

GONIOCYSTS, GONIOCYSTANGIA AND OPEGRAPHA LAMBINONII AND RELATED SPECIES

E. SÉRUSIAUX*

Abstract: The term goniocyst, introduced by Norman in the last century, has been used to designate lichen thalli consisting of algal colonies embedded in a hyphal envelope. It has been applied to the Morioliaceae, '*Botrydina*' and several groups in the Lecideaceae s. lat. A preliminary survey demonstrates that the concept encompasses different structures. Nevertheless, and *ad interim*, the term is here used to describe the small diaspores produced by several species of foliicolous *Opegrapha* in a peculiar organ, the goniocystangium. Four such species are known in *Opegrapha*: *O. dibbenii* sp. nov. in Costa Rica, *O. lambinonii* Sérusiaux in Zaïre, *O. luzonensis* sp. nov. in the Philippines and *O. santessonii* sp. nov. in Zaïre, but foliicolous lichen thalli with goniocystangia are known from undisturbed rain forests at low elevations in four continents.

Introduction

Sérusiaux (1978) described a new foliicolous species of *Opegrapha*, *O. lambinonii*, based on a single collection from Zaïre. In addition to other diagnostic features, this species was characterized by small cup-shaped protuberances (Figs 1-2), abundant on the thallus surface, containing tiny whitish granules (12-25 µm diam); each granule being an algal colony very closely embedded by a network of hyphae. These structures were then considered a type of soralium and termed 'tubuliform soralia'.

These peculiar structures were previously observed, also in *Opegrapha* species, by Santesson (1968) in several collections from the Ivory Coast. He considered them to be a unique organ and named them 'goniocystangia'. Vězda (1977, 1980: 82) maintained this term and adopted 'goniocyst' to designate the soredia.

During the past four years, I have had the opportunity of examining collections of foliicolous lichens from many tropical areas. From all four continents with tropical rain forests, thalli with goniocystangia were discovered and, when fertile, were all demonstrated to belong to *Opegrapha*. Four species of *Opegrapha* with goniocystangia can thus be described. Here I shall try to establish the taxonomy of this group and to describe as precisely as possible their fascinating organs, the goniocystangia, and survey the use of the term 'goniocyst'.

Material and Methods

The collecting of foliicolous lichens is a painstaking task and in spite of the precautions taken for the drying of the leaves bearing them, material is usually badly preserved. Moreover, the climatic conditions of the areas where they are collected demand rapid desiccation of the specimens. The material that was available for this study was scarce and the search for specimens of the group studied

*Chargé de Recherches au Fonds National de la Recherche Scientifique, Département de Botanique, Sart Tilman, B-4000 Liège, Belgium.

among the large collections at my disposal has been long and often fruitless. The main reason is undoubtedly the habitat of these lichens: undisturbed tropical rain forests at low elevations. Few botanists have collected foliicolous lichens in such unexplored places. Even when explored by botanists interested in the foliicolous flora, these forests yield only a few specimens of this group. On the Pacific Coast of Costa Rica, I personally collected several thousand leaves in a \pm undisturbed forest but found only three with *Opegrapha dibbenii*, newly described in this paper.

The material was examined in distilled water, Lugol's iodine, or lactophenol cotton-blue. The measurements of spores, sections and other anatomical structures always refer to water mounts. Photomicrographs were taken with a Leitz Dialux microscope and an Orthomat. Air-dried herbarium material for study with the scanning electron microscope (Philips 501B) was prepared by the critical point drying method, unless otherwise stated.

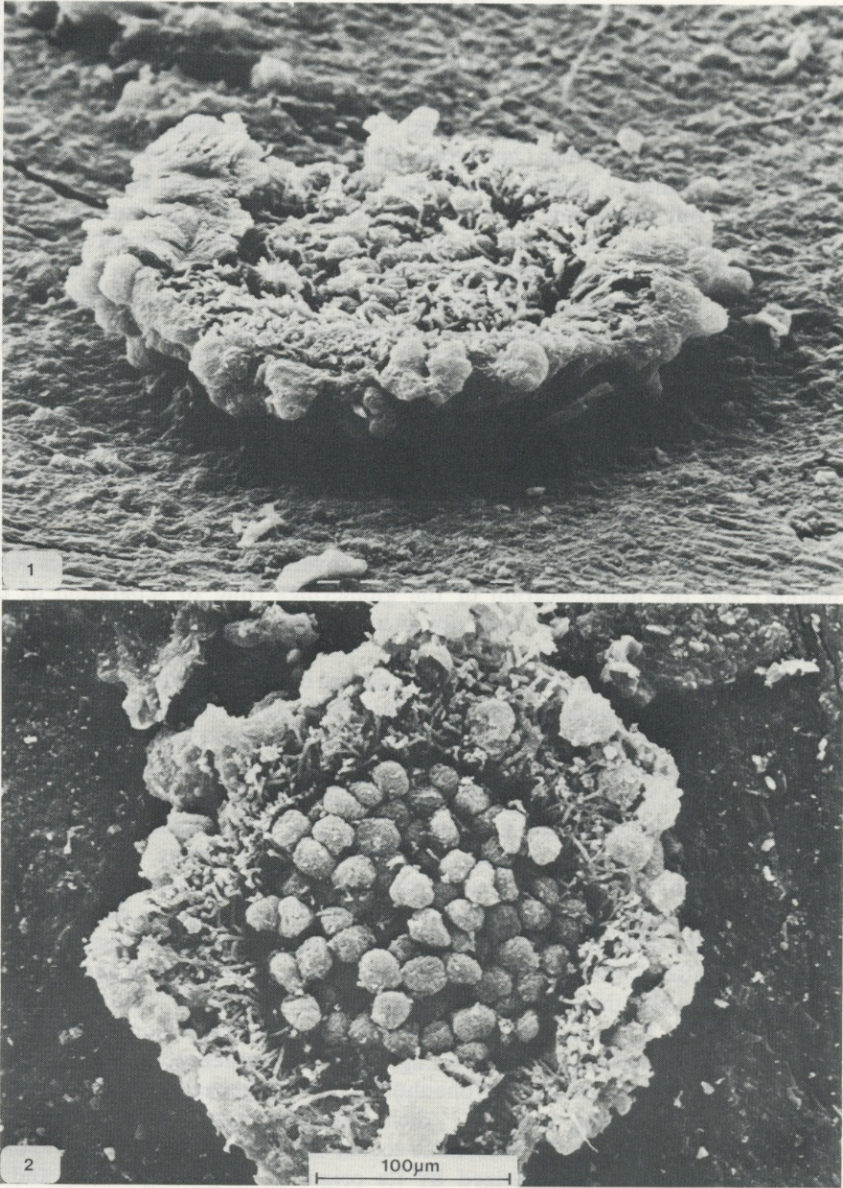
Material studied, beside the specimens of the *Opegrapha lambinonii* group. *Aphanopsis coenosa* (Ach.) Coppins & P. James (Czechoslovakia: Moravia, alt. 300 m, *Vězda* Lich. Sel. Exs. no. 535, LG— isoparatypus of *Lecidea praecox* *Vězda*). *Bacidia apiahica* (Müll. Arg.) Zahlbr. (New Zealand: Waitakere Range near Auckland, *Bartlett* 18596, LG). *B. scutellifera* *Vězda* (Zaire: Kivu, Irangi, réserve de l'IRSAC, sur la rive droite de la rivière Luhoho, c. 850 m, *Lambinon* 72/20, LG). '*Botrydina vulgaris*' Bréb. ex Meneghinio, glomerules associated with *Omphalina luteovirellina* (Pilát & Nannf.) M. Lange (British Isles, Nethybridge, Abernethy Forest, 1968, *James*, BM). *Catillaria mirabilis* *Vězda* (Zaire: Haut-Zaire, route Kisangani-Bengamisa, km 29, alt. 200–500 m, *Lisowski* 44380, LG; Kivu, Irangi, réserve de l'IRSAC, sur la rive droite de la rivière Luhoho, c. 850 m, *Lambinon* 78/265, LG; Shaba, plateau des Muhila, *Malaise* 2056 e, LG). *Micarea prasina* Fr. (Belgium: Anlier, *Sérusiaux* 4979 & *Rose*, LG). *Placynthiella uliginosa* (Schrader) Coppins & P. James (Belgium: Spa, Fagnes de Malchamps, *Lambinon* 67/569, LG). *Vezeadaea aestivalis* (Ohlert) Tsch.-Woess & Poelt (British Isles: herb. Leighton, BM). *V. rheocarpa* Poelt & Dobbeler (Austria: südliches Burgenland, c. 250 m, in Lich. Alp. no. 293, LG—isotypus).

What is a goniocyst?

As far as I am aware, the term goniocyst was first introduced by Norman (1871a: 13) to describe the thallus in the family Moriolaceae. In modern treatises (e.g. Ozenda & Clauzade 1970: 140), the Moriolaceae are described as pyrenomycetes producing multicellular spores and lichenized with cyanobacteria. The cyanobacterial colonies are wrapped in and very tightly embedded by hyphae; they therefore appear as small brownish granules (10–100 μm diam) provided with a continuous envelope; these bodies were named 'goniocysts' by Norman. If the envelope was discontinuous, they were termed 'goniocystula'. The original text of Norman (1871a: 13, infrapaginal note) reads as follows:

Goniocysta = capsula nuda hyphosa, distincte angulosa-reticulata, vulgo saturate colorata, gonidia includens. Nucleus thallinus = corpusculum subglobosum, celluloseum, a massa thallina integrum separandum, demum confluens, gonidia nuda v. goniocystula tecta vulgo includens. Goniocystula = capsula in nucleo thallino v. massa cellulari inclusa, textura obsolete hyphosa, vulgo pallida, gonidia fovens.

Norman (1871a) described three genera belonging to the Moriolaceae (*Moriola*, *Spheconisca* and *Bifrontia*) and nine species, mainly corticolous or overgrowing mosses and plants fragments. Norman (1871b, 1871c, 1876), Hedlund (1895), Nyman (1895), Bachmann (1925) and Keissler (1927) carried on the study of this family. The only recent analysis of the group is that of Eriksson (1981: 100–102) which deals with just two species described by Norman. The species selected as the type of *Moriola* (*M. descensa* Norman) by Clements & Shear (1931: 287) was shown to be identical with the non-lichenized fungus *Melanomma subdispersum* (P. Karsten) Berl. & Vogl.; the so-called goniocysts of Norman were over-ripe ascomata containing algal cells (of which several different species are frequent on



Figs 1-2. *Opegrapha lambinonii* (Zaire, Lambinon 78/265), goniocystangia. 1, Lateral view. 2, View from above. Same scale for both pictures.

the host surface in the type-collection). Eriksson therefore chose another species as the lectotype of *Moriola*, *M. pseudomyces* (Norman) Norman, and examined the type collection. He concluded that this was a lichenized fungus producing goniocysts but unfortunately added no further details. I did not have the oppor-

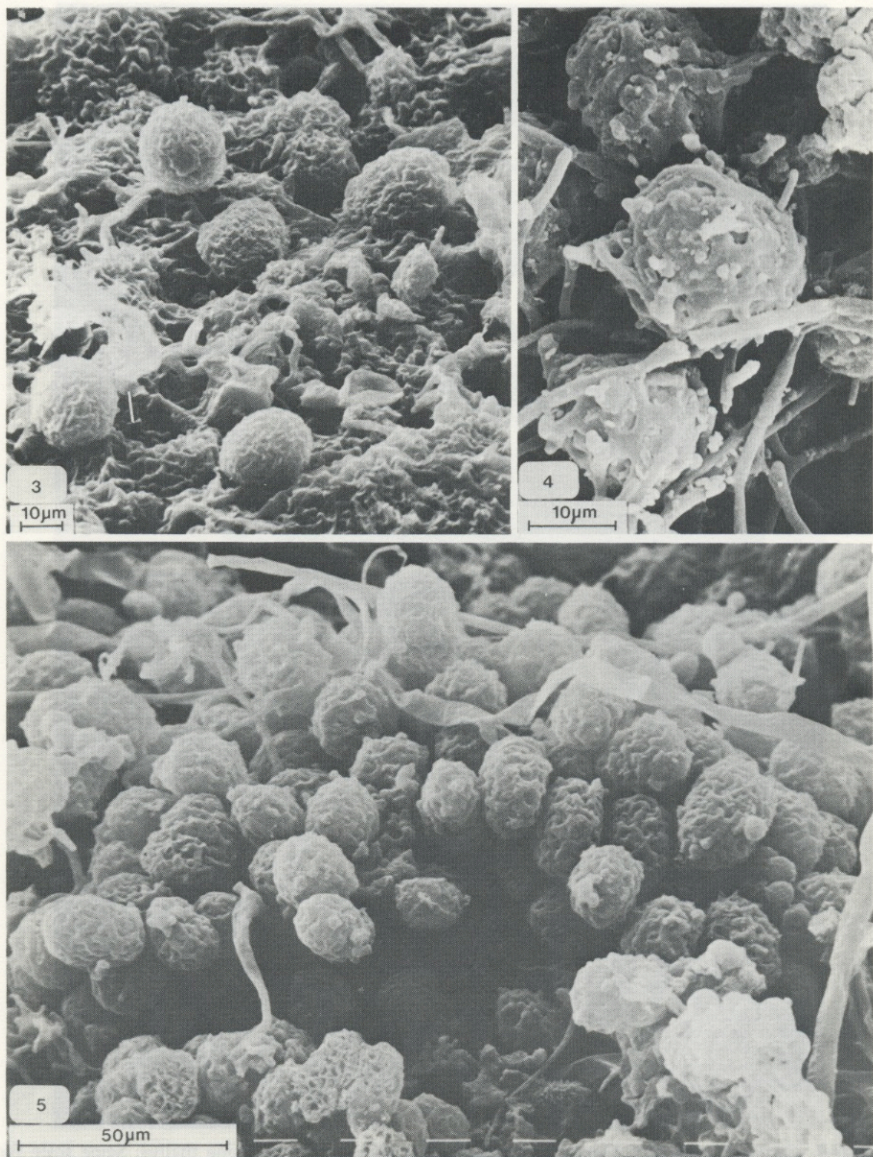
tunity to examine any specimen of Moriolaceae, of which no recent collections are known (Henssen, pers. comm.) but doubt from the data available that the *Moriola* goniocysts have the same structure as those of the *Opegrapha lambinonii* group.

The term goniocyst has also been used to describe the glomerules associated with the basidiomycete genus *Omphalina* Quélet (for example by Poelt & Jülich 1969: 332–333, within *O. grisella*; see Lange 1981 for typification and delimitation of the genus), but this is not done consistently, even within one author's work. These glomerules are often called 'Botrydina' in the lichenological literature. Acton (1909) was the first to demonstrate that 'Botrydina' was in fact a lichenized colony of the alga *Coccomyxa*; and Gams (1962) and Poelt & Oberwinkler (1964) showed conclusively that the carpophores of several *Omphalina* species are associated with such glomerules. Using TEM, Boissière (1980) and Honegger & Brunner (1981) proved that the hyphae of the 'Botrydina' glomerules really belong to a basidiomycete as they have typical dolipores. These glomerules are spherical or elongate (Fig. 16), measure 20–300 µm long and always have a paraplectenchymatous cortex with leptodermatous cells (see Acton 1909 and Jaag 1933 for good illustrations, and Fig. 17). In her excellent paper, Acton described the origin (contact between an algal cell and a single hypha which swells up enormously around the alga until it completely covers it and then undergoes septa formation) and the multiplication of the glomerules (due to separation of the partners which then multiply). I am not aware of any other study on the biology of the 'Botrydina' glomerules.

In the Lecideaceae s. lat., the term goniocyst has been introduced more recently. I have noted the following usages: Ozenda (1963: 32), *Placynthiella uliginosa*; Poelt & Hertel (1968: 210), *Pachyascus lapponicus*; Poelt & Döbbeler (1975: 332) and Tschermak-Woess & Poelt (1976: 77), several species of *Vezdaea*; Vězda (1980: 82, 1983: 61), one species of *Catillaria* s. lat. and several species of *Bacidia* s. lat., mainly foliicolous; and Coppins (1983: 24), a few species of *Micarea*. Although not used in the original description of the genus, the thallus of *Bryostigma* could also be described as consisting of goniocysts ('algae hyphis reticulatim circumdat'); the taxonomic position of the genus is still unknown (Poelt & Döbbeler 1979) but it can perhaps be included in the Arthoniaceae.

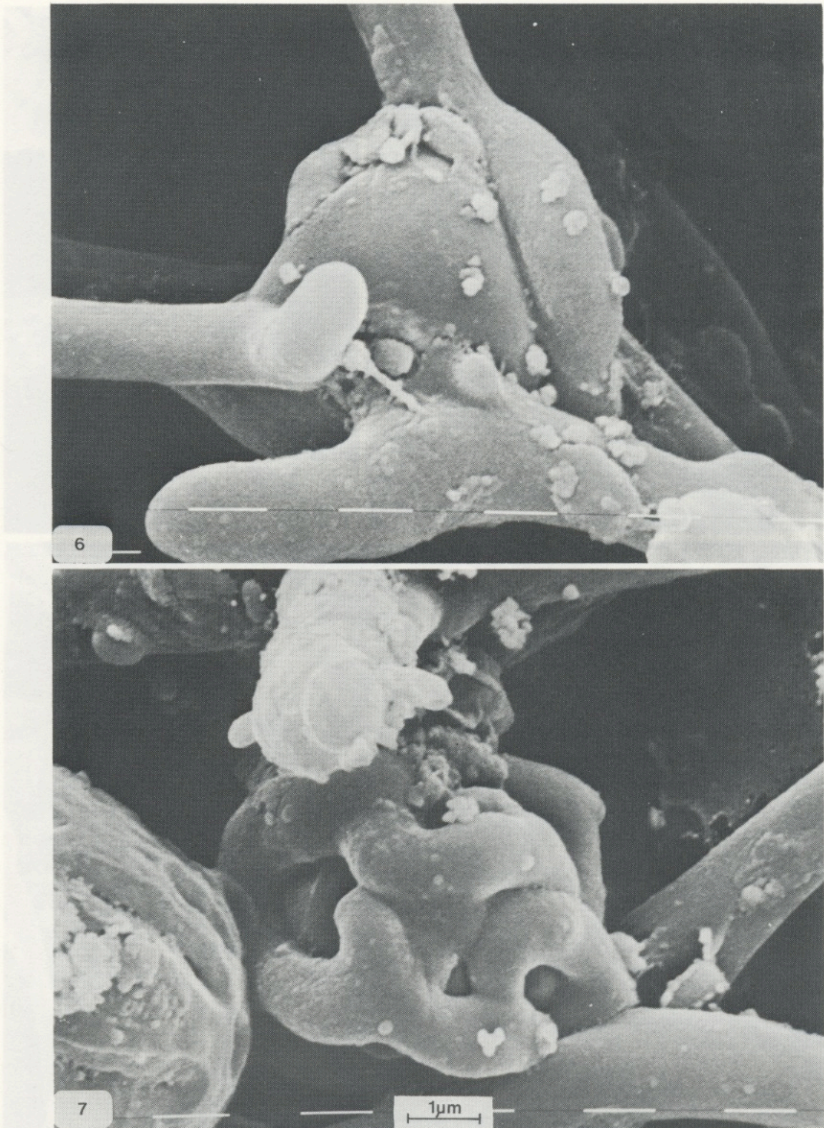
Vězda (1980: 82) is the only modern author to give a definition of the goniocyst (when describing the thallus of *Catillaria mirabilis*; Fig. 3–5): 'Die keugeligen, 15–25 µm breiten Körnchen sind ihrem Anatomiebau nach Goniocysten: jede Goniocyste besteht aus einer Gruppe kugeliger Algenzellen und einer geschlossenen, paraplectenchymatischen Hyphenhülle. Die Algenzellen sind ± kugelig, 4–6 µm breit, dünnwandig, hellgrün, ± dicht gedrängt; zwischen ihnen verlaufen dünne, septierte Hyphen, die jede Zelle locker umhüllen.' Following Vězda, a goniocyst is therefore characterized by its origin (a single algal cell) and its anatomical structure (a paraplectenchymatous envelope completely surrounding the algal colony).

My observations (Figs 6–7) of the origin of the goniocysts in *Catillaria mirabilis* ± concur with Vězda's statement. SEM photographs of very young thalli or of margins of older ones show that, at the early stages of goniocyst formation, the algal cell is rapidly and completely enwrapped by the hyphae. No haustorium or extracellular binding substance could be observed. There is no doubt that the



FIGS 3–5. *Catillaria mirabilis*, view of the thallus. 3, Lateral view of a young thallus with five goniocysts on a hyphae-carpet. 4, Closer view of the goniocysts. 5, Aggregated goniocysts in an old and almost collapsed goniocystangium. The long bandage-like hyphae belong to a dematiaceous hyphomycete, presumed to be a saprophyte.

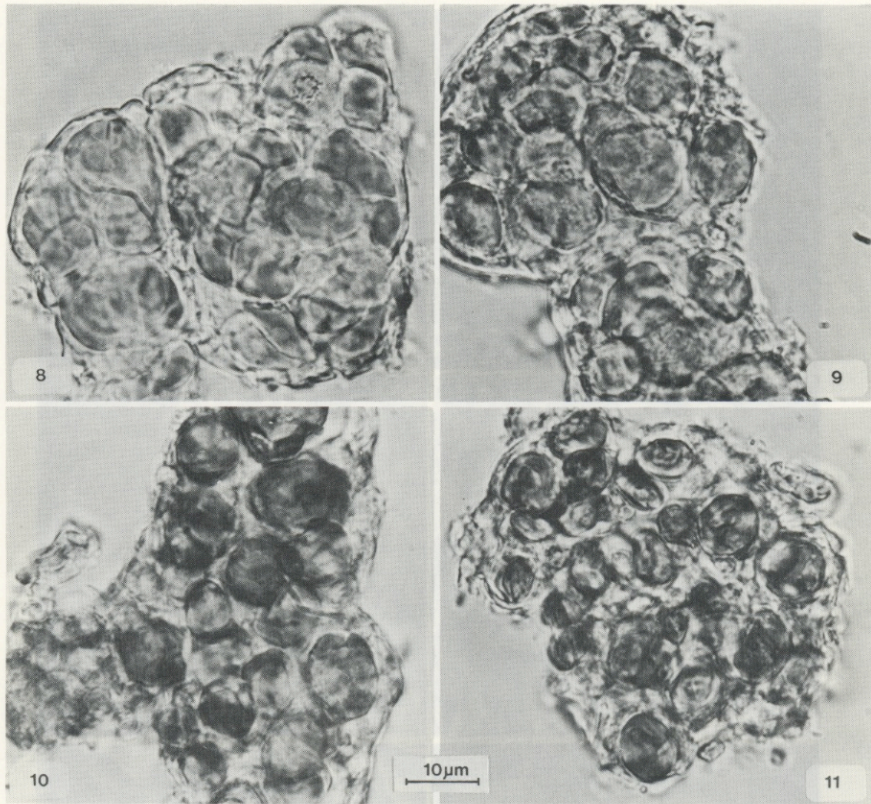
goniocyst originates from a single algal cell. As described by Vězda (1980: 80–82), these goniocysts are dispersed (Fig. 3), \pm agglomerated (Fig. 5) over a network of free hyphae (hypothallus), or arranged in cup-shaped structures ('goniocystangia', see below) to promote their dispersal. SEM photographs also show that the



FIGS 6-7. *Catillaria mirabilis*. Goniocyst formation, as seen in a very young thallus. Same scale for both pictures.

hyphal envelope is not strictly paraplectenchymatous: the hyphae, although tightly appressed around the algal cells, remain discrete.

The goniocysts described in several *Vezdaea* species have a rather similar structure but the hyphal envelope shows a tendency to be more paraplectenchymatous (Fig. 11, and Poelt & Döbbler 1975: 344, Fig. 21 & 22 in *V. rheocarpa*). Attention must be drawn to the diversity of the so-called 'goniocysts' in that genus: in some



Figs 8–11. Goniocysts in several species of Lecideaceae s. lat. 8, *Placynthiella uliginosa*. 9, *Aphanopsis coenosa*. 10, *Micarea prasina*. 11, *Vezdaea aestivalis*. Same scale for all pictures.

species (e.g. *V. aestivalis*) they are formed at the thallus margins only and this formation does not occur in all specimens; in other species like *V. rheocarpa*, goniocysts constitute the whole thallus and are provided with extraordinary spines (Fig. 15). I did not study the ontogeny of the goniocysts of *Vezdaea*.

In other groups of Lecideaceae s. lat. from which goniocysts have been described, the glomerules are typically paraplectenchymatous, especially in *Placynthiella uliginosa* (Fig. 8), *Aphanopsis coenosa* (Fig. 9), and *Micarea prasina* (Fig. 10) (see Coppins 1983: 24 for more details of the goniocysts in *M. prasina* and related species). How these goniocysts are formed is a matter of speculation as no ontogenetic studies have yet been carried out on these species.

A further group in which goniocysts are described is the *Bacidia phacodes* aggr. (Vězda 1983: 61–62). The thallus of these species is made of small glomerules (goniocysts) of various shape. The apothecial anatomy, asci and ascospores are almost identical for all of them, thus leaving little doubt about the homogeneity of the aggregate. The thallus glomerules seem, however, to be quite different from one species to another. In *Bacidia scutellifera* (Fig. 18), the glomerules are

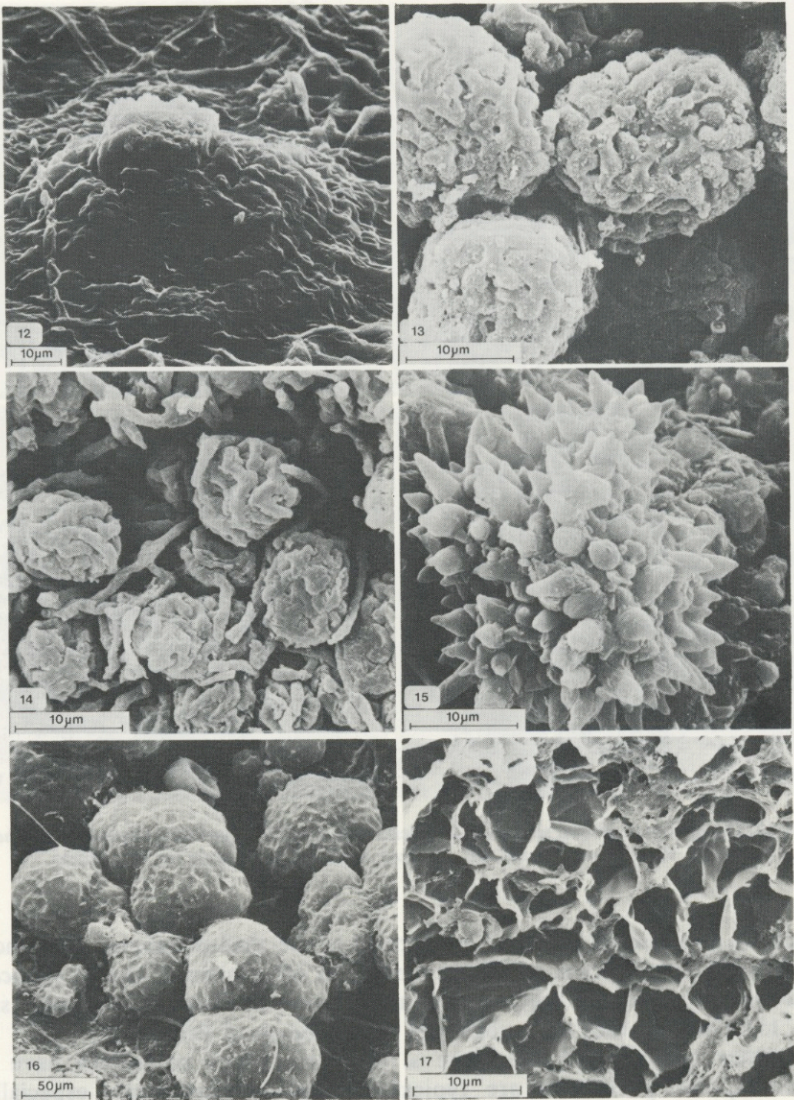
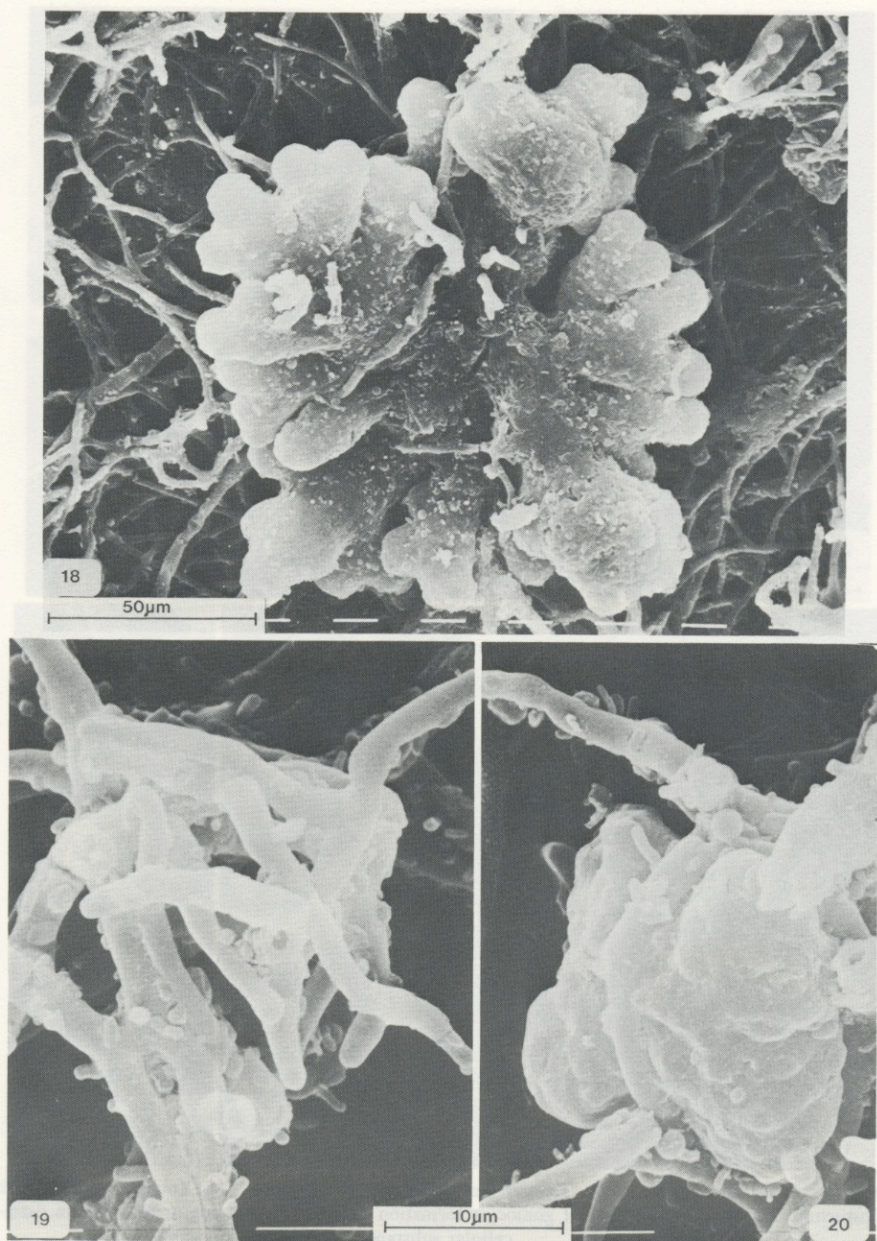
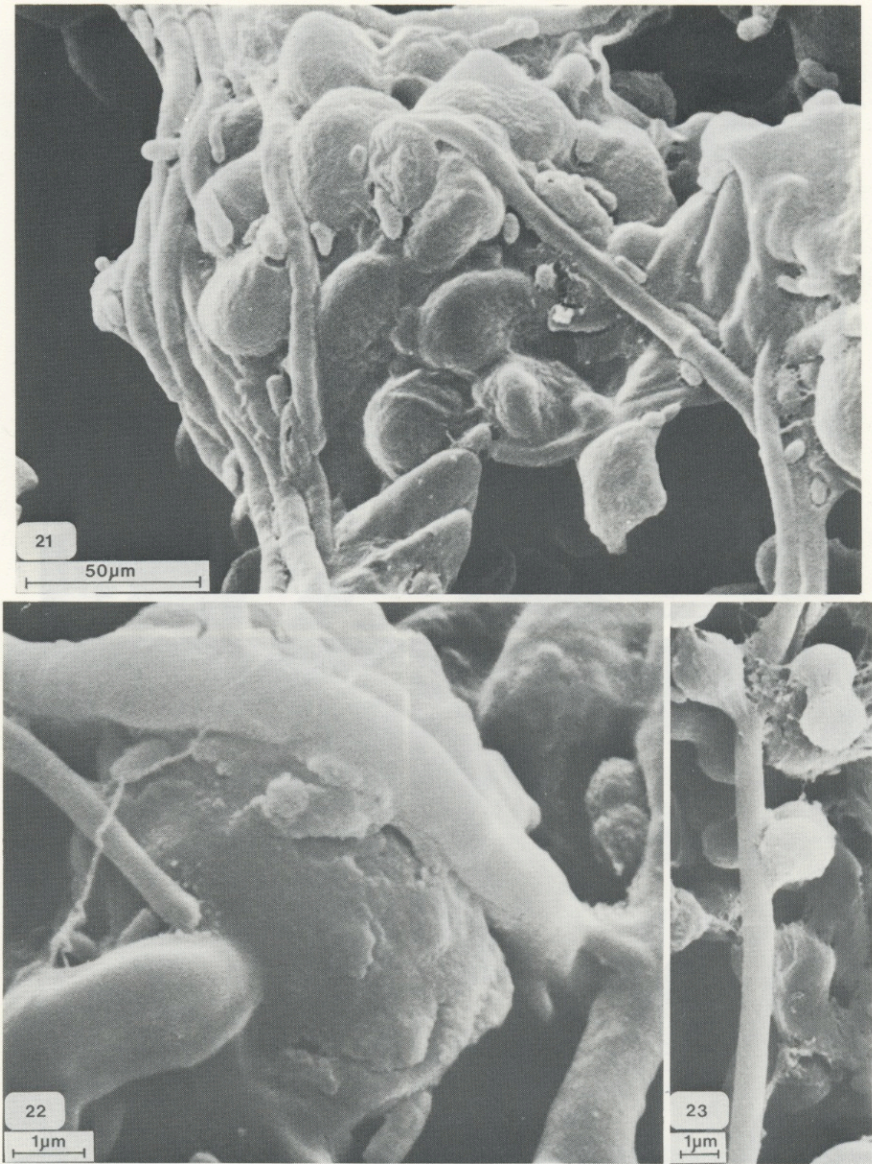


FIG. 12. Early stage of goniocystangium in *Opegrapha lambinonii* (Zaire, Lambinon 78/265). 13, Mature goniocyst in *O. lambinonii* (same collection). 14, Mature goniocyst in *Opegrapha* sp. (New Guinea, Mt Manke, *van Zanten*). 15, Mature goniocyst in *Vezdaea rheocarpa*. 16-17, Goniocysts in '*Botrydina*'. 16, Young goniocysts. 17, Cross-section of a mature goniocyst.

initiated by the wrapping of algae (Figs 19-20); the surface of the glomerule is rather smooth (Fig. 18) and no haustoria were observed by me. In a collection referred to as *Bacidia apiahica*, the glomerules were also initiated by the capture of an algal cell but, at least in some cases, the secretion of an extra-cellular substance first bound the alga to the hyphae (Fig. 23) and haustoria were easily and



FIGS 18–20. *Bacidia scutellifera*. 18, Upper view of a mature goniocyst. 19–20, Early stages of goniocyst formation.



FIGS 21-23. *Bacidia apiahica*. 21, Lateral view of a mature goniocyst. 22, Young goniocyst with haustorium. 23, Very early stages of goniocyst formation showing the binding of algae by an extracellular substance.

regularly observed (Fig. 22). (Rather similar SEM pictures were published by Ahmadian *et al.* 1978.) SEM photographs of the fully grown glomerules (Fig. 21) show a surface shaped by the algal cells trapped within them and a network of embedding hyphae with no tendency to be paraplectenchymatous.

Is there a difference between a goniocyst and a soredium?

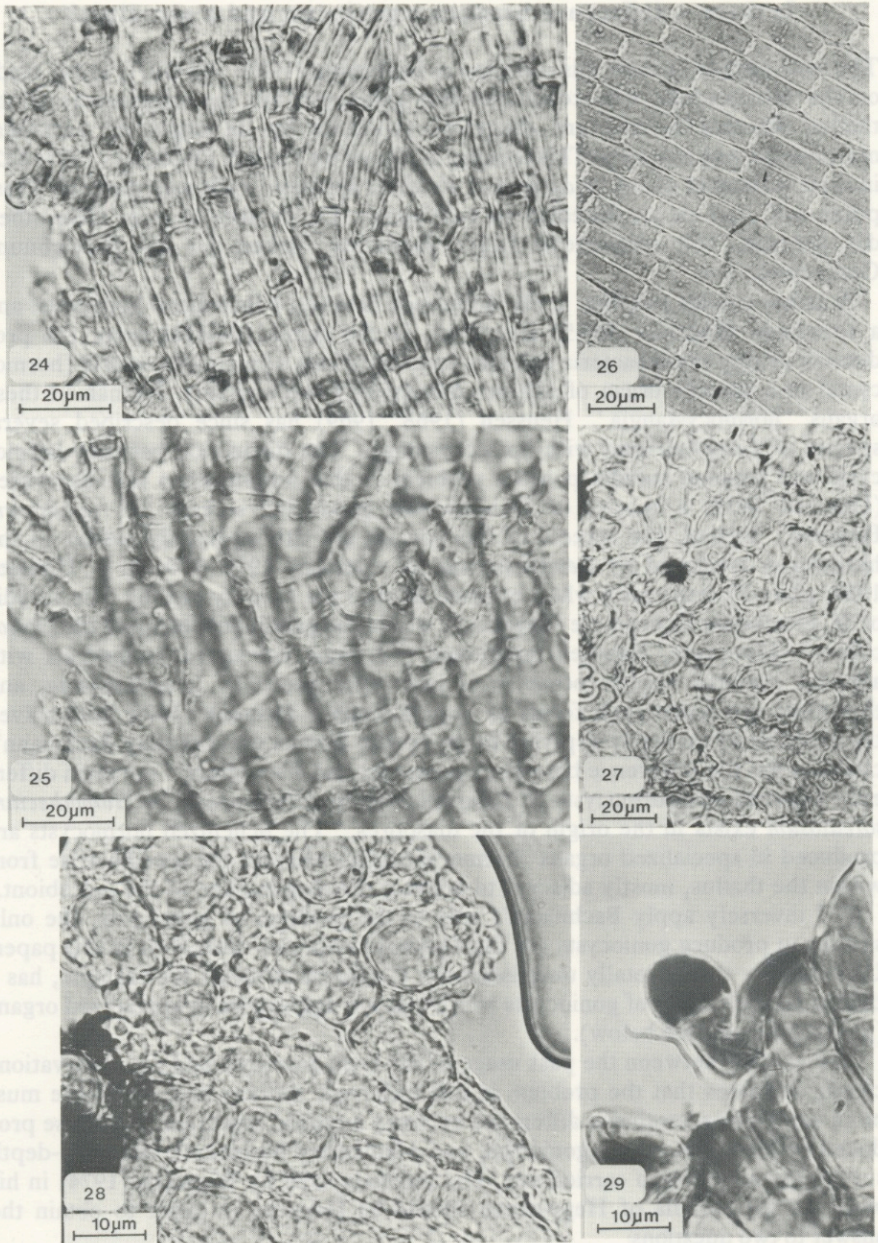
The only author to raise this question is Bachmann (1925: 184–187), in his study on the Morioloraceae, who concluded that goniocysts are the components of the thallus whereas soredia are diaspores produced by an organ of particular morphology and anatomy. This opinion is shared by Poelt & Döbbeler (1975: 332) in their statement about *Micarea* and *Vezdaea* species: 'Faßt man diese als Diasporen auf, sind sie als Soredien zu bezeichnen. Da sie aber in ihrer Gesamtheit das normale, voll entwickelte Lager darstellen, ziehen wir die Bezeichnung Goniocysten vor.'

A rather similar problem is the difference between a lichenized hormocyst and a soredium. Degelius (1945) described, in the genus *Lempholemma*, the production of tiny cyanobacteria colonies embedded into a gelatinous matrix (hormocysts) in a specific organ of distinct morphology and anatomy. He named these organs 'hormocystangia'. Henssen (1968, 1969) has since described several species of *Lempholemma* with hormocystangia. The distinction between hormocysts and genuine soredia posed a problem to that author when she discovered (Henssen 1979) a species of *Homothecium* producing soredia (*H. sorediosum* Henssen). Indeed, the soredia of this species are extraordinarily similar to the hormocysts produced by *Lempholemma* (cf. Henssen 1979: 270 fig. 8, Henssen 1969: plate 2), especially when external hyphae are entirely lacking (the soredia of *H. sorediosum* incorporate fungal cells within the gelatinous sheath of the *Nostoc* colony). Moreover, Henssen mentioned that some lichenized hormocysts with adjacent external hyphae occur in at least one species of *Lempholemma*, and that these are transitional forms to typical soredia. Henssen (1979: 266) solved the problem by inversely applying to the couple hormocyst-soredium Bachmann's criterion for the difference between a goniocyst and a soredium: 'the main difference between the hormocysts of *Lempholemma* and the soredia of *Homothecium sorediosum* exists in the origin of the diaspores.' The lichenized hormocysts are produced in specialized organs (hormocystangia) whereas the soredia arise from within the thallus, mostly adjacent to actively dividing hyphae of the mycobiont.

If I inversely apply Bachmann's rule to the problem of goniocysts, the only species to produce goniocysts are the *Opegrapha* species dealt with in this paper. Undoubtedly this is totally unsatisfactory: *Catillaria mirabilis* for example, has a thallus entirely made of goniocysts which also are aggregated in specialized organs (goniocystangia, see below).

The conflict between the past usage of the term goniocyst and my observations clearly indicates that the problem is still unsolved. Authors feel that there must be in one way or another a difference between a typical soredium (e.g. those produced by Parmeliaceae), a goniocyst, and a lichenized hormocyst, but no in-depth survey has so far been carried out. The methods used by Wetmore (1974) in his work on the soredia of Heppiaceae should be followed in order to obtain the answer to two questions:

(1) What initiates the structure? In the Parmeliaceae, according to Beltman (1978), the algal divisions are responsible for the formation of soredia. Contrariwise, in *Catillaria mirabilis* the goniocysts are initiated by the capture of an algal cell by the hyphae. The alga is then for good and all trapped within the hyphal envelope. This contrasts sharply with the apparent photobiont ability to escape



FIGS 24–29. 24–25, View of the same portion of the thallus of *Opegrapha lambinonii* (Zaire, Lambinon 78/265). 24, Optical section at the algal level. 25, Surface view showing the network of hyphae. 26, View of the alga in the thallus of *Opegrapha sartessonii* (holotype); hyphae removed by preparation in K, then washed in water. 27, View of the alga in the thallus of *Opegrapha* sp. (New Guinea, Mt Manke, van Zanten). 28, Squash preparation of a gonocystangium of *Opegrapha dibbenii*. 29, Partly dissected thallus of a free-living *Phycopeltis* with a young sporangium (Zaire, Lambinon 78/265).

the constraints of the mycobiont in the artificial synthesis of lichens (see Ahmadjian *et al.* 1978, Ahmadjian & Jacobs 1982).

(2) What is the degree of intimacy between the alga and the fungus? When we consider the presence of haustoria it is well known that the structural links between the partners of the lichen symbiosis can be very different (see Honegger 1984). Almost nothing is known on this topic for species producing goniocysts.

Nevertheless, and *ad interim*, I shall restrict the term goniocyst(s) to the diaspore(s) produced in the cup-shaped structures in the foliicolous species of *Opegrapha* dealt with here.

***Opegrapha lambinonii* and related species**

Thallus

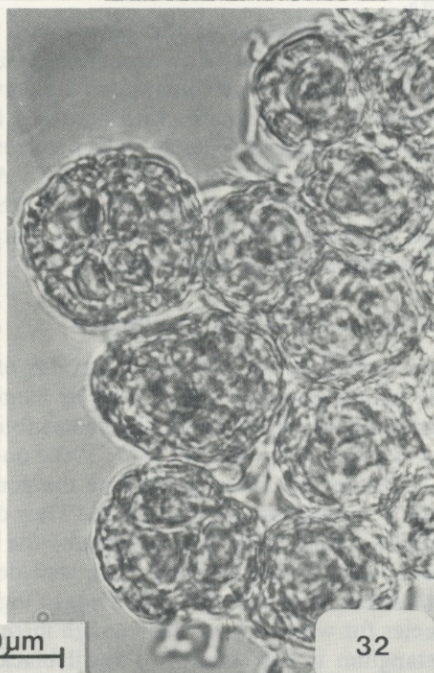
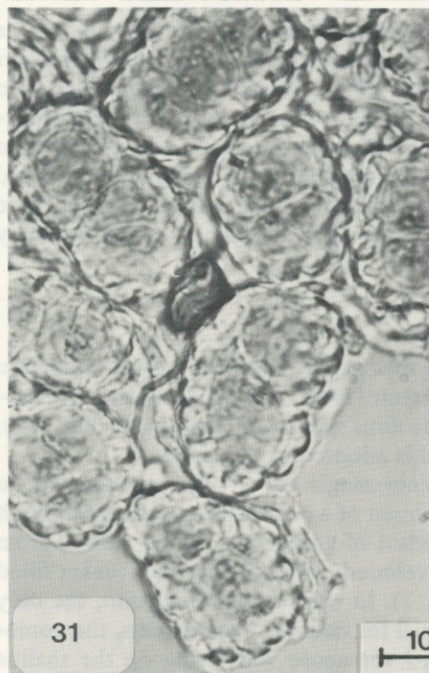
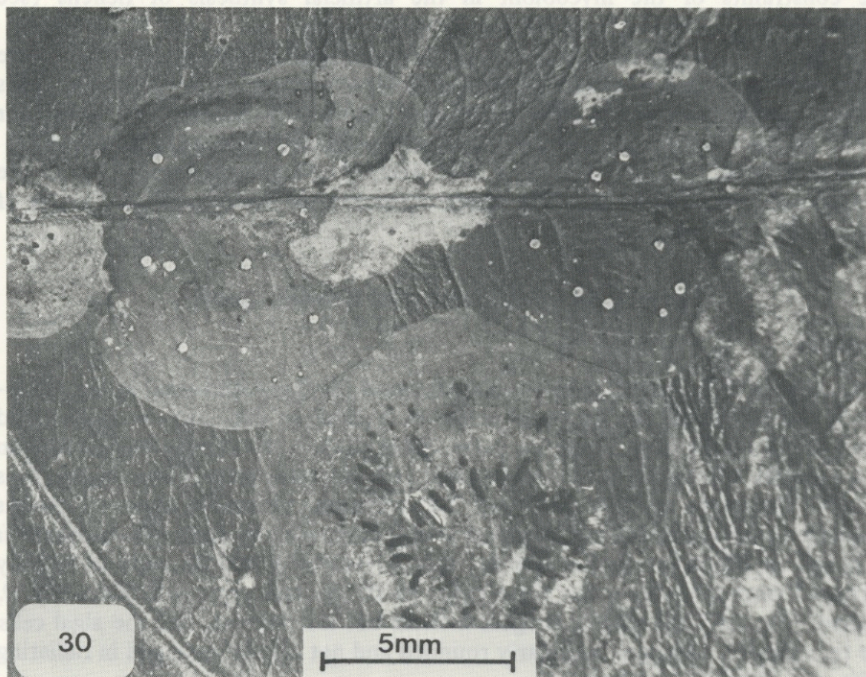
As in most foliicolous lichens with *Phycopeltis* (Trentepohliaceae) as the photobiont, the thallus of the *Opegrapha* species treated in this paper is shaped and 'dominated' by the alga. In sterile parts of the thallus, the fungus is usually seen as a network of hyphae covering the algal cells or intruding between them (Figs 24–25). Haustoria are not observed. Nevertheless, two main types of thallus anatomy can be distinguished. The first is well illustrated by *Opegrapha santessonii* (Fig. 26) in which the thallus is very regular—almost a perfect circle of radially arranged rows of rectangular algal cells. In the second type, illustrated by *O. dibbenii* (Fig. 27), the thallus is again a circle but less regular, and the algal cells are rectangular, oblong or angularly rounded and not clearly arranged in radiating rows.

The identification of the phycobiont to *Phycopeltis* is purely speculative as no culture was made. Accompanying African specimens of *Opegrapha lambinonii* and *O. santessonii* are numerous free-living *Phycopeltis*-like algae, which also develop as circular plates with regularly arranged rows of cells. Numerous sporangia are produced (Fig. 29) which correspond to the description of sporangia in *Phycopeltis* (see Printz 1940: plate XX). Although sporangia were never observed in lichenized thalli with goniocystangia, there is little doubt in my mind that these algae belong to the same species as that involved in the lichen system built by *O. lambinonii* and *O. santessonii*.

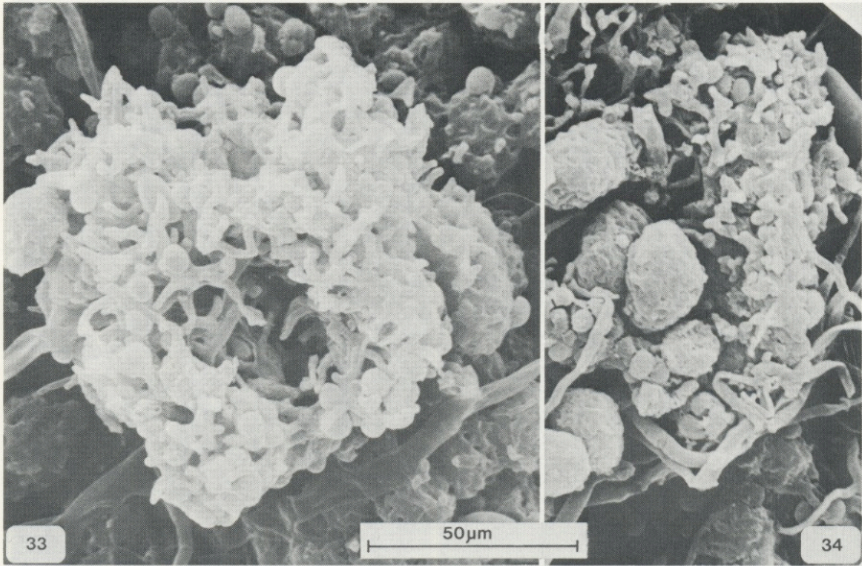
Goniocystangia and goniocysts

As quoted in the preceding sections of this paper, the term goniocystangium (pl.: goniocystangia) was created by Santesson (1968: 176) to designate the cup-shaped structures on the thalli of some foliicolous species of *Opegrapha* (Fig. 1–2). It was retained by Vězda (1977, 1980) and is adopted in this paper.

In the species investigated here the goniocystangia are circular, cup-shaped (to slightly funnel-shaped) structures. They consist of a carbonaceous outer wall with a white-hyphal collar which contains the mass of goniocysts. When viewed from above, the whole structure, when well-developed, looks like a small basket filled with straw litter and numerous eggs (Fig. 2). In *Opegrapha lambinonii*, the only species for which I have had enough material for detailed examination, the goniocystangium is first seen as a small black, ±verrucose wart lying on the thallus surface. It later ruptures at the apex (Fig. 12), by which time it is already filled



10µm



Figs 33–34. *Catillaria mirabilis* (Zaire, Lisowski 44380). 33, Young gonicystangium still without any gonicysts. 34, Margin of an older gonicystangium.

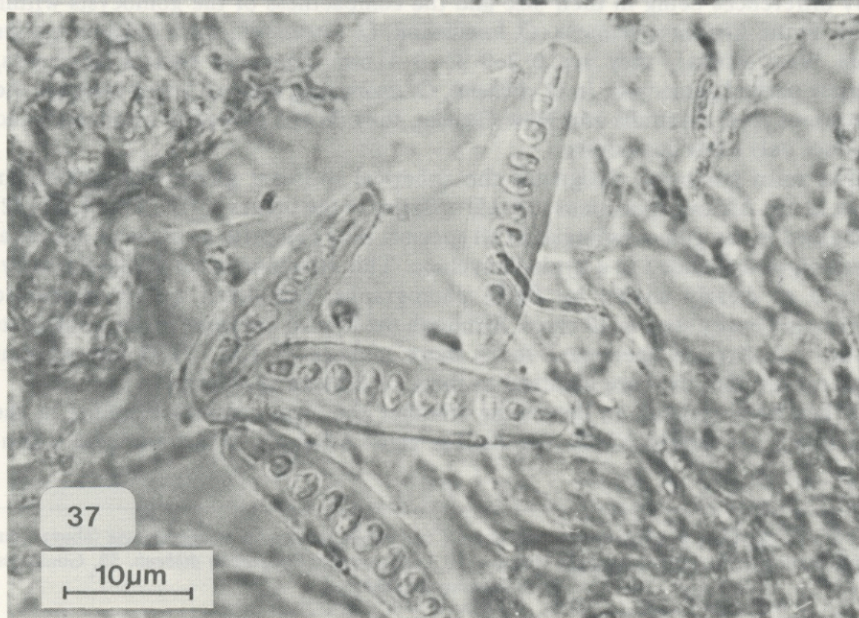
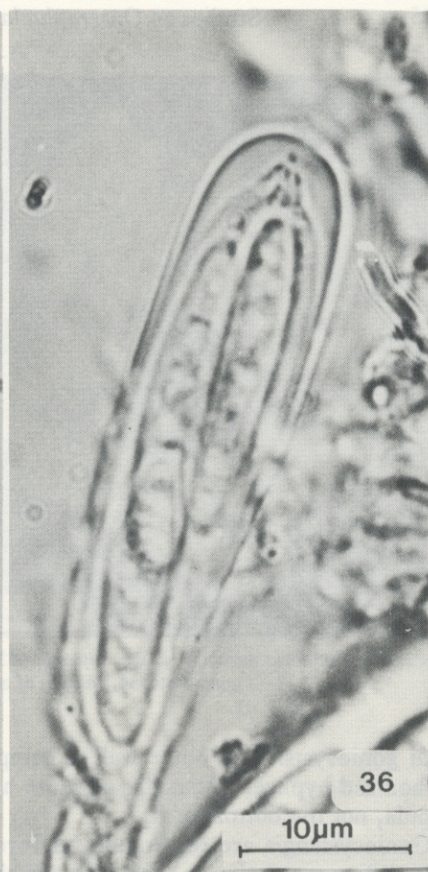
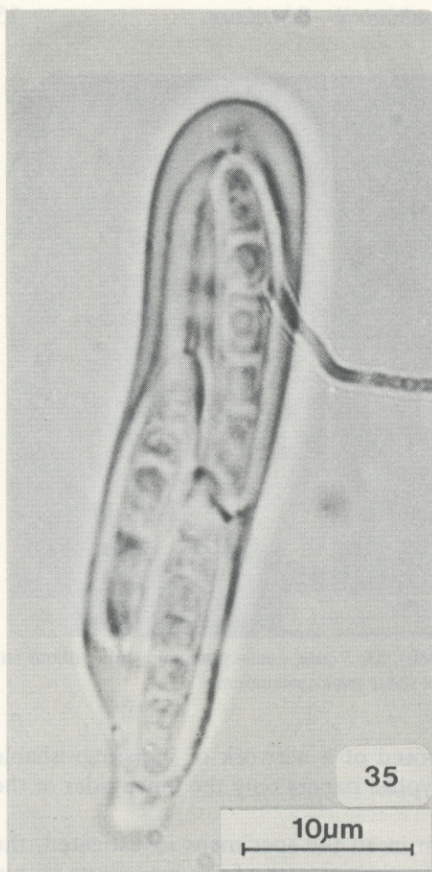
with gonicysts. The outer wall is composed of a network of indistinguishable carbonized hyphae. The collar of white hyphae papers only the inner sides of the cupula, not the bottom of it.

Gonicystangia are remarkably uniform in all the specimens investigated, the only differences being in their size and the compactness of the gonicysts within them. In the African specimens (*O. lambinonii*, *O. santessonii*, and a dubious species from West Africa), they are 0.2–0.3(–0.4) mm diam and contain numerous, densely packed gonicysts. In *O. dibbenii*, *O. luzonensis*, and to a lesser extent in the specimens from Australia and New Guinea, they do not exceed 0.1 mm diam and produce only a few gonicysts.

The term gonicyst designates the spherical to \pm oval glomerules (15–25 μ m diam in the African specimens; 10–15(–20) μ m in the others) (Figs 13–14, 31–32) contained in the gonicystangia. In all species, they comprise a colony of spherical green algae embedded in a hyphal envelope. This envelope is not paraplectenchymatous as clearly shown by SEM photographs. Individual tightly appressed hyphae are easily seen in all cases. Although the hyphal envelope of the gonicysts in the non-African specimens looks more globose in LM, SEM photographs demonstrate that they are identical to those of African specimens.

It has been difficult to determine whether the algal colonies included in the gonicysts are produced by the thallus alga. Attempts to demonstrate unam-

Figs 30–32. 30, *Opegrapha santessonii* (holotype), two sterile thalli with gonicystangia (above), one fertile thallus without gonicystangia (below). 31, Gonicysts of *Opegrapha dibbenii*. 32, Gonicysts of *O. lambinonii* (holotype).



biguously a connection between the thallus alga and the goniocyst alga in species of which I had enough material (*O. lambinonii* and *O. santessonii*) have failed. In *O. dibbenii*, however, squash preparations of a goniocystangium show globose algal cells encircled by hyphae linked directly to rectangular cells typical of the thallus (Fig. 28). This was observed several times and, although it is impossible to tell which of the partners initiates the goniocyst, demonstrates that the alga is the same in the thallus and in the goniocyst. This also indicates that the algal cells included in a fully developed goniocyst are all descended from a single cell. The definition of a goniocyst by Vězda (1980), primarily designed for *Catillaria mirabilis*, similarly applies in this case: a single algal cell is trapped by the fungus and all successive daughter cells (aplanospores?) cannot escape the structure.

Catillaria mirabilis is the only other species certainly known to produce goniocystangia (Figs 5, 33, 34), although they are totally different from those of *Opegrapha*. They first appear as an ill-defined cupula of hyaline interwoven hyphae, devoid of goniocysts. The hyphae of the upper margin differentiate into globose cells but the outer wall remains loose and uncoloured. How the goniocysts succeed in getting aggregated into the structure is unknown to me. The goniocystangia of this species are fragile structures: larger ones are always damaged and their precise role is thus unclear. Indeed what use can this organ provide to the lichen as its whole thallus consists of goniocysts, easily dispersed by running water or by any animal feeding on the leaf surface?

When producing ascomata, the species studied here (especially *O. lambinonii* and *O. santessonii*) produce few if any goniocystangia. In contrast, thalli with numerous goniocystangia are usually sterile (Fig. 30).

Ascomata

The ascomata of this group are typically non-stromatic lirellae, opening by a longitudinal split, with a carbonaceous excipulum. The excipulum is present only laterally, being totally absent below the hypothecium. The hamathecium is composed of branched and anastomosed paraphysoids which are rather stout, being up to $1.5\text{--}2.0\ \mu\text{m}$ thick, quite irregular and sometimes swollen to $2.5\ \mu\text{m}$, especially within the epithecium. The asci are claviform to ovoid, typically bitunicate, with an exoascus that swells strongly in potassium hydroxide solution; the endoascus is slightly amyloid along its whole length and a strongly amyloid ring is easily seen at the apex (asci first mounted in K, then in Lugol's iodine (Figs 35–36). Ascus dehiscence is fissitunicate, at least in *O. lambinonii*, the only species investigated in this respect.

The ascospores are fusiform, transversely septate, and develop a thick gelatinous sheath. When ripe, they are brown to dark brown; the septa are then obscured and the sheath vanishes. An ornamentation is then easily seen in LM and is most probably diagnostic for each species; the material available was unfortunately too scanty to permit SEM observations. The spores reach their maximum length only

FIGS 35–37. 35, 36, Ascus structure of *Opegrapha lambinonii* (Zaire, Lambinon 78/265), mounted first in K then in Lugol's iodine, showing the apical amyloid ring and the amyloid endotunica. 37, Immature spores of *Opegrapha santessonii* (holotype), mounted in K and showing the gelatinous sheath.

after the darkening of their outer walls: thus, fully septate hyaline and smooth spores are shorter and usually narrower than brown, ornamentated ones. On account of the ascus structure and that of the hamathecium and excipulum, the position of the species dealt with here in the genus *Opegrapha* Ach. nom. cons. is the most satisfactory (see Hawksworth *et al.* 1983 for a general account of the Opegraphales and Opegraphaceae; see also Henssen *et al.* 1979 for illustration and some comments on the amyloid ring in the Lecanactidaceae and the Roccellaceae). Although widespread in the tropical regions (as either lichenized or lichenicolous fungi), the genus *Opegrapha* is still poorly known. Further studies might demonstrate its heterogeneity and the necessity to transfer these species to another genus. The foliicolous species may be related to the lichenicolous ones, for example *O. parasitica* and *O. pertusariicola*.

Pycnidia

In spite of their external aspect, the numerous verrucae present on the thallus of all species investigated are not pycnidia. I found them only in one collection (*Opegrapha* sp., Ivory Coast, *Aké Assi* 1260). They are small black verrucae, 60–80 µm in diam, lying on the thallus. Conidiogenous cells are numerous, almost rectangular, 5–6 × 2 µm, enteroblastic, phialidic but not proliferating. Conidia arise singly and terminally and are bacilliform, 3–4 × 1 µm.

Key to recognized species

- 1 Asci 4-spored; ascospores non-loculate, 5-7-septate, never exceeding 21 µm long, papillose when mature **O. lambinonii** (p. 19)
- Asci usually 8-spored; ascospores loculate, mostly at least 7-septate, always exceeding 22 µm long, not papillose but irregularly rugose or striate when mature 2
- 2(1) Thallus usually large, reaching 15 mm in diam; lirellae 0.4–2.0 mm long; spores (8-)9-septate, 26–36 × 5–7 µm when hyaline, reaching 39 × 8 µm and with an irregularly rugose surface when mature. **O. santessonii** (p. 21)
- Thallus small, never exceeding 3–4 mm in diam, or larger but dispersed in small patches; lirellae never exceeding 0.8 mm; spores 9-or more-septate, with a distinct irregular longitudinal ornamentation when mature 3
- 3(2) Thallus in distinct rounded patches; lirellae 0.2–0.4 mm long; spores 9–11(-12)-septate, 28–32 × 3–4.5 µm when hyaline but reaching 42 × 6 µm when mature **O. dibbenii** (p. 19)
- Thalli dispersed in small inconspicuous patches; lirellae 0.5–0.8 mm long; spores (7-)9-septate, 22–27 × 4–5 µm when hyaline but reaching 30 × 5 µm when mature **O. luzonensis** (p. 21)

***Opegrapha dibbenii* Sérusiaux sp. nov.**

Thallus epiphyllus, tenuis, continuus, 3–4 mm diam, brunneus, plerumque verrucis minutis nigris et gonicystangiis instructus. Apothecia lirellina, 0·2–0·4 mm longa, lineares, nigra. Excipulum ex hyphis nigris dense intricatis formatum, sub strato ascigero deficiens; hypothecium indistinctum; hymenium hyalinum, I+ rufescens; paraphysioideae ramosae anastomosantesque, 1·5–2·0(–2·5) μm crassae; asci 6–8–spori; sporae fusiformes, 9–11(–12)–septatae, loculatae, primum incoloratae, laevigatae, ad septa non constrictae et 28–32 \times 3–4·5 μm , deinde nigro-brunneae, irregulariter striatae, ad centrales loculas inflatae et usque ad 42 \times 6 μm metientes. Alga ad *Phycopeltis* pertinens. Typus: Costa Rica, Sérusiaux 3359 (LG).

(Fig. 38)

Thallus foliicolous, \pm circular but with an irregular outline and an effuse margin, usually 3–4 mm diam, very rarely more, greenish brown to brown, rather dull, surface usually covered with minute (less than 0·05 mm in diam) black verrucae. *Gonicystangia* \pm abundant, sometimes absent, 0·1 mm diam; gonicysts few, loosely packed in the gonicystangia. *Ascomata* lirelliform, abundant, always simple, straight or slightly curved, 0·2–0·4 mm long with an excipulum distinctly spreading on the thallus surface where it forms an irregular outline, black, opening by a longitudinal split. Excipulum black or very dark brown, made of intricated hyphae with carbonized walls, absent under the hypothecium layer; hypothecium indistinct; hymenium hyaline, I+ reddish. *Paraphysoids* branched and anastomosed, 1·5–2·0 μm thick, locally inflated up to 2·5 μm ; asci clavate to ovoid, two-layered, with initially 6–8 spores but only 4–6 reaching maturity. *Ascospores* fusiform, with rounded ends, 9–11(–12)–septate, tending towards locular, at first hyaline, smooth, not constricted at the septa and 28–32 \times 3–4·5 μm , later becoming brown, with an outer surface marked with irregular longitudinal lines, constricted at the septa and reaching 42 \times 6 μm . *Phycobiont*: a species of *Phycopeltis* with irregularly arranged rows of rectangular cells, or without any rows of cells.

This lichen is named in honour of Dr M. J. Dibben who organized the field trip in Costa Rica during which this species was collected.

Specimen examined: **Costa Rica**: Puntaneras prov., on the Pacific Coast, Puerto Quepos, Parque Nacional de la Punta Catedral, primary forest along the beach, on leaves of unknown shrubs, 1979, Sérusiaux 3359 (LG- holotype; MIL- isotype).

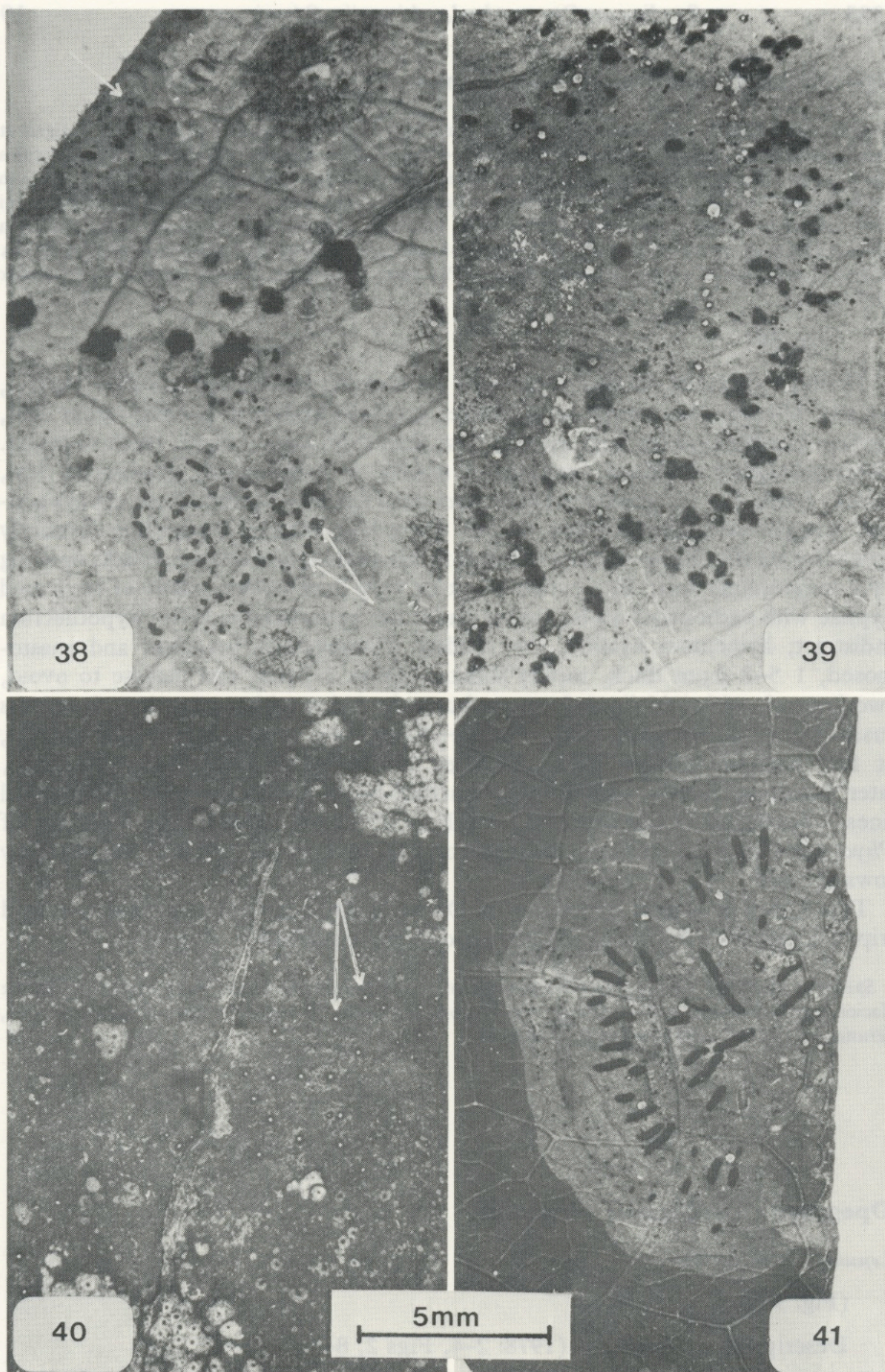
***Opegrapha lambinonii* Sérusiaux**

Lejeunia, n.s. 90: 2(1978).

(Fig. 39)

Description in Sérusiaux (1978: 2–4, Figs 2, 8–11).

Specimens examined: **Zaire**: Kivu, IRSAC reserve, on the north side of the Luhoho river, \pm 850 m, undisturbed rain forest, foliicolous on *Garcinia smeathmanii*, *Lambinon* 72/18 (LG-holotype); *loc. cit.*, foliicolous on leaves of an unknown shrub, *Lambinon* 78/265 (LG, BM, US, hb Vězda), 78/266 (LG) and 78/267 (LG); *loc. cit.*, on leaves of *Gilbertiodendron dewevrei*, *Lambinon* 78/297 (LG).



Figs 38–41. 38, *Opoglypha dibbenii* (holotype). 39, *O. lambinonii* (holotype). 40, *O. luzonensis* (holotype). 41, *O. santessonii* (holotype). Same scale for all pictures. Arrows point to goniocystangia.

***Opegrapha luzonensis* Sérusiaux sp. nov.**

Thallus epiphyllus, indistinctus, dispersus, usque ad 10 mm diam, brunneus, verrucis minutis nigris et goniocystangiis instructus. Apothecia lirellina, 0·5–0·8 mm longa, lineares, nigra. Excipulum ex hyphis nigris dense intricatis formatum, sub strato ascigero deficiens; hypothecium indistinctum; hymenium hyalinum, I+ rufescens; paraphysioideae ramosae anastomosantesque, 1–1·5 µm crassae; asci (4–6)–8-sporei; sporae fusiformes, (7–)9-septatae, loculatae, ad septa non constrictae, primum incoloratae, laevigatae et 22–27 × 4–5 µm metientes, deinde nigro-brunneae, irregulariter striatae et usque ad 30 µm metientes. Alga ad *Phycopeltem* pertinens. Typus: Philippines, Elmer 16963 (FH).

(Fig. 40)

Thallus foliicolous, ± circular, not exceeding 10 mm diam, dispersed, made of small irregular patches of 1–4 mm in diam, patches slightly effigurate to crenulate, matt, grey-brown to pale brown, margins provided with minute (less than 0·05 mm in diam) black verrucae. *Goniocystangia* ± abundant, but not present on all thallus patches, 0·1 mm diam; goniocysts usually rather few. *Ascomata* lirelliform, rare, simple or very rarely bifurcate, straight or slightly curved, 0·5–0·8 mm long, 0·1–0·15 mm wide, black, opening by a longitudinal split. Excipulum black or dark brown, made of densely intricated hyphae with carbonized walls, absent under the hypothecium layer; hypothecium indistinct; hymenium hyaline, I+ reddish. *Paraphysoids* branched and anastomosed, 1–1·5 µm thick, sometimes inflated at the apices; asci clavate to ovoid, two-layered, with (4–6)–8 spores. *Ascospores* fusiform, with rounded ends, (7–)9-septate, locular, at first colorless, smooth and 22–27 × 4–5 µm, later brown and with irregular longitudinally striated surface and reaching 30 µm long. *Phycobiont*: a species of *Phycopeltis* with very irregularly arranged rows of rectangular to rounded cells.

Specimen examined: Philippines, Luzon, prov. Sorsogon, Mt Bulusan, Irosin, 1916, Elmer 19963 (FH-holotype; LG-isotype).

***Opegrapha santessonii* Sérusiaux sp. nov.**

Thallus epiphyllus, tenuis, continuus, 3–15 mm diam, brunneus, verrucis minutis nigris et goniocystangiis instructus. Apothecia lirellina, 0·4–2·0 mm longa, lineares, nigra. Excipulum ex hyphis nigris dense intricatis formatum, sub strato ascigero deficiens; hypothecium nigricans; hymenium hyalinum, I+ rufescens; paraphysioideae ramosae anastomosantesque, 1·5–2·0(–2·5) µm crassae; asci (6–)8-sporei; sporae fusiformes, (8–)9-septatae, loculatae, primum 26–36 × 5–7 µm, ad septa non constrictae, incoloratae et laevigatae, deinde nigro-brunneae, rugatae et usque ad 39 × 8 µm metientes. Alga ad *Phycopeltem* pertinens. Typus: Zaire/Kivu, Lambinon 72/23 (LG).

(Fig. 41)

Thallus foliicolous, circular or semi-circular if growing on the leaf edge or along a scar, 3–15 mm diam, sometimes more, sharply delimited at the margins, brown to greenish brown; upper surface shiny, provided with extremely small (less than 0·05 mm in diam) black verrucae usually quite abundant and arranged in concentric rings. *Goniocystangia* usually abundant, absent on very few thalli which are then well provided with ascocarps, circular, 0·3(–0·4) mm diam, 0·1–0·15 mm high; goniocysts usually numerous and densely packed in the goniocystangia. *Ascomata* lirelliform, rare to abundant, linear or very rarely bi- or quadri-furcate, prominent, straight, 0·4–2·0 mm long, 0·1–0·2 mm wide, usually radiately

arranged on the thallus, black, opening by a longitudinal split. Excipulum black or very dark brown, made of densely intricated hyphae with carbonized walls, absent under the hypothecium layer; hypothecium blackish and hymenium hyaline, I+ reddish. *Paraphysoids* branched and anastomosed, $1.5-2.0(-2.5)$ μm thick, locally inflated up to $2-2.5$ μm , especially at the tips; asci clavate to ovoid, two-layered, (6-)8-spored. *Ascospores* fusiform, with rounded ends, with a thick, distinctly two-layered wall, (8-)9-septate, locular, at first hyaline, smooth, $26-36 \times 5-7$ μm , later becoming dark brown and irregularly but mainly longitudinally worn and rugose, and reaching 39×8 μm . *Phycobiont*: a species of *Phycopeltis* with long rectangular cells ($25 \times 30 \times 4-6$ μm), very regularly arranged in radiate rows.

The lichen is named in honour of Professor R. Santesson who first discovered goniocystangia.

Specimens examined: **Zaire**: Kivu, IRSAC reserve, on the north side of the Luhoho river, ± 850 m, undisturbed rain forest, foliicolous on *Grossera multinervis*, *Lambinon* 72/23 (LG-holotype); *loc. cit.*, on leaves of unknown shrub, *Lambinon* 78/265 (LG). Haut-Zaire, km 78 of the road Kisangani-Bafwaswende, dense and undisturbed rain forest, *Lisowski* 43172 (hb Vězda); *loc. cit.*, km 21 N of Kisangani and 4 km E of Bawi, secondary forest, *Lisowski* 43069 and 43194 (hb Vězda); *loc. cit.*, km 29 of the road Kisangani-Bengamisa, *Lisowski* 44380 (hb Vězda, 3 collections). Yangambi, near the University campus (Unaza), *Woolhouse* s.n. (hb Henderson).

Undetermined thalli

Itemized here are collections of sterile foliicolous thalli that most probably belong to the *Opegrapha lambinonii* group. They all have *Phycopeltis* as phycobiont and produce typical goniocystangia. As they are not fertile, they cannot be irrefutably assigned to any of the species described in this paper. Nevertheless, assemblages of collections can be made on the basis of the morphology and the anatomy of the thallus and the goniocystangia. Some of these assemblages might represent additional taxa within the group.

(1) Collections referable to either *Opegrapha lambinonii* or *O. santessonii*. They have a phycobiont with very regularly arranged rows of large and rectangular cells, and large (0.3 mm diam) goniocystangia with densely packed goniocysts. These two features are typical of *O. lambinonii* and *O. santessonii*.

Specimens examined: **Zaire**: Kivu, Irangi, IRSAC reserve, north side of the river Luhoho, ± 850 m, undisturbed rain forest, foliicolous on *Brazzea longipedicellata*, *Lambinon* 72/20 (LG); *loc. cit.*, foliicolous on *Scaphopetalum dewevrei* var. *suborophila*, *Lambinon* 78/262 and 78/299 (both LG); *loc. cit.*, foliicolous on *Puelia ciliata*, *Lambinon* 78/263 (LG). Maniema, 8 km NW of Lubutu, dense primary rain forest near Anza river, *Lisowski* 40326 (hb Vězda). Maiko National Park, N of Ubukala village, side of the Lubutu river, primary rain forest, *Lisowski* 45054 (LG). Haut-Zaire, Kisangani, 21 km ad septentrionem versus a Kisangani, prope vicum Bawi, alt. 200-500 m.s.m., epiphylla in sylvia virginea, *Lisowski* 43069 [Vězda, Lich. Sel. Exs. no. 1479, sub *Opegrapha lambinonii*.] (LG). Km 29 of the road Kisangani-Bengamisa, 200-500 m, *Lisowski* 44380 (hb Vězda, LG). Bas-Uele, 5 km W of Likati, forest near a river, *Lisowski* 46533 (LG). Wangata, *Staner* L 458 (LG).

(2) The following four collections have thalli very similar to those of *O. lambinonii* or *O. santessonii* but they are somewhat smaller and less shiny. One of them (*Aké Assi* 12965) has some ascomata which are simple, straight and $0.4-0.5$ mm long. A few spores were seen; they are 8 per ascus, fusiform and \pm locular,

7-septate, with a thick two-layered wall, not constricted at the septa and $28\text{--}33 \times 8 \mu\text{m}$. There is little doubt that it represents a new species but the material is far too scanty to permit a satisfactory description.

Specimens examined: **Ivory Coast:** Forest E of Sakré, *Aké Assi* 12965 (hb Vězda). Banca Forest, *Aké Assi* 12600 (hb Vězda). Yapo Forest, *Hendrickx* 7343B (BR, cited by Sérusiaux 1978: 4).—**Guinea:** Macenta, 600–700 m in silviis secundariis, *Lisowski* s.n. (hb Vězda).

(3) In the large collections of foliicolous lichens from New Guinea that are available to me, a few thalli with goniocystangia were found. They are \pm circular, reaching 3–5 mm diam, usually continuous, but either with an indistinct margin or brown and easily seen one, green to greenish brown, rather dull, with very abundant minute verrucae scattered all over the surface; goniocystangia few to abundant, 0.1–0.15 mm, with few goniocysts. Unfortunately, none of these collections is fertile.

Specimens examined: **New Guinea:** Madang, hills W of Yoro (=Mugamat), 100–300 m, foliicolous on unknown shrubs, 1980, *Demoulin* 5940 & *Smeets* (LG). Mt Manke, vicinity of Bulolo, 14–1500 m, rain forest, *van Zanten* s.n. (hb Vězda). Mt Kaisenik, vicinity of Wan, 1500 m, rain forest, *van Zanten* s.n. (LG).

(4) Scanty or badly developed specimens.

Specimens examined: **Colombia:** Cauca River, 1894, *Denton* (FH, cited by Sérusiaux 1978: 4).—**Brazil:** Amazonas, Regenwälder am Rio Negro, zwischen 100–200 km oberhalb von Manaus, 40 m, *Kalb* 310 (LG).—**Zaire:** Haut-Zaire, Yangambi, Esali island on the Zaire river, *Lisowski* 47946 (LG).—**Australia:** Queensland, Davies Creek, Atherton Tableland, SE of Mareeba, virgin rain forest, *Weber* L-54923 (hb Vězda).—**Thailand:** Khaoyai National Park, deep valley with tropical forest, 1979, *Demoulin* 5468 (LG).

Lichenicolous fungi

As with many foliicolous lichens, the species of the *Opegrapha lambinonii* group host several parasymbiotic or parasitic fungi. They can be quite abundant and diverse: in the collection *Lambinon* 78/265 (Zaire: Kivu), *Opegrapha lambinonii* is attacked by at least five different pyrenomyces. They usually occur on or inside the thallus, but, in one collection (New Guinea: Mt Manke, *van Zanten* s.n.), a small cleistocarpic pyrenomyces was found (ascmata hyaline, 50–60 μm in diam, asci bitunicate, spores 8 per ascus, muriform, $5\text{--}8 \times 2\text{--}3 \mu\text{m}$) growing on the goniocysts.

The identification of those fungi proved to be difficult, even to the generic level. The only species identified so far is the hyphomycete *Ampullifera foliicola* Deighton (description in Hawksworth 1979: 199–201) that was found on *Opegrapha lambinonii* (Zaire: Kivu, *Lambinon* 78/297) and on *O. santessonii* (Zaire: Haut-Zaire, *Lisowski* 43069). In both cases, the fungus is extremely abundant but causes relatively little damage to its host.

I wish to thank Dr V. Demoulin, Mr A. Henderson, Professor J. Lambinon and Dr A. Vězda for placing most valuable collections at my disposal. I am also indebted to the curators of herbaria (mainly BM, FH and G) for allowing me to study material in their care, and grateful to Drs B. J. Coppins and D. L. Hawksworth for assistance in preparing my manuscript for publication. SEM micrographs were taken at the Jardin Botanique National de Belgique with a microscope Philips 501 B; I thank Professor E. Petit, Dr J. Rammeloo and M. Verhaegen for their active co-operation in this regard.

REFERENCES

- Acton, E. (1909) *Botrydina vulgaris*, Brébisson, a primitive lichen. *Ann. Bot. Lond.* **23**: 579–585.
- Ahmadjian, V. & Jacobs, J. B. (1982) Artificial re-establishment of lichens. III. Synthetic development of *Usnea strigosa*. *J. Hattori bot. Lab.* **52**: 393–399.
- Ahmadjian, V., Jacobs, J. B. & Russell, L. A. (1978) Scanning electron microscope study of early lichen symbiosis. *Science, N. Y.* **200**: 1062–1064.
- Bachmann, E. (1925) Die Morioloaceen. *Nyt Mag. Naturvid.* **63**: 170–228.
- Beltman, H. A. (1978) Vegetative Strukturen der Parmeliaceae und ihre Entwicklung. *Bibl. lich., Lehre* **11**: 1–193.
- Boissiere, J. C. (1980) Un vrai Basidiolichen européen: l'*Omphalina umbellifera* (L. ex Fr.) Quél. Étude ultrastructurale. *Cryptogamie, bryol. lichén.* **1**: 143–149.
- Clements, F. E. & Shear, S. L. (1931) *The Genera of Fungi*. New-York: Hafner.
- Coppins, B. J. (1983) A taxonomic study of the lichen genus *Micarea* in Europe. *Bull. Br. Mus. nat. Hist., Bot.* **11**: 17–214.
- Degelius, G. (1945) Lichinisierete Hormocysten, ein neuer Diasporentypus der Flechten. *Svensk bot. Tidskr.* **39**: 419–430.
- Eriksson, O. (1981) The families of bitunicate ascomycetes. *Opera bot.* **60**, 1–209.
- Gams H. (1962) Die Halbflechten *Botrydina* und *Coriscium* als Basidiolichenen. *Öst. bot. Z.* **109**: 376–380.
- Hawksworth, D. L. (1979) The lichenicolous Hyphomycetes. *Bull. Br. Mus. nat. Hist., Bot.* **6**: 183–300.
- Hawksworth, D. L., Sutton, B. C. & Ainsworth, G. C. (1983) *Ainsworth & Bisby's Dictionary of the Fungi*. Seventh Edition. Kew: Commonwealth Mycological Institute.
- Hedlund, T. (1895) Ueber die Flechtengattung *Moriola*. *Bot. Zbl.* **63**: 376–377.
- Henssen, A. (1968) *Thyrea radiata*, eine *Lempholemma*-Art mit Hormocystangien. *Ber. dt. bot. Ges.* **81**: 176–182.
- Henssen, A. (1969) An interesting new species of *Lempholemma* from Canada. *Lichenologist* **4**: 99–104.
- Henssen, A. (1979) New species of *Homothecium* and *Ramalodium* from S. America. *Bot. Notiser* **132**: 257–282.
- Henssen, A., Renner, B. & Vobis, G. (1979) *Sagenidium patagonicum*, a new South American lichen. *Lichenologist* **11**: 263–270.
- Honegger, R. (1984) Cytological aspects of the mycobiont-photobiont relationship in lichens. *Lichenologist* **16**: 111–127.
- Honegger, R. & Brunner, U. (1981) Sporopollenin in the cell walls of *Coccomyxa* and *Myrmecia* photobionts of various lichens: an ultrastructural and chemical investigation. *Can. J. Bot.* **59**: 2713–2734.
- Jaag, O. (1933) *Botrydina vulgaris* Bréb., eine Lebensgemeinschaft von Moosprotonen und Grünalgen. *Bull. Soc. bot. Suisse* **42**: 169–185.
- Keissler, K. (1927) Über die als Pilze anzusehenden Arten unter den Norman'schen Morioloaceen. *Nyt Mag. Naturvid.* **65**: 77–92.
- Lange, M. (1981) Typification and delimitation of *Omphalina* Quel. *Nord. J. Bot.* **1**: 691–696.
- Norman, J. M. (1871a) Fuliginosae lichenosae eller Moriolei. *Bot. Notiser* **1871**: 9–20.
- Norman, J. M. (1871b) Allelositismus eller det förhållandet, att en organism för utförandet af sina livsfunktioner begagnar införlifvade främmande organ, samtillhöra en heterogen organism. *Bot. Notiser* **1871**: 46–53.
- Norman, J. M. (1871c) Utdrag ur utländska arbeten. Allelositismus. *Bot. Notiser* **1871**: 82–85.
- Norman, J. M. (1876) Nonnullae observationum ulteriorum Moriolorum. *Bot. Notiser* **1876**: 161–176.
- Nyman, E. (1895) 4. En *Moriola*-likmande laf. *Bot. Notiser* **1895**: 242–244.
- Ozenda, P. (1963) Lichens. *Handb. Pflanzenanatomie* **6**(9): 1–199.
- Ozenda, P. & Clauzade, G. (1970) *Les Lichens. Étude biologique et flore illustrée*. Paris: Masson.
- Poelt, J. & Döbbeler, P. (1975) Über moosparasitische Arten der Flechtengattung *Micarea* und Poelt, J. & Döbbeler, P. (1975) Über moosparasitische Arten der Flechtengattung *Micarea* und *Vezdaea*. *Bot. Jahrb. Syst.* **96**: 328–352.
- Poelt, J. & Döbbeler, P. (1979) *Bryostigma leucodontis* nov. gen. et spec., eine neue Flechte mit fast unsichtbaren Fruchtkörpern. *Pl. Syst. Evol.* **131**: 211–216.
- Poelt, J. & Hertel, H. (1968) *Pachyascus lapponicus* nov. gen. et spec., eine bemerkenswerte Flechtengattung unklaren Anschlusses. *Ber. dt. bot. Ges.* **81**: 210–216.
- Poelt, J. & Jülich, W. (1969) *Omphalina grisella*, ein weiterer lichensierter Blätterpilz in den Alpen. *Herzogia* **1**: 331–336.
- Poelt, J. & Oberwinkler, F. (1964) Zur Kenntnis der flechtenbildenden Blätterpilze der Gattung *Omphalina*. *Öst. bot. Z.* **111**: 393–401.

- Printz, H. (1940) Vorarbeiten zu einer Monographie der Trentepohliaceae. *Nytt Mag. Naturvid.* **80**: 137–210.
- Santesson, R. (1968) Lavar. Some aspects on lichen taxonomy. *Svensk Naturv.* **1968**: 176–184.
- Sérusiaux, E. (1978) Contribution à l'étude des lichens du Kivu (Zaire), du Rwanda et du Burundi. II. Espèces nouvelles de lichens foliicoles. *Lejeunia, n.s.* **90**: 1–18.
- Tschermak-Woess, E. & Poelt, J. (1976) *Vezeadaea*, a peculiar lichen genus, and its phycobiont. In *Lichenology: Progress and Problems* (D. H. Brown, D. L. Hawksworth & R. H. Bailey, eds), 89–105. London and New-York: Academic Press.
- Vězda, A. (1961) *Lecidea praecox*, eine neue Flechten-Art aus der Verwandtschaft von *Lecidea uliginosa* (Schrad.) Ach. *Preslia* **39**: 1–4.
- Vězda, A. (1977) *Lichenes Selecti Exsiccati*. Fasc. LX (nos. 1476–1500). Průhonice: Instituto Botanico Academiae Scientiarum Českoslovacae.
- Vězda, A. (1980) Foliicole Flechten aus Zaire. Die Arten der Sammelgattungen *Catillaria* und *Bacidia*. *Folia geobot. phytotax. bohemoslovaca* **15**: 75–94.
- Vězda, A. (1983) Foliicole Flechten aus der Kolchis (West-Transkaukasien, UdSSR). *Folia geobot. phytotax. bohemoslovaca* **18**: 45–70.
- Wetmore, C. M. (1974) New type of soredium in the lichen family Heppiaceae. *Bryologist* **77**: 208–215.

Accepted for publication 30 April 1984