

BELGIAN RECORDS OF LABOULBENIALES FROM AQUATIC INSECTS (3) – SPECIES FROM *DRYOPS LURIDUS*

ANDRÉ DE KESEL¹ & DANNY HAELEWATERS²

¹ Botanic Garden Meise, Domein van Bouchout, 1860 Meise, Belgium (adk@br.fgov.be)

² Department of Organismic and Evolutionary Biology, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138, USA

Summary

Data and illustrations are presented on *Cantharomyces denigratus*, *Cantharomyces italicus*, and *Helodiomyces elegans*. All three taxa are new for Belgium and were exclusively found on the aquatic beetle *Dryops luridus* (Coleoptera, Dryopidae). Although the parasites can occur simultaneously on a single host specimen, the two species of *Cantharomyces* show a distinctive distribution pattern on male and female hosts. The gender related infection pattern of *Cantharomyces denigratus* cannot be explained by copulation of the host. Two opposing hypothesis are given as to whether *C. denigratus* and *C. italicus* should be considered conspecific. A lectotype for *C. denigratus* is indicated.

Samenvatting

Dit artikel presenteert gegevens en illustraties van *Cantharomyces denigratus*, *Cantharomyces italicus* en *Helodiomyces elegans*. Deze drie parasieten zijn nieuw voor België en werden uitsluitend gevonden op de waterkever *Dryops luridus* (Coleoptera, Dryopidae). Hoewel de drie soorten tegelijkertijd kunnen voorkomen op één individu, vertonen beide *Cantharomyces* soorten een matig tot sterk verschillend distributiepatroon op de mannelijke en vrouwelijke gastheer. *Cantharomyces denigratus* vertoont een infectiepatroon dat niet verklaard kan worden door transmissie tijdens copulatie van de gastheren. Twee hypothesen worden gegeven om te verklaren of *C. denigratus* en *C. italicus* twee aparte soorten zijn of eerder groeivormen van slechts één soort.

Keywords: Laboulbeniales, *Cantharomyces*, *Helodiomyces*, position specificity, growth forms, *Dryops*.

Introduction

In two previous papers (De Kesel & Werbrouck 2008, De Kesel & Haelewaters 2012), nine species of Laboulbeniales from aquatic beetles were reported from the Waelenhoek nature reserve (Niel, Belgium). Further sampling and investigation at this site has revealed that the host *Dryops luridus* (Erichson, 1847) (Coleoptera, Dryopidae) is often simultaneously infected with three parasite species belonging to two different genera, i.e. *Helodiomyces* F. Picard and *Cantharomyces* Thaxter. All three species are highly host-specific and were not yet recorded from Belgium. In this paper we present descriptions and illustrations of these three taxa, as well as host-gender related distribution patterns. Additionally, because Thaxter (1931) did not specify a type specimen for *C. denigratus*, we decided to examine Thaxter's original material and designate a lectotype.

Materials and methods

Detailed information on the collecting site, sampling, storing, and identifying parasites is given in De Kesel & Werbrouck (2008). Identity of the host and sex determination was done using Drost *et al.* (1992). For specific nomenclature, terminology, or extensive iconography and receptacle cell numbering of *Cantharomyces* and *Helodiomyces*, we refer to Santamaría (2003) and Tavares (1985). Drawings were made using an Olympus BX51 with drawing tube.

Thallus density was measured following a method described in De Kesel (1995). Thallus positions of *Cantharomyces italicus* and *C. denigratus* were determined using a stereoscope (at 50×). All positions on infected specimens were charted separately and combined into a cumulative thallus distribution map for both sexes (fig. 5, dorsal and ventral view). Macro images

with high depth of field were obtained by focus stacking using a Canon 5D mkII with MP-E65mm macro lens and merging the images with Zerene Stacker software (Pmax).

Results and descriptions

Cantharomyces denigratus Thaxter.

Mem. Am. Acad. Arts Sci., 16 (1): 27 (1931)

Select. icones: Thaxter 1931 (Pl. I figs. 1-2); Siemaszko & Siemaszko 1933 (Pl. X fig. 6); Santamaría 1992 (figs. 5-7); Majewski 1994 (Pl. 105: 6-9); Santamaría 2003 (fig. 18). **Fig. 1a-f.**

Thallus pale and blackish brown, 141-173 µm in length. Receptacle composed of three cells. Cell I small, inflated, pale to almost hyaline, distally black. Cell II obtriangular, twice as high as cell I, ventral side (in left view) s-shaped, dorsal side convex, entirely black except for the area under cell VI. Cell III broad, 2× wider than high, entirely brownish, the lower abaxial side blackened. Primary appendage simple, tapering upwards, basal cell trapezoidal, pale brown, with laterally build in antheridium, apically carrying a simple branch composed of a short series of more cylindrical and hyaline cells. Perithecial stalk (cell VI) hyaline, slightly higher than cell III, distinctly constricted above the base, broadening upwards. Basal cells of the perithecium not clearly defined. Perithecium 70-92 × 33-43 µm, pale brownish, sub-symmetrical, ovoid, broadest in the middle, tapering towards the rounded apex; abaxial pair of apical wall cells distally wider than the adaxial ones, ostiolum hyaline, pointing in dorsal direction. Ascospores fusiform, two-celled, hyaline, with slime sheath, thicker at the base of the larger cell, 42-47 × 5.0-5.8 µm.

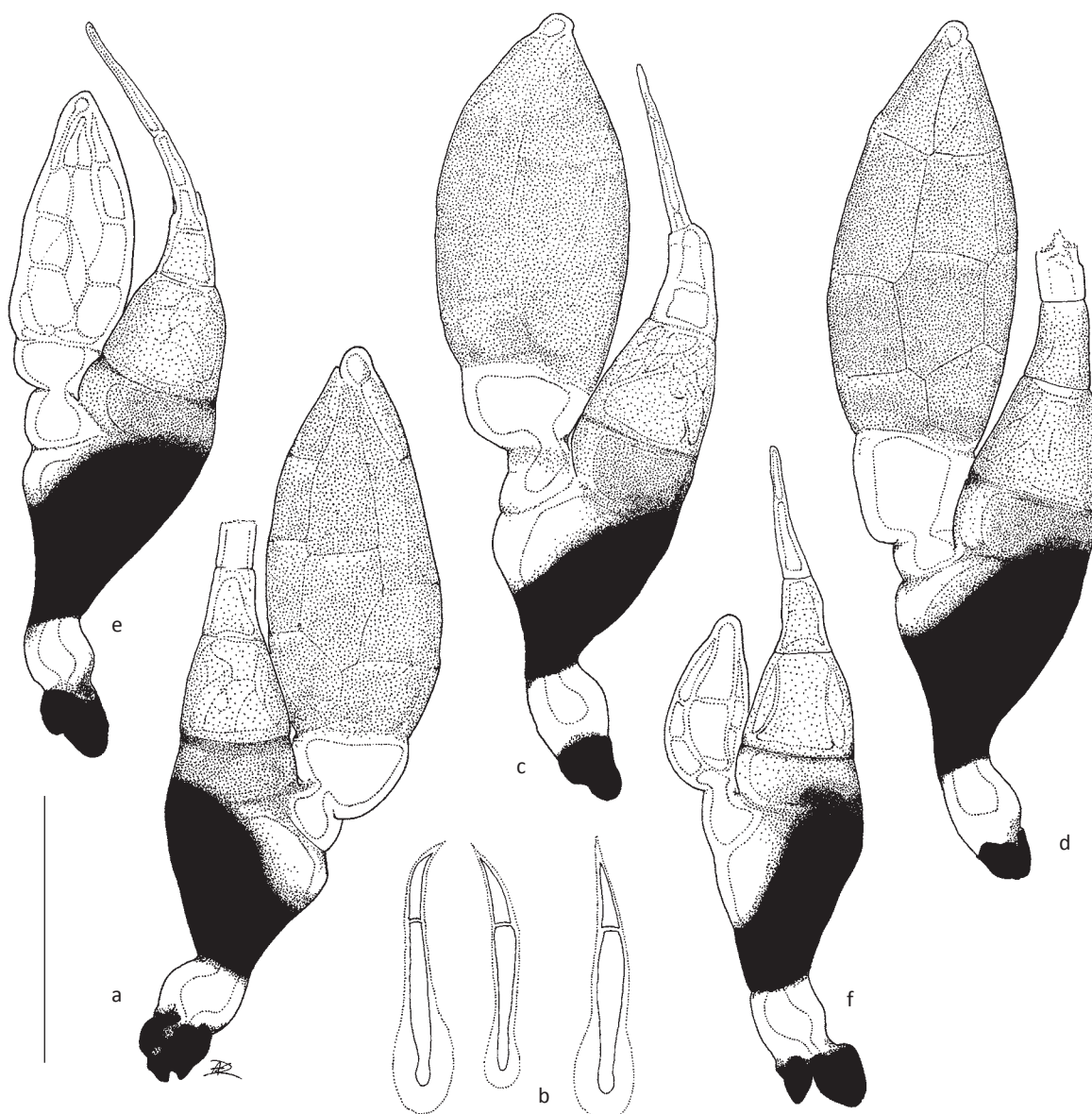


Fig. 1. *Cantharomyces denigratus* Thaxt., taken from *Dryops luridus*. **a.** mature thallus from antenna (A. De Kesel 6138b); **b.** spores with slime sheath (A. De Kesel 6138b); **c.** & **d.** mature thalli from abdominal sternite (A. De Kesel 6154); **e.** young thallus from abdomen (A. De Kesel 6149a); **f.** young thallus from abdomen (A. De Kesel 6149b). Scale bar = 50 µm.

Studied material: On *Dryops luridus* (Erichson, 1847), Niel (B), Walenhoek, in ponds (old clay-pits) and their edges lined with trees, 10.vii.2013, A. De Kesel 6138(a,b); ibidem, 21.viii.2014, A. De Kesel 6144, 6145, 6147, 6165, 6167; ibidem, 28.viii.2014, A. De Kesel 6149(a,c), 6163; ibidem, 5.ix.2014, A. De Kesel 6154, 6155(b).

Lectotype

ENGLAND, Hampshire County, New Forest National Park, vii.1911, F. Muir, on *Dryops griseus* (Erichson, 1847) [as *Parnus griseus*], Thaxter 2116, slide FH848 (5 thalli from tip abdomen).

Specificity and geographical distribution

Found on several species of *Dryops* Olivier, 1791 (Coleoptera, Dryopidae). To date only reported from Europe: England (type), Poland, Ukraine, Sweden, and Spain (Huggert & Eriksson 2010).

Infection pattern and transmission

We confirm Majewski's (1994) and Santamaría's (2003) observations that *Cantharomyces denigratus* occurs much more frequently on males than on females (fig. 4, 15/4). We found an infection frequency in females of 4/11 with a thallus density of just 4 immature thalli on 4 individuals. Males have a much higher infection frequency (fig. 4, 15/17) with a thallus density of 66 thalli on 15 individuals. Females carry *Cantharomyces denigratus* in various places (fig. 5), once on the last abdominal sternite and only occasionally on the distal part of the elytra. Males, on the other hand, are predictably infected on the last abdominal sternite and to a lesser degree on the prothorax, pronotum, legs, and antenna. The morphology of *Cantharomyces denigratus* seems independent of host gender and position on the host.

The observed infection pattern of *C. denigratus* (fig. 5)

is deeply gender related. In general, gender related infection patterns are caused by spore transmission during copulation. Transmission occurs mainly between infected body parts that touch during mating behavior, hence leading to a different thallus distribution on males and females. How infections with *Cantharomyces denigratus* are systematically generated on the abdomen of males' abdomen, and not equally so on the females' elytra, remains unclear.

Thaxter (1931) mentions the co-occurrence of *C. denigratus* and *Helodiomyces elegans* on *Dryops luridus*.

***Cantharomyces italicus* Speg.**

An. Mus. nac. Hist. natl. B. Aires 27: 42 (1915)

Select. icones: Spegazzini 1915 (fig. 6); Thaxter 1931 (Pl. I figs. 3-4); Siemaszko & Siemaszko 1933 (Pl. X fig. 7); Colla 1934 (fig. 16); Huldén 1983 (fig. 28); Santamaria 1992 (figs. 8-9); Majewski 1994 (Pl. 105: 1-5); Santamaría 2003 (fig. 19). **Fig. 2a-f.**

Thallus brownish yellow, 117-185 μm in length. Receptacle composed of three cells. Cell I elongate, broadest at the apex, pale yellowish to almost hyaline, distally darker. Cell II 0.8-2 \times higher than broad, brownish yellow. Cell III isodiametric, to slightly flattened, smaller than cell II, with the same pigmentation. Primary appendage simple, tapering upwards into a simple branch composed of a short series of cylindrical and hyaline cells; its basal cell trapezoidal, caudally less pigmented, with internal antheridium and subapical exit at the abaxial side. Perithecial stalk (cell VI) higher than cell III, distinctly constricted above the base, broadening upwards, often pigmented under the constriction. Basal cells of the perithecium not clearly defined. Perithecium 65-95 \times 24-31 μm , slightly pigmented, sub-symmetrical, elongate, broadest under the middle, tapering towards the rounded apex; abaxial pair of upper wall cells distally widened, ostiolum hyaline, pointing dorsally. Ascospores fusiform, two-celled, hyaline, with slime sheath, slightly thicker around the base of the larger cell, 49-55 \times 4.2-5.5 μm .

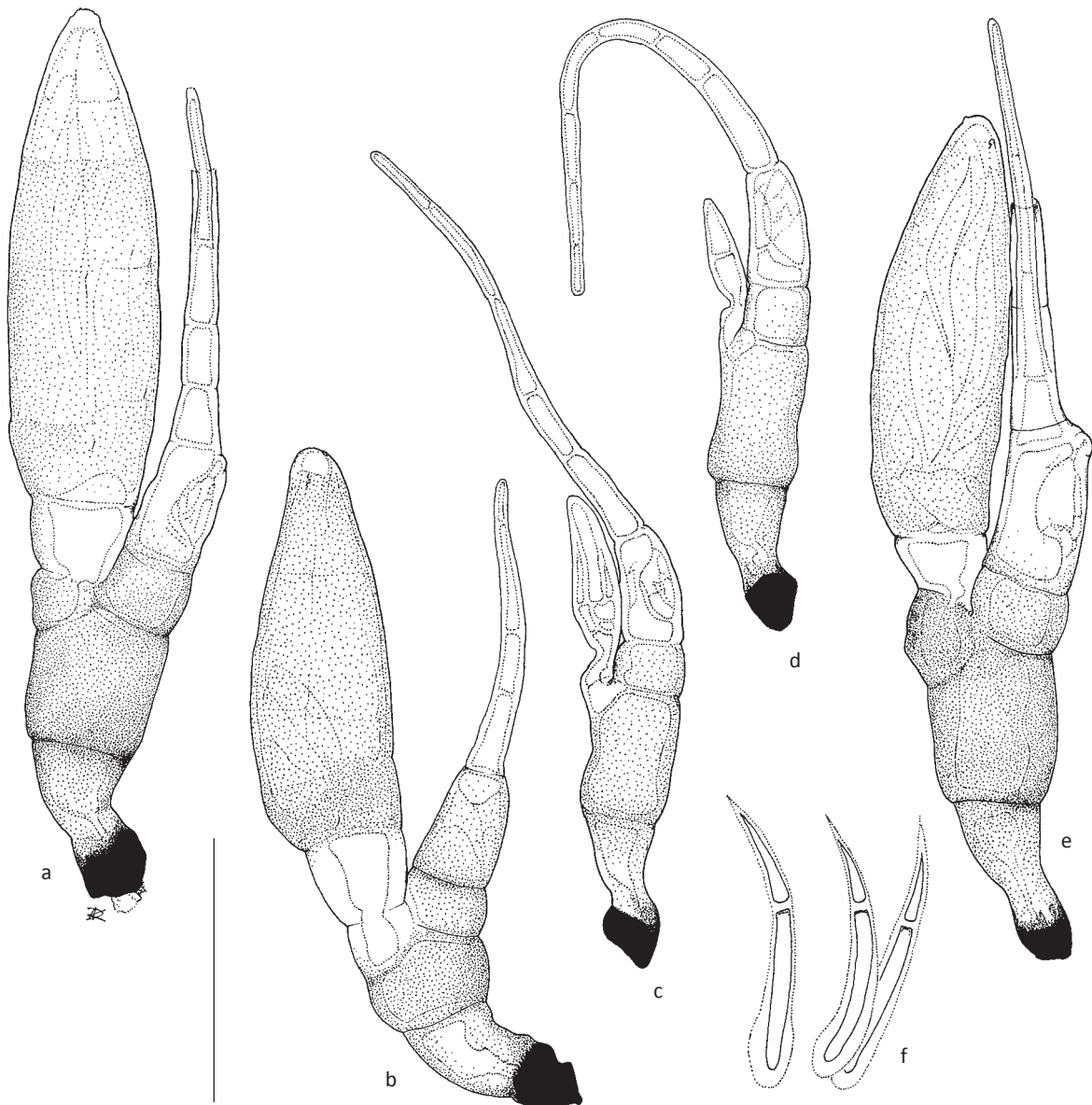


Fig. 2. *Cantharomyces italicus* Speg., taken from *Dryops luridus*. **a.** mature thallus from elytra (A. De Kesel 6142); **b.** mature thallus from elytra (A. De Kesel 6140); **c.** & **d.** young thalli from pronotum (A. De Kesel 6150); **e.** mature thallus from pronotum (A. De Kesel 6150); **f.** spores with slime sheath (A. De Kesel 6142). Scale bar = 50 μm .

Studied material: On *Dryops luridus*, Niel (B), Walenhoek, in ponds (old clay-pits) and their edges lined with trees, 10.vii.2013, A. De Kesel 6140, 6141, 6142; ibidem, 21.viii.2014, A. De Kesel 6146, 6148, 6166; ibidem, 28.viii.2014, A. De Kesel 6149(b), 6150, 6152(a), 6162, 6164.

Specificity and geographical distribution

Found on several species of *Dryops* (Coleoptera, Dryopidae). To date only reported from Europe: Italy, England, Poland, Ukraine, Germany, Finland, Russia, Spain, and Sweden (Huggert & Eriksson 2010, Santamaría 2003, Spaggiari 1915).

Infection pattern and transmission

Majewski (1994) and Santamaría (2003) state that *Cantharomyces italicus* is rare on males and mostly confined to the elytra, pronotum and the distal part of females. In our samples *Cantharomyces italicus* occurs on males and females in almost identical frequency (fig. 4). Taken together, all female hosts bore 125 thalli, while males only carried 45. Unlike with *C. denigratus*, *C. italicus* is not strictly confined to males or females. Both sexes are routinely infected on their dorsal side (fig. 5); mostly on the distal part of the elytra, but also up to the base of the elytra and the pronotum. The distribution of thalli is clearly not identical on males and females. Females were not infected on the lower side of the entire integument, whereas males carry most of *C. italicus* thalli on the prothorax and the legs. The infection pattern of *C. italicus* on males and females is compatible with spore transmission and direct infection during copulation.

Huldén (1983), Scheloske (1969) and Majewski (1994) reported thalli of *C. italicus* on the abdomen or distal part of the body.

Helodiomyces elegans F. Picard

Bull. Soc. mycol. Fr. 29: 558 (1913)

Select. icones: Picard 1913 (Pl. XXX: 11-12); Thaxter 1931 (Pl. LIII fig. 14); Siemaszko & Siemaszko 1933 (Pl. X, fig. 14); Balazuc 1973 (fig. 2); Rossi 1975 (fig. 7); Huldén 1983 (fig. 17); Tavares 1985 (Pl. 20: b-d, Pl. 21: c); Santamaría & Girbal 1987 (fig. 7); Santamaría 1989 (Lám. I: c-e); Majewski 1994 (Pl. 2: 1-7); Santamaría 2003 (fig. 84). **Fig. 3a-e.**

Thallus very pale yellowish, 370-682 µm in length (from foot to ostium). Receptacle S-shaped or bent, composed of a series of 18-31 superposed, flattened, and somewhat rectangular cells, gradually wider towards the apex; the basal cell elongate. Primary appendage at the apex of the receptacle, composed of a complex of filamentous branchlets; antheridia not seen (see Santamaría 2003, fig. 84a). Peritheciium 85-208 × 62-133 µm, sub-symmetrical, ovoidal, broadest under the middle, gradually narrowing towards the ostium, the latter with 4 prominent, cylindrical and elongate prolongations of the lips. Perithecial wall composed of 5 vertical series of outer wall cells, 4 of which composed of 13-15 cells; some of the lower abaxial ones with simple or once-forked slender appendages. Fifth series of perithecial wall cells at the adaxial side and composed of 5 cells. Ascospores 68-82 × 5.3-7.0 µm, with constricted slime sheath near the primary septum, basal cell (forming foot) shorter than apical cell.

Studied material: On *Dryops luridus*, Niel (B), Walenhoek,

in ponds (old clay-pits) and their edges lined with trees, 28.viii.2014, A. De Kesel 6151(a,b,c), 6152(b,c,d); ibidem, 5.ix.2014, A. De Kesel 6155(a), 6156.

Specificity and geographical distribution

Found exclusively on *Dryops* (Coleoptera, Dryopidae). Initially reported from France (Picard 1913), in many European countries (Santamaría *et al.* 1991), with the most recent reports in Sweden (Huggert & Eriksson 2010), Hungary (Majewski 2008), and the Netherlands (Haelewaters *et al.* 2012). Outside Europe known only from Algeria (Maire 1916).

Infection pattern and transmission

Helodiomyces elegans was found on males and females (fig. 4, 4/2). In most cases it occurred on specimens already infected with either *C. denigratus* or *C. italicus*. Picard (1913) and Balazuc (1973) did not mention any other Laboulbeniales co-occurring with *Helodiomyces elegans* on Dryopidae.

Discussion

Cases with three genera of Laboulbeniales occurring on a single host are excessively rare and reported only from Diptera (Rossi 1982) and Carabidae (Rossi 1992). Infections involving representatives of two genera on a single host specimen, like the one on *Dryops luridus* (Dryopidae) are less exceptional and have been reported occasionally from Carabidae, Catopidae, Haliplidae, Hebridae (Hemiptera), and Staphylinidae (Majewski 1994, Haelewaters unpublished records). In aquatic beetles infected with *Chitonomyces* it is more common to have one parasite genus with several, up to six, (phylogenetic) species on a single host specimen (Thaxter 1896, see Goldmann & Weir 2012). To date, only Thaxter (1931) and Siemaszko & Siemaszko (1933) mention simultaneous infections with two of the three above-mentioned taxa known on Dryopidae. To our knowledge this is the first report of all three species on a single *Dryops luridus*. Three males and one female of the 28 infected *Dryops luridus* carried all three parasite species (fig. 4).

Two species or two morphotypes?

Majewski (1994) and Santamaría (2003) agree that *Cantharomyces denigratus* and *C. italicus* are independent species and not growth forms of the same taxon. Growth forms of Laboulbeniales are more and more recognized and accepted (e.g. Rossi & Kotrba 2004, Rossi & Proaño Castro 2009, Santamaría & Faille 2009). They may be related to the position on the host, the sex of the host, or both. In some cases growth forms can be morphologically very diverse and 'convincing', and hence may be wrongly given species rank (Scheloske 1969).

The reason we accept *Cantharomyces denigratus* and *Cantharomyces italicus* as two separate species is based on the fact that they, regardless of host gender, do sporadically grow closely among each other. Such observations are very rare, but would not be conceivable if both taxa were strictly position related growth forms. From the few thalli we found growing outside their more commonly infected areas, the morphology of both *Cantharomyces italicus* and *Cantharomyces denigratus* is stable, i.e. without intermediate forms and independent from host gender or location on the host. Although both species seem to have a rather strict distribution pattern

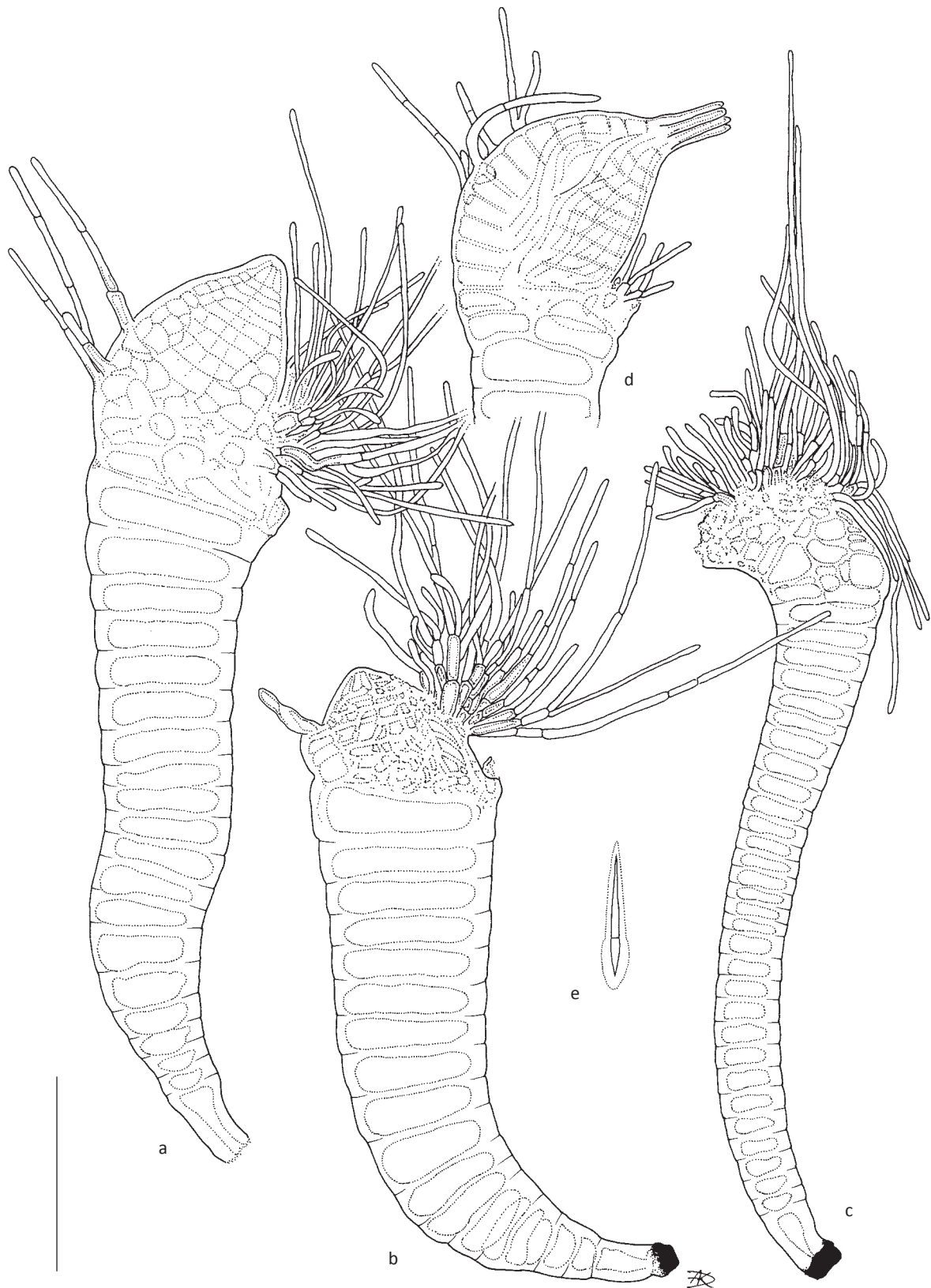


Fig. 3. *Helodiomyces elegans* F. Picard, taken from *Dryops luridus*. **a.** mature thallus from right metafemur (A. De Kesel 6156); **b.** mature regenerating thallus from right metafemur (A. De Kesel 6156); **c.** young thallus from left elytron (A. De Kesel 6155); **d.** detail of a fully mature perithecium with ostiolar prolongations, specimen taken from right mesocoxa (A. De Kesel 6152d); **e.** spore with the basal cell smaller (A. De Kesel 6152d). Scale bar = 100 μ m.

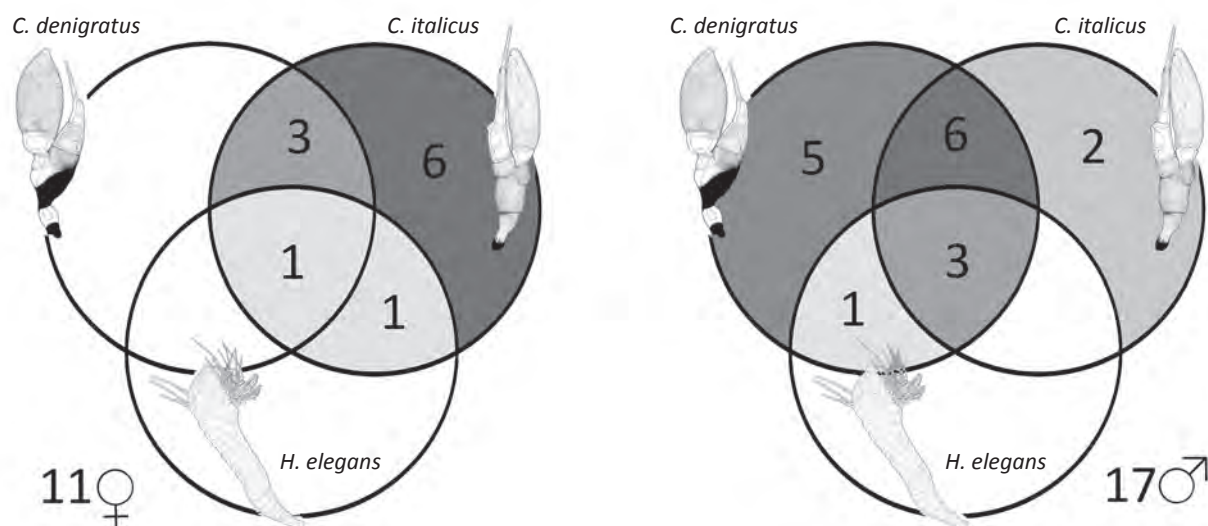


Fig. 4. Venn diagram showing the three species of Laboulbeniales found on *Dryops luridus* and the way they co-occur on males (right) and females (left). Darkness of the sections corresponds with increasing numbers of beetles.

(fig. 5), it is exactly their capacity to develop outside the usual area that speaks in favor of their status as species, rather than position related growth forms. However, those we found were often immature and we have no proof that morphs are restricted to only one location. The main argument in favor of a single species hypothesis is based on the unexplained gender-related distribution pattern of *C. denigratus*. In some cases a single parasite species shows a different but complementary distribution pattern on male and female hosts. This is the result of direct spore transmission between infected hosts during copulation. In terrestrial beetles it is during and after the copulation period that the differences between males and females become obvious. Whereas females are most often parasitized on their elytra, males are infected on abdominal sternites, meta-, meso-, prothorax, and the elytra. The fact that males are also infected on their elytra is explained by the random attempts of males to copulate with either females or males (Scheloske 1969, Frank 1982, for aquatic beetles also Goldmann & Weir 2012). Since females do not exhibit this behavior, their

abdominal sternites are not or hardly ever infected. Examples are found in *Clivina fossor* (Linnaeus, 1758) with *Laboulbenia clivialis* Thaxt., or *Pogonus chalceus* (Marshall, 1802) with *Laboulbenia slackensis* Cépède & F. Picard (De Kesel 1995, 1997). In aquatic beetles the same phenomenon of gender related thallus distribution exists. Often it is rendered more complex by the presence of several highly specific phylogenetic species (*Chitonomyces*) each with position related pairs of morphotypes (Goldmann & Weir 2012). With the Laboulbeniales from *Dryops luridus*, we observe a very similar combination of elements as presented by Goldmann & Weir (2012).

We cannot explain the observed distribution patterns of *Cantharomyces denigratus* and *C. italicus* separately (fig. 5). This is mainly due to the fact that *C. denigratus* is rarely present on the elytra of the females and *C. italicus* is completely missing from the last abdominal sternite of the males. Accepting *C. denigratus* and *C. italicus* as conspecific taxa, i.e. being two morphotypes of a single phylogenetic and phenotypically plastic species, renders



Fig. 5. Cumulative locations of thalli of *Cantharomyces italicus* (white circles) and *Cantharomyces denigratus* (yellow triangles) on females (11) and males (17) of *Dryops luridus*. Patterns show the absence of *C. italicus* from the abdomen of males and females. *C. denigratus* is almost entirely restricted to the male's last abdominal sternite. Scale bar = 1 mm.

the distribution of thalli on males and females complementary, logical, and perfectly in accordance with spore transmission during copulation; *Cantharomyces denigratus* is probably a position specific morphotype from the abdominal sternites.

This paper presents two opposing hypotheses. One is purely based on morphology while the other combines morphology with aspects of the biology of the host and the parasite. Considering recent finds of Goldmann & Weir (2012) and the extreme specificity of both taxa, it is most likely that the 'one species hypothesis' will be right. There is no doubt that the answer will come from a molecular phylogenetic analysis. In the meantime more male and female *Dryops luridus* should be collected and screened to confirm the consistency of the observed gender-related distribution patterns of both *Cantharomyces*.

Acknowledgements

We are grateful to Walter Rossi for providing information on simultaneous infections involving three genera of Laboulbeniales on one host, Donald H. Pfister for critically reading the manuscript, and Cyrille Gerstmanns for assistance during fieldwork in 2013.

References

- BALAZUC J. (1973) – Laboulbeniales de France. *Bulletin Mensuel de la Société Linnéenne de Lyon* **42** (9): 244-256.
- COLLA S. (1934) – Laboulbeniales, Peyritsiaceae, Dimorphomycetaceae, Laboulbeniaceae Heterothallaceae, Laboulbeniaceae Homothallaceae, Ceratomycetaceae. Fasc. 16: 1-157. In: Flora Italica Cryptogama, pars I: Fungi. Eds. P. A. Saccardo and H. Dalla Costa. Società Botanica Italiana, Firenze. R. S. Casciano.
- DE KESEL A. (1995) – Population dynamics of *Laboulbenia clivialis* Thaxter (Ascomycetes, Laboulbeniales) and sex-related thallus distribution its host *Clivina fossor* (Linnaeus, 1758) (Coleoptera, Carabidae). *Bull. Ann. Soc. Ent. Belg.* **131**: 335-348.
- DE KESEL A. (1997) – Contribution towards the study of the specificity of Laboulbeniales (Fungi, Ascomycetes), with particular reference to the transmission, habitat preference and host-range of *Laboulbenia slackensis*. Biologie. PhD thesis, University of Antwerp.
- DE KESEL A. & WERBROUCK T. (2008) – Belgian records of Laboulbeniales from aquatic insects. *Sterbeekia* **28**: 48-54.
- DE KESEL A. & HAELEWATERS D. (2012) – Belgian records of Laboulbeniales from aquatic insects (2) – *Chitonomyces aculeifer*. *Sterbeekia* **31**: 16-18.
- DROST M.B.P., CUPPEN H.P.J.J., VAN NIEUKERKEN E.J. & SCHREIJER M. (1992) – De Waterkevers van Nederland. Uitgeverij K.N.N.V., Utrecht. 280 p.
- HUGGERT L. & ERIKSSON O.E. (2010) – Laboulbeniales i Sverige av Lars Huggert (1942-2003). Umeå University. Ove Eriksson, 96pg. ISBN 978-91-7459-066-1.
- GOLDMANN L. & WEIR A. (2012) – Position specificity in *Chitonomyces* (Ascomycota, Laboulbeniomycetes) on *Laccophilus* (Coleoptera, Dysticidae): a molecular approach resolves a century-old debate. *Mycologia* **104** (5): 1143-1158.
- HAELEWATERS D, NUYTINCK J. & DE KESEL A. (2012) – Laboulbeniales in Nederland: een introductie. *Natuurhistorisch Maandblad* **101** (5): 88-93.
- HULDÉN L. (1983) – Laboulbeniales (Ascomycetes) of Finland and adjacent parts of the U.S.S.R. *Karstenia* **23**: 31-136.
- MAIRE R. (1916) – Deuxième contribution à l'étude des Laboulbeniales de l'Afrique du Nord. *Bull. Soc. Hist. Nat. Afrique N.* **7**: 6-39. Pls. 1, 2.
- MAJEWSKI T. (1994) – The Laboulbeniales of Poland. *Polish Botanical Studies* **7**: 1-466.
- MAJEWSKI T. (2008) – Atlas of the geographical distribution of Fungi in Poland. Fascicle 4. Laboulbeniales. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, pp 240.
- PICARD F. (1913) – Contribution à l'étude des Laboulbeniacées d'Europe et du nord de l'Afrique. *Bull. Soc. Mycol. France* **29**: 503-571. Pls. XXIX-XXXII.
- ROSSI W. (1975) – Su alcune Laboulbeniali (Ascomycetes) nuove per l'Italia. *Giorn. Bot. Ital.* (Nuovo Giorn. Bot. Ital. n.s.) **109**: 71-85.
- ROSSI W. (1982) – Laboulbeniali della Sierra Leone (Ascomycetes). *Accademia Nazionale dei Lincei Quaderno* **255**: 9-22 + pl. I-III.
- ROSSI W. (1992) – Nuove o interessanti Laboulbeniali (Ascomycetes) parassite di Carabidi italiani (Insecta, Coleoptera). *Webbia* **46** (2): 277-290.
- ROSSI W. & KOTRBA M. (2004) – A new polymorphic species of *Laboulbenia* parasitic on a South American fly. *Mycol. Res.* **108**: 1315-1319.
- ROSSI W. & PROAÑO CASTRO A.C. (2009) – New species of *Rhachomyces* from Ecuador, one of which is dimorphic. *Mycologia* **101** (5): 674-680.
- SANTAMARÍA S. (1989) – El orden Laboulbeniales (Fungi, Ascomycotina) en la Península Ibérica e Islas Baleares. *Edicions especials de la Societat Catalana de Micologia*. Vol. 3 (Barcelona). 396 p.
- SANTAMARÍA S. (1992) – New and interesting Laboulbeniales (Fungi, Ascomycotina) from Spain. *Nova Hedwigia* **54** (3-4): 479-492.
- SANTAMARÍA S. (2003) – Flora Mycologia Iberica. Vol. 5. Laboulbeniales, II. *Acompsomyces-Ilyomyces*. Real Jardín Botánico Madrid & J. Cramer. 344 pp.
- SANTAMARÍA S. & GIRBAL J. (1987) – Contribución al conocimiento de los Laboulbeniales (Ascomycotina) ibéricos, II. *Anales Jard. Bot. Madrid* **44** (1): 11-22.
- SANTAMARÍA S. & FAILLE A. (2009) – New species of *Laboulbenia* and *Rhachomyces* (Laboulbeniales, Ascomycota), some of them polymorphic, parasitic on termiticolous ground beetles from tropical Africa. *Nova Hedwigia* **89** (1-2): 97-120.
- SCHLOSKE H.W. (1969) – Beiträge zur Biologie, Ökologie und Systematik der Laboulbeniales (Ascomycetes) unter besonderer Berücksichtigung des Parasit-Wirt-Verhältnisses. *Parasitol. Schriftenreihe* **19**: 1-176.
- SIEMASZKO J. & SIEMASZKO W. (1933) – Owadorosty polskie i palearktyczne. (Laboulbeniales polonici et palaearctici.). III. *Polskie Pismo Entomol.* **12**: 115-138. Tab. IX-X.
- SPEGAZZINI C. (1915) – Segunda contribución al conocimiento de las Laboulbeniales italianas. *Anales Mus. Nac. Hist. Nat. Buenos Aires* **27**: 37-74.
- TAVARES I.I. (1985) – Laboulbeniales (Fungi, Ascomycetes). *Mycologia Mem.* **9**: 1-627.
- THAXTER R. (1896) – Contribution towards a monograph of the Laboulbeniaceae. *Mem. Amer. Acad. Arts Sci.* **12** (3): 187-429.
- THAXTER R. (1931) – Contribution towards a monograph of the Laboulbeniaceae. Part V. *Mem. Amer. Acad. Arts Sci.* **16**: 1-435. Pls. I-LX.