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REVISION OF THE LIVERWORT GENUS *ASTERELLA* P.Beauv. (MARCHANTIALES, AYTONIACEAE) IN CONTINENTAL EURASIA, MALESIA AND JAPAN

Thesis submitted in fulfilment of the degree of PhD

by

DAVID GEOFFREY LONG

TRINITY COLLEGE DUBLIN

September 2000

DECLARATION

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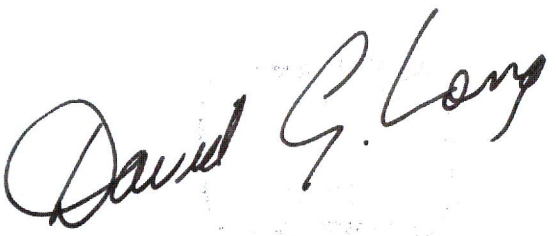

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SUMMARY

This study constitutes a taxonomic revision of the genus *Asterella* in Eurasia. *Asterella* belongs to the family Aytoniaceae in the Chambered Liverworts (Marchantiales). It is poorly understood taxonomically and a worldwide revision of the c. 158 described species is badly needed. Its gametophyte is morphologically complex and rich in qualitative characters; the sporophyte is highly reduced but shows great diversity in spore ornamentation patterns. Marchantiales are among the earliest land plants but relationships and phylogeny are poorly understood.

Aytoniaceae is well-defined, its five genera are poorly defined, *Asterella* by only one unique character, the cage-like pseudoperianth. Centres of diversity of *Asterella* are the neotropical mountains and the Sino-Himalaya. In Eurasia 69 species have been described, 52 of these from Asia. The genus has a complicated and confused nomenclatural history; until fairly recently it was known under the name *Fimbriaria*.

The study has four main objectives: to define the taxonomic characters of the genus; to describe the spores of the Eurasian species in detail using SEM; to provide a morphological taxonomic revision of the Eurasian species; and to attempt phylogenetic reconstruction within *Asterella* and its sister-genera using cladistic analysis.

Study of the taxonomic characters shows the great range of discontinuous (discrete) characters available and how these have been used as 'key' characters. Many continuous characters show phenotypic plasticity. Discrete characters are therefore favoured in taxonomic studies. The ornamentation characters offered by *Asterella* spores under SEM are the most diverse and elaborate in the bryophytes; spore sizes appear to be highly plastic. Spores are described and illustrated for all the Eurasian species and a key based on spore characters is provided.

A morphological taxonomic revision of available Eurasian material is presented, based on both field and herbarium studies. Culture of plants and cytological studies were difficult and yielded little useful data. Subgenera and sections are defined. Sixteen species are accepted and described in detail, along with keys to subgenera and species (including regional keys), detailed synonymy and typification, including designation of many new lectotypes. Spore ornamentation proved vital in identifying old fragmentary type specimens. For each species geography and ecology are summarised. Where appropriate detailed notes on typification, nomenclature, synonymy, *etc.* are given. Excluded taxa are listed and discussed.

The revision demonstrates a major advance in knowledge of Eurasian *Asterella*: huge reduction in names due to past over-description; the existence of two undescribed species; the importance of characters such as sexual condition and spore ornamentation, and the plasticity of many quantitative characters; clarification of phytogeography with a number of highly localised endemics and several widespread taxa.

Phylogenetic reconstruction is attempted using parsimony analysis of nineteen discrete morphological characters. Based on molecular evidence, *Targionia* (Targioniaceae) is used as an outgroup and the 'sister-genera' *Cryptomitrium*, *Mannia*, *Plagiochasma* and *Reboulia* are treated as part of the ingroup. The analysis resulted in 52 most parsimonious trees, grouped in 4 islands. Four almost identical clades occurred in all trees, three of which agree with accepted infrageneric groups; however, the relationship of these varies between trees. The paraphyly of *Asterella*, as suggested by molecular phylogenies, is supported, with the 'sister genera' nested within. Some but not all of the accepted infrageneric groups are supported, and some congruences and incongruences with molecular trees are displayed. Individual clades cannot be defined by unique synapomorphies.

CHAPTER 1: INTRODUCTION, BACKGROUND, OBJECTIVES AND HISTORICAL REVIEW

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1.1 INTRODUCTION

The present study arose from the author's participation in the Himalayan botanical research programme at the Royal Botanic Garden Edinburgh. Field work under this programme facilitated collection of many bryophytes and made possible a monographic research project on Himalayan Bryophyta. Revision of *Asterella*, a genus well-represented in the Himalaya, was suggested by Dr Riclef Grolle, Friedrich Schiller Universität, Jena, Germany. Its suitability for monographic study was supported by (a) enormous confusion over the number of taxa of *Asterella* in Asia and their distinction; (b) the opportunity to study and collect material in the field; and (c) the scope for using 'new' characters not used by previous workers, such as spore ornamentation. Grolle (*pers. comm.*) indicated that, although he had undertaken much preliminary work on the genus *Asterella*, he was not able to develop the study along the lines he felt were essential. Grolle's published work on the genus consisted of a series of nomenclatural notes and short taxonomic papers (Grolle, 1975a, 1975b, 1981, 1989), but no major revision.

A preliminary survey of the genus worldwide suggested that Eurasia would make a natural study-area for the project with around 70 names to deal with, leaving the species from America, Africa and Australasia/ Oceania as possible subjects for additional monographs.

1.2 BACKGROUND AND RATIONALE

Asterella P.Beauv. is a genus of perhaps 80 species worldwide, the second largest genus of Marchantiales (the 'Chambered Liverworts'), after *Riccia* L. Over 150 names have been published in *Asterella* or under several generic synonyms. It has been classified next to *Cryptomitrium* Austin ex Underw., *Mannia* Opiz and *Reboulia* Raddi, also in Aytoniaceae, but differs strikingly in its female gametophores (reproductive branches), which have a cage-like pseudoperianth surrounding each sporogonium, borne within an involucre under the lobes of the carpocephalum (receptacle). When ripe, spores are released from the dehisced capsule through the slits in the pseudoperianth. The genus is striking in its morphological gametophytic complexity, giving rise to a very large number of discontinuous characters, for example the diversity of sexual conditions and branching patterns. The spores also show great diversity of sculpturing patterns.

Asterella has two main centres of diversity, in the mountains of tropical America (especially Mexico) and in eastern Asia, with smaller centres in Africa and Australasia.

Possibly as a result of a slow (in geological time) rate of post-glacial spread in Europe and the specialised habitat requirements of many species, *Asterella* is not present in the British Isles and is rare in Europe. It is not a familiar genus to many European bryologists. In the wild, the genus displays two main "life-strategies", (a) xeromorphic species with thick leathery thalli which are capable of drought-tolerance, can grow in very extreme habitats and are long-lived, producing sporophytes only occasionally, and (b) hygromorphic species, with thin delicate thalli, not capable of drought tolerance, growing in shaded humid or moist habitats and producing sporophytes frequently; these species sometimes also show specialised vegetative perennating tubers. These patterns fit quite well into the system of "Bryophyte Life Strategies" of During (1979). The xeromorphic taxa are "Perennial Stayers" and the hygromorphic taxa are "Perennial Shuttle Species" with regular interruptions in the life cycle caused by climatic or anthropogenic factors.

Some *Asterella* species are adapted to highly specialised habitats, for example *A. lindenbergiana* (Corda ex Nees) Arnell grows in alpine snow-beds and *A. saccata* (Wahlenb.) A.Evans in xerothermic sites enriched by gypsum or ultrabasic minerals; however the precise ecology of many species is unknown. Some Asiatic taxa display weedy characteristics, growing as opportunists on sides of road-cuttings, on footpaths, terraces of rice paddies *etc.* Like other Marchantiales, they are scarcely ever found on living or dead wood, and in forest habitats are confined to rocks and soil.

There are several reasons why this monograph is needed, and why the following rationale has been adopted:

Firstly, the genus itself has a very confused and chequered nomenclatural and taxonomic history, at different periods being widely known under the now synonymous names of *Fimbriaria* and *Hypenantron*. This history has never been properly documented with the correct application of names and synonyms confirmed, which is an essential precursor to a taxonomic revision.

Secondly, the full range of characters available in the genus *Asterella* has never been fully documented and utilised. It is likely both that some characters used in the past are too variable or phenotypically plastic, and also that other very useful characters have never been detected or have been under-utilised. Past taxonomic studies have often been made exclusively on dried herbarium material, which by its very nature in Marchantiales is at best difficult to work with, and at worst totally inadequate for even the most basic taxonomic measurements and judgements. The latter scenario sadly applies to much of the old herbarium material on which most early taxonomic work on *Asterella* is founded. Study of living plants in the field, and of copious recently-collected good-quality fertile material, has presented an excellent opportunity to re-evaluate and re-write the

taxonomy of *Asterella*. Hence all the taxonomic characters available in *Asterella* had to be evaluated afresh.

Thirdly, modern SEM techniques have allowed a whole new suite of potentially very useful characters to become available in *Asterella*. The great ranges of size and sculpturing of spores in Marchantiales, greater than in any other group of liverworts (and probably bryophytes), have been known for many years (*e.g.* Miyoshi, 1966), but only with the advent of SEM technology have these characters been utilised to their full potential for taxonomy. Long (1998) has demonstrated their enormous potential in *Asterella* taxonomy and classification, so that SEM is now an essential component of this type of study.

Fourthly, there is an urgent need for a comprehensive taxonomic revision of *Asterella* in Eurasia. A modern approach to taxonomic revision in Marchantiales has been pioneered by Hélène Bischler in Paris, particularly on *Plagiochasma* and *Marchantia* (Bischler, 1977, 1978, 1979a, 1979b, 1982, 1984, 1986, 1987, 1988; Bischler-Causse, 1989, 1993). Her monographic studies have utilised a variety of techniques including karyotype analysis and SEM; in general she used as broad a spectrum of characters as possible and applied numerical analyses (such as multivariate analysis) on the resulting data. These studies demonstrated that in *Plagiochasma* and *Marchantia*, reduction to synonymy of many names was necessary. Both Bischler's work on these genera and the preliminary work by Grolle on *Asterella* suggested that similar critical revision in this genus would yield similar far-reaching results.

Without a sound taxonomy, it is impossible to understand biogeography. By the 'old' taxonomy, *Asterella* in Asia comprised numerous local endemics. From the above studies on *Marchantia* and *Plagiochasma* this pattern seemed most unlikely and no well-founded statements on 'true' endemism, disjunction, centres of speciation, *etc.* could be made for *Asterella* in Asia. There is also a global need in liverworts for accurate and thorough revisionary studies, particularly in tropical and warm-temperate regions of the world, such as Tropical America, Africa and the Indian Subcontinent where good bryophyte floras are almost non-existent. In such regions it is extremely difficult to identify bryophytes and not easy for students to take up bryology. Much of the past taxonomy was uncritical with acceptance of large numbers of poorly described and probably superfluous taxa. Similarly, without careful revisions and floras, it is hard or impossible to conduct thorough biodiversity inventories, and consequently conservation of important hotspots is difficult to support scientifically.

Fifthly, classification and phylogeny of Marchantiales in general is of great topical interest and is controversial because of the conflicting evolutionary signals from different datasets (possibly due to homoplasy). Classification and evolution of *Asterella* within the Marchantiales, as well as infrageneric classification and evolution within *Asterella*, have not been satisfactorily evaluated and no generally agreed classification or phylogeny exists at either level.

The large number of discontinuous characters available in *Asterella* has been demonstrated by Leitgeb (1881), Evans (1920), Grolle (1989), Perold (1994c) and others. These characters, primarily those of thallus structure, branching patterns, ventral scales, sexuality, carpocephalum and spores, should make *Asterella* an excellent subject for application of cladistic studies. Techniques of nucleotide sequencing are only now being introduced into studies of Marchantiales and are likely to yield a wealth of new data.

1.3 OBJECTIVES

The major objectives of the study, based on the needs described above, are:

- to review the taxonomic and nomenclatural history of the genus *Asterella* and its traditional classification, to evaluate its status as a genus and its differences with related genera, and to review past taxonomic work on *Asterella* in the study area (see Chapter 1)
- to review the characters used in the taxonomy of the Marchantiales and *Asterella* in the past, and the effects the choice of characters has had on taxonomy (see Chapter 2).
- to review the applications of Scanning Electron Microscopy (SEM) in the taxonomy of the Marchantiales and *Asterella* (especially as regards spore ornamentation) and apply such methods to the Eurasian species of *Asterella* (see Chapter 3).
- to revise the genus *Asterella* in the study area, providing descriptions, illustrations, keys, summaries of distribution and ecology, revised synonymy, correct nomenclature, discussion on particular taxonomic and nomenclatural problems, and lists of specimens studied (see Chapter 4).
- to attempt to reconstruct the phylogeny of *Asterella* and its Eurasian species using morphological cladistic analysis (see Chapter 5)

1.4 HISTORICAL REVIEW

1.4.1 The higher categories of Bryophytes and *Asterella*

Asterella belongs to the long-established Division (or Subkingdom) Bryophyta of the plant kingdom. Within this Division, the traditional subdivision (Schofield, 1985) into the three classes Bryopsida (mosses), Hepaticopsida (Liverworts) and Anthocerotopsida (Hornworts) has recently been undermined by the discovery of gametangia and sporophytes on possibly the most 'primitive' Bryophyte known, *Takakia* S.Hatt. & Inoue. Some of the unusual features of *Takakia*, particularly its combination of liverwort-like gametophytic characters with some *Andreaea*- (moss-)like sporophyte features, have led to the segregation of a fourth class of Bryophyta, the Andreaeopsida, including *Takakia* (Murray, 1988; Smith & Davison, 1993).

However, this change is only the latest in a long history of instability in the application of higher categories (especially families) in the bryophytes. At the time of

Engler & Prantl's *Die Natürlichen Pflanzenfamilien* (Schiffner *et al.*, 1893–1895) these higher categories were fewer than now and the balance (at the family level) was greatly in favour of subdividing mosses as opposed to liverworts. Schiffner had only two major subdivisions: Class Hepaticae (liverworts) and Class Musci (mosses).

In Schiffner's system, *Asterella* (as *Hypenantron*) was placed in the Family Marchantiaceae. This equates with Schuster's (1984b) Subclass Marchantiidae – an upgrading of two "levels" in the hierarchy. Within Schuster's Subclass Marchantiidae are three orders: Sphaerocarpales (3 genera, c 27 species), Monocleales (1 genus, 2 species) and Marchantiales (28 genera, c 360 species), of which *Asterella* belongs to the last, by far the largest in numbers of genera and species (Schuster 1984a, 1992b, 1992c). The circumscription of Marchantiales at Ordinal level is relatively stable as they are a well-defined group. However, below this level, the classification into families and in some cases genera is much less stable; it has changed much in the past two centuries and is by no means finally settled.

No hierarchical system of subdividing liverworts was proposed before 1800. The year 1821 saw the publication of S.F. Gray's *Natural Arrangement of British Plants* (Gray, 1821) which presented several innovations including many new generic names and also the first hierarchical classification of liverworts into five major groups (four thalloid and one leafy): Ricciadeae, Targionideae, Anthocerideae, Marchantiadeae and Jungermannideae. *Asterella* was not treated but the related *Reboulia hemisphaerica* (called *Strozzius hemisphericus* (L.) S.F.Gray) was placed in the group Marchantiadeae.

A year later, Dumortier (1822) published his new classification in which *Fimbraria* (later spelled *Fimbriaria*), together with *Marchantia*, *Conocephalus* and *Lunularia,* were placed in the group Cephalotheceae. Soon after, yet another classification was published, by Reichenbach (1828), where *Fimbriaria* was classed as follows: Ordo II Musci; Formatio II Sporangiobrya; Familia XXVII Jungermanniea; B Epiphyllina. In 1829, Corda published a review of the genera of Hepaticae*: Generum Hepaticarum. Die Gattungen der Lebermoose,* which proposed yet another classification, placing *Fimbraria* in the Class Stromatopterideae, Order Marchantiaceae.

The period 1830–1845 saw some stabilisation of the classification; the terms "Tribe" or "Order" became more general. For example, Bischoff (1835), Lindley (1836) and Nees (1838) classed *Fimbriaria* in the Tribe Marchantieae, while Endlicher (1836) placed it in his Ordo Marchantiaceae. This degree of subdivision was accepted until Trevisan (1877) placed *Hypenantron* in a new Tribe Hypenantreae along with *Rhacotheca*, distinct from the sister-tribes Marchantieae and Grimaldieae.

The first major breakthrough in subdividing the Marchantiales was made by Leitgeb (1881) in his classic and very detailed *Untersuchungen über die Lebermoose* wherein "Marchantiaceen" were subdivided into three groups:

1. Riccieen (*Riccia*, *Ricciocarpus*, *Oxymitra*)
2. Corsinieen (*Corsinia*, *Boschia*)

3. Marchantieen
   a) Astroporae (*Clevea*, *Sauteria*, *Peltolepis*).
   b) Operculatae (*Plagiochasma*, *Reboulia*, *Grimaldia*, *Duvalia*, *Fimbriaria* [= *Asterella*])
   c) Targionieae (*Targionia*, *Cyathodium*)
   d) Compositae (*Fegatella* (?), *Lunularia*, *Dumortiera*, *Preissia*, *Marchantia*).

This system was adopted and further elaborated by Schiffner (1893–1895) as part of Engler & Prantl's *Die Natürlichen Pflanzenfamilien*. The Marchantiales were divided into two Families, Ricciaceae and Marchantiaceae, and the latter was split into three Subfamilies. The division into families and subfamilies was primarily based on the positioning of the sporophytes: within the thallus, on sessile receptacles or in elaborate specialised stalked receptacles. The third and largest of these subfamilies, the Marchantioideae, were further divided into Leitgeb's three informal groups primarily on characters of the air pores of the thallus and on the mode of dehiscence of the sporogonium. *Asterella* (under Schiffner's name *Hypenantron*) was classed in the group Operculatae, *i.e.* those genera with the capsule circumscissile, dehiscing by an operculum (lid).

Since Leitgeb and Schiffner's time the trend has been to increase the number of families within the Order Marchantiales, and also to divide the Order into Suborders. Leitgeb's "Group" Operculatae was given familial rank by Cavers (1910–1911) as Aytoniaceae, by Evans (1923) as Rebouliaceae and by Müller (1939–1940) as Grimaldiaceae.

Bischler (1998) has provided a detailed description of the Order Marchantiales as now defined, and the currently accepted subdivision of Marchantiales into families and genera has been summarised by Schuster (1984b) and Bischler (1998) (see Table 1.1). Accepted in this system are five suborders and fifteen families, in contrast to Schiffner's two families. However, many of the differences between the two classifications are essentially of name and rank and do not reflect any major taxonomic advance. Leitgeb's *Astroporae* are the same as Schuster's Cleveaceae except that *Exormotheca* has been segregated into its own family; Leitgeb's *Operculatae* corresponds exactly with the family Aytoniaceae.

Recent molecular studies, however, are beginning to cast doubts about morphological subdivisions of Marchantiales, for example, the study by Wheeler (2000) brings into question the whole subordinal divisions of Marchantiales as defined by Schuster (1984b); it also undermines the segregation of Monocleales and Sphaerocarpales as orders separate from Marchantiales. However, many families of Marchantiales were not included in Wheeler's study, *e.g.* Conocephalaceae, Wiesnerellaceae and Exormothecaceae, and full reclassification of Marchantiales based

on molecular studies is not yet possible. His study, nevertheless, supports Aytoniaceae as a natural monophyletic group, but is not resolved enough to identify an outgroup for Aytoniaceae and does not include enough *Asterella* species to identify well-supported clades within the genus. For further discussion see Chapter 5.

The family Aytoniaceae is defined and distinguished from other families of Marchantiales (Table 1.2), primarily by characters of the thallus (simple pores, absence of gemmae), archegoniophore (dorsal or terminal in position, with or without a rhizoid furrow in the stalk, compound receptacle pores, involucre bilabiate, bilobed or entire) and sporophyte (capsule dehiscing by a lid). The closest relatives are not well-established, but may be Cleveaceae and possibly Conocephalaceae.

Table 1.1. Modern classification of genera within Order Marchantiales, based on morphological studies (from Grolle (1983), Schuster (1984b) and Bischler (1998))

Suborder Marchantiineae	
Family	Cleveaceae
	Genus *Athalamia*
	Genus *Sauteria*
	Genus *Peltolepis*
Family	Aytoniaceae
	Genus *Plagiochasma*
	Genus *Reboulia*
	Genus *Mannia*
	Genus *Cryptomitrium*
	Genus *Asterella*
Family	Lunulariaceae
	Genus *Lunularia*
Family	Conocephalaceae
	Genus *Conocephalum*
Family	Wiesnerellaceae
	Genus *Wiesnerella*
Family	Exormothecaceae
	Genus *Exormotheca*
	Genus *Stephensoniella*
Family	Aitchisoniellaceae
	Genus *Aitchisoniella*
Family	Marchantiaceae
	Genus *Bucegia*
	Genus *Neohodgsonia*
	Genus *Marchantia*
	Genus *Preissia*
	Genus *Dumortiera*
Family	Monoseleniaceae
	Genus *Monoselenium*
Suborder Targioniineae	
Family	Targioniaceae
	Genus *Targionia*
Family	Cyathodiaceae
	Genus *Cyathodium*
Suborder Monocarpineae	
Family	Monocarpaceae
	Genus *Monocarpos*
Suborder Corsiniineae	
Family	Corsiniaceae
	Genus *Corsinia*
	Genus *Cronisia*
Suborder Ricciineae	
Family	Ricciaceae
	Genus *Riccia*
	Genus *Ricciocarpus*
Family	Oxymitraceae
	Genus *Oxymitra*

Table 1.2 Differences between Aytoniaceae and possible related families of Marchantiales
Based on data from Müller (1951–1958), Schuster (1984a, 1984b, 1992c), Bischler (1998).

	Aytoniaceae	Cleveaceae	Lunulariaceae	Conocephalaceae	Exormothecaceae	Marchantiaceae
Gametophyte						
basic chromosome no.	9	9	9	9	8	9
thallus pores	simple	simple	simple	simple	simple	compound
pore thickening	weak	stellate or absent	absent	absent	absent	absent
rows ventral scales	2	undefined	2	2	2	2–6
stalk position	dorsal or terminal	dorsal or terminal	terminal	terminal	terminal	terminal
no. rhizoid furrows	0 or 1	0, 1 or 2	0	1 or 2	1	1–4
receptacle pores	compound	simple or absent	absent	compound	simple	compound or absent
androecia	scattered/ cushion	scattered/ cushion	cushion	cushion	scattered	stalked
paraphyses in androecia	present	absent	absent	absent	absent	absent
involucre	bilabiate, bilobed or entire	bilabiate	tubular	tubular	tubular	bilabiate
pseudoperianth	present or absent	absent	absent	absent	absent	present or absent
stalk elongation	after fertilisation	after fertilisation	after fertilisation	after fertilisation	after fertilisation	before fertilisation
gemmae	absent	absent	present	present	absent	present or absent
Sporophyte						
capsule wall thickening	present or absent	present	absent	present	present	present
capsule dehiscence	lid	irregular valves	4 regular valves	irregular valves	irregular valves	irregular valves
spore: elater	4:1	4:1	>4:1	4:1 or <4:1	1:1 or 4:1	>4:1

1.4.2 The family Aytoniaceae and its genera

As discussed above, the Aytoniaceae is a long-established well-defined family; its main features are summarised in Table 1.2. Its most important defining character (synapomorphy) is the dehiscence of the sporogonium by a lid. Other features (Bischler, 1998) include the ability to produce apical thallus tubers, the frequent occurrence of ventral branching, a thallus with air chambers in one to several layers and ventral scales often with tapering appendages.

However, it remains unclear which are the close relatives of Aytoniaceae; Schuster (1992c) gave the Cleveaceae followed by the Exormothecaceae as the closest families. Bischler (1998) in her morphological cladistic study gave the sister group of the Aytoniaceae as a clade containing Wiesnerellaceae, Conocephalaceae, Lunulariaceae and Marchantiaceae. Wheeler (2000), on the other hand, using molecular cladistics, concluded that Aytoniaceae was sister-group to a clade which included several different families: Cleveaceae, Monocleaceae, Targioniaceae and Ricciaceae (one of these according to Schuster's classification was placed in a different subclass, and two in different suborders of Marchantiales!). Thus, currently, there is no consensus on the relationships of the Aytoniaceae. Several of the most likely related families are compared in Table 1.2. Cleveaceae is distinguished by the lack of or presence of only simple receptacle pores and capsule dehiscence by irregular valves. Better sampling at the molecular level offers the best hope to resolve the question of the relationships of Aytoniaceae.

Before describing and comparing the species of *Asterella*, it is important first to define the genus and establish its monophyly. Within the Aytoniaceae five genera are currently recognised (Grolle 1983a). The major differences are tabulated in Table 1.3 and keyed out below. The four sister-genera are then discussed briefly, particularly any taxonomic or classificatory problems which may parallel those found in *Asterella*, and to examine whether *Asterella* is monophyletic.

Besides being by far the largest of the five genera in number of species, *Asterella* is also the most polymorphic: out of the ten characters tabulated in Table 1.3, *Asterella* is polymorphic for seven, the only constant features being the apical position of the peduncle, the single rhizoid furrow and the pseudoperianth. In fact, the last is the only unambiguous distinguishing feature of *Asterella*. In contrast, *Plagiochasma* is polymorphic for only one of the ten characters, and is uniquely defined by two of them (dorsal peduncles and absence of rhizoid furrow). The other three genera have no unique distinguishing features and are only defined by a combination of characters. Thus, without the pseudoperianth character, only two genera (*Plagiochasma* and *Asterella sensu lato*) could be defined in Aytoniaceae. This lack of unique defining characters gives cause for concern; for example that *Cryptomitrium*, *Mannia* and *Reboulia* could be derivatives of *Asterella*, or are of questionable distinctness from each other. *Cryptomitrium* in particular, shows some striking similarities to some *Asterella*

species, for example *Cryptomitrium oreades* Perold has spores very similar to *Asterella palmeri* (Austin) Underw. and *A. grollei* D.G. Long. Thus the monophyly of *Asterella* rests solely on one character and might therefore be questioned. However, this character (the pseudoperianth) is such a striking and distinctive feature of all *Asterella* species, that its use to define *Asterella* as a solidly-based genus has never been questioned, which implies an assumed monophyly of the genus on morphological criteria.

Key to Genera of Aytoniaceae

1. Peduncle dorsal on thallus and without rhizoid furrow **1. *Plagiochasma***
+ Peduncle terminal in apical notch of thallus and with 1 rhizoid furrow 2

2. Pseudoperianth present .....**5. *Asterella***
+ Pseudoperianth absent 3

3. Air pores with 4–6 rings of cells; peduncle with air chambers; receptacle deeply lobed; androecia surrounded by scales; spores yellow .....**2. *Reboulia***
+ Air pores with 1–3 rings of cells; peduncle without air chambers; receptacle shallowly lobed; androecia without scales; spores black or brown 4

4. Receptacle hemispherical; involucre skirt-like .....**3. *Mannia***
+ Receptacle flat-topped; involucre bilabiate .....**4. *Cryptomitrium***

Table 1.3 Differences between genera of Aytoniaceae
Based on data from Bischler (1998) and Schuster (1992c).

	Plagiochasma	*Reboulia*	*Mannia*	*Cryptomitrium*	*Asterella*
Androecium type	cushions	cushions	cushions/ scattered	scattered	cushions/ scattered
Androecial scales	present	present	absent	absent	absent or present
Peduncle position	dorsal	apical	apical	apical	apical
Peduncle air chambers	absent	present	absent	absent	absent or present
No. rhizoid furrows	0	1	1	1	1
Receptacle shape	depressed hemispheric	depressed hemispheric	depressed hemispheric	discoid	discoid/ hemispheric
Involucre	bilabiate	bilabiate	cup	bilabiate	entire or cleft flap
Pseudoperianth	absent	absent	absent	absent	present
Spore colour	black/ brown	yellow	black/ brown	black/ brown	black/ brown/ yellow
Spore primary ornamentation	regularly areolate	regularly areolate	saccate/ irregularly areolate	irregularly/ regularly areolate	smooth/ ridged/ regularly/ irregularly areolate



Fig. 1.1 a, *Plagiochasma appendiculatum* (Nepal, *Long 21640*); b, *Reboulia hemisphaerica* (India, Sikkim, *Long 22725*).

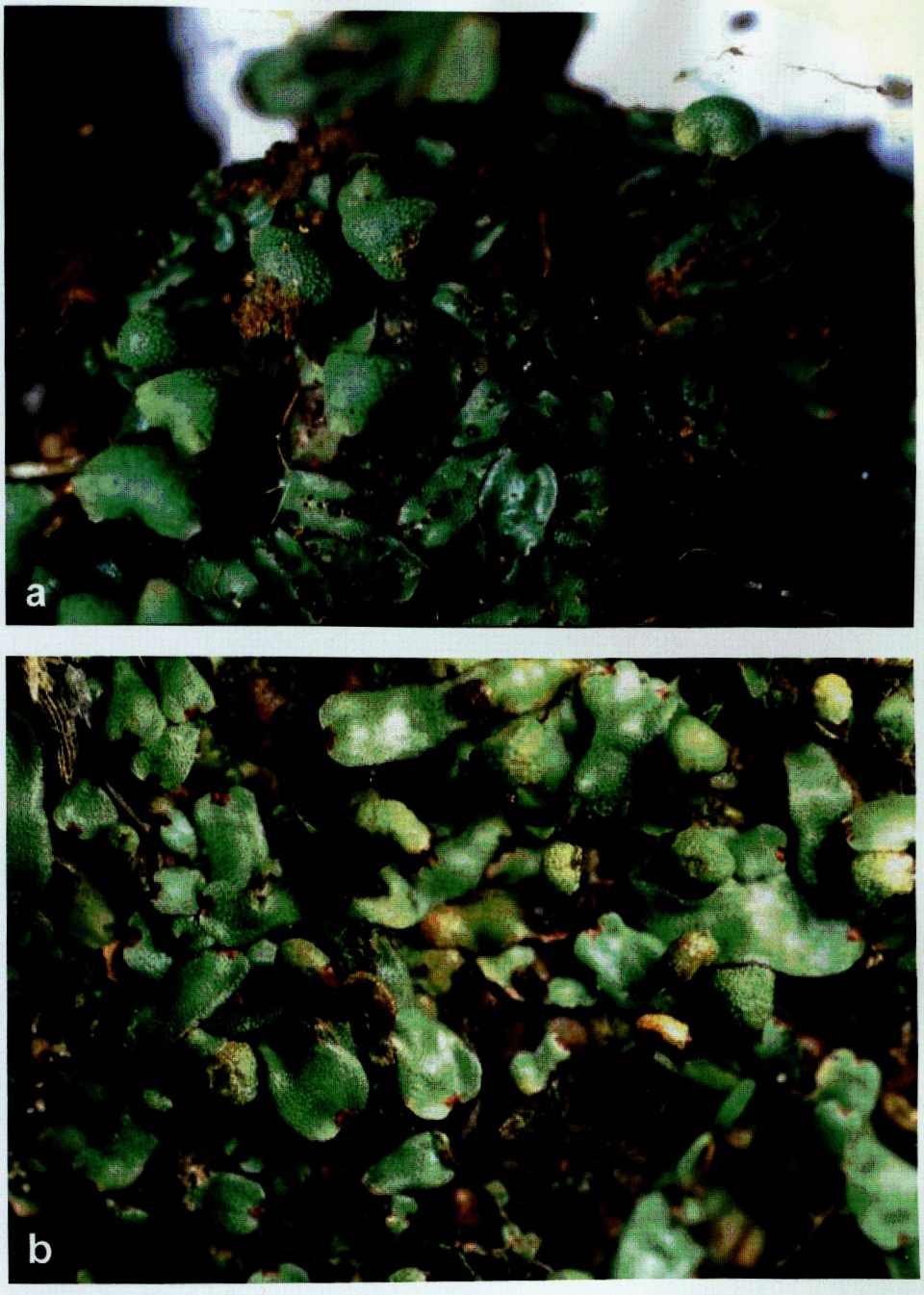

Fig. 1.2 a: *Mannia androgyna* (Madeira, *Long 25074*);
b: *Asterella wallichiana* (Japan, Iriomote, *Yamaguchi 11383*).

Plagiochasma

Plagiochasma Lehm. & Lindenb. in Lehmann, Novarum et Minus Cognitarum Stirpium Pugillus Quartus 13, 1832. (*nom. cons.*).

Type: *P. cordatum* Lehm. & Lindenb. (*type cons.*)

Plagiochasma (Fig. 1.1a), the type genus of Aytoniaceae, is perhaps the most distinctive of the five genera and is readily separated (Table 1.3) by its leathery, strongly xeromorphic thalli; dorsal position of the archegoniophores on the thallus, absence of a rhizoid furrow in the stalk; and the subspherical receptacles with strongly bivalved involucres. The generic name has been conserved against the earlier *Aytonia* from which the family takes its name.

Apart from an earlier monograph of the American species (Evans, 1915), the genus has recently been studied in depth by Bischler (1977, 1978, 1979a, 1979b) and Baudoin & Bischler (1978, 1979a, 1979b), who divided it into two subgenera, based primarily on air pore structure. They recognised a total of sixteen species worldwide. The genus is typical of warm-temperate and tropical regions of the world, a reflection of its xeromorphic adaptations.

Reboulia

Reboulia Raddi, Opuscoli Scientifici (Bologna) 2: 357, 1818.

Type: *R. hemisphaerica* (L.) Raddi

Reboulia (Fig. 1.1b) is distinctive in its relatively smooth thallus, glaucous-green in colour with purplish margins, and its depressed-hemispheric, lobed receptacles which lack pseudoperianths. Anatomically, a striking diagnostic feature is the presence of air chambers in the peduncle. *Reboulia* has been described in detail in many Floras, *e.g.* Macvicar (1912), Kashyap (1929–1934), Müller (1951–1958) and Paton (1999).

In recent years it has been considered to be a monospecific genus, *e.g.* by Müller (1951–1958), with taxa such as *Mindal pangiensis* Kashyap from the Himalaya and *Reboulia javanica* Nees from Java treated as synonyms of *R. hemisphaerica* (L.) Raddi. This view has been challenged recently by Hicks (1992) who reinstated *Reboulia queenslandica* (Steph.) Hicks for some plants from Australia. Schuster (1992c) treated and described several infraspecific taxa under *R. hemisphaerica*, these differing primarily in disposition of androecia and archegoniophores.

These sexual differences parallel those in species of *Asterella*. The type of *Marchantia hemisphaerica* L., a Dillenian specimen, has been shown by Schuster (1992c) to be par-autoicous 'paroicous' (see 2.5.9 for terminology) with androecial cushions median on the thallus immediately posterior to the base of the archegoniophore. *Reboulia queenslandica* differs in having "terminal autoicy" with the androecial cushions terminating abbreviated terminal branches and thus in time appearing *lateral* to the continuing female branch. *R. hemisphaerica* subsp. *sabaliana* R.M.Schust. from Florida, U.S.A. and subsp. *orientalis* R.M.Schust. from Japan, show ventral autoicy similar to that

found in *Asterella multiflora* (Steph.) Kachroo, with androecia terminal on main thalli and archegoniophores borne on short ventral branches or innovations. Unfortunately these recently-described taxa were not compared with earlier segregates when described. Schiffner (1900) showed that "terminal autoicy" can occur in *R. javanica* Nees; Douin & Douin (1918) gave it as an important character of their *R. charrieri* C. & R. Douin and *R. occidentalis* C. & R. Douin; Kashyap (1916) described it in *Mindal pangiensis* Kashyap, and Schuster (1992c: fig. 941.1) illustrated it in his *Reboulia hemisphaerica* subsp. *acrogyna* R.M.Schust.

A world revision of *Reboulia* is clearly much needed, incorporating, if possible, cultivation studies of different populations from around the world. The description of new specific and infraspecific taxa seems premature.

Mannia

Mannia Opiz, Naturalientausch [12] (Beiträge zur Naturgeschichte [1]): 646, 1829.

Type: *Mannia michelii* Opiz, *nom. illeg.* [= *M. androgyna* (L.) A.Evans (see Long & Grolle, 2000)]

Mannia (Fig. 1.2a) is a genus estimated to comprise possibly eight to ten species worldwide, though, according to Engel (1990) there are six species and according to Schuster (1992c) around eighteen species. All are northern hemisphere taxa except for the South African *M. capensis* (Steph.) S.W.Arnell. Although a much smaller genus than *Asterella,* its constituent species provide some interesting parallels with those of *Asterella*, especially in the presence of xeromorphic and hygromorphic taxa and some striking spore ornamentation patterns which are species-specific. It requires a comprehensive revision worldwide, especially in Asia where several local taxa exist which may prove to be minor variants of more widespread species. Some taxa are highly aromatic with a smell quite different to that of *Asterella* (such as *M. fragrans* with its strong smell of cedar oil). The terpenoids and other chemical constituents of both genera require thorough investigation.

The subgeneric/ generic subdivision of *Mannia* has long been confused. Müller (1905–1916) used the name *Grimaldia* (for the European *G. fragrans* (Balb.) Corda, *G. dichotoma* Raddi *nom. illeg.* and *G. pilosa* (Hornem.) Lindb.) and kept apart *Neesiella* for *N. rupestris* (Nees) Schiffn. by virtue of its broader thinner thalli with thin-walled air pores and inconspicuous ventral scales, though he (Müller, 1951–1958) later united both under *Grimaldia*.

Shimizu & Hattori (1954) took a broader view and united both *Neesiella* and *Cryptomitrium* under *Mannia*. Their subgenus *Mannia* included the xeromorphic species such as *M. fragrans* (Balb.) Frye & L.Clark, *M. dichotoma* S.W.Arnell and *M. californica* (Gottsche) L.C.Wheeler, with compact chlorenchyma containing crowded vertical supplementary partitions in the air chambers, thick-walled epidermal cells and 3–4-lobed

receptacles. Their second subgenus *Cryptomitrium* differed in its loose chlorenchyma without crowded supplementary partitions in the air chambers, mesophytic habit, thin-walled epidermal cells and receptacles which are not 3–4-lobed. This subgenus was subdivided into two sections: sect. *Neesiella*, including *Mannia rupestris* (Nees) Frye & L.Clark and *M. pilosa* (Hornem.) Frye & L.Clark with autoicous inflorescences and subspherical receptacles, and Sect. *Cryptomitrium* with par-autoicous inflorescence and flat receptacles. However they did not formally transfer the species of *Neesiella* and *Cryptomitrium* to *Mannia*.

Odrzykoski & Szweykowski (1981) have demonstrated enzyme polymorphism in *Mannia fragrans* in Poland and Germany, analysed by starch gel electrophoresis. Using this technique they demonstrated that there are two chemical races in eastern Europe. These races or 'cryptic species' are indistinguishable morphologically, but show two striking geographical patterns, which may be explicable in terms of isolation and migration of distinct genotypes. This approach to "genetic biogeography" has been applied to several thalloid liverworts and to some mosses (*e.g.* Shaw 1995). It has not yet been applied to *Asterella*. It could be usefully tried out in individual species, particularly for weedy species in which some populations may be actively expanding their ranges, or for disjunct populations of widespread species.

Cryptomitrium

Cryptomitrium Austin ex Underw., Bulletin of the Illinois State Laboratory of Natural History 2: 36, 1884. Type: *C. tenerum* (Hook.) Austin ex Underw.

A rare genus of three species: *C. tenerum* from U.S.A. (Washington, California), Mexico, Costa Rica, Guatemala, Argentina and Chile, *C. himalayense* Kashyap from India (North West Himalaya, Sikkim, South India) as well as Nepal and China (Yunnan), and *C. oreades* Perold from South Africa (Perold, 1994d).

Cryptomitrium is morphologically similar to some species of *Mannia* and has sometimes been united with it (Shimizu & Hattori, 1954). The differences (Table 1.3) lie primarily in the structure of the involucre. The American and Asiatic *Cryptomitrium* species are highly hygromorphic and at first glance in the field resemble the species of *Asterella* sect. *Brachyblepharis* (*e.g. A. khasyana*) in their delicate thalli and flat-topped receptacles.

Cryptomitrium tenerum has been studied in detail by Abrams (1899) and Haupt (1942). *C. himalayense* was treated by Mehra & Sokhi (1977), while Kachroo & Kaul (1971) compared the two species.

1.4.3 Review of the genus *Asterella* and its species

Asterella P.Beauv., in Cuvier (ed.), Dictionnaire des Sciences Naturelles 3:257, 1805 "1804". Lectotype: *A. tenella* (L.) P.Beauv. [= *Marchantia tenella* L.].

For generic synonymy see Chapter 4 (4.5.1.1)

Asterella (Fig. 1.2b) is distinguished (Table 1.3) from the other genera of Aytoniaceae primarily by the presence of a deeply divided pseudoperianth around the sporogonium. In addition, many species of *Asterella* have a characteristic fishy smell, which may derive from a terpenoid but has not yet been identified chemically. Pseudoperianths are also reported (Schuster, 1992c) in Marchantiaceae (*e.g. Marchantia* and *Preissia*) but are not deeply incised cage-like structures as in *Asterella*. The *Asterella* pseudoperianth appears to be unique amongst the Hepaticopsida. The homology of the structures in the two families requires investigation (see Chapter 5).

Asterella is the second largest genus of Marchantiales with about one hundred and thirty-five species described under *Asterella* and its synonyms. Engel (1990) estimated the genus to have about 80 species, probably a realistic provisional total. It is by far the largest genus in Aytoniaceae, greatly outnumbering the combined total for all the other genera.

A short review of taxonomy of the genus worldwide is given below, including important literature and the species reported from different continents.

Nomenclatural and taxonomic history of the genus *Asterella*

Both taxonomically and nomenclaturally the genus *Asterella* has had a troubled history. Taxonomically it has been confused with the related genus *Mannia* because of the close similarity of the vegetative thalli; nomenclaturally it has been known principally under three names *Asterella*, *Fimbr(i)aria* and *Hypenantron*. Also, the name *Asterella* has, in the past, been applied to another related genus (now known as *Reboulia*) as a well as to a genus of Fungi. The genus *Fimbriaria* has also been used for a genus of Algae. The taxonomic confusion over generic identity was cleared up by Nees (1820, 1838) but the nomenclatural uncertainty has only just been put to rest by the conservation of the generic name *Asterella* with a new type (Long & Grolle, 1992a, 1992b). The purely nomenclatural parts of the history of *Asterella* (*e.g.* typification) are dealt with in Chapter 4. The development of knowledge of *Asterella* as a genus can be summarised in four phases:

- Phase 1: 18th century, up to and after Linnaeus' *Species Plantarum* (1753).
- Phase 2: 1800 to the *Synopsis Hepaticarum* of Gottsche, Lindenberg & Nees (1844–1847).

- Phase 3: 1850 to 1900 (but including Stephani's *Species Hepaticarum* (1898–1925)).
- Phase 4: 20th century.

Phase 1: 18th century, up to and after Linnaeus: polynomials and *Marchantia*.

Although references to thalloid liverworts exist in herbal literature dating back to Ancient Greek times, under names such as *Lichen* and *Pulmonaria* (Scott, 1987), they were often confused with lichens in ancient times and few are identifiable with certainty to modern genera (Schuster, 1966). Certainly, none appears to correspond to *Asterella* as now recognised. Before Linnaeus' *Species Plantarum* (1753) the most important works to describe Hepaticae in any systematic and detailed way were the *Nova Plantarum Genera juxta Tournefortii Methodum Disposita* of Micheli (1729) and the *Historia Muscorum* of Dillenius (1741).

Linnaeus, although highly influential in the classification of the Hepaticae as the originator of the binomial system and for providing the starting-point for modern liverwort nomenclature, was not well-versed in hepaticology, and treated liverworts as "Cryptogamia Algae" (Isoviita, 1970). As noted by Schuster (1966): "Linnaeus' lack of familiarity with the hepatics is evident from the fact that he took the natural genus *Marchantia*, as defined by Micheli (including *M. polymorpha* L. and *M. paleacea* Bertol.), and placed in it such diverse elements as *Reboulia*, *Asterella*, *Conocephalum*, and *Lunularia*." Most of Linnaeus' work on liverworts was taken from the earlier works of Micheli and Dillenius, especially the latter (Isoviita, 1970).

Micheli (1729) did not describe any *Asterella* species as the genus was not discovered in Europe until shortly before 1805. The first clear description of a species of *Asterella* I have traced in the literature is that of Dillenius (1741) which is of a North American species, under the name of '*Lichen pileatus parvus carinatus, capitulis fimbriatis'. (The small channelled liverwort, with fringed caps).* Dillenius (*l.c.*) described and illustrated this species (the first published illustration of an *Asterella*) from a plant collected in Virginia in the early 18th century by J. Clayton and named "*Lichen terrestris pileatus* Clayt. n. 377". Earlier, Gronovius (1739) in the first edition of his *Flora Virginica,* had treated Clayton's plant under Micheli's "*Hepatica vulgaris major, vel officinarum, Italiae*", which, as explained by Evans (1920), equates with *Conocephalum conicum* (L.) Dumort. Hence Dillenius (1741) was the first to recognise the distinctiveness of Clayton's plant, stating (translation):

> "Towards the thallus tips the thallus gives rise to a black thread-like pedicel one inch long, without a capsule, on which sits a small, rotund, apiculate capitulum enclosed at the margin by pure-white fimbriae; colour above partly red-brown, below white. Fimbriae composed of slender pellucid ligules, [Fig.] a, b, attached in the margin of the capitulum; in function lightly separating, colour of lower part white, upper part becoming purple."

This, combined with his illustration showing dissected pseudoperianth lobes, and the inclusion of "capitulis fimbriatis" in his polynomial, confirms that Dillenius realised the importance of the pseudoperianth in distinguishing Clayton's plant from other known liverworts.

Linnaeus (1753) based his treatment of this plant on Dillenius' (1741) description and illustration and gave it a binomial: *Marchantia tenella* L. (the first published binomial for an *Asterella* species). However, he did not grasp the importance given by Dillenius to the "fimbriae" and left the plant in the very large genus *Marchantia* (Table 1.4), which also included *M. hemisphaerica* L. (later segregated as *Reboulia*) and other species belonging to *Marchantia* in the modern sense. Gronovius (1762), in the second edition of *Flora Virginica*, followed Dillenius' taxonomy but used Linnaeus' polynomial (not his binomial) as a name, and placed Dillenius' and Clayton's polynomials as synonyms. After Linnaeus, the binomial system was adopted for all newly described taxa. However, no accepted generic identity was established for *Asterella* before 1800.

Table 1.4 Past generic placements of six species which have been included in *Asterella* and its synonyms

Showing how authors on Marchantiales have treated *Asterella* between 1753 and the present day. Before *Asterella* was established its constituent species were treated under several different generic names at different periods. The examples shown are the type species of the respective generic names.

Author	***Marchantia tenella* L. 1753**	***Marchantia hemisphaerica* L. 1753**	***Fimbraria marginata* Nees 1820**	***Hypenantron ciliatum* Corda 1829**	***Rhacotheca azorica* Bisch. 1844**	***Octokepos khasyanum* Griff. 1849**
Linnaeus (1753)	*Marchantia*	*Marchantia*	–	–	–	–
Schwägrichen (1814)	*Marchantia*	*Marchantia*	–	–	–	–
Raddi (1818)	–	*Rebouillia*	–	–	–	–
Nees (1820)	*Fimbraria*	–	*Fimbraria*	–	–	–
Gottsche et al. (1844–7)	*Fimbriaria*	*Reboulia*	*Fimbriaria*	*Fimbriaria*	*Rhacotheca*	–
Trevisan (1853)	–	*Reboulia*	*Hypenantron*	–	–	–
Trevisan (1877)	*Hypenantron*	*Asterella*	*Hypenantron*	*Hypenantron*	*Rhacotheca*	–
Schiffner (1893–5)	*Hypenantron*	*Reboulia*	*Hypenantron*	*Hypenantron*	*Hypenantron*	*Hypenantron*
Stephani (1898–1924)	*Fimbriaria*	*Reboulia*	*Fimbriaria*	–	*Fimbriaria*	*Fimbriaria*
Evans (1920)	*Asterella*	*Reboulia*	*Asterella*	*Asterella*	*Asterella*	*Asterella*

Phase 2: 1800 to the *Synopsis Hepaticarum* of Gottsche, Lindenberg & Nees (1844–1847): confusion of generic names and adoption of *Fimbriaria*.

The name *Asterella* was coined and first validly published by the French botanist Palisot de Beauvois (1805) who included in it two species: *A. tenella* (L.) P.Beauv. (*Marchantia tenella* L.) and *A. hemisphaerica* (L.) P.Beauv. (*Marchantia hemisphaerica* L.). His description translates as follows:

> "*Asterella*, genus of plants of the family Hepaticae, of my system.
> *Character: male flowers*: umbel rounded, borne on a fleshy peduncle, without perichaetium, florets several, sessile, with 6 to 10 divisions enclosing a mass of elastic threads to which are attached the grains of the fertile powder.
> *Female flowers*: membranous, cupuliform, sessile, adhering to the epidermis, containing several rounded seeds, flattened and concave.
> The genus is a dismemberment of *Marchantia* L. It contains 2 species.
> *Asterella tenella* Dill., tab. 75, fig. 4.
> *Asterella hemisphaerica*, Dill. tab. 75, fig. 2."

Several conclusions can be drawn from this; firstly that Beauvois interpreted the receptacle (carpocephalum) as "male flowers", and the spores as pollen; secondly, what he called "female flowers" are clearly the gemma cups of *Marchantia sensu stricto*, as such structures are unknown in either of the two constituent species he included; thirdly, the "6 to 10 divisions" of the "florets" clearly describe the pseudoperianth now considered unique to *Asterella* in the modern sense. The name *Asterella* presumably derives from this pseudoperianth, though Beauvois' second species, *Asterella* [= *Reboulia*] *hemisphaerica* lacks such a structure. Beauvois probably realised that Linnaeus' *Marchantia* was heterogeneous but his "dismemberment" was poorly researched and supported. The relatively obscure place of publication, too, did not lead to the adoption of the genus *Asterella* by other contemporary botanists.

Also in 1805 came the first published record for a European member of the genus, in the third edition of *Flore Française* of Candolle & Lamarck (1805) under the name *Marchantia fragrans*. Their description was of plants collected by Schleicher near Branson in Kanton Valais, Switzerland. Unfortunately, Candolle & Lamarck identified these with *Marchantia fragrans* Balb., described from Italy in 1804 (which is now known as *Mannia fragrans* (Balb.) Frye & L.Clark) and the epithet *fragrans* therefore cannot be used for Schleicher's plant. This confusion is exacerbated by the close vegetative similarity between the genera *Mannia* and *Asterella* when specimens lack carpocephala, which later led to much nomenclatural confusion. Candolle & Lamarck made no reference to Beauvois' new genus *Asterella*.

In 1810 and 1812 this pattern of misapplication of names was repeated with the discovery of a second European species, this time from Norway, described under *Marchantia pilosa* by Wahlenberg (1812) in *Flora Lapponica*. Unfortunately, this name was taken from Hornemann's (1810) *Flora Danica* where the Swedish plant illustrated on t. 1426. as *Marchantia pilosa* Hornem. is clearly a *Mannia* (now *M. pilosa* (Hornem.) Frye & L.Clark). Wahlenberg's plant, with "calyptra exserta fimbriata" clearly refers to an *Asterella* and is correctly *A. gracilis* (F.Weber) Underw.

Meanwhile, Wahlenberg in 1811 had published a short report on bryophytes from Kamchatka in the North West Pacific collected by Tilesius on a Russian expedition between 1803 and 1805 (probably 1804). Amongst these was the new liverwort *Marchantia saccata* Wahlenb. which he compared to *M. pilosa* Hornem. He illustrated a dissected pseudoperianth. Soon after, Wallroth (1815) equated this with the European *Marchantia fragrans*, but used the latter epithet for it rather than *saccata*.

In 1814 C.F. Schwägrichen published his *Historia Muscorum Hepaticarum Prodromus,* a review of all known liverwort names. He did not recognise Beauvois' *Asterella* but kept *A. tenella* under *Marchantia* (Table 1.4) along with the new *M. ludwigii* Schwägr. [long regarded as an *Asterella* but shown by Grolle (1975a) to be *Mannia triandra* (Scop.) Grolle] along with *Marchantia pilosa* Hornem. [= *Mannia pilosa* (Hornem.) Frye & L.Clark], *M. saccata* Wahlenb., *M. tenella* L. and *M. fragrans* Balb. [= *Mannia fragrans* (Balb.) Frye & L.Clark]. The result was that several taxa belonging to both *Mannia* and *Asterella* were firmly entangled under *Marchantia*.

The following year, Weber (1815) essentially repeated but expanded on what Schwägrichen had done; amongst 20 species of *Marchantia* he described a new species *M. gracilis* F.Weber from Uppsala in Sweden where it had been collected by Wahlenberg, Mohr and Weber. This was to be the first new validly published *Asterella* species from Europe.

In 1818, Raddi published his *Novarum vel rariorum ex cryptogamia stirpium in agro florentino collectarum decades duo*, a description mostly of Marchantiales growing around Florence in Italy. Amongst these was the new genus *Rebouillia* Raddi with the single species *Rebouillia hemisphaerica* (L.) Raddi, based on *Marchantia hemisphaerica* L.(Table 1.4). Raddi made no mention of Beauvois' *Asterella hemisphaerica* (L.) P.Beauv. (which is based on the same type). However, after Raddi's publication, *Reboulia* [*orthography changed by* Nees von Esenbeck 1846 *and later conserved*] has almost without exception been used for *M. hemisphaerica* L. Since then, *Asterella* has been used only very rarely for *M. hemisphaerica*, by Trevisan (1877) (see Table 1.4).

The first real clarification of generic identity came from Nees von Esenbeck (1820) in his *Sylloge Observationum Botanicarum*, in which he accepted four species under a new genus *Fimbraria* (Table 1.4). These were *Fimbraria marginata* Nees described as a new species from the Cape, *F. saccata* (based on *Marchantia saccata* Wahlenb.) from Kamchatka, *F. fragrans* (Balb.) Nees (based on *Marchantia fragrans* Balb.) from Europe

and *F. tenella* (L.) Nees (based on *Marchantia tenella* L.) from North America. *F. marginata* was described in detail, the others were transferred into the new genus with little description. Nees defined the genus by the following "essential" characters, translated as:

> "Fruit receptacle with a peduncle, bearing fruit pointing downwards beneath. Calyptra saccate, laterally split, hanging down. Capsule circumscissile, sessile. Spores with elaters."

Nees also suggested that a further three species, *M. gracilis* F.Weber, *M. ludwigii* Schwägr. and *M. pilosa* Hornem., might belong to *Fimbriaria*, but that further study was needed. Like his contemporaries, he ignored the name *Asterella* completely. *Fimbraria* rapidly gained acceptance, *e.g.* by Dumortier (1822), Sprengel (1827), Lindenberg (1829) and Endlicher (1836), although its spelling was altered to *Fimbriaria* by Steudel in 1826, an orthography which was subsequently generally adopted.

In 1829, Corda, in his *Generum Hepaticarum. Die Gattungen der Lebermoose* accepted *Fimbriaria* with only two species, *F. tenella* and *F. paleacea* (Bertol.) Corda [the latter now *Marchantia paleacea* Bertol.], as well as a new genus *Hypenantron* Corda with a single constituent species *H. ciliatum* Corda [now treated as a synonym of *Asterella saccata* (Wahlenb.) A.Evans] based on material collected in Switzerland by Heller. *Hypenantron*, however, was soon reduced to synonymy of *Fimbriaria*, *e.g.* by Endlicher (1836–1841) and Gottsche, Lindenberg & Nees (1844–1847) and did not gain any general acceptance at the time, although it subsequently reappeared.

This period between 1830 and 1845 saw an increasing number of works including descriptions of both known and new species under the now well-established genus *Fimbriaria*. Works such as Lehmann & Lindenberg (1832), with six *Fimbriaria* species and one variety (including three new species from the Indian region), Lehmann (1834), Bischoff (1835) (with very detailed descriptions of the European *F. fragrans* auct. non (Balb.) Nees and the American *F. tenella* (L.) Nees), Taylor (1837) and Montagne (1838a). Nees (1838), in his *Naturgeschichte der Europäischen Lebermoose*, gave particularly detailed generic description and species descriptions for the European *Fimbriaria* taxa.

Two further genera were published at this time but were only short-lived (see Table 1.4): *Rhacotheca* described by Bischoff (in Seubert, 1844) from the Azores with one species *R. azorica* Bisch. [= *Asterella africana* (Mont.) A.Evans] and *Octokepos* Griff. described posthumously by Griffith (1849) from North-east India, containing a single species, *O. khasyanum* Griff. [= *Asterella khasyana* (Griff.) Pandé *et al.*].

The culmination of this period of rapid bryological exploration and discovery was the synthesis published by the three leading European hepaticologists of the day, Gottsche, Lindenberg and Nees von Esenbeck (1844–1847) in their monumental *Synopsis*

Hepaticarum. In this work a total of 25 species of *Fimbriaria* were treated (as well as *Rhacotheca azorica* Bisch. which was kept separate) from all continents of the world (Table 1.4). The genus was then shown to be worldwide in distribution and tidily circumscribed by its "perianth" [= pseudoperianth] character.

Phase 3: 1850 to Stephani's *Species Hepaticarum* (1898–1925): further confusion and disagreement on correct generic name in Europe; resurrection of both *Hypenantron* and *Asterella* then rehabilitation of *Fimbriaria*.

In a significant but long ignored (due to its rarity in libraries) publication, *Herbarium Cryptogamicum Trevisianum*, Trevisan (1853) pointed out that the liverwort genus *Fimbriaria* was a later homonym of the algal genus *Fimbriaria* Stackhouse, and he therefore rejected its use in the Hepaticae. He replaced it by resurrecting *Hypenantron* Corda (Table 1.4) and relegating "*Fimbriaria* Nees 1820– non Stackh. 1809" to synonymy. Trevisan made new combinations for the European species under *Hypenantron*: *H. fragrans* (Balb.) Trevis. and *H. pilosum* (Taylor) Trevis. as well as the South African *H. marginatum* (Nees) Trevis. He retained *Reboulia* in the now-established sense of Raddi.

The only major authors to follow this re-introduction of *Hypenantron* as an accepted substitute for *Fimbriaria* were Kuntze (1891) and Schiffner (1893–1895) in the first part of Engler & Prantl's *Natürlichen Pflanzenfamilien* (Table 1.4) and again Schiffner (1898) in his *Conspectus Hepaticarum Archipelagi Indici*.

At about the same time two other conflicting solutions were proposed. The first, by Lindberg (1868), was to resurrect *Asterella* as a substitute for *Reboulia* and maintain *Fimbriaria* in Nees' sense. Although subsequently followed by Dumortier (1874) and Lindberg (1875), this proposal never gained general acceptance and was soon superseded by Lindberg himself (1879) in reinstating *Reboulia* for *M. hemisphaerica*.

The second proposal was published by Trevisan (1874) in his *Nuovo censo delle Epatiche italiane*, in which he changed his mind from his 1853 paper and rejected *Hypenantron* in favour of *Asterella*; he was the first author to use *Asterella* as a replacement name for the "rejected" *Fimbraria* Nees. He proposed new combinations for the European species: *Asterella bonjeanii* (De Not.) Trevis., *A. fragrans* (Balb.) Trevis., *A. pilosa* (Taylor) Trevis. and *A. raddii* (Corda ex Nees) Trevis., as well as the American *A. elegans* (Spreng.) Trevis. He retained *Reboulia* in Raddi's sense for *R. hemisphaerica*. Three years later, he (Trevisan, 1877) reverted to his previous (1853) adoption of *Hypenantron*. In his 1877 paper, Trevisan included 23 species under *Hypenantron* and a further two under *Rhacotheca* which he maintained for the Macaronesian plants (Table 1.4).

Lindberg in his *Musci Scandinavici* (1879) favoured Trevisan's 1874 option and he stuck to the genera *Asterella* and *Reboulia*. This was the starting point of the "Scandinavian Proposal" which was followed almost without exception by Scandinavian

authors, and later by American authors (see "Phase 4" below). The other European hepaticologists (except for Schiffner), on the other hand, favoured the system of the *Synopsis Hepaticarum* (Gottsche *et al.*, 1844–1847), to maintain *Fimbriaria* instead of *Asterella* or *Hypenantron* along with *Reboulia* (the "European Proposal"). Le Jolis (1895), in a study of liverwort nomenclature, argued for the latter course of retaining *Fimbriaria* and rejecting *Asterella* on the grounds of its confused application to two different generic entities.

The author who came to dominate European hepaticology at this time was the German Franz Stephani (1842–1927). Stephani was a prolific author who had access to many new collections in the late 19th and early 20th centuries, such as the herbarium of E. Levier. His major work was the 6-volume *Species Hepaticarum* in the first part of which (Stephani, 1898–1900) he treated 69 species under *Fimbriaria* (Table 1.4) as well as providing an "Uebersicht der Arten" (conspectus of the species) arranged into four main groups and 15 smaller groups. Nineteen of these were described as new species, though no key was provided. In the final sixth volume (Stephani, 1917–1925) he added a further 22 species of *Fimbriaria*. *Species Hepaticarum* was not illustrated, although Stephani prepared extensive *Icones* (Geissler, 1982), which are of great value in interpreting his descriptions. The originals are preserved in Geneva and published as a microfiche (Stephani, 1985). His citation of material was extremely brief *e.g.* "Cuba (Wright)" for *Fimbriaria austini* Underw. He gave no ecological information. Stephani's output of new taxa with relatively brief descriptions has been much criticised by later workers, especially Schuster (1966).

Phase 4: 20th century; retention of *Fimbriaria* in Europe, adoption of *Asterella* in Scandinavia and North America.

Three alternative proposals regarding the correct name for *Asterella* survived into the 20th century: (a) the Trevisan/ Schiffner proposal using *Hypenantron*; (b) the European proposal using *Fimbriaria*, and (c) the Scandinavian proposal using *Asterella*. The first of these was last used by Schiffner (1900) in his "*Hepaticae der Flora von Buitenzorg*". Thereafter, Schiffner changed to the European system and used *Fimbriaria*, *e.g.* Schiffner (1902, 1908, 1939).

As Stephani had opted for the second "European Proposal" (to stick with *Fimbriaria*), this system became very entrenched in Europe, used in some countries almost to the present day. For example, it was used in Europe by Boulay (1904), Müller (1905–1916, 1939–1940, 1951–1958), Cavers (1910–1911), Casares-Gil (1919), Meylan (1924), Pavletic (1955), Allorge & Jovet-Ast (1958), Szweykowski (1958), Pilous & Duda (1960), Boros (1968) and Mohan (1984). In Asia, too, it was the favoured system, see, *e.g.* Horikawa (1931, 1934, 1936), Herzog (1930), Kashyap (1929–1934) and Chopra (1943). In America, however, it did not last beyond Spruce (1885–1886) and Underwood (1884). This proposal has now been formally rejected (Long & Grolle 1992a, 1992b).

The third option, after nearly a century of debate, has now been finally accepted worldwide in all important recent works such as Schuster (1953–1958, 1992c) for North American species, Hässel de Menéndez (1963) for South American species, Schljakov (1982) for Soviet species, Grolle (1976) for European species, Arnell (1963) for South African species, Campbell (1965) for New Zealand species, Pandé *et al.* (1954) for Indian species and Shimizu & Hattori (1952, 1953a,b) for Japanese species.

This proposal was at first followed only in Scandinavia, *e.g.* by Lindberg (1879), Lindberg & Arnell (1889), Arnell (1892), Kaalaas (1898), Joergensen (1934), and Mårtensson (1955–1956). Surprisingly few other European authors adopted the system (exceptions are Massalongo (1886), Breidler (1894) and Heeg (1894)), before Grolle (1976) finally established its use in his definitive European check-list. Outside Scandinavia, it quickly found favour in North America, first by Underwood (1895a), then Howe (1898) and especially Evans (1919, 1920, 1923) in his outstanding works on North American species of the genus (Table 1.4). Elsewhere, the system was slower to gain acceptance: in Japan by Hattori (1944), Shimizu & Hattori (1952, 1953a) and all workers thereafter, in India by Kachroo (1952a,b, 1954) and Pandé *et al.* (1954). Now this generic name has been formally accepted worldwide (Long & Grolle, 1992a,b).

This presumed new-found stability, both taxonomic and nomenclatural, may prove to be short lived. Long *et al.* (2000), in using molecular phylogenetics to look at relationships of *Asterella* to other genera of Aytoniaceae and other Marchantiales, have found evidence from chloroplast DNA sequences which suggests that *Asterella* is not a monophyletic genus, but that the sister-genera *Cryptomitrium*, *Mannia*, *Plagiochasma* and *Reboulia* are derived from it, presumably by loss of the pseudoperianth. If these results are further supported by other studies, *Asterella* may have to be dismembered into several smaller genera, defined by different characters than those used at present, or merged into a large single genus incorporating the whole of Aytoniaceae. If the latter course were adopted, *Asterella*, as the earliest available generic name, would be retained for the whole redefined genus.

Asterella species worldwide

Compilation of the *Index Hepaticarum* (Bonner, 1962, 1965, 1977) has highlighted the large number of names validly published in *Asterella* and its synonyms. Table 1.5 shows that Bonner accepted 86 names in *Asterella*, as well as many others not combined into *Asterella* but lurking under *Fimbriaria*. The last world monograph was Stephani's *Species Hepaticarum* (1898–1900, 1917–1925) and since then the problem has been so large that no-one has undertaken the task of untangling the chaos.

As Table 1.5 also shows, prior to Stephani, a few monographs and check-lists covered the genus worldwide: *e.g.* at the time of Linnaeus only one species was known (*A. tenella*) and even at the time of Gottsche, Lindenberg & Nees (1844–1847) it had only risen to 24 species. Since then, all the important progress in *Asterella* has been made at

the continental, country or even regional levels. One or two authors have worked on more than one continent, such as Schiffner (Europe and Asia) and Evans (America and Europe), but few looked at the Indian, African or Australasian taxa apart from local workers.

Table 1.5 Number of *Asterella* / *Fimbriaria* species in world monographs and check-lists
Showing growth of number of accepted *Asterella* names by continent
(names under *Asterella* or its synonyms)

Author	Europe	Asia	Australasia	Africa	America	World
Micheli (1729)	0	0	0	0	0	0
Dillenius (1741)	0	0	0	0	1 (polynomial)	1
Linnaeus (1753)	0	0	0	0	1	1
Schwägrichen (1814)	0	1	0	0	1	2
Weber (1815)	2	1	0	1	1	5
Sprengel (1827)	0	1	0	1	2	4
Gottsche et al. (1844–1847)	7	7	2	3	5	24
Trevisan (1877)	6	7	2	3	5	23
Stephani (1898–1924)	6	23	18	14	29	90
Bonner (1962–1977)	9	38	11	5	23	86

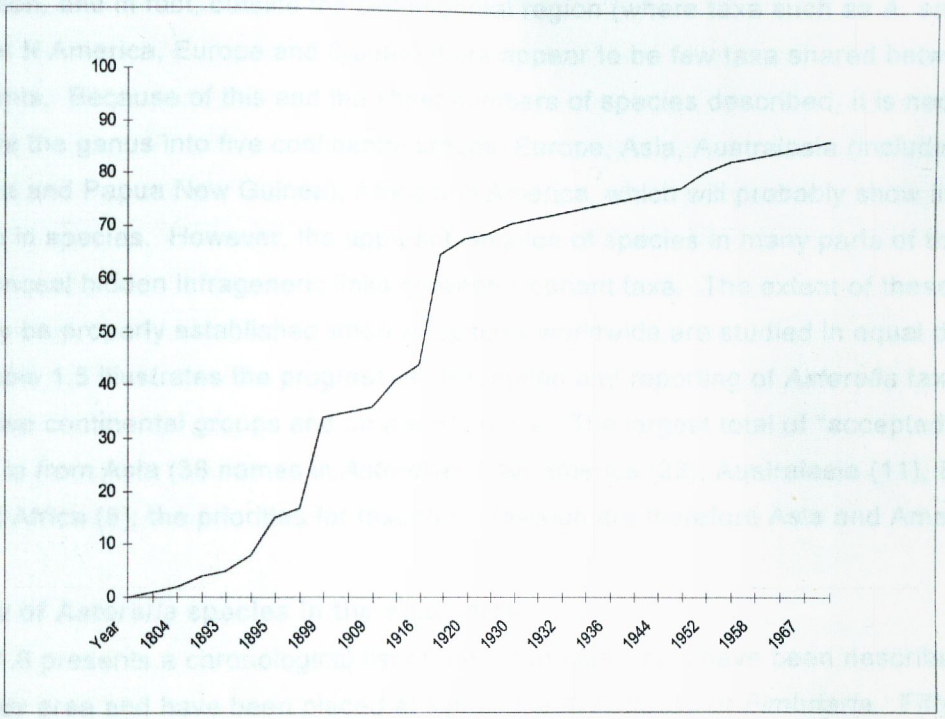

Fig. 1.3 Rate of description of new species of *Asterella* from Eurasia; cumulative total of described species plotted against time from 1753 to 1999.

Table 1.5 and Fig. 1.3 illustrate the steady progress of discovery and description of new *Asterella* taxa, and how their numbers mushroomed between 1899 and 1917. The major reason for this proliferation of names was the reluctance of bryological authors, especially Stephani, to equate similar plants from different countries under a single name. Only from the time of Evans (1920) has a broader outlook been taken. Even within continents, such as India, China and Japan, many new species have been described without reference to related taxa: an example is *Fimbriaria mussuriensis* Kashyap in India, *F. purpureo-capsulata* Herzog & C.E.O.Jensen in China and *Asterella crassa* Shimizu & S.Hatt. in Japan, species closely related to each other and possibly synonymous but described in isolation from the three regions.

However, continental isolation does seem to have played a major role in *Asterella* speciation, and in fact, outside the circumboreal region (where taxa such as *A. saccata* occur in N America, Europe and Siberia) there appear to be few taxa shared between continents. Because of this and the sheer numbers of species described, it is necessary to divide the genus into five continental groups: Europe, Asia, Australasia (including Oceania and Papua New Guinea), Africa and America, which will probably show little overlap in species. However, the apparent isolation of species in many parts of the world may conceal hidden infrageneric links between vicariant taxa. The extent of these links will only be properly established when all species worldwide are studied in equal detail.

Table 1.5 illustrates the progressive description and reporting of *Asterella* taxa in these five continental groups and on a world basis. The largest total of "accepted" names is from Asia (38 names in *Asterella*), then America (23), Australasia (11), Europe (9) and Africa (5); the priorities for taxonomic revision are therefore Asia and America.

Review of *Asterella* species in the study area

Table 1.6 presents a chronological list of names of taxa which have been described from the study area and have been placed at some time in *Asterella* or *Fimbriaria*. Fifty-two have been described from Eastern Asia and Malesia (Table 1.6) and a number of others described from elsewhere have been reported such as *Asterella gracilis* (F.Weber) Underw. and its synonyms. No revision has ever been undertaken of purely Asiatic *Asterella* taxa. The only revisionary studies have been as part of world revisions, particularly Gottsche *et al.* (1844–1847) and Stephani (1898–1925). Gottsche *et al.* recorded seven species from Asia as a whole and Stephani twenty-three (Table 1.5). Of the names accepted under *Asterella* by Bonner (1962, 1965, 1977), 38 are based on Asiatic types. The real number of taxa in Asia has never been evaluated but is likely to be much lower than 38.

Europe. Surprisingly, at the time of Linnaeus' *Species Plantarum* (1753) the only known species of *Asterella* as now defined was a North American species, *Marchantia tenella* L. The first Eurasian species to be described, *Marchantia saccata* Wahlenb. (now *Asterella*

saccata (Wahlenb.) A.Evans) was discovered not in Europe but in Kamchatka, now in the Russian Far East, probably in 1804. The first discovery in Europe was also of *A. saccata*, in Switzerland by J.C. Schleicher, at about the same time, although the name *Marchantia fragrans* Balb. was wrongly applied to it. A second species was reported by Wahlenberg (1812) as *Marchantia pilosa* Hornem. from Norway, again a misidentification. Wahlenberg's plant was the same as *Marchantia gracilis* F.Weber, validly published as a new species from Sweden in 1815.

The relatively late discovery and recognition of the genus in Europe was probably due to the rarity of *Asterella* in much of Europe (including its total absence from Britain and some other countries). In contrast, *Asterella tenella* is a locally abundant and conspicuous hepatic throughout the eastern United States and was not missed by the early American botanical explorers such as Clayton.

In Europe twelve species have been described but one of these (*F. raddii* Nees) is probably based on a mislabelled non-European type specimen. Two American names *A. elegans* (Spreng.) Trevis. and *A. tenella* were in the distant past misapplied to European plants. Four species are now recognised, well-known, and described in detail in many floras. These are: *A. saccata*, *A. gracilis* (F.Weber) Underw., *A. lindenbergiana* (Corda ex Nees) Arnell and *A. africana* (Mont.) A.Evans. The first three of these were distinguished by Nees (1838) and by the time of the *Synopsis Hepaticarum* (Gottsche *et al.* 1844–1847) all four were known, although the nomenclatural confusion was only cleared up relatively recently. The most thorough revision of European species was provided by Müller (1905–1916, 1951–1958). Grolle (1976, 1983b) has now provided authoritative European check-lists for Hepaticae.

Table 1.6 Species of *Asterella* described from the study area

A chronological list of names belonging to *Asterella*, described in *Asterella*, *Marchantia*, *Fimbriaria*, *Hypenantron*, *Octokepos* and *Rhacotheca*.

	Name	Publication Date	Type Locality
1	*M. saccata* Wahlenb.	1811	Kamchatka
2	*M. ludwigii* Schwägr.	1814	Europe
3	*M. gracilis* F.Weber	1815	Sweden
4	*F. fragrans* Nees	1820	Europe
5	*F. nana* Lindenb.	1829	Switzerland
6	*H. ciliatum* Corda	1829	Switzerland
7	*F. sanguinea* Lehm. & Lindenb.	1832	Nepal
8	*F. viridis* Lehm. & Lindenb.	1832	Nepal
9	*F. wallichiana* Lehm. & Lindenb.	1832	Burma
10	*F. marginata* var. *minor* Lehm. & Lindenb.	1832	Nepal
11	*F. nepalensis* Taylor	1837	Nepal
12	*F. pilosa* Taylor	1838	Sweden, Switzerland
13	*F. lindenbergiana* Corda ex Nees	1838	Austria
14	*F. lindenbergiana* ß *angustior* Nees	1838	Switzerland
15	*F. raddii* Nees	1838	'Italy'
16	*F. bonjeanii* De Not.	1838	Italy
17	*F. africana* Mont.	1840	Canary Is.
18	*M. umbonata* Wallr.	1841	Germany
19	*F. leptophylla* Mont.	1842	S India (Nilgherries)
20	*R. azorica* Bisch.	1844	Azores
21	*F. blumeana* Nees	1846	Java
22	*O. khasyanum* Griff.	1849	NE India (Khasia)
23	*F. vesiculosa* Austin	1869	Japan
24	*F. pusilla* Mitt.	1888	Yemen (Socotra)
25	*A. kiaerii* Kaal.	1893	Norway
26	*F. persica* Steph.	1894	Iran
27	*H. venosum* var. *macrosporum* Schiffn.	1898	Sumatra
28	*H. venosum* var. *macrosporum* forma *purprascens* Schiffn.	1898	Sumatra
29	*H. venosum* var. *macrosporum* forma *viridis* Schiffn.	1898	Sumatra
30	*H. vulcanicum* Schiffn.	1898	Java
31	*F. angusta* Steph.	1899	S India (Coorg)
32	*F. maculata* Steph.	1899	NW India (Dehra Dun)
33	*F. multiflora* Steph.	1899	NW India (Kaurran)
34	*F. parvipora* Steph.	1899	NW India (Kashmir)
35	*F. zollingeri* Steph.	1899	Java
36	*F. silachorensis* Schiffn.	1908	Iran
37	*F. calciatii* Gola	1914	NW India (Kashmir)
38	*F. mussuriensis* Kashyap	1916	NW India (Mussoorie)
39	*F. pathankotensis* Kashyap	1916	NW India (Pathankot)
40	*F. butleri* Steph.	1917	N India (Darjeeling)
41	*F. cruciata* Steph.	1917	Japan
42	*F. gollanii* Steph.	1917	NW India (Dehra Dun)
43	*F. indica* Steph.	1917	S India (Mysore)
44	*F. latifrons* Steph.	1917	Lombok
45	*F. levispora* Steph.	1917	Philippines

Table 1.6 (contd.)

Name	Publication Date	Type Locality
46 *F. mescarana* Steph.	1917	S India (Coorg)
47 *F. papulosa* Steph.	1917	NW India (Mussoorie)
48 *F. reticulata* Kashyap	1917	NW India (Kashmir)
49 *F. valida* Steph.	1917	China (Kweichow)
50 *F. yoshinagana* Horik.	1929	Japan
51 *F. purpureo-capsulata* Herzog & C.E.O.Jensen	1930	China (Sichuan)
52 *F. reflexa* Herzog	1930	China (Sichuan)
53 *F. angusta* var. *macrolepis* Herzog	1930	China (Yunnan)
54 *F. liukiuensis* Horik.	1931	Ryukyu Islands
55 *F. gangetica* Kashyap	1932	India
56 *F. monospiris* Horik.	1934	Taiwan
57 *F. koreana* Horik.	1936	Korea
58 *F. mysorensis* Chopra	1938	S India (Mysore)
59 *A. odora* S.Hatt.	1944	Japan
60 *A. crassa* Shimizu & S.Hatt.	1951	Japan
61 *A. chichibuensis* Shimizu & S.Hatt.	1952	Japan
62 *A. mitsuminensis* Shimizu & S.Hatt.	1952	Japan
63 *A. pusilla* Shimizu & S.Hatt.	1952	Japan
64 *A. sanoana* Shimizu & S.Hatt.	1953	Japan
65 *A. umbelliformis* Shim. & Hatt.	1953	Japan
66 *A. ludwigii* var. *major* Inoue & Shimizu	1968	Japan
67 *A. kashyapii* Chopra (*nom. nov.* for *F. reticulata* Kashyap)	1969	India
68 *A. limbata* D.G.Long & Grolle	1994	Sumatra
69 *A. grollei* D.G.Long	1999	Nepal

The early recognition of the European species has meant that for the last 150 years these species have been widely collected, recorded and studied throughout Europe and a great deal is known about their distribution and ecology. However, as with the North American taxa, the evolutionary interest and worldwide taxonomic and phytogeographic relationships of the European species are considerable and still little-understood.

Important regional floras, check-lists and floristic reports for *Asterella* in Europe are: Scandinavia: Wahlenberg (1812); Hartman (1832); Lindberg (1868, 1879); Arnell (1928); Arnell (1956); Finland: Auer (1944); Koponen *et al.* (1977); Norway: Arnell (1892); Kaalaas (1892–1893, 1898); Joergensen (1934); Sweden: Mosen (1870); Tolf (1891); Mårtensson (1955–1956); Iceland: Hesselbo (1918); Germany: Wallroth (1815); Hübener (1834); Reimers (1940); Poland: Limpricht (1877); Kornas (1952); Szweykowski (1958); Browicz & Szweykowski (1958); Czechoslovakia: Dedecek (1886); Pilous & Duda (1960); Austria: Breidler (1894), Heeg (1894); Hungary: Boros & Rouppert (1941); Boros (1968); Romania: Mohan (1984); Yugoslavia: Pavletic (1955); Greece: Bory (1832), Coppey (1908); Italy: Notaris (1838–1839, 1858), Milde (1864), Trevisan (1874); Massalongo &

Carestia (1880), Massalongo (1886), Zodda (1912); Corsica: Camus (1895), Hebrard (1993); Switzerland: Meylan (1924); France: Candolle & Lamarck (1805), Kremer (1863), Héribaud (1899), Boulay (1904), Culmann (1923), Castelli (1954), Theurillat *et al.* (1985), Hebrard (1988); Spain: Spruce (1850), Casares-Gil (1919), Allorge (1956), Allorge & Jovet-Ast (1958).

Macaronesia. Only two *Asterella* names have been used in Macaronesian floristics, *Fimbriaria africana* Mont. described in 1840 from the Canary Islands, and *Rhacotheca azorica* Bisch. in 1844 from the Azores. These were synonymised by Leitgeb (1881) and *Asterella africana* (Mont.) A.Evans is now a well-known taxon throughout Macaronesia. Many of these islands have been thoroughly explored by bryologists and hence there are many reports of *A. africana*: *e.g.* Ade & Koppe (1942), Allorge & Allorge (1948, 1950), Allorge & Jovet-Ast (1958), Arnell (1961), Bryhn (1908), Dirkse *et al.* (1993), Düll (1980), Eggers (1982), Koppe & Düll (1982, 1986), Luisier (1909), Mitten (1870), Montagne (1840, 1856), Pitard & Corbière (1907), Schiffner (1901, 1902, 1939), Sérgio (1973), Seubert (1844) and Sjögren (1978).

Middle East. *Asterella* appears to be a rare genus throughout Asia Minor, SW Asia and Arabia. Only three species have been described from the region (Table 1.6): two from Iran, *Fimbriaria persica* Steph. and *F. silachorensis* Schiffn., and one from the island of Socotra in Yemen, *F. pusilla* Mitt. A fourth species, *Fimbriaria caucasica* Steph. is based on a mislabelled type specimen originating from Australia (Grolle, 1975b) and is therefore excluded.

Frey & Kürschner (1991) published a check-list of all South-west Asian bryophytes in which they listed four species for the region: *A. elegans* (Spreng.) Trevis., *A. gracilis* (F. Weber) Underw., *A. pappii* (Gola) Grolle and *A. persica* (Steph.) M.Howe, together with several synonyms. They did not deal with *F. silachorensis* Schiffn., but in a previous paper (Frey, 1974) this was synonymised under *A. gracilis*.

Frey *et al.* (1991) revised *Asterella* in SW Asia and described the three above accepted species in detail, including SEM micrographs of spores, illustrations and a key. They clarified the confusion between *A. persica* (Steph.) M.Howe and *A. pappii* (Gola) Grolle, the latter an African species also occurring on Socotra for which *F. pusilla* Mitt. is a synonym. The mainland Arabian specimens (previously referred to *A. pappii* (Long, 1987)) they included in *A. persica*, otherwise restricted to Iran. They also concluded that records of *A. elegans* (Spreng.) Trevis., an American species, from Turkey (Bornmüller (1931); Henderson & Prentice (1969)) are based on misidentifications of *A. gracilis* (F.Weber) Lindb.

Reports of *Asterella* from the Middle East are as follows:
Turkey: Walther (1967); Henderson & Prentice (1969); Frey *et al.* (1991); Caucasus: Meyer & Grolle (1968); Vana (1982); Iran: Stephani (1894); Schiffner (1908); Frey (1974);

Frey *et al.* (1991); Arabia (including Socotra): Mitten (1888); Townsend (1969), Long (1987), Frey & Kürschner (1988); Frey *et al.* (1991).

For other countries in the region, *e.g.* Iraq, Afghanistan, the genus has not yet been recorded. A recent report of *Asterella lindenbergiana* (Corda ex Nees) Arnell from Turkey (Gökler & Öztürk, 1991) has been shown by Grolle (*in litt.*) to be an error for *Corsinia coriandrina* (Spreng.) Lindb.

Indian Region. Of the 52 names coined for *Asterella* species from Asia (Table 1.6), 23 are from the Indian Region (Asia 3). In addition, a number of taxa described from elsewhere have been recorded in the literature from India: *A. vulcanica* (Schiffn.) Kachroo & Bapna, *A. blumeana* (Nees) Kachroo and *A. elegans* (Spreng.) Trevis. No comprehensive attempt has yet been made to evaluate these names.

The earliest taxa published from the Indian region resulted from collections by Nathaniel Wallich in Nepal, Burma and elsewhere. These were passed via W.J. Hooker to Lehmann & Lindenberg in Germany who published them in their *Pugillus Quartus* in 1832: *Fimbriaria sanguinea* Lehm. & Lindenb., *F. viridis* Lehm. & Lindenb., *F. wallichiana* Lehm. & Lindenb. and *F. marginata* Nees var. *minor* Lehm. & Lindenb. A few years later, one of these collections was described again by Taylor (1837) as *F. nepalensis* Taylor. In 1842 the first South Indian species, *Fimbriaria leptophylla* Mont., was described by C. Montagne. Next came a new genus, *Octokepos khasyanum* Griff. from the Khasia Hills, discovered and described by Griffith (1849), published posthumously. Between 1899 and 1917 no fewer than ten new Indian taxa were described by Stephani, one by Gola (1914b) and two by Kashyap.

A large volume of literature has been published on Indian *Asterella*; many are papers on morphology and taxonomy of a few species, or on allied subjects such as abnormal receptacles, antibiotic activity *etc.* However, all these suffer from the same problem: the lack of even a preliminary taxonomic revision. The reasons for this lack of a sound taxonomy are several: (1). in the 19th century the first twelve taxa to be described from the region were all circumscribed by European authors and in the early 20th century, Stephani continued to describe new taxa (a further five). The types of all these species were not available to Indian workers. (2). The published descriptions by European authors, especially Stephani, were very inadequate and rarely attempted to relate a new taxon to others already in existence. (3). The necessary field studies, so important in the taxonomy of the Marchantiales, were never done by the early workers. (4). Many important characters were not studied.

S.R. Kashyap was the one early author who worked with *living* plants in Asia (North-west Himalaya). His distinction of taxa largely corresponds to those accepted in this revision but because he was not able to study types he applied the correct name to only one of his species in his (1929–1934) *Liverworts of the Western Himalayas and the Panjab Plain*. Since Kashyap, the confusion has persisted. For example, Chopra (1943) published a

check-list for India with 24 species of *Fimbriaria*; Pandé *et al.*(1954) listed the same number; Parihar (1962) listed 21 species of *Asterella;* Kachroo *et al.* (1977) listed 23 species. The only authors to attempt any significant synonymising were Udar & Jain (1983) who reduced seven names to synonymy under *A. wallichiana* (Lehm. & Lindenb.) Grolle. Virtually no other Indian *Fimbriaria* or *Asterella* names have been synonymised in the literature to date.

Many of the published references to Indian *Asterella* are floristic reports or check-lists which are listed below under geographical regions/ countries. Almost none contains any detailed taxonomy. Without thorough revision of the taxa, and checking the identity of some of the voucher specimens, the published phytogeographic interpretations (see below) are almost meaningless.

Floristic Reports including records of *Asterella* are:
Pakistan: Hameed (1942), Furuki *et al.* (1993); NW Himalaya: Gola (1914b), Kashyap (1916, 1917, 1929–1934), Srivastava (1979), Bir (1970), Kanwal (1977); Nepal: Lehmann & Lindenberg (1832); Taylor (1837), Banerji (1958), Grolle (1966), Noguchi *et al.* (1966), Hattori (1968, 1975); Darjeeling: Chopra (1938b); Bhutan: Long & Grolle (1990); Assam: Griffith (1849), Kachroo (1952a, 1952b); Central India: Murty & Bhargava (1969), Lal & Parihar (1979), Gautam & Thakur (1981), Pandé & Srivastava (1952), Patidar (1988); S India: Montagne (1842, 1856), Chopra (1938a), Joshi & Birardar (1984), Udar & Jain (1984); Thailand: Giesy & Richards (1959).
Taxonomic Revision: Udar & Jain (1983).
Phytogeography: Kachroo (1954, 1969), Pandé (1958).
Threatened species: Udar & Srivastava (1983).
SEM: Udar & Jain (1983), Nath & Asthana (1992).

In spite of this wealth of literature, no definitive list of *Asterella* species can be given for India and adjacent countries. Hence the important questions of taxonomic and phytogeographic relationships between India, China, Malesia and Japan have not yet been addressed. These will be dealt with in the taxonomic revision (Chapter 4).

China. In contrast to India, little has been published on Chinese *Asterella*. There is no *Flora* covering the whole of China for the Marchantiales. The most up-to-date check-list is that of Piippo (1990) which lists the number of taxa recorded for each Province, including Taiwan. Her totals are as follows: Yunnan 2 species, Sichuan 4 species, Liaoning 1 species, Taiwan 2 species. One species, *Fimbriaria purpureo-capsulata* Herzog & C.E.O.Jensen, from Sichuan, is synonymised with *Asterella mussuriensis* (Kashyap) Verd.; *Asterella tenella* (L.) P.Beauv., reported from Taiwan by Kuo & Chiang (1988), is excluded from China and Asia. Two recent papers (Long, 1999) and Whittemore *et al.* (1998) added two further species of *Asterella* to the Chinese bryoflora.

Stephani described only one species of *Fimbriaria*, *F. valida* Steph., from China, in 1917, and that is the earliest name for the region although it is a synonym of *Reboulia hemisphaerica* (L.) Raddi. Between 1914 and 1918, the Austrian H. Handel-Mazzetti explored Western China for plants, and collected several *Asterella* specimens which were worked up by T. Herzog in Jena. From these were published three new taxa in 1930. Since then, only two more species, *Fimbriaria monospiris* Horik. from Taiwan, and *F. koreana* Horik., from Korea, have been described, both by the Japanese bryologist Y. Horikawa in 1934 and 1936. Recently Long (1999) reported the new species *Asterella grollei* from Qinghai Province.

The only other important papers dealing with *Asterella* from the region are from Korea and Taiwan, as follows:
Taiwan: Horikawa (1934), Kamimura (1952b), Kuo & Chiang (1988);
Korea: Horikawa (1936), Choe (1975), Gao & Chang (1983).

Malesia. The Malesian region (excluding Papua New Guinea) is undoubtedly rich in the genus *Asterella*, but has suffered greatly from lack of collections. Nine names have been published for *Asterella* taxa from the region, three from Java, four from Sumatra, one from Lombok and one from the Philippines. Three of the names from Sumatra are infraspecific however, leaving six species. The earliest was *Fimbriaria blumeana* Nees, described in 1846 in the *Synopsis Hepaticarum*. However, the genus (as *Fimbriaria*) was reported twice before that time from Java, by Reinwardt *et al.* (1824), and by Nees von Esenbeck (1830), as *Fimbriaria tenella* (L.) Nees, based on a collection from Java made by Reinwardt. Nees (in Gottsche *et al.*, 1844–1847) realised that the American *F. tenella* was not the same as the Javan material and described it afresh as *Fimbriaria blumeana* Nees.

F. blumeana is a particularly interesting taxon. Many authors have applied this name in the Indian region for the species often called *Asterella khasyana* (Griff.) Pandé *et al.* by other authors. The identity of these two species has never been firmly established and requires careful study. Part of the problem is the rarity of *A. blumeana* (Nees) Kachroo in Malesia and the lack of good herbarium material.

Schiffner (1898) is the next important author, as he described three infraspecific taxa under the species *Hypenantron venosum* (Lehm. & Lindenb.) Trevis. Like *Asterella tenella* (L.) P.Beauv., *A. venosa* (Lehm. & Lindenb.) A.Evans is a new world species, and its presence in Malesia has never been reliably confirmed. Some of the collections included by Schiffner in *H. venosum* were later redescribed by Stephani in 1899 as *Fimbriaria zollingeri* Steph., and thereafter the epithet *venosa* was not maintained for Javan material.

Around this time *Hypenantron vulcanicum* Schiffn. was described from Java, *Fimbriaria latifrons* Steph. from Lombok and *F. levispora* Steph. from the Philippines. These names have never been widely taken up. They are poorly-known species which

need re-collection and careful study. The most recent Malesian *Asterella* to be described, *A. limbata* D.G.Long & Grolle (1994) is based on a type from Sumatra.

Important literature on Malesian *Asterella*:
Java: Reinwardt, Blume & Nees (1824), Nees von Esenbeck (1830), Sande Lacoste (1856), Schiffner (1893, 1898, 1900); Sumatra: Schiffner (1898), Long & Grolle (1994); Borneo: Long & Grolle (1994); Philippines: Tan & Engel (1986).

Japan. Twelve taxa of *Asterella* have been described from Japan. The first species, *Fimbriaria vesiculosa* Austin, was published by the American bryologist C.F. Austin in 1869, following an American expedition to the North-west Pacific. In 1917 Stephani described his only Japanese species, *Fimbriaria cruciata* Steph. Both these taxa have never been studied in detail by other authors.

The next important worker was the distinguished Japanese bryologist Y. Horikawa, who explored many of the richer parts of Japan, such as the Ryukyu Islands, for the first time. He described two new species from Japan, *Fimbriaria yoshinagana* Horik. from Shikoku and *F. liukiuensis* Horik. from Okinawa. In the 1950's S. Hattori and D. Shimizu began their detailed work on Japanese Marchantiales and published a series of papers including seven new species of *Asterella*. Later on they realised that some of these might be synonymous with Indian species, but because of the inadequacy of published descriptions from India, they could not be certain. Their new taxa were published with detailed descriptions and figures which has made subsequent interpretation much easier. Three of their names were synonymised by Long (1997b).

The main challenge now is to make the detailed comparisons of the Japanese taxa with continental Asiatic taxa. No Japanese liverwort Flora has yet been published, although two species are illustrated in Inoue's (1976) *Illustrations of Japanese Hepaticae, Vol. 2*.

Important publications for Japan are:
Austin (1870), Horikawa (1931, 1934), Hattori (1944), Shimizu & Hattori (1952, 1953a), Kamimura (1952a), Hattori & Shimizu (1955), Hattori & Mizutani (1959), Seki (1964), Miyoshi (1966), Mizutani & Hattori (1969), Yamaguchi (1985), Saito (1974), Inoue (1976), Furuki & Inoue (1984), Furuki & Higuchi (1988), Long (1997).

Northern Asia. The vast area of Siberia is largely unknown to western bryologists and undoubtedly the two *Asterella* species occurring in Arctic America and Greenland must be widespread here: *A. gracilis* and *A. saccata*. Indeed, *Marchantia saccata* Wahlenb. was first collected from Kamchatka by Tilesius around 1804, more or less at the same time that Schleicher discovered it in Europe.

The most important *Flora* for the region is that of Schljakov (1982) who described and illustrated three European species: *A. saccata*, *A. gracilis* and *A. lindenbergiana*. The only other species occurring in Russia is *A. leptophylla*, an Indian species which just gets into the Soviet Far East (Gambaryan, 1988, 1992). *A. saccata* has also been reported from the Ukraine by Zerov (1964), and from Siberia by Lindberg & Arnell (1889) under the name *Fimbriaria fragrans* Nees. *A. gracilis* has been reported from the Czukotka Peninsula of Eastern Siberia by Abramova *et al.* (1982).

1.5 DISCUSSION & CONCLUSIONS

Asterella belongs to the family Aytoniaceae in the Chambered Liverworts (Marchantiales). It is poorly understood taxonomically and a worldwide revision of the estimated 80 species is badly needed. It is morphologically very complex and rich in striking qualitative characters such as spore ornamentation patterns.

The family Aytoniaceae is well-defined, but studies of its position within Marchantiales, especially its closest relatives, have produced conflicting conclusions. The five genera of Aytoniaceae are poorly defined, with many overlapping characters. *Asterella* is particularly polymorphic in these generic characters and is reliably distinguished only by its pseudoperianth. The traditional classification of Aytoniaceae is undermined by recent molecular phylogenetic studies, as yet incomplete. Its smaller genera, particularly *Mannia* and *Cryptomitrium*, show significant similarities and parallels with *Asterella*.

Asterella appears to have two centres of diversity, Eastern Asia and America; however, many existing names probably require synonymising. Sixty-nine taxa have been described from the study area, 52 of these from Asia. In Europe, Macaronesia and the Middle East the genus is well-known taxonomically, with a wealth of floristic literature. In India, China and Malesia taxonomy is very confused and distributions doubtful (many so-called 'endemics' are probably synonyms).

The genus has a very confused and complicated nomenclatural history, from its earliest recognition by Dillenius in 1741. Since then it has been known under several different generic names which have only recently stabilised as *Asterella*.

The overriding needs for study of *Asterella* are (1) to define the taxonomic characters, (2) to describe the spores of all taxa using SEM, (3) to undertake a morphological taxonomic revision to define the taxa, synonymy and biogeography of all taxa, and (4) to attempt to reconstruct phylogenies at family, genus and species level.

CHAPTER 2: TAXONOMIC CHARACTERS

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2.1 INTRODUCTION

As outlined in Chapter 1, the genus *Asterella* is very complex morphologically and numerous characters, both qualitative and quantitative, are available for taxonomic study. The primary aims of this chapter are to (1) to describe the morphological features of the genus *Asterella*; (2) review the morphological characters used in major studies on *Asterella*, and the effects the choice of characters by past workers might have had on taxonomy; then (3) to evaluate knowledge of the stability or phenotypic plasticity of the morphological characters.

2.2 MORPHOLOGY OF *ASTERELLA*

The morphological features of *Asterella* have been divided into three groups: vegetative features of gametophyte, reproductive features of gametophyte and features of the sporophyte (see also Appendix I). For a formal generic description see Chapter 4.

2.2.1 Vegetative features of gametophyte

Thallus. The plants in *Asterella* are thalloid (Fig. 1.2b), forming either dense interwoven mats or growing as scattered stems over soil, rocks or other bryophytes. The plants may be highly aromatic, sometimes with a pungent smell likened to rotten fish.

Vegetative branches. The thallus is composed of branches or segments which branch in several ways: terminal branches (dichotomies), terminal innovations marked by a constriction and ventro-lateral branches which are stipitate-based and arise from the ventral surface of the midrib; these may arise some distance from the growing point or almost at the apex. Branch shape may be linear to obovate; the apex is notched at the growing point. In transverse section the thallus may be thick and v-shaped to almost flat (Figs. 2.1b, 2.3d). The midrib is variably differentiated but is the thickest part of the thallus and is more prominent ventrally. The thallus margins are normally entire and straight or shallowly sinuate; in some xeromorphic species they become strongly inrolled when dry. The thallus is normally green above, except on the margins which are often reddish pigmented; the ventral surface is often strongly pigmented. The upper surface (Fig. 2.3b) may be smooth or reticulated with the outlines of the air chambers; air pores (Fig. 2.3c) may be visible as small raised dots within these reticulations.

Specialised vegetative propagulae are unknown in *Asterella*, but some species form specialised tuberous apices which act as organs of perennation and possibly dispersal.

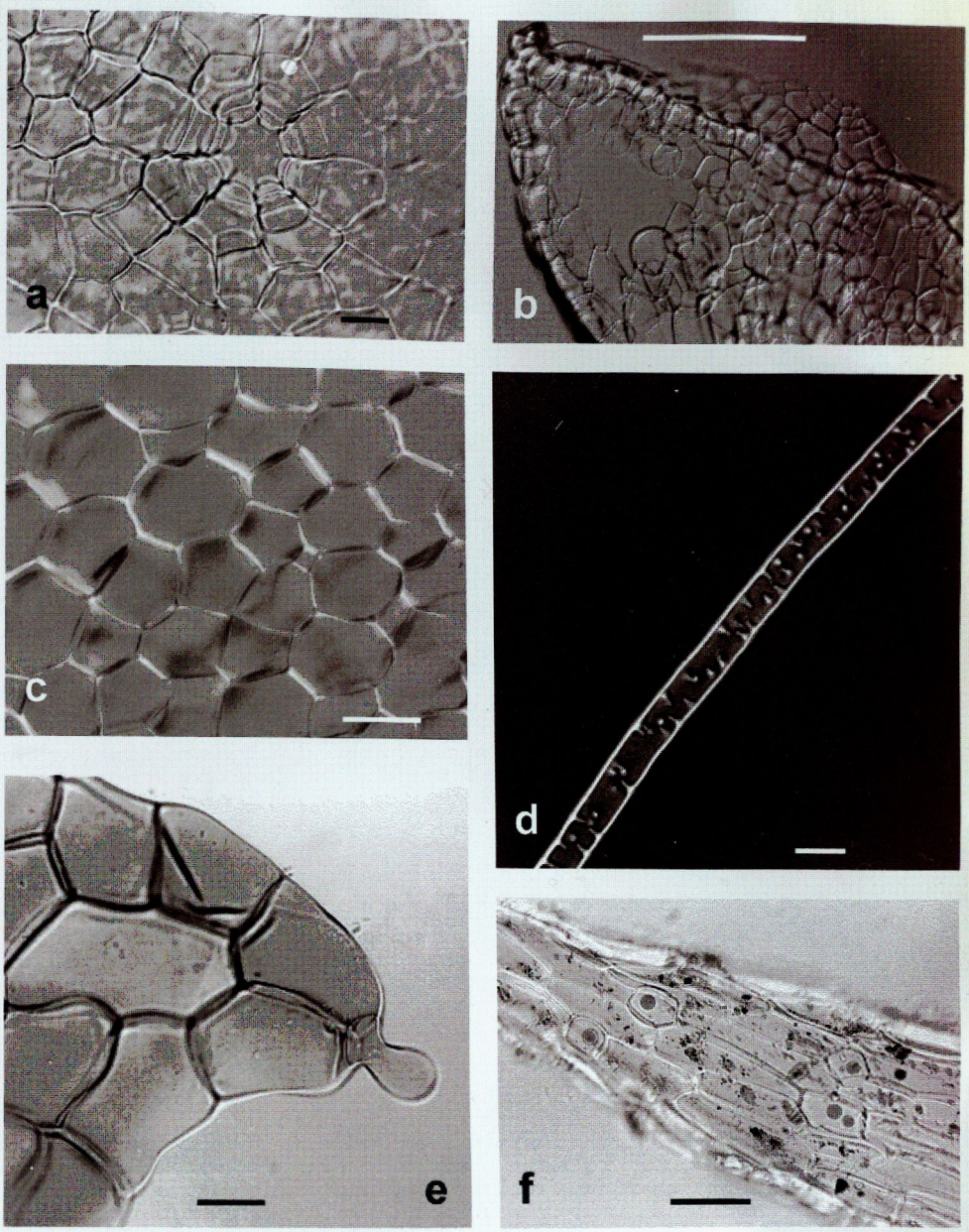

Fig. 2.1. Morphology of *Asterella* under LM (i). a, epidermal pore in surface view; b, t.s. margin of thallus with air chamber and epidermal pore; c, t.s. cells of basal tissue; d, pegged rhizoid; e, apex of ventral scale with slime papilla; f, part of pseudoperianth lobe showing oil cells. a, c, d, *A. wallichiana*, Japan, Iriomote, *Long 24920*; b, e, *A. wallichiana*, Japan, Iriomote, *Long 24903*; f, *A. limbata*, Sumatra, *Meijer B8977*. Scale bars: a, c, d, e = 20µm ; f = 100µm; b = 0.4mm.

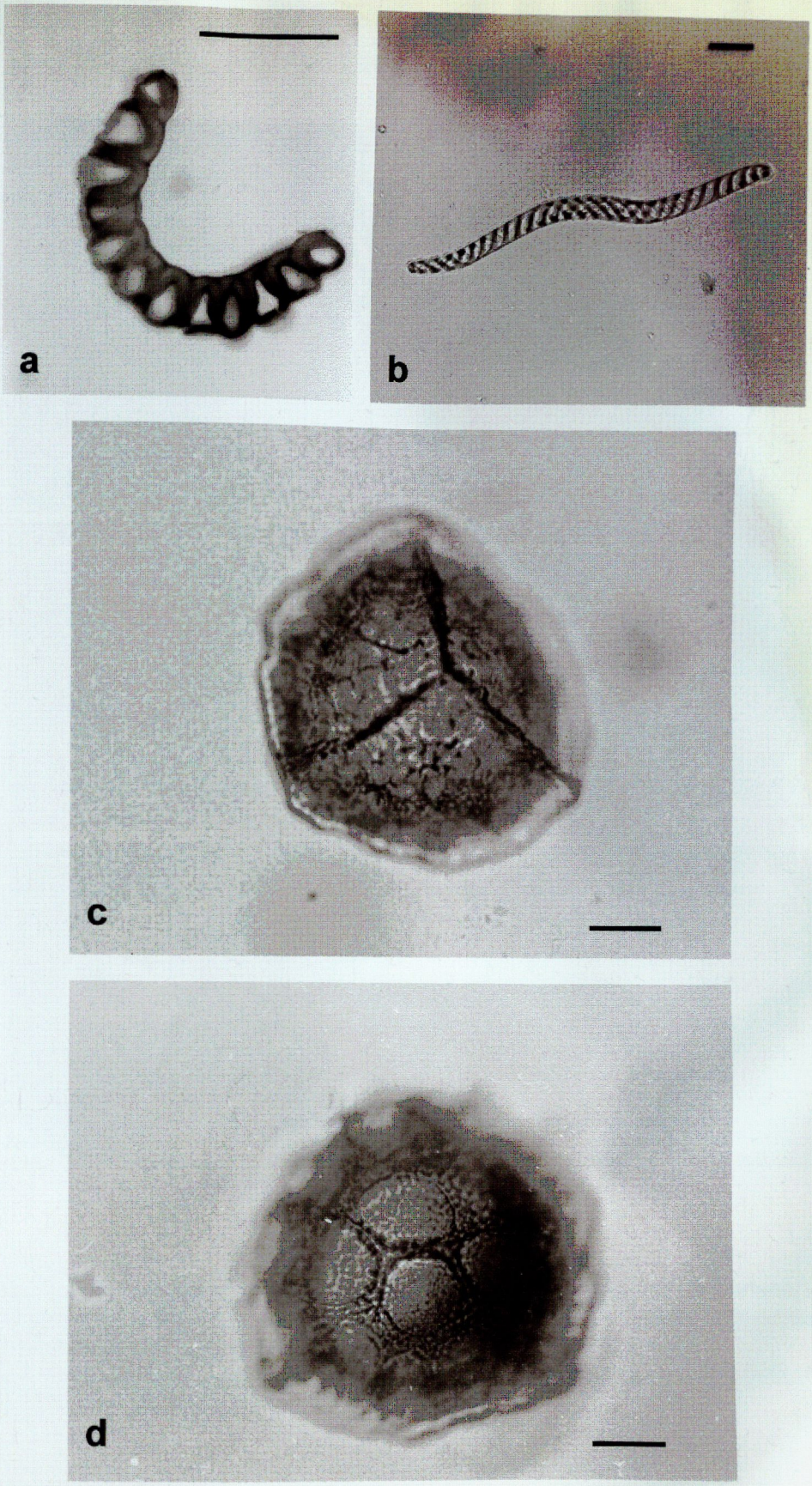

Fig. 2.2. Morphology of *Asterella* under LM (ii). a, t.s. pseudoperianth lobe; b, elater; c, spore, proximal view; d, spore, distal view. a, *A. wallichiana*, Japan, Iriomote, *Long 24903*; b, *A. limbata*, Sumatra, *Meijer B8977*; c, d, *A. limbata*, Sabah, *Menzel et al. 4214*. Scale bars: b, c, d = 20μm; a = 0.2mm.

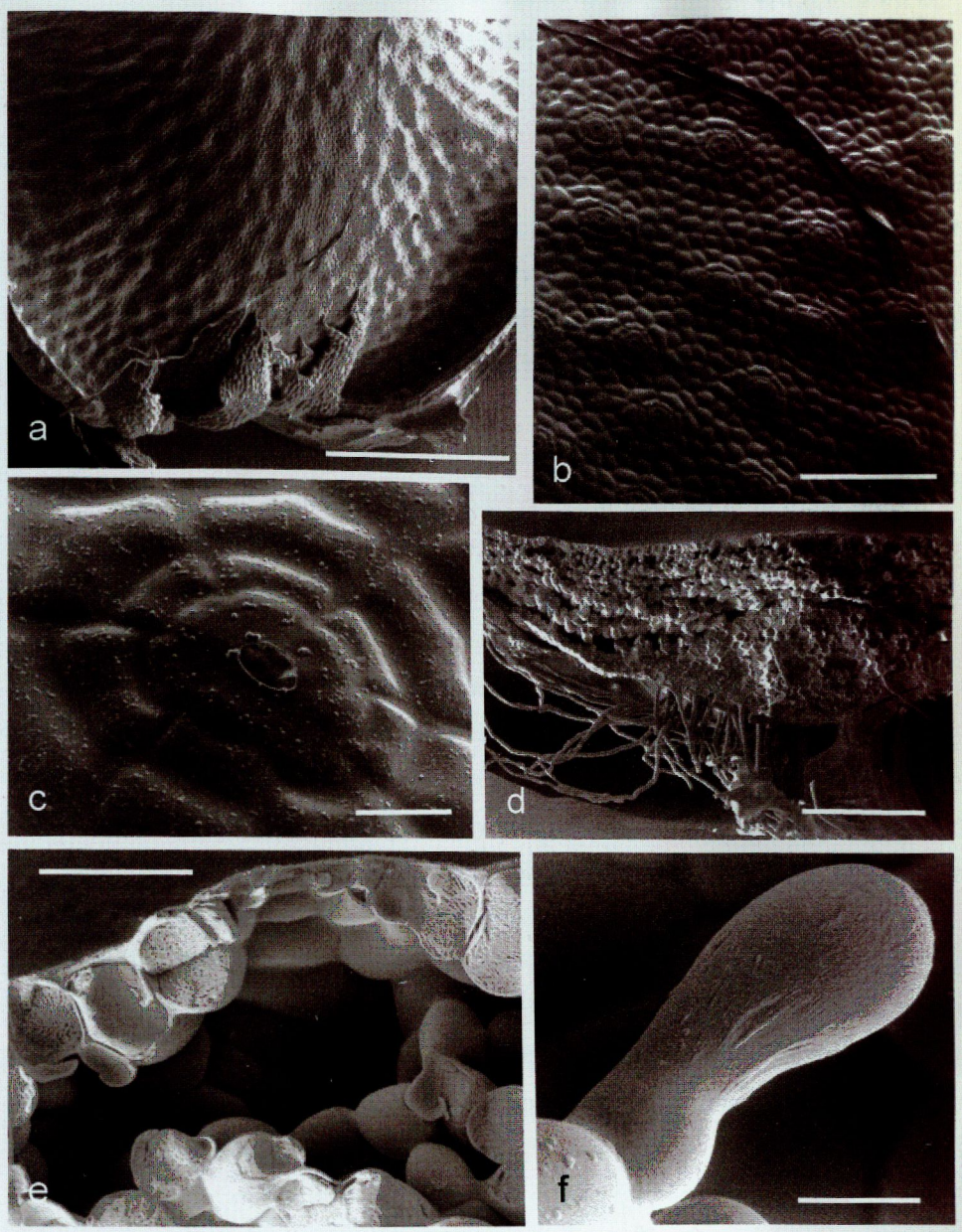

Fig. 2.3 Morphology of *Asterella* under SEM. a, apex of thallus, dorsal surface, showing tips of ventral scale appendages; b, dorsal epidermis showing air pores; c, air pore; d, t.s. thallus; e, t.s. air chamber and pore; f, slime papilla.
a–f, *A. wallichiana*, Japan, Iriomote, *Long 24903*. Scale bars: a, 1mm; d, 500μm; b, 200μm; e, 50μm; c, 20μm; f, 10μm.

Dorsal epidermis. The upper surface of the thallus is covered by an epidermis one cell thick. The cells are irregularly rectangular in shape (Fig. 2.1a), mostly with thin walls though sometimes thickened at the angles. In addition to the epidermal cells there are scattered oil cells and air pores. Oil cells are smaller in size than normal epidermal cells, more or less isodiametric and contain a single large oil body.

Air pores. The air pores (Figs. 2.1a, 2.3c,e) connect the inner air chambers of the thallus with the atmosphere. Normally each air chamber has one air pore which is often raised above the surface of the thallus. In surface view the pore has an inner aperture surrounded by one to several concentric rings of curved elongated cells which form radiating rows, the cells increasing in width and radial length outwards. The walls are often somewhat thickened.

Assimilation tissue. Beneath the epidermis is the green photosynthetic assimilation tissue (Figs. 2.1b, 2.3d,e) or aerenchyma which consists of air chambers in one to several layers bounded by one-layered walls of thin-walled chlorophyllose cells. This tissue can occupy from between one third to two thirds of the thickness of the thallus. The air chambers may be almost vertical to obliquely spreading towards the thallus margins and overlapping. They may be clearly defined or irregular and forming spongy tissue. Sometimes the chambers contain free chlorophyllose filaments or partitions. Scattered oil cells are usually present.

Basal compact tissue. Beneath the assimilatory layer the remaining tissue forms a compact layer (Figs. 2.1c, 2.3d) without air chambers and chloroplasts. This layer is thickest along the middle of the thallus and constitutes an ill-defined midrib; towards the margins it gradually become thinner and often does not extend to the thallus margin. The cells are irregular in shape and size and are thin-walled. A fungal mycorrhiza is often present in this layer, as are scattered oil cells. The lowest layer (lower epidermis) is poorly differentiated and does not contain oil cells or air pores. It is often red-pigmented. In the median part of the thallus the lower epidermis bears rhizoids and ventral scales.

Rhizoids. Rhizoids (Figs. 2.1d, 2.3d) are borne only on the lower epidermis amongst the ventral scales. Rhizoids are colourless and unicellular. Two types occur, smooth and pegged. The smooth ones apparently function primarily to anchor the thallus to the substrate. The pegged rhizoids have internal peg-like thickenings and may have water-holding properties.

Ventral scales. Ventral scales occur in two longitudinal rows along the ventral surface of the thallus. They are often reddish-pigmented. In xeromorphic species the thallus inrolls during dry periods and the scales become exposed and are considered to offer protection to the thallus. At the apex of the thallus the growing point is protected by the recurved tips of the ventral scales. Each scale consists of a lower scale body and one or two apical appendages. The scale body is strongly oblique, somewhat semicircular in shape with a decurrent outer (adaxial) margin. It varies considerably in size between species. The margin is often entire, occasionally lobed or toothed, but often bears one to several small slime papillae (Figs. 2.1e, 2.3f) which are often lost

in older dry specimens. The cells are usually elongate-rectangular and are often much longer towards the outer margin and base of the body. Sometimes the outer marginal cells are thin walled, forming a hyaline border. Oil cells are usually present and conspicuous. The scale appendages (Fig. 2.3a) are usually clearly differentiated from the scale body and may be rounded, triangular or linear. At the base they are sometimes constricted. They may be lobed or toothed and may bear oil cells along the margins. The apex may be rounded or acute, sometimes of several uniseriate elongated cells and may end in a single slime papilla. Cells are usually elongate-rectangular. Oil cells may be absent or present.

2.2.2 Reproductive features of gametophyte

Cytology. Cytological studies have been conducted for very few species of *Asterella* (see Chapter 4.3, 4.4). The chromosomes are very small and difficult to prepare for cytological analysis. Basic numbers of 9,10 and 18 have been reported (Kachroo, 1969; Tatuno, 1955, 1960; Perold 1994c). They have rarely been used to distinguish species. However, at the generic and family levels, Bornefeld (1987) has analysed chromosome number and type over the Marchantiales and in conjunction with morphological data has used this information to construct a hypothetical evolutionary tree.

Sexual condition (Fig. 2.4). Sexual condition has in the past been both poorly observed and imprecisely defined in *Asterella*. Stephani (1898–1900) classed his *Fimbriaria* species simply as 'monoica' or 'dioica'. He did not subdivide the monoicous species into categories but usually did indicate where the peduncle and androecia were borne on the thallus.

Evans (1920) defined three sexual conditions, dioicous (sexes on separate plants), paroicous (androecia borne on main thallus immediately posterior to base of stalk of archegoniophore) and autoicous (androecia borne on same plant as archegoniophore but not immediately posterior to base of stalk). This division into three types has been maintained by Grolle (1989), Frey *et al.* (1991), Schuster (1992c) and Perold (1994c) who have consistently distinguished between 'paroicous' species and 'autoicous' ones.

Wyatt & Anderson (1984) provided a glossary of sexual terminology in bryophytes, and defined the paroicous condition as a subdivision of the monoicous condition with 'archegonia and antheridia contained in the same inflorescence but not mixed together'. In the so-called 'paroicous' *Asterella* species the antheridia are borne dorsally on the main thallus (which in some cases can continue vegetative growth) whilst the archegonia are borne on a separate modified branch system, the archegoniophore. Thus the archegonia and antheridia are never in the same inflorescence in *Asterella* which can never therefore be paroicous. Strictly, these *Asterella* species exhibit a variant of the autoicous condition which has not been clearly defined. In fact, none of Wyatt & Anderson's subdivisions of the autoicous condition can strictly apply to the conditions found in *Asterella* and new terms have had to be introduced.

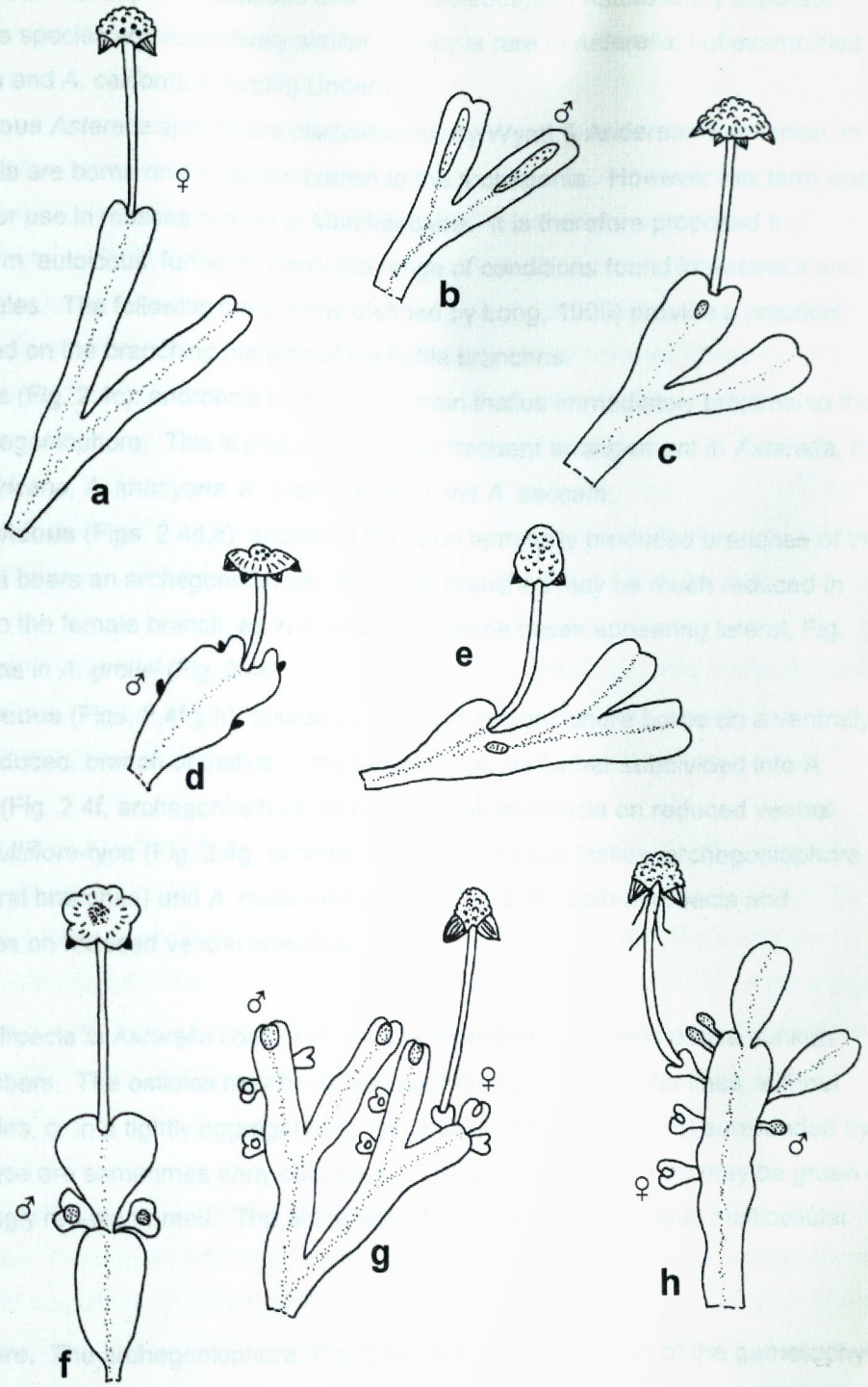

Fig. 2.4 Diagrammatic representation of sexual conditions in Eurasian *Asterella* species. a, b, dioicous; c, par-autoicous; d, e, terminal-autoicous; f–h, ventral-autoicous. a, *Asterella wallichiana*, female plant; b, *A. wallichiana*, male plant; c, *A. khasyana*; d, *A. limbata*; e, *A. grollei*; f, *A. leptophylla*; g, *A. multiflora*; h, *A. mussuriensis*.

Four main types of sexual condition are found in *Asterella*:

i. **dioicous** (Figs. 2.4a,b). Wyatt & Anderson subdivided the dioicous condition into three categories (heterodioicous, pseudautoicous and phyllodioicous). In *Asterella* the separate sexes of dioicous species are vegetatively similar. Dioicy is rare in *Asterella*, but exemplified by *A. wallichiana* and *A. californica* (Austin) Underw.

All **monoicous** *Asterella* species are *cladautoicous* by Wyatt & Anderson's definition, in that the antheridia are borne on a separate branch to the archegonia. However this term was really intended for use in mosses and not in Marchantiales. It is therefore proposed to subdivide the term 'autoicous' further to clarify the range of conditions found in *Asterella* and other Marchantiales. The following three terms (defined by Long, 1999) provide a practical subdivision based on the branching patterns of the fertile branches.

ii. **par-autoicous** (Fig. 2.4c): androecia borne on the main thallus immediately proximal to the base of the archegoniophore. This is probably the most frequent arrangement in *Asterella*, for example in *A. africana, A. khasyana, A. lindenbergiana* and *A. saccata*.

iii. **terminal-autoicous** (Figs. 2.4d,e): androecia borne on terminally produced branches of the same thallus that bears an archegoniophore. The male branches may be much reduced in size compared to the female branch, as in *A. limbata* (in some cases appearing lateral, Fig. 2.4d), or larger, as in *A. grollei* (Fig. 2.4e).

iv. **ventral-autoicous** (Figs. 2.4f,g,h): androecia and/or archegoniophore borne on a ventrally derived, often reduced, branch of thallus. This category may be further subdivided into *A. leptophylla*-type (Fig. 2.4f, archegoniophore on main thallus, androecia on reduced ventral branches), *A. multiflora*-type (Fig. 2.4g, androecia terminal on main thallus, archegoniophore on reduced ventral branches) and *A. mussuriensis*-type (Fig. 2.4h, both androecia and archegoniophores on reduced ventral branches).

Androecia. Androecia in *Asterella* consist of clusters of protruding ostioles above sunken antheridial chambers. The ostioles may be loosely aggregated or in irregular lines, without surrounding scales, or in a tightly aggregated raised cushion (Figs. 1.2b, 2.4b) surrounded by short scales (these are sometimes early caducous). The androecial cushions may be green or sometimes strongly red-pigmented. The antheridial chambers have numerous multicellular paraphyses.

Archegoniophore. The archegoniophore (Fig. 2.4a) is a modified branch of the gametophyte consisting of a stalk (peduncle) and receptacle (carpocephalum). It typically arises from the apical notch of the main thallus or a branch and thereby terminates growth of that branch. Vegetative growth may then be continued by a ventral innovation from the same branch. Only rarely (as in *A. grollei*, Fig. 2.4e) is a new growing point produced from the archegoniophore-bearing branch which produces a 'half-branch' from one side of the apical notch (Long 1999).

Stalk (peduncle). The stalk (Fig. 2.4a) is an elongated smooth or weakly ribbed green or pigmented tube with a single deep longitudinal furrow which contains pegged rhizoids. It varies considerably in length between and within species. In transverse section there is little

differentiation, except in a few species where vestigial air chambers occur in a longitudinal strip. The stalk typically bears a 'beard' of linear scales at its apex, and scattered scales throughout its length and sometimes in a ring at its base. These are normally elongated, one cell thick and only a few cells broad. They may contain scattered oil cells.

Carpocephalum. The carpocephalum or receptacle (Fig. 2.4a) contains air chambers and air pores on its dorsal surface. In Aytoniaceae the air pores are 'compound' (barrel-shaped) in contrast to the simple pores of the vegetative branches. The receptacle displays a variety of shapes and sizes, from almost flat and disc-like, to umbrella-shaped, hemispheric or conical, which may change during development. The carpocephalum is either green or red pigmented. The margin may be almost unlobed to deeply lobed. The upper surface may be smooth to warted. The air chambers may occur all over the surface or be restricted to a central boss or dome.

Involucre. Beneath each carpocephalum lobe is an involucre, a thin bistratose flap of tissue enclosing 2–4 archegonia. The free margin of the involucre may be entire or bilobed.

Archegonia. Fertilisation in Aytoniaceae occurs before stalk elongation. After fertilisation of one archegonium per involucre (some involucres often remain unfertilised) the sporophyte develops inside a pseudoperianth.

Pseudoperianth. The pseudoperianth (Figs. 2.1f, 2.2a) develops after fertilisation from the archegonial stalk (Bischler, 1998). It has a unistratose cup-shaped base (closely enveloping the capsule) consisting of thin-walled cells; oil-cells may be present or absent. The upper part is divided into lanceolate lobes which may be free or remain united at the apex which has a small orifice. The lobes usually have oil cells and the margins are often revolute when dry. They are often whitish in colour or reddish-pigmented.

2.2.3 The sporophyte

Capsule. The sporophyte of *Asterella* is extremely reduced, consisting of a globose capsule borne on a bulbous foot with an extremely short seta which never elongates. The capsule wall is unistratose, composed of brown cells without thickenings. The capsule dehisces in the upper 1/3 by a lid composed of thick-walled cells; the lid may be regular and disc-like but is more usually irregularly fragmenting. The capsule contains spores and elaters in the ratio of 4:1; spores number between 2500 and 3500 per capsule (Bischler, 1998; Patidar *et al.*, 1988).

Spores. The spores (Figs. 2.2c,d) are subglobose and unicellular but very large in size in comparison to other bryophytes (up to 160μm in diameter). They are produced in tetrads but become free when dispersed. In colour they range from yellow to orange, brown, red-brown or black. They display (under SEM) a hemispheric distal face and a proximal face usually with a distinct trilete mark, a well-defined proximal pole and three flat faces (facets). The distal and proximal surfaces may have similar or dissimilar sculpturing. The sculpturing may be in the form

of wavy ridges, in some species these anastomose and form irregular areolae. In other species the areolae are regular and complete. The areolae and their walls (muri) may be smooth or pitted, or with larger alveolate reticulation.

At the junction of proximal and distal surfaces is the equatorial rim which may bear a well-developed smooth wing. The equator where it meets the trilete marks may have three, small to large, apertures. The proximal facets may be flat or have a single conspicuous bulge. In alete species the trilete mark and proximal pole are absent and the proximal surface may be flat or somewhat concave.

Spore characters are reviewed in detail in Chapter 3.

Elaters. Elaters (Fig. 2.2b) are hygroscopic linear structures which have a role in explosive spore dispersal at capsule dehiscence. They are normally whitish or yellowish in colour. They are thin-walled but show 1 to 3 spiral thickenings along their length.

2.3 CHARACTER ASSESSMENT

There are two major criteria individual characters must meet in order to be useful for taxonomy and classification:

a. they must display a measurable difference between taxa, either as discontinuous (discrete) characters which display one of several clearly distinct character states, or as continuous characters in which taxa are distinguished by mean values for these character states (*e.g.* length and breadth).

b. they must be stable and not significantly phenotypically plastic.

The first can be measured by traditional taxonomic methods of observation and measurement, both on living plants and herbarium specimens using microscopy and other techniques. The second is much more difficult to assess. Three main approaches can be used to assess stability: firstly by assessing evidence presented by other workers; secondly by direct observation of the plants, preferably living plants under field conditions; and thirdly by experimentally testing character stability under laboratory conditions in culture. These are considered below.

2.3.1 Characters used in major studies on *Asterella*

Over the centuries during which Marchantiales have been studied, new characters have continuously come to light and have been incorporated into classifications. This process is by no means complete and it is important to look for new characters by careful observation, and by application of new techniques not yet tested in *Asterella*.

Before evaluating the value of characters used in this study, the characters used by earlier workers on the genus will be briefly reviewed to reveal any selection, weighting or neglect of certain characters by past authors. This may shed light on how past taxonomic conclusions (especially delimitation of new taxa) were governed by choice of characters.

Five earlier workers, from 1838 to 1994, who have published detailed revisions of *Asterella* species, were selected for this review:

1. Nees' *Naturgeschichte der Europäischen Lebermoose* Vol. 4 (1838).

2. Stephani's *Species Hepaticarum* (1898–1925).

3. Evans' *The North American Species of Asterella* (1920).

4. Grolle's *Verzeichnis der Lebermoose Europas und benachbarter Gebiete* (1976) and *Über Asterella subg. Brachyblepharis in Lateinamerika* (1989).

5. Perold's *Studies in the Marchantiales (Hepaticae) from Southern Africa. 6. The genus Asterella (Aytoniaceae: Reboulioideae) and its four local species* (1994c).

These revisions were scanned for morphological characters used in species distinction. One hundred and seven characters were identified; these are listed in three groups:

V: vegetative characters of gametophyte (55 characters of branches, ventral scales, *etc.*)

R: reproductive characters of gametophyte (37 characters of sexuality, androecia, archegoniophores, carpocephala, pseudoperianth, *etc.*)

S: characters of sporophyte (15 characters of capsule, spores, elaters)

These characters are listed in Appendix I and their use by the five authors scored according to their presence/absence and importance: 0 for characters not used, 1 for standard characters used in species descriptions, and 2 for 'key' characters used in keys, diagnoses, infrageneric grouping *etc.* The characters tabulated in Appendix I are also classified into continuous (with quantitative values) or discontinuous (with discrete values). The totals of these in the vegetative, reproductive and sporophyte character categories were also calculated; these are also presented in the summary tables in Appendix I.

Comparison of vegetative, reproductive and sporophytic characters used in major studies on *Asterella*.

In *Asterella*, the use of gametophytic characters greatly outnumbers use of sporophytic characters, which is the case in most other bryophytes (Appendix I). The lack of use of sporophytic characters may be because they are apparently more conserved evolutionarily and therefore evolving much more slowly and much less variable. Within the gametophytic characters utilised in *Asterella*, numbers are equally divided between vegetative and reproductive characters.

Over the 156 years spanned by this sample, the total number of characters used has increased: Nees (1838) used 58 characters; Perold (1994) used 93 characters. However, whereas the utilised vegetative characters have increased from 23 to 48 over that timescale, reproductive characters have increased only from 24 to 30 and sporophyte characters from 11 to 15. Earlier workers therefore appear to have selectively chosen reproductive and sporophytic characters and ignored or neglected many vegetative characters. However, in apparent contradiction to this, few of the sporophytic characters have been regarded as 'key' characters compared to both the vegetative and reproductive characters of the gametophyte.

What has changed most significantly over these years is the great increase in the number of 'key' characters as defined above: Nees (1838) and Stephani (1898–1925) used only 5 and 4 characters respectively in their classifications of *Asterella* species. The most recent authors in contrast have used over 20 'key' characters.

It would therefore appear that the five selected authors fall into two groups: Nees/Stephani and Evans/Perold/Grolle in terms of character utilisation. The large increase in vegetative characters between these two groups of workers supports the view that it was Evans (1920) who made the 'quantum leap' in *Asterella* taxonomy by introducing many new characters to distinguish and group his taxa. Stephani, in contrast, by using few characters, created a very artificial classification and was not able to reliably define or classify species with the characters he chose. This is discussed further below.

In terms of character selection, there is little to choose between Nees and Stephani. Between the three recent authors, there is a steady but modest increase in all types of characters; this is greatest in sporophyte characters (11 up to 15) almost certainly due to the advent of SEM. However, the total number of key characters has scarcely increased since Evans, again confirming his extremely thorough study of *Asterella*.

The use of continuous and discontinuous characters in *Asterella* taxonomy.

The summary tables in Appendix I show that out of the 107 characters scored, 41 of these are continuous and 66 are discontinuous. From this it might be concluded that continuous characters are quite important in *Asterella* taxonomy. However, very few of the continuous characters have been used as key characters: Nees (1838), Stephani (1898–1925), and Grolle (1976, 1989) in fact used no continuous characters as key characters, Evans (1920) used only 3 (out of 22) and Perold 5 (out of 24 key characters she recognised). This shows a significant bias towards discontinuous characters. This is perhaps natural, as discontinuous characters by their very nature do not overlap and are easy to define, for example spore ornamentation groups are much easier to define than spore size categories where there is considerable within-species variation and between-species overlap (see Chapter 3).

Stephani's taxonomy of *Asterella*

If it is Evans who made the most significant advances in *Asterella* systematics, it is unfortunately Stephani who has most influenced the history of taxonomic study of the genus. He therefore deserves particular consideration. In Table 1.6 fifteen of the 69 taxa described from Eurasia were described by Stephani, outnumbering those of any other author. In Chapter 4 only three of these species (*A. persica*, *A. multiflora* and *A. cruciata*) are maintained. At the time when Stephani studied *Asterella* (in preparation of his world monograph of Hepaticae, *Species Hepaticarum*) what was needed throughout the Hepaticae was a review and synthesis of all the earlier names described by the 19th century workers such as Lehmann, Lindenberg, Nees, Taylor and Montagne. Instead Stephani did the exact opposite; he did not carefully re-evaluate the earlier taxa but embarked on a spate of description of new taxa based on collections made by field workers in India, China, Japan and other parts of the world. Thus, what might have been a manageable task became almost unmanageable as new names proliferated and the old ones remained obscure. Why did he both produce a poor classification and describe so many taxa no longer accepted? Was he just a careless worker or did he use the wrong characters?

Stephani's choice of characters

Stephani's *Species Hepaticarum* (1898–1925) was included in the character analysis outlined above. His preamble to the revision of *Fimbriaria* has been translated as follows, in order to try to understand the rationale behind his character selection and weighting.

'The genus is split here into a number of sections, on the form of the *capitulum*, which places the *fruiting-head* as the most reliable character to distinguish the species; not rarely only one perianth is fertile and as development of the capitulum depends on fertilisation, and sterile heads remain very rudimentary, such heads are not to be relied on for certain identification.'

'After the *capitulum* are the *height of the assimilation layer* in comparison to *height of the midrib*; this [midrib] and its *ventral development*; also the structure of the *pores* and *epidermis* are the best features as they are the most constant. The *thallus* itself can vary rather widely and in shady localities is considerably thinner, so that thallus size, which in the *Ricciae* is very reliable, and the relationship of the thickness of the thallus to its width, cannot be utilised in our genus.'

'The inflorescence is perhaps monoecious in all species of the genus, also in those here described as dioecious; in all cases unfortunately not preserved so that the male branches can be found attached to the female thallus; it must be that these male branches have become detached from others and that in these plants the older parts have become destroyed and the connection between branches lost below.'

'Little reliable are the *colour* of the *peduncle* and the *perianth*; in sunny places many species have intensively-coloured organs, those in shade become pale. The *husk-scales* on the *peduncle* are easily lost and could possibly exist in many species in which I have not seen them. Thickness and length of the peduncle is very variable, so that at first sight one may think that one has a quite different species at hand; finally the *elaters* vary quite extraordinarily in length in one and the same capsule.'

In summary, the characters Stephani considered most important in his classification were those of the scale appendages (shape, apex and margin) and carpocephalum shape. Comparison of these with those ranked as important in recent revisions shows that although these are still important characters many others, not stressed by Stephani, now rank as equally or more important. It is also clear that Stephani recognised that certain characters were phenotypically plastic and unreliable, especially colour. From Appendix I it is apparent that he observed a wide range of characters of gametophyte and sporophyte, but that he used only very few of these in his classification.

A major problem was that he was not able to study living plants and therefore could not study variability of some species in wild populations, for example carpocephalum shape can change greatly during its development, *e.g.* in Section *Brachyblepharis* the carpocephalum starts off as globose, then becomes conical, then finally flat when mature. Stephani apparently was not aware of this and placed closely-related members of this section in four different groups. Had he used more 'key' characters this might have been avoided. For the same reason *A. wallichiana* was treated by him under seven different names in five different groups.

There are other reasons why Stephani described many species more than once. Firstly, he never tried to key species out individually and perhaps did not attempt to discriminate them critically. This may have been due to his biogeographical assumptions that collections from different continents or subcontinents (*e.g.* India, China and Japan) could not possibly be conspecific and he did not bother to look for differences between them. Other characters, because of the relatively poor dried specimens he had to work with, were misinterpreted, for example he rejected sexuality as unimportant but frequently mis-observed it due to inadequate material. Other characters now known to be informative, were overlooked or rejected, *e.g.* spore ornamentation, oil cells and slime papillae on ventral scales, characters of pseudoperianth, *etc.* (Appendix I).

Character stability

As mentioned above, Stephani did realise that some traits displayed by *Asterella* specimens were variable within individual species and unreliable as a means of distinguishing them. However, he also used other characters such as air chamber structure which are now considered to be phenotypically plastic (for example in hygromorphic and xeromorphic forms of some species).

Evaluation of character stability has never been critically studied in *Asterella*, as it is very difficult to test experimentally. Most of the evidence on character stability is anecdotal rather than statistical, based on observation of natural variation of characters in the field, particularly by recent workers who were able to carry out field studies on living plants.

Another reason why character stability has not been studied in *Asterella* is the wealth of discontinuous characters available which have proved reliable over the years and assumed to be stable. Continuous characters such as thallus dimensions, cell sizes and spore sizes are hard to measure especially in herbarium specimens and vary greatly within single specimens. Therefore it has been assumed that this variability within specimens will be mirrored within taxa so making these characters unreliable. This may indeed be a logical assumption but it has not been demonstrated statistically.

Variation in particular characters of individual species of *Asterella* and other Marchantiales may be of three principal types:

a. *phenotypic plasticity*, where the same organ/ character may manifest itself in different character states under different climatic or other conditions, *e.g.* variable development of pigment in light and shade.

b. *seasonal dimorphism*, where the same plant may produce different states of the same character at different seasons *e.g.* xeroshoots and hygroshoots in *Asterella dominicensis*.

c. *developmental changes*, where the same organ may change its morphology during normal development, *e.g.* changes in morphology of the carpocephalum as it matures.

All three types can cause difficulties in interpreting specimens of *Asterella*, but it is the first which is hardest to detect and potentially the most misleading. As stated by Szweykowski (1978): 'the problem of recognising the amount of environmentally evoked variability is a fundamental one'. Two authors in particular have listed characters in *Asterella* they regarded as phenotypically plastic based on observations on dried material: Stephani and Evans.

Stephani (1898–1925: 85–86) listed the following characters as unreliable in *Asterella*:

Thallus	thickness
	breadth: thickness ratio
Peduncle	colour
	breadth
	length
Pseudoperianth	colour
Elaters	length

Similarly, Evans (1920: 250–259) urged caution in the taxonomic use of certain characters in *Asterella* due to their supposed variability within the same species, population or even on individual plants:

Epidermis	cell size
	wall thickening
Air pores	abundance
	size
	number of surrounding cells
Ventral scales	shape
	size
Pseudoperianth	number of lobes
	colour
Spores	size
	colour
	ornamentation
Elaters	length
	diameter.

Neither of these authors carried out any experimental work to support this or quantify the variation, and it is not clear to what extent their observations were based on living or dried plants. There is an obvious need to test these characters using living plants under controlled experimental conditions. What appears to be the case, however, is that continuous characters (such as thallus size, spore diameter, *etc.*) appear to have been considered more phenotypically plastic in the past and for that reason workers have tended to use them rarely as key characters.

The only series of measurements available in the present study with which to test this is spore diameter which is assessed in Chapter 3. In the present study an attempt was made to study phenotypic plasticity in two *Asterella* species, *A. africana* and *A. lindenbergiana*. Though unsuccessful, this study is described briefly below. However, some past studies in other bryophytes and Marchantiales (see 2.3.3) may be a useful guide for assessing plasticity of *Asterella* characters.

2.3.2 Observations on living plants

Observations were made in the field for several species of *Asterella* where large populations over several square metres in extent were present in single relatively uniform habitats, *A. khasyana*, *A. wallichiana* and *A. mussuriensis* on walls in Darjeeling in August 1992; *A. grollei* on soil in China July 1997 and *A. palmeri* and *A. californica* on soil in California, March and April 1998. Notes were made on variability of size and colour within individual colonies. The following characters were noted as especially variable (at least 10 or more plants were measured and the ranges given):

Branch length and width: in *A. khasyana* 3–6 x 2–2.5mm, in *A. wallichiana* 10–20 x 3.5–4.5mm, in *A mussuriensis* 4–11 x 2.5–4mm; in *A. grollei* 12–20 x 6–8mm

Colour of thallus: development of purplish pigment is very variable in individual populations.

Thallus texture: in *A. californica* thick and leathery in dry sites, thinner in more mesic sites.

Stalk length: 2.0 to 5.3mm in *A. palmeri.*

Carpocephalum shape: in *A. khasyana* spherical when young, becoming conical then flat-topped when mature.

The variability of these and other continuous characters is apparent also from measurements of dried herbarium material of individual species (Chapter 4). For example, in the closely related species *A. africana*, *A. cruciata*, *A. khasyana* and *A. leptophylla*, branch widths are recorded as 3.5–8mm, 2–5mm, 0.8–4mm and 3.2–5mm respectively and stalk lengths 6–30mm, 0.8–3mm, 3.3–17.2mm and 15–35mm respectively. Thus none of these species can be distinguished on branch width, only *A. cruciata* can be distinguished on stalk length. However, without experimental study in a controlled environment, it is not possible to conclusively prove that such variability is due to phenotypic plasticity. However, it does demonstrate that such continuous characters should not be used unless a wide sample of specimens has been studied to establish the range of within-species variation.

2.3.3 Experimental work on phenotypic plasticity

Smith (1979) reviewed experimental approaches in bryophyte taxonomy and stressed the importance of cultivation experiments to rigorously test infraspecific variability of taxa and phenotypic plasticity of characters. These approaches have been considered more fully by McQueen (1991) who pointed out that these methods have been little-used partly because of cultivation difficulties. Their prime value is to 'help to determine the amount of phenotypic plasticity and to differentiate between genotypic and phenotypic effects' (McQueen, 1991).

Two main approaches have in the past been used to assess phenotypic plasticity in bryophytes, which are here designated the 'parallel culture method' and 'clonal transplant method'. In the first, genetically different populations are grown under uniform conditions; in the second genetically identical samples are grown under different conditions. Examples of their use in liverworts (but none specifically in *Asterella*) are given below.

a. 'Parallel cultures'

This method has involved transplanting different populations of the same or related taxa into uniform conditions outdoors or in laboratory conditions, in order to test if the plants maintain their different characteristics when grown together. In liverworts the parallel culture approach was pioneered by Buch (1928) on *Scapania* and other genera of leafy liverworts. He showed, by growing different populations of *Scapania* under semi-controlled, semi-natural conditions, that characters such as leaf dentition, stem internode length and anthocyanin development were strongly environmentally controlled. Similar effects were demonstrated in the *Lophozia ventricosa* (Dicks.) Dumort. group (Buch, 1933) where genetically distinct clones responded differently when grown under uniform conditions.

Hatcher (1967) cultured 5 isolated populations of *Lophocolea heterophylla* (Schrad.) Dumort. under identical conditions and demonstrated that the observed morphological differences were influenced both by genetic and environmental factors. Szweykowski & Krzakowa (1969) used this technique on populations of *Plagiochila asplenioides* (L.) Dumort. *s.l.* and showed that the two most distinctive morphological forms in Poland (defined by stem and leaf characters) maintained their differences when grown under uniform conditions. They concluded that the observed differences were genetically based not environmentally induced. Similarly, Szweykowski & Bobowicz (1978) showed that different clones of *Conocephalum conicum* (L.) Dumort. showed significant morphological differences in ventral scale characters (*e.g.* pigmentation) when cultivated together. They later (Szweykowski & Bobowicz 1979) extended this study, using more samples and characters both of the thallus and ventral scales, and showed that Polish populations of *Conocephalum conicum* could be divided into two different races characterised by 'narrower, shorter thalli' and 'broader, usually longer thalli' (a reflection of differing growth rates), but also differing in a combination of ventral scale characters. These two races showed different geographical ranges within Poland.

b. 'Clonal transplants'

The second approach (here designated 'clonal transplant method') has involved growing genetically identical plants under different environmental regimes, normally in culture where the conditions can be carefully controlled and monitored.

An early review using this approach for Marchantiales was given by Douin & Davy de Virville (1924) who demonstrated clear environmental modifications in thallus anatomy, ventral scale size and shape, development of epidermal air pores when genetically identical plants of *Conocephalum conicum* were subjected to different conditions of light and humidity.

Zehr (1980) continued some of Buch's early work on *Scapania* and showed that in the *S. nemorosa* group, characters such as ventral lobe decurrence, leaf dentation, gemma morphology and oil body number were variable under different culture conditions. Guerke (1978) performed growth-chamber experiments on *Jubula* and found that the culture medium had a greater influence on morphological characters than had light quantity, quality or duration. Vogelpoel (1982) demonstrated that in the *Lophocolea bidentatal cuspidata* complex, the same clone could be induced to produce asexual, female and bisexual plants by environmental

manipulation in growth chambers, and the two species, previously distinguished by sexual condition, were united as a result.

This approach has commonly been used in developmental studies, *e.g.* role of photoperiod and temperature in induction of antheridiophores and archegoniophores in *Lunularia*, *Marchantia* and *Reboulia* by Benson-Evans (1964) and Koevenig (1973), and in *Asterella tenella* by Bostic (1981). The last found that archegoniophores were copiously produced under conditions of short days and low temperatures.

Both parallel cultures and clonal transplants have been widely used in mosses to demonstrate both genetic races and phenotypic plasticity, as in *Dicranum* by Briggs (1965), *Climacium* and *Weissia* (Shaw 1987a, b). Hoddinot & Bain (1979) used clonal transplants in six species of mosses to show the effects of canopy light as opposed to direct sunlight (ratio of Red: Far Red light) on gametophyte growth. Their results showed varying responses in different genera. Schwabe (1976) has reviewed studies on the effects of photoperiodism on vegetative growth and reproduction in thalloid liverworts. For example, etiolation was induced by darkness, low-intensity light and far-red light in *Marchantia polymorpha*; drought-resistance was promoted by long days and vegetative growth promoted by short days in *Lunularia cruciata*; sexual reproduction (gametophore production) was promoted by long days in *Marchantia polymorpha* and *Lunularia cruciata*. All these influences could therefore induce changes in characters used in taxonomy such as thallus length, breadth and thickness, thallus branching, *etc.* In wild habitats such influences could be brought about by local phenomena such as shading by trees, shrubs or rocks. It is likely that such effects also apply to *Asterella* species although this has not been experimentally tested.

Materials and methods

Culture of four samples of two *Asterella* species (*A. africana* and *A. lindenbergiana*) was attempted in growth chambers. Growing thallus tips were removed from fresh living plants and placed on coarse sterile sand in transparent plastic tubs with lids, following the method of Frahm & Nordhorn-Richter (1984). Before the experiment, these specimens had been growing for several months at 15^{0}C in a Swan SSC-20-F-SE Growth Chamber using Osram L 13W/20 cool white tubes, at approx. 3500 lux under a daily cycle of 14 hours day and 10 hours night, watered occasionally with distilled water.

A *Asterella africana* (Mont.) A.Evans: Gran Canaria, *Rae 14*

B *Asterella africana* (Mont.) A.Evans: Madeira, *Long 25073*

C *Asterella lindenbergiana* (Corda ex Nees) H. Arnell: Norway, *Long 19989*.

D *Asterella lindenbergiana* (Corda ex Nees) H. Arnell: Switzerland, *Long 25639*.

A single growth cabinet with four shelves was used with 24 tubs on each shelf. Shelf 1 (top) and shelf 3 were unshaded. Shelves 2 and 4 were shaded with a layer of white muslin cloth. Each shelf contained 24 tubs arranged randomly. Shelves 1 & 2 contained 12 tubs each of *A. africana* samples A and B. Shelves 3 & 4 contained 12 tubs each of *A. lindenbergiana*

samples C & D. The temperature was maintained at 15°C and the daily cycle at 14 hours day and 10 hours night.

It was intended to measure changes in thallus length, thallus breadth, thallus thickness, dry weight, air chamber development and ventral scale development, against differences in both light intensity and quality between the shelves with the genetically identical samples. However it became apparent that the experiment was significantly flawed due to (a) variation of light intensity and temperature throughout the growth chamber due to internal reflections and non-isolation of the shelves; (b) probable variation in light intensity and quality due to variable levels of condensation on the undersides of the lids of the tubs depending on position of shelves and positions of tubs on each shelf. Ideally the tubs should have been left open to avoid condensation but this would have resulted in rapid contamination of cultures by other bryophytes and algae, and the need for much more watering; (c) no instruments for locally measuring light intensity, light quality and temperature either on individual shelves or inside the tubs were available for use.

Results and conclusions

Under conditions of bright light as described above the plants grew apparently 'normally' with no sign of etiolation. However, no induction of androecia or archegoniophores was noted over one year. On the shaded shelves thalli of both species became longer and narrower but no detailed measurements were made as light intensity, light quality and temperature could not be measured for the different treatments. It is not known if the etiolation effects were caused by differences in light intensity or light quality, or both, or what influence local differences in temperature within the growth chamber may have had (the more brightly lit tubs were probably warmer within, than the shaded ones, due to local greenhouse effects).

2.4 DISCUSSION AND CONCLUSIONS

The complex morphology of *Asterella* is typical of Marchantiales and offers the taxonomist a remarkable range of characters for descriptions of species, keys, classifications of species into subgenera and sections, numerical and cladistic analysis. They can be conveniently grouped into vegetative, reproductive and sporophytic characters. The complexity of sexual conditions in conjunction with branching patterns is noteworthy.

Study of characters used by a range of past workers on the genus shows that discontinuous characters are more numerous than continuous ones, and that the former have been favoured as 'key' characters. In the past, reproductive and sporophytic characters were favoured in taxonomy, but recent workers have found many more useful vegetative characters. Modern techniques such as SEM have also provided new suites of characters. The most prolific of past workers was Stephani, who described many ill-founded species based on very few characters some of which are unreliable or were misinterpreted.

Information on phenotypic plasticity of some characters has been gleaned from several sources, and the conclusion is that continuous characters of the gametophyte, such as length and breadth, are readily modified by local environmental influences such as shading and light quality. This still remains to be experimentally demonstrated in *Asterella* though it has been in

other genera of bryophytes including Marchantiales. Continuous characters of the sporophyte (spores) are analysed for their taxonomic utility in Chapter 3.

The over-riding conclusion, therefore, is that the extensive range of discontinuous characters available in *Asterella* should be regarded as more reliable for taxonomy and classification than continuous characters which are likely to be more phenotypically plastic.

CHAPTER 3: SPORE MORPHOLOGY

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3.1 INTRODUCTION

The utilisation of spore characters in bryophyte systematics is a relatively new approach which has developed this century along with increasing sophistication of the microscope. Early workers such as Roth (1904–1905) for mosses and Müller (1905–1916) for liverworts recognised that useful differences between spores of related species could be observed with the light microscope, for example the European species of *Fossombronia* were primarily distinguished by striking differences in the surface ornamentation of their large spores. In several liverwort genera, species could be distinguished by diameter and colour of spores (Müller, 1905–1916).

Only in the last 30 years have such studies become more widespread with workers such as Erdtman (1957, 1965) adopting a more systematic approach covering both pollen (in Angiosperms and Gymnosperms) and spores (in bryophytes and other lower land plants). These studies have continued to use Light microscopy (**LM**), but have increasingly used Scanning Electron Microscopy (**SEM**) and Transmission Electron Microscopy (**TEM**) to study in much greater detail the surface ornamentation and wall structure respectively of pollen and spores.

TEM has been much less-widely utilised in spore ornamentation studies in bryophytes than SEM. It has been widely used in evolutionary studies, particularly in comparing the gametophytes of major groups of bryophytes with each other and with other lower land plants such as green algae (Duckett, 1986; Garbary, Renzaglia & Duckett, 1993). The characters studied, such as sperm architecture, cell membranes and organelles, symbiosis, are significant at these higher levels but much less appropriate and practical for taxonomy of individual groups of bryophytes.

TEM's most frequent application regarding spores has been in the study of the layering of the spore wall (Clarke, 1979), for example in the Jungermanniales by Heckman (1970) and in the genus *Riccia* by Thaithong (1982). Relatively few studies have combined TEM with SEM in spores, *e.g.* Gambardella (1987) for *Fossombronia*. Duckett (1986) pointed out that similar surface features of spores could have arisen in different ways developmentally, and stressed the importance of this dual approach where possible. However, he has also indicated (*pers. comm.*) that the large thick-walled spores of Marchantiales are extremely difficult to embed in resin for TEM.

Two papers published in the 1960's on spore ornamentation in Bryophytes using LM gave very detailed and revealing insights into the importance of this source of taxonomic data: Erdtman (1965) and Miyoshi (1966). Erdtman reviewed the whole of the Bryophyta, concentrating on spore diameters and aperture types. He showed that *Asterella* and several other genera of Marchantiales have among the largest spores of the Bryophyta, often 100µm or more in diameter. In most mosses and many Jungermanniales the spores are much smaller, often under 40µm. In *Asterella*, Erdtman (1965) looked only at two European species and did not illustrate the ornamentation.

The landmark paper of Miyoshi (1966) described and illustrated (using LM) spores of a wide range of Japanese Liverworts and Hornworts in great detail. This paper clearly demonstrated for the first time the enormous potential of spores for the provision of characters for distinguishing species and genera in the liverworts, and their potential use in phylogeny. He stressed that 'In Marchantiales the spores show a greater variation in diameter and sculpture than in any other groups of Hepaticae' (Miyoshi, 1966).

Miyoshi in particular pointed out the usefulness of many spore characters in distinguishing species and genera. He used these characters to produce a key to Japanese Marchantiales which included two *Asterella* species (*A. odora* and *A. pusilla*). The key characters were colour, size, polarity (similarity/ dissimilarity of ornamentation on proximal/ distal surfaces), presence/ absence of a trilete mark and type of exine ornamentation, *e.g.* reticulation (double in *Asterella*, *Plagiochasma* and *Targionia*; single in *Reboulia* and *Riccia*) and saccate ornamentation (in *Mannia*, *Peltolepis*, *Wiesnerella* and *Sauteria*).

Within Hornworts and Liverworts he defined five Spore Types. Marchantiales were represented in three of these, Types I, III and V. Jungermanniales were represented in Types II, III, IV and V. *Asterella*, *Mannia*, *Reboulia* and *Plagiochasma* all fell within Spore Type I. He suggested that some characters, *e.g.* number of cells, polarity and presence/ absence of a trilete mark, were significant at the generic and family levels.

Miyoshi also considered that these spore characters were significant in phylogeny of the Hornworts and Liverworts; he presented four phylogenetic trees, for Hornworts, Marchantiales, Metzgeriales and Liverworts as a whole. In the liverwort tree, 'Type I' spores (unicellular, anisopolar, trilete), as in some Aytoniaceae, were considered primitive. His 'Type V' spore (multicellular, isopolar and without a trilete mark), as in *Conocephalum*, was considered to be the most advanced of any Hepaticae. In the Marchantialean phylogenetic tree, *Riccia* was placed as basal, leading to *Plagiochasma* from which three separate lines evolved: one to the other genera of Aytoniaceae, one to *Conocephalum* and the third to other families of Marchantiales (including Cleveaceae, Wiesnerellaceae and Marchantiaceae). In cladistic terms, Aytoniaceae is presented as paraphyletic in this tree.

Other characters, such as ornamentation details, were regarded as less significant evolutionarily, in that the same ornamentation type could appear in quite unrelated families, genera and species. However, these latter characters were useful in characterising individual species.

Miyoshi's review therefore was a milestone in the study of liverwort spores, and on it subsequent workers have been able to base more detailed work. Another wide-ranging study of

liverwort spores is that of Gupta & Udar (1986). Like Miyoshi, their study used only LM, but is nevertheless the most comprehensive review of spores of Indian Marchantiales to date. They illustrated striking differences between genera (*Riccia*, *Cyathodium*, *Targionia*, *Athalamia*, *Asterella*, *Cryptomitrium*, *Plagiochasma*, *Reboulia*, *Exormotheca*, *Conocephalum*, *Dumortiera* and *Marchantia*) as well as between selected species of some of these genera, for example three species of *Asterella*.

The most recent spore studies have now almost exclusively used SEM. They have been largely of two types: (a) more general papers describing techniques and covering a range of genera and selected species, and (b) studies comparing a range of species within a single genus. The most useful general paper is that of Taylor, Hollingsworth & Bigelow (1974) which described techniques in detail, and provided spore micrographs and descriptions for four genera and species of Marchantiales: *Targionia hypophylla* L., *Asterella tenera* (Mitt.) R.M.Schust., *Marchantia berteroana* Lehm. & Lindenb. and *Neohodgsonia mirabilis* (H.Perss.) H.Perss. They also provided a practical terminology for the important characters they described (see 3.7 below).

Boros, Jarai-Komlodi, Toth & Nilsson (1993) have updated the *Atlas of Recent European Bryophyte Spores* to include some SEM pictures of spores, including the Marchantialean genera *Targionia*, *Reboulia*, *Conocephalum*, *Preissia* and *Riccia*. For other Indian Marchantiales, in the genera *Exormotheca, Aitchisoniella, Conocephalum*, *Cryptomitrium*, *Asterella*, *Sauteria* and *Athalamia*, Udar & Srivastava (1984) and Nath & Asthana (1992) have provided a useful overview and high-quality micrographs.

Perhaps more useful, however, has been the second type of study, where SEM of spores has been used for delimiting and characterising species within particular genera. Two workers have been the clear leaders in this respect: Hélène Bischler in Paris and Sarie Perold in Pretoria. Bischler's monographic studies on *Plagiochasma* and *Marchantia* (Bischler, 1977, 1978, 1979a; Bischler-Causse, 1989, *etc.*) have used spore SEM as an important taxonomic tool. Perold (1989) began her South African Marchantialean studies on *Riccia*, where spore SEM was emphasised. Later this approach was extended to other genera such as *Mannia*, *Exormotheca*, *Asterella*, *Cryptomitrium* and *Plagiochasma* (Perold, 1994a, b, c, d, 1995, 1999). Many of the differences observed at high resolution under SEM can also be seen under light microscope in sufficient detail to be of practical taxonomic value.

Within *Asterella*, the papers by Miyoshi (1966), Grolle (1989), Frey *et al.* (1991), Nath & Asthana (1992), Long (1997, 1999), Long & Grolle (1994) and Perold (1994b) have already demonstrated the great diversity of size, colour and ornamentation within even a relatively small range of species of the genus. However, in spite of Miyoshi's (1966) phylogenetic analysis from LM spore studies, only one author (Bischler, 1998) has used SEM spore characters in a phylogenetic analysis of Marchantiales. The four characters she scored were spore number per capsule, spore size, polarity and ornamentation of distal face, out of a total of 43 morphological characters. The published consensus tree was used for tracing character evolution, with the following conclusions (for Marchantiales as a whole): spore number per capsule suggested that few spores per capsule is the plesiomorphic condition, and many spores is apomorphic; spore size did not show any correlation with evolutionary trends; spores with similar proximal/distal

ornamentation appear to be plesiomorphic and have evolved to dissimilar ornamentation in several different lineages; distal ornamentation patterns were complex and did not show any clear apomorphic and plesiomorphic states. Hence it would appear that spore characters as defined by Bischler (1998) are relatively uninformative for phylogenetic reconstruction, perhaps due to frequent character reversals and homoplasy.

As a foundation for the present study, spores of a worldwide range of *Asterella* species were studied in order to define 'Spore-types' for the whole genus. Eight 'Spore Types' have been defined in *Asterella* (Long, 1998), from study of seventeen taxa. Of these, eleven were European and Asiatic taxa, the remainder were American and African species. Five of the eight Spore Types were reported from European and Asiatic species. This work also demonstrated the constancy of four selected spore characters, their value in taxonomy at the species level, their value in interpreting type specimens and their potential value in infrageneric classification within *Asterella*. This study is expanded below to include all the European and Asiatic taxa, utilising the same characters and Spore Types.

From molecular studies of *Asterella* and related genera, Long *et al.* (2000) presented evidence that the four sister-genera to *Asterella* (*Cryptomitrium*, *Mannia*, *Plagiochasma* and *Reboulia*) evolved from within *Asterella* and in cladistic terms are nested within it and should therefore not be used as outgroups. Spores of these genera are therefore also treated to provide data for the cladistic analysis in Chapter 5.

3.2 OBJECTIVES

The aims of the present study were to investigate the value of spore characters (primarily as observed under SEM) in the taxonomy of Eurasian species of *Asterella,* especially:

- to identify useful spore characters and to assess their constancy within individual species
- to look for taxonomic differences between species
- to classify spore types found in European and Asian *Asterella* species
- to provide data for phylogenetic reconstruction in *Asterella*

The value of spores as a practical tool in synonymizing particular problematic *Asterella* taxa is discussed in Chapter 4; their value in phylogenetic reconstruction within Aytoniaceae is dealt with in Chapter 5.

3.3 TAXON SELECTION, MATERIALS, METHODS AND CHARACTER SELECTION

3.3.1 Taxon selection

This study of spores includes all the European and Asiatic species of *Asterella* accepted in the taxonomic revision (Chapter 4) and the sister-genera *Cryptomitrium*, *Mannia*, *Plagiochasma* and *Reboulia*. The following Eurasian representatives of these genera have therefore been included in the study: *Cryptomitrium himalayense* Kashyap, *Mannia androgyna* (L.) A.Evans, *Reboulia hemisphaerica* (L.) Raddi and *Plagiochasma appendiculatum* Lehm. & Lindenb.

3.3.2 Materials

Full details of the specimens used for LM and SEM studies are given in Appendix V. It has not been possible to get plants in culture to produce ripe spores, therefore all spore studies are based on dried herbarium material, especially recently-collected material. Where possible, copious sporophytes were collected, to reduce the need for damaging old and historic specimens. However, for type specimens and species not personally collected in the field, all studies are based on older (sometimes inadequate) herbarium material. No differences in ornamentation were observed between specimens of the same species collected recently and 100 to 150 years ago.

Of the *Asterella* species names listed in Table 1.6, spores of type specimens were studied for most. For a few critical taxa *e.g. Fimbriaria pathankotensis* Kashyap, *F. gangetica* Kashyap, *F. mysorensis* R.S.Chopra and *F. calciatii* Gola, types were not available for study. Although for each species spores of only a few specimens were used to illustrate spore morphology, many more specimens were studied under SEM, often merely to confirm identification.

3.3.3 Methods

Light Microscopy

a. Observation of spore colour. Observation of colour of spores was made under a Wild Stereomicroscope, using where possible a recently-dehisced mature dry capsule from a dry herbarium collection. Where possible colour was recorded for up to ten different specimens of each taxon. No colour chart was used.

b. Measurement of spore diameter. Measurement of spores was attempted on dry spores using a calibrated eyepiece micrometer and oil-immersion objective. A limited range of spore samples was measured before LM measurement was abandoned because of difficulties in focussing on the equatorial plane of the spores and also due to swelling of the spores caused by moisture absorption. To test the value and limitations of LM spore measurements, spores of *Asterella wallichiana* from Iriomote, Japan were used: (i) to test the degree of swelling caused by wetting dry spores, dry spores of a single collection (*B.S.E. 201*, E) were placed on a slide under a coverslip; water was added from a pipette and the increasing diameter of individual spores was measured against time for 90 minutes; and (ii) to compare spore measurement under LM and SEM for populations of a single species from a single geographical area, ten spores from each of five herbarium collections from Iriomote were measured dry under LM and ten spores from the same five collections measured under SEM (as described below).

c. Observation of ornamentation. LM observations of ornamentation were made on moist spores on a glass slide with coverslip using a x50 oil-immersion objective on a compound microscope.

Scanning Electron Microscopy

The methodology used for the SEM study of spores followed that of Taylor *et al.* (1974). Specimens were first examined under a stereomicroscope to locate sporophytes. In recent material, well-prepared collections had some sporophytes already dissected out and placed in a mini-packet for protection. On old specimens, capsules were often inconspicuous and hidden

amongst thalli and debris, or, more often, capsules had already dehisced and the spores dispersed amongst soil. Undehisced capsules often contained only immature spores and consequently were unsuitable for SEM. Ideally, capsules about to dehisce or partly dehisced were optimal for SEM.

A few spores were removed from one or more capsules using a fine moistened brush and spread on an aluminium SEM stub covered by either double-sided sellotape or a carbon disc. For old specimens and types, only a few spores were mounted, whereas for recent collections tens or even hundreds of spores were studied to assess variation. Stubs and spores were then coated with gold/palladium in a sputter-coater prior to study. Acetolysis, a technique for cleaning pollen grains and spores of extraneous material (Clarke, 1979) has been shown to have no beneficial effects on liverwort spores, and in some cases actually damages the sporoderm (Miyoshi, 1966; Taylor *et al.*, 1974). It was therefore not attempted.

On many old specimens, it was found that by carefully examining the dust, soil and plant debris at the bottom of the specimen packets, some spores could usually be found. These could be individually removed by a fine-tipped moist brush and transferred to an aluminium stub. In some cases (rarely) more than one spore type was found in a single packet, but usually the contamination was of spores of a different genus and by removing 10 to 20 spores, those which were *Asterella* could be identified. Fortunately, most *Asterella* species are normally abundantly fertile and few critical type specimens yielded no spores at all. In some cases it was possible to examine one or more duplicates of a type collection, further corroborating the spore type.

SEM studies were performed both on a JEOL JSM T200 Scanning Electron Microscope and more recently on a Zeiss DSM 962 Digital Scanning Electron Microscope at RBG Edinburgh. Coated stubs were introduced to the SEM and scanned at low magnification to pinpoint mature spores at correct orientations (for distal, proximal and lateral views). A low voltage 5kV or sometimes 10kV was normally used to cut down on charging of the spores. A selection of the spores were photographed at various magnifications (x350 to x2000). In the Zeiss SEM images were stored initially on CD-ROM and also printed as (temporary) video prints. Selection was then made of the best images from each stub for photography on Ilford Technical Pan Film. Descriptions of ornamentation were made from photographic prints. Images selected for reproduction were later scanned from photographic negatives using Adobe Photoshop software on a PC and prepared for publication using Microsoft Powerpoint.

Measurements of spores were made using the SEM Video Printer facility. Stubs were quickly scanned and video prints made of ten spores of each specimen. The chosen spores were aligned so that the equatorial diameter could be measured consistently (Fig. 3.1). Diameter was calculated for each spore using the calibrated scale on the video print. Magnification of x1000 was ideal for most species.

Where possible, measurements of spores were made for ten collections of each taxon, or in some cases for up to 5 collections from putative synonyms or plants from different geographical regions to look for discontinuities (depending on availability). The resulting mean measurements were incorporated into the species descriptions in Chapter 4. The measurements from *A. wallichiana* spores from Iriomote, Japan were used for comparison with the LM measurements.

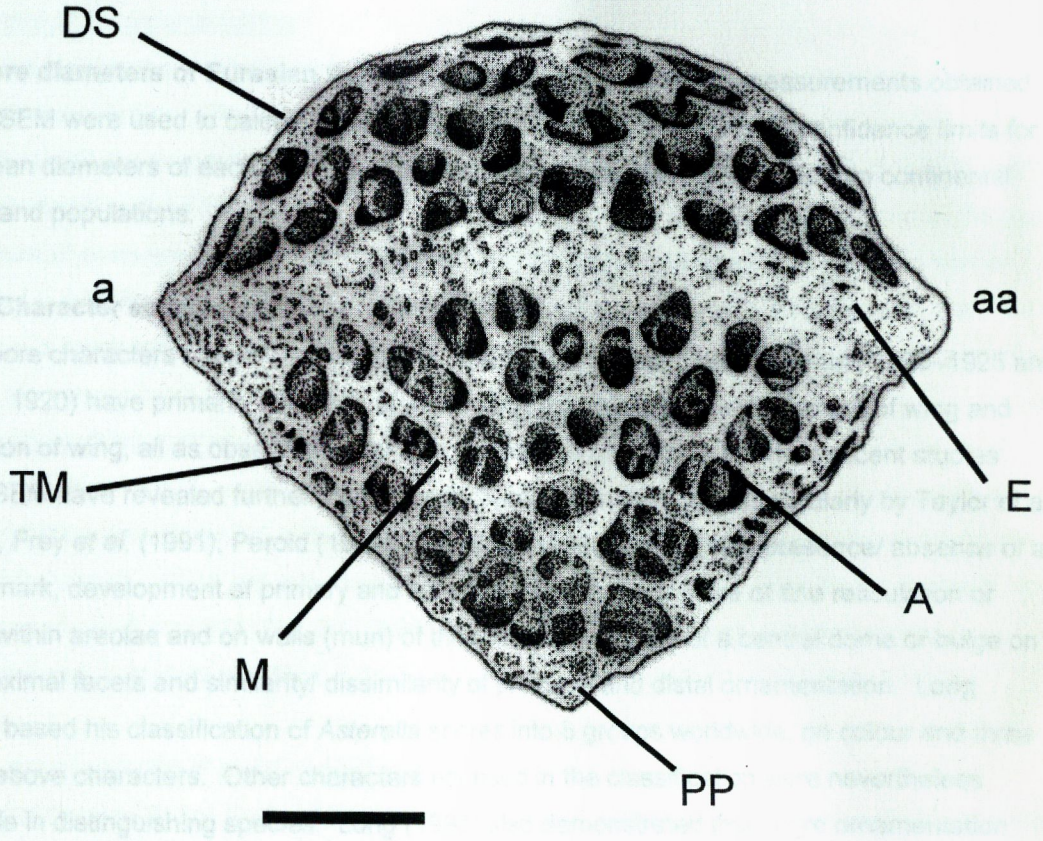

Fig. 3.1 Spore of *Asterella mussuriensis* (India, Mussoorie, *Duthie 309*) in side view. A = areole; DS = distal surface; E = equator; M = murus; PP = proximal pole; TM = trilete mark; a—aa = equatorial diameter. Scale bar = 20µm.

Analysis of spore diameter data

a. Comparison of LM and SEM measurements. For five populations of *A. wallichiana* from Iriomote, Japan, LM and SEM measurements were tabulated. Using Microsoft Excel, means, standard deviations and 99.9% confidence values for the means were calculated for each sample. Two-way analysis of variance (ANOVA) (Sokal & Rohlf, 1995) was undertaken using Datadesk Version 6.0 statistical software to compare spore diameters as measured by SEM and LM, and to test whether treatment of spores and/or collector caused any effect on observed spore diameter, and if there was any interaction between these factors. This was undertaken using Bonferroni Post Hoc tests to establish the effects of the two factors studied, and any interactive effect between the two factors. An interactive plot was produced from this.

b. Spore diameters of Eurasian *Asterella* species. For all taxa the measurements obtained under SEM were used to calculate means, standard deviations and 99.9% confidence limits for the mean diameters of each taxon. For three species these were subdivided into continental and island populations.

3.3.4 Character selection

The spore characters used by early workers on *Asterella* (Nees, 1838; Stephani, 1898–1925 and Evans, 1920) have primarily been colour, diameter, ornamentation, development of wing and crenation of wing, all as observed under light microscope (Appendix I). More recent studies using SEM have revealed further useful spore characters in *Asterella*, particularly by Taylor *et al.* (1974), Frey *et al.* (1991), Perold (1994c) and Long (1998), for example presence/ absence of a trilete mark, development of primary and secondary areolae, presence of fine reticulation or pores within areolae and on walls (muri) of the areolae; presence of a central dome or bulge on the proximal facets and similarity/ dissimilarity of proximal and distal ornamentation. Long (1998) based his classification of *Asterella* spores into 8 groups worldwide, on colour and three of the above characters. Other characters not used in the classification were nevertheless valuable in distinguishing species. Long (1998) also demonstrated that spore ornamentation characters were constant for a range of species, and that they were valuable both in distinguishing and synonymising critical species and were potentially useful in classification of species.

All possible characters derived both from published work and my own observations on *Asterella* spores, were studied. The eleven characters below were found to be of value, both for *Asterella* species and its four sister- genera included in the study.

a. Colour

Colour was recorded into three broad categories: black, brown (including red-brown and purplish-brown) and yellow (including orange-yellow).

b. Size (equatorial diameter)

Spores were measured across the equator (Fig. 3.1). It was assumed that in t.s. the spores are circular and that the equatorial diameter can be measured in any side-view.

c. Shape

Spores of Marchantiales are formed in tetrads resulting from a meiotic division and their shape in most species reflects this development: they are roughly spherical in outline with a hemispheric outer (distal) surface and with three proximal facets separated by a trilete mark, converging at a pointed proximal pole. Spores were classed as trilete (Fig. 3.11d), weakly trilete (with faint trilete mark (Fig. 3.22c)) or alete (Fig. 3.21d); in *Asterella* most are trilete though *A. gracilis* has alete spores.

d. Similarity/ dissimilarity of proximal and distal ornamentation)

Two states of this character were observed: ornamentation similar on both surfaces as in *A. grollei* and *A. wallichiana* (Figs. 3.5, 3.6, 3.7 and 3.8); ornamentation dissimilar, as in *A. leptophylla*. (Fig. 3.12).

e. Primary distal ornamentation

The most highly ornamented *Asterella* spores display three 'levels' of ornamentation: primary, secondary and tertiary. Primary ornamentation is commonly in the form of large shallow areolae, which are demarcated by low ridges (muri). In *A. wallichiana* (Figs. 3.6, 3.7, 3.8) and two other species the primary ornamentation consists of coarse wavy ridges, which may be deep or shallow or even hardly developed at all when the spores appear almost smooth. In some species (*A. gracilis*, Fig. 3.21) the ridges form incomplete areolae and it is considered that this condition is intermediate between the ridged and areolate conditions. In *Mannia androgyna* (Fig. 3.22d) the spores have large swollen saccate protruberances.

f. Secondary distal ornamentation

In some species (*e.g. A. wallichiana* and *A. multiflora*, Figs. 3.6, 3.7, 3.8, 3.20) no secondary ornamentation was observed, but in many species with reticulate spores there are numerous secondary 'alveoli', which are cup-shaped reticulations, relatively small and varying in depth. In species such as *A. saccata* (Fig. 3.4) this is the only type of reticulation, whilst in others (eg. *A. khasyana* and *A. leptophylla* (Figs. 3.11 and 3.12) the alveoli are contained within primary areolae.

g. Fine ornamentation of distal ridges/ muri/ sacs

The finest ornamentation on the ridges, muri and sacs of spores of *Asterella* and related genera is in the form of minute striations, reticulations or papillae (*e.g. A. wallichiana* Figs. 3.6, 3.7, 3.8) or minute pits as on the muri of *A. mussuriensis* and several other species (Figs. 3.19a, b).

h. Equatorial rim development

The equatorial rim or 'wing' of the spore was in the past considered to be an important character as it appeared under light microscope as a distinct wing; *e.g.* the South African *A. marginata* was characterised by its spore wing. Under SEM it can be seen that the presence of a rim correlates with the presence of a trilete mark and it represents a slightly thickened junction between the distal and proximal surfaces (*e.g. A. persica*, Fig. 3.16c). Only rarely is it thin and wing-like. In *A. gracilis* it is absent (Fig. 3.21). In some species it is relatively flat, in others it is wavy in side-view. The rim is defined here by a clear discontinuity in ornamentation.

i. Equatorial apertures

These apertures were found to be relatively rare in *Asterella*, but three small apertures terminating the trilete ridges are found in several southern hemisphere species such as *Asterella*

drummondii (Australia), *A. marginata* (South Africa) and *A. macropoda* (South America). They are also found in the related genera *Mannia* (Fig. 3.22c), *Reboulia* and *Plagiochasma*. In the Sino-Himalayan *A. grollei* (Fig. 3.5b, e) the apertures are much larger. Their function is unknown but may relate to water uptake or germination. They were recorded as present or absent.

j. Proximal bulge development

Proximal bulges were observed in several species such as *A. blumeana* (Fig. 3.13e, h) and A. *cruciata*. Other species have flat or weakly curved proximal facets (Fig. 3.19c).

3.4 RESULTS

Results obtained for both LM and SEM are described under quantitative and qualitative types. The taxon names used are 'accepted names' as defined in Chapter 4.

3.4.1 Quantitative spore data

Spore diameter measurement. As explained under 3.3.2, even at high power under LM the problem of focussing on the equatorial plane of the spore meant that accurate measurements were difficult to obtain and this approach was eventually abandoned in favour of measurement under SEM (see below). The results of the spore wetting experiment are given in Appendix II. The hygroscopic nature of the dry spores meant that they readily absorbed water and increased in diameter under the light microscope making consistent measurement difficult. A single dry spore of *Asterella wallichiana* increased in diameter by 16.2% over 90 minutes. Even without wetting, the heating of the spore under a microscope caused it to absorb water from the atmosphere and begin to swell.

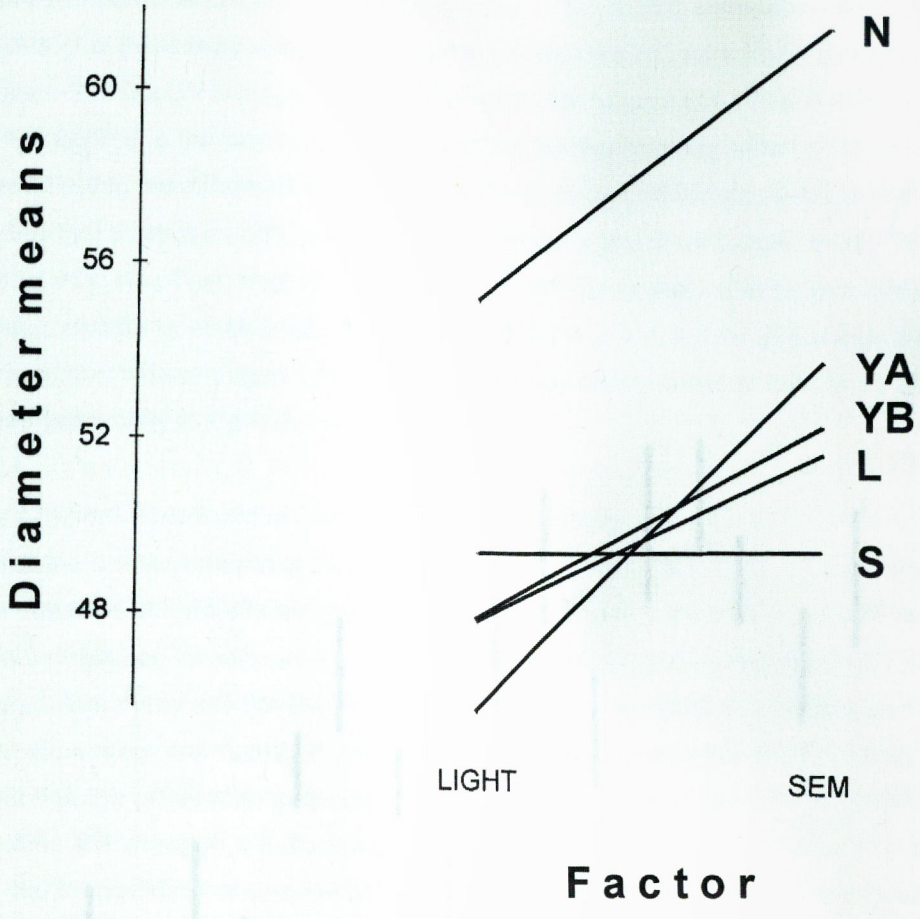

Fig. 3.2 Interactive plot from two-way ANOVA of spore diameter means of five collections of *Asterella wallichiana* from Iriomote, Japan, showing interaction of factors 'treatment' (LM/SEM) with 'collector'. N = *Nagamasu,* YA = *Yamaguchi A*, YB = *Yamaguchi B*, L = *Long*, S = *Saito.*

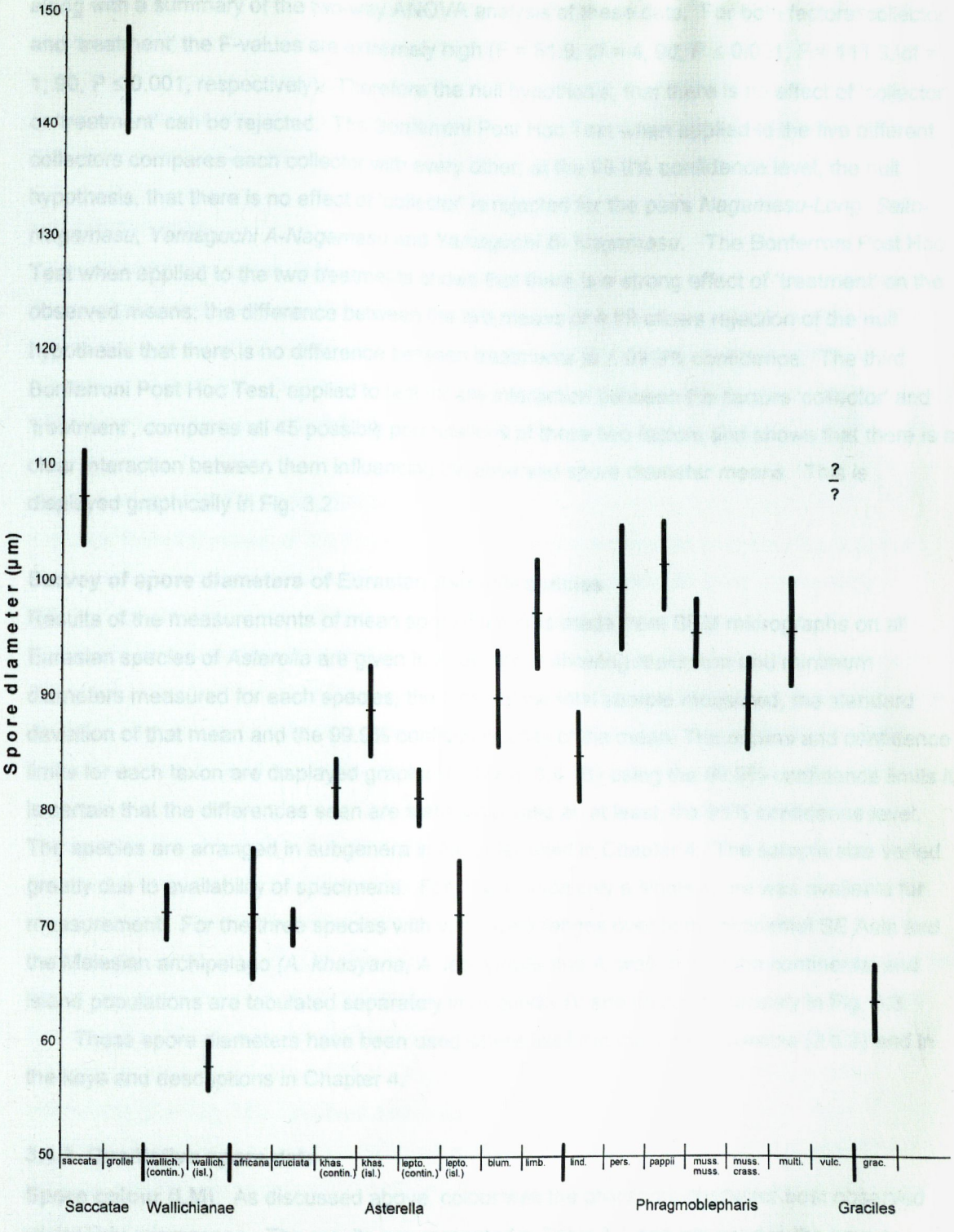

Fig. 3.3 Mean values of spore diameter for Eurasian *Asterella* species showing 99.9% confidence limits. Species are grouped into subgenera. For *A. vulcanica* only a single spore was measured.

Comparative LM/SEM spore diameter analysis. Comparative LM/SEM spore diameter measurements of five samples of *A. wallichiana* from Iriomote Island are given in Appendix III, along with a summary of the two-way ANOVA analysis of these data. For both factors 'collector' and 'treatment' the F-values are extremely high ($F = 51.9$, $df = 4, 90$, $P \leq 0.001$; $F = 111.5$, $df = 1, 90$, $P \leq 0.001$, respectively). Therefore the null hypothesis, that there is no effect of 'collector' or 'treatment' can be rejected. The Bonferroni Post Hoc Test when applied to the five different collectors compares each collector with every other; at the 99.9% confidence level, the null hypothesis, that there is no effect of 'collector' is rejected for the pairs *Nagamasu-Long*, *Saito-Nagamasu*, *Yamaguchi A-Nagamasu* and *Yamaguchi B- Nagamasu*. The Bonferroni Post Hoc Test when applied to the two treatments shows that there is a strong effect of 'treatment' on the observed means; the difference between the two means of 4.99 allows rejection of the null hypothesis that there is no difference between treatments at ≥ 99.9% confidence. The third Bonferroni Post Hoc Test, applied to test for any interaction between the factors 'collector' and 'treatment', compares all 45 possible permutations of these two factors and shows that there is a clear interaction between them influencing the observed spore diameter means. This is displayed graphically in Fig. 3.2.

Survey of spore diameters of Eurasian *Asterella* species

Results of the measurements of mean spore diameters made from SEM micrographs on all Eurasian species of *Asterella* are given in Appendix IV showing maximum and minimum diameters measured for each species, the mean of the total sample measured, the standard deviation of that mean and the 99.9% confidence limits of the mean. The means and confidence limits for each taxon are displayed graphically in Fig. 3.3. By using the 99.9% confidence limits it is certain that the differences seen are statistically valid at, at least, the 95% confidence level. The species are arranged in subgenera in the order used in Chapter 4. The sample size varied greatly due to availability of specimens. For *A. vulcanica* only a single spore was available for measurement. For the three species with very broad ranges over both continental SE Asia and the Malesian archipelago *(A. khasyana*, *A. leptophylla* and *A. wallichiana*) the continental and island populations are tabulated separately in Appendix IV and plotted separately in Fig. 3.3.

These spore diameters have been used where useful in the keys to species (3.5.3) and in the keys and descriptions in Chapter 4.

3.4.2 Qualitative spore data

Spore colour (LM). As discussed above, colour was the only spore character best observed under light microscope. The results are presented in Table 3.1 and are used in the keys to species (3.5.3) and in the keys and descriptions in Chapter 4.

Spore ornamentation (LM). Figs. 2.2c, d illustrate the proximal and distal ornamentation visible under LM of a spore of *Asterella limbata* (compare with SEM of this species in Fig. 3.14).

Spore ornamentation (SEM). The results of the SEM study of a large number of samples of all 16 species of *Asterella* are presented as selected micrographs in Figs. 3.4 to 3.21 showing where possible distal ornamentation, proximal ornamentation and details at higher magnification from several different specimens which display the observed spectrum of within-species

variation. Micrographs of the other four genera included in the study are shown in Fig. 3.22. From these micrographs the major qualitative differences between the taxa are summarised in Table 3.1. The Spore Types described by Long (1998) are shown in Table 3.2 with the addition of three new Types IX, X and XI for the sister-genera *Reboulia*, *Plagiochasma*, *Cryptomitrium* and *Mannia*. Type IV is omitted as it is not represented in the study-area.

These results are incorporated where useful in the keys to species (3.5.3) and in the keys and descriptions in Chapter 4.

3.5 DISCUSSION

3.5.1 Quantitative spore data.

Spore diameter measurement. Accurate measurement of spore diameter under LM is difficult due to the problem of focussing on the equatorial plane. This is much more precise and repeatable under SEM. Consistent measurement of spore diameter under LM is also made very difficult by the changes in diameter caused by moisture content (Appendix II).

Comparative LM/SEM spore diameter analysis.

It is clear from the results of the comparative LM/SEM spore diameter analysis (Fig. 3.2) that measurement of spores of *Asterella wallichiana* on Iriomote under LM gives consistently different results from measurement under SEM. The SEM measurements are usually higher. Due to the problems described above in measuring under LM, it is likely (but not proven) that the SEM measurements are more accurate. The two-way ANOVA analysis shows three things, that at 99.9% confidence level there is a demonstrable effect of 'treatment', of 'collector' and an interactive effect between 'collector' and 'treatment' on the observed spore diameter means.

In the analysis of 'treatment', the F-ratio is 111 which means that the chance of the observed differences being due to natural variation is almost nil, and the null hypothesis, that 'treatment' has no effect on observed spore diameters, is therefore rejected. The Bonferroni Post Hoc tests attempt to ascertain what this effect is. For 'treatment', the effect is that SEM gives larger diameters than LM. For 'collector', Nagamasu's collection is different because of his larger diameters than the other collectors. The interactive plot (Fig. 3.2), however, shows that for Long, Nagamasu and Yamaguchi's collections, the difference between LM and SEM measurements are significant and similar. However, for Saito's collection, LM and SEM treatments give very little observed difference in spore diameter.

Thus it may be the case that Saito's specimens were collected or dried differently from those of the other three collectors, reducing the observed difference caused by the 'treatment' method.

Population differences in *A. wallichiana* on Iriomote

ANOVA analysis using both LM and SEM treatments shows that in the five samples studied, there are statistically significant differences between spore diameters of individual populations (as sampled by different collectors) of *A. wallichiana* on Iriomote (Appendix III).

Thus, on Iriomote, spore diameter of *Asterella wallichiana* populations vary in a different manner to that of the qualitative characters. Because of the close proximity of all the localities it

could be argued that there are unlikely to be separate genetically distinct races on such a small island, although this was not further investigated by tests such as isozyme analysis. In contrast, the differences in spore diameter between populations of *A. wallichiana* from different islands and different parts of continental SE Asia (see below) would be easier to explain by regional genotypic differentiation. On Iriomote it would appear that the observed differences in spore diameter between populations are more likely due to phenotypic plasticity. Even if these differences had a genetic basis, the value of spore diameter as a precise descriptive character is still greatly undermined.

There are four possible explanations for the high within-species variation but low within-population variation:

i) Individual populations (or groups of populations) on Iriomote could be genetically isolated and uniform, with the resulting spore diameters representing significant genetic differences between these populations.

ii) Spore diameter may be extremely phenotypically plastic, and depend on local growth effects. This might be influenced by niche microclimate, favourable sites producing more vigorous plants with larger spores. These differences could also be due to climatic differences between the years of sampling.

iii) Spore diameter could reflect maturity of an individual population when the collection was made; the samples with smaller spores may be immature.

iv) Spore diameter may change according to age of collection.

The first of these hypotheses could be supported by evidence of cryptic infraspecific variation ('sibling speciation') reported in other Marchantiales. This phenomenon has been reviewed by Bischler & Boisselier-Dubayle (1997), who reported 'sharp isozyme differentiation in several morphologically uniform thallose liverwort taxa'. Occasionally, slight morphological differences have been reported between such populations but spore diameter has not been one of these. Bischler & Boisselier-Dubayle (1997) also attempted to correlate these differences with 'life strategy traits' (for example populations behaving as colonists, shuttlers and perennial stayers as defined by During (1992)) but failed to detect any. Examples of sibling speciation in other Marchantiales have been described in *Conocephalum conicum* by Akiyama & Hiraoka (1994) and Odrzykoski (1995) and in *Mannia fragrans* by Odrzykoski & Szweykowski (1981). It has not yet been reported in *Asterella*.

The third and fourth hypotheses are not supported by the current evidence. Although the *Saito* collection made in 1973 has spores smaller than the others (Appendix III), the *Nagamasu* collection made in 1982 has larger spores than the *Long* and *Yamaguchi* collections made in 1993, ruling out a correlation between age and spore diameter. In all samples studied the spores appeared to be fully mature.

The second hypothesis (phenotypic plasticity) is perhaps the most plausible on current evidence but testing the hypotheses is necessary, and would require an approach such as looking for chemical markers in different populations and relating these patterns to spore diameter.

Survey of spore diameter of Eurasian *Asterella* species

a. Differences between species. From Appendix IV it can be seen that for many Eurasian species of *Asterella* (*e.g. A. africana, A. blumeana, A. leptophylla* and *A. persica*), there is a large within-species range of spore diameters. However, Fig. 3.3 illustrates that some species (*e.g. A. grollei*) have very distinct ranges of spore diameter, others overlap with both related and unrelated species, but the species ranges do show some correlation with classification. Subgenus *Saccatae* (*A. saccata* and *A. grollei*) have larger spores than all other species. Spores of Subgenus *Asterella* are mostly smaller than those of Subgenus *Phragmoblepharis*. Subgenus *Graciles* (*A. gracilis*) has small spores. It appears from Fig. 3.3 that subgenus *Asterella* shows much greater variability (c 1/3 greater) in spore diameter than the other large subgenus, subg. *Phragmoblepharis*, especially when *A. lindenbergiana* is removed from subg. *Phragmoblepharis*, which is suggested by the morphological cladistic analysis in Fig. 5.5 (but not by the molecular trees in Long *et al.* (2000)). Spore diameter appears therefore to be of low taxonomic value in subg. *Phragmoblepharis*, but of greater value in subg. *Asterella* and much greater value in subg. *Saccatae*.

Some pairs of related species (*A. africana/ A. cruciata; A. persica/ A. pappii; A. mussuriensis/ A. multiflora*) cannot be distinguished on spore diameter means as the confidence limits overlap; other pairs (*A. saccata/ A grollei; A. leptophylla/ A. blumeana*) are clearly distinct. For all three of the species for which continental and island populations are plotted separately, the means of the two are significantly different, especially *A. wallichiana*. Thus, in spite of the broad observed ranges in diameter measured for many species, the confidence limits of the means show that the differences for some species are significant and that diameter therefore has taxonomic value.

b. Differences between populations. For the three widespread Asiatic species (*A. khasyana, A. leptophylla* and *A. wallichiana)* there appear to be differences between the populations from continental SE Asia and those from the Malesian archipelago on spore diameter measurements. This difference is most marked in *A. wallichiana*, where the populations from Japan, the Philippines and Taiwan have consistently smaller diameters than those from continental Asia.

Therefore, in some widespread taxa, within-species differences in spore diameter are significant and may reflect regional within-species genetic variation. At present these differences are not known to correlate with other morphological differences, but it may suggest that 'sibling speciation' (Bischler & Boisselier-Dubayle, 1997) is present. Other tools, e.g. isozyme analysis, should be applied to a representative geographical sample of populations to test this. Morphological or chemical correlations should be sought by more detailed investigation.

3.5.2 Qualitative spore data.

Spore colour (LM). The results presented above show that the application of light microscopy is of value primarily in recording spore colour. This is best observed under a high-power stereomicroscope. Spore colour appears to be a reliable character which varies little between populations of one species.

Spore ornamentation (LM). Comparison of the ornamentation visible under LM of a spore of *Asterella limbata* with the SEM micrographs of that species (compare Figs. 2.2c, d with Fig. 3.14) shows that LM offers little other than illustrating that it is areolate. However, for practical identification, LM is adequate for characterising the primary ornamentation pattern.

Spore ornamentation (SEM). The large numbers of spore samples studied under SEM confirm that most qualitative characters recorded are remarkably constant for different populations of single species and are therefore very valuable in characterising individual taxa. Some characters (*e.g.* secondary ornamentation) were not present in all taxa. Other characters (*e.g.* saccate ornamentation) were seen only in some of the other genera studied and not in *Asterella*.

a. Shape. *A. gracilis* was the only *Asterella* species observed with alete spores. In *Mannia androgyna* the spores were very weakly trilete.

b. Similarity/ dissimilarity of proximal/ distal ornamentation. This appears to be a very significant character which sharply differentiates groups of *Asterella* species. In that genus most species have similar sculpturing on both surfaces except for *A. khasyana* and related species where it is sharply different. The latter condition also exists in *Mannia androgyna*.

c. Primary distal ornamentation. This character displayed some very striking differences which appear to correlate well with some other spore characters. It appears to be highly consistent within species, though in *A. wallichiana* the degree of ridging is variable: some populations from Japan and Taiwan have much less ridged to almost smooth spores. In *A. grollei* the spores vary from ridged (Nepal) to incompletely areolate (China). Both these examples suggest that there is geographical variation in spore ornamentation, but as yet this has not been clearly correlated with differences in gametophyte morphology.

Muri were not present in all taxa, and the homology of the muri of areolate spores with the ridges of ridged spores is not unequivocal. However, in most areolate taxa the morphology of the muri was distinctive. Significant variation was noted in *A. mussuriensis* where the muri varied greatly in thickness between populations. The almost lamelliform muri of *Cryptomitrium himalayense* were unique amongst the genera studied.

d. Secondary distal ornamentation. This generally consisted of small areolae or alveoli but some species displayed no secondary ornamentation and could not be scored.

e. Fine ornamentation of distal ridges/ muri/ sacs. These surfaces displayed fine striations, reticulations or papillae, or were finely pitted. The primary areola muri of *Reboulia* and *Plagiochasma* are distinct from those of *Asterella* in lacking minute pits, though the ridges of *A. wallichiana* and *A. grollei* also lack pits, as do the sacs of *Mannia androgyna*.

f. Equatorial rim development. This proved difficult to measure consistently as it is often indistinctly differentiated from the distal surface. It is most conspicuous in *Mannia androgyna*.

g. Equatorial apertures. These were observed in *A. grollei*, where they are large and unlike those in any other known species. In *A. vulcanica* small apertures appear to be present but only a single spore of this species was available for study. The spores are very similar to those of several southern hemisphere *species* (*e.g. A. drummondii* and its Australasian relatives) which all have equatorial pores. This observation requires confirmation in *A. vulcanica*. Small pores

are also present in *Mannia androgyna*, *Plagiochasma appendiculatum* and *Reboulia hemisphaerica*.

h. Proximal bulge development. In some species (*e.g. A. blumeana*) these were very pronounced, in others poorly defined and difficult to score.

3.5.3 Taxonomic differences between *Asterella* species.

The qualitative results presented in Table 3.1 and Figs. 3.4 to 3.21, along with the spore measurements displayed in Fig 3.3, give a wealth of information for discriminating the Eurasian species of *Asterella*. In fact most species can be identified from their spores alone (see key below). Apart from diameter, which is quite variable in some species, most other characters are discrete and vary little within a species.

Decisions on synonymy made in this study on individual species have in most cases relied heavily on the results of the spore studies. Three examples have been illustrated in Long (1998): the synonymizing of *A. crassa* under *A. mussuriensis,* the synonymizing of *A. levispora* under *A. wallichiana* and the discrimination of *A. blumeana* from *A. khasyana*. These and other decisions on synonymy are more appropriately discussed in Chapter 4 under individual species, and the precise significance of spores explained there in each case.

The most important qualitative and quantitative spore differences have been incorporated into the key to species and descriptions of species given in Chapter 4. However, a key based solely on spore characters is presented here:

Key to *Asterella* species using colour and SEM spore characters

Note: ornamentation patterns refer to distal surface of spore unless otherwise indicated

1. Spores with coarse ridges to almost smooth; conspicuous areolae or alveoli absent (in *A. saccata* ridges with minute reticulations 1–5µm diameter) 2
+ Conspicuous areolae or alveoli present 4

2. Spores black, 135–160µm diameter, with large equatorial apertures ..... **2. A. grollei**
+ Spores yellow, brown or red-brown, 40–125µm diameter, without equatorial apertures 3

3. Spores yellow, 90–125µm diameter; ridges with minute reticulations ..... **1. A. saccata**
+. Spores brown or red-brown, 40–105µm diameter, ridges (sometimes very weakly developed) with minute striations to almost smooth, never reticulate **3. A. wallichiana**

4. Spores alete, ± hollowed proximally without trilete mark or proximal point; equatorial rim absent ..... **16. A. gracilis**
+ Spores trilete, tapering to distinct proximal point and with distinct trilete ridges; equatorial rim present 5

5. Spores brown, red-brown or purplish-brown 6
+ Spores yellow or orange-yellow 10

6. Large primary areolae present, 15–25µm diameter, smooth and pitted but without alveoli ..... **14. A. multiflora**
+ Primary areolae present or absent; when present over 10µm diameter; secondary alveoli 2–7µm diameter, deep, conspicuous 7

7. Primary areolae (over 10µm diameter) absent or indistinct on distal surface 8
+ Primary areolae ± distinct on distal surface 9

8. Primary areolae absent; secondary alveoli ± uniform, 4–6µm diameter **10. A. lindenbergiana**
+ Primary areolae indistinct (more distinct on proximal facets); alveoli very irregular in size, 2–7µm diameter ..... **11. A. persica**

9. Distal muri thin and irregular; areolae 10–17µm diameter, poorly-defined towards margin ..... **12. A. pappii**
+ Distal muri thick and regular; areolae 6–15µm diameter, clearly defined to margin **13. A. mussuriensis**

10. Primary areolae indistinct distally; distal surface with a 'crown' of bulges **8. A. blumeana**
+ Primary areolae present distally; distal surface rounded, without bulges 11

11. Distal areolae smooth, without alveoli (angles of muri alveolate) ..... **15. A. vulcanica**
+ Distal areolae densely alveolate 12

12: Spores orange-yellow, mostly 60–75µm diameter 13
+ Spores yellow, mostly 75–110µm diameter (rarely smaller *in A. khasyana*) 14

13. Proximal facets ± uniformly sculptured with alveoli, without larger areolae on proximal bulge ..... **4. A. africana**
+ Proximal facets unevenly sculptured with alveoli and prominent larger areolae on proximal bulge ..... **5. A. cruciata**

14. Proximal bulge usually conspicuous; spores 55–90µm diameter ..... **7. A. leptophylla**
+ Proximal bulge very low or absent; spores mostly 75–110µm 15

15. Spores mostly 75–100µm diameter; muri usually narrow and acute ..... **6. A. khasyana**
+ Spores 85–110µm; muri broad and rounded ..... **9. A. limbata**

3.5.4 Classification of Spore Types found in European and Asian *Asterella* species

As discussed above (3.1) the value of spore colour and ornamentation in classifying *Asterella* species has been established by Long (1998). In that study eight Spore Types were recognised; these are incorporated into Table 3.2 as Spore Types I to VIII. For cladistic analysis (Chapter 5) the genera *Reboulia*, *Plagiochasma*, *Mannia* and *Cryptomitrium* are included. The spores of none of these genera can be accommodated within the eight *Asterella* Spore Types; three new Spore Types IX to XI are defined (Table 3.2) using the data from Table 3.1.

Four characters (colour, shape, similarity/ dissimilarity of proximal/ distal ornamentation and distal ornamentation type) have been selected (Long, 1998) as the most useful characters for defining Spore Types in *Asterella*, as they are available in all taxa and can be consistently scored. Two of these (shape and similarity/dissimilarity) are characters Miyoshi (1966) considered to be of evolutionary significance in Hepaticae. In Table 3.2 all sixteen Eurasian *Asterella* species are classified under this system. Representatives of seven of the eight Spore Types are found in the Eurasian taxa, with six species with Type VII spores. The significance of Spore Types lies in infra-generic subdivision of *Asterella*, and in possible evolutionary relationships between different groups of species.

The data presented in Tables 3.1 and 3.2 are also used in infrageneric classification (Chapter 4) and in phylogenetic reconstruction (Chapter 5).

3.6 CONCLUSIONS

As in other Marchantiales, the highly ornamented spores in *Asterella* offer a range of characters with great potential value in taxonomy and classification.

Spores can be observed under both LM and SEM. The former is useful only in scoring spore colour; the latter is useful for measuring diameter and observing a range of qualitative ornamentation characters. In total ten different characters can be scored for individual specimens: colour, diameter, shape, similarity/ dissimilarity of proximal/ distal ornamentation, primary ornamentation, secondary ornamentation, fine ornamentation, development of equatorial rim (wing), presence/ absence of equatorial apertures and development of proximal bulges.

Spore diameter is of value in defining some species, but not others, especially some closely related species-pairs. Individual specimens show quite low variation, but different populations, even those growing in close proximity, can show large statistically significant between-population variation in diameter but low within-population variation. Several hypotheses could explain this; the favoured one is high phenotypic plasticity of spore diameter. However, for species with broader geographical ranges, there are clear geographically-correlated differences in spore diameter. These require further study.

Qualitative characters appear to be more constant, both within individual populations and between different populations of the same species, especially colour and details of ornamentation; which provide a reliable suite of characters. Most Eurasian species can be distinguished by spores alone.

Spores provide good characters for practical identification, as some can be observed under LM. Their longevity and durability (in contrast to the gametophytes) means that they can be

extremely useful in identifying and synonymising problem taxa and old specimens. Spores also provide valuable data for grouping species, classification and evolutionary studies.

3.7 GLOSSARY OF SPORE TERMINOLOGY (see Fig. 3.1)

In reviewing past work on spore ornamentation, there is no great consistency of terminology for the important characters. The following papers have provided glossaries of terms, and these have been used to obtain a consensus terminology which is given below: Boros *et al.* (1993), Miyoshi (1966), Slageren (1985) and Taylor *et al.* (1974).

Alete: lacking trilete angles on proximal surface

Alveolus (plural *alveoli*): fine reticulum (secondary reticulation)

Anisopolar: having proximal and distal surfaces of spore with dissimilar ornamentation.

Aperture: persistent opening in spore wall (usually on equator)

*Areola (*plural *areolae)*: coarse reticulum (primary reticulation)

Distal surface: convex surface of spore, facing outwards when the spores are still united in tetrads

Equator: rim of spore where proximal and distal surfaces meet

Exine: main outer layer of sporoderm

Facet: one of three proximal surfaces between trilete angles

Intine: inner layer of sporoderm

Isopolar: having proximal and distal surfaces of spore with similar ornamentation (= apolar in Miyoshi (1966))

Murus (plural *muri*): ridge between areolae on proximal or distal surfaces

Ornamentation: surface ornamentation of sporoderm

Pit: minute perforation of sporoderm

Pore: aperture

Proximal surface: pointed surface of spore, facing inwards when spores still united in tetrads

Reticulate: with surface network of ridges (= areolate)

Ridge: murus (on proximal and distal surfaces)

Sporoderm: spore wall

Striate: with slender linear ridges on proximal or distal surfaces

Trilete: spores with three clear proximal angles converging at the proximal pole

Table 3.1 Qualitative spore characters of Eurasian species of *Asterella* and related genera

Species	Colour	Shape	Proximal/ distal ornamentation similarity	Primary distal ornamentation
A. saccata	yellow-brown	trilete	similar	wavy ridges
A. grollei	black	trilete	similar	wavy ridges or irregularly areolate
A. wallichiana	brown or red-brown	trilete	similar	wavy ridges (to almost smooth)
A. africana	orange-yellow	trilete	dissimilar	regularly areolate
A. cruciata	orange-yellow	trilete	dissimilar	regularly areolate
A. khasyana	pale yellow	trilete	dissimilar	regularly areolate
A. leptophylla	yellow	trilete	dissimilar	regularly areolate
A. blumeana	yellow	trilete	± dissimilar	corona with weak areolae
A. limbata	yellow	trilete	dissimilar	regularly areolate
A. lindenbergiana	purplish-brown	trilete	similar	regularly alveolate
A. persica	dark red-brown	trilete	similar	regularly areolate
A. pappii	red-brown	trilete	similar	regularly areolate
A. mussuriensis	dark red-brown	trilete	similar	regularly areolate
A. multiflora	brown	trilete	similar	regularly areolate
A. vulcanica	yellow	trilete	similar (probably)	regularly areolate
A. gracilis	yellow	alete	similar	irregularly areolate
Reboulia hemisphaerica	yellow	trilete	similar	regularly areolate
Plagiochasma appendiculatum	brown	trilete	similar	regularly areolate
Cryptomitrium himalayense	brown	trilete	similar	irregularly areolate
Mannia androgyna	yellow	weakly trilete	dissimilar	saccate

Table 3.1 (contd.).

Species	Secondary distal ornamentation	Fine ornamentation of ridges, muri, sacs	Equatorial rim	Equatorial apertures	Proximal bulges
A. saccata	alveolate	weakly pitted	narrow	absent	absent
A. grollei	absent	smooth or weakly papillate	narrow	large	absent
A. wallichiana	absent	papillate or striate	narrow	absent	absent
A. africana	shallowly alveolate	pitted	present	absent	present
A. cruciata	shallowly alveolate	pitted	present	absent	present
A. khasyana	shallowly alveolate	± pitted	present	absent	absent or weak
A. leptophylla	shallowly alveolate	pitted	present	absent	present
A. blumeana	shallowly alveolate	pitted	broad	absent	present
A. limbata	shallowly alveolate	pitted	present	absent	absent
A. lindenbergiana	absent	± smooth	narrow	absent	absent
A. persica	deeply alveolate	pitted	narrow, conspicuous	absent	absent
A. pappii	deeply alveolate	pitted	narrow, conspicuous	absent	absent
A. mussuriensis	deeply alveolate	pitted	narrow, conspicuous	absent	absent
A. multiflora	absent	densely pitted	broad	absent	absent
A. vulcanica	absent	smooth	broad	present (?)	absent (?)
A. gracilis	shallowly alveolate or 0	minutely pitted	absent	absent	absent
Reboulia hemisphaerica	none	papillate	present	present	absent
Plagiochasma appendiculatum	none	papillate	absent	present	absent
Cryptomitrium himalayense	none	smooth	conspicuous	absent	absent
Mannia androgyna	none	finely papillate	conspicuous	present	absent

Table 3.2 Spore Types of Eurasian species of *Asterella* and related genera
Based on Long (1998) and Long *et al.* (2000) and Table 3.1.

Spore type	Distal spore ornamentation	Spore shape	Proximal/ distal ornamentation similarity	Spore colour	Species studied
I	ridged; ridges smooth, not pitted	trilete	similar	black	*A. grollei*
II	ridged (to almost smooth); ridges finely papillate, striate or almost smooth	trilete	similar	brown, red-brown	*A. wallichiana*
III	ridged; ridges finely reticulate	trilete	similar	yellow-brown	*A. saccata*
V	regularly areolate (alveolate in *A. lindenbergiana*); muri pitted	trilete	similar	brown, red-brown, purplish-brown	*A. lindenbergiana* *A. multiflora* *A. mussuriensis* *A. pappii* *A. persica*
VI	regularly areolate; muri pitted	trilete	similar	yellow	*A. vulcanica*
VII	regularly areolate; muri pitted	trilete	dissimilar	yellow, orange-yellow	*A. africana* *A. blumeana* *A. cruciata* *A. khasyana* *A. leptophylla* *A. limbata*
VIII	irregularly areolate; muri pitted	alete	similar	yellow	*A. gracilis*
IX	regularly areolate; muri not pitted	trilete	similar	pale brown or yellow	*Reboulia* *Plagiochasma*
X	irregularly lamellate-areolate; muri not pitted	trilete	similar	brown	*Cryptomitrium himalayense*
XI	saccate; sacs finely papillate	weakly trilete	dissimilar	brown or red-brown	*Mannia androgyna*

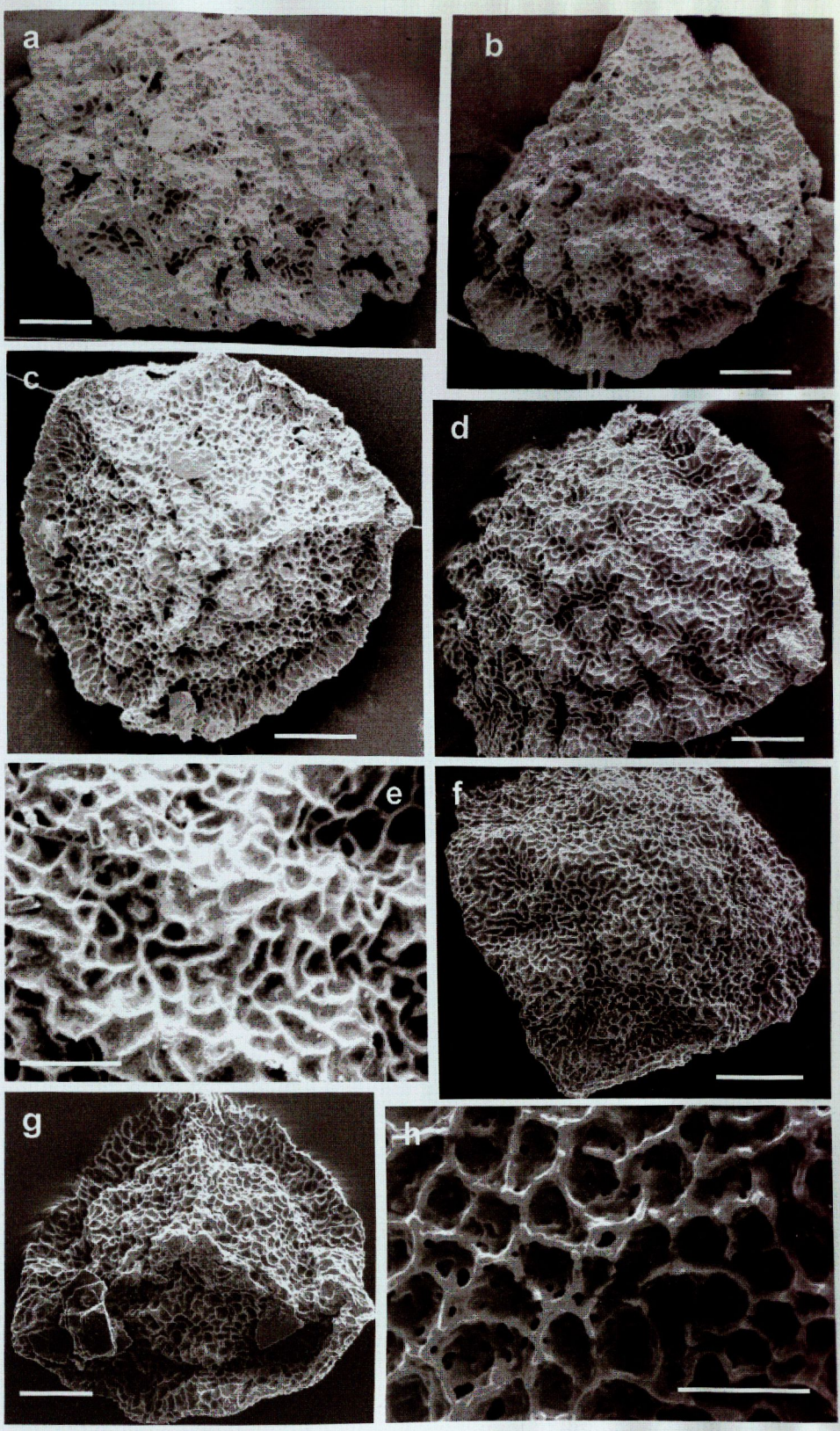

Fig. 3.4. *Asterella saccata* spores. b, c, g, proximal views; a, d–f, h distal views; a, b, Hungary, *Boros s.n.*; c–e, Austria, *Schiffner 1201a*; f–h, Switzerland, *Geissler 8959*. Scale bars: a–d, f, g, 20µm; e, h, 5µm.

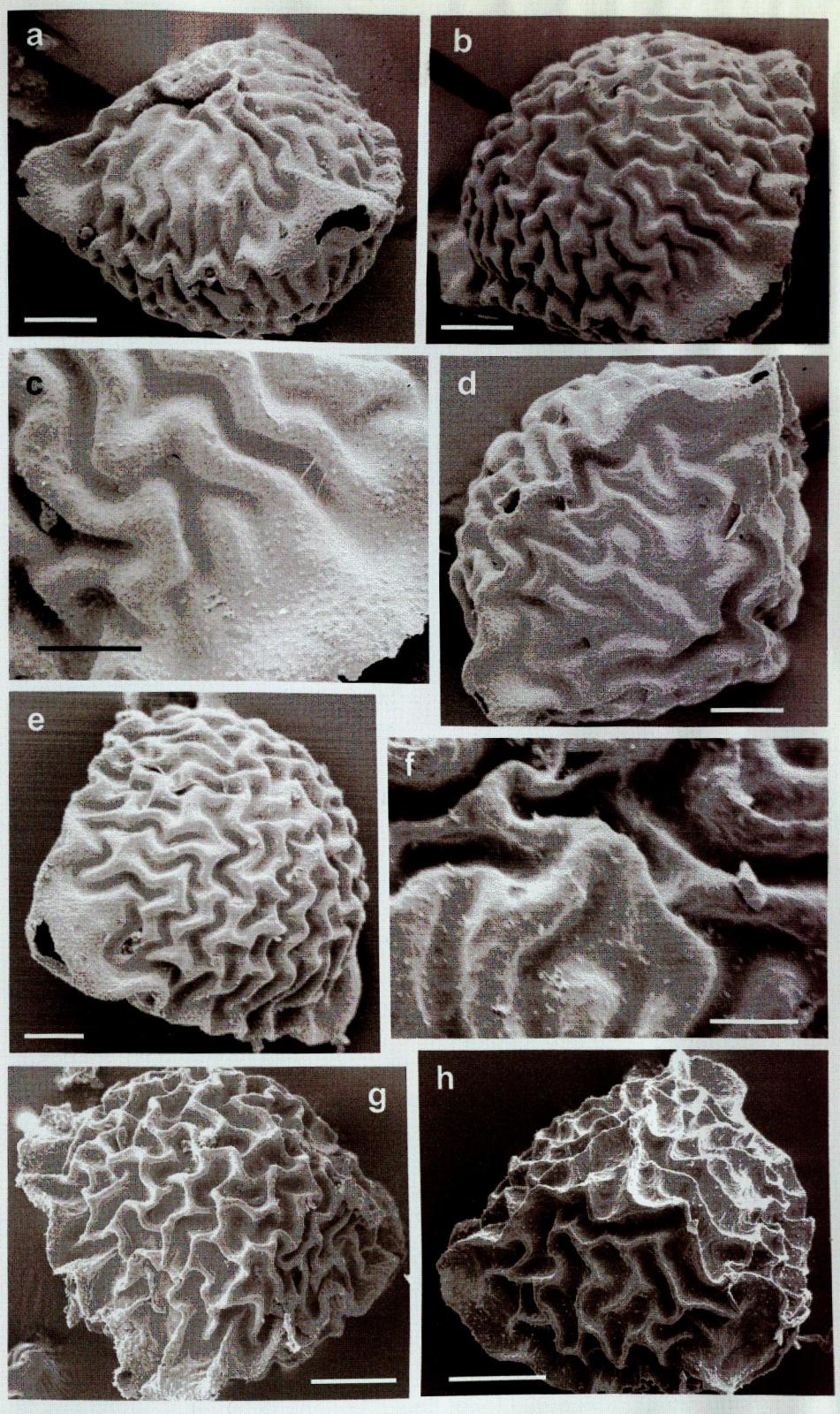

Fig. 3.5. *Asterella grollei* spores. a, d, h, proximal views; b, c, e, f, g, distal views; a–d, Nepal, *Long 20777* (type); e, f, Nepal, *Long 22238*; g, China, Qinghai, *Long 26953*; h, China, Qinghai, *Long 26964*. Scale bars: a, b, d, e, g, h, 20µm; c, f, 10µm.

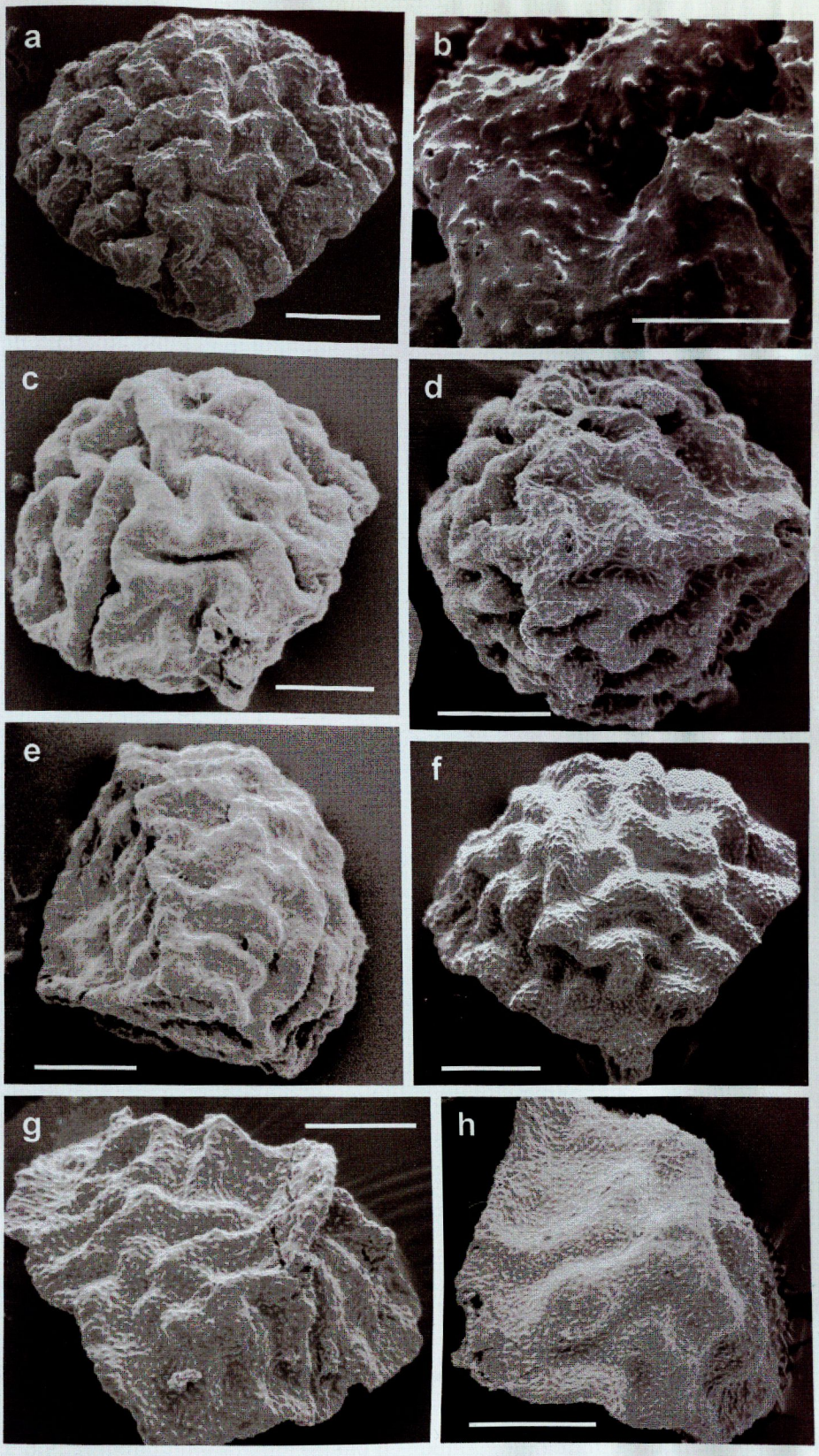

Fig. 3.6. *Asterella wallichiana* spores (i) from continental SE Asia. **a, b, c, f, g, h,** distal views; d, e, lateral views. a, b, Pakistan, *Nishimura 9420*; **c,** India, *Gollan 3764* (syntype of *F. gollanii*); d, India, *Duthie 42* (lectotype of *F. maculata*); **e, Nepal, *Wallich s.n.*** (lectotype of *F. sanguinea*); f, Nepal, *Long 21197*; **g, Nepal, *Wallich s.n.*** (isotype of *F. nepalensis*); h, Bhutan, *Griffith 1094*. **Scale bars: a, d, f, g, h, 20µm; b, c, e,** 10µm.

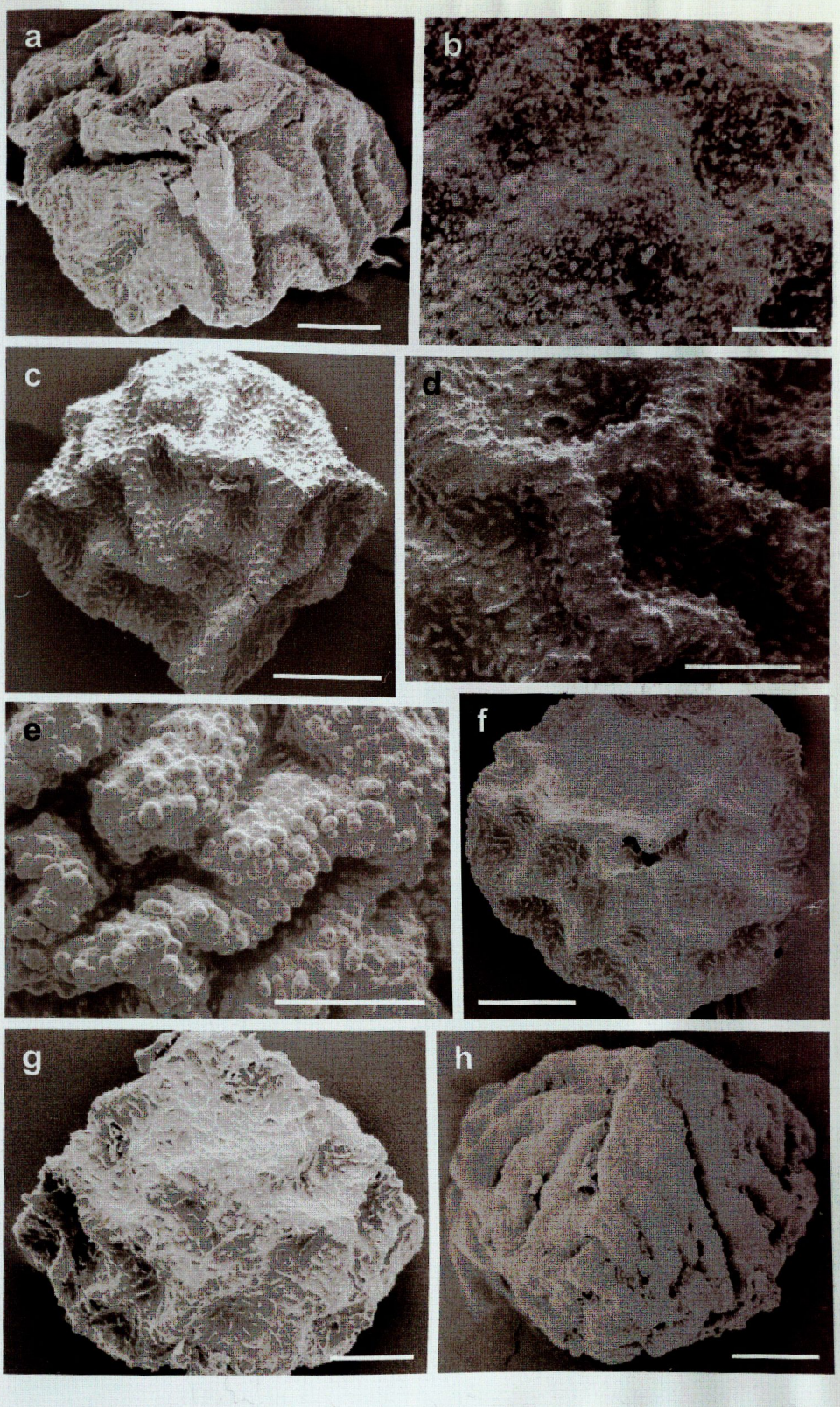

Fig. 3.7. *Asterella wallichiana* spores (ii) from continental SE Asia. f, proximal view; a, b, d, e, g, distal views; c, h, lateral views. a, India, *Lowrie s.n.* (holotype of *F. angusta*); b, Burma, *Wallich s.n.* (lectotype of *F. wallichiana*); c, d, Thailand, *Touw 8904a*; e, China, Yunnan, *Long 18882*; f, g, China, Yunnan, *Handel-Mazzetti 235* (isosyntype of *F. angusta* var. *macrolepis*); h, 'Italy', *Raddi s.n.* (lectotype of *F. raddii*). Scale bars: a, c, f, g, h, 20µm; d, e, 10µm; b, 5µm.

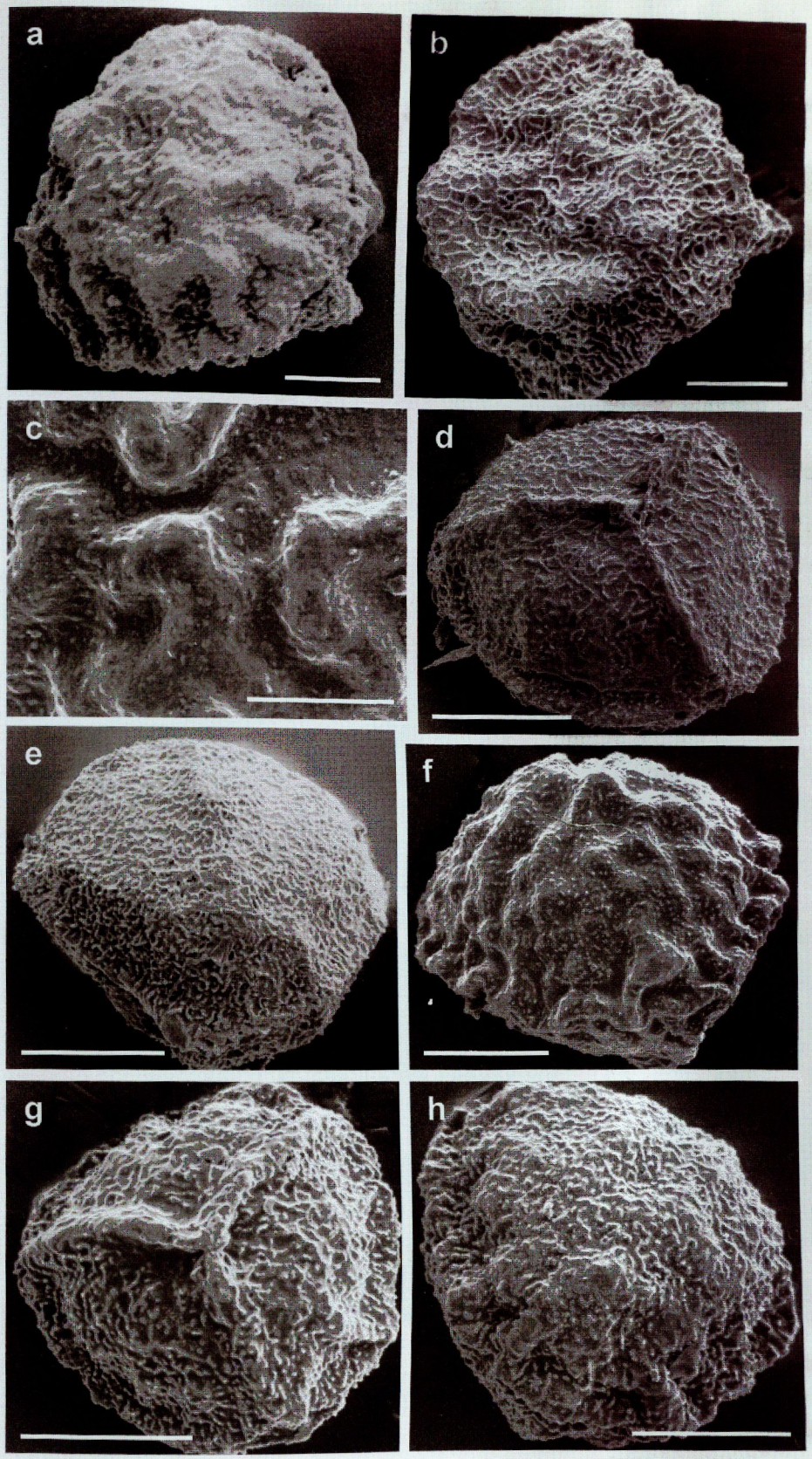

Fig. 3.8. *Asterella wallichiana* spores (iii) from Asiatic islands. d, g, proximal views; a, b, c, e, f, h, distal views; a, Taiwan, *Warburg s.n.*; b, Taiwan, *Faurie 52*; c, Philippines, *Curran 6533* (lectotype of *F. levispora*); d, e, Japan, Iriomote, *Long 24903*; f, Japan, Okinawa, *Yamaguchi 11385*; g, h, Japan, Iriomote, *Yamaguchi 11383*. Scale bars: b, d–h, 20μm; a, c, 10μm.

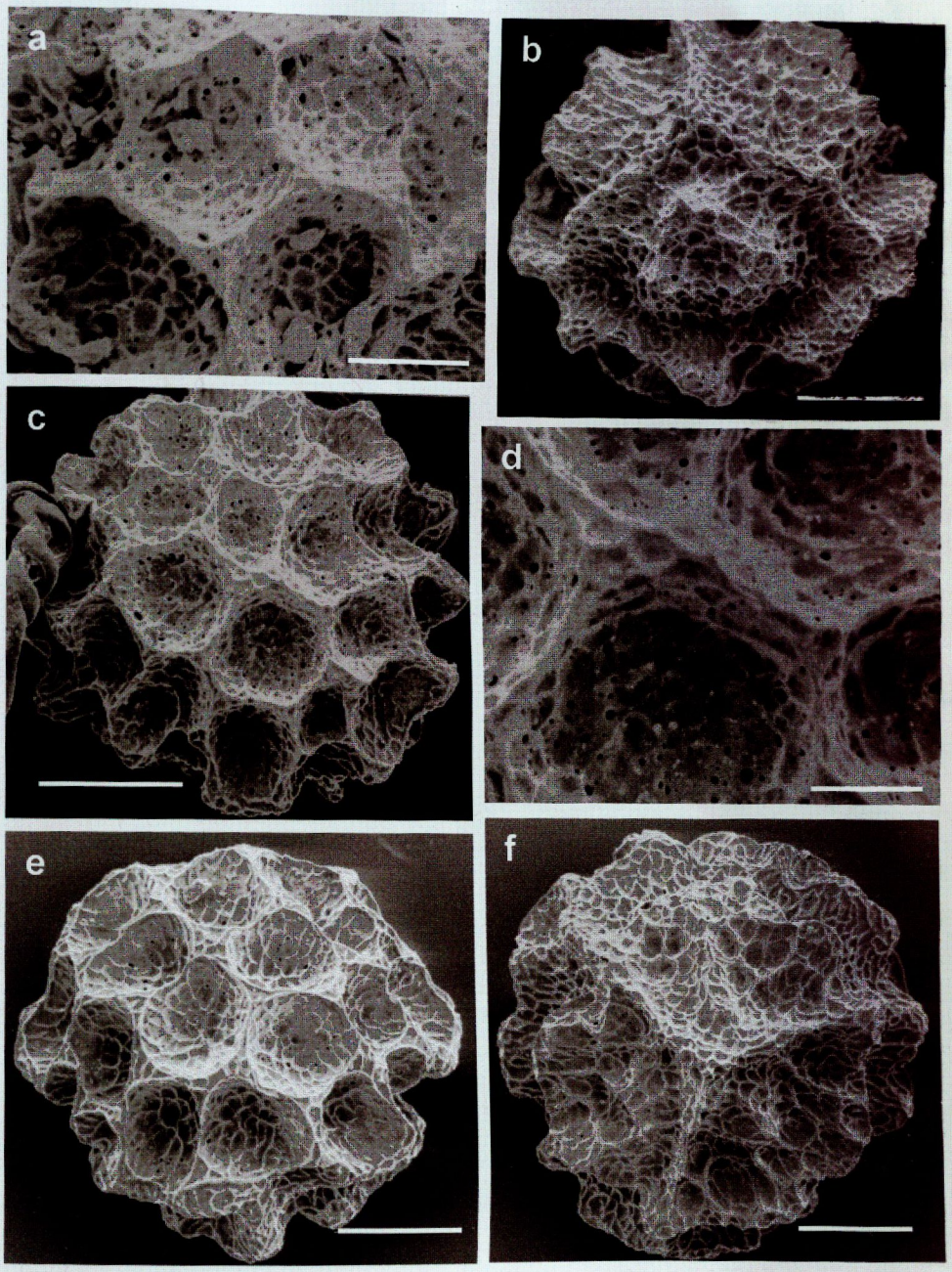

Fig. 3.9. *Asterella africana* spores. b, f, proximal views; a, c, d, e, distal views; a, Canary Islands, *Bornmüller 3003*; b–d, Corsica, *Jovet-Ast & Bischler 711032*; e, f, Madeira, *Clement & Fraile 2264*. Scale bars: b, c, e, f, 20µm; a, 10µm; d, 5µm.

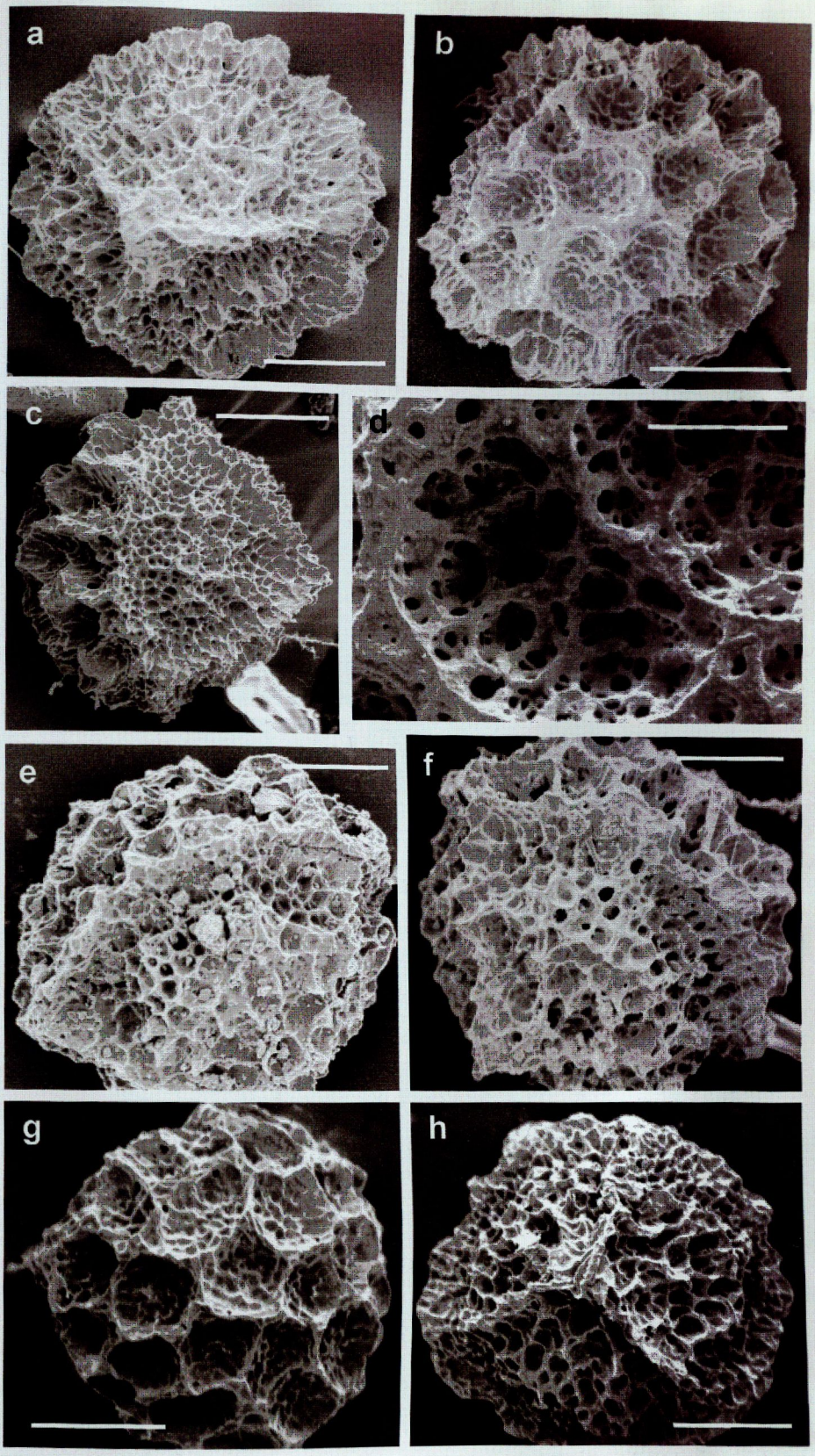

Fig. 3.10. *Asterella cruciata* spores. a, h, proximal views; b, d, g, distal views; c, e, f, lateral views. a–c, China, Yunnan, *Handel-Mazzetti 8603*; d, Japan, *Long 24716*; e, Japan, *Sakurai 9* (lectotype of *F. cruciata*); f, Japan, *Hattori 3124* (holotype of *A. odora*); g, h, Japan, *Shimizu 19642* (holotype of *F. mitsuminensis*). Scale bars: a–c, e–h, 20μm; d, 5μm.

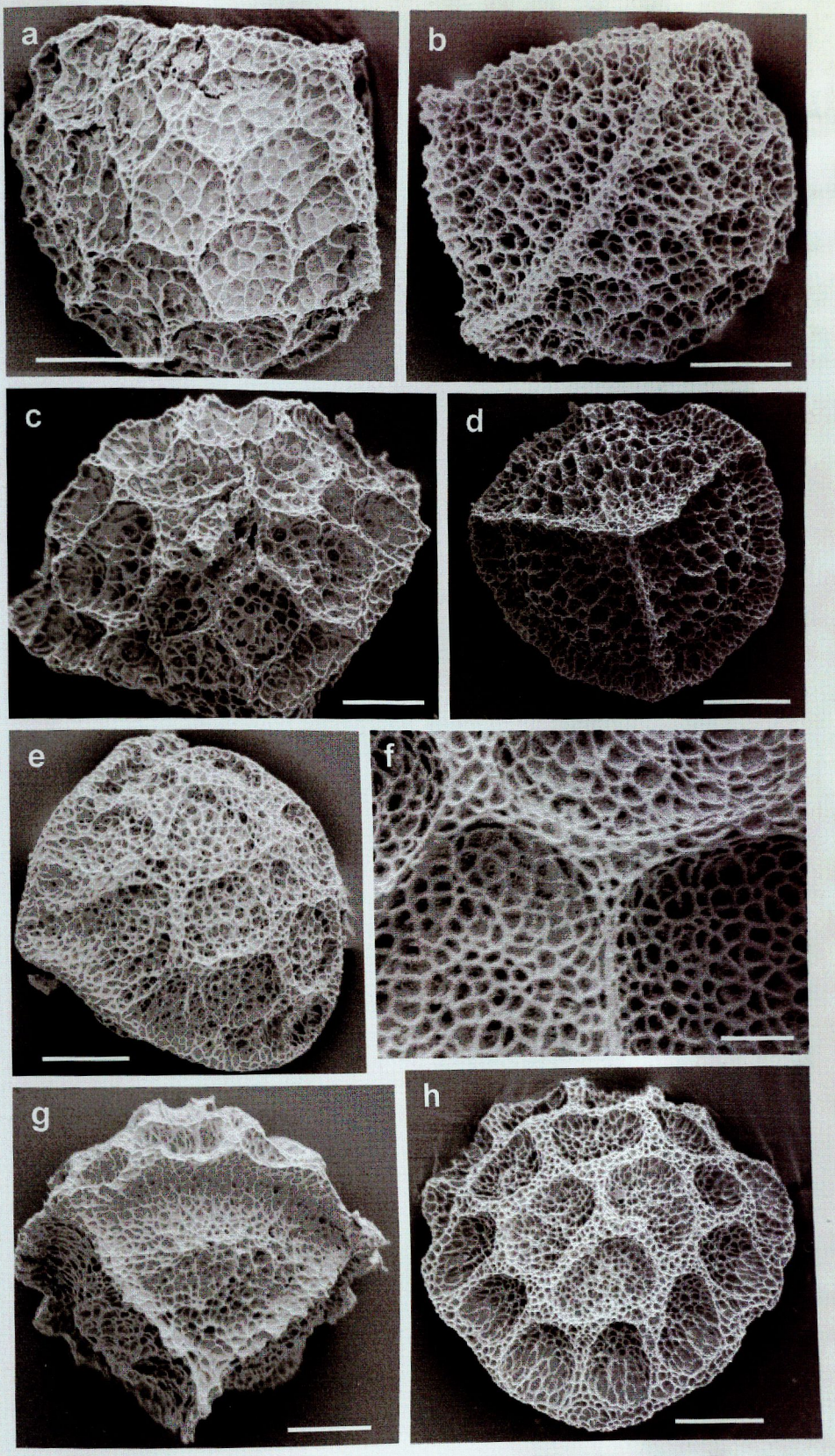

Fig. 3.11. *Asterella khasyana* spores. d, proximal view; a, c, e, f, h, distal views; b, g, lateral views. a, India, *Griffith 100* (lectotype of *O. khasyanum*); b, India, *Butler 4640* (isotype of *F. butleri*); c, India, *Gollan 3888* (lectotype of *F. papulosa*); d, Bhutan, *Long 10653*; e, Java, *Postumus 10436*; f, Java, *Massart 1722*; g, Sumatra, *Schiffner 19* (lectotype of *H. venosum* var. *macrosporum*); h, Sumatra, *Meijer 8722*. Scale bars: a–e, g, h, 20µm; f, 5µm.

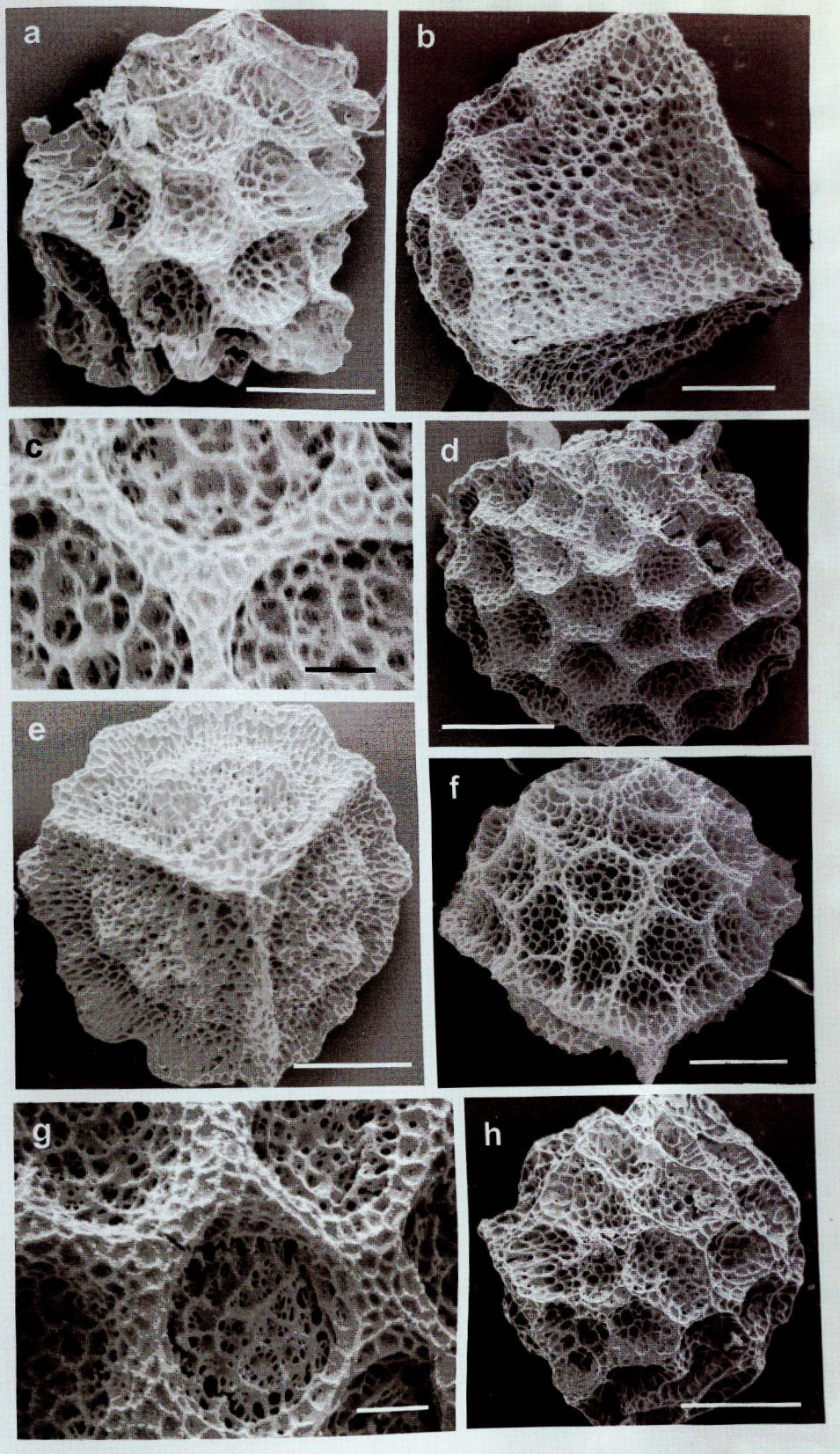

Fig. 3.12. *Asterella leptophylla* spores. e, proximal view; a, c, d, f, g, h, distal views; b, lateral view. a, India, *Perrottet s.n.* (lectotype of *F. leptophylla*); b, c, India, *Gamble 14904*; d, e, Nepal, *Long 20594*; f, Nepal, *Long 17510*; g, China, Yunnan, *Long 18578*; h, Japan, *Shimizu s.n.* (holotype of *A. umbelliformis*). Scale bars: a, b, d, e, f, h, 20µm; c, g, 5µm.

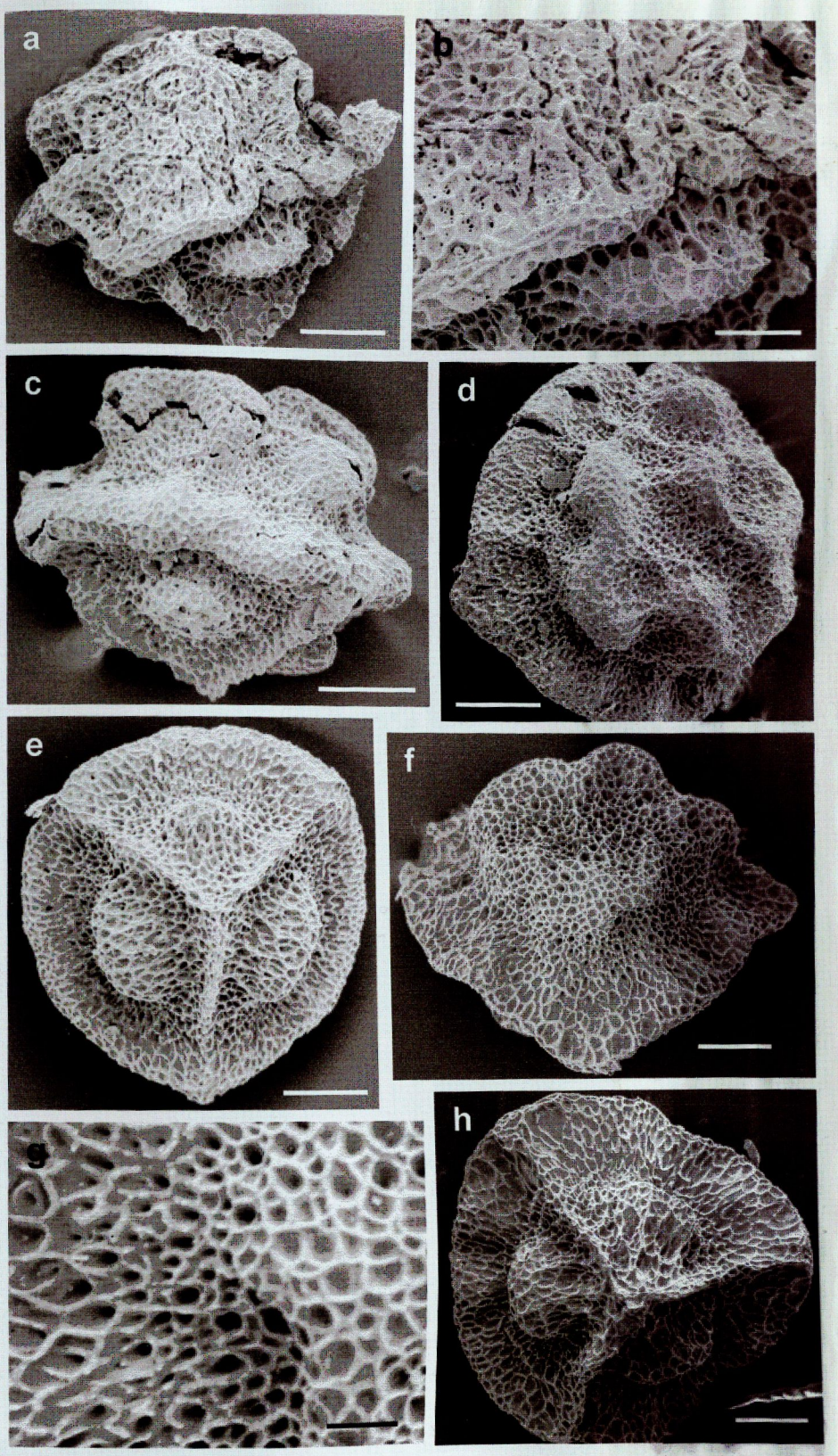

Fig. 3.13. *Asterella blumeana* spores. e, h, proximal views; d, f, g, distal views; a, b, c, lateral views. a, b, Java, *Reinwardt s.n.* (lectotype of *F. blumeana*); c–e, Celebes, *Kjellberg 6H*; f–h, Lombok, *Elbert 1143*. Scale bars: a, c–f, h, 20µm; b, 10µm; g, 5µm.

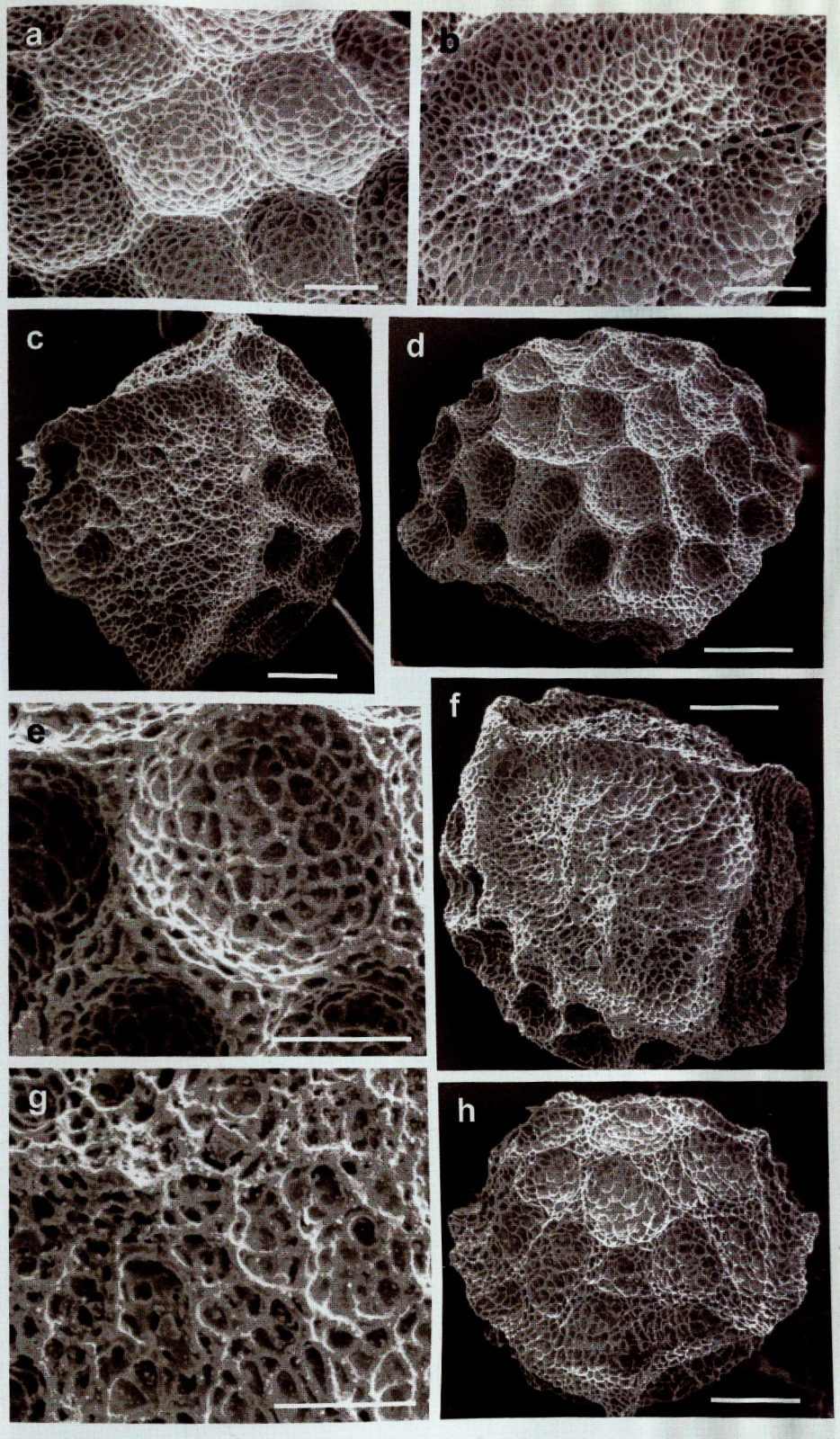

Fig. 3.14. *Asterella limbata* spores. b, g, proximal views; a, d, e, h, distal views; c, f, lateral views. a, b, Sumatra, *Meijer B8884*; c, Sumatra, *Meijer B8927*; d–g, Sumatra, *Meijer B8977* (holotype of *A. limbata*); h, Sabah, *Menzel et al. 4212*. Scale bars: c, d, f, h, 20µm; a, b, e, g, 10µm.

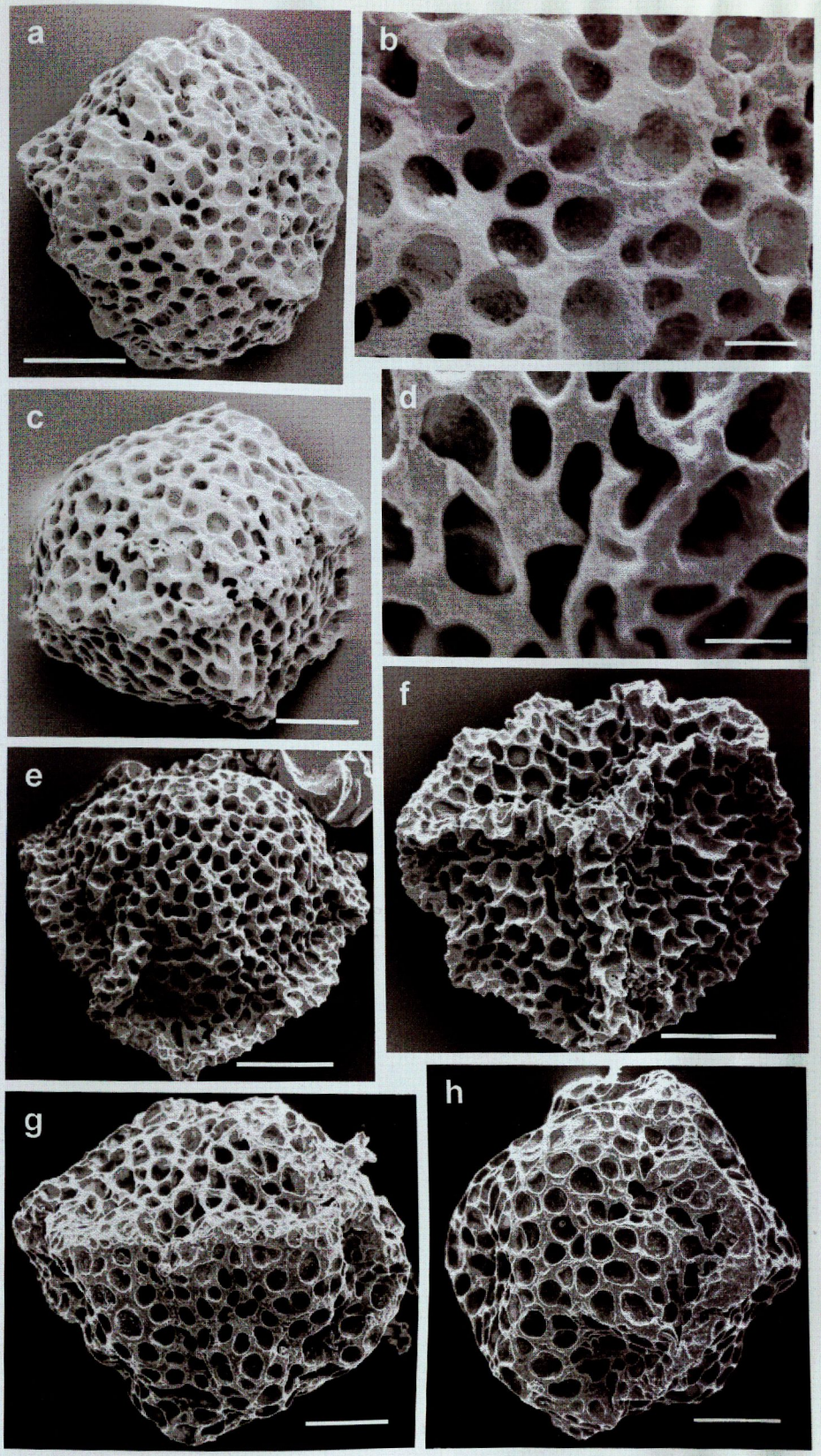

Fig. 3.15. *Asterella lindenbergiana* spores. f, proximal view; a, b, d, e, h, distal views; c, g, lateral views. a–c, Austria, *Schiffner 1199*; d, Romania, *Boros s.n.*; e, f, Sweden, *Smith 3693*; g, h, Switzerland, *Geissler 9807*. Scale bars: a, c, e–h, 20µm; b, d, 5µm.

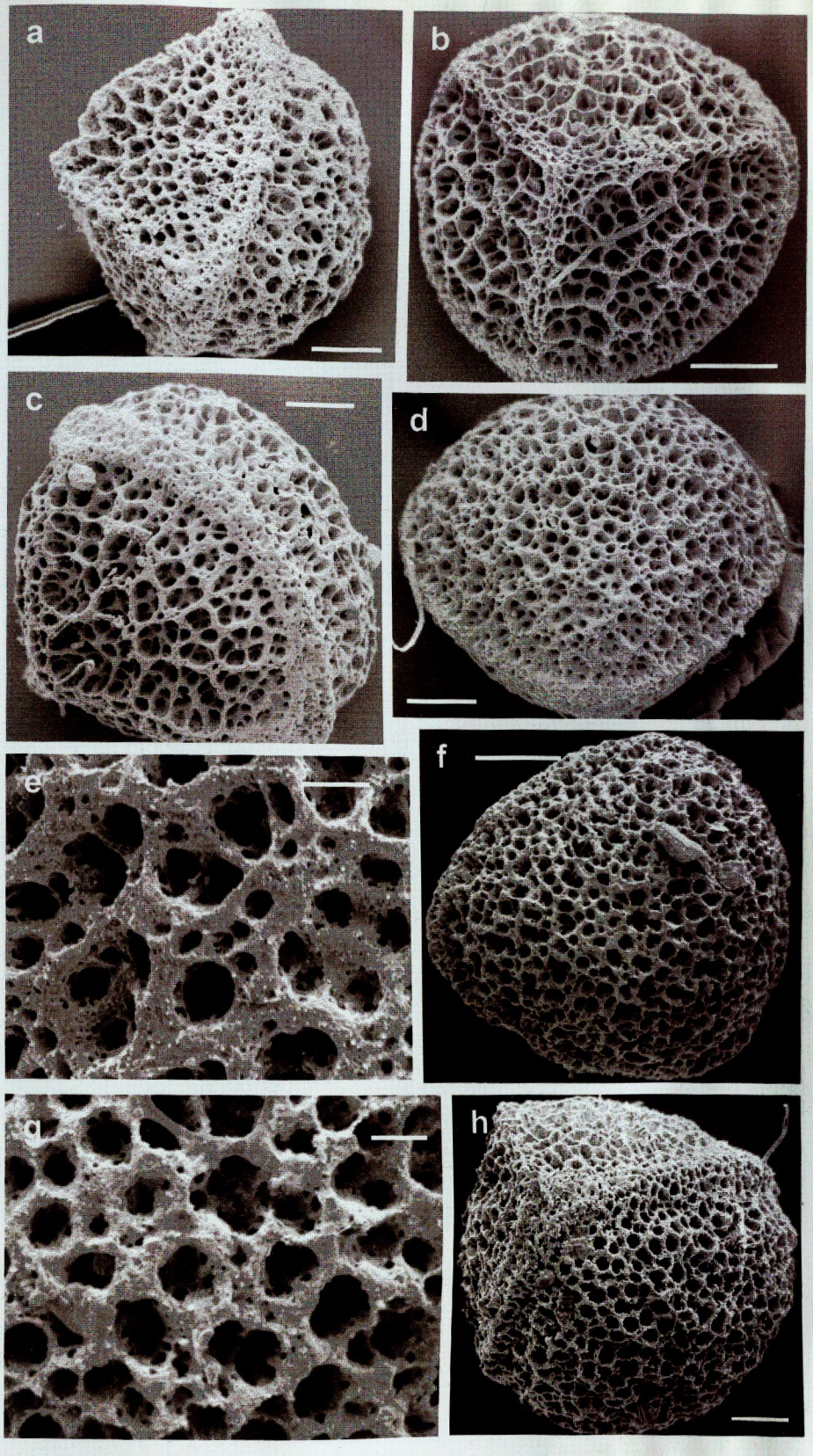

Fig. 3.16. *Asterella persica* spores. b, proximal view; d– g, distal views; a, c, h, lateral views; a, Iran, *Haussknecht s.n.* (isotype of *F. persica*); b–e, Iran, *Stapf s.n.*; f–h, Saudi Arabia, *Collenette 7503*. Scale bars: a–d, f, h, 20µm; e, g, 5µm.

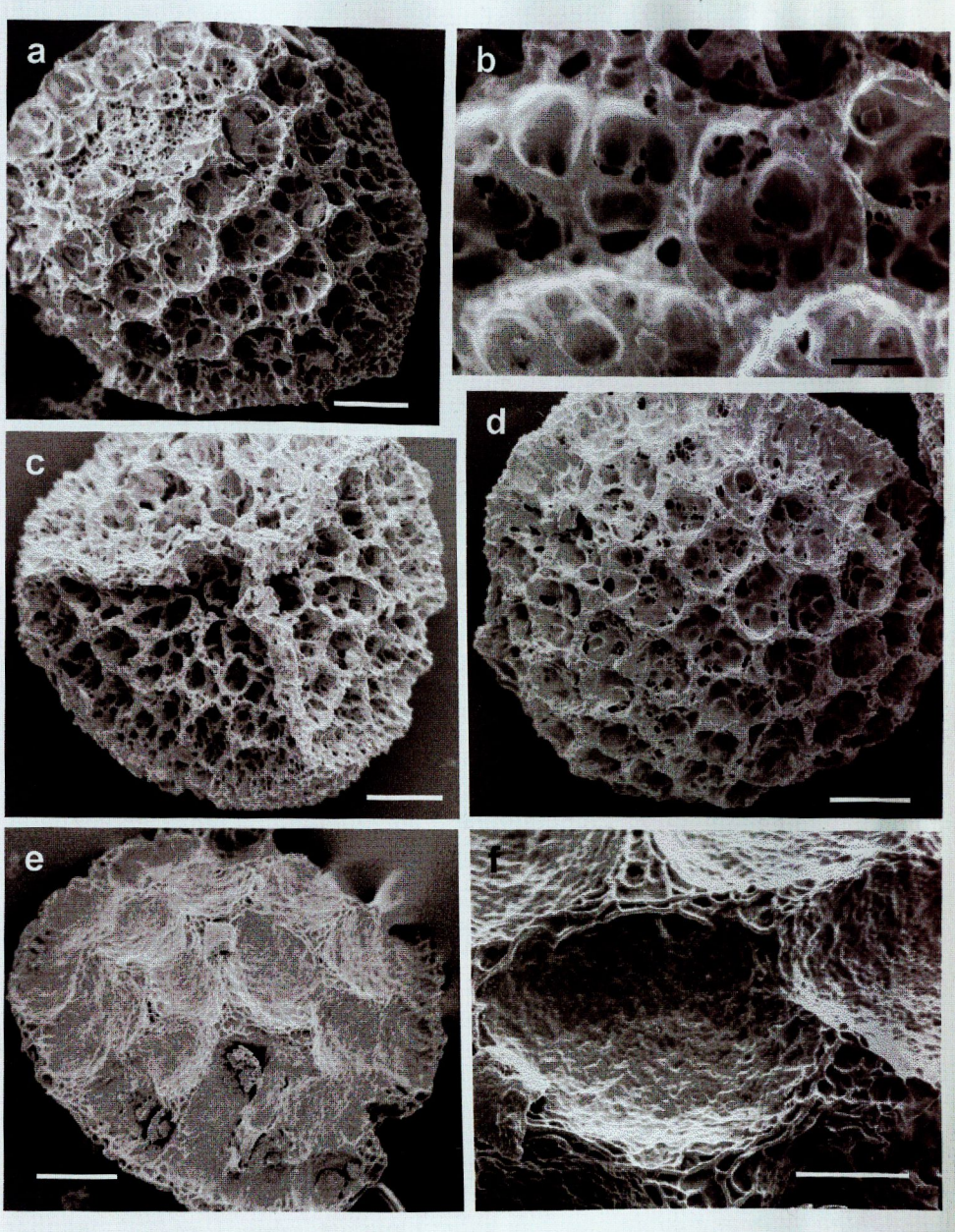

Fig. 3.17. *Asterella pappii* and *Asterella vulcanica* spores. c, proximal view; a, b, d, e, f, distal views; a–d, *Asterella pappii*, Ethiopia, *Schimper A3*; e, f, *Asterella vulcanica*, Java, *Schiffner 17* (lectotype of *F. vulcanica*). Scale bars: a, c, d, e, 20µm; f, 10µm; b, 5µm.

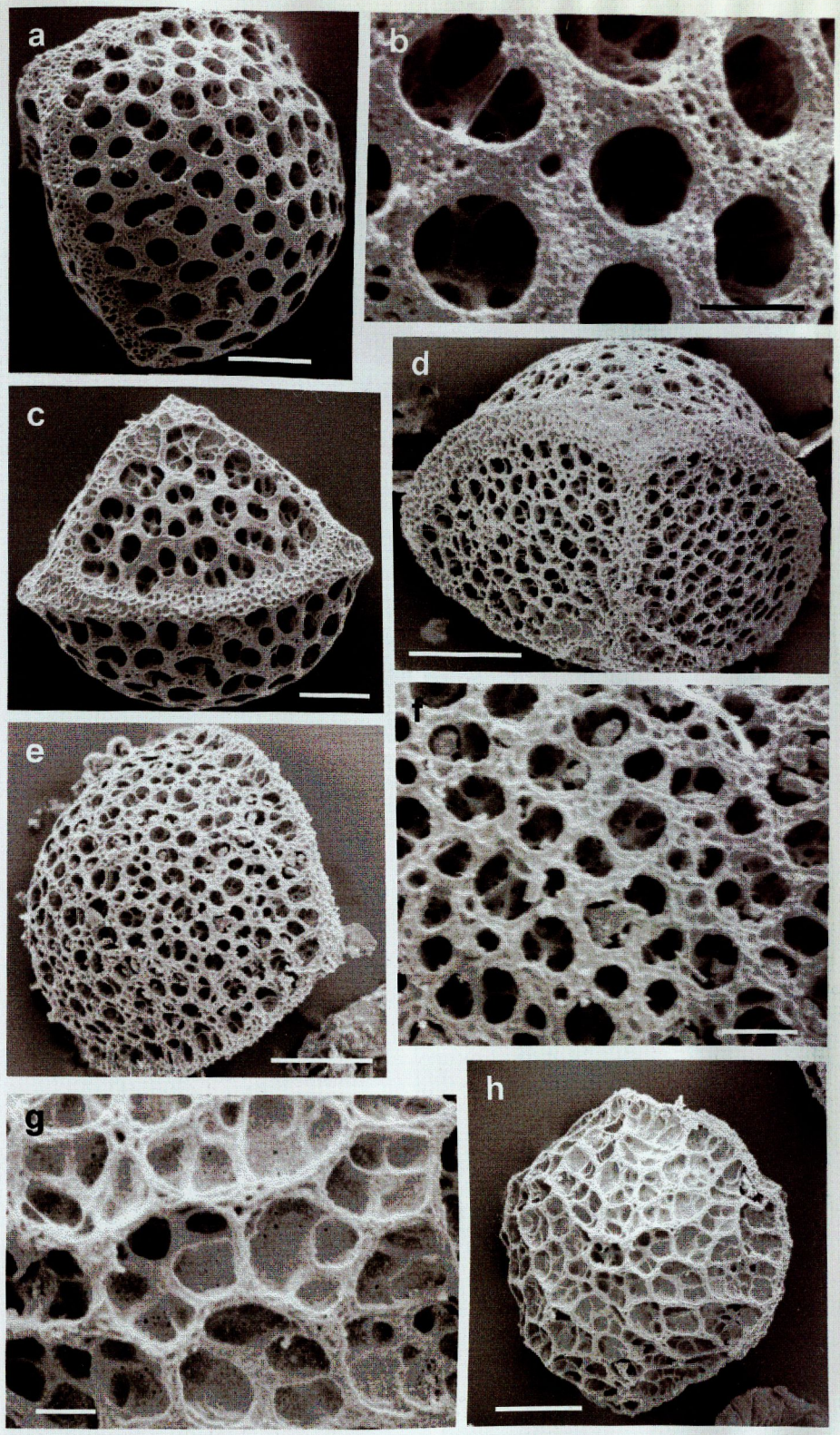

Fig. 3.18. *Asterella mussuriensis* ssp. *mussuriensis* spores. a, b, e–h, distal views; c, d, lateral views. a–c, India, *Duthie 309*; d–f, China, Sichuan, *Handel-Mazzetti 2721*; g, h, China, Sichuan, *Handel-Mazzetti 2288* (isotype of *F. purpureo-capsulata*). Scale bars: a, c, d, e, h, 20µm; b, f, g, 5µm.

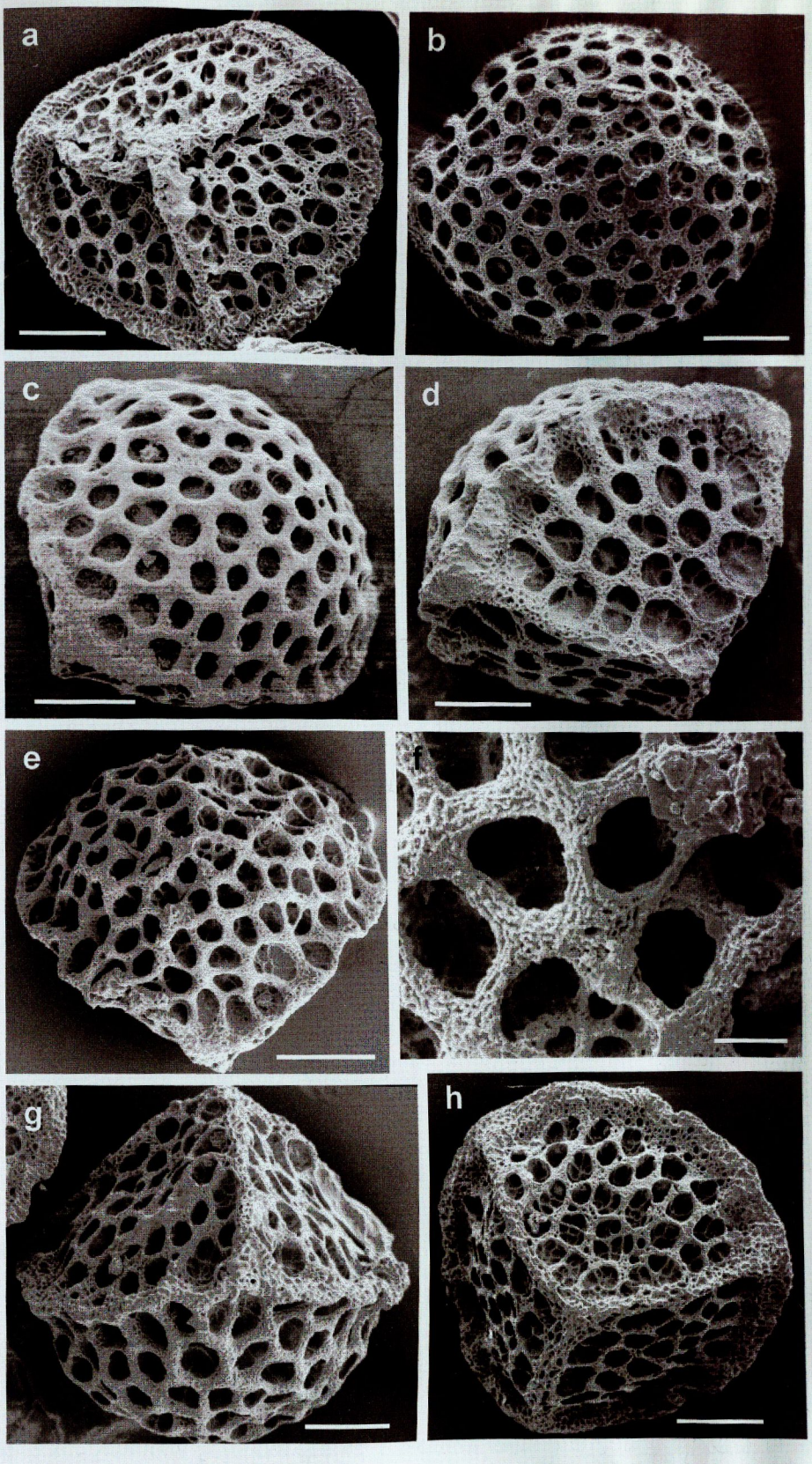

Fig. 3.19. *Asterella mussuriensis* ssp. *crassa* spores. a, h, proximal views; b, c, e, f, distal views; d, g, lateral views. a, b, Japan, *Shimizu 19297* (holotype of *A. crassa*); c, d, Japan, *Kitagawa 15912*; e–h, Japan, *Long 24799*. Scale bars: a–e, g, h, 20µm; f, 5µm.

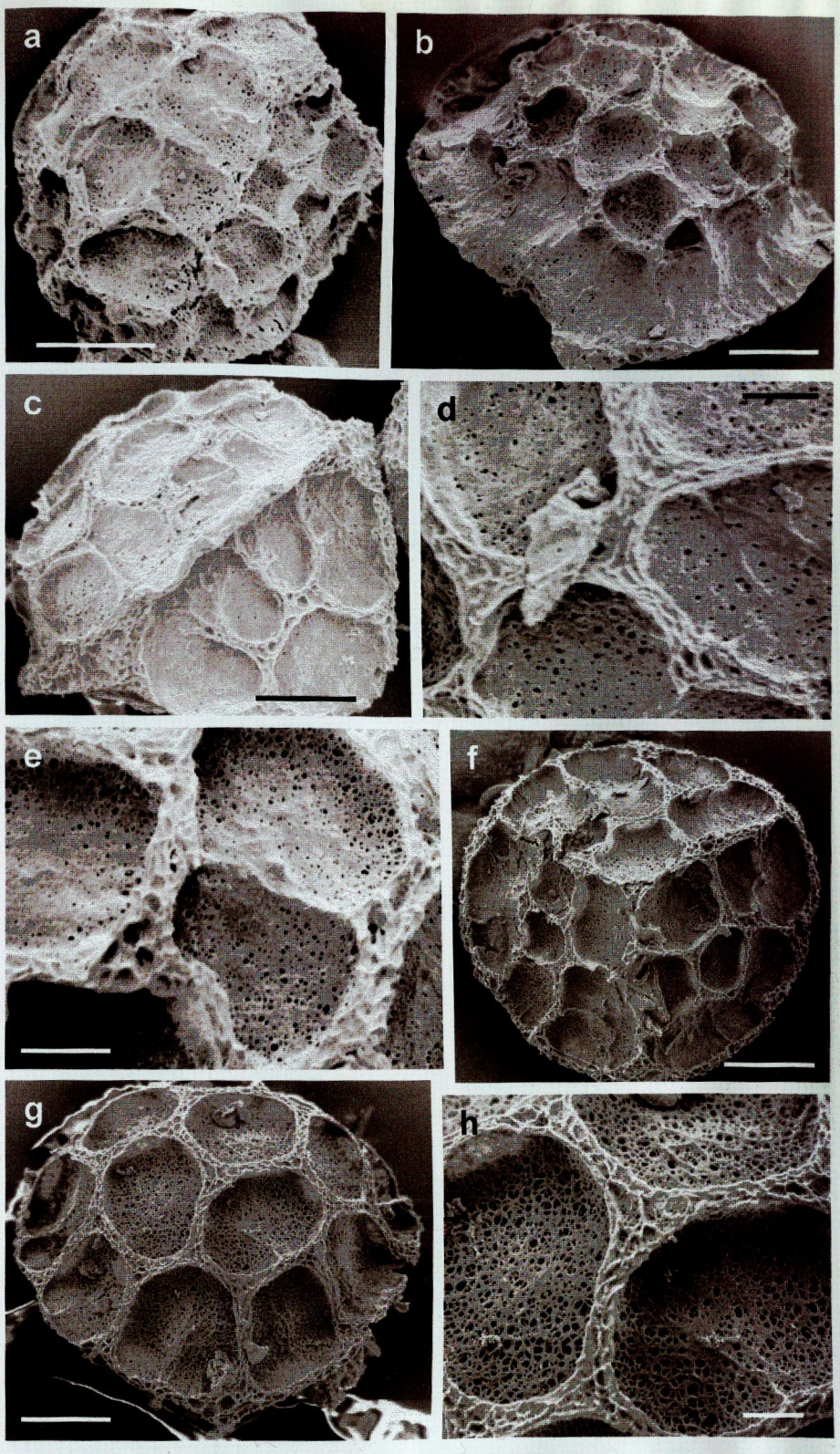

Fig. 3.20. *Asterella multiflora* spores. f, proximal view; a, b, d, e, g, h, distal views; c, lateral view. a, India, *Gamble 24032* (isolectotype of *F. multiflora*); b, India, *Dyal s.n.*; c, d, India, *E.Long 50*; e, India, *Khan 3213*; f–h, Nepal, *Townsend 92-155*. Scale bars: a, b, c, f, g, 20µm; d, e, h, 5µm.

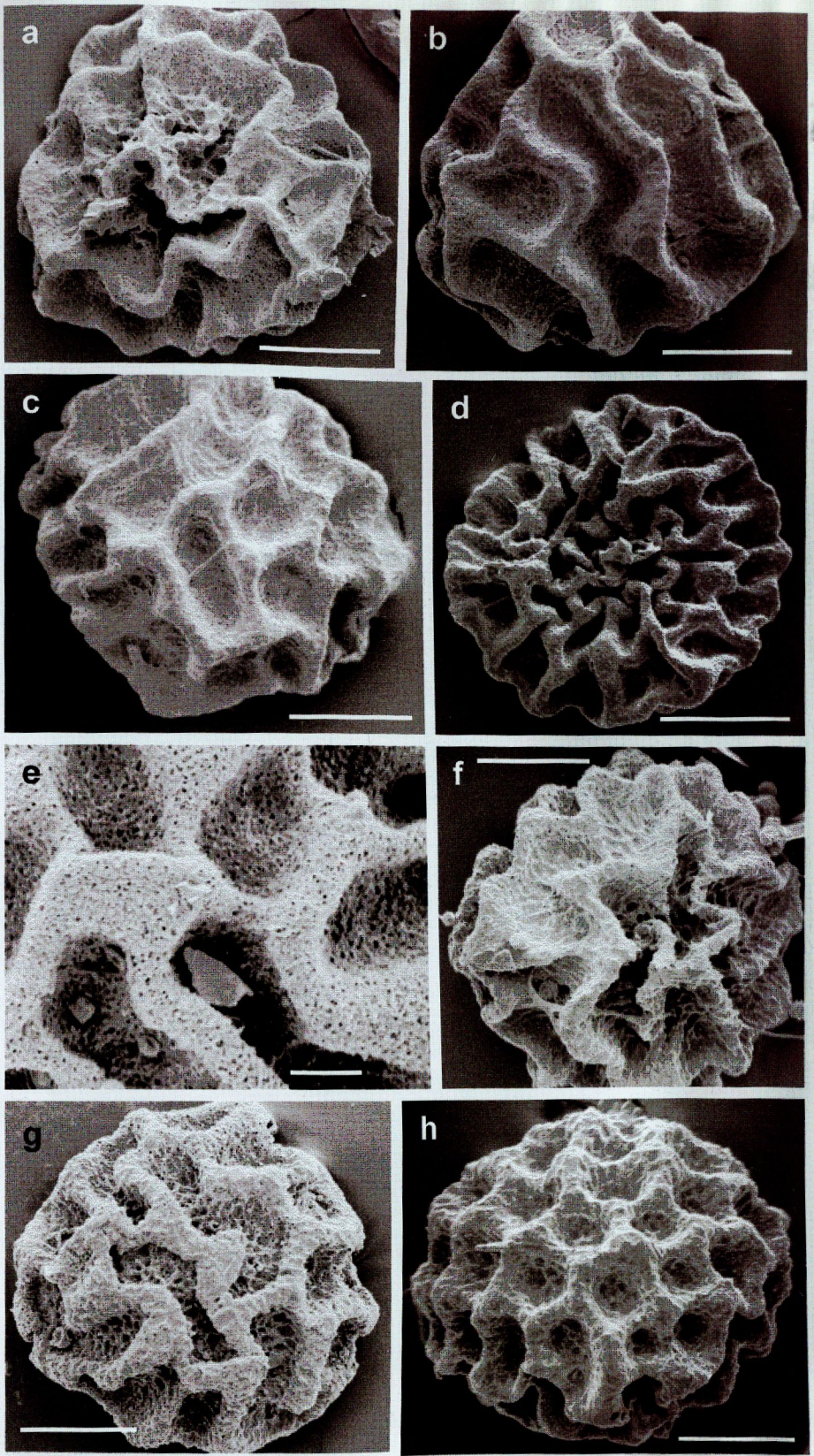

Fig. 3.21. *Asterella gracilis* spores. a, d, f, proximal views; b, c, e, g, h, distal views. a–c, Sweden, *Fröding s.n.*; d, Siberia, *Nilsson-Ehle s.n.*; e, India, *Duthie 13385* (lectotype of *F. parvipora*); f, g, Japan, *Sasaki, HJE 851*; h, Japan, *Shimizu s.n.* (isotype of *A. ludwigii* var. *major*). Scale bars: a–d, f–h, 20µm; e, 5µm.

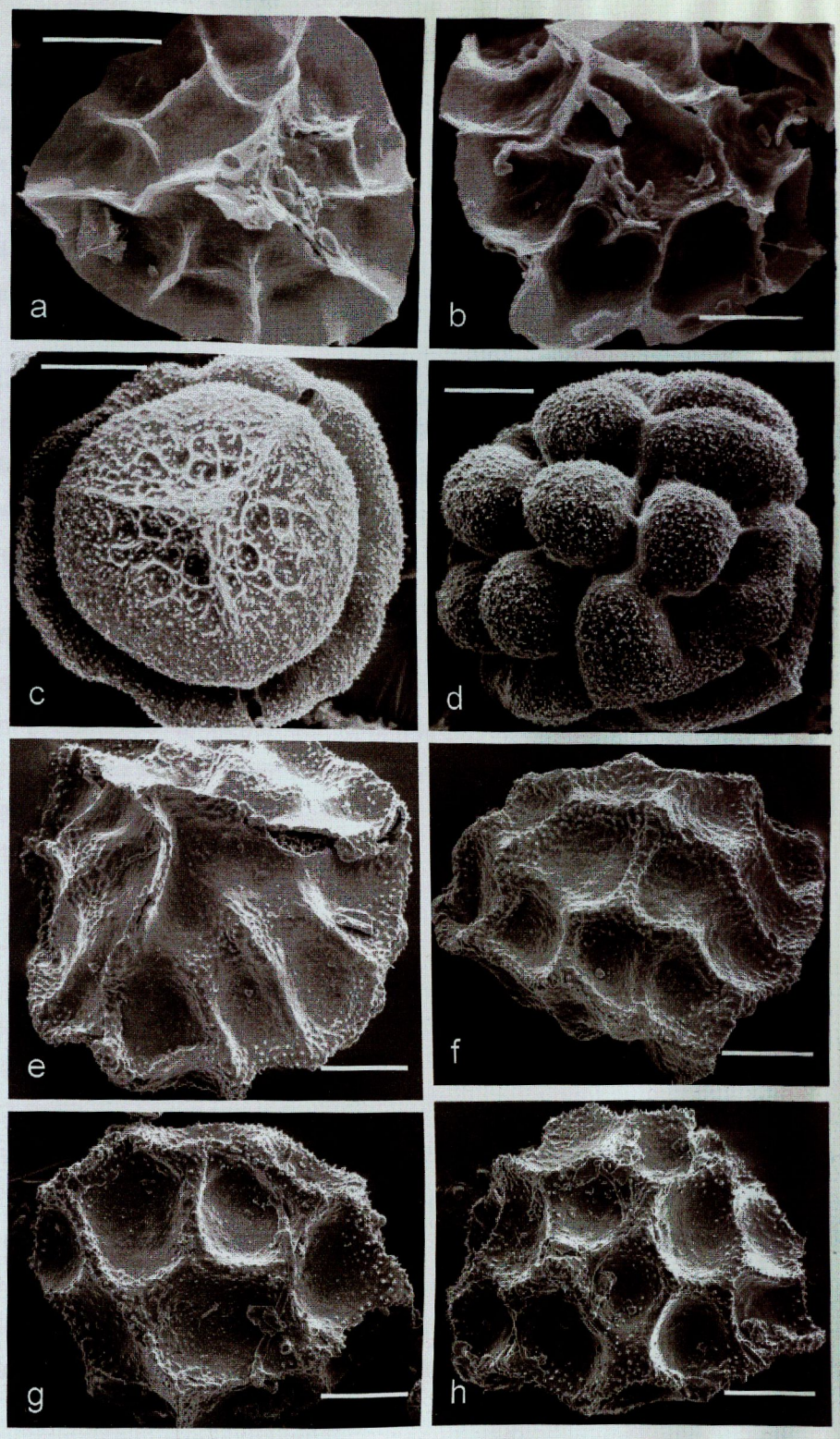

Fig. 3.22. *Cryptomitrium, Mannia, Reboulia* and *Plagiochasma* spores. a, c, e, proximal views; b, d, f, h, distal views; g, lateral view. a, b, *Cryptomitrium himalayense*, Nepal, *Long 22043*; c, d, *Mannia androgyna*, Madeira, *Long 25074*; e, f, *Reboulia hemisphaerica*, India, Sikkim, *Long 22556*; g, h, *Plagiochasma appendiculatum*, Bhutan, *Long 8132*. Scale bars: a–h, 20µm.

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4.1 INTRODUCTION

This chapter provides a new taxonomic treatment of *Asterella* in Europe and Asia, using mostly new data from living plants, herbarium specimens and electron microscopy. The background and rationale for this revision has been given in Chapters 1 and 2, and the results of the studies on spores in Chapter 3.

4.2 OBJECTIVES

To revise the genus *Asterella* in the study area, providing keys to species, correct nomenclature for all accepted names, revised synonymy (accounting for and typifying all names from the study-area where necessary), descriptions and illustrations of all species, summaries of distribution and ecology, discussion on particular taxonomic and nomenclatural problems, and lists of specimens studied.

4.3 MATERIALS AND METHODS

The study-area is shown on Fig. 4.1. It comprises the whole of Europe and Asia, excluding Papua New Guinea. Using the global subdivisions of *Index Muscorum* (Wijk, Margadant & Florschütz, 1959–1969) it includes EUR (Europe), AS1 (Northern Asia), AS2 (China, Taiwan and Japan), AS3 (India, Sri Lanka and Indo-China), AS5 (Arabia, Socotra and Middle East) and AS4 (Malesia) except for Papua New Guinea. It also includes Macaronesia but excludes North Africa. This area was chosen as a 'natural' unit of manageable size for a detailed revision. It excludes the three other areas of the world which will necessitate future revision in *Asterella*: Africa, America and Australasia (including Oceania and Papua New Guinea).

All available relevant material of *Asterella* and its generic synonyms has been studied. This material consists both of living plants (in the field and in cultivation) and herbarium specimens.



Fig. 4.1 The study-area

Living Material. Participation in several expeditions and other trips between 1990 and 1996, and gifts of living material from other bryologists, has enabled living material to be studied, collected and photographed and in some cases brought into cultivation as follows:

Europe: *A. gracilis*, *A. lindenbergiana, A. saccata*

Macaronesia: *A. africana.*

Himalaya: *A. grollei*, *A. khasyana*, *A. leptophylla*, *A. multiflora*, *A. mussuriensis* subsp. *mussuriensis*, *A. wallichiana.*

China : *A. grollei, A. leptophylla*, *A. mussuriensis* subsp. *mussuriensis*, *A. wallichiana.*

Japan: *A. cruciata, A. leptophylla*, *A. mussuriensis* subsp. *crassa*, *A. wallichiana.*

Herbarium material. Numerous specimens have been collected by the author and these specimens are preserved in E with many duplicates in JE and elsewhere. Other material has been generously sent by bryologists worldwide during their own fieldwork.

Herbarium specimens have been borrowed from the following herbaria: B, BM, BR, CBM, E, F, FH, G, H, HIRO, JE, KUN, KYO, L, LD, MANCH, NICH, NMW, NY, PC, S, STR, TENN, TO, U, UBC, UPS, W, WU. Abbreviations follow the *Index Herbariorum* (Holmgren *et al.*, 1990). Many of these contain important historical herbaria with type materials which are particularly important for lectotypifying and synonymising. The most important sources of types have been the Natural History Museum, London (*Hooker* herbarium), Farlow Herbarium at Harvard (*Schiffner* and *Taylor* herbaria), Geneva (*Stephani* herbarium), Jena (*Herzog* and *Grolle* herbaria), Hiroshima (*Horikawa* herbarium), Paris (*Montagne* herbarium), Stockholm (*Lehmann & Lindenberg* herbaria), Strasbourg (*Nees* herbarium) and Vienna (*Lindenberg* and *Handel-Mazzetti* herbaria).

All herbarium specimens cited, including types, have been studied by the author. Where types could not be located they are indicated by '*n.v.*' (non vidi).

Methods

a. Bibliographic studies

At the generic level, the detailed review of the history of the names *Asterella* and *Fimbriaria* and several other synonyms (see Chapter 1) was undertaken by searching libraries (mostly at Edinburgh and Geneva) for important literature on the classification of liverworts from 1729 to the present day. Particular attention was made to the orthography of *Fimbraria/ Fimbriaria,* and to the species included by different authors in the past under *Asterella* and the other genera of Aytoniaceae, and any typifications made of these genera. Other uses of the generic names *Asterella* and *Fimbriaria* were also noted (*i.e.* where the names were used for species now considered to belong to other genera of Aytoniaceae such as *Reboulia*). The validity of the various generic names (*e.g. Dictyochiton)* was also checked against the *International Code of Botanical Nomenclature* (Greuter *et al.*, 2000).

At the species level, all literature relating to *Asterella* and its synonyms worldwide was searched using libraries, bryological bibliographies, *Index Hepaticarum* and any other sources. Dossiers consisting of photocopied extracts from literature were compiled for all published names worldwide, especially those from the study area. Particular note was paid to validity of the names under the *International Code of Botanical Nomenclature* (Greuter *et al.*, 2000) and any problems identified. Publications including descriptive morphology, anatomy, spore SEM, cytology, nomenclature, phytogeography, *etc.* were selected, and any relevant data extracted. Likely sources of type material were pinpointed from the literature, and any available information on distribution. All published illustrations were photocopied. Published synonymy was noted but not accepted until relevant type material had been studied. Preliminary lists of *Asterella* species for the study area were drawn up. Author abbreviations were checked against Brummitt & Powell (1992).

b. Field Methods

Study of living material in field. Over a number of visits to eastern Asia, Europe and Macaronesia, considerable experience was gained in finding *Asterella* material in the field. In China, for example, little *Asterella* had been collected by previous workers, yet on two expeditions to Yunnan *Asterella* was found to be a common genus. Important too, was the ability to identify species in the field, so that notes on their ecology could be made, and any potential new taxa could be recognised as such on the spot, as with *Asterella grollei* when first discovered in East Nepal. For all taxa, notes were made on colour, texture, reproduction, *etc.* and particular efforts were made to collect material with ripe sporophytes (for future SEM study of spores).

Specimens were collected using a knife, soil was removed as far as possible without losing the integrity of the plants, and specimens were transferred to paper packets. Specimens were air-dried where possible, but during trips in the rainy-season, heat-drying using kerosene stoves was necessary. Specimens were given temporary reference numbers in the field, and all data recorded on the spot, such as substrate, ecology, altitude, and longitude and latitude mostly using a portable Global Positioning System navigator. When dry, specimens were bundled tightly and stored in sealed polythene bags for shipment to UK.

Close-up photography was attempted for all species using a Canon SLR camera mounted on a monopod made from a large tent-peg, using a macro lens and hand-held electronic flash. Film used was Kodachrome 64 and Fuji Sensia.

c. Herbarium Methods

Study of dried material. Most old herbarium specimens were too fragmentary or small for very detailed study. Types in particular had to be damaged as little as possible by study. These older (especially type) collections were mostly checked for two key characters by which virtually all could be identified: sexual condition (as discussed in Chapter 2) and spore morphology

under SEM (see Chapter 3). Both these characters could be reliably observed with minimal damage to specimens.

Detailed taxonomic studies, involving much dissecting and sectioning for preparing descriptions and illustrations, were done as far as possible on my own recently-collected specimens. However, for some species (*e.g. A. limbata* and *A. vulcanica*) very little material exists and only older collections were available for study.

Thalli bearing sporophytes were observed under a Wild Stereo-microscope and spores removed for study as described in Chapter 3. For all other observations, herbarium specimens were soaked in cold tap water for 2 to 4 hours before study, to allow thalli to regain their full size and natural shape; this proved difficult for very old collections which were often too brittle to regain their natural appearance. Observations on whole plants were made under a Wild Stereo-microscope, and drawings made freehand. Measurements of branches, *etc.* were made using a calibrated eyepiece micrometer on the Stereo-microscope.

For each preparation, the following semi-permanent prepared slides were made using Hoyer's Fluid (Anderson, 1954).

a. Transverse section of thallus (both hygroshoots and xeroshoots where they were present); made freehand using a razor blade and mounted needle under the Stereo-microscope, then transferring the sections with a fine paintbrush to a slide.
b. Upper epidermis of thallus; by peeling the epidermis off with fine forceps.
c. Ventral scales; by removing these from near thallus apex with fine forceps.
d. Transverse sections of androecia.
e. Transverse section of archegoniophore (stalk).
f. Scales (basal, median and upper) from the stalk.
g. Involucre; removed using forceps and flattened on slide.
h. Pseudoperianth; removed intact then flattened on slide.
I. Capsule; spores squeezed out and capsule wall flattened.
j. Spores and elaters.

Light microscope studies. Observations were made under a Zeiss Standard 25 compound light microscope, with calibrated eyepiece micrometer. Both prepared slides and fresh water-mounted slides were used for observation and measurement. At least five different collections of each species were used for detailed dissection, description and measurement. 5 to 10 measurements of each character, per sample studied, were made. Quantitative characters were scored as minima and maxima, with exceptional measurements added in brackets, *e.g.* archegoniophore 1.5–3(–5)mm long.

Character selection. All available characters, as described in Chapter 2, were observed and recorded, and the observations and measurements incorporated into the species descriptions.

Drawings and photographs. Drawings were made both freehand and using a camera lucida. Photography from prepared slides was done using a 35mm camera attachment on a Zeiss microscope, using Ilford Technical Pan film.

Taxonomic decisions and synonymy. Using only a few characters, such as thallus shape in transverse section, ventral scale appendage morphology, sexual condition and spore ornamentation, known to be important from previous studies (see Chapter 2), a preliminary synonymy was developed early on, and it was discovered that all recent collections could be more or less definitively characterised using these characters. The stability of this preliminary system was tested using additional morphological characters from thallus, ventral scales, carpocephalum, *etc.* Species were also loosely classified into informal groups such as the '*Brachyblepharis* group', *etc.* Within these groups individual species or putative species were compared in more detail, *e.g. A. mussuriensis* with *A. crassa*, *A. wallichiana* with *A. levispora*, *A. liukiuensis*, *A. monospiris etc.*

At the same time as these detailed studies were being made, a systematic survey was made of older collections and types from a wide range of herbaria. On such specimens only a limited range of key characters were observed in order to (a) establish synonymy of the many redundant names (and locate the earliest available epithet for each accepted species) and (b) fill in all details of geographical distribution of species. Spore SEM (see Chapter 3 and Long (1998)) was very important in dealing with these older specimens.

d. Laboratory Methods

Cultivation. Cultivation methods for growing *Asterella* plants in growth cabinets were described in Chapter 2. Cultivated plants were found to be of little value for taxonomic studies because (a) the thalli often became slightly etiolated and did not assume the normal 'wild' morphology, and (b) cultivated plants almost never produced mature carpocephala and sporophytes. Due to limitations of time, facilities and available living material, the more significant experimental opportunities presented by cultivated *Asterella* material, namely (i) testing of character stability and phenotypic plasticity, and (ii) molecular taxonomic studies, could not be taken up in this study.

Cytology. Chromosome counts were obtained from the literature (Kachroo, 1969; Tatuno, 1955, 1960) and a number of new counts were made. Only a limited range of cultivated material was available for study, and no living material of *A. blumeana*, *A. grollei*, *A. limbata*, *A, pappii*, *A. persica*, *A. saccata* and *A. vulcanica* was available.

Specimens studied were (see Appendix V for collection details):

A. khasyana India (Sikkim) *Long 22420*

A. leptophylla India (Sikkim) *Long 22914*

A. lindenbergiana Norway *Long 19989*

A. wallichiana China (Yunnan) *Long 23589*

A. wallichiana Japan (Iriomote) *Long 24903*

The method used for chromosome counting was mitotic squashes of growing points of thalli and staining with lacto-propionic orcein, following the method of Newton (1989). Shoot tips were fixed in a mixture of equal volumes of absolute alcohol, glacial acetic acid and chloroform, and stored in small tubes in a refrigerator. Gelatin-coated 'sub-slides' were prepared, lacto-propionic orcein stain was prepared and used to stain excised growing points which were then firmly squashed under a coverslip using a needle. Several squashes had to be performed on individual slides before a good preparation was obtained. *Asterella* chromosomes were found to be particularly small and difficult to observe and many squashes yielded no counts at all. Slides were examined under a compound microscope and good preparations made semi-permanent by ringing with rubber solution. Karyotypes were counted and photographed.

Electron microscopy. See Chapter 3.

4.4 RESULTS

Bibliographic research. The results of the bibliographic searches, where useful, have been incorporated into the taxonomic accounts. Most published descriptions were found to be inadequate in various ways: older descriptions by Stephani and others were woefully brief and gave only a very superficial account of the taxon; others were inaccurate, especially in describing sexual condition. Many more recent publications gave only brief descriptions, often ignoring important characters. Other published descriptions were clearly drawn up from earlier literature sources, as particular errors had been copied. Because of the poor literature base, the descriptions below have been drawn up almost entirely from new observations on specimens.

Field collections. Field collection was extremely successful in most areas visited, particularly Japan, China, Sikkim, Darjeeling, Nepal, Madeira, Norway and Switzerland. In all these places all the known indigenous *Asterella* taxa were located and collected; in some case significant new records were made, such as *A. gracilis* new to southern Italy, *A. mussuriensis* and *A. wallichiana* new to Sikkim and to Darjeeling district, *A. khasyana*, *A. leptophylla* and *A. mussuriensis* new to Bhutan. Particularly significant was the discovery of a new species in East Nepal, *A. grollei*, and its later discovery in China. In all of these areas both living material and dried material with mature sporophytes containing ripe spores were collected. Twelve out of the 16 accepted species in Europe and Asia were collected, in total 202 collections of *Asterella*. Numerous data were recorded about the plants themselves, their reproduction and their habitats, and many photographs were taken.

Herbarium. Herbarium studies constituted the major part of the research project. For many species, the available collections were more than adequate, but for a few, notably *A. blumeana*, *A. limbata, A. pappii* and *A. vulcanica*, more collections are desirable to give a more complete and reliable account of the species and their variation. For example, in *A. vulcanica*, only a single spore was detected on only one collection for SEM study. In total, over 1500 herbarium specimens were studied, identified and annotated. All specimens were tabulated on data sheets; all types were annotated as such, listed and from them lectotypes selected where needed.

From the herbarium material studied detailed record sheets were completed, with measurements and sketches, and incorporated into the species descriptions.

Laboratory. No significant results have yet been obtained from cultivated material, although some have been used for molecular studies reported elsewhere (Long *et al.*, 2000). The ability to grow *Asterella* species in culture (as described in Chapter 2) is in itself significant and could be of benefit to future in-vitro research.

Cytology. Only limited success was achieved with cytological studies, with the following results:

A. lindenbergiana n=9 (Fig. 4.2)

A. wallichiana n=9 (Fig. 4.2)

For both these species there were 8 larger chromosomes and one small 'm' chromosome. Squashes of *A. khasyana* and *A. leptophylla* were unsuccessful, despite repeated attempts. An explanation may be that at the time of fixation, the shoot apex cells were not actively dividing.

Review of existing literature on cytology within the Marchantiales (*e.g.* Bornefeld, 1987) suggested that its main use is at the generic and family level, rather than at the level of distinguishing species. To some extent this was borne out by other workers' results: counts by Tatuno (1955, 1960) for *A. lindenbergiana*, *A. mussuriensis* subsp. *crassa*, *A. cruciata*, *A. khasyana* and *A. leptophylla* all gave n=9, with one of these a small 'm' chromosome; by Kanwal (1976) for *A. mussuriensis* gave n=9 and two counts by Kachroo (1969) gave n=18 for *A. khasyana* and *A. leptophylla*. It was not possible to examine vouchers for these counts so to some extent the identifications should be treated with caution, particularly as two different workers reported different counts for *A. khasyana*. There is little doubt that in *Asterella*, n=9 is the predominant chromosome number. Because of the minute size of the chromosomes, techniques such as Giemsa C-banding are unlikely to be successful, in contrast to other liverworts, such as *Pellia*, with much larger, strongly banded chromosomes (Newton, 1989).

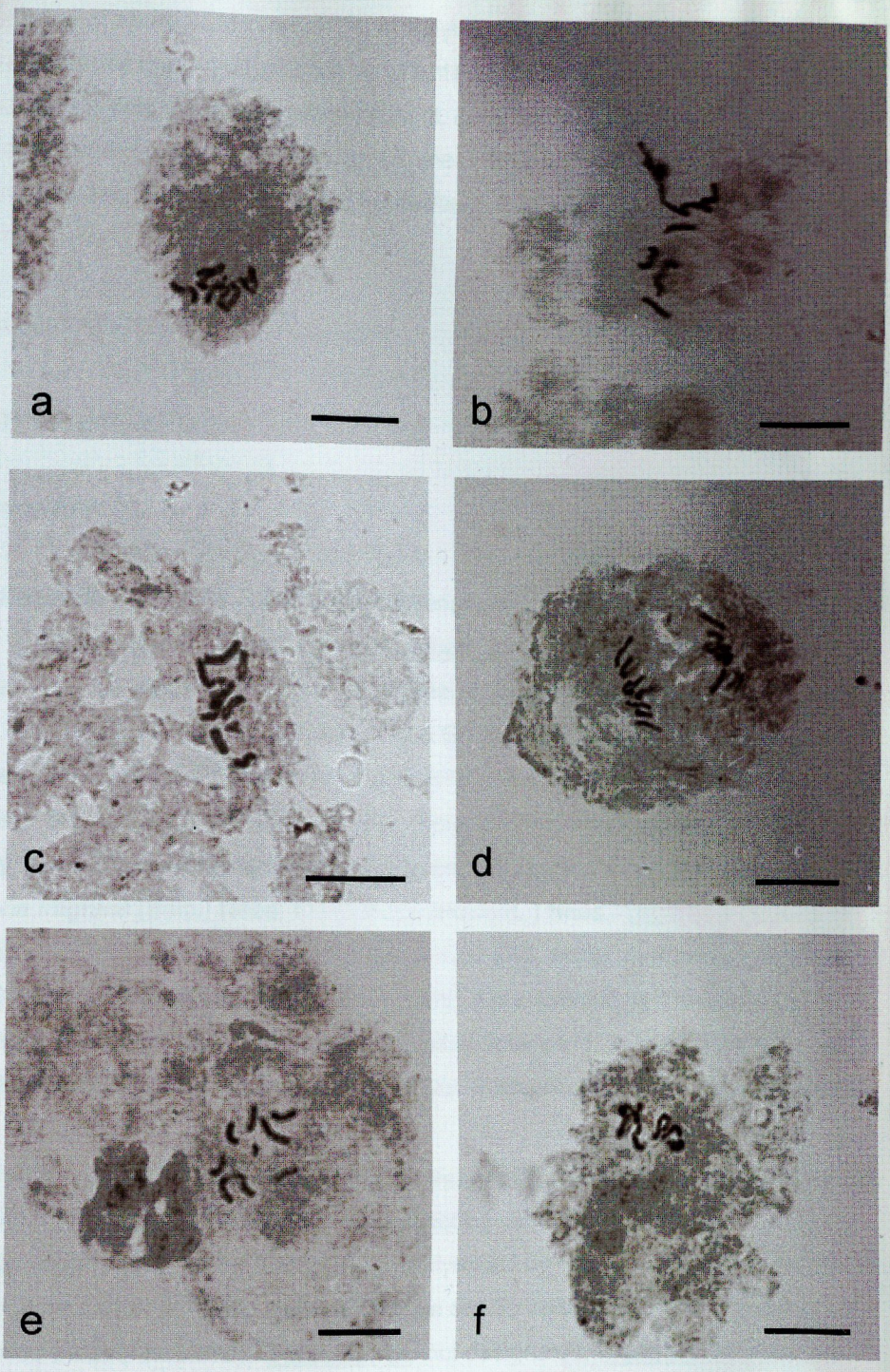

Fig. 4.2 Chromosome preparations of *Asterella* species. a, *Asterella lindenbergiana*, Norway, *Long 19989;* b–e, *Asterella wallichiana*, Japan, Iriomote, *Long 24903*; f, *Asterella wallichiana*, China, Yunnan, *Long 23589*; a, c, e, f, metaphase; b, late prophase; d, late anaphase. Scale bars = 10μm.

SEM. The results are presented in Chapter 3, but with a descriptive paragraph incorporated into the species accounts below. A particularly valuable discovery made during this study was the practical value of spore SEM in resolving synonymy. This study has been described by Long (1998). Because many old types are fragmentary and may lack important characters such as sexual condition, the spores, when present, can provide very conclusive evidence of the identity of the name in question. For many names described by Stephani, and for the early Himalayan names described by Lehmann & Lindenberg, the spores were crucial in resolving the synonymy.

4.5 TAXONOMIC ACCOUNT

4.5.1 The genus *Asterella*

Generic synonymy

Asterella P.Beauv. in Cuvier (ed.), Dictionnaire Sciences Naturelles 3: 257, 30 Jan. 1805 '1804'. Type species: not designated. Constituent species: 1. *Asterella tenella* (L.) P.Beauv.; 2. *Asterella hemisphaerica* (L.) P.Beauv. Lectotype: *Marchantia tenella* L. [= *A. tenella* (L.) P.Beauv.] (type conserved (Long & Grolle, 1992b)).

Syn: *Fimbraria* Nees, Horae Physicae Berolinenses 44, 1820; *hom. illeg.* (Art. 53.1) non *Fimbriaria* Stackhouse 1809 (Rhodophyta). Type species: not designated. Constituent species: 1. *Fimbraria marginata* Nees; 2. *Fimbraria saccata* (Wahlenb.) Nees; 3. *Fimbraria fragrans* (Balb.) Nees; 4. *Fimbraria tenella* (L.) Nees. Lectotype (Evans, Contributions from the U.S. National Herbarium 20: 248, 1920): *Fimbraria marginata* Nees. [= *Asterella marginata* (Nees) S.W.Arnell]. Synonymised by Trevisan (1874).

Syn.: *Fimbriaria* Nees mut. Steudel, Nomenclator Botanicus ed. 1, 2: 165, 1824, orth. var., *hom. illeg.* (Art. 53.1) non *Fimbriaria* Stackhouse 1809 (Rhodophyta). Type: *Fimbraria* Nees.

Syn: *Hypenantron* Corda in Opiz (ed.), Naturalientausch [12] (Beiträge zur Naturgeschichte. [1]): 648; after 21 Sept. 1829(–1830). Type species: *Hypenantron ciliatum* Corda. [= *Asterella saccata* (Wahlenb.) A.Evans]. Synonymised by Nees (1838) under *Fimbriaria*.

Syn.: *Dictyochiton* Corda, in Nees, Naturgeschichte der Europäischen Lebermoose 4: 259, 1838, *nom. inval.* (Art. 34.1d). Type species: not designated. Constituent species: *Dictyochiton pilulare* Corda, in Nees, Naturgeschichte der Europäischen Lebermoose 4: 280, 1838, *nom. inval.* (Art. 34.1c).

Syn.: *Rhacotheca* Bisch., in Seubert, Flora Azorica 12, 1844. Type species: *Rhacotheca azorica* Bisch. [= *Asterella africana* (Mont.) A.Evans]. Synonymised by Leitgeb (1881) under *Fimbriaria*.

Syn.: *Octokepos* Griff., Notulae ad Plantas Asiaticas 2: 343, 1849. Type: *Octokepos khasyanum* Griff. [= *Asterella khasyana* (Griff.) Pandé *et al.*]. Synonymised by Mitten (1861) under *Fimbriaria*.

Notes on generic typification and orthography

A historical account of *Asterella* and its synonyms was given in detail in Chapter 1.4. but excluded typification and orthography.

a. The type of the genus *Asterella*

Asterella was first validly published by Palisot de Beauvois (1805) who included in it two species: *A. tenella* (L.) P.Beauv. (*Marchantia tenella* L.) and *A. hemisphaerica* (L.) P.Beauv. (*Marchantia hemisphaerica* L.). In 1818, Raddi described the unispecific genus *Rebouillia* [*Reboulia* Raddi *orth. mut.* Nees 1846, *orth. cons.*] to accommodate one of the two elements in the protologue of *Asterella*, namely *Marchantia hemisphaerica*.

Grolle (1983a) argued that this act of Raddi (1818) in segregating *Marchantia hemisphaerica* L. as a new unispecific genus *Reboulia*, automatically typified *Asterella* according to the 'residue principle', by *Marchantia tenella* L., the only other element in its protologue. Following changes to the '*Berlin Code*' of nomenclature (Greuter *et al.*, 1988), effective lectotypification by the 'residue principle' could not be accepted (Art. 7.11) and Long & Grolle (1992a, b) re-evaluated the typification of *Asterella*.

Long & Grolle (1992a, b) located an early typification of *Asterella* (unfortunately conflicting with the long-held traditional usage), by Leman (1823) who stated that *Marchantia tenella* L. was placed in *Fimbraria* Nees, and that *M. hemisphaerica* L. was 'type' of both '*Rebouillia*' Raddi [*Reboulia* Raddi *orth. mut.* Nees] and *Asterella* P.Beauv.; this statement constituted a formal typification of *Asterella* by *M. hemisphaerica*, although Leman did not indicate that he intended '*Rebouillia*' to be relegated to synonymy of *Asterella*. The existence of this typification necessitated the conservation of the genus *Asterella* and its traditionally accepted type *Marchantia tenella* L. as proposed by Long & Grolle (1992a, b).

b. Orthography of *Fimbraria* and *Fimbriaria*

Nees von Esenbeck (1820) originally used the spelling *Fimbraria*. This spelling was only rarely used up until Taylor (1837). Steudel in 1824 'corrected' the spelling to *Fimbriaria* and this orthography predominated in publications up to Stephani (1898–1899, 1917–1925). In this form it became accepted by Nees von Esenbeck himself (Nees, 1838; Gottsche, Lindenberg & Nees, 1844–1847).

Although *Fimbraria* Nees is now considered a synonym of *Asterella* P.Beauv. 1805, they have different types and for this reason the former name could theoretically be resurrected should *Asterella* be subdivided in future. Le Jolis (1895) advocated retention of the name *Fimbriaria* and rejection of *Asterella* on the grounds of its confused application to two different generic entities. This suggestion was followed by several authors, mostly European, including

Stephani (1898–1899, 1917), Müller (1951–1958) and Kashyap (1929–1934). However, *Fimbriaria* has never been formally proposed for conservation, nor has *Asterella* been formally proposed for rejection.

Long & Grolle (1992a) considered the legitimacy of *Fimbraria* Nees and concluded that *Fimbraria* Nees is an illegitimate homonym of *Fimbriaria* Stackhouse, as implied by Trevisan (1853) and apparently supported by Underwood (1895) and Bonner (1962) and therefore concluded that it could not be legitimately used in the Hepaticae.

c. Notes on *Dictyochiton* and *D. pilulare*

Dictyochiton Corda and *D. pilulare* Corda were never legitimately published. They were based on an unpublished and annotated drawing made by Corda, studied by Nees and briefly described by him (Nees, 1838) in two footnotes under *Fimbriaria nana* Lindenb. Therein he treated *D. pilulare* (p. 280) as a doubtful synonym of *Fimbriaria nana*, itself now considered a synonym of *Athalamia hyalina* (Sommerf.) S.Hatt. (Grolle, 1981). However in his second footnote (p. 282), Nees noted that Corda's drawing was annotated '*Marchantia pilularis* Wahlenb. Fl. Lapp.' Such a name does not exist in *Flora Lapponica* (Wahlenberg, 1812) and Nees concluded that Corda intended *Marchantia pilosa* Wahlenb. which was published there. This illegitimate name is now a synonym of *Asterella gracilis*. It appears therefore that Corda intended to propose *Marchantia pilosa* Wahlenb. as the type species of a new genus *Dictyochiton*. This seems a likely though academic conclusion; *Dictyochiton*, though never validated, is best treated as a synonym of *Asterella* rather than *Athalamia*. Müller (1951–1958) also treated it as a synonym of *Fimbriaria ludwigii* (= *A. gracilis*).

Generic description of *Asterella*

Thallus prostrate, terrestrial, medium-sized to large, in some species with pungent 'fishy' smell when bruised or crushed. *Vegetative branches* green, often purplish-pigmented especially beneath, ± unbranched to copiously branched, thin and delicate not drought-resistant (hygromorphic) to thick and leathery, drought-resistant (xeromorphic). Surface of thallus flat or weakly channelled, often glossy, usually ± reticulate from bulging sub-dorsal air chambers, often forming a pattern of curved radiating reticulations from midrib to margin. Midrib not to moderately strongly defined above. Dorsal pores slightly elevated though usually inconspicuous. *Branching* of three types: 1. terminal innovations from constriction at apex of thallus; 2. dichotomous symmetrical terminal branches without constrictions; 3. subapical or intercalary asymmetrically produced stipitate-based branches arising from amongst rhizoids on ventral side of midrib. All branches linear to heart-shaped, margins entire or wavy, when dry sometimes inrolling over thallus, apex notched. Midrib weakly to strongly prominent beneath, bearing numerous hyaline rhizoids and two rows of small to large, ± distant to imbricate, ventral scales, these sometimes exserted beyond margins and apical notch and recurved. *Dorsal epidermis* single-layered, cells thin-walled or with distinct trigones at angles. Oil-cells usually

scattered. *Air pores* mostly one per air chamber where these reach the upper surface of the thallus, sometimes raised in bulge above each chamber, surrounded by collapsed cell remains and with 4–8 radial rows of cells in concentric rings around pore; cells of each ring sometimes partly overlapping those of adjacent ring, those of innermost ring with bulging inner face, radial walls of cells sometimes somewhat thickened but not stellate. *Assimilation tissue* green, composed of tubular air chambers, apparently (in transverse section) in 1–several layers, but mostly arising on edge of basal compact tissue and radiating outwards and upwards; air chambers over midrib almost vertical, those of wings almost horizontal, often overlapping; separated by thin walls of tissue containing occasional oil-cells which contain a single large globose oil-body; air chambers sometimes with free filaments. *Basal compact tissue* colourless often mycorrhizal, forming a convex band along lower part of midrib; cells irregularly rounded-hexagonal; oil-cells scattered, especially in lower epidermis. *Rhizoids* colourless, borne amongst ventral scales along basal tissue of midrib, of two types, smooth and pegged, the latter with internal peg-like wall thickenings. *Ventral scales* borne amongst rhizoids in two rows on midrib, colourless or violet to purplish pigmented, asymmetric, one cell thick throughout, composed of a broad semicircular basal part with long decurrent curved margin on median (adaxial) side, and 1 or 2 lanceolate to ovate appendages often somewhat constricted at point of insertion on scale body, cells of scale usually rectangular and with scattered isodiametric oil-cells in basal part and sometimes in appendage, margin of basal part of scale with few to many slime-papillae. *Vegetative perennation* of either xeromorphic persistent thalli or of tubers formed by short ventral stipitate-based branches with short swollen midrib and vestigial thallus wings.

Sexuality: androecia and archegoniophores borne on separate plants (dioicous) or on separate branches of the same plant (monoicous). *Androecia* borne directly on dorsal surface of thallus, on main thallus or on small to large ventral stipitate-based branches, in raised cushions or as scattered line or irregular groups of antheridial chambers, rarely reduced to scaly fleshy protruberances on margin of thallus (vestigial terminal branches), cushions with or without marginal scales; ostioles protruding as raised conical papillae; paraphyses present, pluricellular; antheridia ellipsoid on short stalk. *Archegoniophore* borne as an extension of vegetative thallus from apical notch of a normal vegetative branch, a reduced terminal branch, or a reduced ventral intercalary branch, terminating growth of that branch or in a few species thallus lobe on one side (rarely both sides) of archegoniophore continuing as a vegetative innovation (half-shoot), or thallus producing a ventral stipitate-based innovation at apex close to archegoniophore, continuing vegetative growth. Archegoniophore comprising a stalk (peduncle) and terminal carpocephalum (receptacle). *Stalk* erect, single, rarely paired, usually pale green or brownish in colour, often in part purplish pigmented, delicate to rigid, often weakly longitudinally ribbed; in transverse section ellipsoid to circular, without or rarely with air chambers, with a weakly-differentiated epidermis, medulla of hexagonal thin-walled cells, oil-cells absent; stalk with a single deep longitudinal rhizoid furrow containing dense pegged rhizoids; stalk with or without ring of scales around base, glabrous or with scattered scales

along its length, usually with a dense ring of scales around apex, scales linear to lanceolate, with scattered oil-cells. *Carpocephalum* green or reddish-tinged, usually subglobose when young becoming conical, ovoid or flattened and inversely saucer-shaped when mature, central upper part conical or forming a rounded boss, often coarsely papillate or warted, outer (lower) part smooth to warted, sometimes ± unlobed, more often shallowly to deeply divided into 2–6 lobes; carpocephalum with air-chambers and compound (barrel-shaped) pores, air-chambers often bulging at least in central upper part; under surface of lobes bearing a single involucre. *Involucre* flap-like, borne on ventral surface of each lobe, when young small, containing 2–4 archegonia of which only one becomes fertilised to form a sporogonium; mature involucre often expanded, narrow to broad, containing and partly sheathing a single pseudoperianth and sporogonium, bistratose except for free margin, with numerous oil-cells; free margin entire or bilobed. *Pseudoperianth* colourless or purplish pigmented, formed of cup-shaped undivided base and subequal lobed upper part; basal part closely enclosing sporogonium, often hidden by involucre, constricted or not at insertion of lobes, formed of unistratose rectangular thin-walled cells and scattered isodiametric oil-cells; lobes hyaline, brownish or pinkish, delicate, brittle, exserted from involucre, 5–18, lanceolate, tapering to a smooth or mammillose point, attached at apex when young with a central orifice, becoming free or remaining attached at apex when mature; margins of lobes revolute when dry, involute when moist, composed of a single layer of cells often strongly thickened on inner and radial walls, thickened at angles, with scattered oil-cells.

Capsule globose, usually black or blackish-brown, with very short seta, dehiscing when ripe in upper 1/3 to 1/4 as an irregular or regular, discoid cap; wall brown, unistratose, cells irregularly rectangular, thin-walled, without thickenings in walls or at angles; cells of lid smaller, irregularly shaped, with large strongly thickened trigones. *Spores* yellow, orange, brown or black, subglobose, with rounded outer (distal) face, equatorial rim or wing, and three proximal facets defined by sharp to rounded trilete ridges; equator occasionally with 3 apertures at junction with trilete ridges; distal face often strongly ornamented with reticulations (areolae and alveoli) or ridges and finer pores or papillae, rarely almost smooth; proximal facets flat or with a median bulge, usually less prominently ornamented than distal face, reticulate or ridged, rarely almost smooth. *Elaters* usually yellow or brownish, linear, weakly sigmoidally curved, with tightly coiled bispiral (sometimes unispiral or trispiral) thickenings throughout. *Chromosome number* mostly n = 9.

4.5.2 Infrageneric groupings

The infrageneric classification within *Asterella* is also considered in Chapter 5. No well-established stable groupings are in general use and the system used here is necessarily interim, using available morphological evidence. The Subgenera and Sections adopted here in part follow Grolle (1976, 1983a) but incorporate additional evidence from spore studies

(described in Chapter 3) and new morphological evidence *e.g.* characters of the pseudoperianth and capsule lid considered important. The use of molecular data (see Long *et al.*, 2000) will almost certainly provide new evidence to amend these groupings in future.

The following classification is defined by the characters used in the key below. It is based as far as possible on a worldwide range of species, not purely on Eurasian taxa. The type species of the genus, *A. tenella* (L.) P.Beauv. is not present in Eurasia. It is automatically referred to Subg. *Asterella* Sect. *Asterella*.

Subg. *Saccatae*
Subg. *Wallichianae*
Subg. *Asterella*
Sect. *Brachyblepharis*
Subg. *Phragmoblepharis*
Subg. *Graciles*

Key to subgenera in Eurasia

1. Pseudoperianth lobes free or caducous at maturity; spores yellow to orange-yellow 2
+ Pseudoperianth lobes remaining firmly joined at apex; spores brown, red-brown to black, rarely yellowish 3

2. Mature carpocephalum hemispheric; lid of capsule disc-like, entire; spores proximally alete, distally irregularly and incompletely areolate ..... **Subg. *Graciles***
+ Mature carpocephalum flat or umbrella-shaped; lid of capsule irregularly fragmenting; spores proximally trilete, distally with regular, complete areolae or (in *A. blumeana*) with bulging 'crown' ..... **Subg. *Asterella* Sect. *Brachyblepharis***

3. Spores distally regularly areolate or alveolate ..... **Subg. *Phragmoblepharis***
+ Spores distally ridged (ridges sometimes finely reticulate) 4

4. Dioicous; pseudoperianth without median constriction ..... **Subg. *Wallichianae***
+ Autoicous; pseudoperianth with median constriction ..... **Subg. *Saccatae***

4.5.3 Keys to species

Key to *Asterella* species in Eurasia for specimens with ripe spores

1. Pseudoperianth lobes becoming free or caducous at maturity; spores yellow to orange-yellow 2
+ Pseudoperianth lobes remaining firmly joined at apex; spores brown, red-brown to black, yellowish only in *A. saccata* and *A. vulcanica* 8

2. Spores proximally alete, distally irregularly and incompletely areolate; carpocephalum hemispheric ..... **16. *A. gracilis***
+ Spores proximally trilete, distally with regular complete areolae or (in *A. blumeana*) with bulging 'crown'; carpocephalum flat and disc-shaped or inversely saucer-shaped to umbrella-shaped 3

3. Spores non-areolate distally, with bulging 'crown' ..... **8. *A. blumeana***
+ Spores regularly and completely areolate distally 4

4. Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) 5
+ Sexual condition ventral-autoicous or terminal-autoicous (androecia not borne closely proximal to base of archegoniophore) 7

5. Carpocephalum umbrella-shaped; pseudoperianth lobes (5–) 6, brittle and often caducous ..... **4. *A. africana***
+ Carpocephalum almost flat; pseudoperianth lobes 7–15, neither brittle nor caducous .. 6

6. Archegoniophore 0.8–3 (–6.8)mm; carpocephalum deeply lobed; pseudoperianth lobes 9–15; spores 60–75µm diameter ..... **5. *A. cruciata***
+ Archegoniophore 3.3–17.2mm; carpocephalum shallowly lobed; pseudoperianth lobes 7–9; spores 75–100µm diameter ..... **6. *A. khasyana***

7. Sexual condition ventral-autoicous (androecia on short ventral shoots, never on branch bearing an archegoniophore) ..... **7. *A. leptophylla***
+ Sexual condition terminal-autoicous (androecia produced as short vestigial terminal branches along margin of thallus which also bears an archegoniophore) .. **9. *A. limbata***

8. Spores yellow or yellowish-brown 9
+ Spores black, brown, red-brown or purplish-brown 10

9. Spores distally with low wavy ridges ..... **1. *A. saccata***

\+ Spores distally areolate ..... **15. *A. vulcanica***

10. Spores distally with coarse wavy ridges to almost smooth 11

\+ Spores distally areolate or minutely alveolate 12

11. Spores black, 135–160µm diameter; sexual condition terminal-autoicous .. **2. *A. grollei***

\+ Spores brown to red-brown, 40–105µm diameter, sexual condition dioicous **3. *A. wallichiana***

12. Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) ..... **10. *A. lindenbergiana***

\+ Sexual condition ventral-autoicous 13

13. Both androecia and archegoniophores borne on very small ventral branches up to 2 x 2mm 14

\+ Androecia on main thallus or on small to large ventral branches; archegoniophores on small to medium-sized ventral branches up to 6.4 x 3.2mm 15

14. Carpocephala with low rounded warts as broad as tall **13a. *A. mussuriensis*** subsp. ***mussuriensis***

\+ Carpocephala with tall warts at least twice as tall as broad **13b. *A. mussuriensis*** subsp. ***crassa***

15. Archegoniophores borne on small ventral branches 1.2–2.9mm long; spores with few broad shallow primary areolae not subdivided into alveoli ..... **14. *A. multiflora***

\+ Archegoniophore borne on small to large ventral branches; spores densely alveolate, with or without larger areolae 16

16. Spores distally lacking regular complete primary areolae but with dense irregular alveoli ..... **11. *A. persica***

\+ Spores distally with regular complete primary areolae, these subdivided into alveoli **12. *A. pappii***

Key to *Asterella* species in Eurasia for specimens without ripe spores

1. Sexual condition par-autoicous with androecia borne closely proximal to base of archegoniophore 2
+ Sexual condition ventral-autoicous or terminal-autoicous or dioicous with androecia not borne closely proximal to base of archegoniophore (in *A. grollei* androecia closely lateral to base of archegoniophore) 7

2. Thalli mostly thin and delicate; carpocephala flat, disc-shaped or umbrella-shaped at maturity 3
+ Thalli mostly thick and leathery; carpocephala hemispheric to bluntly conical at maturity 5

3. Carpocephalum umbrella-shaped; pseudoperianth lobes (5–) 6, brittle and often caducous ..... **4. *A. africana***
+ Carpocephalum almost flat at maturity; pseudoperianth lobes 7–15, neither brittle nor caducous 4

4. Archegoniophore stalk 0.8–3 (–6.8)mm; carpocephalum deeply lobed; pseudoperianth lobes 9–15 ..... **5. *A. cruciata***
+ Archegoniophore stalk 3.3–17.2mm; carpocephalum shallowly lobed; pseudoperianth lobes 7–9 ..... **6. *A. khasyana***

5. Thallus apex bearded with conspicuous ventral scales; carpocephalum bluntly conical; pseudoperianth with median constriction and 8–10 lobes ..... **1. *A. saccata***
+ Thallus apex not bearded with conspicuous ventral scales; carpocephalum hemispheric; pseudoperianth without median constriction, lobes 6–18 6

6. Thalli 2–4mm broad, with narrow thick wings; pseudoperianth divided to 4/5 into 6–8(–12) lobes ..... **16. *A. gracilis***
+ Thalli 6–9mm broad with broad attenuate wings; pseudoperianth divided to just below middle into 16–18 lobes ..... **10. *A. lindenbergiana***

7. Thalli mostly thin and delicate; carpocephala flat or umbrella-shaped 8
+ Thalli mostly thick and leathery; carpocephala hemispheric to bluntly conical 10

8. Sexual condition terminal-autoicous (androecia produced as short vestigial terminal branches along margin of thallus which also bears an archegoniophore) .. **9. *A. limbata***

\+ Sexual condition ventral-autoicous or sometimes also terminal-autoicous in *A. blumeana* (androecia on short ventral or terminal shoots, never on margins of branch bearing an archegoniophore) 9

9. Ventral scale appendages 350–490µm long, with cells 42–67µm long; receptacle 3.5–6mm diameter, moderately deeply lobed; pseudoperianth lobes usually 9–12 (Himalaya, India, China, Japan, Korea, E Russia) ..... **7. *A. leptophylla***

\+ Ventral scale appendages c. 800µm long, with cells 70–85µm long; receptacle 2.8–4mm diameter, shallowly lobed; pseudoperianth lobes 7–10 (Java, Celebes, Sunda Islands) ..... **8. *A. blumeana***

10. Sexual condition terminal-autoicous, with androecia borne closely lateral to base of archegoniophore on a terminal half-dichotomy ..... **2. *A. grollei***

\+ Sexual condition dioicous or ventral-autoicous 11

11. Sexual condition dioicous ..... **3. *A. wallichiana***

\+ Sexual condition ventral-autoicous 12

12. Ventral scale appendages broad, obtuse ..... **15. *A. vulcanica***

\+ Ventral scale appendages lanceolate, acute 13

13. Both androecia and archegoniophores borne on very short ventral branches up to 2 x 2mm 14

\+ Androecia on main thallus or on short to long ventral branches; archegoniophores on short to medium-sized ventral branches up to 6.4 x 3.2mm 15

14. Carpocephala with low rounded warts as broad as tall (Himalaya, China)
13a. *A. mussuriensis* subsp. ***mussuriensis***

\+ Carpocephala with tall warts at least twice as tall as broad (Japan)
13b. *A. mussuriensis* subsp. ***crassa***

15. Archegoniophores borne on short ventral branches 1.2–2.9mm long (Himalaya)
14. *A. multiflora*

\+ Archegoniophore borne on short to long ventral branches 2.6–6.4mm long (Iran, Arabian Peninsula, Socotra) ..... **11. *A. *persica*** and **12. *A. *pappii***

* only reliably distinguished by spore ornamentation; see under *A. persica*.

Key to *Asterella* species in Europe, Macaronesia, the Middle East and Northern Asia for specimens with ripe spores

1. Pseudoperianth lobes becoming free at maturity, sometimes caducous; spores yellowish 2
+ Pseudoperianth lobes remaining firmly joined at apex; spores brown, red-brown to black, yellowish only in *A. saccata* 3

2. Spores proximally trilete, distally with regular complete areolae; carpocephalum umbrella-shaped ..... **4. *A. africana***
+ Spores proximally alete, distally irregularly and incompletely areolate; carpocephalum hemispheric ..... **16. *A. gracilis***

3. Spores yellowish-brown; carpocephalum conical; pseudoperianth with median constriction and 8–10 lobes ..... **1. *A. saccata***
+ Spores brown, red-brown or purplish-brown; carpocephalum hemispheric; pseudoperianth without median constriction, lobes 9–18 4

4. Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) ..... **10. *A. lindenbergiana***
+ Sexual condition ventral-autoicous (androecia not borne closely proximal to base of archegoniophore) 5

5. Spores distally lacking regular complete primary areolae but with dense irregular alveoli ..... **11. *A. persica***
+ Spores distally with regular complete primary areolae, these subdivided into alveoli **12. *A. pappii***

Key to *Asterella* species in Europe, Macaronesia, the Middle East and Northern Asia for specimens without ripe spores

1. Sexual condition ventral-autoicous (androecia not borne closely proximal to base of archegoniophore) ..... **11. *A. persica** and **12. *A. pappii**
+ Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) 2

2. Pseudoperianth lobes remaining firmly joined at apex 3
+ Pseudoperianth lobes becoming free, sometimes caducous, at maturity 4

3. Thallus apex bearded with conspicuous ventral scales; carpocephalum conical; pseudoperianth with median constriction and 8–10 lobes ..... **1. *A. saccata***
+ Thallus apex not bearded with conspicuous ventral scales; carpocephalum hemispheric; pseudoperianth without median constriction, lobes 16–18 **10. *A. lindenbergiana***

4. Carpocephalum umbrella-shaped; pseudoperianth lobes (5–) 6, brittle and often caducous; spores with large regular and complete distal areolae, proximally trilete **4. *A. africana***
+ Carpocephalum hemispheric; pseudoperianth lobes 6–8 (–12), not brittle or caducous; spores irregularly and incompletely areolate distally, proximally alete .....**16. *A. gracilis***

* only reliably distinguished by spore ornamentation; see under *A. persica*.

Key to *Asterella* species in the Indian region and China for specimens with ripe spores

1. Pseudoperianth lobes free at maturity; spores yellow to orange-yellow 2
+ Pseudoperianth lobes remaining firmly joined at apex; spores brown, red-brown to black (yellow-brown in *A. saccata*) 5

2. Spores proximally alete, distally irregularly and incompletely areolate; carpocephalum hemispheric ..... **16. *A. gracilis***
+ Spores proximally trilete, distally with regular complete areolae; carpocephalum flat and disc-shaped 3

3. Sexual condition ventral-autoicous (androecia borne on short ventral branches) **7. *A. leptophylla***
+ Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) 4

4. Stalk of archegoniophore 0.8–3 (–6.8)mm; carpocephalum deeply lobed; pseudoperianth lobes 9–15; spores 60–75µm diameter ..... **5. *A. cruciata***
+ Stalk of archegoniophore 3.3–17.2mm; carpocephalum shallowly lobed; pseudoperianth lobes 7–9; spores 75–100µm diameter ..... **6. *A. khasyana***

5. Spores distally coarsely ridged; sexual condition dioicous, terminal-autoicous or par-autoicous 6

\+ Spores distally areolate; sexual condition ventral-autoicous 8

6. Spores brown to red-brown, 40–105µm diameter; sexual condition dioicous; pseudoperianth not constricted ..... **3. *A. wallichiana***

\+ Spores black or yellow-brown, 95–160µm diameter; sexual condition terminal-autoicous or par-autoicous; pseudoperianth with median constriction 7

7. Spores yellow-brown, 95–125µm diameter; sexual condition par-autoicous, with androecia borne proximal to base of archegoniophore; carpocephalum elongate-hemispheric ..... **1. A. saccata**

\+ Spores black, 135–160µm diameter; sexual condition terminal-autoicous, with androecia borne closely lateral to base of archegoniophore on a terminal half-dichotomy; carpocephalum rounded-conical ..... **2. *A. grollei***

8. Spores with numerous deep primary areolae; both archegoniophores and androecia borne on short ventral branches ..... **13. *A. mussuriensis*** subsp. ***mussuriensis***

\+ Spores with few shallow primary areolae; archegoniophores borne on short ventral branches; androecia terminal on main thallus or large ventral branches **14. *A. multiflora***

Key to *Asterella* species in the Indian region and China for specimens without ripe spores

1. Pseudoperianth lobes becoming free at maturity 2

\+ Pseudoperianth lobes remaining firmly joined at apex 5

2. Sexual condition ventral-autoicous (androecia borne on reduced ventral branches) **7. *A. leptophylla***

\+ Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) 3

3. Carpocephalum hemispheric ..... **16. *A. gracilis***

\+ Carpocephalum flat and disc-shaped 4

4. Stalk of archegoniophore 0.8–3 (–6.8)mm; carpocephalum deeply lobed; pseudoperianth lobes ..... **5. *A. cruciata***

\+ Stalk of archegoniophore 3.3–17.2mm; carpocephalum shallowly lobed; pseudoperianth lobes 7–9 ..... **6. *A. khasyana***

5. Sexual condition dioicous, terminal-autoicous or par-autoicous 6

\+ Sexual condition ventral-autoicous 8

6. Sexual condition dioicous; pseudoperianth not constricted ..... **3. *A. wallichiana***

\+ Sexual condition terminal-autoicous or par-autoicous; pseudoperianth with median constriction 7

7. Sexual condition par-autoicous, with androecia borne proximal to base of archegoniophore; carpocephalum elongate-hemispheric ..... **1. A. saccata**

\+ Sexual condition terminal-autoicous, with androecia borne closely lateral to base of archegoniophore on a terminal half-dichotomy; carpocephalum rounded-conical **2. *A. grollei***

8. Both archegoniophores and androecia borne on short ventral branches **13a. *A. mussuriensis* subsp. *mussuriensis***

\+ Archegoniophores borne on short ventral branches; androecia terminal on main thallus or large ventral branches ..... **14. *A. multiflora***

Key to *Asterella* species in Malesia and Indo-china for specimens with ripe spores

1. Carpocephalum ± hemispheric; pseudoperianth lobes remaining firmly joined at apex; spores brown or yellow 2

\+ Carpocephalum flat and disc-shaped or inversely saucer-shaped; pseudoperianth lobes becoming free at maturity; spores yellow to orange-yellow 3

2. Dioicous; spores 40–105µm diameter, brown or red-brown, distally coarsely ridged **3. *A. wallichiana***

Ventral-autoicous; spores 110–150µm diameter, yellow, distally with large areolae **15. *A. vulcanica***

3. Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) ..... **6. *A. khasyana***

\+ Sexual condition ventral-autoicous or terminal-autoicous (androecia not borne closely proximal to base of archegoniophore) 4

4. Sexual condition terminal-autoicous (androecia produced as short vestigial terminal branches along margin of thallus which also bears an archegoniophore) **9. *A. limbata***

\+ Sexual condition ventral-autoicous (androecia on short ventral shoots, never on branch bearing an archegoniophore) 5

5. Spores 55–90µm diameter, regularly and completely areolate distally . **7. *A. leptophylla***

\+ Spores 70–100µm diameter, non-areolate distally, with bulging crown ... **8. *A.blumeana***

Key to *Asterella* species in Malesia and Indo-china for specimens without ripe spores

1. Carpocephalum ± hemispheric; pseudoperianth lobes remaining firmly joined at apex 2

\+ Carpocephalum flat and disc-shaped or inversely saucer-shaped; pseudoperianth lobes becoming free at maturity 3

2. Sexual condition dioicous; stalk of archegoniophore 1.5–5mm long, without air chambers in transverse section; pseudoperianth lobes 7–12 ..... **3. *A. wallichiana***

\+ Sexual condition ventral-autoicous; stalk of archegoniophore 10–28mm, with vestigial air chambers in transverse section; pseudoperianth lobes 12–16 ..... **15. *A. vulcanica***

3. Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) ..... **6. *A. khasyana***

\+ Sexual condition ventral-autoicous or terminal-autoicous (androecia not borne closely proximal to base of archegoniophore) 4

4. Sexual condition terminal-autoicous (androecia produced as short vestigial terminal branches along margin of thallus which also bears an archegoniophore) **9. *A. limbata***

\+ Sexual condition ventral-autoicous or sometimes also terminal-autoicous in *A. blumeana* (androecia on short ventral or terminal shoots, never on margins of branch bearing an archegoniophore) 5

5. Scale appendage 350–490μm long, with cells 42–67μm long; receptacle 3.5–6mm diameter, moderately deeply lobed; pseudoperianth lobes usually 9–12
7. *A. leptophylla*

\+ Scale appendage c. 800μm long, with cells 70–85μm long; receptacle 2.8–4mm diameter, shallowly lobed; pseudoperianth lobes 7–10 ..... **8. *A. blumeana***

Key to *Asterella* species in Japan for specimens with ripe spores

1. Spores yellow to orange-yellow, with dissimilar sculpturing on proximal and distal surfaces; pseudoperianth lobes becoming free at maturity 2

\+ Spores brown or red-brown, with similar sculpturing on proximal and distal surfaces; pseudoperianth lobes remaining firmly joined at apex 4

2. Spores proximally alete, distally irregularly and incompletely areolate; carpocephalum hemispheric ..... **16. *A. gracilis***

\+ Spores proximally trilete, distally with regular complete areolae; carpocephalum flat or umbrella-shaped 3

3. Spores 60–75μm diameter, with irregularly crenate equatorial rim and trilete ridges; sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) ..... **5. *A. cruciata***

\+ Spores 55–90μm diameter, with smooth equatorial rim and trilete ridges; sexual condition ventral-autoicous (androecia borne on short ventral branches)
7. *A. leptophylla*

4. Spores distally ridged to almost smooth; sexual condition dioicous ..... **3. *A. wallichiana***

\+ Spores distally areolate; sexual condition ventral-autoicous
13b. *A. mussuriensis* subsp. *crassa*

Key to *Asterella* species in Japan for specimens without ripe spores

1. Pseudoperianth lobes becoming free at maturity 2

\+ Pseudoperianth lobes remaining firmly attached at apex 4

2. Sexual condition ventral-autoicous (androecia borne on reduced ventral branches)
7. *A. leptophylla*

\+ Sexual condition par-autoicous (androecia borne closely proximal to base of archegoniophore) 3

3. Stalk of archegoniophore 0.8–3 (–6.8)mm; carpocephalum flat, deeply lobed; pseudoperianth with 9–15 lobes divided to just below half-way ..... **5. *A. cruciata***

\+ Stalk of archegoniophore 8–16(–27)mm; carpocephalum hemispheric, shallowly lobed; pseudoperianth of 6–9 lobes divided to c. 4/5 ..... **16. *A. gracilis***

4. Sexual condition dioicous ..... **3. *A. wallichiana***

\+ Sexual condition ventral-autoicous ..... **13b. *A. mussuriensis*** subsp. ***crassa***

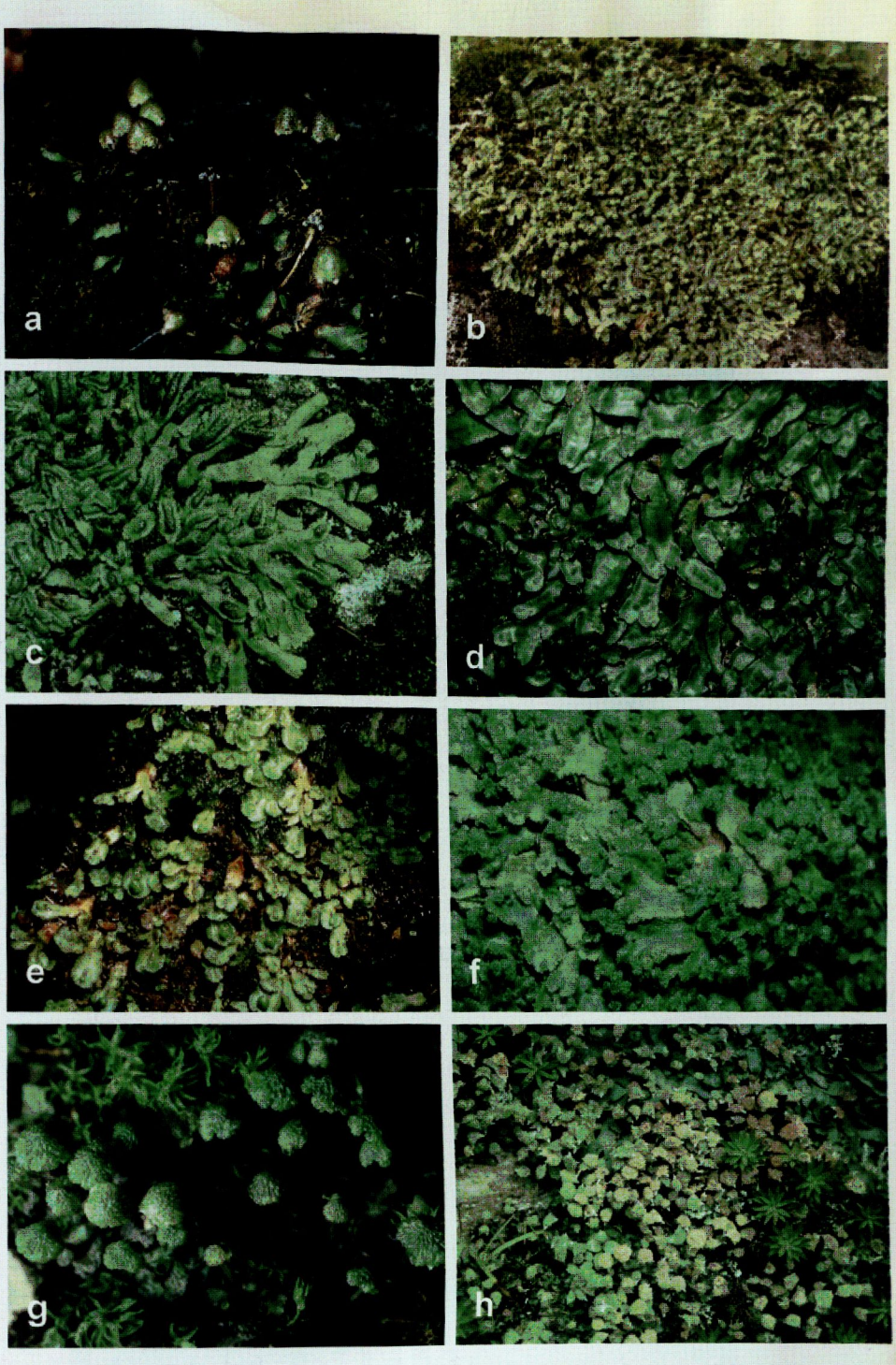

Fig. 4.3 Photographs of *Asterella* species. a, *A. grollei* (Nepal, *Long 20777*); b, *A. wallichiana* , female (India, Sikkim, *Long 22980*); c, *A. wallichiana,* male (India, Sikkim, *Long 22980*); d, *A. wallichiana* (Japan, Okinawa, *Long 24821*); e, *A. africana* (Madeira, *Long 25073*); f, *A. cruciata* (Japan, Honshu, *Long 24789*); g, *A. leptophylla* (India, Sikkim, *Long 22907*); h, *A. khasyana* (Nepal, *Long 20448*).

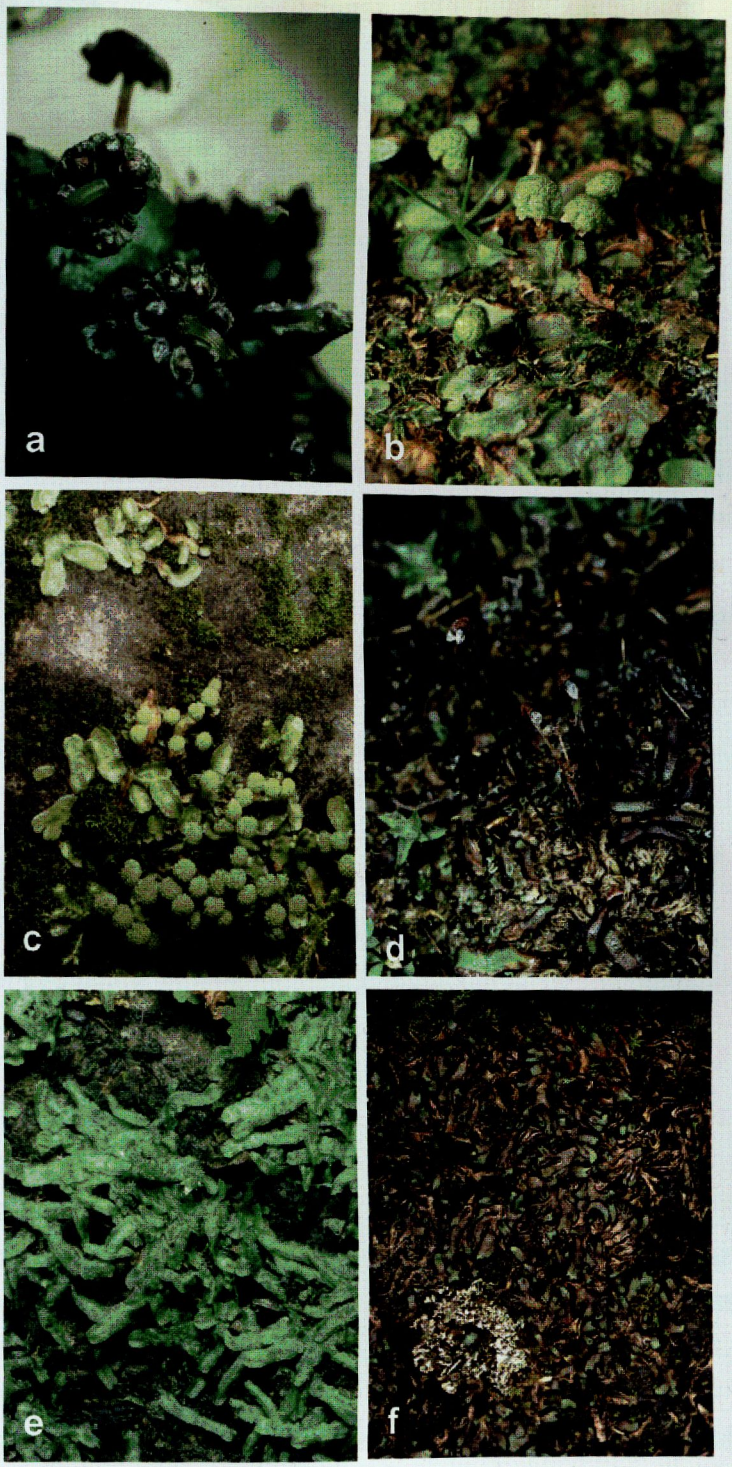

Fig. 4.4 Photographs of *Asterella* species. a, *A. leptophylla* (India, Sikkim, *Long 22907*); b, *A. lindenbergiana* (Switzerland, *Long 25647*); c, *A. mussuriensis* subsp. *mussuriensis* (India, Darjeeling, *Long 23048*); d, *A. mussuriensis* subsp. *mussuriensis* (Nepal, *Long 21541*); e, *A. mussuriensis* subsp. *crassa* (Japan, Honshu, *Long 24697*); f, *A. gracilis* (Switzerland, *Long 25664*).

4.5.4 Species accounts

SUBGENUS *SACCATAE*

Asterella subgenus *Saccatae* (Grolle) D.G. Long, Journal of Bryology 22: 13, 2000.

Basionym: *Asterella* section *Saccatae* Grolle, Feddes Repertorium 87: 171, 1976.

Type: *A. saccata* (Wahlenb.) A.Evans

Thalli xeromorphic, without strong smell; *vegetative branches* terminal and with ventral innovations; *assimilation tissue* with a single layer of air chambers or with 'spongy tissue' below; *ventral scale appendages* 1 or 2 per scale, lanceolate, not constricted, entire or toothed.

Sexual *condition* par-autoicous or terminal-autoicous; *androecia* aggregated in cushions; *carpocephalum* tall-hemispheric or rounded-conical; shortly-lobed or almost unlobed; *involucre* with free margin with median cleft; *pseudoperianth* laterally compressed when young, transversely constricted, lobes united at apex, divided approximately to half-way.

Capsule lid fragmenting irregularly; *spores* of types I and III, yellow-brown or black, with ridged ornamentation similar on proximal and distal surfaces, trilete, with distinct proximal pole; *elaters* 2-spiral.

Note: this is a heterogeneous subgenus defined primarily by the large shortly-lobed carpocephala, pseudoperianths compressed and constricted, and ridged spores However, the two constituent species differ in thallus anatomy, number of ventral scale appendages, sexual condition and spore colour.

1. Asterella saccata (Wahlenb.) A.Evans, Contributions from the United States National Herbarium 20: 276, 1920.

Basionym: *Marchantia saccata* Wahlenb., Der Gesellschaft Naturforschender Freunde zu Berlin Magazin für die neuesten Entdeckungen in der gesammten Naturkunde 5: 196, 1811. Type citation: 'Hab. in Kamtschatka inter Encalyptam vulgarem in terra humosa, uti videtur ad rupes siccas'. Type specimen: Kamschatka, *Tilesius s.n.* (S, herb. Swartz, **lectotype**, selected by Grolle (1976)).

Syn.: *Fimbraria saccata* (Wahlenb.) Nees, Horae Physicae Berolinenses 45, 1820.

Syn.: *Hypenantron saccatum* (Wahlenb.) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 440, 1877.

Syn.: *Marchantia fragrans* Schleich. [Plantae Cryptogamae Helveticae Cent. 3: 64, 1805, *nom. nud.*] ex DC. in Lam. & DC., Flore francaise 4: 423, 1805, *hom. illeg.* non Balb. 1804. Type citation: 'Le citoyen Thore a découvert cette espèce aux environs de Dax, dans les lieux ombragés et humides, sur le revers des fossés; il observe qu'elle émet une odeur forte et résineuse: depuis lors, je l'ai recue de M. Schleicher qui l'a trouvée en abondance aux environs de Branson, dans le Valais, et j'en aivu des énchantillons envoyés du mont

Saint-Gothard au C. Desfontaines.'; type specimen: [Switzerland, Kt. Valais] 'Copiose circa Branson. *Schleicher 64* 'a P.DC." (G–15274, **lectotype designated here**; isolectotypes BM, E, G-15270, G-15271, G-16980, G-16999) *non Marchantia fragrans* Balb. Memorie della Accademia delle Scienze di Torino (Ser.2) 7: 76, 1804. [= *Mannia fragrans*].

Syn.: *Hypenantron ciliatum* Corda, in Opiz (ed.) Naturalientausch [12] (Beiträge zur Naturgeschichte. [1]): 648; after Sept. 1829(–1830). Type citation: 'Helvetia lect. et communicat. a e Holl.' Type specimen: *n.v.*; synonymised by Nees (1838) under *Fimbriaria fragrans*.

Syn.: *Marchantia umbonata* Wallr., Linnaea 14: 686, 1841 '1840'. Type citation: An schroff abgedachten Bänken eines Gypshügels am südlichen Harze stellenweise sehr häufig... [leg. Wallroth]. Type specimen: *n.v.*; synonymised by Stephani (1898–1900).

Syn.: *Fimbriaria umbonata* (Wallr.) Wallr. [Linnaea 14: 686, 1841, *nom. nud. in syn.*] ex Nees in Gottsche, Lindenberg & Nees, Synopsis Hepaticarum 559, 1846.

Syn.: *Fimbraria fragrans* sensu Nees, Horae Physicae Berolinenses 45, 1820, *pro parte*.

Syn.: *Hypenantron fragrans* sensu Trevis., Herbarium Cryptogamicum Trevisianum 32, 1853.

Syn.: *Asterella fragrans* Trevis., Rendiconti del' Istituto Lombardo di Scienze e Lettere 7: 785, 1874, *nom. nov.* for *Marchantia fragrans* Schleich. ex DC. non Balb.

Thalli scattered amongst bryophytes and lichens, forming loose patches, strongly xeromorphic, not aromatic. *Vegetative branches* mostly arising as terminal dichotomies, but also innovating from ventral surface at apex; branches broadening towards apex, 7–10(–20) x 2–3mm, thick and leathery (all xeroshoots), green but not glaucous above with dark reddish wavy margins, notched at apex (but notch often hidden by scale appendages), in transverse section 0.6–1.0mm thick at midrib; branches c 2x as broad as thick; midrib broad, thick, suddenly contracted into narrow thallus wings. Upper surface concave or channelled (rarely almost flat) with undulate margins strongly inrolled when dry revealing conspicuous whitish ventral scale appendages overtopping margins and forming a conspicuous white tuft at thallus apex, surface weakly raised above air chambers in radiating lines from middle of thallus, air pores not visible; lower surface dark purple-red. *Dorsal epidermis* cells small, 20–45 x 6–10µm, walls thin, with small to moderately large trigones; oil cells few. *Air pores* raised on low epidermal domes, with orifice12–25µm diameter, cells in 6–7 rows of 2 concentric rings; inner cells 7–17µm in radial length, 7–20µm in width; outer cells 10–25µm in radial length, 15–30µm wide. *Assimilation tissue* 0.4–0.5mm thick at midrib, 1/4 to almost 1/2 thickness of thallus, of 1 layer of tall narrow air chambers, vertical over midrib, becoming oblique and overlapping in thallus wings; air chambers over midrib with short filamentous outgrowths below air pores; cells of partitions 15–25µm broad; oil cells scattered, sometimes abundant. *Basal compact tissue* 0.4–0.6mm thick in midrib, often more than 2x as thick as assimilation tissue, cells variable in size, 20–50µm diameter, thin-walled; oil cells abundant. *Rhizoids* smooth and pegged 7–22µm diameter. *Ventral scales* obliquely semicircular, with dark purple body with broad hyaline curved median

side, 1100–1800 x 500–750µm (largest towards shoot apex); cells of body rectangular with rounded ends, 50–100 x 17–37µm, becoming much shorter (25–30µm long) in hyaline border especially close to margin; hyaline margin irregularly bluntly toothed on upper half of scale, without slime-papillae; oil cells 6–16, 22–40µm diameter; appendages hyaline, (1–)2 per scale, equal or one much smaller, lanceolate, 550–1100 x 250–350µm, quickly tapering above broad base, not constricted, 6–14 cells broad at insertion, margin entire or with a few blunt teeth towards base; cells of base of appendage short, 25–42 x 17–25µm, those of apex elongate up to 110µm long, apex of a single elongate cell; oil cells absent or occasionally 1–2 at base.

Sexual condition par-autoicous and terminal-autoicous. *Androecia* borne on main thallus proximal to base of archegoniophore, or on separate terminal branch without an archegoniophore; not uncommonly archegoniophore without an associated androecium; main thallus sometimes with more 2 or more older androecia postical to archegoniophore; androecium forming a low weakly-defined elliptic to elongate cushion, variable in length, up to 1.8 x 0.4mm, sometimes reduced to a single ostiole; ostioles often widely spaced, tall, conical-cylindric, 250–400 x 80–100µm, often purplish pigmented, without peripheral scales. *Archegoniophore* terminating main thallus branches; vegetative growth often continued by an apical ventral innovation. *Stalk* orange-yellow, smooth, rigid, 3.5–15(–20) x 0.3–0.4mm, rounded-triangular in transverse section, with rhizoid furrow 125–175µm deep, containing very few pegged rhizoids; medullary cells thin-walled, 12–20µm diameter, becoming slightly larger, pigmented and with thicker walls towards epidermis; epidermal cells small, brown-pigmented, 7–12µm diameter; stalk glabrous but surrounded at base by dense cushion of hyaline scales arising on thallus and on base of stalk; scales linear, 1.3–2.6mm long, 120–280µm broad at or just above base, at widest part 4–8(–11) cells broad, occasionally deeply bifid, margin entire, apex composed of a uniseriate row of cells for about 1/4 of its total length. *Carpocephalum* green, elongate-hemispheric (tall dome-shaped) when fresh, becoming narrowly bluntly conical when dry or old, 2.2– 5 x 1.6–3mm (including pseudoperianth), shortly (1–)2–4-lobed, the lobes almost vertical or up to 20° to stalk; apical dome with low rounded warts, lobes smooth, with sinuate distal margin. *Involucre* 0.9–1.1 mm from base to free margin, with broad bluntly v-shaped median cleft 0.7–0.9mm deep; margin weakly sinuate. *Pseudoperianth* white, compressed laterally when young, 2.35–2.75mm long; basal cup subglobose, 1.25–1.4mm long; cells of base rectangular, 70–130 x 35–45µm; lobes 8–10, 1.1–1.35 x 0.35–0.5mm, strongly constricted at insertion when mature, united at apex, margins recurved when dry, lobe cells 75–210 x 25–40µm; oil cells absent.

Capsule 1.2–1.4mm diameter; cells of urn shortly rectangular, 30–60 x 20–40µm, thin-walled; cells of lid not seen. *Spores* (light microscope) yellow-brown, 95–125µm diameter. *Spores* (SEM) Type III: trilete, without equatorial apertures; with similar proximal and distal sculpturing, on distal surface with weak primary wavy ridges with minute reticulations 1–5µm diameter, not pitted; muri absent; equatorial rim narrow; proximal facets flat, with ornamentation as on distal surface. *Elaters* yellowish, 170–310 x 20–30µm, rounded at ends, bispiral. *Chromosome number* unknown.

Illustrations: Schuster (1992c Fig. 957); spores Fig. 3.3.

Distribution and phytogeography (Fig. 4.5).

In the study area *A. saccata* has been confirmed from Europe (Austria, Switzerland, Czech Republic, Slovakia, Italy, Macedonia, Hungary, Germany); Russia (Siberia, Amur, Kamchatka) and China (Xinjiang). Reports which have not been confirmed are from Spain (Casares-Gil, 1919), France (Spruce, 1850; Boulay, 1904), Greece (Bory, 1832), Romania (Mohan, 1984), Poland (Szweykowski, 1958) and Ukraine (Zerov, 1964).

Outside the study area *A. saccata* is reported from the U.S.A., Alaska, Canada and Greenland (Underwood, 1884, 1895; Evans, 1920, 1923; Frye & Clark,1937–1947; Schuster, 1992c; Schuster & Damsholt, 1974).

Asterella saccata has long been known for its highly localised distribution; it shows an atypical Arctic-alpine distribution in that it is infrequent in the Arctic, whilst in Europe it shows a Southern Continental distribution. In central and eastern Europe Suza (1940) considered it to be a 'xerothermophyte descendent of an Arctic-alpine flora surviving at lower altitudes in warm calcareous sites' on account of its absence from truly alpine habitats in the Alps and its apparent preference for xerothermic sites at lower altitudes. Some authors such as Boros (1938) regarded it as a Mediterranean element (in Hungary). Reimers (1940) explained it as an Arcto-tertiary species whose distribution became fragmented during the last ice-age, and which was unable to spread since then.

In North America *Asterella saccata* has a similar specialised distribution (Steere, 1937) which is predominantly Arctic-alpine (Alaska and Rockies) but with a very disjunct occurrence in the east in Minnesota, an area considered by Steere and others to have remained as an unglaciated refugium. Its present rarity therefore may be the result of the extremely slow rate of recolonisation due to its large spores and lack of vegetative propagules, together with the highly specialised habitat requirements.

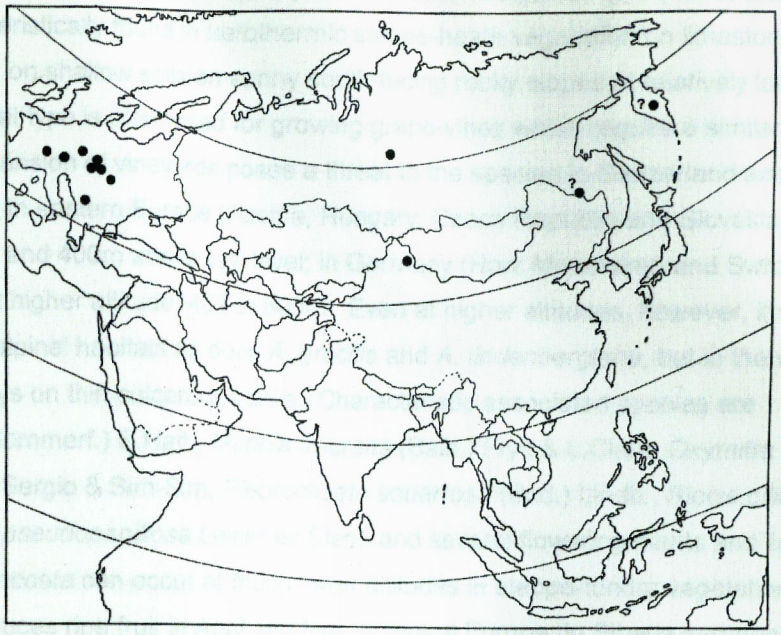

Fig. 4.5 Distribution of *Asterella saccata* in Eurasia, based on specimens studied. ? indicates an unlocalised specimen.

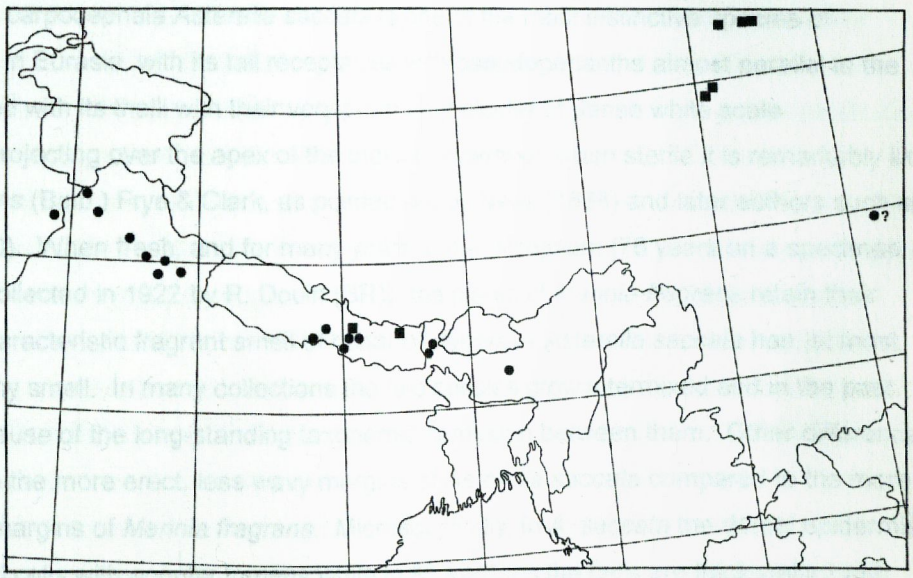

Fig. 4.6 Distribution of *Asterella grollei* and *A. multiflora* in Eurasia, based on specimens studied. ■ = *Asterella grollei* ● = *Asterella multiflora*. ? indicates an unlocalised specimen.

Ecology and phenology

The ecology of *Asterella saccata* and associated species has been studied in detail by several workers in central and eastern Europe, notably Boros (1925, 1938), Reimers (1940) and Suza (1940). It is characteristically found in xerothermic steppe-heath vegetation on limestone, dolomite or gypsum, on shallow soils on sunny south-facing rocky slopes at relatively low altitudes. This habitat type is often used for growing grape-vines which require a similar aspect and climate and expansion of vineyards poses a threat to the species in Switzerland and possibly elsewhere. In eastern Europe (Austria, Hungary, Czech Republic and Slovakia) it occurs between 180 and 400m above sea level; in Germany (Harz Mountains) and Switzerland the species grows at higher altitude, 465 to 800m. Even at higher altitudes, however, it does not occur in typical 'alpine' habitats as does *A. gracilis* and *A. lindenbergiana*, but in the warm sunny S-facing valleys on thin calcareous soils. Characteristic associated species are *Athalamia hyalina* (Sommerf.) S.Hatt., *Mannia fragrans* (Balb.) Frye & L.Clark, *Oxymitra incrassata* (Brotero) Sergio & Sim-Sim, *Pleurochaete squarrosa* (Brid.) Lindb., *Riccia ciliifera* Link ex Lindenb., *R. pseudopapillosa* Levier ex Steph.and several flowering plants and lichens. In Arctic regions *A saccata* can occur at much lower altitudes in steppe-tundra vegetation.

A. saccata produces ripe fruit in April and May in central Europe; in Siberia sporophyte production is during the early summer months (June and July).

Asterella saccata has been classed as a 'Vulnerable' species in Europe by Schumacker & Martiny (1995).

Taxonomic notes

When bearing carpocephala *Asterella saccata* is one of the most distinctive species of Marchantiales in Eurasia, with its tall receptacles with pseudoperianths almost parallel to the stalk, combined with its thalli with their very prominent cluster of dense white scale appendages projecting over the apex of the thallus. However, when sterile it is remarkably like *Mannia fragrans* (Balb.) Frye & Clark, as pointed out by Nees (1838) and later authors such as Reimers (1940). When fresh, and for many years in the herbarium (76 years on a specimen from France collected in 1922 by R. Douin (BR)), the plants of *Mannia fragrans* retain their strong very characteristic fragrant smell of cedar oil, whereas *Asterella saccata* has, at most, only a faint fishy smell. In many collections the two species grow intermixed and in the past that was the cause of the long-standing taxonomic confusion between them. Other differences in the thalli are the more erect, less wavy margins of *Asterella saccata* compared to the more inrolled wavy margins of *Mannia fragrans*. Microscopically, in *A. saccata* the dorsal epidermis has thin-walled cells with angular lumens while in *M. fragrans* the cells are thick-walled with rounded lumens. In transverse section the thallus *of A. saccata* has tall clearly-defined air chambers sharply differentiated from the basal tissue; in *Mannia fragrans* the assimilation tissue is spongy with more irregular chambers in several layers, which intergrade into the compact basal tissue (Reimers, 1940).

Reimers (1940) described and illustrated these differences accurately; however, in some other works some features of *A. saccata* have been erroneously described: the assimilation tissue *of A. saccata*, according to Evans (1920) followed by Schuster (1992c) is composed of 2–3 layers of air chambers above the keel; however as shown by Reimers (1940), *A. saccata* has a single layer of narrow tall chambers; the air pores have often been described as having 2–3 rings of cells whereas 1–2 is typical; the involucre according to Evans (1920) is 'entire or more or less sinuate' and according to Schuster (1992c) is 'entire or ± sinuous'; however study of many specimens confirms that in fact the involucre is deeply cleft in two beneath the sporogonium.

Historical and nomenclatural notes

(a) The nomenclature of *Asterella saccata* in Europe has until comparatively recently been confused. Evans (1920) presented the history thoroughly, and demonstrated that the epithet *fragrans*, for over a century used for this plant, had to be rejected in favour of *saccata*. The epithet *fragrans* was first coined by Balbis (1804) as *Marchantia fragrans* based on material he collected in northern Italy; this is the plant now known as *Mannia fragrans* (Balb.) Frye & L.Clark.

Soon after Balbis' discovery, Schleicher collected, near Martigny in Switzerland, a plant he called *Marchantia fragrans*, assuming it to be the same as Balbis'. This plant was soon after described by DeCandolle in 1805, who unfortunately accepted Schleicher's identification and clearly accepted the Balbis name *Marchantia fragrans* for it. This double application of *Marchantia fragrans* to two different entities took many years to untangle. De Candolle cited his name as *Marchantia fragrans* Balb. ex Schleich. cent.3 n.64 but his description clearly describes Schleicher's plant which is an *Asterella*: 'le réceptacle est en forme de cone obtus, divisé en cinq ou six lobes profondes'. He did not directly refer back to Balbis' publication, but his name is an illegitimate homonym of Balbis'.

Wallroth (1815) reinforced this confusion by using *Marchantia fragrans* Balb. for the Swiss plant and he was the first to illustrate Schleicher's material with a very fine plate illustrating the conical carpocephalum and pseudoperianth with a median constriction. Thus the name *fragrans* became firmly linked to the Swiss plant. Meanwhile, in the midst of this confusion, Wahlenberg (1811) described *Marchantia saccata* as a new species from Kamchatka. Wallroth (1815) astutely synonymised *Marchantia saccata* under *M. fragrans*, but this act was ignored by subsequent authors for many years.

Nees (1820) introduced the name *Fimbraria fragrans*, and by reference to descriptions of Weber (1815) and particularly the figure of Wallroth (1815) clearly based his concept on Schleicher's Swiss plant. However he included *Marchantia fragrans* Balb. as a synonym (presumably assuming that it was the same plant) so that *Fimbraria fragrans* (Balb.) Nees must be typified by Balbis' name and type. Many later authors have used the name '*Fimbriaria fragrans* Nees' 1820 as though it were a *nomen novum* for *Marchantia fragrans* Schleich. ex DC., but this cannot be upheld.

Bischoff (1835) also retained the name *Fimbriaria fragrans* Nees, and clearly described and illustrated the Swiss plant; he also followed Nees in citing the Italian plant of Balbis and was not aware that the latter belonged to a different genus. However, Nees (1838) later discovered his own mistake (and that of many earlier authors) and pointed out the erroneous past application of the epithet *fragrans* to two different plants. He now restricted *Fimbriaria fragrans* to Schleicher's plant from Switzerland and pointed out that Balbis' *Marchantia fragrans* was '*Grimaldia fragrans* Balb.'

Both Lindenberg (1829) and Nees (1838) explicitly excluded Wallroth's synonymising of *Marchantia saccata* under *Fimbriaria fragrans*, without explanation, and *Marchantia saccata* was forgotten by European authors for many more years.

Trevisan (1853) made the combination *Hypenantron fragrans*, citing *Fimbriaria fragrans* Nees as basionym. He made no reference to *Marchantia fragrans* of Balbis or DeCandolle. However, it would appear that *Hypenantron fragrans* has to be typified by *Marchantia fragrans* Balb., through *Fimbriaria fragrans* (Balb.) Nees, as neither Trevisan nor Nees clearly excluded the Balbis element. However, he later (Trevisan, 1874) transferred the epithet again, this time to *Asterella* and under *Asterella fragrans* he gave *Marchantia fragrans* Schleich. as basionym. This makes it clear that *Asterella fragrans* Trevis. is based on the Swiss plant described by DeCandolle, and it can therefore stand as a valid *nomen novum* for the Swiss plant. This is the first valid publication of the epithet *fragrans* for the Swiss plant.

Three years later Trevisan (1877) reverted to his adoption of *Hypenantron fragrans*; he also included *Hypenantron umbonatum* and *Hypenantron saccatum* in that publication as independent species, both of which are earlier validly published epithets (1841 and 1811) than *fragrans* which was not validated until 1874 for the Swiss plant.

Lindberg (1872) and Lindberg & Arnell (1889) in their studies of bryophytes of Russia and Siberia found the same taxon and realised that these plants, which they published under the names *Fimbriaria fragrans* and *Asterella fragrans*, were almost certainly the same as *Marchantia saccata* described from Kamchatka. However, they did not take the step of adopting the latter epithet. Many other authors after 1870 also continued to use the epithet *fragrans* for the plant in spite of its proven ambiguity, for example, *Fimbriaria fragrans* was maintained by Dumortier (1874), Massalongo & Carestia (1880), Stephani (1898–1900), Boulay (1904), Müller (1905–1916), Casares-Gil (1919), Meylan (1924), Reimers (1940), Schiffner (1940); and *Asterella fragrans* was used by Trevisan (1874), Massalongo (1886), Breidler (1894), Underwood (1895) and Lindberg & Arnell (1889).

The author who thoroughly investigated this long catalogue of confusion was Evans (1920) whose excellent description and historical account of *Asterella saccata* settled the matter conclusively. A few Europeans up to Schiffner (1940) continued to use the epithet *fragrans*, but since then *A. saccata* has become the universally accepted name.

(b) Grolle (1976: 180) typified *Marchantia saccata* by a 'holotype'. As Wahlenberg (1811) did not designate a type, a lectotype is required. The designation of a 'holotype' by Grolle is now considered as effective lectotypification (Art. 9.8).

(c) The type of *Marchantia umbonata* Wallr. was presumably destroyed in Berlin. Reimers (1940) had studied it however, and confirmed its synonymy with *Fimbriaria fragrans*.

Specimens examined: see Appendix V.

2. Asterella grollei D.G.Long, Bryologist 102: 169, 1999. Type citation: Nepal, Sankhuwasbha District, Nehe Kharka, S. side of Barun Khola, 27° 45'N, 87° 10'E, 3735m, steep eroding calcareous slope of gully below cliffs; on friable soil, 29 Sept. 1991, *Long 20777* (E, holotype; JE, isotype). Type specimen: as above.

Thalli forming yellow-green patches up to 6cm diameter usually mixed with other mosses and Marchantiales, mostly on thin calcareous soils often overlying rocks; when crushed with faint smell of rotten fish. *Vegetative branches* mostly terminal in origin, but also occasionally innovating from ventral branch at apex beneath an archegoniophore; branches broad and flat, moderately leathery (all xeroshoots); 12–20 x 6–10mm, yellow-green above with red-purple margins, conspicuously notched at apex, in transverse section 0.6–1.5mm thick, branches 2.5–5x as broad as thick; midrib broad, flat or channelled, gradually tapering into broad thallus wings. Upper surface flat or concave, margins weakly upturned when moist, becoming inrolled when dry, surface with conspicuous radiating lines above air chambers, air pores raised, visible with x20 lens. Lower surface and older parts of thallus brown-purple. *Dorsal epidermis* cells irregularly rectangular, often rounded at ends, 30–75 x 20–40µm, walls thin to moderately thickened and with distinct trigones at angles; oil cells scattered. *Air pores* raised above epidermal surface, with orifice 10–20µm across; cells in 6–8 rows of 3–4 concentric rings; cells of innermost ring 10–12µm in radial length, 7–20µm wide; cells of outermost ring 15–30µm in radial length, 27–50µm wide. *Assimilation tissue* 0.4–0.9mm thick, 1/2 to 2/3 thickness of thallus, of an upper layer of regular narrow to broad air chambers, these containing a few short free filaments under air pores, and below this a spongy layer with irregular interconnecting air spaces; regular air chambers extending into thallus wings and overlapping obliquely; cells of partitions 25–40µm diameter; oil cells absent. *Basal compact tissue* 0.2–0.8mm thick, less than half thickness of assimilation tissue ; cells irregular in size, 25–40µm in diameter; oil cells absent. *Rhizoids:* smooth rhizoids 12–37µm diameter; pegged rhizoids 12–25µm diameter. *Ventral scales* obliquely elongate-semicircular, with purple body with narrow hyaline curved median side, very large, 1.8–3.0 x 0.85–1.3mm; cells of body rectangular with truncate or acute ends, 70–155 x 27–40µm, walls weakly thickened, becoming shorter and thin-walled in hyaline margin and much longer and narrower at extreme base; margin entire or with a few short blunt

teeth near base of appendage, with numerous obovoid slime papillae, 10–19 on curved (median) side and 3–7 on straight (outer) side; oil cells 6–13, 22–45µm diameter; scale appendages usually 1 occasionally with a second smaller appendage, or appendage unequally bifid; appendages narrowly lanceolate, 600–900 x 100–200µm, quickly narrowing above base, not constricted and 4–7 cells wide at base, margin entire or with a few blunt marginal teeth (in Qinghai material often with numerous blunt teeth); cells similar to those of scale body but up to 75µm broad; apex of a single row of 3–5 elongate cells, slime papillae absent, oil cells absent or 1(–2) near base.

Sexual condition terminal-autoicous (very rarely also par-autoicous); androecia borne on main thallus (appearing lateral to base of archegoniophore), on a terminal half-dichotomy produced when archegoniophore is initiated; most fertile branches with both sexes or occasionally only male or only female; male half-dichotomy continuing vegetative growth; very occasionally also a few ostioles produced proximal to base of archegoniophore. *Androecia* forming a poorly defined low slightly raised rounded cushion, white or reddish, 0.8–1.6 x 0.6–0.8mm, on male-only branches sometimes U-shaped, up to 2.4mm diameter; ostioles conical-cylindric, 250–350 x 100–150µm, surrounded by inconspicuous short reddish scales. *Archegoniophore* borne in apical notch of main branch, quickly becoming pseudo-lateral by elongation of an adjacent half-dichotomy which produces 1(–2) androecia then continues vegetative growth. *Stalk* 5–15.5 x 0.5–0.6mm, rounded in transverse section with low ridges, with rhizoid furrow 180–260µm deep; medullary cells thin-walled, 17–40µm diameter, becoming larger and with slightly thickened walls towards epidermis; epidermal cells smaller, 17–25µm, brown pigmented and thick-walled; stalk naked at base, above with scattered elongate hyaline or purple scales, with a small beard of longer scales at the apex; scales linear, those at apex 1000–2400 x 40–80 µm, for most of length of a single row of elongate cells, in middle part of 2 rows, entire and without oil-cells. *Carpocephalum* when young green, becoming pinkish or brownish-red-tinged when mature, broadly rounded-conical, 3.6–5mm tall x 5–7mm diameter, without differentiated apical dome or boss, almost unlobed but shallowly depressed between immersed sporogonia, conspicuously warted all over with low warts, lower rim crenate with bulging air-chambers; 4–7 sporogonia immersed in lower part of carpocephalum, (rarely two produced from single involucre), directed at 45–60° to stalk. *Involucre* reduced to narrow flap beneath and closely enveloping lower surface of pseudoperianth base and sporogonium, 1.3–1.9mm (?or more) from base to free margin, c 0.6mm wide, with median cleft 250–350µm deep. *Pseudoperianth* borne in lower part of receptacle, 2.3–2.6mm long; lower part globose, completely immersed, closely enveloping sporogonium, 1.3–1.7mm long; upper (lobed) part laterally exserted, compressed especially when young; cells of base rectangular, 110–255 x 27–40µm; lobes usually 10, white or purplish tinged at apex, 1.3–1.7 x 0.3–0.4mm, with conspicuous constriction at insertion, cells elongate with acute ends, 85–180 x 22–37µm, remaining firmly attached at apex, oil cells absent.

Capsule 1.3–1.5mm diameter; cells of urn rectangular, 60–135 x 30–55µm, thin-walled; cells of lid not seen. *Spores* (light microscope) black, 135–160µm diameter. *Spores* (SEM)

Type I: trilete, with large equatorial slit-like apertures at ends of trilete marks; with similar proximal and distal sculpturing, on distal surface with conspicuous wavy ridges which are almost smooth but become papillose towards the equatorial apertures; reticulation and pits absent; equatorial rim narrow but conspicuous, strongly wavy in side view; proximal facets ± flat or somewhat convex, with ornamentation as on distal surface. *Elaters* yellowish, 125–260 x 17–20µm, gradually tapering to rounded ends, bispiral. *Chromosome number* unknown.

Illustrations: Figs. 4.7, 4.8; spores Fig. 3.4.

Distribution and phytogeography (Fig. 4.6).

Asterella grollei is only known from the study-area, from Central and East Nepal and from NW China (Qinghai Province). It appears to be a Sino-Himalayan endemic but it may be a relict species surviving around the fringes of the Tibetan plateau.

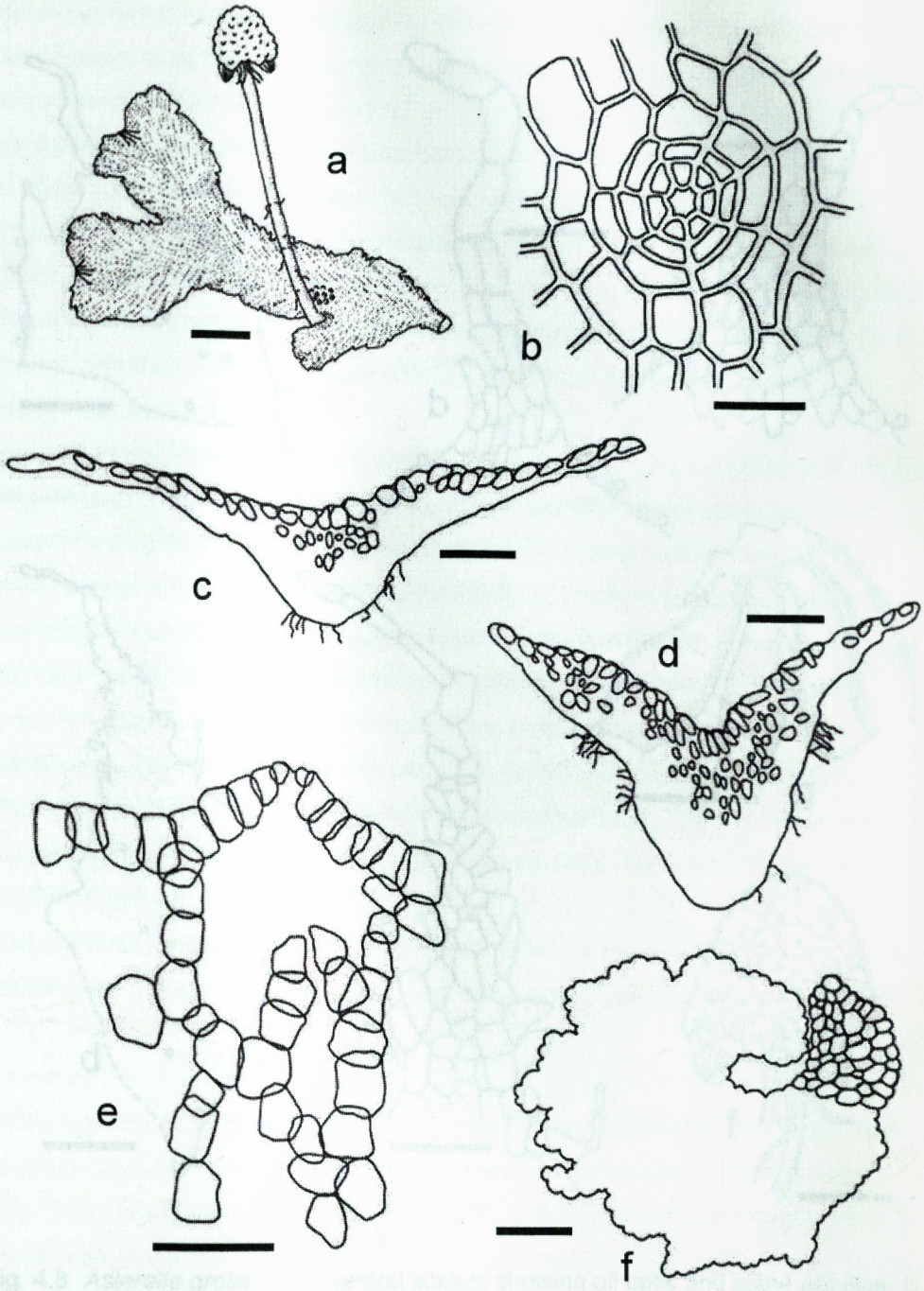

Fig. 4.7 *Asterella grollei* a, thallus showing terminal autoicy, androecium and archegoniophore; b, air pore from dorsal epidermis of thallus; c, d, transverse sections of thallus; e, t.s. of upper assimilation tissue with air pore, air chamber and two free filaments; f, t.s. stalk of archegoniophore. a–f, Nepal, *Long 20777*. Scale bars: a = 5mm; c, d = 1mm; e, f = 100µm; b = 50µm.

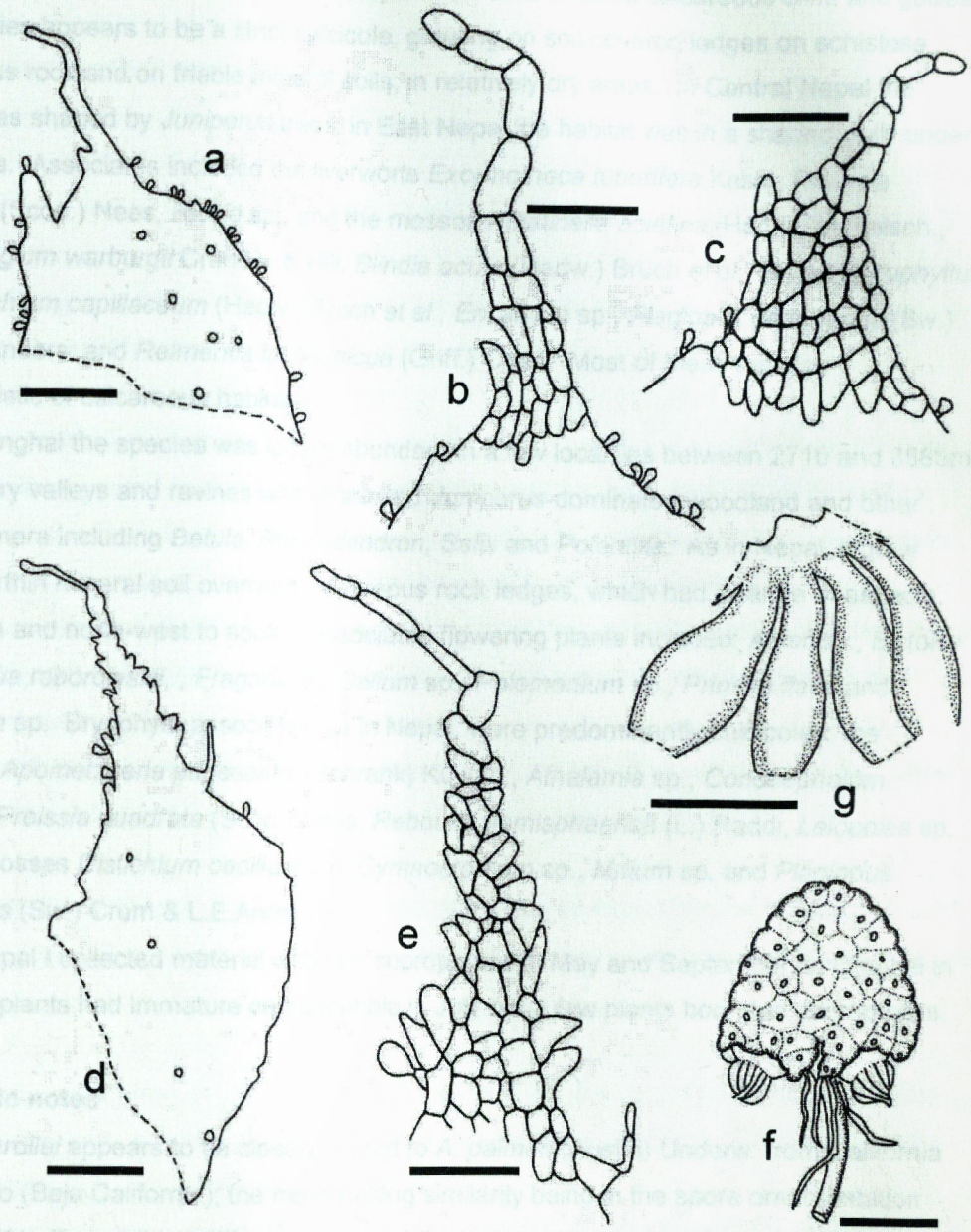

Fig. 4.8 *Asterella grollei* . a, d, ventral scales, showing oil cells and slime papillae; b, c, e, ventral scale appendages; f, mature carpocephalum showing pseudoperianths; g, part of pseudoperianth. a–c, f, g, Nepal, *Long 20777;* d, e, China, *Long 27215.* Scale bars: f = 2mm; g = 1mm; a, d = 0.5mm; b, c, e = 200μm..

Ecology and phenology

In both Nepal and Qinghai *Asterella grollei* has been found at high altitudes around or below the treeline, often associated with dry coniferous forests: in Nepal from 3680 to 3735m, in *Juniperus*/ *Rhododendron campanulatum* forest in Central Nepal, and just above the limit of *Abies* forest in the Barun Khola in East Nepal in an area of steep calcareous cliffs and gullies. The species appears to be a strict calcicole, growing on soil-covered ledges on schistose calcareous rock and on friable mineral soils; in relatively dry areas. In Central Nepal the habitat was shaded by *Juniperus* trees; in East Nepal the habitat was in a shaded gully under large cliffs. Associates included the liverworts *Exormotheca tuberifera* Kash., *Preissia quadrata* (Scop.) Nees, *Riccia* sp., and the mosses *Abietinella abietina* (Hedw.) M.Fleisch., *Anoectangium warburgii* Crundw. & Hill, *Blindia acuta* (Hedw.) Bruch *et al.*, *Bryoerythrophyllum* sp., *Distichium capillaceum* (Hedw.) Bruch *et al.*, *Encalypta* sp., *Plagiopus oederianus* (Sw.) Crum & Anders. and *Reimersia inconspicua* (Griff.) Chen. Most of these are also characteristic of calcareous habitats.

In Qinghai the species was locally abundant in a few localities between 2710 and 3585m, in steep dry valleys and ravines with *Picea* and *Juniperus*-dominated woodland and other woody genera including *Betula, Rhododendron, Salix* and *Potentilla*. As in Nepal, it grew mostly on thin mineral soil overlying calcareous rock ledges, which had a range of aspects from north and north-west to south. Associated flowering plants included: *Aster* sp., *Bistorta* sp., *Cacalia roborowskii, , Fragaria* sp.,*Galium* sp., *Polemonium* sp., *Primula flava* and *Thalictrum* sp. Bryophyte associates, as in Nepal, were predominantly calcicoles: the liverworts *Apometzgeria pubescens* (Schrank) Kuwah., *Athalamia* sp., *Conocephalum conicum*, *Preissia quadrata* (Scop.) Nees, *Reboulia hemisphaerica* (L.) Raddi, *Leiocolea* sp. and the mosses *Distichium capillaceum*, *Gymnostomum* sp., *Mnium* sp. and *Plagiopus oederianus* (Sw.) Crum & L.E.Anderson.

In Nepal I collected material with ripe sporophytes in May and September; in Qinghai in July most plants had immature carpocephala in July but a few plants bore ripe sporophytes.

Taxonomic notes

Asterella grollei appears to be closely related to *A. palmeri* (Austin) Underw. from California and Mexico (Baja California); the most striking similarity being in the spore ornamentation (Long, 1999). Two striking differences are (a) the truly par-autoicous sexual condition of *A. palmeri*, as opposed to the terminal-autoicous condition of *A. grollei* and (b) the presence of an assimilatory strip with air chambers in the stalk of *A. palmeri* which is absent from *A. grollei*. However, other important characters shared by both taxa are: (1) the fact that archegoniophore production does not limit vegetative growth which is continued by a terminal half-dichotomy with the old archegoniophore becoming pseudo-lateral; and (2) the pseudoperianth which is flattened when young and when mature has a distinct constriction at the base of its lobes. The highly-specialised branching pattern found in *A. grollei* and *A. palmeri* has not been described

for *Asterella* previously, and the published descriptions and illustrations of *A. palmeri* (Howe, 1899; Evans 1920, 1923; Frye & Clark (1937–1947)), are inaccurate.

Of other Eurasian species *A. grollei* is most closely allied to *A. saccata*, which also shows the same pseudoperianth characters, but differs in its often par-autoicous sexual condition, in its very different spore ornamentation and the lack of half-dichotomy innovations.

Specimens examined: see Appendix V.

SUBGENUS *WALLICHIANAE*

Asterella Subgenus *Wallichianae* D.G. Long, Lindbergia 26: 43, 2000.

Type: *A. wallichiana* (Lehm. & Lindenb.) Grolle

Thalli xeromorphic or somewhat hygromorphic, aromatic; *vegetative branches* mostly terminal with occasional ventral innovations; *assimilation tissue* of an upper layer of tall broad air chambers and a lower layer of spongy tissue; *ventral scale appendages* 1(2), lanceolate to broadly ovate, acute to obtuse, constricted at base, margin weakly toothed.

Sexual condition dioicous; *androecia* forming cushions; *carpocephalum* rounded-conical, almost unlobed; *involucre* with free margin entire; *pseudoperianth* not compressed or constricted, lobes united at apex, divided to middle.

Capsule lid fragmenting irregularly; *spores* type II, brown or red-brown, coarsely ridged on both surfaces, trilete with conspicuous proximal pole; *elaters* 1(–2)-spiral.

Note: *Asterella wallichiana* is placed in its own subgenus on account of its dioicous sexual condition, brown or red-brown spores with coarsely ridged ornamentation, and mostly 1-spiral elaters.

3. Asterella wallichiana (Lehm. & Lindenb.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Grolle, Ergebnisse des Forschungs-Unternehmens Nepal Himalaya 1: 262, 1966.

Basionym: *Fimbriaria wallichiana* Lehm. & Lindenb., Novarum et Minus Cognitarum Stirpium Pugillus Quartus 4, 1832. Type citation: Crescit in solo calcareo [leg. Wallich]. Type specimens (see note on typification below): [Myanmar] India Oriental, Burma, *Wallich s.n.*(S, herb. Lehmann, **lectotype selected here**; S, herb. Lehmann; LD, herb. Lehmann; STR, herb. Nees, isolectotypes); *Fimbriaria wallichiana* n.sp. Near the images of Pingee, Burma, *Wallich* in Wall. Numer. List 7664 (K-W, isolectotype); Pengee in Ava No. 21 (GL-herb. Scoular, isolectotype); No. 21, Penghee, near the Iriwaddi, Burma, *Wallich* (BM, isolectotype); 'Nepal', *Wallich*, No. 8 [Lindenberg 8659], No. 11 [Lindenberg 8661], (W, herb. Lindenberg, ?isolectotypes); F. *wallichiana* L. & L. Original von Lehmann, aus dem

Meissnerischen Herbar (FH, herb. Jack, isolectotype); *F. wallichiana* L. & L. No. 10, bricks near the Images at Pengee, 10 Jan. 1827, Sir W.J. Hooker 1843 (FH, herb. Taylor, isolectotype); *F. wallichiana*, from Irrowoddy, *Wallich*, December 1834, 21 *Marchantia*, Pingee, ad rupes, Irrowoddy (FH, herb. Taylor, isolectotype); Images at Pengee, 10 Jan. 1827, ex herb. Taylor (NY, isolectotype).

Syn.: *Hypenantron wallichianum* (Lehm. & Lindenb.) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 441, 1877.

Syn.: *Fimbriaria sanguinea* Lehm. & Lindenb., Novarum et Minus Cognitarum Stirpium Pugillus Quartus 5, 1832 Type citation: 'Habitat in India orientali'. Type specimens (see note on typification below): Nepal, *Wallich*, N. 30, herb. Lindenberg 8663-a (W, **lectotype selected here**); Nepal *Wallich* No. 30 ex herb. Hooker (LD, isolectotype); India Oriental, ex herb. Hook. 1831 sub no. 30 (S, herb. Lehmann, isolectotype); Nepalia, [*Wallich*] (STR, herb. Nees, isolectotype); Ind. Or. ex herb. Hook. (FH, herb. Taylor, isolectotype); Nepalia, *Wallich* in Wall. Numer. List 7665 (K-W, isolectotype); **syn. nov.**

Syn.: *Asterella sanguinea* (Lehm. & Lindenb.) Kachroo, Journal of the Hattori Botanical Laboratory 19: 4, 1958.

Syn.: *Fimbriaria viridis* Lehm. & Lindenb., Novarum et Minus Cognitarum Stirpium Pugillus Quartus 6, 1832. Type citation: 'Habitat in Nepalia'. Type specimens (see note on typification below): No. 33 Nepal [*Wallich*] *F. viridis* n.sp., herb. Lindenberg 8665 (W, **lectotype selected here**); India Oriental. Ex herb. Hook. sub no. 33 1831,(S, herb. Lehmann, isolectotype); Nepal, *Wallich* ex herb. Hookeri No. 33 (S, herb. Lehmann, isolectotype); *Fimbriaria viridis* nob., Herbarium Lehmannianum (PC, herb. Montagne, isolectotype); No. 33 Herb. Hook. *F. viridis* n.sp. Nepal L[ehmann] 1831 (LD, herb. Lehmann, isolectotype); Nepal *Wallich* in Wall. Numer. List 7662 (K-W, isolectotype); *Fimbr. viridis*, Nepal (STR, herb. Nees, isolectotype); synonymised by Udar & Jain (1983).

Syn.: *Hypenantron viride* (Lehm. & Lindenb.) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 441, 1877.

Syn.: *Asterella viridis* (Lehm. & Lindenb.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Grolle, Ergebnis Forsch.-Unternehmen Nepal Himalaya 1: 262, 1966.

Syn.: *Fimbriaria marginata* Nees var. *minor* Lehm. & Lindenb., Novarum et Minus Cognitarum Stirpium Pugillus Quartus 3, 1832. Type citation: none. Type specimens (see note on typification below): [Nepal, *Wallich*] No. 22 ex herb. Hook. (S, herb. Lehmann, **lectotype selected here**); Herb. Hook. sub no. 22 e Nepalia (S, JE, isolectotypes); No. 22, (W, herb. Lindenberg 8635, isolectotype); *F. marginata* ß nobis olim Nepalia *Wallich* (LD, herb. Lehmann, isolectotype); Nepalia, *Wallich* in Wall. Numer. List 7663 (K-W, isolectotype); synonymised with *F. nepalensis* by Gottsche, Lindenberg & Nees (1846).

Syn.: *Fimbriaria nepalensis* Taylor, Transactions of the Linnean Society of London 17: 387, 1837. Type citation: In Nepaliae; unde exemplaria solo calcareo affixa misit cl. Wallichius. Specimina etiam sub nomine ex Herbario Hookeriano nuper recepi.' Type specimen:

Nepal, *Wallich*, 1820, with *Bryum coronatum* Schwaeg. (FH, herb. Taylor, **lectotype selected here**); Nepal, Loomphogora, on a brick-wall, leg. *Wallich* ex herb. Spruce (S, H-SOL, isolectotypes); Nepal, [*Wallich*] ex herb. Hooker (E, isolectotype); Nepal, *Wallich*, (S, NY, G-10505, BM, isolectotypes); synonymised by Udar & Jain (1983).

Syn.: *Asterella nepalensis* (Taylor) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Kachroo, Journal of the Hattori Botanical Laboratory 19: 3, 1958.

Syn.: *Hypenantron nepalense* (Taylor) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 440, 1877.

Syn.: *Fimbriaria raddii* Corda ex Nees, Naturgeschichte der Europäischen Lebermoose 4: 289, 1838. Type citation: 'Bei Florenz, (Raddi a. a. O.)'. Type specimen: Prope Fiorent. leg. *Raddi* (STR, **lectotype selected here**); **syn. nov.**

Syn.: *Asterella raddii* (Corda ex Nees) Trevis., Rendiconti del' Istituto Lombardo di Scienze e Lettere Ser. 2, 7: 785, 1874.

Syn.: *Hypenantron raddii* (Corda ex Nees) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 441 1877.

Syn.: *Fimbriaria angusta* Steph., Species Hepaticarum 1: 104, 1899. Type citation: 'India orientalis, Coory [=Coorg] (Lowrie)'. Type specimens: S. India, Coorg, Sept. 1895, *A.E. Lowrie*, comm. Brotherus (G-10430, **lectotype, selected here**; FH, BM isolectotypes); synonymised by Udar & Jain (1983).

Syn.: *Asterella angusta* (Steph.) Mahab. & Bhate, Journal of the University of Bombay 13(5): 5, 1945.

Syn.: *Fimbriaria maculata* Steph., Species Hepaticarum 1: 104, 1899. Type citation: Himalaya, Sansidara. 3000' engl. (Duthie).' Type specimen: Dehra-Dun, Sansidara, 2–3000ft., Dec. 1891, *J.F. Duthie 42-bis* (G-10493, **lectotype, selected here**); ibid. *J.F. Duthie 307* (G-10485, syntype); Sansidhara, below Mussoorie, 3–5000 ft., 10 ix 1895, *J.F. Duthie s.n.* (G-10494, syntype); **syn. nov.**

Syn.: *Asterella maculata* (Steph.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Parihar, University of Allahabad Studies, Botany Section, 1961–1962: 27, 1962.

Syn.: *Hypenantron javanicum* Schiffn., Die Hepaticae der Flora von Buitenzorg 1: 21 (1900). Type citation: 'Java, Tjibodas, ohne nähere Angabe des Standortes von Prof. Goebel 1889 erhalten.' Type specimen: Java, Tjibodas, *Goebel* (FH, **lectotype selected here**); **syn. nov.**

Syn.: *Fimbriaria gollanii* Steph., Species Hepaticarum 6: 13, 1917 '*gollani*'. Type citation: 'Himalaya, Gollan legit.' Type specimens: Dehra Dun, Mohand Pass, Siwalik Range, on rocks, 1600 ft., 14 Oct. 1901, *W. Gollan* in Bryotheca E. Levier 3212 (G-10457, **lectotype selected here**; NY, isolectotype); Dehra Dun, Siwalik Range, damp rocks a little below below Mohan Village, 1480ft., 14 x 1900, *W. Gollan* in Bryotheca E. Levier 3762 (E, G-

10463, syntypes); Dehra Dun, Mohand Pass, Siwalik Range, on rocks, 1600ft., 14 x 1900, *W. Gollan* in Bryotheca E. Levier 3775 (G-10458, syntype); Dehra Dun, Mohand Pass, Siwalik Range, on stone walls, 2500 ft., 27 x 1900, *W. Gollan* in Bryotheca E. Levier 3215 (JE, PC, G-10462 syntypes); ibid. *W. Gollan* in Bryotheca E. Levier 3211 (G-10461, syntype), 3764 (BM, BR, G-10459, syntypes), 3804 (FI, syntype); 3763 (BM, G-10460, syntype); Mussoorie, Arnigadh Estate, on banks at Khetwala, 5500ft., very common, 13 ix 1900, *W. Gollan* in Bryotheca E. Levier 3878 (BM, syntype); ibid. 3880 (JE, syntype); synonymised by Udar & Jain (1983).

Syn.: *Asterella gollanii* (Steph.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Parihar, University of Allahabad Studies, Botany Section, 1961–1962: 27, 1962.

Syn.: *Fimbriaria indica* Steph., Species Hepaticarum 6: 14, 1917. Type citation: 'India orientalis, Mysore. (Gollan legit.)'. Type specimens: Mysore (Ind. Mer.), Bangmai, Hassan District, 5 Sept. 1903 leg. *Inayat Khan*, ex hb. W. Gollan in Bryotheca E. Levier 4515 (G-10476, **lectotype selected here**); Mysore (Ind. Mer.), Suklespur (Hassan distr.), 5 ix 1903, leg. *Inayat Khan* ex hb. W. Gollan in Bryotheca E. Levier 4520 (G-10474, syntype); **syn. nov.**

Syn.: *Asterella indica* (Steph.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Parihar, University of Allahabad Studies, Botany Section, 1961–1962: 27, 1962.

Syn.: *Fimbriaria mescarana* Steph., Species Hepaticarum 6: 15, 1917. Type citation: 'India orientalis. (Pfleiderer legit.)' Type specimen: [India, Karnataka] Coorg (SW India) prope Mescara [=Mercara], Oct. 1906, *J. Pfleiderer* in Bryotheca E. Levier 5142 (G-10495, **lectotype selected here**; FI, isolectotype).; synonymised by Udar & Jain (1983).

Syn.: *Asterella mescarana* (Steph.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Parihar, University of Allahabad Studies, Botany Section, 1961–1962: 28, 1962 '*mercarana*'.

Syn.: *Fimbriaria levispora* Steph., Species Hepaticarum 6: 15, 1917. Type citation: 'Philippinae Insulae. Luzon. (Merrill legit.)'. Type specimen: Philippines, Luzon, Bataan Prov., on rocks along streams, April 1907, *H.M. Curran 6533* (G-15227, **lectotype selected here**, BM, JE, NY, isolectotypes); **syn. nov.**

Syn.: *Asterella levispora* (Steph.) H.A.Mill., Phytologia 47: 320, 1981.

Syn.: *Fimbriaria reflexa* Herzog, in Handel-Mazzetti, Symbolae Sinicae 5: 4, 1930. Type citation: 'S. [Sichuan]: Schotterwände der wtp. St. bei Beidjeho im Becken von Yenyüen, Kalk, 2500m, 15.v.1914 (2237)'. Type specimen: Prov. Setschwan austro-occid.: in altiplanitiei ad oppidum Yenyüen regione calide temperata, ad parietas glareae pr. vic. Beidjeho, substr. calceo, alt. 2500m, 15.v.1914, *Handel-Mazzetti* (Diar. Nr. 449) No. 2237 (JE, **lectotype selected here**; W, WU, isolectotypes); **syn. nov.**

Syn.: *Asterella reflexa* (Herzog) P.C.Chen *comb. inval.* [see note 431 in Piippo (1990)].

Syn.: *Fimbriaria angusta* Steph. var. *macrolepis* Herzog, in Handel-Mazzetti, Symbolae Sinicae 5: 3, 1930. Type citation: Yunnan: In der wtp. St. bei Yünnanfu, 1900–1950m, an einer Sandsteinwand zwischen Sidian und Dolo, 19.ii.1914, (235) und an Kanaldämmen bei Butji, 6.iii.1914 (1978).' Type specimens: Yünnan, prope urbem Yünnanfu, in regionis calide temperatae limo humido ad aggeres canalorum pr. vic. Butji, substr. calcifero, alt. 1900m, 6.3.1914, *Handel-Mazzetti* (Diar. N. 88) Nr. 1978 (JE, **lectotype, selected here**; E, W, WU, isolectotypes); Yünnan, prope urbem Yünnanfu, in regionis calide temperatae, rupe abrupta inter vicos Sidian et Dolo, substr. arenaceo, alt. 1950m, 19.2.1914, *Handel-Mazzetti* (Diar. nr.43) Nr. 235 (E, S, W, WU, syntypes); **syn. nov.**

Syn.: *Asterella angusta* (Steph.) Mahab. & Bhate var. *macrolepis* (Herzog) Piippo, Journal of the Hattori Botanical Laboratory 68: 133, 1990.

?Syn.: *Asterella angusta* (Steph.) Mahab. & Bhate var. *jamesii* Joshi & Birardar, Journal of the Hattori Botanical Laboratory 56: 49, 1984, *nom. inval.* (Art. 36.1). Original material: not indicated.

Syn.: *Fimbriaria gangetica* Kashyap, Liverworts of the Western Himalayas and the Panjab Plain, 1 (Supplement): 5, 1932. Type citation: Garhwal, near Gaurikund; Pipal Koti; Bhuki; common in the Bhagiratha valley above Bhatwari.' Type specimen: *n.v.*; synonymised by Udar & Jain (1983).

Syn.: *Asterella gangetica* (Kashyap) Parihar, University of Allahabad Studies, Botany Section, 1961–1962: 27, 1962.

Syn.: *Fimbriaria mysorensis* R.S.Chopra, Proceedings of the Indian Academy of Sciences 7B: 241, 1938. Type citation: 'Mysore, 1913 (Buttler), 75.' Type specimen: *n.v.*; synonymised by Udar & Jain (1983).

Syn.: *Asterella mysorensis* (R.S.Chopra) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 9, 1954, *comb. inval.* Art. 33.2] ex Kachroo & Bapna, Journal of the Indian Botanical Society 56: 75, 1977.

Syn.: *Fimbriaria liukiuensis* Horik., Journal of Science of the Hiroshima University Ser. B, Div. 2, 1: 55, 1931. Type citation: 'Liuku: Shuri, Insl. Okinawa (Y. Horikawa, no. 2552, Dec. 1930–type)'. Type specimen: Japan, Ryukyu, Isl. Okinawa, Shuri, 30.xii.1930, *Y. Horikawa 2552* (HIRO, **holotype**); **syn. nov.**

Syn.: *Asterella liukiuensis* (Horik.) Horik., Hikobia 1: 79, 1951.

Syn.: *Fimbriaria monospiris* Horik., Journal of Science of the Hiroshima University Ser. B, Div. 2, 2: 113, 1934. Type citation: 'Formosa: Mt. Chipon (Miharashi-Kiriyama), prov. Taito (Y. Horikawa, no. 10455–Typus, Dec. 1932).' Type specimen: Taiwan, Prov. Taito, Mt Chipon, Miharashi-Kiriyama, 30 xii 1932, *Y. Horikawa 10455* (HIRO, **holotype**); **syn. nov.**

Syn.: *Asterella monospiris* (Horik.) Horik., Hikobia 1: 79, 1951.

Description

Thalli forming large patches 15–30cm diameter or more, forming closely intermingled greyish-green patches with new shoots growing over old ones, often on rocks and walls, sometimes

rheophytic; with fishy smell when crushed. *Vegetative branches* mostly terminal (though often little-branched), old parts becoming yellow then brown and decaying; ventral branches occasional arising from narrow stipitate base from ventral surface of older parts of thallus (more frequent when plants drought-stressed), apical innovations occasional; branches somewhat hygromorphic to xeromorphic, somewhat leathery in texture. Normal somewhat hygromorphic current year's shoots long and narrow linear, somewhat undulate, parallel-sided, without constrictions, 1.2–2.5cm long, 1.7–4.5(–6)mm broad, bright green above, sometimes with purple border, weakly notched at apex with tips of scale appendages recurved over growing point; in transverse section 0.8–1.5mm thick, 3–4 x as broad as thick, midrib inconspicuous. Upper surface flat or slightly concave, without median groove; margins undulate, not reflexed when dry, surface without bulges over air chambers but with air pores visible as dots under a lens. Lower surface green or red, especially at margins. Xeroshoots sometimes produced seasonally by ventral branching or apical innovations; shorter and much narrower than normal shoots, strongly red-pigmented and with stout midrib and narrow wings which become reflexed on drying. *Dorsal epidermis* cells irregularly rectangular, 25–80 x 20–50µm, wall slightly thickened and with small trigones at angles; oil cells scattered. *Air pores* prominent, conical, with orifice 15–35µm, with cells in 6–8 rows of 2–3 rings of transversely elongated little-curved cells; innermost cells 7–12µm in radial length, 12–25µm wide; outer cells 10–20µm in radial length, 20–50µm wide. *Assimilation tissue* 250–500µm thick, 1/4 to 1/3 thickness of thallus at midrib, of a single upper layer of broad, tall air chambers overlying a spongy layer of smaller irregular air chambers; upper chambers with free filaments 2–4 cells long below pores, cells of partitions 25–40µm diameter; oil cells few. *Basal compact tissue* 550–1000µm thick, about twice as thick as assimilation tissue, colourless but with broad central band of red cells showing ring-like pits; cells 20–35µm diameter; oil cells numerous. *Rhizoids*: smooth rhizoids 15–25µm diameter; pegged rhizoids 7–25µm diameter. *Ventral scales* asymmetrically semi-ovate with decurrent base on adaxial side; body dark red with paler marginal band, 750–1300 x 450–700µm; median cells of body rectangular with pointed ends, 50–145 x 20–30µm, towards margin shorter and thin-walled, in decurrent base much longer and narrower; margins entire and with 1–2 slime papillae on upper part of straight (abaxial) margin; oil-cells 1–6 in body, 32–50µm diameter; scale appendage 1(–2), lanceolate to broadly ovate, 600–900 x 140–460µm, apex acute to obtuse, base slightly to strongly constricted, 5–7 cells wide, margin usually with 1(–2) linear or lanceolate acute 1–4-celled marginal teeth bearing a terminal slime papilla, or with a single large ovate to lanceolate lobe on one side; cells broad, 50–135 x 22–55µm; oil-cells absent or 1–2 in appendage.

Sexual condition dioicous with male and female plants mostly growing as separate patches, occasionally intermixed, vegetatively similar; androecia produced terminally but not limiting growth of main shoot and becoming dorsal as growth continues; archegoniophore terminal on main branch of female plant. *Androecia* in conspicuous raised green or red-purple cushions, 3.5–9 x 1–1.4mm; rounded to linear, often V-shaped or Y-shaped at a branch; ostioles rounded-conical, 80–150 x 120–200µm, without scales. *Archegoniophore* terminating

growth of female branch; vegetative growth of female plant continuing by older terminal branches and/ or by ventral shoots. *Stalk* whitish-green when young, becoming purplish or blackish, short, 1.5–5 x 0.35–0.45mm, in transverse section rounded with shallow rhizoid furrow 0.08–0.15mm deep; medullary cells 12.5–30µm diameter, with slightly thickened walls; epidermal cells slightly smaller; stalk with a few caducous scales at base, scattered median scales and an inconspicuous beard at apex; median scales linear-lanceolate, 0.5–1.45mm long, basal part 60–150µm broad, 2–4 cells broad; margin entire; occasionally with a single oil-cell. *Carpocephalum* when young subglobose, when mature broadly hemispherical to somewhat flattened and cushion-shaped, pale green or pinkish tinged, 4–6mm diameter (including pseudoperianths), shallowly 2–5-lobed, the lobes spreading at an angle of 60–90° to stalk; the broad crown without any differentiated central dome, uniformly warted on crown and lobes with weakly protruding air-chambers; lobes with sinuate-crenate distal margin. *Involucre* conspicuous, 1–1.2mm broad from free margin to base of stalk, margin sinuate-crenate but not cleft, sometimes with a few small air chambers along free margin. *Pseudoperianth* white or pinkish, 2–2.3mm long; basal cup 0.8–1.05mm long; cells of base rectangular, 70–120 x 30–75µm; lobes 7–12, lanceolate, 1.2–1.4 x 0.3–0.5mm, strongly united at apex into short tubular beak; lobe cells 70–160 x 18–40µm, somewhat thick-walled, at apex much shorter; oil cells 4–10 in each lobe, absent from base or with a few in upper part.

Capsule dark brown, 1.1–1.2mm diameter; cells of urn rectangular, 70–120 x 25–55µm; cells of lid subquadrate, with large trigones. *Spores* (light microscope) brown to red-brown, 40–105µm diameter. *Spores* (SEM) Type II: trilete, without equatorial apertures, with similar proximal and distal ornamentation; distal surface with coarse, shallow to deep, wavy ridges to almost smooth, finely striate or papillose, without reticulation; proximal facets ± flat, not bulging, with ornamentation as on distal surface; trilete ridges rounded; equatorial rim narrow and weakly defined, wavy in side view. *Elaters* 135–260 x 12–17µm, mostly 1-spiral, larger ones sometimes 2-spiral in median part. *Chromosome number n*=9 (newly reported here).

Illustrations: Fig. 4.9; spores Figs. 3.5, 3.6, 3.7.

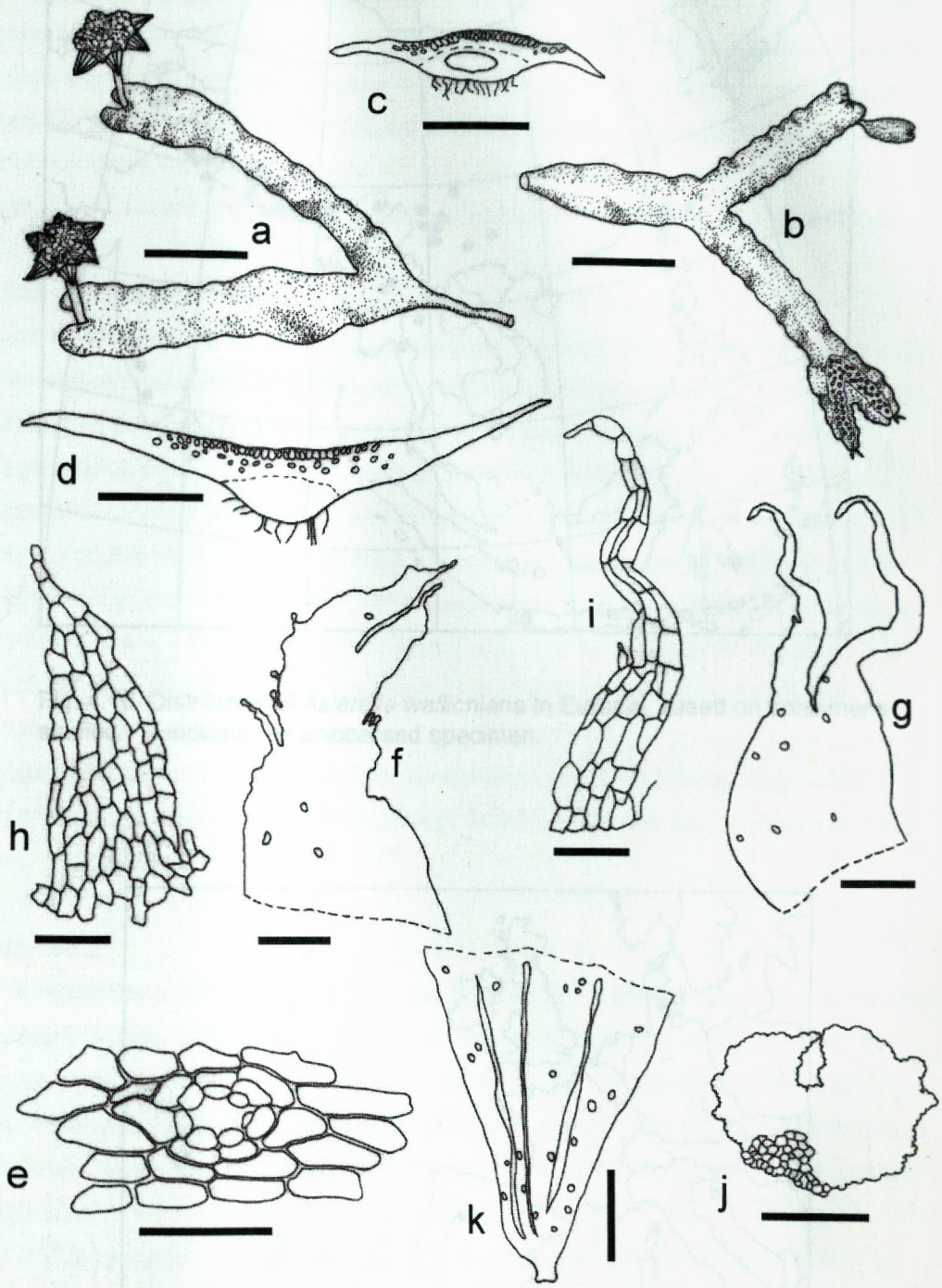

Fig. 4.9 *Asterella wallichiana*. a, female plant with two carpocephala; b, male plant with bifurcate androecium; c, d, t.s. thallus; e, air pore; f, g, ventral scales showing oil cells; h, i, ventral scale appendages; j, t.s. stalk of carpocephalum; k, part of pseudoperianth. a, c, e, Nepal, *Long 21197*; b, Nepal, *Long 20330*; f, h, Japan, Iriomote, *Long 24920*; g, i, China, Yunnan, *Long 19123*; d, j, k, Nepal, *Long 21255*. Scale bars: a, b = 5mm; c, d = 1mm; k = 400μm; f, g, j = 200μm; e, h, i = 100μm.

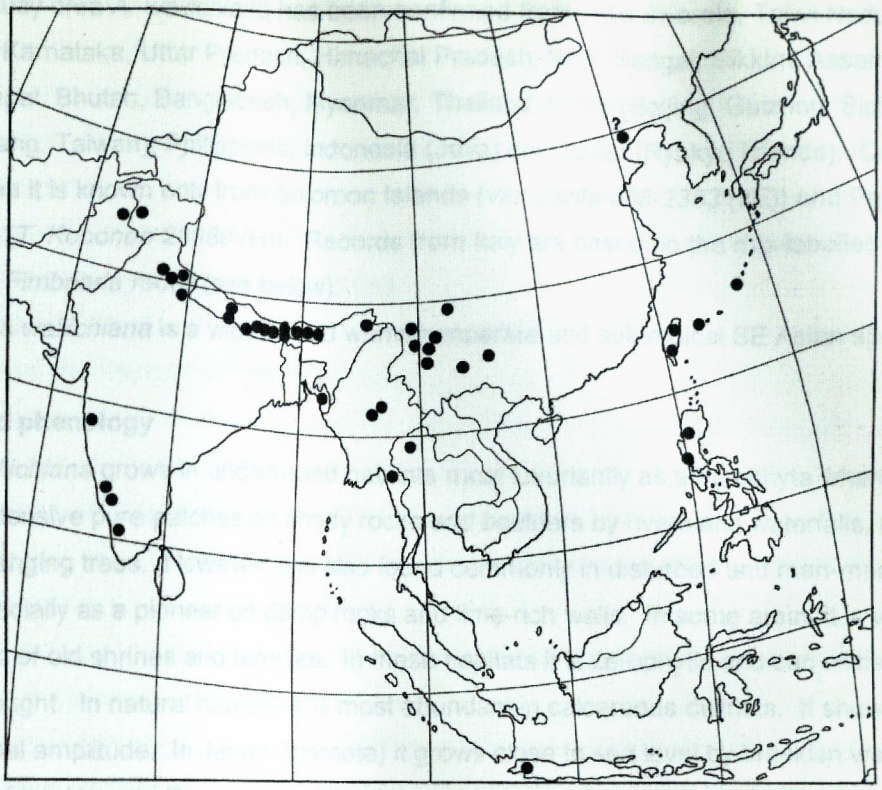

Fig. 4.10 Distribution of *Asterella wallichiana* in Eurasia, based on specimens studied. ? indicates an unlocalised specimen.

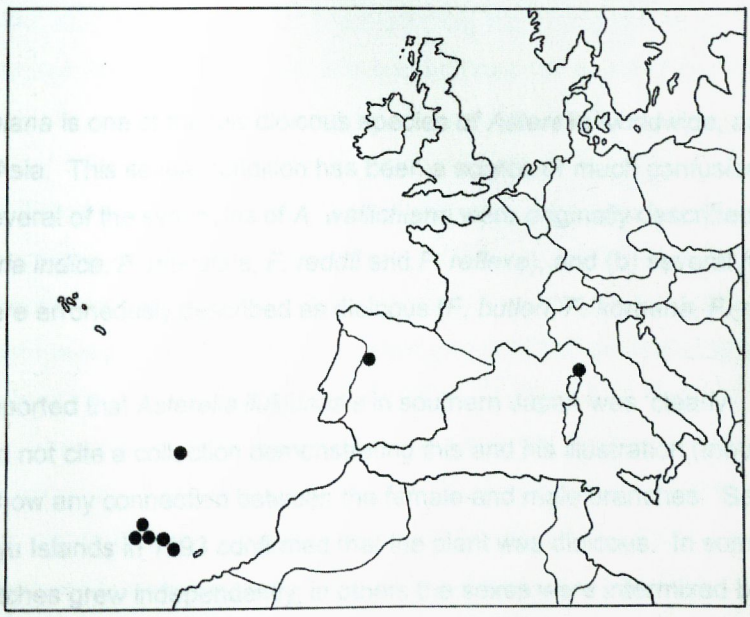

Fig. 4.11 Distribution of *Asterella africana* in Eurasia, based on specimens studied.

Distribution and phytogeography (Fig. 4.10).

Within the study area *A. wallichiana* has been confirmed from India, (Kerala, Tamil Nadu, Maharastra, Karnataka, Uttar Pradesh, Himachal Pradesh, West Bengal, Sikkim, Assam); Pakistan, Nepal, Bhutan, Bangladesh, Myanmar, Thailand, China (Beijing, Guizhou, Sichuan, Yunnan, Xizang, Taiwan); Philippines, Indonesia (Java) and Japan (Ryukyu Islands). Outside the study area it is known only from Solomon Islands (*van Zanten 68-2383* (JE)) and Papua New Guinea (*T. Koponen 28980* (H)). Records from Italy are based on the mis-labelled type specimen of *Fimbriaria raddii* (see below).

Asterella wallichiana is a widespread warm-temperate and subtropical SE Asian species.

Ecology and phenology

Asterella wallichiana grows in undisturbed habitats most luxuriantly as a rheophyte where it can form very extensive pure patches on shady rocks and boulders by rivers and waterfalls, usually under overhanging trees. However, it is also found commonly in disturbed and man-made habitats especially as a pioneer on damp rocks and lime-rich walls. In some areas it is very characteristic of old shrines and temples. In these habitats it is xerophytic and can withstand seasonal drought. In natural habitats it is most abundant in calcareous districts. It shows a wide altitudinal amplitude. In Japan (Iriomote) it grows close to sea level by brackish water in the estuary of the Urauchi River. In the Himalayas it occurs in the subtropical and warm temperate zones, from 490 to 1620m in East Nepal, up to 2700m in Bhutan. In Yunnan it occurs between 2140 and 3120m.

Although dioicous, male and female colonies are often mixed and carpocephala and sporophytes common. Single-sex patches however may be extensive, up to a metre or more in diameter.

Taxonomic notes

Sexuality. *A. wallichiana* is one of the few dioicous species of *Asterella* worldwide, and the only dioicous species in Asia. This sexual condition has been a source of much confusion in the past, because (a) several of the synonyms of *A. wallichiana* were originally described as monoicous (*Fimbriaria indica*, *F. maculata*, *F. raddii* and *F. reflexa*), and (b) several monoicous *Asterella* species were erroneously described as dioicous (*F. butleri*, *F. koreana*, *F. reticulata*, *F. yoshinagana*).

Inoue (1976) reported that *Asterella liukiuensis* in southern Japan was 'clearly monoecious'. He did not cite a collection demonstrating this and his illustration (Inoue 1976, plate 70) does not show any connection between the female and male branches. Searching in the field in the Ryukyu Islands in 1993 confirmed that the plant was dioicous. In some colonies male and female patches grew independently; in others the sexes were intermixed but no definite connection was established between them. The question remains open therefore, as to whether *A. wallichiana* in Japan may on occasion be monoicous as well as dioicous.

Infraspecific variation

A. wallichiana, as well as being the most widespread Asiatic species, is also the most variable and it is not surprising that some variants have been described as species. The following characters show variation which is at least partly correlated with geography:

a. ventral scale appendage shape: Himalayan and Chinese collections have narrower acute scale appendages; those from Iriomote have broader often obtuse scale appendages; those from Okinawa and Taiwan are variable in these characters, for example the type of *A. monospiris* has narrow lanceolate appendages.

b. length of stalk of carpocephalum: 2–5mm in Sino-Himalayan specimens, shorter in specimens from the Ryukyu Islands (1.5–3mm).

c. carpocephalum wartiness: carpocephala can vary from almost smooth to moderately warted.

d. spore size varies from 44–68µm (Iriomote), 49–75µm (Taiwan), 60–68µm (Okinawa), 49–98µm (Himalaya), 65–84µm (China), 58–72µm (Indo-china) and 53–62µm (Philippines and Solomon Islands). In general spores from island populations are smaller than those of continental specimens.

e. spore colour: this correlates with size, the larger spores of continental specimens are brown while those of the island populations are red-brown.

Although there do appear to be some differences between continental and island populations which correlate, most notably spore size and colour, it is not possible yet to define any clear discontinuities as so many characters overlap; for example though Taiwanese and Japanese specimens have similar spores, their ventral scale appendages are different: those from Taiwan are more like those of continental specimens. The plants from Iriomote Island, Southern Japan are quite distinctive and may represent an isolated clone which differs from specimens from both Okinawa to the east and Taiwan to the west.

Until more detailed studies are carried out (incorporating if possible molecular studies) it is considered premature to subdivide *A. wallichiana* into sibling species and it is treated here in its broadest sense.

Historical and nomenclatural notes

Correct name and synonyms.

Of all species of *Asterella* worldwide, *A. wallichiana* as treated here in a broad sense, has the greatest number of synonyms. The oldest names were four published simultaneously by Lehmann and Lindenberg (1832), viz. *Fimbriaria wallichiana*, *F. sanguinea*, *F. viridis* and *F. marginata* var. *minor*. However the most widely used name over the past century for the species in the Indian region has been *Fimbriaria angusta* Steph. published in 1899, *e.g.* by Kashyap (1916, 1929–1934); Chopra (1938b), Mahabale & Bhate (1945). In other parts of its range the species has been known under other names *e.g. F. liukiuensis* in Japan, *F. monospiris* in Taiwan, *F. levispora* in the Philippines, *A. nepalensis* in Nepal *etc.* Some recent authors have used the name *A. sanguinea* (*e.g.* Noguchi *et al.*, 1966; Grolle, 1966; Long & Grolle, 1990).

A choice had to be made between *A. sanguinea*, *A. viridis* and *A. wallichiana* for this species. The last has been chosen for three reasons: (1) seven of the synonyms were already synonymised by Udar & Jain (1983) under *A. wallichiana* (including *F. viridis* but not *A. sanguinea*), (b) the name *F. sanguinea* has been widely misapplied in Asia to what is correctly called *A. multiflora* (Steph.) Kachroo and (c) *F. wallichiana* is based on better type material than the other two.

Types of Lehmann & Lindenberg names.

As the earliest name for this species, *Fimbriaria wallichiana* Lehm. & Lindenb. was described along with the three other synonyms mentioned above, in Lehmann's *Pugillus Plantarum* (1832), and as the information in the protologues of each of these is rather scanty, it is important to consider (a) the origin of the material studied by Lehmann & Lindenberg and (b) other external evidence as to the precise origin of the original material of the four taxa.

Lehmann (1832: iii–vi) in the *Praemonenda* to this volume profusely thanked William Jackson Hooker, Professor of Botany in Glasgow, for his kindness during his (Lehmann's) visit to Glasgow in the summer of 1830. Lehmann was allowed to study the the liverworts in Hooker's herbarium, and was given one specimen of every species represented by more than one example. Hence the *Wallich* specimens, though initially given to Hooker to study and write up, were actually investigated and described by Lehmann.

Lehmann also acknowledged the help and co-operation of J.B.G. Lindenberg in the preparation of the work. Lindenberg was Prefect of the district of Bergedorf near Hamburg and Lehmann described him as 'my nearest neighbour'. In the final paragraph of the *Praemonenda* the active collaboration of Lindenberg is further implied as Lehmann uses 'we' and 'to us' in discussing the work.

More precise information on the original *Wallich* material of the four taxa is given in Gottsche, Lindenberg & Nees's *Synopsis Hepaticarum* (1846), as follows:

(i) *F. wallichiana*: 'Crescit solo calcareo in Burma Indiae orientalis (Wallich in Hb. soc. Angl., Hook. hb. n. 8. 10. 11. Hooker in Hb. L., Lg. et N.); in terra nuda montium Nilagiricorum (Perrottet in Hb. M.).' (Gottsche, Lindenberg & Nees 1846: 566). Thus the original material used by Lehmann and Lindenberg in 1832 had probably been seen in the Herbarium of the East India Company [now K-W], Hooker's herbarium [now BM], herb. Lehmann [now in S, LD] and herb. Lindenberg [now W]. The original locality is Myanmar (Burma). The *Perrottet* material was probably not seen until after 1832.

Udar & Jain (1983) cited a type and isotype of *Fimbriaria wallichiana* in the Naturhistorisches Museum, Wien, but did not specify a particular specimen. It is clear, both from material in Lehmann's herbarium (LD, S) and from the details given in Gottsche, Lindenberg & Nees (1846) that the specific epithet was intended to apply to Wallich's plant from Myanmar. The material in Lindenberg's herbarium in Vienna is in fact labelled 'Nepal' which may be a labelling error but creates some doubt about the provenance of Lindenberg's

material. The specimen in S selected here as lectotype is clearly labelled 'Burma' and bears sporophytes with ripe spores making it the most suitable choice.

(ii) *F. sanguinea*: 'Habitat in India orientali (Wallich in Hb. Hk. n. 30, L. et N.)' (Gottsche, Lindenberg & Nees 1846: 567). Thus the original locality is uncertain, and the original specimens studied were in the herbaria of Hooker, Lehmann and Nees. Nees, however, may not have received specimens until after 1832.

(iii) *F. viridis*: 'Habitat in Nepalia (Wallich in Hb. Hk. n. 33, L., Lg. et N.).' (Gottsche, Lindenberg & Nees 1846: 568). Thus the original locality is Nepal, and the original specimens studied were in the herbaria of Hooker, Lehmann, Lindenberg and Nees. Nees, however, may not have received specimens until after 1832.

(iv) *F. marginata* var. *minor*: 'Habitat in Nepalia, ubi solo calcareo legit Wallich. (Hb. Taylor et Hooker, L., Lg., G. et N.)' (Gottsche, Lindenberg & Nees 1846: 560, sub. *Fimbriaria nepalensis*). Thus Gottsche, Lindenberg and Nees considered that var. *marginata* was the same as Taylor's *Fimbriaria nepalensis* (published in 1837); the original locality is Nepal and the original specimens studied were in the herbaria of Taylor, Hooker, Lehmann, Lindenberg and Nees. Taylor and Nees, however, may not have received specimens until after 1832.

The origin of *Fimbriaria raddii*.

Fimbriaria raddii Corda ex Nees. This species was described from 'Bei Florenz', Italy, collected by Raddi. In its original detailed description, Nees (1838: 292) commented that *F. raddii* was so close to *F. nepalensis* (itself probably synonymous with *Fimbriaria wallichiana* L. & L.) that they might be considered as identical except for the provenance and the 3–4 times longer peduncle of the latter species. Stephani (1899) noted that he could not locate a type in the Berlin Museum, but that from Nees' description, was in no doubt that *F. raddii* was unique amongst the European species. Müller (1951–1958) suggested that it was a modification of *A. saccata*.

Study of the spores of the type of *F. raddii* (located by Riclef Grolle in STR) and a wide range of material of *A. wallichiana* confirms that they are synonyms. Because *A. wallichiana* has never been collected or reported since from Europe or the Middle East, Raddi's specimen must have been mislabelled and probably derived from Asiatic material collected by Wallich.

Later synonyms.

Stephani (1899, 1917), as well as accepting all the earlier names, re-described *A. wallichiana* in the *Species Hepaticarum* no fewer than six times: as *Fimbriaria angusta*, *F. maculata*, *F. gollanii*, *F. indica*, *F. mescarana* and *F. levispora*, from various parts of India and the Philippines. Thereafter it was described again in 1900 by Schiffner from Java and by Herzog in 1916 twice from China.

Kashyap was the first non-European bryologist to study *Fimbriaria* in Asia, and more importantly the first to record observations made on fresh material in the field. He correctly recognised that there was only one dioicous species in the NW Himalaya and used the name

F. angusta Steph. for it. He was not, however, able to equate the earlier synonyms of Stephani and Lehmann & Lindenberg and Taylor with this plant as he had no access to type material and the earlier descriptions were very inadequate.

The result has been that the one widespread dioicous *Asterella* species in East Asia has been widely misunderstood because of the plethora of different names applied to it, the poor descriptions of these (*e.g.* some synonyms were described as monoicous), and the lack of study of living plants. This confusion has persisted until very recent times, and *A. wallichiana* has been reported to the present day under a variety of names: *A. angusta* by Joshi & Birardar (1984) and Piippo (1990); *A. angusta* var. *macrolepis* by Piippo (1990); *A. nepalensis* by Grolle (1966); *A. reflexa* by Piippo (1990); *A. sanguinea* by Grolle (1966), Noguchi *et al.* (1966) and Long & Grolle (1990); *A. viridis* by Grolle (1966) and Piippo (1990); *A. wallichiana* by Grolle (1966) and Gupta & Udar (1986); *A. levispora* by Miller (1981), Tan & Engel (1986); *A. liukiuensis* by Inoue (1976); *A. monospiris* by Seki (1964), Kuo & Chiang (1988), Piippo (1990). As a result, the very wide distribution of this species in E Asia has not been recognised before.

Specimens examined: see Appendix V.

SUBGENUS *ASTERELLA*

Asterella subgenus *Asterella*

Type: *A. tenella* (L.) P.Beauv.

Thalli hygromorphic, sometimes with seasonal xeroshoots, usually strongly aromatic; *vegetative branches* terminal and ventral; *assimilation tissue* of one to several layers of spreading, overlapping air chambers; *ventral scale appendages* single, rarely two, oblong to lanceolate, rarely ovate, acute to obtuse, constricted or not at base, margins entire, rarely toothed.

Sexual condition par-autoicous, ventral-autoicous or terminal-autoicous; *androecia* of scattered ostioles or weakly cushion-forming; *carpocephalum* hemispheric to almost flat, rarely conical, lobes shallow to deep; *involucre* with free margin entire or cleft; *pseudoperianth* not compressed or constricted, lobes free at apex, divided approximately to half.

Capsule lid fragmenting irregularly; *spores* of type VII, yellow or orange-yellow, regularly areolate distally, proximally dissimilar, trilete, with distinct proximal pole; *elaters* 2- or 3-spiral.

This subgenus is defined by its hygromorphic thalli, free pseudoperianth lobes and yellow spores with dissimilar proximal and distal areolate sculpturing. Section *Asterella*, of which the north American *A. tenella* is the only representative, is not known in the study-area.

SECTION *BRACHYBLEPHARIS*

Asterella section *Brachyblepharis* (Gottsche *et al.*) D.G.Long, Journal of Bryology 22:113, 2000.

Basionym: *Fimbriaria* subgenus *Brachyblepharis* Gottsche *et al.*, Synopsis Hepaticarum 569 (1846).

Syn.: *Asterella* subgenus *Brachyblepharis* (Gottsche *et al.*) Grolle, Feddes Repertorium 87: 246, 1976.

Type: *A. leptophylla* (Mont.) Grolle

Characters as for subgenus, but with carpocephalum flat or umbrella-shaped, not hemispheric when mature; involucre with entire free margin; elaters mostly 2-spiral.

4. Asterella africana (Mont.) A.Evans, Contributions from the United States National Herbarium 20: 250, 1920.

Basionym: *Fimbriaria africana* Mont., in Webb & Berthelot, Histoire naturelle des Iles Canaries 3 (2, sect. ult.): 61, 1840. Type citation: 'In insula Canaria a clarr. Webb et Berthelot detecta.' Type specimen: Canary Islands, *Webb & Berthelot s.n.* (PC, lectotype [herb. Montagne]; FI, G, PR, S, isolectotypes); lectotype designated by Grolle (1976).

Syn.: *Rhacotheca azorica* Bisch. in Seubert, Flora Azorica 12, 1844. Type citation: 'In insulis azoricis'; Type specimen: *n.v.*; synonymised by Leitgeb (1881).

Syn.: *Hypenantron africanum* (Mont.) Kuntze, Revisio generum plantarum 1: 89, 1891.

Syn.: *Fimbriaria intermedia* Mont., Annales des sciences naturelles: botanique, Sér. 10: 334, 1838, *nom. inval.* (Art. 34.1). Type citation: Algeria, *Roussel*. Original material (?): Algeria, ex herb. Montagne (BM, G); synonymised by Montagne (1840).

Description

Thalli forming patches up to 6(–10)cm diameter, all shoots hygromorphic, thin and delicate (hygroshoots), with strong fishy smell when bruised. *Vegetative branches* of terminal dichotomies and occasional ventral intercalary branches with stipitate base. Xeromorphic branches and tubers unknown. Branches oblong to heart-shaped, 8–10mm long, 3.5–8mm broad, broadest towards apex, pale green above, sometimes pinkish along margins, apices notched; in transverse section thallus 0.6–0.85mm thick at midrib, 5–10x as broad as tall; midrib c 1/5 width of thallus, gradually tapering laterally into thin thallus wings. Upper surface almost flat, areolate in radiating rows away from weakly-defined midrib. Apex conspicuously notched. Margins sinuate. *Dorsal epidermis* cells irregularly rectangular, 25–57 x 22–49µm, thin-walled, without trigones, in transverse section 30–52µm tall; oil cells frequent in epidermis, rounded-quadrate to rounded-hexagonal, 27–42µm diameter, oil body 0.4–0.8 diameter of oil cell; marginal cells at branch apex 22–39 x 32–45µm. *Air pores* with orifice 20–25µm

diameter, and with 6–8 rows of cells in 2–3 concentric rings; cells of innermost ring 7.5–12.5 µm in radial length, 15–22µm wide; cells of outermost ring, 20–27µm in radial length, 22–32 µm wide; cell walls thin. *Assimilation tissue* 0.2–0.25mm thick, less than half thickness of thallus above midrib; air chambers tall and thin over midrib, elongated and overlapping outwards in thallus wings; cells of air chamber partitions 40–75µm in diameter in transverse section. *Basal compact tissue* 0.25–0.3mm high; cells 25–50µm diameter, thin-walled. *Rhizoids*: smooth rhizoids mostly broad, 20–37µm diameter; pegged rhizoids narrow, 10–15µm diameter. *Ventral scales* small, not or slightly overlapping, hyaline or purplish, with body 400–1000 x 480–840 µm, cells of body 35–160 x 20–40µm; oil cells 8–13, scattered, 20–40µm diameter; irregularly crenate on curved adaxial margin, abaxial margin entire or with 1–3 hyaline papillae, these sessile or borne on a 2–3-celled cilia-like stalk; scale appendage single, oblong or weakly oblong-lanceolate, 620–800 x 130–300µm, 8–11 cells wide at insertion, apex obtuse or bluntly pointed, not or weakly constricted at base, cells smaller than in scale body, 40–100 x 25–40µm, margin entire or 2-toothed near apex, without slime papillae; apex terminating in a single blunt cell; oil cells 2–4 in appendage.

Sexual condition par-autoicous with fertile branches bearing a single archegoniophore and androecium. *Androecia* borne 0.4–1.6mm proximally to base of archegoniophore on a fertile branch. Androecia shortly linear, round or triangular, forming a weakly-defined raised cushion; ostioles bluntly conical, 60–180 x 75–125µm. *Archegoniophore* borne from apex of midrib in apical notch of branch, always terminating vegetative growth; vegetative growth ceasing or taken over by ventral innovations. *Stalk* 6–30 mm long, thin and delicate, whitish green, 460–600µm diameter at middle, weakly 10–12-ribbed; rhizoid furrow 200–260µm deep, medullary cells 17–37µm diameter, epidermal cells 15–30µm diameter; stalk without scales along its length, but with scattered scales around base and dense scales around apex; basal scales lanceolate, 600–900 x 140–180µm, with 1–2 oil cells and 2–3 marginal slime papillae; apical scales similar but more linear-lanceolate, 800–1200 x 50–120µm, with fewer oil cells and slime papillae. *Carpocephalum* green, umbrella-shaped, 4(–5)-lobed; 3–4mm diameter; central part elevated as an umbonate boss 1–1.5mm diameter; lobes 1–5 large, bearing a fertilised sporogonium, and 1–4 vestigial lobes; large lobes cuneate, spreading umbellately at 45–60° to stalk, with truncate-rotund apex, air chambers weakly prominent on central boss and lobes. *Involucre* (fertilised) c 1mm from base to free margin, free margin undivided. *Pseudoperianth* c colourless, thin and delicate, 2mm long; undivided basal part 0.9–1mm long, cells 60–80 x 25–50µm, thin-walled; lobes (5–) 6, each 0.8–1.1 x 0.4–0.5mm, free at maturity, some or all lobes deciduous at junction with basal part before capsule dehiscence; margins remaining ± flat when dry; cells of lobes 105–170 x 20–35µm; oil cells absent in basal part and lobes.

Capsule 1.2–1.5mm diameter; cells of urn 60–100 x 40–50µm. *Spores* (light microscope) orange-yellow, 60–75µm diameter. *Spores* (SEM) Type VII: trilete, without equatorial pores; proximal and distal surfaces with dissimilar sculpturing; on distal surface with large shallow areolae 12–21µm diameter, containing smaller alveoli and pits; muri broad and rounded, alveolate; equatorial rim conspicuous; proximal facets flat with a pronounced central bulge on

each; facets without primary areolae but with ± uniform, dense secondary alveoli which do not form distinct areolae, but are distinctly larger on the median bulges. *Elaters* 275–350 x 10µm, bispiral. *Chromosome number* unknown.

Illustrations: Montagne (1840: Plate 3, Fig. 2); spores Fig. 3.8.

Distribution and phytogeography (Fig. 4.11).

In the study area confirmed from southern Europe (Spain, Corsica, Sardinia) and Macaronesia: Madeira, Azores, Canary Islands. Outside the study-area it has been reported from North Africa (Algeria, Morocco and Tunisia) by Gatefosse & Werner (1932), Gottsche, Lindenberg & Nees (1846), Jelenc (1967), Jovet-Ast (1955), Jovet-Ast & Bischler (1972), Montagne (1838b, 1856) and others. Remarkably it was discovered only recently on continental Europe (Rupidera Giraldo & Elias Rivas, 1996); there is no evidence that this represents a recent expansion of range. The record from France (Duell, 1983) refers to Corsica.

This distribution is classed as Southern Mediterranean-Atlantic (see Ratcliffe 1968). In Europe it has been classed as 'Vulnerable' by Schumacker & Martiny (1995) though they inaccurately described the ecology and perceived threats.

Ecology and phenology

Asterella africana appears to be an obligate hygrophyte which can only occur where there is regular water seepage. It is usually found in forest or scrub, especially Lauraceae-dominated forest and *Erica arborea/ Myrica* shrubberies in Macaronesia, and also in shady *Pinus canariensis* forest in the Canary Islands and *Pinus* plantations on Madeira. Typically in these habitats it grows on wet rocks and banks, particularly along streams and water courses. It can also grow in ravines on wet rocks, cliffs and boulders. Substrates normally appear to be acidic, such as granite in Spain, but in the Canaries it grows on basaltic rocks. Associates are many, but include *Reboulia hemisphaerica* (L.) Raddi, *Plagiochasma rupestre* (J.R. & G. Forst.) Steph., *Anacolia webbii* (Mont.) Schimp., *Trichostomum brachydontium* Bruch, *Marchesinia mackaii* (Hook.) Gray, *Andoa berthelotiana* (Mont.) Ochyra, *Hypnum cupressiforme* Hedw., *Philonotis rigida* Brid., *Calypogeia fissa* (L.) Raddi, *Epipterygium tozeri* (Grev.) Lindb., *Fissidens taxifolius* Hedw., *Saccogyna viticulosa* (L.) Dumort. and *Selaginella denticulata* (L.) Spring.

The plant is most frequent at lower altitudes, on Madeira and the Azores down to sea level; on Tenerife it is recorded up to 1700m and on Madeira to 1600m. In Spain and Corsica it is restricted to lower altitudes (Spain 300 to 425m; Corsica 150 to 730m). This may be explained by the oceanic influence in Macaronesia which permits warm temperate plants to grow at much greater altitudes than further east in the Mediterranean where this influence is much less.

Asterella africana is most conspicuous during the winter months when moist weather facilitates growth, fertilisation and sporophyte development; ripe spores are therefore most often present from January to May.

Taxonomic notes

Asterella africana is not closely related to any of the other European species of *Asterella*. In Sect. *Brachyblepharis* it is related to the other species with par-autoicous sexual condition, but it differs from all other members of that Section in its distinctive pseudoperianth, which usually has only (5–) 6 lobes which are delicate, flat and brittle, and frequently caducous before capsule dehiscence. The most closely allied species is perhaps the tropical African *A. dissoluta* (Steph.) Grolle which has similar thalli and carpocephala; however it is clearly distinct in having 8–12 pseudoperianth lobes which are rigid, have distinctly revolute margins when dry, and are not brittle and shed before capsule dehiscence; *A. dissoluta* also has larger spores 80–105µm diameter.

In Asia the most closely allied species is *A. cruciata* which has the same sexual condition and similar deeply lobed carpocephala and small orange-yellow spores; it differs however in its broader, rounded ventral scale appendages which are constricted at the base; the very short peduncle, more numerous (9–15) pseudoperianth lobes which are not brittle and caducous, and strongly crenate-dentate muri of the spore reticulations.

Historical and nomenclatural notes

Following the description of *Fimbriaria africana* in 1840, there was little confusion over the identity of the only Macaronesian *Asterella* species, apart from its description from the Azores as a distinct genus *Rhacotheca* in 1844. This was synonymised by Leitgeb (1881). In North Africa it was named as *Fimbriaria intermedia* by Montagne, but this name was never validated. Early collections from Corsica, however, were not equated with the Macaronesian plant and were wrongly ascribed to the American species *Fimbriaria elegans* Spreng. by several authors, *e.g.* Notaris (1838–1839), Dumortier (1874) and Massalongo (1886).

Specimens examined: see Appendix V.

5. Asterella cruciata (Steph.) Horik., Hikobia 1: 79, 1951.

Basionym: *Fimbriaria cruciata* Steph., Species Hepaticarum 6: 12, 1917. Type citation: 'Japan, leg. Uematsu.' Type specimen (see notes below): '*Fimbriaria cruciata* St. n.sp. Japonia, Tokyo, 28 ii 1908, *Sakurai 9*, G-15200 (**lectotype,** selected by Long (1997)).

Syn.: *Asterella odora* S.Hatt., Botanical Magazine. (Tokyo) 58: 44, 1944. Type citation: 'Tokyo: Koisikawa-ku, Kamihuzimae-tyo (S. Hattori, no. 2505, 21. Oct. 1938; no. 3124–

typus, 23. Dec. 1939, cum spor.).' Type specimen: Japan, Honshu, Tokyo, Koishigawa, Kamifujimaye, on soil, 23 Dec. 1939, *S. Hattori 3124* (NICH-15906, **holotype**); synonymised by Long (1997).

Syn.: *A. chichibuensis* Shimizu & S.Hatt., Journal of the Hattori Botanical Laboratory 8: 46, 1952. Type citation: [Japan, Honshu] 'Saitama Prefecture: Chichibu, Hashitate, ca. 350 m. alt., on rocks and on soil in the calcareous region, Oct. 25, 1950, Coll. D. Shimizu, no. 18650–Typus! in Herb. Hattori Bot. Lab.'. Type specimen: Japan, Honshu, Saitama Prefecture, Hashitate, ca. 350m alt., on rocks, Oct. 25, 1950, *D. Shimizu s.n.* (NICH-18650, **holotype**); synonymised by Long (1997).

Syn.: *A. mitsuminensis* Shimizu & S.Hatt., Journal of the Hattori Botanical Laboratory 8: 48, 1952. Type citation: 'Japan [Honshu]. Saitama Prefecture: Chichibu, Mt. Mitsumine, ca. 600m. alt., on rocks, Nov. 25, 1951, Coll. D. Shimizu, no. 19642–Typus! in Herb. Hattori Bot. Lab.'. Type specimen: Japan, Honshu, Saitama Pref., Chichibu Mts., Mt. Mitsumine, ca. 550 m alt., on rock, Nov. 25, 1951, coll. *D. Shimizu s.n.* (NICH-19642, **holotype**); synonymised with *A. odora* by Shimizu & Hattori (1953a).

Description

Thalli forming often extensive patches up to 30cm diameter, all shoots thin and delicate, hygromorphic (hygroshoots); strongly smelling of rotten fish. *Vegetative branches* of regular terminal dichotomous branches and occasional ventral intercalary branches with stipitate base. Xeromorphic branches and tubers unknown. Branches oblong or heart-shaped, 10– 25 x 2–5mm, broadest towards apex, pale green above, sometimes pink or purplish along margins, lower surface often purplish, in transverse section 0.3–0.5mm thick at midrib; midrib c 1/3 to 1/6 width of thallus; gradually tapering laterally into thallus wings. Upper surface almost flat, areolate in curved radiating rows from midrib to margins. Apex conspicuously notched. Margins sinuate. *Dorsal epidermis* cells irregularly rectangular, 35–62 x 15–37µm, walls sometimes with small trigones; oil-cells scattered in epidermis, similar in shape but smaller, 25–30µm diameter, oil body almost filling cell; marginal cells 12–35 x 15–50µm. *Air pores* with orifice 25–30µm diameter, surrounded by 6–8 radial rows of cells in 2(–3) rings; cells of innermost ring 5–7.5µm in radial length, 15–20µm wide; cells of outermost ring, 12.5–25µm in radial length x 25–42µm wide; cell walls thin. *Assimilation tissue* 0.2–0.25mm thick, approximately half thickness of thallus at midrib; air chambers vertical above midrib, elongated and overlapping towards thallus margin; cells of air chamber partitions 20–40µm in diameter. *Basal compact tissue* 0.15–0.3mm thick; cells 15–40µm diameter, thin-walled. *Rhizoids:* smooth rhizoids 7.5–20µm diameter, pegged rhizoids 4–22µm diameter. *Ventral scales* not or slightly overlapping, often purplish, with body 500–1000 x 500–650µm, cells 37–115 x 20–45µm, longest in decurrent base; oil cells 4–19, 22–37µm diameter; margin entire or with 1–2 hyaline papillae on outer (abaxial) margin; appendage simple or sometimes deeply bifid, oblong, spathulate or ovate, 300–650 x 135–300µm, apex rounded or bluntly pointed; base weakly to strongly constricted, 4–6 cells wide at base, cells more irregular in shape than in

scale body, 30–100 x 25–55µm; apex usually with a conspicuous hyaline papilla and sometimes 1–2 additional papillae on margin; oil-cells 1–6 in appendage.

Sexual condition par-autoicous with fertile branches bearing single or not infrequently paired archegoniophores and single androecium. *Androecia* borne immediately proximal to or up to 0.8 mm from base of archegoniophore; androecia forming distinct cushions which are rounded, elliptic, linear or Y-shaped, variable in size but usually somewhat raised and conspicuous; ostioles almost cylindric, 75–125 x 60–75µm. *Archegoniophore* borne from apex of midrib in apical notch of branch, always terminating vegetative growth; vegetative growth ceasing or taken over by ventral innovations. *Stalk* very short, 0.8–3 (–6.8)mm, thin and delicate, pale green, 490–630µm diameter, strongly longitudinally 7–12-ribbed, ribs up to 150µm tall; rhizoid furrow 200–250µm deep; medullary cells 18–37µm diameter, with scattered oil cells just below epidermis; epidermal cells 12.5–25µm diameter; stalk with cluster of scales around apex and a few scattered scales along stalk; scales hyaline or purplish, linear, 400–600 x 40–100µm, 2–4 cells wide at base, occasionally deeply bifid into 2 linear lobes, sometimes with a single oil cell and 1–2 apical and marginal hyaline papillae. *Carpocephalum* flattened when mature, deeply irregularly 3–5-lobed, 1.8–3.5mm diameter; central part forming a low raised boss 0.8–1mm diameter; lobes truncate or rounded, mostly 2–5 large, and 1–3 remaining small and vestigial, air chambers conspicuous as raised radiating bulges reaching to margin; central boss with raised wart-like air chambers. *Involucre* (fertilised) 0.7–1mm from base to free margin; margin undivided. *Pseudoperianth* colourless, with undivided base less than half total length (0.7mm), cells of base 70–175 x 30–45µm; lobes 9–15, lanceolate, 0.95–1.15 x 0.3–0.4mm, free at maturity, not deciduous; cells of lobes 10–200 x 17–25µm; oil cells absent or 1–2 per lobe.

Capsule globose, c 1.2mm diameter; cells of urn 100–175 x 60–10µm; cells of lid 25–45µm. *Spores* (light microscope) orange-yellow, 60–75µm diameter. *Spores* (SEM) Type VII: trilete, without equatorial pores; proximal and distal surfaces with dissimilar sculpturing; on distal surface with large shallow areolae 9–15µm diameter containing smaller alveoli and pits; muri narrow and acute, weakly alveolate; equatorial rim conspicuous, with irregularly crenate outline in polar view; proximal facets flat with a low central bulge on each; facets with dense secondary alveoli which become larger and form larger areolae on the median bulges; trilete ridges irregularly toothed. *Elaters* 170–250 x 7.5–8.5µm, bispiral. *Chromosome number* (*A. chichibuensis*): n=9 (Tatuno, 1955).

Illustrations: Inoue (1976: Plate 169); spores Fig. 3.9.

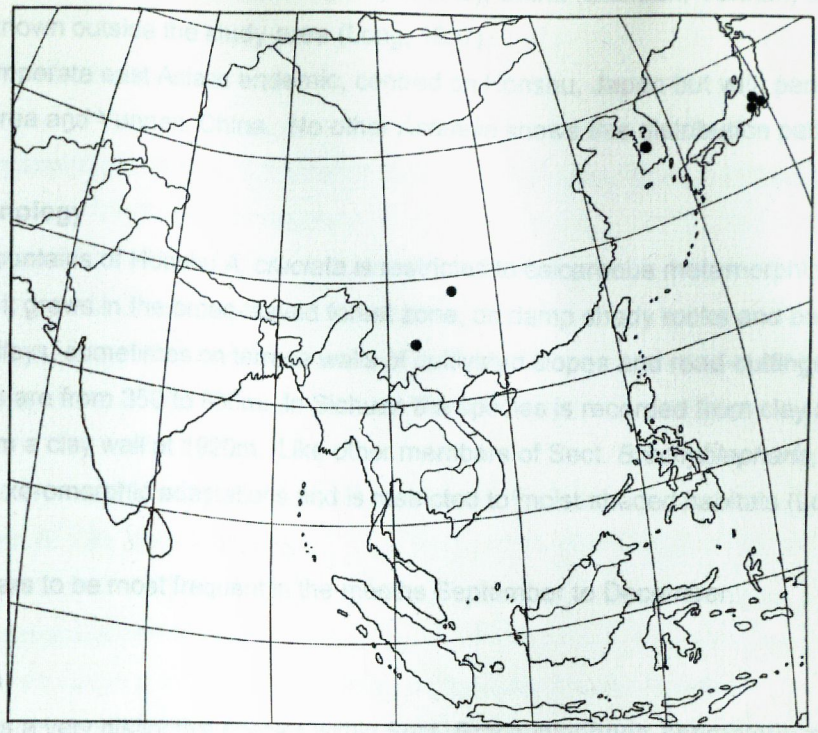

Fig. 4.12 Distribution of *Asterella cruciata* in Eurasia, based on specimens studied. ? indicates an unlocalised specimen.

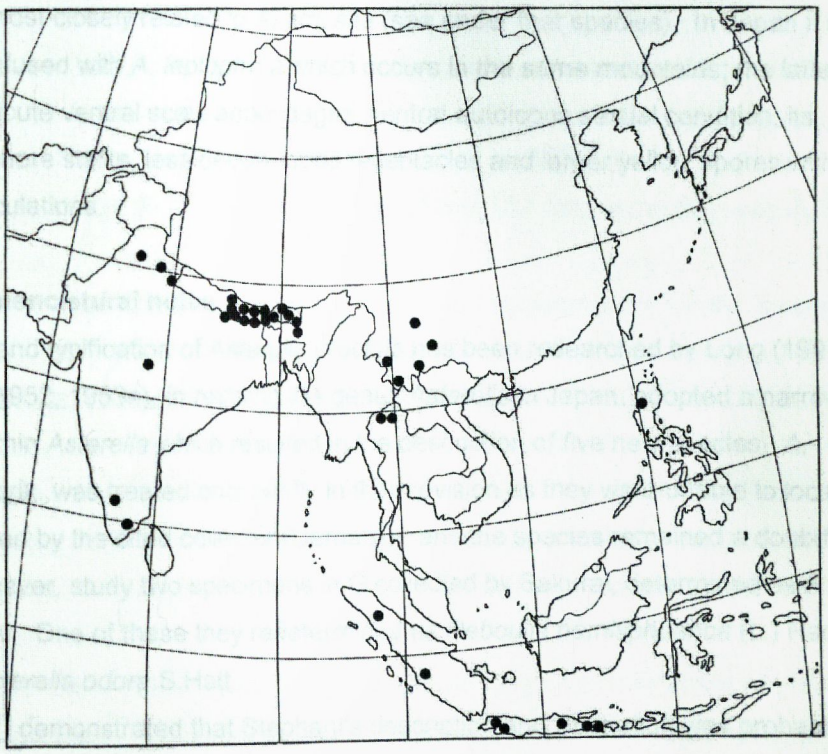

Fig. 4.13 Distribution of *Asterella khasyana* in Eurasia, based on specimens studied.

Distribution and phytogeography (Fig. 4.12).

Asterella cruciata has been confirmed from Japan (Honshu), China (Sichuan, Yunnan) and Korea and is not known outside the study-area (Long, 1997).

It is a cool-temperate east Asiatic endemic, centred on Honshu, Japan but with peripheral occurrences in Korea and Yunnan, China. No other *Asterella* shows this distribution pattern.

Ecology and phenology

In the Chichibu Mountains of Honshu *A. cruciata* is restricted to calcareous metamorphic substrates, where it grows in the broad-leaved forest zone, on damp shady rocks and banks, often in stream valleys, sometimes on terrace walls of cultivated slopes and road cuttings. Recorded altitudes are from 350 to 900m. In Sichuan the species is recorded from clay soil, and in Yunnan from a clay wall at 1920m. Like other members of Sect. *Brachyblepharis, A. cruciata* shows no xeromorphic adaptations and is restricted to moist shaded habitats (Long, 1997).

Fruiting appears to be most frequent in the months September to December.

Taxonomic notes

Asterella cruciata is a very distinctive species within Sect. *Brachyblepharis*; characterised by the blunt often broad ventral scale appendages constricted at base, the par-autoicous sexual condition, the very short stalks of the archegoniophores, the deeply-lobed carpocephala, the numerous (9–15) pseudoperianth lobes and the spores with highly ornamented dentate reticulations. It is most closely related to *A. africana* (see under that species). In Japan it is only likely to be confused with *A. leptophylla* which occurs in the same mountains; the latter differs in its linear acute ventral scale appendages, ventral-autoicous sexual condition, its longer archegoniophore stalks, less deeply lobed receptacles and larger yellow spores with almost smooth reticulations.

Historical and nomenclatural notes

The nomenclature and typification of *Asterella cruciata* has been researched by Long (1997). Shimizu & Hattori (1952, 1953a), in revising the genus *Asterella* in Japan, adopted a narrow species concept within *Asterella* which resulted in the description of five new species. *A. cruciata* (Steph.) Horik. was treated only briefly in their revision as they were unable to locate any material collected by the cited collector (Uematsu), and the species remained a doubtful one. They did, however, study two specimens in G collected by Sakurai, determined as *F. cruciata* by Stephani. One of these they redetermined as *Reboulia hemisphaerica* (L.) Raddi and the other as *Asterella odora* S.Hatt.

Long (1997) demonstrated that Stephani's description and illustration was probably partly based on the *Reboulia* element, but in the greater part based on the *Asterella* element; Stephani also cited this material under the wrong collector. *Fimbriaria cruciata* was therefore lectotypified with the *Sakurai* collection and *Asterella odora*, *A. chichibuensis* and *A.*

mitsuminensis treated as synonyms. This synonymy is supported by SEM study of spores of the type specimens of the three taxa (see Chapter 3).

Specimens examined: see Appendix V.

6. Asterella khasyana (Griff.) Pandé, K.P.Srivast. & Sultan Khan, Journal of the Hattori Botanical Laboratory 11: 7, 1954 '*khasiana*'.

Basionym: *Octokepos khasyanum* Griff., Notulae ad Plantas Asiaticas (2): 343, 1849; Type citation: 'Infra rupem in Pinetis Moflong, Collium Khasyensium parce legi, mense Nov. 1835.' Type specimens: Moflong, Khasyah, *Griffith 100* (BM, **lectotype selected here**; Khasia, Moflong, herb. *Griffith 100*, herb. EIC KD 1095 (BM, NY, isolectotypes); Moflong, 5900 ft., *Griffith* (TCD, isolectotype).

Syn.: *Fimbriaria khasyana* (Griff.) Mitt., Journal of the Proceedings of the Linnean Society. Botany. London 5: 126, 1861 '*khasiana*'.

Syn.: *Fimbriaria venosa* auct. Asiat. non Lehm. & Lindenb.; Sande Lacoste, *Synopsis Hepaticarum Javanicarum* 99, 1856.

Syn.: *Hypenantron venosum* auct. Asiat. non (Lehm. & Lindenb.) Trevis.; Schiffner, Denkschriften der kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Wien 67: 156, 1898.

Syn.: *Hypenantron venosum* (Lehm. & Lindenb.) Trevis. var. *macrosporum* Schiffn., Schiffner, Denkschriften der kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Wien 67: 156, 1898. Type citation: Sumatra occid.: In monte Singalang; in sylvis primaevis ad decliv. orient. secus torrentem ad terram. Regio nubium, alt. ± 2000 m s. m. - 24.7. 1894 (C.fr.) ([V. Schiffner] No. 19). Type specimen: Sumatra occid., In Monte Singlang, ad ripas torrentis, 24.vii.1894, 2000m, *V. Schiffner*, Iter Ind. 1893–94, No. 19 (FH, **lectotype selected here**; BM, WU, isolectotypes); **syn. nov**.

Syn.: *Hypenantron venosum* (Lehm. & Lindenb.) Trevis. var. *macrosporum* Schiffn. forma. *purpurascens* Schiffn., Schiffner, Denkschriften der kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Wien 67: 156, 1898 Type citation: Sumatra occid.: In monte Singalang; in sylvis primaevis ad decliv. orient. secus torrentem ad terram. Regio nubium, alt. ± 2000 m s. m. - 24.7. 1894 ([V. Schiffner] No. 20). Type specimen: Sumatra occid., In Monte Singlang, ad ripas torrentis, 24.vii.1894, 2000m, *V. Schiffner*, Iter Ind. 1893–94, No. 20 (FH, **lectotype selected here**; G-15377, isolectotype); **syn. nov.**

Syn.: *Hypenantron venosum* (Lehm. & Lindenb.) Trevis. var. *macrosporum* Schiffn. forma *viridis* Schiffn., Schiffner, Denkschriften der kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Wien 67: 156, 1898, *nom. superfl.* = forma *macrosporum*. Type: as for var. *macrosporum*.

Syn.: *Fimbriaria zollingeri* Steph., Species Hepaticarum 1:103, 1899. Type citation: Java (Zollinger, Stahl, Schiffner). Type specimens: Java, in Mte. Sijeng, *Zollinger s.n.*, herb. Stephani, ex herb. Wien, G-15374 (**lectotype, selected here**); Java, Prov. Preanger. In decliv. austral. montis Pangerango; ad declivia humida umbrosa pr. Lebak-Saät, rarum 9.v.1894, 2193m, *V. Schiffner* It. Ind. 1893/94 No. 18 (L, WU, PC, FH, G-15381, 15384, syntypes); [Java] in Casuarinetis, M. Idjeng, *U. Zollinger 2843* (L, PC, FH, G-14972, 15186, 15382, 24653, 24654, syntypes); Java, *Zollinger*, herb. Lindenberg 8671 (W, syntype), 8672 (W, syntype)'; Java, herb. Stephani, ex herb. Heidelberg (G-15372, syntype); Sumatra occid., In Monte Singlang, ad ripas torrentis, 24.vii.1894, 2000m, *V. Schiffner*, Iter Ind. 1893–94, No. 19 (FH, BM, WU, syntypes); **syn. nov.**

Syn.: *Hypenantron zollingeri* (Steph.) Schiffn., Die Hepaticae der Flora von Buitenzorg 23, 1900.

Syn.: *Asterella zollingeri* (Steph.) Verd., Annales Bryologici 10: 124, 1937.

Syn.: *Fimbriaria butleri* Steph., Species Hepaticarum 6: 12, 1917. Type citation: 'Sikkim Himalaya. (Butler legit)'. Type specimen: Darjeeling (Sikkim Himalaya) 7000ft. Sept. 1901 *E. Butler* in Herb. Levier 4640 (G-10456, **lectotype, selected here**; FI, isolectotype); **syn. nov**.

Syn.: *Asterella butleri* (Steph.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Parihar, University of Allahabad Studies Botany Section 1961–1962: 27, 1962.

Syn.: *Fimbriaria papulosa* Steph., Species Hepaticarum 6: 16, 1917. Type citation: Himalaya, Mussoorie, Gollan legit. Type specimen: Mussoorie, 1901, *Gollan* in Bryotheca E. Levier 3888 (G-10510, **lectotype selected here**); Mussoorie, *Gollan* in Bryotheca E. Levier 3889 (G-10511, syntype); Mussoorie, *Gollan* in Bryotheca E. Levier 3895 (G-10509, syntype); **syn. nov**.

Syn.: *Asterella papulosa* (Steph.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Kachroo, Journal of the Hattori Botanical Laboratory 19: 4, 1958.

Syn.: *Asterella blumeana* auct. plur. non (Nees) Kachroo; Kachroo, Journal of the Hattori Botanical Laboratory 12:36–38, 1954; Grolle in Flora of East Himalaya 3: 241, 1975; Kachroo, Journal of the Indian Botanical Society 56: 73, 1977; Gupta & Udar, Bryophytorum Bibliotheca 29: 69, 1986.

Syn.: *Fimbriaria blumeana* auct. plur non Nees; Stephani, Species Hepaticarum 89, 1899; Kashyap, Liverworts of the Western Himalayas and the Panjab Plain 62, 1929–1934.

Description

Thalli mostly thin and delicate, forming dense patches 3–5cm or more diameter; shoots mostly hygromorphic (hygroshoots) but also producing short tuber-like xeroshoots under drought conditions; with strong fishy smell when bruised. *Vegetative branches* of regular terminal dichotomous branches, and occasional ventral intercalary branches with stipitate base, rarely

terminal innovations with basal constriction. Hygroshoots oblong or heart-shaped, 3–6 x 2–4mm, 5–10 x as broad as tall, broadest towards apex, green above, often reddish along margins and beneath; in transverse section 0.35–0.4mm thick; midrib 1/5 to 1/7 width of thallus, gradually tapering laterally into thallus wings. Upper surface flat, areolate in curved rows towards margin; apex notched; margins sinuate-crenate, inrolling when dry. *Xeroshoots* produced either as short stipitate-based ventral branches, or as the thickened terminal part of a hygroshoot which quickly withers behind, always vegetative, not producing archegoniophores or androecia, mostly strongly purplish pigmented, shortly oblong, 1.2–2.2 x 0.8–1.0mm, 1–2 x as broad as tall, consisting of a much-expanded thick fleshy midrib, and very narrow purple thallus wings, in transverse section thick and fleshy, with proportionally thicker basal compact tissue; apex with no apical notch, but with purplish ventral scale appendages recurved over growing point and conspicuous from above; midrib much broader than in hygroshoots, 3/4 to 3/5 width of thallus, very prominent beneath and densely covered with purple ventral scales. *Dorsal epidermis* cells irregularly rectangular, 42–77 x 25–50µm, thin-walled, sometimes thickened at angles; oil-cells scattered, 27–37µm diameter, with a single large oil body less than half diameter of cell; marginal cells at branch apex 15–30 x 20–52µm. *Air pores* with orifice 20–30µm diameter, surrounded by 5–7 radial rows of cells in 2 rings; cells of inner ring 7.5–22µm in radial length, 10–32µm wide; cells of outermost ring 12.5–32µm in radial length x 27–52µm wide. *Assimilation tissue* 0.15–0.22mm thick in both hygroshoots and xeroshoots, approximately half thickness of midrib in hygroshoots; air chambers absent in xeroshoots. Air chambers in hygroshoots in a single layer above midrib, towards margins elongated and overlapping. Cells of air chamber partitions 15–40µm diameter. *Basal compact tissue* 0.17–0.2mm thick in hygroshoots, ± equalling thickness of assimilation tissue but in xeroshoots up to 0.3mm, distinctly thicker than assimilation tissue and forming the major part of the thallus; cells 20–50µm diameter, thin-walled. *Rhizoids:* smooth rhizoids 10–25µm diameter, pegged rhizoids 7.5–20µm diameter. *Ventral scales* often purplish, scarcely overlapping, body 450–800 x 500–900µm, cells 32–130 x 25–48µm, longest in decurrent base, shorter and broader just below appendage; oil cells in scale body 3–8, scattered, 22–37µm diameter; margin entire, without teeth or hyaline papillae; appendage single, undivided, lanceolate, 300–475 x 100–160µm, apex acute, ending in a single cell, base not constricted, 5–6 cells wide; margins entire; cells similar to those of upper part of scale body; oil cells 1–3 in appendage.

Sexual condition par-autoicous with archegoniophore(s) and androecia produced together at apex of fertile branches. *Androecia* borne immediately proximal to base of archegoniophore; androecium rounded, elliptic or shortly-linear, forming a well-defined cluster or low cushion bearing several protruberant ostioles, surrounded by a few scales when young; ostioles conical to shortly cylindric, 100–250 x 100–125µm. *Archegoniophore* borne from apex of midrib in apical notch of branch, always terminating vegetative growth; vegetative growth ceasing or taken over by ventral innovations. *Stalk* erect, 3.3–17.2mm, thin and delicate, often purplish, 380–540µm diameter, with 6–10 narrow acute ridges up to 100µm tall; rhizoid furrow 175–250µm deep; medullary cells 20–40µm diameter; stalk with ring of scales at apex, very

few scales along stalk (borne on ridges), naked at base; scales hyaline or pinkish, linear, 300–700 x 40–70µm, cells uniseriate throughout or biseriate in lower half, entire and without marginal hyaline papillae, without oil cells. *Carpocephalum* almost flat when mature, 3.5–5mm diameter, central part forming a low raised dome but not a distinct boss; lobes shallow, apex truncate but with strongly crenate margin due to protruding air chambers, lobes mostly 1–4 with fertilised archegonia and 1–3 vestigial, lacking a sporophyte; whole receptacle strongly warted with large protruding air chambers. *Involucre* 1.1–1.2mm from base to free margin in radial length; free margin entire. *Pseudoperianth* hyaline, 2–2.2mm long, undivided basal part slightly less than half total length (0.9–1mm), cells of base 180–250 x 35–50µm; lobes 7–9, lanceolate, 0.95–1.2 x 0.2–0.3mm, free at maturity; cells of lobes 55–160 x 27–42µm; oil cells absent.

Capsule globose, c 0.8–1mm diameter, cells of urn 37–62 x 30–45µm; cells of lid irregularly rounded, 35–50µm diameter. *Spores* (light microscope) pale yellow, 75–100µm diameter. *Spores* (SEM) Type VII: trilete, without equatorial pores; proximal and distal surfaces with dissimilar sculpturing; on distal surface with large shallow areolae 11–23µm diameter containing smaller alveoli and somewhat pitted; muri narrow and acute, alveolate; equatorial rim conspicuous; proximal facets flat without or with a very weak central bulge on each; facets without primary areolae except towards the proximal pole but with dense secondary alveoli. *Elaters* 150–215 x 10–12.5µm, bispiral. *Chromosome number n* = 18 (Kachroo, 1969, as *A. blumeana*).

Illustrations: Pandé et al. (1954: Fig. 3); spores Fig. 3.10.

Distribution and phytogeography (Fig. 4.13).

A. khasyana has been confirmed from Pakistan, India (Tamil Nadu, Madhya Pradesh, Himachal Pradesh, Uttar Pradesh, West Bengal, Sikkim, Assam); Nepal; Bhutan; China (Sichuan, Yunnan), Thailand, Indonesia (Java, Sumatra) and the Philippines. Many literature reports of *A. blumeana* from the Indian subcontinent refer to this species.

The only confirmed records from outside the study area are from tropical Africa (Burundi and Uganda) (Long, 2000). Collections from Papua New Guinea require further study. Grolle & Piippo (1984) and Piippo (1988) treated *Asterella shimizuana* Inoue (described from Papua New Guinea) as a synonym of *A. khasyana*. It was distinguished (from *A. zollingeri*) when first described (Inoue, 1967) by its ventral scale appendages and air pore structure. These characters have not been re-examined in detail, but preliminary study of spore ornamentation has revealed an apparent difference between the taxa. Several problematic taxa of *Asterella* occur in Papua New Guinea and the whole genus there requires revision. For the time being, *A. shimizuana* is not treated as a synonym of *A. khasyana*, and Papua New Guinea is excluded from its distribution.

Its distribution is tropical and subtropical SE Asian, extending to tropical Africa.

Ecology and phenology

Generally a warm-temperate and subtropical species, common only in warm moist forest habitats, such as Chestnut (*Castanopsis*) forest, Evergreen oak forest (*Quercus lamellosa* Sm. and *Q. semecarpifolia* Sm.), *Rhododendron* forest (*R. arboreum* Sm.) and *Schima wallichii* (DC.) Korthals forest in the Himalaya. In forests the plant is usually found on damp substrates such as streamsides, banks and wet rock outcrops. Substrates appear to be neutral to acidic. Equally commonly the plant grows in degraded or anthropogenic areas, such as overgrazed or burned hillsides, on terrace walls of paddy fields, on banks besides roads and footpaths, on river banks, and in towns and villages on damp walls of buildings, and on old religious buildings and monuments. In open sites in particular, the plants are usually in moist shady niches although these may be seasonally dry (see below).

Its altitudinal range is typically 1200–2500m and it is rarely found below 1000m (in Yunnan, Thailand down to 700m); exceptionally it can occur at higher altitudes (up to 2940m in Nepal). In the Himalaya the related species *A. leptophylla* takes over in similar habitats at higher altitudes though the two occasionally occur together.

In the Sino-Himalayan region the majority of spore-bearing collections were made between September and November, in the post-monsoon period, although a few collections made at other times of the year also had ripe sporophytes. In Thailand a similar pattern emerges, whereas in Java and Sumatra fruiting appears to take place at any time of year.

A striking feature of *A. khasyana* (and *A. leptophylla*, *q.v.*) is its ability to produce tuber-like xeroshoots as a response to drought stress. These are produced both as modifications of tips of normal vegetative thalli, and as short stipitate-based ventral shoots produced at the shoot apex. In some specimens these ventral branches are quite large and conspicuous, in others they are minute and hidden amongst the rhizoids near the shoot apex. It seems likely that with the death of the main thallus (hygroshoot) these xeroshoots would be released and able to act as vegetative dispersal agents. *A. khasyana* frequently grows in somewhat disturbed anthropogenic habitats where such propagules would be easily spread by human disturbance. The tubers also function as organs of perennation enabling *A. khasyana* to colonise habitats which, though moist during the summer monsoon season, would become completely dry during much of the remainder of the year. Thus these tubers may have a dual role of perennation and dispersal which may explain why *A. khasyana* is one of the most successful and widespread members of the genus in Asia.

Taxonomic notes

A. khasyana is a very distinctive member of Sect. *Brachyblepharis*. In its par-autoicous sexual condition it is similar to *A. cruciata* and *A. africana* in Eurasia. *A. cruciata* differs in its deeply-lobed receptacles borne on very short stalks, its more numerous (9–15) pseudoperianth lobes and its smaller spores with crenate-dentate muri; the two appear to be exclusive in distribution. *A. africana* differs in its more deeply lobed less warted receptacles, its fewer, delicate, caducous pseudoperianth lobes and its smaller spores. *A. blumeana*, from Malesia,

does overlap in distribution with *A. khasyana*, and sometimes the two grow together which may account for the past confusion between the two; *A. blumeana* however, differs in its ventral-autoicy and in its spores which lack primary distal areolae. *A. leptophylla* shows much congruence of range with *A. khasyana*, although normally it grows at higher altitudes; like *A. blumeana* it is easily distinguished by its par-autoicous sexuality and less warted receptacles.

Related species with par-autoicous sexuality from other continents are *A. dissoluta* (Steph.) Grolle from tropical Africa,. which differs in its deeply lobed less warted receptacles and more numerous pseudoperianth lobes. *A. chilensis* (Nees & Mont.) A.Evans, from Argentina and Chile, has not been studied, but from the literature (Hässel de Menendez, 1962) appears to be quite closely related to *A. khasyana*, differing in its narrower, often bilobed ventral scale appendages, less warted receptacles and slightly smaller spores. However, it would appear to be much more temperate species than *A. khasyana*, reported from approx. 33 to 45°S. (Hässel de Menendez, 1962) *A. venosa* (Lehm. & Lindenb.) A.Evans, a widespread species in South America, differs in its shorter, oblong ventral scale appendages (Hässel de Menendez, 1962) which are constricted at the base, its almost unlobed and weakly warted receptacles and in its smaller spores. *A. tenera* (Mitt.) R.M.Schust. from New Zealand and Australia differs in its narrower ventral scale appendages and smaller spores.

Historical and nomenclatural notes

Asterella khasyana was originally described by William Griffith (posthumously) in his *Notulae ad Plantas Asiaticas* in 1849 as *Octokepos khasyanum* although in that work the genus was spelled in three different ways: *Octaskepas*, *Octoskepos* and *Octokepos*. The last of these has been accepted as the intended orthography. Griffith's description and illustration were very detailed. He correctly described the pedunculate receptacle as female and the sessile receptacle as male, borne close to the base of the peduncle. The pseudoperianth he called 'interior involucre' and described it as 8-valved. He also accurately described the rhizoid furrow, the capsule and its dehiscence, the elaters and spores.

Griffith's type specimens have been labelled using two different systems, his own 'field numbers' and also 'Kew Distribution' numbers added many years after collection when his herbarium was posthumously sorted, divided and distributed from Kew as part of the East India Company Herbarium. The types bear the field number '100' and others 'KD1095' but both are parts of the original collection from Moflong in the Khasia Hills of Assam.

Although the epithet *khasyana* has continued to be used for Indian plants over the years (*e.g.* Mitten, 1860–1861; Stephani, 1898–1900; Pandé *et al.*, 1954), Stephani's application of the name *F. blumeana* to other collections of *A. khasyana* from India has led to much confusion and misunderstanding of the taxonomy and distribution of *A. khasyana* in SE Asia. Since Stephani, both names have continued to be recognised in India (*e.g.* Kashyap, 1929–1934) along with more taxa described by Stephani (*Fimbriaria butleri* and *F. papulosa*) from India. Schiffner (1898) added a further name into the equation: *Hypenantron venosum*, a

tropical American species, which he reported from Indonesia. These plants were soon after placed by Stephani under another new name, *Fimbriaria zollingeri*.

Study of types of all these names has now clarified the situation, and the much wider distribution of *A. khasyana* is now revealed. Perhaps the most significant breakthrough is in resolving the true identity of the oldest of the confused names, *F. blumeana* (see under *Asterella blumeana*). This species has been found (Long, 1998) to have unique spore ornamentation (quite different from that of *A. khasyana*) and the name is now restricted to purely Malesian plants.

Numerous syntypes exist for *Fimbriaria zollingeri*, most of which are clearly par-autoicous. However, one syntype (G-15375) belongs to the recently described *Asterella limbata* D.G.Long & Grolle. The lectotype (G-15374) was selected for three reasons: (a) it is clearly par-autoicous, belonging to *Asterella khasyana*, (b) it is annotated by Stephani, and (c) it was collected by Zollinger.

Specimens examined: see Appendix V.

7. Asterella leptophylla (Mont.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11:8, 1954, *comb. inval.* Art. 33.2] ex Grolle, Feddes Repertorium 87: 246, 1976.

Basionym: *Fimbriaria leptophylla* Mont., Annales des sciences naturelles; botanique. Sér. 2, 18: 16, 1842. Type citation: 'Ad terram in sylvis umbrosis juxta ripas rivulorum montium circa Kaitie lecta. [Perrottet]' Type specimens: [S India] Ad terram in silvis umbrosis secus rivulas Kaitien Neel-Gherrien cl. *Perrottet s.n.* (PC (herb. Montagne), **lectotype selected here**); Neelgherries, *Perrottet*, (G-10479, G-10480, G-10481, G-10483, G-24207, PC (herb. Roussel), BM (herb. Schimper) isolectotypes); Neel-Gherrien, ex herb. Montagne (BM (herb. Hampe), BR, NY (herb. Mitten), FH (herb. Sullivant), MANCH (herb. Carrington), G-14971, G-10482, isolectotypes); Neel-Gherries, ex herb. Montagne from Sir W.J. Hooker 1843 (FH (herb. Taylor), isolectotype).

Syn.: *Hypenantron leptophyllum* (Mont.) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 441, 1877.

Syn.: *Fimbriaria reticulata* Kashyap, Journal of the Bombay Natural History Society 25: 279, 1917. Type citation: 'Kashmir, 8,000 ft. in a shady place along the road.' Type specimen: *n.v.*; **syn. nov**.

Syn: *Asterella reticulata* (Kashyap) Pandé *et al.*, [Journal of the Hattori Botanical Laboratory 11: 9, 1954, *comb. inval.* Art. 33.2] ex Kachroo, Journal of the Hattori Botanical Laboratory 19: 4, 1958., *hom. illeg.* non *A. reticulata* Evans.

Syn.: *Fimbriaria yoshinagana* Horik., Science Reports of the Tohoku Imperial University, Ser. 4 Biology, 4: 395, 1929. Type citation: [Japan] 'Shikoku: Masunokawa-yama, Hongawa-mura, prov. Tosa (T. Yoshinaga, no. 2–type, Aug. 1928).' Type specimen: presumed destroyed (not traced in HIRO); **syn. nov**.

Syn.: *Asterella yoshinagana* (Horik.) Horik., Hikobia 1: 79, 1951.

Syn.: *Fimbriaria koreana* Horik., Botanical Magazine, Tokyo 50: 201, 1936. Type citation: Korea, Mt. Kongôzan, prov. Kôgen (Y. Horikawa, Aug. 5, 1935). Type specimen: Korea, Prov. Kôgen, Mt. Kongo, 5 viii 1935, *Horikawa 14916* (HIRO, **lectotype selected here**); **syn. nov.**

Syn.: *Asterella koreana* (Horik.) Horik., Hikobia 1: 79, 1951.

Syn.: *Asterella pusilla* Shimizu & S.Hatt., Journal of the Hattori Botanical Laboratory 8: 50, 1952. Type citation: 'Japan. Saitama Prefecture: Chichibu, the Jumonji pass, ca. 1800m. alt., on rocks, Nov. 21, 1951, Coll. D. Shimizu, no. 19643–Typus in Herb. Hattori Bot. Lab.' Type specimen: Japan, Saitama Prefecture: Chichibu, the Jumonji pass, ca. 1800 m alt., on rocks, Nov. 21 1951, *Shimizu s.n.* (NICH-19643, **holotype**); synonymised by Gambaryan (1988).

Syn.: *Asterella sanoana* Shimizu & S.Hatt., Journal of the Hattori Botanical Laboratory 9: 25, 1953. Type citation: [Japan, Honshu] 'On wet chert ledge in shade, 1280m. alt., Ikura, Nagano Prefecture, August 31, 1952, Coll. D. Shimizu, Typus in Herb. Hattori Bot. Lab.' Type specimen: On wet chert ledge in shade, 1280m alt., Ikura, Nagano Prefecture, Aug. 31, 1952, *Shimizu s.n.* (NICH-52791, **holotype**); Chikuma River, Ikura near Azusayama, Nagano County, 1280m, wet chert cliff and its base, viii 1952, *D. Shimizu* & *S. Sano* in Hep. Jap. Exsicc. Ser. 5 No. 203 (JE, UBC, H, TENN, G, L, B, W, LD, isotypes); synonymised by Konstantinova *et al.* (1992).

Syn.: *Asterella umbelliformis* Shimizu & S.Hatt., Journal of the Hattori Botanical Laboratory 9: 25, 1953. Type citation: [Japan, Honshu] 'On soil in sheltered places, mesophilous, 1120m. alt., the Hatcho pass, Chichibu Mts., Saitama Prefecture, August 21, 1952, Coll. D. Shimizu, Typus in Herb. Hattori Bot. Lab.' Type specimen: Japan, Saitama Prefecture: Chichibu Mts., Hatcho Pass, ca. 1120m, August 21 1952, *Shimizu s.n.* (NICH-52802, **holotype**); synonymised by Konstantinova *et al.* (1992).

Syn.: *Asterella kashyapii* Maheshw., Taxon 18: 599, 1969. [*nom. nov.* for *Fimbriaria reticulata* Kashyap non *Asterella reticulata* A.Evans]. Type: *Fimbriaria reticulata* Kashyap.

Description

Thalli in small patches 2–6cm diameter; shoots mostly hygromorphic, thin and delicate (hygroshoots).but producing short tuber-like xeroshoots under drought conditions; aromatic when crushed. *Vegetative branches* of occasional terminal dichotomous branches and frequent ventral intercalary branches with stipitate base. Hygroshoots mostly heart-shaped to spathulate, more rarely oblong, 5–12 x 3.2–5mm, broadest near apex, tapering to stipitate base; vegetative growth continued mostly by ventral branches produced close to apex of shoots, occasionally by dichotomous branches, one branch of which remains vegetative, the other producing an archegoniophore; hygroshoots green above, often pinkish at margins and beneath, in transverse section 0.4–0.6mm thick at midrib, gradually tapering laterally into wings. Upper surface flat, faintly areolate in curved rows; apex notched; margins sinuate and

undulate; midrib 1/4 to 1/3 width of thallus at its broadest point, proportionally broader in tapering base of branch. *Xeroshoots* produced mostly as short stipitate-based ventral branches, more rarely as the thickened terminal part of a hygroshoot which withers behind, always vegetative, not producing androecia or archegoniophores, concave and dark bluish-green above, convex and dark purple pigmented below and on margins above, broadly spathulate or suborbicular, 1.3–2.2 x 1.4–2.5mm, 3–4 x as broad as tall, consisting of a broad thick fleshy midrib and narrow thick wings; midrib with compact basal tissue and an assimilatory layer with compact air chambers and air pores; apex without apical notch but with recurved tips of ventral scale appendages covering growing point; midrib much broader than in hygroshoots, c 1/2 width of thallus, beneath densely covered with dark purple ventral scales. *Dorsal epidermis* cells irregularly rectangular, 25–70 x 12–40µm, thin-walled or thickened at angles; oil cells 20–27µm diameter; marginal cells at branch apex 12–30 x 25–37µm. *Air pores* with orifice12.5–25(–37)µm diameter, surrounded by 6–8 radial rows of cells in 2–3(–4) concentric rings; cells of innermost ring 12.5–25µm in radial length x 30–35µm wide; cells of outermost ring 25–30µm in radial length x 30–75µm wide. *Assimilation tissue* 0.22–0.35mm thick in hygroshoots, usually occupying just over 50% thickness of thallus. Air chambers narrow and vertical in one layer over midrib, towards margins elongated and overlapping; cells of partitions 22–50µm diameter. *Basal compact tissue* 0.17–0.27mm thick in hygroshoots (up to 0.35mm in xeroshoots); cells 20–50µm diameter, thin-walled. *Rhizoids*: smooth rhizoids 12–25µm diameter; pegged rhizoids 8–20µm diameter. *Ventral scales* not overlapping, reddish, body 500–1000 x 700–1050µm, cells 52–88 x 15–32µm; oil cells 4–12 in scale body, mostly on adaxial side, 22–35µm diameter; margin entire but often (? always) with a single hyaline papilla on abaxial margin just below appendage; scale appendage single, undivided, oblong-lanceolate, 350–490 x 150–230µm, apex obtuse except for single terminal hyaline papilla, base not constricted, 3– 6 cells wide; margin of appendage crenate to denticulate; cells mostly shorter and broader than those of scale body, 42–67 x 15–50µm; oil cell single or absent in appendage.

Sexual condition ventral-autoicous with male branches much smaller than vegetative and female branches, 1–3 produced ventrally towards base of branch (this usually bearing a usually single archegoniophore). *Androecia* on small heart-shaped or elliptic ventral branches, often partly hidden by wings of main shoot, mostly emergent, 1.3–2.8 x 0.8–2.2 mm, consisting of small ellipsoid raised cushion with a reduced wing on either side (this sometimes almost absent); cushion 125–150µm tall, surrounded by a few reddish linear scales, bearing prominent ostioles 60–115 x 80–125µm; androecial branches sometimes bearing a secondary ventral male shoot and/or a new vegetative innovation without an androecium. Androecia often lost by sporophyte maturity. *Archegoniophore* borne from apex of midrib in apical notch of branch, always terminating vegetative growth; vegetative growth ceasing or taken over by ventral innovations. *Stalk* erect, delicate, often pinkish, 15–35mm, 500–800µm diameter, with 6–10 rounded to acute ridges 50–125µm tall; rhizoid furrow 200–250µm deep; medullary cells 25–42µm diameter. Stalk with a few scales towards base and a ring of scales at apex; when

mature almost naked except at apex; scales linear, 600–900 x 75–100µm, 3–4-seriate below, 1-seriate at apex, apex with a single hyaline papilla, margin entire except for occasional hyaline papillae, oil cells absent or occasionally 1. *Carpocephalum* disc-shaped, flat when mature except for conspicuous low central raised boss, 3.5–6mm diameter; with 4–5(–8) lobes, unequal in size, ± rectangular, moderately deep. Air chambers weakly raised over whole surface of receptacle and lobes, producing a crenulate margin to lobes. *Involucre* 1.6–1.9mm from base to free margin; margin entire. *Pseudoperianth* hyaline or pinkish-tipped, 2–2.2 mm long, undivided basal cup c 1mm long, cells of base 150–225 x 20–37µm, with scattered oil cells; lobes (8–)9–12(–15), 1–1.3 x 0.35–0.5mm, free at maturity; cells of lobes 85–160 x 17–30µm; oil cells 3–9 per lobe, mostly towards the base.

Capsule globose, 1.3–1.7mm diameter; cells of capsule urn 50–105 x 37–55µm, thin-walled; cells of cap much smaller, irregular in shape, 25–35µm diameter. *Spores* (light microscope) yellow, 55–90µm diameter. *Spores* (SEM) Type VII: trilete, without equatorial pores; proximal and distal surfaces with dissimilar sculpturing; on distal surface with large shallow areolae 11–23µm diameter, containing smaller alveoli and pits; muri broad and rounded, alveolate; equatorial rim conspicuous; proximal facets flat with a pronounced central bulge on each; facets without primary areolae but with dense secondary alveoli. *Elaters* 225–290 x 10–12µm, bispiral. *Chromosome number* n = 9 (Tatuno, 1955, as *A. umbelliformis*; Tatuno, 1955, as *A. sanoana*; Tatuno, 1955, as *A. pusilla*); n = 18 (Kachroo, 1969, as *A. reticulata)*.

Illustrations: Shimizu & Hattori (1953a: Fig. 5) ; spores Fig. 3.11.

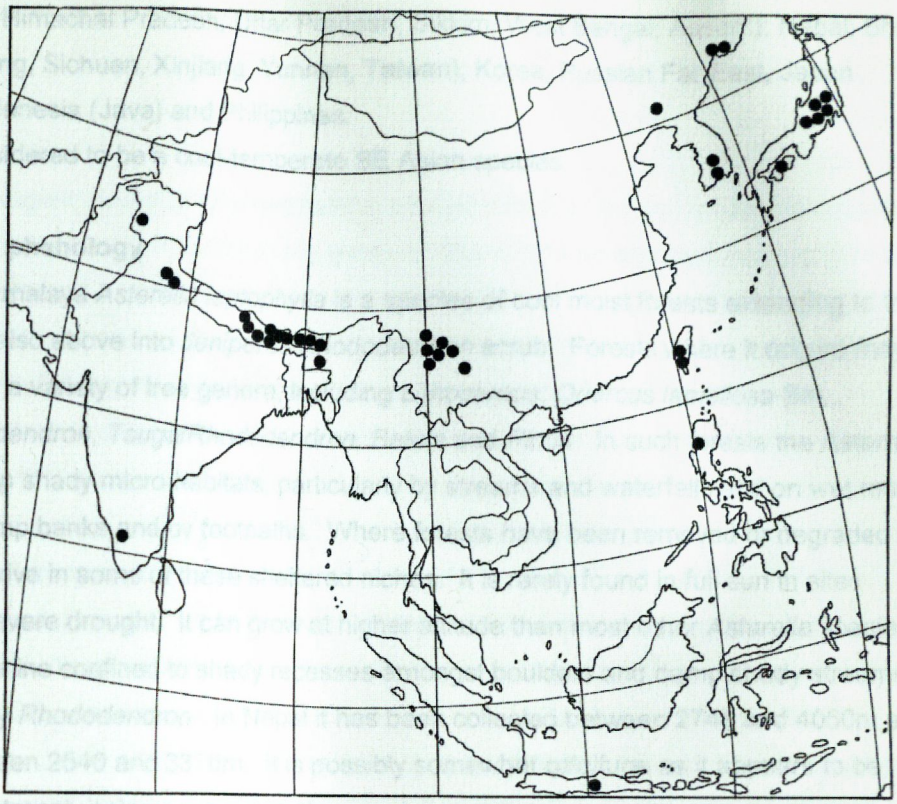

Fig. 4.14 Distribution of *Asterella leptophylla* in Eurasia, based on specimens studied.

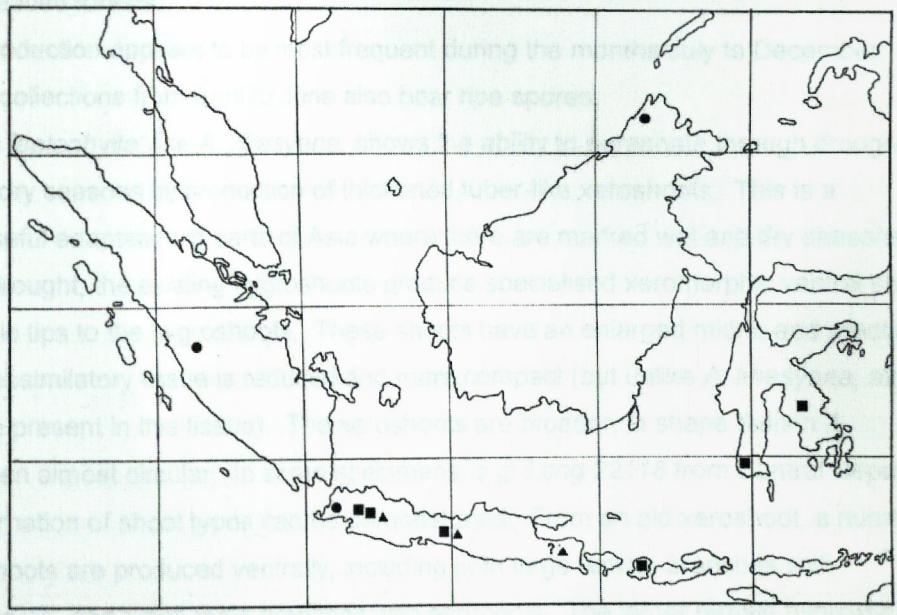

Fig. 4.15 Distribution of *Asterella blumeana, A. limbata* and *A. vulcanica* in Eurasia, based on specimens studied. ■ = *A. blumeana* ● = *A. limbata* ▲ = *A. vulcanica*. ? indicates an unlocalised specimen.

Distribution and phytogeography (Fig. 4.14)

A. leptophylla is only known from the study-area and has been confirmed from Pakistan, India (Tamil Nadu, Himachal Pradesh, Uttar Pradesh, Sikkim, West Bengal, Assam); Nepal; Bhutan; China (Liaoning, Sichuan, Xinjiang, Yunnan, Taiwan), Korea, Russian Far East, Japan (Honshu), Indonesia (Java) and Philippines.

It is considered to be a cool-temperate SE Asian species.

Ecology and phenology

In the Sino-Himalaya *Asterella leptophylla* is a species of cool moist forests extending to the tree line and also above into *Juniperus*/*Rhododendron* scrub. Forests where it occurs may be dominated by a variety of tree genera, including *Lithocarpus*, *Quercus lamellosa* Sm., *Abies*/*Rhododendron*, *Tsuga*/*Rhododendron*, *Betula* and *Pinus*. In such forests the *Asterella* grows in damp shady micro-habitats, particularly by streams and waterfalls and on wet rocks, on soil on damp banks and by footpaths. Where forests have been removed or degraded the plant can survive in some of these sheltered niches. It is rarely found in full sun in sites exposed to severe drought. It can grow at higher altitude than most other *Asterella* species, above the treeline confined to shady recesses amongst boulders and damp shady streamsides under shrubby *Rhododendron*. In Nepal it has been collected between 2745 and 4050m and in Yunnan between 2540 and 3370m. It is possibly somewhat calcifuge as it appears to be absent from strongly calcareous substrates.

In other parts of its range much less is known about its ecology but in Taiwan, the Philippines and Japan it occurs at lower altitudes, from 1000 to 2300m, whilst in the Russian Far East it occurs down to sea level. As far as is known, it is restricted in all these areas to moist broad-leaved forests.

Spore production appears to be most frequent during the months July to December, though a few collections from April to June also bear ripe spores.

Asterella leptophylla, like *A. khasyana*, shows the ability to perennate through drought conditions or dry seasons by production of thickened tuber-like xeroshoots. This is a particularly useful adaptation in parts of Asia where there are marked wet and dry seasons. At the onset of drought, the existing hygroshoots produce specialised xeromorphic ventral shoots, or xeromorphic tips to the hygroshoots. These shoots have an enlarged midrib and practically no wing; the assimilatory tissue is reduced and more compact (but unlike *A. khasyana*, air chambers are present in this tissue). The xeroshoots are broader, in shape than in *A. khasyana*, often almost circular. In some specimens, *e.g. Long 22116* from Central Nepal, the seasonal alternation of shoot types can be demonstrated. From an old xeroshoot, a number of fertile hygroshoots are produced ventrally, including both large female branches with archegoniophores, and small male branches with androecia. The larger female hygroshoots, in turn, produce several ventral xeroshoots at the start of the next dry season.

In other habitats where moisture is available throughout the year, xeroshoots are not present at all. This clearly is an adaptation which broadens the potential ecological spectrum

of the species. For example, in Himalayan forest sites, *Asterella leptophylla* is able to grow in undisturbed forests in its hygromorphic state in damp shaded niches; where the forests are cleared or degraded, the species can adapt to the newer seasonally dry niches and survive the deforestation.

Taxonomic notes

In the Indian region, *A. leptophylla* has been confused with *A. khasyana* mostly, though the species are very distinct. *A. khasyana* is generally found at lower altitudes, has more linear thallus branches and has a par-autoicous sexual condition. In *A. leptophylla* the androecial branches are often inconspicuous or lost by the time the spores are ripe, but the heart-shaped or spathulate fertile branches and absence of androecia immediately proximal to the archegoniophore are diagnostic. More closely-related is the much more restricted *A. blumeana*; for differences see below.

Historical and nomenclatural notes

The various synonyms of *A. leptophylla* are a reflection of its discovery in different regions of South-east Asia: *Fimbriaria leptophylla* in southern peninsular India, *F. reticulata* in the West Himalaya, *F. koreana* in Korea, and *F. yoshinagana*, *A. pusilla*, *A. sanoana* and *A. umbelliformis* in Japan. Some of these have already been reduced to synonymy elsewhere, for example, Hattori & Mizutani (1959) synonymised *A. pusilla*, *A. sanoana* and *A. umbelliformis* under *A. yoshinagana*. *Asterella kashyapii* was proposed as a new name for *Fimbriaria reticulata* Kashyap, but was unnecessary due to the existence of the much earlier *A. leptophylla*.

Specimens examined: see Appendix V.

8. Asterella blumeana (Nees) Kachroo, Journal of University of Gauhati, 3: 130, 1952.

or: *Asterella blumeana* (Nees) Pandé *et al.*, Journal of the Indian Botanical Society 31: 348, 1952 [after 2 viii 1952].

Basionym: *Fimbriaria blumeana* Nees, in Gottsche, Lindenb. & Nees, Synopsis Hepaticarum 564 1846. Type citation: 'Habitat in Java insula, unde cl. Reinwardt attulit (Hb. N.)'. Type specimen: Java, *Reinwardt s.n.* [as *Fimbriaria tenella* Reinw., *F. pilosa* N. ab E.] (STR, herb. Nees, **lectotype**, selected here; S, isolectotype).

Syn.: *Hypenantron blumeanum* (Nees) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4:441, 1877.

Description

Thalli forming extensive patches 5–10cm diameter in hygrophytic forms or smaller patches in drier habitats; both xeroshoots and hygroshoots produced, these sometimes alternating

according to seasons or habitat; smell not recorded. *Vegetative branches* thin and delicate (hygroshoots), linear to obovate or spathulate, 10–50 x 2.5–4(–7)mm, mostly of terminal dichotomies without basal constrictions and terminal innovations with basal constrictions; ventral innovations with stipitate base infrequent; branches green above often with purple margins, apex notched, in transverse section branches 0.35–0.5mm thick at midrib; midrib narrow, 1/6–1/8 width of thallus. Xeroshoots similar to hygroshoots but thicker and leathery in texture and more pigmented. *Dorsal epidermis* cells irregularly rectangular, 37–62 x 17–30µm; oil cells 27–37µm diameter; marginal cells at branch apex 10–20 x 12–27µm. *Air pores* with orifice 20–27µm diameter; surrounded by 6–10 radial rows of cells in 3–4 rings; cells of innermost ring 12.5–25µm in radial length x 10–27µm wide; cells of outermost ring 12.5–25µm in radial length x 45–50µm wide. *Assimilation tissue* 0.2–0.3mm thick in hygroshoots, occupying over 50% of thickness of thallus. Cells of partitions 20–50µm diameter. *Basal compact tissue* 0.15–0.2mm thick; cells 25–35µm diameter. *Rhizoids*: smooth rhizoids 17–32µm diameter; pegged rhizoids 7.5–22µm diameter. *Ventral scales* (only fragmentary scales studied) red, with body up to c1200 x 1000µm; cells of body 60–90 x 25–45µm, oil cells 2–3 (or possibly more); margins apparently entire, slime papillae not seen; appendage oblong, c 800 x 150µm, apex ?acute, base 4–5 cells wide, not constricted, margins ?entire, cells 70–85 x 22–35µm; oil cells not seen in appendage.

Sexual condition both terminal-autoicous and ventral-autoicous on individual plants; male branches usually much smaller than vegetative and female branches. *Androecia* on small heart-shaped or fish-tail shaped branches which are produced both ventrally and terminally, always with a basal constriction; consisting of a small elliptic raised cushion with reduced wings at either side; androecial branches sometimes bearing a ventral vegetative innovation. *Archegoniophore* borne both at apex of main thallus branches and on small ventral innovations near apex of branches, always terminating vegetative growth; vegetative growth ceasing or taken over by ventral innovations. *Stalk* erect, 13–28mm, 450–550µm diameter, with c 6 acute ridges 50–125µm tall; rhizoid furrow 150–250µm deep; medullary cells 20–25µm diameter. Stalk glabrous or with a few scales at base, at apex with ring of scales hidden between involucres; scales few but quite long, 1.2–1.8mm, 2–3-seriate with 2–3 uniseriate cells at apex; slime papillae and oil cells not seen. *Carpocephalum* flat, disc-shaped, 2.8–4mm diameter, with rounded central boss, shallowly 3–5-lobed, of which 2–4 lobes develop sporogonia; air chambers weakly prominent as tubercles over whole surface of receptacle, producing a crenulate margin to lobes. *Involucre* 1.2–1.3mm from base to free margin; margin not divided. *Pseudoperianth* 2.2–2.3mm long; undivided basal cup c 1mm long; cells of base up to 160 x 50µm; lobes 7–10, brownish white (in old specimens), 1.2–1.3 x 0.2–0.35mm, free at maturity; cells of lobes 100–200 x 25–40µm; oil cells absent in base and lobes.

Capsule c 1.2mm diameter; cells of wall of urn 50–120 x 35–55µm; cells of cap much smaller, to 55µm diameter. *Spores* (light microscope) yellow, 70–100µm diameter. *Spores* (SEM) Type VII: trilete, without equatorial pores; proximal and distal surfaces with proximal and distal surfaces with slightly dissimilar sculpturing, on distal surface without primary areolae but

with prominent bulges ± in the shape of a corona, almost uniformly covered in shallow alveoli 1.5–3µm diameter and pits; muri absent; equatorial rim conspicuous especially from proximal pole; proximal facets flat with a very pronounced central bulge on each; facets without primary areolae but with dense secondary alveoli which become larger towards proximal pole. *Elaters* 180–245 x 10–12µm, bispiral. *Chromosome number* unknown.

Illustrations: none ; spores Fig. 3.13.

Distribution and phytogeography (Fig. 4.15).

Specimens of *Asterella blumeana* have been seen only from Indonesia (Java); Celebes and the Sunda Islands (Lombok). It is unknown outside the study area.

A local tropical Malesian endemic.

Ecology and phenology

Very poorly-known; reported from stones of a temple and under overhanging rocks, probably always in (at least seasonally) moist shaded habitats. Altitudes reported from 1200 to 2650m.

Specimens with mature sporophytes have been collected in May, June, July and October.

Taxonomic notes

The above description is based only on old rather fragmentary herbarium specimens. Details of ventral scales in particular are poor, and further collections are much needed to improve the description. There is no doubt that within Sect. *Brachyblepharis*, *Asterella leptophylla* is the most closely allied species. The most reliable differences are in the spore characters, with the corona-like distal bulges in *A. blumeana* strikingly different from the regular and complete distal areolae of *A. leptophylla*.

In the gametophytes there appear to be several differences between the species, but these should be used with caution until more material of *A. blumeana* is studied. The differences are: (a) ventral scale appendages longer in *A. blumeana*, c 800µm, in *A. leptophylla* 350–490µm; (b) scale appendage cells longer in *A. blumeana*, 70–85µm, in *A. leptophylla* 42–67µm; (c) carpocephalum smaller in *A. blumeana,* 2.8–4mm diameter; in *A. leptophylla* 3.6–6mm diameter; (d) receptacle lobes shallow in *A. blumeana,* moderately deep in *A. leptophylla*; (e) pseudoperianth lobes fewer, 7–10, in *A. blumeana,* 9–12 in *A. leptophylla*.

Historical and nomenclatural notes

The names *Asterella blumeana* and *Fimbriaria blumeana* have been widely misapplied in the Indian region to what is correctly *A. khasyana*. This misapplication was first perpetrated by Stephani (1899) and subsequently followed by many others, *e.g.* Kashyap (1929–1934), Kachroo (1954), Gupta & Udar (1986) and others. Originally, Gottsche *et al.* (1844–1847) applied the name *Fimbriaria blumeana* only to Reinwardt's original collection from Java. Stephani (1898–1900) included under this name plants from the NW Himalaya and based

much of his description on the latter. Schiffner (1900) realised that Stephani had misapplied the name *F. blumeana* to another taxon (in Schiffner's opinion *Fimbriaria zollingeri*, now *Asterella khasyana)* and he restricted the former name to two collections from Java, the type specimen collected by Reinwardt and a specimen collected by Zollinger from Gunung Idjeng. Unfortunately Schiffner's correct interpretation was ignored by later authors. However, the lack of good material meant that no advance was made until the striking spore differences were demonstrated by Long (1998) using SEM, corroborating preliminary conclusions made by Grolle (*pers. comm.*) from light microscope observations.

There is uncertainty over the exact date of the combination *Asterella blumeana*.

Specimens examined: see Appendix V.

9. Asterella limbata D.G.Long & Grolle, Journal of Bryology 18: 287, 1994. Type citation: Sumatra, Mt. Korinchi, 2500–3000m, subalpine vegetation with *Vaccinium*, vii 1956, *W. Meijer B8977* (JE, **holotype**; L, isotype); type specimen: as above.

Description

Thalli in close dull green patches up to 2cm diameter or as scattered thalli; smell not recorded. *Vegetative branches* of regular terminal dichotomies without any basal constriction and occasional ventral branches with stipitate base, thin and delicate, hygromorphic (hygroshoots); xeromorphic branches and tubers unknown. Branches heart-shaped to oblong, 3–6mm long, 2–4.2mm broad, more rarely up to 8mm long and little-branched, usually broadest towards apex, in transverse section 0.45–0.75mm thick over midrib, gradually tapering laterally into thin thallus wings. Upper surface of thallus not channelled, almost flat but weakly reticulate and bulging above air chambers which form curved radiating rows away from narrow weakly defined midrib. Margins of thallus not inrolling when dry. Older parts of thalli short-lived. Apices of branches shallowly notched. Midrib thin, narrow, c 1/5 width of thallus. *Dorsal epidermis* cells rectangular-hexagonal, 50–90 x 24–50µm, walls thin, without trigones; oil cells scattered but conspicuous, 29–40µm diameter, oil-body usually 0.2–0.5 diameter of cell; marginal cells at apex 12–22 x 34–59µm. *Air pores* with orifice 20–30µm diameter, surrounded by 6–8 radial rows of cells in 3–4 concentric rings; cells of innermost ring transversely rectangular, 6–10µm in radial length x 12–17µm wide; cells of outermost ring 19–30µm in radial length x 36–50µm; pore cells thin-walled except for radial walls weakly thickened at angles. *Assimilation tissue* 0.2–0.4mm thick and ± half thickness of thallus in middle of thallus; air chambers narrow, vertical above midrib, spreading and overlapping towards thallus wings; cells of air-chamber partitions very variable in size, 25–75µm diameter in transverse section; oil-cells occasional. *Basal compact tissue* 0.2–0.4mm high; cells 24–68µm diameter; oil-cells occasional. *Rhizoids:* smooth rhizoids 20–30µm diameter; pegged rhizoids 6–30µm diameter. *Ventral scales* small, not overlapping, wine-red; scale body 600–

900 x 500–600µm, cells 60–135 x 24–44µm longest at base; oil-cells scattered, 27–37µm diameter; margin entire except for a single minute 1-celled hyaline papilla on outer margin of scale just below insertion of appendage; scale appendage always single, bluntly oblong-lanceolate 250–380 x 200–220µm, 5–9 cells broad at base and not constricted, cells smaller than in scale body, 49–80 x 29–50µm; margin entire but occasionally shortly and bluntly 2-toothed at apex; apex terminating in a single rounded cell; oil cells 2–4 in appendage.

Sexual condition terminal-autoicous with fertile branches bearing both 2–4 androecia and 1–2 archegoniophores. *Androecia* borne apically on a short vestigial terminal branch which then ceases growth and becomes lateral to main vegetative axis, often several androecia borne along margin of a single thallus branch, each usually protruding from a marginal constriction, often also as a terminal branch on one of the main thallus lobes close to the archegoniophore. Ventrally each androecium is a fleshy, densely scaly extension of the branch midrib, lacking thallus wings in its terminal part and thus protruding from a notch in the thallus wing as an inconspicuous short fleshy point. In some branches bearing a single archegoniophore there may be three or four androecial branches at intervals along the margins of the thallus. Antheridia immersed, c 250 x 150µm, above each a low bluntly conical ostiole c 150 x 150µm. *Archegoniophore* borne from apex of midrib in apical notch of branch, always terminating vegetative growth; vegetative growth ceasing or taken over by ventral innovations. *Stalk* 6–8mm long, pale green or reddish tinged, slender, delicate, 330–380µm diameter at middle, weakly 6–9-ribbed; rhizoid furrow 120–150µm deep; medullary cells 29–37(–49)µm diameter, outermost cells smaller, 17–29µm diameter; stalk with scattered deflexed-spreading narrow lanceolate often reddish scales along its length, each 800–900µm long, 2–3 cells wide at base, with 1–3 scattered oil-cells; apex of stalk with a dense ring of scales. *Carpocephalum* green or reddish tinged, subglobose when young, inversely saucer-shaped when mature with rim shortly 3–6-lobed; 3.5–4mm diameter; central part elevated as a low boss c 1.5mm diameter; lobes spreading, truncate or rounded with crenate margin, mostly 1–4 large, bearing a fertilised sporogonium, and 1–5 vestigial, bearing an unfertilised archegonium and small involucre; central boss with bulging air-chambers and pores; rim and lobes with low elongate spreading air chambers and pores to margin. *Involucre* a pouch-like flap, 1.8–2mm from base to free margin, margin sinuate. *Pseudoperianth* hyaline, c 2.2mm, basal part slightly less than half total length, with oil cells only near insertion of lobes, cells 60–100 x 35–60µm; lobes 8–11, radiating laterally, lanceolate, 1.2–1.35 x 0.27–0.4mm, becoming free before capsule dehiscence; cells 100–120 x 20–30µm; oil-cells 8–12 per lobe, up to 65µm long at base of lobe, becoming smaller to c 30µm near apex.

Capsule globose c 1.3mm diameter, dehiscing irregularly by a cap in upper 1/4; wall unistratose, cells 45–100 x 30–50µm; cells of lid 25–37µm diameter. *Spores* (light microscope) yellow or pale brownish, 85–110µm diameter. *Spores* (SEM) Type VII: trilete, without equatorial pores; proximal and distal surfaces with dissimilar sculpturing; on distal surface with large shallow areolae 15–25µm diameter containing smaller alveoli and pits; muri broad and rounded, alveolate; equatorial rim conspicuous, 8–10µm wide, wing weakly crenate

and finely granular-papillose; proximal facets flat with no or only a very low central bulge on each; facets without very poorly-defined primary areolae but with dense secondary alveoli. *Elaters* 210–320 x 12µm, with bispiral thickenings. *Chromosome number* unknown.

Illustrations: Fig. 4.16; spores Fig. 3.14.

Distribution and phytogeography (Fig. 4.15).

A. limbata is known only from Indonesia (Sumatra and Java) and Malaysia (Sabah).

A tropical Malesian endemic.

Ecology and phenology

Several important details of the precise ecological preferences of this species, as well as vegetative perennation, remain to be investigated (Long & Grolle, 1994). Recorded altitudes (Mount Kinabalu 1500–1700m and Mount Korinchi 2000–3000m) indicate that it is a taxon of warm temperate zones, growing in forest, sometimes in ravines. It is probably similar in aspects of its ecology to other better-known members of Sect. *Brachyblepharis* in its relative lack of adaptation to drying-out: the thalli are thin and delicate and usually grow on wet rocks, damp soil, walls *etc.* in shady habitats where a regular moisture supply is available.

Ripe sporophytes have been collected in July and September.

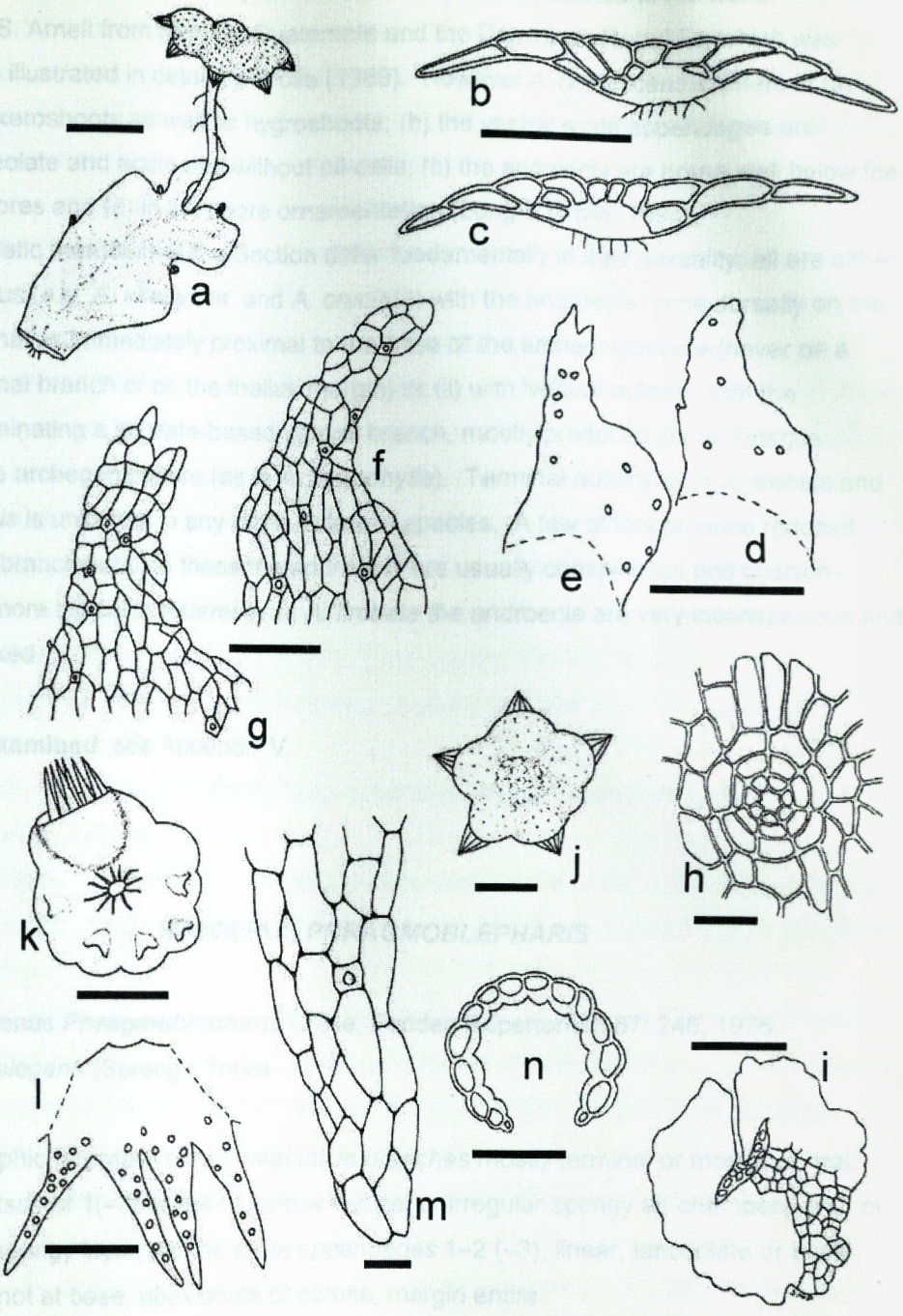

Fig. 4.16 *Asterella limbata*. a, plant habit with androecia and archegoniophore; b, c, t.s. thallus; d,e, ventral scales showing oil-cells and marginal slime-papilla; f, g, ventral scale appendages; h, air pore of dorsal epidermis; i, t.s. peduncle showing rhizoid furrow; j, carpocephalum from above showing protruding pseudoperianths; k, carpocephalum from below showing five undeveloped involucres and a single developed involucre containing a sporogonium and pseudoperianth; l, part of pseudoperianth showing undivided basal part, four segments free at tips, and distribution of oil-cells; m, apex of pseudoperianth segment with a single oil-cell; n, transverse section of pseudoperianth segment. a, j–n, Sumatra, *Meijer 8977*; b–g, Sumatra, *Meijer 8925*; h, l, Sabah, *Menzel et al. 4212.* Scale bars: a, j, k = 2mm; b, c, l = 1mm; d, e = 0.5mm; f, g = 0.2mm; l = 200µm; n = 100µm; h, m = 50µm.

Taxonomic notes

In its distinctive terminal autoicy *A. limbata* is most closely related to *Asterella dominicensis* S. Arnell from Mexico, Guatemala and the Dominican Republic, which was described and illustrated in detail by Grolle (1989). However *A. dominicensis* differs in (a) production of xeroshoots as well as hygroshoots; (b) the ventral scale appendages are narrowly lanceolate and acute and without oil-cells; (c) the androecia are borne well below the archegoniophores and (d) in the spore ornamentation (Long & Grolle, 1994).

Other Asiatic members of the Section differ fundamentally in their sexuality: all are either (i) par-autoicous (*e.g. A. khasyana* and *A. cruciata*) with the androecia borne dorsally on the midrib of the thallus immediately proximal to the base of the archegoniophore (never on a vestigial terminal branch or on the thallus margin) or (ii) with 'ventral autoicy', with the androecia terminating a stipitate-based ventral branch, mostly produced some distance proximal to the archegoniophore (as in *A. leptophylla*). Terminal autoicy as in *A. limbata* and *A. dominicensis* is unknown in any other *Asterella* species. A few others produce reduced terminal male branches but in these the androecia are usually conspicuous and cushion-shaped as is more typical in *Asterella*. In *A. limbata* the androecia are very inconspicuous and easily overlooked.

Specimens examined: see Appendix V.

SUBGENUS *PHRAGMOBLEPHARIS*

Asterella subgenus ***Phragmoblepharis*** Grolle, Feddes Repertorium 87: 246, 1976.

Type: *A. elegans* (Spreng.) Trevis.

Thalli xeromorphic, aromatic or not; *vegetative branches* mostly terminal or mostly ventral; *assimilation tissue* of 1(–3) layers of narrow vertical or irregular spongy air chambers, with or without lower spongy layer; *ventral scale appendages* 1–2 (–3), linear, lanceolate or ovate, constricted or not at base, apex acute or obtuse, margin entire.

Sexual condition par-autoicous or ventral-autoicous; *androecia* cushion-like; *carpocephalum* hemispheric, shortly to deeply lobed; *involucre* with free margin entire, sinuate-lobed, emarginate or deeply cleft; *pseudoperianth* not flattened or constricted, lobes united at apex, divided approximately to half.

Capsule lid fragmenting irregularly; *spores* type V or VI, dark brown, red-brown or yellow, with regularly and completely areolate or alveolate ornamentation similar on proximal and distal surfaces, trilete, with distinct proximal pole; *elaters* (1–)2-spiral.

Subgenus *Phragmoblepharis* is heterogeneous in several characters (*e.g.* involucre division, spore colour), but is united by its xeromorphic thalli, hemispheric carpocephala, united pseudoperianth lobes and areolate spores with similar sculpturing on both surfaces. Grolle (1976) segregated some species as Sect. *Pappiae* and Sect *Lindenbergianae*. Subdivision into sections is necessary but must be based on a broader survey of species worldwide. This is likely to result in recognition of four or more sections.

10. Asterella lindenbergiana (Corda ex Nees) Arnell, Lebermoosstudien in Nördlichen Norwegen: 2, 1892.

Basionym: *Fimbriaria lindenbergiana* Corda ex Nees, Naturgeschichte der Europäischen Lebermoose 4: 266, 283, Sept. 1838. Type citation: [Austria, Switzerland] 'auf den Alpen Salzburgs und der Schweiz; Herr Lindenberg fand sie unter Funck'schen Exemplaren der *Rebouilia hemisphaerica* aus dem Salzburgischen, und Herr Kützig auf dem Faulhorn in der Schweiz bei 6000' Höhe und auf dem Gemmi, (nach Herrn Hampe's Herbarium)'. Type specimen: Austria, Salzburg, *Funck s.n.* (W, lectotype, selected by Grolle (1976)).

Syn.: *Fimbriaria lindenbergiana* Corda ex Nees var. ß *angustior* Nees, Naturgeschichte der Europäischen Lebermoose 4: 283, 1838. Type citation: [Switzerland] 'Die Form ß auf dem Faulhorn und der Bachalpe in der Schweiz, (Kützing in Herrn Hampe's Herbarium)'. Type specimen: *n.v.*.

Syn.: *Fimbriaria major* Hampe in Nees, Naturgeschichte der Europäischen Lebermoose 4: 283, 1838, *nom. nud.* in syn.

Syn.: *Marchantia alpina* Schleich., *Catalogus Plantarum in Helvetia* ed. 3, 36, 1815, *nom. nud.*; synonymised by Nees (1838). Original material: [Switzerland] *Schleicher s.n.*, (BR, herb. Dumortier).

Syn.: *Fimbriaria bonjeanii* De Not., Memorie della Reale Accademia delle Scienze di Torino, Ser.2, 1: 335, 1839. Type citation: [France] 'In monte Cenisio ad Lacum detexit Bonjean, et mecum communicavit sub nomine *Marchantiae hemisphaericae*'. Type specimen: Mt. Cessit., *Bonjean s.n.* in herb. Hampe (BM, isotype).

Syn.: *Asterella bonjeanii* (De Not.) Trevis., Rendiconti del' Istituto Lombardo di Scienze e Lettere 7: 785, 1874.

Syn.: *Hypenantron bonjeanii* (De Not.) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 440, 1877.

Description

Thalli creeping over humus and bryophytes often forming conspicuous pale green patches up to 5cm diameter, when fresh with strong smell of rotten fish. *Vegetative branches* mostly terminal and regularly dichotomous, occasionally also producing a stipitate-based ventral innovation at apex beneath an archegoniophore; branches broad and flat, oblong to obovate, robust and leathery in texture but thin and not strongly xeromorphic, 10–30 x 3–8mm, pale green above with reddish margins, conspicuously notched at apex, in transverse section 1.0–

1.6mm thick, branches 4–5x as broad as thick; midrib stout, semicircular to triangular in transverse section, abruptly narrowing into broad thin thallus wings. Upper surface flat, without or with very shallow median channel, margins wavy, weakly upturned when moist becoming inrolled when dry, surface almost smooth with weak lines of low bulges over air chambers, air pores minutely raised. Lower surface and older parts of thallus red or red-brown. *Dorsal epidermis* cells irregularly rectangular, 30–60 x 20–40µm, walls thin, without trigones; in transverse section crenately bulging on upper surface; oil cells scattered. *Air pores* raised above surface, with orifice 17–35µm diameter, with surrounding cells strongly bulging inwards; cells in 6–8 rows of 2–3 concentric rings; cells of innermost ring 12–17µm in radial length, 15–25µm wide; cells of outermost ring 22–30µm in radial length, 17–45µm wide. *Assimilation tissue* 0.25–0.55mm thick, 1/4 to 1/3 thickness of thallus at midrib, of a spongy layer of irregular rounded air chambers in 2–3 layers; towards margins these chambers long, narrow and obliquely overlapping; free filaments absent; cells of partitions 25–40µm diameter; oil cells many. *Basal compact tissue* occupying the whole of the midrib, 0.65–1.1mm thick, more than twice thickness of assimilation tissue; cells variable in size, 25–45µm diameter; oil cells numerous. *Rhizoids*: smooth rhizoids 12–30µm diameter; pegged rhizoids 10–25µm diameter. *Ventral scales* semicircular, with purple body without pale marginal band, very large, 1400–2400 x 900–1200µm; median cells of body linear with acute ends, 80–200 x 15–27µm, walls weakly thickened, towards margin becoming shorter and strongly curved, often 'clustered' with several terminating together in a short point bearing slime papillae; margin irregularly crenate and with abundant, often paired slime papillae, 15–30 on curved (adaxial) side and 8–20 on straight (abaxial) margin; oil cells numerous, 15–40, 17–32µm diameter; scale appendages 1(–2), shortly oblong-lanceolate, 250–550 x 50–100µm, not (or very weakly) constricted and 5–10 cells broad at base, margin entire but usually with 1–6 slime papillae near base; cells proportionately shorter and broader than those of scale body, irregular in size and shape, 20–75 x 25–45µm; apex of 1–2 short rounded cells, oil cells absent or occasionally 1 at base.

Sexual condition usually par-autoicous. *Androecia* borne proximally to base of archegoniophore along midrib of main thallus; sometimes androecia borne along a separate terminal branch; androecium consisting of a low raised purplish ridge 0.6–2.8 x 0.2–0.5mm, sometimes V-shaped up to 2.4 x 1.2mm; ostioles clustered together or scattered, low and rounded, 150–200 x 225–250µm, without scales. *Archegoniophore* terminating main thallus branch, inhibiting further vegetative growth except for occasional ventral innovations beneath the apex. *Stalk* moderately stout, red-brown when mature, 10–25 x 0.8–1.1mm, in transverse section ellipsoid with very deep rhizoid furrow 0.4–0.8mm deep, often stellately divided within stalk; medullary cells small, 15–30µm diameter, thin-walled; epidermal cells similar in size but reddish and with thicker walls; stalk with scattered pendant scales throughout, denser at base of stalk but not forming a dense ring, scales linear, 0.9–1.5mm long x 20–80µm, mostly 2 cells wide, occasionally 4–8 cells wide in middle; around apex of stalk a conspicuous reddish pendant beard with similar scales up to 3mm long. *Carpocephalum* hemispheric, reddish-green, 3–5mm diameter, deeply 2–4-lobed, the lobes inclined at an angle of c 30° to stalk;

apical dome distinctly warted with low rounded warts, lobes smooth with sinuate distal margin. *Involucre* 1.2–1.3mm from base to free margin, with free margin deeply sinuate-lobed, indentations 0.1–0.3mm, rounded, otherwise entire. *Pseudoperianth* white, usually tinged pink, 2.6–2.9mm long; basal cup 1–1.2mm long; cells of base lax-rectangular, 100–200 x 30–50µm; lobes 16–18, some of these incompletely separated, 1.6–1.75 x 0.15–0.35mm, not constricted at insertion, strongly united at apex into short blunt tubular beak, margins narrowly recurved, lobe cells narrow rectangular, 75–180 x 20–30µm, towards apex much shorter and mammillately bulging outwards around beak; oil cells absent from base and lobes.

Capsule globose, dark red-brown, 1–1.3mm diameter; cells of urn rectangular, 75–125 x 25–45µm, thin-walled; cells of lid subquadrate, 30–37µm diameter, thick-walled. *Spores* (light microscope) purplish-brown, 80–100µm diameter. *Spores* (SEM) TYPE V: trilete, without equatorial apertures, with similar proximal and distal sculpturing; distal surface without primary areolae, but densely and deeply alveolate with ± uniform alveoli 4–6µm diameter; pits absent; muri broad, flat and smooth; equatorial rim narrow; proximal ornamentation similar to distal; facets ± flat, trilete ridges rounded. *Elaters* dark red-violet, 80–175 x 12–17µm, rigid, slightly tapering to abruptly rounded-truncate ends; 1-spiral at ends, mostly 2-spiral in middle. *Chromosome number* n = 9 (Tatuno, 1960; Arnell, 1956; confirmed here).

Illustrations: Müller (1951–1958: Fig. 70); spores Fig. 3.15.

Distribution and phytogeography (Fig. 4.17).

In the study area the species is restricted to Europe and has been confirmed from Austria, Italy, France, Germany, Poland, Switzerland, Roumania, Slovakia, Slovenia, Norway and Sweden. Additional literature records exist from Spain (Allorge, 1956) and Finland (Müller, 1951–1958; Arnell 1956; Koponen *et al.*, 1977). The record from Turkey (Gökler & Öztürk, 1991) refers to *Corsinia coriandrina* (Spreng.) Lindb. (Grolle, *pers. comm.*). Outside Europe *A. lindenbergiana* is known from the U.S.A., Canada and Alaska (Evans, 1920, 1923).

Phytogeographically, in Europe it is a truly Alpine species with its stronghold in the Alps; it is absent from Greenland, Siberia and in Scandinavia becomes rare in the Arctic. In North America it occurs only in the Rocky Mountains from Washington north to southern Alaska.



Fig. 4.17 Distribution of *Asterella lindenbergiana* in Eurasia, based on specimens studied.

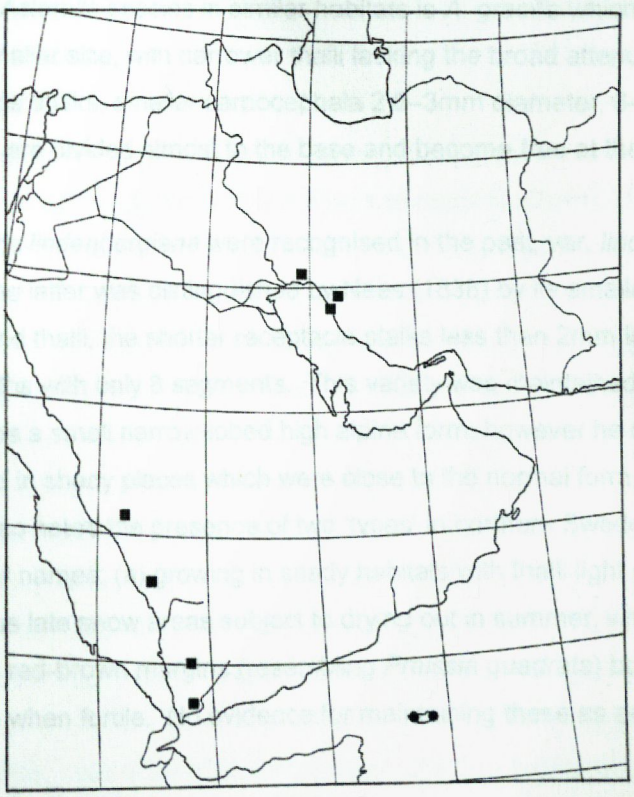

Fig. 4.18 Distribution of *Asterella persica* and *A.pappii* in Eurasia, based on specimens studied. ● = *A. pappii* ■ = *A. persica*

Ecology and phenology

Asterella lindenbergiana is a typical Alpine species in favouring high altitudes in the Alps of central Europe typically from 1800 to 2750m above sea level; in Scandinavia it can occur at much lower altitudes, sometimes descending to the tree-line, or in northern latitudes to as low as 150m. In eastern Europe (Czech Republic) it has been recorded down to 1400m. It is a calcicole, usually found on limestone, though not growing directly on the rock but in humus-filled crevices, small caves, rock ledges, under boulders, *etc.* where it obtains shade and moisture. It is particularly characteristic of snow-bed vegetation and late-snow hollows. Typical associates in these habitats are the liverworts *Athalamia hyalina, Marchantia polymorpha* subsp. *montivagans, Peltolepis quadrata, Preissia quadrata* and the mosses *Brachythecium glaciale*, *B. reflexum*, *Distichium capillaceum, Orthothecium chryseum, O. rufescens*, *Pohlia cucullata, Scorpidium turgescens* and *Tayloria froehlichiana* (Schiffner, 1939).

In alpine habitats *A. lindenbergiana* is in active growth during the summer months and produces ripe sporogonia from June to October.

Taxonomic notes

(1) Ventral tubers similar to those of *Conocephalum conicum* (L.) Dumort. were reported by Evans (1920) from North American material. These could not be found on any of the European specimens examined.

(2) In Europe *A. lindenbergiana* is not likely to be confused with other species. In snow-bed vegetation it can grow with other Marchantiales such as *Athalamia hyalina* and *Preissia quadrata* but when lacking carpocephala it can readily be distinguished by its strong fishy smell when fresh. The only other *Asterella* species in similar habitats is *A. gracilis* which can be distinguished by its much smaller size, with narrower thalli lacking the broad attenuate wings, by its more slender receptacle stalks, smaller carpocephala 2.6–3mm diameter, 6–8 pseudoperianth lobes which are divided almost to the base and become free at the tips, and yellow spores.

(3) Two varieties of *Fimbriaria lindenbergiana* were recognised in the past, var. *lindenbergiana* and var. *angustior* Nees. The latter was distinguished by Nees (1838) by its smaller size in all parts, more deeply channelled thalli, the shorter receptacle stalks less than 2mm long, and fewer (2 or 3) pseudoperianths with only 8 segments. This variety was maintained by Schiffner (1939), and was described as a small narrow-lobed high alpine form; however he noted that intermediate plants occurred in shady places which were close to the normal form. Mårtensson (1955–1956) also noted the presence of two 'types' in northern Sweden, but did not give these formal rank or names: (a) growing in shady habitats with thalli light green and shining, and (b) in calcareous late snow areas subject to drying out in summer, with thalli dark green, less shining and with red-brown margins (resembling *Preissia quadrata*) but easily separable from that species when fertile. No evidence for maintaining these as accepted taxa has been found.

Historical and nomenclatural notes

There has been confusion over the date of publication of *Fimbriaria bonjeanii* De Not. According to Geissler & Natali (1990: 88) the De Notaris paper was published 'mese di settembre del 1838' (*i.e.* in mid September 1838.). According to Stafleu & Cowan (1976–1988), Volume 4 of Nees was also published in Sept. 1838. However, unpublished research by Grolle (*pers. comm.*) suggests that the date of 1839 (Stafleu & Cowan, 1976–1988) for *Memorie della Reale Accademia delle Scienze di Torino, Ser.2*, 1: 335, is correct, not 1838. There is no evidence for the date September 1838 given in Geissler & Natali (1990). Thus Nees' *F. lindenbergiana* was probably published in 1838 and De Notaris' *F. bonjeanii* in 1839.

Geissler (*pers. comm.*) has also researched the type locality of *Fimbriaria bonjeanii* 'In monte Cenisio ad Lacum', which, though in Italy at the time of publication, is now just within France.

Specimens examined: see Appendix V.

11. Asterella persica (Steph.) M.Howe, Bulletin of the Torrey Botanical Club 25: 191, 1898. Basionym: *Fimbriaria persica* Steph., Hedwigia 33: 7, 1894. Type citation: Persia, sine loco natali. leg. Haussknecht. Ex herb. Rabenhorst, dedit Dr. G. Winter. Type specimen: Persia, *Haussknecht* (G-15258, lectotype, selected by Grolle (1976)); BM, G-14590, isolectotypes); Persia, prope Schahpur, *C. Haussknecht*, herb. Juratzka, as *Fimbriaria haussknechtii*, (W, JE, isolectotypes); Persia austro-occ., Schahpur, ad rupes, iii 1867, *C. Haussknecht s.n.* (JE, isolectotype).

Description

Thalli forming semi-pure patches mixed with other bryophytes, mostly on soil or soil-covered rocks. *Vegetative branches* mostly ventral in origin, but with occasional terminal dichotomies; branches 10–16 (–20) x 3–4.1mm, thick and leathery (all xeroshoots), bluish-green above with dark purple margins, rounded and scarcely notched at apex, in transverse section 1.05–1.55mm thick, branches 2.5–3x as broad as thick; midrib broad, gradually tapering into thallus wings. Upper surface weakly concave with raised undulate margins, strongly inrolled when dry, not reticulate and air pores not visible above. Branches dark purple beneath. *Dorsal epidermis* cells 30–100 x 20–40µm, with or without small trigones; oil cells scattered. *Air pores* with orifice 17–30µm diameter, cells in 5–7 rows of 2–3 concentric rings; innermost cells 10–13µm in radial length, 12–25µm wide; outermost cells 20–27µm in radial length, 25–52µm wide. *Assimilation tissue* dense, 0.25–0.45mm thick, 1/5 to 1/4 thickness of thallus, of 1 layer of tall narrow air chambers over midrib and 1–3 layers of obliquely ascending air chambers in thallus wings; air chambers over midrib with short 1–2-celled mammilla-like outgrowths (very short filaments) below air pores; cells of air chamber partitions 25–35µm diameter; oil cells

frequent. *Basal compact tissue* thick, 0.8–1.1mm tall; cells 15–45µm diameter; oil cells occasional. *Rhizoids*: smooth rhizoids 15–35µm diameter; pegged rhizoids 8–25µm diameter. *Ventral scales* with dark red body with paler inner margin, 900–1050 x 750–1000µm; cells of body 37–130 x 18–37µm, becoming narrower, paler and thin-walled along curved median margin; oil cells 9–12, mostly around inner margin, 25–40µm diameter; margin denticulate to subentire with short irregular teeth bearing a slime papilla, slime papillae 2–8 on each side, 1–2-celled; scale appendages 1–2 per scale, narrowly lanceolate, 550–1100 x 125–175µm, 4–8 cells wide at insertion, not constricted, apex filiform, of 1–2 uniseriate cells, appendage cells longer and narrower than scale body cells, 60–150 x 15–35µm, margin entire or occasionally with a slime papilla at extreme base, oil cells absent or 1 at base.

Sexual condition ventral-autoicous; androecia median to subapical, borne on main thallus or large ventral branches; archegoniophore terminating a ventral branch. *Androecia* cushion-like, green to dark purple, rounded to linear-elliptic, 1.2–2.4 x 0.8–1mm, without marginal scales; antheridia not seen; ostioles tall, conical, widely spaced, 200–270 x 150–250µm. *Archegoniophore* borne on female branches spathulate to oblong, 3.6–6.4 x 2.8–3.2mm, otherwise similar to vegetative branches. *Stalk* 6–28 x 0.6–0.85mm, with rhizoid furrow 200–300µm deep; medullary cells 15–40µm diameter; epidermal cells 12.5–25µm diameter; stalk naked at base but with scattered linear scales in lower half when young; scales linear, 1.1–1.4mm long x 80–105µm wide, up to 4 cells wide; apex of stalk bearded with longer scales 2.2–4mm long. *Carpocephalum* rounded and subglobose when young, becoming depressed-hemispheric or broadly dome-shaped when mature, 3.5–4.5mm broad (excluding pseudoperianths), deeply 3–5-lobed with usually 3–4 lobes fertile, lobes spreading at 40–50° to stalk; dome coarsely warted with projecting air chambers; lobes with smooth unwarted distal margin. *Involucre* conspicuous ventrally beneath lobes, 1.2–1.5mm from base to free margin, with weakly sinuate or straight free margin with conspicuous median emargination or cleft 300–500µm deep. *Pseudoperianth* brownish-white or pinkish tinged, 2.5–3.5mm long; undivided basal cup 1.3–1.8mm long, cells of base 170–275 x 30–45µm; lobes 9–13, 1.1–1.7 x 0.35–0.65mm, united at apex into a tubular beak, margins recurved when dry, lobe cells 75–175 x 15–25µm; beak cells with papilla-like outgrowths of cells projecting inwards; oil cells absent or 1–4 in lobes.

Capsule c 1mm diameter (not seen undehisced); cells of urn rectangular, 50–10 x 25–45µm; cells of lid subquadrate, 30–50µm diameter, with large trigones. *Spores* (light microscope) dark red-brown, 80–130µm in diameter. *Spores* (SEM): Type V: trilete, without equatorial apertures; proximal and distal surfaces with similar sculpturing, distal surface without regular complete primary areolae, but with numerous irregular alveoli very variable in size (2–7µm diameter) and minute pits; muri broad and flat, pitted; equatorial rim narrow but conspicuous; proximal facets flat, with primary reticulation slightly more clearly defined than on distal surface. *Elaters* 120–180 x 10–17µm, bispiral. *Chromosome number* unknown.

Illustrations: Frey et al. (1991: Fig. 9); spores Fig. 3.16.

Distribution and phytogeography (Fig. 4.18).

Asterella persica is not known outside the study area, where it has been confirmed from Iran (Prov. Fars), North Yemen and Saudi Arabia (Asir Mountains).

It may be considered as a warm-temperate Middle Eastern endemic.

Ecology and phenology

A strict xerophyte growing in arid habitats on soil and rock, invariably where shaded as amongst large boulders or in crevices on cliffs. Recorded altitides are 2300m in Yemen and 2040–2130m in Saudi Arabia.

Sporophytes appear to mature during the winter months, from January to April.

Taxonomic notes

Asterella persica is very closely related to *A. pappii*; the most striking difference between the two is the spore ornamentation as seen under SEM: in *A. persica* the distal surface of the spores lacks clearly-defined primary areolae but is covered with numerous irregularly-sized alveoli, in *A. pappii* the distal surface has a clear network of large ± uniformly-sized primary areolae. Vegetatively the two species appear to differ only in their ventral scales: appendages longer in *A. persica* (550–1100µm) than *A. pappii* (300–500µm), with longer cells in *A. persica* (37–130µm) than *A. pappii* (5–60µm); in *A. persica* the cells of the scale appendages appear to be distinctly longer than those of the scale body, whereas in *A. pappii* they are subequal; in *A. persica* the scale body has 9–12 oil cells while in *A. pappii* there are 8–18. These and other differences (such as size of thalli and length of stalk) between the two species should be treated with great caution as they may reflect in part stature differences due to phenotypic plasticity.

Historical and nomenclatural notes

Grolle (1976: 180) typified *Fimbriaria persica* by a 'holotype'. As Stephani (1894) did not designate a type, a lectotype is required. The designation of a 'holotype' by Grolle is now considered as effective lectotypification (Greuter *et al.*, 1994, Art. 9.8).

Specimens examined: see Appendix V.

12. Asterella pappii (Gola) Grolle, Feddes Repertorium 87: 246, 1976.

Basionym: *Fimbriaria pappii* Gola, Annali di Bot. 13: 64, 1914. Type citation: [Ethiopia] Eritrea-Assaorta; sull'altipiano dell'Agametta a.m. 1000 sm. 13. iii. 1893 (Pappi), n. 3132; Hamasen: tra Filfil e Moglio m 1000 sm, 1. iv. 1909 (Fiori).; Type specimen: Äthiopien, Eritrea-Assaorta, sull'altipiano del Agametta, 1000m, 13.iii.1893, *Pappi 3132* (FI, lectotype fide Frey & Kürschner (1988), *n.v.*).

Syn.: *Hypenantron pappii* (Gola) Cufod., Phyton (Horn) 4: 79, 1952.

Syn.: *Fimbriaria pusilla* Mitt., in Balfour, Transactions of the Royal Society of Edinburgh 31: 33, 1888. Type citation: [Yemen] 'Socotra. Common on the rocks in many places. [Balfour] B.C.S. n. 1327' ; type specimen: Socotra, *Balfour* (NY, herb. Mitten, lectotype), Socotra, Feb.–March 1880, *B. Balfour 1327* (BM, isotype); synonymised by Frey & Kürschner (1988).

Description

Thalli forming pure patches or mixed with mosses on soil. *Vegetative branches* mostly ventral in origin; terminal dichotomies rare; branches 5–12 x 1.2–2.4 mm (up to 4.0mm broad in Ethiopian material), thick and leathery (all xeroshoots), bluish-green above with purple margins, rounded and weakly notched at apex, in transverse section 0.8–1mm thick; branches 1.5–2x as broad as thick; midrib broad, suddenly contracted into thallus wings. Upper surface concave with raised undulate margins, which become strongly inrolled and tubular when dry, smooth, not reticulate and air pores not visible above. Lower surface dark red-purple. *Dorsal epidermis* cells 50–110 x 25–50µm, without trigones; oil cells scattered. *Air pores* weakly raised, with orifice 15–20µm diameter, cells in mostly 6 rows of (1–)2 concentric rings; innermost cells 10–15µm in radial length, 15–25µm wide; outermost cells 20–25µm in radial length, 30–50µm wide. *Assimilation tissue* 0.2–0.3mm thick at midrib, 1/4 to 1/3 total thickness of thallus, of 1 layer of tall narrow air chambers over midrib and 1–3 overlapping layers obliquely ascending narrow air chambers in thallus wings; air chambers over midrib with short 1–2-celled filamentous outgrowths below air pores; cells of partitions 20–35µm diameter; oil cells scattered. *Basal compact tissue* 0.5–0.75mm thick in midrib, more than 2x as thick as assimilation tissue; cells 20–40µm diameter. *Rhizoids*: smooth rhizoids 15–25µm diameter; pegged rhizoids 10–20µm diameter. *Ventral scales* with very dark purple-red body with paler margins, 800–1000 x 700–800µm; cells of body 60–120 x 25–45µm, becoming narrower and more thin-walled towards curved (median) margin; oil cells 8–18, scattered, 30–45µm diameter; margin denticulate with short irregular blunt teeth, these often bearing an apical slime-papilla; slime-papillae 2–4 on each side, 1–2-celled; scale appendages mostly 2 per scale, equal or occasionally one much smaller, narrowly lanceolate, 400–1000 x 150–250µm, 4–6 cells wide at insertion, not constricted, apex filiform, of 2–3 uniseriate cells, appendage cells subequal to body cells, margin entire or with a single tooth and/or slime papilla near base; oil cells absent or 1 near base.

Sexual condition ventral-autoicous; androecia median to subapical, borne on small to large ventral branch; archegoniophore terminating a ventral branch. *Androecia*, cushion-like, green, elliptic, rarely linear, 1–1.2 x 0.6–0.8mm, without marginal scales; antheridia not seen; ostioles tall, conical, widely spaced, 200–250µm tall and broad. *Archegoniophore* borne on ventral female branch which is spathulate to oblong, 2.6–6 x 2–3mm, otherwise similar to vegetative branches. *Stalk* 2.5–5.2 x 0.55–0.7mm, with rhizoid furrow 165–200µm deep; medullary cells 15–30µm diameter; epidermal cells 12–25µm diameter; stalk scales linear, 0.75–1.9mm long x 40–90µm wide, 1–2 cells wide; scales of apical beard similar. *Carpocephalum* depressed hemispheric, 3.6–4mm diameter, deeply 3–4-lobed, lobes spreading at 40–45° to stalk, central dome warted; lobes with entire distal margin without warts. *Involucre* 1–1.2mm from base to free margin, with smooth free margin and median emargination. *Pseudoperianth* brownish or pinkish-tinged, 2.4–2.5mm long; undivided basal cup c 1mm long, cells of base 85–125 x 25–40µm; lobes 9–11, 1.4–1.5 x 0.3–0.55mm, united at apex into a tubular beak, margins recurved when dry, lobe cells 60–160 x 20–50µm; beak cells with papilla-like outgrowths of cells projecting inwards; oil cells absent. *Capsule* c 1.2mm diameter (not seen undehisced); cells of urn quadrate to rectangular, 35–55µm long; cells of lid subquadrate, 30–37µm diameter, with large trigones. *Spores* (light microscope) red-brown, 97–108µm diameter. *Spores* (SEM) Type V: trilete, without equatorial apertures; proximal and distal surfaces with similar sculpturing, distal surface with regularly sized complete primary areolae 9–17µm diameter ± distinctly defined, these containing secondary alveoli and pits; muri broad and flat, regularly pitted; equatorial rim narrow but conspicuous; proximal facets flat, with ornamentation as on distal surface. *Elaters* 210–250 x 12–17µm, mono- or bispiral. *Chromosome number* unknown.

Illustrations: Frey et al. (1991: Fig. 8); spores Fig. 3.17).

Distribution and phytogeography (Fig. 4.18).

In the study area only known from Yemen (Socotra); elsewhere only reported from Ethiopia (Gola, 1914a; Cufodontis, 1952; Frey & Kürschner, 1988; Frey, Grolle & Kürschner, 1991). Records for Saudi Arabia and North Yemen in Long (1987), Kürschner (1989) and Frey & Kürschner (1988, 1991) all refer to *A. persica*.

It may be considered as a dry tropical NE-African species, extending to the island of Socotra.

Ecology and phenology

A strict xerophyte recorded on Socotra from soil and soil-covered rocks on limestone escarpment, at altitudes of 560 and 790m. In Ethiopia it is recorded from 1000m.

From the limited material available spore production appears to be in the winter months, February and March in both Ethiopia and Socotra.

Taxonomic notes

Very closely allied to *A. persica*; for differences see under that species. So little material of this species is available for study that it is uncertain if the vegetative differences between the two species are significant. The Ethiopian material studied appears to be more robust and with broader thalli than Socotran collections. Further collections and observations on living plants are much-needed.

Historical and nomenclatural notes

The oldest name for this species is *Fimbriaria pusilla* Mitt. published in 1888 based on Socotran material collected by Balfour in 1880. However, the name *Asterella pusilla* cannot be used for this species as the name already exists [*A. pusilla* Shimizu & S.Hatt. 1952] for a Japanese species which is now a synonym of *A. leptophylla* (Mont.) Grolle. *Fimbriaria pappii* is the earliest available name.

13. Asterella mussuriensis (Kashyap) Verd., Annales Bryologici 8: 156, 1935.

Basionym: *Fimbriaria mussuriensis* Kashyap, Journal of the Bombay Natural History Society 24: 345, 1916. Type citation: [India, Uttar Pradesh] 'Moist shady places, Mussoorie.'

Type specimen: Mussoorie, June 1913, *Kashyap 74*, ex Panjab University (JE, ?isotype).

Description

Thalli growing as scattered stems amongst other bryophytes or forming small patches 3–6cm broad on rocks and soil. *Vegetative branches* elongate, 4–11(–45) x 2.5–4mm, mostly ventral in origin with narrow stipitate base, also with occasional terminal innovations, thick and leathery (all xeroshoots), with purple edges, rounded and very shortly notched at apex, appearing segmented with basal constrictions; in transverse section 0.5–0.8mm thick. Upper surface flat or slightly concave with raised margins, strongly inrolled when dry, green but becoming dark purple in open habitats and when older, not reticulate, with minute whitish pores. Branches green or purple beneath. *Dorsal epidermis* cells 30–50 x 12.5–27µm. *Air pores* with orifice 25–35µm diameter; cells in 7–10 rows of 3–4 concentric rings; innermost cells 7.5–12.5µm in radial length, 12.5–20µm in width; outermost cells 20–27µm in radial length, 27–50µm in width. *Assimilation tissue* 0.2–0.35mm thick, less than half thickness of thallus, of 1(–3) layers of small air chambers over midrib, and 1–2 layers of larger obliquely ascending air chambers in thallus wings; uppermost chambers of midrib often with short 1–2-celled mammilla like ingrowths of green tissue below air pores; cells of air chamber partitions 7.5–20µm wide. *Basal compact tissue* 0.3–0.45mm thick; cells 25–50µm diameter; oil cells abundant. *Rhizoids*: smooth rhizoids 15–25µm diameter; pegged rhizoids 7.5–15µm diameter. *Ventral scales* with body strongly vinous red-pigmented but with paler margins, 700–1000 x 650–1200µm, cells of body 32–75 x 20–25µm, becoming paler, narrower and more thin-walled towards curved (median) margin; oil cells mostly close to margins, 5–15(–23) per body, 30–

40µm diameter; margin entire except for 4–6 slime papillae on each side; scale appendages 1–2 per scale, narrowly lanceolate, 350–500 x 75–125µm, 3–4(–5) cells wide at insertion, not constricted, apex bluntly acute, cells 50–80 x 25–45µm, margin entire, without slime papillae, oil cells absent.

Sexual condition ventral-autoicous with androecia and archegoniophores borne on usually numerous short ventral branches, produced along main thallus, female and male branches randomly mixed, becoming lateral by elongation of main thallus; both androecia and archegoniophores limiting further vegetative growth. *Androecia* cushion-like, purplish, on short ventral branches similar in size to female branches but with reduced or no wings, surrounded by scattered reddish lanceolate scales 175–200 x 90–150µm, similar to ventral scale appendages; ostioles bluntly conical, 100–125µm tall and broad. *Archegoniophore* terminal on short ventral branches, occasionally terminal on main branch; female branches heart-shaped, green above, purple below, c 2 x 2mm on narrow stipe c 1mm long, with distinct wings. *Stalk* 7.5–12mm long, 390–480µm diameter at middle; rhizoid furrow 200–240µm deep; medullary cells 20–42µm diameter; epidermal cells 15–20µm diameter; stalk with few scattered linear scales along its length and more numerous long hanging hyaline scales at apex; apical scales narrow linear-subulate, 1.8–3.8mm long, mostly 2 cells broad but at base up to 6 cells broad; margin entire except for a few slime papillae towards base; oil cells absent. *Carpocephalum* rounded, green and subglobose when young, when mature 3–4.2mm diameter, depressed-hemispheric with central dome, margin shortly to deeply lobed with 1–4 large lobes bearing sporogonia and 1–2 vestigial lobes; large lobes cylindric, borne at 45–50° to stalk; dome strongly warted with protruding air chambers and pores, becoming purple-tinged and often completely purple when mature; lobes with fewer warts and almost smooth at apex. *Involucre* hyaline or reddish tinged, 1–1.1mm from base to free margin, free margin coarsely crenate, with median cleft 350–400µm deep. *Pseudoperianth* white or pale purplish, 1.9–2mm long; undivided basal cup 0.85–0.9mm long, cells of base 120–210 x 17–45µm; lobes 8–11, 1.05–1.1 x 0.2–0.25mm, united at apex into a tubular beak, margins revolute when dry, lobe cells 50–125 x 17–25µm; beak cells mammillose internally; oil cells absent or up to 7 per lobe. *Capsule* 1.2–1.4mm diameter; cells of urn 37–85 x 22–50µm; cells of lid irregularly quadrate, 25–55µm diameter, with conspicuous trigones. *Spores* (light microscope) dark red-brown, 80–110µm diameter. *Spores* (SEM) Type V: trilete without equatorial apertures; proximal and distal surfaces with similar sculpturing; on distal surface with large conspicuous areolae 6–15µm diameter densely packed with deep alveoli and pitted; muri broad and flat, alveolate; equatorial rim narrow but conspicuous; proximal facets flat, with conspicuous thickened trilete ridges. *Elaters* 130–195 x 12.5–20µm, distinctly broader at middle, mostly bispiral. *Chromosome number* (subsp. *mussuriensis*): n=9 (Kanwal, 1976); (subsp. *crassa*): n=9 (Tatuno, 1955).

Key to subspecies of *A. mussuriensis*

1. Mature carpocephala with low rounded warts as broad as tall, deeply lobed with fewer warts on lobes 13a. subsp. ***mussuriensis***

\+ Mature carpocephala with tall warts at least twice as tall as broad, lobes short, warted to apex 13b. subsp. ***crassa***

13a. *Asterella mussuriensis* (Kashyap) Verd. subsp. ***mussuriensis***

Syn.: *Fimbriaria purpureo-capsulata* Herzog & C.E.O.Jensen, in Handel-Mazzetti, Symbolae Sinicae 5: 4, 1930. Type citation: [China] 'S. [Sichuan]: Auf nackter Kalkerde der Hg. St. auf dem Liuku-liangdse, 27°48', zwischen Yenyüen und Kwapi, 3450–3550 m, 17.v.1914 (2288).' Type specimen: Prov. Setschwan, austro-occid.: in montis Liuku-liangdse 27°48', inter oppidum Yenyüen et castellum Kwapi regione temperata, ad terram nudum, substr. calceo, alt. ca. 3450–3550m, 17.v.1914, *Handel-Mazzetti* (Diar. Nr. 459) Nr. 2288 (JE, **lectotype selected here**; WU, W, isolectotypes); synonymised by Piippo (1990).

Description

As for the species, but vegetative branches mostly short, up to 11mm; mature carpocephala with low rounded warts as broad as tall on central dome, carpocephala deeply lobed with fewer warts on lobes.

Illustrations: Fig. 4.19; spores Fig. 3.18.

Distribution and phytogeography (Fig. 4.20).

In the study area this subspecies confirmed from Pakistan, India (Himachal Pradesh, Uttar Pradesh, West Bengal, Sikkim); Nepal; Bhutan and China (Sichuan, Yunnan). Reports have also been published from S. India (Chopra, 1938a; Joshi & Birardar, 1984).

Phytogeographically the species is temperate E-Asiatic; this subspecies is Sino-Himalayan.

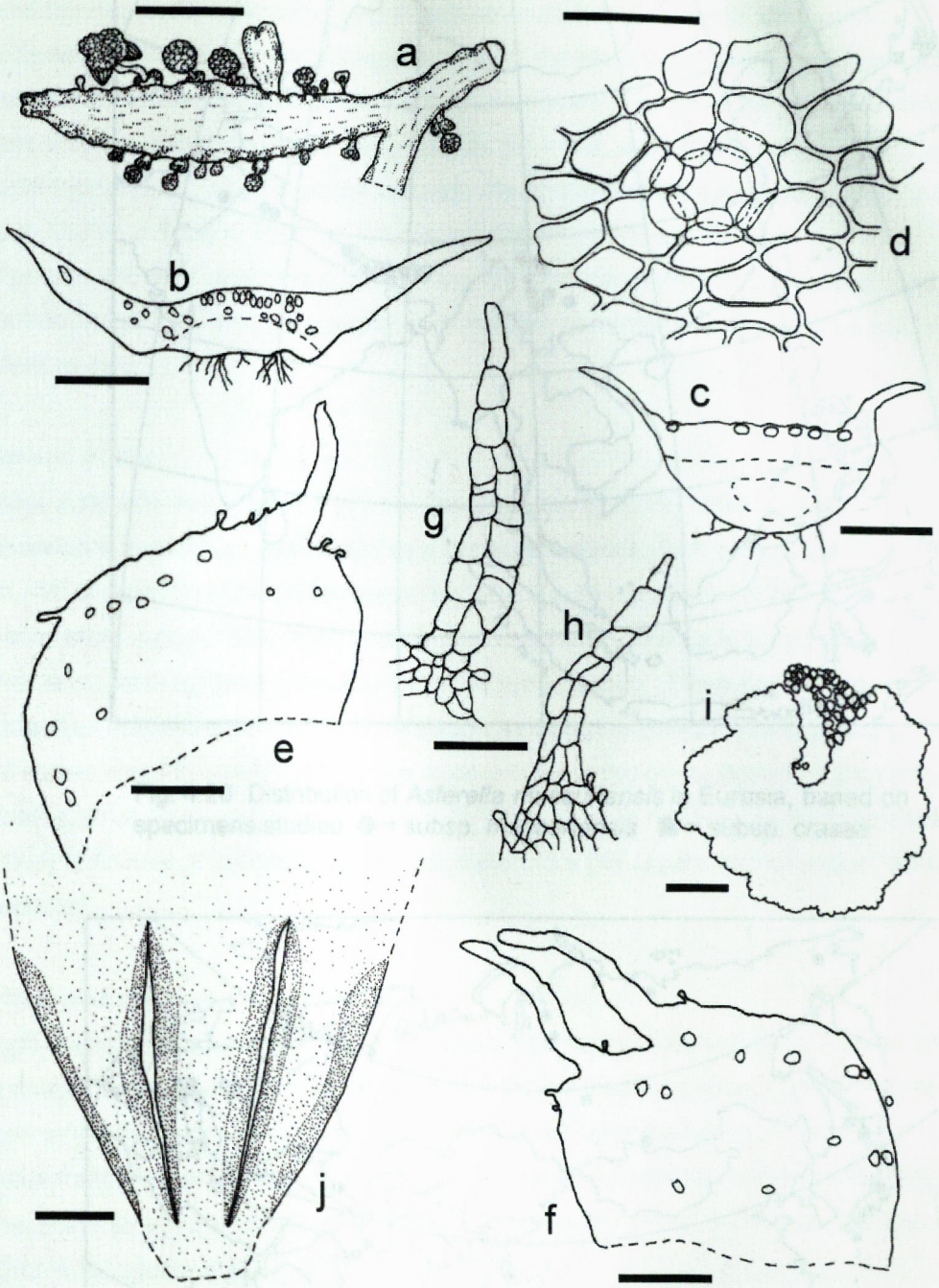

Fig. 4.19 *Asterella mussuriensis* subsp. *mussuriensis*. a, fertile plant with male and female ventral branches; b, c, t.s. thallus; d, air pore; e, f, ventral scales with oil cells and marginal slime papillae; g, h, ventral scale appendages; i, t.s. stalk of carpocephalum; j, part of pseudoperianth. a, b, h, India, Darjeeling, *Long 22351*; c, d, g, Nepal, *Long 21541*; e, f, i, j, China, Yunnan, *Long 18931*. Scale bars: a = 5mm; b, c = 500µm; e, f, j = 200µm; g, h, i = 100µm; d = 50 µm.

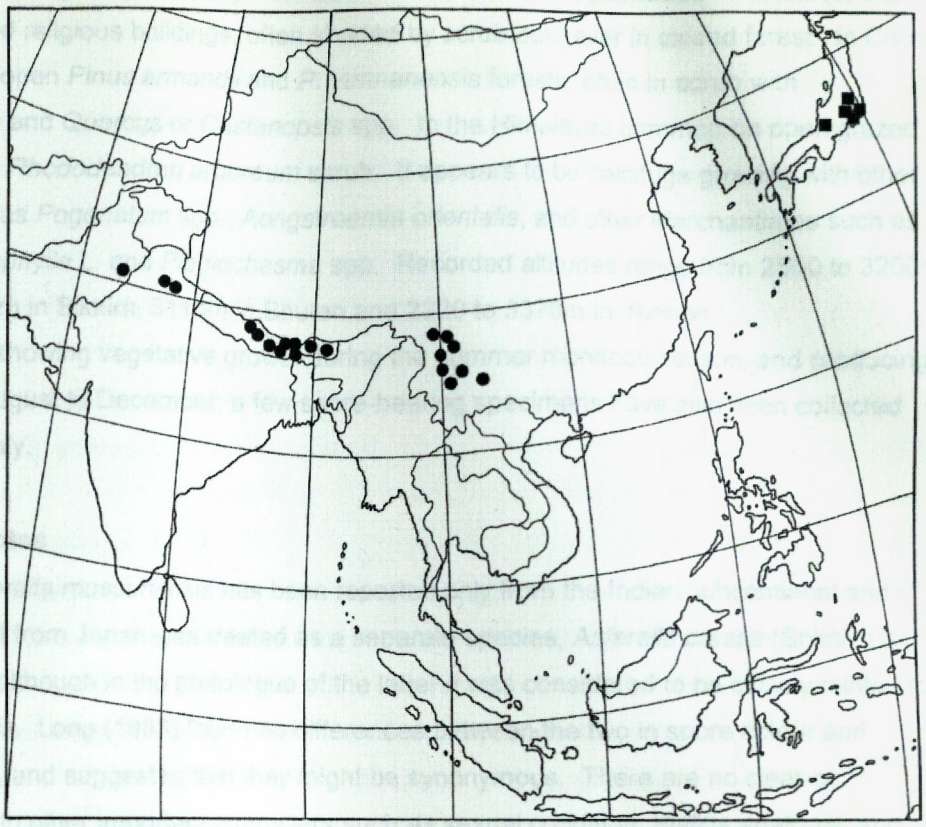

Fig. 4.20 Distribution of *Asterella mussuriensis* in Eurasia, based on specimens studied ● = subsp. *mussuriensis* ■ = subsp. *crassa*

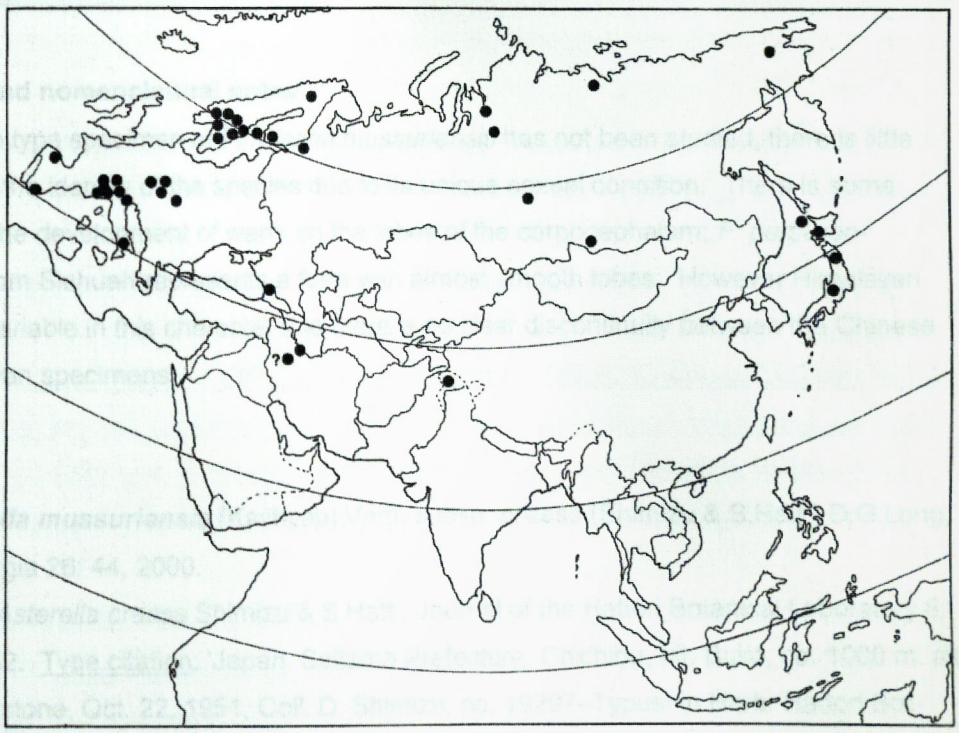

Fig. 4.21 Distribution of *Asterella gracilis* in Eurasia, based on specimens studied.

Ecology and phenology

A xerophyte, growing in open sunny habitats in turf on banks and pathsides on hillsides, often on old walls and religious buildings, often shaded by scrub but never in closed forest. In China recorded from open *Pinus armandii* and *P. yunnanensis* forests, often in scrub with *Rhododendron* and *Quercus* or *Castanopsis* spp. In the Himalayas common on open grazed hillsides and in *Rhododendron arboreum* scrub. It appears to be calcifuge growing with other pioneers such as *Pogonatum* spp., *Aongstroemia orientalis*, and other Marchantiales such as *Targionia hypophylla* L. and *Plagiochasma* spp. Recorded altitudes range from 2500 to 3200m in Nepal, 1830m in Sikkim, 3110m in Bhutan and 2220 to 3370m in Yunnan.

Typically showing vegetative growth during the summer monsoon season, and producing spores from August to December; a few spore-bearing specimens have also been collected from April to July.

Taxonomic notes

Until now, *Asterella mussuriensis* has been reported only from the Indian subcontinent and China; material from Japan was treated as a separate species, *Asterella crassa* (Shimizu & Hattori, 1952) although in the protologue of the latter it was considered to be closely related to *A. mussuriensis*. Long (1998) found no differences between the two in spore colour and ornamentation, and suggested that they might be synonymous. There are no clear-cut discontinuities in other important characters such as sexual condition, thallus anatomy, and ventral scales, the only reliable differences appear to be in the development of protruding air-chambers (warts) on the carpocephalum and its lobes. These relatively minor differences are most likely indicative of geographical races and therefore the Japanese material is retained as a subspecies.

Historical and nomenclatural notes

Although the type specimen of *Fimbriaria mussuriensis* has not been studied, there is little doubt about the identity of the species due to its unique sexual condition. There is some variation in the development of warts on the lobes of the carpocephalum; *F. purpureo-capsulata* from Sichuan represents a form with almost smooth lobes. However Himalayan material is variable in this character and there is no clear discontinuity between the Chinese and Himalayan specimens.

13b. *Asterella mussuriensis* (Kashyap) Verd. subsp. ***crassa*** (Shimizu & S.Hatt.) D.G.Long, Lindbergia 26: 44, 2000.

Basionym.: *Asterella crassa* Shimizu & S.Hatt., Journal of the Hattori Botanical Laboratory 8: 48, 1952. Type citation: 'Japan. Saitama Prefecture: Chichibu, Mt. Buko, ca. 1000 m. alt., on limestone, Oct. 22, 1951, Coll. D. Shimizu, no. 19297–Typus! in Herb. Hattori Bot. Lab.'. Type specimen: Japan, Saitama Prefecture, Prov. Musashi, Chichibu District, Mt.

Buko ca. 1000m, bluff of limestone, 22 Oct. 1951, *Shimizu s.n.* (NICH-19297 holotype; JE, S, isotypes).

Description

Differs from subsp. *mussuriensis* in its often much longer ribbon-like thalli up to 45mm long; carpocephala with tall warts at least twice as tall as broad; lobes of carpocephalum short, warted to apex.

Illustrations: Shimizu & Hattori (1952: Fig. 2); spores Fig. 3.19.

Distribution and phytogeography (Fig. 4.20).

This subspecies is endemic to Japan (Honshu).

Ecology and phenology

Subsp. *crassa* appears to be more highly ecologically specialised than subsp. *mussuriensis*. On Honshu it appears to favour volcanic and metamorphic rock substrates, at least some of which are calcareous, and occurs in the evergreen broad-leaved forest zone between 250 and 800m altitude, sometimes in quite shaded sites though these will be seasonally dry.

Fruiting appears to be in the summer and autumn, August to October.

Taxonomic notes

See above under subsp. *mussuriensis*.

Specimens examined: see Appendix V.

14. Asterella multiflora (Steph.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Kachroo, Journal of the Hattori Botanical Laboratory 19: 3, 1958.

Basionym: *Fimbriaria multiflora* Steph., Species Hepaticarum 1: 124, 1899. Type citation: [India] 'N.W. Himalaya (Duthie, Gamble).' Type specimen: NW Himalaya, Saharanpur district, Kaurran Pass, i 1893, *J.S. Gamble 24032* (G-10496, **lectotype selected here**; BM, JE, S, PC, FH, isolectotypes); NW Himalaya, Mohand Pass, Siwalik Range, 1500–2500ft., 5 i 1892, *J.F. Duthie* 41-bis (G-10497, syntype); NW Himalaya, Mohand Pass (Siwalik Range), infra Mussoorie, 1500–2500 ft., 5 i 1892, *J.F. Duthie 306* (G-10502, JE, syntypes).

Syn.: *Fimbriaria pathankotensis* Kashyap, Journal of the Bombay Natural History Society 24: 344, 1916. Type citation: [India, Punjab] 'Pathankot, on the side of a pond.' Type specimen: *n.v.*; **syn. nov**.

Syn.: *Asterella pathankotensis* (Kashyap) Verd., Annales Bryologici 8: 156, 1935.

Syn.: *Asterella sanguinea* auct. p.p. non (Lehm. & Lindenb.) Kachroo; Stephani, Species Hepaticarum 1: 124, 1899; Kashyap, Liverworts of the Western Himalayas and the Panjab Plain 1: 67, 1929; Kachroo, Journal of the Hattori Botanical Laboratory 12: 42–43, 1954.

Description

Thalli usually creeping amongst other bryophytes or forming semi-pure patches on rocks and soil. *Vegetative branches* mostly ventral in origin; terminal dichotomies and terminal innovations less frequent; branches 5–22 x 2–5mm, thick and leathery (all xeroshoots), 0.5–0.6mm thick; pale bluish-green above with purplish margins, rounded and shallowly notched at apex. Upper surface flat or weakly concave with raised undulate margins, strongly inrolled when dry, not reticulate but with air pores visible as minute whitish dots. Branches mostly dark purple beneath. *Dorsal epidermis* cells 37–105 x 27–58µm, with or without small trigones; oil cells abundant. *Air pores* with orifice 17–37µm diameter, cells in 5–8 rows of 2–4 concentric rings; innermost cells 10–17µm in radial length, 22–37µm wide; outermost cells 17–27µm in radial length, 45–62µm wide. *Assimilation tissue* 0.2–0.25mm thick; less than half thickness of thallus, of 1–2 layers of small air chambers over midrib and 1–3 layers of larger obliquely ascending air chambers in thallus wings; uppermost air chambers of midrib often with short 1-celled mammilla-like ingrowths of green tissue below air pores; cells of air chamber partitions 33–40µm diameter. *Basal compact tissue* 0.3–0.4mm thick; cells 23–37µm diameter; oil cells occasional. *Rhizoids*: smooth rhizoids 12.5–37µm diameter; pegged rhizoids 10–23µm diameter. *Ventral scales* with body strongly reddish-pigmented but with paler margins, 450–800 x 500–650µm; cells of body 47–80 x 15–35µm, becoming paler, narrower and more thin-walled towards curved (median) margin; oil cells 3–9, close to margin, 25–35µm diameter; margin entire except for 1–5 slime papillae on each margin (often caducous); scale appendages 1–2 per scale, narrowly lanceolate, 400–650 x 75–125µm, 3–4 cells wide at insertion, not constricted, apex filiform, of 2–3 linear uniseriate cells, appendage cells 55–130 x 15–47µm; margin entire or sometimes with a single slime papilla near base; oil cells absent.

Sexual condition ventral-autoicous with androecia borne at apex of main branches or large ventral branches; archegoniophores borne on short ventral branches usually close to branch apex; both androecia and archegoniophores limiting further vegetative growth. *Androecia* cushion-like, green, 1–1.4mm diameter, without marginal scales, but partly covered by reflexed purplish ventral scale appendages; antheridia ellipsoid, 340–460 x 160–220µm, with conical apex; ostioles bluntly conical, 90–150 x 100–125µm. *Archegoniophore* terminal on short ventral branches; female branches heart-shaped, 1.2–2.9 x 0.8–2.5mm, with short broad thin wings and a short stipe, 1–3 borne near apex of each fertile branch. *Stalk* short, 1.7–9mm long, 350–450µm diameter, with rhizoid furrow 140–220µm deep; medullary cells 12.5–27µm diameter, epidermal cells 12.5–22µm diameter; stalk with scattered linear scales throughout, scales 300–600 x 40–50µm, uniseriate at base and apex, biseriate in middle, entire, without oil cells; scales of apical beard similar but longer, 0.9–2mm long. *Carpocephalum* rounded and

subglobose when young, when mature becoming cushion-shaped (forming a somewhat flattened dome), 2–2.5mm diameter (excluding pseudoperianths), often oblique due to few fertile lobes developing; deeply 1–2(–4)-lobed with lobes spreading at 45–60° to stalk; dome and dorsal side of fertile lobes coarsely warted with protruding air chambers. *Involucre* conspicuous ventrally, 1.1–1.2mm from base to free margin, with coarsely sinuate free margin with median emargination 100–150µm deep. *Pseudoperianth* white or pale brownish, sometimes purplish tinged; 2.1–2.7mm long; undivided basal cup 0.9–1.1mm long, cells of base 120–240 x 30–45µm; lobes 8–10, 1.2–1.6 x 0.25–0.45mm, united at apex into a tubular beak, margins revolute when dry, lobe cells 70–160 x 25–37µm; beak cells with slime-papilla like outgrowths internally; oil cells absent in base and lobes.

Capsule c 1mm diameter; cells of urn rectangular, 50–75 x 37–50µm; cells of lid subquadrate, 20–50µm diameter, with conspicuous trigones. *Spores* (light microscope) brown, 75–115µm diameter. *Spores* (SEM) Type V: trilete, without equatorial apertures, with similar proximal and distal sculpturing; on distal surface with conspicuous large flat-bottomed areolae 12–25µm diameter, smooth within and without secondary ornamentation but densely pitted; muri broad, flat and alveolate; equatorial rim broad; proximal facets flat, with ornamentation as on distal surface. *Elaters* 120–225 x 12.5–17µm, mostly monospiral but some bispiral. *Chromosome number* unknown.

Illustrations: Pandé *et al.* (1954: Fig. 1); spores Fig. 3.20.

Distribution and phytogeography (Fig. 4.6).

Not known outside the study area; specimens have been confirmed from Pakistan, India (Uttar Pradesh, West Bengal, Assam), Nepal and China (Sichuan). Its occurrence in China is newly confirmed. Although it was reported from Sichuan by Herzog (1930) and Piippo (1990), these records are both based on *Handel-Mazzetti 2721* which is *A. mussuriensis*. However, a specimen labelled 'Turkestania, Ssy-zuan, Ja-szzhon, 30 March 1893' *G.I. Potanin 38* (JE)) is undoubtedly from Sichuan where Potanin was collecting at that time (Coats, 1970) .

A subtropical/warm-temperate Sino-Himalayan endemic.

Ecology and phenology

Asterella multiflora appears to be a weedy species of the subtropical and warm temperate zones of the Himalaya. Its recorded altitudes are from 240 to 2000m. Its habitats are mostly in urban situations or on open or scrubby valley slopes; it typically grows on soil banks, rocks or walls, sometimes by rivers, drains or ponds. It is associated with other Marchantiales such as *Plagiochasma appendiculatum* Lehm. & Lindenb., *Riccia discolor* Lehm. & Lindenb. and occasionally *Asterella mussuriensis*.

Taxonomic notes

Asterella multiflora is a very distinctive species in that it is the only autoicous Asiatic species with androecia terminal on the main thallus branches and with the archegoniophores borne on short ventral shoots. Its receptacles are similar to those of *A. mussuriensis* but the beard around the apex of the stalk is composed of much shorter scales in *A. multiflora*. Under the SEM the spores are particularly striking and unique amongst Asiatic species.

Historical and nomenclatural notes

There is a history of confusion surrounding this species, largely due to the fact that Stephani in his *Species Hepaticarum* described *Fimbriaria multiflora* as a new species, but also treated the same taxon under the older name *Fimbriaria sanguinea* Lehm. & Lindenb. This was a misapplication of the name *F. sanguinea*, which rightly is a synonym of *Asterella wallichiana*. Stephani's treatment confused later workers such as Kashyap who re-described the species again under the name *Fimbriaria pathankotensis*.

Specimens examined: see Appendix V.

15. Asterella vulcanica (Schiffn.) 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: 75, 1977.

Basionym: *Hypenantron vulcanicum* Schiffn., Denkschriften der kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Wien 67: 155, 1898. Type citation: [Indonesia] 'Java: Prov. Preanger. Prope Garut, inter saxa vulcanica in monte ignivomo Gunung-Guntur. Parce *Rebouliae* intermixtum. Regio pluvialis, alt. ± 800 m s.m. - 11.2.1894 (c.fr.) (No. 17)'. Type specimen: Java: Prov. Preanger, Prope Garut. Inter saxa vulcanica in monte Gunung-Guntur. Parce Rebouliae intermixtum. 11.ii.1894. ± 800 m.s.m., *V. Schiffner* Iter Indicum 1893/94 No. 17 (FH, herb. Schiffner, **lectotype selected here**; W, isolectotype).

Syn.: *Fimbriaria vulcanica* (Schiffn.) Steph., Species Hepaticarum 1: 114, 1899 '*vulcania*'.

Description

Thalli robust, forming extensive mats on soil, rocks and other bryophytes. *Vegetative branches* mostly ventral, stipitate based, also with apical innovations and occasional terminal dichotomies; somewhat xeromorphic, linear-oblong to obovate, 8–28 x 2.5–8mm, pale green above with dark red margins, inconspicuously notched at apex (except when archegoniophore produced); in transverse section 1.1–2.0mm thick, 2.5–4 x as broad as thick; midrib inconspicuous. Upper surface flat or broadly U-shaped, without median channel, margins almost flat, inrolling when dry; surface smooth with air chambers not prominent but forming weak curved radiating lines, air pores raised but not easily visible. Lower surface dark red-

purple. *Dorsal epidermis* of irregularly rectangular cells 40–62 x 30–45µm, walls slightly thickened, without or with very small trigones; oil cells frequent, large, 37–52µm diameter. *Air pores* conically raised in transverse section, pore elliptic, 30–50 x 12.5–25µm, with cells in 7–9 rows of 3–5 rings of straight transversely rectangular strongly differentiated overlapping cells, innermost cells 12.5–15µm in radial length, 20–30µm broad; outermost cells 20–35µm in radial length, 37–55µm wide. *Assimilation tissue* 400–550µm thick, 1/4 to 1/3 thickness of thallus, of an upper layer of tall chambers and lower spongy layer; upper air chambers tall, broad only below conical air pore where they are packed with short free filaments; partition cells 17–45µm diameter; lower spongy air chambers small; oil-cells numerous, large, to 50µm diameter. *Basal compact tissue* 650–1500µm thick, distinctly thicker (up to 4x) than assimilation tissue, often with broad red-pigmented median band; cells 20–40µm diameter; oil-cells few. *Rhizoids*: smooth rhizoids 15–35µm diameter; pegged rhizoids 10–30µm diameter. *Ventral scales* ovate with long-decurrent adaxial base, large, body dark red, somewhat paler at margins, 1000–2030 x 530–800µm, median cells of scale body rectangular, 65–175 x 20–40µm, towards margins shorter and thin-walled, often deflexed obliquely outwards, in decurrent base much longer and narrower; margins entire, without slime-papillae; oil cells 11–20, 45–55µm diameter; scale appendage single (rarely 2), ovate, 440–940 x 220–580µm, apex obtuse, constricted and 7–11 cells wide at base, median cells shorter and broader than cells of body, 65–130 x 40–85µm, margins entire, with obliquely deflexed marginal cells; oil-cells 1–3.

Sexual condition ventral autoicous with androecia borne on short to long ventral branches archegoniophore on small to large ventral branch. *Androecia* of raised rounded dark red-purple cushions 0.6–0.9mm diameter, or linear up to 5mm long, without scales; ostioles up to 37, bluntly conical, 150–200µm tall and broad. *Archegoniophore* terminal on ventral branch, inhibiting further vegetative growth which is usually continued by ventral innovations. *Stalk* long, slender, dark red-brown, 10–28 x 0.6–0.75mm, in transverse section rounded when young becoming deeply folded and ± cruciform with 4 large ribs when older; rhizoid furrow 0.25–0.8mm, about half diameter of stalk; medullary cells 20–40µm diameter, smaller around rhizoid furrow; 1–6 air chambers 50–75µm diameter present in rib opposite rhizoid furrow; epidermal cells smaller and with thicker highly red-pigmented walls; stalk naked at base, with a few red scales along its length, at apex with a dense beard of long scales at apex; scales narrowly linear, 1.3–3.2 x 0.07–0.15mm, whitish in lower half, reddish in upper half, long-tapering and 1 cell broad at both ends, up to 4 cells broad in middle, margins entire. *Carpocephalum* tall rounded-hemispheric, 5–5.8mm tall (including pseudoperianth), 4–4.2mm diameter, without differentiated central dome, coarsely warted throughout, conspicuously 2–4-lobed, the lobes pointing downwards almost vertically at 10–20° to stalk, lobes warted, with entire distal margin. *Involucre* forming a conspicuous broad flap on underside of carpocephalum lobes, 1.3–1.5mm from base to free margin, free margin entire, not sinuate. *Pseudoperianth* usually reddish tinged; basal united part 1.05–1.3mm, 1/3 to 2/5 total length of pseudoperianth, cells of basal part rectangular, 150–275 x 20–40µm, thin-walled; lobes 12–16, lanceolate, 2–2.25 x 0.25–0.55mm, firmly attached at apex at maturity, margins recurved when

dry, lobe cells linear, 160–225 x 135–65µm, thick-walled, becoming shorter towards apex; oil-cells absent from base and lobes.

Capsule brown, c 1.4mm diameter, on very short basal stalk; with upper part of urn irregularly fragmenting and lobed, without well-defined lid; cells of urn rectangular, 50–120 x 30–60µm, thin-walled; cells of lid fragments with large trigones. *Spores* (light microscope) pale yellow, 110–150µm diameter, conspicuously winged equatorially. *Spores* (SEM) Type VI: trilete; small equatorial apertures present; with similar proximal and distal ornamentation; distal surface with large areolae 18–30µm diameter, smooth, without alveoli; muri alveolate, especially at angles; equatorial rim conspicuous; proximal facets with similar ornamentation though large areolae incomplete. *Elaters* yellowish, 200–255 x 15–18µm, 2-spiral in middle part, 1-spiral at ends. *Chromosome number* unknown.

Illustrations: Fig. 4.22; spores Fig. 3.17.

Distribution and phytogeography (Fig. 4.15).

In the study area known only from Indonesia (Java); records from south India (Chopra, 1938a; Pandé, *et al.*, 1954; Kachroo *et al.*, 1977) have not been confirmed and must be regarded as extremely doubtful. Outside the study area a specimen has been confirmed from Papua New Guinea. The record from New Caledonia (Miller *et al.*, 1983) requires confirmation.

Currently considered to be a tropical Malesian endemic.

Ecology and phenology

On Java reported from volcanic rocks at 800m and also from the stones of an old temple. On Papua New Guinea collected at 3500m, on damp humus near a spring. Javan specimens collected in January have very immature carpocephala; the Papua New Guinea specimen has a few ripe and several unripe sporogonia in late April.

In one collection of *A. vulcanica* (*Warburg 14917*) small bulbil-like shoots were seen on the ventral surface of two separate thalli. These appear to be very young ventral branches consisting of a short fleshy stem covered with dense reddish scales. It is possible that these could become detached and act as vegetative propagules, as was described in *A. lindenbergiana* by Evans (1920).

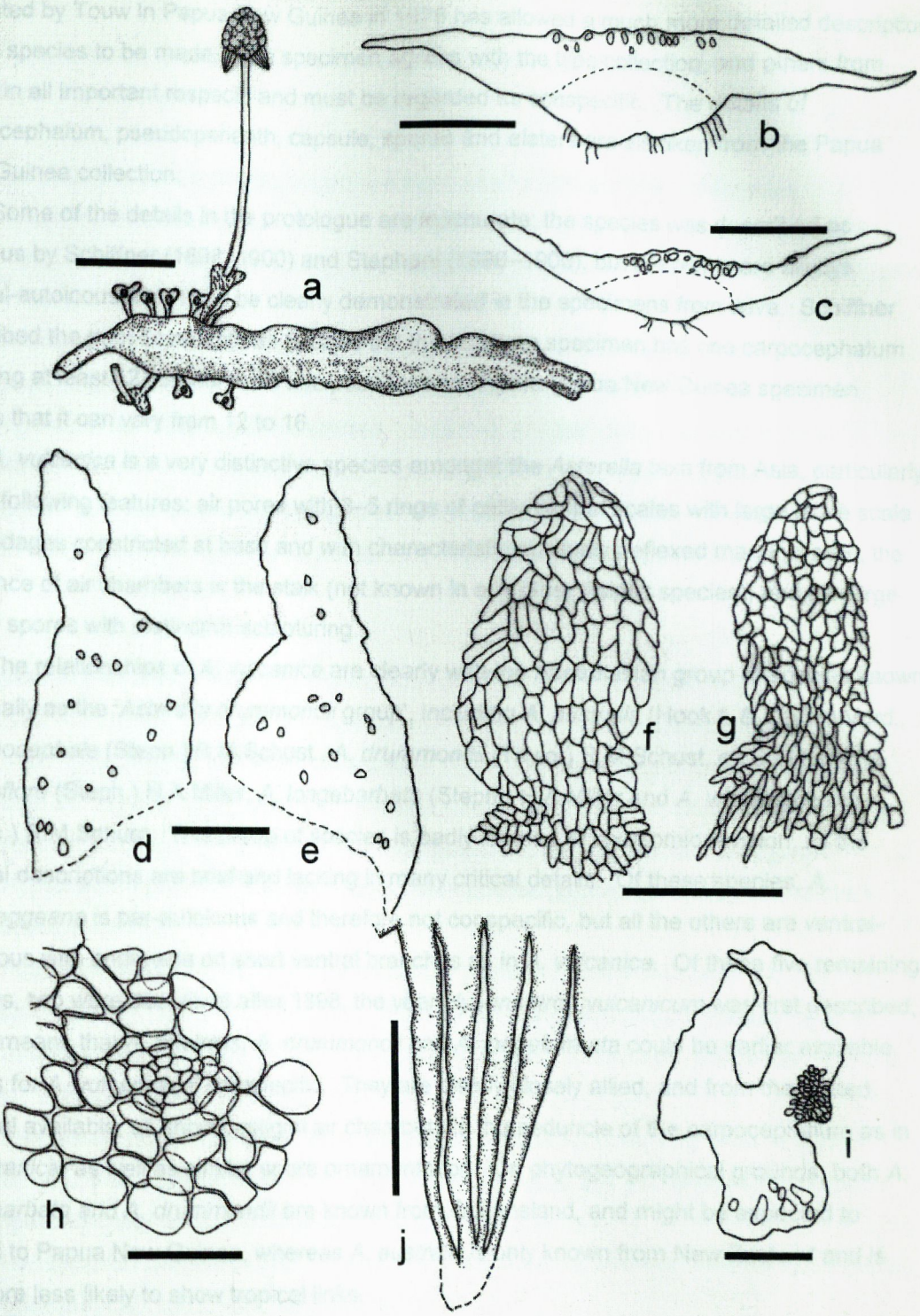

Fig. 4.22 *Asterella vulcanica*. a, fertile plant with male and female branches and carpocephalum; b, c, t.s. thallus; d, e, ventral scales showing oil cells; f, g, ventral scale appendages; h, air pore; i, t.s. stalk of carpocephalum showing vestigial air chambers; j, part of pseudoperianth. a, b, f, i, j, Papua New Guinea, *Touw 16628*; c, d, e, g, h, Indonesia, Java, *Warburg 14917*. Scale bars: a = 10mm; b, c, j = 1mm; d, e, f, g = 400µm; i = 200µm; h = 100µm.

Taxonomic notes

The original description of this species is very scanty as so little material was available; the lectotype contains only one mature carpocephalum in a fragile condition. The material collected by Touw in Papua New Guinea in 1975 has allowed a much more detailed description of the species to be made. This specimen agrees with the type collection, and others from Java, in all important respects and must be regarded as conspecific. The details of carpocephalum, pseudoperianth, capsule, spores and elaters are all taken from the Papua New Guinea collection.

Some of the details in the protologue are inaccurate: the species was described as dioicous by Schiffner (1898, 1900) and Stephani (1898–1900), but the plants are always ventral-autoicous which can be clearly demonstrated in the specimens from Java. Schiffner described the pseudoperianth as 8-lobed but the holotype specimen has one carpocephalum showing at least 12 segments on one pseudoperianth; the Papua New Guinea specimen shows that it can vary from 12 to 16.

A. vulcanica is a very distinctive species amongst the *Asterella* taxa from Asia, particularly in the following features: air pores with 3–5 rings of cells; ventral scales with large ovate scale appendages constricted at base and with characteristic obliquely deflexed marginal cells; the presence of air chambers in the stalk (not known in any other Asiatic species), and the large yellow spores with distinctive sculpturing.

The relationships of *A. vulcanica* are clearly with the Australasian group of species known informally as the '*Asterella drummondii* group', including *A. australis* (Hook.f. & Taylor) Verd., *A. conocephala* (Steph.) R.M.Schust., *A. drummondii* (Taylor) R.M.Schust. ex D.G.Long, *A. heteroflora* (Steph.) H.A.Miller, *A. longebarbata* (Steph.) H.A.Miller and *A. whiteleggeana* (Steph.) R.M.Schust. This group of species is badly in need of taxonomic revision, as the original descriptions are brief and lacking in many critical details. Of these species, *A. whiteleggeana* is par-autoicous and therefore not conspecific, but all the others are ventral-autoicous with androecia on short ventral branches as in *A. vulcanica*. Of these five remaining species, two were described after 1898, the year *Hypenantron vulcanicum* was first described, which means that *A. australis*, *A. drummondii* and *A. longebarbata* could be earlier available names for *A. vulcanica*, if conspecific. They are clearly closely allied, and from the limited material available, all show vestigial air chambers in the peduncle of the carpocephalum as in *A. vulcanica*, as well as similar spore ornamentation. On phytogeographical grounds, both *A. longebarbata and A. drummondii* are known from Queensland, and might be expected to extend to Papua New Guinea, whereas *A. australis* is only known from New Zealand and is therefore less likely to show tropical links.

Two things are clear: more material of *A. vulcanica* is badly needed, to assess its variation and distribution, and a revision of Australasian *Asterella* is needed to establish the identity of the Australian taxa and the possible synonymy of *A. vulcanica*.

Specimens examined: see Appendix V.

SUBGENUS *GRACILES*

Asterella Subgenus *Graciles* D.G. Long, Journal of Bryology 22:113, 2000.

Type: *Asterella gracilis* (F.Weber) Underw.

Thalli xeromorphic, not aromatic; *vegetative branches* mostly terminal dichotomies, occasionally ventral; *assimilation tissue* of a single layer of tall air chambers; *ventral scale appendages* 1–2, lanceolate to oblong, not constricted at base, apex acute to obtuse, margins weakly toothed.

Sexual condition par-autoicous; *androecia* ill-defined, of scattered ostioles; *carpocephalum* hemsipheric, shallowly lobed; *involucre* with free margin deeply cleft; *pseudoperianth* not flattened or constricted, lobes free at apex, divided almost to base,

Capsule lid disc-like, not fragmenting; *spores* type VIII, yellow, with irregularly and incompletely areolate ornamentation on distal surface, proximal surface with similar ornamentation, but lacking trilete ridges and proximal pole (alete); *elaters* 3-spiral.

16. Asterella gracilis (F.Weber) Underw., Botanical Gazette (Crawfordsville) 20: 61, 1895.

Basionym: *Marchantia gracilis* F.Weber, Historiae Muscorum Hepaticorum Prodromus 105, 1815. Type citation: [Sweden] 'Gottsundae prope Upsaliam cum ill. Wahlenbergio et beato Mohrio legi.' Type specimen: Gottsundae prope Upsaliam, *Wahlenberg, Mohr & Weber s.n.* (S-H10008 lectotype; STR, W, isolectotypes) [fide Grolle (1976)], *n.v.*

Syn.: *Hypenantron gracile* (F.Weber) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 440, 1877.

Syn.: *Fimbriaria pilosa* Taylor, Transactions of the Linnean Society of London 17: 386, 1837, *nom. illeg.* (Art. 52.1) - including type of the earlier name *Marchantia gracilis* F.Weber.

Syn.: *Asterella pilosa* (Taylor) Trevis., Rendiconti del' Istituto Lombardo di Scienze e Lettere, Ser. 2, 7: 785, 1874, *nom. illeg.* (Art. 52.1).

Syn.: *Marchantia pilosa* Wahlenb., Flora Lapponica 399, 1812, *hom. illeg.* [non *M. pilosa* Hornem., Flora Danica 8(24): 7, t. 1426, 1810]. Type citation: [Norway] Hab. in rupibus irrigatis inferalpinis Nordlandiae rarius. Type specimen: *n.v.*.

Syn.: *Hypenantron pilosum* (Taylor) Trevis. Herbarium Cryptogamicum Trevisianum II (Musci, Hepaticae): 32, 1853, *nom. illeg* (Art. 52.1).

Syn.: *Marchantia polycephala* Schleich., Catalogus Plantarum in Helvetia ed.2, 31, 1807, *nom. nud.*; synonymised by Nees (1838) under *Fimbriaria pilosa*.

Syn.: *Fimbriaria schleicheriana* Corda, in Nees, Naturgeschichte der Europäischen Lebermoose 4: 273, 1838, *nom. illeg.* (Art. 34.1). Type citation: none; Type specimen: *n.v.*; synonymised by Nees (1838) under *Fimbriaria pilosa*.

Syn.: *Dictyochiton pilulare* Corda, in Nees, Naturgeschichte der Europäischen Lebermoose 4: 280, 1838, *nom. illeg.* (Art. 34.1). Type citation: none; Type specimen: *n.v.*; synonymised by Müller (1951–1958).

Syn.: *Fimbriaria vesiculosa* Austin, Proceedings of the Academy of Natural Sciences of Philadelphia (1869): 230, 1869. Type citation: 'Japan. Com. Rodgers, N. Pac. Expl. Exped.' Type specimen: [Japan] N. Pac. Expl. Expd., *Rodgers s.n.* (MANCH, herb. Carrington, **lectotype selected here**; G-15289, isolectotype); **syn. nov**.

Syn.: *Fimbriaria parvipora* Steph., Species Hepaticarum 1:116, 1899. Type citation: [NW India] 'Kaschmir Liddar Valley 13000' engl. (Duthie).' Type specimen: Kashmir, Liddar Valley, Jonsal nullah, 13–14000 p., 31.vii.1893, *J.F. Duthie 13385* (G-10514, **lectotype selected here**); **syn. nov**.

Syn: *Fimbriaria silachorensis* Schiffn., Oesterreichische Botanische Zeitschrift 58: 229, 1908. Type citation: [Iran] 'Persia occid. In alpibus districtus Silachor ad terram inter *Bryum pallens* Sw. VI. 1902 legit Th. Strauss.' Type specimen: Persia occid., In alpibus districtus Silachor, vi 1902, *Strauss 5* (FH, herb. Schiffner, **lectotype selected here**; JE, isolectotype); synonymised by Frey (1974).

Syn: *Asterella silachorensis* (Schiffn.) R.M.Schust., The Hepaticae and Anthocerotae of North America 6: 226, 1992.

Syn.: *Asterella parviflora* Parihar, University of Allahabad Studies Botany Section 1961–1962: 28, 1962, *nom. nud.* err. pro *A. parvipora*.

Syn.: *Asterella parvipora* (Steph.) Pandé *et al.* [Journal of the Hattori Botanical Laboratory 11: 8, 1954, *comb. inval.* Art. 33.2] ex Kachroo, Journal of the Hattori Botanical Laboratory 19: 4, 1958.

Syn.: *Fimbriaria ludwigii* auct. non (Schwägr.) Limpr. ex Müll.Frib.

Syn.: *Asterella ludwigii* auct. non (Schwägr.) Underw. ex A.Evans

Syn.: *Asterella ludwigii* (Schwägr.) Underw. ex A.Evans var. *kitadakensis* Shimizu & S.Hatt., Journal of the Hattori Botanical Laboratory 14: 102, 1955, *nom. inval.* (Art. 36.1). Type citation: [Japan, Honshu] 'collected on Mt. Kitadake (type)'. Type specimen: *n.v.*.

Syn.: *Asterella ludwigii* (Schwägr.) Underw. ex A.Evans var. *major* Inoue & Shimizu, Memoirs of the National Science Museum, Tokyo 1: 49, 1968. Type citation: [Japan, Honshu] 'Mt. Hayachine, Iwate Pref., ca. 1100m alt., on wet, gravelly soil: leg. D. Shimizu, *s.n.*, June 20, 1967 (TNS; duplicate in MASS, JE, NY, G). Type specimen: Japan, Mt. Hayachine, Iwate Pref., ca. 1100 m. alt., on wet gravelly soil. 20 June 1967. *Shimizu s.n.* (G, isotype).

Description

Thalli creeping over humus and other bryophytes, rarely forming small purplish-green patches; without fishy smell. *Vegetative branches* mostly terminal dichotomies, with occasional stipitate-based ventral branches; branches fleshy, xeromorphic, linear to obovate, 6–15(–20)x 1.2–3(–4.6)mm, dark green above with red-purple margin, in exposed sites narrower and purplish-tinged throughout, in more mesic sites broader and green throughout; inconspicuously

notched at apex; in transverse section 0.5–0.8mm thick, 2–3x as broad as thick (but appearing proportionally thicker when margins are upturned or inrolled); midrib inconspicuous, tapering into thallus wings. Upper surface weakly concave, sometimes almost flat, when fresh, without median groove, margins weakly undulate, weakly upturned becoming strongly inrolled when dry, surface with low radiating bulges when moist, air pores minute but conspicuous when dry. Lower surface red-purple. *Dorsal epidermis* cells subquadrate, 25–40µm long and broad, walls thin, without trigones; oil-cells scattered. *Air pores* slightly raised above surface, with orifice 20–35µm diameter, with cells in 5–7 rows of 1(–2) rings of curved differentiated cells, innermost cells 12.5–20µm in radial length, 17–35µm wide; outer ring little differentiated from epidermal cells in shape and size. *Assimilation tissue* 250–350µm thick, about half thickness of thallus at midrib, of a single layer of tall broad air chambers; towards margins these chambers overlapping obliquely; free filaments not seen; cells of partitions 20–40µm wide; oil-cells few. *Basal compact tissue* 200–450µm thick, more or less equal in thickness to assimilation tissue, colourless; cells irregular in shape and size, 25–60µm across, thin-walled; oil-cells abundant. *Rhizoids*: smooth and pegged rhizoids 10–27µm diameter. *Ventral scales* semicircular, body red-purple without clearly differentiated border, 1100–1450 x 550–850µm; median cells of body linear with acute ends, 45–100 x 17–35µm, shorter, paler and with thinner walls towards margin, longer and narrower in decurrent base; margins irregularly and remotely crenate-dentate, adaxial margin with 6–12 slime papillae, abaxial margin with 2–7 slime papillae; oil cells 6–15, 20–30µm diameter; scale appendages 1(–2), often very unequal or with 1 or 2 large teeth, lanceolate to oblong, 300–650 x 100–200µm, not constricted and 8–13 cells wide at base, cells 27–75 x 12.5–35µm; margin of appendage with a few blunt to acute 1–2-celled or occasionally larger acute teeth, slime papillae not seen; apex acute or rounded, oil cells absent (rarely 1 at base).

Sexual condition par-autoicous with androecia borne on main thallus proximal to base of archegoniophore, sometimes also on separate terminal branches with no archegoniophore. *Androecia* reddish, diffuse, ill-defined along mid-line of thallus, composed of an ill-defined single or double line 1–2 mm long, 0.1–0.4mm broad; ostioles 3–10, taller than broad, 175–200 x 125–150µm, without surrounding scales. *Archegoniophore* terminating main thallus branch, inhibiting further vegetative growth except for occasional ventral innovations near apex. *Stalk* slender, brown, 8–16 (–27) mm long, 500–650µm diameter, rhizoid furrow deep, 0.25–0.35mm, about half diameter of stalk; medullary cells 17–40µm diameter, becoming smaller, thick-walled and pigmented outwards; scales and apical beard absent. *Carpocephalum* hemispheric, green or often reddish tinged, 2.6–3mm diameter when mature, shallowly 2–4-lobed, the lobes pointing downwards at 20–40° to stalk; the broad rounded crown almost smooth when fresh, when dry with low rounded warts, the lobes smooth, with sinuate-crenate distal margin. *Involucre* inconspicuous, 0.5–0.8mm from base to free margin, with free margin deeply cleft to its insertion opposite apex of stalk, margin otherwise entire. *Pseudoperianth* colourless, 1.8–2.4mm long; basal united part very short, 0.35–0.45mm; cells of base laxly rectangular 120–230 x 15–35µm; lobes 6–8(–12), slender, lanceolate, white, free at maturity

though some incompletely separating, 1.45–2 x 0.25–0.5mm, not constricted at base, margins flat both moist and dry, with long flexuous filiform flat point; lobe cells rectangular 75–135 x 12–25µm; oil cells absent from base and lobes.

Capsule brown, 1.1–1.3 mm diameter with large regular discoid lid 1–1.1mm diameter and straight line of dehiscence; cells of urn 60–110 x 20–40µm, thin-walled, becoming much shorter at mouth; cells of lid subquadrate, 30–50µm, walls little thickened. *Spores* (light microscope) yellow, 55–70µm diameter. *Spores* (SEM) Type VIII: alete, without trilete mark, equatorial rim and apertures absent; proximal and distal surfaces with similar sculpturing, on distal surface consisting of large irregular incomplete primary areolae 9–17µm diameter which show indistinct subdivisions into secondary alveoli or are smooth, with scattered minute pits; muri broad and rounded, pitted; proximal surface ± hollowed, without trilete ridges or proximal point; with similar ornamentation to distal surface, without bulges. *Elaters* yellowish, long, 250–320 x 10–12.5µm, gradually tapering, 3(–4)-spiral. *Chromosome number n* = 18 (Tatuno 1960, as *A. ludwigii*, probably based on European material).

Illustrations: Frey *et al.* (1991: Fig.1); spores Fig. 3.21.

Distribution and phytogeography (Fig. 4.21)

In the study area specimens have been confirmed from Europe (Norway, Sweden, Finland, France, Switzerland, Spain, Italy, Germany, Czech Republic, Poland, Georgia, Russia), Siberia, Iran, NW India and Japan (Hokkaido, Honshu). It has also been reported from Iceland (Gottsche *et al.*, 1844–1847; Hesselbo, 1918); Austria (Gottsche *et al.*, 1844–1847); Slovakia (Suza, 1940); Yugoslavia (Pavletic, 1955); Turkey (Schiffner, 1908) and N. Korea (Gao & Chang, 1983). Outside the study area it is widespread in the U.S.A., Canada, Alaska and Greenland (Evans, 1923; Steere, 1937; Schuster, 1992c; Schuster & Damsholt, 1974).

Its phytogeography has been described as an arctic-alpine (Schuster & Damsholt, 1974) with a disjunct holarctic distribution, with outposts in the mountains of NW Turkey, NW & N Iran (Frey *et al.*, 1991). In North America Steere (1937) mapped the distribution of *A. gracilis* which shows a typical Arctic-alpine distribution (though the species is rare in the American Arctic (Alaska) but widespread in Greenland); it is abundant in the Rocky Mountains but (like *A. saccata*) has a major disjunction in the east close to Lake Superior, in what is argued by Steere and others (*e.g.* Schuster, 1992c) is an unglaciated refugium. Its absence elsewhere may be explained by its inability in post-glacial times to colonise formerly glaciated areas. In Europe, Suza (1940) described at as arctic-alpine, but considered it to be a post-glacial relict in its lower localities in the xerothermic regions of Germany, Bohemian massif and the western Carpathians.

Ecology and phenology

Asterella gracilis is generally considered to be both a xerophyte and a calciphyte (Schuster & Damsholt, 1974). It grows in very exposed sites in the Arctic and usually on mountains

elsewhere, sometimes up to high altitudes. In the European mountains the recorded altitudes are from 320 to 2500m; in Scandinavia up to 1200m; in the Middle East (Iran) from 2100 to 2300m, in Kashmir reported from 3900m, in Japan from 1000 to 1100m. In the Arctic, as in Iceland and Alaska, it can grow down to sea level. The plant usually grows as scattered stems or almost pure mats on soil or humus, often mixed with other bryophytes, often on rock shelves, cliff ledges, soil amongst boulders and sometimes in late snow areas. It often grows in very exposed strongly insolated sites which undergo periodic desiccation. The substrate is usually calcareous, such as basalt, limestone and weathered schist. Associated species often include other Marchantiales, for example in Greenland Schuster & Damsholt (1974) reported the associates *Peltolepis quadrata* (Saut.) Müll.Frib., *Sauteria alpina* (Nees) Nees, *Athalamia hyalina* (Sommerf.) S.Hatt. and *Preissia quadrata* (Scop.) Nees; in Scandinavia associates include *Mannia pilosa* (Hornem.) Frye & L.Clark, *Peltolepis quadrata*, *Preissia quadrata* and *Sauteria alpina* (Mårtensson, 1955–1956).

Because of its ecological preferences for arctic-alpine habitats, *A. gracilis* normally is in active growth only through the spring and summer months and spore maturity therefore occurs most frequently in summer and autumn (May to September).

Taxonomic notes

Nees (1838) pointed out that the pseudoperianth in *A. gracilis* was divided almost to the base into long tapering segments. This important difference with all other European and Asiatic species, in which the divisions only reach to 50–60%, was overlooked by later authors. Also distinctive are the following features: (a) the little-differentiated cells around the air-pores; (b) the margins of the pseudoperianth lobes which remain flat when dry (as also in *A. africana*), (c) the highly-differentiated circular lid of the capsule, and (d) the elaters which are very tightly coiled and have 3(–4) spiral bands, in contrast to most other *Asterella* species which commonly have 1 or 2 bands. The spores in *A. gracilis* are also unique amongst the species treated here, suggesting that it is quite isolated from other Eurasian species.

As noted by Evans (1920) *Asterella gracilis* was last century confused with the exclusively North American *Asterella tenella* (L.) P.Beauv. and was reported from several European countries under the latter name. Both Grolle (1976) and Schuster (1992c) considered it closely related to *A. tenella* and therefore placed it in Subg. *Asterella* along with *A. tenella,* which is the type species of the genus. However, it is now clear that the similarities between the two are somewhat superficial, and there are several striking differences (Table 4.1) which suggest that they are not closely related, and in fact better placed in separate subgenera. *A. tenella* is more closely allied to species traditionally placed in Subg. (now Sect.) *Brachyblepharis*, whereas *A. gracilis* appears to be isolated and unique within the genus, meriting its own subgeneric status.

When bearing carpocephala *Asterella gracilis* is readily distinguished from other arctic-alpine species of *Asterella* as outlined above; when sterile it is most likely to be confused with other genera of Marchantiales rather than other *Asterella* species, especially *Mannia pilosa* (Hornem.) Frye & L.Clark with which it often grows (Mårtensson, 1955–1956). According to

Schuster (1992c) *Mannia pilosa* differs in the median cells of the ventral scale body which are 13–17µm wide with those in the scale appendage broader, 18–23µm wide; in *A. gracilis* the cells of both the body and appendage are of a similar size, 18–36µm wide.

Table 4.1 Differences between *Asterella gracilis* and *A. tenella*

	Asterella gracilis	***Asterella tenella***
Xeromorphism	xeromorphic	hygromorphic
Smell	non-aromatic	aromatic
V. scale appendages	not constricted	constricted
Pseudoperianth lobing	to base	to just below middle
Pseudoperianth lobe margins	flat	recurved
Pseudoperianth lobe apex	flat, finely pointed	boat-shaped, blunt
Involucral lobing	deeply cleft	undivided
Capsule lid	circular, unlobed	irregular, lobed
Spore diameter	55–70µm	86–120µm
Spore shape	alete	trilete
Spore areolae	irregular, incomplete	regular, complete
Spore areola diameter	9–17µm	18–27µm
Elater spirals	mostly 3-spiral	mostly 2-spiral

Historical and nomenclatural notes

As was the case with *Asterella saccata* (q.v.) J.C. Schleicher was the first to discover this species in Europe in Switzerland in the early 19th century; he distributed it under the name *Marchantia polycephala* but without any valid publication. Wahlenberg (1812), who discovered this taxon soon after in northern Norway, published it under the name *Marchantia pilosa* Hornem. which unfortunately was a misidentification as Hornemann's collection was a *Mannia* (*M. pilosa* (Hornem.) Frye & L.Clark) and the epithet *pilosa* cannot be retained for the *Asterella*. However, for many years the epithet *pilosa*, based on Wahlenberg's plant, was in general use for this taxon, for example by Taylor (1837), Nees (1838), Gottsche *et al.* (1846), Limpricht (1877), Kaalaas (1892–1893), Stephani (1898–1900), Boulay (1904), Müller (1905–1916) and Schiffner (1940).

Soon after Wahlenberg's discovery two further names applied to this species appeared: *Marchantia ludwigii* Schwägr. (Schwägrichen, 1814) and *Marchantia gracilis* F.Weber (Weber, 1815). The first of these was based on collections now identified by Grolle (1975a) as *Mannia triandra* (Scop.) Grolle from the Sudety Mountains (Poland/ Czech Republic border); thus the

use of the epithet *ludwigii* in *Fimbriaria* and *Asterella* cannot be maintained. Weber's name *Marchantia gracilis*, based on material from Sweden, therefore becomes the earliest valid name for this widespread species, as established by Grolle (1975a). However, the epithet *ludwigii* became the accepted successor to *Fimbraria pilosa* for this taxon, for example by Evans (1920, 1923), Joergensen (1934), Frye & Clark (1937–1947), Müller (1951–1958), Schuster (1953–1958), Mårtensson (1955–1956), Arnell (1956), Flowers (1961), Schuster & Damsholt (1974) and Steere & Inoue (1978). Grolle's (1975a) work necessitates the further change to *Asterella gracilis*, which is now generally established as the accepted name for the plant, *e.g.* by Koponen *et al.* (1977), Frey *et al.* (1991) and Schuster (1992c).

Grolle (1976) typified *Marchantia gracilis* by a 'holotype', but as Weber (1815) did not designate a type, a lectotype should have been selected. The designation of a 'holotype' by Grolle is now considered as effective lectotypification under I.C.B.N. (Art. 9.8).

Specimens examined: see Appendix V.

4.5.5 Excluded taxa and doubtful records from Eurasia

Excluded taxa (names in *Asterella* and *Fimbriaria* reported from the study area which belong to other genera of Marchantiales).

1. *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 delle 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.' (TO, lectotype selected here), (*non vidi*, fide Grolle, *unpublished ms.*).

= *Mannia androgyna* (L. emend. Lindb.) A.Evans, fide Grolle (*in litt.*)

2. *Asterella fasciata* (Myrin ex Hartm.) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 439, 1877.

Syn: *Reboulia fasciata* (Myrin ex Hartm.) Fr., Summa Vegetabilium Scandinaviae 102, 1845.

Basionym: *Marchantia fasciata* Myrin ex Hartm., Handbok i Skandinaviens Flora Ed. 2, 366, 1832. Type citation: [Norway] 'Lpl. - N. Nordl.' Type specimen: BM, G (*n.v.*) fide Grolle ms.

= *Mannia pilosa* (Hornem.) Frye & L.Clark fide Grolle (pers. comm.).

3. *Fimbraria fragrans* (Balb.) Nees, Horae Physicae Berolinenses 45, 1820

Basionym: *Marchantia fragrans* Balb., Memorie della Accademia delle Scienze di Torino (Ser.2) 7: 76, 1804.

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

The name *Fimbraria fragrans* was for many years misapplied to *Asterella saccata*, as has been discussed at length under that species, but rightly applies only to *Mannia fragrans*.

4. *Asterella hemisphaerica* (L.) P.Beauv. in Cuvier (ed.), Dictionnaire des Sciences Naturelles 3: 258, 1805 '1804'.

Basionym: *Marchantia hemisphaerica* L., Species Plantarum Ed. 1, 1138, 1753.

= *Reboulia hemisphaerica* (L.) Raddi

See note under next species.

5. *Asterella javanica* (Nees) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 439, 1877.

Basionym: *Reboulia javanica* Nees, in Gottsche, Lindenberg & Nees, Synopsis Hepaticarum 549, 1846. Type citation: 'Ad parietes templorum montis Dieng latis densissimisque stratis, Julio cum fructu perfecto.' Type specimen: *n.v.*

= *Reboulia hemisphaerica* (L.) Raddi

For a short time during the late 19th century, the generic name *Asterella* was used for what is now called *Reboulia*, and both *R. hemisphaerica* and *R. javanica* were included under *Asterella* by Trevisan (1877). Although Schiffner (1893–1895) kept *R. javanica* separate from *R. hemisphaerica*, most subsequent authors, *e.g.* Stephani (1898–1900), Müller (1951–1958) have united them as a single taxon.

6. *Asterella kiaerii* Kaal., Nyt Magazin for Naturvidenskaberne 33: 78, 1893. Type citation: [Norway] 'paa Norges vestkyst I faa exemplaar I en underjordisk hule paa oen Lammetun I Dalsfjorden I Sondfjord (60^0 15'n.br.).af kaptein Landmark (27de august 1890). Exemplarerne er sendte af samleren til hr. laege F. Kiaer, I hvis herbarium jeg har fundet den.' Type specimen: *n.v.*

Syn.: *Fimbriaria kiaerii* (Kaal.) Steph., Species Hepaticarum 1: 140, 1899.

= *Conocephalum conicum* (L.) Lindb. fide Joergensen (1934).

7. *Asterella latifrons* (Steph.) H.A.Mill., Phytologia 47: 320, 1981.

Basionym: *Fimbriaria latifrons* Steph., Species Hepaticarum 6: 15, 1917. Type citation: 'Lombock. (Sunda Archipelagus.) (Elbert legit.)' Type specimen: Lombok, Rindjani-Vulkangebirge, NNO Seite, Andjar Fluss, oberhalb; Monsun Hochwald, 1400–1530m, humus Sand, 19.5.1909, *J. Elbert 1388* (G-15225, **lectotype selected here**; FH, isolectotype); *Elbert 1145* (G-15226, syntype).

= *Reboulia hemisphaerica* (L.) Raddi; **syn. nov.**

Note: In Stephani's herbarium (G) are three syntypes of *Fimbriaria latifrons*, of which two represent *Reboulia hemisphaerica* and one is an *Asterella* species but poor and unidentifiable. The material of *Reboulia hemisphaerica* bears sporophytes and one of these is selected as lectotype in order to satisfactorily synonymise the name.

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

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

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

= *Mannia triandra* (Scop.) Grolle.

Grolle (1975a) has shown that this name has been long misapplied to what is now correctly called *Asterella gracilis* (F.Weber) Underw. (q.v.).

9. *Asterella nana* (Lindenb.) C.Massal., Annuario del Reale Istituto Botanico di Roma 2: 146, 1886.

Basionym: *Fimbriaria nana* Lindenb., Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum 14 (Suppl.) 109, 1829. Type citation: '*Marchantia nana* Schleich. Cat. Plant. Exsiccat. a. 1821. Hab. in Helvetia'. Type specimen: Switzerland ('Helvetia'), *Schleicher s.n.* (W, lectotype ['holotype'] selected by Grolle (1981)).

Syn.: *Hypenantron nanum* (Lindenb.) Trevis., Memorie del' Istituto Lombardo di Scienze e Lettere 4: 440, 1877.

= *Athalamia hyalina* (Sommerf.) S.Hatt.

Grolle 1981: 325 showed that *Fimbriaria nana* Lindenb. is a synonym of *Athalamia hyalina*. Although he typified it by a 'holotype' this act counts as effective lectotypification (Berlin amendment to I.C.B.N. (Greuter *et al.*, 1994)).

10. *Fimbriaria paleacea* (Bertol.) Corda in Opiz, Naturalientausch [12]: 648, 1829.

Basionym: *Marchantia paleacea* Bertol., Opuscoli Scientifici (Bologna) 1: 242, 1817.

= *Marchantia paleacea* Bertol.

11. *Fimbriaria valida* Steph., Species Hepaticarum 6: 17, 1917. Type citation: China. (Fortunat legit.)' Type specimen: Chine, Kouy Tcheou; Pin fa, 5 Avril 1904, *P. Cavalerie 1756*, Sur rochers (PC, ?type).

= *Reboulia hemisphaerica* (L.) Raddi; synonymised by Piippo (1990).

Doubtful records from study-area:

1. *Asterella caucasica* (Steph.) H.Buch *et al.*, Annales Bryologici 10: 8, 1938.

Basionym: *Fimbriaria caucasica* Steph., Species Hepaticarum 1: 132, 1899. Type citation: 'Caucasus (Moyston)' ; type specimen: Caucasus, Moyston, *D. Sullivan* (G-14589).

Stephani gave the type as 'Caucasus (Moyston)'; Muller (1951–1956) included it as a European species. However Grolle (1975b, 1976) showed that this type originated from Victoria, Australia.

2. *Asterella elegans* (Spreng.) Trevis.

A number of reports of the West Indian *Asterella elegans* (mostly as the synonym *Fimbriaria elegans* Spreng.) exist from the study area, *e.g.* from Corsica (Notaris (1838–1839), Dumortier (1874), Massalongo (1886)), Turkey (Bornmüller (1931), Wettstein (1889), Henderson & Prentice 1969). These are undoubtedly misidentifications; those from Corsica may refer to *A. africana* while those from Turkey possibly refer to *Mannia androgyna* (L.) A.Evans (Frey & Kürschner, 1991).

A separate variety of this species was described from Nepal:

Fimbriaria elegans var. *orientalis* Gottsche *et al.*, Synopsis Hepaticarum 565, 1846. Type citation: 'in Nepalia in terra argillosa rubra a cl. Wallich lecta est. (Hb. L. et Lg.). Type specimen: not located.

This taxon most likely is a synonym of *Asterella wallichiana*.

3. *Asterella tenella* (L.) A.Evans

Several early reports of the North American *Marchantia tenella* L. and *Fimbriaria tenella* (L.) Nees from Europe exist (Italy, Poland, Sweden, Switzerland, Portugal, see Casares-Gil (1915)), Notaris (1838–1839), Hübener (1834), Reinwardt *et al.* (1824)). These may refer to *Asterella gracilis* though no species of *Asterella* is yet recorded from Portugal. Erroneous records also exist from Asia (Java and Taiwan, see Nees (1838), Reinwardt *et al.* (1824), Kuo & Chiang (1988), Yang & Lee (1964)). Those from Java were later (Gottsche *et al.*, 1844–1847) described as *Fimbriaria blumeana* Nees.

5. *Asterella venosa* (Lehm. & Lindenb.) A.Evans

This tropical American species was erroneously recorded (as *Hypenantron venosum* (Lehm. & Lindenb.) Trevis.) from Java by Sande Lacoste (1856) and Schiffner (1898). These records refer to *Asterella khasyana*.

4.5.6 Ecology

In the past fairly detailed ecological accounts have been published for the four European species: *i.e. A. africana* (Rupidera Giraldo & Elias Rivas, 1996), *A. lindenbergiana* (Schiffner, 1939), *A. saccata* (Boros, 1925, 1938; Reimers, 1940; Suza, 1940) and *A. gracilis* (Mårtensson, 1955–1956; Schuster & Damsholt, 1974). In the Middle East and Asia very little has been published until recently, when some details have appeared for *A. grollei* (Long, 1999), *A. cruciata* (Long, 1997) and *A. limbata* (Long & Grolle, 1994). Earlier reports for Asia are very scanty, and in some cases misleading, for example Kashyap (1916) described *Asterella wallichiana* as 'very xerophilous' whereas in fact it is most luxuriant as a rheophyte on moist river banks and by waterfalls. For several taxa almost no ecological information is available, especially *A. blumeana* and *A. vulcanica*.

In common with many other Marchantiales, *Asterella* species typically behave as pioneers, colonising bare soil and rock substrates, never on organic substrates other than creeping over living bryophytes. Two factors appear to be important for many of the species, humidity and substrate acidity/ alkalinity. The most moisture-sensitive species are those with hygromorphic thalli, particularly the five species in Sect. *Brachyblepharis*. Moderately hygromorphic or slightly xeromorphic are *A. wallichiana* and *A. lindenbergiana*; the remaining seven species are typically xeromorphic. These tendencies are reflected in thallus morphology: xerophytes are thick and leathery, hygrophytes thin and delicate. Some species may be seasonal xerophytes or produce xeromorphic tubers. The hygrophytes (except *A. lindenbergiana*) tend to be species of forest habitats, where they grow on shady rocks, walls and streamsides. The xerophytes are more often found at high altitudes (*e.g. A. gracilis*) or in arid areas amongst rocks or dry scrub. In general, altitude reflects the type of habitat: species requiring cool moist forests such as *A. leptophylla* are found at higher altitudes in the Himalaya than they are farther north in Russia and Japan. Similarly Arctic-Alpine species such as *A. gracilis* are found at much lower altitudes in the Arctic than in the European mountains.

Many *Asterella* species are strict calciphiles, growing on limestone, gypsum or calcareous schist (*e.g. A. grollei, A. saccata, A. lindenbergiana, A. gracilis*) or on limy walls (*A. wallichiana*). For several species such as *A. blumeana* and *A. vulcanica* the substrate preferences remain unknown. Others, such as *A. africana*, *A. khasyana* and *A. mussuriensis* subsp. *mussuriensis* appear to be strictly calcifuge.

4.5.7 Distribution and phytogeography

Previous treatments of *Asterella* in Asia (*e.g.* Stephani, 1898–1900; Kashyap, 1929–1934; Kachroo, 1954; Pandé *et al.*, 1954) have listed numerous species considered as 'local endemics' and relatively few very widespread species. Kachroo (1954) stated that there were 21 endemic species in India alone. This contrasts with Europe where the taxonomy and distributions have been well-established for over a century. As a result of the present taxonomic revision of Asiatic taxa, more accurate distributions and phytogeography are now apparent, with a mixture of widespread and localised taxa.

Of the sixteen species now recognised in Eurasia, seven are classed as widespread and nine as localised. Of the widespread species, two occur in three continents, Europe, Asia and N. America (*A. saccata*, *A. gracilis*, Figs. 4.5, 4.21) as Arctic-alpines; two occur in two continents (*A. lindenbergiana*, an Alpine species in Europe and N. America; *A. khasyana*, Fig. 4.13, a tropical/ subtropical species in Asia and Africa) and three in only one continent, Asia, of which one is warm-temperate/ subtropical (*A. wallichiana*, Fig. 4.10) and two are cool-temperate (*A. leptophylla* and *A. mussuriensis*, Figs. 4.14, 4.20).

The nine localised species display several different distributions: three species (*A. blumeana*, *A. limbata* and *A. vulcanica*, Figs. 4.15) are tropical Malesian endemics; two (*A. grollei* and *A. multiflora*, Fig. 4.6) are Sino-Himalayan endemics, of which the former is cool temperate and the latter subtropical/ warm-temperate; one (*A. cruciata*, Fig. 4.12) is a cool-temperate Japanese/Chinese endemic; one (*A. persica*, Fig. 4.18) is a warm-temperate Middle-Eastern endemic; one (*A. pappii*, Fig. 4.18) is a tropical NE-African endemic and one (*A. africana*, Fig. 4.11) is a Mediterranean-Atlantic species.

4.6 DISCUSSION AND CONCLUSIONS

Taxonomic revision of *Asterella* in Eurasia utilised a wide range of material, mostly herbarium specimens which were studied using light microscopy. The amount of material available for each taxon varied widely. Many qualitative and quantitative characters were studied and recorded, and these data used to prepare keys and descriptions. From the 67 taxa previously described from Eurasia, 14 species were accepted and two new species described. The remainder were synonymised. One species was subdivided into two subspecies. The species were grouped in five subgenera. Study of type specimens necessitated designation of many new lectotypes.

This taxonomic revision shows that former species concepts have been too narrow. Redefinition of species has clarified the phytogeography greatly, with some local endemics and other very widespread species.

The classification adopted is admittedly somewhat arbitrary, being based on selected characters such as spore ornamentation and sexual condition which appear to be relatively stable and subdivide the taxa into easily-definable groups. This classification is effectively a hypothesis of relationships, some of which it is hoped reflect phylogeny. It is possible to test this classification by techniques of phylogenetic reconstruction (see Chapter 5).

The taxonomic revision is incomplete in that for several species very little material has been available for study, and large parts of the continent are poorly-explored for specimens: Sri Lanka, south India, Thailand, Myanmar (Burma), Taiwan, and Malesia, *e.g.* Sumatra, Java, Celebes, Philippines and the Malayan Peninsula. A number of problematic species occur in Java and Borneo which need further materials to deal with adequately. Papua New Guinea was deliberately excluded from the study area as it has several problematic *Asterella* taxa which require much further collecting; these may have links with Australasian species.

CHAPTER 5: PHYLOGENETIC RECONSTRUCTION

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5.1 INTRODUCTION

In Chapter 4.5.2 a classification of Eurasian species of *Asterella* into Subgenera and Sections was adopted as a practical way of grouping the species, based on selected characters considered to be both important and useful, such as pseudoperianth lobe attachment, carpocephalum shape, capsule dehiscence and spore colour and ornamentation pattern. This classification made no pretence of reflecting phylogeny, though some of the characters used might be expected to be phylogenetically informative.

Attempts to reconstruct phylogenies are now an integral part of systematics, and cladistic analysis has become a widely championed tool for this reconstruction, using both morphological and molecular datasets, or 'combined analyses' using both types of data. A more traditional approach used in the past for investigating phylogeny, the use of fossil evidence, is very difficult to undertake in bryophytes because of their lack of secondary thickening and consequent poor preservation (Schuster, 1966; Krassilov & Schuster, 1984). Most past phylogenetic debate in liverworts was based on comparative morphology (*e.g.* Cavers 1910–1911). In spite of the lack of fossil evidence, phylogeny of thalloid liverworts has been hotly debated since the time of Goebel (1915–1918) and Wettstein (1903–1908), with conflicting theories of evolution in Marchantiales, the 'Antithetic Theory' (Leitgeb, 1881) and 'Homologous Theory' (Wettstein, 1903–1908) which have been summarised by Bischler (1998). By the Antithetic Theory, Marchantiales underwent progressive elaboration from a simple acarpocephalate *Riccia*-like ancestor; by the Homologous Theory, gametophytes have been gradually reduced in elaboration, with *Riccia* consequently considered highly derived from former carpocephalate ancestors.

These debates on morphology have shed little light on the position of Aytoniaceae in Marchantiales, or on the relationships of genera within the Aytoniaceae, nor have studies using other types of data, for example cytological data (Bornefeld, 1987) or phytochemical data (Schier, 1974; Whittemore, 1991).

Cladistic analysis minimises the number of shared similarities explained by parallel or convergent evolution (*i.e.* minimises homoplasy) (Farris, 1983). The theoretical direction of evolution for each character used is usually ascertained by "outgroup comparison" *i.e.* by including an organism outside the group under study, the 'ingroup', which should be monophyletic (Nixon & Carpenter, 1993). Monophyletic groups include all, and only, descendants of a common ancestor. Paraphyletic groups include some, but not all, descendants of a common ancestor. Mishler & Churchill (1984, 1985) pioneered the application

of cladistic methods to Bryophyta, focussing particularly on their origin, and incorporated a wide spectrum of data. More recently, cladistic analyses have been widely applied in bryophytes, attempting to reconstruct phylogenies over land plants as a whole, over the Bryophyta as a group, and to many examples within the mosses and liverworts: relationships between families, genera and species, and even at the infraspecific level. Both morphological and molecular data (nucleic acid sequences) have now been widely utilised (*cf.* Newton et al., 2000).

Within Marchantiales, the molecular studies have been summarised by Bischler (1998), but they have not considered *Asterella* or Aytoniaceae in any detail. A radical new molecular phylogenetic reconstruction has been presented by Wheeler (2000), using a selection of families and genera. Wheeler used plastid and nuclear DNA sequences, and included three species of *Asterella* and one each of the sister-genera *Cryptomitrium*, *Reboulia* and *Plagiochasma*. In his combined (plastid and nuclear DNA) analysis, strong support was indicated for Aytoniaceae as a monophyletic family; however, the three species of *Asterella* did not form a monophyletic group. His studies did not identify a single outgroup for Aytoniaceae, the sister-group being a large clade including the families Monocleaceae, Targioniaceae, Cleveaceae and Ricciaceae. His trees conflicted strongly in many ways with the classification of Schuster (1984b) and the morphological cladistic trees of Bischler (1998), for example in the derived, not basal, position of *Riccia*.

More recently, Long *et al.* (2000) have investigated the phylogeny of genera of Aytoniaceae in more detail, using two chloroplast DNA sequences (*mat*K coding region and *trn*L intron). Sixteen species of *Asterella* were sampled, along with species of *Cryptomitrium*, *Mannia*, *Plagiochasma* and *Reboulia*. The study strongly supported Wheeler's conclusion that the Aytoniaceae is monophyletic, but produced well-supported evidence that *Asterella* is paraphyletic, with its four putative sister-genera nested within it and derived by two or three separate evolutionary events involving loss of the assumed synapomorphy, the pseudoperianth. Thus, all five 'genera' of Aytoniaceae in fact represent cladistically only a single broad '*Asterella*'. The study also demonstrated that the major molecular clades within Aytoniaceae have distinctive spore ornamentation patterns, and some of the infrageneric groupings of *Asterella* inferred from spore characters (Long, 1998) were supported. The traditional grouping of genera of Aytoniaceae into subfamilies Reboulioideae and Aytonioideae was not supported. The far-reaching taxonomic implications of this study have not been adopted here, as a clear subdivision of Aytoniaceae into smaller genera, with good morphological markers for recognition, cannot yet be made due to limited sampling of species of *Asterella*, *Cryptomitrium* and *Mannia*. Furthermore, the identification of an outgroup for Aytoniaceae has not yet been resolved.

The major cladistic analysis of Marchantiales using morphological data is that of Bischler (1998) which incorporated all families and genera. She used genera or subgenera as her terminal taxa, not individual species, and thereby made assumptions of monophyly of these taxa. *Asterella* was a sister-group to *Mannia*; Aytoniaceae was monophyletic with its sister-group a large clade including Wiesnerellaceae, Conocephalaceae, Lunulariaceae and Marchantiaceae. No conclusions about relationships of species within *Asterella* are possible from this study. Bischler's phylogeny is based on 41 characters, of which 14 are vegetative

characters of the gametophyte, 17 are reproductive characters of the gametophyte, and 12 are sporophyte characters.

The above molecular and morphological phylogenetic studies show congruent as well as conflicting results. A morphological phylogenetic study of Aytoniaceae is attempted, to test the congruence with molecular data, with a view to formulating an infrageneric classification of species of *Asterella* and evaluating relationships of the four 'sister-genera' to *Asterella*.

5.2 MATERIALS AND METHODS

Data utilised in this analysis are taken from the following sources: for *Asterella* from the present study and (spores) from Long (1998); for the other genera some data (*e.g.* spore data) is directly taken from observations on herbarium specimens in E, and from literature sources, particularly Bischler (1998) and Hässel de Menéndez (1962), Müller (1951–1958), Paton (1999), Perold (1999) and Schuster (1992c); as well as Kachroo & Kaul (1971), Kashyap (1915) and Mehra & Sokhi (1977) for *Cryptomitrium*; Bischler (1977, 1978, 1979a) for *Plagiochasma*.

The methodology of cladistic analysis has been set out in detail by Wiley *et al.* (1991) and used in many phylogenetic studies on bryophytes (*e.g.* Bischler (1998), Newton *et al.* (2000)). This approach was followed and the steps are outlined below. Other types of analysis were not performed, for example Neighbour-joining and Maximum likelihood, the former because individual characters cannot be traced, and the latter as it is applicable primarily to molecular datasets. Cladistic parsimony analysis is by far the most widely-used method for morphological datasets.

5.3 PHYLOGENETIC RECONSTRUCTION

5.3.1 Ingroup selection

The ingroup used in this study is Aytoniaceae, not *Asterella*, due to the strongly supported monophyly of Aytoniaceae and the paraphyly of *Asterella* demonstrated by molecular studies (Long *et al.*, 2000). It is fundamental to cladistic analysis that the ingroup be monophyletic (Nixon & Carpenter, 1993). The ingroup therefore includes the sixteen Eurasian species of *Asterella* studied, along with a single Eurasian representative of the four other genera of Aytoniaceae, *Cryptomitrium himalayense* Kashyap, *Mannia androgyna* (L.) A.Evans, *Plagiochasma appendiculatum* Lehm. & Lindenb. and *Reboulia hemisphaerica* (L.) Raddi.

However, this geographically restricted choice of *Asterella* species could create problems for cladistic analysis: it is theoretically impossible to demonstrate monophyletic groups within the ingroup unless all possible members of that ingroup are included in the analysis. Rarely is this possible in practice and normally it is considered acceptable to select representative species to cover the complete range of morphological variability of the ingroup rather than every taxon. Selecting on a geographical basis may not encompass the total range of variation over the estimated 80 species of *Asterella*. Nevertheless, the present study includes all the current subgenera defined in *Asterella*, and as far as is known is a good representation of the genus.

5.3.2 Outgroup selection

The outgroup method is used in cladistic analysis for determining character polarity, *i.e.* which character states are plesiomorphic and which are apomorphic (Nixon & Carpenter, 1993). Selecting the outgroup can be problematic. The outgroup must be one or more taxa outside the monophyletic ingroup and must have comparable characters which can be scored in both outgroup and ingroup taxa. Recent molecular study (Long *et al.*, 2000) used *Athalamia hyalina* (Sommerf.) S.Hatt. (Cleveaceae) and *Targionia hypophylla* L. (Targioniaceae) as outgroups for Aytoniaceae. *Targionia* was selected for this study as it clearly lies outside Aytoniaceae and can be scored across a wide range of morphological characters shared with Aytoniaceae.

5.3.3 Character selection and coding of character states

For cladistic analysis, discontinuous characters are strongly favoured as they can be easily coded as discrete states (Wiley *et al.*, 1991). Quantitative characters have been much less-used in cladistic analysis, although in groups where few discontinuous characters are available, quantitative characters have been subdivided into arbitrary states then coded 0, 1, 2 *etc.* The arbitrary nature of such data means that the resulting analyses are arbitrary. Stevens (1991) has criticised many past workers for using such subdivision of continuous data, and also pointed out that some characters treated as discontinuous are essentially quantitative. Stevens advocated more thorough analysis of quantitative data, so that character states can be 'delimited by carefully analysed discontinuities (not necessarily absolute gaps) in the variation'.

In the present study, *Asterella* was found to contain many discontinuous characters (see Appendix I) and no quantitative characters were included in the analysis. The main reason for this exclusion is that many of the quantitative characters, such as dimensions of the thallus, spore diameter, *etc.* vary continuously over the whole genus and cannot readily be subdivided meaningfully for coding; in addition some appear to show phenotypic plasticity. The nineteen characters selected have all been considered in Chapter 2 (morphological characters) or Chapter 3 (spore characters). Six are vegetative characters of the gametophyte, seven are reproductive characters of the gametophyte, and six are characters of the sporophyte. The definition of the adopted character states and their coding is summarised in Appendix VI. Some of these characters were used in a similar but broader study of Marchantiales by Bischler (1998). The resulting matrix is presented in Appendix VII. For four characters (6, 7, 8 and 10) a few species exhibit polymorphism, *e.g. Asterella blumeana* is polymorphic for sexual condition, androecial position and peduncle position; such polymorphisms are coded '1&2' , *etc.*

There are some problems associated with selecting morphological characters and a more detailed survey of the Aytoniaceae might reveal more potentially informative characters. Bischler (1998) discussed some characters excluded from her study, because of practical difficulties in observation, such as biochemical characters (*e.g.* the characterstic fishy smell of many *Asterella* species), ploidy level, characters of antheridia and archegonia, embryonic development patterns. Others which she utilised are apparently uninformative (non-variable) within Aytoniaceae (according to her coding of them), such as air chamber structure, oil-cell presence, rhizoid morphology, timing of fertilization, receptacle pore structure, seta length, spore:elater ratio, spore number per capsule and spore germination pattern.

Some important and potentially informative characters of the ingroup or part of the ingroup were omitted as they were absent in outgroups and/or some members of the ingroup and therefore polarity could not be unambiguously ascertained by outgroup comparison; for example, characters of pseudoperianth, absent from the sister-genera and outgroup. There are also problems in defining single characters and character states; some characters in reality could possibly be broken down into smaller characters, for example air pores are anatomically complex structures and the simple division by number of rings of pores is a crude system; ventral scale appendage shape and sexual condition could perhaps be subdivided into two or more characters. There are also possible problems of homology between outgroup and ingroup, for example it is assumed that the sessile involucre of *Targionia* is homologous with the carpocephalum-borne involucres in Aytoniaceae.

The problem of 'inapplicable data' arises with several characters, for example character 13 (pseudoperianth), where in some taxa that particular character is absent. Pennington & Gemeinholzer (2000) have discussed three different ways in which such characters may be coded: Applied to character 13, their Method A (single multistate) would score pseudoperianth absent as 0 and pseudoperianth present, fused at apex would score 1 and pseudoperianth present, free at apex would score 2. Method B (two characters) would break the character into two, the first being pseudoperianth absent (0) or pseudoperianth present (1), and the second pseudoperianth fused (0) or pseudoperianth free at apex (1). By this method, the genera *Targionia*, *Cryptomitrium*, *Mannia*, *Plagiochasma* and *Reboulia* would all be scored as non-applicable (*i.e.* with a question mark). Method C (Absence/Presence coding) would break the character into two: free pseudoperianth present/absent and fused pseudoperianth present/absent.

Pennington & Gemeinholzer (2000) dismissed Method C because the two subdivided characters are logically dependent on each other (a species with a free pseudoperianth present will inevitably score absent for the other type of pseudoperianth). Method B if applied would introduce numerous question marks into the data matrix, which introduces problems of optimisation. In the example above, *Targionia*, *Cryptomitrium*, *Mannia*, *Plagiochasma* and *Reboulia* will become optimised as possessing one state of pseudoperianth, a structure which none of them possesses. Thus their preferred scoring method for this type of data is Method A, using a single multistate character, and this method has been used here.

The above problems have the effect of restricting the data matrix to well-known, informative characters present in all taxa. This selectivity may have an effect on the results of parsimony analysis. Therefore caution should be exercised in interpreting morphological cladistic trees in Marchantiales. An extremely conservative view (*e.g.* Esser *et al.*, 1997) would be to recognise (as named higher taxa in a formal classification) only those clades defined by a unique apomorphy, in the case of Aytoniaceae as genera, subgenera and sections. Because of homoplasy, such an approach is rarely possible in reality as higher taxa can often only be defined by combinations of two or more characters.

5.3.4 Parsimony analysis

Analysis has been carried out on Macintosh computers using two software packages: PAUP 4.0b2a (Swofford, 1998) for parsimony analysis of data and tree searching, and MACCLADE 3.01 (Maddison & Maddison, 1992) for tabulating the data matrix, tree analysis and tracing of characters. The data matrix (Appendix VII) includes 21 taxa and 19 characters.

Phylogenetic trees were generated from unordered character states using PAUP (Swofford, 1998). Most parsimonious trees were first obtained with heuristic searches with SIMPLE addition sequence with TBR (tree bisection-reconnection) swapping and MULTREES on. A majority rule consensus tree was computed using PAUP. Because of the very low branch support normally found on morphological trees (due to the very short branch-lengths) bootstrap analysis (Felsentein, 1985) was not performed.

5.3.5 Character evolution

Character evolution was analysed for three characters in MACCLADE using the majority-rule consensus tree computed from the most parsimonious trees obtained. For these characters, (1 Thallus Branching, 9 Androecium type and 14 Capsule dehiscence) evolution of their different character states were traced on the cladogram. Optimisation (ACCTRAN or DELTRAN) was not used.

5.4 RESULTS

The heuristic analysis using *Targionia hypophylla* as outgroup resulted in 52 most parsimonious trees distributed among four tree islands (46, 2, 2 and 2 trees, respectively); tree length = 91 steps; Consistency Index = 0.54; Retention Index = 0.63. All characters in the matrix were informative. Four of the 52 trees, one from each island (trees 30, 47, 50 and 51) are shown in Figs. 5.1, 5.2, 5.3 and 5.4. The main difference between the four islands is that Island 1 (see Fig. 5.1) is less resolved, with a large polytomy absent from the other three islands.

Tree 30 (Island 1, Fig. 1) shows four major clades: '*Phragmoblepharis*' (*A. persica*, A. pappii, *A. mussuriensis, A. multiflora* and *A. vulcanica*); '*Brachyblepharis*' (*A. blumeana, A. limbata, A. leptophylla, A. africana, A. cruciata* and *A. khasyana*) to which *A. wallichiana* is sister; '*Saccatae*' (*A. saccata, A. grollei* and *A. lindenbergiana*) and 'Residue' (*A. gracilis*, *Mannia*, *Cryptomitrium*, *Reboulia* and *Plagiochasma*). '*Phragmoblepharis*' is basal and sister to the rest of the ingroup, which is itself unresolved.

Tree 47 (Island 2, Fig. 5.2) is more resolved and shows the same four major clades, except that *A. wallichiana* is sister to '*Saccatae*' rather than to '*Brachyblepharis*' and '*Brachyblepharis*' is sister to the rest of the ingroup.

Tree 50 (Island 3, Fig. 5.3) is also resolved with '*Phragmoblepharis*' sister to the rest of the ingroup; *A. wallichiana* is sister to '*Brachyblepharis*', *Plagiochasma* and *Mannia* also change position outside the 'Residue' clade.

Tree 51 (Island 4, Fig. 5.4) is also resolved into the same four major clades; however, '*Saccatae*' (with the addition of *A. wallichiana* and *Plagiochasma*) becomes basal and sister to the rest of the ingroup.

The majority rule consensus tree is shown in Fig. 5.5. The percentage values show the proportion of the most parsimonious trees in which that branch is present. Those branches with values below 100% are ones which would show no bootstrap support in a strict consensus tree. This tree displays similar topology and the same polytomy as in Tree 30 (Fig. 5.1). '*Phragmoblepharis*' is basal and sister to the rest of the ingroup. *A. wallichiana* is basal to the '*Brachyblepharis*' clade, as in Tree 30.

Results of tracing character evolution for three characters (1, 9, 14) are presented in Figs. 5.6 to 5.8, mapped on the majority rule consensus tree, which in topology closely resembles trees of Island 1 (*cf.* Fig. 5.1). However, none of the four major clades in any of the trees obtained can be defined by a unique apomorphy, for example in Fig. 5.6 ventral thallus branching defines the '*Phragmoblepharis* clade' but that character state also appears homoplasiously in *A. leptophylla* in the '*Brachyblepharis*' clade.

5.5 DISCUSSION

Comparison of the four selected trees (Figs. 5.1 to 5.4), representative of the four islands, shows that three major clades ('*Phragmoblepharis*', '*Brachyblepharis*' and '*Saccatae*') are consistently seen in all four. However, the relative position of these three clades changes between the four trees. In the consensus tree '*Phragmoblepharis*' is sister to the rest of the ingroup, as in tree 30. These three clades correspond to the established subgenera and sections recognised in Chapter 4, with three anomalies: (a) *Asterella lindenbergiana*, which is tradionally placed in Subgenus *Phragmoblepharis*, here nests with *A. saccata* and *A. grollei* (Subgenus *Saccatae*); (b) *Asterella wallichiana* (in Chapter 4 treated as a distinct Subgenus *Wallichianae*) which in the consensus tree and trees 30 and 50 is sister to '*Brachyblepharis*'; in trees 47 and 51 it is sister to '*Saccatae*'; (c) *Asterella gracilis*, which belongs to the 'Residue' clade along with *Mannia*, *Cryptomitrium*, *Reboulia* and *Plagiochasma*. In the consensus tree and trees 30 and 47 the 'Residue' form a single clade; in trees 50 and 51 this breaks down, in tree 51 *Plagiochasma* moves into the '*Saccatae*' clade. However, in the accepted classification of *Asterella*, *A. gracilis* is recognised as unique and is placed in its own subgenus '*Graciles*'.

It is the position of the four 'sister genera' which is perhaps most surprising. They are clearly nested within *Asterella* which thereby becomes paraphyletic; however their relationship to each other varies: in trees 30, 47 and the Consensus tree, they are nested in the same clade with *A. gracilis*; in trees 50 and 51 *Mannia* and *Plagiochasma* move out of this clade.

When the consensus tree (Fig. 5.5) is compared with the single most parsimonious molecular tree of Long et al. (2000), some congruences and some incongruences are observed. Congruences are: (a) Subgenus *Phragmoblepharis* is defined in both; (b) Section *Brachyblepharis* is defined in both; (c) Subgenus *Wallichianae* (*A. wallichiana*) is sister to Section *Brachyblepharis* in both; and (d) *Asterella gracilis* nests with *Mannia* in both. Incongruences are: (a) *A. lindenbergiana* is nested in Subg. *Phragmoblepharis* in the molecular tree, it is nested with Subg. *Saccatae* in the morphological consensus tree; (b) *A. grollei* is basal to Aytoniaceae in the molecular tree but not in the morphological consensus tree; (c) *Cryptomitrium* is not nested with *Plagiochasma*, *Reboulia* and *Mannia* in the molecular tree as it is in the morphological consensus tree.

Evolution of selected characters.

Character 1, Thallus Branching. Fig. 5.6 (0 = mostly terminal; 1 = mostly ventral). Of the two defined character states, 'mostly terminal' is plesiomorphic; 'mostly ventral' branching has evolved twice, in Subgenus *Phragmoblepharis* and in *A. leptophylla*.

Character 9 Androecium type. Fig. 5.7 (0 = diffuse; 1 = weak cushion; 2 = defined cushion). Of the three character states 'defined cushion' is plesiomorphic; diffuse androecia have evolved once, in the *A. gracilis*/ *Mannia*/ *Cryptomitrium* clade; 'weak cushions' have evolved twice, in the *A. saccata*/ *A. grolleii*/ *A. lindenbergiana* clade and in *A. africana* in the '*Brachyblepharis*' clade.

Character 14 Capsule dehiscence. Fig. 5.9 (0 = irregular cap, 1 = regular cap; 2 = valves). The presence of a cap defines Aytoniaceae; a 'regular' cap has evolved once, in the *A. gracilis*/ *Mannia*/ *Cryptomitrium* clade.

5.6 CONCLUSIONS

Based on morphological cladistic analysis:

(a) *Asterella* is a paraphyletic genus, with its four 'sister genera' nested within it.

(b) These 'sister genera' have evolved in a single clade within *Asterella*, most closely allied to *A. gracilis*.

(c) The accepted grouping of *Asterella* species into subgenera is largely supported, with some anomalies, but the relationship of these to each other is not unambiguously resolved.

(d) Comparison of the morphological consensus tree with the molecular tree shows some congruences: similar resolution of subgenus *Phragmoblepharis* and Section *Brachyblepharis*; *A. wallichiana* is sister to Section *Brachyblepharis* in both; and *A. gracilis* is placed alongside *Mannia* in both. Incongruences are the different placement of *A. lindenbergiana, A. grollei* and *Cryptomitrium* in the trees, and the placement of *Mannia*, *Cryptomitrium*, *Reboulia* and *Plagiochasma* in one clade in the morphological tree.

(e) Because of homoplasy the major clades cannot be defined by unique apomorphies, but only combinations of characters. Tracing of character evolution can pick out those character states which are important in defining particular clades: *e.g.* mostly ventral branching identifies Subg. *Phragmoblepharis*; the *A. gracilis*/ *Mannia*/ *Cryptomitrium* clade is identified by two synapomorphies, diffuse androecia and capsule dehiscence by a regular cap; the *A. saccata*/ *A. grolleii*/ *A. lindenbergiana* clade is identified by weakly defined androecial cushions.

There are several inherent limitations to this study, which might be addressed in a future more detailed molecular/ morphological investigation:

a. the need to find other outgroup(s) for Aytoniaceae

b. the need to look for additional informative morphological characters

c. the need to sample a wider range of ingroup species

d. the possible value of a combined analysis using molecular and morphological data, for the same terminal taxa, should be considered

e. the possible value of mapping morphological character evolution (eg. pseudoperianth loss) onto a molecular or combined tree in order to assess which characters have been least subjected to character reversals (homoplasy).

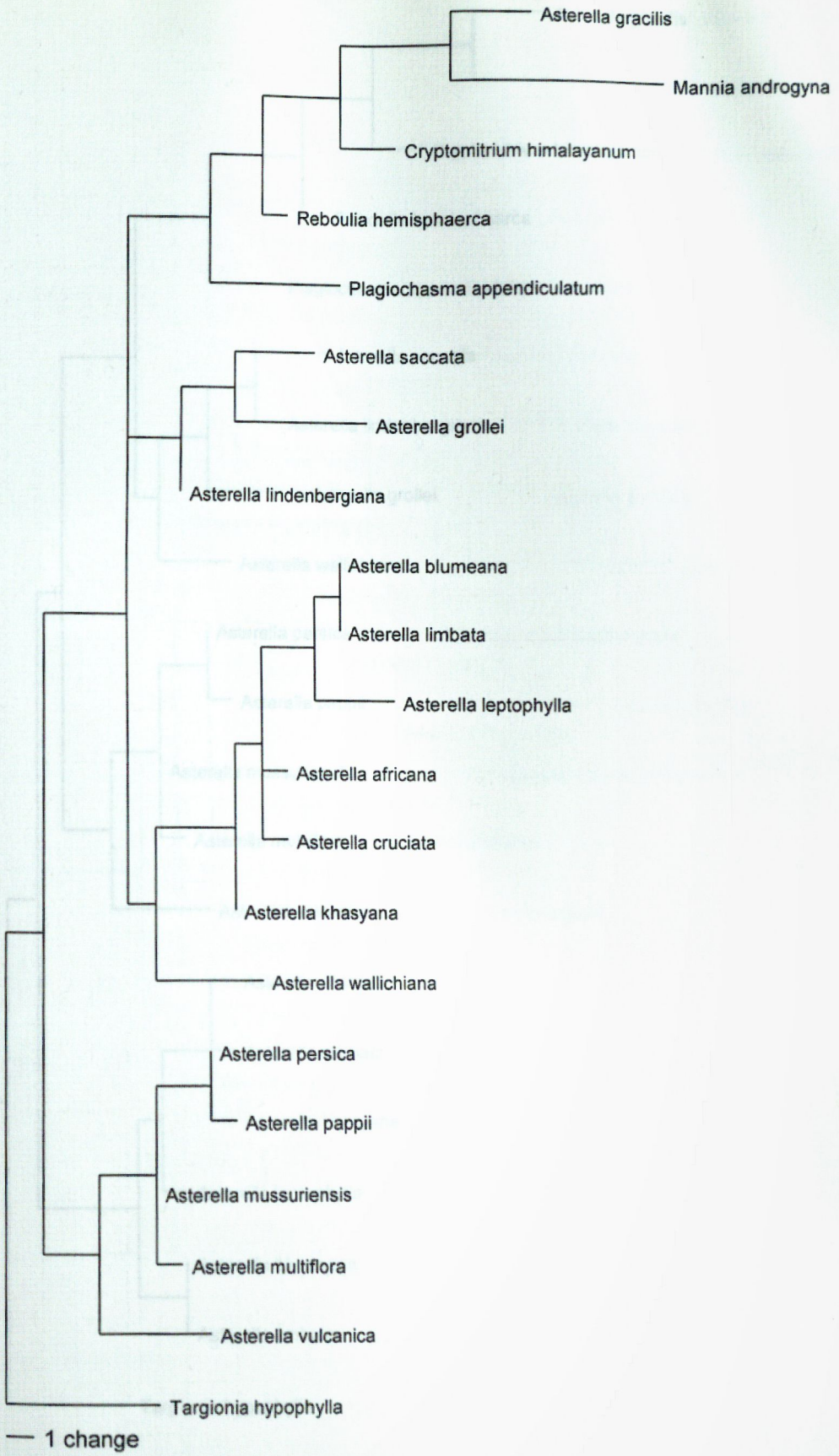

Fig. 5.1 Tree 30 (Island 1), one of 52 most parsimonious trees (length = 91 steps; C.I. = 0.54; R.I. = 0.63) derived from morphological dataset of 19 characters for 21 taxa based on a heuristic search using unweighted parsimony.

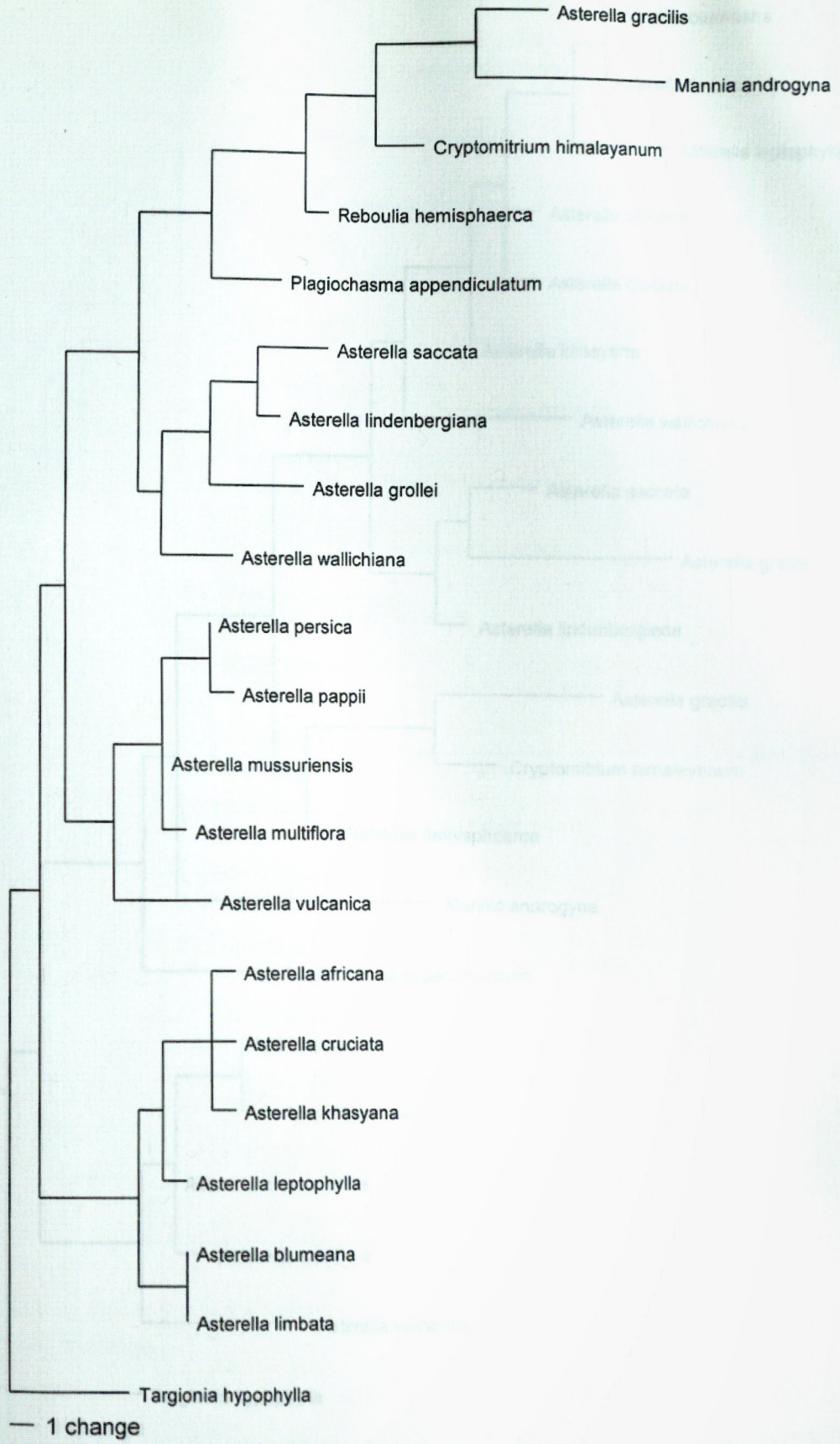

Fig. 5.2 Tree 47 (Island 2), one of 52 most parsimonious trees (length = 91 steps; C.I. = 0.54; R.I. = 0.63) derived from morphological dataset of 19 characters for 21 taxa based on a heuristic search using unweighted parsimony.

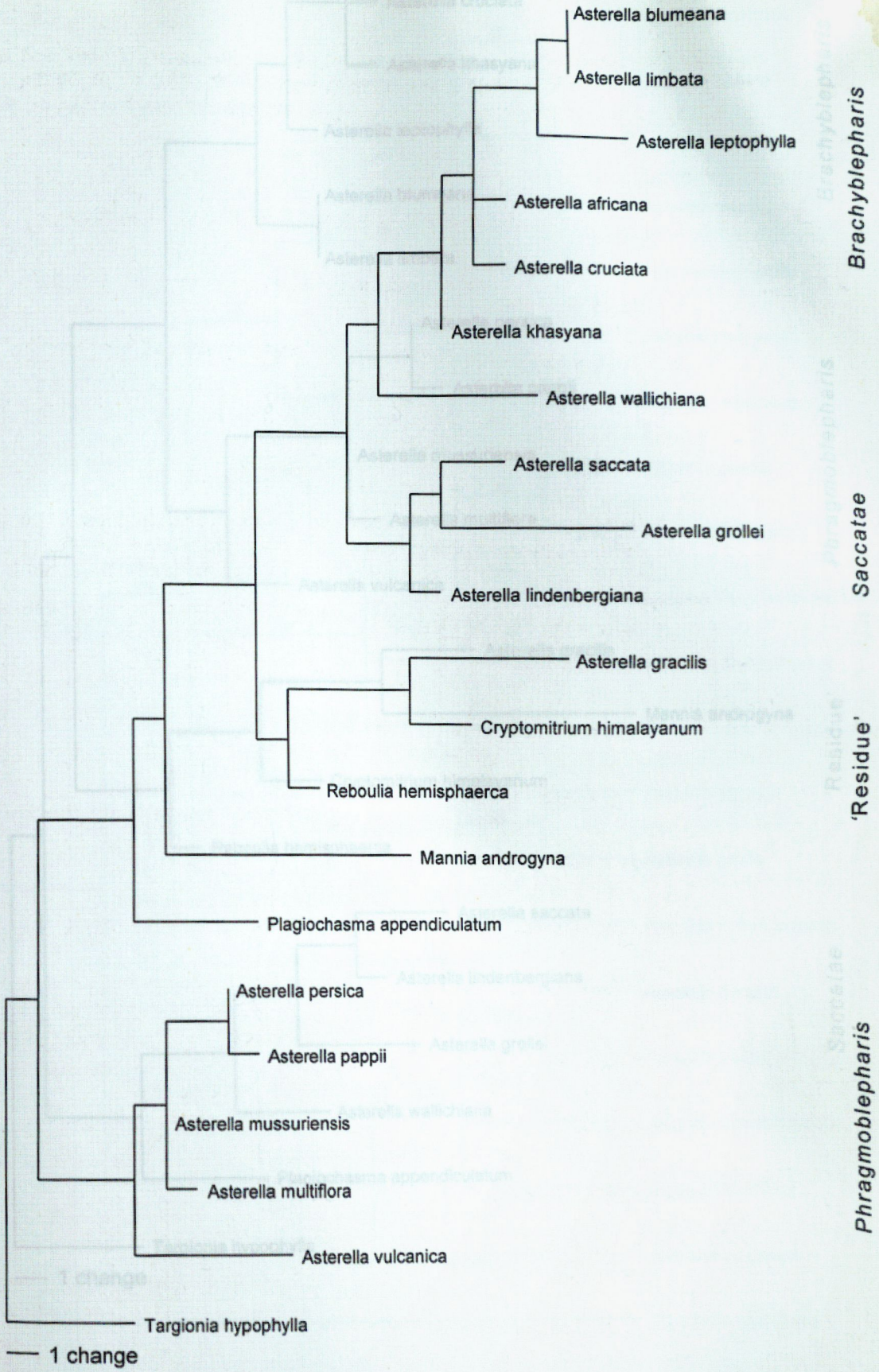

Fig. 5.3 Tree 50 (Island 3), one of 52 most parsimonious trees (length = 91 steps; C.I. = 0.54; R.I. = 0.63) derived from morphological dataset of 19 characters for 21 taxa based on a heuristic search using unweighted parsimony.

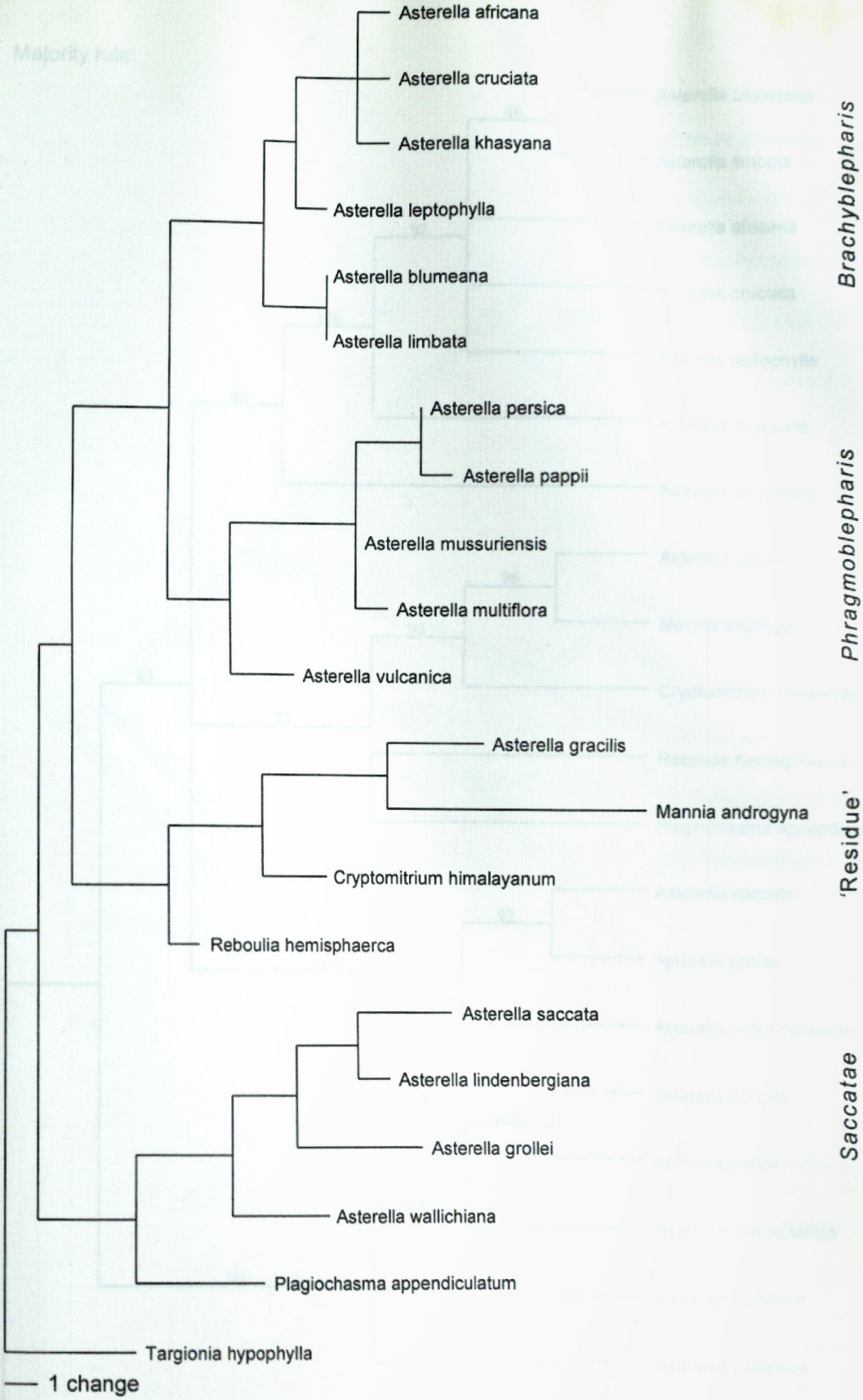

Fig. 5.4 Tree 51 (Island 4), one of 52 most parsimonious trees (length = 91 steps; C.I. = 0.54; R.I. = 0.63) derived from morphological dataset of 19 characters for 21 taxa based on a heuristic search using unweighted parsimony.

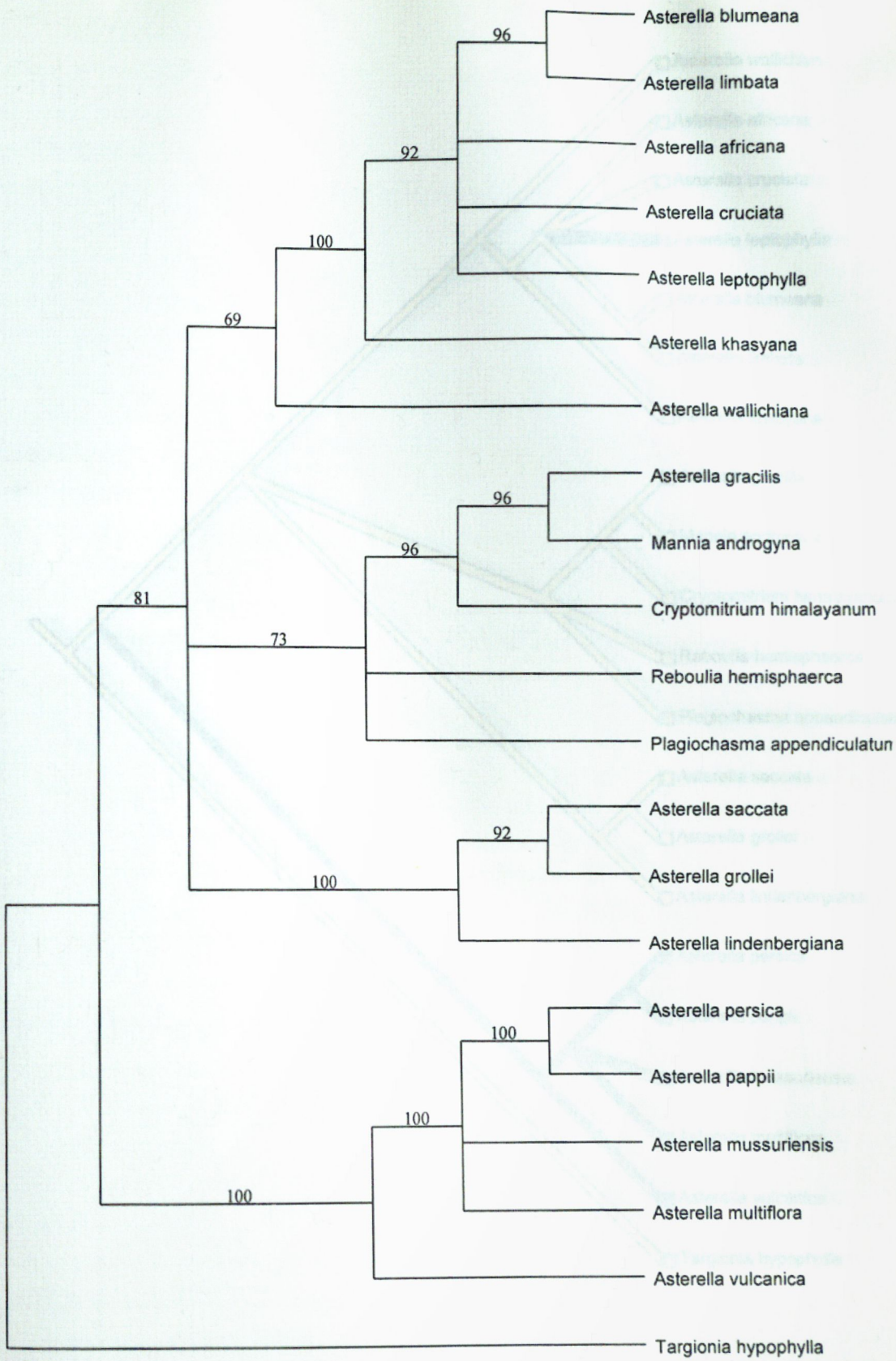

Fig. 5.5 Majority rule consensus tree of 52 most parsimonious trees (length = 91 steps; C.I. = 0.54; R.I. = 0.63) derived from morphological dataset of 19 characters for 21 taxa based on a heuristic search using unweighted parsimony. The percentage values show the proportion of the most parsimonious trees in which that branch appears.

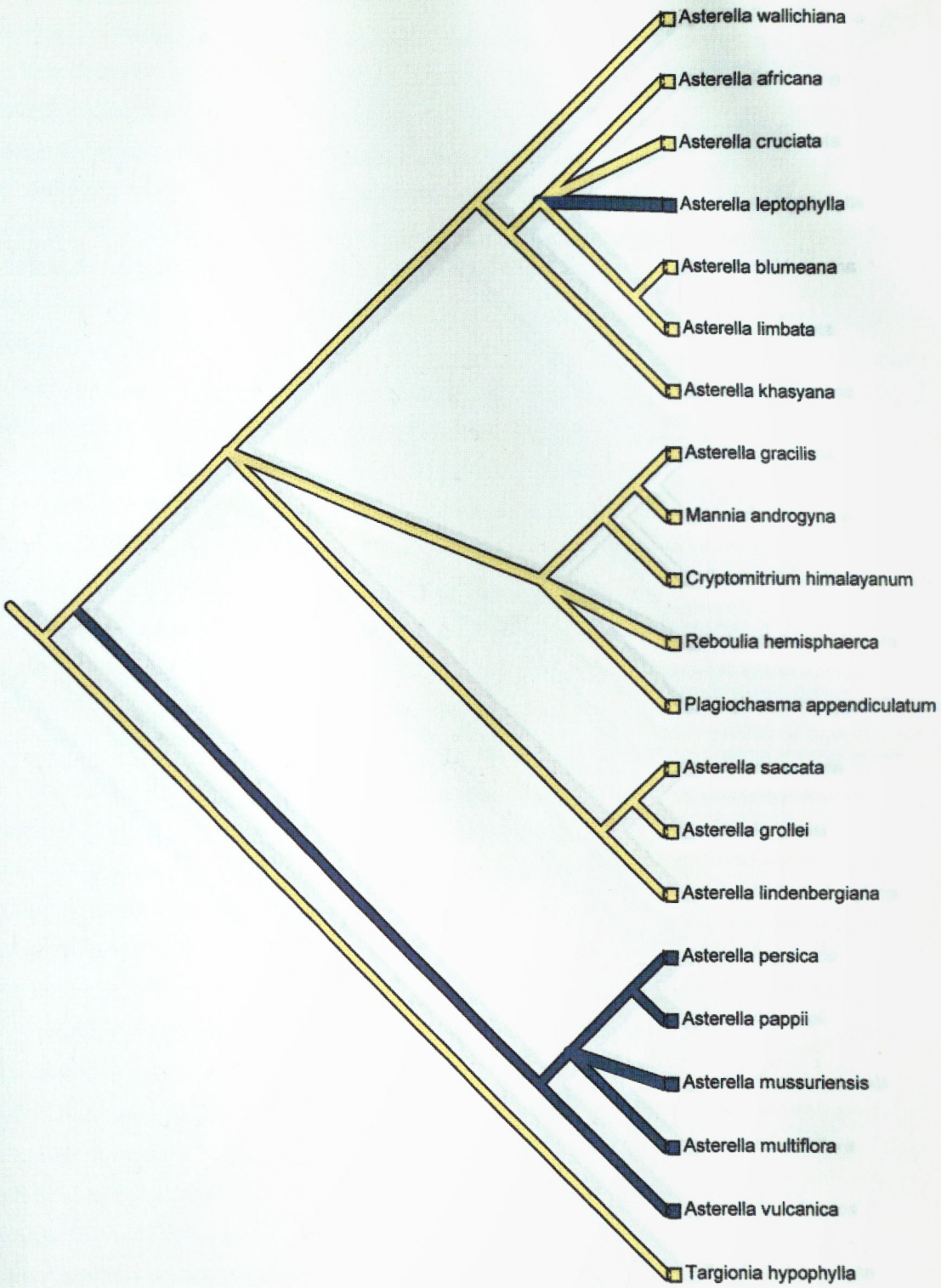

Fig. 5.6. Evolution of character 1, thallus branching, shown on majority rule consensus tree. Yellow = 'mostly terminal'; blue = 'mostly ventral'.

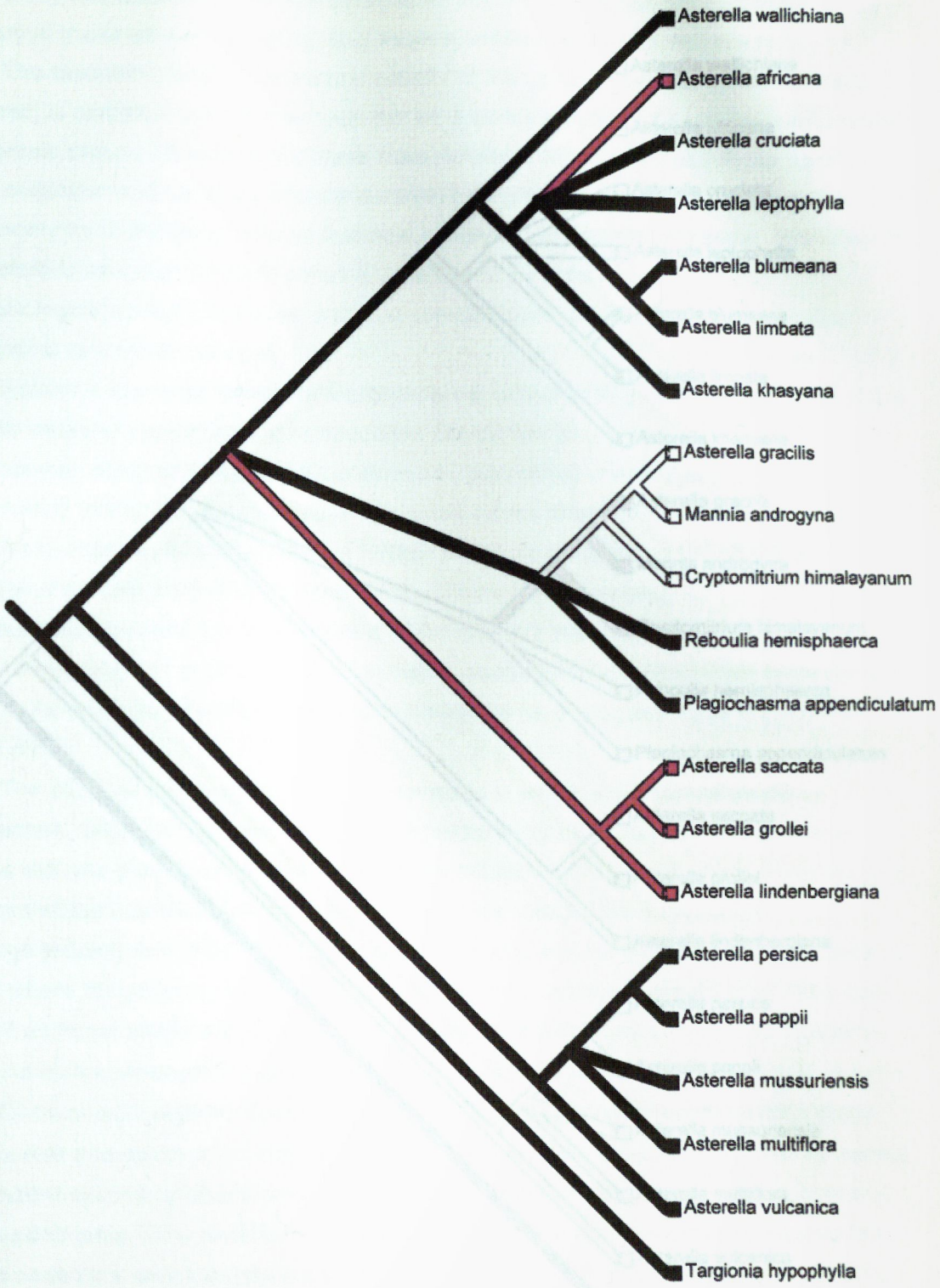

Fig. 5.7. Evolution of character 9, androecium type, shown on majority rule consensus tree. White = 'diffuse'; pink = 'weak cushions'; black = 'defined cushions'.

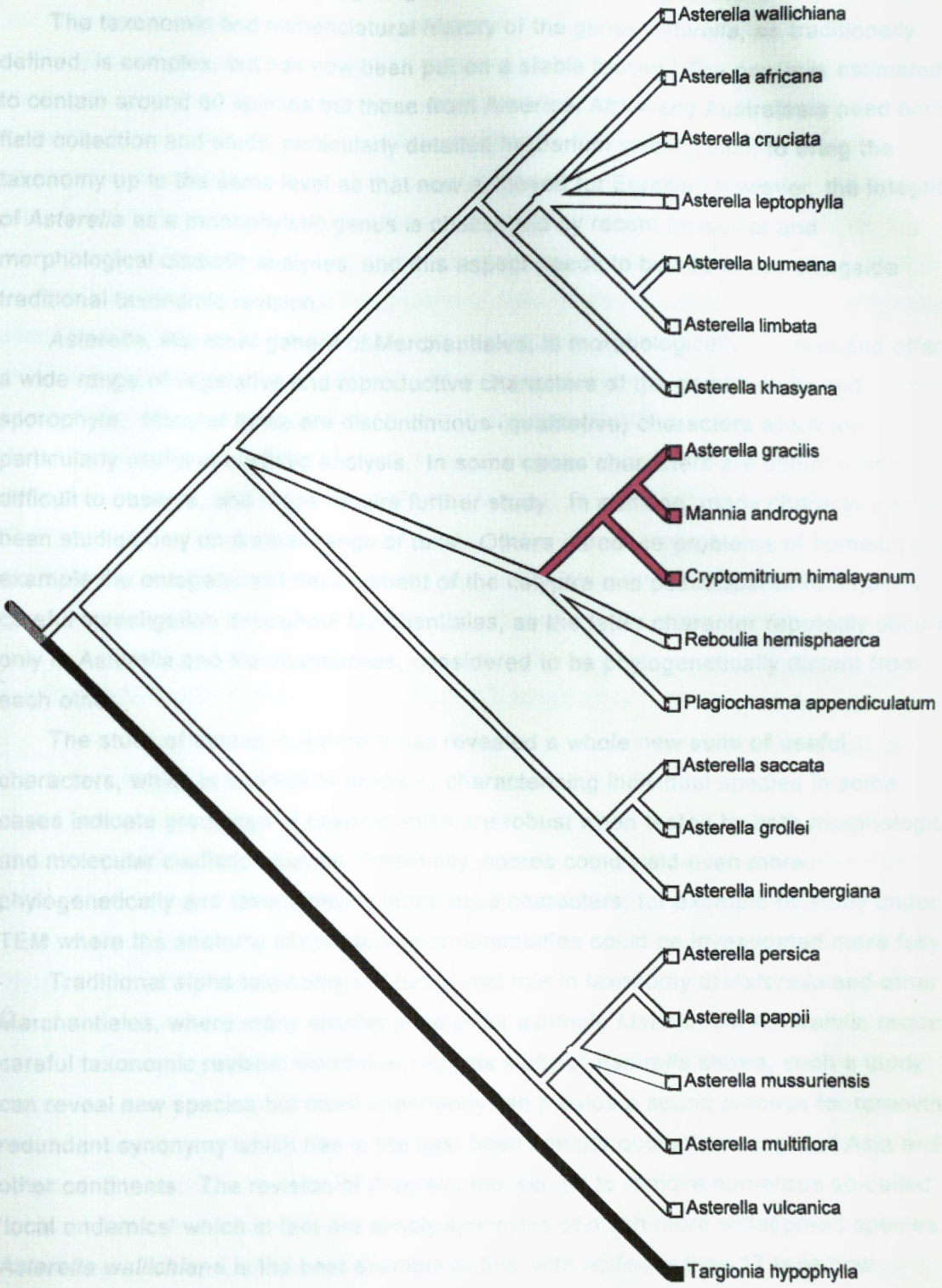

Fig. 5.8. Evolution of character 14, capsule dehiscence, shown on majority rule consensus tree. White = 'irregular cap'; pink = 'regular cap'; black = 'valves'.

CHAPTER 6: GENERAL CONCLUSIONS AND IMPLICATIONS

6.1 GENERAL CONCLUSIONS

The study has addressed the overall aims as set out in Chapter 1.6 and has broadly achieved these as well as highlighting several areas meriting further study.

The taxonomic and nomenclatural history of the genus *Asterella*, as traditionally defined, is complex, but has now been put on a stable footing. The genus is estimated to contain around 80 species but those from America, Africa and Australasia need both field collection and study, particularly detailed herbarium investigation, to bring the taxonomy up to the same level as that now achieved for Eurasia. However, the integrity of *Asterella* as a monophyletic genus is challenged by recent molecular and morphological cladistic analyses, and this aspect needs to be addressed alongside traditional taxonomic revision.

Asterella, like other genera of Marchantiales, is morphologically complex and offers a wide range of vegetative and reproductive characters of the gametophyte and sporophyte. Many of these are discontinuous (qualitative) characters which are particularly useful in cladistic analysis. In some cases characters are complex and difficult to observe, and these require further study. In addition, many characters have been studied only on a small range of taxa. Others introduce problems of homology, for example the ontogeny and development of the calyptra and pseudoperianth requires careful investigation throughout Marchantiales, as the latter character reputedly occurs only in *Asterella* and Marchantiaceae, considered to be phylogenetically distant from each other.

The study of spores in *Asterella* has revealed a whole new suite of useful characters, which in addition to precisely characterising individual species in some cases indicate groupings of species which are robust when tested by both morphological and molecular cladistic analysis. Potentially, spores could yield even more phylogenetically and taxonomically informative characters, for example by study under TEM where the anatomy of the surface ornamentation could be investigated more fully.

Traditional alpha taxonomy still has a vital role in taxonomy of *Asterella* and other Marchantiales, where many smaller genera, for example *Mannia* and *Athalamia*, require careful taxonomic revision worldwide. As this study of *Asterella* shows, such a study can reveal new species but more importantly can provide a sound process for removing redundant synonymy which has in the past been a major obstacle throughout Asia and other continents. The revision of *Asterella* has served to remove numerous so-called 'local endemics' which in fact are simply synonyms of much more widespread species. *Asterella wallichiana* is the best example of this, with no fewer than 17 taxa now synonymised under it. This detailed characterisation of species also reveals a wealth of

new biogeographic data: the redefined species show striking patterns of distribution, both widespread species and others of more restricted distribution, patterns which correlate with those of other species of plants (*e.g.* Sino-Himalayan species). Such revision also yields much more detailed ecological data about individual species, especially where study of plants in the field is possible.

The morphological cladistic analysis attempted on *Asterella*, together with recent molecular studies, shows the potential for this approach at both levels, and future use of combined datasets. Phylogenetic investigation needs to operate at several levels: firstly to clarify the overall evolutionary position of Marchantiales within liverworts and bryophytes, and then to provide a robust phylogeny of all the Marchantiales. In turn this will greatly help in resolving the evolutionary relationships of Aytoniaceae and its five component genera, and ultimately their subgenera and species. Progress to date has undermined the integrity of the five genera of Aytoniaceae but has not provided a viable alternative. It would appear that *Asterella* is paraphyletic, but the molecular and morphological tree topologies, though showing some striking congruences, also show some important incongruences, for example as to whether the 'sister-genera' of *Asterella* arose as a single evolutionary event (marked by loss of the pseudoperianth) or by two or three separate processes of reduction, as is implied by the molecular trees. The question therefore remains open as to whether Aytoniaceae is represented cladistically by a single genus (*Asterella sensu lato*) or whether it can be subdivided into two or more smaller genera using other key characters yet to be identified.

6.2 BROADER IMPLICATIONS AND FUTURE RESEARCH

6.2.1 Future taxonomic and phylogenetic studies

In the study area, there are several major gaps in this taxonomic study, primarily due to lack of field work, both in particular areas such as the Malesian archipelago and Indo-china, but also for several rare and inadequately understood species of *Asterella*, particularly *A. blumeana*, *A. limbata* and *A. vulcanica*. Perhaps the most potentially interesting of the under-collected parts of Asia (left out of this study for that reason) is Papua New Guinea, where the few specimens studied suggest that at least four species occur, and that these are of considerable interest. At least one of these (*A. vulcanica*) shows strong affinities with some Australasian species, and thereby provides an interesting link between northern hemisphere and southern hemisphere species of *Asterella*.

Outside the study area, three monographic treatments of *Asterella* are required: for Australasia, Africa and America. As pointed out in Chapter 1, America, particularly the Neotropics, is likely to reveal the greatest diversity of morphology. However,

revision for all three continents is highly desirable if the full evolutionary and biogeographical picture of *Asterella* and Aytoniaceae is to be achieved. All three continents provide interesting links (e.g. in spore ornamentation) between the two hemispheres which may provide clear evolutionary links. Species such as the Asiatic *Asterella grollei*, a highly localised taxon which shows strong morphological links with species in other continents (*A. muscicola* in Africa and *A. palmeri* in America), pose interesting evolutionary and biogeographical questions which can only be investigated by a global approach.

As in Asia, many of these other regions of the world are poorly-collected for *Asterella*, and collection for taxonomic revision can also provide material for DNA extraction for a global molecular phylogenetic study. Although north temperate species such as *A. gracilis* and *A. saccata* are circumboreal, tropical species of the genus appear to be restricted to single continents, with the exception of *A. khasyana* recently discovered in Africa. The global approach will enable the following biogeographic question to be addressed: did the tropical species of *Asterella* arise independently on each continent?

6.2.2 Studies below the species level

The present study has shown that species such as *A. khasyana*, *A. leptophylla* and *A. wallichiana* show infraspecific variation across their range which can be demonstrated by spore and other characters. In *A. wallichiana* it is particularly striking, where characters such as spore size, spore colour and morphology of ventral scale appendages appear to vary in ways which correlate to some extent with geography, but nevertheless do not show clear discontinuities which can be easily recognised taxonomically. In addition, preliminary molecular studies in *A. wallichiana* and *Reboulia hemisphaerica* reveal significant differences between isolated populations. This suggests that 'cryptic' or 'sibling' speciation may be widespread in Aytoniaceae as has been demonstrated in other genera of Marchantiales including *Mannia* and *Conocephalum*. This is likely to be a fruitful area for further research, particularly as there appear to be some morphological markers which may or may not correlate with 'cryptic' molecular discontinuities. *Asterella wallichiana* in south-east Asia would be an excellent species for such a study. It would require considerable field work and collection of herbarium and DNA vouchers over the range of the species. Other techniques, such as analysis of isozymes or secondary products, could also be brought to bear on the problem.

A related problem which this study was unable to address fully, was the apparent phenotypic plasticity of some characters in *Asterella*, particularly quantitative characters such as thallus dimensions and spore size. The results presented in Chapter 3 on

variation in spore diameter were inconclusive, as some variation was considered to be due to phenotypic plasticity (variation of *A. wallichiana* on the island of Iriomote) but there was also evidence of genotypically-based variation in spore diameter correlated with geography across the whole range of the species. Experimental work on characters such as this, to study the phenotypic and genotypic bases for this variation, could be of considerable interest.

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Appendix I Characters used in taxonomy of *Asterella* by selected monographers

Showing the 'key' characters (characters used in keys, diagnoses, infrageneric groupings *etc.*) and general descriptive characters used by five important authors from 1838 to 1994 in distinguishing species of *Asterella*. V = vegetative characters; R = reproductive characters of gametophyte; S = sporophyte characters. C = continuous characters; D = discontinuous characters. 0 = not used; 1 = used in species descriptions; 2 = used as 'key' character

Char. No.	Part of plant	Main Characters used	Cont./ Disc.	Nees (1838)	Stephani (1898-1925)	Evans (1920)	Grolle (1976, 1989)	Perold (1994)
V01	Thallus	smell fresh	D	1	0	0	0	0
V02		colour	D	1	1	1	1	2
V03		shape	D	1	1	0	1	1
V04		dimorphism	D	0	0	0	1	0
V05		texture	D	2	1	2	2	1
V06		branching	D	1	1	2	1	1
V07		shape in ts	D	2	1	1	1	1
V08		length	C	1	1	1	1	2
V09		breadth	C	1	1	2	1	2
V10		thickness	C	0	1	0	0	1
V11	Upper surface	flatness/ convexity	D	2	1	1	1	1
V12		reticulation	D	1	0	0	1	1
V13	Wings	development in t.s.	D	1	1	1	1	1
V14		margin	D	1	1	2	1	1
V15	Midrib	width in relation to thallus	C	1	1	1	1	0
V16	Epidermis	cell diameter	C	0	0	1	0	1
V17		cell thickening	D	1	1	1	1	1
V18		oil cells + / -	D	0	0	2	1	1
V19	Pores	pore:chamber ratio	C	0	0	2	0	0
V20		no. / area	C	0	0	0	0	1
V21		pore size	C	1	1	1	0	1
V22		number of rings	D	0	1	1	1	1

Appendix I (cont'd)

Char. No.	Part of plant	Main Characters used	Cont./ Disc.	Nees (1838)	Stephani (1898-1925)	Evans (1920)	Grolle (1976, 1989)	Perold (1994)
V23	Pores	number of rows of cells	D	1	1	1	1	1
V24		inner cell length	C	0	0	0	0	1
V25		inner cell width	C	0	0	0	0	1
V26		outer cell length	C	0	0	0	0	1
V27		outer cell width	C	0	0	0	0	1
V28		wall thickening	D	0	0	2	1	2
V29	Assimilation layer	thickness (in midrib)	C	1	1	1	1	2
V30	Air chambers	no. layers (in midrib)	D	0	0	1	1	2
V31		breadth	C	0	0	0	0	1
V32		shape	D	0	1	1	2	2
V33		free filaments + / -	D	0	1	2	2	2
V34	Basal tissue	thickness	C	0	0	1	1	1
V35		cell diameter	C	0	0	0	0	1
V36		mycorrhiza	D	0	0	1	0	0
V37	Ventral scales	distance apart	C	0	1	0	0	0
V38		colour	D	1	1	1	1	1
V39		shape	D	1	0	1	1	1
V40		length	C	0	0	1	0	1
V41		breadth	C	0	0	1	0	1
V42		exsertion at thallus apex/ margin	D	2	1	2	0	1
V43		cell length	C	0	0	0	1	1
V44		cell width	C	0	0	0	1	1
V45		no. oil cells	D	0	0	1	1	1
V46		no. slime papillae	D	0	0	0	1	1
V47	Appendages	number	D	0	1	2	2	2
V48		shape	D	1	2	1	2	2
V49		apex shape	D	1	2	1	2	2
V50		length	C	0	0	1	0	1

Appendix I (cont'd)

Char. No.	Part of plant	Main Characters used	Cont./ Disc.	Nees (1838)	Stephani (1898-1925)	Evans (1920)	Grolle (1976, 1989)	Perold (1994)
V51	Appendages	breadth	C	0	0	1	1	1
V52		basal constriction	D	0	1	1	2	1
V53		margin	D	0	2	1	2	2
V54		cell length	C	0	0	1	0	1
V55		cell width	C	0	0	1	0	1
R01	Chromosome number	n	D	0	0	0	0	1
R02	Sexuality	sexuality	D	0	1	2	2	2
R03	Androecia	position	D	1	1	2	2	1
R04		marginal scales	D	0	0	1	1	1
R05	Peduncle	position on thallus	D	1	1	1	1	1
R06		colour	D	1	1	1	1	1
R07		length	C	1	1	1	1	1
R08		width	C	0	0	0	0	1
R09		ridges	D	1	1	0	1	0
R10		air chambers	D	0	1	0	0	1
R11		scales + / -	D	1	1	1	2	1
R12	Basal scales	+ / -	D	1	1	1	1	1
R13		colour	D	1	1	1	1	1
R14		shape	D	1	1	1	1	1
R15	Apical scales	+ / -	D	1	1	1	1	2
R16	Carpocephalum	colour	D	1	1	1	1	0
R17		shape	D	2	2	1	2	2
R18		length	C	1	1	0	0	0
R19		width	C	1	0	1	0	1
R20		lobing	D	1	1	2	1	2
R21		papillosity	D	1	1	2	1	2
R22		marginal air chambers	D	0	1	0	2	0
R23	Lobes	length	C	0	1	0	1	0
R24		margin	D	1	1	1	0	0
R25	Involucre	division (lobing)	D	0	1	1	2	0

Appendix I (cont'd)

Char. No.	Part of plant	Main Characters used	Cont./ Disc.	Nees (1838)	Stephani (1898-1925)	Evans (1920)	Grolle (1976, 1989)	Perold (1994)
R26	Pseudoperianth	colour	D	1	1	2	2	1
R27		shape	D	1	1	0	0	1
R28		orientation	D	1	1	2	0	1
R29		total length	C	1	0	0	0	1
R30		exsertion from involucre	C	1	1	0	0	2
R31		no. lobes	D	1	1	2	2	2
R32		lobe length	C	0	0	0	0	1
R33		lobe width	C	0	0	0	0	1
R34		attachment at apex	D	1	0	2	2	2
R35		apical surface	D	0	0	0	2	1
R36		cell length	C	0	0	0	0	1
R37		cell width	C	0	0	0	0	1
S01	Capsule	colour	D	1	1	1	1	1
S02	Wall	thickening	D	1	1	0	1	1
S03		cell shape	D	0	0	0	1	1
S04		cell diameter	C	1	1	0	1	1
S05	Elaters	colour	D	1	1	1	1	1
S06		length	C	1	1	1	0	1
S07		width	C	0	0	2	1	1
S08		shape	D	1	1	1	1	1
S09		number of spirals	D	1	1	1	1	1
S10	Spores	colour	D	1	1	2	2	2
S11		diameter	C	0	1	1	1	2
S12		ornamentation (light. mic.)	D	1	1	2	2	2
S13		wing + / -	D	1	1	2	1	1
S14		wing crenation	D	1	1	1	1	1
S15		ornamentation (SEM)	D	0	0	0	2	2

Appendix I (cont'd.) Summary of types of characters used in past revisions of *Asterella*
V characters = vegetative characters of gametophyte; R = reproductive characters of gametophyte;
S = sporophyte characters; type 1 characters = general descriptive characters, type 2 = key characters;
T = totals

	No. V (veg.) characters (out of total 55)			No. R (repr.) characters (out of total 37)			No. S (spor.) characters (out of total 15)			Total no. Characters (out of total 107)		
	1	2	T(V)	1	2	T(R)	1	2	T(S)	1	2	T
Nees (1838)	19	4	23	23	1	24	11	0	11	53	5	58
Stephani (1898-1925)	24	3	27	25	1	26	12	0	12	61	4	65
Evans (1920)	29	10	39	14	8	22	7	4	11	50	22	72
Grolle (1976, 1989)	27	8	35	13	10	23	11	3	14	51	21	72
Perold (1994)	36	12	48	22	8	30	11	4	15	69	24	93

Appendix I (cont'd.) Summary of use of continuous versus discontinuous characters in past revisions of *Asterella*

Character type	No. continuous	No. discontinuous
V (vegetative)	25	30
R (reproductive)	11	26
S (sporophye)	4	11
Total	40	67

Appendix II Increase in diameter of a single dry spore of *Asterella wallichiana* (*B.S.E. 201*) by moistening, measured under LM

Time (mins.)	Diameter (µm)	% swelling
0	38.3	0
8	40.7	6.3
14	42.0	9.7
18	44.5	16.2
24	44.5	16.2
27	44.5	16.2

Appendix III Analysis of spore diameter under LM and SEM

Comparative LM/SEM spore diameters of *Asterella wallichiana* specimens from Iriomote, Japan

Sample	*Long 24903* LM	*Long 24903* SEM	*Nagamasu s.n.* LM	*Nagamasu s.n.* SEM	*Saito s.n.* LM	*Saito s.n.* SEM	*Yamaguchi 11381* LM	*Yamaguchi 11381* SEM	*Yamaguchi 11383* LM	*Yamaguchi 11383* SEM
1	49.4	51.5	54.3	58.3	50.6	50.9	44.5	51.5	46.9	56.1
2	48.2	54.5	51.9	59.1	49.4	47.9	43.2	53.8	46.9	53.8
3	48.2	50.0	53.1	63.6	46.9	48.3	45.7	53.0	46.9	50.0
4	49.4	54.5	54.3	68.2	46.9	55.5	45.7	56.1	50.6	50.7
5	46.9	50.0	59.3	64.4	48.2	47.9	48.2	51.5	45.7	53.0
6	46.9	50.7	59.3	61.4	49.4	49.0	43.2	54.5	48.2	48.5
7	49.4	51.5	51.9	62.9	51.9	51.3	44.5	51.5	44.5	56.1
8	44.5	50.0	53.1	59.8	50.6	47.5	42.0	57.6	50.6	53.0
9	45.7	54.5	54.3	58.3	49.4	48.7	46.9	56.8	45.7	51.5
10	48.2	50.0	54.3	62.1	50.6	50.2	45.7	54.5	53.1	48.5
Mean	47.7	51.7	54.5	61.8	49.4	49.7	45.0	54.1	47.9	52.1
SD	1.66	2.00	2.66	3.13	1.65	2.42	1.86	2.25	2.71	2.77
99.9% conf. level	2.51	3.02	4.02	4.73	2.49	3.65	2.81	3.40	4.09	4.18

Appendix III (cont'd.)

Two-way ANOVA analysis of LM/SEM spore diameter data

Source	df	Sums of squares	Mean square	F-ratio	Probability
Collector	4	1158.37	289.59	51.92	≤ 0.0001
Treatment	1	621.50	621.50	111.45	≤ 0.0001
Cllr/Trt	4	226.50	56.62	10.15	≤ 0.0001
Error	90	501.97	5.58		
Total	99	2508.29			

1. Expected spore diameter means for data on 'collector'

Collector/ collection	Expected diameter mean	Spore count
Long 24903	49.70	20
Nagamasu s.n.	58.20	20
Saito s.n.	49.56	20
Yamaguchi A (11381)	49.52	20
Yamaguchi B (11383)	50.02	20

Bonferroni Post Hoc Tests

	Difference	Probability
Nagamasu - Long	8.49	0
Saito - Long	-0.14	1.0000
Saito - Nagamasu	-8.64	0
Yamaguchi A - Long	-0.18	1.0000
Yamaguchi A - Nagamasu	-8.67	0
Yamaguchi A - Saito	-0.03	0.9999
Yamaguchi B - Long	0.31	0.9999
Yamaguchi B - Nagamasu	-8.18	0
Yamaguchi B - Saito	0.46	0.9996
Yamaguchi B - Yamaguchi A	0.49	0.9992

Appendix III (cont'd.)

2. Expected spore diameter means for data on 'Treatment'

Treatment	Expected diameter mean	Spore count
LM	48.90	50
SEM	53.89	50

Bonferroni Post Hoc Test

	Difference	Probability
SEM - LM	4.99	0

3. Expected spore diameter means for data on 'collector'/'treatment' interaction

Collector/Treatment	Expected spore diameter mean	Spore count
Light, *Long*	47.68	10
Light, *Nagamasu*	54.58	10
Light, *Saito*	49.39	10
Light, *Yamaguchi A*	44.96	10
Light, *Yamaguchi B*	47.91	10
SEM, *Long*	51.72	10
SEM, *Nagamasu*	61.81	10
SEM, *Saito*	49.72	10
SEM, *Yamaguchi A*	54.08	10
SEM, *Yamaguchi B*	52.12	10

Appendix III (cont'd.)

Bonferroni Post Hoc Tests

	Difference	Probability
Light, *Nagamasu* - Light, *Long*	6.90	0
Light, *Saito* - Light, *Long*	1.71	0.99
Light, *Saito* - Light, *Nagamasu*	-5.19	0. 0002
Light, *Yamaguchi A* - Light, *Long*	-2.72	0.4095
Light, *Yamaguchi A* - Light, *Nagamasu*	-9.62	0
Light, *Yamaguchi A* - Light, *Saito*	-4.43	0.0028
Light, *Yamaguchi B* - Light, *Long*	0.23	1.0
Light, *Yamaguchi B* - Light, *Nagamasu*	-6.67	0
Light, *Yamaguchi B* - Light, *Saito*	-1.48	0.9997
Light, *Yamaguchi B* - Light, *Yamaguchi A*	2.95	0.2500
SEM, *Long* - Light, *Long*	4.04	0.0108
SEM, *Long* - Light, *Nagamasu*	-2.86	0.3065
SEM, *Long* - Light, *Saito*	2.33	0.7450
SEM, *Long* - Light, *Yamaguchi A*	6.76	0
SEM, *Long* - Light, *Yamaguchi B*	3.81	0.0225
SEM, *Nagamasu* - Light, *Long*	14.13	0
SEM, *Nagamasu* - Light, *Nagamasu*	7.23	0
SEM, *Nagamasu* - Light, *Saito*	12.42	0
SEM, *Nagamasu* - Light, *Yamaguchi A*	16.85	0
SEM, *Nagamasu* - Light, *Yamaguchi B*	13.90	0
SEM, *Nagamasu* -SEM, *Long*	10.09	0
SEM, *Saito* - Light, *Long*	2.04	0.9271
SEM, *Saito* - Light, *Nagamasu*	-4.86	0.0006
SEM, *Saito* - Light, *Saito*	0.33	1
SEM, *Saito* - Light, *Yamaguchi A*	4.76	0.0009
SEM, *Saito* - Light, *Yamaguchi B*	1.81	0.9856
SEM, *Saito* - SEM, *Long*	-2.00	0.9424
SEM, *Saito* - SEM, *Nagamasu*	-12.09	0
SEM, *Yamaguchi A* - Light, *Long*	6.40	0
SEM, *Yamaguchi A* - Light, *Nagamasu*	-0.50	1
SEM, *Yamaguchi A* - Light, *Saito*	4.69	0.0011
SEM, *Yamaguchi A* - Light, *Yamaguchi A*	9.12	0
SEM, *Yamaguchi A* - Light, *Yamaguchi B*	6.17	0
SEM, *Yamaguchi A* - SEM, *Long*	2.36	0.7203
SEM, *Yamaguchi A* - SEM, *Nagamasu*	-7.73	0
SEM, *Yamaguchi A* - SEM, *Saito*	4.36	0.0037
SEM, *Yamaguchi B* - Light, *Long*	4.44	0.0028
SEM, *Yamaguchi B* - Light, *Nagamasu*	-2.46	0.6339
SEM, *Yamaguchi B* - Light, *Saito*	2.73	0.4016
SEM, *Yamaguchi B* - Light, *Yamaguchi A*	7.16	0
SEM, *Yamaguchi B* - Light, *Yamaguchi B*	4.21	0.0061
SEM, *Yamaguchi B* - SEM, *Long*	0.40	1
SEM, *Yamaguchi B* - SEM, *Nagamasu*	-9.69	0
SEM, *Yamaguchi B* - SEM, *Saito*	2.40	0.6863
SEM, *Yamaguchi B* - SEM, *Yamaguchi A*	-1.96	0.9553

Appendix IV Mean diameters (µm) of spores of Eurasian *Asterella* species measured under SEM

Species	*saccata*	*grollei*	*wallichiana* (contin.)	*wallichiana* (islands)	*africana*	*cruciata*	*khasyana* (contin.)	*khasyana* (islands)
No. spores measured	60	30	270	200	30	110	90	60
Min.	81.8	134.5	43.9	42.4	58.3	57.6	63.6	74.2
Max.	126.5	161.6	106.1	81.1	85.6	84.8	98.5	101.5
Mean	107.0	143.7	71.2	57.6	70.9	69.6	82.0	88.6
SD	9.29	6.99	11.65	9.95	8.38	4.64	7.17	8.15
99.9% conf. level	4.26	4.78	2.33	2.31	5.73	1.53	2.61	3.74

Species	*leptophylla* (contin.)	*leptophylla* (islands)	*blumeana*	*limbata*	*lindenbergiana*	*persica*	*pappii*
No. spores measured	80	60	60	40	50	70	10
Min.	66.7	50.0	68.2	81.8	66.7	78.8	97.0
Max.	97.0	92.4	103.0	109.1	100.0	131.7	107.6
Mean	81.2	70.9	89.8	97.1	84.9	99.6	101.7
SD	6.77	10.69	9.20	8.63	7.98	13.20	2.65
99.9% conf. level	2.54	4.90	4.22	4.98	4.01	5.46	4.01

Species	*mussuriensis* ssp. *m.*	*mussuriensis* ssp. *crassa*	*multiflora*	*vulcanica*	*gracilis*
No. spores measured	180	30	70	1	90
Min.	70.4	83.3	75.0	-	53.0
Max.	121.7	107.6	117.4	-	74.2
Mean	95.7	90.0	95.8	109.1	65.1
SD	11.98	5.38	11.73	-	4.87
99.9% conf. level	3.01	3.68	4.85	-	1.77

Appendix V: Eurasian *Asterella* specimens studied

Specimens cited are additional to types cited in Chapter 4. Herbarium abbreviations follow the *Index Herbariorum* (Holmgren *et al.*, 1990).

1. Asterella saccata (Wahlenb.) A. Evans

MACEDONIA: Treska-Schlucht SW von Skopje, 1971, *Poelt* 10116 (JE).

ITALY: Meran, Tirol, *Schimper* (BM); Meran, Tyrol, *Sauter* in herb. Jack (G); Appenines, herb. Stephani (G-15267); Piemont, herb. Belanger (G-15268); Piedmont, ex herb. Menzies (E); Piedmont, 1806, *Bridel* s.n. (H-SOL).

HUNGARY: Z-Ungarn, in terra humosa ad saxa calcarea montis Remetehegy supra Mariaremete, 400m, 1934, *Szepesfalvi* s.n. (JE ex ABSH); Budapest, in humosis inter saxa dolomit, montis Kiskecskehegy, 350m, iii 1934, *Boros*, Plant. Hungar. Exsicc. s.n. (E); Comit. Fejér, in monte Szolokó, prope Csákvár, in terra humosa umbrosa i. saxa dolomitica, ca. 200m, iii 1937, *Boros* in Verdoorn, Hep. Sel. Crit. Ser. II, 502 (BM, BR, G, GOET, H, U); Comit. Pest., in humosis inter saxa dolomit. montis Vas-hegy prope Csövár, 300–350m, iii 1951, *Boros*, Plant. Hungar. Exsicc. s.n. (E).

AUSTRIA: Niederösterreich, bei Rothenhof, Stein a/ Donau, c 300m, iv 1893, *Baumgartner* s.n. (G); In locis apricis prope Krems, solo schistoso, 200–300msm, *Baumgartner* in Krypt. Exsicc. 282 (BM, G-17008, GL); Niederösterreich, sonnige Hänge in der Weinbergregion (Schiefer) oberhalb Stein an der Donau, 250–300m, (a) iv 1900, (b) xi 1900, *Baumgartner*, in Schiffner Hepat. Europ. Exsicc. 1201a (E, G, U), 1201b (E, G, WU, U); Niederösterreich, sonnige Abhänge bei Stein an der Donau, 300m, iv 1900, *J. Baumgartner* s.n. (BR).

SWITZERLAND: Helvet?, *Lammers* 35 (E); Kanton Valais, 1829, *Thomas*, (BR); [Valais]: Branson, 1840, *Muret* s.n. (G).; Valais: sur la terre au Mont Valeyres [=Follatères] pres Sion, iii 1864, *J. Rome* s.n. (G); Wallis [= Valais] Branson, iv 1868, *M. Bernet* s.n. (G); Valais: coteaux des Folateires, vis a vis de Martigny, iii 1873, *T. Brown* s.n. (G); Valais: Folateres, iii 1873, *H. Bernet* s.n. (G); Valais: Folateres, v 1885, *H. Bernet* 195 (G); Valais, dans les vignes de Martigny, iv 1885, *Bernet* s.n. (E); Valais: Vignes près de Martigny, 475m, iv 1887, *H. Bernet* s.n. (G); Valais: Côteaux arides à la Bâtia et à Branson près de Martigny, iv 1887, *H. Bernet* s.n. (E, G, U); Valais: Branson pres Martigny, 450m, iv 1887, *H. Bernet* s.n. (DBN); Valais: Branson, 1896, herb. Müller Arg. (G); Valais: collines arides, Montorge près Sion, 650m, ii 1897, *G. Colomb-Duplan* (G-15275); Valais: Montorge pres Sion, iv 1897, *G. Colomb-Duplan* s.n.(DBN); Valais: adret de la Valleé du Rhône, entre Masembroz et Saillon, bas du coteau sur affleurement de quartzites, 650m, orientation SE, [feuillle de Morcles 1:25000 No. 305: 579.1/ 113.1], iii 1980, *A. Dutoit* s.n. (G-195168); Valais: Mazembroz (Fully), sous un rocher siliceux dans la steppe, 550m, iii 1980, *R. Delarze* s.n. (G-148276); Valais: Sion, Mont d'Orge, steppes a' *Ephedra*, 740m, v 1981, *Geissler* 7737 (G); Valais: Fully, Follatères, 600m, iii 1983, *Geissler* 8949 (G);

Valais: Sion, Mont d'Orge, steppe, 800m, iii 1983, *Geissler* 8959 (G); Valais, Fully, Les Taches, sol nu, 5725/1083, 560m, iii 1990, *Geissler* 15221 (G); Valais, Fully, Follatères, Solnu, 5720/10798, Transect I,2, 465m, v 1990, *Geissler* 15249 (G); Valais: Fully, Follatères, 5921/ 10805, terre nue dans pelouse à annuelles, 490m, iii 1991, *Geissler* 15649 (G, E); Valais: Fully, terre nue, 57225/ 1983(3), Transect II,17, 630m, iii 1991, *Geissler* 15658 (G); Valais: Sion, Mont d'Orge, 5921/ 1198, versant S, steppe, 700m, ii 1992, *Geissler* 16333 (G); Valais, Follatères, near Branson N of Martigny, 490m, sunny rocky slopes with vineyards, on thin soil on rocks, 11 viii 1994, *Long, Geissler & Maier* 25667 (E); Valais, Niedergampel, 700m, 18 iv 1999, *F. Rüegsegger* s.n. (E).

CZECH REPUBLIC: W-Mähren, Tisnov, in solo calcareo, 1942, *Smarda* in Crypt. Cechoslov. Exsicc. No. 33 (JE ex PRC).

SLOVAKIA: Slovakia merid., opp. Nitra, ad saxa calcarea montis Zobor (Pleska), ca. 350msm, 11 iv 1934, *Suza* in Bryophyta Cechoslovaca Exsiccata Ser. V, 201 (BR, G-243982, H, U).

GERMANY: [Sachsen-Anhalt, Harz] Agro Halensis, ex herb. Sprengel in herb. Jack (G-16990); [Sachsen-Anhalt, Harz] In montis gypsaceis prope Steigerthal, Mai, *Hampe* s.n. (BM); [Sachsen-Anhalt, Harz] Prope Nordhausen, 1897, *Vocke* s.n., ex herb. Stephani (BM, G); [Sachsen-Anhalt, Harz] Bezirk Erfurt, Südl. Vorland des Harzes, Nordhausen, flachgründiger Rasen ca. 750m südöstl. Steigerthal am Südfuss des Breiten-Bergen, v 1975, *Günther* s.n. (E ex JE).

RUSSIA: Amur, Poddale, v 1855, *Maximowicz* s.n. (H-SOL); Sibiria, Jenisei, Nikulina, 60° 20' N lat., in monte calcares Stolba, vii 1876, *H.W. Arnell* s.n. (S); Rossia, Permska gavernem, Kunzur, pa Kalk, 18 vi 1876, *H.W. Arnell* s.n. (LD).

CHINA, XINJIANG: c 20km N of Qinghe on road to Qinghe Forestry Station and Mongolian border, S Altai Mts., 46°45'N, 90°20'E, 4700 ft., soil on N side of road, *Caragana/ Artemisia* scrub on rocky hills, 28 vii 1993, *A.T. Whittemore et al.* 4610 (MO).

2. Asterella grollei D.G.Long

NEPAL: C Nepal, Nuwakot District, Thare Danda ridge 2km S of Thare Pati, 27° 59'N, 85° 29'E, 3680m, *Juniperus/ Rhododendron campanulatum* forest, on soil ledges under calcareous schist outcrop, 1 v 1992, *Long* 22238 (E).

CHINA, QINGHAI: Maqin County, valley north of Jungun Naichong, 34°33'48"N, 100°33'28"E, 3570m, damp rocky side gully in dry valley; on shady rock face, 10 vii 1997, *Long* 26943 (E); ibid., on damp soil on N-facing rocks, 10 vii 1997, *Long* 26950 (E); Jungun Naichong, between Dawu and Huang He, 34°38'53"N, 100°36'37"E, 3545m, valley with *Picea* and *Juniperus* woodland; on shady N-facing eroded mineral soil bank, 10 vii 1997, *Long* 26953 (E); ibid., 34°38'50"N, 100°36'41"E, 3585m, valley with *Picea* and *Juniperus* woodland; on S-facing soil on

limestone bank under *Juniperus*, 10 vii 1997, *Long* 26964-a (E); S of Radja on slopes of Huang He valley, 34°39'29"N, 100°37'34"E, 3730m, steep ravine in *Picea* forest; on calcareous rock ledges, 12 vii 1997, *Long* 26968 (E); Huzhu County, Jiading Xiang, near Langshidang Village, Langshidanggou Valley, 36°55'43"N, 101°22'17"E, 2710m, *Betula* woodland on valley slope; soil on calcareous rock outcrop, 23 vii 1997, *Long* 27203 (E); near Nanzhangzhagon Village, upper Zhalonggou Valley, 36°46'17"N, 102°32'44"E, 2735m, *Betula/ Juniperus* woodland on limestone; on shady NW-facing banks, 24 vii 1997, *Long* 27215 (E); Jiading Xiang, Gangzigou Valley, 36°45'05"N, 102°37'49"E, 2820m, *Juniperus/ Betula* woodland; on bank of stream on limestone, 25 vii 1997, *Long* 27259 (E); Jiading Xiang, upper Gangzigou Valley, 36°45'24"N, 102°37'02"E, 2990m, limestone gully with *Betula* and *Juniperus*; on shady E-facing bank, 25 vii 1997, *Long* 27285 (E).

3. Asterella wallichiana (Lehm. & Lindenb.) Grolle

PAKISTAN: Rawalpindi District, Bharatium, 6.5km from Panjar towards Kashmir, 520m, pine forests on steep rocky slope with *P. roxburghii* dominant. On rocks, 18 Oct. 1976, *R.B. Faden, A.J. Faden & E. Nasir* 76/192 (F); Mt Toli Pir (E of Rawalkot), Punch, Azad Kashmir, 2400m, on soil, trail-bank, 9 ix 1991, *N. Nishimura* 9420 (CBM).

INDIA, KERALA: Cote Malabar, *Belanger* 5 (S).
INDIA, TAMIL NADU: In terra nuda montium Nilagiricorum, *Perrottet*, herb. Lehmann ex herb. Montagne (S).
INDIA, MAHARASHTRA: Prope vicum Khandalla in montibus Bhor Ghat, ad terram humidam secus rivulum, ± 600m, 19 x 1893, *V. Schiffner* Iter Ind. 1893/94 No. 16 (FI, FH, WU, G-10532).
INDIA, KARNATAKA: Hassan District, Suklespur [= Sakleshpur], 5 ix 1903, *Inayat Khan* in Bryotheca E. Levier 4520 (BR, FI), 4519 (FI, G-10437), 4571 (FI); Hassan District, Bargmai, 6 ix 1903, *Inayat Khan* in Bryotheca E. Levier 4514 (FI, G-10435), 4516 (G-10436); ibid. 5 ix 1913, *Inayat Khan* in Bryotheca E. Levier 4513 (FI, G-10475); Balee Kannoor [= Bale-Honnur 13°22'N, 75°27'E] , 9 ix 1903, *Inayat Khan* in Bryotheca E. Levier 4517 (FI); Aldoor, 9 ix 1903, *Inayat Khan* in Bryotheca E. Levier 4518 (G-10439); Solebale, 10 ix 1903, *Inayat Khan* in Bryotheca E. Levier 4522 (G-10500); Koppa, 11 ix 1903, *Inayat Khan* in Bryotheca E. Levier 4510 (FI), 4509 (FI, G-10432, G-10433).
INDIA, NW: without locality, *Royle* s.n. (LIV); NW Himalaya, *Falconer*, KD 1092-a (H-SOL).
INDIA, HIMACHAL PRADESH: Simla [1840], *Griffith*, KD 1093 (BM, BR, FH, H-SOL, NY, S, G-10530); Simla District, Mt. Jako, 9800ft., 11 viii 1904, *W. Gollan* in Bryotheca E. Levier 4619 (BM).on rocks; Simla, E. Panjab, 7008ft., on ground, 26 iii 1906, *E. Long* 86.90 in Bryotheca E. Levier 5690 (BM, FI).
INDIA, UTTAR PRADESH: Mussoorie, 6-7000 ft., 26 ii 1892, *W. Gollan* in Bryotheca E. Levier 308 (G-10508); Throughout Tunnily Pass, Deyrah Dhoon, *W. Griffith* 212 (BM), 265 (BM, NY). Dehra Dun, 2300ft., viii 1894, *J.S. Gamble* 24973 (FH, G-10506); Mussoorie, Arnigadh Bot. Gardens, 5500ft., 13 xii 1895, *W. Gollan* in Bryotheca E. Levier 3890 (FI, G-10452), 215 (FI, G-10507), 1294 (BM, LD); Dehra-Dun, Arnigadh, prope Mussoorie, 6-7000 ft., xii 1895, *W. Gollan*

in Bryotheca E. Levier 1297 (G-10487), 1294 (G-10491); Mussoorie, Arnigadh Bot. Gardens, 5500 ft., vi 1896, *W. Gollan* in Bryotheca E. Levier 3892 (G-10464); Mussoorie, Arnigadh Gov. Botan. Gardens, on banks, 5500 ft., 10 ix 1900, *W. Gollan* in Bryotheca E. Levier 3871 (BR, G-10486); Mussoorie, Arnigadh Estate, on banks at Khetwala, 5550 ft., 13 ix 1900, *W. Gollan* in Bryotheca E. Levier 3878 (G-10467), 3880 (G-10466); On road to Mussoorie, Arnigadh Estate, on open rocks, 5550 ft., 14 ix 1900, *W. Gollan* in Bryotheca E. Levier 3897 (G-10468); Mussoorie, Respana Valley, 1735m, on rocks on Bala Hissar Estate, 5 x 1900, *W. Gollan* in Bryotheca E. Levier 3873 (BR, FI); Mussoorie, on road leading to Khetwala, a little above Arnigadh Garden, 5550ft.,12 x 1900, *W. Gollan* in Bryotheca E. Levier 3879 (BM); Dehra Dun, Mohand Pass, Siwalik Range, 2500ft., on stone walls, 27 x 1900, *W. Gollan* in Bryotheca E. Levier 3218 (BM, G-10440), 3217 (G-10438); Mussoorie to Rajpore road near Barlowganj, on earthy bank, 5900 ft., 7 xi 1900, *W. Gollan* in Bryotheca E. Levier 3886 (G-10465); Mussoorie, Arnigadh Govt. Botanic Gardens, 5500ft., on earthy banks, 14 xi 1900, *W. Gollan* in Bryotheca E. Levier 3885 (FI, JE); Mussoorie, hill above Arnigadh Bot. Gardens, on rocks, 6000 ft., 24 xii 1900, *Amar Singh* in Bryotheca E. Levier 3887 (G-10451); Mussoorie, 1700–1800m, iii 1907, *J. Capra* in Bryotheca E. Levier 6495 (G-10526), 6496 (FI, G-10528), 6497 (FI, G-10529), 6498 (FI), 6499 (FI); Mussoorie, Sahasardhara, 1000m, ad rupes, *R.S. Chopra* in Verdoorn, Hep. Sel. Crit. Ser. 1, No. 2 (BM, BR, F, FH, G-10431, H, JE, L, LD, MANCH, NY, S, U, W); Mussoorie, on soil, ix 1930, *R.S. Chopra* s.n. (FH); Mussoorie, on exposed rocks, ix 1930, *R.S. Chopra* s.n. (E, GL, FH); Mussoorie, 6–7000ft., on dry exposed rocks, ix 1930, *R.S. Chopra* 263 (JE, W), 272 (S, W), 274 (JE, S); Mussoorie, Landour, 6500 ft., viii 1935, *R.R. Stewart* 15012 (NY); Mussoorie, near Landour, 6-7000 ft., *R.R. Stewart* s.n. (NY); Lucknow, ix 1952, S.K. Pande s.n. (S); Mussoorie, near Charleville, 2000m, on vertical face of rock at roadside, 13 ix 1964, *R.A. Maas Geesteranus* 14505-a (L, MO); Naini Tal, Corbett Tiger Reserve, valley of Ramganga River, 380m, on termitery in broad-leaved forest, ii 1995, *T. Arts* s.n. (E).

INDIA, WEST BENGAL: Kurseong District, Siliguri–Darjeeling road above Sukna, 26°48'N, 88°21'E, 440m, degraded subtropical forest, on bank by road, 3 vii 1992, *Long* 22343 (E); Darjeeling, Chowrasta Square, 27°02'N, 88°16'E, 2235m, on large roadside wall, 4 vii 1992, *Long* 22350 (E); ibid. 9 viii 1992, *Long* 23047 (E); Mungpoo Quinine Factory, 26°58'N, 88°23'E, 1190m, on shady wall, 3 viii 1992, *Long* 23030 (E).

INDIA, SIKKIM: West District, tributary of Rathong Chhu, Tingdong near Gerathang, SE of Yoksam, 27°21'N, 88°14'E, 1510m, shady mixed broad-leaved forest, on shady wall by stream, 7 vii 1992, *Long* 22411 (E); West District, Norbugang near Yoksam, 27°22'N, 88°13'E, 1830m, on old wall of chorten, 28 vii 1992, *Long* 22939 (E); East District, Gangtok, 27°20'N, 88°37'E, 1830m, on roadside wall in town, 30 vii 1992, *Long* 22962 (E); East District, near Bitu, N of Gangtok, 27°21'N, 88°37'E, 1745m, degraded hillside, on wall by roadside, 31 vii 1992, *Long* 22980 (E); North District, N bank of Rate Chhu, N of Gangtok, 27°23'N, 88°37'E, 1675m, steep river valley, on stonework of culvert, 31 vii 1992, *Long* 22996 (E); East District, Namnam area, SE ouskirts of Gangtok, 27°19'01"N, 88°36'57"E, 1720m, degraded *Schima* forest; on wall of culvert by road, 6 vii 1996, *Long* 26298 (E); North District, 2km east of Phodong, NW of Gangtok, 27°24'N, 88°35'E, 1740m, degraded evergreen broad-leaved forest; on wall by road, 11 vii 1996, *Long* 26352 (E); North District, south bank of Myang Chhu bridge, 4km S of Naga, S

side of Tista valley, 27°31'N, 88°36'E, 1610m, evergreen broad-leaved forest; on wet rocks by road, 11 vii 1996, *Long* 26353 (E); North District, Bop, between Chungthang and Maltin, 27°33'08"N, 88°40'05"E, 1960m, steep valley with patches of evergreen broad-leaved forest; on wet rocks by waterfall, 12 vii 1996, *Long* 26369 (E).

INDIA, ASSAM: Mishmee, *W. Griffith* 19, KD 1090 (BM); Mishmee, *W. Griffith* s.n. (BM, H-SOL); Mishmee Mts., *W. Griffith* 16 (BM); Assam Tea Department, *Kurz* 1227 (NY); Assam, leg. *A.D.* 1227, herb. Goebel (G-10503).

NEPAL: Hänge gegen Pele, an feuchten Felsen, subtropische Stufe, 1962, *J. Poelt* s.n. (JE); Kalingchok, on boulder by road on sunny slope, 1970, *Kanai et al.* NICH-327945 (JE).

NEPAL, WEST: Lumbini Zone, Gulmi District, below conflux of Andhi Khola and Kali Gandaki, near suspension bridge, 27°55'N, 83°26'E, 510m, on limestone rocks, S-facing slope, in woodland on steep slope, 4 x 1991, *K.A. Lye* 17513 (E); Walin, 720m, on soil, 9 xi 1988, *M. Higuchi* 18518 (TNS).

NEPAL, CENTRAL: Gebiet von Kathmandu, zwischen Dolagath und Huxe, 1962, *J. Poelt* H112 (JE); Sundarijal, 1400m, 21 ix 1988, *M. Higuchi* 16802-b (TNS); Kathmandu Valley, Godawari, Botanical Garden, 1520m, on stone wall, 27 ix 1988, *M. Higuchi* 16903 (TNS); Kathmandu Valley, Godaveri, near Royal Botanic Garden, 1560m, on wall of shrine, 9 x 1989, *Long* 17603 (E); Kathmandu District, footpath above Sundarijal, 27°44'N, 85°25'E, 1420m, on wall by path, 4 v 1992, *Long* 22279 (E); Makawanpur District, Siwalik Range, 15km S of Hetauda, 27°19'N, 85°00'E, 490m, steep rocky valley with scrub, on shady rock face by road, 29 x 1991, *Long* 21636 (E); Makawanpur District, 2km N of Hetauda, 27°27'N, 85°03'E, 550m, steep scrubby slope, on rock face, 29 x 1991, *Long* 21641 (E); Kathmandu District, Swayambunath Temples, 1400m, on brickwork of monument, 4 x 1999, *Long* 28924 (E); Kathmandu District, Pashupatinath Temples, 1300m, on old shady wall, 6 x 1999, *Long* 28936 (E).

NEPAL, EAST: Dschiddarré, westlich über dem Charnawati, 1968, *J. Poelt* s.n. (JE); Near Nesum above Dobhan, Tamur Valley, 27°20'N, 87°37'E, 1320m, cultivated slopes, earth bank under trees, 31 viii 1989, *Long* 16529 (E); Taplejung District, foot of Ghunsa Khola near confluence with Tamur River, 27°32'N, 87°49'E, 1710m, steep wooded river bank, on shady rock face, 5 ix 1989, *Long* 16617 (E); Sankhuwasabha District, E side of Arun Valley, Khandbari, 27°22'N, 87°13'E, 1100m, on damp shady wall in town, 18 ix 1991, *Long* 20302 (E); Sankhuwasabha District, E side of Arun Valley, ridge S of Bhotebas, 27°26'N, 87°11'E, 1430m, open cultivated slopes, 18 ix 1991, *Long* 20330 (E); Sankhuwasabha District, Hatiya, Upper Arun Valley, 27°44'N, 87°20'E, 1620m, on mani wall in village, 13 x 1991, *Long* 21197 (E); Sankhuwasabha District, Arun River gorge S of Hatiya, 27°43'N, 87°22'E, 1290m, deep shady gorge, on wet rock face, 14 x 1991, *Long* 21216 (E); Sankhuwasabha District, E side of Arun Valley, above Chokkrang Bridge near Syiksilla, 27°38'N, 87°22'E, 1430m, dry degraded and cultivated slopes, on rocky bank under shrubs, 15 x 1991, *Long* 21241 (E); Sankhuwasabha District, Karmanam, E side of Arun Valley near foot of Pawa Khola, 27°36'N, 87°22'E, 1345m, open cultivated hillside , on large boulder, 16 x 1991, *Long* 21255 (E).

BHUTAN: Bhotan [1838], *W. Griffith* 17, KD 1091 (BM, NY); Bhotan, *Griffith* KD 1085 (NY), 1093 (BM), 1094 (BM, NY); Linje [Mongar District], *Griffith* 181 (BM); Linge, wet rocks, *Griffith* 101 (NY); Bhootan cliffs, *Griffith* 17 (BM); Bhotan, *Griffith* s.n. (G-10536); Tongsa District, Longte Chu 2km above Chendebi, 27°27'N, 90°20'E, 2500m, riverside scrub, on limestone boulder, 22 v 1979, *Long* 8108 (E, JE); Bumthang District, Bumthang Chu, 2km N of Byakar Dzong, 27°34'N, 90°43'E, 2700m, open *Pinus wallichiana* forest, on soil amongst boulders by river, 2700m, 8 vii 1979, *Long* 8709 (E, JE, NY, U); Thimphu District, E bank of Thimphu Chu near Lanjupakha Bridge, 2330m, roadside on river bank,on retaining wall, 8 ix 1999, *Long* 28580 (E); Punakha District, Mo Chu valley between Rimchu and Tashithang, 27°42'38"N, 89°46'14"E, 1575m, Warm broad-leaved forest on river bank, on silty rocks by river under trees, 25 ix 1999, *Long* 28768 (E).

BANGLADESH: Chittagong District, Sitakunda, Chandranath Hill below temple, 150m, steep wooded hillside, on brickwork of wall, 11 x 1998, *Long* 28179 (E).

MYANMAR (BURMA): Martaban, *R. Scott* 2690 (BM); Maymyo, Thowndong Railway Station 2200ft., on bank of stream, xii 1903, *Ram Sarup* in Bryotheca E. Levier 4548 (S).

THAILAND: Payap, limestone massive Doi (Mt.) Chiengdao,19°25'N, 98°55'E, 1000m, deciduous forest on NNE slope, on rocks, 4 xii 1965, *A. Touw* 8904-a (L, JE); Chiangmai, Mt. Doi Tung, 1200m, on stone walls in the precinct of the temple (Wat Doi Tung), 1967, *N. Kitagawa* T-12476 (JE), T-12477 (JE); Doi Chiengdao, on rocks, vi 1968, *Beusekom* B71 (L); Prov. Chiangmai, Chiangmai District, Doi Sutep, Phu Ping Palace, 1400m, hill evergreen forest zone, on rock, 14 x 1979, *N. Kitagawa* 24263 (E, KYO).

CHINA, TIBET (XIZANG): Laide, near Ridong, 2600m, on ground, 8 x 1982, *D.C. Chang* 7724, HKAS H9436 (KUN).

CHINA, SICHUAN: Chiang-pei, Pei-Chi, ad saxa sicca, ix 1941, *P.C. Chen* s.n. (JE); Mt Emei, 2300m, 1942, *P.C. Chen* 5494 (JE).

CHINA, YUNNAN: Supra Ngulukö ad urbem Lidjiang (Likiang), 3100–3400m, rupestribus, calceo, 10 vi 1915, *H. Handel-Mazzetti* 6697-b (W, WU); in demissis subtropicis fluminis Djinscha-djiang (Yangtse), ad orientem urbis Yungbei, in faucibus supra vicum Hsindschwang, 1400m, ad terram abruptam, calceo, 31 x 1916, *H. Handel-Mazzetti* 13012 (JE, W, WU); Yangbi County, along Qinqqiaohe stream, 1.2km N of junction of Xierhe Rivers, 25°36'N, 100°02'E, badly disturbed areas, vertical surface of rocks along stream, 14 vi 1984, *P.L. Redfearn Jr., S. He & Y.-G. Su* 137 (E, SMS); Bei Han Chang, between Dali and Lijiang, 2360m, on shady rock face by road, 24 ix 1990, *Long* 18494 (E); Lijiang District, below Wen Bi Shan SW of Lijiang, 2540m, slopes with young *Pinus yunnanensis* forest, common on clay banks by tracks and on silty boulder by stream, 3 x 1990, *Long* 18759 (E), 18761 (E); Yulong Shan, foot of Gang Ho Ba valley, 3120m, edge of flat open valley, on bank under shrubs, 4 x 1990, *Long* 18819 (E); Yulong Shan, Baishui Valley N of Lijiang, 2850m, calcareous soil bank of road cutting, 5 x 1990, *Long* 18859 (E); between Baishui and Heishui, N of Lijiang, 2900m, open slopes with *Quercus* and

Pinus yunnanensis, on crumbling calcareous road cutting, 6 x 1990, *Long* 18882 (E); Yulong Shan, valley above Baishui, N of Lijiang, 3015m, damp valley with *Pinus/Quercus*, on shady limestone rock face, 7 x 1990, *Long* 18905 (E); near Naou Jan, between Dali and Lijiang, 2140m, open degraded hillside, on calcareous soil bank of gully, 14 x 1990, *Long* 19123 (E); Lijiang Prefecture, Long Pang, Yangtze Valley, 27°06'26"n, 100°03'47"E, 1984m, in village, on damp clay bank by well, v 1993, *Long* 23589 (E); Diqing Prefecture, Wong Shui River above gorge, 28°24'26"N, 99°46'09"E, 3060m, cultivated river valley, on shady rock face under trees, v 1993, *Long* 23778 (E); Diqing Prefecture, Wong Shui River above gorge, 28°24'00"N, 99°45'50"E, 3050m, cultivated river valley, on dry vertical bank, v 1993, *Long* 23785 (E); Diqing Prefecture, Geza, below village, 28°12"N, 99°43'E, 2930m, wet tufa outcrop, in crevices in tufa, v 1993, *Long* 23898 (E); Diqing Prefecture, between Zhongdian and Geza, 28°10'N, 99°43'E, 2915m, roadside rocks, 3 x 1994, *McBeath* s.n. (E); Diqing Prefecture, San-ba, 27°30'N, 100°02'E, 2960m, damp shaded earth, 12 x 1994, *McBeath* s.n. (E); Diqing Prefecture, Haba Shan, 27°22'N, 100°08'E, 2960m, moist banks in semi-shade, 13 x 1994, *McBeath* s.n. (E).
CHINA, GUIZHOU: Gau-chouen, *Cavalerie* 8036 (JE); Ngan-shun, 1900–1920, *Cavalerie* 8036 (JE).
CHINA, BEIJING: Peking municipality, Yenching County, Petaling, 100m N of the Great Wall, on soil, iv 1972, *G. Een* 1 (JE, S).
CHINA, TAIWAN: Nord-Formosa, beim Dorf Sintiam, xii 1887, *O. Warburg* s.n. (FH-13865 'type'); Nord-Formosa, beim Dorfe Sintiam, xii 1887, *O. Warburg* 1468 (FH-14861); Taito-cho, Taikanko (E coast), xii 1899, *Miyake* 154 (JE); Mt Kushaku, distr. Taipeh, vi 1903, *Faurie* 52 (BM, JE, FH, FI, PC); Wulai, S of Taipei, Tung Hou Chi, iii 1965, *Iwatsuki* 247718 (JE); Tailyuko Gorge, along trail across river from Chan-an-chia, limestone area, on cliff, iii 1965, *Iwatsuki* 248369 (JE); Tailuko Gorge, betweem Tienhsing and Li-sue, limestone area, on soil, iii 1965, *Iwatsuki* 247623 (JE); Ha-lien Co., Shyu-lin village, Tien-hsiang, above Tien-hsiang Temple, c 400m, secondary subtropical rainforest on slope, 25 x 1970, *T. Koponen* 18405 (H); Miaoli Hsien, Tafu Hsiang, Tunghsien Tsun at foot of Manabang Shan, c 800m, on soil covering boulder along a stream, 20 xi 1977, *S. Lin* in Bry. Taiwan Exsicc. Ser.2, 53 (F, H, L, UBC).

PHILIPPINES: Philippinen, *Cuming* 2195 (BM, G); Philippinen, herb. *Hugo Dohl* (JE); Luzon, Laguna Prov., Botoan, Majayjay Town, on soil, partially shaded, moist, in field, 6 i 1979, *A.R. Alvarez Jr.* O-79041 (JE); Luzon, Asin, vicinity of Baguio, 1300m, limestone rocks by road, shaded loamy soil, xi 1993, *B.O.Van Zanten* 93.11.3444b (E).

JAPAN, RYUKYU ISLANDS: Amami-Oshima Island, iv 1970, *K. Saito* s.n. ex TNS 19131 (JE). Okinawa Island, Kunigami-son, Hiji River valley below Hiji Falls, 25 & 30m, river valley with evergreen broad-leaved forest, on soil bank under shrubs by river, abnd on shady vertical rocks by river, 8 ix 1993, *Long & Yamaguchi* 24811 (E), 24821 (E); Okinawa Island, Nago-shi, Sukuda, Todoroki Falls, c 50m, 24 x 1993, *T. Yamaguchi* 11279 male, 11280 female (E); Okinawa Island, Nago-shi, Sukuda, Todoroki Falls, 30m, 2 i 1994, *T. Yamaguchi* 11385, 11386 (E).
JAPAN, RYUKYU ISLANDS, IRIOMOTE: Iriomote, 100m, on moist rocks along stream, 19 vii 1971, *D. Shimizu* s.n. (JE); Shirahama, c 10m, on moist rock along small stream, in dense

forest, 11 I 1973, *H. Inoue* in Bry. Sel. Exsicc. 201 (E, F, G, H, JE, L, LD, MO, S, TENN, U, UBC); Along R. Nakama, c 70m, on boulder in river bed, 21 iii 1973, *K. Saito* s.n. (H, UBC); Mariudono, 50m, on rocks, 24 i 1975, *M. Mizutani & I. Yoshimura* in Hep. Jap. Exs. Ser. 22, 1051 (BM, L, S, UBC, TENN, F, G-210959); Sonai, 10m, on rocks, 23 i 1975, *M. Mizutani & I. Yoshimura* in Hep. Jap. Exs. Ser. 22, 1052 (H, L, S, UBC, TENN, BM, F, G-210960); Iriomote, 9 iii 1982, *Nagamasu* s.n. (KYO); Nakama River about 4km west of Ohtomi, 5m alt., on wet silt-covered boulders by river, 23 xii 1985, *R. Suda & T. Furuki*, in Bryoph. Asia Fasc. 2, 43 (G-382011, H, UBC); Urauchi River, Kanpirei Falls, 80m, river valley with evergreen broad-leaved forest, on boulders and rocks along river rapids, 11 ix 1993, *Long & Yamaguchi* 24903 (E); Urauchi River 3km above Kanpirei Falls, 100m, Open river bank in forest, on large boulders, 11 ix 1993, *Long & Yamaguchi* 24920 (E); Tributary of Urauchi River 3km above Kanpirei Falls, 105m, valley with evergreen broad-leaved forest, abundant on boulders by stream, 12 ix 1993, *Long & Yamaguchi* 24927 (E); Urauchi River 6.5km above Kanpirei Falls, 160m, shady evergreen forest, on boulder in small side-stream, 13 ix 1993, *Long & Yamaguchi* 24968 (E); Tributary of Nakama River 2.5km NW of Otomi, 5m, stream in evergreen broad-leaved forest, on boulder, 13 ix 1993, *Long & Yamaguchi* 24992 (E); Urauchi River, Kanpirei Falls, 60m alt., on mesic boulder in open site, 31 xii 1993, *T. Yamaguchi* 11377 (E); 11378 (E); 11381 (E); 11382 (E); 11383 (E); 11384 (E).

4. Asterella africana (Mont.) A. Evans

FRANCE, CORSICA: Bastia, Nonza S., 150m, v 1971, *Jovet-Ast & Bischler* 711032 (JE).

SPAIN: Salamanca, Mieza, 'La Barca', 350m, pared de granito por donde resbala el agua, ii 1995, *Rupidera Giraldo* s.n. (SALA, E).

SPAIN, CANARY ISLANDS: Ins. Canariensis, *Bourgeau* (H-SOL); Ins. Canarie, *de la Perrardiere* 17 (G); Iles Canaries, *Ant. Couverand* 1830 (G); Ins. Canarias, in humidis, *Trumpff* s.n. (BM)

SPAIN, CANARY ISLANDS, GRAN CANARIA: San Mateo, vi 1897, *Cook* in Schiffner Hep. Europ. Exsicc. 1196 (E, G); San Mateo, 900m, iv 1901, *Bornmüller* in Pl. exsicc. Canarienses 1962 (G), 1969 (BR); Ca 5km SW of Arucas, Barranco de Jimenez, UTM 445-3105, 600–700m, moist barranco with planted trees, 16 iii 1989, *Dirkse* s.n. (herb. Dirkse); Upper part of barranco from Cuevas de Corcho to Valsendero, UTM 440-3100, 1200–1300m, dry to moist barranco with big boulders and grassy ledges, 16 iii 1989, *Dirkse* s,n. (herb. Dirkse); Near the Cuevas de Corcho, 1.5km SSW of Lanzarote, UTM 440-3095, 1300m, shaded rocks and ledges, 16 iii 1989, *Dirkse* s.n. (herb. Dirkse); Between Cuevas de Corcho and Barranco del Andén, UTM 440-3095, 1400m, NE-facing rocks along road, 17 iii 1989, *Dirkse* s.n. (herb. Dirkse); Between Pico de las Nieves and Roque Nublo, S of artificial lake, UTM 440-3090, 1600–1700m, rocky outcrops and small periodic streams, 21 iii 1989, *Dirkse* s.n. (herb. Dirkse); Barranco del Agua, 12km W of Telde, UTM 445-3095, 1000–1100m, stony slopes and moist ledges, 25 iii 1989, *Dirkse* s.n. (herb. Dirkse); Barranco de Guyadeque, W of Ingenio near Montana de los Tierros,

UTM 445-3085, 1000–1100m, dry stony slopes and boulders, 26 iii 1989, *Dirkse* s.n. (herb. Dirkse); Barranco del Anden, NE of the Moriscos mountain, UTM 440-3095, 1400–1500m, moist slopes, 30 iii 1989, *Dirkse* s.n. (herb. Dirkse); E of San Isidro, UTM 445-3100, 900–950m, N-facing slopes with *Cytisus proliferus* and some *Castanea sativa* trees, 1 iv 1989, *Dirkse* s.n. (herb. Dirkse); 2km west of San Mateo, 1000m, damp rocks on roadside, locally abundant, 10 v 1994, *D.A.H. & S.J. Rae* 14 (E).

SPAIN, CANARY ISLANDS, TENERIFE: Tegueste el Viejo, in udosis sylvaticus, iii 1855, *Bourgeau* Pl. Canarienses (ex itinere secundo) 1598 (BM, G); Guimar, Barranco Anavigo, 600–700m, vii 1901, *Bornmüller* in Pl. exsicc. Canarienses 1933 (G); Aguamansa, Orotava Valley, 1000m, on shaded wall with *Reboulia*, *Anacolia webbii* etc., iii 1977, *Long* 5696 (E); SW of Guimar, La Ladera, UTM CS-5530, 800m, deep ravine with dry river bed, 30 iii 1985, *Dirkse* 4080 (herb. Dirkse); SW of La Esperanza, SW slopes of the Montaña Grande, UTM CS-6045, 1100–1200m, pine forest on steep slopes, 17 iii 1987, *Dirkse* 5588 (herb. Dirkse); Barranco del Agua, 3–5 km W of Guimar, UTM 355-3130, 900–1200m, deep ravine with dry laurel forest of *Picconia*, *Visnea*, *Jasminum*, *Arbutus* and *Maytenus*, 27 iii 1991, *Dirkse* 6678 (herb. Dirkse); Anaga, el Pijaral, UTM 380-3155, 800m, NW, barranco door *Laurus*-bos, 30 iii 1984, *Dirkse* 4190 (herb. Dirkse), 4188 (herb. Dirkse); Anaga Mts, NW, slopes of El Pijaral, UTM CS-8055, 750m, very steep and wet slopes of barranco through evergreen forest of Lauraceae, 25/26 iii 1985, *Dirkse* 3969 (herb. Dirkse), 3333 (herb. Dirkse); Anaga Mts., Vueltas de Taganana, UTM CS-8055, 700–800m, earth-covered rocks and moist gravel banks, exp. NE, 2 iv 1986, *Dirkse* 5594 (herb. Dirkse); Anaga Mts., N slope of the Taborno, near the road to Carboneras, UTM CS-5575, 900–1000m, Erica forest, 8 iii 1987, *Dirkse* 5589 (herb. Dirkse); Anaga Mts., N slope of the Roque de los Pasos, Vueltas de Taganana, UTM CS-5580, 700–800m, deep wooded ravines, 8 iii 1987, *Dirkse* 5590 (herb. Dirkse); Valle de la Orotava, los Organos, S of Aguamansa, UTM CS-5035, 1100m, deep barranco through *Pinus canariensis* forest, 28 iii 1985, *Dirkse* 3856 (herb. Dirkse); Valle de la Orotava, near Camino de Chasna, UTM CS-5035, 800m, steep NE slope with remnant of evergreen Lauraceae forest, 29 iii 1985, *Dirkse* 3792, 4150 (herb. Dirkse); Valle de la Orotava, SW of Realejos, UTM CS-4035, 650m, small barranco in steep N-facing slope, 29 iii 1985, *Dirkse* 4142 (herb. Dirkse); Valle de la Orotava, E of Aguamansa, near Los Organos, UTM CS-5035, 1050m, dry waterfall, 5 iv 1985, *Dirkse* 3765 (herb. Dirkse); Valle de la Orotava, E of Aguamansa, barranco near the Piscifactoria, UTM CS-5035, 1000m, dry river bed, 5 iv 1985, *Dirkse* 3729 (herb. Dirkse); Valle de la Orotava, along the road to the Cañadas, near the 'Marguerita' (rock-flower), UTM CS-4530, 1700–1800m, dry barranco through upper *Pinus canariensis* forest, 5 iv 1985, *Dirkse* 3756 (herb. Dirkse); Valle de la Orotava, pine forest W of the road to the Cañadas, UTM CS-5035, 1350–1400m, boulders and banks, exp. N, 23 iii 1986, *Dirkse* 5595 (herb. Dirkse); Valle de la Orotava, Aguamansa, La Caldera, UTM CS-3550, 1200–1300m, road banks, stony barranco, 12 iii 1987, *Dirkse* 5591 (herb. Dirkse); Valle de la Orotava, Ladera de Tigaiga, SW of Los Realejos, UTM CS-3540, 500–1100m, dry *Erica- Myrica* woodland with small springs, 14 iii 1987, *Dirkse* 5592 (herb. Dirkse); Monte de las Mercédes, c 2km W van de Taborno, NW, 800m, steile Barranco door *Laurus*-bos, 30 iii 1984, *Dirkse* 4189, 4191, 4192 (herb. Dirkse); Monte de las Mercédes, near the Llano de los Viejos, UTM CS-7055, 750m, Barranco through evergreen forest of Lauraceae,

23 iii 1985, *Dirkse* 3507, 3510, 3521, 3561 (herb. Dirkse); Monte de las Mercédes, steep NW-facing slope of the Taborno, UTM CS-7555, 900–950m, barranco through evergreen forest of Lauraceae, 24 iii 1985, *Dirkse* 3435 (herb. Dirkse).

SPAIN, CANARY ISLANDS, LA PALMA: Without locality, in humidis, *Bourgeau* Plant. Canar. 121 (BM, BR, G, OXF); Cumbre Nueva, 1100m, v 1902, *Bornmüller* in Pl. Exsicc. Canar. 3003 (GL); Los Tiles, in faucibus, 400m, iii 1906, *Pitard* Pl. Can. 760 (G); Barranco del Agua, SW of Los Sauces, UTM 225-3185, 400–500m, deep dark ravine with boulders, 6 iii 1990, *Dirkse* s.n. (herb. Dirkse); Barranco de la Galga, UTM 225-3180, 350–500m, wooded ravine, exp. NE, remnants of laurel forest, road banks, 7 iii 1990, *Dirkse* s.n. (herb. Dirkse); Cumbre Nueva, along road from Santa Cruz to Los Llanos de Aridane, UTM 225-3170, 760m, E slopes with small ravines through *Erica* woodland with some *Laurus*, 9 iii 1990, *Dirkse* s.n. (herb. Dirkse); Fuente de los Mimbreros, SW of Barlovento, UTM 220-3190, 750m, steep N-facing rocks with laurel forest, wet rocks, 11 iii 1990, *Dirkse* s.n. (herb. Dirkse); Barranco Gallegos, SW of Barlovento, UTM 220-3185, 760–840m, deep ravine with laurel forest, *Laurus*, *Ocotea*, *Persea* & *Appolonias*, 11 iii 1990, *Dirkse* s.n. (herb. Dirkse); Cumbre Nueva, between the Reventón and the Ovejas, UTM 220-3175, 1400m, small rocky outcrop in pie forest with some *Myrica* & *Cistus*, 15 iii 1990, *Dirkse* s.n. (herb. Dirkse); Barranco de Juan Diaz, S of Franceses, UTM 220-3190, 800m, *Erica arborea* shrubland, dense, cultivated, with some *Myrica faya*, 16 iii 1990, *Dirkse* s.n. (herb. Dirkse); Barranco Carmona, c 2km W of Roque Faro, UTM 215-3185, 1050–1100m, dry ravine, N-facing, in open pine forest with some *Erica arborea*, *Myrica* & *Laurus*, 18 iii 1990, *Dirkse* s.n. (herb. Dirkse); Barranco de Izcagua, c 4km E of Puntagarda, UTM 210-3185, 1250m, dry basaltic slopes in open pine forest, burnt some years ago, 20 iii 1990, *Dirkse* s.n. (herb. Dirkse); Barranco de la Galga, near Cubo de la Galga, UTM 225-3180, 600m, laurel forest on steep slope of deep barranco, 16 i 1992, *Dirkse* s.n. (herb. Dirkse); Barranco de Taburiente, NE slopes of the Bejenado, UTM 215-3175, 1100–1250m, dry pine forest with small barrancos, 22 i 1992, *Dirkse* s.n. (herb. Dirkse).

SPAIN, CANARY ISLANDS, GOMERA: Between el Cedro and the Garajonay, 1200m, boulders and earth-covered rocks in a dry barranco through laurel forest, exp. east, 26 iii 1986, *Dirkse* 5593 (herb. Dirkse); Between el Rejo and the Fuente Agando, near the Ermita de Nostra Señora de Gouadeloupe, 800m, boulders and banks along a small stream through laurel forest, exp. steep NE, 26 iii 1986, *Dirkse* 5507 (herb. Dirkse); Valle de Hermigua SW of the tunnel, near Espigon de Ibosa, UTM BS-8010, 750–950m, steep northern slope with laurel forest, *Erica arborea* and *Myrica faya*, partly eroded, 12 iii 1988, *Dirkse* s.n. (herb. Dirkse); Chorros de Epina, near Epina, UTM BS-7015, steep NW slope of Montaña de la Zarza, *Erica- Myrica* forest, 14 iii 1988, *Dirkse* s.n. (herb. Dirkse); La Laguna Grande, UTM BS-7510, 1100–1200m, steep N slopes with *Myrica-Ilex* forest, moist barrancos, 15 iii 1988, *Dirkse* s.n. (herb. Dirkse); Between Vallehermosa and las Rosas, Barranco de los Zarzales, UTM BS-7515, 250–400m, steep N-facing slopes with shrubs, 20 iii 1988, *Dirkse* s.n. (herb. Dirkse); Barranco del Vallehermosa, SE of Banda de las Rosas, UTM BS-7515, 500–700m, 20 iii 1988, *Dirkse* s.n. (herb. Dirkse); Barranco del Cedro, between the Campamento and the Ermita, UTM BS-8010, 900–1000m, 22 iii 1988, *Dirkse* s.n. (herb. Dirkse).

SPAIN, CANARY ISLANDS, HIERRO: Fuento del Lomo, inside filling well on N wall near water retaining ledges, viii 1964, *T.J. Bines* 81 (E); El Golfo, Los Palos Blancos, S of los Llanitos, UTM 195-3070, 950–1000m, *Erica-Myrica* forest on steep N-facing slope, dominance of *Urtica morifolia*, 14 iii 1991, *G.M. Dirkse* s.n. (herb. Dirkse); El Chijo, W parts of the Petraje, c 3km W of Valverde, UTM 205-3075, 800–950m, dry *Erica-Myrica* shrubland with small ravine, 17 iii 1991, *G.M. Dirkse* 6676 (herb. Dirkse); Hoya de Fileba, UTM 205-3070, 1330m, steep N-facing slopes with *Erica - Myrica* forest, 19 iii 1991, *Dirkse* s.n. (herb. Dirkse).

PORTUGAL, MADEIRA: without locality, *Mandon* 21 (G); ibid., *Fritze* 1021 (G); Without locality, *Mandon* s.n. (BM); Without locality, *Heer* s.n. (BM); Without locality, vii 1852, *Milne* s.n. (BM). Camacha, iii 1880, *R. Fritze* s.n. (BM); Rabacal, Ribeira Grande, Levodo Bo. do Risco, 32° 45'N, 17° 07'W, 1070m, moist basaltic levada wall in *Laurus azorica / Erica arborea* forest, iii 1992, *Perry* 8402 (NMW); ibid., 1070m, dripping basalt cliff behind levada in *Laurus azorica / Erica arborea* forest, iii 1992, *Perry* 8416 (NMW); Achada do Texeira, 32° 45'N, 16° 55'W, 1600m, on shaded roadside cutting between Santana and Pico co Ruiva, iii 1992, *Perry* 8431 (NMW); Levado do Curral, near Chamorra, c 44km NW of Funchal, vertical rock face with running water above levada, 300m, v 1993, *Clement* & *Fraile* 2264 (E); 1km N of Poiso Pass on road to Ribeiro Frio, 1230m, shady conifer plantation, on damp soil-covered rocks by road, 20 i 1994, *Long* 25073a (E); Between Poiso Pass and Ribeiro Frio, 2km above Ribeiro Frio, 1080m, steep open rocky slopes with *Erica* scrub, on wet rocks by road, 21 I 1994, *Long* 25094 (E); Ribeiro Frio, valley S of village, 900m, valley in laurel forest, on mossy rocks by levada, 21 I 1994, *Long* 25117 (E); Ribeiro Frio, by Levada do Furado, 875m, steep sloping laurel forest, on wet rocks by levada, 23 I 1994, *Long* 25185 (E).

5. Asterella cruciata (Steph.) Horik.

CHINA, SICHUAN: Hwa-lung-chiao prope Chungking [= Chongqing], in terra argillosa, skiophila, v 1940, *P.C. Chen* s.n. (JE-H3346); Chongqing City, Bai residence, roadside, on soil, 7 xi 1989, *Cao Tong & Li Qian 41340* (IFP).

CHINA, YUNNAN: in urbe Yünnanfu [= Kunmimg], muris, 1920m, 22 xii 1915, *H. Handel-Mazzetti* 8603 (E, JE, W, WU); Kunming City, Western Mountains, between Gaorao and Yangjia stockaded village, on damp soil, 21 xi 1964, *Xu Wen-Xuan 64101* (IFP).

KOREA: Korea, 13 xii 1978, *Hattori* (JE-H2444).

JAPAN, HONSHU: Japonia, No. 1562 as *Asterella minuta* Lindb. ex herb Lindberg (BM, S). Prov. Tokyo, 21 xi 1909, *H. Sakurai* s.n. (JE); Tokyo Prefecture, foot of Mt. Tenso, along R. Akigawa, alt. 600–700m, deciduous forest, on moist shaded limestone rock, 10 x 1979, *S.R. Gradstein & H. Inoue* 3094 (U); Saitama Pref., Chichibu, Kagemori, 25 xi 1950, *D. Shimizu* NICH 58650 (JE); Saitama County, Ochiai of Otaki, Chichibu Mts., 480m, on rock crevices and on soil in shade, 31 viii 1952, *D. Shimizu* in Hep. Jap. Exsicc. Ser. 6, 252 (H, G, BM, UBC, NY, S, W, LD, B, TENN, L, JE); Saitama Pref., Chichibu Mts., 600m, 2 xi 1952, *Hikuma* NICH-64335 (JE);

ibid., 570m, 2 xi 1952, *Hikuma* NICH 60725 (JE), 60726 (JE); Saitama Pref., Chichibu Mts., 570m, 1952, *Hikuma* NICH 60725 (JE); Saitama Pref., Chichibu Mts., Mt. Mitsumine, 900m alt., on wet rock in shady places with *Conocephalum conicum*, x 1959, *H. Inoue* s.n. (S); Saitama Prefecture, Chichibu Mts., Mt. Mitsumine ca. 800m, *H. Inoue* 8523 (TENN); Saitama Prefecture, Chichibu-gun, Hinata-ohya below Mt. Ryokami, 705m, terraced cultivated slope, on base of wall, 5 ix 1993, *Long & Furuki* 24716 (E); Saitama Prefecture, Chichibu-gun, Ohwa, Arakawa River below Mt. Mitsumine, 375m, forested rocky river bank, on damp mossy rocks by road, 6 ix 1993, *Long & Furuki* 24789 (E).

6. Asterella khasyana (Griff.) Pandé *et al.*

INDIA, TAMIL NADU: Madura [= Madurai] district, environs de Shembagarma, 2000m, 1910, *Velle* 261 (PC); Madura district, Palni Hills, Kodaikanal and surrounding region, 1650m, 1932, *Foreau* 138 (JE); Nilghiris, Ootacamund, 2600m, auf nassen Felsen, x 1909, *Meebold* 11777 (JE, G-10471).

INDIA, MADHYA PRADESH: Pachmari, on roadsides, moist soil, ix 1985, *Kaul* 1 (JE).

INDIA, NW HIMALAYA: without locality, herb. *Falconer* KD1092-b (H), KD1092 (FH, NY, G-10525).

INDIA, HIMACHAL PRADESH: Simla, *Griffith* KD 1097 (NY); Simla, *Stolitzka* 398 ex herb München (G-10444); Simla Distr., Mashobra, 8000ft., on ground, xi 1906, *E. Long* 32 in Bryotheca E. Levier 5696 (FI); ibid., *E. Long* 64 in Bryotheca E Levier 5695 (BM).

INDIA, UTTAR PRADESH: Kumaon, *Strachey* & *Winterbottom* s.n. (BM); Mussoorie, 4-6000 ft., ix 1895, *J.F. Duthie* 1949 (G-15380); Mussoorie, Arnigadh Botanic Gardens, 1800m, on earthy banks, 1900, *W. Gollan* in Levier 3885-b (JE); Mussoorie, water canal of Arnigadh Botanic Gardens, 5575 ft., on damp rocks, 5 x 1900, *W. Gollan* in Bryotheca E. Levier 3876 (BR); Mussoorie, hill above Arnigadh Garden, 6000ft., 12 ix 1900, *W. Gollan* in Bryotheca E. Levier 3868 (G-10445), 3901 (NY, G-10469); Mussoorie, Arnigadh Estate, dry bank at Khetwala, 5600 ft., 5 x 1900, *W. Gollan* in Bryotheca E. Levier 3874 (G-10446); Mussoorie, Respana Valley, on a shady bank close to Arnigadh Garden, 5500 ft., 6 x 1900, *W. Gollan* in Bryotheca E. Levier 3875 (G-10447); Arnigadh, on earthy banks in Govt. Bot. Gardens, 5500ft., 11 xi 1900, *W. Gollan* in Bryoth. E. Levier 3899 (FI, G-10454); Mussoorie, on earthy bank in Gov. Bot. Garden, Arnigadh, 5500 ft., 27 ix 1901, *W. Gollan* in Bryotheca E. Levier 3867 (G-10512); Mussoorie, on banks, Simla road below Charleville Hotel, 5500 ft., 29 xi 1903, W. Gollan in Bryotheca E. Levier 4522bis (G-10455); Mussoorie, 1700–1800m, iii 1907, *J. Capra* in Bryotheca E Levier 6495 (FI); Mussoorie, 6000-7000 ft., ix 1930, *R.S. Chopra* s.n. (FH); Mussoorie, Baslansar, 1800m, on earth bank, 22 ix 1964, *R.A. Maas Geesteranus* 14627 (H, JE, L, MO); Nainital, 6000 ft., ix 1932, *S.K. Pandé* s.n. (S).

INDIA, WEST BENGAL: Darjeeling, 2215m, 4 ix 1875, *Clarke* s.n. (BM); Darjeeling, 2300m, xi 1881, coll.? (BM, JE); 'Sikkim' [probably Darjeeling district] *S. Kurz* 2458 (BM); Peydong [= Pedong 27°09'N, 88°37'E] 'Sikkim', 4000ft., x 1896, *G. King's Collector* 89-96 (BM, BR, G-10441, 10442); 'Sikkim' prope Kurseong, 5500ft., 2 x 1898, *Decoly & Schaul* in Bryotheca E. Levier 210 (FI)l 'Sikkim' Himalaya, prope Kurseong, Sonada, 7000ft., 3 viii 1899, *Rev. P. Decoly & Schaul*,

in Bryotheca E. Levier 596 (BR, NY, TENN); Badamtam, 910m, 2 xi 1900, *A.C. Hartless* in Bryotheca E. Levier 3259 (BM, BR, FI, PC, G-15379); Himalayas near Darjeeling, 7400ft. Found in road-cutting between railway station and bazaar, Ghoom, about 4 miles from Darjeeling. On a vertical wall of rock clothed with plants such as *Selaginella*, *Marchantia*, mosses etc. Fairly moist situation. A species of dwarf habit, not common, 10 ix 1901, *E.J. Butler* No. 1 (as *F. parvipora*) in Bryotheca E. Levier 4636 (FI, G-10515); Near Darjeeling, 7410ft. Same locality as No. 1. Resembles No. 1, ix 1901, *E.J. Butler* No. 12 (as *F. parvipora*) in Bryotheca E. Levier 4637 (FI, G-10519); Himalayas near Darjeeling, about 6900ft., extends to 7500ft., Auckland Road between Darjeeling and Ghoom. Fairly common. Dwarf habit. Occurs usually buried in mosses clothing rocks often in a fairly dry situation. ix 1901, *E.J. Butler* No. 8 (as *F. parvipora*) in Bryotheca E. Levier 4638 (FI, G-10518); Jorpokhari near Darjeeling, 6000 ft., n.d., *S.K. Pandé* s.n. (S); Darjeeling, 2290m, viii 1967, *D.M. Henderson* D6 (E); Darjeeling Town below Observatory Hill, 27°02'N, 88°16'E, 2245m, on damp roadside wall, 4 vii 1992, *Long* 22357 (E); Between Ghoom and Tiger Hill, 26° 59'N, 88° 17'E, 2460m, slopes with *Cryptomeria* and degraded oak scrub, on wet rocks by stream, 5 vii 1992, *Long* 22362 (E); Senchal, near reservoirs, 26° 59'N, 88°16'E, 2340m, degraded *Quercus lamellosa* forest, on soil on wet soft schist rock outcrop, 5 vii 1992, *Long* 22387 (E); Tenzing Rock near Roy Villa, between Darjeeling and Lebong, 27° 03'34"N, 88° 16'37"E, 2060m, cleared evergreen *Castanopsis* forest, on shady rock by road, 6 vii 1992, *Long* 22391 (E); Barnesbeg Tea Estate below Takvar, 27°06'N, 88°16'E, 1130m, footpath in tea garden, on bank, 7 vii 1992, *Long* 22405 (E); 12km above Mungpoo, 26°59'N, 88°18'E, 1975m, degraded *Quercus/Castanopsis* forest, on damp shady roadside wall, 3 viii 1992, *Long* 23021 (E); Mungpoo Quinine Factory, 26°58'N, 88°23'E, 1190m, on brick wall around base of cultivated *Aesculus*, 3 viii 1992, *Long* 23031 (E); 5km W of Sukia Pokhari, W of Ghum, 26°59'N, 88°09'E, 2090m, open degraded hillside, on crumbling roadside bank, 5 viii 1992, *Long* 23041 (E).

INDIA, SIKKIM: [North District] Lachen, 6000ft., *J.D. Hooker* s.n. (H-SOL); West District, tributary of Rathong Chhu, Tingdong near Gerathang SW of Yoksam, 27°21'N, 88°14'E, 1510m, shady mixed broad-leaved forest, on damp rocky bank by road, 7 vii 1992, *Long* 22412 (E); West District, near Yoksam, 27°22'N, 88°13'E, 1860m, cultivated slope, on small chorten, 8 vii 1992, *Long* 22420 (E); East District, Gangtok, 27°20'N, 88°37'E, 1830m, on roadside wall in town, 30 vii 1992, *Long* 22961 (E); East District, near Bitu, N of Gangtok, 27°21'N, 88°37'E, 1745m, degraded hillside, on wet rocks by road, 31 vii 1992, *Long* 22970 (E); North District, N bank of Rate Chhu N of Gangtok, 27°33'N, 88°37'E, 1660m, steep river valley, on shady wet cliff, 31 vii 1992, *Long* 22995 (E); North District, below Phodong Gompa, NW of Gangtok, 27°24'N, 88°35'E, 1830m, *Schima* forest, on wet rock face, 31 vii 1992, *Long* 23004 (E); East District, Namnam area, SE ouskirts of Gangtok, 27°19'01"N, 88°36'57"E, 1720m, degraded *Schima* forest; on shady wet rocks by path, 6 vii 1996, Long 26297 (E); East District, between Gangtok and Karponang, 5km from Gangtok 27°21'N, 88°37'E, 2090m, on damp wall by road, 8 vii 1996, *Long* 26306 (E); East District, Deorali Sanctuary below Gangtok, 27°18'28"N, 88°36'35"E, 1600m, *Schima/ Castanopsis* woodland; on damp roadsiode rocks, 9 vii 1996, *Long* 26323 (E); East District, near Bitu, N of Gangtok, 27°22'42"N, 88°38'38"E, 1765m, steep valley with degraded warm broad-leaved forest; on shady rack face by road, 10 vii 1996, *Long* 26343

(E); North District: Bop, between Chungthang and Maltin, 27°33'08"N, 88°40'05"E, 1960m, steep valley with patches of evergreen broad-leaved forest; on wet rocks by waterfall, 12 vii 1996, *Long* 26380 (E).

INDIA, ASSAM: Khasia, regio subtrop., 1220m, *J.D. Hooker & T. Thomson* 1677 (BM, FH, G-10478, NY, PC); In ripis umbrosis Cherra, Khasyah Mts., [1835-6], *Griffith* 211 (BM); Khasia, Churra, *Griffith* 80, KD 1096 (NY).

NEPAL: Without locality: Nepal, herb. Arnott (GL).

NEPAL, CENTRAL: Langtang area, Trisuli Ganga Valley N, below Dhunche and on way to Barkhu, 1800m, 26 viii 1986, *J. Poelt* H3049 (JE), *J. Poelt* H3050 (JE); Kathmandu Valley, Godawari, Botanical Garden, 1520m alt., on soil, 4 ix 1988, *M. Higuchi* 15402 (TNS); Kathmandu Valley, Mt. Jamakok, 2000m alt., on stone wall, 11 ix 1988, *M. Higuchi* 15587 (TNS); Langtang National Park, Dhunche, 2000m, on stone wall, 13 ix 1988, *M. Higuchi* 15726 (TNS); Langtang National Park, Dhunche, 2000m, on cliff, 14 ix 1988, *M. Higuchi* 15855 (TNS); Kutumsang–Gul Bhanjyang, 2100–2500m, on soil, 20 ix 1988, *M. Higuchi* 16685 (TNS); Jiri, 2000m, on soil, 4 x 1988, *M. Higuchi* 17122 (TNS); Jiri–Shivalaya, 2000–2200m, on soil, 5 x 1988, *M. Higuchi* 17175 (TNS); Rasuwa District, slopes of Trisuli Khola below Dhunche, 28°07'N, 85°18'E, 1980m, terraced cultivated hillside, under boulder by path, 22 iv 1992, *Long* 22003 (E); Rasuwa District, hillside above Syabru, 28°07'N, 85°22'E, 2430m, on stonework of chorten by path, 28 iv 1992, *Long* 22141 (E); Nuwakot District, ridge N of Kutumsang, 27°57'N, 85°29'E, 2940m, degraded *Quercus semecarpifolia*/*Rhododendron arboreum* forest; on thin soil on rock face, 2 v 1992, *Long* 22253 (E); Sindhupalchok District, Chipling Village, 27°52'N, 85°28'E, 2300m, cultivated slopes, on rocky bank of terrace, 3 v 1992, *Long* 22267 (E); Sindhupalchok District, Pati Bhanjyang, 27°50'N, 85°28'E, 2140m, degraded area, on steep rocky bank, 3 v 1992, *Long* 22268 (E); Nuwakot District, Chisapani N of Sheopuri Lekh, 27°48'N, 85°27'E, 2200m, degraded hillside with scrub, on vertical rock wall by path, 3 v 1992, *Long* 22269 (E); Kathmandu District, above Sundarijal, 27°44'N, 85°25'E, 1940m, steep rocky hillside, on rocks by path, 4 v 1992, *Long* 22274 (E); Mahabharat Range, S of Kathmandu, Pharphing to Phakel, 27° 35'N, 85° 13'E, 1700m, damp shady bank, clay soil, under shrubs, 28 ii 1996, *M.F. Watson* 96-7b (E).

NEPAL, EAST: Près de Thazi, 1900m, 13 ix 1954, *A. Zimmermann* 1221 (G); Vorhimalaya, Jassá, feuchte Erdwand, 1962, *J. Poelt* H113 (H, JE); Vorhimalaya, westlich unterhalb Thodung, 2000–2500m, 1962, *J. Poelt* H150 (JE); Vorhimalaya, Dudh Kosi Tal, zwischen Pemgara and Kamptega, 1962, *J. Poelt* H213 (JE); Kulekham–Chisapani Gari, 1800m, 1970, *Kanai* NICH 327960 (JE); Between Hile and Chitre, 2050m, on soil, 1972, *Iwatsuki* 185 (JE); Between Papung and Bir Gaon, 1850m and 1750m, on bank and on soil, 1972, *Iwatsuki* 2100 [NICH 313074] (JE), *Iwatsuki* 2124 [NICH 313150] (JE); Between Bir Gaon and Dingla, 1300m, on soil, 1971, *Iwatsuki* 2175 [NICH 313132] (JE); Ilam, 1200m, on soil, 4 xi 1988, *M. Higuchi* 18290 (TNS); Junbesi, 2500m, on soil, 20 x 1988, *M. Higuchi* 18067-b (TNS); Tamur River between Tawa and Chirwa, 27°29'N, 87°45'E, 1300m, open scrubby hillside, on damp gravelly bank, 2 ix 1989, *Long* 16560 (E); Ghunsa Khola near Amjilassa, 27°34'N, 87°52'E, 2500m, open hillside, on damp rocks on soil, 5 ix 1989, *Long* 16635 (E); Ghunsa Khola between Amjilassa and

Kyapra, 27°37'N, 87°53'E, 2600m, *Quercus semecarpifolia*/ *Rhododendron* forest, on bank, 6 ix 1989, *Long* 16642 (E); Kabeli Khola bridge, Yamphudin, 27°27'N, 87°55'E, 1720m, open river valley, on crumbling rock face under trees, 24 ix 1989, *Long* 17207 (E); ibid., steep wooded bank, on wet cliff, 25 ix 1989, *Long* 17236 (E); Lower slopes of Dobala Danda above Yamphudin, 27°27'N, 87°56'E, 1920m, ravine in warm broad-leaved forest, on wet rocks by waterfall, 26 ix 1989, *Long* 17284 (E); Between Nesum and Buje Daurali, 27°20'N, 87°36'E, 2570m, burnt oak forest, on open bank, 4 x 1989, *Long* 17509 (E); Sankhuwasabha District, E side of Arun Valley between Khandbari and Bhotebas, 27°24'N, 87°12'E, 1120m, cultivated slopes, on wall, 18 ix 1991, *Long* 20308 (E); Sankhuwasabha District, E side of Arun Valley between Manebhanjyang and Bhotebas, 27°25'N, 87°12'E, 1145m, degraded *Castanopsis* forest, on steep damp bank under scrub, 18 ix 1991, *Long* 20312 (E); Sankhuwasabha District, E side of Arun Valley near Bhotebas, 27°26'N, 87°11'E, 1940m, degraded evergreen oak (*Castanopsis*) forest, on bank by path, 19 ix 1991, *Long* 20345 (E); Sankhuwasabha District, E side of Arun Valley between Kuwapani and Fururu, 27°28'N, 87°15'E, 1960m, degraded forest on ridge, on bank under *Lyonia* etc., 21 ix 1991, *Long* 20448 (E); Sankhuwasabha District, Arun Valley below Num, 27°34'N, 87°17'E, 920m, subtropical forest slopes, on damp shady rocks, 22 ix 1991, *Long* 20478 (E); Sankhuwasabha District, between Shidua and Tashigaon, 27° 36'N, 87° 16'E, open hillside, on terrace of paddy fields, 23 ix 1991, *Long* 20499 (E); Sankhuwasabha District, near Hatiya, upper Arun Valley, 27°44'N, 87°20'E, open hillside, on large boulder, 12 x 1991, *Long* 21176 (E); Sankhuwasabha District, E side of Arun Valley, above Chokkrang Bridge near Syiksilla, 27° 38'N, 87° 22'E, dry degraded and cultivated slopes, on soil on shady rocks, 15 x 1991, *Long* 21235; Sankhuwasabha District, S slopes of Pawa Khola, W of Panch Pokhari Khola, 27° 35'N, 87° 24'E, degraded hillside, on stone terrace wall, 17 x 1991, *Long* 21262 (E); Taplejung District, S end of Milke Danda ridge between Noondaki and Gupha Pokhari, 27° 18'N, 87° 29'E, 2830m, degraded *Rhododendron arboreum* forest, on steep rocky bank, 24 x 1991, *Long* 21540 (E); Taplejung District, ridge NE of Gupha Pokhari, 27° 17'N, 87° 31'E, 2845m, degraded *Rhododendron arboreum* forest, on rocky bank, 25 x 1991, *Long* 21542 (E); Terathum District, S slope of Tinjure Danda ridge between Chauki and Door Pani, 27° 10'N, 87° 26'E, 2820m, open cleared hillside, on shady rocky slope, 27 x 1991, *Long* 21630 (E); Terathum District, Basantapur, 27° 06'N, 87° 24'E, 2260m, degraded slopes, in eroded gully, 27 x 1991, *Long* 21633 (E).

BHUTAN: Gaylegphug district, Gaylegphug-Surey road 26km N of Gaylegphug, 26°58'N, 90°32'E, 1300m, soil in crevice of shady wall, 2 vi 1979, *Long* 8204 (E); Chukka district, 2km N of Takhti Chu, lower Raidak Valley, 26°56'N, 89°36'E, 2050m, wet warm broad-leaved forest, on rock face, 26 vii 1979, *Long* 8827 (E), 8828 (JE); Gaylegphug district, W bank of Chabley Khola, 55km post, 27°05'N, 90°35'E, 1700m, cool broad-leaved forest, on roadside rock face, 27 iii 1982, *Long* 10653 (E, JE); Thimphu District, Drugyel Dzong, Paro Chu, 27°30'11"N, 89°19'24"E, 2650m, rocky bank with shrubs, in soil crevices of small chorten, 18 ix 1999, *Long* 28698 (E); Punakha District, 2km above Lometsawa, 2270m, warm broad-leaved forest, on damp wall by stream, 25 ix 1999, *Long* 28766 (E).

CHINA, SICHUAN: in montis Lungdschu-schan prope urbem Huili, regione calide temperata, in fruticetis ad vic. Djifangkou, arenaceo, 2875m, 17 ix 1914, *H. Handel-Mazzetti* 5227-a (E, JE, WU).

CHINA, YUNNAN: Luchun County, Lao Bean, 1900m, 12 x 1973, *M. Zang* 459, HKAS H6843 (KUN, IFP); Rei Li, Nanjingli, 770m alt., on ground, 9 vii 1977, *X.J. Li* 126, HKAS H7359 (KUN, IFP); Changyüan County, bat cave, on soil, 30 ix 1980, *S.Y. Zeng* 80-1355, HKAS H7364 (KUN, IFP); Changyüan County, bat cave, on soil, 3 ix 1980, *S.Y. Zeng* 80-1376 (IFP); Kunming, Bamboo Temple, 1700m, on ground, 20 x 1981, *M. Zang* 81-46, HKAS H8134 (KUN, IFP); ibid. 1900m, on ground, 20 x 1981, *M. Zang* 81-76, HKAS H10174 (KUN); Dulong River, 1400m, on ground, 7 viii 1982, *D.C. Zhang* 1734, HKAS H5377 (KUN, IFP); Dulong River, Xian Ju Dang, 1600m, on rock, 23 viii 1982, *M. Zang* 3146 (KUN, IFP); Dulong River, 1650m, 24 viii 1982, *M. Zang* 3284, HKAS H8383 (KUN, IFP); Kunming Municipality, Qiongzhusi (Bamboo) Temple, 25°04'N, 102°37'E, 2100–2300m, broadleaf evergreen forest with *Pinus yunnanensis* and shrubs on ridge, clay soil in open, W-facing slope, 30 vii 1984, *P.L. Redfearn Jr., S. He & Y.-G. Su* 2177 (SMS); Xishuangbanna, Menghai Co., Nannuo Mtn., 1400–1500m, old tea grove and adjacent wooded N-facing slopes, some large trees 4–5ft. in diameter present, on shaded soil of NW-facing road bank, 30 xii 1986, *P.L. Redfearn Jr. et al.* 34251 (SMS, E).

THAILAND: Chieng Dao, path to 'Hill Station', c 760m, xii 1957, *Richards* 5464 (PC); Chiengmai, Doi Chiengdao, on trail up to Tea Factory, 700m, on side cut in earth, 7 xii 1957, *T. Smitinand* 4047 (L, JE); Prov. Chiengmai, Doi Sutep, evergreen forest, in earth, 1 xii 1959, *T. Smitinand* 6202 (L, JE); Payap, Doi (Mt.) Suthep, granitic massive W of Chiengmai, 18°50'N, 98°55'E, 1000–1100m, humid evergreen forest along streamlet, on wet rocks, 27 xi 1965, *A. Touw* 8448 (L); Payap, granitic massive Doi (Mt.) Inthanon, 18°35'N, 98°30'E, 1650m, on banks along path in open hill evergreen forest, 21 xii 1965, *A. Touw* 10273 (L); Payap, Doi (Mt.) Suthep, granitic massive W of Chiengmai, summit region of Doi Pui, 18°50'N, 98°55'E, 1650–1685m, open evergreen forest with *Pinus khasya*, on weathered bricks, 29 xi 1965, *A. Touw* 8785 (L); Payap, Doi (Mt.) Suthep, granitic massive W of Chiengmai, summit region of Doi Buak Ha, 18°50'N, 98°55'E, 1550m, evergreen forest, loamy bank at roadside, 2 i 1966, *A. Touw* 10347 (L); Lamphun, middle elevation of Mt. Doi Khun Tan, 1100m, on moist rock in evergreen forest, 1967, *Tagawa & Kitagawa* T12029 (JE); Prov. Chiangmai: Doi Sutep (Doi Pui), Chiangmai Distr., hill evergreen forest near the top of the mountain, 1500m, on soil, 14 x 1979, *N. Kitagawa* T-24232 (E, KYO); Prov. Chiang Mai, Distr. Muang, Doi Sutep, just below summit on the NE side along the dirt road to Doi Pui, 1575m, shaded soil embankment, primary evergreen forest, granite bedrock, 24 ix 1988, *J.F. Maxwell* B-63 (L).

INDONESIA, JAVA, WEST: Tjiburrum, 2193m, 1894, *V. Schiffner* 10864 (FH); Sur le Pangerango, ii 1895, *J. Massart* 1722 (FH, herb. Schiffner); Parois de rochers a Tjipanao sur le Gedeh, i 1895, *J. Massart* 1639 (FH, herb. Schiffner); Buitenzorg, 1924, *Goebel* s.n. (JE); Kantang Batak, 1927, *Burgeff* 8228 (JE); Kandang Badak, 4 v 1906, *D.H. Campbell* s.n. (NY, UBC); Kandang Badak, 2150m, terrestrial, 19 iii 1952, *R. van der Wijk* 506 (L); Gedeh, Tjibodas, leg. Sapilius, ex herb Fleischer (MANCH); Res. Priangan, G. Gede, Ajer Panas, 2150m, ad

rupes fontes calid. (50°C), viii 1930, *V. Schiffner* in Verdoorn, Hep. Sel. Crit. Ser 9, 403 (BM, BR, G, JE, PC, MANCH, H, L, NY, S, U, LD, TENN, F); Tjibodas, 1909, *Domin* s.n. (JE); Gedeh, Tjibodas, 1913, *M. Fleischer* s.n. (JE); Gedeh Tjibodas, i 1918, *Fleischer* 49 (B); Mt Gedeh, 1920, *W. Seifrig* 45 (NY); Gegerbintang Mt. ridge near Tjibodas, 1700m, primary mt. forest - mossy forest, on a steep sunny slope, 15 iii 1954, *W. Meijer* B5507 (BM, JE, PC), 5607 (NY); INDONESIA, JAVA, EAST: Res. Pasoeroean in mm. Tengger, inter Tosari et lac. mont. Ranoe Pani, 1900-2350m, vi 1930, *Fr. Verdoorn* 1800 (NY); Idjen bei Pindak, iv 1925, *D.O. Posthumus* 10436 (FH) .

INDONESIA, SUMATRA, CENTRAL: Mt Korinchi, ravine of Sungai Kering, 1600–1700m, 31 vii 1956, *W. Meijer* B8722 (JE, L); ibid. 2000m, vii 1956, *W. Meijer* B8894 (L).

PHILIPPINES: Luzon, Prov. Benguet, Baguio, 4500 ft., wet bank in shaded ravine, x/xi 1905, *E.D. Merrill 4994* (G-15185).

7. Asterella leptophylla (Mont.) Grolle

PAKISTAN: Mt. Toli Pir (E of Rawalkot), Punch, Azad Kashmir, 2400m, on soil, trail-bank, 9 ix 1991, *N. Nishimura* 9411 (CBM); ibid. *N. Nishimura 9429* (CBM).

INDIA, SOUTH: without locality, *Beddome* 443 (BM).
INDIA, TAMIL NADU: Nilgiri Mountains, *Schmidt* s.n. (BM); Ootacamund, *Schmidt* s.n, (NY); Madras, Nilgiris, Ooty, 2300m, viii 1885, *J.S. Gamble* 16656 (BM, JE); Nilgiris, Naduvatam, 6000ft., x 1884, *J.S. Gamble* 14904 (BM).
INDIA, HIMACHAL PRADESH: Simla, banks, Annandale, [xii 1840], *W.Griffith* 23 (BM); Simla district, Mt. Jako, near Bonnie Moon House, 7600 ft., on stone walls, 9 viii 1904, *W. Gollan* in Bryotheca E. Levier 5689 (FI, G-10450); Simla, Mt. Jako, 7800ft., on earthy banks, 16 viii 1904, *W. Gollan* in Bryotheca E. Levier 4706 (FI, G-10492); Simla Distr., Mount Jako, on earthy banks, 7700ft., 22 viii 1904, *W. Gollan* in Bryotheca E. Levier 5865 (FI); ibid. 5866 (FI), ibid. 4705 (FI, G-10490); Simla, Mount Jako, on earthy banks, 7700 ft., 23 viii 1904, *W. Gollan* in Bryotheca E. Levier 5685 (G-10477), 5686 (G); Simla Distr., Mount Jako, on earthy banks, 7900ft., 26 viii 1904, *W. Gollan* in Bryotheca E. Levier 5687 (BM, FI); ibid. 4704 (FI, G-10489); Simla District, E. Punjab, Mashobra, 8000 ft., on rocks, xi 1906, *E. Long* 49, in Bryotheca E. Levier 5693 (BM, FI, G-10472), 5692 (G-10473); Simla District, Mussoorie, moist shady rocks, ix 1957, *Chopra* s.n. (JE).
INDIA, UTTAR PRADESH: NW India, Deoban Range (Jaunsar–Bahar), 7–8000ft., x 1879, *J.F. Duthie* 50 in Bryotheca E. Levier (G-15389); ibid. *Duthie* in Bryotheca E. Levier 310 (G-15184); Jaunsar, Mundali, 8000ft., xi 1894, *J.S. Gamble* 25043 (BM, G-10443); Dehra Dun, Arnigadh prope Mussoorie, 6–7000ft., xii 1895, *W. Gollan* in Bryotheca E. Levier 1296 (FI, G-10484); Mussoorie, Arnigadh, on banks in Govt. Bot. Gardens, 5500ft., 10 ix 1900, *W. Gollan* in Bryotheca E. Levier 3872 (FI); Mussoorie, 1800–2100m, on moist rocks, ix 1930, *Chopra* s.n. (E, BM, GL, JE).

INDIA, SIKKIM: Sikkim temp., 1830m, *Hooker* 1679-b (BM); Sikkim, 12–13000 ft., *S. Kurz* 2222 (BM); Sikkim, *S. Kurz* 2052 (BM); Sikkim 7000ft., *S. Kurz* 2419 (BM); West District, Rathong Chhu Valley, between Prek Chhu and Bakhim, 27°25'N, 88°11'E, degraded *Quercus lamellosa* forest, on underside of boulder, 2710m, 8 vii 1992, *Long* 22459 (E); West District, Tsoka, E slope of Chhurong Chhu valley, 27°26'N, 88°11'E, cleared *Tsuga* forest, on bank of path under *Rhododendron arboreum*, 3050m, 9 vii 1992, *Long* 22469 (E); West District, Chhurong Chhu valley between Tsoka and Jamlinghang, 27°27'N, 88°09'E, 3475m, ravine in *Abies densa/ Rhododencron* forest, on soil on shady bank, 9 vii 1992, *Long* 22503 (E); West District, near bridge below Chaunrikhiang, 27°32'N, 88°08'E, 4215m, rocky river bank, on soil under rock overhang, 16 vii 1992, *Long* 22618 (E); West District, between Phedang and Tsoka, S of Dzongri, 27°26'N, 88°10'E, 3495m, *Abies/Rhododendron* forest, on shady soil-covered rocks in small gully, 26 vii 1992, *Long* 22907 (E); West District, below Tsoka, 27°25'N, 88°11'E, 2940m, *Tsuga/Lithocarpus* forest, on shady soil bank by path, 26 vii 1992, *Long* 22914 (E); North District, east bank of Tista above Rabom, N of Chungthang, 27°39'N, 88°36'E, 2370m, evergreen broad-leaved forest on steep slope; on rock face by road, 16 vii 1996, Long 26503 (E).

INDIA. ASSAM: Khasia Mts., *J.D. Hooker & T. Thomson* s.n. (NY).

NEPAL, CENTRAL: Langtang area, on way Khangjung to Sangsa (E of Khangjung), towards Pang Sang Lekh, 2500–2600m, pastures, rocks, open woods, 28 viii 1986, *J. Poelt* H3053 (JE); Langtang area, ± N-exposed slopes towards Langshisa Glacier, SE Langshisa Kharka, 4200–4300m, 17 ix 1986, *J. Poelt* H3051 (JE); Langtang area, S of Langtang Khola, S of Chamky, 3000–3200m, very humid mixed *Abies* forest on N-exposed slope, 5 ix 1986, *J. Poelt* H3052 (JE); Langtang National Park, Dhunche–Shin Gompa, 3000–3200m, on base of tree trunk, 14 ix 1988, *M. Higuchi* 15951 (TNS); Langtang National Park, Tharepati Pass–Kutumsang, 2900m, on soil, 19 ix 1988, *M. Higuchi* 16563 (TNS); Rasuwa District, N bank of Langtang Khola above Syabru, 28°09'N, 85°25'E, 2200m, dry rocky wooded river bank, on rocks, 23 iv 1992, *Long* 22042 (E); Rasuwa District, Langtang Village, 28°12'N, 85°31'E, 3460m, on turf amongst stones of house, 26 iv 1992, *Long* 22091 (E); Rasuwa District, N bank of Langtang Khola below Lama Hotel, 28°09'N, 85°25'E, 2200m, *Betula alnoides*/ bamboo woodland, on boulder by river, 27 iv 1992, *Long* 22116 (E); Nuwakot District, ridge N of Kutumsang, 27°57'N, 85°29'E, 2940m, degraded *Quercus semecarpifolia*/ *Rhododendron arboreum* forest, on thin soil on rock face, 2 v 1992, *Long* 22251 (E).

NEPAL, EAST: Below Thudam, 3350m, in forest, 22 vi 1972, *Iwatsuki* 1536 (JE); Between Nessum and Bhuje, 2750m, on bank, 1972, *Iwatsuki* 2289 (JE); Sete–Goem, 3100m, on soil, 8 x 1988, *M. Higuchi* 17479 (TNS); Junbesi–Charamka, 3570m, on soil, 11 x 1988, *M. Higuchi* 17712 (TNS); Tinjure Danda ridge between Door Pani and Chauki, 27°10'N, 87°26'E, 2960m, open hillside, mossy bank by path, 29 viii 1989, *Long* 16476-b (E); Forested ridge between Gupha Pokhari and Buje Daurali, 27°18'N, 87°33'E, 2910m, wet mixed forest, on steep bank by path, 30 viii 1989, *Long* 16494 (E); ibid., 2880m, wet mixed *Rhododendron* forest, on dripping mica-schist cliff, 30 viii 1989, *Long* 16504 (E); Ghunsa, by second large waterfall above village, 27°40'N, 87°57'E, ravine in *Abies*/*Rhododendron* forest, on shaded crumbling bank, 3450m, 14

ix 1989, *Long* 16893 (E); Betwen Nesum and Buje Daurali, 27°20'N, 87°36'E, burnt oak forest, on open bank, 2570m, 4 x 1989, *Long* 17510 (E); Sankhuwasabha District, forested ridge between Tashigaon and Kauma, 27°37'N, 87°14'E, 2745m, mixed mossy cool evergreen broad-leaved forest, on bank by path, 25 ix 1991, *Long* 20594 (E); Sankhuwasabha District, near Kauma, S of Shipton La, 27°39'N, 87°13'E, 3275m, mossy *Rhododendron* forest, on vertical bank, 25 ix 1991, *Long* 20625 (E); Sankhuwasabha District, Nehe Kharka, S side of Barun Khola, 27°45'N, 87°10'E, 3710m, steep hillside with degraded scrub, on soil under *Juniperus*, 30 ix 1991, *Long* 20822 (E); Sankhuwasabha District, N bank of Barun Khola above Pemathang Kharka, 27°45'N, 87°11'E, 3470m, margin of *Abies/Rhododendron* forest, on soil amongst roots at base of *Abies*, 8 x 1991, *Long* 21030 (E); Sankhuwasabha District, upper slopes of E bank of Saldim Khola, NW of Hatiya, 27°44'N, 87°18'E, 2760m, *Tsuga/Rhododendron* forest, on stump, 12 x 1991, *Long* 21167 (E); Taplejung District, Milke Danda ridge between Manebhanjang and Suke Pokhari, 27°26'N, 87°28'E, 3515m, cleared *Rhododendron* forest, on bank, 23 x 1991, *Long* 21502 (E).

BHUTAN: Deothang district, 8km N of Tschilingor, N of Deothang, 27°04'N, 91°25'E, 2400m, moist evergreen oak forest, on shady rock face, 26 vi 1979, *Long* 8566 (E, JE); Bumthang District, between Zhurig and Resang La, 27°27'N, 90°48'E, 2930m, *Tsuga/ Rhododendron* forest in small valley, on shady soil bank, 14 ix 1999, *Long* 28662 (E); Thimphu District, Drugyel Dzong, Paro Chu, 27°30'11"N, 89°19'24"E, 2650m, rocky bank with shrubs, on soil in rock crevices, 18 ix 1999, *Long* 28701 (E); Thimphu District, summit of Chelai La, 27°22'N, 89°20'E, 3780m, *Rhododendron* scrub, on shaded soil bank, 19 ix 1999, *Long* 28720 (E); Ha District, summit of Chelai La, 27°22'N, 89°20'E, 3780m, open rocky hillside, on soil bank by chorten, 19 ix 1999, *Long* 28727 (E); Thimphu District, slopes below Tangu Monastery, Thimphu Chu, 27°35'N, 89°38'E, 2820m, *Quercus semecarpifolia* forest; on shady soil bank, 20 ix 1999, *Long* 28740 (E); Thimphu District, valley above old Motithang Hotel, Thimphu, 27°28'59"N, 89°35'34"E, 3000m, *Pinus wallichiana* forest, on shady bank, 28 ix 1999, *Long* 28840(E); Thimphu District, valley above old Motithang Hotel, Thimphu, 27°29'31"N, 89°35'06"E, 3470m, *Picea* forest, on shady bank, 28 ix 1999, *Long* 28842(E); Thimphu District, above Pajoding monasteries, 27°29'30"N, 89°34'30"E, 3700m, Juniper/ Rhododendron scrub, on shady bank, 28 ix 1999, *Long* 28843(E).

CHINA, LIAONING: Kuan Dian County, Xiang Shui valley, below Hu Li Mountain, Bai Shi Li Zi Reserve, 124°52'E, 40°50'N, 900-1000m, deep crevice in rock face near stream, N-facing, 21 viii 1993, *A.T. Whittemore et al.* 4979 (MO).

CHINA, SICHUAN: montis Lungdschu-schan prope urbem Huili, ad. vic. Djifangkou, 2875m, 17 ix 1914, *H. Handel-Mazzetti* 5227-c (E, WU); in altiplanetei ad oppidum Yenyuen regione temperata, in fovea profunda prope vicum Kalapa, 27° 40', calceo, 2800m, 17 v 1914, *H. Handel-Mazzetti* 11122 (WU); Yen Yuan Co., 3200m, under *Quercus* forest, 10 viii 1983, *L.S. Wang* 83-949, HKAS-H8340 (KUN).

CHINA, YUNNAN: Kunming Municipality, vicinity of Daxiao, 43 km N of Kunming, 25°22'N, 102°45'E, 2200m, disturbed slopes with *Pinus armandii*, *Keteleeria* etc., shaded clay soil, E-

facing slope, 28 vii 1984, *P.L. Redfearn Jr., S. He & Y.-G. Su* 1977 (SMS); Songming Co., ca. 48.5km N of Kunming, 25°22'N, 102°45'E, 2100m, moist ravines and dry slopes wityh remnant broadleaf evergreen *Keteleeria-Pinus* forest, shaded clay soil along small stream bank, 28 vii 1984, *P.L. Redfearn Jr., S. He & Y.-G. Su* 2028 (SMS); Zhongdian (Chungtien) district, river valley in Bi Ta Hai Forest Reserve, 3370m, margin of *Pinus* forest and flat marshy valley floor, on wet rocks by small waterfall in tributary stream, 26 ix 1990, *Long* 18578 (E); Zhongdian (Chungtien) district, tributary valley 20km S of Zhongdian, 3260m, steep scrubby river valley, shady bank of path under scrub, 1 x 1990, *Long* 18722 (E); Bi Ye Go valley, N of Yangtze bridge at Lou Swang, 2895m, small valley with damp bamboo and scrub, on shady bank by stream, 2 x 1990, *Long* 18753 (E); between Baishui and Heishui, N of Lijiang, 2850m, open slopes with *Quercus* and *Pinus yunnanensis*, on shady acid soil bank under *Coriaria*, 6 x 1990, *Long* 18887 (E); Yulong Shan, slope below Ha Lan Gon Lake, Wen Hai Mountain, 3180m, steep slope with *Pinus yunnanensis*, on soil bank in gully, 9 x 1990, *Long* 18995 (E); Tsang (Cang) Shan, path from Shi Jo village to Huadianba, 2665m, hillside with *Pinus yunnanensis* and *P. armandii*, on shady rocks in gully, 16 x 1990, *Long* 19204 (E); Tsang (Cang) Shan, Huadianba, 2920m, on bank under shrubs in village, 17 x 1990, *Long* 19206 (E); Tsang (Cang) Shan, valley N of Huadianba, 2910m, degraded *Lithocarpus* forest, on shady bank of path near river, 17 x 1990, *Long* 19223 (E).

CHINA, TAIWAN: Ali Shan, x 1970, *Lai* 4010 (B); Chia-yi Co., Mt A-li, valley on S slope, c2300m, 13 x 1970, *T.Koponen* 16870 (H, JE); Chia-yi Co., Mt A-li, on NW slope, 1800–2000m, along railway and trails in planted *Cryptomeria japonica* wood on NW slope, on cliff, 14 x 1970, *T. Koponen* 17117 (H); Pingtung, Mt. Peitawu, ca 2000m alt., on moist soil in evergreen forest, 13 x 1993, *T. Yamaguchi* 11278 (E).

INDONESIA, JAVA: Goen. Soembing, crater at top, 3200m, 15 v 1927, *Docters van Leeuwen-Reijnvaan* 8847 (NY).

PHILIPPINES: Luzon, Prov. Benguet, Panai to Baguio, 6000 ft., on damp cliffs, x/xi 1905, *E.D. Merrill* 4935 (G-15183, NY) det. Grolle.

KOREA: Noimtchi, vi 1906, *Faurie* 50 (BM, FH, G-15373); Prov. Gyeongsangnam-do, Yeongju-gun, Heuibang Temple, 500–600m, on soil, 1976, *D.-M. Choi* 2 (JE).

JAPAN, HONSHU: Nagano Prefecture, Mt. Ontake, ca. 1250m, on shaded soil among rocks (chert), viii 1953, S. Hattori in Hep. Jap. Ser. 9, 402 (B, F, G, L, W, TENN); Nagano Prefecture, Miwa, 1120m, on rock, 12 viii 1953, *D. Shimizu* s.n. (JE); Nagano Prefecture, Mt. Yatsugatake, 2210m, on rock, 20 viii 1953, *D. Shimizu* s.n. (JE); Saitama Prefecture, Chichibu Mts., Mt Ryogami, 1000m, on rock, viii 1954, *D. Shimizu* s.n. (JE); Tochigi Prefecture, Nikko City, along the Ooyagawa (volcanic area), ca. 700m, 7–10 x 1977, *N. Kitagawa* 15902 (KYO), 15964 (KYO); Saitama Prefecture, Chichibu-gun, between Kiyotaki Hut and Ryokami Shrine, Mt. Ryokami, 1675m, *Quercus/ Rhododendron* forest on steep slope, in wet crevices of rock face, 5 ix 1993,

Long & *Furuki* 24769 (E); Saitama Prefecture, Chichibu-gun, near Hatcho Pass, Mt. Ryokami, 1275m, shady broad-leaved forest, on damp wall, 6 ix 1993, *Long* & *Furuki* 24796 (E).

RUSSIA: Primorski Kraj, Primorskaja, 9 ix 1953, *V.N. Vorosilov* 7158 (JE); Primorye Territory, Vladivostok, rocks along the sea coast, 31 viii 1962, *Bardunov* LV44 (JE); Primorye Terriotory, "Kedrovaya Pad" State Reserve, on rock, 12 x 1974, *S.K. Gambaryan* s.n. (MO); Primorye Territory, Reserve 'Kedrovaya Pad', oak forest, on exposed soil, 18 viii 1977, *S.K. Gambaryan* 43 (JE); Primorye Territory, Moryak Rybolov, rocks, in niches stones, 11 ix 1977, *L.V. Bardunov* 42 (JE); S of Primorye Territory, Vityaz Bay, coastal rocky exposures, humid shady sites with mud substrate, 13 x 1978, *L.V. Bardunov* 47 (JE); Primorye Territory, reserve 'Kedrovaya Pad', on rocky exposures, 19 viii 1982, *S.K. Gambaryan* 46 (JE); Primorye Territory, cliff Golubiny, in clefts, 21 viii 1982, *S.K. Gambaryan* 45 (JE).

8. Asterella blumeana (Nees) Kachroo

INDONESIA, JAVA, WEST: Buitenzorg, s. data (L); Mt. Gede [= Gunung Gedeh], above Air Panas, 2200m, Pantja wulu, under overhanging rocks along the Tjikundal, vii 1953, *Meijer* B4181 (JE, L, PC, S).
INDONESIA, JAVA, CENTRAL: Dieng-Plateau [= Djeng], 2000m, between stones of the Hindu temples, v 1954, *Meijer* B5691 (JE, L).
INDONESIA, SULAWESI (CELEBES): Porema, 1400m, x 1929, *G. Kjellberg* 6h (S); Porema, 1200m, x 1929, *Kjellberg* 1Ha (S); SW Celebes, Gunung Bonthain [= Gunung Lompobattang], c1900m, vi 1921, *Bünnemeyer* 12168 (L, B [ex Bogor], JE).
INDONESIA, SUNDA ISLANDS: Lombok, Rindjani-Vulkangebirge, N Seite, Putihtal, Barranco der Rindjani-Caldera, 2400–2650m, quellenreich, nebelfeucht, v 1909, *J. Elbert* 1143 (L, JE, G15228).

9. Asterella limbata D.G.Long & Grolle

INDONESIA, SUMATRA: Mt. Korinchi, ravine of Sungai Kering, 2000m, vii 1956, *W. Meijer* B8884 (JE, L); Mt. Korinchi, 2500–3000m, subalpine vegetation with *Vaccinium*, vii 1956, *W Meijer* B8925 (L), B8927 (JE, L), B8977 (Type, JE, L).
INDONESIA, JAVA: Java, *Prof. Stahl* 35 (G-15375; syntype of *Fimbriaria zollingeri* Steph.).

SABAH: Kota Belud district, Kinabalu Park, slopes of Gunong Kinabalu (30–40°SW) near Cascade Waterfall, lower montane forest, on sedimentary rocks, 1500–1700m, 4 ix 1986, *M. Menzel, J.-P. Frahm, W. Frey* & *H. Kürschner* 4214 (B).

10. Asterella lindenbergiana (Corda ex Nees) H.Arnell

SLOVENIA [formerly Yugoslavia]: Julische Alpen, an humusbedeckten Kalkfelsen am Hangart [Slovenian-Italian border], 2200–2300m, viii 1884, *J. Breidler* s.n. (G).

ITALY: Valsesia [Val de la Thuile], Piccolo S. Bernardo [= Petit Saint-Bernard], ad lacum Verney, 1900–2000m, *Vaccari* s.n. (JE, ex FI).

ROUMANIA: Bucegi Gebirge, supra Cabana Malaesti Sept., 1700–1900m, 1962, *Boros* s.n. (JE); Bucegi-Gebirge, subalpine Stufe in der Umgebung des Bucsoi und der Maest-Hütte, vii 1973, *Günther* s.n. (JE).

AUSTRIA: Salzburg, *Sauter* s.n. (BM); Salzburg, Unterberg, int. saxa, *Sauter* s.n., herb. Hampe (BM); In Schneekesseln um die Salzburger Spitze des Unterberges (5500') sehr selten, im August, leg. *Dr. Sauter*, in Gottsche & Rabenhorst Hep. Eur. 369 (BM, BR, G). [Tirol] Am Klein Röthestein [= Rettenstein S of Kitzbühel] auf nacktem Schneeboden unter Felsblöcken, 6000', *Sauter* s.n., herb, Schimper (BM); [Niederösterreich] In alpe Schneeberg, in fossis et valleculis nivosis regionis alpinae, solo calcareo humoso, ca. 1850m, fruct. m. Sept., *Baumgartner*, Krypt. Exsicc. 2473 (BM, G, H, U); [Kärnten] Heiligenblut, 1860, *Jack* s.n. (H-SOL); [Kärnten] Heiligenblutertauern, 'Vom Hohen Thor'[= Hochtor, summit of Grossglocknerhochalpenstrasse], viii 1860, *Jack* 264 (G); Niederösterreich, Schneeberg in Schneegruben von Ochsenboden, ca. 1850m, ix 1886, *Beck* s.n. in herb. Jack (G); Steiermark: Lopernstein bei Mitterndorf, Kalk, 1950m, vii 1886, *J. Breidler* s.n. (G); Tirol, Gschnitztal, am Mutterjoch, auf von Schneewasser durchtränkten, steinigen Boden, 2300m, (a) viii 1903, (b) ix 1905, *Schiffner & Handel-Mazzetti* in Schiffner, Hep. Europ. Exsicc. 1198a (E, G), 1198b (E, G); Salzburg: Heiligenbluther Tauern, Hochthor, auf Erde zwischen Geröll und Steinblöcken (Schiefer und Serpentin), ca. 2200m, ix 1905, *J. Baumgartner* in Schiffner. Hep. Eur. Exsicc. 1199 (G); Osttirol: Matrei, Steiner Alm, ob Sudetendeutsche Hütte, Felsnische, 2750m, viii 1988, *Geissler* 13644 (G).

SWITZERLAND: Schweiz, 1870, *Jack* (H-SOL); [Valais] alp. Gemmi, *Nees*, herb. Gottsche (H-SOL); [Schwyz] zwischen Geitenberg und Robuzlialp [Muotathal], *Hegetschweiler* s.n. ex herb. Jack (G); [Bern] Faulhorn, 6000 ft., 'aus dem Meissnerschen Herbar', ex herb Jack (G-15229); Kt. Graubünden [=Grisen] Splügen, 1839, *Muhlenbeck* s.n. (BM, G); [Valais] Gemmi, 1839, *Blanchee* s.n. (G); [Valais] Gemmi, viii 1842, *Mühlenbeck* s.n. (G); [Bern] Fisialp (Kanderthal) bei Thun, vii 1846, *J. Müller* s.n.(G); [Valais] La Gemmi, 1848, *Lesquereux* s.n. (G); Kt. Uri: auf Gampele, oberhalb Schattdorf, x 1870, *Gisler* s.n. in herb. Jack (G); Kt. Uri: Andermatt, ix 18?, *Gisler* s.n. (G); [Valais] Daubensee, viii 1881, *G. Davies* s.n. (BM, H-SOL); [Valais] au sommet de la Gemmi, 2329m, viii 1888, *H. Bernet* s.n. (DBN, G); [Bern] Bachalp, Faulhorn, Bern 2300m, 9 viii 1905 *P. Culmann* (BR); Kt. Bern, zwischen Bachsee und Faulhorn, auf Erde in Felsspalten unter Felsblöcken, 2300–2600m, viii 1906, *Culmann* in Schiffner Hep. Europ. Exsicc. 1200 (E, G); Kt. Vaud: Bex, Les Martinets, 2200m, ix 1918, *Meylan* s.n. (G-15230); [Graubünden= Grison] Parc National [Engadin], Val Tantermozza, 2600m, 1923, *C. Meylan* s.n. (G); [Graubünden= Grison] Parc National [Engadin], Val Nüglia, 2600m, vii 1926, *C. Meylan* s.n. (G); Kt. Vaud: Bex, Pont de Nant, la Chaux, 2000m, ix 1980, *Geissler* 7651 (G); Kt. Ticino: Quinto, V. Piora, A. Carorescio, dolina, 2200m, viii 1983, *Geissler* 9534 (G); Kt. Ticino: Quinto, Val Piora, Ganon, bordo di ruscello, 2200m, viii 1983, *Geissler* 9542 (G); Kt. Bern: Lenk, Iffigensee, Felsnische,

2080m, viii 1983, *Geissler* 9796 (G); Kt. Bern: Lenk, Iffighorn, Ca-Rohboden, 2350m, viii 1983, *Geissler* 9807 (G); Kt. Vaud: Bex, Vallon de Pont de Nant, sous le col des Perris Blancs, ébouli, 2450m, x 1983, *Geissler* 9992 (G); Kt. Ticino: Quinto, E Passo del Sole, 7027/ 1544, ruscello, 2240m, ix 1984, *Geissler* 10717 (G); Kt. Ticino: Quinto, Sotto P. Colombe, 7019/ 1545, valletta nivale, 2300m, viii 1985, *Geissler* 11408 (G); Kt. Valais: V. de Réchy, comm. de Nax, 6053/ 1495, base d'un rocher, 2370m, viii 1985, *Geissler* 11444 (G); Kt. St. Gallen: Alt St. Johann, Tierwiis, 7431/ 2347, Felsen, 2060m, viii 1986, *Geissler* 11840 (G); Kt. St. Gallen: Alt St. Johann, E Gluristal, 7412/ 2251, Schneeboden, 1860m, viii 1986, *Geissler* 11877 (G); Kt. St. Gallen: Allt St. Johann, E Gluristal, 7413/ 2248, Schneeboden, 2000m, viii 1986, *Geissler* 11886 (G); Kt. Valais: Leukerbad, Seestutz, N Daubensee, 6138/ 1414, Felsnische, 2200m, x 1986, *Geissler* 12359 (G);Kt. Valais, Gemmi Pass, near cable car station, 2280m, limestone plateau, in rock crevices by footpath, 10 viii 1994, *Long, Geissler & Maier* 25633 (E); Kt. Valais, near Lämmernsee, Gemmi Pass, 2300m, limestone valley slopes, crevices on low limestone ridge, 10 viii 1994, *Long, Geissler & Maier* 25639 (E); Valais, near Lämmernsee, Gemmi Pass, 2330m, limestone valley slopes, late snow hollow on low limestone ridge, 10 viii 1994, *Long, Geissler & Maier* 25647 (E); Kanton Uri, Chracken, Klausenpass, 46° 52'00"N, 08° 54' 00"E, Grid. 708191, 2000m, on thin turf among limestone outcrops in N-facing alpine grassland, 7 ix 1994, *N.G. Hodgetts* 3050 (herb. Hodgetts), 3014 (herb. Hodgetts).

SLOVAKIA: Galizien, Hohe Tatra, Umgebung der Felsgrotte 'Magóra' auf Humus über Kalk, 1400–1600m, x 1907, *Raciborski* in Schiffner Hep, Europ. Exsicc. 1197 (E, G).

POLAND: Tatry, na wapieniach pod Wielka Turnia w dol. Malej Laki, razem z *Bucegia*, *Sauteria*, *Peltolepis*, 2 viii 1910, M. Raciborski in Hep. Pol. Exsicc. 6 (BR).

GERMANY: [Bayern] Karwendel Gbge, 5600 ft., *Sendtner* s.n. in herb. Jack (G); Bayern, Berchtesgaden, am Schossmalhorn, c 1800m, viii 1920, *Difenb.* s.n. (GL); Bayern, Bayrische Alpen, Wettersteingebirge, Osterfelderkopf, near Alpspitze, S of Garmisch-Partenkirchen, TK 8532/1, c 2000msm, soily crevice, limestone outcrop, viii 1985, *A.R. Perry* 2316 (NMW).

FRANCE: Voisinage du Grand Lac au Lutaret, 189 viii 1922, *R. Douin* (BR); Haute-Savoie: St Gervais, Lac Jovet supérieur désseché, 2195m, ii 1978, *Geissler* 3588 (G); Isère, Les Deux Alpes, prés du refuge communal de la Fée, sous la Grande Sûre, 2230m, dans un pâturage très fréquenté par le troupeaux, sur humus noir abrité sous une pierre, vii 1981, *de Sloover* 35082 (BM, BR, H, U); Hautes-Alpes: Abriès, Lac Egourgéou, roche calcaire, 2390m, viii 1984, *Geissler* 10535 (G).

NORWAY: Finmark, 1851, *Hartman* (H-SOL); [? Norway] Vom Lynfuntkväl, viii 1868, herb. *Leithe* (BM); Tromsö, Flöifjeld, viii 1890, *Jörgensen* s.n. (GL); Bardo, Storfjeld, 10 viii 1891, *H. Arnell* (BR); Nordland, Salten, 67°05'N, 300m, viii 1893, *Hagen* s.n. (JE ex LD); Sör-Trondelag District, Dovrefjell National Park, valley on NW side of N Knutsho, on bank near snow-melt stream, 1480m, vii 1991, *Long* 19989 (E).

SWEDEN: Nordvestra Härjedalens fjällomade, Hilagsfjallet, viii 1912, *Smith* s.n. (GL); Torne Lappmark, Juckasjärvi sn. Sjangeli, Ruopsuok, in alveis nivalibus ca 950m, viii 1927, *H. Smith* in Cryptogamae Exsiccatae ed. Mus. Hist. Nat. Vind. 3693 (BM, BR, G, H, U); Härjedalen, Storsjö sn, N. Gröndörrsstöten, ca. 1000m, vii 1931, *R. Florin* s.n. (G); Lapponia lulensis, Kvikkjokk parish, Virihaure region, Tjargesvare, under rock, 600m, 13 vii 1946, *Martensson* s.n. (E); Lapponia lulensis: Jokkmokke parish, Vaisa region, 4km W of Lake Slappejaure, viii 1947, *O. Mårtensson* s.n. (G); Jämtland, Undersaker parish, Neadalen, Ekorr-Hammaren, SW-slope, 1100m, viii 1950, *Smith & Martensson* s.n. (E); Härjedalen: Storsjö parish, Isengälda NW slope of peak 1475, under and among slate boulders, 1350m, viii 1950, O. *Mårtensson* s.n. (G); Torne Lappmark: Torneträsk region, Kärketjårro, slope towards Låktatjåkka stopping place, among boulders, 700 m, viii 1951, *O. Mårtensson* s.n. (G); Pite Lappmark, Arjeplog Parish: N slope of Mt. Kaptjotakko, c 800m alt., vi 1960, *S. Arnell* s.n. (E).

11. Asterella persica (Steph.) M.Howe

IRAN: Prov. Fars, Kleine Wadi's der Halbinsel von Buschir unter überhängenden Felsen, iv 1885, *Stapf* s.n. (BM, JE); Prov. Fars, zwischen grossen Felsen-blöcken auf den Hügeln über der grossen Naphtha-Quelle von Daleki, viel Schatten, iv 1885, *Stapf* s.n. (BM, JE).

SAUDI ARABIA: Dalaghan Park, 25km S of Abha, damp soil under boulder on open granite outcrop, 7000 ft., ii 1986, *Collenette* 5640a (E, JE), 5641b (E); Jabal Ibrahim, part way up SW face, shady crevice, 6700 ft., iv 1990, *Collenette* 7503 (E).

YEMEN: Quelle bei el Mechader über Menacha, 2306m, 11 iii 1889, G.H.D. (G-13369, G13371); Quelle bei Bet el Magrab (Menacha), 2400m, 7 viii 1889, G.H.D. (G); El Mechader über Menada, 1889, *Schweinfurth* s.n. (JE); Wadi Warizan, E side of Jabal Sami, off Taizz to Aden road, 2300m, i 1983, *Gordon* 24 (E, JE).

12. Asterella pappii (Gola) Grolle

YEMEN, SOCOTRA: Majah escarpment, Hammaderoh, NE Socotra, 2600 ft., 6 iv 1967, *A.R. Smith* B3a (E); Above Qaysoh, S of Qalansiyah, 560m, steep N-facing limestone escarpment, on soil, 30 I 1990, *A.G. Miller* 10509 (E).

13. Asterella mussuriensis (Kashyap) Verd.

13a. subsp. **mussuriensis**

PAKISTAN: Sheikhupura, viii 1933, *Sultan Ahmed* 1 (FH).

INDIA, HIMACHAL PRADESH: District Simla, E Panjab, Mount Jako, 7700 ft., on earthy banks, 23 viii 1904, *W. Gollan* in Bryotheca E. Levier 4703 (BM, FH, FI, G-10516).

INDIA, UTTAR PRADESH: Mussoori, 5–7000 ft., 1864, *W. Bell* 224 (E); Mussoorie, 6-700 ft., 2 I 1892, *J.F. Duthie* in Bryotheca E. Levier 309 (G-10501); Arnigadh prope Mussoorie, 6-7000 ft., xii 1895, *W. Gollan* in Bryotheca E. Levier 1298 (G-15378); Mussoorie, above Chajuri Gardens, 6000 ft., inter Barbulas, 10 x 1899, *W. Gollan* in Bryotheca E. Levier 3891 (FI, G-10453); Mussoorie, on road side leading to Khetwala a little above Arnigadh Garden, 5550 ft., 12 ix 1900, *W. Gollan* in Bryotheca E. Levier 3879 (G-10449); Mussoorie, damp shady rocks near head of Arnigadh Garden Canal, 5575 ft., 5 x 1900, *W. Gollan* in Bryotheca E. Levier 3876 (G-10448); Mussoorie, Respana Valley, shady bank close to Arnigadh Garden, 5500 ft., 6 x 1900, W. Gollan in Bryotheca E. Levier 3875 (BM); Distr. Mussoorie, Dhanoulti, on rocks, 8000 ft., 10 xii 1903, *Bahadru* in Bryotheca E. Levier 4522ter (G-10498); Mussoorie, 6–7000 ft., on moist soil, ix 1930, *R.S. Chopra* s.n. (JE, W); ibid, on moist soil amongst mosses, ix 1930, *R.S. Chopra* 548 (JE, S, W); ibid. on moist rocks, amongst moss, ix 1930, *R.S. Chopra* s.n. (E, GL, FH, MANCH, BM); Mussoorie, viii 1933, *R.S. Chopra* in Verdoorn, Hep. Sel. Crit. Ser. 7, No. 343 (BM, BR, G, GOET, H, F, JE, L, LD, MANCH, NY, S, U, W); Mussoorie, E of Landour Dhobi Ghat, 5500-6500 ft., 25 viii 1934, *R.R. Stewart* 14482-b (NY); Mussoorie, near Charleville, 2000m, on vertical face of rock at roadside, 13 ix 1964, *R.A. Maas Geesteranus* 14505-b (L, MO).
INDIA, WEST BENGAL: Darjeeling, Chowrasta Square, 27°02'N, 88°16'E, 2235m, on large roadside wall, 4 vii 1992, *Long* 22351; ibid. 9 viii 1992, *Long* 23048 (E).
INDIA, SIKKIM: West District, Norbugang near Yoksam, 27°22'N, 88°13'E, 1830m, on old wall of chorten, 28 vii 1992, *Long* 22940 (E).

NEPAL, CENTRAL: De Simigaon au col, forêt, 2340m, 15 ix 1954, *A. Zimmermann* 1310 (G); angtang area, S-exposed slopes on way from Khanjing–Syarpa, 3200m, pasture, rocks, 30 viii 1986, *J. Poelt* H3054 (JE); Langtang National Park, Tharepati Pass to Kutumsang, 3300m alt., on soil, 19 ix 1988, *M. Higuchi* 16447 (TNS); Langtang National Park, Syabru–Dhunche, 2200–2500m, on soil, 12 xi 1988, *M. Higuchi* 18740 (TNS).
NEPAL, EAST: Bahskall östlich Panepa, 1962, *J. Poelt* H-111 (JE); Vorhimalaya, östlich Jumbesi, 1962, *J. Poelt* H120 (JE); Vorhimalaya, Likhukhola-Tal, gegen Sete (–Lamjura), 1962, *J. Poelt* H115 (JE); Between Shewaden and Papung, 2350m, on soil, 29 vi 1972, *Z. Iwatsuki* 2069 (H, L, JE); Between Nessum and Bhuje, 1300–2700m, 3 vii 1972, *Z. Iwatsuki* 2288 (UBC, JE, NY, S, G-102726); Junbesi, 2500m alt., on soil, 20 x 1988, *M. Higuchi* 18067-a (TNS); Shidua Ridge above Hille, 27°03'N, 87°24'E, 2270m, soil bank on open grassy hillside, 27 viii 1989, *Long* 16407 (E); Terathum District, Tinjure Danda Ridge between Door Pani and Chauki, 27°10'N, 87°26'E, 2960m, open hillside, mossy bank by path, 29 viii 1989, *Long* 16476-a (E); Foot of Ghunsa Khola near confluence with Tamur River, 27°32'N, 87°49'E, 1750m, steep wooded river bank, open soil bank, 5 ix 1989, *Long* 16618 (E); Taplejung district, Milke Danda ridge between Suke and Koping, 27°21'N, 87°29'E, 3080m, degraded hillside with *Rhododendron arboreum*, on rocky bank by path, 23 x 1991, *Long* 21530 (E); Taplejung district, S end of Milke Danda ridge between Noondaki and Gupha Pokhari, 27°18'N, 87°29'E, 2830m, degraded *Rhododendron arboreum* forest, on steep rocky bank, 24 x 1991, *Long* 21541 (E); Terathum District, S slope of Tinjure Danda ridge, between Chauki and Door Pani, 27°10'N, 87°26'E, 2835m, open cleared hillside, on dry rocky slope, 27 x 1991, *Long* 21628 (E).

BHUTAN: Thimphu District, summit of Dochong La, 27°29'N, 89°45'E, 3110m, cleared forest, on mani wall, 19 iv 1982, *Long* 10939 (E); Thimphu District, Serbithang, Thimphu Chu valley, 27°25'10"N, 89°39'19"E, 2500m, open slope with regenerating *Pinus wallichiana* forest, on soil bank, 9 ix 1999, *Long* 28581; Thimphu District, summit of Dochu La, 27°29'N, 89°45'E, 3040m, *Tsugal Rhododendron* forest, on chorten by road, 10 x 1999, *Long* 28584 (E); Bumthang District, Chume Chu below Chume, 27°29'32"N, 90°47'27"E, 2630m, steep river bank with *Pinus wallichiana*, on bank, 11 ix 1999, *Long* 28600 (E); Bumthang District, between Zhurig and Resang La, 27°27'N, 90°47'E, 2860m, open slope with scattered Rhododendrons, in turf, 12 ix 1999, *Long* 28617 (E); Bumthang District, above Shingkar, Ura, 27°30'N, 90°57'E, 3420m, cleared, grazed *Picea* forest, on soil bank, 15 ix 1999, *Long* 28679 (E); Thimphu District, Drugyel Dzong, Paro Chu, 27°30'11"N, 89°19'24"E, 2650m, rocky bank with shrubs, on soil bank, 18 ix 1999, *Long* 28704 (E); Thimphu District, slopes below Tangu Monastery, Thimphu Chu, 27°35'08"N, 89°38'46"E, 2760m, *Quercus semecarpifolia* forest; on soil bank by path, 20 ix 1999, *Long* 28733 (E); Thimphu District, valley above old Motithang Hotel, Thimphu, 27°28'59"N, 89°35'34"E, 3000m, *Pinus wallichiana* forest, on shady bank, 28 ix 1999, *Long* 28841 (E).

CHINA, SICHUAN: in montis Lungdschu-schan prope urbem Huili regione calide temperata,in fruticetis vic. Djifangkou, arenaceo, 2875m, 17 ix 1914, *H. Handel-Mazzetti* 5227-b (JE, W, WU); Prope castellum Kwapi, N of Yenyüen, 27°53'N, 2750m, rupibus calceo, 30 v 1914, *H. Handel-Mazzetti* 2721 (E, JE, S, W, WU); Sichuan, Mu Li County, 3100m, 13 viii 1980, Gao Chien 20229 (MO).

CHINA, YUNNAN: supra vicum Ganhaidse ad urbem Lidjiang (Likiang) in regione temperate via cava versus Nguluko, arenacea, 3250m, 22 vii 1914, *H. Handel-Mazzetti* 4324 (W, WU); supra Ngulukö ad urbem Lidjiang (Likiang), 3100–3400m, 10 vi 1915, *Handel-Mazzetti* 6697-a (E, WU); Lijiang, Elephon Mts., 2600m, on ground, 30 vii 1985, *X.-J. Li* 85166, HKAS H-4867 (KUN); Lijiang County, km20 at Lijiang-Bai-Han-Chang highway (12km SW of Lijiang) 26°48'N, 100°09'E, ravine sloping SW with *Rhododendron/Quercus* scrub, 2700m, 4 viii 1985, *T. Koponen* 42730 (MO); Summit of pass E of Nan-Hua, E of Dali, 2450m, open eroded hillside with scattered *Pinus* and *Osteomeles*, on soil on shady bank, 23 ix 1990, *Long* 18479 (E); Zhongdian (Chungtien) district, river valley in Bi Ta Hai Forest Reserve, 3360m, open scrubby *Pinus* forest on river bank, on soil bank, 26 ix 1990, *Long* 18542 (E); ibid. 3370m, margin of *Pinus* forest and flat marshy valley floor, on exposed soil bank, 26 ix 1990, *Long* 18580 (E); Lijiang District, above temple, Wen Bi Shan SW of Lijiang, 2775m, *Pinus armandii* forest, on soil bank by path, 3 x 1990, *Long* 18797-b (E); Yulong Shan, below Ma Huang Ba, above Shu Song village, 3140m, hillside with *Pinus/Quercus* scrub, on acid soil bank by path, 8 x 1990, *Long* 18931 (E); Yulong Shan, Wen Hai Mountain above Camellia Temple, 2980m, slopes with *Pinus yunnanensis* forest, on boulder, 9 x 1990, *Long* 18967 (E); Tsang (Cang) Shan, path below Longquan Peak, above Dali, 3320m, open slopes with *Rhododendron*/bamboo scrub, on bank, 15 x 1990, *Long* 19152 (E); Tsang (Cang) Shan, path from Shi Jo village to Huadianba, 2365m, open grazed hillside, on bank with *Pogonatum* etc.,16 x 1990, *Long* 19199 (E); Kunming

Prefecture, small valley above Qiongzhu (Bamboo) Temple W of Kunming, 2220m, dry *Lithocarpus*/ *Castanopsis* forest, on wall of old tank, 22 v 1993, *Long* 23556 (E).

13b. **Asterella mussuriensis**

subsp. **crassa** (Shimizu & S.Hatt.) D.G.Long

JAPAN, HONSHU: Tokio, 1879, *Nordenskjöld* s.n. (G-15325, JE); Saitama Prefecture, Nakatsugawa in Chichibu Mts., c 800m, 30 vii 1965, *Z. Iwatsuki & A.J. & E. Sharp* 2115 (JE, TENN); Pref. Tochigo, Nikko City, along the Ooyagawa (volcanic area), ca. 700m, 7 x 1977, *N. Kitagawa* 15912 (KYO); Kyoto City, in the campus of Kyoto University, in greenhouse, 2 ii 1982, *N. Kitagawa* s.n. (KYO); Chiba Prefecture, Mt. Nokogiri, southern Boso Peninsula, 250m, evergreen broad-leaved forest, shady rock face of volcanic tuff rocks, 29 viii 1993, *Long* & *Furuki* 24697 (E); Saitama Prefecture, Deai, Nakatsu River in Nakatsu Gorge, 800m, gorge in wet broad-leaved forest, on soil on limestone rock ledges, 6 ix 1993, *Long* & *Furuki* 24799 (E).

14. Asterella multiflora (Steph.) Kachroo

PAKISTAN: Lahore, Panjab, 700ft., on the sides of a drain, iii 1931, *Devi Dyal* s.n. (W); Pathankot, Jurdaspur District, Punjab, by stream, 1000 ft., 12 ii 1917, *R.R. Stewart* 1129 (NY).

INDIA, HIMACHAL PRADESH: Simla, *Griffith*, KD 1087 (BM, JE, FH, S, H-SOL, G-10521, G-10524); Iwatamukti, rupicola, ad fluminis ripam, hygrophila, 1700m, iii 1931, *R.S. Chopra* in Verdoorn, Hep. Sel. Crit. Ser. 7, 344 (BM, BR, F, G, GOET, H, JE, L, LD, U, W); Jawalamukhi, on banks at ponds, iii 1931, *D. Dyal* s.n. (FH); ibid. 4–5000ft., on moist rocks, iii 1931, *D. Dyal* s.n. (FH, JE); Jawalamukki, 4–5000 ft., xi 1931, *D. Dyal* 3586 (GL).
INDIA, UTTAR PRADESH: Syree [near Dehra Dun] [xi 1840], *Griffith* 21, KD 1089 (BM); Dehra Doon, *Griffith* KD 1086 (BM, NY); Simon Borge, *Griffith* KD 1087 (BM, NY); Tumsuly Pass, Deyrah Dhoon, *Griffith* 227 (BM); Kheree Pass, Dhera Dhoon, *Griffith* 220 (BM); SW Kumaon, Kodtwara District, on rocks near Kodtwara [= Kotdwara], 2000 ft., 18 i 1901, *Kabir Khan* in Bryotheca E. Levier 3213 (BM, BR, JE, FI, G-10517); Nainital, 6000 ft., ix 1834, S.K. Pandé s.n. (S).
INDIA, WEST BENGAL: Darjeeling, on stone or rocks, 6600ft., 4 ix 1904, *E. Long* 50 in Bryotheca E. Levier 4716 (BM, FI, G-10520); Tista Valley above Melli Bazaar 27°05'N, 88°27'E; 240m, open valley; on roadside wall, 3 vii 1996, *Long* 26266 (E).
INDIA, ASSAM: Gauhati, 10 x 1950, *P. Kachroo* s.n. (JE, TENN, NY, GL).

NEPAL, CENTRAL: Nepal, *Wallich* in herb. Lindenberg 8663-b (W); Nepal, *Wallich* (G-24423) In montibus prope Khatmandu, ii–iv 1900, *K.N. Rana* in Bryotheca E. Levier 2558 (BM, MANCH, G-10499); Godaweri Botanical Gardens near Kathmandu, 27° 35'N, 85° 23'E, 1500m, on rock, 2 xii 1985, *M.J. Wigginton* 1402a (E); Mt. Phulchowki, SE Kathmandu, 1700–2000m alt., Wegböschung im NW-expon. Hangwald, 5 ii 1990, *J. Eggers* 1-8 (JE); Kathmandu Valley,

Gokarna Safari Park, 1350m, an beschatteter senkrechter Ziegelmauer des Hotelgartens, 14 ii 1990, *J. Eggers* 4-31 (JE); Makawanpur District, Siwalik Range, 15km S of Hetauda 27°19'N, 85°00'E, 490m, steep rocky valley with scrub, on shady rock face by road, 29 x 1991, *Long* 21637 (E); c73 km from Kathmandu on way to Pokara, c 1212m, on a bank near the road, 3 iii 1992, *C.C. Townsend* 92-155 (E); Royal Chitwan National Park, S of Meghauli, W of Tiger Tops Jungle Lodge, 27° 32'N, 84° 04'E, 200m alt., mixed deciduous woodland dominated by *Shorea robusta*, shaded damp soil face, 7 iii 1996, *M.F. Watson* 96-19 (E); Kathmandu District, Pasupatinath Temples, 1300m, on old shady wall, 6 x 1999, *Long* 28935 (E).

CHINA, SICHUAN: 'Turkestania' - Ssy-zuan [= Sichuan], Ja-szzhon, 30 iii 1893, *G.I. Potanin* 38 (JE).

15. Asterella vulcanica (Schiffner) Kachroo & Bapna

INDONESIA, JAVA, CENTRAL: Z-Java, Prov. Jogjakarta, Tjandi Borobudur near Magelang, on stones of the building, 1954, *W. Meijer* B5654 (L, JE); Borobudur-Tempel, i 1887, *O. Warburg 14917* (FH, det. Schiffner).
INDONESIA, JAVA, EAST: O-Java, 1924, *Goebel* s.n. (JE, S).

PAPUA NEW GUINEA: West Sepik District, Star Mountains, Sili' Katibin, granodiorite area NW of Mt. Auriga, c 5°S, 141°05'E, on humus soil near spring, exposed, 3500m, 24 iv 1975, *Touw 16628* (L).

16. Asterella gracilis (F. Weber) Underw.

SPAIN: [Andalucia, Prov. Granada] Sierra Nevada, Barranco de San Juan, (Vic. Pico Veleta), vii 1847, *Schimper* s.n., herb. Hampe, as *Fimbriaria semiglobosa* Bisch. in litt. (BM); [Asturia] Picos de Europa, 1930, *Buch* (H);

ITALY: Montes ad Verbanum [= Lago Maggiore] herb. *Hampe* (BM); Prov. Novara, sui Muri nei dintorni di Riva (Valsesia), iv 1861, *Carestia* in Erb. Critt. Ital. Ser. II, 956 (BM); Prov. Bolzano, am Guslan, Brünnel, Süd Tirol, Bozen [= Bolzano], herb. Hampe (BM); Campania, Prov. Salerno, Mont Cervati, between summit and Madonna della Neve, 1850m, xi 1994, *Long* & *Duckett* 25775 (E); Piemonte: Bardonecchia, Vallone de Rochemolles above the Scarfiotti refuge, 2500m, thin soil in rock crevice on steep N-facing slope, 30 vii 1997, *T.L. Blockeel* 26-404 (herb. Blockeel).

FRANCE: Autour du Grand Lac pres le Lautarec, 18 viii 1922, *R. Douin* (BR); Mont-Cenis (Savoie), talus au bord d'un sentier, sous-sol de schiste lustré, 2150m, vii 19644, *L Castelli* s.n. (E).

SWITZERLAND: [Kt. Bern] Faulhorn, viii 1841, *Mühlenbeck*, herb. Pearson (BM); Kt. Ticino: Ai muri ed alle ripe a Brione presso Minusio [Locarno] nel Cantone Ticino, v 1860, *Daldini* in Erb. Critt. Ital. 464 (BM, G-15263); [not traced] Stantashorn, 6500 ft., vi 1906, *Byron* s.n. (BM); Kt. Ticino: Quinto, V. Piora, Taneda di Sopra, Sorgente, 6962/ 1573, 2310m, viii 1984, *Geissler* 10648 (G); Kt. Ticino: Intragna, Carbozzei di Sotto, 69615/ 1187, 370m, muro, v 1985, *Geissler* 11051 (G); Kt. Ticino: Quinto, Pian Murinascia, 6988/ 1557, pascolo roccioso, 2070m, viii 1984, *Geissler* 11366 (G); Kt. Valais: Leukerbad, Lämmernboden, 6114/ 1386, Erdblösse, 2330m, viii 1987, *Geissler* 12862 (G); Kt.Valais: Gemmi Pass, near Lämmernsee, 2330m, limestone valley slopes, ledges on low limestone ridge, 10 viii 1994, *Long, Geissler & Maier* 25664 (E).

CZECH REPUBLIC: Schlesisch-mährisches Gesenke, Kessel, Glimmerschieferfelsen, vii 1870, *Limpricht* G-14595 del[ineavit] Stephani, rev. Grolle; G-14596; Nord-Böhmen, am Südabhange des Kleisberges bei Haida, an sonniger Stelle auf Humus über Felsen (Phonolith), 550–600m, v 1896, *Schmidt* in Schiffner, Hep Europ. Exsicc. 1202 (U).

GERMANY: [Sachsen-Anhalt] Hercynia, Bodegebirge, v 1847, *Hampe* (BM); in valle Bodethal, juxta Winzenburg, *Hampe* (BM).

POLAND: Silesia, im Weistritztal (1500') bei Charlottenbrunn, an sonnigen Stellen mit *Woodsia ilvensis* zwischen Gerölle, vi 1860, *Milde* in Rabenhorst Hep. Eur. 161 (BM, BR); Silesia, Weistritzthal, vi 1860, *Milde* s.n. (BM, H-SOL).

NORWAY: Norvege, *Hornemann* '*Marchantia pilosa* Horn. Original' (G-15260). nb. this specimen annotated as not type by Grolle; Norvege, in terra Nordlandiae, *Sommerfelt* 41 (G-15261, G-14591); Norvege, 1826, *Sommerfelt* s.n. (BR); Norvegia, 1841, *Blytt* s.n. as *Marchantia alpina* Myrin (G-15265); Falkensten prope Horten, ad terram in fissuris rupium, v 1898, *Kaalaas* in Bryotheca E. Levier s.n. (TENN); Falkensten by Horten, v 1898, *Kaalaas* (BM); S. Myensauch, Opd., Vangolien in fissuris rupium, 850m, viii 1900, *Hagen* s.n. (GL); Hordaland, Grytehorgi, rocky ground, 22 vi 1950, *E.F. Warburg* s.n. (OXF); Oppland District, Jotunheimen, limestone valley with caves, SW of Bovertun, 1030m, on damp soil on limestone rocks, vii 1991, *Long* 20009 (E).

SWEDEN: Suecia, *Arnell* s.n., ex herb. Stephani (BM); Upsaliae, 1804, *Mohr* s.n. herb. Turner (BM); Smaland, Jönköping, Dunkchallai, v 1829, *A. Arvén* s.n. (G); Upsaliae ad Gottsunde, Majo 1831 et 1832, ubi specimena sua legerunt *Weberus*, ex herb. Myrin (BM); Upsaliae, vi 1839, *Ångström* s.n. (BM); Gottsundabergen Upsaliae, vi 1840, *Ångström* s.n. (BM, BR); ad Upsaliam, vi 1845, *Ångström* s.n. (BM); Prov. Jämtland, Sueciae, vi 1846, *Sjögren* s.n. (BM); Laxfjället, Lappon. Umens., vii–viii 1854–1855, *Ångström* s.n. (BM, BR, G); Lapponia, *Ångström* 65, herb. Schimper (BM); Stockholm, fiss. rup., vii 1857, *Lindberg* s.n. (BM); Närke, Ullaviklint, 1870, *Hartman* s.n. (GL); Malpd. [?], Sundsvaelsberget, 1874, *Arnell* (BM); Upsala Gottsundabergen, v 1879, *Seth* 9 (GL); Jönköping, iv 1886, *Arnell* (BR); Jönköping, on earth-covered rocks, v 1888, *Arnell* in Husnot, Hep. Gall. 170 (BM, BR, GL, G-17029); Jönköping, on an earth-covered rock,

ix 1890, *Arnell* (FH); Vrm. [Varmland] N. Rada, v 1896, *Fröding* s.n. (FH); Varmland, N. Rada, Fl. Rada, vi 1897, *Fröding* s.n. (GL); Lapponia tornensis, Karesundo parish,Pältsa region, at the base and SE of the southern peak, vii 1948, *Mårtensson* s.n. (G-14588).

FINLAND: Ins. Aland, Libyberg, vi 1878, *F.O. Bomasson* s.n. (BM, G); Alandia, Saltviks sn. Berg i klippspringor, 60° 15'N, 20° 05'E, 5 vi 1878, *J.O. Bomansson*, Hep. Exsicc. S.O. Lindbergii 309 (BM, E); Alandia, 'Saltvik sn, Ersberg i klippspringor', 60° 15'N, 20° 05'E, 2 vi 1878, *J.O. Bomansson*, Hep. Exsicc. S.O. Lindbergii 319 (BM, E); Finlandia austr., Lojo, Skröddarla, viii 1878, *Lindberg* s.n. (BM); Varsinais-Suomi, Raisio, Nuorik-kala, 300m west-northwest of the Nuorikkala farm house, eastern slope of a sunny hill, in rock crevices, vi 1968, *Tapio Laine* s.n. (E).

RUSSIA: Irkutsk, *Turczaninow* s.n. (H-SOL); [Karelia] Ladoga, Sortavala, app. Fenniae, vi 1874, *S.O. Lindberg* s.n. (BM); [Karelia] Ladoga, Kirjavalaks, vi 1874, *S.O. Lindberg* s.n. (BM, G-14593); Karelian Republic, Karelia ladogensis, Sortavala, 'Kirjavalaks, Kotomäki, ad terram fere nudam vel perfecte nudam supra praeruptas parvas aridas, vere solum humiectatas', 61° 40'N, 30° 40'E, vi 1874, *S.O. Lindberg* in Hep. Exsicc. S.O. Lindbergii 320 (BM, E); Siberia, Jenisei, Antsiferona, 59° 10' N lat., vi 1876, *H.W. Arnell* s.n. (S); Sibiria, Jenisei, Plachino, 68° 05'N lat., vii 1876, *H.W. Arnell* s.n. (S); Sibiria, Jenisei, Tolstoinos, 70° 10' N lat., viii 1876, *H.W. Arnell* s.n. (S); Sibiria, in valle flum. Lena, Kumachsur, 70°30' lat. bor., vii 1898, *Nilsson-Ehle* s.n. (LD, S); Siberia, 1979, *Abramova* s.n. (ALA); Chukotka, vi 1979, leg. ? (ALA).

GEORGIA: Caucasus, Abchasien, Suchumi, Kelasuri, Seitentälchen des Kelasuritales, vii 1966, *Meyer & Meyer* 8520 (JE).

IRAN: Mazandaran, Kelardasht, 2300m, Weg zum Alam-Kuh, Shahrezamin, auf Erde, vi 1977, *Kürschner & Frey* 2-456 (JE).

JAPAN: Hokkaido, [Yezo Nord, ile plate] Rebunshiri, v 1893, *Faurie* 9463 (FH); Hokkaido, Sankakuyama, Sapporo-shi; in crevices of andesite rocks in sunny places, c250m, vi 1969, *T. Sasaki* in Hep. Jap. Exsic. ser. 18, 851 (F, G, H, L, S, TENN, U, UBC).

Appendix VI Characters and character state codes for cladistic analysis

Vegetative characters of gametophyte

For further definition and discussion of gametophytic characters and character states see Chapter 2.2.

1 *Branching* (0 = mostly terminal; 1 = mostly ventral). Often both types of branch occur in individual specimens and taxa; normally one type predominates and is scored as such.

2 *Thallus t.s.* (0 = 3–10x wider than tall; 1 = 1–3x wider than tall). This character is a reflection of hygromorphy/ xeromorphy and is normally clearly assignable to one or other category.

3 *Pore rings* (0 = 1(2); 1= 2–3; 2 = 3–6). Each air pore is surrounded by concentric rings of cells which are relatively constant for each species. The score 0 is assigned to species where most pores have only one ring; occasionally a few have two; 1 is scored where there are 2 or 3 rings and the score 2 given where all air pores have 3 or more cell rings.

4 *Scale appendage number* (0 = 1(–2); 1 = 1 or 2; 2 = 2 or 3). The number of ventral scale appendages can vary on single specimens; 0 is scored where appendages are mostly single, with occasionally some scales with two appendages; 1 is scored where both 1 and 2 appendages are common, and 3 scored for taxa where 2 and 3 appendages occur.

5 *Scale appendage shape* (0 = lanceolate, filiform, acute; 1 = ovate, broadly oblong, obtuse; 2 = transversely ovate, obtuse).

6 *Appendage constriction* (0 = absent; 1 = present). In some species the scale appendages are constricted just above their point of insertion on the sale body. *Asterella wallichiana* is polymorphic for this character; some specimens have appendages which are somewhat constricted at the base.

Reproductive characters of gametophyte

7 *Sexual condition* (0 = dioicous; 1 = terminal-autoicous; 2 = ventral autoicous; 3 = par-autoicous). These terms are defined in Chapter 2.2.2. This is normally constant for individual species but polymorphisms occur in *A. blumeana* and *Reboulia hemisphaerica*.

8 *Androecial position* (0 = main thallus; 1 = base of stalk; 2 = ventral branch). The position of the androecium on the thallus branches is constant for each species; polymorphisms occur in *A. blumeana, A. persica* and *A. multiflora*.

9 *Androecium type* (0 = diffuse; 1 = weak cushion; 2 = defined cushion). In most species the antheridial ostioles are aggregated into cushions; in three taxa they are diffusely arranged.

10 *Peduncle position* (0 = absent; 1 = dorsal; 2 = pseudoterminal; 3 = terminal on main branch; 4 = terminal on ventral branch). Polymorphisms for this character occur in *A. blumeana, Cryptomitrium himalayense* and *Reboulia hemisphaerica*.

11 *Carpocephalum shape* (0 = absent; 1 = depressed; 2 = hemispheric; 3 = discoid or umbrella-shaped). Carpocephala are absent in *Targionia hypophylla*; the shape of the carpocephalum is distinctive for individual species, however the distinction between 'depressed' and 'hemispheric' is somewhat arbitrary.

12 *Involucre type* (0 = 2-valved/ bilabiate; 1 = tubular; 2 = cup; 3 = cleft flap; 4 = entire flap). There are some doubts about the homology of the involucre, particularly in the genera other than *Asterella*, for example in *Targionia* where it is borne directly on the thallus.

13 *Pseudoperianth* (0 = absent; 1 = present, fused at apex; 2 = present, free at apex).

Sporophyte characters

For definition of spore characters see Chapter 3.3 and 3.7.

14 *Capsule dehiscence* (0 = irregular cap, 1 = regular cap; 2 = valves).

15 *Elater spirals* (0 = 3-spiral mostly; 1 = 2-spiral mostly; 2 = 1-spiral mostly). This character is somewhat variable within individual specimens and species; the number of spirals is scored at the middle of the elater. The score reflects the majority state.

16 *Spore colour* (0 = black; 1 = brown; 2 = yellow). These limits are arbitrary; 'brown' includes pale brown and red-brown; 'yellow' includes yellow-brown spores.

17 *Spore shape* (0 = alete; 1 = weakly trilete; 2 = strongly trilete).

18 *Proximal/ distal similarity/ dissimilarity* (0 = similar; 1 = dissimilar).

19 *Primary ornamentation of spores* (0 = saccate; 1 = ridged; 2 = irregularly areolate; 3 = regularly areolate).

Appendix VII Data matrix for cladistic analysis

For definition of character state codes see Appendix VI.

Character Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
A. saccata	0	1	1	1	0	0	3	1	1	3	2	4	1	0	1	2	2	0	1
A. grollei	0	0	2	0	0	0	1	0	1	2	2	3	1	0	1	0	2	0	1
A. wallichiana	0	0	1	0	0	0&1	0	0	2	3	1	4	1	0	2	1	2	1	1
A. africana	0	0	1	0	1	0	3	1	1	3	3	4	2	0	1	2	2	1	3
A. cruciata	0	0	1	0	1	1	3	1	2	3	3	4	2	0	1	2	2	1	3
A. khasyana	0	0	1	0	0	0	3	1	2	3	3	4	2	0	1	2	2	1	3
A. leptophylla	1	0	1	0	1	0	2	2	2	3	3	4	2	0	1	2	2	1	3
A. blumeana	0	0	2	0	1	0	1&2	0&2	2	3&4	3	4	2	0	1	2	2	1	3
A. limbata	0	0	2	0	1	0	1	0	2	3	3	4	2	0	1	2	2	1	3
A. lindenbergiana	0	0	1	0	0	0	3	1	1	3	2	4	1	0	1	1	2	0	3
A. persica	1	1	1	1	0	0	2	0&2	2	4	1	3	1	0	1	1	2	0	3
A. pappii	1	1	1	2	0	0	2	2	2	4	1	3	1	0	1	1	2	0	3
A. mussuriensis	1	0	2	1	0	0	2	2	2	4	1	3	1	0	1	1	2	0	3
A. multiflora	1	0	2	1	0	0	2	0&2	2	4	1	3	1	0	2	1	2	0	3
A. vulcanica	1	0	2	0	1	1	2	2	2	4	2	4	1	0	1	2	2	0	3
A. gracilis	0	1	0	0	0	0	3	1	0	3	2	3	2	1	0	2	0	0	2
Mannia androgyna	0	1	1	1	0	0	2	0	0	4	1	2	0	1	0	2	1	1	0
Cryptomitrium himalayense	0	0	2	0	0	0	3	1	0	2&3	3	0	0	1	0	1	2	0	2
Reboulia hemisphaerica	0	0	2	2	0	0	1&3	1	2	2&3	1	0	0	0	0	2	2	0	3
Plagiochasma appendiculatum	0	0	1	0	2	1	1	0	2	1	1	0	0	0	0	1	2	0	3
Targionia hypophylla	0	0	2	0	0	0	2	2	2	0	0	0	0	2	1	1	0	1	3