

Allopatric speciation illustrated: The hypogean genus *Geotrechus* Jeannel, 1919 (Coleoptera: Carabidae: Trechini), with description of four new species from the Eastern Pyrenees (Spain)

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Abstract

We present a study of the eastern group of species of the genus *Geotrechus* (Coleoptera, Carabidae, Trechini), combining molecular and morphological approaches. Four new species are described from caves of the Pyrenees of Catalonia, Spain. Two of the new species belong to the *Geotrechus ubachi* group sensu novo, like all the species previously known. A new group, the *Geotrechus delioli* group, is proposed for two new species merged until now with *Geotrechus seijasi* Español. The molecular study is based on a combination of fragments of four mitochondrial and two nuclear genes. We discuss the distribution of the group and provide a potential scenario of diversification, favouring the hypothesis of allopatric speciation for this old and speciose group of Pyrenean microendemic biota.

Key words

Trechinae, new species, subterranean environment, Pyrenees, Spain, molecular phylogeny, modes of speciation.

1. Introduction

Although a number of speciation modes have been reported to lead to diversification of troglobites, speciation due to geographic isolation (= allopatry) is assumed to be the dominant speciation mode prevailing in subterranean ecosystems (e.g. BARR & HOLSINGER 1985; CULVER & KANE 2005; see JUAN et al. 2010 for a review).

Recent investigations on Palearctic terrestrial cave fauna highlight the monophyly of exclusive subterranean lineages (FAILLE et al. 2010a, 2013b; RIBERA et al. 2010). Nevertheless, some studies underline the possibility of dispersal of beetles fully adapted to subterranean

environments during favourable climatic windows (BARR 1967; SOKOLOV 2012; RIZZO et al. 2013b; FAILLE et al. 2015), making the puzzle of present-day distribution of cave-adapted insects more complex by adding the possibility of secondary contact events.

The genus *Geotrechus* was described by JEANNEL (1919) for a number of subterranean species with “anophthalmous” features, in opposition to the troglobitic “aphaenopsian” species of the genus *Aphaenops* Bonvouloir, 1861 characterized by a slender body form and an extreme elongation of body parts, legs and antennae

(JEANNEL 1941). Diagnostic characters of *Geotrechus* include the presence of frontal furrows and a robust appearance, with short legs and antennae (COIFFAIT 1962). JEANNEL (1919) considered the genera *Aphaenops* and *Geotrechus* as two closely related but distinct lineages. Most of the 23 known species of *Geotrechus* are hypogean microendemisms, and although some species can be locally abundant in caves, most of them are usually endogean localized at the entrance of the cavities (JEANNEL 1926b, 1941). Some species can also be found under large stones in forests, when hydric conditions are favourable. A molecular study showed the polyphyly of *Geotrechus* as well as the two subgenera *Geotrechus* and *Geotrechidius* Jeannel, 1947 (FAILLE et al. 2010a). The two subgenera were recently considered as synonyms (QUÉINNEC & OLLIVIER 2011). *Geotrechus* species are more common on the French slope of the Pyrenees, and only 6 of them are known from the Spanish side (MORAVEC et al. 2003; SERRANO 2013). The first Spanish species described was *Geotrechus ubachi*, as endemic from the valley of Segre river, Lleida, Eastern Pyrenees (ESPAÑOL 1965).

In this paper we focus on the eastern group of the species of *Geotrechus*, composed until now by three species: *Geotrechus ubachi*, *G. seijasi* Español, 1969 and *G. puigmalensis* Lagar, 1981. This eastern group of species has a particular interest as one of the species (*G. deliotti* sp.n. under the name *G. seijasi*, FAILLE et al. 2010a) is known to have diverged early in the evolution of the hypogean lineage of Pyrenean Trechini. The morphological revision coupled with a molecular analysis led to the discovery of four new species, well differentiated into two species groups.

2. Material and methods

2.1. Taxon sampling, morphological study, DNA extraction and sequencing

Specimens were collected by hand or by mean of pitfall traps containing water saturated in salt or propylene glycol, known to preserve DNA (RUBINK et al. 2003; LÓPEZ & OROMÍ 2010) (Table 1). Apart from the two epigeal species of *Trechus*, all the samples were taken in natural or artificial (mine) caves. The detailed protocol is described by FAILLE et al. (2010b). Extractions of single specimens were non-destructive, using the DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany). After extraction, specimens were mounted on card and the genitalia stored in water-soluble dimethyl hydantoin formaldehyde resin (DMHF) or in Canada balsam on transparent cards, pinned beneath the specimen.

Pictures were taken with microscopes Olympus CH and Olympus szx16, coupled with a camera Olympus c5060wz. Serial pictures were combined using the CombineZP software, and finally processed using Adobe Photoshop CS.

Vouchers and DNA samples are kept in the collections of various institutions and of the authors.

For DNA studies, we used specimens of 5 of the 6 species of the *G. ubachi* and *G. deliotti* groups, with the exception of *G. boumortensis* sp.n., some specimens of the Pyrenean lineage of hypogean Trechini (*Aphaenops* and *Geotrechus*), including the type species of *Aphaenops* (*A. leschenaulti* Bonvouloir, 1862), and *Geotrechus* (*Geotrechus discontinnyi* Fairmaire, 1867); the tree was rooted on two species of *Trechus* belonging to a different group of Trechini (JEANNEL 1927; FAILLE et al. 2010a).

We amplified fragments of four mitochondrial genes: 3' end of cytochrome c oxidase subunit (*cox1*); a single fragment including the 3' end of the large ribosomal unit (*rrnL*), the whole tRNA-Leu gene (*trnL*) and the 5' end of the NADH dehydrogenase 1 (*nad1*); and two nuclear genes (internal fragment of the large ribosomal unit 28S rRNA (*LSU*) and the 5' end of the small ribosomal unit 18S rRNA (*SSU*) (details of primers used in Table 2). Sequences were assembled and edited using Sequencher TM 4.8 (Gene Codes, Inc., Ann Arbor, MI). Some sequences were already available and taken from previous studies (FAILLE et al. 2010a, 2011a, 2013a,b) (Table 1). New sequences have been deposited in EMBL database with Accession Numbers KT892652–KT892676 (Table 1).

2.2. Phylogenetic analyses

We aligned the sequences using the MAFFT online v.7 and the Q-INS-i algorithm (KATO & STANDLEY 2013). Maximum likelihood analyses were conducted on a combined data matrix with RAxML GUI (STAMATAKIS 2006; STAMATAKIS et al. 2008; SILVESTRO & MICHALAK 2012), with four partitions corresponding to the *cox1*, *rrnL*+*trnL*+*nad1*, *SSU* and *LSU* fragments and with a GTR+I+G evolutionary model, and the default values for other parameters of the search (STAMATAKIS et al. 2008). Independent runs of single markers were set up to look for possible incongruence between the markers. All the topologies obtained were congruent and in accordance with the one presented in Fig. 25. BEAST 1.7 (DRUMMOND et al. 2012) was used to obtain an ultrametric phylogenetic tree and ages of diversification. We used as priors the rates estimated for the same gene fragments in previous work on Carabidae based on a set of fossils and biogeographic events (ANDÚJAR et al. 2012; FAILLE et al. 2013b).

2.3. Abbreviations

Institutes and collections. **IBE:** Institute of Evolutionary Biology, Barcelona (Spain); **MNHN:** Muséum national d'Histoire naturelle, Paris (France); **MZB:** Museu de Ciències Naturals (Zoologia), Barcelona (Spain); **ZSM:** Zoologische Staatssammlung, München (Germany); **CXB:** coll. X. Belles (Barcelona, Spain); **CCB:** coll. C. Bourdeau (Rebique, France); **CAF:** coll. A. Faille (Paris, France); **CFL:** coll. Fresneda-Lagar (Llesp, Spain).

Table 1. Sequenced specimens, with localities, collectors, codes and sequence accession numbers (new sequences in bold). Sequences of *Geotrechus deliotti* sp.n. from Cova d'En Manent (MNHN-AF89) were previously published under the name *G. seijasi* (FAILLE et al. 2010a, 2011a).

Species	Locality	Code	SSU	LSU	cox1	rrnL	tRNA-Leu	nad1
Aphaenops Bonvouloir, 1862								
Aphaenops Bonvouloir, 1862 (s.str.)								
<i>Aphaenops leschenaulti</i> Bonvouloir, 1861	Grotte de Castelmouly – Bagnères-de-Bigorre (France-65)	MNHN-AF1	FR733945	GQ293593	GQ293629	GQ293739	GQ293757	GQ293822
Hydraphaenops Jeannel, 1926								
<i>Aphaenops ehlersi</i> (Abeille de Perrin, 1872)	Goueil-di-Her – Arbas (France-31)	MNHN-AF64	FR733957	GQ293589	GQ293646	FR729571	FR729571	FR729571
Geotrechus Jeannel, 1919								
<i>Geotrechus deliotti</i> sp.n.	Cova d'en Manent – Isòvol (Spain-Girona)	MNHN-AF89	GQ293529	GQ293598	FR733905	KT892663	KT892663	KT892663
<i>Geotrechus deliotti</i> sp.n.	Mines de Cortàs – Isòvol (Spain-Girona)	ZSM-L228	KT892673	KT892664	KT892656	—	—	—
<i>Geotrechus deliotti</i> sp.n.	Mines de Cortàs – Isòvol (Spain-Girona)	ZSM-L1000	KT892674	KT892665	—	—	—	—
<i>Geotrechus discontignyi</i> (Fairmaire, 1863)	France - Bagnères-de-Bigorre – Grotte du Tuco	MNHN-AF92	FR733966	GQ293560	FR733901	FR729572	FR729572	FR729572
<i>Geotrechus incantatus</i> sp.n.	Cova de les Encantades – Toloriu (Spain-Lleida)	IBE-L227	KT892675	KT892666	—	—	—	—
<i>Geotrechus incantatus</i> sp.n.	Cova de les Encantades – Toloriu (Spain-Lleida)	IBE-L227b	—	KT892667	KT892657	—	—	—
<i>Geotrechus puigmalensis</i> Lagar, 1981	Cova de les Encantades del Puigmal – Queralbs (Spain-Girona)	IBE-L222	KT892677	KT892672	KT892655	KT892661	KT892661	KT892661
<i>Geotrechus sarpedon</i> Faille, Fresneda, Bourdeau 2013	Grotte inférieure d'Oxibar – Camou-Cihigue (France-64)	ZSM-L445	KT892679	HG315029	HG315032	HG315028	HG315028	HG315028
<i>Geotrechus seijasi</i> Español, 1969	Fou de Bor – Bellver de Cerdanya (Spain-Lleida)	ZSM-L1065	—	KT892671	KT892654	KT892662	KT892662	KT892662
<i>Geotrechus ubachi</i> Español, 1965	Avenc del Xato – Llinars (Spain-Lleida)	ZSM-L553	KT892678	KT892670	KT892658	—	—	—
<i>Geotrechus victorjai</i> sp.n.	Cova d'Espades – La Nou de Berguedà (Spain-Barcelona)	ZSM-L302	KT892676	KT892668	KT892652	KT892659	KT892659	KT892659
<i>Geotrechus victorjai</i> sp.n.	Cova d'Espades – La Nou de Berguedà (Spain-Barcelona)	ZSM-L304	—	KT892669	KT892653	KT892660	KT892660	KT892660
Trechus Clairville, 1806								
<i>Trechus obtusus</i> Erichson, 1837	Madeira, Estrada de Nicho (Portugal)	IBE-AF2	FR733976	FR733997	HE817937	FR729579	FR729579	FR729579
<i>Trechus quadristriatus</i> (Schränk, 1781)	Egea, Collau de la Plana del Turbón (Spain-Huesca)	IBE-AF96	GQ293534	GQ293619	FR733908	GQ293743	GQ293745	GQ293841

Table 2. Primers used in the study.

Gene	Name	Sense	Sequence	Reference
<i>cox1</i>	Jerry (M202)	F	CAACATTTATTTGATTTTTGG	SIMON et al. 1994
	Pat (M70)	R	TCCA(A)TGCACTAATCTGCCATATTA	SIMON et al. 1994
	Chy	F	T(A/T)GTAGCCCA(T/C)TTTCATA(T/C)GT	RIBERA et al. 2010
	Tom	R	AC(A/G)TAATGAAA(A/G)TGGGCTAC(T/A)A	RIBERA et al. 2010
<i>rrnL-nad1</i>	16saR (M14)	F	CGCCTGTTA(A/T)CAAAAACAT	SIMON et al. 1994
	16Sa	R	ATGTTTTGTTAAACAGGCG	SIMON et al. 1994
	16Sb	R	CCGGTCTGAACCTCAGATCATGT	SIMON et al. 1994
	ND1A (M223)	R	GGTCCCTACGAATTTGAATATATCCT	SIMON et al. 1994
<i>LSU</i>	D1	F	GGGAGGAAAAGAACTAAC	OBER 2002
	D3	R	GCATAGTTCACCATCTTTC	OBER 2002

Measurements. LE: Length of elytra; LP: Length of pronotum; WE: Maximum width of elytra; WH: Maximum width of head; WP: Maximum width of pronotum; WPB: Width of pronotal base.

3. Taxonomy

Our study revealed the presence of seven species, belonging to two groups morphologically and molecularly very well characterized.

3.1. Group of *Geotrechus ubachi* sensu novo

A group of species well characterized by the shape of median lobe of aedeagus with apex rounded, the pronotum with hind angles simple and the maxillary palpus with the penultimate segment glabrous. This species group is composed by all previously known species: *G. ubachi*, *G. seijasi* and *G. puigmalensis*, and by two new species described herein.

3.1.1. *Geotrechus ubachi* Español, 1965

Figs. 7, 17

Geotrechus (Geotrechidius) ubachi Español, 1965: 136

In the original description the holotype was not designated. Therefore, and although the specimens are labelled “Typus” and “Paratypus”, all the 9 specimens included in the description have to be considered syntypes, contrary to the opinion of VIÑOLAS & MASÓ (2014). The species was described from two localities; we choose the lectotype from Avenc del Xato (Fig. 1) and consequently this locality as the type locality. The Avenc del Xato is the first locality sampled, where 8 of the 9 syntypes were found. The last specimen from the second locality (Bòfia de la Matella de les Planes) is lost (*G. Masó* personal communication), and it is now attributed to the new species *G. boumortensis* **sp.n.** described below. Moreover only 5 specimens are deposited in the collection of MZB (VIÑOLAS & MASÓ 2014). These specimens are designated as type series. As specified by VIÑOLAS & MASÓ (2014), the date of collecting of the paralectotypes is 4.X.1964, but the specimens are labelled 25.X.1964.

Type series. Lectotype ♂ of *Geotrechus ubachi* Español, 1965 (present designation); Llinàs, Avenc del Xato, 2.V.1964, Subils, Escolà & Senent leg., 1 specimen (MZB). «Av. del “Xato” / Llinars (Oliana) / 2-V-64 / Subils-Escolà-leg.». «Typus» «*Geotrechus / ubachi / Español / F. Español det.*» «1 (♂)» «78-0731 MZB» (Aedeagus in microscopic preparation); we added a red rectangular label «LECTOTYPUS / *Geotrechus ubachi* Español, 1965 / Faille, Bourdeau, Bellès & Fresneda des. 2015». Paralectotypes: Llinàs, Avenc del Xato, 4.X.1964, Subils, Escolà & Pintó leg., 4 exx. (MZB). «Avenc del “Xato” / Llinàs – Oliana / 25-X-64 / Lleida leg.» «Subils / Escolà / Pinto leg.» «*Geotrechus / ubachi / Español / F. Español det.*» «Paratypus» «2' ♀» «78-0732 MZB»; «Avenc del “Xato” / Llinàs – Oliana / Lleida 25-X-64 / leg.» «2-V-64 / Subils / Escolà / Senent leg.» «*Geotrechus / ubachi / Español / F. Español det.*» «Paratypus» «78-0733 MZB»; «Avenc del Xato / Llinàs Oliana / 25-X / Lleida 64» «Subils / Escolà / Pinto leg.» «*Geotrechus / ubachi / Español / F. Español det.*» «Paratypus» «75-5114 / MZB»; «Avenc del Xato / Llinàs Oliana / 25-X-64 / Lleida» «Subils / Escolà / Pinto leg.» «*Geotrechus / ubachi / Español / F.*

Español det.» «Paratypus» «2' ♀» «75-5115 / MZB»; we added a red rectangular label to these four specimens: «PARALECTOTYPUS / *Geotrechus ubachi* Español, 1965 / Faille, Bourdeau, Bellès & Fresneda des. 2015» (MZB).

Additional material and bibliographic data. Llinars, Avenc del Xato (ESPAÑOL 1965; BELLÉS 1973, 1978); 13.XI.2011, Bourdeau & Fresneda leg., 1 ♀, ZSM-L553 (CCB). Same locality, 11.VI.2013 Bourdeau & Fresneda leg., 1 ♀ (CFL); same locality, 25.IV.2014, Bourdeau & Faille leg., 1 ♂ (CAF).

Type locality. «España. Lérida: avenc del Xato, Llinàs, cerca de Oliana, sector oriental del Solsonés, ...» (ESPAÑOL 1965). UTM (WGS 84): 31T 364666 4665596, 1269 m (Fig. 1).

Diagnosis. Anophthalmous and depigmented. **Size:** Mean length (2 specimens): 4.67 mm (1 male), 4.25 mm (1 female). **Colour:** Yellowish brown. **Chaetotaxy:** Surface of elytra with a periscutellar seta, three setae on the disk, four humeral setae, four setae along lateral margin and two preapical setae. Marginal setae of pronotum present, the basal ones located before the hind angle. Ventral pubescence limited to one seta on each half sternite. **Head:** Glabrous except few scattered setae, elongate; mandibles long and thin giving to the species a “hydraphaenopsian” appearance (length (M/F): 0.9/0.9 mm; WH: 0.68/0.65 mm). Maxillary palpus elongated, the penultimate segment glabrous. Labrum bisinuate. **Antennae:** Proportionally long. Length (M/F): 3.5/2.8 mm; a few setae on the first antennomere, densely pubescent from the second antennomere. Articles IX to XI much longer than wide. **Pronotum:** Proportions (M/F): WP:LP = 0.75/0.82, WP:WPB = 1.67/1.75, WP:WH = 1.1/1.08, WE:WP = 1.93/2. Elongated, faintly narrowing towards base (length: 1.0/0.85 mm; WP: 0.75/0.7 mm); sides faintly arcuate, maximum width in the anterior quarter, without any distinct puncture. Pronotal hind angles moderately acute, turned up; basal margin sinuate. **Elytra:** Proportions (M/F): WE:LE = 0.5/0.56. Glabrous, elongated, lateral margin bordered by a gut all along the elytra, turned up and especially pronounced in the anterior part in the shoulders angles, which are blunt (length: 2.77/2.5 mm; WE: 1.45/1.4 mm). Striation faded on the side, internal striae faintly impressed. **Legs:** Proportionally long, pubescent, tibiae straight. Male pro-tarsomeres 1–2 dilated. **Male genitalia** (Fig. 17): Median lobe of aedeagus slightly curved in lateral view, with basal bulb and apex rounded, apical lamella present; parameres with two setae. Inner sac elongate without any strongly sclerotized copulatory piece.

Affinities. The species shares with the four other species all the characters of the *G. ubachi* group sensu novo. Although the new species *G. boumortensis* **sp.n.** was not available for DNA study, external and internal morphology suggest that these two species – *G. boumortensis* **sp.n.** and *G. ubachi* – could be regarded as two sister species originated by the isolation on the two sides of the Segre river. They differ by various characters among which the size, the shape of the labrum and the male genitalia.



Figs. 1–6. Type localities of *Geotrechus* spp. **1:** Avenc del Xato, type locality of *G. ubachi*. **2:** Avenc de Pla Fornesa, type locality of *G. boumortensis* **sp.n.** **3:** Fou de Bor, type locality of *G. seijasi* (photo: F. Fadrigue). **4:** Cova de les Encantades del Puigmal, type locality of *G. puigmalensis*. **5:** Cova d'Espades, type locality of *G. victoriai* **sp.n.** (photo: L. Auroux). **6:** Cova de les Encantades de Toloriu, type locality of *G. incantatus* **sp.n.**

Distribution and ecology. The Avenc del Xato (Fig. 1) is located in the Serra dels Obacs, not far from the Pla de les Guàrdies (Llinars, Odén), on the left edge of the Segre River. It is a very narrow 17 meters-deep pit opened in puddingstone. The bottom (1 m²) is humid and covered by a mix of stones, ground and organic debris. The species coexists with the Leptodirini (Col., Leiodidae, Cholevinae) *Speonomites mengeli* (Jeannel, 1910).

3.1.2. *Geotrechus boumortensis* Faille, Bourdeau, Bellés & Fresneda sp.n.

Figs. 8, 18

Type series. Holotype ♂: Spain, Lleida, La Guàrdia d'Ares, Avenc de Pla Fornesa, 3.I.1987, Escolà & Comas leg. (coll. Comas). «Holotypus / *Geotrechus boumortensis* sp.n.sp.n. / Faille, Bourdeau, Bellés & / Fresneda det. 2015» [red rectangular label (printed)], genitalia dissected and mounted in a separate label pinned with the specimen. – Paratype: 1 ♀, same data as holotype (CAF). «Paratypus / *Geotrechus boumortensis* sp.n.sp.n. / Faille, Bourdeau, Bellés & / Fresneda det. 2015» [red rectangular label (printed)].

Type locality. Lleida, La Guàrdia d'Ares, Avenc de Pla Fornesa, UTM (WGS 84): 31T 354295 4681553, 1495 m (Fig. 2).

Diagnosis. Anophthalmous and depigmented. **Size** (2 specimens): 3.79 mm (1 male), 3.79 mm (1 female). **Colour:** Yellowish brown. **Chaetotaxy:** Surface of elytra with a periscutellar seta, three setae on the disk, four humeral setae, four setae along lateral margin and two preapical setae. Marginal setae of pronotum present, the basal ones located before the hind angle. **Head:** Glabrous except some scarce setae, elongate; mandibles long and thin (length (M/F): 0.79/0.79 mm; WH: 0.54/0.54 mm). Penultimate segment of maxillary palpus glabrous. Labrum right. **Antennae:** Proportionally long. Length (M/F): 2.58/2.54 mm; a few setae on the first antennomere, densely pubescent from the second antennomere. **Pronotum:** Proportions (M/F): WP: LP = 0.8/0.8, WP: WPB = 1.49/1.87, WP: WH = 1.16/1.16, WE: WP = 1.94/1.94. Elongated, faintly narrowing towards base (length: 0.75/0.75 mm; WP: 0.63/0.63 mm); sides faintly arcuate, maximum width in the anterior quarter, without any distinct puncture. Pronotal hind angles moderately acute, right; basal margin right. **Elytra:** Proportions (M/F): WE: LE = 0.54/0.54. Glabrous, elongated, without lateral margin bordered all along the elytra, shoulders angles blunt (length: 2.25/2.25 mm; WE: 1.21/1.21 mm). Striation obsolete except for the internal stria, faintly impressed. **Legs:** Proportionally long, pubescent, tibiae straight. Male protarsomeres 1–2 dilated. **Male genitalia** (Fig. 18): Median lobe of aedeagus elongate, slightly curved in lateral view, thinner at apex which is slightly turned up; apical lamella present; parameres with two setae. Inner sac without any strongly sclerotized copulatory piece.

Etymology. The specific epithet refers to the Serra de Boumort, massif where the type locality of the new species is located.

Affinities. The external morphology, especially the shoulders angles blunt, the elongated pronotum and the thin and long mandibles (“*Hydraphaenops*-like” appearance), together with the geographic position of the new species suggest that it could be close to *G. ubachi*, although this hypothesis should be confirmed in the future by molecular approaches.

Distribution and ecology. *Geotrechus boumortensis* sp.n. is known with certainty from the type locality only: the shaft of Pla Fornesa. The species is endemic from the Serra del Boumort. The type locality (Avenc de Pla Fornesa) is located between the basins of Barranc del Llop and Riu de la Guàrdia, northern slope of Serra de Prada; it is located on the right edge of the Segre river, eastern extremity of the Serra del Boumort. The species occurs in the deep part of the cave. Avenc de Pla Fornesa is a 16 meters-deep shaft, with humidity close to saturation, located at 1500 m of altitude. The specimens were observed walking around the calcite part of the deepest part of the shaft (Comas personal communication). This cave is rich in hypogean fauna, it is the type locality of the Pterostichini *Zariquieya boumortensis* Faille, Fresneda & Bourdeau, 2011 (Col., Carabidae), which co-occurs with the Leptodirini *Troglocharinus fonti* (Jeannel, 1910) (Col., Leiodidae, Cholevinae) (FAILLE et al. 2011b).

Remarks. We did not study the cotype specimen from La Bòfia de la Matella de les Planes, which could not be located at MZB (VIÑOLAS & MASÓ 2014; G. Masó personal communication): Cabó, Bòfia de la Matella de les Planes, 29.XI.1964, Senent & Escolà leg., 1 specimen (MZB) (ESPAÑOL 1965). Nevertheless, and because of the geographic position of the cave, it is likely that the specimen of *Geotrechus* from this locality belongs to the new species. The Bòfia de la Matella de les Planes is located in the Cabó valley, south-west of the Tossal del Morro, in the middle of a ravine going down from the Serra de Sant Joan, around the Inglada stream. It is a 22 meters-deep shaft with a scree slope at its bottom. The only specimen collected in this locality was included in the type series of *G. ubachi* by ESPAÑOL (1965), and is also quoted by BELLÉS (1973, 1978) as *G. ubachi*.

3.1.3. *Geotrechus seijasii* Español, 1969

Figs. 9, 14

Geotrechus (Geotrechidius) seijasii Español, 1969: 89

Type series. Espagne, Lleida, Bellver de Cerdanya, Fou de Bor, 16.IV.1965, Seijas leg., 1 ♀ holotype fixed by monotypy (ICZN, 1999: article 73.1) (MZB) (ESPAÑOL 1969).

Additional material and bibliographic data. Bellver de Cerdanya, Fou de Bor, Seijas, Ribera, Ubach, Poderós, Victoria, Comas & Bellés leg. (BELLÉS 1973); Bellés (1978); 29.III.1970, Bellés leg., 1 ♂, 1 ♀ (CXB) (BELLÉS & DÉLIOT 1981); 1 ♂, same data, J. Comas leg. (CAF); 2.V.1970, Fadrique leg., 3 exx. (CFL); 5.IV.1972, Fadrique leg., 1 specimen (CFL); 30.IV.1972, Muniesa leg., 1 specimen (CFL); 18.XII.1978, Fadrique leg., 2 exx. (CFL); 4.VI.2014, ECA-MZB leg., MZB 2014 2433, ZSM-L1065, 1

♂ (MZB); Bellver de Cerdanya, Forat de les Gralles, Gaudin & Henrot leg., MZB 87-8435, 1 ♀ (MZB) (ESPAÑOL 1977); BELLÉS & DÉLIOT (1981).

Type locality. «Lérida: Fou de Bor, Bellever de Cerdanya, ...» (ESPAÑOL 1969). UTM (WGS 84): 31T 401236 4688060, 1145 m (Fig. 3).

Diagnosis. Anophthalmous and depigmented. **Size** (3 specimens): 3.43 mm (2 males), 4.2 mm (1 female). **Colour:** Yellowish brown. **Chaetotaxy:** Surface of elytra with a periscutellar seta, three setae on the disk, four humeral setae, four setae along lateral margin and two preapical setae. Marginal setae of pronotum present, the basal ones located before the hind angle. Ventral pubescence limited to one seta on each half sternite (1 specimen of Forat de les Gralles with 1 seta in the middle of each segment). **Head:** Glabrous except some scarce setae, round, temples protruding; mandibles short (length (2M/F): 0.7/0.7 mm; WH: 0.55/0.6 mm). Penultimate segment of maxillary palpus glabrous. Labrum right, in some specimens slightly concave or indented in its median part. **Antennae:** Proportionally long. Length (M/F): 2/2.17 mm; a few setae on the first antennomere, densely pubescent from the second antennomere. **Pronotum:** Proportions (2M/F): WP:LP = 0.87/0.9, WP:WPB = 1.66/1.7, WP:WH = 1.05/1.05, WE:WP = 1.98/1.9. Short, cordiform, narrowing towards base (length: 0.67/0.7 mm; WP: 0.58/0.63 mm); sides faintly arcuate, maximum width in the anterior quarter, without any distinct puncture. Pronotal hind angles moderately acute; basal margin faintly bisinuate. **Elytra:** Proportions (2M/F): WE:LE = 0.56/0.56. Glabrous, oval, broadest almost at mid-length; shoulders rounded (length (2M/F): 2.07/2.13 mm; WE: 1.15/1.2 mm). Striation obsolete except for the internal striae, faintly impressed. **Legs:** Proportionally short, pubescent, tibiae straight. Male protarsomeres 1–2 dilated. **Male genitalia** (Fig. 14): Median lobe of aedeagus slightly curved in lateral view, apical lamella present; parameres with two to three setae. Inner sac without any strongly sclerotized copulatory piece. [All measurements were taken from three specimens (2 ♂♂, 1 ♀) from the type locality.]

Affinities. *Geotrechus seijasi* shares all the characters of the *G. ubachi* group: median lobe of aedeagus with rounded apex and maxillary palpus glabrous. Contrary to *G. ubachi* and *G. boumortensis* **sp.n.**, it is a “*Geotrechus*-like” species, stocky, with short mandibles, legs and antennae. It differs from the two following species by the shape of elytra, head and median lobe of aedeagus and the length of antennae.

Distribution and ecology. The two caves where *G. seijasi* occurs are close to each other and located on the northern slope of the Serra del Cadí, at its eastern extremity which is connected with the Serra del Moixeró. The type locality, Fou de Bor cave (Serrat de la Quera), is a huge subterranean system (more than 2 km length)

(CANALS et al. 1970) (Fig. 3). The species was found in the deepest part of the cave, walking on the humid clay. The second locality, the Forat de les Gralles is a 54 meters-vertical shaft compound of two successive pits with a large landing in between. *Geotrechus seijasi* was found at the bottom of the first pit walking around between stones and clay. The hypogean Leptodirini (Col., Leioididae, Cholevinae) *Ceretophyes cenarroi* (Español, 1955) occurs in the two caves.

All the other localities given in BELLÉS & DÉLIOT (1981) for *G. seijasi* referred to the two species of the “*G. delioli* group” described below.

3.1.4. *Geotrechus puigmalensis* Lagar, 1981

Figs. 10, 15

Geotrechus puigmalensis Lagar, 1981: 32

Type series. Holotype ♀ labelled: «Cova de les / Encantades / Querals / 10.8.1973 / F. Fadrique / leg. / SIE» [rectangular white label (ms Lagar)], «Holotipo» [rectangular red label (i)], «col. Lagar» [rectangular white label (i)], «*Geotrechus / puigmalensis / n. sp. / LAGAR det.*» (CFL).

Additional material and bibliographic data. Girona, Querals, Cova de les Encantades del Puigmal, Fadrique leg. (BELLÉS 1973 sub *G. seijasi*); 9.VIII.2004, Fadrique leg., 1 ♀ (MZB: 2004-1283) (PRIETO & AGULLÓ 2010); 2.XI.2006, Agulló, Fadrique & Prieto leg., 1 ♀ (MZB: 2006-0888) (PRIETO & AGULLÓ 2010); 2.XI.2006, Fadrique leg., 1 ♂ (MZB: 2006-0893) (PRIETO & AGULLÓ 2010); 4.X.2009, Fadrique & Faille leg., IBE-L222, 1 ♂ (MZB).

Type locality. «... cova de Les Encantades, a 2.100 m., Querals, Ripollès, ...» (LAGAR 1981). UTM (WGS 84): 31T 427171 4690534, 2240 m (Fig. 4).

Diagnosis. Anophthalmous and depigmented. **Size** (1 specimen): 3.73 mm (male). **Colour:** Yellowish brown. **Chaetotaxy:** Surface of elytra with a periscutellar seta, three setae on the disk, four humeral setae, four setae along lateral margin and two preapical setae. Marginal setae of pronotum present, the basal ones located before the hind angle. **Head:** Glabrous except some scarce setae, round, temples protruding; mandibles short (length (M): 0.77 mm; WH: 0.65 mm). Penultimate segment of maxillary palpus glabrous. Labrum right, slightly indented in its median part. **Antennae:** Proportionally long. Length (M): 2.38 mm; a few setae on the first antennomere, densely pubescent from the second antennomere. **Pronotum:** Proportions (M): WP:LP = 0.88, WP:WPB = 1.74, WP:WH = 0.94, WE:WP = 2.02. Short, narrowing towards base (length: 0.69 mm; WP: 0.61 mm); sides regularly arcuate, maximum width in the anterior quarter, without any distinct puncture. Pronotal hind angles moderately acute; basal margin right. **Elytra:** Proportions (M): WE:LE = 0.54. Glabrous, oval, broadest at posterior third; shoulders marked although rounded (length (M): 2.27 mm; WE: 1.23 mm). Striation obsolete except for the internal striae, faintly impressed. **Legs:** Proportionally short, pubescent, tibiae straight. Male protarsomeres 1–2 dilated.

Male genitalia (Fig. 15): Median lobe of aedeagus curved in lateral view, apical lamella present; parameres with three setae. Inner sac without any strongly sclerotized copulatory piece.

Affinities. This species is morphologically close to *G. seijasi*, differing from it by longer antennae and elytra shape which is less parallel and increasing in width until the last third of the length. It also differs by the shape of the median lobe of aedeagus, which is more curved (Figs. 14, 15).

Remarks. PRIETO & AGULLÓ (2010) described the male of *G. puigmalensis* with a specimen from the type locality (Cova de les Encantades del Puigmal) and included a figure of the genitalia, which however does not seem to agree with that of our specimen also from the type locality (Fig. 15). The shape of the genitalia figured by PRIETO & AGULLÓ (2010) (with the basal part straight and a recurved apex) is more similar to that of the western species *G. dequaei* Dupré, 1988 or *G. picanyoli* Español & Escolà, 1981. Unfortunately, the authors compared their *G. puigmalensis* to a specimen of *G. seijasi* from a cave (Cova de les Encantades de Toloriu) that is not the type locality of the species. It turns out that the species occurring in this cave is not *G. seijasi* but a new species (*G. incantatus* sp.n.), which is described below.

Distribution and ecology. La Cova de les Encantades del Puigmal is located on the southern slope of the Puigmal peak, basin of the Barranc de l'Estremera, tributary of the Freser river (Queralls, Girona) (Fig. 4). This cave is located at 2200 meters in a karstic area. It is one of the highest caves of Pyrenees known to host hypogean Invertebrates. PRIETO & AGULLÓ (2010) report a temperature of the cave of 7.4°C to 8.5°C but the annual mean temperature estimate is ca 3.8°C (D. Sánchez-Fernández personal communication). The hygrometry is close to saturation (PRIETO & AGULLÓ 2010). Two species of hypogean Leptodirini coexist with *G. puigmalensis*: *Parvospeonomus delarouzei* (Fairmaire, 1860) and *Perriniella bofilli* Zariquiey, 1924 (SALGADO et al. 2008), as well as the Cholevini *Choleva fagniezi brevistylis* Jeannel, 1923 (LAGAR 1981) (Col., Leiodidae, Cholevinae).

3.1.5. *Geotrechus victorai* Faille, Bourdeau, Bellés & Fresneda sp.n.

Figs. 11, 16

Type series. Holotype ♂ labelled: «La Nou de Berguedà / Berguedà (Cat) / 2.IX.2010» [rectangular white label (printed)], «Cova d'Espades / F. Fadrique» [rectangular white label (printed)], «DNA extraction code / ZSM-L304» [rectangular white label (printed)], «*Geotrechus / victorai* / Faille, Bourdeau, Belles & Fresneda n. sp. / HOLOTYPE» [rectangular red label (printed)] (MZB). – Paratypes: same locality than the holotype, 12.VIII.2010, Auroux leg., 1 ♂, ZSM-L302; same locality and data than the holotype, Comas & Fadrique leg., 1 ♀ (spare in 95° ethanol); same locality, 7.VIII.2013, Auroux, leg. 2 ♀♀; same locality, 24.IX.2010,

Auroux, leg., 1 ♂, 2 ♀♀; same locality, 1.VIII.2012, Meseguer & Auroux leg., 2 ♀♀ (ZSM-L1080 & ZSM-L1080bis); same locality, X.2013, Auroux leg., 1 ♀ (ZSM-L1079) (CAF, CCB, coll. J. Comas, CFL, CXB, MNHN, MZB, ZSM).

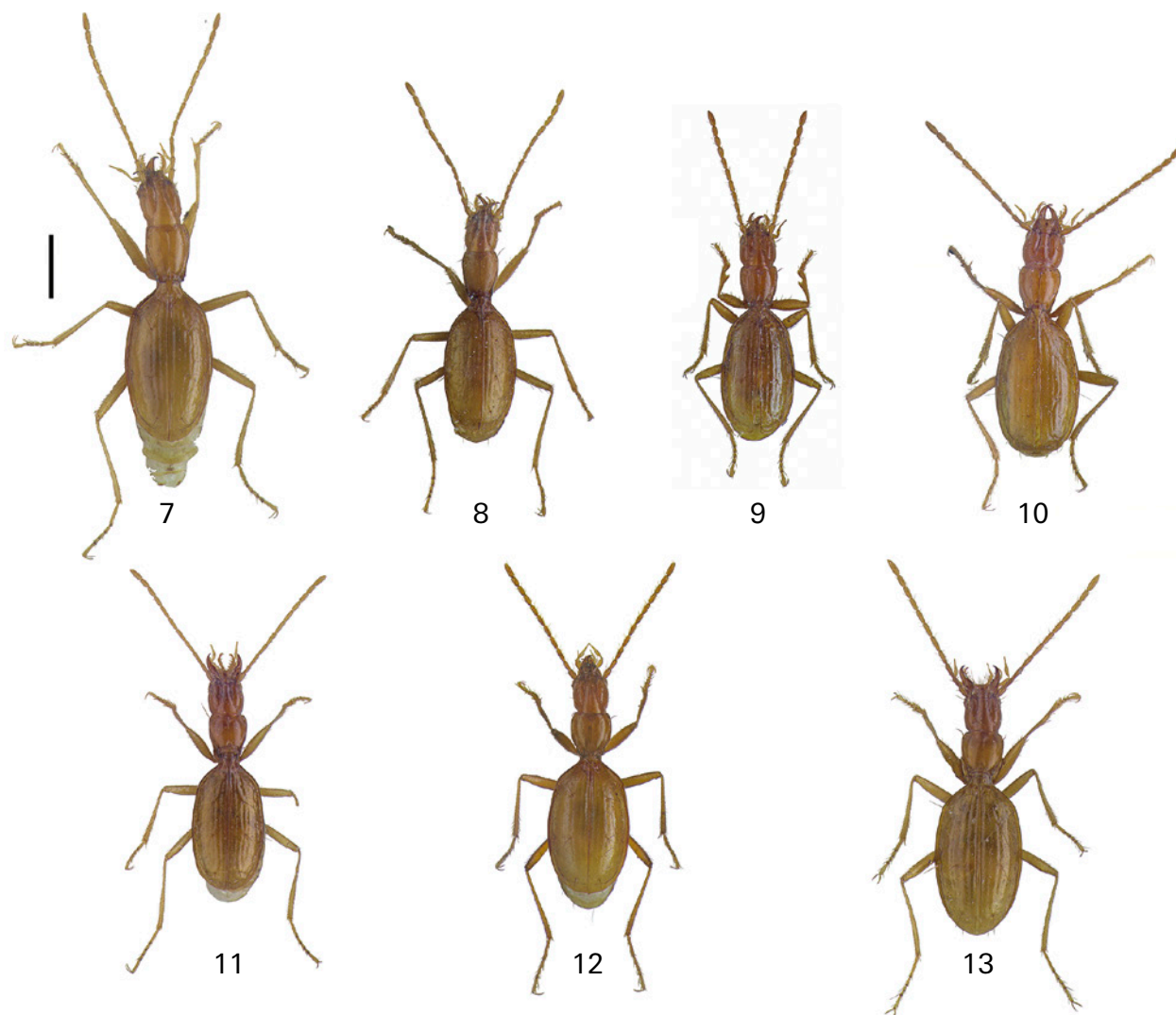
Type locality. Spain, Barcelona, La Nou de Berguedà, Cova d'Espades, UTM (WGS 84) 31T 409751 4669900, 1415 m (Fig. 5).

Diagnosis. Anophthalmous and depigmented. **Size** (2 specimens): 3.54 mm (HT♂), 3.39 mm (PT♂). **Colour:** Yellowish brown. **Chaetotaxy:** Surface of elytra with a periscutellar seta, three setae on the disk, four humeral setae, four setae along lateral margin and two preapical setae. Marginal setae of pronotum present, the basal ones located before the hind angle. Ventral pubescence limited to one seta on each half sternite. **Head:** Glabrous except some scarce setae, moderately elongate; (length (HTM/PTM): 0.71/0.71 mm; WH: 0.54/0.57 mm). Penultimate segment of maxillary palpus glabrous. Labrum slightly convex, indented in its median part. **Antennae:** Length (HTM/PTM): 2.25/2.18 mm; a few setae on the first antennomere, densely pubescent from the second antennomere. **Pronotum:** Proportions (HTM/PTM/Mean): WP:LP = 0.95/0.95/0.95, WP:WPB = 1.91/1.91/1.91, WP:WH = 1.13/1.07/1.1, WE:WP = 1.93/1.82/1.87. Regularly narrowing towards base (length (HTM/PTM): 0.64/0.64 mm; WP: 0.61/0.61 mm); sides faintly arcuate, maximum width in the anterior quarter, without any distinct puncture. Pronotal hind angles marked although not acute; basal margin slightly sinuate. **Elytra:** Proportions (HTM/PTM): WE:LE = 0.54/0.54. Glabrous, lateral margin bordered by a small gut all along the elytra, turned up; humeral angles faintly pronounced, blunt (length (HTM/PTM): 2.18/2.04 mm; WE: 1.18/1.11 mm). Striation obsolete except for the internal stria, faintly impressed. **Legs:** Proportionally short, pubescent, tibiae straight. Male protarsomeres 1–2 dilated. **Male genitalia** (Fig. 16): Median lobe of aedeagus short, slightly curved in lateral view, with basal bulb and apex rounded, apical lamella present; parameres with two setae. Inner sac without any strongly sclerotized copulatory piece.

Etymology. The new species is dedicated to Josep Manuel Victòria, speleologist of the Associació Catalana de Biospeleologia and SIE group of Speleology (Barcelona), in recognition of his important work of caving for more than 50 years.

Affinities. Morphologically, the species seems to be close to *G. seijasi*. Nevertheless the molecular results indicate that it is closer to *G. ubachi*. The species shares with *G. ubachi* the head with flat temples and the conformation of the lateral margin of the elytra, which is well developed and turned up.

Distribution and ecology. The species is only known from the type locality, the Cova d'Espades (La Nou de



Figs. 7–13. *Geotrechus* spp., habitus. **7:** *G. ubachi*, Avenc del Xato. **8:** Holotype of *G. boumortensis* sp.n., Avenc de Pla Fornesa. **9:** *G. seijasi*, Fou de Bor. **10:** Holotype of *G. puigmalensis*, Cova de les Encantades del Puigmal. **11:** *G. victorai* sp.n., Cova d'Espades. **12:** *G. deliotti* sp.n., Cortàs Mine. **13:** *G. incantatus* sp.n., Cova de les Encantades de Toloriu (scale bar: 1 mm).

Berguedà) (Fig. 5). The specimens were found walking on the clay and under stones in the deepest part of the cave; one specimen was sampled with a pitfall trap containing wine and salt (L. Auroux personal communication).

3.2. Group of *Geotrechus deliotti* sensu novo

A species group created in the present work for two species also well characterized by the shape of the pronotum with hind angles acute before the base, the median lobe of aedeagus short, with sharp apex (Fig. 19–23), the inner sac with a faintly sclerotized copulatory piece forming a conspicuous gut and the penultimate article of maxillary palpus with a few setae. The two species of the group were until now confused with *G. seijasi*.

3.2.1. *Geotrechus deliotti* Faille, Bourdeau, Bellés & Fresneda sp.n.

Figs. 12, 19–22

Type series. Holotype ♂ labelled: «Cerdagne (SP) / Isovol / 07.07.2004» [rectangular white label (printed)], «Mine inf de Cortàs / Deliot & Faille rec.» [rectangular white label (printed)], «M1» [rectangular white label (ms)], «*Geotrechus deliotti* sp.n. / Faille, Bourdeau, Bellés / & Fresneda det. 2015 / HOLOTYPE» [rectangular red label (printed)] (MZB). – Paratypes: Isòvol, Cortàs mines, 7.VII.2004, 8 ♂♂, 5 ♀♀, Déliot & Faille leg. (MZB, ZSM, MNHN, CAF); same locality, 17.X.2009, Bourdeau, Faille & Fresneda leg., 1 ♂ (ZSM-L228) (CAF); same locality, 17.V.2011, Bourdeau & Fresneda leg., 3 ♂♂, 3 ♀♀ (CFL); 17.IX.2011, Fresneda leg., 13 ♂♂, 8 ♀♀ (CFL, CXB); same locality, 24.IV.2014, Bourdeau & Faille leg., 1 ♂, 6 ♀♀ (CAF); same data, 1 ♂ (ZSM-L1000), 1 ♀ (spare in 95° ethanol) (ZSM); same locality, 13 ♂♂, 17 ♀♀, 10.XI.2001, 10.XI.2004, 18.X.2009, 17.V.2011, 14.IV.2012, 25.IV.2014, C. Bourdeau leg. (CCB).

Additional material and bibliographic data. Isòvol, Mines Superior i Inferior de Cortàs, 29.V.1980 & 1.I.1981, Déliot leg.

(BELLÉS & DÉLIOT 1981 sub *G. seijasi*). – Isòvol, Cova d'Olopte, 13.IV.1968, Castell leg., 1 ♂, (MZB 87-8436) (MZB) (BELLÉS 1973 sub *G. seijasi*; BELLÉS & DÉLIOT 1981 sub *G. seijasi*). Isòvol, Cova “B” d'Olopte, 3.V.1980, Déliot leg. (BELLÉS & DÉLIOT 1981 sub *G. seijasi*); same locality, 23.VIII.1992, Escoll & Fresneda leg., 1 ♀ (CFL); same locality, 1.V.1981, 1 ♂ (CCB). – Isòvol, Cova d'en Manent, Viñas & Ribera leg. (BELLÉS 1973 sub *G. seijasi*; BELLÉS 1978 sub *G. seijasi*; BELLÉS & DÉLIOT 1981 sub *G. seijasi*); same locality, 28.VIII.1966, Gonzalez & Viñas, F. Español leg., 1 ♂, 1 ♀ (Coll. Daffner in ZSM); same locality, 30.XII.1981 / 1.V.1981, 4 ♂, 2 ♀ (CCB); same locality, 7.VII.2004 (MNHN-AF89), Déliot & Faille leg. (CAF). – Lleida, Prullans, Cova d'Anes, Viñas, González, Lagar, Bertrán, Comas & Bellés leg. (BELLÉS 1973 sub *G. seijasi*; BELLÉS 1978 sub *G. seijasi*; BELLÉS & DÉLIOT 1981 sub *G. seijasi*); 1/2.XI.1969, Lagar leg., 1 ♂, 4 ♀♀ (CFL); same data, X. Bellés leg., 1 ♂, 1 ♀ (CXB); same locality, VI.1970, I. Gonzalez, 1 ♂ (MZB 87-8434) (MZB); same locality, VII.1967, Viñas, 1 ♂, MZB 87-6723 (MZB); same locality, 23.XII.1981 / 2.V.1981, 3 ♂, 1 ♀ (CCB); same locality, 7.VII.2004, Déliot & Faille, 1 ♀ (CAF).

Type locality. Girona, Isòvol, Mines de Cortàs, UTM (WGS 84): 31T 401088 4693767, 1226 m.

Diagnosis. Anophthalmous and depigmented. **Size** (HT/5M/5F): 3.88/3.78/3.94 mm. **Colour:** Yellowish brown. **Chaetotaxy:** Surface of elytra with a periscutellar seta, three setae on the disk, four humeral setae, four setae along lateral margin and two preapical setae. In some specimens very short and sparse setae are present on the elytra. Marginal setae of pronotum present, the basal ones located before the hind angle. Ventral pubescence limited to one seta on each half sternite. **Head:** Glabrous except some scarce setae, round with prominent temples; (length (HT/5M/5F): 0.88/0.79/0.87 mm; WH: 0.6/0.59/0.6 mm). Penultimate segment of maxillary palpus short, dilated at the apex, with a few setae. Labrum regular, slightly convex, without indentation in its median part. **Antennae:** Length (HT/5M/5F): 2.24/2.22/2.14 mm; a few setae on the first antennomere, densely pubescent from the second antennomere. **Pronotum:** Proportions (HT/5M/5F): WP:LP = 0.89/0.91/0.93, WP:WPB = 1.6/1.64/1.63, WP:WH = 1.07/1.08/1.08, WE:WP = 2,13/2.03/2.05. Cordiform, slightly constricted and narrowing towards base (length (HT/5M/5F): 0.72/0.7/0.7 mm; WP: 0.64/0.64/0.65 mm); sides faintly arcuate, maximum width in the anterior quarter, without any distinct puncture. Pronotal hind angles acute, dentate before the basal margin, in some specimens forming a sharp tooth; basal margin slightly sinuate. Fore angles well-marked, protruding. **Elytra:** Proportions (HT/5M/5F): WE:LE = 0,6/0.57/0.56. Glabrous, smooth, without striae, lateral margin slightly bordered; maximum width in the middle. Humeral angles pronounced, blunt (length (HT/5M/5F): 2.28/2.29/2.36 mm; WE: 1.36/1.3/1.33 mm. **Legs:** Proportionally short, pubescent, tibiae straight. Male protarsomeres 1–2 dilated. **Male genitalia** (Figs. 19–22): Median lobe of aedeagus short, strongly curved in lateral view, with basal bulb stocky and rounded, and sharp apex. Apical lamella present; parameres thick with four setae. Inner sac with a faintly sclerotized copulatory piece forming a sharp gut. **Variability:** The anterior angles of the pronotum are

more or less protruding depending on the specimen. Very short setae are present on the elytra of some populations (Manent, Anes, Olopte). Some differences are also observed on the median lobe of aedeagus (Figs. 19–22). Further detailed investigations of the different populations of *G. deliotti* would be required to evaluate the potential structuration between them.

Etymology. The new species is dedicated to our late friend Philippe Déliot who studied in detail this area of the Pyrenees, and discovered the population of Cortàs.

Affinities. *Geotrechus deliotti* sp.n. and the species described below, *G. incantatus* sp.n. are closely related, and share unique characters like the penultimate maxillary palpus pubescent, the very peculiar conformation of the hind angles of the pronotum or the shape of the median lobe of aedeagus. This clade is the sister group of the previously treated *G. ubachi* species group (Fig. 25). *G. deliotti* sp.n. differs from *G. incantatus* sp.n. by the shape of the median lobe of the aedeagus, the pronotum, the outline of elytra and the length of the antennae.

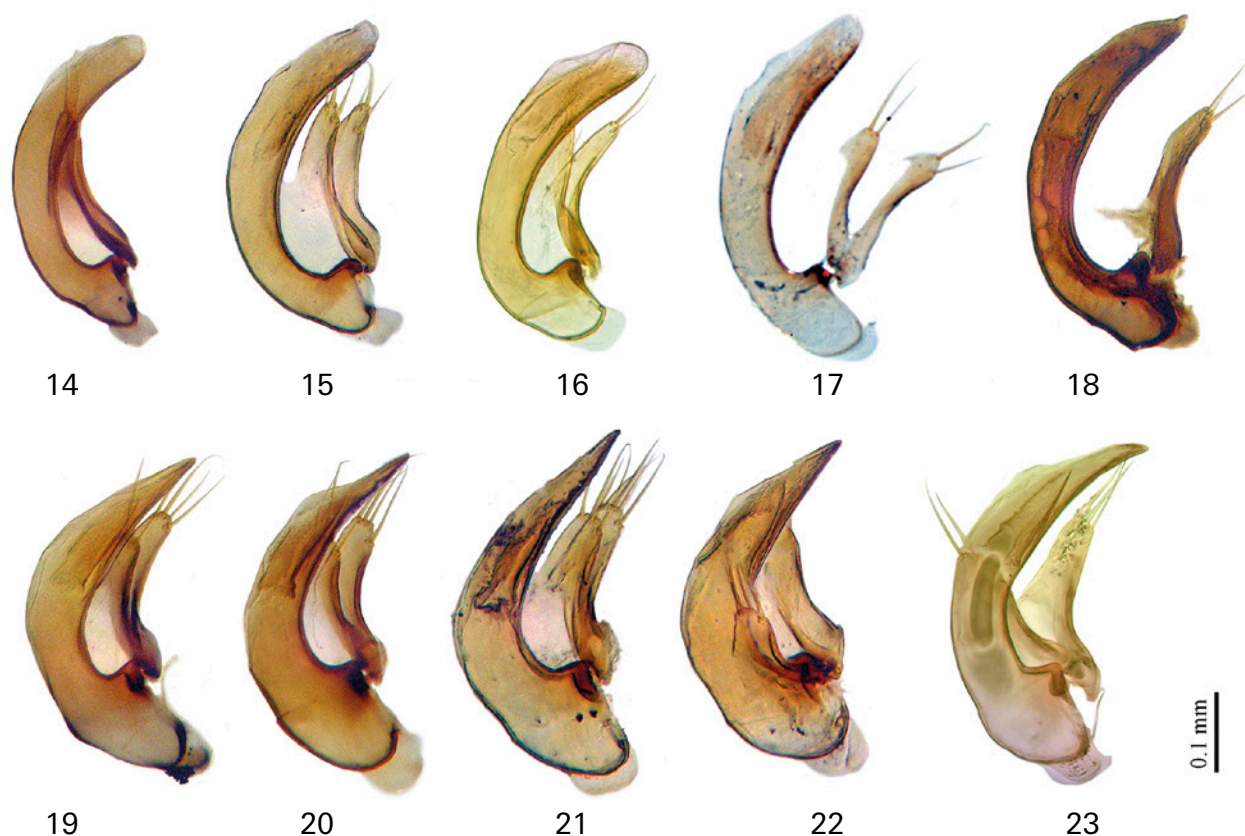
Distribution and ecology. All the caves where *Geotrechus deliotti* sp.n. occurs are located in the drainage basin of the Riu Duran, a right-edged tributary of the Segre River, on the Tossal d'Isòvol (Cova d'en Manent) and the Mont Cortàs (Cortàs mines and Coves d'Olopte). Cortàs mines are old manganese mines, and, strikingly, it is in one of these artificial cavities that the species is most common. The other caves are small, with high humidity and quite constant temperature all along the year. *G. deliotti* sp.n. coexists with the Leptodirini (Col., Leiodidae, Cholevinae) *Ceretophyes riberaei* (Español, 1967) in Olopte caves and Manent cave, whereas this species is lacking in Cortàs mines. The Anes cave is located at 1300 m on the right edge of Segre River, in the upper part of Torrent d'Anes, a tributary of Segre River, close to Prullans. The cave consists of a single 335 meters-long meander, very humid, with numerous lithogenic formations. Despite the vicinity of Isòvol, there are no Leptodirini in this cave.

3.2.2. *Geotrechus incantatus* Faille, Bourdeau, Bellés & Fresneda sp.n.

Figs. 13, 23

Type series. Holotype ♂ labelled: «Toloriu / 17.X.2009» [rectangular white label (printed)], «Cova des Encantades / C.B., J. & M. F. A.F.» [rectangular white label (printed)], «DNA extraction code / ZSM-L227bis» [rectangular white label (ms)], «*Geotrechus incantatus* sp.n. / Faille, Bourdeau, Bellés / & Fresneda det. 2015 / HOLOTYPE» [rectangular red label (printed)]. – Paratypes: Lleida, Toloriu, Cova de les Encantades, VIII.1969, Viñas leg., 1 ♂ (MZB 85-2907) (aedeagus lacking) (MZB); same locality, 17.X.2009, Bourdeau, Fresneda, Escoll & Faille leg., 1 ♂ (ZSM-L227); same locality, 14.IV.1981 / 2.V.1981 / 17.X.2009, 8 ♂, 4 ♀, C. Bourdeau leg. (CCB).

Additional material and bibliographic data. Lleida, Toloriu, Cova de les Encantades, Castell & Viñas leg. (BELLÉS 1973, 1978



Figs. 14–23. *Geotrechus* spp., aedeagus in lateral view. 14: *G. seijasi*. 15: *G. puigmalensis*. 16: *G. victoraii* sp.n. 17: *G. ubachi*. 18: Holotype of *G. boumortensis* sp.n. 19: *G. deliotti* sp.n., Cova d'Anes. 20: *G. deliotti* sp.n., Cortas Mine. 21: *G. deliotti* sp.n., Cova d'En Manent. 22: *G. deliotti* sp.n., Cova d'Olopte. 23: *G. incantatus* sp.n. (scale bar: 1 mm).

sub *G. seijasi*; BELLÉS & DÉLIOT 1981 sub *G. seijasi*; PRIETO & AGULLÓ 2010 sub *G. seijasi*; same locality, 17.X.2009, Bourdeau, Escoll, Fresneda & Faille leg., old trap, rests of 24 ex. (CAF); Toloriu, Avenc de la Cabana d'en Garraba, 22.XII.1974, Fadrique leg., 1 specimen and remains (elytra) of a second specimen (CFL).

Type locality. Lleida, Toloriu, Cova de les Encantades (= Cova d'en Vinyoles, Cova de Coll de Ser), UTM (WGS 84): 31T 385614 4689403, 1551 m (Fig. 6).

Diagnosis. Anophthalmous and depigmented. **Size** (HT/3M): 3.96/3.88 mm. **Colour:** Yellowish brown. **Chaetotaxy:** Surface of elytra with a periscutellar seta, three setae on the disk, four humeral setae, four setae along lateral margin and two preapical setae. Marginal setae of pronotum present, the basal ones located before the hind angle. Ventral pubescence limited to one seta on each half sternite. **Head:** Glabrous except some scarce setae, round with prominent temples; (length (HT/3M): 0.76/0.76 mm; WH: 0.58/0.58 mm). Penultimate segment of maxillary palpus short, dilated at the apex, with a few setae. Labrum regular, slightly convex, without indentation in its median part. **Antennae:** Length (HT/3M): 2.49/2.46 mm; a few setae on the first antennomere, densely pubescent from the second antennomere. **Pronotum:** Proportions (HT/3M): WP:LP = 0.94/0.94, WP:WPB = 1.67/1.67, WP:WH = 1.16/1.16, WE:WP =

2.06/1.98. Short, regularly curved and narrowing towards base (length (HT/3M): 0.71/0.71 mm; WP: 0.67/0.67 mm); sides gradually arcuate, maximum width in the anterior quarter, without any distinct puncture. Pronotal hind angles faintly acute before the basal margin, never forming a sharp tooth; basal margin slightly sinuate. Fore angles blunt, never protruding. **Elytra:** Proportions (HT/3M): WE:LE = 0.55/0.55. Glabrous, oval, smooth, without distinct striae, maximum width after the middle; lateral margin slightly bordered. Humeral angles blunt (length (HT/3M): 2.49/2.42 mm; WE: 1.38/1.33 mm). **Legs:** Proportionally short, pubescent, tibiae straight. Male protarsomeres 1–2 dilated. **Male genitalia** (Fig. 23): Median lobe of aedeagus long, regularly curved in lateral view, with basal bulb stocky and rounded, and sharp apex turned-in at its extremity. Apical lamella present; parameres thick with two to three setae. Inner sac with a faintly sclerotized copulatory piece forming a sharp bevelled gut.

Etymology. The specific epithet refers to the type locality, the Cova de les Encantades.

Affinities. The new species is geographically and morphologically close to *G. deliotti* sp.n., mainly differing by the shape of the median lobe of the aedeagus and the pronotum.

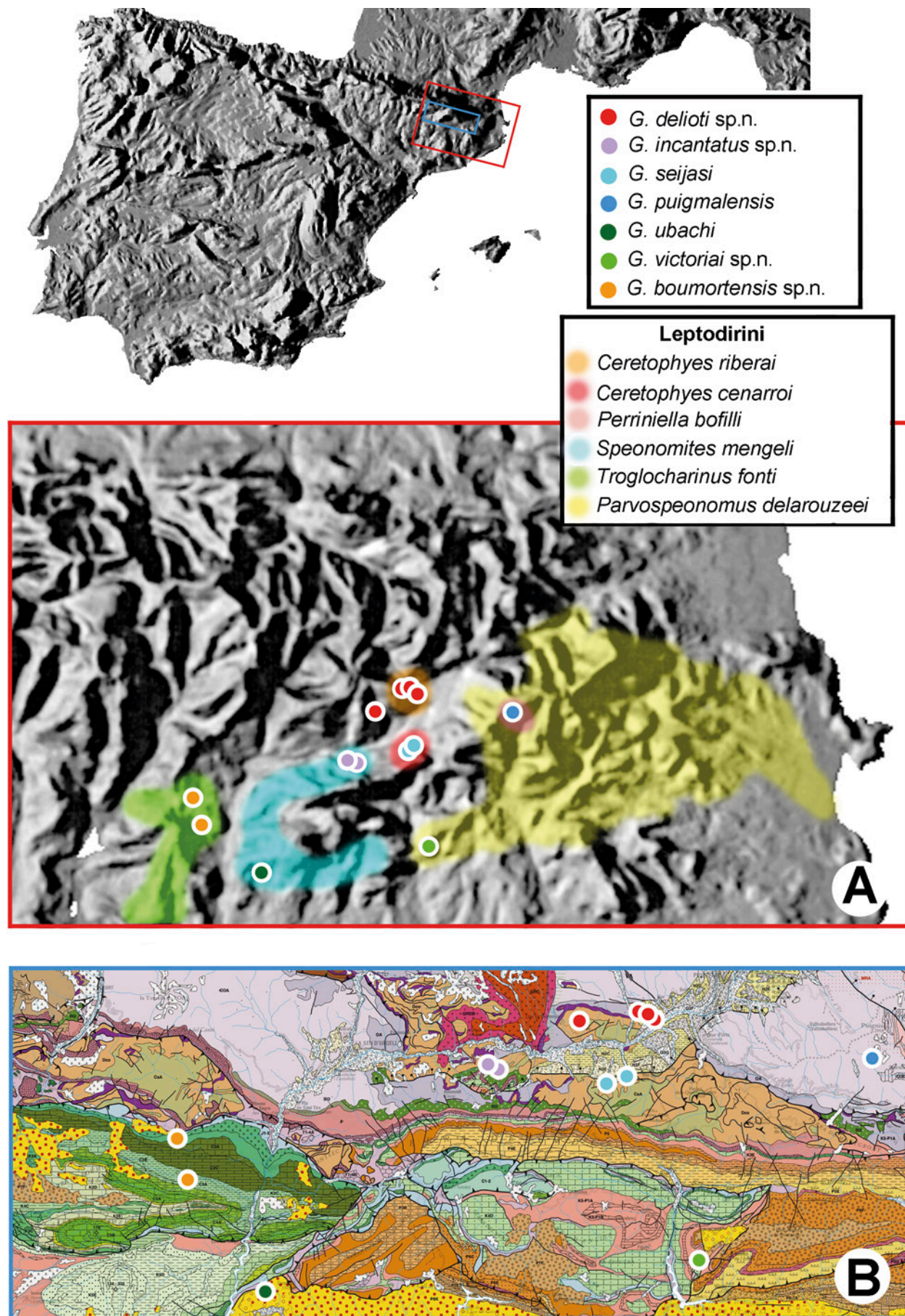


Fig. 24. Map of Pyrenees showing the distribution of the 6 *Geotrechus* species compared to the distribution of Leptodirini (A) and the geological structure of the area (B).

Distribution and ecology. The Cova de les Encantades is located south-west of Toloriu, north-east of the Coll de Ser, Serra de Cava, northern foothills of Serra del Cadí (Fig. 6). The cave is 228 meters long; the ground is covered with stones and very humid clay where the specimens were found walking around. Cova de les Encantades is the type locality of the Leptodirini (Col., Leiodidae, Cholevinae) *Speonomites mengeli* (Jeannel, 1910). Avenc de la Cabana d'en Garraba (425 m in length, 62 m deep) is located East of Toloriu, close to the village, in the Torrent de la Barguja. It is an active pit, with a stream flowing inside. *S. mengeli* also occurs in this cave.

4. Phylogenetic results and discussion

4.1. Molecular phylogeny of the species of the *G. ubachi* and *G. delioli* groups

The molecular phylogeny (Fig. 25) is in accordance with the morphology regarding the separation of the species and supports the two species groups “*G. ubachi*” and “*G. delioli*” recognized on the basis of the synapomorphies listed above (shape of pronotum and aedeagus, pubescence of maxillary palpus).

Although unambiguously unrelated to the type species of the genus, *Geotrechus discontignyi* (Fairmaire, 1863), we choose to temporarily let the Spanish eastern species in the polyphyletic genus *Geotrechus* Jeannel, 1919. A revision of the systematics of the Pyrenean lineage (Faille et al. in preparation) will probably lead to the reorganization of the present genera into monophyletic units.

The molecular phylogeny strongly supports the two clades corresponding to the two groups *G. ubachi* and *G. delioli*, which are unambiguously sister clades.

The *G. ubachi* clade is composed of four species. *Geotrechus seijasi* is sister to a clade grouping *G. puigmalensis*, *G. ubachi* and *G. victoraii* **sp.n.** Surprisingly, the most morphologically derived *G. ubachi* is sister of *G. victoraii* **sp.n.** (divergence at Plio-Pleistocene) both isolated on the southern slopes of the Serres de Cadí-Moixeró.

The *G. delioli* clade, composed of *G. delioli* **sp.n.** and *G. incantatus* **sp.n.**, is also well supported (Fig. 25, green clade) and some differences between the two populations of *G. delioli* are evidenced. Further studies on this species including other localities would be needed to test if the populations are genetically structured.

4.2. Biogeography and modality of speciation of the group

According to the temporal reconstruction of the diversification of the lineage obtained with the rates used in

previous study on Trechini (Faille et al. 2014), the separation of the two clades *G. ubachi* and *G. delioli* has to be dated at ca. 16±5 MY, in the late Miocene (Fig. 25). The values obtained for the other Pyrenean cave Trechini are in accordance with the date estimates reported in previous studies (Faille et al. 2011a, 2013b).

Present day distribution (Fig. 24) and timing of divergence events (Fig. 25) argue for allopatric mode of speciation, a pattern classically observed for subterranean fauna: geographical isolation of the species south of the Segre River, crossed ones by one species, *G. delioli*.

The *G. ubachi* and *G. delioli* species groups are widely distributed in the southeastern Pyrenean mountains (Fig. 24). The western limit of the clade is the Serra de Boumort (La Guàrdia d'Ares and Cabó, *G. boumortensis* **sp.n.**), isolated by the Noguera Pallaresa valley. The eastern limit is the Riu Freser valley, southern slope of the Puigmal massif. The southernmost localities are located in the Serra dels Obacs (surroundings of Llinars), Odén (Avenc del Xato, *G. ubachi*) and in the Serra de Catllaràs, in the vicinity of La Nou de Berguedà, left side of the Llobregat River (*G. victoraii* **sp.n.**). In the north, the group reaches the right side of the Segre River, a narrow area between Prullans and Isòvol (*G. delioli* **sp.n.**) and a small massif on the Northern slope of Serra del Cadí (*G. incantatus* **sp.n.**) (Fig. 24).

Here we present a tentative explanation for the diversification of the group, although the wide confidence interval for the dating of the splits (Fig. 25) and the lack of *G. boumortensis* in the molecular analyse does not allow to unambiguously discard alternative scenarios. The *G. ubachi* + *G. delioli* clade might have appeared at the end of Oligocene or in Early Miocene, ca 20–30 My (dating of geological periods according to the International Stratigraphic Chart, 2012) and might have split during the Miocene (Fig. 26). The two species of the *G. delioli* subclade might have been isolated by the Segre River during Miocene, at end of the Messinian (ca 5 My). The diversification of the *G. ubachi* subclade might have occurred between the Tortonian-Messinian (ca 7 My) and the Pleistocene. The formation of the Segre valley led to the isolation of the two subclades (Fig. 26). The digging of this valley started at the end of Burdigalian (15.97 My), following the E/W syncline collapsed at the foot of the Serra de Cadí. The two groups *G. ubachi* and *G. delioli* were separated by a valley of deep gorges and lakes, under a wet tropical climate, with progressively drier periods. The deepest sediments of these lake basins (Cerdanya, Bellver and Seu d'Urgell) are dated from Vindobonien (AGUSTI & ROCA 1987), from Langhian (ca 16 My) to early Tortonian (11.6 My).

The *G. ubachi* subclade might have dispersed on the massifs south of Segre and Puigmal; the split between *G. ubachi* and *G. victoraii* **sp.n.** occurred late and might be related to the glacial episodes which let moraines in La Nou de Berguedà surroundings.

If further investigations confirm the phylogenetic affinities between *G. ubachi* and *G. boumortensis* **sp.n.** suggested by the external morphology, we could hypothesize

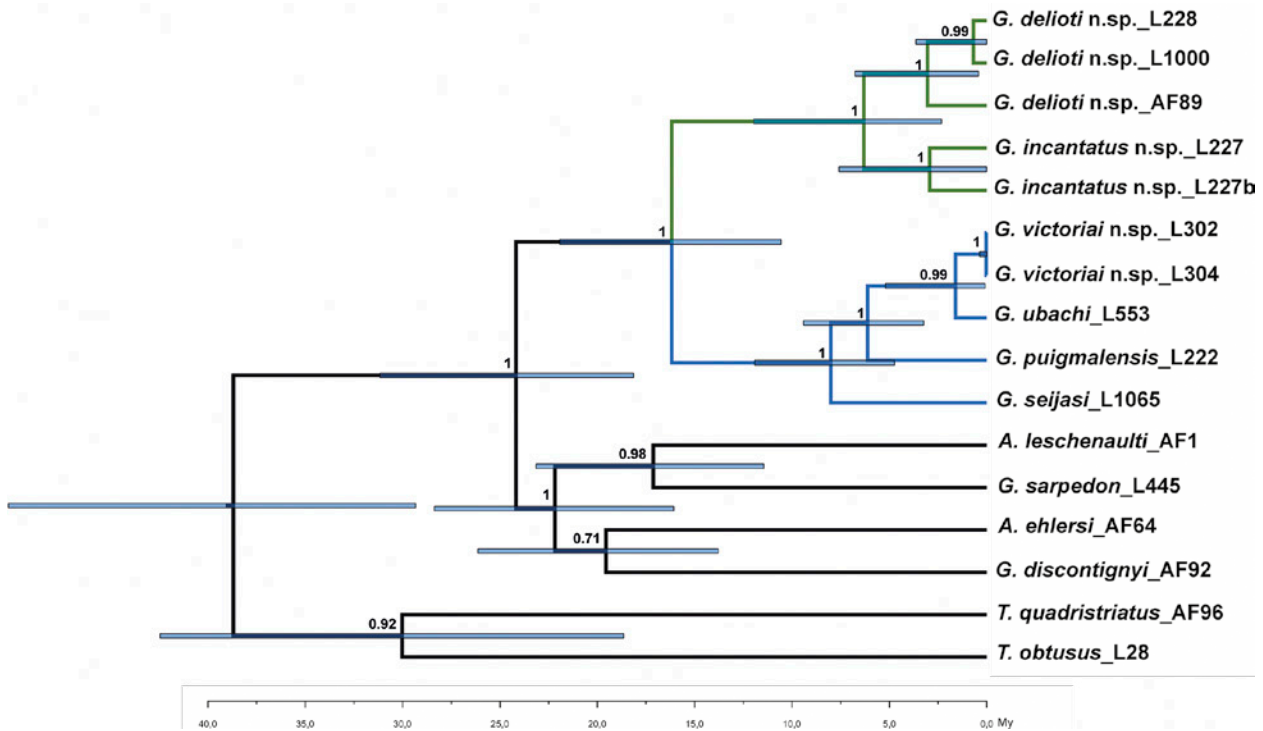


Fig. 25. Ultrametric time-calibrated tree obtained with *beast* for the combined dataset. Blue bars, 95% confidence intervals of the estimated ages for the node. Blue: *G. ubachi* group, green: *G. deliotti* group. Above nodes, posterior probabilities values when superior to 0.7. See Table 1 for locality data of the specimens.

a recent Pleistocene split during one of the glacial cycles which let imprints of the Andorran glacier until the Seu d'Urgell lake; Valira flooded in numerous streams crossing over the alluvial sediments (TURU et al. 2007) forming a large area of scree similar to MSS (Milieu Souterrain Superficiel, JUBERTHIE et al. 1980; ORTUÑO et al. 2013), an environment which nowadays is favorable for dispersal of hypogean fauna. Such ecological conditions could have allowed the crossing of the valley in the same conditions than what occurred for gave de Pau (Peyrouse, France) and gave d'Ossau (Rébénacq, France), at the level of moraine fronts, for the species *Geotrechus gallicus* (Delarouzeé, 1857) and *Aphaenops (Hydraphaenops) pandellei* (Linder, 1859) (JEANNEL 1948).

The allopatric isolation of *G. incantatus* **sp.n.** (Toloriu) is easier to explain; there is no discordance between the geological layers of the two sides of the Segre River; the presence of a long thrust fault together with alluvial sediments southern of this area indicate a change of the course of the Segre leading to the isolation of this population. This split is dated from the Messinian (ca 5 My) (Fig. 25).

Because of the wide confidence intervals, alternative scenarios like a simultaneous splitting into four clades might be considered. In case of a scenario of simultaneous splitting, we would expect to obtain a comb between these four clades. However, the topology clearly supports (with posterior probabilities of 1) two species groups (as well as the subsequent subdivisions of these clades), which are difficult to explain if the splits were simultaneous. The

two species group *G. deliotti* and *G. ubachi* are also morphologically very well characterized, strengthening the hypothesis of a previous split into two subclades and a single crossing of the Segre valley. Finally, the role of rivers as strong barriers to dispersal for Pyrenean cave beetles was recently acknowledged for another Trechini of the genus *Aphaenops* (FAILLE et al. 2015).

Molecular results recently obtained on the second most speciose radiation of Pyrenean cave beetles, the Leptodirini (Leiodidae, Cholevinae), suggest a similar evolution of the group in this area, especially in Cerdanya (RIBERA et al. 2010). Leptodirini and Trechini are often sympatric in the Pyrenean karstic areas. The comparison of the molecular chronology of the species of the *G. ubachi* subclade and the Leptodirini occurring in the same area suggest that the same geological history equally impacted the two groups, as the speciation events are synchronous in both of them. During Langhian, the digging of the Segre valley isolated on the right edge the species *Geotrechus deliotti* **sp.n.** & *Ceretophyes riberai* (Español, 1967) from the species *Geotrechus seijasii* & *Ceretophyes cenarroii* (Español, 1955) (restricted to Bellver area, on the left edge). On the other hand the Serra del Obacs massif is characterized by the pair *Geotrechus ubachi* & *Speonomites mengeli* (Jeannel, 1910).

Geotrechus incantatus **sp.n.** belongs to the *G. deliotti* subclade but coexists with *Speonomites mengeli* on the restricted area of Toloriu, where they were already present before the modification of the course of the Segre River during the Messinian.

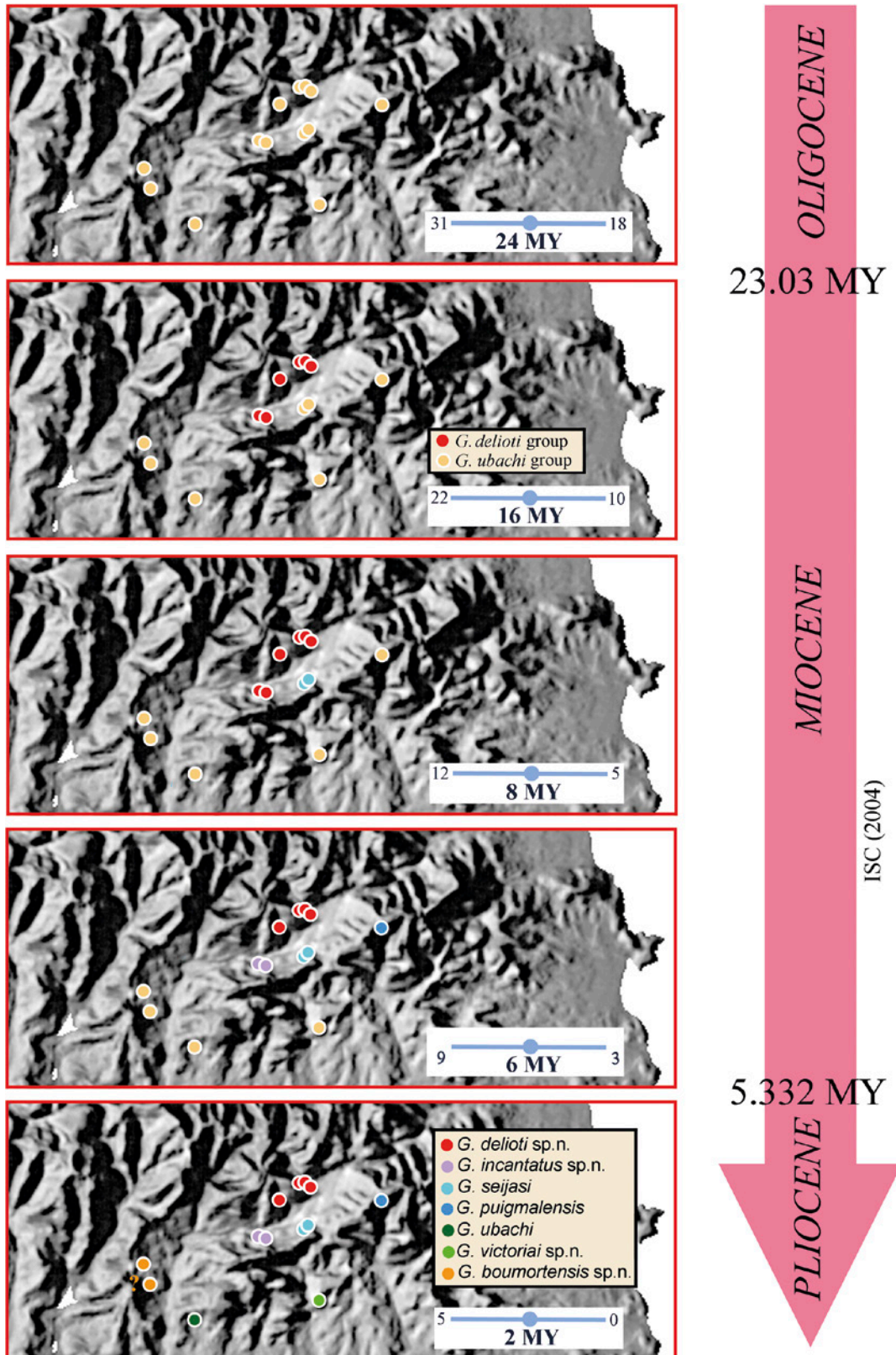


Fig. 26. A scenario of allopatric speciation of the present day *Geotrechus* species during geological times. Blue bars, 95% confidence intervals of the estimated ages for the nodes of Fig. 25.

Geotrechus puigmalensis, which belongs to the *G. ubachi* subclade, coexists with *Perriniella bofilli* Zariquiey, 1924, which is close to the genus *Ceretophyes*.

On the Serra de Boumort, *G. boumortensis* sp.n. co-occurs with *Troglocharinus fonti* (Jeannel, 1910). *Troglocharinus* is a genus with a western origin much more

recent (ca 12 My) than *Ceretophyes* and *Perriniella*, confirming the role of the Segre River as a strong barrier to dispersal of eastern Leptodirini as well as for the Trechini of the *G. ubachi* subclade with an eastern origin posterior to 15 My.

Geotrechus victoriai **sp.n.** is sympatric to the Leptodirini *Parvospeonomus delarouzei* (Fairmaire, 1860), a species with a very old south-eastern origin (Oligocene), reaching here its western limit.

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