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Sergio Santamaria

Universitat Autònoma de Barcelona, Bellaterra, Spain

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LABOULBENIALES ON SEMIAQUATIC HETEROPTERA. A NEW SPECIES OF *TRICEROMYCES* (ASCOMYCOTA, LABOULBENIALES) ON *MICROVELIA* (HETEROPTERA, VELIIDAE) FROM SPAIN

SERGIO SANTAMARIA

Unitat de Botànica, Facultat de Ciències, Departament de Biologia Animal, Biologia Vegetal i Ecologia,
Universitat Autònoma de Barcelona, 08193–Bellaterra, Barcelona, Spain
(sergi.santamaria@uab.es)

ABSTRACT

A new species of fungal genus *Triceromyces* (Laboulbeniales) is described: *Triceromyces benjaminii*. The description is based on several thalli found on the insect host *Microvelia pygmaea* (Heteroptera, Veliidae), collected in two localities from SE Spain. Characteristics of male and female thalli of this dioecious species are discussed and compared with other dioecious taxa. The characteristics of male thalli require some adjustment in generic limits. This is the first species of *Triceromyces* known to parasitize a species of *Microvelia*, a semiaquatic heteropteran genus. The new species is described and illustrated with line drawings and photographs. A table collates information on synonymy, hosts, geographical distribution, and salient references pertinent to taxa of Laboulbeniales parasitic on semiaquatic Heteroptera.

Key words: Ascomycota, dioecism, Heteroptera, Laboulbeniales, *Microvelia*, morphology, Spain, taxonomy, *Triceromyces*.

INTRODUCTION

Laboulbeniales Engler, an order of fungal parasites, are known to parasitize Heteroptera (true bugs), a lineage in the insect order Hemiptera. Several alternative classifications are in use for the Hemiptera–Heteroptera–Homoptera lineage of Insecta. Traditionally, Hemiptera have been divided into two suborders, Heteroptera and Homoptera (Brues et al. 1954). Subsequently, new classifications have emerged, and modern studies using molecular methods have further changed the classical view of hemipteran systematics, although the monophyly of the group is strongly supported (Yoshizawa and Saigusa 2001).

In the absence of a unified system, two classifications deserve mention: the “Tree of Life, web project” (<http://tolweb.org/treelphylogeny.html>) divides the so called hemipteroid assemblage into four suborders: Sternorrhyncha (psyllids, whiteflies, aphids, coccids), Auchenorrhyncha (cicadas, leafhoppers, treehoppers, fulgoroids), Coleorrhyncha (Peloridiidae), and Heteroptera (true bugs). The alternative classification, based on the studies by Sorensen et al. (1995), divides order Hemiptera into suborders Sternorrhyncha, Clypeorrhyncha (incl. Auchenorrhyncha), Archaeorrhyncha (incl. the fulgoroids, i.e., Fulgoromorpha), and Prosorrhyncha (incl. Heteroptera and Coleorrhyncha). Regardless of the classification used, Heteroptera continue to be a natural, isolated, and well defined group.

Heteroptera are divided into seven infraorders (Enicocephalomorpha, Dipsocoromorpha, Gerromorpha, Nepomorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha) based upon the studies of Schuh (1979) and Wheeler et al. (1993). Among aquatic Heteroptera, Laboulbeniales are only known by genus *Coreomyces* (Thaxter 1902) parasitizing family Corixidae (Nepomorpha). Among terrestrial Heteroptera, Laboulbeniales are known on four genera: (1) *Lasiochilus pallidulus* Reuter (Anthocoridae, Cimicomorpha) from Grenada Island (West Indies) is parasitized by *Cupulomyces lasiochili* (Thaxt.) R.K.Benj. (Benjamin 1992) [= *Stigmatomyces lasiochili* Thaxt. (Thaxter 1917); = *Hesperomyces lasiochili* (Thaxt.) Thaxt. (Thaxter 1931); = *Acompsomyces lasiochili* (Thaxt.) I.I.Tav. (Tavares 1985)]; (2) *Myodocha unispinosa* Stål (Lygaeidae, Pentatomomorpha) from Guatemala is parasitized by *Corethromyces myodochae* Thaxt. (Thaxter 1931); (3) *Coptosoma* spp. (Pentatomidae, Pentatomomorpha) from Madagascar, Fiji, and the Solomon Islands are parasitized by *Polyandromyces coptosomalis* Thaxt., *Coptosoma* spp. from Cameroon are parasitized by *P. coptosomalis* var. *minor* Thaxt. (Thaxter 1931), as is an undetermined pentatomid from Ecuador (Benjamin 1967); and (4) *Macroscytus fraterculus* Horváth (Cydnidae, Pentatomomorpha) from Japan is parasitized by *Majewskaia japonica* Y.B.Lee & K.Sugiy. (Lee and Sugiyama 1986). Semiaquatic Heteroptera, currently included in suborder Gerromorpha, provide the greatest number of insect hosts for Laboulbeniales (Table 1), including members of families Hebridae, Hydro-metridae, Macroveliidae, Mesovelidae, and Veliidae.

Studies on Laboulbeniales parasitizing semiaquatic Heteroptera attracted the attention of Richard K. Benjamin who published eight contributions on this topic. In 1967, Benjamin described in detail the species of *Laboulbenia* known on these insects, including two species parasitizing *Velia*, two new species on *Microvelia*, four new species on *Rhagovelia*, and two new species on *Macrovelia* (Table 1). In the second contribution, Benjamin (1970) described *Autophagomyces poissonii* and *Dioicomycetes mesoveliae* on *Mesovelia*, and described the new genus *Prolixandromyces* with two species attacking *Velia*. The third Benjamin report was published in 1979, where he studied genus *Rhizopodomyces*, including seven species, two on *Merragata* and five on *Hebrus*, six of them new to science. Benjamin (1981) added three new species to genus *Prolixandromyces* parasitic on *Velia*. In 1986, Benjamin treated *Triceromyces* (see below). In the sixth part of the series, Benjamin (1993) studied *Tavaresiella* and described three new species on Hebridae. After, Benjamin (1998) added new observations and described four new species of *Triceromyces*

Table 1. List of Laboulbeniales described on semiaquatic Heteroptera, with synonyms, hosts, geographical distribution, and selected references.

<i>Autophagomyces</i> sp.	<i>Microvelia</i> (Veliidae)	France (Poisson 1957)
<i>Autophagomyces mesoveliae</i> Poisson nom. inval.	<i>Mesovelia</i> (Mesoveliidae)	USA (Benjamin 1970)
<i>Laboulbenia drakei</i> R.K.Benj.	<i>Mesovelia</i> (Mesoveliidae)	France (Poisson 1957)
<i>Laboulbenia hemipteralis</i> Thaxt.	<i>Rhagovelina</i> (Veliidae)	Panama (Benjamin 1967)
<i>Laboulbenia leechii</i> R.K.Benj.	<i>Velia</i> (Veliidae)	Argentina (Thaxter 1912)
<i>Laboulbenia macroveliae</i> R.K.Benj.	<i>Microvelia</i> (Veliidae)	Mexico, USA (Benjamin 1967)
<i>Laboulbenia microveliae</i> R.K.Benj.	<i>Macrovelia</i> (Macroveliidae)	USA (Benjamin 1967)
<i>Laboulbenia rhagoveliae</i> R.K.Benj.	<i>Microvelia</i> (Veliidae)	Mexico, USA (Benjamin 1967)
<i>Laboulbenia titschackii</i> Poisson nom. inval.	<i>Rhagovelina</i> (Veliidae)	Mexico, Panama (Benjamin 1967)
<i>Laboulbenia truxalii</i> R.K.Benj.	<i>Velia</i> (Veliidae)	Peru (Poisson 1954)
<i>Laboulbenia uhleri</i> R.K.Benj.	<i>Rhagovelina</i> (Veliidae)	Mexico (Benjamin 1967)
<i>Laboulbenia usingeri</i> R.K.Benj.	<i>Macrovelia</i> (Macroveliidae)	USA (Benjamin 1967)
<i>Laboulbenia veliae</i> Thaxt.	<i>Rhagovelina</i> (Veliidae)	Panama (Benjamin 1967)
<i>Monandromyces australis</i> R.K.Benj.	<i>Velia</i> (Veliidae)	Argentina (Thaxter 1912)
<i>Monandromyces elongatus</i> R.K.Benj.	<i>Microvelia</i> (Veliidae)	Australia, Flores Island (Benjamin 1999)
<i>Monandromyces falcatus</i> R.K.Benj.	<i>Pseudovelina</i> (Veliidae)	Sumatra (Benjamin 1999)
<i>Monandromyces longispinae</i> R.K.Benj.	<i>Microvelia</i> (Veliidae)	New Guinea (Indonesia) (Benjamin 1999)
<i>Monandromyces microveliae</i> (Thaxt.) R.K.Benj.	<i>Pseudovelina</i> (Veliidae)	Madagascar, Malawi, Tanzania (Benjamin 1999)
= <i>Autophagomyces microveliae</i> Thaxt.	<i>Microvelia</i> (Veliidae)	Sumatra (Thaxter 1931, Benjamin 1999)
<i>Monandromyces neoalardi</i> R.K.Benj.	<i>Neoalardus</i> (Veliidae)	Malaysia (Benjamin 1999)
<i>Monandromyces polhemorum</i> R.K.Benj.	<i>Microvelia</i> (Veliidae)	Timor (Benjamin 1999)
<i>Monandromyces protuberans</i> R.K.Benj.	<i>Microvelia</i> (Veliidae)	Australia (Benjamin 1999)
<i>Monandromyces pseudoveliae</i> R.K.Benj.	<i>Pseudovelina</i> (Veliidae)	Madagascar (Benjamin 1999)
<i>Monandromyces tenuistipitis</i> R.K.Benj.	<i>Microvelia</i> (Veliidae)	New Guinea (Indonesia) (Benjamin 1999)
<i>Monandromyces umbonatus</i> R.K.Benj.	<i>Microvelia</i> (Veliidae)	Timor (Benjamin 1999)
<i>Prolixandromyces</i> sp.	<i>Rhagovelina</i> (Veliidae)	Nigeria, Sierra Leone (Rossi 1982)
<i>Prolixandromyces corniculatus</i> R.K.Benj.	<i>Velia</i> (Veliidae)	El Salvador, Mexico (Benjamin 1970)
<i>Prolixandromyces lingulatus</i> R.K.Benj.	<i>Velia</i> (Veliidae)	Nicaragua (Benjamin 1981)
<i>Prolixandromyces rhinoceralis</i> R.K.Benj.	<i>Velia</i> (Veliidae)	Nicaragua (Benjamin 1981)
<i>Prolixandromyces tenuis</i> R.K.Benj.	<i>Velia</i> (Veliidae)	Costa Rica (Benjamin 1981)
<i>Prolixandromyces triandrus</i> Santam.	<i>Velia</i> (Veliidae)	Spain, Portugal (Santamaria 1988, 1992), France (Balazuc 1990)
<i>Prolixandromyces veliae</i> R.K.Benj.	<i>Velia</i> (Veliidae)	Mexico (Benjamin 1970), Nicaragua (Benjamin 1981)
<i>Rhizopodomyces</i> sp.	<i>Hebrus</i> (Hebridae)	Mexico (Benjamin 1979)
<i>Rhizopodomyces basifurcatus</i> R.K.Benj.	<i>Hebrus</i> (Hebridae)	Mexico (Benjamin 1979)
<i>Rhizopodomyces californicus</i> R.K.Benj.	<i>Merragata</i> (Hebridae)	USA (Benjamin 1979)
<i>Rhizopodomyces erectus</i> R.K.Benj.	<i>Hebrus</i> (Hebridae)	Costa Rica (Benjamin 1979)
<i>Rhizopodomyces geniculatus</i> R.K.Benj.	<i>Hebrus</i> (Hebridae)	Costa Rica, USA (Benjamin 1979)
<i>Rhizopodomyces merragatae</i> Thaxt.	<i>Merragata</i> (Hebridae)	Guatemala (Thaxter 1931), USA (Benjamin 1967)
<i>Rhizopodomyces mexicanus</i> R.K.Benj.	<i>Hebrus</i> (Hebridae)	Costa Rica, Mexico (Benjamin 1979)
<i>Rhizopodomyces polhemusii</i> R.K.Benj.	<i>Hebrus</i> (Hebridae)	Mexico (Benjamin 1979), Spain (Santamaria 1993)
<i>Tavaresiella hebri</i> T.Majewski	<i>Hebrus</i> (Hebridae)	Mexico (Benjamin 1979)
<i>Tavaresiella majewskii</i> R.K.Benj.	<i>Timasius</i> (Hebridae)	Poland (Majewski 1981)
<i>Tavaresiella polhemi</i> R.K.Benj.	<i>Timasius</i> (Hebridae)	Sumatra (Benjamin 1993)
<i>Tavaresiella santamariae</i> R.K.Benj.	<i>Hebrus</i> (Hebridae)	Sumatra (Benjamin 1993)
<i>Triceromyces balazucii</i> T.Majewski	<i>Hebrus</i> (Hebridae)	Flores Island, Madagascar, Spain (Benjamin 1993), Poland (Majewski 1994)
<i>Triceromyces benjaminii</i> Santam.	<i>Microvelia</i> (Veliidae)	Poland (Majewski 1981)
<i>Triceromyces biformis</i> R.K.Benj.	<i>Mesovelina</i> (Mesoveliidae)	Spain (described here)
= <i>Dioicomyces verruculosus</i> T.Majewski		Philippines (Benjamin 1986), Japan (Majewski 1988)
<i>Triceromyces bullatus</i> R.K.Benj.		
= <i>Dioicomyces yongboi</i> T.Majewski	<i>Mesovelina</i> (Mesoveliidae)	Philippines (Benjamin 1986), Japan (Majewski 1988)
<i>Triceromyces elongatus</i> R.K.Benj.	<i>Hydrometra</i> (Hydrometridae)	India, Kenya, Madagascar, Sri Lanka, Timor (Benjamin 1998)
<i>Triceromyces floridanus</i> R.K.Benj.	<i>Hydrometra</i> (Hydrometridae)	USA (Benjamin 1998)
<i>Triceromyces hebri</i> R.K.Benj.	<i>Hebrus</i> (Hebridae)	Mexico (Benjamin 1986), Spain (Santamaria 1993)
<i>Triceromyces hydrometrae</i> R.K.Benj.	<i>Hydrometra</i> (Hydrometridae)	USA (Benjamin 1986), Spain (Santamaria 1989), Portugal (Santamaria 1992), Sierra Leone (Rossi 1994), Australia, Kenya, Madagascar, Malaysia, Peru, Tanzania, Timor (Benjamin 1998), Algeria (Santamaria and Rossi 1999), Canary Islands (Santamaria et al. 1991)

Table 1. Continued.

<i>Triceromyces lithophilus</i> R.K.Benj.	<i>Hydrometra</i> (Hydrometridae)	Madagascar (Benjamin 1998)
<i>Triceromyces poissonii</i> (R.K.Benj.) R.K.Benj. = <i>Autophagomyces poissonii</i> R.K.Benj. = <i>Dioicomyces mesoveliae</i> R.K.Benj.	<i>Mesovelia</i> (Mesoveliidae)	Mexico, Nicaragua, USA (Benjamin 1970, 1986)
<i>Triceromyces terrestris</i> R.K.Benj.	<i>Hydrometra</i> (Hydrometridae)	Madagascar (Benjamin 1998)

parasitizing *Hydrometra* (see below). In his last contribution to Laboulbeniales on semiaquatic Heteroptera, Benjamin (1999) erected a new genus, *Monandromyces*, based on *Autophagomyces microveliae* Thaxt. (Thaxter 1931) (not *A. hemipteralis* as mentioned in the abstract, a *nomen nudum* used as a notation on the slide by Thaxter [Benjamin 1999: 90]; not *A. micronectae*, a *nomen nudum* mentioned in error by Poisson [1954: 81]), to accommodate 11 species, seven parasitizing *Microvelia* spp., one species parasitizing *Neoalardus*, and two species parasitizing *Pseudovelia* (see Table 1).

Triceromyces was described by Majewski (1981) with a single species, *T. balazucii*, parasitizing *Hebrus ruficeps* (Thomson) from Poland. Important information on the genus was added by Benjamin (1986) who described four new species: *T. hebri* on *Hebrus* sp. from Mexico, *T. hydrometrae* on *Hydrometra australis* Say (as *H. martini* Kirkaldy) from the USA, *T. biformis* and *T. bullatus* on *Mesovelia vittigera* Horváth from the Philippine Islands; he further proposed a new combination, *T. poissonii*, to accommodate two species previously described in *Autophagomyces* (*A. poissonii*) and *Dioicomyces* (*D. mesoveliae*) from material collected on *Mesovelia mulsanti* White in the USA, Mexico and Nicaragua. In that paper, Benjamin described the interesting phenomenon of trioecy, the presence of both monoecious and dioecious morphs, for the three *Triceromyces* species parasitizing *Mesovelia*. This feature was not previously known in any member of Laboulbeniales.

Later, Majewski (1988) described the dioecious morphs of *T. biformis* and *T. bullatus* as *Dioicomyces verruculosus* and *D. yongboi*, respectively, occurring on *Mesovelia vittigera* from Iriomote Island (Japan). In the same work, Majewski reported, with reservation, *A. poissonii*, from the same locality as *D. yongboi*. According to Benjamin (1998) this fungus may represent the monoecious morph of *T. biformis*. Later, Majewski (1994) reported *T. balazucii* from another locality in Poland. Santamaria (1993) mentioned the presence of *T. hebri* in Spain. Santamaria (1989, 1992) reported *T. hydrometrae* from Spain and Portugal, and Rossi (1994) from Sierra Leone.

Benjamin (1998) published four new species of *Triceromyces* parasitic on *Hydrometra*: *T. floridanus* on *H. australis* Say from the USA, *T. elongatus* on several species of *Hydrometra* from Africa, *T. lithophilus* on *H. cavernicola* J.T. & D.A. Polhemus, and *T. terrestris* on *H. phytophila* J.T. & D.A. Polhemus, both from Madagascar, and also added reports of *T. hydrometrae* from five continents. Lastly, Santamaria and Rossi (1999) reported *T. hydrometrae* from Algeria.

In this study we describe *T. benjaminii*, a new dioecious species of *Triceromyces* parasitic on *Microvelia pygmaea* (Dufour) collected in a river and in a rushing stream from two localities in SE Spain. In addition to the formal description we discuss some characteristics that diverge slightly

from those of the last emended generic description of Benjamin (1998), but we do not consider these discrepancies to warrant the description of a new genus.

MATERIALS AND METHODS

Fungal specimens were isolated from two collections of *Microvelia pygmaea* preserved in vials of 70% ethyl alcohol and sent to the author by entomologists A. Millán and C. Hernando. Permanent slides were prepared following the methods described by Santamaria (1998). Slides were kept at BCB, the herbarium that houses the author's collection. Observations were made using a differential interference contrast (DIC) microscope and drawings prepared with the help of a drawing device mounted on the microscope.

TAXONOMY

***Triceromyces benjaminii* Santam., sp. nov.**

Fig. 1–17

Dioecius. Mas.—Dilutus luteolus praeter pedem denigratum et aream suffusam in cellularum *II* et *III* inferis areis. Receptaculum tricellulare, ex una elongata basali cellula constans, quae cellulas *II* et *III* sustinet, lateraliter adnatas et plus minusve parallelas inter se. Cellula *II* sustinens unam fere isodiametricam, sterilem cellulam et unum terminale, arcuatum antheridium. Cellula *III* leviter longior quam cellula *II*, sustinens appendicem ex quattuor superpositis cellulis constantem; infima cellula longior quam latior atque longissima appendicis; tres cellulae superae plus minusve complanatae, praecipue summa cellula, quae dua antheridia sustinet, dorsale antheridium brevius, arcuatum, spiniforme processum in interiore latere ferens, quod est reliquum originalis apicis ascosporae. Tota longitudo a pede ad antheridium terminans cellulam *II*, 38–48 μ m. Tota longitudine a pede ad antheridium terminans cellulam *III*, 55–68 μ m. **Femina.**—Luteolus ad dilutum succineum praeter pedem denigratum et aream suffusam in cellularum *II* et *III* inferis areis. Receptaculum tricellulare, ex una elongata basali cellula constans, quae cellulas *II* et *III* sustinet, lateraliter adnatas et plus minusve parallelas. Cellula *III*, leviter longior quam cellula *II*, sustinens appendicem, 33–40 μ m longam, ex 4(–5) superpositis, longioribus quam latioribus cellulas constantem; distalis cellula spiniforme processum ferens, quod est reliquum originalis apicis ascosporae. Perithecialis cellula stipitis (*VI*) 23–48 μ m longa. Perithecium, 98–120 $\times$ 23–38 μ m (cellulis *VII* et basalibus cellulis, *m*, *n* et *n'* inclusis), cum fusiformi, extra convexo, latiore prope medium corpore, abrupte constricto prope trichogyni reliquum et lateraliter flexum collum formans. Peritheci apex acutus atque asymmetricus. Peritheci subapicalis area diagonaliter directam excrescentiam includens, quae cristiforme processum deliniat et duas bene definitas et obtusas protuberationes in ambobus lateribus faciens. Haec excrescentia derivatur ex suprema cellula parietalium cellularum seriei oriunda a cellula *m*. Trichogyni reliquae prope basem quartae cellulae seriei parietalium cellularum. Tota longitudo a pede ad peritheci apicem 135–185 μ m.

Dioecious. Male.—Pale yellowish except for the blackened foot and the deep brown suffusion in lower areas of cells *II* and *III*. Receptacle three-celled, consisting of an elongated basal

Fig. 1–11. *Triceromyces benjamini*.—1, 5. *BCB SS2084*.—2–4, 6, 11. *BCB SS2402c*.—7–8. *BCB SS2402e* = HOLOTYPE.—9. *BCB SS2402f*.—10. *BCB SS2402b*.—11. Mature female thalli; in Fig. 7 the diagonally orientated outgrowth is labelled with an “*”.—2–4. Three successive early stages of development in female thalli.—5–6, 8. Three mature males.—9. Young female with developing trichogyne (*tr*).—10. Immature female with trichogyne (*tr*) showing the formation of a diagonally orientated outgrowth from an upper wall cell in the row originated from cell *m* (*). (Key to figure labels: *I*, basal cell of receptacle; *II*, suprabasal cell of receptacle; *III*, stalk cell of perithecius; *VII*, secondary stalk cell of perithecius; *an*, antheridium; *m*, *n*, and *n'*, perithecial basal cells; *sx*, spinous process, the remainder of original ascospore apex; *tr*, trichogyne; *ts*, trichogyne scar; *w1*–*5*, tiers of outer wall cells). (Scale bar = 50 μ m for all figures).

Fig. 12–17. *Triceromyces benjaminii*.—12. BCB SS2084.—13–15. BCB SS2402e HOLOTYPE; 16–17. BCB SS2402f.—12, 13, 17. Mature females (see Fig. 1–11 for key).—13. Ascospore (s) visible in the neck channel.—14–16. Male thalli, with spermatia (sp) indicated in Fig. 14. (Scale bars: Fig. 12–13, 17: bar in Fig. 12 = 50 μ m; Fig. 14–16, bar in Fig. 14 = 50 μ m).

cell (*I*) subtending the cells *II* and *III*, which are laterally adnate and more or less parallel to one another. Cell *II* supporting one almost isodiametric sterile cell and one terminal, more or less arcuate antheridium (Fig. 6: *an*). Cell *III*, which is slightly longer than cell *II*, supporting the appendage which consists of four superposed cells, the lowermost cell being longer than broad and the longest cell of the appendage; the three cells above being more or less flattened, especially the uppermost cell which supports two antheridia, the dorsal antheridium being shorter, arcuate and bearing on the inner side one spine-like process (Fig. 6, 8: *sx*), that represents the remainder of the original ascospore apex. Total length from foot to antheridium terminating the cell *II*, 38–48 μ m. Total length from foot to antheridium-terminating cell *III*, 55–68 μ m. *Female*.—Yellowish to pale amber except for the blackened foot and the deep brown suffusion in lower areas of cells *II* and *III*. Receptacle three-celled, consisting of an elongated basal cell (*I*) subtending the cells *II* and *III*, which are laterally adnate and more or less parallel to one another. Cell *III*, which is slightly longer than cell *II*, supporting the primary appendage, 33–40 μ m in length, consisting of 4(–5)

superposed, longer than broad cells; the distal cell bearing a terminal spine-like process, which represents the remainder of the original ascospore apex (Fig. 1, 12: *sx*). Perithecial stalk cell (*VI*) 23–48 μ m in length. Perithecium, 98–120 $\times$ 23–38 μ m (including cell *VII*, and basal cells *m*, *n* and *n'*), with a fusiform, externally convex body that is broadest near the middle, that is abruptly constricted at the level of the trichogynic remnant and forms a laterally bent neck. The perithecial apex is acute and asymmetric. The subapical area includes a diagonally orientated outgrowth, which draws a ridge-like process and which forms two well-defined, blunt protuberances at each side (Fig. 7: *). This outgrowth is derived from an upper cell of the wall cell row originated from cell *m* (Fig. 11: *). Trichogyne with an ovoid, transversely septate basal part, and a lobate apex (Fig. 10: *tr*). The trichogynic remnant is located near the base of the fourth cell of the *m* row (Fig. 1, 7, 13: *ts*). Total length from foot to perithecial tip 135–185 μ m.

Etymology.—Named for Richard K. Benjamin, a scholar of Laboulbeniales.

Holotype.—SPAIN: ALMERIA; Sorbas, Los Molinos del río Aguas, Aguas river; Oct 2002; C. Hernando; on legs and antennae of *Microvelia pygmaea* (Dufour); *BCB SS2402e*.

Isotypes.—Data as for the holotype; *BCB SS2402a–SS2402d*, and *SS2402f*.

Paratypes.—SPAIN: MURCIA; Cieza, Rambla del Moro; 14 Oct 1986; A. Millán; on antennae of *M. pygmaea*; *BCB SS2084*.

Notes and observations.—Benjamin (1998) redefined the genus *Triceromyces* including monoecious, trioecious and dioecious species. Thalli of monoecious species, or females in dioecious species or in dioecious forms of trioecious species, have a three-celled receptacle, where cell *I* subtends laterally adnate and parallel cells *II* and *III*. Cell *I* is defined by Benjamin (1998) as a small cell; moreover, in comparison with the cells *II* and *III* above, it might be considered a rather minute cell. In females of *T. benjaminii*, a dioecious species, cell *I* is as long or longer than cells *II* and *III*.

Benjamin (1998) included as a generic character the secondary division of cell *III* into an upper, nucleate cell and a lower, empty segment. This characteristic is not observed in *T. benjaminii*.

The primary appendage, above cell *III*, is obviously sterile in females of dioecious species (or in dioecious forms of trioecious species) and has a variable number of cells. The primary appendage of female thalli in *T. benjaminii* is four (Fig. 1, 9–13) or rarely five-celled (Fig. 7), and may be compared with the two, rarely three-celled primary appendages of females of dioecious forms in trioecious species, as *T. biformis*, *T. bullatus*, or *T. poissonii*. Nevertheless, *T. benjaminii* is unique among them, because the appendage is spinose, bearing the remainder of the original ascospore apex on its top (Fig. 1, 7, 12: *sx*). A similar spinose process is only known in young females of *T. hydrometrae* (Benjamin 1986), and in mature thalli of *T. floridanus* (Benjamin 1998), two monoecious species.

The number of cells for each vertical row of perithecial wall cells is variable from four to five in the species of *Triceromyces*. This number is difficult to establish in *T. benjaminii* due to its poorly defined septa, but we can see five cells in all rows except in the row originated from cell *n'*, that only has four cells (Fig. 1, 7). The perithecial basal cells, *m*, *n*, and *n'*, are rather elongated, forming about a quarter of the total perithecial length in *T. benjaminii*. Cell *VII* is wedge-shaped and very inconspicuous (Fig. 1, *VII*). These characteristics are variable in all known species of *Triceromyces*.

The perithecial apex and neck in *T. benjaminii* include important characteristics for distinguishing this species from others but are difficult to compare. Broad similarities to the long, even snout-like, apices of species parasitizing Hydrometridae are noteworthy.

However, *T. benjaminii* is most distinctive in relation to its unique male thalli. Male thalli of dioecious forms and species consist of an unbranched, one-celled receptacle subtending several superposed cells terminated by a single, simple, sometimes spinose antheridium (Benjamin 1998). As can be seen in Fig. 5, 6, 8, and 14–16 and from the taxonomic description, males of *T. benjaminii* are very different from this definition. The receptacle is identical to those in females, two antheridia (one of them spinose, Fig. 6 and 8) terminate a

four-celled primary appendage, and a single antheridium is above a single cell formed from cell *II* (Fig. 6: *an*).

In conclusion, *T. benjaminii* shows many peculiar characteristics, especially in male thalli, and it is debatable whether this species should be included in genus *Triceromyces* or if a new genus should be erected. We are waiting for additional species, probably on *Microvelia*, that validate the importance of such characters and the necessity for a separate genus.

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LITERATURE CITED

- BALAZUC, J. 1990. Catalogue actuel des Laboulbéniales (Ascomycètes parasites) de la France métropolitaine. *L'Entomologiste* **46**: 219–232.
- BENJAMIN, R. K. 1967. Laboulbeniales on semi-aquatic Hemiptera. *Laboulbenia*. *Aliso* **6**: 111–136.
- . 1970. Laboulbeniales on semiaquatic Hemiptera. II. *Autophagomyces*, *Dioicomyces*, and *Prolixandromyces* gen. nov. *Aliso* **7**: 165–182.
- . 1979. Laboulbeniales on semiaquatic Hemiptera. III. *Rhizopodomycetes*. *Aliso* **9**: 379–409.
- . 1981. Laboulbeniales on semiaquatic Hemiptera. IV. Addenda to *Prolixandromyces*. *Aliso* **10**: 1–17.
- . 1986. Laboulbeniales on semiaquatic Hemiptera. V. *Triceromyces*: with a description of monoecious–dioecious dimorphism in the genus. *Aliso* **11**: 245–278.
- . 1992. *Cupulomyces*, a new genus of Laboulbeniales (Ascomycetes) based on *Stigmatomyces lasiochili*. *Aliso* **13**: 355–364.
- . 1993. Laboulbeniales on semiaquatic Heteroptera. VI. The genus *Tavaresella*. *Aliso* **13**: 559–576.
- . 1998. Laboulbeniales on semiaquatic Heteroptera. VII. Addenda to species of *Triceromyces* on Hydrometridae and further observations on dioecism in the order. *Aliso* **17**: 1–21.
- . 1999. Laboulbeniales on semiaquatic Heteroptera. VIII. *Monandromyces*, a new genus based on *Autophagomyces microveliae* (Laboulbeniales). *Aliso* **18**: 71–91.
- BRUES, C. T., A. L. MELANDER, AND F. M. CARPENTER. 1954. Classification of insects, keys to the living and extinct families of insects, and to the living families of other arthropods. *Rev. Ed. Bull. Mus. Comp. Zool. Harvard* **108**: 1–917.
- LEE, Y. B. AND K. SUGIYAMA. 1986. On a new genus of the Laboulbeniales: *Majewskia*. *Mycologia* **78**: 289–292.
- MAJEWSKI, T. 1981. Rare and new Laboulbeniales from Poland. VI. *Acta Mycol* **16** (1980): 141–153.
- . 1988. Some Laboulbeniales (Ascomycotina) collected in Japan II. Species on semiaquatic Hemiptera from Iriomote Island. *Trans. Mycol. Soc. Japan* **29**: 151–160.
- . 1994. The Laboulbeniales of Poland. *Polish Bot. Stud.* **7**: 1–466.
- POISSON, R. 1954. Sur une Laboulbéniale ectoparasite de *Velia osborniana* Kirkaldy (Hemipt. Veliidae) *Laboulbenia* (s. g. *Velio-mycetes* nov.) *titschacki* n. sp., pp. 81–82. In E. Titschack [ed.], Beiträge zur Fauna Perus, vol. 4. Gustav Fischer, Jena, Germany.
- . 1957. Faune de France. 61. Hétéroptères aquatiques. P. Lechevalier, Paris, France. 263 p.

- ROSSI, W. 1982. Laboulbeniali della Sierra Leone (Ascomycetes). *Accad. Naz. Lincei, Quaderno* **255**: 9–22, Plates I–IV.
- . 1994. A new contribution to the knowledge of the Laboulbeniales (Ascomycetes) from Sierra Leone. *Accad. Naz. Lincei, Quaderno* **267**: 5–17.
- SANTAMARIA, S. 1988. *Prolixandromyces triandrus* sp. nov. (Laboulbeniales) from Spain. *Mycotaxon* **32**: 433–437.
- . 1989. El orden Laboulbeniales (Fungi, Ascomycotina) en la Península Ibérica e Islas Baleares. *Ed. Espec. Soc. Catalana Micol.* **3**: 1–396.
- . 1992. Laboulbeniales (Ascomycotina) ibéricos. Nuevos datos corológicos. *Orsis* **7**: 139–144.
- . 1993. New and interesting Laboulbeniales (Fungi, Ascomycotina) from Spain, II. *Nova Hedwigia* **56**: 409–422.
- . 1998. Laboulbeniales, I. *Laboulbenia. Fl. Mycol. Iber.* **4**: 1–186.
- , J. BALAZUC, AND I. I. TAVARES. 1991. Distribution of the European Laboulbeniales (Fungi, Ascomycotina). An annotated list of species. *Treb. Inst. Bot. Barcelona* **XIV**: 1–123.
- AND W. ROSSI. 1999. New or interesting Laboulbeniales (Ascomycota) from the Mediterranean region. *Plant Biosystems* **133**: 163–171.
- SCHUH, R. T. 1979. [Review of Cobben's] Evolutionary trends in Heteroptera. *Syst. Zool.* **28**: 653–656.
- SORENSEN, J. T., B. C. CAMPBELL, R. J. GILL, AND J. D. STEFFEN-CAMPBELL. 1995. Non-monophyly of Auchenorrhyncha ('Homoptera'), based upon 18S rDNA phylogeny: eco-evolutionary and cladistic implications within pre-Heteropterodea Hemiptera (s.l.) and a proposal for new monophyletic suborders. *Pan-Pacific Entomol.* **71**: 31–60.
- TAVARES, I. I. 1985. Laboulbeniales (Fungi, Ascomycetes). *Mycol. Mem.* **9**: 1–627.
- THAXTER, R. 1902. Preliminary diagnoses of new species of Laboulbeniaceae. V. *Proc. Amer. Acad. Arts* **38**: 7–57.
- . 1912. New or critical Laboulbeniales from the Argentine. *Proc. Amer. Acad. Arts* **48**: 153–223.
- . 1917. New Laboulbeniales, chiefly dipterophilous American species. *Proc. Amer. Acad. Arts* **52**: 647–721.
- . 1931. Contribution towards a monograph of the Laboulbeniaceae. Part V. *Mem. Amer. Acad. Arts* **16**: 1–435.
- WHEELER, W. C., R. T. SCHUH, AND R. BANG. 1993. Cladistic relationships among higher groups of Heteroptera: congruence between morphological and molecular data sets. *Entomol. Scand.* **24**: 121–137.
- YOSHIZAWA, K. AND T. SAIGUSA. 2001. Phylogenetic analysis of paraneopteran orders (Insecta: Neoptera) based on forewing base structure, with comments on monophyly of Auchenorrhyncha (Hemiptera). *Syst. Entomol.* **26**: 1–13.