

Rhachomyces (Ascomycota, Laboulbeniales) parasites on cave-inhabiting Carabid beetles from the Pyrenees

by

Sergi Santamaria^{1*} and Arnaud Faille²

¹Unitat de Botànica, Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia, Facultat de Ciències, Universitat Autònoma de Barcelona, 08193-Bellaterra (Barcelona), Spain

²C.P.50. UMR 5202 du CNRS / USM 601, Origine, Structure et Évolution de la Biodiversité, Muséum National d'Histoire Naturelle, Dept. Systématique et Évolution, Bat. Entomologie, 45 rue Buffon, 75005 Paris, France

With 55 figures and 1 table

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Abstract: The species of *Rhachomyces* parasitizing species of the cave-dwelling genera *Aphaenops*, *Geotrechus* and *Hydraphaenops* (Trechini) from the Pyrenees (France and Spain) are studied. Examination of many collections and revision of literature reveal that five species of *Rhachomyces* are involved. *Rhachomyces aphaenopsis* is the most common and a fairly variable species, including the synonyms *R. dedyi* and *R. jeannelii*. Previous reports of other taxa like *R. hypogaeus*, *R. stipitatus*, *R. stipitatus* var. *pallidus* and *R. maublancii* must be removed from the list of Pyrenean parasites of Trechini beetles as they also refer to *R. aphaenopsis*. The status of *R. girardii* is validated by addition of a Latin diagnosis. *Rhachomyces pyrenaicus*, which was only known from the type, was collected again on another host and locality. Additionally, two new species are described: *R. ilerdensis* on *Geotrechus seijasi* from Spain and *R. spadiceus* on *Aphaenops* spp. from France. The characteristics of extant species are discussed and defined, with special emphasis on *R. aphaenopsis*. Other taxa are compared when necessary to eliminate the confusion accumulated by old records in the literature. Hosts and localities are also reviewed to offer up-to-date information for all species studied of *Rhachomyces* occurring in the Pyrenees.

Introduction

The genus *Rhachomyces* was erected in 1895 by Thaxter to accommodate six species previously described in the genus *Acanthomyces*, a preoccupied name (Thaxter 1892). Many new species were successively added, and Tavares (1985) reported 70 species (including 8 not validly described), 3 varieties, and 2 subspecies in her monograph.

*corresponding author, e-mail: sergi.santamaria@uab.es

Species described later and hence not included by Tavares are: *R. kenodactyli* W.Rossi and *R. moorei* W.Rossi (Rossi 1984), *R. insularis* T.Majewski & K.Sugiy. (Majewski & Sugiyama 1985), *R. calypso* Balazuc (1986), and *R. pyrenaicus* Santam. (Santamaria 1989), the last described species in this genus to date. Typical hosts are Carabid beetles, but 13 species parasitize species of the Staphylinidae (Tavares 1985).

Among the species of fungi parasitizing Carabidae, those inhabiting cave-dwelling insects have attracted the attention of several authors (Lepesme 1942, Boyer-Lefèvre 1965, 1966, Balazuc 1970, Balazuc & Juberthie 1983, Santamaria 1989). Such fungi fascinate mycologists because the hosts are highly specialized and adapted to cavernicolous life, comprising an important number of endemic or rare species. Many laboulbeniologists were also entomologists, and therefore they linked the curiosity for these beetles with that of their parasites. Moreover, it is broadly accepted that biotrophic parasites, as the Laboulbeniales, have evolved together with their hosts (Tavares 1985).

Among all cave-inhabiting beetles, the tribe Trechini (Coleoptera Carabidae Trechinae) deserve emphasis because it includes the most important troglobiotic species of *Rhachomyces*. The tribe Trechini is considered as a Gondwanian group and now may also be found in New Zealand, Europe, North America, and Africa. Two main migrations of Trechini into Europe occurred during the Tertiary (Jeannel 1942). Some species of the first migration reached the Pyrenees, and colonized the frequent subterranean biotopes yielding species of *Aphaenops*, *Geotrechus* and *Hydraphaenops*, which are presently parasitized by *Rhachomyces*. These three genera are found in karstic areas of the Pyrenees and are mainly diversified in the northern part of the range along the Pleistocene glaciation boundaries. A few species were described from the southern slope of the chain. *Aphaenops* and *Hydraphaenops* are very highly modified. All of them are completely blind, unpigmented and apterous. These hygrophilous species live in all karstic areas, in caves, cracks or MSS (“Milieu Souterrain Superficiel”, Juberthie et al. 1980) from high altitude cold chasms (e.g. *H. penacollaradensis*, *A. hidalgoi*, *A. loubensi*, *A. valleti*, etc.) to relatively warm low altitude stations (e.g. *A. cerberus* and *A. crypticola*). Some species in the subgenus *Geaphaenops* are endogenous. The species belonging to the genus *Geotrechus* are less modified in shape and live, like *Geaphaenops*, in the deep soil and at the entrance of caves. All are extremely hygrophilous.

The study of species of *Rhachomyces* on these hosts from the Pyrenees has been the subject of some papers (Boyer-Lefèvre 1965, 1966, Balazuc & Juberthie 1983, Santamaria 1989), where a large amount of information was given, including some mistakes, making reassessment necessary (see Table 1). The aim of this work is to provide an up-to-date list of extant species of *Rhachomyces* parasitizing the troglobiont genera *Aphaenops*, *Geotrechus*, and *Hydraphaenops* in the Pyrenees, including hosts and localities, with corrections when necessary, and with an attempt to define the taxonomic framework of fungal species.

Materials and methods

Host insects were collected by several entomologists, and were preserved dry or in 70% ethanol. As indicated in SPECIMENS EXAMINED, some of these insects are kept in entomological collections of

Museums as “Museu de Zoologia de Barcelona, Spain” (MZB) and “Muséum National d’Histoire Naturelle, Paris” (MNHN). Fungi were prepared following methods described in previous works (Santamaria 1998). Slides are kept in the BCB Mycotheca (at the institutional address of the senior author) or in PC (“Muséum National d’Histoire Naturelle”, at Paris, for slides indicated as duplicates in specimens examined). Some of the fungi are included in DMHF (dimethyl hydantoin formaldehyde), and kept pinned with their host insects by means of a plastic label. Photographs were made using a Jenoptik ProgRes 10 Plus digital camera on a Leica DMR microscope equipped with differential interference contrast optics (DIC). We have also carried out an exhaustive search of references in relation to the species treated here. For the host systematic treatment we have followed Lorenz (2005), except for the genus name *Aphaenops*. The genus was described as *Aphoenops*, and Lorenz (2005) follows strictly this treatment for precedence; but with the support of articles 23.9 and 58 of International Code of Zoological Nomenclature (Ride et al. 1999) the term *Aphaenops* is preferable and here adopted. For a better reading and easy understanding, authorities and systematic arrangement of hosts are omitted, but can be found in specialized literature like Lorenz (2005). A map with localities is provided (Fig. 1), to complement the data included in Table 1. Coordinates in the map and in Table 1 are in decimal degrees. The original language is respected in toponymy, with the following meanings: **Av.**, Aven (french) = Avenc (catalan) = Gouffre (french) = Sima (spanish) = Chasm (english); **Cv.**, Cueva (spa.) = Cova (cat.) = Cave (eng.); **Gr.**, Grotte (fr.) = Grotto (eng.) = Gruta (spa.).

Results and discussion

Rhachomyces Thaxter, Proc. Amer. Acad. Arts 30: 467. 1895

In the genus *Rhachomyces* the main axis of the thallus is formed laterally from cell II, so it is in truth a secondary axis (sax, Fig. 5). The primary appendage (pa) is the lowermost appendage, above the cell III and the dark spore or primary septum (a, Fig. 5). Cells of the secondary axis divide laterally to develop cells of the tertiary axis, which form the base for the appendages. Three types of appendages (regardless of the primary appendage) can be found in a thallus of *Rhachomyces*, and their characteristics must be included in the descriptions of species, besides the characteristics of the secondary axis and the perithecium. These appendages were defined by Tavares (1985) as follows: (1) **type a** - long, dark, sterile appendages, low in the axis (sa “a”, Fig. 4); (2) **type b** - short to long, very variable sterile appendages, high in the axis (sa “b”, Fig. 2), and often indistinguishable from those of type a; and (3) **type c** - the antheridial appendages (an, Fig. 5). Tavares (1985) also defined a fourth type, called **d**, but these are branches arising from the secondary axis, and therefore are better denominated as tertiary axes. The perithecium has an outer wall consisting of 4 vertical rows of cells strongly unequal in height.

Rhachomyces aphaenopsis Thaxter, Proc. Amer. Acad. Arts 41: 314. 1905 (as “*Aphanopsis*”) Figs 2-22

Type. - In FH. On the elytra of *Aphaenops cerberus*, nearly always immature, Ariège, France; Sharp Collection, Type, No. 1142 [not seen].

= *Rhachomyces jeannelii* Cépède & F.Picard, Bull. Sci. France Belgique 42: 253. 1908 (as ‘*Jean-neli*’).

Ind. loc. - Sur *Aphaenops Jeanneli* Abeille, grotte d’Oxibar, commune de Camoucihigue, canton de Tardets-Sorholus, Basses-Pyrénées, et sur *A. bucephalus* Dieck, grotte de Liqué, commune de Moulis, canton de St-Girons, Ariège. (Collection Jeannel). [According to Lepesme (1941: 487) the type is the material on *A. jeannelii*.]

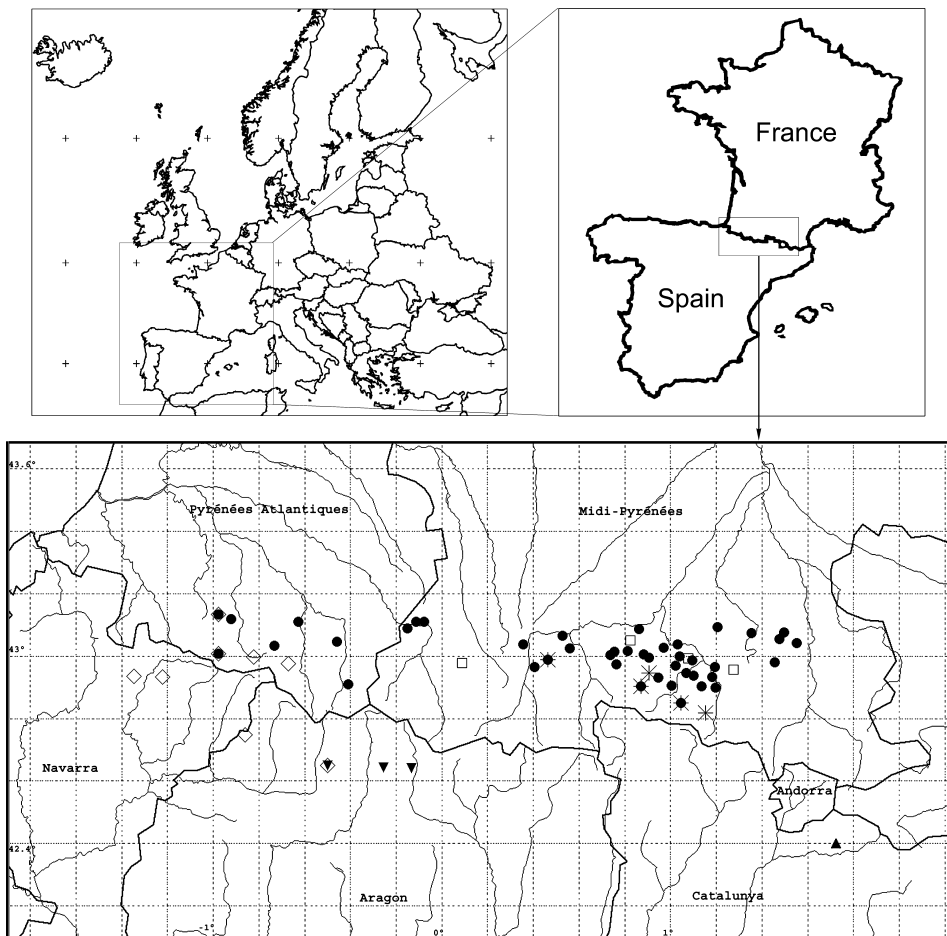


Fig. 1. Geographical location of the Pyrenees in Europe and known distribution of species of *Rhachomyces*. Symbols represent: ▼, *R. pyrenaicus*; *, *R. spadiceus*; =, *R. girardii*; ●, *R. aphaenopsis*; ▲, *R. ilerdensis*; □, *Rhachomyces* sp.

= *Rhachomyces aphaenopsis* var. *jeannelii* (Cépède & F.Picard) F.Picard, Bull. Trimestriel Soc. Mycol. France 1913: 555. 1913 (as “Jeanneli”)

= *Rhachomyces dedyi* Lepesme, Bull. Trimestriel Soc. Mycol. France 58: 71. 1942, nom. inval.

Type. - Sur *Aphaenops Hustachei* Jeann. (sic), de la grotte de l’Haiouat de Pelou, à Haut-Nistos, Hautes-Pyrénées.

SPECIMENS EXAMINED. - FRANCE. ARIÈGE: Balaguères, Av. de S^{te} Catherine, on *A. cerberus*, 14.XII.2003, leg. A.Faille, BCB-SS-E321 (+ duplicate in MNHN). Ibidem, on *A. cerberus bruneti*, 15.III.1959, leg. J.Vives, BCB-JGXE69. Ibidem, on *A. pluto sinister*, 5.IX.1960, leg. M.Z.B., BCB-SS-E50. Balaguères, Gouffre de Peyrère, on *A. bucephalus*, 5.VI.2004, leg. A.Faille, BCB-SS-E344 (in DMHF at MNHN). Bordes sur Lez, Gr. de Pétiliac, on *A. bouilloni*, 19.IX.2003, leg. A.Faille, BCB-SS-E345. Cazavet, Gr. de L’Estelas, on *A. cerberus*, 7.VII.2003, leg. A.Faille, BCB-

Table 1. Reports of *Rhachomyces* species on *Geotrechus*, *Aphaenops* and *Hydrphaenops* from the Pyrenees arranged by localities, including first references and new records. Asterisks in Locality and Host columns indicate that some material from these localities and/or hosts have been studied here. Species of *Rhachomyces* are reported as originally published according to abbreviations: aph (*R. aphaenopsis*), ded (*R. dedyi*), gir (*R. girardii*), hyp (*R. hypogaeus*), ile (*R. ilerdenensis*), jea (*R. jeannelii*), mau (*R. maublancii*), pal (*R. stipitatus* var. *pallidus*), pyr (*R. pyrenaicus*), sp. (*Rhachomyces* indet.), spa (*R. spadicus*), sti (*R. stipitatus*). Emendations or comments about fungal determinations must be searched in the text. Coordinates (Coord. Long./Lat. column) are in decimal degrees in agreement with the map (Fig. 1). In the Rhach. spp. column, the square brackets indicate an erroneous identification (all, except that of *R. ilerdenensis*, reidentified as *R. aphaenopsis*). In References column the superscript H or L indicates that corrections for host determination or locality have been made in the table. An asterisc alone in the References column indicates new records.

Localities	Coord. Long./Lat.	Rhach. spp.	Hosts	References
SPAIN - Huesca				
Ansó; Gamueta, Av. G12* and G171 *	-0.8615/42.7473	gir	<i>A. loubensi</i> *	Santamaria (1989: 9)
Ansó; Gamueta, Av. G3*	-0.8615/42.7473	gir	<i>A. loubensi</i> *	Balazuc et al. (1983: 40)
Ansó; Zuriza, Av. G20*	-0.8615/42.7473	gir	<i>A. loubensi</i> *	Santamaria (1989: 9)
Biescas; Sierra Tendeñera, Sima del Gel*	-0.2552/42.6444	pyr	<i>A. hidalgoi</i> *	Santamaria (1989: 6)
Torla; Sierra Tendeñera, Bujaruelo, Sima T1*	-0.1333/42.6414	pyr	<i>A. hidalgoi</i> *	Santamaria (1989: 6)
Villanúa; Peña Collarada, Sima (s.n.)*	-0.4989/42.6499	pyr	<i>H. penacollaradensis</i> *	*
Villanúa; Peña Collarada, trou Souffleur*	-0.4989/42.6499	gir	<i>A. valletti</i> *	*
SPAIN - Lleida				
Prullans, Cova d'Amnes*	1.7243/42.4000	[aph] ile	<i>G. sejasi</i> *	Balazuc at al. (1983: 39)
SPAIN - Navarra				
Erroibar, Mezkititz, Cueva Alta del Espinal*	-1.3452/42.9354	gir	<i>A. ochsi</i> *	Balazuc et al. (1982: 406)
Garralda, Cueva de Garralda*	-1.3452/42.9354	gir	<i>A. ochsi</i> *	*
Villanueva de Aezkoa, Sierra de Abodi*	-1.2227/42.9336	gir	<i>A. ochsi cabidochei</i> *	*
FRANCE				
Grottes des Pyrénées		[hyp]	<i>Geotrechus</i> sp.	Jeannel (1926: 229)
FRANCE - Ariège				
"locality not reported"		aph	<i>A. cerberus</i>	Thaxter (1905: 314)
Aigues Juntas, Gr. de Les Cloutets	1.4753/43.0550	aph	<i>A. cerberus inaequalis</i>	Balazuc (in litt.)
Alos, Gouffre Lacoste	1.1348/42.9039	aph	<i>A. pluto</i>	Boyer-Lefèvre (1965: 129) ^H

Localities	Coord. Long./Lat.	Rhach. spp.	Hosts	References
Alos, Gouffre de Courrèze	1.1348/42.9039	sp.	<i>A. cerberus bruneti</i>	Boyer-Lefèvre (1965: 128) ^{III}
		sp.	<i>G. saulcyi demauxi</i>	Balazuc (in litt.)
Alzen, Gr. de Montagne	1.4562/42.9811	[mau]	<i>G. saulcyi demauxi</i>	Boyer-Lefèvre (1965: 129) ^{II}
Alzen, Gr. de Soullisquet	1.4562/42.9811	[mau]	<i>G. saulcyi demauxi</i>	Boyer-Lefèvre (1965: 129) ^{II}
		sp.	<i>G. orpheus subparallelus</i>	Boyer-Lefèvre (1965: 129) ^{III}
		aph	<i>A. cerberus*</i>	*
Balagnères, Av. de S ^e Catherine*	1.0215/42.9699	aph	<i>A. cerberus bruneti*</i>	Santamaria (1989: 8) ^I
		aph	<i>A. pluto sinester*</i>	*
		aph	<i>Aphaenops</i> sp.	Boyer-Lefèvre (1965: 126)
		[sti]	<i>H. ehlersi</i>	Boyer-Lefèvre (1965: 126) ^{III}
Balagnères, Gouffre de Peyrière*	1.0215/42.9699	aph	<i>A. bucephalus*</i>	*
Bordes sur Lez, Gr. de Pétiliac*	1.0215/42.9699	aph	<i>A. bouilloni*</i>	Balazuc (1970: 686) ^I
		[ded]	<i>A. bouilloni*</i>	Boyer-Lefèvre (1965: 125) ^{II}
		sp.	<i>A. carrerei*</i>	Boyer-Lefèvre (1965: 125) ^{III}
Bordes sur Lez, Gr. du Trapech d'en Haut*	1.0462/42.8508	spa	<i>A. carrerei*</i>	*
		spa	<i>A. mariaerosae*</i>	*
		aph	<i>A. bucephalus</i>	Lepesme (1941: 487) ^I
Cazavet, Gr. de L'Estelas*	1.0385/43.0003	aph	<i>A. cerberus*</i>	Cépède & Picard (1908: 253) ^I
		aph	<i>A. cerberus bruneti</i>	Lepesme (1941: 487)
		[hyp]	<i>G. orpheus subparallelus</i>	Boyer-Lefèvre (1965: 129) ^{III}
Cazavet, Gr. de Peïllot	1.0385/43.0003	aph	<i>A. cerberus bruneti</i>	Lepesme (1944: 68) ^I
Encourtiech, Mine d'Encourtiech	1.1934/42.9665	[pal]	<i>A. cerberus</i>	Boyer-Lefèvre (1965: 124) ^{II}
Engomer, Gouffre de Pique Grand	1.0679/42.9458	aph	<i>A. tirsias robustus</i>	Boyer-Lefèvre (1965: 126) ^{II}
Galey, Escarchein, Gr. d'Escarchein*	0.9059/42.9456	spa	<i>A. crypticola*</i>	*
		[sti]	<i>A. cerberus</i>	Boyer-Lefèvre (1966: 780) ^I
		[sti]	<i>Aphaenops</i> sp.	Boyer-Lefèvre (1965: 127) ^I
		aph	<i>H. pecoudi*</i>	*
Lacourt, Gouffre Barroti*	1.1813/42.9332	[pal]	<i>A. cerberus inaequalis</i>	Boyer-Lefèvre (1965: 129) ^{II}
Loubens, Gr. du Portel	1.5526/43.0425	[pal]	<i>A. cerberus inaequalis</i>	Boyer-Lefèvre (1965: 129) ^{II}
Mas d'Azil, Gr. de Lafage	1.3537/43.0746	aph	<i>A. cerberus</i>	Boyer-Lefèvre (1965: 129) ^{II}

Localities	Coord. Long./Lat.	Rhach. spp.	Hosts	References
Mas d'Azil, Gr. de Peyrounard*	1.3537/43.0746	aph aph [pal] aph aph aph [hyp] sp. aph aph aph sp. [sti] [sti] [pal] sp. aph aph aph aph [jea] [ded] [jea] sp. aph [jea] [jea] [sti]	<i>A. cerberus</i> * <i>A. tirsias tispiphone</i> <i>A. cerberus inaequalis</i> <i>A. cerberus inaequalis</i> * <i>G. orpheus</i> * <i>G. orpheus bouilloni</i> * <i>G. orpheus bouilloni</i> * <i>A. cerberus bruneti</i> <i>A. pluto</i> <i>Aphaenops</i> sp. <i>G. saulcyi</i> <i>G. orpheus</i> <i>A. cerberus</i> <i>Aphaenops</i> sp. <i>A. cerberus inaequalis</i> <i>G. orpheus</i> <i>A. cerberus</i> <i>A. pluto</i> * <i>Aphaenops</i> sp. <i>H. pecoudi</i> * <i>Aphaenops</i> sp. <i>A. cerberus</i> <i>Aphaenops</i> sp. <i>G. trophonius</i> ? <i>A. cerberus</i> * <i>A. bucephalus bonasus</i> <i>Aphaenops</i> sp. <i>A. cerberus</i>	* Balazuc (1970: 680) ^{III} . Boyer-Lefèvre (1965: 129) ^{III} . Boyer-Lefèvre (1965: 129) ^{III} . * Santamaria (1989: 8) Boyer-Lefèvre (1965: 129) Boyer-Lefèvre (1965: 129) ^{III} . Boyer-Lefèvre (1965: 120) Boyer-Lefèvre (1965: 127) Boyer-Lefèvre (1965: 120) Boyer-Lefèvre (1965: 127) Balazuc (1970: 693) ^L Boyer-Lefèvre (1965: 127) ^L Balazuc (ined.) Boyer-Lefèvre (1965: 126) Lepesme (1941: 487) ^L * Boyer-Lefèvre (1965: 127) * Boyer-Lefèvre (1965: 127) Balazuc (1970: 686) ^L Boyer-Lefèvre (1965: 127) ^L Boyer-Lefèvre (1965: 127) ^{II} * Cépède & Picard (1908: 253) ^{II} Boyer-Lefèvre (1965: 126) Balazuc (1970: 693)
Mérigon, Gr. de la Quère*	1.2069/43.0929			
Montégut en Couserans, Gr. du Plagnol de la Plagne	1.0945/42.9874			
Montegut-Plantaurel, Plantaurel Montgauch, Av. de la Coumat de la Roque Moullis, Aubert, Gr. d'Aubert (= Gr. du Sendé)*	1.4964/43.0767 1.0760/42.9935 1.1011/42.9381			
Moullis, Gr. de Labouiche	1.1011/42.9381			
Moullis, Gr. de Las Séchos Moullis, Gr. de Liqué*	1.1011/42.9381 1.1011/42.9381			

Localities	Coord. Long./Lat.	Rhach. spp.	Hosts	References
Moulis, Gr. de Moulis	1.1011/42.9381	aph	<i>G. orpheus</i>	Balazuc (1970: 680) ^L
Moulis, Gr. des Fadettes*	1.1011/42.9381	aph	<i>A. cerberus</i> *	*
Moulis, Poudac de la Baoussou	1.1011/42.9381	sp.	<i>Aphaenops</i> sp.	Boyer-Lefèvre (1965: 127) ^L
Orgibet, forêt d'Orgibet	0.9453/42.9308	aph	<i>A. sioberae giselae</i>	
			<i>A. vandeli</i>	
Prat-Bonrepaux, Gr. de Gaujac	1.0322/43.0370	[hyp]	<i>G. orpheus microcephalus</i>	Balazuc & Juberthie (1983: 100)
Prat-Bonrepaux, Gr. de Peyort	1.0322/43.0370	aph	<i>A. cerberus</i>	Boyer-Lefèvre (1965: 126) ^H
		aph	<i>A. tiresias proserpina</i>	Boyer-Lefèvre (1965: 120) ^L
		[hyp]	<i>G. orpheus subparallelus</i>	Boyer-Lefèvre (1965: 120) ^H
		sp.	<i>Aphaenops</i> sp.	Boyer-Lefèvre (1965: 126) ^H
		sp.	<i>G. saulcyi metallorum</i>	Boyer-Lefèvre (1965: 126) ^L
Rivièrevert, Ancienne mine des Cabesses	1.2744/42.9561	aph	<i>A. sioberae colluvii</i>	Balazuc (ined.)
Saint-Lary, forêt de Saint-Lary	0.8721/42.9038	aph	<i>A. vandeli</i> *	Balazuc & Jubert. (1983: 100)
Saint-Lary, MSS S100*	0.8721/42.9038	aph	<i>A. vandeli</i> *	*
Saint-Lary, SL1*	0.8721/42.9038	spa	<i>A. vandeli</i> *	*
Salsein, Gr. de Payssa*	1.0046/42.9069	aph	<i>A. vandeli</i> *	Boyer-Lefèvre (1965: 125) ^H
		aph	<i>A. sioberae</i> *	*
Seix, Gr. des Bordes de Crues*	1.1518/42.8192	spa	<i>A. carrerei boui</i> * <i>A. laurenti</i> *	*
Soueix-Rogalle, Rogalle, Gr. d'Ardet	1.1972/42.8992	aph	<i>A. cerberus</i>	Boyer-Lefèvre (1965: 124) ^H
FRANCE – Haute Garonne				
Arbas, Gr. de Pène Blanche	0.9059/42.9945	aph	<i>A. cerberus bruneti</i>	Lepesme (1941: 487)
Arbas, Gr. du Goueil di Her*	0.9059/42.9945	aph	<i>A. tiresias</i> *	Lepesme (1941: 487)
		aph	<i>A. tiresias proserpina</i>	*
		aph	<i>H. ehlersi</i> *	Lepesme (1941: 487)
		aph	<i>H. ehlersi longiceps</i> *	Boyer-Lefèvre (1965: 124) ^H
Arbon, Gr. des Chevaux	0.7379/43.0034	sp.	<i>A. crypticola</i>	Lepesme (1944: 68) ^L
Aspet, Gouillou, Gr. de Gouillou	0.8123/43.0166	aph	<i>A. crypticola</i>	Balazuc (1970: 680) ^L
Aspet, Gr. de Baléjon	0.8123/43.0166	aph	<i>G. orpheus consorranus</i>	Balazuc (1970: 680) ^L
		sp.	<i>G. orpheus consorranus</i>	*
Chéin-Dessus, Gr. d'Artigouli*	0.8823/43.0068	aph	<i>A. jauzoni</i> *	*

Localities	Coord. Long./Lat.	Rhach. sp.	Hosts	References
Couret, Gr. de la Bouhadère	0.8248/43.0514	sp.	<i>Aphaenops</i> sp.	Boyer-Lefèvre (1965: 125) ^L
Izaut-de-l'Hôtel, Gr. de la Maouro*	0.7554/43.0153	aph	<i>A. crypticola</i> *	*
Juzet-d'Izaut, Gr. de Mount*	0.7620/42.9736	sp.	<i>A. crypticola</i> *	Boyer-Lefèvre (1965: 124) ^{HL}
Montespan, Gr. de la Hountaou	0.8625/43.0874	aph	<i>A. crypticola</i> *	Balazuc (1970: 680) ^L
Saleich, Gr. de Laspugues	0.9693/43.0272	aph	<i>G. orpheus consorranus</i>	Boyer-Lefèvre (1965: 125) ^{HL}
St-Bertrand-de-Comminges, Gr. de la	0.5585/43.0262	[hyp]	<i>A. cerberus inaequalis</i>	Boyer-Lefèvre (1965: 123) ^H
Coumo Nero		sp.	<i>G. orcinus henroiti</i>	Boyer-Lefèvre (1965: 123) ^H
			<i>A. crypticola</i>	
FRANCE – Hautes Pyrénées				
Aventignan, Gr. de Gargas	0.5285/43.0647	aph	<i>G. orcinus</i>	Balazuc (1970: 680) ^L
Bagnères de Bigorre, Gr. de Castelmouly	0.0870/42.9791	[pal]	<i>A. crypticola</i>	Boyer-Lefèvre (1965: 123) ^{HL}
Ilhet, Gr. d'Ilhet	0.4056/42.9664	sp.	<i>G. discontignyi</i>	Balazuc (ined.) ^L
Labastide, Gr. de Labastide*	0.3568/43.0386	[pal]	<i>A. crypticola</i>	Boyer-Lefèvre (1965: 123) ^{HL}
		aph	<i>A. hustachei</i> *	*
		sp.	<i>A. crypticola</i>	Boyer-Lefèvre (1965: 123) ^{HL}
Labastide, Grande Gr. de Labastide*	0.3568/43.0386	aph	<i>A. hustachei</i> *	*
Lourdes, Av. de Haiou	-0.0770/43.1112	aph	<i>G. gallicus bigerricus</i>	Balazuc (1970: 680) ^L
Nistos, Bas Nistos, Gr. de l'Eglise*	0.4636/42.9886	aph*	<i>G. orcinus</i> *	*
		ded]	<i>G. serrulatus</i>	Boyer-Lefèvre (1965: 120)
		[ded]	<i>H. longicollis</i>	Boyer-Lefèvre (1965: 120)
		[hyp]	<i>G. orcinus elongatus</i>	Boyer-Lefèvre (1965: 120)
		[hyp]	<i>G. serrulatus</i>	Boyer-Lefèvre (1965: 120)
Nistos, Haut-Nistos, Gr. de Haut-Nistos*	0.4636/42.9886	aph	<i>A. hustachei</i> *	Boyer-Lefèvre (1965: 123) ^{HL}
(= Moumouch ou Haiouat)		[ded]	<i>A. hustachei</i> *	Lepesme (1941: 487) ^L
		[pal]	<i>A. hustachei</i> *	Boyer-Lefèvre (1965: 123) ^{HL}
		spa	<i>A. crypticola</i> *, <i>A. hustachei</i> *	*
		[sti]	<i>A. hustachei</i> *	Lepesme (1941: 487)
Peyrouse, doline de Soulabère	-0.1126/43.1113	aph	<i>G. jeanneli</i>	Balazuc (1970: 682)
		aph	<i>G. jeanneli renaudeti</i>	Balazuc (ined.) ^L

Localities	Coord. Long./Lat.	Rhach. spp.	Hosts	References
Saint-Pé-de Bigorre, Pène de la Hèche, Isarce	-0.1509/43.0889	aph	<i>G. jeanneli</i>	Balazuc (1970: 680) ^L
Saint-Pé-de Bigorre, Rieulhès, Gr. de la Pale*	-0.1509/43.0889	aph	<i>A. linderi</i> *, <i>G. gallicus</i> *	*
Saint-Pé-de Bigorre, Rieulhès, montagne de la Pale et bois de Subercarrère	0.1509/43.0889	aph	<i>G. gallicus bigerricus</i> , <i>G. jeanneli</i>	Balazuc (1970: 680) ^L
FRANCE – Pyrénées Atlantiques				
Arette, Gr. d' Ambielle	-0.7330/43.0338	[hyp]	<i>A. ludovici baretosanus</i>	Boyer-Lefèvre (1965: 122) ^H
Asasp-Arros, Av. d' Asasp	-0.6285/43.1109	[hyp]	<i>G. gallicus gaudini</i>	Boyer-Lefèvre (1965: 120) ^H
Aussurucq, Gr. d' Istaurdy*	-0.9784/43.1348	sp.	<i>G. gallicus gaudini</i>	Balazuc (ined.) ^L
		aph	<i>A. jeanneli</i> *	Santamaria (1989: 8)
		gir	<i>A. alberti</i> *	*
		[jea]	<i>A. jeanneli</i> *	Balazuc (ined.)
		sp.	<i>A. jeanneli</i> *	Boyer-Lefèvre (1965: 121) ^H
Bielle, Aspeigt	-0.4597/43.0471	aph	<i>G. gallicus superstes</i>	Balazuc (1970: 680) ^L
Camou-Cihigue, Gr. d'Oxibar*	-0.9210/43.1190	[jea]	<i>A. alberti</i>	Boyer-Lefèvre (1966: 779)
		[jea]	<i>A. jeanneli</i> *	Cépède & Picard (1908: 253)
		gir	<i>A. ochsi reymondi</i>	Balazuc (1970: 686)
Larrau, Av. de Phista	-0.9779/43.0089	gir	<i>A. ochsi reymondi</i>	Lepesme & Temp. (1948: 206)
Larrau, Gorges d'Holçarté, Gr. d' Ayssaguer	-0.9779/43.0089	gir	<i>H. vasconicus giraudi</i>	Boyer-Lefèvre (1965: 120)
		[pal]	<i>A. ochsi reymondi</i>	Boyer-Lefèvre (1965: 130)
Larrau, Gr. Aker-Lecia	-0.9779/43.0089	gir	<i>A. gallicus</i>	Balazuc (1970: 680) ^L
Laruns, bois de Couscouilla	-0.4084/42.9091	aph	<i>A. loubensi jeanneli</i> *	*
Lées-Athas, Gouffre Bétap*	-0.6718/42.9766	gir	<i>A. loubensi</i> *	Boyer-Lefèvre (1965: 130)
Sainte Engrâce, Pierre St. Martin*	-0.8241/42.9974	gir	<i>A. ochsi cabidochei</i> *	Boyer-Lefèvre (1966: 782)

SS-E324 (+ duplicate in MNHN). Idem, 3.IX.1970, leg. J.Comas, BCB-SS-E29, BCB-JGXE47. Lacourt, Gouffre Barroti, on *H. pecoudi*, 10.X.2003, leg. A. Faille, BCB-SS-E346 (in DMHF at MNHN). Mas d'Azil, Gr. de Peyrounard, on *A. cerberus*, 27.VII.2003, leg. A.Faille, BCB-SS-E327 (+ duplicate in MNHN). Mérigon, Gr. de la Quère, on *A. cerberus inaequalis*, collecting date unknown, leg. M.Z.B., BCB-SS-E49. Ibidem, on *G. orpheus*, 21.VII.2003, leg. A.Faille, BCB-SS-E326 (+ duplicate in MNHN). Ibidem, on *G. orpheus bouilloni*, collecting date unknown, leg. M.Z.B., BCB-SS-E57. Moulis, Aubert, Gr. d'Aubert (= Gr. du Sendé), on *A. pluto*, 25.IV.2003, leg. A.Faille, BCB-SS-E334 (+ duplicate in MNHN). Ibidem, on *H. pecoudi*, collecting date unknown, leg. M.Bouillon, BCB-SS-E347 (in DMHF at MNHN). Moulis, Gr. de Liqué, on *A. cerberus*, 15.VI.2003, leg. A.Faille, BCB-SS-E332. Moulis, Gouffre des Fadettes, on *A. cerberus*, 11.IV.2004, leg. A.Faille, BCB-SS-E323. Saint-Lary, MSS S100, on *A. vandeli*, 23.IV.1985, leg. A. Faille, BCB-SS-E313. Salsein, Gr. de Payssa, on *A. vandeli*, 8.XII.2003, leg. A.Faille, BCB-SS-E320. Ibidem, on *A. sioberae*, 8.V.1991, leg. E. Queinnec, BCB-SS-E352 (in DMHF at MNHN). HAUTE GARONNE: Arbas, Gr. du Goueil di Her, on *A. tiresias*, 17.IV.2003, leg. A.Faille, BCB-SS-E322 (+ duplicate in MNHN). Idem, 19.X.1989, leg. A.Faille, BCB-SS-E333. Ibidem, on *H. ehlersi*, 19.X.1989, leg. A.Faille, BCB-SS-E335. Ibidem, on *H. ehlersi longiceps*, 5.IX.1943, leg. M.Z.B., BCB-SS-E51. Chein-Dessus, Gr. d'Artigouli, on *Aphaenops* sp., collecting date unknown, leg. A.Faille, BCB-SS-E339. Izaut-de-l'Hôtel, Gr. de la Maouro, on *A. crypticola*, 11.XI.1987, leg. A.Faille, BCB-SS-E319 (+ duplicate in MNHN). Juzet-d'Izaut, Gr. de Mount, on *A. crypticola*, 2.I.1988, leg. A. Faille, BCB-SS-E329 (+ duplicate in MNHN). HAUTES PYRÉNÉES: Labastide, Gr. de Labastide, on *A. hustachei*, 23.VIII.1948, coll. MNHN, BCB-SS-E338. Labastide, Grande Gr. de Labastide, on *A. hustachei*, collecting date unknown, coll. MNHN, BCB-SS-E341 (in DMHF at MNHN). Nistos, Bas Nistos, Gr. de l'Eglise, on *G. orcinius*, collecting date unknown, leg. M.Bouillon, BCB-SS-E342. Nistos, Haut-Nistos, Gr. de Haut-Nistos, on *A. hustachei*, 4.XI.2003, leg. A.Faille, BCB-SS-E325. Idem, 9.VI.1990, leg. A.Faille, BCB-SS-E336. Saint-Pé-de Bigorre, Rieulhès, Gr. de la Pale, on *A. linderi*, V.1994, leg. P. de Koninck, BCB-SS-E351 (in DMHF at MNHN). Ibidem, on *G. gallicus*, 21.V.1988, leg. A.Faille, BCB-SS-E328 (+ duplicate in MNHN). PYRÉNÉES ATLANTIQUES: Aussurucq, Gr. d'Istaurdy, on *A. jeanneli*, 9.VII.1989, leg. A. Faille, BCB-SS-E330 (+ duplicate in MNHN). Idem, 25.V.2004, leg. A.Faille, BCB-SS-E349 (in DMHF at MNHN). Idem, 1.VIII.1941, leg. M.Z.B., BCB-SS-E48. Camou-Cihigue, Gr. d'Oxibar, on *A. jeanneli*, 3.V.1988, leg. A.Faille, BCB-SS-E331 (+ duplicate in MNHN).

Thaxter (1908) compared *R. aphaenopsis* with *R. hypogaeus* (Thaxt.) Thaxt. (Thaxter 1895), and defined as its distinctive characters the “closely septate appendages about the base of the perithecium, and the long clear rich dark brown appendages of the usual type which arise from the axis and are as long near its base as near its summit” (Thaxter 1908: 422). Cépède & Picard (1908) described *R. jeannelii*, a species posteriorly reduced to a variety of *R. aphaenopsis* by Picard (1913). Lepesme (1942) supported the similarity of *R. aphaenopsis* with *R. hypogaeus*, but mentioned that closely arranged septa not only occur in the main appendages but also in appendages located near the thallus base; he also regarded “the perfect regularity” of the perithecium as the best specific character. In the same paper, Lepesme described *R. dedyi*, an obviously related species, but invalid because of a lacking Latin diagnosis. Boyer-Lefèvre (1965, 1966) published many observations on *R. aphaenopsis* as well as for other species of *Rhachomyces* that she collected in the Pyrenees. Unfortunately, many of her identifications must now be revised. Other publications added new records or observations for *R. aphaenopsis*, in an effort to refine its description as well as to clarify the status of some related taxa (Balazuc 1970, Santamaria 1989). Until now, it has been largely accepted that *R. aphaenopsis* was a variable species, which parasitizes the genera *Aphaenops*, *Geotrechus*, and *Hydraphaenops* in the Pyrenees in France and Spain (Santamaria et al. 1991). But the amount of data published does not clarify at all its status, its distribution and those of some “sister” taxa synonymized or not with it, or confused with it. Now, we have at our disposition a very large number of specimens and we begin to understand the topic.

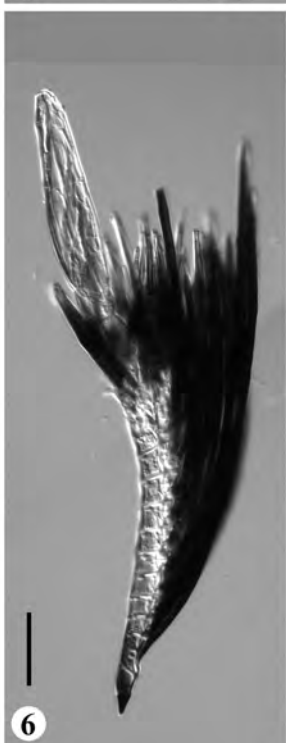
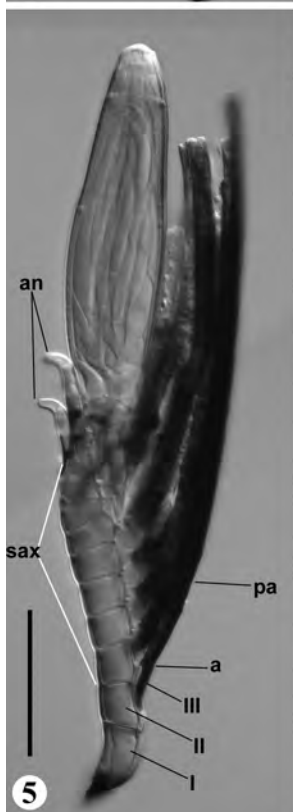
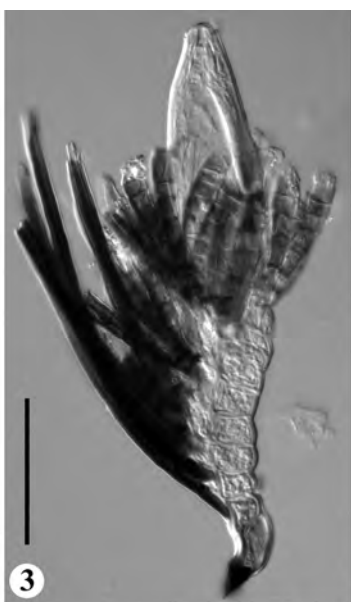
Considering *R. aphaenopsis* as a variable species is a poor start and our purpose is now to fix its diagnostic characteristics. Figures 2-4 represent thalli from the same host and locality from where Thaxter had described the species; some characters emphasized by himself, referring to the appendages, are clearly seen and these, after our observations of many thalli must be accepted as the “only” usable to distinguish the species. In these thalli (Figs 2-4), the number of cells in the main axis ranges from 8 to 12, the appendages in the base (type “a”) are long (even extending beyond the perithecium, Fig. 4), dark and bending towards the posterior side of the thallus; the appendages near and below the perithecium are shorter and paler than others and show several closely septate cells in the base (Fig. 2, sa “b”). Typically, the perithecium leans towards a direction opposite to that of the bent appendages (“a” in Figs 2, 4). When more thalli, from other hosts than “typical” *A. cerberus*, are added to the study, some variability becomes visible. As seen in Figs 5-7, the number of cells in the axis ranges from 8 to 16 or even more (Fig. 6). The colour of the appendages varies from pale brown, reddish brown, to blackish brown (Fig. 6). The shape of the perithecium seems irrelevant for taxonomy (contradicting with what Lepesme 1942 had suggested). Antheridial appendages (type “c”) show a broad black basal septum, a nearly square supporting cell, and a falcate antheridium (Fig. 16). A slight variation has been observed in these appendages among the material studied, but is not a good diagnostic characteristic, because similar antheridial appendages may be found in other species of *Rhachomyces* (e.g. *R. hypogaeus*, see Fig. 51).

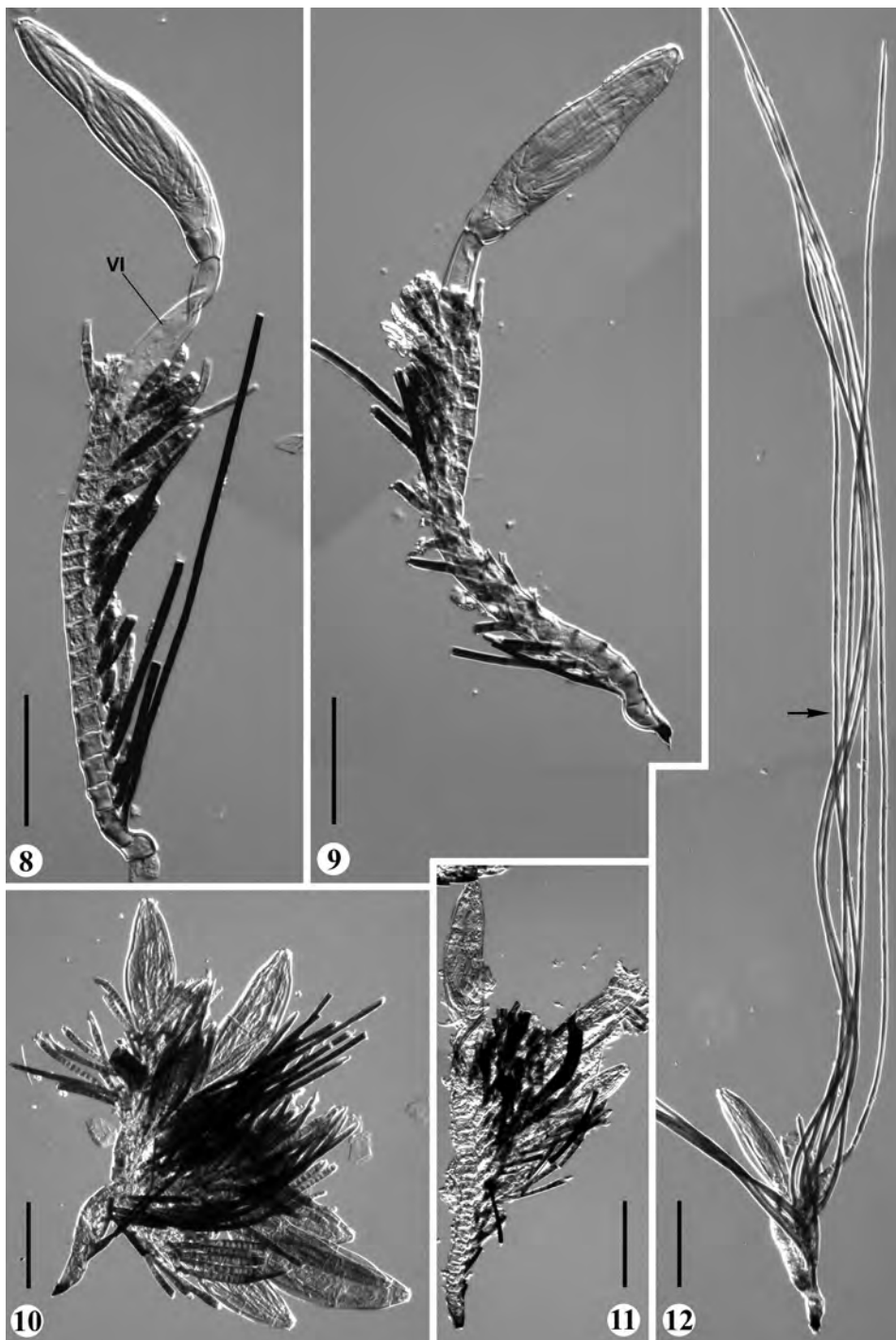
In Table 1 the column “Rhach. spp.” lists abbreviations for all recorded species. Among them are some with square brackets like [ded] (*R. dedyi*), [hyp] (*R. hypogaeus*), [jea] (*R. jeannelii*), [mau] (*R. maublancii*), [pal] (*R. stipitatus* var. *pallidus*), and [sti] (*R. stipitatus*). All these records must be corrected as concerning *R. aphaenopsis*. *Rhachomyces dedyi*, described by Lepesme (1942, see above), must be included among the synonyms of *R. aphaenopsis* because it represents abnormally branched thalli (Figs 10-11), by means of its growth on unsuitable locations of the

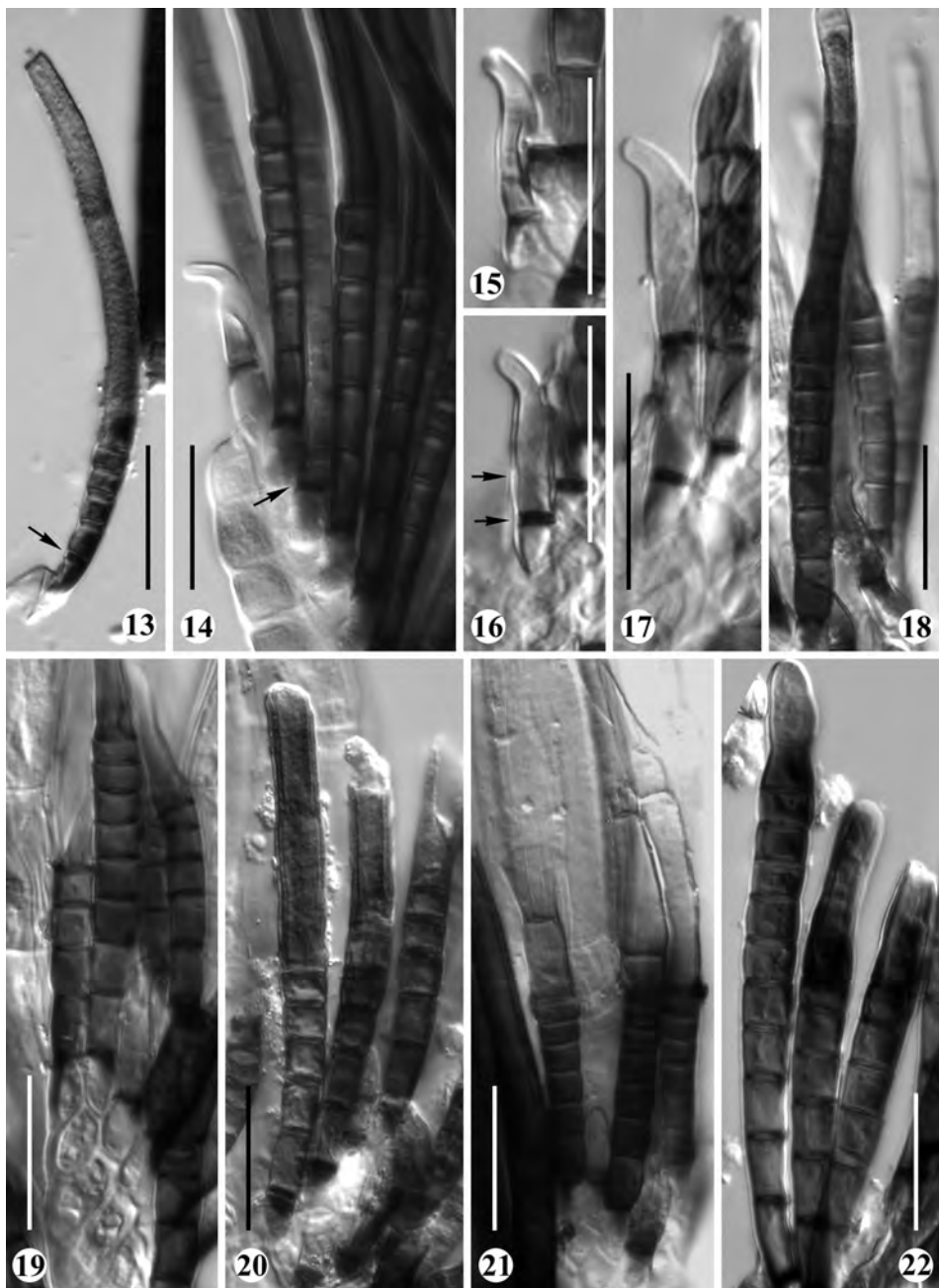
Figs 2-7. *Rhachomyces aphaenopsis*. 2-4. Typical mature thalli showing the two types of sterile appendages (sa “a” and sa “b”). 5. Mature thallus (I: basal cell, II: suprabasal cell, III: terminal cell, a: primary septum, an: antheridium, pa: primary appendage, sax: secondary axis). 6-7. Mature thalli. Scale bars = 50 µm. [2-3. SS-E321, 4. SS525b, from *Aphaenops cerberus*; 5. SS-E326, from *Geotrechus orpheus*; 6. SS-E339, from *Aphaenops* sp.; 7. SS605, from *Geotrechus orpheus bouillonii*].

Figs 8-12. *Rhachomyces aphaenopsis*. 8-9. Mature thalli with elongated perithecial stalk cell (VI) (“*stipitatus*” type). 10-11. Mature thalli with branched secondary axis and several perithecia (“*dedyi*” type). 12. Mature thallus with very elongated sterile appendages (arrow) (“*jeannelii*” type). Scale bars = 100 µm. [8-9. SS-E327, from *Aphaenops cerberus*; 10. SS-E330, 11. SS596, 12. SS-E331, from *Aphaenops jeanneli*].

Figs 13-22. *Rhachomyces aphaenopsis*. Details of appendages. 13. A broken sterile appendage of type “a” showing de broad and constricted basal septum (arrow). 14. One antheridial appendage and many sterile appendages of type “a” with broad basal septa (arrow). 15-17. Antheridial appendages; arrows in Fig. 16 point to septa, the lower is the basal broad septum and the upper separates the intermediate or supporting cell from the antheridium. 18-22. Sterile appendages of type “b”. Scale bars = 25 µm. [13, 20. SS-E329, from *Aphaenops crypticola*; 14, 22. SS-E331, from *Aphaenops jeanneli*; 15-17. SS-E321, from *Aphaenops cerberus*; 18-19. 21, SS-E339, from *Aphaenops* sp.].







host body (like mouth parts, tarsi or antennae) or by damage (Fig. 11). Appendages of such forms follow the typical outline (Fig. 22). *Rhachomyces hypogaeus* has been repeatedly reported on *Aphaenops* spp. and, especially, on *Geotrechus* spp. This species (Figs 47, 50, 51) must be restricted to parasites of *Typhlotrechus* spp. living in ex-Yugoslavian caves (Balazuc 1988). Its characteristics and especially those of the appendages (Fig. 50) show that the species is different. *Rhachomyces jeannelii* is a synonym of *R. aphaenopsis*, despite the enormous appendages that we see in the thalli from the type locality and host (Fig. 12), because this character is not invariable and the remaining details show a normal *R. aphaenopsis*. More surprising are the reports of the three other species: *R. maublancii* Lepesme ex W.Rossi (Lepesme 1942, Rossi 1979) parasitizing *Duvalius* in Italy; *R. stipitatus* var. *pallidus* Maire (1912), a doubtful taxon described on *Duvalius (Trechopsis) iblis* from Algeria; and *R. stipitatus* Thaxter. (Thaxter 1900) parasitizing species of *Duvalius* in the Mediterranean area. All records of these three taxa from the Pyrenees must be considered as erroneous determinations of or confusions with thalli of *R. aphaenopsis* having long-stalked perithecia (Figs 8-9).

Different arguments determine the identification of thalli parasitizing *Geotrechus seijasi* in Spain. These had been classified as *R. aphaenopsis* by Santamaria (1989). Balazuc et al. (1983) reported this species for the first time from the same locality and host, supporting the determination with a photograph (lam. I, fig. 3; Balazuc et al. 1983). Indeed, this image represents the most typical form of *R. aphaenopsis*; but we discovered that the photograph was taken from the slide BCB-JGXE47b, made from (see above in the specimens examined) *A. cerberus* collected in France (Cv. L'Estelas, Ariège). Reexamination of these slides convinced us of the necessity to describe a new species, *R. ilderdensis*, treated later in this paper.

We conclude that characteristics of secondary sterile appendages (types "a" and "b") are most important to distinguish *R. aphaenopsis*. The cells (4 to 10 or even more) located in the base of these appendages are short, flattened, squarish or slightly longer than broad, having closely and constricted septa (Figs 13-22), with a broad and black lowermost septum (Fig. 13, arrow); upper cells may be longer, even very much longer. The original statement of Thaxter (1908, see above) seems to be most appropriate.

***Rhachomyces girardii* Lepesme & G.Temp. ex Santam., sp. nov. - MycoBank MB510311** Figs 23-32

Rhachomyces girardii Lepesme & G.Temp., Bull. Trimestriel Soc. Mycol. France 63: 205. 1948 (as '*Girardi*') (nom. inval. Art. 36).

= *Rhachomyces girardii* Lepesme & G.Temp. in G.Temp., Sci. & Mont. (Trav. Comité Sci. Commiss. Médit. Sect. Sud-Ouest, Club Alpin Franç.) 58 (Suppl.): 24. 1947 (as "*Girardi*") [nom. inval.]

= *Rhachomyces girardii* G.Temp., Procès-Verbaux. Soc. Linn. Bordeaux 93: 209. 1946 (as "*Girardi*") [nom. nud.]

Ind. loc. - Sur *Aphaenops Ochsi* L. Gaudin subsp. *Reymondi* Colas et Gaudin, de la grotte d'Ayssaguer, aux environs de Larrau (Basses-Pyrénées), mai 1936 et mai 1938. Type et cotypes dans la collection Lepesme; cotypes dans la collection Tempère (Lepesme & Tempère 1948: 206). [The collections containing the type material are lost - Balazuc, pers. comm.]

NEOTYPE (here designated). - In BCB. FRANCE. PYRÉNÉES ATLANTIQUES: Sainte Engrâce, Pierre St. Martin, on *Aphaenops ochsi cabidochei*, 3.IX.2003, leg. A.Faille, BCB-SS-E317.

Tota longitudo thalli 306-1226 μm . Secundarius axis e 12-29 superpositis cellulis rubidis vel atrobrunneis confectus. Omnes cellulae in secundario axe 2-3 appendices ferentes, et plerumque 1 vel 2 antheridii appendices et 1 secundariam appendicem, oppositè ordinatas. Antheridii appendices, quae constant e cellula basilari brunnea, cellula intermedia fusca angusta et longitudine variabili, atque ex uno antheridio dilute brunneo ampulliformi terminali. Steriles secundariae appendices, quae constant ex cellulo basilari et 3-5 denigratis cellulis, quarum distalis cum terminali parte diluta, maturitate destructa. Perithecium 128-216 \times 39-77 μm , apice conico, abrupte distincto super duas series ventrales cellularum parietalium, quae cylindricum corpus formant.

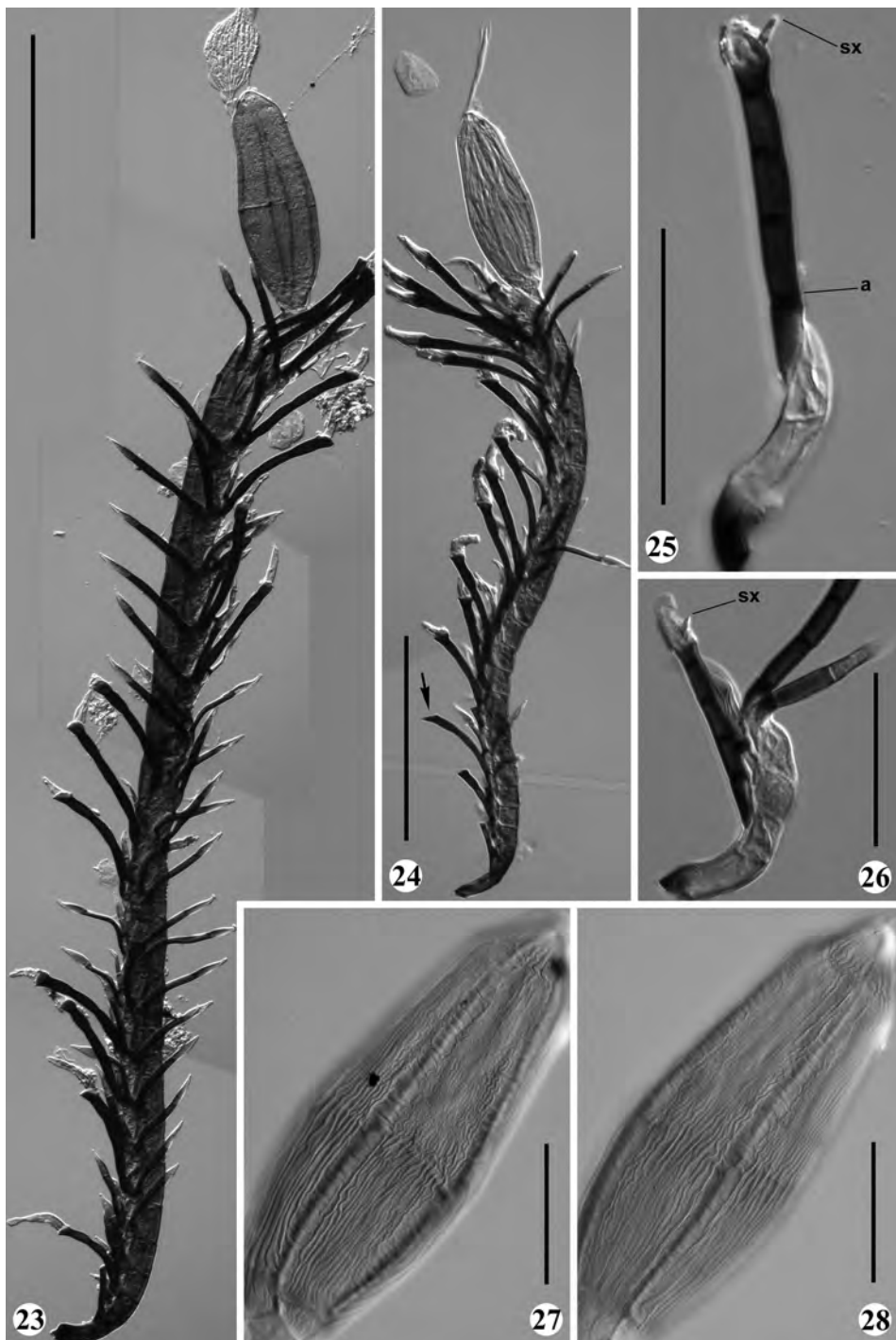
Total length from foot to perithecial apex 306-1226 μm . Secondary axis consisting of 12-29 reddish to dark brown superposed cells. Each cell in secondary axis giving rise to 1-2 antheridial appendages and one sterile secondary appendage. Antheridial appendages consisting of a brown basal cell, a variably elongated and narrow intermediate cell, and one pale brown, flask-shaped terminal antheridium. Secondary sterile appendages consisting of 3-5 superposed blackened cells, where the distal one bears a pale portion which deteriorates with age. Perithecium 128-216 \times 39-77 μm , with a cylindrical venter and a distinct conical apex, formed by the two upper wall cell tiers.

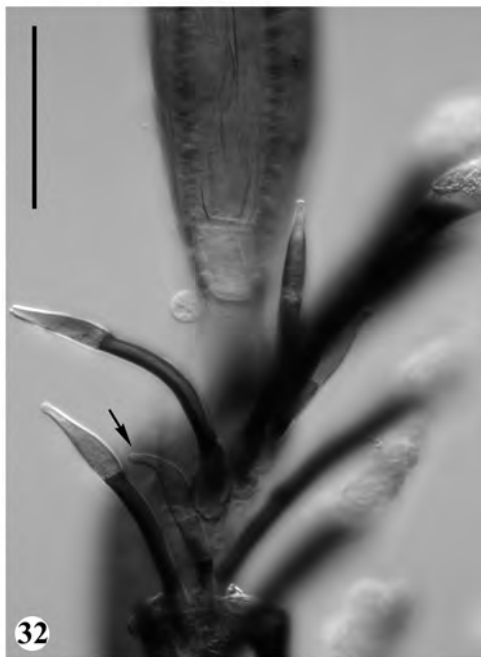
SPECIMENS EXAMINED. - FRANCE. PYRÉNÉES ATLANTIQUES: Aussurucq, Gr. d'Istaurdy, on *A. alberti*, 25.V.2004, leg. C.Bourdeau, BCB-SS-E350 (in DMHF at MNHN). Léés-Athas, Gouffre Bétap, on *A. loubensi jeannei*, collecting data unknown, leg. MNHN, BCB-SS-E354 (in DMHF at MNHN). Sainte Engrâce, Pierre St. Martin, on *A. loubensi* and on *A. ochsi cabidochei*, 3.IX.2003, leg. A.Faille, BCB-SS-E316-317 (+ duplicates in MNHN). SPAIN. HUESCA: Ansó; Gamueta, Av. G12, on *A. loubensi*, VII.1981, leg. M.Z.B., BCB-SS42. Idem, Av. G171, on *A. loubensi*, 18.VII.1982, leg. A.Inglés, BCB-SS47/2. Idem, Av. G3, on *A. loubensi*, 22.VIII.1982, leg. O.Escolà, BCB-JGXE42ab, BCB-SS40. Ansó; Zuriza, Av. G20, on *A. loubensi*, X.1981, leg. A.Inglés, BCB-SS43. Villanúa; Peña Collarada, trou Souffleur, on *A. valleti*, 25.VIII.1981, leg. P.Vallet, BCB-SS2538 (in DMHF at MNHN). NAVARRA: Erroibar, Mezkiritz, Cueva Alta del Espinal, on *A. ochsi*, collecting data unknown, leg. M.Z.B., BCB-SS597. Garralda, Cueva de Garralda, on *A. ochsi*, 26.V.2004, leg. A.Faille, BCB-SS2536 (+ duplicate in MNHN). Villanueva de Aezkoa; Sierra de Abodi, on *A. ochsi cabidochei*, 28.VIII.2004, leg. A.Faille, BCB-SS2539 (in DMHF at MNHN).

This is a very well characterized species which parasitizes several species of *Aphaenops* from the Pays Basque caves (western Pyrenees, both Spanish and French slopes) and from the Aragonese caves (central Pyrenees, only Spanish slope). The species was described without the mandatory Latin diagnosis, and although it has been reported several times after (see Table 1), the invalidity was not corrected until now. This

Figs 23-28. *Rhachomyces girardii*. 23-24. Mature thalli. 25-26. Very immature thalli with original spinose spore apex (sx) and primary septum (a) labelled. 27-28. Detail of striated surface of perithecium. Scale bars in 23 and 24 = 200 μm , Scale bars in 25-28 = 50 μm . [23. JGXE42a, 24-28. SS-E316, from *Aphaenops loubensi*].

Figs 29-32. *Rhachomyces girardii*. Details of appendages. 29. Detail of cells in secondary axis bearing three appendages (*, **), both sterile and antheridial (an: antheridium). 30. Distal portion of sterile appendages appearing deteriorate (arrow). 31. Sterile appendages in the upper thallus where the distal cell begins to distend (arrow). 32. Antheridial appendages which one unusually shortened (arrow). Scale bars = 50 μm . [29-30, 32. SS2536, from *Aphaenops ochsi*; 31. SS-E316, from *Aphaenops loubensi*].





species is unrelated to *Rh. aphaenopsis*. Tavares (1985) compared *R. girardii* with *Rh. thalpii* Thaxt. (Thaxter 1908) because of the shared characteristic of appendages with enlarged apices which are a result of breakdown of their cell walls. This trait is also seen in *R. pyrenaicus* (Figs 37-39) and in *R. reveilletii* Balazuc (1970) (Figs 48, 52, 53) which we consider as close relatives, whereas *R. thalpii* (of which we have seen one slide kept in our collection) does not seem related with it.

Rhachomyces girardii cannot be confused with any other species because of its special traits. The longer thalli may be seen on the host even with the naked eye because of their large size (up to 1226 μm in length, Fig. 23) and their dark color contrasting with the pale amber-brown host cuticle. Nevertheless, the length varies greatly (\bar{x} = 717.5 μm) (306 μm in the smallest specimen); the characters of the appendages type “a” and “c” clearly define the species. Each cell in the secondary axis bears 2-3 appendages (Fig. 29, *, **), usually one or two antheridial appendages (type “c”) and one sterile secondary appendage (type “a”), pointing in opposite directions at least primarily (Figs 29-30). Antheridial appendages consist of a brownish basal cell, a dark intermediate narrow cell of variable length, and one pale brown terminal flask-shaped antheridium (Fig. 29, an). Sometimes we found some unusually short antheridial appendages under the perithecium (Fig. 32, arrow). The sterile secondary appendages consist of a basal cell and about 3-5 blackened cells, where the distal one has a pale terminal portion (Fig. 31, arrow) which deteriorates with age in a broad, apparently sticky (because of the dirt that can be seen) amorphous mass (Fig. 30, arrow), which later may be broken in old thalli showing then a truncated and tilt apex (Fig. 24, arrow). The perithecium is also characteristic by its conical apex, abruptly tapering above the two perithecial wall cells of the venter. A striated surface in the perithecium is apparent with DIC optics (Figs 27-28), a characteristic already shown in the drawings by Lepesme & Tempère (1948) but not yet described.

The primary appendages have received little attention when describing new species of *Rhachomyces*, and in this species there is a detail that represents an important addition to the knowledge of the genus. The original spore apex is seen as a little brown spine in young thalli (Figs 25-26, sx), a character not described in any other species of the genus. We do not know whether such a characteristic has taxonomic significance for other species of Laboulbeniales, as for example those included in the subtribe Stigmatomycetinae (Tavares 1985).

***Rhachomyces ilerdensis* Santamaria, sp. nov. - MycoBank MB510316 Figs 33-36**

Tota longitudo thalli 224-307 μm . Secundarius axis ex 10-15 superpositis cellulis luteolis vel dilute brunneis confectus. Tertiarius axis ex maxime 5 cellulis confectus, conspicuus in summo thallo. Antheridii appendices e septo nigro constricto oriunda, e cellula minuta, brunnea, quadrata, atque ex antheridio terminali ampulliformi, lateraliter flexo compositae. Appendices steriles secundariae ex latere thalli sub perithecio exorientes, e septo basilari nigro, crasso et constricto oriunda, ex aliquot cellulis alternantibus elongatis et brevibus atrobrunneis compositae. Perithecium 108-159 \times 35-61 μm , robustum, ovoideum, cum ventre lato, collo indistincto et apice obtuso composita.

Thallus yellowish to pale brown, consisting of a curved basal cell (27-40 \times 12-17 μm ; \bar{x} = 31.9 \times 14.8 μm) and 10-15 superposed cells which form the secondary axis, each cell including a more or less conspicuous darkened stigma. Total length from foot to

perithecial apex 224-307 μm (\bar{x} = 261.1 μm). Tertiary axis chiefly apparent on the uppermost thallus, under the perithecium, where rows of up to five cells may form (Fig. 34). Secondary appendages up to 170 μm in length, only of one type (“a” = “b”) arising at one side of the thallus and below the perithecium; with a black, thick and constricted basal septum and consisting of several alternating long, 12-36 μm (\bar{x} = 17.8 μm in length) and short, 5-9 μm (\bar{x} = 7.7 μm in length), dark brown cells. Antheridial appendages (type “c”) interspersed among the secondary appendages, though more abundant under the perithecium, consisting of a black, constricted septum, a small, brown, squarish intermediate or supporting cell (6-10 μm , \bar{x} = 7.8 μm) in length, and a terminal, flask-shaped, laterally bent antheridium, 12-23 μm (\bar{x} = 17.5 μm) in length. Perithecium stout, ovoidal, 108-159 \times 35-61 μm (\bar{x} = 126.8 \times 46.8 μm), with a broad venter, an indistinct neck and a blunt apex. Perithecial stalk cell very short (30-35 μm ; \bar{x} = 31.2 μm), hidden among the appendages.

ETYMOLOGY: *L. ilterdensis*, named after Ilerda, the Latin name for Lérida (Lleida), province in Spain, where the fungus and its host live.

SPECIMENS EXAMINED: SPAIN. LLEIDA (LÉRIDA): Prullans, Cova d’Annes, on *G. seijasi*, 1.XI.1969, leg. J.Comas, BCB-SS522, BCB-JGXE48a (ISOTYPES), BCB-JGXE48b (HOLOTYPE). Ibidem, VI.1970, leg. M.Z.B., BCB-SS34. Ibidem, VII.1967, leg. M.Z.B., BCB-SS35, BCB-SS36.

Although Balazuc (1970) initially expressed some doubts about the identity of thalli collected on *Geotrechus* as *R. aphaenopsis*, the scarcity of his material did not allow a taxonomic conclusion. As mentioned above in the discussion of *R. aphaenopsis*, thalli collected on *Geotrechus seijasi* had been classified as *R. aphaenopsis* in part by a misconception and by using an incorrect photograph. Santamaria (1989) returned on the topic but did not change the initial classification. Moreover, his fig. c was drawn rather imprecisely; appendages type “b”, under the perithecium, would represent the typical closely septate *R. aphaenopsis*.

The new species is described with emphasis on several details which now appear relevant. Sterile appendages of *R. ilterdensis* do not show differentiation into the two types, “a” or “b”, whereas in *R. aphaenopsis* the appendages of type “a” (Figs 13-14) clearly differ from those of type “b” (Figs 18-22). The typical short lower cells in the appendages of *R. aphaenopsis* are not present in *R. ilterdensis*, where the first and second cells are longer than broad, and the third cell is short and flattened (Fig. 36). This arrangement of appendage cells predominates, but even when it varies (Fig. 35) we never found short cells like in *R. aphaenopsis*. Other not less important characters that distinguish the two species can only be understood with the study of a large series of thalli. Septa in the appendages of *R. ilterdensis* are little or not constricted. The basal septum of such appendages is particularly thick and very often marked with a central indentation, which probably represents a central pore (Fig. 35, arrow), different from that of *R. aphaenopsis* (see Figs 13-14, 18-22). In fact our species should rather be compared with *R. hypogaeus* (parasite on *Typhlotrechus* spp. from ex-Yugoslavian countries) or *R. richardii* (Balazuc) Balazuc in Santam. et al. (= *R. hypogaeus* subsp. *richardii*, Santamaria et al. 1991; parasite on *Speotrechus mayeti* from France) (Figs 47, 49-51, 54-55). As a further justification of the new species, its host appears geographically isolated from the other *Rhachomyces*-bearing beetles in the Pyrenees (see map, Fig. 1).

TYPE. - In BCB. On *Aphaenops (Cerbaphaenops) hidalgoi* Español & Comas (Coleoptera, Carabidae, Trechinae). Sima del Gel, terme municipal de Biescas, a la Sierra Tendeñera, Osca (Espanya), 27/8/82, J.Hidalgo leg., Col·lecció J.Comas (prep. JGXE91 -Holotypus-). [A photograph of the slide of the type was published in the protologue with number XEJG69; further changes in BCB herbarium lead now to a new number for the holotype: JGXE91.]

SPECIMENS EXAMINED. - SPAIN. HUESCA: Biescas; Sierra Tendeñera, Sima del Gel, on *A. hidalgoi*, 27.VIII.1982, leg. J.Hidalgo, BCB-JGXE91 (Type), and BCB-SS524. Torla; Sierra Tendeñera, Bujaruelo, Sima T1, on *A. hidalgoi*, 8.VIII.1979, leg. O.Escolà, BCB-SS539. Villanúa; Peña Collarada, Sima (without name), on *H. penacollaradensis*, collecting data unknown, leg. C.Bourdeau, BCB-SS2537.

With the new record reported here, the species can be confirmed and its area of distribution remains restricted to the central Aragonese Pyrenees. The typical host, *A. hidalgoi*, seems unrelated with the second host, *H. penacollaradensis*, but the revision of the systematics of Pyrenean Trechinae in progress suggests that these two species may be close (A. F., unpublished data). It is interesting that *R. girardii* (see above) and *R. pyrenaeus* have been collected in very close localities (at “Peña Collarada”, Spain), although on different hosts.

This species, when described (Santamaria 1989), was regarded as close to *R. girardii* because of similar secondary sterile appendages, both species having deteriorate apices. Nevertheless, clear affinities are unknown because the differences are fairly strong. The close distribution areas of both species might indicate a relationship, though it is not supported by morphological traits.

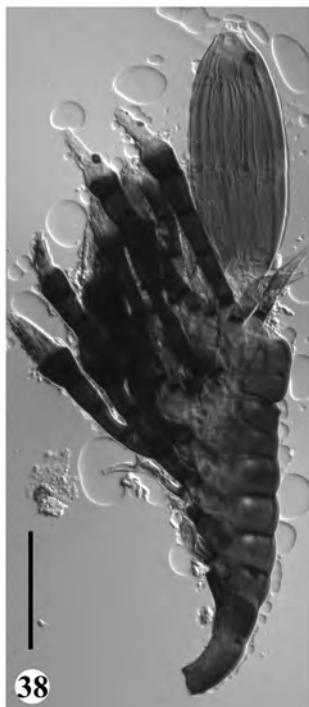
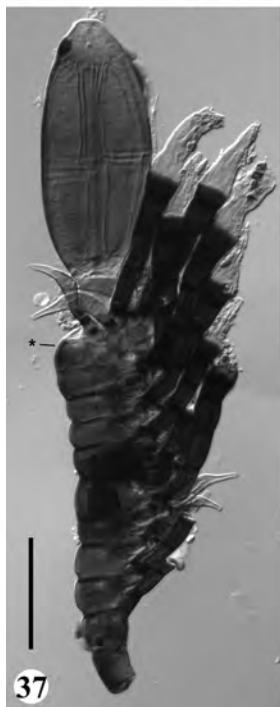
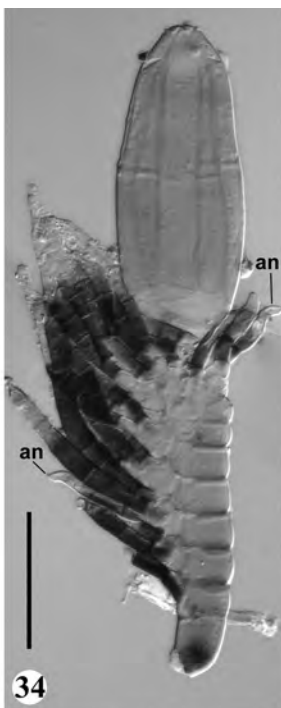
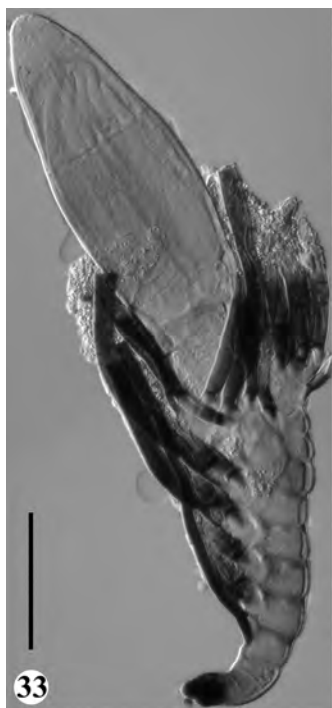
Rhachomyces pyrenaeus is a very distinct species due to the shape of the two types of appendages (sterile and antheridial), a darkened axis and by shape and location of perithecium (Figs 37-39).

Rhachomyces spadiceus Santamaria & Faille, sp. nov. - MycoBank MB510317

Figs 40-46

Tota longitudo thalli 734-928 µm. Thallus atrobrunneus, e cellula basilari elongata, inflata, luteola ad dilute brunnea atque 19-27 cellulis superpositis axem secundarium formantibus confectus. Cellula suprabasalis (II) parva, trapezoidea, complanata vel fere isodiametrica, brunnea, sed magis pallens quam cellulae superiores, basaliter lata et apicem versus decrescens. Tertiarius axis ex unaquaque cellula constans, quae ut appendicem sustinens cellula fungitur. Omnes cellulae axis secundarii 2-4 cellulas spiraliter dispositas proferunt, quae antheridii appendices et appendices secundarias steriles, plerumque oppositae ordinatae gerunt. Antheridii appendices ex septo basilari nigro constricto oriundae, e cellula intermedia angusta et longitudine variabili, atque ex uno antheridio terminali falciformi, quod cellulis cingentibus pallidius est compositae. Appendices steriles secundariae e septo basilari nigro, constricto oriundae, ex aliquot cellulis superpositis, longitudine variabilibus atrobrunneis confectae. Appendices secundariae longitudine variabilissimae, ubi integrae, longitudinem dimidio totius thalli similem attingentes. Perithecium elipsoideum ad ovoideum, 124-167 × 30-47 µm, ventre leviter inflato, collo indistincto et apice obtuso. Perithecii stipes typice conspicue elongatus.

Figs 33-36. *Rhachomyces ilderdensis*. Figs 37-39. *Rhachomyces pyrenaeus*. - *R. ilderdensis*. 33-34. Mature thalli (an: antheridia). 35-36. Sterile appendages with broad basal septum (arrows). - *R. pyrenaeus*. Mature thalli. In Fig. 37 the asterisc indicates the protuberant upper thallus because of the subterminal perithecium, a diagnostic character. Scale bars in 33-34 and 36-39 = 50 µm; Scale bar in 35 = 25 µm. [33., JGXE48; 34-36. JGXE48b, holotype; from *Geotrechus seijasi*] [37-38, JGXE91, holotype, from *Aphaenops hidalgoi*; 39. SS2537, from *Hydraphaenops penacollaradensis*].



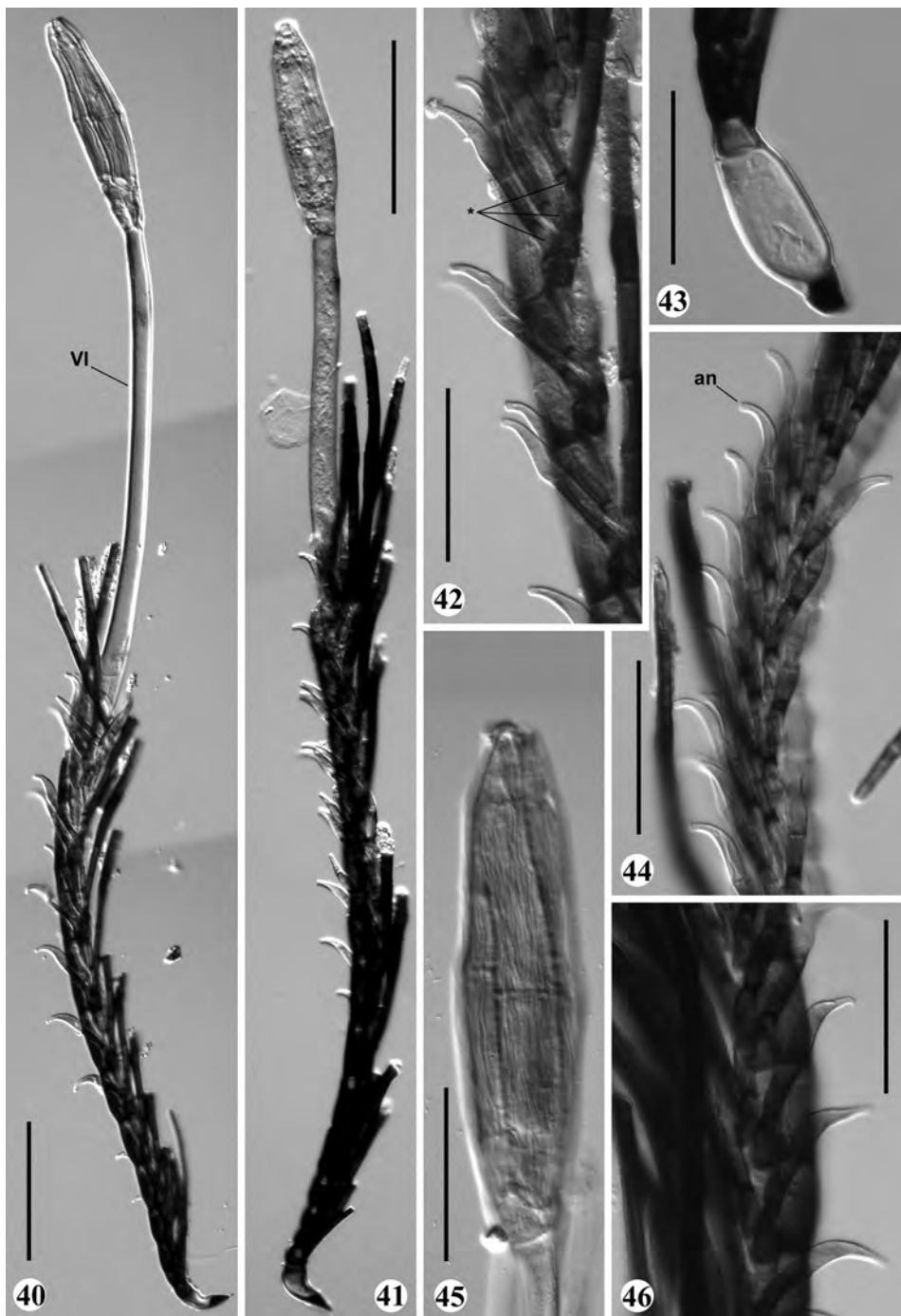
Thallus dark brown, consisting of an inflated, elongated, straight to curved, yellowish to pale brown basal cell, 31-42 × 13-15 μm (\bar{x} = 36.1 × 13.7 μm) (Fig. 43) and 19-27 superposed cells which form the secondary axis, each cell including an inconspicuous pale stigma. Suprabasal cell (II) small, 9-11 × 10-13 μm (= 10.2 × 11.6 μm), trapezoid, flattened to almost isodiametric, brownish, but paler than the cells above, broad below and narrowing towards the apex (Fig. 43). Total length from foot to perithecial apex 734-928 μm (\bar{x} = 806.9 μm). Tertiary axis consisting of single cells that function as supporting cells for the appendages. Secondary appendages, only of one type (“a” = “b”), arising from a black constricted basal septum and consisting of several superposed variably elongated dark brown cells. Secondary appendages very variable in length, reaching, when unbroken, a length to about half the total length of the thallus. Antheridial appendages (type “c”) arising from a black, constricted basal septum, consisting of a narrow, variable in length (15-19 μm, \bar{x} = 17.3 μm), intermediate or supporting cell, and a terminal, falcate antheridium (23-28 μm, \bar{x} = 26 μm in length), which is paler than the surrounding cells (Fig. 43). Each cell of the secondary axis bearing 2-4 tertiary, helically arranged cells, which give rise to antheridial appendages and secondary sterile appendages (Figs 42, 44, and 46). Usually, the antheridial appendages and the secondary sterile appendages are orientated in opposite directions (Figs 40, 44). Perithecium ellipsoidal to ovoidal, 124-167 × 30-47 μm (\bar{x} = 148.1 × 36.2 μm), with slightly inflated venter, indistinct neck and blunt apex. Perithecial surface striated (Fig. 45). Perithecial stalk typically conspicuously elongated, 213-351 μm (\bar{x} = 250.1 μm).

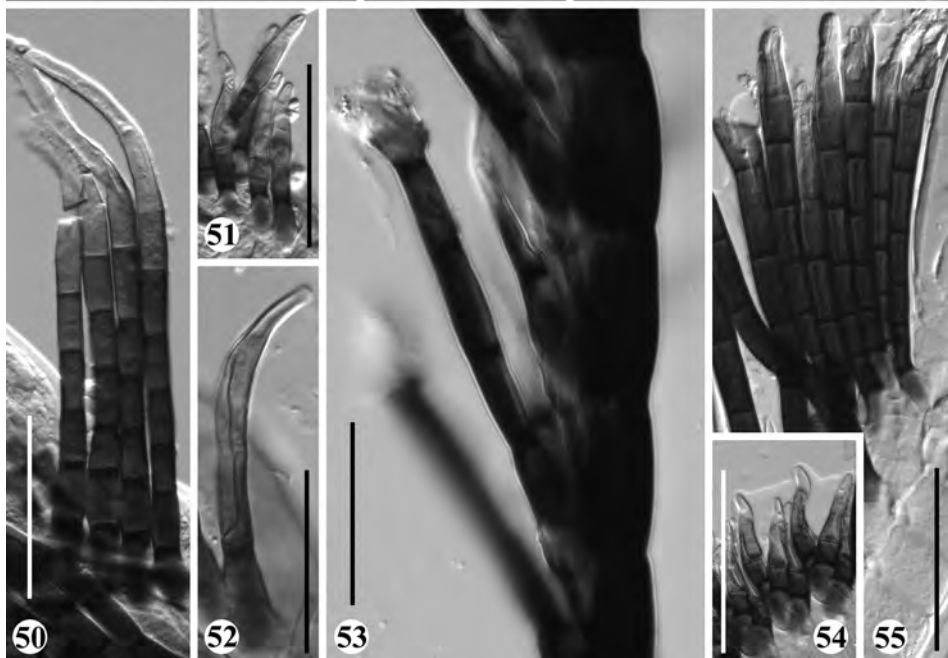
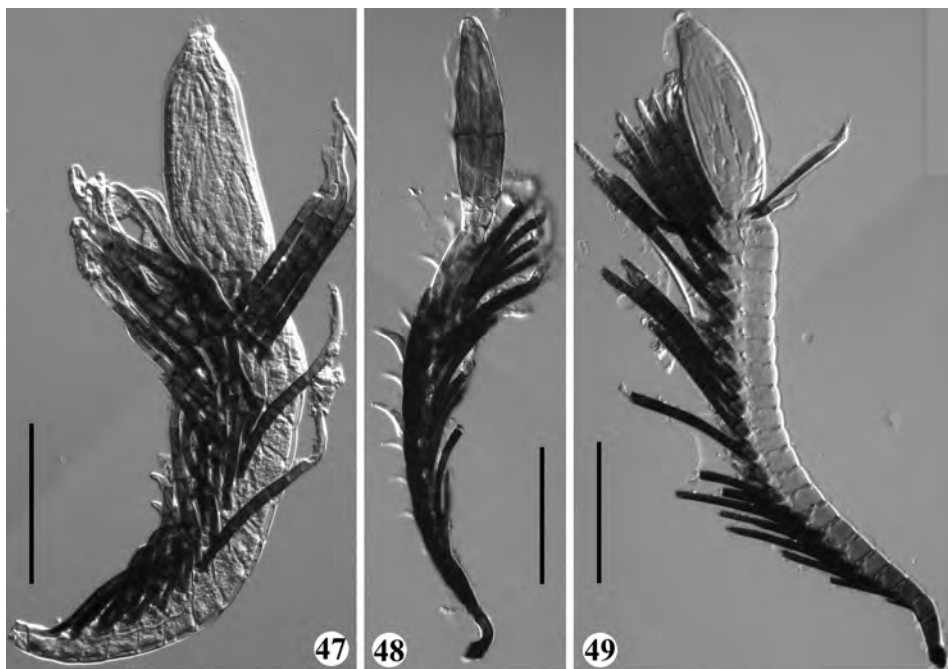
ETYMOLOGY. L., *spadiceus*, referring to the overall color of the fungus, a deep reddish-brown.

SPECIMENS EXAMINED. FRANCE. ARIÈGE: Bordes sur Lez, Gr. du Trapech d'en Haut, on *A. carrerei*, 2.X.2003, leg. A.Faille, BCB-SS-E318 (+ duplicate in MNHN). Idem, on *A. mariaerosae*, 2.X.2003, leg. A.Faille, BCB-SS-E343. Galey, Escarchein, Gr. d'Escarchein, on *A. crypticola*, 4.X.2004, leg. A.Faille, BCB-SS-E314a/314b (+ duplicate in MNHN). Saint-Lary, MSS S100, on *A. vandeli*, 23.IV.1985, leg. A.Faille, BCB-SS-E313 (+ duplicate in MNHN). Saint-Lary, SL1, on *A. vandeli*, 15.VI.2004, leg. A.Faille, BCB-SS-E315 (HOLOTYPE) (+ duplicate in MNHN -ISOTYPE-). Seix, Gr. des Bordes de Crues, on *A. carrerei boui*, V.1993, leg. E. Queindec, BCB-SS-E353 (in DMHF at MNHN). Idem, on *A. laurenti*, 16.X.2004, leg. A.Faille, BCB-SS-E348. HAUTES PYRÉNÉES: Nistos, Haut-Nistos, Gr. de Haut-Nistos (= Moumouch or Haiouat), on *A. crypticola*, 9.VI.1990, leg. G. Corbaz, BCB-SS-E337 (+ duplicate in MNHN). Idem, on *A. hustachei*, 4.XI.2003, leg. A.Faille, BCB-SS-E325.

Figs 40-46. *Rhachomyces spadiceus*. 40-41. Mature thalli with typically elongated perithecial stalk cell (VI). 42. Detail of cells in secondary axis bearing antheridial appendages (*). 43. Detail of basal and suprabasal cell of receptacle. 44, 46. Details of arrangement of antheridial (an) and sterile appendages. 45. Striated surface of perithecium. Scale bars in 40-41 = 100 μm, Scale bars in 42-46 = 50 μm. [40, 42. SS-E314b, 41, 45. SS-E314a, from *Aphaenops crypticola*; 43, 44, 46. SS-E315, from *Aphaenops vandeli*, holotype].

Figs 47, 50-51. *Rhachomyces hypogaeus*. Figs 48, 52-53. *Rhachomyces reveilletii*. Figs 49, 54-55. *Rhachomyces richardii*. - *R. hypogaeus*. 47. Mature thallus. 50. Sterile appendages. 51. Antheridial appendages. - *R. reveilletii*. 48. Mature thallus. 52. Antheridial appendage. 53. Sterile appendage. 49, 54-55. *R. richardii*. 49. Mature thallus. 54. Antheridial appendages. 55. Sterile appendages. Scale bars in 47-49 = 100 μm; Scale bars in 50-55 = 50 μm. [47, 50-51, SS588, Slovenia: Lipica, from *Typhlotrechus circovichii*] [48, 52-53. SS-E340, France: Gr. du Brudour, Vassieux-en-Vercors, from *Trichaphaenops gounellei*] [49, 54-55. JGXE28, France: Gr. de la Coquelière, St. André de Cruzières, from *Speotrechus mayetii*].





This species is an interesting novelty in view of the fact that the geographical area of its troglolithic hosts has been so intensively studied. The species might have been confused by other authors who studied these fungi and hosts (see under introduction) because it parasitizes many different hosts and has been found in several cavities. *Rhachomyces spadiceus* has outstanding characteristics and cannot be confused with any other extant species. The only species morphologically close to *R. spadiceus* is *R. reveilletii* (parasite of *Trichaphaenops* in the French Alps), but the appendages are different (Figs 52-53) amongst other characteristics (Fig. 48).

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