

Further new lichen species producing campylidia or complex conidiomata

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Summary: Three new foliicolous lichen species are described: *Byssoloma lueckin-gii* SÉRUSIAUX (from Papua New Guinea and Costa Rica), *Woessia arvidssonii* SÉRUSIAUX (from Ecuador), both producing typical campylidia, and *W. pseudohyphophorifera* R. LÜCKING & SÉRUSIAUX (from Costa Rica and St. Lucia), producing a new type of conidiomata, named brush-like conidiomata. Campylidia are shown to be ecological adaptations to the dispersal of conidia by rain water in the Tropics. The new combination *Woessia defecta* (VĚZDA) SÉRUSIAUX is introduced.

Key words: *Byssoloma*, campylidia, conidiomata, foliicolous lichens, *Woessia*

Introduction

The study of lichens from tropical areas, especially of foliicolous species, highlighted the occurrence of conidiomata of very complex anatomy, named campylidia by MÜLLER ARGOVIENSIS (1881) and which were left unstudied for over seventy years. Such asexual means of reproduction were first observed in lecideoid genera belonging to the Ectolechiaceae and Pilocarpaceae (SÉRUSIAUX 1986; VĚZDA 1986). Similar organs were later found in two further families: the Aspidotheliaceae (APTROOT & SIPMAN 1993) and the Arthoniaceae (LÜCKING 1995).

In the course of studying large collections of foliicolous lichens from several parts of the world, campylidia were found in two genera in which they were so far unknown, and a further type of conidiomata («brush-like conidiomata») was discovered in a species belonging to one of them. These species all proved to be new for science and this paper deals with their description. This paper also provides the results of field observations on the biological role of campylidia.

Table 1 provides a summary of the lichen genera producing campylidia.

Material and methods

The material was observed in tap water, in Lugol's iodine solution, in lactophenol cotton-blue (LCB) or in brilliant cresyl blue (CRB). The measurements given in this paper always refer to preparations in water, unless otherwise stated.

Description of new species

Byssoloma lueckingii SÉRUSIAUX spec. nov.

Byssoloma subdiscordans species insignis praesentia campylidiorum (efferentium 1-septata conidia), ascosporis longioribus et conidiis bifusiformibus.

Type: PAPUA NEW GUINEA. Madang prov.: Bunapas Mission, epiphyllous on *Mangifera* by a village near the Ramu river, 25 m, 4.II.1980, Demoulin 5907 & Smeets (LG – holotype).

(Fig. 1-2)

Thallus epiphyllous, covering rather large portions of the leaves (up to 2-3 cm in diam.), dispersed, formed of small irregular patches, 0.2-0.4 mm in diam., rarely forming a continuous thallus, greenish grey to whitish, sometimes almost white, without any visible prothallus or with a white or translucent one. *Photobiont* most probably a species of Chlorococcaceae, with green spherical cells, 8-12 μm .

Apothecia numerous, circular, rarely contiguous, 0.2-0.4(-0.6) mm in diam., 0.1-0.15 mm in height, with a flat, bluish black disc, and a whitish to slightly brownish byssoid margin, which is already seen in very young apothecia. Excipulum byssoid, spreading laterally over the thallus surface and becoming gradually thinner towards the edge, made of loosely interwoven pachydermatous hyphae, 2-4 μm thick, without any crystals. Epi-thecium greenish olivaceous, K \pm more greenish. Hymenium uncoloured, partly brownish in old apothecia, 50-60 μm thick. Hypothecium brownish, especially in central parts of the apothecium, K- or K+ purplish brown. Hamathecium of branched and anastomosed paraphyses. Asci clavate, typically constricted at their base and usually with a short stipe, 40-55 μm , 8-spored. *Ascospores* ellipsoid, with rounded ends, sometimes bent and slightly deformed, or \pm stretched, 3-septate, distinctly constricted at the septa when mounted in a 10% K solution, with a thin but distinct halo, 16-20 \times 4-5 μm .

Campylidia few but always present, helmet-shaped but at the top abruptly terminating in a point, 0.3-0.4 mm high (apical point included), with a socle c. 0.15 mm in diam., bluish black or with a slight bluish green

tinge. In cross sections, the following »tissues« can be distinguished: (1) socle araneous, made of loosely interwoven hyphae, sometimes containing a few algal cells; (2) walls made of tightly interwoven hyphae, completely surrounding an internal cavity, at least in young campylidia, as the inner wall tends to disintegrate in mature campylidia; (3) conidiogenous layer developing on the inner concave part of the cavity. Conidiogenous cells numerous, rectangular and slightly inflated at their base; *conidia* abundantly produced, arising singly at the apices of the conidiogenous cells, ellipsoid, 1-septate but with the proximal cell smaller and with a rather acute end, and the distal cell much larger and with a rounded end, always constricted at the septum, $9-11 \times 3-4 \mu\text{m}$.

Pycnidia rare, flask-shaped, *c.* 0.05 mm in diam., with a blackish blue wall. Conidiogenous cells slightly swollen; conidia bifusiform or slightly clavate at one end, $4-5 \times 1 \mu\text{m}$.

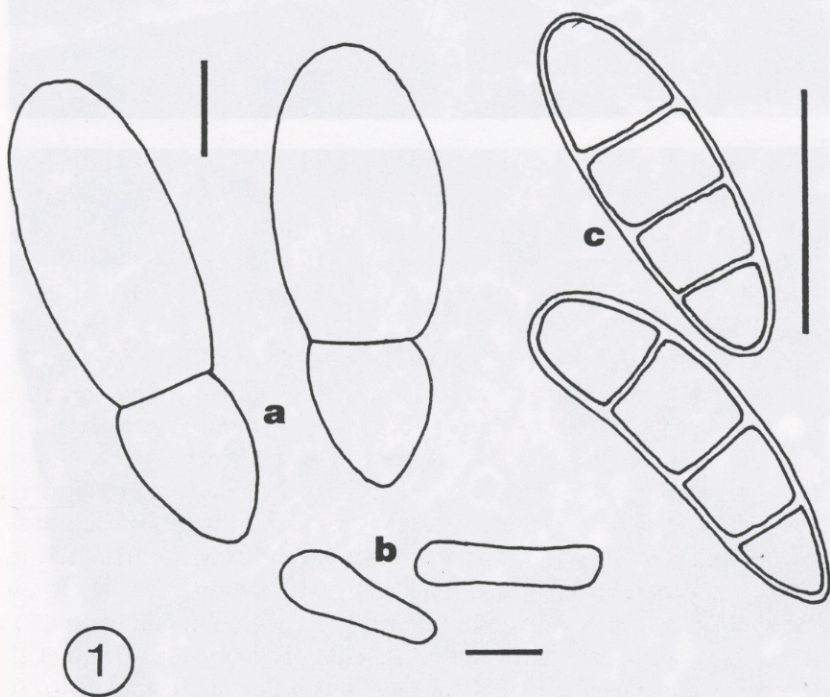


Fig. 1. *Byssoloma lueckingii* SÉRUSIAUX (holotypus). (a) Conidia produced by the campylidia (scale bar = $2 \mu\text{m}$). (b) Conidia produced by the pycnidia (scale bar = $2 \mu\text{m}$). (c) Ascospores (scale bar = $10 \mu\text{m}$).

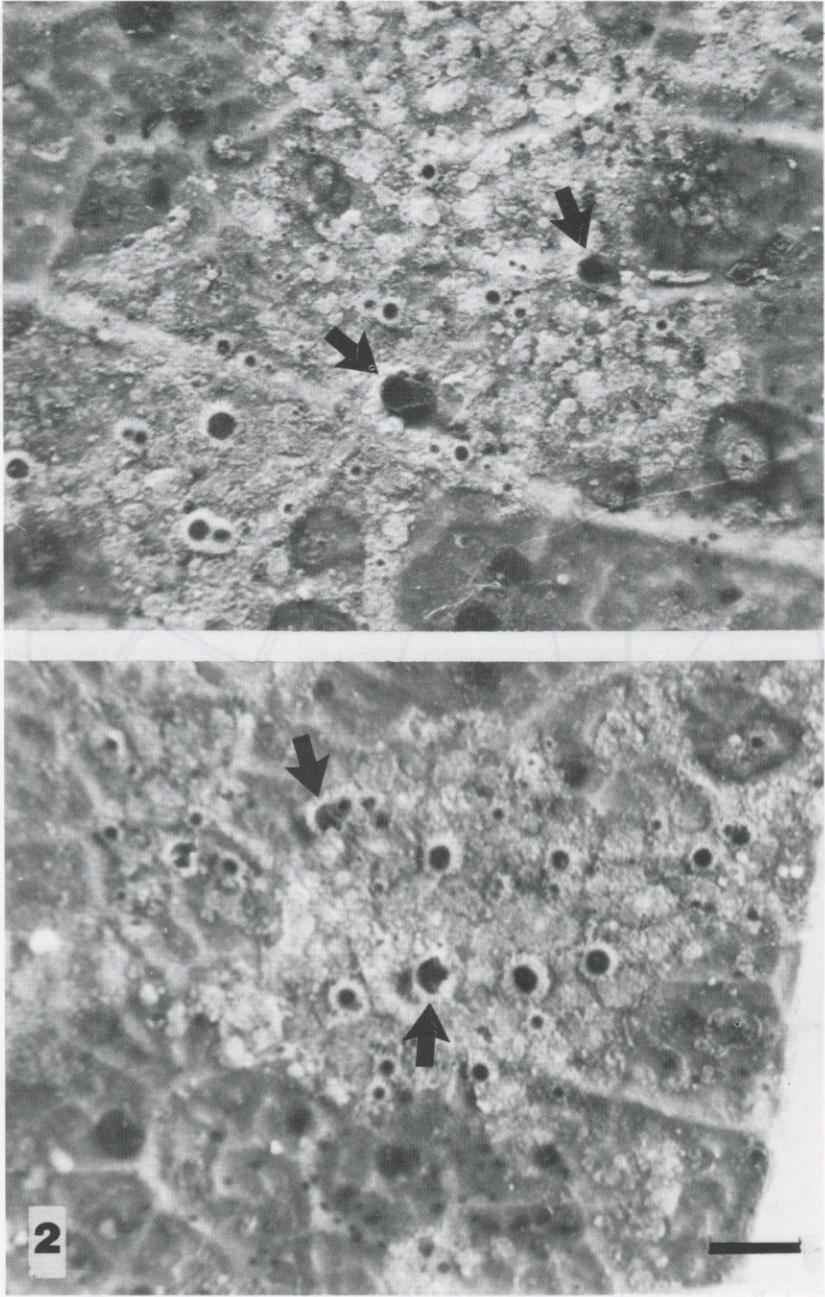


Fig. 2. *Byssoloma lueckingii* SÉRUSIAUX (holotype). General habit. Arrows point to campylidia. Scale bar = 1 mm.

This fascinating species has already been mentioned by LÜCKING (1992: 162) under »Genus *sp. a*, familiae *Ectolechiaceae*«, on the basis of two collections from Costa Rica. LÜCKING correctly described the campylidia as blackish and apically pointed and the conidia as 1-septate and drop-shaped (see his drawings of conidia on fig. 62 h). The specimen 88-523 was pictured (fig. 61 f): an apothecium referred to *Byssoloma subdiscordans* is clearly seen. This collection has been studied and is definitely conspecific with a larger one, gathered in Papua New Guinea in 1980 and which I had left as »*Byssoloma cum campylidiis*« for a long time. It is time to describe it and it is a pleasure for me to name it after Dr Robert Lücking, a brilliant lichenologist who has made most valuable contributions to our knowledge of foliicolous lichens.

The campylidia produced by this species appear to belong to the *Pyrenotrichum splitgerberi*-type as circumscribed by SÉRUSIAUX (1986: 27-29): the conidiogenous layer develops on the inner concave part of a closed cavity that is stretched upwards by the growth of one section of its outer wall. The cavity thus has the shape of a flattened crescent. The conidia accumulate within the cavity and are able to escape it either through a crack that seems to appear in the upper parts of the inner wall of the campylidium, or through the disintegration of that wall. The scarce material available does not allow a thorough investigation of the means of dispersal of the conidia but the observations I have made tend to demonstrate similar ways of dispersal to those seen in the campylidia produced by species of *Calopadia* VĚZDA and *Lasioloma* R. SANT. The anatomy of the campylidia is, however, simpler as there is no differentiation of the wall (in *Calopadia* and in *Lasioloma*, the wall carrying the conidiogenous layer differentiates into an inner paraplectenchymatous part and an outer part that remains arachnoid).

This species is referred to the widely occurring genus *Byssoloma* TREVIS., although the ascus-type, so typical of the genus (known as the *Byssoloma*-type sensu HAFELLNER (1984: 315), has not been clearly observed. In spite of careful examination, the ascus-type could not be determined with certainty; such a situation is not rare with tropical lichens from the lowland rainforest, and seems to be due to the difficulties in drying the specimens quickly enough. However, all other details point to that genus (byssoid margin, hamathecium, ascospores) and I feel rather confident that it does belong to it.

It is nevertheless a surprise to have a *Byssoloma* species producing campylidia. The genus is very common and diverse in the tropics: many species have already been described and none of them produce campylidia. I expect that many more species belonging to that genus will have to be des-

cribed in the future. For example, more than 20 species occur in Papua New Guinea, most of which are still undescribed.

B. lueckingii can be confused with the common *B. subdiscordans* (NYL.) P. JAMES which has very similar thallus and apothecia. The ascospores of the latter are, however, smaller ($10\text{-}17 \times 3\text{-}5 \mu\text{m}$) and the conidia are typically obpyriform-clavate; without campylidia, these criteria are the only way to distinguish it with absolute certainty from *B. lueckingii*.

B. lueckingii is known from three localities, one along the northern coast of Papua New Guinea, and the other two in Costa Rica. It is remarkable that it is so far known only from highly artificial sites, growing on planted trees by villages or in fruit tree plantations. Although intensively prospected, the virgin rain forests in both countries did not yield any material of this new species.

Additional specimens examined: COSTA RICA. Puntarenas prov.: Golfito village, Golfo Dulce, epiphyllous on *Mangifera* in a fruit tree plantation, 50 m, VI.1988, Lücking 88-523 (hb. Lücking). Alajuela prov.: Fortuna village, E slope of Arenal volcano, epiphyllous on leaves of *Citrus* by a village, 250 m, XII.1991, Lücking 91-4889 (hb. Lücking, LG).

***Woessia arvidssonii* SÉRUSIAUX spec. nov.**

Woessia species insignis praesentia conchiformium campylidiorum acicularia et longissima conidia efferentium.

Type: ECUADOR. Pastaza: Mera, Rio Alpayacu, epiphyllous in a mountain rain forest, 1100 m, 24.II.1972, Arvidsson 290 & Nilson (GB - holotype).

(Fig. 3-7)

Thallus epiphyllous, forming poorly delimited patches over the leaf surface, overgrowing other epiphyllous plants (liverworts or other lichens), including dying ones, or more frequently along leaf asperities, formed of greenish, deeply incised goniocysts (sensu lato; see SÉRUSIAUX 1985), each branch up to $c. 100 \times 20 \mu\text{m}$; goniocysts \pm erect or forming small coralloid bushes in the best preserved thalli; prothallus always present, membranous and almost translucent. *Photobiont* most probably a species of Chlorococcales, with green spherical cells, $5\text{-}8 \mu\text{m}$ in diam.

Apothecia rare, absent on thalli producing campylidia, circular, never contiguous, $0.2\text{-}0.4 \text{ mm}$ in diam., $0.15\text{-}(0.2) \text{ mm}$ in height, with a flat

Fig. 3-5. *Woessia arvidssonii* SÉRUSIAUX (holotype). General habit. (3) Thallus with apothecia. (4) Thallus with campylidia (arrows). (5) Details of two campylidia, seen from above and showing the typical fan-shaped part of the structures. Scale bar = 0.1 mm .

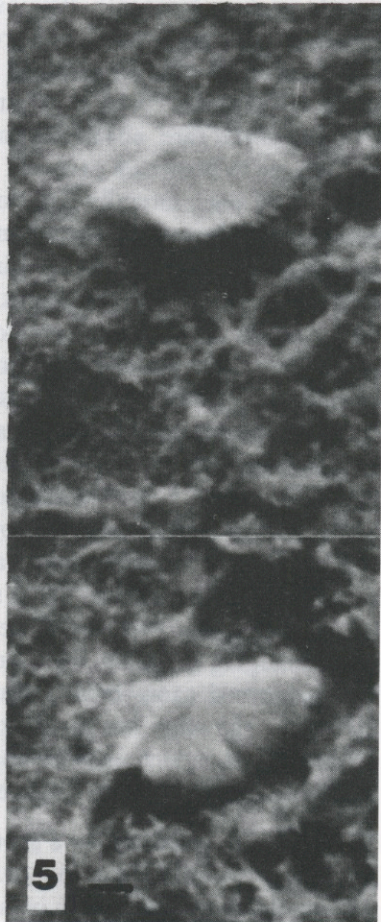
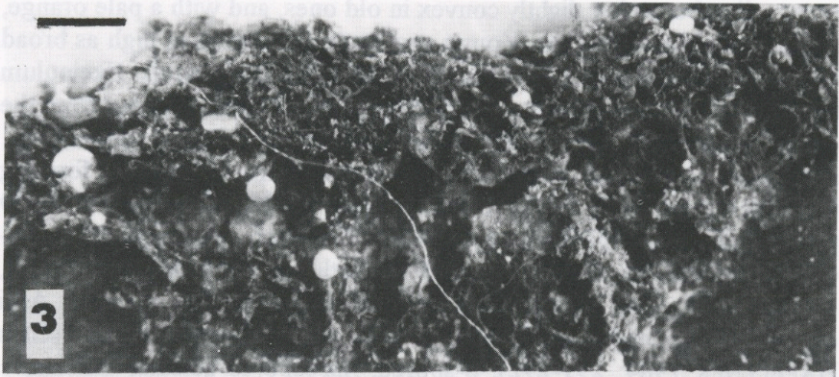


Fig. 3. *Leptogium* sp. (SEM). Fig. 4. *Leptogium* sp. (SEM). Fig. 5. *Leptogium* sp. (SEM).

orange disc, becoming slightly convex in old ones, and with a pale orange, slightly prominent margin. Young apothecia are almost as high as broad and have convex flanks, and therefore look like tiny barrels. Excipulum typically paraplectenchymatous, although rows of cells radiating from the centre can be easily seen, with cellular lumina up to c. 10-15 μm in diam. at the edge, colourless, present under the hypothecium and thereby forming the base of apothecia, 50-55 μm thick under the hypothecium and 10-20 μm laterally in old apothecia. Epithecium indistinct, colourless. Hypothecium colourless, less than 15 μm thick. Hamathecium of simple paraphyses, 1-2 μm thick, with several septa and with apices swollen to 5 μm . Asci clavate, up to 50-60 μm in height, close to the *Lecanora*-type (sensu HAFELLNER 1984: 291-292), 8-spored. *Ascospores* acicular-filiform, \pm straight or more frequently flexuose, slightly inflated in the upper half and gradually tapering towards the proximal end, spirally arranged in the asci and their distal ends all gathered together in the upper part of the ascus, thinly 3-7-septate, 50-55 \times 1.5 μm .

Campylidia rare, absent on thalli producing apothecia, formed of two pale orange to brownish parts: an ovoid pycnidium with a shell-shaped or fan-shaped part, laterally fixed on the upper part of the pycnidium and bending over the ostiole. Pycnidium ovoid, 0.15 mm in diam. and up to 0.2 mm in height, with its base \pm immersed into an araneous network of hyphae that anchor it to the thallus, with a paraplectenchymatous wall, 30-40 μm thick, colourless; conidiogenous layer lining the bottom of the cavity; conidiogenous cells numerous, cylindrical; *conidia* abundantly produced, arising singly at the apices of the conidiogenous cells, coiled up in the cavity but mostly turning towards the ostiole, filiform-sigmoid, remaining non-septate until they reach their final size, up to 20-septate when ripe, 120-160 \times 1.5 μm . Ostiole present, central, usually obstructed by the upper parts of conidia, protected by the fan-shaped part of the campylidium that bends over it. Fan-shaped part orange brown, paler on its inner side and more brownish on its outer side, up to 0.7 \times 0.5 mm, fringed on its lateral edges, made of a colourless, paraplectenchymatous »tissue« at its base, changing gradually into periclinally hyphae towards its edge. In the best preserved campylidia, a plateau develops on the other edge of the ostiole (= the edge not carrying the fan-shaped part that bend over it), made of a paraplectenchymatous »tissue« at its base and also changing gradually into periclinally hyphae towards its edge.

This new species belongs to a group species of *Bacidia* s. l., known as the *Bacidia phacodes*-group (VĚZDA 1983: 61): thallus made of goniocysts s. l., apothecia pale orange to orange brown, excipulum typically paraplectenchymatous, simple paraphyses with swollen apices, ascospores acicular

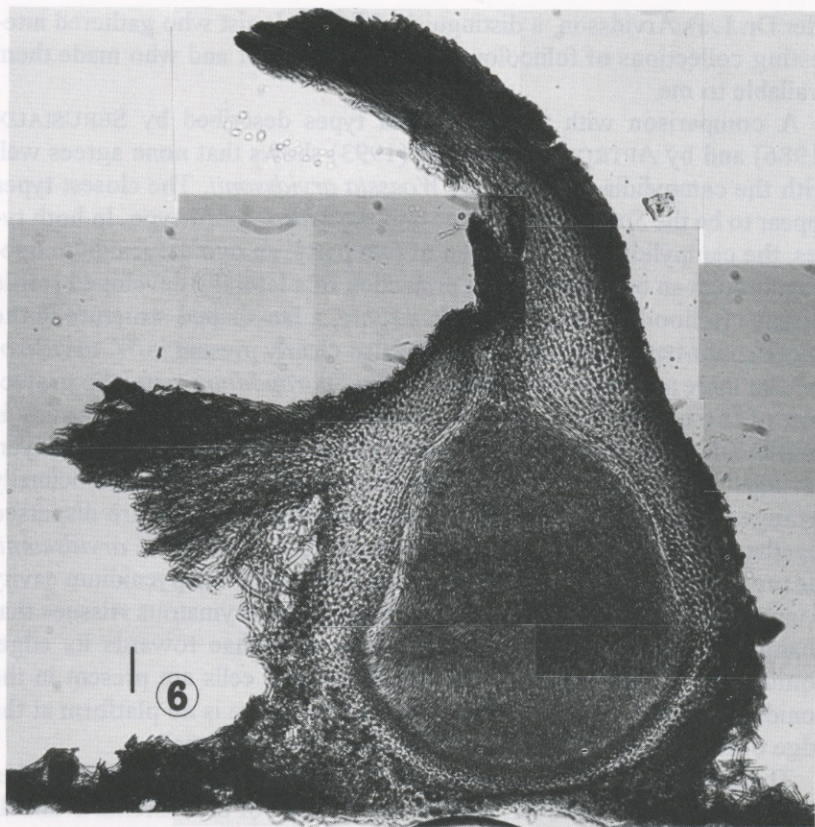


Fig. 6. *Woessia arvidssonii* SÉRUSIAUX (holotype). Cross-section through a mature campylidium, mounted for five minutes in CRB. Scale bar = 20 μ m.

and spirally arranged in the asci, filiform-sigmoid conidia forming a coiled mass in the pycnidia. LUMBSCH (1991) has demonstrated that their ascus-type does not belong to the *Bacidia*-type and is much closer to the *Lecanora*-type. VĚZDA (1990) has described the new genus *Bacidina* VĚZDA to accommodate that group of species, but the earlier generic name *Woessia* D. HAWKSW. & POELT is available for it and taken up by SÉRUSIAUX & DIEDERICH (in prep.). Indeed, the type species (*W. fusarioides* D. HAWKSW., POELT & TSCH.-WEOSS) is typical *Bacidia arnoldiana* KÖRB. (isotype in IMI 253748!) that also belongs to that group.

Woessia arvidssonii is the first described representative of that genus to produce campylidia. I think there is no reason to exclude it from that genus on the sole basis that it does develop genuine campylidia instead of »usual« pycnidia, as all other characters fit well into that group. It is named

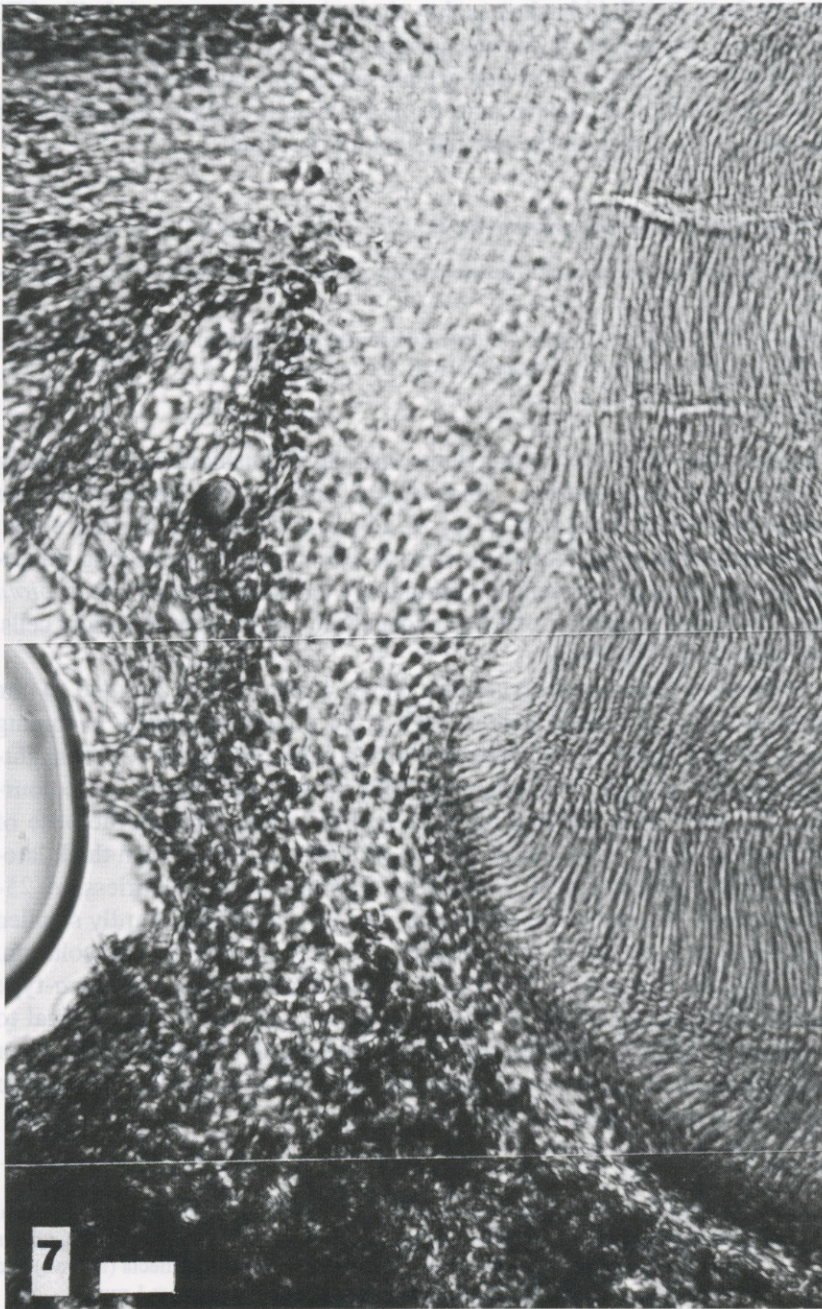
after Dr. Lars Arvidsson, a distinguished lichenologist who gathered interesting collections of foliicolous lichens in Ecuador and who made them available to me.

A comparison with the campylidia types described by SÉRUSIAUX (1986) and by APTROOT & SIPMAN (1993) shows that none agrees well with the campylidia produced by *Woessia arvidssonii*. The closest types appear to be the *Sporopodium*-type and the *Musaespora*-type. In both types, the campylidia are composed of two parts: an ovoid pycnidium opening through an ostiole under the protection of a laterally developed sterile »tissue« (a hood in the *Sporopodium*-type, a fan-shaped structure in the *Musaespora*-type); such an anatomy is also clearly present in *W. arvidssonii*. But there are major differences: in the *Sporopodium*-type, the protection of the ostiole is secured by a convex hood, the pycnidium cavity is multilocular and photobiont cells are present in the conidiogenous layer, the small lateral platform at the edge of the ostiole is made of anticlinally arranged hyphae, and conidia are small and lacrimiform and are dispersed together with photobiont cells in a sticky globose mass. In *W. arvidssonii*, the protection of the ostiole is a fan-shaped »tissue«, the pycnidium cavity is unilocular, the platform is made of a paraplectenchymatous »tissue« that changes gradually into periclinally arranged hyphae towards its edge, conidia are filiform-sigmoid, and no photobiont cells are present in the conidiogenous layer. In the *Musaespora*-type, there is no platform at the edge of the ostiole and the conidia are oval and very small.

Thalli carrying typical campylidia described above together with apothecia were not seen. However, careful examination of the material available convinced me that thalli with campylidia and those with apothecia belong to the same species: they are absolutely identical. Such a situation is commonplace in species producing campylidia (SÉRUSIAUX 1986: 5) and is best explained by the hypothesis that thalli which invest into an asexual way of reproduction (e. g. campylidia) neglect the sexual way (apothecia).

However, the closely related *Woessia defecta* (VĚZDA) SÉRUSIAUX comb. nov. [Basionym: *Bacidina defecta* VĚZDA, *Nova Hedwigia* 58: 124 (1994)], described from several collections from Africa and Central & South America, is also present in the same collection. Its thallus is also made of deeply incised goniocysts; they are, however, more appressed and

Fig. 7. *Woessia arvidssonii* Sérusiaux (holotype). Details of the cross-section through a mature campylidium, mounted for five minutes in CRB, showing the conidiogenous layer, the paraplectenchymatous wall and the araneous network of hyphae. Scale bar = 10 μ m.



do not form coralloid bushes as they do in the best preserved thalli of *W. arvidssonii*. Moreover, *W. defecta* produces typical scutelliform isidia (see fig. 8 in VEŽDA 1994: 139) that are present in this collection.

W. arvidssonii is known only from the type locality in Ecuador, in a mountain rain forest on the eastern flank of the Andes.

***Woessia pseudohyphophorifera* R. LÜCKING & SÉRUSIAUX spec. nov.**

Woessia species insignis praesentia pedicellatorum pycnidiorum filiformia conidia efferentium.

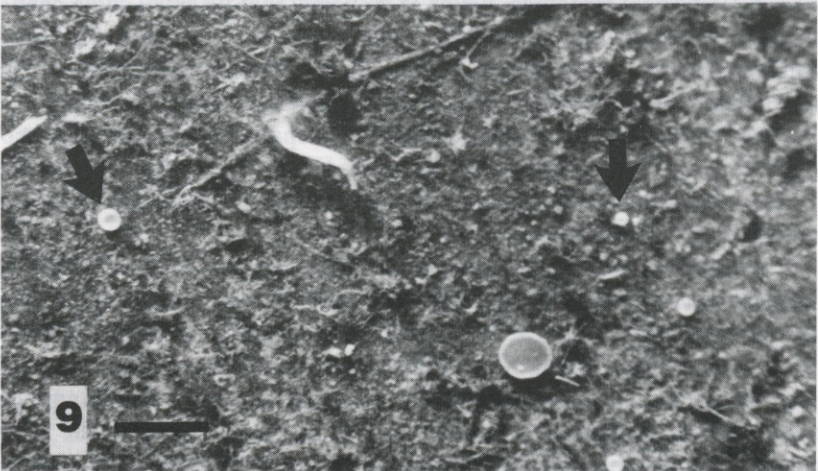
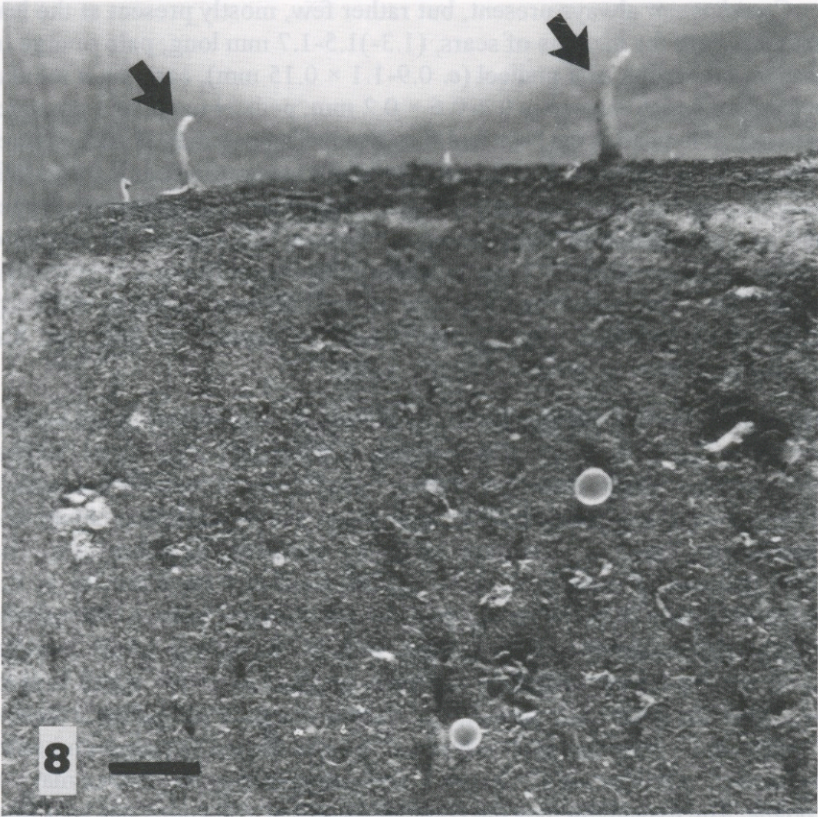
Type: WEST INDIES. St. Lucia: Quillesse Forest reserve, foliicolous on a fern in a virgin forest, 300-350 m, II.1993, Sérusiaux s. n. (LG – holotype).

(Fig. 8-12)

Thallus epiphyllous or hypophyllous, usually inconspicuous but reaching 1.5-2 cm in diam., sometimes almost absent, made of appressed goniocysts (sensu lato; see SÉRUSIAUX 1985) 10-15 μm in diam., and therefore with a minutely rugose surface (best seen at 40x under the dissecting microscope), green to pale greenish, without any visible prothallus. *Photobiont* most probably a species of Chlorococcaceae, with green spherical cells, less than 10 μm in diam.

Apothecia rare or absent, circular, never contiguous, 0.2-0.4(-0.5) mm in diam., c. 0.15 mm in height, with a flat pale orange disc, becoming brownish and convex in old ones, and with a paler (but never white) slightly prominent margin. Excipulum typically paraplectenchymatous, colourless, present under the hypothecium and therefore forming the base of apothecia, 40 μm thick under the hypothecium and 40-60 μm thick laterally. Epitecium indistinct, colourless. Hypothecium colourless, c. 25-30 μm thick. Hamatecium of simple, septate paraphyses, hardly swollen at apices, c. 2 μm thick and swelling to c. 2.5 μm in a 10% K solution. Asci slightly clavate, 25-30 μm in height, close to the *Lecanora*-type (sensu HAFELLNER 1984: 291-292), 8-spored. *Ascospores* cylindrical to fusiform, straight or slightly bent, sometimes slightly inflated in the upper half and gradually tapering towards the proximal end, spirally arranged in the asci, 3(-5)-septate, 16-23 \times 1-1.5 μm .

Fig. 8-9. *Woessia pseudohyphophorifera* R. LÜCKING & SÉRUSIAUX (holotype). General habit. (8) Thallus with two apothecia and two over-mature conidiomata (pedicels without the pycnidium; arrows). (9) Thallus with young apothecia (arrows) and a mature one, and with an immature conidioma. Scale bar = 1 mm.



Conidiomata always present, but rather few, mostly present at the leaf margins, or at the margins of scars, (1.3-)1.5-1.7 mm long, pale orange to orange, consisting of a pedicel (c. 0.9-1.1 × 0.15 mm), carrying a tubular pycnidium which measures 0.4-0.6 × 0.2 mm; pedicel made of a compact network of hyphae at the base, but mostly periclinally arranged in the upper part; sterile »tissue« of the tubular pycnidium made of a cupule of periclinally arranged ± pachydermatous hyphae (named here the palisadic hyphae) and of a conidiogenous layer lining the bottom of its inner side; conidiogenous cells not observed; *conidia* very numerous, forming a hygroscopic mass when ripe, coiled up as in a wool ball, filiform-sigmoid, distinctly clavate at the proximal end, apparently with 5-7 septa when fully ripe, but usually seen as non-septate, 55-65 × 1 µm.

The conidiomata of this species are so far unique in lichenized fungi as they are made of a rather long pedicel carrying a cupular pycnidium. In the best preserved specimens, there is a distinct constriction separating the pedicel from the cupular pycnidium. At an early stage, the pycnidium is closed and therefore appears as a paint-brush carried by a pedicel; the palisadic hyphae then encompass completely the conidial mass and form the tip of the structure. There is, however, no genuine ostiole and I believe that conidia are not able to disperse at that stage. Indeed, the growth of the conidial mass enables the pycnidium to »open« at its weakest point, which is at its tip, where the palisadic hyphae do not form a compact and robust »tissue«. A fully ripe pycnidium is thus made of a tulip-shaped cupule with hardly agglutinated hyphae at its margins, and containing an enormous mass of conidia. The pycnidium plus the conidial mass that protrudes out of it then form a cylindrical structure, which is so heavy that its small socle cannot maintain it upwards anymore and it bends down. Any mechanical pressure leads to a rupture: old pedicels are thus seen without any pycnidium. This also means that the conidial mass may disperse as a single diaspore.

When moistened, the conidial mass can be separated from the cupule by a needle under the dissecting microscope. Even after such a preparation, we have been unable to examine the conidiogenous layer which was still hidden by the numerous conidia.

This species was already mentioned by LÜCKING (1992: 132), but left formally undescribed as the material was sterile. It was compared to *Bacidia permira* VĚZDA (1975: 419), which was based on a single collection from Tanzania (hb. Vězda – holotype!). The conidiomata of the latter are quite different and indeed very close to the hyphophores of the Gomphillaceae: filiform, multiseptate conidia are externally produced on the lower side of a flattened bent cilium. *B. permira* has never been reported since its description but its ascomata put it aside from all other lichen genera.

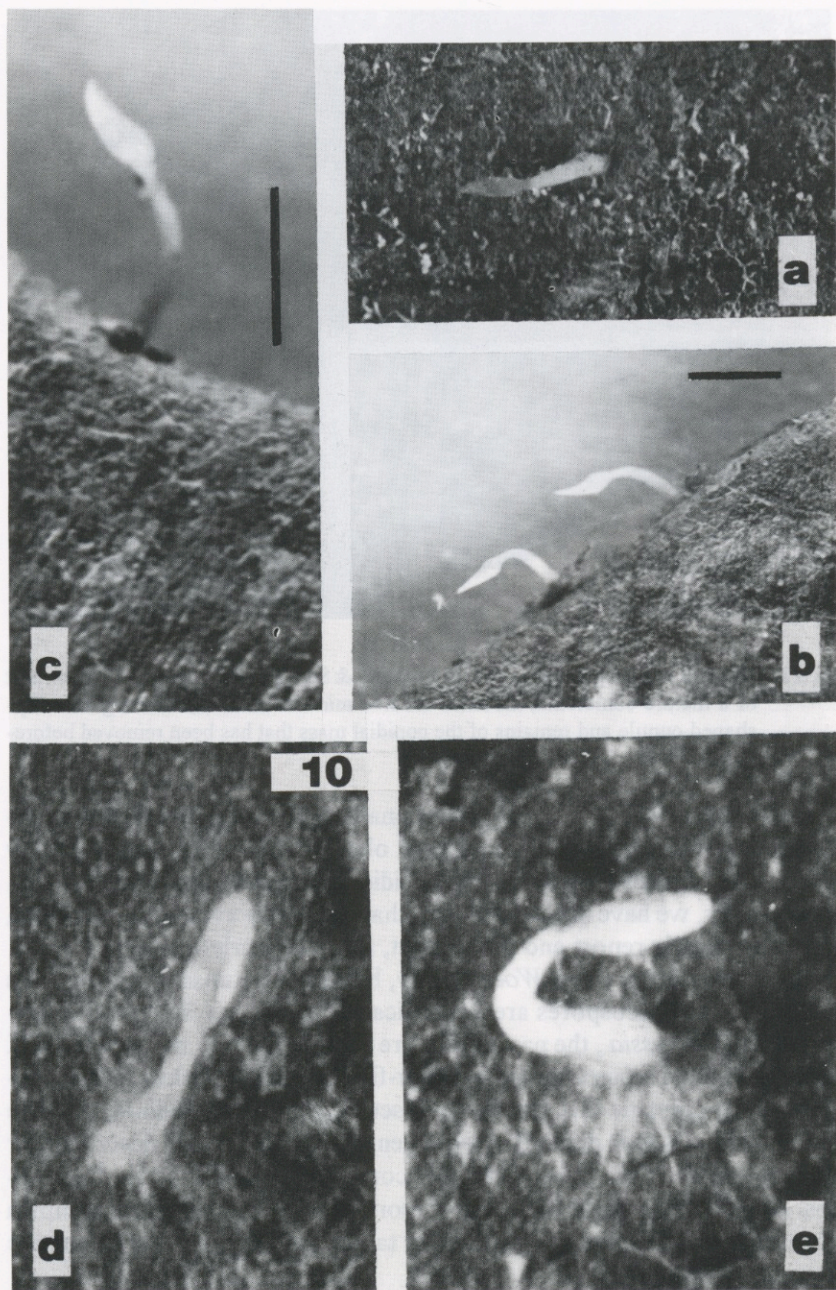


Fig. 10. *Woessia pseudohyphophorifera* R. LÜCKING & SÉRUSIAUX (holotype). Sequence of maturation of the conidiomata (a to e). Scale bar = 1 mm.

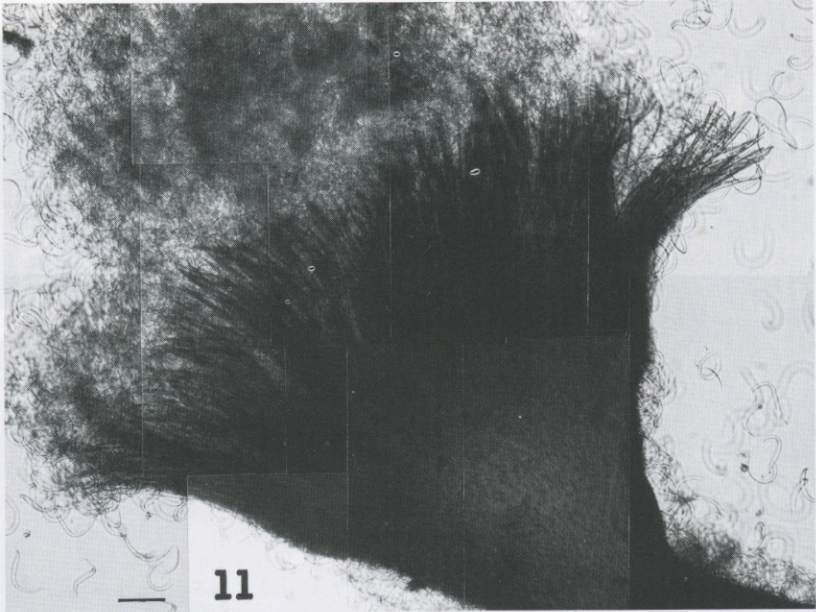


Fig. 11. *Woessia pseudohyphophorifera* R. LÜCKING & SÉRUSIAUX (holotype). Upper part of a mature conidioma, mounted for five minutes in CRB, showing the tulip-shaped cupule and remains of the conidial mass that has been removed beforehand (above). Scale bar = 20 μ m.

LÜCKING (1992: 132) has provisionally named this species *pseudohyphophorifera*, and, although detailed observations on the material now available clearly demonstrate that its conidiomata cannot be compared with hyphophores, we have decided to keep that epithet to avoid any confusion between its early report and the present, formal description.

Its position in the genus *Woessia* may, however, be unsatisfactory as its paraphyses and ascospores are not typical of that genus. In typical representatives of *Woessia*, the paraphyses are capitate and do not swell in a K solution, and the ascospores are acicular-filiform. Nevertheless, other characteristics point to that genus: the ascus-type, the excipulum, and the conidia. There is little doubt that more genera will have to be described for the tropical lecideoid lichens and this could be the case also for this species. However, we prefer to wait until more material is available to confirm our observations on this species, and to take a final decision on its generic status.

The diversity of the asexual means of reproduction in tropical lecideoid genera has now grown larger with those of *Woessia pseudohyphophorifera*



Fig. 12. *Woessia pseudohyphorifera* R. LÜCKING & SÉRUSIAUX (holotype). Details of the margin of the tulip-shaped cupule of the upper part of a mature conidioma, mounted for five minutes in CRB. Scale bar = 10 μ m.

as they do not fit in any other types described so far. The following types were known (see SÉRUSIAUX & LAMBINON 1994 for a short review): (1) flask-shaped pycnidia; (2) flask-shaped pycnidia with a long beak and the ostiole at its tip; (3) conidiogenous cilia; (4) campylidia.

W. pseudohyphorifera is known from one locality in St. Lucia in the West Indies and from another one in Costa Rica. At both localities, it is

found in virgin rain forests but, in Costa Rica at least, it is able to survive the disturbance of its habitat.

Additional specimens examined: COSTA RICA. Heredia prov.: La Selva protection zone, epiphyllous on leaves of a dicotyledon in secondary vegetation and in primary forest, 50 m. IX.1991, Lücking 91-1246 p. p. & 91-5429 (hb. Lücking).

Notes on the biological role of campylidia

Campylidia are now known in several unrelated groups of lichenized fungi (Arthoniales, Melanommatales, Lecanorales; cf. Table 1), and, as quoted by LÜCKING (1995), there is no chance that they are homologous organs: »A strong selective advantage must be postulated for these structures to have evolved independently in such different groups.«. Indeed, close anatomical examination of these highly complex conidiomata show that they have only three features in common: they are dorsiventral, they are geotropically orientated, and they react strongly to humidification.

Their geotropic orientation was carefully examined during a field trip in Papua New Guinea in 1992, together with my friends and colleagues Drs A. Aptroot, P. Diederich & H. Sipman. These field observations mainly dealt with campylidia produced by *Badimia*, *Lasioloma* and *Musaespora* species. When present on large leaves, all campylidia point towards the petiole (also observed by LÜCKING 1995), which is where the main flow of rain water comes from. Observations on small leaves are less clear but such leaves are not heavy enough to be immobile in the rainforest understory or to be able to »come back« to their original position after any disturbance; in such situations, the direction of the water flow on the leaf surface is not constant and campylidia are thus puzzled by the variations. When growing on branches or on trunks, campylidia are always orientated upwards, and are again facing the main water flow. I also confirm LÜCKING's observations that, upon application of water, campylidia unfurl the »tissues« that protect the ostiole or the crack through which the conidia can escape them. This means that when water runs over the surface of the substratum on which they grow, campylidia act as small cupules or receptacles for the water. Conidia are then able to spread out over the droplets surface and be dispersed.

LÜCKING (1995) has also argued that the orientation of the campylidia might be a way to use the splash-cup mechanism (BRODIE 1951) to disperse their conidia. I have no definite observations to support my hypothesis (collecting water droplets to let the conidia spread out over their surface) instead of the splash-cup one (organizing a surface on which the rain water would have the most efficient mechanical impact to disperse the conidia)

and indeed both mechanisms could work well with the morphology of the campylidia. I do not, however, accept his statement that campylidia are mostly produced by foliicolous species because the living leaves provide the only surface that can be reached by direct rain in the forest understory, until further evidence is available. I have the feeling that campylidia are mostly known in foliicolous species just because there is more interest nowadays in foliicolous tropical taxa than in corticolous ones. KALB & VĚZDA (1987) have, for example, described campylidia in several corticolous species from Brazil.

Field observations of the recently described *Placopsis auriculata* LUMBSCH & KASHIWADANI (LUMBSCH *et al.* 1993) provide further data to support the function of campylidia. This species, known so far from the mountains of Papua New Guinea, is easily characterized by its helmet-shaped soralia, very close to campylidia in appearance: they are erect, concave lobes producing soredia on their inner side (see Fig. 3-6 in LUMBSCH *et al.* 1993: 288). When I first saw this species in the field in 1992, I immediately labelled it as »*Placopsis cum campylidiis*«. I only realized my mistake when I examined it in the laboratory: the so-called campylidia do not produce conidia but soredia. This species was found growing on road cuttings on the outskirts of a forest, together with several *Gyalidea* species. It is remarkable to note that its concave soralia were all pointed upwards, facing the water flow or the rain droplets. They most probably use the same mechanisms to disperse their soredia as do genuine campylidia. Thus *Placopsis auriculata* is a further lichen producing dorsiventral, geotropically orientated structures to disperse its asexual diaspores.

Campylidia are produced by lichenized fungi only in the tropics, and in subtropical or wet and warm temperate regions (Macaronesia, Western Caucasus, etc.). In such areas they are very rare: in Madeira for example, the only species so far known to develop campylidia is *Tapellaria epiphylla* (MÜLL. ARG.) R. SANT. The basic reason for this remains obscure, whatever the functional mechanism of campylidia is.

In their discussion about the origin of campylidia, MALCOLM & VĚZDA (1994: 523) argue that there are two hypotheses »competing« for the origin of campylidia: the »ontogenetic« versus the »phylogenetic« one. They claim that I have proposed »... that campylidia originate from apothecia ontogenetically.«. There is clear evidence that it is the case in the genus *Badimia* VĚZDA (see Fig. 1-15 in SÉRUSIAUX 1986), but those observations do not provide any reason for a competition between the two hypotheses: campylidia are produced in unrelated groups of lichenized fungi and are analogous structures designed to disperse asexual diaspores; I would be surprised, therefore, that they have the same phylogenetic history.

Table 1. Genera known to produce campylidia and their family position. All genera mentioned comprise species which all produce campylidia, except for those marked with *.

Genus	Family position
* <i>Arthonia</i> ACH.	Arthoniaceae; only one species described with campylidia (LÜCKING 1995)
<i>Badimia</i> VĚZDA	Assigned to the Ectolechiaceae by VĚZDA (1986) but referred to the Pilocarpaceae by SÉRUSIAUX (1986) because of its ascus-type, confirmed by APTROOT & SIPMAN (1993) and by LÜCKING <i>et al.</i> (1995)
<i>Badimiella</i> MALCOLM & VĚZDA	Ectolechiaceae (MALCOLM & VĚZDA 1994), without data on ascus type; family position to be confirmed
<i>Barubria</i> VĚZDA	Ectolechiaceae (VĚZDA 1986)
* <i>Byssoloma</i> TREVIS.	Pilocarpaceae (HAFELLNER 1984); only one species described with campylidia by SÉRUSIAUX (this paper)
<i>Calopadia</i> VĚZDA	Ectolechiaceae (SÉRUSIAUX 1986; VĚZDA 1986)
<i>Lasioloma</i> R. SANT.	Ectolechiaceae (SÉRUSIAUX 1986; VĚZDA 1986); formerly referred to Lasiolomataceae (HAFELLNER 1984) but this family has been reduced into synonymy with Ectolechiaceae (VĚZDA 1986)
* <i>Loflammia</i> VĚZDA	Ectolechiaceae (SÉRUSIAUX 1986; VĚZDA 1986)
<i>Logilvia</i> VĚZDA	Ectolechiaceae (VĚZDA 1986)
<i>Musaespora</i> APTROOT & SIPMAN	Aspidotheliaceae (APTROOT & SIPMAN 1993)
<i>Sporopodium</i> MONT.	Ectolechiaceae (HAFELLNER 1984; VĚZDA 1986)
<i>Tapellaria</i> MÜLL. ARG.	Ectolechiaceae (VĚZDA 1986)
* <i>Woessia</i> D. HAWKSW. & POELT	Family position to be determined; only one species with campylidia (SÉRUSIAUX, this paper)

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