
A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Coenogonium* (*Ostropales: Coenogoniaceae*), with a world-wide key and checklist and a phenotype-based cladistic analysis

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A treatment of filamentous and crustose species of the lichen genus *Coenogonium* in Costa Rica is presented, reporting a total of 48 taxa, including seven of unresolved taxonomic status. Eight species and one form are described as new to science: *C. aciculatum* Lücking & Aptroot sp. nov., *C. barbatum* Lücking, Aptroot & Umaña sp. nov., *C. byssothallinum* Aptroot & Lücking sp. nov., *C. kalbii* Aptroot, Lücking & Umaña sp. nov., *C. luteocitrinum* Rivas Plata, Lücking & Umaña sp. nov., *C. magdalenae* Rivas Plata, Lücking & Lizano sp. nov., *C. saepincola* Aptroot, Sipman & Lücking sp. nov., *C. siquirrense* f. *denticulatum* Rivas Plata & Lücking f. nov., *C. strigosum* Rivas Plata, Lücking & Chaves sp. nov. The following new combinations and nomenclatural novelties are introduced: *C. antonianum* Lücking, Aptroot & Sipman nom. nov., *C. atroluteum* (Vain.) Lücking, Aptroot & Sipman comb. nov., *C. bacilliferum* (Malme) Lücking, Aptroot & Sipman comb. nov., *C. degeneri* (Kalb & Vezda) Kalb & Lücking comb. nov., *C. eximium* (Vezda) Kalb & Lücking comb. nov., *C. frederici* (Kalb) Kalb & Lücking comb. nov., *C. isidiatum* (G. Thor & Vezda) Lücking, Aptroot & Sipman comb. nov., *C. isidiigerum* (Vezda & Osorio) Lücking, Aptroot & Sipman comb. nov., *C. isidiosum* (Breuss) Rivas Plata, Lücking, Umaña & Chaves comb. nov., *C. luteolum* (Kalb)

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Kalb & Lücking comb. nov., *C. nepalense* (G. Thor & Vezda) Lücking, Aptroot & Sipman comb. nov., *C. perminutum* (Malme) Lücking, Aptroot & Sipman comb. et stat. nov., *C. persistens* (Malme) Lücking, Aptroot & Sipman comb. et stat. nov., *C. pertenua* (Stirt.) Kalb & Lücking comb. nov., *C. pocsii* (Vezda & Farkas) Lücking, Aptroot & Sipman comb. nov., *C. pusillum* (Mont.) Lücking, Aptroot & Sipman comb. nov., *C. pyrophthalmum* (Mont.) Lücking, Aptroot & Sipman comb. nov., *C. stenosporum* (Malme) Lücking, Aptroot & Sipman comb. nov., *C. stramineum* (Aptroot & Seaward) Lücking, Aptroot & Sipman comb. nov., *C. subdentatum* (Vezda & G. Thor) Rivas Plata, Lücking, Umana & Chaves comb. nov., *C. subdilatatum* (Malme) Lücking, Aptroot & Sipman comb. nov., *C. subfallaciosum* (Vezda & Farkas) Lücking, Aptroot & Sipman comb. nov., *C. subsquamosum* (Aptroot & Seaward) Lücking, Aptroot & Sipman comb. nov., *C. tavaresianum* (Vezda) Lücking, Aptroot & Sipman comb. nov., and *C. weberi* (Vezda) Lücking, Aptroot & Sipman comb. nov. *Coenogonium complexum* Nyl. is established as a synonym of *C. tuckermanii*. Ten species are new records for Costa Rica. A phenotype-based cladistic analysis of 54 taxa using 49 characters supports merging *Dimerella* with *Coenogonium* and suggests polyphyletic origin of species with filamentous thallus structure. As additional result of our studies, we present a world-wide working key to the 82 accepted species of *Coenogonium* and an updated checklist including the status of 186 further names in *Coenogonium* and its twelve generic synonyms *Biatorinopsis*, *Byssiplacea*, *Coenogoniomycella*, *Coenogoniomyces*, *Coenomycogonium*, *Didymopycnomycetes*, *Dimerella*, *Flabellomyces*, *Holocoenis*, *Lecaniopsis*, *Microphiale*, and *Mycocoenogonium*.

Key words: *Dimerella*, lichens, new combinations, new species

Introduction

Coenogonium Ehrenb., in its present circumscription, is a fairly large genus of more than 80 species of chiefly tropical lichens. The genus is characterized by biatorine (rarely zeorine), yellow to orange or brown apothecia with paraplectenchymatous excipulum, partially amyloid hymenium (I+ blue then quickly sordid green then red-brown), thin-walled unitunicate asci, 1-septate or rarely non-septate ascospores, and trentepohlioid photobiont (Ehrenberg, 1820; Nylander, 1859, 1862a-c; Hariot, 1891; Dodge, 1933, 1953; Malme, 1934, 1937; Santesson, 1952; Uyenco, 1963a-b, 1965; Vezda, 1969, 1994, 2004; Vezda and Poelt, 1975; Kalb and Vezda, 1980; Xavier Filho *et al.* 1983; Thor and Vezda, 1984; Vezda and Farkas, 1988; Awasthi, 1991; Harada and Vezda, 1997; Lücking, 1999a, 2007; Lücking and Kalb, 2000; Lücking and Kalb, 2001; Alvarez Andrés and Carballal Durán, 2001; Brodo *et al.*, 2001; Kauff and Lutzoni, 2002; Malcolm, 2004; Seaward and Aptroot, 2004; Harada *et al.*, 2004).

Coenogonium originally only included species with filamentous thallus, while crustose taxa were separated in the genus *Dimerella* Trev. (with the illegitimate homotypic synonyms *Biatorinopsis* Müll. Arg. and *Microphiale* Zahlbr.). However, thallus morphology in this group is more diverse than implied by the simple separation of filamentous versus crustose and suggests

that the taxa traditionally assigned to *Coenogonium* form various, unrelated lineages. This and the fact that the filamentous and crustose taxa have exactly the same type of apothecia, while the morphological differences are due to the photobiont rather than based on mycological characters, led Lücking and Kalb (2000) to unite both genera under the older name *Coenogonium*, a proposal that has been accepted by some workers (Lücking and Kalb, 2001, 2002; Kauff and Lutzoni, 2002; Harada *et al.*, 2004; Malcolm, 2004, 2005; Esslinger, 2005), but opposed by others, which either consider the morphological differences sufficient to maintain both genera or opt to propose *Dimerella* for conservation over *Coenogonium* (Alvarez Andrés and Carballal Durán, 2001; Osorio, 2001; Brodo *et al.*, 2001; Breuss, 2002; Seaward and Aptroot, 2004; Ryan and Nimis, 2004; Van Herk and Aptroot, 2004; Vezda, 2004).

Species of *Coenogonium* usually grow on organic substrata, including bark, bryophytes, and leaves, and many species are typically or at least facultatively foliicolous (Vezda and Farkas, 1988; Lücking, 1999a, 2007; Lücking and Kalb, 2000). The foliicolous taxa are rather well-known taxonomically and keys for their identification are readily available (Vezda and Farkas, 1988; Lücking, 1999a, 2006). The filamentous taxa have been revised by Uyenco (1963a-b) and in part by other workers (Nylander, 1862a-c; Harriot, 1891; Malme, 1937; Santesson, 1952; Dodge, 1933, 1953; Xavier Filho *et al.*, 1983; Lücking, 1999a), but studies of abundant collections and revision of type material are urgently needed to clarify the status of some of the names and to obtain a clear picture of how many species are to be accepted, in particular in the *C. linkii* group. Except for regional treatments by Malme (1934) and Awasthi (1991), no synopsis or key exists so far for the crustose corticolous species, and their taxonomy is much less settled, partly due to the fact that the taxonomically important pycnidia and conidia are rarely observed in these species.

In spite of the fact that species of *Coenogonium* are well-characterized and easily recognized by their apothecial morphology and anatomy, no less than 12 generic names have been established for this group, eight of which refer to filamentous and four to crustose taxa (Table 1). These synonyms correspond to four groups: the *C. linkii* group of species with conspicuous, filamentous thallus (*Coenogonium*, *Byssioplaca*, *Holocoenis*, *Coenogoniomycella*, *Coenogoniomyces*, *Coenomycogonium*), the *C. epiphyllum* group of species with 'pilose' thallus (*Mycocoenogonium*), the *C. luteum* group of crustose species with narrowly ellipsoid ascospores, (*Dimerella*, *Biatorinopsis*, *Microphiale*), and the *C. subluteum* group of crustose species with broadly ellipsoid ascospores (*Lecaniopsis*, *Didymopycnomycetes*).

Lichens which are unrelated to *Coenogonium* have been repeatedly mistaken for that genus because of their filamentous growth (Glück, 1896; Simmer, 1899; Smith, 1906; Schade, 1932; Skuja and Ore, 1933; Puymaly, 1935; Koppe, 1937; Grummann, 1963; Dodge, 1966). Most of these belong to *Cystocoleus* or *Racodium* (Koppe, 1937). *Coenogonium missouriense* described from the United States (Davis, 1994) is a similar case; we have not seen material of that taxon but the described sheath-like hyphal arrangement around the algal filaments and the spinose ascospores preclude any relationship with *Coenogonium*.

Table 1. *Coenogonium* and its generic synonyms (in chronological order). Names provided with an asterisk are illegitimate according to ICBN Art. 52.1 and 52.2 (see also Lücking and Hawksworth, 2006).

Genus name	Author	Year	Type species	Species group
<i>Coenogonium</i>	Ehrenb.	1820	<i>C. linkii</i> Ehrenb.	<i>linkii</i> group
<i>Byssioplaca</i>	A. Massal.	1860	<i>B. feeana</i> A. Massal.	<i>linkii</i> group
<i>Dimerella</i>	Trev.	1880	<i>D. lutea</i> (Dicks.) Trev.	<i>luteum</i> group
<i>Biatorinopsis</i> *	Müll. Arg.	1881	<i>B. lutea</i> (Dicks.) Müll. Arg.	<i>luteum</i> group
<i>Microphiale</i> *	(Stiz.) Zahlbr.	1905	<i>M. lutea</i> (Dicks.) Zahlbr.	<i>luteum</i> group
<i>Holocoenis</i>	Clem.	1909	<i>H. leprieurii</i> (Mont.) Clem.	<i>linkii</i> group
<i>Lecaniopsis</i>	(Vain.) Zahlbr.	1926	<i>L. perminuta</i> (Vain.) Zahlbr.	<i>subluteum</i> group
<i>Coenogoniomyces</i> *	Cif. & Tomas.	1954	<i>C. linkii</i> Cif. & Tomas.	<i>linkii</i> group
<i>Coenogoniomycella</i> *	Cif. & Tomas.	1954	<i>C. linkii</i> Cif. & Tomas.	<i>linkii</i> group
<i>Coenogonogonium</i>	Cif. & Tomas.	1954	<i>C. interpositi</i> Cif. & Tomas.	<i>linkii</i> group
<i>Mycocoenogonium</i>	Cif. & Tomas.	1954	<i>M. curvuli</i> Cif. & Tomas.	<i>epiphyllum</i> group
<i>Didymopycnomyces</i>	Cavalc. & A.A.1972 Silva		<i>D. hyalinus</i> Cavalc. & A.A. Silva	<i>subluteum</i> group
<i>Flabellomyces</i>	Y. Kobayashi	1982	<i>F. amazonicus</i> Y. Kobayashi	<i>linkii</i> group

Although being most abundant and diverse in the tropics, *Coenogonium* has been a favorite object for morpho-anatomical and ecophysiological studies, including thallus growth (Karling, 1934; Redinger, 1934), apothecial development (Schwendener, 1862), ultrastructure (Meier and Chapman, 1983), photobiont and resynthesis in culture (Uyenco, 1963a, 1965; Stocker-Wörgötter, 1997), photosynthesis (Thomas and Nash, 1996; Thomas *et al.*, 1997), and the importance of filamentous thalli as home for diatoms and other microorganisms (Lakatos *et al.*, 2004). Müller Argoviensis (1881) even used his erroneous interpretation of the thallus organization of filamentous *Coenogonium* to oppose Schwendener's theory of the symbiotic nature of lichens.

In this paper we present the results of a survey of the genus *Coenogonium* in Costa Rica, within the frame of the TICOLICHEN

biodiversity inventory (Lücking *et al.*, 2004). Foliicolous species were treated in detail in an earlier paper (Lücking, 1999a) and are also featured in a forthcoming Flora Neotropica monograph on foliicolous lichenized fungi (Lücking, 2006), but are included here for sake of completeness. As in the preceding papers of this series (Chaves *et al.*, 2004; Lücking *et al.*, 2007; Nelsen *et al.* 2006), we present an updated checklist of species and descriptions and discussions of new taxa, including a revision of the material reported by Müller Argoviensis (1894) and Dodge (1933). We also used this opportunity to present the results of a phenotype-based phylogenetic study that supports the merging of *Coenogonium* and *Dimerella*, and for the first time, a world-wide working key to all species of the genus is provided, completed by a world-wide checklist of names described in *Coenogonium* and its synonyms and their current nomenclatural and taxonomic status, based on extensive literature studies and revision of selected material. For this purpose, types or authentic materials have been checked for many taxa, unless otherwise stated in the key and in the appendices.

Notes on the taxonomy of *Coenogonium* species

The crustose taxa of *Coenogonium*, formerly included in *Dimerella*, are traditionally separated by the following set of characters: apothecial size, apothecial color, hymenium height, ascospore size, ascospore arrangement, conidial size, and conidial septation. This renders the taxonomy of the numerous species described quite difficult, since most of these characters are either qualitative or continuous, while quantitative and discrete characters to separate the species are only found in few taxa. In addition, important characters such as apothecial color can be affected by the way of collecting and processing specimens; most species have very pale apothecia in life and only get their vivid colors after drying. While these colors are specific if specimens are handled properly, they can be altered when fully hydrated specimens are dried in a plant press or in a heated drier. Such specimens often have unnaturally dark and translucent apothecia. Another problem is that, while the pycnidia and conidia are very diverse in shape and size, they are absent from many specimens, and thus their diagnostic features cannot be used when identifying the bulk of the material or assessing taxonomy at the species level.

With these problems in mind, during our studies we have come across a couple of additional characters that were useful for separating species. One is the width of the ascospores and the relationship of length to width, which turned out to be species specific. Most crustose species of *Coenogonium* can be assigned to two major groups: species with ascospores relatively narrow, not

exceeding 2.5 μm , and species with wider ascospores, exceeding 2.5 μm and usually up to 4.5 μm broad (Fig. 1). The first are mostly biserially arranged within the asci, while the second are more or less uniseriate. Ascospores are mostly 6-12 μm in length, but in a few taxa exceed that range, with extreme values reaching 25 μm . A survey of apothecial sizes across individuals, specimens, and species, revealed that three size classes can be distinguished: small (0.1-0.3 mm), medium-sized (0.3-0.8 mm), and large (0.8-2 mm). Specimens and species with apothecial sizes intermediate between these categories are rare.

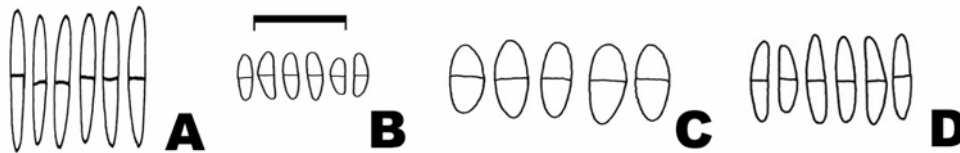
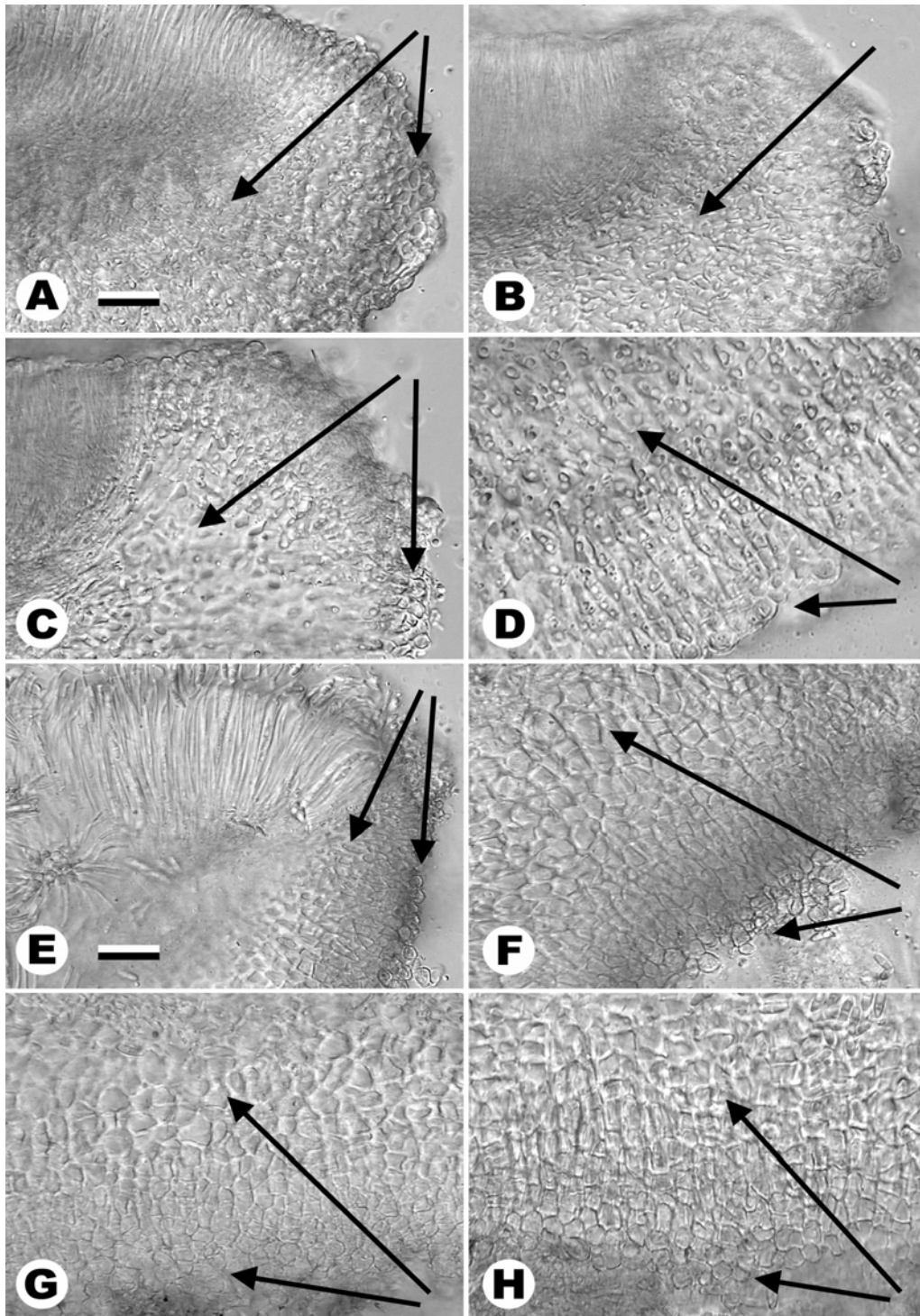


Fig. 1. Ascospores in *Coenogonium*. **A.** *Coenogonium aciculatum*. **B.** *Coenogonium byssothallinum*. **C.** *Coenogonium luteum*. **D.** *Coenogonium siquirrense*. Scale = 10 μm .

We also found that the excipulum structure provides additional, unexplored data. Typically, the excipulum is paraplectenchymatous, with the cells more or less radiately or somewhat labyrinthically arranged. The cells are usually small (3-7 μm diam.) and rather thick-walled (pachydermatous), but the peripheral excipular cells tend to be larger and thin-walled (leptodermatous) and anticlinally arranged in some species. The cell structure seems to be species-specific, and most taxa have rather small, thick-walled cells with little differentiation towards the periphery (Fig. 2A-D). However, large and thin-walled cells throughout the excipulum were found in *Coenogonium siquirrense* and *C. strigosum* (Fig. 2E-H).

The taxonomic value of some other characters often used to distinguish species of *Coenogonium*, such as the iodine reaction of the hymenium and asci, could not be confirmed by us. All the species tested had more or less the same iodine reaction (Lugol's solution): I+ blue then quickly turning sordid green then turning orange brown. This reaction is often called 'hemiamyloid', but differs clearly from the 'hemiamyloid' reaction seen in most Arthoniales, where

Fig. 2. Excipular structure in *Coenogonium*. **A-D.** *Coenogonium luteum*, showing lateral (A-C) and basal (D) excipulum; note the internal thick-walled, pachydermatous cells with small lumina and the outermost thin-walled, leptodermatous cells (arrows). **E-H.** *Coenogonium strigosum*, showing lateral (E) and basal (F-H) excipulum; note the internal thin-walled, pachydermatous cells with large lumina and the external, very thin-walled, ultraleptodermatous cells (arrows). Scale = 20 μm .



the hymenium reacts first I+ orange-red and, after adding KOH, KI+ blue.

While the taxonomy of crustose species of *Coenogonium* is notoriously difficult because of the few characters available and the absence of diagnostic pycnidia and conidia in most collections, the taxonomy of the filamentous taxa has suffered from a lack of understanding of the taxonomic importance of photobiont and mycobiont characters. The only synoptical papers available for this group are Nylander's (1862a-c) early treatments, Dodge's (1933) paper on the foliose and fruticose lichens of Costa Rica (with a key to neotropical filamentous species of *Coenogonium*), and Uyenco's (1963a) thesis and subsequent paper on North American species (Uyenco, 1963b).

Uyenco's (1963a) thesis is the most thorough treatment of this group, including the analysis and culture of photobionts of North American taxa and lengthy discussions on the taxonomic value of characters, such as photobiont cell size and apothecial morphology and anatomy. However, this work has to be used with care, since it contains many errors that raise doubt with respect to the conclusions of the author. For example, the apothecial sizes given for some species are undoubtedly wrong, such as up to 7.5 mm in *C. acrocephalum* or 1-5 mm in *C. leprieurii*; no species of this group has apothecia wider than 1.5 mm, and mostly they are below 1 mm. In the key to the accepted species of *Coenogonium* (Uyenco, 1963a), *C. acrocephalum* is said to be distinguished from *C. leprieurii* by its different thallus morphology, but in the description its thallus is given as dimidiate, which is another word for shelf-like, i.e. as in *C. leprieurii*. In the discussion of *C. acrocephalum*, it is said to be related to *C. leprieurii*, but differing by its larger spores; however, those of *C. leprieurii* are given as $5.5-10 \times 2-4 \mu\text{m}$ and those of *C. acrocephalum* as $7.5-9 \times 2-3 \mu\text{m}$, thus perfectly within the range of *C. leprieurii*. According to Dodge (1933), *C. acrocephalum* should differ from *C. leprieurii* by its pale apothecia and slightly broader photobiont cells ($16-20 \mu\text{m}$ vs. $11-16 \mu\text{m}$), and Uyenco (1963a) also mentions biserially vs. uniserially arranged ascospores; we have thus maintained *C. acrocephalum* as a separate species on the basis of these characters for the moment, but restudy of the type is required.

Another example is *Coenogonium botryosum*, which is given as different from *C. moniliforme* because of its different photobiont and smaller, uniserially arranged ascospores. However, in the same work, Uyenco (1963a) describes the photobiont of *C. botryosum* as very similar to *Physolinum moniliforme* (the photobiont of *C. moniliforme*), but then states it to be a *Trentepohlia*, without having actually cultured the photobiont of any of the two species. Interestingly enough, *Physolinum moniliforme* is now included in *Trentepohlia* (López-Bautista *et al.*, 2002; López-Bautista and Chapman, 2003). As for the ascospores, the size ranges for *Coenogonium botryosum* and

C. moniliforme are almost identical, and the ascospores of *C. moniliforme* are given as uni- or biserially arranged. Although we have not seen the original material of *C. botryosum*, we therefore strongly suspect it to be conspecific with *C. moniliforme*.

The thallus of *Coenogonium disjunctum* is given as shelf-like or crustose in the key, but as pannose in description, the latter being correct. *Coenogonium implexum* is compared to *C. interplexum* and said to be distinguished mainly by its larger and wider paraphyses. However, the main differences between the two are the pannose thallus with very densely arranged filaments (see for example the excellent color photograph in Kantvilas and Jarman, 1995: 55) and the larger ascospores in *C. implexum*.

Since the description of thallus shapes in filamentous *Coenogonium* is quite confusing in the literature, we are using the terms and definitions as follows:

shelf-like or **dimidiate**: projecting horizontally from the substrate and forming a semi-circle or rarely a complete circle, very similar to polyporean fungi; apothecia usually produced on the underside; examples: *Coenogonium leprieurii*, *C. linkii*, *C. congense* (Fig. 3A-B).

beard-shaped or **caespitose**: projecting horizontally from the substrate or rarely pendulous, not forming a semi-circle but narrow and elongate; apothecia usually produced on the underside; example: *Coenogonium barbatum* (Fig. 3C-D).

pannose: forming a more or less rounded cushion of densely woven filaments loosely attached to, and easily removed from the substrate; apothecia usually produced on the upper side, rarely on both sides when parts of the thallus underside are exposed; example: *Coenogonium implexum* (Fig. 3E; see also fig. 24 in Kantvilas and Jarman, 1995: 55).

prostrate: forming an irregular crust of loosely woven filaments basally attached to the substrate and impossible to remove without partly damaging the thallus; apothecia produced on the upper side; examples: *Coenogonium interplexum*, *C. interpositum* (Fig. 3F).

felt-like or **'pilose'**: forming a thin crust of irregular filaments attached to the substrate, from which a short and dense layer of erect filaments ('hairs') emerges; apothecia produced on the upper side; examples: *Coenogonium ephyllum*, *C. ciliatum*, *C. curvulum* (Fig. 3G).

appressed filamentous: forming a thin crust of very densely woven filaments attached to the substrate, at first glance appearing crustose and filamentous nature only visible at lens magnification; apothecia produced

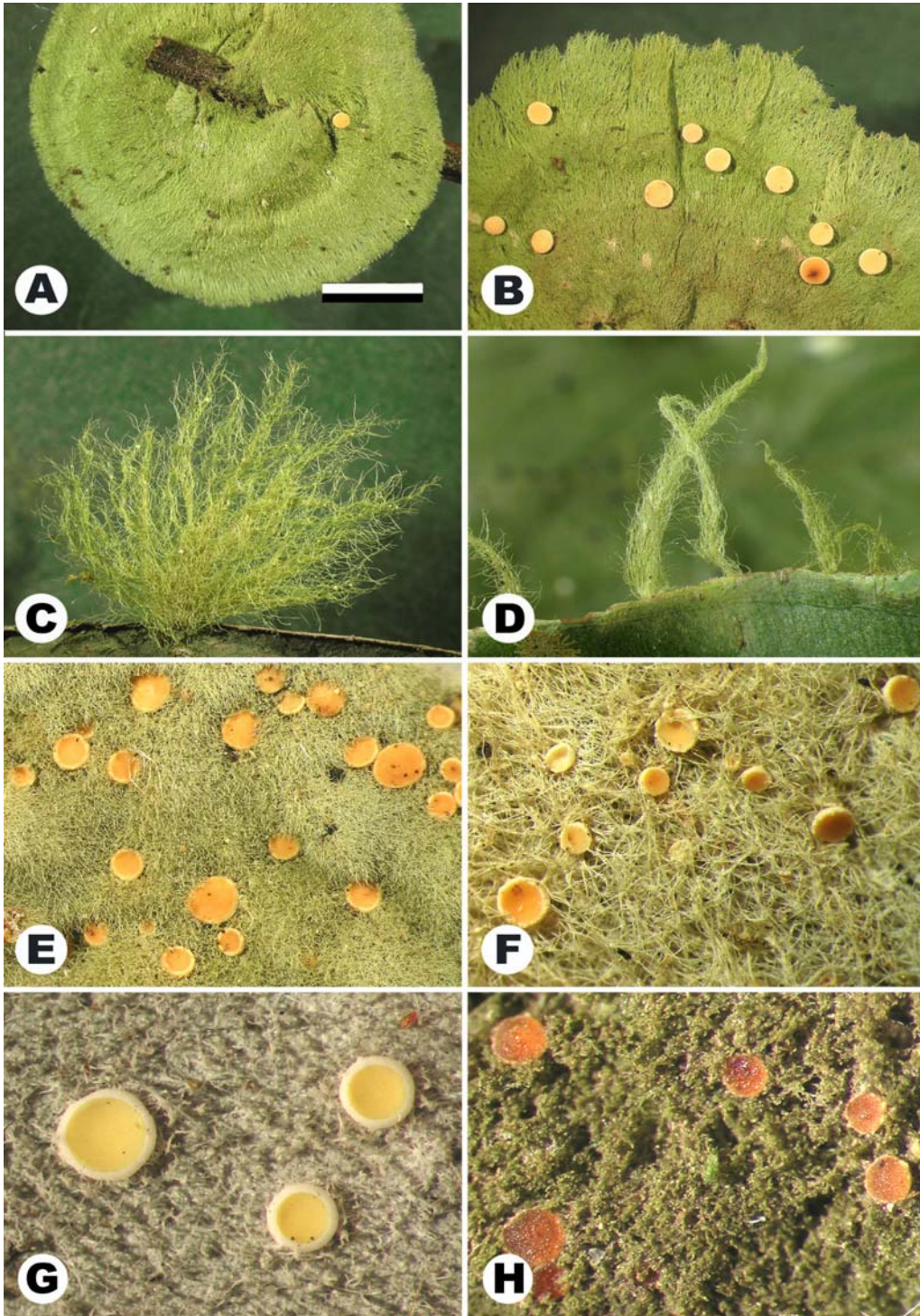


Fig. 3. Growth forms in filamentous *Coenogonium* species. **A-B.** *Coenogonium congense* (shelf-like). **C.** *Coenogonium barbatum* (beard-shaped). **D.** *Coenogonium* aff. *barbatum* (beard-shaped). **E.** *Coenogonium implexum* (pannose). **F.** *Coenogonium disjunctum* (prostrate). **G.** *Coenogonium epiphyllum* (felt-like). **H.** *Coenogonium moniliforme* (appressed filamentous). Scale for A = 4 mm, for B = 2 mm, for C-D = 3 mm, for E-H = 0.7 mm.

on the upper side; examples: *Coenogonium moniliforme*, *C. flavoviride*, *C. antonianum* (Fig. 3H).

In our phylogenetic approach, we interpret the thallus of *Coenogonium* species as modified from a non-lichenized thallus of *Trentepohlia*, which typically consists of two elements: a basal, horizontal, crustose thallus adnate to the substrate, and vertically projecting, free filaments. Recent studies suggest that the way these two elements are developed and combined is partially species-specific for the *Trentepohlia* taxa and partially dependent on the mycobiont. Thus, in the filamentous species of the *Coenogonium linkii* group, it is the vertical filamentous elements which are well-developed, while the basal crustose elements are reduced. In the crustose species, on the other hand, only the basal horizontal element is present. Of specific interest are then the taxa with felt-like and appressed filamentous thallus, which traditionally have been included in the filamentous '*Coenogonium*' species. In the felt-like or 'pilose' species of the *C. epiphyllum* group, both thallus elements are present and rather well-developed, although the vertical filaments are short and resemble hairs. Apothecial and pycnidial characters suggest closer relationship of these taxa with the *C. linkii* group, and hence the erect 'hairs' are interpreted as homologous to the filamentous thallus in the latter species. In the appressed-filamentous taxa of the *C. moniliforme* group, however, only one element is present, and an ad hoc decision of whether this represents the horizontal or vertical element of the *Trentepohlia* is not possible. However, apothecial and pycnidia characters suggest that this group is more closely related to crustose species, and because of that and the much branched and strongly appressed nature of the 'filaments', we interpret these as homologous to the basal, crustose element, rather than to the vertical, truly filamentous element.

Material and methods

Phenotype-based phylogenetic analysis. — After assembling a list of the currently accepted species of *Coenogonium*, 54 were selected for the phylogenetic analysis (Table 2), excluding a number of taxa of doubtful status or for which too little information on taxonomically important characters was available. Preliminary circumscriptions were compiled from original literature, and world-wide material from several herbaria (B, BM, F, G, GZU, H, M, S,

STU, TUR, UPS, hb. Kalb, hb. Lücking, hb. Vezda) was examined to produce the final data matrix. A set of 49 characters was extracted, with most characters coded in binary fashion (Wiley *et al.*, 1991; Poe and Wiens, 2000; Lücking *et al.*, 2005), except for quantitative features for which unordered multistate characters were defined (Table 3). Gaps were treated either as additional character (for inapplicable data) or as missing data (in case of taxa for which information on apothecia or pycnidia was unavailable). No character weighting was applied.

Table 2. Taxa used in the phenotype-based phylogenetic analysis. COEN = taxa with filamentous thallus, DIME = taxa with crustose thallus.

<i>Petractis luetkemulleri</i> (outgroup)		
(COEN) <i>antonianum</i>	(DIME) <i>eximium</i>	(DIME) <i>pulchrum</i>
(COEN) <i>ciliatum</i>	(DIME) <i>flavum</i>	(DIME) <i>roumeguerianum</i>
(COEN) <i>curvulum</i>	(DIME) <i>frederici</i>	(DIME) <i>siquirrense</i>
(COEN) <i>disjunctum</i>	(DIME) <i>fuscescens</i>	(DIME) spec. A
(COEN) <i>epiphyllum</i>	(DIME) <i>geralense</i>	(DIME) spec. A
(COEN) <i>flavoviride</i>	(DIME) <i>hypophyllum</i>	(DIME) <i>stenosporum</i>
(COEN) <i>implexum</i>	(DIME) <i>isidiatum</i>	(DIME) <i>subdentatum</i>
(COEN) <i>interplexum</i>	(DIME) <i>isidiiiferum</i>	(DIME) <i>subfallaciosum</i>
(COEN) <i>interpositum</i>	(DIME) <i>isidiiigerum</i>	(DIME) <i>subluteum</i>
(COEN) <i>leprieurii</i>	(DIME) <i>isidiosum</i>	(DIME) <i>subsquamosum</i>
(COEN) <i>linkii</i>	(DIME) <i>kawanae</i>	(DIME) <i>subzonatum</i>
(COEN) <i>moniliforme</i>	(DIME) <i>fallaciosum</i>	(DIME) <i>tanzanicum</i>
(COEN) <i>tuckermanii</i>	(DIME) <i>labyrinthicum</i>	(DIME) <i>queenslandicum</i>
(DIME) <i>atroluteum</i>	(DIME) <i>luteolum</i>	(DIME) <i>tavaresianum</i>
(DIME) <i>bacilliferum</i>	(DIME) <i>luteum</i>	(DIME) <i>usambarense</i>
(DIME) <i>dilucidum</i>	(DIME) <i>minimum</i>	(DIME) <i>vezdanum</i>
(DIME) <i>disciforme</i>	(DIME) <i>pineti</i>	(DIME) <i>weberi</i>
(DIME) <i>degeneri</i>	(DIME) <i>pocsii</i>	(DIME) <i>zonatum</i>

From the resulting matrix (Table 4), trees were reconstructed by means of maximum parsimony using PAUP 4.0b10 (Swofford, 2003). To explore alternative topologies, the data set was analyzed both completely and once including apothecial characters only (24). Based on previous molecular phylogenetic studies (Kauff and Lutzoni, 2002), *Petractis luetkemulleri* was chosen as outgroup. The shortest trees were searched by means of heuristic search, using random stepwise addition with 100 replicates and tree-branching-regrafting (TBR) as branch swapping algorithm. If searches resulted in multiple parsimonious trees, both strict and majority rule consensus trees were computed to inspect the degree and nature of conflict between individual trees.

Table 3. List and definition of characters and character states used in the phenotype-based phylogenetic analysis. Note that character coding is binary, i.e. all character complexes used in the descriptions are dissolved into individual characters. Thus, a shelf-like filamentous thallus would code as 1001110 for characters 1-7, and yellow-orange apothecia would code as 0110 for characters 26-29, and so forth.

No.	Group	Character	Character states and coding
1.	Horizontal filaments	reduction	0 = absent / 1 = present (crustose)
2.	Horizontal filaments	photobiont type	0 = <i>Trentepohlia</i> / 1 = <i>Physolinum</i> (<i>moniliforme</i> type)
3.	Horizontal filaments	morphology	0 = angular-rounded / 1 = cylindrical (<i>antonianum</i> type)
4.	Vertical filaments	development	0 = absent (crustose) / 1 = present
5.	Vertical filaments	length	0 = short (<i>epiphyllum</i> type) / 1 = long (<i>interplexum</i> type)
6.	Vertical filaments	thallus morphology	0 = adnate / 1 = shelf-like (<i>linkii</i> type)
7.	Vertical filaments	density	0 = loose / 1 = dense (<i>implexum</i> type)
8.	Thallus	surface verrucae/ridges	0 = absent / 1 = present
9.	Thallus	fungal hairs	0 = absent / 1 = present
10.	Thallus	prothallus	0 = absent / 1 = present
11.	Thallus	prothallus color	0 = white / 1 = yellow
12.	Thallus	color	0 = green / 1 = yellow
13.	Thallus	apothecial position	0 = on thallus / 1 = on algal-free mycelium
14.	Thallus	thallus position	0 = upper surface / 1 = lower surface (hypophyllous)
15.	Isidia	cylindrical isidia	0 = absent / 1 = present (<i>isidiosum</i> type)
16.	Isidia	disc-shaped isidia	0 = absent / 1 = present (<i>isidiiferum</i> type)
17.	Isidia	disc-shaped isidia type	0 = irregular / 1 = regularly rounded
18.	Apothecia	zeorine margin	0 = absent / 1 = present (<i>fuscescens</i> type)
19.	Apothecia	basal algal cells	0 = absent / 1 = present (<i>kawanae</i> type)
20.	Apothecia	(short) stipe	0 = absent / 1 = present
21.	Apothecia	obconical shape	0 = absent / 1 = present (<i>antonianum</i> type)
22.	Apothecia	urceolate shape	0 = absent / 1 = present (<i>minimum</i> type)
23.	Apothecia	lobulate margin	0 = absent / 1 = present (<i>Petractis</i> type)
24.	Apothecia	denticulate margin	0 = absent / 1 = present (<i>subdentatum</i> type)
25.	Apothecia	pilose margin	0 = absent / 1 = present (<i>ciliatum</i> type)
26.	Apothecia	disc color carneous	0 = absent / 1 = present
27.	Apothecia	disc color yellow	0 = absent / 1 = present
28.	Apothecia	disc color orange	0 = absent / 1 = present
29.	Apothecia	disc color brown	0 = absent / 1 = present
30.	Apothecia	apothecia translucent	0 = absent / 1 = present
31.	Apothecia	apothecia bright	0 = absent / 1 = present
32.	Apothecia	margin color dark	0 = absent / 1 = present
33.	Apothecia	disc pruina	0 = absent / 1 = present

Table 3 continued. List and definition of characters and character states used in the phenotype-based phylogenetic analysis. Note that character coding is binary, i.e. all character complexes used in the descriptions are dissolved into individual characters. Thus, a shelf-like filamentous thallus would code as 1001110 for characters 1-7, and yellow-orange apothecia would code as 0110 for characters 26-29, and so forth.

No.	Group	Character	Character states and coding
34.	Apothecia	Diameter	0 = < 0.3 mm / 2 = 0.3-0.8 mm / 4 = > 0.8 mm (1, 3 = interm.)
35.	Apothecia	hymenium height	0 = < 40 μ m / 2 = 60-80 μ m / 4 = > 100 μ m (1, 3 = interm.)
36.	Ascospores	septa	0 = present / 1 = absent
37.	Ascospores	length	0 = < 6 μ m / 2 = 9-12 μ m / 4 = > 20 μ m (1, 3 = interm.)
38.	Ascospores	width	0 = < 2 μ m / 2 = 2.5-3 μ m / 4 = > 4 μ m (1, 3 = interm.)
39.	Ascospores	length-width ratio	0 = < 2 / 1 = 2-5 / 2 = 5-10 / 3 = > 10
40.	Ascospores	ascospore arrangement	0 = biseriate / 1 = irregular / 2 = uniseriate
41.	Apothecia	ascospore shape	0 = straight / 1 = curved (<i>curvulum</i> type)
42.	Pycnidia	tubular shape	0 = absent / 1 = present
43.	Pycnidia	club-shaped apex	0 = absent / 1 = present
44.	Pycnidia	globose shape	0 = absent / 1 = present
45.	Pycnidia	applanate shape	0 = absent / 1 = present
46.	Pycnidia	labyrinthical chambers	0 = absent / 1 = present
47.	Conidia	septa	0 = absent / 1 = present
48.	Conidia	length	0 = < 3 μ m / 1 = 3-6 μ m / 2 = 6-10 μ m / 4 = > 10 μ m
49.	Conidia	width	0 = < 1 μ m / 1 = 1-2 μ m / 2 = > 2 μ m

Bootstrap and Jackknife analysis were performed for all analyses, using 1000 replicates and 75% resampling in case of Jackknife analysis.

New and otherwise interesting species of *Coenogonium* in Costa Rica

A total of 48 taxa of *Coenogonium* are known from Costa Rica at this point, including seven of unresolved taxonomic position (Table 5), which represent more than 50% of the diversity known world-wide. Ten taxa are described as new, and five names are excluded from the Costa Rican checklist (see below).

Table 4. Data matrix for 55 taxa and 49 characters for the phenotype-based phylogenetic analysis.

<i>Petractis luetkemuellerei</i>	0000---000-00000-1100110011100000113541100-000020
<i>coen_antonianum</i>	0010---000-00000-001100000010000010000010????????
<i>coen_ciliatum</i>	0001000000-00000-0000000101000100320322000-010022
<i>coen_curvulum</i>	0001000000-00000-000000001100000001010101????????
<i>coen_disjunctum</i>	1--1100---000---001000000110000022032200????????
<i>coen_epiphyllum</i>	0001000000-00000-00000000100000022011020????????
<i>coen_flavoviride</i>	01-0---000-00000-0010000001010000000000200-000010
<i>coen_implexum</i>	1--1101---000---000000000110000031022110????????
<i>coen_interplexum</i>	1--1100---000---0010000001100000220110200-100021
<i>coen_interpositum</i>	1--1100---000---0010000001100000221110200-100021
<i>coen_leprieurii</i>	1--1110---000---0010000001100000211110100-100021
<i>coen_linkii</i>	1--1110---000---0010000001100000310110100-100021
<i>coen_moniliforme</i>	01-0---000-00000-001000000110000011022120????????
<i>coen_tuckermanii</i>	1--1100---000---000000000110000032012010????????
<i>dime_atroluteum</i>	0000---000-00000-00000000101001031020200????????
<i>dime_bacilliferum</i>	0000---000-00000-000000000100000032041300????????
<i>dime_degeneri</i>	0000---100-00000-000000000110000123033100????????
<i>dime_dilucidum</i>	0000---000-00000-000000001000000010120200-000132
<i>dime_disciforme</i>	0000---000-000011????????????????????????????
<i>dime_eximium</i>	0000---000-00000-000000000100000410211100-000021
<i>dime_fallaciosum</i>	0000---000-01000-000000001100000410221100-000021
<i>dime_flavum</i>	0000---000-00000-00000000010000004101211011000011
<i>dime_frederici</i>	0000---000-00000-00000000010000022022020????????
<i>dime_fuscens</i>	0000---000-00000-1100100000110000020101100-000010
<i>dime_geralense</i>	0000---000-01000-0000000001000000310101000-000011
<i>dime_hypophyllum</i>	0000---000-00100-0000001001000000210313000-000022
<i>dime_isidiatum</i>	0000---000-00010-0000000010000001032110????????
<i>dime_isidiiferum</i>	0000---000-000010000000000100000021010100????????
<i>dime_isidiigerum</i>	0000---001000010-000000000100000043041310????????
<i>dime_isidiosum</i>	0000---000-00010-00000000101000021021200????????
<i>dime_kawanae</i>	0000---001000000-0100101001010000110330100-000022
<i>dime_labyrinthicum</i>	0000---000-00000-0000000001000100220303100-011011
<i>dime_luteolum</i>	0000---000-00000-000000001000000430120100-000011
<i>dime_luteum</i>	0000---000-00000-0000000001100000420221100-000011
<i>dime_minimum</i>	0000---000-00000-000010000101100001032100????????
<i>dime_pineti</i>	0000---000-00000-000000001100000110220100-000021
<i>dime_pocsii</i>	0000---001000000-0000000001100000320202000-000031
<i>dime_pulchrum</i>	0000---011000000-00000000010000042031210????????
<i>dime_queenslandicum</i>	0000---000-01000-000000001000000210101000-000010
<i>dime_roumaeguerianum</i>	0000---001000000-00000000010000034023010????????
<i>dime_siquirrense</i>	0000---001000000-000000000100100310101000-000011
<i>dime_spec_A</i>	0000---000-00010-00000000100000021031310????????
<i>dime_spec_B</i>	0000---000-00010-00000000010000041032110????????
<i>dime_stenosporum</i>	0000---000-10000-000000000110000021020300????????
<i>dime_subdentatum</i>	0000---000-00000-0000001001100000220101100-000011
<i>dime_subfallaciosum</i>	0000---000-01000-0000000001100000210101000-000001
<i>dime_subluteum</i>	0000---000-00000-0000000010100000110220200-000132
<i>dime_subsquamosum</i>	0000---001010000-00000000100010043032200????????
<i>dime_subzonatum</i>	0000---001001000-0000001001000100210120100-000011
<i>dime_tanzanicum</i>	0000---000-00000-0000000001100000120202100-000021
<i>dime_tavaresianum</i>	0000---100-00000-00000000011000024032210????????
<i>dime_usambarensis</i>	0000---000-00000-000000000100000110211000-000010
<i>dime_vezdanum</i>	0000---000-00000-00000000010000002101111010000011

Table 4 continued. Data matrix for 55 taxa and 49 characters for the phenotype-based phylogenetic analysis.

<i>Petractis luetkemulleri</i>	0000---000-00000-1100110011100000113541100-000020
<i>dime weberi</i>	0000---000-00000-000000001000000044033010????????
<i>dime zonatum</i>	0000---001000000-0000000000100000110220200-000132

***Coenogonium aciculatum* Lücking & Aptroot, sp. nov.** (Figs 1A, 5A-B)

Mycobank number: 501130.

A *Coenogonio bacillifero* apotheciis fulvis et ascosporis minoribus differt.

Type: COSTA RICA, Cartago, Tapantí National Park, Mirador, 1800 m, Lücking 1325 (CR, **holotype**; F, **isotype**).

?*Microphiale lutea* f. *stenospora* Zahlbr. in Magnusson & Zahlbruckner, Ark. Bot. 31A(1): 58 (1944).

Thallus crustose, corticolous, continuous, thin, smooth, greenish grey, 10-20 mm diam., with cartilaginous corticiform layer; prothallus absent. *Photobiont Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 5-9 µm diam. *Apothecia* sessile, rounded, 0.5-0.7 mm diam. and 120-150 µm high; disc plane, bright yellow; margin thin, not prominent, smooth, yellow. *Excipulum* paraplectenchymatous with radiating cell rows, 40-70 µm broad, colorless, I+ sordid yellow-green; cells isodiametric and thin-walled, 5-7 µm diam. *Hypothecium* 15-25 µm high, pale yellowish. *Hymenium* 50-60 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 45-55 × 4-6 µm. *Ascospores* biseriate, oblong-acicular, 1-septate, 14-18 × 1.5-2 µm, 7-10 times as long as broad. *Pycnidia* not observed. *Chemistry:* not tested. *Ecology:* Corticolous in understory of montane rain forest.

Coenogonium aciculatum is a distinctive species due to its bright yellow apothecia (disc and margin) and its rather long and narrow ascospores. The bright yellow apothecia recall those of *C. subzonatum* and the newly described *C. luteocitrinum*, but those species have much shorter and broader ascospores (6-10 × 2-3.5 µm). Long and narrow ascospores are rare in the genus and otherwise found in the following taxa: *C. bacilliferum* (ascospores larger, 18-25 × 2-3 µm), *C. hypophyllum* (thallus hypophyllous, apothecia pale yellow,

Table 5. Species and subspecific taxa of *Coenogonium* currently known from Costa Rica. For detailed Ticolichen collection data, consult the online database at http://emuweb.fieldmuseum.org/botany/search_crf.php.

Taxa
<i>Coenogonium aciculatum</i> Lücking & Aptroot sp. nov.
<i>Coenogonium bacilliferum</i> (Malme) Lücking, Aptroot & Sipman comb. nov. ; new to Costa Rica.
<i>Coenogonium barbatum</i> Lücking, Aptroot & Umaña sp. nov.
<i>Coenogonium</i> aff. <i>barbatum</i> Lücking, Aptroot & Umaña.
<i>Coenogonium byssothallinum</i> Aptroot & Lücking sp. nov.
<i>Coenogonium ciliatum</i> Kalb & Lücking, Bot. Jahrb. Syst. 122: 29 (2000); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium confervoides</i> Nyl., Flora 41: 380 (1858); reported from Costa Rica by Dodge (1933).
<i>Coenogonium</i> aff. <i>confervoides</i> Nyl.
<i>Coenogonium congensense</i> C. W. Dodge, Ann. Missouri Bot. Gard. 40: 350 (1953); new to Costa Rica.
<i>Coenogonium</i> aff. <i>congensense</i> C. W. Dodge.
<i>Coenogonium dilucidum</i> (Kremp.) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium disjunctum</i> Nyl., Bot. Zeitschr. 20: 178 (1862); reported from Costa Rica by Uyenco (1963a).
<i>Coenogonium eximium</i> (Vezda) Lücking, Aptroot & Sipman comb. nov. ; new to Costa Rica.
<i>Coenogonium fallaciosum</i> (Müll. Arg.) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium geralense</i> (P. Henn) Lücking, Fl. Neotrop. Monogr. (in press); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium hypophyllum</i> (Vezda) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium</i> cf. <i>implexum</i> Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 92 (1862).
<i>Coenogonium interplexum</i> Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 92 (1862); reported from Costa Rica by Dodge (1933), Uyenco (1963a), Lücking (1999a).
<i>Coenogonium</i> aff. <i>interplexum</i> Nyl. A.
<i>Coenogonium</i> aff. <i>interplexum</i> Nyl. B.
<i>Coenogonium</i> aff. <i>interplexum</i> Nyl. C.
<i>Coenogonium interpositum</i> Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 91 (1862); reported from Costa Rica by Dodge (1933), Lücking (1999a).
<i>Coenogonium isidiatum</i> (G. Thor & Vezda) Lücking, Aptroot & Sipman comb. nov. ; new to Costa Rica.
<i>Coenogonium isidiiferum</i> (Lücking) Lücking in Lücking <i>et al.</i> , Lichenologist 33: 201 (2001); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium isidiosum</i> (Breuss) Rivas Plata, Lücking, Umana & Chaves comb. nov. ; new to Costa Rica.
<i>Coenogonium kalbii</i> Aptroot, Lücking & Umaña sp. nov.

Table 5 continued. Species and subspecific taxa of *Coenogonium* currently known from Costa Rica. For detailed Ticolichen collection data, consult the online database at http://emuweb.fieldmuseum.org/botany/search_crf.php.

Taxa
<i>Coenogonium lepriurii</i> (Mont.) Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 89 (1862); reported from Costa Rica by Dodge (1933), Uyenco (1963a), Lücking (1999a).
<i>Coenogonium linkii</i> Ehrenb. in Nees von Esenbeck, Horae Phys. Berol.: 120 (1820); reported from Costa Rica by Dodge (1933), Uyenco (1963a), Lücking (1999a).
<i>Coenogonium lisowskii</i> (Vezda) Lücking in Lücking <i>et al.</i> , Lichenologist 33: 201 (2001); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium luteocitrinum</i> Rivas Plata, Lücking & Umaña sp. nov.
<i>Coenogonium</i> aff. <i>luteolum</i> (Kalb) Kalb & Lücking.
<i>Coenogonium luteum</i> (Dicks.) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium magdalenae</i> Rivas Plata, Lücking & Lizano sp. nov.
<i>Coenogonium minimum</i> (Müll. Arg.) Lücking, Fl. Neotrop. Monogr. (in press); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium moniliforme</i> Tuck., Proc. Amer. Acad. Sci. 5: 416 (1862); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium nepalense</i> (G. Thor & Vezda) Lücking, Aptroot & Sipman comb. nov. ; new to Costa Rica.
<i>Coenogonium pusillum</i> (Mont.) Lücking, Aptroot & Sipman comb. nov. ; new to Costa Rica.
<i>Coenogonium roumeguerianum</i> (Müll. Arg.) Kalb, Sched. Lich. Neotrop. 13: 3 (2001); new to Costa Rica.
<i>Coenogonium saepincola</i> Aptroot, Sipman & Lücking sp. nov.
<i>Coenogonium squirrense</i> (Lücking) Lücking, Fl. Neotrop. Monogr. (in press); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium squirrense</i> f. <i>denticulatum</i> Rivas Plata & Lücking f. nov.
<i>Coenogonium strigosum</i> Rivas Plata, Lücking & Chaves sp. nov.
<i>Coenogonium subdentatum</i> (Vezda & G. Thor) Rivas Plata, Lücking, Umana & Chaves comb. nov. ; new to Costa Rica.
<i>Coenogonium subdilutum</i> (Malme) Lücking, Aptroot & Sipman comb. nov. ; new to Costa Rica.
<i>Coenogonium subluteum</i> (Rehm) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium subzonatum</i> (Lücking) Lücking & Kalb, Biblioth. Lichenol. 78: 254 (2001); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium tuckermanii</i> Mont., Ann. Sci. Nat. Bot., Ser. 4, 7: 143 (1857); reported from Costa Rica by Uyenco (1963a) as <i>C. complexum</i> .
<i>Coenogonium vezdanum</i> (Lücking) Lücking, Fl. Neotrop. Monogr. (in press); reported from Costa Rica by Lücking (1999a).
<i>Coenogonium zonatum</i> (Müll. Arg.) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000); reported from Costa Rica by Lücking (1999a).

with cream-colored, denticulate margin, ascospores broader, $13-20 \times 2-3 \mu\text{m}$), and *C. labyrinthicum* (foliicolous, apothecia yellow but ascospores shorter, $10-14 \times 1.8-2 \mu\text{m}$, pycnidia labyrinthical). We have thus not hesitated in formally describing this new taxon, although knowing it only from a single collection.

We have not seen the type of *Microphiale lutea* f. *stenospora* from Hawaii, but according to the description (Magnusson and Zahlbruckner, 1944), it is very likely that it deals with the same taxon. The apothecia are given as deep yellow and the ascospores as $16-18 \times 1.5-2 \mu\text{m}$. No other species of *Coenogonium* has such long and narrow ascospores, being almost ten times as long as broad.

***Coenogonium barbatum* Lücking, Aptroot & Umaña, sp. nov.** (Figs 1C, 2C)
Mycobank number: 501131.

A *Coenogonio linkii* thallo caespitoso et cellulis algarum maioribus differt.

Type: COSTA RICA, Heredia, La Selva Biological Station, Arboleda, 50-100 m, 1998, Lücking 98-99 (CR, **holotype**; B, F, INB, USJ, **isotypes**); *ibid.*, Lücking 98-79, 98-81, 98-101 (F, **paratypes**).

Thallus filamentous, projecting horizontally from substrate (leaves), caespitose, beard-shaped, composed of several tufts of filaments connected at the base, with a single point of attachment, yellowish green, up to 10 mm long and broad, ecorticate; prothallus absent. *Photobiont Trentepohlia*, cells cylindrical, in distinct filaments, $40-60 \times 15-20 \mu\text{m}$ diam. *Apothecia* substipitate, rounded, 0.3-0.6 mm diam. and 100-150 μm high; disc soon convex, pale yellow to yellow-orange; margin thin, not prominent, smooth, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 30-60 μm broad, colorless, I+ sordid yellow-green; cells isodiametric and thin-walled, 3-7 μm diam. *Hypothecium* 10-20 μm high, colorless. *Hymenium* 60-70 μm high, colorless, I+ blue then quickly sordid green then reddish brown. $\times 2-3 \mu\text{m}$, 3-3.5 times as long as broad. *Pycnidia* not observed. *Chemistry*: no substances detected by TLC. *Ecology*: Foliicolous in understory of lowland rain forest.

Coenogonium barbatum is here described as a new species because of its distinctive growth form. The thallus projects horizontally from the substrate, but is not shelf-like and semi-circular as in *C. linkii* or *C. leprieurii*, but rather beard-shaped, resembling a tiny *Usnea*. The new species is otherwise similar and closely related to *C. linkii* and *C. congense*; both produce semi-circular thalli, and while the first has biserially arranged ascospores, the second often has a thinly pilose apothecial margin, at least in the present material. For a long time we considered *C. barbatum* to be a form of *C. linkii* or *C. congense*, but the new species is known from a very rich collection growing on several leaves of a single plant. It has not been found elsewhere at the type locality, whereas

both *C. linkii* and *C. congense* are very common at this site. This strongly suggests that a different mycobiont and possibly also a different species of *Trentepohlia* photobiont are involved in the beard-shaped taxon. Indeed, the *Trentepohlia* photobiont of *C. barbatum* has unusually wide cells of a type rarely found in the genus (Dodge, 1933; Uyenco, 1963a-b) and at the type locality occurs only in one other species, *C. confervoides*.

Another beard-shaped form was found at the same locality. It differs from *C. barbatum* in the 'unbranched' thallus composed of a single tuft of photobiont filaments only (Figs. 1D, 2D), and in the different photobiont itself, being a *Trentepohlia* with narrower cells. The taxon was found twice on leaves and bark but unfortunately without apothecia, which precludes a formal description. It is here filed as *C. aff. barbatum*.

***Coenogonium byssothallinum* Aptroot & Lücking, sp. nov.** (Fig. 1B, 5C-D)
Mycobank number: 501132.

A *Coenogonio flavoviride* thallo tenue obscuriore differt.

Type: COSTA RICA, Limón, Hitoy Cerere Biological Reserve (La Amistad Caribe Conservation Area), near Pandora, 150 m, lowland rainforest zone, on tree in secondary forest, overgrowing a sorediate *Thelotrema* family, 9 March 2004, Aptroot 60109 (INB, **holotype**; ABL, **isotype**).

Thallus appressed filamentous, corticolous, continuous, very thin, green, 10-20 mm diam., ecorticate; prothallus absent. *Photobiont Trentepohlia*, cells angular-rounded, in distinct filaments, 7-12 × 5-8 µm diam. *Apothecia* sessile, rounded, 0.15-0.25 mm diam. and 60-70 µm high; disc plane, pale yellow-brown; margin thin, not prominent, smooth, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 20-40 µm broad, colorless, I+ sordid yellow-green; cells isodiametric and thin-walled, 3-5 µm diam. *Hypothecium* 10-15 µm high, colorless. *Hymenium* 30-35 µm high, colorless, I+ blue then quickly sordid green then reddish-brown. *Asci* 25-30 × 4-6 µm. *Ascospores* irregularly biserial, ellipsoid, 1-septate, 4-6 × 1.8-2 µm, 2.5-3 times as long as broad. *Pycnidia* not observed. *Chemistry*: not tested. *Ecology*: Corticolous in understory of lowland rain forest.

This new species belongs in a small group of taxa with appressed filamentous thallus, possibly related to *Coenogonium moniliforme* but with very small apothecia and extremely small ascospores. So far, two other taxa are known in this group: the foliicolous *C. flavoviride*, with a thicker, bright green thallus and moniliform photobiont cells, and the foliicolous *C. antonianum* (≡ *C. madagascarensis* Vezda nom. illeg., see below), with a thallus formed by a photobiont with cylindrical cells and slightly larger, orange apothecia. *Coenogonium byssothallinum* has a photobiont intermediate between those two species, while its apothecia are very similar to those of *C. flavoviride*. The

thallus of the latter is very different in color and texture, and that species also produces abundant pycnidia, thus far unknown in *C. byssothallinum*.

Coenogonium confervoides Nyl., Flora 41: 380 (1858). (Fig. 4H)

?*Coenogonium andinum* Karst. in Nyl., Bot. Zeit. 20: 178 (1862).

Representative material examined: COSTA RICA, Heredia, La Selva Biological Station, STR trail, 50 m, 1998, Lücking 98-61, 98-63, 98-63 (hb. Lücking).

Thallus filamentous, projecting horizontally from substrate (bark and leaves), more or less shelf-like, with rather wide interspaces between individual filaments, yellow-green, up to 20 mm long and 30 mm broad, ecorticate; prothallus absent. *Photobiont Trentepohlia*, cells cylindrical, in distinct filaments, 30-50 × 15-20 µm diam. *Apothecia* substipitate, rounded, 0.3-1 mm diam. and 150-200 µm high; disc flat, yellow; margin distinct, not prominent, denticulate, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 µm broad, colorless, I+ sordid yellow-green; cells isodiametric and thin-walled, 3-7 µm diam. *Hypothecium* 10-30 µm high, colorless to pale yellowish. *Hymenium* 50-60 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 45-55 × 4-6 µm. *Ascospores* irregularly biseriata, ellipsoid, 1-septate, 6-8 × 2.5-3 µm, 2.5-3 times as long as broad. *Pycnidia* not observed. *Chemistry*: no substances detected by TLC. *Ecology*: Insufficient data available.

The present material is similar to *Coenogonium linkii* s.str. but distinguished by various characters: larger apothecia with yellow (vs. yellow-orange) disc and denticulate (vs. smooth) margin, more irregularly shelf-like thallus with large interspaces between filaments (vs. regularly shelf-like, compact thallus lacking interspaces), and a *Trentepohlia* photobiont with very large and wide cells (20-30 × 5-10 µm in *C. linkii*).

For the time being, we have adopted the name *Coenogonium confervoides* for this form. The latter, as well as *C. andinum*, was listed as a synonym of *C. linkii* by Uyenco (1963a), but both differ from *C. linkii* s.str. in their much wider photobiont cells. Since in our present, rather rich material, the mycobiont and photobiont characters are strongly correlated, we have decided to use an available name, rather than describing new taxa, until the taxonomy and nomenclature of these species can be clarified by studying more material from different regions. The species was also found in material from Brazil (Cáceres *et al.*, in prep.).

Coenogoniumacrocephalum (not known from Costa Rica) is very similar to *C. confervoides* in thallus morphology and photobiont type, but differs in having non-septate ascospores and apothecia with smooth margin;

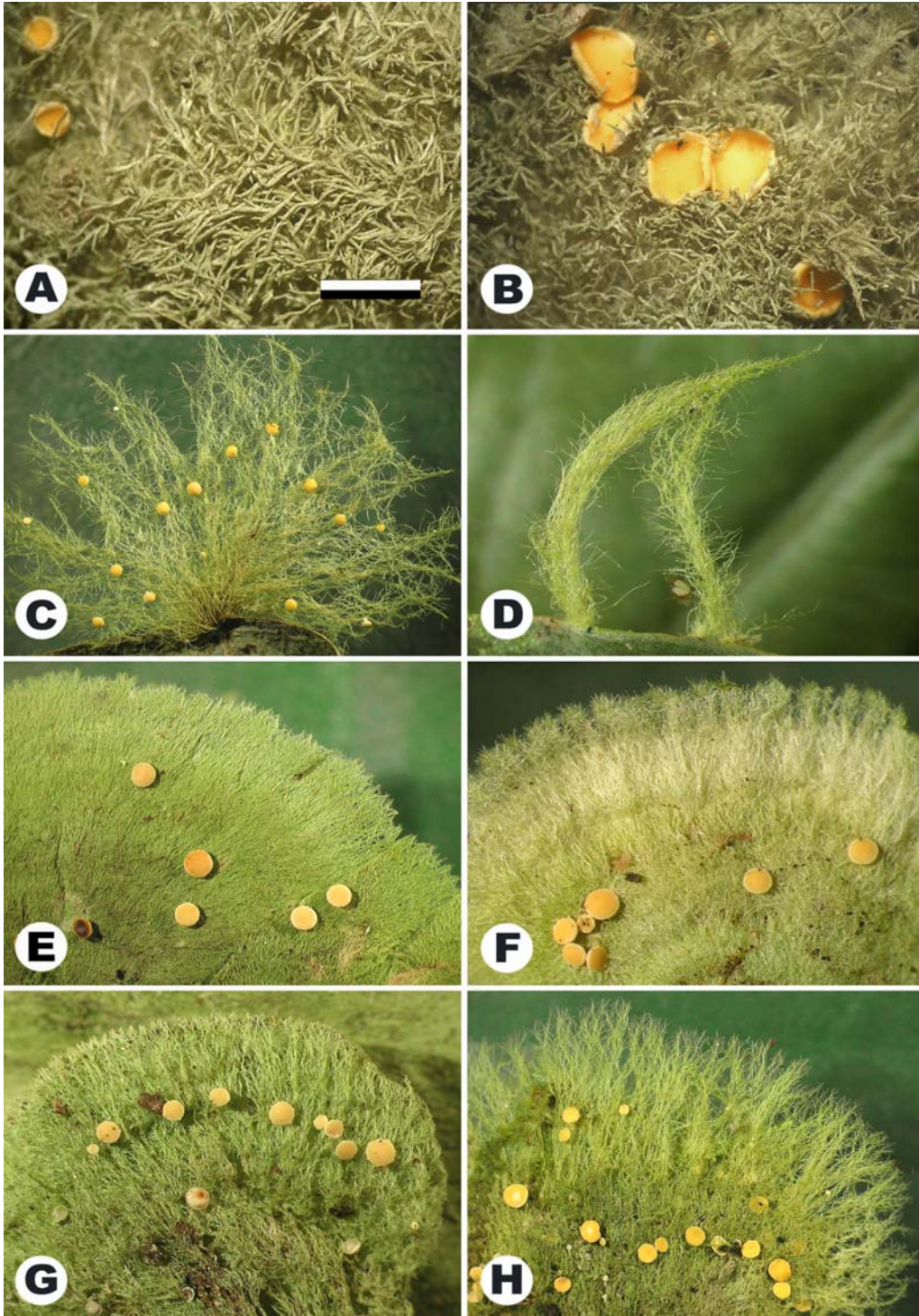


Fig. 4. Habit of *Coenogonium* species. **A-B.** *Coenogonium tuckermanii* (Nelsen 3613). **C.** *Coenogonium barbatum* (isotype). **D.** *Coenogonium* aff. *barbatum*. **E.** *Coenogonium congense*. **F.** *Coenogonium* aff. *congense*. **G.** *Coenogonium linkii*. **H.** *Coenogonium confervoides*. Scale for A-B = 1 mm, for B = 3 mm, for D = 1.5 mm, for E-H = 2 mm.

there is a slight chance that the imperfectly known *C. andinum* might actually be synonymous with the latter, rather than with *C. confervoides*.

Coenogonium congense C.W. Dodge, Ann. Missouri Bot. Gard. 40: 350 (1953). (Figs 3A-B, 4E)

Representative material examined: COSTA RICA, Heredia, La Selva Biological Station, SHO trail, 50-100 m, 1998, Lücking 98-11, 98-12, 98-15 (F); *ibid.*, CES trail, 50-100 m, 1998, Lücking 98-33 (F); *ibid.*, STR trail, 50 m, 1998, Lücking 98-69 (F).

Thallus filamentous, projecting horizontally from substrate (mostly bark), very regularly shelf-like, rather thin and compact, with no interspaces between individual filaments, usually bright to dull green, up to 30 mm long and 40 mm broad, ecorticate; prothallus absent. *Photobiont Trentepohlia*, cells cylindrical, in distinct filaments, 15-25 × 5-7 µm diam. *Apothecia* substipitate, rounded, 0.3-1 mm diam. and 150-200 µm high; disc soon convex, yellow-orange; margin thin, not prominent, smooth to thinly pilose, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 µm broad, colorless; cells isodiametric and rather thick-walled in inner parts, 3-7 µm diam., radiately elongate and thin-walled in the periphery, 5-12 × 3-5 µm. *Hypothecium* 15-30 µm high, colorless. *Hymenium* 50-60 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 45-55 × 4-6 µm. *Ascospores* uniseriate, ellipsoid, 1-septate, 5-8 × 2.5-3 µm, 2-3 times as long as broad. *Pycnidia* globose, creme-colored; conidia non-septate, fusiform-ellipsoid, 5-8 × 1.5-2 µm. *Chemistry*: no substances detected by TLC. *Ecology*: Corticolous and sometimes foliicolous in understory of lowland rain forest.

Uyenco (1963a) did not have access to the type material and therefore excluded this taxon from her study. Based on the description given by Dodge (1953), the present material fits the type of *Coenogonium congense*, which was verified during a recent visit of the first and second author to FH. The species is apparently very closely related to *C. linkii* but seems to differ in the constantly uniseriate (vs. biseriolate) ascospores and the very compact filaments leaving no interspaces (less compact in *C. linkii* s.str.). The thallus morphology and apothecial anatomy is exactly the same as in *C. leprieurii*, but that species has non-septate ascospores.

In our material from Costa Rica, *Coenogonium congense* was the most abundant of the species with filamentous, shelf-like thallus.

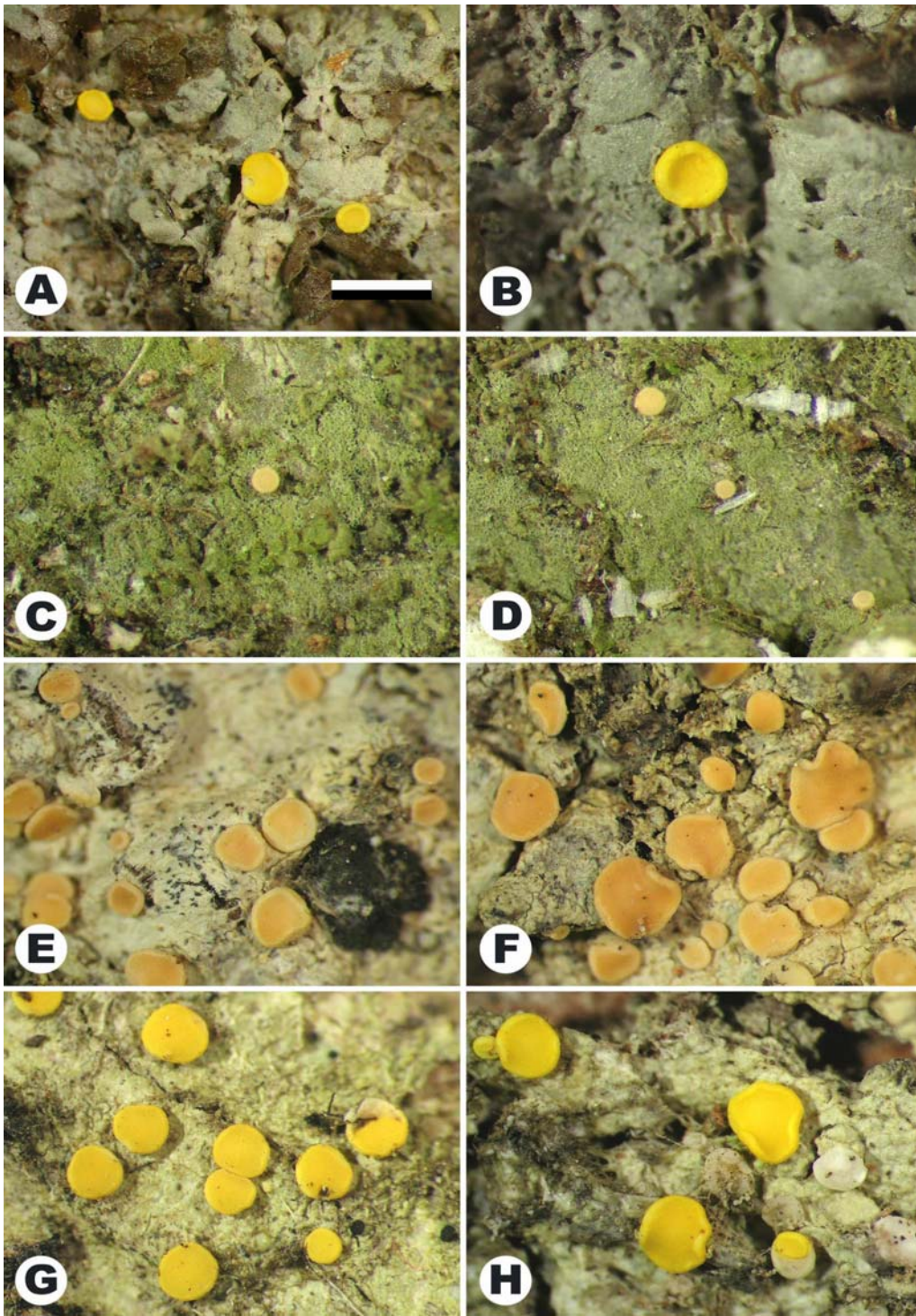


Fig. 5. Habit of *Coenogonium* species. **A-B.** *Coenogonium aciculatum* (holotype). **C-D.** *Coenogonium byssothallinum* (holotype). **E-F.** *Coenogonium kalbii* (paratype). **G-H.** *Coenogonium luteocitrinum* (holotype). Scale for A and C-D = 0.7 mm, for B = 0.4 mm, for E-H = 1 mm.

A probably undescribed species, which is somehow intermediate between *Coenogonium congense* and *C. confervoides*, remains unnamed at the moment and is here treated as *C. aff. congense* (Fig. 4F). It agrees with *C. congense* in the uniseriately arranged ascospores but has apothecia with a denticulate margin, the thallus is more nitidous, and the arrangement of the photobiont filaments is quite different, leaving distinct interspaces along the margin, which appears slightly zonate. The thallus and apothecia are more similar to *C. confervoides*, but that species has biseriately arranged ascospores and a different photobiont with much broader cells.

Coenogonium* cf. *implexum Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 92 (1862).

Representative material examined: COSTA RICA, Limón, Hitoy Cerere Biological Station (La Amistad Caribe Conservation Area), 40 km S of Limón, forest trail above station, 83° 02' W, 9° 40' N, 130 m, lowland to submontane rainforest zone, on trunks in disturbed primary forest, 9 Mar 2004, Sipman 51598 (B, INB).

Thallus filamentous, pannose, very densely woven, with little interspaces between individual filaments, yellow-green, up to 50 mm across, ecorticate; prothallus absent. *Photobiont* *Trentepohlia*, cells cylindrical, in distinct filaments, 25-35 × 10-15 µm diam. *Apothecia* sessile, rounded, 0.5-1 mm diam. and 150-200 µm high; disc flat, yellow-orange; margin thin, not prominent, smooth, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 µm broad, colorless; cells isodiametric and rather thick-walled in inner parts, 3-5 µm diam., radiately elongate and thin-walled in the periphery, 3-7 × 3-5 µm. *Hypothecium* 20-30 µm high, colorless. *Hymenium* 60-80 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 55-75 × 5-7 µm. *Ascospores* uniseriate, ellipsoid, 1-septate, 8-12 × 2.5-3.5 µm, 2.5-3.5 times as long as broad. *Pycnidia* not observed. *Chemistry*: no substances detected by TLC. *Ecology*: Corticolous in understory of temperate to tropical rain forest.

This species was reported by Müller Argoviensis (1894), Dodge (1933), and Uyenco (1963a), for Costa Rica, and specimens fitting the North American material of this taxon (Brodo *et al.*, 2001) have been found in Costa Rica by us. However, comparison with gatherings from Australasia suggest that *Coenogonium implexum* s.str. is restricted to that area and that the American material represents a distinct species. As exemplified by the color photograph in Kantvilas and Jarmann (1995), *C. implexum* has a very densely woven

thallus which forms rather thick, pannose, almost circular tufts on the substrate. This type of thallus is unknown from any other species in the genus and most closely resembles the shelf-like, yet thinner, thalli of *C. congense* and *C. leprieurii*. The New World material is closer to *C. disjunctum*.

Coenogonium interplexum Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 92 (1862).

Thallus filamentous, prostrate and effuse, irregularly woven, with large interspaces between individual filaments, yellow-green, up to 40 mm across, ecorticate; prothallus absent. *Photobiont Trentepohlia*, cells cylindrical, in distinct filaments, 25-40 × 10-15 µm diam. *Apothecia* substipitate, rounded, 0.3-1.0 mm diam. and 150-200 µm high; disc flat, yellow-orange; margin thin, not prominent, smooth, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 µm broad, colorless; cells isodiametric and rather thick-walled in inner parts, 3-7 µm diam., radiately elongate and thin-walled in the periphery, 5-10 × 3-5 µm. *Hypothecium* 20-30 µm high, colorless. *Hymenium* 70-80 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 60-70 × 4-6 µm. *Ascospores* uniseriate, ellipsoid, 1-septate, 6-9 × 2-3 µm, 2.5-3.5 times as long as broad. *Pycnidia* globose, creme-colored; conidia non-septate, fusiform-ellipsoid, 5-8 × 1.5-2 µm. *Chemistry*: no substances detected by TLC. *Ecology*: Corticolous and sometimes foliicolous in understory of lowland montane rain forest.

Coenogonium interplexum forms the center of another group of taxonomically difficult, filamentous species of the genus, including also *C. disjunctum*, *C. implexum*, *C. pannosum*, and *C. velutinum*. Among these, *C. velutinum* is characterized by its pruinose apothecia; *C. pannosum* has very narrow ascospores (1.5-2 µm), while those of *C. disjunctum* are larger than those of the other species of this group (10-14 × 2.5-3.5 µm). *Coenogonium implexum* is easily distinguished from *C. interplexum* by its very compact, pannose thallus, with very densely woven, short filaments; this species is often confused in the literature.

Uyenco (1963a-b) describes *Coenogonium interplexum* as having a smooth apothecial margin. We found one specimen in our material with strongly stipitate apothecia and denticulate margins [COSTA RICA, Heredia, La Selva Biological Station, SHO trail, 50-100 m, 1998, Lücking 98-98 (hb. Lücking)]; the ascospores were extremely small, measuring only 5-6 µm in length. Another set of specimens [COSTA RICA, Heredia, La Selva Biological Station, Arboleda, 50-100 m, 1998, Lücking 98-6, 98-7, 98-22, 98-25, 98-27, 98-45, 98-56, 98-82 (hb. Lücking)] agree with *Coenogonium interplexum* in all characters except for the distinctly pannose instead of prostrate thallus. In some of these, the photobiont has narrow cells (15-25 × 5-7 µm), while in others the

cells are larger (20-40 × 10-15 µm). Due to the sparse material and the insufficient knowledge of type specimens, it was not possible to evaluate these differences taxonomically or assign any of the available names to these forms, and they are here treated as *C. aff. interplexum* A (denticulate apothecia, small ascospores), *C. aff. interplexum* B (pannose thallus, photobiont cells 10-15 µm wide) and *C. aff. interplexum* C (pannose thallus, photobiont cells 5-7 µm wide).

Coenogonium kalbii Aptroot, Lücking & Umaña, **sp. nov.** (Fig. 5E-F)
Mycobank number: 501133.

A *Coenogonio geralense* apotheciis pallide aurantiacis et conidiis angustioribus differt.

Type: COSTA RICA, Puntarenas, Restaurant Río Brujo, about 10 km before Río Grande de Terraba, along Interamerican Highway, 350 m, 2 Jan 1979, Kalb & Plöbst s.n. (hb. Kalb 35086, **holotype**). Additional material examined: COSTA RICA, Puntarenas, Surroundings of Las Cruces Tropical Botanical Garden, Fila Cruces Ridge, about 4 km SSE of San Vito, 1300 m, 31 Dec 1978, Kalb & Plöbst s.n. (hb. Kalb, **paratype**). Cartago, Tapantí National Park, Mirador, 1800 m, Lücking 1327 (F, **paratype**). Cartago, Río Macho village (La Amistad Pacífico Conservation Area), Orosi Valley, 30 km SE of San José and 15 km SE of Cartago, road from Orosi to Tapantí near park entrance, 83° 48' W, 9° 46' N, 1100 m, montane rainforest zone, exposed roadside trees, on bark (lower trunk), 11 April 2003, Grube 11742 (GZU, INB, **paratypes**).

Thallus crustose, corticolous, continuous, thin, smooth, yellowish green, 10-30 mm diam., with cartilaginous corticiform layer; prothallus absent. *Photobiont Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 5-10 µm diam. *Apothecia* sessile, rounded to slightly irregular in outline, 0.5-0.8(-1) mm diam. and 120-160 µm high; disc plane, pale orange; margin thin, not prominent, smooth to rough, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-70 µm broad, colorless, I+ sordid yellow-green; cells isodiametric and thin-walled, 5-7 × 3-5 µm. *Hypothecium* 15-30 µm high, colorless to pale yellowish. *Hymenium* 60-70 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 55-65 × 5-7 µm. *Ascospores* irregularly biseriate, narrowly ellipsoid, 1-septate, 6-8 × 2-2.5 µm, 3-3.5 times as long as broad. *Pycnidia* observed in one collection, wart-shaped, 0.05-0.1 mm diam. *Conidia* broadly ellipsoid-bacillar, non-septate or seemingly 1-septate, 3-4 × 1-1.5 µm. *Chemistry*: no substances detected by TLC. *Ecology*: Corticolous in more exposed situations in lower montane rain forest.

This new species belongs in the taxonomically difficult group centered around *Coenogonium geralense*, including species with medium-sized to large apothecia, rather small and narrow (6-9 × 1.5-2.5 µm), more or less biserially arranged ascospores, and minute conidia. The species within this group mostly differ in their apothecial colors, together with other characters. Thus, *C.*

geralense and the foliicolous *C. queenslandicum* have apothecia with pale to bright yellow discs lacking an orange tinge, and smaller conidia in the latter ($2\text{--}2.5 \times 0.5\text{--}0.7 \mu\text{m}$). The apothecia of *C. siquirrense* are bright orange and feature an excipulum with very large, thin-walled peripheral cells. In *C. subdentatum*, the apothecia are pale yellow-brown and have a denticulate margin, whereas the newly described *C. luteocitrinum* features bright yellow apothecia with smooth margin and narrower conidia (up to $2.5 \mu\text{m}$ broad). The foliicolous *C. subfallaciosum* comes closest to *C. kalbii* but produces abundant pycnidia with smaller ($2 \times 1.2 \mu\text{m}$) conidia, and its apothecia are frequently marginally hypophyllous on a mycelium free of algae. *Coenogonium stenosporum*, *C. nepalense* and *C. atroluteum* are also similar but have longer ascospores ($7\text{--}13 \mu\text{m}$ long), and the latter has brown apothecial margins; conidia are unknown in these species.

Coenogonium kalbii is a rather non-descript species known from four well-developed collections made in the southern parts of Costa Rica. As many other species in the genus, it seems to prefer humid, shaded microsites in the lowland to lower montane rainforest. The smaller collection was chosen as the holotype since it is the one that produces pycnidia.

Coenogonium linkii Ehrenb. in Nees von Esenbeck, Horae Phys. Berol.: 120 (1820). (Fig. 4G)

Representative material examined: COSTA RICA, Heredia, La Selva Biological Station, STR trail, 50 m, 1998, Lücking 98-68 (F).

Thallus filamentous, projecting horizontally from substrate (mostly bark), very regularly shelf-like, rather thin and compact, with few and narrow interspaces between individual filaments, usually bright green, up to 25 mm long and 30 mm broad, ecorticate; prothallus absent. *Photobiont* *Trentepohlia*, cells cylindrical, in distinct filaments, $15\text{--}25 \times 5\text{--}7 \mu\text{m}$ diam. *Apothecia* substipitate, rounded, 0.5-1.2 mm diam. and 150-200 μm high; disc flat to convex, yellow-orange; margin thin, not prominent, smooth, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 μm broad, colorless; cells isodiametric and rather thick-walled in inner parts, 3-7 μm diam., radiately elongate and thin-walled in the periphery, $5\text{--}12 \times 3\text{--}5 \mu\text{m}$. *Hypothecium* 15-30 μm high, colorless. *Hymenium* 50-60 μm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* $40\text{--}55 \times 4\text{--}6 \mu\text{m}$. *Ascospores* irregularly biseriata, ellipsoid, 1-septate, $6\text{--}9 \times 2\text{--}3 \mu\text{m}$, 2.5-3.5 times as long as broad. *Pycnidia* globose, creme-colored; conidia non-septate, fusiform-ellipsoid, $5\text{--}7 \times 1.5\text{--}2 \mu\text{m}$. *Chemistry*: no substances detected by TLC. *Ecology*: Corticolous and foliicolous in understory of lowland to montane rain forest.

Coenogonium linkii is the oldest name available for a taxonomically difficult complex of species forming filamentous, shelf-like thalli and producing 1-septate ascospores. In spite of the tendency to lump all these taxa into a single species, our material clearly shows correlations between mycobiont and photobiont characters that indicate that several taxa are involved, differing in apothecial color and morphology, ascospore arrangement within the asci, arrangement of the filaments, and photobiont type. Thus, at present we distinguish the following four taxa: *C. congense*, with uniseriately arranged ascospores, apothecia with yellow-orange disc and smooth to thinly pilose margin, and very compact thallus leaving no interspaces and featuring a photobiont with narrow cells; *C. aff. congense*, differing from the preceding species by its apothecia with yellow disc and denticulate margin and its less compact, shiny thallus leaving distinct interspaces along the margin; *C. confervoides*, with apothecia similar to those of *C. aff. congense*, but biseriately arranged ascospores and a photobiont having very large and broad cells; and *C. linkii* s.str., with biseriately arranged ascospores, apothecia with yellow-orange disc and smooth margin, and a photobiont with intermediate cell size leaving interspaces in the thallus. In the material studied by us so far, these differences seem to hold, but a revision of world-wide material is urgently needed to clarify the taxonomy of species in this and the *C. interplexum* aggregate.

***Coenogonium luteocitrinum* Rivas Plata, Lücking & Umaña, sp. nov.**

Mycobank number: 501134.

(Figs 5G-H)

A *Coenogonio geralense* apotheciis flavo-luteis differt.

Type: COSTA RICA, Puntarenas, La Amistad International Park, Altamira Station (La Amistad Pacífico Conservation Area), Talamanca Ridge, 20 km N of San Vito near Finca Colorado, trail to Casa Coca, 83° 00' W, 9° 02' N, 1600-1800 m, montane rainforest zone, secondary forest and open secondary vegetation dominated by *Cecropia*, on bark (fallen branch), 1 July 2002, Lücking 15269b (INB, **holotype**; F, **isotype**). Additional material examined: GUATEMALA, on bark of *Mimosaceae*, Quedensley 2061 (F). COSTA RICA, Puntarenas, La Amistad International Park (La Amistad Pacífico Conservation Area), Altamira Station, 20 km N of San Vito near Finca Colorado, access road to station, 83° 00' W, 9° 01' N, 1350-1450 m, montane rainforest zone, roadside pasture with living fence posts, on bark (stem base) of *Vismia*, 29 Jun 2002, Sipman 48010j (B, INB, **paratypes**). VENEZUELA, Mérida, Distr. Libertador, Monte Zerpa, a few km before Mérida, above "Hechincera", 8° 40' N, 71° 10' W, 2200 m, primary cloud forest, 14 Aug 1989, Kalb *et al.* s.n. (hb. Kalb 29467, **paratype**). Distr. Campo Elías, El Pedregal, about 50 km NW of Mérida, 8° 40' N, 71° 05' W, 2000 m, remnants of cloud forest, 4 Aug 1989, Kalb *et al.* s.n. (hb. Kalb 34861, **paratype**).

Thallus crustose, corticolous, continuous, thin, smooth, pale greenish, 10-15 mm diam., with cartilaginous corticiform layer; prothallus absent. *Photobiont Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 6-10 µm diam. *Apothecia* sessile, rounded to slightly irregular in

outline, 0.5-0.8 mm diam. and 150-200 μm high; disc plane, bright yellow; margin thin, not prominent, smooth, bright yellow. *Excipulum* paraplectenchymatous with radiating cell rows, 50-70 μm broad, colorless, I+ sordid yellow-green; cells isodiametric and thick-walled, in peripheral parts partially elongated and thin-walled, 3-7 \times 3-5 μm . *Hypothecium* 20-30 μm high, pale yellowish. *Hymenium* 50-70 μm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 45-65 \times 6-8 μm . *Ascospores* irregularly biseriate, narrowly ellipsoid, 1-septate, 6-10 \times 2-2.5 μm , 3-4 times as long as broad. *Pycnidia* not observed. *Chemistry*: no substances detected by TLC. *Ecology*: Corticolous in more exposed situations in montane rain forest.

Coenogonium luteocitrinum is closely related to *C. geralense*, a chiefly foliicolous species, with which it shares the medium-sized, yellow apothecia and small, narrowly ellipsoid, biseriate ascospores. However, differences are found in the color and shape of the apothecia, those of *C. geralense* being paler yellow with creme-colored margin and having a more concave disc and slightly prominent margin. Also, pycnidia are regularly present in the latter but have not been found in *C. luteocitrinum*, in spite of careful search. The bright yellow apothecia are similar to those of *C. subzonatum* (foliicolous, apothecia denticulate, ascospores 2.5-3.5 μm broad, uniseriate), *C. labyrinthicum* (foliicolous, ascospores 10-14 \times 1.8-2 μm , pycnidia labyrinthical), and the newly described *C. aciculatum* (ascospores 14-18 \times 1.5-2 μm).

Coenogonium luteocitrinum seems to be a relatively abundant and widespread taxon, being known also from Venezuela (see collections cited above) and Brazil (Cáceres *et al.*, in prep.; Kalb, pers. comm. 2000); it is therefore astonishing that no name was available for this species.

Coenogonium* aff. *luteolum (Kalb) Kalb & Lücking (see below).

Representative material examined: COSTA RICA, Puntarenas, La Amistad International Park (La Amistad Pacífico Conservation Area), Altamira Station, 20 km N of San Vito near Finca Colorado, access road to station, 83° 00' W, 9° 01' N, 1350-1450 m, montane rainforest zone, roadside pasture with living fence posts, on bark (stem base) of *Vismia*, 29 Jun 2002, Sipman 48010j (B, INB; filed under *Coenogonium luteocitrinum*).

Thallus crustose, corticolous, continuous, thin, smooth, pale greenish grey, 5-10 mm diam., with cartilaginous corticiform layer; prothallus absent. *Photobiont Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 6-9 μm diam. *Apothecia* sessile, rounded to slightly irregular in outline, 0.5-0.8 mm diam. and 150-200 μm high; disc plane to slightly concave, yellow; margin thin, slightly prominent, uneven, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 μm broad,

colorless, I+ sordid yellow-green; cells isodiametric and thick-walled, in peripheral parts partially elongated and thin-walled, $3-7 \times 3-6 \mu\text{m}$. *Hypothecium* 15-30 μm high, colorless to pale yellowish. *Hymenium* 70-80 μm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 60-70 \times 6-8 μm . *Ascospores* uniseriate, ellipsoid, 1-septate, 9-13 \times 2.5-3.5 μm , 3-4 times as long as broad. *Pycnidia* not observed. *Chemistry*: not tested.

This taxon is known from one small collection only and could not be identified with any of the species accepted here. It is morphologically similar to *Coenogonium luteolum* described from Madeira (Kalb and Hafellner, 1992), but that taxon has larger apothecia with smooth margin. In the key it comes closest to the new species *C. saepincola*, which differs by its smaller apothecia with pale yellow-orange disc and denticulate margin and its white thallus.

Coenogonium luteum (Dicks.) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000). Figs. 1C, 2A-D

Representative material examined: COSTA RICA, San José, Interamerican Highway near El Empalme, S side of highway at road to San Pablo, 2200 m, montane rainforest zone, 28 Dec 1978, Kalb & Plöbst s.n. (hb. Kalb 35085, 35086). San José, Genesis II Cloud Forest Reserve, 2500 m, Jul 1997, Lücking 97-57 (F). San José, Los Santos Forest Reserve, Cerro de la Muerte Biological Station (Pacífico Central Conservation Area), Talamanca Ridge, km 93 on road (ruta 2) from Cartago to San Isidro, trail to summit, 83° 45' W, 9° 34' N, 3100-3400 m, upper montane cloud forest zone, partly disturbed subparamo shrub and low forest, on bark (lower trunk), 3 July 2002, Lücking s.n. (F). Cartago, Tapantí National Park, Macizo de la Muerte Section, Cerro de la Muerte (La Amistad Pacífico Conservation Area), Talamanca Ridge, Villa Mills, km 95 on road (ruta 2) from Cartago to San Isidro, trail behind Restaurante La Georgina (Sendero La Danta), 83° 43' W, 9° 33' N, 3100 m, upper montane rainforest zone, disturbed oak forest, on bark (lower trunk) of *Quercus*, 12 April 2003, Trest 1466a (F, INB, WIS).

Thallus crustose, corticolous, continuous, thin, smooth, pale greenish, 20-50 mm diam., with cartilaginous corticiform layer; prothallus absent. *Photobiont Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 6-10 μm diam. *Apothecia* sessile, rounded to slightly irregular in outline, (0.5-)0.8-2 mm diam. and 200-250 μm high; disc concave, orange; margin thin, slightly prominent, smooth, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 μm broad, colorless, I+ sordid yellow-green; cells isodiametric and thick-walled, in peripheral parts partially elongated and thin-walled, $3-7 \times 3-6 \mu\text{m}$. *Hypothecium* 20-30 μm high, pale yellowish. *Hymenium* 60-70 μm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 55-65 \times 6-8 μm . *Ascospores* irregularly uniseriate, broadly ellipsoid, 1-septate, 7-11 \times 2.5-3.5 μm , 2.5-3.5 times as long as broad. *Pycnidia* wart-shaped, 0.05-0.1 mm diam. *Conidia* broadly ellipsoid-bacillar, non-septate, 3-5 \times 1.5-2 μm . *Chemistry*: no substances

detected by TLC. *Ecology*: Corticolous and muscicolous in upper montane rain forest and subparamo, widespread in temperate regions.

This taxon has been greatly confused in the literature and available collections, at one point or the other including all specimens with large, vividly colored apothecia. *Coenogonium luteum* in the strict sense is characterized by its large apothecia with more or less concave, orange disc, excipulum with rather small, thick-walled cells, broadly ellipsoid ascospores of the *C. subluteum* type, and non-septate, small conidia. For some time we thought *C. luteum* s.str. to be a strictly temperate to subtropical taxon, but tropical collections from higher elevations, often overgrowing bryophytes, perfectly match specimens from North America and Europe. Most similar are *C. eximium* (ascospores 2-2.5 μm broad), *C. luteolum* (disc yellow, conidia shorter), and *C. fallaciosum* (apothecia plane, pale yellow to pale orange).

***Coenogonium magdalenae* Rivas Plata, Lücking & Lizano, sp. nov.**

Mycobank number: 501135.

(Figs 6A-B)

A *Coenogonio luteo* apotheciis pallide flavis margine aspero et prothallo albido differt.

Type: COSTA RICA, San José, Leonel Oviedo Ecological Reserve (Cordillera Volcánica Central Conservation Area), Central Valley, San José, University campus north of church in San Pedro, adjacent to Escuela de Biología, main trail through reserve, 84° 03' W, 9° 56' N, 1200 m, lower montane moist forest zone, oldgrowth secondary forest, on bark (lower trunk), 22 April 2003, Lücking 16288 (USJ, **holotype**; F, **isotype**). Additional material examined: San José, Leonel Oviedo Ecological Reserve (Cordillera Volcánica Central Conservation Area), Central Valley, San José, University campus north of church in San Pedro, adjacent to Escuela de Biología, main trail through reserve, 84° 03' W, 9° 56' N, 1200 m, lower montane moist forest zone, oldgrowth secondary forest, on bark (lower trunk), 4 November 2002, Lücking 15680b (F, **paratype**), 22. April 2003, Lücking 16278 (F, **paratype**), Lücking 16283 (USJ, F, **paratypes**), 8 March 2004, Aptroot 60015 (ABL, INB, **paratypes**).

Thallus crustose, corticolous or muscicolous, continuous, thin, smooth, pale greenish, 30-70 mm diam., with cartilaginous corticiform layer; white prothallus present. *Photobiont* *Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 6-9 μm diam. *Apothecia* sessile with strongly constricted base, rounded, 0.7-1.3 mm diam. and 300-400 μm high; disc plane to concave, pale yellow; margin thin, prominent, with irregular surface to minutely denticulate, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 μm broad, colorless, I+ sordid yellow-green; cells partially elongated and thin-walled, in innermost parts isodiametric and thick-walled, 7-15 \times 5-8 μm . *Hypothecium* 20-30 μm high, colorless. *Hymenium* 70-90 μm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 65-80 \times 4-6 μm . *Ascospores* irregularly uniseriate, ellipsoid, 1-septate, 6-10 \times 2.5-3.5 μm , 2-3 times as long as broad. *Pycnidia* not observed. *Chemistry*:

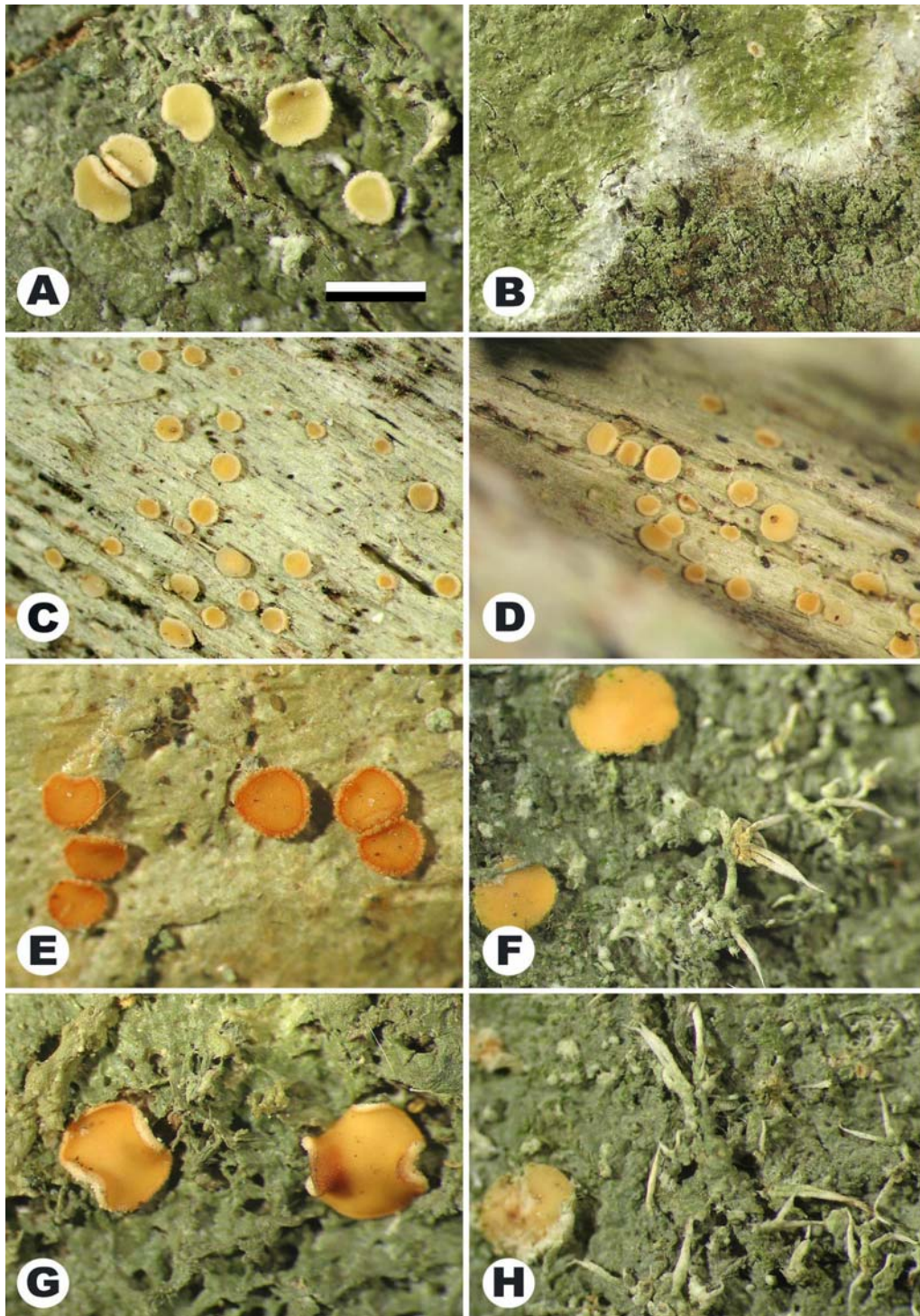


Fig. 6. Habit of *Coenogonium* species. **A-B.** *Coenogonium magdalenae* (isotype). **C-D.** *Coenogonium saepincola* (isotype). **E.** *Coenogonium siquirrense* f. *denticulatum* (isotype). **F-H.** *Coenogonium strigosum* (holotype). Scale for A and E-H = 0.7 mm, for B-D = 1 mm.

no substances detected by TLC. *Ecology*: Corticolous in understory of lower montane moist forest.

This new species is dedicated to Magdalena Pavlich, mycologist and botanist at the Universidad Peruana Cayetano Heredia in Lima, Peru, for her contributions to Peruvian mycology and botany and for her support to make the visit of the first author to The Field Museum possible.

Coenogonium magdalenae belongs in the group of *C. luteum* and related species, characterized by rather large apothecia with high hymenia and small, ellipsoid, more or less uniseriate ascospores. *Coenogonium luteum* itself lacks a prothallus and has more vividly colored, yellow-orange apothecia with smooth margin. *Coenogonium luteolum* also lacks a prothallus and further differs by its more vividly yellow apothecia with smooth margin. The latter two species are also characterized by their very small, non-septate conidia, whereas pycnidia have not been found in the material of *C. magdalenae*. The newly described *C. strigosum*, which was found at the same locality, agrees with *C. magdalenae* in its ascospore type, large apothecia, and white prothallus, but the apothecia are yellow-orange with plane to undulate disc and evanescent margin, and the excipulum features very large peripheral cells.

Coenogonium saepincola Aptroot, Sipman & Lücking **sp. nov.** (Figs 6C-D)
Mycobank number: 501136.

A *Coenogonio pineti* apotheciis margine denticulato et thallo albido differt.

Type: COSTA RICA, Limón, Hitoy Cerere Biological Reserve (La Amistad Caribe Conservation Area), near Pandora, 150 m, lowland rainforest zone, on wooden poles along meadows along access road, 10 March 2004, Aptroot 60242 (INB, **holotype**; ABL, **isotype**). Limón, Hitoy Cerere Biological Reserve (La Amistad Caribe Conservation Area), 40 km S of Limón, 83° 02' W, 9° 40' N, 130 m, lowland rainforest zone, on wooden posts of fence between road and pasture, 10 March 2004, Sipman 51664 (B, INB, **paratypes**).

Thallus crustose, lignicolous, continuous, very thin, smooth, white to very pale greenish, 10-20 mm diam., with cartilaginous corticiform layer; prothallus absent. *Photobiont* *Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 6-10 µm diam. *Apothecia* sessile, rounded, 0.3-0.5 mm diam. and 100-120 µm high; disc plane, pale yellow-orange; margin thin, not prominent, denticulate, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, colorless, I+ sordid yellow-green; cells isodiametric and thin-walled, 3-5 µm broad. *Hypothecium* 10-20 µm high, colorless to pale yellowish. *Hymenium* 50-60 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 45-55 × 5-7 µm. *Ascospores* irregularly

uniseriate, ellipsoid, 1-septate, $8-10 \times 2.5-4 \mu\text{m}$, 2.5-3 times as long as broad. *Pycnidia* not observed. *Chemistry*: no substances detected by TLC. *Ecology*: Lignicolous in exposed situations of lowland rain forest.

Coenogonium saepincola is rather similar to the foliicolous taxa of the *C. subluteum* group in having medium-sized, rather pale apothecia and relatively broad, more or less uniseriately arranged ascospores. It differs from other species in this group by its lignicolous growth on fence posts, its more or less white thallus, and its denticulate apothecial margins. Other species in this group have smooth apothecial margins, except *C. subzonatum* which differs by its bright yellow apothecia. Most closely related among the corticolous taxa are *C. pineti*, with smooth apothecial margins and greenish thallus, and *C. frederici*, which also has smooth apothecial margins and a pale salmon-colored disc. *Coenogonium stramineum* from the Seychelles agrees with *C. saepincola* in the rather pale apothecia with denticulate margin and the relatively broad ascospores, but its apothecia are smaller (0.2-0.35 mm diam.) and its thallus is greenish and corticolous.

The new species is known from two rather rich collections on fence posts in the lowland rainforest zone near the Caribbean coast of Costa Rica.

***Coenogonium siquirrense* f. *denticulatum* Rivas Plata & Lücking, f. nov.**

Mycobank number: 501137.

(Fig. 6E)

A *Coenogonio siquirrense* f. *siquirrense* apotheciis margine denticulato differt.

Type: COSTA RICA, Heredia, La Selva Biological Station, El Atajo Trail (SAT), 50-100 m, 5 March 2004, Lücking 17075 (CR, **holotype**; F, USJ, **isotypes**).

Thallus crustose, corticolous, continuous, thin, smooth, pale yellowish green, 30-50 mm diam., with cartilaginous corticiform layer; white prothallus present. *Photobiont* *Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 6-10 μm diam. *Apothecia* sessile, rounded, 0.6-1.2 mm diam. and 150-200 μm high; disc plane, pale to bright orange with darker marginal zone; margin thin, not prominent, minutely denticulate, creme-colored to pale orange. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 μm broad, colorless, I+ sordid yellow-brown; cells partially elongated and thin-walled, very large in peripheral parts, up to $20 \times 10 \mu\text{m}$. *Hypothecium* 15-25 μm high, colorless to pale yellowish. *Hymenium* 50-70 μm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* $45-55 \times 5-7 \mu\text{m}$. *Ascospores* irregularly biseriately, ellipsoid, 1-septate, $6-10 \times 2-3 \mu\text{m}$, 3-3.5 times as long as broad. *Pycnidia* not observed. *Chemistry*: no substances detected by TLC. *Ecology*: Corticolous in understory of lowland rain forest.

The several corticolous collections assigned to this new form agree with the foliicolous populations in all characters (thallus color, white prothallus, apothecial color, ascospore type), except that the apothecial margin is

persistently denticulate. We restudied about 50 foliicolous collections, many of them originating from the same locality, and the apothecial margins are always smooth to very minutely irregular. Experience with other species suggests that the nature of the surface of the apothecial margin might be a specific feature, but since the collections agree in all other characters with the foliicolous specimens having smooth margins, we follow the concept of Lücking (2007) and recognize them at the level of forma for the time being.

***Coenogonium strigosum* Rivas Plata, Lücking & Chaves, sp. nov.**

Mycobank number: 501138. (Figs 2E-H, 6F-H)

A *Coenogonio siquirrense* apotheciis pallidioribus et ascosporis latioribus differt.

Type: Costa Rica, San José, Leonel Oviedo Ecological Reserve (Cordillera Volcánica Central Conservation Area), Central Valley, San José, University campus north of church in San Pedro, adjacent to Escuela de Biología, main trail through reserve, 84° 03' W, 9° 56' N, 1200 m, lower montane moist forest zone, oldgrowth secondary forest, on bark (lower trunk), 4 November 2002, Lücking 15678 (USJ, **holotype**; F, **isotype**), 15679 (F, **paratype**), 15680a (F, **paratype**).

Additional material examined: COSTA RICA, Limón, Hitoy Cerere Biological Reserve (La Amistad Caribe Conservation Area), near Pandora, 150 m, on wet volcanic rock along stream, 9 March 2004, Aptroot 60103 (ABL, INB, **paratypes**). Puntarenas, La Amistad International Park (La Amistad Pacífico Conservation Area), Altamira Station, 20 km N of San Vito near Finca Colorado, interpretative trail behind station (Sendero Gigantes), 83° 01' W, 9° 02' N, 1500-1600 m, montane rainforest zone, secondary vegetation dominated by *Cecropia*, on bark, 30 Jun 2002, Sipman 48035 (B, INB, **paratypes**).

Thallus crustose, corticolous or muscicolous, continuous, thin, smooth to irregularly setose, olive green, 50-100 mm diam.; white prothallus present. Thick, setalike structures present on the type specimen but absent in most other collections, acute, unbranched or irregularly bifurcate, 0.5-2 mm long, 100-200 µm thick at base and 25-50 µm thick in upper part, olive green and with smooth surface in lower part, pale grey to white and with minutely pilose surface in upper part; in section formed by densely interwoven to parallel hyphae, with loosely woven outer layer in upper part; lower part filled with algal cells except for outermost pseudocortex formed by parallel hyphae. *Photobiont Trentepohlia*, cells angular-rounded, in irregular plates or short threads, 6-9 µm diam. *Apothecia* sessile, rounded to irregular in outline, 0.8-1.5 mm diam. and 250-350 µm high; disc plane to undulate, pale to dark yellow-orange; margin thin, not prominent, evanescent, with irregular surface to minutely denticulate, creme-colored. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 µm broad, colorless, I+ sordid orange-brown; cells partially elongated and thin-walled, very large in peripheral parts, up to 20 × 10 µm. *Hypothecium* 20-30 µm high, colorless. *Hymenium* 60-80 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 60-80 × 4-6 µm. *Ascospores* uniseriate, ellipsoid, 1-septate, 6-10 × 2.5-3 µm, 2.5-3.5

times as long as broad. *Pycnidia* not observed. *Chemistry*: no substances detected by TLC. *Ecology*: Corticolous in understory of lowland to lower montane rain forest.

Coenogonium strigosum is another new species in the *C. luteum* group. The latter lacks a prothallus and has apothecia with concave disc and smooth margin. *Coenogonium luteolum* also lacks a prothallus and differs by its yellow apothecia with smooth margin. The new *C. magdalenae* was found at the same locality and differs by its more prominent apothecia with pale yellow, concave disc and distinct, slightly prominent margin. *Coenogonium strigosum* differs from all those species also by its very large and thin-walled peripheral excipulum cells. Such an excipulum is otherwise only known from *C. siquirrense*, which agrees with *C. strigosum* in several other features but differs by the vividly orange apothecia with dark orange zone in the periphery of the disc and the narrower ascospores (2-2.5 μm broad).

The most characteristic feature of the type of *Coenogonium strigosum* are the strange setae, in their nature so far unknown in the genus. Anatomically, they distantly resemble the cylindrical isidia known from some other species in the genus. However, they are much larger and do not seem to function as dispersal organs but rather might have importance in increasing the photosynthetic surface of the thallus. Species of *Coenogonium* often overgrow bryophytes and then may appear strigose due to the strands of substrate enclosed by the thallus. The setae of *C. strigosum* also somehow give this impression, but in section reveal that they are part of the lichen thallus and only enclose fungal hyphae and algal cells of the same type as the rest of the thallus.

The species is mostly corticolous, but one collection was found saxicolous.

Coenogonium tuckermanii Mont., Ann. Sci. Nat. Bot., Ser. 4, 7: 143 (1857).

(Figs 4A-B)

Coenogonium complexum Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 90 (1862).

Representative material examined: COSTA RICA, Cartago, Chirripó National Park (La Amistad Pacífico Conservation Area), trail from San Gerardo to Crestones, Filo Cementerio de la Máquina. 9° 29' N, 83° 29' W, 2400 m, 15 Mar 2000, Sipman V11 (INB; F). Additional material examined: COSTA RICA, Cartago, Río Macho village (La Amistad Pacífico Conservation Area), Orosi Valley, 30 km SE of San José and 15 km SE of Cartago, road from Orosi to Tapantí near park entrance, 83° 48' W, 9° 46' N, 1100 m, montane rainforest zone, exposed roadside trees, on bark (lower stem), 11 Apr 2003, Nelsen 3613 (F, INB).

Thallus filamentous, pannose, yellowish green, 20-30 mm diam., ecorticate. *Filaments* in central parts solitary, in peripheral parts forming bundles of 15-25 individual filaments agglutinated by a dense net of thin, richly branched mycobiont hyphae; filaments in central parts accompanied by partly free, rather thick (up to 2.5 μm), straight mycobiont hyphae. *Photobiont*

Trentepohlia, cells cylindrical, in distinct filaments, 30-50 × 5-8 µm diam. *Apothecia* sessile, rounded to slightly irregular in outline, 0.5-1.2 mm diam. and 150-200 µm high; disc plane to convex, yellow-orange; margin distinct, prominent, smooth to rough, creme-colored to pale yellow. *Excipulum* paraplectenchymatous with radiating cell rows, 50-100 µm broad, colorless, I+ sordid yellow-green; cells isodiametric and thick-walled, 7-15 µm diam. *Hypothecium* 15-25 µm high, colorless. *Hymenium* 50-60 µm high, colorless, I+ blue then quickly sordid green then reddish brown. *Asci* 45-55 × 4-6 µm. *Ascospores* uniseriate, fusiform-ellipsoid, 1-septate, 6-10 × 2.5-3.5 µm, 2.5-3 times as long as broad. *Pycnidia* not observed. *Chemistry*: not tested. *Ecology*: Corticolous in lower montane and montane rain forest.

This species was first believed to represent a new taxon, until we examined type material of *Coenogonium* in the Nylander herbarium and came across two available names, *C. tuckermanii* and *C. complexum*, described from Venezuela and Bolivia, respectively. Both exhibit exactly the same morphological and anatomical features as the Costa Rican material, and *C. tuckermanii* antedates *C. complexum* by two years. Uyenco (1963a) gives *C. tuckermanii* as a name of doubtful application, although she apparently saw the type. The material is sterile but well-developed and perfectly displays the agglutinate terminal filaments. Uyenco (1963a) uses the name *C. complexum* this taxon, but in her key, she does not mention the agglutinate filaments but instead separates *C. complexum* based on apothecial characters only, probably because she interpreted this feature as an algal character. However, the filament bundles are held together by a dense net of mycobiont hyphae, and thus this is a character of the mycobiont and not the photobiont. Except for the agglutinate hyphae, *C. tuckermanii* is most similar to *C. disjunctum*, but has also smaller ascospores.

Names of species of *Coenogonium* excluded from the Costa Rican checklist

Coenogonium complexum Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 90 (1862). Reported from Costa Rica by Uyenco (1963a). The taxon is here established as a synonym of *C. tuckermanii*.

Coenogonium depressum Müll. Arg., Flora 64: 525 (1881). Reported from Costa Rica by Dodge (1933). The type is non-lichenized and thus belongs to *Trentepohlia* (Uyenco, 1963a). The Costa Rican material reported by Dodge is sterile and thus cannot be identified to species.

Coenogonium heterotrichum Müll. Arg., Bull. Soc. Roy. Bot. Belg. 32: 162 (1893). Reported from Costa Rica by Müller Argoviensis (1894) and Dodge (1933). The type is only partially lichenized and sterile (Uyenco,

1963a), and hence the name must be considered a nom. dub. The Costa Rican material is sterile and hence cannot be identified to species.

Coenogonium interponendum Nyl. in Polakowsky, J. Bot. Brit. For. 15: 225 (1877). Reported from Costa Rica by Dodge (1933); considered a synonym of *C. interplexum* (Uyenco, 1963a). The Costa Rican material reported by Dodge is sterile and thus cannot be identified to species.

Coenogonium pannosum Müll. Arg., Flora 64: 234 (1881). Reported from Costa Rica by Dodge (1933). The distinctive feature of this taxon are its very narrow ascospores; since the Costa Rican material reported by Dodge is sterile, his identification is untenable.

Coenogonium subvirescens (Nyl.) Nyl., Flora 57: 72 (1874); *Coenogonium leprieurii* var. *subvirescens* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 89 (1862). The taxon was reported from Costa Rica by Dodge (1933); the type was studied by us and is sterile (see also Uyenco, 1963a), and hence the name must be considered a nom. dub. The description of the Costa Rican material by Dodge suggests that it might at least in part be identical with *C. aff. interplexum* C (see above).

Phenotype-based phylogenetic analysis

The phenotype-based cladistic analysis of 49 characters (38 being parsimony informative) resulted in 720 equally most parsimonious trees with a length of 216 steps each (CI = 0.38, HI = 0.62). Since the topology of all 720 trees was the same except for details in the terminal clades, one of the trees was selected to display the phylogram with branch lengths; all nodes recovered in the strict consensus tree are indicated (Fig. 7).

The species traditionally classified in *Coenogonium* fall onto two distant, monophyletic clades, viz. the *C. linkii* plus *C. epiphyllum* group and the *C. moniliforme* group, while the taxa traditionally included in *Dimerella* form two paraphyletic grades, the *Coenogonium* clades nested within them. Certain smaller groups are recovered in the phylogram: the monophyletic *C. disciforme* group (disc-shaped isidia), the paraphyletic *C. epiphyllum* group ('pilose' thallus with upright setae formed by photobiont), the monophyletic *C. flavum* group (tubular pycnidia), and the monophyletic *C. subluteum* group (uniseriately arranged ascospores and bacillar, 1-septate conidia). Other groups appear polyphyletic, such as the taxa with cylindrical isidia and those with unusually broad ascospores. Species with zeorine apothecia (*C. fuscescens*) or algae in the basal excipulum (*C. kawanae*) are located at the very base of the tree. Species representing *Dimerella* s.str., i.e. with crustose thallus and lacking any particular features, such as tubular pycnidia or disc-shaped isidia, do not

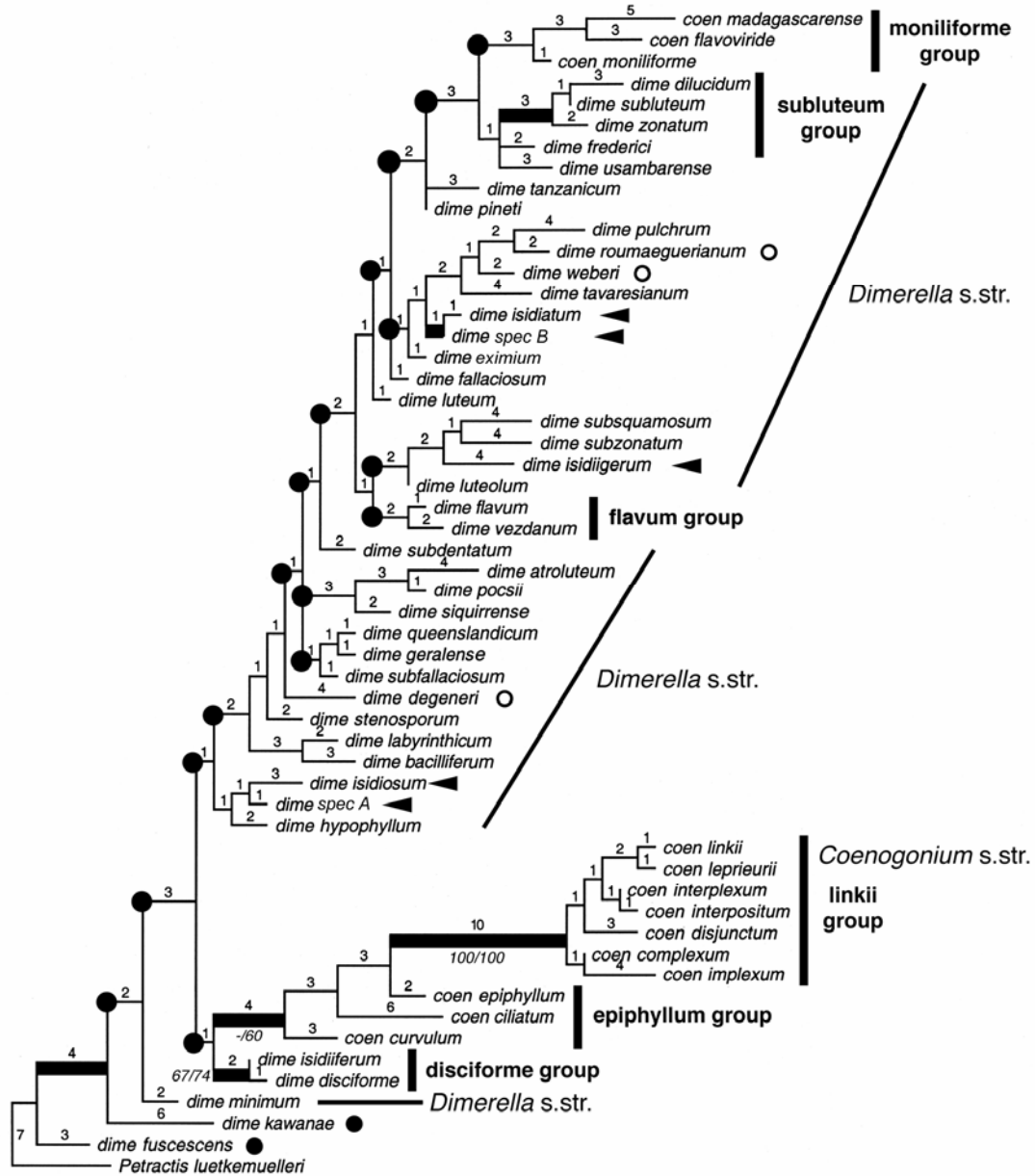


Fig. 7. One of several most parsimonious trees showing phylogeny of *Coenogonium* species based on cladistic analysis of 49 phenotype characters. Selected branches with significant Bootstrap and Jackknife support are indicated by thick lines; black circles indicate nodes recovered in strict consensus tree. Values above branches represent branch lengths.

form a monophyletic clade, but are found at three positions in the tree, with the bulk of the taxa forming two large, paraphyletic grades.

In spite of the high degree of resolution reflected in the strict consensus of the 720 trees (100% nodes indicated in Fig. 7), support for most of the clades is low or absent. The only strongly supported clade is that of the *Coenogonium linkii* group or *Coenogonium* s.str. Some support is also found for a clade including *Coenogonium* s.str. and the *C. epiphyllum* group, the *C. disciforme* clade, and the *C. subluteum* clade when excluding *C. frederici*.

When including only apothecial characters (24 out of 49; 17 parsimony informative), only a small part of the groups is recovered in the majority rule consensus of 120760 equally most parsimonious trees with a length of 133 steps each (Fig. 8). The *C. subluteum* and *C. moniliforme* groups remain almost unchanged, and the core of the *C. linkii* group remains intact while also including *C. epiphyllum*. Most other groups are dispersed over the tree, in particular the remainder of the *C. linkii* and *C. epiphyllum* groups, the *C. disciforme* group, and the *C. flavum* group. The base of the tree is invariably formed by a paraphyletic assemblage of the three species *C. fuscescens*, *C. kawanae*, and *C. minimum*. Overall, there is no support for any of the clades, and the strict consensus of the 120760 trees (not shown) has absolutely no resolution at all, indicating a very high degree of homoplasy in the apothecial characters (CI = 0.304, HI = 0.696) between the filamentous and crustose taxa.

The analysis thus does not support the separation of two genera including filamentous (*Coenogonium*) versus crustose species (*Dimerella*), especially if only apothecial characters are concerned (as demonstrated by the strict consensus tree of the analysis of apothecial characters alone). The filamentous taxa are polyphyletic, and the crustose taxa form a paraphyletic backbone in which the filamentous taxa are nested. For sake of nomenclatural stability, and to retain the name *Dimerella* for the bulk of crustose species, the name *Coenogonium* could be restricted to the species of the *C. linkii* and *C. epiphyllum* groups. In that case, however, applying a strict monophyly criterion, the three species of the *C. moniliforme* group would have to be transferred to *Dimerella*, and four new genera would have to be established for the species of the *C. disciforme* group and for *C. fuscescens*, *C. kawanae*, and *C. minimum*.

Taking into consideration that phenotype data have limitations in terms of phylogenetic information compared to molecular data, and the latter are not available for most species so far, at this point we see no support for a generic rearrangement that would permit to continue the use of the name *Dimerella* for the bulk of the crustose species, and at the same time allow to introduce four new generic names. This would be a purely nomenclatural solution to satisfy

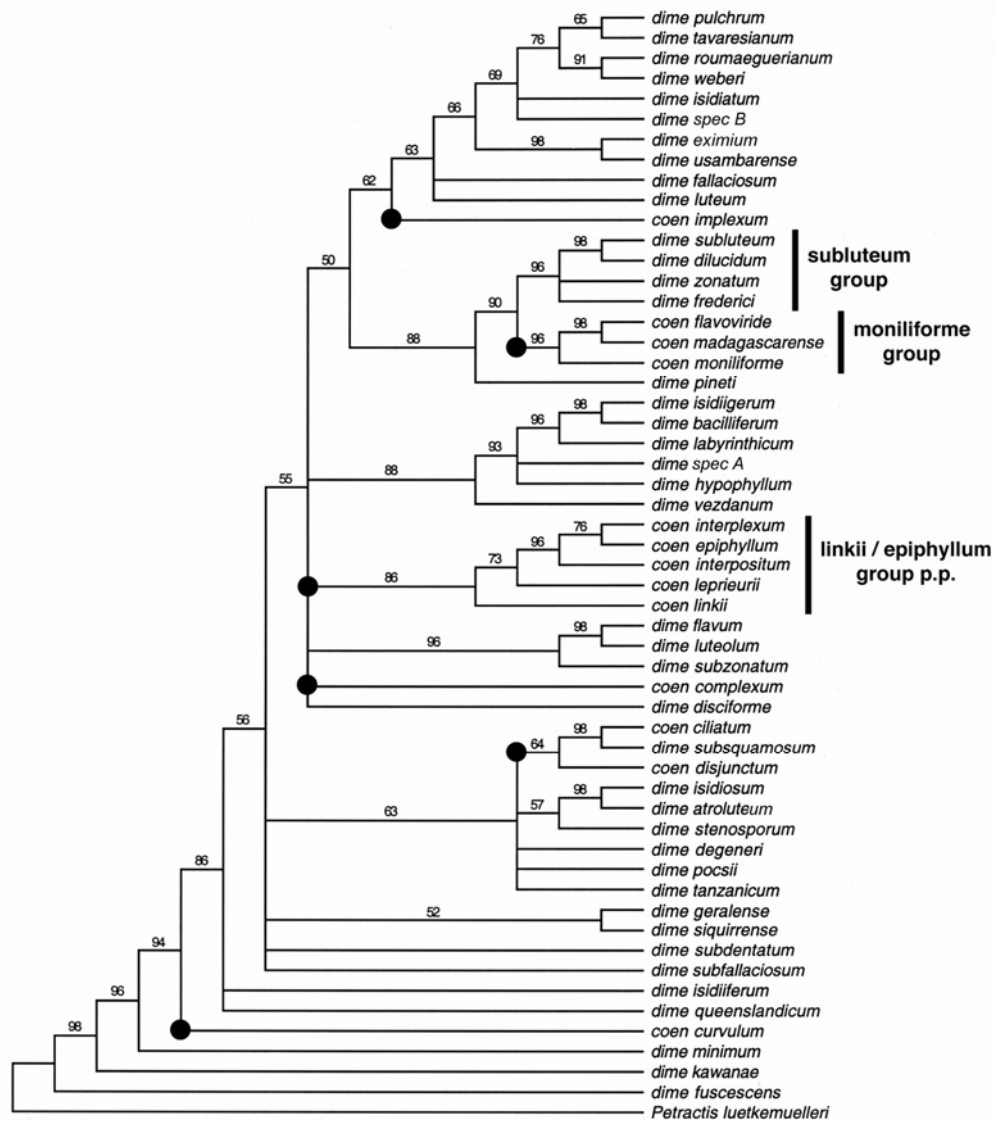


Fig. 8. Majority rule consensus tree showing phylogeny of *Coenogonium* species based on cladistic analysis of 24 phenotype characters (apothecia only). Black circles indicate branches including filamentous taxa.

mostly those used to the names of the two common temperate species *Dimerella lutea* and *D. pineti*, but would not reflect the very close relationship and partial polyphyly of both *Coenogonium* and *Dimerella*. We therefore

follow Lücking and Kalb (2000) to recognize only one genus, *Coenogonium*, and the remaining necessary combinations are given here:

- Coenogonium antonianum** Lücking, Aptroot & Sipman **nom. nov.** Mycobank 501139. Bas.: *C. madagascarensis* Vezda, Acta Mus. Richnov., Sect. Natur. 11: 58 (2004); nom. illeg., ICBN Art. 53.3 [non *C. madagascariensis* Hue, Bull. Soc. Bot. France, Ser. 10, 57: 285 (1910). = *C. interpositum*].
- Coenogonium atroluteum** (Vain.) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501140. Bas.: *Gyalecta atrolutea* Vain., Ann. Soc. Fauna Fl. Fenn. 7(2): 70 (1890). Syn.: *Microphiale atrolutea* (Vain.) Zahlbr., Catal. Lich. Univ. 2: 693 (1924); *Dimerella atrolutea* (Vain.) Malme, Arkiv Bot. 26A(13): 6 (1934).
- Coenogonium bacilliferum** (Malme) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501141. Bas.: *Dimerella bacillifera* Malme, Arkiv Bot. 26A(13): 5 (1934); *Microphiale bacillifera* (Malme) Zahlbr., Catal. Lich. Univ. 10: 229 (1939).
- Coenogonium degeneri** (Kalb & Vezda) Kalb & Lücking **comb. nov.** Mycobank 501142. Bas.: *Dimerella degeneri* Kalb & Vezda, Folia Geobot. Phytotax. 15: 310 (1980).
- Coenogonium eximium** (Nyl.) Kalb & Lücking **comb. nov.** Mycobank 501143. Bas.: *Lecidea lutea* var. *eximia* Nyl., Lich. Nov.-Gran. Prodr.: 54 (1863). Syn.: *Biatorinopsis lutea* var. *eximia* (Nyl.) Müll. Arg., Flora 64: 102 (1881); *Dimerella eximia* (Nyl.) Vezda, Folia Geobot. Phytotax. 4: 445 (1969).
- Coenogonium frederici** (Kalb) Kalb & Lücking **comb. nov.** Mycobank 501144. Bas.: *Dimerella frederici* Kalb, Folia Geobot. Phytotax. 15: 310 (1980).
- Coenogonium isidiatum** (G. Thor & Vezda) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501145. Bas.: *Dimerella isidiata* G. Thor & Vezda, Folia Geobot. Phytotax. 19: 72 (1984).
- Coenogonium isidiigerum** (Vezda & Osorio) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501146. Bas.: *Dimerella isidiigera* Vezda & Osorio in Vezda, Sched. Lich. Sel. Exs. 94: 2 (1989).
- Coenogonium isidiosum** (Breuss) Rivas Plata, Lücking, Umana & Chaves **comb. nov.** Mycobank 501147. Bas.: *Dimerella isidiosa* Breuss, Linzer Biol. Beitr. 34: 1063 (2002).
- Coenogonium luteolum** (Kalb) Kalb & Lücking **comb. nov.** Mycobank 501148. Bas.: *Dimerella luteola* Kalb, Herzogia 9: 62 (1992).
- Coenogonium nepalense** (G. Thor & Vezda) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501149. Bas.: *Dimerella nepalensis* G. Thor & Vezda, Folia Geobot. Phytotax. 19: 74 (1984).
- Coenogonium perminutum** (Malme) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501150. Bas.: *Dimerella diluta* var. *perminuta* Malme, Arkiv Bot. 26A(13): 8 (1934); *Microphiale perminuta* (Vain.) Zahlbr. in Engler & Prantl, Nat. Pflanzenfam., Ed. 1, 1: 25 (1905); *Lecaniopsis perminuta* (Vain.) Zahlbr. in Engler & Prantl., Nat. Pflanzenfam., Ed. 2, 8: 147 (1926).
- Coenogonium persistens** (Malme) Lücking, Aptroot & Sipman **comb. et stat. nov.** Mycobank 501151. Bas.: *Dimerella lutea* f. *persistens* Malme, Arkiv Bot. 26A(13): 5 (1934).
- Coenogonium pertenuis** (Stirt.) Kalb & Lücking **comb. nov.** Mycobank 501152. Bas.: *Baeomyces pertenuis* Stirt., Trans. Glasgow Soc. Field Natural. 1: 17 (1873).
- Coenogonium pocsii** (Vezda & Farkas) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501153. Bas.: *Dimerella pocsii* Vezda & Farkas, Folia Geobot. Phytotax. 23: 193 (1988).

- Coenogonium pusillum** (Mont.) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501154. Bas.: *Biatora pusilla* Mont. in Ramon de la Sagra, Hist. d'Île de Cuba, Bot.: 109 (1842). Syn.: *Dimerella pusilla* (Mont.) R. Sant. & Vezda, Folia Geobot. Phytotax. 4: 445 (1969).
- Coenogonium pyrophthalmum** (Mont.) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501155. Bas.: *Biatora pyrophthalma* Mont., Ann. Sci. nat., Bot., ser 2, 20: 357 (1843). Syn.: *Dimerella pyrophthalma* (Mont.) Vezda, Folia Geobot. Phytotax. 4: 446 (1969).
- Coenogonium stenosporum** (Malme) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501156. Bas.: *Dimerella stenospora* Malme, Arkiv Bot. 26A(13): 7 (1934).
- Coenogonium stramineum** (Aptroot & Seaward) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501157. Bas.: *Dimerella straminea* Aptroot & Seaward in Seaward & Aptroot, Lichenologist 36: 121 (2004).
- Coenogonium subdentatum** (Vezda & G. Thor) Rivas Plata, Lücking, Umana & Chaves **comb. nov.** Mycobank 501158. Bas.: *Dimerella subdentata* Vezda & G. Thor in Vezda, Sched. Lich. Sel. Exs. 94: 3 (1989).
- Coenogonium subdilutum** (Malme) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501159. Bas.: *Dimerella subdiluta* Malme, Arkiv Bot. 26A(13): 6 (1934); *Microphiale subdiluta* (Malme) Zahlbr., Catal. Lich. Univ. 10: 230 (1939).
- Coenogonium subfallaciosum** (Vezda & Farkas) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501160. Bas.: *Dimerella subfallaciosa* Vezda & Farkas in Vezda, Sched. Lich. Sel. Exs., Fasc. 98: 2, no. 2429 (1990).
- Coenogonium subsquamosum** (Aptroot & Seaward) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501161. Bas.: *Dimerella subsquamosa* Aptroot & Seaward in Seaward & Aptroot, Lichenologist 36: 122 (2004).
- Coenogonium tavaresianum** (Vezda) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501162. Bas.: *Dimerella tavaresiana* Vezda, Folia Geobot. Phytotax. 4: 446 (1969).
- Coenogonium weberi** (Vezda) Lücking, Aptroot & Sipman **comb. nov.** Mycobank 501163. Bas.: *Dimerella weberi* Vezda, Folia Geobot. Phytotax. 8: 311 (1973).

World-wide key to the species of *Coenogonium*

The following key gives access to all species of *Coenogonium* that have been verified by us in this study (see Appendix 1). Due to the large number of species, we have assembled a skeleton key for quick access to the major groups (Table 6).

The character entries used in this key are based on our own experience with the studied material, but due to the lack of important features, such as pycnidia and conidia, in many specimens, including types, this treatment and key must be considered a preliminary working key. In some instances when a species could not be assigned unambiguously to a key couplet, it is keyed out within both alternatives. Extracting a key for foliicolous taxa only was not found feasible, since most of the species are at least facultatively foliicolous, and typically foliicolous species are not rarely also found on bark. Information on world distribution is given when known, and origin of types is indicated (country). Types or authentic material have been checked unless otherwise stated in the key.

Table 6. Skeleton key to morphological species groups in *Coenogonium*.

Thallus type	Special features	Ascospores	Apothecial size	Key entry	Group
pilose	—	—	—	3	<i>epiphyllum</i>
appressed filamentous	—	—	—	6	<i>moniliforme</i>
filamentous shelf-like	—	non-septate	—	13	<i>leprieurii</i>
"	—	1-septate	—	14	<i>linkii</i>
filamentous prostrate	—	non-septate	—	20	<i>interpositum</i>
"	—	1-septate	—	21	<i>interplexum</i>
byssoid	—	—	—	29	<i>pulchrum</i>
crustose	isidia	—	—	31	<i>isidiatum</i>
"	tubular pycnidia	—	—	37	<i>flavum</i>
"	zeorine apothecia	—	—	38	<i>fuscescens</i>
"	biatorine apothecia	12-25 µm	—	40	<i>wrightii</i>
"	"	6-12 × 4.5-6 µm	—	53	<i>roumeguerianum</i>
"	"	6-12 × (2.5-)3-4.5 µm	small	56	<i>pineti</i>
"	"	"	medium	60	<i>subluteum</i>
"	"	"	large	66	<i>luteum</i>
"	"	6-12 × 1.5-2.5(-3) µm	small	71	<i>lisowskii</i>
"	"	"	medium	75	<i>stenosporum</i>
"	"	"	large	87	<i>eximium</i>

1a. Thallus filamentous (sometimes forming closely appressed mats) or felt-like and pilose with short, upright algal threads resembling hairs 2
 1b. Thallus crustose, glabrous or very rarely with finely byssoid surface caused by fungal (not algal!) hairs 30

2a. Thallus felt-like and pilose, with crustose basal thallus and short, upright algal threads resembling hairs (*Coenogonium epiphyllum* group) 3
 2b. Thallus filamentous (sometimes forming closely appressed mats) 5

3a. Apothecial margin pilose (hairs formed by fungal hyphae); disc pale to bright yellow; hymenium 70-80 µm high; ascospores 10-15 × 3-3.5 µm; pycnidia common, appanate; conidia non-septate, 7-8 × 2-2.5 µm (Neotropics; type: Brazil) **Coenogonium ciliatum**
 3b. Apothecial margin glabrous, smooth; disc pale yellowish; hymenium 40-65 µm high; ascospores 6-10 × 2-3 µm; pycnidia and conidia unknown 4

4a. Ascospores curved, 7-10 × 2-2.5 µm; apothecia 0.1-0.3 mm diam. (Neotropics and eastern Paleotropics; type: Indonesia) **Coenogonium curvulum**
 4b. Ascospores straight, 6-8 × 2-3 µm; apothecia 0.3-0.8 mm diam. (eastern Paleotropics; type: Philippines) **Coenogonium epiphyllum**
 [= *Dimerella pilifera* (≡ *Coenogonium piliferum*)]

5a. Thallus appressed-filamentous, forming a closely adnate crust, the filamentous nature only visible under lens magnification; algal filaments often moniliform.....	6
5b. Thallus distinctly filamentous, either prostrate or pannose or dimidiate-caespitose and then shelf- or beard-shaped.....	11
6a. Algal filaments moniliform or at least distinctly constricted at septa; ascospores 1-septate	7
6b. Algal filaments cylindrical, not constricted at septa; ascospores 1-septate or non-septate	9
7a. Ascospores $4-6 \times 1.8-2 \mu\text{m}$; apothecia 0.15-0.25 mm diam.; conidia non-septate, $3-3.5 \times 0.7-1 \mu\text{m}$; thallus bright yellow-green (Neotropics; type: Brazil).....	Coenogonium flavoviride
7b. Ascospores $8-12 \times 3-4 \mu\text{m}$; apothecia 0.2-0.4 mm diam.; conidia unknown; thallus yellow-green to dark green.....	8
8a. Algal filaments distinctly moniliform (pantropical; type: Cuba)	Coenogonium moniliforme
8b. Algal filaments constricted at septa but not moniliform; cells longer than broad (Neotropics and eastern Paleotropics; type: Australia - not seen)	Coenogonium botryosum
9a. Ascospores non-septate, $8-10 \times 2.5-4 \mu\text{m}$; apothecia 0.4-0.6 mm diam. (amphipacific; type: Australia - fide Uyenco 1963).....	Coenogonium ornatum
9b. Ascospores 1-septate, $4-6 \times 1.8-2 \mu\text{m}$; apothecia 0.15-0.35 mm diam.	10
10a. Apothecia substipitate, obconical, orange, 0.25-0.35 mm diam. (African Paleotropics; type: Madagascar).....	Coenogonium antonianum
..... (\equiv <i>Coenogonium madagascarense</i> Vezda nom. illeg.)	
10b. Apothecia sessile, pale yellow-brown, 0.15-0.25 mm diam. (Neotropics; type: Costa Rica)	Coenogonium byssothallinum
11a. Thallus projecting horizontally from substrate, shelf- or beard-shaped	12
11b. Thallus loosely or closely attached to substrate, prostrate or pannose	19
12a. Ascospores non-septate	13
12b. Ascospores 1-septate	14
13a. Ascospores uniseriate; apothecia substipitate, with uneven margins; thallus thin, very compact, in single layer, filaments without interspaces; filaments 5-10 μm wide (pantropical; type: French Guiana).....	Coenogonium leprieurii
13b. Ascospores biseriate; apothecia sessile, with smooth margins; thallus thick, in several layers, filaments leaving interspaces; filaments 10-15 μm wide (Neotropics; type: Brazil - fide Uyenco 1963).....	Coenogoniumacrocephalum
14a. Thallus caespitose, beard-shaped	15
14b. Thallus dimidiate, shelf-like.....	16

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- 15a. Thallus composed of several tufts of algal filaments connected at the point of attachment; apothecia common (Neotropics; type: Costa Rica)..... **Coenogonium barbatum**
 15b. Thallus composed of single tuft of algal filaments; apothecia unknown
 **Coenogonium aff. barbatum**
- 16a. Ascospores uniseriate; algal filaments 10-25 μm wide 17
 16b. Ascospores biseriata; algal filaments 5-10 μm wide..... 18
- 17a. Apothecia yellow-orange, with flat to convex disc and smooth margin; filaments 10-15 μm wide (pantropical; type: Brazil) **Coenogonium linkii**
 17b. Apothecia yellow, with flat disc and denticulate margin; filaments 15-25 μm wide (Neotropics; type: Mexico - fide Dodge 1933 and Uyenco 1963) .. **Coenogonium confervoides**
- 18a. Thallus very compact, thin, leaving no interspaces between filaments, opaque; apothecia with smooth to thinly pilose margin and yellow-orange disc (Neotropics and African Paleotropics; type: Democratic Republic of Congo)..... **Coenogonium congensense**
 18b Thallus loose, thicker, with distinct interspaces between filaments especially at the margin, slightly nitidous; apothecia with denticulate margin and mostly yellow disc (Costa Rica)
 **Coenogonium aff. congensense**
- 19a. Ascospores non-septate 20
 19b. Ascospores 1-septate 21
- 20a. Ascospores uniseriate, 8-12 μm long; apothecia sessile, with flat disc (Neotropics and eastern Paleotropics; type: New Zealand - fide Uyenco 1963) **Coenogonium tomentosum**
 20b. Ascospores biseriata, 5-10 μm long; apothecia stipitate, with flat to convex disc (pantropical; type: Reunion) **Coenogonium interpositum**
- 21a. Algal filaments forming closely agglutinated, club-shaped tufts at the thallus periphery (Neotropics; type: Venezuela)..... **Coenogonium tuckermanii** (= *C. complexum*)
 21b. Algal filaments solitary or aggregated in tufts but not closely agglutinated and club-shaped 22
- 22a. Apothecia pruinose (Neotropics; type: Chile: Juan Fernandez Isls. - fide Uyenco 1963).....
 **Coenogonium velutinum**
 22b. Apothecia non-pruinose 23
- 23a. Ascospores 10-14 μm long, biseriata (Neotropics and eastern Paleotropics; type: Cuba)
 **Coenogonium disjunctum**
 23b. Ascospores 5-10(-12) μm long, more or less uniseriate..... 24
- 24a. Thallus filaments very densely woven, forming a compact mat; apothecia sessile; ascospores 8-12 μm long (Neotropics and eastern Paleotropics; type: Australia)
 **Coenogonium implexum**
 24b. Thallus filaments loosely woven, forming an irregular and effuse mat; apothecia sessile to substipitate; ascospores 6-10 μm long 25

25a. Ascospores 1.5-2 µm broad; apothecial margin evanescent (Neotropics; type: Brazil)	
.....	Coenogonium pannosum
25b. Ascospores 2-4 µm broad; apothecial margin persistent (<i>C. interplexum</i> aggr.)	26
26a Thallus pannose, forming dense mats easily detached from substrate	27
26b Thallus prostrate, irregularly woven and not easily detached from substrate	28
27a Apothecial margin denticulate; cells of algal filaments 5-10 µm wide (Costa Rica)	
.....	Coenogonium aff. interplexum C
27b Apothecial margin uneven; cells of algal filaments 10-15 µm wide (Costa Rica)	
.....	Coenogonium aff. interplexum B
28a Ascospores 6-10 µm long; apothecia substipitate, margin smooth (pantropical; type: Colombia)	Coenogonium interplexum
28b Ascospores 5-7 µm long; apothecia strongly stipitate, margin denticulate (Costa Rica)	
.....	Coenogonium aff. interplexum A
29a. Thallus with finely byssoid surface caused by fungal hairs. — Apothecia 1-1.3 mm diam.; disc orange; ascospores 11-18 × 2.5-3 µm; pycnidia and conidia unknown (Neotropics; type: Brazil)	Coenogonium pulchrum (= <i>Dimerella chiodectonoides</i>)
29b. Thallus glabrous	30
30a. Thallus with disc-shaped or cylindrical isidia	31
30b. Thallus lacking isidia	36
31a. Thallus with disc-shaped isidia by disintegration of the original thallus	32
31b. Thallus with cylindrical to coralloid isidia formed by thallus outgrowths	33
32a. Disc-shaped isidia very regularly rounded, leaving 'punched' holes in the thallus (eastern Paleotropics; type: Thailand)	Coenogonium disciforme
32b. Disc-shaped isidia irregularly rounded, the thallus 'dissolving' (Neotropics; type: Costa Rica)	Coenogonium isidiiferum
33a. Ascospores 20-24 µm long (Neotropics; type: Uruguay)	Coenogonium isidiigerum
33b. Ascospores 8-14 µm long (if 15-18 µm long, cf. <i>Coenogonium</i> spec. A from Brazil; Kalb, pers. comm. 2000)	34
34a. Ascospores 2.5-3 µm broad, 4-5 times as long as broad; disc brownish yellow (Neotropics; type: Nicaragua)	Coenogonium isidiosum
34b. Ascospores 3-4 µm broad, 2.5-3.5 times as long as broad; disc orange to red	35
35a. Isidia in dense cushions, branched, up to 0.7 mm long; disc orange-red (Brazil)	
.....	<i>Coenogonium</i> spec. B (Kalb, pers. comm. 2000)
35b. Isidia dispersed, rarely branched, up to 0.3 mm long; disc orange (Neotropics and eastern Paleotropics; type: Nepal)	Coenogonium isidiatum

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36a. Pycnidia tubular, setiform. — Disc pale yellow; ascospores 8-10 × 2.5-3.5 μm; conidia non-septate, 3-3.5 × 1.2-2 μm	37
36b. Pycnidia wart-shaped or absent.....	38
37a. Pycnidia straight, with thickened, yellow apex due to accumulation of conidial mass; conidia 1.5-2 μm broad (Neotropics and eastern Paleotropics; type: New Zealand)	Coenogonium flavum
37b. Pycnidia irregular, with acute apex and inflated base; conidia 1.2-1.5 μm broad (Neotropics; type: Ecuador)	Coenogonium vezdanum
38a. Apothecia zeorine, with algiferous thalline margin. — Apothecia 0.2-0.3 mm diam.; disc red-brown; ascospores 6-9 × 1.8-2 μm; conidia non-septate, 2.5-3 × 1 μm (eastern Paleotropics; type: New Zealand)	Coenogonium fuscescens
38b. Apothecia biatorine, lacking algiferous thalline margin (but sometimes with algal cells in basal excipulum)	39
39a. Ascospores (10-)12-20(-25) μm long, at least 12 μm long on average but usually exceeding that length	40
39b. Ascospores 6-12 μm long	53
40a. Ascospores 18-25 μm long, at least 20 μm long on average. — Disc yellow	41
40b. Ascospores (10-)12-20 μm long.....	42
41a. Apothecia 0.3-0.5 mm diam.; ascospores 3-4 μm broad (eastern Paleotropics; type: Japan)	Coenogonium wrightii
41b. Apothecia 0.5-1 mm diam.; ascospores 2-3 μm broad (Neotropics; type: Brazil)	Coenogonium bacilliferum
42a. Apothecia small, 0.1-0.3 mm diam. — Disc brown	43
42b. Apothecia medium-sized to large, 0.3-3 mm diam.	44
43a. Apothecia urceolate, translucent, 0.1-0.2 mm diam.; ascospores 3-4 μm broad (Neotropics; type: Costa Rica).....	Coenogonium minimum
43b. Apothecia flat, opaque, 0.2-0.3 mm diam.; ascospores 4-5 μm broad (Neotropics and African Paleotropics; type: Tanzania).....	Coenogonium subdilucidum
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Footnotes to the key:

¹*Biatorinopsis pallidula* was recombined as *Coenogonium pallidulum* by Vezda (1969), apparently a lapsus since this taxon has a crustose thallus. The type material was considered conspecific with *C. luteum* by Galloway (1985), but the apothecia are much smaller than in the latter. If one accepts apothecial size as species-specific feature, then *Biatorinopsis pallidula* could be an earlier name for *Dimerella frederici* (\equiv *Coenogonium frederici*).

²We have not seen original material of *Biatorinopsis membranacea*, but according to the description, this taxon might be conspecific with *Coenogonium fallaciosum* and then provide an earlier name for that species. *Biatorinopsis savesiana* and *Lecidea planella* are also similar according to their descriptions, but it is uncertain whether those belong to *Coenogonium* at all.

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Appendix 1. Currently accepted names in *Coenogonium* sensu Lücking and Kalb (2000).

1. ***Coenogonium aciculatum*** Lücking & Aptroot, this paper.
2. ***Coenogonium acrocephalum*** Müll. Arg., *Flora* 64: 525 (1881).
3. ***Coenogonium antonianum*** Lücking, Aptroot & Sipman, this paper.
4. ***Coenogonium atroluteum*** (Vain.) Lücking, Aptroot & Sipman, this paper.
5. ***Coenogonium bacilliferum*** (Malme) Lücking, Aptroot & Sipman, this paper.
6. ***Coenogonium barbatum*** Lücking, Aptroot & Umaña, this paper.
7. ***Coenogonium botryosum*** C. Knight in Bailey, *Synops. Queensl. Fl. Suppl.* 1: 74 (1886).
8. ***Coenogonium byssothallinum*** Aptroot & Lücking, this paper.
9. ***Coenogonium ciliatum*** Kalb & Lücking, *Bot. Jahrb. Syst.* 122: 29 (2000).
10. ***Coenogonium confervoides*** Nyl., *Flora* 41: 380 (1858).
11. ***Coenogonium congensense*** C. W. Dodge, *Ann. Missouri Bot. Gard.* 40: 350 (1953).
12. ***Coenogonium curvulum*** Zahlbr., *Ann. Crypt. Exot.* 1: 164 (1928).
13. ***Coenogonium degeneri*** (Kalb & Vežda) Kalb & Lücking, this paper.
14. ***Coenogonium dilucidum*** (Kremp.) Kalb & Lücking, *Bot. Jahrb. Syst.* 122: 32 (2000).

15. **Coenogonium disciforme** Papong, Boonbragob & Lücking ined.
16. **Coenogonium disjunctum** Nyl., Bot. Zeitschr. 20: 178 (1862).
17. **Coenogonium epiphyllum** Vain., Ann. Acad. Sci. Fenn., Ser. A, 15: 156 (1921).
18. **Coenogonium eximium** (Vezda) Kalb & Lücking, this paper.
19. **Coenogonium fallaciosum** (Müll. Arg.) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000).
20. **Coenogonium flavoviride** Cáceres & Lücking, Nova Hedwigia 70: 219 (2000).
21. **Coenogonium flavum** (Malcolm & Vezda) Malcolm, Australasian Lichenology 54: 19 (2004).
22. **Coenogonium frederici** (Kalb) Kalb & Lücking, this paper.
23. **Coenogonium fuscescens** (Vezda & Malcolm) Malcolm, Australasian Lichenol. 54: 19 (2004).
24. **Coenogonium geralense** (P. Henn) Lücking, Fl. Neotrop. Monogr (in press) (2006).
25. **Coenogonium hypophyllum** (Vezda) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000).
26. **Coenogonium implexum** Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 92 (1862).
27. **Coenogonium interplexum** Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 92 (1862).
28. **Coenogonium interpositum** Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 91 (1862).
29. **Coenogonium isidiatum** (G. Thor & Vezda) Lücking, Aptroot & Sipman, this paper.
30. **Coenogonium isidiiferum** (Lücking) Lücking in Lücking *et al.*, Lichenologist 33: 201 (2001).
31. **Coenogonium isidiigerum** (Vezda & Osorio) Lücking, Aptroot & Sipman, this paper.
32. **Coenogonium isidiosum** (Breuss) Rivas Plata, Lücking, Umana & Chaves, this paper.
33. **Coenogonium kalbii** Aptroot, Lücking & Umaña, this paper.
34. **Coenogonium kawanae** (H. Harada & Vezda) H. Harada in Harada *et al.*, Lichenology 2(2): 127 (2004).
35. **Coenogonium labyrinthicum** Lücking & Kalb, Biblioth. Lichenol. 78: 254 (2001).
36. **Coenogonium leprieurii** (Mont.) Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 89 (1862).
37. **Coenogonium linkii** Ehrenb. in Nees von Esenbeck, Horae Phys. Berol.: 120 (1820).
38. **Coenogonium lisowskii** (Vezda) Lücking in Lücking *et al.*, Lichenologist 33: 201 (2001).
39. **Coenogonium luteocitrinum** Rivas Plata, Lücking & Umaña, this paper.
40. **Coenogonium luteolum** (Kalb) Kalb & Lücking, this paper.
41. **Coenogonium lutescens** (Vezda & Malcolm) Malcolm, Australasian Lichenology 54: 19 (2004).
42. **Coenogonium luteum** (Dicks.) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000).
43. **Coenogonium magdalenae** Rivas Plata, Lücking & Lizano, this paper.
44. **Coenogonium minimum** (Müll. Arg.) Lücking, Fl. Neotrop. Monogr (in press) (2007).
45. **Coenogonium moniliforme** Tuck., Proc. Amer. Acad. Sci. 5: 416 (1862).
46. **Coenogonium nepalense** (G. Thor & Vezda) Lücking, Aptroot & Sipman, this paper.
47. **Coenogonium ornatum** Müll. Arg., Bull. Herb. Boissier 4: 96 (1896).
48. **Coenogonium pannosum** Müll. Arg., Flora 64: 234 (1881).
49. **Coenogonium perminutum** (Malme) Lücking, Aptroot & Sipman, this paper.
50. **Coenogonium persistens** (Malme) Lücking, Aptroot & Sipman, this paper.
51. **Coenogonium pertenuae** (Stirt.) Kalb & Lücking, this paper.
52. **Coenogonium pineti** (Schrad. ex Ach.) Lücking & Lumbsch in Lücking *et al.*, Mycologia 96: 290 (2004).
53. **Coenogonium pocsii** (Vezda & Farkas) Lücking, Aptroot & Sipman, this paper.
54. **Coenogonium pulchrum** (Müll. Arg.) Kalb, Sched. Lich. Neotrop. 13: 3 (2001).

55. **Coenogonium pusillum** (Mont.) Lücking, Aptroot & Sipman, this paper.
56. **Coenogonium pyrophthalmum** (Mont.) Lücking, Aptroot & Sipman, this paper.
57. **Coenogonium queenslandicum** (Kalb & Vezda) Lücking in Lücking *et al.*, *Lichenologist* 33: 201 (2001).
58. **Coenogonium roumeguerianum** (Müll. Arg.) Kalb, *Sched. Lich. Neotrop.* 13: 3 (2001).
59. **Coenogonium rubrifusum** (Vezda & Malcolm) Malcolm, *Australasian Lichenol.* 56: 25 (2005).
60. **Coenogonium saepincola** Aptroot, Sipman & Lücking, this paper.
61. **Coenogonium siquirrense** (Lücking) Lücking, *Fl. Neotrop. Monogr* (in press) (2007).
62. **Coenogonium siquirrense** f. **denticulatum** Rivas Plata & Lücking, this paper.
63. **Coenogonium stenosporum** (Malme) Lücking, Aptroot & Sipman, this paper.
64. **Coenogonium stramineum** (Aptroot & Seaward) Lücking, Aptroot & Sipman, this paper.
65. **Coenogonium strigosum** Rivas Plata, Lücking & Chaves, this paper.
66. **Coenogonium subdentatum** (Vezda & G. Thor) Rivas Plata, Lücking, Umana & Chaves, this paper.
67. **Coenogonium subdilutum** (Malme) Lücking, Aptroot & Sipman, this paper.
68. **Coenogonium subfallaciosum** (Vezda & Farkas) Lücking, Aptroot & Sipman, this paper.
69. **Coenogonium subluteum** (Rehm) Kalb & Lücking, *Bot. Jahrb. Syst.* 122: 32 (2000).
70. **Coenogonium subsquamosum** (Aptroot & Seaward) Lücking, Aptroot & Sipman, this paper.
71. **Coenogonium subzonatum** (Lücking) Lücking & Kalb, *Biblioth. Lichenol.* 78: 254 (2001).
72. **Coenogonium tanzanicum** (Vezda & Farkas) Lücking & Kalb, *Bot. J. Linn. Soc.* 139: 177 (2002).
73. **Coenogonium tavaresianum** (Vezda) Lücking, Aptroot & Sipman, this paper.
74. **Coenogonium tomentosum** Müll. Arg., *J. Linn. Soc. Lond. Bot.* 32: 206 (1896).
75. **Coenogonium tuckermanii** Mont., *Ann. Sci. Nat. Bot., Ser. 4*, 7: 143 (1857).
76. **Coenogonium usambarensense** (Vezda & Farkas) Lücking & Kalb, *Biblioth. Lichenol.* 78: 255 (2001).
77. **Coenogonium velutinum** Zahlbr. in Skottsberg, *Nat. Hist. Juan Fernandez*, 2 (Bot.), 3(11): 332 (1924).
78. **Coenogonium vezdanum** (Lücking) Lücking, *Fl. Neotrop. Monogr* (in press) (2007).
79. **Coenogonium weberi** (Vezda) Lücking, Aptroot & Sipman, this paper.
80. **Coenogonium wrightii** (Vezda) H. Harada & Lumbsch in Harada *et al.*, *Lichenology* 2(2): 127 (2004).
81. **Coenogonium zonatum** (Müll. Arg.) Kalb & Lücking, *Bot. Jahrb. Syst.* 122: 32 (2000).

Appendix 2. Further names described in *Coenogonium* and its generic synonyms (*Biatorinopsis*, *Byssioplaca*, *Coenogoniomycella*, *Coenogoniomyces*, *Coenomycogonium*, *Didymopycnomycetes*, *Dimerella*, *Flabellomyces*, *Holocoenis*, *Lecaniopsis*, *Microphiale*, *Mycocoenogonium*) and their current taxonomic and nomenclatural status (types or authentic material seen unless otherwise stated). 'Nom. dub.' indicates that material is lichenized but cannot be identified to genus or species level due to absence of ascomata and/or conidiomata.

- Biatorinopsis brachyspora* Müll. Arg., Lichenes Epiphylli Novi: 16 (1890). = ?*Coenogonium squirrense*.
- Biatorinopsis diluta* (Pers.) Müll. Arg., Flora 64: 103 (1881). = *Coenogonium pineti*.
- Biatorinopsis epiphylla* Müll. Arg., Flora 64: 103 (1881). = *Coenogonium subluteum*.
- Biatorinopsis foliicola* (Kremp.) Müll. Arg., Flora 64: 103 (1881). = ?*Coenogonium zonatum*.
- Biatorinopsis lutea* (Dicks.) Müll. Arg., Flora 64: 102 (1881). = *Coenogonium luteum*.
- Biatorinopsis lutea* var. *eximia* (Nyl.) Müll. Arg., Flora 64: 102 (1881). = *Coenogonium eximium*.
- Biatorinopsis membranacea* (Fée) Müll. Arg., Flora 64: 103 (1881); not seen. = ?*Coenogonium fallaciosum*.
- Biatorinopsis microspora* Müll. Arg., Flora 64: 103 (1881). = *Coenogonium dilucidum*.
- Biatorinopsis minima* Müll. Arg., Bull. Soc. Bot. Belg. 30: 74 (1891). = *Coenogonium minimum*.
- Biatorinopsis myriadella* (Nyl.) Müll. Arg., Bull. Soc. Bot. Belg. 31: 35 (1892). = *Cryptolechia myriadella* (Nyl.) D. Hawksw. & Dibben.
- Biatorinopsis pallidula* Müll. Arg., Bull. Soc. Bot. Belg. 31: 34 (1892); not seen. = ?*Coenogonium frederici*.
- Biatorinopsis planella* (Nyl.) Müll. Arg., Rev. Mycol. 9(34): 4 (1887); not seen. = ?*Coenogonium fallaciosum*.
- Biatorinopsis pulchra* Müll. Arg., Flora 64: 102 (1881). = *Coenogonium pulchrum*.
- Biatorinopsis roumegueriana* Müll. Arg., Rev. Mycol. 9(34): 4 (1887). = *Coenogonium roumeguerianum*.
- Biatorinopsis savesiana* Müll. Arg., Rev. Mycol. 9(34): 4 (1887); not seen. = ?*Coenogonium fallaciosum*.
- Biatorinopsis subincolerella* (Nyl.) Müll. Arg., Hedwigia 31: 283 (1892). = *Cryptolechia subincolorella* (Nyl.) D. Hawksw. & Dibben.
- Biatorinopsis torulosa* Müll. Arg., Rev. Mycol. 10: 114 (1888). = *Coenogonium moniliforme*.
- Biatorinopsis zonata* Müll. Arg., Lich. Epiphylli Novi: 16 (1890). = *Coenogonium zonatum*.
- Byssioplaca feeana* A. Massal., Atti Reale Ist. Veneto Sci. Lett. Arti, Ser. 3, 5: 252 (1860). = *Coenogonium* sp..
- Coenogonomycella linkii* Cif. & Tomas., Atti Inst. Bot. Univ. Lab. Crittog. Pavia, Ser. 5, 10: 291 (1954). = *Coenogonium linkii*.
- Coenogonomycetes linkii* Cif. & Tomas., Atti Inst. Bot. Univ. Lab. Crittog. Pavia, Ser. 5, 10: 290 (1954). = *Coenogonium linkii*.
- Coenogonium afrum* A. Massal., Mem. Reale Ist. Veneto Sci. 10: 43 (1861); fide Uyenco (1963). = nom. dub. (partially lichenized).
- Coenogonium andinum* P. Karst. in Nyl., Bot. Zeitschr. 20: 178 (1862); not seen. = ?*Coenogonium confervoides*.
- Coenogonium boninense* M. Satô, J. Jap. Bot. 8: 390 (1933). = *Coenogonium leprieurii*.
- Coenogonium cancellatum* Leight., Trans. Linn. Soc. London 27; 172 (1869); fide Uyenco (1963). = nom. dub. (partially lichenized).
- Coenogonium cancellatum* var. *candida* Sambo, Nuovo Giorn. Bot. Ital., N. Ser., 44 (1937); not seen. = nom. dub.
- Coenogonium complexum* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 90 (1862). = *Coenogonium tuckermanii*.
- Coenogonium confervoides* var. *arborum* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 92 (1862); fide Uyenco (1963). = nom. dub. (partially lichenized).
- Coenogonium consimile* Vain., Hedwigia 38, Beibl. 3: 124 (1899); not seen. = nom. dub.

Coenogonium controversum Pers. in Gaudichaud, Voy. Uranie, Bot., 7: 214 (1826). = *Coenogonium linkii*.
Coenogonium deightonii C. W. Dodge, Ann. Missouri Bot. Gard. 40: 349 (1953). = *Coenogonium interpositum*.
Coenogonium deplanatum Kremp., Flora 59: 250 (1876); fide Uyenco (1963). = non-lichenized *Trentepohlia*.
Coenogonium depressum Müll. Arg., Flora 64: 525 (1881); fide Santesson (1952), Uyenco (1963). = non-lichenized *Trentepohlia*.
Coenogonium dialeptizum Stirt., Proc. Phil. Soc. Glasgow 11: 103 (1879); fide Santesson (1952); Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium dialeptum Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 90 (1862); fide Santesson (1952); Uyenco (1963). = non-lichenized *Trentepohlia*.
Coenogonium diffractum Kremp., Flora 59: 250 (1876); fide Uyenco (1963). = non-lichenized *Trentepohlia*.
Coenogonium ebeneum (Dillwyn) Smith, Handb. Brit. Lich.: 75 (1921). = *Cystocoleus ebeneus* (Dillwyn) Thwaites.
Coenogonium echinus Müll. Stuttg., Bot. Zeitschr. 15: 387 (1857); fide Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium effusum Kremp., Flora 59: 250 (1876); fide Uyenco (1963). = non-lichenized *Trentepohlia*.
Coenogonium flavicans (Vezda & Farkas) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000). = *Coenogonium geralense*.
Coenogonium germanicum Glück, Allgemeine Botanische Zeitschrift 5: 189-194 (1896); not seen. = ?*Cystocoleus ebeneus* (Dillwyn) Thwaites.
Coenogonium heterotrichum Müll. Arg., Bull. Soc. Roy. Bot. Belg. 32: 162 (1893); fide Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium himalayense G. Pant & D. D. Awasthi, Biblioth. Lichenol. 40 (Addendum): 2 (1991). = not a *Coenogonium*; apothecia are described as black and ascospores as septate and acicular; most probably belongs in Lecanorales.
Coenogonium inflexum Hook. f., Handb. New Zeal. Fl.: 581 (1867); fide Uyenco (1963). = *Coenogonium implexum*.
Coenogonium interplexum f. *contextum* Stirt., Proc. Phil. Soc. Glasgow 10: 297 (1877). = *Coenogonium interplexum*.
Coenogonium interponendum Nyl. in Polakowsky, J. Bot. Brit. For. 15: 225 (1877); fide Uyenco (1963). = *Coenogonium interplexum*.
Coenogonium leprieurii var. *lamellifera* Vain., Ann. Acad. Sci. Fenn., Ser. A, 15: 157 (1921). = *Coenogonium leprieurii*.
Coenogonium leprieurii var. *panniforme* Vain., J. Bot. 34: 204 (1896). = *Coenogonium leprieurii*.
Coenogonium leprieurii var. *subvirescens* Nyl., Ann. Sci. Nat. Bot., Ser. 4, 16: 89 (1862) = *Coenogonium subvirescens*; fide Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium linkii Fée, Index Fungorum Database (typographic error). = *Coenogonium linkii*.
Coenogonium linkii var. *leprieurii* Mont., Crypt. Guyan.: 47 (1851). = *Coenogonium leprieurii*.
Coenogonium madagascarense Vezda, Acta Mus. Richnov., Sect. Natur. 11: 58 (2004), nom. illeg., ICBN Art. 53.3 (non *C. madagascariense* Hue) = *Coenogonium antonianum*.
Coenogonium madagascariense Hue, Bull. Soc. Bot. France, Ser. 10, 57: 285 (1910). = *Coenogonium interplexum*.

- Coenogonium missouriense* J. S. Davis, Bryologist 97: 188 (1994). = not a *Coenogonium*.
Coenogonium nigropunctatum Kurok. [Index Fungorum Database]; typographic error for *Coenogonium nigromaculatum*.
Coenogonium nigrum (Huds.) Zahlbr., Ann. Naturhist. Mus. Wien 25: 241 (1911); not seen. = ?*Cystocoleus ebeneus* (Dillwyn) Thwaites.
Coenogonium pallidulum (Müll. Arg.) Vezda, Folia Geobot. Phytotax. 4: 446 (1969); not seen. = ?*Coenogonium frederici*.
Coenogonium pallidum (Müll. Arg.) Vezda [Index Fungorum Database]; orthographic error for *Coenogonium pallidulum*.
Coenogonium patagonicum Müll. Arg., Flora 71: 47 (1888); fide Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium piliferum (Vezda) Kalb & Lücking, Bot. Jahrb. Syst. 122: 32 (2000). = *Coenogonium epiphyllum*.
Coenogonium pulvinatum Kremp., Verh. Zool.-Bot. Ges. 26: 445 (1876); fide Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium retistriatum Leight., Trans. Linn. Soc. London 27: 172 (1869); fide Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium rigidulum Müll. Arg., Flora 65: 490 (1882); fide Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium schmidlei Simmer, Allg. Bot. Zeitschr. 5: 190 (1899); not seen. = ?*Cystocoleus ebeneus* (Dillwyn) Thwaites.
Coenogonium simplex Müll. Arg., Lich. Epiphylli Novi: 16 (1890); fide Santesson (1952); Uyenco (1963). = non-lichenized *Trentepohlia*.
Coenogonium subtorulosum Müll. Arg., J. Linn. Soc. Lond. Bot. 32: 207 (1896). = nom. dub. (partially lichenized).
Coenogonium subvirescens (Nyl.) Nyl., Flora 57: 72 (1874); fide Uyenco (1963). = nom. dub. (partially lichenized).
Coenogonium tenuissimum Kremp., Nuov. Giorn. Bot. Ital. 7: 25 (1875); fide Santesson (1952); Uyenco (1963). = nom. dub. (partially lichenized).
Coenomycogonium interpositi Cif. & Tomas., Atti Inst. Bot. Univ. Lab. Crittog. Pavia, Ser. 5, 10: 292 (1954). = *Coenogonium interpositum*.
Didymopycnomycetes hyalinus Cavalc. & A. A. Silva, Publ. Inst. Micol. Univ. Fed. Pernambuco 647: 17 (1972). = *Coenogonium subluteum*.
Dimerella atrolutea (Vain.) Malme, Arkiv Bot. 26A(13): 6 (1934). = *Coenogonium atroluteum*.
Dimerella bacillifera Malme, Arkiv Bot. 26A(13): 5 (1934). = *Coenogonium bacilliferum*.
Dimerella bonariensis Malme, Arkiv Bot. 26A(13): 4 (1934). = *Coenogonium pyrophthalmum*.
Dimerella chiodectonoides Kalb, Sched. Lich. Neotrop. 10: 7 (1988). = *Coenogonium pulchrum*.
Dimerella cubana De Lesd., Bull. Soc. Bot. France 78: 729; typographic error for *Biatorinopsis cubana*. = *Coenogonium pusillum*.
Dimerella degeneri Kalb & Vezda, Folia Geobot. Phytotax. 15: 310 (1980). = *Coenogonium degeneri*.
Dimerella dilucida (Kremp.) R. Sant., Symb. Bot. Upsal. 12(1): 394 (1952). = *Coenogonium dilucidum*.
Dimerella diluta (Pers.) Trevis., Rendic. R. I. Lomb. Sci Lett., ser. 2, 13: 66 (1880). = *Coenogonium pineti*.

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