Three new species of *Laboulbenia* from Roland Thaxter's backlog of slides and a brief review of Laboulbeniales associated with Chrysomelidae

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Abstract: Three new species of Laboulbenia parasitic on Chrysomelidae are described from material mounted by Roland Thaxter (1858–1932). These are L. bilobata on Lema spp. from Brazil and Trinidad; L. longipilis from Cameroon; and L. pfisteri on Ivongius sp. from Madagascar. The following species of Laboulbenia on Chrysomelidae are illustrated for the first time: L. macarthurii, L. minuscula, L. nodostomatis, L. obesa, and L. philippina, all of which were described by Thaxter in 1914. A list of all 69 described Laboulbeniales associated with Chrysomelidae is presented in tabulated form.

Key words: Ascomycota, Farlow Herbarium, leaf beetles, parasitic fungi, Roland Thaxter, taxonomy

INTRODUCTION

Sixty-six species of Laboulbeniales, belonging to three genera, have been described previously on Chrysomelidae with the exclusion of a few obvious synonymies. The genus *Laboulbenia* with 55 species is by far best represented, followed by the genus *Dimeromyces* with 10 species; the genus *Rickia* is represented by a single species only (TABLE I). Most of these species were described by Roland Thaxter (1914, 1920), whose huge slide collection is deposited at the Farlow Herbarium (Harvard University).

Thaxter condensed his contribution in five monographic volumes (1896, 1908, 1924, 1926, 1931), in which he described hundreds of new species and reported most of those previously described in 21 nonillustrated papers published between 1890 and 1920 in the *Proceedings of the American Academy of Arts and Sciences.* He died in 1932 before he was able to publish a sixth volume that was intended as a comprehensive treatment of the genus *Laboulbenia.* Benjamin (1971, p 8) wrote in this connection: "Unfortunately, Prof. Thaxter left no manuscript for the latter work and the illustrations were in early stages of preparation. Thus, all species of *Laboulbenia* that he described subsequent to the publication of Part 2 of the monograph never were illustrated." Among these are all species of *Laboulbenia* parasitic on Chrysomelidae, most of which were described in 1914 (only one in 1912). Moreover, many of the new species of *Laboulbenia* that Thaxter intended to describe in his sixth volume are parasitic on Chrysomelidae.

Restudy of Thaxter's collection is an important approach for supplementing the missing illustrations and describing new species, which were considered as new but never published by Thaxter. In this paper we report the results of our review of the *Laboulbenia* species parasitic on Chrysomelidae. Because one of the major problems we have faced during our work was the absence of any iconography for some of the species, photographs also are provided for five species that had not been illustrated (FIG. 1). These species are *Laboulbenia macarthurii* Balazuc (formerly *L. papuana* Thaxt.; Thaxter 1914, Balazuc 1971), *L. minuscula* (Thaxt.) Thaxt., *L. nodostomatis* Thaxt., *L. obesa* (Thaxt.) Thaxt. and *L. philippina* Thaxt.

We emphasize the age of Thaxter's collection; most of the slides used for this paper are more than 100 y old. This explains some artifacts (formation of crystals, medium drying out) that we have encountered during our survey of the collection and that are seen in some of the photographs. To our surprise, we noticed that some of the measurements in Thaxter's contributions differ from our measurements of the same slides. For example, the length from foot to perithecial apex of Laboulbenia macarthurii (as L. papuana) is reported as 200-228 µm (Thaxter 1914), based on the single slide "MCZ No. 2511" (FH 00313330); the only fully complete and mature thallus on this slide, however, measures 272 µm. Actually, the specimen used for FIG. 1E measures 278.18 µm (slide FH 00313329). We do not know the origin of these differences. As we study more slides we will be able to discover whether this was a simple error on Thaxter's part or whether there was a systematic problem with some of the measurements he provided.

The number of *Laboulbenia* species parasitic on Chrysomelidae that Thaxter had planned to describe as new was much higher than the three presented in this paper. However, some of Thaxter's "new" species have

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been described by other scientists in the meantime (i.e. *L. metrionae* Balazuc, *L. grayi* Balazuc, *L. flabelliformis* K. Sugiy. & T. Majewski); others cannot be described due to the poor condition of the slides, and some species we decided not to describe for the lack of valuable information about the host insect or because we are not convinced they are accurate species.

MATERIALS AND METHODS

Observations and measurements of thalli and their components were made with Thaxter's original slides deposited in the Farlow Herbarium (FH), using an Olympus BX40 light microscope with Olympus XC50 digital camera and Micro-Suite special edition software 3.1 (Soft Imaging Solutions GmbH). Photography was done at the Harvard Center for Biological Imaging with a Zeiss AxioImager microscope running on ZEN software.

TAXONOMY

Laboulbenia bilobata Haelew. & W. Rossi, sp. nov. FIG. 2A

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Typification: BRAZIL, Para, 1911, *W.M. Mann*, on *Neolema gracilis* (Lacordaire 1845) (subfamily Criocerinae), slide FH 00313316 (HOLOTYPE).

Etymology: From Latin, referring to the presence of two distinct and unusual lobes.

Description: Receptacle short, stout because of short cells I, II and III, all of which are distinctly broader than long. Cell I subtrapezoidal, almost hyaline, contrasting with the dark cells above. Cell II irregularly triangular. Cell III quadrangular or subtrapezoidal, distinctly oblique. Cell IV about twice as long as broad, forming a rounded protrusion exceeding for nearly half of its length the insertion cell. The latter obliquely shifted inward. Cells II, III and IV brownish, paler on the inner side, deeply darkened externally, making these cells almost indistinguishable in mature thalli. Cell V small and much paler than the surrounding cells of the receptacle. Basal cell of outer appendage large, pentagonal in outline, giving rise to two branches that repeatedly divide dichotomously. The result is a dense tuft of short branchlets, which are mostly hyaline but brownish near the base. Basal cell of inner appendage much smaller, giving rise to a tuft of branchlets similar to those of the outer appendage. Antheridia hyaline, elongate and bottle-shaped, found on inner and outer appendage. Cell VI small in immature thalli, but soon developing abnormally outward, forming a protrusion similar in shape and size to but paler than the one formed by cell IV. Perithecium deep brown, wholly free, subcylindrical or slightly inflated, its basal cells forming a short and

hyaline stalk; the tip hyaline, contrasting, slightly enlarged; the apex subtended by two superposed hyaline and tooth-like projections, the upper arising externally from one of three rounded lips, one of which is distinctly larger. Length from foot to perithecial apex 140–190 μ m. Perithecium: 85–125 \times 20–29 μ m. Longest appendage 90 μ m.

Other specimens examined: TRINIDAD, St Augustine, 20–30 Apr 1929, *P.J. Darlington Jr.*, on the elytra of "*Lema*" sp., slide FH 00313317 (PARATYPE). Three fully mature and seven other thalli at various stages of development were examined.

Commentary: This species is strikingly different from any other in the genus because of the unusual growth of cell VI; at first one might think it belongs to another genus. However, young thalli show very clearly that it does belong to the genus *Laboulbenia* and that the growth of cell VI occurs as the thallus matures. For cell IV bulging outward and for the dark cell and of cells II and III it is likely allied to the two other species parasitic on American Criocerinae (i.e. *L. bruchii, L. rhinoceralis*). The peculiar projections at the perithecial apex recall those of the latter. The name given to this species is the one written on the slide label by Thaxter.

Laboulbenia longipilis Haelew. & W. Rossi, sp. nov. FIGS. 2B, C

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Typification: CAMEROON, Littoral Region, Sakbayeme, *s. d.*, *s. c.*, "on elyt. small yel. flat chrysomelid"[sic], slide FH 00313334 (HOLOTYPE). Two fully mature thalli were examined.

Etymology: From the Latin terms *longus* = long and *pilus* = hair, referring to the long and hair-like outer appendage.

Description: Thallus long and slender, light brown with much darker perithecium, appendage, and the almost hyaline basal cell of the latter. Cells I and II subcylindrical, elongate, the latter about $1.3 \times$ as long as the former, the area of the septum between these two cells distinctly darker. Cell III subtrapezoidal, small in comparison to cells I and II. Cell IV shorter than cell III. Cell V lens-shaped, not reaching cell III. Insertion cell dark and thick. Outer appendage extremely long and slender, up to 940 µm long, consisting of a large basal cell with the inner side distinctly convex, followed by two short cells of the same length divided by dark and constricted septa; the other cells forming the appendage much more elongate. Inner appendage consisting of a small basal cell, bearing distally a pair of elongate cells, each of which produces a bottle-shaped antheridium. Cell VI similar to cell III in shape and size. Perithecium fusiform, regularly and not abruptly tapering to the tip, which is darker only on the posterior side, ending in three rounded lips, the anterior of which is

Genus	Species	Host subfamily ^a
Dimeromyces	alaucophorae Thaxt. 1914	Galerucinae
Dimeromyces	auriculatus Thaxt. 1920	Galerucinae
Dimeromyces	geminander Thaxt. 1920	Galerucinae
Dimeromyces	helicoideus Thaxt. 1920	Alticinae
Dimeromyces	hermeophagae Thaxt. 1914	Alticinae
Dimeromyces	homophoetae Thaxt. 1914	Alticinae
Dimeromyces	hyperacanthae Thaxt. 1920	Galerucinae
Dimeromyces	longitarsi Thaxt. 1914 (= bordei Maire 1920)	Alticinae
Dimeromyces	nigricaulis Thaxt. 1920	Galerucinae
Dimeromyces	rigidus Thaxt. 1920	Galerucinae
Laboulbenia	arietina Thaxt. 1914	Alticinae
Laboulbenia	armata Thaxt. 1914	Alticinae
Laboulbenia	bertiae Balazuc 1975	Chrysomelinae
Laboulbenia	bilobata Haelew. & W. Rossi	Criocerinae
Laboulbenia	biondii W. Rossi & Cesari 1979	Alticinae
Laboulbenia	bergii Speg. 1917	Alticinae
Laboulbenia	braziliensis Thaxt. 1914	Alticinae
Laboulbenia	bruchii (Speg. 1912) Thaxt. 1914	Criocerinae
Laboulbenia	chaetocnemae (Thaxt. 1914) Thaxt. 1915	Alticinae, Cryptocephalinae
Laboulbenia	cephaloleiarum Balazuc & Demaux 1973	Alticinae
Laboulbenia	cristatella Thaxt. 1914	Alticinae
Laboulbenia	cryptocephali W. Rossi 1994	Cryptocephalinae
Laboulbenia	diabroticae Thaxter 1914 (= boggianii [Speg.1917])	Galerucinae
Laboulbenia	dislocata (Thaxt. 1914) Thaxt. 1915	Alticinae
Laboulbenia	disonichae Speg. 1912 (= tucumanensis Speg. 1912)	Alticinae
Laboulbenia	dorstii Balazuc 1975	Alticinae
Laboulbenia	durantonii Balazuc 1975	Chrysomelinae
Laboulbenia	epitrichis (Thaxt. 1914) Thaxt. 1915	Alticinae
Laboulbenia	flabelliformis K. Sugiy. & T. Majewski 1987	Alticinae
Laboulbenia Laboulbenia	fuliginosa Thaxt. 1914	Alticinae Alticinae
Laboulbenia Laboulbenia	funebris Thaxt. 1914	
Laboulbenia	grayi Balazuc 1975	Alticinae
Laboulbenia	halticae Thaxt. 1914	Alticinae
Laboulbenia	hermeophagae Thaxt. 1914	Alticinae
Laboulbenia	homophoetae (Speg. 1912) Thaxt. 1914	Alticinae, Galerucinae
Laboulbenia	hottentottae Thaxt. 1914	Criocerinae
Laboulbenia	idiostoma Thaxt. 1914	Alticinae
Laboulbenia	indohi K. Sugiy. & T. Majewski 1987	Clytrinae
Laboulbenia	lacticae Thaxt. 1912	Alticinae
Laboulbenia	longipilis Haelew. & W. Rossi	unknown
Laboulbenia	macarthurii Balazuc 1971 (= $papuana$ Thaxt. 1914) ^b	Criocerinae
Laboulbenia	maecolaspidis W. Rossi & Cesari 1979	Eumolpinae
Laboulbenia	manobiae Thaxt. 1914	Alticinae
Laboulbenia	metrionae Balazuc 1978	Cassidinae
Laboulbenia	minuscula (Thaxt. 1914) Thaxt.1915	Alticinae
Laboulbenia	monocestae Thaxt. 1914	Galerucinae
Laboulbenia	monoleptae Balazuc 1975	Galerucinae
Laboulbenia	motasii Balazuc 1975	Alticinae
Laboulbenia	nisotrae (Thaxt. 1914) Thaxt. 1915	Alticinae
Laboulbenia	nodostomatis Thaxt. 1914	Eumolpinae
Laboulbenia	obesa (Thaxt. 1914) Thaxt. 1915	Alticinae
Laboulbenia	oedionychi Thaxt. 1914	Alticinae
Laboulbenia	opima W. Rossi 2011	Eumolpinae
Laboulbenia	parasyphraeae W. Rossi & Bergonzo 2008	Alticinae
Laboulbenia	partita Thaxt. 1914 (= Eumisgomyces dohrnii Speg. 1915)	Alticinae

TABLE I. Laboulbeniales described thus far on Chrysomelidae, including the three species described in this paper (in boldface)

Genus	Species	Host subfamily ^a
Laboulbenia	paumomuae (Speg. 1915) Balazuc 1975	Galerucinae
Laboulbenia	percolaspidis A. Weir & W. Rossi 2001	Eumolpinae
Laboulbenia	pfisteri Haelew. & W. Rossi	Eumolpinae
Laboulbenia	philippina Thaxt. 1914	Eumolpinae
Laboulbenia	podontiae Thaxt. 1914	Alticinae
Laboulbenia	rhinoceralis Thaxt. 1914	Criocerinae
Laboulbenia	rigidula Speg. 1917	Chrysomelinae
Laboulbenia	sebaetheos Speg. 1915	Alticinae
Laboulbenia	skirgielloae Balazuc 1975	Alticinae
Laboulbenia	systenae Speg. 1917	Alticinae
Laboulbenia	temperei Balazuc 1973	Alticinae
Laboulbenia	trinidadensis (Thaxt. 1914) Thaxt. 1915	Alticinae
Laboulbenia	yurikoi K. Sugiy. & T. Majewski 1985	Alticinae
Rickia	borneoensis K. Sugiy. & Hiroy. Yamam. 1982	Galerucinae

^a Many entomologists now agree that the tribe Alticini belongs in the subfamily Galerucinae (Bouchard et al. 2011). However, the relationship between these two leaf-beetle groups is not yet clear and its study represents an area of active research regarding Chrysomelidae phylogeny (Biondi and D'Alessandro 2012). Therefore, to facilitate understanding, we have decided to adopt the "traditional" taxonomy of these host beetles from the literature on Laboulbeniales, in which these insects were treated as a subfamily (Alticinae).

^bWhen Thaxter (1914) described *Laboulbenia papuana* on *Lema* sp., he had already used this name for a species occurring on a ground beetle (family Carabidae) from New Guinea (see Thaxter 1899, p 193). It was only until Balazuc (1971) that this "mistake" was reported and solved.

distinctly shorter. Length from foot to perithecial apex about $373 \,\mu\text{m}$. Perithecium $122-127 \times 30-33 \,\mu\text{m}$. Outer appendage $808-940 \,\mu\text{m}$.

Commentary: Laboulbenia longipilis is easily distinguished from any other species parasitic on Chrysomelidae by the long outer appendage and the elongate habit. Because of these striking characters we decided to describe it, although Thaxter gave no information about the host taxonomy, except that it was a chrysomelid. On the other hand, the number of "small yel[low], flat" species of Chrysomelidae from Cameroon may not be very high. We maintained the name of the species written on the label by Thaxter himself.

Laboulbenia pfisteri Haelew. & W. Rossi, sp. nov. FIG. 2D

MycoBank MB809150

Typification: MADAGASCAR, *s. d.*, *s. c.*, on the elytra of "stout pale" *Ivongius* sp. (subfamily Eumolpinae), slide FH 00313335 (HOLOTYPE). Eleven mature and four immature thalli were examined.

Etymology: Named for Donald H. Pfister, mycologist and curator of the Farlow Herbarium at Harvard University, in honor of his exceptional service in the curation of the fungal collection.

Description: Thallus short and compact, wholly brown with much paler cells I and II and appendages. Cell I relatively short and tapering to the foot. Cell II slightly longer, gradually broadening from below upward. Cell III short and compact, about as long as it is wide. Cell IV about the same size as cell III. Cell V small, not reaching cell III, distinctly paler than the surrounding cells. Insertion cell blackish and thick, attached to the posterior margin of the perithecial wall. Outer appendage consisting of two superimposed, almost hyaline cells, separated by a black septum, and of three simple and robust branches, one of which is borne from the distal inner angle of the lower of these two cells, the other two from the upper cell. A second blackish septum is found at the base of the outermost branch. Inner appendage consisting of a small basal cell, which gives rise to two small cells, slightly longer than broad, each bearing one, rarely two antheridia; the latter are flask-shaped and unusually dark brown. Cell VI small and almost isodiametric. Perithecium stout, almost wholly free, hardly inflated, slightly enlarged in its upper portion, strongly tapered at the blackish tip, the apex distinctly turned outward, with three rounded lips, the inner of which is distinctly larger and bearing small papillae. Length from foot to perithecial apex 135-155 µm. Perithecium $65-83 \times 25-33 \mu m$. Longest appendage 225 µm.

Commentary: Only five species of Laboulbenia have been described so far on Eumolpinae. These are L. nodostomatis, L. philippina, L. maecolaspidis, L. percolaspidis and L. opima. Laboulbenia pfisteri is easily distinguished from the latter three South American species by cells III and IV, which are undivided in these species while they are clearly separated in the new

TABLE I. Continued

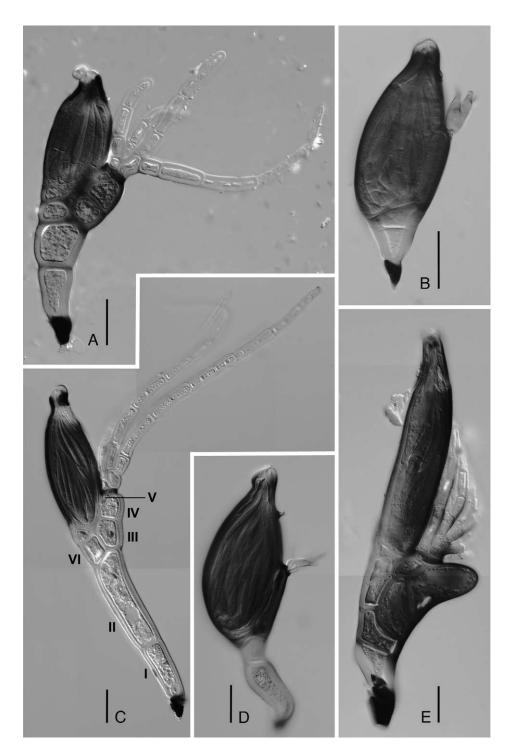


FIG. 1. A. Laboulbenia nodostomatis Thaxt. (FH 00313315). B. L. minuscula (Thaxt.) Thaxt. (FH 00313327). C. L. *philippina* Thaxt. (TYPE, FH 00313323), with labeled cells I to V of the receptacle and the basal cell of the perithecium (VI). D. L. obesa (Thaxt.) Thaxt. (TYPE, FH 00313337). E. Laboulbenia macarthurii Balazuc (formerly L. papuana Thaxt.) (FH 00313329). Scale bars = 25 μm.

species (Thaxter 1914, Rossi and Cesari Rossi 1979, Weir and Rossi 2001, Rossi 2011). It is also clearly different from *L. philippina*, which has an elongate habit and long branchlets (up to 470 μ m) on both the outer and inner appendages (FIG. 1C). *Laboulbenia* *nodostomatis* (FIG. 1A) shares with *L. pfisteri* a short habit, but has a bifurcate outer appendage and above all the inner appendage consists of two branchlets, which are absent in the new species. Thaxter provided no name on the slide label.

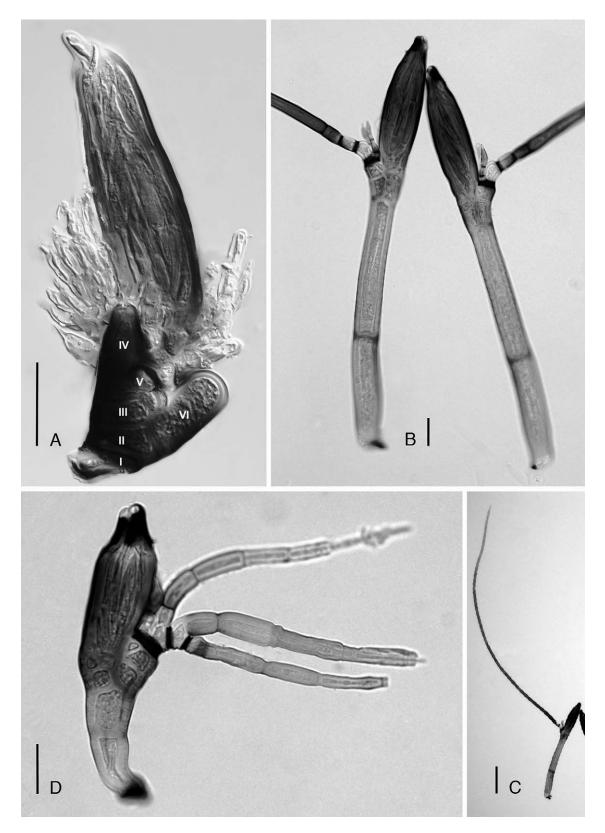


FIG. 2. A. *Laboulbenia bilobata* sp. nov. (PARATYPE, FH 00313317), with labeled cells I–V of the receptacle and the abnormally protruded basal cell of the perithecium (VI). B, C. *L. longipilis* sp. nov. (HOLOTYPE, FH 00313334). D. *L. pfisteri* sp. nov. (HOLOTYPE, FH 00313335). Scale bars: A, B, D = $25 \mu m$; C = $100 \mu m$.

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