Phylogeny and Taxonomy of the Complex Thalloid Liverwort family Cleveaceae Cavers

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DECLARATION

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

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ABSTRACT

Liverworts (Phylum Marchantiophyta) form the earliest diverging lineage of extant land plants and hold a key position in the evolutionary history of land plants. The family Cleveaceae, first defined in 1881 by Leitgeb by its complex thallus anatomy and star-shaped epidermal pores with strongly thickened radial walls, is now included within Marchantiopsida (Complex Thalloid Liverworts). The family is widely distributed in warm temperate to arctic regions throughout the Northern Hemisphere, but very rare in South America and absent from Australia and New Zealand.

Since Cleveaceae was described, the number and names of genera and species recognized within the family have changed many times, with three genera currently accepted: *Athalamia* (12 to 15 species), *Sauteria* (2 to 5 species) and *Peltolepis* (1 or 2 species). However, no robust phylogenetic frame work or taxonomic monographs of the family have previously been undertaken and the species diversity within the genera remains uncertain.

The study presents the first robust phylogenetic framework for the family, based on three chloroplast genes (*psb*A, *rpo*C1 and *rps*4) and one nuclear ribosomal region (26S) sequenced for 54 ingroup accessions representing a substantial part of the geographic range of the family (except South America) and a large part of its morphological diversity. Samples sequenced include the type species of the three currently accepted genera as well as those of previously synonymised genera; *Clevea*, *Spathysia*, *Gollaniella* and *Sauchia.* The current circumscription and relationships of the genera were tested using Maximum Parsimony, Bayesian and Likelihood inferences.

Cleveaceae was strongly supported as monophyletic with four main lineages resolved within the family, two corresponding to *Peltolepis* and *Sauteria* and two composing a polyphyletic *Athalamia*. The latter is therefore divided into a more narrowly defined *Athalamia* and a fourth genus, for which *Clevea* is the earliest published name.

Inferred evolutions of twelve morphological characters, that are useful or have been used in classifications of Cleveaceae, were reconstructed using maximum parsimony and maximum likelihood methods. The misleading influence of homoplasy on past morphological classifications and phylogenies is discussed.

The study also presents the first worldwide taxonomic revision of Cleveaceae based on around 2300 specimens studied, including all available type specimens. The monographic work is based on morphological and anatomical characters reviewed using dissecting, compound and scanning electron microscopes including both herbarium and fresh material collected on field excursions during the study. Ventral scale morphology, position and aggregation of androecia and shape of receptacle were found to be valuable characters in generic and species delimitation. The traditional definition of genera of Cleveaceae based mainly on two characters (carpocephalum stalk position and anatomy) was rejected. A total of seven species were recognized from 25 formerly described names including one new necessary combination: *Clevea hyalina* (Sommerf.) Lindb., *C. spathysii* (Lindenb.) Müll.Frib., *C. pusilla* (Steph.) Rubasinghe & D.G.Long comb. nov., *Athalamia pinguis* Falc., *Sauteria alpina* (Nees) Nees, *S. spongiosa* (Kashyap) S.Hatt., and *Peltolepis quadrata* (Saut.) Müll.Frib. Nine excluded and doubtful species are listed along with reasons for their exclusion. Generic and species keys are presented based on vegetative, reproductive and spore morphological characters. For each genus and species, descriptions, illustrations, and distribution maps are given along with ecological, taxonomic and nomenclatural notes.

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Please

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

CHAPTER -1-INTRODUCTION

1.1. Introduction and background to the study

Extant bryophytes (liverworts, hornworts and mosses) form a group of plants comprising more than 15,000 described species worldwide (Beike & Rensing 2010; Vanderpoorten & Goffinet 2009). They are a diverse group of land plants of small stature but major ecological importance. They occur in all continents; in extremely cold tundra regions, deserts, near hot water springs and in the tropics, occupying xeric to mesic and aquatic (though not marine) niches, with the greatest diversity thriving in specialized moist micro-environments. They have the greatest biomass in cool temperate regions where, for example, the single moss genus *Sphagnum* is estimated to contain roughly 16% of the earth's carbon (Renzaglia et al. 2007). Although they play very important ecological roles, such as reducing erosion along streams, water and nutrient cycling in tropical forests and insulating the arctic permafrost, bryophytes rarely receive the same level of attention as angiosperms, pteridophytes or gymnosperms due to their small size (Vanderpoorten & Goffinet 2009).

Bryophytes have been an ecologically significant component of life on land for over 400 million years (Mishler 2001; Renzaglia et al. 2007). Since the Ordovician and Devonian periods, bryophytes have existed continuously to the present day and may have played a significant role in shaping the earth's atmosphere and biosphere (Renzaglia et al. 2007; Wellman & Gray 2000). Although small, their gametophytes and solitary unbranched sporogonia are remarkably diverse, and show a range of innovative adaptations to life on land. After flowering plants, bryophytes are the most diverse and species-rich lineages of embryophytes (Mishler 2001; Renzaglia et al. 2007; Wellman & Gray 2000).

Classification within the three groups of bryophytes has constantly been changing for over two centuries. In the first half of the 18th century, very little was known about the morphology and anatomy of bryophytes until Dillenius (1741) first described moss capsules (Steere 1947). However, *Fundamentum historiae naturalis muscorum frodosorum* by Johannes Hedwig (1782) is thought to be the real beginning of bryology (Price 2007; Shaw & Renzaglia 2004). Studies of mosses have gradually advanced since then. Although hepatics were not scientifically investigated until the nineteenth century, the study of liverworts or “hepaticology” is thought to be post-Linnaean (Schuster 1966). The thallus of some liverworts like *Marchantia* showed some resemblance to the lobes of the liver, which led to the naming of the group ‘Hepaticae’ or, as more commonly known in familiar language, the ‘Liverworts’. According to the physician Platearius (1497), Hepatica is so called because “it is particularly a helper of the liver” (in Howe 1894). However, this is a source of possible confusion with the angiosperm genus ‘Hepatica’ and no evidence has been found to support Platearius’s view to date (Howe 1894; Schuster 1966).

In the earlier classifications of bryophytes a very small number of morphological characters were considered adequate to define families, genera and species. This may be due to the dominant influence of Linnaeus (1753), who gave prime importance to sexual characters (Schuster 1966). However, with time, the number and type of characters used in bryophyte classifications have gradually but greatly increased. They include morphological, anatomical, cellular and intracellular ultrastructural, ontogenic, chromosomal and chemical characters. Large scale cladistic analyses performed using these morphological, ultrastructural and biochemical data, suggested a paraphyly for bryophytes and a basal position for liverworts (Bremer 1985; Kenrick & Crane 1997; Mishler & Churchill 1985), although few studies suggested a monophyly (Qiu 2008 and references therein). However, evolutionary relationships within the three groups of bryophytes remained uncertain until the application of molecular data (Heinrichs 2009; He-Nygrén et al. 2006; Waters et al. 1992).

Most recent molecular phylogenetic studies using multigene super-matrices and many advanced analytical methods and evolutionary models such as parsimony, likelihood, Bayesian inference supported the monophyly of embryophytes: the group containing liverworts, mosses, hornworts and tracheophytes, where a basal position is supported for bryophytes (Brown & Lemmon 2008; Dombrovska & Qiu 2004;

Friedman & Cook 2000; Qiu et al. 2006 2007). These multigene phylogenetic studies have firmly confirmed the paraphyly for bryophytes and have also unambiguously supported liverworts as the basal-most lineage in land plants (Brown & Lemmon 2008; Dombrovska & Qiu 2004; Friedman & Cook 2000; Forrest et al. 2006; Karol et al. 2001; Qiu 2008; Qiu et al. 1998, 2006, 2007; Turmel et al. 2002). Most of the earlier morphological phylogenetic analayses predicted mosses as sister to tracheophytes, considering hydroids and leptoids, the conductive tissue in some mosses (e.g. Polytricaceae) to be homologous with the xylem and phloem in tracheophytes (Bremer 1985; Kenrick & Crane 1997; Mishler & Churchill 1985). Recent molecular phylogenetic analyses have confirmed that hornworts are sister to tracheophytes and their mostly nutritionally independent sporophyte is a key character supporting this position (Qiu 2008; Qiu et al. 2006).

According to the most recent classification scheme, based on both morphological and molecular data, proposed by Crandall-Stotler et al. (2009), the three groups of ‘bryophytes’; liverworts, mosses and hornworts are recognized as three phyla: Bryophyta (mosses), Marchantiophyta (liverworts) and Anthocerotophyta (hornworts). Despite their paraphyletic position, the three phyla are still frequently kept together in a single group “Bryophytes” (Crandall-Stotler 1980; Schofield 1985), because (1) they share many fundamental structural features (e.g. prostrate growth habits are common in all three phyla and absence of a true (cutin-containing) cuticle and cutinized walls in the mature haploid generation) and (2) they display reproductive features (e.g. external source of water is necessary for their motile sperm to facilitate fertilization and their unbranched sporophytes have a single sporangium) that are unifying and innovative, as the only land plants with a dominant gametophytic generation. Their highly specialised vegetative and reproductive innovations and their basal position in land plant phylogeny demonstrate why studies of bryophytes are crucial to an understanding of the evolution of the land plant genome and morphological innovations of land plants (Goffinet & Shaw 2009; Qiu et al. 2006; Shaw & Renzaglia 2004).

1.2 The Phylum Marchantiophyta (Liverworts)

Liverworts form the earliest diverging lineage of land plants and therefore are the sister group to all other extant land plants (Groth-Malonek & Knoop 2005; Qiu et al. 1998, 2006, 2007) (Fig. 1.1). The earliest liverwort lineages are thought to have evolved from aquatic algal ancestors (Charophycean green algae) (Brown & Lemmon 2008; Buck & Goffinet 2000; Hernick et al. 2008; Karol et al. 2001; Kenrick & Crane 1997; Nishiyama & Kato 1999; Shaw & Renzaglia 2004; Vanderpoorten & Goffinet 2009). These oldest known extant group of terrestrial embyrophytes are often considered as “living fossils” (Brown & Lemmon 2008). The earliest confirmed land plant fossil is thought to be of an ancient liverwort dating to the middle Ordovician Period of the Palaeozoic Era, about 475 million years ago. This is thought to be the first evidence for the existence of embryophytes (Buck & Goffinet 2000; Djamali et al. 2008; Edwards et al. 1995; Goffinet & Shaw 2009; Shaw & Renzaglia 2004; Qiu et al. 1998).

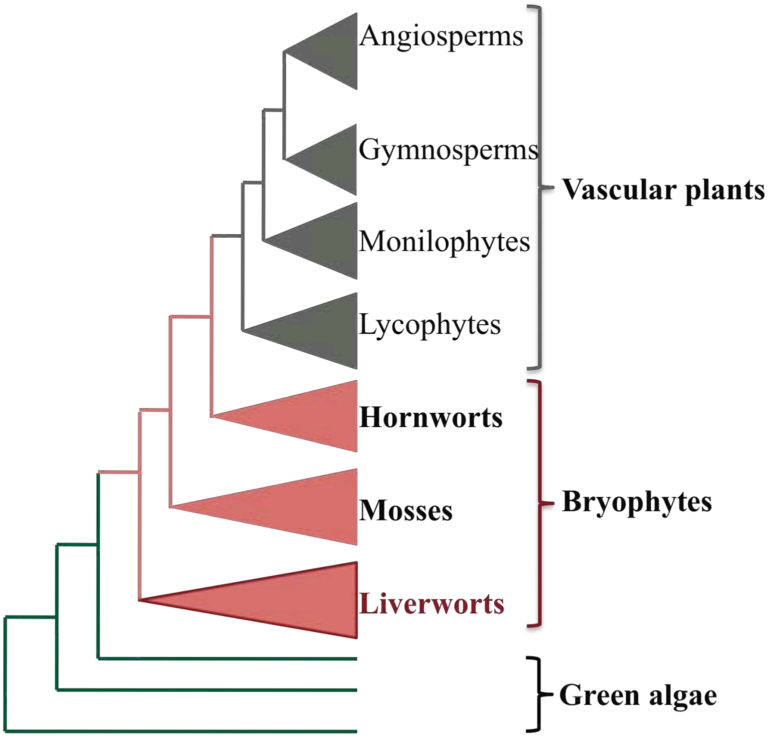


Figure 1.1 Liverworts: the earliest diverging lineage of land plants (phylogram from a maximum likelihood analysis of a seven-gene, 192-taxon matrix). (Modified from Qiu et al. 2007).

In spite of this antiquity, liverworts are morphologically among the most complex and diverse of all bryophytes and there are about 6000–8000 species of extant liverworts. This makes it difficult to study and understand their evolutionary relationships (Davis 2004; Crandall-Stotler & Stotler 2009, 2005; He-Nygrén et al. 2006). The seminal publications of Hofmeister (1851) and Leitgeb (1874–1881) laid the foundations for morphological studies of liverworts. Many taxonomists have since then contributed much more detailed descriptions of many groups of liverworts (Goffinet & Shaw 2009 and references therein). However, according to Goffinet & Shaw (2009), “the majority of liverwort taxa are known only at the level of a taxonomic description”. Furthermore, the phylogenetic structure of most liverwort groups is yet to be investigated using molecular data (Davis 2004; Crandall-Stotler et al. 2009).

Traditionally, liverworts have been subdivided into the marchantioid group (complex thalloids), and the jungermannioid group (simple thalloids and leafy liverworts). These groups have been recognised in most classification systems and have been accepted as natural groups. However, Schiffner (1893) divided the Jungermanniod group into Jungermanniales anakrogynae, including mainly simple thalloids and Jungermannilaes akrogynae including leafy liverworts. He based this division on differences in archegonial position and development. These two groups were elevated into orders by Lotsy (1909); Metzgeriales (anakrogynae) and Jungermanniales (akrogynae). Schuster (1953) recognized two subclasses within liverworts: Marchantiidae and Jungermanniidae. His subclass Jungermanniidae contained two orders Jungermanniales (leafies) and Metzgeriales (simple thalloids). However, Crandall-Stotler and Stotler (2000) recognized them as classes: Marchantiopsida and Jungermanniopsida, the latter divided into two subclasses, Metzgeriidae (simple thalloid liverworts) and Jungermanniidae (leafy liverworts).

The incorporation of molecular data along with phylogenetic analytical methods such as cladistics, have resulted in recent revolutionary changes to the morphology-based phylogenetic groupings of liverworts and thus have brought a lot of new insights to liverwort phylogeny. These recent molecular studies demonstrated that many morphological characters previously used to define taxa within liverworts are homoplasious. However, in most instances the incongruence between traditional morphology-based classifications and molecular phylogenies are attributed to faulty interpretations of homology (Crandall-Stotler et al. 2009). There has also been debate over the assumed monophyly of liverworts. Analysis of complete 18s-rRNA sequences supported the paraphyly of liverworts with Jungermanniopsida resolved as a separate lineage (Capesius & Bopp 1997) whereas *rbc*L data suggested a monophyly for the group (Lewis et al. 1997). However, more recent molecular studies employing multigene super-matrices, including nuclear, mitochondrial and chloroplast regions and morphological data have confirmed the monophyly of the liverworts and three lineages within the liverworts (Crandall-Stotler et al. 2005, 2009; Forrest & Crandall-Stotler 2005; Forrest et al. 2006; Heinrichs et al. 2005; He-Nygrén et al. 2006; Qiu et al. 2006, 2007). However, the three different gametophyte types: leafy, simple thalloid and complex thalloid, which were used to define the major groupings within liverworts and believed to be three monophyletic groups, is not accepted. The three gametophyte types refer to a type of morphological organization but do not form natural groupings, e.g. leafy morphologies are distributed across all three major liverwort lineages. *Haplomitrium* and *Treubia* (leafy morphology) have resolved in a monophyletic group, which is sister to all other liverworts. However, complex thalloid morphology is recovered as a monophyletic group and is the first diverging lineage after *Haplomitrium* and *Treubia* (Crandall-Stotler et al. 2009; Forrest et al. 2006; Heinrichs et al. 2007; He-Nygrén et al. 2006).

The three lineages recognized within the phylum Marchantiophyta in recent analyses are recognized as Classes in the most recent classification systems of liverworts: Haplomitriopsida Stotler & Crand.-Stotl., Marchantiopsida Doweld and Jungermanniopsida Stotler & Crand.-Stotl (Crandall-Stotler et al. 2009) (Fig. 1.2).

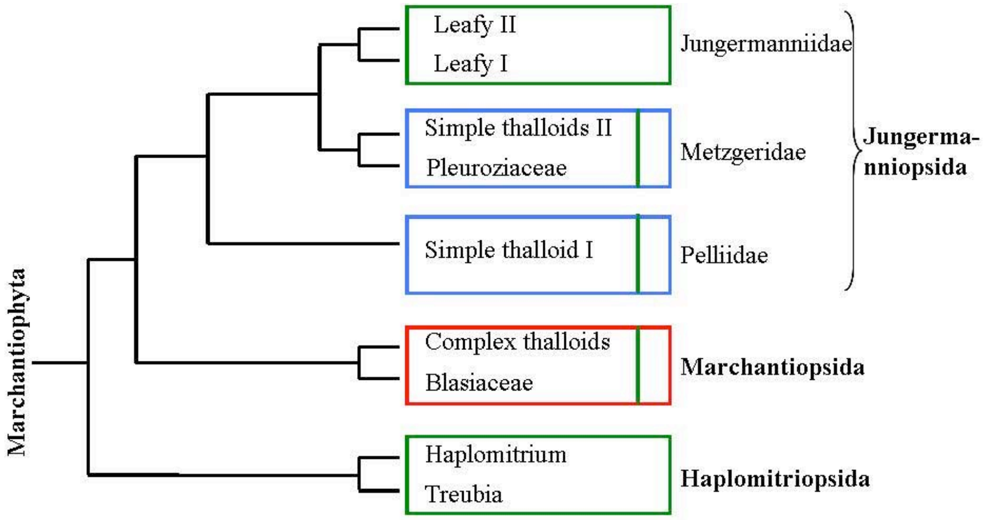


Figure 1.2. The three traditional morphological groups are not supported by molecular phylogeny of liverworts (Modified from Forrest et al. 2006).

Taxa traditionally classified as "simple thalloids" have resolved as a polyphyletic group. The simple thalloids, with leafy morphology, *Haplomitrium* and *Treubia*, which were never classified as closely-related in the past, have resolved in a monophyletic group which is sister to all other liverworts. It is believed that the Class Haplomitriopsida diverged from the rest of the liverworts in the early Devonian period (Heinrichs et al. 2007). This group therefore occupies a very important position in the early evolution of liverworts in particular and of land plants in general (Crandall-Stotler et al. 2009; Forrest et al. 2006; Renzaglia et al. 2007). It includes three extant taxa; *Treubia*, *Apotreubia* and *Haplomitrium*. Although they are morphologically quite different, they share several key characters such as tetrahedral apical cells, copious mucilage secreting epidermal cells, leaf-wings formed from a single leaf initial, and the anacrogynous position of gametangia (Crandall-Stotler et al. 2009; Forrest et al. 2006; Heinrichs et al. 2005; He-Nygrén et al. 2006; Qiu et al. 2006, 2007; Renzaglia et al. 2007) (Fig. 1.2).

Jungermanniopsida is paraphyaletic and includes three major lineages, considered as subclasses: Pelliidae assigned to Simple Thalloids I, Metzgeriidae including the Simple Thalloid group II and Jungermanniidae containing leafy liverworts (Fig. 1.2). The subclass Pelliidae He-Nygrén et al. includes taxa that are mostly simple thalloids without internal differentiation into air chambers and as well as some leafy forms. Leafy taxa in Pelliidae contain leaves developed from one primary initial, they are never lobed and not arranged in 2 ranks. The subclass Metzgeriidae Barthol.-Began, comprises mostly simple thalloid forms, without air chambers; or if leafy, leaves develop from three primary initials and are arranged in 2 ranks. *Pleurozia*, which was long classified as a leafy liverwort, has resolved sister to the simple thalloid group Metzgeriidae. However, *Pleurozia* is the only leafy liverwort that possesses a lenticular apical cell, a character shared with other simple thalloids in Metzgeriidae. Most of the ‘true leafies’ form a monopyletic group in the subclass Jungermanniidae Engl., which very rarely includes thalloids. In Jungermannioid taxa leaves are developed from 2 primary leaf initials which are frequently divided into two or more lobes (Crandall-Stotler et al. 2009; Forrest et al. 2006; Heinrichs et al. 2005; He-Nygrén et al. 2006; Qiu et al. 2006, 2007;Renzaglia et al. 2007) (Fig. 1.2).

Complex thalloids are the only ‘traditional’ group resolving as monophyletic. It comprises two subclasses: Blasiidae He-Nygrén et al. and Marchantiidae Engl. However, taxa of complex thalloids or Marchantiidae have complex thalli, with or without internal differentiation, with or without air chambers and air pores, ventral scales present or absent, rhizoids may be smooth or smooth and pegged, and antheridia either embedded in the dorsal part of the thallus, in cushions on the thallus, or in stalked receptacles (antheridiophores), sporophytes on stalked receptacles or borne dorsally on thallus or embedded in thallus, etc (Crandall-Stotler et al. 2009). Blasiidae which includes *Blasia* and *Cavicularia*, that were earlier, grouped within the simple thalloids due to their simple thalli, lacking dorsiventral differentiation, is resolved as sister to the rest of the complex thalloids. However, they share several key characters with the complex ventral scales, true calyptra and cuneate apical cells (Crandall-Stotler et al. 2009; Forrest et al. 2006; Heinrichs et al. 2005; He-Nygrén et al. 2006; Qiu et al. 2006, 2007; Renzaglia et al. 2007) (Fig. 1.2).

The Subclass Marchantiidae is subdivided into four orders: Sphaerocarpales, Neohodgsoniales, Lunulariales and Marchantiales (Crandall-Stotler et al. 2009). The latest classification of the order Marchantiales includes 15 families with 27 or 28 genera and approximately 355 species (Table 1.1) (Bischler 1998; Crandall-Stotler et al. 2009). According to Bischler (1998) the genera of Marchantiales are clear-cut entities and each genus is unambiguously defined by a number of morphological features. This view has changed somewhat through recent molecular studies (Forrest et al 2006). According to the most recent classification of liverworts by Crandall-Stotler et al. 2009, the family Cleveaceae is placed in the class Marchantiopsida, subclass Marchantiidae, order Marchantiales. The current accepted classification of complex thalloid liverworts (Subclass Marchantiidae) within the liverworts (Phylum Marchantiopsida) is shown in Table 1.1.

Table 1.1 Classification of complex thalloid liverworts (Subclass Marchantiidae) within the liverworts (Class Marchantiopsida) (Crandall-Stotler et al. 2009).

Class	Subclass	Order	Family	Genus
Marchantiopsida	**Marchantiidae**	Sphaerocarpales	Sphaerocarpaceae	*Sphaerocarpos*
				Riella
				Geothallus
		Neohodgsoniales	Neohodgsoniaceae	*Neohodgsonia*
		Lunulariales	Lunulariaceae	*Lunularia*
		Marchantiales	Marchantiaceae	*Bucegia*
				Marchantia
				Preissia
			Aytoniaceae	*Asterella*
				Cryptomitrium
				Mannia
				Plagiochasma
				Reboulia
			Cleveaceae	***Athalamia***
				Sauteria
				Peltolepis
			Monosoleniaceae	*Monosolenium*
			Conocephalaceae	*Conocephalum*
			Cyathodiaceae	*Cyathodium*
			Exormothecaceae	*Aitchisoniella*
				Exormotheca
				Stephensoniella
			Corsiniaceae	*Corsinia*
				Cronisia
			Monocarpaceae	*Monocarpus*
			Oxymitraceae	*Oxymitra*
			Ricciaceae	*Riccia*
				Ricciocarpos
			Wiesnerellaceae	*Wiesnerella*
			Targioniaceae	*Targionia*
			Monocleaceae	*Monoclea*
			Dumortieraceae	*Dumortiera*

1.3 The Family Cleveaceae Cavers.

1.3.1 Introduction and General Morphology

Cleveaceae is a complex thalloid liverwort family in the phylum Marchantiophyta, class Marchantiopsida (Table 1.1). The family is well-defined morphologically by a combination of several morphological characters: presence of simple epidermal pores with thickened radial walls, ventral scales of the thallus with a single, tapering, ill-defined appendage, air chambers of the thallus without photosynthetic filaments, capsule wall with well-defined annular bands and the irregular dehiscence of the capsule wall (Fig. 1.3, A-E).

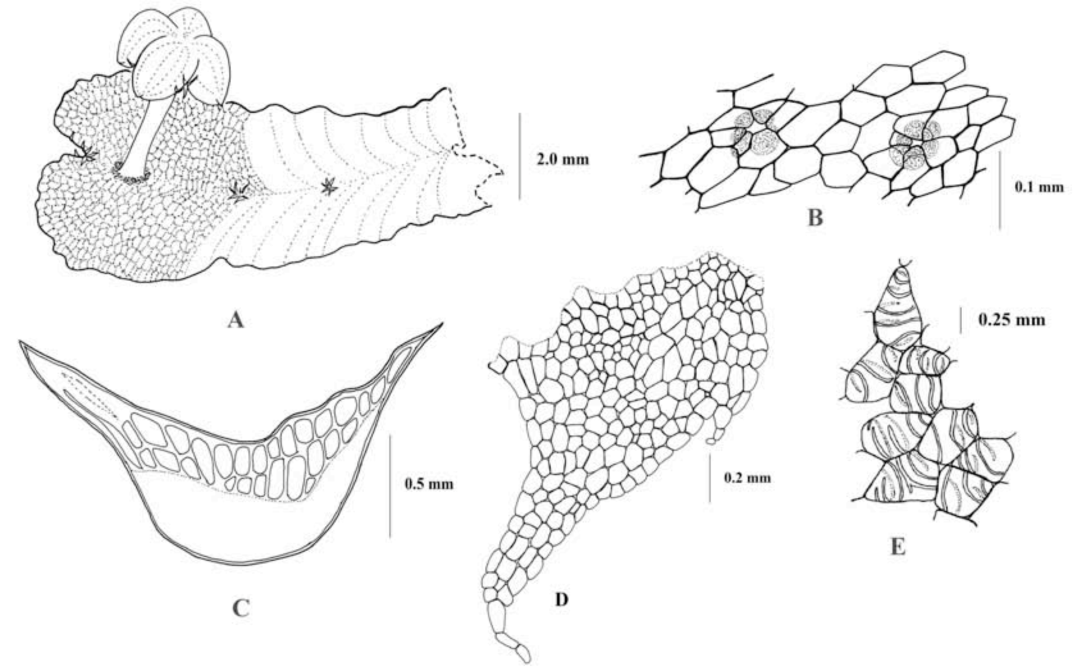


Figure 1.3. General morphology of Cleveaceae: (A) gametophytic thallus with a carpcephalum; (B) air pores; (C) transverse section of thallus; (D) ventral scales; (E) cells of sporophyte capsule wall with annular bands.

1.3.2 A taxonomic history of Cleveaceae

Our modern concept of Cleveaceae has its origins in Leitgeb's "Untersuchungen über die Lebermoose" (1881). His family Marchantiaceae encompassed what is now treated as the whole Order Marchantiales, and included three 'groups': Astroporae, Operculatae and Compositae. Leitgeb (1881) was the first to place the three genera *Clevea* Lindb., *Sauteria* (Nees) Nees and *Peltolepis* Lindb. together in a single 'Gruppe', Astroporae (also called Astroporenreihe). These three genera were originally described by different workers; *Clevea* (described by Lindberg, 1868), *Sauteria* (Nees 1838) and *Peltolepis* (Lindberg, 1876) and had not been assigned to a single group before Leitgeb (1881). However, Lindberg in his "Utredning af de under namen af *Sauteria alpina* sammanblandade former [Investigation of the mixed forms under the name *Sauteria alpina*]" (1877), dismantled the species that were erroneously named under the earlier described name *S.alpina* into the three genera; *Clevea* (*Marchantia hyalina* Sommerf. ≡ *Clevea hyalina* (Sommerf.) Lindb. = *Sauteria suecica* Lindb.), *Sauteria* (*Lunularia alpina* Nees ≡ *Sauteria alpina* (Nees) Nees = *Clevea hyalina* Lindb.) and *Peltolepis* (*Sauteria alpina* Lindb. non (Nees) Nees, *Sauteria grandis* Lindb. ≡ *Peltolepis grandis* Lindb. = *P. quadrata* (Saut.) Müll.Frib.). These three genera together formed Leitgeb's group Astroporae. The name Astroporae derives from the fact that the radial walls of the cells (arranged in a single ring) surrounding the thallus air-pores are normally strongly thickened, giving the pore a star-like appearance in surface view. This is still a key diagnostic character for Cleveaceae, which comprises the same three genera. However, Leitgeb also mentioned that the three genera are very similar in vegetative appearance.

Falconer (1848, 1851) described a new genus named *Athalamia* (from India) in Marchantiales. Although *Athalamia* was described before the group Astroporae, this genus was overlooked by many authors and was not assigned to Cleveaceae or any other group until quite recently (Shimizu & Hattori 1954).

The most detailed early classification of liverworts was that of Schiffner (1893). In his treatment of Marchantiaceae in the Engler and Prantl's "Die natürlichen Pflanzenfamilien” he divided the complex thalloid liverworts (Marchantiaceae) into two broad groups mainly based on presence and absence of a carpocephalum. He formed three sub-orders, Corsinioideae, Targionioideae and Marchantioideae, separating Marchantioideae from the rest due to the fact that they bear their sporogonia in stalked carpocephala (receptacles). His sub-order Marchantioideae included Leitgeb’s three ‘groups’: Astroporae, Operculatae and Compositae. According to Schiffner (1893) the group Astroporae included four genera: *Peltolepis*, *Sauteria*, *Clevea* and *Exormotheca*.

Conspectus of Astroporae (Cleveaceae) translated from Schiffner (1893)

A. Sporophytes united into stalked carpocephala ……..……III. Marchantioideae

a. Air pores simple, star-shaped due to strong radial thickening of walls of surrounding cells, air chambers without chlorophyll-rich filaments (like *Riccia*), or air pores not star-shaped, very large, the air chambers containing unbranched filaments and epidermis of each chamber pustule-shaped or conically raised; capsule always dehiscing by long longitudinal slits (mostly irregularly 4-lobed) ……………………...…III.1. Astroporae

α Upper side of the thallus not distinctly reticulate; air chambers without filaments

I. Stalk of carpocephalum with 2 rhizoid furrows ….5. *Peltolepis*

II. Stalkof capocephalum with 1 rhizoid furrow ……...6. *Sauteria*

III. Salk of capocephalum without rhizoid furrow ……...7. *Clevea*

β Upper side of the thallus distinctly reticulate. Each reticulation bearing a pustular or conical protuberances of the epidermis, which opens by a large, round air pore; air chambers with unbranched chlorophyll-rich filaments within ………………………………………………….…….8. *Exormotheca*

The genus *Exormotheca* was later removed from Cleveaceae and placed in a new family Exormothecaceae by Müller (1940). It differs from Cleveaceae in having 1) assimilation tissue with air chambers elevated and basally occupied by densely crowded, chlorophyllose filaments in one layer, 2) air pores surrounded by thin-walled cells, and 3) epidermis raised as conical protuberances over air chambers

(Grolle 1972; Perold 1999). Recent molecular studies support the exclusion of the genus from Cleveaceae (Forrest et al. 2006).

Following Schiffner's elaboration of Leitgeb's classification, other authors followed this system, although some re-named Astroporae: Solms-Laubach (1899) as the group Cleveideae, and Lotsy (1909) as subgroup Astroporen under the subfamily Clevieae.

Cavers (1910-1911), in his synthesis of bryophyte classification, described the new family Cleveaceae to replace Leitgeb's Astroporae and placed this on an equal rank with the other six families of Marchantiales recognized at that time (Ricciaceae, Corsiniaceae, Targioniaceae, Monocleaceae, Aytoniaceae and Marchantiaceae). He included the genus *Gollaniella* which was introduced by Stephani (1905) into the Cleveaceae. However, the genus *Gollaniella* was relatively short-lived and was finally synonymised under *Athalamia* by Kashyap (1929). Cavers noted that there is no doubt that the four genera (*Clevea*, *Sauteria*, *Peltolepis* and *Gollaniella* = *Athalamia*) formed a natural group.

Kashyap (1915), in his taxonomic studies on Western Himalayan liverworts, at first accepted Stephani's genus *Gollaniella*, but later (Kashyap 1929) placed it in synonymy of *Athalamia*. Since then *Gollaniella* has only briefly been recognized, by Shimizu & Hattori (1953). However, Kashyap (1916) also described a new related genus, *Sauchia*, which he considered to be closely allied to *Sauteria*. Verdoorn (1932) in his classification of liverworts returned to the use of Leitgeb's Astroporae which contained five genera, *Athalamia*, *Clevea*, *Sauteria*, *Peltolepis* and *Sauchia*.

A thorough review of the classification of Marchantiales was published by Evans (1923) in which he replaced Leitgeb's "Astroporae" with a new family Sauteriaceae including *Clevea*, *Sauteria* and *Peltolepis*; he made no reference to the earlier Cleveaceae of which Sauteriaceae later become a superfluous synonym, and essentially used the same characters as earlier authors to distinguish the three genera.

Conspectus of Sauteriaceae (Evans 1923)

Antheridia born in a more or less elongate and vaguely defined median group without paleae

Female receptacle becoming dorsal, the stalk without a rhizoid-furrow, the paleae with few or no slime-papillae ……………………… 1. *Clevea*

Female receptacle terminal, the stalk with one rhizoid furrow, the paleae with numerous slime-papillae ……………………..………. 2. *Sauteria*

Antheridia born on a definite sessile receptacle with marginal paleae; female receptacle terminal, the stalk with two rhizoid furrows ...……….……… 3. *Peltolepis*

Shimizu and Hattori (1953) returned to the correct use of Cleveaceae for the family; they also resurrected *Gollaniella* Steph. and described a new species *Gollaniella nana* in their "Marchantiales of Japan I"; however they added the comment that "we see no very good reason for generic division between *Athalamia* and *Clevea*" and they considered both genera, together with *Gollaniella*, to be very closely allied to each other. However, following Kashyap's (1915) detailed morphological description of *A. pinguis*, Shimizu and Hattori (1954) united the three genera, stating that they did not find any morphological characters of generic rank to keep them separated. However, for this genus they used the name *Athalamia* because it antedates *Clevea* by 17 years, so they were thus the first authors to relegate *Clevea* to the synonymy of *Athalamia*. They also reduced Kashyap's *Sauchia* to a synonym of *Sauteria*, noting that although it differed from *Sauteria* in having thin-walled cells around the air pores and in its delicate texture, they did not consider these differences sufficient to separate them as two genera. Consequently Shimizu and Hattori (1954) in the "Marchantiales of Japan II" recognized only three genera in Cleveaceae, *Athalamia*, *Sauteria* and *Peltolepis*, listing 15 species worldwide under *Athalamia*, 6 species under *Sauteria* and 2 under *Peltolepis*.

Up to the present day, subsequent authors have followed Shimizu & Hattori's treatment. For example, Müller (1954), in "Die Lebermoose Europas" in using the name Cleveaeae, commented that "Die ältere Familienbezeichnung Astroporae kann nicht etwa deshalb nicht bleiben, weil die Bezeichnung nicht für alle Gattungen zutrifft, wie vereinzelt angegeben wird, sondern, weil nach den Nomenklaturregeln die Familiennanmen nach dem Namen einer Gattung der betreffenden Familie gawählt werden sollen" [the older family name Astroporae cannot be used since the description does not hold for all the genera….and according to the rules of nomenclature the family named after the name of a genus of the family is to be chosen]. He separated the three genera by the key characters listed in Table 1.4, adding to those used by earlier authors.

Conspectus of the family Cleveaceae (translated from Müller 1954).

1. Thallus light green, with scattered oil-body cells in basal tissue and the ventral scales, those on the margins with slime papillae. Scales on the archegonial stalk ovate, with slime-papillae. Carpocephalum stalk with 1 rhizoid furrow. Spores-blackish brown .……..…………….……… *Sauteria*
2. Thallus green to reddish without oil-body cells.
   a) Stalk of the carpocephalum without rhizoid furrows, always in the middle of the upper surface of thallus. Scales of archegonial stalk narrow-lanceolate. Antheridia born along the thallus. Spores rust-red ………………………………………………………………..….. *Clevea*
   b) Stalk of the carpocephalum at apex of thallus with 2 rhizoid furrows. Scales around the archegonium stalk ovate, small. Antheridia in cushions in paroicous arrangement. Spores blackish-brown……………………..……………………………….....*Peltolepis*

Schuster (1958) also followed Müller (1954) and Shimizu & Hattori (1953, 1954) in recognising *Athalamia*, *Sauteria* and *Peltolepis*. He distinguished Cleveaceae from the rest of the Marchantialean families by the following characters: air-pores simple, stellate, the peripheral cells in 1 ring, with ± thickened radial walls; air chambers in several layers, the walls forming the chlorenchyma without chlorophyllose filaments; ventral scales with a single, tapering ill-defined appendage; archegoniophores conspicuously divided into (2–3) 4–7 deeply bilabiate involucres, each with a single archegonium; androecia (except in *Peltolepis*) of a series of loosely organized antheridia, each antheridium with a conspicuous elevated ostiole above it; capsule wall splitting irregularly, with well-defined annular bands; spores with coarse, contiguous papillae. Schuster (1992) in his later treatment of the family gave a more detailed key to the genera and maintained the union of *Gollaniella* and *Clevea* under *Athalamia*.

Udar (1958) in “Indian Sauteriaceae” supported reduction of *Clevea* and *Gollaniella* as synonyms of *Athalamia* and confirmed the synonymy of *Sauchia* under *Sauteria*. More recently, Udar (1960) in the “Studies in Indian Sauteriaceae II” discussed the nomenclatural tangles of the family and favoured retention of Evans’ (1923) Sauteriaceae stating that “it appears more appropriate to follow Sauteriaceae as proposed by Evans (1923) since Cleveaceae as a family name now typifies a genus no longer recognized”. This view is not acceptable under the rules and regulations of ICBN (Art. 11) where the correct name that must be adopted is the earliest legitimate one at the same rank. Sokhi and Mehra (1973), in a study on comparative embryology of *Athalamia pinguis* Falc. and *A. pusilla* (Steph.) Kashyap agreed with Udar (1958, 1960) and incorrectly adopted Sauteriaceae in their work. Grolle (1972, 1983) in his thorough treatments of nomenclature of families of Hepaticopsida, correctly accepted the name Cleveaceae as the valid family name.

A summary of the genera of the modern Cleveaceae recognized in publications over the past 130 years is given in Table 1.2.

Table 1.2. Genera of Cleveaceae recognized in publications over the past 130 years.

Author	Year	Name	Rank	Genera recognised
Leitgeb	1881	Astroporae	Group	*Clevea*, *Sauteria*, *Peltolepis*
Schiffner	1893	Astroporae	Group	*Clevea*, *Sauteria*, *Peltolepis*, *Exormotheca*
Solms-Laubach	1899	Cleveideae	Group	*Clevea*, *Sauteria*, *Peltolepis*
Lotsy	1909	Clevieae Astroporen	Subfamily Subgroup	*Athalamia*, *Sauteria*, *Peltolepis*
Cavers	1911	Cleveaceae	Family	*Clevea*, *Sauteria*, *Peltolepis*, *Gollaniella*
Kashyap	1915	Cleveaceae	Family	*Athalamia*, *Sauteria*, *Peltolepis*, *Sauchia*
Evans	1923	Sauteriaceae	Family	*Clevea*, *Sauteria*, *Peltolepis*
Verdoon	1932	Astroporae	Family	*Athalamia*, *Clevea*, *Sauteria*, *Peltolepis*, *Sauchia*
Shimizu & Hattori	1953	Cleveaceae	Family	*Athalamia*, *Clevea*, *Sauteria*, *Peltolepis*, *Gollaniella*
Shimizu & Hattori	1954	Cleveaceae	Family	*Athalamia*, *Sauteria*, *Peltolepis*
Müller	1954	Cleveaceae	Family	*Clevea*, *Sauteria*, *Peltolepis*
Schuster	1958	Cleveaceae	Family	*Athalamia*, *Sauteria*, *Peltolepis*
Udar	1958	Sauteriaceae	Family	*Athalamia*, *Sauteria*, *Peltolepis*
Schuster	1992	Cleveaceae	Family	*Athalamia*, *Sauteria*, *Peltolepis*
Crandall-Stotler	2009	Cleveaceae	Family	*Athalamia*, *Sauteria*, *Peltolepis*

1.3.3 Historical review of *Athalamia*, its synonyms and its species

The genus *Athalamia* was described in 1848 (Falconer, 1848, 1851) as a new genus of Marchantiales from India. He stated that it was a very distinct new genus, characterized by the absence of a common receptacle and the erect 'flowers'. Falconer further stated that it was most closely allied to *Lunularia*, in the dehiscence of the sporangium and elongated pedicel. The only species he included from North Western Himalayas of India (Mussoorie) was named as *A. pinguis* Falc. However, the name *Athalamia* was overlooked for many years and was first accepted as a genus by Shimizu & Hattori (1954).

At around the same time, Griffith (1849) described *Plagiochasma pedicellatum* Griff. from India, which was made into a new combination *Clevea pedicellatum* by Lindberg (1882). However, Shimizu & Hattori (1954), in their revision of Cleveaceae, placed it as a doubtful species. This species has still not been finally confirmed as a member of Cleveaceae.

In 1868 Lindberg, in *Musci novi Scandinavici*, created the new genus *Clevea* Lindb., in which he included one species, *Clevea hyalina* (Sommerf.) Lindb. This became the accepted name for the genus from 1868 until it was relegated to synonymy under *Athalamia* by Shimizu and Hattori (1954). However, the first description of the plant now known as *Athalamia hyalina* was given under the misapplied name *Marchantia cruciata* L. (now *Lunularia cruciata* (L.) Lindb.) by Sommerfelt (1826) in "Supplementum Florae Laponnicae". Sommerfelt's material came from Norway (Nordland) and he later (Sommerfelt 1833) realised his mistake and formally described the specimen as a new species *Marchantia hyalina* Sommerf. Lindberg's *Clevea hyalina* (1868) was based on Sommerfelt's *Marchantia hyalina*, which is therefore the basionym of *Athalamia hyalina*. Lindberg (1868) also included two other species he had earlier described as distinct species, *Clevea suecica* Lindb. and *Sauteria seriata* Lindb. as new synonyms of *C. hyalina*. Shimizu and Hattori (1954) much later added *Plagiochasma erythrosperum* Sull., *Sauteria limbata* Aust., *Fimbriaria nana* Lindenb. and *Grimaldia punicea* Wallr. (1840) as further synonyms under *Athalamia hyalina* (Sommerf.) S.Hatt. However, Lindberg (1868), mentioned that *Clevea* is different from *Athalamia* Falc. in having a porose thallus, erect receptacles with connate base, elongate seta, strong calyptra, etc. (“a quo diversa est *Athalamia* Falc., fronde eporosa, receptaculis propriis erectis et absi connatis, seta longa et elongate conica, calyptra magna, etc.”)

Leitgeb (1881) in his treatment on Marchantiales, did not mention *Athalamia* but continued with the name *Clevea*. Spruce (1884) added a new species to the genus, *Clevea andina* Spruce, from the Ecuadorean Andes. Stephani (1895) described *C. pulcherrima* from Ethiopia, *C. robusta* from Chile and *C. chinensis* from China (1906) as three new species. They were later combined as *Athalamia pulcherrima*, *Athalamia robusta* and *Athalamia chinensis* respectively by Shimizu and Hattori (1954). However, Bischler (2005) later synonymised *C. robusta* under *Athalamia andina* (Spruce) S.Hatt.

Schiffner (1893), in his classification of liverworts accepted *Clevea* Lindb. and placed *Athalamia* as a doubtful genus under Astroporae, but pointed out that it was doubtlessly related to *Clevea* and also noted within brackets that it could be identical with *Aytonia* (which is a synonym of *Plagiochasma* in Aytoniaceae). Cavers (1910-1911), while renaming the family Astroporae as Cleveaceae, ignored or overlooked the genus *Athalamia* and treated only *Clevea*. Kashyap (1915) recognized *Athalamia* in his work on Western Himalayan liverworts; he re-examined *A. pinguis* Falc. and agreed with Schiffner (1893) that it was very closely allied to *Clevea*. Kashyap (1916) described a second species, *Athalamia dioica*, from the Western Himalayas of India (Pangie).

Stephani (1917) described a new species *Clevea trabutiana* from Algeria. Earlier (Stephani 1905) he had described the new genus *Gollaniella*, containing one species *Gollaniella pusilla* Steph. which was later transferred to *Athalamia* by Kashyap (1929) as *Athalamia pusilla* (Steph.) Kashyap. A second species of *Gollaniella* was described by Shimizu and Hattori (1953) which was named *G. nana* Shimizu & S. Hatt. This combination lasted only one year, becoming *Athalamia nana* (Shimizu & S. Hatt.) S. Hatt. when *Clevea*, *Gollaniella* and *Athalamia* were united under the earliest validly published generic name *Athalamia* (Shimizu & Hattori 1954).

Herzog (1930) described a new species *Clevea handelii* from China (Yunnan) which was later combined as *Athalamia handelii* (Herz.) S.Hatt. in 1954. Müller (1940) transferred *Marchantia spathysii* Lindenb. (1829), described from Greece, to the genus *Clevea* as *C. spathysii* (Lindenb.) Müll.Frib.; subsequently Shimizu and Hattori (1954) re-combined it as *Athalamia spathysii* (Lindenb.) S. Hatt., including *Plagiochasma rousselianum* Mont. (1838) and *Clevea rousseliana* (Mont.) Leitgeb as synonyms. Trabut (1942) described another new Mediterranean species *Clevea crassa* from Algeria, but Müller (1954) remarked, "*Clevea crassa* Trabut (1942) aus dem algerischen Atlasgebirge unterscheidet sich von *C. hyalina* nur durch stärkere, herzförmige Verdickungen der Radialwände der Atemöffnungen nom. inval. = *A. hyalina*" (*Clevea crassa* Trabut (1942) from the Algerian Atlas Mountains differs from *C. hyalina* only by having stronger, heart-shaped thickenings of the radial walls of the air pores). The species is not validly published according to ICBN (Art. 36.1).

Shimizu and Hattori (1954) also described a new species from Japan, *Athalamia glauco-virens*. However, after several years of culture studies by Shimizu and Hattori on *A. nana* and *A. glauco-virens*, they confirmed that the two species are conspecific, considering *A. nana* to be a modification occurring in damp, shady sites and concluded that the differences between the two species are merely ecological (Hattori & Mizutani 1959). They also pointed out that this species is closely related to the Chinese *A. chinenis* and the Indian *A. pusilla* (Steph.) Kashyap.

All described species now treated under *Athalamia* and their type localities are listed in Table 1.3.

Table 1.3. Chronological table of *Athalamia* species and their type localities.

Basionym	**Year of publication**	**Type locality**
Marchantia hyalina Sommerf.	1826	Norway
Marchantia spathysii Lindenb.	1829	Greece
Plagiochasima pedicellatum Griff.	1847	India
Athalamia pinguis Falc.	1848	India
Clevea andina Spruce.	1884	Ecuador
Clevea pulcherrima Steph.	1895	Ethiopia
Clevea robusta Steph.	1898	Chile
Clevea chinensis Steph.	1906	China
Athalamia dioica Kashyap	1916	India
Clevea trabutiana Steph.	1917	Algeria
Gollaniella pusilla Steph.	1929	India
Clevea handelii Herzog.	1930	China
Gollaniella nana Shimizu & S. Hatt.	1954	Japan
Athalamia glauco-virens Shimizu & S. Hatt.	1954	Japan
Athalamia pygmaea R.M. Schust.	1985	U.S.A.

1.3.4 Historical review of *Sauteria,* its synonyms and its species

The genus *Sauteria* was created by Nees (1838) and was dedicated to A. Sauter (1800-1881), a medical doctor of Mittersill (Germany). Nees included one species *Sauteria alpina* (Nees) Nees, which he had earlier (1830) described as *Lunularia alpina* Nees. When he described *L. alpina* (1830), he noted that it shares similarities with *Marchantia spathysii* Lindb. which is now recognized as *Athalamia spathysii*. A year later, a second species was described in the genus by Montagne (1839); *Sauteria berteroana* Mont. from Chile. He found it distinct from *S. alpina* by the shape of ventral scales and the length of the capsule (Montagne 1839). However, Grolle (1985) created a new combination, *Sauteria chilenesis* (Lindenb. ex Mont.) Grolle based on *Grimaldia chilensis* Lindenb. ex Mont. (Montagne 1839), which itself had *Neesiella chilensis* (Lindenb. ex Mont.) Steph., *Sauteria berteroana* Mont. (Montagne, 1839) and *Grimaldia debilis* Bisch. ex Gottsche (Gottsche et al. 1844) as synonyms. He noted that the name *S. berteroana* Mont. is an invalid name (Art. 34.1).

Kashyap (1916) described a new genus *Sauchia*, represented by single species *Sauchia spongiosa*, endemic to the Himalayas. The genus was named after the Sauch Pass where it was found. He considered the plant to be connecting link between the Astroporae of Leitgeb and the '*Exormotheca* line'. The species was originally described from scanty material. However, the same author, after collecting more material in 1928, was able to expand the original description (Kashyap 1929). Comparing *Sauchia* with its ally *Sauteria*, Kashyap remarked that the former differed in having thin-walled cells around the pores, and in its more delicate texture. A second species of *Sauchia, S. japonica,* was described from Japan by Shimizu and Hattori (1953), who stated that "*Sauchia* seems to be very closely related to *Sauteria*." After careful examination of a specimen of *Sauteria alpina,* the same authors concluded that there were no characters of generic value to keep them separated and that they represented one and the same natural taxon, the genus *Sauteria*. The species were thus combined as *Sauteria spongiosa* (Kashyap) S.Hatt. and *S. japonica* (Shimizu & S.Hatt.) S.Hatt. (Shimizu & Hattori 1954).

A new variety *japonica* of *Sauteria alpina* was described by Shimizu and Hattori (1954). They noted that the Japanese form is distinct from the European type in the nature of the female receptacle and thickening of radial walls of the cells around the pores. Later, after discovering *S. alpina* on the island of Rishiri in Japan, and with careful examination with the local variety (var. *japonica*) Shimizu (1955) decided it is no longer merely a variety of *S. alpina* but a distinct species. The new species was named *Sauteria yatsuensis* S. Hatt. He also mentioned that this species was more closely related to *S. spongiosa*.

Austin (1869) described *Sauteria crassipes* Aust. as a new species in *Sauteria*. In his original description he noted, "I have doubtfully referred this species to *Sauteria*. It resembles *Preissia* very much, - also, in some respects, *Duvalia* [=

Mannia].” The specimen he examined was from Japan, and was too immature to give a complete description of the sporophyte. The species has not been re-examined or collected since Austin’s original diagnosis, and unfortunately the original specimen cannot be located. Stephani remarked, “Dies Pflanze liegt in keinem öffentlichen Herbar Americas oder Europas und scheint ganz verloren gegangen zu sein; nach der nichtssagenden Diagnose des Autors, die ich oben übersetzt habe, dürfte sie kaum wieder zu erkennen sein” (This plant is not located in any public herbarium in Americas or Europe and seems to have been lost entirely, but after the meaningless diagnosis of the author, which I have already translated, it can scarcely be known) (Stephani 1900).

Perold (2003) described a new species from Malawi, Nyika National Park named *Sauteria nyikaensis* Perold. However, the species was described from scanty material and the author did not observe androecia. All described *Sauteria* species and their type localities are given in Table 1.4.

Table 1.4. Chronological table of *Sauteria* species and their type localities.

Basionym	**Year of publication**	**Type locality**
Lunularia alpina Nees	1830	Slovania
Grimaldia chilensis Lindenb. ex Mont.	1839	Chile
Sauteria crassipes Aust.	1869	Japan
Sauchia spongiosa Kashyap	1916	India
Sauchia japonica Shimizu & S. Hatt.	1953	Japan
Sauteria alpina var. *japonica* Shimizu & S. Hatt.	1954	Japan
Sauteria nyikaensis Perold.	2003	Malawi

1.3.5 Historical review of *Peltolepis*, its synonyms and its species

The genus *Peltolepis* was first described by Lindberg (1876), his first publications appeared in daily news papers (Morgonbladet – Helsingfors, 1875-1876a; Helsingfors Dagblad 1875-1876b) and briefly in Bot. Notiser (1876). Lindberg (1875), while examining specimens of *S. alpina*, from Saltdalen (Norway), realised the specimens were mixed with another species, and named it *Sauteria grandis* Lindb. Later (1876) he realized that this species belonged to a different genus and named it *Peltolepis grandis* Lindb. Later (1877) he included *Sauteria alpina* (non Nees) Lindb. as a synonym. Müller (1940) described a new species, *Peltolepis quadrata* (Saut.) Müll. Frib. based on *Sauteria quadrata* Saut. described by Sauter from Asutria (1860) and included *P. grandis* Lindb. as a synonym.

Shimizu and Hattori (1954) described a new variety *japonica* Shimizu & S. Hatt. of *P. quadrata*, from Japan. They described the new variety as a local species representing the European type in the Far East. Later Hattori (in Hattori & Shimizu 1955), elevated it to species level *Peltolepis japonica* (Shimizu & S.Hatt.) S.Hatt. considering its small size, not so firm texture, shape of ventral scales, larger spores, flattened receptacle lacking air pores and the chromosome number as distinct features. Schuster (1992) included *Sauteria* auct. (before 1876) as a synonym under the genus *Peltolepis*. Bischler (1998) in her treatment of Marchantiales removed *Peltolepis* from Cleveaceae and on her evidence (from a morphological cladistic study, see Chapter 3) incorrectly classified *Peltolepis* under the family Monosoleniaceae by Grolle and Long (2000); this transfer was shown to be erroneous by Forrest et al. (2006) who confirmed its placement within Cleveaceae. In this study *Peltolepis* resolved remote from *Monosolenium*, the type genus of Monosoleniaceae. The species of *Peltolepis* and their type localities are given in Table 1.5.

Table 1.5. Chronological table of *Peltolepis* species and their type localities.

Basionym	Year of publication	Type locality
Sauteria quadrata Saut.	1860	Austria
Sauteria grandis Lindb.	1875	Norway
Peltolepis quadrata var. *japonica* Shimizu & S.Hatt.	1954	Japan

1.3.6 Geographical distribution of Cleveaceae

All three genera of Cleveaceaeare are widely distributed in warm temperate to arctic regions throughout the Northern Hemisphere. However in the southern hemisphere Cleveaceae is much rarer, *Peltolepis* is absent and *Athalamia* and *Sauteria* are both represented by 1 or 2 species in the Andes and the African mountains. Some taxa e.g. *Athalamia hyalina*, have a amphizonal distribution. *Peltolepis* shows the most sporadic distribution pattern in the family, mainly circumboreal. *Sauteria* shows a similar pattern of distribution as *Athalamia*. The general distribution of the family is illustrated in Figs. 1.4, 1.5 and 1.6.

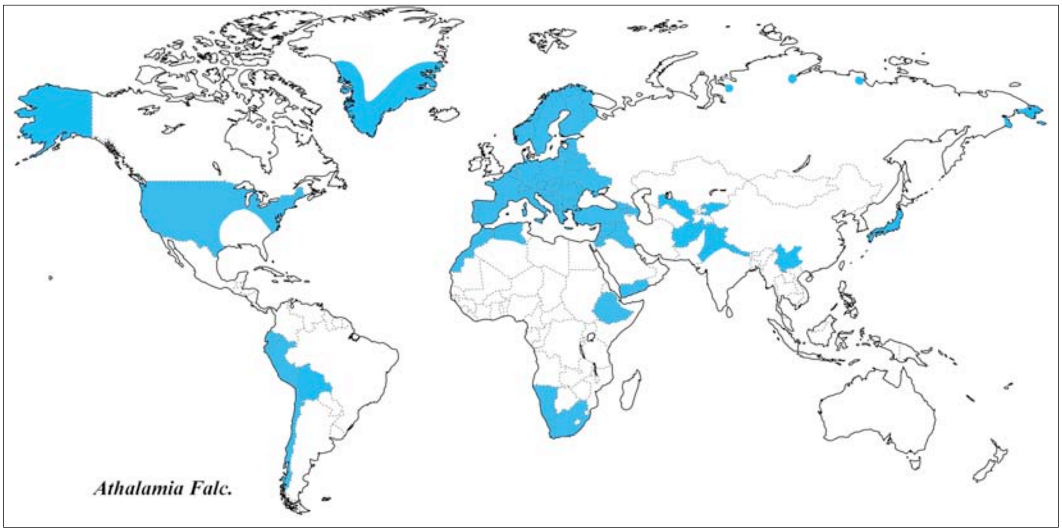


Figure 1.4. Geographical distribution of *Athalamia* Falc. (Adapted from Bischler 1998).

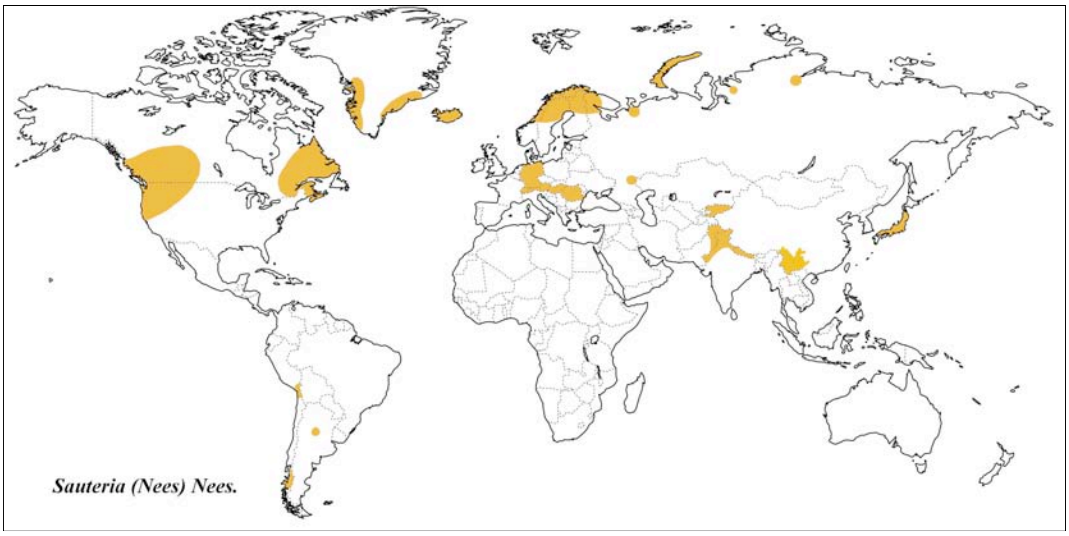


Figure 1.5. Geographical distribution of *Sauteria* (Nees) Nees. (Adapted from Bischler 1998).

Figure 1.6. Geographical distribution of *Peltolepis* Lindb. (Adapted from Bischler 1998).

1.4 Objectives of the study

As described above the family Cleveaceae is distinct from other families of complex thalloid liverworts by a combination of morphological characters and also it is well-supported as a monophyletic group in molecular studies. However, since the inception of the family (as Astroporae) by Leitgeb (1881), the number and names of genera within the family have changed over the past 130 years. Recently the family has become relatively stable, with three genera *Athalamia*, *Sauteria* and *Peltolepis* accepted (Crandall-Stotler et al. 2008, 2009; Damsholt 2002; Grolle 1983; Koponen et al. 1977; Schuster 1958, 1984, 1992; Schljakov 1981; Shimizu & Hattori 1954, 1955) (Table 1.2). Species numbers in the three genera of Cleveaceae are uncertain; Bischler estimated *Athalamia* to have 12-15 species, *Sauteria* 5 and *Peltolepis* 1 or 2.

The main character commonly used by many authors to distinguish the three long accepted genera of Cleveaceae is the rhizoid furrow number in the carpocephalum stalk (Damsholt 2002; Evans 1929; Müller 1954; Schiffner 1893; Schuster 1992). No world revision of Cleveaceae has been published since Stephani (1898 – 1900) although many of the species were reviewed by Shimizu & Hattori (1953, 1954, 1955, 1959). There is no established classification for genera and species of Cleveaceae, which make the identification of genera and species difficult. Many local endemics have been described, which may not be distinct. The phylogenetic relationships within Cleveaceae have yet to be studied.

Therefore, the aims of the present study were to:

1. Review the taxonomic and nomenclatural history of Cleveaceae and its genera (Chapter 1)
2. Review morphological characters of Cleveaceae and its genera (Chapter 2)
3. Construct a phylogeny for Cleveaceae and test the current three-genus subdivision of the family (Chapter 3)
4. Carry out an alpha-taxonomic revision of the family (Chapter 4)
5. Discussion and conclusions about the main phylogenetic and taxonomic findings of the research and suggestions for future work (Chapter 5)

CHAPTER-2-MORPHOLOGICAL CHARACTERS OF CLEVEACEAE

2.1 Morphological characters in taxonomy

Morphological characters are features of external form or appearance of a plant which traditionally provide most of the characters essential for plant identification, description, classification and for hypothesizing phylogenetic relationships. These features have been used for a much longer time than molecular evidence, and have constituted the primary source of taxonomic evidence since the beginnings of plant systematics (Judd et al. 2002; Stuessy 2009). Morphological characters are still the most popular ones used in plant taxonomic studies, and they play a major role in taxonomic keys, Floras and also in field identification. Although molecular data are very important tools in inferring evolutionary relationships among organisms, morphological data still provide the foundation for most of the classification systems today and will probably continue to be the main discriminatory feature for both the identification and grouping of plants. This is mainly due to the fact that they are readily recognizable by eye and easily described. Usually in the field, a trained botanist with access to appropriate literature and a hand lens can identify a plant (including bryophytes) in part or completely to family, genus and species by examining its external morphology.

Micheli’s (1729) *Nova Plantarum Genera juxta Tournefortii Methodum Disposita* and Dillenius’s (1741) *Historia Muscorum* mark the first most important detailed taxonomic works on liverworts (in Long 2006) but no member of Cleveaceae was known to those workers. The first species described of what is now Cleveaceae was Sommerfelt’s (1833) *Marchantia hyalina* (later *Clevea hyalina*). However, the first detailed morphological study of Cleveaceae was by Leitgeb (1881), who first united the three genera *Clevea*, *Sauteria* and *Peltolepis* under a single group; Astroporae. Although a few other morphological studies of Cleveaceae have been carried out since then (Arnell 1963; Bergdolt 1926; Schiffner 1893; Schuster 1992; Shimizu & Hattori 1953, 1954, 1955; Sokhi & Mehra 1973) they were based on a limited number of species and samples, focusing on a few characters related to carpocephalum stalk, position of archegoniophore, radial wall thickening of air pores and number of air chamber layers in the assimilatory tissue. No world revision of Cleveaceae has been published since Stephani (1898-1900). Although many species were reviewed by Shimizu and Hattori (1954), they mainly focused on synonymising *Clevea* under *Athalamia*, no morphological studies on these species were carried out, except for their newly described Japanese species.

2.2 Objectives

The main objective of Chapter 2 is to explore all morphological characters in the described species and genera of Cleveaceae from all over the world. This morphological survey will be used for the study of character evolution in Chapter 3 and to support the taxonomic revision of the family undertaken in Chapter 4.

2.3 Materials and methods

2.3.1 Materials

Herbarium material of all described species as well as fresh material collected on field excursions during the study (Appendix, 2.1) was used to study the morphological and anatomical characters.

Herbarium material. Herbarium specimens of Cleveaceae were requested on loan from many major herbaria around the world. A list of the chosen herbaria and the number of specimens of received is given in Chapter 4, Table 4.1.

Fresh material. Collection of fresh material was very important for the study of ecology and habitat preferences of the species. Herbarium specimens of liverworts are not always easy to work with; they lose some important characters such as oil cells, colour and smell with time. Variation in size cannot easily be measured except in the field and also photographs of living material can play an important role in taxonomic studies. Localities for fieldwork were chosen from the literature, annotations on herbarium specimens, online databases and advice from personal contacts. Details of specimens collected during field excursions are given in Appendix 2.1.

Spores. Spore material was obtained from mature dehisced capsules from dried herbarium material. Spores from almost all the described species, including some type specimens, were included in the study.

2.3.2 Methods of observation

2.3.2.1 Herbarium material

Herbarium specimens were soaked in water before observation. Length of soaking depended on the age of the material; older specimens took a longer time. The moist specimen was dissected using fine forceps and a needle. Transverse sections of thalli were prepared manually using a razor blade and a freezing microtome was used where necessary. Epidermal peels were removed with fine forceps or with a needle. Rhizoids and ventral scales were removed with a pair of fine forceps for microscopic study. Preparations were normally mounted in water on a microscope slide. For anatomical drawings and photographic studies, slides were mounted with glycerine, covered with a cover-slip and sealed with nail varnish.

2.3.2.2 Fresh material

Field notes were prepared on texture, colour and odour of all the collected material. Specimens were collected using a knife and placed in paper packets. Soil was removed before packing the sample. Notes on substrate, ecology and vegetation were recorded. Each specimen collected was given a reference number. Longitude and latitude data were recorded using a Garmin 12XL Global Positioning System navigator (GPS). Photographs were taken using a Nikon COOLPIX 995 digital camera in the field. Voucher specimens for the living collections were air-dried followed by deep-freezing at -30ºC for three to five days to prevent infestation and then could be taken into the herbarium for study.

All specimens available (both herbarium and fresh) were initially observed using a stereo dissecting microscope with long arm stand (Leica MZ8). Observations of detailed cellular characters were made using a Zeiss Standard 20 compound microscope. Since the gametophytes of most taxa in Cleveaceae are extremely delicate, some fine structures like air-pores and air chambers were observed under the Scanning Electron Microscope (SEM) using the variable pressure technique. Cellular measurements were made using the Carl Zeiss Axiovision system, version 4.8).

2.3.2.3 Spore material

Spores from mature dehisced capsules, selected under a stereo microscope, were transferred onto 12 mm carbon discs mounted on 12.5 mm aluminium pin stubs using fine forceps and a fine moistened brush. Spore colour was recorded for each specimen observed. The prepared stubs were then placed in the chamber of a K575x sputter coater (Emitech). The chamber was then vacuumed and after reaching the High vacuum status, argon gas was sprayed at $2x10^{-2}$ mbar for 20 seconds. The specimens were then coated with gold palladium at a deposition of 12 nm with a rate of 25 mA for 1 minute. The stubs were then observed under a LEO Supra 55VP digital scanning electron microscope. Suitable spores were selected under low magnification and then observed under higher magnification with a working distance between 5 and 9 mm and a scanning voltage (EHT) of 5kV. Scanning was done at 1024 x 768 resolution with ‘pixel average noise reduction’, once the focusing was adjusted. Images were printed out for measurement of spores.

2.4 Morphological and anatomical characters of Cleveaceae

The characters observed in Cleveaceae are grouped into three categories; vegetative, reproductive and sporophyte characters. Photographs and illustrations are presented where possible.

2.4.1 Vegetative characters

Thallus: Gametophytic plants of Cleveaceae are thalloid, dorsiventral in structure, and in section show three main regions; a dorsal epidermis, an assimilatory region with a series of air chambers beneath which is a basal storage region bounded by a ventral epidermis which bears ventral scales and rhizoids (Fig. 2.1).

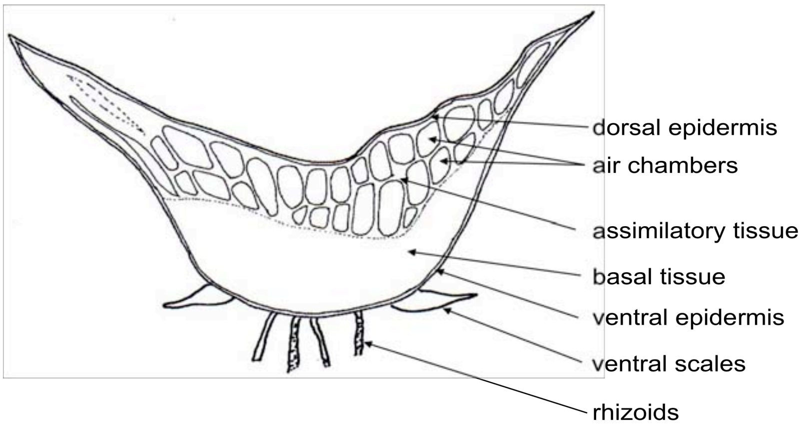


Figure 2.1. Schematic diagram of t.s. of gametophytic thallus of Cleveaceae.

Plants are small to medium in size; 2−15 mm long, 1−10 mm wide. They form close, tightly packed mats or loose spreading mats covering a considerable area of substrate. Thalli are normally linear or lingulate (tongue-shaped) to obovate (broadened towards the apex) in shape (Fig. 2.2). In general, plants are fragile and delicate, particularly *Sauteria* having extremely delicate thalli but *Athalamia pinguis* having firmer, thick and fleshy thalli.

Colour of the thallus varies from dark or light green, to yellowish or whitish green. Most species develop a purple tinge towards the margins which can extend onto the dorsal surface of the thallus with age. However, *Clevea spathysii* (syn. *Athalamia spathysii*, See Chapter 4) develops a characteristic blackish purple colour in its margin and ventral scales whereas *Sauteria* does not show any trace of purple coloration in its light translucent greenish to yellowish thalli (Fig. 2.2).

In most species, the upper surface of the thallus is slightly concave along the mid-line, although a clear midrib cannot be observed from above. However, the thallus is sometimes almost flat. Margins of the thallus in Cleveaceae are normally undulating but in a few species such as *C. spathysii* and *C. pusilla* the margin is not or only very slightly undulating. However, upon drying, margins roll up inwards, exposing the ventral scales.

Vegetative branching: The most commonly observed branching in Cleveaceae is by terminal dichotomies where the thallus divides into two branches at its apex. These branches can be either symmetrical or asymmetrical. However, vegetative branches arising from ventral innovations can be observed in some species. These ventral branches are normally smaller in size and obovate in shape. Similar reduced ventral branches bearing antheridia occur in some species (see below).

Dorsal epidermis and air pores: The dorsal surface of the thallus is usually marked with shallow spreading grooves marking polygonal areas, which are visible to the naked eye (Fig.2.2.). These polygonal markings correspond to the underlying air chambers. Each polygon contains a slightly raised (or sometimes not raised) air pore at the middle. However, these markings are difficult to detect without a hand lens in fleshy thallii. The dorsal epidermis is composed of thin- or thick-walled, often polygonal shaped cells, sometimes with trigones (triangular thickenings) in the angles (Fig. 2.3). Oil cells are rarely found scattered in the dorsal epidermis.

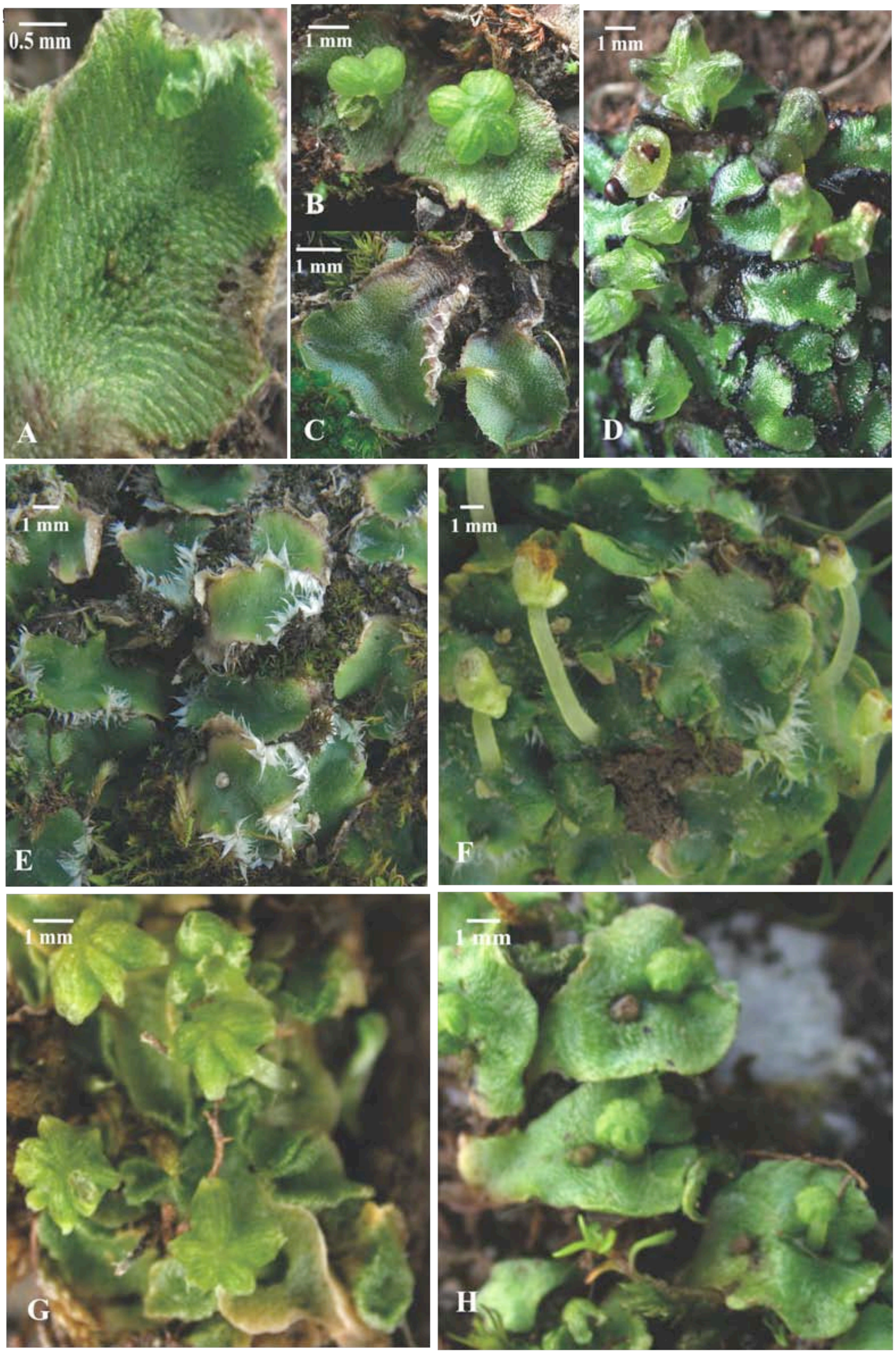


Figure 2.2. Morphology of Cleveaceae I. A) Dorsal surface with shallow spreading grooves (*C.hyalina* 02-08SR, Switzerland-E); B) lingulate shaped thalli with umbrella-shaped carpocephala (*C.hyalina* 02-08SR, Switzerland-E); C) Male plants with closely aggregated androecia (*C hyalina* Long 39966, China-E); D) cup-shaped carpocephala with upturned lobes, sporophytes and blackish purple margins of thalli (*C. spathysii* 08-09SR, Spain -E); E, F) large white ventral scales protruding along margins and cup-shaped carpocephala (*A.pinguis* Long 40305, China-E); G) Yellowish-green thalli lacking purple colouration with umbrella shaped carpocephala (*S.alpina* 10-08SR, Switzerland-E); H) obovate thalli with antheridia arranged into discs (*P.quadrata* 07-08SR, Switzerland-E).

Air pores, which connect the underlying air chambers with the external atmosphere, are ‘simple’ in Cleveaceae. In some species they are slightly elevated above the dorsal epidermis. These air pores are surrounded by a single row of 4–7 cells. In most cases, the radial walls of the surrounding cells are thickened and have a star-like appearance under the compound microscope (Fig. 2.4). However, radial wall thickening was found to vary from slight to strong within the same species and in some species like *C. spathysii*, *C. pusilla* and *S. spongiosa* radial wall thickenings are either absent or very slight and not stellate. In the latter case these air pore surrounding cells look very similar to normal epidermal cells (Fig. 2.4).

Assimilatory tissue: The assimilatory tissue in Cleveaceae consists of 1 to 3 layers of air chambers which lack photosynthetic filaments (Fig. 2.3). However, near gametangia only a single layer of chambers is observed. Air chambers are normally wide and polygonal in shape, except in *Athalamia pinguis* where they are narrow and slit-like (Fig. 2.3, D). Thickness of the assimilatory tissue varies within species. The air chambers can be tightly packed or loose, sometimes taking up most of the internal space of the thallus making it spongy as in *Sauteria spongiosa* (Fig. 2.3, E).

Basal tissue and midrib: The basal tissue, found between the assimilatory tissue and the ventral epidermis, is whitish to colourless and composed of spherical to polygonal shaped thin-walled cells. Oil cells are rarely found scattered in the basal tissue. Thickness of the basal tissue varies considerably; it can be thinner, subequal to or thicker than the assimilatory tissue (Fig. 2.3).

The ventral epidermis is usually made up of a single layer of spherical to polygonal, thin- or thick-walled cells and is normally brownish in colour. However, sometimes the ventral epidermis is not well-differentiated from the basal tissue. In most species, the midrib region is slightly visible viewed from below and it gradually passes into the thallus wings. However in *A. pinguis*, the midrib strongly protrudes and is conspicuous from below and it rather suddenly passes into the wings on either side.

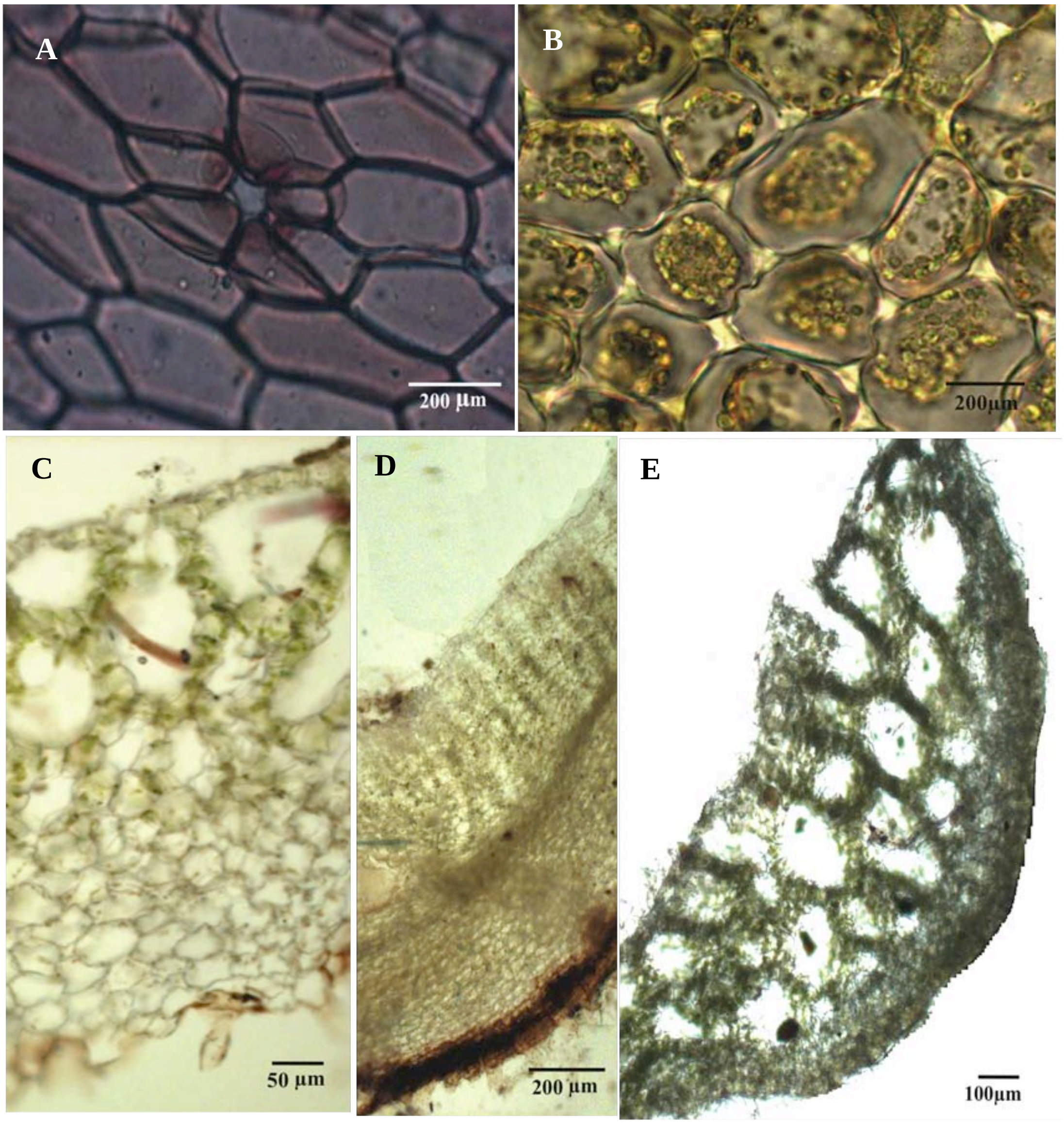


Figure 2.3. Morphology of Cleveaceae II. A) polygonal epidermal cells and an air pore (*C. hyalina* 01-07SR, Scotland-E); B) Epidermal cells with trigones at corners (*C. spathysii*, 06-09SR, Spain-E); C) polygonal shaped air chambers and hyaline basal tissue (*C. pusilla*, Chopra, 24, India-JE); D) Narrow slit-like air chambers (*A. pinguis*, Higuchi 19772, Pakistan-TNS); E) Wide assimilatory tissue taking up most of the space of the thallus (*S. spongiosa* Long 30427, Nepal-E).

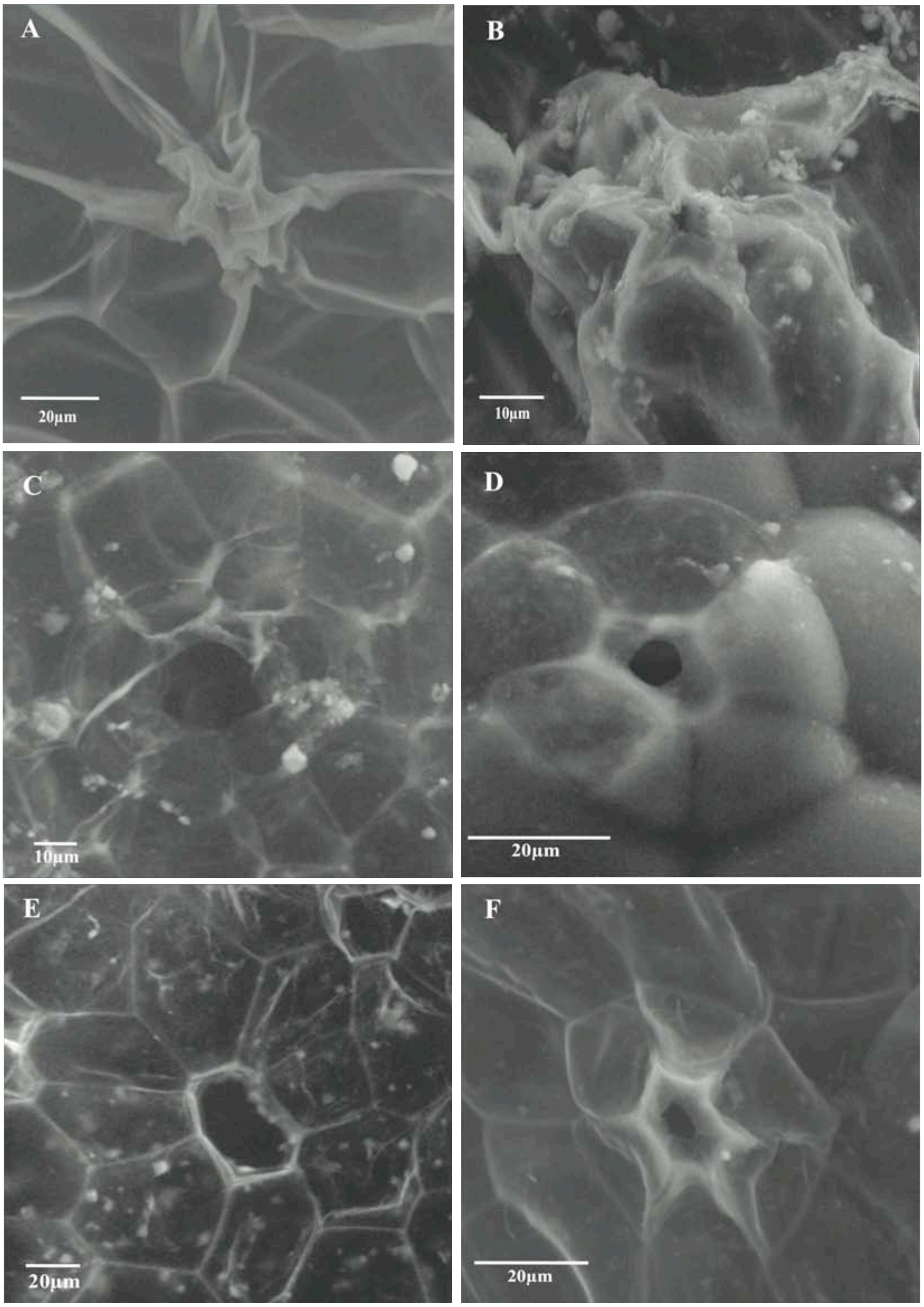


Figure 2.4. Air-pores of Cleveaceae. A, B, F) air pores with strongly thickened radial walls (A-*C. hyalina*, 01-07SR, Scotland-E; B-*A. pinguis*, Higuchi,-TNS; F-*P. quadrata*, 07-08SR, Switzerland-E); C, D, E) air pores lacking radial wall thickenings (C-*A. pusilla*, Chopra, 8054, India-W; D-*C. spathysii*, SR03-09, Spain-E; E- *S. alpina*, SR12-08, Switzerland-E).

Ventral scales: Liverworts lack specialised tissues for water conduction (Bischler & Jovet-Ast 1981). In complex thalloids liverworts, water uptake is believed to be by means of capillary action amongst ventral scales and rhizoids (Bischler & Jovet-Ast 1981). It has been hypothesized that ventral scales may have evolved from slime papillae as an adaptation to protect the apical dividing cell from desiccation (Schuster 1992). In many complex thalloid liverworts, ventral scales consists of a body and 1-3 appendages. However, in Cleveaceae the scales are usually lanceolate to ovate in shape with an appendage which is not well-differentiated (Fig. 2.5). They are one cell thick and the cells are usually uniform in size and shape in the body and appendage area. In most species, ventral scale cells are polygonal and thin walled. However, in *A. pinguis* and *C. spathysii*, ventral scale cells are rectangular in shape and thick-walled (Fig. 2.5).

Ventral scales usually bear slime papillae on their margins; these are mucilage producing cells, which are thought to provide added protection from damage and desiccation (Renzaglia et al. 2000; Crum, 2001). They are sessile and found on the margin of the ventral scales (Fig. 2.5). However, in *C. spathysii*, *C. pusilla* and *A. pinguis* slime papillae are mostly lacking from the ventral scales (or rarely up to 2).

Oil bodies, or membrane bound distinctive bodies, were observed in ventral scales of some species (Fig. 2.5). These oil bodies occur singly in specialised cells which are scattered in the ventral scale. Oil body containing cells can be smaller than or the same size as the surrounding cells. They are isodiametric and mostly found in the body of the scale. However, in *C. hyalina*, *A. pinguis* and *P. quadrata* ventral scale oil bodies are absent. These oil bodies are thought to contain ethereal oils, and produce distinct types of odour. However, a distinctive smell was not evident in any species within the family.

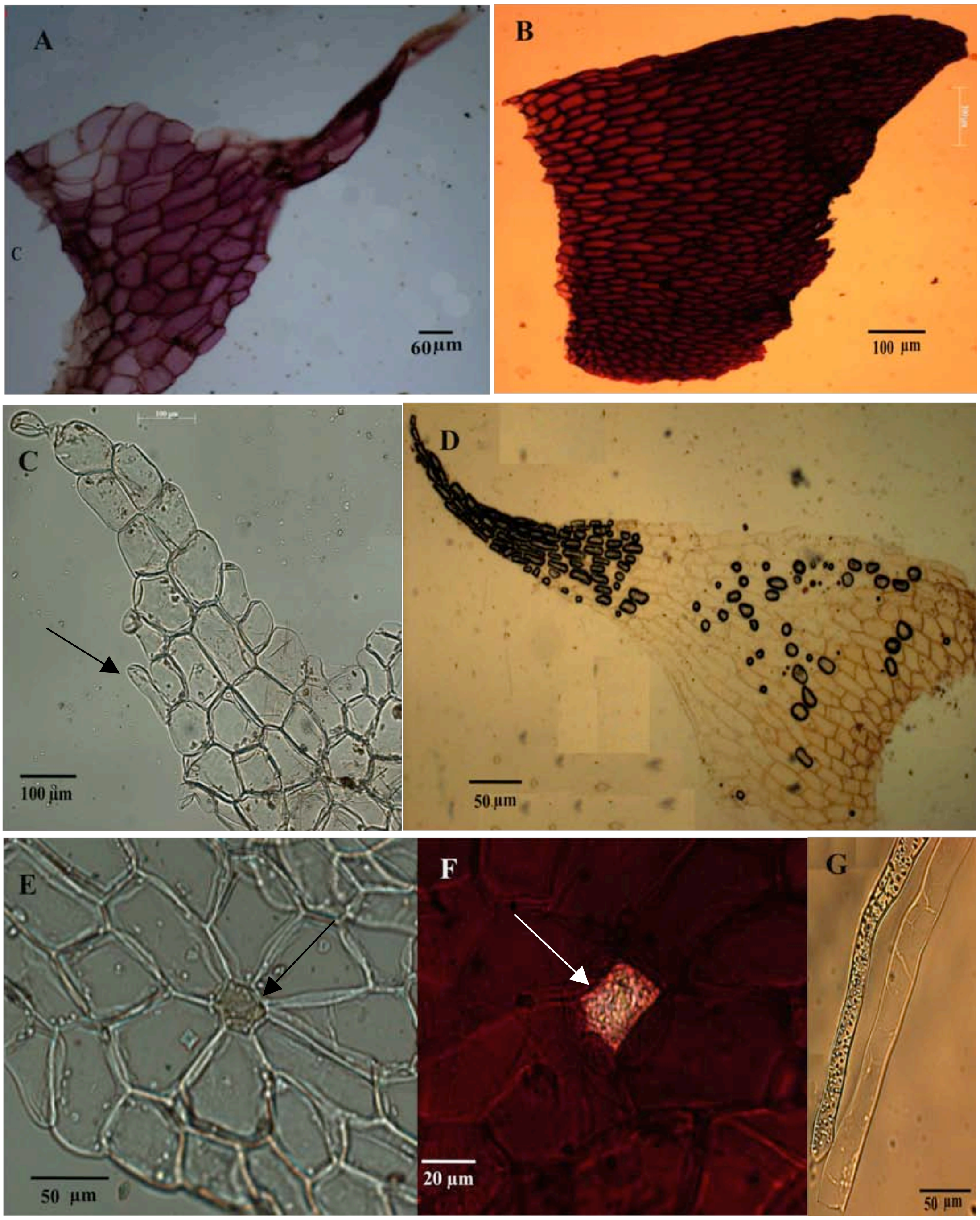


Figure. 2.5. Ventral scale morphology in Cleveaceae. A) purplish hyaline, lanceolate scale with polygonal shaped cells and ill defined appendage (*C. hyalina,* 01-07SR, Scotland-E); B) blackish purple, ovate shaped ventral scale with rectangular shaped cells (*C. spathysii*, Volk 861, Namibia-JE); C) silvery white scales with slime papillae on margins (*S. spongiosa,* Katagiri 1173, Japan-HIRO); D) large, hyaline, lanceolate scale with rectangular shaped cells (*A. pinguis*, Higuchi 19772, Pakistan-TNS); E,F) Oil bodies (E-*S. alpina*, Breidler *s.n.*, Austria-W; F-*C. spathysii* Volk 861, Namibia-JE); G) smooth & pegged rhizoids (*S. alpina*, Breidler *s.n.*, Austria-W).

Ventral scales in Cleveaceae are mostly hyaline, tinged purplish in colour. This purplish coloration is believed to be due to anthocyanin production in the cells, as a response to exposure to high light intensities. It is thought they may protect the ventral epidermis from drying out (Schuster 1992). However, in some species of Cleveaceae, they were silvery white in colour and no purple pigmentation was observed even when growing under high light intensities. In *Clevea spathysii*, scales develop a characteristic blackish-purple colour even when growing in shady conditions (Fig. 2.5).

In most liverwort taxa, ventral scales are arranged in 2 or more distinct rows which may have evolved from a 1-ranked condition (Crum 2001; Schuster 1992). In Cleveaceae, ventral scale arrangement is of two distinct types: scales arranged in 2-4 distinct rows on either side of the midrib region, or arranged in ill-defined longitudinal rows on the midrib region. When in distinct rows, they are normally dense and overlapping, and in most species in addition to these main rows, an additional band of smaller scales was found scattered on the midrib region (Fig. 2.6).

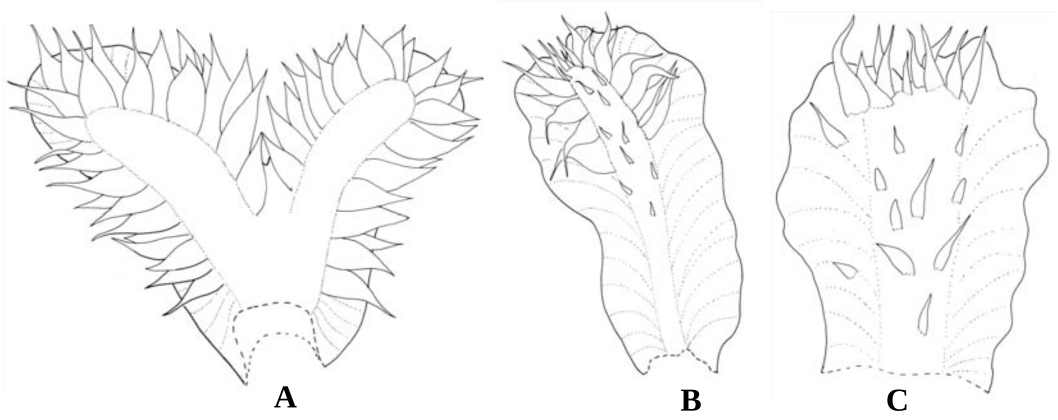


Figure 2.6. Ventral scale arrangements in Cleveaceae. A) in distinctly arranged rows alongside the midrib region; B) in distinctly arranged rows alongside the midrib region with a second type of smaller scales on the midrib region; C) in ill-defined rows on the midrib region.

Ventral scale protrusion (i.e. the amount scales protrude when observed from above) varied within species of Cleveaceae. In *Sauteria* and *Peltolepis*, protrusion was observed only at the thallus apex (Fig. 2.2, G & H) or scales were barely visible from above. In *Clevea* and *Athalamia* species ventral scales protrude conspicuously near the apical thallus region (Fig. 2.2, C & D). An extreme condition of ventral scale protrusion was shown in *A. pinguis*, with its large white scales projecting beyond the thallus margin along a considerable length of the thallus (Fig. 2.2, E).

Rhizoids: A large number of rhizoids are scattered on the ventral thallus surface, arising from the ventral epidermal cells along the midrib region. Both pegged and smooth rhizoids are found in Cleveaceae. Rhizoids are normally hyaline or can be brownish towards the base (Fig. 2.5, G).

2.4.2 Reproductive characters of the gametophyte

Sexual condition: The sexual condition in most species of Cleveaceae is autoicous: both archegonia and antheridia born on the same plant. The only dioicous species is *Clevea hyalina*, in which archegonia and antheridia are always borne on separate plants. Here the male plants were found to be slightly smaller than the female plants, displaying weak sexual dimorphism. Three different spatial relationships of antheridia and archegonia were observed in autoicous plants (Fig. 2.7), exactly as described for *Asterella* by Long (2006): (a) par-autoicous, antheridia born immediately proximal to the base of the archegoniophore, (b) terminal-autoicous: antheridia and archegonia born on different terminal branches of the same plant and (c) ventral-autoicous: androecia born on a reduced ventral branch. The dioicous condition is hypothesized to be the primitive sexual condition in liverworts with an evolutionary trend to have gametes borne more close together where the sexual reproduction is more easily accomplished (Crum 2001; Schuster 1992).

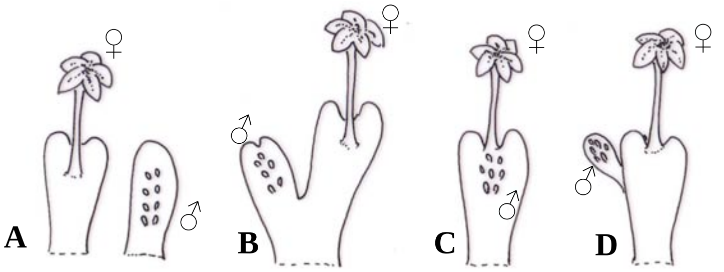


Figure 2.7. Sexual conditions in Cleveaceae. A) Dioicous; B) Terminal-autoicous; C) Par-autoicous; D) Ventral-autoicous.

Androecia: Androecia are never borne on antheridiophores but are always sessile with antheridial chambers sunk below the dorsal surface of the thallus. Antheridia are borne in these sunken chambers. Each androecium consists of a group of ostioles which protrude above the upper epidermis (Fig. 2.8, H) and can be purplish to hyaline or greenish. In most species of Cleveaceae androecial ostioles are closely aggregated or in zig-zag rows (Fig. 2.8, A & D). In *Peltolepis quadrata* they are aggregated into a raised disc (Fig. 2.8, E). Androecial scales are present in *Clevea hyalina* and *P. quadrata* (Fig. 2.8, C & E) and all other species lack androecial scales, even in the fresh condition.

Archegoniophore: The archegoniophore in Cleveaceae consists of a stalk and a receptacle which is called the carpocephalum. Elongation of the stalk takes place after fertilization in order to uplift the carpocephalum for spore dispersal (Bischler 1998). There are different hypotheses regarding the origin of the carpocephalum. According to Crum (2001), archegoniophores are modified branch systems of the thallus. Crum (2001) also argued that when archegoniophores are terminal, the carpocephalum develops very close to the growing point and that its stalk is a continuation of that branch. However, he suggested that in the case of dorsal archegoniophores these are dorsal outgrowths, hence quite different in origin. In most complex thalloid liverworts the carpocephalum stalk usually contains 1 or more rhizoid furrows which are narrow grooves along the length of the stalk, they contain numerous pegged rhizoids and are thought to facilitate water conduction into the carpocephalum (Bischler & Jovet-Ast 1981). Crum (2001) observed that the stalk of terminal carpocephala always contains 1 or more rhizoid furrows which represent a continuation of the ventral surface of the thallus. On the other hand, dorsal archegoniophores lack a rhizoid furrow because they are mere dorsal outgrowths of the thallus. This applies both in Cleveaceae (*Athalamia* and *Clevea*) and in Aytoniaceae (*Plagiochasma*) where all species have dorsal archegoniophores and lack rhizoid furrows. In *Sauteria* and *Peltolepis*, the archegoniophore is terminal, borne in the apical notch and has one and two rhizoid furrows in the stalk respectively (Fig. 2.9, B & C). In *Athalamia* and *Clevea*, the archegoniophores are dorsal and lack a rhizoid furrow (Fig. 2.9, A). When the archegoniophore is terminal, one or both of the thallus lobes on either side often continues to grow. When the archegoniophores are dorsal, several may be produced in succession along the mid-line of a single branch. The carpocephalum stalk is normally smooth, greenish to hyaline or sometimes with a purplish tinge at the base.

Scales are absent from the base of the stalk; however in most species a 'beard' of scales is found at the top of the stalk under the carpocephalum. These apical stalk scales can be hyaline or purplish, usually lanceolate in shape. They usually bear slime papillae on the margins, sometimes only on one side and uneven in distribution. However, in *Peltolepis* and *Sauteria*, 4–many slime papillae are evenly distributed on both sides of the scales (Fig. 2.9, D, E, F)

The carpocephalum is normally greenish to yellowish in colour, with 2–8 lobes, with or without air pores on the dorsal surface. In most species the carpocephalum is ±umbrella shaped and the lobes are directed downwards (Fig. 2.2, B, G, H). However, in *Clevea spathysii*, *C. pusilla* and *Athalamia pinguis*, the carpocephalum is cup-shaped with lobes directed upwards (Fig. 2.2, D, F& Fig. 2.8, D). Each lobe of the carpocephalum ends in a bilabiate involucre and after fertilization contains a very shortly stalked, spherical sporophyte (Fig. 2. 10).

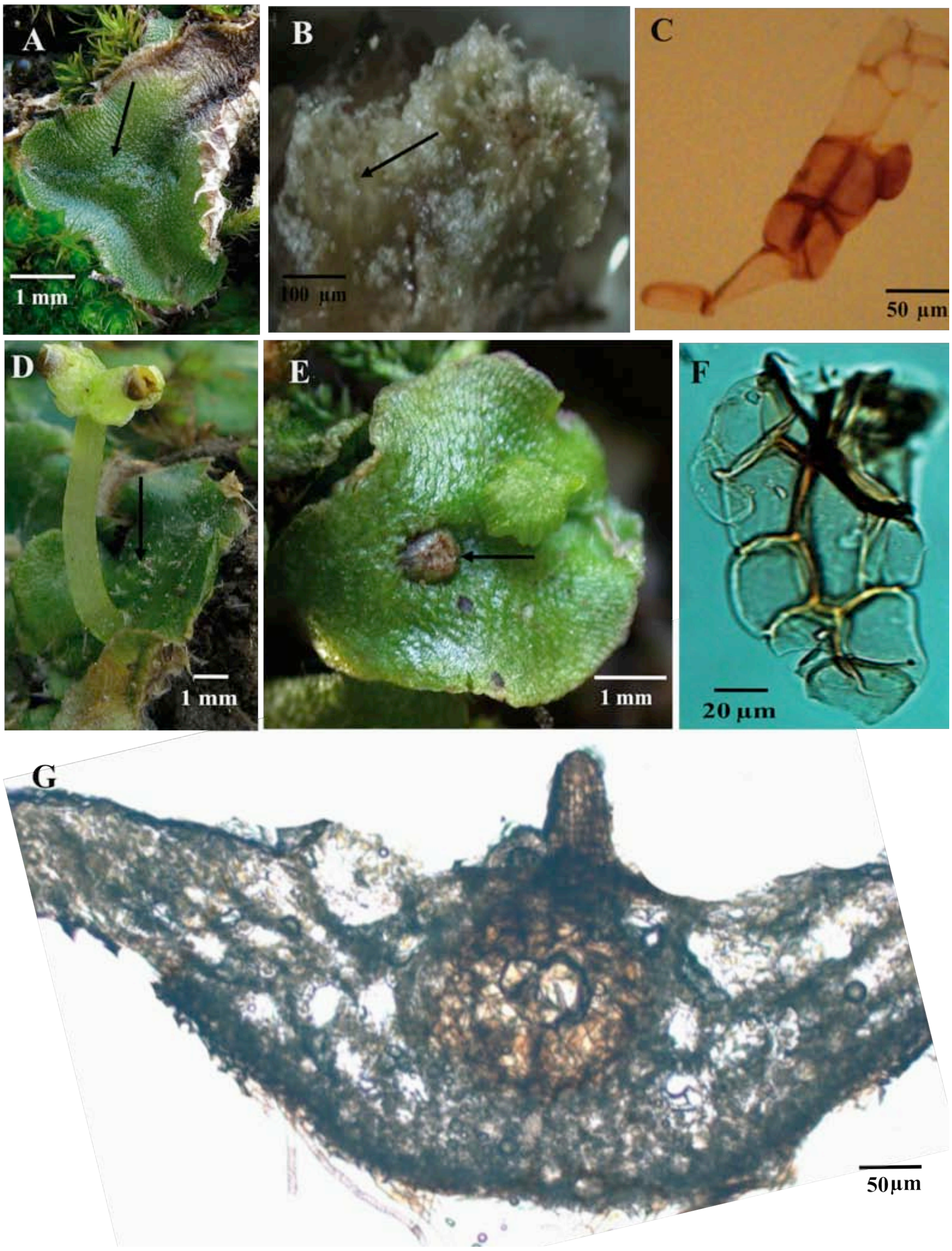


Figure 2.8. Morphology of Cleveaceae III. A) Closely aggregated androecia in zig-zag rows (*C. hyalina,* Long 39966, China-E); B) Androecia born on a reduced ventral branch (*S. spongiosa,* Katagiri 1173, Japan-HIRO); C, F) Antheridial scales from (*C. hyalina*, Long & Duckett 25774, Italy-E; *P. quadrata,* 08-08SR, Switzerland-E); D) Closely aggregated antheridia behind the archegonium (*A. pinguis,* Long 40305, China-E); E) Antheridia aggregated into a raised disc behind base of stalk (*P. quadrata,* 07-08SR, Switzerland-E); G) Sessile androecium embedded in the thallus with an ostiole protruding above dorsal surface (*C. hyalina,* 01-07SR, Scotland-E).

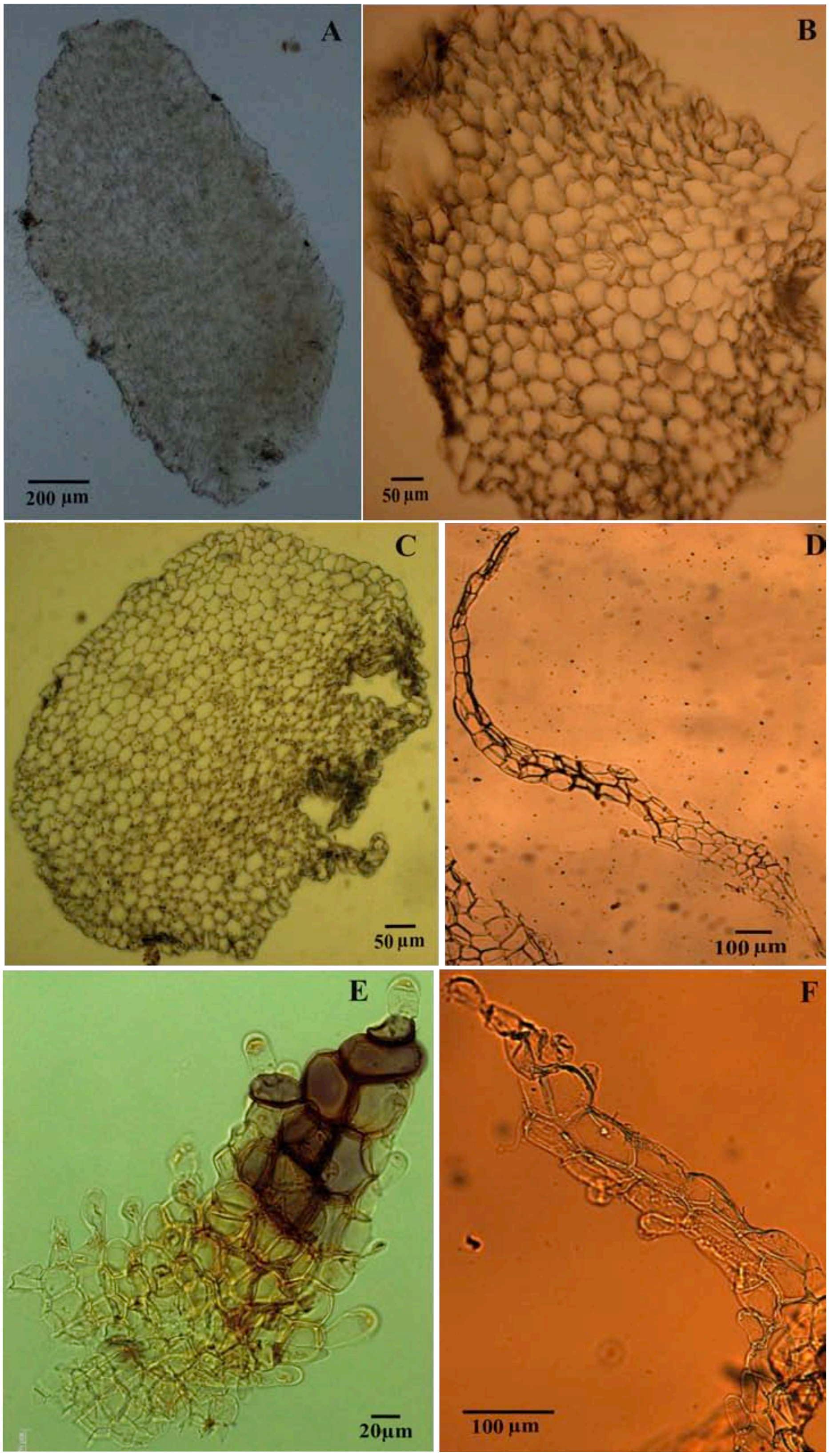


Figure 2.9. Morphology of Cleveaceae IV. T.S. of archegoniophore stalk A) lacking rhizoid furrow, B) with one rhizoid furrow, C) with two rhizoid furrows, (A-*A. pinguis* Kashyap *s.n.*, India-E; B-*S. spongiosa,* Katagiri 2806, Japan-HIRO; C-*P. quadrata,* 14-08SR, Switzerland-E); D, E, F) Apical stalk scales with slime papillae (D-*C.hyalina,* 01-07SR, Scotland-E; E-*P. quadrata,* 14-08SR, Switzerland-E; F-*S. alpina,* Breidler *s.n.*, Austria-W).

2.4.3 Sporophyte characters

Capsule: The sporophyte of Cleveaceae is highly reduced – a capsule borne on the lobes of the carpocephalum and protected by the lobes of the gametophytic involucre. The capsule is globose and is borne on a very short fleshy seta (Fig. 2.10). The capsule is yellowish-green when young and turns brownish or blackish brown with maturity. The capsule wall is one cell thick and the cells are rhomboidal in shape with annular thickenings that are visible on tangential and radial walls, and semi-annular thickenings which are U-shaped. The capsule lacks any distinct dehiscence lines or markings and splits irregularly longitudinally into a variable number of irregular valves during spore dispersal.

Spores: Spores are produced in tetrads during the meiotic division of spore mother cells. In most liverworts, these spore tetrads (Fig. 2.11, A) remain united until all wall layers are completely formed, resulting in a well recognizable convex outer or distal surface and a flatter inner or proximal surface with three distinct trilete markings representing the union of the tetrad. Spores are eventually separated from the tetrad before dispersal (Schuster 1966).Three layers can be recognized in the liverwort spore coat: the innermost layer, intine; the middle layer, exine; and the outermost layer, perine (Lietgeb 1881; Miyoshi 1966; Nath & Asthana 1992; Schuster 1966). The outermost perine is marked by prominent sculpturing. These sculptures offer important diagnostic features in many species of liverworts, especially complex thalloids (Miyoshi 1966). In Cleveaceae the spores are unicellular (Miyoshi 1966) and in most species sculpturing on distal and proximal surfaces with a trilete mark is hardly distinguishable (Fig2.11, B). The colour of mature spores varies from reddish to dark or blackish-brown. Spores in Cleveaceae are usually densely ornamented with hemispherical projections or domes, and the entire surface of the spore is finely granular (Fig. 2.11). These granules are sometimes more dense at the apex of the domes. These domes are thought to emerge independently from the spore surface (Gambardella 1986). They vary in size and shape, according to Gambardella (1986) this variation is due to the uneven deposition of granules around their margins. In *Athalamia pinguis* ornamentation is different from other species; they are ornamented with a reticulate pattern formed by joining of projections (Fig. 2.11, D), whereas all species of *Clevea*, *Peltolepis* and *Sauteria* show a fairly uniform ornamentation pattern. Spore size in Cleveaceae varies from 40–76 µm.

Elaters: Elaters are thought to help in spore dispersal acting as springs uncoiling rapidly at capsule dehiscence (Schuster 1966). However according to Bischler and Jovet-Ast (1981), their function is to loosen spores in the sporophyte and enhance maturation. In Cleveaceae, elaters are usually brownish in colour and have 2-3 helical thickening bands. Branched elaters were occasionally observed in *Clevea hyalina* and *Sauteria spongiosa* (Fig. 2.10).

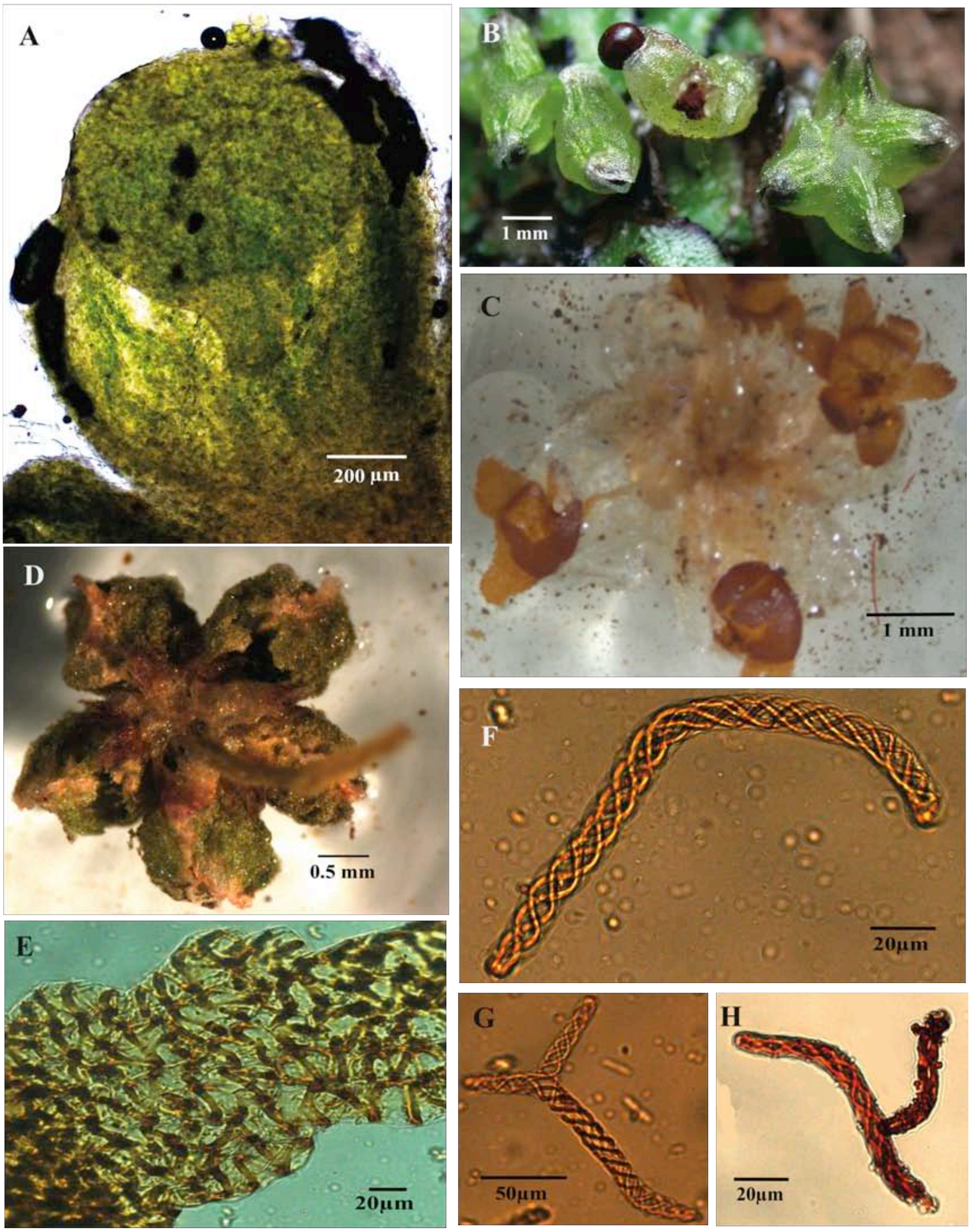


Figure 2.10. Morphology of Cleveaceae V. A) young globose capsule with bulbous foot with bivalved involucre around (*S. alpina*, 10-08SR, Switzerland-E); B) Mature capsules & bivalved involucre (*C. spathysii*, 01-09SR, Spain-E); C) Capsules dehisced into irregular valves (*S. spongiosa*, Miehe 13164, Nepal-JE); D) Lower surface of a mature carpocephalum showing bivalved involucres (*P. quadrata*, Katagiri 1174, Japan-HIRO); E) Spore wall with annular and semi annular thickenings (*S. spongiosa*, Katagiri 1173, Japan-HIRO); F,G,H) Elaters (G, F-*S. spongiosa*, Katagiri 1173, Japan-HIRO; H-*C. hyalina* , 01-07SR, Scotland-E).

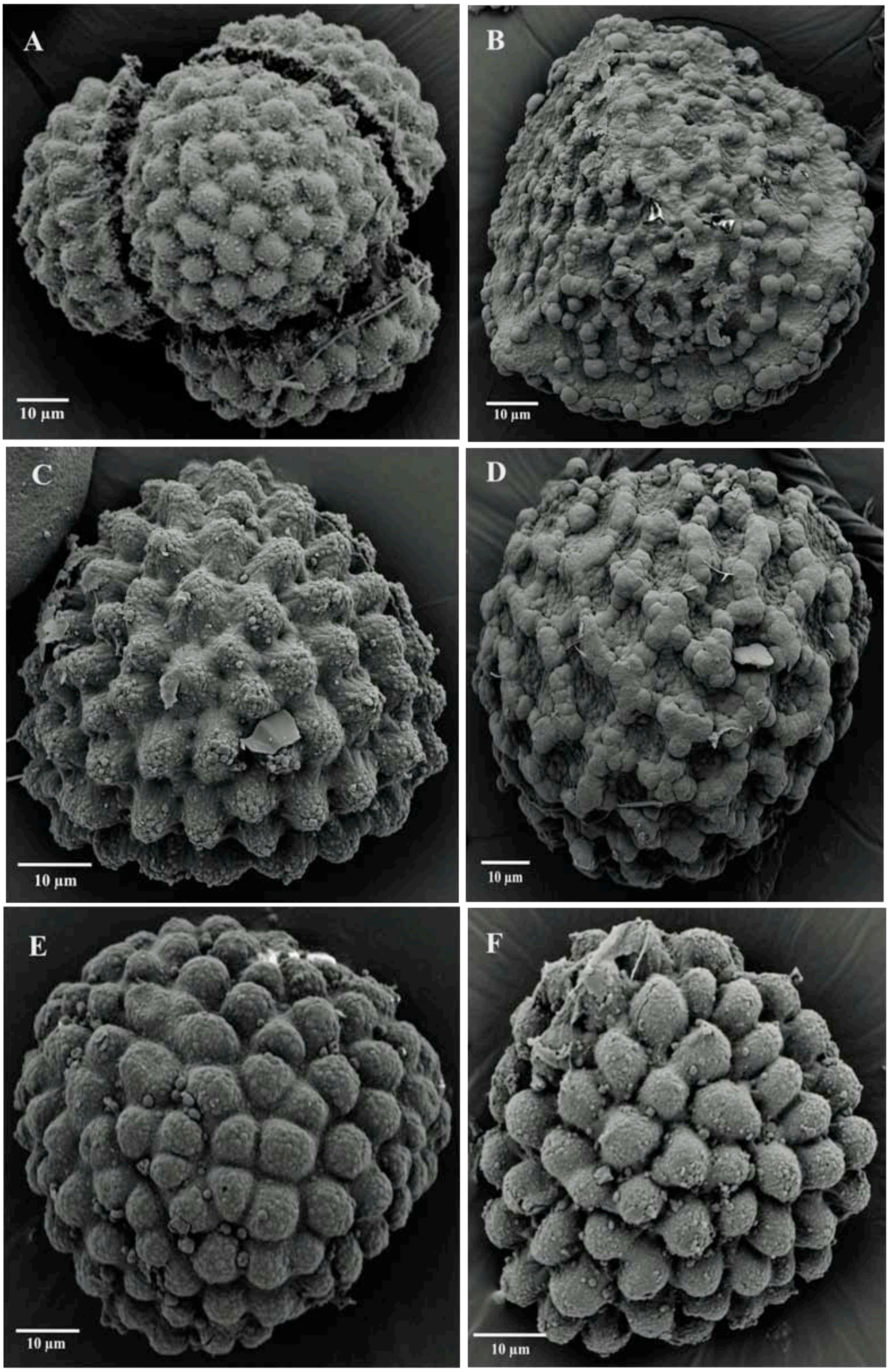


Figure 2.11. Spore morphology in Cleveaceae. A) young spore tetrad (*P.quadrata,* Froehlich *s.n*., Austria-S); B) proximal surface with hardly visible trilete mark (*A. pinguis*, Poelt s.n., Nepal-JE); C) distal surface ornamented with domes and granules (*C. hyalina*, Schuster & Damsholt 70-2699, Greenland-F); D) distal surface of ornamented with reticulate bands (*A. pinguis,* Poelt s.n., Nepal-JE) E) distal surface ornamented with domes and granules (*P. quadrata*, Baumgartner 8357, Austria-W); F) distal surface ornamented with domes and granules (*S. alpina*, Anzi, *s.n*., Austria-MANCH).

2.5 Discussion and Conclusions

The few morphological studies carried out on Cleveaceae in the past have mostly been based on a limited number of observed samples and species (Bergdolt 1926; Schiffner 1893; Schuster 1992; Shimizu & Hattori 1953, 1954, 1955). Leitgeb (1881) emphasized the radial wall thickenings of epidermal pores in *Clevea*, *Sauteria* and *Peltolepis* and placed the three genera in one group, the Astroporae (Chapter, 1). However, the present study shows that this character is variable within and between species (Appendix 2.2) indeed some species do not show radial wall thickenings at all. It was also observed that the lack of radial wall thickening could successfully be used in species identification e.g. *C. spathysii* and *C. pusilla*. Similarly the length and width of the thallus and receptacle stalk length and width, used to separate species in the past; *Athalamia nana* (now *Clevea pusilla*, see Chapter 4), *A. glauco-virens* (now *C. pusilla*, see Chapter 4) and *A. chinensis* (now *C. pusilla*, see Chapter 4) (Stephani 1906; Shimizu & Hattori 1953, 1954, 1955), were found to vary considerably within species, hence could not be used as key characters.

Although Shimizu and Hattori (1954) synonymised *Clevea* and *Athalamia* based on the fact that both genera posess a furrow-less archegoniophore, many other differences have been observed that readily separate the two genera even in the sterile condition. *Athalamia* differs from *Clevea*, *Sauteria* and *Peltolepis* in having a distinctly thick, firm thallus, conspicuous large whitish ventral scales protruding along the thallus margins (Fig. 2.2, E), spore ornamentation with reticulate bands, (Fig. 2.11, B,D) and in its narrow, slit-like air chambers (Fig. 2.3, D); it can easily be identified even in the sterile condition.

Species delimitation within *Sauteria* was in the past mainly based on the number of layers of air chambers in the assimilatory tissue, number of lobes and presence of air chambers in the carpocephalum and the position of the androecia: *S. spongiosa*, air chambers mostly in 1 layer, carpocephala with 2−4 lobes, with or without air pores and chambers, androecia on reduced ventral branches; *S. yatsuensis*, air chambers in 2–3 layers, carpocephala with 4−5 lobes, without pores and air chambers, androecia on a different branch or behind the carpocephalum, radial pore walls not thickened; *S. japonica*, air chambers in 2–3 layers, carpocephala with 1−4 lobes, with some pores and air chambers, androecia on reduced ventral branches (Shimizu & Hattori 1953, 1954, 1955; Schuster 1992). All the above mentioned characters except the position of androecia were observed to be highly variable and hence they cannot reliably be used in species delimitation. Comparison of these earlier described species in detail reveals that most of these species are morphologically very similar. However, presence of androecia on a reduced ventral branch (ventral-autoicy) and the spongy texture of the thallus separate *S. spongiosa* from *S. alpina*. Further, *Sauteria* was regarded as the only genus in Cleveaceae with ventral scale oil bodies, which was thought to be a key character distinguishing the genus (Schuster 1992; Shimizu & Hattori 1954). However, this observation has proved to be inaccurate in the present study, since some species of *Clevea* also have ventral scale oil bodies. However, the characteristic translucent yellowish-green thalli with whitish, decolorate margins, devoid of any purple coloration, its extremely delicate texture and silvery white ventral scales is distinctive for *Sauteria* and separates it from other genera of Cleveaceae even in the sterile condition.

It is evident that the limited availability of material, and in some instances lack of material of other taxa for comparison, has led in the past to the misguided description of many local endemics, as also happened in *Asterella* (Long 2006). This study is the first to include all the described species world-wide within Cleveaceae and it clearly shows that many characters used in species delimitation in the past are variable and can overlap within and between these described species. However, this study also revealed some more stable characters especially in ventral scale morphology such as arrangement, protrusion, colour, oil bodies, and also position and aggregation of androecia, shape of air chambers, colour and texture of thallus. These characters can be successfully used as key characters in defining species and genera within Cleveaceae. For complete descriptions of genera and species see Chapter 4.

CHAPTER-3-MOLECULAR PHYLOGENY AND GENERIC DELIMITATION OF THE LIVERWORT FAMILY CLEVEACEAE

3.1 A summary of the current taxonomic and phylogenetic status of Cleveaceae

The family Cleveaceae was first formally described by Cavers (1910−1911) but had earlier been defined by Leitgeb (1881) as the ‘Gruppe’ Astroporae (or Astroporenreihe) within a much broader family Marchantiaceae. The family was characterized primarily by its star-shaped epidermal pores with strongly thickened radial walls in the surrounding cells. The concept of Cleveaceae has been maintained ever since Cavers (1910−1911) and the family is well-defined by the following combination of morphological characters: presence of pores with thickened radial walls in the surrounding cells, air chambers of the thallus without photosynthetic filaments, ventral scales with a single tapering ill-defined appendage, capsule with irregular dehiscence and capsule wall with well-defined annular bands. According to the most recent classification system by Crandall-Stotler et al. (2009), the family Cleveaceae is placed in the class Marchantiopsida, subclass Marchantiidae, order Marchantiales (Chapter 1). The family name Cleveaceae has been almost universally used since Cavers (1910−1911) although Evans (1923) and Udar (1958) used the illegitimate family name Sauteriaceae. The genera recognized within Cleveaceae have changed over the years, but the family has become relatively stable, with three genera *Sauteria* (Nees) Nees, *Athalamia* Falc. and *Peltolepis* Lindb. accepted (Crandall-Stotler et al. 2008, 2009; Damsholt 2002; Grolle 1983; Koponen et al. 1977; Schljakov 1981; Schuster 1958, 1984, 1992; Shimizu & Hattori 1954, 1955).

A current conspectus of genera of Cleveaceae based on Grolle (1972, 1983) and Schuster (1984, 1992).

Cleveaceae Cavers, New Phytol. 10: 42. 1911. – Type: *Clevea* Lindb.

1. *Sauteria* Nees, Naturg. Europ. Leberm., 4: 139. 1838. – Type: *Sauteria alpina* (Nees) Nees

= *Sauchia* Kashyap, J. Bombay Nat. Hist. Soc. 24: 437. 1916. – Type: *Sauchia spongiosa* Kashyap (≡ *Sauteria spongiosa* (Kashyap) Shimizu & S.Hatt.); synonymised by Shimizu & Hattori (1954).

2. *Athalamia* Falc., Ann. Mag. Nat. Hist. ser. 2, 1: 375. 1848; Trans. Linn. Soc. London 20: 397. 1851 (detailed description). – Type: *Athalamia pinguis* Falc.

= *Clevea* Lindb., Notiser Sällsk. Fauna Fl. Fenn. Förhandl. 9: 28. 1868. – Type species: *Clevea hyalina* (Sommerf.) Lindb.; synonymised by Shimizu & Hattori (1954).

= *Gollaniella* Steph., Hedwigia 44: 74. 1905. – Type: *Gollaniella pusilla* Steph. (≡ *Athalamia pusilla* (Steph.) Kashyap); synonymised by Kashyap (1929).

3. *Peltolepis* Lindb., Morgonbladet (Helsingfors) 1876 (106): [1]. 1876; Helsingfors Dagblat 1876 (139): [2]. 1876; Bot. Notiser 1876: 123. 1876; Bot. Notiser 1877: 73. 1877 (detailed description). – Type species: *Peltolepis grandis* (Lindb.) Lindb. (= *P. quadrata* (Saut.) Müll.Frib.).

The family Cleveaceae, described over 129 year ago (Leitgeb 1881), has not been studied in detail in past molecular phylogenetic studies of liverworts. However, Cleveaceae has been used as a sister group in some studies; Schill, 2006 (using one accession, *Athalamia hyalina*), Boisselier-Dubyle et al. 2002 (using two accessions, *Athalamia spathysii* and *Sauteria alpina*) Long et al. 2000 (using one accession, *Athalamia hyalina*), or for support for major studies in liverworts; Forrest et al. 2006 (using four accessions, *Athalamia hyalina*, *A. pinguis*, *Sauteria alpina* and *Peltolepis quadrata*), and Wheeler 2000 (using two accessions, *Athalamia hyalina* and *Peltolepis quadrata*). These studies were focused largely on ordinal and familial relationships and the limited sampling did not permit consideration of generic relationships within Cleveaceae.

Species numbers in the three genera currently recognized within Cleveaceae are uncertain; Shimizu & Hattori (1954) and Bischler (1998) estimated *Athalamia* to have 12–15 species, *Sauteria* 5 or 6 and *Peltolepis* 1 or 2. As described in Chapter 2 & 4, many local species have been described in different geographic parts of the world. However, these species have not been closely studied or compared with existing species, which was one of the main reasons for taxonomic confusions within the family.

The circumscription of the genera *Sauteria* and *Peltolepis* has remained largely unchanged since they were first described, except for the relatively brief appearance of *Sauchia* Kashyap (now synonymized under *Sauteria*). In contrast, *Athalamia* has largely been treated as synonymous with *Clevea*, which was relegated to synonymy under *Athalamia* by Shimizu & Hattori (1954), a concept widely followed since (Crandall-Stotler et al. 2008, 2009; Damsholt 2002; Grolle 1983; Grolle & Long 2000; Koponen et al. 1977; Schljakov 1981; Schuster 1958, 1984, 1992; Shimizu & Hattori 1955). The later proposed genus *Gollaniella* Steph. enjoyed only brief recognition until it was synonymized by Kashyap (1929) under *Athalamia*.

3.2 Objectives

The family Cleveaceae has not been studied in detail in molecular phylogenies. The morphological classifications put forward by earlier workers (Bischler 1998; Shimizu & Hattori 1954) have never been tested by a molecular phylogenetic approach and character evolution within the family is yet to be investigated.

The main objectives of the present study were:

- To undertake a detailed molecular phylogenetic analysis on the family Cleveaceae and its constituent genera.
- To test the current three-genus subdivision of the family and provide a stable backbone classification to underpin the morphological study (Chapter 3)

- To test the relationships between the genera of Cleveaceae as well as those between almost all the widely-recognised species in the family.
- To evaluate the congruence between morphological and molecular approaches and to determine the extent of homoplasy through mapping morphological characters on phylogenetic trees.

3.3 Materials and Methods

3.3.1 Taxon sampling

Silica dried material collected on field excursions were mainly used for DNA extractions. Herbarium specimens were used to extract DNA from those taxa for which silica dried material was unavailable. In the field, samples were thoroughly cleaned to remove algae, fungi and soil debris and the young green thallus tips up to 5mm long were dried in silica gel. Voucher specimens were prepared in paper packets and deposited in the Royal Botanic Garden Edinburgh (E). Voucher information of all plant material used in molecular analysis is given in Appendix 3.1.

3.3.2 Ingroup and Outgroup taxa

Ingroup taxa. Fifty four accessions from Cleveaceae were used in the study: *Athalamia* (28 accessions/5 species), *Sauteria* (15/3) and *Peltolepis* (11/1). These represent a substantial part of the geographical distribution of the family except for South America and also encompass a very large part of its morphological diversity; they include the type species of the three traditionally accepted genera as well as those of the synonymized genera *Clevea*, *Spathysia*, *Gollaniella* and *Sauchia*.

***Outgroup taxa*.** Outgroup taxa were selected based on the comprehensive multi-locus molecular phylogenetic study of liverworts carried out by Forrest et al. (2006). This analysis shows (Fig. 3.1) that the sister group to Cleveaceae contains *Monosolenium*, *Conocephalum*, *Cyathodium*, *Exormotheca*, *Corsinia*, *Ricciocarpos*, *Riccia*, *Wiesnerella*, *Targionia*, *Dumortiera* and *Monoclea*. The family Aytoniaceae forms a strongly supported clade which subtends the clade including Cleveaceae.

Therefore, twenty outgroup accessions covering both these clades were included in the current study: *Monoclea* (1 accession/1 species), *Conocephalum* (2/2), *Corsinia* (1/1), *Dumortiera* (2/1), *Exormotheca* (1/1), *Monosolenium* (1/1), *Ricciocarpos* (1/1), *Riccia* (2/2), *Targionia* (2/1), *Wiesnerella* (1/1), *Asterella* (2/2), *Mannia* (2/2), *Plagiochasma* (2/2).

All ingroup sequences (54) were newly generated for this study. Voucher information and accession numbers of all taxa used in the study are given in Appendix 3.1. Outgroup sequences downloaded from the nucleotide database of the National Centre for Biotechnology (http://www.ncbi.nlm.nih.gov/) are indicated in Appendix 3.1.

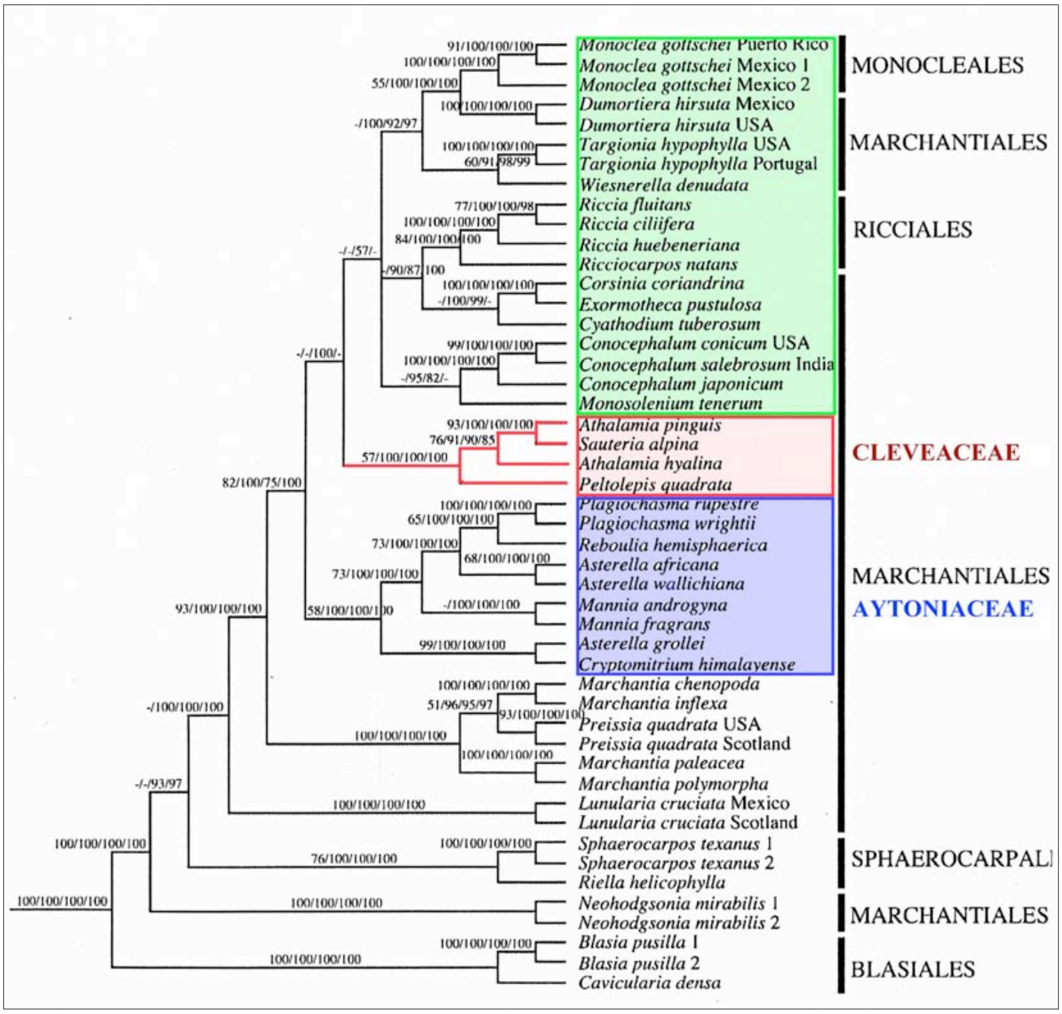


Figure 3.1. Marchantiopsida (based on the topology from the 5 partition Bayesian analysis). Numbers above branches are Maximum Parsimony Bootstrap support values/ homogeneous Bayesian Posterior Probabilities/5-partition Bayesian Posterior probablities/14-partition Bayesian Posterior Probabilities (Adapted from Forrest et al. 2006).

3.3.3 Molecular Markers

Three loci of the chloroplast genome: *rpo*C1, a ~700 base pair (bp) fragment of a ~3000 bp RNA polymerase gene; *psb*A, including the intergenic spacer from trnK, the photosystem II protein gene and the intergenic spacer to trnH; *rps*4, the small ribosomal protein gene and its 3´spacer region, and one locus of the nuclear genome: 26S, a ~1000 bp fragment from the 5´ end of the nuclear ribosomal large subunit, were sampled. These regions, referred to as *psb*A, *rpo*C1, *rps*4 and 26S, were chosen because they have proved informative in distinguishing liverwort species in previous publications (e.g. Forrest et al. 2005, 2006) and/or have provided species level resolution for liverworts in plant barcoding trials (Chase et al. 2007; Hollingsworth et al. 2009).

3.3.4 DNA extraction and Polymerase Chain Reaction (PCR)

DNA extraction. Silica dried samples collected during field excursions were mainly used for DNA extractions. Herbarium specimens were used to extract DNA from those taxa for which silica dried material was unavailable.

Specimens were placed in 2.0ml Eppendorf tubes with a 3mm Retsch cone ball in each tube. A mixer mill (Retsch® MM300) at 20/sec frequency for 2x30 sec., was used to grind up dry plant material for DNA extraction since it is considered to be most effective for both silica gel dried material and herbarium specimens. Extractions were carried out using Plant DNeasy kits (QIAGEN) following the manufacturer’s protocol except that in the final two steps elution was performed with 75 µl of Buffer AE. DNA was electrophoresed in 1% agarose TBE gels, stained with SYBRsafe^{TM} (Invitrogen) and visualised under UV light.

PCR amplification. Primers LP1 and LP5 (Chase *et al*., 2007) were used to amplify and sequence the *rpo*C1 region, primers trnK2F, 501F, 576R and trnHR (Forrest & Crandall-Stotler 2004) for the *psb*A region, primers rps5 (Nadot et al.

1994) and trnAS (Cox et al. 2000) for the *rps*4 region and primers OF and 12R (Shaw 2000) for the 26S region (Table 3.1).

Table 3.1. Primers used in PCR and sequencing reactions.

Gene region	Primer	Direction	Sequence	Source
*rpo*c 1	LP1	F	5´ TATGAAACCAGAATGGATGG	Chase et al. (2007)
	LP5	R	5´ CAAGAAGCATATCTTGASTYGG	Chase et al. (2007)
*psb*A-*trn*H	501F	F	5´ TTT CTC AGA CGG TAT GCC	Forrest & Crandall-Stotler (2004)
	trnK2F	F	5´ GAC GAG TTC CGG GTT CGA	Forrest & Crandall-Stotler (2004)
	576R	R	5´ TGG AAT GGG TGC ATA AGG	Forrest & Crandall-Stotler (2004)
	trnHR	R	5´ GAA CGA CGG GAA TTG AAC	Forrest & Crandall-Stotler (2004)
*rps*4	rps5	F	5´ ATG TCC CGT TAT CGA GGA CCT	Nadot et al. (1994)
	trnAS	R	5´ TAC CGA GGG TTC GAA TC	Cox et al. (2000)
26S	OF	F	5´ ACC CGC TGT TTA AGC ATA T	Manos Lab in Shaw (2000)
	12R	R	5´ ATC GCC AGT TCT GCT TAC CA	Manos Lab in Shaw (2000)

For the *rpo*C1 region, PCR mixes had a total volume of 20 µl, and contained 0.6 µl of 1.5 mM $MgCl_2$, 10 pmol of each primer (Table 1), 2 µl of 2 mmol of each dNTP, 2 µl of 10x Bioline NH_4 Reaction Buffer, 0.2 µl of 100x BSA, 0.2 units Biotaq DNA polymerase (Bioline), and c. 1 µl DNA extract. The thermocycling profile consisted of a 1 min denature at 94 ^{o}C, then 40 cycles of denaturing at 94 ^{o}C for 30 sec, annealing at 50 ^{o}C for 40 sec, and extending at 72 ^{o}C for 40 sec, with a final 5 min extension at 72 ^{o}C followed by a 10 ^{o}C holding stage.

For the *psb*A region, PCR mixes had a total volume of 25 µl, and contained 1.25 µl of 1.5 mM $MgCl_2$, 7.5 pmol of each primer, 2.5 µl of 2 mmol dNTPs, 2.5 µl of 10x Bioline NH_4 Reaction Buffer, 0.125 units Biotaq DNA polymerase, and 1 µl DNA extract. The thermocycling profile consisted of a 1 min denature at 94 ^{o}C, then 40 cycles of denaturing at 94 ^{o}C for 45 sec, annealing at 48 ^{o}C for 45 sec, and extending at 60 ^{o}C for 2 min, with a final 7 min extension at 72 ^{o}C followed by a 10 ^{o}C holding stage.

For rps4 and 26S regions, PCR mixes had a total volume of 20 µl and contained 0.6 µl of 1.5 mM $MgCl_2$, 20 pmol of each primer, 2 µl of 2 mmol dNTPs, 2 µl of 10x Bioline NH_4 Reaction Buffer, 0.4 units Biotaq DNA polymerase, 0.2 µl of 100x BSA and 1 µl DNA extract. The thermocycling profile consisted of a 1 min denature at 94 °C, then 40 cycles of denaturing at 94 °C for 45 sec, annealing at 48 °C for 45 sec, and extending at 60 °C for 2 min, with a final 7 min extension at 72 °C followed by a 10 °C holding stage.

PCR products were electrophoresed in 1% agarose TBE gels, stained with SYBERSafe ™, and visualized under UV light. PCR products were cleaned using either illustra™ DNA and Gel Band purification kits (GE Healthcare), and eluted in 25-30 µl of elution buffer EB (QIAGEN) or 2 µl ExoSAP-IT™ (USB Corp., Ohio) and 5 µl of PCR product. The ExoSap cleanup protocol consisted of 15 min incubation at 37.0 °C followed by enzyme inactivation at 80 °C for a further 15 min and a 10.0 °C holding stage.

3.3.5 DNA sequencing and aligning

DNA Sequencing. For all the regions, cycle sequencing was performed using 1 µl of PCR product, 0.33 µl primer (10µM), 2 µl of 5x sequencing buffer (Applied Biosystems, Inc., Foster City, CA) and 1µl BigDye® Terminator v3.1 Cycle sequencing Kit (Applied Biosystems, Inc., Foster, CA). The BigDye® Terminator v3.1 protocol consisted of 25 cycles of denaturing at 95 °C for 30 sec, annealing at50 °C for 20 sec and extending at 60 °C for 4 mins, followed by a 4 °C holding stage. Samples were then run at the University of Edinburgh’s Gene Pool Sequencing service on ABI capillary sequencers.

Sequence Alignment. Electropherograms were assembled using Sequencher ™ 4.6 (Gene Codes Corporation), forward and reverse sequences were aligned into a contig, checked for ambiguities and edited manually if required. Once the consensus from the contig was completed, it was exported as a text file which was used to generate a new contig and subsequently exported from Sequencher in NEXUS format.

Sequences were aligned using MUSCLE (MUltiple Sequence Comparison by Log-Expectation, Edgar 2004) and optimized manually using Se-Al v 2.0a11 (Rambaut 2002). Separate alignments were made for *psb*A, *rpoC*1, *rps*4 and 26S genes. The total length of individual sequences for *psb*A, *rpoC*1, *rps*4 and 26S ranged between 1490 – 1161bp, 451 – 838bp, 1153 – 664bp and 1169 – 1024bp respectively. Regions of ambiguous alignment and incomplete data (i.e. beginnings and ends of the sequenced regions) were identified and excluded from further analyses. The four regions were compiled into a single matrix using Mesquite v. 2.72 (Maddison & Maddison 2010).

3.3.6 Phylogenetic Analysis

It has been proven by many recent studies that the use of more than one molecular marker is desirable when deducing phylogenetic relationships and reconciling evolutionary behavior of molecular and morphological characters (Chase et al. 2007; Crandall-Stotler et al. 2005; Crandall-Stotler et al. 2009; Forrest & Crandall-Stotler 2005; Forrest et al. 2006; Heinrichs et al. 2005; He-Nygrén et al. 2006; Nickrent et al. 2004; Qiu et al. 2006; Qiu et al. 2007; Samigullin et al. 1999). However, whether data sets should be analysed separately or combined in a simultaneous analysis depends on the degree of incongruence of data matrices (Buckley & Cunningham 2002; Cunningham 1997; de Queiroz et al. 1995; Huelsenbeck & Bull 1996). An earlier method used to test the compatibility of data sets was to compare the trees obtained from different matrices by comparing the topologies (Farris et al. 1995). However, to test the strength of incongruence between data partitions, different statistical tests have been developed (Cunningham 1997). The incongruence length difference (ILD) test of Farris *et al*. (1995) has proven to be best able to distinguish between the degree of incongruence among data sets, and is widely used in parsimony analyses (Barker & Lutzoni 2002; Cunningham 1997; Hipp et al. 2004; Möller et al. 2009).

Both methods were used to tests the congruence between the four data sets used in this study: *rpoC*1, *psb*A, *rps*4 and 26S. Each data set was first independently analysed and the topologies were compared. All analyses yielded almost identical topologies with no hard incongruencies between them (Appendix 3.2). Data sets were then tested using the IDL test (Farris et al. 1994; 1995) which is implemented as a partition homogeneity test in PAUP* 4.0b10 (Swofford 2002), on 1000 replicates of repartitioning using heuristic search with asis sequence addition and tree bisection-reconnection (TBR) on (Möller et al. 2009; Yuan et al. 2005). The data sets were confirmed as congruent (all p values were greater than 0.05): *rpoC*1 vs. *psb*A (p=0.63); *rpoC*1 vs. *rps*4 (p=0.91); *rpoC*1 vs. 26S (p=0.95); *psb*A vs. *rps*4 (p=0.26); *psb*A vs. 26S (p=0.21); *rps*4 vs. 26S (p=0.1).

The total amount of data in the combined data set ranged from 807–3708 bp per accession. Several gaps inserted in the data matrix due to indel events (insertion/deletion) meant the final alignment had a length of 3809 bp.

The matrices were analysed using three commonly applied methods of phylogenetic analyses: maximum parsimony (MP), Bayesian Inference (BI) and maximum likelihood (ML) on unordered and equally weighted characters.

Maximum Parsimony. Maximum Parsimony is one of the most widely used methods for inferring phylogenies (Felsenstein 2004; Lemey et al. 2009). Maximum Parsimony is based on the assumption that common characters are shared by taxa due to inheritance from a common ancestor and that evolution took place with the least number of character state changes. Therefore in MP analysis the most likely tree is the one that minimizes the number of evolutionary steps required to explain a data set (Hall 2008; Hillis et al. 1994; Lemey et al. 2009). Parsimony methods permit rapid exploration of alternative tree toplogies and the software which applies the method (e.g. PAUP, Swofford 2002) is highly efficient. However, when large numbers of data are accumulated MP analyses can produce misleading results and are particularly prone to a phenomenon known as ‘long-branch attraction’, i.e. reconstruction of clades composed of unrelated taxa that share common characters due to homoplasy rather than clades of related taxa with characters shared due to common ancestry. Model-based methods such as Bayesian and Likelihood have an advantage over parsimony because they are less susceptible to long-branch attraction (Hall 2008; Hillis et al. 1996; Lemey et al. 2009).

MP analyses were performed using PAUP* 4.0b10 (Swofford 2002), mounted on an Apple Macintosh G4, using Fitch criteria. For all analyses, heuristic searches were performed initially using unweighted, unordered characters with 10000 random sequence addition replicates using tree bisection-reconnection (TBR) branch swapping, saving 10 trees per replicate, with MULTREES on, steepest descent off. Gaps were treated as missing in all analyses. Initial trees yielded were filtered using best fit. The shortest most parsimonious trees (MPTs) saved were further optimized with TBR, MULTREES and STEEPEST DESCENT off, with no limit on the number of trees saved. Branch lengths and tree scores were calculated from one of the most parsimonious trees based on an assumption of accelerated transformation optimization (ACCTRAN). Strict and Majority rule consensus trees were computed. Bootstrapping was carried out to evaluate the robustness of the clades, with 10000 bootstrap replicates, using a heuristic search with one random sequence addition and TBR branch swapping (Fig. 3.2).

Bayesian Inference (BI) and Maximum Likelihood (ML). These methods are based on explicit models of sequence evolution and can be regarded as similar approaches in inferring phylogenies although they differ in some ways. Both ML and BI methods are based on the likelihood function; a quantity that is proportional to the probability of observing the data on a tree, and similar models of sequence evolution can be used in both methods (Hall 2008; Huelsenbeck et al. 2002). Maximum Likelihood considers observed data as fixed observation and searches for a single tree that maximizes the probability of observing the data on a given tree (Hall 2008; Pagel 1999). Maximum Likelihood estimates correspond to those that provide the most probable description of the observed data, given the model of evolution (Pagel 1999). However, because ML explores more likely trees (higher points) by moving on a landscape using an heuristic search strategy, it is possible to get trapped on a point even though there can be a better set of trees elsewhere in the landscape (just in the same way as MP analyses can get trapped) (Hall 2008). However, unlike ML, BI incorporates posterior probabilities i.e. prior probabilities estimated based on a model in its search for the best set of trees. Bayesian Inference searches for the tree that maximizes the probability of the tree, considering the data and model of evolution. The most commonly used program that incorporates BI analysis, MrBayes (Huelsenbeck & Ronquist 2007), uses the Metropolis-coupled Monte Carlo Markov Chain (MCMC) method; a set of independent searches that approximate posterior probability distribution of trees and is computationally very efficient. Once the best set of trees which are consistent with the model and the data are found, posterior probabilities of clades can be obtained by summarizing the results with a majority rule consensus tree (Hall 2008; Huelsenbeck et al. 2002). Due to its computational efficiency and flexibility of specifying priors, BI has become one of the most commonly used methods for inferring phylogenies.

BI analyses were performed using MrBayes version 3.1.2 (Huelsenbeck & Ronquist 2007) on unordered and equally weighted characters. A model of substitution was selected independently for each locus using MrModeltest version 2.3 (Nylander 2004) based on the Hierarchical Likelihood Ratio Test (hLRT) and the Akaike’s Information Criterion (AIC). Data partitions were made according to the gene with the following model parameters: the General Time Reversible model of evolution with a gamma distribution of rate variation among sites and a proportion of invariant sites (GTR+I+G) for *psb*A and 26S regions and the Hesegawa-Kishino-Yano substitution model with gamma distribution of rate variation among sites (HKY+G) for *rpoC*1 and *rps*4 as selected by hLRT and AIC information. The MCMC chains were run for one million generations, with two independent parallel analyses, with one tree sampled every 100 generations (10000 trees). Posterior Probabilities for both runs were compared to check if convergence was reached, and the Burn-in was determined by visualizing the likelihood parameter against generation time using Tracer v1.5 (Rambaut & Drummond 2009). The first 2000 trees were discarded as Burn-in from both runs. A majority consensus tree was constructed using PAUP* (Fig. 3.3). Bayesian posterior probability (BPP) support values 95% or higher were regarded as significant (e.g. Forrest et al. 2006), although some authors discuss lower values (Nickrent et al. 2004).

GARLI (Genetic Algorithm for Rapid Likelihood Inference) (Zwickl 2008) was used to find the maximum likelihood tree for the data, using the General Time Reversible model of evolution, with a gamma distribution of rate variation among sites and a proportion of invariant sites (GTR+I+G) and with parameters estimated during the search. Estimated parameters of the likeliest tree were: -lnL = (15280.0645), Base=(0.2892 0.1866 0.2198) Rmat=(1.1140 2.6371 1.0371 1.5179 4.8820) Rates=gamma Shape=0.4785 Pinvar= 0.5953 and ML bootstrapping was run with 500 replicates (Fig. 3.4).

3.3.7 Character reconstruction

Mapping the character states of living organisms onto phylogenies is widely used in inferring ancestral states (Brooks & McLennan 1991; Cunningham et al. 1998). Reconstruction of characters over evolutionary trees makes it possible to understand the imprint of historical events and to describe how character states evolved (Pagel 1999). The ancestral states are traced using statistical models that unfold the evolutionary history of state changes. Maximum Parsimony and ML are the most widely used methods of reconstructing ancestral states (Cunningham et al. 1998; Pagel 1999). The MP criterion chooses the ancestral state so that it minimizes the number of evolutionary transitions required to explain the character state of the species. It does not take branch lengths into account. Although the MP criterion is most successful when there are fewer character changes and with short branches, its performance weakens with higher rates of character evolution and with long branches (Cunningham et al. 1998; Pagel 1999). Maximum likelihood uses a Markov approach which estimates rates at which a character makes changes among its probable states as it evolves through time. The Markov-transition model in ML considers both the length of branches in the tree and rates of evolution when searching for the most probable explanation of the observed data (Cunningham et al. 1998; Maddison & Maddison 2010; Pagel 1999). Therefore ML works better with high rates of character changes and long branches and also estimates the relative probability of each character state at every node (Cunningham et al. 1998).

Twelve morphological characters, including those traditionally used for distinguishing genera and those found to show distinct patterns of variation, were scored (Table 3.2) and their evolution was reconstructed over the most likey topology (Fig. 3.4). Morphological data matrix is given in Appendix 3.3. Character evolution reconstructions were made in Mesquite v. 2.74 (Maddison & Maddison 2010), using both MP with character states modelled as unordered and ML with a Markov k-state one-parameter model (Mk1, Lewis 2001) implemented in the programme.

Table 3.2. Morphological characters and character states used in character reconstructions

Character	**Characters state codes**
(a) Number of rhizoid furrows	0=none; 1=one; 2=two; 3=carpocephalum absent
(b) Position of archegonia/archegoniophore	0=terminal; 1= dorsal
(c) Radial wall thickening	0=absent; 1=present;?=air pores absent
(d) Air chamber width and shape	0=wide &polygonal; 1=narrow & slit-like
(e) Sexual condition	0=autoicous; 1=dioicous
(f) Androecial scales	0=absent; 1=present
(g) Androecial aggregation	0=scattered; 1=closely aggregated; 2=cushion; 3=disc; 4= stalked receptacle; 5=open-groove
(h) Androecial position	0=main thallus; 1=ventral branch
(i) Secondary pigmentation	0=absent; 1=present
(j) Ventral scale arrangement	0=ill-defined rows; 1=distinct rows;?=scales absent
(k) Ventral scale protrusion	0=only at apex; 1=apical region; 2=along margins; ?=scales absent
(l) Ventral scale oil bodies	0=absent; 1=present;?=ventral scales absent

3.4 Results

3.4.1 Phylogenetic inference

Maximum Parsimony, Bayesian Inference and Maximum Likelihood Analyses. Of the total 3809 unambiguously aligned sites of the final data matrix, 3109 (81.62%) were constant. Of 700 (18.38%) variable sites, 275 (8.90%) were parsimony uninformative and 425 (9.11%) were parsimony informative. Inferences under the parsimony optimality criterion resulted in 154 equally parsimonious trees (MPTs) of 1313 steps, with a consistency index (CI) of 0.637, and a retention index (RI) of 0.861 (Fig. 3.2). A single optimal tree was obtained under the ML criterion (Figure 3.4). Bayesian inference yielded a majority rule tree with most of the branches strongly supported (Fig. 3.3). MP, ML and BI analyses recovered very similar tree topologies. Most clades were well-supported in all three analyses, with the exception of the clade containing *Peltolepis*, *Sauteria* and *Athalamia*, which received a posterior probability of 0.8, or 80%, but was not supported in the maximum parsimony and Likelihood analyses (Figs. 3.2, 3.3, 3.4).

The family Cleveaceae is resolved as a monophyletic group with strong support in MP, ML and BI analyses (Figs. 3.2, 3.3, 3.4); four major lineages receive 100% support from all three analyses. *Peltolepis* and *Sauteria* were both resolved as robust monophyletic groups (with 100% support), whereas *Athalamia* as currently defined was resolved as polyphyletic, with two strongly supported clades (Fig. 3.2). *Athalamia hyalina*, *A. spathysii* and *A. pusilla* formed a lineage sister to the clade containing *Peltelepis*, *Sauteria*, *Athalamia pinguis* and *A. handelii*. *Athalamia pinguis* and *A. handelii* were resolved as sister taxa sharing a unique common ancestor with *Sauteria* (Fig. 3.2).

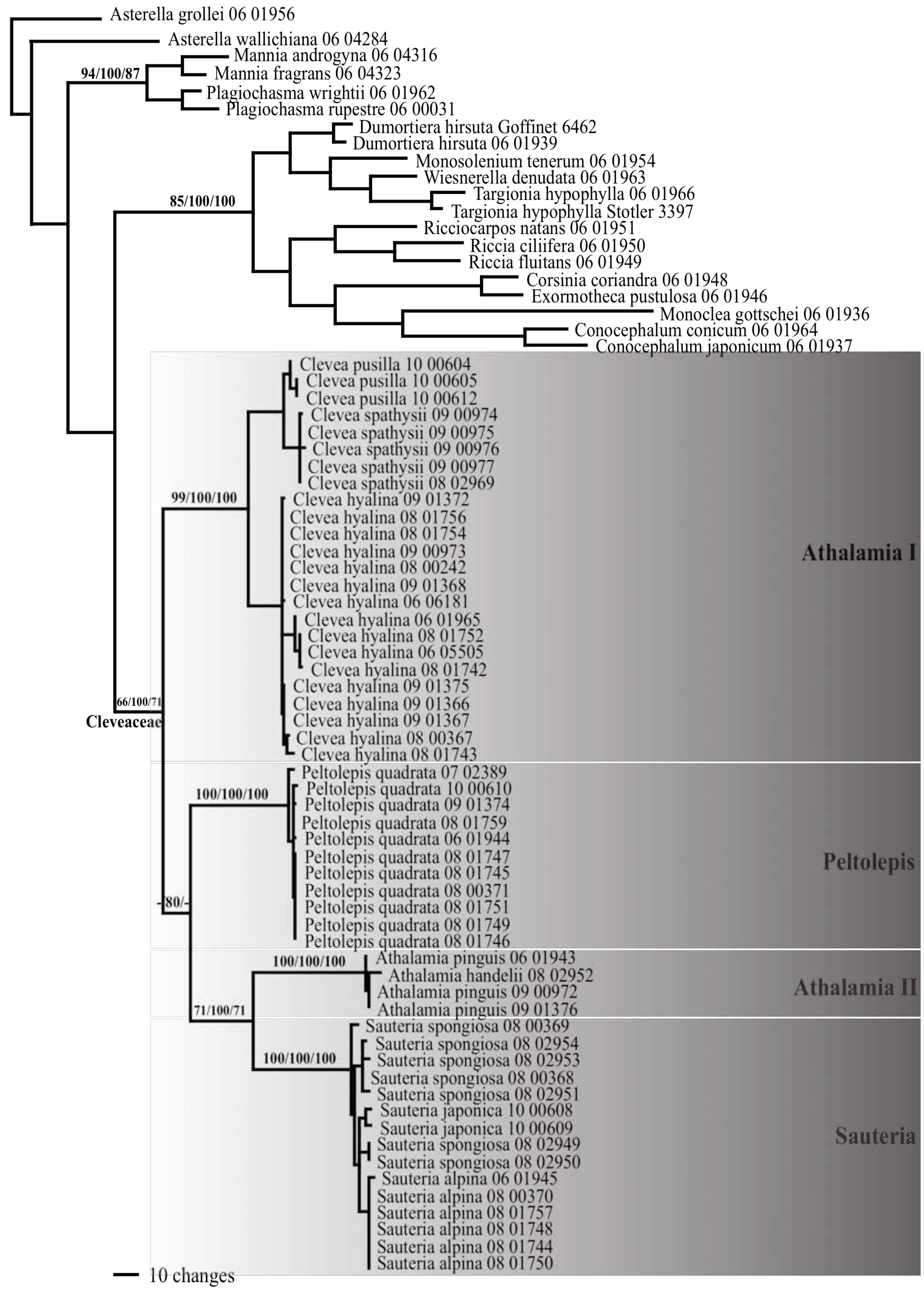


Figure 3.2. Phylogram (one of 154 equally parsimonious trees) with major clades highlighted and annotated. Numbers above branches indicate Maximum Parsimony Bootstrap Support (PS) values, Bayesian Posterior Probabilities (BPP) and Maximum Likelihood Bootstrap Support (ML). The tree had a length of 1313 steps, CI=0.637 and RI=0.548.

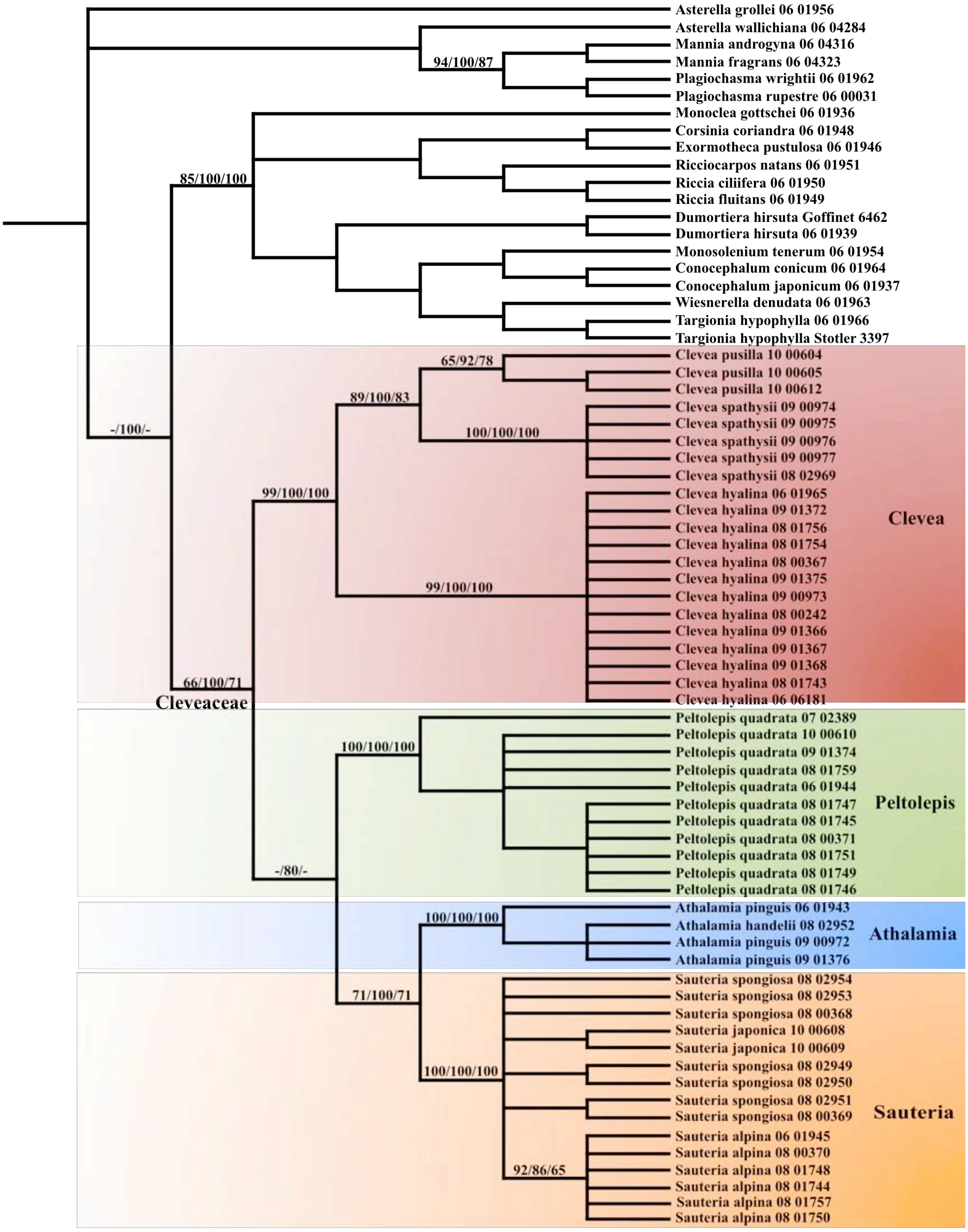


Figure 3.3. Bayesian majority tree with major clades highlighted and annotated. Numbers above branches represent Maximum Parsimony Bootstrap Support (PS) values, Bayesian Posterior Probabilities (BPP) and Maximum Likelihood Bootstrap Support (ML).

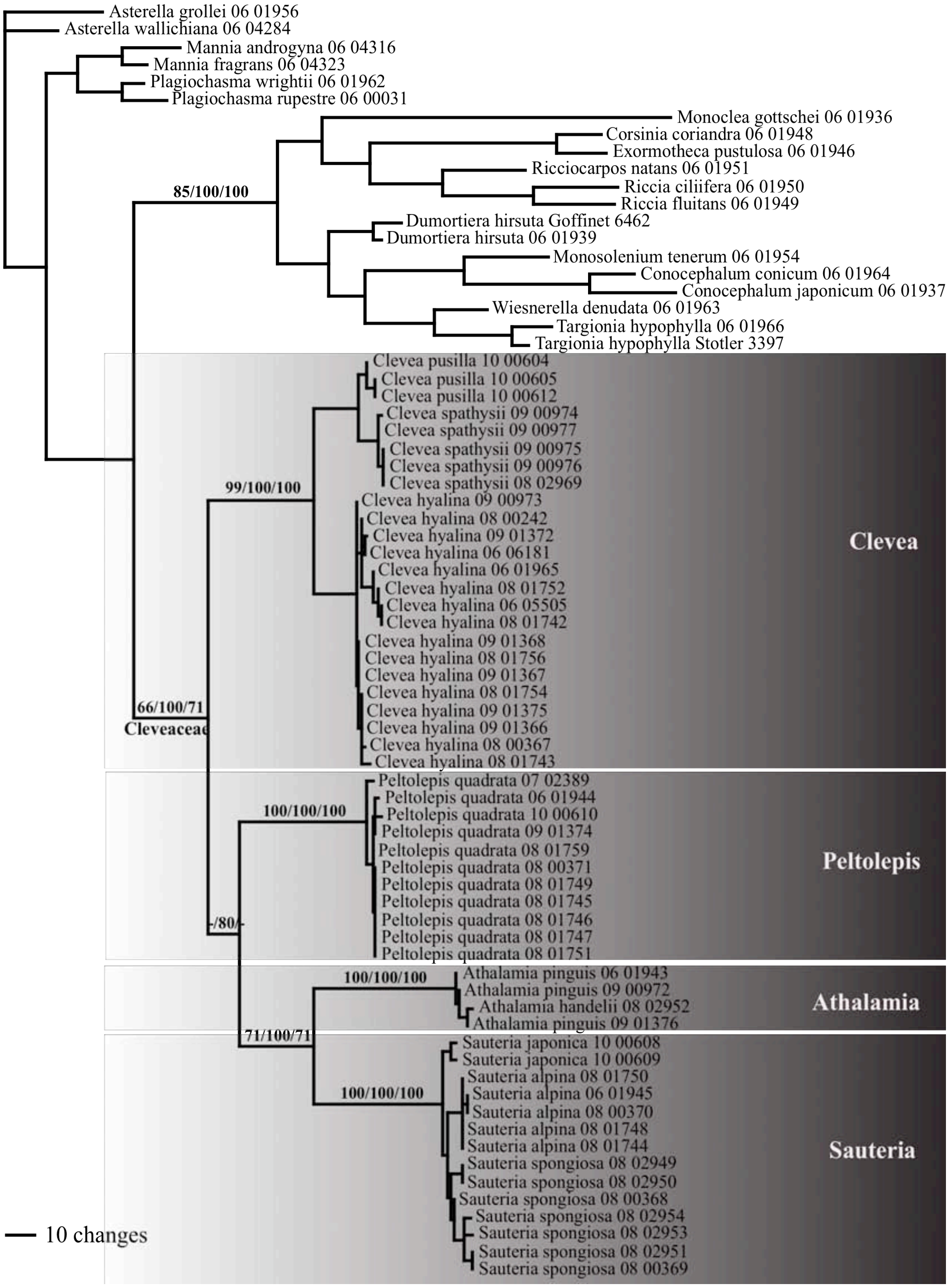


Figure 3.4. Likelihood tree with major clades highlighted and annotated. Numbers above branches represent Maximum Parsimony Bootstrap Support (PS) values, Bayesian Posterior Probabilities (BPP) and Maximum Likelihood Bootstrap Support (ML).

3.4.2 Reconstruction of ancestral states in Cleveaceae

3.4.2.1 Distribution of characters across taxa

Within the ingroup taxa, *Clevea* and *Athalamia* lack a rhizoid furrow, while *Sauteria* has one and *Peltolepis* two. In the outgroup, *Plagiochasma wrightii* and *P. rupestre* have no rhizoid furrows, *Asterella*, *Mannia*, *Conocephalum conicum* and *Exormotheca pustulosa* have one rhizoid furrow, and *Dumortiera hirsuta*, *Monosolenium tenerum* and *Wiesnerella denudata* have two furrows. However, *Corsinia coriandrina*, *Monoclea gottschei*, *Targionia hypophylla*, *Riccia fluitans* and *Ricciocarpos natans* lack a carpocephalum stalk. The character states were scored as 0=none; 1=one; 2=two; ?=carpocephalum stalk absent

Except *Clevea* and *Athalamia* in the ingroup, all other taxa have terminal archegoniophores. In the outgroup all taxa except *Plagiochasma*, *Corsinia coriandrina*, *Riccia fluitans* and *Ricciocarpos natans* (which have dorsal archegoniophores or archegonia dorsal on the thallus) have terminal archegoniophores. The character states were scored as 0=terminal; 1=dorsal.

Radial wall thickening was observed in *Clevea hyalina*, *Peltolepis*, *Athalamia* and rarely in *Sauteria alpina.* All other species in the ingroup lack radial wall thickening. In the outgroup, with the exception of *Monoclea* and *Monosolenium* (which lack air pores), all other species lacked radial wall thickenings. The character states were scored as 0=absent; 1=present;?=air pores absent.

All taxa in the ingroup except *Athalamia pinguis* have wide, polygonal air chambers and all taxa in the outgroup except *Dumortiera*, *Monoclea* and *Monosolenium* (which lack air chambers (Bischler 1998; Schuster 1992) have wide, polygonal air chambers. The character states were scored as 0=wide & polygonal; 1=narrow & slit-like; ?=air chambers absent

Except *C. hyalina*, all other ingroup species were autoicous. All outgroup taxa except *Asterella wallichiana*, *Mannia fragrans*, *Conocephalum conicum* and *Monoclea gottschei* were autoicous. The character states were scored as 0=autoicous; 1=dioicous.

Androecial scales are present in *Clevea hyalina* and *Peltolepis* but lacking in all other ingroup taxa. In the outgroup all taxa except *Asterella grollei*, *Wiesnerella* and *Plagiochasma* have antheridial scales. The character states were scored as 0=absent; 1=present.

All taxa within the ingroup except *Peltolepis*, which has androecia aggregated into a disc, have closely aggregated antheridia. This character is polymorphic in the outgroup taxa; in *Riccia fluitans* – scattered, *Corsinia*, *Ricciocarpos*, *Exormotheca* – open grooves, *Asterella*, *Plagiochasma*, *Mannia androgyna* – cushions, *Mannia fragrans* – disc, and *Monoclea* and *Dumortiera* – receptacles (antheridiophores) (Bischler 1998; Bischler-Causse et al. 2005; Schuster 1992). The character state was scored as 0=scattered; 1=closely aggregated; 2=cushion; 3=disc; 4=receptacle; 5=open groove.

All ingroup taxa except *Sauteria spongiosa* had antheridia on the main thallus. In the outgroup, with the exception of *Targionia*, all species had antheridia on the main thallus, while *Plagiochasma* was polymorphic for the character. The character states were scored as 0=main thallus; 1=ventral branch.

Except *Sauteria* and *Athalamia* in the ingroup and *Corsinia coriandrina*, (Bischler-Causse et al. 2005), *Monoclea* (Schuster 1992) and *Dumortiera* (Bischler-Causse et al. 2005) in the outgroup, secondary pigmentation was present. The character states were scored as 0=absent; 1=present.

All included taxa, except *Monoclea* (Bischler 1998; Campbell 1898), have ventral scales, arranged either in distinct rows or ill-define rows. Within the outgroup, except *Ricciocarpos natans* and *Corsinia coriandra*, all taxa have ventral scales arranged in distinct rows (Bischler-Causse et al. 2005; Schuster 1992). The character states were scored as 0=ill-defined rows; 1=distinct rows; ?= ventral scales absent.

The degree of ventral scale projection beyond the thallus margin shows variation within ingroup taxa. *Clevea hyalina* has ventral scale protrusions in the apical region, *Athalamia hyalina* and *A. handelii* have ventral scale protrusion along their margins while *Sauteria* and *Peltolepis* have protrusions only at the apex. Within the ougroup, except *Exormotheca pustulosa* (with protrusions along margins) and *Monoclea gottschei* (ventral scales absent), all other species have ventral scales protrusions only at their apices (Bischler-Causse et al. 2005; Schuster 1992). The character states were scored as 0=only at apex; 1=apical region; 2=along margins; ?=scales absent.

Clevea spathysii, *C. pusilla* and *Sauteria* have oil-bodies in their ventral scales, whereas in *C. hyalina*, *Peltolepis* and *Athalamia* ventral scale oil-bodies are absent. In the outgroup taxa, except *Dumortiera hirsuta*, *Riccia fluitans* and *Monoclea gottschei* (ventral scales absent), species have ventral scale oil-bodies. The character states were scored as 0=absent; 1=present; ?=ventral scales absent.

A morphological data matrix showing the distribution of characters across taxa is presented in Appendix 3.3

3.4.2.2 Ancestral character states in Cleveaceae

a) Number of rhizoid furrows in archegoniophore

An ancestral condition without a rhizoid furrow in Cleveaceae is reconstructed with ML as marginally more likely (proportional likelihood 0.6026) than one (0.2254) or two furrows (0.1181). Likelihood reconstructions then shows a gaining of a furrow in *Sauteria* (0.9629), and doubling in *Peltolepis* (0.9585) (Fig. 3.5,i). According to MP the ancestral condition is uncertain, either none or one (Fig. 3.5,ii).

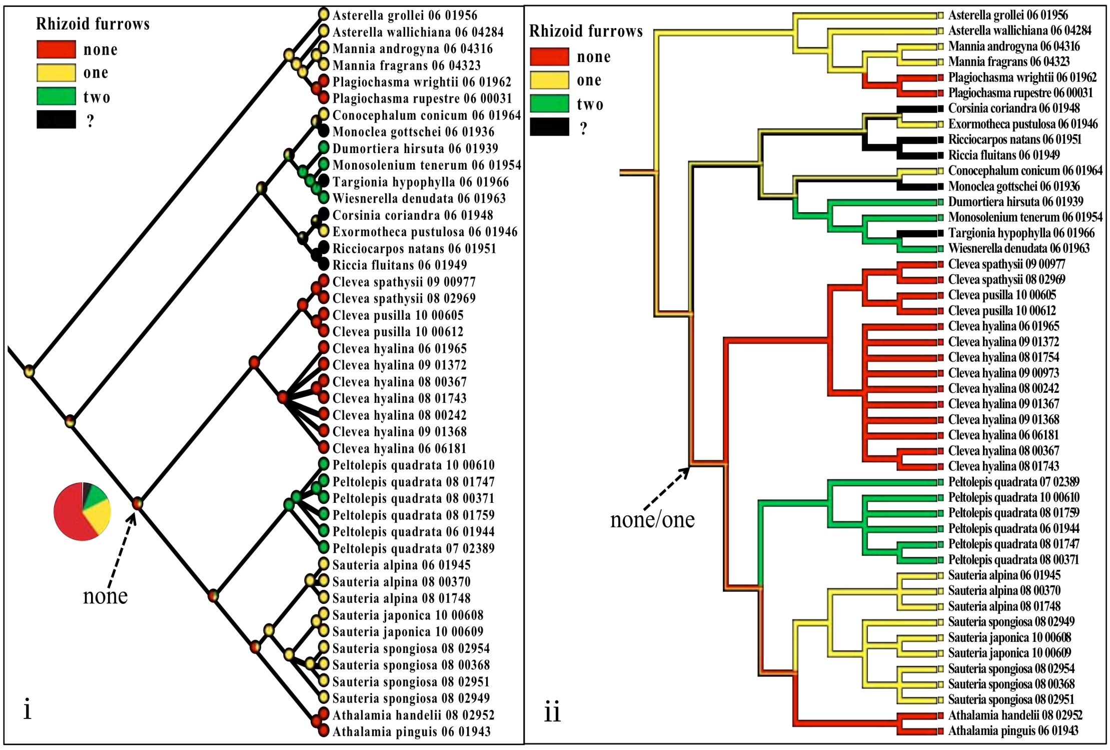


Figure 3.5. Reconstruction of number of rhizoid furrows in the carpocephalum stalk mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

b) Archegonia/ archegoniophore position

A terminal position of the archegoniophore was reconstructed with ML as more likely to be the ancestral state for Cleveaceae (proportional likelihood 0.7380) than a dorsal position (0.2620), with two independent changes to dorsal in *Clevea* (0.9379) and in *Athalamia* (0.9380) (Fig. 3.6, i). The MP criterion shows the same pattern, with a terminal position ancestral (Fig. 3.6, ii).

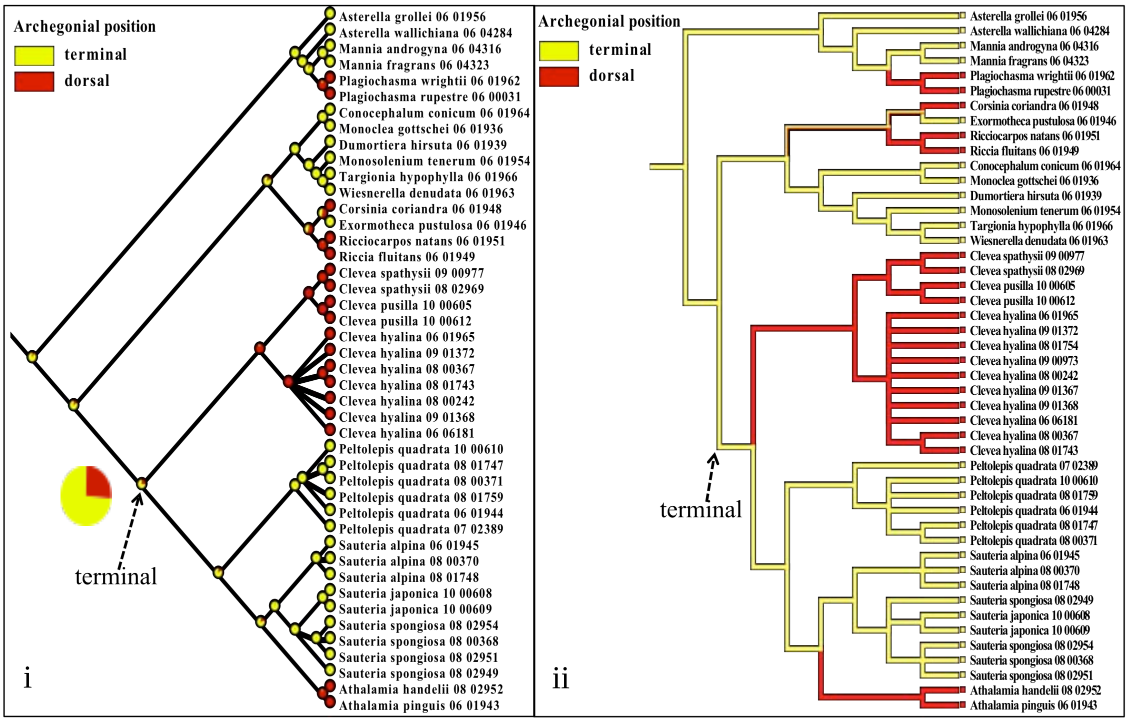


Figure 3.6. Reconstruction of archegonia/archegoniophore position mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

c) Thickening of radial walls of epidermal pores

Pore wall thickening was reconstructed by ML as more likely to be absent in the ancestor to Cleveaceae (proportional likelihood 0.6436) than present (0.3545). The character shows a change to presence in the Cleveaceae clade with two reversals in *C. spathysii*/*C. pusilla* (0.9854) and *Sauteria* (0.9756) clades (Fig. 3.7, ic). The MP criterion reconstructed the character as uncertain, either absent or present (Fig. 3.7, ii).

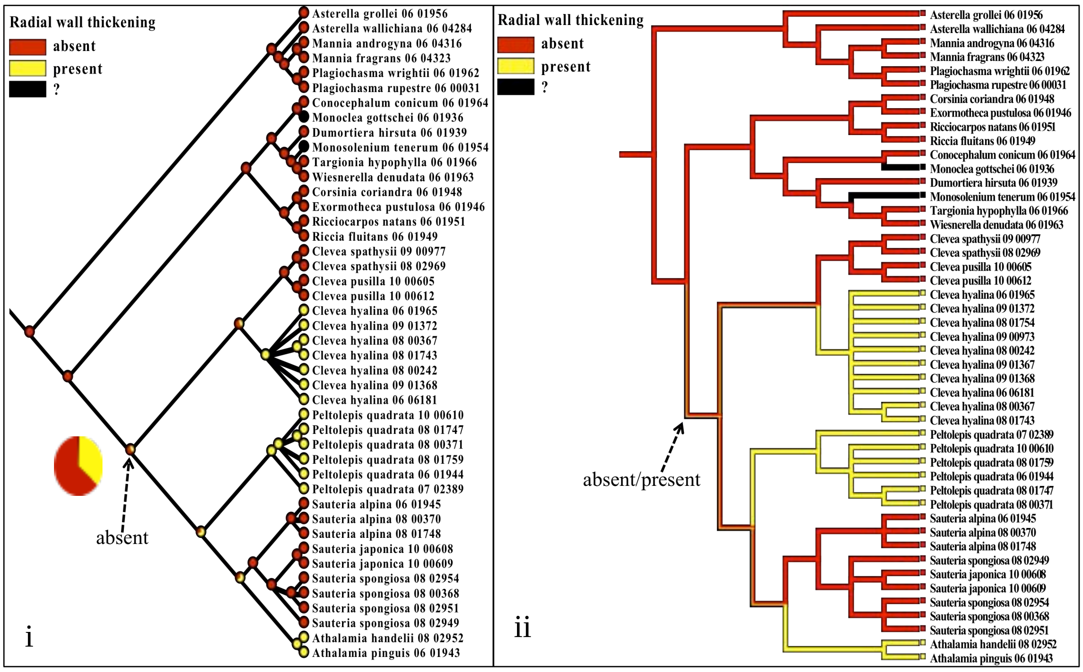


Figure 3.7. Reconstruction of radial wall thickening of air-pores mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

d) Width and shape of air chambers

Polygonal air chambers were reconstructed by ML as present in the ancestor to Cleveaceae (proportional likelihood 0.9998), with a single change to narrow air chambers in *Athalamia* (0.9723) (Fig. 3.8, i). The MP reconstruction showed the same pattern, with a single change to narrow air chambers and an ancestral state of polygonal air-chambers (Fig. 3.8, ii).

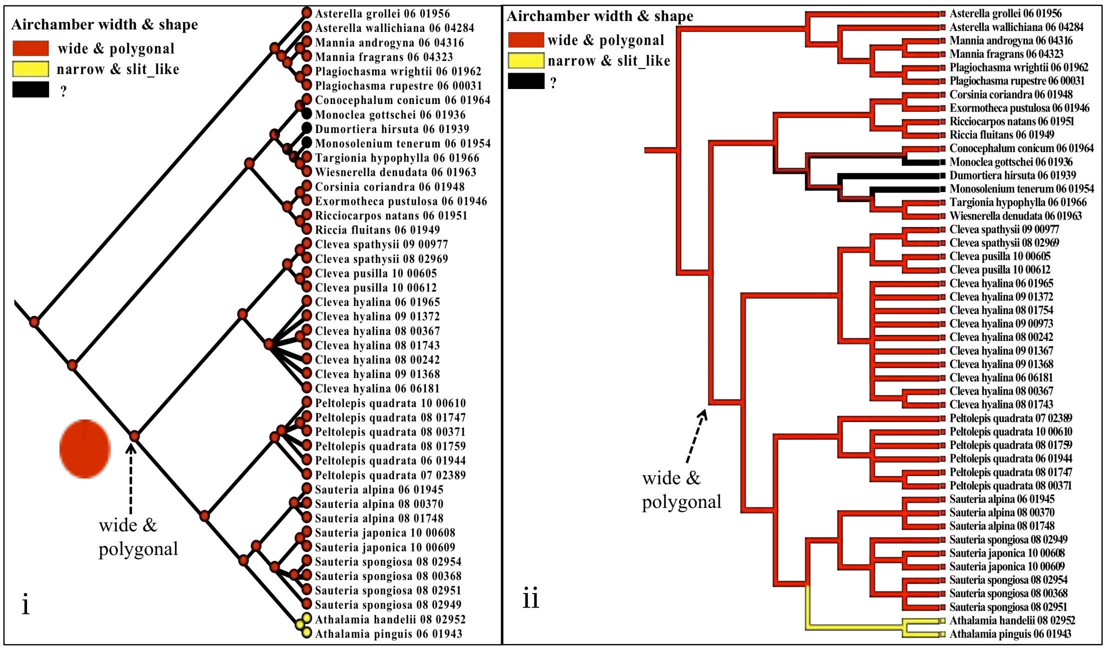


Figure 3.8. Reconstruction of air-chamber width and shape mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

e) Sexual condition

The autoicous sexual condition was reconstructed by ML as the ancestral state for Cleveaceae (proportional likelihood 0.9733), with an independent change to the dioicous state in *Clevea hyalina* (0.9999) (Fig. 3.9, i). The MP criterion also reconstructed the ancestral state as autoicous (Fig. 3.9, ii).

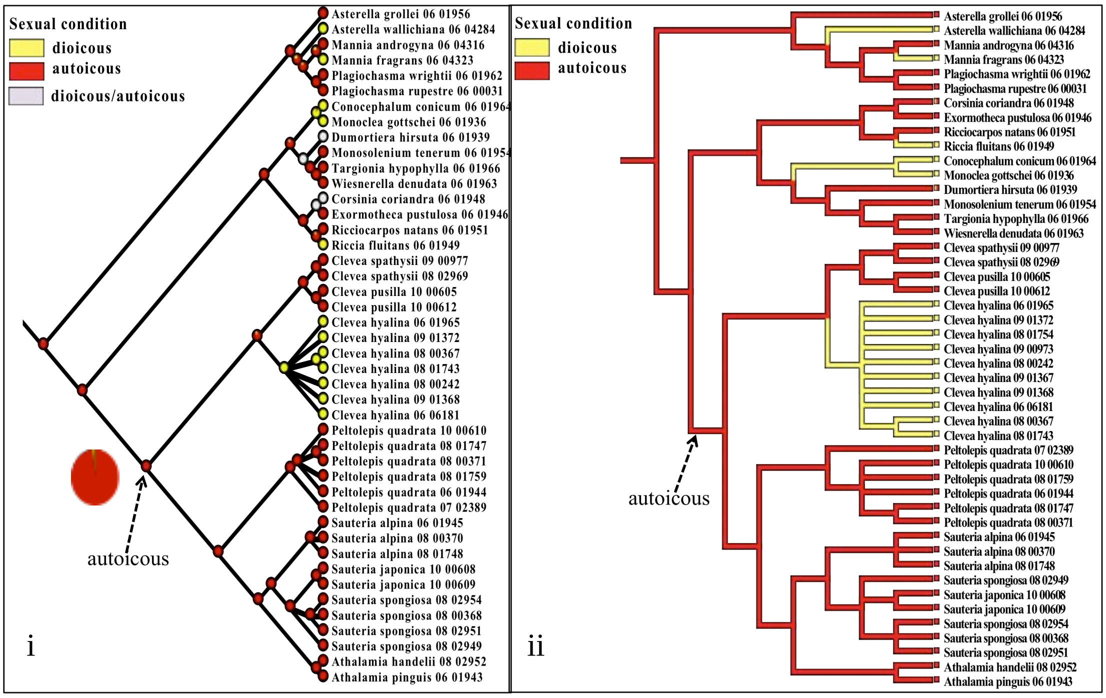


Figure 3.9. Reconstruction of sexual conditions mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

f) Androecial scales

An ancestral condition of absence of androecial scales in Cleveaceae is marginally more likely (proportional likelihood 0.7960) than presence (0.2040). Likelihood reconstruction showed an absence of scales in the Cleveaceae with two gains in *Clevea hyalina* (0.9999) and *Peltolepis* clades (0.9410) (Fig. 3.10, i). According to MP criterion the ancestral condition was absence of scales, with independent gains in *Clevea* and *Peltolepis* (Fig. 3.10, ii).

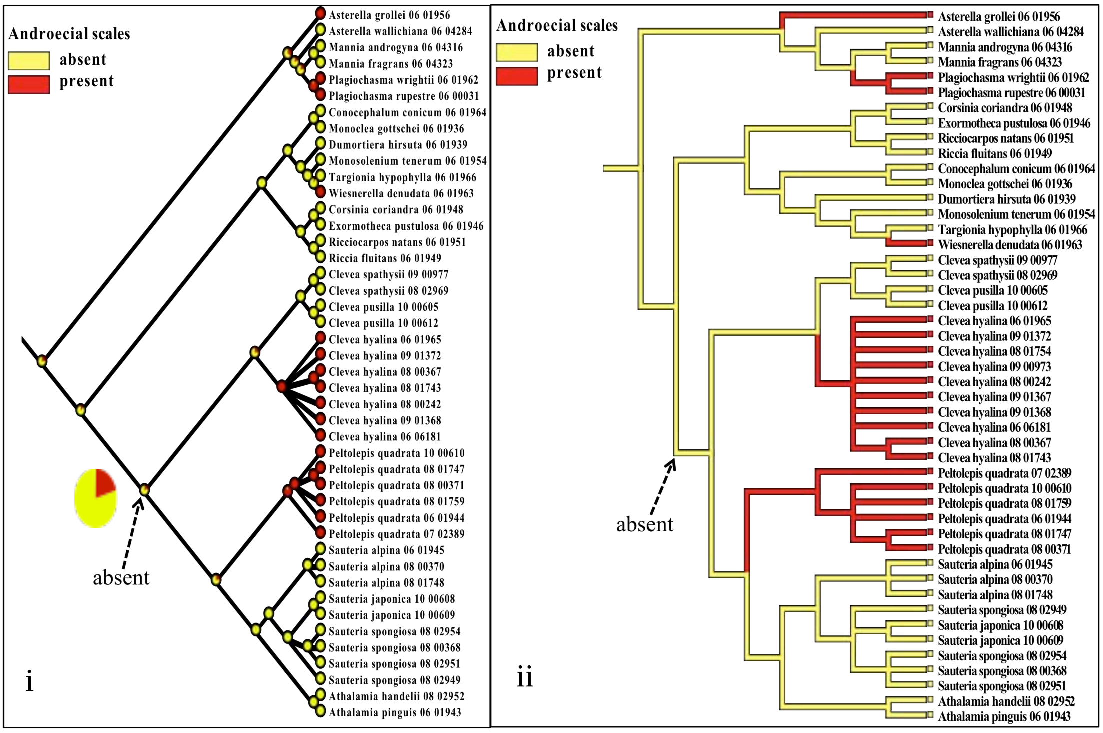


Figure 3.10. Reconstruction of androecial scales mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

g) Androecial aggregation

The closely aggregated condition was reconstructed using ML to be marginally more likely to be the ancestral state (proportional likelihood 0.9240) than aggregated into a disc (0.0212) (Fig. 3.11, i). According to the MP criterion, the ancestral condition was either closely aggregated or in a cushion (Fig. 3.11, ii).

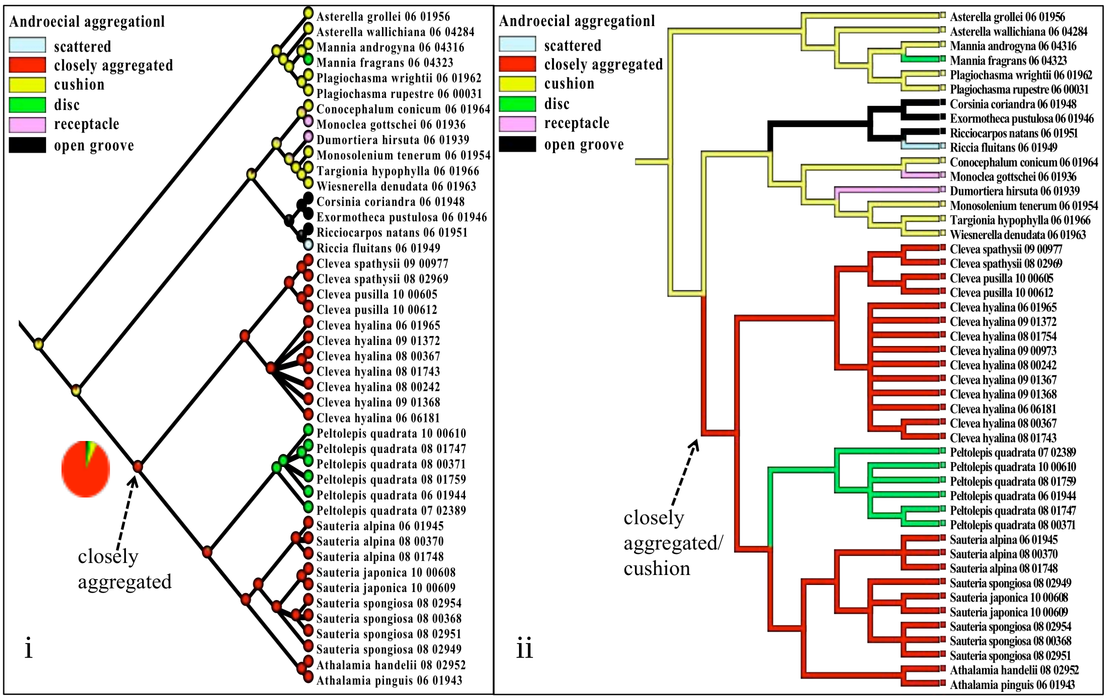


Figure 3.11. Reconstruction of androecial aggregation mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

h) Androecial position

An ancestral state of androecia on the main thallus was reconstructed using ML as more likely (proportionally more likely (0.9999). Antheridial position changed in the *Sauteria spongiosa* clade (0.9991) (Fig. 3.12, i). The MP criterion also reconstructed androecia on the main thallus as ancestral (Fig. 3.12, ii).

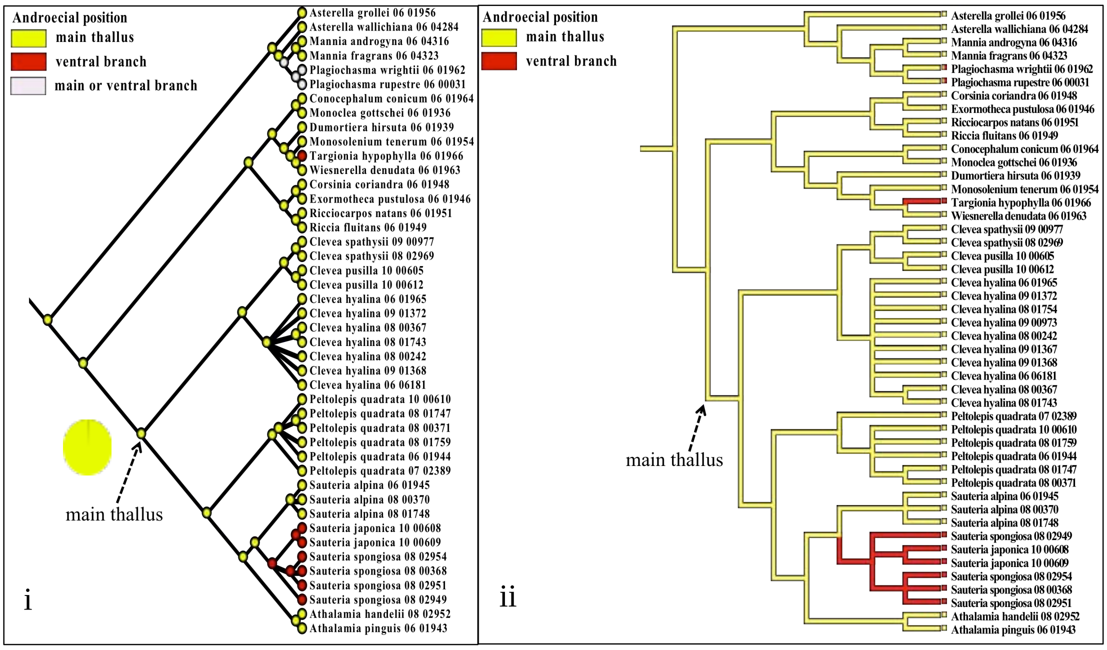


Figure 3.12. Reconstruction of androecial position mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

i) Thallus secondary pigmentation

Thallus secondary pigmentation was reconstructed using ML as present in the ancestor to Cleveaceae (proportional likelihood 0.9945), with a change to absent in the *Sauteria*/*Athalamia* lineage (0.9396) (Fig. 3.13, i). According to MP reconstruction, the ancestral state is also reconstructed as presence of secondary pigmentation, with a single loss in the *Sauteria*/*Athalamia* clade (Fig. 3.13, ii).

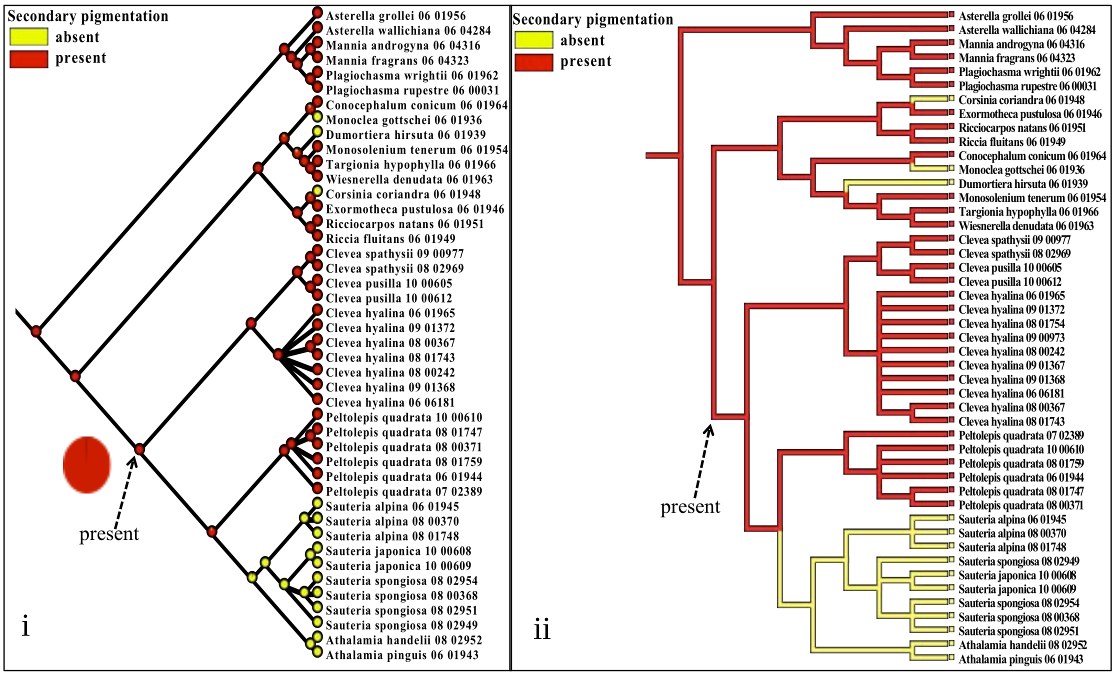


Figure 3.13. Reconstruction of secondary pigmentation mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

j) Ventral scale arrangement

Ventral scales arranged in distinct rows was reconstructed by ML as the ancestral state to Cleveaceae (proportional likelihood 0.9465), with changes to ill defined rows in *Clevea pusilla* (0.9571) and the *Peltolepis/Sauteria/Athalamia* clade (0.5137) and a reversal back to distinct rows in *Athalamia* (0.9761) (Fig. 3.14, i). The MP criterion shows a similar pattern with two changes in the Cleveaceae (Fig. 3.14, ii).

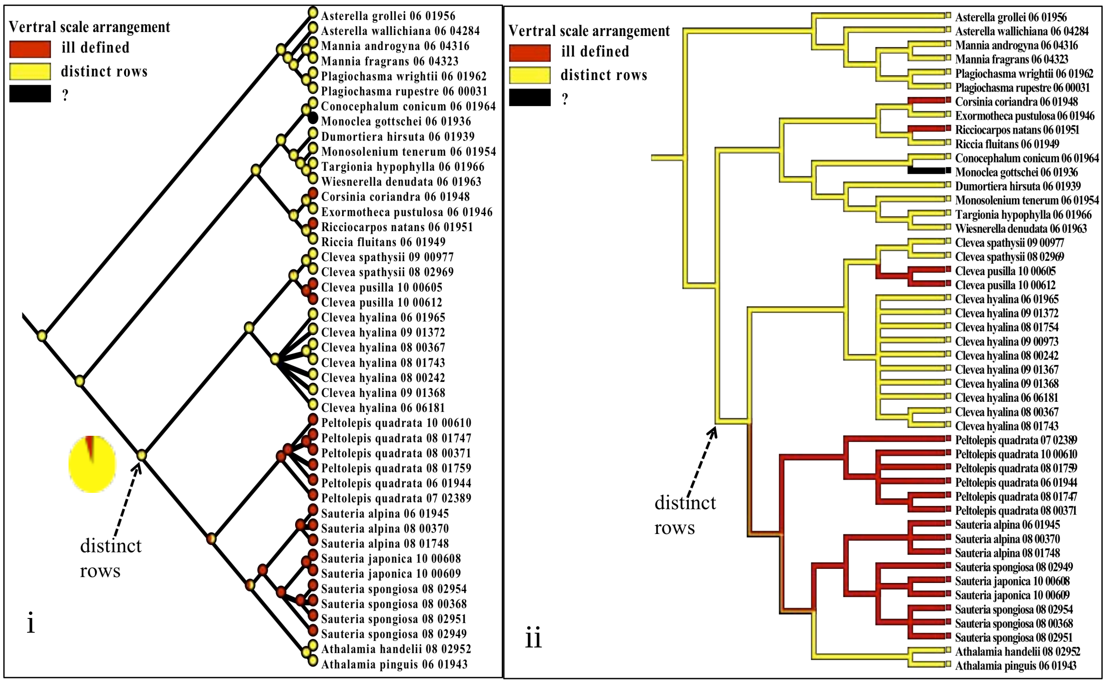


Figure 3.14. Reconstruction of ventral scale arrangement mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

k) Ventral scale protrusion

Ventral scale protrusion was reconstructed by ML as lacking (or only at apex) in the ancestor to Cleveaceae (proportional likelihood 0.9785), with apical protrusion evolving in *Clevea* (0.9808) and marginal protrusion in *Athalamia* (0.9811) (Fig. 4.15, ik). The MP criterion also showed the ‘only at apex’ state as ancestral to Cleveaceae (Fig. 4.15, ii).

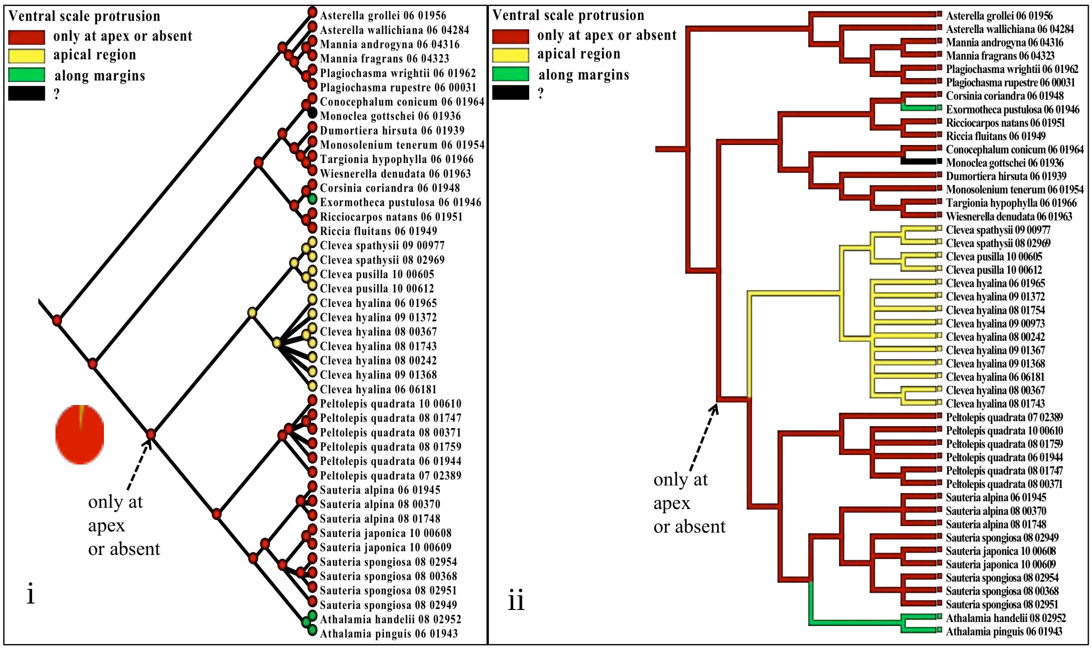


Figure 3.15. Reconstruction of ventral scale protrusion mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

l) Ventral scale oil bodies

Presence of oil bodies in ventral scales was reconstructed by ML as more likely to be present in the ancestor to Cleveaceae (proportional likelihood 0.6306) than absent (0.3668), with independent losses in *Clevea hyalina* (0.9999), *Athalamia* (0.9850) and *Peltolepis* (0.9850), followed by regain in *Sauteria* (0.9665), *Clevea spathysii* and *C. pusilla* (0.9743) (Fig. 4.16, i). Using the MP criterion, the ancestral state was reconstructed as uncertain, either absent or present (Fig. 4.16, ii).

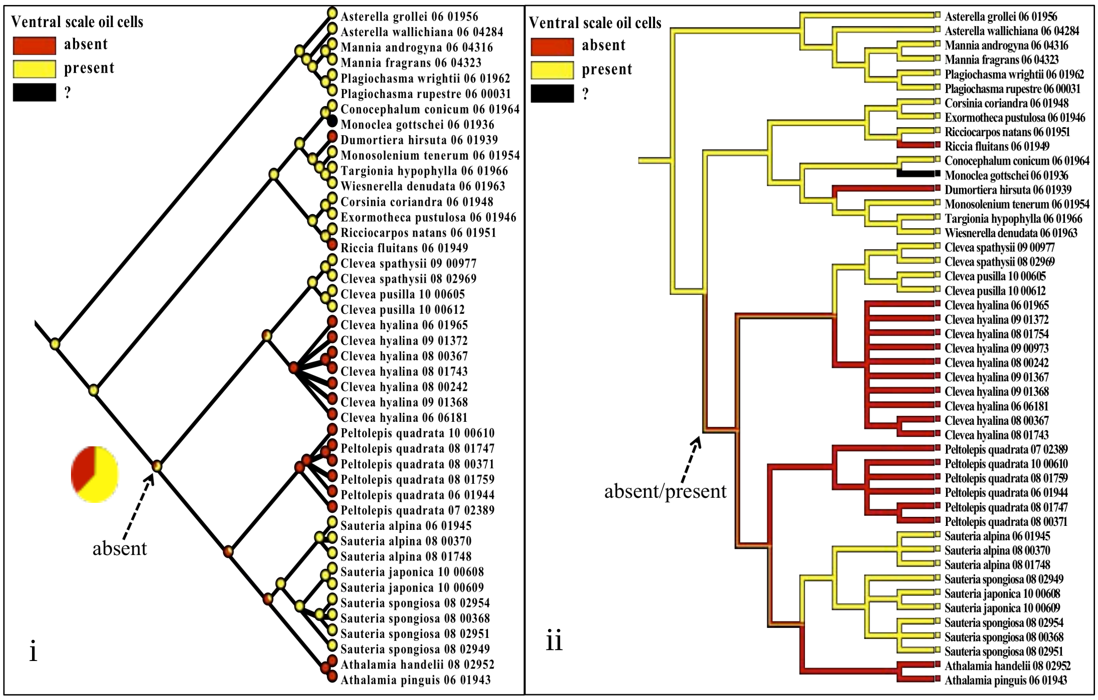


Figure 3.16. Reconstruction of ventral scale oil-bodies mapped across the most likely topology derived from ML analysis of the three plastid regions (*psb*A, *rpo*C1 and *rps*4) and one nuclear region (26S) using, i) maximum likelihood with pie charts at nodes representing proportional likelihood for each state ii) maximum parsimony with branch colour indicating the ancestral character reconstruction.

3.5 Discussion and conclusions

3.5.1 Phylogenetic relationships of genera of Cleveaceae

Cleveaceae comprises four well-supported monophyletic lineages corresponding to the currently accepted genera *Peltolepis*, *Sauteria* and two clades comprising a polyphyletic *Athalamia*. Phylogenetic support for the recognition of *Athalamia* in its current sense is therefore lacking. The name *Athalamia* must be applied to the clade composed of *A. pinguis* (the type species of the genus *Athalamia*) and *A. handelii* (*Athalamia* I in Fig.3.2), which form the sister-group to *Sauteria*. The earliest available generic name for the clade composed of *A. hyalina*, *A. spathysii* and *A. pusilla* (*Athalamia* II in Fig. 3.2) is *Clevea*, which must be resurrected for these species – viz. *Clevea hyalina*, *Clevea spathysii* and *Clevea pusilla*. Recognition of *Clevea* distinct from *Athalamia* is a reversal of the synonymising of those two genera by Shimizu and Hattori (1954). As *Clevea* was widely recognized before that time, new combinations are not necessary except for one species *A. pusilla* (Steph.) Kashyap., which has never been placed in *Clevea* before. The name *Clevea pusilla* (Steph.) Rubasinghe & D.G.Long, is therefore presented as a new combination (Rubasinghe et al. 2011 in press). *Peltolepis, Sauteria* and *Athalamia sensu stricto* are phylogenetically distinct strongly supported (Figs, 3.2, 34.3, 3.4) and morphologically well-defined genera (Fig. 3.20). Merging two (*Athalamia* & *Sauteria*) or all three genera would obfuscate significant transformations between them, such as in the position of the archegonia and in its stalk anatomy. Therefore a four-genus solution: *Clevea*, *Athalamia*, *Sauteria* and *Peltolepis*, is recommended to reconcile molecular and morphological data.

Within *Clevea*, three well-supported monophyletic groups were resolved and these represented three well-known species within the genus: *C. hyalina* (the type of the genus), *C. spathysii* and *C. pusilla* (Fig. 3.3). The lack of molecular structure within *Peltolepis* and *Athalamia* was consistent with their status as monotypic genera. However specific delimitation within *Sauteria* was ambiguous, with *S.*

spongiosa and *S. japonica* comprising a polytomy (Fig. 3.3). However, *S. alpina* was resolved as a monophyletic group with strong MP, BI and ML support.

Leitgeb (1881) considered Cleveaceae as one of the end-points of several lines of increasing gametophyte complexity, starting with the ‘simple’ *Riccia* through a *Corsinia*-like form to *Clevea* then *Peltolepis* (‘Astroporae’= Cleveaceae). Within the ‘Astroporae’, *Clevea* was considered ancestral to *Peltolepis* and *Sauteria* was placed between them. This ‘antithetic’ theory of liverwort evolution was followed by Schiffner (1893) and Cavers (1910−1911) who published a phylogenetic tree of Marchantiales, with *Clevea* giving rise to two lines of evolution, on one hand to *Gollaniella* [= *Clevea pusilla*], on the other to *Sauteria* then *Peltolepis* (Fig. 3.17). Following Goebel’s (1910), opposing ‘homologous’ theory, which explained the evolution of Marchantiales by reduction rather than elaboration, Kashyap (1914, 1915) proposed a phylogeny which showed several lines of reduction from an ancestral *Marchantia*, one of these leading to *Sauteria* then *Clevea* and *Athalamia* (Fig. 3.17). Goebel’s theory was further elaborated by Bergdolt (1926) in relation to Cleveaceae, and he illustrated a line of evolution by reduction from Marchantiaceae leading to *Peltolpis grandis* (=*P. quadrata*), *Sauteria alpina*, *Clevea hyalina* and *Clevea rousseliana* (= *C. spathysii*), *Athalamia pinguis* and finally *Riccia* species (Fig. 3.17). Although Schuster (1992) noted that there are discrepancies in generic delimitations in Cleveaceae, he did not develop the phylogenetic implications of this. Bischler (1998), using her evidence from morphology based phylogenetic analysis, suggested a paraphyletic Cleveaceae with *Peltolepis* removed from Cleveaceae and placed close to *Monosolenium*. Differences in position of androecia and archegonial stalk structure were regarded strong enough characters in this separation (Bischler, 1998). Based on Bischler’s (1998) evidence, *Peltolepis* was placed in Monosoleniaceae by Grolle & Long. (2000). However this transfer was shown to be erroneous by Forrest et al. (2006) who confirmed its placement within Cleveaceae using phylogenetic inference from sequence data; in that study *Peltolepis* was only distantly related to *Monosolenium* (Fig. 3.7), the type genus of Monosoleniaceae (Forrest et al. 2006).

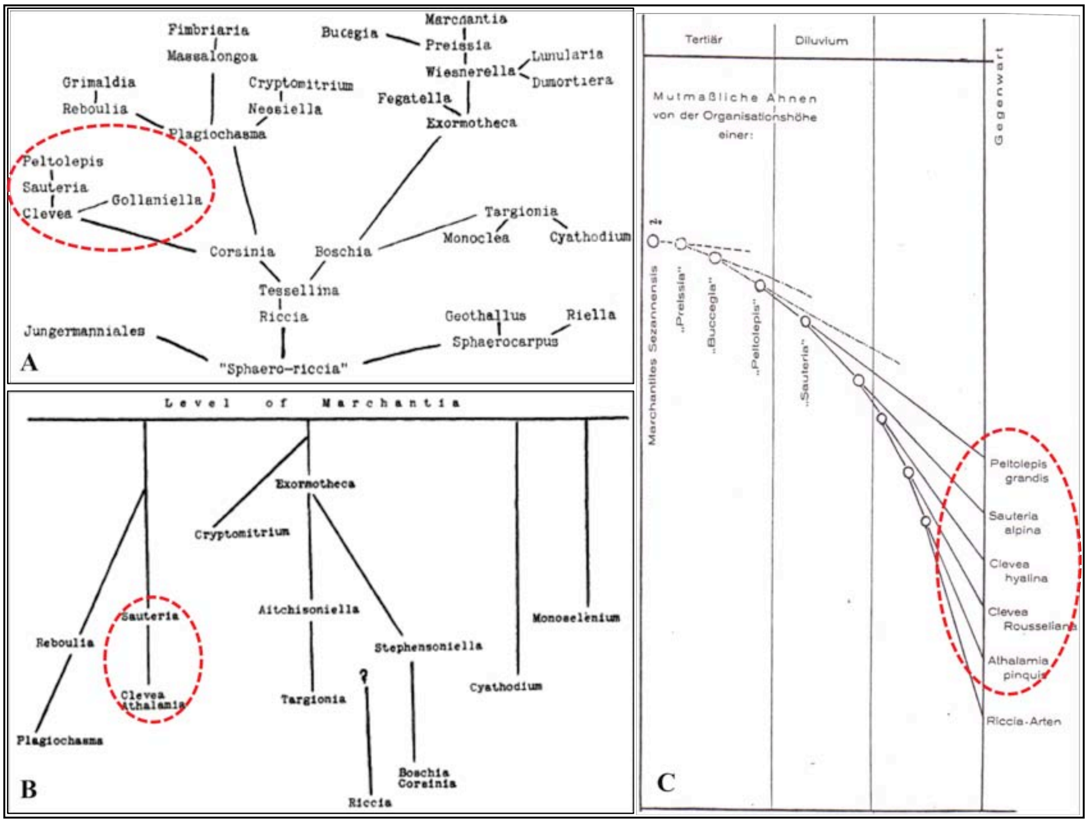


Figure 3.17. Phylogenetic hypotheses of evolution of Cleveaceae by A) Cavers (1910), B) Kashyap (1914) and C) Bergdolt (1926).

The present molecular phylogenetic analysis is the most detailed phylogeny for the family Cleveaceae and the first molecular study taking into consideration its generic relationships to date. The sampling of Cleveaceae possible for this study is much wider than that used by Wheeler (2000) and Forrest et al. (2006) and makes possible the testing of relationships of the genera of Cleveaceae, as well as almost all the widely-recognised species in the family. This study further strengthens the support for the monophyly of the family. However, the published morphology-based phylogenetic hypotheses are not congruent with this molecular phylogenetic analysis (Figs. 3.2, 3.3, 3.4). *Clevea*, the earliest diverging genus, is now resolved as sister to *Peltolepis*, *Sauteria* and *Athalamia* with strong support from all analyses. Although MP, BI and ML tree topologies indicate *Peltolepis* as the next diverging genus within the family, the clade comprising *Peltolepis*, *Athalamia* and *Sauteria* is not well-supported, hence the relationships between these three genera remain unresolved.

Therefore, further analysis with more samples and loci are necessary to confirm this relationship. However, *Athalamia* and *Sauteria* were resolved as closely related with significant MP, BI and ML support. Phylogenetic relationships resolved from the present analysis do not support any of the other three hypothesis of evolution of genera discussed above, although the ancestral position of *Clevea* is supported as in Leitgeb's scheme, and the derived position of *Athalamia* as proposed by Bergdolt.

3.5.2 Character evolution within Cleveaceae

One of the clearest conclusions emerging from recent phylogenetic studies on complex thalloid liverworts is the remarkable incongruence between morphology-based topologies (e.g. Bischler 1998) and those obtained with molecular data (e.g. Boisselier-Dubayle et al. 2002; Long et al. 2000; Schill et al. 2010; Wheeler 2000). This can only be explained by extensive homoplasy throughout the group and frequent reversals demonstrated by characters traditionally regarded as important in classification, such as xeromorphy/ hygromorphy, elaboration of reproductive branches, anatomy of air chambers and air pores. Because of this, it is scarcely surprising that the relatively few characters used to delimit genera in Cleveaceae should also have been subject to reversals in the past. This appears to be true for the characters formerly considered to be the most important for distinguishing genera in Cleveaceae.

In past morphology-based classifications of complex thalloids liverworts, position of the archegoniophore on the thallus and the number of rhizoid furrows in the carpocephalum stalk were considered to be key characters in defining many genera (Bischler 1998). In Cleveaceae these characters were the most important ones used in generic delimitation: *Sauteria*; with a single rhizoid furrow and terminal archegoniophore, *Peltolepis*; with two rhizoid furrows and terminal archegoniophore and *Clevea*; later included in *Athalamia* by virtue of the same two characters, without rhizoid furrow and archegoniophore dorsal on the thallus (Evans 1923; Müller 1954; Schiffner 1893; Shimizu & Hattori 1954; Schuster 1992).

However, morphological character reconstruction does not support a linear progression of these two characters, but shows that the two characters were subjected to reversals in the past (Figs. 3.5, 3.6, 3.19). Maximum likelihood reconstruction supported a furrow-less archegoniophore to be the ancestral condition in Cleveaceae, meaning that a furrow was gained independently in *Sauteria* with a doubling in *Peltolepis*. The main function of the rhizoid furrow (which is thought to be a modified branch of the thallus) is thought to be transport of water up to the carpocephalum (Bischler 1998; Crum 2001; Schuster 1992). However, there is a tendency for the carpocephalum stalk to become longer along the line of *Clevea*, *Athalamia* and then to *Peltolepis* and *Sauteria*. It can be assumed that in the ancestor to Cleveaceae, the stalk was short and the carpocephalum was nearer to the thallus and long distance water conduction was not necessary. There is also a tendency to have more lobes in the carpocephalum in *Sauteria* and *Peltolepis*, which may have required additional water supply towards the carpocephalum. A terminal archegoniophore was reconstructed as ancestral to Cleveaceae with two independent changes to a dorsal position in *Clevea* and *Athalamia* (Fig. 3.6). A continuous production of archegoniophores is facilitated by having them on the dorsal surface of the thallus rather than terminal, meaning more spore production and higher dispersal efficiency. It can therefore be assumed that the ancestor to Cleveaceae had a terminal archegoniophore which later evolved to the dorsal position, as better reproductive and dispersal strategies. The clear implication of this picture is that the above two characters used in the past to unite *Athalamia* and *Clevea* prove to be homoplastic which greatly weakens the evidence for uniting the genera as proposed by Shimizu and Hattori (1954) (Fig. 3.18). In fact, the genera can readily be separated by other characters shown in Figure 3.20.

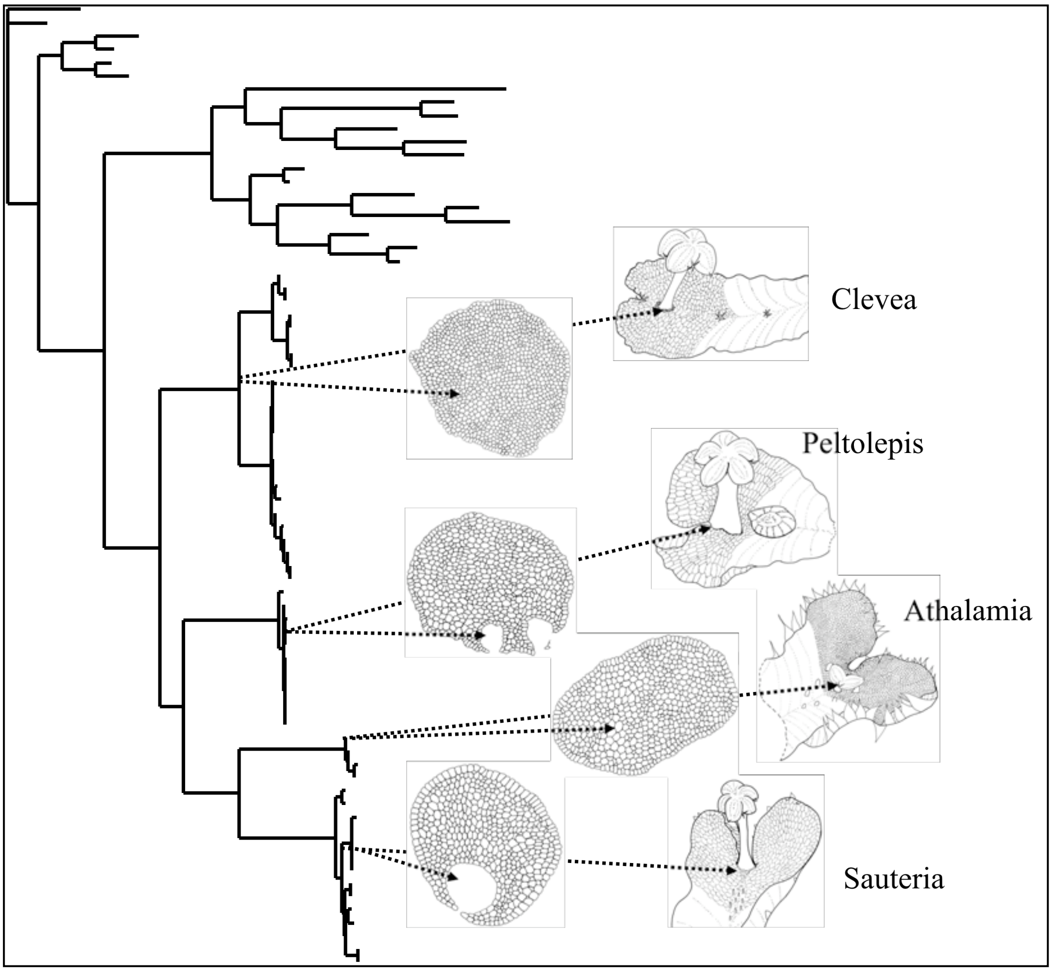


Figure 3.18. Distribution of character states of number of rhizoid furrows and the archegonial position within Cleveaceae.

Leitgeb (1881) united *Clevea* (described by Lindberg, 1868), *Sauteria* (Nees, 1838) and *Peltolepis* (Lindberg, 1876) due to the fact that in all three genera, radial walls of air pores are thickened so that it gives a star-like appearance (stellate air-pores). However, this character was found to be very variable within and between genera of Cleveaceae. Some species of *Clevea*, e.g. *C. spathysii* and *C. pusilla* (Fig. 3.19) completely lack stellate thickenings on their air pores. In *Sauteria*, thickened radial walls were rarely observed and found to be very weak when observed. The strongest thickenings were observed in *Athalamia pinguis*. Although *Clevea hyalina* showed thickened radial walls, the degree of thickening varied from very slight to strong, probably depending on environmental conditions. This agrees with Bergdolt's (1926) observations on lack of radial wall thickenings in *C. rousseliana*

(= *C. spathysii*) and in *C. chinensis* (= *C. pusilla*), however present observations conflict with his comment on *Peltolepis grandis* (= *P. quadrata*) having the weakest thickenings (Bergdolt, 1926). Although Leitgeb's definition is not tenable according to these observations, stellate pore walls are a good practical character in identifying some taxa of the family. According to likelihood character reconstructions (Fig. 3.7, i), lacking pore wall thickenings is the ancestral condition in Cleveaceae and presence of star-like pores is an apomorphy for the family.

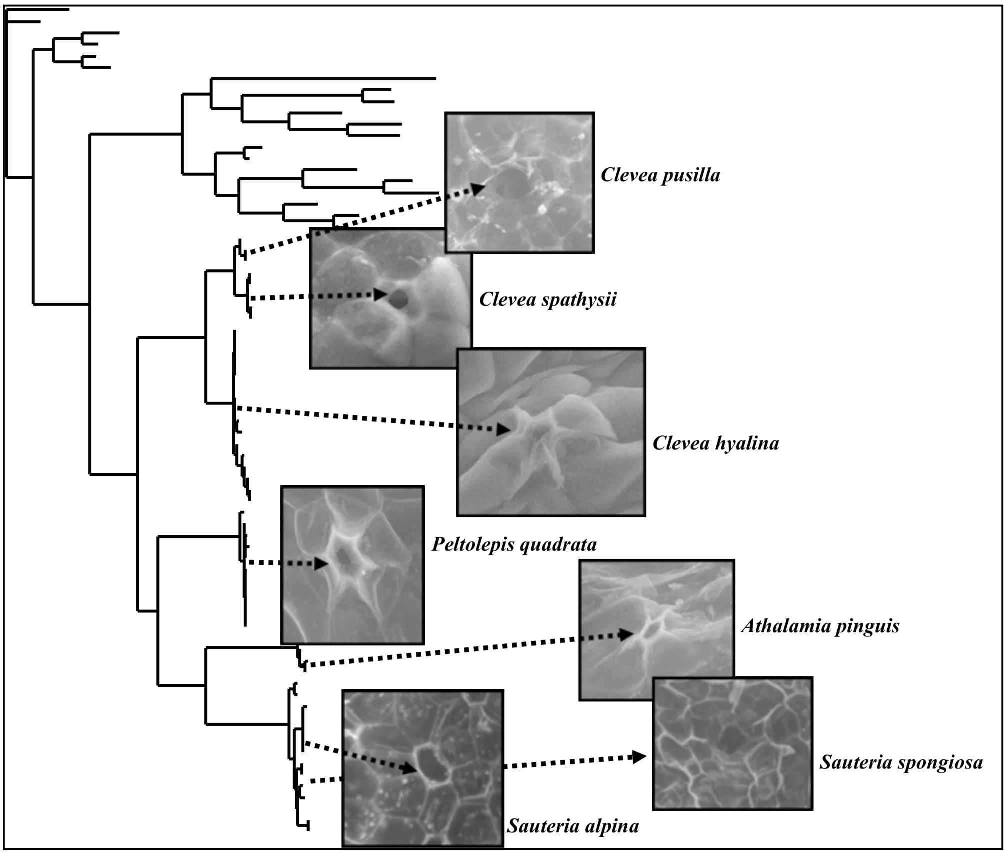


Figure 3.19. Scanning Electron Microscopic (SEM) photographs showing the variation of radial wall thickening within Cleveaceae.

Kashyap (1914), the first author to consider in detail the relationships of *Athalamia*, pointed out that *A. pinguis* was related to both *Clevea* and *Sauteria*, but also showed similarities to *Riccia* in its narrow, slit-like air chambers (Fig.3.8). Bergdolt (1926), also noted that *A. pinguis* is greatly reduced and is closest to Ricciaceae by its narrow, slit-like air chambers (Fig.3.17). However, wide, polygonal shaped air chambers observed in the rest of the Cleveaceae members was reconstructed as the ancestral state in the family with a single change to narrow, slit-like air chambers evolving in *A. pinguis* (Fig. 3.8).

Antheridial scales were not noticed in Cleveaceae by previous workers on the family (Evans 1923; Leitgeb 1881; Lindberg 1868; Solms-Laubach 1899) except Bergdolt (1926). However, Bergdolt considered antheridial scales to be more reduced than archegonial scales (Bergdolt 1926); they were observed in two species of Cleveaceae: *C. hyalina* and *P. quadrata*. However, Bergdolt (1926), who noticed antheridial scales in *C. hyalina* and *P. quadrata*, commented that in *Sauteria alpina* and *Clevea rousseliana* (= *C. spathysii*) antheridial scales have completely disappeared due to loose antheridial arrangement. However, absence of antheridial scales was reconstructed as more likely to be the ancestral condition in Cleveaceae with two independent changes in *C. hyalina* and *P. quadrata* with antheridial scales present.

Bischler (1998), suggested two hypotheses as to the evolution of aggregation of antheridia; antheridia in open grooves gave rise to either scattered antheridia in *Riccia* or to loosely aggregated antheridia, then to antheridia in cushions and finally to antheridiophores. However, antheridial aggregation in Cleveaceae showed two distinct patterns: loosely aggregated on the thallus or aggregated into a disc which was only observed in *Peltolepis*. *Clevea*, *Sauteria* and *Athalamia* showed loosely aggregated antheridia i.e. antheridia developed in irregular rows on the midrib but not sharply separated from the surrounding tissue into a cushion and not as randomly scattered as in *Riccia*. This character was reconstructed as ancestral in Cleveaceae with close aggregation into a disc evolving in *Peltolepis* (Fig. 3.10). Another distinctly variable character observed in Cleveaceae was the position of the antheridia. All species except *Sauteria spongiosa* had their antheridia borne on the main thallus either on a separate branch or behind the archegonia. In *S. spongiosa* antheridia were found on a small ventral branch (ventral-autoicous condition). According to character reconstructions, antheridia borne on the main thallus was ancestral to Cleveaceae with a transfer to ventral branch evolving in *S. spongiosa* (Fig.3.12).

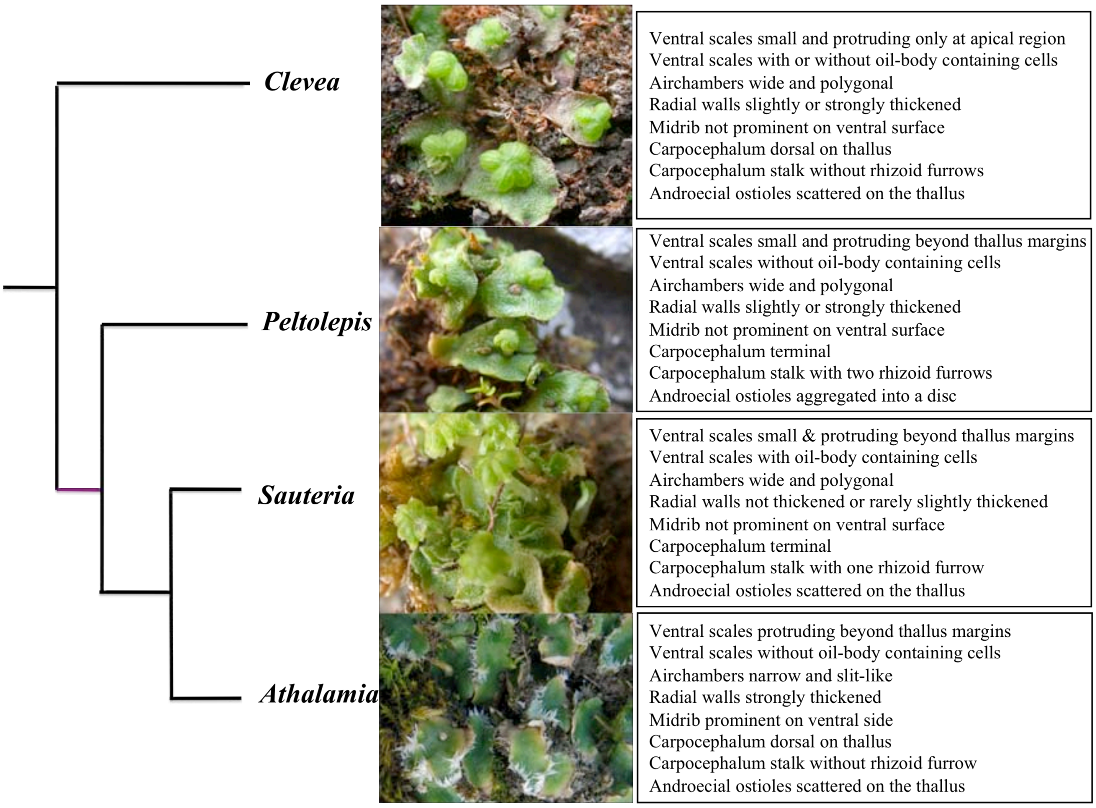
Presence of secondary pigmentation is normally considered as a xeromorphic character, and an adaptation to filter high light intensities (Schuster 1992; 1984). However, within Cleveaceae, *Sauteria* and *Athalamia* did not exhibit any form of secondary pigmentation on the gametophytic thallus whereas all other species showed at least slight purple colouration with *C. spathysii* developing a blackish-purple colour. Lack of secondary pigmentation was reconstructed as a secondary change in Cleveaceae, evolving in the *Sauteria*, *Athalamia* clade.

Ventral scales of Marchantiales are hypothesized to have originated from slime papillae, as an adaptation to protect the apical dividing cell from desiccation (Bischler 1998; Schuster 1992). The assumption that these scales enhance drought tolerance still remains unproven (Bischler 1998). However, Schuster (1992) suggested that scales arranged in distinct rows could be an early derivation in liverworts and small ventral scales in ill-defined rows, a secondary reduction in taxa invading moist habitats. However, ventral scales in Cleveaceae showed considerable diversity in arrangement, degree of protrusion beyond the thallus and in the presence or absence of ventral scale oil-body containing cells. In *Clevea hyalina*, *C. spathysii* and *A. pinguis* ventral scales were arranged in distinct rows (2–4), whereas in *C. pusilla*, *Sauteria* and *Peltolepis* they were arranged in ill-defined longitudinal rows. Scales arranged in distinct rows was reconstructed as ancestral to Cleveaceae by both maximum likelihood and maximum parsimony methods, with three independent changes to an ill-defined arrangement in *C. pusilla*, *Sauteria* and *Peltolepis* (Fig. 3.13). *Athalamia pinguis* showed a marked variation with respect to protrusion of ventral scales, with its long, white scales protruding beyond the thallus margins for a considerable length of the main thallus. This type of conspicuous ventral scale protrusion was not observed in any other species in the family. In *Clevea*, ventral scales protruded in the apical region, but they were not as conspicuous as in *Athalamia* and these projections were not seen along the thallus margin. However, in *Sauteria* and *Peltolepis*, ventral scale protrusions are mostly absent or sometimes visible only at the apex, and this was reconstructed as the ancestral condition in Cleveaceae. According to character reconstructions, apical protrusion evolved in *Clevea* and then marginal protrusion in *Athalamia* (Fig. 3.14). Ventral scale oil bodies also showed distinct variation within Cleveaceae. *Sauteria* was well known for having ventral scale oil bodies and this has been used as a key character in the past (Bergdolt 1926; Müller 1954; Schuster, 1992). However, ventral scale oil bodies in *C. pusilla* and *C. spathysii* have gone unnoticed in the past. Presence of ventral scale oil bodies was reconstructed as the ancestral state in Cleveaceae, with three changes to absence of oil-body containing cells evolving in *C. hyalina*, *P. quadrata* and *A. pinguis* (Fig. 3.15).

It is clear from the results of the present molecular phylogeny and character reconstructions that most characters used in the past as key characters in generic delimitation were homoplastic and have been subject to frequent reversals in the past.

3.5.3 Generic characters in a revised Cleveaceae

Re-assessment of morphological characters shows that for the four robust clades resolved from the molecular phylogeny, each has a unique combination of characters (Fig. 3.20). Ventral scale protrusion, presence of secondary pigmentation, aggregation of androecia, width and shape of air chambers were found to be useful generic characters in the revised Cleveaceae and they were also supported by character reconstructions as apomorphies within the family.



Ventral scales small and protruding only at apical region
Ventral scales with or without oil-body containing cells
Airchambers wide and polygonal
Radial walls slightly or strongly thickened
Midrib not prominent on ventral surface
Carpocephalum dorsal on thallus
Carpocephalum stalk without rhizoid furrows
Androecial ostioles scattered on the thallus

Ventral scales small and protruding beyond thallus margins
Ventral scales without oil-body containing cells
Airchambers wide and polygonal
Radial walls slightly or strongly thickened
Midrib not prominent on ventral surface
Carpocephalum terminal
Carpocephalum stalk with two rhizoid furrows
Androecial ostioles aggregated into a disc

Ventral scales small & protruding beyond thallus margins
Ventral scales with oil-body containing cells
Airchambers wide and polygonal
Radial walls not thickened or rarely slightly thickened
Midrib not prominent on ventral surface
Carpocephalum terminal
Carpocephalum stalk with one rhizoid furrow
Androecial ostioles scattered on the thallus

Ventral scales protruding beyond thallus margins
Ventral scales without oil-body containing cells
Airchambers narrow and slit-like
Radial walls strongly thickened
Midrib prominent on ventral side
Carpocephalum dorsal on thallus
Carpocephalum stalk without rhizoid furrow
Androecial ostioles scattered on the thallus

Figure 3.20. Results of morphological re-assessment of genera of Cleveaceae: four genera, each represented with a unique combination of characters. Morphologically well defined *Sauteria* and *Athalamia* cannot easily be merged.

To reconcile morphological and molecular data, a revised generic delimitation is presented, recognizing four genera within the family: *Clevea*, *Athalamia*, *Sauteria* and *Peltolepis*. The four genera are redefined as follows (with a full conspectus of the genera and their synonym in Chapter 4):

1. *Clevea* Lindb. 1868
    = *Spathysia* Nees ex Trevis. 1877
    = *Gollaniella* Steph. 1905
2. *Peltolepis* Lindb. 1876
3. *Athalamia* Falc. 1848
4. *Sauteria* Nees 1838
    = *Sauchia* Kashyap 1916

Key to redefined genera of Cleveaceae

1. Ventral scales protruding at apex or along margins of thallus; carpocephalum dorsal on thallus; carpocephalum stalk without rhizoid furrow; androecial ostioles scattered on thallus 2

1. Ventral scales hidden under margins of thallus; carpocephalum terminal in apical notch of thallus; carpocephalum stalk with 1 or 2 rhizoid furrows; androecial ostioles scattered or closely aggregated on thallus 3

  2. Ventral scales small, projecting only at apex of thallus; air chambers in thallus t.s. large, polygonal 1. ***Clevea***

  2. Ventral scales large, projecting at apex and along margins of thallus; air-chambers in thallus t.s. narrow and slit-like 3. ***Athalamia***

3. Thallus with secondary pigmentation along margins; ventral scales without oil body containing cells; carpocephalum stalk with 2 rhizoid furrows; androecial ostioles in well-defined disc 2. ***Peltolepis***

3. Thallus without secondary pigmentation; ventral scales with oil-body cells; carpocephalum stalk with 1 rhizoid furrow; androecial ostioles loosely aggregated along thallus 4. ***Sauteria***

3.5.4 Conclusions

Thalloid liverworts with a complex anatomy and with star-shaped epidermal pores with strongly thickened radial walls in the surrounding cells have traditionally been accommodated within the Cleveaceae, composed of three genera: *Athalamia*, *Peltolepis* and *Sauteria*. Based on phylogenetic inferences from three chloroplast genes (*psb*A, *rpo*C1 and *rps*4) and one nuclear gene (26S), sampled for 54 accessions (9 species), the circumscription and the relationships of these genera was tested, using 18 species from 10 other families as outgroups. Four main lineages were resolved, two corresponding to *Peltolepis* and *Sauteria* and two comprising a polyphyletic *Athalamia.* The latter is here divided into *Clevea* and a narrowly defined *Athalamia*. Morphological character reconstructions showed that the two characters used to unite the two genera; the position of the archegoniophore and the

number of rhizoid furrows, have been subjected to reversals in the past. These two characters, used as key characters in traditional definition of genera of Cleveaceae, are therefore rejected. Inferred evolutions of twelve morphological characters, that are useful or have been used in classifications of Cleveaceae, were reconstructed using maximum parsimony and maximum likelihood methods. Misleading influence of homoplasy on past morphological classifications and phylogenies were discussed. A key to the re-defined genera of Cleveaceae is presented including newly found morphological characters.

CHAPTER-4-TAXONOMIC REVISION OF THE FAMILY CLEVEACEAE

4.1 Introduction

"Taxonomy is dynamic, beautiful, frustrating and challenging all at the same time" (Stuessy 2009). The Swiss botanist A. P. de Candolle (1778–1841), first used the word 'taxonomy' to describe the science of plant classification, and it includes the methods, principles and rules of classification of any group of organisms (Stace 1989; Stuessy 2009). Taxonomy has a long history; therefore a taxonomist must be able to utilise past concepts and literature, to deal with older work on a subject group, and also understand and incorporate new material and discoveries from the present. Taxonomy can utilise data from a wide variety of fields such as morphology, anatomy, chemistry, ecology and molecular biology. Because knowing the identity of organisms under study is so important, taxonomy is an essential tool for applied or experimental studies in almost all the fields of biology.

The term "systematics" was thought to be synonymous with taxonomy in the past (Stuessy 2009). Systematics is defined by Simpson (2006) as a "science that includes and encompasses traditional taxonomy, the description, identification, nomenclature and classification of organisms". The most important new application of systematics today is to infer phylogenetic or evolutionary relationships among groups of organisms. May (2004) aptly stated that "taxonomy provides the bricks and systematics the plan, with which the house of the biological sciences is built". While taxonomy deals with naming of organisms, systematics deals with classifying organisms according to their evolutionary relationships or phylogeny.

The purposes of a taxonomic revision are to circumscribe all of the known taxa in the study group, to account for all names ever applied within the group, to provide descriptions of all of the recognised taxa, to provide the means for their identification (keys, illustrations) and to communicate that information to potential users.

4.2 Objectives

Cleveaceae is a family of complex thalloid liverworts encompassing three currently recognized genera: *Athalamia*, *Sauteria* and *Peltolepis*. The number of species in each genus has not been reliably established, but from published literature has been estimated at between 15 and 20, according to various sources (see Chapter 1). Most of these species have traditionally been assigned to the genus *Athalamia*. The species-level taxonomy of the family has been very inadequately researched with the result that many local 'endemics' described in the literature have not been revised in a global context and many of them may prove to be synonyms or minor variants of more widespread species, as was the case in *Asterella* in the related family Aytoniaceae (Long 2006).

Past taxonomic treatments of Cleveaceae were restricted to relatively narrow geographic regions, consequently covering only a fraction of the total species. No world treatment of Cleveaceae has been published since Stephani (1898–1900) in his *Species Hepaticarum*. Although many of the species were reviewed by Shimizu & Hattori (1953, 1954) and Hattori & Shimizu (1955), only a few of them were treated in any detail, the major focus of their work being to synonymise existing *Clevea* species under *Athalamia*. Hence a comprehensive taxonomic revision of the family is now considered essential before the species can be reliably identified and their biogeography evaluated. The alpha-taxonomic revision undertaken in the present study is the first monograph of Cleveaceae on a worldwide scale.

The family Cleveaceae is well-supported as a monophyletic group both morphologically (Crandall-Stotler et al. 2009) and in molecular phylogenies (Forrest et al. 2006), however the differences between the three traditionally recognized genera *Athalamia*, *Sauteria* and *Peltolepis* are much less clear morphologically (Schuster 1992) and require re-evaluation. Difficulties in defining and identifying the species and genera within the family stem from the paucity of useful and clear-cut morphological characters used to define the genera - many of the characters traditionally used to define the species are continuous and often overlap.
The main objectives of Chapter 3 are:

- To circumscribe all the taxa in the family Cleveaceae and resolve areas of taxonomic confusion
- To evaluate the status of the ‘local’ species described
- To provide taxonomic keys to genera and accepted species
- To provide descriptions of genera and species, clarify accepted taxa and synonyms, and provide illustrations where useful
- To evaluate the ecology and biogeography of the accepted taxa and provide distribution maps

4.3 Materials and Methods.

4.3.1 Materials

Literature sources. A literature survey is an essential part of any taxonomic research project. A thorough literature survey was carried out to locate the protologues (i.e. the original descriptions), of all the taxa in the family Cleveaceae. For a family and its constituent genera that have been known for over a century, a considerable body of published literature exists. It is very important to review how and on what basis these genera and species were originally defined and named, and also to evaluate differences in past taxonomic treatments. Some of the results of this literature survey were presented as part of the taxonomic history of the family Cleveaceae in Chapter 1.

Herbarium material. The use of herbarium material in taxonomic work, especially in a taxonomic revision, is fundamental. Observations of type specimens are crucial to correct application of names. In bryophyte taxonomy it is often only herbarium material that is available for scientific study since dry specimens can be preserved indefinitely, in contrast to living plants which may be difficult or impossible to obtain from the wild, and are very rarely kept in cultivation. Almost all taxonomic researchers utilising morphological and anatomical characters have had to study these primarily from herbarium material. In cataloguing localities to establish species distributions, and to re-find populations especially of rarer species, herbarium material plays an essential role.

Herbarium material from many herbaria around the world was requested on loan for the study. A list of these herbaria and the number of specimens of Cleveaceae received is given in Table 4.1 and all the specimens studied are given in Appendix 4.1

Table 4.1. Acronyms and names of herbaria and number of specimens of Cleveaceae received from each

Herbarium	**No. of specimens**
B - Botanischer Garten und Botanisches Museum Berlin-Dahlem, Germany	84
BG - University of Bergen, Norway	94
BM - The Natural History Museum, London, U.K.	150
BR - National Botanic Garden of Belgium, Meise, Belgium	49
E - Royal Botanic Garden Edinburgh, U.K.	124
F - Field Museum of Natural History, Chicago, Illinois, U.S.A.	48
FH - Harvard University, Cambridge, Massachusetts, U.S.A.	122
G - Conservatoire et Jardin botaniques de la Ville de Genève, Switzerland	93
H - University of Helsinki, Finland	79
JE - Friedrich-Schiller-Universität, Jena, Germany	86
KYO - Kyoto University, Kyoto, Japan	02
MANCH - University of Manchester, U.K.	24
NICH - Hattori Botanical Laboratory, Nichinan, Japan	26
NY - New York Botanical Garden, Bronx, New York, U.S.A.	136
O - Botanical Museum, Oslo, Norway	145
PC - Muséum National d'Histoire Naturelle, Paris, France	34
S - Swedish Museum of Natural History, Stockholm, Sweden	197
TNS - National Museum of Nature and Science, Tsukuba, Japan	19
U - Nationaal Herbarium Nederland, Herbarium Utrecht, Netherlands	02
UPS - Uppsala University, Uppsala, Sweden	607
W - Naturhistorisches Museum, Wien, Austria.	83
WU - Universität Wien, Austria	33

Living material. Collection and observation of living material is very important for taxonomic revision of liverworts since some characters (e.g. colour, smell, oil bodies) are lost during drying. In addition, variation in size cannot easily be measured except in the field. This is a particular problem in complex thalloid liverworts where much of the natural morphology is distorted by drying and is difficult to re-establish fully by re-hydrating dry specimens. Photographs of living plants are hence particularly useful in these taxonomic studies since they can show the exact appearance and colour of the plants in the field. Due to the occurrence of many published taxa of Cleveaceae in remote and inaccessible parts of the world, and limitations of time and funding, only fieldwork in Europe was possible in this study. However, specimens for all three recognized genera of Cleveaceae were collected on successful field excursions in Switzerland, Spain and Scotland. In addition, some living specimens from Spain, Japan and China were supplied by colleagues from their field work. Localities for fieldwork were chosen from literature, annotations on herbarium specimens, on-line databases and advice from personal contacts.

4.3.2 Methods

a) Herbarium methods

Dry specimens of delicate thalloid liverworts such as Cleveaceae, particularly when old, are among the most difficult of all bryophytes to work with due to their fragility and problems of rehydration (D. Long, pers. comm.). The quality of available herbarium material varied depending on the quality and condition of the plants when collected, the age of the specimen and drying methods used by the collectors and the curation methods applied in different herbaria. Specimens for detailed morphological and anatomical studies were selected after carefully reviewing the loans received. Old and delicate herbarium material was observed without dissection to avoid damaging the specimens, hence most old specimens were not used for detailed anatomical studies. Five to ten specimens of each species, preferably from copious recent collections, were chosen for detailed study.

Herbarium material was retrieved by soaking in water for a variable period of time (30mins-12hrs), depending on the condition of the specimen. This is the most frequently used method for reviving herbarium material (Long 2000; McLean 1916; Schill 2006). Extra care was taken when handling type specimens so that damage was minimised. All the herbarium specimens received were studied, identified and annotated with the correct name, except for some that were so fragmentary as to be unidentifiable or that clearly belonged to genera outside Cleveaceae.

b) Field methods

Members of Cleveaceae generally grow in mountainous regions on open treeless slopes, and especially favour moist shaded soil under boulders and rock outcrops, particularly of limestone and other calcareous rocks. Since the plants are small and are often hidden under rocks, they can be difficult to locate in the field. Following collection, a hand lens was used to make preliminary identifications in the field. Field notes on texture, colour, odour, size, etc. were made for all collected specimens. Notes on substrate, ecology and dominant vegetation were also recorded, where possible. Digital photographs were taken using a Nikon Coolpix 995 digital camera. All specimens collected were given temporary reference numbers. Georeferencing data were recorded using a Garmin 12XL Global Positioning System Navigator (GPS). Specimens were collected using a knife and placed in paper packets after removing surplus soil from the sample. The specimens collected in the field were immediately air-dried. Before incorporation into the herbarium, specimens were re-packeted, fully labelled and deep-frozen at -30°C for three to five days to prevent infestation and could then be used for study.

c) Microscopic methods

Specimens were first observed under a Stereo dissecting microscope with a long arm stand (Leica MZ8; 10445538 PLAN 1.0x). Most macro-morphological characters were observed and measurements obtained using this microscope. For observation and measurement of detailed and fine anatomical characters such as transverse sections of thallus and stalk, epidermal peels, ventral scales, scales from the stalk, capsule wall, etc., a Zeiss Standard 20 compound microscope was used.

d) SEM studies

The scanning electron microscope (SEM) gives a three dimensional representation at a range of magnifications of the object examined (Heywood 1971) and has become an essential tool in a wide range of biological research such as palynology, parasitology, bryology, etc. It has revolutionised morphological classifications in some groups of plants and animals. The ‘new’ characters drawn from it are now widely and successfully used in systematic and phylogenetic studies of most groups of bryophytes (Burreson & Reece 2006; Clabrese 2006; Gallego et al. 2000; Long 1999; Long et al. 2000; Mishler 1985b).

A Leo Supra 55VP scanning electron microscope at the Royal Botanic Garden Edinburgh was used to observe spore morphology in the present study. SEM combined with the Variable Pressure technique was used to observe epidermal pores and ventral scales using both fresh and herbarium material.

e) Drawings and photographs

The camera lucida is an optical device that projects a reflection of the object being viewed on to a piece of paper. It allows the user to see both the object and the drawing surface simultaneously, making it possible to trace the outline of the object on the drawing surface. This technique has been successfully used in numerous bryological studies, especially in taxonomic revisions (Long 2000; Mogensen 1981; Schill 2006). In this study, all drawings were made using a camera lucida mounted on a stereo dissecting microscope for macro-morphological characters and on a Zeiss Standard 20 compound microscope for micro-morphological characters. Drawings were then traced on to A3 tracing film and scanned using an Epson Expression 10000 XL scanner.

Digital photographs of fine structures were obtained using Zeiss AxioVision software in conjunction with a Zeiss Axioskop compound microscope.

f) Character selection

Specimens of all treated species were studied before characters were selected. The number of specimens studied in detail for anatomical characters, using prepared slides and dissections, varied from 5 to 10 and for each character 5 to 10 measurements were made. Both qualitative and quantitative characters were observed (as described in Chapter 2). All the characters available were observed and measured and data recorded in Excel spreadsheets.

4.4 Species concepts

All disciplines of plant sciences ultimately depend on the correct identification and naming of plants. Thus a unified method of naming plants became essential to facilitate the scientific understanding of plants. The basis for today's botanical nomenclature was put forward by Linnaeus in 1753, in his *Species Plantarum*. Linnaeus' rationale mainly insists on the reality, objectivity and constancy of species and is of great importance in the history of biology (Mayr 1957). His work is the starting point for liverwort nomenclature (but not mosses) though he was not an authority on liverworts and based his treatment on seminal publications particularly Micheli's (1729) *Nova Plantarum Genera* and Dillenius' (1741) *Historia Muscorum* (in Isoviita, 1970).

Trends in the development of a modern species concept. As Mayr (1957) discusses, there exists a variety of "species concepts" or "species definitions" depending on the choice of criteria. The English word "species" comes from the identical Latin word "species" which means "kind"; the term was used for things that look different (Eldredge & Cracraft 1980; Nixon & Wheeler, 1990). Linnaeus (1758) applied this term for "particular kinds of generic entities" (in Eldredge & Cracraft, 1980). According to Nixon & Wheeler (1990), the species is a particular kind of biological entity in its simplest meaning. There is a massive amount of literature on species concepts available. However, Mann (1999) noted that “the more that I examine the plethora of species concepts and definitions that are available, the more I come to the conclusion that there is substantial agreement between many of them”. According to Mann (1999), this agreement between species concepts is “because species are real and that they do exist”.

Species concepts group together, as a species, individuals that have in common with one another certain factors that they do not share with individuals outside that group (other species) (Levin 2000; Nixon & Wheeler 1990). These factors include morphological links, genetic similarities, an ability to interbreed, or the sharing of a common ancestor or evolutionary history. In most cases, morphological similarity reflects genetic similarity and ability to interbreed; all three normally reflect common ancestry, with some exceptions mostly in the case of morphology (Mann 1999; Nixon & Wheeler 1990). This partly explains the “substantial agreement” between species concepts noted by Mann (1999). However, it is the many cases where species concepts do not agree that fuels ongoing debate about the relative merits of different species concepts. A brief discussion of species concepts most relevent to the current study is necessary.

One of the simplest and most widely used species concepts is the ‘typological species concept’. Here the species are determined and organisms are assigned to species, based upon the distribution of observable morphological or phenetic characters (Bischler & Boisselier-Dubayle 2000; Mayr 1957; Simpson 1951). This results in morphologically defined species in practical taxonomy (Mayr 1957; Stuessy 2009). However, here species are defined solely by the degree of morphological difference, without reference to evolutionary history (Baum & Donoghue 1995).

Another very widely accepted species concept is the ‘biological species concept’, put forward by Ernst Mayr that had great impact on species concepts in recent times (Ridley 2004; Stuessy 2009). According to Mayr (1957, 1969) the biological species concept defines a species as “groups of interbreeding natural populations that are reproductively isolated from other such groups". According to this concept, the species is "the unit of evolution" (Ridley 2004) or "genetically integrated, cohesive, and comparable units of evolution" (Mishler 1985a).

Almost all the other species definitions proposed recently are primarily based on Darwinian concepts as it became clear that morphological data alone were not sufficient for determining variation and identifying species. Great advances in genetic techniques have improved the tools for defining species (Bischler & Biosselier-Dubayle 2000). The 'phylogenetic species concept', widely used in many different groups of organisms (Stuessy 2009), defines a species as "a basal group of organisms all of whose genes coalesce more recently with each other than with those of any organisms outside the group" (Baum & Donoghue 1995). Monophyly is the centrepiece of this phylogenetic species concept and molecular sequence data is the basis for tracing this common ancestor (Nixon & Wheeler 1990).

Any of these species concepts may be additionally qualified by adopting a "broad" or "narrow" species concept. A narrow species concept applies criteria for dividing up species more stringently, leading to the recognition of larger numbers of species in a genus, whereas a broad concept allows for more variation within a species, dividing species only when there is a clear and strong boundary, leading to fewer species within a genus.

Species concepts in bryophytes. In the past, bryologists preferred the typological species concept, and most liverwort taxa were defined based on morphological criteria alone (Bischler & Boisselier-Dubayle 2000; Heinrichs et al. 2009). However, with time many variants were described based on morphological and ecological variations as well as disjunct geographic ranges, which reduced many of the local taxa to synonyms of widespread bryophyte species (Heinrichs 2002, 2009). As Bischler & Biosselier-Dubayle (2000) observed, "in recent taxonomic treatments, widespread species often have lists of several tens of synonyms. But similar cases did not always receive similar treatments". In many of the past classification systems, even slight morphological differences were given high weight and were recognized taxonomically. However, according to Bischler & Biosselier-

Dubayle (2000) “species delimitation varies among taxonomists”. Bischler (1989, 1984), in her revision of *Marchantia* L., has incorporated ecological and morphological differences in species definitions. According to Bischler (1989, 1984) every taxonomic group described may comprise several genetically different components. Bischler (1989) remarked “most of the described species are probably comprised of several genetically different components. […..] Structural variations are not the same, but by no means can these different kinds of populations be distinguished on a structural basis. Further subdivision of the taxa as defined here, is not thought likely to contribute to a better understanding of these plants. […..] with these considerations in mind, a broad species concept has been adopted”. According to Bischler (1989) “they (species) have to be morphologically recognizable, even if their structure might be genetically heterogenous”.

There is an increasing trend to use DNA sequence data to test morphology-based taxonomic concepts (Heinrichs et al. 2009 and references therein). More recent studies on liverworts tend use a combination of morphological and molecular evidence to define species (Boisselier-Dubayle 2000; Heinrichs 2002; Heinrichs et al. 2009; Schill 2006; Vanderpoorten 2006). However, the morphological species concept is still widely used in bryophytes (Heinrichs et al. 2004, 2009)

Species concepts in the current study. Some systematists find the morphological or the typological species concept inadequate and reject it, mainly due two practical problems. First, some individuals, despite been strikingly different morphologically, are found to be conspecific due to one of many factors such as sexual dimorphism, age differences, or polymorphism (Heinrichs et al. 2009, 2004; Vanderpoorten 2006). The second problem is cryptic species: some individuals which are clearly genetically different lack morphological differences (Heinrichs et al. 2009; Vanderpoorten 2006). Cryptic speciation has been recognised in many bryophyte taxa (Vanderpoorten 2006) and Heinrichs et al. (2009), noted that there is a “phylogenetic structure that follows a geographical rather than a morphological pattern” in bryophytes. Because of these problems, a typological species is not always a meaningful biological entity. Despite these weaknesses, some argue that the typological method should be followed to distinguish “archetypes” when studying the diversity of nature and classifying it into species (Mayr 1957). Moreover, for most of the history of plant systematics, morphology was normally the only information available to taxonomists (Judd et al. 2002; Stuessy 2009), and still is very often used in taxonomic work. Hence the great majority of described species are effectively typological species, defined and recognised by diagnostic characters (Mayr 1957; Ridley 2004), although some taxonomists do use morphological criteria as secondary indications of reproductive isolation (Mayr 2004; Stuessy 2009). Therefore, the typological species concept is the most useful in terms of ease of application, but not in terms of describing biological reality.

The biological species concept has its own weaknesses mainly due to the lack of universality (Mishler 1985a). Taxonomists who adopted this concept have followed a variety of “standards”: some would identify every polymorph variant as a species; some would identify every morphologically different population a species and some would identify geographically isolated populations as species (Baker 1970; Baum 1995). Part of this disagreement concerns the term “reproductively isolated” (Baum 1995). When most rigidly applied, this term could be taken to mean that two species must be unable to produce viable and fertile offspring under any circumstances, including deliberate human assistance (Baker 1970; Baum 1995; Donoghue 1985). A more relaxed definition could describe two species that never form offspring under natural conditions but may begin to do so if their habitat is disturbed or their ranges changed. Some animal biologists may favour the former, but plant biologists tend to favour more relaxed definitions because of the ease with which hybrids may be formed in some plant genera (Baker 1970; Donoghue 1985). There are practical difficulties to applying the biological species concept, because only a limited number of plants can be cultivated, and it is impractical to test whether every possible hybrid combination can be produced and would be viable (Baker 1970).

The phylogenetic species concept, as discussed above, is mainly based on molecular evidence to test groups of organisms that share a common ancestry. However, sequencing every individual of every organism for DNA is not practically plausible. Moreover, it is not clear how to deal with taxa that form a paraphyletic group which are otherwise morphologically well-defined (Brummitt 2002).

According to Ruse (1998), the best way to characterise a species is “to make a virtue of plureism,” which can be done by incorporating as many different independent aspect as possible such as morphological, molecular characteristics, ecological and breeding systems. Mann (1999) supported Ruse’s (1998) view and noted that this total evidence approach, which is known as the ‘Waltonian concept,’ is a better solution to avoid difficulties arising from limited available material and time. The species concept in the present study used a combination of morphological and molecular data and searched for a general consensus. In this study, as in many modern studies discussed above, morphological characters were used to define species, combined with DNA sequence data to test their relationships. The final outcome was the one that reconciled morphological and molecular data.

4.5 Taxonomic account

4.5.1 The family Cleveaceae

Cleveaceae Cavers, New Phytol. 10: 42, 1911. ≡ Marchantiaceae ‘Gruppe’ Astroporae Leitgeb., Untersuchungen über die Lebermoose VI, 1881. ≡ Cleveideae Solms-Laubach, Botanische Zeitung, 57: 15, 1899. ≡ Marchantiaceae (Bisch.) Lindl. subfam. Clevieae Lotsy, Vorträge Bot. Stammesgesch. 2: 103, 114, 1909. – Type: *Clevea* Lindb.

= Sauteriaceae A.Evans, North Amer. Flora 14 (1): 35, 1923, *nom. illeg.* (Art.52.1). – Type: *Sauteria* Nees.

Description:

Plants small to medium sized, delicate to fragile or firm and fleshy, upper surface light to dull green or yellowish to whitish green with margins purplish to dark purple or green to whitish, slightly to strongly undulate. Branching terminal (dichotomous) or sometimes ventral. Thalli flat to slightly concave along middle, linear to lingulate or ovate to obovate in shape. Upper epidermis with or without shallow spreading polygonal grooves representing underlying air chambers, each polygon with a slight to non raised air pore. Pores simple, surrounded by a single ring of 4–8 cells, radial wall of the bounding cells slightly to strongly thickened to stellate (star-like) or not thickened and hardly differentiated from the normal epidermal cells. Ventral surface green to purplish or yellowish, midrib slightly to strongly protruding below, gradually to suddenly passing into narrow to broad wings. Ventral scales lanceolate to ovate, arranged in 2–4 distinct rows or randomly distributed on midrib region, dense and overlapping or scattered, hyaline to purplish, dark purple or hyaline to silvery white, protruding only at apical region or along the margins; cells polygonal or rectangular, thin-walled, with or without oil cells; margin smooth, with 0–3(–6) slime papillae; appendage 1 (very rarely 2), weakly differentiated (body gradually narrowed into the acute or acuminate appendage), acuminate, acute to obtuse, cells in appendage and body similar. Rhizoids arising from ventral epidermal cells along the midrib region, both smooth and pegged, hyaline and occasionally brownish towards the base.

Thallus with assimilatory layer well-developed; air chambers wide and polygonal or narrow and slit-like, 1–3 layers, without photosynthetic filaments. Storage tissue thin to thick, hyaline, in layer beloe assimilatory tissue; cells rounded to polygonal, sometimes with dark coloured oil bodies. Mycorrhizal tissue not observed in storage layer. Specialised asexual reproduction absent.

Plants dioicous or autoicous. Androecia embedded in thallus below dorsal epidermis; ostioles loosely aggregated, in regular zig-zag lines or in a tightly aggregated raised disk, sessile (never on antheridiophore), ostioles greenish to whitish or purplish, with or without androecial scales. Archegonia borne on archegoniophores which are terminal or dorsal, 1–4(–6) on one thallus; carpocephalum stalk hyaline, delicate, greenish to yellowish or sometimes with purplish tinge at base, fleshy, smooth. Stalk t.s. with 0, 1 or 2 rhizoid furrows, cells polygonal, thin-walled. Apical stalk scales present, purple and hyaline or hyaline, with 1–4 slime papillae. Carpocephalum greenish to yellowish, smooth or warted, cup- or umbrella-shaped (sometimes horizontal), with or without simple air pores and air chambers, deeply lobed; lobes 1–6(–8), pointing up, down or horizontal, each lobe terminating in a bilabiate ivolucre. Capsule globose, dark brown to blackish brown when mature; wall one cell thick, without lines of dehiscence, tearing into irregular longitudinal valves, without a lid, cells with annular and semi-annular thickenings; stalk very short, up to 0.25 mm; calyptra surrounding base of capsule stalk, very thin, inconspicuous, cup-shaped.

Spores reddish brown to blackish brown under light microscope. Tetrad scar absent or sometimes weakly visible, proximal and distal surfaces weakly distinguishable. Outer surface ornamented with deep to shallow sacs (saccate) or projections, sometimes with papillae and areoles on sacs. Elaters reddish-brown to blackish brown, with 2–3 spiral thickenings, usually 3-spiral at middle.

Chromosome number mostly n = 9, 18 or 36 (Fritsch 1991).

Distribution:

The distribution of Cleveaceae based on confirmed herbarium specimens: Afghanistan, Algeria, Argentina, Austria, Bolivia, Bosnia & Herzegovina, Bulgaria, Canada, Chile, China, Croatia, Ecuador, Finland, France, Georgia, Germany, Greece, Greenland, Hungary, Iceland, India, Iraq, Italy, Japan, Jordan, Mexico, Mongolia, Morocco, Namibia, Nepal, Norway, Oman, Pakistan, Peru, Poland, Portugal, Romania, Russia, Slovakia, Spain, Svalbard, Sweden, Switzerland, United Kingdom (Scotland), United States of America (Alaska, California, Colorado, Minnesota, New England, Nevada, Texas, Utah, Vermont, Washington), Yemen, Yugoslavia and Zimbabwe. According to literature Cleveaceae is also recorded from Montana, U.S.A. (Hong et al. 1998), Oregon, U.S.A (Hong 1978), Tanzania (van den Berghen 1965) and Turkey (Cetin 1988). However, Cleveaceae is not recorded from New Zealand and Australia. Figure 4.1 shows the worldwide distribution of the family Cleveaceae based on confirmed herbarium specimens.

Cleveaceae was not recorded from the British Isles until Long & Rothero (2003) discovered *Clevea hyalina* in the eastern Scottish Highlands. The family occurs as far north as land extends, the most northerly point being Ellesmere Island, 82.52° N where *Clevea hyalina* was collected (R.M. Schuster 35080).

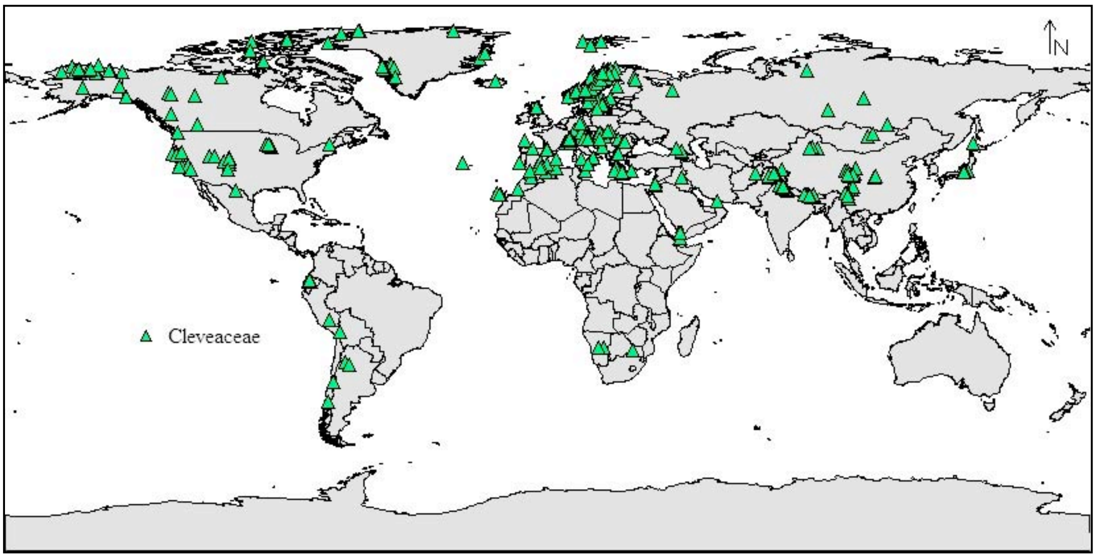


Figure 4.1. Geographical distribution of the family Cleveaceae based on confirmed herbarium material.

Ecology:

Cleveaceae normally occur on high mountains with an alpine climate and also at lower elevations particularly in the Arctic. In contrast, *C. spathysii* occurs at low elevations in the Mediterranean region and *C. hyalina* shows an amphizonal distribution. There are very few records of *Clevea* from the tropics. They normally grow on calcareous substrates, on steep slopes, under boulders, near snow-beds, along streams or sometimes near hot springs e.g. *Athalamia pinguis*.

Taxonomic note:

Cleveaceae is delimited from related families by a combination of morphological characters: presence of simple air pores with ± thickened radial walls in surrounding cells, ventral scales with a single ill-defined appendage, air chambers in 1–several layers without photosynthetic filaments, the delicate, translucent carpocephalum stalk, capsule wall with well-defined annular bands and its irregular splitting.

Nomenclatural note:

Cleveaceae was published by Cavers (1911) to replace Leitgeb's 'group' Astroporae (1881) described as part of Marchantiaceae, then defined in a much broader sense than now. Evans (1923) used the name Sauteriaceae, which is an illegitimate name according the rules of ICBN (2006) and is a superfluous synonym of Cleveaceae.

4.5.2 The genera and species of cleveaceae

Based on molecular phylogeny, morphological and SEM studies presented in Chapters 2 and 3, the family Cleveaceae comprises four genera: *Athalamia*, *Clevea*, *Sauteria* and *Peltolepis*. Table 4.2 gives a summary of the four genera and seven species accepted in the family in this study.

Table 4.2. Synopsis of genera and species of Cleveaceae

Family	Genus	Species	Authors
Cleveaceae	*Athalamia*	*Athalamia pinguis*	Falc.
	Clevea	*Clevea hyalina*	(Sommerf.) Lindb.
		Clevea spathysii	(Lindenb.) Müll.Frib.
		Clevea pusilla	(Steph.)Rubasinghe & D.G.Long
	Sauteria	*Sauteria alpina*	(Nees) Nees
		Sauteria spongiosa	(Kashyap) S.Hatt.
	Peltolepis	*Peltolepis quadrata*	(Saut.) Müll.Frib.

4.5.3 Keys to the genera and species of Cleveaceae

Key to genera of Cleveaceae (Androecia and/or archegonia present).

1. Ventral scales protruding at apex or/and along margin of the thallus; carpocephala dorsal; carpocephalum stalk without rhizoid furrow; androecial ostioles scattered on the thallus 2

\+ Ventral scales hidden under margins of thallus; carpocephalum terminal in apical notch of thallus; carpocephalum stalk with 1 or 2 rhizoid furrows; androecial ostioles scattered or in sharply defined, raised discs 3

2. Ventral scales small (≤1.0 mm); projecting only at apical region of thallus; air chambers in thallus t.s. wide, polygonal ***Clevea***

\+ Ventral scales large (≥1.0 mm), conspicuously projecting at apex and along margins of thallus; air chambers in thallus t.s. narrow, slit like ***Athalamia***

3. Thallus with secondary pigmentation; ventral scales without oil body containing cells; carpocephalum stalk with 2 rhizoid furrows; androecial ostioles in sharply defined, raised discs ***Peltolepis***

\+ Thallus without secondary pigmentation; ventral scales with oil body containing cells; carpocephalum stalk with 1 rhizoid furrow; androecial ostioles loosely aggregated along thalllus ***Sauteria***

Key to genera of Cleveaceae (sterile thalli)

1. Ventral scales large (≥1.0 mm), white to hyaline, conspicuously projecting at apex and along margins of the thallus for most (≥ 2/3) of the length, air chambers in thallus t.s. narrow (≤ 0.1mm) and slit-like ***Athalamia***

\+ Ventral scales small (≤1.0 mm), hyaline or purple, projecting only at apical region or hidden under margins of the thallus; air chambers in thallus t.s. wide (≥0.1mm), polygonal 2

2. Dorsal surface yellowish to whitish-green, lacking purple pigmentation, fine to spongy in texture; ventral scales silvery white, with oil body containing cells ***Sauteria***

\+ Dorsal surface green to purplish, always with purple pigmentation, delicate or firm and robust; ventral scales purple and hyaline, with or without oil body containing cells 3

3. Thalli delicate, linear to lingulate, margins strongly to slightly undulate; ventral scales mostly dense and overlapping, mostly in distinct rows, projecting at apical region ***Clevea***

\+ Thalli firm, mostly obovate, margins very slightly to not undulate; ventral scales scattered, never in distinct rows, always hidden under margins of the thallus and never projecting along margins ***Peltolepis***

Key to genera of Cleveaceae (androecia and archegonia and/or spores present)

1. Always par-autoicous; androecia on well-defined disc; carpocephalum stalk with two rhizoid furrows ***Peltolepis***

\+ Dioicous or par-autoicous, ventral-autoicous or terminal-autoicous; androecia loosely aggregated on thallus; carpocephalum stalk with one rhizoid furrow or rhizoid furrow lacking 2

2. Gynoecia formed at an apical notch; carpocephalum stalk with one rhizoid furrow ***Sauteria***

\+ Gynoecia dorsal on thallus; carpocephalum stalk without rhizoid furrow 3

3. Gynoecial scales purple and hyaline; spores reddish-brown with dense protrusions covering the entire spore surface ***Clevea***

\+ Gynoecial scales hyaline; spores blackish-brown with band-like projections joining to form a reticulate pattern ***Athalamia***

Key to accepted species of Cleveaceae

1. Ventral scales large (≥1.0 mm), white to hyaline, projecting at apex and along margins of the thallus; air chambers in thallus t.s. narrow, slit-like ***Athalamia pinguis***

\+ Ventral scales small (≤1.0 mm), hyaline and/or purple, projecting only at apical region or hidden under margins of the thallus; air chambers in thallus t.s. wide, polygonal 2

2. Dorsal surface yellowish to whitish-green, lacking purple pigmentation; ventral scales silvery white, with oil body containing cells 3

\+ Dorsal surface green and purple, with purple pigmentation; ventral scales hyaline and purple, with or without oil body containing cells 4

3. Thallus thin, ca. 100 μm; dorsal surface without wide pores; branching mostly apical (rarely ventral); par-autoicous with androecia behind carpocephalum or on separate branch on the same thallus (very rarely on a small ventral branch) ***Sauteria alpina***

\+ Thallus thick, 300–900 μm; dorsal surface with wide conspicuous pores; branching mostly ventral (rarely terminal); ventral-autoicous with androecia borne on a small ventral branch (very rarely behind carpocephalum) ***Sauteria spongiosa***

4. Thalli firm, not fragile, margins very slightly to not undulate; ventral scales scattered, without oil body containing cells, never in distinct rows, always hidden under margins of the thallus and never projecting along margins ***Peltolepis quadrata***

\+ Thalli delicate and ragile, margins slightly to strongly undulate; ventral scales mostly dense and overlapping, with or without oil body containing cells, mostly in distinct rows, projecting at apical region 5

5. Dioicous; radial walls of spores thickened (rarely not thickened); androecial scales present; carpocephalum stalk long, 1.5–20 mm; receptacle umbrella shaped, with 2–6(–7) lobes, pointing downwards, ventral scales without oil body containing cells ***Clevea hyalina***

\+ Autoicious; radial walls of pores not thickened (rarely very slightly thickened); androecial scales lacking; carpocephalum stalk short, 0.4–2.0 mm; receptacle cup-shaped, with 1–3 lobes, pointing upwards, ventral scales with oil body containing cells 6

6. Thalli small to medium, 2–13 x 2–9 mm; thick, 300–900 µm; ventral scales dark purple (rarely hyaline and dark purple), dense and overlapping, in 3 or 4 distinct rows ***Clevea spathysii***

\+ Thalli small, 1–6 x 1–4 mm; thin, ca. 100 µm; ventral scales light to dark purple and hyaline, scattered on ventral surface, not in distinct rows ***Clevea pusilla***

4.6 Description of genera and species

4.6.1 The genus *Clevea*

Clevea Lindb., Notiser Sällsk. Fauna Fl. Fenn. Förhandl. 9: 28, 1868. – Type**:** *Clevea hyalina* (Sommerf.) Lindb.

= *Spathysia* Nees [Naturg. Europ. Leberm. 4: 178, 1838. *nom. inval.* (Art. 34.1 (b))] ex Trevis., Memorie Real. Istit. Lombardo Sci. Mat. Nat. ser. 3, 4: 439, 1877. – Type: *Spathysia lindenbergii* Trevis. *nom. illeg.* (≡ *Marchantia spathysii* Lindenb. ≡ *Clevea spathysii* (Lindenb.) Müll.Frib.); synonymised by Grolle (1983).

= *Gollaniella* Steph., Hedwigia 44: 74, 1905. – Type: *Gollaniella pusilla* Steph. (≡ *Clevea pusilla* (Steph.) Rubasinghe & D.G. Long); *syn nov.*

Description:

Thalli small to medium, linear-lingulate, delicate, light to dull green, non-aromatic; vegetative branches usually terminal, often dichotomous, with ventral innovations; branches (1.1–)2–12.8(–6.4) mm long, (1.2–)2–5.3(–9) mm wide; margin slight to strongly undulate, greenish to purplish or dark purple above; dorsal surface with shallow spreading polygonal grooves, each polygon demarcating an underlying air chamber, each polygon with not to slightly raised air pore at middle; air pores simple, 0.01–0.03 mm in diameter, surrounded by a single row of (4–)5–6(–7) cells, radial walls slightly to strongly thickened, rarely not thickened, normal epidermal cells thick- or thin-walled, rectangular or polygonal, (0.02–)0.07–0.09(–0.10) mm long, (0.02–)0.03–0.04(–0.05) mm wide; thallus in t.s. (0.1–)0.3–0.9 mm thick, flat to slightly concave along mid-line, assimilatory tissue well developed, (0.02–)0.15–0.4(–0.8) mm thick, with 1–3 layers of wide, polygonal air chambers, without photosynthetic filaments; storage tissue hyaline, well developed, without oil cells (rarely with dark coloured oil cells); midrib not strongly protruding on ventral surface, (0.2–)0.5–1.5(–2.0) mm wide, gradually passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells.

Ventral scales hyaline and purplish or blackish purple, in 2–3(–4) longitudinal rows on either side of the midrib or randomly arranged on the midrib region, dense and overlapping or scattered, lanceolate or ovate, 0.03–0.1 mm long, (0.02–)0.4–0.75(–0.87) mm wide, with a single ill-defined appendage, sometimes the appendage not differentiated from the body which narrows gradually into an acute tip, unistratose, cells in body and appendage similar, uniform, thin- or thick-walled, polygonal or rectangular, 0.035–0.1(–0.15) mm long, 0.025–0.05(–0.09) mm wide, without oil cells, margins entire with or without slime papillae. Ventral scales protruding beyond apical region of thallus.

Plants dioicous, terminal-autoicous or par-autoicous. Androecia dorsal, in distinct rows or loosely scattered, never in cushions, 6–12, on separate male plant or on the same plant behind base of archegoniophore or on a different terminal branch; ostioles conspicuous, greenish or purplish, with or without androecial scales. Archegoniophores dorsal, 1–4 on each plant, along mid-line; stalk light green to hyaline, rarely with a purple tinge at base, 0.4–20.0 mm long, smooth, without rhizoid furrow, cells in t.s. thin-walled, apical stalk scales present, hyaline and purplish-tinged, linear or linear-lanceolate, 1.0(–2.0) mm long, 0.1(–0.2) mm wide, cells thin-walled, without oil cells, with or without marginal slime papillae; carpocephalum smooth or warted, umbrella- or cup-shaped, 1.2–5.6 mm long, 1.0–3.2 mm wide, bearing 1–6 lobes, lobes pointing downwards, horizontally or upwards.

Capsule dark brown, globose, wall unistratose, cells rhomboidal, 0.4–7.0 μm^2, with annular and semi-annular spiral thickenings.

Spores reddish brown, 41.6–58.8 μm diameter.

Elaters brown, 0.14–0.22 mm long.

Distribution:

Clevea is a small genus with 3 species. It has a nearly worldwide distribution although it is not recorded from Australia and New Zealand. According to confirmed herbarium specimens the genus occurs in: Afghanistan, Algeria, Argentina, Austria, Bulgaria, Canada, Chile, China, Ecuador, Finland, France, Georgia, Germany, Greece, Greenland, Hungary, India, Iraq, Italy, Japan, Jordan, Mexico, Morocco, Namibia, Nepal, Norway, Oman, Peru, Portugal, Romania, Russia, Slovakia, Spain, Svalbard, Sweden, Switzerland, United Kingdom (Scotland), U.S.A. (Alaska, California, Colorado, Minnesota, Washington, Nevada, Utah, New England), Yemen, Yugoslavia, Zimbabwe. Based on literature *Clevea* is also recorded from Oregon, Montana and Turkey. Figure 4.2 shows the geographic distribution of the genus *Clevea* based on confirmed herbarium material.

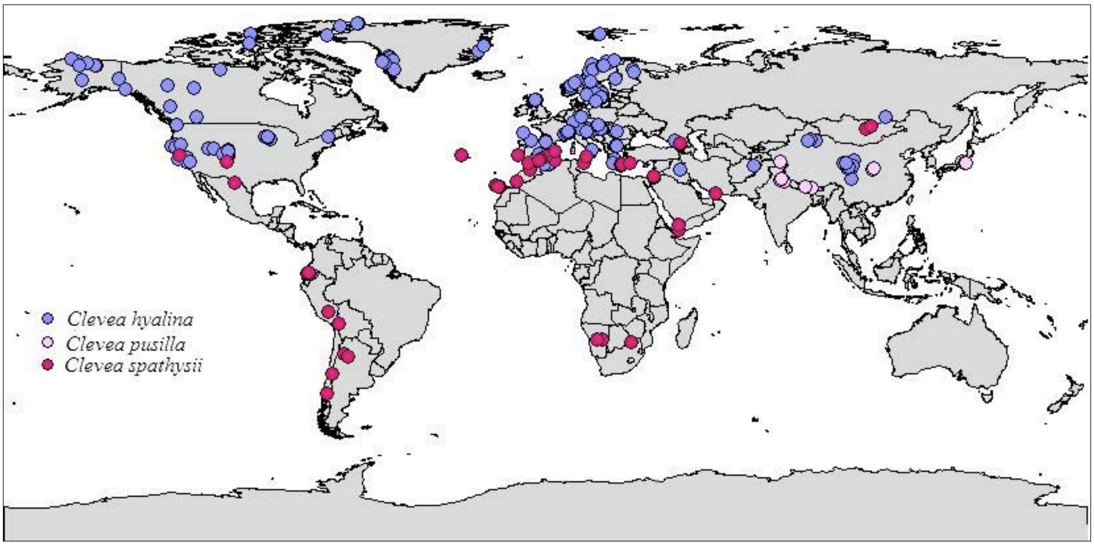


Figure 4.2. Distribution of the genus *Clevea* based on confirmed herbarium material.

Ecological notes:

Thalli of *Clevea* form large to medium sized closely intermingled, irregular shaped patches on exposed limestone rocks or under shaded moist boulders on thin soil. The patches are normally dense and are often mixed with other bryophytes.

Taxonomic notes:

The genus *Clevea* was coined by Lindberg (1868), and since its inception was the favoured name until it was relegated to synonymy under *Athalamia* by Shimizu and Hattori (1954). Since that time *Clevea* has been consistently treated as a synonym of *Athalamia* (Crandall-Stotler et al. 2008, 2009; Damsholt 2002; Grolle 1983; Grolle & Long 2000; Koponen et al. 1977; Schljakov 1981; Schuster 1958, 1984, 1992; Shimizu & Hattori 1955). Molecular and morphological studies carried out during the present study (see Chapter 3) show that the two genera are genetically and morphologically isolated and stand on their own. The main reason for combining the two genera by earlier authors was that both genera have dorsal gynoecia and lack a rhizoid furrow in the carpocephalum stalk. *Clevea* can easily be distinguished from *Athalamia* even in sterile condition by its ventral scales, texture of the thallus and when fertile by spore ornamentation pattern. *Spathysia* Nees ex Trevis. (1877) never gained acceptance as a genus and *Gollaniella* Steph. gained only brief recognition until synonymised by Kashyap (1929) under *Athalamia*.

Key to *Clevea* species:

1. Plants dioicous; radial walls of air pores slightly to strongly thickened (very rarely not thickened); ventral scales hyaline, often purplish but never becoming blackish-purple, lacking oil cells; antheridia in distinct zig-zag rows (6–12), archegoniophore stalk long, 1.5–20 mm, apical stalk scales with 2–4 slime papillae at the base, evenly distributed on either side of margin; carpocephalum umbrella-shaped with 2–6 descending, rarely horizontal lobes ……………………………………………………………...…*C. hyalina*

\+ Plants monoicous; radial walls of air pores not thickened (very rarely slightly thickened); ventral scales blackish purple sometimes hyaline near apex, with oil cells (rarely absent); antheridia randomly arranged; archegoniophore stalk short, 0.4–2.0 mm, apical stalk scales without slime papillae or rarely with 1–2 unevenly distributed slime papillae; carpocephalum cup-shaped with 1–3 ascending, rarely horizontal, lobes….…………………………………...….. 2

2. Thalli medium sized, 2–13 x 2–9mm, 300–900µm thick; ventral scales blackish purple (sometimes hyaline at apex), arranged in distinct rows, ovate, dense and overlapping……………………...………………..… *C. spathysii*

\+ Thalli small, 1–6 x 1–4mm, c.100µm thick; ventral scales pale purple and hyaline, very rarely becoming blackish purple, irregularly arranged, not in distinct rows, ovate to lanceolate, loosely scattered on the midrib and scarcely overlapping………………………………………………………..… *C. pusilla*

1. *Clevea hyalina* (Sommerf.) Lindb. Not. Sällsk. pro Fauna et Flora Fennica 9:291, 1868. ≡ *Marchantia cruciata* Sommerf., Suppl. Florae Lapponicae 79, 1826, *nom. illeg.* non L. ≡ *Marchantia hyalina* Sommerf., Magazin Naturvidensk. (Christiana) II. Ser., I, fasc. 2: 234, 1833. ≡ *Sauteria hyalina* (Sommerf.) Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 23: 561, 1867. ≡ *Athalamia hyalina* (Sommerf.) S. Hatt., J. Hattori Bot. Lab. 12: 54, 1954. – Type citation (Sommerfelt, 1826): [Norway] "in terra rupium et in collibus ad pedes montium callidissimarum Saltdalen Nordlandiæ…". – Type specimen: [Norway] Nordland: Saltdal, Saltdalen. S. C. Sommerfelt s.n. (O-23080, lectotype selected by Grolle (1976)).

= *Sauteria suecica* Lindb., in Gottsche & Rabenhorst, Hep. Eur. no. 347, 1866. ≡ *Sauteria seriata* Lindb., Hedwigia 5(3): 33, 1866; *nom. illeg.* (Art. 52.1). ≡ *Clevea hyalina* (Sommerf.) Lindb. var. *suecica* (Lindb.) Lindb., Bot. Not. 7: 78, 1877. ≡ *Clevea suecica* (Lindb.) Lindb., Musci Scand. 9: 1, 1879. – Type citation: [Sweden] "von Herrn Cleve auf der insel Gotland in der Parochie Boge im Juli 1864, von Herrn Lindberg später im Mai 1865 auf der Insel Oeland gefunden; sie wächst daselbst sehr reichlich auf nassen grasigen Stellen des Alvarits (kalkgründiger Sinöden). Früher hatte sie Herr Lindberg schon (Aug.1856) auf der Alpe Tjiatjak in Pitea-Lappland gesammelt". – Type specimens: [Sweden] Öland, prope Resmo. 1865. *Lindberg, s.n.* (G-00112928, Lectotype selected here); Vickleby, 1865, *Lindberg*, *s.n.* (G-00112927, syntype); Gotland, in der Parochie Boge, Juli 1864, *Cleve s.n.* (JE, syntype); Ins. Gotland, Boge, Julii 1864, *P.T. Cleve s.n.* (B-123667, syntype); synonymised with *Clevea hyalina* by Lindberg (1868).

= *Clevea trabutiana* Steph. Sp. Hepat. 6: 5, 1917. ≡ *Athalamia trabutiana* (Steph.) S. Hatt., J. Hattori Bot. Lab. 12: 54, 1954. – Type citation: [Africa] "Algeria (Trabut legit.)". – Type specimens: [Africa] Algeria, 1907, *Trabut s.n.* (G-00112668, lectotype, selected here); Algeria, Trabut, 1907 (G-00067398, syntype); Algeria: Oran, Tiaret, auf Sandboden, Mai 1907, *Trabut s.n.* (G-00067399, syntype); synonymised with *Athalamia hyalina* by Grolle (1976).

= *Clevea crassa* Trabut., Rev. Bryol. Lichénol. 12: 7, 1942, *nom. illeg.* (Art. 36.1). ≡ *Athalamia crassa* S.Hatt., in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 54, 1954, *nom. illeg.* (Art. 36.1). – Original citation: [Algeria] "Sur les grés humides, à Gertoufa prés Tiaret.” – Original material: [Algeria] Gertoufa prés Tiaret [*Trabut s.n.*] (BR–4139); synonymised by Schuster (1992).

= *Clevea hyalina* (Sommerf.) Lindb. var. *kernii* Müll.Frib. ex Kern, Jahresber. Schles. Ges. (1908) 86: 14. – Type citation: [Italy] “auf lehmiger erde in kleinen Felshöhlen des Monte Canale bei Collina, 1800m (13 vii 07). – Auf Kalkfelsen nahe der Forcella Monumens am Monte Coglians, 2300m”. – Type specimen: *n.v.* (specimen not located)*;* synonymised by Müller (1940).

Description:

Thalli small to medium, linear (particularly in male plants) to lingulate, flat to slightly concave along mid-line, delicate, light to dull green above, usually with purple tinge towards the margins, turning brown or blackish-brown with age; vegetative branching usually terminal, often once dichotomous, ventral branches not uncommon, especially in male plants, thalli sometimes simple; branches of female plants 2–13 mm long, 2–5 mm wide, branches of male plants 2–13 mm long, 1–4 mm wide; margins slightly to strongly undulate, green or with a purple tinge, turning whitish-brown with age; dorsal epidermis with thin-walled, rectangular or elongate-polygonal cells 40–100 μ m long, 30–50 μ m wide, dorsal surface with shallow spreading polygonal grooves representing underlying air chambers, each polygon with single slightly raised air pore at middle; air pores simple, 12.0–29.5 μm in diameter, surrounded by a single row of 6–7 cells, radial walls slightly to strongly thickened; thallus t.s. (0.1–)0.3–0.87 mm thick at midrib, assimilatory tissue well developed, (0.15–)0.25–0.81 mm thick, with 1–3 layers of wide polygonal to rectangular air chambers, without photosynthetic filaments; storage tissue hyaline, well developed, without oil cells; midrib not strongly protruding on ventral surface, 0.6–1.7 mm wide, gradually narrowing into wings.

Rhizoids smooth and pegged, arising from ventral epidermal cells.

Ventral scales hyaline and purplish (never becoming blackish purple), in two longitudinal rows on either side of the midrib, dense and overlapping at apical region, lanceolate, 0.4–0.93 mm long, 0.35–0.82 mm wide, with a single ill-defined appendage, unistratose, cells in body and appendage similar, uniform, thick-walled, polygonal sometimes rounded, 38.3–78.2 μm long, 23.5–44.5 μm wide, slime papillae 0–2, margin entire, oil cells absent, with additional slightly smaller similar-shaped scales scattered on midrib region.

Sexual condition dioicous, male and female plants in separate colonies or rarely intermixed, vegetatively similar or sometimes male plants smaller. Androecia dorsal, in zigzag rows, 6–12, ostioles greenish to brownish, conspicuous, androecial scales one for each ostiole towards the marginal side of the thallus, hyaline and purplish, 0.03 mm long. Archegoniophores dorsal, 1–4 along the mid line; stalk cylindrical, hyaline or greenish, slightly purplish at base, smooth, 1.5–20 mm long, round in t.s., 0.3–0.85 mm in diameter, without rhizoid furrow, cells thin-walled, polygonal to isodiametric; apical stalk scales present, hyaline to purplish, 0.6–1.0 mm long, 0.1–0.2 mm wide, linear, with 2–4 slime papillae distributed evenly on either side at the base of the scale; carpocephalum light green to yellowish green, umbrella shaped, 2.2–5.0 mm in diameter, with 2–6 lobes pointing downwards, rarely horizontal, each involucre containing one sporophyte. Capsule globose, foot bulbous, short, up to 0.5–0.6 mm, dehiscing by several irregular valves, wall unistratose, cells spindle-shaped, 38–86 mm long, 18–37 mm wide, with annular and semi-annular thickenings.

Spores reddish brown, 44.4–58.8 µm in diameter, usually ± triangular in outline, rarely almost spherical, distal surface convex, proximal face flatter, trilete mark not or rarely slightly visible, densely covered with hemispherical domes, 3.0–6.67 µm high, obtuse, rarely acute, spaces between domes deep and wide, with 4–6 cavities around each dome, entire surface finely granular, granules rarely aggregated at the tip of domes. Elaters brown, 150–225 µm long, 8.6–11.4 µm wide, sometimes once-branched. Chromosome number n= 9 (Fritsch 1991).

Illustrations: Figures, 4.3; 2.2 (A, B, C); 2.3 (A); 2.4 (A); 2.5 (A); 2.8 (A, C, G); 2.9 (D); 2.10 (H); 2.11 (C)

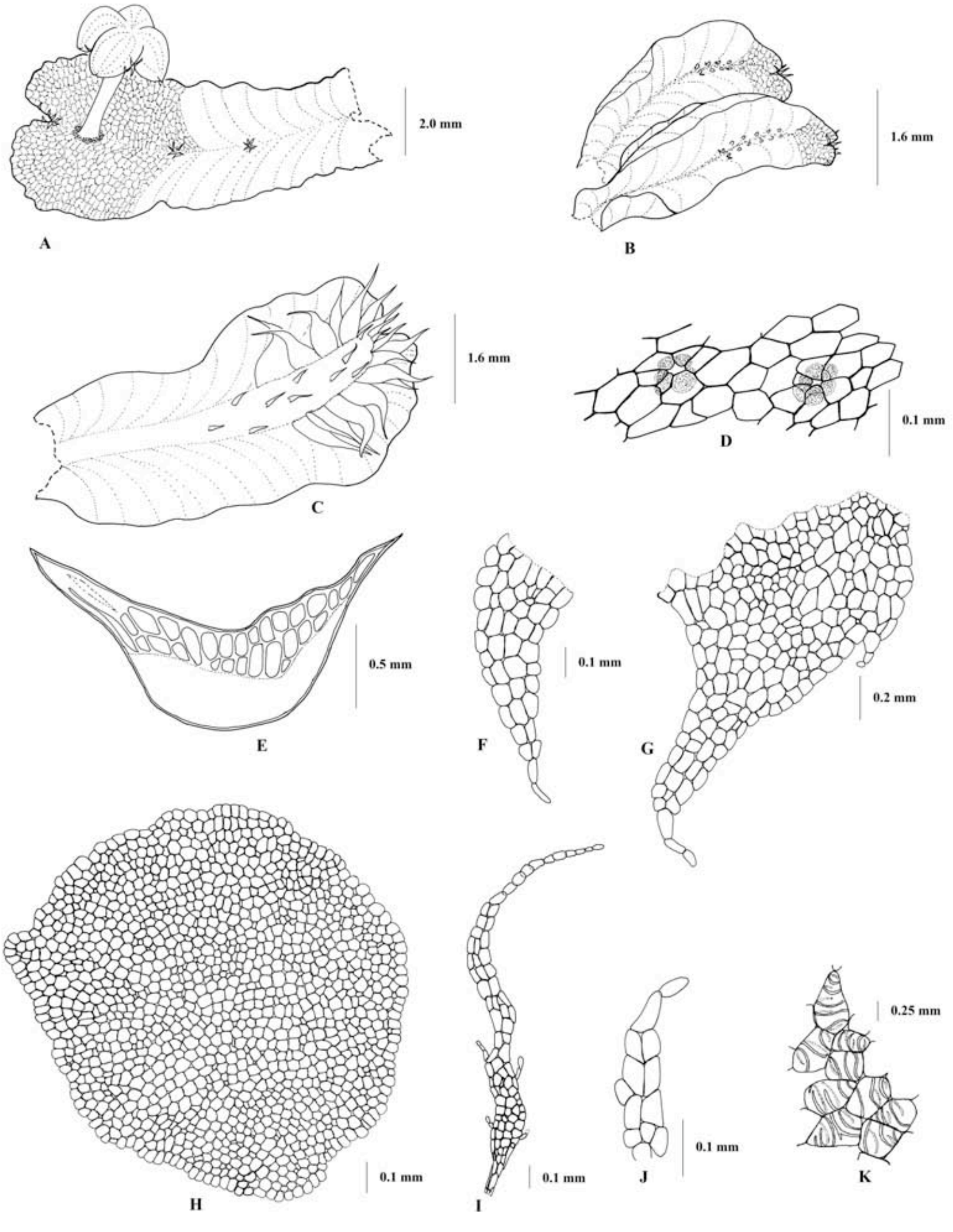


Figure 4.3. ***Clevea hyalina*****. A) dorsal surface of a ♀ plant showing archigoniophore; B) dorsal surface of a ♂ plant showing androecia; C) thallus ventral surface showing ventral scale distribution; D) air pores from dorsal epidermis of thallus; E) transverse section of thallus; F) a venral scale from the median region of the thallus; G) ventral scale from alongside the midrib; H) transverse section of apical stalk; I) apical stalk scale; J) antheridial scale; K) cells of the spore wall. A–I, K, Scotland,** ***Rubasinghe & Long 01–07SR*****; J, Italy,** ***Long & Duckett 25774*****.**

Distribution:

The distribution of *Clevea hyalina* based on confirmed herbarium specimens: Afghanistan (Tscharika), Algeria (Tiaret), Austria, Bulgaria, Canada (Alberta, Bathurst Island, British Columbia), China, Croatia, Finland, France, Georgia, Germany, Greece, Greenland, Hungary, Iraq, Italy, Morocco, Norway, Romania, Russia, Slovakia, Svalbard, Sweden, Switzerland, U.K., U.S.A. (Alaska, Colorado, Minnesota, Utah, Vermont, Virginia, Washington) and Yugoslavia (Fig. 4.4). Based on literature it is also recorded from Montana and Idaho in the U.S.A. and Turkey.

Clevea hyalina is arctic-alpine in distribution extending north at least up to 82° 32' (Schuster 1992). It shows a nearly worldwide distribution but is not recorded from South America, most of Africa, Australia, New Zealand, and tropical South-east Asia.

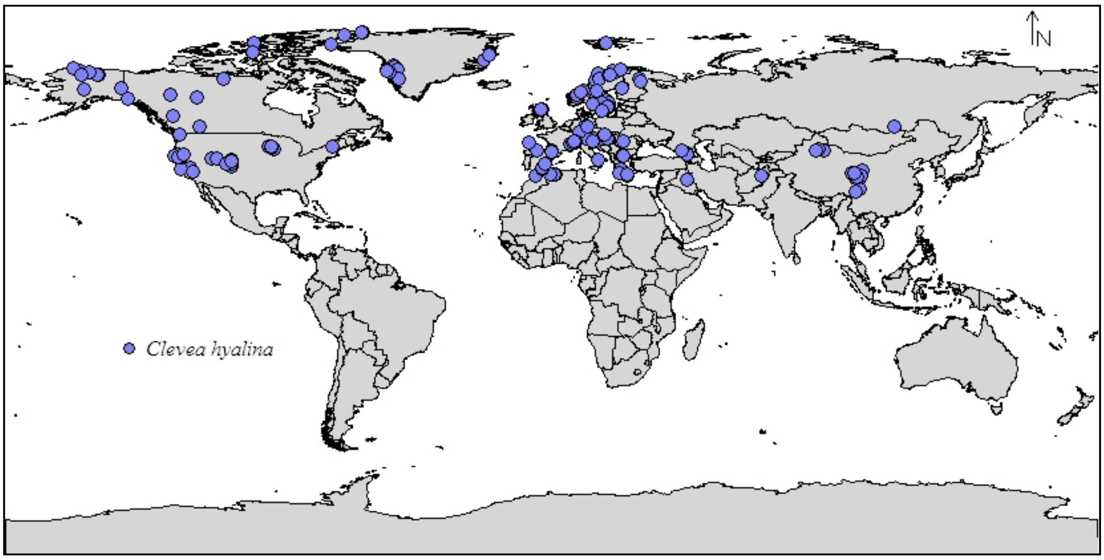


Figure 4.4. Geographical distribution of *Clevea hyalina* based on confirmed herbarium material.

Ecological Notes:

Clevea hyalina grows on thin mineral soil over friable limestone, on exposed slopes (e.g. Braemar, Scotland), under boulders on very high mountains (e.g. Gemmi, Switzerland), on ledges of eroding crags (Spain). Observations on the population in Braemar during the study suggested that this species is highly seasonal, growing during the winter months and produce reproductive structures during early spring but becoming inconspicuous in dry summer months when it shrivels up and disappears into the soil crust.

Taxonomic notes:

Clevea hyalina is distinct from the other two species of *Clevea* and also from the rest of the Cleveaceae by its sexual condition – it is the only dioicous species in the family. The male plants are rather rare (or perhaps less conspicuous) and smaller than the female plants and often occur in separate patches. It is the only species where androecial scales were observed. *C. hyalina* is also characterized by the nature of ventral scales and the texture of the thallus.

Nomenclatural notes:

The first description of *Marchantia hyalina* by Sommerfelt (1826) was given under the misapplied name *Marchantia cruciata* L. (now *Lunularia cruciata* (L.) Lindb.); Sommerfelt (1833) later corrected his misidentification by giving it the new name *Marchantia hyalina* Sommerf. Although the 1833 publication contained no description, the name is validly published by reference to the earlier 1826 description and is typified by the 1826 specimen. Lindberg's *Clevea hyalina* (1868) was thus based on Sommerfelt's *M. hyalina* which was collected from Norway.

Sauteria seriata was published by Lindberg shortly after he published *S. suecica* in 1866 and the protologue made it clear it was based on the same type as *S. suecica*; it is therefore a superfluous name (Art. 52.1).

Athalamia crassa S. Hatt., treated here as a synonym, was published as a substitute name for the illegitimate *Clevea crassa* Trabut. However, both these names are illegitimate as they did not include a Latin diagnosis. Müller (1954) stated that this species (described from the Algerian Atlas Mountains) was different from *C. hyalina* only by the stronger, heart shaped thickening of radial walls of the air pores "*Clevea crassa* Trabut (1942) aus dem algerischen Atlasgebirge unterscheidet sich von *C. hyalina* nur durch stärkere, herzförmige Verdickungen der Radialwände der Atemöffnungen". Grolle (1976) also noted that this was probably a synonym of *C. hyalina*.

The name *Clevea hyalina* var. *kernii* was first applied as a herbarium name by Karl Müller to plants collected by F. Kern who later formally described it (Kern, 1908). However, the specimens cited by Kern (1908) were carefully studied again by Müller (1940). He confirmed that the original material collected from Monte Canale is *Clevea hyalina* but doubted that the differences given by Kern were adequate to distinguish it as a variety. Consequently he Müller (1954) did not even mention it in his ‘Lebermoose Europas’.

2. *Clevea spathysii* (Lindenb.) Müll.Frib., Hedwigia 79: 75, 1940. ≡ *Marchantia spathysii* Lindenb., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14 (Suppl.); 104, 1829. ≡ *Dumortiera spathysii* (Lindenb.) Nees, Naturg. Europ. Leberm. 4: 171, 1838. ≡ *Athalamia spathysii* (Lindenb.) S.Hatt. in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 54, 1954. – Type citation: [Greece] “Corcyra insula, ad terram, cl. Spathys primus legit.” – Type specimen: Greece, Corfu, *Spathys s.n.* (W, holotype, *n.v.;* STR, isotype, *n.v.*, fide Grolle (1976)-not seen).

= *Plagiochasma rousselianum* Mont., Ann. Sc. Nat. 10: 334, 1838. ≡ *Clevea rousseliana* (Mont.) Steph., Sp. Hepat. 1: 68, 1898. – Type citation: [Algeria] “in vallibus umbrosis occidentalibus, imprimis loco Boudjareah dicto et non multum ab urbe distanti, ad margines viarum hanc speciem detexit cl. Roussel.” – Type specimen: Algeria: *Roussel s.n.* (G-00112976, isotype); synonymised with *Clevea spathysii* by Müller (1940).

= *Sauteria limbata* Austin, Proc. Acad. Nat. Sci. Philadelphia 21: 229, 1870. ≡ *Clevea limbata* (Austin) Solms ex Steph., Sp. Hepat. 1: 70, 1898. – Type citation: [U.S.A.] "California, Bolander. (No. 4619)". – Type specimen: [U.S.A] Under wet rocks, California, 17 iii 1834, *Bolander 4619* (MANCH, lectotype selected here); *syn. nov.*

= *Clevea andina* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 569, 1884. ≡ *Athalamia andina* (Spruce) S.Hatt. in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 54, 1954. – Type citation: [Ecuador] “Andes Quitenses, in terra rupium umbrosa humida juxta pontem fluvii Pastasa “de Baños” dictum, etiam loco simili prope Ambato, alt. 2000–2800m, rarissime.” – Type specimens:

[Ecuador] Ambato in rupibus, cum Plagiochasmate etc., *Spruce s.n.* (MANCH, EM445848, lectotype, selected here); [Ecuador] Andes, Quito, Baños, 7000m, *Spruce s.n.* (G-00112899, syntype); *syn. nov.*

= *Clevea robusta* Steph. Spec. Hepat. 1: 69, 1898. ≡ *Athalamia robusta* (Steph.) S.Hatt. in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 54, 1954. – Type citation: "Chile. Valparaiso in humo (leg. P. Dusén)." – Type specimen: Chile, Valparaiso in humo, xi 1879, *Dusén 143* (G-00112727, holotype); synonymised under *Athalamia andina* by Bischler (2005).

= *Athalamia pygmaea* R.M. Schust., Phytologia, 57(6): 411, 1985. – Type citation: [U.S.A.] "Near Boot Spring, Chisos Mts., Big Bend Natl. Park, Texas (RMS-81-1251a)." – Type specimens: Texas: Big Bend National Park: Chisos Mts., below and above Boot Springs, 24.12.1981, *R.M Schuster 81-1251a* (F, holotype); *syn. nov.*

Description:

Thalli small to medium, oblong-ovate to linear, flat to slightly concave along mid-line, delicate to fleshy, pale green to dark green above, usually dark purple towards the margin, vegetative branching terminal, usually once dichotomously branched or simple, ventral branches not uncommon; branches 4.8–12.8 mm long, 1.6–6.4 mm wide; margins slightly to not undulate, rarely strongly undulate, dark to blackish purple, sometimes light purple to rarely green; dorsal epidermis with thin-walled, hyaline, polygonal to isodiametric cells usually with distinct trigones, 0.02–0.10 mm long, 0.01–0.07 mm wide, dorsal surface with shallow spreading hexagonal to polygonal grooves representing underlying air chambers, each with a very slightly raised to not raised air pore at middle; air pores simple, 7.33–11.37(–20.0) μm in diameter, surrounded by a single row of 4–5(–6) cells, radial walls not thickened (very rarely very slightly thickened); thallus t.s. 0.45–0.87 mm thick over midrib, assimilatory tissue well developed, 0.10–0.75 mm thick, with 1–3 layers of polygonal to rounded air chambers without photosynthetic filaments, storage tissue hyaline, well developed, without oil cells or rarely with dark coloured oil cells; midrib not strongly protruding on ventral surface, 0.2–1.93 mm wide, gradually passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells along midrib region.

Ventral scales dimorphic. Larger scales blackish purple, very rarely hyaline at base or apex of the scale, in 3–4 longitudinal rows on either side of the midrib, dense and overlapping, ovate or obliquely triangular and pointed, rarely lanceolate, 0.5–1.3 mm long, 0.30–0.87 mm wide, with a very weakly defined appendage, unistratose, cells in body and appendage similar, uniform, thick-walled, rectangular, 74.25–120.17 μm long, 25.28–48.13 μm wide, slime papillae 0–1 (–2), margin entire, oil cells present, up to 10, rarely absent. Smaller scales scattered on the midrib region, slightly smaller, similar in shape or rather lanceolate, with an acuminate apex.

Sexual condition par-autoicous and terminal-autoicous. Androecia dorsal, immediately proximal to base of archegoniophore or on a separate terminal branch on the same thallus, ostioles 6–12, scattered, greenish to purplish, antheridial scales absent. Gynoecia dorsal, mostly single or up to 4 in a line; stalk cylindrical, pale green to yellow green, smooth, 0.4–1.9 mm long, round to elliptic in t.s. 0.35–0.80 mm in diameter, without rhizoid furrow, cells thin-walled, polygonal to isodiametric, apical stalk scales present, dark purplish and hyaline, 0.7–2.0 mm long, mostly linear sometimes linear lanceolate, slime papillae not observed; carpocephalum greenish to yellowish green, cup-shaped, 0.9–3.6 mm in diameter, with 1–4 lobes, pointing upwards, rarely horizontal, each involucre containing one sporophyte. Capsule globose, up to 0.6 mm diameter, foot short, bulbous, capsule dehisching by several irregular valves, wall unistratose, cells spindle-shaped, 0.05–0.1 mm long, 0.03–0.07 mm wide with annular and semi-annular thickenings.

Spores reddish brown, 44.4–62.5 μm in diameter, usually spherical, distal surface convex, proximal face flatter, trilete mark not recognizable, densely covered with conical or hemispherical domes, 7.7–11.5 μm high, acute and pointed, rarely obtuse, spaces between domes deep and wide, with 4–6 cavities around domes, fine granules aggregated mostly at the tip of the dome.

Elaters brown, 100–350 μm long, 6.6–10.8 μm wide at middle, bispiral, branching not observed, sometimes bent.

Chromosome number n = 9 (Fritsch 1991).

Illustrations: Figures, 4.5; 2.2 (C); 2.3 (B); 2.4 (D); 2.5 (B, F); 2.10 (B).

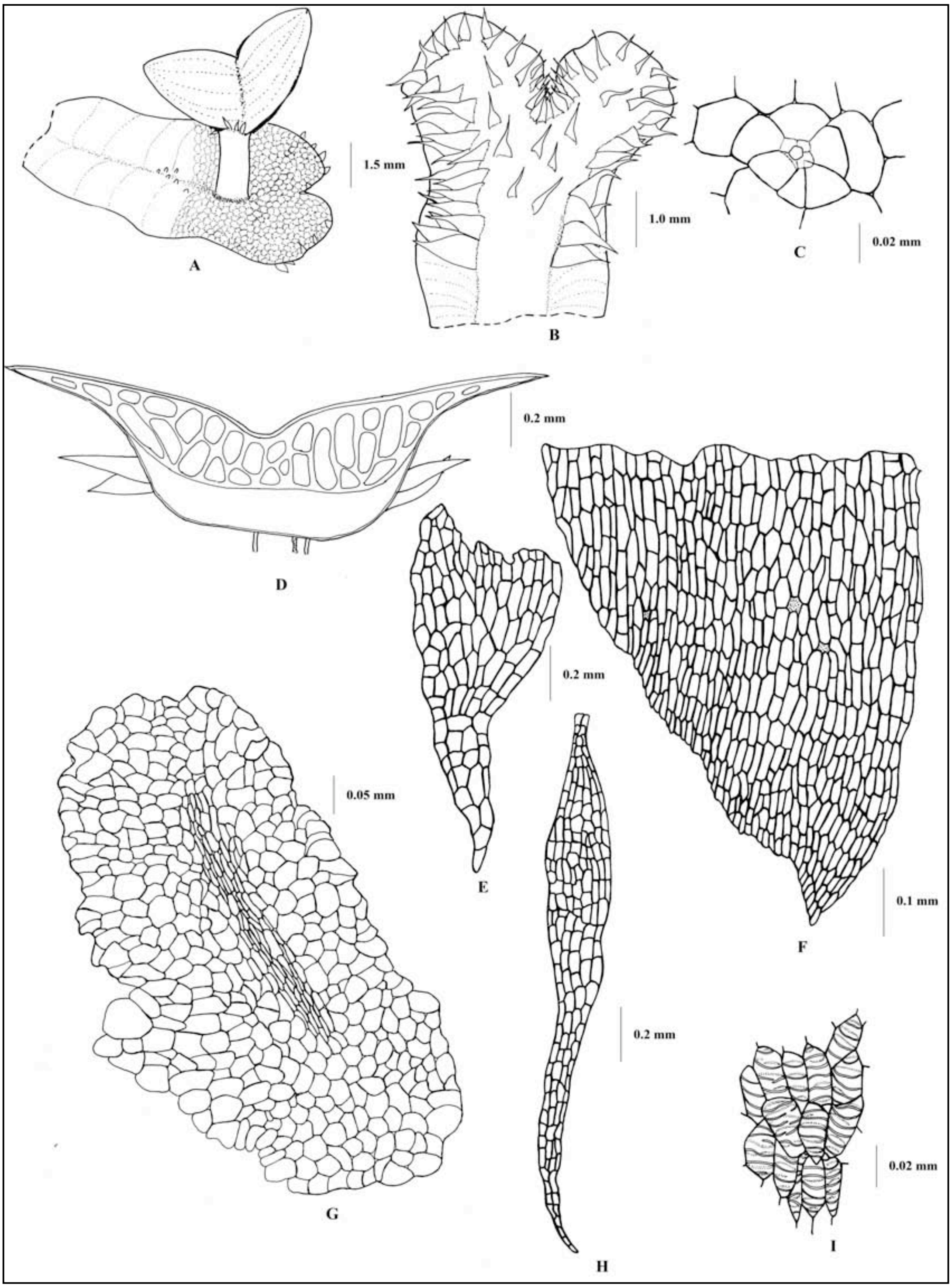


Figure 4.5. ***Clevea spathysii*****. A) dorsal surface of thallus showing archegoniophore and antheridial ostioles; B) thallus ventral surface showing ventral scale distribution; C) air pore from dorsal epidermis of thallus; D) transverse section of thallus; E) ventral scale from median region of thallus; F) ventral scale from alongside midrib; G) transverse section of stalk; H) apical stalk scale; I) cells of spore wall. A–D, Spain,** ***Rubasinghe & 06-09SR*** **(E); F, Namibia,** ***Volk 861*** **(JE); H, Namibia,** ***Volk 904*** **(BM); E,G, Algeria,** ***Douin 4145*** **(BR); I, Namibia,** ***Volk 908*** **(JE).**

Distribution:

The distribution of *Clevea spathysii* based on confirmed herbarium material: Algeria, Argentina, Bolivia, Chile, Ecuador, Georgia, Greece, Italy, Jordan, Mexico, Mongolia, Morocco, Namibia, Oman, Peru, Portugal, Spain, U.S.A. (California, Texas), Yemen and Zimbabwe (Fig. 4.6). Based on literature it is also recorded from Tanzania and Turkey (van den Berghen, 1965).

This is the only species of *Clevea* recorded from southern Africa and South America.

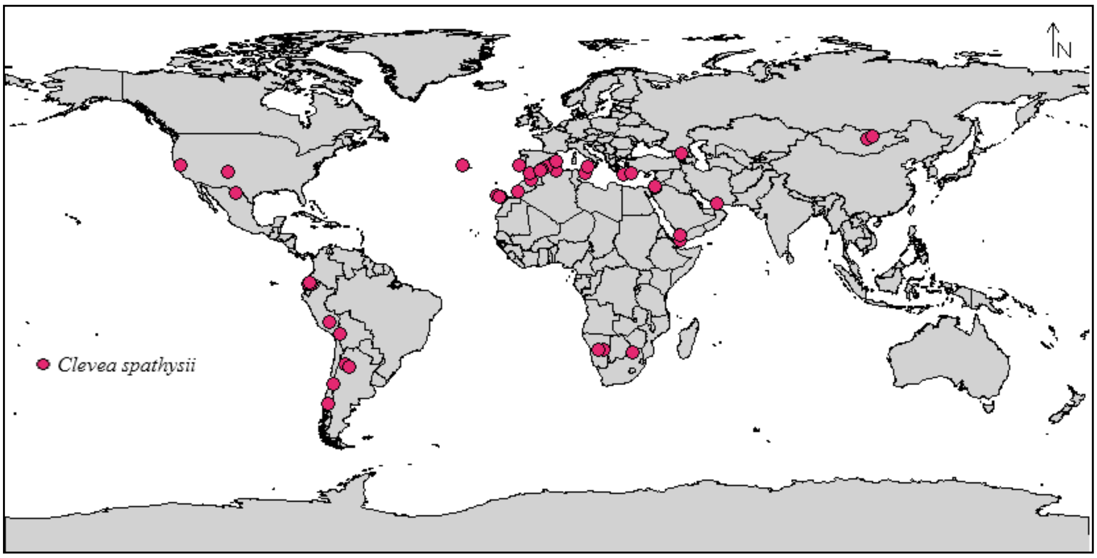


Figure 4.6. Distribution of *Clevea spathysii* based on confirmed herbarium material.

Ecological Notes:

Clevea spathysii forms dense irregular shaped mats on moist shady soil under boulders. It grows on rocky soil or rock crevices near streams, rocks wet from cliff seepage and prefers growing on north facing slopes in Mediterranean climates and is able to tolerate comparatively long periods of desiccation.

Taxonomic notes:

Clevea spathysii can easily be identified in the field by the crystalline green colour and the blackish-purple margins and ventral scales. Although the species tolerates arid conditions, the morphological structure does not show particularly xeromorphic features. The air pores of *C. spathysii* are very delicate and usually lack any radial wall thickenings and are thus easily overlooked. The blackish-purple colour of the ventral scales and the edges of margins is a characteristic feature of this species. It also stands out from the rest of the Cleveaceae in having a crystalline green colour, at least when young.

Nomenclatural Notes:

Lindenberg (1829) described a new species, *Marchantia spathysii* based on a specimen collected by Spathys from Corfu (Greece). Nees (1838) gave a detailed description of this specimen under the name *Dumortiera spathysii*. In his description he erroneously mentioned that the carpocephalum stalk has two rhizoid furrows and the androecia are stalked at maturity, which made its taxonomic position uncertain.

Solms-Laubach (1899) after carefully examining Nees's original specimens confirmed that the androecia of *Dumortiera spathysii* are not stalked but as in other *Clevea* species sunken in the thallus. According to Müller (1940), Nees's description of the antheridium is essentially a young archegonium. Furthermore this species is identical with Montagne's *Plagiochasma rousselianum* (1838), collected by Roussel from Algeria which was later (1898) recombined as *Clevea rousseliana* by Leitgeb.

Sauteria limbata Austin was discussed by Long & Grolle (1994) and considered to be based on a mixture of *Clevea hyalina* and *Asterella californica* (Hampe) Underwood and they pointed out that lectotypification was required to fix the application of the name to the *Clevea* element. However, study of the type of *Sauteria limbata* shows that it is a synonym of *C. spathysii* not *C. hyalina* as suggested by Schuster (1992). Lectotypification has now been done and the name relegated to the synonymy of *Clevea spathysii*.

3. *Clevea pusilla* (Steph.) Rubasinghe & D.G. Long, J. Bryol. 33, 2011 [in press]. ≡ *Gollaniella pusilla* Steph. Hedwigia, 44: 74, 1905. ≡ *Athalamia pusilla* (Steph.) Kashyap, Liverw. W. Himal. & Panjab Plain 1: 87, 1929. – Type citation: [India, Uttaranchal] “Himalaya, Mussurie, Gollan”. – Type specimens: [India, Uttaranchal], Mussoorie (N.W. Himalaya) on roadside between Arnigadh and Khetwala, 5550 ft. 12 Sept. 1900, *W. Gollan s.n.* in Bryotheca E. Levier 3867b (G-00067320, lectotype, selected here); Mussoorie (N.W. Himalaya) Arnigadh Garden, 5500 ft., parce inter Targioniam, Sept. 1900, *W. Gollan s.n.* in Bryotheca E. Levier 3960 (G-00069831, syntype); Mussoorie, Arnigadh botan. Gardens, earthy banks, 5500', 10 Sept. 1900, *W. Gollan s.n.* (G-00069832, syntype).

= *Clevea chinensis* Steph., Nuovo Giorn. Bot. Ital. (ser. 2) 13: 347, 1906. ≡ *Athalamia chinensis* (Steph.) S.Hatt. in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 54, 1954. – Type citation: [China, Shaanxi ‘Schen-Si’ Prov.] “Monte Tui-kio-san, 19 ott. [18]96. –Zu-lu (valle del Lao-y-san), 27 ott. [18]96.–In-kia-po, 16 ott. [18]97. –Han-sun-fu, ott. [18]98. [leg. G. Giraldi]”. – Type specimens: [China, Shaanxi Prov.] China interior, Schen-Si sept., Han-sun-Ku, Oct. 1898. Giraldi s.n. in herb. Levier 1780 (G-00067325, lectotype, selected here); China, Schensi, Hansunfu, Oct. 1898, *Giraldi s.n.* in herb. Levier 2511 (G-00112849, syntype); China Schensi, in catena Lao-y-san, Giraldi s.n. in herb. Levier 1850 (G-00112850, syntype); *syn. nov.*

= *Gollaniella nana* Shimizu & S.Hatt., J. Hattori Bot. Lab. 9: 34, 1953. ≡ *Athalamia nana* (Shimizu & S. Hatt.) S.Hatt. in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 56. 1954. – Type citation: [Japan] “Crevices of limestone cliff, the Jumonjii pass, ca. 1700 m. alt., Chichibu Mts., Saitama Prefecture, August 26, 1952, Coll. D. Shimizu, Typus in Herb. Hattori Bot. Lab.” – Type specimen: Japan, Saitama Pref., Chichibu Mts., Jumonji pass, ca 1700m., 26 August 1952. D. Shimizu s.n. (NICH, holotype); *syn. nov.*

= *Athalamia glauco-virens* Shimizu & S.Hatt., J. Hattori Bot. Lab. 12: 56, 1954. – Type citation: “Among crevices of rocks (mostly clay-slate), south-facing shrubby slope, ca. 1040m. alt., Kita-aiki in Minami-saku District, Nagano County, Middle Japan, August 18, 1953, Coll. D. Shimizu, No. 52767–Type in Herb. Hattori Bot. Laboratory.” – Type specimen: Japan, Nagano-ken, Minamisaku-gun, Kita-aiki-mura, ca. 1060 m. alt., on slate, 18 viii 1953, D. Shimizu 52767 (NICH, holotype); *syn. nov.*

= *Athalamia glauco-virens* Shimizu & S.Hatt. forma *subsessilis* Shimizu & S.Hatt., J. Hattori Bot. Lab. 12: 58, 1954. – Type citation: "Crevices of rocks (clay-slate, phyllite and cherts), south-facing exposed cliffs, ca. 700m. alt., at Kaminakao of Otaki-mura, Chichibu Mts., Saitama County, Middle Japan, September 3, 1953. Coll. D. Shimizu, No. 52755–Type; in Herb. Hattori Bot. Laboratory." – Type specimen: Japan, Saitam-ken, Chichibu-gun, Otakimura Kaminakano, ca. 700m. alt., on rock, 1953 IX 3, D. Shimizu 52755 (NICH, holotype); synonymised with *Athalamia glauco-virens* by Hatttori and Shimizu (1955).

Description:

Thalli small, linear or linear-lingulate, mostly flat, sometimes slightly concave along mid-line, delicate, light green to dull green above, usually dark purple towards the margin, vegetative branching terminal usually 1–3 times dichotomously branched or mostly simple, sometimes with ventral branches; branches 1.0–6.0 (–15.0) mm long, 1.0–4.0 mm wide; margins slightly to strongly undulate, with purplish tinge, sometimes with strong dark purple line along margin; dorsal epidermis with thin-walled, hyaline, polygonal to isodiametric cells usually with distinct trigones at corners, 0.04–0.06 mm long, 0.03–0.05 mm wide, dorsal surface with polygonal markings representing underlying air chambers, each with a very slight to not elevated air pore; air pores simple, (8.0–) 13.0–25.0 μm in diameter, surrounded by a single row of 4–5 (–9) cells, radial walls not thickened, sometimes slightly thickened; thallus t.s. 0.09–0.45 mm thick over midrib; assimilation tissue with 1–3 layers of polygonal to rounded air chambers without photoshynthetic filaments, storage tissue hyaline, well developed, without oil cells; midrib not strongly protruding on ventral surface, 0.2–1.6 mm wide, gradually passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells at midrib regiong.

Ventral scales purplish hyaline or blackish purple, irregularly arranged on midrib region, scattered, ovate to lanceolate, acute to acuminate, 0.4–0.8 mm long, 0.2–0.5 mm wide, with weakly defined appendage, unistratose, cells in body and appendage similar, uniform, thick-walled, rectangular to polygonal, 0.04–0.08 mm long, 0.03–0.04 mm wide, slime papillae 0–2, margin entire, oil cells present, up to 10 when present, rarely absent.

Sexual condition par-autoicous and terminal-autoicous. Androecia dorsal, immediately proximal to base of archegoniophore or on a separate terminal branch of the same plant, ostioles up to 6, scattered, greenish, antheridial scales absent. Gynoecia dorsal, mostly single; stalk cylindrical, pale green to yellowish green, smooth, 0.4–1.9 mm long, round in t.s. 0.35–0.8 mm in diameter, without rhizoid furrow, cells thin-walled, usually isodiametric, apical stalk scales present, purplish and hyaline, 0.4–0.64 mm long, 0.10–0.14 mm wide, linear, slime papillae not observed; carpocephalum greenish, cup-shaped, with 1–3 lobes pointing upwards, rarely horizontal, each involucre with one sporophyte. Capsule globose, foot short, bulbous, dehiscing irregularly with several valves, wall unistratose, cells spindle shaped, 50–70 μ m long, 0.02–0.04 mm wide with annular and semi-annular thickenings.

Spores reddish-brown, 41.6–55.6 μm in diameter, slightly triangular in outline, distal face convex, proximal face flatter, trilete mark not visible to slightly visible, surface densely covered with hemispherical domes, 4.0–5.56 μm high, acute to obtuse, fine granules aggregated at the tip of dome, sometimes tiny pores present at tip, with4–6 cavities around domes, surface except at dome tips mostly smooth.

Elaters brown, 160–248 μm long, 8.0–12.0 μm wide at middle, branching not observed.

Chromosome number n=9 (Fritsch 1991).

Illustrations: Figures, 4.7; 2.3 (C); 2.4 (C).

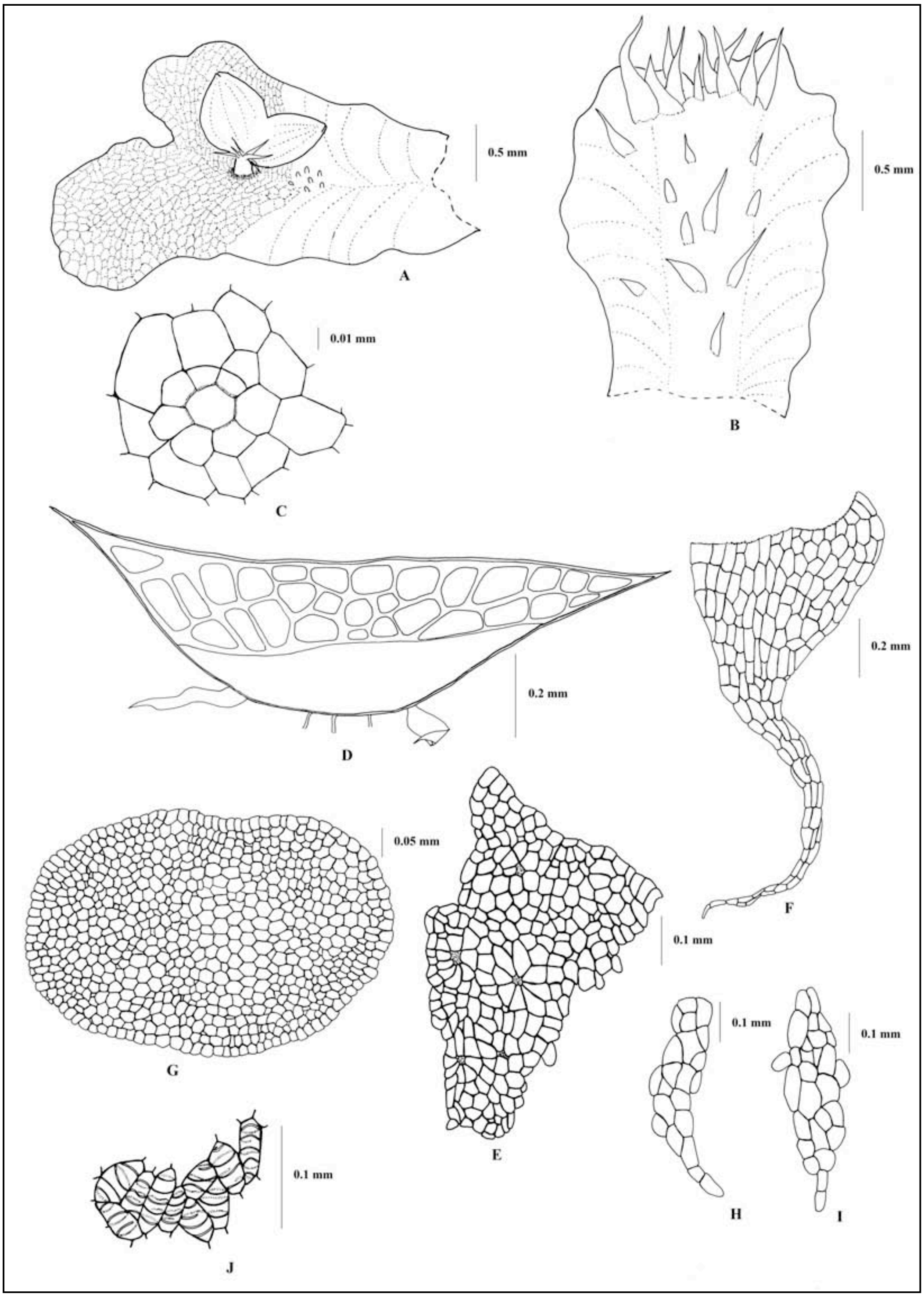


Figure 4.7. ***Clevea pusilla*. A) dorsal surface of thallus showing archegoniophore and antheridial ostioles; B) ventral surface of thallus showing ventral scale distribution; C) air pore from dorsal epidermis of thallus; D) transverse section of thallus; E) ventral scale from median region of thallus; F) ventral scale from alongside midrib; G) transverse section of apex of stalk; H, I) apical stalk scales; J) cells of spore wall. A–C, F, G, H, I, India, *Long 22838* (E); D, India, *Chopra 24* (JE); E, Nepal, *Yoda s.n*. (TNS); J, India, *Gollan 3960* (BM).**

Distribution:

The distribution of *C. pusilla* based on confirmed herbarium specimens: China, India and Japan (Fig. 4.8).

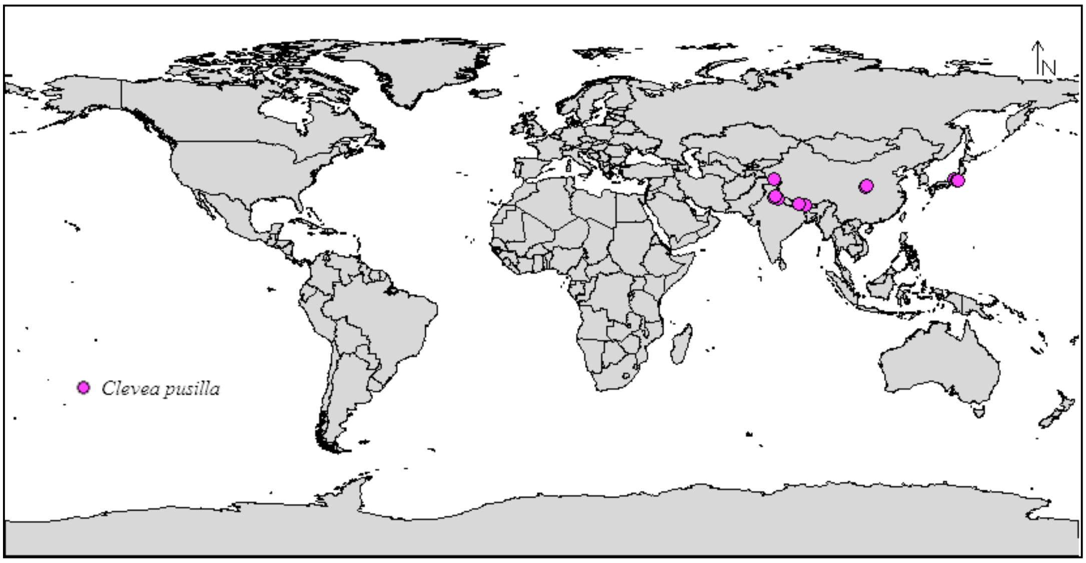


Figure 4.8. Distribution of *Clevea pusilla* based on confirmed herbarium material.

Ecological Notes:

Clevea pusilla prefers growing in rock crevices, mostly clay-slate, or limestone cliffs and is recorded between 600 and 1900m. It is recorded as a common species in the northwest Himalayas (Kashyap, 1929).

Taxonomic Notes:

Clevea pusilla has smaller thalli than the other two species in genus. Its pores are similar to *C. spathysii*; the radial walls are thin and never stellate. The ventral scales are mostly not in distinct rows but scattered on the midrib region which is a distinct difference from the other two species.

Nomenclatural Notes:

The genus *Gollaniella* was proposed by Stephani (1905) from a species collected in Mussoorie in NW India. He included one species *Gollaniella pusilla* in the genus; the original material was collected by W. Gollan. Another species was introduced to the genus by Shimizu and Hattori (1953), *Gollaniella nana* from Japan. However, Kashyap (1929) regarded the two genera *Gollaniella* and *Athalamia* as identical and treated *G. pusilla* under *Athalamia pusilla*. Shimizu & Hattori (1954), considering Kashyap's detailed description of *Athalamia pinguis*, decided that there are no characters of generic value to separate the three genera *Athalamia*, *Clevea* and *Gollaniella* and united all three under *Athalamia*. They mainly focussed on the stellate nature of the radial walls of the three genera, and stated that "whether the pores of thallus are stellate or not should not be considered as a characteristic of generic value". However, they played down the fact that air chambers in *Athalamia* are much narrower and slit-like, and argued that similar air chambers are found in *Clevea* although there they are found only close to the sexual organs and are often not so narrow. In fact, the present study shows that the air chambers of *Athalamia* are unique and much narrower than those of any other genus in the family.

In the same year Shimizu and Hattori (1954) described a new species, *Athalamia glauco-virens* and a new form, *Athalamia glauco-virens* fo. *subsessilis* from Japan. Both taxa were considered to be endemic to Japan.

Stephani (1917) described a new species, *Clevea chinensis* from Schensi Province, China. Shimizu & Hattori (1955) giving a description of that species from Stephani's original diagnosis and his unpublished 'Icones' mentioned that their *C. nana* seems to be related to *C. chinensis*. After rediscovering *Athalamia nana* in a different locality in Japan, the same authors noted that the differences between the two species *A. nana* and *A. glauco-virens* could possibly be ecological, and that they could be closely related to Stephani's *C. chinensis*. The same authors, examining a cultivated population of their forma *subsessilis*, decided that the statistical dimensions of the stalk and spores which they had previously found different from *A. glauco-virens* were phenotypic variations and that they are identical. Furthermore, Shimizu and Hattori (1959), after studying cultures, confirmed that *A. nana*, *A. glauco-virens* and *A. glauco-virens* fo. *subsessilis* were ecological variants of the same species and they synonymised them under *A. nana*. They also noted that this species is probably conspecific with the Indian *A. pusilla* and the Chinese *C. chinensis*, however they were not able to confirm this.

4.6.2 The genus *Athalamia*

Athalamia Falc., Ann. Mag. Nat. Hist. ser. 2, 1: 375, 1848; Trans. Linn. Soc. London 20: 397, 1851 (detailed description). – Type: *Athalamia pinguis* Falc.

Description:

Thalli medium to large, thick and fleshy in the median region, light green above; vegetative branching terminal, once or rarely twice dichotomously branched, ventral branches also common; margins strongly undulate, white to hyaline; dorsal surface without clear markings or with very narrow rectangular to square shaped markings; air pores simple, slightly elevated or rarely not elevated, radial walls strongly thickened and star shaped or slightly to rarely not thickened; assimilatory tissue with one (rarely 2 or 3) layer(s) of narrow, linear slit like air chambers without photosynthetic filaments; midrib strongly protruding on ventral surface, sharply and suddenly passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells at midrib region.

Ventral scales whitish to hyaline with brownish tinge at base, in 4 longitudinal rows on either side of the midrib, dense and overlapping, ovate (rarely lanceolate), with a weakly to very weakly defined appendage, oil cells absent.

Sexual condition par-autoicous and terminal-autoicous. Androecia dorsal, behind or in front of base of archegoniophore, or sometimes on a separate terminal branch on the same plant, ostioles whitish, conspicuous, antheridial scales absent. Gynoecia dorsal; stalk cylindrical, light green or whitish to hyaline, smooth, without rhizoid furrow, cells thin-walled, polygonal to isodiametric, apical stalk scales present, hyaline, lanceolate, slime papillae absent or up to 7 evenly distributed on either side of margin; carpocephalum light green to yellowish green, cup-shaped, with 1–3 lobes, pointing upwards, each involucre with one sporophyte.

Capsule slightly elongated to globose, foot short, dehiscing by several longitudinal valves, wall unistratose, cells cylindrical to spindle shaped, with annular and semiannular thickenings.

Spores blackish brown, triangular to spherical in outline, distal surface convex, proximal face flatter, trilete mark faintly visible, surface with bands of reticulate papillae.

Elaters blackish-brown, branching not observed.

Chromosome number n= 18 (Fritsch 1991).

Distribution:

Athalamia is a monotypic genus distributed around the Tibetan Plateau. Based on the confirmed herbarium specimens the genus is found in China, Mongolia, India, Nepal and Pakistan.

Taxonomic Notes:

Athalamia sensu stricto is distinctly different from *Clevea* with which it was united since 1954. It has robust, thick, fleshy thalli with whitish protruding scales which are characteristic of the genus in addition to the narrow, slit-like air chambers in the t.s. of its thallus. Spores of *Athalamia* are quite different from the other three genera of the family by having reticulate ornamentation. No secondary pigmentation was observed in *Athalamia*, a featured it shares with *Sauteria*. *Athalamia* shares two morphological characters with *Clevea*: dorsal position of the gynoecia and lack of a rhizoid furrow in the carpocephalum stalk; these are the characters which led to the two genera being united in the past but no other significant shared characters were observed between the two genera.

Nomenclatural Notes:

The genus was discovered and described by Falconer (1848, 1851), as ‘a new genus in Marchantieæ”. However his original description was very brief. Schiffner (1909) treated it as a doubtful genus in his group Marchantioidae–Astroporae. He also stated that it was undoubtedly closely related to *Clevea*. The genus was overlooked or ignored by many later authors and was not included in the family Cleveaceae when it was created by Cavers (1911). Shimizu and Hattori (1954) considered it to be identical with *Clevea*.

1. *Athalamia pinguis* Falc., Ann. Mag. Nat. Hist. ser. 2, 1: 375, 1848; Trans. Linn. Soc. London 20: 397, 1851 (detailed description). – Type citation: [India, Himalaya] not indicated. – Type specimen: *n.v.* (specimen not located).

= *Clevea gollani* Levier ex Steph., Sp. Hepat. 6: 5, 1917. – Type citation: [India] "Himalaya (Gollan legit.)". – Type specimens: [India, Uttaranchal] Mussoorie (N.W. Himalaya) Hill above Arnigadh Garden, on rocks in open spots 6000 ft. "Leaves have pale yellow or golden tint when fresh". 12 Sept. 1900. *W. Gollan. 3842* (G 00067324); Mussoorie (N.W. Himalaya) Govt. Bot. Gardens Arnigadh, on banks, 5500 feet, 11 ix 1900, *W. Gollan. 3842*^{b} (G-00112848, lectotype, selected here); synonymised by Kashyap (1929).

= *Clevea handelii* Herzog in Handel-Mazzetti, Symb. Sinic. 5: 2, 1930. ≡ *Athalamia handelii* (Herz.) S.Hatt. in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 54, 1954. – Type citation: [China] "NW-Y[unnan]: An Mauern (Eruptivgestein) der tp. St. [temperierte Stufe] in Ngulukö bei Lidjiang ("Likiang"), 2830m, 9 vi 1915 (6682)." – Type specimen: [China] Prov. Yünnan bor.-occid.: In regionis temperatae in vico Ngulukö ad urbem Lidjiang (''Likiang''), muris, Substr. Eruptivo, 2830 m., 9 vi 1915, *Handel-Mazzetti 6682*, (JE, holotype; E, isotype); *syn. nov.*

Description

Thalli medium to large, broad linear-lingulate or obovate-lingulate, flat, fleshy, light green above, whitish towards the margin, vegetative branching terminal, once or rarely twice dichotomously branched, ventral branches common; branches 5.3–13.0 mm long, 2.0–8.75 mm wide; margins strongly undulate, white to rarely hyaline; dorsal epidermis with thin-walled, hyaline, polygonal to isodiametric cells, 0.04–0.09 mm long, 0.02–0.06 mm wide, dorsal surface without clear markings,; air pores simple, 8.7–32.2 μm in diameter, surrounded by a single row of (4–)5–6(–7) cells, radial walls strongly thickened and star-shaped or rarely slightly to not thickened; thallus t.s. 0.7–1.25 mm thick over midrib, assimilatory tissue with one (rarely 2 or 3) layer(s) of narrow, linear slit like air chambers without photosynthetic filaments, storage tissue hyaline, well developed, without oil cells; midrib strongly protruding on ventral surface, 1.6–3.3 mm wide, sharply and suddently passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells at midrib region.

Ventral scales white to rarely hyaline with brownish tinge at base, in 4 longitudinal rows on either side of the midrib, dense and overlapping, ovate (rarely lanceolate), 1.0–1.7 mm long, 0.09–1.3 mm wide, with a weakly to very weakly defined appendage, unistratose, cells in body and appendage similar, uniform, thin to thick-walled, rectangular, 79.5–158.9 mm long, 25.21–54.0 mm wide, slime papillae 0(–1, very rarely), margin entire, oil cells absent.

Sexual condition par-autoicous and terminal-autoicous. Androecia dorsal, behind or in front of archegonia, or sometimes on a separate terminal branch on the same plant, ostioles 6–12, whitish, conspicuous, antheridial scales absent. Gynoecia dorsal, 1 or up to 4 in a line; stalk cylindrical, light green or whitish to hyaline, smooth, 1.5–8.9 mm long, round to elliptic in t.s. 0.4–0.8 mm in diameter, without rhizoid furrow, cells thin-walled, polygonal to isodiametric, apical stalk scales present, hyaline, 0.1–0.7 mm long, lanceolate, slime papillae absent or up to 7 evenly distributed on either side of margin; carpocephalum light green to yellowish green, cup-shaped, 1.2–2.5 mm in diameter, with 1–3 lobes, pointing upwards, each involucre with one sporophyte. Capsule slightly elongated to globose, foot short, up to 2.4 mm long, dehiscing by several longitudinal valves, wall unistratose, cells cylindrical to spindle shaped, 36.8–73.7 μm long, 18.5–27.4 μm wide, with annular and semiannular thickenings.

Spores blackish brown, 74.3–75.7 μm in diameter, triangular to spherical in outline, distal surface convex, proximal face flatter, trilete mark faintly visible, surface with bands of reticulate papillae, distinctly different from spore ornamentation of other 3 genera.

Elaters blackish brown, (71–)114–214 μm long, 5.7–11.4 μm wide at middle, branching not observed. Chromosome number n= 18 (Fritsch 1991).

Illustrations: Figures 4.9; 2.2 (E, F); 2.3 (D); 2.4 (B); 2.5 (D); 2.8 (D); 2.9 (A); 2.11 (B, D)

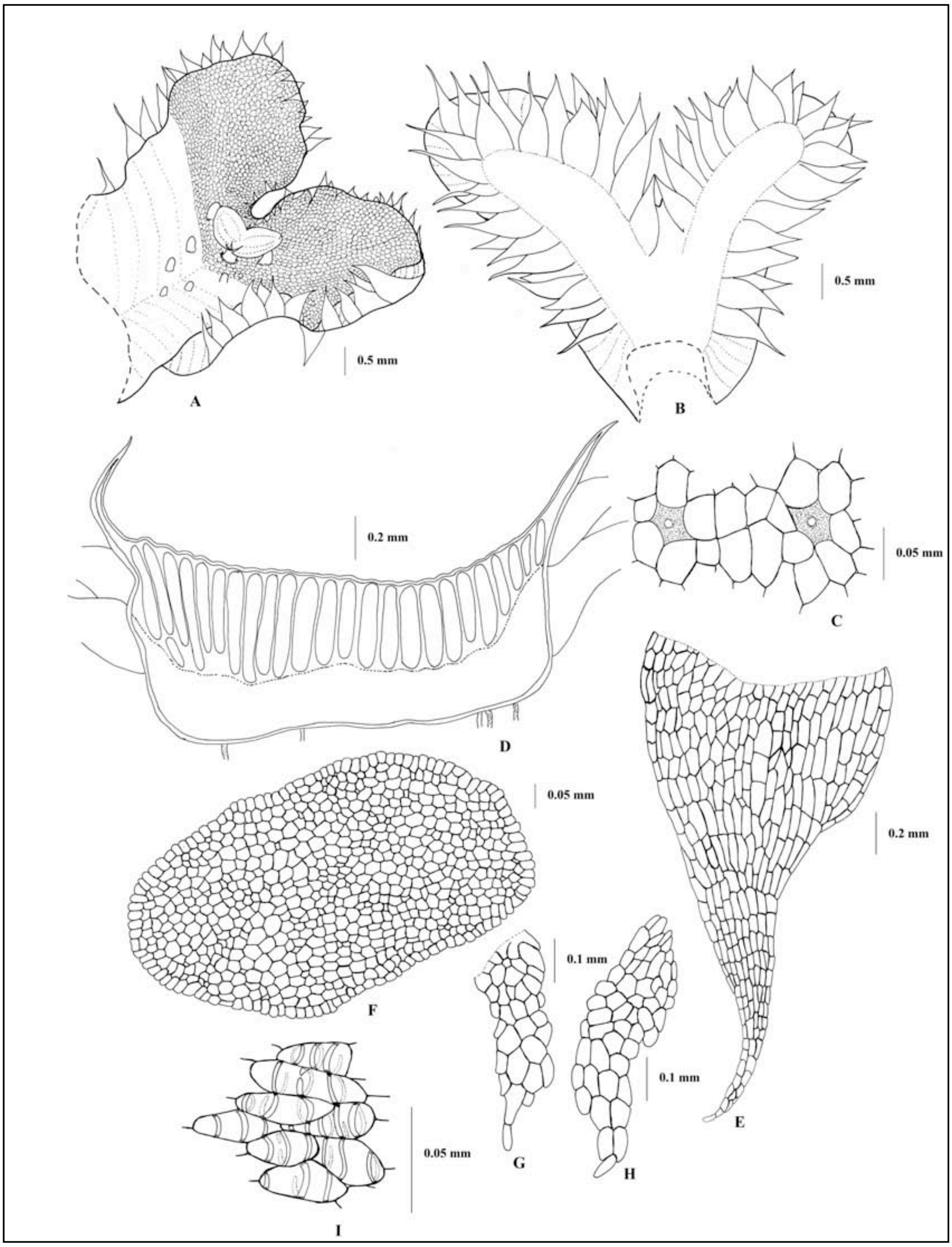


Figure 4.9. ***Athalamia pinguis*****. A) dorsal surface of thallus showing archegoniophore and antheridial ostioles; B) ventral surface of thallus showing ventral scale distribution; C) air pore from dorsal epidermis of thallus; D) transverse section of thallus; E) ventral scale from alongside midrib; F) transverse section of apex of stalk; G, H) apical stalk scales; I) cells of spore wall. A, B, E, G, H, Pakistan,** ***Higuchi 19772*** **(TNS); C, D, F, I; China,** ***Long 18626*** **(E); F, India,** ***Kashyap 354*** **(O).**

Distribution:

Based on confirmed herbarium specimens *A. pinguis* is distributed in: China, Mongolia, India, Nepal and Pakistan (Fig. 4.10).

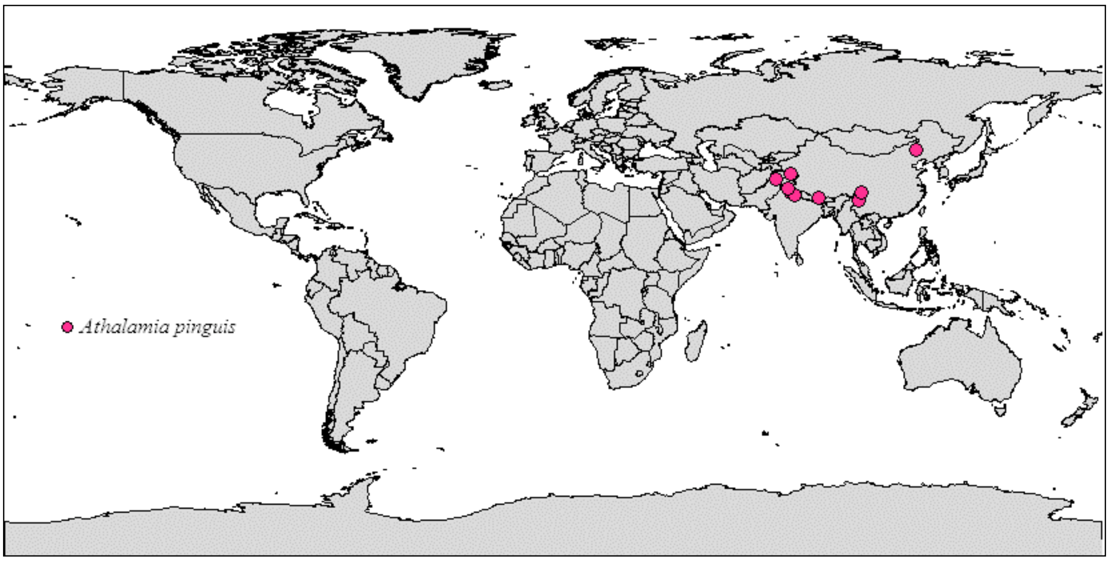


Figure 4.10. Distribution of *Athalamia pinguis* based on confirmed herbarium material.

Ecological notes

Plants grow as large pure patches on rocks or earth especially on limestone (Kashyap 1916). In Yunnan it grows on limestone tufa beside hot springs and in Sichuan on soil in crevices of walls. *Athalamia pinguis* is cited as one of the commonest liverworts in Mussoorie, NW India (Kashyap 1915). Its altitudinal range is 609–3400 m.

Taxonomic notes:

Athalamia pinguis can be easily recognized even in the sterile condition by its large and conspicuous white protruding scales. Plants are very fleshy, normally simple, margins are upturned and the thallus at the middle tends to be concave. Shallow spreading grooves are absent from the dorsal surface of the thallus because of the nature of the air chambers, which are narrow and slit-like. Antheridial ostioles of *A. pinguis* were found to be whitish or light greenish and conspicuous.

Nomenclatural notes:

The genus was discovered and described by Falconer (1848, 1851). However the original description provided by him was very brief and did not include any information on the type specimen. According to Desmond (1992) Falconer was superintendent from 1832 to 1841 of Saharanpur Botanic garden in Uttar Pradesh, about 90 km below the hill station of Mussoorie where a second smaller garden was established. According to Kashyap (1915) *Athalamia pinguis* is one of the commonest livrworts in Mussoorie, so it is very likely that Falconer's type specimen came from Mussoorie.

4.6.3 The genus *Sauteria*

Sauteria Nees, Naturg. Europ. Leberm. 4: 139, 1838. ≡ *Hampea* Nees, Naturg. Europ. Leberm. 4: 139, 1838 (non Schlechtendal 1837, Bombacaceae), *nom. inval*. (Art. 34). – Type: *Sauteria alpina* (Nees) Nees.

= *Sauchia* Kashyap, J. Bombay Nat. Hist. Soc. 24: 437, 1916. – Type: *Sauchia spongiosa* Kashyap; synonymised by Shimizu & Hattori (1954).

Description:

Thalli small, linear or obovate to lingulate, flat to slightly concave along mid-line, fine to spongy, yellowish green to whitish-green above, vegetative branching terminal and ventral, usually simple, rarely once or twice dichotomously branched; branches 2.0–13.0 mm long, 1.0–6.4 mm wide; margins slightly undulate, yellowish to whitish; dorsal epidermis with thick-walled, polygonal to rectangular cells, with chloroplasts, dorsal surface with clear hexagonal markings representing underlying air chambers, sometimes conspicuously areolate; air pores simples, with 1–2 rings of 4–8 cells, radial walls slightly to not thickened, usually with an inner hyaline ring; assimilatory layer well developed, deep, with 1–3 layers of wide polygonal air chambers without photosynthetic filaments; midrib not strongly protruding on ventral surface, gradually passing into wings.

Rhizoids smooth and pegged arising from the ventral epidermal cells along midrib region.

Ventral scales hyaline to silvery white, in 2 distinct rows on either side of midrib or irregularly arranged on midrib region, sometimes arising towards margins, small, ovate to lanceolate, 0.42–0.87 mm long, 0.28–1.01 mm wide, with a weakly defined appendage, unistratose, cells thin-walled, with 1–2 oil cells, slime papillae 2–3.

Sexual condition par-autoicous, terminal-autoicous and ventral-autoicous. Androecia dorsal, loosely scattered, behind archegoniophore or on a separate terminal branch or on a small ventral branch, ostioles greenish to whitish, not conspicuous. Gynoecia originating in an apical notch, one or both lobes may elongate making archegoniophore lateral or terminal, stalk yellowish green to hyaline, smooth, with 1 rhizoid furrow, cells think walled; apical stalk scales hyaline or silvery white, small, linear to ovate, slime papillae 2–many; carpocephalum dull green to yellowish green, umbrella shaped, 2–7 lobed.

Distribution of *Sauteria*:

According to confirmed herbarium specimens, *Sauteria* is distributed in Austria, Canada, China, Finland, France, Germany, Greece, Greenland, Hungary, India, Italy, Japan, Nepal, Norway, Pakistan, Poland, Romania, Russia, Slovakia, Svalbard, Sweden, Switzerland and U.S.A. (Alaska) (Figure 4.11). According to literature it is also recorded from Minnesota in the U.S.A, British Columbia and Alberta in Canada and from the former Yugoslavia. It is not known from the southern hemisphere except for *Sauteria nyikaensis* Perold from Malawi which is a poorly known species of uncertain generic placement (see below under excluded species).

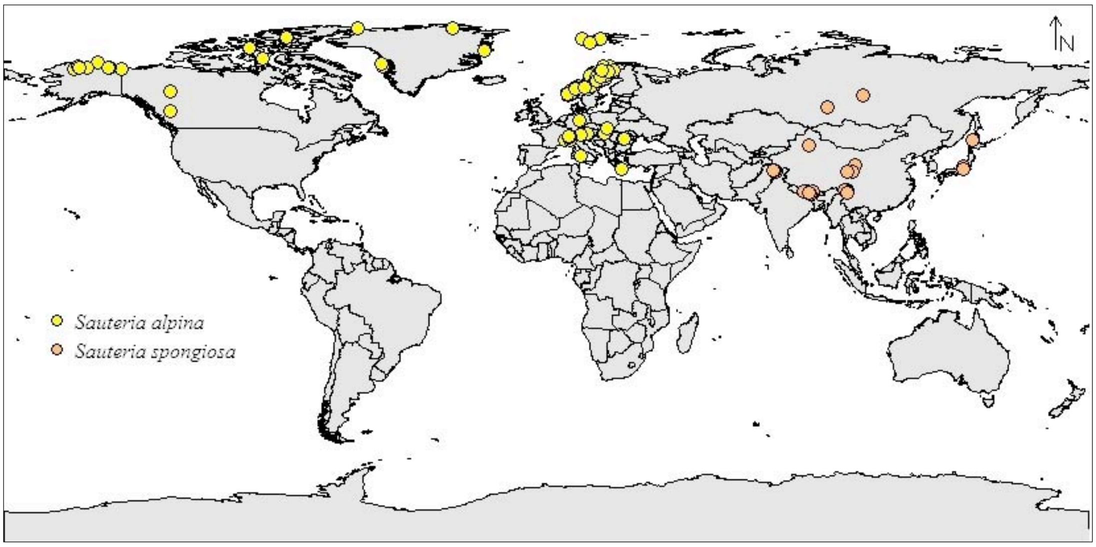


Figure 4.11. Distribution of *Sauteria* based on confirmed herbarium material.

Taxonomic notes:

The silvery white ventral scales with oil body containing cells, and the total lack of secondary pigmentation in the thallus and the carpocephalum stalk with a single rhizoid furrow differentiates *Sauteria* from all other the members of Cleveaceae. The thallus margins become decolorated and the upper surface lacunose with age, and it can be easily spotted when occurring with *Clevea hyalina* and *Peltolepis quadrata* by its yellowish to whitish-green, fleshy, spongy, delicate thalli. Ventral scales tend to be hidden under the thallus margin and are only seen at the apex when young and in older plants when the margins roll upwards. Air pores are different from other three genera in having an inner hyaline ring.

Nomenclatural notes:

Nees, when erecting the genus *Sauteria*, based it on the European plant he had earlier called *Lunularia alpina* Nees (Nees, 1830). The genus *Sauchia* was first described by Kashyap (1916) from the NW Himalaya. Kashyap (1929) noted that *Sauchia* is different from its ally *Sauteria* in having thin walled cells around the pores and its delicate texture. Shimizu & Hattori (1953) described a new species under *Sauchia, S. japonica* stating that it differed from *Sauchia spongiosa* in having 2-3 layers of air chambers, a prominent midrib below and slightly larger spores. However, the same authors a year later remarked that the genus *Sauteria* was very closely related to the Indian *Sauchia* and that it differed from the former only by having slightly thickened or thin radial walls around the pores. Since they did not find any other characters of generic value to keep the two genera separate, *Sauchia* was synonymised under *Sauteria* (Shimizu & Hattori 1954). At the same time, Shimizu & Hattori (1954) described a new variety from Japan; *Sauteria alpina var. japonica*, and noted that the new variety could possibly be a local species of *Sauteria*. However, later this variety was elevated to specific rank as *S. yatsuensis*, and the authors mentioned that it differed from *S. alpina* in having a non-convex receptacle lacking pores, lobes extending 65º-75º with stalk, and radial walls of the pores not so thickened.

Schuster (1985), divided *Sauteria* into three sections: Sectio Sauteria, Sectio Yatsuenses, and Sectio Sauchia; based on the number of layers of air chambers, degree of thickening of radial walls of air pores, presence of air chambers and pores on the receptacle tissue and the position of androecia. He discussed a reduction series in *Sauteria* based on the number of layers of air-chambers in the thallus, position of androecia and presence of air-chambers and air pores in receptacular tissue of carpocephalum (Schuster 1992). In his discussion, Schuster (1985, 1992) placed *S. alpina* as the most advanced in the series, having strongly stellate pores, higher number of layers of air chambers in the thallus, and well-developed receptacular tissue with air chambers and air pores, although he noted the latter character was variable within species. He placed *S. yatsuensis* at an intermediate position and considered *S. spongiosa* the most reduced. However, he noted that only a few specimens had been investigated. The present study showed that the number of air-chambers in the main thallus, presence of air-chambers and pores in receptacular tissue, as well as the degree of radial wall thickening are highly variable characters within species and cannot be successfully used in species identification. The position of androecia and texture of thallus was found to be a good character in specific delimitation withing *Sauteria*. The present study recognised two species within *Sauteria*; *S. alpina* and *S. spongiosa* and after careful examination of other Japanese species they were identified as synonyms of *S. spongiosa*. This identification was further confirmed by the molecular phylogenetic analysis (Chapter 3) which included Indian and Japanese specimens.

Key to species of *Sauteria*

1. Dorsal surface smooth, only older parts areolate, yellowish green, rarely whitish green, delicate and fine, androecia behind archegonia or on a separate terminal branch, rarely on a ventral branch *Sauteria alpina*

\+ Dorsal surface conspicuously areolate, areoles wide, whitish green rarely yellowish green, delicate and spongy, androecia on reduced ventral branches, rarely behind archegoniophore *Sauteria spongiosa*

1. *Sauteria alpina* (Nees) Nees, Naturg. Europ. Leberm. 4: 139, 1838. ≡ *Lunularia alpina* Nees, in Nees & Bischoff, Flora 13: 393, 399, 1830. – Type citation: [Austria, Slovenia] “Habitat in alpibus Germaniae australis; in cataracta Leitrae fluminis minore prope Heiligenblut invenit Alex. Braun; in alpe Pasterze dicta ad rupes, muscis instratam Funkius, amicus carissimus, in Carnioliae alpibus Müllerus, foederis itinerarii sumtibus iter faciens, legit distribuitque.” – Type specimens: [Slovenia] in Carnioliae alpibus *Müller* (Reiseverein no. 4) (STR, lectotype, *n.v.*, selected by Grolle (1976); BP, isolectotype, *n.v.*); [Austria, Salzburg] Pasterzalp, 1821, *Funck s.n.* (syntype, STR, *n.v.*) (not seen).

= *Sauteria alpina* (Nees) Nees var. *angustifrons* Kaal., in Jørgensen, Bergens Mus. Skr. 16: 27, 1934. – Type citation: [Norway, Prov. Troms] “Nordreise, på skifergrus i dalen n.f. Jerta (J[ørgensen] 29.7.[18]93, var. *angustifrons* Ks: thallus 1-3 mm bredt, fruktstilk 5 mm). Kvaenangen: Slirovarre, near sneen, J[ørgensen] 11.8. [18]90, var. *angustifrons*, fr.”. – Type specimen: [Norway] Troms: Nordreise, Reisen, paa skifergrus i dalen nord for Jertafjeld, 29 vii 1893, *E. Jørgensen s.n.* (O-27860, lectotype selected here).

Description:

Thalli small, linear to lingulate, flat to slightly concave along mid-line, delicate to firm (rarely fleshy), light to yellowish green (rarely whitish green) above, vegetative branching terminal and ventral, simple, rarely once or twice dichotomously branched; branches 3.3–8.6 mm long, 2.2–3.6 mm wide; margins slightly undulate, yellowish or rarely whitish; dorsal epidermis with thin-walled, polygonal to rectangular cells, with chloroplasts, 36.1–79.9 µm long, 25.6–35.4 µm wide, dorsal surface with shallow spreading hexagonal grooves representing underlying air chambers, each with a single very slightly to not raised air pore at middle; air pores simple, 14.3–57.1 μm in diameter, surrounded by 1–2 rings of 4–5(–8) cells, radial walls slightly to not thickened, sometimes innermost ring collapsed with time; thallus t.s. 0.9–1.0 mm thick over midrib, assimilatory tissue well-developed, 0.51–0.58 mm thick, with 1–3 layers of polygonal air chambers without photosynthetic filaments, storage tissue hyaline, well developed, rarely with 1–2 oil cells; midrib not strongly protruding on ventral surface, 0.8–1.4 mm wide, gradually passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells at midrib region.

Ventral scales hyaline to silvery white, in 2 distinct rows on either side of midrib or irregularly distributed on midrib region, scattered (dense and overlapping only at apex), ovate to lanceolate, 0.6–0.9 mm long, 0.3–1.0 mm wide, with a very weakly defined appendage, unistratose, cells in body and appendage similar, uniform, thin-walled, polygonal, 65–100 μm long, 42–51 μm wide, slime papillae 2–3, margine entire, oil cells present, 1–2, rarely absent.

Sexual condition par-autoicous and terminal-autoicous, rarely ventral-autoicous. Androecia dorsal, immediately proximal to base of archegoniophore or on separate branch on same plant, very rarely on ventral branch, ostioles up to 6, yellowish green, inconspicuous, antheridial scales absent. Gynoecia in deep apical notch, sometimes both or one of the branches elongating, up to 3; stalk cylindrical, yellowish green, smooth, 3.2–10.4 mm long, round in t.s. 0.4–0.6 mm in diameter, with 1 rhizoid furrow, cells thin-walled, isodiametric, apical stalk scales present, hyaline to silvery white, 0.44–0.92 mm long 0.07–0.13 mm wide, linear to ovate, slime papillae 6 to many, evenly distributed on either side; carpocephalum dull green to yellowish green, umbrella-shaped, 2.1–2.7 mm in diameter, with 2–6 lobes, pointing downward rarely horizontal, each involucre with one sporophyte. Capsule globose, foot bulbous, short, up to 0.47 μm long, dehiscing by several irregular valves, wall unistratose, cells cylindrical to spindle shaped, 47.9–69.1 μm long, 22.0–32.8 μm wide, with annular and semi-annular thickenings. Spores reddish brown, 60.0–66.7 μm in diameter, triangular, distal surface convex, proximal surface slightly flatter, trilete mark slightly to not visible, densely covered with hemispherical domes, 4.2–5.0 μm high, obtuse, spaces between domes narrow, without deep cavities around domes, entire surface covered with evenly distributed fine granules.

Elaters brown to dark brown, 127–300 μm long, 7.3–14.5 μm wide at middle, sometimes branched, sometimes bent.

Chromosome number n=36 (Fritsch 1991).

Illustration: Figures 4.12; 2.2 (G); 2.4 (E); 2.5 (E, G); 2.9 (F); 2.10 (A); 2.11 (F).

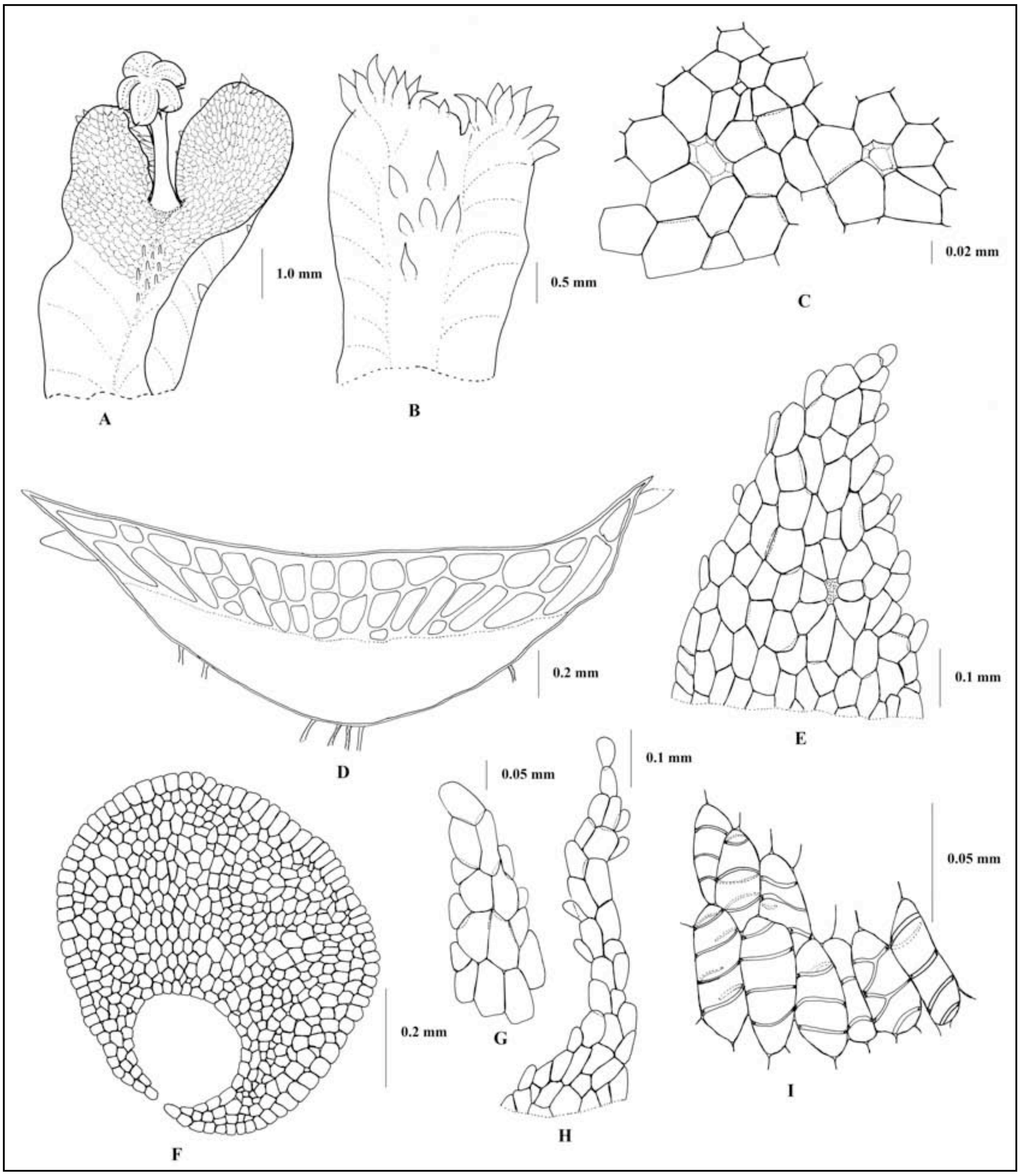


Figure 4.12. ***Sauteria alpina*. A) dorsal surface of thallus showing archegoniophore and antheridia; B) thallus ventral surface showing ventral scale distribution; C) air pores from dorsal epidermis of thallus; D) transverse section of thallus; E) ventral scale from median region of thallus; F) transverse section of apex of stalk; G, H) apical stalk scales; I) cells of the spore wall. A, Austria, *Wettstein & Patzelt 1070* (W); B, E, I, Austria, *Breidler s.n.* (W); C, D, F, Switzerland, *Rubasinghe & Long 10-08SR* (E); G, H, Austria, *M. Anzi s.n.* (W).**

Distribution:

The distribution of *Sauteria alpina* based on confirmed herbarium specimens: Austria, Canada, Finland, France, Germany, Greece, Greenland, Hungary, Italy, Norway, Poland, Romania, Slovakia, Svalbard, Sweden, Switzerland, U.S.A (Alaska) (Fig. 4.13). It is not recorded from the British Isles, Africa, Asia or South America. Its distribution is mainly holarctic. Although various authors have previously recorded *Sauteria alpina* from the Himalaya (Kashyap 1929), China and Japan (Shimizu & Hattori 1955), no evidence was found to prove the occurrence of *S. alpina* in these countries from the material observed and it is likely that these records refer to *S. spongiosa*.

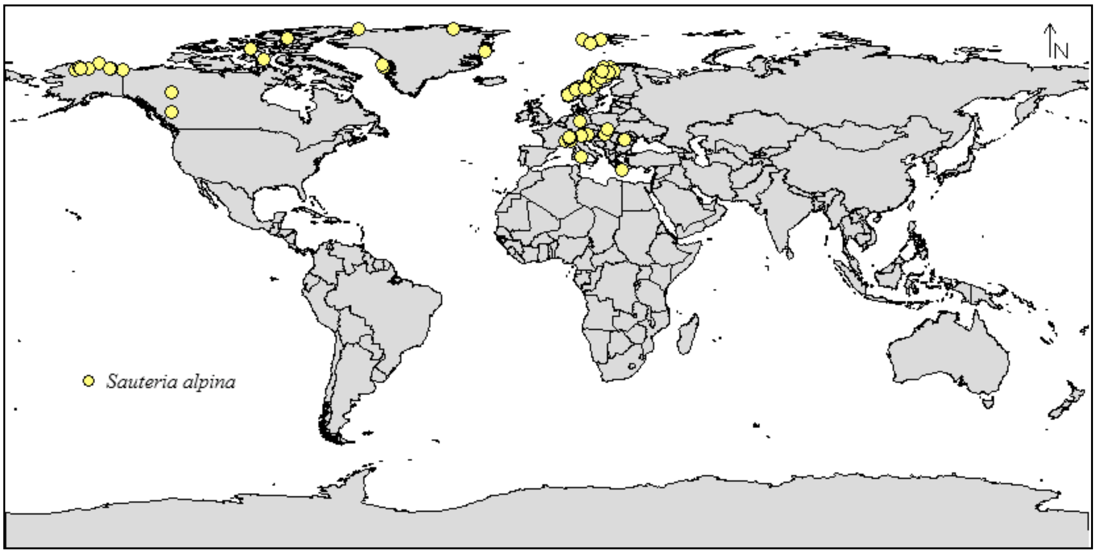


Figure 4.13. Geographic distribution of *Sauteria alpina* based on confirmed herbarium material.

Taxonomic notes:

Sauteria alpina can be differentiated from the other species of Cleveaceae by its extremely delicate texture and the light to translucent green to yellowish colour.

Ecological Notes:

Sauteria alpina is confined to arctic and alpine sites, in damp crevices of limestone cliffs.

2. ***Sauteria spongiosa*** (Kashyap) S.Hatt., in Shimizu & Hattori, J. Hattori. Bot. Lab. 12: 62, 1954. ≡ *Sauchia spongiosa* Kashyap, J. Bombay Nat. Hist. Soc. 24: 347, 1916. – Type citation: [India, Himachal Pradesh] “Moist shady rocks on the Chamba–Pangie road, 10,000 feet.” – Type specimen: *n.v.* (specimen not located).

= *Sauchia japonica* Shimizu & S.Hatt., J. Hattori Bot. Lab. 9: 34, 1953. ≡ *Sauteria japonica* (Shimizu & S.Hatt.) S.Hatt., in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 62, 1954. – Type citation: “Hab. On moist agglomerates in exposed places, ca. 2800 m. alt., near summit of Yatsu Volcano, Nagano Prefecture, August 13, 1952, Coll. D. Shimizu.” – Type specimen: *n.v.* (not seen).

= *Sauteria alpina* (Nees) Nees var. *japonica* Shimizu & S.Hatt., J. Hattori Bot. Lab. 12: 64, 1954. ≡ *Sauteria yatsuensis* S. Hatt., in Hattori & Shimizu, J. Hattori Bot. Lab. 14: 99, 1955. – Type citation: [Japan] “Among rock crevices and moist surface of agglomerate bluff facing west by south, ca. 2500 m. alt., Mt. Yatsu, Nagano County, August 22, 1953, Coll. D. Shimizu, No. 52828–Type, Nos. 52745–52747.” – Type specimen: *n.v.* (not seen).

Description:

Thalli small, obovate to lingulate, rarely linear-lingulate, flat to slightly concave along mid-line, delicate and spongy, whitish green (rarely yellowish green) above, vegetative branching terminal and ventral, often with numerous small ventral branches, rarely once or twice dichotomously branched, branches 1.5–7.7 mm long, 0.9–3.9 mm wide; margins slightly undulate, light green to whitish green, (rarely yellowish green); dorsal epidermis with thin-walled polygonal cells, with chloroplasts 67.2–80.0 μm long, 41.6–70.5 μm wide, dorsal surface with hexagonal markings corresponding with underlying air chambers, conspicuously areolate; air pores simple, 0.02–0.04 mm in diameter, surrounded by 1–2 rings of 7–8(–9) cells, radial walls not thickened (rarely very slightly thickened), innermost ring usually collapsed, sometimes both layers collapsed making pores visible even to naked eye; thallus t.s. 0.5–0.8 mm thick over midrib, assimilatory tissue well developed, usually occupying ½ of entire thickness, with 1–3 layers of isodiamtric, wide, air chambers without photosynthetic filaments, occupying 2/3 of the entire thickness, storage tissue hyaline, oil cells not observed; midrib not strongly protruding on ventral surface, 0.2–1.4 mm wide, gradually passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells at the midrib region.

Ventral scales hyline to silvery white, irregularly arranged on ventral surface, usually arising at margins at apex, scattered (dense and overlapping only at apex), ovate to lanceolate, 0.4–0.8 mm long, 0.28–0.30 mm wide, with a very weakly defined appendage, sometimes appendage not defined, unistratose, cells in body and appendage similar, uniform, thin-walled, polygonal or rectangular, 54.2–78.6 µm long, 48.7–67.5 µm wide, slime papillae 2–3, margins entire, oil cells present, 1–2, rarely absent.

Sexual condition ventral-autoicous, rarely par-autoicous. Androecia loosely scattered, dorsal on a short ventral branch, very rarely behind base of archegoniophore (par-autoicous), up to 6, ostioles whitish, conspicuous, antheridial scales absent. Gynoecia in deep apical notch, sometimes both or one of the terminal branches elongating, up to 3; stalk cylindrical, yellowish green to whitish green, smooth, 7.0–13.0 mm long, round in t.s. 0.5–0.6 mm in diameter, with 1 rhizoid furrow, cells thin-walled, isodiametric, apical stalk scales present, hyaline to silvery white, 0.69–0.77 mm long 0.14–0.16 mm wide, linear to ovate, slime papillae 2–6, evenly arranged on either side; carpocephalum dull green to yellowish green, umbrella shaped, 1.7–3.5 mm in diameter, with 2–6 lobes, pointing downwards or horizontal, each involucre with one sporophyte. Capsule globose, foot bulbous, capsule dehiscing into several irregular valves, wall unistratose, cells spindle shaped, 82.4–91.8 µm long, 20.0–28.7 µm wide, with annular and semi-annular thickenings. Spores reddish brown, 63.3–76.9 µm in diameter, triangular, distal surface convex, proximal surface slightly flatter, trilete mark weakly visible, densely covered with hemispherical domes, up to 3.6 µm high, obtuse, spaces between domes narrow, without deep cavities around domes, entire surface covered with granules, evenly distributed. Elaters brown, 130–367 µm long, 6.7–10.0 µm wide at middle, branching not observed. Chromosome number n=36 (Fritsch 1991).

Illustrations: Figures, 4.14; 2.3 (E); 2.5 (C); 2.8 (B); 2.9 (B); 2.10 (C, E, F, G).

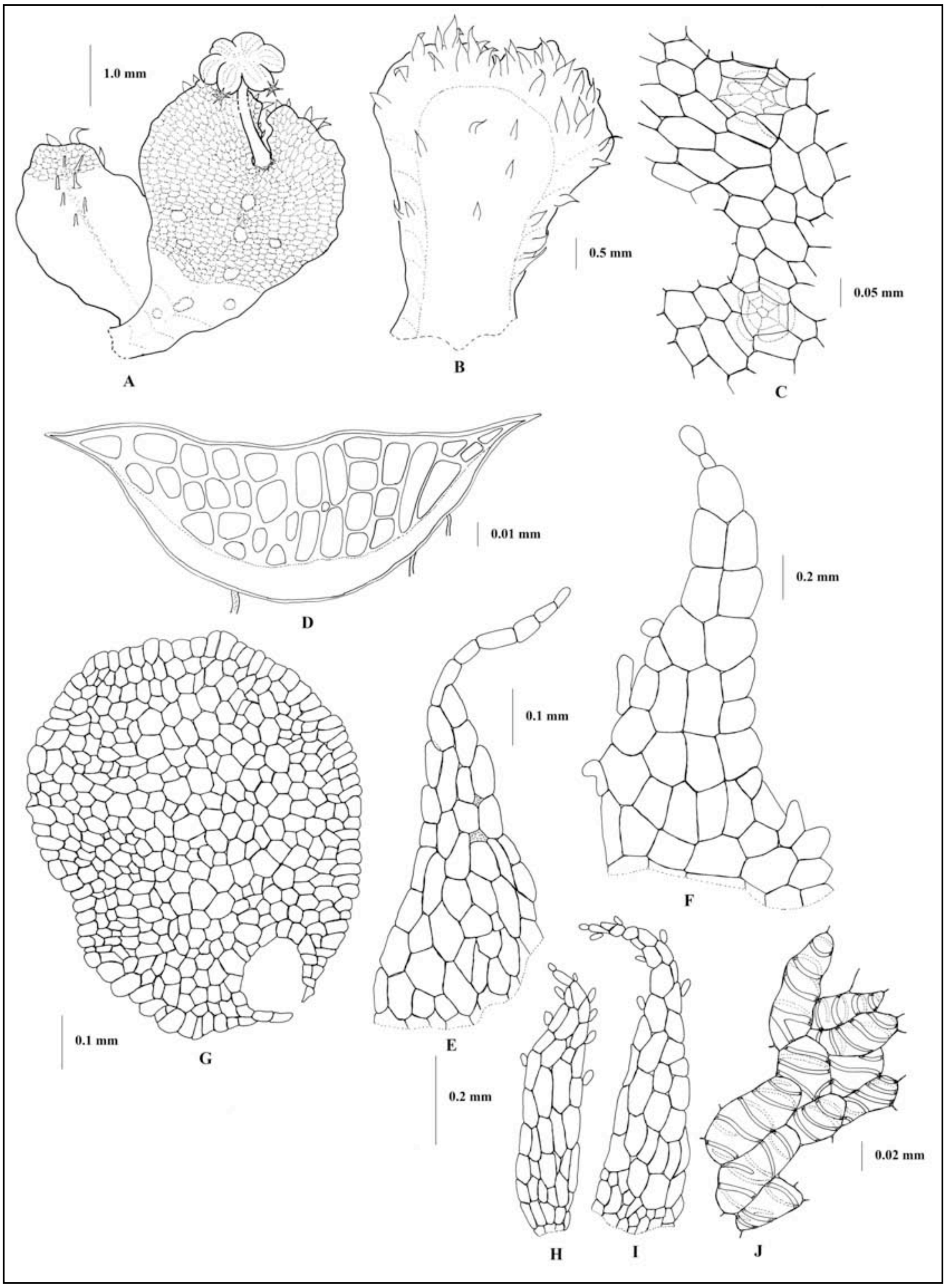


Figure 4.14. ***Sauteria spongiosa*** **A) dorsal surface of thallus showing archegoniophore with an antheridial branch attached; B) thallus ventral surface showing ventral scale distribution; C) air pores from dorsal epidermis of thallus;D) transverse section of thallus; E, F) ventral scale from median region of thallus; G) transverse section of apex of stalk; H, I) apical stalk scales; J) cells of spore wall. A, D, E, F Nepal,** ***Long 30427*** **(E); B, C, G, J, Japan,** ***Katagiri 1173*** **(HIRO); H, I, China,** ***Long 24012*** **(E).**

Distribution:

Sauteria spongiosa is restricted to eastern Asia and is found in China, India, Japan, Nepal, Pakistan and Russia (Fig. 4.15).

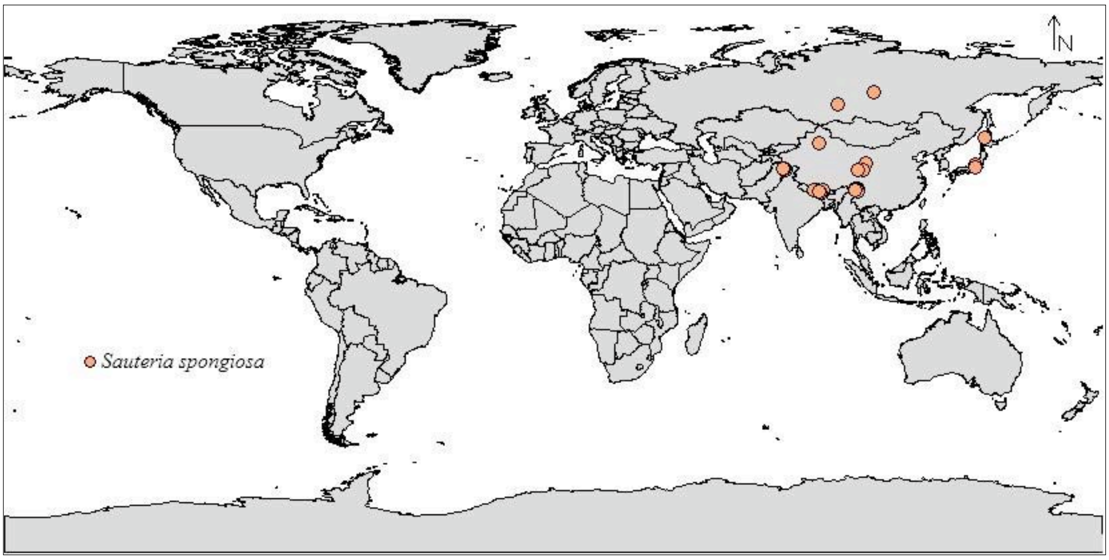


Figure 4.15. Geographical distribution of *Sauteria spongiosa* based on confirmed herbarium material.

Ecological Notes:

Sauteria spongiosa was found to grow on steep, damp, stony limestone slopes and on shady rocks near streams between 1900 and 4390 m.

Taxonomic Notes:

Sauteria spongiosa is distinct from *S. alpina* in its thicker, spongy texture, and bt its conspicuously lacunose dorsal surface. This is due to the disintegration of cells around the pores. Although mature plants of *S. alpina* may show lacunae on older parts of the thallus, here in *S. spongiosa* they occur despite the age. Carpocephala are similar in both taxa. When antheridia are present, they are mostly on a reduced ventral branch in *S. spongiosa* where they occur behind carpocephala or on a different terminal branch in *S. alpina*. However, it should be noted that androecia occurring behind the carpocephala were observed on rare occasions in *S. alpina*.

Nomenclatural Notes:

Kashyap (1916) described *Sauchia* as a new genus, named after the Sauch Pass (India) where he first discovered it, including a single species *Sauchia spongiosa*. He did not specify a type specimen and his original description is very brief. He later gave a more detailed description (Kashyap 1929) after collecting additional material.

Shimizu & Hattori (1953) added a second species to the genus, *Sauchia japonica*. A year later (1954) the same authors, reduced *Sauchia* Kashyap to synonymy of *Sauteria*. They also introduced a new variety *Sauteria alpina* var. *japonica* (Shimizu & Hattori 1954), which was later elevated to species rank as *Sauteria yatsuensis* (Hattori & Shimizu 1955). They also noted that this species is closely related to the Indian *S. spongiosa* and also to *S. japonica*. The distinctions they found between these three species: number of layers of air chambers, number of involucres, androecial position, were vague and mostly overlapping.

4.6.4 The genus *Peltolepis*

Peltolepis Lindb., Morgonbladet (Helsingfors) 1876 (106): 1, 1876; Helsingfors Dagblat 1876 (139): 2, 1876; Bot. Notiser 1876: 123, 1876; Bot. Notiser 1877: 73, 1877 (detailed description). – Type: *Peltolepis grandis* (Lindb.) Lindb. (= *P. quadrata* (Saut.) Müll.Frib.)

Description:

Thalli medium to large or sometimes small, obovate to lingulate, flat to slightly concave along mid-line, firm, rarely delicate, robust, light or bright green to dull green above, vegetative branching terminal and ventral, usually once or twice dichotomously branched; margins slightly undulate, greenish to purplish; dorsal epidermis with thin-walled, polygonal cells, with chloroplasts, sometimes with oil cells, dorsal surface with shallow spreading polygonal grooves representing underlying air chambers, each with a slightly raised air pore at the middle; air pores simple, surrounded by a single ring of 5–7 cells, radial walls slightly to strongly thickened, occasionally not thickened; assimilatory tissue well developed, with 2–3 layers of polygonal air chambers without photosynthetic filaments, storage tissue greenish to hyaline, well developed, oil cells not observed; midrib not strongly protruding on ventral surface, gradually passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells along midrib region.

Ventral scales purple and hyaline (never blackish purple), in irregular rows on the midrib region, scattered, ovate, with a single ill-defined appendage, unistratose, cells in body and appendage similar, uniform, thin to thick-walled, polygonal, slime papillae 2 –4, margin entire, oil cells absent.

Sexual condition par-autoicous, occasionally terminal-autoicous. Androecia dorsal, immediately proximal to base of archegoniophore, occasionally on a separate terminal branch, in well defined, oval shaped, raised tuberculate discs, 1–3 along midline of the thallus, antheridial scales around the androecial cushion, small, purplish, ovate to elongate, obtuse apex, with 4–6 slime papillae. Gynoecia terminal, in a deep apical notch, (one or both lobes occasionally elongating as in *Sauteria*); stalk cylindrical, hyaline and greenish, slightly purplish at base, with 2 rhizoid furrows, cells thin-walled, polygonal to isodiametric, apical stalk scales present, hyaline to purplish, lanceolate, with 2–4 slime papillae, evenly arranged on either side; carpocephalum light green, umbrella-shaped, deeply lobed, with 4–8 lobes, lobes pointing downwards or rarely horizontal, each involucre bilabiate, with a short, up to (0.2–0.5) mm long stalk, sporophyte globose to cylindrical, fleshy.

Capsule globose, foot short, bulbous, dehiscing by irregular valves.

Spores reddish brown, usually triangular, rarely spherical, distal surface convex, proximal surface flatter, trilete mark occasionally visible, densely covered with hemispherical domes, obtuse or acute, spaces between domes narrow or wide, deep or shallow, with or without deep cavities around the domes, entire surface covered with fine granules or granules aggregated at the tip of domes.

Elaters brown, 2–3-spiral, branching not observed.

Chromosome number n = 9 (Schuster, 1992)

Distribution: see under *P. quadrata*

Taxonomic Notes:

Peltolepis differs from the other three genera of Cleveaceae in having androcecia in compact, well-defined, raised, oval discs, and having two rhizoid furrows in the carpocephalum stalk. In sterile condition the plants can be distinguished by the texture of the thallus and the nature of the ventral scales.

Nomenclatural Notes:

Peltolepis was first described by Lindberg in newspapers (Morgonbladet (Helsingfors) 1876 and Helsingfors Dagblat 1876). He gave a brief description in Bot. Notiser (1876), however the first detailed description of the genus was published in Bot. Notiser (1977).

1. ***Peltolepis quadrata*** (Saut.) Müll.Frib., Hedwigia 79: 74, 1940. ≡ *Sauteria quadrata* Saut., Flora (Regensburg) 43: 351, 1860; Mittheil. Ges. Salzb. Landesk. 11: 27, 1871. – Type citation: “[Austria] an Felsen in der Nähe der Schneefelder und am Grunde tiefer Felsenkessel des Untersbergs (5000–5500’). [leg. Sauter]”. – Type specimens: [Austria, Salzburg] Untersberg, *Sauter s.n* (W-6084, holotype); [Austria, Salzburg] Felsenkessel am Untersberg, 6000', *Sauter s.n.* (W-2008-1126, isotype).

= *Sauteria grandis* Lindb., Morgonbladet [Helsinki] 1875 (76): 1 (5 Apr.), 1875; Helsingfors Dagblad 1875 (91A): 2 (6 Apr.), 1875; Bot. Not. 1875: 92 (15 May), 1875. ≡ *Peltolepis grandis* (Lindb.) Lindb., Bot. Notiser, 1877: 74, 1877. – Type citation: “anträffad endast på Dovre och i Saltdalen i Norge, samt på Spetsbergen”. – Type specimen: *n.v.*; synonymised by Müller (1940).

= *Peltolepis sibirica* Lindb., Acta Soc. Fauna Fl. Fenn. 2(3): 4, 1882. ≡ *Peltolepis grandis* (Lindb.) Lindb. var. *sibirica* (Lindb.) Lindb., Kongl. Svenska Vetenskapsad. Handl. (n.s.) 23(5): 12, 1889. –. Type citation: locis argillosis ad rivulos alpinos, juxta Dudinka fluminis Jenisei (Julii 28, 1876, J. Sahlberg). – Type specimen: *n.v.* (not locatted); synonymised by Müller (1940).

= *Peltolepis grandis* (Lindb.) Lindb. var. *angustifrons* Lindb., Kongl. Svenska Vetenskapsad. Handl. (n.s.) 23(5): 13, 1889. – Type citation: [Norway]

“Perfecte eadem formam in regione betulina montis Knudshö, ad cataractam parvam rupis micaceae supra Kongsvold in Dovrefjeld Norvegiae, Julii 16, 1882 legumus, R. Fritze et S.O.L[indberg].” – Type specimen: Sǿr-Trǿndelag, Dovre: “Kongsvold, reg. Betul., ad catarrhactas parvas up. Micac hic illic ubique parce”, Juli 1882, *Fritz & Lindberg* (JE, S, isotypes) synonymised by Schuster, 1992.

= *Peltolepis quadrata* (Saut.) Müll.Frib. var. *japonica* Shimizu & S.Hatt., J. Hattori. Bot. Lab. 12: 69, 1954. ≡ *Peltolepis japonica* (Shimizu & S.Hatt.) S.Hatt., in Hattori & Shimizu, J. Hattori. Bot. Lab. 14: 103, 1955. – Type citation: [Japan, Honshu] “Among rock crevices or moist surface of agglomerate cliff along mountain stream running down east, 2250–2300 m. alt., near the uppermost limit of coniferous forest, Mt. Yatsu, Nagano County, Middle Japan, August 21, 1953, Coll. D. Shimizu 52826.” – Type specimen: [Japan, Honshu] Among rock crevices and damp surfaces of agglomerate cliffs, along mountain brook, 2280m alt., near the uppermost limit of conifer forest, Akadake Peak of the Yatsu volcano, Nagano County. *Shimizu s.n.*, August 21, 1953 (W, isotype); *syn. nov*.

Description:

Thalli small to medium, obovate to lingulate, flat to slightly concave along mid-line, firm, rarely delicate, robust, light green to dull green above, vegetative branching terminal and ventral, usually once or twice dichotomously branched; branches 2.0–13.0 mm long, 2.0–9.0 mm wide; margins slightly undulate, greenish to purplish, purplish colour extending over thallus with age; dorsal epidermis with thin-walled, polygonal cells, with chloroplasts, 32.0–65.4 μm long, 18.2–30.3 μm wide, dorsal surface with shallow spreading polygonal grooves representing underlying air chambers, each with a slightly raised air pore at the middle; air pores simple, 22.4–34.8 μm in diameter, surrounded by a single ring of 5–7 cells, radial walls slightly to strongly thickened, occasionally not thickened; thallus t.s. 0.71–1.02 mm thick over midrib, assimilatory tissue well developed, 0.51–0.59 mm thick, with 2–3 layers of polygonal air chambers without photosynthetic filaments, storage tissue greenish to hyaline, well developed, oil cells not observed; midrib not strongly protruding on ventral surface, 0.7–1.6 mm wide, gradually passing into wings.

Rhizoids smooth and pegged, arising from the ventral epidermal cells at midrib region.

Ventral scales purple and hyaline (never becomes blackish purple), in irregular rows on the midrib region, scattered, ovate, 0.4–1.5 mm long, 0.2–0.5 mm wide, with a single ill-defined appendage, unistratose, cells in body and appendage similar, uniform, think to thick-walled, polygonal, 31.5–67.3 μm long, 30.4–39.7 μm wide, slime papillae 2–4, margin entire, oil cells absent.

Sexual condition par-autoicous, rarely terminal-autoicous. Androecia dorsal, immediately proximal to base of archegoniophore, occasionally on a separate terminal branch, in well defined, oval shaped, raised discs, 1 –3 borne along midline of the thallus, antheridial scales small, 0.15–0.25 mm long, 0.05–0.08 mm wide, ovate to elongate, obtuse apex, each with 2–5 slime papillae, 4–6 borne around androecial disc. Gynoecia terminal, in a deep apical notch, (one or both lobes occasionally elongating as in *Sauteria*); stalk cylindrical, hyaline and greenish slightly purplish at base, 5.8–9.74 mm long, 0.39–0.52 mm in diameter, with 2 rhizoid furrows, cells thin-walled, polygonal to isodiametric, apical stalk scales present, hyaline to purplish, lanceolate, 0.35–0.48 mm long, 0.10–0.11 mm wide, with 2–4 slime papillae, evenly arranged on either side; carpocephalum light green, umbrella shaped, 0.2–4.2 mm in diameter, with 4–8 lobes pointing downwards or horizontal, each involucre with one sporophyte. Capsule globose, foot short, bulbous, dehiscing by irregular valves. Spores reddish brown, 41.7–55.6 μm in diameter, usually triangular, rarely spherical, distal surface convex, proximal surface flatter, trilete mark occasionally visible, densely covered with hemispherical domes, 4.4–5.5 μm high, obtuse or acute, spaces between domes narrow or wide, deep or shallow, with or without deep cavities around the domes, entire surface covered with fine granules or granules aggregated at the tip of domes. Elaters brown, 40.0–268.0 μm long, 8.0–12.0 μm wide, branching not observed. Chromosome number n =9 (Schuster 1992)

Illustrations: Figures 4.16; 2.2 (H); 2.4 (F); 2.8 (E, F); 2.9 (C, E); 2.10 (D); 2.11 (A, E).

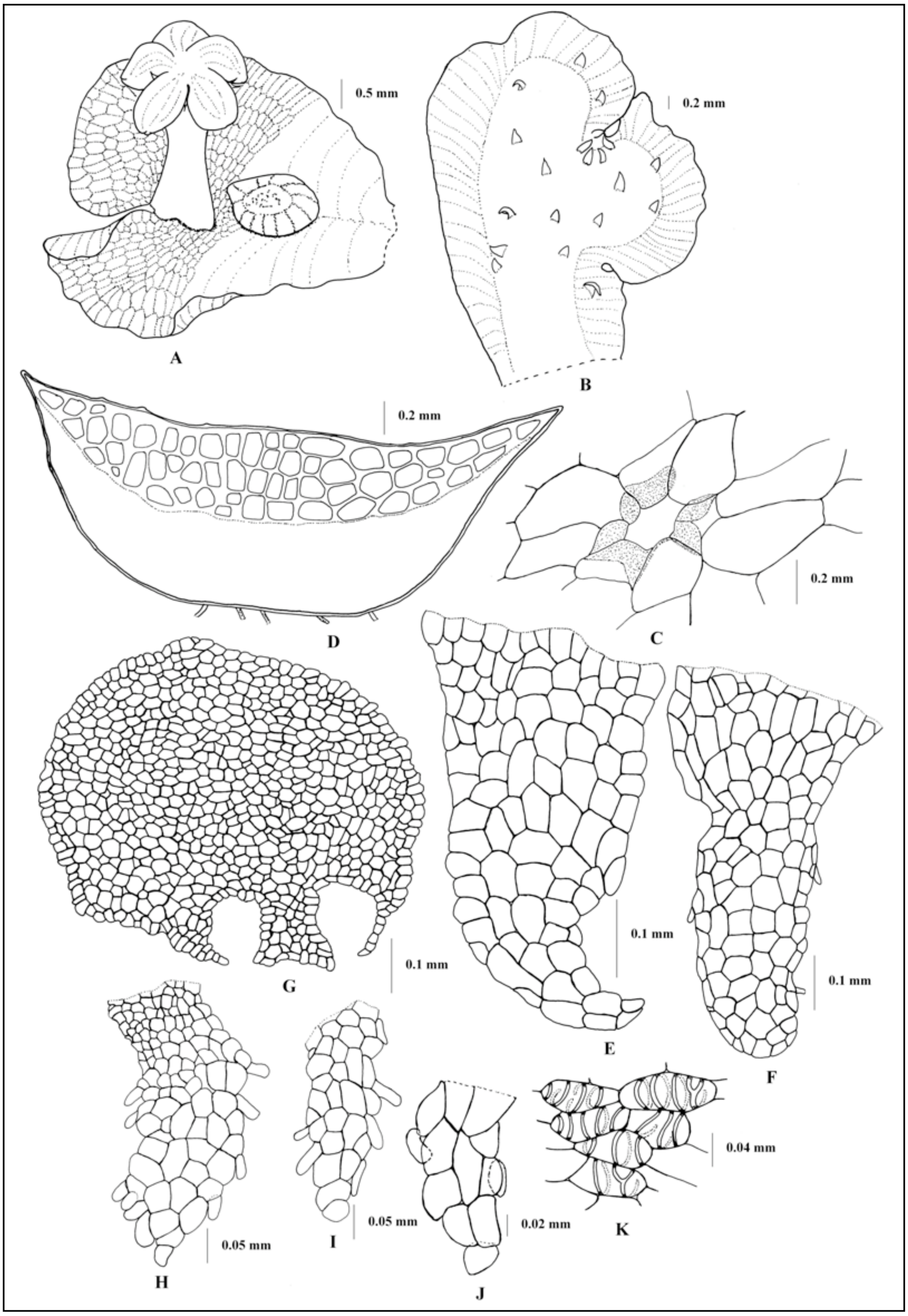


Figure 4.16. ***Peltolepis quadrata*****. A) dorsal surface of thallus showing carpocephalum and androecial cushion; B) ventral surface of thallus showing ventral scale distribution; C) air pore from dorsal epidermis of thallus; D) transverse section of thallus; E, F) ventral scales from median region of thallus; G) transverse section of apex of stalk; H, I) apical stalk scales; J) cells of spore wall. A, B, C, Switzerland,** ***Rubasinghe & Long 08-08SR*** **(E); D–J, Switzerland,** ***Rubasinghe & Long 08-14SR*** **(E); K, Sweden,** ***Arnell & Jensen s.n.*** **(W).**

Distribution:

Peltolepis quadrata is the most sporadically distributed species of Cleveaceae and is holarctic in range. The distribution of *P. quadrata* based on confirmed herbarium specimens: Austria, Bosnia & Herzegovina, Finland, France, Germany, Greenland, Hungary, Iceland, Italy, Japan, Norway, Poland, Russia (Siberia), Slovakia, Sweden, Switzerland, U.S.A. (Alaska) (Fig. 4.17). According to literature it is also recorded from Minnesota, U.S.A.

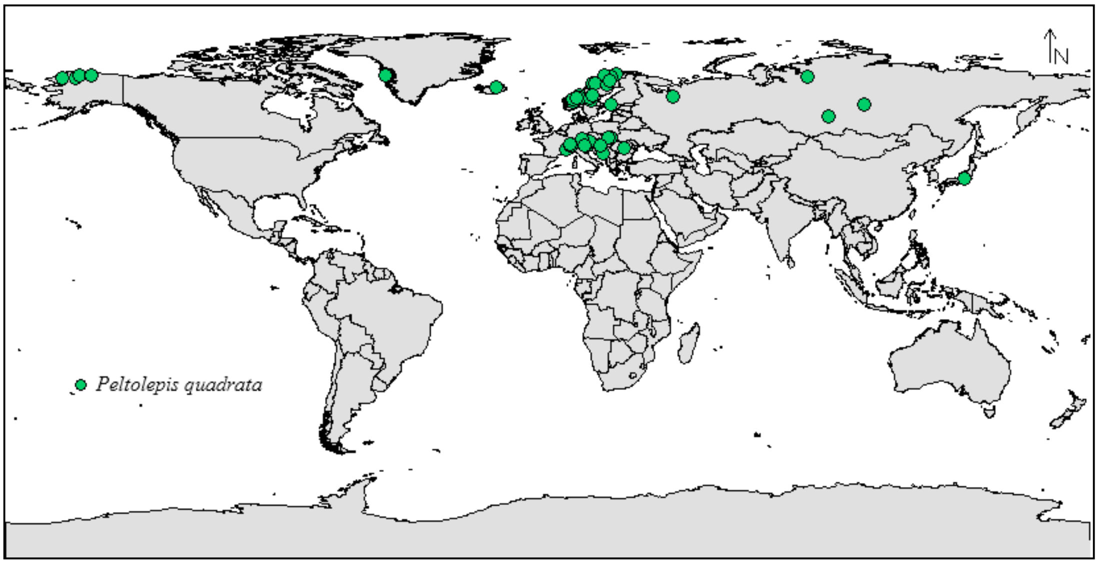


Figure 4.17. Distribution of *Peltolepis quadrata* based on confirmed herbarium material.

Ecological Notes:

It prefers calcareous soil, on damp rock crevices, particularly near snow beds.

Taxonomic Notes:

Peltolepis quadrata sometimes occurs admixed with *Clevea hyalina* and *Sauteria alpina* (e.g. in Switzerland, Norway and Alaska) but can easily be distinguished from them by its firm, robust, obovate, dark green and purplish (usually) thalli, with scattered purplish to hyaline small ventral scales which are hidden under the margin. *Clevea hyalina* tends to be fragile, light green and purplish with prominent shallow spreading grooves on the thallus, with tufts of purplish and hyaline scales projecting beyond the margin at the thallus apex, whereas *S. alpina* has yellowish to whitish thalli, and their ventral scales are never pigmented and also contain oil bodies which are lacking from the other two species. Apart from *C. hyalina*, *P. quadrata* is the only other species where antheridial scales were observed. These scales are purplish and very small and can be easily overlooked. *Peltolepis quadrata* is also the only species with raised androecial discs.

Nomenclatural Notes:

Lindberg (1875) described a new species of *Sauteria* Nees, *S. grandis* Lindb. from Norway. While recognizing this new species he noticed that it was different from *Sauteria alpina* in having two rhizoid furrows in the carpocephalum stalk and also by the arrangement of antheridia. Later (1876) he placed this species in his new genus *Peltolepis* under the name *Peltolepis grandis.* However, Müller (1940) realized that the earlier epithet *quadrata* (described earlier as *Sauteria quadrata* from Austria in 1860) referred to the same species and had nomenclatural priority so he made the new combination *Peltolepis quadrata*.

Peltolepis quadrata var. *japonica* was first described as a variety of *P. quadrata* (Shimizu & Hattori, 1954), differing only by its smaller size of the thallus and convexity of the female receptacle from the type. Later (1955) the same authors elevated it to species level considering the chromosome number (n=18), small size and not so firm texture of the thallus, shape of the ventral scales, size of the spores and the flatness of the female receptacle. This species is included as new synonym of *P. quadrata*.

4.7 Excluded and doubtful taxa

1. *Athalamia dioica* Kashyap., J. Bombay Nat. Hist. Soc. 24: 348, 1916. – Type citation: [India] “Common in Pangie, 8000 ft.”– Type specimen: *n.v.* (specimen not located).

This species was described without a designated type specimen and no original material has been available for study. In his brief description Kashyap (1916) indicated that the species was dioicous but doubtfully distinct from *Athalamia* *pinguis*. However, no mention of carpocephala or illustrations of the species were provided. Of the members of Cleveaceae known from the North-west Himalaya, the thick, fleshy, oblong thallus and the slightly exserted capsule described most suggest *A. pinguis*. The sexual condition could have been erroneously described as dioicous (with limited material this could easily happen). Without a type specimen its position cannot be confirmed.

2. *Clevea hyalina* (Sommerf.) Lindb. var. *californica* M.Howe, Mem. Torrey Bot. Club 7: 38, 1899. – Type citation: [U.S.A., California] “Doolan’s Creek Cañon, near Ukiah, May 13, 1896, (Howe, no. 765).” – Type specimen: *n.v.* (specimen not located).

Howe (1899) included *Sauteria limbata* Austin. p.p. as a synonym of this variety but study of the lectotype of *S. limbata* shows that it is a synonym of *Clevea spathysii* not *C. hyalina* (see above under *Clevea spathysii*). It is very likely that var. *californica* is a synonym of *C. hyalina* or *C. spathysii* but the type specimen has not been studied.

3. *Clevea hyalina* (Sommerf.) Lindb. fo. *rufescens* S.W.Arnell, Ark. Bot. 4 (6): 123, 1959; *nom. inval*. (Art. 37.1). – Type citation: [Svalbard] "Kingsbay (Malmgren); Zeppelinfjellet, the slope above Ny-Ålesund; rocks above Gluudneset; the bird cliff below Haavimbfjell; Blomstrandhalvöya, immed. N of London [leg. S. Arnell & O. Mårtensson]". – Type specimens: *n.v.* (specimen not located).

This forma was described without a designated type specimen so the name is invalidly published. The author described it as different from *C. hyalina* by having purple scales, but ventral scales are commonly purlish tinged in typical *Clevea hyalina*, so there seems no justification in recognizing it at any rank. It is therefore almost certainly a synonym of *Clevea hyalina*.

4. *Clevea pedicellata* (Griff.) Lindb., Acta Soc. Fauna Fl. Fenn. 2 (3): 11, 1882. ≡ *Plagiochasma* (*Antrocephalus*) *pedicellatum* Griff., Not. Pl. Asiat.2: 331, 1849. – Type citation: [India] "Assam" [leg. Griffith]. – Type specimen: *n.v.* (specimen not located). Synonymised under *Clevea hyalina* by Lindberg (1882).

This species is only known from Griffith’s (1847) original description and illustrations, based on a specimen from Assam in NE India. It is difficult to determine the status of the species from his illustrations. However it is very unusual to have scales on the carpocephalum stalk in Cleveaceae. Griffith described the archegoniophores as dorsal and also that the ventral scales were red pigmented, both of which could suggest *Plagiochasma* in Aytoniaceae, and it is unlikely to be a member of Cleveaceae. Without a type specimen its position cannot be determined.

5. *Clevea pilati* Lorb., Jahrb. Wiss. Bot. 80: 569, 1934. *nom. inval*. (Art. 32.1). – Type citation: none.

Lobeer (1934) listed 10 species of leafy and thalloid liverworts based on chromosome studies. Several of these are new names but without any formal description as new species, including one apparently belonging to Cleveaceae which he named *Clevea pilati*. However, no description, type or locality details were provided so the name is without taxonomic standing.

6. *Clevea pulcherrima* Steph., Engl. Bot. Jahrb. 20: 303, 1895. ≡ *Athalamia pulcherrima* (Steph.) S.Hatt., in Shimizu & Hattori, J. Hattori Bot. Lab. 12: 54, 1954. – Type citation: “Abyssinien: an Felsen (Schimper, n. 772)“. – Type specimen: [Ethiopia] Abyssinia, W. Schimper 772. (G-00067323, holotype).

Stephani’s (1895) protologue, based on Schimper’s original collection, describes a robust dioicous plant with stellate air pores and gynoecia produced dorsally in a row. This would partly fit both *Clevea hyalina* in Cleveaceae and the genus *Plagiochasma* in Aytoniaceae; it is not clear from the description which family it belongs to. Van den Berghen (1965) gave a brief description and illustration based on a specimen he identified as *Athalamia pulcherrima* collected by Beccari in Ethiopia in 1870 (G). Beccari's plant is sterile but has the appearance of the genus *Athalamia* s.str. with its large prodruding ventral scales, rather than *Clevea*, but it is not clear if Van den Berghen compared it with Stephani's type. Clearly these collections represent two different genera and species, neither of which can be reliably identified. Field work in Ethiopia to recollect these plants is highly desirable.

7. *Sauteria chilensis* (Lindenb. ex Mont.) Grolle., J. Hattori. Bot. Lab. 58: 200, 1985.
≡ *Grimaldia chilensis* Lindenb. ex Mont., in Orbigny, Voy. Amér. Mérid., Bot. 7(2): 53, 1839 ≡ *Neesiella chilensis* (Lindenb. ex Mont.) Steph. Sp. Hepat. 1: 95, 1898. – Type citation: [Chile, Prov. Valparaiso] "Ad terrain locis humidis prope Quillota, praesertim loco *Cerro de Mallaca* dicto exeunte Septembri legit Bertero, misitque sub no. 1129." – Type specimen: [Chile, Prov. Valparaiso], prope Quillota, Cerro de Mallaca, Bertero 1129 (PC, lectotype; BM, G-17151, STR, isotypes, designated by Grolle (1985)).

= *Sauteria berteroana* Mont. [Voy. Amér. Mérid., Bot. 7(2): 53, 1839. nom. inval. (Art. 34.1)] ex Gottsche, Lindenb. & Nees, Synop. Hepat. 541, 1846. ≡ *Sauteria 'bertoroi'* Mont., in Lindb., Bot. Not. 1877: 74, 75, 1877; nom. inval. (Art. 61) [orthographic variant of *S. berteroana*]. – Type citation: "Habitat in regni Chilensis montium "la Leona" dictorum pascuis locisque glareosis (Bertero in Hb. Delessert n. 354, M[ontagne] and N[ees])". – Type specimen: Chile, Prov. Curicó, in Monte la Leona, leg. Bertero in Hb. Delessert n. 354, (PC, lectotype, designated by Grolle (1985).

= *Grimaldia debilis* Bisch. ex Gottsche, Lindenb. & Nees, Synop. Hepat. 552, 1844. – Type citation: [Chile] "Habitat ad terram in pascuis locis glareosis in Monte la Leona in Chili, ubi Sept. mense a. 1828 a Bertero sub. n. 354 lecta est. – Type specimen: *n.v.* (not seen).

Grolle's (1985) new combination, *Sauteria chilensis*, was based on his study of the type specimens, and he concluded that it was genuinely a *Sauteria* (Grolle, 1975, 1985). However, from Hässel de Menéndez's (1962) description and illustrations of *Sauteria berteroana* it is evident that she has included under that name specimens of more than one taxon including *Clevea spathysii*. Several specimens identified as *Sauteria chilensis* were studied and the branching pattern (terminal, dichotomous), blackish-purple overlapping ventral scales arranged in two rows along the midline of the thallus, shorter carpocephalum stalk (up to 100µm) and smaller 4–5-lobed receptacle makes these specimens distinctly different from *Sauteria* but quite similar to *Mannia* (Aytoniaceae). *Sauteria* typically lacks any purple pigmentation, although it is sometimes 1–2-dichotomously branched the branches are never sharply forked, and the air pores are very rarely thickened. The spores described by Hässel de Menendez (1962) seem rather similar to some *Mannia* species (Schill 2006, pp. 67, 68). It is clear that some of these South American plants require further collection and study to untangle the confusion. Without further work, particularly collection and study of living plants in the field, *Sauteria chilensis* must remain a poorly-known species.

8. *Sauteria crassipes* Austin, Proc. Acad. Nat. Sci. Philadelphia 21: 229, 1869. – Type citation: “Japan, on hillsides. Com. Rodgers, N. Pac. Expl. Exped.” – Type specimen: *n.v.* (specimen not located).

Austin (1869) doubtfully referred this species to *Sauteria* with a question mark. He also noted that it “resembles *Preissia* very much – also in some respects *Duvalia* [= *Mannia*]”. According to his description the carpocephalum stalk is very thick at the apex and bears scales, it also has filamentous scales at the base and involucres tinged purple. These characters suggest strongly that this species does not belong to Cleveaceae. However, if a type specimen can be located its taxonomic position should be readily clarified.

9. *Sauteria muelleri* Gottsche, Rev. Bryol. 15: 23, 1888. *nom. inval.* (Art. 32.1). – Original citation: [France] “Val de Cogne, Courmayeur (Müller)". – Original material: *n.v.* (specimen not located).

This was described from the MontBlanc region without any description. Further collections and observations are required to confirm the status of the species, which probably belongs to one of the well-known species from the European Alps – *Clevea hyalina*, *Peltolepis quadrata* or *Sauteria alpina*.

10. *Sauteria nyikaensis* Perold, Bothalia 33 (2): 166–167, 2003. – Type citation: Malawi, 1033: Nyika National Park, Jalawe viewpoint, (–BD), on soil, in a cavity under rock overhang, at altitude 2343 m, 3 April 2000, *Keokemoer* 1874 (PRE, holotype) with *Lunularia cruciata* (L.) Dumort. ex Lindb. and *Plagiochasma eximium* (Schiffn.) Steph. – Type specimen: *n.v.* (not seen).

This species was described from immature material and its sexual condition is not known. It was placed in *Sauteria* as the thallus lacks pigment, the ventral scales contain oil body cells and the immature archegoniophore stalk contains a single rhizoid furrow. However, mature material is needed to confirm its placement in *Sauteria* and to clarify its relationship with other species of *Sauteria*. No other member of *Sauteria* is known from Africa.

4.8 Dispersal and Phytogeography

Dispersal in bryophytes is facilitated by spores, asexual propagules and gametophytic fragments (Longton 1997). However, in Cleveaceae dispersal is mainly by spores, although vegetative thalli may survive adverse conditions and rejuvenate and spread vegetatively when the conditions are better. This was observed in the *Clevea hyalina* population near Braemar (Scotland) where thalli shrivelled and disappeared in the soil crust during dry summer months, but reappeared and re-commenced growth and reproduction in the winter and early spring. According to Bischler (1998) in Cleveaceae each capsule produces 2000–3000 spores, and these are 40–70 µm in diameter; this agrees well with the 44–76 µm range observed in the current study. Studies have shown that this range is too large for wind dispersal (Schuster 1966, 1992) and to achieve successful wind dispersal, spores must be ≤ 25 µm in diameter (Zanten & Gradstein 1988). Therefore, it can be assumed that these spores of Cleveaceae mainly disperse by water, by soil and/or step-by-step dispersal

(Schuster 1992; van Zanten & Gradstein 1988). Nevertheless, their long distance dispersal cannot be excluded (van Zanten & Gradstein 1988). The larger spore size is thought to increase the duration of spore viability, which is an adaptive feature to withstand unfavourable seasons or conditions. Hence, over long periods of time, these large, long-lived spores might be as effective overall as dispersal units as small, short-lived spores.

Members of Cleveaceae are calcicoles, and therefore their distribution mirrors the distribution of calcareous rocks and soils. This suggests that for effective dispersal of these plants to new areas, their spores would have had to cross extensive intervening acidic habitats, and therefore range extension would have been sporadic and unpredictable. Perhaps linked to this is the fact that most species of Cleveaceae, such as *Sauteria alpina* and *Peltolepis quadrata*, show a discontinuous distribution and often occur in very isolated localities. However, some species have clearly been able to adapt to a wide range of environmental conditions. For example, *Clevea hyalina* is mostly arctic in distribution, reaching as far north as land extends (Ellesmere Island, 82.52° N), but also occurs south to the Mediterranean region. According to Schuster (1983), this wide climatic range is an important factor "allowing certain taxa to persist under marginal climatic or edaphic regimes".

Clevea spathysii shows a transoceanic distribution, occurring in North, Central and South America, southern Africa, Europe and Mongolia. The present distribution of this species may be explained by two different hypotheses as described by van Zanten & Gradstein (1988). The first hypothesis is ancient vicariance, with former very wide distributions having contracted due to climate change and/or continental drift; the alternative hypothesis is long distance dispersal in comparatively recent times. Schuster (1983) has argued that continental drift has been an important factor affecting the disjunct distribution of phylogenetically old species, but there is no evidence (such as fossil remains) for this in the case of Cleveaceae. Bisexual spores are assumed to be more effective for species dispersal than unisexual spores, because theoretically, dispersal of only a single bisexual spore is needed to establish a new population (Schuster 1983; van Zanten & Gradstein 1988). Most taxa in Cleveaceae are autoicous and by this argument may be more effective long-distance dispersers. However *Clevea hyalina* is dioicous, and therefore would require both a male and a female spore landing within short distance of each other for successful long-distance dispersal. However, *C. hyalina* has a very broad distribution range, so its past dispersal has not been impeded by its dioicy (Fig. 4.18).

Cleveaceae is widely distributed in warm temperate to arctic regions throughout the Northern Hemisphere, with only a single confirmed species in the Southern Hemisphere, in the Andes of South America and the African mountains; it is not recorded from Australia and New Zealand (Fig. 4.18). As a result of the present taxonomic clarifications, two distinct biogeographic patterns can be identified in Cleveaceae: a widespread group and a localised Asian group, although neither is monophyletic (see Chapter 3, Fig. 3.3). The widespread group comprises *Clevea spathysii*, *C. hyalina*, *Sauteria alpina* and *Peltolepis quadrata*, all of which occur in Europe and North America, and are the only representatives of Cleveaceae on either continent. Of these four species, *P. quadrata* and *S. alpina* both show an exclusively arctic-alpine distribution, whereas *C. hyalina* shows an amphizonal distribution as noted above and *Clevea spathysii* is the most tolerant of warm, relatively arid conditions. This tolerance might have allowed *C. spathysii* to cross the equator (see Mao et al. 2010 for a similar example among gymnosperms), into both South America and Africa, on each of which it is the only Cleveaceae species (apart from poorly known local endemics whose status needs checking). Of the group of four widespread species, all except *S. alpina* extend into Asia as well. Hence this group forms a biogeographic unit whose distribution is almost that of the whole family.

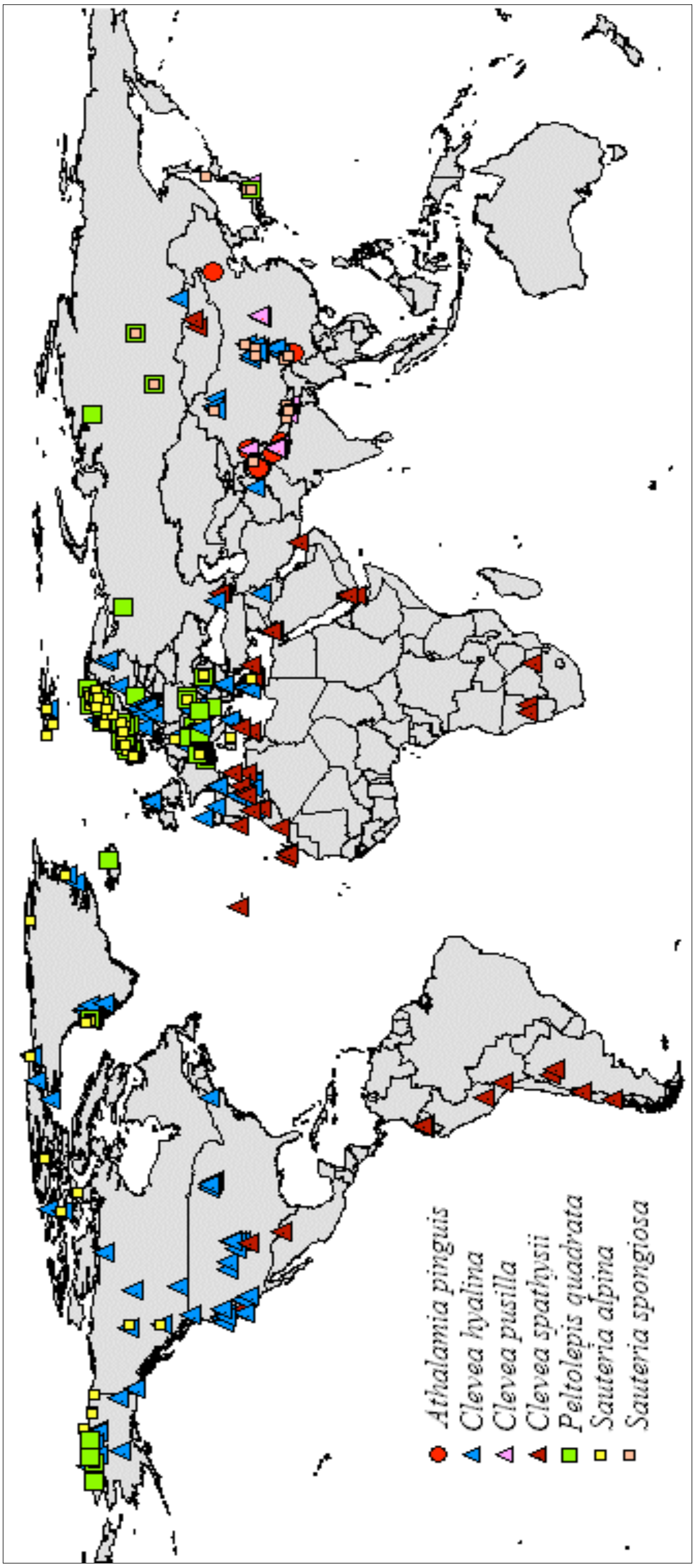


Figure 4.18. Distribution of species of Cleveaceae based on confirmed herbarium material.

The second biogeographic group comprises *Clevea pusilla*, *Sauteria spongiosa* and *Athalamia pinguis*, all of which have a restricted or localised distribution in and around the Sino-Himalaya, Tibetan Plateau and Japan. Therefore, Cleveaceae has a clear centre of diversity in Asia, where all species except *Sauteria alpina* occur. The assemblage of species endemic to Asia is non-monophyletic, rejecting a hypothesis that this local diversity arose by recent radiation (as occurred, for example, in *Rhododendron* (Milne 2004; Milne et al. 2010). One possible explanation for this pattern is that higher Cleveaceae diversity in Asia reflects lower extinction rates in this region during the Pliocene and Pleistocene, as is the case for many Angiosperms (Milne & Abbott 2002; Wen 1999). However, the wide climatic range and high cold tolerance observed in many of the family makes this hypothesis seem unlikely. Instead, the distribution better fits a hypothesis that Cleveaceae originated in Asia, with multiple lineages then moving out of this region across the northern hemisphere. If such an origin can be assumed, a reasonable hypothesis to explain modern Cleveaceae distributions is that three of the genera have migrated westwards to Europe and/or eastwards across Beringia to North America, with three species achieving circumboreal distributions in common with many other boreal bryophytes (Shaw 2001). Tertiary land connections across Beringia and the North Atlantic occupied high latitudes, favouring cool-adapted taxa especially as the Earth gradually cooled from the late Eocene onwards (Milne & Abbott 2002, and references therein). The precise routes of migration for these species remain unknown, because the timescales involved are not known (Abbott et al. 2000).

The effects of Pleistocene ice ages may have reduced Cleveaceae diversity in some areas; however the paucity of records from regions such as northern Asia at least partly reflects under-collecting. According to Hong (1987), most liverwort taxa that are distributed along the northern Pacific coast of Asia (including Japan) and North America (including Alaska to California, and the western part of Montana) could have survived during the Pleistocene period due to the lack of glaciation. *Peltolepis quadrata* may be an example of this as it remains absent from former glaciated regions, such as the British Isles. The fourth of the widespread species, *Clevea spathysii*, is adapted to warmer climates, and may therefore have achieved its distribution by a slightly different route, moving between continents during climatic optima such as the Eocene period, when conditions on the North Atlantic Land Bridge would have been equable to subtropical biota (Milne & Abbott 2002, and references therein).

It is clear that the wide range of factors that influenced the present day distribution patterns of these species cannot be fully understood by analyzing distribution maps based solely on herbarium material and also with our limited knowledge of their dispersal strategies. For example, there are more records of Cleveaceae from Europe (Fig. 4.1) than from other continents, but the main reason for this is surely that it is the most extensively studied area for bryophytes in the world (Hodgetts 1996). However, this study has included a greater number of specimens and speceis world-wide than any other work on the family, and gives invaluable insight to species limits and distributions. This provides a ground work for future research; future collections will refine our knowledge of the family's distribution within currently poorly sampled areas such as northern Asia, Africa and South America, and may determine the status of doubtful local endemics. The production of a dated phylogeny for this family would give a clearer picture of the origin, diversification and routes of migration within this interesting group.

4.9 Discussion and Conclusions

The present taxonomic revision accepts four genera within the family Cleveaceae: *Athalamia*, *Clevea*, *Sauteria* and *Peltolepis*. This means that *Clevea,* which was synonymised under *Athalamia* since 1954 (Shimizu & Hattori, 1954), is resurrected. Texture of the thallus, nature of ventral scales and reproductive structures showed distinct discontinuities between the genera.

Three species of *Clevea*, and one species of *Athalamia* of the formely fourteen published species, have been accepted, of which one required a new combination. The other names were synonymised or listed under doubtful or excluded species. One species of *Peltolepis* of two previously recognized species was accepted. Two species of *Sauteria*, out of seven previously published species, were accepted. Other names were considered as synonyms or listed under doubtful or excluded species.

Many herbarium specimens were studied to build up as complete a geographical overview and assessment of morphological variation for each species as possible. This is the first alpha taxonomic revision for Cleveaceae, and since all taxa have been observed in one study, the generic and species delimitations within the family should be more consistently applied. Ranges of variation within and between species have become clearer. Key characters to identify these taxa were defined and taxonomic keys prepared to facilitate identification all the taxa within the family. Most previous studies carried out in narrow geographical areas usually did not compare closely related taxa from elsewhere (Bischler 1998; Schuster 1992; Shimizu & Hattori 1954, 1955). Such narrow studies resulted in geographically localized taxa (local endemics). The present study shows that most of these local endemics in fact belong to more widespread taxa (eg. *Clevea spathysii*) which necessitated synonymisation.

Many authors who had described local species used a narrow species concept involving emphasis on continuous quantitative characters, e.g. for *Peltolepis japonica*. The present study shows that many of these features of size display significant phenotypic plasticity. However, other quantitative gametophytic characters such as thallus thickness and texture were found to be distinct for particular genera and species. For example, several gametophytic characters of *Athalamia* such as texture and anatomy are quite distinct and did not overlap with the other three genera of the family.

Spore ornamentation patterns have successfully been used as highly informative diagnostic characters at the species level in taxonomic revisions of other complex thalloids liverworts such as *Asterella* and *Mannia* (Long 1998, 2000; Schill 2006). However, spore ornamentation patterns in Cleveaceae did not provide distinguishing characters between genera except that the spores of *Athalamia* were different from those of the other three genera.

CHAPTER-5-DISCUSSION AND CONCLUSIONS

5.1 Polyphyletic Athalamia and re-alignment of genera within Cleveaceae

Although the number and names of genera and species recognized within the Cleveaceae have changed many times, since the definition of the family as ‘Gruppe’ Astroporae by Leitgeb (1881) and then formally by Cavers (1910−1911), a robust phylogenetic framework has never been established before. Phylogenetic inference based on three chloroplast genes (*psb*A, *rpo*C1 and *rps*4) and one nuclear ribosomal region (26S), strongly supported a monophyletic Cleveaceae with four main lineages resolved within the family. Two genera; *Peltolepis* and *Sauteria* were resolved as monophyletic groups, as traditionally recognised. However, *Athalamia* was resolved as polyphyletic with two lineages, one included the type of the genus *Athalamia*; *A. pinguis*, and a second clade comprising species later synonymised under *Athalamia* by Shimizu & Hattori (1954). Therefore, the oldest available generic name for this second lineage, *Clevea*, was resurrected. The two main characters considered when uniting the two genera, archegoniophore position and number of rhizoid furrows in the carpocephalum stalk, were proved to be homoplastic by morphological character reconstructions which did not support this traditional synonymy. Furthermore, morphological re-assessment recognised distinct characters; ventral scale protrusion, shape and width of air chambers, presence of secondary pigmentation, androecial aggregation, which readily separated the four genera. Therefore, the present study, while rejecting the traditional synonymy of *Clevea* under *Athalamia*, recognised four genera strongly supported by molecular and morphological data within Cleveacae: *Athalamia*, *Clevea*, *Sauteria* and *Peltolepis*. This phylogenetic analysis included 54 ingroup accessions representing all currently widely accepted species, covering a large part of its morphology and a substantial part the geographic range of the family. Samples included type species of the three genera as well as all previously synonymised genera. However, this phylogenetic framework could be improved by wider sampling, especially from South America and Africa.

5.2 Present taxonomic circumscription of Cleveaceae and suggestions for future research

Based on the observed material, several formerly assumed endemic taxa were synonymised as they belong to more widespread species. This revision included more than 2300 specimens collected worldwide and thus gives a much more soundly-based picture of genus and species distributions. The family is widely distributed in warm temperate to arctic regions throughout the Northern Hemisphere with some species occurring as far north as land extends, the most northerly (82.52° N) occurrence known being on Ellesmere Island in Arctic Canada. However, Cleveaceae is rare and represented by only 1 or 2 species in the Andes of South America and the African mountains and is not recorded from Australia and New Zealand. The genus *Athalamia* which was until recently thought to have a widespread circumboreal distribution now has a highly restricted distribution in East Asia following the re-segregation of *Clevea*.

Some doubtful taxa such as *Clevea pulcherrima* (from Ethiopia) and *Sauteria chilensis* (from Chile) require further discovery, collection and research to confirm their status and more field studies are vital to understand these poorly-known taxa. It is also necessary to relocate species which are only known from type collections or and/or that have been described using very scanty or immature material such as *Sauteria nyikaensis* (from Malawi), *Clevea pedicellata* (India) and *Sauteria crassipes* (Japan). In the light of the phylogenetic framework and the worldwide taxonomic monograph provided in the present study, further research should be carried out to fill the gaps in other aspects such as breeding systems, population genetics and spore dispersal strategies of the family.

Additional work on the widely-distributed species in the family (for example *Clevea hyalina*) looking at possible genetic/ geographic differentiation within the species or cryptic speciation is now possible using genetic markers such as microsatellites. Sampling at the population level over the whole range of such species would be necessary for such a study. In the genus *Sauteria*, the molecular results show that the differences between *S. alpina* (Europe, North America) and *S.*

spongiosa (East Asia) may be more complicated than their taxonomic status as two allopatric species (as adopted here) indicates. This would require more field sampling, more detailed morphological study and more intensive molecular study. Constraints of time and limitations of sampling did not permit more detailed investigations of this type in the present study. However, it is hoped that this study is a major leap forward in our understanding of the phylogeny and taxonomy of the Cleveaceae, and that this will provide a springboard for more intensive studies of the many remaining intriguing questions provided by this unique and fascinating family of plants.

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Appendix 2.1. Species collected and their locality descriptions. Species/ collection number/ country/ location/ habitat description/altitude

***Clevea hyalina* (Sommerf.) S.Hatt.**

Clevea hyalina: Rubasinghe & Long 01-07SR; U. K., South Aberdeenshire: Creag a' Chlamhain, Crathie. South-east facing, steep limestone slope; on exposed flat rocks. 433 m.

Clevea hyalina: Rubasinghe & Long 08-09SR;U.K. South Aberdeenshire: north slope of Craig Leek, near Braemar. On steep limestone rocks. 553 m.

Clevea hyalina: Rubasinghe & Long 03-08SR; Switzerland, Canton Vaud, North facing limestone valley; under damp boulder below snow patch, 2196m

Clevea hyalina: Rubasinghe & Long 04-08SR; Switzerland, Canton Valais, Rocky alpine limestone slopes; on damp soil under boulders, 2306m

Clevea hyalina: Rubasinghe & Long 05-08SR; Switzerland, Canton Valais, Rocky alpine limestone slopes; on damp soil under boulders, 2306m

Clevea hyalina: Rubasinghe & Long 14-08SR; Switzerland, Canton Valais, Steep limestone slopes; under damp boulder near snow bed, 2169m

Clevea hyalina: Rubasinghe & Long 16-08SR; Switzerland, Canton Valais, Limestone slope; under shady boulder, 2249m

***Clevea spathysii* (Lindenb.) Müll.Frib.**

Clevea spathysii: Rubasinghe & Long 01-09SR; Spain, Prov Murcia, El Valla, north facing slope, under rock over hang, 142 m.

Clevea spathysii: Rubasinghe & Long 02-09SR; Sierra Cabrera: Spain, Prov. Almeria, S side of Cortijo Grande, N-facing slopes, under shady rock ledges, 246m.

Clevea spathysii: Rubasinghe & Long 03-09SR; Spain, Prov. Almeria, South of Rodalquilar (Cabo de Gata). under shady boulder, 242 m.

Clevea spathysii: Rubasinghe & Long 04-09SR; Spain, Prov. Almeria, South of Rodalquilar (Cabo de Gata). under shady boulder, 91 m.

Clevea spathysii: Rubasinghe & Long 05-09SR; Spain, Prov. Almeria, Barranco de Requera: under boulders near stream, 252 m.

Clevea spathysii: Rubasinghe & Long 06-09SR; Spain, Prov. Almeria, Barranco de Requera: under boulders near stream, 252 m.

Clevea spathysii:Rubasinghe & Long 06-09SR; Spain, Prov. Almeria, Barranco de Requera: noth facing rock overhangs, 70 m.

***Sauteria alpina* (Nees) Nees:**

Sauteria alpina: Rubasinghe & Long 06-08SR; Switzerland, Canton Valais, Rocky limestone slopes; on damp soil under boulders, 2296m

Sauteria alpina: Rubasinghe & Long 11-08SR; Switzerland, Canton Valais, Steep limestone slopes; damp crevices of limestone cliff, 2199m

Sauteria alpina: Rubasinghe & Long 13-08SR; Switzerland, Canton Valais, Steep limestone slopes; under damp boulder near snow bed, 2169m

Peltolepis quadrata (Saut.) Müll. Frib.

Peltolepis quadrata: Rubasinghe & Long 07-08SR; Switzerland, Canton Valais, Rocky limestone slopes; in deep crevice under boulders, 2210m

Peltolepis quadrata: Rubasinghe & Long 07-08SR; Switzerland, Canton Valais: Rocky limestone slopes; in deep crevice under boulders, 2210 m.

Peltolepis quadrata: Rubasinghe & Long 08-08SR; Switzerland, Canton Valais, Rocky limestone slope; under huge shady boulder near snow bed, 2196m

Peltolepis quadrata: Rubasinghe & Long 098-08SR; Switzerland, Canton Valais, Rocky limestone slope; under shady boulder near snow bed, 2196m

Peltolepis quadrata: Rubasinghe & Long 10-08SR; Switzerland, Canton Valais, Steep limestone slopes; under rock overhang by snow patch, 2162m

Peltolepis quadrata: Rubasinghe & Long 12-08SR; Switzerland, Canton Valais, Steep limestone slopes; under damp boulder near snow bed, 2169m

Peltolepis quadrata: Rubasinghe & Long 15-08SR; Switzerland, Canton Valais, Limestone terraces with pavement; in deep fissure, 2279m

Appendix 2.2. Selected morphological characters in Cleveaceae.

Species	***C. hyalina***	***C. spathysii***	***C. pusilla***	***A. pinguis***	***S. alpina***	***S. spongiosa***	***P. quadrata***
Thallus shape	linear-lingulate	linear-oblong-ovate	linear-lingulate	linear-obovate-lingulate	linear-lingulate	obovate to lingulate	obovate to lingulate
Branching	apical dichotomous & ventral	apical dichotomous & ventral	apical dichotomous & ventral	apical dichotomous & ventral	apical dichotomous & ventral	apical dichotomous & ventral	apical dichotomous & ventral
Branch length/mm	2–13	4.8–12.8	1.0–6.0 (–15.0)	5.3–13.0	3.3–8.6	1.5–7.7	2.0–13.0
Branch width/mm	2–5	1.6–6.4	1.0–4.0	2.0–8.75	2.2–3.6	0.9–3.9	2.0–9.0
Thickness of thallus/mm	(0.1–)0.3–0.87	0.45–0.87	0.09–0.45	0.7–1.25	0.9–1.0	0.5–0.8	0.71–1.02
Colour dorsal surface	light to dull green	pale to dark green	light to dull green	light green	light to yellowish green	whitish green	light to dull green
Flatness-dorsal surface	flat to slightly concave at middle	flat to slightly concave at middle	flat, rarely slightly concave at middle	flat	flat to slightly concave at middle	flat to slightly concave at middle	flat to slightly concave at middle
Texture	delicate	delicate to fleshy	delicate	fleshy	delicate to fine	delicate & spongy	firm
Width of wings/mm	0.5-2.5	0.5-2.5	0.2-1.5	1.2 - 2.5	0.2-1.5	0.2-1.5	0.5-2.0
Margin colour	green- purple	purple to blackish purple	purple to greenish purple	white to hyaline	greenish to yellowish	light to whitish green	green to purple
Midrib width/mm	0.6–1.7	0.2–1.93	0.2–1.6	1.6–3.3	0.8–1.4	0.2–1.4	0.7–1.6
Midrib protrusion	not strong	not strong	not strong	strong	not strong	not strong	not strong

Appendix 2.2. Morphological characters of Cleveaceae cont….

Species	***C. hyalina***	***C. spathysii***	***C. pusilla***	***A. pinguis***	***S. alpina***	***S. spongiosa***	***P. quadrata***
Midrib passing into wings	gradual	gradual	gradual	sudden & sharp	gradual	gradual	gradual
Shape of aircharmbers	polygonal & rectangular	Polygonal & rectangular	polygonal & spherical	Narrow & slit-like	polygonal	polygonal & spherical	polygonal
Width of assimilatory layer	(0.15–)0.25–0.81	0.10–0.75	0.03–0.40	0.7–1.25	0.51–0.58	0.4–0.6	0.51–0.59
Number of layers of airchambers	1−3	1−3	1−3	1(−3)	1−3	1−4	2−3
Pore elevation	slight	very slight to not elevated	very slight to not elevated	slight to not elevated	very slight to not elevated	very slight to not elevated	slight to not elevated
Pore size/μm	12.0–29.5	7.33–11.37(–20.0)	(8.0–) 13.0–25.0	8.7–32.2	14.3–57.1	20.2–40.0	22.4–34.8
Number of rings around pores	1	1	1	1	1	1	1
Number of cells around pores	6-7	4–5(–6)	4–5 (–9	(4)–)5–6(–7)	14.3–57.1	7–8(–9)	5–7
Radial wall thickening	slight to srong	absent, rarely very slight	absent, rarely very slight	slight to strong	very slight or absent	very slight or absent	slight to strong
Distinct rows of ventral scales	present	present	absent	present	absent	absent	absent
Number of rows of ventral scales	2	3–4	–	4	–	–	–

Appendix 2.2. Morphological characters of Cleveaceae cont…..

Species	***C. hyalina***	***C. spathysii***	***C. pusilla***	***A. pinguis***	***S. alpina***	***S. spongiosa***	**P. quadrata**
Ventral scale projection	apical region	apical region	apical region	along thallus margins	only at apex	only at apex	only at apex
Distance apart	dense & overlapping	dense & overlapping	scattered	dense & overlapping	scattered	scattered	scattered
Colour of ventral scales	hyaline & purple	dark to blackish purple	hyaline & purple or dark purple	whitish to hyaline	silvery white	silvery white	hyaline & purple
Secondary type of ventral scales	present	present	absent	absent	absent	absent	absent
Oil cells in ventral scales	absent	present	present	absent	present	present	absent
Length of ventral scales/mm	0.4–0.93	0.5–1.3	0.4–0.8	1.0–1.7	0.6–0.9	0.4–0.8	0.4–1.5
Ventral scale cell shape	polygonal	rectangular	rectangular & polygonal	rectangular	polygonal	polygonal to rectangular	polygonal
Ventral scale shape	lanceolate	ovate or obliquely triangular	ovate - lanceolate	lanceolate	ovate to lanceolate	ovate to lanceolate	ovate
Slime papilae on ventral scales	0–2	0–1 (–2)	0–2	0(–1)	2–3	2–4	2–4
Body & appendage distinction	vague	very vague	vague	vague	vague	very vague	very vague
Number of appendages	1–2	1	1–2	1	1	1	1
Appendage shape	acuminate	acute, rarely acuminate	Acuminate to acute	acuminate	acuminate to acute	acuminate to acute	acute

Appendix 2.2. Morphological characters of Cleveaceae cont…..

Species	***C. hyalina***	***C. spathysii***	***C. pusilla***	***A. pinguis***	***S. alpina***	***S. spongiosa***	***P. quadrata***
Sexuality	dioicous	monoicious	monoicious	monoicious	monoicious	monoicious	monoicious
Androecial position	main thallus on separate plant	main thallus, behind♀/separate branch	main thallus, behind♀/separate branch	main thallus, behind ♀/separate branch	main thallus, behind ♀/separate branch	on a short ventral branch	main thallus, behind ♀/separate branch
Antheridial scales	present	absent	absent	absent	absent	absent	absent
Archegonial position	dorsal	dorsal	dorsal	dorsal	terminal	terminal	terminal
Stalk colour	hyaline-greenish sometimes slightly purplish at base	hyaline-greenish sometimes slightly purplish at base	pale green–yellowish green	greenish hyaline	greenish yellow	yellowish to whitish green	hyaline-greenish sometimes slightly purplish at base
Stalk length/mm	1.5–20	0.4–1.9	0.4–1.9	1.5–8.9	3.2–10.4	7.0–13.0	5.8–9.74
Stalk width/mm	0.3–0.85	0.35–0.80	0.35–0.8	0.4–0.8	0.4–0.6	0.5–0.6	0.39–0.52
Number of rhizoid furows	0	0	0	0	1	1	2
Apical stalk scale colour	purple-hyaline	purple-hyaline	purple-hyaline	light green to hyaline	silvery white to hyaline	silvery white to hyaline	purple-hyaline
Slime papillae on apical stalk scales	2–4 mostly at base	0(–1)	0(–1)	2–7 even on margins or absent	6– many even on margins	2–6 even on margins	2–4(- many)-even on margin
Receptacle shape	umbrella	cup-shaped	cup-shaped	cup-shaped	umbrella	umbrella	umbrella

Appendix 2.2. Morphological characters of Cleveaceae cont….

Species	***C. hyalina***	***C. spathysii***	***C. pusilla***	***A. pinguis***	***S. alpina***	***S. spongiosa***	***P. quadrata***
Receptacle diameter/mm	2.2–5.0	0.9–3.6	0.81–2.8	1.2–2.5	2.1–2.7	1.7–3.5	0.2–4.2
Number of lobes	1–6	1–4	1–3	1–3	2–6	2–6	4–8
Lobe orientation	pointing down, rarely horizontal	pointing up (rarely horizontal)	pointing up (rarely horizontal)	pointing up (rarely horizontal)	pointing down or horizontal	pointing down or horizontal	pointing down or horizontal
Capsule colour	dark brown	dark brown	dark brown	dark brown to blackish brown	dark brown	dark brown	dark brown
Spore colour	Reddish brown	reddish brown	reddish brown	Blackish brown	reddish brown	reddish brown	reddish brown
Spore size/µm	44.4–58.8	44.4–62.5	41.6–55.6	74.3–75.7	60.0–66.7	63.3–76.9	41.7–55.6
Spore ornamentation	dense domes	dense domes	dense domes	reticulate bands	dense domes	dense domes	dense domes

Appendix 3.1. Voucher information (species, DNA accession number, country of origin, collector, and GenBank accession numbers for *rpoc*1/*rps*4/*psb*A/26S). All vouchers deposited at E.

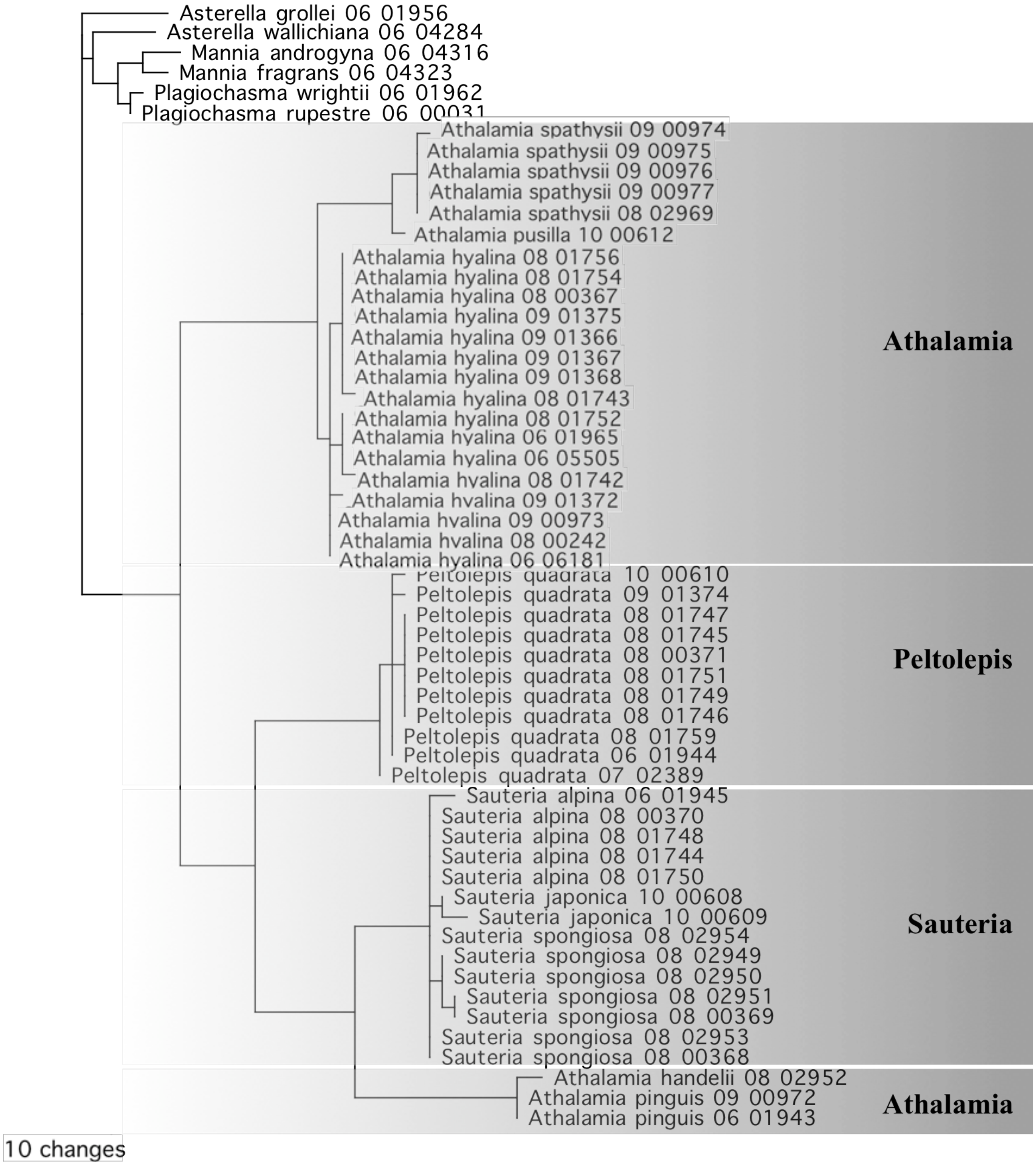
***Clevea hyalina* (Sommerf.) S.Hatt.**
*C. hyalina*_03_08, Switzerland: Canton Vaud, Rubasinghe & Long 03-08SR, HQ225538/HQ225510 /HQ225571: EDNA08_01742
*C .hyalina*_ 05_08, Switzerland: Canton Valais, Rubasinghe & Long 05-08SR, HQ225539/HQ225511/HQ225572: EDNA08_01743
*C. hyalina*_ 16_08, Switzerland: Canton Valais, Rubasinghe & Long 16-08SR, HQ225540/HQ225512/HQ225573: EDNA08_01752
*C. hyalina*_ 24_226, Greece: Peloponnese, T.L. Blockeel 24/226, —/—/HQ225574: EDNA08_01754
*C. hyalina*_ 28262, United Kingdom: South Aberdeen, Long & Rothero 28262, —/—/HQ225575: EDNA08_01756
*C. hyalina*_ 82, Austria: Carinthia Schill, Köckinger & Müller 82, HQ225541/HQ225513/HQ225576:EDNA06_05505
*C. hyalina*_ 01_07, United Kingdom: South Aberdeen, Rubasinghe & Long 01-07 SR, HQ225542/HQ225514/HQ225577:EDNA08_00242
*C. hyalina*_ 3496, Romania: Bucegi Mountains, S. Stefanut 3496, HQ225543/HQ225515/HQ225578: EDNA08_00367
*C. hyalina*_ 60, Austria: Carinthia, D.B. Schill 60, HQ225544/HQ225516/HQ225579: EDNA06_01965
*C. hyalina*_ 6181, U.S.A.: Utah, J.G. Duckett s.n., HQ225547/—/HQ225580: EDNA06_06181
*C. hyalina*_ 35604, United Kingdom: South Aberdeen, D. G. Long 35604, —/—/HQ225581: EDNA09_01375
*C. hyalina*_ 10507, Morocco: Bab-Taza, M. J. Cano & R.M. Ros 10507, —/—/HQ225582:EDNA09_01368
*C. hyalina*_ 08_09, United Kingdom: South Aberdeen, Rubasinghe & Long 08-09 SR, HQ225545/HQ225517 /HQ225583EDNA09-00973
*C. hyalina*_4856, Spain: Albacete, Sierra del Calar del Mundo, R. M. Ros & O. Werner., HQ225546/HQ225518/HQ225584: EDNA09_01367
*C. hyalina*_10501, Morocco: Bab-Taza, R. M. Ros 10501, —/—/HQ225585: EDNA09_01366
*C. hyalina*_1372, Italy: H.Freih.v.Handel-Mazetti s.n., —/—/—: EDNA09_01372
***Clevea pusilla* (Steph.) Rubasinghe & D.G.Long**
*C. pusilla*_22838, India: Sikkim, D.G.Long, 22838, —/—/—: EDNA10_00612
*C. pusilla*_24, India: Dehra Dun, S. Chopra, 24, —/—/—: EDNA10_00604
*C. pusilla*_605, India: Dehra Dun, S. Chopra, s.n., —/—/—: EDNA10_00605
***Athalamia pinguis* Falc.**
*A. pinguis*_30889, India: Uttaranchal, D. G. Long 30889, HQ623623/DQ220677/DQ265747: EDNA06_01943
***A. handelii* (Herzog) S.Hatt.**
*A. handelii*_18626, China: Yunnan, D.G. Long 18626, HQ225548/HQ225519 /HQ225586: EDNA08_02952
***Clevea spathysii* (Lindenb.) Müll.Frib.**
*C. spathysii*_1176, Italy: Sicily, V. Schiffner 1176, HQ225549/—/HQ225587: EDNA08_02969
*C. spathysii*_01_09, Spain: Murcia, Rubasinghe & Long 01-09 SR, HQ225550/HQ225520/HQ225588: EDNA09_00974
*C. spathysii*_06_09, Spain: Almeria, Rubasinghe & Long 06-09 SR, HQ225551/HQ225521/HQ225589: EDNA09_00977
*C. spathysii*_02-09, Spain: Almeria, Rubasinghe & Long 02-09 SR, HQ225552/—/HQ225590: EDNA09_00975
*C. spathysii*_05-09, Spain: Almeria, Rubasinghe & Long 05-09 SR, HQ225553/HQ225522/HQ225591: EDNA09_00976
*C. spathysii*_15873, Portugal: Algarve, D.G. Long 15873, —/—/HQ225592: EDNA08_01776

***Peltolepis quadrata* (Saut.) Müll.Frib.,**
*P. quadrata*_ 3494, Romania: Bucegi Mountains, S. Stefanut 3494, HQ225554/HQ225523/HQ225593: EDNA08_00371
*P. quadrata*_ 07-08, Switzerland: Canton Valais, Rubasinghe & Long 07-08 SR, HQ225555/HQ225524/HQ225594: EDNA08_01745
*P. quadrata*_ 08-08, Switzerland: Valais, Rubasinghe & Long 08-08SR, HQ225556/HQ225525/HQ225595: EDNA08_01746
*P. quadrata*_ 09-08, Switzerland:Valais, Rubasinghe & Long 09-08 SR, HQ225557/HQ225526/HQ225596; EDNA08_01747
*P. quadrata*_ 12-08, Switzerland: Valais, Rubasinghe & Long 12-08 SR, HQ225558/HQ225527/HQ225597: EDNA08_01749
*P. quadrata*_ 15-08, Switzerland: Valais, Rubasinghe & Long 15-08 SR, HQ225559/HQ225528/HQ225598: EDNA08_01751
*P. quadrata*_ 35918, China: Yunnan, D.G. Long 35918, HQ225560/HQ225529/HQ225599: EDNA07_02389
*P. quadrata*_ 13223, Greenland, Disko island, D.G. Long 13223, HQ225561/HQ225530/HQ225600: EDNA08_01759
*P. quadrata*_ 31360, Norway: Prov. Sogn og Fjordane,, D.G. Long 31360, HQ225562/HQ225531/HQ225601:EDNA09_01374
*P. quadrata*_ 31360, Norway: Prov. Sogn og Fjordane,, D.G. Long 31360, HQ225562/HQ225531/HQ225601:EDNA09_01944
*P. quadrata*_ 1174, Japan, Honshu, Nagano-ken, Ina-shi Mt, T. Katagiri, 1174, —/—/—:EDNA10_00610
***Sauteria alpina* (Nees) Nees,**
*S. alpina*_06-08, Switzerland: Valais, Rubasinghe & Long 06-08 SR, HQ225563/—/HQ225602: EDNA08_01744
*S. alpina*_11-08, Switzerland: Valais, Rubasinghe & Long 11-08 SR, HQ225564/HQ225532/HQ225603: EDNA08_01748
*S. alpina*_13-08, Switzerland: Valais, Rubasinghe & Long 13-08 SR, HQ225565/HQ225533/HQ225604: EDNA08_01750
*S. alpina*_13130, Greenland: Disko Island, D.G.Long 13130, HQ225566/—/HQ225605; EDNA08_01757
*S. alpina*_64, Austria: Carinthia, D. B. Schill 64, HQ225567/HQ225534/HQ225606: EDNA06_01945
*S. alpina*_3498, Romania: Bucegi mountains, Babele Peak, S. Stefanut, 3498, —/—/—: EDNA08_00370
***S. spongiosa* (Kashyap) S.Hatt.**
*S. spongiosa*_35772, China: Yunnan, D.G. Long 35772, HQ225568/HQ225535/HQ225607: EDNA08_00368
*S. spongiosa*_30427, Nepal: Rasuwa District, D.G. Long 30427, HQ225569/HQ225536/HQ225608: EDNA08_00369
*S. spongiosa*_24012, China: Yunnan, D.G. Long 24012, HQ225570/HQ225537/HQ225609: EDNA08_02949
*S.spongiosa*_30427, Nepal: Rasuwa District, D.G. Long 30427, —/—/—: EDNA08_02951
*S. spongiosa*_20626, Nepal: Sankhuwasabha district, D.G. Long 30427, —/—/—: EDNA08_02953
*S. spongiosa*_20876, Nepal: Sankhuwasabha district, D.G. Long 20876, —/—/—: EDNA08_02954
*S. spongiosa*_30450, Nepal: Rasuwa District district, D.G. Long 30450, —/—/—: EDNA08_02950
*S. spongiosa*_1173, Japan: Honshu, Nagano-ken, Ina-shi Mt, T. Katagiri, 1173, —/—/—: EDNA10_00608
*S. spongiosa*_2806, Japan: Honshu, Yamanashi-ken, T. Katagiri, 2806, —/—/—: EDNA10_00609
***Asterella grollei* D.G.Long**
*A. grollei*_30251, Nepal, Lalitpur District, D.G. Long 30251, AM920036*/DQ220675*/DQ265745*: EDNA06_04284
***Asterella wallichiana* (Lehm. & Lindenb.) Grolle,**
*A. wallichiana*_27203, China: Qinghai, D.G. Long 27203, FJ173781*/DQ220674*/DQ265744*: EDNA06_01956
***Mannia androgyna* (L.) A.Evans,**
M. androgyna _20, Portugal: Madeira, D.B. Schill 20, AM919995*/DQ220686*/DQ265756*: EDNA06_04316

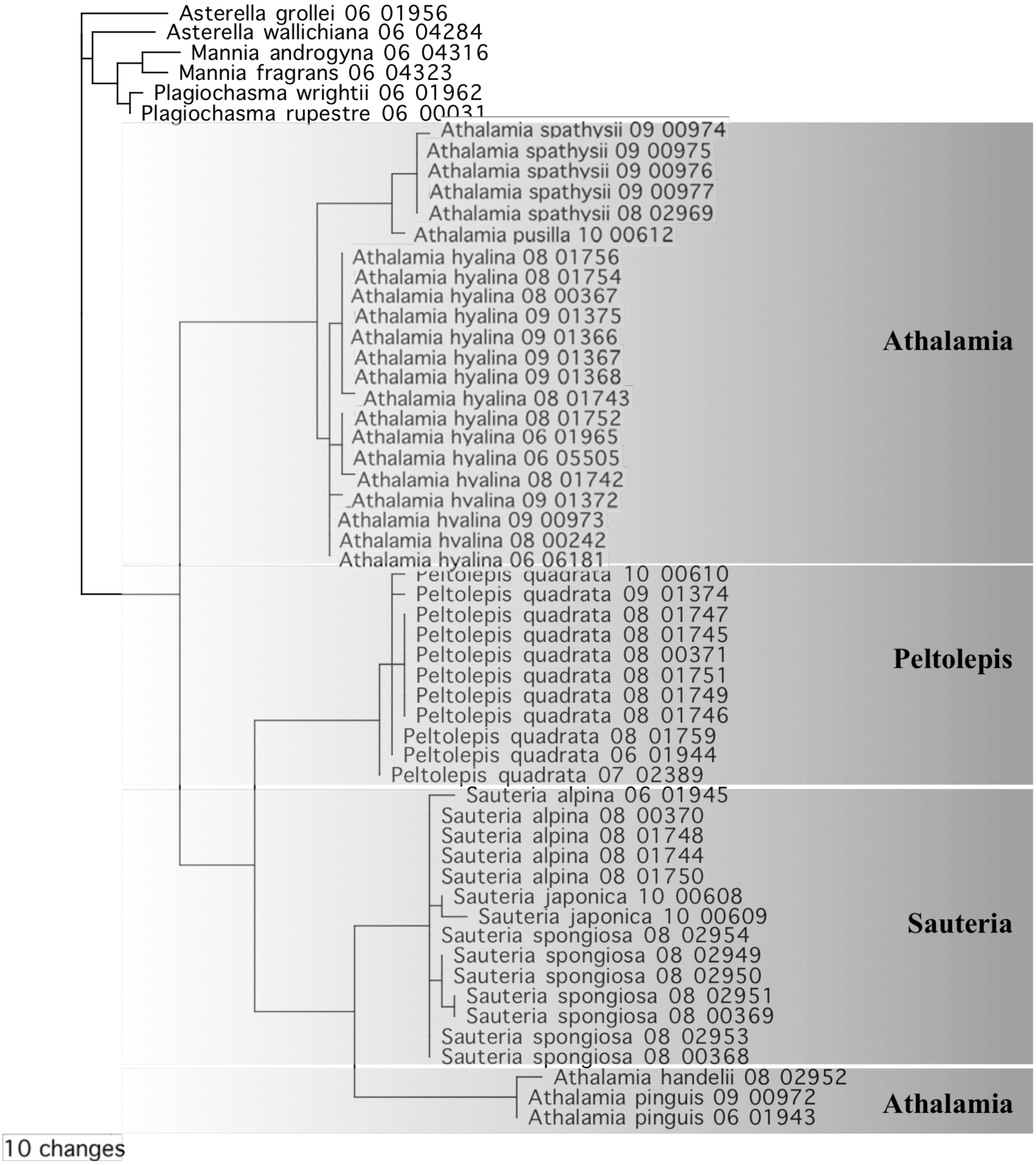
***Mannia fragrans* (Balbis) Frye & L. Clark,**
*M. fragrans*_34, Switzerland: Valais, D.B. Schill 34, AM920016*/DQ220687*/DQ265757*: EDNA06_04323
***Plagiochasma rupestre* (J.R. & G. Forst.) Steph.,**
*P. rupestre*_5, Portugal: Madeira, D.B. Schill 5, AM920000*/DQ220694*/DQ265763*: EDNA06_00031
***Plagiochasma wrightii* Sull.,**
*P. wrightii*_29636, Mexico: Veracruz State, Long *et al.* 29636, FJ173797*/DQ220695/DQ265764:EDNA06_01962
***Conocephalum conicum* (L.) Underw.s.lat.**
*C. conicum*_30975, India, Uttaranchal, D.G. Long 30975, —/DQ220678*/DQ265748*: EDNA06_01964
***Conocephalum japonicum* (Thunb.)Grolle**
*C. japonicum*_30724, Nepal, D.G. Long 30724, —/DQ220679*/DQ265749*: EDNA06_01937
***Monoclea gottschei* Lindb.**
*M. gottschei*_29637, U.S.A., Mexico, Veracruz, Long, Garcia & de Luna, 29637, —/DQ220690*/DQ265760*: EDNA06_01936
***Corsinia coriandrina* (Spreng.) Lindb.**
*C. coriandrina*_9, Portugal, Madeira, D.B. Schill, 9, —/DQ220680*/DQ265750*: EDNA06_01948
***Exormotheca pustulosa* Mitt.**
*E. pustulosa*_8, Portugal, Madeira, D.B. Schill, 8, —/DQ220684*/DQ265754*: EDNA06_01946
***Ricciocarpos natans* (L.) Corda**
*R. natans*_20467, Australia, Victoria, Seppelt, 20467, —/DQ220698*/DQ265767*: EDNA06_01951
***Riccia ciliifera* Lindenb.**
*R. ciliifera*_37, Switzerland, D.B.Schill, 37, —/DQ220696*/DQ265765*: EDNA06_01950
***Riccia fluitans* L.**
*R. fluitans*_1949, U.S.A., Iowa, Cady, s.n., —/DQ220697*/DQ265766*: EDNA06_01949
***Dunortiera hirsuta* (Sw.) Nees**
D. hirsuta _6462, U.S.A, Goffinet, 6462, —/AY608061*/DQ607940*
*D. hirsuta*_29627, U.S.A., Mexico, Veracruz, Long, Garcia & de Luna, 29627, —/DQ220683*/DQ265753*: EDNA06_01939
***Monosolenium tenerum* Griff.**
*M. tenerum*_1954, Germany, Gradstein, s.n., —/DQ220691*/—: EDNA06_01954
***Targionia hypophylla* L.**
*T. hypophylla*_11, Portugal, Madeira, D.B.Schill, 11, —/DQ220700*/DQ265769*: EDNA06_01966
*T. hypophylla*_3397, U.S.A., California, Stotler & Crandall-Stotler, 3397,—/AY688805*/AY507514*
***Wiesnerella denudata* (Mitt.) Steph.**
*W. denudata*_30337, Nepal, D.G.Long, 30337, —/DQ220701*/—: EDNA06_01963

Accession numbers denoted with * were downloaded from the nucleotide database of National Centre for Biotechnology Information (http://www.ncbi.nlm.nih.gov/); all others were generated for this project.

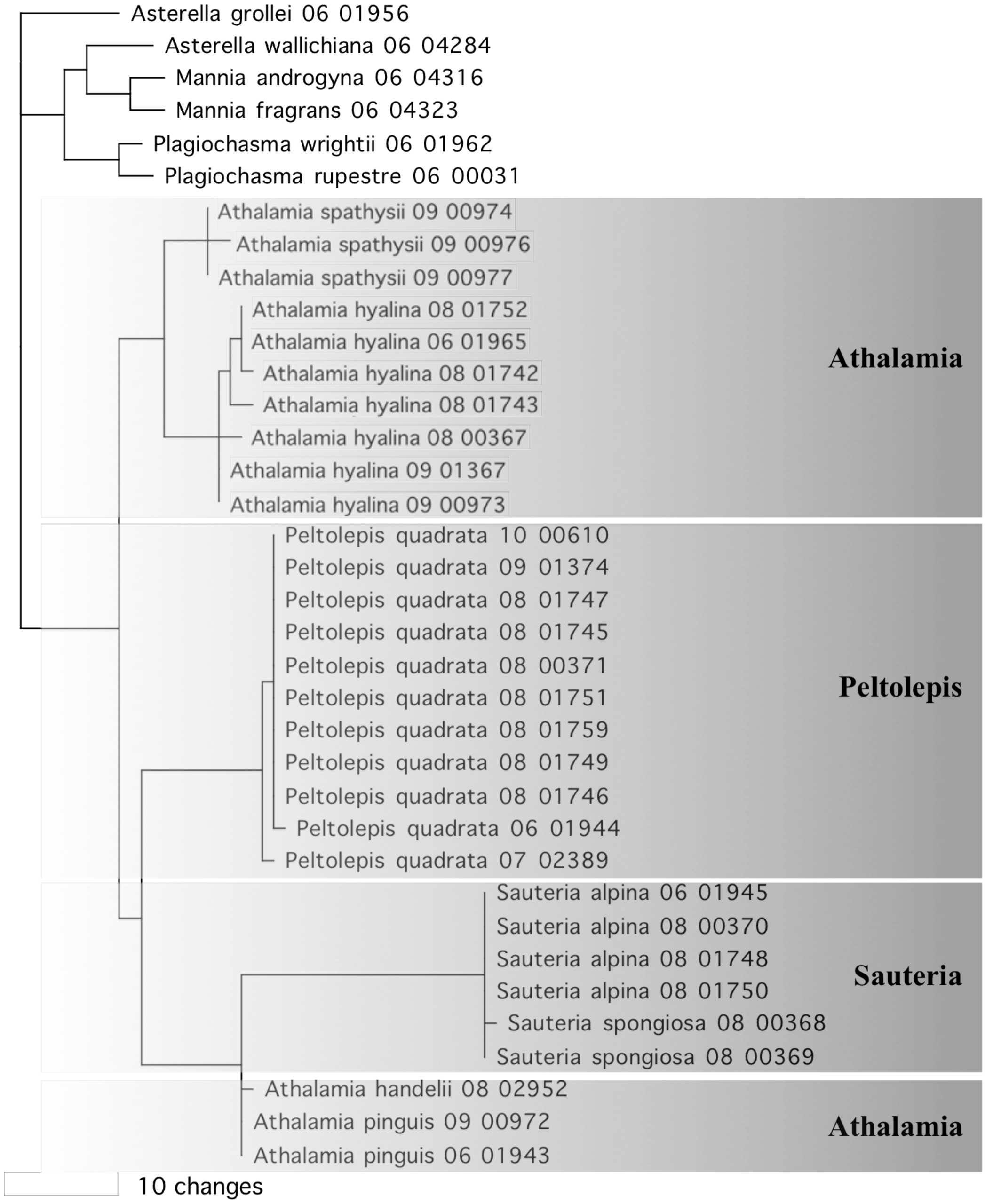
Appendix 3.2. Results of initial maximum parsimony analysis of separate regions: *psb*A, *rpo*C1, *rps*4 & 26S.



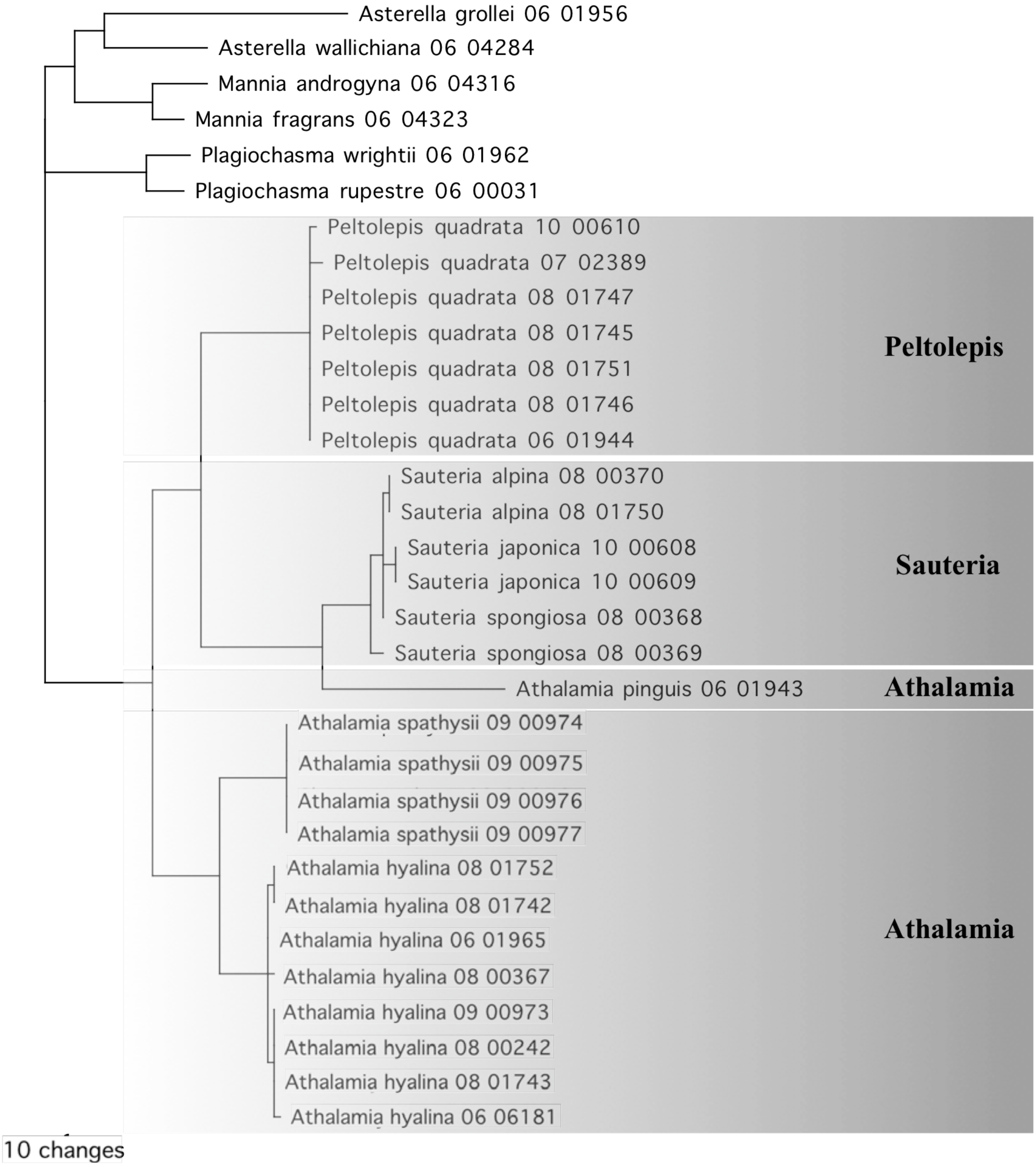
Phylogram (one of 04 equally parsimonious trees) from *psb*A region, with major clades highlighted. Four currently recognised genera are annotated. Tree length=538, CI=0.686, RI=0.881.



Phylogram (one of 6821 equally parsimonious trees) from *rpo*C1 region, with major clades highlighted. Four currently recognised genera are annotated. Tree length=120, CI=0.783, RI=0.963.



Phylogram (one of 410 equally parsimonious trees) from *rps*4 region, with major clades highlighted. Four currently recognised genera are annotated. Tree length=121, CI=0.752, RI=0.914.



Phylogram (one of 100 equally parsimonious trees) from 26S region, with major clades highlighted. Four currently recognised genera are annotated. Tree length=255, CI=0.725, RI=0.8

Appendix 3.3. Morphological data matrix showing the distribution of characters across the taxa used in character reconstructions. 1=Number of rhizoid furrows; 2=Archegonia/archegoniophore position; 3=Thickening of radial walls of epidermal pores; 4=width& shape of air chambers; 5=sexual condition; 6=androecial scales; 7=androecial aggregation; 8=androecial position; 9=thallus secondary pigmentation; 10=ventral scale arrangement; 11=ventral scale protrusion;12=vetral scale oil bodies.

	Character states											
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Clevea spathysii 09 00977	0	1	0	0	1	0	1	0	1	1	1	1
Clevea spathysii 08 02969	0	1	0	0	1	0	1	0	1	1	1	1
Clevea pusilla 10 00605	0	1	0	0	1	0	1	0	1	0	1	1
Clevea pusilla 10 00612	0	1	0	0	1	0	1	0	1	0	1	1
Clevea hyalina 08 01752	0	1	1	0	0	1	1	0	1	1	1	0
Clevea hyalina 06 01965	0	1	1	0	0	1	1	0	1	1	1	0
Clevea hyalina 09 01372	0	1	1	0	0	1	1	0	1	1	1	0
Clevea hyalina 08 00367	0	1	1	0	0	1	1	0	1	1	1	0
Clevea hyalina 08 00242	0	1	1	0	0	1	1	0	1	1	1	0
Clevea hyalina 09 01368	0	1	1	0	0	1	1	0	1	1	1	0
Clevea hyalina 08 01743	0	1	1	0	0	1	1	0	1	1	1	0
Clevea hyalina 06 06181	0	1	1	0	0	1	1	0	1	1	1	0
Peltolepis quadrata 10 00610	2	0	1	0	1	1	3	0	1	0	0	0
Peltolepis quadrata 07 02389	2	0	1	0	1	1	3	0	1	0	0	0
Peltolepis quadrata 08 01747	2	0	1	0	1	1	3	0	1	0	0	0
Peltolepis quadrata 08 00371	2	0	1	0	1	1	3	0	1	0	0	0
Peltolepis quadrata 08 01759	2	0	1	0	1	1	3	0	1	0	0	0
Peltolepis quadrata 06 01944	2	0	1	0	1	1	3	0	1	0	0	0
Sauteria alpina 06 01945	1	0	0	0	1	0	1	0	0	0	0	1
Sauteria alpina 08 00370	1	0	0	0	1	0	1	0	0	0	0	1
Sauteria alpina 08 01748	1	0	0	0	1	0	1	0	0	0	0	1

Sauteria japonica 10 00608	1	0	0	0	1	0	1	1	0	0	0	1
Sauteria japonica 10 00609	1	0	0	0	1	0	1	1	0	0	0	1
Sauteria spongiosa 08 02954	1	0	0	0	1	0	1	1	0	0	0	1
Sauteria spongiosa 08 02949	1	0	0	0	1	0	1	1	0	0	0	1
Sauteria spongiosa 08 00368	1	0	0	0	1	0	1	1	0	0	0	1
Sauteria spongiosa 08 02951	1	0	0	0	1	0	1	1	0	0	0	1
Athalamia handelii 08 02952	0	1	1	1	1	0	1	0	0	1	2	0
Athalamia pinguis 06 01943	0	1	1	1	1	0	1	0	0	1	2	0
Conocephalum conicum 06 01964	?	1	0	0	0/1	0	5	0	0	0	0	1
Corsinia coriandra 06 01948	1	0	0	0	0	0	2	0	1	1	0	1
Dumortiera hirsuta 06 01939	2	0	0	?	0/1	0	4	0	0	1	0	0
Exormotheca pustulosa 06 01946	1	0	0	0	1	0	5	0	1	1	2	1
Monoclea gottschei 06 01936	?	0	?	?	0	0	4	0	0	?	3	2
Monosolenium tenerum 06 01954	2	0	?	?	1	0	2	0	1	1	0	1
Ricciocarpos natans 06 01951	?	1	0	0	1	0	5	0	1	0	0	1
Riccia fluitans 06 01949	?	1	0	0	0	0	0	0	1	1	0	0
Targionia hypophylla 06 01966	?	0	0	0	1	0	2	1	1	1	0	1
Wiesnerella denudata 06 01963	2	0	0	0	1	1	2	0	1	1	0	1
Asterella grollei 06 01956	1	0	0	0	1	1	2	0	1	1	0	1
Asterella wallichiana 06 04284	1	0	0	0	0	0	2	0	1	1	0	1
Mannia androgyna 06 04316	1	0	0	0	1	0	2	0	1	1	0	1
Mannia fragrans 06 04323	0	1	0	0	1	1	2	0/1	1	1	0	1
Plagiochasma wrightii 06 01962	0	1	0	0	1	1	2	0/1	1	1	0	1
Plagiochasma rupestre 06 00031	1	0	0	0	0	0	3	0	1	1	0	1

Appendix 4.1 Cleveaceae specimens studied.

Confirmed Name	Specimen name	Country	Locality	Date	Collector	No	Herbarium
Athalamia pinguis Falc.	*Athalamia handelii* (Herzog) S.Hatt.	CHINA	Yunnan, Zhongdian (Chungtien) district: hot spring above Nada Village. In shady crevices of limestone rock outcrop.Alt. 3400m.	27 ix 1990	D.G.Long	18626	E
Athalamia pinguis Falc.	*Athalamia handelii* (Herzog) S.Hatt.	CHINA	Yunnan, NW., Deqen Zang Aut. Pref.: Zhongdian Co,: By hot spring, Stone Bridge, near Zhongdian. Limestone cliff. 3400m.	24 ix 1995	D.F. Chamberlain	s.n.	E
Athalamia pinguis Falc.	*Athalamia handelii* (Herzog) S.Hatt.	CHINA	Yunnan: bor-occid.: In regionis temperatae in vica Ngulukö ad urbem Lidjiang (Likiang). Substr. Eruptivo. 2830m.	9 vi 1915	H. Handel-Mazzetti	(1187) 6682	E, JE, WU
Athalamia pinguis Falc.	*Clevea gollani* Steph.	INDIA	Simla distr. Upper path leading to Tetreat Masholia, 8000 – 8500 ft. – 2138-2590m.	iv 1908	E. Long	58	BM
Athalamia pinguis Falc.	*Clevea gollani* Steph.	INDIA	N. W. India, Mussoorie (N.W. India) hill above Arnigadh Bot. Garden. Alt. 6000 ft. On rocks in open spots.	12 viii 1900.	W. Gollan	s.n. M-7977.	BG
Athalamia pinguis Falc.	*Clevea gollani* Steph.	INDIA	Mussoorie (N.W. Himalaya) Govt. Bot. Gardens Arnigadh, on banks, 5500 f.	11 ix 1900.	W. Gollan	s.n.	BM, G
Athalamia pinguis Falc.	*Clevea gollanii* Steph.	INDIA	Simla Distr. - N. W. Himalaya. Mount Jako, on rocks and earthy banks 7800 ft.	10 viii 1904	W. Gollan	s.n.	O
Athalamia pinguis Falc.	*Clevea gollanii* Steph.	INDIA	Mussoorie. Herb. Karl Müller (1956).	12 ix 1900	[W. Gollan] in herb. E. Levier	s.n. B22252	S
Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	INDIA	Kagar (8000´) W Himalaya On dry exposed rocks.	ix 1930	Bagchi	8059	W
Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	INDIA	Uttaranchal: National district: path from Nainital-Khurpatal road to Land’s End. Open limestone slopes; on thin soil on rocks Alt. c. 2110m	1 ii 2002	D.G. Long	30889	E
Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	INDIA	Mussorie (6-7000) W. Himalaya on dry rocks	ix 1930	R.S.Chopra	s.n.	JE, W, FH
Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	INDIA	Mussoorie, 2000´ Western Himalayas	20 ix 1948	S.K. Pande	s.n.	S

Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	INDIA	Himalaya occ., Mussoorie, rupicola, subxerophila,	1932	S.R. Kashyap	s.n.	G
Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	INDIA	Himalaya Occ., Mussoorie, rupicola, subxerophila, photophila, 2200m	1932	S.R. Kashyap	s.n.	H, F, W, BR, NY, O, JE, FH
Athalamia pinguis Falc.	*Clevea gollani* Steph.	INDIA	Mussoorie (N. W. Himalaya) Hill above Arnigadh Garden, on rocks in open spots 6000 f. Leaves have pale yellow or golden tint when fresh.	12 ix 1900.	W. Gollan	3842b	G
Athalamia pinguis Falc.	*Clevea gollani* Steph.	INDIA	Simla Distr. Mount Jako, on rocks and earthy banks, 7800ft.	10 viii 1904.	W. Gollan,	s.n. BM000890069	BM
Athalamia pinguis Falc.	*Clevea gollani Steph.*	INDIA	Mussoorie (N. W. Himalaya). Hill above Arnigadh Gardens on dry limestone rocks. 5600 – 6000 ft.	15 x 1903.	W. Gollan.	s.n.	BR
Athalamia pinguis Falc.	*Clevea gollani Steph.*	INDIA	Simla distr. (S.E. Panjab) Mount Jako, on rocks and grassy banks, 7700ft.	23 viii 1904	W.Gollan	s.n.	FH
Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	NEPAL	Vorhimalaja, Abies-Rhododendron-Bergwald Östlich Junbesi	1962	J. Poelt	s.n. H117	JE
Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	PAKISTAN	North-West Frontier Prov, Changla Gali (north of Murree), 2420m alt., on soil.	03 viii 1990	M. Higuchi	19387	TNS
Athalamia pinguis Falc.	*Athalamia pinguis* Falc.	PAKISTAN	North-West Frontier Prov, Dunga Gali (north of Murree), 2300m , on stone wall.	20 viii 1990	M. Higuchi	19772	TNS
Athalamia pinguis Falc. + *Clevea pusilla* (Steph.) Rubasinghe & D.G.Long	*Athalamia pinguis* Falc.	INDIA	Himalaya Occ., Mussoorie, rupicola, subxerophila, photophila, 2200m	1932	S.R. Kashyap	s.n. BM000890070	BM
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AFGHANISTAN	Tscharikar, Top Tara, an einer Quelle	12 v 1950,	J.F. Neubauer	280	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Arctic Alaska: Meade River Post Office (Coal Mine) Sandy, calcareous, east-facing bluff above Meade River, south of camp.	15 vii 1973	W.C. Steere, H. Inoue & Z. Iwatsuki	22425	TNS
Clevea hyalina (Sommerf.) Lindb.	*Clevea trabutiana* Steph.	ALGERIA	Oran, Cotterie Espagnole	v 1907	A. Faure	s.n.	E

Clevea hyalina (Sommerf.) Lindb.	*Clevea trabutiana* Steph.	ALGERIA	Algerien: Oran, Tiaret, auf Sandboden.	v 1907	L. Trabut	s.n.	E
Clevea hyalina (Sommerf.) Lindb.	*Clevea trabutiana* Steph.	ALGERIA	Algerien: Oran; Tiaret, auf Sandboden. .	v 1907.	L. Trabut	1177	G, S, B
Clevea hyalina (Sommerf.) Lindb.	*Clevea trabutiana* Steph.	ALGERIA	no locality details	1907	L. Trabut	s.n. G00067398	G
Clevea hyalina (Sommerf.) Lindb.	*Clevea trabutiana* Steph.	ALGERIA	Oran: Tiaret, auf Sandboden.	v 1907.	L. Trabut	s.n.	WU
Clevea hyalina (Sommerf.) Lindb.	*Clevea trabutiana* Steph.	ALGERIA	no locality details	1907	L. Trabut	s.n. G000112668	G
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	AUSTRIA	Carinthia: Völkermarkt, Bleiburg, Petzen, between Kniepsattel and Hochpetzen. In rock crevice. 2007 m.	24 vii 2003	D. Schill, H. Köckinger & U. Müller	82	E
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Gumpeneck im Sölktal 2200m	20 vii 1912	E. Riehmer	s.n.	B
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Niederösterreich: Hundsheimer Berg, Hexenberg, ca 425m auf Erde über Kalkgestein.	22 iv 1956	J. Froehlich	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Niederösterreich: Hundsheimer Berg, Hexenberg, ca 425m auf Erde über Kalkgestein.	20 iv 1941	J. Froehlich	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Niederösterreich: Westhang des Hexenberges nördlich von Hundsheim, ca 350m auf Erde in der pannonischen Heide. 10.2.1957.	31 xii 1960	J. Froehlich	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Niederösterreich:Südlich von Hundsheim, Spetzberg,ca 250-290m auf Erde. 26.8.1956	31 xii 1956	J. Froehlich	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Niederösterreich: Spitzer Berg, sudlich von Hundsheim, ca 250m, auf Erde.	24 iv 1938.	J. Froehlich	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.)S.Hatt.	AUSTRIA	[Lower Austria] Niederösterreich: Sudlich von Hundsheim, Sudwesthang des Spitzer Berges, ca 280 m auf Erde.	22 iv 1956	J. Froehlich	s.n.	TNS

Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Niederösterreich: Südlich von Hundsheim, Südwesthang des Spitzer Berges, ca 280m auf Erde.	22 iv 1956	J. Froehlich	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Kärnten: Großglockner; Umgebung des Glocknerhauses (bes "Böse Platee") unter und an überhängenden Silikatfelsen 2000-2200m.	vii 1902	K. Loitlesberger	s.n.	B, WU, NY
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Burgenland: Kreis Eisenstadt: Steppenveget. Auf. D. Plateau d. Hügel am "Römersteinsbruch" zw. Rust. & St. Margareten. Kalk. C. 200m.	20 vii 1972	R. Düll	s.n.	B, U
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Kalkfelsspallen, Granaten wand, Geissbarh. Obesguryl, Tirol, 2800m. Herbarium Patricia Geissler.1135	10 vii 74	S. Bootenschlege	s.n. G00112901	G
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	AUSTRIA	Niederösterreich: Am Braunsberge bei Hainburg, auf dem durch den Kalk brechenden Quarzitriffe, auf humöser Erde. 250m.	19 ix 1902	V. Schiffner & J Baumgartner.	s.n.	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	AUSTRIA	Neiderösterreich: Am Braunsberge bei Hainburg, auf dem durch den Kalk brechenden Quarzitriffe, auf humoser Erde, 250m.	19 x 1902	V. Schiffner & J. Baumgartner	s.n.	G, WU
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	BULGARIA	Pirin, Raslog, Aufstieg in den Circus Kamenitica, 2200-2500m.	24 vi 1977	F.K. & J. Mayer.	12578	JE
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	BULGARIA	Bulgarien, Pirin-Gebirge, 2500m, Kalkfelsspalten im Kessel nördlich vom Vichsen.	1973	L. Meinunger	s.n. H1039	JE
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	CANADA	Kong Oscars Land, Goose fjord (76° 30´N)	viii 1900	H. G. Simmons.	s.n.	O
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	Banff National Park: Johnson's Canyon. On soil. 1500m, Along path to lower falls in Pinus contorta, Picea glauca, Pseudotsuga menziesii forest. Dry to mesic calcareous rock outcrops exposed along stream.	25 ix 1978	E. Nyhom	335/78	S
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	Banff National Park: Johnson's Canyon. On soil. 1500m, Along path to lower falls in Pinus contorta, Picea glauca Pseudosuga menziesi forest. Sry to mesi calcareous rock out crops exposed along stream with abundant	25 ix 1978	E. Nyhom	Itsi 54	U

			Homalothecium aeneum, Tortula ruralis and Orthotrichum jamesianum.				
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	CANADA	NE Ellesmere Island, The Dean, 5-6 mls. SE of Alert. Basic exposed soil, snow-fed slope below a shallow ravine.	24 vi 1955	R.M Schuster	35178	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	CANADA	Ellesmere I. Moist tundra over clay- shale slope, between Dumbbell Bay and the Dean. S. of Alert.	3 vi 1955	R.M Schuster	35060	F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	Damp clay at base of rocky outcrop, around lemming warren, 1m S of Alert, above Parr Inlet. (n. e. Ellesmere island)	13 vi 1955	R.M Schuster	35080	F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CHINA	Xinjiang Province: Shaded soil, east-facing base of canyonside. Open east facing canyonside open Picea forest with heavily grazed grass-herb understorey. Valley at head of Lake Tian-Chi; elev. 2000 m.	24 vii 1993	A.T. Whittemore with B. Tan, R. L. Hu, J. C. Zhao, R. L. Zhu & M. Sulayman.	4580	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CHINA	Xinjiang Province: Shaded vertical soil beneath root of Picea. Open grassy Picea forest on steep northwest slope. Forest of Hei-lau-pa, near Banjeko, north base of Tien Shan south of Qitai; elev. 2100 m.	25 vii 1993	A.T. Whittemore, B. Tan, R. L. Hu, J. C. Zhao, R. L. Zhu & M. Sulayman.	4601,	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CHINA	Xinjiang Province: Shaded overhang, north facing rock face. Grassland with rosaceous shrubs and scattered Picea deep canyon. 10 km south of Huoxia, on Urumqi-Ulaxitai highway: elev 2300 m.with	11 viii 1993	A.T. Whittemore, B. Tan, R. L. Hu, J. C. Zhao, R. L. Zhu & M. Sulayman	4827	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CHINA	Xinjiang Province: Crevice in south-facing rock of trailbank, just south of upper end of lake. Open east-facing canyon-side, open Picea forest with heavily grazed grass- herb understorey. Valley at head of Lake Tian-Chi; elev. 2000m.	24 vii 1993	A.T. Whittemore, B. Tan, R. L. Hu, J. C. Zhao, R. L. Zhu & M. Sulayman	4584	H, NY
Clevea hyalina (Sommerf.) Lindb.	—	CHINA	Xinjiang Province: Fukang Co., south end of Lake Tian-chi, ca 1940 – 2000m. Dry and open slope in anrrow valley of Picea schrinckiana forest behind the forestry nursery site, underneath disturbed shrubs.	24 vii 1993	B.C. Tan	93-834	E
Clevea hyalina	*Athalamia hyalina*	CHINA	Xinjiang Prov., Tianshan Range, Nanshan	11 viii	BC Tan. & A.	93-1228	E

(Sommerf.) Lindb.	(Sommerf.) S.Hatt.		Bai-Yang Valley, about 55 km S of Urumqi City ca 6800 ft.Picca forest near the spray of waterfall, shaded and wet. B. C.	1993	Whittemore.		
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province: Henan county: Dousong Xiang, Zhilong, Limestone hillside; soil clefts at foot of limestone cliff. Alt. c. 3830 m.	15 vii 1997	D.G. Long	27033	E
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province, Henan County: Xiawate, Zhihoumao Xiang S of Henan. Steep slopes below limestone cliffs; on soil ledges. 3800 m.	15 vii 1997	D.G. Long	27015	E
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province: Maqin county: Chihedana S. of Dawu,. Steep limestone valley; on shady bank uncer Salix. Alt. c. 3910 m.	8 vii 1997	D.G. Long	26900	E
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province: Maqin county: S of Radja on slopes of Huang He valley,, . Steep revine in Picea forest; on calcareous rock ledges. Alt. c. 3730 m. 1997.	12 vii 1997	D.G. Long	26967	E
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province: Maduo county: Ang'lexiao Pass, SE of Huashixia,. Open rocky hillside; on soil bank on hummocky slope. Alt. c. 4635m.	5 vii 1997	D.G. Long	26847	E
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province: Huzhu county: near Nanzhangzhagon villege, upper Zhalonggou valley, *Betula*/ *Juniperus* woodland on limestone; on soil under rock overhang. Alt. c. 2765 m.	24 vii 1997	D.G. Long	27233	E
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province: Maqin county: valley north of Jungun Naichong, . Damp rocky side gully in dry valley; on soil on rocks. Alt. c. 3570 m.	10 vii 1997	D.G. Long	26940	E
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province: Zeku county: below Maixiu Forestry Centre, Langzhang valley, Steep rocky valley with Picea and Juniperus forest; on stream bank under shrubs. Alt. c. 3180m.	17 vii 1997	D.G. Long	27062	E
Clevea hyalina (Sommerf.) Lindb.	Cleveaceae	CHINA	Qinghai Province: Maqin county: Valley north of Jungun Naichong, Damp rocky side gully in dry valley; on damp soul on N-facing rocks. Alt. c. 3570m.	10 vii 1997	D.G. Long	26948	E
Clevea hyalina	Cleveaceae	CHINA	Qinghai Province: Xianghai County: north	2 vii 1997	D.G.Long	26807	E

(Sommerf.) Lindb.			slope of Heka Shan. Steep hillside with Caragana, under wet overhang. 3845m				
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	FINLAND	NW-Le, Kilpisjärvi, SW-Saana, in clivo rupestri, in terra humosa, 650-700 m	14 vii 1958	Laila & H. Roivainen	s.n.	H
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* var. *suecica* (Lindb.)K.Müll.	FINLAND	Karleby, Skattegården, kalkhed.	20 v 1938	A. Hülphers	s.n. B123668	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	FINLAND	Lapp. Ponojensis, ad promontorium Orlow	25 v 1889	A.O. Kihlman	s.n.	H
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	FINLAND	Ks, Salla, Nivajärvi, Hirveäkallio.	14 vii 1934	M. J. Kotilainen.	s.n.	H
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	FINLAND	Pááhkánánkallia in ripa bareale pluminis Kit-kajoki I ca 5.5 km adoccidenteu versus aboppluvia eivs in pluminem Oulankajoki in articula areuasa in pariete alta etad aientem versus ecpaita rupis ± dolamiticae. .	20 vi 1938	Matti Laurila	s.n.	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	FRANCE	Savoie, St. Nichel-de-Nauvienne. Col du Galilies, Salus 2610 m.	6 vii 1992	not known	s.n.	G
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sft.) Lindb.	FRANCE	Hautes – Pyrénées. Baréges, route du Col du Tourmalet, fentes de rochers schisteux. Alt. 1800 m.	8 viii 1974	R.B. Pierrot	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GEORGIA	Caucasus, Georgia: distr. Ducheti, in vicinitate pagi Pasanauri, in valle fluminis Belaia Aragva. Alt. 1200 – 1500 ms.m.	31 vii 1982	V. Vašák.	s.n.	G
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GERMANY	N-Thüringen, Kyffhäuser, Flakenbergplateau bei Rottleben	1952	R. Grolle	s.n.	JE
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	GERMANY	Rottleben, auf Gips der Falkenburgh, Plateau	15 iv 1938	F. & K. Koppe	s.n.	B
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GERMANY	Bezirk Halle, Kreis Merseburg. Kotberg bei Gröst, auf Muschelkalk	10 v 1977	S. Rauschert	s.n. JE-2227	JE
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREECE	Pr. Rethimnon: Aufstieg zum Berg Mavri (Ostabhang d. Nida - Hochebene 20 km südl. Anogia) Südalp. Dornpolsterstufe. Kalk. C. 1540 m.	3 iv 1972	R. Düll	113 a	B

Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREECE	Crete, Pr. Rethimnon: Aufstieg zum Berg Mavri (Ostabhang d. Nida-Hochebene 20 km. sudl. Anögia) Sübalp. Dornpolsterstufe. Kalk. E. 1540 m.	3 iv 1972	R. Düll	113a	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREECE	On soil over rock face in sheltered gully. Peloponnese: Arkadia Mt. Parnon range several km SW of Kosmas. 950-1000m	14 iv 1995	T.L. Blockeel	24/156	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREECE	among limestone rocks at edge of Abies forest. Peloponnese: Ahaia [Arcadia]: Mt. Helmos on the approach to Xirokambos, SE of Kalavryta. 1400m	18 iv 1995	T.L. Blockeel	24/226	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia trabutiana* (Steph.) S.Hatt.	GREECE	Habitat: on soil among sloping limestone slabs. Locality: Crete: Nome of Iraklion: Mt. IDA, slopes above the Nida Plain. Alt. ca 1500m.	ix. 1992	T.L. Blockeel.	21/380	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Foulkefjord (N.V. Grønland). [Foulk Fjord]	11-12 viii 1899	H. G. Simmons	s.n. M-7997	BG
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	GREENLAND	Moist, shady rockcave. Qioqe Pen. Kangerdlugssuak Fj.	23 vii 1956	K. Holmen	16.397	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	GREENLAND	Kap Franklin	20 vii 1899	P. Dusén	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Sønder Strømfjord: on south facing steep slope N. of the air strip; along a small temporary rill.	3 ix 1970	R.M Schuster	70-3208	F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Sønder Strømfjord: on south facing steep slope N. of the air strip; along a small temporary rill.	3 ix 1970	R.M Schuster	70-3209	F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Disko I. : N. side of Nordfjord: Perdlertut, E. and SE. facing slopes	7 viii 1970	R.M Schuster & K. Damsholt	70-2699	F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	W. Greenland: Madglak, Alfred Wegeners Halvo	8 viii 1966	R.M Schuster & K. Damsholt	66-357d	F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Sønder Strømfjord South facing slopes near airstip (38° N)	3 vii 1970	R.M Schuster & K. Damsholt	70-2001	F
Clevea hyalina	*Athalamia hyalina*	GREENLAND	SW. corner of Anap nunâ, NW. of	21 vii 1970	R.M Schuster & K.	70-2418	F

(Sommerf.) Lindb.	(Sommerf.) S.Hatt.		Niaqornarssuaq		Damsholt		
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Sondrestrom Fjord: sunny south facing slopes near air-strip. At head of fjord.	23 vi 1966	R.M Schuster & K. Damsholt	66-038	F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Basalt cliffs near shore, below Skarvefjeld, E. of Godhavn.	27 vii 1966	R.M Schuster & K. Damsholt	66-298	F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Sheltered bank, W side of Delta River, S end of Kuhn Island	12 viii 1990	R.W.M. Corner	s.n.	E
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* Lindbg.	GREENLAND	Aus Gronland.	viii 1830	Vahl	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	HUNGARY	Comit. Fejér. In humosis inter saxa dolom., montis Kölik-hegy prope Csakbereny , 220m	9 vi 1936	Boros	s.n.	S, PC
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	HUNGARY	Budapest. In graminosis apricis planitici Tétényi fensik pr. Pag Budatétény. Alt. cca. 290m. Solo calc.	8 vi 1934	Szepesfalvi	s.n.	H, F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	HUNGARY	Comit. Pest. Budapest. In graminosis apricis planitiei Tétényi fennsik pr. Pag Budatétény. Solo calc. ca. 290m.	8 vi 1934	Szepesfalvi	s.n.	B
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	ITALY	Alagna Valsesia, appie delle rupi sgretolose. Primavera.	1877	A. Carestia	s.n.	E, F
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	ITALY	Campania: Prov. Salerno, Mont Cervati, between summit and Madonna della Neve. Crevices of limestone rocks. Alt. c. 1850 m.	18 xi 1994	D.G.Long & J. G. Duckett	25774	E
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	NORWAY	Finnmark: Alta: Talvik, ved Storevand, Paa skifer.	5 viii 1892	E. Jørgensen	s.n.	O
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	NORWAY	Nordland, Andøy, Vesteraalen: Andøen, ven Dverberg. Paa jord over en kalhøi I myren paa solvarme steder.	25 vii 1904	B. Kaalaas	s.n. M-7989	BG
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	NORWAY	Vesterålen, Dverberg.	25 vii 1904	B. Kaalaas	s.n.	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	NORWAY	Nordland: Rana. Ranen: Hauknaesfjeld I Mo Paa kalk 730m o.h.	5 viii 1894	B. Kaalaas	s.n.	O
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	NORWAY	Nordland, Andøy, Dverberg paa Andø I Vesteraalen. Str.	25 vii 1904	B. Kaalaas	s.n. M-7992	BG

Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* Lindb.	NORWAY	Dovre, Kongsvold	18 vii 73	Berndes & Engelhart	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Sør-Trøndelag: Oppdal, Kongsvold	viii 1883	C. Kaurin	27060	O
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	NORWAY	Sör-Tröndelag district, Dovrefjell National Park: Kongsvoll. On low calcareous cliff. Alt. c. 900m.	6 vii 1991	D.G. Long	19860	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	NORWAY	Prov. Oppland: Skjak District. Valley S of Bismo . Montane dwarf shrub heath; on turfy ledge on rock outcrop. Alt. c. 1061m.	26 vii 2002	D.G.Long, D. Shill, L. Soderstrom & K. Hassel	31421	E
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	NORWAY	Troms: Lyngen. Lyngen, vest for Guolasjavre.	10 viii 1893	E. Jørgensen	s.n.	O
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	NORWAY	Finnmark: Alta. Talvik.	15 vii 1888	E. Jørgensen	s.n.	O
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	NORWAY	Nordland, Fauske, [Nordlands amt, Salten,] Storstenfjeldet. Alt. 380m.	25 viii 1893	I. Hagen	s.n. M-7990	BG
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	NORWAY	Sør-trøndelag: Oppdal, Dovre: Kongsvold.	9 vii 1870.	J.E. Zetterstedt	s.n.	O
Clevea hyalina (Sommerf.) Lindb.	*Marchantia cruciata* L.	NORWAY	Nordland: Saltdal, Saltdalen. Udatert.		S.C. Sommerfelt	s.n. 23080	O
Clevea hyalina (Sommerf.) Lindb.	*Marchantia cruciata* L.	NORWAY	Nordland: Saltdal, Saltd.in latiris montium	v 1823	S.C. Sommerfelt	s.n. 23079	O
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	ROMANIA	Comit. Torda-Aranhos: in rupibus calcariis humidis Kóhasadék (Túr-hasadék) prope pagum Tordatúr, alt. cca 500 m.s.m. Substr. Tithon-calx.	16 x 1914	Gyórffy et Peterfi	s.n.	S, WU
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	RUSSIA	Caucasus centralis: distr. Tyrnyauz, mons Elbrus, loco Staryj Krugozor dicto, 2900 – 3100 m.s.m.	22 vi 1980	V. Vašák	s.n.	G, NY, BR
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SLOVAKIA	Slovakia merid., montes Malé. Karpaty: prope pagum Hradištê pod.Vrátnom, 260-280msm.	v 1937	J. Suza	202	S, B, BR, G, TNS
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* Lindbg.	SLOVAKIA	Slovakia occid., Malé Karpaty: in monte Holý vrch prope opid. Smolenice, solo calcareo., ca 330m.	4 v 1951	J. Šmarda	s.n.	S

Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SPAIN	Prov. Santander, Picos de Europa, in radice montis Peña Vieja (ca 1900m.s.m.), juxta stabulum venatorium regali;in terra nuda		H. Buch.	21.9	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SPAIN	Prov. Jaen: Sierra de Cazorla, slopes above Parador; Crevices of limestone rocks in pine forest. Alt. c. 1650 m.	15 iv 1980	D.G. Long	8931	E
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* Lindb.	SVALBARD	Spitsbergensis:	1868	S. Berggren	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Smrt.)Lindb.	SWEDEN	Gotland: Dacker par Bro.	30 v 1957.	Å. Hovgard	s.n.	TNS
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	SWEDEN	Gotland Suecia. Far Boge.	vii 1864	Cleve	s.n. BM00080061	BM
Clevea hyalina (Sommerf.) Lindb.	*Clevea suecica* Lindb.	SWEDEN	Uppland, Runmarö, Nore	5 v 1921	E. Almquist	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	SWEDEN	Earth-covered limestone pavement near Garde Stenkyrka parish, Gotland	14 vii 1960	E.Nyholm & A.C. Crundwell	s.n.	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina var. suecica* (Lindb.)K.Müll.	SWEDEN	Uppland. Par. Djurö, Runmarö, Sö,derby, in rupibus calcareis.	3 VI 1917	G. Samuelsson	s.n.	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SWEDEN	Torne Lappmark, Torneträskområdet, Tjasinnijaskatjåkko. Skifferbrant.	01 viii 1916	G. Samuelsson	s.n. M–7995	BG
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	SWEDEN	Torne Lappmark: Torneträsk-området, Tjasinn-jaskatjakko ca. 800 m.	1 viii 1916.	G. Samuelsson	s.n.	O
Clevea hyalina (Sommerf.) Lindb.	*Clevea suecica* Lindb.	SWEDEN	Gotland, Bro, vester om Dacker, alvarmark vid landsvägen mellan Visby och Bro	16 iii 1934	H. Persson	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Sauteria hyalina* (Sommerf.) Lindb.	SWEDEN	Öland, Resmo alvar,	9 vii 1867	J. E. Zetterstedt	s.n. B123515	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	SWEDEN	Sweden, Södermanland, Hölö, W of Skoogtorp, escarpment just E of Skräddartorpskarret. Bare soin on shelves in escarpment	21 x 2001	L. Hedenäs	s.n.	S
Clevea hyalina	*Clevea hyalina*	SWEDEN	Jämtland, Kalls, suljätten, södra sidan.	25 vi 1972	N. Hakelier	s.n.	S

(Sommerf.) Lindb.	(Sommerf.) Lindb.						
Clevea hyalina (Sommerf.) Lindb.	*Clevea suecica* Lindb.	SWEDEN	Gotland, Boge	vii 1864	P. J. Cleve	s.n. B123667	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea suecica* Lindb.	SWEDEN	Gotland, Visby, Kopparsvik, kalkhãll.	27 v 1928	P.A. Larsson	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	SWEDEN	Öland, Gärdby, sandfaltet	4 ix 1920	R. Herman	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea suecica* Lindb.	SWEDEN	Öland. Permulllis locis gramiosis et vere humibis prope Resmo.	1865	S. O. Lindberg	s.n. G00112928	G
Clevea hyalina (Sommerf.) Lindb.	*Clevea suecica* Lindb.	SWEDEN	Öland, prope Resmo	1865	S. O. Lindberg	s.n.	G
Clevea hyalina (Sommerf.) Lindb.	*Clevea suecica* Lindb.	SWEDEN	Öland, Vickleby	1865	S. O. Lindberg	s.n. G00112927	G
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.)	SWEDEN	Öland, Resmo	21 v 65	S. O. Lindberg	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	SWEDEN	Ins. Öland.	v 65	S.O.Lindberg	(12/68) BM00080060	BM
Clevea hyalina (Sommerf.) Lindb.	*Sauteria suecica* Lindb.	SWEDEN	Gotland, Boge.	vii 1864	P.T. Cleve	s.n.	JE, WU
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SWITZERLAND	Schweiz, Kanton Wallis: N Rhone, W Lötschbachtunnel, Walliser Felsensteppe zwischen Ober- und Niedergampel, in Felsnische 660m.	1 x 1989	B. Zimmer	1335	B
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SWITZERLAND	Canton Valais: Gemmi Pass, above Leukerbad, near cable car station. Limestone planteau; soil under rock overhang. Alt. c. 2290m.	10 viii 1994	D.G.Long.	25637	E
Clevea hyalina (Sommerf.) Lindb.	*Sauteria hyalina* (Sommerf.) Lindb.	SWITZERLAND	Valais: Dans les vignes pres de Martigny, Branson, 475 m.	12 iv 1887	Dr. H. Bernet	s.n.	G, S
Clevea hyalina	*Athalamia hyalina*	U.K.	Scotland: South Aberdeen: NE corrie of Craig	12 iv 1999	D.G. Long & G.P.	28312	E

(Sommerf.) Lindb.	(Sommerf.) S.Hatt.		Leek near Braemar. Steep rocky limestone hillside; on thin soil on rocks. Grid Ref. 37/187 932. v.– c.92. Alt. c. 510m.		Rothero.		
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.K.	South Aberdeenshire: east slope of Creag a’ Chlamhain near Crathie. Steep limestone slope with Betula; on eroding soil on scree slope. Grid. No. 2683 9549. v.-c. 92. Alt. c. 430m.	31 iii 2006.	D. G. Long et al.	35604	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.K.	South Aberdeen: north slope of Craig Leek, near Braemar. Crumbling limestone slope; soil ledges under limestone blocks. Grid. Ref. 37/185 933. v. –c. 92. Alt. c. 560 m.	1 ii 1999.	D. G. Long & G. P. Rothero	28272	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.K.	South Aberdeen: NE corrie of Craig Leek near Braemar. Small limestone dome; on thin soil crevices. Grid. Ref. 37/186 935. v.-c.92. Alt. c. 490 m.	1 ii 1999.	D.G. Long & G. P. Rothero.	28262	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.K.	S. Aberdeen: E cliffs of Craig Leek, Braemar. SE-facing slope; on crust on top of large flat rocks. Grid: v.-c. 92. Alt. c. 450 m.	15 v 2000	D.G. Long	29141	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.K.	South Aberdeen: Creag a’ Chlamhain, Crathie. South facing slope; large patch growing on bare, base-rich soilamongst broken slabby outcrop of Dalradian limestone. Grid. No. 268 955. v. –c. 92. Alt. c. 450m.	18 v 2005.	E. Holden	s.n.	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.K.	South of Aberdeen: Craig Leek SSSI. Braemar. On open soil on ledges of N-facing limestone crag. Grid: No. 188 932. v.-c. 92. Alt. c. 530m	24 i 1999.	G.P. Rothero	99020	E
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.K.	South Aberdeenshire: Creag a’ Chlamhain, Crathie. South-east facing, steep limestone slope; on exposed flat rocks. 433 m.	24 xi 2007	S. Rubasinghe & D.G.Long	01-07SR	E
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.K.	South Aberdeen: north slope of Craig Leek, near Braemar. On steep limestone rocks. 553 m.	18 iii 2009	S. Rubasinghe & D.G.Long	08-09SR	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	California, Mono County, very moist, shaded soil under boulder. In lodgepole pine forest and adjacent meadows in Hall Natural Area	3 vi 1977	D.H. Norris	48409	H

			near Stanford Research Area Sec 1, T1N, R24E. Elev. Ca. 10,000 ft.				
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	California: Siskiyou County, moist, rather shaded recess under boulder. In red fir, white fir and Jeffrey pine forest near Bear Lake, Sec. 34, T44N, R12W. Elev. 5000-6500 ft.	20 v 1973	D.H. Norris	24235	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	Trinity Co.: Salmon Trinity Alps Primitive Area. ~Trail to and above Long Gulch Lake. T39N R9W Sec. 29 & 32 in Klamath Nat. Forest. Northern slopes with red fir and mountain hemlocks. On soil over moist rock.	27 vii 1980	R. Spjut, D. Norris & J. Koponen.	6299	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	Vermont, Willoghby, Bluff & Overhang. Alt. 1500 f. On earth under limestone ledges.	16-18 vii 1913.	A. W. Evans & A. Lorenz	s.n. M–7999	BG
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	California, Siskiyou County, Very moist, diffusely lit rocks in seepage in red fir, white fir mountain hemlock and whitebark pine forest near Echo Lake north of Red Butte (about 5 air miles north of Seiad Valley. Secs. 7, T18N, R12 W. . Elev. Ca.5600 ft.	28 vii 1980	D. H. Norris.	57562	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	California: Moist, diffusely lit thin soil on outcrop. On large sandstone dome in redwood & Lithocarpus forest along Hwy. 9 ca. 1.5 miles north of Boulder Creek., Elev. Ca. 600 ft.	19 i 1980	D. H. Norris.	55589	H
Clevea hyalina (Sommerf.) Lindb.	*Peltolepis quadrata* (Saut.)Müll. Frib.	U.S.A.	Alaska. Philip Smith mountain quad: W. facing cliffs of Mt. Hulten Brooke Rang, alt. 1200m	29 vii 1982	D.G.Long	11213	E
Clevea hyalina (Sommerf.) Lindb.	*Peltolepis quadrata* (Saut.)Müll. Frib.	U.S.A.	Alaska, Philip Smith mountains Quad: W.ridge of Mt Steers, Brooks Range Alt. 1250m	30 vii 1982	D.G.Long	11276	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	California, Del Norte County, Moist, shaded cliff. In mixed conifer forest with open serpentine areas near Doctor Rock Sec. 1, T13N, R3E, . Elev. Ca. 5000 ft.	3 x 1977	D.H. Norris	50303	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	California: In Ribes-Amelanchier-Acer subalpine scrub above Terrace and Upper cliff	13 vi 1979	D.H. Norris	s.n.	H

			Lakes. Sec.31 T39N, R5W & Sec. 36, T39N R6W. Elev. Ca. 6200-6400ft. Moist diffusely lit thin soil on cliff.				
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	California, Siskiyou County, moist, diffusely lit cliff above lake on north-facing slopes with red fir and mountain hemlock along trail to long GulchLake and on cirque walls above lake southwest of Callahan. Secs. 29 & 32, T39NR9W. Elev. 6400-6800 ft.	25 vii 1980	D.H. Norris	57486	H
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	California: Modoc. Co.: In douglas fir, ponderosa pine and white fir forest on volcanic outcrop about 16 miles east of Medicine Lake on road to Beeler Reservoir. Moist, rather shaded soil under boulder.	23 iv 1972	D.H. Norris.	s.n.	H
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	Utah: Mount Baldy above Snowbird, east of Salt Lake City. On soil under boulders. Alt. c. 10,500 ft.	01viii 2004	J.D. Duckett	s.n.	E
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	Reno: On thin calcareous soil over talus (calcareous) and bases of east facing shaded bluffs, 3 m north of Reno, Houston Co.	14 v 1947.	R. M. Schuster	6752	G, H, S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Minnesota. Over moist, shaded sandstone bluff, on thin sandy soil, 1.5 miles S. of Brownsville, Houston Co.	9 v 1948	R.M Schuster	13472	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Minnesota: Over moist shaded thin sandy soil of sandstone bluff, 1.5 m. s. of Brownsville, Houston co. (a few male plants; female plants; pH 7.1)	9 v 1948	R.M Schuster	13473	F, S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Minnesota, On thin soil ledges 1 mile south of Lake City, Wabasha Co. ph 7.7	9 v 1948	R.M. Schuster	10068	H, S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Minnesota: On moist E. facing soil over sandstone bluffs, 1 mi.s. of Lake City, Wabasha Co. pH 7.5.	9 v 1948	R.M. Schuster	4761	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Minnesota; Over rather exposed moist soil near summit of bluff just south of Wacouta, Goodhue Co. Occurring with arhegonia; a few carpocephala.	13 v 1950.	R.M. Schuster	18004a.	E
Clevea hyalina	*Athalamia hyalina*	U.S.A.	Utah, Daggett Co. Spirit Lake, Uintah Mts.,	2 viii 1952.	S. Flowers	8157	NY

(Sommerf.) Lindb.	(Sommerf.) S.Hatt.		10300 ft. on wet soil under Talus. Ex Herb. Seville Flowers				
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	Colorado: Gunnison Co. north-east exposure, quartzite cliffs along East River just below Emerald Lake; spruce-fir subalpine forest, ca. 10,500 ft. alt.	13 vii–1 viii 1955.	W. A. Weber	s.n.	G
Clevea hyalina (Sommerf.) Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	Anacortes; Washington Park. Shaded earth in open terrace shelf.	24 iv 1982	W. B. Schofield & T. Mc Intosh	77296	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Alaska: East Oumalik and vicinity. In trundra W of camp and on cut bank silt cliffs across river, at loop.	3-10 vii 1951	W. C. Steere	15430	NY
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Custer. Humboldt Peak. Wet soil along streamlet. 12,000ft.	4 vii 1941	W. Kiener	10208	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Mt. Lady Washington (Colorado). Larimer Co. 12000 ft.	3 ix 1933	W. Kiener	1529	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Saguache county. Kit Carson Peak. Soil among rocks 13500 ft.	27 viii 1938	W. Kiener	6501	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Longs Peak. Larier Co. Streamlet among grasses. 11100ft.	1 vii 1941	W. Kiener	10203a	F
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Colarado: Park Co., on moist soil of trailside bank just below Wheeler Lake, head of Platte Gulch, north of Mt. Lincoln, 12300ft. Alt.	3 vii 1954	W.A. Weber	8844	FH
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Gunnison Co.: north-east exposure, quartzite cliffs along East River just below Emerald Lake; spruce-fir subalpine forest, ca. 10,500 ft. alt.	13 viii 1955	W.A. Weber	s.n.	O
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Colorado: Boulder Co.: Four Mile Canyon at Salina 6500ft.alt.	30 iv 1959	W.A.Weber	s.n.	S
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Alaska: about 80 miles South of Umiat; Kurupa Lake, Endicott Mountains, Brooks Range, 3000-5000ft. alt. tundra and limestone cliffs SE corner of lake.	20 viii 1974	Z. Iwatsuki	3335	NY
Clevea hyalina (Sommerf.) Lindb.	*Clevea hyalina* (Sommerf.) Lindb.	USA	Alaska. On limestone and calcite cliff with southern exposure, about 20 miles south of Chicken, Taylor Highway. Altitude approx. 2000 ft.	30 vi 1960	H.T. Shacklette	s.n.	S

Clevea hyalina (Sommerf.) Lindb.	—	USA	Alaska: Mt. Hayes Quadrangle, Mile 237 Richardson Highway, 2 miles north of Donnelly, 525 m, On a vertically exposed organic layer overlying on rock outcrop.	25 vii 1967	L.A. Viereck	8342	S
Clevea hyalina (Sommerf.) Lindb.	*Sauteria alpina* (Nees) Nees	YUGOSLAVIA	Jugoslawien: Slowenien, Juliske Alpi, 2000-2050m. Mangartska Scala, Kammgebiet alpine Stufe, auf Kalk.	4 ix 1977	R. Dull	s.n.	JE
Clevea hyalina (Sommerf.) Lindb. + *Sauteria alpina* (Nees) Nees	*Clevea hyalina* (Sommerf.) Lindb.	CANADA	Dumbell Bay, near Alert, Ellesemere I. Moist depression, dry Saxifraga caespitosa slope (over shale talus).	13 vi 1955	R.M Schuster	35080	F
Clevea hyalina (Sommerf.) Lindb. + *Sauteria alpina* (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREECE	On soil among sloping limestone slabs, Nome of Raklion: mt. DA slopes above the Nida plain. 1500m	01 x 1992	T.L. Blockeel	21/380	E
Clevea hyalina (Sommerf.) Lindb. + *Sauteria alpina* (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	Disko I. : Disko Fjord, Kuanerssuit, irrigated S. facing basaltic slopes	10 vii 1970	R.M Schuster & K. Damsholt	70-2146	F
Clevea hyalina (Sommerf.) Lindb. + *Sauteria alpina* (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	NORWAY	Nordland, Rana, Ranen: Hauknaesfjeld i Mo. Alt. 730 m. Paa Kalk.	05 viii 1894	B. Kaalaas	s.n. M– 988	BG
Clevea hyalina (Sommerf.) Lindb.+*Sauteria alpina* (Nees) Nees+*Peltolepis quadrata* (Saut.)Müll. Frib	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Sør-Trøndelag: Oppdal. Strax sǿndenfor Kongsvold ved Driva.	28 vii 1878	F.Kiǽr	27840	O
Clevea hyalina (Sommerf.)Lindb.	*Clevea crassa* Trabut. Fl. Alg.	ALGERIA	Gertoufa prés Tiaret		L. Trabut	s.n. BR-139	BR
Clevea hyalina (Sommerf.)Lindb.	*Athalamia trabutiana* (Steph.) S.Hatt.	ALGERIA	Algerien: Oran; Tiaret, auf Sandboden.	v 1907	L. Trabut	1177	NY
Clevea hyalina	*Athalamia hyalina*	CANADA	Alberta, Banff national Park: Johnson's	25 ix 1978	C.H. Vitt	24054	BR

(Sommerf.)Lindb.	(Sommerf.) S.Hatt.		Canyon. Elev.: 1500m. Along path to lower falls in Pinus contorta-Picea glauca-Pseudotsuga menziesii forest. Dry to mesic calcareous rock outcrops exposed along stream with abundant Homalothecium aeneum Tortula ruralis and Orthotrichum jamesianum.				
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	Head of Tanquary Fjord; 2.5 km S of base camp; 160 m.s.m.. Habitat: moist clay between rocks.	16 vii 1964	G. R. Brassard	1511	NY
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	Northwest Therritories: Bathurst Inlet, near Lodge	29 vii 1979	G. W. Scotter	28370	NY
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	Subalpine area ca. 15 km south of Virginia falls, South Nahanni River.	05 vii 1977	G. W. Scotter	24094	NY
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	CANADA	Mackenzie District; Heart Lake area; ca.1m NE of Mile 80 of the Mackenzie Hwy. Calcareous escarpment.	01 vii 1977	S. Talbot	T3001 -2	NY
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	On “Duck Pond” nunatak, about two miles from nunatak with permanent camp of “Snow Cornice” Project of Arctic Institute of North America, Seward Glacier near Mount Vancouver, St. Elias Mountains.	11 viii 1949	W. C. Steere	14404	NY
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	CHINA	Xinjiang Province: Fukang Co., south end of Lake Tian-chi, ca 1940 – 2000m. Dry and open slope in anrrow valley of Picea schrinckiana forest behind the forestry nursery site, underneath disturbed shrubs.		B.C.Tan	93-834	E, FH
Clevea hyalina (Sommerf.)Lindb.	*Sauteria alpina* (Nees) Nees	CROATIA	Dalmatia.	23 ix 1909	A Latzel	s.n.	FH
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	FINLAND	Lapponia enontekiensis: Kilpisjärvi, S-Saana. 800 m s.m. ad rpem dolomitic.	21 viii 1955	A.J. Huuskonen	31236	BR
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	FRANCE	Hautes-Pyrénées. Baréges. Rpit di Cp; di Tpirmalet. Fentes de rpcjers scjosteix. Alt. 1800 m.	8 août 1974	R.B. Pierrot	3410	BR
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	GEORGIA	Caucasus, Georgia: distr. Dusheti, in vicinitate pagi. Psanauri, in valle flauminis Belaia Aragva. Alt. 1200-1500 m.s.m.	31 vii 1982	V. Vašák	s.n.	BR

Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb. var suecica (Lindb.) Mull. + *Sauteria alpina* (Nees) Nees	GERMANY	Schneeberg, unterm Absturze des Kaiserstaines, 2000 m.	31 ix 1917	J. Baumgartner	s.n.	FH
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	HUNGARY	Comit. Fejér. In humosis inter saxa dolomite. Montis Kólik-hegy prope CSAKBERÉNY. Alt. cca 220. m.s.m.	9 vi 1936.	not known	258259	FH
Clevea hyalina (Sommerf.)Lindb.	*Athalamia trabutiana* (Steph.) S.Hatt.	IRAQ	Clevea trabutiana Hassar-iu Sakran, u vodopadu 2500m	7 vi 1901	R.Hadac	s.n.	UPS
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	MOROCCO	Bab-Taza, Jbel Bouhalla. Repisa de roca con suelo hasta 10cm, pinsapr con cedros. 1800 m.	16 vi 1997	M. J. Cano & R. M. Ros	10507	MUB
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	MOROCCO	Bab-Taza, Jbel Bouhalla, ascensión a pie desde 1595 m. Hendidiura de roca, abetal aclarado con algunos pinos salgareňos. 1700 m.	16 vi 1997	M. J. Cano & R. M. Ros	10504	MUB
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	MOROCCO	Bab-Taza, Jbel Bouhalla. Hendidura, pinsapar. 1700 m.	17 iii 1997	M. J. Cano, M. T. Gallego & R. M. Ros	10501	MUB
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	MOROCCO	Bab-Taza, ascension al Jbel Bouhalla, 1600 mm s.n.m. Habitat. Hendidura en roca a 2 cm de suelo, pinsapar.	16 vi 1997	M.J. Cano & R.M. Ros	s.n.	NY
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SPAIN	Sierra Nevada, Rio Dilar. Station: groupements des fissures de rochers clacires dolomitiques.	17 vii 1988.	J. Margot	44.887.	BR
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SPAIN	Albacete Province, Sierra del Calar del Mundo, Nacimiento del rio Mundo, 1000 m. Talud de tierra, proximidades cauce del rio, 30SH.	30 iii 2009	R. M. Ros & O. Werner	4856	MUB
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S.Hatt.	SPAIN	Albacete Province, Sierra del Calar del Mundo, Umbria de la Fuente de las Raigadas, 1400 m. Talud de tierra protegido en base de rocas, 30 SWH.	20 iii 2009	R. M. Ros & O. Werner	6701	MUB
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Smrft) Lindb. var.	SWEDEN	Uppland: par. Djurö, Runmarö, Söderby, in rupibus siccis calcareis.	3 vi 1917	G. Samuelsson	s.n.	NY

	suecia (Lindb.) K. Mull.						
Clevea hyalina (Sommerf.)Lindb.	*Clevea suecica* Lindb.	SWEDEN	Gotland: Visby	19 v 1908	K.Johanson	s.n.	UPS
Clevea hyalina (Sommerf.)Lindb.	*Clevea suecica* Lindb.	SWEDEN	Gotland: hallmark.	21 v 1908	K.Johanson	s.n.	UPS
Clevea hyalina (Sommerf.)Lindb.	*Clevea suecica* Lindb.	SWEDEN	Västergötland: Kinnekulle; Österplana hed, hällyta på over rodsten VSV om kyrkan.	20 v 1944	N. Abertson	s.n.	UPS
Clevea hyalina (Sommerf.)Lindb.	*Clevea suecica* Lindb.	SWEDEN	Gotland: Boge.	1864	P. S. Cleur	s.n.	UPS
Clevea hyalina (Sommerf.)Lindb.	*Clevea suecica* Lindb.	SWEDEN	Öl. Joisludi, Kalkated.	1 v 1945	S. Arnel	s.n.	UPS
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	SWITZERLAND	Sion, Valais, Suisse. Sous la Cathédrale de Valére. Le Terre siliceuse acide, vers 500 m.	21 vii 1956	J. De Sloover	3163	BR
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S. Hatt.	SWITZERLAND	Canton Vaud: North facing limestone valley; under damp boulder below snow patch. 2196 m.	27 vi 2008	Rubasinghe & D.G.Long	03-08SR	E
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S. Hatt.	SWITZERLAND	Canton Valais: Rocky alpine limestone slopes; on damp soil under boulders. 2306 m.	1 vii 2008	S. Rubasinghe & D.G.Long	04-08SR	E
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S. Hatt.	SWITZERLAND	Canton Valais: Rocky alpine limestone slopes; on damp soil under boulders. 2306 m.	1 vii 2008	S. Rubasinghe & D.G.Long	05-08SR	E
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S. Hatt.	SWITZERLAND	Canton Valais: Steep limestone slopes; under damp boulder near snow bed. 2196 m.	2 vii 2008	S. Rubasinghe & D.G.Long	14-08SR	E
Clevea hyalina (Sommerf.)Lindb.	*Athalamia hyalina* (Sommerf.) S. Hatt.	SWITZERLAND	Canton Valais: Limestone slope; under shady boulder. 2249 m.	3 vii 2008	S. Rubasinghe & D.G.Long	16-08SR	E
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Rich peaty soil in damp, shaded, shallow cave in embankment of Silver Dollar Lake Trail, high above Naylor Lake, alt. 11 300 ft., 10 miles SSW. Georgetown.	29 vii1977	F. J. Hermann	27972	NY
Clevea hyalina (Sommerf.)Lindb.	*Sauteria limbata* Austin	U.S.A.	California: near a lake on the trail to the white chief mine, 1100 ft. above mineral king. Sierra	6 viii 1891	F. V. Coville & F.M. Funston	1511	FH

			Nevada, Juare County Loal.				
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Minnesota. Over rather exposed moist soil near summit of bluff just south of Wacouta, Goodhue Co.	15 v 1950	R. M. Schuster.	18004a.	NY
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Colorado: Boulder Co.: Four mile Canyon at Salina 6500ft.alt.	30 iv 1959	W. A. Weber	B1331	NY
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	On vertical back of ravine, near river. Alaska: Meade River \post office (Coal mine), approximately 70miles south of Barrow	2-5 vii 1963	W. C. Steere.	63-44,	NY
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Alaska: On south-facing slope of ridge north of Umiat. Umiat and vicinity, Colville River in wet tundra and on ridges.	30 vi–6 vii 1974	W.C. Steere & Z. Iwatsuki	s.n.	NY
Clevea hyalina (Sommerf.)Lindb.	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Alaska: Umiat and vicinity, Colville River, in wet tundra and on ridges. South facing slope near oil well no. 2, 300 – 525, ft. alt.	1 vii 1974	W.C. Steere & Z. Iwatsuki	2207	NY
Clevea hyalina (Sommerf.)Lindb. + *Sauteria alpina* (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	Northwest Territories, District of Franklin, Bathurst Island, vicinity of base camp. 10 m w. of Goodsir I nlet. On silty soil in crevice, SW side of mound, polygmarrea 1.5 m NW of base camp.	11 vii 1974	N. G. Miller	7610	FH
Clevea hyalina (Sommerf.)Lindb.+Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	British Columbia. Shoulder of Pope's Peak, 6500ft. Wet earth.	July 3, 1913	G.G. Conklin & A.H. Brinkman	795	FH
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Clevea chinensis* Steph.	CHINA	China interior, Schen-si sept., Han-sun-Ku	x 1898	Giraldi	s.n. G00067325	G
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Clevea chinensis* Steph.	CHINA	China, Schensi in catena Lao-y-san	1898	Giraldi in herb. E. Levier 1850	s.n. G00112850	G
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Clevea chinensis* Steph.	CHINA	China, Schensi, Hansunfu	1898	Giraldi in herb. Levier 2511	s.n. G00112849	G
Clevea pusilla (Steph.) Rubasinghe	*Athalamia pusilla* Falconer	INDIA	Vorderindien, Dehradun 2000´	no date	R.S. Chopra	24	S

& D.G.Long							
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Gollaniella pusilla* Steph.	INDIA	Mussoorie (N.W. Himalaya) on roadside between Arnigadh and Khetwala, 5550 ft., Gollan s.n. in Bryotheca E. Levier 3867b	12 ix 1900	W. Gollan	s.n. G00067320	G
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Gollaniella pseudocaccula* Hnsp.	INDIA	Mussoorie (N. W. Himalaya). Arnigadh, earthy banks in Gov. Bot. Gardens, 5500ft.	14 x 1903	W. Gollan	s.n. G00067321	G
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Gollaniella pusilla* Steph.	INDIA	Mussoorie (N.W. Himalaya) Arnigadh Garden, 5500 f.	ix 1900	W. Gollan s.n.	G00069831	G
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Gollaniella pusilla* Steph.	INDIA	Mussoorie. Arnigadh botan. Gardens, earthy banks 5500	10 ix 1900	W. Gollan	s.n. G00069832	G
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*A. glauco-virens* Shimizu & Hatt. fo. *subsessili*s Shimizu & Hatt	JAPAN	Crevices of south facing exposed cliffs of clay-slate, phillite and chert, ca. 700m alt., at Kaminakao of Otaki, Chichibu Mts., Saitama County	3 ix 1953	D. Shimizu	s.n.	G
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*A. glauco-virens* Shimizu & Hatt. fo. *subsessili*s Shimizu & Hatt	JAPAN	Crevices of south-facing exposed cliffs of clay-slate, phillite and chert, ca. 700 m. alt., at Kaminakao of Otaki, Chichibu Mts., Saitama County	3 ix 1953	D. Shimizu	s.n.	H
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*A. glauco-virens* Shimizu & Hatt. fo. *subsessili*s Shimizu & Hatt	JAPAN	Crevices of south-facing exposed cliffs of clay-slate, phillite and chert, ca. 700 m alt., at Kaminakao of Otaki, Chichibu Mts., Saitama County	3 ix1953	D. Shimizu	B13522	S, B
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Gollaniella nana* Shimizu et Hatt.	JAPAN	Saitama Pref.: Chichibu Mts., Jumonji Pass, Ca 1700m.	26 viii 1952.	D. Shimizu.	52806	NICH
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Athalamia glauco-virens* Shimizu & Hatt.	JAPAN	Obi, Nichinan-Shi, Miyazaki-ken: Nagano-ken, Minamisaku-gun, Kita-aiki-mura, ca. 1060 m alt., on slate.	18 viii 1953	D. Shimizu.	52767	NICH
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*A.glauco-virens* Shimizu & Hatt. fo. *subsessili*s Shimizu & Hatt	JAPAN	Saitama-ken, Chichibu-gun, Otaki-mura, Kaminakano, ca 700 m alt., on rock.	3 ix 1953	D. Shimuzu	52755	NICH

Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*A.glauco-virens* Shimizu & Hatt. fo. *subsessilis* Shimizu & Hatt	JAPAN	Obi, Nichinan-Shi, Miyazaki-ken):Saitama-ken, Chichibu-gun, Otaki-mura, Kaminakao, ca 1700m alt., on rock	28 viii 1953	D. Shimuzu	52768	NICH
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Athalamia nana* (Hatt. et Shim.) Hatt. et. Shim.	JAPAN	1400m	10 viii 1956	T. Kodama	s.n.	TNS
Clevea pusilla (Steph.) Rubasinghe & D.G.Long	*Athalamia pusilla*	NEPAL	Namdu, ca. 1500 m.	iv 1963	K. Yoda	s.n.	TNS
Clevea pusilla (Steph.)Rubasinghe &D.G.Long	*Athalamia*	INDIA	Sikkim, W. District: Samiti Lake (Bungmoteng Chho), foot of Onglakthang Glacier. Grassy hillside with calcareous schist boulders; on shady soil under boulder. 4405 m.	23 vii 1992	D.G. Long	22838	E
Clevea pusilla (Steph.)Rubasinghe &D.G.Long	*Athalamia pusilla* (Steph.) Kashyap	INDIA	Dehra Dun (2000') United provinces India. On a shady wall.	viii 1930	R. S. Chopra	24	BM, JE, FH
Clevea pusilla (Steph.)Rubasinghe &D.G.Long	*Athalamia pusilla* (Steph.) Kashyap	INDIA	Dehra Dun 2000´ United provinces India. On a shady wall	viii 1930	R. S. Chopra	8054	W
Clevea pusilla (Steph.)Rubasinghe &D.G.Long	*Gollaniella pusilla Steph.*	INDIA	Mussoorie, Hill above Anigadh Gardens in dense shade under large boulders, 6000 ft.	6 x 1900.	W. Gollan	3848	BM
Clevea pusilla (Steph.)Rubasinghe &D.G.Long	*Gollaniella pusilla* Steph.	INDIA	Mussoorie; (N.W. Himalaya) Arnigadh Garndens, amongst Targionia, rare, 5500 ft.	ix 1900.	W. Gollan	3960	BM
Clevea pusilla (Steph.)Rubasinghe &D.G.Long	*A. glauco-virens* Shimizu & S.Hatt. fo. *subsessilis* Shimizu & S.Hatt	JAPAN	Crevices of south-facing exposed cliffs of clay-slate, phillite and chert, ca. 700 m alt., at Kaminakao of Otaki, Chichibu Mts., Saitama County	3 viii 1953	D. Shimizu	s.n.	B, W
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	—	not known	v 1894	Herb. Jack	s.n. G00112988	G
Clevea spathysii (Lindenb.) Müll.	*Clevea rousseliana* (Mont.) Steph.	MOROCCO	North Africa. Herb. Karl Müller (1956).	1913	not known	s.n.	S

Frib.						B123819	
Clevea spathysii (Lindenb.) Müll. Frib.	*Plagiochasma rousselianum* Mont.	ALGERIA	Mte. Environs d'Alger.	no date	L. Trabut	s.n. G00112963	G
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	ALGERIA	no locality, comm. Massalongo	no date	not known	s.n. G00112986	G
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia andina* (Spruce) S.Hatt.	ARGENTINA	Provincia Catamarca, Dep. Belén, Cumbres de Las Bayas, Quebrada del Totoral-Granadillas, 2300 m	26 i 1952	H. Sleumer	2147	B, S
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia andina* (Spruce) S.Hatt.	ARGENTINA	Catamarca: S. Ambato 900 msm, steiles schattiges Ufer mit Plagiochasma und Farnen.	5 vi 1976	O. Volk	6/0670.	JE
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia andina* (Spruce) S.Hatt.	BOLIVIA	Dep. La Paz, Prov. Pacajes, Estacion Jencial Campero, 3800 m	4 iii 1921	E. Asplund	52	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia andina* (Spruce) S.Hatt.	ECUADOR	Ambato in rupibus, aum Plagiochasmate tc. (=H74 Bauos). Spruce Herb.	no date	R. Spruce	s.n. EM445848	MANCH
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia andina* (Spruce) S.Hatt.	ECUADOR	Quito-Banos. 7000 m.	no date	R. Spruce.	s.n. G00112899	G
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia andina* (Spruce) S.Hatt.	ECUADOR	Pstura de Banos. Cum J 73. xH 74. Spruce Herb.	no date	not known	s.n. EM65002	MANCH
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia andina* (Spruce) S.Hatt.	ECUADOR	Puente de Banos. H73Spruce Herb.	no date	not known	s.n.	MANCH
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea hyalina* (Sommerf.) Lindb.	GEORGIA	Ossetia, Balka, Terek River	22 v 1881	V.F. Brotherus	s.n. G00112920	G
Clevea spathysii	*Clevea rousseliana*	GREECE	Crete 'Creta', Konnithades	4 iv 1921	G. Samuelsson	s.n.	S

(Lindenb.) Müll. Frib.	(Mont.) Steph.						
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	GREECE	Creta. Komithades. Från ett ex. i iksmuseet. Exemplaret av Jensen först bestämt till Fimbriaria Africana + Fossombronia caespiticiformis.	4 iv 1921	G. Samuelsson	s.n.	UPS
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea spathysii* (Lindenb.) Müll. Frib.	GREECE	Grekland: Rhodes, Philerimos, vid källan nedom acropolis	11 iii 1961	S. Arnell	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea spathysii* (Lindenb.) Müll. Frib.	GREECE	Rhodos, Philerimos.	15 iii 1961.	S. Arnell	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea spathysii* (Lindenb.) Müll. Frib.	GREECE	Rhodos, Philerimos.	9 iii 1961.	S. Arnell	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	ITALY	Insel Linasa, sudl v. Sizilien, Grotte dei Colombi	2 iii 1906.	S. Sommier	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	ITALY	Insula sic. Linosa (olim Aethusa) as parietes antri didi, “ Grotla dei Colombi”	2 iii 1906	S. Sommier	s.n.	BR
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	ITALY	Insula Linosa (olim Aethusa) inter sicilian et African. In rupibus, loco docto Giotta dei Colibi.	2 iii 1906.	S. Sommier	s.n.	FH
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	ITALY	Insula Linosa intis Sicilium et Africum. Grotta l dei Colombi	2 iii 1906.	S. Sommier	s.n.	WU
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	JORDAN	Kerak: Wadi Areva, Fenan; Fenan; Fahrt zum Wadi Rathje. 320m, zwischen Sandsteinen.	8 iii 1986	U. Bairele & H. Kürschner	86-223	B
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	JORDAN	Kerak: Wadi Areva, Fenan; Fenan; Fahrt zum Wadi Rathje. 320m, zwischen Sandsteinen.	8 iii 1986	U. Bairele & H. Kürschner	86-285	B
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	JORDAN	Prov. Amman: Wadi Heidean between Dhiban and Madaba. 400m, calcareous rocks.	1 iv 1980	W. Frey & H. Kürschner	80-54	B

Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia hyalina* (Sommerf.) S.Hatt.	MONGOLIA	Zentral-Aimak, östlicher Chentej auf Felsen am Sorgol-Gol, einem Bebenfluß des Kerulen	5 viii 1983	Juneck	s.n. JE-2676	JE
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	MOROCCO	Taderrast (Oued Massa) Souss.	no date	Gattefossé	s.n.	PC
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	MOROCCO	Ain Cheggag prés Fez fin	iv 1913	Mouret	s.n.	PC
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	NAMIBIA	Windhoek, Kalkfels-Überhang ex cult.	iv 1978	O. Volk	589	BM
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	NAMIBIA	Felsüberhänge, Glimmerschiefer, Gobabispad, WIN 70, pH.6.9	24 iii 1974.	O. Volk	904	BM
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	NAMIBIA	Farm Windhoek, schattige Felsüberhänge am Kuiseb, Glimmerschiefer.	1973	O. Volk	485	JE
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	NAMIBIA	10 km östlich Windhoek, Tälchen an der Straße nach Gobabeis, schattige Glimmer-schiefer-Uberhänge und Treppen, Boden sehr humos, dunkel, Staubboden.	1974	O. Volk	908	JE
Clevea spathysii (Lindenb.) Müll. Frib.	Athalamia spathysii (Lindenb.) S.Hatt.	NAMIBIA	S.W Africa (Namibia). Frauenstein, Glimmerschiefer schattige Uberhänge und Treppen über 1. Rivier.	3 iii 1974	O. Volk	861	JE
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	OMAN	Oman; Ayn Sih, Wadi al-Ayn, On rocks wet from cliff seepage. Alt. c. 465m.	19 iii 1982	M.D. Gallagher & P. R. Sichel	6399-37a	JE
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	OMAN	Ayn Sih, Wadi al-Ayn. On rocks wet from cliff seepage. Alt. c. 465 m.	19 iii 1982	M. D. Gallagher & P. R. Sichel	6399 – 37a	G
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	OMAN	Ayn Sih Alt. 465 m. In rocks wet from clif seepage.	19 iii 1982	M. D. Gallagher & P. R. Sichel	6399-37a	E
Clevea spathysii (Lindenb.) Müll.	*Athalamia spathysii*	OMAN	Sultanate Of Oman: Ayn Sih, Wadi al-Ayn, On rocks wet from cliff seepage. Alt. c. 465	19 iii 1982.	M. D. Gallagher & P. R. Sichel	6399-37a	E

Frib.	(Lindenb.) S.Hatt.		m.				
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea andina* (Spruce) S. Hatt.	PERU	Dept. Cuzco, Prov. Urubamba, Chincheros; courtyard of informant, community of Cuper. 3800 m.	5 ii 1982	S. King, E. Franquemont, C. Franquemont & C. Sperling	209	F
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea roussseliana* (Mont.) Steph.	PORTUGAL	San Sorge, above Uzelina.	2 viii 1965	A.E. Smooker	11	BM
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	PORTUGAL	Algarve Ribeira das Merces, Fonte Filipe nr. Amendoeira. Uncer rock overhang by stream in wooded valley. Alt. c. 400 m.	25 iii 1989.	D.G. Long.	15873	E
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	SPAIN	Gran Canaria, prope Tafira, ca 400 m.s.m.	30 iii 1901	J. Bornmüller	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	SPAIN	Gran Canaria, San Mateo, in rupestribus, ca 900 m.s.m.	3 iv 1901	J. Bornmüller	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	SPAIN	Gran-Canaria, Tafira, 400 m	1 iv 1901	J. Bornmüller	s.n.	G, S, B
Clevea spathysii (Lindenb.) Müll. Frib.	Clevea spathysii (Lindenb.) Müll. Frib.	SPAIN	Prov. Murcia, El Valle (Albereia de Toires): N. facing slope, under rock over hang. 142 m.	08 iii 2009	S. Rubasinghe & D.G.Long	01-09SR	E
Clevea spathysii (Lindenb.) Müll. Frib.	Clevea spathysii (Lindenb.) Müll. Frib.	SPAIN	Prov. Almeria, Sierra Cabrera: south side of Catijo Grende, noth-facing slopes, under moist shady rock sledges. 246 - 1600 m.	10 iii 2009	S. Rubasinghe & D.G.Long	02-09SR	E
Clevea spathysii (Lindenb.) Müll. Frib.	Clevea spathysii (Lindenb.) Müll. Frib.	SPAIN	Prov. Almeria, South of Rodalquilar (Ca bo de gata). under shady boulder. 242 m.	11 iii 2009	S. Rubasinghe & D.G.Long	03-09SR	E
Clevea spathysii (Lindenb.) Müll. Frib.	Clevea spathysii (Lindenb.) Müll. Frib.	SPAIN	Prov. Almeria, South of Rodalquilar (Ca bo de gata). under shady boulder. 91 m.	11 iii 2009	S. Rubasinghe & D.G.Long	04-09SR	E
Clevea spathysii (Lindenb.) Müll. Frib.	Clevea spathysii (Lindenb.) Müll. Frib.	SPAIN	Prov. Almeria, Barranco de Requera: under boulders near stream. 252 m.	12 iii 2009	S. Rubasinghe & D.G.Long	05-09SR	E
Clevea spathysii	Clevea spathysii	SPAIN	Prov. Almeria, Barranco de Requera: under	12 iii 2009	S. Rubasinghe &	06-09SR	E

(Lindenb.) Müll. Frib.	(Lindenb.) Müll. Frib.		boulders near stream. 252 m.		D.G.Long		
Clevea spathysii (Lindenb.) Müll. Frib.	Clevea spathysii (Lindenb.) Müll. Frib.	SPAIN	Prov. Almeria, Barranco de Requera:noth facing rock overhangs. 70 m.	13 iii 2009	S. Rubasinghe & D.G.Long	07-09SR	E
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	SPAIN	Tenerife, Puerto de la Cruz, el barranco,	17 iii 1958	S. Arnell	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea spathysii* (Lindenb.) Müll. Frib.	SPAIN	Gran Canaria, La Calzada	8 iii 1959	S. Arnell	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea spathysii* (Lindenb.) Müll. Frib.	SPAIN	Tenerife, Puerto de la Cruz, el barranco below Hotel Tauro,	27 iii 1958	S.Arnell	s.n.	S
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	SPAIN	Mallorca, La Calobra, torrent de Pareis. Creux d'une balme.	9 iv 1965	not known	4126	BR
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	SPAIN	Tenerife: Las Mercedes, ad rupes humidas secus “caharcdulam”. Lat. Sept. . Alt. supra mare 600m.	21 v 1908	not known	s.n.	O
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea hyalina* (Sommerf.) Lindb.	U.S.A.	Mexico: Vicinity of Santa Fe: Arroye Hondo. 2200m	12 x 1936	B. G. Arséne	23283	F
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia pygmaea* Schust.	U.S.A.	Texas: Big Bend National Park: Chisos Mts., below and above Boot Springs.	24 xii 1981	R.M Schuster	81-1251a	F
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	YEMEN	Nordjemen: bei Suq-ad Dabab SE Taizz. 1200m, Felsausbisse 93-1030	27 viii 1993	A.N. Al-Gigri & H. Kürschner	s.n.	B
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	YEMEN	Yemen Arab Republic: in shade of rock on a shrubby hill between Mefhek and Ban Mansour c. 20 km ESE of Ibb, 1500m.	22 i 1978	J.R.I. Wood	2187	JE, E
Clevea spathysii (Lindenb.) Müll. Frib.	*Athalamia spathysii* (Lindenb.) S.Hatt.	ZIMBABWE	S.W. Matopos. Silorzwe. Under overhaning Granite Rocks on Kopje.	6 i 1963	H. Wild	5942	BM
Clevea spathysii	*Clevea rousseliana*	ALGERIA	not known.		Herb Montagne	s.n.	G

(Lindenb.) Müll. Frib.	(Mont.) Steph.					G00112978	
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	ALGERIA	Ad rupes opacas prope Birmandreis, ditionis Algeriensis.	ii 1866	Major Paris	s.n.	BR, G
Clevea spathysii (Lindenb.) Müll. Frib.	*Plagiochasma rousselianum* Mont.	ALGERIA	not known.		Montagne	543 G00112980	G
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	ALGERIA	not known.		Roussel	s.n. G00112976	G
Clevea spathysii (Lindenb.) Müll. Frib.	*Plagiochasma rousselianum* Mont.	ALGERIA	Mte.Environs d'Alger.		Trabut	s.n.	BR, G
Clevea spathysii (Lindenb.) Müll. Frib.	*Plagiochasma rousselianum* Mont.	ALGERIA	In locis umbraisn montis Thoudjoush propi Algerian.	1836-1837	Feb&main,	s.n.	BR
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea andina* Spruce	ECUADOR	Andes, Quito, Baños. 7000m	no date	R. Spruce	s.n.	G
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea rousseliana* (Mont.) Steph.	ITALY	Kultiviert im Botanischen Garten zu Prag, aus Material von Sizilien; Palermo, 1901 mit E. Levier	18 i 1902	V. Schiffner	1176	E
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea robusta* Steph.	CHILE	Osorno: Puyehue; in a shelf in the rocks near the lower course of Rio Cjaaleufu? 350 m.s.m.	16 i 1947	B. Sparre	2213	S, JE
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea robusta* Steph.	CHILE	Laguna de Aculeo, en quebrada sombria, sue lo húmedo (al N. de la Laguna)	1 v 1954	Liquenes	3918	F
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea robusta* Steph.	CHILE	Valparaiso in humo		P. Dusén	11/796	G
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea spathysii* (Lindenb.) Müll. Frib.	SPAIN	Gran Canaria, La Calzada, lodrät skuggig berhäll (grotta). .	1959	S. Arnell	s.n.	UPS

Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea spathysii* (Lindenb.) Müll. Frib.	SPAIN	Tenerife: Puerto de la Cruz. El barranco. Stenblock.	17 iii 1958	S. Arnell	s.n.	UPS
Clevea spathysii (Lindenb.) Müll. Frib.	*Clevea spathysii* (Lindenb.) Müll. Frib.	SPAIN	Gran Canaria: La Calzada. el barranco.	8 iii 1959.	S. Arnell	s.n.	UPS
Clevea spathysii (Lindenb.) Müll. Frib.	*Sauteria limbata* Austin	USA	Under wet rocks, California.	17 iii 1834.	Bolander	K4587	MANCH
Peltolepis quadrata (Saut.) Müll. Frib	*Peltolepis quadrata (Saut.) Müll. Frib*	SWITZERLAND	Canton Valais: Rocky limestone slope; under huge shady boulder near snow bed. 2196 m.	2 vii 2008	S. Rubasinghe & D.G.Long	08-08SR	E
Peltolepis quadrata (Saut.) Müll. Frib	*Peltolepis quadrata (Saut.) Müll. Frib*	SWITZERLAND	Canton Valais: Rocky limestone slope; under shady boulder near snow bed. 2196 m.	2 vii 2008	S. Rubasinghe & D.G.Long	09-08SR	E
Peltolepis quadrata (Saut.) Müll. Frib	*Peltolepis quadrata (Saut.) Müll. Frib*	SWITZERLAND	Canton Valais: Steep limestone slopes; under rock overhang by snow patch. 2162 m.	2 vii 2008	S. Rubasinghe & D.G.Long	10-08SR	E
Peltolepis quadrata (Saut.) Müll. Frib	*Peltolepis quadrata (Saut.) Müll. Frib*	SWITZERLAND	Canton Valais: Steep limestone slopes; under damp boulder near snow bed. 2196 m.	2 vii 2008	S. Rubasinghe & D.G.Long	12-08SR	E
Peltolepis quadrata (Saut.) Müll. Frib	*Peltolepis quadrata (Saut.) Müll. Frib*	SWITZERLAND	Canton Valais: Limestone terraces with pavement; in deep fissure. 2279 m.	3 vii 2008	S. Rubasinghe & D.G.Long	15-08SR	E
Peltolepis quadrata (Saut.) Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	SWITZERLAND	Canton Valais: Rocky limestone slopes; in deep crevice under boulders. 2210 m.	1 vii 2008	S. Rubasinghe & D.G.Long	07-08SR	E
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	AUSTRIA	Nord-Tirol:Wattens-Tal; bei der Gotzenser Alpe und ober der Lizum-Alpe gegen das "Halsl" zerstreut zwischen Gras langs der Wasserlaufe. Kalk-1600 bis 1800m	ix 1902 & 1903	H. Handel-Mazzetti	1181	E, B, G
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	AUSTRIA	Nord-Tirol: Ober der Lirum? Bei. 1900m	25 ix 1902	H. Handel-Mazzetti	258924	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	AUSTRIA	Nord-Tirol: bei der Götzenser Alpe und ober der Lizum-Alpe gegen das "Halsl" zerstreut zwischen Gras längs der Wasserläufe. 1600 -	ix 1902 & 1903	H. Handel-Mazzetti	1181	S

			1800 m.				
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	AUSTRIA	Nord-Tirol: Wattens; bei der Götzenser Alpe und ober der Lizum-alpe gegen das "Halsl" zerstreut swischen Gras Längs der Wasserläufe Kalk. 1600 bis	ix 1902-1903	H. Handel-Mazzetti	1080	W
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) K.Müll. Frib.	AUSTRIA	Oberösterreich: Warschengegg-Gebirge in einer Schneegrube 2100m	20 ix1932	J. Baumgartner	8357	W
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	AUSTRIA	Südlich: Südlich unter der Neualmscharte in den Niedere Tauern. 2300 m. auf sandig-lehmiger Ubterlage.	24 viii 1930	J. Froehlich	s.n.	S
Peltolepis quadrata (Saut.)Müll. Frib.	*Sauteria quadrata* Saut.	AUSTRIA	Salzburg, Untersberg,		Sauter	s.n. 6084	W
Peltolepis quadrata (Saut.)Müll. Frib.	Sauteria quadrata Saut.	AUSTRIA	Feljenfejjel des Untersbergs 6000'	1839	Sauter	s.n. 2008-1126	W
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	AUSTRIA	Steiermark: Totes gebirge Loilesberger	viii 1902	Schiffner	258922	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	AUSTRIA	Tirol:Vennakal am Breuner.	viii 1908	Wellstein	258923	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	BOSNIA & HERZEGOVINA	Walder am Fusse des Grijal, 1400m	16 vii 1904	J. Stadlmann & F. Faltis	258931	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	FINLAND	NW - Le, Kilpisjärvi, SW-Saana, in clivo rupestri, in terra humosa, 650 - 700 m.	14 vii 1958	Laila & H. Roivainene	s.n.	H
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	FRANCE	Isére, Les Deux Alpes, vallée de la Selle, au-dessus du refuge de la Fée, partie Sud de la Selle d'En Haut,. 2300 m. paroi siliceuse ruisselante sous une cascade	7 vii 1981	J. L. Sloover	34.503	BR
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	GERMANY	Reichenhall, Bayern.	1909	not known	258919	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	GREENLAND	W5, Disko island, Disko Fjord, near head of Kangikerklak Fjord. Damp soil by waterfall in basalt ravine Alt. 20m	18 viii 1985	D.G.Long	13198	E

Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	GREENLAND	W5: Disko island, Disko Fjord, Ikineq, Kaunerssauit Suvdlaut. Damp bank in ravine on E-facing basalt cliffs. Alt. 40m	18 viii 1985	D.G.Long	13223	E
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	HUNGARY	Comit. Bresso, in valle Malaiest, montis Bucsecs	1 ix 1911	A de Degen	258928	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.)Müll. Frib.	ICELAND	Northeast iceland: Myvatn region: on cliffs, peninsula on E side of lake.	6 vii 1964	W. C. Steere	64-53	NY
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	ITALY	Standort: In Schneegruben auf dem Dürrenstein bei Lunz, Nied. Oest. 1600 m.	28 ix 1930	H. Hans	s.n.	B
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.)Müll. Frib.	JAPAN	Honshu, Nagano-ken, Ina-shi Mt. Senjo, Shinyabusawa pass; ca. 2300 m alt., on wet rock (conglomerate).	14 viii 2008	T. Katagiri	1174	HIRO
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Troms: Storfjord. Skibotn I Lyngen, I lierne ovenfor Skibotngaardene ca. 100m	31 vii 1916	B. Kaalaas	27079	O
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	NORWAY	Nord-Nordland: Helgl. Dunderlandsdalen, Östfjeld	27 vii 1870	Blytt & Arnell	s.n.	UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) K.Müll. Frib.	NORWAY	Oppland District, Jotunheimen: limestone valley with cavers SW of Bovertun. On wet shady rock cleft on calcareous cliffs. Alt. c. 950m	11 vii 1991	D.G .Long	20001	E
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Finnmark:Alta. Talvik, Vasbotnfjeld.	17 viii 1888	E .Jørgensen	27091	O
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Troms: Nordreisa. Reisen,I tvaerdalen nord for Jertafjeld Paa skifergrus	29 vii 1893	E.Jørgensen	27077	O
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	NORWAY	Troms: Tromsö par., Malanger, Haugefjeld i klippspringor i videregionen	18 vii 1891	H. W. Arnell	s.n. B-45883	UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Hedmark: Tynset. Tønset, Tonnfossen. 650m o.h.	30 vii 1910	I. Hagen det. B. Kaalaas	27054	O
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Sondre Trondhjems amt, Opdal. 700m	17 vii 1904	J.H.	258917	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Nordland amt, Salten 300m.	21 viii 1893	J.H.	258918	FH

Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Baevertun, in Felsritzen 1000m	26 viii 1900	K. Loitlesberger	2008-01164	W
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Nordland: Saltdal . Skeiti-axlen, Saltdalen 500m.	12 viii 1889	R.E. Fritz	O27069	O
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	NORWAY	Sør-Trøndelag: Dovre: Konsvold, reg. betul., ad ca tarrhactas parvas rup. Micac. Hic illic, ubique parce UTM grid NQ2	vii 1882.	R. Fritz & S.O.Lindberg	s.n.	E
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis var. angustifrons* Lindb.	NORWAY	Sǿr-Trǿmdelag. Dovre: “Kongsvold, reg. Betul., ad catarrhactas parvas up. Micac hic illic ubique parce” (Atl. Fl. Eur. UTM grid NQ2).	vii 1882.	R. Fritz & S.O.Lindberg	s.n.	JE, S
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	NORWAY	Sør-Trøndelag: Dovre: Konsvold, reg. betul., ad ca tarrhactas parvas rup. Micac. Hic illic, ubique parce UTM grid NQ2	vii 1882.	R. Fritz & S.O.Lindberg	1996-00190	W
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	NORWAY	Sør-Trøndelag: Knudshoe, reg., betul, -alp. (Atl. Fl. Eur. UTM grid NQ2)	vii 1882.	S.O. Lindberg	243	E, G, S
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	POLAND	Tatry, w górnej dolinie Miętusiej w kotle zw. Świstówka, poniźej dol. Mulowej, bardzo obficie (podobnie jak w innych miejscach na wapieniach Tatr) w wysokości okolo 1500 m.	25 viii 1910	Z. M. Raciborski	4	B, FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	POLAND	Tatra Plonica. In rupestribus humosis calcareis pedis montis Wlk. Turnia in valle Dolina Malej Laki. 1300 - 1500 m. Herbarium Dr.-IS A. Boros.	24 vi 1959	not known	s.n.	B
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis (Lindb.) var. sibirica*	RUSSIA	Sibiria, Jenisei, Dudinka	2 viii 1876	H. W. Arnell	s.n.	S
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis var sibirica*	RUSSIA	Krasnoyarsk: Sibiria, Jenisei, Dudinka.	2 viii 1876	H. W. Arnell	s.n. B-45896	UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis (Lindb.) var. sibirica*	RUSSIA	Sibiria, Jenisei, Dudinka	2 viii 1876	H. W. Arnell	s.n. BM000962731	BM
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	RUSSIA	Krasnoyarsk: Sibirien, Jenisei, 15 verst V om Dudinka.	27 vii 1876	H. W. Arnell	n.s.	UPS

Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	RUSSIA	Siberia, Jenisei	not known	H.W. Arnell	s.n. BM000962736	BM
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	SLOVAKIA	Presovský: Bielské Tatry: In saxis prope Široké pole.(1832 m) 1650 m.	23 viii 1951	J. Smarda	n.s.	UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	SLOVAKIA	Bielské Tatry: In saxis calcareis prope široké pole (1832 m). 1650 m.	28 viii 1951	J. Šmarda	s.n.	S
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	SLOVAKIA	Beilske Tatry: In saxis calcareis prope Siroke pole (1832m) ca. 1650m	23 viii 1951	J. Šmarda	5939	W
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	SWEDEN	Lule Lappmark: Jokkmokk par., regio Sarjekensis, Unna Riddavaare.	9 viii 1902	C. Jensen & H. W. Arnell		UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis sibirica* (Lindb.) Lindb.	SWEDEN	Lule Lappmark, Sarekgebiet; am Bache Stora Rissaböck nördlich von Kvickjoch, auf vom Schneewasser durchtränktem Humus in der Weidenregion.	9 viii 1902	H. W. Arnell & C. Jensen	1182	B
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	SWEDEN	Härjedalen: Storsjö par., Skarsjäll, SV-branten av Toppen "1483". 1320 m.	22 viii 1950	O. Mårtensson	s.n. B-45803	UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	SWEDEN	Lule Lappmark: Jokkmokk par., Virikaureområdet, Arasvaer: liten V-brant. 800 m.	18 vii 1946	O. Mårtensson	s.n. B-45831	UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Sauteria alpina* (Nees) Nees	SWEDEN	Jämtland: Åre par., Hadnölforsen. På klippor.	1850	R. Hartman	s.n. B-45812	UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.) Lindb.	SWEDEN	Torne Lappmark: Jukkasjärvi par., Torneträsk-området, Kopparåsen.	viii 1954	S. Arnell & O.Mårtensson	s.n. s.n. B-45842	UPS
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	SWITZERLAND	Gemmi.	1905	C.Meylan	258925	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	SWITZERLAND	Gemmi. 2320m.	ix 1905	C.Meylan	258930	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	SWITZERLAND	Canton Valais: Gemmi, E-facing slopes N of Daubensee. Steep limestone slopes; under rock overhang by snow patch. 2196 m.	2 vii 2008	D.G.Long	37975	E

Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.)Müll. Frib.	SWITZERLAND	Canton Valais: Gemmi, N-facing slopes at Gemmipass. Limestone terraces with pavement; in deep fissure. 2271 m.	3 vii 2008	D.G.Long	37983	E
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.) Müll. Frib.	SWITZERLAND	Canton Valais: Gemmi, below Seestutz, N end of Daubensee. N-facing limestone slope; in deep crevice under limestone boulder. 2209 m.	1 vii 2008	D.G.Long	37949	E
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	SWITZERLAND	2000 m.	x 1933	Maylan	s.n.	S
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	SWITZERLAND	Canton Bern, Unterhalb des Tschingel gletscher, 1950m	21 viii 1905	P. Culman	258929	FH
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	SWITZERLAND	Helvetia, Bern Faulhorn, humicola e. lapides skiophila, c. Fimbriaria. 2300m.	viii 1906	P. Culmann	472	FH, O
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis grandis* (Lindb.)Lindb.	SWITZERLAND	Helvetia, Bern, Faulborn, humicola i. lapides, skiophila c. Frimbriaria, 2300m,	VIII 1906	P.Culmann	10244	W
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.)Müll. Frib.	USA, ALASKA	East Oumalik and vicinity, east facing slope, near lake.	14 viii 1952	G. H. Ward	1427	NY
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis*	USA, ALASKA	Driftwood camp, near headwaters of the Utukok River, north slope of De Long Mountains, Brooks Range.	4-16 viii 1951	W. C. Steere	16754	NY
Peltolepis quadrata (Saut.)Müll. Frib.	*Peltolepis quadrata* (Saut.)Müll. Frib.	USA, ALASKA	Gubic and vicinity, near the confluence of the Chandler and Coville Rivers.	22-25 vii 1951	W. C. Steere	16190	NY
Peltolepis quadrata (Saut.)Müll. Frib. + *Clevea hyalina* (Sommerf.) Lindb.	*Peltolepis quadrata* (Saut.) Müll. Frib.	NORWAY	Prov. Sogn og fjordane: Laerdal District, Eldrevatn.Alt. 1173m	23 vii 2002	D.G. Long, D. Schill, L. Soderstrom & K. Hassel	31360	E
Peltolepis quadrata (Saut.)Müll. Frib. +Sauteria alpina (Nees) Nees	*Peltolepis grandis* (Lindb.)Lindb.	USA, ALASKA	Are between Mt. Arga and Smith Lakes, just west of Etivluk River, Endicott Mountains, Brooks Range. 2000 ft.	11-18 vii 1952	W. C. Steere	18053	NY
Sauteria alpina (Nees) Nees	*Sauteria alpina (Nees) Nees*	SWITZERLAND	Canton Valais: Rocky limestone slopes; on damp soil under boulders. 2296 m.	1 vii 2008	S. Rubasinghe & D.G.Long	06-08SR	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWITZERLAND	Canton Valais: Steep limestone slopes; damp crevices of limestone cliff. 2199 m.	2 vii 2008	S. Rubasinghe & D.G.Long	11-08SR	E

Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWITZERLAND	Canton Valais: Steep limestone slopes; under damp boulder near snow bed. 2196 m.	2 vii 2008	Rubasinghe & D.G.Long	13-08SR	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	—	not known	14 viii 1870	Juratzka	2008-1145	W
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWEDEN	Lappland	viii 1856	S.O. Lindberg	s.n. BM000962728	BM
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	ALASKA	Arctic Coast District, Peters Lake area.	23 vii 1960	W. C. Steere, O.Mårtensson & K.A. Holmen	19636	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	AUSTRIA	Carinthia: Völkermarkt, Bleiburg, Petzen, east of Kniepssattel. In calcareous rock crevice. 2016 m.	24 vii 2003	D. Schill, H. Köckinger & U. Müller	86	E
Sauteria alpina (Nees) Nees	Sauteria alpina (Nees) Nees	AUSTRIA	Radstadtertauern, in 5000' Hohe. Rabenh. Handb. II. 3. p. 10. Lunularia alpina Bischoff in Nov. Act. XVII. 2. T. 67. F. 22-28.(143)		Dr.Sauter	s.n. BM000962729	BM
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	AUSTRIA	Nord-Tirol: Wattental; auf nackter Erde, besonders in Felsritzen in der Nähe der Wasserläufe bei der Götzen ser-und oberhalb der Lizum Alpe Kalk. Ca. 1600 bis 1800m	ix 1902	H. Handel-Mazzetti	s.n.	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	AUSTRIA	Nord-Tirol: Im Martarthal bei Gschnitz in erdigen Felsritren langs der Wasserlanges. Kalk. Ca. 2200m	9 ix 1902	H. Handel-Mazzetti	s.n.	WU
Sauteria alpina (Nees) Nees	Sauteria alpina (Nees) Nees	AUSTRIA	Conf. Rabenh. Hep. Eur. Exsicc. N. 67, 542 ybd bi, 347. Gesammelt auf Erde längs einer feuchten Kalkwand am Grunde der Serloswände in Tirol auf der Waldrast-Alpe (5400 Fuss hoch)	not known	Fr. Arnold	542	W
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Ness	AUSTRIA	Kalkspitz bei Schladming. 2450 m.	21 viii 1877	J. Breidler	s.n. 2008-01152	W
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	AUSTRIA	Tirol: Gschnitztal; am Padster bei Trins, in Felsspalten (Kalk) in der Nähe des Baches. 1700 – 2000m.	viii 1902.	R.v. Wettstein & V. Patzelt	s.n.	WU
Sauteria alpina	*Sauteria alpina*	AUSTRIA	Tirol: Gschniztal; am Padaster bei Trins, in	xiii 1902	Wettstein & V.	1070	E, W

(Nees) Nees	(Nees) Nees		Felsspalten (Kalk) in der Nähe des Baches 1700-200m		Patzelt		
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.)Lindb.	CANADA	Firth River Basin, near mouth of Mancha Creek. Peaty Bank of Firth River near Mancha Creek.	9 viii 1958	A. J. Sharp	MC-58185	NY
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.)Lindb.	CANADA	Wet Calcareous gravelly tundra. Base Camp, 720 05´ N, 940 10´W, Somerset I.	23 vii 1958	D. B. O. Savile	3595	NY
Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	CANADA	Northwest Therritories: District of Franklin, Axel Heiberg Island	21 vii 1980	G.W. Scotter	45598	NY
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.)Lindb.	CANADA	On soil over calcareous rock, near mouth of Ram Creek. Deadmen Valley, South Nahanni River	11 vii 1976	W. C. Steere	76-492	NY
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.) Lindb.	FINLAND	Le: Valtijoki, Gaitkejavre.	03 viii 1966	A.J. Huuskonen	s.n.	H
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.) Lindb.	FINLAND	Lapponia enontekiensis: Guenjarvaarri, Kalkkinokka 10000 m.s.m. ad rupem calcaream una c. Blepharestoma var. brevirete.	12 viii 1966	A.J.Huuskonen	1072	H
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	FINLAND	Lapponia enontekiensis, Naturpark Malla am NW-Ende des Kilpisjärvi, NE-Hang des Pikku-Malla, auf Erde in einer schattig-feuchten Felsspalte einer Dolomitwand, zus. Mit Jung. Polaris 650 m.	31 viii 1990	H.Köckinger	90-524	H
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	FRANCE	Isére, Les Deux Alpes, vallée de la Selle, au-dessus du refuge de la Fée, partie Sud de la Selle d'En Haut,. 2300 m. paroi siliceuse ruisselante sous une cascade	7 vii 1981	J. L. Sloover	34.503	BR
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	GERMANY	Thuringia, Alter Stolberg, Windehäuser Holz.	4 viii 1902	F. Quelle	s.n.	B
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	GREENLAND	W5, Disko island, river E of Arotic Station, Godhavn. Under large boulder by basalt cliffs. Alt. 50m	17 viii 1985.	D.G.Long.	13130	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	GREENLAND	W5, Disko island, Disko Fjord, near head of Kangikerdlak Fjord. Damp soil by waterfall in basalt ravine. 20m	18 viii 1985	D.G.Long.	13197	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	GREENLAND	W5: Disko Island river E of Arctic Station, Godhavn. Under large boulder by basalt cliffs.	17 viii 1985.	D.G.Long.	13130	JE

			Alt.c.50m.				
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	GREENLAND	Heilprin Land, Brönlund Fjord. 20m. Moist, sandy soil near river.	1 viii 1947	K. Holmen	197	UPS
Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.)S.Hatt.	GREENLAND	Thallose hepatic. Sheltered bank W. side of delta river S. end of Kuhn.	12 viiI 1990	R.W.M. Corner	s.n.	E
Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	GREENLAND	West Greenland: Nửgssuaq, west end Nửgssuaq Peninsula	4 vii 1962	W. C. Steere.	62 – 449	TNS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	HUNGARY	Comit. Szepes. Tatra Magna. In rupestribus calcareis 'Faix tisztas'supra 'Drechslerhauschen' montium Meszhegyseg. Alt. cca. 1500-1600 msm	11 ix 1940	not known	s.n.	O
Sauteria alpina (Nees) Nees	*Sauteria alpina* Nees	ITALY	Distr. Champouker (Alp. Cpaj. Piedmout) 1700m,	28 vii 1905	E.L.	s.n.	O
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.) Lindb.	NORWAY	Lapponia enontekiensis: Guonjarvaarri, Kalkkinokka, 1060m s.m. ad terram clacaream.	12 viii 1966.	A.J. Huuskonen.	s.n.	E
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.)Lindb.	NORWAY	Sör-Tröndelag: Kongsvold.	18 vii 1873	Berndes & Engelhart	s.n.	NY
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Nord-Nordland: Helgl. Dunderlandsdalen, Kragestrand.	6 viii 1870	Blytt & Arnell	s.n. B-45772	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Sør-Trøndelag:Oppdal. Kongsvold.	viii 1883	C. Kaurin	27837	O
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Oppland District, Jotunheimen: limestone valley with caves SW of Bovertun. On wet rock ledges on E-facing cliff. Alt. 930m	11 vii 1991	D.G. Long	19998	E
Sauteria alpina (Nees) Nees	Sauteria alpina var. angustifrons Kaal.	NORWAY	Troms: Nordreisa. Reisen, paa skifergrus I dalen nord for Jertafjeld [S.alpina (Nees) Nees var. angustifrons Kaal.]	29/7 1893	E. Jørgensen	s.n. 27860	O
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Troms: Tromsö par., Malanger, Haugefjeld I fjällregionen.	18 vii 1891	H.W. Arnell	s.n. B-45780	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Nordland: Salten, Sörfolden, Dypviks fjeldet (67 15)	22 viii 1893	I. Hagen	s.n. B-45774	UPS
Sauteria alpina	*Marchantia*	NORWAY	Nordland: Salten. Solvaagtind.	vii 1837	J. Ångstöm	s.n.	UPS

(Nees) Nees	*cruciata* L.					B-45775	
Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	NORWAY	Norv. Hordaland, Ulvik, Finse, Sandalsnut.	31 v 1985.	K. Fægri.	s.n. M-7978.	BG
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Sør-Trøndelag: Oppdal. Opdal, søndre del av Lille Elgsjøtangen 1300m. O.h.	17 vii 1907	N. Bryhn & I. Hagen	s.n. 27832	O
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Troms:Tromsø	1841	N.G. Moe	s.n. 27857	O
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Nordland: Rana. Eiteraa, Dunderlandsdal, Ranen	6 viii 1894	R.E. Fritz	s.n 27851	O
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Nordland: Rana. Mæsingen, Dunderlandsdal, Ranen.	14 viii 1894	R.E.Fritz	s.n. 27854	O
Sauteria alpina (Nees) Nees	*Peltolepis grandis* (Lindb.)Lindb.	NORWAY	Sør-Trøndelag: Oppdal. Dovre:Kongsvold	1872	R. Harman	s.n. 27062	O
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Björnfjeld.	3 ix 1938	S. Arnell	s.n. B-45768	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Sör-Tröndelag: "Dovre reg. betul., in fiss. Et cavern. Rup. Micac. Infra Knudshöe, ad viam prope Sprenbaekkan, parce fertilis."	20 vii 1882	S. O. Lindberg & E.Rettig	120	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	NORWAY	Sør-Trøndelag: Dovre reg. betul. In fiss et cavern. Rup. Micac. Infra Knudshoe ad viam prope Sprendbækkan, parce fertilis. NQ2.	20 vii 1882	S. O. Lindberg & E. Rettig	s.n	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	POLAND	Tatry, w górnej dolinie Miętusiej w kotle zw. Świstówka, poniźej dol. Mulowej, bardzo obficie (podobnie jak w innych miejscach na wapieniach Tatr) w wysokości okolo 1500 m.	25 viii 1910	Z. M. Raciborski	3	B
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	ROMANIA	Bucegi-Gebirge.	1970	Meinunger	s.n. JE-1488	JE
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	ROMANIA	Comit. Brassó. In montis Buesecs cacumine Buksoi	30 viii 1911	not known	s.n.	FH
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SLOVAKIA	Presovský: Bielské Tatry: In saxis prope Siroké pole.(1832 m) 1650 m.	23 viii 1951	J. Smarda	85	UPS
Sauteria alpina	*Clevea hyalina*	SVALBARD	Spitsbergen: Bellsund, på östsiden av	15 viii	S. Manum	s.n	O

(Nees) Nees	(Sommerf.) Lindb.		Reinsletta, sydöst for Linenes. Ca.	1962.			
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SVALBARD	Spetserbegn, Kings Bay District, Blomstrandshalvöya, London, nedom klippbrant.	26 vii 1956	S. Arenll & O. Mårtensson	s.n. B-45786	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SVALBARD	Kings bay District, Zeppelinfjällets sluttning ovan Ny-Alesund.	22 vii 1956	S. Arnell O. Mårtensson	s.n. 27866	O
Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	SWEDEN	Lule Lappmark, Junkatjokko.C.fr.	12 viii 1896	A. Cleve	s.n. M-7994.	BG
Sauteria alpina (Nees) Nees	*Sauteria* Nees	SWEDEN	Lappmark	30 vii 1925	F. Vierkapp.	s.n.	WU
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWEDEN	Torne Lappmark: Jukasjärvi par., Torneträsk-området, Vassitjåkko. 1100m. Skifferbrant.	3 viii 1916	G. Samuelsson	s.n. B-45766	UPS
Sauteria alpina (Nees) Nees	*Peltolepis grandis* Lindb.	SWEDEN	Härjedalen: Grönfjället.	vii 1913	H. Smith	s.n.	B
Sauteria alpina (Nees) Nees	*Peltolepis grandis* Lindb.	SWEDEN	Härjedalen: Storsjö par., Härjedalens fjällområdet, Grönfjäll.	vii 1913	H. Smith	B-045806	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* Nees	SWEDEN	Lapponia Tornesis, par. Karesuando:M. S. m. 1000n.r. 592.	11 vii 1929	H. Weimarck	s.n.	JE
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWEDEN	Jämtland, Hotagen, Ansätten	9 viii 1963	N. Hakelier	s.n.	S
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWEDEN	Jämtland: Undersåker par., Nedalen, Ekorrhammaren, SV-branten. 1240 m.	19 viii 1950	O. Mårtensson	s.n. B-45690	UPS
Sauteria alpina (Nees) Nees	*Peltolepis quadrata* (Saut.)Müll. Frib.	SWEDEN	Åsele Lappmark: Vilhelmina par., klimfjäll, Rapsentjåkko, lågalpina bältet, vid bäcken.	24 vii 1964	O. Mårtensson	s.n. B-45693	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWEDEN	Pite Lappmark, Arjeplog: S slope towards lkisjaure near the W end of the lake. 760 m.	3 viii 1955	P. O. Nyman	s.n. B92484	S
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWEDEN	Härjedalen:Tännäs par., Ramundberget. In saxis.		R. Oldberg	s.n. B-45689	UPS
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWEDEN	Torne Lappmark: Jukkasjärvi par., Abisko nationalpark, Kårsavaggejåkk, S: a sidan.	29 vii 1944	S. Arnell & H. Persson	s.n B-45724	UPS

Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.) Lindb.	SWEDEN	Svalbard (Spitsbergen)	1868	S. Berggren	s.n. BM00080062	BM
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWEDEN	Torne Lappmark: Aufstieg von Kopparåsen zum Låktatjåkko. 600 -800 m. an feuchten Felsen.	15 vii 1967	W. Schu	2569	B
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWITZERLAND	auf Gamzuku? Uri (Schweiz)	1 iii - 16 viii 1870	not known	s.n G00120826	G
Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	SWITZERLAND	Canton Valais: Gemmi, slopes of Schafberg above Daubensee. Rocky alpine limestone slopes; on soil under boulder. 2305 m.	1 vii 2008	D.G.Long	37943	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWITZERLAND	Canton Valais: Gemmi, E-facing slopes N of Daubensee. Steep limestone slopes;in damp crevice of limestone cliff. 2199 m.	2 vii 2008	D.G.Long	37977	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWITZERLAND	Canton Valais: Gemmi, slopes of Schafberg above Daubensee. Rocky alpine limestone slopes; on soil under boulder. 2283 m.	1 vii 2008	D.G.Long	37946	E
Sauteria alpina (Nees) Nees	*Sauteria alpina* (Nees) Nees	SWITZERLAND	Schwez: Kanton Bern, am Aufstieg zur Gemmi, von Kandersteg bis zur Paßhohe, auf humus zwischen Felsen (Kalk) 1250 – 2230m	viii 1904, 1906 & 1908	P. Culmann	s.n	E, WU
Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	SWITZERLAND	Valais, Val d'Hérémence, Lac de Dixence, onderaan de stuwdam. Alt. 2130 m. Ecol.: Op aardelaagje, op rotshelling langs de weg. Rem: On original lebel: Clevea hyalina.	13 vii 1988.	T. Arts	16.971 b.	BR
Sauteria alpina (Nees) Nees	*Sauteria alpine* (Nees) Nees	SWITZERLAND	Gemmi	1841	not known	s.n BM000962718	BM
Sauteria alpina (Nees) Nees	*Athalamia hyalina* (Sommerf.) S.Hatt.	U.S.A.	Alaska; Beechey Point Quad: Prudhoe Bay , W. side . Damp soil on open tundra. 10m	2 viii 1982.	D. G. Long.	11396	E
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Alaska: In frost boils, hill top tundra. East Oumalik and vicinity. William Campbell Steere. No. 15579. July 3-10, 1951. Arctic Alaska:Meade River Post Office (Coal Mine) Sandy calcareous, east-facing bluff above Meade River, south camp.	15 vii 1973	W. C. Steere, H. Inoue & Z. Iwatsuki	s.n	NY

Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Alaska: Tundra and shale cliff, west side of Peters Lake. Peters lake vicinity, Franklin Mountains, Brooks Range,3000-4000 ft.alt., boggy tundra and rocky slopes and cliffs.	16 viii 1974	W. C. Steere, H. Inoue & Z. Iwatsuki	3254	NY
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Alaska: Calcareous sandtone on the hill, 300-500 ft. alt. Umiat and vicinity, Colville River,, in wet tundra and on ridges.	July 3, 1974	W. C. Steere, H. Inoue & Z. Iwatsuki	2283	NY
Sauteria alpina (Nees) Nees	*Clevea hyalina* (Sommerf.)Lindb.	U.S.A.	Alaska: Kurupa Lake, Endicott Mountains, Brooks Range,3000 – 3500ft. alt., tundra and limestone cliffs, SE corner of lake. About 80 miles northeast of Umiat.	20 viii 1974	Z. Iwatsuki	3339	NY
Sauteria alpina (Nees) Nees	Sauteria alpina (Nees) Nees	AUSTRIA	Syn. Hep. P. 541 n. 1. Nees ab E. Hep. Eur. IV. P. 143. Conf. Rabenh. Hep Eur. Exice n. 67	not known	M. Anzi	s.n	BM, W, MANCH
Sauteria alpina (Nees) Nees +*Peltolepis quadrata* (Saut.)Müll. Frib.	*Athalamia hyalina* (Sommerf.) S.Hatt. + *Peltolepis grandis*	NORWAY	Sør-Trøndelag, Oppdal, Dovre: Konsgvold.	08 viii 1887.	N. Bryhn	s.n. M-7982.	BG
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Athalamia*	CHINA	Xinjian, China. Soil around rocks, very steep north facing canyonside. Very open Picea forest, very steep rocky valley. Path around base of falls Bai Yang (Poplar) Valley, southwest of Urumqi; ca. 1900m	01 vi 1994	A.T. Whittemore, B. Tan, R. L. Hu, J. C Zhu & M. Sulayman	4837	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Athalamia hyalina* (Sommerf.)S.Hatt.	CHINA	Xinjiang Prov., Tianshan Range, Nange, Nanshan Bai-yang Valley, about 55 km S of Urumqi City, ca 6800 ft. Picea forest near the spray of water fall,shaded and wet.	11 viii 1993.	B. C.Tan.	93-1228	H
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	CHINA	Yunnan Prov., Diqing prefecture: Da Xue Shan, N of Geza, large valley 5km W of pass. Damp stony limestone slope; on flushed turfy bank. 4390m	29 v 1993	D.G. Long	23860	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	CHINA	Yunnan Prov., Diqing prefecture: Da Zue Shan, N of Geza ridge W of pass. Rocky open ridge; on turf under rocks.	29 v 1993	D.G. Long	23815	E
Sauteria spongiosa	*Sauteria*	CHINA	Yunnan Prov., Diqing prefecture: Bai Ma	09 vi 1993	D.G. Long	24194	E

(Kashyap.) Shimizu & S.Hatt.			Shan, above logging road below E pass. Hillside with partly cleared scrub; under rock overhang shaded by dwarf Rhododendron. 4220m				
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	Cleveaceae	CHINA	Qinghai province: Huzhu county: Baishuwia (Juniper) Pass, Steep slope with Rhododendron, Salix & Potentilla scrub; on shady bank of gully. Alt. c. 3520 m.	22 vii 1997	D.G. Long	27143	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria* Nees	CHINA	Yunnan Prov., Diqing prefecture: Bai Ma Shan, valley N of plateau between mid and W passes. Limestone gorge; on turfy bank under shrubs by stream. 4190m.	07 vi 1993	D.G. Long	24119	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	Cleveaceae	CHINA	Qinghai province: Huzhu county: Baishuwia (Juniper) Pass, Steep slope with Rhododendron, Salix & Potentilla scrub; on shady bank of gully. Alt. c. 3520 m.	22 vii 1997	D.G. Long	27143	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	Cleveaceae	CHINA	Qinghai province: Henan county: Zhihoumao Xiang, Xiawate, S of Henan, Steep rocky limestone hillside; on bank at foot of cliff. Alt. c. 3750 m.	15 vii 1997	D.G. Long	26992	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	Cleveaceae	CHINA	Qinghai province: Maqin county: Yangkao, Steep limestone side valley; on damp shady bank under Salix. Alt. c. 3845m.	9 vii 1997	D.G. Long	26920	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	CHINA	Yunnan Prov., Zhongdian (Chungtien) district: Ge Zao area 15km N of Zhongdian. Small rocky limestone hill; on soil on rock outcrop. 3550m.	29 ix 1990	D.G. Long	18691	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria alpina* (Nees) Nees	CHINA	Yunnan Prov., bor-occid.: Ad confines Tibetica sub jugo Dokerla, in regionis frigide temperatae abieto-salicetis. Substr. Granitico. Alt. S.m.ca. 3800-4150m (28º 15´)	17 ix 1915	H. Handel-Mazzetti	8096	WU
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria spogiosa* (Kashyap) S. Hatt.	INDIA	Khasia Mts. 1300m.	1678	J.D. Hooker & T. Thomson	s.n. JE-3360	JE
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	INDIA	Sikkim, West District: Tributary of Prek Chhu opposite Lambi, N of Thangshing. Bouldery gully; on shady soil under boulder. 4065m.	20 vii 1992	D.G. Long	22732	E

Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	INDIA	Sikkim, West District: valley at Lam Pokhari Rest House, E side of Prek Chhu valley. Stream with series of cascades; on wet turfy ledges by waterfall. 4070m.	19 vii 1992	D.G. Long	22715	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauchia spongiosa* Kashyap	INDIA	Kashmir. 7500ft.	4 ix 1920	R. R. Stewart	5927	NY
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Athalamia yatsuensis* S.Hatt.	JAPAN	Jogozawa, Mt. Yatsugatake, Nagano Pref., on wet rock., ca. 2000m	5 viii 1976	S. Ono	3997	TNS
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria spogiosa* (Kashyap) S. Hatt.	NEPAL	Mahalangur Himal, Khumbu. 3800 – 4000m.	1962	Poelt	H72	JE
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Athalamia*	NEPAL	Rasuwa District: near Nyengang Kharka opposite Kyangin Gompa. Rocy valley on steep open mountainside; on earth under large boulder.3970m	14 x 2001	D.G. Long	30601	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Athalamia*	NEPAL	Rasuwa District: Gosainkund, S side of lake. Rocky valley by lake; on soil under rock overhang in block scree. 4290m	07 x 2001	D.G. Long	30450	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Athalamia*	NEPAL	Rasuwa District: between Shin Gompa and Cholang Pati. Shady Abies spectabilis forest; on wet mossy rocks. 3500m	06 x 2001	D.G. Long	30427	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	NEPAL	Sankhuwasabha District: Upper Barun Khola valley; cliffs on S side of Lower Barun Glacier opposite Mera. Rocky clacareous slopes below cliffs; damp turfy laedge under wet cliff. 4440m	03 x 1991	D.G. Long	20913	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	NEPAL	Taplejung District: Ridge of Gupha Pokhari. Mixed Rhododendron forest; on rocky bank by path. 2795m	25 x 1991	D.G. Long.	21552	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	NEPAL	Sankhuwasabha District: Upper valley of tributary N of Barun Khola, NE of Pemathang Kharka. Open rocky alpine valley; on soil in deep cleft between large boulders. 4160m.	09 x 1991	D.G. Long.	21070	E
Sauteria spongiosa	*Sauteria*	NEPAL	Sankhuwasabha District: Near Kauma, S of	25 ix 1991	D.G. Long.	20626	E

(Kashyap.) Shimizu & S.Hatt.			Shipton La. Mossy Rhododendron forest: on vertical bank. 3490m				
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	NEPAL	Sankhuwasabha district: Nehe Kharka, S side of Barun Khola. Steep calcareous gully under huge cliffs; on soil in shady recesses amongst boulders. 3740m	30 ix 1991	D.G. Long.	20799	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	NEPAL	Sankhuwasabha District: Upper Barun Khola valley; tributary valley below Peak 3, above Mera. Open rocky valley; on bank at foot of gully. 4530m	02 x 1991	D.G. Long.	20876	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria spogiosa* (Kashyap) S. Hatt.	NEPAL	Loc. Above Pemdang Kerpo. Alt. 5060m. Hab. Scree S exp mosses and liverworts.	1988	G. & S Miehe	13164	JE
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	PAKISTAN	Northern Areas, Baltistan, Deosai National Park. Valley of Bara Pani River valley. Vicinity of Himalayan wildlife project base camp. On wet soil. Wet, humid soil banks along river. 3861m	22 vii 1998	T.A.J. Hedderson	12239	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	PAKISTAN	Northern Areas, Baltistan, Deosai National Park. Road from Skardu to Astor. About mid-way between Sheosar Lake and Sher Kuli. 4000m.Peaty sides of stream	02 viii 1998	T.A.J. Hedderson	12481	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	PAKISTAN	Northern Areas, Baltistan, Deosai National Park. Valley of Bara Pani River valley. West bank of river across from HWP base camp. Sides of temproary pool. Sedge meadows in valley bottom with pools and occasional bouldery outcrops.3859m	05 viii 1998	T.A.J. Hedderson	12555	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	PAKISTAN	Northern Areas, Baltistan, Deosai National Park. Near junction of Ali Malik and Shatung Rivers. On mud of stream bank. Springy slope and sides of small stream in valley.3955m	06 viii 1998	T.A.J. Hedderson	12661	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	PAKISTAN	Norther Areas, Baltistan, Deosai National park. Bara Pani River Valley. West bank of river across from HWP base camp. Sedge meadows in valley bottom, with pools and occasional boudery outcrops. Mineral soil on sides of temporary pool.	05 viii 1998	T.A.J. Hedderson with Lowe, R.A.W., Petitt, S.C., Shah, M.& Upson, T.M.	12583	E

Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria*	PAKISTAN	Northern Areas, Baltistan, Deosai National Park. Valley of Bara Pani River, north end of ridge just east of river. Wet soil along stream. Wet streamside vegetation and granitic cliffs in gully.3924m	24 vii 1998	T.A.J. Hedderson with Lowe, R.A.W., Petitt, S.C., Shah, M.& Upson, T.M.	12345	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	—	PAKISTAN	Northern Areas, Baltistan, Deosai National Park. Valley of Bara Pani River, north end of ridge just east of river. Vertical stream banks. Wet streamside vegetation and granitic cliffs in gully. 3924m.	24 vii 1998	T.A.J. Hedderson with Lowe, R.A.W. Petitt, S.C., Shah, M.& Upson, T.M.	12333	E
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria yatsuensis* S.Hatt.	JAPAN	Mt. Yatsugatake	27 vii 1922	H. Koizumi	71102	TNS
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria yatsuensis* S.Hatt.	JAPAN	Honshu, Nagano-ken, Mts. Yatsugatake, Mt. Yokodke. 2500 m. on rocks	22 viii 1958	S. Kurokawa	s.n	TNS
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria japonica* (Shimizu & S.Hatt.) S.Hatt.	JAPAN	Honshu, Nagano-ken, Ina-shi Mt. Senjo, Shinyabusawa pass; ca. 2300 m alt., on wet rock (conglomerate).	14 viii 2008	T. Katagiri	1173	HIRO
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria japonica* (Shimizu & S.Hatt.) S.Hatt.	JAPAN	Honshu, Yamanashi-ken, Minamiarupusu-shi, Southern Alps, Mt. Kitadake, traverse from Kitadake Mountain Cottage to Happonba; ca. 3000 m, on moist soil.	24 vii 2009	T. Katagiri	2806	HIRO
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	Sauteria alpina (Nees) Nees	JAPAN	Hokkaido. Kitami Prov., Isl. Rishiri. Yaminaizawa valley above Oniwaki. 550 - 600 m. on rock cliff.	18 viii 1971	Z. Iwatsuki	1978	NICH
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria alpina* (Nees) Nees	RUSSIA	Sibiria, in valle flum Lena.	4 ix 1898	H. Nilsson-Ehle	s.n.	S
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria alpina* (Nees) Nees	RUSSIA	Krasnoyarsk: Sibiria, in valle flum. Lena, Buckeer [?].	4 ix 1898	H. Nilsson-Ehle	s.n. B-45918	UPS
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria alpina* (Nees) Nees	RUSSIA	Krasnoyarsk: Sibiria, Jenisei, Kudinka. Nakna fläckar I videsnår vid flodstranden (69˚ 35´N).	2 viii 1876	H. W. Arnell	s.n. B-45915	UPS
Sauteria spongiosa	*Sauteria alpina*	RUSSIA	Krasnoyarsk: Siberia, Patopooskoje (68˚	25 vii 1876	H. W. Arnell	s.n.	UPS

(Kashyap.) Shimizu & S.Hatt.	(Nees) Nees		35´N).			B-45916	
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria alpina* (Nees) Nees	RUSSIA	Krasnoyarsk: Siberia, Jenisei, Tolstoinos. I dalgångar vid flodstranden där andra länge kvarlegat (70˚ 10´N).	26 viii 1876	H. W. Arnell	s.n. B-45913	UPS
Sauteria spongiosa (Kashyap.) Shimizu & S.Hatt.	*Sauteria alpina* (Nees) Nees	RUSSIA	Krasnoyarsk: Sibirien, Jenisei, Patapovskoja. Nakna fläckar på toppen av turdrakullar (68º 35´).	25 vii 1876	H. W. Arnell	s.n	UPS