The types of *Comatricha anastomosans* Kowalski, *C. filamentosa* Meyl., *C. suksdorffii* Ellis & Everh. var. *aggregata* Meyl. and *Lamproderma longifilum* H. Neubert, Nowotny & K. Baumann were studied. *Comatricha anastomosans* is synonymized with *C. filamentosa*, *C. suksdorffii* var. *aggregata* with *Symphytocarpus confluens* (Cooke & Ellis) Ing & Nann.-Bremek. A new lectotype for *C. filamentosa* is proposed. The synonymy of *L. longifilum* with *C. anastomosans* is confirmed. SEM and light microscope micrographs of spores, capillitia and sporocarps are given.

**Key words:** nivicolous Myxomycetes, *Comatricha*, *Lamproderma*, *Symphytocarpus*, taxonomy.

The revision of type material of nivicolous Myxomycetes (Moreno et al., 2003a, 2003b 2004; Singer et al., 2003, 2004, 2005) is continued with the application of electron microscopy in order to specify the variability of spore ornamentation. We have been able to localize and study the type of *Comatricha anastomosans* described by Kowalski, the type material of Meylan’s *C. suksdorffii* var. *aggregata* Meyl., a specimen of *C. filamentosa* collected by Meylan and the type of *Lamproderma longifilum* H. Neubert, Nowotny & K. Baumann.

Several works on the revision of nivicolous species described by Kowalski have already been published (Singer et al., 2005), in which various taxa have been synonymized: *Trichia synspora* with *T. varia* (Singer et al., 2003), *Diderma nigrum* with *D. asteroides* (Moreno et al., 2003b), *Diacheopsis spinosifila* with *Lepidoderma didermoides* (Moreno et al., 2003a), *D. subcaeruleum* with *D. niveum* (Singer et al., 2004), *Lepidoderma aggregatum* with *L. chailletii* (Moreno et al., 2004) and *Lepidoderma didermoides* with *L. chailletii* (Moreno et al., 2004).

It has been necessary and important to carry out these studies in order to establish the taxonomic position of the species, which were inadequately described and thus obtain new information essential for understanding their taxonomy and applying it to previous chorological and ecological studies.

**MATERIAL AND METHODS**

The collected material was studied with a binocular microscope and, after mounting in Hoyer’s medium, with a Nikon (Optiphot) microscope. Spore measurements were made under the oil immersion objective and include surface structures such as spines or warts.
Scanning electron microscopy (SEM) micrographs were taken in the University of Alcalá de Henares using a Zeiss DSM-950. SEM-preparation was made as sporocarps were rehydrated in concentrated ammonium hydroxide (28–30%) for 30 minutes, dehydrated in aqueous ethanol (70%) for 30 minutes, fixed for 2 hours in pure ethylene glycol dimethyl ether (= 1, 2-dimethoxyethane) and finally immersed in pure acetone for at least 2 hours followed by critical point drying and sputtering with gold-palladium.

The terminology of the spore-producing stages follows Dörfelt & Marx (1990) and Lado & Pando (1997). The spore wall ornamentation as seen in the SEM is described according to the terminology proposed by Rammeloo (1975a, b). The abbreviations for author citations follow Kirk & Ansell (1992).

**TAXONOMY**

**Comatricha alpina** — Figs. 1–5

*Comatricha alpina* Kowalski, Madroño 22 (1973) 152.


*Original description* (Meylan, 1921). Sporanges en touffes et confluentes sur la plus grande partie de leur longueur, libres au sommet, d’un noir intense, très brièvement stipités, de 2 à 3 mm de hauteur. Columelle mal développée, s’effaçant vers la moitié de la hauteur du sporange. Capillitium très lâche, formant à la surface des sporanges libres un réseau très lâche, plus ou moins défini. Spores noires très opaques, de 10 à 13 μm de diamètre, papilleuses.

*Description.* Sporocarps aggregated, forming groups that are laterally fused by the capillitium, stalked, approximately 2 mm high in total; forming pseudoaethalia, black. Hypothallus iridescent silver. Stalk less than 1 mm long, blackish. Peridium evanescent, except for remains which are united at the centre with the capillitium, forming rounded plates of an irregular outline with a radial venation, up to 100 μm in diameter, with a distinct peripheral zone with abundant small perpendicular filiform veins. Columella a continuation of the stalk and concolorous, short, cylindrical, from one third to half the height of the sporotheca, or branching at the base into several branches. Capillitium formed by rigid threads, 2–5(–6) μm in diameter, dark reddish brown to blackish, branched and anastomosed, forming a wide-meshed net, united with the capillitia of the contiguous sporothecae, with abundant spiny free ends. Spores dark brown in mass, brown in transmitted light, globose, 11–14 μm in diameter, densely verrucose to spinulose. With SEM the spore ornamentation is composed of dense baculæ of regular distribution (Figs. 4, 5).

*Observations.* The material designated as type by Kowalski is conserved in a small carton with a piece of card at the bottom to which a small piece of bark is attached (2.5 × 1.5 cm), which bears two groups of sparse sporocarps with few spores. We found abundant remains of hypothallus where sporocarps had been broken off or lost.

Meylan (1921) proposed the new variety *Comatricha suksdorfii* var. *aggregata* because of the tufted sporocarps which are contiguous for most of their length, but free at their bases and apices. Subsequently, Kowalski (1973), after comparing the type of *C. suksdorfii* with his own collections found that his specimens did not fit this species, but resembled Meylan’s type of *C. suksdorfii* var. *aggregata*. He pointed
out that the differences between _C. suksdorfii_ var. _suksdorfii_ and _C. suksdorfii_ var. _aggregata_ were greater than those indicated by Meylan. Kowalski distinguished the former variety by its “widely scattered sporangia 3–4 mm long and stipes about 4 mm tall” and the latter by its “densely aggregated sporangia 1.5–3 mm long and stipes about 1 mm tall”. He considered these differences sufficient to treat _C. suksdorfii_ var. _aggregata_ as a different species which he called _C. alpina_, as the epithet _aggregata_ was already in use by Farr (1957) for another _Comatricha_.

Figs. 1–5. _Comatricha alpina_ (type). 1. Sporocarps; 2. sporocarps with detail of capillitium plate; 3. detail of capillitium; 4. spore; 5. detail of spore ornamentation. Scale bars: 1, 2, 3 = 0.25 mm; 4 = 2 µm; 5 = 1 µm.
Within the scope of the revision of types of nivicolous Myxomycetes that is presently carried out, we have restudied the type of \textit{C. alpina}. Surprisingly, apart from observing confluent sporocarps forming pseudoaethalia, we have observed that the capillitia of the individual sporocarps are partially fused and continuous. Thus, \textit{C. alpina} is in reality a \textit{Symphytocarpus}. Within this genus it matches \textit{S. confluens} (Cooke & Ellis) Ing & Nann.-Bremek., due to its rigid capillitium forming a wide-meshed net with abundant spiny free ends and the presence of the typical rounded plates described above, as indicated by Lister (1911) and Neubert et al. (2000) for this species.

The genus \textit{Symphytocarpus} was proposed by Ing & Nannenga-Bremekamp (1967) in order to group together some species that they segregated from the genera \textit{Amaurochaete}, \textit{Comatricha} and \textit{Stemonitis} and which are characterized mainly by their sporocarps, whose capillitia fuse together to form pseudoaethalia. These authors already indicated that “perhaps \textit{C. suksdorffii} var. \textit{aggregata} should go here too, but as we have not seen specimens of this variety, we cannot decide now”. Later, Neubert et al. (2000) came to the same conclusion, studying Meylan’s type but not associating it with \textit{Symphytocarpus confluens}.

\textit{Symphytocarpus confluens} is a very common species that is cited in literature. It is not nivicolous and, as Schnittler & Novozhilov (1996) indicated recently, “the solid inner wood is the microhabitat of the plasmodia”.

\textit{Collection examined.} SWITZERLAND: Canton Vaud, Granges de Sainte Croix, 1100 m, on dead spruce branch, leg. Ch. Meylan, VIII.1920, LAU (holotype).

\textbf{Comatricha anastomosans — Figs. 6–10}

\textit{Comatricha anastomosans} Kowalski, Mycologia 64 (1972) 362.

\textit{Original diagnosis.} Sporangiis gregariis, commatis, cylindricis vel subglobosis, nigris, 1–3 mm altis; stipite negro, in sporangium pro columella continuo, 1–2 mm in longitudinem; peridio evanescentio, sed acetabulo basilari persistenti, membranaceo, iridescenti, hypothallo nigro vel rubido-brunneo, disciformi vel continuo; columella nigra, attenuata, aliquando ad apicem sporangii attingenti; capillitio copioso, cunnato, reti flaccido formanti, terminis libris perpaucis, rubido-brunneis; sporis globosis, purpureo-brunneis, spinulosis, cum area palidiore, 11–12 μm diam; plasmodio ignoto.

\textit{Description.} Sporocarps aggregated, forming large groups, united laterally by the expanding capillitium, giving the appearance of pseudoaethalia, stalked, 2–3.5 mm high in total (capillitium not expanded), black. Sporotheca 1–2.5 × 1–1.5 mm (capillitium not expanded), ovoid to subglobose. Hypothallus dark brown, shiny, confluent and forming a small blackish brown disc around the base of the stalk. Stalk 1–2 mm long, cylindrical to laterally compressed, slightly widened towards the base, longitudinally striate, with a fibrous base, blackish brown to black. Peridium membranous, generally evanescent except at the base which persists forming a basal cup, iridescent silver; sometimes small fragments attached to the capillitium can be observed. Columella continuous with the stalk and concolorous, reaching up to 3/4 to almost the total height of the sporotheca, generally tapered towards the apex, sometimes truncate. Capillitium formed by flexuous and sinuous threads of 1–2 μm in diameter, dark brown, without main branches, branched and anastomosed, forming a dense wide-meshed net, that expands and intermingles without fusing together with the threads of the capillitia of
Figs. 6–10. Comatricha anastomosans (type). 6. Sporocarp; 7. detail of capillitium; 8, 9. spores; 10. detail of spore ornamentation. Scale bars: 6 = 0.25 mm; 7 = 0.5 mm; 8, 9 = 2 μm; 10 = 1 μm.
adjacent sporocarps. Spores dark brown in mass, violaceous brown by transmitted light, globose, 11–12 μm in diameter, spinulose, with a clearer zone of variable size (germination pore), sometimes forming an almost complete band. With SEM the spore ornamentation is composed of dense, regularly distributed baculae (Figs. 8–10).

**Observations.** The type material is kept in a box at the bottom of which are glued five pieces of bark, three large and two smaller ones; one of the small pieces does not contain any material, but the others do. However, only on one of them the sporocarps are well-formed and not collapsed or parasitized by fungi.

*Comatricha anastomosans* is characterized by its capillitium formed by flexuous and sinuous threads that expand and intermingle with the capillitium of adjacent sporocarps which, however, do not fuse together and by its peridium that persists at the base of the sporotheca to form a basal cup.

Kowalski (1972) placed this species near the genus *Amaurochaete* on basis of its sporocarps having interconnected capillitia that resemble pseudoaethalia. *Comatricha anastomosans* can clearly be separated from *Amaurochaete* by its sporocarps being visibly discrete, while species of the genus *Amaurochaete* have either true aethalia or pseudoaethalia where it is difficult or impossible to distinguish individual sporocarps.

Kowalski also considered *C. suksdorffii* to be the most closely related species in the genus. These two species, apart from sharing the mountainous habitat, have gregarious, black, cylindrical sporocarps, with a long columella that almost reaches the apex of the sporotheca and blackish spores of similar dimensions (11–12 μm diameter in *C. anastomosans* and 10–12 μm in *C. suksdorffii*). However, they can be distinguished by the peridium, capillitium and spore ornamentation. In *C. anastomosans* the peridium always persists at the base as a cup, the capillitium intermingles with that of adjacent sporocarps and the spores are spinulose with light microscope. In *C. suksdorffii* the peridium is entirely evanescent and never forms a basal cup, the capillitium of individual sporocarps is never intermingled and the spore ornamentation appearswarted with light microscope.

Nannenga-Bremekamp (1974) followed by Yamamoto (1998), ascribe to *C. filamentosa* a 3–4 mm long stalk, which does not coincide with Meylan’s description of this species (Meylan, 1921). Some years later, Neubert et al. (2000) concluded that these authors had confused *C. filamentosa* with *C. alta*.

Once again, Kowalski (1975), after studying the type of *C. filamentosa*, suggested that his *C. anastomosans* could be a synonym or a robust variety of *C. anastomosans*. The only differences observed by Kowalski (1975) were the height of the sporocarps (1–2 mm in *C. filamentosa* and 2–6 mm in *C. anastomosans*) and the absence of a pale zone in the spores of *C. filamentosa*. As described below, there is a difference in the height of the sporocarps, but in both species a pale zone on the spores can be observed that corresponds to a germination pore.

Lado (2001) considered the two species synonymous following Kowalski’s own observations (1975), without studying their types.

Comatricha filamentosa — Figs. 11–15


Original diagnosis. Plasmodium? Sporanges en groupes nombreux, d’un brun foncé, de 0.8 à 1 mm de hauteur, elliptiques ou subglobuleux, portés par un stipe de 0.5 à 1 mm s’élevant en colonne, jusqu’au sommet du sporange où elle s’étale parfois comme celle d’un Enerthenema. Capillitium lâchement adhérent à la colonne et tombant avec les spores à la maturité en formant de longues trainées à la surface du support entre les stipes, comme le capillitium des Hemitrichia et Arctyria.

Ce capillitium présente d’ailleurs les mêmes caractères extérieurs, étant formé d’un réseau interrompu de longs filaments anastomosés, peu ramifiés, de grosseur constante, lisses, d’un brun pourpré. Spores de 10 à 12 µm brunes spinuleuses.

Description. Sporocarps aggregated, in large groups, united laterally by the capillitia that expand and give the appearance of pseudoaethalia, stalked, 1.5–3.5 mm high in total, the expanded capillitium black. Sporotheca approximately 1–2.5 \times 1 \text{ mm}, after the capillitium has expanded, subglobose to ovoid. Hypothallus dark brown, shiny, continuous, forming a small blackish brown disc in the base of the stalk. Stalk 0.5–1 mm long, cylindrical to laterally compressed, tapered slightly towards the apex and somewhat widened towards the base, longitudinally striate, with a fibrous base, dark reddish. Peridium membranous, generally evanescent, persisting as a basal cup that can reach up to half the height of the sporotheca, iridescent silver. Columella a continuation of the stalk and concolorous, up to 3/4 the height of the sporotheca to almost reaching the apex, tapered towards the apex. Capillitium formed by flexuous and sinuous threads, 0.5–2 \text{ µm} in diameter, frequently with widenings that are fusiform or in form of a half-moon, dark brown, without primary branches, branched and anastomosed, forming a dense wide-meshed net, that expands and intermingles without fusing together with the threads of the capillitium of adjacent sporocarps. Spores dark brown in mass, violaceous brown with transmitted light, globose, 10–12 \text{ µm} in diameter, spinulose, with a clearer zone of variable size (germination pore). With SEM the spore ornamentation is composed of dense baculae of regular distribution (Figs. 14, 15).

Observations. Two specimens from Meylan with the same collection data have been studied. The first consists of five pieces of bark each of which bears a group of approximately 30–40 sporocarps, stuck on card, within a box (this specimen is considered as the new lectotype). The second specimen is conserved in a match box and consists of four pieces of wood with a group of approximately 20 sporocarps on each, also stuck on card (this specimen is considered the new isolectotype).

After studying Meylan’s specimens, we characterize C. filamentosa by its capillitium of flexuous and sinuous threads forming a net that expands and intermingles with the capillitium-threads of adjacent sporocarps without fusing together, by its short stalk (0.5–1 mm) and by the peridium persisting as a basal cup. This species was first determined by Meylan as C. alta, as can be seen on the labels on the boxes and subsequently corrected to C. filamentosa. Comatricha alta is close to this species but differs principally in its longer stalk (reaching 5 mm) and entirely evanescent peridium. As already mentioned, Neubert et al. (2000) considered C. filamentosa synonymous with C. alta, but they did not study type material.
Figs. 11–15. Comatricha filamentosa (type). 11. Sporocarp; 12. detail of stalk and columnella; 13. detail of capillitium; 14. spore; 15. detail of spore ornamentation. Scale bars: 11, 12 = 0.25 mm; 13 = 40 µm; 14 = 2 µm; 15 = 1 µm.
After revising the available material determined by Meylan in the herbarium LAU, we have created a new lectotype, since the one proposed by Kowalski (1975) can not be found and is possibly lost.

Collections examined. SWITZERLAND: La Grandsonnaz, Le Chasseron, 1450 m, Canton Vaud, on bark of decayed wood, leg. Ch. Meylan, X.1920, LAU (new lectotype and isolectotype).

**Lamproderma longifilum** — Figs. 16–20


**Original diagnosis.** Sporocarpi stiptitata, globosa, gregaria, dua ad quattuor cohaerentia, 1.5 mm in diametro, ad 3 mm in altitudine universa. Hypothallus subfuscus, ad basim stipitis nigro-fuscus vel fuscus, splendens, contura irregulari, sporocystibus communis. Stipes ater, splendens, usque ad 1.5 mm longus, ad acumen 0.15 mm, ad basim 0.5 mm in diametro, in coni modum hypothallo adiunctus. Peridium argentum, iridescent, tenue, cum zonis obscurioribus, crassioribus, ucidis, breviter eminentibus, ad zonas tenues incomposite aperiens, deinde zonae crassiore capillitio coniunctae, lucem orientem versus visum brunnescens, zonae obscurae reticulatae in forma nervi, contura irregulari, in forma stellae. Columella atra, duas partes sporocarpii attingens, forma cylindrica, acumine tenuiore. Capillitium elasticum, tota columella orines, ad partem inferiorem columnellae rubiginosum, fasciatum, circiter 5 μm in diametro, primo reticulum formans, lacunae reticula circiter 40 μm in diametro, deinde sicut ad partem superiorem columnellae filiforme, circiter 1.5 μm in diametro, sine reticulis, plus minusve ramificatum et una simile formatum, ad peridium ex filamentis libere exuuntibus vel rarius zonis crassioribus peridii adnexum compositum, filamenta levia, nigro-brunnea, lucem orientem versus visae brunneae, dense et minute spinuloseae, spinae 0.5 μm non attingentes, 11–12 μm in diametro, porus germinativus distinctus, clarior, paulum emens. Plasmodium ignotum.

**Description.** The only three sporocarps that are conserved appear more or less grouped, stalked, up to 3 mm in total height, black. Sporotheca up to approximately 1.5 mm in diameter, globose. Hypothallus dark brown, shiny, continuous, common to the groups of sporocarps. Stalk up to 1.5 mm long, cylindrical to laterally compressed, tapered slightly towards the apex and somewhat widened towards the base, longitudinally striate, with a fibrous base, dark reddish. Peridium membranous, persistent, golden iridescent, with darker maculae; irregular dehiscence into large flakes. Columella a continuation of the stalk and concolorous, up to 2/3 of the height of the sporotheca, with an obtuse apex. Capillitium formed by flexuous and sinuous threads of 1.5–2 μm in diameter, dark brown, with main branches up to 5 μm in diameter originating along the whole length of the columella, branched and anastomosed, forming a dense net, with few free ends. Spores dark brown in mass, violaceous brown with transmitted light, globose, 11–12 μm in diameter, spinulose, with a clearer zone of variable size (germination pore). With SEM the spore ornamentation is composed of dense baculae of regular distribution (Figs. 19, 20).

**Observations.** The type of *L. longifilum* consists of a piece of wood of Pinus mugo of approximately 3.5 cm of length, with only three sporocarps that conserve abundant remains of peridium attached to the capillitium. At its base, remains of the hypothallus can be found. The substrate is stuck on a white card that is kept in a box of transparent plastic. A microscope slide with two sporocarps is also conserved. *Lamproderma longifilum*
Figs. 16–20. Lamproderma longifilum (type). 16. Sporocarp; 17. detail of capillitium; 18, 19. spores; 20. detail of spore ornamentation. Scale bars: 16 = 0.25 mm; 17 = 0.5 mm; 18, 19 = 2 µm; 20 = 1 µm.
is characterized by its aggregated sporocarps, globose sporotheca with a persistent peridium, cylindrical stalk with the same height as the sporotheca, capillitium formed by flexuous and sinuous dark reddish threads and spores 11–12 \( \mu m \) in diameter, which are spiny, with an ornamentation by SEM formed by dense baculae of uniform distribution.

The type material and two further specimens of \( L. \) longifilum were kindly sent to us by Nowotny for the preparation of SEM photos. Surprisingly, the spore ornamentation with SEM does not agree with photos of the same material published by the authors of the species in the monograph of Neubert et al. (2000). We interpret this as a mistake in the printing of the book and it remains possible that the photos of \( C. \) anastomosans (= \( L. \) longifilum) have been confused with another species of Comatricha (for example \( C. \) fusiformis, which has the type of spore ornamentation consisting of baculae with star-like apices, as shown in the book).


CONCLUSION

Following the study of the type material of \( C. \) suksdorfii Ellis & Everh. var. aggregata Meyl. (1921: 455) we consider \( C. \) alpina synonymous with Symphytocarpus confluens (Cooke & Ellis) Ing & Nann.-Bremek. (Figs. 1–5).

As Kowalski (1975) has already suggested, we agree that \( C. \) anastomosans “is very close, if not identical, with \( C. \) filamentosa”. There are only minimal differences in the height of the sporocarps, 2–3.5 mm in \( C. \) anastomosans (with the capillitium not expanded) and 1.5–3.5 mm in \( C. \) filamentosa (with the capillitium expanded) and there are no significant differences in the dimensions of the sporothecae. We have observed that the sporothecae of \( C. \) anastomosans are 1–2.5 \( \times \) 1–1.5 mm (capillitium not expanded) and of \( C. \) filamentosa 1–1.5 \( \times \) 1 mm (capillitium expanded). We have to point out that the dimensions of the sporocarps of these species are difficult to measure as a result of the tendency of the capillitium to expand. As there are no other significant differences, synonymy of these species is proposed.

We propose the synonymy of Lamproderma longifilum with \( C. \) anastomosans. When Neubert et al. (1989) described \( L. \) longifilum, they noted its similarity to \( C. \) anastomosans. These species are separated, according to these authors, because \( C. \) anastomosans has cylindrical sporothecae, each with a columella that is markedly tapered and reaches almost to the apex, where it gives rise to the capillitium with few free ends. In \( L. \) longifilum the sporothecae are globose, the columella is shorter and is only slightly tapered or blunt, the capillitium has free ends and the peridium shows dark spots.

Neubert et al. (2000), after consulting Meyer who studied Kowalski’s American material of \( C. \) anastomosans, observed similarities in the microscopy of the two species and proposed the synonymy of \( L. \) longifilum with \( C. \) anastomosans. We agree with this view, as the differences between these species do not justify their separation.
The distinct spots, present in all of Neubert’s collections of *L. longifilum* that we have studied, are not present in *C. anastomosans* and *C. filamentosa*, as these specimens were very mature and lacked sporothecae with a complete peridium.

In conclusion we make the following taxonomic proposals:

*Symphytocarpus confluens* (Cooke & Ellis) Ing & Nann.-Bremek. in Nannenga-Bremekamp, Nederlandse Myxomyceten (‘1974’ 1975) 174.

= *Stemonitis confluens* Cooke & Ellis, Grevillea 5 (1876) 51.


= *Comatricha alpina* Kowalski, Madroño 152 (1973) 22.


= *Comatricha anastomosans* Kowalski, Mycologia 362 (1972) 64.


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REFERENCES


