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Source: Integrative Systematics: Stuttgart Contributions to Natural History, 6(1) : 9-37

Published By: Stuttgart State Museum of Natural History

URL: <https://doi.org/10.18476/2023.609967>

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## RESEARCH ARTICLE

# Reconciling morphological and molecular data in a highly convergent group: the Pyrenean radiation of hypogean Trechini (Coleoptera: Carabidae)

ARNAUD FAILLE<sup>1</sup>, JAVIER FRESNEDA<sup>2</sup> & CHARLES BOURDEAU<sup>3</sup>

## Abstract

We provide the first molecular phylogeny based on a thorough taxonomic sampling of all Pyrenean species of the tribe Trechini occurring in the subterranean environment *sensu lato* (soil and cave), with a complete taxonomic inventory of all valid species. Based on this analysis and a careful morphological study, a new classification is proposed. All species of the genera *Aphaenops* Bonvouloir, 1862 and *Geotrechus* Jeannel, 1919 are included in a single genus, *Aphaenops*, which is split into eleven subgenera: subgenus *Aphaenops sensu stricto* (= *Geaphaenops syn. n.*), with type species *Aphoenops leschenaulti* Bonvouloir, 1862; subgenus *Argonotrechus subgen. n.*, with type species *Anopthalmus orpheus* Dieck, 1869; subgenus *Aurigerotrechus subgen. n.*, with type species *Trechus (Anopthalmus) vulcanus* Abeille de Perrin, 1904; subgenus *Ceretotrechus subgen. n.*, with type species *Geotrechus ubachi* Español, 1965; subgenus *Dupreaphaenops subgen. n.*, with type species *Aphaenops vasconicus* Jeannel, 1913; subgenus *Geotrechidius sensu novo*, with type species *Anopthalmus gallicus* Delarouzée, 1857; subgenus *Geotrechus stat. n.*, with type species *Anopthalmus discontignyi* Fairmaire, 1863; subgenus *Hydraphaenops sensu novo* (= *Pubaphaenops*, *Cerbaphaenops syn. n.* and *Simaphaenops syn. n.*), with type species *Anopthalmus ehlersi* Abeille de Perrin, 1872; subgenus *Nafarroaphaenops subgen. n.*, with type species *Aphaenops (Hydraphaenops) giraudi* Ochs, 1938; subgenus *Pyreneotrechus subgen. n.*, with type species *Geotrechus (Geotrechidius) aldensis* Jeannel, 1955; subgenus *Riberaphaenops subgen. n.*, with type species *Geotrechus holcartensis* Genest, 1977. Two of the subgenera are monospecific and were erected to place two morphologically and genetically divergent species, *Aphaenops (Argonotrechus) orpheus* and *Aphaenops (Pyreneotrechus) aldensis*. The former subgenera *Cerbaphaenops* and *Simaphaenops* are included in the large monophyletic subgenus *Hydraphaenops*, the paraphyletic subgenus *Geaphaenops* is included in the subgenus *Aphaenops* and the synonymy of *Arachnaphaenops*, *Cephalaphaenops* and *Pubaphaenops* with *Aphaenops* is confirmed. A full list of species, including 68 new combinations at the generic or subgeneric level, is presented.

**Key words:** Trechinae, hypogean beetles, subterranean evolution, molecular phylogeny, systematics.

## Zusammenfassung

Die vorliegende Arbeit liefert die erste molekular Phylogenie der in den Pyrenäen vorkommenden Arten des Tribus Trechini. Diese basiert auf einer genauen taxonomischen Probennahme aller im weitesten Sinne in unterirdischen Umgebungen (Boden und Höhle) vorkommenden Arten und beinhaltet eine komplette taxonomische Liste aller validen Arten. Auf der Grundlage dieser Analyse und einer sorgfältigen morphologischen Untersuchung wird eine neue Klassifizierung vorgeschlagen. Alle Arten der Gattungen *Aphaenops* Bonvouloir, 1862 und *Geotrechus* Jeannel, 1919 werden in einer einzigen Gattung, *Aphaenops*, zusammengefasst, die in elf Untergattungen aufgeteilt wird: Untergattung *Aphaenops sensu stricto* (= *Geaphaenops syn. n.*), mit der Typusart *Aphoenops leschenaulti* Bonvouloir, 1862; Untergattung *Argonotrechus subgen. n.*, mit der Typusart *Anopthalmus orpheus* Dieck, 1869; Untergattung *Aurigerotrechus subgen. n.*, mit der Typusart *Trechus (Anopthalmus) vulcanus* Abeille de Perrin, 1904; Untergattung *Ceretotrechus subgen. n.*, mit der Typusart *Geotrechus ubachi* Español, 1965; Untergattung *Dupreaphaenops subgen. n.*, mit der Typusart *Aphaenops vasconicus* Jeannel, 1913; Untergattung *Geotrechidius sensu novo*, mit der Typusart *Anopthalmus gallicus* Delarouzée, 1857; Untergattung *Geotrechus stat. n.*, mit der Typusart *Anopthalmus discontignyi* Fairmaire, 1863; Untergattung *Hydraphaenops sensu novo* (= *Pubaphaenops*, *Cerbaphaenops syn. n.* und *Simaphaenops syn. n.*), mit der Typusart *Anopthalmus ehlersi* Abeille de Perrin, 1872; Untergattung *Nafarroaphaenops subgen. n.*, mit der Typusart *Aphaenops (Hydraphaenops) giraudi* Ochs, 1938; Untergattung *Pyreneotrechus subgen. n.*, mit der Typusart *Geotrechus (Geotrechidius) aldensis* Jeannel, 1955; Untergattung *Riberaphaenops subgen. n.*, mit der Typusart *Geotrechus holcartensis* Genest, 1977. Zwei der Untergattungen sind monospezifisch und wurden aufgestellt, um zwei morphologisch und genetisch divergente Arten, *Aphaenops (Argonotrechus) orpheus* und *Aphaenops (Pyreneotrechus) aldensis*, zu klassifizieren. Die früheren Untergattungen *Cerbaphaenops* und *Simaphaenops* werden in die große monophyletische Untergattung *Hydraphaenops* aufgenommen, die paraphyletische Untergattung *Geaphaenops* wird in die Untergattung *Aphaenops* gestellt und die Synonymie von *Arachnaphaenops*, *Cephalaphaenops* und *Pubaphaenops* mit *Aphaenops* wird bestätigt. Eine vollständige Artenliste, einschließlich 68 neuer Kombinationen auf Gattungs- oder Untergattungsebene, wird hier präsentiert.

## Introduction

“*Au premier abord, un Geotrechus orpheus Dieck et un Aphaenops pluto Dieck sembleraient appartenir à deux lignées très distinctes. En réalité, ils sont très proches parents. Et nul meilleur exemple ne saurait être donné pour montrer qu'en systématique il faut terriblement se méfier des caractères dits d'adaptation.*”

(JEANNEL 1943)

Hypogean animals have fascinated evolutionary biologists since more than 200 years. Straddling the border between France and Spain, the Pyrenean chain is recognized as one of the world's hotspots of subterranean biodiversity (CULVER & SKET 2000; CULVER et al. 2006).

Subterranean environments host some of the less known parts of beetle diversity in the Western Palearctic and remain among the most important reservoirs of unknown biodiversity for the area, as evidenced by recent discoveries (e.g., FRESNEDA et al. 2009; CASALE et al. 2012; GUÉORGUIEV 2012; FAILLE et al. 2015a; NJUNJIC et al. 2016; ORTUÑO et al. 2017; HLAVÁČ et al. 2019; LOHAJ & DELIĆ 2019; MAGHRADZE et al. 2019; RIBERA & REBOLEIRA 2019; FAILLE et al. 2021; PIVA 2021; CASALE et al. 2022; FAILLE & BOURDEAU 2022a, 2022b). The species colonizing the hypogean environment share some remarkable morphological features known as troglomorphies: depigmentation, apterism, lack of eyes and elongation of appendages (VANDEL 1964; BARR 1968). Beetles are the most diverse group of insects below ground, and the two main groups of beetles having diversified in the subterranean environments of the Palearctic are Leiodidae Leptodirini and Carabidae Trechini (JEANNEL 1924, 1928; CASALE et al. 1998).

The hypogean Trechini of the Pyrenees form one of the most diverse monophyletic groups of subterranean invertebrates in the Western Palearctic (FAILLE et al. 2010a). The range of the group extends from the Puigmal massif (Cerdanya) in the East to Gipuzkoa in the West, a distance of ca. 360 km in a straight line. The Pyrenean lineage is estimated to have originated during the early Miocene (FAILLE et al. 2013b). Three genera—*Geotrechus* Jeannel, 1919, *Hydraphaenops* Jeannel, 1926 and *Aphaenops* Bonvouloir, 1862—were traditionally recognized, each representing a distinct morphological type, but a molecular study of the group evidenced the non-monophyly of these three genera, highlighting the role of morphological convergence in deeply obscuring the real affinities among taxa (FAILLE 2006; FAILLE et al. 2010a). The phylogeny by FAILLE et al. (2010a) was a first attempt at understanding the origin of the Pyrenean Trechini radiation and testing the monophyly of the above-mentioned three genera, but relationships among species within the radiation were left largely unsolved and could not be tested due to the reduced sampling, which lacked numerous key spe-

cies. Indeed, although hypogean Trechini are the most species-rich group of ground beetles, most of the species are extremely rare in the field and known from few exemplars only (JEANNEL 1926, 1928, 1941, 1943, 1949).

Recently, an update of the classic “Faune de France” volume on carabid beetles by RENÉ JEANNEL (1941) was published (QUÉINNEC & OLLIVIER 2011), in which the authors proposed a rearrangement of the supraspecific classification of Pyrenean subterranean Trechini based partly on the results of FAILLE (2006) and FAILLE et al. (2010a). The authors readopted the view of JEANNEL, considering *Hydraphaenops* (one of the three previously recognized genera) as a subgenus of *Aphaenops*. The genus *Aphaenops* was split into five subgenera: *Aphaenops*, *Geaphaenops* Cabidoche, 1966, *Cerbaphaenops* Coiffait, 1962, *Hydraphaenops* and the new subgenus *Simaphaenops* Quéinnec & Ollivier, 2011. No subgenera were recognized in the other genus, *Geotrechus*, and the former subgenus *Geotrechidius* Jeannel, 1947 was regarded as its synonym.

The present work aims to test the validity of these different hypotheses and provide a general framework for the classification of Pyrenean Trechini, in accordance with the evolutionary history of the group. We do not consider subspecies here unless otherwise stated, and a detailed discussion on the validity of subspecies as well as on the population structure of the most widespread species will be the focus of other publications. Contrary to the recent, highly contentious work by DONABAUER (2019), in which the genus *Trechus* Clairville was split based mainly on previous molecular works with limited sampling and without taking morphology or distribution into account, we here rename clades within a single monophyletic lineage of Trechini based on an analysis including all the known species. The group is divided into unambiguous monophyletic units largely supported by biogeography, morphological synapomorphies or a combination of morphological characters. We strongly disapprove of practices aiming at naming clades without morphological support and based on incomplete sampling of groups the complete history of which has yet to be elucidated—even more so in groups of worldwide distribution such as the genus *Trechus*—particularly if the only motivation is seemingly to create new names in the hope that some of them will be recovered as valid in the future.

By adding new specimens of previously included species and 28 little-known, endemic species to the study, we investigate the relationships between species in the Pyrenean hypogean radiation and propose to divide the two former genera *Aphaenops* (including *Hydraphaenops*) and *Geotrechus* into eleven monophyletic subgenera. By doing so, we aim to provide a clear framework for the study of Pyrenean hypogean ground beetles and for future, detailed revisions of the proposed subgenera. As mentioned above, the possible subspecific status of different populations of some species is not discussed in this contribution and

should be assessed on a case-by-case basis in the context of species-group revisions.

**Material and methods**

**Taxon sampling and DNA extraction**

With 91 species recognized so far (SERRANO 2013; TRONQUET 2014; FAILLE et al. 2015a; MORAVEC et al. 2017; FAILLE & BOURDEAU 2022a, 2022b), the Pyrenean radiation is one of the most speciose groups of hypogean Trechini of the Western Palearctic. Here, we included 91 specimens of 80 species belonging to this radiation, with representatives of all the subgenera recognized in QUÉINNEC & OLLIVIER (2011) and in the present work, together with two outgroups chosen from the genus *Trechus* (Appendix 1). All but two species of *Geotrechus* sensu auct. were included (25/27 spp.), as well as a nearly complete sampling of *Aphaenops* (*Aphaenops* sensu stricto: 12/14 spp.; *Geaphaenops*: 6/6 spp.; *Cerbaphaenops*: 19/22 spp.; *Hydraphaenops*: 14/15 spp.; *Simaphaenops*: 2/4 spp.). Although the genus was described as “*Aphoenops*” (BONVOULOIR 1862), the spelling *Aphaenops* is here conserved for the genus, in accordance with the opinion of previous authors (FAILLE et al. 2010a: Appendix A; QUÉINNEC & OLLIVIER 2011: 163 [status of “nomen protectum” assigned to *Aphaenops*]) and with the latest version of the Palearctic Catalogue of Coleoptera (MORAVEC et al. 2017).

Specimens were collected by hand or using pitfall traps containing propylene glycol to preserve the DNA (RUBINK et al. 2003; LÓPEZ & OROMÍ 2010). We followed the extraction protocol described in FAILLE et al. (2010b); extractions were non-destructive, using the DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany). Extracted exemplars were then mounted on cards, with the genitalia stored in water-soluble resin (DMHF) on a transparent card pinned beneath the specimen. The tree was rooted by two species of *Trechus* known to belong to different groups of Trechini (JEANNEL 1927; FAILLE et al. 2010a).

We amplified fragments of four mitochondrial genes: the 3' end of cytochrome c oxidase subunit I (cox1); a single fragment (16S) including the 3' end of the large ribosomal unit (rrnL), the whole tRNA-Leu gene (trnL) and the 5' end of NADH dehy-

drogenase 1 (nad1), and two nuclear genes: the internal fragment of the large ribosomal unit 28S rRNA (LSU) and the 5' end of the small ribosomal unit 18S rRNA (SSU) (see Table 1 for details of primers used). Sequences were assembled and edited using Sequencher TM 4.8 (Gene Codes, Inc., Ann Arbor, MI) and Geneious Prime 2019.2.3. Some sequences were taken from previous studies (FAILLE et al. 2010a, 2011, 2013a, 2013b, 2015a) (details and accession numbers in Table 2). For eight species, we failed to get all genes from a single exemplar; therefore, we combined two specimens in a single chimera (see asterisks in Table 2 Fig. 1). New sequences have been deposited in the GenBank database (for accession numbers, see Table 2).

**Morphological data**

Earlier classifications (especially JEANNEL 1928) grouped species based on shared general characteristics. We followed this approach by adding more characters; we first took images of 30 characters for each species, later restricting the number to 15 structures identified as phylogenetically more stable, such as the topology of setae, body pubescence, the general shape of the aedeagus, or the labial tooth and ligula. The terminology of the different kinds of elytral setae follows JUBERTHIE et al. (1975): mc: macrochaetae (discal series); t: trichobothria (umbilicate series); tm: the four trichobothria forming the “groupe huméral” sensu JEANNEL (1928).

The retained characters allowed to morphologically describe the groups in accordance with the obtained clades. Characters used to define each subgenus are listed below in their respective diagnoses or in the first sentence of each paragraph concerning the different species groups identified.

Images were taken with Olympus CH and Olympus SZX16 microscopes coupled with an Olympus C5060WZ camera (Olympus, Tokyo, Japan). Composite images were combined using the CombineZP software (Informer Technologies Inc., Dominica) and processed with Adobe Photoshop 7.0 (Adobe, San José, California).

For 10 species, no molecular data were available. We therefore considered their affinities based on morphological similarity, by looking at both external characters and characters of the male genitalia (when known). We studied all described species (and their type series in most cases) of the former genera

**Table 1.** Primers used for gene amplification.

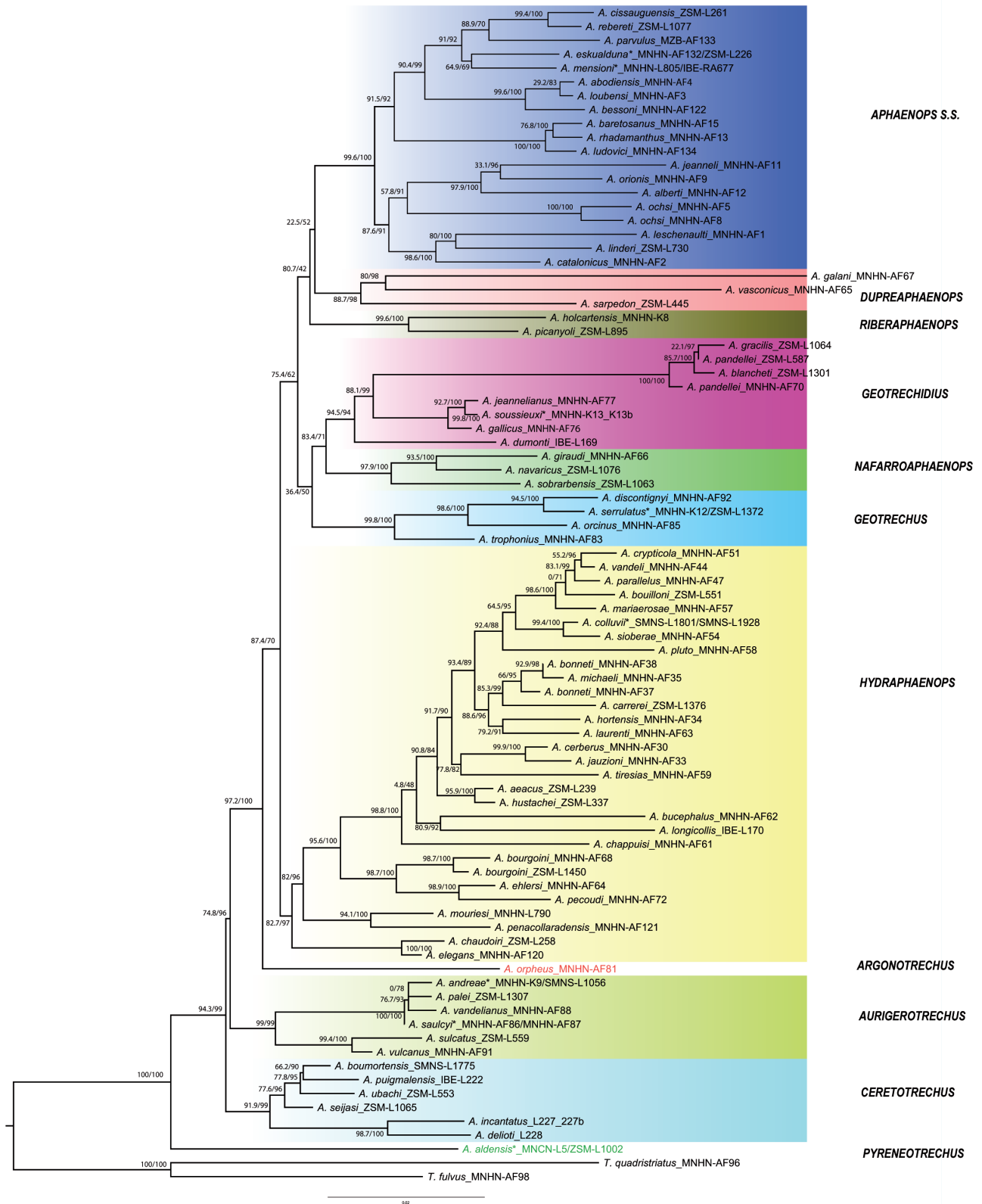
Gene	Name	Sense	Sequence	Reference
cox1	Jerry (M202)	F	CAACATTTATTTTGATTTTTTGG	SIMON et al. (1994)
	Pat (M70)	R	TCCA(A)TGCACTAATCTGCCATATTA	SIMON et al. (1994)
	Chy	F	T(A/T)GTAGCCCA(T/C)TTTCATTA(T/C)GT	RIBERA et al. (2010)
	Tom	R	AC(A/G)TAATGAAA(A/G)TGGGCTAC(T/A)A	RIBERA et al. (2010)
	Ron	F	GGATCACCTGATATAGCATTCCC	SIMON et al. (1994)
rrnL-nad1	16saR (M14)	F	CGCCTGTTTA(A/T)CAAAAACAT	SIMON et al. (1994)
	ND1A (M223)	R	GGTCCCTTACGAATTTGAATATATCCT	SIMON et al. (1994)
SSU	5'	F	GACAACCTGGTTGATCCTGCCAGT	SHULL et al. (2001)
	b5.0	R	TAACCGCAACAACCTTAAAT	SHULL et al. (2001)
LSU	D1	F	GGGAGGAAAAGAACTAAC	OBER (2002)
	D3	R	GCATAGTTCACCATCTTTC	OBER (2002)

Table 2. Material used in the study, with locality data, voucher number and accession numbers of the sequences.

N°	Genus	Subgenus	Species group	Species	code	localities	SSU	LSU	Cox1	rrnL	trnaLeu	NADI
	<i>Aphaenops</i>											
1	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>eskualduna</i>	<i>cisauquensis</i> Faille & Bourdeau, 2008	ZSM-L261	Aven de Lieje Elsau - Barlanès (France-64)		OO564991	OO566888	OO621678	OO621678	OO621678
2	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>eskualduna</i>	<i>eskualduna</i> Coiffait, 1959	MNHN-AF132	Salle de la Verma - Sainte-Engrâce (France-64)		HM921086	HM921079	XX	XX	XX
2	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>eskualduna</i>	<i>eskualduna</i> Coiffait, 1959	ZSM-L226	Salle de la Verma - Sainte-Engrâce (France-64)	OO534259	-	-	OO621676	OO621676	OO621676
3	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>eskualduna</i>	<i>mensoni</i> Lagar, 1976	MNHN-L805	Forat d'a Bufoma - Escuain (Spain-Fuesca)	-	OO564990	OO566868	OO621677	OO621677	OO621677
3	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>eskualduna</i>	<i>mensoni</i> Lagar, 1976	IBE-RA677	Forat d'a Bufoma - Escuain (Spain-Fuesca)	OO534260	-	-	-	-	-
4	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>eskualduna</i>	<i>parvulus</i> Faille, Bourdeau & Fresneda, 2010	MZB-AF133	Cueva d'Esjamiento - Villanua (Spain-Fuesca)	OO534261	HM921085	HM921078	HG315025	HG315025	HG315025
5	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>eskualduna</i>	<i>rebereti</i> A. Gaudin, 1947	ZSM-L1077	MSS - Gères Belesen (France-64)	OO534262	OO564980	-	OO621679	OO621679	OO621679
6	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>jeanneli</i>	<i>alberti</i> Jeannel, 1939	MNHN-AF12	Aven prox. Istaurdy - Aussarueq (France-64)	FR733955	GQ293595	GQ293662	GQ293700	GQ293782	GQ293829
7	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>jeanneli</i>	<i>jeanneli</i> (Abeille de Perrin, 1905)	MNHN-AF11	Aven d'Isaurdy - Aussarueq (France-64)	-	GQ293594	GQ293661	FR729560	FR729560	FR729560
8	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>jeanneli</i>	<i>orionis</i> Fagniez, 1913	MNHN-AF9	Gouffie EL71 - Château-Pignon (France-64)	GQ293507	GQ293592	HM921077	OO621693	OO621693	OO621693
9	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>leschenaulti</i>	<i>catalonica</i> Escolá & Cancio, 1983	MNHN-AF2	Cova des Toscolosses - Bonansa (Spain-Fuesca)	GQ293508	HM921082	GQ293674	GQ293699	GQ293756	GQ293821
10	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>leschenaulti</i>	<i>leschenaulti</i> Bonvoutloir, 1861	MNHN-AF1	Grotte de Castelimoity - Bagnères-de-Bigorre (France-65)	FR733945	GQ293593	GQ293629	GQ293739	GQ293757	GQ293822
11	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>leschenaulti</i>	<i>lindeti</i> Jeannel, 1938	ZSM-L730	Aven de Nabailès - Arthez d'Asson (France-64)	OO534266	OO564989	OO566867	OO621696	OO621696	OO621696
12	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>loubensi</i>	<i>abodiensis</i> Dupré, 1988	MNHN-AF4	Villanueva de Aezkoa - Sierra de Abodi - P70 (Spain-Navarra)	OO534251	GQ293555	GQ293627	OO621674	OO621674	OO621674
13	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>loubensi</i>	<i>bessoni</i> Cabidoche, 1962	MNHN-AF122	Gouffie du Col d'Aras 3 - Bielle (France-64)	OO534255	GQ293554	HM921076	OO621675	OO621675	OO621675
14	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>loubensi</i>	<i>loubensi</i> Jeannel, 1953	MNHN-AF3	Salle de la Verma - Sainte-Engrâce (France-64)	FR733946	HM921083	GQ293660	HG315024	HG315024	HG315024
15	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>ochsi</i>	<i>ochsi</i> L. Gaudin 1925	MNHN-AF8	Sima de Garralda - P10 (Spain-Navarra)	GQ293521	GQ293601	FR733894	GQ293740	GQ293777	GQ293830
15	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>ochsi</i>	<i>ochsi</i> L. Gaudin 1925	MNHN-AF5	Salle de la Verma - Sainte-Engrâce (France-64)	OO534263	GQ293556	GQ293667	OO621695	OO621695	OO621695
16	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>rhadamanthus</i>	<i>baretosanus</i> Jeannel, 1941	MNHN-AF15	Grotte d'Ambielle - Arrette (France-64)	FR733947	GQ293550	GQ293676	GQ293716	GQ293775	GQ293828
17	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>rhadamanthus</i>	<i>ludovici</i> A. Gaudin, 1935	MNHN-AF134	Achama Lezia - Sainte-Engrâce (France-64)	OO534268	HM921088	HM921081	OO621694	OO621694	OO621694
18	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>rhadamanthus</i>	<i>rhadamanthus</i> (Linder, 1860)	MNHN-AF13	Aven de Nabailès - Arthez d'Asson (France-64)	GQ293506	HM921087	HM921080	FR729562	FR729562	FR729562
19	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>argonotrechus</i>	<i>orpheus</i> (Dieck, 1870)	MNHN-AF81	Grotte de la Quère - Mérigon (France-09)	GQ293528	GQ293597	GQ293665	FR729573	FR729573	FR729573
20	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>sautleyi</i>	<i>andreae</i> (Jeannel, 1920) *	MNHN-K9	Grotte Rieux - Massat (France-09)	OO534264	OO564993	-	-	-	-
20	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>sautleyi</i>	<i>andreae</i> (Jeannel, 1920) *	SMNS-L1056	Grotte Rieux - Massat (France-09)	-	-	OO566875	OO621698	OO621698	OO621698
21	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>sautleyi</i>	<i>pateti</i> (Fourès, 1962)	ZSM-L1307	Grotte de Malarnaud - Montseron (France-09)	OO534265	OO564994	OO566876	-	-	-
22	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>sautleyi</i>	<i>sautleyi</i> (Argod-Vallon, 1913) *	MNHN-AF86	Gouffie du Barroti - Lacourt (France-09)	-	-	-	FR729574	FR729574	FR729574
22	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>sautleyi</i>	<i>sautleyi</i> (Argod-Vallon, 1913) *	MNHN-AF87	Grotte du Ker - Riveneret (France-09)	GQ293522	GQ293548	GQ293669	-	-	-
23	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>sautleyi</i>	<i>vandelianus</i> Faille et al. 2022	MNHN-AF88	Aven d'Anglade - Couffens (France-09)	GQ293523	GQ293549	FR733906	GQ293714	GQ293784	GQ293833
24	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>vulcanus</i>	<i>sulcatanus</i> (Coiffait, 1959)	ZSM-L559	Aven de la Tussave - Soueix (France-09)	-	OO564995	OO566878	OO621702	OO621702	OO621702
25	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>vulcanus</i>	<i>vulcanus</i> (Abeille de Perrin, 1904)	MNHN-AF91	Perte du Fustié - Saint-Martin-de-Caralp (France-09)	FR733970	GQ293599	FR733907	GQ293701	GQ293786	GQ293832

N°	Genus	Subgenus	Species group	Species	code	localities	SSU	LSU	Cox1	rrnL	trnaLeu	NADI
26	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Ceretroechus</i>	<i>deltai</i> (Faillie, Bourdeau, Bellès & Fresneda, 2015)	ZSM-L.228	Mines de Cortàs - Isòvol (Spain-Girona)	KT892673	KT892664	KT892656	-	-	-
27	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Ceretroechus</i>	<i>incantatus</i> (Faillie, Bourdeau, Bellès & Fresneda, 2015)*	IBE-L.227	Cova de les Encantades - Tolorú	KT892675	KT892666	-	-	-	-
27	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Ceretroechus</i>	<i>incantatus</i> (Faillie, Bourdeau, Bellès & Fresneda, 2015)*	IBE-L.227b	Cova de les Encantades - Tolorú	-	-	KT892657	-	-	-
28	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Ceretroechus</i>	<i>bomortensis</i> (Faillie, Bourdeau, Bellès & Fresneda, 2015)	SMNS-L1775	Avene de Pla Fomesa - La Guardia d'Ares (Spain-Lleida)	-	-	<b>OQ566874</b>	<b>OQ621700</b>	<b>OQ621700</b>	<b>OQ621700</b>
29	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Ceretroechus</i>	<i>pugnalanensis</i> (Lagar, 1981)	IBE-L.222	Cova de les Encantades del Puigmal - Querarbs (Spain-Girona)	KT892677	KT892672	KT892655	KT892661	KT892661	KT892661
30	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Ceretroechus</i>	<i>sejasi</i> (Español, 1969)	ZSM-L.1065	Fon de Bor - Belver de Cerdanya (Spain-Lleida)	-	KT892671	KT892654	KT892662	KT892662	KT892662
31	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Ceretroechus</i>	<i>ubachi</i> (Español, 1965)	ZSM-L.553	Avene del Xato - Llinars (Spain-Lleida)	KT892678	KT892670	KT892658	<b>OQ621701</b>	<b>OQ621701</b>	<b>OQ621701</b>
32	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Dupreaphaenops</i>	<i>galani</i> (Español, 1968)	MNHN-AF67	Guardexe Koleccia - Usurbil (Spain-Guipuzcoa)	GQ293524	GQ293602	FR733899	GQ293697	GQ293746	GQ293817
33	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Dupreaphaenops</i>	<i>serpillon</i> (Faillie, Fresneda & Bourdeau, 2013)	ZSM-L.445	Grotte inférieure d'Oxibar - Camou-Chigue (France-64)	KT892679	HG315029	HG315032	HG315028	HG315028	HG315028
34	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Dupreaphaenops</i>	<i>vasconicus</i> Jeannel, 1913	MNHN-AF65	Aven d'Isaurdy - Aussurucq (France-64)	GQ293530	GQ293622	GQ293628	GQ293698	GQ293759	GQ293803
35	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>blanchetti</i> (A. Gaudin, 1947)	ZSM-L.1301	Grotte de Capbis - Capbis (France-65)	<b>OQ534267</b>	<b>OQ565003</b>	<b>OQ566889</b>	-	-	-
36	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>dumonit</i> (Español, 1977)	IBE-L.169	Cova de las Cuixas - Villanna (Spain-Huesca)	<b>OQ534269</b>	<b>OQ565000</b>	<b>OQ566869</b>	<b>OQ621688</b>	<b>OQ621688</b>	<b>OQ621688</b>
37	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>gallicus</i> (Delarouze, 1857)	MNHN-AF76	Aven de Nabailis - Arthez d'Asson (France-64)	GQ293518	GQ293557	GQ293670	GQ293724	GQ293769	GQ293798
38	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>gracilis</i> (A. Gaudin, 1947)	ZSM-L.1064	Aven de Licie Elsaüt - Barlanès (France-64)	-	<b>OQ565005</b>	<b>OQ566891</b>	-	-	-
39	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>jeannelianus</i> Faillie et al. 2022	MNHN-AF77	Grotte de la Bouhadère - Saint-Pé-de-Bigorre (France-65)	GQ293517	GQ293558	FR733904	GQ293725	GQ293770	GQ293799
40	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>pandellet</i> (Linder, 1859)	MNHN-AF70	Grotte d'Artegiade - Ribénaucq (France-64)	FR733961	GQ293545	GQ293681	HG315026	HG315026	HG315026
40	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>pandellet</i> (Linder, 1859)	ZSM-L.587	Grotte d'Ambielle - Arette (France-64)	-	<b>OQ565004</b>	<b>OQ566890</b>	<b>OQ621703</b>	<b>OQ621704</b>	<b>OQ621705</b>
41	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>sousseixi</i> (Perreau & Quéinnec, 1987)	MNHN-K.13	Grotte des Fées - Saint-Cricq-du-Gave (France-40)	-	<b>OQ564999</b>	<b>OQ566870</b>	-	-	-
41	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechidius</i>	<i>sousseixi</i> (Perreau & Quéinnec, 1987)	MNHN-K.13b	Grotte des Fées - Saint-Cricq-du-Gave (France-40)	-	-	-	<b>OQ621685</b>	<b>OQ621685</b>	<b>OQ621685</b>
42	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechus</i>	<i>discontigny</i> (Fairmaire, 1863)	MNHN-AF92	Grotte du Tucco - Bagnères-de-Bigorre (France-65)	FR733966	GQ293560	FR733901	FR729572	FR729572	FR729572
43	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechus</i>	<i>orcinus</i> (Linder, 1859)	MNHN-AF85	Gouffre de Peyreigne - Tibrin (France-65)	GQ293519	GQ293559	FR733902	GQ293744	GQ293789	GQ293802
44	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechus</i>	<i>sernulatus</i> (Jeannel, 1946)*	MNHN-K.12	Grotte de l'Église - Nistos (France-65)	<b>OQ534257</b>	-	-	-	-	-
44	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechus</i>	<i>sernulatus</i> (Jeannel, 1946)*	ZSM-L.1372	Grotte de l'Église - Nistos (France-65)	-	<b>OQ564996</b>	<b>OQ566887</b>	-	-	-
45	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Geotrechus</i>	<i>trophonius</i> (Abelle de Perrin, 1872)	MNHN-AF83	Grotte de Tuto Heredo - Merigon (France-09)	FR733968	GQ293561	GQ293631	GQ293715	GQ293766	GQ293825
46	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Hydrapphaenops</i>	<i>chaudoiri</i> (Brisout de Barneville, 1867)	ZSM-L.258	Grotte de Castelmouly - Bagnères-de-Bigorre (France-65)	-	<b>OQ564988</b>	<b>OQ566873</b>	<b>OQ621690</b>	<b>OQ621690</b>	<b>OQ621690</b>
47	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Hydrapphaenops</i>	<i>elegans</i> (A. Gaudin, 1946)	MNHN-AF120	Subterranean river of Artigalou-Arodeis - Esparrós (France-65)	FR733964	GQ293562	FR733900	GQ293703	GQ293754	GQ293816
48	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Hydrapphaenops</i>	<i>aecacus</i> (Saulcy, 1864)	ZSM-L.239	Grotte de Castelmouly - Bagnères-de-Bigorre (France-65)	-	<b>OQ564981</b>	<b>OQ566882</b>	<b>OQ621680</b>	<b>OQ621680</b>	<b>OQ621680</b>
49	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Hydrapphaenops</i>	<i>bonneti</i> Fourès, 1948	MNHN-AF38	Trou du Rantou - Sue-et-Sentenac (France-09)	-	GQ293571	FR733897	GQ293721	GQ293774	GQ293805
50	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Hydrapphaenops</i>	<i>boulloni</i> Coffait, 1955	ZSM-L.551	Grotte de Pétilac - Bordès-sur-Lez (France-09)	<b>OQ534252</b>	ON427719	ON421545	ON660967	ON660967	ON660967
51	<i>Aphaenops</i>	<i>Bonvoutloir</i> , 1862	<i>Hydrapphaenops</i>	<i>bucephalus</i> (Dieck, 1869)	MNHN-AF62	Gouffre de la Peyrère - Balaguères (France-09)	GQ293511	GQ293588	GQ293675	GQ293693	GQ293747	GQ293814

N°	Genus	Subgenus	Species group	Species	code	localities	SSU	LSU	Cox1	rrnL	trnSLeu	NAD1
52	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>carrerei</i> Coiffait, 1953	ZSM-L1376	Grotte de Lameza - Seix (France-09)	-	0Q564987	0Q566885	0Q621681	0Q621681	0Q621681
53	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>cerberus</i> (Dieck, 1869)	MNHN-AF30	Grotte du Scandé - Moulis (France-09)	FR733948	GQ293589	GQ293646	GQ293718	GQ293779	GQ293835
54	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>chappuisi</i> Coiffait, 1955	MNHN-AF61	Grotte de la Maoutro - Izaut-de-l'Hotel (France-31)	GQ293525	GQ293563	GQ293684	FR729569	FR729569	FR729569
55	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>collavii</i> Genest & Juberthie, 1983	SMNS-L1801	MSS Origbet 1380m - Origbet (France-09)	-	-	-	0Q621682	0Q621682	0Q621682
55	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>collavii</i> Genest & Juberthie, 1983	SMNS-L1928	MSS Ravin de la Tire - Argein (France-09)	-	0Q564983	0Q566884	-	-	-
56	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>crypticola</i> (Linder, 1859)	MNHN-AF51	Gouffre de Peyregues - Tibiran-Jaunac (France-65)	0Q534253	GQ293580	GQ293642	ON660973	ON660973	ON660973
57	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>bonneti</i> Genest, 1983	MNHN-AF37	Gouffre du Petit Mirabat - Ericé (France-09)	GQ293513	GQ293570	GQ293638	GQ293720	GQ293773	GQ293804
58	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>hortensis</i> Fourès, 1954	MNHN-AF34	Gouffre du Trapech d'en Haut - Bordes-sur-Lez (France-09)	GQ293512	GQ293572	GQ293641	0Q621683	0Q621683	0Q621683
59	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>lustachi</i> Jeannel, 1917	ZSM-L337	Grotte de l'Ayguat de Pelou - Nistos (France-65)	-	ON427718	ON421544	ON660966	ON660966	ON660966
60	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>jauzioni</i> Faillé, Delhot & Quéinnec, 2007	MNHN-AF33	Grotte d'Artigouli - Estadens (France-31)	-	GQ293581	GQ293640	FR729564	FR729564	FR729564
61	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>laurenti</i> Genest, 1983	MNHN-AF63	Grotte de Bordes de Cnues - Saix (France-09)	FR733956	GQ293569	GQ293634	GQ293719	GQ293767	GQ293813
62	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>longicollis</i> Hoffe, 1931	IBE-L170	Grotte de l'Ayguat de Pelou - Nistos (France-65)	0Q534270	0Q564986	0Q566892	0Q621684	0Q621684	0Q621684
63	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>mariaesae</i> Genest, 1983	MNHN-AF57	Gouffre du Trapech d'en Haut - Bordes-sur-Lez (France-09)	FR733953	GQ293568	GQ293649	GQ293704	GQ293760	GQ293809
64	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>michaeli</i> Fourès, 1954	MNHN-AF35	Grotte de Noël - Seix (France-09)	GQ293515	GQ293585	FR733896	GQ293722	GQ293768	GQ293815
65	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>parallelus</i> Coiffait, 1954	MNHN-AF47	Grotte de Gouillou - Aspet (France-31)	FR733952	GQ293577	GQ293671	GQ293709	GQ293765	GQ293812
66	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>pluto</i> (Dieck, 1869)	MNHN-AF58	Grotte du Scandé - Moulis (France-09)	FR733954	GQ293567	GQ293647	ON660974	ON660974	ON660974
67	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>soberae</i> Fourès, 1954	MNHN-AF54	Grotte de Payssa - Salseim (France-09)	GQ293516	GQ293587	GQ293639	FR729568	FR729568	FR729568
68	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>itresias</i> (Prochard de La Brulerie, 1872)	MNHN-AF59	Gouffre de la Peyrière - Balaguères (France-09)	GQ293527	GQ293596	GQ293658	GQ293713	GQ293748	GQ293800
69	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>crypticola</i>	<i>vandeli</i> Fourès, 1954	MNHN-AF44	Grotte de Payssa - Salseim (France-09)	FR733951	GQ293584	GQ293657	GQ293706	GQ293762	GQ293808
70	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>ehlersi</i>	<i>bourgoini</i> Jeannel, 1946	MNHN-AF68	Grotte de l'Église - Nistos (France-65)	FR733960	GQ293552	GQ293659	GQ293733	GQ293772	GQ293826
71	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>ehlersi</i>	<i>bourgoini</i> Jeannel, 1946	ZSM-L1450	Grotte de Payssa - Salseim (France-09)	-	0Q564984	0Q566881	0Q621692	0Q621692	0Q621692
72	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>ehlersi</i>	<i>ehlersi</i> (Abelle de Perrin, 1872)	MNHN-AF64	Gouffé-di-Hier - Arbas (France-31)	FR733957	GQ293565	GQ293683	FR729571	FR729571	FR729571
73	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>ehlersi</i>	<i>pecoudi</i> A. Gaudin, 1938	MNHN-AF72	Gouffre du Barroti - Lacourt (France-09)	FR733963	GQ293566	GQ293673	GQ293738	-	-
73	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>minos</i>	<i>mouriesi</i> (Genest, 1983)	MNHN-L790	Gouffre VMI - Le Port (France-09)	-	0Q564985	0Q566879	0Q621686	0Q621686	0Q621686
74	<i>Aphaenops</i> Bonvouloir, 1862	<i>Hydraphaenops</i>	<i>minos</i>	<i>penacollarandensis</i> (Dupré, 1991)	MNHN-AF121	Aven El Simistro, Villanúa (Spain-Huesca)	FR733965	GQ293564	0Q566880	GQ293702	GQ293771	GQ293823
75	<i>Aphaenops</i> Bonvouloir, 1862	<i>Najarroaphaenops</i>		<i>giraudi</i> Ochs, 1938	MNHN-AF66	Salle de la Verma - Sainte-Engrâce (France-64)	FR733958	GQ293600	GQ293663	GQ293695	GQ293753	GQ293818
76	<i>Aphaenops</i> Bonvouloir, 1862	<i>Najarroaphaenops</i>		<i>navaricus</i> Coiffait & A. Gaudin, 1950	ZSM-L1076	Gouffre EL71 - Château-Pignon (France-64)	-	0Q564997	0Q566871	0Q621687	0Q621687	0Q621687
77	<i>Aphaenops</i> Bonvouloir, 1862	<i>Najarroaphaenops</i>		<i>sobrarbensis</i> Lagar & Hermandó, 1987	ZSM-L1063	Cueva de Aso - Fanlo (Spain-Huesca)	-	0Q564998	0Q566872	0Q621689	0Q621689	0Q621689
78	<i>Aphaenops</i> Bonvouloir, 1862	<i>Pyreneotrechus</i>		<i>aldensis</i> (Jeannel, 1955)	MNCN-L5	Grotte Budax - Belestia (France-09)	0Q534256	0Q565006	-	0Q621699	0Q621699	0Q621699
78	<i>Aphaenops</i> Bonvouloir, 1862	<i>Pyreneotrechus</i>		<i>aldensis</i> (Jeannel, 1955)	ZSM-L1002	Grotte Budax - Belestia (France-09)	-	-	0Q566877	-	-	-
79	<i>Aphaenops</i> Bonvouloir, 1862	<i>Riberaphaenops</i>		<i>holcartensis</i> Genest, 1977	MNHN-K8	Grotte d'Ambielle - Arette (France-64)	0Q534254	0Q565001	-	0Q621697	0Q621697	0Q621697
80	<i>Aphaenops</i> Bonvouloir, 1862	<i>Riberaphaenops</i>		<i>picanoyi</i> Espanol & Escolá, 1983	ZSM-L895	Cova Mora - San Juan de la Peña (Spain-Huesca)	-	0Q565002	0Q566886	0Q621691	0Q621691	0Q621691
1	<i>Trechus</i> Clairville, 1806											
1	<i>Trechus</i> Clairville, 1806			<i>fulvus</i> Dejean, 1831	MNHN-AF98	Cueva del Pis - Penilla, Santurde de Toranzo (Spain-Cantabria)	FR733972	GQ293613	HE817938	GQ293729	-	-
2	<i>Trechus</i> Clairville, 1806			<i>quadristriatus</i> (Schrank, 1781)	MNHN-AF96	Spain- Egea, Collau de la Plana del Turbón	GQ293534	GQ293619	FR733908	GQ293743	GQ293745	GQ293841



**Fig. 1a.** Phylogram of Pyrenean hypogean Trechini obtained in IQ-TREE using the combined data matrix. Maximum likelihood node supports of the ultrafast bootstraps/SH-aLRT indicated above nodes.



*Aphaenops* (including *Hydrapphaenops*) and *Geotrechus*. Vouchers and DNA samples are kept in the collections of the Muséum National d'Histoire Naturelle (Paris, France) (MNHN), Zoologische Staatssammlung München (Munich, Germany) (ZSM), Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany) (SMNS) and of the authors.

#### Phylogenetic analyses

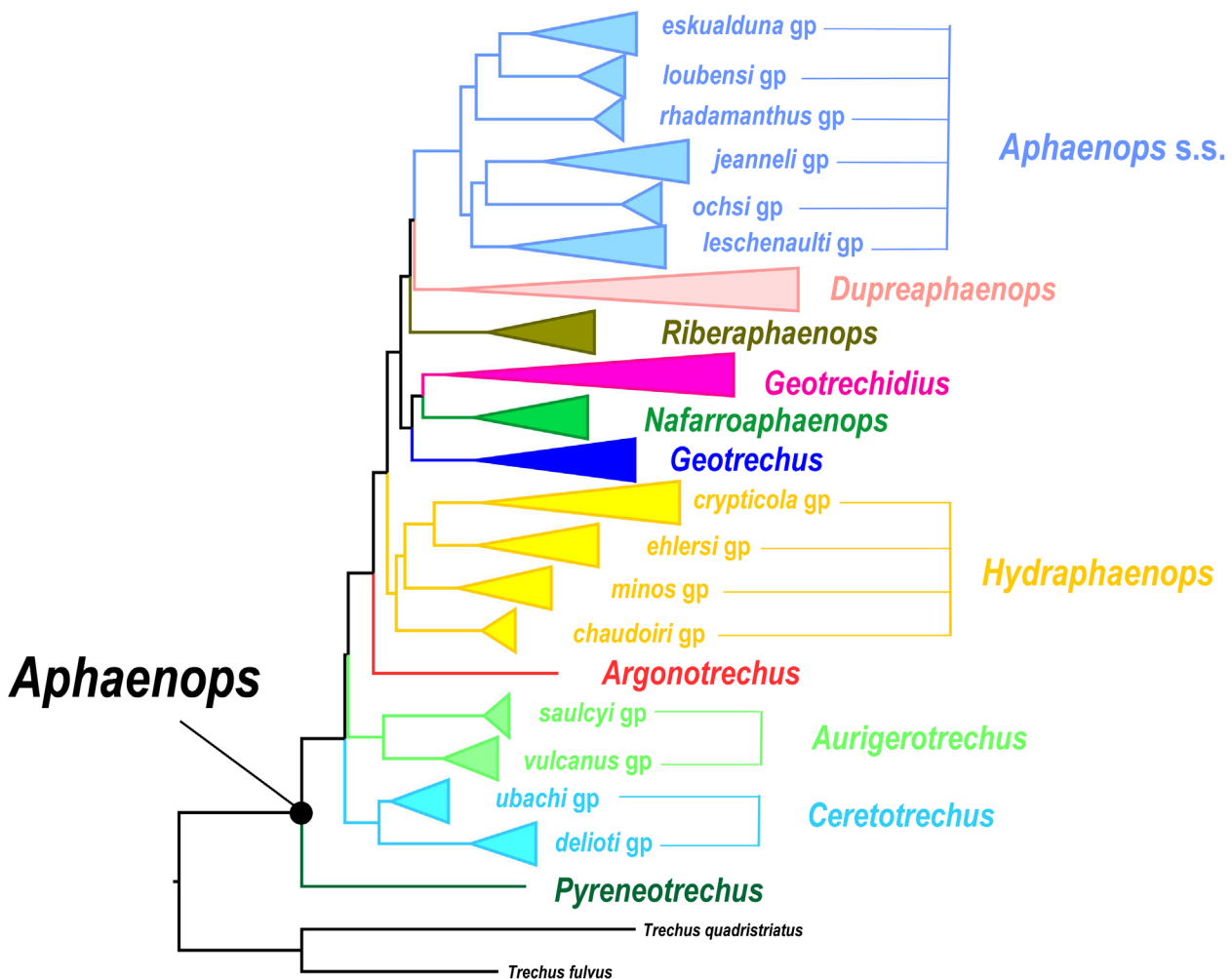
The sequences obtained were aligned using MAFFT online v.7 (KATOHI et al. 2019), with the Q-INS-i algorithm (KATOHI & TOH 2008) and default parameters. The sequence matrix was analysed with a fast maximum likelihood search as implemented in IQ-TREE v1.6 (NGUYEN et al. 2015), with the best evolutionary model (TVM+F+R3) as selected by Modelfinder (KALYANAMOORTHY et al. 2017) using the AIC (Akaike Information Criterion). We assessed topological stability with 1,000 ultrafast bootstraps (UFBoot) and additionally tested branch support using SH-like aLRT with 1,000 replicates (NGUYEN et al. 2015). Maximum likelihood analyses were also conducted on the combined data matrix using RAxML 8.1.2 (STAMATAKIS 2006, 2014). The data set was partitioned by gene, with an independ-

ent GTR+I+G evolutionary model applied to each partition and default values for other parameters of the search. The node support values were obtained with 1,000 bootstrap replicates.

The names of the valid taxa in their new combinations, their authors, publication dates and lists of synonyms and combinations are given in Appendix 1.

## Results

The topologies obtained with RAxML and IQ-TREE were largely congruent, except for minor differences in node support. As we found no incongruence and the topologies were similar, we chose to keep the topology obtained with IQ-TREE (Fig. 1a). The monophyly of this hypogean radiation of Trechini beetles was strongly supported and none of the three traditionally recognized genera was recovered as monophyletic. The polyphyly of the



**Fig. 1b.** Simplified phylogram of the genus *Aphaenops* Bonvouloir and its eleven subgenera.

genera *Aphaenops* and *Geotrechus* and of the subgenera *Hydrapphaenops*, *Cerbapphaenops* and *Geapphaenops*, under their circumscription prior to this work, is evidenced. Some well-defined species groups were recovered. A single species, *Aphaenops aldensis* (Jeannel, 1955), the easternmost species of the group, is sister to the whole Pyrenean radiation, suggesting an eastern origin of the lineage. Apart from this species, the genus *Geotrechus* is split into five well-supported clades.

The reconstructed topology of the Pyrenean subterranean Trechini lineage is consistent with previous results obtained with a smaller sampling coverage (FAILLE et al. 2010a).

Among the characters chosen for the morphological study, the topology of the elytral setae and the distribution of pubescence appeared to be very often informative phylogenetically. The main characters of each of the subgenera newly erected or newly defined herein are listed in Appendix 2.

The molecular phylogenetic results and the nearly complete taxon sampling allow to propose, for the first time, a new classification of the radiation, with the aim to avoid para- or polyphyletic genera and subgenera.

The following section provides brief descriptions of the new subgenera, each of them delimited according to the well-supported clades in the phylogeny. Their main diagnostic morphological characters are given, as well as new names and combinations (see Appendix 1 for a complete list of species in the newly defined genus *Aphaenops*).

The hypogean Pyrenean Trechini comprise 91 species, all of which are here included in a single genus: *Aphaenops* sensu novo; the species previously included in the genus *Geotrechus* are split across eight of the 11 clades of *Aphaenops* (Fig. 1a, b). The name *Geotrechus* is now restricted to the clade of *Aphaenops* containing *Aphaenops (Geotrechus) discontignyi* (Fairmaire, 1863), **comb. n.**, the type species of *Geotrechus*. The subgenus *Hydrapphaenops* sensu novo is extended to all the species previously included in the genera *Cerbapphaenops* and *Simapphaenops*. Some of the species previously recognized as belonging to the genus *Hydrapphaenops* are included in new subgenera. The genus *Geapphaenops* is regarded as a junior synonym of *Aphaenops* s. str., **syn. n.**

These taxonomic changes have generated secondary homonymies, and two species are therefore renamed (see Appendix 1).

### A new classification of the Pyrenean hypogean lineage of *Aphaenops*

#### Genus *Aphaenops* Bonvouloir, 1862

*Aphoenops* Bonvouloir, 1862 (BONVOULOIR 1862: 567), **nomen oblitum**.

#### Type species

*Aphoenops leschenaulti* Bonvouloir, 1862 (BONVOULOIR 1862: 568) (Fig. 2).

#### Diagnosis

The hypogean species of Trechini traditionally gathered in the genera *Aphaenops* (including *Hydrapphaenops*) and *Geotrechus* are all blind, depigmented and apterous. Additionally, they share the following combination of characters:

- labial tooth simple (although slightly bifid when observed at high magnification in some species);
- submentum with six setae;
- protibiae pubescent, without sulcus;
- elytra: marginal umbilicate setae with humeral group not aggregated, the third and the fourth seta distant from the margin of the elytra;
- apex of elytra: first stria running into direction of 5th longitudinal stria;
- endophallus of male genitalia with a simple copulatory piece, asymmetrical and in a lateral position (“anisotopic”, JEANNEL 1928; FAILLE et al. 2013b).

The genus includes 91 species previously included in the former genera *Aphaenops* (subgenera *Aphaenops*, *Geapphaenops*, *Cerbapphaenops*, *Hydrapphaenops* and *Simapphaenops* sensu auct.) and *Geotrechus*.

All representatives are endemic to the Pyrenean area and are found underground, from the soil and MSS (“Milieu Souterrain Superficiel”; JUBERTHIE et al. 1980) to the deepest caves. Some species are preferentially found in the upper part of the karst, under stones, with some species of *Hydrapphaenops* being more common in the deepest areas of the karst.

Here, we list the subgenera in alphabetical order together with diagnostic character states. An exhaustive list of the species can be found in Appendix 1.

#### 1. Subgenus *Aphaenops* sensu stricto

= *Geapphaenops* Cabidoche, 1966, **syn. n.**

This speciose subgenus currently contains 20 species and corresponds to the “groupe *leschenaulti*” sensu JEANNEL (1943) plus *Aphaenops (Aphaenops) alberti* and the species described since then [subgenera *Aphaenops* and *Geapphaenops* sensu QUÉINNEC & OLLIVIER (2011)].

#### Diagnosis

Large bodied species, troglitic or endogean (former *Geapphaenops*) (Fig. 2). Size variable from 5 mm [*Aphaenops (Aphaenops) parvulus*] to 8 mm [*Aphaenops (Aphaenops) loubensi*]. All species of this clade are glabrous and lacking dense pubescence on the head, with the only exception of the aberrant species *Aphaenops (Aphaenops) alberti* from the Arbailles Massif in France (Fig. 8b).



**Fig. 2.** *Aphaenops leschenaulti* Bonvouloir, 1862, the type species of the genus. Scale bar: 2 mm.

Elytra without striae.

#### Distribution

This large and homogeneous clade corresponds to the “Western clade” of FAILLE et al. (2010a). It is distributed in the western part of the Pyrenean chain, from the Pre-

Pyrenees in the Noguera Ribagorçana Valley—*Aphaenops (Aphaenops) catalonicus*—in the East to the Roncevaux area (Navarra)—*Aphaenops (Aphaenops) ochsi*—in the West.

#### Remarks

The clade is geographically and genetically strongly supported. Nevertheless, in spite of the large size and similar overall appearance of species in this subgenus, no unambiguous synapomorphy has been evidenced (FAILLE 2006). However, *Aphaenops* sensu stricto can be split into six species groups, each of which can be characterized morphologically and genetically.

#### 1.1. *Aphaenops (Aphaenops) eskualduna* group

The species of this group are characterized by a round head, labrum slightly or deeply concave, ligula triangular and bearing six (3+3) lateral setae, the presence of a crown of setae on the maxillary palps, and male genitalia elongated, with sagittal aileron present.

The group consists of five species endemic to the Western Pyrenees. It is heterogeneous in size, some species being large [e.g., *Aphaenops (Aphaenops) mensioni*], others very small [e.g., *Aphaenops (Aphaenops) parvulus*] (FAILLE et al. 2010b). Some of the species are known from caves only [*Aphaenops (Aphaenops) mensioni*, *Aphaenops (Aphaenops) parvulus*, *Aphaenops (Aphaenops) eskualduna*], whereas others are more common in the soil and MSS [*Aphaenops (Aphaenops) rebereti*, *Aphaenops (Aphaenops) cissauguensis*].

#### 1.2. *Aphaenops (Aphaenops) jeanneli* group

The species of this group share a salient though moderately acute labial tooth and median lobe of aedeagus with a dilated basal bulb and pointed apex.

Group composed of three troglobitic species from the Western Pyrenees. *Aphaenops (Aphaenops) jeanneli* and *Aphaenops (Aphaenops) orionis* are morphologically close, differing by a combination of morphological characters (shape of head, elytra and median lobe). The third species, *Aphaenops (Aphaenops) alberti*, endemic to the Arbailles Massif, is morphologically divergent, slender, larger in size and with a large, pubescent head (Fig. 8b) that led its descriptor to consider it close to *Aphaenops (Hydraphaenops) bucephalus* from Ariège, which convergently shares a similar facies, especially the large, pubescent head (Fig. 8d) (JEANNEL 1939). This group is localised in the Arbailles Massif (France) and the neighbouring Urkulu, Orbara and Orion massifs (Spain).

#### 1.3. *Aphaenops (Aphaenops) leschenaulti* group

Head large, temples glabrous, two discal setae. Labrum concave, labial tooth smooth, flattened. Labial ligula

prow-shaped, with protruding central bulb. Male genitalia homogeneous in the three species: aedeagal median lobe small, short, with a blunt apex and without an apical lamella, widely open at base (Fig. 5). The aedeagal internal sac is covered with a broad field of uniformly-sized microtrichia.

Three species of the Central Pyrenees: two troglitic [*Aphaenops (Aphaenops) leschenaulti* and *Aphaenops (Aphaenops) catalanicus*], one endogean [*Aphaenops (Aphaenops) linderi*, previously included in the subgenus *Geaphaenops*]. *Aphaenops (Aphaenops) leschenaulti* and *Aphaenops (Aphaenops) linderi* are endemic to the northern slope of the Pyrenees. The first is restricted to the area of Bagnères de Bigorre, whereas the second is found in the Saint Pé area. The third species, *Aphaenops (Aphaenops) catalanicus*, is widespread in Betesa and Bonansa, Huesca, Spain, although always rare in caves (FRESNEDA 1987; FAILLE et al. 2006).

#### 1.4. *Aphaenops (Aphaenops) loubensi* group

Head triangular, labrum concave. Pronotum small, squared; body glabrous, discal series with numerous setae (usually 5–8).

Three large-bodied species from the Western Pyrenees, found in high altitude caves between the Aspe and Iraty valleys in the West (DUPRÉ 1988). A fourth species, *Aphaenops (Aphaenops) valleti*, not available for the molecular part of this work, is tentatively included in this group. Although much smaller, this last species shares many character states with the *Aphaenops (Aphaenops) loubensi* group: high number (10–12) of discal setae and shape and arrangement of setae of labrum and copulatory piece among others. The male genitalia of *Aphaenops (Aphaenops) valleti* are of a similar structure to those of the *Aphaenops (Aphaenops) loubensi* group, although not hooked at the apex (CASALE & GENEST 1986). This species is endemic to the Somota Massif in Huesca province, Spain.

#### 1.5. *Aphaenops (Aphaenops) ochsi* group

This group is characterized by some unique morphological character states, the most relevant of being the triangular shape and the conformation of the labrum with four median setae gathered in the middle (Fig. 8a). Other features (copulatory piece gutter-shaped; protruding ligula, calyx-shaped with eight setae and a prominent, two-lobed central tubercle) are characteristic of *Aphaenops (Aphaenops) ochsi*, but these characters have not been documented for *Aphaenops (Aphaenops) fresnedai*, which is known from a single, poorly preserved female exemplar.

The group consists of two troglitic species from the Central and Western Pyrenees. *Aphaenops (Aphaenops)*

*ochsi* is a widespread species occurring from the Villanúa Valley in the East to the Arce Valley in the West (FAILLE & BOURDEAU 2011). It is found in a great variety of cavities, from warm, low-altitude caves (e.g., the Espoz and Espinal areas on the southern slope of the Pyrenees) to cold, high-altitude caves (e.g., the Pierre Saint Martin Massif at the border between France and Spain). A population of this species was recently discovered far south, in the Sierra de Leyre (DUPRÉ 2017). Many subspecies have been described, some of which were recently synonymized without further explanation (TRONQUET 2014). The status of the numerous populations of *Aphaenops (Aphaenops) ochsi* is in need of revision. The second species, *Aphaenops (Aphaenops) fresnedai*, is known from the female type only, found in a high-altitude abyss in Sierra de Alano (FAILLE & BOURDEAU 2011).

#### 1.6. *Aphaenops (Aphaenops) rhadamanthus* group

Homogeneous morphology, with large head scarcely pubescent, short appendages and parameres with numerous (usually 5–7) setae. Mandibular tooth squared, simple.

This group is composed of three endogean species (former *Geaphaenops*, in part). The species of this group are extremely rare in caves and are found in the ground and occasionally in the MSS, often mixed with species of the subgenus *Geotrechidius*: *Aphaenops (Geotrechidius) gallicus* spp., *Aphaenops (Geotrechidius) jeannelianus* **nom. n.**

### 2. Subgenus *Argonotrechus* subgen. n.

Type species

*Anopthalmus orpheus* Dieck, 1869: 3 (DIECK 1869: 3 [= DIECK 1870: 341]), by present designation (Figs. 3a, 6a).

Diagnosis

This morphologically distinct monospecific subgenus is very well characterized by the convex elytra with deep punctate striae, pronotum with fore angles salient and hind angles acute and divergent, presence of a transverse bulge at the base of the elytra, and bilobate labrum.

Etymology

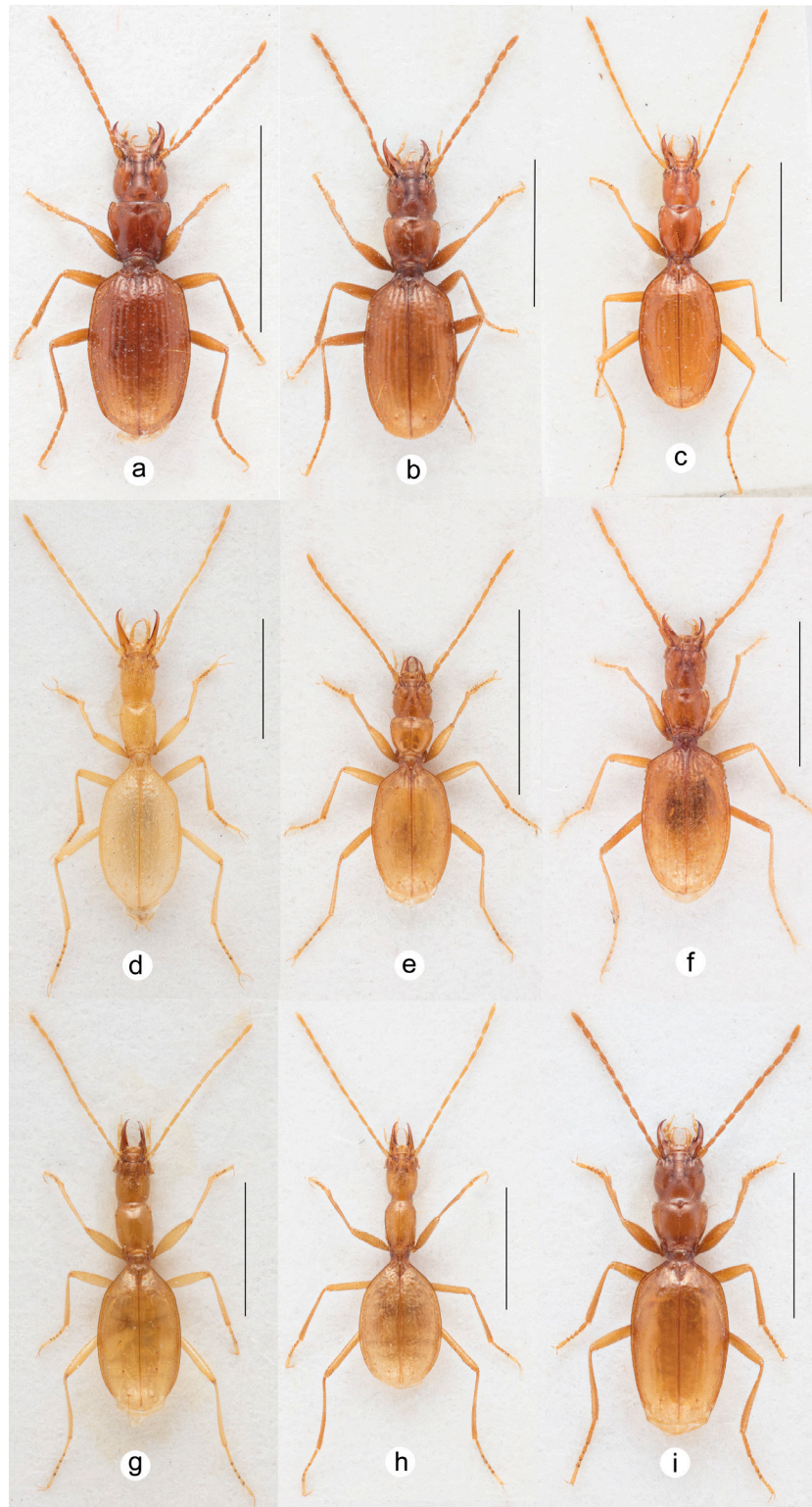
The new name refers to the Argonauts, heroes in Greek mythology, of which Orpheus (the name of the type species) was a member.

Distribution

The only species of this subgenus is quite widespread in Ariège and Haute-Garonne (France).

Remarks

*Aphaenops (Argonotrechus) orpheus* is a common and widespread species, often endogean, which is morpholog-



**Fig. 3.** Type species of the 11 subgenera of *Aphaenops*. **a.** *Aphaenops* (*Argonotrechus*) *orpheus* (Dieck, 1869). **b.** *Aphaenops* (*Aurigerotrechus*) *vulcanus* (Abeille de Perrin, 1904). **c.** *Aphaenops* (*Ceretotrechus*) *ubachi* (Español, 1965). **d.** *Aphaenops* (*Dupreaphaenops*) *vasconicus* Jeannel, 1913. **e.** *Aphaenops* (*Geotrechidius*) *gallicus* (Delarouzée, 1857). **f.** *Aphaenops* (*Geotrechus*) *discontignyi* (Fairmaire, 1863). **g.** *Aphaenops* (*Hydraphaenops*) *ehlersi* (Abeille de Perrin, 1872). **h.** *Aphaenops* (*Nafarroaphaenops*) *giraudi* Ochs, 1938. **i.** *Aphaenops* (*Pyreneotrechus*) *aldensis* (Jeannel, 1955). Scale bars: 2 mm.



**Fig. 4.** A tiny and poorly known species, *Aphaenops holcartensis* (Genest, 1977), type species of the subgenus *Riberaphaenops* **subgen. n.** Scale bar: 2 mm.

ically distinct and genetically isolated from the other species of endogean *Aphaenops*. Ten subspecies have been described, of uncertain status.

### 3. Subgenus *Aurigerotrechus* subgen. n.

#### Type species

*Trechus (Anophthalmus) vulcanus* Abeille de Perrin, 1904 (ABEILLE DE PERRIN 1904: 198), by present designation (Figs. 3b, 6b).

#### Diagnosis

All the species of this clade share median lobe of aedeagus rounded, with sharpened apex, and sagittal aileron of male genitalia faintly developed or absent (Fig. 6b).

#### Etymology

From *aurigera*, auriferous, suggested etymology of Ariège, river and department (France) where the species of this subgenus are endemic.

#### Distribution

The seven species belonging to the subgenus *Aurigerotrechus* **subgen. n.** occur in Ariège, in the French Eastern Pyrenees.

#### Remarks

The clade is subdivided into two well-supported (99/99) groups of species: the *Aphaenops (Aurigerotrechus) vulcanus* group (*Aphaenops vulcanus*, *A. sulcatus*) and the *Aphaenops (Aurigerotrechus) saulcyi* group (*Aphaenops saulcyi*, *A. andreae*, *A. palei*, *A. vanderberghi*, *A. vandelianus* **nom. n.**).

#### 3.1. *Aphaenops (Aurigerotrechus) saulcyi* group

Morphology homogeneous, characterized by a moderate size, body glabrous and short appendages. Species of this group differ from those of the *A. sulcatus* group by having pronotum much narrower at base, with fore angles usually protruding (a character not so marked in *A. vandelianus*), and completely lacking striae.

Five species are recognized in this group so far (former *Geotrechus* in part). The species of this group are mostly found in caves (*A. saulcyi*, *A. andreae*, *A. palei*) or in the ground at the entrance of caves (*A. vandelianus*, *A. vanderberghi*). The status of these last two species is in need of revision, as many intermediate populations have been discovered since their description.

#### 3.2. *Aphaenops (Aurigerotrechus) vulcanus* group

Both species are characterized by elytra with visible remains of striae, pronotum much less constricted and fore angle of pronotum never protruding.

Two close species belong to this group. *Aphaenops vulcanus* is a species widely distributed in the Plantaurel, on both sides of the Ariège River, whereas *A. sulcatus* is known so far only from its type locality Aven de la Tussave (Soueix-Rogalle) (COIFFAIT 1959).

### 4. Subgenus *Ceretotrechus* subgen. n.

#### Type species

*Geotrechus ubachi* Español, 1965 (ESPAÑOL 1965: 136), by present designation (Figs. 3c, 6c).

#### Diagnosis

All species in this clade share elongated elytra, pronotum always longer than wide, striae hardly visible or lacking, humeral angle faintly pronounced. The sagittal aileron of the median lobe of the male genitalia is well developed (Fig. 6c).

#### Etymology

*Ceretotrechus* **subgen. n.** refers to the Ceretania area of the “ceretani” iberic people, cited by classical Greek and Roman historians—POLIBIOS, Πολύβιος “History”, III, 8; ESTRABON,

Στράβων “Geographia”, III, 4,11; PLINIUS “Natural History”, III, 22–23. From this name is derived the actual name of Cerdanya (France and Spain) or Ceret (France) in the Eastern Pyrenees, the probable centre of dispersal of this new subgenus.

#### Distribution

The seven species belonging to the *Ceretotrechus* **subgen. n.** clade occur in the eastern part of the Spanish Pyrenees. The group is distributed in the South-Eastern Pyrenean Mountains between Serra de Boumort and the Puigmal Massif. It reaches Serra dels Obacs in the South and Serra de Catllaràs—on the left bank of the Llobregat River—and the right bank of the Segre River in the North.

#### Remarks

This clade was recently revised by FAILLE et al. (2015a) and contains two, well-characterized groups of species.

#### *Aphaenops (Ceretotrechus) deliotti* group

The two species of this group share pronotum with hind angles acute before the base, median lobe of aedeagus short, with acute apex and penultimate article of maxillary palpi with a few setae.

The two species occur on the right side of the Segre River, a narrow area between Prullans and Isòvol (*G. deliotti*) and a small massif on the northern slope of Serra del Cadí (*G. incantatus*). The ancestor of the group might have become separated on the right (north) bank of the Segre River, later colonizing the distribution area of the other group on the southern bank (FAILLE et al. 2015a).

#### *Aphaenops (Ceretotrechus) ubachi* group

The five species of this group are characterized by the shape of the median lobe of the aedeagus, with apex rounded, pronotum with hind angles simple and maxillary palpi with penultimate segment glabrous.

The species of this group are distributed on the left (south) bank of the Segre River between the Puigmal Massif and the westernmost part of Serra del Boumort.



Fig. 5. *Aphaenops leschenaulti* Bonvouloir, 1862, genitalia.



**Fig. 6.** Morphological diversity of the male genitalia among the different subgenera of *Aphaenops*. **a.** *Aphaenops* (*Argonotrechus*) *orpheus* (Dieck, 1869). **b.** *Aphaenops* (*Aurigerotrechus*) *vulcanus* (Abeille de Perrin, 1904). **c.** *Aphaenops* (*Ceratotrechus*) *ubachi* (Español, 1965). **d.** *Aphaenops* (*Dupreaphaenops*) *vasconicus* Jeannel, 1913. **e.** *Aphaenops* (*Geotrechidius*) *gallicus* (Delarouzée, 1857). **f.** *Aphaenops* (*Geotrechus*) *discontignyi* (Fairmaire, 1863). **g.** *Aphaenops* (*Hydraphaenops*) *ehlersi* (Abeille de Perrin, 1872). **h.** *Aphaenops* (*Nafarroaphaenops*) *giraudi* Ochs, 1938. **i.** *Aphaenops* (*Pyreneotrechus*) *aldensis* (Jeannel, 1955). Scale bars: 2 mm.

### 5. Subgenus *Dupreaphaenops* subgen. n.

#### Type species

*Aphaenops vasconicus* Jeannel, 1913 (JEANNEL 1913: 382), by present designation (Figs. 3d, 6d).

#### Diagnosis

The three species in this group share a pubescent body, long and sickled mandibles and median lobe of male genitalia regularly curved, with a round, blunt apex (Fig. 6d). Labial tooth triangular, flat [*Aphaenops* (*Dupreaphaenops*) *galani*] to slightly protruding [*Aphaenops* (*Dupreaphaenops*) *sarpedon*, *Aphaenops* (*Dupreaphaenops*) *vasconicus*]. This clade was already identified by FAILLE et al. (2013b).

#### Etymology

Named in tribute to ERIC DUPRÉ, who passed away at the beginning of the year, in recognition of his contribution to the knowledge of the cave beetle diversity of the Pyrenees, and more especially the French Basque country.

#### Distribution

The new subgenus groups three species endemic to the Basque country, two in France [Arbailles massif: *Aphaenops* (*Dupreaphaenops*) *vasconicus*, *Aphaenops* (*Dupreaphaenops*) *sarpedon*] and one in Spain, *Aphaenops* (*Dupreaphaenops*) *galani*, the westernmost species of the clade (and of the genus *Aphaenops*), restricted to Guipuzkoa, Spain: Macizo de Andatza and Macizo de Hernio.



## 6. Subgenus *Geotrechidius sensu novo*

*Geotrechidius* Jeannel, 1947 (JEANNEL 1947: 102).

### Type species

*Anophthalmus gallicus* Delarouzée, 1857 (DELAROUZÉE 1857: xciv; JEANNEL 1947: 102) (Figs. 3e, 6e).

### Diagnosis

The seven species of *Geotrechidius sensu novo* are characterized by elytra glabrous or finely hairy [*Aphaenops (Geotrechidius) dumonti*, *Aphaenops (Geotrechidius) pandellei* complex] and without a crenulate humerus. The external morphology is quite homogeneous between *Aphaenops (Geotrechidius) gallicus*, *Aphaenops (Geotrechidius) jeanneli* and *Aphaenops (Geotrechidius) sous-sieuxi*; *Aphaenops (Geotrechidius) dumonti* is also similar to *Aphaenops (Geotrechidius) gallicus*. The external morphology of the species of the *Aphaenops (Geotrechidius) pandellei* complex is very different, especially because of the hydraphaenopsian features likely reflecting a peculiar ecology and feeding behaviour. Surprisingly, the shape of the median lobe of the aedeagus is most similar between *Aphaenops (Geotrechidius) sous-sieuxi*, *Aphaenops (Geotrechidius) jeanneli* and the *Aphaenops (Geotrechidius) pandellei* complex: the median lobe of those species is regularly curved, with a wide and rounded apex. In the two last species, *Aphaenops (Geotrechidius) gallicus* and *Aphaenops (Geotrechidius) dumonti*, the median lobe is different: long, thin and acute at the apex (Fig. 6e).

### Distribution

The name *Geotrechidius sensu novo* is restricted to seven species occurring in the western part of the Pyrenean range. Six species are French endemics, whereas only one (*A. dumonti*) is a Spanish endemic.

### Remarks

The genus *Geotrechus* was split into two by JEANNEL (1947). In the subgenus *Geotrechidius*, he included all species with glabrous elytra without a crenulate humerus. Such characters are found in two species groups: an eastern group (“groupe *vulcanus*” sensu JEANNEL, here assigned to *Aurigerotrechus subgen. n.*) and a western group (“groupe *gallicus*”). At that time, the species of the subgenera *Pyreneotrechus subgen. n.* and *Ceretotrechus subgen. n.*, which share the same morphological features, were not known. The two subgenera, *Geotrechus* and *Geotrechidius*, were later synonymized (QUÉINNEC & OLLIVIER 2011). Here, we restore the name *Geotrechidius* but restrict it to the western group—“groupe *gallicus*” of JEANNEL (1947)—to which we add five species: one Spanish species [*Aphaenops (Geotrechidius) dumonti*], one species located far from the Pyrenees, in the Landes department [*Aphaenops (Geotrechidius) sous-sieuxi*] and three close species occurring in the same area but mor-

phologically divergent, with “hydraphaenopsian” features: *Aphaenops (Geotrechidius) pandellei*, *Aphaenops (Geotrechidius) gracilis* and *Aphaenops (Geotrechidius) blancheti*. These three species are here treated as the *Aphaenops (Geotrechidius) pandellei* complex, as the differences between them are tenuous and their status as distinct species remains to be tested. The status of the various populations and closely-related species of *Aphaenops (Geotrechidius) gallicus* and the *Aphaenops (Geotrechidius) pandellei* complex, respectively, with many subspecies described and recently synonymized, is in need of revision, as suggested by the position of *Aphaenops (Geotrechidius) blancheti* in the tree (Fig. 1a).

## 7. Subgenus *Geotrechus stat. n.*

*Geotrechus* Jeannel, 1919 (JEANNEL 1919: 254).

### Type species

*Anophthalmus discontignyi* Fairmaire, 1863 (FAIRMAIRE 1863: 3; JEANNEL 1919: 254) (Figs. 3f, 6f).

### Diagnosis

Species in this subgenus share head and elytra pubescent, humerus more [*Aphaenops (Geotrechus) discontignyi*, *Aphaenops (Geotrechus) serrulatus*] or less [*Aphaenops (Geotrechus) orcinus*, *Aphaenops (Geotrechus) trophonius*] serrulate (Fig. 3f), and a characteristic median lobe of the aedeagus: long and rounded in its apical part (Fig. 6f). The four species in this clade are morphologically very close.

### Distribution

*Geotrechus stat. n.* is restricted to four species occurring between Gave de Pau in the West and the Salat River in the East.

### Remarks

*Aphaenops (Geotrechus) serrulatus* was regarded as valid by QUÉINNEC & OLLIVIER (2011), but as a synonym of *Aphaenops (Geotrechus) orcinus orcinus* by QUÉINNEC in TRONQUET (2014). Finally, this taxon is in the list of valid species of the genus *Geotrechus* in MORAVEC et al. (2017). *Aphaenops (Geotrechus) serrulatus bona species* is a valid species, genetically and morphologically distinct from *Aphaenops (Geotrechus) orcinus*, which occurs in the same area. As already mentioned by JEANNEL (1949), *A. serrulatus* is closely related to *Aphaenops (Geotrechus) discontignyi* and shares a similar shape of the male genitalia as well as a serrulate humerus.

## 8. Subgenus *Hydraphaenops sensu novo*

*Hydraphaenops* Jeannel, 1926 (JEANNEL 1926: 234).

= *Cerbaphaenops* Coiffait, 1862, **syn. n.**

= *Simaphaenops* Quéinnec & Ollivier, 2011, **syn. n.**



Fig. 7. *Aphaenops* (*Riberaphaenops*) *holcartensis* (Genest, 1977), male genitalia (ssp. *charlesi* Dupré & Bourdeau).

#### Type species

*Anophtalmus ehlersi* Abeille de Perrin, 1872 (ABEILLE DE PERRIN 1872: 15; JEANNEL 1926: 234) (Figs. 3g, 6g).

#### Diagnosis

This subgenus is formed of species of small size, with a pubescent head.

#### Distribution

With 35 species described so far, *Hydraphaenops sensu novo* is the most speciose group of the Pyrenean lineage, the most diverse in Ariège and Haute-Garonne, but occurring from the Ariège Valley in the East to Gave d'Aspe and the Canfranc Valley in the West.

#### Remarks

*Hydraphaenops sensu novo* includes all the species previously included in the subgenera *Cerbaphaenops* and *Simaphaenops*, as well as two groups of species of the subgenus *Hydraphaenops* as previously defined, including the type species *Aphaenops* (*Hydraphaenops*) *ehlersi* (Figs. 3g, 6g, 8c). Four species groups are unambiguously identified.

*Hydraphaenops sensu novo* can be split into four species groups, each of which can be characterized morphologically and genetically.

#### 8.1. *Aphaenops* (*Hydraphaenops*) *chaudoiri* group

The *A. chaudoiri* group is composed of three species endemic to the Central Pyrenees. The two French

species are characterized by sickled mandibles, body densely pubescent except for pronotum, which is glabrous, and aedeagus curved and sharp at apex. *Aphaenops* (*Hydraphaenops*) *alfambrai*, a species known from the female holotype only, found in a high altitude deep shaft in the Revilla area (central Spanish Pyrenees), and which share the same chaetotactic pattern (LAGAR 1979), is tentatively included in this group.

#### 8.2. *Aphaenops* (*Hydraphaenops*) *crypticola* group

This clade is the most speciose group of *Aphaenops* (24 species so far) and includes most of the species of the former subgenus *Cerbaphaenops*. The morphology of the species of this clade is quite homogeneous, composed of slender pale testaceous species with long appendages and head normal, pubescent, harbouring two to six or seven discal setae, with temples moderately swollen behind and mandibles short, shorter than head [“groupe *cerberus*” sensu JEANNEL (1941)]. A few species of the group deviate from this homogeneous morphology and were considered as belonging to other groups: *Aphaenops* (*Hydraphaenops*) *bucephalus* (*Cephalaphaenops* Jeannel), *Aphaenops* (*Hydraphaenops*) *longicollis* (*Hydraphaenops sensu auct.*), *Aphaenops* (*Hydraphaenops*) *chappuisi*—here found sister to the other species of the *A. crypticola* group—and *Aphaenops* (*Hydraphaenops*) *tiresias* (both *Arachnaphaenops* Jeanne), and *Aphaenops* (*Hydraphaenops*) *laurenti* (the only species of the former subgenus *Pubaphaenops* Genest).

The *A. crypticola* group represents the typical “troglobie des parois stalagmitées” (JEANNEL 1941), with some species locally abundant on the wet walls of caves of the northern slope of the Pyrenees; nevertheless, some species are common in the MSS (see JUBERTHIE et al. 1980) [e.g., *Aphaenops (Hydraphaenops) vandeli* in Ariège]. The group is restricted to the French slope of the Pyrenean chain, where it is distributed from west of the Ariège Valley [*Aphaenops (Hydraphaenops) bonneti*] to Gave de Pau [*Aphaenops (Hydraphaenops) aeacus*]. The bulk of the diversity of this group is in Ariège. The clade is subdivided into five subclades: **8.2.1.**, a clade with *Aphaenops (Hydraphaenops) crypticola*, *Aphaenops (Hydraphaenops) pluto* and related species; **8.2.2.**, a clade with all the species of the *Aphaenops (Hydraphaenops) carrerei* group, including the hairy species *Aphaenops (Hydraphaenops) laurenti* (for which a new subgenus had previously been erected, *Pubaphaenops*); **8.2.3.**, a clade with the *Aphaenops (Hydraphaenops) cerberus* group + *Aphaenops (Hydraphaenops) tiresias*; **8.2.4.**, a clade with the western species, *Aphaenops (Hydraphaenops) aeacus* and related species; **8.2.5.**, a clade with low support gathering the divergent species *Aphaenops (Hydraphaenops) bucephalus*, *Aphaenops (Hydraphaenops) longicollis* and sometimes, but not always, *Aphaenops (Hydraphaenops) chappuisi* (see Fig. 1a).

### 8.3. *Aphaenops (Hydraphaenops) ehlersi* group

Species in this group have pronotum and elytra glabrous [*Aphaenops (Hydraphaenops) ehlersi* (Figs. 3g, 8c), *Aphaenops (Hydraphaenops) pecoudi*] or slightly pubescent [*Aphaenops (Hydraphaenops) bourgoini*]. They share a similar shape of the median lobe of the aedeagus, which is curved with apical part narrowed and rounded (Fig. 6g), sickled mandibles and a straight labrum (Figs. 3g, 8c). This clade was already recovered in previous molecular studies (FAILLE 2006; FAILLE et al. 2010a).

A group of three tiny species from Ariège and Haute-Garonne.

### 8.4. *Aphaenops (Hydraphaenops) minos* group

All four species in this group have head and elytra pubescent and pronotum glabrous, median lobe of aedeagus straight, long and progressively sharpened to apex. *Aphaenops (Hydraphaenops) hidalgoi*, formerly assigned to *Cerbaphaenops*, unambiguously belongs to this group and is morphologically close to *Aphaenops (Hydraphaenops) penacollaradensis* (FAILLE 2006: 215). Such proximity is confirmed by the fact that *A. hidalgoi* and *A. penacollaradensis* are the only known hosts of *Rhachomyces pyrenaicus* Santamaria, a parasitic fungus of the Laboulbeniales group (SANTAMARIA & FAILLE 2007).

A cryophilic group present at high altitudes up to almost 3,000 m (FAILLE 2006). It is the group with the

largest distribution, from the Ariège Valley [*Aphaenops (Hydraphaenops) minos*] to Peña Collarada (Spain) and Gourette (France) [*Aphaenops (Hydraphaenops) penacollaradensis*]. The only species occurring at low altitudes is *Aphaenops (Hydraphaenops) minos*, described from the Lombrives cave in the Ariège Valley (France). This group corresponds to the *Simaphaenops* clade in QUÉINNEC & OLLIVIER (2011).

### Remarks

An alternative taxonomic choice regarding the large clade *Hydraphaenops sensu novo* would have been to keep the existing subgenera *Cerbaphaenops* [+ *Aphaenops (Hydraphaenops) longicollis*] and *Simaphaenops* as valid and restrict *Hydraphaenops* to just the *Aphaenops (Hydraphaenops) ehlersi* clade. Such a decision would have implied the creation of a new subgenus for the *Aphaenops (Hydraphaenops) elegans* + *Aphaenops (Hydraphaenops) chaudiroi* clade, without synapomorphies supporting any of these three clades. Finally, the position of *Aphaenops (Hydraphaenops) alfambrai*, known only from the female holotype, is still questionable. Therefore, we chose the conservative option to include all these species in a large subgenus *Hydraphaenops*.

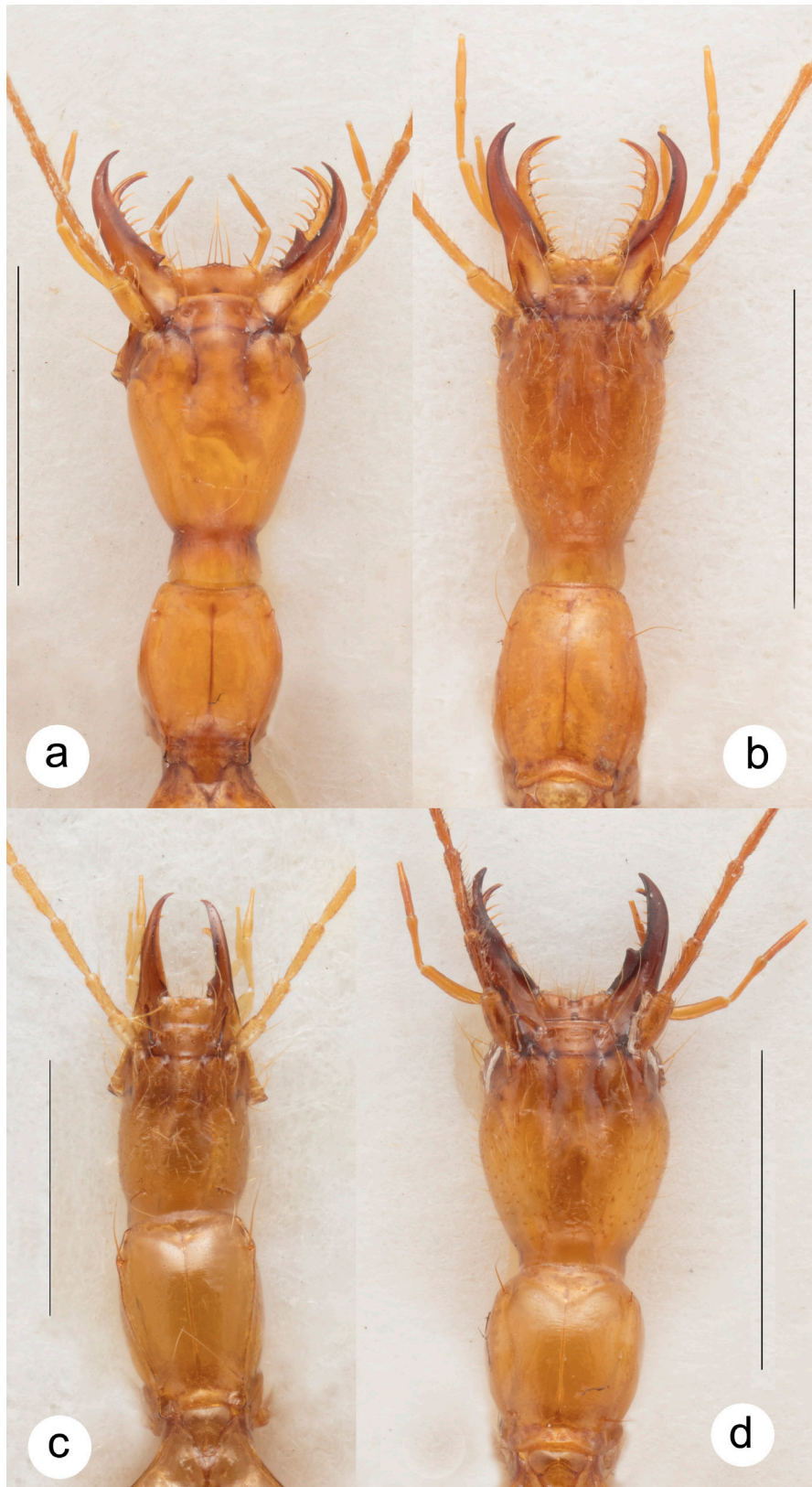
## 9. Subgenus *Nafarroaphaenops* subgen. n.

### Type species

*Aphaenops (Hydraphaenops) giraudi* Ochs, 1938 (OCHS 1938: 26), by present designation (Figs. 3h, 6h).

### Diagnosis

Body size variable (3.3–5.0 mm). Species with a “hydraphaenopsian” appearance: slender and completely [*Aphaenops (Nafarroaphaenops) giraudi*, *Aphaenops (Nafarroaphaenops) navaricus*] or partially [*Aphaenops (Nafarroaphaenops) sobrarbensis*] hairy (Fig. 3h). In spite of an important difference in size, the three species of the clade share a hairy head, oval elytra without pronounced humeral angles, a flattened mental tooth, pronotum much [*Aphaenops (Nafarroaphaenops) giraudi*, *Aphaenops (Nafarroaphaenops) navaricus*] or only slightly longer [*Aphaenops (Nafarroaphaenops) sobrarbensis*] than wide, striae hardly visible or lacking; penultimate labial palpomere tri- or quadrisetose. *Aphaenops (Nafarroaphaenops) giraudi* and *Aphaenops (Nafarroaphaenops) navaricus* share a similar shape of the ligula, with a salient tubercle [lacking in *Aphaenops (Nafarroaphaenops) sobrarbensis*] and median lobe of aedeagus with a rounded apex (Fig. 6h); in *Aphaenops (Nafarroaphaenops) sobrarbensis*, the outline of the median lobe is morphologically divergent from this model, very elongate and bisinuate dorsally, the apex acute and gradually curved upward. The minute species *Aphaenops (Nafarroaphaenops) sobrarbensis*, known from a single locality (Cueva



**Fig. 8.** Differences in the head morphology in the clades *Aphaenops* s. str. [*A. ochsi* (a) vs. *A. alberti* (b)] and *Hydraphaenops* [*A. ehlersi* (c) vs. *A. bucephalus* (d)]. Scale bars: 2 mm.

de Aso in Sercué, Añisclo Valley, Spain) and from just two exemplars, is morphologically and genetically highly divergent and shares few characters with the two other species (*A. giraudi* and *A. navaricus*). Nevertheless, it is unambiguously related to these two species in all analyses; we therefore chose to be conservative and to include it in the same group. Further discoveries might fill the distribution gap between these three species and lead to taxonomic changes regarding *A. sobrarbensis*.

#### Etymology

*Nafarroaphaenops* refers to the Navarra area in euskera language, Nafarroa, Western Pyrenees. The three species of this subgenus occur in this region or in its vicinity.

#### Distribution

The three species belonging to the *Nafarroaphaenops* **subgen. n.** clade occur in the Western part of the Pyrenees: one in France [*Aphaenops* (*Nafarroaphaenops*) *navaricus*], one [*Aphaenops* (*Nafarroaphaenops*) *sobrarbensis*] in Spain. The third species, *Aphaenops* (*Nafarroaphaenops*) *giraudi*, is found on both slopes of the chain.

### 10. Subgenus *Pyreneotrechus* subgen. n.

#### Type species

*Geotrechus* (*Geotrechidius*) *aldensis* Jeannel, 1955 (JEANNEL 1955: 17), by present designation (Figs. 3i, 6i).

#### Diagnosis

Body size small (3.5–4.0 mm). Well characterized by the humeral setae forming a right angle, and median lobe of aedeagus long and slender, with sharpened apex. Elytra with intervals flat, striae hardly visible or absent, humeral angle faintly pronounced. Sagittal aileron well developed, parameres with two setae. Labial tooth rounded.

#### Etymology

The new name refers to the mountain chain where the group diversified, the Pyrenees (France and Spain).

#### Distribution

The only species of this subgenus is located in the Belesta area, eastern Ariège (France).

#### Remarks

*Aphaenops* (*Pyreneotrechus*) *aldensis* is the easternmost species of the group. It was already regarded as a particularly morphologically divergent species by its describer (JEANNEL 1955).

### 11. Subgenus *Riberaphaenops* subgen. n.

#### Type species

*Geotrechus holcartensis* Genest, 1977 (GENEST 1977: 281), by present designation (Figs. 4, 7).

#### Diagnosis

Small-sized: 2.8–3.8 mm. The three species in this subgenus share a similar and peculiar shape of the median lobe of the aedeagus, which is curved and enlarged in its apical part, with an upturned apex (Fig. 7). Prebasilar with six setae, labial tooth triangular, slightly protruding. Body pubescent, pronotum glabrous in *Aphaenops* (*Riberaphaenops*) *picanyoli*.

#### Etymology

Named to honour Ignacio Ribera, for his contribution to the knowledge of the cave beetle diversity of the Pyrenees.

#### Distribution

A clade of three rarely collected, tiny species from the Western Pyrenees. The type subspecies of *Aphaenops* (*Riberaphaenops*) *holcartensis* is known from a single female from Grotte d'Ayssaguer (Larrau), whereas the subspecies *charlesi* is known from a few exemplars from a cave in Arette (Fig. 4). *Aphaenops* (*Riberaphaenops*) *picanyoli* is the southernmost species of this clade, secluded in the conglomerates of Sierra de San Juan de la Peña (Huesca, Spain). The third species, *Aphaenops* (*Riberaphaenops*) *dequaei*, which was lacking for the molecular study, is only known from Cueva del Ponte in Abaurrea Alta (Navarra, Spain).

### Discussion

As a result of a previous molecular phylogenetic analysis, FAILLE et al. (2010a) pointed out that a thorough systematic rearrangement of the classification of the Pyrenean clade of hypogean Trechini was needed, but the partial sampling in that study prevented any taxonomic action. The delimitation of the former three genera, *Aphaenops*, *Hydraphaenops* and *Geotrechus*, was the subject of many hypotheses (e.g., JEANNEL 1920, 1922, 1926, 1941; COIFFAIT 1962; CASALE & LANEYRIE 1982; QUÉINNÉC & OLLIVIER 2011). The phylogeny presented here solves some of the main questions regarding the evolutionary history of the Pyrenean clade by gathering the species in one genus (*Aphaenops*) and many species groups, in order to avoid an artificial classification. The taxonomy proposed here is based on the combination of the molecular phylogeny with morphologically diagnostic character states independent of the convergent adaptive characters resulting from a subterranean lifestyle, as has been done for other lineages of hypogean ground beetles, such as the Trechini genus *Orotrechus* Müller [see discussion by CASALE et al. (1991) when describing a highly modified cave species from Veneto]. Although the topology was highly consistent with the distribution of the species, identifying unambiguous morphological synapomorphies for each new subgenus was at a first glance quite challenging, and it was

often a combination of characters that succeeded in defining the clades. The here-proposed taxonomy strengthens the congruence between the subgenera and species groups and their geographic distribution.

The most unexpected result of the phylogenetic analysis was the division of the former genus *Geotrechus* into eight subgenera, one of which, the monotypic *Pyreneotrechus* with the species *A. (P.) aldensis*, is sister to the whole radiation. This is the easternmost species of the radiation, and all the early splits in the history of the group concern eastern, non-troglobiomorphic species, stocky, without elongation of the appendages, and more common in the soil than in caves: the subgenera *Ceretotrechus* **subgen. n.**, *Aurigerotrechus* **subgen. n.** and *Argonotrechus* **subgen. n.** This suggests an eastern origin of the whole Pyrenean lineage, an assumption also supported by the complete absence of the group in the Cantabrian chain, which is inhabited by other old lineages related to *Trechus* sensu lato (the *Apodualius* clade), is known to have acted as a refugium in the past, and hosts remarkable paleoendemic Trechini ground beetles such as *Iberotrechus* and *Iberotrechodes* (JEANNEL 1913; FAILLE et al. 2021).

The subgenus *Hydraphaenops* **sensu novo** represents the bulk of the diversity of the “eastern clade” (sensu FAILLE et al. 2010a). The early splits of this clade are “hydraphaenopsian” species: two species from the Central Pyrenees [*Aphaenops (Hydraphaenops) elegans* + *Aphaenops (Hydraphaenops) chaudoiri*] and a group of cryophilic species [*Aphaenops (Hydraphaenops) minos* group]. The clade is found at high altitudes along the chain, from the Ariège Valley [*Aphaenops (Hydraphaenops) minos*, the only species found at low altitude, which was probably trapped following the glaciers retreat] to the Ossau Valley (France) and Río Aragón (Spain).

The troglobiomorphic species of the former genus *Aphaenops* belong to two main clades, one in the East (*Aphaenops* subg. *Hydraphaenops* **sensu novo** containing, among others, all the species previously grouped under the name *Cerbaphaenops*) and one in the West (*Aphaenops* sensu stricto).

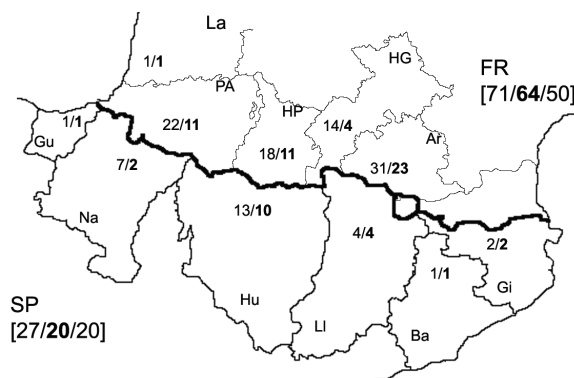
Contrary to the previous views (QUÉINNEC & OLLIVIER 2011), we found *Geaphaenops* to be unambiguously polyphyletic. Adaptation to an endogean way of life led convergently to the same stocky appearance in species of three different groups: the *Aphaenops (Aphaenops) rhadamanthus* group (all species), the *Aphaenops (Aphaenops) eskualduna* group [*Aphaenops (Aphaenops) rebereti*, *Aphaenops (Aphaenops) cissauguensis*] and the *Aphaenops (Aphaenops) leschenaulti* group [*Aphaenops (Aphaenops) linderi*].

Finally, the species of the former genus *Hydraphaenops*, which share a superficially convergent morphology (small appendages, elongated head with sickle mandibles), are now distributed within four subgenera containing most

of the species at the base of the large clade *Hydraphaenops* sensu novo, a few in the three subgenera *Geotrechidius* [*Aphaenops (Geotrechidius) pandellei* complex], *Dupreaphaenops* **subgen. n.** [*Aphaenops (Dupreaphaenops) vasconicus*, *Aphaenops (Dupreaphaenops) galani*] and *Nafarroaphaenops* **subgen. n.** [*Aphaenops (Nafarroaphaenops) navaricus*, *Aphaenops (Nafarroaphaenops) giraudi* and *Aphaenops (Nafarroaphaenops) sobrabensis*].

### Biogeographic patterns

The distribution of hypogean Trechini is heterogeneous along the Pyrenean chain. The highest diversity occurs on the northern slope (France), with 71 species found so far, 64 of which are endemic to this slope (Table 3; Fig. 9). Twenty-seven species occur on the southern slope (Spain), 20 of which are endemic to this slope. Most of the species are local endemics occurring in one department (France) or province (Spain) only. The peak of diversity is observed in Ariège, with 31 species known so far, 23 of which are strict endemics of the department. Only a few taxa are quite widespread, with strong geographic structuration of the populations across the range, highlighting the strong impact of geomorphology on the structure of the populations [see, e.g., FAILLE et al. (2015b) for *A. cerberus*]. The second richest area is the Pyrénées-Atlantiques department (also France), with 22 species but a proportionally lower number of endemic species (11), as this is the area of the chain with the highest number of species occurring on both slopes (Fig. 9). This might be explained by the decrease in altitude in the West, lead-



**Fig. 9.** Diversity of hypogean Trechini by department (France) or province (Spain): number of species/number of endemic species. SP: Spain; FR: France. French departments: La: Landes; PA: Pyrénées-Atlantiques; HP: Hautes-Pyrénées; HG: Haute-Garonne; Ar: Ariège. Spanish provinces: Gu: Guipuzcoa; Na: Navarra; Hu: Huesca; LI: Lleida; Ba: Barcelona; Gi: Girona. In brackets: [number of species per country/number of country endemics/number of endemics per single department or province].

**Table 3.** Diversity and distribution of each subgenus by country.

Subgenus	France	Spain	both	Total
<i>Pyreneotrechus</i>	1	0		<b>1</b>
<i>Ceretotrechus</i>	0	7		<b>7</b>
<i>Aurigerotrechus</i>	7	0		<b>7</b>
<i>Argonotrechus</i>	1	0		<b>1</b>
<i>Hydraphaenops</i>	32	2	1	<b>35</b>
<i>Geotrechus</i>	4	0		<b>4</b>
<i>Geotrechidius</i>	6	1		<b>7</b>
<i>Nafarroaphaenops</i>	1	1	1	<b>3</b>
<i>Riberaphaenops</i>	1	2		<b>3</b>
<i>Dupreaphaenops</i>	2	1		<b>3</b>
<i>Aphaenops</i>	9	6	5	<b>20</b>
<b>Total</b>	<b>64</b>	<b>20</b>	<b>7</b>	<b>91</b>

ing to more homogeneous ecological parameters and a less fragmented limestone cover on both slopes of the chain. Five of the 20 species of *Aphaenops* sensu stricto occur on both slopes of the Pyrenees (*A. loubensi*, *A. ochsi*, *A. orionis*, *A. ludovici* and *A. eskualduna*) (Table 3), whereas only one of the three species of *Nafarroaphaenops* (*A. giraudi*) occurs both in Spain and France. A trans-Pyrenean distribution is extremely rare in the speciose subgenus *Hydraphaenops*, as it has so far only been documented for the westernmost species of the subgenus: the cryophilic *A. penacollaradensis*, described from Peña Collarada (Huesca) but known just from a single specimen on the northern slope, from the Gourette area (Pyrénées-Atlantiques) (DUPRÉ 1991; DUPRÉ & BOURDEAU 1994).

Trans-Pyrenean sister relationships,  
a common occurrence in the Pyrenean lineage of  
subterranean Trechini

Whereas trans-Pyrenean species distributions are unusual, we could identify some examples of trans-Pyrenean sister relationships in hypogean Trechini. Such sister relationships between Spanish and French species in many clades was quite unexpected, as the axial chain of the Pyrenees was considered a barrier between species from the northern and southern slopes and a scenario of independent diversifications on each side of the chain was favoured. A striking example is found in the *Aphaenops* (*Aphaenops*) *leschenaulti* group, with the pair *Aphaenops* (*Aphaenops*) *leschenaulti*-*Aphaenops* (*Aphaenops*) *linderi* from the French Central Pyrenees sister to *Aphaenops* (*Aphaenops*) *catalonicus*, the southernmost species of *Aphaenops* sensu stricto, which reaches the Noguera Ribagorçana Valley on the Spanish side. A trans-Pyrenean dis-

tribution is also observed in the subgenus *Riberaphaenops* **subgen. n.**, with the species *Aphaenops* (*Riberaphaenops*) *holcartensis* (France) vs. *Aphaenops* (*Riberaphaenops*) *dequaei*-*Aphaenops* (*Riberaphaenops*) *picanyoli* (Spain), and in some species of Leptodirini (Coleoptera, Leiodidae, Cholevinae), such as *Bellesia espanyoli* (Auroux & Bellés, 1974) from the Añisclo Valley in Huesca, a true Miocene relict closely related to *Machaeroscelis* Jeannel, 1924 from Ariège in France, the divergence between the two having occurred about 10.5 million years ago (RIBERA et al. 2010).

Apart from these examples, other south versus north speciation events, with distributions perpendicular to the chain, have been identified in other subgenera: *Geotrechidius*, with *Aphaenops* (*Geotrechidius*) *dumonti* as the sister species of all members of the subgenus found on the French slope of the chain; *Aphaenops* (*Dupreaphaenops*) *vasconicus*-*Aphaenops* (*Dupreaphaenops*) *sarpedon* from the Arbailles Massif (Pyrénées-Atlantiques) vs. *Aphaenops* (*Dupreaphaenops*) *galani* from Guipúzcoa (in this case a distribution that did not have to overcome the geographical barrier of the Pyrenean Massif), or *Aphaenops* (*Aphaenops*) *cissauguensis*-*Aphaenops* (*Aphaenops*) *rebereti* vs. *Aphaenops* (*Aphaenops*) *parvulus*. In some cases, species were found at high altitude in the axial chain, acting as a transition link between the taxa from the northern and the southern slopes.

A few groups radiated parallel to the chain, the most diverse being the large *Hydraphaenops* clade, nearly exclusively found on the northern slope. But at the base of the clade is a clade of orophilic and cold-adapted species, the pair *Aphaenops* (*Hydraphaenops*) *penacollaradensis*-*Aphaenops* (*Hydraphaenops*) *mouriesi*, the most cryophilic species of the group, occurring in high altitude caves under snow. Finally, the presence of the clade *Aphaenops* (*Hydraphaenops*) *elegans*-*Aphaenops* (*Hydraphaenops*) *chaudoiri* in low altitude caves of the Central Pyrenees might not be regarded as an exception if we consider the high probability that the species *Aphaenops* (*Hydraphaenops*) *alfambrai*, known from a single female specimen found in a deep abyss located at ca. 2,100 m in the Central Pyrenees, is related to these two species.

This pattern suggests that the high altitude chain might have acted as a refugium from where cave beetles recolonized the low altitude karsts.

A similar biogeographical pattern occurs among the beetle tribe Leptodirini (Leiodidae), whose fauna also has a strong geographical structure, with a fundamental division between the eastern and western sectors of the Pyrenean Massif and a colonization of the subterranean environment that seems to have proceeded from the edges to the centre. Within each large zone, there seems to be a secondary division between the northern and southern slopes of the Pyrenees, which share practically no species

from the subterranean environment, especially in the central part of the range. But there are close north-south faunal links that justify consideration of the entire massif as a biogeographical unit.

### Three shapes, many histories

The phylogeny of the group reflects local diversifications nested within the distribution range of Pyrenean Trechini, and multiple convergence events within the Pyrenean lineage, evidenced by morphology as well as ecology or physiology [see, e.g., the convergent reduction of larval instars among the lineage inferred from the simplification of the ovaries by FAILLE & PLUOT-SIGWALT (2015)].

The fact that none of the three morphologically well-characterized former genera *Aphaenops*, *Hydraphaenops* and *Geotrechus* sensu auct. was recovered as monophyletic illustrates the strong impact of the subterranean environment on morphology, which has led to convergent habitus for historically unrelated but ecologically similar species. The “*Geotrechus* shape” is shared by species scattered across the phylogeny; it should be regarded as plesiomorphic and resulting from more superficial ecologies, with most species occurring in the upper part of the karst or in the soil.

As already mentioned by JEANNEL when dealing with all those species sharing an “hydraphaenopsian” morphology and at that time gathered in the subgenus *Hydraphaenops*: “Ce sous-genre réunit des lignées d’espèces assez disparates mais présentant un ensemble de caractères évolutifs [...] Cet ensemble de caractères est en rapport avec un mode de vie particulier” [“This subgenus brings together lineages of quite disparate species but presenting a set of evolutionary characters [...] This set of characters is related to a particular way of life”] (JEANNEL 1948). The “hydraphaenopsian shape” is indeed shared convergently by species that could be regarded as fissuricolous, highly hygrophilic, adapted to the cracks of unreachable parts of the karst, which would also explain why they are, in most cases, extremely rare in caves, where they appear to occur accidentally only.

The plesiomorphic “geotrechoid shape” shared by species found preferentially in forest endogean environments is repeated in almost all clades; the dispersal of these elements through the most superficial compartments of the subterranean environment (the soil or deep litter layers in forest environments) during favourable paleoclimatic periods could explain the dispersion and speciation phenomena of the entire radiation: locally, they have given rise to various hypogean subclades with convergent adaptations to the various occupied habitats. Paradoxically, a result similar to that of the orthogenetic hypothesis of JEANNEL (1950) is obtained: in all the clades containing troglobiomorphic taxa, the early splits concern “geo-

trechoid” species, with the late arrival of “aphaenopsian” and “hydraphaenopsian” taxa depending on the colonized habitat.

### Conservation

The extension of the name *Aphaenops* to all the underground Trechini of the Pyrenees makes the legal texts, which only concern the species included in the genus *Aphaenops* as defined up to now, obsolete. A case-by-case assessment of the species on the basis of IUCN criteria, and in particular by integrating the notion of threat, is required to identify the taxa requiring appropriate conservation measures.

### New replacement names

The new classification results in two homonymies, which can be solved as follows:

*Aphaenops* (*Geotrechus*) *jeannelianus* Faille, Fresneda & Bourdeau, **nom. n.** for *Geotrechus jeanneli* A. Gaudin, 1938 [nec *Aphaenops jeanneli* (Abeille de Perrin, 1905)].

*Aphaenops* (*Aurigerotrechus*) *vandelianus* Faille, Fresneda & Bourdeau, **nom. n.** for *Geotrechus vandeli* Coiffait, 1959 [nec *Aphaenops vandeli* Fourès, 1954].

A complete catalogue of the hypogean Trechini of the Pyrenees, following the new classification, is given in Appendix 1. The recognized species are listed from SERRANO (2013) and TRONQUET (2014), also considering later contributions (FAILLE et al. 2015a; FAILLE & BOURDEAU 2022a, 2022b); the validity of the recognized subspecies was not tested here and will be the topic of future contributions.

### Acknowledgements

We are grateful to the following people for their help in the field, for providing cave beetles from the Pyrenees, or for the loan of specimens from their private collections: F. ALFAMBRA and the Grupo de Espeleología de Badalona (GEB), L. AUROUX, P. BALART, A. BEDOS, X. BELLÈS, J. P. BESSON†, M. BOF, F. BRÉHIER, H. BRUSTEL, S. CALLY, A. CASALE, O. CAUDRON, J. CHAUVIN, S. CLÉMENT, J. COMAS, O. COURTIN, G. CORBAZ, L. DEHARVENG, M. C. DELMASURE, A. DOLE, E. DUPRÉ†, J. F. ETCHÉPARRE, F. FADRIQUE, C. HERNANDO, S. HUANG, G. JAUZION†, B. JUNGER, V. LEFEBVRE, L. RIGOU, N. VALLA and the Groupe Spéléologique du Couserans (GSC), C. VANDERBERGH, T. DEUVE, A. MANTILLERI, A. TAGHAVIAN (MNH) and G. MASÓ (MZB) are warmly thanked for the loan of material under their care. We thank J. SCHMIDT, A. CASALE and D. WHITMORE for their thoughtful reviews of the manuscript.

We are also grateful to A. BELLERSHEIM (SMNS) and S. HUANG (MNH) for providing us with some of the pictures illustrating this work. Collecting in the Ordesa National Park and Monte Perdido (Huesca, Spain) were carried out under a permit granted by INAGA (N. 24/2012/5229).



This work is dedicated to the memory of our friends P. DÉLIOT, I. RIBERA and E. DUPRÉ, who were fascinated by the study of the cave fauna of the Pyrenees.


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ZooBank registration: <https://zoobank.org/References/A3E11FB8-6712-484F-B926-5A51DBFA6B8E>

Manuscript received: 03.XI.2022; accepted: 13.XII.2022.

**Appendix 1.** List of the species of the genus *Aphaenops* sensu novo.

**Genus *Aphaenops* Bonvouloir, 1862 (nomen protectum) sensu novo**

*Aphaenops* Bonvouloir, 1862 (BONVOULOIR 1862: 567) (**nomen oblitum**)

*Aphaenops* Bonvouloir, 1862 (KRAATZ 1862: XII)

*Cerbaphaenops* Coiffait, 1962 (COIFFAIT 1962: 147), **syn. n.**

*Cephalaphaenops* Coiffait, 1962 (COIFFAIT 1962: 154)

*Arachnaphaenops* Jeanne, 1967 (JEANNE 1967: 20)

*Geaphaenops* Cabidoche, 1966 (CABIDOCHÉ 1966: 520), **syn. n.**

*Pubaphaenops* Genest, 1983 (GENEST 1983: 309)

*Simaphaenops* Quéinnec & Ollivier, 2011 (QUÉINNEC & OLLIVIER 2011: 210), **syn. n.**

**1. Subgenus *Aphaenops* sensu novo**

**1.1. Group *Aphaenops* (*Aphaenops*) *eskulduna***

1.1.1. *Aphaenops* (*Aphaenops*) *cissauguensis* Faille & Bourdeau, 2008, **subgen. comb. n.** – France: Pyrénées-Atlantiques.

1.1.2. *Aphaenops* (*Aphaenops*) *eskulduna* Coiffait, 1959 – France: Pyrénées-Atlantiques; Spain: Huesca.

1.1.3. *Aphaenops* (*Aphaenops*) *mensionii* Lagar, 1976 – Spain: Huesca.

1.1.4. *Aphaenops* (*Aphaenops*) *parvulus* Faille, Bourdeau & Fresneda, 2010 – Spain: Huesca.

1.1.5. *Aphaenops* (*Aphaenops*) *rebereti* A. Gaudin, 1947, **subgen. comb. n.** – France: Pyrénées-Atlantiques.

**1.2. Group *Aphaenops* (*Aphaenops*) *jeanneli***

1.2.1. *Aphaenops* (*Aphaenops*) *alberti* Jeannel, 1939 – France: Pyrénées-Atlantiques.

1.2.2. *Aphaenops* (*Aphaenops*) *jeanneli* (Abeille de Perrin, 1905) – France: Pyrénées-Atlantiques.

1.2.3. *Aphaenops* (*Aphaenops*) *orionis* Fagniez, 1913 – France: Pyrénées-Atlantiques; Spain: Navarra.

**1.3. Group *Aphaenops* (*Aphaenops*) *leschenaulti***

1.3.1. *Aphaenops* (*Aphaenops*) *atalonicus* Escolà & Canció, 1983 – Spain: Huesca.

1.3.2. *Aphaenops* (*Aphaenops*) *leschenaulti* Bonvouloir, 1862 – France: Hautes-Pyrénées.

1.3.3. *Aphaenops* (*Aphaenops*) *linderi* Jeannel, 1938, **subgen. comb. n.** – France: Haute-Pyrénées, Pyrénées-Atlantiques.

**1.4. Group *Aphaenops* (*Aphaenops*) *loubensi***

1.4.1. *Aphaenops* (*Aphaenops*) *abodiensis* Dupré, 1988 – Spain: Navarra.

1.4.2. *Aphaenops* (*Aphaenops*) *bessoni* Cabidoche, 1962 – France: Pyrénées-Atlantiques.

1.4.3. *Aphaenops* (*Aphaenops*) *loubensi* Jeannel, 1953 – France: Pyrénées-Atlantiques; Spain: Huesca, Navarra.

1.4.4. *Aphaenops* (*Aphaenops*) *valleti* Casale & Genest, 1986 – Spain: Huesca

**1.5. Group *Aphaenops* (*Aphaenops*) *ochsi***

1.5.1. *Aphaenops* (*Aphaenops*) *fresnedai* Faille & Bourdeau, 2011 – Spain: Huesca.

1.5.2. *Aphaenops* (*Aphaenops*) *ochsi* L. Gaudin 1925 – France: Pyrénées-Atlantiques; Spain: Huesca, Navarra.

**1.6. Group *Aphaenops* (*Aphaenops*) *rhadamanthus***

1.6.1. *Aphaenops* (*Aphaenops*) *baretosanus* (Jeannel, 1941), **subgen. comb. n.** – France: Pyrénées-Atlantiques.

1.6.2. *Aphaenops* (*Aphaenops*) *ludovici* A. Gaudin, 1935, **subgen. comb. n.** – France: Hautes-Pyrénées; Pyrénées-Atlantiques; Spain: Navarra.

1.6.3. *Aphaenops* (*Aphaenops*) *rhadamanthus* (Linder, 1860), **subgen. comb. n.** – France: Hautes-Pyrénées, Pyrénées-Atlantiques.

**2. Subgenus *Argonotrechus* subgen. n.**

2.1. *Aphaenops* (*Argonotrechus*) *orpheus* (Dieck, 1869), **comb. n.** – France: Ariège, Haute-Garonne.

**3. Subgenus *Aurigerotrechus* subgen. n.**

**3.1. Group *Aphaenops* (*Aurigerotrechus*) *saulcyi***

3.1.1. *Aphaenops* (*Aurigerotrechus*) *andreae* (Jeannel, 1920), **comb. n.** – France: Ariège.

3.1.2. *Aphaenops* (*Aurigerotrechus*) *palei* (Fourès, 1962), **comb. n.** – France: Ariège.

- 3.1.3. *Aphaenops* (*Aurigerotrechus*) *sauleyi* (Argod-Vallon, 1913), **comb. n.** – France: Ariège.
- 3.1.4. *Aphaenops* (*Aurigerotrechus*) *vandelianus*, Faille, Fresneda & Bourdeau, 2023 **nom. n.** for *Geotrechus vandeli* Coiffait, 1959 (nec *Aphaenops vandeli* Fourès, 1954 = *Aphaenops* (*Hydrapphaenops*) *vandeli* Fourès, 1954) – France: Ariège.
- 3.1.5. *Aphaenops* (*Aurigerotrechus*) *vanderberghi* (Perreau & Quéinnec, 1987), **comb. n.** – France: Ariège.
- 3.2. Group *Aphaenops* (*Aurigerotrechus*) *vulcanus sensu novo*
- 3.2.1. *Aphaenops* (*Aurigerotrechus*) *sulcatus* (Coiffait, 1959), **comb. n.** – France: Ariège.
- 3.2.2. *Aphaenops* (*Aurigerotrechus*) *vulcanus* (Abeille de Perrin, 1904) **comb. n.** – France: Ariège.
4. Subgenus *Ceretotrechus* subgen. n.
- 4.1. Group *Aphaenops* (*Ceretotrechus*) *delioli*
- 4.1.1. *Aphaenops* (*Ceretotrechus*) *delioli* (Faille, Bourdeau, Bellès & Fresneda, 2015), **comb. n.** – Spain: Girona.
- 4.1.2. *Aphaenops* (*Ceretotrechus*) *incantatus* (Faille, Bourdeau, Bellès & Fresneda, 2015), **comb. n.** – Spain: Lleida.
- 4.2. Group *Aphaenops* (*Ceretotrechus*) *ubachi*
- 4.2.1. *Aphaenops* (*Ceretotrechus*) *boumortensis* (Faille, Bourdeau, Bellès & Fresneda, 2015), **comb. n.** – Spain: Lleida.
- 4.2.2. *Aphaenops* (*Ceretotrechus*) *puigmalensis* (Lagar, 1981), **comb. n.** – Spain: Girona.
- 4.2.3. *Aphaenops* (*Ceretotrechus*) *seijasi* (Español, 1969), **comb. n.** – Spain: Lleida.
- 4.2.4. *Aphaenops* (*Ceretotrechus*) *ubachi* (Español, 1965), **comb. n.** – Spain: Lleida.
- 4.2.5. *Aphaenops* (*Ceretotrechus*) *victoriai*\* (Faille, Bourdeau, Bellès & Fresneda, 2015), **comb. n.** – Spain: Barcelona.
5. Subgenus *Dupreapphaenops* subgen. n.
- 5.1. *Aphaenops* (*Dupreapphaenops*) *galani* (Español, 1968), **subgen. comb. n.** – Spain: Guipúzcoa.
- 5.2. *Aphaenops* (*Dupreapphaenops*) *sarpedon* (Faille, Fresneda & Bourdeau, 2013), **comb. n.** – France: Pyrénées-Atlantiques.
- 5.3. *Aphaenops* (*Dupreapphaenops*) *vasconicus* Jeannel, 1913, **subgen. comb. n.** – France: Pyrénées-Atlantiques.
6. Subgenus *Geotrechidius* sensu novo
- 6.1. *Aphaenops* (*Geotrechidius*) *blancheti* (A. Gaudin, 1947), **subgen. comb. n.** – France: Hautes-Pyrénées.
- 6.2. *Aphaenops* (*Geotrechidius*) *dumonti* (Español, 1977), **comb. n.** – Spain: Huesca.
- 6.3. *Aphaenops* (*Geotrechidius*) *gallicus* (Delarouzée, 1857), **comb. n.** – France: Hautes-Pyrénées, Pyrénées-Atlantiques.
- 6.4. *Aphaenops* (*Geotrechidius*) *gracilis* (A. Gaudin, 1947), **subgen. comb. n.** – France: Pyrénées-Atlantiques.
- 6.5. *Aphaenops* (*Geotrechidius*) *jeannelianus*, Faille, Fresneda & Bourdeau, 2023 **nom. n.** for *Geotrechus jeanneli* A. Gaudin, 1938 – France: Hautes-Pyrénées.
- 6.6. *Aphaenops* (*Geotrechidius*) *pandellei* (Linder, 1859), **subgen. comb. n.** – France: Hautes-Pyrénées, Pyrénées-Atlantiques.
- 6.7. *Aphaenops* (*Geotrechidius*) *soussieuxi* (Perreau & Quéinnec, 1987), **comb. n.** – France: Landes.
7. Subgenus *Geotrechus* stat. n.
- 7.1. *Aphaenops* (*Geotrechus*) *discontignyi* (Fairmaire, 1867), **comb. n.** – France: Hautes-Pyrénées.
- 7.2. *Aphaenops* (*Geotrechus*) *orcinus* (Linder, 1859), **comb. n.** – France: Haute-Garonne, Hautes-Pyrénées.
- 7.3. *Aphaenops* (*Geotrechus*) *serrulatus* (Jeannel, 1946), **comb. n.** – France: Hautes-Pyrénées.
- 7.4. *Aphaenops* (*Geotrechus*) *trophonius* (Abeille de Perrin, 1872), **comb. n.** – France: Ariège, Haute-Garonne.
8. Subgenus *Hydrapphaenops* sensu novo
- 8.1. Group *Aphaenops* (*Hydrapphaenops*) *chaudoiri*
- 8.1.1. *Aphaenops* (*Hydrapphaenops*) *chaudoiri* (Brisout de Barneville, 1867) – France: Hautes-Pyrénées.
- 8.1.2. *Aphaenops* (*Hydrapphaenops*) *elegans* (A. Gaudin, 1946) – France: Hautes-Pyrénées.
- 8.1.3. Incertae sedis: *Aphaenops* (*Hydrapphaenops*) *alfambrai* (Lagar, 1979) – Spain: Huesca.
- 8.2. Group *Aphaenops* (*Hydrapphaenops*) *crypticola sensu novo*
- 8.2.1. *Aphaenops* (*Hydrapphaenops*) *aeacus* (Saulcy, 1864), **subgen. comb. n.** – France: Hautes-Pyrénées.
- 8.2.2. *Aphaenops* (*Hydrapphaenops*) *bonneti* Fourès, 1948, **subgen. comb. n.** – France: Ariège.
- 8.2.3. *Aphaenops* (*Hydrapphaenops*) *bouilloni* Coiffait, 1955, **subgen. comb. n.** – France: Ariège.
- 8.2.4. *Aphaenops* (*Hydrapphaenops*) *bucephalus* (Dieck, 1869), **subgen. comb. n.** – France: Ariège, Haute-Garonne.
- 8.2.5. *Aphaenops* (*Hydrapphaenops*) *carrerei* Coiffait, 1953, **subgen. comb. n.** – France: Ariège.
- 8.2.6. *Aphaenops* (*Hydrapphaenops*) *cerberus* (Dieck, 1869), **subgen. comb. n.** – France: Ariège, Haute-Garonne.
- 8.2.7. *Aphaenops* (*Hydrapphaenops*) *chappuisi* Coiffait, 1955, **subgen. comb. n.** – France: Haute-Garonne.
- 8.2.8. *Aphaenops* (*Hydrapphaenops*) *colluvii* Genest & Juberthie, 1983, **subgen. comb. n.** – France: Ariège.
- 8.2.9. *Aphaenops* (*Hydrapphaenops*) *corbazi*\* Faille & Bourdeau, 2022b, **subgen. comb. n.** – France: Haute-Garonne.
- 8.2.10. *Aphaenops* (*Hydrapphaenops*) *crypticola*\* (Linder, 1859), **subgen. comb. n.** – France: Haute-Garonne, Hautes-Pyrénées.
- 8.2.11. *Aphaenops* (*Hydrapphaenops*) *hortensis* Fourès, 1954, **subgen. comb. n.** – France: Ariège.
- 8.2.12. *Aphaenops* (*Hydrapphaenops*) *hustachei* Jeannel, 1917, **subgen. comb. n.** – France: Hautes-Pyrénées.
- 8.2.13. *Aphaenops* (*Hydrapphaenops*) *jauzioni* Faille, Déliot & Quéinnec, 2007, **subgen. comb. n.** – France: Haute-Garonne.
- 8.2.14. *Aphaenops* (*Hydrapphaenops*) *laurenti* Genest, 1983, **subgen. comb. n.** – France: Ariège.
- 8.2.15. *Aphaenops* (*Hydrapphaenops*) *longicollis* Joffre, 1931 – France: Hautes-Pyrénées.
- 8.2.16. *Aphaenops* (*Hydrapphaenops*) *mariaerosae* Genest, 1983, **subgen. comb. n.** – France: Ariège.
- 8.2.17. *Aphaenops* (*Hydrapphaenops*) *michaeli* Fourès, 1954, **subgen. comb. n.** – France: Ariège.
- 8.2.18. *Aphaenops* (*Hydrapphaenops*) *parallelus*\* Coiffait, 1954, **subgen. comb. n.** – France: Ariège, Haute-Garonne.

- 8.2.19. *Aphaenops (Hydraphaenops) pluto* (Dieck, 1869), **subgen. comb. n.** – France: Ariège.
- 8.2.20. *Aphaenops (Hydraphaenops) pseudocrypticola* Coiffait, 1947, **subgen. comb. n.** – France: Hautes-Pyrénées.
- 8.2.21. *Aphaenops (Hydraphaenops) riberai*\* Faille & Bourdeau, 2022a, **subgen. comb. n.** – France: Haute-Garonne.
- 8.2.22. *Aphaenops (Hydraphaenops) sinister* Coiffait, 1959, **subgen. comb. n.** – France: Ariège.
- 8.2.23. *Aphaenops (Hydraphaenops) sioberae* Fourès, 1954, **subgen. comb. n.** – France: Ariège.
- 8.2.24. *Aphaenops (Hydraphaenops) tiresias* (Piochard de La Brûlerie, 1872), **subgen. comb. n.** – France: Ariège, Haute-Garonne.
- 8.2.25. *Aphaenops (Hydraphaenops) vandeli* Fourès, 1954, **subgen. comb. n.** – France: Ariège.

\*Remark: the species *A. crypticola* and sister taxa were partially revised recently. The species *A. crypticola* is located between the Aure valley to the West and the Garonne valley to the East. All the populations located between the Garonne valley and the Portet d'Aspet area belong to *Aphaenops parallelus* (Faille & Bourdeau 2022a).

**8.3. Group *Aphaenops (Hydraphaenops) ehlersi sensu novo***

- 8.3.1. *Aphaenops (Hydraphaenops) bourgoini* Jeannel, 1946 – France: Ariège, Haute-Garonne.
- 8.3.2. *Aphaenops (Hydraphaenops) ehlersi* (Abeille de Perrin, 1872) – France: Ariège, Haute-Garonne.
- 8.3.3. *Aphaenops (Hydraphaenops) pecoudi* A. Gaudin, 1938 – France: Ariège.

**8.4. Group *Aphaenops (Hydraphaenops) minos***

- 8.4.1. *Aphaenops (Hydraphaenops) hidalgoi* (Español & Comas, 1985), **subgen. comb. n.** – Spain: Huesca.
- 8.4.2. *Aphaenops (Hydraphaenops) minos* (Linder, 1860), **subgen. comb. n.** – France: Ariège.
- 8.4.3. *Aphaenops (Hydraphaenops) mouriesi* (Genest, 1983), **subgen. comb. n.** – France: Ariège.
- 8.4.4. *Aphaenops (Hydraphaenops) penacollaradensis* (Dupré, 1991), **subgen. comb. n.** – France: Pyrénées-Atlantiques; Spain: Huesca.

**9. Subgenus *Nafarroaphaenops subgen. n.***

- 9.1. *Aphaenops (Nafarroaphaenops) giraudi* Ochs, 1938, **subgen. comb. n.** – France: Pyrénées-Atlantiques; Spain: Navarra.
- 9.2. *Aphaenops (Nafarroaphaenops) navaricus* Coiffait & A. Gaudin, 1950, **subgen. comb. n.** – France: Pyrénées-Atlantiques.
- 9.3. *Aphaenops (Nafarroaphaenops) sobrarbensis* (Lagar & Hernando, 1987), **subgen. comb. n.** – Spain: Huesca.

**10. Subgenus *Pyreneotrechus subgen. n.***

- 10.1. *Aphaenops (Pyreneotrechus) aldensis* (Jeannel, 1955), **comb. n.** – France: Ariège.

**11. Subgenus *Riberaphaenops subgen. n.***

- 11.1. *Aphaenops (Riberaphaenops) dequaei* (Dupré, 1988), **comb. n.** – Spain: Navarra.
- 11.2. *Aphaenops (Riberaphaenops) holcartensis* (Genest 1977), **comb. n.** – France: Pyrénées-Atlantiques.
- 11.3. *Aphaenops (Riberaphaenops) picanyoli* (Español & Escolà, 1983), **comb. n.** – Spain: Huesca.

**Appendix 2.** Summary of the main morphological characters of each subgenus of *Aphaenops sensu novo*. The characters defining the subgenera are listed in the main text.

**Glabrous body and sternites with 2 symmetrical setae**

- Mc1 implanted very far from the base of the elytra, body glabrous, tm1 lower than tm2..... *Pyreneotrechus*,
- ..... *Ceretotrechus*, *Aurigerotrechus*
- Mc1 implanted close to the base of the elytra, elytra only slightly pubescent..... *Argonotrechus*
- Size >5mm, Tm1 always higher than tm2, elytra without striae..... *Aphaenops* (exception: *A. alberti* has a pubescent head)

**Pubescent sternites with 2 symmetrical setae**

- Body fully hairy
- Tm1 lower than tm2 ..... *Geotrechus-Riberaphaenops-Nafarroaphaenops*
- Tm1 higher than tm2 ..... *Dupreaphaenops*
- Elytra glabrous, head pubescent..... *Geotrechidius*
- Head pubescent, pronotum glabrous ..... *Hydraphaenops*

