# *Laboulbenia slackensis* and *L. littoralis* sp. nov. (Ascomycota, Laboulbeniales), two sibling species as a result of ecological speciation

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**Abstract:** *Laboulbenia littoralis* is described from the halobiont *Cafius xantholoma* (Coleoptera, Staphylinidae); it previously was misidentified and not properly documented. Morphologically the new species belongs to a group of carabidicolous taxa similar to *Laboulbenia pedicellata* and especially *Laboulbenia slackensis*. It is generally accepted that the specificity of Laboulbeniales is based on their need for substances from the host. In this relatively strict context, shifts between unrelated hosts are difficult to explain. We present morphological and ecological evidence supporting the hypothesis that these fungi are capable of shifting between unrelated hosts as long as they share the same habitat. Adaptation to a particular environment, combined with a reduced dependence from specific nutrients of the host, explains the proposed interfamilial host shift.

*Key words:* *Cafius*, ecological specificity, host shift, parasitic fungi, plurivory, reproductive isolation, taxonomy

## INTRODUCTION

Laboulbeniales are obligate ectoparasites associated with arthropods. The order consists of 140 genera (Rossi and Santamaría 2012) and about 2050 species, 80% of them reported from Coleoptera (Weir and Blackwell 2005). Among these, the Carabidae (ground beetles) and Staphylinidae (rove beetles) are the most common hosts, accounting for 17 and 47 genera of Laboulbeniales respectively (Frank 1982, Tavares 1985, Rossi and Santamaría 2008). With more than 600 species (Kirk et al. 2008, Rossi 2011) the genus *Laboulbenia* Mont. & C.P. Robin is the largest within the Laboulbeniales.

Most Laboulbeniales have a high degree of host specificity (Benjamin 1971, Tavares 1985). Based on the phylogenetic relatedness of taxa within a host range, specificity has been attributed generally to the need for certain substances from the host (Scheloske 1969, Tavares 1979). Studies directed at understanding the mechanisms governing host specificity and explaining observed host ranges have been limited in part because these fungi can be manipulated only by growing infected insect colonies and artificially introducing a foreign host. An alternative way to investigate host specificity is to examine unrelated insects living in the same habitat. Laboulbeniales infecting co-habiting and stenotopic hosts, which are characterized by having a very strict habitat choice, are interesting in terms of host specificity and ecological speciation. The latter, according to the modern evolutionary synthesis, is the result of the micro-evolutionary process of divergent natural selection between populations exploiting different resources or environments, ultimately leading to reproductive isolation (e.g. Mayr 1942, Dobzhansky 1951, Schluter 2000).

Host and parasite phylogenies often align as a result of codivergence (shared history) (Legendre et al. 2002, Downie and Gullan 2005, Futuyma 2005, Page 1994) but explaining how morphologically similar Laboulbeniales can occur on phylogenetically unrelated hosts is challenging. Field data indicate that plurivorous Laboulbeniales, such as *Laboulbenia ecitonis* G. Blum, can be found only on unrelated hosts occupying the same ecological niche, including Staphylinidae, Histeridae, mites (Acari, Mesostigmata, Uropodidae) and ants (Hymenoptera, Formicidae) (Benjamin 1971). Plurivory is still unexplained and many factors are thought to be involved, including accidental transmission (Scheloske 1969) and adaptation to common nutrients available from the cohabiting hosts (Scheloske 1969, Benjamin 1971). Rossi (2011) and Arndt et al. (2003) suggest that host shifts of *Laboulbenia* species have occurred between Cicindelinae and other Carabidae living in the same habitat, resulting in a number of morphologically similar taxa. Benjamin (1971) suggested in this context that ''successful colonization of a new host is probably a rare event, but it is possible, even likely, that fortuitous parasite transfer has played a role in the evolution of new species groups and even genera.'' Mutations also are thought to allow host shifts, yielding cryptic species with different nutritional requirements (Rossi 2011). The transmission

experiments from Cépède and Picard (1907) showed that *L. vulgaris* Peyr. and *L. pedicellata* Thaxt. (as *L. gracilipes* Cépède & F. Picard) were not able to interchange hosts, even though the hosts belong to the same genus (*Bembidion* Latreille 1802). The major effect of rearing conditions in transmission experiments with Laboulbeniales has been shown in experiments with *L. slackensis* Cépède & F. Picard, which under natural conditions is a host-specific parasite, apparently restricted to the salt mash-inhabiting *Pogonus chalceus* (Marsham, 1802) (De Kesel 1993, 1996). Nonetheless, data from transmission experiments show that it can infect several other Carabidae; it was demonstrated that the development of thalli on these hosts was influenced by the rearing conditions rather than by the host species (De Kesel 1996).

To date we know, from both field observations and laboratory experiments, that the habitat (imposed or chosen by the host) seems to determine the success of ectoparasites. This observation is an important element in considering the ecological specificity of Laboulbeniales (Scheloske 1969, Majewski 1994b, De Kesel 1996). It helps to understand the difference and meaning of a usual host and an occasional host, including why in certain habitats a parasite can be found on an atypical host. Altogether the habitat preference of the host as an important driving force behind specialization and speciation of Laboulbeniales also is recognized. With this in mind we searched for *L. slackensis* in its natural habitat (coastal environments and saltmarshes), aiming to find it on a number of Carabidae. Instead we found infected populations of the staphylinid beetle *Cafius xantholoma* bearing thalli of the newly described *Laboulbenia littoralis*, morphologically similar to *L. slackensis*.

The present paper deals with a number of morphologically similar *Laboulbenia* species occurring on unrelated hosts from these coastal habitats. Our results provide new evidence for habitat-related interfamilial host shifts in the genus *Laboulbenia*.

## Materials and methods

*Morphology.*—Insects were obtained from seaweed and plant debris from above the high water mark along east coast beaches in Belgium and the Netherlands. At each site 40–80 L debris were carefully transferred to a bag and transported to the laboratory. The samples were placed in a large Berlese-Tullgren funnel for 24 h (Domingo-Quero and Alonso-Zaraga 2010). Insects were collected and stored in 90% ethanol. Target hosts were sorted and identified to sex. Screening for infection and removal of thalli was done at 50× magnification with an Olympus SZ61 stereomicroscope. Thalli were mounted in Amann solution (Benjamin

1971), and slides were sealed with transparent fingernail polish. Both insects and microscope slides are deposited at the National Herbarium of Belgium (BR). French and Italian host specimens were studied at the American Museum of Natural History (New York); respective microscope slides are deposited at the Farlow Herbarium, Harvard University (FH). Drawings and measurements were made with an Olympus BX51 light microscope with drawing tube, digital camera and AnalySIS 5 imaging software (Soft Imaging System GmbH). Host taxonomy and classification follows Vorst (2010), unless otherwise cited.

*Biometrics.*—Differences in thallus dimensions and shapes were tested following De Kesel & Van den Neucker (2005). We measured 15 variables and four ratios from at least 30 mature thalli of each species. These parameters were used (abbreviations and explanations are given between parentheses): total thallus length (TL, from foot to perithecial apex); length of the receptacle (RL, from foot to insertion cell); perithecium length (PL, without cell VI); perithecium width (PW); height of cell I (cell I); height of cell II (cell II); height of cell III (cell III); height of cell IV (cell IV); height of the paraphysopodium (par); width of the insertion cell (IC) and length of the appendages (app, intact whenever possible). The length of these septa was measured: septum I–II, septum II–VI; septum II–III; septum of cell III with cells IV and V. To better understand shapes and proportions, these ratios also were calculated: PL/PW; cell I/cell II; cell IV/par and II–VI/II–III. Differences were tested with Student's *t* test (Sokal and Rohlf 1981) with Statistica 10.0. Host species was used as a grouping variable. The significance value was $P < 0.05$. Thalli included in the analysis came from all parts of host integument, regardless of host species or sex.

## Results

*Statistical analysis.*—Significant differences between *Laboulbenia littoralis* and *L. slackensis* were observed for parameters, PL, PW, cell I, cell II, cell III, cell IV, par, IC, app, I–II, II–VI, II–III, III– (IV+V); and ratios, PL/PW, cell I/cell II, cell IV/par, II–VI/II–III (Table I). Tested differences were not significant for two remaining parameters, TL and RL.

## Taxonomy

**Laboulbenia littoralis** De Kesel & Haelew., sp. nov.

Fig. 1

MycoBank MB801461

Illustrations: Balazuc (1974 Fig. 18, ut *L. cafii*), De Kesel (1997 Pl. 20 and 1998 Pl. 1.5 ut *L. cafii*).

*Diagnosis.*—Thallus resembling *Laboulbenia slackensis* but stouter and with the paraphysopodium swollen and equal or taller than cell IV, twice as tall as the andropodium. Dorsal side of the receptacle never straight, always outwardly and prominently bent or kinked at the junction of cells II and III. Appendages

TABLE I. Results of the Student's *t* test to compare parameters and ratios between thalli of *L. littoralis* and *L. slackensis*

| Parameters | *L. littoralis* | | *L. slackensis* | | *t* value | F ratio variances | df[a] | P[a] |
| | Mean (μm) | St. dev. | Mean (μm) | St. dev. | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| TL | 294.56 | 31.98 | 280.74 | 38.99 | 1.56 | 1.49 | 63 | 0.1227 |
| RL | 193.49 | 22.29 | 189.00 | 29.34 | 0.70 | 1.73 | 63 | 0.4888 |
| PL | 145.83 | 14.84 | 126.70 | 15.56 | 5.07 | 1.10 | 63 | 0.0000 |
| PW | 74.12 | 9.03 | 55.58 | 8.21 | 8.65 | 1.21 | 63 | 0.0000 |
| cell I | 51.01 | 8.02 | 63.00 | 9.21 | −5.60 | 1.32 | 63 | 0.0000 |
| cell II | 62.14 | 10.41 | 53.54 | 13.09 | 2.94 | 1.58 | 63 | 0.0046 |
| cell III | 55.57 | 7.68 | 44.60 | 9.07 | 5.27 | 1.40 | 63 | 0.0000 |
| cell IV | 24.12 | 3.75 | 26.42 | 4.39 | −2.28 | 1.37 | 63 | 0.0261 |
| par | 30.59 | 3.14 | 18.26 | 3.00 | 16.07 | 1.10 | 62 | 0.0000 |
| IC | 32.33 | 2.97 | 22.25 | 2.47 | 14.84 | 1.44 | 63 | 0.0000 |
| app | 81.45 | 17.27 | 143.07 | 56.06 | −5.16 | 10.53 | 48 | 0.0000 |
| I-II | 39.68 | 3.70 | 31.33 | 3.63 | 9.18 | 1.04 | 63 | 0.0000 |
| II-VI | 45.77 | 5.24 | 38.09 | 5.02 | 6.04 | 1.09 | 63 | 0.0000 |
| II–III | 24.59 | 4.54 | 17.18 | 3.11 | 7.66 | 2.13 | 63 | 0.0000 |
| III–(IV+V) | 33.79 | 3.27 | 29.00 | 3.74 | 5.51 | 1.31 | 63 | 0.0000 |
| Ratios | | | | | | | | |
| PL/PW | 1.98 | 0.11 | 2.29 | 0.19 | −8.25 | 3.22 | 63 | 0.0000 |
| cell I/cell II | 1.24 | 0.23 | 0.86 | 0.22 | 6.80 | 1.10 | 63 | 0.0000 |
| cell IV/par | 0.79 | 0.12 | 1.46 | 0.21 | −15.57 | 3.11 | 62 | 0.0000 |
| II-VI/II-III | 1.92 | 0.40 | 2.26 | 0.37 | −3.65 | 1.17 | 63 | 0.0005 |

[a] The degrees of freedom (df) and *P* values are provided. Differences are considered significant when $P < 0.05$.

never exceeding the tip of the perithecium; the latter with large, black preostiolar spots.

*Holotype.*—BELGIUM, WEST-VLAANDEREN: Knokke-Heist, Zwin estuary, 28 Apr 2012, parasite on tibia of male *Cafius xantholoma* (Gravenhorst, 1806) (Coleoptera, Staphylinidae, Staphylininae, Staphylinini, Philonthina), *A. De Kesel 5152b* (BR-MYCO 171396-94).

*Etymology.*—From the Latin term *littoralis* = coastal, of or belonging to the coastline [Latin *lītus* = seashore].

*Description.*—Thallus yellow brownish, 225–350 μm long. Receptacle 105–175 μm long, not punctuate, robust, dorsal side outwardly bent or kinked at the junction of cells II and III. Cell I triangular, 35–65 μm long and 35–45 μm wide. Cell II variable in length, 45–90 μm long, up to 1.5 times longer than cell I, 35–45 μm wide at the base, broadening upward, septum II–VI and II–III becoming 35–60 μm and 17–32 μm wide respectively. Cell III about 1.5–2 longer than broad, always slightly shorter than cell II; septum III–(IV+V) often arched or kinked and longer (30–38 μm) than septum II–III. Cells IV and V about the same size and shape, slightly higher than broad, 18–37 μm long. Septum IV–V perpendicular to the insertion cell, never oblique, mostly straight, shorter than the posterior wall of cell IV. Insertion cell black, relatively thick, with age becoming constricted near the posterior side, 30–39 μm. Appendages, both inner and outer, short, forming a dense cluster in older thalli, 70–90 μm long, not exceeding the perithecial apex. Paraphysopodium large, 21–40 μm long, often slightly inflated, up to two times longer than broad, of the same length or longer than cell IV; its outer branch simple, short, always separated by a thick, black and constricted septum, its inner branch sterile and simple, with normal septum. Andropodium isodiametric in mature thalli, at most half the length of the paraphysopodium, producing 1–3 short and slightly inflated branches, each supporting one or two single and moderately pigmented antheridia. Cell VI wider than long, its base twice as long as the base of cell III. Perithecium 105–175 × 50–85 μm, ovate, straight, smooth, two-thirds free, concolorous with the receptacle, mature specimens with large black preostiola spots; perithecial apex asymmetrical, mostly hyaline, with slightly larger and rounded posterior lips and inconspicuous papillae. Spores 63–70 μm long, two-celled, spindle-shaped, with slime sheath, hyaline.

*Specimens and distribution.*—Forty-nine specimens, all on *Cafius xantholoma* (Gravenhorst, 1806) (Coleoptera, Staphylinidae, Staphylininae, Staphylinini, Philonthina).

BELGIUM. WEST-VLAANDEREN: Knokke, coastal, no date, *C. van Volxem* in coll. A. Collart, L103, L104, L105, L106; Knokke-Heist, Zwin estuary (51°21′59.76″N
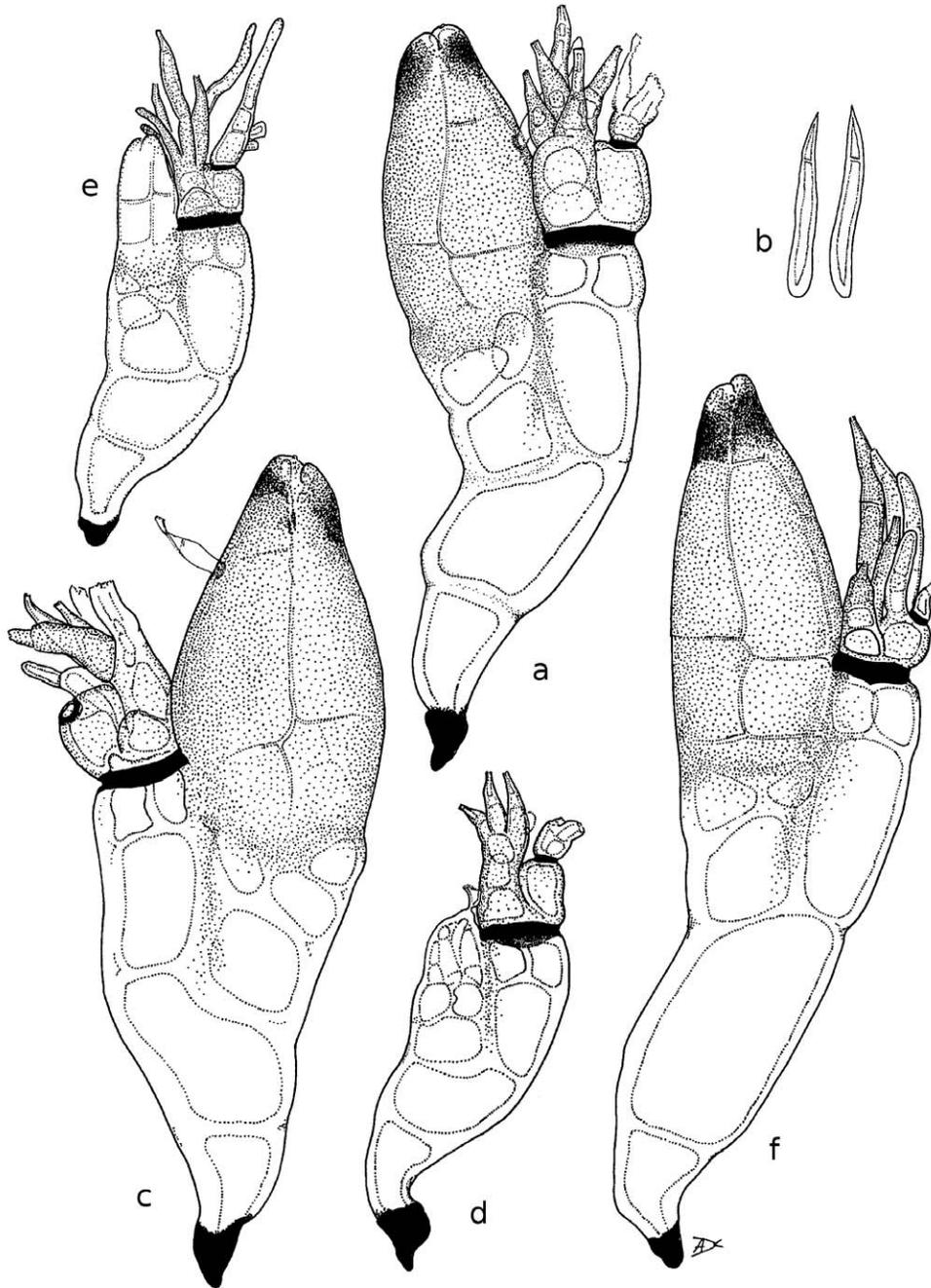
FIG. 1. *Laboulbenia littoralis* from *Cafius xantholoma*. a. Mature thallus from tibia (HOLOTYPE, ADK5152b), b. spores (ADK5152a), c. mature thallus from abdominal tergite, d. juvenile thallus from right elytron (ADK5161), e. juvenile thallus from the prothorax (L103), f. mature thallus from the legs (L106). Bar = 100 μm.

− 3°21′53.57″E), in seaweed and plant debris on the beach, 28 Apr 2012, *A. De Kesel 5148* (PARATYPE), *A. De Kesel 5151a, b* (PARATYPES), *A. De Kesel 5152a*, b (PARATYPES); ibid., 17 May 2012, *A. De Kesel 5155, A. De Kesel 5156, A. De Kesel 5159*.

THE NETHERLANDS. ZEELAND: Nieuwe Sluis (51°24′21,14″N, 3°30′19,08″E), in seaweed bed on a small protected beach near a lock, 9 Apr 2012, *A. De Kesel 5144*.

FRANCE, VENDÉE: mentioned by Balazuc (1974) as *Laboulbenia cafii*, from Pointe de l'Aiguillon (46°16′1.26″N, 1°12′15.59″E), no date, illustrated in Balazuc (1974, p 14 fig. 18); GRANVILLE, at the shore of the ocean, 1 Sep 1937, *M. Bernhauer*, in coll. American Museum of Natural History, *D. Haelew. 117a* (FH 00313193), *117b* (FH 00313194).

ITALY, VENICE: Lido sandbar, no date, *M. Bernhauer*, in coll. American Museum of Natural

History, *D. Haelew. 116a*, (FH 00313190), *116b* (FH 00313190), *116c* (FH 00313192).

*Host ecology and infection data.*—With 44 species listed within *Cafius* Stephens 1829 (sensu stricto), the host *C. xantholoma* belongs to the most species-rich genus of coastal Staphylinidae (Frank and Ahn 2011). It is a European species, sexually dimorphic, exclusively halobiont and the best investigated species in the genus. *Cafius xantholoma* is predacious both as adult and larva and occurs only in deep layers of seaweed beds. The species is capable of producing several generations per year (multivoltinism; Frank and Ahn 2011).

*Cafius xantholoma* reaches relatively high population densities in the seaweed and plant debris along the high water mark (up to 200 individuals per 25 L substrate). Large samples taken in spring (Apr–May) have a parasite prevalence of 10.3% (58 infected beetles out of a total of 559). Parasite prevalence is much higher in males. Females are usually infected only on the tergites, males on their prosternum, abdomen and legs, especially the tibia. There is no evidence for assuming growth-position related morphological differences.

## DISCUSSION

*Morphology.*—*Laboulbenia littoralis* is similar to *L. pedicellata*, a morphologically variable taxon specializing on Carabidae from the subfamilies Trechinae (*Bembidion* Latreille 1802 and allied taxa) and Scaritinae (*Dyschirius* Bonelli 1810). *Laboulbenia pedicellata* is only one member of a well defined group of morphologically similar taxa including, among others, *L. clivinalis* Thaxt., *L. gregaria* W. Rossi, *L. slackensis*, *L. lichtensteinii* F. Picard, *L. parriaudii* Balazuc ex Santam., *L. patrata* Thaxt. and *L. littoralis*. All are recognized by cells IV and V being of equal height, the septum IV, V perpendicular on cell III and a dark, constricted septum separating the paraphysopodium from the abaxial branchlet of the outer appendage. These taxa are found on ripicolous Carabidae (*L. clivinalis, L. slackensis, L. lichtensteinii*), Staphylinidae (*L. gregaria, L. parriaudii, L. littoralis*) and Elateridae (*L. patrata*).

Of the 29 *Laboulbenia* species recorded on Staphylinidae (TABLE II), *L. cafii* and *L. parriaudii* are worth mentioning. All existing Belgian collections of *L. cafii,* taken from *C. xantholoma* (Collart 1945; De Kesel and Rammeloo 1992; De Kesel 1997, 1998) were examined and clearly belong to *L. littoralis*. Consequently *L. cafii* does not occur in Belgium. The illustrated French record as *L. cafii* on the same host (Balazuc 1974) also represents *L. littoralis*. There is no doubt that *L. littoralis* is different from *L. cafii*. Older thalli with severely damaged and deteriorated appendages however may be challenging to identify. It is important that young thalli be observed and compared. *Laboulbenia cafii* does not belong to the *L. pedicellata* group and, unlike *L. littoralis*, is a species that lacks the prominent differentiation of the inner and outer appendages. *Laboulbenia cafii*, taken from *Remus sericeus* Holme, 1837 (as *Cafius sericeus*), was illustrated by Santamaría (1998).

*Laboulbenia parriaudii* was reported from coastal staphylinid hosts, *Bledius arenarius* Paykull 1800 and *Bledius* sp. (Balazuc 1974, Santamaría 1998). This species also fits in the *L. pedicellata* group but differs from *L. littoralis* in having a distinctly asymmetrical perithecial apex and strongly differentiated posterior and anterior lips. The fact that cell III is strongly inflated and that the andropodium and paraphysopodium are dark brown clearly separates it from the new taxon.

Of all taxa reported on Staphylinidae and Carabidae, *L. littoralis* most closely resembles *L. slackensis*. The latter is known from Europe, Africa and Japan and is parasitic on the salt marsh-inhabiting carabid beetles, *Pogonus* Dejean 1821, *Pogonistes* Chaudoir 1871 and *Syrdenus* Dejean 1828 (Coleoptera, Carabidae, Trechinae) (Santamaría et al. 1991, Terada 1998). Compared to *L. slackensis* our data show that the new species has no significantly different average thallus (TL) and receptacle (RL) lengths. Because both belong to the *L. pedicellata* group, the specific differences between them need to be inferred from shapes and proportions within the thallus. A similar approach was used by De Kesel and Van den Neucker (2005) in an attempt to recognize and define forms in *L. flagellata* Peyr.

*Laboulbenia littoralis* is distinguished morphologically from *L. slackensis* by its more robust thallus with an outwardly bent or kinked dorsal side of the receptacle at the junction of cells II and III. This feature is supported by a significantly longer septum II–VI and septum II–III in combination with a significantly smaller ratio of these septa (II–VI/II–III) in *L. littoralis*. The state of these three parameters results in a differently shaped receptacle in both species, regardless of the length of thallus and receptacle or growth position. The bent receptacle of *L. littoralis* is typical and present already in young individuals. *Laboulbenia slackensis*, however, has an erect receptacle in which the dorsal side is straight to slightly concave. The robustness of *Laboulbenia littoralis* also is due to a significantly larger and wider perithecium and smaller PL/PW ratio. This means that, although larger and wider, the perithecium of *L. littoralis* is significantly less elongate than the one of

TABLE II.  *Laboulbenia* species parasitizing on Staphylinidae

| *Laboulbenia* species | Host genus (genera) | Host subfamily[a] | Reference |
|---|---|---|---|
| *achenii* Maire 1920 | *Achenium* | Paederinae | Maire 1920 |
| *atlantica* Thaxt. 1902 | *Lobrathium* | Paederinae | Santamaría et al. 1991 |
| *barbara* Middelh. & Boelens 1943 | *Philonthus* | Staphylininae | Majewski 1994 |
| *bergiana* Speg. 1917 | *Pinophilus* | Paederinae | Spegazzini 1917 |
| *bledii* Thaxt. 1902 | *Bledius* | Oxytelinae | Thaxter 1902 |
| *cafii* Thaxt. 1902 | *Cafius, Phucobius, Remus* | Staphylininae | Santamaría et al. 1991 |
| *cristata* Thaxt. 1892 | *Paederus* + related | Paederinae | Santamaría et al. 1991 |
| *dolicaontis* Maire 1920 | *Dolicaon, Leptobium* | Paederinae | Santamaría et al. 1991 |
| *dubia* Thaxt. 1902 | *Philonthus* | Staphylininae | Santamaría et al. 1991 |
| *geodromici* Baumgartner 1923 | *Geodromicus* [*Psephidonus*] | Omaliinae | Santamaría et al. 1991 |
| *gregaria*[b] W. Rossi | *Philonthus* (s.l.) | Staphylininae | Rossi 2011 |
| *gridellii* S. Colla 1926 | *Platystethus* | Oxytelinae | Colla 1926 |
| *jarrigei* Balazuc 1975 | *Lispinus* | Osoriinae | Balazuc 1975 |
| *kenyensis* W. Rossi & Santam. 2000 | *Mimogonus* | Osoriinae | Rossi & Santamaría 2000 |
| *lathropini* Thaxt. 1912 | *Lathropinus* | Paederinae | Thaxter 1912 |
| *lathropinicola* Speg. 1917 | *Lathropinus* | Paederinae | Spegazzini 1917 |
| *latonae* Thaxt. 1902 | *Pseudocryptobium* [*Latona*] | Paederinae | Proaño Castro & Rossi 2008 |
| *littoralis*[b] De Kesel & Haelew. | *Cafius* | Staphylininae | present paper |
| *micrandra* W. Rossi 2011 | *Lobrathium* | Paederinae | Rossi 2011 |
| *oedichiri* Thaxt. 1902 | *Oedichirus* | Paederinae | Thaxter 1902 |
| *oedodactyli* Thaxt. 1902 | *Oedodactylus* | Paederinae | Thaxter 1899 |
| *parriaudii*[b] Balazuc ex Santam. 1998 | *Bledius* | Oxytelinae | Santamaría 1998 |
| *philonthi* Thaxt. 1893 | *Philonthus* + related | Staphylininae | Santamaría 1998 |
| *platyprosopi* Thaxt. 1902 | *Platyprosopus* | Staphylininae | Thaxter 1902 |
| *quedii* Thaxt. 1893 | *Anaquedius* [*Quedius*] | Staphylininae | Thaxter 1893 |
| *richardii* W. Rossi & Santam. 2000 | *Phlaeopterus, Unamis, Vellica* | Omaliinae | Rossi & Santamaría 2000 |
| *stilicicola* Speg. 1914 | *Rugilus* [Stilicus] | Paederinae | Santamaría 1998 |
| *taenodemae* Thaxt. 1902 | *Taenodema* | Paederinae | Thaxter 1902 |
| *trogacti* W. Rossi 2011 | *Trogactus* | Oxytelinae | Rossi 2011 |

[a] Host classification corresponds with Frank 1982.
[b] Members of the *Laboulbenia pedicellata* group.

*L. slackensis.* Robustness is also seen in the significantly wider upper receptacle of *L. littoralis.* A prominent and easily seen feature is the significantly larger paraphysopodium. Moreover, mature *L. slackensis* often have a perithecial stalk cell (VI) that is longer than broad, an almost evenly pigmented thallus and appendages extending well beyond the perithecial apex.

*Ecological specificity.*—*Laboulbenia littoralis* on *Cafius xantholoma* is collected less than 50 m from salt marshes with vast populations of *L. slackensis* infecting *Pogonus chalceus.* When several morphologically close *Laboulbenia* species infect unrelated hosts in a similar habitat, questions arise about host specificity, transmission, reproductive isolation and identity. We consider *L. littoralis* and *L. slackensis* much more closely related than their hosts (staphylinid versus carabid beetle respectively). Because *C. xantholoma* and *P. chalceus* are both halobiont, locally abundant and mobile, we assume that opportunities exist for

ecological shift from one host to another. In this particular context transmission experiments might be helpful to confirm the identity and the specificity of both *L. slackensis* and *L. littoralis.* Controlled transmission experiments have resulted in successful transfer of *L. slackensis* from *Pogonus chalceus* to other Carabidae but attempts to transfer it to Staphylinidae failed (De Kesel 1996). Although environmental conditions were optimal for the fungus, we think the Staphylinidae tested may not have been sufficiently salt tolerant. With the discovery of an interesting staphylinid host (*C. xantholoma*) from a saline habitat, experiments aiming to transfer *L. slackensis* and *L. littoralis* between Carabidae and Staphylinidae might be successful. In such an event, the morphology of all thalli obtained should be carefully checked and compared with all other species from the *L. pedicellata* group. Because the host and the position on the host are known to induce morphological variation (Tavares 1985, Santamaría and Faille 2009), a molecular analysis including as

many taxa as possible (i.e. from inside and outside the *L. pedicellata* group) is indispensable. This approach will help to define and delimit boundaries between species and provide evidence about the effect of the host species as well as the growth site on thallus morphology.

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