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Research article

New species of *Rhizomyces* (Ascomycota, Laboulbeniales) parasitic on African stalk-eyed flies (Diptera, Diopsidae)

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Abstract. Three new species of *Rhizomyces* Thaxt., parasitic on African stalk-eyed flies, are described. These are *R. forcipatus* W.Rossi & Feijen sp. nov., parasitic on various species of *Centrioncus* Speiser from Ivory Coast, Kenya and Malawi and *Teloglabrus* Feijen from South Africa; *R. ramosus* W.Rossi & Feijen sp. nov., parasitic on *Diopsina nitida* (Adams, 1903) from Uganda; *R. tschirnhausii* W.Rossi & Feijen sp. nov., parasitic on *Diopsina africana* (Shillito, 1940) from Uganda. All previous records of species of *Rhizomyces* are presented in tabulated form with updated host names. A key is presented to all species of *Rhizomyces*. The occurrence of *Rhizomyces* and other taxa of the Laboulbeniales Lindau in the genera of the Diopsidae Billberg is discussed.

Keywords. Afrotropical, Diopsidae, Laboulbeniales, *Rhizomyces*, taxonomy.

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Introduction

About 10% of the approximately 2100 described species of Laboulbeniales Lindau, parasitic fungi of arthropods, is associated with the Diptera Linnaeus, 1758. Among the latter, the Diopsidae Billberg, 1820 (stalk-eyed flies) is one of the many families reported as hosts of the Laboulbeniales. The Diopsidae is one of the two families (together with the Chloropidae Rondani, 1856) from which three different genera of the Laboulbeniales have been recorded: *Laboulbenia* Mont. & C.P.Robin (3 species), *Rhizomyces* Thaxt. (10 species) and *Stigmatomyces* H.Karst. (10 species) (Rossi 1987, 1990a, 1990b). Actually, a diopsid is one of only two insects on which three parasites of three different genera have been found concurrently (Rossi 1982). Moreover, the only fossil species of the Laboulbeniales, *Stigmatomyces succini* W.Rossi, Kotrba & Triebel, was found on a diopsid, *Prosphyracephala succini* (Loew, 1873), in a piece of Baltic amber estimated to be 35 to 55 million years old (Rossi *et al.* 2005).

Rhizomyces is a relatively small genus with ten species described thus far, all of which are parasitic on Afrotropical Diopsidae (Thaxter 1931; Rossi 1990a). The records of these fungi are not numerous

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Table 1. Literature records for the *Rhizomyces* Thaxt. species, indicating host and country. If necessary, host names have been updated to bring them in line with actual views on the taxonomy of Diopsidae. Records of unidentified species (such as *Rhizomyces* sp.) and confusing records were not reported.

	Host	**Country**	**Reference**
Rhizomyces canzonerii W.Rossi	*Diasemopsis* cf. *silvatica* Eggers, 1916	Sierra Leone	Rossi (1990a)
Rhizomyces circinalis Thaxt.	*Diopsis apicalis* Dalman, 1817	Gambia	Thaxter (1918, 1931)
	Diopsis apicalis Dalman, 1817	Togo	Feijen (1978)
	Diopsis mayae Feijen & Feijen, 2017	Malawi, Mozambique, Tanzania	Feijen & Feijen (2017)
Rhizomyces confusus Thaxt.	'*Diopsis*'	Cameroon	Thaxter (1918)
	'*Diopsis*'	South Africa	Thaxter (1918)
	Chaetodiopsis meigenii (Westwood, 1837)	Sierra Leone	Rossi & Leonardi (2018)
Rhizomyces cornutus Thaxt.	*Diopsis punctiger* Westwood, 1837	Cameroon	Thaxter (1918, 1931)
	Diopsis atricapilla Guérin-Méneville,1837–1844	DR Congo	Feijen (1978)
Rhizomyces crispatus Thaxt.	'*Diopsis*'	South Africa	Thaxter (1900, 1931)
	'*Diopsis*'; *Diasemopsis coniortodes* Speiser, 1910	Tanzania	Thaxter (1908, 1931)
	'*Diopsis*'	Togo	Thaxter (1908)
	Diasemopsis interrupta Curran, 1931 *Diasemopsis quadrata* Curran, 1931 *Chaetodiopsis meigenii* (Westwood, 1837)	Cameroon	Thaxter (1931)
	Diasemopsis aethiopica (Rondani, 1873)	DR Congo	Thaxter (1931)
	Diasemopsis aethiopica (Rondani, 1873)	DR Congo	Collart (1947)
	Diasemopsis wolteri Lindner, 1954	Central African Republic	Lindner 1962
	Diasemopsis sp.; *Diasemopsis signata* (Dalman, 1817)	Sierra Leone	Rossi (1990a)
	Diasemopsis aethiopica (Rondani, 1873)	Kenya	Rossi (1990a)
Rhizomyces ctenophorus Thaxt.	*Diopsis longicornis* Macquart, 1835	Liberia	Thaxter (1896)
	Diopsis longicornis Macquart, 1835	Tanzania	Thaxter (1896, 1908)
	Diopsis longicornis Macquart, 1835	Togo	Feijen (1978)
	Diopsis longicornis Macquart, 1835	Sierra Leone	Rossi (1982)
	Diopsis apicalis Dalman, 1817	Sierra Leone	Rossi (1982)
	Diopsis mayae Feijen & Feijen, 2017	Malawi, Mozambique, Tanzania	Feijen & Feijen (2017)
Rhizomyces cucullatus Thaxt.	*Diopsis diversipes* Curran, 1928	DR Congo	Thaxter (1931)
Rhizomyces gibbosus Thaxt.	*Diopsis* sp.	Tanzania	Thaxter (1901)
Rhizomyces gracilis Thaxt.	*Diasemopsis* sp.	Tanzania	Thaxter (1918, 1931)
	Diasemopsis sp.	Sierra Leone	Rossi (1990a)
	Diasemopsis aethiopica (Rondani, 1873)	Kenya	Rossi (1990a)
Rhizomyces kamerunus Thaxt.	*Chaetodiopsis meigenii* (Westwood, 1837)	Cameroon	Thaxter (1918, 1931)

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and four species are known only from the type series. All previous records of identified species of *Rhizomyces* are summarized in Table 1. A few of these records need some comments and clarification:

1) The host insects reported by Thaxter (1918, 1931) as *Diopsis* sp. (in quotation marks in Table 1) should be considered as unidentified stalk-eyed flies.

2) The drawing given by Collart (1947: 27, fig. 8) is taken from Thaxter (1908: pl. 52, fig. 19) (as stated by Collart himself in a note on p. 26). This thallus represents what was later described as *R. confusus* Thaxt. However, the thalli in the pertinent slide in Collart's collection preserved in BR belong to the 'true' *R. crispatus* Thaxt. (André De Kesel pers. comm.).

3) Lindner (1962) reports *R. gracilis* Thaxt. on *Diasemopsis wolteri* Lindner, 1954 from "French Congo, Fort Crampel", but his detailed drawing (Lindner 1962: 4, fig. 2) clearly shows that the fungus is *R. crispatus*. In the same paper *Stigmatomyces* sp. is also reported on *Diopsis planidorsum* Hendel, 1923 and *Diopsis erythrocephala* Westwood, 1837. Again, the parasite can be safely identified as *Stigmatomyces diopsis* Thaxt. by means of the drawing (Lindner 1962: 4, fig. 2) and the photograph (Lindner 1962: 5, fig. 3) accompanying the record.

4) The insect hosts of *R. ctenophorus* Thaxt. from Sierra Leone (Rossi 1982) were reported as *Diopsis thoracica* Westwood, 1837 and *Diopsis tenuipes* Westwood, 1837, but were later identified by H.R. Feijen by their senior synonyms as respectively *Diopsis longicornis* Macquart, 1835 and *Diopsis apicalis* Dalman, 1817; likewise, host *Diopsis thoracica* from Togo (Feijen 1978) becomes *Diopsis longicornis*. This latter species was also erroneously reported as a junior synonym of *Diopsis macrophthalma* Dalman, 1817 (Feijen 1987).

The name *Rhizomyces* was given to the genus for the most peculiar feature of the type species: the presence of rhizoids at the base of the thallus penetrating the cuticle of the host insects. Rhizoids are missing in four of the species described later (*R. confusus*, *R. crispatus*, *R. gracilis*, and *R. kamerunus* Thaxt.).

In the present paper three new species of *Rhizomyces* occurring on Afrotropical Diopsidae are described. Two of these fungi display quite peculiar characteristics: one (*R. ramosus* W.Rossi & Feijen sp. nov.) has a ramified thallus (unique in its genus), the other (*R. forcipatus* W.Rossi & Feijen sp. nov.) has a folded basal cell acting like a forceps.

A key to all the species of *Rhizomyces*, including the new ones, is also given.

Material and methods

The diopsids bearing Laboulbeniales were collected by means of a sweeping net. The flies were placed in 75–80% ethyl alcohol in the field for transport to the laboratory, where they were examined with a dissecting microscope. The thalli of the Laboulbeniales were removed from the hosts by means of an entomological pin (#3) and permanent slides were prepared following the method described by Rossi & Santamaría (2015), with the exception of a few old slides (HF in RMNH) in which Hoyer's medium was used as mounting medium. Holotypes are deposited in the Botanical Museum of Florence (FI), while the host insects are preserved in Naturalis Biodiversity Center, Leiden (RMNH, formerly Rijksmuseum van Natuurlijke Historie).

Photomicrographs were made with a Jenoptik ProgRes 10 Plus digital camera on a Leica DMR microscope equipped with differential interference contrast optics (DIC).

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Results

Order Laboulbeniales Lindau
Suborder Laboulbeniineae Thaxt.
Family Laboulbeniaceae Peyr.

Genus ***Rhizomyces*** Thaxt., 1896

Memoirs of the American Academy of Arts and Sciences 13 (6): 307 (Thaxter 1896).

Type

Rhizomyces ctenophorus Thaxt., *Memoirs of the American Academy of Arts and Sciences* 13 (6): 308 (Thaxter 1896).

Rhizomyces forcipatus W.Rossi & Feijen sp. nov.
MycoBank No: MB827885
Fig. 1A–C

Description

Basal cell hyaline, subsigmoid, more than twice as long as the maximum width, lying flat on the insect, with the black foot placed laterally and flanked by a depression apparently working as a sucker. Suprabasal cell (cell II) variable in size, shape and color, usually smaller and sometimes darker than the basal. Stalk cell of the appendage (cell III) distinctly smaller and darker than cell II, from which it is separated by a slightly oblique septum. Free appendage usually exceeding the perithecial apex, with the axis consisting of 12–16 almost hyaline cells gradually longer and more slender, each bearing a branch arising from the upper, outer angle; these branches consist of an elongate basal cell bearing distally 2–4 bottle-shaped antheridia with darker necks and a one-celled short, hyaline, slender and erect cell which gives rise laterally to a vertical series of 4–8 very slender branchlets; the latter are dark brown, distinctly curved, with hyaline and enlarged tips. Perithecial stalk-cell (cell VI) long, slender, flexuous and hyaline (or almost so). Basal cell region well distinguished, tinged with very pale brown, concolorous with the perithecial venter, consisting of relatively large, subequal cells with their outer margins bulging outwards. Perithecium almost three times longer than maximum width, the venter very slightly inflated, distinctly enlarged below the brownish tip, which tapers rather abruptly to a subspherical apex. Trichogyne consisting of a club-shaped cell from which arise distally 4–5 spreading branchlets which are curved or sigmoid, sometimes bifurcate, gradually tapering towards the apex. Length from foot to perithecial apex 210–345 µm; from foot to the apex of the appendage 250–400 µm; perithecium 70–75 × 25–30 µm; antheridia about 20 µm.

Etymology

From Latin *forceps*, referring to the forceps-like shape and function of the basal cell.

Types

KENYA: Naro Moru river, on *Centrioncus decoronotus* Feijen, 1983, 20 Jul. 1987, *H.R. Feijen* leg. (holo-: FI 4100a; iso-: FI 4100b); same data as preceding except different host specimens (para-: FI 4099, FI 4101, FI 4102).

MALAWI: Mt. Soche, on sternites of male *Centrioncus jacobae* Feijen, 1983, 19 Mar. 1972, *H.R. Feijen* leg. (para-: FI 4103, RMNH-HF-74); same data as preceding except on wing of the same host

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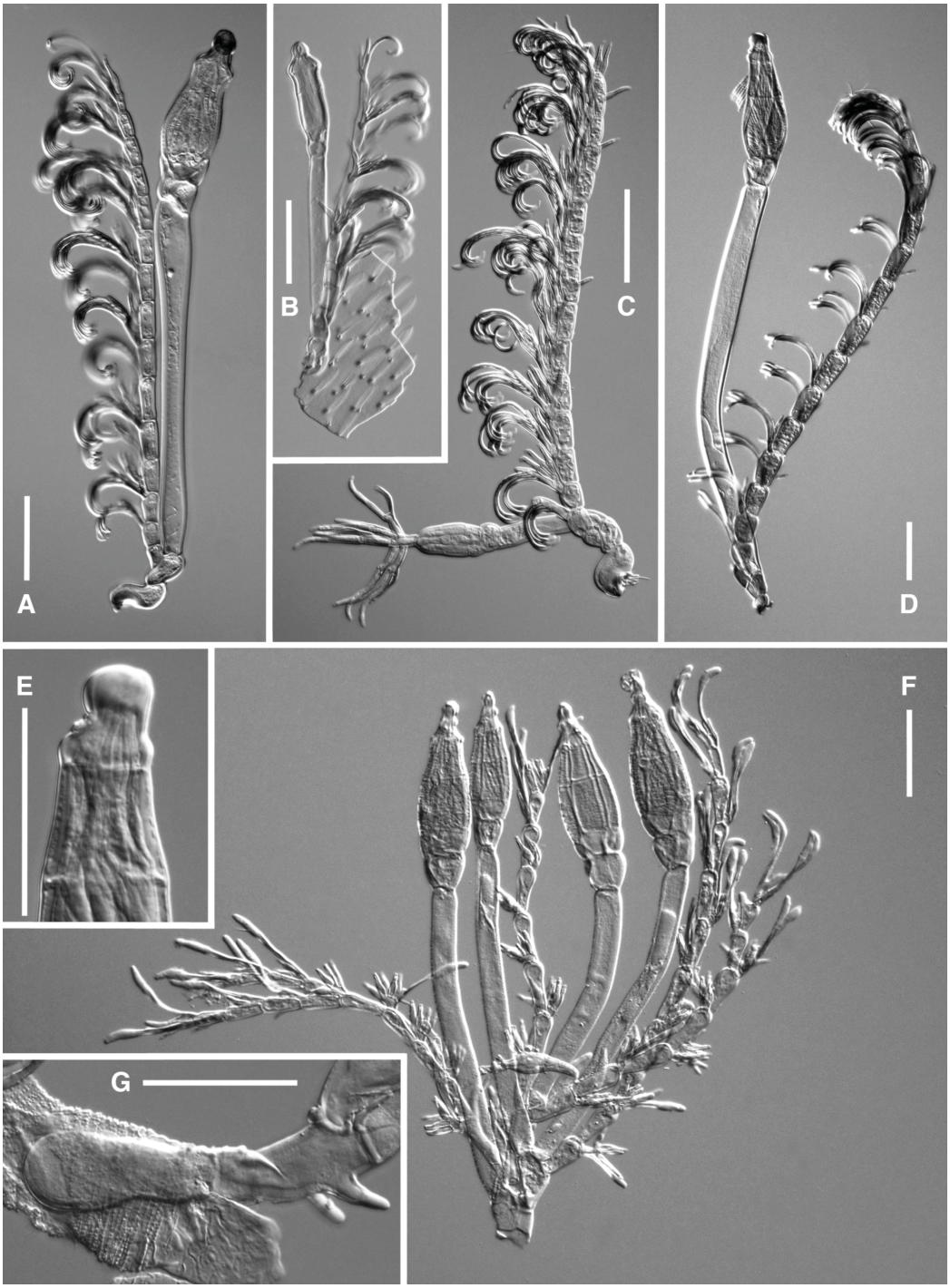

Fig. 1. Photomicrographs of the new species of *Rhizomyces* Thaxt.: **A**. *R. forcipatus* W.Rossi & Feijen sp. nov. (FI 4100a). **B**. Thallus of *R. forcipatus* sp. nov. from the wing of *Teloglabrus* sp. (FI 4125). **C**. Immature thallus of *R. forcipatus* sp. nov. showing the trichogyne and the basal cell holding firmly a piece of the exoskeleton of the host insect (FI 4099). **D**. *R. tschirnhausii* W.Rossi & Feijen sp. nov. (FI 4091). **E**. Upper portion of the perithecium of *R. tschirnhausii* sp. nov. (FI 4090). **F**. *R. ramosus* W.Rossi & Feijen sp. nov. (FI 4201a), amid the four mature perithecia, near the base of the stalk cells, it can be seen a fifth very immature perithecium bearing the trichogyne. **G**. *R. ramosus* sp. nov. (FI 4201a), the pyriform haustorium with remains of the host integument and cell I showing two primordia of new branches. Scale bars: 50 μm.

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specimen (para-: RMNH-HF-90); Mt. Soche, on sternites of male *Centrioncus jacobae*, 7 Jan. 1973, *H.R. Feijen* leg. (para-: RMNH-HF-86 , RMNH-HF-87); same data as preceding except on wing of female *Centrioncus jacobae* (para-: RMNH-HF-88); Mt. Ndirande, on wing of female *Centrioncus jacobae*, 16 Feb. 1974, *H.R. Feijen* leg. (para-: RMNH-HF-73).

IVORY COAST: Amanikro, on the wing of a female *Centrioncus decellei* Feijen, 1983, Sep. 1961 (para-: RMNH-HF-3).

REPUBLIC OF SOUTH AFRICA, Eastern Cape, Hogsback, Tyume Forest, 32.6029° S, 26.9384° E, 1166 m a.s.l., on *Teloglabrus* sp., 10 Apr. 2010, *A.H. Kirk-Spriggs & V. de Swart* leg. (para-: FI 4125, FI 4126); Western Cape, Buffelsbos forest, 33.9026° S, 23.6388° E, 400 m a.s.l., on *Teloglabrus australis* Feijen, 1983, 27 Mar. 2009, *A.H. Kirk-Spriggs* leg. (para-: FI 4129).

Remarks

The description is based on the parasites obtained from the sternites of the host insects; thalli growing on the wings are smaller (180–255 µm from foot to perithecial apex: Fig. 1B). The thalli observed on *Centrioncus jacobae* are paler, more slender and longer on average (up to 550 µm from foot to perithecial apex).

Rhizomyces forcipatus sp. nov. is distinguished from all the other species in the same genus by the peculiar shape and function of the basal cell. The latter is turned in, forming a 'forceps' which grasps a fold of the exoskeleton of the host insect (Fig. 1C).

Rhizomyces forcipatus sp. nov. bears a superficial resemblance with *R. crispatus*. However, the latter species has a stockier habitus, a more luxuriant appendage, a distinctly smaller and darker cell III, a darker and subconical tip of the perithecium, and it obviously differs from the new species in the shape of the basal cell.

The presence of this fungus was already reported on various species of *Centrioncus* Speiser, 1910 and *Teloglabrus* Feijen, 1983 by Feijen (1983).

Rhizomyces forcipatus sp. nov. is found on several species of the genera *Centrioncus* and *Teloglabrus*. This is remarkable, since the species of these genera occur in Afromontane forests and have very limited, allopatric distributions (Feijen 1983). The rate of parasitism came to 17%; however, this figure was lowered by the large *Teloglabrus sanorum* Feijen, 1983 sample of young flies. In female flies, *R. forcipatus* sp. nov. was only found on the wings. In male hosts, the thalli were found on the wings (79%) and on the sterna (30%). Thalli were most often found on both wings together (61%), followed by right wing only (32%). 90% of thalli found on the sterna of males flies were on the left hand side (Table 2).

Rhizomyces ramosus W.Rossi & Feijen sp. nov.
MycoBank No: MB827886
Fig. 1F–G

Description

Basal cell hyaline, usually subcylindrical, distinctly longer than broad, producing more than one suprabasal cell in sequence. The basal cell extends under the integument of the host in a relatively small, ovoid or pear-shaped haustorium. Suprabasal cells irregularly trapezoidal, about as long as the basal, bearing distally the stalk cell of the perithecium paired either with the appendage or with another cell similar in shape and size, from which arise a second perithecium and the appendage. Appendages slender

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Table 2. Prevalence of *R. forcipatus* W.Rossi & Feijen sp. nov. on host species of *Centrioncus* Speiser, 1910 and *Teloglabrus* Feijen, 1983. Given are: totals of hosts examined (♀ and ♂), totals with *Rhizomyces* Thaxt., infection location. (n. a. = not available).

	n ♀	n ♂	infected flies		infected ♀		infected ♂	
			n ♀	n ♂	site	n	site	n
Centrioncus decellei Feijen, 1983	1		1		wings	1		
Centrioncus decoronotus Feijen, 1983	22	20	2	12	n. a.		n. a.	
Centrioncus jacobae Feijen, 1983	33	39	5	13	wings	5	wings	11
							sterna	2
Centrioncus prodiopsis Speiser, 1910	2	2		1			wings	1
Teloglabrus australis Feijen, 1983	23	41	2	8	wings	2	wings	7
							sterna	2
Teloglabrus curvipes Feijen, 1983	2	2	1		wings	1		
Teloglabrus duplospinosus Feijen, 1983		4		1			wings	1
Teloglabrus pelecyformis Feijen, 1983	5	3	1	2	wings	1	wings	1
							sterna	1
Teloglabrus sanorum Feijen, 1983	77	53	3	1	wings	3	sterna	1
Teloglabrus tsitsikamensis Feijen, 1983	1	4		1			wings	1
Teloglabrus trituberculatus Feijen, 1983	3	1	1	1	wings	1	sterna	1
Teloglabrus vumbensis Feijen, 1983	8	4	1		wings	1		
Teloglabrus sp.	18	24	3	5	wings	3	wings	4
							sterna	3

and flexuous, reaching the tip of the perithecium when erect, the main axis consisting of 8–11 club-shaped cells separated by conspicuous constrictions; the appendages can be either simple or bifurcate from the base, sometimes also bearing 1–3 short lateral ramifications made of 1–4 cells. Each cell of the axis bears close to the base of the following a relatively large cell irregularly shaped, which gives rise to antheridia and sterile branchlets. The antheridia are more numerous in the lower portion of the appendage (up to 5 per cell) and are bottle-shaped with darker necks. The sterile branchlets are gradually longer and more numerous in the upper portion (up to 3 and exceptionally 4 per cell): are slender and chestnut brown, with a hyaline distal portion variably enlarged and variably curved. Perithecial stalk-cell (cell VI) very long and slender, of nearly constant diameter, pale amber yellow, with a roughened surface, abruptly distinguished distally from the relatively large and externally prominent basal cell region. Perithecium brownish yellow with the surface roughened by transverse ridges formed by wart-like elevations, broadly pear-shaped, its margins concave distally below a crown of small protuberances which subtend the paler and abruptly tapering tip; the apex is nipple-shaped, subtended on one side by two hemispherical prominences. Up to seven perithecia (six mature and one immature) were seen in a single thallus. Length from the external tegument of the host insect to perithecial apex up to 415 µm; longest appendages 365 µm; perithecia 85–102 × 30–40 µm; haustorium 20–62 × 15–25 µm.

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Etymology

From the Latin '*ramosus*', branched.

Types

UGANDA: Bushenyi distr., Kazinga Channel SE of Katunguru, 0.1292° S, 30.0525° E, 925 m a.s.l., on *Diopsina nitida* (Adams, 1903), 26 Mar. 2012, *M. von Tschirnhaus* leg. (holo-: FI 4109a; iso-: FI 4109b); same data as preceding except different host specimen (para-: FI 4093).

Remarks

Rhizomyces ramosus sp. nov. can be distinguished at first glance from all the other species in the same genus by its ramified thallus, but also the shape and the roughened surface of the perithecia are very characteristic.

The presence of this fungus was already reported on *Diopsina nitida* by Feijen & Feijen (2013).

Rhizomyces tschirnhausii W.Rossi & Feijen sp. nov.
MycoBank No: MB827887
Fig. 1D–E

Description

Basal cell hyaline, relatively small, distinctly wider than tall, with a small black foot placed laterally and flanked by a depression apparently functioning as a sucker. Suprabasal cell (cell II) much larger, yellowish gray, bearing distally the stalk cell of the perithecium (cell VI) paired with the stalk cell of the appendage (cell III). Appendage slender, flexuous, usually sigmoid, seldom exceeding the tip of the perithecium, consisting of 13–17 pale brown cells separated by conspicuous constrictions, the stalk cell subtrapezoidal or irregular, about as long as its maximum width, the others gradually longer, up to twice as long as broad, each bearing, except sometimes the lowest one, a branch arising from the upper, outer angle; these branches consist of a very small basal cell bearing 2–4 slender and relatively small antheridia with darker necks and a one-celled short, hyaline, slender and erect cell that gives rise laterally to a vertical series of slender branchlets; the latter are 2 or 3 in the lower portion of the appendage, up to 5 in the upper portion, black and variably curved, slightly enlarged at the nearly hyaline tips. Stalk-cell of the perithecium very long, erect, subhyaline, nearly uniform. Basal cell region abruptly distinguished, barrel-shaped, orange with a tinge of red, concolorous with the perithecium. The latter about three times longer than the maximum width, its wall cells spirally twisted and marked by transverse striae, the venter slightly inflated, the distal portion tapering gradually and symmetrically to the tip, which is abruptly distinguished, asymmetrical, with one of the lips much larger and hemispherical bulging outwards. Length from foot to perithecial apex 310–710 µm; from foot to the apex of the appendage 310–540 µm; perithecium 100–140 × 35–50 µm; antheridia 16–18 µm; ascospores about 28 µm.

Etymology

Named after Michael von Tschirnhaus, distinguished student of the Diptera and collector of the new species.

Types

UGANDA: Kasese distr., 17 km WNW of Kasese, near Nyakalengrja, 0.3444° N, 30.0394° E, 1630 m a.s.l., on the abdomen of a male of *Diopsina africana* (Shillito, 1940), 21 Mar. 2012, *M. von Tschirnhaus* leg. (holo-: FI 4091); Kabarole distr., crater landscape WNW of Fort Portal, 0.6778° N,

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30.2250° E, 1555 m a.s.l., near the tip of the abdomen of a male of *Diopsina africana*, 13 Mar. 2012, *M. von Tschirnhaus* leg. (para-: FI 4090); Kasese distr., 11 km WNW of Kasese, NW above Kilembe village, 0.2217° N, 29.9900° E, 1555 m a.s.l., on the abdomen of a female of *Diopsina africana*, *M. von Tschirnhaus* leg. (para-: FI 4092).

Remarks

Because of the absence of rhizoids and the slender habitus, *R. tschirnhausii* sp. nov. bears a superficial resemblance with *R. gracilis*, from which it differs for the showy, rounded bulge at the apex of the perithecium, the color of the latter, the stockier and darker cells of the axis of the appendage, and for other minor features. It might be noted that the ascospores are quite small compared with the size of the perithecium: which is a characteristic of all the species in the genus *Rhizomyces*.

Key to all the *Rhizomyces*

It should be noted that *R. cornutus* Thaxt., *R. cucullatus* Thaxt. and *R. gibbosus* Thaxt. are very closely related and the distinguishing characters (in brackets) reported in the key are those given with the original descriptions (Thaxter 1901, 1918, 1931).

1. Thallus not ramified, usually bearing a single perithecium (very rarely 2) 2
− Thallus ramified, bearing more than one perithecium .....***R. ramosus*** W.Rossi & Feijen sp. nov.

2. Perithecium lacking any outgrowth or bulge near the apex 3
− Perithecium bearing an outgrowth or a bulge near the apex 9

3. Perithecial tip abruptly distinguished and blackened 4
− Perithecial tip not abruptly distinguished and not blackened 5

4. Basal cell subsigmoid, bearing a depression ..... ***R. forcipatus*** W.Rossi & Feijen sp. nov.
− Basal cell not as above .....***R. crispatus*** Thaxt.

5. Thallus never reaching 1 mm in length, not bearing a rounded hausorium 6
− Thallus very slender and elongate, exceeding 1 mm in length, bearing a rounded hausorium penetrating the exoskeleton of the host ..... ***R. canzonerii*** W.Rossi

6. Thallus not bearing a haustorium penetrating the exoskeleton of the host 7
− Thallus bearing a ramified haustorium penetrating the exoskeleton of the host .....***R. ctenophorus*** Thaxt.

7. Perithecium symmetrical or almost so 8
− Perithecium distinctly asymmetrical .....***R. confusus*** Thaxt.

8. Perithecial stalk-cell at least 3 times longer than the perithecium; appendage and perithecial apex reaching the same height, more or less ....***R. gracilis*** Thaxt.
− Perithecial stalk-cell about as long as the perithecium; appendage distinctly exceeding in length the perithecial apex .....***R. kamerunus*** Thaxt.

9. Perithecium bearing a rounded bulge or a short outgrowth just below the apex 10
− Perithecium bearing a divergent, elongate, finger-like outgrowth just below the apex ....***R. circinalis*** Thaxt.

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10. Thallus bearing a ramified haustorium penetrating the exoskeleton of the host 11
− Thallus not bearing a haustorium penetrating the exoskeleton of the host ....***R. tschirnhausii*** W.Rossi & Feijen sp.nov.

11a. Perithecial outgrowth "relatively narrow and tooth-like" .....***R. cornutus*** Thaxt.
11b. Perithecial outgrowth "slightly curved outwards, resembling a peaked hood" .... ***R. cucullatus*** Thaxt.
11c. Perithecial outgrowth "broadly rounded and divergent" ..... ***R. gibbosus*** Thaxt.

Discussion

Laboulbeniales are relatively common on African Diopsidae, but are considerably less common on Oriental Diopsidae and are unknown from the extant Holarctic Sphyracephalinae Hennig, 1965. Three reasons can be given for this abundance. Diopsidae live in humid conditions: in rainforests, wet places in savannas and along rivers. Their gregarious behavior is the second factor. Large congregations of thousands of stalk-eyed flies are common and can consist of 10–20 species (Feijen *et al.* 2017). A third factor is the longevity of the Diopsidae. In Africa, the species are often univoltine with a lifespan of around a year. Due to the shift from earlier to later reproducing flies an overlap occurs between the generations. In, for instance, *Diopsis longicornis* this overlap occurred in the paddy fields of Malawi to around 2–3 months. Young flies are, of course, without fungi, but during their lifespan the percentage of parasitism increases: in populations of *Diopsis longicornis*, for example, it can almost reach a 100%, especially in the males (Feijen 1984). Infection rates increase strongly during the aestivation period, suggesting that transmission through non-sexual physical contact in the aggregations is an important mechanism of spread for *Rhizomyces* and other Laboulbeniales infecting diopsids. That high host population density, such as aggregations, can promote a transmission of Laboulbeniales was also seen in *Hesperomyces virescens* Thaxt. infecting the coccinellid beetle *Harmonia axyridis* (Pallas, 1773) (Riddick & Schaefer 2005) and in *Laboulbenia slackensis* Cépède & F.Picard infecting the carabid beetle *Pogonus chalceus* (Marsham, 1802) (De Kesel 1993).

In Asia, species of the genera *Cyrtodiopsis* Frey, 1928, *Teleopsis* Rondani, 1875 and *Megalabops* Frey, 1928 are often multivoltine and have a relatively short lifespan. Wilkinson & Dodson (1997) stated that the average adult ages of two field-caught species of *Cyrtodiopsis* were estimated to be over 30 days. This is likely to form main reason why Laboulbeniales are relatively uncommon in these oriental genera. The short lifespan appears to form the key factor in this case and not the large number of generations per year. This is different from the situation in *Hesperomyces virescens* parasitizing *Harmonia axyridis*. There, Ceryngier & Twardowska (2013) list the host abundance, multivoltinism with overlapping generations, the high level of promiscuity and the overwintering in mass aggregations as factors facilitating the spread of the parasite. However, in this case the multivoltine hosts may live and reproduce for periods as long as three years.

To date, species of *Rhizomyces* have been found only on African Diopsidae of the genera *Centrioncus* Speiser, 1910, *Teloglabrus* Feijen, 1983, *Diasemopsis* Rondani, 1875, *Chaetodiopsis* Séguy, 1955, *Diopsis* Linnaeus, 1775 and *Diopsina* Curran, 1928. It appears that these parasites are more common on the stalkless genera of Diopsidae (*Centrioncus* and *Teloglabrus*) and on the *Diasemopsis* genus-group than on the genera *Diopsis* and *Diopsina*. In *Diopsis*, species of *Laboulbenia* and *Stigmatomyces* are much more common than those of *Rhizomyces*; also, *Rhizomyces* has never been encountered on the thousands of specimens examined of the almost cosmopolitan genus *Sphyracephala* Say, 1828. The species of *Rhizomyces* lacking haustoria only occur in *Centrioncus*, *Teloglabrus*, *Diasemopsis* and *Chaetodiopsis*. These are all more basal branches of the Diopsidae. On the other hand, the parasites of *Rhizomyces* with ramified haustoria are only found in the more derived genus *Diopsis*. This could represent a case of coevolution, if it is assumed that the rhizoidal apparatus of the latter parasites represents an apomorphic

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character. The *Diasemopsis* genus-group and *Diopsis* separated more than 34 million years ago (F.A.A. Feijen, pers. comm.), so this could also give an indication of the age of the two *Rhizomyces* groups. Although several of the very common species of *Diasemopsis* (like *Diasemopsis aethiopica* (Rondani, 1873)) and species of *Diopsis* (like *Diopsis cruciata* Curran, 1934) can be found in large mixed groups for more than half of the year, no horizontal exchange of the parasites of *Rhizomyces* belonging to the two different groups has ever been observed thus far. A horizontal transfer of Laboulbeniales between different hosts can occur according to Scheloske (1969), but he stressed that "die entsprechenden Parasiten dabei nicht zu eng specialisiert sein dürfen" (i.e., the parasites concerned should not be too specialized). Scheloske discussed the possibility of "Ökologische Specifität bei Laboulbeniales" (ecological specificity) and described a case of ants and a beetle living in the nest of these ants that were both parasitized by the same species of *Laboulbenia*. Rossi (2011) also discussed the phenomenon of a host switch (or horizontal transfer) in Laboulbeniales. However, it appears that in the case of the two groups of *Rhizomyces*, these are too specialized to allow for a horizontal transfer between relatively distant taxa of diopsids although these taxa can be found together for long periods in joint aggregations.

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