Baronniesia delioti gen. n. sp. n., a new subterranean Leptodirini from the French Pyrenees (Coleoptera: Leiodidae: Cholevinae)

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Abstract

Baronniesia delioti Fresneda, Bourdeau & Faille gen. n. & sp. n., tribe Leptodirini (Coleoptera, Leiodidae, Cholevinae), is described from the French central Pyrenees (Hautes-Pyrénées, Esparros, subterranean river of Artigaléou-Arodets). The genus is remarkable for the large body size and the strong sexual dimorphism in antennae of its type species. The structure of the aedeagus and the inner sac, with two additional strongly curved feather-like structures, forming an inverted “V”, and the lateral styles with only three spines without other structures, indicates affinities between the new genus and the Antrocharis group, diversified in the eastern part of the Pyrenean range. The limestone area in the central Pyrenees where this new genus was discovered appears to be a contact area between the eastern and western faunas of the Pyrenean cave beetles, both for Leiodidae: Leptodirini and Carabidae: Trechini.

Key words: Baronniesia delioti gen. n. sp. n., Leiodidae, Cholevinae, Leptodirini, subterranean environment, Pyrenees, France

Introduction

The Pyrenees is known to be one of the world’s hot-spots of subterranean biodiversity (Culver et al. 2006). Particularly, two radiations of subterranean Coleoptera occur along the Pyrenean chain: Leiodidae: Cholevinae: Leptodirini and Carabidae: Trechini. Leptodirini are known in the Pyrenees and associated mountain chains by 222 taxa (species and subspecies) included in 28 genera, all of them endemic of this area. This group has fascinated biospeleologists and evolutionary biologists in general since very early, due to its very strong ecological requirements, isolation of populations, morphological differentiation and multiple examples of character convergence. The Pyrenean Leptodirini have been studied in detail by many authors, among them Jeannel (1911, 1924), Dupré (1989, 1990) and Fresneda & Salgado (2006). A recent study suggested the monophyly of all Pyrenean Leptodirini (Fresneda et al. 2007).

During biospeleological explorations in the massif of the Baronnies (Central Pyrenees, France), two of us (CB, AF) discovered an unexpected species of Leptodirini, which should be considered as the only representative of a new genus close to a group of genera with a more eastern distribution.

Material and methods

The terminology of the structures of the inner sac of the aedeagus (Figs. 5–6) follows Jeannel (1924), Bellés (1984), Dupré (1992) and Fresneda (1998):
1) Basal area:
   FAPY “fibras apicales de la pieza en Y”, apical fibers of PY (Fresneda 1998)
   NL “nodule de liaison”, connection nodule (Dupré 1992)
   PY “piece en Y” (Jeannel 1924)

2) Median area:
   BDAM “bolsas dorsales del ápice de la región media”, dorsal sacs of apex of median area (Fresneda 1998)
   FDM “faneres dorsales de la regió mitjana”, dorsal feather-like structures (Bellés 1984)
   FVM “faneres ventrals de la regió mitjana”, ventral feather-like structures (Bellés 1984)
   IVP, inverted V phanerae or feather-like structures

3) Apical area:
   BRA “bandelette de renforcement apical”, reinforcement bands (Jeannel 1924)

**Baronniesia** Fresneda, Bourdeau & Faille gen. n.

**Type species:** *Baronniesia delioti* Fresneda, Bourdeau & Faille sp. n.

**Description.** The type species of this new genus is characterized by its large size, 4.0–5.0 mm long, being one of the largest species of Leptodirini known from the Pyrenean chain. Sexual dimorphism is very accentuated: male with dilated pentameric protarsi, antennomeres 5 to 9 exceptionally wide, forming a sort of blade (Fig. 1), filiform in females (Fig. 2). Elytra strongly punctured; punctures wide and rough, forming poorly defined transverse striae, especially in the front area. Mesoventral carina low, forming an obtuse angle, and not extended on metaventrite. Male genital segment reduced, forming a slightly sclerotized ring with two very long lateral appendices. Width of aedeagus (Fig. 3) decreasing from base to apex in dorsal view, apex rounded with central part truncated; lateral margins sinuate; aedeagus slightly bent in lateral view (Fig. 4), forming an obtuse angle; terminal tip strongly curved; basal part proportionally large. Lateral styles of aedeagus very thin through their entire length; apex simple, with only three spines (Fig. 7). Inner sac of aedeagus with the three sections typical of the *Speonomus* phyletic lineage (Fig. 5) (Jeannel 1910, Dupré 1992, Fresneda 1998, Fresneda & Salgado 2000); reinforcement bands (BRA) only in apical area, very long and reaching the base of the section, which is round and more sclerotized, inserted on two additional large feather-like structures located at the external apical part of the FDM (Fig. 5: BDAM). Median area with dorsal (Fig. 5: FDM) and ventral feather-like structures (Fig. 5: FVM), two additional slightly curved feather-like structures forming an inverted “V” located above FDM and FVM (Fig. 5: IVP), between BDAM. Apical part of PY in basal area (Fig. 5: FAPY), above connection nodule (NL), very thin and elongate; feather-like structures associated with PY with strongly sclerotized and large basal nodule; ventral basal complex very robust and sclerotized. Eighth female urosternite with short and robust apophyse and round apex (Fig. 15). Spermatheca of “type 1” *sensu* Perreau (1989) (Fig. 16), thin and elongated, slightly curved and with two well-differentiated lobes; apical lobe spherical and smaller than basal lobe, with spermathecal gland inserted at the same place as spermiduct. Spermiduct 10–12 times longer than spermatheca, which gets larger close to the insertion with spermatheca and crosses a sclerotized disc at the contact with bursa copulatrix. Main part of spermiduct close to spermatheca strongly curved.

**Etymology.** The name of the new genus refers to the mountainous massif of Baronnies, located north of the central Pyrenees, between the Aure valley and the Adour valley.

**Taxonomic notes.** *Baronniesia* belongs to the Infraflagellates of the *Speonomus* “phyletic series” of Jeannel (1910). However, the new genus is morphologically very isolated from the rest of the Pyrenean fauna. At first glance, it looks like a large *Euryspeonomus breuili* Jeannel, 1919 (Sierra de Aralar, Navarra, Spain) but an accurate examination shows that some genital structures are very different, and similar to *Antrocharis* Abeille de Perrin, 1878 (Ariège, France) and related taxa. The lateral styles of the aedeagus of *Baronniesia* are
very thin through their entire length, with only three spines at the apex. The inner sac of the aedeagus has two additional feather-like structures forming an inverted “V” above the FDM and FVM, and the apical part of PY is very thin and elongate. All these characters allow to link the new genus to the Pyrenean genera of Leptodirini of the *Antrocharis* group (*sensu* Fresneda *et al*. 2007), which is redefined below.

**FIGURES 1–2.** Habitus of *Baronniesia delioti* gen. n. sp. n. 1—male; 2—female.

The *Antrocharis* group was characterized by the following characters (the terminology of the structures of the inner sac of the aedeagus follows Jeannel 1924, Bellés 1984, Dupré 1989, 1992 and Fresneda 1998):

1) The median lobe of the aedeagus in lateral view is curved forming right or obtuse angle, with a strong depression or dorsal sinuosity in the apical third. Until now this character was considered a synapomorphy of the group. The median lobe of aedeagus of *Baronniesia* in lateral view is curved forming an obtuse angle, but without any depression or sinuosity, decreasing regularly from base to apex, and strongly curved in the central part (Fig. 4).

2) Lateral styles of the aedeagus are shorter than the median lobe, very thin through their entire length and each carrying three long spines at the apex (one shorter), without any penicillum, cavity or membranous lamina (Figs. 8–9). The lateral stylus of *Baronniesia* conforms to this morphological structure (Fig. 7).
3) Presence of two additional strongly sclerotized feather-like structures forming an inverted “V”, above the FDM and FVM (Figs. 5–6: IVP). These two feather-like structures are present in *Baronniesia*, which also has two additional structures located laterally of the inverted “V” (Fig. 5: BDAM).

4) The apical part of PY (FAPY), above the connection nodule (NL), is very thin and elongate. *Baronniesia* shares this character with all genera of the *Antrocharis* group (Fig. 5: FAPY). In all the other genera of the Pyrenean Leptodirini (not members of the *Antrocharis* group) the apical part of PY is shorter, broader and conical.

**FIGURES 3–4.** Aedeagus of *Baronniesia delioti* gen. n. sp. n. 3—dorsal view; 4—lateral view.

The *Antrocharis* group includes four genera: *Antrocharis* (two species), *Gesciella* Giachino & Guéorguiev, 1989 (monospecific genus), *Paratroglophyes* Fourès, 1954 (two species) and *Troglophyes* Abeille de Perrin, 1894 in pars sensu Fresneda et al. 2007: *T. aubryi* Coiffait, 1953 with the subspecies *T. aubryi* *vallierensis* Coiffait, 1953 (Fresneda et al. 2007). Coiffait (1953) indicates that the two subspecies of *Troglophyes aubryi* have the apex of the styles each with three spines and a penicillum composed of 7–8 setae. We did not see a penicillum in the numerous specimens from the Anglade cave (locus typicus of *T. aubryi aubryi*) and various MSS (“*Milieu souterrain superficiel*” Juberthie et al. 1980) in the area; all examined specimens have only three spines without penicillum (Fig. 9).

*Eskualdunella delespierrei* Coiffait, 1950b, an enigmatic species from the French Basque country, known by a single specimen, seems to have a similar structure of the stylus apex, as the members of the *Antrocharis* group: three spines without penicillum (Coiffait 1950b: Fig. 11; 1955). But in *Eskualdunella* one of the spines is longer and more robust than the two others.
FIGURES 5–6. Inner sac of aedeagus of Leptodirini. 5—Baronniesia delioti gen. n. sp. n. and 6—Antrocharis querihaci dispar Abeille de Perrin. BDAM, dorsal sacs of apex of median area; BRA, reinforcement bands; FDM, dorsal feather-like structures; FVM, ventral feather-like structures; NL, connection nodule; FAPY, apical fibers of PY; IVP, inverted “V” feather-like structures; PY, “piece en Y”.

In the genus Bathysciola Jeannel, 1910, the species of ovata group (Perreau 2000, Fresneda & Salgado 2006) have the apex of the stylus with only three spines, but the mesoventral keel is extended over the metaventrite, and transverse striae on the elytra are missing. Those characters separate the ovata group from the Antrocharis group and Baronniesia. The species of madoni and zariqueyi groups are closely related to ovata group (Fresneda et al. 2007), and have a variable number of spines in the lateral stylus of the aedeagus (between 5 and 14). In the phylogenetic reconstruction by Fresneda et al. (2007) these groups of Bathysciola are not closely related to the Antrocharis group. The other Pyrenean Bathysciola (lapidicola, meridionalis, larcennei and schiodtei groups) have four spines in the apex of the lateral stylus of the aedeagus (the only exception is one species of the meridionalis group, B. finismillennii Fresneda & Salgado, 2006 with nine spines), and belong to a clade of Leptodirini restricted to the Spanish Basque country (see Fresneda et al. 2007): Josettekia Bellés & Déliot, 1983, Speocharidius Jeannel, 1919, Euryspeonomus Jeannel, 1919 (all with four spines) and Aranzadia Español, 1972 (with about thirty spines).
In all other Pyrenean Leptodirini the number of spines in the apex of the lateral stylus of the aedeagus varies from two to five, but they all have a penicillum, which could be inserted in a depression or not, or be inserted on a membranous lamina.

**FIGURES 7–14.** Apices of lateral styles of aedeagus of Leptodirini. 7—Baronniesia delioti gen. n. sp. n.; 8—Paratroglophyes jeanneli Coiffait; 9—Troglophyes aubryi aubryi Coiffait; 10—Troglophyes gavoyi Abeille de Perrin; 11—Parvospeonomus delarouzeei Faïmaire; 12—Phacomorphus (Phacomorphoides) sioberi sioberi (Coiffait); 13—Speonomus curvipes subcurvipes Abeille de Perrin; 14—Paraspeonomus vandeli Coiffait.
There are two main types of lateral stylus of the aedeagus among the rest of Pyrenean Leptodirini:

1) The Troglophyes type. The apex of the lateral stylus of the aedeagus with two or (more frequently) three long spines, with a dense penicillum formed by numerous short setae. This penicillum may be inserted in a cavity or directly on the integument of the apex of the stylus (Figs. 10–12). In the speluncarum group of Speonomus Jeannel, 1908 the third spine is often concealed by the penicillum. The following groups have the lateral stylus of the Troglophyes type: Bathysciella Jeannel, 1906; Bellesia Fresneda & Hernando, 1994; Ceretophyes Fresneda, 1998; speluncarum (Jeannel, 1947) and ehlersi (Perreau, 2000) groups, and the subgenus Machaeroscelis Jeannel, 1924 of Speonomus; Phacomorphus Jeannel, 1908, including the subgenus Phacomorphoides Dupré, 1989 (Fig. 12); Parvaspeonomus Bellès & Escolà, 1977 (Fig. 11); Perriniella Jeannel, 1910 and Troglophyes Abeille de Perrin, 1894 (Fig. 10). Troglophyes is a para- or polyphyletic genus (Fresneda et al. 2007). All the easternmost species of Troglophyes, T. bedeli Jeannel, 1906, T. g. gavoyi Abeille de Perrin, 1894, T. g. alluaudi Jeannel, 1911, T. ludovici Chobaut, 1903 and T. oblongulus Reitter, 1908, are closely related to Ceretophyes Fresneda, 1998 and Perriniella Jeannel, 1910, unlike the Antrocharis group of genera and T. a. aubryi and T. a. vallierensis of the central Pyrenees.

2) The Trocharanis type. The apex of the lateral stylus of the aedeagus is with three long spines (sometimes five). One can be longer than the other two (Fig. 13: Speonomus curvipes subcurvipes (Abeille de Perrin, 1878)), or two longer than the third one, all three of different size (Fig. 14: Parvaspeonomus vandeli Coiffait, 1952) or all subequal. A dense penicillum formed by numerous long setae inserted on the side or on a more or less developed membranous lamina is always present; in some species the long setae of the penicillum look like a pedunculus or thin extension of the membranous lamina (e.g. in S. carrerei Fourès, 1954). This group is formed by the genus Parvaspeonomus Coiffait, 1952, Speonomus of pyreneus and zophosinus groups (Jeannel 1947), subgenus Metaspeonomus Coiffait, 1959 and Trocharanis Reitter, 1885. All the genera of the southern side of central Pyrenees and coastal ridges of Catalonia (Spain) belong to this group: Lagariella Fresneda, 2000, Naspunitus Fresneda, Hernando & Lagar, 1994, Pallaresiella Fresneda, 1998, Salgadaia Fresneda, 1998, Speonomites Jeannel, 1910, Stygiophyes Fresneda, 1998, Trapezodirus Jeannel, 1924 and Troglocharinus Reitter, 1908 (except the three taxa of the subgenus Antrocharidius Jeannel, 1910 with a secondary loss of penicillin but with the membranous lamina).

Dilated antennae in male of Baronniesia is a character shared with Josettekia angelinae Bellés & Déliot, 1983 and Parvaspeonomus vandeli Coiffait, 1952. Josettekia angelinae has the 9th (especially) and 10th male antennomeres dilated. However, in Josettekia this is not a generic character, as the second species of the genus, J. mendizabali (Bolívar, 1921), does not show any dilatation of the male antennae. Both species of Josettekia have the apex of the lateral stylus with four short spines and lack the two inverted “V” feather-like structures in the inner sac of aedeagus. In P. vandeli only the fourth antennal article of male is dilated, but the lateral stylus of the aedeagus has a membranous lamina and a penicillum, and the inner sac lacks the two inverted “V” feather-like structures.

Phylogenetic analyses. Baronniesia gen. n. and the genus Gesciella (omitted from the previous analyses) were added to the data matrix of Fresneda et al. 2007 (Appendix 1: this paper) with the aim of including both genera in a formal phylogenetic analysis. See Fresneda et al. 2007: 335–344 for the list of the 34 characters and their states. For a list of studied species see Appendix 1 in Fresneda et al. 2007. For composition of groups of terminal taxa sharing identical character states and lumped together for the purposes of analysis see Appendix 2 in this paper. Despite the fact that three new characters were added to the matrix of Fresneda et al. (2007) (see below), this could not help to resolve relationships between Baronniesia and the most closely related taxa (the Antrocharis group). In the new character matrix (Appendix 1) Baronniesia shares all character states with Antrocharis, Gesciella, Paratroglophyes and Troglophyes.

Character 35. Lateral styles of aedeagus: very thin along their entire length (0) and always shorter than the median lobe (Figs. 3–4); or strong along their entire length (1), with the apex more or less thickened and of length ranging from shorter to longer than the median lobe. Coded as missing data (?) for the species with character states 26 (1), 27 (1), 28 (0), 29 (0), 30 (1) and 31 (1), sensu Fresneda et al. (2007). These species
have the apex of the lateral stylus of the aedeagus with two to five spines; when they have three, there is always a penicillum, cavity or membranous lamina.

Character 36. *Apical part of the median region of the inner sac of aedeagus*: with two very sclerotized pieces forming an inverted “V” located above FDM and FVM (Fig. 5: IVP) (1); without inverted “V”, or with other structures (0). In the species with the inner sac of the aedeagus lacking copulating armature (Fresneda et al. 2007: character 16, state 0) character 36 was coded as missing data (?).

Character 37. *Basal region of inner sac of aedeagus*: apical piece of PY (FAPY) above the connection nodule (NL) very thin and elongated (Fig. 5: FAPY) (1) or short and conical (0). In species without PY (Fresneda et al. 2007: character 17, state 0) character 37 was coded as missing data (?).

The extended data matrix was analysed using the same methods as in Fresneda et al. (2007): the shortest trees were heuristically searched in PAUP 4.0b10 (Swofford 2002) with 10,000 tree-bisection-reconnection (TBR) replicas, swapping on all multiple starting trees, and saving all of them. To obtain a higher resolution, data were reweighted successively according to the rescaled consistency index (Swofford, 2002), and a heuristic search conducted on the initial set of the shortest trees (see Fresneda et al. 2007 for details).

The topology of the strict consensus of the 330 reweighted trees (consistency index 0.67, retention index 0.9) was identical to that of Fresneda et al. (2007) (Fig. 17) and, thus, was not affected by addition of three new characters. *Gesciella* and *Baronniesia* appear in the same polytomy with the remaining genera of the *Antrocharis* group, as they share all character states.

**Baronniesia delioti** Fresneda, Bourdeau & Faille sp. n.

(Figs. 1–5, 7, 15–16)

**Type locality.** France, Hautes-Pyrénées, Esparros, subterranean river of Artigaléou-Arodets.


Holotype description. *Habitus and size. Baronniesia delioti* sp. n. is one of the largest species of Pyrenean Leptodirini. Length from anterior edge of pronotum to apex of elytra: 4.54 mm (see Variability). Anophthalmous and depigmented; outline oval, stocky, with pronotum wider than elytra (Fig. 1). All the surface covered by yellowish pubescence, thin and soft; elytral pubescence longer. Punctation of head thin; mandibles very robust with a subapical tooth at internal edge.

**Antennae.** Length 3.50 mm; antennal articles gradually dilated from fourth to ninth, tenth and eleventh articles not dilated; ventral side of the ninth article concave, dorsal side strongly convex. For measurements of antennal articles see Table 1.

**TABLE 1.** Measurements of antennal articles of the holotype male and a single female paratype (40 units = 1 mm).

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**Pronotum.** Strongly transverse (length 1.25 mm, width 2.30 mm), sides very arcuate, maximum width before posterior edge.

**Elytra.** One and half time longer than wide, strongly convex, with dehiscent apices; each elytron regularly curved at apex. Punctation strong and rough, in basal area arranged in transverse striae; in apical half with punctures distributed irregularly.

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8 : Zootaxa 1993 © 2009 Magnolia Press
Legs. Proportionally long; mesotibiae arched, metatibiae straight. Male protarsomeres 1–3 strongly dilated, the first wider than apex of protibia; onychium as long as protarsomeres 1–4 combined.

Mesoventral carina, aedeagus and male genital segment as in the description of the genus.

Female diagnosis. Habitus as in Fig. 2; body smaller than in male (see Variability), pronotum as wide as elytra; outline perfectly oval. Antennae filiform, articles not dilated. For measurements of antennal articles see Table 1. Protarsi tetramerous, non dilated. Urosternite VIII and spermathecal complex as in the description of the genus.

Variability. Body length (measured from anterior edge of pronotum to apex of elytra): male: 4.02–4.54 mm, average 4.30 mm; female 4.01–4.40 mm; average 4.16 mm.

Etymology. This new species is dedicated to our entomologist colleague and friend Philippe Déliot, who died recently.

Distribution and ecology. The new species is only known from a single cave located in the central part of the Pyrenean chain, south of Esparros. The total length of the cave of Artigaléou is more than one kilometer, with two levels of chalk-stoned fossil galleries before reaching the subterranean river. Specimens of *B. delioti* were found only in traps placed near the river. Apparently, the species does not occur in the deeper parts of the cave, and it seems likely that the specimens found were carried from deep soil by water together with *Speonomus bastideus* Coiffait, 1950a and the species of Trechini mentioned below. Hypogean fauna of the Baronnies has never been studied in detail, and there are scarce faunistic data from only three other caves (Jeannel 1928, Coiffait 1950a). To better characterize the ecology of *Baronniesia* it would be necessary to investigate other localities where it could live, probably as an MSS or endogean species together with *Geotrechus discontignyi*, a typical endogean ground beetle also found near the traps.
FIGURE 17. Phylogram of the strict consensus of the 330 trees obtained after successive reweighting of the characters (in the tree, the character weights were reset to unity, so the scale of the branch lengths is uniform across the tree). Taxa with identical character states were lumped in a single terminal taxon except the genera of the *Antrocharis* group (see Appendix 2).
Biogeographical notes. In the area where B. delioti was discovered, the only other known Leptodirini are the species of the *speluncarum* group of the genus *Speonomus*, distributed between the Lez valley (Ariège) and the western Pyrenees, where they have also colonized the southern range in Navarra until the Echo valley (Huesca, Spain).

*Baronniesia delioti* is sympatric with *Speonomus bastideus* (*speluncarum* group) and three species of Trechini: *Hydraphaenops elegans* Gaudin, 1945, *Cerbaphaenops* aff. *aeacus* Saulcy, 1864 and *Geotrechus* *discontignyi canteti* Cabidoche, 1967. The subterranean river of Artigaléou-Arodets is the third known locality of *Speonomus bastideus*, which was so far only known from the caves of Labastide and Diable Rouge, both in Banios, Hautes-Pyrénées.

It may be expected that the two main unrelated groups of cave Coleoptera (Leptodirini and Trechini) living in the same geographical area show some similarities in their patterns of distribution and colonization of the subterranean environment. Both live in the same underground ecosystem, characterized by strict and constant features, and share the area affected by the same climatic conditions and a particular paleogeographic history.

The pattern of distribution of the Pyrenean Trechini is presented in Fig. 18. The species of the subgenus *Aphaenops* Bonvouloir, 1862 have radiated in the western part of the Pyrenean chain, and their diversity increases from Lourdes to the west, the majority of them (including the endogean *Geaphaenops* Cabidoche, 1965) diversified between Lourdes and Saint-Jean-Pied-de-Port (Faille 2006). The eastern-most French species of the subgenus *Aphaenops* is *A. leschenaulti* Bonvouloir, 1862, known from the caves around Bagnères-de-Bigorre. On the contrary, the species of the subgenus *Cerbaphaenops* Coiffait, 1962 have radiated in the eastern part of the Pyrenees between Ariège valley and Bigorre area, and their diversity decreases from east to west (Faille 2006). The surrounding area of Bagnères-de-Bigorre is the contact area.
FIGURE 19. Map of the Pyrenees with distribution areas of taxa with different models of lateral styles of the aedeagus in Leptodirini. The *Antrocharis* type (continuous line): *Antrocharis querilhaci dispar* Abeille de Perrin (a). The *Troglophyes* type (dots and dashes): *Phacomorphus (Phacomorphus) fratyi* (Dupré) (b), *Speonomus (Speonomus) ere* Escolà & Fresneda (c), *Perriniella faurai* Jeannel (d), *Bellesia espanyoli* (Auroux & Bellés) (e) and *Parvospeonomus urgellesi* (Español) (f). The *Trocharanis* type (doted line): *Speonomus (Speonomus) curvipes subcurvipes* (Abeille de Perrin) (g), *Salgadoia brieti* (Jeannel) (h) and *Troglocharinus (Troglocharinus) ferreri ferreri* (Reitter) (i).
between the two main radiations of subterranean cave Trechini, *Aphaenops* in the narrow sense in the west and *Cerbachaenops* in the central-eastern Pyrenees. In this area, the two lineages are represented by *A. (Cerbaphaenops) cryptica* ssp. *aeacus* Saulcy, 1864 and *A. (Aphaenops) leschenaulti* Saulcy, 1864, both sympatric in the cavities around Bagnères-de-Bigorre, in particular the Castelmouly and Tuco caves (Jeannel 1928). While the species of the subgenus *Aphaenops* on the northern slope of the range do not reach the area east of Bagnères-de-Bigorre, on the southern slope some species of this subgenus are distributed further east, till the Ribagorçana valley, where *A. catalonicus* Escolà & Canció, 1983 is present.

The pattern of diversification of the Pyrenean Leptodirini is quite similar, although with some differences (Fig. 19). The species of *Spenonomus* of the *speluncarum* group are distributed from the western Pyrenees to the Aure valley (Sarrancolin, Lortet) and the Labastide area (Artigaléou, Labastide cave). Members of the *speluncarum* group are found again in Ariège, with *S. orgibetensis* Gers, 1989 (*speluncarum* group sensu Gers, 1989: Fig. 1D), the two species of the *ehlersi* group, *S. ehlersi* Abeille de Perrin, 1872 and *S. opisthonoxyus* Gers & Dupuis, 1988 (Gers & Dupuis 1988: Fig. 3C), and the subgenus *Machaeroscelis*. The distribution area of the *speluncarum* group and related Leptodirini are thus extended to the east. The presence of other genera apparently related to the *speluncarum* group (*Ceretophyes, Parvospeonomus, Perriniella, and Troglophyes*) in the eastern part of the Pyrenees is very remarkable. A revision of the north Pyrenean Leptodirini would be necessary to elucidate this biogeographical enigma.

When Leptodirini are compared to troglobitic Trechini, the main difference in their distribution is that in Leptodirini the contact area of the two groups, the western one (*Spenonomus* of *speluncarum* and *ehlersi* groups, *Machaeroscelis, Bathysciella and Phacomorphus*) and the central-eastern one (*Paraspeonomus, Trocharanis* and *Spenonomus* of the *pyreneus* group) is extended to the east until Ariège. The area between Ariège and Bigorre seems to be an overlapping area of distribution for the Leptodirini of the *Trocharanis* type and those of the *Spenonomus* of the *speluncarum* group. The lineage of the *Antrocharis* group of genera seems to have originated in this contact area, but we do not know whether from the western or the eastern group. The coincidence of the same contact area for the eastern and western Pyrenean groups of Leptodirini and Trechini suggests the same geologic and climatic causes.

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References

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Appendix 1. Data matrix used in the phylogenetic analysis. Terminal taxa with identical character states were pooled except for the genera of the Antrocharis group (see Appendix 2 for the composition of the groups, and Fresneda et al. (2007) for the definition of characters 1–34).

Characters 0000000001111111111222222223333333

Speonomus pyreneus gr. 1111101100100111110?0111001100111011
Speonomus speluncarum gr. 1111101100100111110?0111001100111011
Paraspeonomus gr. 1111101100100111110?0111001100111011
Speocharidius gr. 1111101100100111110?0111001100111011
Euryspeonomus gr. 1111101100100111110?0111001100111011
Antrocharis 1111101100100111110?0111001100111011
Baronniessia gen. n. 1111101100100111110?0111001100111011
Gesciella 1111101100100111110?0111001100111011
Paratroglophyses 1111101100100111110?0111001100111011
Troglophyses a. aubryi/a. vallie 1111101100100111110?0111001100111011
Bathysciola series IV 11111111001000111110?0111001100111100
Speocharinus gr. 1111111101110010001101000001000100???
Quaestus gr. 11111111011100100011010000011001001??
Catops 000 00100??0001000000?0000000?000????
Speonemadus 000 00000??0010000000?0000000?000????
Breuilia 1111111101110010001101000001000100???
Breuilites 11111111011100100011010000011001001??
Espanoliella 11111111011100100011010000011001001??
Oresigenus 11111111011100100011010000011001001??
Q. (Amphogeus) escalerai 11111111011100100011010000011001001??
Anillochlamys 11111111011100100011010000011001001??
Ovobathysciola 11111111011100100011010000011001001??
Paramillochlamys 11111111011100100011010000011001001??
Pseudospeonomus 11111111011100100011010000011001001??
Speleochlamys 11111111011100100011010000011001001??
Patriziella 11111111011100100011010000011001001??
Notidocharis 0111110110110000001100000001001011??
Speonomidius 11111111011100100011010000011001001??
Bathysciola ovata gr. 11111111011100100011010000011001001??
T. (Antrocharidius) 1111101100100111110?0111001100111011

Appendix 2. Composition of the groups of terminal taxa sharing identical character states.

Quaestus gr.: Q. (Amphogeus) cantabricus, Q. (Quaestus), Q. (Quaesticulus), Q. (Speogeus), Q. (Samanolla), Cantabrogeus, Leonesiella.
Speocharinus gr.: Speocharinus, Quaestus (Asturianella), Bathysciola series IV: B. madoni gr., B. zariqueyi gr.
Speocharidius gr.: Speocharidius, Bathysciola larcennei gr.
Paraspeonomus gr.: Bellesia, Lagariella, Paraspeonomus.
Speonomus pyreneus gr.: Naspunius, Pallaresiella, Salgadoa, Speonomites, Stygiophyes, Trapezodirus, Troglocharinus (Troglocharinus), Speonomus pyreneus gr.
Speonomus speluncarum gr.: Ceretophyes, Parvospeonomus, Perriniella, Phacomorphus, Speonomus (Batinoscelis), Speonomus speluncarum gr., Troglophyses partim.