Granitzersatz, schattige Überhänge, Farm Quelldamm bei Kalkfeld, Otjiwarongo Nr.110, 1973, *Volk* 467 (JE); 10km westlich Okahandja, Granitkuppe, Granitblockhalde, Ueberhaenge, SW-exponiert, 17 ii 1974, *Volk* 828 (JE); 10 km west of Okahandja (B2), prominent granite hill next to rest stop, 1407 m, 21°57'33.6"S, 16°50'29.7"E, under boulder on thin soil layer on granite stone, 11 iii 2004, *D.B.Schill & J.Clarke* 124 (E); 10 km west of Okahandja (B2), prominent granite hill next to rest stop, 1411 m, 21°57'33.3"S, 16°50'30"E, on granite, 11 iii 2004, *D.B.Schill & J.Clarke* 125 (E); Waterberg Plateau Park, on trail to viewpoint, rocky hillside, 1567 m, 20°30'15.4"S, 17°14'33.6"E, on soil under stone, 11 iii 2004, *D.B.Schill & J.Clarke* 127 (E).

SOUTH AFRICA, SW-Afrika, sine loco speciali, 1974, *Volk* s.n. (H1256) (JE). **Free State Province,** Oranje Frijstaat, Bloemfontein, 29 x 1963, *K.H. Rechinger* 5369 (B74548) (S); Botanical Garden Bloemfontein, not cultivated part on hill, with stomata, 4 xii 1980, *O.H. Volk* 81/062 (BOL); Eaglesnest, Bloemfontein, 5.3. 29, *Potts* 1266 (F); O.F.S., Prov. Trompsberg, around boulders, base on S. aspect of outcrop, Ranoid Veld, 4 mls S of Trompsberg, 14 ii 1955, *E. Schelpe* 5282 (BOL). **Gauteng Province**, Pretoria, amongst rocks, Magaliesberg range Wanderboom, 20 iv 1929, *M.Bosman* 199 (NY, F). **[Kwa Zulu-Natal Province],** South-East Africa, Mountains near Mooi River, viii 1880, *W. Nelson* 339 p.p. (BM). **[Mpumalanga Province],** Transvaal, Prov. Lydenberg, 15 miles N.E. of Lydenberg, *D.E.Schelpe* 5906 (BOL). **[Northern Cape Province]**, Kap-Provinz (an der Grenze zu Namibia), Augrabies-Faelle des Oranje, Granitfelsen, Ueberhaenge, pH 5.8, 29 vi 1973, *Volk* 554 (JE); Cape Province, Kuruman division, just east of Brethy Mine, 5500ft., in damp rock crevices and under overhanging rocks in kloof, 3 vii 1961, *E.G.H.Oliver* 1450 (BM, S, BOL); Kanoo, Three Sisters, *D.E.Schelpe* 5860 (BOL). **[North-West Province]**, Magalis-Gebirge (Transvaal), Rustenburgklook (Schlucht), 28 xi 1954, *B.J.Cholnoky* (B74545) (S). **[Western Cape Province]**, Kap-Provinz, Montagu, Cogmans Kloof, 19 ix 1951, *S.Arnell* 791 (JE, S, BOL); Kap-Provinz, Montagu, Cogmans Kloof, 19 ix 1951, *S.Arnell* 795 (F, JE, BOL); Cape Province, Montagu, Cogmans Kloof, 19 ix 1951, *S.Arnell* 798 (BOL); Cape Provinz, Montagu, Kam Kloof, 20 ix 1951, *S.Arnell* 825 (S); Cape Provinz, Montagu, Cogmans Kloof, 19 ix 1951, *S.Arnell* 806 (S);

Clanwilliam, on Farm Mertenhof, Bidouw Valley, on slope facing east below a Bushman Cave, 1500 ft., 24 vii 1961, *E.G.H. Oliver* 1465 (BOL).

TANZANIA, Uluguru Mountains, 1480m, on dry open rocks near Hululu Falls, S of Bunduki, 25 iii1973, *T. Pocs* 6902/A (JE).

ZIMBABWE, S.Rhodesia, Khami Ruins, near Bulawayo, locally common on shelterd earthly ledges, 5000 ft., 30 vi 1953, *E.Schelpe* 3926 (BM, BOL).

CYPRUS, near Ayia, on the road from Kannaviou to Stavros, western Troodos, 21 vi 2003, *T. L. Blockeel* s.n. (E).

PROBABLY ERRONEOUS LOCALITIES: Brasil, 1874, *Raddi* s.n. (BM); Brasil, *Raddi* s.n. (BM).

UNKNOWN LOCALITIES: Wasserfall, Kumakala, 24, s.n. (669239) (BM); In agris olyvifonervis?, *Welwitsch* s.n. (NY); Veri 1844, *Messano* s.n. (S); Herbarium Lehmann s.n. (B7422) (S); *Savi* s.n. (B74423) (S); *Savi* s.n. (B74421) (S); Ex-Herbarium A. de Mercey (669090) (BM).

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

FINLAND, **[Finland Proper Region]**, Varsinais-Suomi, Velkua, Pohjakylä, Mustaluoto, in calcareous rock crevice, 29 v 1962, *T. Laine* s.n. (S).

NORWAY, [Buskerud County], Drammen, Mai 1881, *N. Brylen* s.n. (B74915) (S).

RUSSIA, **Siberia**, **[Krasnoyarsk Territory]**, Jenisei, inter Krasnojarsk, Jenisseisk prope pagum Makokovo, 18.6.1876, *H. W. Arnell* s.n. (B24528) (S); Jenissei, inter Krasnojarsk et Jeniseisk, prope pagum Makokovo, 18 vi 1876, *H. W.Arnell* s.n. (H1306) (JE); Jenisei, inter Krasnojarsk et Jeniseisk, prope pagum Makokovo, 18 vi 1876, *Arnell* s.n. (B24527) (S); Jenisei, Makakovo, 18 vi

1876, *Arnell* s.n. (B24526) (S); Jenisei, Futjanova, 23 ix 1876, *Arnell* s.n. (B74776) (S); Jenisei, Fatjanova, 64°5'n.lat., 25 ix 1976, *Arnell* s.n. (S); Jenisei, *Arnell* s.n. (BM); Jenisei, Futjanova, 23 ix 1876, *Arnell* s.n. (B74778) (S).

U.S.A., Alaska, [North Slope Borough]: Arctic Alaska, Umiat and vicinity, Colville River, 69°22'N, 152°08'W, in wet tundra and on ridges, on soil, steep south-facing ridge, 30 vi – 6 vii 1974, *W.C. Steere & Z. Iwatsuki* 74-29 (JE, NY); Colville River, 69°22'N, 152°08'W, on soil, steep south-facing ridge, in wet tundra and on ridges, 30 vi –6 vii 1974, *Steere, Inoue & Iwatsuki* 74-29 (NY). **Iowa,** Allamakee County: 3 miles south of Harpers Ferry, over moist thin soil on face of bluff, with *Woodsia obtusa* and *Reboulia*, 14 v 1950, *Schuster* 18059 (F). **Michigan**, Machnide Kelt., on limestone cliff, 6 vii 99, *Harper* s.n. (1040238)(F). **Minnesota**, Houston County: 3.4 miles S of Brownsville, over rather dry, exposed, east-facing, soil-covered sandstone ledges, with mature carpocephala, pH7.3, spores 55–60u at time of dehiscence of capsule, thallus sections with ventral tissue high, keeled, ventral scales with oil-cells, 31 v 1949, *Schuster* 14326 (F); 3 miles N of Reno, on thin sandy calcareous soil over talus and crevices at bases of east facing bluffs, occurring with *Mannia rupestris*, 14 v 1947, *Schuster* 6754 (F). Lake County: N-America, Carubou Falls, 6 vii 1926, *G. H. Conklin 2554* (F). Wabasha County: two miles S of Lake City, on bluff, 19 v 1950, *Schuster* s.n. (1133340)(F); 1 mile south of Lake City, on moist sandstone bluffs, in shade, 15 v 1947, *Schuster* 13516 (F); 1 miles S of Lake City, on thin soil over E-facing calcareous bluffs, with immature carpocephala, occurring with *Cryptogramma stelleri*, *Corydalus areus*, near *Clevea hyalina* and *Mannia rupestris*, *Conocephalum*, 9 v 1948, *Schuster* 4672 (F). Washington County: Nearctic, over sandstone wall, about 1 mile s. of Stillwater, occurring with Pellaea glabella, 11 vi 1950, *Schuster* 18130 (NY, F); Along narrow cut going into St. Croix River, circa 3.5 miles N of Stillwater, over moist thin soil, mature carpocephala and spores, 11 vi 1950, *Schuster* 18136 (F); Over sandy, moist soil over sandstone cliffs, 3 miles north of Stillwater, with mature carpocephala, v 1947, *Schuster* 14051 (F). Winona County: Winona, wet ground, 19 vi 1888, *Holzinger* s.n. (268657) (NY); Over crest of sandstone bluff, below "The needle", near S.Lake Winona, Winona, occurring with carpocephala and spores (rare), with *Preissia quadrata*, 7 v 1948, *Schuster* 17254 (F); Over friable moist, sunny sandstone ledges, along Whitewater River in Whitewater State Park, capsules, Spores areolate, 52–58–60u, Antheridial disks terminal, 15 v 1950, *Schuster* 18009 (JE, NY, S, F); Whitewater State Park, across Whitewater River, from picknick area, over moist, rather exposed, friable sandstone cliffs and ledges, pH7.8, a few carpocephala, spores and capsules on slide, 29 v 1949, *Schuster* 14225 (F); Whitewater State Park, over moist, exposed friable sandstone cliffs (Jordan sandstone), at end of trail 5, pH, two measurements, 7.6 and 7.9, occurring with *Preissia quadrata*, 30 v 1949, *Schuster* 14315 (F); Whitewater State Park, over moist sandstone bluff, along Whitewater R., 15 v 1950, *Schuster* 18009b (F); Whitewater State Park, over Jordan sandstone along Whitewater River, near end of trail 5, with carpocephala, 17 v 1949, *Moore* 19958 (F); Whitewater State Park, over exposed, somewhat sunny, relatively dry rapidly disintegrating, friable sandstone faces of cliff along Whitewater River, pH7.6, occurring with *Preissia commutata* intermingled, with carpocephala mature, 29 v 1949, *Schuster* 14227 (F); Witewater R. in Whitewater State Park, over moist sunny sandstone, with *M. triandra*, 15 v 1950, *Schuster* 18009a (1124472) (F).

CANADA, **Yukon Territory**, along Duncan Creek near Keno Hill about 30 miles northeast of Mauo, ledge on bank, common, 5 vii 1949, *Calder & Billard* 4265 (NY). On earth at the summit of the Rocky and Selkirk Mountains, 7500 ft., Underwood Herbarium, s.n. (268874) (NY).

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

AUSTRIA, **Styria**, Central Alps, Knittelfeld, Rachau, Rachaugraben, next to path, c. 800m, on rocks in crevices, S-W- exposure, 23 vii 2003, *D.B.Schill, H.Köckinger & U.Müller* 77 (E), Central Alps, Knittelfeld, Rachau, Rachaugraben, next to path, c. 800m, on rocks in crevices, S-W- exposure, 23 vii 2003, *D.B.Schill, H.Köckinger & U.Müller* 78 (E).

FRANCE, [Rhône-Alpes], Ardèche, Banne, Pont du Granzon, fissures de tables calcaires, 21 iii 2005, *V. Hugonnot* s.n. (E); France, Ardèche, Labeaume, Peyroche, dans les joints des couches calcaires, en position verticale, sur des terrasses surplombant le cours de la Beaume, avec Timmiella, Weissia, Reboulia, 150 m, 18 iv 2004, *Hugonnot* s.n. (E).

U.S.A., Arizona, [Gila County]: Sierra Ancha, 1550m, Parker Creek Experimental Forest, natural drainages, oak chaparral zone, common on quartzite ledges, 1937, *Little* 4507 (JE). Mohave County: Pipe Spring, 4500ft., red sandstone ledges, very dry, 29 v 1944, *Flowers* 2729 (NY). [Pima County]: Molino Basin, Sta. Catalina Mts., Coronado Natl. Forest, above Tucson, 4300 ft., thin soil over rocks, oak woodland zone, 22 iii 1979, *Schuster* 79-211 (F); Mt. Lemon, 1 km above Molino Canyon, Sta. Catalina Mts., in quebrada, soil over exposed rocks, pine-oak zone, 27 xii 1981, *Schuster* 81-302 (F). [Santa Cruz County]: Pajarita Mountains, 12 miles west of Nogales, 19 iii 1941, *Gross* s.n. (NY); Sycamore Canyon, on moist shaded place, 29 viii 1938, *Goodding* 131 (NY). **California**, Fresno County: Tollhouse Road between Tollhouse and MT-Rest Guard Station, 2800ft. (840m), soil, base of granite outcrop, 26 iv 1980, *T. Doyle* 2744 (NY, F). [Los Angeles County]: Pasadena, West?side, 4000ft., trail to Wilson's Peak, iv 1893, *McClatchie* s.n. (NY); Pasadena, 21 iv 1893, *McClatchie* #316 (NY); Trail to Wilson's Peak, at 4000ft., *McClatchie* s.n. (575651) (NY). [Mariposa County]: Yosemite valley, 1866, *Bolander* s.n. (575639) (NY); Yosemite valley region, 1896, *Cooke Jr.* s.n. (5755653) (NY); *Bolander* s.n. (575640) (NY); *Bolander* s.n. (575647) (NY); 1864–70, *Bolander* s.n. (575648) (NY). Tulare County: Sequoia National Park, below Amphitheater Point, 36°31'43"N, 118°46'30"W, c. 1190m, steep wooded hillside, on wet banks by small waterfall, 4 iv 1998, *Long* 27577 (E). **North Carolina,** Jackson County: Cedar Cliff Mountain, East Fork of Tuckaseegee R., ca. 4600 ft., along NC rte 281, thin soil over partly sunny dry ledges, with *Cheilanthese lanosa*, occurring with *Reboulia hemispherica*, sterile, 1 ix 1953, *Schuster* 29498 (F); Cedar Cliff Mt., East Fork of the Tuckaseegee River, exposed rock outcrop, 5 vi 1951, *Anderson* 9896 (F); Cedar Cliff Mt., East Fork of the Tuckaseegee River, along Rte 281, thin soil over partly sunny dry ledges, occurring with *Cheilanthes lanosa* and *tomentosa*, *Woodsia obtusa*, *Talinum teretrifolium*, 1 ix 1953, *Schuster* 29498a (F). [Polk County]: Tryon, N.C., White Oak Mountain, on earth among rocks, 5 iv 1929, *Evans* s.n. (268682), F). **Tennessee,** Polk County: 300m, crevices of siliceous bluff, 1956, *Sharp & Robinson* 563 (JE, NY, F); Moist crevice on shale cliff, 19 iii 1939, *Sharp* s.n. (268687) (NY). **Texas**, Gillespie County: Enchanted Rock, growing on thin soil over granite, 18 ii 1961, *Ellison* 151 (268765) (NY).

CANADA, [**British Columbia**], on earth at the summit of the Rocky and Selkirk Mountains, 7500 ft., Underwood Herbarium, s.n. (268874) (NY).

LESOTHO, **Maseru District**, above the Liphiring River near the village of Mahlabatheng, 7km north-west of Roma, Maseru District, 1600m, 29°25'S, 27°40'E, shaded by shrubs under a low sandstone ledge, E-facing, 24 iv 1997, *J.G.Duckett & W.Matcham* 5149a (E).

NAMIBIA, Frauenstein, Glimmerschiefer, Ueberhang Ufer, schattig, 16 ix 1974, *Volk* 862 (JE). **Khomas Region**, Windhoek, 10 km E of Windhoek on road to Gobabis, little valley, overhang, 1788 m, 22°34'26.4"S, 17°10'4.8"E, on soil on ledge below rock, 9 iii 2004, *D.B.Schill & J.Clarke* 112 (E); Windhoek, 10 km E of Windhoek on road to Gobabis, little valley, overhang, 1788 m, 22°34'26.8"S, 17°10'4.5"E, on ledge on rocky bank, 9 iii 2004, *D.B.Schill & J.Clarke* 114 (E); Windhoek, on road to Matchless Mine, little river valley, on banks, 1920 m, 22°40'30"S, 16°51'5.9"E, on soil under big boulder, 10 iii 2004, *D.B.Schill & J.Clarke* 119 (E); Windhoek, on road to Matchless Mine, little river valley, on banks, 1891 m, 22°40'37.1"S, 16°51'4.1"E, in rock crevice on big boulder, 10 iii 2004, *D.B.Schill & J.Clarke* 120 (E). **Otjozondjupa Region**, Otavi-Bergland, Rietfontin, Dolomitfelsen, Ueberhaenge, schattig, 11 iv 1974, *Volk* 943 (JE); Otjiwarongo, Farm Oros, on hillside behind farm, W-facing, 1574 m, 20°14'2.3"S, 17°7'42.7"E, under rock, 13 iii 2004, *D.B.Schill & J.Clarke* 128 (E); Otjiwarongo, Farm Oros, on hillside behind farm, W-facing, 1577 m, 20°14'2.3"S, 17°7'42.7"E, under rock, 13 iii 2004, *D.B.Schill & J.Clarke* 130 (E); Otjiwarongo, Farm Oros, on hillside behind farm, W-facing, 1576 m, 20°14'2.3"S, 17°7'42.6"E, on soil under rock, 13 iii 2004, *D.B.Schill & J.Clarke* 131 (E); Otjiwarongo, Farm Oros, on hillside behind farm, W-facing, 1573 m, 20°14'1.3"S, 17°7'43"E, under pile of rocks on soil, 13 iii 2004, *D.B.Schill & J.Clarke* 133 (E).

SOUTH AFRICA, [Gauteng Province], Pretoria district, Hennops River Valley 23 i 1955, *Meeuse* 9621 (F, BOL).

TANZANIA, [Morogoro Region], Uluguru Mt., 1240m, on shady rocks near waterfalls, Morningside, 17 v 1972, *T.Pocs* 6571/B (JE); Uluguru Mt. near Morogoro, riverine forest, rocky type, near Bahati Camp, along the Morogoro river, 600m, on stony soil, 1 v 1972, *T.Pocs* 6561/q (JE)

CHINA, Yunnan, Fugong County, CN, Gaoligong Shan Range, southern end of the Hengduan Shan, Nu Jiang (Salween River) watershed, above dirt road about 2–3 km south of Fugong near Guqian and Mugujia Village, 1275 m, 26°51'54.5"N, 98°52'00.6"E, along flume on steep hillside, ruderal vegetation with remnants of secondary hardwood forest, on filtered marble boulders, 21 iv 2004, *J. R. Shevock* 24912 (E); Fugong County, CN, Gaoligong Shan Range, southern end of the Hengduan Shan, Nu Jiang (Salween River) watershed, above dirt road about 2–3 km south of Fugong near Guqian and Mugujia Village, 1275 m, 26°51'54.5"N, 98°52'00.6"E, along flume on steep hillside, ruderal vegetation with remnants of secondary hardwood forest, on filtered marble boulders, 21 iv 2004, *J. R. Shevock* 24925 (E).

JAPAN, [Honshu Island, Kanto Region], Saitama Prefecture, Chichibu District, Otakimura, Kami-nakao, c. 700m, on soil among rocks of hedge, 4 viii 1958, *Inoue* 38/66 (NICH); Chichibu District, Ootakimura, Kaminkao, c. 750m, sunny crevice…, sandstone, 2 ix 1952, s.n. (52817) (NICH); Saitama Prefecture, Chichibu District, Ootakimura, Kaminkao, c. 750m, 2 ix 1952, *Shimizu 52818* (NICH).

LEBANON, Antelias, holes on hard limestone boulder, 7 ii 1943, *P.H.Davis* 5247 (E, BM).

INDIA, *Stewart* s.n. (NY); *Stewart* s.n. (NY); Ind. Orient, *Stewart* s.n. (NY). **[Himachal Pradesh],** Himalaya occ., Kyelang, ad rupes, xerophila, photophila, c. 3000m, vii 1933, *P.N.Mehra* 345 (JE, NY, BM, G, S); Chenab valley, regio temp., 8000 ft, *Thomson* 1680 (BM, NY). **Uttaranchal**, Gangotri, on path to Gomukh, 3335 m, 30°59'37.7"N, 78°59'22.6"E, in hollow at bottom of cliff, 13 xi 2004, *D. B. Schill & J. Clarke* 164 (E); Road from Uttarkashi to Rishikesh, next to roadside, 1032 m, 30°43'53.5"N, 78°21'02.3"E, on rock, 14 xi 2004, *D. B. Schill & J. Clarke* 165 (E). **[Uttar Pradesh]**, Saharanpur (N.W.India), Gor. Botan. Gardens, on rockwork in open air, 990ft., 13 ii 1901, *W.Gollan* 3214 (JE, BM, G, S); Saharanpur (N.W.India), Gor. Botan. Gardens, on rockwork in open air, 990ft., 13 ii 1901, *W.Gollan* 3214b (BM); Cawnpore (Allahabad), Ind. Or., from rockwork in Memorial Garden, c.fr., 23 ii 1903, *Giel* 4213 (010540) (G).

PAKISTAN, **[North-West Frontier Province]**, NW-Himalaya, Chitral, Jambatai, 4000' ft, 6 v 1895, *Harries* 16939 (G, BM); Jambatai, 4000 ft., 6 v 95, *Harries* 16939 (BM). **[Panjab Province]**, Panjab, Lahore, ad fossae lapides, nunc xerophila, nunc subhygrophila, xi 1929, *R.S.Chopra* 3 (JE, G, BM, S, NY); Vorder-Indien, Lahore, Panjab, 1929, *Chopra* s.n. (B74740) (S).

YEMEN ARAB REPUBLIC, Towillah, c. 2530m, soil in shady gully on sandstone cliffs, 31 iii 1981, *Long & Miller* 10169 (E, JE). **[Ibb governorate]**, Jibla, wadi in town, c. 2100m, on shaded soil by wadi, 10 iv 1981, *Long & Miller* 10261 (E).

4. *Mannia fragrans* (Balbis) Frye & L.Clark

AUSTRIA, Hutweidenboden, 1 iv 1956, *Froehlich* s.n. (S). **Carinthia**, Austrian Alps, Kärnten, *Breidler* s.n. (725042) (BM). **Lower Austria**, sonnige Haenge in der Weinbergregion (Schiefer) oberhalb Stein an der Donau, 250–300m, iv 1900, *J. Baumgartner* 1187a (E, NY, S, JE); Sonnige Haenge in der Weinbergregion (Schiefer) oberhalb Stein an der Donau, 250–300m, 19 xi 1901, *J. Baumgartner* 1187b (E, NY, S, JE); Rothenhof nächst Stein an der Donau, 300 m, 1897, *J. Baumgartner* s.n. (H1296) (JE); Sonniger Hügel bei Rothenhof nächst Stein/Donau, Schiefer, ca. 300 m, 4 iv 1897, *J. Baumgartner* s.n. (E); Sonnige Hügel bei Rothenhof nächst Stein, 300m, 4 iv 1897, *Baumgartner* s.n. (S); Wachau, nördlich von Rotenhof ca. 300m auf Erde, 19 ii 1939, *Froehlich* s.n. (S); Bei Rotenhof an der Wachau, ca. 300m, auf Erde, 19 iii 1939, *Froehlich* s.n. (S);

Bei Rotenhof an der Wachau, ca. 300m, auf Erde, 12 iii 1939, *Froehlich* s.n. (S); Südlich von Hundsheim, Spitzerberg, 250–290m auf Erde, 26 viii 1956, *Froehlich* s.n. (S); Nordwestlich von Hundsheim auf dem Südwestrücken des Hexenberges ca. 300m auf der Erde im steinigen, pannonischen Heideboden, 1 v 1956, *Froehlich* s.n. (S); Spitzer Berg, südlich von Hundsheim, ca. 250m, auf Erde, 24 iv 1938, *Froehlich* s.n. (S); Südlich von Hundsheim, Südwesthang des Spitzberges, ca. 275m auf Erde, 22 iv 1956, *Froehlich* s.n. (S); Braunsberg bei Hainburg, Quarzitriff auf der Südseite auf Erde, 5 iv 1941, *Froehlich* s.n. (S); Braunsberg bei Hainburg auf Erde, 24 iv 1938, *Froehlich* s.n. (S); Westlich von Pulkau, ca. 375m, auf Erde, 20 iv 1939, *Froehlich* s.n. (S); Göttweiher-Berg, 1871, *Erdingern* s.n. (B74582) (S). **Salzburg**, Lungau, sonnseitiger Abhang bei Mur, ca. 1200m, 24 viii 1880, *Breidler* s.n. (S); Sonnseitiger Abhang bei Mur in Lungau, 1200m, 25 viii 1878, *Breidler* s.n. (S); Im Lungau, Abhaenge bei Mur, ca. 1200 m, 24 viii 1878, *Breidler* s.n. (JE). **Styria,** ex Herbarium *Stephani* s.n. (NY); In einem ..bei Graz, iv 1875, *Breidler* s.n. (NY); Graz, Flurufer an einem Wiesenrain, 250 m, April 1875, *Breidler* s.n. (669107) (BM); An einem Wiesenrain bei Graz, 27 iv 1875, Hb. S.O. Lindberg, s.n. (S). **Tyrol,** *Sauter* s.n. (NY); Windisch Matrei, 1877, G.D./ Herbarium H Pearson, s.n. (725079) (BM); Windisch Matrei, s.n. (725046) (BM); Auf Kalkboden des Blaser (Matrei in Tirol), auf Kalkboden eines begrasten Abhanges auf dem Blaser in einer Hoehe von 6500 Fuss, 24 xiii 1871, *Arnold* 517 (JE); Tirolia australis, ad terram aridam collium apricorum montis Guntschna prope Bolzanum, solo porphyraceo, *Sauter* 1139 (BM, NY, S, F, E). **Upper Austria,** Steyr, *Schimper* s.n. (725062) (BM); Auf verwitterter feuchter Erde der Nagelfluh-Huegel bei Steyr, *Sauter* 332 (JE); Linz, an Wärmeplätzen am St. Martin mit Pulsatilla, Carex humilis, Globularia etc., 16 iii 1951, *Barikant?* s.n. (JE). **Vienna**, Nördling nächst Wien, 14 iv 1822, *Juratzka* s.n. (725049) (BM); Abhänge bei Mädling nächst Wien, 14 iv 1890, *Juratzka* s.n. (S).

CZECH REPUBLIC, Central Bohemia Region, distr. Doutnáč, in clivo stepposo, c. 200m, 16 v 1967, *J. Váňa* s.n. (JE); Distr. Benešov, collis Hláska supra flumen Horní Sázava, 2 vii 1935, *Suza* 2 (S). [**Prague**], Podbaba bei Prag, 13 iii 1884, *Schiffner* s.n. (B74703) (S). [**South Moravia Region**], Moravia occid., Tišnov (p.

vicum Drásov), in solo calcareo in cumulo Drásovský kopeček, c. 310m, 2 v 1937, *Šmarda* 82 (S); Mähren, Heiligen Berg pr Mikulov, v 1913, *Podpera* s.n. (S).

FRANCE, [Rhône-Alpes], Lyon, s.n. (725066) (BM); Bessans (Savoie), vallée de la Lombarde, 2450 m, sur la terre sèche (schistes lustrés), 10 viii 1952, *L. Castelli* 9 (S).

FINLAND, [Southern Finland, Tavastia Proper Region], South Häme province, Lammi, Lamminjärvi-Halila Natura 2000-area, F10325008, Halilankallio SE/S-facing steep rock crevice with dry herb meadow vegetation, on road terraces, 27°E 6776000: 3395061, on shallow soil on rock terraces, often on base of ferns such as *Asplenium septentrionale*, fairly abundant, 24 x 2005, *S. Laaka-Lindberg* 22-2005 (E).

GERMANY, Baden-Württemberg, Bilstein im Hoellental, bei Albungen a.d. Werra, 9 vii 1956, *K. Meyer* s.n. (JE); Bilstein bei Albungen, schoener Rasen, 2 x 1904, F. Quelle s.n. (JE); Baden, Kaiserstuhl, am Schneckenberg bei Achkauen?, Sommer 37, *G.Herzog* s.n. (JE); Baden, auf humosen Stellen des Hohentwiel, c. fr., iv 1898, *Herzog* s.n. (S); Baden, bei Heidelberg, 1844, *Buhse* s.n. (S); Baden, Heidelberg, 1844, *Buhre* s.n. (JE); Baden, Heidelberg, 1844, *Buhse* s.n. (NY); Baden, Heidelberg, in valle Ludwigsthal prope Schriesheim, 1845, *Bischoff* s.n. (BM); Heidelberg, *Buhse* s.n. (S); Heidelberg, 1836, *Buehinger* s.n. (S); Heidelberg, *Funck* s.n. (72508) (BM); Heidelberg, 22 ix 84, *Schimper* s.n. (E); Heidelberg, ..., Trevirauns?, 1830 , *Bischoffs* s.n. (BM); Heidelberg, 1830, *Bischoff* s.n. (725017) (BM); Heidelberg, s.n. (725072) (BM); Heidelberg, 1861, *Mettenius* s.n. (NY); Circa Heidelberg, *Bischoff* s.n. (725075) (BM); Prope Heidelberg, *Bischoff* s.n. (S); Baden, bei Schriesheim, *G. W. Bischoff* s.n. (725082) (BM); Eboulis granitiques des côtes incultes dans la vallée Ludwigsthal près de Schriesheim aux environs de Heidelberg, iii1849, *Arnold* 1388 (BM); Bei Schriesheim im Ludwigsthal, an felsigen Abhängen, Hb. Schimper, s.n. (725059) (BM); In valle Ludwigsthal prope Schriesheim, x 1835, s.n. (JE); Schriesheim, Ludwigsthal, *Bischoff* s.n. (725073) (BM); Ludwigsthal, *Bischoff* s.n. (BM); Im Ludwigsthale bei Schriesheim, iii 1850, *G. W. Bischoff* 473 (BM, NY); Im Ludwigsthale bei Schriesheim, an Granit in der Gessellschaft von *Riccia* *bischoffii*, iv 1836, Herb. *Hampe* s.n. (BM); Vom Eingang in das Ludwigsthal, auf Granit, iii 1828, *Hirtz*? s.n. (JE). **Bavaria**, *Herbarium Helmgren* s.n. (S); Eichstätt, iv 62, *Arnold* s.n. (BM); Bei Eichstaett in Mittelfranken, *Arnold* 83 (JE, BM, NY, F, S); Eichstätt, iv 1862, *Arnold* s.n. (BM); Auf steinigem, karg begrastem Boden der Bergabhänge zwischen Eichstätt und dem Tiefenthale, c.fr., 15 v 1860, *Arnold* 83b (S); Schwabelweisser Berghaenge bei Regensburg, 370m, auf Humus ueber Dolomit, 9 iv 1907 and 1909, *Familler* 1190 (JE, S, NY); Regensburg, Dolomit bei Schwabelweiß, 380m, iv 1907, *Familler* s.n. (S); Regensburg, auf Dolomithumus der Schwabelweisser Berghänge, 370m, 9 iv 1907, *Familler* 606 (S); Regensburg, auf Dolomithumus der Schwabelweiser Hänge, 370m, iv 1907, *Familler* s.n. (S); Bayrischer Jura, Felshänge ober Neuessing im Altmühltale, vi 1907, *Familler* s.n. (S); Niederbayern, auf Granit unter Passau-Ilzstadt, ix 1912, *Familler* 606b (S). **Lower Saxony,** Niedersachsen, Harz Mountains, Einhornhöhle, Brandkopfe, NE of Schwarzfeld, 51°38'N, 10°25'E, S-facing dolomite cliff overlooking lake, on friable soil, 28 x 2005, *J. G. Duckett* s.n. (E). **Saxony,** Dresden, s.n. (E); Sachsen, Hb. Hugo Dahl, Schmalkalden, *Krieger* s.n. (JE). **Saxony-Anhalt**, near Nebra, west of Wangen, NSG Steinklöbe, south-east slopes, c. 200m, on thin soil layer of open, exposed boulders, 20 xi 2002, *D.B.Schill & H.-J. Zündorf 2* (E); Near Nebra, west of Wangen, NSG Steinklöbe, south-east slopes, c. 201m, on thin soil layer of open, exposed boulders, 20 xi 2002, *D.B.Schill & H.-J. Zündorf 3* (E); Bezirk Halle, Unteres Unstruttal, Nebra, auf Felspodesten ca. 3km nordwestl. Klein Wangen, am Suedhang der Steinkloebe (am westl. Ende des Steilhanges), 8 v 1966, *K.-F. Guenther* s.n. (E). **Thuringia,** Ex-DDR, Heinrichstein im Oberen Saaletal, 1970, *Meinunger* s.n. (JE); Auf Detritus der Steinkloebe bei Nebra, 23 v 1970, *J.Hueneck* s.n. (JE); Bezirk Erfurt, suedl. Vorland des Harzes, Nordhausen, Kalk-Berg nordoestl. Krimderode, flachgruendiger, suedexponierter Rasen am Hangfuss, 6 v 1975, *K.-F. Guenther* s.n. (E).

HUNGARY, Kultivat des Jenaer Botan. Gartens vom 30 iv 1973, 1972, *A. Boros et Vadja* s.n. (H1295) (JE); M. Synto, Medzi Skalky, 29 viii 1890, *A. Kmet* s.n. (E); M. Synto, Medzi Skalky, 29 viii 1890, *A. Kmet* s.n. (JE); M. Synto, Medzi Skalky, 29 viii 1890, *A. Kmet* s.n. (B74620) (S); M. Synto, Medzi Skalky, 29 viii 1890, *A. Kmet* 25 (JE). Hungary? Podbabal bei Tray?, xi 84, *Schiffner* s.n. (E); S-

Ungarn, Villányer Gebirge, Nagyharsányi Berg, Kalkfelsritzen und offener Humus auf Kalk, 350 m, 3 iv 1975, *Pócs* s.n. (H1433) (JE); Balatonfüred, 18 v 1972, *Z. Vajda* s.n. (JE); Ungarn, Steingerthal, 22 vii 1879, *S. Hochhausen* s.n. (S). **Borsod[-Abaúj-Zemplén County]**, 350m, in humosis inter saxa calc. montis Kisfarkaskö prope Kácsfürdö, 11 vi 1933, *A. Boros* s.n. (JE); In humosis inter saxa calc. montis Kisfarkaskö prope KÁCSFÜRDÖ, c.350m, 11 vi 1933, *A. Boros* s.n. (S). **Fejér County**, in humosis inter saxa dolom. supra "Báracháza" prope Csákvár, 200m, 15 iv 1934, *A. Boros* s.n. (S); In humosis inter saxa dolomit. montis Lóingató-hegy prope pagum Óbarok, 250m, 7 iv 1940, *A. Boros* s.n. (S). **Komárom[-Esztergan County]**, in humosis inter saxa calc. montis Wallstrich-tetö, 380–385m, prope pagum VÉRTESSOMLÓ, 22 iv 1935, *A. Boros* s.n. (JE); In humosis inter saxa calc. Montis Wallstrich-tetö, 385m, prope pagum Vértessomló, 380m, 22 iv 1935, *A. Boros* s.n. (S); In humosis inter saxa calc. montis Wallstrich-tetö, 385m, prope pagum Vértessomló, 380m, 22 iv 1935, *A. Boros* s.n. (S); In humosis inter saxa dolomit. merid. Montis Kecskekö prope Gyermely, c. 250m, 25 iii 1941, *A. Boros* s.n. (S); In humosis inter saxa dolomit. Merid. montis Kecskekö prope Gyermely, 250m, 25 iii 1941, *A. Boros* s.n. (F); In humosis inter saxa calc. ad monum, "Turul" in monte Kő-hegy prope Bánhida, c. 300m, 1 v 1938, *A. Boros* s.n. (E); In humosis inter saxa calc. Montis Gadóz supra pag. Vágesztes, 350m, 29 iv 1935, *A. Boros* s.n. (S); In humosis inter saxa dolomit. supra Köhányás-puszta prope pag. Vágesztes, 350m, 14 v 1933, *A. Boros* s.n. (S); In monte Turnhegy supra Barihiola, 12 v 1921, *Degen* s.n. (S); In humosis inter saxa calcarea montis Öregkö prope BAJÓT, c. 3-375m, 5 iv 1936, *A. Boros* s.n. (S). [**Nógrád County**], Filakovo. Ragačské kopce, Tilil, 2 iv 1956, *Z. Pilous* s.n. (S). **Pest County,** in humosis inter saxa calc. Montis Ferenchegy, "Vérhalom", ad Budapest, 260m, 23 iv 1933, *A. Boros* s.n. (S); Centr, in declivibus montis "Kiscsikóvár" supra pag. Pomáz, c. 450m, solo andes, 10 iii 1934, *Szepesfalvi* s.n. (S); In humosis montis Kis Csikóvár ad Pomáz, 21 iii 1920, *De Degen* s.n. (S); Berg Matyashegy bei Budapest, c. 280m, feuchte Stellen zwischen Kalkfelsen, 25 iii 1926, *A.Boros* s.n. (JE); Budakalász, Hungariae centr., c. 250m, in terra humosa calc. versus montem "Ezuesthegy", x 1926, *J. Szepesfalvi* 926 (E, F, S); In humosis inter saxa calc. montis Pilishegy supra pag. Pilisszántó, c. 600m, 20 iii 1927, *A. Boros* s.n. (E); In humosis inter saxa calc. Montis Pilishegy supra Pilisszántó, c. 680m, 12 vi 1932, *A. Boros* s.n. (BM); In humosis inter saxa calc. montis Remetehegy ad Máriaremete, 300–400m, 19 iv 1925, *A. Boros* s.n. (JE); In humosis inter saxa calc. montis, Remetehegy ad Máriareuete, 300–400m, 19 iv 1925, *A. Boros* s.n. (S); In humosis inter saxa montis Remetehegy ad Mária-Remete, 28 iii 1926, de *Degen* s.n. (S). **Veszprém County**, in humosis inter saxa calc. Adv. Montem Vár-hegy pr, CSESZNEK, 320m, 27 iii 1939, *A. Boros* s.n. (S); In humosis inter saxa calcar. Vallis cuha-völgy pr. Osesznek, 400 m, 7 vi 1928, *A. Boros* s.n. (E). **Zala County**, in humiosis inter saxa basalt, "Páholy" montis Badacsony prope Badacsony, c. 400m, 29 iv 1956, *A. Boros* .n. (E).

ITALY, *Balbis* s.n. (B36643); N.Italien, Mediolani, Herb.Aongstr., s.n. (S). [**Lombardy**], ad muror agrorum prope Varese, 25 ix 1878, *Marmazelli?* s.n. (669111) (BM); Pte. Molinello (près Come), 24 vii 1896, *F.A.Artaria* s.n. (E); C. 400m, an sonnigen Abhaengen des Castel Baradello bei Como, 4 iii 1902, *F.A.Artaria* 1188 (E, S, JE, NY); Prov. Comensis, valle di Sa. Martino (Como), 8 i 1848, *F.A.Artaria* s.n. (E); Prov. Comensis, Castel Bernadetto près de Côme, 1 vi 1902, *F. A. Artaria* s.n. (669110) (BM); Prov. Comensis, Castel Bernadetto,.., 25 xii 1895, *Artaria* s.n. (NY); Sulla terra nei luoghi soleggiati presso Como, Primavera 1880 et 1881, *Anzi* 1118 (F, BM, NY); Auf Erde an dem Weg von Limonta nach Bellagio am Comersee, iv 1908, *Müller* s.n. (S). **Piedmont,** à Turin, de la Grand Jardin de Valentin, café T. Le petit...jardin Botaniques sur les rochers, viii 1812, *Bernet* s.n. (NY); Vercellis (Pedemont.), *Cesati* 63 (JE). [**Trentino-South Tyrol**], Meran, Weg zur Naifschlucht, *Bäumler* 18 (S); Ad terrum humidam prope Meran, Tirol, *Bamberger* s.n. (725032) (BM); Meran, *Mim* s.n. (JE); Meran, *Schimper* s.n. (725067) (BM); Tyrol, Meran, *Stephani* s.n. (72504) (BM); An sonnigen felsigen Abhaengen auf fettem Humus allgemein verbreitet um Kratsch bei Meran (Tirol), waechst neben *Celtis*, *Colutea*, *Fraxinus ornus*, *Sempervivum*, *Riccia Bischoffi*, gesammelt in der Naehe der Villa Maurer, *H.Lohse* 261 (JE, BM, NY, S, F). Tirol, sonnige Abhaenge bei Gratsich bei Meran, 18 vi 1864, *H. Lohse* 261 (NY). An sonnigen Abhängen bei Gratsich im Tirol, 18 iii 1864, *Lohse* s.n. (S); Um Gratsich bei Meran, Tirol, an sonnigen, lockeren Abhängen, mit *Riccia ciliata*, *Oxymitra*, 18 iii 1864, *Milde* s.n. (S). [**Varese**], entre Ceresio et Pianver Borguana près de Pto. Ceresio, Lac de Lugano, 8 ii 1896, *Artaria* s.n. (S).

NORWAY, *s.n.* (725037) (BM). **[Østlandet Region]**, Insel Horedöen bei Kristiana, auf duerrem, sonnigen Huegeln am Meeresufer, 1892, *B. Kaalaas* 1189 (E, JE, NY, S, BG); In insula Horedöen, ..., ad terram aridane..., solo calcareo, 2 v 1896, *Kaalaas* s.n. (BM); Horedöen bei Kristiana, 24 iv 1892, *Kaalaas* s.n. (B74862) (S); Norway, Horedöen bei Kristiana, 24 iv 1892, *Kaalaas* s.n. (M-5827) (BG); Horedöen bei Kristiana, 24 iv 1892, *Kaalaas* s.n. (M-5826) (BG); Horedön auf Kristiana, 21 v 1911, *Kaalaas* s.n. (S); Auf der Hovedøen pr. Christiana, an sonnigen Abhängen (Kalkunterlage), 2 v 1896, *Kaalaas* s.n. (M-5823) (BG); Horedö bei Christiana, 24 iv 1892, *Kaalaas* s.n. (M-5828) (BG); Horedö bei Christiana, 24 iv 1892, *Kaalaas* s.n. (M-5829) (BG).

POLAND, **[Lesser Poland]**, Przegorzaly pod Krakowem, na humusie śród slonecznych skal wapiennych, 21 ii 1910, *Zb. M. Raciborski* 5 (S).
[Lower Silesia, Swidnica County], Striegauer Berge, Siles?, Hb. Lindberg, (725048) (BM); Striegau, auf Erde, an sonnigen Stellen, 26 iv 1864, *J. Zimmermann* s.n. (S).

ROMANIA, Cernatal, ca. 500m, 1916, *Herzog* s.n. (S). **[Alba County]**, Transsilvania, distr. Alba, ad terram in jugo montis "Piatra" e fissures Cheile Rîmeţului, solo calcareo, c. 1250m, 2 xii 1940, *Bunea* 3146 (BM, S, JE).

SWEDEN, Gotland Island, Torsburgen, 15 v 1957, *Å. Hovgard* s.n (S); Nickarvejun, Hejdeby, 15 v 1957, *Å. Hovgard* s.n. (S); Grogansbergel, 9 vi 1957, *Å. Hovgard* s.n. (S). **Jämtland county**, Alsens sn, Rödeberget, 22 vi 1964, *Hakelier* s.n. (S). **[Örebro County]**, Närke, Glanshammar, c. 300m NO om kyrkan, på jord på kalkklippa, 6 v 1986, *Hakelier* s.n. (S); Närke, Glanshammar sn, c. 300m NO om kyrkan, jord på kalkklippa, 22 v 1964, *Hakelier* s.n. (S). **Östergötland county**, V. Tollstads sn, Omberg, Alvastra branter, 17 iv 1964, *Hakelier* s.n. (S). **Södermanland County**, Vårdinge socken, Stillens östra strand, 2.4km SSO om Vårdinge kyrka och 1 km SSO om Ustaggård, Hög, exponerad klippbrant, delvis med urkalkstensinslag, I fuktspricka på jord, 9 xi 1975, *Kers* 4530 (S); Halla socken, vid Baldersnäs, norr om Hallbosjön, 1.8km ONO om Halla kyrka och 200m ONO om torpet Baldersnäs, På krönet av urkalkstensåsen, Öppet parti av hällmark omgivet av gran/tallskog, svagt sluttande hällmark, invid Bovista tomentosa, 9 iii 1975, *Kers* 4388 (S). **[Stockholm County]**, Srm. Utö sn, Utö, Kroka strax om vägen nära gården, SO-exposition (al semua lokal *Clevea hyalina*, *Mannia pilosa* o. *Reboulia*), 21 v 1944, *Arnell & Persson* s.n. (S).

SWITZERLAND, [Canton Vaud], Roche (Cant. Waacht), *Hausknecht* s.n. (JE); Aigle (Cant. Waacht), *Hausknecht* s.n. (JE). **[Graubünden]**, an Mauern bei Flims, 1858, *Killian* s.n. (725031) (BM). **Valais**, Commun dans les vignes près de Martigny, 475m, 12 iv 1887, *Bernet* s.n. (F); Martigny, *H. Bernet* s.n. (669113) (BM); Commun dans les vignes près de Martigny, 475m, 12 iv 1887, *H. Bernet* s.n. (S, NY); Follateres, near Branson N of Martigny, c.480m , sunny rocky slopes with vineyards, on bark, 11 viii 1994, *Long* 25677 (E); Follateres, near Branson N of Martigny, c.480m, sunny rocky slopes with vineyards, on bark, 11 viii 1994, *Long* 25664 (E); La Bâtiaz et Branson, 475m, 12 iv 1887, *H. Bernet* s.n. (S, NY); La Bâtiaz et Branson, 475m, 12 iv 1887, *Bernet* s.n. (F); Martigny, La Bâtiaz, 550m, 46°06'20.6"N, 07°04'09.9"E, on S-facing grassland slope, on ground next to path, 17 iii 2003, *D.B.Schill & M.Price 57* (E); Martigny, La Bâtiaz, 550m, 46°06'20.2"N, 07°04'09.8"E, on S-facing grassland slope, on ground, 17 iii 2003, *D.B.Schill & M.Price 59* (E); Follatères, terre nue dans pelouse à annuelles, 490m, 5721/10805, 12 iii 1991, *P. Geissler* 15648 (G); Fully, Follatères, talus (transecte I, S), 5724/10805, 500m, 12 iii 1991, *P. Geissler* 15647 (G); Follatères, Steppe, 700m, 5726/1087, 20 vi 1990, *P. Geissler* 15301 (G); Fully, Follatères, Steppe, transecte 2, 10, 520m, 5725/11085, 10 vi 1989, *P. Geissler* 13873 (G); Fully, Follatères, Les Taches, transecte II, sous 11, sol, steppe rocheuse, 620m, 5724/1084, 4 ii 1990, *P. Geissler* 15205 (G); Fully, Les Follatères, 470m, 46°07'30.9"N, 07°05'05.5"E, next to path, on S-facing vertical rock face with thin soil layer, 17 iii 2003, *D.B.Schill, M.Price & E.Maier 40* (E); Fully, Les Follatères, 472m, 46°07'30.9"N, 07°05'05.5"E, on big boulder with thin soil layer, S-exposed, dry, 17 iii 2003, *D.B.Schill, M.Price & E.Maier 42* (E); Fully, Les Follatères, 473m, 46°07'30.9"N, 07°05'05.5"E, next to path, on grassy ground, 17 iii 2003, *D.B.Schill, M.Price & E.Maier 44* (E); Fully, Les Follatères, 480m, 46°07'30.9"N, 07°05'05.5"E, next to path, on way up, on grassy ground, S-facing and exposed, 17 iii 2003, *D.B.Schill, M.Price & E.Maier 47* (E); Fully, Les

Follatères, 475m, 46°07'30.8"N, 07°04'59.7"E, next to path, on grassy ground, S-facing and exposed, 17 iii 2003, *D.B.Schill, M.Price & E.Maier 48* (E); Fully, Les Follatères, 597m, 46°07'30.4"N, 07°04'41.4"E, next to path, on way up, on soil on grassy slope, S-facing, 17 iii 2003, *D.B.Schill, M.Price & E.Maier 50* (E); Fully, Les Follatères, 632m, 46°07'33.8"N, 07°04'47.2"E, on grassland slope, on ground, S-facing, 17 iii 2003, *D.B.Schill, M.Price & E.Maier 51* (E); Fully, Les Follatères, 645m, 46°07'40.5"N, 07°05'00.4"E, on grassland slope, on boulder with thin soil layer, S-facing, 17 iii 2003, *D.B.Schill, M.Price & E.Maier 55* (E); Fully, Valais, Follatères, pelouse à Stipa chevelue, 5723/1833 (Tr. II, 16), 630m, 12 iii 1991, *P. Geissler* 15661 (G); Follatères, La Forcla, Steppe dans chinaie pubescente, 910m, 5720/1087, 20 vi 1990, *P. Geissler* 15284-15286 (G); Fully, Branson, Follatères, 600m, 13 iii 1983, *P. Geissler* 8948 (G); Fully, Planches de Mazembros, Steppe, 540m, 5772/1117, 14 iv 1991, *P. Geissler* 15691 (G); Fully, Valais, Les Planches, balme, (II 10+), 630m, 57252/10842, 5 v 1990, *P. Geissler* 15270 (G); Fully, Les Planches, sol nu, 630 m, 5724/1084, 1 v 1990, *P. Geissler* 15261 (G); Fully, Corbassière, Saxifrago-Stipetum, 1040m, 5729/1096, 19 x 1990, *P. Geissler* 15618-15619 (G); Fully, Valais, Forèt de la Lui, pelouse à annuelles, 580m, 5721/10815, *P. Geissler* 15653 (G); Sion, Mont d'Orge, Steppe, 750m, 21 iii 1983, *P. Geissler* 8955 (G); Sion, Mont d'Orge, Steppe, 700m, 5921/1198, 22 ii 1992, *P. Geissler* 16334 (G); Mont d'Orge, 742m, 46°13'55"N, 07°20'16"E, on grassy slope, open dry grassland with Opuntia nana, S-facing, 18 iii 2003, *D.B.Schill & M.Price 62* (E); Sion, Mont d'Orge, 701m, 46°13'55"N, 07°20'16"E, open dry grassland slope, on ground, S-facing, 18 iii 2003, *D.B.Schill & M.Price 64* (E); Sion, Chateauneuvre, 556m, 46°13'15.9"N, 07°18'52.5"E, on grassy slope, amongst grasses, on ground, S-facing, 18 iii 2003, *D.B.Schill & M.Price 60* (E); Ob Granges, Trockenhang, 600m, 18 iv 1972, *P. Geissler* 0159 (G); Grengiols, Valais, Blaws Egg, Trockenrasen, 1050m, 6491/1365, 16 vi 1985, *P. Geissler* 11151 (G). [**Ticino**], alle pendici soleggiate nei dintorno di Locarno, al Lago Maggiore, Spring 1859, *Daldini* 268 (669115) (BM); Pr. Locarno, ad Verbanum, *Duthy?* s.n. (NY).

U.S.A., Forchiels?, 5 miles n. Dr. Colino colo.?, 5 iii 1896, *Baker* 6 (NY); Springfield, Mis., limestone rocks, 4 ii 1891, *Weller* s.n. (NY). **Alaska,** [North Slope Borough]: Arctic Alaska, Philip Smith Mountains Quad, lower W slope of

Mt Steere, Brooks Range, c. 1050m, 68°29', 149°25', on soil on dry rocky slope, 30 vii 1982, *Long* 11262 (E); Philip Smith Mountain Quad, W ridge of Mt Steere, Brooks Range, 68°29', 149°25', c. 1250m, on damp cliff ledge, 30 vii 1982, *Long* 11277 (E); [Fairbanks North Star Borough]: Big Delta Quad, Munson's Slough, Mi 39.2, Richardson Hwy., 64°28'N, 146°59'W, 20 vii 1991, *A. R. Perry & B. M. Murray* 8007 (E); [Yukon-Koyukuk Census Area]: Black River Quad, second tier bluffs on Porcupine River, 66°59'10"N, 142°49'20"W, 4 vi 1996, *B. M. Murray* 96-132 (E). **Colorado**, *J. S. Brandegee* s.n. (268775) (NY). [La Plata County]: Southern Colorado, upper La Plata River wooft?, 13 vii 1898, *C. F. Baker, F. S. Earle & S. M. Tracy* s.n. (268776) (NY). **Georgia**, Columbia County: Appling, mossy edge of pool, on granite outcrop, 8 miles E., 13 iii 1939, *Hermann* 10115 (NY, F). **Illinois**, Lermont, on thin soil of limestone rocks, iii 1903, *E. J. Hill* s.n. (223450) (F); Loes Bluff, Sangamon, Ill., *Hall* s.n. (F). [Rock Island County]: Arsenal at Rock Island, 25 iv 1899, *T. E. Savage* s.n. (NY); Arsenal at Rock Island, 25 iv 1899, *T. E. Savage* 7297 (NY); Rock Island Arsenal, 25 iv 1899, *T. E. Savage* s.n. (1136288) (F). **Iowa**, Muscatine, x 1896, *B.S.* s.n. (NY); Blue Mts., Otis, *C. R. Barnes* 3235 (F); Faguette, on wooded hillside, 28 x 1902, *B. Fink & C. Green* s.n. (268740) (NY). Dubuque County: hill back of Dubuque County, 17 iv 1937, *Conard* s.n. (268741) (NY); Hills back of Dubuque, 17 iv 1937, *H. S. Conard* s.n. (F). Emmet County: 6 m S of Estherville, on a prairie knoll in Emmet County, 19 iv 1942, *B. O. Wolden* s.n. (268773) (NY); 6 m S of Estherville, on a prairie knoll in Emmet County, 19 iv 1942, *B. O. Wolden* s.n. (268783) (NY). Jackson County: iv 1909, *A. O. Thomas* 7228 (NY); iv 1909, *A. O. Thomas* s.n. (268735) (NY). Linn County: Palisades State Park, 27 v 1933, *Conard* s.n. (NY); Palisadess State Park, 27 v 1933, *H. S. Conard* s.n. (1173581) (F). Lyon County: Gitchie Manitou State Preserve, extreme NW corner of Iowa, bordered by South Dakota to N & W, NE ¼ , Sec. 11, T100N, R48W, 43°30'N, 96°36'W, 1290 ft., Sioux quartzite outcrops with occasional *Quercus macrocarpa* & *Fraxinus pennsylvanica*/*Symphoricarpos*, *Rhus*/*Andropogon* spp., *Bromus inermis*, *Setaria*, *Bouteloua gracilis*, *Artemisia* spp., *Woodsia*, abundant *Opuntia* & *Selaginella rupestris*/*Mannia fragrans*, *Schistidium*, *Hedwigia*, *Tortula*, *Ceratodon* on soil and rocks in exposed habitats, 23 ix 1989, *D. Horton, L. Hunter, T. O'Brien & P.-Z. Zheng* 30033 (F). Winneshiek County: Kendalville, upper Iowa River, Iowa-Minn line, 25 vi 1936, *Conard* s.n. (NY). **Kansas,** Chautauqua County: 1 ½ mi NE Sedan, shallow sandy soil, open oak wooded, prairie hillside, 5 iv 1952, *R. L. McGregor* 5340 (NY); 3 mi NE Sedan, oak woods, shady soil, 26 iii 1948, *R. L. McGregor* 1216 (NY). Coffey County: 2 miles SW Le Roy, sandy soil, 4 xi 1948, *R. L. McGregor* 1239 (NY). Douglas County: 3 miles SE Baldwin City, sandy soil, 4 ii 48, *R. L. McGregor* 1225 (NY); 12 mi of Lawrence, hole in the rock, on sandy soil, 13 x 1951, *R. L. McGregor* 5246 (NY); 12 miles south of Lawrence, Area known as Hole-in-the-Rock, soil in oak-hickory prairie, 18 x 1959, *H. L. Smith* 85 (NY). Elk County: 10 miles of Busby, edge of oak woods, sandy soil, 4 x 1948, *R. L. McGregor* 1283 (NY). Ellsworth County: 6 miles southeast of Kanopolis, growing on high ground, on thin soil over sandstone, abundant, 27 vi 1962, *Ellison* 1430 (NY); 6 miles southeast of Kanopolis, growing on high ground over thin soil on sandstone, abundant, 27 vi 1962, *Ellison* 1432 (NY); 6 miles southeast of Kanopolis, growing on high ground on thin soil over sandstone, among grass, abundant, 27 vi 1962, *Ellison* 1435 (NY); 2 mi. E. 6 mi. S. Kanapolis, Kansas Area of Dakota sandstone outcrops, shaded banks, 3 v 1952, *R. L. McGregor* 5454 (NY); 3 Mi NE Senesco, moist sandstone rock, 13 iv 1948, *R. L. McGregor* 1309 (NY); 2 mi. N., 4 ¼ mi. W. Langley, Kansas Area of Dakota Sandstone outcrop, on shaded sandy banks, 3 v 1952, *R. L. McGregor* 5447 (NY); 5 mi E Carneiro, sandy soil below sandstone outcrop, 30 iv 1949, *R. L. McGregor* 2782 (NY). Greenwood County: 1 mile NE Fall River, , margin of sandstone outcrop, oak woods, 4 x 1948, *R. L. McGregor* 1293 (NY). Jefferson County: 1 mile W Medina, oak woods, sandy soil, 4 ii 1948, *R. L. McGregor* 1235 (NY). Labette County: 5 miles SW Dennis, sandy soil, roadside bank, 4 x 1948, *R. L. McGregor* 1265 (NY). McPhersons County: 2 Mi., NW Lindsborg, Kansa Area of Dakota Sandstone outcrop, shaded moist banks, 3 v 1952, *R. L. McGregor* 5457 (NY). Montgomery County: Elk City, sandstone country and soil, *R. H. Thompson* 35 (NY); 6 mi of Elk City, oak woods, sandy soil, *R. L. McGregor* 1181 (NY). Reosho County: 2 miles E, ½ miles N Chanate, sandy soil, 4 ix 1948, *R. L. McGregor* 1257 (NY). Rice County: 1 mi. E Senesco, sandy soil, Prairie, 30 iv 1949, *R. L. McGregor* 2714 (NY). Saline County: 2 miles NW Brookville, sandy soil, prairie, 30 iv 1949, *R. L. McGregor* 2694 (NY). Wilson County: 1 mi. NE Neodesha, on shallow sandy soil over sandstone outcrop, a few small colonies, 5 iv 1952, *R. L. McGregor* 5331 (NY); 1 mile NE Reodesha, Wilson County, oak wood, on sandy soil at margin of sandstone outcrop, 4 x

1948, *R. L. McGregor* 1271 (NY). Woodson County: 2 mi, NW Yates Center, sandy soil, pasture, 4 ix 1948, *R. L. McGregor* 1242 (NY); 2 miles NW Yates, sandy soil, pasture, 4 ix 1948, *R. L. McGregor* 1242 (NY); 5 miles east of Toronto, Fegan Lake, Woodson County State Park, soil in oak forest, 10 x 1959, *H. L. Smith* 49 (NY). **Minnesota,** Chippewa County: on Sioux quartzite, 6 miles east of Montevideo, 29 vi 1952, *Gier* 5402 (NY). Cottonwood County: c. 2 mi W of US 71, c. 14.5 mi N of Windom, c. 400m, 44°05'40"N, 95°04'30"W, seasonally dry, flat, Sioux quartzite outcrop on N side of road, 28 ix 1991, *Buck* 20875 (NY). Hennepin County: over sandy exposed hillside terrace overlooking Minnesota River, near Ninemile Creek, occurring with androecia and capsules, 1–8 v 1950, *Schuster* 18020 (NY); On exposed, dry, sunny, shady knolls above the Minnesota R., near Ninemile Cr., with Pasque Flower, *Bryum argenteum*, v 1947, *Schuster* 1001 (F); Near Ninemile Creek, over sandy exposed hillside terrace overlooking Minnesota River, occurring with androecia and capsules, 1–8 v 1950, *Schuster* 18020 (F). Winona County: Laird's, sand rock, in shade moist, 31 v 1890, *Holzinger* 14 (NY); Winona, Beck's, sand cliff, 29 v 1890, *Holzinger* 18 (NY); Whitewater State Park, over exposed, rather dry soil at crest of bluff, with prairy plants, occurring with androecia, apparently plants male and dioecious, 15 v 1950, *Schuster* 18028 (F). **Missouri**, Clay County: on wooded slope, east of Oldham's mine, N4S26 TS1N R31W, 12 viii 1951, *Gier* 5092 (NY). Franklin County: St Peter sandstone bluffs and open cedar glades, Pacific, NE ¼ sec. 12, T. 43 N, R. 2E, abundant on open soil in glade, *Redfearn, Jr.* 20766 (NY). Jefferson County: on soil in limestone outcrops in exposed places along Bark Creek, 15 xi 1941, *Meyer* 106 (NY); On soil on limestone outcrops in exposed places along Bark Creek, 15 xi 1941, *Meyer* 106 (NY). LaClede County: "Indian Grave", high west-facing bluff above Niangua River, SW ¼ SW ¼ sect. 32, T.36N, R.17W, open soil, top of bluff, common, 2 i 1975, *Redfearn Jr.* 29775 (F). St. Louis: *Eggert* s.n. (669246) (BM). **Nebraska**, s.n. (268792) (NY). Cass County: South Bend. Nebr., ix 1889, *H. J. Webber* 11 (268659) (NY). Lancaster County: Lincoln, 4 ml. South, 1240 ft., 41°N, thin soil on rocky ground, 16 iv 1943, *Kiener* 13784 (NY). Sarpy County: on broken soil of bluffs, 1100 ft, S of Gretna, 6 v 1945, *Kiener* 18908 (F). **New Jersey**, Woodbridge, Ct., on black soil in crevices of trap rock, iv 1891, *A. W. Evans* 121 (BM, NY, F). Pallisades, 1871, *Austin* s.n. (268650) (NY); On wet rocks, Palisades, v 1858, *C.F.Austin* (268671) (NY).

Bergen County: Rocky places, near Closter, also in Illinois, *Hall* 133 (BM, NY, F); Closter on rocks in hilly places, 1858, *Hall* s.n. (NY). **New Mexico**, Galleries baûon, 15 ii 1927, *Frère G. Arsène* 19069 (BM).Nouveau Mexique, Gallinas Canon S. puits pétrole, 15 ii 1927, *Arsène* 19070 (S, F). [Santa Fe County]: Santa Fe, *Fendler* 136b (NY); Santa Fe, Arroyo Horcho?, 2200m, 12 x 1936, *Arsène* 23284 (NY, F). [Sierra County]: New Mexico, Hot Springs, 9 miles from Las Vegas, xi 1926, *Arsène* 19093 (NY, S). **New York,** Adirondack Mts., on sunny moderately moist, west and south-facing slopes of hill nw. of Pea leeville, associated with Preissia quadrata and Selaginella rupestris, etc., 28–30 iii 1945, *Schuster* s.n. (NY, F). Albany County: Ravena, on thin soil over massive limestone, old field, c. 300 ft., 28 x 1970, *Smith & Dean* 46141 (NY); Vic. Clarksville, c. 450 ft., thin soil over massive limestone, 10 iii 1973, *Smith & Herrick* 49144 (NY); Clarksville, 1 xi 1975, *Smith & Starck* 51854 (NY, S); Albany Schoharie, *Peck & R. Wateburg* (268673) (NY). [Bronx County]: New York, Bronx, Plott Haven?, ii 1897, *Saniab* s.n. (268806) (NY). [New York County]: *Stephani* s.n. (BM), New York City, on rocks in a sunny field, Jerome Ave, near Fleetwood, 20 iii 1896, *Saniab* s.n. (NY); N.Y.City, Jerome Avenue, near Fleetwood, on rocks in a sunny field, 20 iii 1896, *Saniab* 14 (2688020) (NY). Montgomery County: fields, southeast side of Nelliston, c. 380 ft., thin soil over massive limestone, 7 v 1960, *Smith & Carr* 30062 (NY). Saratoga County: Lester Park, c. 325 ft., thin soil over massive limestone, 22 v 1976, *S. J. Smith & D. J. Starck* 52299 (NY, S). Westir County: Mott Harven, Westir Co. N. Y., loose ground on top of rocks, *M. S. Saniab* (268649) (NY). **North Carolina,** Burke County: Schw., Salem, Torrey Hb., s.n. (268667) (NY). **Conneticut**, Litchfield County: New Milford, Ct., moist bank, 24 iii 1910, *Nichols* 68 (BM); Conneticut to Iowa and Texas, also in Europe, thin soil on rocks, s.n. (NY). **Oklahoma**, Cadelo County: Floor?, Devil's Canyon, 22 ii 1958, *Z. Z. Wellbourne* 2 (F). Comanche County: Wichita Wild Life Refuge, on sandy soil over granite, 10 iv 1963, *Ellison* 1580 (NY). **Pennsylvania**, *Rau* s.n. (669244) (BM). Lancaster County: Lancaster, 1861, *J. C. Porter* s.n. (268648) (NY). **Tennessee**, Rutherford County: Murfreesboro, Snail Shell Cave, 31 iii 1934, *Sharp* 34294 (NY, S, F). **Texas**, Burnet Country: sandy soil, over granite, 1 mi. E of Marble Falls, 23 i 1982, *R. M. Schuster* 82-231 (F); Granite Mountain, 1 mi. west of Marble Falls, growing on thin dry sandy soil over granite rock, dry and rolled up when collected, common in this area, 3 iv 1962, *Ellison* 1107 (NY). Denton County: Post Oak Belt, south of Denton about 5 miles, ½ mile west of Highway 77, 7 iii 1948, *Whitehouse* 19363 (NY). Hood County: Post Oak B lt., 2 miles northwest of Granbury on bluff above Barzos River, sandy soil, 16 iii 1947, *Whitehouse* 17858 (NY). Travis County: Eastern North America, Texas, , Brackenridge Tract, Austin, on Lake Austin Bolvd., well drained soil, opening in woods, 8 ii 1982, *R. M. Schuster* 82-423 (F). **Utah**, San Juan County: Devils Canyon, ca. 6500 ft, on dry soil under overhanging sandstone rocks, oak and yellow pine belt, 25 vi 1952, *Flowers* 8060 (NY). **West Virginia,** Grant County: Petersburg, W. Va., on thin soil over sloping rock, *Gray* 7458 (NY). **Wisconsin**, Dane County: near Mazomanie, rather dry hillside, 5 x 1936, *P. Snure* s.n. (NY); Madison, on dry hills, 1 vi 1891, *Cheney* 6 (NY). Dodge County: 2 miles S of Mayville, T11N, R16E, Sect. 1, SW¼ , NW¼, on limestone outcrops, open pasture at top of Niagara Dolomite escarpment, 29 iii 1973, *Nee & Hansen* 5639 (NY). Grant County: 3 miles N of Mt Ida, T6N, R3W, Sect. 6, SW¼, NW¼, with *Selaginella rupestris* in open sandy pasture on S facing slope below *Pinus banksiana* stand, 7 iv 1973, *Nee* 5680 (NY). St Croix County: over strongly insulated, s. facing talus slopes, on soil at the bases of clumps of Prairie grasses, Apple River Canyon, near Somerset, occurring with a few androecia (terminal at this stage), *Bryum argenteum, Viola pedatifida*, etc., 26 vi 1949, *R. M. Schuster* 15011 (NY); Apple River Canyon, near Somerset, over strongly insolated, s. facing talus slopes, on soil at the bases of clumps of Prairie grasses, occurring with a few androecia (terminal at this stage), *Bryum argenteum, Viola pedatifida*, 26 vi 1949, *R. M. Schuster* 15011 (F, NY).

CANADA, **Alberta**, Red Deer Area, Dry Island Buffalo Jump Provincial Park, along Red Deer River, in xeric prairie of *Artemisia-Festuca scabrella-Agropyron-Stipa comata* with *Eleagnus angustata-E. commutata-Symphocarpus alba* shrubs along banks of steep gully, 23 ix 1978, *Vitt* 24013 (NY). **Ontario,** Durham County: sandy soil in poor hilly pasture, abundant, Cavan Twshp. LA6, 1.5 miles W of Millbrook, 17 iii 1957, *H. Williams* 871 (F); South slope of sandy knoll, between tufts of thin grass, fully exposed, hilly pastureland, never ploughed, 1.5 miles W of Millbrook, 17 iii 1957, *H. Williams* 878 (F); On dry sandy soil in open pasture, W. of Millbrook, 24 v 1958, *R. F. Cain & H. Williams* 5122 (F); 1.5 miles

W of Millbrook, dry open soil of poor pasture gravely under. Cavan Twshp., v 1957, *H. Williams* 954 (F).

GREENLAND, West Greenland, Søndre Strømfjord, on south facing steep slope, N. of the air strip, along a small temporary rill, 3 ix 1970, *Schuster* 70-3201 (F); Søndre Strømfjord, on south facing steep slope, N. of the air strip, along a small temporary rill, 3 ix 1970, *Schuster* 70-3204 (F).

CHINA, [Beijing Region], Beijing, Mutianyu 'Great Wall', ca. 90 km NE Beijing, 530 m, 40°25'52.5"N, 116°33'52.2"E, auf Lehmblößen im Laubwald (*Quercus liatungensis*, *Quercus mongolica*), 15 viii 2004, *H. Kürschner & D. Wagner* 04-858 (E). **[Shaanxi Region]**, China interior, provincia Schensi septentr., in alveo arenoso amnis San-huo prope Sche-kin-tsuen, 3 iv 1897, *Rev. Jos. Giraldi* s.n. (det. Massalongo 148) (JE, BM, NY).

INDIA, Uttaranchal, Gangotri, on path to Kedartal, on bank next to path, ca. 3200 m, on ground, 11 xi 2004, *D. B. Schill & J. Clarke* 157 (E); Gangotri, on path to Kedartal, on bank next to path, ca. 3200 m, on ground, 11 xi 2004, *D. B. Schill & J. Clarke* 158 (E); Gangotri, on path to Kedartal, on vegetated bank below juniper bushes to the right of path, ca. 3300 m, on soil, 11 xi 2004, *D. B. Schill & J. Clarke* 159 (E); Gangotri, on path to Kedartal, on bank next to path, ca. 3330 m, 30°59'11.8"N, 78°56'13.7"E, on ground, 11 xi 2004, *D. B. Schill & J. Clarke* 160 (E); Gangotri, on path to Kedartal, on vegetated bank next to path, ca. 3330 m, 30°59'11.8"N, 78°56'13.7"E, on ground, 11 xi 2004, *D. B. Schill & J. Clarke* 161 (E); Gangotri, on path to Kedartal, next to path, 3341 m, 30°59'10.8"N, 78°56'13.4"E, on soily bank, fragrant, 11 xi 2004, *D. B. Schill & J. Clarke* 162 (E).

JAPAN, Chubu Region, Aichi Prefeture: cervices of stone-walls in exposed places, c. 300m, Tomiyama in Kita-shidara District, Aichi County, 25 iv 1954, *N.Takaki* 274 (JE, BM, NY, S). **[Honshu, Kanto Region]**, Saitama Prefecture: Chichibu, Tochimoto, 780m, rock crevices in exposed places, 27 viii 1952, *Shimizu* 52809 (NICH). Chichibu Mts, Tochimoto, c. 700–800m, 9 ix 1952, *Shimizu* 52808 (NICH); Saitama-shi, Midori-ku, Nakao, 26 x 2003, *M. Itouga* s.n. (E); Tokyo, Koisigawa-ku, 15 xi 1940, *Hattori* 6202 (TNS); Tokyo, 1897, *Miyake* 71 (NY).

MONGOLIA, Chubsugul-Aimak bei Alag-Endene in Felsritzen, 1900m ue. M., 12 vii 1983, *S.Huneck* s.n. (JE); Chubsugul-Aimak, bei Alag-Erdene am Egiin-Gol, zwischen Felsbloecken, 1900m ue. M., 12 vii 1983, *S.Huneck* s.n. (H2673) (JE); Zezerleg (Stadt), in Felsspalten zwischen Granitbloecken, 27 vi 1978, *Huneck* MVR-2 (JE); Chögnö-Tarna-Uul, vi 1988, *S.Huneck* s.n. (JE).

RUSSIA, Siberia, **[Chita Province]**, Rossia asiatica, Transbaikalia, Regio Czitaënsis, distr. Nerczinskij-Zavod, prope vicum Ivanovka, in terra declivitatis lapidosae siccae, in umbra arborum (*Ulmus scabra*), 9 vii 1956, *I.I. Abramov* 71 (E, S). **[Krasnoyarsk Territory]**, Jenissei, Antsiferova, 59°10' N, 1876, *H. W.Arnell* s.n. (H4337) (JE); Jenisei, Antsiferova, 59°10' N, 27 vi 1876, *Arnell* s.n. (B74729) (S); Jenisei, Antsiferova, 59°10' N, 27 vi 1876, *Arnell* s.n. (B74730) (S); Jenisei, Antsiferova, 59°10' N, 27 vi 1876, *Arnell* 6a (S); Jenisei, Antsiferova, 59°10'n.lat., 27 vi 1876, *Arnell* s.n. (BM); Jenisei, Antsiferova, 59°10'n.lat., 27 vi 1876, *Arnell* s.n. (NY); Jenisei, Antsiferova, 59°10'n.lat., 27 vi 1876, *Arnell* 49 (NY). **[Karelia Republic]**, Karelia ladog., Farfielala?, Pullinvuori, ad terr. in fissuris rufium, viii 1876, *Brotherus* s.n. (B74864) (S). **[Saratov Province]**, URSS, Regio ciswolgensis, distr. Saratov. Montes dysyj, in silva, 8 v 1927, *Janischevskij* s.n. (S).

UNKNOWN LOCALITIES, Siniplow?, 1860–62, *Gagliardi* s.n. (669114) (BM); *Lohse* s.n. (669108) (BM); *Bischoff* L53, 793 (JE); *De Notaris* s.n. (725076) (BM); *De Notaris* s.n. (725033) (BM); *De Notaris* s.n. (725071) (BM); *Bischoff* s.n. (725084) (BM); Hookera optono, s.n. (669279) (BM); *Grimaldia dichotoma* (no data), s.n. (E).

5. *Mannia asiatica* Schill & D.G.Long

INDIA, [Uttaranchal], NW-India, Kumaun, Ralan Valley, 13000-14000', 24 viii 1884, *Duthie* 311 (G); NW-India, Kumaun, Ralan Valley, 13–14000', 24 viii 1884, *Duthie* 3757 (BM).

CHINA, **Qinghai Province**, Henan County: Xiawate, Zhihoumao Xiang S of Henan, 34°31'20"N, 101°31'13"E, ca. 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, ca. 3830 m, limestone hillside, soil clefts at foot of kimestone 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, ca. 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, ca. 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, ca. 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, ca. 3585 m, valley with *Picea* and *Juniperus* woddland, 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, ca. 3570 m, steep limestone side valley, on bank under *Salix*, 10 vii 1997, *D.G. Long* 26951-b (E). Tongren County: Shuangpenxi Xiang, Kuohelongwa Valley, 35°31'42"N, 102°14'32"E, ca. 3200 m, degraded scrubby *Picea* woodland, on shady bank, 24 vii 1997, *D.G. Long* 27126 (E).

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

6. *Mannia triandra* (Scop.) Grolle

*indicates bearded or slightly bearded *M. triandra* specimens

AUSTRIA, Austria/Italy, auf Trockenmauern unter dem Brenner beim Klarerhof, iv 1942, *Gams* s.n. (S). **Carinthia**, Gutschekogel, SW Eberstein, S-slope, c. 800m, 46°47'36.7"N, 14°33'07.3"E, in calcareous shaded rock crevice in conifer forest, 25 vii 2003, *D.B.Schill, H.Köckinger & U.Müller* 87 (E); Nockberge, west of Erlacher Hütte, c. 1670m, 13 vii 2003, *H.Köckinger* s.n. (E). **Lower Austria**, Schneeberg, unter dem Kaiserstein, ca. 2000m, auf Erde über Kalkgestein, 21 ix 1940, *Froehlich* s.n. (S); Schneeberg, unter dem Kaiserstein, ca. 2000m, auf Kalkgestein, 25 ix 1938, *Froehlich* s.n. (S); Auf dem Hochkar südwestlich der Hütte, ca. 1550m, auf Humus über Kalk, 5 x 1930, *Froehlich* s.n. (S); Wiesenbachtal am noerdlichen Fusse der Reisalpe, c. 550m, Erdbrueche am Wege, Kalk, 14 vi 1906 and 1908, *J.Baumgartner* 1193 (E, JE, S, NY). **Salzburg,** s.n. (BM); *Braun* s.n. (BM); *Schimper* s.n. (BM); *Hampe* s.n. (S); In muris, *Schimper* s.n. (BM); Austrian Alps, *Stephani* s.n. (g) (BM); Obertauern, SE Hundskogel, Ca-Schneeboden, 2100m, 19 vii 1988, *Geissler* 13268 (G); Pottenstein nächst Muggendorf bei Salzburg, 1793, in den Höhlungen der Stadtwand, *Funck* s.n. (c) (BM); 'Ad ipso' Herbarium Lehmannium, s.n. (S-B22546) (S); 'Ad ipso' Herbarium Lehmannium, s.n. (S-B22547) (S); mur cerb. Salisburgia ad Sazach, *Schimper* s.n. (f) (BM); Felsspalten Pinzgau, *Sauter* s.n. (i) (BM). **Styria,** *Breidler* s.n.* (B74802) (S); Ex-Herbarium Stephani, s.n. (NY); 1879, *Breidler* s.n.* (B74805) (S); Australian Alps, *Breidler* s.n. (BM); Schlossberg in Weilenstein, c. 400m, 18 v 1879, *Breidler* s.n. (JE); Schlossberg in Weitenstein, 18 v 1879, *Breidler* s.n. (S); Bei Weitenstein, 9 vi 1908, *Glowacki* s.n. (S); Sonnige Abhänge bei Weihenstein, c. 400m, auf Kalk, v 1879, *Breidler* s.n. (BM); Flumberg bei Triffes, 25 v 1897, *Glowaki* s.n. (S); Stockluken bei Wildalpe, 1892, *Breidler* s.n. (H1297) (JE); Trofaiach, Tragößß-Oberort, Haringgraben (Hochschwab), beginning of Marienklamm, c. 850m, in calcareous rock crevices, 23 vii 2003, *D.B.Schill, H.Köckinger & U.Müller* 79 (E); Eisenerzer Alps, Vordernberger Mauern, Krumpen, above the 'Hirnalm', next to path, 1037m, 47°28'46.6"N, 14°58'06.1"E, on ground on grassy, stony slope, 23 vii 2003, *D.B.Schill, H.Köckinger & U.Müller* 81 (E). **Tyrol**, Kaisergebirge bei Kufstein, an Kalkfelsen, ca. 1980m, 9 viii 1905, *Schinnerk* s.n. (S); Nord-Tirol, Gschnitztal, Martartal bei Gschnitz, in Felsspalten, Kalk, ca. 1800m, viii 1902, *Schiffner & Patzelt* 1191b (S). **Upper Austria**, Steyr, *Sauter* s.n. (BM); Auf Kalkgrus bei Steyr, gesellig mit *Grimaldia fragrans*, *Sauter* 26 (JE, BM, NY); An schattigen Nagelfluhfelsen und Huegeln bei Steyr in Tyrol, *Sauter* 85 (JE, S).

CROATIA, [Dubrovnik-Neretva County], Dalmatien, Ragusa, v 1911, *Bäumler* s.n. (S); Dalmatien, Ragusa, an der Eisenbahn S.Stefano- Ćajković, ca. 40m, 23 iv 1912, *Latzel* 569 (S).

CZECH REPUBLIC, **[Hradek Ksálové Region]**, Riesengebirge, Oberlangenau, Kr. Hohenelbe, SO-Hang des Stimmesberges, bei 500m, auf Urkalk, 1 vi 1942, *Futschig* s.n.* (B74794) (S).

FRANCE, **[Auvergne]**, Cantal, Gazilien, s.n. (b) (BM). **[Provence-Alpes-Côte d'Azur]**, Alpes maritime, Au de Grasse, Canton de Bar, ½ km en Pont du Louge, 23 vii 1953, *Arnell* s.n. (S); Alpes Maritimes, Saint Vallier de Thiey, Col de la Lèque, peloux rases à Genista villarsii sur calcaire dolomitique, 695 m, *V. Hugonnot* VH03353 (E).

GERMANY, **Bavaria**, Auf feuchter Erde unter Dolomitwaenden bei Beyniz? in Oberfranken, 26 v 1861, *Arnold* 182 (JE, BM, NY); Beyniz in Oberfranken, Dolomitfelsen, 2 v 1866, Herb. *Hampe* s.n. (c) (BM); Fränkische Alb, Dolomitfelsen bei Pottenstein, 390m, 4 v 1941, *Gauckler* s.n.* (B74791) (S); Dolomit bei Pottenstein, 1863, *Arnold* s.n. (S); München, b. Einzieol?, 12 viii 56, *Molander* s.n.* (JE); Weichenfeld?, 1 vi? 55, *Arnold* s.n. (d) (BM); Bavarian Alps, Königsee, *Stephani* s.n. (e) (669301) (BM); Almbachklam bei Berchtesgarden, 400–500m, viii 1910, *Familler* s.n. (S). **Thuringia**, Kreis Schleiz, Bleilochfelsen N Saalestausee, 26 vi 1978, *L.Meinunger* 7108 (JE).

ITALY, Gardasee, *Mihs*? s.n. (JE).**[Trentino-South Tyrol]**, Tirol, in Mauerritzen neben der Ponalestrane bei Riva am Gardasee, iv 1908, *Müller* s.n. (S); Südtirol, Prentino, S.Marco, in den Ritzen von Steinmauern (Kalk) bei der Slavini di Marco, ca. 180m, 23 vii 1911, *Kern* s.n. (S); Südtirol, Prentino, Serravalle, an der

Deike einer Felshöhle (Kalk) mit *Soligeria* und *Eucladium*, ca. 150m, 23 vii 1911, *Kern* s.n. (S).

POLAND, **[Lower Silesia]**, Schlesien, Riesengebirge, *Kerratehl?* s.n. (NY).

SLOVAKIA, Slovenský Ráj, pag. Ztratená, vallis Čierná dolinka, 580m, vi 1978, *Pilous* s.n. (NY);

SLOVENIA, Carniolia, solo calcareo in valle Kanker, 500m, *Robič* s.n. (BM). **[Goriška Region]**, Küstenland, Čepovan, 700–800m, auf Humus und Sandboden ueber Dolomit, v 1905, *K.Loitlesberger* 1192 (JE, S, NY). **[Inner Carniolia Region]**, Austro-Hungarica, Carniolia, in rupestribus prope Zwischenwassern et Idria, solo calc., 328m, *Deschmann* 1138 (BM, NY, S, G).

SWEDEN, **Jämtland County**, Offerdals sn, Riseberget, 31 viii 1964, *Hakelier* s.n. (S). **[Örebro County]**, Västmanland, Grythyttans sn, kalkberget Ö om Brunnsjön, östra stupet på jord på avsats i starkt skuggigt läge, 11 vii 1964, *Hakelier* s.n. (S).

SWITZERLAND, **Glarus**, *Winter* s.n.* (b) (669298) (BM); Tödi, *Stephani* s.n.* (669299) (BM). **[Ticino]**, Nelle commessure di un muro vetusto eposto a tramontana a Locarno, Lago Maggiore, 6 iv 1857, *Cesati* s.n. (d) (BM); A. Carorescio, pascolo, 2200m, 7012/1553, 8 viii 1985, *Geissler* 11383 (G).

U.S.A., North America, Bethlehem, *Rau* s.n. (S); On slate and limestone rocks in ravines, New York and Canada, *Peck, Macoun* 134 (F). **Illinois**, [Cook County]: Lemont, crevices of limestone cliff, 6 v 1903, *Hill* 10 (F). Jackson County: bluffs near north entrance to Giant City State Park, 20–22 viii 1958, *Miller* 5689 (NY). Rock Island County: Port Byron, 28 v 1897, *Harper* s.n. (H1296) (JE); Port Bryon, 28 v 1897, *Harper* s.n. (NY); Port Byron, 28 v 1897, *E. & T. Harper* s.n. (F); Port Byron, Barber's Creek, on cliffs in crevasses in rock, 23 v 1904, *E. & T. Harper* s.n. (268812) (NY); Port Byron, on cliffs in crevasses in rocks, 23 v 1904, *E. & T. Harper* s.n. (F). **Indiana**, Putnam County: Fern cliff, sandstone exposure, 1958, *Miller* 5760 (NY). **Michigan**, Ontonagon County: Porcupine Mountains, at base of cliff above talus? Slope, Carp Lake, 20–27 viii 1935, *Nichols & Steere* s.n. (268808) (NY). **Minnesota**, s.n. (268818) (NY); s.n. (268819) (NY); Bear breek, 6 vii 1896, *Holzinger* s.n. (268830) (NY). Goodhue County: over moist soil on exposed bluff south of Wacouta, 15 v 1950, *Schuster* 18007 (F). Houston County: Over rather dry soil on steep, strongly insulated sandy soil at crest of bluff, 1.5 miles south of Brownsville, xeromorphic extreme, mature carpocephala, pH8, occurring with *Mannia rupestris* intermixed, *Oxalis violaceae*, *Liothospermum canescens*, *Viola pedatifida*, 9 v 1948, *Schuster* 13480a (S); Over rather dry soil on steep, strongly insolated sandy soil at crest of bluff, 1.5 miles S of Brownsville, mature carpocephala, *M. rupestris* intermixed, *Oxalis violaceae*, *Liothospermum canescens*, *Viola pedatifida*, 9 v 1948, *Schuster* 13480 (F); 3.4 miles S of Brownsville, over rather shaded, rather moist talus slopes and ledges, on thin soil over sandstone, 31 v 1949, *Schuster* 14327 (F); 3 miles south of La Crescent, on moist, shaded sandstone wall, one or two intermingled plants of *M. pilosa*, 15 v 1947, *Schuster* 13544 (F); 3 miles N of Reno, on thin calcareous soil over east facing talus and bases of bluffs, occurring with *M. pilosa*, 14 v 1947, *Schuster* 6754a (F). Washaba County: on shaded, moist, thin soil over narrow sandstone ledges, at foot of large bluffs south of Lake City, pH 7.5, occuring with carpocephala, 9 v 1948, *Schuster* 10063 (S). Washington County: Over shaded moist thin soil in crevices of sandstone cliffs, 3 miles N of Stillwater, along St Croix R., with carpocephala, v 1947, *Schuster* 14055 (F); Nearctic, over thin soil on marrow, moist ledges, and in sheltered cavities in moist limy sandstone ledges, along St. Croix River, circa 3 miles north of Stillwater, 11 vi 1950, *Schuster* 18139 (NY, S); In crevices and moist cavities, on shaded, high sandstone bluffs at edge of St. Croix R., 2–3 miles north of Stillwater, 30 v 1947, *Schuster* 14825 (NY, S); On moist, shaded calcareous sandstone, about 3 miles N. of Stillwater, 2 v 1947, *Schuster* 10009a (S, F); Over thin soil on narrow, moist ledges and in sheltered cavities in moist limey sandstone ledges, along St. Croix R., ca. 3 miles N of Stillwater, mature capsules, 11 viii 1950, *Schuster* 18139 (F); Sandstone bluffs 2–3 miles N of Stillwater, along St Croix R., in shally shaded depressions of rock wall, c. capsules, v 1949, *Schuster* 14825 (F). Winona County: "Mt. Faith", John Latch State Park, over moist soil over bluff, 12 v 1950, *Schuster* 18058 (F); Whitewater River in Whitewater State Park, over moist exposed sandstone ledges, with capsules, 15 v 1950, *Schuster* 18010 (F).

New Jersey, Bergen County: Closter, New Jersey, 1873, *Austin* 134 (NY). **New York,** Athaea ?, Rocks, west bank of Fall br. at free hollow, just below falls, 1888, *Boville* s.n. (268825) (NY). Schuyler Country: Watkins Glen, 26 vi 1857, *Brewer* s.n.* (268816) (NY). **North Carolina,** McDowell County: Eastern United States, damp rocks, near waterfall above Linville Caverns, just W. of Route 221, 9 vii 1958, *Schuster* 40369 (S); Linville Taverns, over thin moist humus, on limestone ledges, just above entrance to the caverns, occurring with very few capsules, 1 v 1955, *Schuster* 34741 (F); On soil over shaded damp calcareous ledges, just to the right of the entrance to Linville Caverns, ca. 2800 ft., Route 221, sterile, 27 vii 1953, *Schuster* 29061 (F); At Linville Caverns, Rte 221, in small patches, with *Gymnostomum aeruginosum*, over shaded limestone bluff, with old carpocephala, spores typical, 27 vii 1953, *Schuster* 28800 (F); Damp rocks, at mouth of Linville Caverns, just W of Route 221, 9 vii 1958, *Schuster* 40370 (F); Damp rocks, at mouth of Linville Caverns, just W of Route 221, 9 vii 1958, *Schuster* 40371 (F). **Ohio**, [Clark County]: *Austin* 189 (268829) (NY); *Leroy* s.n. (NY); *Biddle* s.n. (NY); 1878, *Biddlecome* s.n. (268834) (NY); Springfield, 12 v 1877, *Pearson* s.n. (BM); Springfield, 12 v 1899, *Biddlecome* s.n. (NY); Springfield, 15 vi 1886, *Spence* 118 (NY); Near Springfield, 5 vi 1877, *Haines* s.n. (93043) (NY); Springfield, 15 vi 1886, *Spence* s.n. (F); Springfield, 15 vi 1886, *Spence* 118 (F). **Pennsylvania**, *Rau* s.n. (b) (BM). **Vermont**,Willoughby, 1500ft., on limestone, on the Bluffs, where it was somewhat damp and shady, 16–18 vii 1913, *Evans & Lorenz* s.n. (268817) (NY).

CANADA, On slate and limestone rocks in ravines, New York and Canada, *Peck &Macoun* 134 (BM, NY). **Ontario**, Lake region and Ontario, vi 1876, *Macoun* 2532 (NY); Lake region and Ontario, vi 1869, *Macoun* 13 (NY); Belville, on calcareous rocks, vi 1869, *Macoun* 187 (NY); Belville, 1873, *Macoun* s.n. (109379) (NY); Crevices of wet limestone rocks along the Moira above Belleville, rare, 6 vi 1862, *Macoun* 145 (NY). **Yukon Territory**, Dawson, slope of Moosehide Mtn., along side of path, wet sandy gravel, rare but common locally, 1 vii 1949, *Calder & Billard* 3443 (NY).

CHINA, Qinghai Province, Henan County: Ningmute Xiang, Ningmute, 34°29'40"N, 101°10'09"E, ca. 3450 m, steep river bank with *Juniperus*, under

Sibiraea, 16 vii 1997, *D.G. Long* 27056 (E). Zeku County: below Maixiu Forestry Centre, Langzhang Valley, 35°15'52"N, 101°53'37"E, ca. 3180 m, steep rocky valley with Picea and Juniperus forest, on stream bank under shrubs, 17 vii 1997, *D.G. Long* 27059 (E).

JAPAN, **Hokkaido Region**, *Faurie* 5552 (BM); Hidako, Samani-cho, Tashirozawa, on soil, 29 v 1970, *Kobayashi* s.n. (S); Hidaka, Samani-cho, Tashirozawa, on soil, 23 v 1970, *Kobayashi* s.n.* (B74813) (S); In crevices of andesite cliff, ca. 250m above sea-level, Sankaku-yama, Sapporo-shi, Hokkaido, *Sasaki & Kudo* 932* (F, G, S); Sapporo-shi, Sankakuc. 250m, in crevice of andesite, sunny place, 15 v 1972, *Sasaki & Kudo* 10524* (NICH); Tokachi-shicho, Onbetsucho, Satonbetsu, 300m, on humus, 31 v 1981, *Takida* 569* (NICH).

RUSSIA, NW of Europes part of Russia, Bychegda, composite forest, in puddle, 8 ix 1930, *M. Vlasov* s.n. (JE). [**Krasnoyarsk Territory**], Sibiria, Jenisei, Mjelnitsa, 65°50'N lat., 12 vii 1876, *H. W. Arnell* s.n. (B74772) (S). [**Murmansk Province**], Murmansk Region, Lapland Reserve, Salnyc tundras, 10 viii 1986, *E.N.Andrejeva* s.n. (JE). [**Taymyr Autonomous Okrug**], Northern Sibiria, Putorana Plateau, vii 1980, *E.N.Andrejeva* 144* (JE); Northern Siberia, Norilsk Region, Tundra belt of Talnach Mt., 5 viii 1993, *E.N.Andrejeva* s.n. (JE).

UNKNOWN LOCALITIES, *Neesiella rupestris*, ex Schimper, per Stirton, vii 1884, s.n. (E); De not? (BM); *Sauter* s.n. (BM); *Nees* s.n. (BM); *Nees* s.n. (b) (BM); *Grimaldia*, Hb. W. Mitten 1906, *Kumam* 3757 (NY).

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

AUSTRIA, **Carinthia**, Völkermarkt, Bleiburg, Petzen, Knieps, N-side of summit, 2014m, 46°30'14.1"N, 14°45'45.3"E, in calcareous rock crevice, 24 vii 2003, *D.B.Schill, H.Köckinger & U.Müller* 83 (E); Völkermarkt, Bleiburg, Petzen, east of Kniepssattel, 2016m, 46°30'19.2"N, 14°46'12.2"E, in calcareous rock crevice on stony, grassy slope, 24 vii 2003, *D.B.Schill, H.Köckinger & U.Müller* 84 (E);

Völkermarkt, Bleiburg, Petzen, east of Kniepssattel, 2016m, 46°30'19.1"N, 14°46'12.3"E, in calcareous rock crevice on stony, grassy slope, 24 vii 2003, *D.B.Schill, H.Köckinger & U.Müller* 85 (E); Karnische Alpen, Friaul, Felshaenge des Monte Canale, 2200 m, 10 vii 08, *Kern* s.n. (B74762) (S). **Tyrol**, Gschnitztal, Martartal bei Gschnitz, in Felsspalten, Kalk, c. 1800m, viii 1902, *V.Schiffner & V. Patzelt* 1191a. (E, NY); Gschnitztal, Martartal bei Gschnitz, in Felsspalten, Kalk, ca. 1800m, viii 1902, *Schiffner & Patzelt* 1191a (S); Innsbruck, Hafelekan, ca. 2300m, Kalkvegetation, 4 viii 1951, *Gams & Sjörs* s.n. (S); N-Tiroler Alpen, Grethenweg am Hafelekar, 2300m, 4 viii 1951, *H. Gams* s.n. (B74761) (S). [**Vorarlberg**], An der Douglashütte bei der Scesaplana, 1924, *K. Müller* s.n. (H1307) (JE); Bei der Douglashütte bei der Scesaplana, auf Kalkfelsen, viii 1924, *K. Müller* s.n. (B74751) (S).

ESTONIA, **Saaremaa County**, Estonian SSR, Lõo, alvar, 13 vi 1989, *L. Hedenäs* E-18 (B74763) (S).

FINLAND, [**Lapland Province**], Pohjois-Pohjanmaa, Tornio, Kalkkimaa, W end of the cliffs on SW side of Tuppivaara, Q=7312:520, c. 30m, amongst other bryophytes in moss mat on thin layer of mixed humus and mineral soil over exposed sloping face of dolomite-bearing rock, 18 vi 1972, *E. & M. Ohenoja* s.n. (S).

FRANCE, [Rhône-Alpes], Bessans (Savoie), vallée de Ribon, sur schistes lustrés, 2900m, 6 viii 1952, *L. Castelli* 10A (B74769) (S); Bessans (Savoie), vallée de Ribon, sur schistes lustrés, 2600m, 4 vii 1952, *L. Castelli* 10C (B74769) (S).

GERMANY, **Bavaria**, Oberbayern, Watzmann, 3 viii, *D. V.*s.n. (JE).

ITALY, [**Trentino-South Tyrol**], Nord-Italien, Suedtirol, bei Sulden, 15 viii 1902, *Quelle* s.n. (H1305) (JE); Mt Pelmo, Prov. Bellamo, *Massalongo* s.n. (B24386).

NORWAY, 1833, *Regnell* s.n. (BM); Nordlandis, ad interactam Bardofossen in mulangendalea Nordlandia Norveg. Jun., *A.F. Regnell* s.n. (B74904) (S).

[Finnmark County], Finnmark, earth-covered limestone rocks, west side of Altafjord, ca. 8 km north of Kåfjord, 2 viii 1976, *E. Nyholm & A. C. Crundwell* s.n. (E). **[Nordland County]**, Nordlands, amt Salten, Fauske, Lägäflun, 67°/0' lat. bor., 26 viii 1893, *J. Hagen* (F); Nordlands amt Salten, Förfolden, Dyperik, 67°5' lat. bor., 19 viii 1893, *Hagen* s.n. (S); Nordf. Salten, Boodfjelt?, 27 viii 1869, *Schlegel & Arnell* s.n. (S); N. Helgl., Dunderlandsdalen, 4 viii 1870, *Blytt & Arnell* s.n. (S); N.Helgl. Mo, Selfordfied ?, 19 vii 1870, *Blytt & Arnell* s.n. (S). **[Oppland County]**, Dovre, vii 1857, *Hirlen* s.n. (g) (BM); Dovre, Kongsvolt, 1872, *Rok.Hu* s.n. (NY); Dovre, Kongsvolt, Rok. Hu (NY); Kongsvolt, 1873, *Brandes* s.n. (S); Drinftuen ask Kongsvold, 1834, *Rok. Hu* s.n. (B74912) (S). **[Troms County]**, Tromsoe amt, Tromsoe, 11 vii 1891, *Arnell* s.n. (NY); Tromsö amt, Bardo, Bergkletten i tallneg, 9 viii 1891, *Arnell* s.n. (S); Tromsö amt, Nordreizen?, Tavrovive? I videreg, 18 viii 1891, *Arnell* s.n. (S).

SLOVAKIA, Hohe Tatra, Beläer Kalkalpen beim ‚Eisernen Tore', sehr spärlich, 1603 m, 27 vii 1910, *I. Györffy* s.n. (725087) (BM).

SWEDEN, Srm?, bagnhäred, Fänsåker, 20 v 1946, *Arnell* s.n. (S).
Gotland County, Nickarvejun, Hejdeby, 15 v 1957, *Å.Hovgard* s.n. (S); Hejdeby, 1957, *Å.Hovgard* s.n. (H1299) (JE); Nickarve prom. Hejdeby, 14 v 1957, *Å.Hovgard* s.n. (S); Kräklingbo sn, Torsburgen, 1957, *Hakelier* s.n. (H1303) (JE); Kräklingbo sn, Torsburgen, 15 v 1957, *Hakelier* s.n. (S); St. Karlsö, Röjserhajd, 10 viii 1943, *Persson* s.n. (S); Follingbo sn, vid Storvidemeyr, 13 v 1957, *Hakelier* s.n. (S); Östergarns sn, Grogarnsberget, Lammbetad mark, 17 v 1946, *Pettersson* s.n. (S); Visby, Langähage På ....Follingbo, 16 v 1952, s.n. (S); Strovidemyr pron. Follingbo, 27 v 1955, *Å. Hovgard* s.n. (B74832) S. **Jämtland County**, Haerjedalen, Taennaes sn, Froestsjoeberget, soedra sidan, 15 viii 1964, *Hakelier* s.n. (NY); Häredalen, Tännäs, Skenörsfjället, södra sidan, 31 viii 1975, *Hakelier* s.n. (S); Häredalen, Tännäs sn, Hamrafjället, östra sidan, 12 viii 1965, *Hakelier* s.n. (S); Häredalen, Tännäs sn, Fröstsjöberget, södra sidan, 15 viii 1964, *Hakelier* s.n. (S).Undersåkers sn, ca. 500m Ö om Säterråvallen nära vägen till Vålådalen, kalkklippa, 25 vi 1964, *Hakelier* s.n. (S); Jämtland, Åre sn, Ulvsberget, södra sidan, 22 viii 1964, *Hakelier* s.n. (S); Lyle. Tärna sn, Mieskatfjället, 25 vii 1934, *Uggla* s.n. (S). **[Kalmar County]**, **Öland**, Resmo sn,

alvaret strax O om kyrkbyn, mellan tuvor i alvarstepp, 7 vi 1942, *Albertson* s.n. (S); Bei Resmo, 24 v 1865, *Lindberg* s.n. (S); Resmo sn, 17 vi 1928, *Hülphers* s.n. (S); Resmo alvar, på Kalkhallar nud grund jordhetåckning, 18 vi 1928, *Hülphers* s.n. (S); Resmo alvar, 12 vi 1920, *Medelius* s.n. (S); Resmo alvar, 17 vi 1928, *Medelius* s.n. (S); Borgby alvar, 10 vi 1920, *Medelius* s.n. (S); Borgby alvar, 1920, *Medelius* s.n. (H1298) (JE); Böda sn, Lalngaloaud?, 2 v 1944, *Albertson* s.n. (S); Böda sn, Strandtorps, 14 vi 1928, *Hülphers* s.n. (S); Hullenstad sn, Gösslunche alvar, 9 vi 1920, *Medelius* s.n. (S); Hartlösa sn, Bjärby alvar, 18 vi 1920, *Medelius* s.n. (S); Högsrum asvar sogn, Karums alvar, 22 v 1983, *Hallingbäck* s.n. (E). **[Norbotten County]**, Torne Lappmark, Jukkasjärvi socken, Abisko nationalpark, Nuolja, nordsluttningen (12a), 29 vii 1944, *Persson* s.n. (S); Torne Lappmark, Jukkasjärvi socken, Torneträskområdet, Nissonjåkks kanjon, 4 viii 1944, *Persson* s.n. (S); Torne Lappmark, Jukkasjärvi socken, Abisko nationalpark, Slåttatjåkko, O-sluttningen, reg. Alp., 15 viii 1944, *Persson & Gjaerevoll* s.n. (S); Torne Lappmark, Jukkasjärvi socken, Abisko nationalpark, Kårsavaggejåkk, S:a sidan, 29 vii 1944, *Arnell & Persson* s.n. (S); Jukkasjärvi, *Rodlofriano* s.n. (S); Torne Lappmark, Torneträsk-området, Vassitjakko, bravt ca. 700m, 12 viii 1927, *Samuelsson* s.n. (S); Lapponia tornensis, in reg. Lacus Torneträsk, Låktatjakko, in supikes? Schistosis, 2 vii 1927, *Samuelsson & Zander* s.n. (S); Torne Lappmark, Björkliden, 19 vii 1941, *Hülphers* s.n. (S); Torne Lappmark, Tjasinnjarkatjåkko, skifferbrant, ca. 800m, 1 viii 1916, *Samuelsson*, s.n. (S); Torne Lappmark, Nuolja, 16 vii 1944, *Hülphers* s.n. (S); Torne lappmark, par. Jukkasjaervi, Tjasinnjaskatjåkko, 1 viii 1916, *Samuelsson* s.n. (NY); Pite Lappmark, Silbotjåkkå, rock crevices near the river, 500–575m, 16°15'E, 66°31'N, 5 viii 1998, *Thingsgaard & Damsholt* 98-150 (E); Pite Lappmark, Vuoggatjålmejaure, Reti, ostrikan?, 16 vii 1932, *Arwidsson* s.n. (S); Pite Lappmark, Sulitelma, vii 1938, *Uggla* s.n. (S); Lule lappm., Njammats pr. Krikkjokk, 15 vii 1891, *Nyman* s.n. (S); Pite Lappland, Arjeplog s:n Sulitelma, 1938, *Uggla* s.n. (H1304) (JE). **[Stockholm County]**, Upland, Djurö, Munkön, kalkhällar, 28 v 1916, *Samuelsson* s.n. (S); Upland, Djurö, Runmarö, Kalkeberg nära Hvitträsk, 26 v 1927, *Larsson* s.n. (S); Uppland, Djurö socken, Runmarö, Kalkberg norr om Kila, provet innehåller *Mannia fragrans* åtminstone som inblandning, 28 vii 1976, *Johansson* s.n. (S); Södermanland, Bälinge parish, 1.5km NE Nynäs, among mosses on limestone, 8 vi 1980, *Thor* 1712 (S). **[Västra**

Götaland County], Västergötland, Karleby sn, 1944, *Hülphers* s.n. (H1302) (JE); Västergötland, Karleby, 15 v 1944, *Albertson* s.n. (S); Västergötland, Karleby sn, Djupedalen, mydla påckalkhällar, 12 x 1937, *Larsson* s.n. (S); Västergötland, Karleby sn, Karlbg hed, 1 vi 1944, *Albertsson* s.n. (S); Värtugull., Karleby kalkkea jordtäckt kalkhull, 19 vi 1944, *Hülphers* s.n. (S).

SWITZERLAND, Valais, Bernice, Mte. Gemmi, Herb. *Shuttleworth* 1877 (BM).

GREENLAND, **West Greenland**, Sondĕstrom Fjord, sunny south facing slopes, near air strip, 66°50'N, ca. 50°30'W, at head of Fjord, with Solenostoma polaris, 23 vi 1966, *Schuster* 66-041 (F); Sondĕstrom Fjord, sunny south facing slopes, near air strip, 66°50'N, ca. 50°30'W, at head of Fjord, 23 vi 1966, *Schuster* 66-047 (F); Sondĕstrom Fjord, sunny south facing slopes, near air strip, 66°50'N, ca. 50°30'W, at head of Fjord, 23 vi 1966, *Schuster* 66-045 (F); SW corner of Anap nunâ NW of Niaqornarssuag, 69°55'N, 50°33'W, 21 vii 1970, *Schuster* 70-2404 (F).

U.S.A., **Alaska**, **[Nome Census Area]**, Bendeleben Quad., Darby Mts., Mt. Omilak, saddle on E shoulder, 65°01'07"N, 162°34'05"W, ± flat saddle, on ground, 1 vii 1997, *B. M. Murray* s.n. (E). **[North Slope Borough]**, Arctic Alaska, in vicinity of Ogoturuk Creek and its mouth, south of Cape Thompson, Chukchi Sea, near southwest end of Brooks Range, 68°07'N, 165°55'W, on side of frost hummock in tundra, 21 vii 1963, *W. C. Steere* 63-526 (NY); Driftwood Camp, near headwaters of the Utukok River, north slope of De Long Mountains, Brooks Range, approx. 68°53'N, 161°10'W, on soil, frost boil,12 viii 1951, *W. C. Steere* 16805 (NY); Driftwood Camp, near headwaters of the Utukok River, north slope of De Long Mountains, Brooks Range, approx. 68°53'N, 161°10'W, 4 viii –6 viii 1951, *W. C. Steere* 16525 (NY); Lupine River, Brooks Range (68°45'N, 148°20'W), in headwater area of Sagavanirktok River, south of Prudhoe Bay, 500–1500m, 26 vii 1973, *Iwatsuki* 1166 (NY); Vicinity of Umiat, Colville River (69°22'N, 152°10'W), North side of Umiat Mountains, 140–250m, 25 vi 1973, *W. C. Steere, Inoue & Iwatsuki* 323 (NY); Gubic and vicinity, near the confluence of the Chandler and Colville Rivers, approx. 69°28'N, 151°30'W, hillside, 23 vii 1951, *W. C. Steere* 16145 (NY); East Oumalik and vicinity, approx. 69°48'N, 155°23'W, on bare frost boil, high tundra, 3-10 vii 1951, *W. C. Steere* 15373-3d (NY); East Oumalik and vicinity, approx. 68°48'N, 161°10'W, on bare frost boil, high tundra, 3-10 vii 1951, *W. C. Steere* 15272 (NY); Liberator Lake, north slope of De Long Mountains, Brooks Range, 68°52'N, 158°22'W, on north-facing ridge south of lake, 19 vii –25 vii 1961, *W. C. Steere* 610725-12 (NY); Liberator Lake, north slope of De Long Mountains, Brooks Range, 68°52'N, 158°22'W, on silt in frost boil, north slope of Liberator Ridge, 19 vii –25 vii 1961, *W. C. Steere* 610725-19 (NY). Firth River Basin, near mouth of Mancha Creek, 68°40'N, 141°W, in crevices of rock outcrop, lower Mancha Creek, 5 viii 1958, *Sharp* MC-58144U (NY); Firth River Basin, near mouth of Mancha Creek, 68°40'N, 141°W, crevices of soil in bluff, 11 viii 1958, *Sharp* MC-58222a (NY); Firth River Basin, near mouth of Mancha Creek, 68°40'N, 141°W, peaty bank of Firth River near Mancha Creek, 9 viii 1958, *Sharp* MC-58185b (NY). **[Northwest Arctic Borough]**, Boreal Alaska, Ambler River Region, moist slatey limestone rock pile, 1000', north facing slope west of waterfall, Mountains E. of Ruby Creek, 1.5 miles S. of Bornite, ca. 67°03'N, 156°54'W, 25 vi 1976, *Lewis* 1537 (F).

CANADA, **North-West Territories**, Banks Island, Bernard River, a few miles south of its aprupt turn southward, 73°23'N, 121°50'W, on vertical silt bank above Bernard River, 1 viii –4 viii 1963, *W. C. Steere* 63-908 (NY).

RUSSIA, **[Krasnoyarsk Territory]**, Siberia, Jenissei, inter Krasnojarsk et Jeniseisk, prope pagum Makokovo, 58°N, 1876, *H. W.Arnell* s.n. (H1300) (JE); Jenissei, Dudinka, 69°35'N, 27–30 vii 1876, *H. W.Arnell* s.n. (H1301) (JE). **[Sakha Republic]** Siberia, In valle flum. Lena, Kumachsur, 70°30' lat.bor., 31 vii 1898, *Nilsson-Ehle* s.n. (S, NY).

UNKNOWN LOCALITIES, 6 viii, Schneibstein, *Quelle* s.n. (JE); Oben an Aggarstein, Schneilstein? 6.8., *F.Quelle* s.n. (JE).

Appendix II. Morphological phylogeny and character evolution

1. Characters and character state codes used for morphological phylogeny

Vegetative characters of gametophyte

1 Thallus margin (0 = narrow and rather parallel; 1 = sinuate; 2 = undulate, crenate, wavy)

2 Thallus areolation (0 = absent; 1 = present)

3 Assimilation tissue (0 = compact; 1 = loose)

4 Oil bodies in ventral scales (0 = present; 1 = absent)

5 Scale appendage Number (0 = predominately 1; 1 = 1 or 2; 2 = 2, 3 and 4)

6 Appendage constriction (0 = absent; 1 = present)

7 Aromatic (0 = weakly aromatic; 1 = strongly aromatic)

Reproductive characters of gametophyte

8 Sexual condition (0 = par-autoicous; 1 = terminal autoicous; 2 = male- ventral autoicous; 3 = female-ventral-autoicous; 4 = dorsal autoicous; 5 = dioicous)

9 Androecium type (0 = diffuse, scattered; 1 = weak cushion or cluster; 2 = defined cushion; 3 = disc)

10 Position of androecium (0 = dorsal; 1 = base of stalk; 2 = ventral; 3 = terminal)

11 Peduncle position (0 = terminal on main thallus; 1 = terminal on ventral thallus, 2 = dorsal; 3 = absent)

12 No of rhizoidal furrows (0 = none; 1 = one; 2 = two; 3 = not applicable)

13 Carpocephala head (0 = naked; 1 = inconspicuously bearded; 2 = conspicuously bearded; 3 = not applicable)

14 Shape of carpocephalum (0 = hemispherical; 1 = umbrella-shaped; 2 = conical; 3 = discoid; 4 = subglobose to globose; 5 = absent)

15 Involucre (0 = cup-shaped; 1 = flap; 2 = entire flap; 3 = bilabiate or bivalved; 4 = tubular)

16 Pseudoperianth (0 = absent: 1 = present)

Sporophyte characters

17 Capsule dehiscence (0 = entire/regular lid; 1 = fragmenting/decaying/irregular lid; 2 = valves)

18 Spore shape (0 = alete; 1 = weakly trilete; 2 = strongly trilete)

19 Proximal/distal ornamentation (0 = isopolar; 1 = anisopolar)

20 Proximal disc (0 = present; 1 = absent)

21 Equatorial pores (0 = absent; 1 = inconspicuous, 2 = conspicuous)

22 Fine distal ornamentation (0 = pits; 1 = without pits)

23 Fine distal ornamentation (0 = papillate; 1 = areolate/alveolate; 2 = spongy; 3 = smooth)

24 Primary distal ornamentation (0 = saccate, 1 = ridges; 2 = regularly areolate; 3 = incompletely areolate; 4 = lamellate)

2. Data matrix for morphological phylogeny

Taxon Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Mannia androgyna	0	0	0	0	1	0	0;1	3;4	0;1	0	0;1	1	0	0	0	0	0	1	1	0	2	0	0	0
Mannia asiatica	0	0	1	0	1	0	0	1	1	3	0	1	0;1	0	0	0	0	1	0	1	1;2	0	1	3
Mannia californica	0	0	0	0	1	0	0	3;4	0;1	0	0;1	1	0	0	0	0	0	1	1	0	2	1	0	1;3
Mannia fragrans	0	0	1	0	1	0	1	5	3	3	0	1	2	0	0	0	0	0	0	1	2	0	0	2
Mannia pilosa	1	1	1	1	1	0	0	2	1	2	0	1	2	4	0	0	0	0	0	1	1	0	2	3
Mannia sibirica	0	1	0;1	0	1	0	0	1	1	3	0	1	2	0	0	0	0	1	1	0	2	1	0	1;2
Mannia triandra	1	1	1	0	1	0	0	0;1	1	1;3	0	1	0	4	0	0	0	0	0	1	1	0	2	3
Asterella africana	1	1	0	0	0	0	0	0	1	1	0	1	2	1	2	1	1	2	1	1	0	0	1	2
Asterella californica	2	0	1	0	2	0	1	5	2	0	0	1	0	0	1	1	1	2	0	1	0	0	1	1
Asterella gracilis	2	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	0	1;3	3
Asterella grollei	?	0	1	0	0	0	1	1	1	3	0	1	1	2	1	1	1	2	0	1	2	1	0	1
Asterella lateralis	?	0	0	0	1	0	?	2;3	1	2	1	1	1	1	2	1	1	2	0	1	0	0	1	2
Asterella palmeri	2	0	0	0	0	0	?	0	1	1	1	1	0	2	2	1	0	2	0	1	2	1	0	1
Asterella saccata	0	0	1	0	1	1	0	0;1	1	1	0	1	0	2	1	1	1	2	0	1	0	1	1	1
Asterella tenella	1	0	1	0	1	0	1	0	1	1	0	1	0	2	2	1	0	2	0	1	2	1	0	3
Asterella wallichiana	2	0	1	0	0	0;1	1	5	2	0	0	1	1	0	2	1	1	2	0	1	0	1	0	1
Cryptomitrium himalayense	2	1	1	0	0	0	0	0	0	1	0	1	0	3	3	0	0	2	0	1	0	1	3	4
Cryptomitrium tenerum	2	1	1	0	0	0	0	0	0	1	0	1	0	3	3	0	0	2	0	1	0	1	3	4
Plagiochasma rupestre	2	0	0	0	1	1	0	1	2	0	2	0	2	0	3	0	1	2	0	1	1	1	0	2
Plagiochasma wrightii	2	0	0;1	0	0	1	0	1	2	0;2	2	0	2	0	3	0	1	2	0	1	1	1	0	1;3
Reboulia hemisphaerica	2	0	0	0	2	0	0	0;1	2	1;3	0	1	2	0	3	0	1	2	0	1	2	1	0	2
Athalamia hyalina	2	1	1	1	0	0	0	5	0	0	2	0	0	0	4	0	2	1	0	1	0	0	0	3
Targionia hypophylla	0	0	0	0	0	0	1	2	1	2	3	3	3	5	2	0	2	0	1	0	0	0	1	2

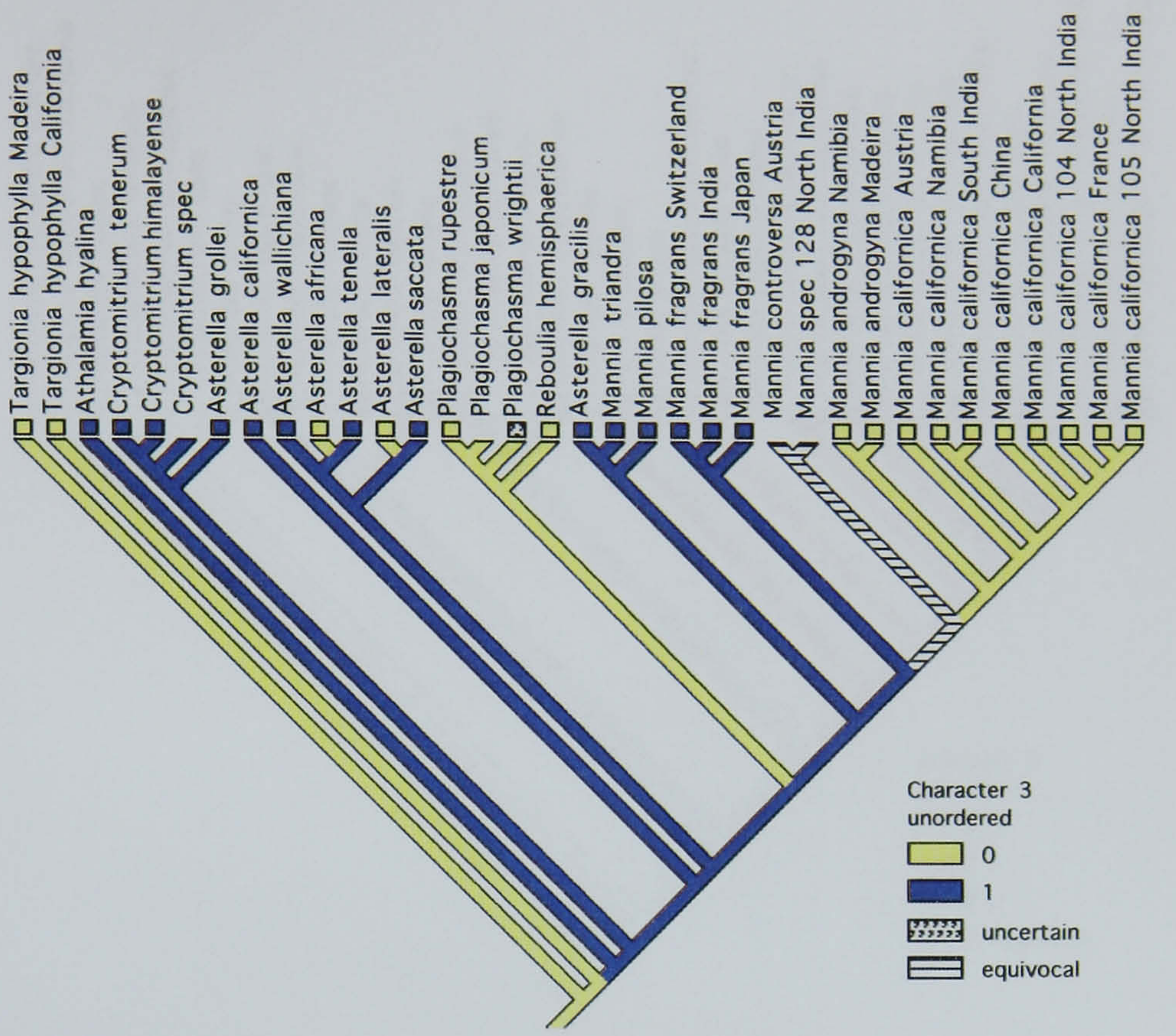
3. Characteristics of the morphological matrix

Parameter	Morphological dataset
Number of taxa	23
Length of most parsimonious trees, steps	142
Number of most parsimonious trees	76
Consistency Index (CI)	0.54
Homoplasy Index (HI)	0.62
Retention Index (RI)	0.61
Rescaled consistency Index (RC)	0.33

4. List of characters, states, steps and the Consistency Index (CI) used in the character evolution

Character	States	Steps	CI
1	3	6	0.33
2	2	5	0.20
3	2	5	0.20
4	2	2	0.50
5	3	7	0.29
6	2	2	0.50
7	2	6	0.17
8	6	10	0.40
9	4	7	0.43
10	4	10	0.30
11	4	4	0.75
12	3	3	0.67
13	4	8	0.38
14	6	9	0.56
15	5	8	0.50
16	2	4	0.25
17	3	3	0.67
18	3	4	0.50
19	2	3	0.33
20	2	2	0.50
21	3	6	0.33
22	2	6	0.17
23	4	7	0.43
24	5	11	0.36

5. Character evolution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Asterella wallichiana
Asterella africana
Asterella tenella
Asterella lateralis
Asterella saccata
Plagiochasma rupestre
Plagiochasma japonicum
Plagiochasma wrightii
Reboulia hemisphaerica
Asterella gracilis
Mannia triandra
Mannia pilosa
Mannia fragrans Switzerland
Mannia fragrans India
Mannia fragrans Japan
Mannia controversa Austria
Mannia spec 128 North India
Mannia androgyna Namibia
Mannia androgyna Madeira
Mannia californica Austria
Mannia californica Namibia
Mannia californica South India
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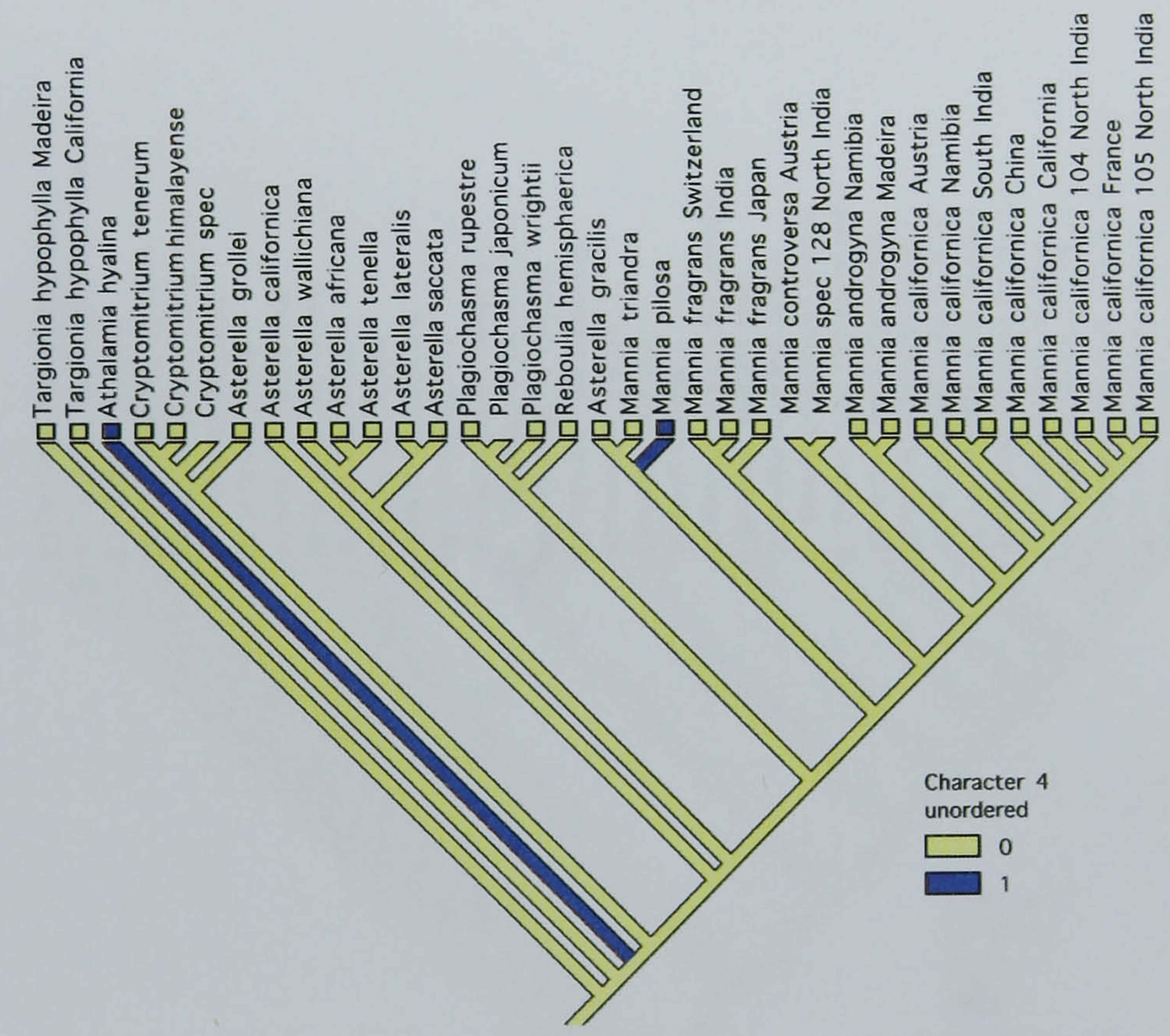
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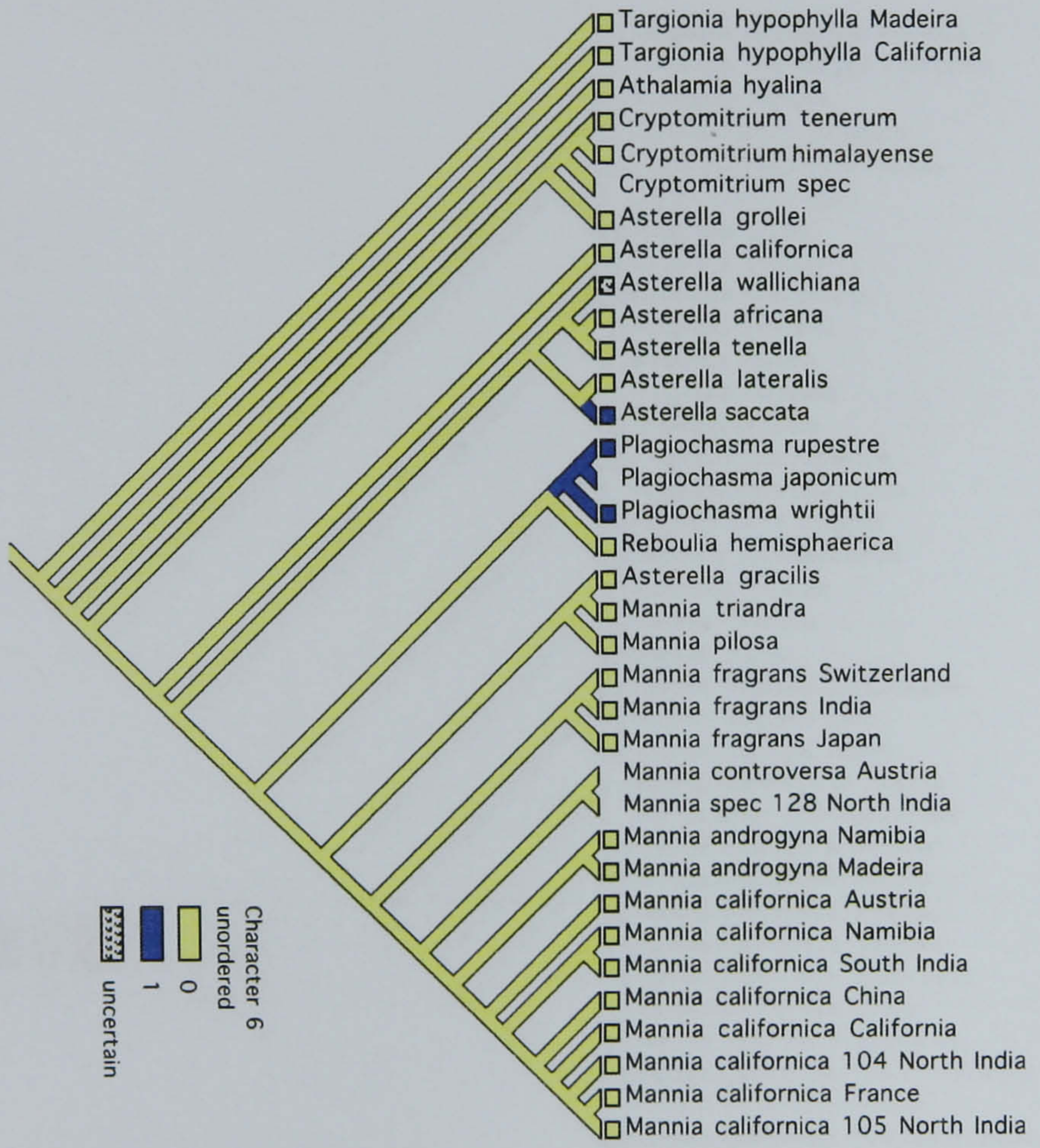
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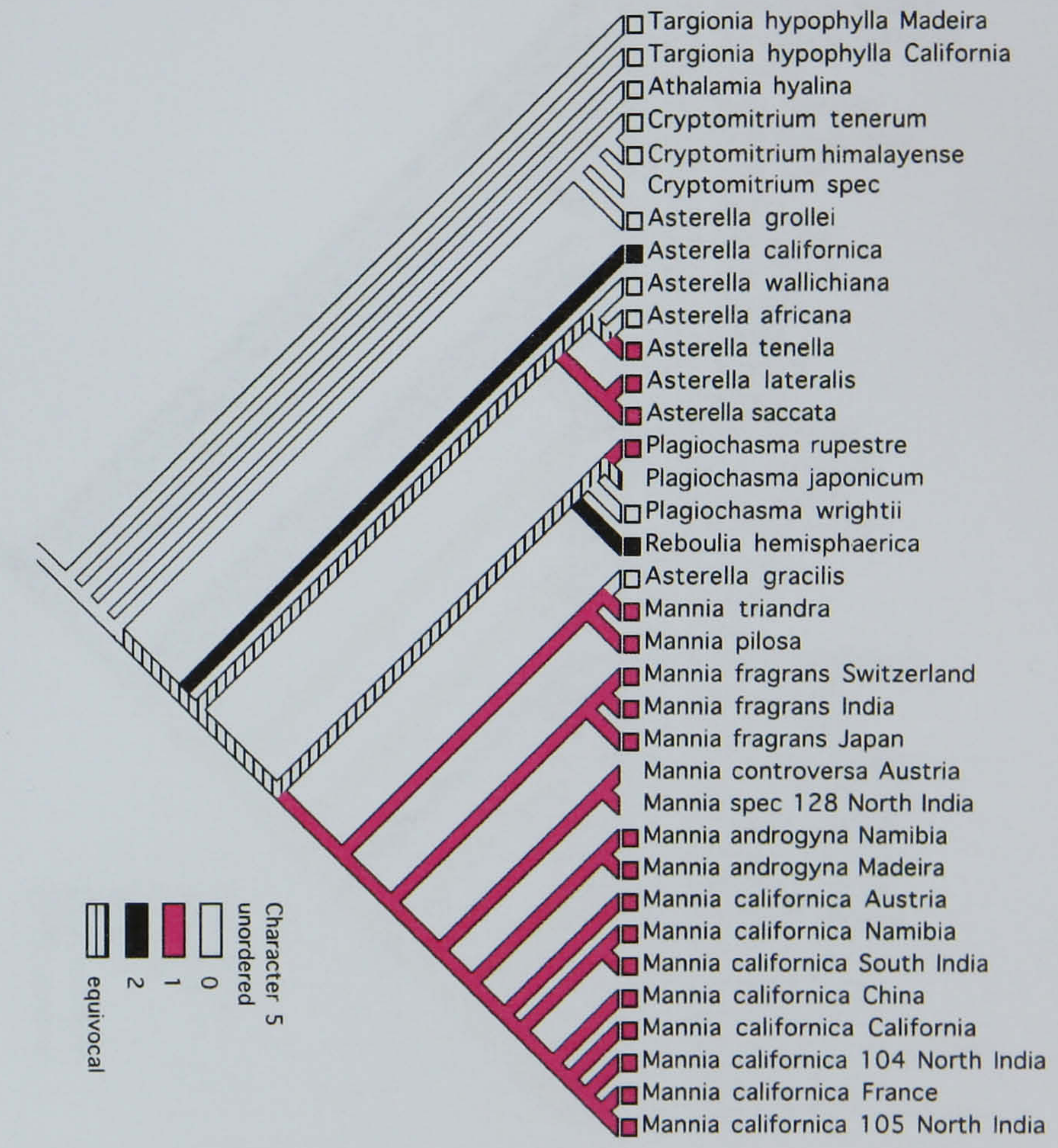
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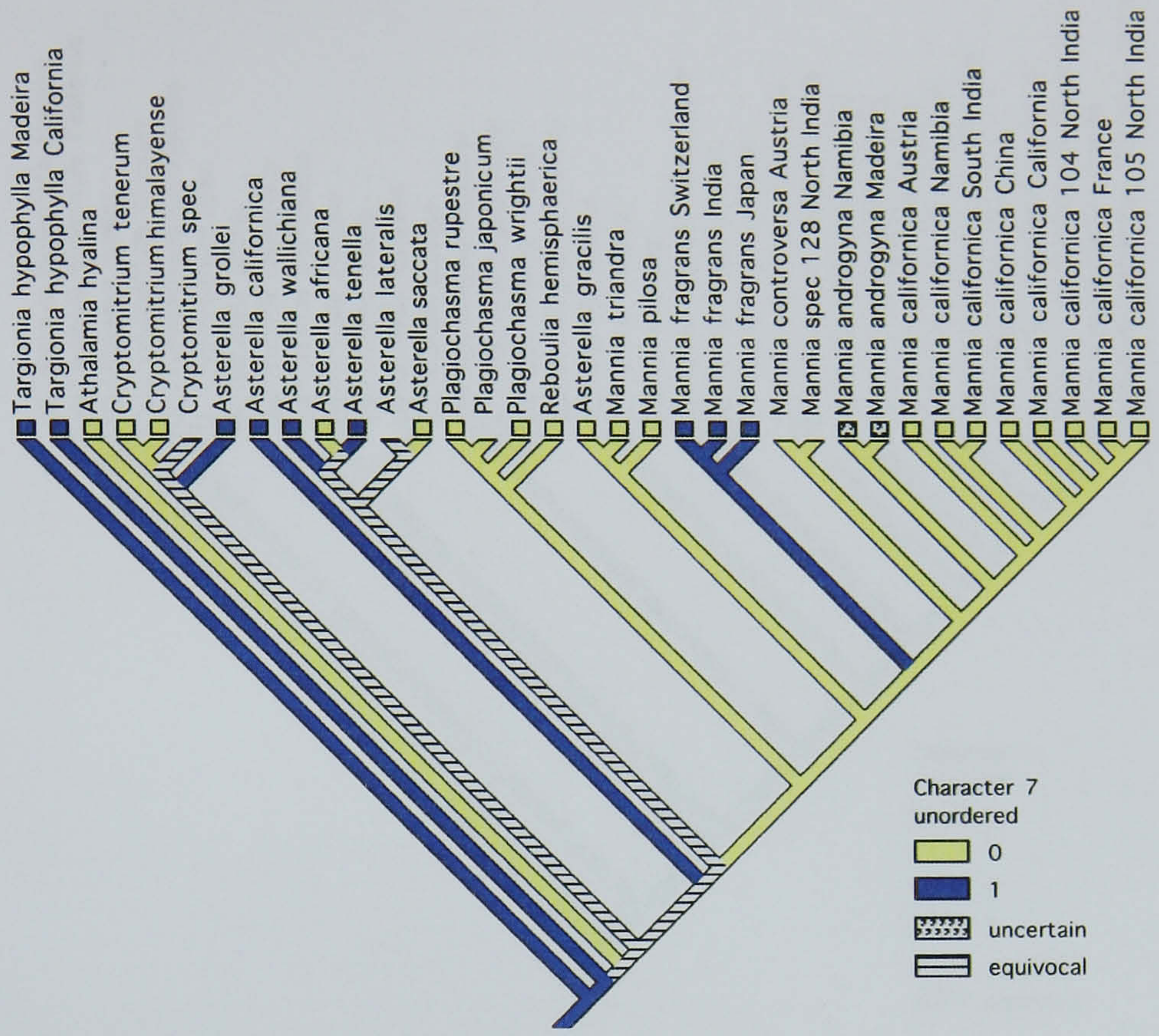
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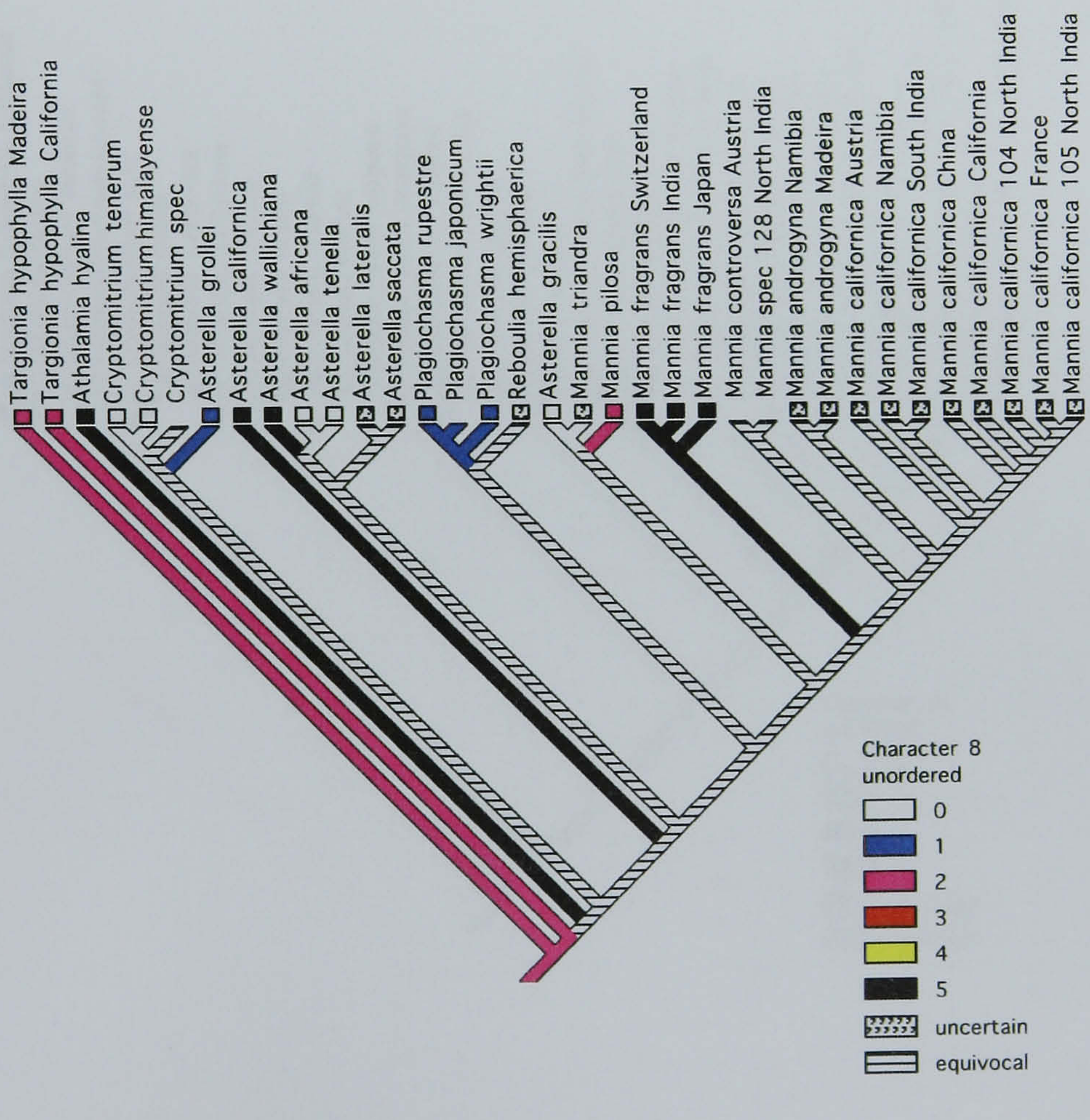
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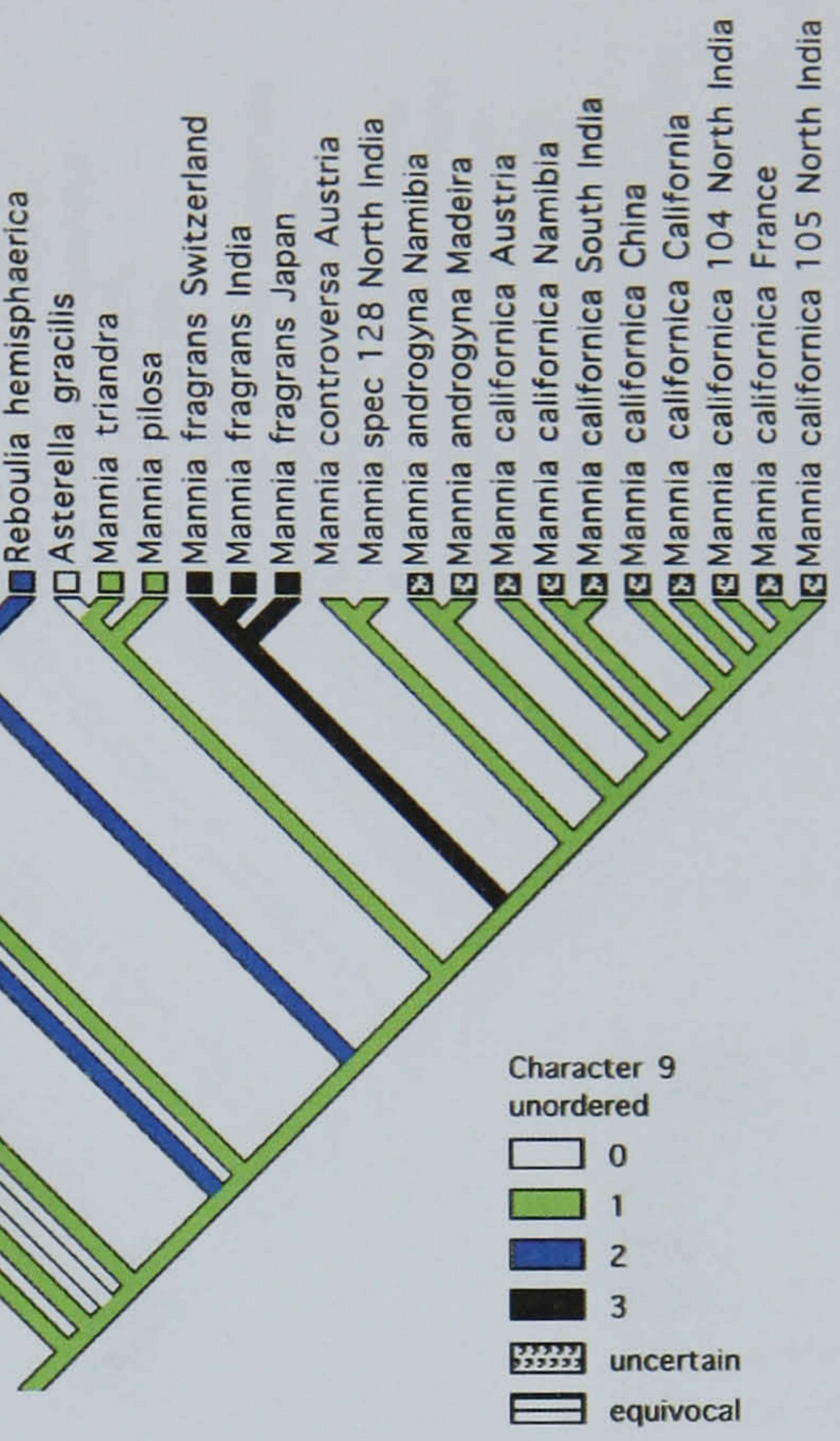
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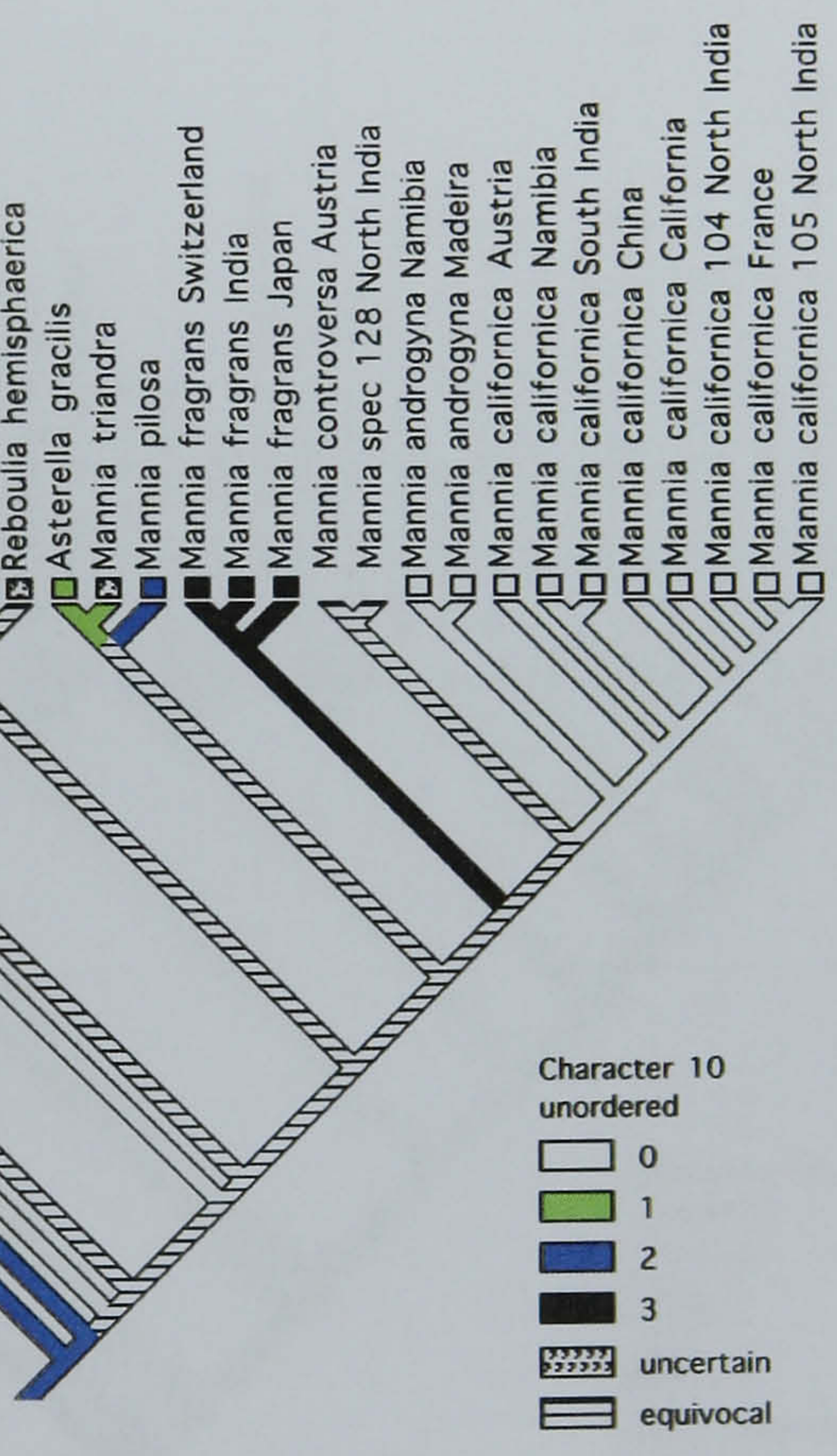
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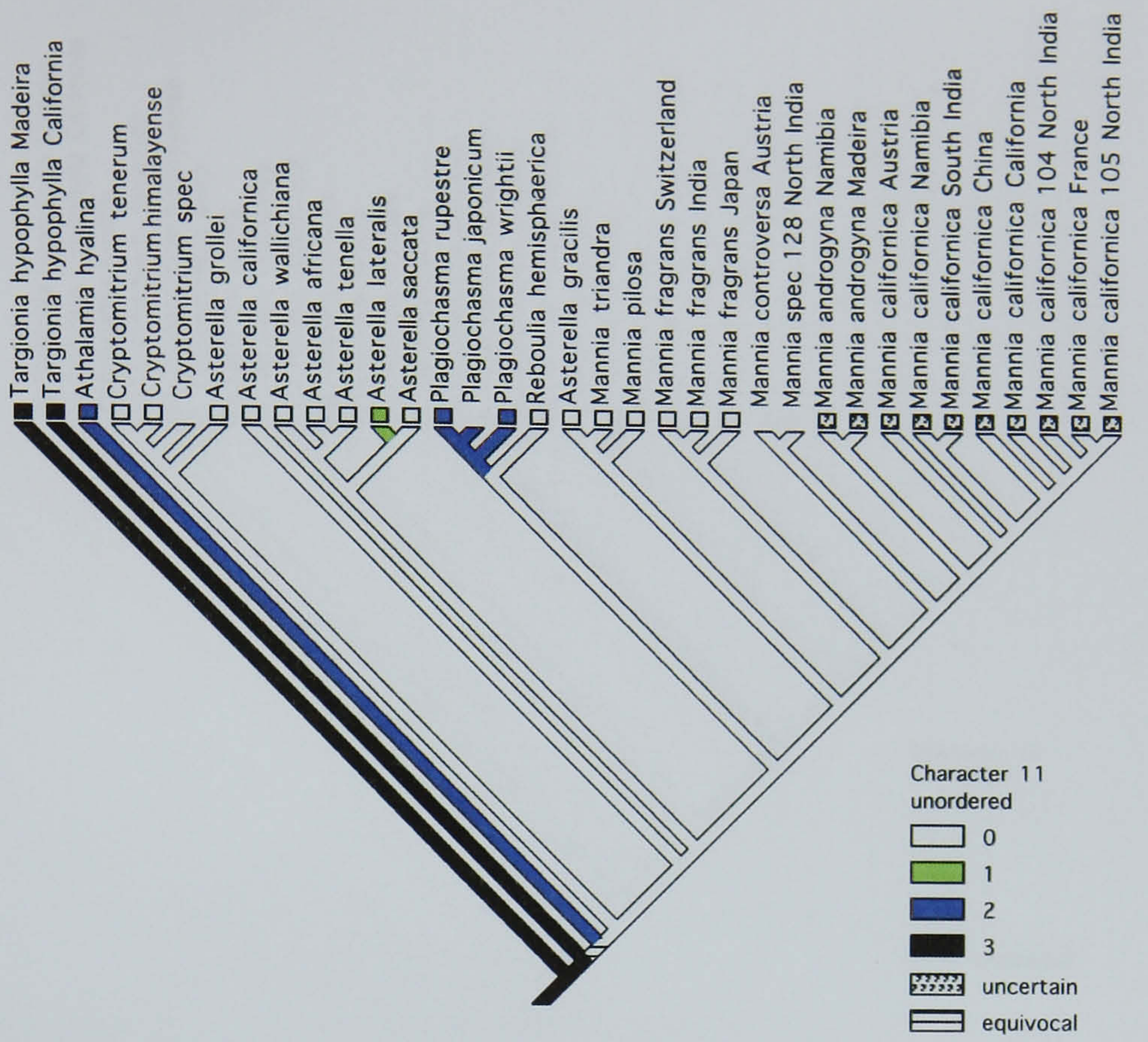
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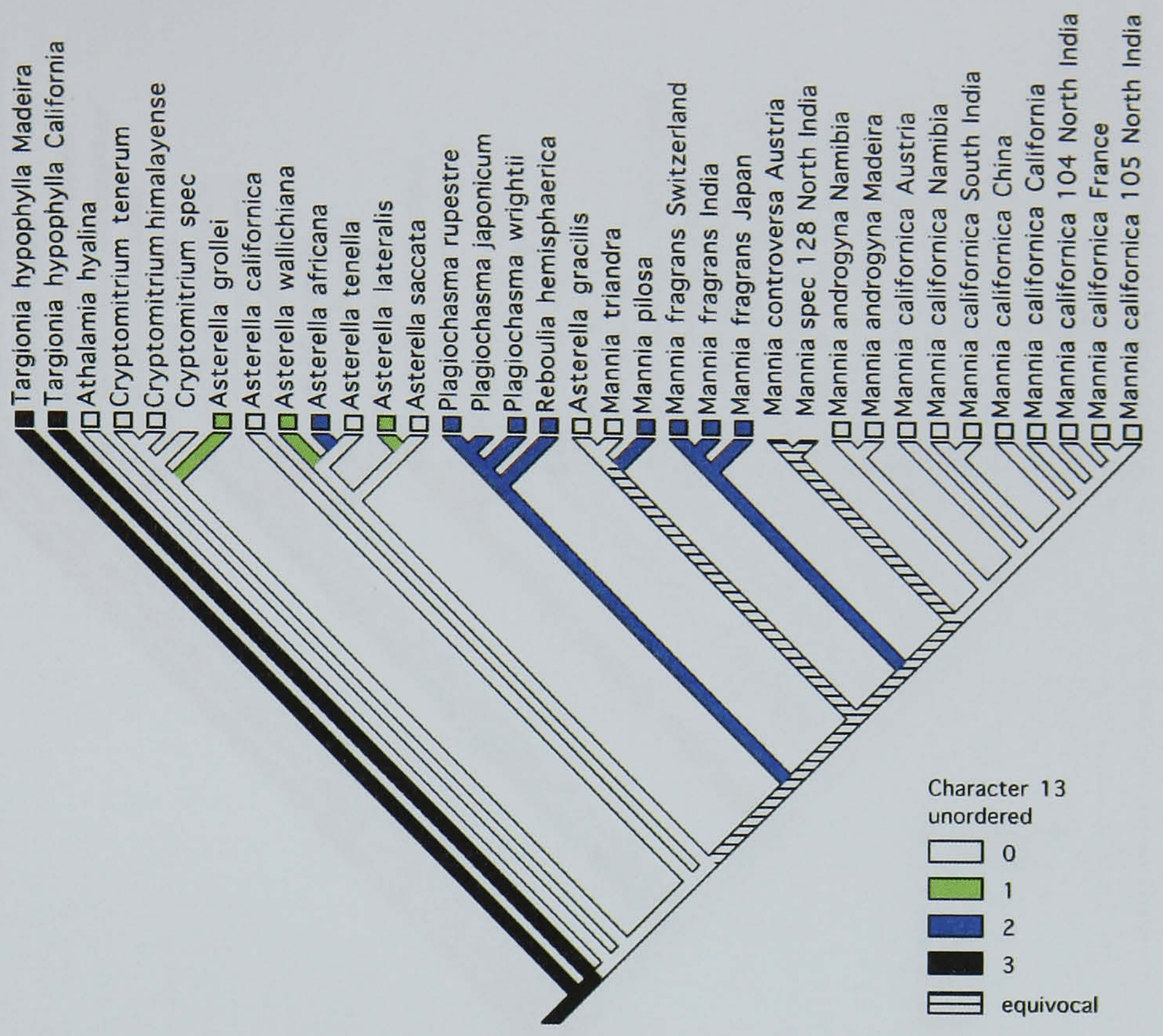
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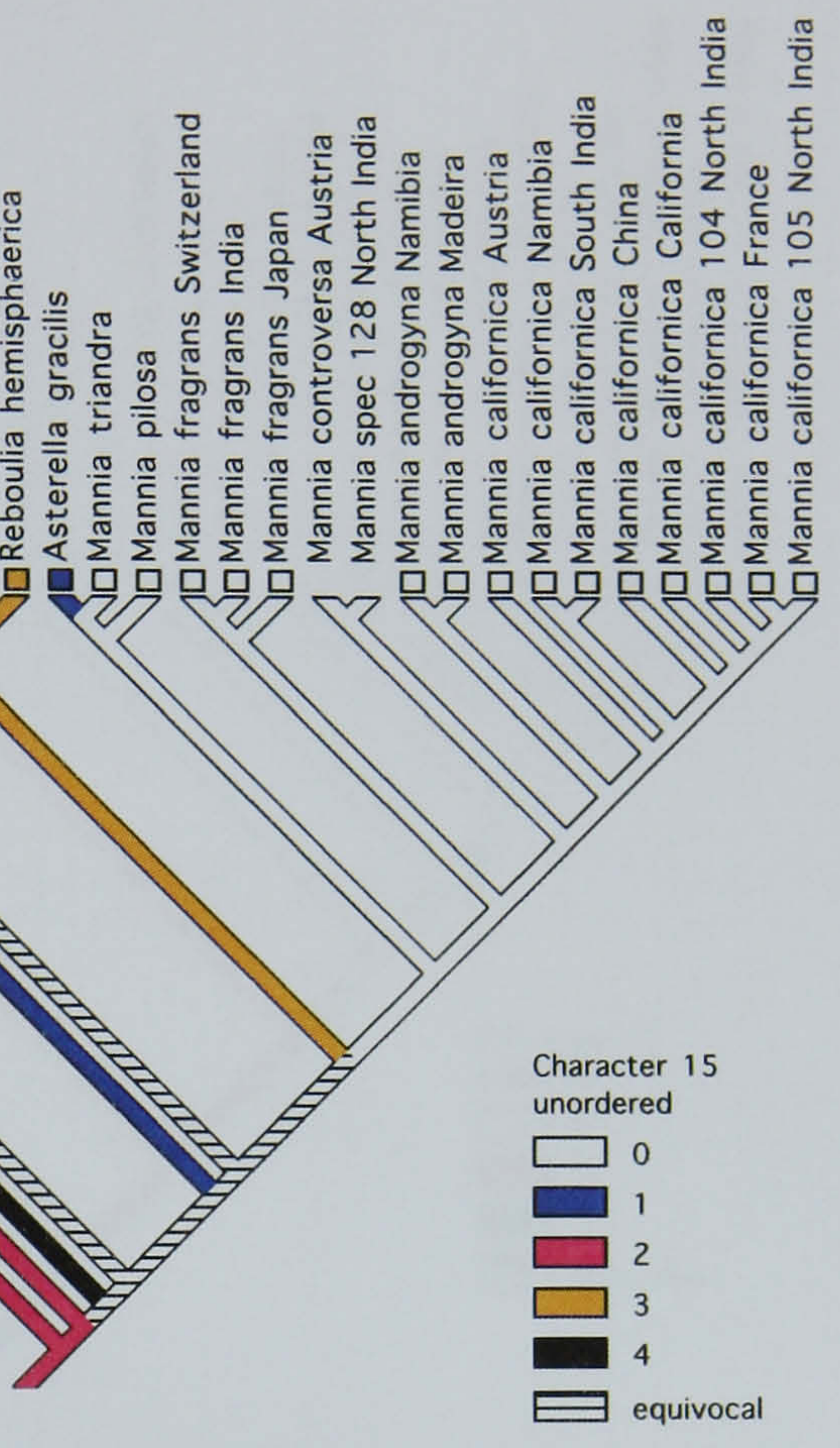
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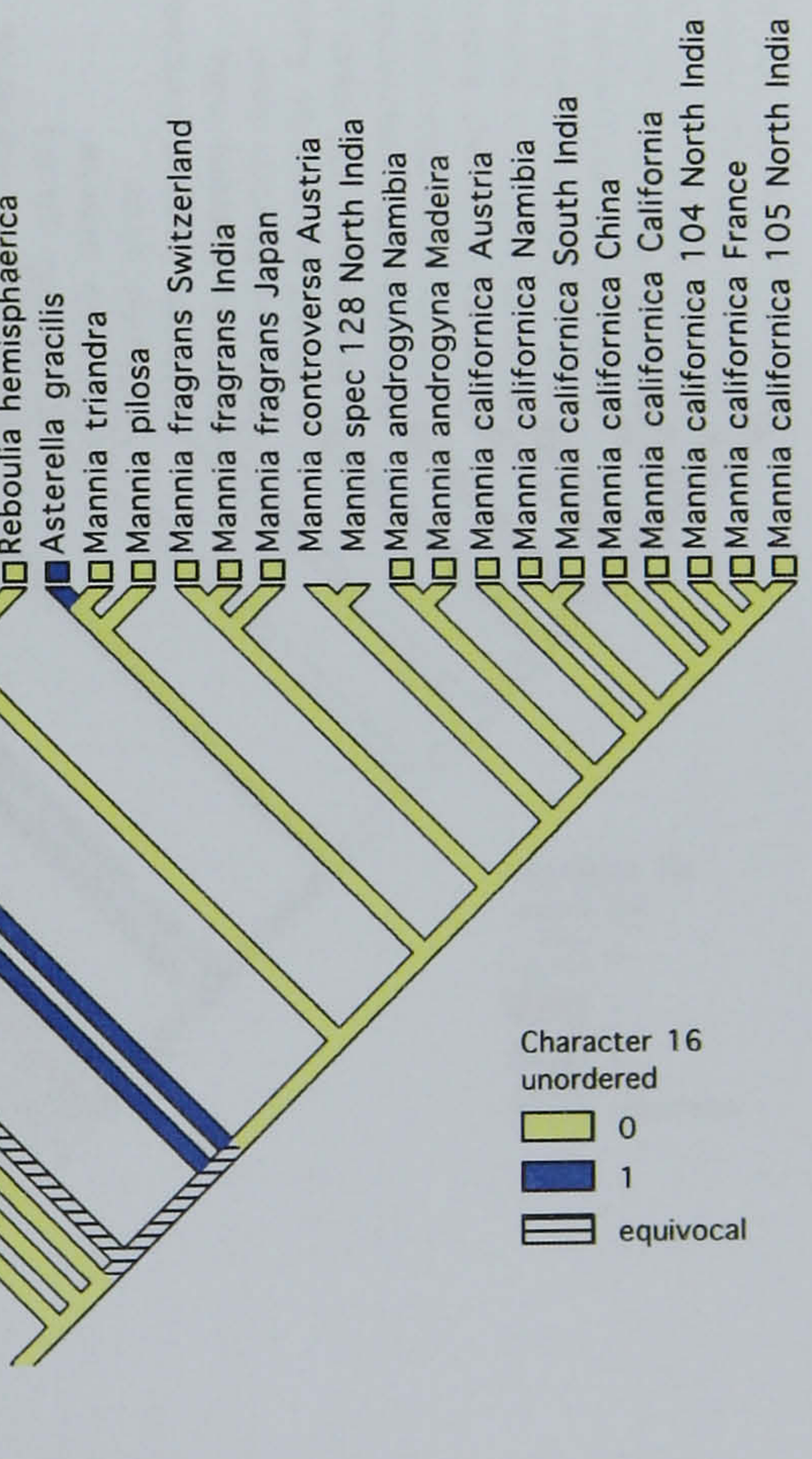
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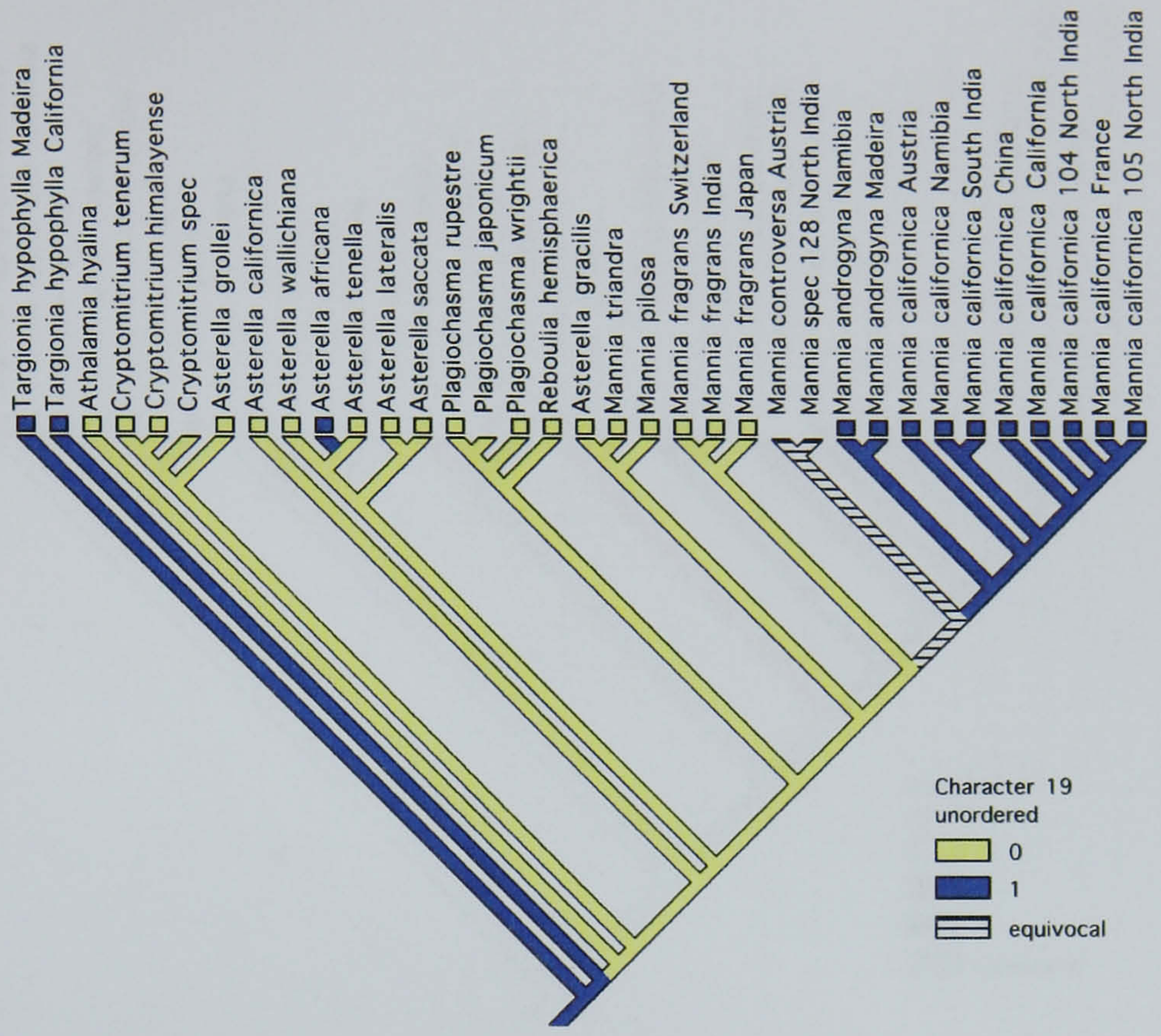
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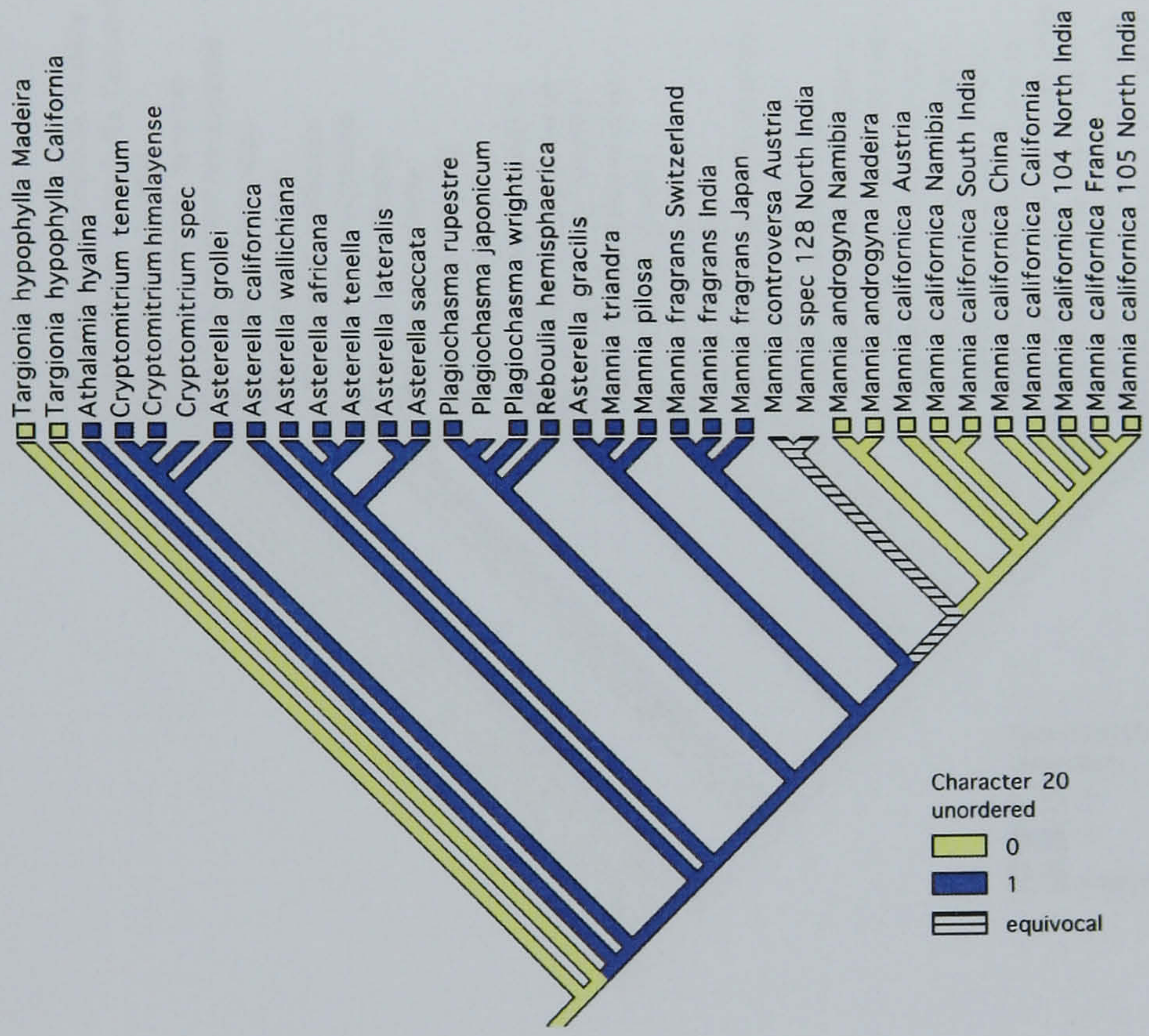
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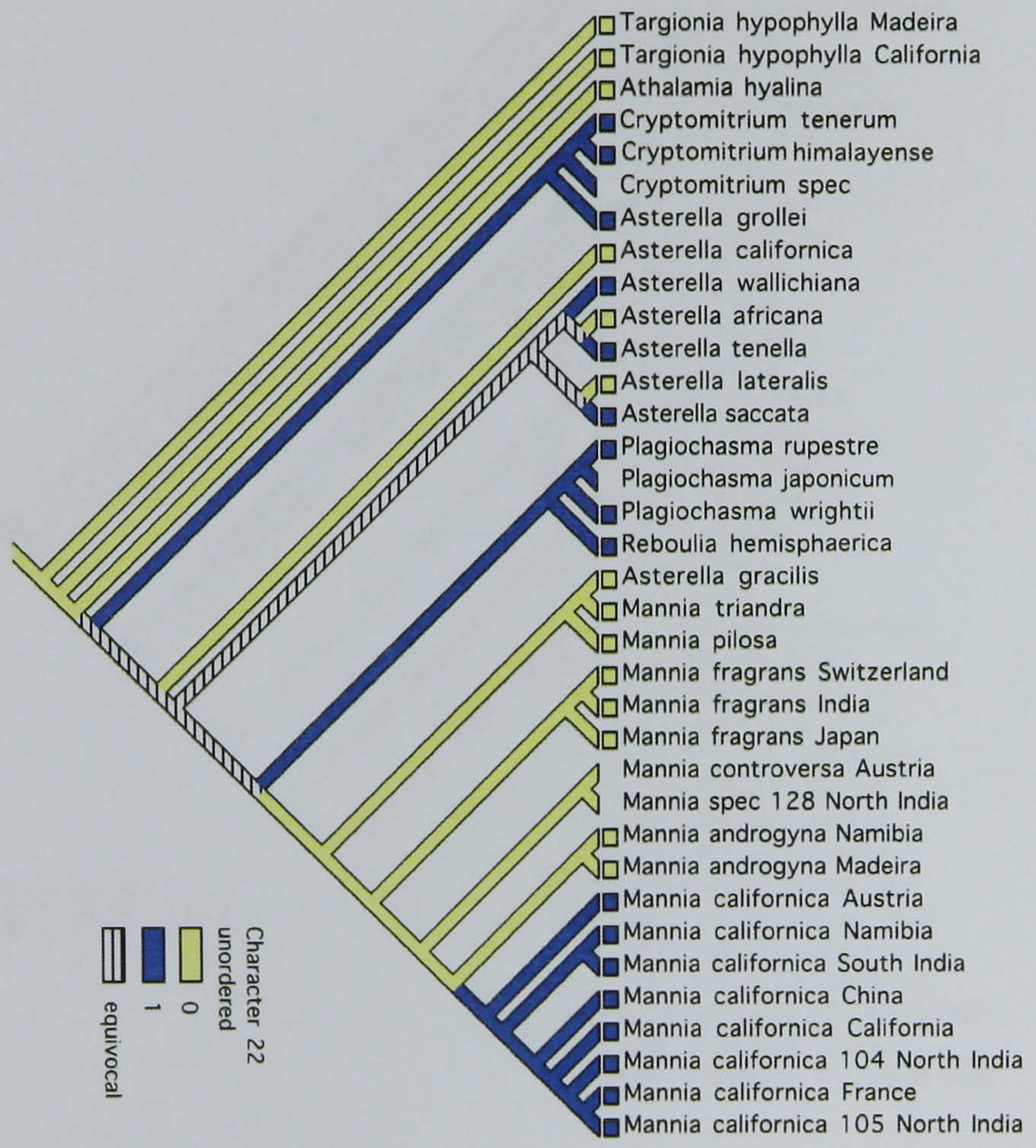
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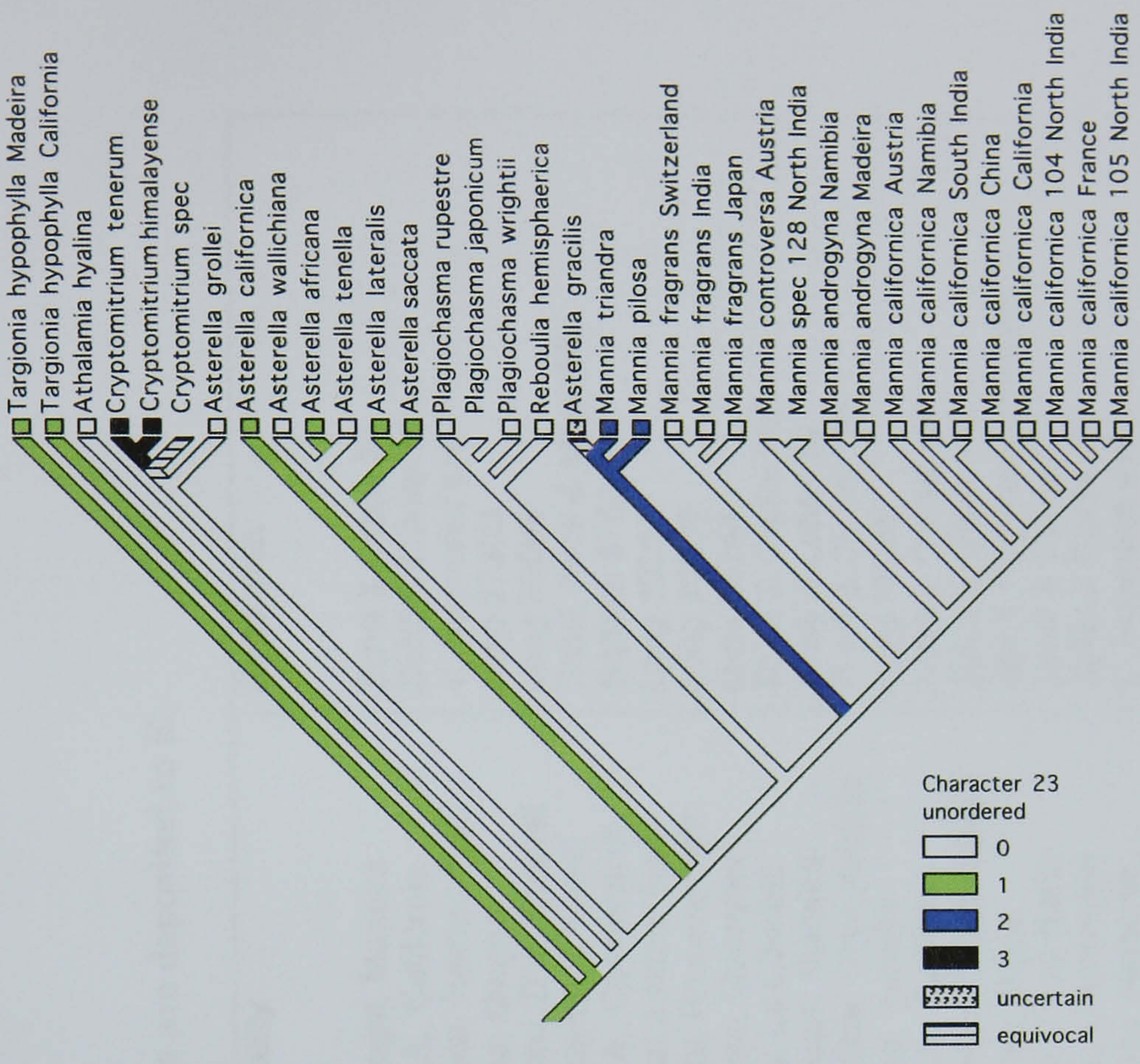
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Appendix III. Molecular phylogeny

1. Liverwort material used for DNA analyses. Voucher specimens are deposited in E.

Taxon	DNA sample No.	Locality	Collection
Aytoniaceae			
Asterella africana (Mont.) A.Evans	Schill 18	Portugal, Madeira	*Schill & Lobos* 29
Asterella californica (Hampe) Underw.	Schill 74	U.S.A., California	*Schill & Clarke* 104
Asterella gracilis (F.Weber) Underw.	HUGO 2	France, Haute-Loire	*V. Hugonnot* s.n.
Asterella grollei D.G.Long	H37	China, Qinghai	*Long* 27203
Asterella lateralis M.Howe	H257	Mexico, Dist. Federal	*Long* 29598
Asterella saccata (Wahlenb.) A.Evans	Schill 41	Switzerland, Valais	*Schill, Price & Maier* 58
Asterella tenella (L.) P.Beauv.	H363	U.S.A., Connecticut	*Goffinet* 8750
Asterella wallichiana (Lehm.) Grolle	H317	Nepal, Lalitpur Distr.	*Long* 30251
Cryptomitrium himalayense Kashyap	H346	Nepal, Rasuwa Distr.	*Long* 30559
Cryptomitrium tenerum (Hook.) Austin ex Underw.	H276	Mexico, Querétaro	*Long* 29748
Cryptomitrium spec.	Schill 116	Peru, La Libertad	*Schill & Clarke* 180
Mannia androgyna (L.) A.Evans	Schill 20	Portugal, Madeira	*Schill & Lobos* 29
Mannia androgyna (L.) A.Evans	Schill 87	Namibia, Otjozondjupa	*Schill & Clarke* 124
Mannia californica (Gottsche) L.C.Wheeler	H639	China, Yunnan	*Long* 35035
Mannia californica (Gottsche) L.C.Wheeler	Schill 72	U.S.A., California	*Schill & Clarke* 102
Mannia californica (Gottsche) L.C.Wheeler	Schill 91	Namibia, Otjozondjupa	*Schill & Clarke* 131
Mannia californica (Gottsche) L.C.Wheeler	Schill 55	Austria, Styria	*Schill, Köckinger & Müller* 77
Mannia californica (Gottsche) L.C.Wheeler	Schill 95	India, Tamil Nadu	*Schill & Clarke* 144
Mannia californica (Gottsche) L.C.Wheeler	Schill 105	India, Uttaranchal	*Schill & Clarke* 165
Mannia californica (Gottsche) L.C.Wheeler	HUGO	France, Ardèche	*V. Hugonnot* s.n.
Mannia californica (Gottsche) L.C.Wheeler	Schill 104	India, Uttaranchal	*Schill & Clarke* 164
Mannia californica (Gottsche) L.C.Wheeler	KOE	Austria, Carinthia	*Köckinger* s.n.
Mannia controversa Meyl.	DUE	Austria, Carinthia	*Duell* s.n.
Mannia fragrans (Balbis) Frye & L.Clark	Schill 34	Switzerland, Valais	*Schill, Price & Maier* 58

Mannia fragrans (Balbis) Frye & L.Clark	ITO	Japan, Honshu	*Itouga* s.n.
Mannia fragrans (Balbis) Frye & L.Clark	Schill 103	India, Uttaranchal	*Schill & Clarke* 162
Mannia pilosa (Hornem.) Steph.	Schill 63	Austria, Carinthia	*Schill, Köckinger & Müller* 85
Mannia triandra (Scop.) Grolle	Schill 65	Austria, Carinthia	*Schill, Köckinger & Müller* 87
Mannia spec.	Schill 128	India, Uttaranchal	*Schill & Clarke* 163
Plagiochasma rupestre (Forst.) Steph.	Schill 5	Portugal, Madeira	*Schill* 5
Plagiochasma wrightii Sull.	H264	Mexico, Vrracruz	*Long* 29636
Plagiochasma japonicum (Steph.) C.Massal.	Schill 98	India, Tamil Nadu	*Schill & Clarke* 147
Reboulia hemisphaerica (L.) Raddi	Schill 31	Switzerland, Valais	*Schill, Price & Maier* 46
Cleveaceae			
Athalamia hyalina (Sommerf.) S.Hatt.	Schill 60	Austria, Carinthia	*Schill, Köckinger & Müller* 82
Targioniaceae			
Targionia hypophylla L.	Schill 11	Portugal, Madeira	*Schill & Lobos* 19
Targionia hypophylla L.	Schill 75	U.S.A., California	*Schill & Clarke* 106

2. Alignment of *Mannia* and related taxa for *trn*L-F and 26S. *Trn*L-F matrix from 1-684 (excluded regions: 1-11, 249-301, 655-684), gap matrix from 685-693, 26S matrix from 694-1922 (excluded regions: 694-710, 769-774, 1274-1320, 1433-1447, 1485-1499, 1847-1857, 1880-1922). '*' excluded regions; '?' missing data, '-' gap.

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Targionia_hypophylla_California       ??????????ATTGGTAGACGCTGCGAACTTAATTTAATTGAGCTTTAGTCGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Athalamia_hyalina                     ????TCGAAA-TTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCCACTAAATGACTGTTTTCAAA   [79]
Plagiochasma_rupestre                 ????????TTATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCCACTAAATGATTGTTTTCAAA   [80]
Plagiochasma_wrightii                 ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Plagiochasma_japonicum                ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCCACTAAATGATTGTTTTCAAA   [80]
Reboulia_hemisphaerica                ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Cryptomitrium_tenerum                 ????TCGAAA-TTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCTACTAAATGATTGTTTTCAAA   [79]
Cryptomitrium_himalayense             ????TCGATA-TTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCTACTAAATGATTGTTTTCAAA   [79]
Cryptomitrium_spec_Peru               ????????TA-TTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCTACTAAATGATTGTTTTCAAA   [79]
Asterella_grollei                     AAAATCGAAAATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCTACTAAATGATTGTTTTCAAA   [80]
Asterella_californica                 ????TCGATA-TTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCAACTAAATGATTGTTTTCAAA   [79]
Asterella_wallichiana                 ?????TCGATATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCCACTAAATGATTGTTTTCAAA   [80]
Asterella_africana                    ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Asterella_tenella                     ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Asterella_lateralis                   ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Asterella_saccata                     AAAAATCCTTATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTCGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Asterella_gracilis                    ?????????????GGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_pilosa                         ??AATCGTTA-TTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [79]
Mannia_triandra                       ?????????A-TTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAATTAAATGATTGTTTTCAAA   [79]
Mannia_fragrans_Switzerland           ?????TCGATATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_fragrans_India                 ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_fragrans_Japan                 ?????????ATTTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_androgyna_Namibia              ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_androgyna_Madeira              ????TCGTATATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_controversa_Austria            ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_spec_128_North_India           ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_californica_Austria            ?AAAGTCGATATTGGTAGACGCTGCGGACTCAATTTAATTGAGCTTTAGTTGAGAAATCAACTAAATGATTGTTTTCAAA   [80]
Mannia_californica_California         ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATTAACTAAATGATTGTTTTCAAA   [80]
Mannia_californica_Namibia            ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATTAACTAAATGATTGTTTTCAAA   [80]
Mannia_californica_France             ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATTAACTAAATGATTGTTTTCAAA   [80]
Mannia_californica_China              ??????????ATTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATTAACTAAATGATTGTTTTCAAA   [80]
Mannia_californica_104_North_India    ????????????TTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATTAACTAAATGATTGTTTTCAAA   [80]
Mannia_californica_105_North_India    ?????????????GGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATTAACTAAATGATTGTTTTCAAA   [80]
Mannia_californica_South_India        ?????????ATTTGGTAGACGCTGCGGACTTAATTTAATTGAGCTTTAGTTGAGAAATGAACTAAATGATTGTTTTCAAA   [80]
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[                                                   90        100       110       120       130       140       150       160]
[                                                   .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira             TTCAGGGAAACCTAGGATGAAAAAAA--GATAAATATTAGGTAATTCTGAGCCAAATTTTGTATGCTAAGACAAAATAGG   [157]
Targionia_hypophylla_California          TTCAGGGAAACCTAGGATGAAAAAAA--GATAAATATTAGGTAATTCTGAGCCAAATTTTGTATGCTAAGACAAAATAGG   [158]
Athalamia_hyalina                        TTCAGGGAAACCTAGGTTGAAAAAAAAAGAAAAAGATTAGGTAATCCTGAGCCAAATTTTGTGTACTAAAACAAAATAGG   [159]
Plagiochasma_rupestre                    TTCAGGGAAACCTTGGATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAAATTTTGTGTGCTAAAACAAAATAGG   [159]
Plagiochasma_wrightii                    TTCAGGGAAACCTTGGATGAAAAAAA--GATAAAGATTAGGTAATCCTGAGCCAAATTTTGTGTGCTAAAATAAAATAGG   [158]
Plagiochasma_japonicum                   TTCAGGGAAACCTTGGATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAAATTTTGTATGCTAAAACAAAATAGG   [159]
Reboulia_hemisphaerica                   TTCAGGGAAACCTTCTATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAAATTTTGTGTGCTAAAACAAAATAGG   [159]
Cryptomitrium_tenerum                    TTCAGGGAAACCTTGGATGAACAAAAAA----AAGATTAGGTAATCCTGAGCCAAATTTTGTGTGCTAAAACAAAATAGG   [155]
Cryptomitrium_himalayense                TTCAGGGAAACCTTGGATGAACAAAAAA----AAGATTAGGTAATCCTGAGCCAAATTTTGTGTGTTAAAACAAAATAGG   [155]
Cryptomitrium_spec_Peru                  TTCAGGGAAACCTTGGATGAACAAAAAA----AAGATTAGGTAATCCTGAGCCAAATTTTGTGTACTAAAACAAAATAGG   [155]
Asterella_grollei                        TTCAGGGAAACCTTGGATGAAAAAAAAA--TAAACATTAGGTAACCCTGAGCCAAATTTTGTGTGCTAAAACAAAATAGG   [158]
Asterella_californica                    TTCAGGGAAACCTTGGATGAAAAAAAA-GAGAAAGATTAGGTAATCCTGAGCCAAATTTTGTGTGCTAAAACAAAATAGG   [158]
Asterella_wallichiana                    TTCAGGGAAACCTAGGATGAAAAAAAAA--TAAAGATTAGGTAATCCTGAGCCAAATTTTGTATGCTAAAGCAAAATAGG   [158]
Asterella_africana                       TTCAGGGAAACCTTGGATGAAAAAAAA-GAAAAAGATTAGGTAATCCTGAGCCAAATTTTGTATGCTAAAACAAAATAGG   [159]
Asterella_tenella                        TTCAGGGAAACCTTGGATGAAAAAAAA-GAAAAAGATTAGGTAATCCTGAGCCAAATTTTGTATGCTAAAACAAAATAGG   [159]
Asterella_lateralis                      TTCAGGGAAACCTTGGATAAAAAAAA--GACAAAGATTAGGTAATCCTGAGCCAAATTTTGTATGCTAAAACAAAATAGG   [158]
Asterella_saccata                        TTCAGGAAAACCTTGGATGAAAAAAAAAGATAAAGATTAGGTAATCCTGAGCCAAATTTTGTTTG-TATACTAAAATAGG   [159]
Asterella_gracilis                       CTCAGGGAAACCTTGGATGAAAAAAA--GATAAAGATTAGGTAATCCTGAGCCAAATTTTGTGTGGTAAAACAAAATAGG   [158]
Mannia_pilosa                            TTCAGGGAAACCTTGGATGAAAAAAA--GATAAAGATTAGGTAATCCTGAGCCAAATTTTGTGTACTAAAACAAAATAGG   [157]
Mannia_triandra                          TTCAGGGAAACCTTGGATGAAAAAAA-------AGATTAGGTAATCCTGAGCCAAATTTTGTGTGGTAAAAAAAAATAGG   [152]
Mannia_fragrans_Switzerland              TTCAGGGAAACCTTGGATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAATTTTTGTATGCTAAAACAAAATAGG   [159]
Mannia_fragrans_India                    TTCAGGGAAACCTTGGATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAATTTTTGTATGCTAAAACAAAATAGG   [159]
Mannia_fragrans_Japan                    TTCAGGGAAACATTGGATGAAAAAAAA-GATAAAGATTAGGTAATCTTGAGCCAATTTTTGTATGCTAAAACAAAATAGG   [159]
Mannia_androgyna_Namibia                 TTCAGGGAAACCTTGGATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAATTTTTGTATGCTAAAACAAAATAGG   [159]
Mannia_androgyna_Madeira                 TTCAGGGAAACCTTGGATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAATTTTTGTATGCTAAAACAAAATAGG   [159]
Mannia_controversa_Austria               TTCAGGGAAACCTTGAATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAATTTTTGTGTGCTAAAACAAAATAGG   [159]
Mannia_spec_128_North_India              TTCAGGGAAACCTTGGATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAATTTTTGTGTGCTAAAACAAAATAGG   [159]
Mannia_californica_Austria               TTCAGGGAAACCTTGGATGAAAAAAAA-GATAAAGATTAGGTAATCCTGAGCCAATTTTTGTATGCTAAAACAAAATAGG   [159]
Mannia_californica_California            TTCAGGGAAACCTTTGATGAAAAAAAA-GAGAAAGATTAGGTAATCCTGAGCCAATTTTTGTATGTTAAAACAAAATAGG   [159]
Mannia_californica_Namibia               TTCARGGAAACCTTTGATGAAAAAAAA-GAGAAAGATTAGGCAATCCTGAGCCAATTTTTGTATGTTAAAACAAAATARG   [159]
Mannia_californica_France                TTCAGGGAAACCTTTGATGAAAAAAAA-GAGAAAGATTAGGCAATCCTGAGCCAATTTTTGTATGTTAAAACAAAATAGG   [159]
Mannia_californica_China                 TTCAGGGAAACCTTTGATGAAAAAAAA-GAGAAAGATTAGGCAATCCTGAGCCAATTTTTGTATGTTAAAACAAAATAGG   [159]
Mannia_californica_104_North_India       TTCAGGGAAACCTTTGATGAAAAAAAA-GAGAAAGATTAGGCAATCCTGAGCCAATTTTTGTATGTTAAAACAAAATAGG   [159]
Mannia_californica_105_North_India       TTCAGGGAAACCTTTGATGAAAAAAAA-GAGAAAGATTAGGCAATCCTGAGCCAATTTTTGTATGTTAAAACAAAATAGG   [159]
Mannia_californica_South_India           TTCAGGGAAACCTTTGATGAAAAAAAA-GAGAAAGATTAGGCAATCCTGAGCCAATTTTTGTATGTTAAAACAAAATAGG   [159]
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[                                                170       180       190       200       210       220       230       240]
[                                                 .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira             TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTTTTATAA-------AAAAAA---AATAAAAATG--AAACTAA-T   [224]
Targionia_hypophylla_California          TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TA-A--------AAAAAA---ATTAAAAATT--AAACTAA-T   [222]
Athalamia_hyalina                        TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TATAAA------AAAAAATG-ATTAAATTAA--AAATGAA-T   [228]
Plagiochasma_rupestre                    TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TATAAAGATGA-AAAGAATC-GTGAAAAATT--GTATTAA-T   [233]
Plagiochasma_wrightii                    TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TATAAAGATGA-AAAGAATT-GTGAAAAATT--GTATTAA-T   [232]
Plagiochasma_japonicum                   TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TATAAAGATGA-AAAGAATC-GTGAAAAATT--GTATTAA-T   [233]
Reboulia_hemisphaerica                   TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TCTCAAAATGA-AAAGAATC-ATGAAAAATT--GTACTAA-T   [233]
Cryptomitrium_tenerum                    TGCAGAGACTCAAAGAAAACTATCCTAACGTAATTTT-TATAAAAATGA-AAAAAATG-ATTAAAAATA--GTATTAA-T   [229]
Cryptomitrium_himalayense                TGCAGAGACTCAAAGAAAACTATCCTAACGTAATTTT-TATAAAAATGAGAAAAAATG-ATTAAAAATA--GTATTAA-T   [230]
Cryptomitrium_spec_Peru                  TGCAGAGACTCAAAGAAAACTATCCTAACGTAATTTT-TATCAAAATGAGAAAAAATG-ATTAAAAATA--GTATTAA-T   [230]
Asterella_grollei                        TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TATCAAAATGC-AAAAAATG-ATATTAATTT--CTATTAA-T   [232]
Asterella_californica                    TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATTAAAAAAAATG-ATGAAAAATG--GTACTAA-T   [233]
Asterella_wallichiana                    TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT----CAAAATGC-AAAAAATG-ATGAAAAATT--ATACTAA-T   [229]
Asterella_africana                       TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TATCAAAATGA-AAAAAATG-ATGAAAAATT--ATACTAA-T   [233]
Asterella_tenella                        TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TATCAAACTGA-AAAAAATG-ATGAAAAATT--GTACTAA-T   [233]
Asterella_lateralis                      TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATTAAAATGA-AAAAAATT-ATTAAAAATT--GCACTAA-T   [232]
Asterella_saccata                        TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTAT-TATCAAAATAA-AAAGAATG-ATTAAAAATT--CTACTAAAT   [234]
Asterella_gracilis                       TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAAATG-ATGAAAAATT--GTACTAA-T   [231]
Mannia_pilosa                            TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAAATG-ATGAAAAATT--GTACTAA-T   [230]
Mannia_triandra                          TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAAATG-ATGAAAAATT--GTACTAA-T   [225]
Mannia_fragrans_Switzerland              TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAATTGTACTAATAATTTAATACTAA-T   [235]
Mannia_fragrans_India                    TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAATTGTACTAATAATTTAATACTAA-T   [235]
Mannia_fragrans_Japan                    TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAATTGTACTAATAATTTAATACTAA-T   [235]
Mannia_androgyna_Namibia                 TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAAATG-ATAAAAAATT--GTACTAA-T   [232]
Mannia_androgyna_Madeira                 TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAAATG-ATAAAAAATT--GTACTAA-T   [232]
Mannia_controversa_Austria               TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAAATG-ATGAAAAATT--GTACTAA-T   [232]
Mannia_spec_128_North_India              TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAAATG-ATGAAAAATT--GTACTAA-T   [232]
Mannia_californica_Austria               TGCAGAGACTCAAAGAAAACTATCCTAACGAAATTCT-TATCAAAATG--AAAAAATG-ATGAAAAATT--GTACTAA-T   [232]
Mannia_californica_California            TGCAGAGACTCAAAGAAAACTATTCTAACGAAATTAT-TATCAAAATG--AAAAAATT-TTGAAAAATT--GTACTAA-T   [232]
Mannia_californica_Namibia               TGCAGAGACTCAAAGAAAACTATTCTAACGAAATTAT-TATCAAAATG--AAAAAATG-TTGAAAAATT--GTACTAA-G   [232]
Mannia_californica_France                TGCAGAGACTCAAAGAAAACTATTCTAACGAAATTAT-TATCAAAATG--AAAAAATT-TTTAAAAATT--GTACTAA-T   [232]
Mannia_californica_China                 TGCAGAGACTCAAAGAAAACTATTCTAACGAAATTAT-TATCAAAATG--AAAAAATG-TTCAAAAATT--GTACTAA-T   [232]
Mannia_californica_104_North_India       TGCAGAGACTCAAAGAAAACTATTCTAACGAAATTAT-TATCAAAATG--AAAAAATT-TTTAAAAATT--GTACTAA-T   [232]
Mannia_californica_105_North_India       TGCAGAGACTCAAAGAAAACTATTCTAACGAAATTAT-TATCAAAATG--AAAAAATT-TTTAAAAATT--GTACTAA-T   [232]
Mannia_californica_South_India           TGCAGAGACTCAAAGAAAACTATTCTAACGAAATTAT-TATCAAAATG--AAAAAATG-TTGAAAAATT--GTACTAA-G   [232]
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[                                                250       260       270       280       290       300       310       320]
[                                                .         .         .         .         .         .         .         .]
                                                *****************************************************
Targionia_hypophylla_Madeira            AGATTAAT----------------------------TACTCCA---------------------------TAAATGTATA   [249]
Targionia_hypophylla_California         AGATTAAT-----------------------------------------------------TACTC--A-TAAATGTATA   [246]
Athalamia_hyalina                       AGATTAAT-----------------------------------------------------TACTA--A-TAAATGTTTT   [252]
Plagiochasma_rupestre                   AATTTAATACTA-----TTA---------------CTACTAA---GTAGTAATAGATTAATTACTA--A-TAAATCT-AT   [286]
Plagiochasma_wrightii                   AATTTAATACTA-----TTA---------------CTACTAATTAGTAGTAATAGATTAATTACTA--A-TAAATCT-AT   [288]
Plagiochasma_japonicum                  AATTTAATACTA-----TTA---------------CTACTAATTAGTAGTAATAGATTAATTACTA--A-TAAATCT-AT   [289]
Reboulia_hemisphaerica                  AATTTCATACTAATAGATTA---------------TTACTAATTAGTAGTAATAGATTAATTACTA--A-TAAATCCTAG   [295]
Cryptomitrium_tenerum                   AAATTAAT-----------------------------------------------------TACTA--A-TAAATAGTAT   [253]
Cryptomitrium_himalayense               AAATTAAT-----------------------------------------------------TACTA--A-TAAATGG-AT   [253]
Cryptomitrium_spec_Peru                 AAATTAAT-----------------------------------------------------TACTA--A-TAAATGG-AT   [253]
Asterella_grollei                       AGATTAATACTAAT---TTAG-------------------------TACTA-----TTAATTATTA--G-TAAATGT-AT   [275]
Asterella_californica                   AAATTAATACTAATAGT--------------------------TAATACTAATATAATAATTACTA--G-TAAATGT-AT   [283]
Asterella_wallichiana                   AATATAATATTAATAGATTAGTAATA---------------ATTAGTACTAATAGATTAATTAGTA--G-TAAATAT-AT   [290]
Asterella_africana                      AATTTAATCTAAATAGATTAGTAGTATT------AGTAGTAATTAGTACTAATCAATTAATTACTA--G-TAAATAT-AT   [303]
Asterella_tenella                       AATCTAATATACATAGATTAGTAGTA---------------ATTCGTATTAATCGATTAATTACTA--G-TAAATAT-TT   [294]
Asterella_lateralis                     AATTTAATACTAATAGATTA--------------ATAGTAATT-AGTACTAATAGATTAATTACTA--G-TAAATAT-AT   [293]
Asterella_saccata                       AATTGAATACAAATAGATTA--------------GTAAGAATT-AGTACTAATAGATTAATTACTA--G-TAAATAT-AT   [295]
Asterella_gracilis                      AATTTAAT--------ATTA-------------------------------ATAGATTAACTAGTACAG-TAAATAT-AT   [270]
Mannia_pilosa                           AATTTAATACTAATAGATTAA-----------------------------------TTAA----TA--G-TAAATAT-AT   [267]
Mannia_triandra                         AATTTAATAATAAT---TTAATATTAATAGATTA-------------ACTAGTA----------TA--G-TAAATAT-AC   [275]
Mannia_fragrans_Switzerland             AGTTTAATACTAATAGTTTA--------------GTACTAATTTAGTACTAGTAGATTAATGACTA--G-TAAATAT-AT   [297]
Mannia_fragrans_India                   AGTTTAATACTAATAGTTTAATACTAATAGTTTAGTACTAATTTAGTACTAGTAGATTAATGACTA--G-TAAATAT-AT   [311]
Mannia_fragrans_Japan                   AGTTTAATACTAATAGTTTA--------------GTACTAATTTAGTACTAGTAGATTAATGACTA--G-TAAATAT-AT   [297]
Mannia_androgyna_Namibia                AATTTAATATTAATAGTTTA--------------GTACTAATTTAGTACTACTAGATTAATTACTA--G-TAAATAT-AT   [294]
Mannia_androgyna_Madeira                AATTTAATATTAATAGTTTA--------------GTACTAATTTAGTACTACTAGATTAATTACTA--G-TAAATAT-AT   [294]
Mannia_controversa_Austria              AATTTAATACTAATAGTTTA--------------GTACTAATTTAATATTACTAGATTAATTACTA--G-TAAATAT-AT   [294]
Mannia_spec_128_North_India             AATTTAATACTAATAGTTTA--------------GTACTAATTTAATATTACTAGATTAATTACTA--G-TAAATAT-AT   [294]
Mannia_californica_Austria              AAATTAATACTAATAGTTTA--------------GTACTAATTTAATACTACTAAATTAATTACTA--G-TAAATAT-AT   [294]
Mannia_californica_California           AATTTAATACTAAT--TTTA--------------GTACTAATTTAAGACTACTAGATTAATTACTA--G-TAAATAT-AT   [292]
Mannia_californica_Namibia              AATTTAATACTAAT--TTTA--------------GTACTAATTTAAGACTACTAGATTAATTACTA--G-TAAATAT-AT   [292]
Mannia_californica_France               AAATTAATACTAAT--TTTA--------------GTATTAATTTAAGACTACTAGATTAATTACTA--G-TAAATAT-AT   [292]
Mannia_californica_China                AATTTAATACTAAT--TTTA--------------GTACTAATTTAAGACTACTAGATTAATTACTA--G-TAAATAT-AT   [292]
Mannia_californica_104_North_India      AAATTAATACTAAT--TTTA--------------GTATTAATTTAAGACTACTAGATTAATTACTA--G-TAAATAT-AT   [292]
Mannia_californica_105_North_India      AAATTAATACTAAT--TTTA--------------GTATTAATTTAAGACTACTAGATTAATTACTA--G-TAAATAT-AT   [292]
Mannia_californica_South_India          AATTTAATACTAAT--TTTA--------------GTACTAATTTAAGACTACTAGATTAATTACTA--G-TAAATAT-AT   [292]
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[                                                330       340       350       360       370       380       390       400]
[                                                  .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira           AATTTATTTTT--TATTACTAAAAAAAAAATTTTA----------ATTATTAAATTAT------AAATAGACGAGGATAA   [311]
Targionia_hypophylla_California        AATTACTTTTT--TAGTATTAAATTATATTTAAAA----------ATAAATAAATTAT------AAATAGACGAGGATAA   [308]
Athalamia_hyalina                      CATTACTTAAA--ATTGTAATAAAATAATCTAAAA----------ACGATTAAACTAT------TAATAGACGAGGATAA   [314]
Plagiochasma_rupestre                  TAATTATTTAA--ATA-----------------------------------------------------GACGAGGATAA   [311]
Plagiochasma_wrightii                  TAATTATTTAA--ATA-----------------------------------------------------GACGAGGATAA   [313]
Plagiochasma_japonicum                 TAATTATTTAA--ATA-----------------------------------------------------GACGAGGATAA   [314]
Reboulia_hemisphaerica                 TCATTATTTAA--ATAGTAATAAAATTATTTAATA----------AC-----AACTAT------TAATAGACGAGGATAA   [352]
Cryptomitrium_tenerum                  TAATTTTTTAA--AGAGTAATAAAATAATTTAAAA----------ACTATTAAACTAT------TAATAGACGAGGATAA   [315]
Cryptomitrium_himalayense              TAATTTTTTAA--AGAGTAATAAAATAATTTAAAA----------ACTATTAAACTAT------TAATAGACGAGGATAA   [315]
Cryptomitrium_spec_Peru                TTATTATTTAA--AGAGTAATAAAATAATTTAAAA----------ACTATTAAACTAT------TAATAGACGAGGATAA   [315]
Asterella_grollei                      TAATTATTGAA--AGAGTATTAAAATCATTTAATA----------ATTATTAAACTAT------TCATAGACGAGGATAA   [337]
Asterella_californica                  TCATTATTTAA--ATAGTAATAAAATCATTTAATA----------ACTATTAAACTAT------GAATAGACGAGGATAA   [345]
Asterella_wallichiana                  TAATTATTTAA--ATAGTAATACAATCATTTAATG----------AC-----AACTAG------TAATAGACGAGGATCA   [347]
Asterella_africana                     TAATTATTTAAT-ATAGTAATAAAATCATTTAATG----------AC-----AACTAT------TAATAGACGAGGATCA   [361]
Asterella_tenella                      GAAAAATTTAA--ATAATAATAAAATCATTTAATG----------AC-----AACTAT------TAATAGGCGAGGATCA   [351]
Asterella_lateralis                    TAATTATTTAA--ATAATAATAAAATTATTTAATG----------AC-----AACTATTAATAGTAATAGACGAGGATAA   [356]
Asterella_saccata                      TAATTATTTATTAGTAATAATAAAATCATTTAATG----------AC-----AATTAT------TAATAGACGAGGATAA   [354]
Asterella_gracilis                     ATTTTATTTAA--ATAGTAATAAAATTATTGAATA----------AC-----AACTAT------AAATAGACGAGGATAA   [327]
Mannia_pilosa                          AATT-ATTTAA--ATAGTAATAAAATCATTTAATA----------AC-----AACTAT------TAATAGACGAGGATAA   [323]
Mannia_triandra                        TATTTATTTAA--ATAGTAATAAAATCATTGAATA----------AC-----AACTAT------AAATAGGCGAGGATAA   [332]
Mannia_fragrans_Switzerland            TAATTATTTAA--ATAGTAATAAAATCATTTAATA----------AT-----AACTAT------TAATAGACGAGGATAA   [354]
Mannia_fragrans_India                  TAATTATTTAA--ATAGTAATAAAATCATTTAATA----------AT-----AACTAT------TAATAGACGAGGATAA   [368]
Mannia_fragrans_Japan                  TAATTATTTAA--ATAGTAATAAAATCATTTAATA----------AT-----AACTAT------TAATAGACGAGGATAA   [354]
Mannia_androgyna_Namibia               TAATTATTTAA--ATAGTAATAAAATCATTTAATATCATTTAATAAT-----AACTAT-----ATAATAGACGAGGATAA   [362]
Mannia_androgyna_Madeira               TAATTATTTAA--ATAGTAATAAAATCATTTAATATCATTTAATAAT-----AACTAT-----ATAATAGACGAGGATAA   [362]
Mannia_controversa_Austria             TAATTATTTAA--ATAGTAATAAAATCATTTAATA----------AT-----AACTAT-----ATAATAGACGAGGATAA   [352]
Mannia_spec_128_North_India            TAATTATTTAA--ATAGTAATAAAATCATTTAATA----------AT-----AACTAT-----ATAATAGACGAGGATAA   [352]
Mannia_californica_Austria             TAATTATTTCA--ATAGTAATAAAATCATTTAATA----------AT-----AACTAT-----ATAATAGACGAGGATAA   [352]
Mannia_californica_California          TAATTATTTAA--ATAGTAATAAAATCATTTAATC----------AT-----AACTAT-----ATAATAGACGAGGATAA   [350]
Mannia_californica_Namibia             TAATTATTTAA--ATAATTATAAAATCATTTAATC----------AT-----AACTAT-----ATAATAGACGAGGATAA   [350]
Mannia_californica_France              TAATTATTTAA--ATAGTAATAAAATCATTTAATC----------AT-----AACTAT-----ATAATAGACGAGGATAA   [350]
Mannia_californica_China               TAATTATTTAA--ATAGTAATAAAATCATTTAATC----------AT-----AACTAT-----ATAATAGACGAGGATAA   [350]
Mannia_californica_104_North_India     TAATTATTTAA--ATAGTAATAAAATCATTTAATC----------AT-----AACTAT-----ATAATAGACGAGGATAA   [350]
Mannia_californica_105_North_India     TAATTATTTAA--ATAGTAATAAAATCATTTAATC----------AT-----AACTAT-----ATAATAGACGAGGATAA   [350]
Mannia_californica_South_India         TAATTATTTAA--ATAATTATAAAATCATTTAATC----------AT-----AACTAT-----ATAATAGACGAGGATAA   [350]
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[                                               410       420       430       440       450       460       470       480]
[                                                .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira            AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [388]
Targionia_hypophylla_California         AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [385]
Athalamia_hyalina                       AGATAGAGTCCGTTTTTACAAATGAATTTTAACAACAATGAAAA--TTGGCAGTAAAATGAAAATCCGTTGGCTTTAAAG   [392]
Plagiochasma_rupestre                   AGATAGAGTCCATTTTTACAAGTGAATTTTAACAGCAATGTAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [388]
Plagiochasma_wrightii                   AGATAGAGTCCATTTTTACAAGTTAATTTTAACAGCAATGTAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [390]
Plagiochasma_japonicum                  AGATAGAGTCCATTTTTACAAGTTAATTTTAACAGCAATGTAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [391]
Reboulia_hemisphaerica                  AGATAGAGTCCATTTTTACAAGTTAAATTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [429]
Cryptomitrium_tenerum                   AGATAGAGTCCGTTTTTACAAGTTAATTTGAGCAACAATGAAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [392]
Cryptomitrium_himalayense               AGATAGAGTCCGTTTTTACAAGTTAATTTGAGCAACAATGAAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [392]
Cryptomitrium_spec_Peru                 AGATAGAGTCCGTTTTTACAAGTTAAATTTAGCAACAATGAAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [392]
Asterella_grollei                       AGATAGAGTCCGTTTTTACAAGTTA-TTTTAACAACAATGCAAA--TTG-CAGTAAAATGAAAATCCGTTGGCTTTAAAG   [413]
Asterella_californica                   AGATAGAGTCCATTTT-ACAAGTTAATTTTAACTACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [421]
Asterella_wallichiana                   AGATAGAGTCCATTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [424]
Asterella_africana                      AGATAGAGTCCATTTTTACAAGTTAATTTTAACAACAATGCAAATTTTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [440]
Asterella_tenella                       AGATAGAGTCCATTTTTACAAGTTAAATTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [428]
Asterella_lateralis                     AGATAGAGTCCATTTTTACAAGTTAATTTTAATAACAATGCAAA--T-G-TAATAAAATGAAAATCCGTTGGCTTTAAAG   [432]
Asterella_saccata                       AGATAGAGTCCATTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAACAAAATGAAAATCCGTTGGCTTTAAAG   [431]
Asterella_gracilis                      AGATAGAGTCCATTTTTACAAGTTAATTTGAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [404]
Mannia_pilosa                           AGATAGAGTCCATTTTTACAAGTTAATTTTAACAACAATACAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [400]
Mannia_triandra                         AGATAGAGTCCATTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [409]
Mannia_fragrans_Switzerland             AGATAGAGTCCATTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [431]
Mannia_fragrans_India                   AGATAGAGTCCATTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [445]
Mannia_fragrans_Japan                   AGATAGAGTCCATTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [431]
Mannia_androgyna_Namibia                AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [439]
Mannia_androgyna_Madeira                AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [439]
Mannia_controversa_Austria              AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [429]
Mannia_spec_128_North_India             AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [429]
Mannia_californica_Austria              AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [429]
Mannia_californica_California           AGATAGAGTCCGTTTTTACAAGTTAAATTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [427]
Mannia_californica_Namibia              AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [427]
Mannia_californica_France               AGATAGAGTCCGTTTTTACAAGTTAAATTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [427]
Mannia_californica_China                AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [427]
Mannia_californica_104_North_India      AGATAGAGTCCGTTTTTACAAGTTAAATTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [427]
Mannia_californica_105_North_India      AGATAGAGTCCGTTTTTACAAGTTAAATTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [427]
Mannia_californica_South_India          AGATAGAGTCCGTTTTTACAAGTTAATTTTAACAACAATGCAAA--TTG-TAGTAAAATGAAAATCCGTTGGCTTTAAAG   [427]
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[                                          490       500       510       520       530       540       550       560]
[                                            .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira          ACCGTGAGGGTTCAAGTCCCTCTACCCCCA-TTCAGTTATATTTTTATTTTAACATAAAAA-------GTTGACACAATT   [460]
Targionia_hypophylla_California       ACCGTGAGGGTTCAAGTCCCTCTACCCCCAG-TCAGTTCTATTTTTATTTTAACATAAAAAGAAAAAAGTTGACACATTT   [464]
Athalamia_hyalina                     ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTAAGTTTTTATAA-AATTTTAATAAACAA-------GTTGACACATTT   [464]
Plagiochasma_rupestre                 ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGACCA-AAATTGAATAACCACAAAA---GTTGACACATTT   [464]
Plagiochasma_wrightii                 ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGACCA-AAATAAAA-AAAAAA-------GTTGACACATTT   [461]
Plagiochasma_japonicum                ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTAACCA-AAATGGAATAAAAAAAA-----GTTGACAGATTT   [465]
Reboulia_hemisphaerica                ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATAA-AAATTGACTAAAAAAA------GTTGACACATTT   [502]
Cryptomitrium_tenerum                 ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTTAGAC-AAATTGAATAAAAAA-------GTAGATAAACTT   [464]
Cryptomitrium_himalayense             ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTTAGAC-AAATTGAATAAAAAA-------GTTGACAAACTT   [464]
Cryptomitrium_spec_Peru               ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTTAGAC-AAATTTAATAAAAAA-------GTTGACACACTT   [464]
Asterella_grollei                     ACCGTGAGGGTTCAAGTCCCTCTACCCCCAATTCAATTTGTATAT-AAATTTCATAAAAAA-------ATTGACA---TA   [482]
Asterella_californica                 ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTAAGAA-AAATTGAATAAAAAA-------GTTGACACATTT   [493]
Asterella_wallichiana                 ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGAACA-AAATTGAATAAAAAAA------GTTGACACATTT   [497]
Asterella_africana                    ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTTATAA-AAATTGAATAAAACAAA-----GTTGACACATTT   [514]
Asterella_tenella                     ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTTATAA-AAATTGAATAAA----------GTTGACACATTT   [497]
Asterella_lateralis                   ACCGTGAGGGTTCAAGTCCCTCTACCCCCAATTCAATTTTGATCA-AAATTGAATAAAAAA-------GTTGACACATTT   [504]
Asterella_saccata                     ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTTATAA-AAATTGAATAAAAAA-------ATTGACACTATT   [503]
Asterella_gracilis                    ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTGGATTTTGAACC-AAGTTGAATAAAAAA-------GTTGACACTTTT   [476]
Mannia_pilosa                         ACCGTGAGGGTTCAATTCCCTCTACCCCCAGTTCAATTTTGAGCA-AAGTTGAATAAAAAAA------GTTGACAAGTTT   [473]
Mannia_triandra                       ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGAACC-AAGTTGAATAAAAAA-------GTTGACACTTTT   [481]
Mannia_fragrans_Switzerland           ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATCA-AAATTGAATAAAAAAA------GTTGACACATTT   [504]
Mannia_fragrans_India                 ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATCA-AAATTGAATAAAGAAAA-----GTTGACACATTT   [519]
Mannia_fragrans_Japan                 ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATCA-AAATTGAATAAAAAAA------GTTGACACATTT   [504]
Mannia_androgyna_Namibia              ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATCA-AAATTGAATAAAAAAA------GTTGACACATTT   [512]
Mannia_androgyna_Madeira              ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATCA-AAATTGAATAAAAGAAA-----GTTGACACATTT   [513]
Mannia_controversa_Austria            ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTCATCA-AAATTGAA--------------------------   [482]
Mannia_spec_128_North_India           ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTCATCA-AAATTGAATAAAGAAAA-----GTTGACACATTT   [503]
Mannia_californica_Austria            ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATCA-AAATTGAATAAAAAAA------GTTGACACATTT   [502]
Mannia_californica_California         ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGCTCAATTTTGATGA-AAATTGAATAAGAAA-------CTTGACACTTTT   [499]
Mannia_californica_Namibia            ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATTA-AAATTGAATAAAAAA-------GTTGACACTTTT   [499]
Mannia_californica_France             ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGCTCAATTTTGATTA-AAATTGAATAAAAAA-------GTTGACACTTTT   [499]
Mannia_californica_China              ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATTA-AAATTGAATAAAAAA-------GTTGACACTTTT   [499]
Mannia_californica_104_North_India    ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGCTCAATTTTGATTA-AAATTGAATAARAAA-------GTTGACACTTTT   [499]
Mannia_californica_105_North_India    ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGCTCAATTTTGATTA-AAATTGAATAARAAA-------GTTGACACTTTT   [499]
Mannia_californica_South_India        ACCGTGAGGGTTCAAGTCCCTCTACCCCCAGTTCAATTTTGATTA-AAATTGAATAARAAA-------GTTGACACTTTT   [499]
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[                                              570       580       590       600       610       620       630       640]
[                                              .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira          TTTCTT-TTTATGT--------------TAAAATAAAAA-TAAGAAAAA-A-A--------ATtGCCGGGATAGCTCAGT   [514]
Targionia_hypophylla_California       TTTCTT-TTTATGT--------------TAAAATAAAAA-TAAGAAAAA-A-A--------ATTGCCGGGATAGCTCAGT   [518]
Athalamia_hyalina                     TTTMTT-TTTATGTTTTTCTTTTTATGCTATAATAATAA-AAAGAAAAACA-A--------ATtGCCGGGATAGCTCAGT   [533]
Plagiochasma_rupestre                 TTTATT-TTTATGT-------------CTAAAATAATCAAAAAGTAAAACATAAGTAAAAAAT-GCCGGGATAGCTCAGT   [529]
Plagiochasma_wrightii                 TTTATT-TTTATGT--------------TAAAATAATAA-AAAGTAAA-CATA-GTAAAA-AT-GCCGGGATAGCTCAGT   [521]
Plagiochasma_japonicum                ATTATT-TTTATGT--------------TAAAATAAACA-AAAGTAAA-GATA-GTAAAA-AT-GCCGGGATAGCTCAGT   [525]
Reboulia_hemisphaerica                TTTATT--TTATGT--------------TAAAATAATCA-GAAGTAAAA-ATA-CTAAAA-AT-GCCGGGATAGCTCAGT   [561]
Cryptomitrium_tenerum                 TTTTTTTATTATGT--------------TAAAATAAAAA--AAGTAAAA------------AT-GCCGGAATAGCTCAGT   [515]
Cryptomitrium_himalayense             TTTTTTTATTATGT--------------TAAAATAAAAA-AAAGTAAAA------------AT-GCCGGAATAGCTCAGT   [516]
Cryptomitrium_spec_Peru               TTTTTT-ATTATAT--------------TAAAATAAAAA-AAAGTAAAA------------AT-GCCGGAATAGCTCAGT   [515]
Asterella_grollei                     TTTATT-ATTATTTTTTT-TTTTT-------------------GTAATA-ATAATTAAAA-AT-GCCGGAATACCTCAGT   [538]
Asterella_californica                 TTTATT-TTTATGT--------------TAAAATAATCA-AAAGTAAAA------------AT-GCCGGGATAGCTCAGT   [544]
Asterella_wallichiana                 TTTCTT-TTTATGT--------------TAAAATAATCA-AAAGTAAAA-ATA-GTAAAA-AT-GCCGGGATAGCTCAGT   [557]
Asterella_africana                    TTACTT-TTTATAT--------------TAAAATAATCATAAAGTAAAA------------AT-GCCGGGATAGCTCAGT   [566]
Asterella_tenella                     TTTCTT-TTTATGT--------------TAAAATAATCATAAAGTAAAA-ATA-GTAAAA-CT-GCCGGGATAGCTCAGT   [558]
Asterella_lateralis                   TTGATT-TTGATGT--------------TAAAATAATAA-AAAATAAAA-ATA-GTAAAA-AT-GCCGGGATAGCTCAGT   [564]
Asterella_saccata                     TTTATT-TTTATGT--------------TAAAATAATAA-AAAATAAAA-ATA-GTAATA-AT-GCCGGGATAGCTCAGT   [563]
Asterella_gracilis                    TTTATT-TTTATGT--------------TAAAATAACGA-AAAGTCAAA------------AT-GCCGGGATAGCTCAGT   [527]
Mannia_pilosa                         ATTATT-TTTATGT--------------TAAAATAATGA-AAAGTATAA------------AT-GCCGGGATAGCTCAGT   [524]
Mannia_triandra                       TTTATT-TTTATGT--------------TAAAATCATGA-AAAGTAAAA------------AT-GCCGGGATAGCTCAGT   [532]
Mannia_fragrans_Switzerland           TTGATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [555]
Mannia_fragrans_India                 TTGATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [570]
Mannia_fragrans_Japan                 TTGATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [555]
Mannia_androgyna_Namibia              TTTATT-TTTATGT--------------TAAAATGATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [563]
Mannia_androgyna_Madeira              TTTATT-TTTATGT--------------TAAAATGATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [564]
Mannia_controversa_Austria            -------------------------------------------TAAAAA------------AT-GCCGGGATAGCTCAGT   [506]
Mannia_spec_128_North_India           TTTATT-TTGATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [554]
Mannia_californica_Austria            TTTATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [553]
Mannia_californica_California         TTTATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [550]
Mannia_californica_Namibia            TTTATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [550]
Mannia_californica_France             TTTATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [550]
Mannia_californica_China              TTTATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [550]
Mannia_californica_104_North_India    TTTATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [550]
Mannia_californica_105_North_India    TTTATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [550]
Mannia_californica_South_India        TTTATT-TTTATGT--------------TAAAATAATCA-AAATAAAAA------------AT-GCCGGGATAGCTCAGT   [550]
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[                                                650       660       670       680       690       700       710       720]
[                                                .         .         .         .         .         .         .         .]
                                                     ******************************         *****************
Targionia_hypophylla_Madeira            TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGT????????1?10101???????????AACAAGGATTCCCCTA   [594]
Targionia_hypophylla_California         TGGTAGAGCAGARGAMTGAAAATCCTCGCTGGTTACCCAAGTTT??1?10101????AAGAACTAACAAGGATTCCCCTA   [598]
Athalamia_hyalina                       TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTTAAAT???0110101???????AACTAACGAGGATTCCCCTA   [613]
Plagiochasma_rupestre                   TGGTAGA?????????????????????????????????????010111?????????????????AAGGATTCCCCTA   [609]
Plagiochasma_wrightii                   TGGTA???????????????????????????????????????010111?????????????????AAGGATTCCCCTA   [601]
Plagiochasma_japonicum                  TGGTAGAGCAGACGACTGAAAATCCTCGTGTCACCAGTTCA???010111????????????????CAAGGATTCCCCTA   [605]
Reboulia_hemisphaerica                  TGGTAGAGCAGAGGACTGA?????????????????????????010110111?????????CTAACAAGGATTCCCCTA   [641]
Cryptomitrium_tenerum                   TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTTCAAAT010110101???????AACTAACAAGGATTCCCTTA   [595]
Cryptomitrium_himalayense               TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTTCAAAT000110101???????AACTAACAAGGATTCCCTTA   [596]
Cryptomitrium_spec_Peru                 TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTAC????000110101????AGAAACTAACAAGGATTCCCTTA   [595]
Asterella_grollei                       TGGTAAAGCAAAGGACTGAAAATCCTCATGTCACCAGTTC????010110101???????????AACAAGGATTCCCCTA   [618]
Asterella_californica                   TGGTAGAGCAGACGACTGAAAATCCTCGTGTCACCAGTTCAAAT000110101?????GAAACTAACAAGGATTCCCCTA   [624]
Asterella_wallichiana                   TGGTAGAGCAGACGACTGAAAATCCTCGTGTCACCAGTCAAA??010110111????AAGAACTAACAAGGATTCCCCTA   [637]
Asterella_africana                      TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGT??????010110111????????????ACAAGGATTCCCCTA   [646]
Asterella_tenella                       TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTACAAAT010110111??????GAACTAACAAGGATTCCCCTA   [638]
Asterella_lateralis                     TGGTAGAGCAGACGACTGACCATCCTCGTGTCACCAGTACAAA?01011011??????AGAACTAACAAGGATTCCCCTA   [644]
Asterella_saccata                       TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTAAAAT?010110111TAGAAAGAACTAACAAGGATTCCCTTA   [643]
Asterella_gracilis                      TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTTAAA??110110111??????GAACTAACAAGGATTCCCTTA   [607]
Mannia_pilosa                           TGGTAGAGCAGAGGACTGAAAATCCACGTGTCACCAGT??????110110111???AAGAAACTAACAAGGATTCCCTTA   [604]
Mannia_triandra                         TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTTCA???110110111?????????????CAAGGATTCCCTTA   [612]
Mannia_fragrans_Switzerland             TGGTAGAGCAGA????????????????????????????????110000111????AGAAACTAACAAGGATTCCCTTA   [635]
Mannia_fragrans_India                   TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTTCAATT110000111?????AGAACTAACAAGGATTCCCTTA   [650]
Mannia_fragrans_Japan                   TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTC?????110000111???????AACTAACAAGGATTCCCTTA   [635]
Mannia_androgyna_Namibia                TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTACAAAT110110010????AAGAACTAACAAGGATTCCCTTA   [643]
Mannia_androgyna_Madeira                TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTCA????110110010???????????????AGGATTCCCTTA   [644]
Mannia_controversa_Austria              TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTTCAAAT110110110???GAGACTAGACAAGAGATTCCCCTA   [586]
Mannia_spec_128_North_India             TGGTAGAGCAGACGACTGAAAATCCTCGTGTCACCAGT??????110110110??????????????????ATTCCCCTA   [634]
Mannia_californica_Austria              TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTTCAAAT110110110???????AACTAACAAGGATTCCCTTA   [633]
Mannia_californica_California           TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGT??????110110110????AGAAACTAACAAGGATTCCCTTA   [630]
Mannia_californica_Namibia              TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTC?????110110110??????????TAACAAGGATTCCCTTA   [630]
Mannia_californica_France               TGGTAGAGC???????????????????????????????????110110110????AGAAACTAACAAGGATTCCCTTA   [630]
Mannia_californica_China                TGGTAGAGCAGACGACTGAAAATCCTCGTGTCACCAGTC?????110110110????AAGAACTAACAAGGATTCCCTTA   [630]
Mannia_californica_104_North_India      TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTCA????110110110????AAGAGCTAACAAGGATTCCCTTA   [630]
Mannia_californica_105_North_India      TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGT??????110110110???AAGAAACTAACAAGGATTCCCTTA   [630]
Mannia_californica_South_India          TGGTAGAGCAGAGGACTGAAAATCCTCGTGTCACCAGTCA????110110110???????AACTAACAAGGATTCCCTTA   [630]
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[                                             730       740       750       760       770       780       790       800]
[                                              .         .         .         .         .         .         .         .]
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Targionia_hypophylla_Madeira          GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCGCGT-GGT--CATTTAGGCGGCGCGAGTTGTAGTCTGGAG   [671]
Targionia_hypophylla_California       GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGC-TGT--CATTTAGGCGGCGCGAGTTGTAGTCTGGAG   [675]
Athalamia_hyalina                     GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCCCGT-CGTAGTCGATTTGCGGCGGGAGTTGTAGTCTGGAG   [692]
Plagiochasma_rupestre                 GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT-----TTCGGCGACGCGAGTTGTAGTCTGGAG   [683]
Plagiochasma_wrightii                 GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT-----TTCGGCGGCGCGAGTTGTAGTCTGGAG   [675]
Plagiochasma_japonicum                GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT-----TTCGGCGGCGCGAGTTGTAGTCTGGAG   [679]
Reboulia_hemisphaerica                GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT-----TTCGGCGACGCGAGTTGTAGTCTGGAG   [715]
Cryptomitrium_tenerum                 GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [668]
Cryptomitrium_himalayense             GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGTgCGT------TCTGCGGCGCGAGTTGTAGTCTGGAG   [670]
Cryptomitrium_spec_Peru               GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT------TCTGCGGCGCGAGTTGTAGTCTGGAG   [668]
Asterella_grollei                     GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT------TTTGCGGCGCGAGTTGTAGTCTGGAG   [691]
Asterella_californica                 GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGTGT-CGT-----TTCGGCGGCACGAGTTGTAGTCTGGAG   [698]
Asterella_wallichiana                 GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGC-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [710]
Asterella_africana                    GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCAC-CGT------TTCGCGGCGCGAGTTGTAGTCTGGAG   [719]
Asterella_tenella                     GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGC-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [711]
Asterella_lateralis                   GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGC-CGT------TTCGCGGCGCGAGTTGTAGTCTGGAG   [717]
Asterella_saccata                     GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGC------TTCGCGGCGCGAGTTGTAGTCTGGAG   [716]
Asterella_gracilis                    GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT------TCTGCGGCGCGAGTTGTAGTCTGGAG   [680]
Mannia_pilosa                         GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGTG---TTTCCGCGGCGCGAGTTGTAGTCTGGAG   [680]
Mannia_triandra                       GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT------TTTGCGGCGCGAGTTGTAGTCTGGAG   [685]
Mannia_fragrans_Switzerland           GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT-----TTCCGCGGCGCGAGTTGTAGTCTGGAG   [709]
Mannia_fragrans_India                 GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT-----TTCCGCGGCGCgAGTGGTATTCTGGAA   [724]
Mannia_fragrans_Japan                 GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT------TCKGCGGCGCGAGTTGTAGTCTGGAG   [708]
Mannia_androgyna_Namibia              GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGC-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [716]
Mannia_androgyna_Madeira              GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGC-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [717]
Mannia_controversa_Austria            GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-GCG---TTTTCCGCGACGCGAGTTGTAGTCTGGAG   [662]
Mannia_spec_128_North_India           GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGTCGTC---TTTCGTGCGACGCGAGTTGTAGTCTGGAG   [711]
Mannia_californica_Austria            GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAAAATCGCGT-CGT----TTCCGGCGGCGCGAGTTGTAGTCTGGAG   [708]
Mannia_californica_California         GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCGCGT-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [703]
Mannia_californica_Namibia            GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCGCGTgCGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [704]
Mannia_californica_France             GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCGCGT-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [703]
Mannia_californica_China              GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCGCGT-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [703]
Mannia_californica_104_North_India    GTAGCAGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCGCGT-CGT------TCCGCGACGCGAGTTGTAGTCTGGAG   [703]
Mannia_californica_105_North_India    GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCGCGT-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [703]
Mannia_californica_South_India        GTAGCGGCGAGCGAACCGGGAGAAGCCCAGCTTGAGAATCGCGT-CGT------TCCGCGGCGCGAGTTGTAGTCTGGAG   [703]
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[                                              810       820       830       840       850       860       870       880]
[                                                .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira          AAGTGTCCTCTGCGGCGGACCTGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCAGGAC   [751]
Targionia_hypophylla_California       AAGTGTCCTCTGCGGCGGACCTGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCAGGAC   [755]
Athalamia_hyalina                     AAGTGTCCTCTGCAGCGGACCTGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAG   [772]
Plagiochasma_rupestre                 AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCAGGAC   [763]
Plagiochasma_wrightii                 AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [755]
Plagiochasma_japonicum                AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [759]
Reboulia_hemisphaerica                AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [795]
Cryptomitrium_tenerum                 AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTTCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [748]
Cryptomitrium_himalayense             AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTTCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [750]
Cryptomitrium_spec_Peru               AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTTCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [748]
Asterella_grollei                     AAGTGTCCTCTGCGGCGGACCCGGCTCAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [771]
Asterella_californica                 AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [778]
Asterella_wallichiana                 AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [790]
Asterella_africana                    AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [799]
Asterella_tenella                     AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [791]
Asterella_lateralis                   AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [797]
Asterella_saccata                     AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTTCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [796]
Asterella_gracilis                    AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAaGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [760]
Mannia_pilosa                         AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [760]
Mannia_triandra                       AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [765]
Mannia_fragrans_Switzerland           AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [789]
Mannia_fragrans_India                 AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [804]
Mannia_fragrans_Japan                 AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [788]
Mannia_androgyna_Namibia              AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [796]
Mannia_androgyna_Madeira              AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [797]
Mannia_controversa_Austria            AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [742]
Mannia_spec_128_North_India           AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [791]
Mannia_californica_Austria            AAGTGTCCTCTGCGGCGGACCCGGCTTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [788]
Mannia_californica_California         AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [783]
Mannia_californica_Namibia            AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [784]
Mannia_californica_France             AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [783]
Mannia_californica_China              AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [783]
Mannia_californica_104_North_India    AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [783]
Mannia_californica_105_North_India    AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [783]
Mannia_californica_South_India        AAGTGTCCTCTGCGGCGGACCCGGCCTAAGTCCCCTGGAAAGGGGCGTCAGAGAGGGTGAGAACCCCGTCGGGCCGGGAC   [783]
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[                                              890       900       910       920       930       940       950       960]
[                                                .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira            CCTGCCGCTCCACGAGGCACTGTCAACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [831]
Targionia_hypophylla_California         CCTGCCGCTCCACGAGGCACTGTCAACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [835]
Athalamia_hyalina                       CCTGCTGCTCCACGAGGCACTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [852]
Plagiochasma_rupestre                   CCTGCCGCTCCACGAGGCGCTGTCGATGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [843]
Plagiochasma_wrightii                   CCTGCCGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [835]
Plagiochasma_japonicum                  CCTGCCGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [839]
Reboulia_hemisphaerica                  CCTGCCGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [875]
Cryptomitrium_tenerum                   CCTGCTGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGAGGGAGGTAAATTCCTTCCAAG   [828]
Cryptomitrium_himalayense               CCTGCTGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGAGGGAGGTAAATTCCTTCCAAG   [830]
Cryptomitrium_spec_Peru                 CCTGCTGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGAGGGAGGTAAATTCCTTCCAAG   [828]
Asterella_grollei                       CCTGCTGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [851]
Asterella_californica                   CCTGCTGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [858]
Asterella_wallichiana                   CCTGCCGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [870]
Asterella_africana                      CCTGCCGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [879]
Asterella_tenella                       CCTGCCGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [871]
Asterella_lateralis                     CCTGCCGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [877]
Asterella_saccata                       CCTGCCGCTCCACGAGGCGCTGTCGACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [876]
Asterella_gracilis                      CCTGCTGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [840]
Mannia_pilosa                           CCTGCTGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [840]
Mannia_triandra                         CCTGCTGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [845]
Mannia_fragrans_Switzerland             CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [869]
Mannia_fragrans_India                   CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [884]
Mannia_fragrans_Japan                   CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [868]
Mannia_androgyna_Namibia                CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [876]
Mannia_androgyna_Madeira                CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [877]
Mannia_controversa_Austria              CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [822]
Mannia_spec_128_North_India             CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [871]
Mannia_californica_Austria              CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGCGGGAGGTAAATTCCTTCCAAG   [868]
Mannia_californica_California           CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [863]
Mannia_californica_Namibia              CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [864]
Mannia_californica_France               CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [863]
Mannia_californica_China                CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [863]
Mannia_californica_104_North_India      CCTGCCGCTCCACGAGGCGCCGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [863]
Mannia_californica_105_North_India      CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [863]
Mannia_californica_South_India          CCTGCCGCTCCACGAGGCGCTGTCTACGAGTCGGGCTGTTTGGGAATGCAGCCCTAAGTGGGAGGTAAATTCCTTCCAAG   [863]
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[                                                970       980       990       1000      1010      1020      1030      1040]
[                                                .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira            GCTAAATACTGGCGGGAGACCGATAGCAAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAGA   [911]
Targionia_hypophylla_California         GCTAAATACTGGCGGGAGACCGATAGCAAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAGA   [915]
Athalamia_hyalina                       GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [932]
Plagiochasma_rupestre                   GCTAAATACAGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [923]
Plagiochasma_wrightii                   GCTAAATACAGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [915]
Plagiochasma_japonicum                  GCTAAATACAGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [919]
Reboulia_hemisphaerica                  GCTAAATACAGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [955]
Cryptomitrium_tenerum                   GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [908]
Cryptomitrium_himalayense               GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [910]
Cryptomitrium_spec_Peru                 GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [908]
Asterella_grollei                       GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [931]
Asterella_californica                   GCTAAATACCGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [938]
Asterella_wallichiana                   GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [950]
Asterella_africana                      GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [959]
Asterella_tenella                       GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [951]
Asterella_lateralis                     GCTAAATACGGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [957]
Asterella_saccata                       GCTAAATACAGGCGGGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [956]
Asterella_gracilis                      GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [920]
Mannia_pilosa                           GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTCAAAAA   [920]
Mannia_triandra                         GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [925]
Mannia_fragrans_Switzerland             GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [949]
Mannia_fragrans_India                   GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [964]
Mannia_fragrans_Japan                   GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [948]
Mannia_androgyna_Namibia                GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [956]
Mannia_androgyna_Madeira                GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [957]
Mannia_controversa_Austria              GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [902]
Mannia_spec_128_North_India             GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [951]
Mannia_californica_Austria              GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [948]
Mannia_californica_California           GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [943]
Mannia_californica_Namibia              GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [944]
Mannia_californica_France               GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [943]
Mannia_californica_China                GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [943]
Mannia_californica_104_North_India      GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [943]
Mannia_californica_105_North_India      GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [943]
Mannia_californica_South_India          GCTAAATACAGGCGAGAGACCGATAGCGAACAAGTACCGCGAGGGAAAGATGAAAAGGACTTTGAAAAGAGAGTTAAAAA   [943]
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[                                             1050      1060      1070      1080      1090      1100      1110      1120]
[                                             .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira          GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTGGTGTGCGCCCCGGTCGGATGCGGAACGGCGTA-AGCTGGTC   [990]
Targionia_hypophylla_California       GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTGGTGTGCGCCCCGGTCGGATGCGGAACGGCGTA-AGCTGGTC   [994]
Athalamia_hyalina                     GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTTCAGCTGGTC   [1012]
Plagiochasma_rupestre                 GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1002]
Plagiochasma_wrightii                 GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [994]
Plagiochasma_japonicum                GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [998]
Reboulia_hemisphaerica                GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGAG-AGCTGGTC   [1034]
Cryptomitrium_tenerum                 GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [987]
Cryptomitrium_himalayense             GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [989]
Cryptomitrium_spec_Peru               GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [987]
Asterella_grollei                     GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGGCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1010]
Asterella_californica                 GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1017]
Asterella_wallichiana                 GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1029]
Asterella_africana                    GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1038]
Asterella_tenella                     GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1030]
Asterella_lateralis                   GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1036]
Asterella_saccata                     GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1035]
Asterella_gracilis                    GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [999]
Mannia_pilosa                         GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCA-AGCTGGTC   [999]
Mannia_triandra                       GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1004]
Mannia_fragrans_Switzerland           GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1028]
Mannia_fragrans_India                 GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1043]
Mannia_fragrans_Japan                 GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1027]
Mannia_androgyna_Namibia              GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1035]
Mannia_androgyna_Madeira              GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1036]
Mannia_controversa_Austria            GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [981]
Mannia_spec_128_North_India           GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGCG-AGCTGGTC   [1030]
Mannia_californica_Austria            GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGCCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1027]
Mannia_californica_California         GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGGCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1022]
Mannia_californica_Namibia            GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGGCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1023]
Mannia_californica_France             GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGGCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1022]
Mannia_californica_China              GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGGCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1022]
Mannia_californica_104_North_India    GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGGCCCGGTCGGATGCGGGACGGCGTG-AGCCGGTC   [1022]
Mannia_californica_105_North_India    GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGGCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1022]
Mannia_californica_South_India        GTGCTTGAAATTGCTGGGAGGGAAGCGAATGGAGGCCTCGTGTGCGGCCCGGTCGGATGCGGAACGGCGTG-AGCTGGTC   [1022]
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[                                                          1130      1140      1150      1160      1170      1180      1190      1200]
[                                                          .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira          CGCCGCTCGACGCGGGGTGCTGGTCAGCGTGGGCTTCT----TTGG-CGGGATAAACG---TTGGCGCGTGCAAGCCTTA   [1062]
Targionia_hypophylla_California       CGCCGCTCGACGCGGGGTGCTGGTCAGCGTGGGCTTCT----TTGG-CGGGATAAACG---TTGGCGC-TGCAAGCTTTA   [1065]
Athalamia_hyalina                     CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTTTTGTTTCCGG-CGGGATAAAAG---TCGGTCTTT----------   [1078]
Plagiochasma_rupestre                 CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTCCT----CCGG-CGGGACAAAAG---TCAGCCTTT----------   [1064]
Plagiochasma_wrightii                 CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTCCT----CCGG-CGGGACAAAAG---TCAGCCTTC----------   [1056]
Plagiochasma_japonicum                CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTCCT----CCGG-CGGGACAAAAG---TCAGCCTTT----------   [1060]
Reboulia_hemisphaerica                CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTTCC----CCGG-CGGGACAAAAG---TCGGCCTTT----------   [1096]
Cryptomitrium_tenerum                 CGCCGCTCGACGCGGGGTGCTGGTCGGCGTGGGCTTCT----TGGG-CGGGACAAAAG---TCTGCCTTC----------   [1049]
Cryptomitrium_himalayense             CGCCGCTCGACGCGGGGTGCTGGTCGGCGTGGGCTTCT----TGGG-CGGGACAAAAG---TCTGCCTTC----------   [1051]
Cryptomitrium_spec_Peru               CGCCGCTCGACGCGGGGTGCTGGTCGGCGTGGGCTTCT----TGGG-CGGGACAAAAG---TCAGCCTTC----------   [1049]
Asterella_grollei                     CGCCGCTCGACGCGGGTTGCTGGTCGGCGTGGGCTTCT----TCGG-CGGGACAAAAG---TCCGTCTTC----------   [1072]
Asterella_californica                 CGCCGCTCGACGCGGGGTGCTGGTCGGCGTGGGCTTTT----CCGG-CGGGACAAAAG---TCGGCCTTC----------   [1079]
Asterella_wallichiana                 CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTTCC----CCGG-CGGGACAAAAG---TCGGCCTTC----------   [1091]
Asterella_africana                    CGCCGCTCGACGCGGGGTGCTGGTCGGCGTGGGCTTCC----CCGG-CGGGACAAAAG---TCGGCCTTC----------   [1100]
Asterella_tenella                     CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTTCC----CCGG-CGGGACAAAAG---TCGGTCTTC----------   [1092]
Asterella_lateralis                   CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTTCC----TCGG-CGGGACAAAAG---TGTAGCTT-----------   [1097]
Asterella_saccata                     CGCCGCTCGACGCGGGGCGCTGGTCGGCGTGGGCTTCT----TCGG-CGGGACAAAAG---TCGGCCTTT----------   [1097]
Asterella_gracilis                    CGCCGCTCGACGCGGGGTGCTGGTCGACGTGGGCTCCT----CCGG-CGGGACAAAGG---TCGGCCATTCAA-------   [1064]
Mannia_pilosa                         CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCT----CCGGGCGGGACAAAGGTCGTCGGCCTTC----------   [1065]
Mannia_triandra                       CGCCGCTCGACGCGGGGTGCTGGTCGACGTGGGCTCCT----CCGG-CGGGACAAAGG---TCGGCCTTC----------   [1066]
Mannia_fragrans_Switzerland           CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCT----CGGG-CGGGACAAAAG---TCGGCCTTC----------   [1090]
Mannia_fragrans_India                 CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCT----CGGG-CGGGACAAAAG---TCGGCCTTC----------   [1105]
Mannia_fragrans_Japan                 CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCT----TCGG-CGGGACAAAAG---TCGGCCTTC----------   [1089]
Mannia_androgyna_Namibia              CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCT----TCGG-CGGGACAAAAG---TCAGCCATC----------   [1097]
Mannia_androgyna_Madeira              CGCCGCTCGACGCGGGGCGCTGGTCAACGTGGGCTCCT----TCGG-CGGGACAAAAG---TCAGCCATC----------   [1098]
Mannia_controversa_Austria            CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCC----TCGG-CGGGACAAAAG---TCGTGCTCT----------   [1043]
Mannia_spec_128_North_India           CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCT----TCGG-CGGGACAAAAG---TCGGCCCTTG---------   [1093]
Mannia_californica_Austria            CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCC----TCGG-CGGGACAAAAG---TCGGTCATC----------   [1089]
Mannia_californica_California         CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCT----TGGG-CGGGACAAAAG---TCGGGCATC----------   [1084]
Mannia_californica_Namibia            CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCC----TCGG-CGGGACAAAAG---TCGGGCATC----------   [1085]
Mannia_californica_France             CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCC----TCGG-CGGGACAAAAG---TCGGGCATC----------   [1084]
Mannia_californica_China              CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCC----TCGG-CGGGACAAAAG---TCGGGCATC----------   [1084]
Mannia_californica_104_North_India    CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTTTT----TCGG-CGGGACAAAAG---TCGGTCATC----------   [1084]
Mannia_californica_105_North_India    CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCC----TCGG-CGGGACAAAAG---TCGGGCATC----------   [1084]
Mannia_californica_South_India        CGCCGCTCGACGCGGGGCGCTGGTCGACGTGGGCTCCC----TCGG-CGGGACAAAAG---TCGGGCATC----------   [1084]
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[                                         1210      1220      1230      1240      1250      1260      1270      1280]
[                                            .         .         .         .         .         .         .        .]
                                                                                                             *******
Targionia_hypophylla_Madeira              ACCGGTTTGCGGGTGTTGG--CCGAT--GCCGTCGGGGAGGCTGAGGA---------TCTTGAAGTGCGCGTCCCCTTTT   [1129]
Targionia_hypophylla_California           ACCGGTTTGCGG-CGCCAG--CCGAT--GCCGTCGGGGAGGCTGAGGAATGAACCCCTCTTGAAGTGCGCGTTCCTCTTT   [1140]
Athalamia_hyalina                         -----TTGTCGGG--CCGG--CCGAT--GCCGTCGGGGAGGCCGAGGAAT----------CGAAGTGCGCGCCCTTTGTA   [1137]
Plagiochasma_rupestre                     -------TGTGG---CTGG--CCGAT--GCCGTCGAAGGGGCCGAGGAAA----------CGAAGTGCGCGCCTCCCTTT   [1120]
Plagiochasma_wrightii                     -------AGTGG---CTGG--CCGAT--GCCGTCGAAGGGGCCGAGGAAA----------CGAAGTGCGCGCCCCTCTTT   [1112]
Plagiochasma_japonicum                    -------CGTGG---CTGG--CCGAT--GCCGTCGAAGGGGCCGAGGAAA--A-------CGAAGTGCGCGCCCTTCT--   [1115]
Reboulia_hemisphaerica                    -------TGTGG---CCGG--CCGAT--GCCGTCGAGGAGGCCGAGGAAA--AC------TGAAGTGCGCGCC-------   [1147]
Cryptomitrium_tenerum                     -------TGTGG---CAGG--CCGAT--GCCGTCTAGGAGGCCGAGGAAA----------CGAAGTGCGCGTCCTCCG--   [1103]
Cryptomitrium_himalayense                 -------TGTGG---CAGG--CCGAT--GCCGTCTAGGAGGCCGAGGAAA----------CGAAGTGCGCGTCCTCCG--   [1105]
Cryptomitrium_spec_Peru                   -------AGTGG---CAGG--CCGAT--GCCGTCTAAGAGGCCGAGGAAA----------CGAAGTGCGCGTCCTCCG--   [1103]
Asterella_grollei                         -------AGTGGG--CGGG--CCGAT--GCCGTCGAGGAGGCCGAGGGAA---------TCGAAGTGCGCGTCCTCCG--   [1128]
Asterella_californica                     -------AGTGG---CCGG--CCGAT--GCCGTCGGAGAGGCCGAGGAA----------CCGAAGTGCGTGCCTGCGGGT   [1135]
Asterella_wallichiana                     -------AGTGG---CCGG--CCGAT--GCCGTCGAGGAGGCCGAGGAA-----------CGAAGTGCGCGTCCCCCCCT   [1146]
Asterella_africana                        -------AGTGG---CCGG--CCGAT--GCCGTCGAGGAGGCCGAGGAA-----------CGAAGTGCGCGTCCCCCCC-   [1154]
Asterella_tenella                         -------AGTGG---CCGG--CCGAT--GCCGTCGAGGAGGCCGAGGAA-----------CGAAGTGCGCGTCCCCCCC-   [1146]
Asterella_lateralis                       ----------------------------GCCGTCGAGGAGGCCGAGGAA-----------CGAAGTGCGCGCCC-TCT--   [1135]
Asterella_saccata                         -------CGTGG---CCGG--CCGAT--GCCGTCGAGGAGGCCGAGGAA-----------CGAAGTGCGCGCCCCTATTT   [1152]
Asterella_gracilis                        -----CGAGTGG---TCGG--CTGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCCTCCGG   [1121]
Mannia_pilosa                             -------AGTGG---TCGAGACTGATATGCCGTCCGAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCTCC--G   [1122]
Mannia_triandra                           -------AGTGG---TCGG--CTGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCTCC--G   [1119]
Mannia_fragrans_Switzerland               -------AGTGG---CCGG--CCGAT--GCCGTCGGAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCCCTCGG   [1145]
Mannia_fragrans_India                     -------AGTGG---CCGG--CCGAT--GCCGTCGGAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCCCTCGG   [1160]
Mannia_fragrans_Japan                     -------AGTGG---CCGG--CCGAT--GCCGTCGGAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCCCTCGG   [1144]
Mannia_androgyna_Namibia                  -------AGTGG---CCGG--CCGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCCTCTCC   [1152]
Mannia_androgyna_Madeira                  -------AGTGG---CCGG--CCGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCCTCTCC   [1153]
Mannia_controversa_Austria                -------AGTGG---CCGG--CCGAT--GCCGTCGAGGGGGCCGAGGAA-----------CGAAGTGCGCGCCCTC----   [1094]
Mannia_spec_128_North_India               -------AGTGGG--CCGG--CCGAT--GCCGTCGAGGGGGCCGAGGAA-----------CGAAGTGCGCGCCCTCTCGG   [1149]
Mannia_californica_Austria                -------AGTGG---CCGG--CCGAT--GCCGTCGGAGGGGCCGAGGAA-----------CGAAGTGCGCGCCCCATTTT   [1144]
Mannia_californica_California             -------AGTGA---CCGG--CCGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGTCCGGTTTC   [1139]
Mannia_californica_Namibia                -------AGTGG---CCGG--CCGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGTCCGGTT--   [1138]
Mannia_californica_France                 -------AGTGG---CCGG--CCGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGTCCGGTTGG   [1139]
Mannia_californica_China                  -------AGTGG---CCGG--CCGAT--GCCGTCGAGGGGGCCGAGGAA-----------CGAAGTGCGCGTCCGGTTGG   [1139]
Mannia_californica_104_North_India        -------AGTGA---CCGG--CCGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGTCCGGTTGG   [1139]
Mannia_californica_105_North_India        -------AGTGG---CCGG--CCGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGTCCGGTT--   [1137]
Mannia_californica_South_India            -------AGTGG---CCGG--CCGAT--GCCGTCGAAGGGGCCGAGGAA-----------CGAAGTGCGCGTCCGGTTTT   [1139]
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[                                              1290      1300      1310      1320      1330      1340      1350      1360]
[                                              .         .         .         .         .         .         .         .]
                                      ****************************************
Targionia_hypophylla_Madeira          TG----GGGACGGGGCCTCCGTT--------------MGGAGGTCACCTGCGTACTCGGGACGCTGGCGTTGTGGGCTTT    [1191]
Targionia_hypophylla_California       CGG-GAGGGGCGGGGCATTCCTCTTTC------GGGAGGAGTGCCACCTGCGTACTCGGGACGCTGGCGTTGTGGGCTTT    [1213]
Athalamia_hyalina                     AAA-AKTGGKCGGGCTCCCCCCT----------CCACGGGGGAGCACMTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1206]
Plagiochasma_rupestre                 TT--TGGGGGCGGGCCTCCCCCCCYTTC-----GCGGGGGGGAGCACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1193]
Plagiochasma_wrightii                 ------GGGGCGGGCTCCCT------------------AGGGAGCACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1168]
Plagiochasma_japonicum                -------GGGCGGGCTCCCCTTCAC-------------GGGGAGCACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1176]
Reboulia_hemisphaerica                ----CTCGGGCGGGCTCCCT------------------CGGGAGTACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1205]
Cryptomitrium_tenerum                 -------GGACGGGCTCTCTCTCTC---------GGGAGTAGAGCACCTGCGCACTCGAGACGCCGGCGTAGTGGGCTTT    [1167]
Cryptomitrium_himalayense             -------GGACGGGCTCTCTCTCTC---------GGGAGTAGAGCACCTGCGCACTCGAGACGCCGGCGTAGTGGGCTTT    [1169]
Cryptomitrium_spec_Peru               -------GGACGGGCTCTCTCTCTCTCG-----GGGGAGTAGAGCACCTGCGCACTCGAGACGCCGGCGTAGTGGGCTTT    [1171]
Asterella_grollei                     -------GGACGGGTCCCGCC------GCTCGAAAGAGTTGGGGCACCTGCGCACTCGAGACGTCGGCGTAGTGGGCTTT    [1195]
Asterella_californica                 TTTCCGCGGGCGGACTCCTC------------------CGGGAGTTCCTGCGTACTCGGGACGCCGGCGTAGTGGGCTTT    [1197]
Asterella_wallichiana                 TCGGGGAGGACGGGTTCCCCCTCTCT------CGGGAGGGGGAGCACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1220]
Asterella_africana                    ----GGGGGACGGGTTCTCTTC----------------GGAGAACACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1214]
Asterella_tenella                     ----GGGGGACGGGTCCTCTTC----------------GGAGGACACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1206]
Asterella_lateralis                   ------CGGGCGGGCTCCTTCG------------------GGAGCACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1191]
Asterella_saccata                     TTT---GGGGCGGGTTCCCCTTTCCCTTCGCGGGGGGAGTGGAGCACCTGCGCACTCGGGACGCCGGCGTAGTGGGCTTT    [1229]
Asterella_gracilis                    -------GGGCGGGCTCCTTC----------------ACGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1178]
Mannia_pilosa                         -------GGGCGGGCTCCTC------------------CGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1177]
Mannia_triandra                       -------GGGCGGGCTCCTTC----------------ACGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1176]
Mannia_fragrans_Switzerland           -------GGGCGGGCTCCCT------------------CGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1200]
Mannia_fragrans_India                 -------GGGCGGGCTCCCT------------------CGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1215]
Mannia_fragrans_Japan                 -------GGGCGGGCTCCCT------------------CGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1199]
Mannia_androgyna_Namibia              -------GGGGGGGCGGGCTCCTTTT-----------GCGGGAGCACCTGCGCACTCGAGACGTCGGCGTAGTGGGCTTT    [1214]
Mannia_androgyna_Madeira              -------GGGGGGGCGGGCTCCTTTT-----------GCGGGAGCACCTGCGCACTCGAGACGTCGGCGTAGTGGGCTTT    [1215]
Mannia_controversa_Austria            -------GGGCGGGCTCCCCTT------------CACGGGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1155]
Mannia_spec_128_North_India           -------GGGCGGGCTCCCTT---------------CACGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1207]
Mannia_californica_Austria            T------GAGGCGGGCTCCTTTT-------------GCGAGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1205]
Mannia_californica_California         -------GGGCGGGCTCTCTT----------------CGGGGAGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1196]
Mannia_californica_Namibia            -------GGGCGGGCTCTCTCTCTCTTT------CGGGGGAGGGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1205]
Mannia_californica_France             -------GCGGGCTCTTCTCTCTTT--------CGGGGGGAGGGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1204]
Mannia_californica_China              -------GCGGGCTTCCTCTCTTCTCT--------GGGGGGGRGCACMTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1204]
Mannia_californica_104_North_India    -------GCGGGCAATCTCTCTTT--------CGGGGGGGGGTGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1204]
Mannia_californica_105_North_India    -------GGGCGGGCTCT-TCTCTCTTT-----CGGGGGGAGGGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1204]
Mannia_californica_South_India        -------GGGCGGGCTCTCTCTCTCTCTTT----CGGGGGAGGGCACCTGCGCACTCGGGACGTCGGCGTAGTGGGCTTT    [1208]
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[                                            1370      1380      1390      1400      1410      1420      1430      1440]
[                                            .         .         .         .         .         .         .         .]
                                                                                                               *********
Targionia_hypophylla_Madeira        TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGT-------   [1264]
Targionia_hypophylla_California     TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACAT-------   [1286]
Athalamia_hyalina                   TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGTGGCAAACCCACACGTTTTG-   [1285]
Plagiochasma_rupestre               TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTAT-----   [1268]
Plagiochasma_wrightii               TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTT------   [1242]
Plagiochasma_japonicum              TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTATTTTTT   [1256]
Reboulia_hemisphaerica              TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTAA-----   [1280]
Cryptomitrium_tenerum               TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCAC---------   [1238]
Cryptomitrium_himalayense           TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCAC---------   [1240]
Cryptomitrium_spec_Peru             TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCAC---------   [1242]
Asterella_grollei                   TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTTT-----   [1270]
Asterella_californica               TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTT------   [1271]
Asterella_wallichiana               TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTGT-----   [1295]
Asterella_africana                  TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTTT-----   [1289]
Asterella_tenella                   TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTTTTTTC-   [1285]
Asterella_lateralis                 TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTTT-----   [1266]
Asterella_saccata                   TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTTT-----   [1304]
Asterella_gracilis                  TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTTGA-----   [1253]
Mannia_pilosa                       TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTT-------   [1250]
Mannia_triandra                     TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACAT-------   [1249]
Mannia_fragrans_Switzerland         TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTTT-----   [1275]
Mannia_fragrans_India               TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTTT-----   [1290]
Mannia_fragrans_Japan               TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACGTTT-----   [1274]
Mannia_androgyna_Namibia            TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTT-------   [1287]
Mannia_androgyna_Madeira            TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTT-------   [1288]
Mannia_controversa_Austria          TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCTGCAAACCCACTT-------   [1228]
Mannia_spec_128_North_India         TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCTGCAAACCCACTT-------   [1280]
Mannia_californica_Austria          TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTT-------   [1278]
Mannia_californica_California       TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTCGAG----   [1272]
Mannia_californica_Namibia          TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTTTAG----   [1281]
Mannia_californica_France           TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTCTAG----   [1280]
Mannia_californica_China            TCATCTGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTCGAG----   [1280]
Mannia_californica_104_North_India  TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTCGAG----   [1280]
Mannia_californica_105_North_India  TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTCTAG----   [1280]
Mannia_californica_South_India      TCATCCGACCCGTCTTGAAACACGGACCAAGGAGTCTAACATGCATGCGAGCCGGTGGGCGGCAAACCCACTTGAG----   [1284]
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[                                         1450      1460      1470      1480      1490      1500      1510      1520]
[                                            .         .         .         .         .         .         .         .]
                                     *******                                      ***************
Targionia_hypophylla_Madeira         -------GAGGCG--CAAATAACTT--GACT-GGTGTGATCCTTTTTTTCTTTCGAGGAGAAGAGGTGCAACATCGACCG   [1332]
Targionia_hypophylla_California      -------GAGGCG--CAAATAACTT--GACT-GGTGTGATCCTTTCCCTCTTTCGGGAGGGCGAGGTGCAACATCGACCG   [1354]
Athalamia_hyalina                    ------AGAGGCG--CAAATAACTT--GATAAGGTGTGATCCTCG--------------AGAGGGGTGCAACATCGACCG   [1341]
Plagiochasma_rupestre                ------AGAGGCG--AAAATAACTT--GACAGGGTGTGATCCTCCTCC------------GCGGGGTGCAACATCGACCG   [1326]
Plagiochasma_wrightii                ------AGAGGCG--AAAATAACTT--GACAGGGTGTGATCCTCCTCC------------GCGGGGTGCAACATCGACCG   [1300]
Plagiochasma_japonicum               TATAAAAGAGGCG--AAAATAACTT--GACA-GGTGTGATCCTCCTCC------------GCGGGGTGCAACATCGACCG   [1319]
Reboulia_hemisphaerica               -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCTCCT-------------AGCGGGGTGCAACATCGACCG   [1335]
Cryptomitrium_tenerum                -------GAGGCG--AAAATAACTT--GACT-GGTGTGATCCTCCTTTT----------AGCGGGGTGCAACATCGACCG   [1296]
Cryptomitrium_himalayense            -------GAGGCG--AAAATAACTT--GACT-GGTGTGATCCTCCTTTT----------AGCGGGGTGCAACATCGACCG   [1298]
Cryptomitrium_spec_Peru              -------GAGGCG--AAAATAACTT--GACT-GGTGTGATCCTCCTTCT----------AGCGGGGTGCAACATCGACCG   [1300]
Asterella_grollei                    -------GAGGCG--AAAATAACTT--GACT-GGTGTGATCCTCGCTG-----------GGCGGGGTGCAACATCGACCG   [1327]
Asterella_californica                -------GAGGCG--AAAATAACTT--GACT-GGTGTGATCCTCGTTTTT---------AGCGGGGTGCAACATCGACCG   [1330]
Asterella_wallichiana                -------GAGGCG--CAAATAACTT--AACA-GGTGTGATCCTCCTTTTTCK-------AGCGGGGTGCAACATCGACCG   [1356]
Asterella_africana                   -------GAGGCG--CAAATAACTT--AACG-GGTGTGATCCTCCCCTTTTTTGG----AGCGGGGTGCAACATCGACCG   [1353]
Asterella_tenella                    -------GAGGCG--CAAATAACTT--AACG-GGTGTGATCCTTC------------------GGGTGCAACATCGACCG   [1335]
Asterella_lateralis                  -------GAGGCG--CAAATAACTT--AACA-GGTGTGATCCCCTTC-------------GCGGGGTGCAACATCGACCG   [1321]
Asterella_saccata                    -------GAGGCG--CAAATAACTT--AACA-GGTGTGATCCCCTTT--------------CGGGGTGCAACATCGACCG   [1358]
Asterella_gracilis                   -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCTCTCTCTCTTCATAGGGAGCGGGGTGCAACATCGACCG   [1321]
Mannia_pilosa                        -------GAGGCG--AAAATAACTTGAGACA-GGTGTGATCCTCTCCTCTTCC------GGGGGGGTGCAACATCGACCG   [1314]
Mannia_triandra                      -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCTCT--------------AATGGGGTGCAACATCGACCG   [1303]
Mannia_fragrans_Switzerland          -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCCCTCTCG----------ACCGGGGTGCAACATCGACCG   [1333]
Mannia_fragrans_India                -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCCCTCTCG----------ACCGGGGTGCAACATCGACCG   [1348]
Mannia_fragrans_Japan                -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCCCTCTCG----------ACCGGGGTGCAACATCGACCG   [1332]
Mannia_androgyna_Namibia             -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCTCTTTTG----------AGCGGGGTGCAACATCGACCG   [1345]
Mannia_androgyna_Madeira             -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCTCTTTTG----------ACCGGGGTGCAACATCGACCG   [1346]
Mannia_controversa_Austria           -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCCCTTG------------ACCGGGGTGCAACATCGACCG   [1284]
Mannia_spec_128_North_India          -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCCCTTG------------ACCGGGGTGCAACATCGACCG   [1336]
Mannia_californica_Austria           -------GAGGCG--AAAATAACTT--GACA-GGTGTGATCCCTCTC------------GGGGGGGTGCAACATCGACCG   [1334]
Mannia_californica_California        ------AGAGGCG--AAAATAACTT--GACAGGGTGTGATCCCCTT--------------GGGGGGTGCAACATCGACCG   [1328]
Mannia_californica_Namibia           ------AGAGGCG--AAAATAACTT--GACAGGGTGTGATCCTCCTG------------GGGGGGGTGCAACATCGACCG   [1339]
Mannia_californica_France            ------AGAGGCG--AAAATAACTT--GACAAGGTGTGATCCCCTCCTCGT--------GGGGGGGTGCAACATCGACCG   [1342]
Mannia_californica_China             ------AGAGAGGCgAAAATAACTT--GACAGGGTGTGATCCCCTCCTCGG-------AGGGGGGGTGCAACATCGACCG   [1345]
Mannia_californica_104_North_India   ------GGAGGCG--AAAATAACTT--GACAGGGTGTGATCCCCTCCTTAG-------AGGGGGGGTGCAACATCGACCG   [1343]
Mannia_californica_105_North_India   ------AGAGGCG--AAAATAACTT--GACARGGTGTGATCCCCTCCTCGT--------GGGGGGGTGCAACATCGACCG   [1342]
Mannia_californica_South_India       ------AGAGGCG--AAAATAACTT--GACAGGGTGTGATCCCCTCCTCGT--------GGGGGGGTGCAACATCGACCG   [1346]
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[                                                     1530      1540      1550      1560      1570      1580      1590      1600]
[                                                        .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira             ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1412]
Targionia_hypophylla_California          ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1434]
Athalamia_hyalina                        ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1421]
Plagiochasma_rupestre                    ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1406]
Plagiochasma_wrightii                    ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1380]
Plagiochasma_japonicum                   ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1399]
Reboulia_hemisphaerica                   ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1415]
Cryptomitrium_tenerum                    ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1376]
Cryptomitrium_himalayense                ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1378]
Cryptomitrium_spec_Peru                  ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1380]
Asterella_grollei                        ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1407]
Asterella_californica                    ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1410]
Asterella_wallichiana                    ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1436]
Asterella_africana                       ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1433]
Asterella_tenella                        ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1415]
Asterella_lateralis                      ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1401]
Asterella_saccata                        ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1438]
Asterella_gracilis                       ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1401]
Mannia_pilosa                            ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1394]
Mannia_triandra                          ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1383]
Mannia_fragrans_Switzerland              ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1413]
Mannia_fragrans_India                    ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1428]
Mannia_fragrans_Japan                    ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1412]
Mannia_androgyna_Namibia                 ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1425]
Mannia_androgyna_Madeira                 ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1426]
Mannia_controversa_Austria               ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1364]
Mannia_spec_128_North_India              ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1416]
Mannia_californica_Austria               ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1414]
Mannia_californica_California            ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1408]
Mannia_californica_Namibia               ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1419]
Mannia_californica_France                ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1422]
Mannia_californica_China                 ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1425]
Mannia_californica_104_North_India       ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1423]
Mannia_californica_105_North_India       ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1422]
Mannia_californica_South_India           ACCATGATCTTCTGTGAAAGGTTCGAGTAAGAGCATGCCTGTTGGGACCCGAAAGATGGTGAACTATGCCTGAGCAGGGC   [1426]
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[                                               1610      1620      1630      1640      1650      1660      1670      1680]
[                                               .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira           GAAGCC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTTGGGTATA-GGGGCG   [1490]
Targionia_hypophylla_California        GAAGCC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTTGGGTATA-GGGGCG   [1512]
Athalamia_hyalina                      GAAGCC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1499]
Plagiochasma_rupestre                  GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1484]
Plagiochasma_wrightii                  GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1458]
Plagiochasma_japonicum                 GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1477]
Reboulia_hemisphaerica                 GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1493]
Cryptomitrium_tenerum                  GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1454]
Cryptomitrium_himalayense              GAAGTCcAGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1457]
Cryptomitrium_spec_Peru                GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1458]
Asterella_grollei                      GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1485]
Asterella_californica                  GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1488]
Asterella_wallichiana                  GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1514]
Asterella_africana                     GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1511]
Asterella_tenella                      GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1493]
Asterella_lateralis                    GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1479]
Asterella_saccata                      GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1516]
Asterella_gracilis                     GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1479]
Mannia_pilosa                          GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1472]
Mannia_triandra                        GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1461]
Mannia_fragrans_Switzerland            GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1491]
Mannia_fragrans_India                  GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1506]
Mannia_fragrans_Japan                  GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1490]
Mannia_androgyna_Namibia               GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1503]
Mannia_androgyna_Madeira               GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1504]
Mannia_controversa_Austria             GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1442]
Mannia_spec_128_North_India            GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1494]
Mannia_californica_Austria             GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1492]
Mannia_californica_California          GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1486]
Mannia_californica_Namibia             GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1497]
Mannia_californica_France              GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1500]
Mannia_californica_China               GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1503]
Mannia_californica_104_North_India     GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATAAGGGGCG   [1502]
Mannia_californica_105_North_India     GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1500]
Mannia_californica_South_India         GAAGTC-AGAGGAAACTCTGGTGGAGGCTCGTAGCGATACTGACGTGCAAATCGTTCGTCAGACTCGGGTATA-GGGGCG   [1504]
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[                                          1690      1700      1710      1720      1730      1740      1750      1760]
[                                             .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira         AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCCGGAGCA-TGA-GGAGTTTCATC   [1568]
Targionia_hypophylla_California      AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCCGGAGCA-TGA-GGAGTTTCATC   [1590]
Athalamia_hyalina                    AAAGACTMATCGAACCATCTAGTAGCTGGTTCCCTCcGaAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1577]
Plagiochasma_rupestre                AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1562]
Plagiochasma_wrightii                AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1536]
Plagiochasma_japonicum               AAAGACTAATCGAACCATCTAGTAGCTGGTTCCYTCCGAAGTTTCCCTCAGGATAGCTGGAGCAGCGA-GGAGTTTCATC   [1556]
Reboulia_hemisphaerica               AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1572]
Cryptomitrium_tenerum                AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1532]
Cryptomitrium_himalayense            AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1535]
Cryptomitrium_spec_Peru              AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1536]
Asterella_grollei                    AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1564]
Asterella_californica                AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1566]
Asterella_wallichiana                AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1592]
Asterella_africana                   AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1589]
Asterella_tenella                    AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1571]
Asterella_lateralis                  AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGA-GGAGTTTCATC   [1557]
Asterella_saccata                    AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CAAAGGAGTTTCATC   [1595]
Asterella_gracilis                   AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1558]
Mannia_pilosa                        AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1551]
Mannia_triandra                      AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1540]
Mannia_fragrans_Switzerland          AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1570]
Mannia_fragrans_India                AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1585]
Mannia_fragrans_Japan                AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1569]
Mannia_androgyna_Namibia             AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1582]
Mannia_androgyna_Madeira             AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1583]
Mannia_controversa_Austria           AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1521]
Mannia_spec_128_North_India          AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1573]
Mannia_californica_Austria           AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1571]
Mannia_californica_California        AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1565]
Mannia_californica_Namibia           AAAGACTAATCGAACCATCTAGTAGCTGGTTCCYTCCGAAGTTTCCcTCAGgATAGCTGGAGCA-CGAAGGAGTTTCATC   [1576]
Mannia_californica_France            AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1579]
Mannia_californica_China             AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1582]
Mannia_californica_104_North_India   AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGGA-CGAAGGAGTTTCATC   [1581]
Mannia_californica_105_North_India   AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1579]
Mannia_californica_South_India       AAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCCTCAGGATAGCTGGAGCA-CGAAGGAGTTTCATC   [1583]
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[                                                   1770      1780      1790      1800      1810      1820      1830      1840]
[                                                   .         .         .         .         .         .         .         .]

Targionia_hypophylla_Madeira            AGGTA-AAGCGAATGATTAGAGGCCT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1640]
Targionia_hypophylla_California         AGGTA-AAGCGAATGATTAGAGGCCT-CGGGGGTGAAA--CACCCTCGCAC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1663]
Athalamia_hyalina                       AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAWA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1649]
Plagiochasma_rupestre                   AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1634]
Plagiochasma_wrightii                   AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1608]
Plagiochasma_japonicum                  AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTMTCAAACTTTAAATAGGT-GAG   [1628]
Reboulia_hemisphaerica                  AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1644]
Cryptomitrium_tenerum                   AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1604]
Cryptomitrium_himalayense               AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1607]
Cryptomitrium_spec_Peru                 AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAMA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1608]
Asterella_grollei                       AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACTCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1636]
Asterella_californica                   AGGTAgAAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACTCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1639]
Asterella_wallichiana                   AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1664]
Asterella_africana                      AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGATGAAA--CATCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1661]
Asterella_tenella                       AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1643]
Asterella_lateralis                     AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACTCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1629]
Asterella_saccata                       AGGTA-AAGCGAATGATTAGAGGCATgCGGGGGTGAcA--CACTCTCG-AC-CTtATTCTCAAACTTTAAATAGGTAGAG   [1670]
Asterella_gracilis                      AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1630]
Mannia_pilosa                           AGGTA-AAGCGAATGATTARAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGTaGAG   [1624]
Mannia_triandra                         AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1612]
Mannia_fragrans_Switzerland             AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGtGAAA--CACCCTCG-AC-CT-ATTCTCMAACTTTAAATAGGT-GAG   [1642]
Mannia_fragrans_India                   AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1657]
Mannia_fragrans_Japan                   AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-ACgCT-ATTCTCAAACTTTAAATAGGT-GAG   [1642]
Mannia_androgyna_Namibia                AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1654]
Mannia_androgyna_Madeira                AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1655]
Mannia_controversa_Austria              AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1593]
Mannia_spec_128_North_India             AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1645]
Mannia_californica_Austria              AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1643]
Mannia_californica_California           AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1637]
Mannia_californica_Namibia              AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCTTCG-AC-tT-ATTCTCAAACTTTAAATAGGT-GAG   [1648]
Mannia_californica_France               AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1651]
Mannia_californica_China                AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1654]
Mannia_californica_104_North_India      AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1653]
Mannia_californica_105_North_India      AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-CT-ATTCTCAAACTTTAAATAGGT-GAG   [1651]
Mannia_californica_South_India          AGGTA-AAGCGAATGATTAGAGGCAT-CGGGGGTGAAA--CACCCTCG-AC-MT-ATTCTCAAACTTTAAATAGGT-GAG   [1655]
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[                                            1850      1860      1870      1880      1890      1900      1910      1920]
[                                            .         .         .         .         .         .         .         .  ]
                                          ***********                      *******************************************
Targionia_hypophylla_Madeira        ATCCGAC-----------GGGGTTGCTTAAGTGAACCCC-CGGCGGAGAATCCAAACTG??????????????????????? [1710]
Targionia_hypophylla_California     ATCCGAC-----------GGGGTTGCTTAAGTGAACCCC-CGGCGGAGAATCCAAACTGC?????????????????????? [1733]
Athalamia_hyalina                   ATCCGTTTTTTAAAAAGAGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCG???????????????????????????? [1730]
Plagiochasma_rupestre               ATCCGATTTTT-------GGGGTTGCTCGATTGAACCCC-CGGCGGAGAATCCGA??????????????????????????? [1708]
Plagiochasma_wrightii               ATCCGATTTTT-------GGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCG???????????????????????????? [1682]
Plagiochasma_japonicum              ATCACTGATTTTGTA--TGGGGTTGCTTGATTGAACCCC-CGG??????????????????????????????????????? [1707]
Reboulia_hemisphaerica              ATCCGAC-----------GGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGTCCA????????????????????? [1714]
Cryptomitrium_tenerum               ATCCGTT-----------GGGGTTGCTTGATTGAACCCC-CGGCGGAGCATCCG???????????????????????????? [1674]
Cryptomitrium_himalayense           ATCCGTT-----------GGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCG???????????????????????????? [1677]
Cryptomitrium_spec_Peru             ATCCGTT-----------GGGGTTGCTTGATTGAACCCCCCGGCGGAGAATCCGAAC????????????????????????? [1679]
Asterella_grollei                   ATCCGAC-----------GGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCC????????????????????????????? [1706]
Asterella_californica               ATCCGAT----------GCGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGC??????????????????????? [1710]
Asterella_wallichiana               ATCCGATT---------CGGGGTTGCTTGACTGAACCCC-CGGCGGAGAATCCG???????????????????????????? [1736]
Asterella_africana                  ATCCGA-----------CGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCC????????????????????????????? [1731]
Asterella_tenella                   ATCCGACA---------CGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAAC????????????????????????? [1715]
Asterella_lateralis                 ATCCGATTT--------CGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGCTCCAGTGGGCCATTTTGGGTAGC [1702]
Asterella_saccata                   ATCCGATC---------CGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGCTCC???????????????????? [1742]
Asterella_gracilis                  ATCCGTTT---------CGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGCT?????????????????????? [1702]
Mannia_pilosa                       ATCCGTTT------GCGCGGGTGTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGCTCCAA?????????????????? [1699]
Mannia_triandra                     ATCCGTTT---------CGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGA??????????????????????????? [1684]
Mannia_fragrans_Switzerland         ATCCGTTTTTTT-----CGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGC??????????????????????? [1718]
Mannia_fragrans_India               ATCCGTTTTTTT-----CGGGGTTGCTTGATTGMACCCC-CGGCGGAGCATCACGCAAC??????????????????????? [1733]
Mannia_fragrans_Japan               ATCCGTTTTTT-----GCGGGGTTGCTTGATTGAACCCC-CGGCGG???????????????????????????????????? [1718]
Mannia_androgyna_Namibia            ATCCGCGTT---------GGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACG???????????????????????? [1726]
Mannia_androgyna_Madeira            ATCCGCGTT---------GGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCG???????????????????????????? [1727]
Mannia_controversa_Austria          ATCCGTTT---------CGGGGTTGCTTGATTGAACCCC-CGGCGG???????????????????????????????????? [1665]
Mannia_spec_128_North_India         ATCCGTCT---------CGGGGTTGCTTGATTGMAACCCGCGGCGGAG?????????????????????????????????? [1718]
Mannia_californica_Austria          ATCCGTTTTGAT-----CGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAA?????????????????????????? [1719]
Mannia_californica_California       ATCTAT--------CGGGGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGA??????????????????????????? [1710]
Mannia_californica_Namibia          ATCTAT-------CCGGGGGGGTTGCTTGATTGMACCCC-CGGCGGAGCAATCCG??????????????????????????? [1722]
Mannia_californica_France           ATCTAT--------CGGGGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAA?????????????????????????? [1724]
Mannia_californica_China            ATCTAT--------CGGGGGGGTTGCTTGATTGMACCCC-CGGCGGAGCATCCGCAACGT?????????????????????? [1727]
Mannia_californica_104_North_India  ATCTAT--------CGGGGGGGTTGCTTGATTGMACCCC-CGGCGGAGAATCCGA??????????????????????????? [1726]
Mannia_californica_105_North_India  ATCTAT--------CGGGGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGCTCC???????????????????? [1724]
Mannia_californica_South_India      ATCTAT-------GCGGGGGGGTTGCTTGATTGAACCCC-CGGCGGAGAATCCGAACGTCCA????????????????????? [1729]
```

3. ***Trn*L-F gap matrix analysed in Chapter 5**

Position Species	123456789
Targionia hypophylla Madeira	??1?10101
Targionia hypophylla California	??1?10101
Athalamia hyalina	??0110101
Plagiochasma rupestre	010111???
Plagiochasma wrightii	010111???
Plagiochasma japonicum	010111???
Reboulia hemisphaerica	010110111
Cryptomitrium tenerum	010110101
Cryptomitrium himalayense	000110101
Cryptomitrium spec. Peru	000110101
Asterella grollei	010110101
Asterella californica	000110101
Asterella wallichiana	010110111
Asterella africana	010110111
Asterella tenella	010110111
Asterella lateralis	01011011?
Asterella saccata	010110111
Asterella gracilis	110110111
Mannia pilosa	110110111
Mannia triandra	110110111
Mannia fragrans Switzerland	110000111
Mannia fragrans India	110000111
Mannia fragrans Japan	110000111
Mannia androgyna Namibia	110110010
Mannia androgyna Madeira	110110010
Mannia controversa Austria	110110110
Mannia spec. 128 North India	110110110
Mannia californica Austria	110110110
Mannia californica California	110110110
Mannia californica Namibia	110110110
Mannia californica France	110110110
Mannia californica China	110110110
Mannia californica 104 North India	110110110
Mannia californica 105 North India	110110110
Mannia californica South India	110110110

Gap position

1= 209
2= 210
3= 217-218
4= 219
5= 230-231
6= 337-355
7= 356-365
8= 368-372
9= 384

4. Characteristics of *trn*L-*trn*F and 26S sequence matrices

* based on alignment matrix excluding ambiguous regions.

Parameter	Program	trn*L*-trn*F*	26S	Combined
Number of taxa	PAUP	35	35	35
Length range (total)(bp)	PAUP	516-606	1059-1136	1582-1712
Length mean (total)(bp)	PAUP	571.7	1084	1655.7
Length range (ingroup)(bp)	PAUP	516-606	1106-1059	1582-1712
Length mean (ingroup)(bp)	PAUP	573.1	1080.8	1653.9
Length range (outgroup)(bp)	PAUP	548-572	1109-1136	1657-1688
Length mean (outgroup)(bp)	PAUP	557.3	1118	1675.3
Aligned length (bp)	PAUP	684	1229	1913
Aligned length (bp)-ambiguous	PAUP	581	1076	1657
G + C content, mean (%)	PAUP	28.14	57.75	47.52
Sequence divergence (*Asterella*) (bp)*	PAUP	13-53	7-32	21-84
Sequence divergence (*Asterella*) (%)*	PAUP	2.5-10.5	0.7-3.2	1.4-5.6
Sequence divergence (*Plagiochasma*) (bp)*	PAUP	10-12	6-10	18-21
Sequence divergence (*Plagiochasma*) (%)*	PAUP	2.1-2.5	0.6-0.9	1.2-1.4
Sequence divergence (*Cryptomitrium*) (bp)*	PAUP	4-12	2-5	6-17
Sequence divergence (*Cryptomitrium*) (%)*	PAUP	0.8-2.3	0.2-0.5	0.4-1.1
Sequence divergence (*Mannia*) (bp) *	PAUP	0-33	0-32	0-66
Sequence divergence (*Mannia*) (%)*	PAUP	0-6.5	0-3.2	0-4.3
Sequence divergence (*M. californica*) (bp) *	PAUP	0-18	0-32	0-43
Sequence divergence (*M. californica*) (%)*	PAUP	0-3.9	0-3.2	0-2.9
Sequence divergence (ingroup) (bp) *	PAUP	0-53	0-44	0-85
Sequence divergence (ingroup) (%)*	PAUP	0-10.5	0-4.3	0-5.7
Sequence divergence (outgroup) (bp)*	PAUP	20-62	15-54	35-116
Sequence divergence (outgroup) (%)*	PAUP	3.9-12.2	1.5-5.3	2.3-7.6
Sequence divergence (in/outgroup) (bp)*	PAUP	43-71	33-69	82-133
Sequence divergence (in/outgroup) (%)*	PAUP	9-14.5	3.3-6.8	5.5-8.8
Number of variable sites (bp)*	PAUP	184	142	326
Number of variable sites (%)*	PAUP	32	13	20
Number of constant sites (bp)*	PAUP	406	933	1339
Number of constant sites (%)*	PAUP	68	87	80
Number of informative sites (bp)*	PAUP	112	88	200
Number of informative sites (%)*	PAUP	19	8	12
Number of uninformative sites (bp)*	PAUP	72	54	126
Number of uninformative sites (%)*	PAUP	13	5	8
Transitions (minimum) *	MacClade	389	452	458
Transversions (minimum)*	MacClade	517	562	555
Transitions/Transversions*	MacClade	0.75	0.8	0.81
Length of most parsimonious trees, steps*	PAUP	375	315	697
Number of most parsimonious trees*	PAUP	9	33	20
Average number of steps per character	PAUP	0.65	0.29	0.42
Consistency Index (CI), including uninformative characters*	PAUP	0.69	0.58	0.62
Homoplasy Index (HI), including uninformative characters*	PAUP	0.31	0.42	0.37
Retention Index (RI) *	PAUP	0.76	0.74	0.74
Rescaled consistency Index (RC) *	PAUP	0.52	0.43	0.47

5. Model selection results for Bayesian analysis

Based on the Akaike Information Criterion (AIC) and the hLRTs (hierachical Likelihood Ratio Tests) in the program Modeltest (POSADA & CRANDALL 1998), with -ln likelihood and parameters for each partition in the data matrix given.

Partition	Modeltest	-ln likelihood	Parameter values
*trn*L-F (AIC)	TVM+I+G	2833.51	statefreq = (0.4182, 0.1166, 0.1391, 0.3261), revmatpr = fixed (1.1970, 1.1576, 0.6562, 1.4212, 1.1576, 1.000), ratepr = variable, nst = 6, rates = invgamma, pinvar = 0.4448, shape = 1.0741
*trn*L-F (hLRTs)	F81+G	2842.68	statefreq = (0.4071, 0.1334, 0.1526, 0.3069), revmatpr = fixed (1, 1, 1, 1, 1, 1), ratepr = variable, nst = 1, rates = invgamma, pinvar = 0, shape = 0.2930
*trn*L-F gap	-	-	statefreq = fixed (0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1), revmatpr = fixed (1.0, 1.0, 1.0, 1.0, 1.0, 1.0), ratepr = variable, nst = 2, rates = invgamma
26S	TrN+I+G	3243.0432	statefreq = (0.2287, 0.2307, 0.3382, 0.2024), revmatpr = fixed (1.000, 3.2367, 1.000, 1.000, 9.6107, 1.000), ratepr = variable, nst = 6, rates = invgamma, pinvar = 0.7395, shape = 0.5253

TVG = Tamurei Nei Model

F81 = Felsenstein 1981 Model

TrN = Transversional model

I = proportion of invariable (static, unchanging) sites in a dataset

G = Gamma distributed site-to-site rate variation

statefreq = base frequencies (A, C, G, T)

revmat = for the six substitution rates of the rate matrix (AC, AG, AT, CG, CT, GT)

ratepr = prior for site-specific rate models

nst = number of states

rates = model of gamma shaped rate variation across sites

pinvar = the proportion of invariable sites

shape = gamma distribution shape parameter.