Monographic studies on *Cryphaea* (Bryopsida)

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**Academic dissertation**

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On Dec. 21, 2001 at 12 o’clock

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This thesis comprises


And the author’s publications upon which the synopsis is largely based:

A synopsis of the genus *Cryphaea* (Cryphaeaceae, Bryopsida)

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The genus *Cryphaea* (Cryphaeaceae, Bryopsida) comprises 30 species including two new species described from China after revisions. Twenty-three specific or infraspecific names were reduced to synonymy. The taxonomic status of five species was changed and the necessary new combinations were made. Twenty-five names were lectotypified or neotypified. The identities of five specific epithets remain unknown because no type material was found. In this synopsis, the research history, morphology and anatomy, phylogeny, ecology, and phytogeography of *Cryphaea* are reviewed. The morphological and anatomical characters are discussed in detail. The variation range of each character is clarified. The phylogenetic analysis is based on 42 morphological characters using the closely related genera *Cryptodontopsis* Dixon, *Dendrocyphaea* Paris & Schimp. ex Broth., and *Schoenobryum* Dozy & Molk. as outgroups. Based on the phylogenetic studies, morphological characters are evaluated in terms of evolutionary significance for further studies. Two subgenera and three sections are suggested in *Cryphaea*. An artificial key to all *Cryphaea* species is provided for identification. Seven geographic distributional patterns are recognized for the extant species of the genus. The group is speculated to have originated in West Gondwanaland (Africa-South America) around the Late Cretaceous to early Tertiary (ca. 70–60 m.y. BP). The genus exhibits a high level of endemism and some species should be listed as globally endangered bryophytes.

Key words: Bryopsida, *Cryphaea*, Cryphaeaceae, ecology, nomenclature, phylogeny, phytogeography, taxonomy, typification

This synopsis is based on the following articles, which are referred to by their Roman numerals in the text:


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1. Introduction

Cryphaea F.Weber (Cryphaeaceae, Bryopsida) is a genus distributed in Asia (I, II), Europe, Africa, North and South America, Australia, and Oceania (III) and from the sea level to ca. 6500 m in altitude. All its species are exclusively epiphytic on tree trunks, branches, and exposed roots. Wijk et al. (1959, 1969) and other supplemented “Index of Mosses” files of Missouri Botanical Garden (Crosby et al. 1992, Crosby & Magill 1994, 1997) listed over 140 names within Cryphaea. Recently Crosby et al. (1999) recognized 57 taxa for this genus. I tried to study types of all taxa except those transferred to other genera by previous authors. Twenty-three new synonymizations and five new combinations are made. Twenty-five names were lecototypified or neotypified. Five species are listed as doubtful taxa because no type material was found (I, II, III). In total, thirty species are recognized, including two new species reported from China (I, II).

Because of the relatively high infrageneric variability, Cryphaea, clearly the largest genus of the family Cryphaeaceae, is also the key genus in understanding the still problematic evolution and generic relationships within the family. The genus has never been thoroughly studied or satisfactorily circumscribed and therefore species of Cryphaea have often been confused with other genera such as Cryptidium (Mitt.) A.Jaeger (Robinson 1972, Buck 1998, III), Cyptodon M.Fleisch. (Enroth 1995), Cyptodontopsis Dixon (I), Dendrocyphaea Broth. (Griffin et al. 1982, Enroth 1995, III), Forssstroemia Lindb. (Stark 1987), and Sphaerothecia M.Fleisch. (Manuel 1977, Rao 2000).

Since Brotherus (1925), the genus has never been the subject of a detailed systematic treatment, although there are a few floristic or regional revisions (Manuel 1973, 1981, Scott et al. 1976, Enroth 1990, 1995, 1996, Beever et al. 1992, León & Horton 1996, Buck 1998, León 1999a). The taxa of Africa and Asia, however, remained unstudied. I initiated my studies on Cryphaea with the Chinese species (I) and then revised the Asian taxa (II). The most recent paper (III) revises the taxa distributed outside Asia. The present synopsis summarizes the results and my understanding of this genus, treating its taxonomic history, morphological and anatomical features, ecology, phytogeography, generic delimitation and infrageneric taxonomy in the light of phylogenetic analyses. I also describe the methodology employed in my research. An appendix lists the specific and infraspecific epithets of the genus.

2. Historical Outline

The generic name Cryphaea was first published in a key by Weber in 1814 (‘1813’). He emphasized the mitriform calyptera as a generic character and transferred Neckera heteromalla Hedw. to Cryphaea. Bridel (1819) defined the genus by an immersed capsule, a double peristome with 16 separate teeth and the same number of alternating segments, and the mitriform and glabrous calyptera. Bridel (1819) also moved Neckera heterophylla Brid., N. filiformis Hedw., and N. sphaerocarpa Hook. (= Sphaerothecia sphaerocarpa (Hook.) M.Fleisch.) to Cryphaea. Müller (1851) recognized Cryphaea only as a section of the larger genus Pilotorichum P.Beauv. The section comprised three subsections Dichotomaria, Eucryphaea (≡ Cryphaea), and Dendropogon (≡ Dendropogonella). Three of Bridel’s four
species of *Cryphaea* were placed in the Subsect. *Eucryphaea* and eleven taxa were added by Müller himself. He excluded *Cryphaea heterophylla* (Brid.) Brid. from this group and resurrected the name *Neckera heterophylla*. A few years later, Mitten (1859) raised *Cryphaea* to the generic level again and recognized three sections: *Eucryphaea* (= *Cryphaea*), *Acrocryphaea* (= *Schoenobryum*), and *Dendropogon* (= *Dendropogonella*). Later, Mitten (1869) included one more section into this genus: *Philudora* (= *Dendrocryphaea*).

The generic concept of *Cryphaea* was widely accepted until Brotherus (1905), who raised *Acrocryphaea*, *Dendropogon*, and *Dendrocryphaea* to the generic level, thus excluding them from *Cryphaea*. Brotherus (1905) recognized two sections in *Cryphaea*: Sect. I. *Sphaerothecium*, with a single species *Cryphaea sphaerocarpa* (Hook.) Brid.; and Sect. II. *Eucryphaea*, consisting of 53 taxa. Brotherus emphasized the double peristome, ovate to elliptic upper laminal cells, and erect secondary stems as generic characters of *Cryphaea*. He noted that the description of *C. ravenellii* Austin, a species with a single peristome, was consistent with the genus *Forssstroemia*. Fleischer (1906–1908) accepted Brotherus’s concept of *Cryphaea* but later (Fleischer 1914) excluded sect. *Sphaerothecium* and another species from *Cryphaea* by establishing two new genera: *Sphaerothecielia* to accommodate *Cryphaea sphaerocarpa* and *Cryphaeaphilium* to accommodate *Cryphaea molle* Dusén (which actually belongs in the Meteoriaceae, *vide* Crosby et al. 1999). In the same 1914 paper, Fleischer established within *Cryphaea* the section *Cryphaeella M.Fleisch.*, consisting of *C. consimilis* Mont., *C. tahitica* Besch., and *C. tenella* Hornsch. *Cryphaea* was revised again by Brotherus (1925) and was divided into three sections *Obovatothecium* S.Okamura ex Broth. (with one species), *Eucryphaea* (with 49 taxa), and *Cryphaeella* (with 5 species). In addition to the characters Brotherus emphasized for *Cryphaea* in 1905, he now mentioned the capsule shapes and spore size to separate it from *Sphaerothecielia*.

Since 1925, very few modifications have been made. Robinson (1972) reduced the genus *Cryphidium* to the synonym of *Cryphaea*. However, Buck (1998) and I (III) recognize the genus *Cryphidium*. Manuel (1982) provided a key to identify *Cryphaea* from other genera within the Cryphaeaceae by the combination of lateral sporophytes, broadly ovoid to narrowly ellipsoid theca, exosporic spores, and erect stems. Manuel (1973) included the peculiar *C. ravenellii* within *Cryphaea* and subsequently appreciated that the genus encompasses both single- and double-peristomate species. In my most recent paper (III), I proposed the new genus *Monocryphaea* to accommodate *C. ravenellii*. In the present paper, two subgenera and three sections are suggested for *Cryphaea* based on the cladistic studies. The ecology and phytogeography of the genus are discussed based on the results of the phylogenetic studies and the label information of the examined herbarium specimens. A hypothesis of geographic origin and age of *Cryphaea* is speculated.

### 3. Material and Methods

This synopsis is based on the taxonomic revisions (I–III), for which I studied ca. 3300 specimens kept in the Helsinki herbaria H, H-BR, H-SOL and borrowed from B, BM, CAN, CANB, COLO, CAS, DBN, DS, DUKE, E, EGR, F, FH, FT, G, GB, GOET, GRO, HAL, HBG, HIRO, JE, KUN, L, MANCH, MEXU, MICH, MO, NICH, NY, PE, PC, RO, S, STR, TNS, US, and W. All specimens were observed for gross morphology in both dry and wet
condition under a dissection microscope. Capsules, calyptrae, and opercula were measured and illustrated from moist specimens under the dissection microscope unless otherwise indicated. Leaves, perichaetial leaves, peristomes, and other anatomical details were examined, measured, and illustrated under a compound microscope.

Morphological variation was studied for each selected character. Because of the diversity of levels at which development occurs, comparative studies of development can be confusing (Mishler & Luna 1991). Therefore, the measurements were standardized. A few criteria were adopted: (1). The first 5–10 specimens from each country (if possible) were measured for each species; (2). Leaves were removed from an area 5–15 mm below stem apex and from the middle of branches; (3). Cell sizes refer to the size of the lumina.

According to the species concept applied in my work, species were delimitated from each other by at least one clearly non-intergrading character or a combination of characters. No infraspecific taxon is recognized, because the quantitative differences employed by previous authors to recognize infraspecific taxa were found to be continuous and, I think, of no taxonomic significance.

The geographic distributions of all species were mapped according to countries or states (one mark for each country or state). The distribution maps were made using the VISIO 2000 programme. The illustrations were first drawn by hand and scanned in HP ScanJet 6200C. The scanned pictures were then traced and processed by the FreeHand 9 and PhotoShop 6 programmes.

In the present paper, the morphology and anatomy of the genus are summarized. Phylogenetic analyses were performed using NONA (Goloboff 1993) and Winclada (version 0.9.9+ (BETA), Nixon 1999). Forty-two characters were used. Three closely related genera are employed as outgroups in the analysis.

4. MORPHOLOGY AND ANATOMY

Morphological and anatomical characters and their variation in Cryphaea are here discussed in detail. The terminology mostly follows La Farge-England (1996) and Newton & De Luna (1999) unless otherwise indicated.

Life form and growth form. – Plants of Cryphaea usually grow in dense or loose turfs or occasionally in cushions on the trunks, branches, twigs, or exposed roots of trees or shrubs. The plants are usually 1–6 cm in height, although the largest specimens occasionally reach a length of 10 cm and the smallest may be as short as 0.5 cm. Most species have a more or less stout habit, but a few taxa are slender.

Branching pattern. – As in most of the pleurocarpous mosses, Cryphaea has a monopodial branching pattern. Most species are pinnately or tripinnately branched, some taxa are irregularly branched, but a few species (Cryphaea glomerata, C. filiformis, C. omeiensis, C. orizabae) are almost unbranched.

Stolons and stems. – The stolons (primary stems) are usually very slender, inconspicuous, green to dark brown, usually covered with reduced, scale-like leaves, rarely naked, and
appresses along the substrate. Stems (secondary stems) are formed by a sudden turning of stolons perpendicularly from the substrate. The stolons are continued by buds at the stem base, which can develop in different directions from the same stem and thus form a dense ‘community’. The stems are sometimes curved at their tips. Epidermal and cortical cells are small and strongly incrassate, whereas the medullary cells are much larger and relatively thin-walled. No central strand was observed in any species (Fig. 1). Paraphyllia were not seen. Pseudoparaphyllia are present.

**Fig. 1.** Transverse section of stem of *Cryphaea jamesonii* Taylor (from Angeles Cárdenas 4214, H) – Scale: 0.2 mm.

**Leaves.** – The stem leaves are imbricate, loosely imbricate, or irregularly spreading (with flexuose apices) when dry, but rapidly become erect-patent to spreading when moist. The leaves are spirally arranged around the stem, and may be dense or loose. Leaf shapes vary from ovate to lanceolate, and the leaf apex ranges from acuminate, to acute, setaceous, or rarely obtuse (*Cryphaea ovalifolia*). The leaves are mostly smooth, rarely plicate (*C. chlorophylllosa*), and usually concave, at least at the base. Leaf bases are decurrent, usually cordate, rarely truncate (*C. attenuata*). In cross section, the leaf lamina is unistratose, whereas the costa is 2–3-stratose (Fig. 2). The branch leaves are usually smaller, but otherwise similar to the stem leaves. However, in some species the branch leaves have a much shorter costa, a narrower lamina, more distinctly prorate cells, or more strongly denticulate apices than the stem leaves. The leaf margins are entire in the lower leaf portion but vary from entire to coarsely denticulate at the leaf apex. They are usually recurved in the lower leaf portion (1/3–4/5) or occasionally plane throughout.

**Leaf costa.** – The leaf costa is single in all members of this genus, usually unforked, but a few species (*Cryphaea amurensis, C. songpanensis*) have a bifurcate costa occasionally. The costa is conspicuous in all species, mostly ending below the leaf apex (0.25–0.75 of leaf length), but a few species have a percurent costa (to apex), and four species (*C. clandestina, C. consimilis, C. parvula, and C. pilifera*) possess an excurrent costa that forms a short to long arista. The costa in the branch leaves is usually similar to that in the stem leaves, but in some species (e.g., *C. attenuata*) it can be distinctly shorter.
Fig. 2. Transverse section of leaf of *Cryphaea lanceolata* P. Rao & Enroth (from the holotype: *T. Koponen 46842, H*!). – a: The whole leaf, basal portion; – b: Costal area. – Scale A for a: 0.4 mm; scale B for b: 50 µm.

**Leaf cells.** – The laminal cells are exclusively incrassate, mostly coarsely to minutely prorate in their upper ends, or rarely smooth. Most members of *Cryphaea* have differentiated inner basal cells that are usually linear, but occasionally rectangular. Only three species lack distinctly differentiated specialized inner basal cells (*C. acuminata, C. consimilis, C. parvula*). The differentiated inner cells can be just a few at the leaf base, or the group can extend from leaf base to apex. Usually the group covers the lower half of the leaf. The alar cells are more or less differentiated, subquadrate or round and with one or two cells elongate at basal ends, often in obvious rows. The upper lamina cells are usually shorter than the inner basal and apical cells. The marginal cells are usually shorter than the inner laminal cells.

**Pseudoparaphyllia.** – Pseudoparaphyllia usually occur around branch primordia or branch bases or occasionally lack from some of these positions. They are usually filamentous (uniseriate), or rarely biseriate at base (*Cryphaea chlorophyllosa, C. rutenbergii, C. songpanensis*). Their length mostly ranges between 80–180 µm, occasionally slightly longer than 200 µm (*C. obovatoarpa*), and rarely reaching 400 µm long (*C. apiculata*).

**Rhizoids.** – Rhizoids are fairly uniform in the genus. They usually occur on stolons, rarely on leaves (mainly along the dorsal costa), and are smooth, unbranched, and hyaline to brownish.
Reproduction. – Asexual propagula have not been observed in the genus. León (1999b) cultured spores and fragments of *Cryphaea jamesonii* and found that its reproductive strategy “seems to be a great reproductive effort input (RE) in sexual reproduction and apparently lack asexual reproduction”, which seems to be the common feature of *Cryphaea*.

Sexual condition. – All species are exclusively autoicous.

Perigonia. – The perigonia in the genus are solitary in leaf axils, small, bud-like, and inconspicuous. The perigonal leaves are ovate to ovate-acuminate, concave, and ecostate.

Perichaetium position. – Most species in *Cryphaea* are pleurocarpous, but a few species (*Cryphaea chlorophyllosa*, *C. clandestina*, *C. ovalifolia*, *C. tenella*) seem to be cladocarpous. It is difficult to determine which is pleurocarpous or cladocarpous in *Cryphaea* because the fertile branches in all species are very short and more or less swollen compared with vegetative branches. In addition, no subperichaetial branch primordia were observed on the fertile branches. Theoretically, I agree with La Farge-England (1996) on the concept of pleurocarpy and cladocarpy. I could not find any difference between the “pleurocarpous taxon” (*Cryphaea patens*) and “cladocarpous taxa” (*Cryphaea filiformis*, *C. glomerata*, *C. orizabae*, *C. tenella*) which were listed so in her study (La Farge-England 1996: 176–177). However, as stated in La Farge-England (1996), the juvenile leaf development at the base of fertile branches seems to be a good and practical criterion to determine the perichaetial position type. The juvenile leaves at the base of fertile branches are similar to stem leaves in cladocarpous taxa (*C. chlorophyllosa*, *C. clandestina*, *C. ovalifolia*, *C. tenella*) and the fertile branches are often slightly elongate. On the contrary, the juvenile leaves at fertile branch bases (actually the outermost perichaetial leaves) are distinctly different from stem leaves in pleurocarpous taxa.

Perichaetial leaves. – The perichaetial leaves are of specific significance in *Cryphaea*. They grow on a short and more or less swollen fertile branch, and are mostly longer than the sporophyte, rarely only reaching about half of the sporophyte (*C. consimilis*). The outermost perichaetial leaves are very small, uniformly ecostate; their apices vary from acute to setaceous, rarely obtuse. The perichaetial leaves gradually increase in length from the outer layers to the inner ones. The upper portions of the inner perichaetial leaves mostly abruptly form awns, which can be very short (e.g., less than 1/10 of the leaf length in *C. hygrophila*) to quite long (e.g., almost half of the leaf length in *C. pilifera*); rarely the leaves gradually narrow to the acumina (*C. orizabae*), in which case an awn-like structure may also be formed. The inner laminal cells are usually linear, occasionally rectangular (e.g., *C. glomerata*). The marginal cells are usually shorter than the inner ones, shortly rectangular or subquadrate, but are not always differentiated from the inner cells. The cells in the leaf shoulders are abruptly or gradually shorter than adjacent linear cells, but in some taxa the shoulder cells are undifferentiated.
**Perichaetial leaf costa.** – The costal development in the perichaetial leaves can be of the three types described in Table 1 and illustrated in Figures 3 and 4. The distributions of the perichaetial leaf types in the cladogram are shown in Figure 6.

**Fig. 3.** Examples of costal types in perichaetial leaves. – A: Type Ia (*Cryptobelia obovatocarpa* S.Okamura); – B: Type Ib (*C. heteromalla* (Hedw.) F.Weber); – C: Type Ic (*C. filiformis* (Hedw.) Brid.). See text for explanations.

**Capsule.** – Spore capsules are frequent in *Cryptobelia*. The capsules are erect, symmetric, and immersed in the perichaetial leaves because of the short seta. They are mostly elongate-obloid or obloid, but in a few species ellipsoid, rarely cylindrical (*C. brevipila, C. rhacomitrioides, C. rutenbergii*). The exothecial cells are usually subquadrate to rectangular above and irregular below. The urn mouth usually has a dark red ring, and is rarely undifferentiated. Stomata are absent in most of the species, but a few taxa have a few present at the urn base (*C. glomerata, C. songpanensis*). Crum & Anderson (1981) made a similar observation: “stomata none or few, at the extreme base of the urn”. However, Manuel (1973, 1981) reported “stomata phaneroporous on neck, infrequent” as a generic feature, something that I have not observed. It seems that stomata are reduced in *Cryptobelia* and of no diagnostic significance.
Fig. 4. Examples of costal types in perichaetial leaves. – A: Type II (*Cryphaea rhacomitri-oides* Müll.Hal.); – B: Type III (*C. rutenbergii* Müll.Hal.). See text for explanations.

**Peristome.** – The peristome in the genus is double, usually hyaline, but occasionally yellowish brown. In most species the peristome teeth become erect when moist but are closed when dry (hygrocastique). However, the opposite reaction to humidity changes (xerocastique) is also present in the genus. Two species (*C. hygrophila* and *C. ramosa*) have a different peristome type: the exostome teeth in these two species are open but their endostome segments are closed to form a dome when moist. I termed this type of peristome “semi-hygrocastique”. The exostome teeth are sixteen, lanceolate, usually 200–400 µm, rarely
shorter than 200 µm (C. amurensis and C. tenella) or longer than 500 µm (C. hygrophiila, C. parvula, C. protensa, C. ramosa, and C. rhacomitrioides). They are usually papillose, rarely smooth, their median lines are usually distinct more or less in a zigzag pattern, or indistinct, rarely perforated/cracked (C. amurensis, C. chlorophyllosoa, C. clandestina, C. ovalifolia, and C. tenella). The endostome segments are also sixteen and alternate to the exostome teeth, mostly linear, and shorter than the exostome teeth.

**Table 1. Types of perichaetial leaf costa development in Cryphaea.**

<table>
<thead>
<tr>
<th>Type</th>
<th>Relevant Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type I: Costa initiated in the leaf base of the outer leaves, gradually getting longer in the inner leaves. This type can be further divided into three subtypes:</td>
<td></td>
</tr>
<tr>
<td>Subtype Ia. Costa not reaching leaf tip even in the innermost leaves (Fig. 3A).</td>
<td>C. obovatocarpa</td>
</tr>
<tr>
<td>Subtype Ib. Fully costate in the inner leaves (Fig. 3B).</td>
<td>C. acuminata, C. amurensis, C. clandestina, C. glomerata, C. nervosa, C. heteromalla, C. lanceolata, C. ovalifolia, C. protensa, C. razzii, C. tenella</td>
</tr>
<tr>
<td>Subtype Ic. Fully costate in the leaves of middle layers, but lower portion of costa gradually disappearing in the leaves of inner layers. The further in the leaves, the shorter the costa (Fig. 3C).</td>
<td>C. chlorophyllosoa, C. filiformis, C. omeiensis, C. songpanensis</td>
</tr>
<tr>
<td>Type II. Costa initiated at leaf apex of the outer leaves, tapering downwards and disappearing well above leaf base (Fig. 4A).</td>
<td>C. attenuata, C. brevipila, C. consimilis, C. gracillima, C. jamesonii, C. orizabae, C. parvula, C. patens C. pilifera, C. ramosa, C. rhacomitrioides</td>
</tr>
<tr>
<td>Type III: Ecostate or irregularly discontinuously costate along the median line of the lamina (Fig. 4B).</td>
<td>C. apiculata, C. hygrophiila, C. rutenbergii</td>
</tr>
</tbody>
</table>

**Columella.** – The columella is persistent after the release of spores in all members of Cryphaea. The length of the columella is mostly above half of the theca, or even reaches the urn mouth in some species (e.g., C. lanceolata).

**Operculum.** – In my previous studies (I, II, III), opercula are found to be not only conical, but also rostellate, and even rostrate in a few species (C. brevipila, C. ovalifolia, C. parvula, C. songpanensis). The surface of the operculum is always smooth.
The term “mitrate” was used to describe the calyptra of *Cryphaea heteromalla*, the type of the genus, and the mitriform calyptra was emphasized when establishing the genus (Weber 1814 (1813)). This term was also used by Manuel (1982), who considered it as an “important” character to distinguish the Cryphaeaceae from the Leucodontaceae. A detailed examination of all species of *Cryphaea* shows that the mitriform calyptra could be very short as in *Cryphaea glomerata* and *C. nervosa* or quite long as in *C. heteromalla* and *C. parvula*. In addition, there are two species, *C. hygrophiha* and *C. ramosa*, which have somewhat different calyptrae. I employed the term “campanulate” to describe them (cf. Fig. 24 of III).

**Annulus.** – In the current genus, annuli are present in most of its members, and usually consists of 1–3 rows of thick-walled cells. However, an annulus is absent in some species (*Cryphaea chlorophyllosa, C. ovalifolia, C. tenella*).

**Spores.** – All spores in the genus are globose or subglobose, mostly between 18–40 µm in diameter, with a few species having spores more than 40 µm (*C. apiculata, C. gracillima, C. obovatorcarpa, C. protensa, C. ragazzii*). The surface of the spores is sparsely to densely papillose, or rarely smooth (*C. rhacomitrioides*) when observed under the compound microscope.

### 5. Phylogenetic analysis

**TAXA AND METHOD**

The analysis is based on morphological characters. All 30 species of *Cryphaea* were included, using three closely related genera of the Cryphaeaceae as outgroups: *Cypodontopsis* Dixon, *Dendrocrysthia* Paris & Schimp. ex Broth., and *Schoenobryum* Dozy & Molk. Because *Schoenobryum* is the only acrocarpous moss and seems to be the most plesiomorphous taxon among the outgroups, it thus is used to root the tree. The morphological data for *Cypodontopsis levellii* (Thér.) P. Rao & Enroth, *Dendrocrysthia lamynnana* (Mont.) P. Rao, and *Cryphaea* species were compiled from the specimens studied for and cited in my previous papers (I, II, III). Four specimens were examined for *Schoenobryum concavifolium* (Griff.) Gangulee: *Bandeira 516* (H); *Dusén s. n.* (H); *Hegewald 7065* and *8484* (H). In total the study is based on 33 taxa and 42 characters. The cladistic analyses were executed with NONA (Goloboff 1993) within the Winclada shell (version 0.9.9+ (BETA), Nixon 1999). Optimal trees were found by heuristic searches with TBR branch swapping using NONA with the options “hold*; hold/100; mult*1000;”, which randomize the order of the taxa, create weighted Wagner trees, and submit them to branch swapping (TBR), storing in the memory up to 100 trees, and repeating the process 1000 times. Different options “hold*; hold / 150; mult*200;” were tried but resulted in the same optimal trees. Winclada was employed to edit the data matrix, analyze the trees resulting from the NONA search, and to diagnose and map the characters and their states. Jackknife and Bremer support values were calculated to explore the reliability or “strength” of the individual clades. Jackknife (Farris 1997) analysis was run by using the parsimony jackknife program xac with the option “1000*/5”, which means that the number of replicates was 1000, it was done using branch-swapping (*) and the
The number of random addition sequences per replicate was 5. The Bremer support values (Bremer 1994) were calculated using TreeRot (Sorenson 1999) in conjunction with PAUP* (Swofford 1999).

**Characters, Coding, and Data Matrix**

All characters were coded as unordered, nonadditive, and unweighted. Thus the direction of character state transformations in multi-state characters was not judged a priori. The purpose is to prevent a bias towards the characters and minimize assumptions about character evolution before analysis. Quantitative character states are delimited arbitrarily with special consideration on the extreme cases. For example, most of the capsules are shorter than 2.5 mm in length but there are a few species with even the smallest one longer than 2.7 mm, I then delimit the state at 2.7 mm in length. The character state was coded as “?” if the information was unknown for a taxon (e.g., calyptra). The data matrix is given in Table 2. The characters and character states employed are listed below. Characters were enumerated from 0, corresponding with the numbers shown on the cladogram of Figure 7.

**Characters and Their States**

0. Habitat: aquatic (0); terrestrial (1)
1. Size of mature plants: small, under 6 cm long (0); large, 6–10 cm (1); very large, ≥ 11 cm (2).
2. Stem leaf apex: obtuse (0); acute (1); acuminate (2); setaceous (3).
3. Leaf margins near apex: entire or weakly crenate (0); denticulate (1); variable from entire to denticulate in the same species or even within an individual plant (2).
4. Leaf margins: plane (in at least most of the stem leaves) (0); recurved, never plane (1).
5. Leaf costa length: excurrent, forming an arista (0); percurrent, or costa reaching leaf apex but usually longer than 0.8 of the leaf length (1); shorter than 0.75 the leaf length (2).
6. Leaf costa type: never forked (0); sometimes forked (1).
7. Upper leaf laminal cell shape: round to elliptic (0); at least partially rhombic (1); linear (2).
8. Upper leaf laminal cell size (average in length). Upper leaf laminal cells are relatively uniform within the species of *Cryphaea*, so average values are adopted here, the measurement method is given under the MATERIAL AND METHODS section: small, ≤ 8 µm (0); medium-sized, 9–15 µm (1); large, 16–20 µm (2); very large, > 21 µm (3).
9. Apical leaf cell shape: round or short elliptic (0); rhombic (1); elongate elliptic or linear (2).
10. Specialized inner leaf lamina cells. Specialized inner cells usually linear, rarely rectangular, can be restricted to the basal area or reaching to leaf tip, or not clearly differentiated: indistinct (0); restricted to basal half of leaves (1); reaching above the middle of the leaves but not to leaf apex (2); reaching to leaf apex (3).
11. Leaf laminal cell ornamentation: smooth (0); minutely prorate (1); strongly prorate (2); papillose projecting at cell middle (3).
12. Costa of branch leaves: similar to stem leaves (0); much shorter than that in stem leaves (1).
13. Perichaetial position: acrocarpous (0); cladocarpous (1); pleurocarpous (2).
Table 2. Data matrix of the character states used in the cladistic analyses of *Cryphaea*

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 11111 11112 22222 22223 33333 33334 4</td>
</tr>
<tr>
<td></td>
<td>0 12345 67890 12345 67890 12345 67890 1</td>
</tr>
</tbody>
</table>

*S. concavifolium* 1 02012 00121 10000 23302 12010 00010 21102 12101 2
*Cyp. leveillei* 0 20101 00001 30211 23302 01010 10010 20104 12100 2
*D. lamyana* 0 00002 00001 00101 23311 01010 01010 11112 11110 1

*C. acuminata* 1 02012 00120 10211 33101 12110 11011 00102 02211 2
*C. amurensis* 1 02012 12223 21211 23122 00010 11010 11110 00011 2
*C. apiculata* 1 13012 00121 22211 01101 12110 01010 01103 11212 1
*C. attenuata* 1 12211 02323 21211 21001 00210 10010 01102 01211 1
*C. brevifila* 1 02201 01201 10211 21110 11000 10000 20102 01210 1
*C. chlorophyllosa* 1 01001 01102 12101 11122 00110 10011 00011 00010 2
*C. clandestina* 1 03110 02322 10101 33011 00110 10000 11101 10210 1
*C. consimilis* 1 03000 00100 00211 21101 10010 00010 00102 02210 2
*C. filiformis* 1 02002 00201 20211 21112 12210 10010 01211 11111 2
*C. glomerata* 1 02002 00101 12211 13101 12110 10100 01102 12211 2
*C. gracilima* 1 03120 02323 20211 21102 11110 11101 00102 12112 1
*C. heteromalla* 1 01012 00101 10211 23101 11010 01101 00102 01110 1
*C. hygrophila* 1 11012 00101 12211 00201 10211 01111 10124 01110 1
*C. jamesonii* 1 13111 00323 10211 31001 10010 11101 00103 02210 2
*C. lanceolata* 1 02111 00121 11211 13002 11210 11??1 00101 02111 1
*C. nervosa* 1 02211 00121 20211 23122 01010 11011 00101 11111 2
*C. obovatocarpa* 1 02002 00101 10211 32122 01110 11000 01101 02112 2
*C. omeiensis* 1 03111 00101 01211 21112 11101 10001 00101 01101 1
*C. orizabae* 1 02002 00221 20211 11302 12210 00010 11103 12211 2
*C. ovalifolia* 1 00001 01201 12101 03122 01010 10000 20012 00010 2
*C. parvula* 1 03000 00120 00211 11002 10010 10010 20104 01210 1
*C. patens* 1 01211 00101 00211 31111 11110 10010 01102 02211 1
*C. pilifera* 1 13200 00221 11211 31002 11010 11010 00103 01111 2
*C. protensa* 1 12012 00321 10211 13102 11101 01010 00104 12212 1
*C. ragazzii* 1 02012 02323 12211 13101 11110 11010 01103 12212 1
*C. rosa* 1 12012 00121 10211 10101 10211 01111 01124 02112 2
*C. rhamomitioides* 1 12201 01311 12211 21101 11000 10010 01104 02211 0
*C. rutenbergii* 1 12201 01311 10211 10102 11000 10001 00102 02211 1
*C. songpanensis* 1 03012 10222 21101 33111 01210 11??1 21101 02111 2
*C. tenella* 1 02001 01211 10101 13121 00010 10010 00010 00010 2

14. Leaves at fertile branch base: similar to stem leaves (0); different from leaves (1).
15. Costa of the outermost perichaetial leaves: partially present (0); absent (1).
16. Apices of the outermost perichaetial leaves: obtuse (0); acute (1); acuminate (2); setaceous (3).
17. Costa of inner perichaetial leaves: absent (0); strong at apex, disappearing below (1); strong at leaf base, disappearing above (2); present throughout leaf (3).
18. Acumen of inner perichaetial leaves: acumen formed by an abrupt contraction from the lamina, and longer than 1/2 of the leaf length (0); acumen abruptly formed, between ½–1/5 of the leaf length (1); acumen very short, less than 1/10 of the leaf length (2); apices acuminate and acumen gradually forming an awn, sometimes no clear awn formed (3).
19. Specialized marginal cells (when differentiated clearly shorter than inner cells) of inner perichaetial leaves: undifferentiated (0); differentiated, marginal cells in 1–5 rows (1); strongly differentiated, marginal cells in more than 6 rows (2).
20. Laminal cell ornamentation in inner perichaetial leaves: smooth (0); minutely prorate (1); strongly prorate (2).
21. Shoulders of inner perichaetial leaves: narrower than lower portion (0); wider (1).
22. Shoulder cells in inner perichaetial leaves. The shoulder cells are usually shorter and wider than the cells in the lower leaf portion: undifferentiated (0); gradually differentiated (1); sharply differentiated (2).
23. Lumina of basal cells of inner perichaetial leaves: smooth (0); porose (1); with internal papilla-like thickenings (2).
24. Capsule shape: cylindrical, L/D (length/diameter) ratio 3.5–5.0 (0); obloid to ellipsoid, L/D ratio 1.8–3.5 (1).
25. Capsule size (in length). Capsules are usually small in Cryphaea, mostly varying between 1–2.4 mm in length. Two species, C. hygrophiila and C. ramosa, have relatively large capsules, between 2.7–3.8 mm: small, ≤ 2.6 mm (0); large, > 2.7 mm (1).
26. Urn mouth becoming dark red, forming a striking ring: no (0); yes (1).
27. Seta length: less than 100 µm (0); between 100 – 350 µm (1).
28. Shape of calyptra: mitriform (0); campanulate (1).
29. Calyptra surface: smooth throughout (0); upper cells prorate (1).
30. Calyptra margin: entire (0); lobed asymmetrically (1).
31. Operculum shape: conical (0); rostellate (1); rostrate (2).
32. Columella: long, ≥ 0.7 the theca length (0); short, < 0.7 the theca length.
33. Annulus: absent (0); present (1).
34. Peristome type: hygrocastique (0); xerocastique (1); semi-hygrocastique (2).
35. Length of exostome teeth (max.): very short, < 200 µm (0); short, 200–300 µm (1); of median length, 300–400 µm (2); long, 400–500 µm (3); very long, > 500 µm (4).
36. Color of exostome teeth: whitish (0); yellowish-brown (1).
37. Median line of exostome teeth. The median lines of the exostome teeth seem related with the division of the teeth, three situations are found within the concerned taxa: at least partially cracked (0); distinct but not cracked (1); indistinct (2).
38. Exostome ornamentation. The peristome teeth are usually papillose, or smooth in the lower portion, or rarely smooth throughout when observed under a compound microscope: smooth throughout (0); smooth below, papillose above (1); papillose throughout (2).
39. Endostome: absent (0); present (1).
40. Spore size (maximum size): small, < 25 µm (0); medium-sized, 25–40 µm (1); large, > 40 µm (2).
41. Spore ornamentation: smooth (0); sparsely papillose (1); densely papillose (2).
RESULTS

The phylogenetic analysis resulted in three most parsimonious trees (MPT) with a length of 279 steps (Fig. 5). The consistency index (CI) was 0.26 and the retention index (RI) 0.47. In all the three MPTs, *Cryphaea* was supported as a monophyletic group. There are no fundamental differences between the topologies of these three MPTs. In the strict consensus tree two nodes collapse (Fig. 6). In Figure 6, Jackknife values above 50% are included. The Bremer support value (decay index) was one for each clade if not otherwise assigned in the figure. The Bremer support value indicates how many extra steps are required before the clade is lost from the strict consensus tree of near-minimum length cladograms (Bremer 1994).

The first MPT is arbitrarily chosen for the detailed analysis of character state changes (Fig. 7), which is also the MPT most closely corresponding with the strict consensus tree topologically. The character state transitions presented on Figure 7 are unambiguous ones only.

**Fig. 5.** The three most parsimonious trees (MPTs) resulting from the analysis of the data matrix including 33 taxa and 42 characters (L = 279, CI = 0.26, RI = 0.47).
Fig. 6. The strict consensus tree based on the three MPTs (L = 281, CI = 0.26, RI = 0.47). Jackknife values (when > 50%) are marked below the relevant clades. Bremer support values (when > 1) are shown above the clades. *CT indicating the costa type of inner perichaetial leaves. See text for explanations.
Fig. 7. One of the 3 MPTs. Character states marked on the tree are only unambiguous changes. Nonhomoplasious character states are marked with "■". Homoplasious character states are marked with "□". Numbers above the symbol indicate character numbers, below are state numbers. See text for explanations.
cladogram of figure 7. In addition, characters with a high value of RI (≥ 0.5) include: 0, 1, 4, 5, 6, 7, 8, 11, 17, 18, 19, 21, 23, 24, 25, 27, 28, 33, 34, 36, 41, whereas characters with a high value of CI (≥ 0.5) are found in 0, 6, 18, 24, 25, 28, 33, 34, 39 (Table 3).

From the topology of the tree (Fig. 7), Cypodontopsis and Dendrochrysea form a sister group to all members of Cryphaeae. The genus Cryphaeae is supported as a monophyletic taxon by the conical operculum (31) and the papilla-like thickenings of basal cells of inner perichaetial leaves (23). Furthermore, two plesiomorphic character states, the aquatic habitat (0) and small laminal cells (8), can be employed to well separate the sister group from the ingroup.

Table 3. A brief view of the character diagnoses (*L = Steps of character on the MPT of Fig. 7; *S = Synapomorphy without homoplasy if marked with “x” (synapomorphic state if marked with “s”, autapomorphy if with “a”); *u = uniform between sister group and ingroup).

| Character number | 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 4 4 | 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 |
| L*              | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| S*              | x a x s u* a a s s x x x s x x x a |
| Cl ≥ 0.5        | x x u x x x x x x x x |
| RI ≥ 0.5        | x x x x x x x x x x x x x x x x x x x x x x x x x x x x |

Within the ingroup (cf. Figs. 6, 7), two major groups (Groups A and B) can be distinguished according to the cladogram. Group A, including C. filiformis and C. orizabae, can be defined by three apomorphies, including large and distinctly prorate laminal cells (8, 11), and the inner perichaetial leaf costa strong at apex and vanishing downwards (17). This clade is sister to all other Cryphaeae taxa.

In Group B, four major clades can be roughly recognized (B1-B4). B1, including a single species, Cryphaeae glomerata, is actually a taxon on the node between A and B2. The clade B2-B4 is supported by the porose cell lumina of the inner perichaetial leaves (23), recurved stem leaf margins (4), and a longer columella (32). Within B2-B4, B2 is supported only by the whitish exostome teeth (36). The clade B3-B4 is supported by the large and sparsely papillose spores (40, 41). Finally, the species of clade B4, starting with C. apiculata, have setaceous leaf apex (2) and distinct median line of exostome teeth (37). All these four major clades lack enough support by jackknife values.

However, several lineages within clades B2 and B4 are supported by synapomorphies and/or in some cases the used indices indicate a support as well. In B2, B2I can be defined by strongly differentiated marginal cells of the inner perichaetial leaves (19). Within B2I, C. amurensis and C. songpanensis is supported by the occasionally forked costa (6). Another branch, C. chlorophyllosa-C. tenella, is supported by the absence of an annulus (33). This branch is strongly supported both by a high jackknife value (87%) and a high Bremer support value (3).

In the clade B4, the branch C. hygrophiha-C. ramosa is well supported by the large capsule (25), the campanulate calyptra (28), and the semi-hygrocastique peristome (34). Both
jackknife (75%) and Bremer support values (3) are reasonably high for this lineage. Another branch, _C. brevipila-C. rutenbergii_, is supported by the cylindrical capsule (24). This branch is supported by a moderate Bremer index (2) but without enough support of jackknife values. The other branch, _C. consimilis-C. parvula_, is supported by a moderate jackknife value (51%) though lacking support from any synapomorphic character state.

**EVOLUTIONARY TRENDS IN CHARACTERS**

The character states mapped on the MPT (Fig. 7) display some interesting evolutionary trends in _Cryphaea_. These may be helpful for understanding the systematic position of each genus in the Cryphaeaceae.

**Gametophyte.** The plants (1) seem to have evolved from small to large, especially in clade B4. The stem leaf margins (4) evolved from plane to recurved, with four reversals. The leaf costa (5) evolved from a short (subpercurrent) costa to a percurrent one, which have occurred once within B2 and B4 each; in the clade B2, two reversals happened, whereas in clade B4, the percurrent costa have further developed into incurrent ones (occurring three times independently). The leaf apices and acumina (2, 3) exhibit a trend from acuminate in the basal taxa to setaceous in the distal groups, occasionally reduced to acute or obtuse; the margins of the leaf acumen are basically entire, but gradually evolved to denticate, particularly in clade B4. The upper leaf laminal cells (7, 8, 11) evolved from oval to linear (three times) or rhombic (2 times) in distal groups; cell size was large in the basal taxa, then evolved to medium-sized, but in some taxa reversed to large-sized (four times) or evolved to very large size in distal groups; the ornamentation of the cells evolved from distinctly prorate to minutely prorate or smooth, but with four reversals. The leaf inner laminal cells (linear or rectangular) (10) were originally found below the leaf middle in the basal group, but frequently evolved to above leaf middle or even to the leaf apex (seven times), or occasionally reduced to indistinct (two times). The branch leaves (12) are mostly similar to stem leaves, but a much short costa in the branch leaves is evolved in some species (five times).

**Sporophyte, perichaetial leaves, and calyptra.** _Cryphaea_ is basically pleurocarpous (13) but three reversals (cladocarpous) occurred independently. The inner perichaetial leaves (17, 18, 19, 20, 21, 22) exhibit an interesting evolutionary trend: in the basal clade the costa is strong at the leaf apex, tapering downwards and failing near leaf base then evolved to fully costate (a character state occurring in the outgroups) in B1 and B2, but in B3-B4 the costa development trend evolved back into the same state as in the basal group, or developed into the ecostate type (occurring 2 times independently); the arista evolved from short to long, with the longest ones in the distal group; marginal cells developed from undifferentiated to strongly differentiated; laminal cells evolved from distinctly prorate to minutely prorate smooth (largely in B4); leaf shoulders are wider than lower portion in the basal and most taxa of _Cryphaea_ but with two clades reduced to narrower ones (a character state occurring in the hypothetical sister group of this genus, cf. Fig. 7), shoulder cells developed generally from sharply differentiated to gradually differentiated and undifferentiated; lumina of basal cells evolved from having papilla-like internal thickenings to porose (mainly in B2) or smooth (mainly in B4). As regard to the types of perichaetial leaves (Fig. 6), in both B1 and B2 they are uniformly of the type I. In B3 and B4 they are of all the three types. The two species in the
basal clade (C. filiformis, C. orizabae), however, have different types (II, Ic), which makes the evolutionary interpretation of the perichaetial leaf types ambiguous.

The urn mouth of the capsule (26) developed from undifferentiated to differentiated into a dark red ring. The seta (27) evolved from short to long but with reversals in two distal groups (in B2 and B4). The calyptra (28, 29, 30) seems to develop from short to long mitriform, and to campanulate in one lineage, from upper cells prorate to smooth (occurring six times independently), and frequently from entire margin to lobed (five times independently). The operculum (31) in Cryphaea was getting short (conical) when comparing with the outgroups (rostrellate or rostrate), the conical operculum is actually a common feature for most of the species, but with frequent reversals (occurring seven times independently). The columella (32) developed from short to long in the genus, though frequently reversed (8 times independently). The peristome type (34) seems to evolve from hygrocastique to semi-hygrocastique or xerocastique. The exostome teeth (35, 36, 37) were getting shorter in the clade B2 but longer in B4, and evolved from yellowish brown to whitish in color; the median lines of the teeth developed from indistinct to distinct or even to cracked in some distal clades (mainly in Australasian species). The spores (40, 41) evolved from medium-sized to small in the distal clades of B2 and B4, and from densely papillose to sparsely papillose mainly in B3 and B4.

6. TAXONOMIC TREATMENT

Cryphaea F.Weber


Notes on nomenclature — The genus was published in Weber 1814 (1813), which is actually a descriptive key to 43 genera, on three printed sheets, not paged, which was dated in 1813 but published in 1814. However, the author’s name of Cryphaea has long been erroneously attributed to Mohr as pointed out by Buck (1998). The name Cryphaea appeared indeed first in Weber 1814 (1813) and was listed as “Cryphaea Web”, but Weber stated that Mohr (1806) used the name Cryphaea as a subdivision of Neckera:

“A Neckera, ob diversitatem calytrae genera propria separandas putavi Cryphaeas et Ptychodres, quas subdivisiones Neckerae his nominibus, in Ann. of bot. II. notavit amicus Mohr”.

I checked the citation and found no such a name as Cryphaea used in Mohr’s paper, as Buck (1998) argued. Another possible misleading factor might be Brotherus (1905, 1925) who cited the genus as “Cryphaea Mohr in Web. Tab. Synopt. musc. (1803)”. I checked all pertinent documents and found no such a paper. It was obviously an erroneous citation of Weber 1814 (1813). However, Weber (1814) established the genus obviously based on the calyptra study of Mohr (1806) and as a matter of fact the “mitraeform” calyptra was emphasized for Cryphaea in his key.
Plants usually growing in dense or loose turfs, occasionally in cushions, exclusively epiphytic on trunks or branches of trees or shrubs, or on exposed roots, yellowish green, bright green, dark green, or brownish, mostly stout, a few species slender. Stolons (primary stems) creeping along substrate, very slender, mostly inconspicuous, bearing small, scale-like leaves, usually with dense, smooth, and unbranched rhizoids on the side facing substrate. Stems (secondary stems) erect or sometimes curved at tip, ca. (0.5–) 1–6 (–10) cm tall, densely to sparsely branched, rarely unbranched, in cross section with 2–5 brownish cortical cells sharply demarcated from hyaline, larger, thin-walled medullary cells, central strand absent. Branching mostly pinnate, sometimes irregular. Stem leaves ovate to lanceolate, apices acute to setaceous, usually concave in lower portion, imbricate to loosely appressed when dry, erect-patent to spreading when moist. Leaf margins entire to denticulate near apex, entire below, plane, or recurved in lower portion. Costa single, rarely forked occasionally (C. amurenensis and C. songpanensis), in most species ending below 0.75 of leaf length, sometimes percurrent, rarely excurrent. Leaf cells incrassate, inner basal (juxtacostal) cells usually specialized, linear to rectangular, rarely slightly or not differentiated, specialized inner cells usually restricted to lower ½ of lamina, occasionally extending to leaf apices, cells from distinctly prorate to smooth; apical cells usually longer than upper laminal cells; upper laminal cells usually elliptic, sometimes round, rhombic, or linear when inner basal cells reach apex; alar cells usually indistinct from adjacent upper laminal cells but often distinct from inner basal cells, usually subquadrate or rounded, forming obvious rows. Branch leaves smaller, usually similar to stem leaves, but sometimes costa much shorter (C. attenuata), lamina narrower (C. chlorophylllosa), or leaf cells more distinctly prorate (C. lanceolata). Pseudoparaphyllia filamentous, uniseriate, rarely biseriate at base, mostly 80–180 µm long. Paraphyllia absent.

Plant pleurocarpous, occasionally cladocarpous. Autoicous. Perigonia solitary in leaf axils, inconspicuous, bud-like; perigonal leaves ovate, ecostate, laminal cells linear or rhombic, prorate. Perichaetia frequent, monosetose, in clusters, mostly growing in 1–3 rows along one side of stems or branches; fertile branches very short, slightly to clearly swollen. Outer perichaetial leaves ovate to oblong-lanceolate; margins incurved; outermost leaves ecostate, apex usually acute to acuminate, rarely obtuse or setaceous; laminal cells usually linear in inner part, rectangular in marginal part, prorate to smooth. Inner perichaetial leaves oblong, above usually abruptly narrowed into a short to long arista, occasionally gradually forming an acumen which may be ending in a short awn; laminal cells mostly linear, sometimes rectangular, prorate to smooth, marginal cells usually short rectangular, or not specialized, in some species becoming hyaline on margins, basal cells usually wide, smooth, but sometimes brownish, with a few internal papilla-like thickenings, cells on laminal shoulders often shorter than adjacent cells, in some species not specialized, ecostate, partially costate to fully costate. Capsules immersed, erect, mostly elongated obloid, occasionally cylindrical or ellipsoid; stomata absent, rarely present in urn base; exothecial cells thin-walled, usually subquadrate above, irregular below. Seta very short, from absence to 0.35 mm long. Peristome hygrocastique, occasionally xerocastique, rarely semi-hygrocastique, double, hyaline to yellowish-brown; exostome teeth usually 170–600 µm long, lanceolate, median line usually distinct, or indistinct, rarely perforated/cracked along median line, papillose or smooth; endostome segments narrowly lanceolate to linear, usually shorter than exostome teeth, papillose or smooth. Annulus often present, rarely absent, formed by 1–3 rows of thick-walled cells. Columella persistent, usually reaching above ½ of theca length. Operculum conic,
rostellate, or rostrate, smooth. Calyptra short to long mitriform, rarely campanulate, entire, or split up one side, naked, but upper cells usually prorate, rarely smooth. Spores exosporic, ± globose, mostly 18–40 µm, occasionally bigger, coarsely papillose to smooth.

6.1. SYNOPSIS OF THE SUBDIVISIONS OF Cryphaea

The phylogenetic studies shed new light on the subdivision of Cryphaea. The analyses seem to support the monophyly of the genus, with C. filiformis-C. orizabae as its basal clade. Thus the early subdivision of the genus into three sections (Brotherus 1925), Obovatothecium S.Okamura, Eucryphaea Broth., and Cryphaeella M.Fleish., is unacceptable. Based on the cladograms (Fig. 5–7) and the above analyses, the basal clade (C. filiformis-C. orizabae) seems stable and can be well separated from other taxa. Superficially, the two species are quite similar to and seem somewhat related with the genus Schoenobryum. Sterile material of C. filiformis is actually “very difficult to separate from Schoenobryum concavifolium” (Buck 1998). I have been convinced that two subgenera can be relatively safely recognized within Cryphaea: the basal clade as one subgenus and the remaining taxa as the other. Within Group B, B1 and B2 are stable among all three MPTs (Fig 5, 6). B3 and B4, however, should be united as a single group. Although a few lineages in B2 and B4 are well supported, their relationships with sister groups remain largely unresolved, which may imply heterogeneity among the lineages within the major clades. As we know, “these reconstructions are estimates based on parsimony considerations, they are not observed facts” (Kitching et al. 1998). Thus, in the present study, I recognize two subgenera and three sections in Cryphaea. Molecular, ultrastructural, and biochemical characters, and a wider sampling of the whole family seem necessary for a satisfactory and more detailed subdivision of the genus.

Subgenus Filiformes P. Rao subg. nov.

Folia caulis plana, nullo modo recurvata, cellulae laminales magnae, 16–20 µm longae, distincte prorateae. Costa foliorum perichaetialium interiorum robusta ad apicem, decrescens deorsum, deest supra basin, cellulae distales marginalesque laminae foliorum perichaetialium valde breviores quam cellulae aliae laminae.

Type: Cryphaea filiformis (Hedw.) Brid.

Stem leaves plane, not recurved; laminal cells large, 16–20µm long, distinctly prorate. Costa of inner perichaetal leaves strong at apex, tapering downwards, failing above leaf base, cells in leaf shoulders sharply shorter than in lower leaf portion.

Taxa: C. filiformis, C. orizabae.

Subgenus Cryphaea

25
Stem leaves recurved, rarely plane, laminal cells usually small, 9–15 µm long, occasionally large, or very large (> 21 µm), minutely prorate to smooth, rarely distinctly prorate. Inner perichaetal leaves fully costate, occasionally failing above leaf base, rarely tapering upwards and failing below leaf apex (C. obovatocarpa), cells in leaf shoulders gradually shorter or not specialized, rarely abruptly shorter (C. acuminata, C. apiculata).

SECTION GLOMERATAE P. RAO SECT. NOV.

Planta parva, 0.5–2.0 cm alta. Margines foliorum caulis planae. Capsula ellipsoidea. Folia perichaetialia interioria admodum costata, cellulae laminales rectangulares, cellulae marginales non differentiatae, lumen cellularum basalium multipapillosum. Peristomium flavobrunneum. Annulus praesens.

Type: Cryphaea glomerata Sull.

Plants small, 0.5–2.0 cm tall. Stem leaf margins plane. Capsule ellipsoid. Inner perichaetal leaves fully costate, laminal cells rectangular, marginal cells not specialized, lumina of basal cells with papilla-like thickenings. Peristome yellowish brown. Annulus present.

Taxon: C. glomerata.

SECTION OBOVATOTHECIUM S.OKAMURA EX BROTH. EMEND. P. RAO

Type: Cryphaea obovatocarpa S.Okamura
[Type of Cryphaea obovatocarpa S.Okamura: Japan. Tango, Maruda in Maruyae-mura, 10. I. 1911 S. Okamura s.n. (lectotype nov. PC-Cardot!), see note below].

Plants medium-sized, up to (3–)5–6 cm tall. Stem leaf margins plane or recurved. Capsule obloid or ellipsoid. Inner perichaetal leaves fully costate (except in C. chlorophyllosa, C. obovatocarpa), laminal cells linear, marginal cells strongly differentiated (≥ 5 rows), rarely undifferentiated (C. acuminata, C. lanceolata), lumina of basal cells porose or smooth, rarely with papilla-like thickenings (C. songpanensis). Peristome whitish, rarely yellowish (C. nervosa). Annulus absent or present.

Note on typification. — I failed to find the types of Cryphaea obovatocarpa in the loans of NICH where S. Okamura’s specimens are supposed to be housed (Sayre 1977) but I saw a syntype hosted in PC (II), which I designate as the lectotype of the name.


SECTION CRYPHAEA
Type: *Cryphaea heteromalla* (Hedw.) F.Weber

Plants large, up to (5–)7–10 cm tall. Stem leaf margins recurved, rarely plane. Capsule cylindrical, obloid, or ellipsoid. Inner perichaetial leaves fully costate, or strong at apex and vanishing downwards, laminal cells linear, marginal cells not specialized, rarely differentiated (1–5 rows), lumina of basal cells smooth, occasionally porose or with papilla-like thickenings. Peristome whitish, or yellowish brown. Annulus present.


### 6.2. AN ARTIFICIAL KEY TO THE SPECIES OF *CRYPHAEA*

1. Leaf apices obtuse .................................................. *C. ovalifolia*
1. Leaf apices acute, acuminate to setaceous ................................. 2
2. Costa of stem leaves less than 0.7 of leaf length .......................... 3
2. Costa of stem leaves excurrent or longer than 0.8 of leaf length .......... 16
3. Stem leaf margins plane .................................................. 4
3. Stem leaf margins recurved .............................................. 7
4. Costa of perichaetial leaves strong at base, tapering upwards, disappearing below apex; marginal cells of perichaetial leaves strongly differentiated, in 7–12 rows .......................................................... *C. obovatoacarpa*
4. Costa of perichaetial leaves present throughout, or strong at apex, tapering downwards, rarely reaching to leaf base; marginal cells of perichaetial leaves not or weakly differentiated, in 1–3 row .............................................................. 5
5. Stem leaves wide-oblong below, abruptly acuminate; inner perichaetial leaves wide (0.55–1.22 mm) .............................................. *C. orizabae*
5. Stem leaves ovate, acuminate; inner perichaetial leaves narrow (0.45–0.68 mm) .... 6
6. Marginal laminal cells of inner perichaetial leaves not distinctly different from the inner cells (rectangular), costa of innermost perichaetial leaves strong, present throughout, awn short (< 0.2 of leaf length) ......................................................... *C. glomerata*
6. Marginal laminal cells of inner perichaetial leaves distinctly different from the inner cells (linear), costa of innermost perichaetial leaves strong at apex but failing at lower portion, awn long (ca. 0.35 of leaf length) .............................. *C. filiformis*
7. Inner basal linear cells of stem leaves extending from leaf base to apex .......... 8
7. Inner basal linear cells restricted to below the middle of leaves, or indistinct ........ 11
8. Stem leaves ovate-acuminate or ovate-lanceolate .................................. 9
8. Stem leaves oblong-acuminate .............................................. 10
9. Stem leaves larger, ≥1.5 mm long; peristome ca. 320 µm long; spores ca. 50 µm in diameter .......................................................... *C. gracillima*
9. Stem leaves smaller, ≤0.9 mm long; peristome ca. 270 µm long; spores ca. 35 µm in diameter ............................................... *C. songpanensis*
10. Stem leaves ≥2 mm long, costa stout, cells slightly prorate; exostome teeth brownish, long, ca. 430–450 µm long; spores ca. 38 µm in diameter ............................. *C. ragazzii*
10. Stem leaves <1.5 mm long; costa weak; cells distinctly prorate; exostome teeth whitish, very short, ca. 170–180 µm long; spores ca. 26 µm in diameter .................. C. amurensis
11. Leaf apices cuspidate or abruptly acuminate .............................................. 12
11. Leaf apices acute or gradually acuminate .................................................. 13
12. The widest part of stem leaves above leaf middle; inner basal cells distinct, linear .............................................................. C. apiculata
12. The widest part of stem leaves below the leaf lower 1/3 portion; inner basal cells indistinct, oblong to rectangular .............................................. C. acuminata
13. Costa of inner perichaetial leaves stout, present throughout; peristome hygrocastique ........................................................................................................... 14
13. Inner perichaetial leaves ecostate; peristome semi-hygrocastique .................. 15
14. Apical cells of stem leaves round to elliptical; spores smaller, ca. 16 µm; exostome teeth shorter, ca. 370 µm long ................................................................. C. heteromalla
14. Apical cells of stem leaves linear; spores larger, ca. 45 µm; exostome teeth longer, ca. 550 µm long ................................................................. C. protensa
15. Leaves oblong acuminate; awn of inner perichaetial leaves distinct, > 0.3 of the leaf length ................................................................. C. ramosa
15. Leaves ovate acuminate; awn of inner perichaetial leaves indistinct, < 0.1 of the leaf length ................................................................. C. hygrophila
16. Costa excurrent, forming a clear arista ............................................................. 17
16. Costa percurrent, not excurrent ........................................................................ 20
17. Central linear cells differentiated from stem leaf base to apex ............. C. clandestina
17. Central linear cells restricted to lower half of leaf or undifferentiated .............. 18
18. Stem leaves large, > 2.2 cm long, inner basal cells linear, very different from surrounding rectangular to elliptical .................................................. C. pilifera
18. Stem leaves small, < 0.9 cm long, leaf inner basal cells irregularly quadrate, not distinct from surrounding cells .................................................. 19
19. Exostome teeth shorter, ca. 380 µm; awn of inner perichaetial leaves shorter, ca. ½ the lamina length ................................................................. C. consimilis
19. Exostome teeth longer, ca. 520 µm; awn of inner perichaetial leaves longer, ca. 2/3 the lamina length ................................................................. C. parvula
20. Upper laminal cells of stem leaves vermiculate or linear-rhomboideal .............. 21
20. Upper laminal cells of stem leaves oval .................................................. 24
21. Leaves lanceolate ................................................................. 22
21. Leaves ovate-acuminate .............................................................................. 23
22. Stem leaves lanceolate, costa in branch leaves much shorter than that in stem leaves; margin near apices entire to denticulate, upper marginal cells linear .......................................................... C. attenuata
22. Stem leaves ovate lanceolate, costa in branch leaves similar to stem leaves; margin near apices denticulate; upper marginal cells elliptical .................................. C. jamesonii
23. Stem leaves smaller, ca. 1.0×0.5 mm, glossy, marginal cells round to elliptic, laminal cells distinctly prorate, margin near apices entire to denticulate .............. C. nervosa
23. Stem leaves larger, ca. 1.7×0.8 mm, plicate, marginal cells linear; laminal cells smooth, margin near apices entire ................................................. C. chlorophylloosa
24. Capsule cylindrical; stem leaf margins plane (at least in most leaves) ............. 25
24. Capsule obloid or ellipsoid; stem leaf margins recurved, never plane ............. 27
25. Operculum rostrate; costa of stem leaves always reaching leaf tip .......... \textit{C. brevipila}
25. Operculum conical; costa of stem leaves sometimes disappearing below leaf tip ..... 26
26. Stem leaves broadly ovate-acute; exostome teeth shorter, ca. 320–400 µm ..............
................................................................. \textit{C. rutenbergii}
26. Stem leaves oblong-acuminate; exostome teeth longer, ca. 400–520 µm ..............
................................................................. \textit{C. rhacomitrioides}
27. Stem leaves lanceolate ......................................................... 28
27. Stem leaves ovate-acute(- acuminate) ............................................. 29
28. Costa of branch leaves similar to that in stem leaves; exostome teeth perforated / cracked
    along median lines; annulus absent ........................................... \textit{C. tenella}
28. Costa of branch leaves much shorter than that in stem leaves; exostome teeth not
    perforated / cracked; annulus present ....................................... \textit{C. lanceolata}
29. Leaf apex abruptly acuminate; laminal cells distinctly prorate; exostome teeth shorter, ca.
    180–210 µm ............................................................................. \textit{C. omeiensis}
29. Leaf apex acute to acuminate; laminal cells minutely prorate to smooth; exostome teeth
    longer, ca. 380–400 µm ............................................................... \textit{C. patens}

7. \textbf{ECOLOGY AND PHYTOGEOGRAPHY}

7.1. \textbf{ECOLOGY}

As epiphytes, \textit{Cryphaea} species occupy trunks, branches, or exposed roots of trees and
shrubs. The survival of each species is dependent on its ability of dispersal and colonization,
the availability of suitable substrate, i.e., host plants to which it can become affixed and
persist, and the general environmental conditions of the site (e.g., climatic conditions). A
thorough study of the label information of all the specimens examined and the biological
observations depict some of \textit{Cryphaea}’s ecological features.

Most \textit{Cryphaea} species are confined to oceanic to suboceanic areas. Very few taxa can
survive inner continental areas and are represented by a few scattered occurrences. All species
of \textit{Cryphaea} seem to prefer a humid environment, though three taxa were reported from a few
localities in relatively dry regions: \textit{Cryphaea brevipila}, \textit{C. pilifera}, and \textit{C. filiformis}. The first
two taxa were collected in “dry areas” of Ecuador and Bolivia, respectively, and the last one
in semi-arid deciduous forests in Honduras.

Though mainly confined to oceanic/suboceanic areas, \textit{Cryphaea} species seem to be
adapted to seasonal or periodical desiccation. The following structural features, as discussed
in the section \textit{MORPHOLOGY AND ANATOMY}, most probably function to resist or retard
desiccation: (1) the plants usually grow in dense turfs or cushions so as to form many
capillary spaces, which can prevent rapid water loss; (2) the leaves are imbricate when dry;
(3) the inner basal cells of leaves are usually linear so as to appress to the stem tightly when
dry; (4) the capsules are immersed in perichaetial leaves because of the short seta (cf.
Hedenäs 2001); (5) the columella is persistent to keep the capsule from collapsing when dry.

From label information, though somewhat sporadic and insufficient, we get a general
picture of the host plants colonized by \textit{Cryphaea}. The European \textit{C. heteromalla} seems only to
grow on broadleaf trees such as Acer, Betula, Buxus, Castanea, Fraxinus, Populus, Quercus, Salix, Sambucus, Ulmus in deciduous forests. The African species, however, grow both on angiosperm trees such as Erica, Olea, Phoenix and on gymnosperms such as Juniperus and Podocarpus. Most Australasian taxa are found on Fuchsia among other plants including Eucalyptus, Leptospermum, Salix, Syzygium. In America the species of Cryphaea grow on various trees and shrubs in different types of forests. Cryphaea glomerata and C. nervosa, the two U.S.A. endemics, occupy similar habitats and are often found growing together on twigs, trunks, or dead branches or logs of Celtis, Quercus, Cedrus, and Juniperus in mesic forests of the Coastal Plain (Manuel 1973). Strangely enough, both of them, especially C. glomerata, are very common species in the eastern U.S.A. but are not found elsewhere. In the Neotropics, Cryphaea apiculata is epiphytic on tree bark in mixed subparamo-forest, Pinus-Quercus forest, and also on trees and shrubs of grassland. Cryphaea attenuata occurs on trunks or branches in Pinus-Alnus forests. Cryphaea consimilis grows on trunks or branches of Nothofagus, Populus, Quercus, and Fuchsia, mainly in lowland Nothofagus dominated forests. Cryphaea filiformis is encountered on twigs, branches and trunks of Citrus, Ximenia etc. in different types of habitats from hardwood-Taxodium swamps, tropical hardwood hammocks, semi-arid forests, to Citrus orchards. Cryphaea patens, with numerous collections from a wide geographic area, is epiphytic on trees in various types of forests such as Cupressus, Quercus-Pinus, Liquidambar-Quercus forests, and some ‘humid’ forests. It is interesting to find that C. pilifera can grow on spiny shrubs (Berberis, Bernadizia, Hesperomeles) and trees in pine plantations. Cryphaea hygrophila and C. ramosa seem to prefer trees or shrubs among grasslands or near the treeline of upper montane forest or subalpine forest (Whitmore 1998) at an altitude around 2800–4000 m, sometimes found together with C. filiformis. Cryphaea rhacomitrioides prefers humid lower montane forest and is frequently found on Alnus trunks. Some species are found dominant on tree trunks or branches in the highland forests among other epiphytes in the local bryoflora (e.g., C. pilifera, C. ramosa), but some other species are highly endemic ones (C. consimilis, C. gracillima, C. attenuata). As for Asian Cryphaea species, most of them are only known from a few collections. From the current information it can be concluded that C. obovatocarpa prefers to grow on Morus, C. songpanensis on Abies, and C. lanceolata on deciduous trees or shrubs. Cryphaea clandestina was found on “sunny twigs” in very wet rain forest (Enroth 1990) and C. amurenensis grows on trunks and twigs of Abies, Picea, Betula, Populus, Padus, Alnus, in forests in flood valleys, often with Neckera pennata and Leucodon pendulus (Ignatov et al. 2000).

Capsules are frequently produced in the Cryphaea species. In addition to their autoicous sexual condition, another possible reason for this is the inability of asexual reproduction in the genus. Spores seem undoubtedly to be the most important means of reproduction and dispersal. The different types of peristomes may have developed to control the spore release effectively in different environments. In a few species (C. apiculata, C. gracillima), multicellular spores have been observed (Crum 2001) and these may be adaptations for quick and continued growth once they have dispersed. However, according to our current knowledge about the distribution of the genus, its species still seems unsuccessful in colonizing most regions of the world. Possible explanations for this include: (1) Ineffective spore dispersal. Because the species mainly inhabit humid forests, the dispersal of spores by wind may be restricted by the moist, wind-breaking forest habitat (Crum 2001) and a relatively large size of the spores; (2) Lacking specialized asexual reproduction; (3)
Atmospheric pollution. As pointed out by Dickson (1973), partial or total elimination of many common bryophytes (such as *Cryphaea heteromalla*, *Leucodon sciuroides*, and *Uloa crispa*) from areas downwind of sources of atmospheric pollution has been convincingly demonstrated. The recent decrease of corticolous species was most probably caused by air pollution; (4) The general crisis in tropical bryology: the rapid destruction of plant life in tropical countries (Schultze-Motel 1982); (5) Fluctuations in climate and vegetation in the long history, which might destroy the suitable habitats of *Cryphaea* species and cause subsequent fragmentation and extinction of their populations. Further biological and ecological studies may be necessary to explore other possible causes such as the abilities of spore germination and competition with other species of the same ecological niches.

It seems difficult for *Cryphaea* species to survive in dry areas (as in western Asia, North & West Africa, western Australia, and western North America). Their distributions are also limited in regions where the climate is too hot or too cold seasonally (as in Southeast Asia). Additionally, dark dense forests (as in tropical lowland rain forests) are not very suitable habitats for them. Thus, most of the specimens were collected from deciduous, humid forests at high elevations (around 3000 m) in tropical areas (such as *C. patens*) and at low elevation (below 500 m) of temperate areas (such as *C. glomerata*, *C. heteromalla*). Generally speaking, *Cryphaea* is habitat sensitive and prefers a humid, cool, and relatively high light environment. This may partly explain why the uprisng Andes and its surroundings areas have become the current diversity and distribution center of this genus.

### 7. 2. Phytogeography

*Cryphaea* species are distributed from tropical montane to oroboreal regions, from the sea level to above 6000 m in altitude. Within this wide geographic range, however, most individual species have highly specific distributional patterns (Fig. 8). The total numbers and the number of endemics for each geographical area are indicated in Figure 8. Almost all individual species exhibit restricted patterns of distribution, with only one exception, *C. jamesonii* occurring in both the Neotropics and Africa. Five species are represented in eastern Asia (seven species in the whole Asia, *cf. I, II*) and known from very few collections. There are a bit more collections of eastern African and Australian species but far from numerous. In central and southern Europe, though large number of collections, only one species, *C. heteromalla*, has been found. Similarly, in North America, abundant specimens were collected of only two species, *C. glomerata* and *C. nervosa*, on the eastern Coast Plain of U.S.A. The diversity center of the genus seems to be in the Neotropics, where 13 species are recognized, with some species (e.g., *C. patens*, *C. filiformis*) of a relatively wide distributional range and some dominant taxa (e.g., *C. pilifera*, *C. ramosa*) on tree trunks or branches among other epiphytes in the local bryofloras.

In regard to the vertical distribution, some species seem to be flexible but others are more rigorous. However, for those species known only from a few collections, it is premature to draw any conclusions regarding their vertical distribution ranges. The species of *Cryphaea* can be tentatively divided among seven main distributional patterns. A summary for their altitudinal and geographical ranges is given in Table 4 for easy reference.
Fig. 8. Species distribution of the genus *Cryphaea*. The total number of species for each region is given below and the number of endemic species is given above.

**Southeast Asian Endemics**
The genus is poorly represented in Asia (I, II). *Cryphaea lanceolata*, *C. omeiensis*, and *C. songpanensis* are all endemic to the interior hilly areas of China. *Cryphaea lanceolata* is represented by a few collections, whereas the latter two species are known only from the types. *Cryphaea obovatocarpa* occurs mainly in central and southern Japan; there is a single specimen known from Taiwan. *Cryphaea amurensis* is known from a few collections, and *C. clandestina* is only known from the types.

**Australasian Distribution**
In Australian and Oceanian region (III), New Zealand seems to be the diversity center of *Cryphaea*, where all five species are found from both North and South Islands. *Cryphaea acuminata* and *C. chlorophyllosa* are endemic to New Zealand. *Cryphaea parvula* is mainly distributed in New Zealand (200–1000m) but with a few collections from Tasmania. *Cryphaea ovalifolia*, however, has frequently been collected in Victoria, Australia but “its geographic range in New Zealand is fairly wide, too” (Enroth 1995) (100–150 m). *Cryphaea tenella* has frequently been collected in New South Wales and Queensland of Australia (40–800 m) and New Zealand (around 200 m) and it also occurs on Tahiti and New Caledonia.

**African Distribution**
Most African species are distributed in eastern African countries (III). *Cryphaea razazzii* is

<table>
<thead>
<tr>
<th>Species</th>
<th>Geographical Distributions</th>
<th>Altitudinal Range (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. amurensis</em></td>
<td><strong>SE</strong> <strong>ASIAN ENDEMICS</strong> Russia (Khabarovsk)</td>
<td>430–1000</td>
</tr>
<tr>
<td><em>C. clandestina</em></td>
<td>Papua New Guinea</td>
<td>2400</td>
</tr>
<tr>
<td><em>C. lanceolata</em></td>
<td>China</td>
<td>1600–2500</td>
</tr>
<tr>
<td><em>C. obovatomarpa</em></td>
<td>Japan / China (Taiwan)</td>
<td>100–400 / 1500–2000</td>
</tr>
<tr>
<td><em>C. omeiensis</em></td>
<td>China</td>
<td>1000–1200</td>
</tr>
<tr>
<td><em>C. songpanensis</em></td>
<td>China</td>
<td>2900–2930</td>
</tr>
<tr>
<td><em>C. acuminata</em></td>
<td>New Zealand</td>
<td>100–1500</td>
</tr>
<tr>
<td><em>C. chlorophyllosa</em></td>
<td>New Zealand</td>
<td>≤ 300</td>
</tr>
<tr>
<td><em>C. ovatifolia</em></td>
<td>Australia and New Zealand</td>
<td>100–150</td>
</tr>
<tr>
<td><em>C. parvula</em></td>
<td>New Zealand and Australia (Tasmania)</td>
<td>200–1000</td>
</tr>
<tr>
<td><em>C. tenella</em></td>
<td>Australia, New Zealand, New Caledonia, and Tahiti</td>
<td>40–800</td>
</tr>
<tr>
<td><em>C. protensa</em></td>
<td><strong>AFRICAN DISTRIBUTION</strong> E* African countries</td>
<td>1500–3225</td>
</tr>
<tr>
<td><em>C. ragazzii</em></td>
<td>Mozambique</td>
<td>?</td>
</tr>
<tr>
<td><em>C. rutenbergii</em></td>
<td>E African countries and Madagascar</td>
<td>1200–2400</td>
</tr>
<tr>
<td><em>C. heteromalla</em></td>
<td><strong>EURASIAN-N</strong> <strong>AFRICAN DISTRIBUTION</strong> European countries, e.g., Ireland / Spain</td>
<td>30–190 / 200–1000</td>
</tr>
<tr>
<td></td>
<td>African countries, e.g., Tanzania</td>
<td>2300</td>
</tr>
<tr>
<td><em>C. glomerata</em></td>
<td><strong>EN</strong> <strong>AMERICAN DISTRIBUTION</strong> U.S.A.</td>
<td>300–1000</td>
</tr>
<tr>
<td><em>C. nervosa</em></td>
<td>U.S.A.</td>
<td>130–1050</td>
</tr>
<tr>
<td><em>C. consimilis</em></td>
<td><strong>NEOTROPICAL DISTRIBUTION</strong> <strong>LOWLAND DISTRIBUTION</strong> Chile</td>
<td>20–730</td>
</tr>
<tr>
<td><em>C. filiformis</em></td>
<td>CS* American countries and U.S.A. (Florida)</td>
<td>200–1000</td>
</tr>
<tr>
<td></td>
<td><strong>LOWLAND TO SUBALPINE DISTRIBUTION</strong></td>
<td></td>
</tr>
<tr>
<td><em>C. brevipila</em></td>
<td>S* American countries</td>
<td>300–3300</td>
</tr>
<tr>
<td><em>C. orizabae</em></td>
<td>CS American countries</td>
<td>350–2100</td>
</tr>
<tr>
<td><em>C. patens</em></td>
<td>CS American countries</td>
<td>100–6500</td>
</tr>
<tr>
<td><em>C. rhacomiroides</em></td>
<td>Argentinia and Brazil</td>
<td>940–2100</td>
</tr>
<tr>
<td></td>
<td><strong>UPPER MONTANE TO SUBALPINE DISTRIBUTION</strong></td>
<td></td>
</tr>
<tr>
<td><em>C. apiculata</em></td>
<td>CS American countries</td>
<td>1420–3600</td>
</tr>
<tr>
<td><em>C. attenuata</em></td>
<td>C* American countries</td>
<td>2100–2880</td>
</tr>
<tr>
<td><em>C. gracilima</em></td>
<td>CS American countries</td>
<td>2600–3335</td>
</tr>
<tr>
<td><em>C. hygrophiha</em></td>
<td>Bolivia</td>
<td>2900–3750</td>
</tr>
<tr>
<td><em>C. pilifera</em></td>
<td>S American countries</td>
<td>1800–4000</td>
</tr>
<tr>
<td><em>C. ramosa</em></td>
<td>S American countries</td>
<td>2100–4000</td>
</tr>
<tr>
<td><em>C. jamesonii</em></td>
<td><strong>NEOTROPICAL-AFRICAN DISJUNCTION</strong> CS American and E African countries</td>
<td>400–3000</td>
</tr>
</tbody>
</table>
endemic to Mozambique, known only from the type. *Cryphaea protensa* is confined to middle-eastern African countries (AFR2), the collections coming mainly from Tanzania (1800–3225 m) and Ethiopia (2700–3000 m) but also from the neighboring Kenya and Malawi (1500–1700 m) from middle to high montane forests. *Cryphaea rutenbergii* was first reported from Madagascar but was later found to be widely distributed along eastern to south coast regions of Africa, with many collections from Tanzania (1600–2300 m). Other specimens I examined are from Ethiopia (2100–2400 m), Kenya (1850–2300 m), Malawi (1700 m), Uganda (1440–1480 m), and South Africa (1200–1400 m).

**Eurasian-North African Distribution**
The European and fairly common *C. heteromalla* has a relatively wide distribution (III), from southernmost Sweden and Denmark in the north, Ireland (30–190 m) and U.K. (10–160 m) in the west, Iran and West Russia in the east, and a single specimen was examined from each of Algeria and the mossy forest of Tanzania (2300 m), which is the southernmost known locality.

**Eastern North American Distribution**
Two endemics are found in eastern North America: *Cryphaea glomerata* and *C. nervosa*. Both grow on the southeastern Coastal Plain of the U.S.A. with their major distribution in the Gulf Plain from Florida to Texas. *Cryphaea glomerata* extends further north than does *C. nervosa* into states such as Ohio and Virginia and enters into more southern part of Florida as well (Manuel 1973, III).

**Neotropical Distributions**
*Cryphaea* reaches its greatest diversity in the Neotropics. The main distributional areas are from Mexico and Caribbean areas to Venezuela, Colombia, then along the west coastal countries, Ecuador, Peru, Bolivia, then North Argentina, to southernmost Brazil. According to their vertical distribution information, three sub-patterns may be recognized.

- **Lowland Distribution**
  Two species are confined to Neotropical lowlands. *Cryphaea filiformis* is mainly distributed in Mexico and Caribbean Islands but is also found from southern Florida of U.S.A. and South American countries. Its appearance in Colombia and Venezuela is expected but further studies should be made to explore if it is really missing from the central South America areas and has “jumped” to the southernmost Brazil and Uruguay. This is actually a common pattern, maybe the Amazonian lowlands are not suitable habitats for these species or maybe they are simply undercollected.

  On the southwestern coast, another Neotropical lowland species, *C. consimilis*, is endemic to Chile and occurs in humid forests.

- **Lowland to Subalpine Distribution**
  There are four species occurring in a wide range of elevations from lowlands, lower and upper mountains, to subalpine areas. *Cryphaea brevipila* has a relatively wide altitudinal range in South American countries, though it is represented by a limited number of collections. It has
been found from Colombia, Ecuador (3000–3200 m), Peru (300–3300 m), Bolivia (400 m), and Argentina, but mainly from Brazil. The species was recorded from both dry and wet areas. Another more widely distributed species is *C. patens*, which occurs in the high montane areas of southern Mexico (2000–6500 m), the Caribbean Islands (Dominican Republic) (1020 m), Guatemala (1590–3500 m), El Salvador (1300 m), Costa Rica (1500 m), and the South American countries of Colombia (1500–2470 m), Venezuela (2000 m), Ecuador (3000–3300 m), Peru, Chile (260 m), Bolivia, Paraguay (100–200 m), Argentina (500 m), and Brazil (200–1200 m). Many collections come from Mexico and Colombia but it is not rare in Brazil and Paraguay either.

*Cryphaea orizabae* is distributed mainly in southern Mexico, Guatemala, and the Caribbean Islands (Dominican Republic) (350–2100 m) but it is also found in southernmost Brazil (ca. 450 m). Further study is necessary to clarify if this distributional pattern is really disjunct or simply due to undercollection. *Cryphaea rhacomitrioides* has a more narrow distributional area, mainly in northern Argentina and with one collection from neighboring Brazil.

- **Upper Montane to Subalpine Distribution**

Six species are currently found only growing in the upper montane to subalpine regions. *Cryphaea apiculata* has been found from a relatively wide area (AM2, 4, 5) with a moderate number of collections. This species seems to inhabit mainly Bolivia (2400–3600 m), Peru (2300–3200 m), and Ecuador (1800–3600 m). A few collections are known from Mexico (1420–1510 m), and only a single specimen from each of Guatemala (1800 m), Colombia (3200 m), and Guyana.

Both *Cryphaea pilifera* and *C. ramosa* have the same distribution range (AM4) from Venezuela, Colombia, Ecuador, Peru, and Bolivia. They usually form dominant communities on tree trunks, branches, and twigs in the Neotropical montane forests. They are frequently found growing together. But *C. pilifera*, as mentioned under the Ecology subsection, can also survive in drier habitats such as roadside trees and montane scrub.

*Cryphaea gracillima* is clearly a rare and endangered species. In Bolivia (2600 m) it is only known from the type material. It is newly reported from Costa Rica (3335) and Ecuador, where it is represented by one specimen from each country (III).

*Cryphaea attenuata* seems fairly rare. I only saw a couple of specimens from Mexico at 2880 m of elevation (III). It was reported from Guatemala (ca. 2700 m) and Costa Rica (2450 m) by Manuel (1981), one specimen being known from each country. Manuel (1981) also recorded a specimen from lower altitude (2100 m) of Mexico.

*Cryphaea hygrophila* is endemic to the highlands of Bolivia.

**Neotropical–African Disjunction**

*Cryphaea jamesonii* is the only continental disjunct species in the genus. The geographic range of this species in America is fairly wide, reaching from Mexico and the Caribbean Islands to the northern South American countries (AM2–5) in upper montane forests between 1450–3400 m. Its distribution in Africa exhibits a tricentric pattern: mainly in mesic montane forests of the eastern African countries of Uganda (2400 m), Kenya (2750 m), eastern Zaire (2500 m), Rwanda (2000–3000 m), and Tanzania (1900–3100 m); it is also found in the lowland forests of South Africa (400–1250 m); and one collection is from the island
Madagascar (1200–2400 m). However, no collections are known from the western African countries.

7.3. HYPOTHESIS OF ORIGIN

No fossil specimens have ever been found of *Cryphaea* (cf. Dickson 1973, Miller 1980, 1984, 1987, Krassilov & Schuster 1984, Oostendorp 1987). The following hypothesis regarding the origin of the genus is therefore based on the distributional patterns of the extant species and on the results of the phylogenetic analysis.

As a whole, the extant species of the genus have a Pantropical disjunct distribution (Fig. 8). Most Pantropical disjuncts have a relatively old origin between the Jurassic and Mid-Cretaceous (ca. 190–100 m.y. BP) in Gondwanaland, before the break off of Madagascar and the Indian subcontinent (Menzel & Schulze-Motel 1987). However, the absence of *Cryphaea* from the Indian subcontinent and the areas along its rafting route suggests that the genus evolved after the separation of Indian subcontinent from Africa. According to the maps presented by Audley-Charles et al. (1981), the possible timing would have been around 70–60 m.y. BP (Late Cretaceous to early Tertiary) when the intercontinental gap was sufficiently wide to prevent long distance dispersal.

From the above phylogenetic and phytogeographical analyses, a relatively strong floristic affinity between Neotropics and Africa can be seen. Apart from the evidence that *Cryphaea jamesonii* is distributed in both continents, two other African species are closely related with the Neotropical vicariant species: *Cryphaearagazzii-C. gracillima, C. rutenbergii-C. rhacomitrioides* (cf. B3, B4 of Fig. 6.). Additionally, *C. protensa* is probably on the node between *C. apiculata* and the *C. ragazzii-C. gracillima* clade (Fig. 7). African-American disjunctions have been a much studied topic of bryologists in the past thirty years (e.g. Schofield & Crum 1972, Zander 1972, Bizot & Pócs 1979, Gradstein et al. 1983, Schuster 1983, Menzel & Schulze-Motel 1987, Delgadillo 1993). Delgadillo (1993) presented three hypotheses for this distribution pattern: (1) Land connection hypothesis; (2) Long-distance dispersal hypothesis; (3) Secondary dispersal center hypothesis.

As discussed under the subsection ECOLOGY, species of *Cryphaea* are likely to have a low ability for long-distance dispersal. The land connection hypothesis seems a good explanation for the affinity of South American-African *Cryphaea* taxa, though long-distance dispersal might have occurred in some ‘recent’ species (see below). The evidence suggests that these taxa are of a common Gondwanalandic origin, which evolved and spread before South America had drifted far away in the Late Cretaceous (Delgadillo 1993). Additionally, the cladograms (Figs. 5–7) indicate that the most primitive species (*C. filiformis-C. orizabae*) of the extant taxa are from the Neotropics, and the current distribution and diversity center undoubtedly lies in this area. It thus seems plausible to speculate that the common ancestor of *Cryphaea* might have occurred in South America-Africa around the Late Cretaceous to early Tertiary (ca. 70–60 m.y. BP). Deductions from the two different points of view seem to come to the same conclusion.

Based on the above hypothesis, the genus *Cryphaea* can be deduced to have occurred first in South America-Africa (Neotropic-Paleotropical). Then *Cryphaea* species were dispersed via the two continents while they were drifting away from each other. Africa rafted species to Eurasia, while the South American taxa disseminated to Caribbean islands and North
America. As for the distribution on New Zealand, Australia and Oceania Islands, the simplest explanation is to assume that *Cryphaea* evolved somewhere in the South America-Antarctic-Australia chain of continents around the Late Cretaceous to the Late Eocene (cf. Fig. 7.5 of Cox and Moore 1993: 186–187). Subsequent development and speciation have shaped the group to the current situation. This hypothesis is largely supported by the cladograms (Fig. 6, 7) especially in clade B3 and B4.

In the parsimony evolutionary consideration (Fig. 6, 7), the basal subgenus, *Filiformes*, as mentioned above, occurs in the Neotropics. Within the subgenus *Cryphaea*, dispersal routes can be hypothesized for the three recognized sections. Section *Glomeratae*, with only one species, is endemic to the eastern Coastal Plain of the U.S.A. It may be a local speciation of an early separation from a close ancestor of the basal taxa. Section *Obovatothectum*, comprising most of the Australian-Oceanic and Southeast Asian species, has an Australasian-Asian-North American pattern and seems to suggest a dispersal route from Australasia to Southeast Asia with recent speciation in Asia (e.g., *Cryphaea obovatocarpa*) and South Pacific Islands (e.g., *C. chlorophyllosa-C. tenella* clade). This section, however, includes a species of North American endemics (*C. nervosa*), whose distribution route remains ambiguous. It is related with the Southeast Asian taxa (*C. amurensis-C. songpanensis*). These species seem unlikely to be distributed via long distance dispersal. This America-Southeast Asia pattern is similar to the angiosperm genus *Magnolia* and *Liriodendron* (cf. Cox and Moore 1993: 38–39), and thus these species can be explained as evolutionary relics, though fossil evidence is lacking of *Cryphaea*. Section *Cryphaea* exhibit a Pantropical distribution pattern with South American-African taxa as the basal group, which is consistent with the hypothesis above. The basal species are from the Neotropics and African. The European dominant species, *C. heteromalla*, shows a close relationship with the African species. Two closely related vicariant species between Chile-New Zealand (*C. consimilis-C. parvula*) are presented in this section as expected. The most apomorphic species *C. clandestina*, from Papua New Guinea, may be a new speciation from the gene pool of a South American taxon. It is interesting that two vicariant species (*C. patens-C. omeiensis*) occur between the Neotropics and Asia. They may be speciations from an earlier wide-spread extinct ancestor or close relatives. However, the South America-Africa disjunct *C. jameonii*, sitting on a distal branch and thus seeming to be a relatively ‘recent’ species, might be a result of long-range dispersal by chance, the explanation being congruent with the fact that the species has relative small spores (15–26 µm). Another possible explanation could be that a lot of the evolution within the genus occurred before the two continents were effectively separated from each other, since the clade *C. rutenbergii-C. rhacomitrioides* is also relatively ‘recent’.

Formal methods for reconstruction of the ancestral areas have been proposed (e.g. Bremer 1992). The use of these methods requires a robust hypothesis of phylogeny for the group of interest but also on a larger scale in order to make reliable conclusions about ancestral distribution for the whole group and particularly the most basal node. As a robust hypothesis of the phylogeny of the family Cryphaeaceae is currently lacking I did not attempt to make a formal analysis of the ancestral areas of the genus *Cryphaea*.

The extant species thus could be habitat/climatic relics (as some Southeast Asian species) or evolutionary relics (as some African taxa), because *Cryphaea* as a habitat/climate sensitive group could be partially or totally eliminated during the history if suitable habitats were destroyed.
8. CONCLUSIONS

*Cryphaea* appears to be a monophyletic taxon. The genus can be defined by the following features: plants exclusively epiphytic; stems ‘erect’, developed from shoots by turning 90° from stolons which are prostrate on the substrates, central strand absent; pseudoparaphyllia filamentous; leaves costate, inner basal cells specialized (linear or rectangular); capsule erect, immersed; seta very short (≤ 0.35 mm); calyptra mitriform (rarely campanulate), naked, smooth or with upper cells prorate; peristome double; operculum mostly conic; columella persistent; and asexual propagula absent.

The circumscription of *Cryphaea* has been amended in my studies. The exclusion of *C. leveillei* (I) and *C. ravenelii* (III) from the genus renders *Cryphaea* a genus with only double-peristomate species. An aquatic species, *C. lamyana*, was transferred to *Dendrocryphaea* (III), which leaves the genus more uniform in terms of habitat ecology. *Cryphaea* then can be well separated from other genera of the family. *Cypodontopsis* (I), *Monocryphaea* (III), and *Schoenobryum* are distinct from *Cryphaea* by the single peristomes; *Cystodon* and *Dendrocryphaea* (III) occupy aquatic habitats; *Cryphidium* has round apices of the stem leaves; *Pilotrichopsis* and *Dendropogonella* can be separated from *Cryphaea* by the long and pendent stems; *Sphaerotheciella* differs from *Cryphaea* by the endospore germination with precocious, intracapsular protonematal development (II, Rao 2000).

A comprehensive phylogenetic analysis of the genus was made based on 42 morphological characters. The indices of the most parsimonious trees (Fig. 5, 7) show a relatively low resolution (CI = 0.26, RI = 0.47). Most of the characters display considerable homoplasies.

Character diagnosis of the phylogenetic studies shows that the following apomorphic character states developed within the genus: excurrent or occasionally forked costa of stem leaves (5, 6), rhombic laminal cells (7), cylindrical or large capsules (24, 25), campanulate calyptra (28), conic operculum (31), and the absence of annulus (33). Autapomorphic character states were developed in a few species such as *Cryphaea obovotocarpa* (costa of inner perichaetial leaves tapering upwards (17)) and *C. hygrophi/a* (inner perichaetial leaves having very short awn, less than 1/10 of the leaf length (18)). Furthermore, some characters are found to be phylogenetically informative for this group, such as margins and costa of stem leaves (4, 5), laminal cell shape, size, and ornamentation (7, 8, 11), costa, apices, marginal cells, and shoulders of inner perichaetial leaves (17, 18, 19, 21), length of seta (27), peristome type (34), color of exostome teeth (36), size and ornamentation of spores (40, 41). Additionally, the variation scope has been clarified for all the characters in question. For example, previously both single and double peristomes were included in *Cryphaea* but now the single peristome species are excluded from the genus. The length of the exostome teeth ranges between 150–600 µm and their median lines vary from cracked to indistinct. This information about the characters provides a basis for the further studies of this family in generic delimitation. In addition, three types of costa are described in the genus (cf. Fig. 6), which might prove to be an interesting character for the future studies.

Based on the cladistic studies, two subgenera and three sections are tentatively recognized for *Cryphaea*. However, it is necessary to explore more informative characters such as ultrastructural, biochemical, and molecular data to achieve a more satisfactory result. Simultaneously, a thorough revision of other genera in Cryphaeaceae seems critical for a confident subdivision of the genus.
The favorite habitats of *Cryphaea* species include humid, cool, and relatively high light environments, usually in tropical highland forests and temperate oceanic/suboceanic areas. Seven distributional patterns are recognized for this genus with the Neotropics as its diversity center.

Because of the lack of fossil evidence, the origin of *Cryphaea* cannot be deduced with confidence. However, its present distributional pattern, phylogenetic studies, and the palaeogeographical evidence furnished support for the postulation: the ancestor of this genus occurred in West Gondwanaland (Africa and South America) around the Late Cretaceous to early Tertiary (ca. 70–60 m.y. BP).

The high level of endemism suggests that species of *Cryphaea* may be climatic or evolutionary relics (Cox and Moore 1993). The following species should be considered as endangered taxa because they are known only from very few collections and seem to be globally threatened: *Cryphaea amurensis, C. clandestina, C. lanceolata, C. obovotocarpa, C. omeiensis, and C. songpanensis* of Asia (I, II); *Cryphaea ragazii* of Africa; *Cryphaea chlorophyllosa* of Australasia; *Cryphaea attenuata, C. brevipila, C. gracillima*, and *C. hygrophila* in the Neotropics (III). In the cladogram (Fig. 7), most of the taxa mentioned above are separated by high numbers of character state transitions or steps, and a more detailed analysis may therefore show that they also represent the genus best (cf. Bisang & Hedenäs 2000). The taxonomic, phylogenetic, ecological, and phytogeographical studies of *Cryphaea* establish a basic ground for further analysis of the mechanisms of its speciation and supplies a scheme for its conservation (cf. Hedenäs 1996). The genus, with great morphological variation, seems to be critical to our understanding of the evolutionary relationships of the Cryphaeaceae, a family comprising acrocarpy, cladocarpy, and pleurocarpy.

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REFERENCES


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INDEX TO THE SPECIFIC AND INFRASPECIFIC EPITHETS OF CRYPHAEA

This index includes only the names that were recognized as Cryphaea in Crosby et al. (1999), and newly treated taxa. Based on my previous studies (I, II, III), accepted names are in boldface. Newly described species are marked with sp. nov. New synonyms and combinations are marked with syn. nov. and comb. nov. respectively. Newly lectotypified or neotypified names are indicated with “*”. Doubtful species are marked with a question mark “?”. For easy reference, the currently accepted names are provided in parentheses ( ) behind synonyms and excluded taxa. The Roman numeral(s) at the end of each item indicate the paper in which the concerned species were treated.

acuminata III
amurensis II
apiculata III
arborea* (= C. heteromalla). III
attenuata III
boliviana*, syn. nov. (= C. ramosa). III
bollei*, comb. nov. (= Pseudoleskeopsis bollei). III
brachycarpa*, syn. nov. (= C. apiculata). III
brevidens* (= C. tenella). III
brevipila III

caldensis*, syn. nov. (= C. jamesonii). III
chlorophyllosa III
clandestina II
consimilis* III.

exigua, syn. nov. (= C. jamesonii) III

fasciculosa, syn. nov. (= C. ramosa) III
filiformis III
furcinervis ? III

glomerata III
gglomerata var. scabra* (= C. filiformis) III
gracillima* III

henryi, syn. nov. (= Cyptodontopsis leveillei). I
heteromalla II, III
hortonae syn. nov. (= C. hygrophiila). III
hygrophiila* III.
hygrophiila var. nitens*, syn. nov. (= C. hygrophiila). III

intermedia*, syn. nov. (= C. patens). III

jamesonii III

lamyana, comb. nov. (= Dendrocryphaea lamyana). III
lanceolata, sp. nov. I
leptopteris, syn. nov. (= C. patens). III
leucocolea (= Cryphidium leucocoleum). III
leveillei, comb. nov. (= Cyptodontopsis leveillei). I
longicuspis, syn. nov. (= C. jamesonii). III
lorentziana ? III

macrospora, syn. nov. (= C. apiculata). III
malmei*, syn. nov. (= C. rhacomiroides). III
manoclada syn. nov. (= C. patens). III
microspora*, syn. nov. (= C. hygrophiila). III
mosenii, syn. nov. (= C. patens). III
nervosa III
nitens (=C. hygrophila). III

obovatocarpa I, II
omeiensis sp. nov. II
orizabae III
ovalifolia* III

parvula III
patens III
patens var. dilatata*, syn. nov. (= C. patens). III
pendula* (= C. glomerata). III
pilifera III
protensa* III
pusila? III

raddiana? III
ragazzii* III
ramosa* III
ravenelii, comb. nov. (= Monocryphaea ravenelii). III.
rhacomitrioides* III
rhacomitrioides var. gracilis*, syn. nov. III.
robusta, syn. nov. (= C. rutenbergii). III
rutenbergii* III

scariosa (= Papillaria scariosa). III
schiedeana? III
sinensis, comb. nov. (= Sphaerotheciella sinensis). II.
songpanensis I, II
subglabra, syn. nov. (= C. tenella). III

tahitica, syn. nov. (= C. tenella). III
tenella* III
tenuicaulis, syn. nov. (= C. pilifera). III.
tenuiretis*, syn. nov. (= C. jamesonii). III.