

THE NATURE AND ORIGIN OF CAMPYLIDIA IN LICHENIZED FUNGI

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Abstract: The campylidia hypothesis, first introduced by Müller Argoviensis (1881) and recently restored by Vězda (1983), for the erect helmet-shaped structures found on foliicolous lichens and usually known as 'Pyrenotrichum' is adopted as being the most satisfactory. In the *Badimia pollilensis* aggregate, campylidia are shown to derive from primordia identical to those of the apothecia. In the genus *Sporopodium*, algal cells are included in the conidiogenous layer and are dispersed together with conidia. This also seems to be the case in the genus *Loflammia*. Short descriptions are given for the most common campylidium known as 'Pyrenotrichum splitgerberi' and for another not yet assignable to a peculiar genus. *Loflammia demoulinii* sp. nov. is described from New Guinea.

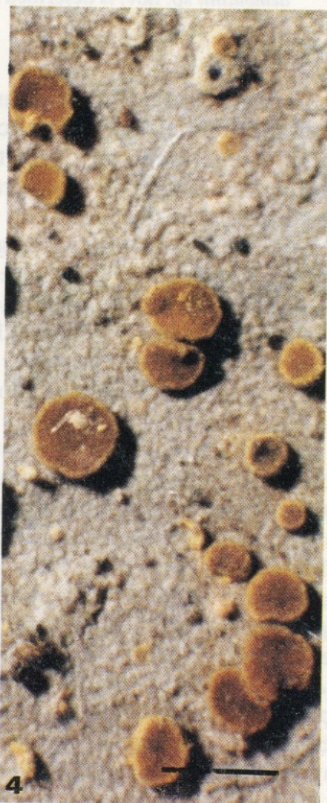
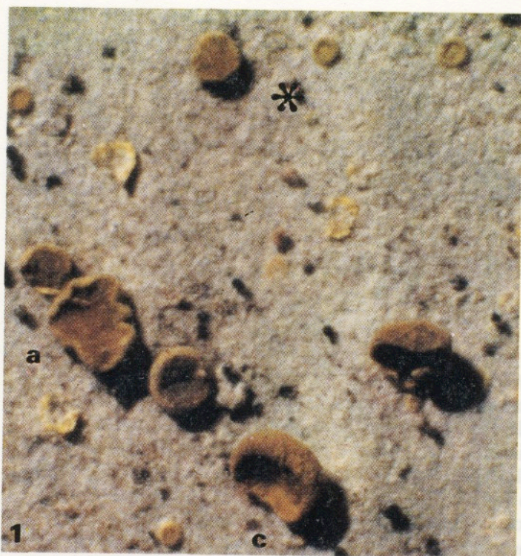
Introduction

Anyone working on foliicolous lichens or liverworts will be familiar with the erect and helmet-shaped structures found attached to lichen thalli. They are usually very frequent, sometimes covering entire leaves in monospecific stands. However, the monograph by Santesson (1952) on foliicolous lichens does not deal with them as he regarded them as the conidiomata of the lichen parasitic or parasymbiotic genus *Pyrenotrichum*. Seventy years earlier, Müller Argoviensis (1881) termed these structures 'campylidia' and considered them to be a part of the lichen which carries them and analogous with pycnidia. Except by Malme (1935), this hypothesis has not been adopted by later workers and has never been restudied thoroughly. However Vězda (1983) in his work on foliicolous lichens in the Caucasus (U.S.S.R.) restored that idea.

In 1980 Dr V. Demoulin gathered an extraordinary collection of foliicolous lichens in New Guinea in which these structures are particularly abundant. Even a superficial examination reveals—and this is what struck me most—that they have the same colour as the apothecia of the lichen on which they grow. This is obvious in species such as: *Loflammia flammea* (syn. *Lopadium flammeum*) whose 'campylidia' have the red colour of the apothecia; *Sporopodium phyllocharis* var. *flavescens* whose 'campylidia' have the bright yellow colour of the apothecia and of the prothallus; *Badimia elegans* (syn. *Bacidia elegans*) whose 'campylidia' are vivid yellow-brown like the apothecia (Figs 1-4); and *Badimia pollilensis* (syn. *Bacidia pollilensis*) whose 'campylidia' are pale orange like the apothecia. These observations motivated my work on these fascinating structures.

This paper was ready to be submitted for publication when Dr A. Vězda sent me a copy of his work on the new genera he recognizes amongst the

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FIGS 1-4. *Badimia elegans*. 1, Apothecia (a) and campylidia (c). 2, Three mature campylidia. 3, Young and almost mature campylidia. 4, Young and mature apothecia. Note that both structures have the same colour and how very alike are young apothecia (Fig. 1*) and young campylidia (Fig. 3*). Scales: 1-3 = 2 mm; 4 = 1 mm.

foliicolous representatives of the Lecideaceae *s. lat.* (Vězda 1986). His paper also deals with campylidia which he considers to be phylogenetically derived from apothecia. The aims of my paper are not the same: Dr Vězda takes for granted the fact that the 'campylidia' are the conidiomata of the lichens on which they grow, whilst I will attempt to rule out the hypothesis of their parasitic or parasymbiotic nature. For this purpose, this paper concentrates on the *Badimia pollilensis* agg. where I have been able to demonstrate that the campylidia derive ontogenetically from the apothecia, and *Sporopodium* where I have demonstrated that the conidia produced are dispersed with the photobiont diaspores. The five main types of campylidia so far encountered are also reviewed, but this must be considered provisional as all the material available has not yet been thoroughly investigated.

It is beyond the scope of this paper to offer a complete description of the campylidia, more particularly the way in which the conidia are produced, following the recent concepts of Minter *et al.* (1982, 1983). Similarly, the nomenclatural implications of the demonstration that the taxa described in *Pyrenotrichum* and other related genera are anamorphs of particular lichens will not be pursued here.

Methods

The material was observed in tap water, either in Lugol's iodine solution, in lactophenol cotton-blue (LCB), or in ammoniacal erythrosin. The measurements given in this paper always refer to preparations in water. The photomicrographs were taken with a Leitz Dialux microscope and an Orthomat, or with a Zeiss microscope. Air-dry herbarium material for study with the scanning electron microscope (SEM) (Philips 501 B) was prepared by the critical point method.

Historical Background

The first mention of campylidia in the literature is the description of the new genus *Pyrenotrichum* by Montagne (1843: 376). The genus is typified by *P. splitgerberi* Mont., the only described species at that time. Montagne (1843: 376–377) considered his new genus a lichen parasite ('ad crustam lichenum parasitans') which he compared to *Cliostomum* and *Endotrichum*. This type of campylidium is by far the most frequent: according to Santesson (1952: 40–41), it is found on six species of *Tapellaria* (all foliicolous) and on nine species of *Lopadium* (foliicolous and corticolous). As stated by Hawksworth (1981: 59–64), only two further epithets are validly published in the genus: *P. staurosporum* (Keissler) R. Sant. which corresponds to the campylidia of the exclusively foliicolous genus *Lasioloma*, and *P. foliicola* (Vainio) R. Sant. which corresponds to the campylidia of the *Badimia pollilensis* agg. Besides these, Santesson (1952) mentions six further species, not formally published. He considered *Pyrenotrichum* to be a parasitic, parasymbiotic, or at least a lichenicolous genus of Coelomycetes. Hawksworth (1981) illustrated *P. splitgerberi* and *P. staurosporum*, but was uncertain as to their biological relationship, pointing out that the photobiont layer and mycobiont were continuous from the thallus of the presumed host and that the association appeared to be lichenized.

Campylidia were also described several times as basidiomycetes belonging to the Aphyllophorales, in the genera *Cyphella* Fries nom. rejic. and *Chlorocyphella* Speg. (whose type, *C. subtropica* Speg., is identical with *Pyrenotrichum splitgerberi*, fide Santesson 1952: 49). The shape and the habit of the most common type of campylidium (*P. splitgerberi*) explain this confusion, but of course no basidia are found in the campylidia. This confusion continued until the works of Keissler (1927, 1933, in Zahlbruckner *et al.* 1929).

Fée (1873) sometimes confused campylidia with apothecia. He described the campylidia represented by *Pyrenotrichum splitgerberi* as *Lecidea irregularis* (Fée 1873: 318; fide Hawksworth 1981: 60) and as *L. lunulans* (Fée 1873: 319; fide Santesson 1952: 528*).

As alluded to above, Müller Argoviensis (1881) was the first author to express the opinion that these structures are organs peculiar to the lichens on which they are found. He considered them analogous to pycnidia and introduced the term campylidium (pl. campylidia) to name them. He described the conidiogenous cells as 'basidia' and the conidia as 'acrospores', i.e. born at the apex. His observations are rather accurate as the conidia proliferate at the apex of conidiogenous cells and this process can easily be confused with the production of basidiospores. In his original paper, Müller Argoviensis mentions campylidia in *Gyalectidium xantholeucum* Müll. Arg. (i.e. *Sporopodium xantholeucum* (Müll. Arg.) Zahlbr.), *G. dispersum* Müll. Arg. (i.e. *S. phyllocharis* (Mont.) Massal.), and *Lopadium melaleucum* Müll. Arg. (i.e. *Tapellaria nana* (Fée) R. Sant.). Until the reappraisal by Vězda, Malme (1935) had been the only author to maintain the campylidium hypothesis after Müller d'Argoviensis first description. Malme described them associated with *Lopadium perpallidum* (Nyl.) Zahlbr. and emphasized the interlacing ('umschlingen') of conidia with algae. He compared these 'kleine Bälle' with soredia and assumed they propagated the lichen thallus as a whole.

Vainio (1921, 1923) described the 'conidangia' of two species of *Sporopodium* without reference to Müller Argoviensis' paper, and hence without using the term 'campylidium': *S. mastophorum* Vainio (1921: 92) (i.e. *S. argillaceum* (Müll. Arg.) Zahlbr. and *S. glaucopheopsis* Vainio (1923: 134) (i.e. *S. xantholeucum* (Müll. Arg.) Zahlbr.). Also worth mentioning here is the original description of *Bilimbia mastophoriza* Vainio (1921: 80) (i.e. *Bacidia micrommata* (Krempelh.) R. Sant) in which Vainio indicates the presence of 'pycnidia and conidangia (spermogonia)'. According to Santesson (1952: 459-460), these structures actually grow on a *Sporopodium* and are independent of the *Bacidia* described. There is consequently no doubt that the conidangia briefly described by Vainio are campylidia.

Finally, between 1961 and 1972, several Brazilian authors, the most important being the late Professor A. C. Batista, described no less than 37 new genera of imperfect mainly foliicolous lichens (Vobis & Hawksworth 1981: 267). So far no comprehensive survey of these genera has been attempted but

*This statement needs to be checked as Fée described *Lecidea lunulans* with 'des scutelles émergentes jaunâtres', a colour which *Pyrenotrichum splitgerberi* never has. This discrepancy will be solved by the study of the type of *Lecidea lunulans* and of the campylidia of *Lopadium foliicola* (Fée) R. Sant. with which Santesson puts *Lecidea lunulans* in synonymy.

there is little doubt that some of these genera are members of Asterothyriaceae producing hyphophores (see Vězda 1979) or campylidia. It is obvious, for example, that *Acleistomyces rionegrensis* Bat. *et al.* (Batista 1961) is a campylidium. The hypothesis that the campylidia are a lichen-forming coelomycete was also sustained by Mameli-Calvino (1930) and by Rizzini (1952) for *Pyrenotrichum splitgerberi*, as noted by Hawksworth (1981).

Parasitism or Parasymbiotism

That the *Pyrenotrichum* species are parasites must be ruled out as there is no gall formation, thallus deformation, or necrosis around these structures. However, the fact that the thalli covered by numerous *Pyrenotrichum* are usually almost or totally devoid of apothecia could be interpreted as a depressing effect of an invading parasite. This observation, commonplace on foliicolous material, is not incompatible with the campylidia hypothesis. Indeed, it is not aberrant to affirm that a species, or a thallus of a species, which invests into an asexual way of multiplication (in this case the campylidia), would neglect the sexual way.

However, the hypothesis of parasymbiotism (lichenization of a fungus with an algal population which is already lichenized with another fungus) must be examined seriously. Hawksworth (1981:63) has recently raised this idea for *Pyrenotrichum*. Two cases can be distinguished (see Hawksworth *et al.* 1979, Hawksworth & Hill 1984: 7): in the first one, the parasymbiotic fungus invades its host, from which it presumably obtains carbohydrates but does little damage to it (e.g. *Arthonia glaucomaria* on *Lecanora rupicola*, *Sphinctrina turbinata* on *Pertusaria* species); in the second, the invading fungus associates with the photobiont of a developed lichen thallus and with it builds a different thallus. This is seen in, for example, *Arthrorhaphis citrinella* on *Baeomyces rufus*, *Lecidea insidiosa* on *Lecanora varia*, *Diploschistes caesioplumbeus* on *Lecanora gangaleoides*, *D. muscorum* on *Cladonia* species, *Blarneya hibernica* on *Enterographa crassa* and on two species of *Lecanactis*. These cases are all beyond question regarding the presence of two different fungi: either two types of ascomata are present or a new thallus is built by the invading fungus; two networks of hyphae are easily distinguished, even if they are lichenized with the same algal population. The situation with *Pyrenotrichum* is altogether different. I have carefully examined the *Pyrenotrichum* species that are available to me and, like Hawksworth (1981), failed to demonstrate two hyphal networks and found no discontinuity between the *Pyrenotrichum* structure and the lichen thallus on which it grows. Moreover, as already mentioned, some *Pyrenotrichum* taxa (*P. bicolor* R. Sant. *nom. nud.*, *P. irregularis* R. Sant. *nom. nud.* and *P. foliicola* (Vainio) R. Sant.) have the same colour as the apothecia of the thallus carrying them, and most probably the same pigments; the pigments are unidentified but those from the apothecia and campylidia run together in t.l.c. Thus, to uphold the parasymbiotism theory, one would have to admit that the invader which confiscates the lichen photobiont also adopts the pigments which the lichen produces for its own fructifications; this scenario seems most unlikely and cannot be upheld.

Observations

At this stage of my investigations, I can add only one type of campylidia to the four recognized by Santesson (1952: 41): (1) produced by *Badimia pollilensis* and related species, corresponding to *Pyrenotrichum foliicola*; (2) produced by *Sporopodium*, corresponding to *Pyrenotrichum irregulare*; (3) produced by *Loflammia flammea* and *L. demoulinii*, corresponding to *Pyrenotrichum bicolor*; (4) corresponding to *Pyrenotrichum splitgerberi*, produced in several genera; (5) a new type, found on an unnamed foliicolous lichen from New Zealand.

I shall discuss the first two cases here as they clearly demonstrate that campylidia are lichen conidiomata.

The campylidia of *Badimia pollilensis* and of *B. elegans*

The genus *Badimia* was described by Vězda (1986) to accommodate several foliicolous species maintained in *Bacidia* by Santesson (1952). My studies of this aggregate agree with Vězda's description except that I assign its ascus type to the *Byssoloma*-type of Hafellner (1984: 315), rather than to the *Sporopodium*-type. In all species examined, including the type-species (*Badimia dimidiata* (Bab.) Vězda; syn. *Bacidia dimidiata* (Bab.) R. Sant.), the amyloid thallus contains a distinct I+ dark blue 'Rohrenstruktur', not found in the *Sporopodium*-type. I therefore suggest that this new genus belongs to the Pilocarpaceae and not to the Ectolechiaceae.

Vězda (1986) transferred six species known to produce campylidia referable to *Pyrenotrichum foliicola* to *Badimia**. The material available to me in sufficient amounts to perform detailed studies includes *Badimia pollilensis* and *B. elegans*.

Badimia pollilensis (Vainio) Vězda

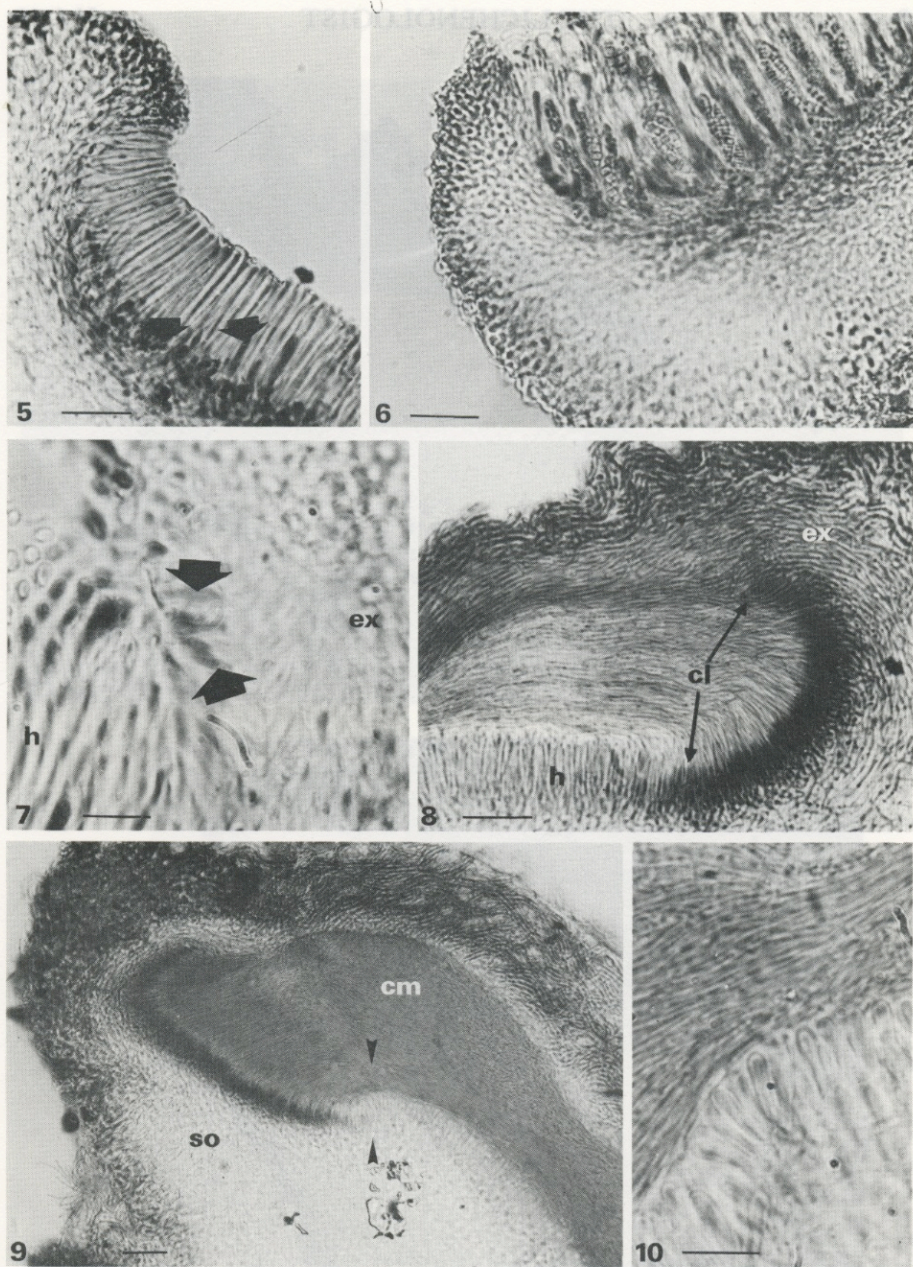
Material studied: New Guinea: W of Yoro (=Mugamat), Madang prov., 100–300 m elev., epiphyllous, 1980, Demoulin 5930 & Smeets (LG).

(Figs 5–12)

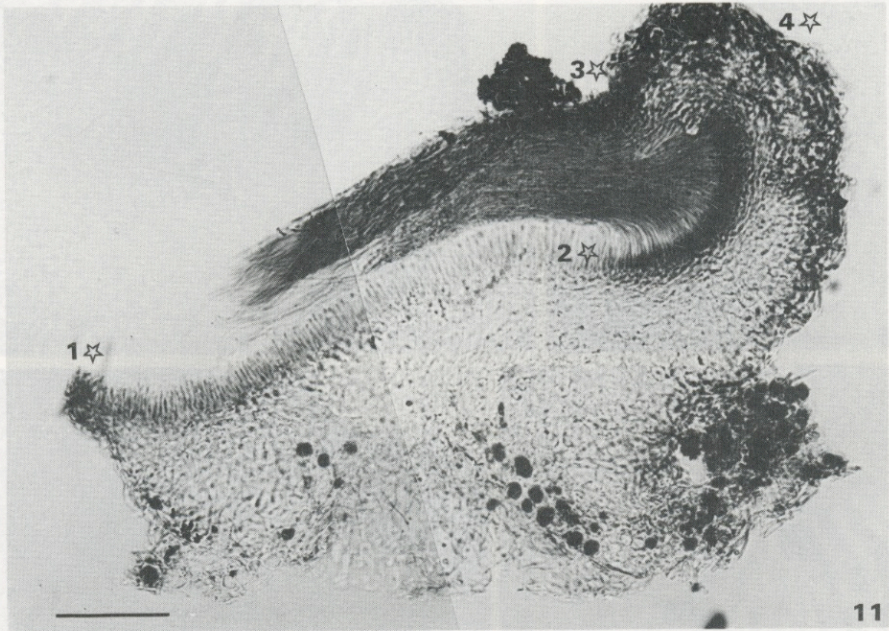
Thallus forming \pm regular patches, to 3 cm diam, usually continuous, pale greenish-grey or bluish, densely verrucose (verrucae hemispherical or conical, ± 0.1 mm diam), without prothallus, 20–30 μ m thick.

*As indicated by Vainio (1921: 83), the type-collection of *Cyphella foliicola* Vainio is a thallus of *Badimia pollilensis* on which four campylidia are present. I have not sectioned any of them to preserve that collection, but there is no doubt in my mind that the campylidia of *Badimia pollilensis* described in this paper are identical to those of the type-collection of *Cyphella foliicola*. Several other collections studied by Vainio (no 21536, 21540, 21549, TUR!) also bear campylidia annotated as *Pyrenotrichum foliicola* by Santesson.

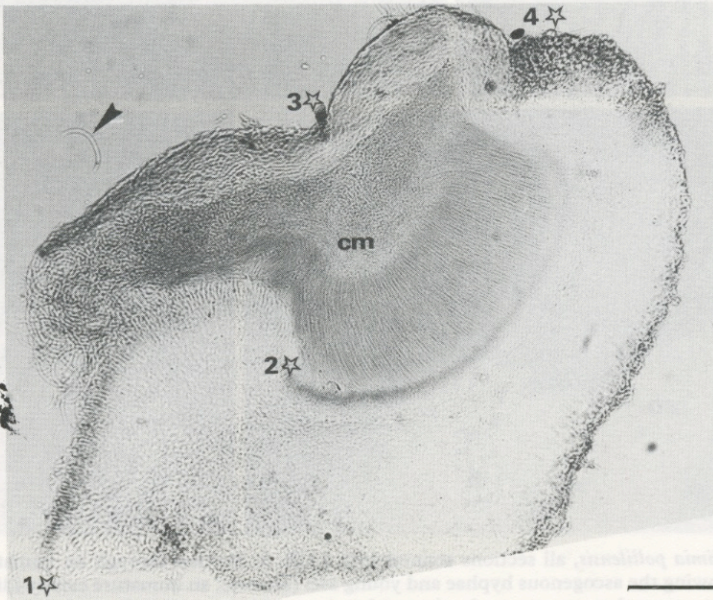
Cyphella foliicola Vainio, *Ann. Acad. Sci. fenn.*, A, 15: 83 (1921); type: Philippines, Island of Polillo, 1909, Robinson, [herb. Vainio 32926] (TUR!).—*Chlorocyphella foliicola* (Vainio) Keissler, *Ann. naturhist. Mus. Wien* 41: 159 (1927).—*Pyrenotrichum foliicola* (Vainio) R. Sant., *Symb. bot upsal.* 12(1): 41 (1952). A thallus of *Badimia elegans*, with several damaged campylidia, is also present in this collection. Of course, the type of *Cyphella foliicola* is represented by the thallus of *Badimia pollilensis*.



FIGS 5–10. *Badimia pollilensis*, all sections stained with LCB. 5, Section through an immature apothecium, showing the ascogenous hyphae and young asci (arrows); an immature campyloidium would be similar except that ascogenous hyphae and asci would be absent. 6, Section through a mature apothecium, with 8-spored asci. 7, Section through an immature campyloidium, showing rows of rectangular cells (arrows) developing between the 'excipulum' (ex) and the 'hamathecium' (h) and what would be the first conidiogenous cells. 8, Section through a young campyloidium, showing the conidiogenous layer (cl), the 'hamathecium' (h) and the contiguous 'excipulum' (ex) developing into the hood of the structure. 9, Section through an almost completely developed campyloidium showing the exuberant conidial mass (cm) and the still paraplectenchymatous socle (so). 10, Detail view of a portion of Fig. 9 (between the arrows), showing the conidia (above) and the layer of clavate hyphae derived from the 'hamathecium' (below). Scales: 5, 6, 8, 9 = 20 μ m; 7, 10 = 10 μ m.



11



12

FIGS 11 & 12. *Badimia pollilensis*, both sections stained with LCB. 11, Section through a young campylidium, with a still typical apothecium anatomy. 12, Mature campylidium; arrow points to a conidium; cm=conidial mass. Numbered stars in both figures refer to homologous tissues.

Scales: 11 = 50 μ m; 12 = 100 μ m.

Apothecia frequent on thalli that have few, if any, campylidia, 0.3–0.5 mm diam, strongly constricted at the base; disc pale orange, rarely brownish, sometimes with a pinkish tinge, without pruina, plane to slightly convex when old; margin at first very distinct and slightly prominent, always paler than the disc and without pruina. Excipulum encrusted with granular hyaline crystals in the most inner parts (crystals not dissolving in 10% KOH), not exceeding 50 μm in lateral parts but reaching 70 μm below the hypothecium, for the most part typically paraplectenchymatous (spherical to isodiametric mesodermatous cells) but distinct rows of cells radiating from the apothecial centre are visible, the cells changing from \pm rectangular in the most inner parts of the apothecium to distinctly globose at its surface. Hypothecium hyaline, \pm 20 μm thick; hymenium 50–60 μm thick, hyaline; epithecium layer absent. Paraphyses mostly simple, 1.5 μm thick, slightly inflated (not clavate) at the apices (up to 2.5 μm thick), very coherent, hardly separating from each other in 10% KOH; asci clavate, of the *Byssoloma*-type, 8-spored; spores fusiform, 3-septate, 9–13 \times 3.5–5 μm with a \pm distinct halo (Fig. 6).

Campylidia frequent on thalli that have few, if any, apothecia; when mature looking like an obliquely erect scale with a thick podgy upper margin, sometimes arched in a way transforming the structure into a half a funnel; lowest part very pale orange and smooth whereas the upper parts are more orange and have an arachnoid whitish surface; 0.8–1.3 mm wide and 0.4–0.6 mm deep (when seen from above) and up to 0.5 mm high (measure taken perpendicularly to the thallus surface). In cross-sections, mature campylidia appear (Fig. 12) as obliquely raised cupulae, fixed by a large socle (600–700 μm long) and hooded on their upper side by a thick tissue that encompasses the conidial mass. Four different plectenchymatous layers are easily distinguished*.

- (1) The socle and the outer parts (half to two-thirds of the total height) are made of medullary tissue.
- (2) At and around the fold at the upper side of the campylidium, a strongly encrusted dismantled paraplectenchyma with \pm globose cells forms the hood; it is usually separated from the downward part of the hood by a small but distinct furrow; the downward part of the hood is made of long, regular and periclinally arranged hyphae.
- (3) At the inner lowest side of the structure, usually taking up a convex shape, is a layer of short (\pm 15 \times 2 μm) hyphae regularly arranged anticlinally with clavate (to 3–4 μm) apices, thus giving a finely papillose surface (Fig. 10). In mature campylidia this layer appears as a thick lip to the cupula containing the conidiogenous layer and the conidial mass. At its lowest side, this lip is terminated by a mass of irregularly interwoven hyphae containing a few crystals.
- (4) The conidiogenous layer is present on the inner cupulate side and is always covered by the campylidium hood, except in those which are badly damaged; conidiophores simple or branched, made of rectangular cells (\pm 10 \times 4 μm), forming a regularly arranged layer together with the

*All campylidia when seen in cross-section have no symmetry; conventionally the inner side (or part) of a campylidium is the side where the conidia are ejected.

conidiogenous cells and a few (but always present) paraphyses that are inflated ($2-3\ \mu\text{m}$) at the apices; conidial mass usually enormous, accumulated under the hood and orientated downwards towards the fissure that separates the inferior part of the hood and the socle.

Conidia abundantly produced, arising singly at the apices, hyaline, at first filiform and simple, then flexuose and convoluted, $95-115 \times 1.5\ \mu\text{m}$, 11-17-septate with crooks or clasps at both ends and with 5-7 pedicellate ($3-4\ \mu\text{m}$ long) appendages, each terminated by a tiny ($1-2\ \mu\text{m}$ diam) sticky mass, spread along their length.

Examination of campylidium ontogeny clearly demonstrates that they arise from primordia that would otherwise be assigned to immature apothecia. Early stages are impossible to distinguish from immature apothecia. Immature campylidia (i.e. not yet producing conidia) are small cupulae with tissues identical to the well-developed 'excipulum' and 'hamathecium' of immature apothecia, except for the absence of ascogenous hyphae. Young campylidia (i.e. with a few conidia) are slightly raised cupulae with a swollen margin, appearing like malformed apothecia.

The onset of conidium production has not been observed with certainty, despite numerous young campylidia having been sectioned. No doubt it is a rapid process, as the youngest campylidia observed already have numerous conidia (Fig. 11). The same rapidity occurs with ascospore production. This is perhaps not surprising as foliicolous lichens have a short life-expectancy as the leaves on which they grow persist for only 4-6 years. Anyway, the conidiophores and conidiogenous cells appear between the 'excipulum' and the 'hamathecium', or at the expense of the 'hamathecium', along about one-quarter of the inner circumference of the immature 'apothecium' (Figs 7, 8). They proliferate rapidly, and soon produce filiform conidia that remain agglutinated. This mass spreads towards the centre of the 'apothecial disc', pushing the 'hamathecium' that progressively becomes thinner. Simultaneously the 'excipulum' adjacent to the conidiogenous zone is activated: it becomes thicker and forms a cushion-like swelling that spreads towards the centre of the 'apothecium' and over the conidial mass. The hood of the mature campylidium is thus already formed. Soon afterwards, the base of the 'apothecium' (i.e. below the 'hypothecium' at its centre) grows up laterally in a way that lifts the conidial zone. At this moment, this zone has spread to about half the total circumference of the 'apothecium' and the contiguous 'excipulum' has reached its maximum development. The other part of the 'excipulum' tends to disintegrate and lose its typical anatomy.

All the processes described above continue until the structure that is then a typical mature campylidium is produced, especially the upheaval (at maturity the structure can be almost vertical). At maturity, therefore, the campylidium has its conidiogenous zone perched on its upper parts, just under the enormous hood initiated by the contiguous 'excipulum'. The parts of the hood that have spread over the conidial mass towards the centre of the former disc do not amalgamate with the tissue derived from the 'hamathecium'. Thus, a fissure persists between both tissues and is used by the conidia to escape from the campylidium.

It is obvious that, amongst the different tissues making up the campylidium, only the conidiophores and conidiogenous cells do not derive from a tissue present in the young 'apothecium'. The campylidium development can therefore be summarized as in Table 1 and Figs 11 & 12. Such an ontogeny leaves no doubt concerning the true nature of campylidia: they do belong to the lichen on which they grow, and they are highly specialized conidiomata. One might, however, argue that the campylidia are deformed apothecia thwarted from their original objective (production and dispersion of ascospores) by an invading fungus. This fungus would intrude into the apothecium between its excipulum and hymenium, stop the formation of asci, and produce its own conidia. This hypothesis seems unreasonable for two reasons: (1) the very site where the conidiogenous layer starts is hard to reach, even for an infectious agent, and (2) two types of hyphae are not seen at any stage of the development.

TABLE 1. Comparison of the features of immature and mature campylidia in *Badimia pollilensis*

Immature campylidium (identical with immature apothecium)	Mature campylidium
(1) Immature hymenium: reduced to a hamathecium (no asci, only paraphyses present)	(1) Inner and lowest part: tissue made of short hyphae antically arranged with a papillose surface
(2) Hypothecium and medullary tissue below	(2) Basal tissue (making the socle) carrying all the others, present at the base and on the outer part up to half to two-thirds of the total height
(3) Excipulum adjacent to the future conidial zone	(3) Hood of the structure, including the layer of periclinally arranged hyphae covering the conidial mass
(4) Excipulum not adjacent to the future conidial zone	(4) Almost vanished, remnants present at the base of (1)

The conidia produced by the campylidia are very unusual. Vainio (1921: 83) briefly described them as the 'basidiospores' of *Cyphella foliicola*. As far as I am aware, no conidia with crooked ends and with lateral pedicellate gelatinous mass are known in any other group of fungi.

The role of those lateral appendages is unclear. They might act as suckers for the fixation of the conidia on the leaf surface, but of course this cannot be easily demonstrated. It must be noted that these appendages are invisible when the conidia are tightly packed within the campylidia; this is evident when observed in this position with the SEM. Anastomosis of the appendages of two close conidia has also been observed, thus they might also be responsible for the coherence of the conidial mass.

Badimia elegans (Vainio) Vězda

Material studied: **New Guinea:** W of Yoro (= Mugamat), Madang prov., 100–300 m elev., epiphyllous, 1980, *Demoulin* 5937, 5938, 5940 & *Smeets* (LG).

(Figs 1–4, 13–37)

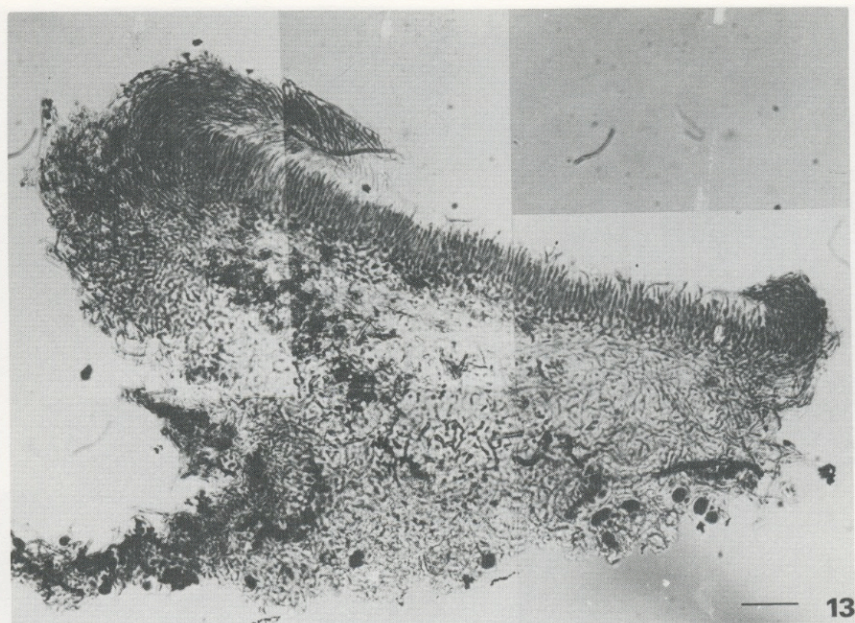
Thallus forming large \pm circular patches, to 4 cm diam, usually continuous, smooth (when not attacked by dematiaceous Hyphomycetes, which is frequent), pale bluish, 20–40 μ m thick, usually with a distinct prothallus made of stretched bunches of hyphae.

Apothecia frequent on thalli that have few, if any, campylidia, 0.4–0.7 mm diam, strongly constricted at the base; disc yellow-orange to orange-brown, brown when old, with a very thin yellowish pruina, slightly concave to plane; margin at first rather thick and prominent, yellow to orange-brown, usually distinctly paler than the disc, covered by a yellow pruina. Excipulum strongly encrusted with yellow-brown crystals; these crystals lose their colour but do not dissolve in 10% KOH, although they dissolve in boiling LCB and can re-crystallize into long yellow needles; excipulum 40–50 μ m thick in lateral parts, much more (up to 80 μ m) in basal parts below the hypothecium, made of long mesodermatous hyphae \pm radiating from the centre of the apothecium, much more irregular in lateral parts where the hyphae become interwoven, more globose and less densely agglutinated (gaps are clearly seen in sections prepared in lactophenol and boiled; these gaps were probably filled with crystals). Hypothecium pale reddish-brown or sometimes almost hyaline, not exceeding 25 μ m in thickness, with a thin layer containing yellow crystals underneath; hymenium 50–60 μ m thick, hyaline or with a few yellow crystals; epithecium seen as a distinct layer of yellow to orange-brown crystals. Paraphyses mostly simple (rarely branched near the base), 1.5 μ m thick, slightly or distinctly inflated at the apices (up to 2.5 μ m), very coherent, hardly separating from each other in 10% KOH; asci clavate, of *Byssoloma*-type, 8-spored; spores fusiform, 3-septate, 11–14 (–16) \times (3–)4–5 μ m, with a distinct halo.

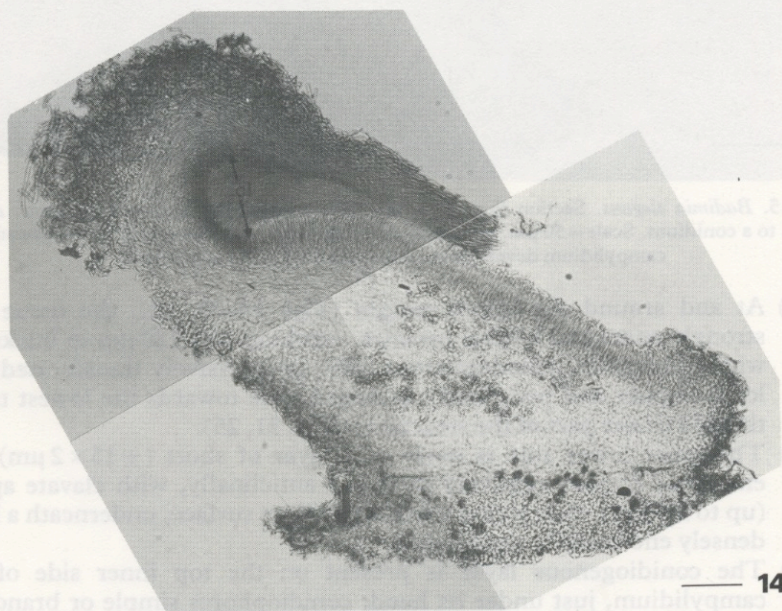
Campylidia frequent on thalli that have few, if any, apothecia, crescent-shaped and erect when mature (Fig. 22), looking like a small funnel, with a thick upper edge, of which one side (about one-third of the total diameter) has been removed; lowest part rather thin and yellow whereas the upper is thicker, with a much coarser surface, and orange-brown; 0.9–1.3 (–1.4) mm wide, up to 0.7 mm deep (when seen from above) and about 0.4–0.6 mm at maximum height (perpendicular to the thallus surface).

Mature campylidia appearing in cross-sections (Fig. 15) as erect, obliquely orientated structures, with a large base (to 400 μ m) tapering towards their summit but folded at about two-thirds of their length like a swan's neck, and thus covering the enormous conidial mass. Four different plectenchymas are distinguishable:

- (1) The socle and the outer parts up to half of the total height are made of medullary tissue slightly encrusted with yellow-brownish crystals (these crystals, as well as those cited below, behave in the same way as those contained in the apothecia) (Fig. 17).



13



14

FIGS 13 & 14. *Badimia elegans*, both sections stained with LCB. 13, Section through an immature (=not yet producing conidia) campylidium. 14, Section through a young (=already producing conidia) campylidium. Both campylidia still have the typical apothecium anatomy; cl = conidiogenous layer. Scales: 13 = 20 μm ; 14 = 50 μm .

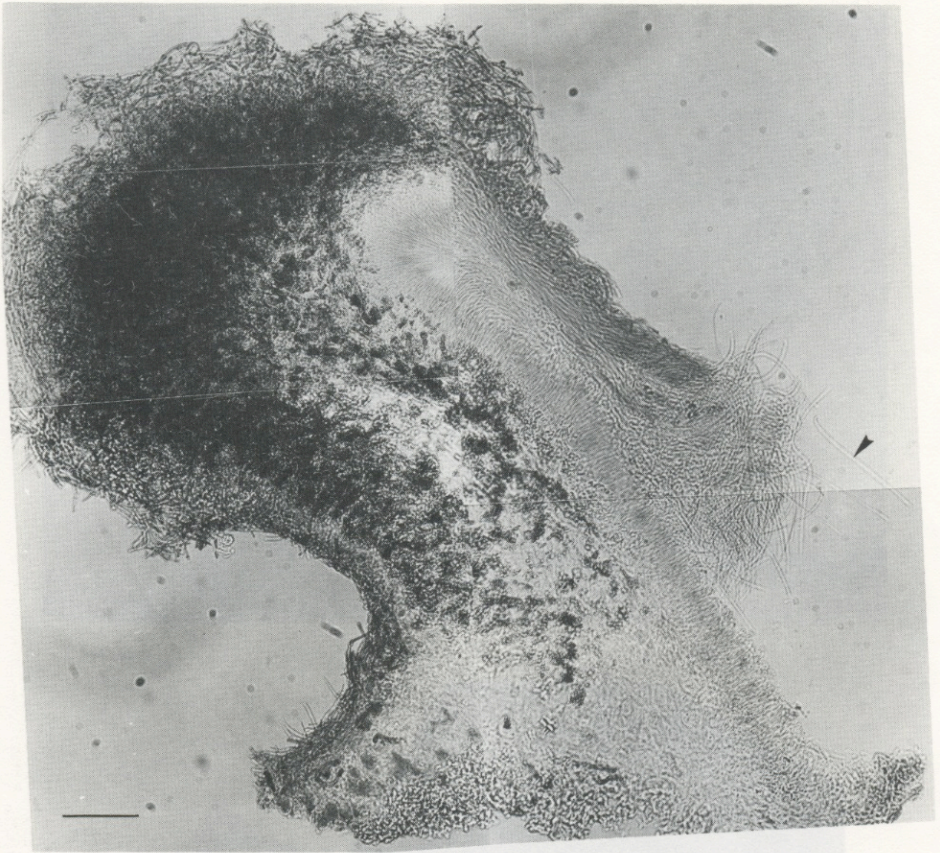
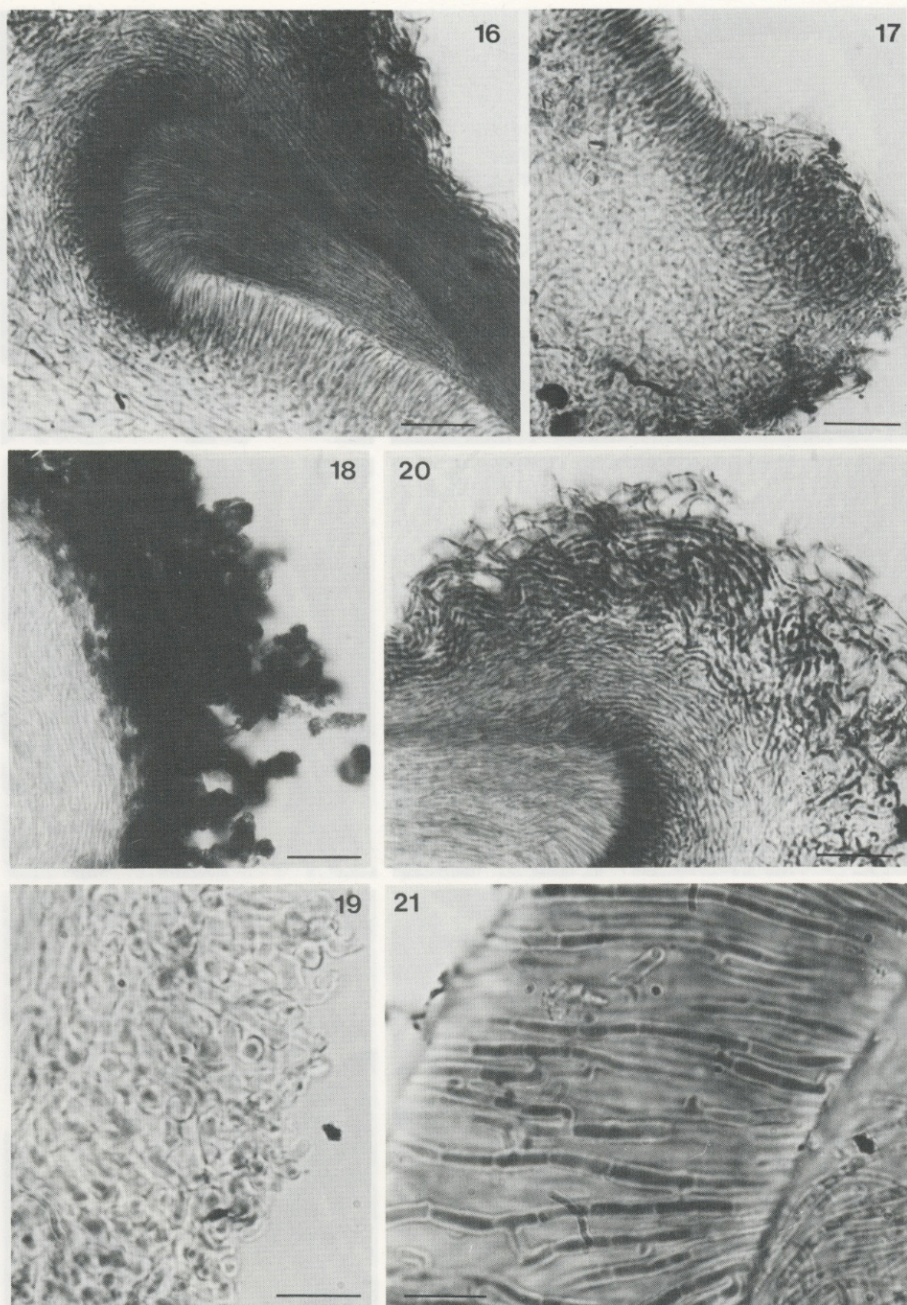
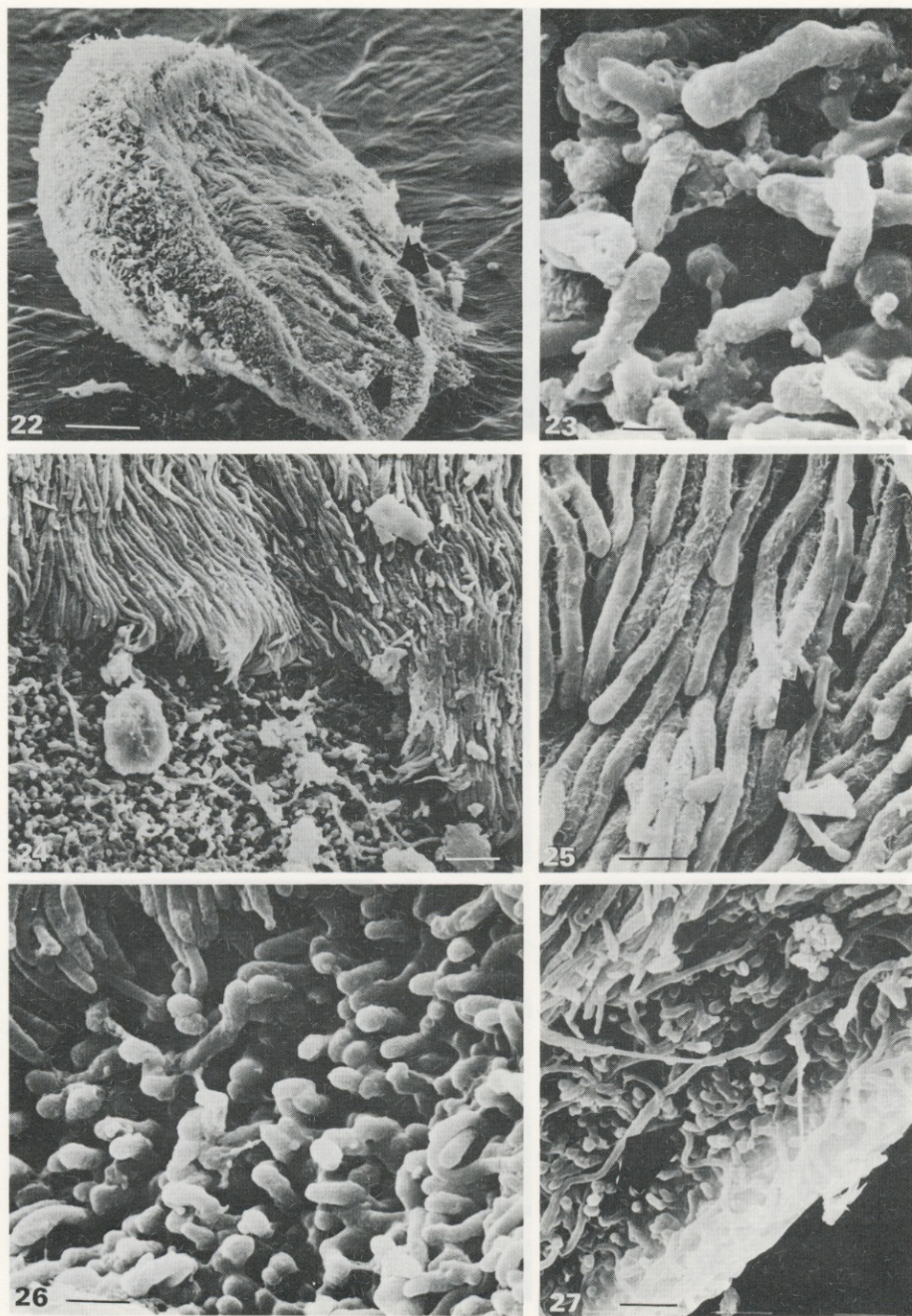


FIG. 15. *Badimia elegans*. Section through a mature campylidium, mounted in water. Arrow points to a conidium. Scale = 50 μm . Note that although Figs 13–15 represent successive steps in campylidium development, the scale for Fig. 13 is different.

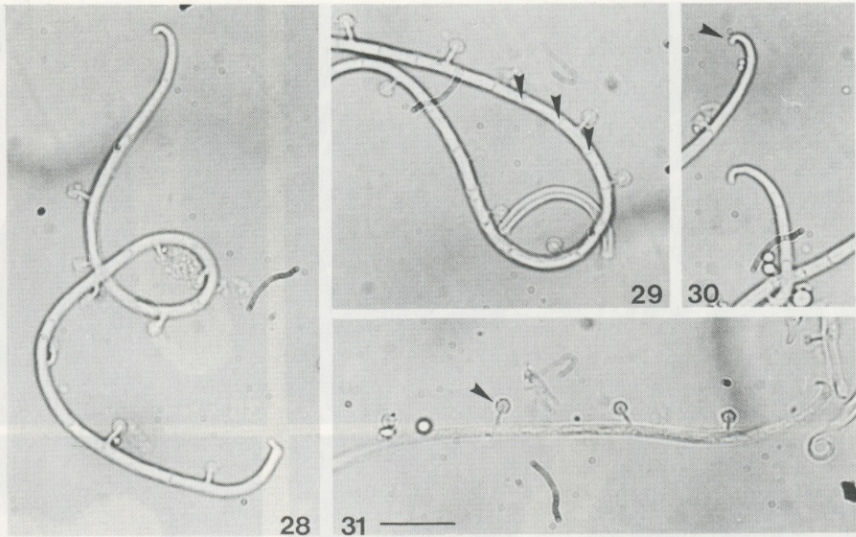
- (2) At and around the upper margin (Figs 18–20, 23), the tissue is a strongly encrusted hyphal network, reaching 100–120 μm in thickness, with \pm elongated leptodermatous cells, progressively transformed into long, regular and periclinally arranged ones towards the lowest tip of the fold (inner part of the structure) (Figs 21, 25).
- (3) The inner lower side is made of a layer of short ($\pm 15 \times 2 \mu\text{m}$) and encrusted hyphae regularly arranged anticlinally, with clavate apices (up to 3.5 μm), thus giving a finely papillose surface; underneath a layer densely encrusted is clearly seen.
- (4) The conidiogenous layer is present on the top inner side of the campylidium, just under its hood; conidiophores simple or branched, made of rectangular cells (9–10 \times 4 μm), forming a regularly arranged layer together with the conidiogenous cells and a few paraphyses inflated (2.0–2.5 μm) at their apices; conidial mass notable, oriented downwards towards the fissure (Fig. 16).



FIGS 16–21. *Badimia elegans*, all sections, except 18, stained with LCB; 18 mounted in water. 16, Detail view of the conidiogenous layer in a young campyloidium. 17, Detail view of the base of the ‘excipulum’, not adjacent to the conidiogenous layer, of a young campyloidium; also seen here is the medullary tissue that makes the socle of the structure. 18, View of the ‘excipulum’, adjacent to the conidiogenous layer, of a young campyloidium, as mounted in water; the hyphae are encrusted with crystals (black). 19, Same as 18 but after mounting in LCB and boiling; the hyphae are \pm globose to elongated. 20, View of the ‘excipulum’ of a young campyloidium over the conidiogenous layer; the hyphae are distinctly elongated. 21, View of the long periclinally arranged hyphae that form the campyloidium hood over the conidial mass. Scales: 16, 17, 20 = 20 μ m; 18, 19, 21 = 10 μ m.



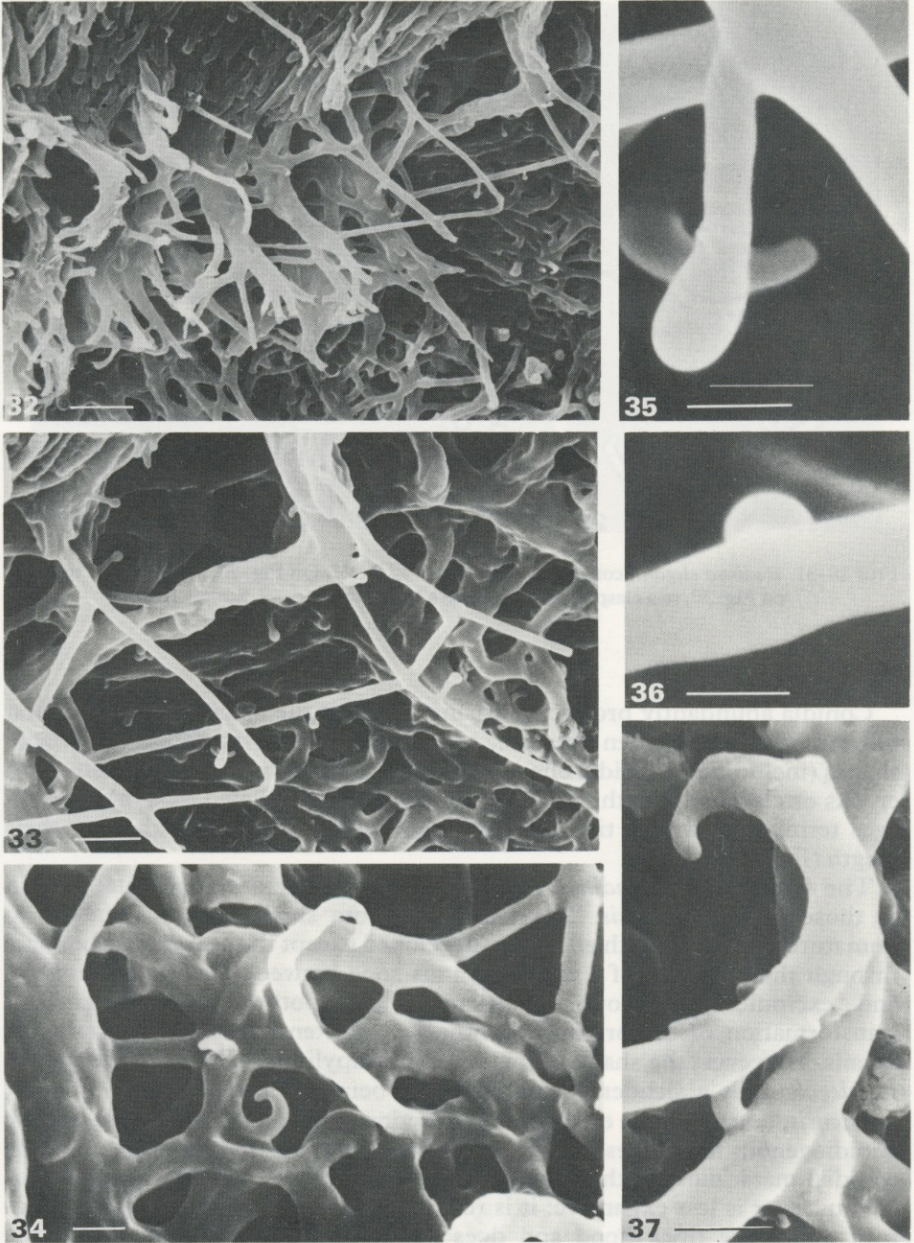
FIGS 22–27. *Badimia elegans*. 22, General lateral view of a mature campyloidium; this specimen is rather unusual as it does not have a crescent shape; arrows point to the fissure through which conidia extrude. 23, Detail view of the hyphae of the upper podgy part of a mature campyloidium (same hyphae as in Fig. 19). 24, Detail view of the fissure of an immature campyloidium; hood of periclinally arranged hyphae (above) and layer of anticlinally arranged hyphae (below). 25, Closer view of the periclinally arranged hyphae of Fig. 24 (same hyphae as in Fig. 21); arrows point to a conidium. 26, Closer view of the anticlinally arranged hyphae of Fig. 24. 27, Detail view of the lower margin of a mature campyloidium; arrows point to conidia. Scales: 22 = 200 μ m; 23 = 2 μ m; 24 = 20 μ m; 25, 26 = 5 μ m; 27 = 10 μ m.



FIGS 28–31. *Badimia elegans*, conidia mounted in 10% KOH. On Fig. 29, arrows point to septa; on Fig. 30, to a clasper; on Fig. 31, to a lateral appendage. Scale = 10 μ m.

Conidia abundantly produced, arising singly at the apices, hyaline, at first filiform and simple, then flexuose, convoluted and wavy, adopting variable shapes (including helicoidal ones), 110–120 \times 1.5–2.0 μ m, 11–17-septate, with crooks or claspers at both ends and 5–9 shortly pedicellate (2–3 μ m) appendages terminated with a tiny (1–2 μ m diam) sticky mass, spread along their length (Figs 28–37).

The campylidia of *Badimia elegans* follow the same developmental pattern as those of *B. pollilensis*. They originate from small cupules identical to immature apothecia (with all tissues developed except the ascogenous hyphae) through the initiation of a conidiogenous zone between the 'hamathecium' and 'excipulum' on about one-quarter of the 'apothecium' diameter. The transformation of the original 'apothecial' plectenchymas is similar in all details. However, the shape of the mature campylidia is slightly different: in *B. elegans* it is a slender structure, never being 'corpulent' as it is in *B. pollilensis*, due to a more exuberant production of conidia. In *B. pollilensis*, the conidiogenous layer lines the bottom of a large cupule that occupies, with the conidial mass, most of the campylidium volume. In *B. elegans*, the conidiogenous layer is less expansive: it is restricted to the upper parts of the structure under the thick hood and does not hollow out a cupule within the campylidium. Of course a further difference between the campylidia of these two species is their colour (pale orange in *B. pollilensis* and yellow-brown in *B. elegans*), which is also the major difference between their apothecia. The conidia themselves provide a further diagnostic criterion: they tend to be longer and their lateral appendages smaller in *B. elegans*.



FIGS 32–37. *Badimia elegans*, conidia as seen in SEM. 32, Conidial mass as seen near the fissure of a mature campylidium. 33, Detail view of the upper right portion of Fig. 32. 34, Detail view of a compact conidial mass. 35 & 36, Detail view of the lateral appendages. 37, Detail view of a conidium clasper; note the anastomosis of two conidia via their lateral appendages. Scales: 32 = 10 μ m; 33 = 5 μ m; 34, 37 = 2 μ m; 35, 36 = 1 μ m.

The campylidia of *Sporopodium phyllocharis* (Mont.) Massal.

(Figs 38–50)

Sporopodium Mont. comprises four species of exclusively foliicolous lichens and was monographed in a masterly manner by Santesson (1952). Even sterile, *Sporopodium* is easily identified by its thallus structure; as described by Santesson, the upper part 'consists of globose cells of different sizes which are irregularly arranged and not formed into any distinct layer' (Fig. 41). Such cells are also seen on the lowest parts of the excipulum; this is very characteristic of the genus.

All described species are said (Santesson 1952: 40–41) to bear *Pyrenotrichum irregulare* R. Sant. *nom. nud.* of which the only available diagnostic detail is the production of pyriform, simple or 1-septate conidia. All campylidia observed by me on *Sporopodium* thalli produce simple or 1-septate, pyriform to lacrimiform conidia, sometimes with one end truncated. They most probably represent what Santesson had in mind when mentioning *P. irregulare*.

I concentrated my study on *Sporopodium phyllocharis*, the only species of which I had enough material. Campylidia here do not ontogenetically derive from apothecia (whose ontogeny is very well documented by Henssen 1981: 178–181, plates 10.30, 10.31 & 10.32; results confirmed by my studies). I will therefore concentrate on the campylidia here.

Material studied: **New Guinea:** W side of Manam Island, above Jogari, Madang prov., \pm 400 m elev., epiphyllous, 1980, *Demoulin* 5860 & *Smeets* (LG).

Thallus forming \pm regular patches, to 1 cm diam, much more when thalli become contiguous, pale blue to \pm greenish blue, farinose and slightly verrucose, extending on a filamentous radiating white prothallus which is always conspicuous.

Campylidia very abundant and regularly distributed over the thallus surface (Fig. 39), 0.2–0.3 mm broad (at the base) and rarely more than 0.35 mm in total height, pale brown with a \pm conspicuous orange tinge, sometimes with white pruina (mainly near the base), appearing as small hoods covering tiny but rather deep cupules that are fringed, at their lower side, by a platform. This platform is oblique or almost vertical in mature campylidia and is turned up at its lower side; these campylidia recall the ventilating-pipes of a steamer or the periscopes of submarines.

The campylidium is roughly composed of two parts (Fig. 38): a pyriform cavity included into a socle and connected through a narrow canal to the upper lateral 'mouth' of the structure. The existence of a tube and not of a fissure is easily demonstrated by serial cross-sections; the contact between the cavity and the mouth is seen only in sections made in the median plane. The campylidium usually has a distinct socle (sometimes forming a small cushion at the base) filled with large amounts of crystals, containing several algal cells and with a surface typical of the genus (globose cells).

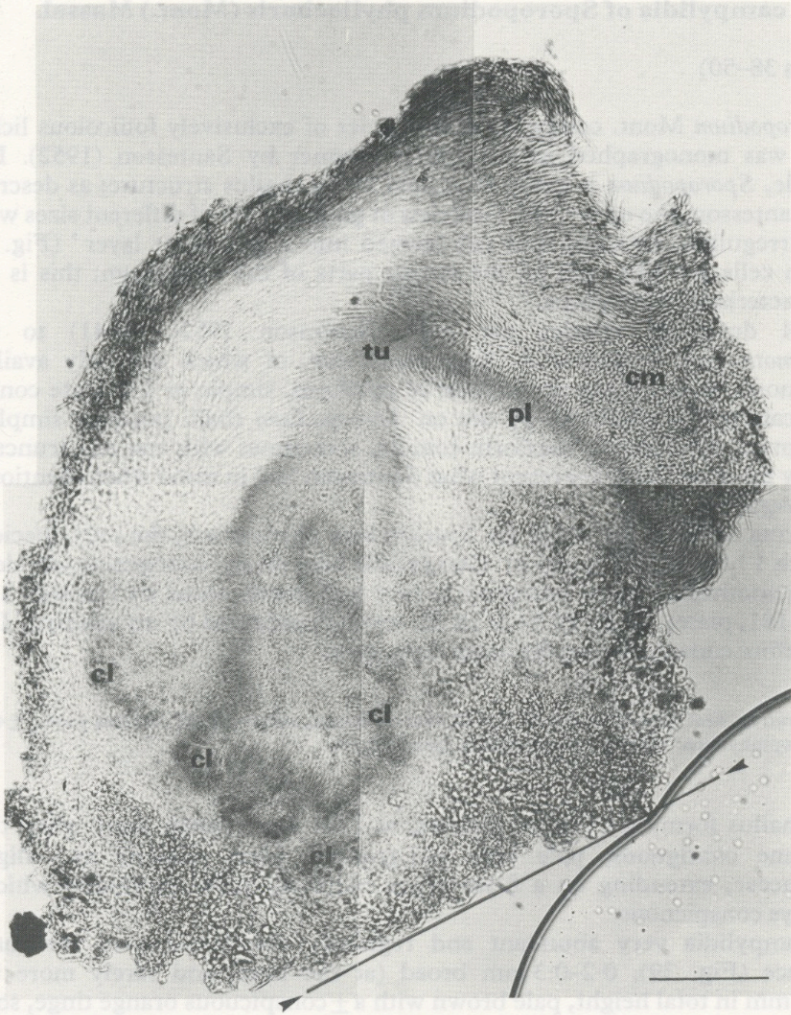
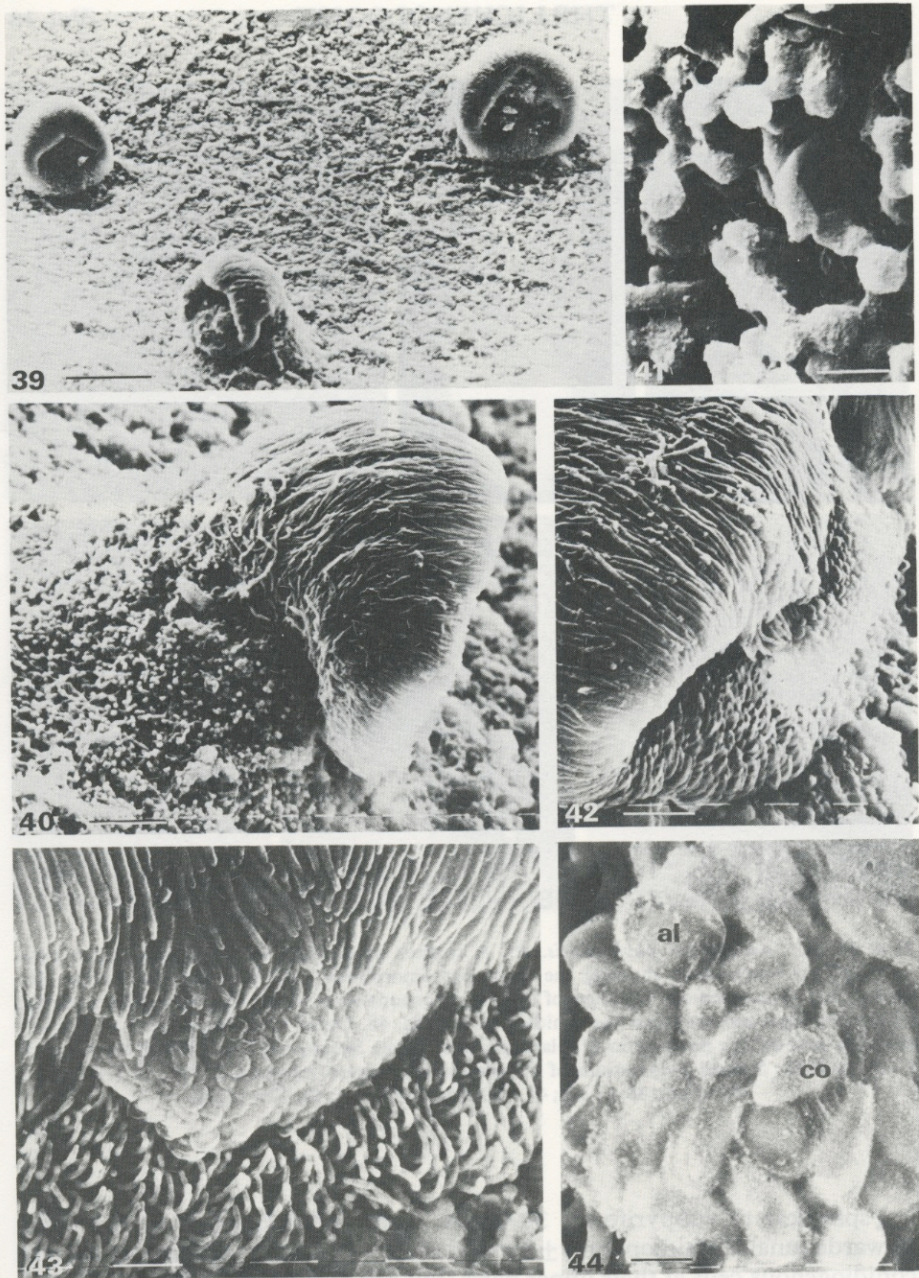
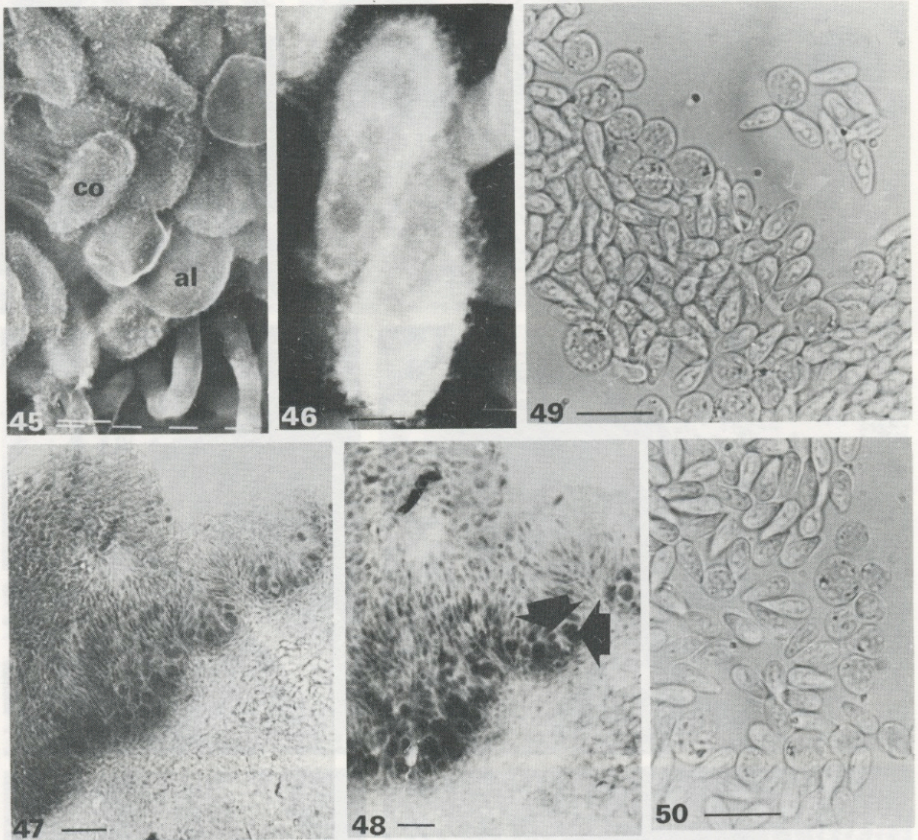


FIG. 38. *Sporopodium phyllocharis*, cross-section through a mature campylidium, mounted in LCB. The line indicated by two arrows represents the surface of the leaf on which the campylidium grows; cm = conidial mass; cl = conidiogenous layer; tu = tube joining the conidiogenous cavity with the outside; pl = platform of anticlinally arranged hyphae. Scale = 50 μ m.

Hood made of rather regularly periclinally arranged long hyphae, with a thin but coloured outer wall; terminal part (the part covering the mouth of the structure) more brittle because of the more loosely agglutinated hyphae. The platform is made of very regularly anticlinally arranged hyphae, simple but with distinct anastomoses, leptodermatous and not inflated at the apices. The cavity is multilocular and lined with the conidiogenous layer. Each locule



FIGS 39–44. *Sporopodium phyllocharis*. 39, General view of three mature campylidia on a thallus surface. 40, Lateral view of a mature campylidium, showing the hood of periclinally arranged hyphae (right) and the base covered by typically globose cells (left). 41, Closer view of the thallus surface. 42 & 43, Upper detail views of the conidia–algae globose mass at the mouth of the structure. On Fig. 43, the periclinally arranged hyphae of the hood are above and the anticlinally arranged hyphae of the platform are below. 44, Closer view of the conidia–algae mass; al = alga; co = conidium. Scales: 39 = 200 μm ; 40 = 50 μm ; 41 = 5 μm ; 42 = 20 μm ; 43 = 10 μm ; 44 = 2 μm .



FIGS 45–50. *Sporopodium phyllocharis*. 45, A further detail view of the conidia–algae mass (al=alga; co=conidium), showing the arachnoid amorphous layer covering the conidia. 46, Closer view of two conidia. 47, View of the conidiogenous layer within the campylidium cavity, with many algal cells between the conidiogenous cells. 48, Detail view of a portion of Fig. 47, showing (arrows) the production of aplanospores by algae. Sections in Figs 47 & 48 stained with LCB. 49 & 50, Squash preparations of the conidia–algae mass, mounted in 10% KOH. Scales: 45 = 2 μ m; 46 = 1 μ m; 47 = 20 μ m; 48 = 10 μ m; 49, 50 = 10 μ m.

is \pm spherical to subpyriform, 30–80 μ m diam and connected to the main upwards canal. Conidiophores \pm rectangular, \pm 10 \times 3 μ m, supporting several conidiogenous cells at their upper parts (but not necessarily at the same level) as well as 0–2 paraphyses. Paraphyses reaching 20–25 \times 1–2 μ m, always emerging from the top of conidiophores; as their bases are inflated and colarette remain, they are apparently proliferations of old, no longer functioning, conidiogenous cells. It seems unlikely that what I describe as ‘paraphyses’ represent a second type of conidium as they are not present in the conidial mass at the mouth of the campylidium.

Conidia abundantly produced, arising singly at the apices of conidiogenous cells, pyriform to \pm lacrimiform with the proximal (relatively to the conidiogenous cell) end truncated, $5-7 \times 2.5-3.5 \mu\text{m}$, hyaline, simple or 1(-3)-septate (usually only the first septum is complete; the two others are not always present and are due to the thickening of the inner wall which thus mimics septa). Conidia with an arachnoid amorphous layer on their outer surface (when seen with the SEM, Fig. 46), agglutinated at the opening of the canal into a sticky globose mass that also contains algae (see below) (Figs 42-45).

Conidiogenesis not studied in detail but probably following this pattern: first holoblastic conidial ontogeny, septum delimitation, schizolytic secession, enteroblastic conidiogenous cell proliferation followed by another holoblastic conidial ontogeny; two colarettes being the maximum observed: afterwards the conidiogenous cell degenerates into paraphysis production.

Algae present within the conidiogenous layer (Figs 47, 48) not in great quantities but always seen, as green spherical cells (6-8-10 μm diam, producing aplanospores which are evacuated to the mouth of the campylidium together with the conidia; they are clearly seen in squash preparations of the conidial ball (Figs 49, 50) as well as on its surface (when seen in SEM, Figs 44, 45).

Nothing in the structure of the campylidia described above indicates that they belong to the lichen thallus on which they grow, especially as they are abundant on thalli devoid of apothecia. One could thus infer a depressing effect from the invading fungus producing the campylidia. However, as already stated in the first section, this observation—very frequent with *Sporopodium*—can be interpreted as the limited resources of the fungus being expended on asexual rather than sexual reproduction. Moreover, the base of the campylidium has a surface very typical of *Sporopodium* (globose cells; Fig. 40). But by far the most convincing argument to assign these campylidia to the lichen carrying them is the photobiont presence in the conidiogenous layer and in the conidial mass at the campylidium mouth. Such a dispersal strategy would hardly be expected in a non-lichenized fungus. As far as studies with a light microscope on herbarium material can tell, the algae in the campylidia and in the thallus are the same. Finally, one should not forget that the alga is also present in the epithecium where it undergoes the same development pattern, i.e. the production of aplanospores. Henssen (1981: 181) was unable to demonstrate that the epithecial algae are dispersed with the ascospores, and I can confirm her statement. With conidia, the situation is different as both partners are agglutinated into the same mass at the campylidium mouth. The dispersal from a campylidium of conidia and algae agglutinated together has already been described by Malme (1935), but in different conditions. Malme observed long conidia individually wrapped over a single algal cell; as far as I know, no further study has ever been attempted on the campylidia of the species involved, *Lopadium perpallidum* (Nyl.) Zahlbr.

I cannot demonstrate any ontogenetical link between the apothecia and the campylidia in *Sporopodium*. The campylidia begin as small thalline verrucae and develop their complex structure without any homology with apothecia.

The campylidia of *Loflammia demoulinii* Sérusiaux

(Figs 51–60)

This new species, formally described below, is closely related to *L. flammea* (i.e. *Lopadium flammeum*). It is rather abundant in New Guinea and is here used to describe the campylidia referred to *Pyrenotrichum bicolor* R. Sant. *nom. nud.* The following observations were made from the holotype material.

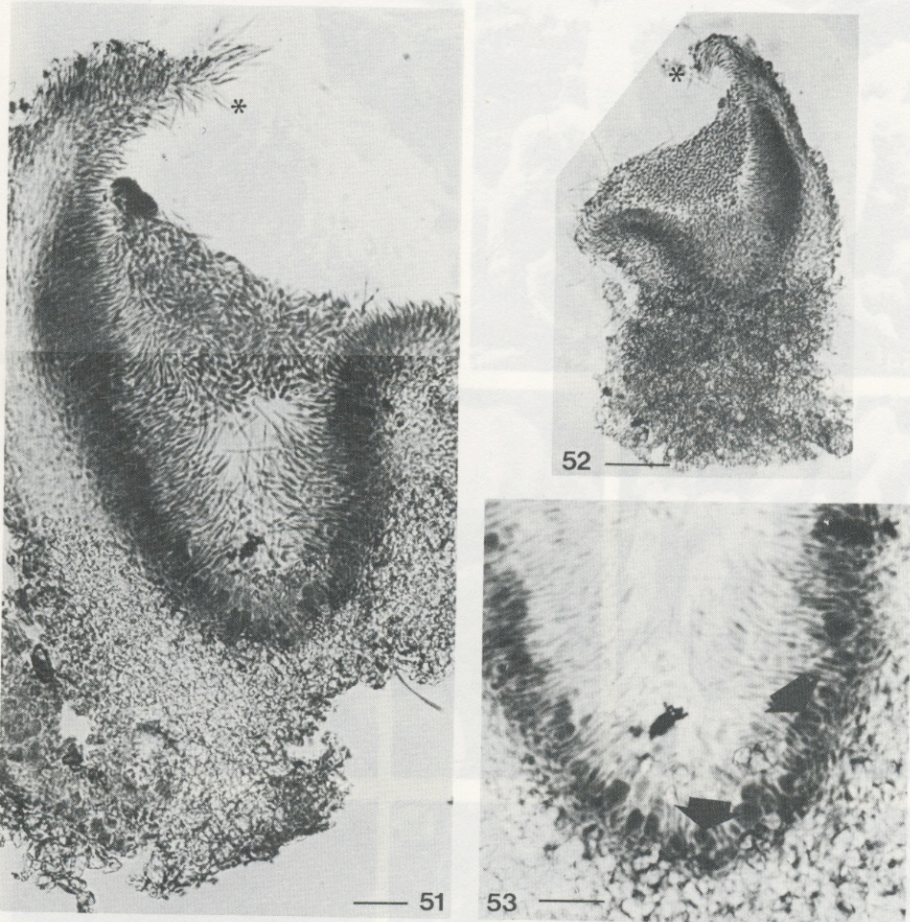
Campylidia usually very numerous and regularly distributed over the thallus surface, in habit very similar to those of *Sporopodium phyllocharis* as they are small hoods covering tiny cupules fringed at their lower side by a \pm horizontal platform (Figs 51–55). The socle is almost cylindrical (140–180 μm diam, measure taken near the base) and rather high (80–120 μm), strongly encrusted with angular crystals but nevertheless covered, at least in parts, by a hyphal layer containing algae. In the middle part, the socle is hollowed into a large funnel lined by the conidiogenous layer. On one side, the socle is extended by a long inclined hood (reaching 140–180 μm , measured from the socle top) and on the other side by a \pm horizontal platform. Hence the whole structure has the shape of a large, laterally open, funnel overtopped by a long hood. At its base the hood is 25–40 μm thick and is typically paraplectenchymatous (cells angular to isodiametric, 3–5 μm , mesodermatous) but, progressively upwards, the cells get longer and are periclinally orientated. At the tip, these hyphae have a thinner wall and are less agglutinated, recalling a 'paint-brush'. The conidiogenous layer lines the bottom of the funnel up to half the height of the hood and up to the inner margin of the platform. Above this conidiogenous zone remain only paraphysis-like hyphae (long, simple hyphae with non-inflated apices; Fig. 56); they line the whole inner part of the campylidium up to the hood tip where they participate in the hyphal-brush formed by the campylidium wall. On the lower platform, these hyphae are anticlinally arranged and form a compact layer; as they are rounded (but not inflated) at the apices, they give the surface a papillose aspect.

Conidiophores simple or branched, rectangular, 10 \times 3–4 μm , with 1–2 conidiogenous cells on their apices and usually a long (maximum measured: 40 \times 1 μm) paraphysis, laterally implanted a few micrometres under the apex. Conidiogenous cells rectangular but usually inflated near the base.

Conidia abundantly produced, arising singly at the apices of the conidiogenous cells, ellipsoid to obovoid, with their proximal part more tapering and their distal more rhomboidal, simple, 5–9 \times 1.5–2.0 μm , with a discontinuous granulate-arachnoid amorphous layer on their outer surface (when seen with the SEM; Figs 57–60).

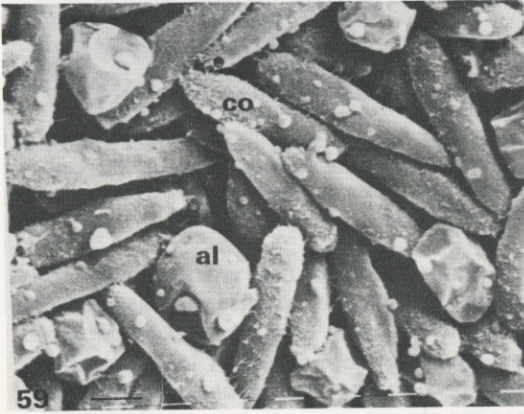
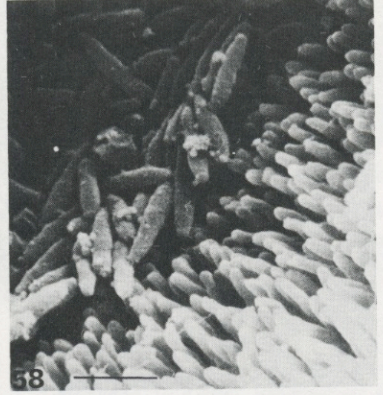
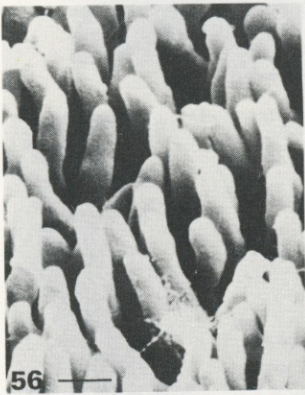
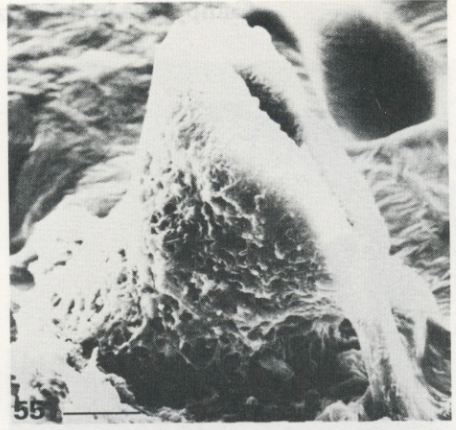
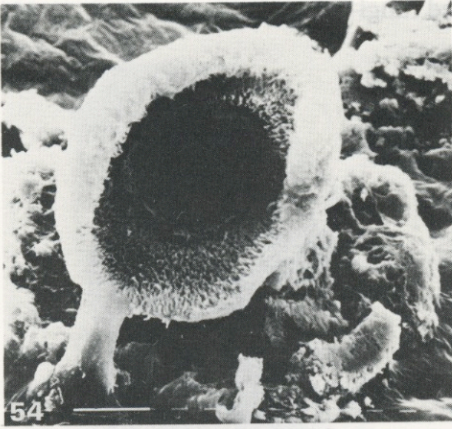
In most of the campylidia examined, algae (identical to those of the thallus) are present between the conidiophores where they undergo active cell division: small chains of 2–4 cells have been observed (Fig 53).

The campylidia of *Loflammia demoulinii* can be regarded as small funnels laterally open and set into a crystal-encrusted socle. Their morphology is not far removed from that of normal pycnidia. Most lichen species have ostiolate conidiomata (pycnidia), immersed or not in the thallus. The particularity of



FIGS 51–53. *Loflammia demoulinii*. Cross-sections of a mature campylidium, stained with LCB. On Fig. 53, arrows point to the aplanospore-producing algae that are present in the conidiogenous layer. On Figs 51 & 52, the 'paint-brush' of the summit is indicated by a star. Scales: 51, 53 = 20 μm ; 52 = 50 μm .

the pycnidia of species like *Loflammia demoulinii* is that they are not ostiolate but funnel-shaped. Nothing in their structure, however, justifies their assignment to an invading fungus instead of to the lichen itself. The conidia of *Loflammia demoulinii* accumulate at the funnel opening, sometimes in large numbers. Contrary to those of *Sporopodium phyllocharis*, they are not agglutinated into a compact guttule (Figs 58, 59). Algae are always present amongst the conidia, as spherical green cells, 3–5 μm . They most probably derive from the algae present in the conidiogenous layer of the campylidium, but they could also originate from the environment. Such wide open campylidia can easily act as efficient collectors of any diaspores present at the leaf surface and it is not rare to see more than 10 different spores, conidia, pollen grains or even remains of the conidial masses of *Asterothyriaceae* hyphophores in the campylidium.

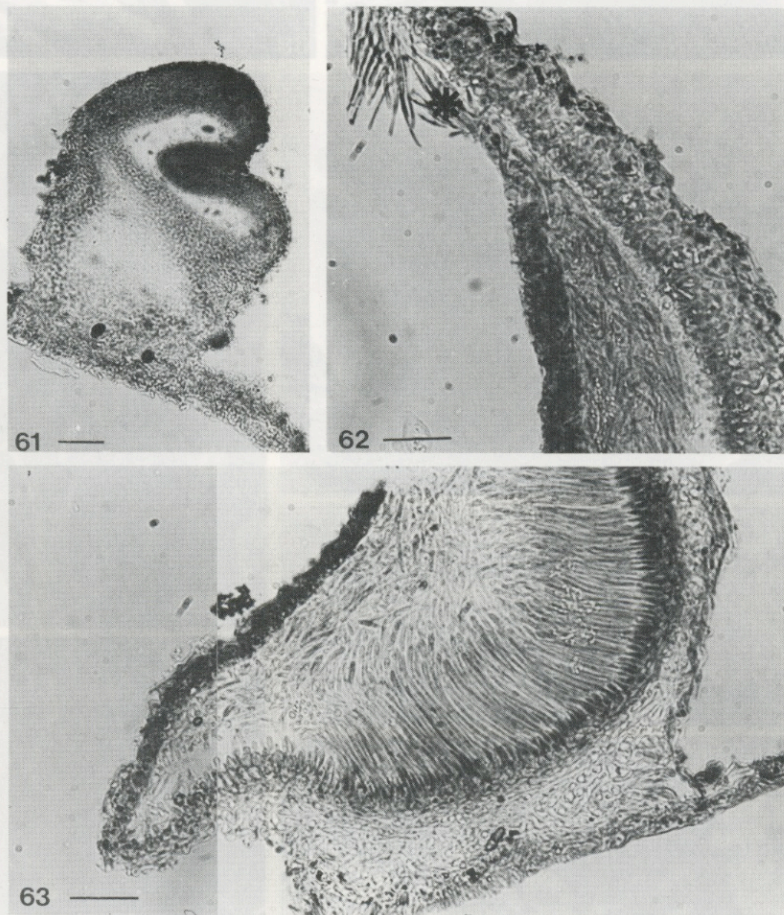


FIGS 54–60. *Loflammia demoulinii*. 54, 55, Front and lateral view of a mature campylidium; the 'stake' that seems to support it is an artefact. 56, Detail view of the anticlinally arranged hyphae of the platform. 57, Detail view of a conidiogenous cell. 58, Detail view of the conidia lying on the platform of the campylidium. 59, Closer view of a portion of Fig. 58, showing algae (al) and conidia (co). 60, Closer view of the conidial surface with their granulate-arachnoid surface. Scales: 54,55 = 50 μm ; 56,59 = 2 μm ; 57,60 = 1 μm ; 58 = 10 μm .

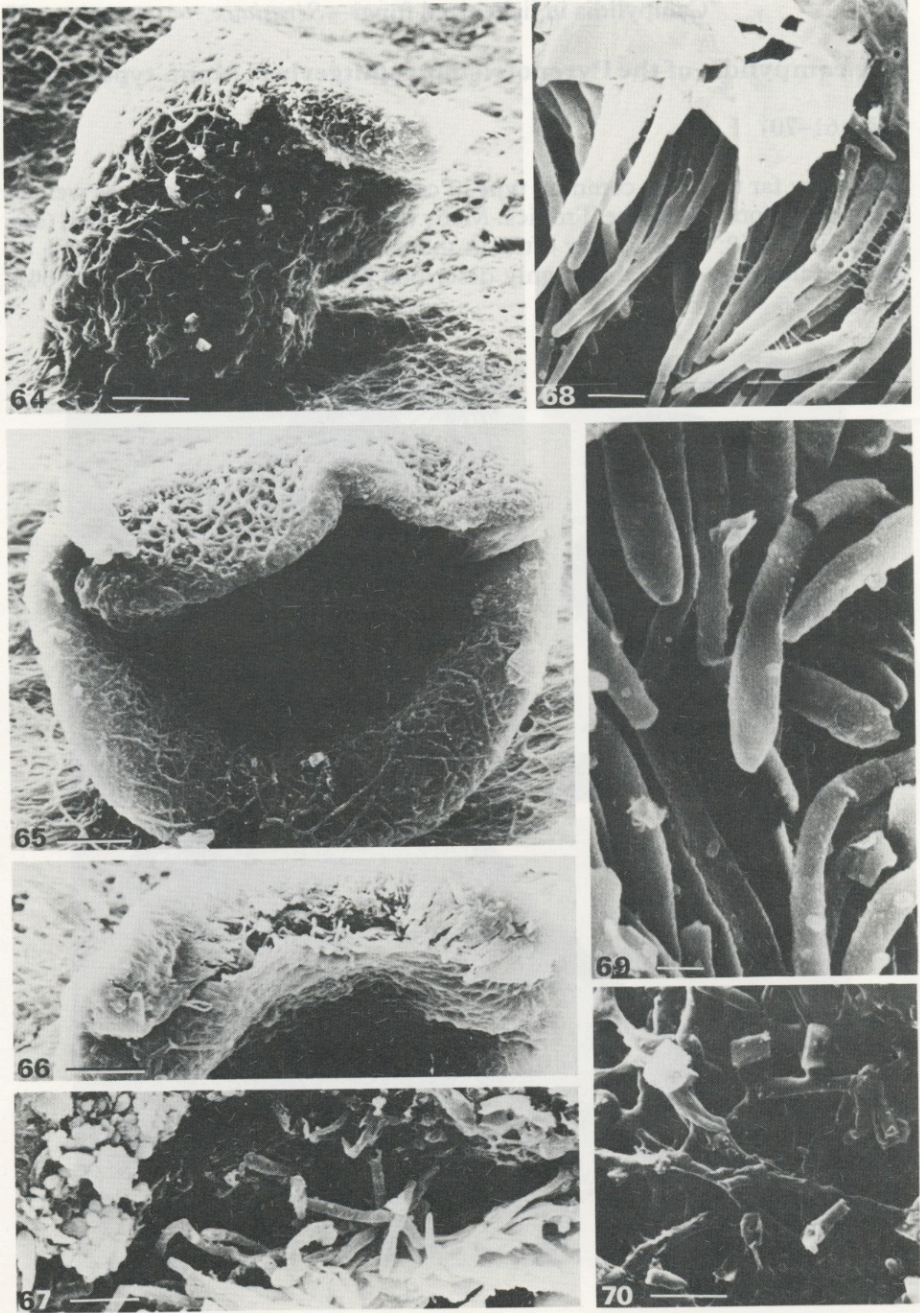
The campylidia of the *Pyrenotrichum splitgerberi* Mont. type

(Figs 61–70)

This is by far the most common type of campylidia found on leaves as well as on bark and on rock in the Tropics. Many different species produce them (see Santesson 1952: 40–41), very often in the absence of apothecia. This type of campylidium has been thoroughly described by Hawksworth (1981: 59–64),



FIGS 61–63. Campylidia of the '*Pyrenotrichum splitgerberi*' type. All sections stained in LCB. 61, Cross-section of an immature campylidium, showing the typical flat goatskin shape of the structure. 62, Cross-section of the upper parts of a campylidium, showing the upper 'paint-brush' and the crack (star) through which conidia can escape the structure. 63, Cross-section of the base of the same campylidium as in Fig. 62, showing that the structure is entirely closed. Scales: all = 20 μ m.



FIGS 64-70. Campylidia of the '*Pyrenotrichum splitgerberi*' type. 64, Lateral view of a mature campyloidium, showing the arachnoid outer surface. 65, Front view of an almost mature campyloidium, not yet fully developed. 66, Upper front view of the crack appearing near the campyloidium summit (see also Fig. 62). 67, Detail view of a portion of Fig. 66, showing the conidia emerging through the crack. 68, Detail view of the 'paint-brush' of a campyloidium summit (see on Fig. 62 for the position of this 'paint-brush'). 69, Detail view of the conidia. 70, Detail view of the arachnoid outer surface of a campyloidium. Scales: 64-66 = 50 μ m; 67, 70 = 10 μ m; 68 = 5 μ m; 69 = 2 μ m.

and the only emendation I wish to make is that the conidiogenous layer remains entirely confined within the structure (Fig. 63). Indeed the young campylidium first appears as a socle topped by a flat goatskin-shaped cavity (Fig. 61). In cross-section, the cavity has the shape of a flattened crescent. At this stage there is no contact between the cavity and the atmosphere. The conidiogenous layer develops on the inner concave part of the cavity and on both sides a layer of anticlinally arranged hyphae with rounded apices occurs. As its walls grow, the cavity stretches upwards. The arachnoid tissue that carries the conidiogenous layer (i.e. the concave side) differentiates into an inner paraplectenchymatous part and an outer part that remains arachnoid. Meanwhile the tissue on the other, convex, side of the cavity remains thinner and does not undergo differentiation. In old specimens, the differentiated wall tends to bend over the structure. Most herbarium specimens have inclined-geniculate or even appressed campylidia; this is an artefact due to the pressing of the leaves on which those lichens live during curation. Better curated collections have erect or slightly bent campylidia (confirmed by field observations). The non-differentiated wall does not grow upwards as fast as the differentiated one; a longitudinal crack consequently appears near the summit (Figs 62, 66) and the conidia that accumulate into the cavity can escape from the campylidium through this; this is hard to demonstrate on herbarium material but seems most probable. In any event, the non-differentiated wall is more fragile and is lacking in old campylidia.

The conidia produced by campylidia with this morphology belong to two different types:

- (1) Conidia simple, filiform to arcuate, slightly clavate, 5–8 septate, $50\text{--}80 \times 2\text{--}3 \mu\text{m}$. Campylidia with such conidia are referable to '*Pyrenotrichum splitgerberi* Mont.' and are typical of the genera *Tapellaria* Müll. Arg. and *Calopladia* Vězda.
- (2) Conidia branched (2–4 branches arising at a single locus about halfway along the conidium, arms at acute angles), $60\text{--}80 \times 2\text{--}3 \mu\text{m}$. Such campylidia represent '*Pyrenotrichum staurosporum* (Keissler) R. Sant.', illustrated and described by Hawksworth (1981: 63–64), and are produced by the genus *Lasioloma* R. Sant. alone.

Nothing in the ontogeny or in the structure of these campylidia proves that they belong to the lichen on which they grow, except that it is impossible to distinguish two types of hyphae, which would be the case if there were parasymbiotic coelomycete invading the lichen. I am consequently inclined to believe that these structures are also a part of the lichen itself.

Material studied in detail:

'*Pyrenotrichum splitgerberi*': **U.S.A.:** Louisiana, Fricke's Cave, S of Franklinton, boggy hardwood forest, 1976, *Sérusiaux* 1805 [associated with *Calopladia puiggarii* (Müll. Arg.) Vězda] (LG).—**New Guinea:** Madang prov., between Bunapas Mission and Bunapas, rain forest at sea-level, 1980, *Demoulin* 5912 & *Smeets* (no apothecia seen) (LG).

'*Pyrenotrichum staurosporum*': **Zaire:** Kivu, Irangi, IRSAC reserve on the right side of the Luhoho river, 850 m, rain forest, on leaves of *Brazzea longipedicellata*, 1972, *Lambinon* 72/20 [associated with *Lasioloma arachnoideum* (Krempelh.) R. Sant.] (LG).

The campylidium of an unknown New Zealand species

Material studied: New Zealand: Coromandel Peninsula, Castle Rock Scenic Reserve, on a fern, 1982, Bartlett 18893 (LG).

(Figs 71–79)

This collection of foliicolous lichens from New Zealand includes a curious type of campylidium described below, although I am unable to assign it to a precise species or even genus at this time. Indeed these campylidia have a conidiogenous layer located in their upper half and, when mature, are totally exposed to the air; this is not the case in the four types described above. Besides these campylidia, the only collection so far available contains *Porina semecarpi* Vainio, a most probably undescribed species of *Trichothelium*, *Byssoloma leucoblepharum* (Nyl.) Vainio and *Bacidia subundulata* (Stirton) R. Sant. (i.e. *Byssoloma subundulatum* (Stirton) Vězda).

The campylidia grow on thalli identical to those connected with the apothecia of *Bacidia subundulata* but with the material available it has been impossible to see the campylidia and the apothecia on the same thallus. In *B. subundulata*, the apothecia are hypophyllous and are connected with an epiphyllous thallus via a hyphal network growing over the leaf margin (see Santesson 1952: 453–455). The campylidia described here are epiphyllous.

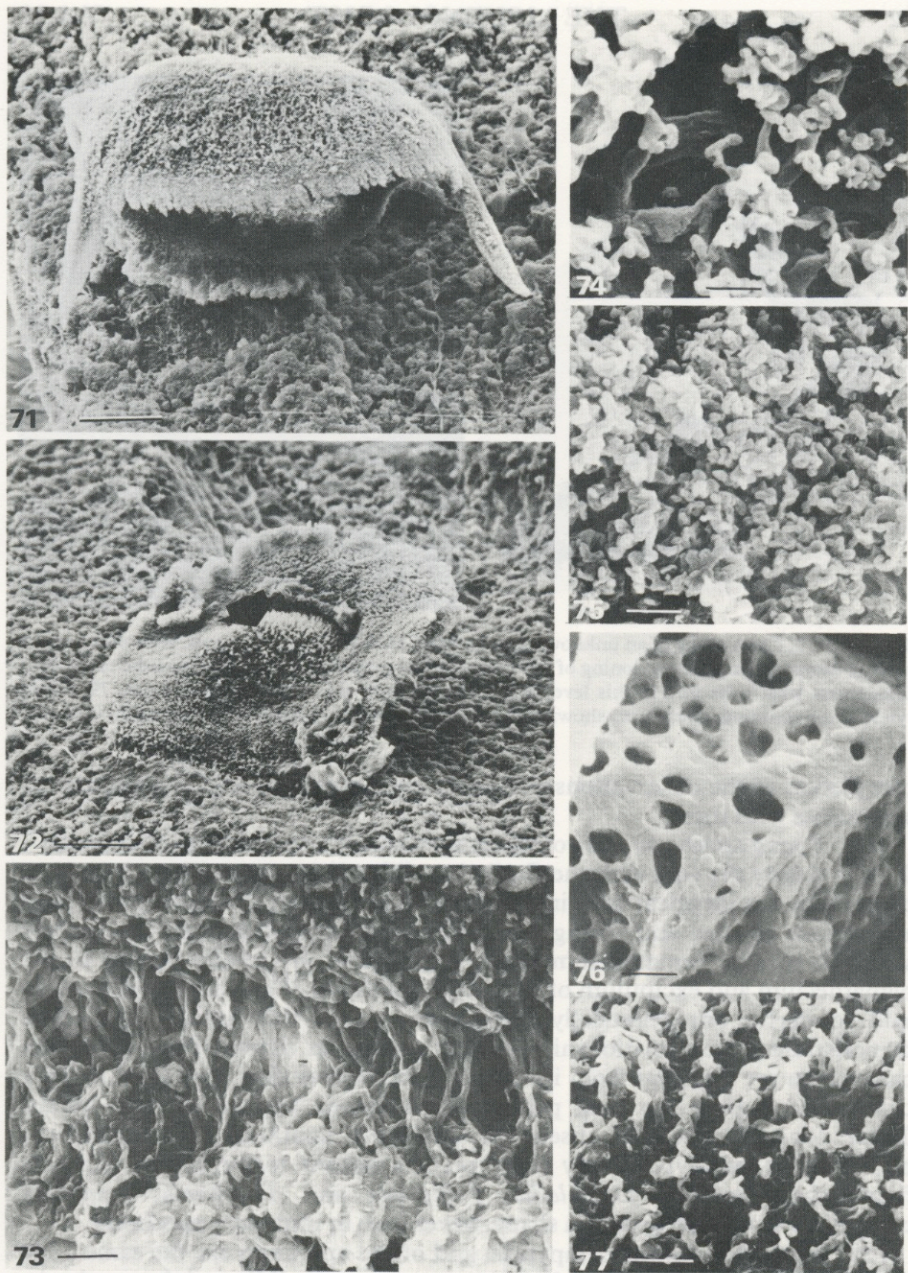
Thallus greenish-grey, sometimes with a bluish tinge, surface matt, \pm farinose, without any cortex, 15–30 μm thick. Campylidia not very numerous, erect, reaching 0.6 mm in height and 0.7 mm broad at the base when mature, rather square, slightly concave (on the inner side) and extended by a long triangular cilium (to 0.3 mm long when preserved) at both the upper corners (Fig. 71); whitish to very pale orange on the concave side and pale orange on the convex; surface smooth or almost smooth in young campylidia but finely rugose in old ones due to the vermiform proliferation of the superficial hyphae of the arachnoid tissue that covers the campylidia (Figs 74, 75). Except for this typical outer surface, the campylidia are composed of paraplectenchymatous tissue (Fig. 76).

Conidiogenous layer a circular (\pm 0.2 mm diam) slightly convex surface, located on the upper part of the concave side (Fig. 72), orange-brown and shiny. In mature campylidia, this layer is totally exposed, whereas in young ones the upper part of the structure is bent back over it (perhaps an artefact of the curating of the specimens). Conidiophores and conidiogenous cells forming a regularly arranged layer without any paraphyses; conidiogenous cells rectangular, 6–8 \times 2 μm , producing 1–3 conidia at or near their apices, probably by sympodial proliferations.

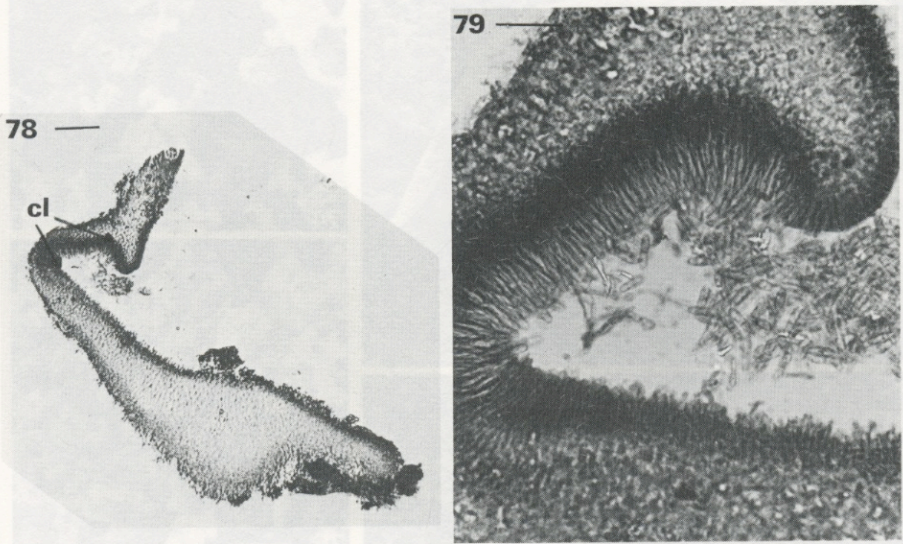
Conidia not abundant, hyaline, bacilliform to narrowly ellipsoid, 1-septate, usually constricted at the septum, 9–11 \times 3 μm .

Discussion

In his recent paper, Vězda (1986) claims that campylidia are phylogenetically derived from apothecia. As a copy of that paper was received after the



FIGS 71-77. Campylidia of an unknown species from New Zealand. 71, Upper view of an undamaged, almost mature campylidium, showing the two cilia. 72, Lateral view of a mature campylidium, with the conidiogenous zone (arrow points to it); this campylidium is partly damaged as the two cilia have been destroyed. 73, Outer base of a campylidium, showing the continuity between the structure (above) and the thallus (below) on which it grows. 74 & 75, Detail view of a campylidium outer surface, showing the hyphae vermiform proliferations. 76, View of a cross-section through a campylidium, showing its paraplectenchymatous tissue. 77, Detail view of the conidiogenous layer; no conidia are present (they were probably removed by the preparation of the specimen for SEM observation). Scales: 71, 72 = 100 μ m; 73 = 10 μ m; 74-76 = 2 μ m; 77 = 10 μ m.



FIGS 78 & 79, Campylidia of an unknown species from New Zealand. 78, Cross-section through a mature campylidium; the sectioning of the structure has caused its bending at the level of the conidiogenous layer—the fold at this level is thus an artefact; cl = conidiogenous layer. 79, Detail view of the conidiogenous layer, showing the 1-septate conidia. Scales: 78 = 100 μ m; 79 = 20 μ m.

completion of the observations presented here, it is pertinent to compare his arguments with them.

(1) 'Young apothecia and young campylidia are impossible to distinguish'. This is clearly the case with the *Badimia pollilensis* aggregate where immature campylidia are identical with immature apothecia apart from the presence of ascogenous hyphae and young asci. Immature campylidia have a cupulate shape in which 'hamathecium' and 'excipulum' are totally similar to the hamathecium and excipulum of immature apothecia. Thus campylidia can be said to derive ontogenetically from apothecia in this group. I failed to demonstrate such a relationship in other genera: in *Sporopodium*, immature campylidia are different from immature apothecia as they very early in their development grow the long periclinally arranged hyphae of their hoods. These long hyphae are absent in immature apothecia. In *Loflammia*, primordia of campylidia very early become hollow to form their ultimate funnel-shape and in *Calopladia*, *Lasioloma* and *Tapellaria*, immature campylidia have a flat goatskin shape, never seen in immature apothecia.

(2) 'The colour of the campylidia and of the apothecia are the same'. No doubt this is the most striking link between the campylidia and the apothecia. This suggests that the same fungus is involved in both structures.

(3) 'The base and the sides of the campylidia have the same paraplectenchymatous 'tissue' as the apothecia'. In the *Badimia pollilensis* aggregate, it is obvious that campylidia and apothecia have similar tissues as they originate from identical primordia; in *Sporopodium*, the campylidium base has a surface typical of the genus and the socle anatomy is very close to that of the

apothecia. The same similarity can be observed with *Loflammia*, *Calopladia*, *Lasioloma* and *Tapellaria*. Thus with this argument one could be inclined to follow Vězda and say that all campylidia are derived from apothecia.

(4) 'In the *Badimia pollilensis* aggregate, campylidia and apothecia contain the same crystals'. As campylidia ontogenetically derive from apothecia in this group, they certainly contain the same crystals, as is to be expected.

(5) 'In *Calopladia* species, the core of the campylidia and of the apothecia have the same aeruginose color'. This is true for most specimens I have examined.

Do campylidia then derive from apothecia? There is no doubt for those produced by the *Badimia pollilensis* group. Does this type of campylidia represent a primitive one? And do the others represent more evolved ones, thus making it impossible to be sure of their origin? These remain unanswered questions, but undoubtedly the structures referred to *Pyrenotrichum* in the past are now seen to be highly specialized conidiomata of tropical lichenized fungi, mainly as foliicoles. If they could all be demonstrated to derive from apothecia initially, this very unusual origin would be a criterion to distinguish them from pycnidia; otherwise, what would be the difference between a pycnidium and a campylidium? The fate of the conidiomata of *Barubria fuscorubra* (Vězda) Vězda is revealing as they were first described as pycnidia (Vězda 1975: 122–123) prior to their more recent assignment as campylidia (Vězda 1986).

More work is needed to understand thoroughly the campylidia and their unusual biology. Indeed, as also observed by Vězda (1986), in almost all lichen thalli examined, campylidia are all almost perfectly orientated in the same direction; in other words all the campylidia openings face the same direction. The reasons for this remains obscure.

Appendix

Loflammia demoulinii Sérusiaux sp. nov.

A *Loflammia flammea* (Müll. Arg.) Vězda differt thallo verruculoso, apotheciis brunneo-nigris et hypothecio K+ brunneo.

Typus: **New Guinea**, Madang prov., between Bunapas Mission and Bunapas, rain forest at sea-level, 1980, *Demoulin* 5912 & *Smeets* (LG—holotypus).

Thallus forming irregular or circular patches up to 15 mm diam, without prothallus, ± continuous or not, pale green to almost white, shiny, with numerous small (less than 50 µm diam) hemispherical white verrucae.

Apothecia few, circular, 0.2–0.3(–0.35) mm diam, very strongly constricted at the base, up to 0.2 mm high; disc brownish-black to almost black, but not carbonaceous, not pruinose, with a distinct, slightly to non-prominent margin, very pale brown, smooth or rarely downy. *Excipulum* well developed, paraplectenchymatous, with irregular or rectangular (rarely isodiametric) cells, sometimes ± arranged radially from the centre of the apothecia, hyaline in thin sections, 50–60 µm high in lateral parts and up to 65–70 µm under the hypothecium. *Hypothecium* impossible to distinguish from the centre (core) of

the apothecium, aeruginose when seen in sections, turning brown in K, 80–100 μm high; a brownish (in K!) layer in connection with the hypothecium exists between the hymenium and the excipulum in the lateral parts of the apothecium. *Hymenium* hyaline, 110–120 μm high; paraphyses numerous, richly branched and anastomosed, forming a dense network between and around the asci. *Asci* clavate, imbedded in a gel vigorously I+ dense blue, with a well developed I+ blue tholus but usually with a distinct 'chambre oculaire'. *Spores* single in each ascus, muriform, fusiform to oblong, 77–85 \times 11–18 μm , with a thick (to 5 μm in 10% KOH) gelatinous sheath.

Campylidia described above (see pp. 24–26).

Photobiont: most probably a species of Chlorococcaceae; cells green and globose, 4–10 μm diam.

Additional specimen: New Guinea, Madang prov., W of Yoro (= Mugamat), 100–300 m elev., on leaves of palm-tree, 1980, Demoulin 5943 & Smeets (LG).

This species is close to *Loflammia flammea* (Müll. Arg.) Vězda from which it can be distinguished by its thallus (*L. flammea* has a dispersed, smooth thallus), by the colour of the apothecial disc (*L. flammea* has a reddish disc), and by the hypothecium reaction to K (brown-red in *L. flammea*). The campylidia of *L. flammea* also have this reddish colour; they were assigned to *Pyrenotrichum bicolor* R. Sant. nom. nud. by Santesson (1952: 40–41).

The inclusion of this new species in the recently described genus *Loflammia* Vězda necessitates some emendation of the genus diagnosis. Indeed, Vězda has described this new genus as having a dispersed thallus, red apothecial disc and K+ red excipulum and hypothecium. I think these discrepancies are acceptable as in other respects *L. flammea* and *L. demoulinii* are extremely similar.

I wish to thank sincerely Dr V. Demoulin who placed his important lichen collections from New Guinea at my disposal; without these, this study would have been impossible. Several other collectors in the tropics have allowed me to study their specimens; amongst them I especially want to thank Ir. P. Bamps, Dr J. K. Bartlett and Professor J. Lambinon. I am much indebted to Dr A. Vězda for sending me an advance copy of his paper 'Neue Gattungen der Familie Lecideaceae s. lat. (Lichenes)', and also the curators of herbaria (mainly G, TUR, UPS and S) for rapid and easy access to the collections in their care. I am also very grateful to Dr B. J. Coppins and Professor D. L. Hawksworth for assistance in preparing my manuscript. SEM photographs were taken at the Jardin Botanique National de Belgique with a Philips 501B microscope; I thank Professor E. Petit, Dr J. Rammeloo and M. Verhaegen for their active cooperation in this regard.

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