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Hidden biodiversity revealed by collections-based research—Laboulbeniales in millipedes: genus *Rickia*

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Abstract

Nine new species of the genus *Rickia* parasitizing Diplopoda are described: *R. appendicifera* from Iran on *Chiraziulus, R. candelabriformis* from Australia and New Zealand on several Spirostreptida, *R. galatheae* from New Zealand on *Eumastigonus*, *R. gigas* from Tanzania on '*Spirostreptus*' and *Archispirostreptus*, *R. lophophora* from Tanzania on some genera of Spirostreptidae, *R. obelostrepti* from Tanzania on *Obelostreptus*, *R. odontopygiidarum* from Tanzania on Odontopygidae, *R. platessa* from Singapore and Thailand on Pachybolidae, and *R. rhynchophora* from Australia on *Trigoniulus*. This nearly triples the previously known number of species of *Rickia* species on millipedes; all 14 species are treated in this study with photomicrographs, additional observations on previously described taxa and comments. A key to these species is also provided. The Laboulbeniales species were found on millipede specimens preserved mostly at the Natural History Museum of Denmark, from samples collected between 1916 to the present.

Key words: Ascomycota, Diplopoda, Julida, parasitic fungi, Spirobolida, Spirostreptida

Introduction

Taxonomy provides the foundation to understand biodiversity and such derived biological disciplines as biogeography, ecology, ethology and evolution (Causey *et al.* 2004, Wheeler *et al.* 2004). Type specimens are the faithful custodians of taxon identity, contributing the fundamental proofs for solving systematic issues, and their preservation and availability for study over time is a duty of scientific collections. An estimated 2.5–3 billion specimens are deposited in natural history collections worldwide (Ariño 2010). This number is, however, clearly underestimated, since each plant, animal or fungal specimen may harbour several parasites. For example, Peterson *et al.* (1980) prepared 3000 specimens of feather mites from bird skins (families Apodidae and Hemiprocnidae) in several ornithological museum collections and described 47 new species of mites from this material. Chlebicki (1995) found 27 species of plant parasitic fungi on *Dryas* in Polish herbaria.

A further remarkable example of this phenomenon is provided by Laboulbeniales on millipedes (Diplopoda)—all species here described were obtained from millipede hosts deposited in museum collections, most of them in the zoological collections of the Natural History Museum of Denmark (ZMUC).

Developing only on living arthropods, ectoparasitic fungi of the order Laboulbeniales have chitinous cell walls that assure their preservation both in dry and alcohol-preserved hosts (Santamaria 2001). Taxonomy of the Laboulbeniales is mainly based on morphological features of the thallus, which is attached to the surface of its host (Tavares 1985). In the last decades, phylogenetic analysis using DNA sequences has decisively contributed to clarify the biogeographic history and the roles of dispersal and vicariance, clarifying aspects of morphological taxonomy of sibling species, which often mask the biodiversity patterns and their evolutionary relations (Giribet 2015). Among Laboulbeniales, the development of DNA extraction methods has confirmed their fungal origin within filamentous Ascomycetes (Weir & Blackwell 2001) and has contributed to the clarification of "position specificity" and cryptic diversity (Goldmann & Weir 2012, Goldmann *et al.* 2013). Collections-based research has used only morphological taxonomic characters to

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unveil and document new laboulbenialean diversity (Weir & Blackwell 2001). Efficient methods for extracting DNA from museum material have only very recently been developed (Haelewaters *et al.* 2015).

Four genera of Laboulbeniales are known to occur on millipedes: *Diplopodomyces, Troglomyces, Triainomyces* and *Rickia.* The two first genera were treated in previous papers (Santamaria *et al.* 2014; Enghoff & Santamaria 2015). The present study is devoted to the genus *Rickia* Cavara, which with 161 species (counting those described here) is one of the largest known genera within the Laboulbeniales. Thaxter (1926: 445–450) made an extensive analysis of the species of *Rickia* known heretofore. These species have a wide variety of hosts, including Acarina, Orthoptera, Hymenoptera, Coleoptera, Blattaria and Diplopoda (Tavares 1985, Weir 1998). Although the genus is widespread, its species seem to prefer tropical regions, which have the largest known diversity of *Rickia* species associated with arthropods (Weir & Hammond 1997, Santamaria & Espadaler 2015).

Up to now five species of *Rickia* were known on millipedes, viz., *R. dendroiuli* W. Rossi *in* W. Rossi & Balazuc *ex* W. Rossi from Italy (Rossi & Balazuc 1977), *R. laboulbenioides* De Kesel *in* De Kesel, Haelewaters & Gerstmans from The Netherlands and Belgium (De Kesel *et al.* 2013), *R. pachyiuli* M. Bechet & I. Bechet from Romania (Bechet & Bechet 1986), *R. siddhartha* Balazuc *in* W. Rossi & Balazuc from Sri Lanka (Rossi & Balazuc 1977), and *R. uncigeri* Scheloske from Germany (Scheloske 1969) and Poland (Majewski 1974). They all parasitize cylindrical millipedes (superorder Juliforma); the Asian *Rickia siddhartha*, parasitizes a species of the order Spiropstreptida, family Harpagophoridae, the other four species were found on European hosts of the order Julida, family Julidae.

This contribution describes nine new species of the genus *Rickia*, discovered and isolated from millipedes from 14 countries on four continents and includes also revision of the previously known species of *Rickia* on millipedes. This material represents a sampling effort done by generations of biologists from 1916 to date whose collections have been preserved in Museums.

Material and Methods

Most of the millipede hosts were found by examining with a dissecting microscope part of the zoological collections of the Natural History Museum of Denmark (ZMUC). Hosts are preserved in 70% ethanol. Permanent slides were prepared following previously described methods (Benjamin 1971), with the modifications reported in Rossi & Santamaria (2015), and are kept in the BCB Mycotheca of the Universitat Autònoma de Barcelona (BCB-slides), and in the Mycological collection Herbarium of the Natural History Museum of Denmark, University of Copenhagen (C-F-slides). Millipede specimens with attached fungi are kept in the Zoological collections of the Natural History Museum of Denmark (ZMUC) when nothing else is indicated. Photomicrographs were made with a Jenoptik ProgRes 10 Plus digital camera on a Leica DMR microscope equipped with differential interference contrast optics (DIC). Images were processed with Photoshop CS5 software and Dpx View Pro for its included feature of extended focus function. Specimens for scanning electron microscopy (SEM) were transferred to 100% ethanol, then critical point-dried in a Tousimis Autosamdi 815, serie A, mounted on aluminum stubs, coated with platinum/palladium and studied in a JEOL JSM-6335F scanning electron microscope. Type slides of *Rickia dendroiuli* and *R. siddhartha* were borrowed from Walter Rossi's collection (FI, Firenze Herbarium, Italy).

The terminology used in the descriptions follows Thaxter (1926) and Tavares (1985); although we have adopted some abbreviations concerning the denomination of the thallus cell series: **a**, anterior series; **m**, median series; **p**, posterior series; subindexed with numbers as adequate, $\mathbf{a}_1 \ldots \mathbf{a}_n$, $\mathbf{m}_1 \ldots \mathbf{m}_n$, and $\mathbf{p}_1 \ldots \mathbf{p}_n$, increasing from the foot to the apex. We adopt the term phialide to refer the flask-shaped terminal portion of antheridia, where spermatia are formed, according to Tavares (1985).

Cells and thallus elements were labeled in the figures with abbreviations mostly following Tavares (1985). Alphabetical guide to abbreviations: **a**, primary septum (original septum of spore); **an**, antheridium (pointing to the phialide); **apc**, appendiculate cell; $\mathbf{a}_n$, cells of anterior series; $\mathbf{m}_n$, cells of median series; **pa**, primary appendage; $\mathbf{p}_n$, cells of posterior series; **sa**, secondary appendage; **sc an**, stalk cell of antheridium; **tr**, trichogyne; **trs**, trichogyne scar; $\mathbf{w}_n$, perithecial wall cells; **I**, basal cell of thallus; **VI**, stalk cell of perithecium.

Notes on measurement standards

The lack of clearly delimited standards for measurements of different parts of the thallus in the specialized literature introduces uncertainty that often leads to confusion and difficulty in comparing descriptions of species. For any description of Laboulbeniales two measurements are mandatory: the total length of thallus and the length × width of

the perithecium. Depending on the species, other measurements may include antheridia (only the phialide or flask-shaped portion, without the stalk), appendages (unbroken and fully developed), ascospores (with the sheath), and other features depending on whether the measured part represents a striking feature worth mentioning.

The measurements here presented are standardized as following: (1) total length of the thallus, from the base of the darkened foot to the apex of the most apical perithecium; (2) length × width of perithecium, length from the base of perithecial basal cells -m, n, n' and VII, not including cell VI- to the apex, and maximum width; (3) length × width of the antheridium, only including the phialide (the flask-shaped portion), not the stalk and the appendiculate cells; and (4) secondary appendages, only the length of the uppermost cell without including the appendiculate cell.

Taxonomic treatment

Rickia appendicifera Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 1−5)
Mycobank MB 815401

Diagnosis:—Receptacle triseriate, a: 2, m: 2, p: 2(–3). Primary appendage conspicuous, consisting of a dark brown, straight, slightly constricted, rigid fragment, about twice as long as any of the other similar parts, i.e., secondary appendages and antheridia. Median series with m_1 twice as long as m_2.

Type:—IRAN. Chiraz, clayey mountain north of the city, on *Chiraziulus kaiseri* (Mauriès 1983) (Cambalidae), 16 February 1937, *E.W. Kaiser* leg., C-F-95116, C-F!, **holotype designated here**; BCB-SS·E602ab, d, BCB!, **isotypes designated here**.

Etymology:—*appendicifera*, meaning "bearing an appendage"; referring to the conspicuous primary appendage, especially remarkable when the thalli are seen on the host cuticle under a dissecting microscope.

Thallus hyaline except for the dark brown foot, the base of appendages and the stalk cells of antheridia. Total length 78−94 µm. Receptacle triseriate. Basal cell twice as long as broad, its distal part wedged between the lower cells of the marginal series, separated by oblique septa from cells a_1 and p_1.

Anterior series consisting of two cells. Cell a_1 triangular in section, lacking appendages or initial appendiculate cells. Cell a_2 triangular to trapezoidal in section, including on its upper-inner corner the perithecial stalk-cell (Fig. 1, VI), bearing on the outer-upper corner one antheridium with its appendiculate cell (Fig. 3, an; Fig. 5, apc, scan).

Median series consisting of two cells, rounded at both extremes, fully surrounded by the two lateral series, borne just above a_1 and p_1 and ending slightly above p_2 (Fig. 1). Cell m_1 2–3 times as long as m_2.

Posterior series composed of 2(–3) cells (Fig. 1). Cell p_1 without appendages, similar to a_1. Cell p_2 longer than broad, bearing (1–)2(–3) secondary appendages (very rarely one of these is replaced by a single antheridium) on its outer-upper corner and the primary appendage on its top. When more than one secondary appendage is present, they are overlapping. Cell p_3, if present, bears a secondary appendage similarly as p_2. Basal cell of primary appendage 1.5 times as long as broad, bearing the terminal long cell, the latter with a sallow base, a rather long, dark brown, and constricted middle part, which is about twice as long as analogous parts of the secondary appendages, and a hyaline, short, often damaged terminal portion (Fig. 2, pa).

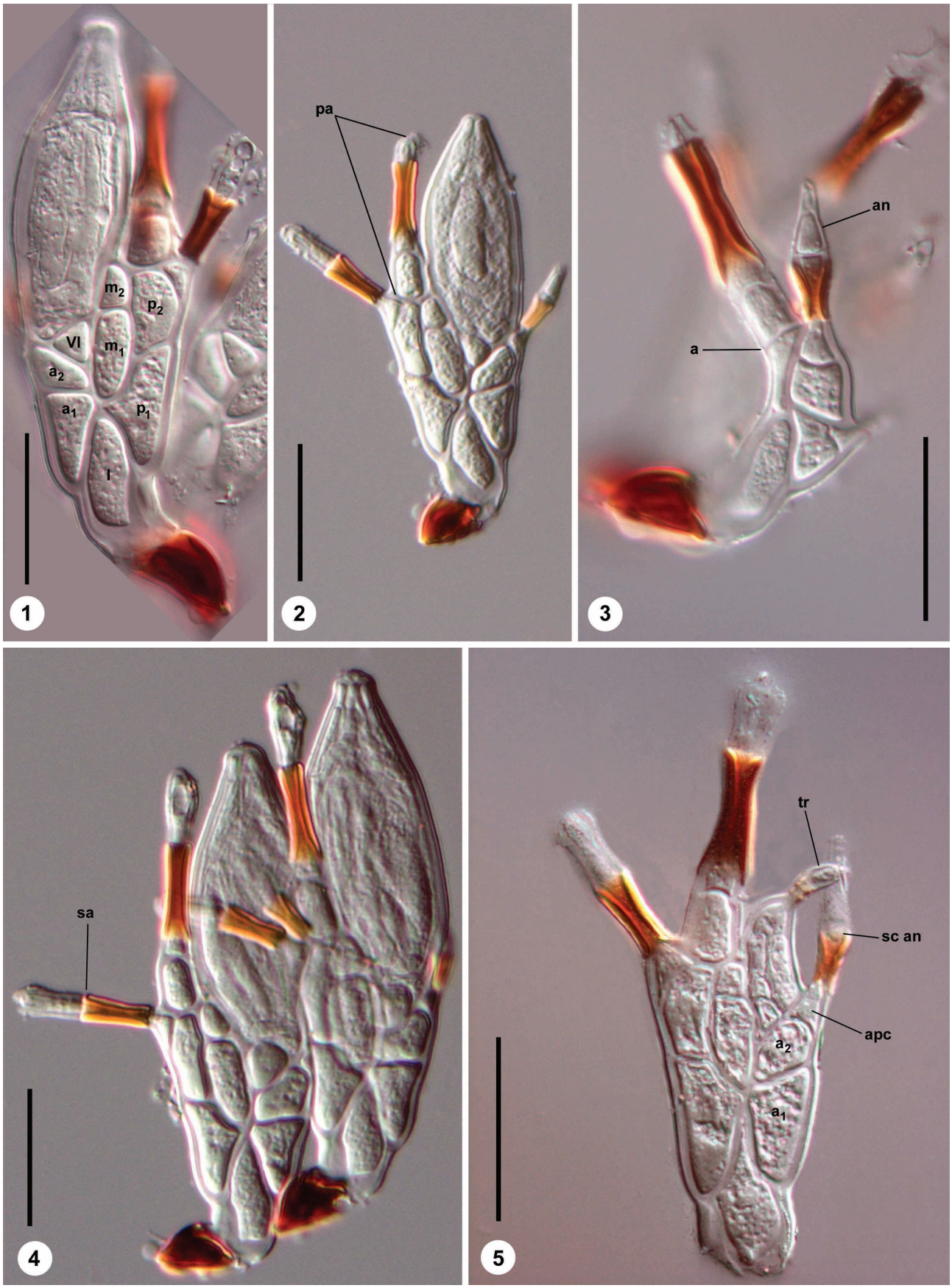
Antheridium 7–11 × 3–4 µm, typically isolated on cell a_2, above a subtriangular hyaline appendiculate cell, an elongate dark brown and basally constricted stalk-cell, and the terminal flask-shaped phialide (Fig. 3, an; Fig. 5, apc, scan).

Secondary appendages 17–23 µm, consisting of a hyaline distal portion contrasting with a dark brown lower part, which is constricted near the septum of separation from the appendiculate cell (Fig. 4, sa).

Perithecium 42–54 × 19–24 µm, solitary, stout, ovoid, entirely hyaline (even the trichogyne scar), with a slightly differentiated short neck and a blunt apex with rounded and poorly defined lips.

Discussion:—Determining the position of the primary septum in this species is not easy, because the basal cell of the primary appendage does not show the usual dome-shaped form as in the remaining species of *Rickia* included in this work. We have defined the position of primary septum (Fig. 3, a) in agreement with what mature thalli or even sporelings show. This species appears absolutely isolated among the other species in this study. A short trichogyne was observed on an immature thallus, pointing towards the antheridium (Fig. 5, tr).

Position on host:—*Rickia appendicifera* is randomly distributed on the host; thalli were found on the head, antennae, the dorsal part of body rings, and the legs, the highest density around the most anterior pairs of legs.



FIGURES 1–5. *Rickia appendicifera*. Figs 1–2. Nearly mature thalli. Figs 3 and 5. Immature thalli. Fig. 4. Two paired mature thalli. (Figs 1, 5, SS·E602b; Figs 2, 4, C-F-95116; Fig. 3, SS·E602a.) (For interpretation of abbreviations see under materials and methods.) Scale bars for Figs 1, 3, 5 = 20 µm; for Figs 2, 4 = 25 µm.

Notes on hosts:—*Chiraziulus kaiserii* belongs to order Spirostreptida, family Cambalidae. *Chiraziulus* has two known species, both endemic in Iran, and is the only cambalid genus occurring in the western Palaearctic region, being isolated from its presumed closest relative by more than 7000 km distance (Reboleira *et al.* 2015).

Rickia candelabriformis Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 6–10, 60)
Mycobank MB 815402

Diagnosis:—Receptacle biseriate; a: 3, p: 4(–5). Cells I, a_1 and p_1 delineating a curious form reminiscent of a two-armed candelabrum. Only one antheridium on cell p_1, with a long, strongly inwardly (towards the thallus) curved neck.

Type:—AUSTRALIA. Tasmania, St Columba Falls, 27.1 km 256'W St. Helens, S41º17'7.2" E147º55'33.7", 335 m.a.s.l., eucalypt/casuarinas woodland, on indeterminate Iulomorphidae (Spirostreptida), 7 March 2006, *N.Scharff & T. Szüts* leg., C-F-95089, C-F!, **holotype designated here**; BCB-SS·E600a, c, BCB!, **isotypes designated here**.

Etymology:—*candelabriformis*, meaning "shape of candelabrum", the ensemble of cells I, a_1 and p_1 resembles the shape of a simple candelabrum with only two arms.

Thallus hyaline to pale yellowish except for the dark brown foot, the trichogyne scar, and the septa separating the appendiculate cells from appendages. Total length 134–174 µm. Receptacle biseriate. Basal cell four times as long as broad, narrowly ovate, surrounded on both sides for about ¾ of its upper length by cells a_1 and p_1 from which it is separated by strongly oblique, nearly vertical septa. The outline in this part of the thallus is abruptly indented at the transition between cell I and both lower cells of the marginal series, resulting in the distinct shape from which the epithet of species has been derived (Figs 6–7, arrows).

Anterior series consisting of three cells (Fig. 6). Cell a_1 broadly triangular in section, about 2.5 times as long as broad, never with appendages. Its upper side reaching the same level as the top of cell I. Cells a_2 and a_3 flattened, each giving rise to a flattened and elongated appendiculate cell bearing a secondary appendage. Cell a_3 bearing the perithecium and a very inconspicuous perithecial stalk-cell (cell VI) on its upper-inner corner (Fig. 8, VI).

Posterior series consisting of 4(–5) cells. Cell p_1 nearly identical in shape and size to cell a_1, but it is worth mentioning that it supports the unique antheridium of the thallus on its outer-upper corner, including a minute appendiculate cell and a bigger stalk-cell, both concolorous with the pale receptacle (Figs 7, 9–10). Cell p_2 very variable in shape and size, with a secondary appendage with an appendiculate cell on its upper-outer corner. Cell p_3, which sometimes divides forming a p_4, usually lacks appendages or rarely bears only one; it varies greatly in size depending on whether it is undivided (then it is longer than broad) or if the additional p_4 is also formed, in which case both cells appear shortened. The upper cell of the series (p_4 or p_5) supports the primary appendage, including its dome-shaped basal cell, a constricted and dark brown septum, and the distal elongated cell, which is similar to any secondary appendage (Fig. 8, pa).

Antheridium 8–12 × 3–5 µm, typically isolated on p_1, above a minute triangular appendiculate cell, a bigger stalk-cell, and the terminal flask-shaped phialide ending in a rather long, strongly inwardly incurved efferent neck (Figs 7, 9–10, an).

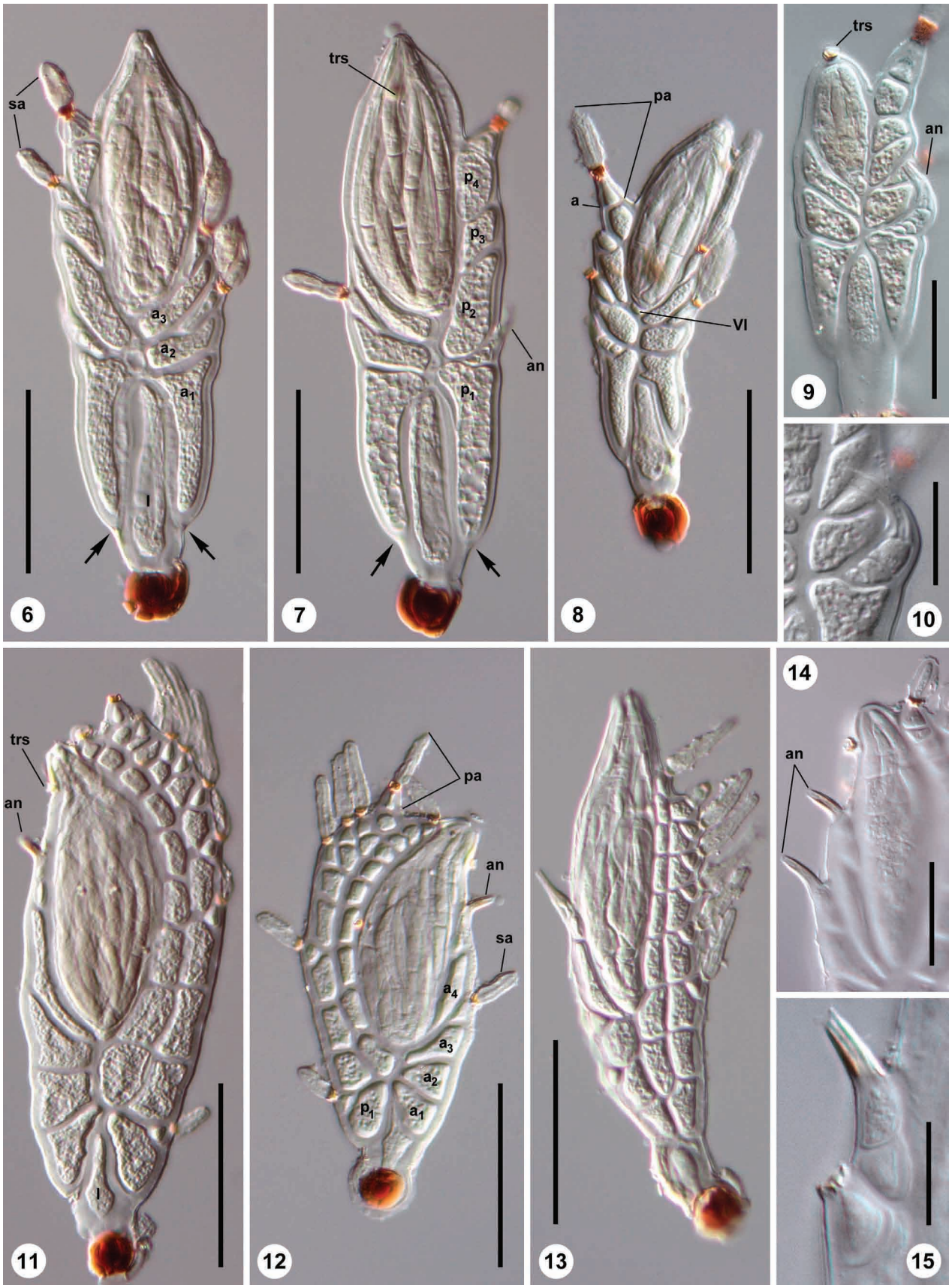
Secondary appendages, 21–43 µm, deteriorate easily, hyaline, soft, delicate, slightly expanded by pressure of coverslip, separated from respective appendiculate cells by dark brown and constricted septa (Fig. 6, sa).

Perithecium 65–82 × 27–32 µm, solitary, ovoid, entirely hyaline, except for the tan trichogyne scar present on the side where the short neck is slightly differentiated; apex blunt (Fig. 7, trs).

Discussion:—Some thalli differ from the above description in having two perithecia and a variable number of cells in the series, but these specimens are very uncommon and could be considered abnormal by damage and subsequent unusual cell divisions. This species may be compared with *R. rhynchophora* if we only look at the base of thallus, but remaining characters are very different. The sucker-like shape of the foot of a sporeling and of two immature thalli can be seen on the SEM image of Fig. 60.

Position on host:—Thalli are found randomly along the body rings, legs and head, including antenna and clypeus. Female hosts are highly infected on the first pairs of legs. Three thalli were found in a male gonopod (C-F-95099).

Notes on hosts:—The Australian fauna of Iulomorphidae is extremely poorly known, and numerous species and genera still await description. Even the delimitation of Iulomorphidae vis-à-vis Cambalidae is dubious (Enghoff *et al.* 2015). *Eumastigonus* (see also *R. galatheae* sp.nov.) is endemic in New Zealand (Korsós & Johns 2009).



FIGURES 6–10. *Rickia candelabriformis*. Figs 6–8. Mature thalli, arrows in Figs 6 and 7 indicate a diagnostic characteristic, from which the species takes his name. Fig. 9. Immature thallus. Fig. 10. Detail of antheridium. (Figs 6, 7, SS·E600a; Fig. 8, SS·E589a; Figs 9–10, SS·E593a.) **FIGURES 11–15**, *Rickia galatheae*. Figs 11–13. Mature thalli. Figs 14–15. Details of antheridia. (Figs 11, 14–15, SS·E598a; Fig. 12, C-F-95088; Fig. 13, SS·E595a.) (For interpretation of abbreviations see under materials and methods.) Scale bars for Figs 6–8, 11–13 = 50 µm; for Figs 9, 14 = 20 µm; for Figs 10, 15 = 10 µm.

Additional collections examined:—AUSTRALIA. SE QLD, Lamington NP near O'Reilly's Gesthouse, rainforest, on *Victoriocambala* sp. (Spirostreptida, Iulomorphidae), 13–17 April 2002, *N.Scharff* & *S.Larsen* leg., BCB-SS·E589ac, BCB-SS·E591 (BCB!). Tasmania, Newall creek, Franklin-Gordon Wild Rivers, N.P. 9.67 km 177' Queenstown, *Notophagus* rainforest, S42º09'37.1" E145º32'20.1", 159 m.a.s.l., on Iulomorphidae indet. (Spirostreptida), 14 March 2006, *N.Scharff* & *T. Szuts* leg., BCB-SS·E593ac (BCB!). Tasmania, Weldborough Pass Scenic Reserve, 28.6 Km 280WNW St Helens, *Notophagus* rainforest, S41º12'59.8" E147º56'18.2", 480 m.a.s.l., on Iulomorphidae indet. (Spirostreptida), 6–7 March 2006, *N.Scharff* & *T. Szuts* leg., BCB-SS·E594 (BCB!). Tasmania, Cradle Mountain, Lake St Clair N.P., near Waldheim cabins, 22.6 Km 202SWS Moina, *Notophagus* rainforest, S41º38'28.5" E145º56'26.5", 926 m.a.s.l., on *Amastigogonus* sp. (Spirostreptida, Iulomorphidae), 3–5 March 2006, *N.Scharff* & *T. Szuts* leg., BCB-SS·E597 (BCB!). NEW ZEALAND. Ak: Waitakere Ranges Regional Park, Kauri Grove Track, S36º57.795' E174º30.876', on *Eumastigonus* sp. (Spirostreptida, Cambalidae), 2 February 2011, *A.Solodovnikov* & *L.Vilhelmsen* leg., BCB-SS·E592ac (BCB!).

Rickia dendroiuli W. Rossi *in* W. Rossi & Balazuc *ex* W. Rossi (Figs 52–53)

This species was validated with designation of the holotype by Rossi (1986) to correct its absence in the original description (Rossi & Balazuc 1977). The type material comes from Italy and was found on *Cylindroiulus latzeli* (Berlese 1884) (as *Dendroiulus*) (Julida, Julidae). The authors compared their species with *Rickia uncigeri* Scheloske and mentioned many differences between them. On the basis of our studied material the number of cells for each series is 3(a), 11(m), and 8(p), which does not differ significantly from what was described in the protologue (3–4 a, 9–10 m, 7 p).

The species of *Rickia* parasitizing family Julidae, order Julida, constitute a group of closely related species: *R. dendroiuli*, *R. laboulbenioides*, *R. pachyiuli*, and *R. uncigeri*. Distinguishing these species may be difficult, and careful observation is needed. Only *R. laboulbenioides* is easily and readily distinguished from others by specific characters such as, for example, the shape and size of the primary appendage and the subtending cell. *Rickia dendroiuli* may be distinguished from *R. pachyiuli* and *R. uncigeri* by the median series of the receptacle. The median series of *R. pachyiuli* consists of 11–12 cells, of which 7–8 cells are located below the base of the perithecium, whereas in *R. dendroiuli* and *R. uncigeri* there are only two cells in this position. In *R. dendroiuli*, the upper part of the median series (approx. the 3–4 distal cells) clearly curves towards the posterior side of the thallus overlapping cell p_7 and causing the primary appendage to point obliquely in an angle of about 45º as to the perithecial axis (Fig. 53, arrow). This character is not mentioned in the original description although it is visible in the illustrations. We consider it important to distinguish *R. dendroiuli* from the other two species.

Rickia dendroiuli has been recorded from England (Berkshire) growing on *Cylindroiulus punctatus* (Leach 1815) (Storey 2009), but the several fine images of the fungus show that the species in question is *R. laboulbenioides*, not *R. dendroiuli.* The host of *R. dendroiuli*, *C. latzeli,* previously known as *Dendroiulus latzeli*, belongs to order Julida, family Julidae, and is largely widespread in Italy where it is endemic.

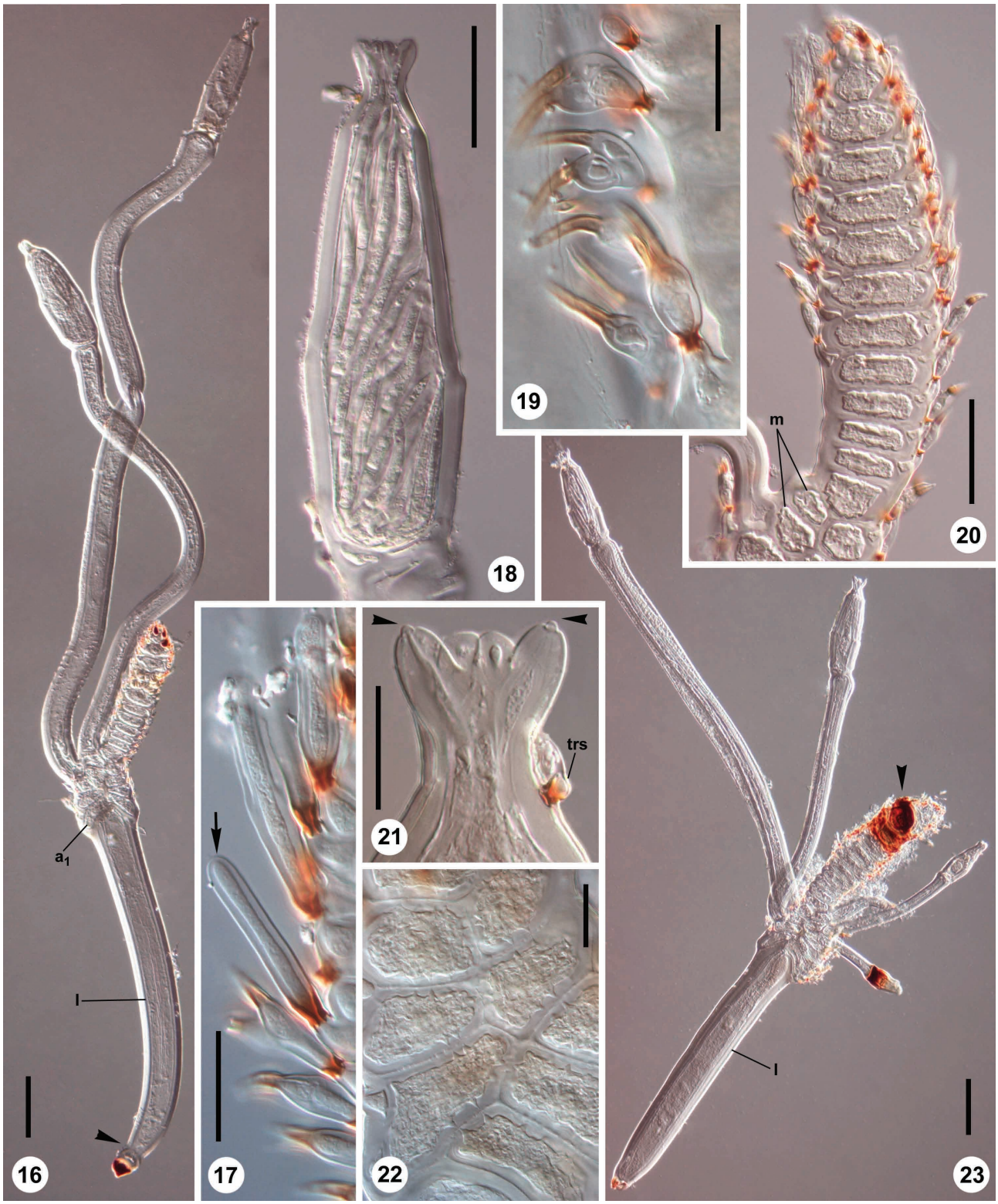
Position on host:—Many thalli on the anterior legs (pairs 1–12), sometimes also on the ventral parts of the corresponding body rings, a few thalli also found on legs further back (to the middle of the millipede's body) and on the head, antennae and mouthparts (Enghoff & Santamaria 2015).

Collections examined:—ITALY. Roma, Canale Monterano, on *Cylindroiulus (Dendroiulus) latzeli* (Berlese 1884), 17 April 1976, *W.Rossi* leg., WR586 -paratype-. Veneto, Montello, between Treviso and Belluno, on *C. latzeli*, 2 October 2010, *L. Bonato et al.* leg.

Rickia galatheae Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 11–15)
Mycobank MB 815403

Diagnosis:—Receptacle triseriate, a: 4, m: (7–)9, p: (8–)10(–12). Uppermost cell of anterior series (a_4) bearing a single antheridium, without a stalk cell, terminating in a brownish, outwardly curved, efferent neck. Median series flanking the dorsal side of the perithecium, consisting of subequal cells, with approximately parallel sides.

Type:—NEW ZEALAND. Wellington Porirua PA, on *Eumastigonus distinctior* Chamberlin 1920 (Spirostreptida, Cambalidae), 14 December 1951, *Galathea II expedition*, C-F-95088, C-F!, **holotype designated here**; BCB-SS·E598a, c, BCB!, **isotypes designated here**.



FIGURES 16–23. *Rickia gigas*. Fig. 16. Mature thallus with two mature perithecia; slight geniculation near the darkened foot is seen (arrowhead). Fig. 17. Detail of secondary appendages (arrow). Fig. 18. Detail of mature perithecium. Fig. 19. Detail of antheridia. Fig. 20. Lateral branch of the posterior series of cells. Fig. 21. Perithecial apex at high magnification showing rounded papillae (arrowheads). Fig. 22. Detail of receptacle cells to show the several pores connecting them (see the pointed, triangular or arrow-head sized expansions of cytoplasm in the wall cells). Fig. 23. Mature thallus with up to five perithecia, the two of the left mature, and darkening of lateral branch (arrowhead). (Figs 16, 21, 23, C-F-95086; Fig. 17, SS·E578b; Fig. 18, SS·E576d; Figs 19, 22, SS·E578c; Fig. 20, SS·E576c.) (For interpretation of abbreviations see under materials and methods.) Scale bars for Figs 16 and 23 = 100 µm; for Figs 17, 19, 21–22 = 20 µm; for Figs 18, 20 = 50 µm.

Etymology:—*galatheae*, named after the "Galathea II" expedition (Bruun *et al.* 1956) during which part of the host material was collected. We wish to emphasize these interesting finding sponsored by the Danish government through the important Galathea expeditions.

Thallus hyaline except for the dark brown foot, the trichogyne scar, the septa separating the appendiculate cells from appendages and often, the pale brown efferent necks of antheridia located along the perithecium on a_4 (Figs 11–12, 14, an). Total length 112–133 µm. Receptacle triseriate. Basal cell 1.5 times as long as broad, base cylindrical, upper part acute, embedded between a_1 and p_1, reaching about the middle of these cells, or higher (Fig. 11, I).

Anterior series consisting of four cells (Fig. 12). Cell a_4 subtending perithecium, narrow and elongate, reaching half of the perithecium length, supporting an appendiculate cell giving rise to an antheridium (Fig. 11–12, an). Cell a_3 with a secondary appendage (Fig. 12, sa), which rarely may be replaced by an antheridium (Fig. 14, an). The septum under the antheridia is neither constricted nor darkened, in contrast to septa below the secondary appendages. Cells $a_{1–2}$ may support a secondary appendage each, although this is very variable, being more common on a_2.

Median series consisting of (7–)9 cells, forming a row lining the margin of the perithecium as far as to leave free only its tip. The cells of this series are rather similar in length and breadth—an outstanding feature for this species. The upper cell of the series bears a secondary appendage with an appendiculate cell. The series (m_1) begins just above a_1 and p_1.

Posterior series consisting of (8–)10(–12) cells. Upper cell of the series bearing the primary appendage, which consists of a dome-shaped basal cell and a distal filamentous cell separated by a brown constricted septa (Fig. 12, pa). The primary appendage is similar to the secondary appendages. Appendages may be present on any of the cells of the series, but are most common on the distal cells, i.e., those above p_3.

Antheridia 12–15 × 3–6 µm, usually a single one for any mature thallus, rarely two (Fig. 14, an) (see above the description for the anterior series), borne on cell a_4, above an appendiculate cell, without a stalk cell, with a conspicuous efferent neck, straight to variably curved, outwardly directed, more or less suffused with brown (Fig. 15).

Secondary appendages 11–30 µm, entirely hyaline, soft, delicate and easily deteriorating, with a constricted brownish septum which separate them from appendiculate cells.

Perithecium 58–80 × 22–28 µm, solitary, ovoid to broadly fusiform, hyaline, except for the tan trichogyne scar present on the outer side, where the slightly differentiated and short neck begins (Fig. 11, trs). Apex blunt, slightly bent towards the ventral side. Stalk and basal cells of the perithecium indistinguishable.

Position on host:—Thalli are mostly located on the posterior margin of the body rings, the so-called limbus, and also on some legs, as well as on the head, including the clypeus and the antennal insertion.

Discussion:—This small, beautiful new species is distinct from all others included in this study, although *R. appendicifera* and *R. candelabriformis* were also found to parasitize millipedes of the family Cambalidae (see under *R. candelabriformis* for notes on the host). The antheridium, sometimes two, located on the ventral margin, bearing a conspicuous brown efferent neck, and the median series of cells, reminiscent of a backbone, are two characters that very easily distinguish this species from others in the genus.

We found a gross resemblance to *R. spathulata* Thaxt., a species described from a mite of the genus *Celanopsis* from the Amazon (Thaxter 1926). The number of cells in each series is similar except for the anterior series where *R. galatheae* has fewer cells. The presence of a single antheridium in front of the perithecium is a character shared by both species but, despite this, the relation of these species seems unlikely based on hosts and geographical distribution. Moreover, from the morphological point of view there are some important differences such as the shape of the secondary appendages, the location and orientation of perithecium, and the shape of the uppermost cell of the posterior series subtending the primary appendage.

Additional collections examined:—NEW ZEALAND. South of the Island, Tasman Dist., Kahurangi N.P., Flora Saddle, 4º11'24.3"S 172º44'28.8"E, 970 m.a.s.l., litter and logs, on *Eumastigonus* sp. (Spirostreptida, Cambalidae), 7 March 2010, *N. Scharff* & *G. Hormiga* leg., BCB-SS·E587 (BCB!). Milford Sound, 44º40'S 167º56'E, on *Eumastigonus* cf. *insulanus* (Spirostreptida, Cambalidae), 16 January 1952, *Galathea II expedition* leg., BCB-SS·E595ab (BCB!).

Rickia gigas Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 16–23, 61–65)
Mycobank MB 815404

Diagnosis:—Receptacle triseriate, a: 3–4, m: 2–3, p: 3–4 (+ 8–14 of lateral branch). Very large species, often exceeding 2000 µm in length. Posterior series extending in a free, lateral branch of 8–14 cells. Antheridia solitary or in pairs scattered on the thallus. Perithecial apex bearing two protuberant lobes and two short lips.

Type:—TANZANIA. Tanga, just outside Amboni Caves, on *Archispirostreptus gigas* (Peters 1855) (Spirostreptida, Spirostreptidae), 7

August 1974, *I. B. & H. Enghoff* leg., C-F-95086, C-F!, **holotype designated here**; BCB-SS·E576ad, f, BCB!, **isotypes designated here**.

Etymology:—*gigas*, a Latin noun in apposition meaning "giant", referring to the large size of the species and its main host.

Thallus hyaline except for the dark brown foot, the trichogyne scar, the septa separating the appendiculate cells from appendages and antheridia, and the antheridial efferent necks. Total length (379–)657–2189 µm. Receptacle triseriate. Basal cell cylindrical, slightly broadened at the distal end, usually very elongated, up to 13 times as long as broad, reaching up to 734 µm of total length, straight to variably curved (Figs 16, 23, I), showing a slight geniculation next to the darkened foot (Fig. 16, arrowhead).

Anterior series consisting of 3–4 superposed, slightly outwardly inflated, and variably shaped cells (Fig. 16).

Median series consisting of 2–3 cells (Fig. 20, m), arising below cells a_2 and p_2, each with a distal appendiculate cell and secondary appendages, which are difficult to distinguish in mature specimens, each consisting of a brown base and a deteriorate apex, mostly similar to the remaining secondary appendages in the thallus.

Posterior series consisting of a basal part with 3–4 cells similar to those of the anterior series, and a free lateral flat branch (110–)245–325 µm long, which consists of a basal large, isodiametric cell, and (7–)10–13 superposed, flattened cells, 2–3 times as broad as long cells (Figs 20, 63). This branch is broadest near its midlength; each cell on both sides with appendiculate cells, which randomly support appendages or antheridia above constricted and brown septa (Fig. 17), except for the outer side of the 2–5 lower cells, which bear neither antheridia nor appendages. Sometimes this free branch appears strongly tinged with brown, may be by deterioration (Fig. 23, arrowhead).

Antheridia 16–19 × 5–7 µm, above a trapezoidal to squarish stalk cell, with outwardly curved, more or less brownish, efferent necks. By pairs (Fig. 64) or isolated, vertically superposed on the outer sides of lower cells of the marginal series, including the free branch of the posterior series (Figs 17, 19).

Secondary appendages 34–63 µm, hyaline except for the diffuse brown base, above the constricted septum, which separates them from the appendiculate cells (Fig. 17, arrow). Short, with parallel margins and rounded distally when young, quickly deteriorating, disorganizing and becoming dirty with maturation and ageing of the thallus. Following the same pattern of distribution on the thallus as the antheridia, except that they are absent from cells of the anterior series.

Perithecia 166–292 × 50–89 µm, up to five on the same thallus (Fig. 23), formed primarily from the anterior series, but also from the posterior and even, but rarely, from the median series (Fig. 16). Ovoid, with maximum breadth near 1/3 of its height (Fig. 65), gradually tapering towards an abruptly distinguished neck and, when seen in front view, a symmetrical tip showing two large outer lobes (Fig. 18), each having small rounded apical papillae (Fig. 21, arrowheads), and two inner rather short lips (Fig. 62). Persistent trichogyne brown scar at upper outer margin of neck (Figs. 21, 62, trs). Perithecial basal cells very flattened and inconspicuous. Perithecial stalk cell (VI) usually very elongate (up to 1087 µm), up to 22 times as long as broad, more or less flexuous, with parallel sides, inflated at the two ends (Fig. 16), especially under the perithecium, sometimes deeply pigmented with brown at the base, when ageing. Ascospores 70–103 µm.

Position on host:—Thalli grow mostly on the legs, but can also be found on the dorsal parts of the first body rings.

Notes on hosts:—*Archispirosteptus gigas* is one of the World's largest millipedes, reaching 260 mm in length and 19 mm in diameter. It is widespread in eastern tropical Africa (Mwabvu *et al.* 2010). '*Spirostreptus' hamatus* is a moderate-sized spirostreptid, up to 10 cm long and 5 mm diameter, it occurs in the Tanzanian Eastern Arc mountains (Enghoff *et al.* in press). The genus name is cited among inverted commas because the name *Spirostreptus* has been re-interpreted (Hoffman *et al.* 2001) to apply to a different group of species, and no other genus name is currently available for *hamatus* and several other species.

Discussion:—The number of appendiculate cells vary from one to three on the cells of lateral series, each bearing one secondary appendage, a solitary antheridium or one group with paired antheridia (Fig. 19). Thalli found on *Spirostreptus hamatus* Demange 1970 (BCB-SS·E578ac) are smaller than those on *Archispirostreptus gigas* that we regard as the typical, representing what may be considered a varietal extreme of the species in relation to measurements and number of cells. The receptacle cells show conspicuous and numerous pores connecting them, which is exceptional and never previously described for any of the Laboulbeniales (Fig. 22). It is interesting also to remember that, with the exception of dimorphic yeasts, all filamentous ascomycetes show a simple pore between cells according to scholarly mycological textbooks (e.g., Webster & Weber 2007: 227). Also it is worth mentioning that our SEM studies show no evidence of a haustorium penetration below the foot attachment after removal of the thallus (Fig. 61). So far it seems

incomprehensible how these fungi can acquire nourishment and grow without a haustorium, essential for a biotrophic fungi, as the Laboulbeniales are known to be. The apparent absence of a penetration into the host constitute a huge challenge in the interpretation of the entire biology of Laboulbeniales and their interaction with the host. Ongoing studies on this matter will clarify this discussion.

Archispirostreptus gigas is commonly kept as a pet and goes under the name of "African Giant Black" (AGB). *Rickia gigas* may infect *A. gigas* kept in terraria which has long been reported as an aesthetic problem at internet forums and wikis of enthusiasts. The identification of the culprit as a laboulbenial fungus was previously made (Hughes pers. comm.).

Rickia gigas is among the world's largest Laboulbeniales with thalli surpassing 2 mm in length. Only two species seem to be significantly larger: the largest is *Laboulbenia kunkelii* (Giard) Thaxt. reaching 4 mm (Giard 1892) followed by *Rhachomyces mattiroloi* Colla (=*R. longissimus* Thaxt.) with 3.5 mm (Thaxter 1931). In the same size class as *R. gigas* we find *Rhizomyces canzonerii* W. Rossi with 2.1 mm (Rossi 1990), *Rhachomyces giachinoi* W. Rossi with 1.9 mm (Rossi 2006), *Trianomyces hollowayanus* W. Rossi & A. Weir with 1.85 mm (Rossi & Weir 1998), *Tettigomyces gracilis* with 1.5 mm (Thaxter 1926), *Stigmatomyces limnophorae* Thaxt. with 1.43 mm (Rossi *et al.* 2013), and *Filariomyces forficulae* Shanor with 1.2 mm (Shanor 1952). The number of species approaching 1 mm of length is relatively big in the genus *Rickia*: *R. apiculifera* Thaxt., *R. biseriata* Thaxt., *R. coelostomatis* Thaxt., *R. passalina* Thaxt., etc. (Thaxter 1926).

Additional collections examined:—TANZANIA. E Usambara Mts. Amani, 1000 m, on '*Spirostreptus*' *hamatus* Demange 1970 (Spirostreptida, Spirostreptidae), 1 August 1979, *M. Stoltze* leg., BCB-SS·E578ac (BCB!), C-F-92242 (C-F!). From pet trade, no further information, on *Archispirostreptus gigas*, C-F-92226 (C-F!). Pwani region, Kisarawe District, Ruvu South Forest Reserve, on *A. gigas* (no date and collector information), C-F-95117 (C-F!). Rubeho Mts, forest 5 km SW Madizini, on '*S.*' *hamatus*, 10–24 September 1993, *M. Andersen* leg., C-F-95118 (C-F!).

Rickia laboulbenioides De Kesel *in* De Kesel *et al*. (Figs 54–55)

Described from *Cylindroiulus latestriatus* (Curtis 1845) (Julida, Julidae) from The Netherlands and Belgium (De Kesel *et al*. 2013), *R. laboulbenioides* is very different from any other known species of the genus parasitizing millipedes. It was compared with *R. uncigeri* in the protologue. The specific epithet seems very appropriate because of the overall resemblance with *Laboulbenia*, particularly concerning the enlarged terminal portion of median and posterior series of cells of the receptacle, and the greatly elongated primary appendage and supporting cell.

According to De Kesel *et al.* (2013), the number of cells per series is a: 2, m: 4(–5), and p: (3–)4. If the new material studied is compared with images in the protologue there are some details of the primary appendage as well as others that deserve to be mentioned. We count six cells in the posterior series. The upper part of this series of cells may appear a little disorganized but we suggest that p_5 forms the base for the large cell which supports the primary appendage. This enlarged cell might correspond to cell p_6, located below the primary septum and the primary appendage which consists of the dome-shaped basal cell separated by a darkened and constricted septum from the terminal portion, a conspicuously and filamentous elongated cell very similar to secondary appendages (Fig. 54). The filamentous terminal portion of the primary appendage was not described in the original description, and secondary appendages of our material are much longer than mentioned by De Kesel *et al.* (2013).

The geographical distribution of this species is extended to Portugal, Spain, Italy and Denmark, in part parasitizing other species of *Cylindroiulus*. See under *R. dendroiuli* for the correction of a record from England reported in a web page of images.

Cylindroiulus is a large genus of Julidae. *Cylindroiulus punctatus* and *C. latestriatus* are widespread in western Europe, whereas *C. perforatus* and *C. dahli* are limited to the Iberian peninsula (plus the Azores Islands for *C. dahli*).

Position on host:—Mostly found in the first pair of legs and scarcely over the posterior legs, in case of high infection it is also distributed in the ventral part of the body rings.

Collections examined:—DENMARK. Western Jutland, Nørholm Skov, on *Cylindroiulus punctatus* (Leach 1815) and *C. latestriatus* (Curtis 1845), 23 June 1988, *H. Ruhberg* leg. ITALY. Veneto, Montello, between Treviso and Belluno, on *C. latzeli*, 2 August 2010, *L. Bonato et al.* leg., C-F-95111 (C-F!). PORTUGAL. Algarve, Monchique, on *C. perforatus* (Verhoeff 1900), 9 June 1987, *P. T. Bailey* leg., BCB-SS2686ae (BCB!). Algarve, Cerro da Cabeça, Moncarapacho, Olhão, on a female of *Cylindroiulus* sp., 14 February 2015, *S. Reboleira* leg., C-F-95095 (C-F!). SPAIN. Pontevedra, Eiras, O Rosal, Finca Río Miño, on *C. dahli* Demange 1970, 25 March 2004, *S. T. Gregory* leg., BCB-SS2687 (BCB!).

Rickia lophophora Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 24–29)
Mycobank MB 815405

Diagnosis:—Receptacle triseriate, a: 3, m: 3, p: 1–3 (+ 5–8 of lateral branch). Posterior series extending in a free, lateral branch of 5–7 cells. Antheridia solitary or in pairs scattered on the thallus. Perithecia elongate subfusiform. Perithecial apex bearing two small lobes and two short lips. Secondary appendages and antheridia with a strongly constricted and dark brown base.

Type:—TANZANIA. West Usambara, Mts. Mazumbaion, on Spirostreptidae indet. (new genus near *Trachystreptus* or *Attemsostreptus*), 1 August 1980, *M. Stoltze & N. Scharff* leg., C-F-92260, C-F!, **holotype designated here**; BCB-SS·E573bc, BCB!, **isotypes designated here**.

Etymology:—*lophophora*, from the Greek "lophos" crest, and "phoros" bearing. Referring to the crest-like lateral branch.

Thallus hyaline except for the dark brown foot, the trichogyne scar, and the lower portion of the secondary appendages and antheridia. Total length 177–254 µm. Receptacle triseriate. Basal cell twice as long as broad.

Anterior series consisting of 3 superposed, variably shaped cells (Fig. 27). Cell a_2 with two secondary appendages on the outer, upper corner. Cell a_3 bearing three appendiculate cells, superposed in a vertical row, each giving rise to secondary appendages or to 1–2 antheridia on the distal one (Fig. 29).

Median series consisting of 3 cells, topped with 1–2 antheridia, secondary appendages, or not rarely with one perithecium (Fig. 29).

Posterior series consisting of a basal part with 1–3 cells, each bearing 1–3 secondary appendages and/or single to paired antheridia. Rarely, cells $p_{2–3}$ may develop a perithecium (Fig. 29, arrow). The series extends in a free lateral flat branch 68–119 µm long, consisting of a basal trapezoidal cell, and 5–8 superposed, flattened cells. There are neither appendages on the basal cell of this branch nor on the ventral side of the lowermost 3 cells. Remaining cells of this branch bear 1–2 appendages or, less commonly, single antheridia. When two appendiculate cells are borne by the same cell, they appear more or less overlapped, especially those on the upper cells of the branch. The uppermost cell is terminated by the short and rounded primary appendage which is flanked by secondary appendages with their respective appendiculate cells.

Antheridia 19–29 × 4–7 µm, single (Fig. 26) or paired (Fig. 25) above the elongated stalk cell which is similar in shape to the lower segment of secondary appendages, above the septum which separates them from the appendiculate cells. Each antheridium with a more or less laterally curved, brownish, short efferent neck.

Secondary appendages 26–33 µm, rounded and broadened distally, deteriorate with ageing, hyaline at the distal end and reddish deep brown at the basal 2/3 of their total length; abruptly narrowing towards the constricted septum which separate them from the appendiculate cells (Fig. 24).

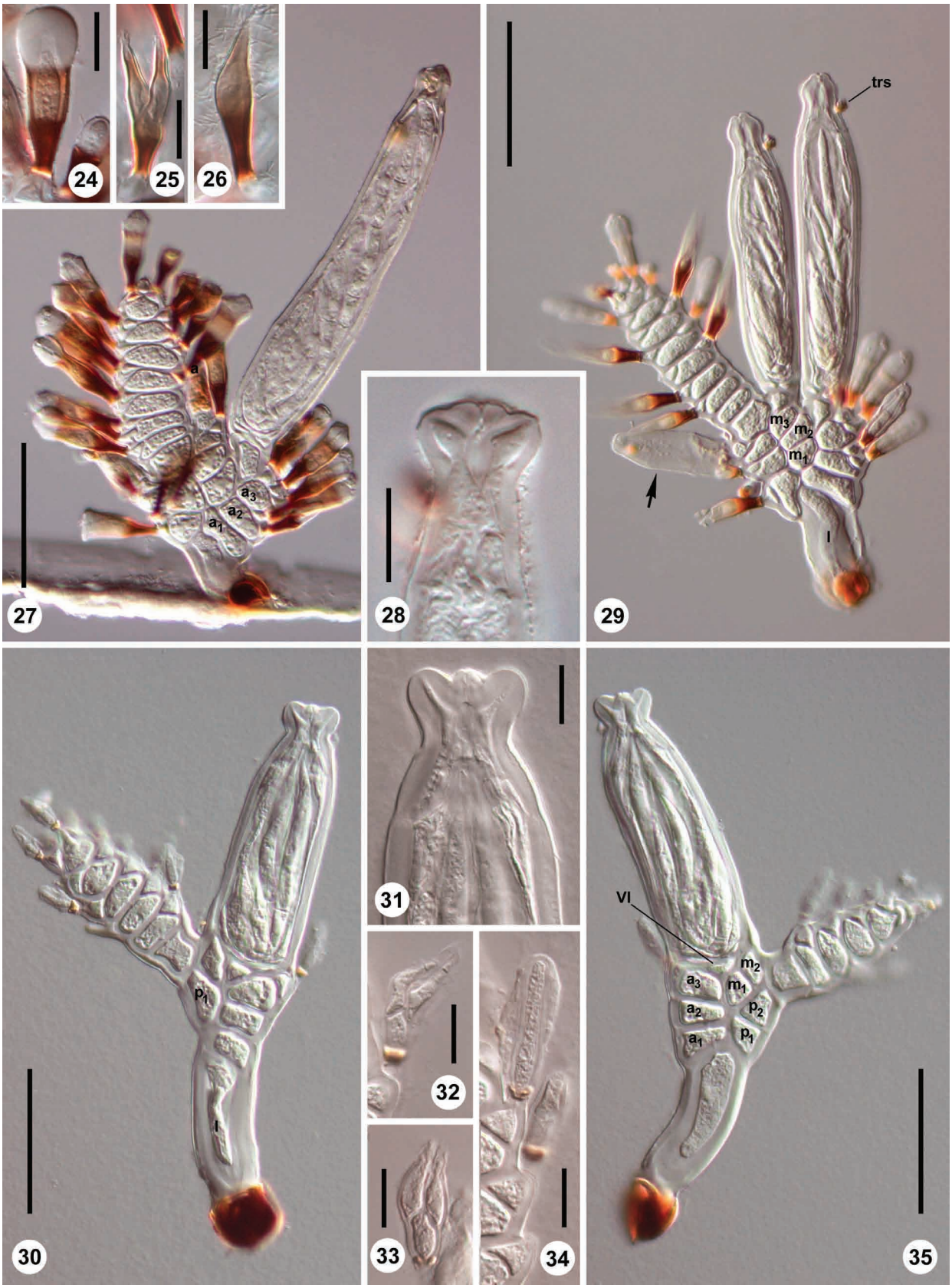
Perithecia 97–150 × 21–32 µm, up to three on the same thallus, formed primarily from the anterior series as usual, but also from the median and even, although rarely, from the posterior series. Perithecium body long and narrow, fusiform to cylindrical, with a slightly inflated venter, gradually tapering or broadening towards the apex and at the level between cells w_2 and w_3, then abruptly differentiated in a neck right under the asymmetrical tip which bears 4 protuberances, i.e. two outer lobes and two inconspicuous inner lips (Fig. 28). A persistent trichogyne brown scar is found at upper outer margin of the neck (Fig. 29, trs). Perithecial basal cells very flattened and inconspicuous. Perithecial stalk cell (VI) very small, variable.

Position on host:—Thalli are found on the body rings, along the trunk, mainly seated at the limbus, with some also in the suture of the prozone and metazone. This species forms conspicuous infections on its hosts with thalli growing typically on the posterior edges of the body rings.

Notes on hosts:—Spirostreptidae is a large family of mainly tropical millipedes. *Obelostreptus proximospinosus* has been recorded from several mountain blocks in the Eastern Arc system (Enghoff *et al.* in press).

Discussion:—The examined material is quite uniform; only the thalli found on *Obelostreptus* (cf.) *proximospinosus* Krabbe 1982 (BCB-SSE574ac) are distinctly larger, with lateral branches of the posterior series with up to 12 cells, whereas typical thalli have 5–8 cells.

Rickia lophophora belongs to the same group of species as *R. gigas*, *R. obelostrepti* and *R. odontopygiidarum*, sharing with these the free lateral branch of the posterior series of the receptacle and the morphology of the perithecial apex. It differs from *R. gigas* and *R. odontopygiidarum* for the fusiform perithecia, inconspicuous protuberances on the perithecial tip, secondary appendages with a strongly constricted and dark brown base, and stockier antheridia with less differentiated efferent necks. It can be easily distinguished from *R. obelostrepti* by the pale and simple lateral branch of the posterior series of the latter.



FIGURES 24–29. *Rickia lophophora*. Fig. 24. Detail of a secondary appendage. Fig. 25. Detail of a set of paired antheridia. Fig. 26. Detail of a solitary antheridium. Figs 27, 29. Mature thalli. In Fig. 29, a young, probably aborted perithecium is indicated with an arrow. Fig. 28. Perithecial apex. (Figs 24–28, SS·E572a; Fig. 29, C-F-92260.). **FIGURES 30–35.** *Rickia obelostrepti*. Figs 30, 35. Mature thalli. Fig. 31. Perithecial apex. Figs 32–33. Detail of paired antheridia. Fig. 34. Detail of secondary appendages. (All Figs from slide SS·E579b.) (For interpretation of abbreviations see under materials and methods.) Scale bars for Figs 24–26, 28, 31–34 = 10 µm; for Figs 27, 29, 30, 35 = 50 µm.

Additional collections examined:—TANZANIA. Iringa region/district, New Dabaga/Ulangambi F.R., 1908 m, 08°00’26.6’’S 35°56’06.1’’E, on Spirostreptida indet., 19–26 October 2000, BCB-SS·E572ac (BCB!). Uluguru Mts., Lupanga West, 1900 m, on *Obelostreptus* (cf.) *proximospinosus* Krabbe, 1982 (Spirostreptida, Spirostreptidae), 1 July 1981, BCB-SS·E574ac (BCB!). Uluguru Mts., Lupanga East, 1600 m, on *Eiphorus* sp. (Spirostreptida, Spirostreptidae), 10 July 1981, BCB-SS·E599 (BCB!), C-F-9509 and C-F-95110 (C-F!).

Rickia obelostrepti Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 30–35)
Mycobank MB 815406

Diagnosis:—Receptacle triseriate, a: 3, m: 1(–3), p: 1–2 (+ 5 of lateral branch). Posterior series extending in a free, lateral branch of 5 cells. Antheridia always paired and only on immature thalli. Perithecial apex with two protuberant lobes and two short lips. Dark brown color only in foot and septa separating the appendiculate cells from appendages and antheridia.

Type:—TANZANIA. Uluguru Mts, Lupanga East, on *Obelostreptus* cf. *proximospinosus* Krabbe, 1983 (Spirostreptida, Spirostreptidae), 19 July 1981, *M. Stoltze & N. Scharff* leg., C-F-95087, C-F!, **holotype designated here**; BCB-SS·E579bc, BCB!, **isotypes designated here**.

Etymology:—*obelostrepti*, referring to the host.

Thallus hyaline except for the dark brown foot and the septa separating the appendiculate cells from appendages and antheridia. Total length 172–204 µm. Receptacle triseriate. Basal cell 2–3 times as long as broad. The basal cell borders distally on the two lower cells of the marginal series or only to the lower cell of the anterior series.

Anterior series consisting of 3 superposed cells (Fig. 35). Cell a_3 developing the perithecium, bearing a big appendiculate cell and a secondary appendage; in immature thalli this cell gives rise to a set of paired antheridia together with the appendiculate cell. Exceptionally cell a_2 supports a group of paired antheridia, and the cell a_1, one appendage.

Median series consisting of 1(–3) cells, not bearing any appendage, antheridia or perithecial initial.

Posterior series consisting of a basal part with 1–2 cells, extending in a free lateral flat branch 73–101 µm long, which consists of an isodiametric basal cell, narrower than the 5 cells above, which are more or less strongly flattened (Figs 30, 35). Each cell of the free branch bearing one appendage on each side. Rarely, the second cell of this branch with one appendage only on the ventral side. The distal cell of the branch with 3 appendiculate cells supporting secondary appendages, probably the one in the center is the primary appendage.

Antheridia 12–15 × 3–4 µm, only seen in immature thalli, arising from cell a_3 and from the cells 3–4 of the free branch of the posterior series, always paired above a trapezoidal stalk cell, entirely hyaline except for the darkened basal septum which separates the set of two antheridia and its stalk cell from the appendiculate cell (Figs 32–33).

Secondary appendages 12–40 µm, soft, delicate, easily deteriorating when ageing, with an obtuse apex, hyaline, except for the darkened basal septum above the appendiculate cell (Fig. 34).

Perithecium 89–101 × 32–36 µm, solitary, formed from the apex of the anterior series. Body subcylindrical, with subparallel sides, abruptly differentiated into a neck at cells w_2 and w_3 level (Fig. 31). Apex symmetric in front view, with two outer lobes contiguous with the two lips which form the tip (Fig. 31). Perithecial stalk cell (VI) triangular in section, minute, located in the corner of cell a_3, above cell m_1, and side by side with cell m_1 or m_2 (Fig. 35, VI).

Position on host:—Thalli are found on the ventral part of the body, directly on legs or among them.

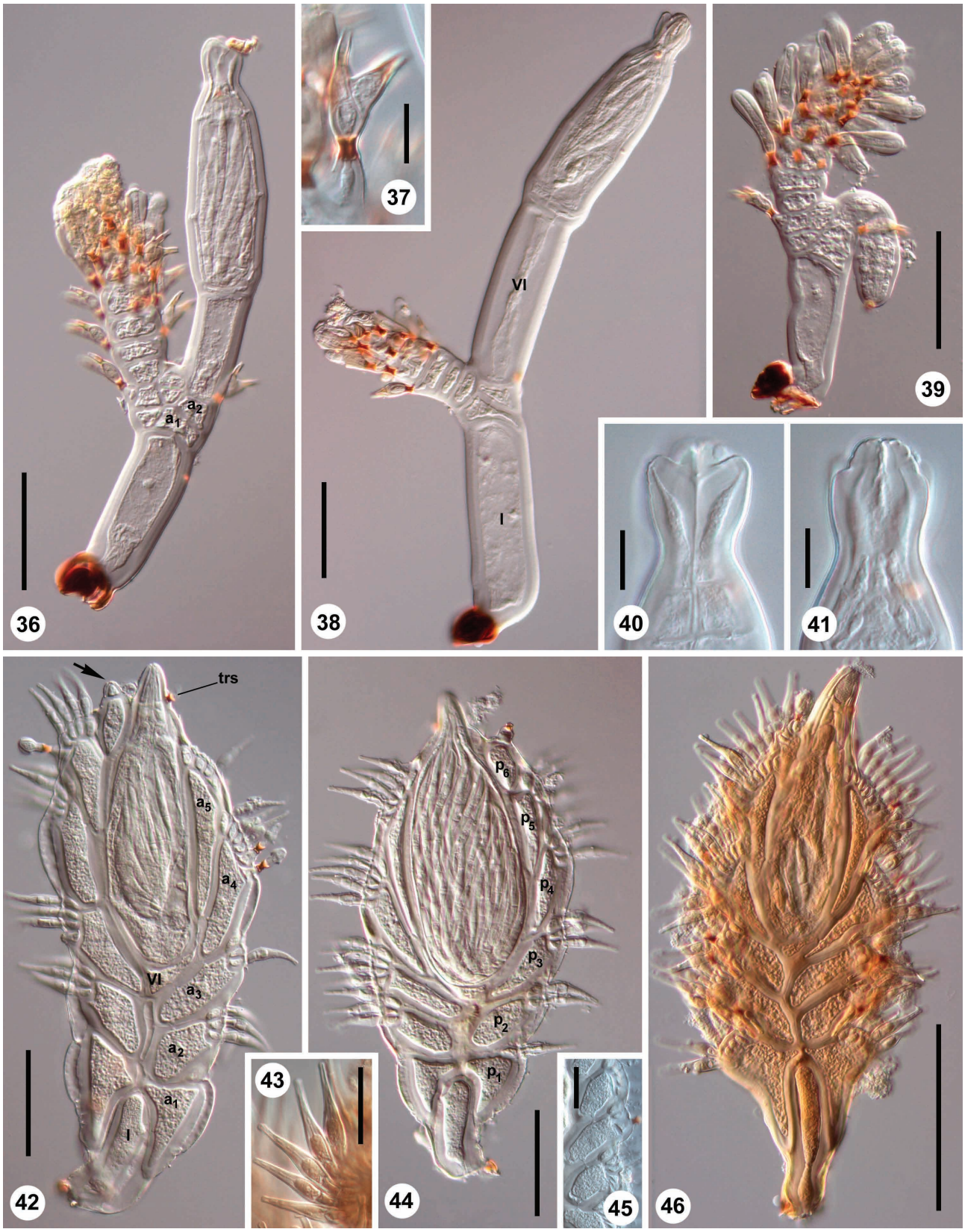
Discussion:—This species may be considered the most reduced in the group including *R. gigas*, *R. lophophora* and *R. odontopygiidarum*. Besides the small size, its pale color and the lateral branch composed of a squarish basal cell, plus no more than 5 cells, separates this species from the other three. This species and *R. lophophora* parasitize the same host and have been found in the same locality, *R. obelostrepti* lives on and between legs whereas *R. lophophora* grows only on the posterior edges of body rings. Neither species coexist on the same individual host and have been found only on the parts of body indicated.

For notes on the host see under *R. lophophora*.

Rickia odontopygiidarum Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 36–41)
Mycobank MB 815407

Diagnosis:—Receptacle triseriate, a: (1–)2, m: (1–)3, p: 1–2 (+ 5–7 of lateral branch). Posterior series extending in a free, lateral branch of (5–)6(–7) cells. Similar to *R. gigas* but smaller and with fewer cells on the receptacle.

Type:—TANZANIA. Tanga Region, Muheza District nilo F.R., 04°55’46’’S 38°39’06’’E, on Odontopoygidae indet. (Spirostreptida), 26 July 2000, C-F-92261, C-F!, **holotype designated here**; BCB-SS·E577bc, BCB!, **isotypes designated here**.



FIGURES 36–41. *Rickia odontopygiidarum*. Figs 36, 38. Mature thalli. Fig. 37. Detail of a set of paired antheridia. Fig. 39. Immature thallus. Figs 40–41. Perithecial apex at two different focusing levels, at right the corrugation of the inner lips is shown. (Figs 36–38, 40–41, C-F-92261; Fig. 39, SS·E577c.). **FIGURES 42–46.** *Rickia platessa*. Figs 42, 44, 46. Mature thalli. The arrow in Fig. 42 points to the dome-shaped basal cell of the primary appendage. Fig. 43. Detail of antheridia. Fig. 45. Detail of appendiculate cells on three receptacular cells. (Fig. 42, SS·E580a; Fig. 43, SS·E590c; Figs 44–45, C-F-92262; Fig. 46, SS·E590b.) (For interpretation of abbreviations see under materials and methods.) Scale bars Figs 36, 38–39, 42, 44, 46 = 50 µm; for Figs 37, 40–41 = 10 µm; for Figs 43, 45 = 20 µm.

Etymology:—*odontopygiidarum*, referring to the host.

Thallus hyaline except for the dark brown foot, the trichogyne scar, the septa separating the appendiculate cells from appendages and antheridia, and the antheridial efferent necks. Total length 248–553 µm. Receptacle triseriate. Basal cell cylindrical, straight, with parallel sides in fully mature thalli (Fig. 38, I) or slightly broadened distally when immature (Fig. 39), variably elongated, up to 5 times as long as broad, reaching up to 210 µm of total length in longer thalli; bordering distally on the two lower cells of the marginal series, or less usually only on the lower cell of the posterior series.

Anterior series consisting of (1–)2 superposed, variably shaped cells (Figs 36, 38).

Median series located above cells a_2 and p_2; consisting of (1–)3 cells, or even absent (Fig. 38).

Posterior series consisting of a basal part with 1–2 cells similar to those of the anterior series, extending in a free lateral branch 87–144 µm long, which consists of (5–)6(–7) superposed, variably flattened (2–3 times as broad as long) cells. This branch is broadened distally, each cell with appendiculate cells which randomly support appendages or antheridia above constricted and dark brown septa (Figs 36, 38).

Antheridia 12–18 × 4–8 µm, above a trapezoidal to squarish stalk cell, with curved, more or less brownish, efferent necks. Paired (Fig. 37) or rarely single, numerous and overlapping on the outer sides of cells of series a and p; but also on the front and rear sides of the lateral branch, where appendiculate cells are horizontally seriate, being crowded towards the distal part of the free branch (Fig. 39).

Secondary appendages 23–48 µm, short, broadened and rounded distally, when deteriorating getting disorganized and their contents may extrude through the broken apex; hyaline except for the brown base and the constricted septum above the appendiculate cells. Following the same pattern of distribution on the thallus as the antheridia, they are abundant on the free branch of the posterior series, rare on the second cell of this series (Fig. 39).

Perithecium 109–193 × 36–62 µm, solitary, formed from the anterior series as usual. Ovoid, its maximum breadth near the third basal part, gradually tapering towards an abruptly distinguished neck and, when seen in front view, a symmetrical tip with two outer lobes and two inner rather conspicuous lips (Fig. 40), often showing corrugated edges (Fig. 41). Perithecial basal cells highly flattened and inconspicuous. Perithecial stalk cell (VI) 47–156 µm long, 2–3, or more times as long as broad, straight, with parallel sides (Fig. 38, VI).

Position on host:—Thalli have been found on the anterior part of the host body, on legs and ventral side of body rings.

Notes on hosts:—The family Odontopygidae is endemic in the Afrotropical region and contains numerous still undescribed genera and species.

Discussion:—This species is evidently related to *R. gigas*, but differs in its smaller size, the reduced number of cells in all the series, the arrangement of antheridia and appendages (overlapped and not superposed vertically as in *R. gigas*), the more cylindrical and unflattened lateral branch of posterior series, the cells of receptacle showing only one pore, not several as in *R. gigas*, the perithecial apical lobes that lack the small papillae which are present in *R. gigas,* and other minor characteristics.

Rickia pachyiuli M. Bechet & I. Bechet (Figs 56–57)

This species was described on *Pachyiulus hungaricus* (Karsch 1881) (Julida, Julidae) from Romania (M.Bechet & I.Bechet 1986). It was compared by the authors with *R. uncigeri*, from which it is separated, according to them, by the greater number of receptacular cells in each series. We confirm that this is the most evident difference: *R. pachyiuli* has 8–9 cells in the anterior series, 11–12 in the median, and 14–15 in the posterior one, whereas *R. uncigeri* has 3 cells in the anterior series, 5–6 cells in the median, and 5–6 in the posterior one.

As a curiosity it is worth mentioning that some of the material we had the opportunity to study was collected about 100 years ago and conserved in 70% ethanol in Vienna (Naturhistorisches Museum Wien, NMW), and have remained up to the present day with no decay in their characteristics and appearance. These are the oldest host specimens from which the first author has had the opportunity to prepare and study useful slides, after more than 30 years of studying laboulbeniales.

Pachyiulus hungaricus is a large julid and is widespread in SE Europe.

Position on host:—The fungus is mostly in the first pairs of legs of the hosts, in highly infected specimens some thalli spread through the dorsal part of the first body rings.

Collections examined:—BOSNIA-HERZEGOVINA. Drinrsprung am Zleb, on *Pachyiulus hungaricus*, August 1916, *Penther* leg., BCB-SS·E582ac (BCB!), host in NMW (see above). SERBIA. Belgrade, Alava mountains, living specimens, *D. Antic* leg.

Rickia platessa Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 42–46)
Mycobank MB 815408

Diagnosis:—Receptacle biseriate, a: 5, p: 6. Perithecium nearly completely embedded between the two series of cells. Antheridia very abundant, forming series of vertical rows on both sides of the thallus. Brown septa only under secondary appendages and not below the antheridia.

Type:—SINGAPORE. Seletar reservoir, Forest, 1°24'N 103°48'E, on *Trigoniulus corallinus* (Gervais 1841) (Spirobollidae, Pachybolidae), 7 November 1991, C-F-92262, C-F!, **holotype designated here**; BCB-SS·E580a, c, BCB!, **isotypes designated here**.

Etymology:—*platessa*, refers to the superficial similarity of this species to a flatfish, especially the plaice, *Pleuronectes platessa*.

Thallus hyaline to reddish brown; if hyaline, then with the exception of the brown foot, the tan trichogyne scar and the brown septa separating the appendiculate cells from appendages; if reddish brown, then uniform without darker colour of parts as mentioned for other thalli. Total length 131–257 µm. Receptacle biseriate. Basal cell about 2.5–3 times as long as broad, clavate, with a narrow, even acute base above a diminutive, point-sized foot. The basal cell borders distally on the lower cells of the two series, flanked by these cells and immersed between them for 2/3 of its total length.

Anterior series consisting of 5 cells (Fig. 42). Cell a_1 triangular in section, opposite and nearly identical to p_1, rarely with one appendage and one antheridium. Cells $a_{2–5}$ on their upper corners with 3–8 lateral antheridia each, and sometimes also 1–2 secondary appendages below. Cell a_3 giving rise to the perithecium.

Posterior series consisting of 6 cells (Fig. 44). Cell p_1 almost identical to the opposite symmetrical a_1, rarely with one antheridium or one secondary appendage on its upper corner. Cells $p_{2–5}$ on their upper corners with 3–8 lateral antheridia each, and sometimes also 1–2 secondary appendages. Cell p_6 supporting the primary appendage including its dome-shaped and very small basal cell (Fig. 42, arrow), separated by a constricted and slightly darkened septum from the inconspicuous distal elongated cell, which is nearly identical to secondary appendages; rarely, cell p_6, also supports one secondary appendage. Primary septum constricted and brown-colored.

Antheridia 18–22 × 4–7 µm, hyaline (Figs 42–44) to reddish brown (Fig. 46), above squarish stalk cells, partially immersed in the thallus, with curved to straight, long efferent necks where rows of spermatia are clearly seen in the discharge channel. Septum separating the stalk cell from the appendiculate cell hyaline and not constricted.

Secondary appendages 14–17 µm, hyaline, short, clavate, above the constricted and brown septa which separate them from the embedded appendiculate cells.

All the appendiculate cells are superposed in vertical-diagonal series and are embedded in the thallus (Figs 43, 45).

Perithecium 77–138 × 30–52 µm, solitary, broadly fusiform, more curved on the dorsal margin, asymmetric, with an acute apex. Surrounded along both margins by the anterior and posterior series of cells, with only the tip free on the posterior margin, and the 1/5 of its length on the anterior margin. A persistent brown trichogyne scar is seen at the upper anterior margin of the neck (Fig. 42, trs). Perithecial basal cells indistinguishable. Perithecial stalk cell (VI) very flattened, triangular in section, located in the upper inner corner of cell a_3 (Fig. 42, VI).

Position on host:—In some specimens of *T. corallinus* from the same sample as the type host, there is an almost complete, regular complement of thallus feet on virtually all body rings of the millipede, but apart from the feet, the thalli are lost. This gives the millipede such a distinctive appearance that it was first assumed by HE to represent a new species.

Notes on hosts:—*Trigoniulus corallinus* is a tropical 'tramp' species that has been recorded from numerous places in the tropics, especially from islands where it has obviously been introduced by man (Shelley & Lehtinen 1999). The unidentified Thai pachybolid is one of many undescribed species currently under study by Piyatida Pimvichai.

Discussion:—This species belongs to the group of species of *Rickia* with biseriate thalli. Although the number of cells per series seems rather constant, the quantity of antheridia, and to a lesser degree of the appendages, is heavily increased in some unusual, maybe teratological thalli.

At the first glance, the two collections included here were considered different species, especially because of the conspicuous differences in the colour of the thalli, hyaline vs. reddish-brown. But in spite of this difference, the morphology is almost identical in the two collections with only minor differences relating to the number of appendages and antheridia above the cells of the receptacle series. Both collections came from the same host family and from neighboring regions which support the idea of co-specificity.

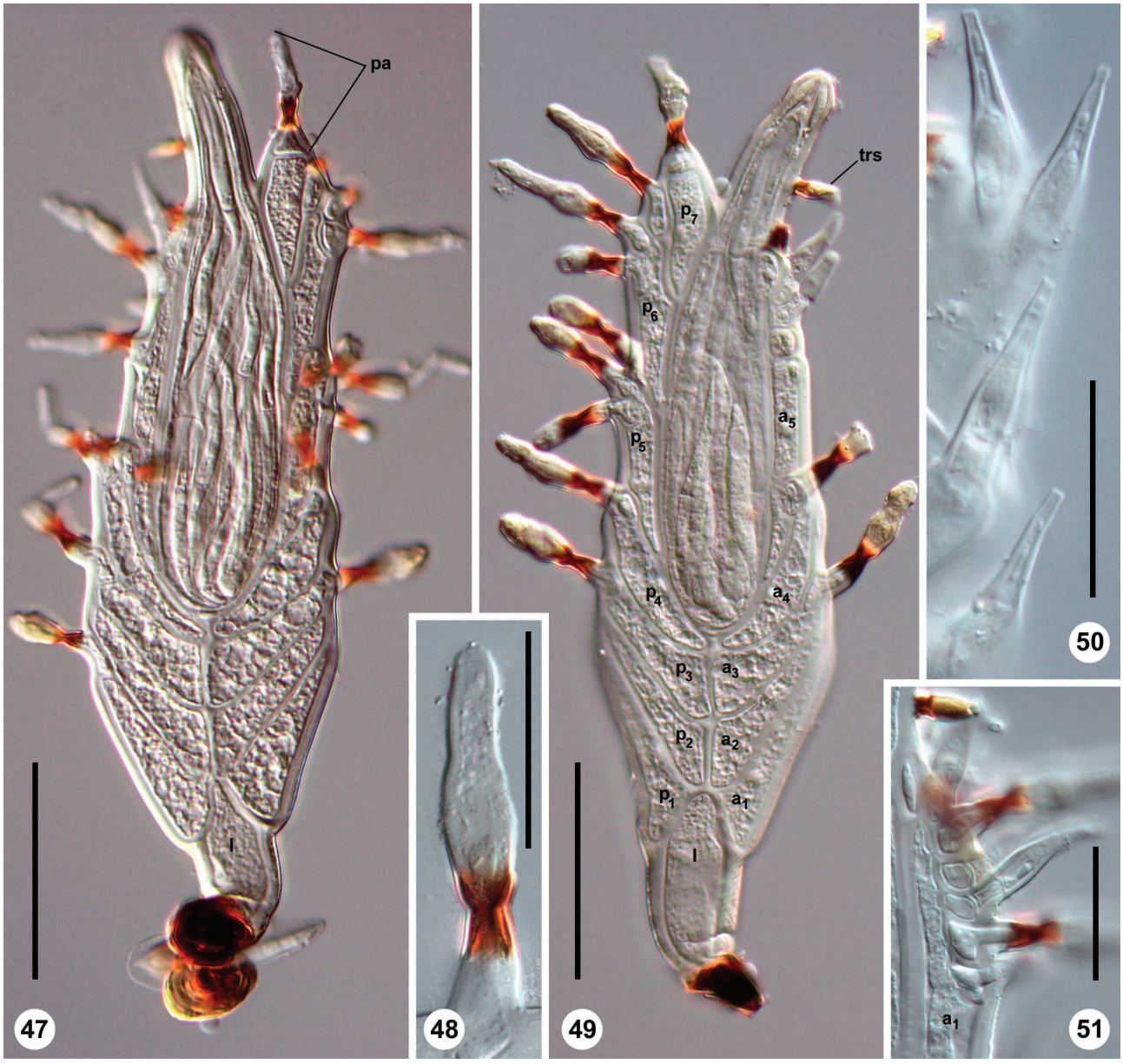
Additional collections examined:—THAILAND. Tham Suae Temple, Krabi, on Pachybolidae indet.

(Spirobolida), 14 January 2013, *Piyatida Pimvichai* leg., BCB-SS·E590ac (BCB!), C-F-95100 (C-F!). Hosts at Chulalongkorn University Museum of Zoology coll.

Rickia rhynchophora Santam., Enghoff, & Reboleira, *sp. nov.* (Figs 47–51)
Mycobank MB 815409

Diagnosis:—Receptacle biseriate; a: 5, p: 7. Cells a_{1-4} and p_{1-4} arranged in a symmetrical, pinnate way along the main, vertical axis of the thallus. Perithecium narrowly ovoid, almost immersed in the receptacle, extending into a snoutlike, bent neck.

Type:—AUSTRALIA. SE Queensland, Lamington NP near O'Reilly's Guesthouse, rain forest, on *Trigoniulus* sp. (Spirobolida, Trigoniulidae), 13–17 April 2002, *N.Scharff* & *S.Larsen* leg., C-F-92263, C-F!, **holotype designated here**; BCB-SS·E588a, c, BCB!, **isotypes designated here**.



FIGURES 47–51. *Rickia rhynchophora*. Figs 47, 49. Mature thalli. Fig. 48. Detail of a secondary appendage. Fig. 50. Detail of antheridia. Fig. 51. Secondary appendages and antheridia with their appendiculate cells arranged laterally to cell a_5. (Figs 47–48, 50–51, SS·E588a; Fig. 49, C-F-92263.) (For interpretation of abbreviations see under materials and methods.) Scale bars Figs 47, 49 = 50 µm; for Figs 48, 50–51 = 20 µm.

Etymology:—*rhynchophora*, meaning "bearing a nose", referring to the snout-like apex of the perithecium extending above the thallus.

Thallus hyaline to pale yellowish except for the dark brown foot, the trichogyne scar, and the septa separating the

appendiculate cells from appendages. Total length 171–237 μm. Receptacle biseriate. Basal cell about two times as long as broad, kite-like in shape, forming a symmetrical base for cells a_1 and p_1 from which it is separated by strongly diagonal septa (Fig. 47, I).

Anterior series consisting of five cells (Fig. 49). Cells $a_{1–4}$, together with cells $p_{1–4}$ of the opposite marginal series arranged symmetrically, diagonally in relation to main thallial vertical axis, with the outer edges pointing upwards, in a pinnate way, side by side, and separated by vertical, straight septa which follow the central axis of the thallus. The pattern of distribution of the appendages is: a_1 always with one appendage, a_2 without appendages; a_3 and a_4 variable, may or may not bear an appendage; a_5 very narrow and elongated bearing from top to bottom one appendage, one or two antheridia, and two or three appendages (Fig. 51). Cell a_4 bears the perithecium and supports an inconspicuous, flattened and wedge-shaped perithecial stalk-cell (cell VI) on its upper-inner corner.

Posterior series consisting of 7 cells (Fig. 49). Cells $p_{5–7}$ very narrow and difficult to distinguish and count because they appear closely connected to the dorsal perithecial wall. Cells $p_{1–2}$ without appendages, cells $p_{3–4}$ each with one appendage (often cell p_3 lacks this appendage), cell p_5 with 2–3 appendages, and cell p_6 with 3–4 appendages. Upper cell of the series (p_7) comparatively big, supporting the primary appendage with its dome-shaped, small, basal cell, a constricted and dark brown septum, and the distal elongated, filamentous cell (Fig. 47, pa), which is nearly identical to the secondary appendages.

Antheridia 16–18 × 5–6 μm, typically 1–2 on a_5 in fully mature thalli. In immature thalli they may be fairly abundant, up to seven associated with the different cells of the a and p series (more often a_4 and p_4, besides a_5). Antheridia hyaline, consisting of a minute trapezoidal appendiculate cell, a cylindrical stalk-cell, and the terminal flask-shaped phialide which bears a conspicuous, straight to curved efferent neck (Figs 50–51).

Secondary appendages 14–34 μm, flask-shaped, with a rather inflated venter and a neck terminating in an obtuse apex, separated from their respective appendiculate cells by dark brown and constricted septa (Fig. 48). Appendiculate cells immersed in the receptacle, vertically superposed.

Perithecium 89–147 × 20–31 μm, solitary, narrowly ovoid, with a narrow neck which extends into a snout-like, slightly laterally bent tip and a rounded apex; entirely pale, except for the tan trichogyne remnant (not only the usual scar) found on the anterior side (Fig. 49, trs); almost immersed and surrounded by the two receptacular series of cells.

Position on host:—Scantily distributed along the dorsal part of the body rings and in the 5th leg.

Notes on hosts:—*Trigoniulus* is a large genus, and many species remain undescribed.

Discussion:—This species resembles *R. candelabriformis* in the biseriate condition of the thallus and the morphology of the lower receptacle, especially the ensemble of cells I, a_1 and p_1, but may be easily distinguished by several characters, especially by the shape of the perithecium and the snout-like tip in *R. rhynchophora*.

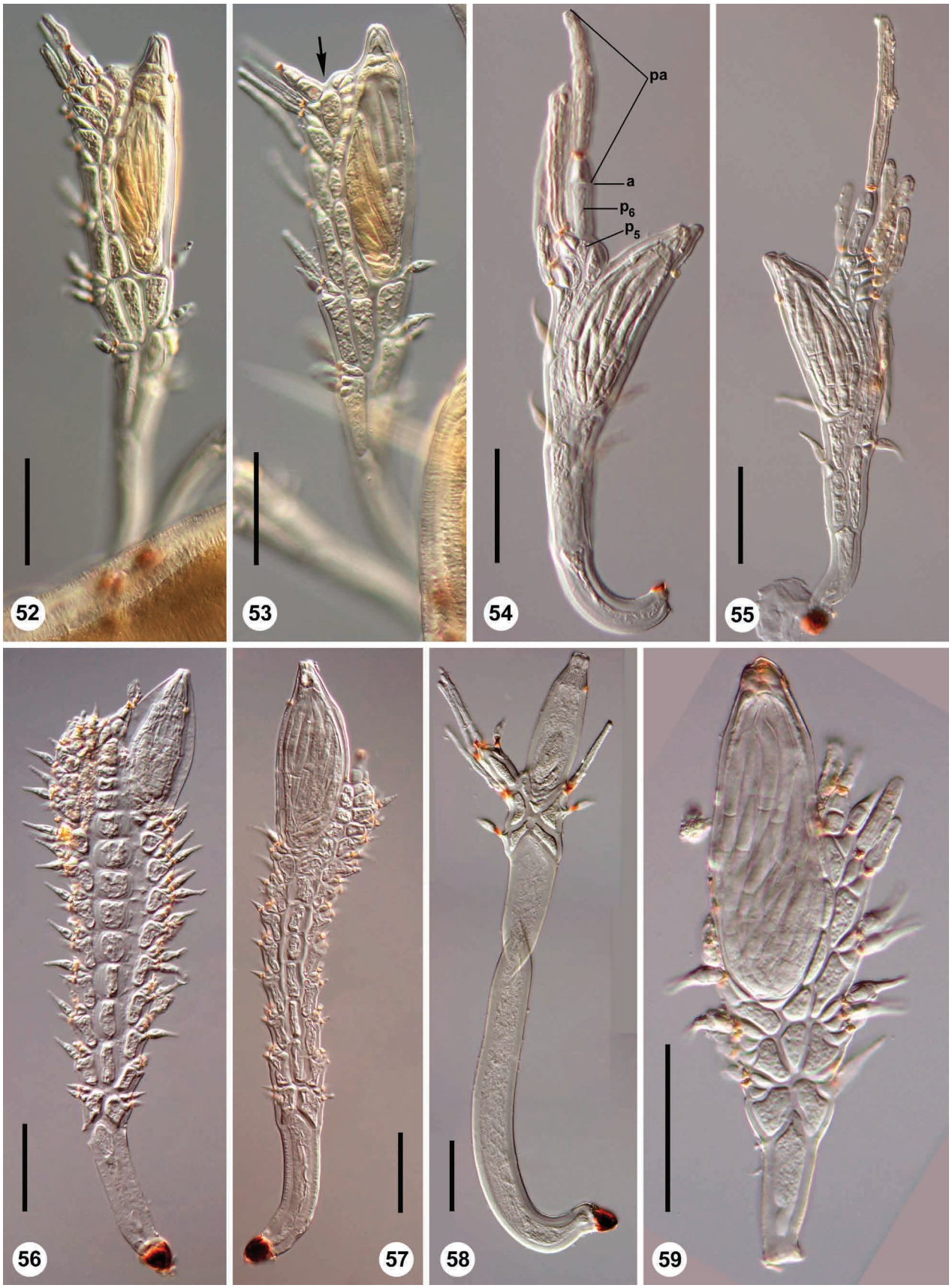
Rickia siddhartha Balazuc *in* W.Rossi & Balazuc (Figs 58, 66)

The type material was described from Sri Lanka on *Ktenostreptus lankaensis* (Humbert 1865) (Spirostreptida, Harpagophoridae) (Rossi & Balazuc 1977). This species is striking and very different from any other by the very elongated cell I, the reduced number of receptacle cells (2a, 1m, 3p), and by the free and elongated cell p_3 which forms a lateral appendage-like prolongation. The material we had the opportunity to study is from the *locus classicus* and has exactly the same collecting data as the material used to describe the species. In the SEM image (Fig. 66) we can see the smooth appearance of the base of appendages (arrows), a characteristic also observed on SEM preparations of other species (Fig. 60, arrow). This may indicate that the more rigid and broad condition of wall cells in these areas of thalli (darkened basal septa in appendages) are more resistant to the critical point drying during preparation of SEM samples.

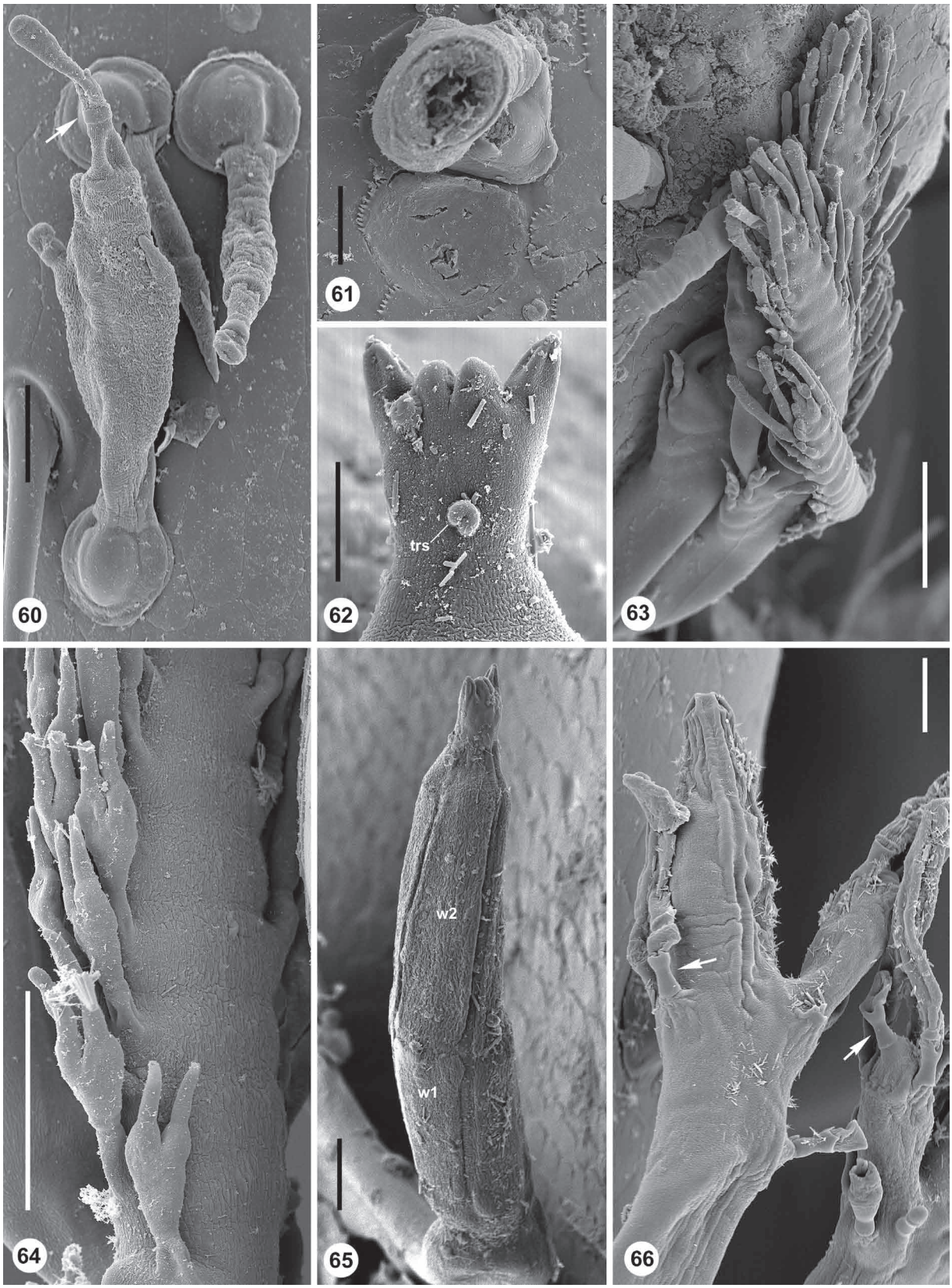
Ktenostreptus lankaensis is a large species, endemic in Sri Lanka.

Position on host:—Thalli were found all over the host, especially in the ventral part of the body.

Collections examined:—SRI LANKA. Sabaragamuwa, Prov. Deerwood Kuruwita, 6 mls NNW Ratnapura, Loc. 90 III, on *Ktenostreptus lankaensis*, 18–21 February 1962, Lund University Ceylon Expedition 1962, *Brick-Andersson-Cederhom* leg., isotype slide borrowed from W.Rossi collection. *Ibidem*, BCB-SS·E601ac (BCB!) and C-F-95090 (C-F!) (host in the Lund University Zoology Museum).



FIGURES 52–59. Species of *Rickia* not described in this paper. Figs 52–53. Mature thalli of *Rickia dendroiuli*. Arrow in Fig. 53 points to the uppermost cell of posterior series, where a diagnostic character is shown (see text). Figs 54–55. Mature thalli of *Rickia laboulbenioides*. Figs 56–57. Mature thalli of *Rickia pachyiuli*. Fig. 58. Mature thallus of *Rickia siddhartha*. Fig. 59. Mature thallus of *Rickia uncigeri*. (Figs 52–53, WR586; Fig. 54, SS2686d; Fig. 55, SS2686e; Fig. 56, SS·E582b; Fig. 57, SS·E582c; Fig. 58, SS·E601b; Fig. 59, SS·E596c.) (For interpretation of abbreviations see under materials and methods.) Scale bars = 50 µm.



FIGURES 60–66. SEM images. Fig. 60. *Rickia candelabriformis*, one immature thallus and two sporelings; the arrow points to the septum between the two cells of the primary appendage. Figs 61–65. *Rickia gigas*; in Fig. 61 a broken foot of a thallus above the scar left by another thallus purposely removed; in Fig. 62 detail of a perithecial apex; in Fig. 63 several thalli showing the flattened appearance of the lateral branches; in Fig. 64 a row of paired antheridia; in Fig. 65 a perithecium showing the two lower tiers of wall cells. Fig. 66. *Rickia siddhartha*, thalli where arrows point to septa between appendiculate cells and the upper cell of secondary appendages. (For interpretation of abbreviations see under materials and methods.) Scale bars Figs 60–62, 66. = 10 µm; for Fig. 63 = 50 µm; for Fig. 64 = 25 µm; for Fig. 65 = 20 µm.

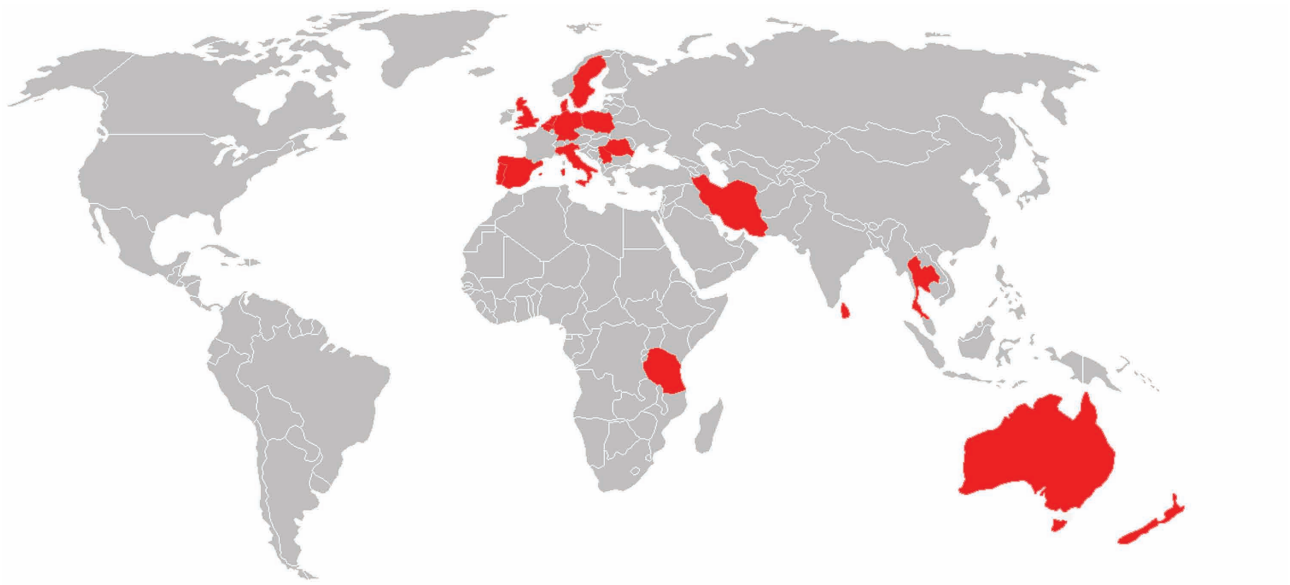
Rickia uncigeri Scheloske (Fig. 59)

Described on *Unciger foetidus* (Koch 1838) from Germany (Scheloske 1969) and reported later from Poland (Majewski 1974), this species should be compared with the other species parasitizing Julidae, i.e., *R. dendroiuli, R. laboulbenioides* and *R. pachyiuli*, as mentioned above. *Rickia uncigeri* has triseriate thalli, without very striking characters, except may be those concerning the median series which consists of cells strongly narrowed towards the apex, following the dorsal wall of perithecium until near its apex.

Unciger foetidus is widespread in Central and Eastern Europe.

Position on host:—May occur all over the body but preferentially on the ventral side of head, as well as the anterior body rings and legs (Scheloske 1969, Majewski 1974, Enghoff & Santamaria 2015).

Collections examined:—DENMARK. Dania, SZ PG64, Sorø Kristiansminde, 55º25'09"N 11º35'11"E, on *Unciger foetidus*, 24 July 2013, *Malene Månsson* leg., BCB-SS·E596ac (BCB!).



FIGURES 67. World distribution of species of *Rickia* on millipedes.

Identification key for species of *Rickia* parasitizing millipedes

1. Species with biseriate thallus.....2
- Species with triseriate thallus.....4
2. Antheridia very numerous in mature thalli, found in vertical series at both sides of the thallus. On Asian Pachyboliidae..... .....*R. platessa*
- Antheridia few in number, 1–2 in mature thalli.....3
3. Antheridium solitary on p_1, with a long, strongly inwardly incurved efferent neck. Anterior series consisting of three cells. On Iulomorphidae and Cambalidae from Australia and New Zealand.....*R. candelabriformis*
- Antheridia otherwise. Anterior series consisting of five cells. On *Trigoniulus* (Trigoniulidae).....*R. rhynchophora*
4. Posterior series of cells extending in a free stalked lateral branch separating and diverging from receptacle and consisting of several superposed cells with appendages and antheridia. Perithecial apex ornate with 2 lobes and 2 lips.....5
- Posterior series without free multicellular branch (at most the uppermost cell of the series diverging from thallus, forming something like an appendage structure). Perithecial apex not ornate.....8
5. Anterior series consisting of (1–)2 cells. Antheridia and appendages crowded at the distal part of free lateral branch, with appendiculate cells arranged horizontally in the four directions from free lateral branch. On African Odontopygidae..... .....*R. odontopygiidarum*
- Anterior series consisting of 3–4 cells. Antheridia and appendages not as above, arranged bilaterally on the free lateral branch, i.e. in two directions. On African Spirostreptidae.....6
6. Thallus gigantic, typically surpassing 1 mm of total length, often 2 mm. Free lateral branch of posterior series consisting of more than 8 cells. On African *Archispirostreptus* and *'Spirostreptus'*.....*R. gigas*
- Thallus smaller, typically less than 250 µm of total length. Free lateral branch of posterior series consisting of 5–8 cells. On other hosts.....7
7. Secondary appendages rounded and broadened distally, darkened at least in 2/3 of their total length. Antheridia almost entirely dark brown, especially at the constricted base. Growing on the posterior edges of body rings. On African Spirostreptidae..... .....*R. lophophora*
- Secondary appendages not broadened distally, hyaline except the darkened basal septum. Antheridia entirely hyaline except for the

darkened basal septum. Growing on and between legs. On African *Obelostreptus* (Spirostreptidae) ..... *R. obelostrepti*

8. Thallus very reduced, series consisting of a: 2, m: 2, p; 2(–3). Primary appendage including a conspicuous, dark brown, and constricted middle part, which is about twice as long as analogous parts of secondary appendages. On Iranian *Chiraziulus* (Cambalidae) ..... *R. appendicifera*
- Characters different from the above 9
9. Median series concealed, consisting of only one diminutive cell. Cell p3 conspicuous, elongated, forming a lateral branch supporting appendages and antheridia. On Sri Lankan *Ktenostreptus* (Harpagophoridae) ..... *R. siddhartha*
- Median series with at least four cells. Characters different from above. On other hosts 10
10. Median series with 11–12 cells, with most (not less than seven) cells located under the level of the base of the perithecium. On European *Pachyiulus* (Julidae) ..... *R. pachyiuli*
- Median series with 4–11 cells, with most cells located above the level of the base of the perithecium, no more than two cells below. On other hosts 11
11. Anterior series consisting of two cells. Uppermost cell of posterior series (p_6) forming a conspicuous free pedicel that serves of base for the primary appendage. On European *Cylindroiulus* (Julidae) ..... *R. laboulbenioides*
- Anterior series consisting of 3 or 4 cells. Other characters not as above 12
12. Anterior series consisting of 4 cells. Median series composed of a backbone-like row of similar cells. Cell a_4 bearing one antheridium directly on the appendiculate cell, without a stalk. On New Zealand *Eumastigonus* (Cambalidae) ..... *R. galatheae*
- Anterior series consisting of 3 cells. Other characters not as above. On European Julidae 13
13. Upper part of median series, i.e. the 3–4 distal cells turning outward, overlapping cell p_7 and stretching the primary appendage in that direction. On European *Cylindroiulus* ..... *R. dendroiuli*
- Different combination of characters . On European *Unciger* ..... *R. uncigeri*

Discussion

Importance of museum collections as a resource for biodiversity research

The genus *Rickia* is the most diverse genus of Laboulbeniales associated with millipedes (Santamaria *et al.* 2014), and 71% of this diversity has been discovered in historical specimens preserved in museum collections. It is clear that large entomological collections hold a huge potential for new findings of Laboulbeniales, thus the number of new taxa present in other collections is far from being known.

Three paradigmatic aspects of this newly discovered biodiversity may be highlighted: (i) *Rickia galatheae* is a remarkable example of long overlooked biodiversity—collected in New Zealand during the world circumnavigation of the famous Danish "Galathea Deep Sea Expedition (1950–1952)", this species has remained attached to the host and undescribed since 1951 and thus has had a "shelf life" of more than 60 years, much more than the average of 21 years reported by Fontaine *et al.* (2012); (ii) a holotype on a holotype—*Rickia appendicifera* is here described from the holotype of the endemic Iranian millipede *Chiraziulus kaiseri* and has remained neglected since the host was described, despite 94% prevalence of the fungus in the large type series (Reboleira *et al.* 2015); (iii) infection of a common pet—*Rickia gigas*, one of the World's largest Laboulbeniales, is here described from the giant African millipede, *Archispirostreptus gigas*, which is frequently kept as a pet; although its presence has been reported as "hairs" in amateur forums, it has evaded scientific study until now. These examples serve as strong arguments to emphasize that the study of Laboulbeniales contributes to a more efficient use of the biological heritage present in museum collections.

With the new species described here, Laboulbeniales infecting millipedes are known from Europe, Asia, Africa, Australia and New Zealand (Fig. 67). So far there is no record from the Americas, but this may merely be an effect of the relatively paucity of American millipede specimens in the ZMUC collection.

Morphological characters of Rickia

Rickia was described by Cavara (1899) for the myrmecophilous species *R. wasmannii* Cavara, a Palaearctic species with a wide distribution (Santamaria & Espadaler 2015). The genus comprises an interesting and unusual large diversity of thallus characters especially those exhibited by antheridia. Also, thallus forms range from compact and rounded to greatly elongate and even ramified.

In the genus *Rickia* the thallus is multiseriate and unilayered, with a receptacle typically consisting of three vertical rows of cells known as anterior (ventral), posterior (dorsal) and median (axial) series. The median series may sometimes be absent (biseriate condition, formerly used as a diagnostic character for the genus *Distichomyces*, now a synonym of *Rickia*), extremely reduced to a single cell or just as well-developed as the two marginal series. Lateral branches from marginal series may be formed and may branch again in some species. The cells of marginal series bear secondary one-celled appendages and flask-shaped antheridia often separated from their respective appendiculate or subtending cells by a constricted brown to blackish septum. The anterior series is, in most species, where the

perithecium is borne. The numbers of cells in the three series is very important and must be precisely defined in descriptions because they serve as good distinguishing features between species inasmuch the numbers are very stable. The cells of the median series rarely produce antheridia or appendages. The main body is flat, only one-cell thick, i.e. unilayered, ribbon-like in elongated types, mostly appressed to the substratum, but sometimes divergent from it, and borne on a single basal cell, often distinguished as an abruptly differentiated stalk attached to the host by the usual darkened foot. Although the cells that constitute the median series, once formed, remain unchanged, except in size and shape, all or a variable number of cells in the two marginal series form, from their upper outer angles, one to several small cells, which give rise to either single secondary appendages or antheridia. In the more complicated situations even six such appendiculate cells may be separated from a single cell of the marginal series; the groups thus formed form a border of a continuous series of smaller cells above and below (see, e.g., *Rickia platessa*). The relative position of these appendiculate cells may not always be the same, even in the same individual, tending to become vertically superposed, horizontally seriate, or crowded, overlapping and even completely concealing one another (their number can then only be estimated by examination of the protruding necks of the antheridia or the projecting ends of the appendages).

The secondary appendages consist of two cells: one appendiculate cell giving rise to a more or less elongated filamentous distal cell. According to Thaxter (1926) in the development of appendages a slight protrusion is separated by a septum, growing out to form the unicellular appendage; the septum becomes variably darkened and constricted; although in certain instances, the base of appendage, the septum, and even the appendiculate cell may become more or less involved in a brown suffusion. The appendage is normally simple and unicellular, rarely branched or septate, and varies greatly in shape and size.

The primary appendage is very similar to secondary appendages, also one-celled, variably short, borne on the distal part of the posterior series above its typically dome-shaped, subtending cell and the primary septum.

Antheridia mostly consist of three cells: an appendiculate cell, a stalk-cell and the flask-shaped phialide on the top. The number of antheridia per thallus varies from one to hundreds depending on the species. Thaxter (1926) mentioned that the development of antheridia from the appendiculate cells is fundamentally the same as that of appendages. The septum above their appendiculate cells may be constricted and darkened exactly as in the appendages, or remain unmodified, more or less immersed in the receptacle together with all or part of the body of the antheridium, where only the neck or part of the venter are free externally. According to Thaxter (1926), the phialide consists of an inner "stalk-" cell and one to several fertile, spermatia-forming cells located inside a venter below the apical, variably elongated neck. Thaxter defined the antheridia of *Rickia* as belonging to the compound type, with two or more closely associated spermatia-forming cells, which discharge through minute pores into the main cavity of the neck. This was accepted by Tavares (1985) and use as a character in the key of her monograph. Trying to clarify this feature, Thaxter (1926) wrote: "the limits of the antheridial cells are at best usually very indistinct, and for the reason that they may be so superposed that there seems to be but a single cell present". Also, Thaxter mentioned that the whole contents of the "antheridium" (i.e. the phialide) may be evanescent, thus disorganizing and appearing to be a continuous cavity like that of the simple antheridia of the Laboulbeniaceae. Moreover, Maire (1916) described *R. peyerimhoffii* as having simple antheridia, but reexamination of material by Thaxter (1926) convinced him that they were compound. In a few cases like *R. macrandra* Thaxter's drawings (Thaxter 1926: figs 60, 62 and 63) show evidently the typical organization of compound antheridia, otherwise the majority of species seem to show simple antheridia. Species with compound antheridia were absent from the material studied. Being regarded as basal for Laboulbeniales taxonomy at the generic level, this character should be carefully analyzed. A generic segregation of *Rickia* regarding the presence of compound antheridia should be considered. Likewise, the systematic relations with suprageneric taxa of its group should be reviewed with molecular approaches.

Perithecia are primarily formed from the anterior series of cells, rarely from others. In species with several perithecia, they may be formed by any of the series of cells of the thallus. The perithecial wall includes four outer cells, distinctly unequal in height, for each vertical row (Thaxter 1926). Mature perithecia are formed even in species lacking antheridia. Trichogynes are well developed and evanescent. The shape of the trichogyne is very variable. Its persistent base, or at least its dark basal septum is usually readily recognizable on the anterior margin of the perithecium. Mature perithecia are very variable in size and shape.

Tavares (1985: 311) defined three or four basic structural types in the genus according to the illustrated species in Thaxter's monograph (1926): a *dichotoma* type, with a slender branched or unbranched receptacle (occurring on Acari and Coleoptera -Erotylidae and Passalidae-); a *filifera* type, showing a uniseriate extension of the receptacle above the perithecium (on Acari as well as on Passalidae); a *berlesiana* type, having a massive multiseriate receptacle of considerable length and usually darkened; and a *perlata* type, which is short and broad (the two latter groups

are widespread). Four of the new species of *Rickia* here described (*R. gigas, R. lophophora, R. obelostrepti* and *R. odontopygiidarum*) may belong to the *filifera* type because the posterior series extends in a branch beside and above the perithecium. It is, however, difficult to reduce all the forms of species of *Rickia* to the four groups described by Tavares.

As is evident from the descriptions and the key, the 14 species included in this study belong to different morphological groups. Relationships between the species are difficult to establish—further studies are needed to clarify it, since currently data are still too scarce. Nevertheless, the identity of hosts and geographical distribution may be helpful. The biseriate condition is found in three species: *R. candelabriformis*, *R. platessa* and *R. rhynchophora*; but these three appear to be very isolated and without apparent close relationships. An evident relationship exists between the four African species which have a free stalked lateral branch borne from the posterior series of the receptacle: *R. odontopygiidarum* on Odontopygidae, and *R. gigas, R. lophophora,* and *R. obelostrepti* on Spirostreptidae. Species parasitizing the family Julidae: *R. dendroiuli, R. laboulbenioides, R. pachyiuli* and *R. uncigeri* also seem to be related having more "usual" morphologies if compared with many other *Rickia* on hosts other than millipedes. The remaining species are as isolated as their hosts.

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