

Polyandromyces coptosomatis (Dimorphomycetaceae, Laboulbeniales): new records, distribution patterns and host–parasite interactions in Brazil

Marília Pereira Rodrigues de Melo & Roger Fagner Ribeiro Melo

¹ Universidade Federal de Pernambuco, Departamento de Micologia, Centro de Ciências Biológicas, Av. da Engenharia, s/n, 50740-600, Recife, Pernambuco, Brazil

e-mail: rogerfrmelo@gmail.com

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An obligate parasitic fungus, *Polyandromyces coptosomatis*, is reported for the first time from Brazil, as a recurrent and persistent infection on the true bug *Antiteuchus tripterus*. *Antiteuchus tripterus* is for the first time reported as host for *P. coptosomatis*. Insect specimens were collected on *Bauhinia forficata*, the Brazilian orchid tree (Fabaceae). Most analyzed insects were infected by the fungus (74 %). The morphology of both female and male thalli is described in detail based on more than 100 examined specimens. In addition, we reveal and describe recurrent aberrant forms. Most thalli were found on male hosts, without any evidence for position specificity, whereas female insects were more intensely parasitized on their genitalia and dorsum. Differences between host sex and infected body parts are presented and discussed. A review on the world occurrences of this species thus far suggests that the records on Pentatomidae and Plataspidae hosts do not overlap, and that their potential distribution might follow a similar pattern.

Keywords: Ascomycota, fungal-insect association, Hemiptera, Peyritschielloideae.

Laboulbeniales (Laboulbeniomycetes, Ascomycota) are biotrophic fungi, mostly associated with true insects (Goldmann & Weir 2018, Haelewaters et al. 2019). They lack a mycelium and form multicellular thalli, which are the result of determinate growth. Unlike necrotrophic entomopathogenic fungi (such as *Cordyceps*, *Beauveria* or *Metarhizium*), they do not kill their hosts to proliferate on their dead cells and tissues — they require living hosts (Benjamin et al. 2004). These fungi can be found as ectoparasites on many arthropods, including Chelicerata, Hexapoda and Myriapoda, with about 2200 species and 141 genera known, reported from all continents except Antarctica (Rossi & Santamaria 2012, Haelewaters et al. 2019). The Laboulbeniales have had a confusing taxonomic history before they were placed in the class Laboulbeniomycetes based on sequence data (Weir & Blackwell 2001). Studies in laboulbeniacean fungi in the last decades have demonstrated the consistency of their phylogenetic positioning among the higher ascomycetes (Schoch et al. 2009, Goldmann & Weir 2018, Haelewaters et al. 2019). One of the most comprehensive historical contributions on South American Laboulbeniales is the work of Spegazzini (1917). To

date, about 150 species have been reported from Brazil (Paoli 1911; Thaxter 1896, 1908, 1926, 1931; Arndt et al. 2003; Bergonzo et al. 2004; Proaño Castro & Rossi 2008; Rossi & Bergonzo 2008; Sosa-Gómez et al. 2010; Barragán et al. 2013, Bernardi et al. 2014, Haelewaters & Rossi 2015, Kaishian & Weir 2018).

Polyandromyces coptosomatis Thaxt. (Peyritschielloideae, Dimorphomycetaceae) is a parasite of terrestrial Pentatomidae and Plataspidae bugs. It is the only species of the genus, described by Thaxter (1920), the epithet *coptosomatis* being derived from the plataspid bug *Coptosoma maculatum* Westw. Members of Dimorphomycetaceae have dioecious thalli, meaning that male and female organs are produced on separate thalli, in contrast to what is more usual in the group (Santamaria 2002). The Peyritschielloideae subfamily (*sensu* Tavares 1985) includes dioecious Laboulbeniales with the male thallus bearing one or more compound antheridia (Thaxter 1920). In *Polyandromyces*, the antheridium is positioned terminally, in contrast to the lateral position in related genera (Tavares 1985).

Species of Laboulbeniales are moderately to highly host specific, and it is known that this speci-

ficity can be influenced by several parameters (De Kesel 1996). Some Laboulbeniales seem to show position and/or sex specificity (Riddick & Schaefer 2005, Goldmann & Weir 2012, Sundberg et al. 2018). Recent studies have shown the phenomena of habitat specificity and host shift in Laboulbeniales (Rossi 2011, De Kesel & Haelewaters 2014, Pfliegler et al. 2016).

Pentatomidae contains the majority of Heteroptera that are pests of crops (Schaefer & Panizzi 2000). *Antiteuchus* (Pentatomidae: Discocephalinae: Discocephalini) is a widespread genus of true bugs with rounded, shiny and smooth bodies. Males are darker, usually in shades of black, and the females present lighter colors, usually variegated with light and dark spots (Ruckes 1964). *Antiteuchus tripterus* Fabricius, mainly found in the Neotropics, can be identified based on differences in the form of the terminal tergal margin in the male, with a raised inner side angle, forming a small, rounded projection fused to the posterolateral angle, and by the reniform parameral lateral lobe (Fernandes & Grazia 2006).

This work presents a severe and recurrent infection of the stink-bug *Antiteuchus tripterus* in Northeastern Brazil caused by *Polyandromyces coptosomatis*, and presents the first record of this species for this country and for this host, with comments on position and sex specificity.

Materials and methods

The host specimens were collected from May to July 2018 from Brazilian orchid trees *Bauhinia forficata* (Fabaceae), in an urban area of Recife, State of Pernambuco, Northeastern Brazil. The insects were removed from trees using entomological tweezers and delicate brushes and preserved in 75 % ethyl alcohol for transportation to the laboratory (Benjamin et al. 2004). Specimens were observed directly from the hosts under a Leica EZ4 stereomicroscope. Thalli were mounted in tap water and/or lactophenol with cotton blue for measurements and identification, and in Polyvinyl-Lactol-Glycerol resin for long-term preservation. Thalli were identified based on morphology, ecology and sexual pattern (Thaxter 1920, Huldén 1983, Tavares 1985). The geographical records of the fungus and its insect hosts were reviewed based on the available literature and from herbarium records at the Global Biodiversity Information Facility (GBIF 2018) database. For the sex and position specificity observations, both binomial (presence or absence of thalli in a given insect/position) and numerical

(number of thalli) data were considered. An analysis of variance (ANOVA) was used in order to evaluate the significance between treatments (host sex and position) on thallus density in the collected specimens. A chi-square goodness of fit test (χ^2) was performed to test the independence of thalli presence/absence on host sex. The main question analyzed was whether there were patterns of occurrence related with host sex, preferred body or a synergy between the two parameters in this parasite-host interaction. In the presented results, infection rates denote the percentage of examined insects with the parasite. The local infection rates relate with the number of insects parasitized in a given body part in relation with all insects examined for that sex and in total. The proportion of male per female number of thalli and number of parasitized insects is also presented.

Stereomicrographs were taken using an Olympus SZ61 stereomicroscope equipped with an Olympus Soft solutions LC20 camera. High-resolution images of morphological characters were taken with an Olympus QColor 3 digital camera mounted on an Olympus BX51 microscope equipped with bright-field and Nomarski interference optics. Images were optimized and cropped in Adobe Photoshop CS Version 8.0 (San Jose, California). Permanent voucher slides are deposited at URM (Herbário Padre Camille Torrend, Departamento de Micologia, Universidade Federal de Pernambuco, Recife, Brazil).

Results and discussion

Host-parasite interaction

Among the 50 studied insects, 26 males and 24 females, thalli were observed on 37 specimens (total infection rate = 74 %), being 21 infected males (male infection rate = 86.76 %) and 16 infected females (female infection rate = 66.67 %). Table 1 presents the results of thalli count and presence/absence per body part and per host sex. Nine hundred and sixty-two thalli of *Polyandromyces coptosomatis* were counted on the studied hosts, 604 on male and 358 on female adults. Only female thalli were counted.

All body parts were positive for the presence of the fungi. The differences in thalli occurrences were significant between body parts in the same sex, for males ($\chi^2 = 752.66$; $P < 0$) and females ($\chi^2 = 441.05$; $P < 0$). The differences between sex considering different body parts were not considered significant, both for thalli occurrence ($F = 1.99$; $F_{\text{crit}} = 4.25$; $P = 0.17$) and for number of infected hosts ($F = 3.57$; F_{crit}

Tab. 1. Distribution and occurrences of *Polyandromyces coptosomatis* thalli on *Antiteuchus tripterus* in Northeastern Brazil, considering host sex, position and infection rates. M male; F female; M/F male per female ratio; T total, n.d. no data.

	Thalli per position				No. of parasitized insects				Local infection rate (%)		Position distribution (%)	
	M	F	M/F	T	M	F	M/F	T	M	F	M	F
Dorsal parts												
Head	27	9	3.00	36	7	1	7.00	8	26.92	4.17	4.47	2.51
Eyes	9	3	3.00	12	3	2	1.50	5	11.54	8.33	1.49	0.84
Antenna	40	5	8.00	45	5	2	2.50	7	19.23	8.33	6.62	1.40
Pronotum	73	24	3.04	97	11	3	3.67	14	42.31	12.50	12.09	6.70
Scutellum	70	64	1.09	134	12	11	1.09	23	46.15	45.83	11.59	17.88
Corium	174	108	1.61	282	16	11	1.45	27	61.54	45.83	28.81	30.17
Hemelytra	7	0	n.d.	7	5	0	n.d.	5	19.23	0.00	1.16	0.00
Laterotergites	47	51	0.92	98	11	7	1.57	18	42.31	29.17	7.78	14.25
Femur	63	1	63.0	64	9	1	9.00	10	34.62	4.17	10.43	0.28
Tibia	32	15	2.13	47	8	3	2.67	11	30.77	12.50	5.30	4.19
Tarsus	13	0	n.d.	13	2	0	NA	2	7.69	0.00	2.15	0.00
Propleuron	25	10	2.50	35	4	2	2.00	6	15.38	8.33	4.14	2.79
Mesopleuron	0	15	0.00	15	0	2	0.00	2	0.00	8.33	0.00	4.19
Metapleuron	7	5	1.40	12	3	2	1.50	5	11.54	8.33	1.16	1.40
Abdomen	14	17	0.82	31	4	5	0.80	9	15.38	20.83	2.32	4.75
Genitalia	3	31	0.10	34	1	6	0.17	7	3.85	25.00	0.50	8.66
Total	604	358			101	58						

= 4.17; $P = 0.06$), pointing to a lack of synergy between these parameters. The correlation between thalli numbers and exposed area for each body part proved to be relevant for the presented data, both for male ($\chi^2 = 764.87$; $P < 0$) and female ($\chi^2 = 394.13$; $P < 0$) hosts, being the distribution pattern statistically significant. Genitalia of females were more parasitized compared to those of males (M/F ratio = 0.10). The corium, the basal portion of the hemelytra, was the body part with more thalli in both sexes (282), but in female hosts, the parasite showed a rather regular preference for this region (30.17 %). The exposed hemelytral membrane was the least parasitized body part. Only one thallus was recorded on femurs from female hosts, against 63 thalli in males, being in this body part the higher value of ratio between sexes for the same body part recorded. The ventral parts of female hosts were more parasitized than in males, despite not reaching a much higher infection ratio. The most common occurrence pattern on females was few thalli grouped at the scutellum and laterally at the laterotergites, while males usually had thalli scattered all over the dorsum, antennae and legs. The number of thalli per body part and the number of infected insects for

males and females is presented in Fig. 1, as well as the most common infection patterns for both sexes.

Taxonomy

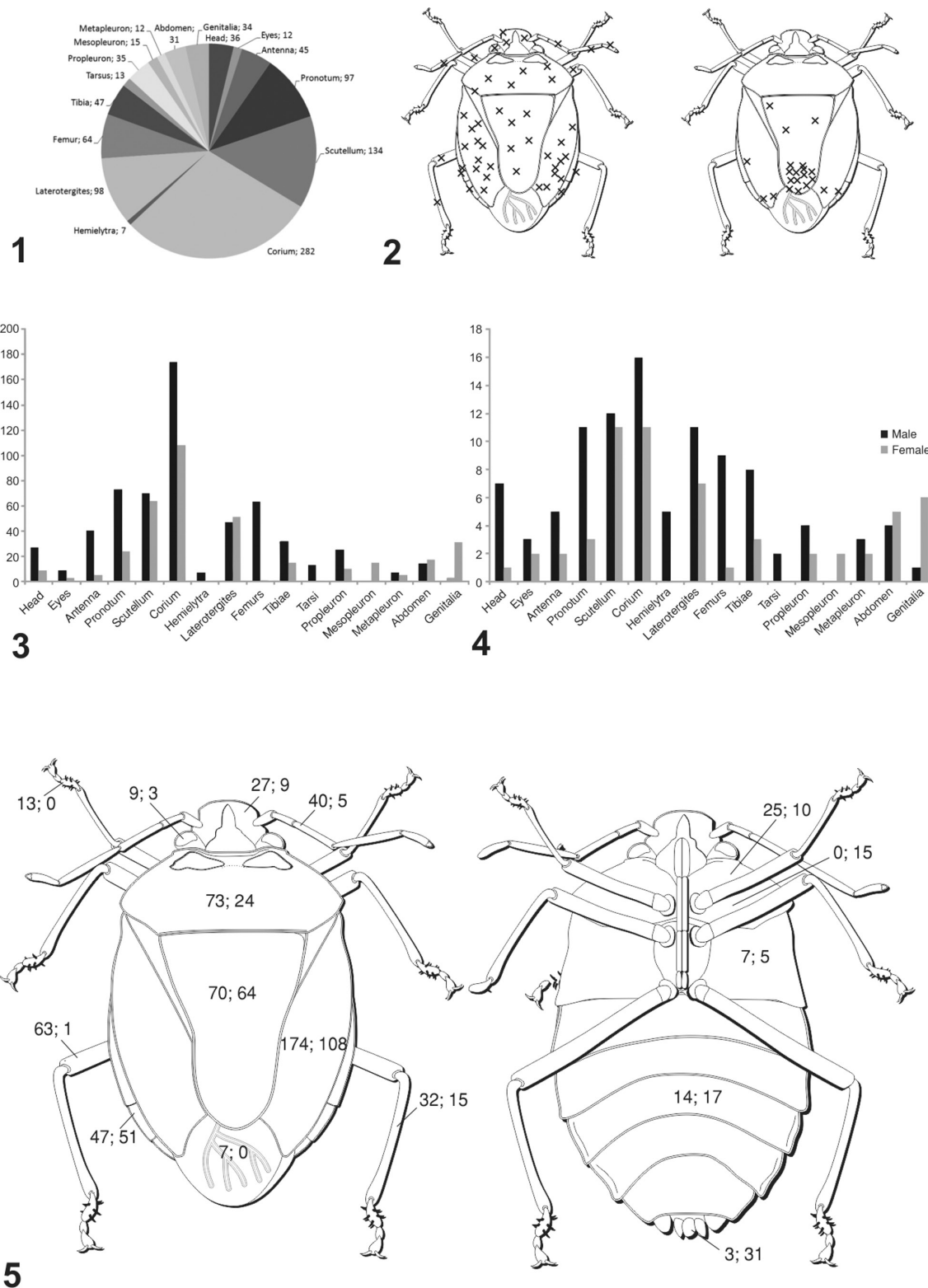
Polyandromyces coptosomatis Thaxt., Proc. Amer. Acad. Arts & Sci. 55(6): 215. 1920. – Figs. 2–3)

Synonyms. *Polyandromyces coptosomatis* var. *coptosomatis* Thaxt., Proc. Amer. Acad. Arts & Sci. 55(6): 215 (1920)

Polyandromyces coptosomatis var. *minor* Thaxt., Proc. Amer. Acad. Arts & Sci. 55(6): 217 (1920)

Eudimeromyces greatheadii Balazuc, Rev. Mycol. 37(5): 253 (1973)

Thalli dioecious. – Male thallus erect, light golden to amber, 160–195 μm long. – Receptacle consisting of three cells, rarely two, hyaline, cyanophilous, 153–155.5 \times 22.5–27.5 μm ; basal cell (I) longer than the others, straight to strongly bent, 35–37.5 \times 10–12.5 μm ; cell II triangular to liver-shaped, complementary in shape with the basal cell, with a tapered upper end, 8–8.5 \times 12.5–13.5 μm ; cell III trapezoid to roughly square shaped, 7–7.5 \times 10.5–11(12.5) μm . – Antheridia endogenous, compound, single, rarely two per thallus, 64–65 μm long; stalk-cell depressed, triangular to mitriform, amber to dark brown, 7.5–8 \times



Figs. 1–5. Occurrence of *Polyandromyces coptosomatis* on *Antiteuchus tripterus* in Brazil. **1.** Number of thalli per body part. **2.** Schematic representation of the most common occurrence pattern of thalli on male (left) and female (right) hosts. **3.** Number of thalli per body part. **4.** Number of infected insects in each body part. **5.** Schematic representation of thalli per body part distribution.

20–21.5 µm, slightly thick-walled; Antheridial venter hyaline, usually non-cyanophilous, 21.5–22.5 µm wide, bearing flask-shaped, strongly cyanophilous antheridial cells, usually 6–9 visible, formed above small, individual basal cells, equally strongly cyanophilous; efferent chamber triangular to dome-shaped, occasionally pigmented, with a light golden coloration, with numerous oily droplets, filled with spermatia at maturity, 12.5–15 × 20–21.5 µm; efferent neck clearly distinguishable, formed after an abrupt constriction atop the efferent chamber, triangular to flask-shaped, straight or curved, 22.5–25 × 7.5–8 µm. – Spermatia bacilli-form, 1.8–2.6 µm long, oozing through the efferent neck at maturity. – Female thallus with a single perithecium and one sterile appendage, erect, light golden to amber, 410–440 µm long. – Receptacle consisting of five obliquely superposed cells, hyaline, cyanophilous, 185–202.5 µm long: basal cell (I) longer than the others, straight to slightly bent, 72.5–80 × 30–32.5 µm; cell II rectangular to doliiform, 35–40 × 12.5–15 µm; cell III rectangular to liver-shaped, somewhat complementary in shape with the cell II, 32.5–37.5 × 12.5–15 µm; cell IV narrowly triangular, oblique, 27.5–30 × 17.5–22.5 µm; cell V strongly depressed, 15–17.5 × 16.5–17.5 µm; cell VI broadly triangular to bullet-shaped, slightly acute to rounded, 25–30 × 16.5–17.5 µm. – Appendage sterile, single, two-celled, hyaline, cyanophilous, 42.5–43 × 35–42.5 µm: lower cell trapezoid to roughly square shaped, 15–18.5 × 20–25 µm; upper cell broadly triangular to bullet-shaped, slightly acute to rounded, 25–27.5 × 15–17.5 µm. – Perithecium single, without clear distinguishable perithecial cells, translucent, light golden to amber, with cyanophily varying with maturation, utriform to lageniform, with the basal-most part strongly bent, forming a right to obtuse angle in relation to the thallus, 355–360 × 16.5–17.5 µm. – Ascospores two-celled, fusiform, 48–65 × 12.5–17.5 µm, the upper cell shorter, (12.5)17.5–20 µm, with a rounded end, and the lower cell longer, 37.5–45 µm, wholly surrounded by a thick gelatinous sheath, especially thick at the acute end; the spores are stuck together after liberation, usually in pairs but occasionally in groups of three to five.

Material examined. – BRAZIL. State of Pernambuco, Recife (8° 02' 46.9" S, 34° 53' 15.43" W), on *Antiteuchus tripterus* feeding on living branches and twigs of *Bauhinia forficata*, 27 June 2018, leg. & det. R.F.R. Melo (URM91827, 91828, 91829, 91830).

Notes: *Polyandromyces coptosomatis* was described by Thaxter (1920) as "*Polyandromyces coptosomalis*" from the legs of *Coptosoma maculatum*

(Plataspidae). Later, it was reported from other Plataspidae and Pentatomidae. The material presented here was scattered on different body parts of *Antiteuchus tripterus* (Pentatomidae). Compared with the type material, the Brazilian specimens are larger, with longer thalli and perithecia. The ascospore measurements could not be compared, since this information was not published in the original description. Some male thalli tend to form two compound antheridia, which was not previously described for this species. Some female thalli form a second, primordial perithecium, which is initiated on cell III but does not develop to maturity. Multiple perithecia can occasionally be observed in other genera that have thalli with a single perithecium, such as *Corethromyces* and *Diphymyces* (Hughes et al. 2004, Rossi & Maca 2006).

Geographical distribution

Polyandromyces coptosomatis has been reported from 13 countries and thus far has a Pantropical distribution, mostly in Africa, Oceania and southern Asia (Fig. 4, Tab. 2). This is the second report from South America and the first one from Brazil. Previously reported host insects were species in the genera *Coptosoma* (Plataspidae), *Acrosternum*, *Antestia*, *Antestiopsis*, *Euryaspis*, *Phoeacia* and *Thyanta* (Pentatomidae). This is the first report of a species of Laboulbeniales for the genus *Antiteuchus*. Benjamin (1967) mentioned *P. coptosomatis* on an "undetermined" plataspid from Ecuador, with no mention of microscopic preparations or further details.

Discussion

Two interesting observations are the high prevalence and recurrence of infection. An infection rate of 74 % can be considered high for this interaction. No other species of Laboulbeniales were recorded on these hosts, and examination of other Pentatomidae at the study site was negative for *Polyandromyces*. In their study of Laboulbeniales on beetles, Weir & Hammond (1997) state that there is no evidence to suggest that each arthropod supports its own unique species of this order. However, using an integrative taxonomy approach, Haelewaters et al. (2018a) suggest that *Hesperomyces virescens*, considered a single species occurring on more than 30 species of ladybirds, is instead made up of multiple different species, each adapted to their individual host species.

Among the parameters that can influence position specificity in Laboulbeniales, those most com-

Tab. 2. Geographic distribution of *Polyandromyces coptosomatis* records, ordered by year.

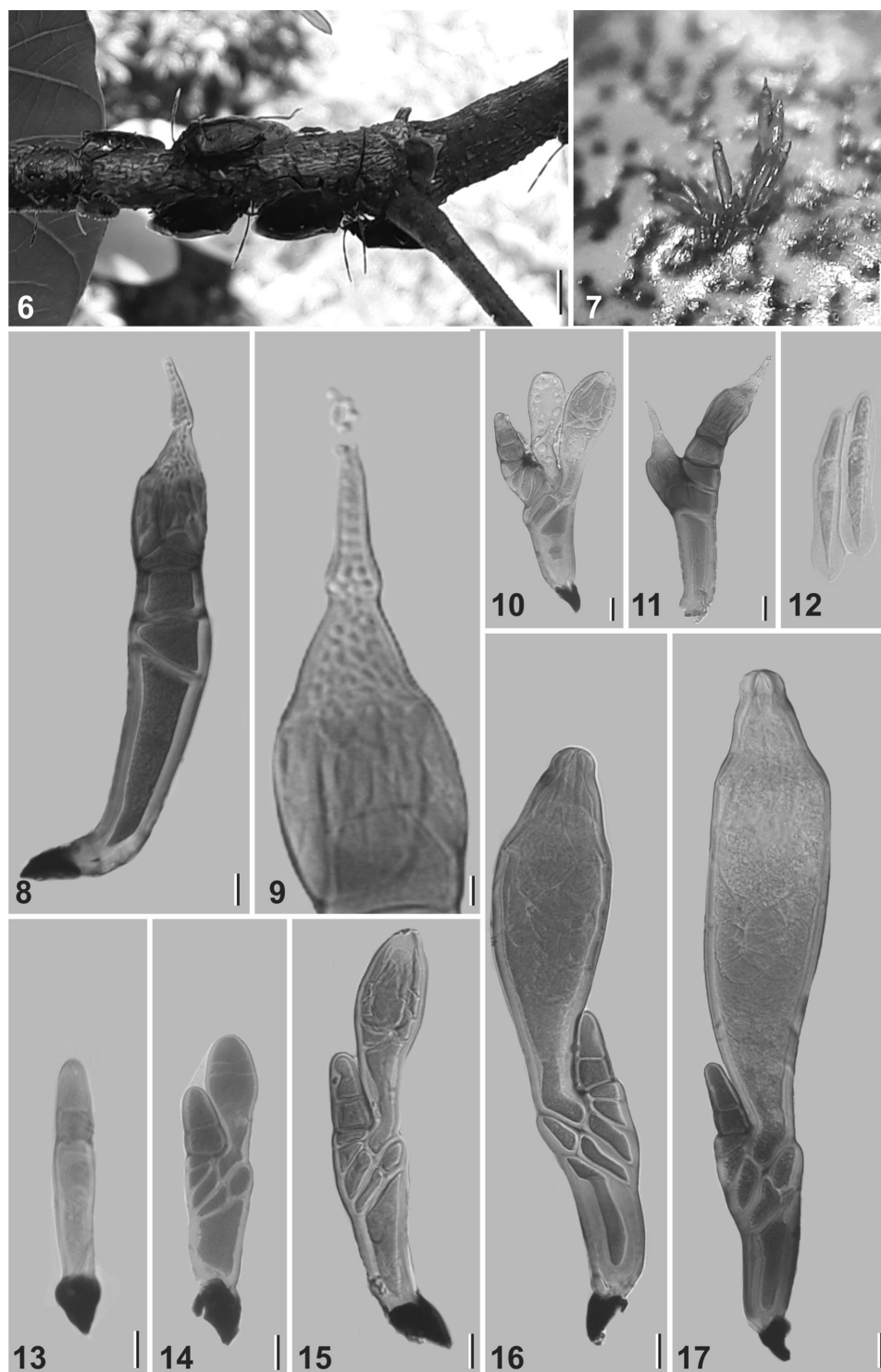
Country	Year	Host species	Host family	Source
Vietnam	1909	<i>Coptosoma cribraria</i>	Plataspidae	Herbarium record
China	1912	<i>Coptosoma cribraria</i>	Plataspidae	Herbarium record
Cameroon	1920	<i>Coptosoma</i> sp.	Plataspidae	Thaxter 1920
Fiji	1920	<i>Coptosoma</i> sp.	Plataspidae	Thaxter 1920
Madagascar ^a	1920	<i>Coptosoma maculatum</i>	Plataspidae	Thaxter 1920
Solomon Islands	1920	<i>Coptosoma</i> sp.	Plataspidae	Thaxter 1920
Uganda	1962	<i>Antestiopsis orbitalis</i>	Pentatomidae	Herbarium record
Tanzania	1963	<i>Antestiopsis orbitalis</i>	Pentatomidae	Herbarium record
Uganda	1972	<i>Euryaspis marshalli</i>	Pentatomidae	Herbarium record
Senegal	1984	n.d.	Plataspidae	Herbarium record
Togo	1990	<i>Acrosternum acutum</i>	Pentatomidae	Herbarium record
Indonesia	1991	<i>Coptosoma cribraria</i>	Plataspidae	Herbarium record
Indonesia	1991	<i>Antestia anchora</i>	Pentatomidae	Herbarium record
St. Vincent and the Grenadines	1992	<i>Thyanta vadosa</i>	Pentatomidae	Herbarium record
South Africa	1997	<i>Antestiopsis orbitalis</i>	Pentatomidae	Van-der-Linde & Rong 1997
Ecuador	2009	<i>Phoeacia</i> sp. nov.	Pentatomidae	Haelewaters et al. 2015
Canary Islands	2011	<i>Acrosternum</i> sp.	Pentatomidae	Haelewaters et al. 2015
Brazil	2018	<i>Antiteuchus tripterus</i>	Pentatomidae	Presented record

^a Type.

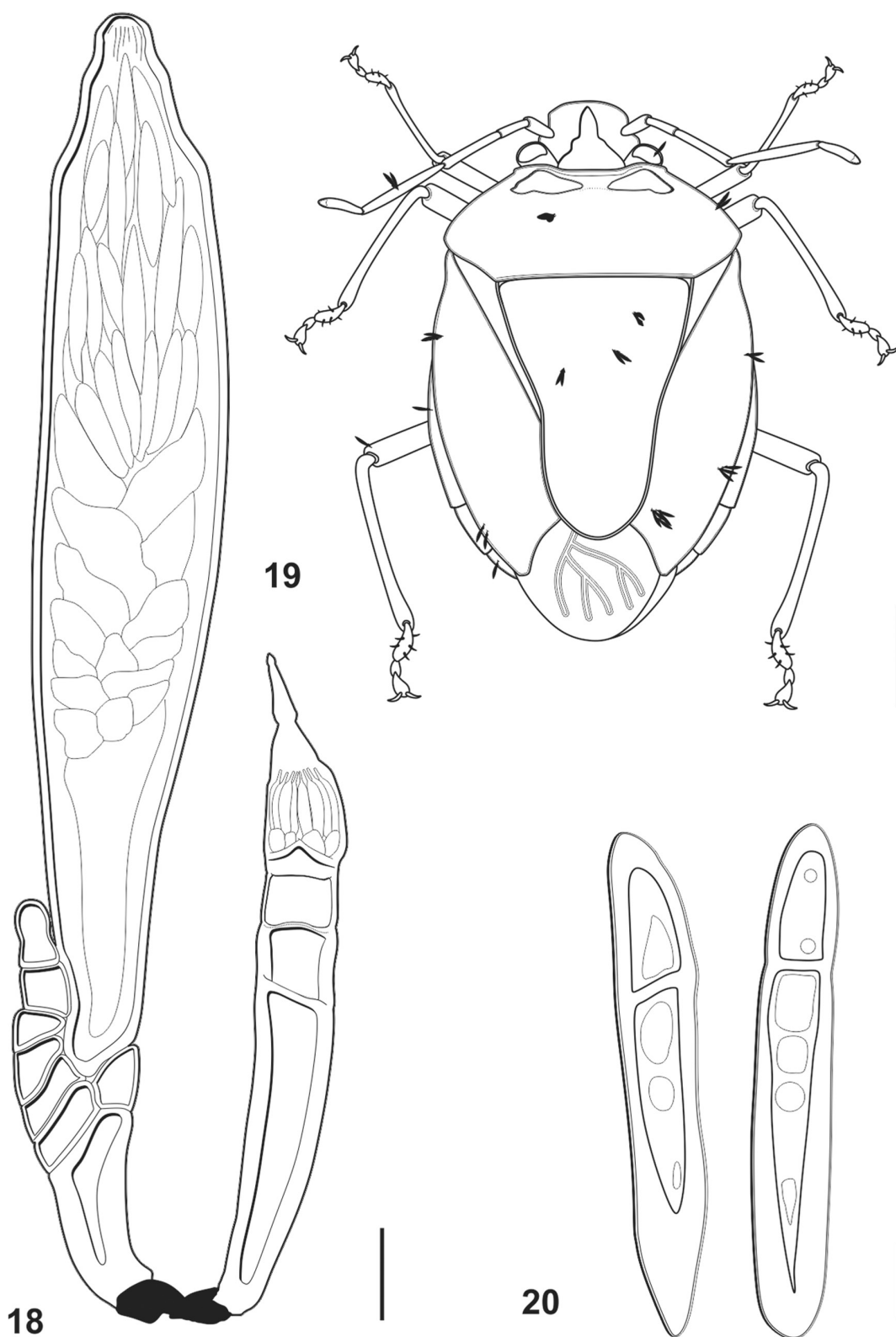
monly assessed are: (1) host feeding and (2) mating behavior; (3) nutrient availability, and (4) characters from the insect integument (Weir & Blackwell 2005). Rossi & Leonardi (2018) presented the interesting study case of *Laboulbenia antemnalis*, associated with termite antennae, in which spore transmission probably occurs by communication contact (antennation), since there is no mating contact between soldiers and workers. The original hypothesis in the present work, on the differences in occurrence patterns related to sex, was that the female would be predominantly infected in its dorsum, due the transmission of parasites during mating. For the studied interaction, this hypothesis was not confirmed, since these numbers were not significantly different. Most thalli found on female venter were associated with the genitalia, which cannot be properly compared with the male hosts, since in males this is an anatomically and physiologically different organ, and with the dorsum, mainly on scutellum and corium. The majority of thalli were found at the corium of both males and females, which lead, aside from the area available for spore implantation, to the hypothesis that the transmis-

sion between hosts occurs by direct contact, given that many individuals share the same twig, touching each other laterally as they move. Thus, this could be regarded as a contact disease. Similarly, Nalepa & Weir (2007) described the infection of *Hesperomyces virescens* on *Harmonia axyridis* (Coleoptera, Coccinellidae) as a “socially transmitted disease” in overwintering aggregations, where the fungus can be transmitted in random contacts. The tendency of mature ascospores to stick to the insect’s cuticle and even to other thalli can facilitate this method of transmission. Also, since females tend to be still when taking care of eggs for a moderate amount of time, they are less likely to move along the trees, exposing less of their body to infection by direct contact (Eberhard 1975). Regarding the association of *Antiteuchus tripterus* and fungi, only an unidentified species of *Penicillium* has been cited, found only on dead insects (Eberhard 1974).

One of the problems regarding understudied groups is to infer or hypothesize host specificity with only a few records scattered in different continents. Haelewaters et al. (2018b) hypothesize that bat fly-associated lineages of Laboulbeniales inde-



Figs. 6–17. *Polyandromyces coptosomatis* from *Antiteuchus tripterus* in Brazil. **6.** Host habit on a living branch of a Brazilian orchid tree *Bauhinia forficata* (bar 5 mm). **7.** Mature thalli on the scutellum of a female host (bar 300 μ m). **8.** Mature male thallus (bar 5 μ m). **9.** Compound antheridium of a mature male thallus, with both efferent chamber and neck filled by spermatia, which can be seen oozing through the ostiole (bar 5 μ m). **10.** Aberrant female thallus, with the primordium of a second perithecium, eventually aborted (bar 20 μ m). **11.** Aberrant male thallus, with two antheridia (bar 20 μ m). **12.** Ascospore pair (bar 10 μ m). **13–17.** Development of the female thallus, from the foot formation at the end of the basal cell up to the production of ascospores inside the mature perithecium (bars 20 μ m).



Figs. 18–20. *Polyandromyces coptosomatis* from *Antiteuchus tripterus* in Brazil. **18.** Female (left) and male (right) thalli, drawn to scale, as seen on the host, arising from the same insertion point (bar 10 μ m). **19.** Schematic representation of one of the infestation patterns, with thalli scattered through the body of a male host (bar 2 mm). **20.** Ascospores in detail (bar 10 μ m).

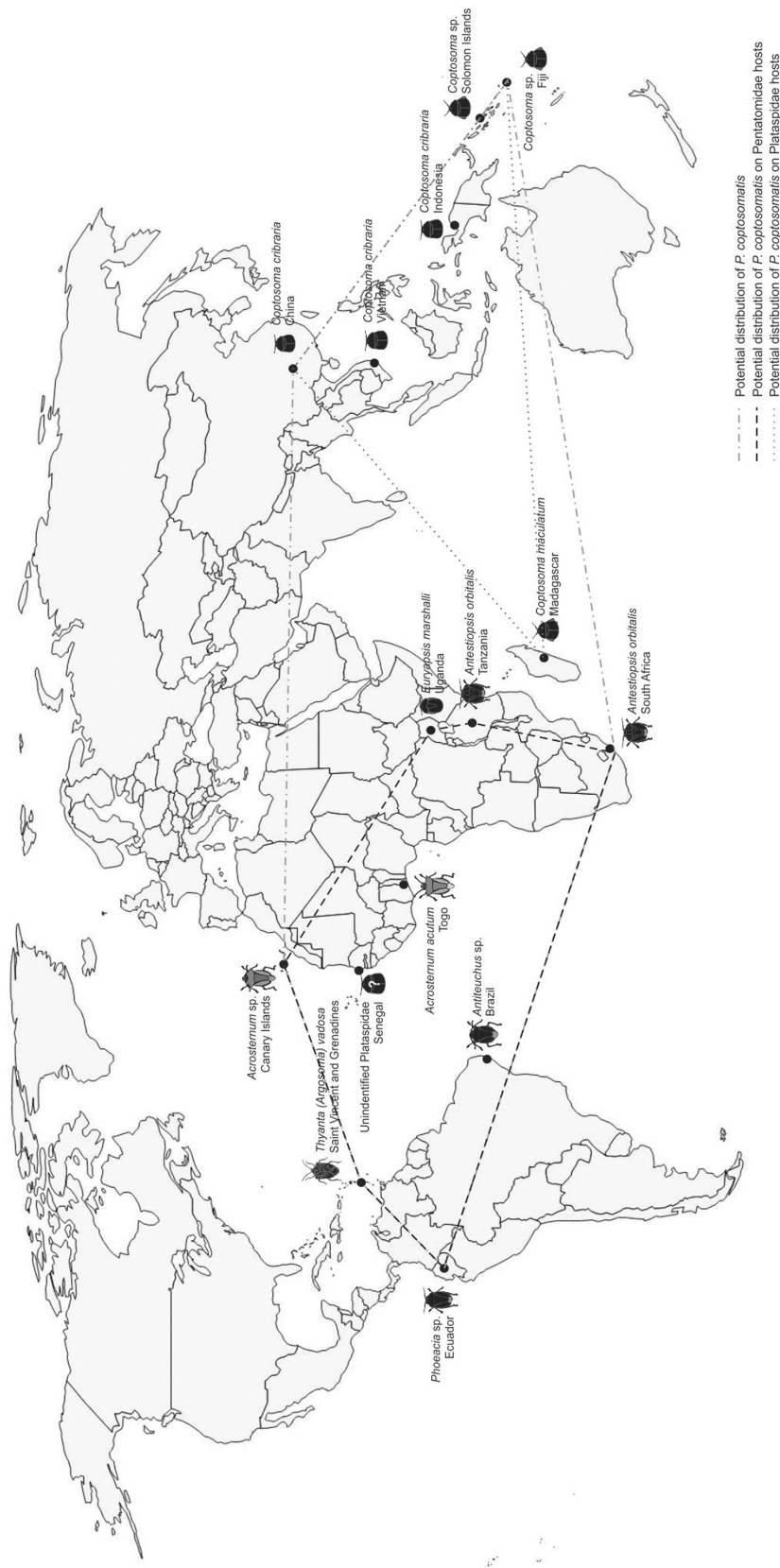


Fig. 21. Worldwide records of *Polyandromyces coptosomatis*. The lines connecting the records represent its potential distribution based on current data and host range/distribution.

pendently evolved from bug-associated lineages, considering, among others, the close relationship between *Nycteromyces* and *Polyandromyces*. To assess whether the heavy infection of this fungus on *A. tripterus* is a recent association (from an evolutionary point of view) will require more intensive field studies, but it is known that some morphological characters of *Polyandromyces*, such as the indistinguishable perithecial cell walls, presumably represent a more derived state. No pattern regarding position specificity could be delimited from records around the world. However, a quick examination suggests that the distribution of host family follows a non-overlapping pattern, with records on Pentatomidae in tropical America and Africa, and on Plataspidae in Oceania and southern Asia.

As with some other groups of biotrophic fungi, thalli of Laboulbeniales cannot be grown in axenic culture, which has contributed to a delay in the generation of molecular data on these fungi (Weir & Blackwell 2001; Haelewaters & Rossi 2015; Haelewaters et al. 2018a,b; Goldmann & Weir 2018; Sundberg et al. 2018). The progress of the study on these parasites will prove invaluable in establishing their host relationship patterns, evolutionary inferences and species diversity.

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