

Phylogenetic studies in the family *Sarcosomataceae* (Ascomycota, *Pezizales*)

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Summary: New phylogenetic studies focused on the family *Sarcosomataceae* support the independence of the genera *Plectania*, *Pseudoplectania*, *Donadinia*, *Sarcosoma*, *Galiella* and *Urnula*. *Galiella* is restricted to the temperate species, while the tropical taxa seem to be more related to the family *Chorioactidaceae*, and are here accommodated in the priority genus *Trichaleurina*. The lineage including the type species of *Urnula* is here shown to include also several morphologically deviant species. The genus *Pseudosarcosoma* is here proposed to accommodate *Sarcosoma latahensis*/*Plectania latahense* in the family *Chorioactidaceae*, since this lineage is not related to the type species of the genus *Sarcosoma*, *S. globosum*.

Keywords: ITS, 28S LSU, phylogeny, *Chorioactidaceae*, *Plectania*, *Pseudoplectania*, *Donadinia*, *Sarcosoma*, *Galiella*, *Urnula*, *Trichaleurina*, *Pseudosarcosoma*.

Introduction

The family *Sarcosomataceae* Kobayasi (KOBAYASI, 1937, *ut "Sarcosomataceae"*) has been based on the genus *Sarcosoma* Casp. KORF (1970) amended the concept of the family and split it into two tribes: *Sarcosomatae* and *Galielleae* Korf. He recognized ten distinct genera: *Sarcosoma* Casp., *Plectania* Fuckel, *Pseudoplectania* Fuckel, *Urnula* Fr., *Galiella* Nannf. & Korf, *Nannfeldtiella* Eckblad, *Chorioactis* Kupfer ex Eckblad, *Neournula* Paden & Tylutki, *Desmazierella* Libert and *Wolfina* Seaver ex Eckblad. The monotypic genus *Korfiella* D.C. Pant & V.P. Tewari, described from India (PANT & TEWARI, 1970; PANT & PRASAD, 2008), was not originally included in the family *Sarcosomataceae*, but, according to the described morphological features, it could be possibly related to it. The genus *Nannfeldtiella* was later considered as a section in *Pseudombrophila* Boud. (BRUMMELEN, 1995; YAO & SPOONER, 2006). More recently PFISTER *et al.* (2008) transferred the latter four genera to the new family *Chorioactidaceae* Pfister. Morphological features alone seem not enough to accurately delimit the five remaining *Sarcosomataceae* genera: *Plectania*, *Sarcosoma*, *Galiella*, *Urnula* and *Pseudoplectania* plus the more recently described genus *Donadinia* Bellem. & Mel.-Howell. All of them show a very similar microscopic arrangement of the excipulum, which is divided into a highly to moderately gelified medullary excipulum made up of a *textura intricata* and an ectal excipulum of *textura subglobulosa-angularis*, with hairs rising from the latter. Another common feature is the presence of the so-called *hymenial hairs*, a non-septate, slightly larger and usually unbranched kind of paraphyses which are generated by the same hyphae of the paraphyses. The only major morphological differences among these genera seem to be the degree of gelification of their flesh and their spore morphology. However, if we compare these features among a representative number of species there are no clear-cut values, but a varying continuum that prevents these characters to be used to define genera. Hence, the combination of characters of each type species needs to be analysed in order to delimit each lineage.

As pointed out by KORF (1957a) the type species of *Sarcosoma* is the European *Sarcosoma globosum* (Schmidel) Casp. (*in* REHM, 1891). This species was originally described from Germany as *Burcardia globosa* Schmidel (SCHMIDEL, 1793), but it seems fairly common in northern Europe (e.g. MARTINSSON & NITARE, 1986; DISSING & ECKBLAD, 2000; NITARE, 2010). It is macroscopically characterized by its general colours, wet gelatinous flesh and globose to turbinate habit, whilst microscopically it presents typical moniloid external hairs and smooth spores (PADEN, 1983; CARBONE, 2009). These features led first PADEN (1983) and then CARBONE *et al.* (2009) to consider *Sarcosoma* as monotypic and therefore to transfer the American species *Sarcosoma*

mexicanum (Ellis & Holw.) Paden & Tylutki and *Sarcosoma latahense* Paden & Tylutki to the genus *Plectania*.

The genus *Galiella* was proposed by Nannfeldt and Korf (*in* KORF, 1957b) to accommodate all the *Sarcosoma*-like fleshy species that present warted spores with callose-pectic markings. The type species is the well known American *Galiella rufa* (Schwein.) Nannf. & Korf characterized by globose to shallow cupulate (sub)sessile apothecia with irregularly toothed margin, reddish-brown to orange-brown hymenium, blackish-brown external surface covered with hairs that give it a felt-like appearance; the flesh is gelatinous and rubbery; microscopically the main feature are the subfusoid ornamented spores (SEEVER, 1928, 1942; BESSETTE *et al.*, 1997; PHILLIPS, 2005). Nannfeldt & Korf (KORF, 1957b) proposed three combinations to this genus: *Galiella javanica* (Rehm) Nannf. & Korf, *Galiella celebica* (Henn.) Nannf., and *Galiella thwaitesii* (Berk. & Broome) Nannf. At present most known species of *Galiella* (including the already cited ones) are widely distributed over tropical areas (PADEN, 1983; CAO *et al.*, 1992; ZHUANG & WANG, 1998), while only few species appear in temperate or boreal latitudes, such as *Galiella rufa* or the north-Asian *Galiella amurensis* (VASSILJEVA, 1950; RAITVIIR, 1965; ZHUANG & WANG, 1998).

The genus *Urnula* Fr. was established by FRIES (1849), and typified by the American species *Urnula craterium* (Schwein.) Fr. (FRIES, 1851). The genus *Urnula* was defined by its habit, and its non-gelatinous flesh consistence (NANNFELDT, 1949; LE GAL, 1958). Several cytological studies followed focusing in the spore's nuclei (BERTHET, 1964; DONADINI, 1987), or the ultrastructure of the ascus apex (BELLEMÈRE *et al.*, 1990). Few species are still accepted in the genus, such as *Urnula hiemalis* Nannf. from Sweden (NANNFELDT, 1949) or *Urnula groenlandica* from Greenland (DISSING, 1981).

The genus *Plectania* was proposed by FÜCKEL (1870) and it is typified by *Plectania melastoma* (Sowerby) Fuckel, an European species originally described as *Peziza melastoma* Sowerby (SOWERBY, 1799) growing on "*Erica vulgaris* & c.". The genus has been divided morphologically by different authors into five sections on the basis of spore morphology only (KORF, 1957b; PADEN, 1983; CARBONE *et al.*, 2012a): *Plectania* sect. *Plectania* with smooth spores; *Plectania* sect. *Plicosporae* Korf with spores transversally furrowed on one side; *Plectania* sect. *Curvatisporae* Korf, with smooth allantoid spores; *Plectania* sect. *Sphaerosporae* Paden (= *Pseudoplectania*) with spherical spores; and *Plectania* sect. *Donadinia* (Bellem. & Mel.-Howell) M. Carbone & Agnello (= *Donadinia*) with ellipsoid cyanophilous ornamented spores.

The genus *Pseudoplectania* was also described by FÜCKEL (1870), who selected the European *Pseudoplectania nigrella* (Pers.) Fuckel (= *Peziza nigrella* Pers.) as its type species. This species has been recently neotypified by CARBONE & AGNELLO (2012). Among the *Sarco-*

somataceae, the genus is mainly characterized by its spherical smooth spores. It was thought to be independent by many authors, (SEEVER, 1928; NANNFELDT, 1949; LE GAL, 1953; SANWAL, 1953; BERTHET, 1964; KREISEL, 1962; ECKBLAD, 1968; RIFAI, 1968; KORF, 1972, 1973). However, other workers (KORF, 1982; PADEN, 1983) considered it to be a synonym of *Plectania* sect. *Sphaerosporae* mainly due to the discovery of a *Conoplea* conidial state in *Pseudoplectania melaena* and because of *Plectania*'s rounded spores in their early development. From that time on, Paden's wide concept of *Plectania* was largely agreed (KORF & ZHUANG, 1991; MEDEL & CHACÓN, 2000; CALONGE & MATA, 2002; CALONGE *et al.*, 2003; BENKERT, 2005; PERÉZ-DE-GREGORIO *et al.*, 2009), as can be seen in the description of *Plectania carranzae* Calonge & Mata and the new combination *Plectania ericae* (Donadini) Roqué. Still other authors (DONADINI, 1987; BELLEMÈRE *et al.*, 1990) argued that *Pseudoplectania* was different on the basis of its ultrastructure and so they decided to preserve it as a separate genus.

Finally, the genus *Donadinia* was proposed by BELLEMÈRE *et al.* (1990), who typified it with *Donadinia helvelloides* (Donadini, Berthet & Astier) Bellem. & Mel.-Howell (\equiv *Urnula helvelloides* Donadini, Berthet & Astier), a species discovered in France and published by DONADINI *et al.* (1973). This genus was primarily characterized by the ultrastructural features of its ascus apex and ornamented spores. The type specimen was recently studied by CARBONE *et al.* (2012a) who reduced *Donadinia*, from a morphological point of view, to a section within *Plectania*. According to these authors, other species putatively related to it could be *Urnula lusitanica* Torrend & Boud. and *Plectania nannfeldtii* Korf, while *Plectania coelopus* (Mont.) Sacc. should be considered a *nomen dubium*. Recently CARBONE *et al.* (2012b) described *Plectania seaveri* M. Carbone, Agnello & La Greca from Bermuda, a species definitely belonging to this lineage in all respects.

The present work aims to further delimit the molecular and morphological concept of the mentioned genera *Plectania*, *Urnula*, *Pseudoplectania*, *Donadinia*, *Sarcosoma* and *Galiella*, as well as to test the morphology-based taxonomy of several species in these genera in light of newly obtained molecular data. Unfortunately, *Korfiella* has not been included due to the temporary absence of available samples.

Material and methods

Morphological study. — The microscopic studies were based on both fresh and dried specimens. Two optical microscopes were used: Olympus CX41 trinocular and Optika B353 trinocular with plan-achromatic objectives 4x, 10x, 40x, 60x, 100x in oil immersion. The following main reagents were used: Melzer's reagent, cotton blue, Congo red, KOH. Water mounts were used for the observation of the pigmentation and measurements. At least 30 spores were measured from each apothecium. Species concepts have been based on the original descriptions and, in some cases, on the type revisions and selections.

DNA extraction, amplification and sequencing. — DNA was extracted and amplified from dried specimens following the methods published before (ALVARADO *et al.*, 2010, ALVARADO *et al.*, 2012). The primers LR1 (TUINEN *et al.*, 1998) and LR7 (VILGALYS & HESTER, 1990) were used to amplify and sequence the 28S nuclear large ribosomal region (nrLSU), while ITS1F and ITS4 (WHITE *et al.*, 1990, GARDES & BRUNS, 1993) were used to amplify the internal transcribed spacer region. Sequences were visually inspected searching for reading errors in MEGA 5.0 (TAMURA *et al.*, 2011). Validated sequences were stored in GenBank under the accession numbers listed in table I.

Phylogenetic analyses. — The sequences obtained were aligned with the closest relatives and their matches obtained with BLAST searches. Sequences were first aligned in MEGA 5.0 software using its ClustalW application and then corrected manually. Final alignments were uploaded in TreeBase (ID13387). Neighbor-joining phylogenetic inference was performed in MEGA 5.0 (pairwise deletion

of gaps, 2000 bootstrap replicates). The aligned loci were loaded in PAUP* 4.0b 10 (SWOFFORD, 2001) and a maximum parsimony phylogenetic tree reconstruction was performed (2000 bootstrap replicates, TBR swapping algorithm, 50 sequence additions per replicate, MulTrees not in effect). Aligned loci were also subjected to MrModeltest 2.3 (NYLANDER, 2004) in PAUP* 4.0b10. The best models were implemented in MrBayes 3.1 (RONQUIST & HUELSENBECK, 2003), where a Bayesian analysis was performed (ITS1-5.8S-ITS2 data partitioned, 2 simultaneous runs, 6 chains, temperature set to 0.2, sampling every 100th generation) until convergence parameters were met after about 2.5M generations. Significance thresholds were above 70% for bootstrap (BP) and 99% for posterior probability (PP).

Studied and sequenced collections

Donadinia helvelloides: FRANCE, Var, Saint Baume, on *Taxus baccata*, spring 1972, *leg.* Donadini & Astier, *det.* P. Berthet (LY P.B. 940, isotype). *Donadinia lusitanica*: ITALY, Apulia, Brindisi, Bosco Zundrano, on mossy sticks of *Pinus halepensis*, 22.02.2010, *leg. et det.* A. Baglivo & D. De Giorgi (TUR-A 195791); GREECE, Kefalovryso, Larissa, on *Pinus halepensis*, 05.01.2000, *leg.* A. Papatsanis, *det.* C. Agnello & M. Carbone (TUR-A 195792). *Donadinia nigrella*: USA, Idaho, Kootenay County, 1100 m a.s.l., 07.05.1985, *leg. et det.* K. Scates & H.E. Barnhardt (TUR-A 195793). *Neournula pouchetii*: ITALY, Apulia, Mesagne (BR), Contrada Manfredonia, in a private garden under *Cedrus atlantica*, 15.03.2009, *leg. et det.* C. Agnello (TUR-A 195798). *Plectania melastoma*: ITALY, Tuscany, Marina di Vecchiano, on *Erica scoparia*, 26.04.2012, *leg. et det.* M. Carbone & G. Cacialli (TUR-A 195783); ITALY, Apulia, Brindisi, Bosco Preti, on *Erica arborea*, 28.04.2012, *leg. et det.* C. Agnello (TUR-A 195784). *Plectania megalocrater*: GREECE, Ziakas Grevena, along with *Quercus cerris* and *Acer pseudoplatanus*, 15.05.2011, *leg.* G. Palatsios, *det.* M. Carbone & C. Agnello (TUR-A 195803). *Plectania cf. melastoma*: USA, Montana, Cedar Creek Trail, moist areas along the trail, under conifers as well as on decaying wood, 31.07.2011, *leg.* J. Harnisch, *det.* M. Carbone & C. Agnello (TUR-A 195785). *Plectania milleri*: USA, Montana, Trego, under *Larix*, 11.06.2011, *leg.* J. Harnisch, *det.* M. Carbone, C. Agnello & J. Harnisch (TUR-A 190823). *Plectania rhytidia*: ITALY, Apulia, Brindisi, Bosco Preti, on *Erica arborea*, 24.04.2012, *leg. et det.* C. Agnello (TUR-A 195786); ITALY, Apulia, Brindisi, Bosco Colemi, on *Quercus ilex* and *Q. suber*, 18.04.2012, *leg. et det.* C. Agnello (TUR-A 195787); ITALY, Apulia, Taranto, Torre Colimena, on *Eucalyptus camaldulensis*, 31.01.2012, *leg. et det.* C. Agnello (TUR-A 195788); NEW ZEALAND, Taupo, vic. Kiko Rd., Tiraki Rd., on soil and litter in *Nothofagus* forest, 21.11.2001, *leg.* K. Petersen & P.R. Johnston, *det.* P.R. Johnston (PDD 75313); NEW ZEALAND, Northland, Native Forests Restoration Trust, Cynthia Hewett Reserve, on litter, 28.11.2006, *leg.* P.R. Johnston & B. Paulus, *det.* P.R. Johnston (PDD 90028). *Plectania zugazae*: SPAIN, Valladolid, Valdestillas, among mosses under *Pinus sp.*, 08.04.2001, *leg.* A. Garcia Blanco & J. Mori, *det.* F.D. Calonge (AVM 1467, private duplicate of the holotype MA-fungi 53068); Spain, Valladolid, Valdestillas, among

Legend of the plates

Plate 1 – 1. *Galiella rufa* (A.D. Parker); 2. *Urnula craterium* (C. Zoldan); 3. *U. hiemalis* (S. Kytöharju); 4. *U. padeniana* (A.D. Parker); 5. *U. campylospora* (G. Gates); 6. *U. mediterranea* (C. Agnello); 7. *Plectania melastoma* (C. Agnello).

Plate 2 – 8. *Plectania zugazae* (A. Garcia Blanco); 9. *P. megalocrater* (G. Palatsios); 10. *P. milleri* (J. Harnisch); 11. *P. rhytidia* (C. Agnello); 12. *Sarcosoma globosum* (J. Vauras); 13. *Pseudoplectania nigrella* (M. Carbone); 14. *P. ericae* (C. Roqué); 15. *P. melaena* (M. Carbone).

Plate 3 – 16. *Donadinia nigrella* (A.D. Parker); 17. *D. helvelloides* holotypus (M. Carbone); 18. *D. lusitanica* (A. Baglivo); 19. *D. seaveri* (F.J. Seaver); 20. *Trichaleurina javanica* (M. Carbone); 21. *T. celebica* (K. Saitoh); 22. *Pseudosarcosoma latahensis* (A.D. Parker); 23. *Neournula pouchetii* (C. Agnello).



PLATE 1



PLATE 2



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PLATE 3

mosses under *Pinus sp.*, 15.04.2007, *leg.* J. Mori & M. Sanz, *det.* A. Garcia Blanco (AVM 2086). *Pseudoplectania nigrella*: AUSTRIA, Carinzia, Boudental, under *Picea abies*, 1050 m a.s.l., 18.05.1976, *leg. et det.* H. Engel (KL BK-4914, neotype); FINLAND, Varsinais-Suomi, Koski, Partela, under *Picea abies*, among litter in *Sphagnum*, 11.05.2005, *leg. et det.* M.-L. Heinonen & P. Heinonen (TUR 169888). *Pseudoplectania melaena*: ITALY, Veneto, Belluno, Bosco del Cansiglio, on old mossy fallen trunks of *Abies alba*, 25.03.2012, *leg. et det.* E. Campo & M. Carbone (MCVE 27433). *Pseudoplectania ericae*: SPAIN, Girona, Can Llaudador, Solius, on buried sticks of *Erica arborea*, 16.01.2007, *leg. et det.* C. Roqué (TUR-A 195789, duplicate of 160120074CRP, pers. herb. C. Roqué); *ibidem*, 17.02.2010, *leg. et det.* C. Roqué (TUR-A 195790, duplicate of 170220101CRP, pers. herb. C. Roqué). *Pseudosarcosoma latahense*: CANADA, British Columbia, Fernie, Island Lake, under conifers, 17.07.2011, *leg.* J. Harnisch, *det.* M. Carbone & C. Agnello (TUR-A 195801). *Trichaleurina javanica*: SEYCHELLES, Praslin, Anse Lazio, on decaying wood, 04.04.2009, *leg. et det.* M. Carbone (TUR-A 195799). *Trichaleurina celebica*: JAPAN, Yokohama, Kanazawa, on log, 24.06.2012, *leg. et det.* K. Saitoh (TUR-A 195800). *Urnula campylospora*: NEW ZEALAND, Bay of Plenty, Te Urewera, Mangapae, UA1 W2, on decaying wood, 24.05.2005, *leg.* B. Paulus & M. Fletcher, *det.* B. Paulus (PDD 83522); NEW ZEALAND, Bay of Plenty, Te Urewera, Te Waiiti, on fallen log, 17.05.2006, *leg.* P.R. Johnston & B. Paulus, *det.* B. Paulus (PDD 88805). *Urnula craterium*: Italy, Veneto, Nevegal (BL), in mixed *Corylus* and *Carpinus* forest at 1150 m a.s.l., 25.04.2008, *leg. et det.* C. Zoldan (TUR-A 195794). *Urnula hiemalis*: FINLAND, Etelä-Häme, Tammela, Syrjänharju, lakeshore under *Picea abies*, *Betula* and *Alnus glutinosa*, 09.IV.2000, *leg.* M.-L. Heinonen & P. Heinonen, *det.* S. Huhtinen (TUR 136909); Perä-Pohjanmaa, Rovaniemi, Pullinpuoli, under *Picea*, *Sorbus* and *Sorbaria sorbifolia*, 26.V.2011, *leg. et det.* T. Kekki (TUR 196076); Etelä-Häme, Tampere, Vestonkatu, 10 m. S of Kaukajärventie, close to the road, on soil under *Picea abies*, *Betula pendula* and near to *Alnus glutinosa*, 22.IV.2012, *leg. et det.* S. Kytöharju, *rev.* M. Carbone (TUR-A 195795). *Urnula mediterranea*: ITALY, Apulia, Brindisi, Bosco Colemi, on *Quercus ilex*, 27.04.2012, *leg. et det.* C. Agnello (TUR-A 195796); FRANCE, Charente-Maritime, Saintes, on sticks under *Acer sp.* and *Quercus sp.*, May 2012, *leg.* P. Tanchaud, *det.* M. Carbone & C. Agnello (TUR-A 195797). *Urnula padeniana*: USA, Washington, Pend Oreille County, Roosevelt Cedar Grove, Forest Service Rd. 302, 48° 46' 04" N, 117° 03' 38" W, on needle duff under old growth *Thuja plicata*, at 1185 m. a.s.l., 11.06.2006, *leg. et det.* A.D. Parker (WTU-F-33051, holotype). *Urnula sp.*: NEW ZEALAND, Auckland, Hunua, Walkman Track, on the ground, 28.07.2002, *leg.* C. Shirley (PDD 81259, as *Plectania sp.*).

Results

Taxonomic results

Pseudosarcosoma M. Carbone, Agnello & P. Alvarado, *gen. nov.* – MB 801353

Diagnosis: Apothecia turbinate to discoid, gelatinous to less gelatinous in age, substipitate, hymenium deep purple to black, external surface grayish to black. Asci operculate, 8-spored, inamyloid, tapering basally with some forked bases; spores elliptical to subcylindrical, smooth, hyaline, oil-dropped to eguttulate at maturity; paraphyses cylindroid, branched, anastomosing, closely septate, with bent or lobed tips; subhymenium of a thick *textura intricata*; medullary excipulum of a loose *textura intricata*; ectal excipulum of *textura angularis*, the most outer cells with brown walls; external hairs branched, septate, smooth, lobed, hyaline to pale brownish-olivaceous.

Type species:

Pseudosarcosoma latahense (Paden & Tylutki) M. Carbone, Agnello & P. Alvarado, *comb. nov.* – MB 801354

Basionym: *Sarcosoma latahense* Paden & Tylutki, *Mycologia*, 61: 686 (1969) [*sub latahensis*].

Synonym: *Plectania latahensis* (Paden & Tylutki) M. Carbone, Agnello & Baglivo, *Riv. Micol.*, 52 (3): 260 (2009).

Donadinia nigrella (Seaver) M. Carbone, Agnello & P. Alvarado, *comb. nov.* – MB 801344

Basionym: *Paxina nigrella* Seaver, *North American Cup-fungi*, (*Operculates*): 208 (1928).

Synonyms: *Macropodia nigrella* (Seaver) Teng, *Zhong Guo De Zhen Jun [Fungi of China]*: 762 (1963); *Helvella nigrella* (Seaver) F.L. Tai, *Syll. fung. sinicorum*: 157 (1979); *Macroscyphus nigrellus* (Seaver) Z.S. Bi, in Bi, Zheng & Li, *Macrofungus Flora of the Mountainous District of North Guangdong*: 26 (1990); *Plectania nannfeldtii* Korf, *Mycologia*, 49 (1): 109 (1957).

Donadinia lusitanica (Torrend & Boud.) M. Carbone, Agnello & P. Alvarado, *comb. nov.* – MB 801347

Basionym: *Urnula lusitanica* Torrend & Boud., in Boudier & Torrend, *Bull. Soc. mycol. Fr.*, 27: 130 (1911).

Synonym: *Plectania lusitanica* (Torrend & Boud.) M. Carbone, Agnello, Baglivo & B. Perić, *Mycol. Monten.*, 14: 9 (2012).

Donadinia seaveri (M. Carbone, Agnello & LaGreca) M. Carbone, Agnello & P. Alvarado, *comb. nov.* – MB 801365

Basionym: *Plectania seaveri* M. Carbone, Agnello & LaGreca, *Mycotaxon*, 120: 318 (2012).

Pseudoplectania carranzae (Calonge & M. Mata) M. Carbone, Agnello & P. Alvarado, *comb. nov.* – MB 801345

Basionym: *Plectania carranzae* Calonge & M. Mata, *Mycotaxon*, 81: 238 (2002).

Urnula mediterranea (M. Carbone, Agnello & Baglivo) M. Carbone, Agnello & P. Alvarado, *comb. nov.* – MB 801346

Basionym: *Plectania mediterranea* M. Carbone, Agnello & Baglivo, *Riv. Micol.*, 52 (3): 252 (2009).

Trichaleurina javanica (Rehm) M. Carbone, Agnello & P. Alvarado, *comb. nov.* – MB 801351

Basionym: *Sarcosoma javanicum* Rehm, in Hennings, *Hedwigia*, 32: 226 (1893).

Synonym: *Galiella javanica* (Rehm) Nannf. & Korf, in Korf, *Mycologia*, 49 (1): 108 (1957).

Trichaleurina celebica (Henn.) M. Carbone, Agnello & P. Alvarado, *comb. nov.* – MB 801352

Basionym: *Bulgaria celebica* Henn., *Monunia*, 1: 30 (1900).

Synonyms: *Galiella celebica* (Henn.) Nannf., in Korf, *Mycologia*, 49 (1): 108 (1957); *Sarcosoma celebicum* (Henn.) Sacc. & P. Sydow, *Syll. fung.*, 16: 771 (1902); *Sarcosoma globosum* var. *celebicum* (Henn.) Kobayasi, *J. Jap. Bot.*, 13: 518 (1937).

Phylogenetic results

ITS inference (fig. 1) suggested the existence of at least six major clades within the *Sarcosomataceae*: *Sarcosoma*, *Plectania*, *Galiella*, *Pseudoplectania*, *Donadinia* and a clade containing *Urnula hiemalis*, *U. craterium*, *U. padeniana*, *Plectania campylospora* and *P. mediterranea*. Most clades were significantly supported by both bayesian and maximum parsimony analyses, although some received supporting values below significance thresholds (e.g. *Pseudoplectania*, *Urnula*).

In turn, combined ITS-LSU inference (fig. 2) significantly supported a similar phylogenetic topology to that suggested by ITS alone. *Galiella javanica*, *G. celebica* and *Sarcosoma latahense* seemed to be closely related to the *Chorioactidaceae* Pfister, while the type species in their respective genera (*G. rufa* and *S. globosum*, respectively) were related to the *Sarcosomataceae*, thus suggesting their transfer to different taxa to accommodate them. In the first case, the existing name *Trichaleurina* seems to be available, while the new taxon *Pseudosarcosoma* is here proposed to accommodate *S. latahense*.

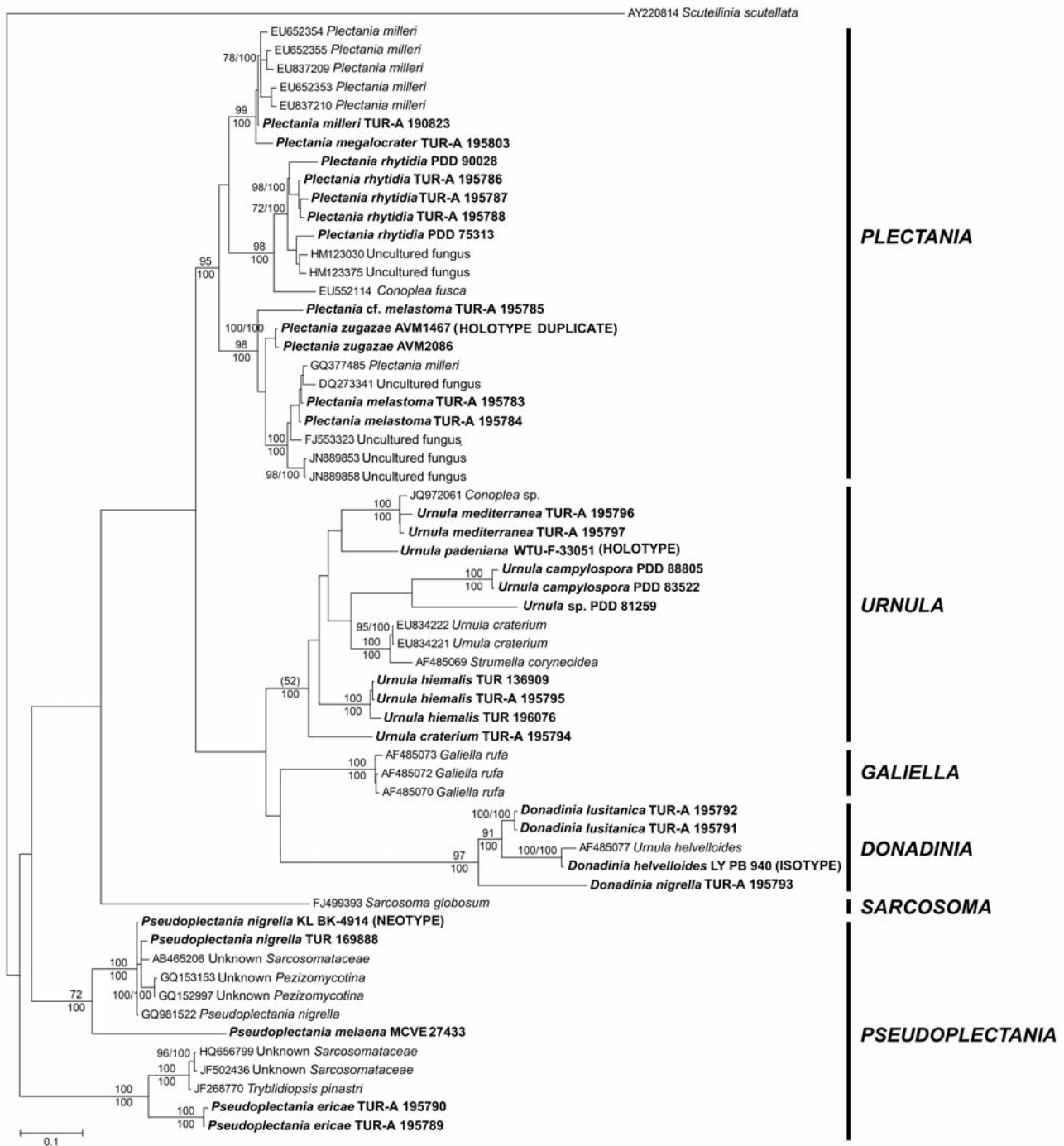


Fig. 1 – Consensus tree resulting from Bayesian ITS analysis of the *Sarcosomataceae* lineages studied. The length of the rooting branch was altered for publishing purposes. Nodes were annotated with maximum likelihood BP (above) and Bayesian PP (below). Only nodes supported (or nearly supported) by both analyses were annotated. **Bold names** belong to samples sequenced in the present study.

Discussion

In the present study, a comprehensive phylogenetic comparison of *Sarcosomataceae* genera has been performed to delimit their respective concepts. Besides the already cited morphological and cytological studies, other major ultrastructural research on *Sarcosomataceae* genera have been published before by LI & KIMBROUGH (1995a, 1995b), SAMUELSON (1975) and SAMUELSON *et al.* (1980). A pioneer phylogenetic approach was conducted by HARRINGTON *et al.* (1999) using 18S nuSSU region. These authors included the north-western American species *Urnula padeniana* — as *Sarcosoma mexicanum* (Ellis & Holw.) Paden & Tylutki —, a *Plectania* sp. from Puerto

Rico, *Pseudoplectania nigrella* (Pers.) Fuckel from Japan, and American collections of *Donadina* sp., *Urnula craterium* and *Galiella rufa*. Using these data, as well as newly obtained 28S nuLSU and RPB2 sequences, PERRY *et al.* (2007) and PFISTER *et al.* (2008) obtained significant support for the new family *Chorioactidaceae* Pfister, sister to the *Sarcosomataceae*.

Present results seem to support previous phylogenetic movements in the genus *Plectania*, such as the combination of *Plectania megalocrater* (Malençon & Le Gal) M. Carbone, Agnello & Konstant., while other species such as *P. mediterranea* M. Carbone, Agnello & Baglivo and *P. campylospora* are here excluded (see below). Results suggest that *P. milleri* and *P. megalocrater* could be considered conspecific, since they display a very close relationship with only 7

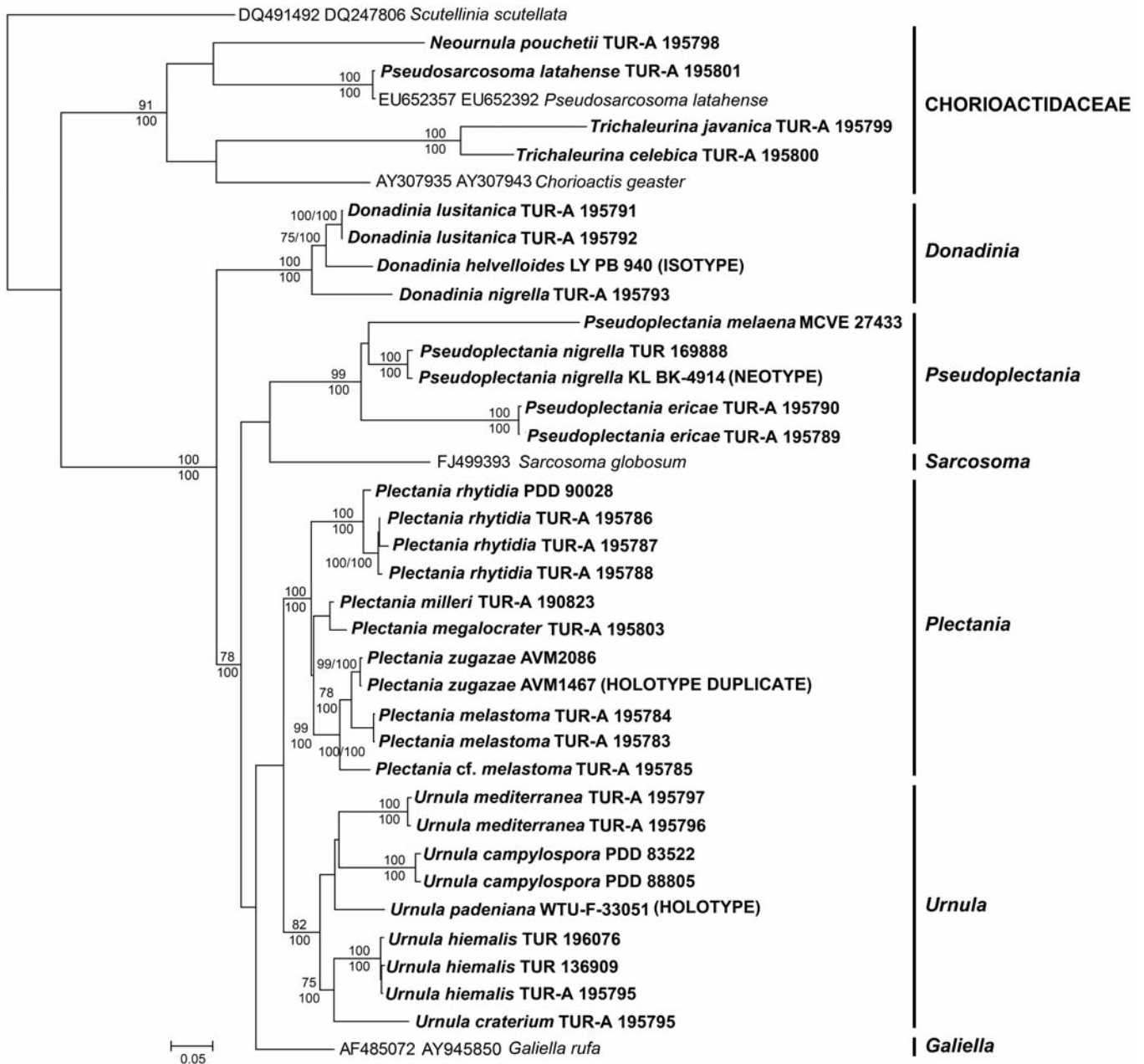


Fig. 2 – Consensus tree resulting from combined Bayesian ITS-28S LSU analysis of the *Sarcosomataceae* and *Chorioactidaceae* lineages studied. The length of the rooting branch was altered for publishing purposes. Nodes were annotated with maximum likelihood BP (above) and Bayesian PP (below). Only nodes supported (or nearly supported) by both analyses were annotated. **Bold names** belong to samples sequenced in the present study.

of 422 bp (1.65%) specifically variable in the only available sequence of *P. megalocrater*. The *P. milleri* sample analyzed was deeply studied by CARBONE *et al.* (2011a), and so was that of *P. megalocrater* by CARBONE *et al.* (2011b). All collections clearly match with their respective protologues, and differ from each other in some morphological, ecological and biogeographical features. If the slight molecular differences are constant or not, it should be addressed by further sequencing of more specimens of both species. However, they seem too low to consider each clade a different species if compared with sister lineages such as *P. melastoma* and *P. zugazae*. With regards to the latter species, we believe that it deserves a small comment because our revision has revealed many common features with *P. melastoma* and also one previously regarded as exclusive of *P. milleri*. In particular, *P. zugazae* microscopic characters are not so different from those of *P. melastoma* (AGNELLO & CARBONE, 2012); most of the

features described in the protologue are confirmed whilst other are amended, such as: mature asci up to 470–490 μm long, spores $Q_m = 1.6$, immature spores fusoid to slightly subfusoid when mature, the surface of the latter being very slightly warted (but this feature must be evaluated with more precise technique like SEM and above all on more mature spores), hymenial hairs present and av. 3.5–4 μm wide, medullary excipulum crossed by brown “*milleri*-type” hairs (see CARBONE *et al.*, 2011a). So, the only really deviant features (from *P. melastoma*) consist in a lower Q , more elliptical spores and also a slight difference in spores size. Macroscopically, it lacks the typical orange granules on the external surface, although the picture here published and water mounts have revealed an evident covering of an encrusting pigment very similar to that one of *P. melastoma*. With regards to the presence of hairs in the medullary excipulum, the first author has recently studied an American col-

TABLE I – Samples sequenced for the present study, GenBank codes

Taxon	Voucher/Strain	ITS	28S nrLSU
<i>Donadinia helvelloides</i>	LY PB 940	JX669834	JX669872
<i>Donadinia lusitanica</i>	TUR-A 195792	JX669810	JX669846
<i>Donadinia lusitanica</i>	TUR-A 195791	JX669811	JX669847
<i>Donadinia nigrella</i>	TUR-A 195793	JX669836	JX669874
<i>Neourmula pouchetii</i>	TUR-A 195798	JX669837	JX669875
<i>Plectania cf. melastoma</i>	TUR-A 195785	JX669804	JX669840
<i>Plectania megalocrater</i>	TUR-A 195803	JX669809	JX669845
<i>Plectania melastoma</i>	TUR-A 195784	JX669814	JX669850
<i>Plectania melastoma</i>	ALV0091	JX669805	JX669841
<i>Plectania milleri</i>	TUR-A 190823	JX669812	JX669848
<i>Plectania rhytidia</i>	TUR-A 195788	JX669816	JX669852
<i>Plectania rhytidia</i>	PDD 90028	JX669832	JX669871
<i>Plectania rhytidia</i>	TUR-A 195786	JX669813	JX669849
<i>Plectania rhytidia</i>	TUR-A 195787	JX669815	JX669851
<i>Plectania rhytidia</i>	PDD 75313	JX669833	
<i>Plectania zugazae</i>	AVM2086	JX669818	JX669855
<i>Plectania zugazae</i>	AVM1467	JX669817	JX669854
<i>Pseudoplectania ericae</i>	TUR-A 195789	JX669822	JX669862
<i>Pseudoplectania ericae</i>	TUR-A 195790	JX669823	JX669863
<i>Pseudoplectania melaena</i>	MCVE 27433	JX669806	JX669842
<i>Pseudoplectania nigrella</i>	KL BK-4914	JX669807	JX669843
<i>Pseudoplectania nigrella</i>	TUR-A 176861		JX669858
<i>Pseudoplectania nigrella</i>	TUR 172564		JX669860
<i>Pseudoplectania nigrella</i>	TUR 169888	JX669821	JX669859
<i>Pseudosarcosoma latahensis</i>	TUR-A 195801	JX669819	JX669856
<i>Trichaleurina celebica</i>	TUR-A 195800	JX669839	JX669876
<i>Trichaleurina javanica</i>	TUR-A 195799	JX669838	JX669861
<i>Urnula campylospora</i>	PDD 83522	JX669830	JX669869
<i>Urnula campylospora</i>	PDD 88805	JX669831	JX669870
<i>Urnula craterium</i>	TUR-A 195794	JX669820	JX669857
<i>Urnula hiemalis</i>	TUR 196076	JX669828	JX669868
<i>Urnula hiemalis</i>	TUR 136909	JX669827	JX669867
<i>Urnula hiemalis</i>	TUR-A 195795	JX669835	JX669873
<i>Urnula mediterranea</i>	TUR-A 195796	JX669808	JX669844
<i>Urnula mediterranea</i>	TUR-A 195797	JX669824	JX669864
<i>Urnula padeniana</i>	WTU-F-33051	JX669825	JX669866
<i>Urnula sp.</i>	PDD 81259	JX669829	

lection (NY 231 *sub Bulgaria mexicana*) which has shown all the features of *P. milleri* but the hairs in the medullary excipulum. We still do not know why some hairs can grow downwards, but we believe that this feature must not be regarded as relevant from a taxonomical point of view. In addition, a putative cryptic species of *P. melastoma* from Canada is here suggested. However, macro- and micromorphological features are extremely similar to those of *P. melastoma* and *P. zugazae* (if not identical but a slightly higher spore's Q), more studies are required in order to ascertain if all this molecular diversity could be considered as intraspecific, and a single species (i.e. *P. melastoma*) can be recognized. The creation of a new section to accommodate *Plectania milleri* or *P. megalocrater* is here suggested, but we prefer to wait for other species before formally establish it.

The section *Plicosporae* of *Plectania* was built around *Peziza rhytidia* Berk. from New Zealand. Other species have been considered in this section, such as the Argentinian *Plectania platensis* (= *Urnula platensis* Speg.) and the French *Urnula torrendii* Boud. RIFAI (1968) considered *Plectania platensis* as independent from *P. rhytidia* because of: (i) smaller spores; (ii) fewer striations in spore surface; (iii) a more branched-ramose apex of the paraphyses; (iv) association with *Eucalyptus*. The first three reasons were deeply investigated and refuted by DONADINI (1985), CONTU & LA ROCCA (1999), and lastly by CARBONE *et al.* (2010) who revised the type specimen of *P. platensis*. In the present work, no genetic differences have been found between *Plectania rhytidia* specimens fruiting exclusively under *Eucalyptus camaldulensis*, *Erica arborea* or *Quercus ilex* / *Quercus suber*, further supporting the already proposed synonymy also from an ecological point of view. The comparison of the Italian collections with those from New Zealand does not reveal any significant genetic or morphological variation.

Plectania sect. *Curvatisporae* was established around the species *Peziza campylospora* Berk. originally described from New Zealand (HOOKER, 1855), and further deeply revised by RIFAI (1968). This author confirmed Korf's hypothesis (KORF 1957a, 1957b) that *Plectania campylospora* and the Australian *Gloeocalyx bakeri* Masee were conspecific. Until now *Gloeocalyx* Masee has been therefore treated as a synonym of *Plectania*. Our results show that *Peziza campylospora* definitely does not belong to the genus *Plectania*, but to a different lineage close to the genus *Urnula*. For that reason *Gloeocalyx* is now considered a late synonym of *Urnula*, and the already existing name *Urnula campylospora* (Berk.) Cooke should be used for this species. For an in-depth morphological study regarding this species see CARBONE & AGNELLO (2013b).

According to literature available many species originally described in *Urnula* have been later transferred to other genera (e.g. *Urnula megalocrater* Malençon & Le Gal, *Urnula lusitanica* Torrend & Boud. or *Urnula platensis* Speg.). As already mentioned in the introduction, according to DISSING (1981) the currently accepted species seem to be *U. craterium*, *U. hiemalis*, *U. groenlandica* — and also a fourth species *Urnula sp.* = *Urnula hiemalis sensu* KEMPTON & WELLS (1974). The Danish author also reported that both *U. hiemalis* and *U. groenlandica* lack hymenial hairs. CARBONE & AGNELLO (2012b, 2013a) argued that hymenial hairs are definitely present in *U. hiemalis*, although sometimes they are rare to infrequent. Our results support the independence of *U. hiemalis* from both the European and American lineages of *U. craterium*. Further studies are required to ascertain if any of these should be described as a new species. Additionally, *Plectania mediterranea* turned out to belong also to the *Urnula* clade and thus the new combination is proposed. Some collections previously treated by American mycologists as *Sarcosoma mexicanum* or *Plectania mexicana*, are here accommodated under

the name *Urnula padeniana* after the revision of the type specimen of *Bulgaria mexicana* (CARBONE *et al.*, 2013), which should be considered a member of the “*campylospora*-complex” being extremely different from *U. padeniana*. The species in the *Urnula* clade show broad morphological differences with *Urnula craterium* (type species of the genus), unveiling the need for further ultrastructural and cytological studies to uncover yet putative common features.

Phylogenetic inference based on the neotype of the type species *Pseudoplectania nigrella*, showed that the genus *Pseudoplectania* is well supported as a sister clade to *Plectania*. BOUDIER (1885) proposed the genus *Melascypha* to accommodate *Melascypha melaena* (Fr.) Boud. (BOUDIER, 1905–1910; BOUDIER, 1907) because of its big size, the presence of a well differentiated stipe, and the morphology of external hairs, paraphyses and spores. However, these features were not considered as relevant by subsequent mycologists who proposed *Melascypha* as a synonym of *Pseudoplectania*. Present results support this synonymy, and the independence of *P. nigrella*, *P. ericae* and *P. melaena*. *Plectania carranzae*, with globose spores, belongs to this genus — as also stressed by CALONGE & MATA (2002) who, however, regarded it a synonym of *Plectania* — and so the new combination *Pseudoplectania carranzae* is here proposed. Lastly, during the final revision of the article we obtained clean ITS and LSU sequences of some collections perfectly matching (macro-microscopically, phenologically and ecologically) the species known as *Pseudoplectania sphagnophila* (Pers.) Kreisel. Our results, not shown here, suggest also the independence of this species.

The results based upon the isotype specimen of *Urnula helvelloides* prove that this species must be regarded as the type of the independent genus *Donadinia*. Results also show that *Urnula lusitanica* (\equiv *Plectania lusitanica*) and *Paxina nigrella* (\equiv *Plectania nannfeldtii*) belong to this clade, as already pointed out by CARBONE *et al.* (2011, as *Plectania* sect. *Donadinia*), and so the two new combinations are proposed. Unfortunately we have not obtained a complete ITS and LSU sequence of *Plectania seaveri* holotype, but a perfectly clean sequence of ITS2 region was successfully obtained using primers ITS3-ITS4 (GenBank KC249999). The separate phylogenetic analysis of ITS1 region revealed that this sequence shows a clear relationship with genus *Donadinia* (data not shown), representing an independent lineage within this clade. Due to its morphological features (see CARBONE *et al.*, 2012b) and also on this partial genetic result, it is here transferred to *Donadinia* as well.

The genus *Galiella* is well supported by phylogenetic inference on the basis of the sequences of its type species *Galiella rufa* previously stored in GenBank. This genus displays a genetic distance similar to that of most other lineages in the *Sarcosomataceae* with almost no intraspecific variability. Two species formerly included in the genus, *G. javanica* and *G. celebica*, seem to be unrelated to the type species, and constitute an independent lineage within the *Chorioactidaceae* (see the discussion below). The old generic name *Trichaleurina* Rehm is here restored for these species, primarily on the morphological study made by the first author on the holotype of the type species *Trichaleurina polytricha* Rehm. *Trichaleurina* was first introduced by REHM (1903) as an infrageneric taxon within *Aleurina* Masee, including three species. Then REHM (1914) raised it at genus level, validating it with the new (and only) species *Trichaleurina polytricha* from the Philippines. Nannfeldt’s unpublished revision concerning *T. polytricha* holotype and also *Urnula philippinarum* holotype led him to consider both as synonyms of *G. javanica*. Our type studies on the former two cited species confirm that they are conspecific to each other and definitely congeneric with the species known as *Galiella javanica* and *G. celebica*. Anyway, at present, we prefer to study more material before state if they are conspecific to *G. javanica*. In fact, very small differences in the external hairs morphology could be useful characters for distinguishing species.

The genus *Sarcosoma*, the core of the family, is here represented by a single sequence of its type species *Sarcosoma globosum*. It seems to be a clearly independent clade within the *Sarcosomataceae*, in accordance with its deviant morphological features (CAR-

BONE, 2009). *Sarcosoma latahensis* was first invalidly described as *Plectania latahense* (PADEN, 1967), then validly assigned to *Sarcosoma* by PADEN & TYLUTKI (1969b), and finally transferred to the genus *Plectania* by CARBONE *et al.* (2009). Genetic results allow concluding that it does not belong to any of these or any other previously described genera, so the new genus *Pseudosarcosoma* is here proposed to accommodate it in the family *Chorioactidaceae*, as defined by PFISTER *et al.* (2008). The latter family has been circumscribed with features that can be summarized as follows: pigmentation, excipular construction without gelified tissue, ascospores with cyanophilic walls or cyanophilic surface ornamentation in the form of ridges or warts, warty external hairs, and in addition multinucleate ascospores and cells of paraphyses. It is pretty obvious that *Trichaleurina* is deviant from this definition because of its jelly flesh, but matches in all other respects (e.g. warty spores and external hairs). The main problem should rise for *Pseudosarcosoma* which shows smooth spores, slightly gelified medullary excipulum and smooth external hairs. As can be seen no morphological striking “chorioactidaceous” features seem to be present in this new genus, although our results put it into this family. It is worth to note that the collections studied by us of *Pseudosarcosoma*, *Neournula* and *Trichaleurina* don’t have the so-called “hymenial hairs” which, to the best of our knowledge, are present in the family *Sarcosomataceae*. The same can be said for the other genera, which, according to PFISTER *et al.* (2008) seem to lack hymenial hairs (or non-septate paraphyses). If this will turn out to be true, this would be an additional feature to delimit both families.

Finally, with regards to the family *Chorioactidaceae*, our genetic studies seem to suggest the independence of the European *Neournula pouchetii* (Berthet & Rioussset) Paden (BERTHET & RIOUSSET, 1965) from the American 28S LSU sequences already stored in GenBank with this name (AY307940). Since this taxon was first described in Europe, the American lineage could be accommodated under the species *N. nordmanensis* Paden & Tylutki (PADEN & TYLUTKI, 1969a). Both species have been regarded as synonyms since PADEN (1972), and further studies are surely needed to clarify this preliminary result.

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