Morphological diversity in the hyphophores of *Gomphillaceae* (*Ostropales*, lichenized Ascomycetes)

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Hyphophores are highly specialized conidia-producing structures characteristic of the *Gomphillaceae*. In this paper the high diversity and variability of these structures is evaluated. New setiform hyphophores of unidentified species of the genera *Calenia*, *Echinoplaca* and *Tricharia* are described. A new grouping is proposed, based on the external morphology and the possible ontogeny of these conidiomata.

Key words: foliicolous-lichens, hyphophores, conidiomata

Introduction

The vegetative diaspores (produced by the thallus) and asexual diaspores (produced by conidiomata) can show great variability within lichens. In some cases both symbionts are involved. This occurs in vegetative structures such as isidia, soredia and propagules such as phyllidia, small squamules and thallus portions that can be dispersed (Vezda, 1972; Büdel and Scheidegger, 1996; Lücking, 1997).

Conidiomata are also diverse. Pycnidia and sporodochia produce spores which can be associated and dispersed with algae or not. Pycnidia are closed structures from which conidia are dispersed through a pore (ostiole), while sporodochia have the conidiogenous area completely exposed. In campylidia, the conidiogenous layer is partially covered by a lobule; while in hyphophores, conidia are generally produced on elevated peduncles and dispersed as diahypha masses (Vezda and Poelt, 1987). In both cases, conidia are frequently found together with algae.

Vobis (1980, 1981, 1992) recognized coelomycetous and hyphomycetous anamorphs in the lichens. Pycnidial conidiomata, sporodochial conidiomata,

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and campylidia are found in both lichenized and non-lichenized ascomycetes. As far as is known, hyphophores are restricted to the *Gomphillaceae*.

Vegetative diaspores such as isidia and pseudoisidia are not common in *Gomphillaceae*. Vězda (1972) mentioned them in *Gyalideopsis anastomosans* and Lücking (1997) described structures similar to isidia on the thallis of *Actinoplaca strigulacea* and *Echinoplaca gemmifera*. Unidentified species of *Echinoplaca* from Argentina and Brazil also show isidia, wich appear as small, conical, orange or pale yellow structures.

Campylidia are asexual reproductive organs, with a complex anatomy similar to that of pycnidia, but partially opened and with the conidiogenous layer covered by a lobule. They are commonly found in *Ectolechiaceae and Pilocarpaceae*, but also in *Arthoniaceae* and *Monoblastiaceae*. Sérusiaux (1995) described in detail the campylidia of one species of *Byssoloma* and two species of *Woessia*. He considered this kind of conidiomata as an adaptation to conidial dispersal in humid tropical regions. In *Gomphillaceae*, campylidia were reported only in *Gyalideopsis hyalina* Lücking; in this species they are tomentose and yellowish white, infundibular or ear-shaped, and elevated over the thallus. However, like isidia, the campylidia of this family are not homologous with those of other lichens, but instead represent highly modified hyphophores.

Pycnidia are slightly sunken or immersed conidiomata, they can be unilocular or plurilocular. They have been observed on young thalli of *Gyalectidium* and *Gomphillus*. Ferraro (2000) showed that in species of *Tricharia* the mature apothecia become converted into conidiomata and the whole structure produces conidia. In this genus the muriform spores can also disintegrate in conidia (Santesson, 1952).

Hyphophores are structures which produce diahyphae, variable in shape, elevated or flattened on the thallus. Vězda (1973) first described them and elucidated their dispersal role. The term "diahyphae", according to Vězda and Poelt (1987), refers to a hypha that ramifies at the apex in several moniliform branches, with marked constrictions at the septa that give the cells the appearance of chain links. Conidiophore diahyphae are dispersed as a mass can group to be dispersed, and these masses or fascicles can contain algae cells. Thus they act as asexual diaspores, sometimes carrying their algal symbiont with them.

Hyphophores have previously been called "sporodochia" or "acervuli", and were interpreted as infertile filaments, imperfect lichens or lichenized mushrooms. Müller Argoviensis (1891) used the term sporodochia in his description of *Actinoplaca strigulacea*.

Vobis *et al*. (1992) distinguished sporodochia from pycnidia, considering both as different types of conidiomata, i.e., different structures that produce conidia; he referred to them as pycnidial conidiomata and sporodochial conidiomata. Santesson (1952) observed hyphophores in several species, but misinterpreted their significance. He described hyphophores as infertile filaments in *Aulaxina multiseptata* and in *Echinoplaca atrofusca*. He considered them as nonlichenized fungi in other cases, and used the name *Cristidium pallidum* for the scaly hyphophores of *Gyalectidium filicinum*. He also called them sporodochia in *Actinoplaca strigulacea*.

In the period between 1961 and 1975, a group of Brazilian researchers, led by Batista described hyphophores as parts of imperfect lichens, although they never used the term hyphophore. These authors contributed much information about many genera of foliicolous lichens, based on their anamorphs. However, only some of their published genera and species names are regarded as valid. Lücking *et al*. (1998) checked all proposed names, assigning them correlative status. Ferraro *et al*. (2001) pointed out that Cavalcante *et al*. (1972) created the genus *Tauromyces* Cavalc. & A.A. Silva based on a hyphophore misinterpreted as a separate lichen.

In the "Dictionary of the fungi" (Kirk *et al*., 2002) hyphophores are considered as "erect stalked peltate asexual sporophores in the *Asterothyriaceae*, *e.g*. *Echinoplaca*, *Gyalideopsis*, *Tricharia*". The term is not included in the list of obsolete terms associated with conidiomata. The term conidiomata is applied to any structure that produces conidia. Sérusiaux (1986) described and illustrated the development of the scaly hyphophores in Argentinian species of *Gyalectidium*. Vězda (1979) classified hyphophores as zygomorphic or radiate, according to their symmetry, and also made comments about the morphology and position of the conidiogenous hyphae.

There are differences in the location of the hyphophores on the thallus. It is quite common to find them centrally on the lichenized thallus, or occurring more or less in circles, as do the scales of *Gyalectidium*. The pedunculate hyphophores may occur anywhere on the thallus, and do not follow an ordered pattern, but in genera such as *Aulaxina*, they are found on the prothallus. It is common to find fungal spores on the thallus and at the base of the hyphophores. In one species of *Echinoplaca*, hyphophores were observed with fungal hyphae and spores germinating on the peduncle without diahyphae.

Material and methods

Hyphophores were mounted in 5% potassium hydroxide (KOH), and coloured with phloxine and lactophenol cotton blue (LCB). In some cases, after

a few minutes, the material was washed again with KOH and coloured once more. The measurements and illustrations were made with the camera lucida of Willd M5 or Zeiss dissecting microscopes. Light micrographs were taken with a Nikon Optiphot 2 microscope.

Results and discussion

Some hyphophore types have been recently observed in material from Argentina and Paraguay and are added to the ones listed by Vězda (1973). The new types correspond to four species of *Echinoplaca*, one species of *Tricharia* and one of *Calenia*. Comments about some variants of the scaly type of hyphophores found in species of the genus *Gyalectidium*, are also added. The classification proposed below considers the degree of adnation as well as the symmetry and the shape of the hyphophore. Three groups with eleven **[1]** – **[11]** different types of hyphophores are established.

Group 1.
Linear, pedunculate or setiform hyphophores.

Example: *Echinoplaca pellicula* (Fig. 1).

[1] Simple (Fig. 2), **[2]** branched (Fig. 11), **[3]** conical or pyramidal (Fig. 26), **[4]** with a hand- or spoon- shaped apex (Figs 3-4), **[5]** with penicillate, retrorse apex, **[6]** with a capitate, head-like apex (pin), **[7]** with an peltate, umbrella-like apex.

Group 2.
Exposed, **sessile** to adnate hyphophores.

Example of *Actinoplaca strigulacea* (Fig. 7) and *Echinoplaca gemmifera*.

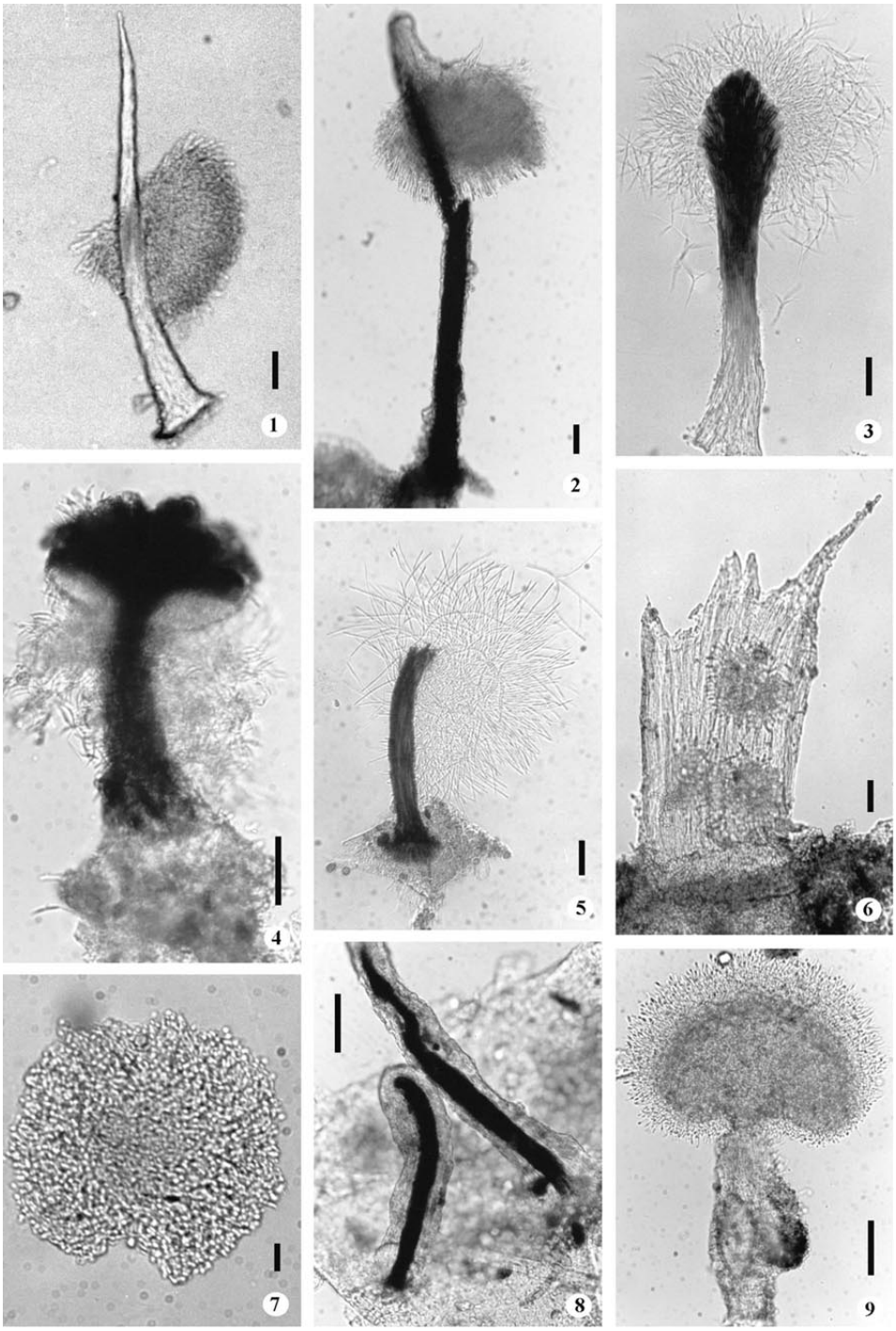
[8] They lack peduncles and the diahyphae masses are borne directly on the thallus.

Group 3.
Adnate hyphophores, covered by a scale.

Example: *Hippocrepidea nigra* and *Gyalectidium fantasticum* (Fig. 6).

[9] Scaly: with broad scales - with an entire upper margin, **[10]** with a lacerate upper margin (Fig. 6), **[11]** with laciniate narrow scales

Figs 1-9. Different types of hyphophores found in specimens of *Gomphillaceae*. **1.** *Echinoplaca pellicula*. **2.** *Tricharia* sp. **3.** *Tricharia planicarpa*. **4.** *Gyalideopsis cochlearifer*. **5.** *Tricharia aulaxinoides*. **6.** *Gyalectidium filicinum*. **7.** *Actinoplaca strigulacea*. **8.** *Gyalideopsis choshuencensis*. **9.** *Gyalideopsis vulgaris*. Bars = 0.05 mm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Linear, pedunculate or setiform hyphophores (Group 1).

In this group, the peduncles resemble hairs, bristles, or setae. Hairs are generally flexible, their tips tapering to a point, with variable length and variable width at the base, white or black pigmented. They can be simple or bifurcated.

Bristles are stiff, shorter than hairs, generally very fragile. Setae are of intermediate length and variable stiffness.

Like the sterile hairs of the thallus in many *Gomphillaceae*, the setiform and pedunculate hyphophores are constituted by hypha fascicles. They can be black, with thick, pigmented walls, or white, with thin and translucent walls. Wall pigments are melanoid, as in other fungi such as the dematiaceous hyphomycetes. These pigments have been little-studied chemically. They are responsible for dark or reddish colours. Only in a few cases, are tannins responsible for these colours in the walls.

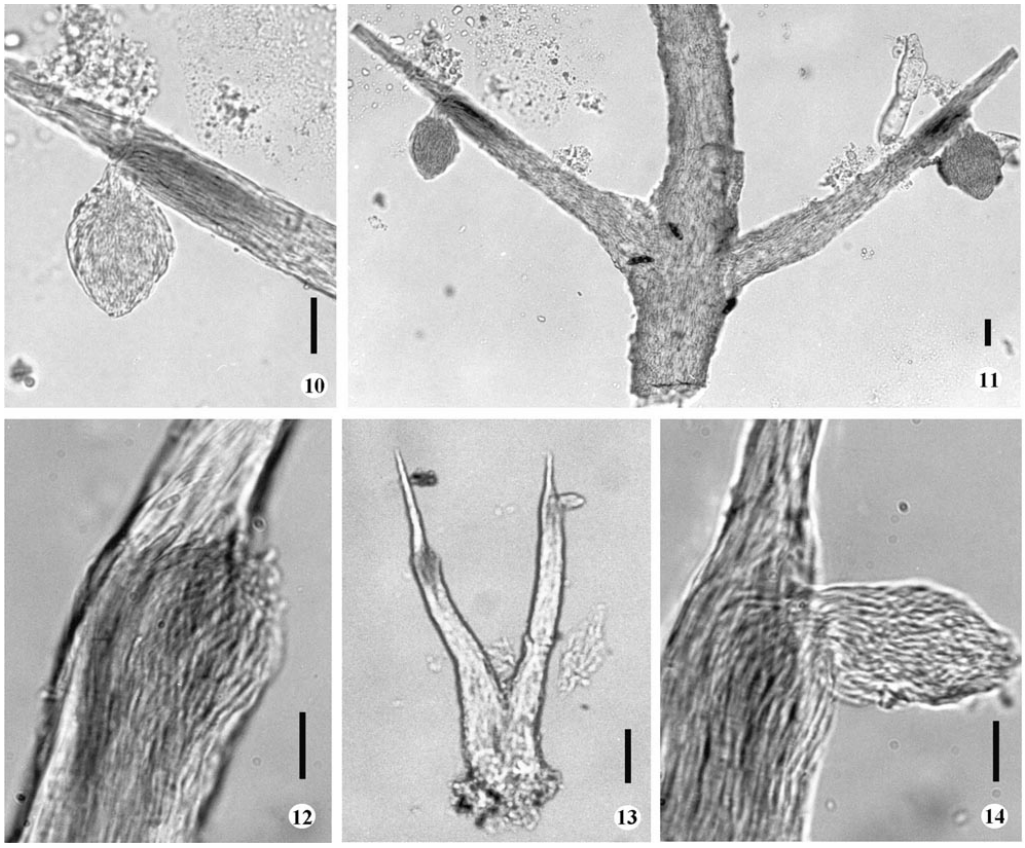
The position of the fascicles of diahyphae supported by the hairs, bristles or setae, can be apical, subapical or intermediate. In the majority of hyphophores with translucent peduncles, the fascicles of diahyphae are located in a darker area. In this area, the hyphae show thick brownish walls, and are pasked tighter than those in the rest of the bristle.

In the genus *Echinoplaca*, many new anamorphs were found, but apothecia were lacking, which impeded identification of species. The specimens are included in this genus because of their generally thick and verrucose thallus, and because of the presence of setiform pedunculate hyphophores.

Commonly, the diahyphae are apical, located at the peduncle apex as in species of *Echinoplaca*, *Calenia* and *Tricharia*. In *Echinoplaca pellicula*, they can be located in the middle of the bristle, which in this species, is clear, acicular with a wide base, producing fusiform simple conidia. Hyphophores similar to those of *E. pellicula* are found in *Echinoplaca* sp. *(O. Popoff 3222*, *CTES)*, (Fig. 1), but the diahyphae masses are subapical, and the seta is thicker and conspicuously curved (Fig. 20).

Branched hyphophores and sterile setae in the thallus do not seem to be common. Vězda (1979) illustrated hyphophores with several branches starting from a common base in *Tricharia cretacea*, and black peduncles with short apical branches in *Tricharia substipitata*. Branched sterile setae are found in *Echinoplaca furcata* and *E. verrucifera*, as well as in *Tricharia ramifera* and *T. armata*.

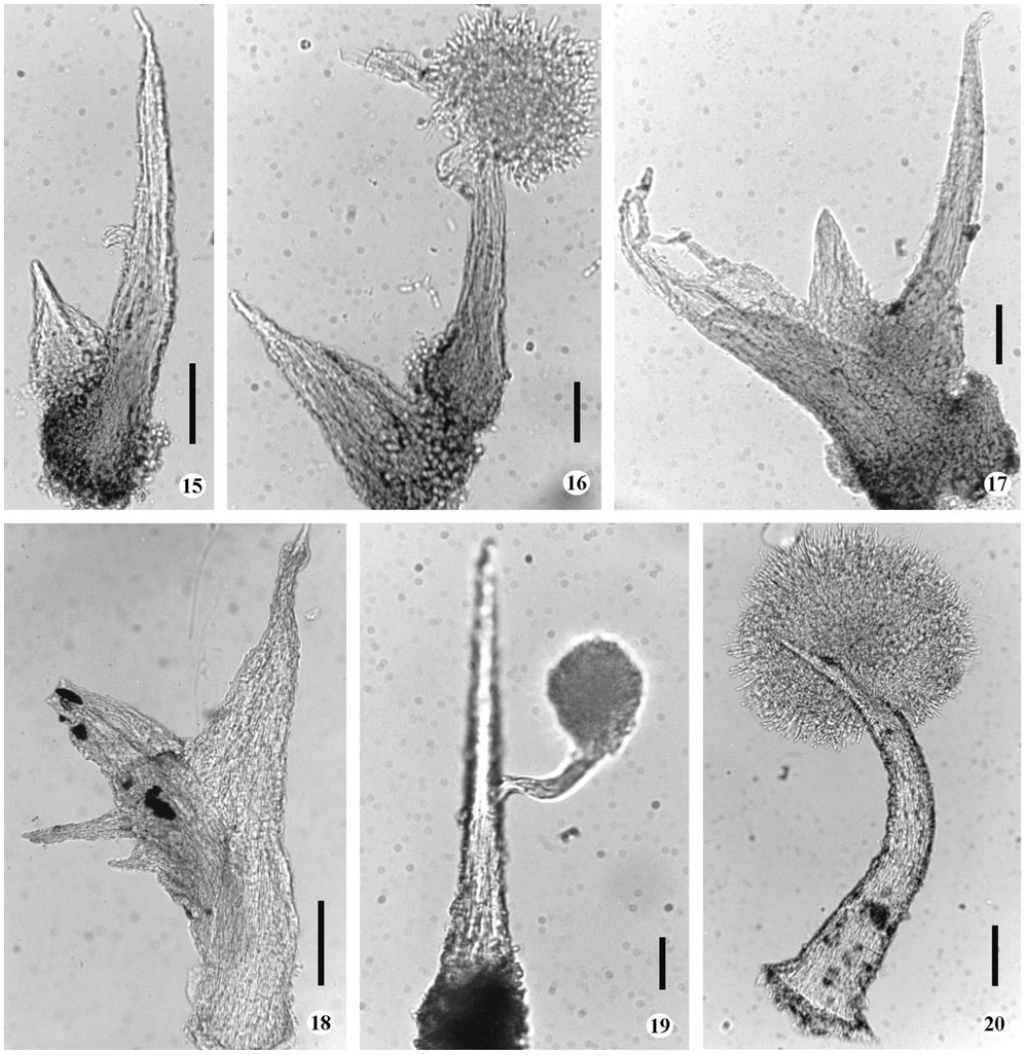
For Argentina, branched hyphophores were first mentioned in *Echinoplaca sp. (L. Ferraro et al. 6082*, CTES*)*, which has a long yellowish



Figs 10-14. Branched hyphophores of *Echinoplaca* sp. (L. Ferraro *et al*. 6082, CTES). **10.** Details of diahyphae at the end of a lateral branch. **11, 13.** View of branched hyphophores. **12, 14.** Details of the origin zone of diahyphae. Bar = 0.1 mm.

brown peduncle, the same color as the sterile setae of the thallus (Figs 10-14). These hyphophores have a long and erect central structure, which carries two ascending branches just above its base (Fig. 11). Diahyphae masses are located in the distal portion of the branches, hanging as racemes on each side of the central axis (Fig. 10). The conidia-producing hyphae are translucent, with narrow walls, and produce short, fusiform conidia.

In another unidentified species, *Echinoplaca* sp. *(O. Popoff 3532*, CTES), fragile, echinate yellowish hyphophores were observed (Figs 15-17). They comprised of two branches of different length, one short and pyriform and the other long and narrow at the apex; both are located in such a way that can only be related at a portion of their rounded bases. Diahypha masses are located on the short branches (Fig. 15), covering them totally, or on the extremities of the



Figs 15-20. Hyphophores of unidentified species of *Echinoplaca*. **15-17.** View of echinate hyphophores of *Echinoplaca* sp. *(O. Popoff* 3532, CTES). **18.** Hyphophores of *Echinoplaca* sp. (*A. Schinini et al*. 36223). **19.** Hyphophores of *Echinoplaca* sp. (*O. Popoff* s/n, CTES). **20.** Hyphophores of *Echinoplaca* aff. *pellicula (Popoff* 3222, CTES). Bar = 0.1 mm.

long branches (Fig. 16). They arise as clusters with a common base (Fig. 17). Short branches, like teardrop-shaped thorns, show an uncinate apex, and can be found solitary on the thallus.

In another *Echinoplaca* sp. *(*collection *O. Popoff s/n*, CTES), the hyphophores (Fig. 19) are transparent, bright, not tinged, and very pointed at the apex, while the base is wide, dark and granular. They show a single

diahyphal mass located on a lateral branch situated in the middle of the main peduncle.

Transparent hyphophores were found in another specimen of *Echinoplaca* from Paraguay (*A. Schinini et al. 36223*, CTES), the material is mature and the diahyphae are absent (Fig. 18). Vězda (1979) describes similar conidia in *Aulaxina minuta* but the peduncles are thicker and totally black. Kalb and Vězda (1988), illustrate hyphophores with apical diahyphae, cup-shaped, for *Echinoplaca campanulata* and *E. lucernifera* species collected in the northern Brazil.

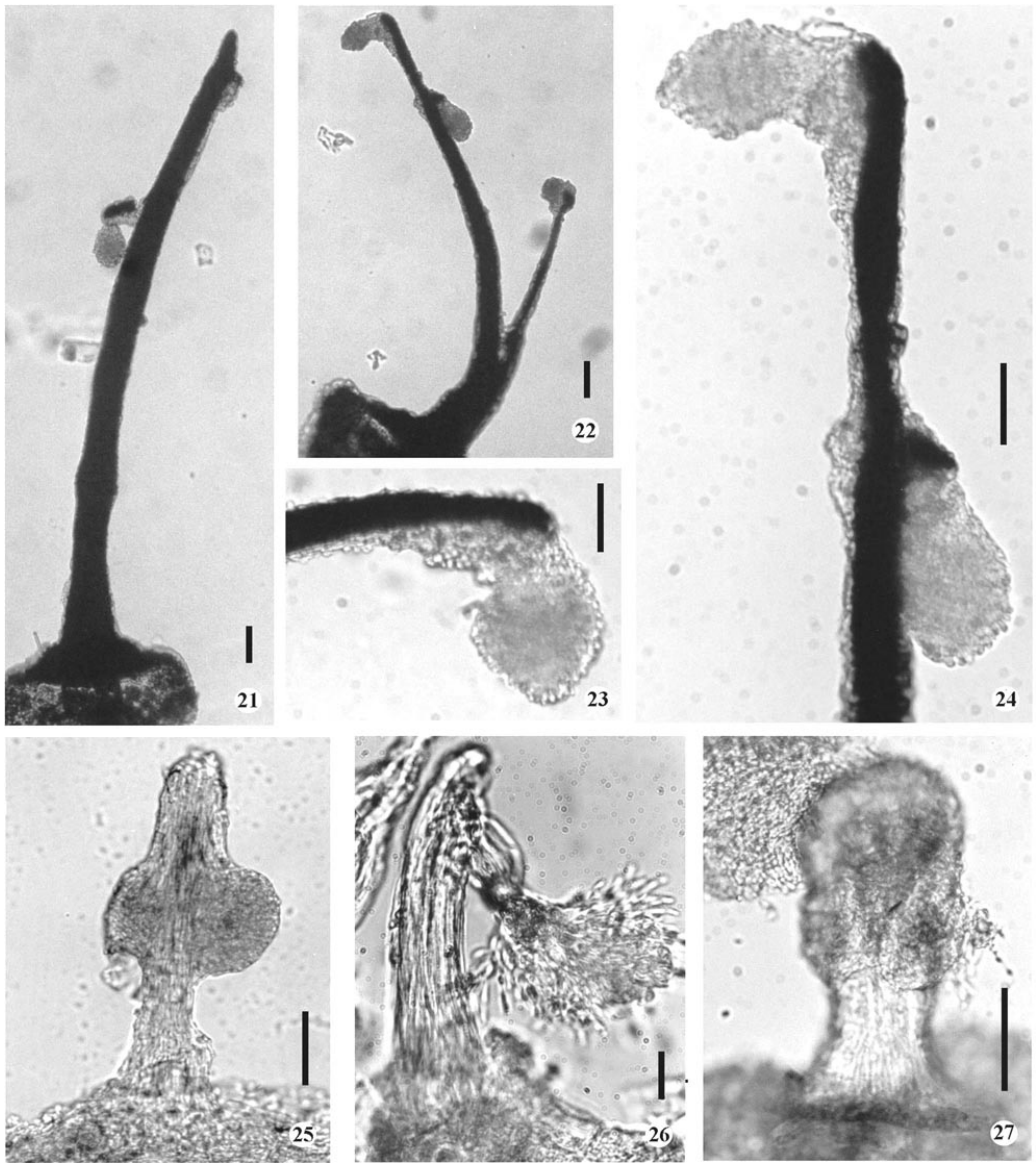
Hyphophores with a long, simple peduncle are found in several species of *Tricharia*. Those observed in a specimen of *Tricharia* sp. *(O. Popoff 3525*, CTES), are pedunculate, simple or branched (Figs 21-24). They are long and black, with robust bases, like sterile hairs. Those with branches bifurcate from a short, common base (Fig. 22). In both, diahypha masses are whitish, somewhat bright, and sessile (Fig. 24) or located at the end of short lateral branches (Fig. 23). They appear in acropetal series, starting more or less at the middle of the peduncle.

They generally are completely black, like in *T. carnea* and *T. farinosa*, while in *T. testacea*, a species that Kalb and Vězda (1988) described from São Paulo, Brazil, they are whitish at the base and black toward the tip. *Tricharia planicarpa*, *T. albostrigosa*, *T. heterella*, and *T. purulhensis* show white pedunculate hyphophores expanded at the apex, which can be white or dark. The shape of the apex is also variable, from cordate to peltate.

The hyphophores of *Gyalideopsis gigantea* Kalb and Vězda (1994) and *Gyalideopsis gigantoides* Sérusiaux (1998) are unusually large. They have peduncles with expanded apices, that resemble spoons, and in the case of the former species, the peduncles are tomentose. In *Gyalideopsis choshuencensis* (Fig. 8) the hyphophores are black, undulate, and the diahyphae are dispersed from the apex to the base, forming a hood-like covering. On the other hand, the apices of *G. cochlearifera* (Fig. 4) resemble dark spoons.

Simple hyphophores with short cylindrical peduncles, and without poimted apices, are found in species of *Aulaxina* (Fig. 5), *Calenia* (Fig. 25), and *Tricharia*. One species, collected in Argentina, close to *Calenia monospora*, shows only the anamorphic state. The hyphophores are small, up to 0.8 mm, white or hyaline, transparent, with diahypha masses hanging from long conidiophorous hyphae down to the base of the peduncle (Fig. 26).

In *Aulaxina corticola*, *Gyalideopsis poeltii* and *Caleniopsis laevigata*, peduncles are wide, short, and black; at the apex they bear very long conidiophorous hyphae that hang down more or less to the middle of the peduncle. Conidiogenous hyphae show thick walls; they are lax, transparent



Figs 21-27. 21-22. General view of hyphophores of *Tricharia* sp. (*O. Popoff* 3525, CTES). **23-24.** Details of diahyphae. **25.** Hyphopore of *Calenia monospora (Ferraro et al*. 6121, CTES). **26.** Hyphophore *of Calenia* aff. *monospora (O. Popoff* 3509, CTES). **27.** *Gyalideopsis* aff. *vulgaris (L. Ferraro et al*. 6181, CTES). Bar = 0.1 mm.

and are positioned downwards, being retrorse-penicillate, with simple, moniliform conidia at the end.

In *Echinoplaca leucotrichoides*, the most common species of the genus in the area studied, the hyphophores are pin-like, with a short, limpid peduncle and a black head. The thallus also has white sterile setae.

Gyalideopsis vulgaris shows pedunculate hyphophores (Fig. 9). The diahyphae are produced at the end of the peduncles, where they form globose masses that can remain erect or bend down. At the wide central portion the peduncles have internal crystals that are sometimes abundant, that they can tear or distort the peduncle. At maturity, the central portion of the peduncle opens and crystals can be clearly seen; the diahyphae placed at the apex grow upward like a feather duster, from which the conidia are dispersed. Groups of algal cells, which easily become detached, are found on the sides of the peduncle. One of the specimens studied (*L. Ferraro et al. 6181*, CTES) has thicker and shorter hyphophores, with larger lateral alga masses (Fig. 27).

A particular kind of hyphophore, and the nicest one in this group, is present in the genus *Gomphillus*. It has a fairly long peduncle, wide at the apex like an umbrella, with the diahyphae placed at the lower part. This type of hyphophore was also observed in two species of *Gyalideopsis* that were not found in the area studied, *G. japonica*, with a long peduncle, and *G. lambinonii* with a very short peduncle.

Sessile Hyphophores (Group 2)

In *Echinoplaca strigulacea* the hyphophores are sessile and hyaline. Diahyphae masses are globose, bright yellowish, occurring as convex, globose structures, directly on the thallus (Fig. 7). Lücking (1997) describes similar, disk-shaped hyphophores in *Echinoplaca gemmifera*.

Adnate Hyphophores (Group 3)

Scaly hyphophores, the first to be described, are usually found in *Gyalectidium* (Fig. 6). In this genus diahyphae are located at the hyphophore base. The hyphophores are several millimeters long and can be easily observed with the unaided eye. The scale can be appresed to the thallus or be erect, depending on moisture conditions. In *G. filicinum* the scales show a lacerate upper margin, with longer lateral extensions. There is a great variability within other species of this genus, for example, the upper margin of the scales can be entire, dentate or laciniate. *Gyalectidium eskuchei* has narrow laciniate scales, placed in a circle over thalline warts, with diahyphae located in the center.

Scales are generally transparent, although in some species they are brown and cartilaginous.

Ferraro *et al*. (2001) reported a long, narrow scale in *Gyalectidium fantasticum*, a species described from Paraguay. Similar hyphophores were reported in the genus *Hippocrepidea* by Sérusiaux (in Aptroot *et al*., 1997), although these were narrower, darker, flexuous, and horseshoe-shaped.

The shape of hyphophores is similar in the genera *Gyalectidium* and *Hippocrepidea*, although their conidia and apothecia are very different.

Conidia are usually produced at the end of conidiophorous hyphae; they are small, hyaline, and most are simple and fusiform. In *Tricharia sp*. conidia are very showy, long, bifurcate or cruciform, with narrow arms. A similar type of conidia was described by Sérusiaux (in Aptroot *et al*., 1997) for *Hippocrepidea nigra* Sérus.

Ontogeny of hyphophore Types

Few published works have dealt with the origin of hyphophores. Sérusiaux (1998) suggested that they derive from or represent structures analogous to the hyphomycetous sporodochia. According to that author, cilia, setae and hyphophores probably originated in sporodochia, which would have undergone change related to different environmental moisture conditions.

Little explanation has been offered for the existence of black, white or transparent hyphophores. It is possible that the white seta gave rise to black setae by means addition of pigments to their walls in response to environmental changes. The factor that most affects setae colour and consistency is light intensity. In the foliose thalli of certain members of *Parmeliaceae*, the thallus becomes thicker and more pigmented in conditions of intense light and exposure to open dry environments. The changes are conspicous when such thalli are compared with specimens growing in dark, closed, humid environments. High light conditions could determine the emergence of dark setae. However, the colour of hyphophores is fairly constant in groups of related species; for example, they are black in *Aulaxina* and *Tricharia sensu str*., while they are white or pale coloured in *Echinoplaca* and *Calenia*.

Sérusiaux (1986b) observed development of scaly hyphophores of *Gyalectidium*. He believed these hyphophores to have an origin similar to that of soralia. Species of this genus have only scaly hyphophores, but as explained above they show a wide variety of hyphophores, with setae of different shapes and colours and branches or diahyphae located at different height and position. It seems that hyphophores originated by processes more complex than those

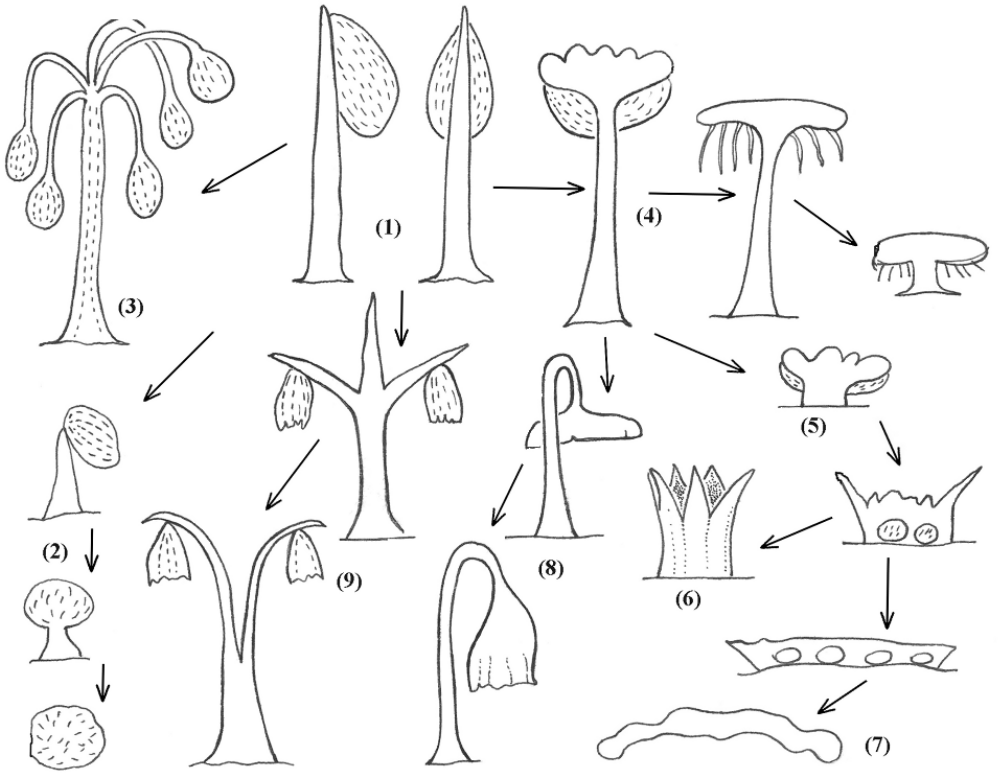


Fig. 28. Possible modifications generating the different shapes of hyphophores.

that originated soredia, but it is possible that environmental factors started the development of the former structures on the thallus.

Taking the studies of Carmichael *et al*. (1980) on hyphomycetes as a base, I hypothesize that hyphophores originated in ciliate, conidia-producing structures. At present, the view of Carmichael *et al*. (1980) is the most acceptable. "sporodochia" or "acervuli" are structures similar to hyphophores, in which the origin of conidia is related to phialidic, conidiogenous hypha, while in *Gomphillaceae* the hyphae apex becomes fragmented and conidial origin is holoblastic.

In this paper (see Fig. 28), starting with the basic pedunculate type (1), all the possible modifications generating the different shapes of hyphophores

are analyzed. One of the most important changes, is the reduction of the peduncle, situating the diahypha masses directly upon the thallus.

Reduction of the setae give rise to shorter setiform and non pedunculate hyphophores (2), as in the case of *Echinoplaca strigulacea*, ehere globose diahypha masses are borne directly upon the thallus.

When conidiophorous hyphae elongate and produce diahypha masses at the apex, a penicillate structure arises (3), as in the hyphophores of *Calenia monospora*. Lücking considers that this is a step in the ontogeny of the hyphophores of this species, which later look like a unique drop.

Apical structures, with forms resembling shields, discs, hads or spoons are produced by differential thickening of the peduncle apex (4). These structures could also undergo peduncle reductions, becoming more or less sessile. It is probable that sessile, scaly hyphophores, which are the common type of hyphophore in *Gyalectidium*, originated in this way (5). In this genus, scales have variable shape, from very wide to laciniate (*G. eskuchei*), with or without sharpened lateral extensions, or narrow and closely adheret to the thallus (7) as in *G. fantasticum* and *G. aurelli* (inéd.). Lateral extensions at the scale margin are also variable, from very long and sharpened, to short and thick. The adnate scale can totally surround the diahypha mass, as in *Gyalectidium yahriae*, producing a tube with dentate margin (6).

The showy hyphophores of *Echinoplaca lucernifera* and *Gyalideopsis gigantea* are setiform. In *E. lucernifera*, the seta curves, producing a cup-shaped structure which is the typical droplet-shaped diahypha of this species. Peduncles can be upright or curved, in the latter case allowing the cups to be placed separately from the thallus or downwards, almost touching it. In *Gyalideopsis gigantea* and *G. gigantoides*, the apical thickening is spoon-shaped.

Other lines would produce by means of the peduncle forking, branched types (9) found in species of *Echinoplaca* and *Tricharia*. Finally, the most derived forms would be those hyphophores that do not show scales or peduncles, in which the diahyphae masses are directly located on the thallus, with or without a scale protecting them.

Conclusions

In *Gomphillaceae*, the hyphophores show variable shapes. They are most commonly macronemate synnemata, pedunculate setiform structures, while the scale-like hyphophores are found only in a few genera.

Hyphophores are usually found in the central area of the thalli, but may also be dispersed or occur at the marginal zone or upon the fungal prothallus.

They can be found together with apothecia in mature thalli. In many species, the young thalli, first produce hyphophores and conidia, before the thallus bears sexual fructifications. There are many species hyphophores producing in which, sexual fructifications are unknown, even though they show well differentiated thalli.

A large number of the hyphophores observed in the family *Gomphillaceae* include algae in the diahypha masses, dispersing both symbionts together. Co-dispersal of algae with conidia was observed also in campylidia *of Sporopodium*, *Tapellaria*, *and Tapellariopsis* (Sérusiaux, 1986a, 1995; Lücking 1999).

A single species can show a certain degree of variation in hyphophores morphology. For example, simple, bristly hyphophores and branched hyphophores may occur on a single thallus. This was observed in some species of *Echinoplaca* and *Tricharia* found in Argentina, for which only hyphophores are known at present. They night represent different stages of development, with the simple seta maturing to producea complex branching structure.
The position of the diahyphae masses on bristly pedunculate hyphophores is variable, depending on the maturity of the conidia-producing hyphae.

In most taxa from Argentina and Paraguay, conidia are generally born at the end of the conidiophorous hyphae. They are small, simple, mostly fusiform and hyaline. Some filiform, cruciform and curved conidia were observed, as occur some species of *Echinoplaca*.

Lücking (pers. com.) carried out a phylogenetic analysis involving 260 species, half of which had hyphophores, and concludes that the setiform type typical of *Echinoplaca pellicula*, is the most primitive. The sessile type, with total reduction of the peduncle as in *Actinoplaca strigulacea*, would be the most evolved. The scale-like hyphophores, as in *Gyalectidium*, cannot be directly related to the other known types. This is an accepted opinion, which was taken as the base of the phylogenetic classification here proposed.

Conidial dispersal may occur individually, when they originate at the apex of conidiogenous hyphae, or the whole diahyphae mass may be dispersed together. The latter case is observed in translucent hyphophores, where the peduncle portion from which the diahyphae masses hang is narrow and fragile. This kind of dispersal is very conspicuous in many species of *Tricharia* where the diahyphae look like "chinese street lamps". This way of dispersing conidial masses as a unique diaspore, was described for the conidia observed in *Woessia pseudohyphorifera* R. Lücking & Sérusiaux (Sérusiaux, 1995). Also, the presence of crystal masses inside the peduncle, as in *Gyalideopsis vulgaris*, can be interpreted as a dispersal strategy.

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