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Update of the knowledge of the Ibero-Balearic hypogean Carabidae (Coleoptera): Faunistics, biology and distribution

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Abstract: The Iberian Peninsula, because of its special location in southern Europe and its abundance and diversity of karst, has a large number of hypogean arthropods, among which, there is a notable presence of Carabidae. Often, new discoveries of exclusive subterranean taxa are added, which are listed in the very briefly discussed catalogues of the Ibero-Balearic fauna. This procedure, which is correct with regard to general catalogues of Carabidae, seems to be insufficient for the hypogean species. The present work updates all faunistic, biological, and chorological information available on the Ibero-Balearic hypogean Carabidae. Finally, according to the distribution of the lineages of the most representative of them, a regionalization of the Iberian Peninsula in biospeleologic districts is proposed.

Zusammenfassung: Aktualisierung des Kenntnisstandes der Ibero-Balearischen hypogäischen Carabidae (Coleoptera): Faunistik, Biologie and Verbreitung. – Aufgrund ihrer besonderen Lage in Südeuropa und der Häufigkeit von Karstgebieten besitzt die Iberische Halbinsel eine große Zahl von hypogäischen Arthropoden, unter denen die Carabidae besonders hervorzuheben sind. Häufig werden Neuentdeckungen exklusiv-subterraner Taxa hinzugefügt, welche in den Katalogen der Ibero-Balearischen Fauna aufgelistet werden, in denen nur sehr wenig Raum für Diskussionen besteht. Diese Verfahrensweise ist im Rahmen von Katalogwerken der Laufkäfer zwar notwendig, erscheint aber hinsichtlich der hypogäischen Arten ungenügend. Diese Arbeit stellt den aktuell verfügbaren Kenntnisstand über Faunistik, Biologie und Chorologie der Ibero-Balearischen hypogäischen Laufkäfer zusammen. Auf der Grundlage der Verbreitung der repräsentativsten Entwicklungslinien der hypogäischen Carabidae wird abschließend eine regionale Gliederung der Iberischen Halbinsel in biospeleologische Bezirke vorgeschlagen.

Key words: Hypogean Carabidae, Iberian Peninsula, faunistics, biology, biogeography.

Introduction

The Iberian Peninsula is a strategic biogeographical region of Europe that, for millions of years, has been a "melting pot" of insect faunae of Eurasian, North African, and Mediterranean origins, and has fostered the emergence of numerous endemic species (ORTUÑO 2002). Much of this endemicity is closely linked to subterranean environments, that favour the geographical isolation of populations and, therefore, their speciation by genetic drift. In this regard, there is a remarkable contribution of subterranean fauna, which is up to 15% of the total diversity of ground beetles of the Iberian Peninsula (1158 species, see SERRANO 2003), a percentage of which represents approximately 37% of the Iberian endemic species of this group of beetles (468 endemic species, see JIMÉNEZ-VALVERDE & ORTUÑO 2007).

But what is meant by subterranean fauna? The number of authors who are removing the word "cavernicolous" from their vocabulary is constantly increasing, because it does not fit the biological reality of the wildlife that inhabits the subterranean hollows. Instead, the most correct word seems to be "hypogean." And yet, without having answered the previous question, we must ask another: What is a hypogean being? The nomenclatural problem we face is that some researchers, employ as synonyms the words "subterranean" and "hypogean" (JUBERTHIE 1983, JUBERTHIE & DECU 1994, GALÁN 2004, SKET 2008, TASAKI 2008, among others), arguing that those two terms define the same biological reality. After many years of subterranean research and, in general, studying the Iberian ground beetle fauna, we disagree with these authors. We consider as subterranean those members of the fauna that develop their full lifecycle underground, regardless of the size of the void or hollow, and regardless of its position in any level or soil horizon. This is true in three layers at different depths and geostructural features, which might not always be present simultaneously in one place. But, if they coincide in the same place, we must also consider the contact or transition areas between these levels. We refer to 1) the caves (Deep Subterranean Environment, or MSP sensu JUBERTHIE 1983) and the network of cracks radiating from them, 2) the interstices called Mesovoid Shallow Substratum (short: MSS) generated by the disintegration of the bedrock, forming a C1 horizon, or by the accumulation of rock fragments (colluvium and alluvium), or of volcanic soils by the erosion of volcanic debris; and finally 3) the soil micro-spaces on the B horizon (low in organic fraction) and in deep areas of the A horizon (more rich in organic fraction). The first two levels that have been cited harbour the hypogean fauna, classically defined as subterranean fauna, while the latter is closely related to the deep areas of the soil environment, and shelters the endogeous fauna. This latter type of fauna is not considered by some authors as subterranean fauna, despite the fact that they develop all their life underground, and share physiological and morphological features with the cave faunas: anophthalmia, depigmentation, and winglessness (CASALE et al. 1998). However, the relationship between endogeous (soil in general) and hypogean environments is very narrow, as evidenced by the frequent presence of epiedaphic or endogeous taxa in the MSS (JUBERTHIE 1983, CASALE et al. 1998, GERS 1998, GALÁN 2001, ORTUÑO & SENDRA 2010). In fact, there are taxa of clear endogenous lineages, as the Anillini, which have jumped from an edaphic level to the MSS, developing hypogean characteristics (ORTUÑO & SENDRA, 2007): elongation of appendages, increase in size, and filiform antennae. Our position on this issue leads us to accept as members of the subterranean fauna both strictly hypogean and endogeous organisms.

On the other hand, hypogean fauna can be classified according to the degree of its association with it. SKET (2008) summarizes the criteria that historically have been taken, and offers a nomenclatural proposal consistent with the current use of these terms and their orthodoxy. Note that this criterion of classification is based primarily on the ecology of the fauna associated with these environments, but not with their degree of morphological adaptation. In this work, we adopt this criterion, and we carry out a revision of the genera and species of troglobiont hypogean Carabidae of the Iberian Peninsula and Balearic Islands, leaving aside the endogeous taxa.

This work of synthesis finds its justification in the following facts: In the first place, the study of hypogean fauna has an important biogeographical and historic value, as it reveals the knowledge of the evolutionary and geological processes that led to the establishment of the fauna in that environment. According to this, the importance of the subterranean environment as a refuge for climatic changes, and as a habitat for relict fauna, can be cited (Jeannel 1926, 1943, Bellés 1987). In the second place, although there are several catalogues of Carabidae of the palaeartic region and the Iberian Peninsula (Löbl & Smetana 2003, Serrano 2003, among others), the new discoveries make an almost constant revision of the general knowledge of this group necessary, as there is not an actualized catalogue of the hypogean Ibero-Balearic Carabidae. Finally, there are other works that have proposed a regionalization of the Iberian Peninsula into biospeleological districts (Español 1969, Zaragoza 1986, Bellés 1987, Galán 1993, Sendra 2003, among others) but none based only on Carabidae, and therefore it is necessary to delimit those regions for this group, in order to establish a precise comparison with the other district proposals. In summary, the importance of the study of this fauna, the increase in the new discoveries, and the lack of a complete synthesis justify a revision of the biology and chorology of this fauna.

Material and Methods

The data here are handled from multiple literature sources, but has been used as basic texts the Palaearctic catalogue (Löbl & Smetana 2003) with appropriate updates (addenda and amendments). The 10 x10 km UTM coordinates relating to the localities of each species were obtained, in some cases (latest articles) from the original publication, but in most cases have been sought through the use of tools such as Google Earth and Digital Cartography of Spain 2.0. The maps have been generated with the MapInfo Professional 7.0 program. Eutroglophile species with hypogean populations were excluded for the regionalization, but not for the faunistic aspects, and therefore this study only refers to the troglobiont species (sensu Sket 2008) that have been found in caves or in the MSS. The same criterion was followed for some species cited in the hypogean environment, which are with all probability endogeous species that have occasionally appeared there. Such is the case of the genera *Microtyphlus* Linder, 1863, *Hypotyphlus* Jeannel, 1937, and *Reicheia* Saulcy, 1862. The citation of *Duvalius lencinai* Mateu & Ortuño, 2006 in the southeast of the Peninsula has also been omitted, as its morphology and distribution suggest that this species could belong to the genus *Trechus* Clairville, 1806.

Results and discussion

Faunistics

The hypogean Ibero-Balearic Carabidae are grouped in four subfamilies: Promecognathinae, Scaritinae, Trechinae and Harpalinae (Table 1). One of the most surprising biospeleological discoveries was the one of a carabid beetle of remarkable dimensions (10–13 mm), assignable to the subfamily Promecognathinae which, in addition to its anophthalmia and slight depigmentation of its heavy integument, shows a very singular characteristic that affects the morphology of maxila: the lack of galea (Mateu 2002). This fact, a remarkable aberration between the Carabidae, was verified in more than 40 specimens (typical series) and in many

Table 1: List of hypogean taxa of Carabidae.

Ibero-Balearic hypogean (caves and MSS) Carabidae (Insecta: Coleoptera)

Promecognathinae LECONTE, 1853

Dalyatini MATEU, 2002

Dalyat mirabilis MATEU, 2002

Scaritinae BONELLI, 1810

Clivinini RAFINESQUE, 1815

Reicheia (Catalanodytes) bellesi LAGAR, 1971
Reicheia (Reicheia) balearica ESPAÑOL, 1974

Trechinae BONELLI, 1810

Trechini BONELLI, 1810

Aphaenops (Aphaenops) abodiensis DUPRÉ, 1988
Aphaenops (Aphaenops) catalonicus ESCOLÀ & CANCIO, 1983
Aphaenops (Aphaenops) loubensi loubensi JEANNEL, 1953
Aphaenops (Aphaenops) mensioni LAGAR, 1973
Aphaenops (Aphaenops) ochsi aezcoaensis DUPRÉ, 1988
Aphaenops (Aphaenops) ochsi cabidochei COIFFAIT, 1959
Aphaenops (Aphaenops) ochsi ochsi L. GAUDIN, 1925
Aphaenops (Aphaenops) ochsi orbaraensis DUPRÉ, 1988
Aphaenops (Aphaenops) orionis meridionalis L. GAUDIN, 1925
Aphaenops (Aphaenops) parvulus FAILLE, BOURDEAU & FRESNEDA 2010
Aphaenops (Aphaenops) valleti CASALE & GENEST, 1986
Aphaenops (Cephalaphaenops) eskualduna COIFFAIT, 1959
Aphaenops (Cerbaphaenops) hidalgoi ESPAÑOL & COMAS, 1985
Aphaenops (Geaphaenops) ludovici A. GAUDIN, 1935
Apoduvalius (Apoduvalius) anseriformis SALGADO & PELÁEZ, 2004
Apoduvalius (Apoduvalius) aphaenopsianus ESPAÑOL & E. VIVES, 1983
Apoduvalius (Apoduvalius) asturiensis SALGADO, 1991
Apoduvalius (Apoduvalius) champagnati SALGADO, 1991
Apoduvalius (Apoduvalius) drescoi JEANNEL, 1953
Apoduvalius (Apoduvalius) espanoli SALGADO, 1996
Apoduvalius (Apoduvalius) franzi JEANNEL, 1958
Apoduvalius (Apoduvalius) lecoqi DEUVE, 1991
Apoduvalius (Apoduvalius) naloni SALGADO, 1993
Apoduvalius (Apoduvalius) negrei JEANNEL, 1953
Apoduvalius (Apoduvalius) purroyi SALGADO, 1987
Apoduvalius (Apoduvalius) salgadoi CARABAJAL, GARCÍA & RODRÍGUEZ, 2002
Apoduvalius (Apoduvalius) serrae E. VIVES, 1976
Apoduvalius (Trichapoduvalius) alberichae ESPAÑOL, 1971
Apoduvalius (Trichapoduvalius) leonensis SALGADO & ORTUÑO, 1998
Duvalius (Duvalius) balearicus HENROT, 1964
Duvalius (Duvalius) berthae JEANNEL, 1910
Duvalius (Duvalius) lencinai MATEU & ORTUÑO, 2006
Duvalius (Trechopsis) ferreri LAGAR, 1976
Geotrechus (Geotrechidius) puigmalensis LAGAR, 1981
Geotrechus (Geotrechidius) seijasi ESPAÑOL, 1969
Geotrechus (Geotrechidius) ubachi ESPAÑOL, 1965
Geotrechus (Geotrechus) dequaei DUPRÉ, 1988
Geotrechus (Geotrechus) dumonti ESPAÑOL, 1977
Geotrechus (Geotrechus) picanyoli ESPAÑOL & ESCOLÀ,1981
Hydraphaenops alfambrai LAGAR, 1979
Hydraphaenops galani ESPAÑOL, 1968
Hydraphaenops penacollaradensis DUPRÉ, 1991
Hydraphaenops sobrarbensis LAGAR & HERNANDO, 1987
Hydraphaenops vasconicus delicatulus COIFFAIT, 1962
Hydrotrechus cantabricus CARABAJAL, GARCÍA Y RODRÍGUEZ, 2000
Paraphaenops breuilianus (JEANNEL, 1916)
Thalassophilus breuili JEANNEL, 1926
Trechus alicantinus ESPAÑOL, 1971
Trechus apoduvalipenis SALGADO & ORTUÑO, 1998
Trechus baztanensis DUPRÉ, 1991
Trechus beltrani TORIBIO, 1990
Trechus beusti (SCHAUFUSS, 1862)
Trechus breuili JEANNEL, 1913
Trechus carrilloi TORIBIO & RODRÍGUEZ, 1997
Trechus escalerai ABEILLE, 1903
Trechus gamae REBOLEIRA & SERRANO, 2009
Trechus gloriensis JEANNE, 1970
Trechus lunai REBOLEIRA & SERRANO, 2009
Trechus machadoi JEANNEL, 1941
Trechus martinezi JEANNEL, 1927
Trechus pecignai TORIBIO, 1992
Trechus pieltaini JEANNEL, 1920
Trechus torressalai ORTUÑO, 2005

Anillini JEANNEL, 1937

Aphaenotyphlus alegrei ESPAÑOL &COMAS, 1985
Hypotyphlus andorranus ESPAÑOL &COMAS, 1984
Hypotyphlus huetei ORTUÑO, 1997
Hypotyphlus sotilloi ESPAÑOL, 1971
Iberanillus vinyasi ESPAÑOL, 1971
Microtyphlus (Microtyphlus) fideli VIÑOLAS Y ESCOLÀ, 1999
Microtyphlus (Microtyphlus) menorquensis COIFFAIT, 1961
Microtyphlus (Speleotyphlus) aurouxi ESPAÑOL, 1966

Microtyphlus (Speleotyphlus) comasi (J. Vives, O. Escolà y E. Vives, 2002)
Microtyphlus (Speleotyphlus) fadriquei (Español, 1999)
Microtyphlus (Speleotyphlus) infernalis Ortuño & Sendra, 2010
*Microtyphlus (Speleotyphlus) jusmeti (*Español, 1971)
Microtyphlus (Speleotyphlus) virgilii (J. Vives, O. Escolà y E. Vives, 2002)

Harpalinae Bonelli, 1810

Pterostichini Bonelli, 1810

Molopina Bonelli, 1810

Henrotius jordai (Reitter, 1914)
Molopidius spinicollis (Dejean, 1928)
Oscadytes rovirai Lagar, 1975
Zariquieya troglodytes (Jeannel, 1924)

Pterostichina Bonelli, 1810

Pterostichus (Lianoe) drescoi Nègre, 1957
Tinautius troglophilus Mateu, 1997
Tinautius exilis Mateu, 2001
Troglorites breuili Jeannel, 1919

Platynini Bonelli, 1810

Galiciotyphlotes weberi Assman 1999

Sphodrini Laporte, 1834

Sphodrina Laporte, 1834

Laemostenus (Antisphodrus) alejandroi Carabajal, García & Rodríguez, 2002
Laemostenus (Antisphodrus) andalusiacus J.Vives & E. Vives, 1982
Laemostenus (Antisphodrus) barrancoi Mateu, 1996
Laemostenus (Antisphodrus) bermejae Fernández-Cortés, 1996
Laemostenus (Antisphodrus) cazorlensis (Mateu, 1953)
Laemostenus (Antisphodrus) lassallei Mateu, 1989
Laemostenus (Antisphodrus) ledereri (Schaufuss, 1865)
Laemostenus (Antisphodrus) levantinus C. Bolívar, 1919
Laemostenus (Antisphodrus) navaricus Vuillefroy, 1893
Laemostenus (Antisphodrus) peleus (Schaufuss, 1861)

Atranopsina Baehr, 1982

Platyderus alhamillensis Cobos, 1961
Platyderus breuili Jeannel, 1921
Platyderus speleus Cobos, 1971
Platyderus torressalai Jeanne, 1996
Platyderus troglodytes Schaufuss, 1863

Zuphiini Bonelli, 1810

Zuphiina Bonelli, 1810

Ildobates neboti Español, 1966

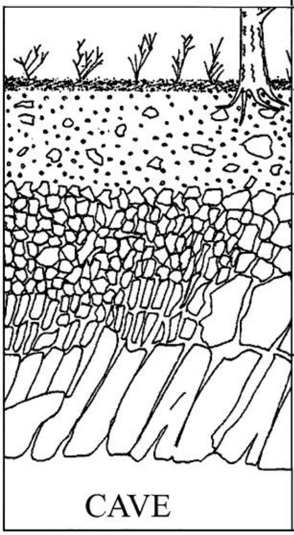
others captured later. This characteristic that perhaps had its origin in a teratology combined with a noticeable founder effect, forces the classification of *Dalyat mirabilis* Mateu, 2002, in a group (tribe Dalyatini) separated from the other Nearctic (*Promecognathus* Chaudoir, 1846) and Afrotopical Promecognathinae (*Axinidium* Sturm, 1843; *Paraxinidium* Basilewsky, 1963; *Metaxinidium* Basilewsky, 1963 and *Holaxinidium* Basilewsky, 1963). In spite of this, the results of molecular studies seem to indicate that *Dalyat* Mateu, 2002, is closer to *Promecognathus* than to South African taxa, confirming the mesozoic origin of this lineage (Mateu & Bellés 2003, Ribera et al. 2005). At the moment, concrete aspects of their biology remain unknown. This species has been found in three cavities of the Mountain range of Gador (Mateu & Bellés 2003), a mountainous formation in the province of Almeria, southeast of Spain (Fig. 2).

In regard to the subfamily Scaritinae, only two species of *Reicheia* Saulcy, 1862, have been found only in caves. In agreement with Bellés (1987), it is very likely that both species are, in fact, endogeous elements, as are their other Iberian relatives. The characteristics of the caves where they have been found, added to the absence of troglobiomorphic characteristics and the endogeous life of the other species of the genus, make this hypothesis very likely. However, since there is no evidence of it, they must be considered within the list of hypogean carabid beetles. Except for this conjecture, nothing is known about the biology of these species, beyond their presence on vegetal rests that are accumulated in some sections of these caves. *Reicheia bellesi* (LAGAR, 1971) is known from the Cave Janet, situated in the south of Tarragona (Northeast of Spain) and *Reicheia balearica* ESPAÑOL, 1974, from the Cova dets Estudiants in the island of Majorca (Balearic archipelago) (Fig. 3).

As it is possible to observe in the listing of species (Table 1), the subfamily that contributes more taxa is the Trechinae (76 species/subspecies), following the same trend as in other places of the planet. In the hypogean environment, we distinguish an unequivocally hypogean contribution, like the one of the Trechini, which contributes with nine genera, whose species have different degrees in the expression of their troglobiomorphic characters. So, some genera are totally hypogean with much modified species with respect to their epigean ancestors (*Aphaenops* BONVOULOIR, 1861; *Hydraphaenops* JEANNEL, 1926 and *Paraphaenops* JEANNEL, 1916). Other genera, including clearly geophilic, sciophile, and hygrophilic representatives, which are also found in epigean environments, and that, nevertheless, also contribute with some exclusive species of hypogean habitats (*Trechus* CLAIRVILLE, 1806; *Thalassophilus* WOLLASTON, 1854; *Duvalius* DELAROUZÉE, 1859). Between these extremes, there are also species that show a more moderate degree of hypogean evolution than in *Aphaenops* and convergent with this one; we are referring to the species of *Geotrechus* JEANNEL, 1919, *Apoduvalius* JEANNEL, 1953, and *Hydrotrechus* CARABAJAL, GARCÍA & RODRÍGUEZ, 2000. The genus *Aphaenops* shows 14 taxa that are located in the Iberian Peninsula, some of which are also shared with France. With respect to the subgeneric division, the Iberian species of *Aphaenops* are grouped in four subgenera: *Aphaenops* s.str.; *Cephalaphaenops* COIFFAIT, 1962; *Cerbaphaenops* COIFFAIT, 1962 and *Geaphaenops* CABIDOCHE, 1965. It is worth indicating that the taxonomic status of some of the populations has not been solved yet (species or subspecies?); for this reason it now seems prudent to follow the same criterion of SERRANO (2003), but with the proper updates (Table 1). The Iberian distribution of *Aphaenops* is circumscribed to the Pyrenean mountain range and pre-Pyrenean reliefs (Fig. 4), inhabiting cavities with very low temperatures; it has also been captured under very big stones (BELLÉS 1987) or in the MSS (GENEST & JUBERTHIE 1983, GERS 1998).

Hydraphaenops contributes five species to the Iberian carabid fauna and, although they show a great similarity with *Aphaenops*, are a group of species with an almost amphibious behaviour (characteristic related to the presence of numerous small setae on the integument). This facilitates a cryptic way of life, in the fissures of rocks surrounded by water (JEANNEL 1926a: 82), behaviour that makes them very hard to locate. This genus, like *Aphaenops*, seems to be polyphyletic (FAILLE et al. 2010). Its distribution is also Pyrenean, although one of the species, the most western, is in the karst of the Basque Montes (Fig. 5).

Paraphaenops is a monospecific genus, with aphaenopsian aspect, that is located towards the south (in the Iberian System, in the province of Tarragona) (Fig. 6), far from the influence of the Pyrenees. In fact, everything points to this genus being phylogenetically very far from *Aphaenops* and *Hydraphaenops* (FAILLE et al. 2010). *Paraphaenops breuilianus* (JEANNEL, 1916) is known from several cavities whose more relevant abiotic characteristics are the high humidity of the substrate and the low temperature. Some morphologic data of the larva are known (JEANNEL 1926b).



Layer	Environment	Fauna
A	Soil	Humicolous / Edaphic
B	Soil	Edaphic / Endogeous
C_1	MSS	Hypogean
C	MSP	Hypogean

Fig. 1: Soil and subsoil layers, and ecological classification of the fauna.

Fig. 2: Distribution of *Dalyat* MATEU, 2002, in the Iberian Peninsula and Balearic Islands.

Fig. 3: Distribution of hypogean *Reicheia* SAULCY, 1862, in the Iberian Peninsula and Balearic Islands.

Fig. 4: Distribution of *Aphaenops* BONVOULOIR, 1861, in the Iberian Peninsula and Balearic Islands.

Fig. 5: Distribution of *Hydraphaenops* JEANNEL, 1926, in the Iberian Peninsula and Balearic Islands.

Fig. 6: Distribution of *Paraphaenops* JEANNEL, 1916, in the Iberian Peninsula and Balearic Islands.

With respect to the genus *Geotrechus*, polyphyletic according to FAILLE et al. (2010), it is typically Pyrenean (Fig. 7). There are very few Iberian species that are known, being located in two subgenera, *Geotrechus* s.str and *Geotrechidius* Jeannel, 1947. In addition, the samplings in the typical localities have provided a very low number of specimens, circumstances that contrast, as is indicated by BELLÉS (1987), with the remarkable diversity and abundance shown by this genus in the French Pyrenees (north slope). Accepting that the Pyrenean karsts are reasonably well sampled, on both slopes, it is reasonable to presume that climatic factors (smaller higher humidity and temperature on the south slope) limit the life of *Geotrechus* to a smaller number of subterranean spaces. This explanation seems reasonable and could also be applied to understanding why the *Aphaenops* and *Hydraphaenops* are more frequent in the French Pyrenees that on the Spanish side. Nothing is known about the biological aspects of the Iberian species of *Geotrechus*.

In the last decades, and thanks to the biospeleological investigation of Prof. J.M. SALGADO, the knowledge of the specific diversity of *Apoduvalius*, an exclusive genus of the Cantabrian range mountains (North of Spain) (Fig. 8) has been increased remarkably. *Apoduvalius* includes a set of anophthalmic Trechini that, seemingly, reminds us of the slightly more streamlined *Trechus*. Leaving aside the characteristics of edeago (isotopic aedeagus) described by JEANNEL (1953) and other authors (CASALE & LANEYRIE 1982, among others), it is possible that this genus is group of *Trechus* sensu lato of different origin, but very specialized to hypogean life (FAILLE et al. 2010). The majority of the species are known from caves, although they are very little abundant, which is why it is thought that its regular habitat could be the MSS. As a reinforcement of this hypothesis, it is worth mentioning that *Apoduvalius lecoqi* DEUVE, 1991, has been captured next to snow (DEUVE 1991), therefore in deposits of colluvia, and probably it may inhabit the MSS. Also the capture of *Apoduvalius espanoli* SALGADO, 1996, in a MSS next to the cave that is its typical locality deserves special mention (CARABAJAL et al. 2001). No other aspect is known about the biology of *Apoduvalius*. *Hydrotrechus*, as the other hypogean genera of Trechini, also is a controversial taxon, which has been recently discussed (ORTUÑO & JIMÉNEZ- VALVERDE in press). At present we will only indicate that it is a single species, *Hydrotrechus cantabricus* CARABAJAL, GARCÍA & RODRÍGUEZ, 2000, which has been recently found in the MSS of a single locality in the Cantabrian Mountains (Cantabria, north of Spain) (Fig. 9). The surface of its integument is profusely covered with plenty of small setae, a characteristic that could qualify it, as happens with *Hydraphaenops*, to live in close contact with subterranean layers of water. This species lives in syntopy with three species of *Trechus*, although a space segregation related to the horizons of the ground is observed among them: *H. cantabricus* in deep and very humid zones of the MSS, *T. carrilloi* TORIBIO & RODRIGUEZ, 1997, in more superficial zones of the MSS, and *T. distigma* KIESENWETTER, 1851, and *T. jeannei* SCIAKY, 1998, in the A horizon, which is much richer in organic matter.

The genus *Duvalius* has a strong representation in eastern eurasiatic geographic areas, maybe because it was its centre of origin. This phyllogenetic lineage reaches the Ibero-Balearic region (Fig. 10), although it only includes the most western representatives of the genus (MATEU & ORTUÑO 2006). There are only four species (two continental and two insular) that are distributed in two subgenera, *Duvalius* s. str., and *Trechopsis* PEYERIMHOFF, 1908. Concrete aspects of the biology of these species are yet unknown.

At present, we accept that there is a hypogean species of *Thalassophilus* in the Iberian Peninsula: *Thalassophilus breuili* JEANNEL, 1926, that like its vicariant *Thalassophilus longicornis* (STURM, 1825), is eyed. It is an enigmatic species, of which only few specimens are known (no higher than half a dozen) that are confined to the subsoil of the north-eastern end of the Betic mountain system of Alicante (Fig. 11). Many caves have been prospected and the findings are almost anecdotal, a circumstance that feeds the hypothesis that they belong to some type of MSS of Spanish Levante (ORTUÑO 2007).

Presently in our knowledge of the Carabidae of the Iberian Peninsula, there are 14 species of *Trechus* that can be considered as strictly subterranean, some of them are known with regularity in caves, and others in MSS and, generally, underneath stones sunk in very fissured soils in diverse places of the Iberian Peninsula (Fig. 12). Some of these species show evident characteristics of the troglobiomorphism process: most evident is anophthalmia (or microphthalmia). But not all the hypogean species show the same intensity in the manifestation of this or other characteristics (depigmentation, gracility, etc.). For example, we will mention two Cantabrian *Trechus*: *T. escalerai* ABEILLE, 1903 (of ampler distribution), and *T. apoduvalipenis* SALGADO & ORTUÑO, 1998 (only known from a cave), with clear morphologic characteristics of adaptation to subterranean environments. Nevertheless, the species of the *Trechus martinezi* – lineage (sensu ORTUÑO & ARILLO 2005), although are all hypogean, have eyes and show very slight characteristics of troglobiomorphism. In any one of these extreme cases they might be considered to be species that are at different moments in subterranean evolution. About the biology of these species, almost nothing is known, although it is worth pointing out that breeding of *Trechus alicantinus* ESPAÑOL, 1971, in controlled conditions made possible some observations about feeding, copula, and the description of the third stage of the larva (ORTUÑO & REBOLEIRA 2010).

The tribe Anillini, in spite of heading the representation of the endogeous Carabidae, contributes to the list of hypogean fauna, in some cases anecdotally (circumstantially) but in other cases relevantly, with taxa that can be considered exclusively hypogean. In the most remarkable cases they show troglobiomorphic characters (almost aphaenopsian), as *Aphaenotyphlus alegrei* ESPAÑOL & COMAS, 1985. This species, exclusive to the reliefs "Platform of the Caroig" (Valencia, east of Spain) (Fig. 13) has again been studied by ORTUÑO & SENDRA (2007), who contributed new data on morphology, systematics, and biology.

Another supposed hypogean Anillini of the genus *Microtyphlus* s. str and *Hypotyphlus*, are thought to be in fact endogeous elements that arrived accidentally at some cavities (ORTUÑO & SENDRA 2007, 2010). The frequency with which they are found in these underground spaces (sometimes only one unit) emphasizes how rare they are in the hypogean environment. The distribution of the cavernicolous elements of these two genera is observed in the following maps (Figs. 14 and 15).

Iberanillus, a monospecific genus, is a very singular taxon, only known from two caves of the "Alineaciones Costeras" (Castellón, east of Spain) (Fig. 16). *Iberanillus vinyasi* ESPAÑOL, 1971, reminds us, because of its general form, of *Geocharis* EHLERS, 1883, of remarkable dimensions (2,75–3,2 mm); its manifest "gigantism", compared with the dimensions that a standard Anillini would show, perhaps is due to an adaptive answer to the hypogean environments which it inhabits (ORTUÑO 2007). As in the case of another Anillini, it is conjectured that perhaps it can be a predator of mites and Collembola (ORTUÑO 2007).

Fig. 7: Distribution of *Geotrechus* JEANNEL, 1919, in the Iberian Peninsula and Balearic Islands.

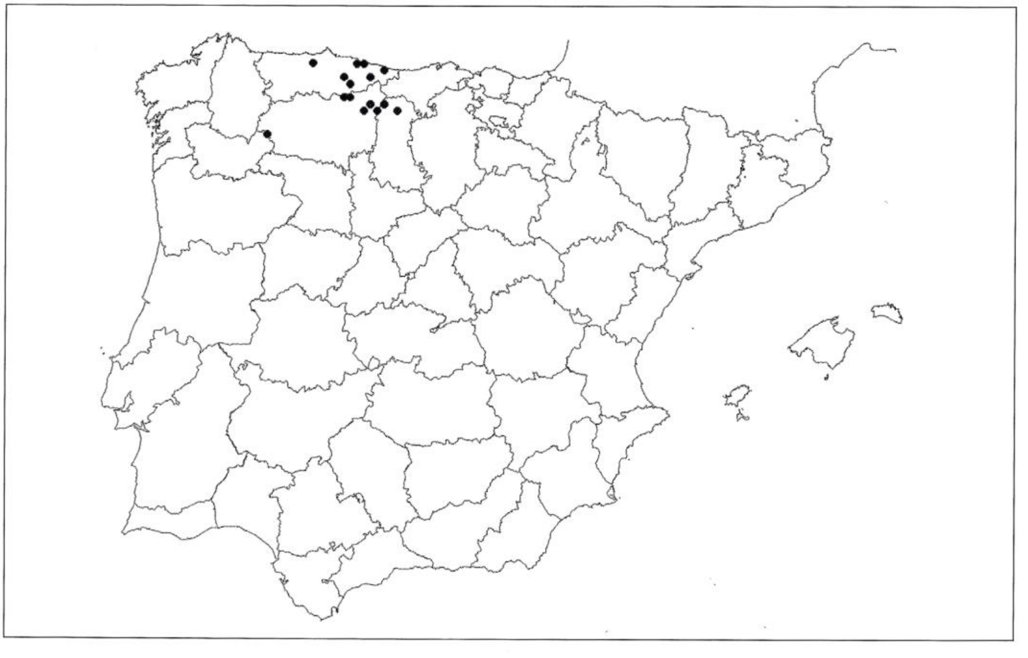


Fig. 8: Distribution of *Apoduvalius* JEANNEL, 1953, in the Iberian Peninsula and Balearic Islands.

Fig. 9: Distribution of *Hydrotrechus* CARABAJAL, GARCÍA & RODRÍGUEZ, 2000, in the Iberian Peninsula and Balearic Islands.

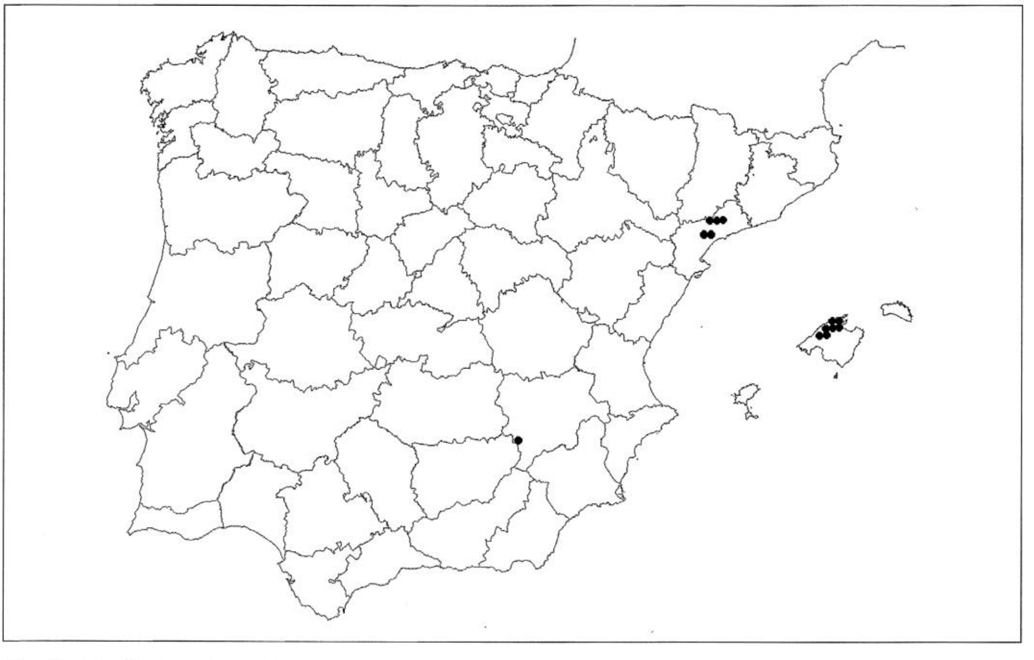


Fig. 10: Distribution of *Duvalius* DELAROUZÉE, 1859, in the Iberian Peninsula and Balearic Islands.

Finally, with respect to the Anillini, the subgenus *Speleotyphlus* JEANNE, 1973, includes a series of species with different degrees from stylisation (troglobiomorphism). This taxon was considered, in origin, to be a generic status (JEANNE 1973), but ORTUÑO & SENDRA (2007) demonstrate that, according to the qualitative characters, they are nothing more than *Microtyphlus* specialized in the hypogean life. The data in hand at the moment indicate a certain geographic coherence, being known from the hypogean environments of diverse reliefs of Spanish Levant (east of Spain) (Fig. 17). On this subject a new article is being prepared (ORTUÑO & SENDRA in prep.) that will shed light on the status of these hypogean species.

The subfamily Harpalinae (sensu LÖBL & SMETANA 2003) contributes four tribes: Pterostichini, Platynini, Sphodrini and Zuphiini.

The hypogean Pterostichini includes seven genera (five endemic to the Ibero-Balearic area) to the hypogean list with only 8 species (Table 1), which supposes that almost the totality of the genera are represented in a monospecific way. The subtribe Molopina (sensu CASALE & RIBERA 2008) contributes four of these species, all of them closely related, and also with *Speomolops sardous* PATRIZI, 1955, endemic from the hypogean environments of Sardinia. Therefore, areas of the western Mediterranean and, in particular, of the north-eastern quadrant of the Iberian Peninsula and the Balearic archipelago, include the majority of the hypogean Molopina.

These, unlike the Pterostichina, conserve a much pigmented integument. *Molopidius* JEANNEL, 1942, with its only species *Molopidius spinicollis* (DEJEAN, 1828), in spite of its constant presence in certain cavities of Gerona and the north of Barcelona (Fig. 18), perhaps should be considered as a humicolous element typical of soils of humid forests (ESPAÑOL 1966, BELLÉS 1987), often very fissured (probable inhabitant of the MSS). The hypogean Molopina of Spain are anophthalmic, except for *Molopidius spinicollis* which is microphthalm.

Henrotius JEANNEL, 1953 is a genus exclusive to the island of Majorca (Balearic archipelago), more concretely of the Mountain range of the Tramontana and its derivations (Fig. 19). Although two species were described, BELLÉS (1976) concluded that it was not possible to distinguish both, due to the great variability and instability of the characters that were used to differentiate them. For this reason, only *Henrotius jordai* (REITTER, 1914) remains in the faunistic listing nowadays. Beyond the accompanying fauna of the cavities where it lives, we do not know any concrete aspects of its biology.

A Molopina with a very restricted distribution is *Zariquieya* JEANNEL, 1924; at present, it is only well-known in three cavities of the province of Gerona (northeast of Spain) (Fig. 20). Its unique species, *Zariquieya troglodytes* (JEANNEL, 1924), is very scarce in these caves, becoming visible (with a low number of individuals) during the rainy season (ESPAÑOL 1946, VIVES 1975, ORTUÑO 1996). It is probably an element of the MSS that flees to bigger spaces when this one drowns (ORTUÑO 1996). The very little known about the biology of this species, from controlled conditions in laboratory, shows that it likes to hunt and to depredate isopods of the genus *Spelaeonethes* VERHOEFF, 1932 (see E. VIVES & M. VIVES 1978), which also appear in two of the cavities where this species is known.

The last genus of Molopina that was added to the Ibero-Balearic catalogue is *Oscadytes* LAGAR, 1975, amidst great controversy about its systematic location. In its description, it was located among the Sphodrini, whereas J. Vives & E. Vives (1982) thought that it was a Pterostichina. With the study of the genitalia of the single species *Oscadytes rovirai* Lagar, 1975, it was definitively located among the Molopina (Fresneda et al. 1997). This species was initially well-known from a cavity of Pre-Pyrenees of Huesca (Fig. 21), but recent searches discovered that its true habitat is the MSS of the surroundings of the typical locality, and perhaps also the network of fissures of the limestone layers of the reliefs that it colonizes (Fresneda et al. 1997), by that it must accede by subterranean cavities. The study of female genitalia reveals a great similarity between *Oscadytes* and *Zariquieya*, being more distant to the other Ibero-Balearic species of Molopina (Fresneda et al. 1997).

The subtribe Pterostichina includes four interesting hypogean Ibero-Balearic species that are distributed in three genera. Two of them are present in the north of the Iberian Peninsula, *Troglorites* Jeannel, 1919, and *Pterostichus* Bonelli, 1810, of the subgenus *Lianoe* Gozis, 1882. The third genus, *Tinautius* Mateu, 1997 is found in the south of the Iberian Peninsula. *Troglorites* includes one Iberian species, *Troglorites breuili* Jeannel, 1919, that is widely present in diverse caves of the karst of the Basque Mountains (North of Spain: Navarre, Alava, and Guipúzcoa) (Fig. 22) and, with evident characteristics of adaptation to hypogean environments (anophthalmia and depigmentation of the integument). The trend in those species is to be macrocephalic, a peculiarity that is more or less pronounced in different populations. This characteristic has made possible the designation of subspecies which, recently, has begun to be studied critically again (Ortuño et al. in press).

Similarly, although not as widely distributed, *Pterostichus (Lianoe) drescoi* Nègre, 1957, is located in caves of Picos de Europa (North of Spain) (Fig. 23). It is also depigmented and anophthalmic, and plays the important role of predator in these subterranean habitats. Its scarcity in the caves can be an indication that it is an element of the MSS (Bellés, 1987). There are two recognized subspecies (Jeanne 1964, Español 1966b, Serrano 2003) that, according to our criterion, might be of doubtful validity. Beyond certain observations of capture, concrete aspects of their biology are not known.

Recently, there was a surprising discovery of two hypogean Pterostichina in karst of the Betic reliefs (Andalusia, the south of Spain) (Fig. 24). Both these species were placed in a new genus: *Tinautius* Mateu, 1997. The first of them, *Tinautius troglophilus* Mateu, 1997, has an eye that shows slight depigmentation. According to Mateu (1997) this genus could have certain taxonomic relations with *Troglorite*s, being more similar to *Troglorites ochsi* Fagniez, 1921, from the Marine Alps that to the species of the north of Spain. Years later, a second Pterostichina *Tinautius exilis* Mateu, 2001, which was also included in this same genus, was discovered in a cave in Almeria (Mateu 2001). This species shows major adaptations to hypogean life: anophthalmia, integument depigmentation, stylisation of the body, and an umbilicate series with long flageliform setae. The specimens of both sexes exhibit a notable autapomorphy, the extension of metatrochanter, finishing in a point (Mateu 2001). Nothing is known of the biology of this species.

The tribe Platynini includes an exceptional hypogean species, for which a new genus had to be created: *Galiciotyphlotes* Assmann, 1999. At the moment, this species, *Galiciotyphlotes weberi* Assmann, 1999, is only known from the mountain ranges of "Los Ancares" and "El Caurel" (Galicia, the northwest of Spain) (Fig. 25). Although Assmann (1999) systematically located this species among the Perigonini, Ortuño & Salgado (2000) propose their location

Fig. 11: Distribution of hypogean *Thalassophilus* WOLLASTON, 1854, in the Iberian Peninsula and Balearic Islands.

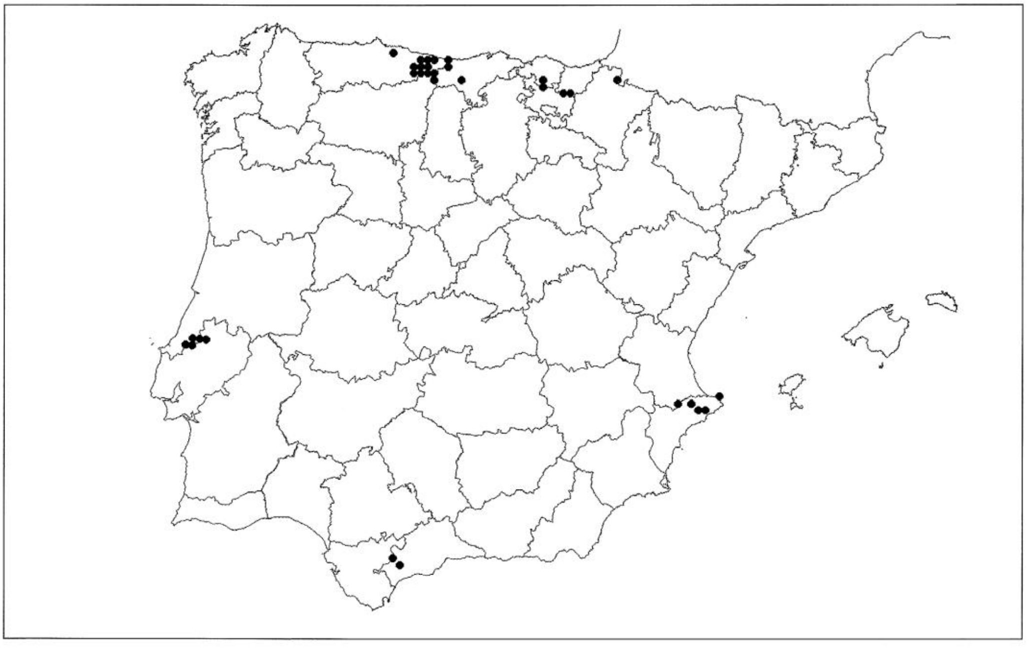


Fig. 12: Distribution of hypogean *Trechus* CLAIRVILLE, 1806, in the Iberian Peninsula and Balearic Islands.

Fig. 13: Distribution of *Aphaenotyphlus* ESPAÑOL & COMAS, 1985, in the Iberian Peninsula and Balearic Islands.

Fig. 14: Distribution of the *Microtyphlus* s. str. LINDER, 1863, found in caves in the Iberian Peninsula and Balearic Islands.

between the Platynini, based on a detailed study of morphology and masculine and feminine genitalia, which makes it the first western paleartic hypogean of this tribe. We do not know anything about its biology, although it could be an inhabitant of the MSS that, circumstantially, can reach the caves.

The Sphodrini constitutes a very well represented tribe in the Ibero-Balearic region, with some troglophilic elements which are a constant in the caves. The best example is *Laemostenus (Pristonychus) terricola* (HERBST, 1783) because of its wide distribution and perseverance in the hypogean environment, which surely turns it into an important trophic competitor of the strictly hypogean species. In spite of this, Sphodrini also contributes to the list of hypogean fauna with 15 species, ten of them are *Laemostenus* BONELLI, 1810, of the subgenus *Antisphodrus* SCHAUFUSS, 1865, which belong to the subtribe Sphodrina, and five of the genus *Platyderus* STEPHENS, 1827, which belong to the subtribe Atranopsina. All of them constitute a set of eyed carabid beetles (but with trends to the microphthalmia) and, generally, with few morphological specialisations for hypogean life. However, these 15 species show a clear fidelity to hypogean habitats.

The subgenus *Antisphodrus* includes a series of hypogean species throughout a mountainous arc that, by the south, east, and north, surrounds part of the Iberian Peninsula, from Cadiz to Galicia, but without exceeding the northern limits of the valley of Ebro (Fig. 26). The absence of hypogean species in a large extent of the Iberian system, among them the *Antisphodrus*, has not been explained yet, neither in the group of the Carabidae nor in other taxonomic groups. All the Iberian species of *Antisphodrus* belong to the *Laemostenus (A.) navaricus* group sensu CASALE, (1988) and present a greater number of species in the Betic System and its ramifications (from Cadiz to Albacete), where there are six species, in caves or MSS with atmospheres related to this one (underneath stones partially buried on very fissured grounds): *L. (A.) ledereri* (SCHAUFUSS, 1865); *L. (A.) cazorlensis* (MATEU, 1953) (with three subspecies); *L. (A) andalusiacus* J. VIVES & E. VIVES, 1982 (with two subspecies); *L. (A.) barrancoi* MATEU, 1996; *L. (A.) bermejae* FERNÁNDEZ CORTÉS, 1996 y *L. (A.) alejandroi* CARABAJAL, GARCÍA & RODRÍGUEZ, 2002. In the most eastern derivations of the Iberian system, next to the Mediterranean coasts, there are another two species, the most extended being *L. (A.) levantinus* C. BOLÍVAR, 1919, typical of caves (Valencia and Castellón, east of Spain); the most located, *L. (A.) lassallei* MATEU, 1989, lives in the MSS of "Puertos de Beceite" (Teruel-Tarragona, east of Spain). Finally, to complete the list of hypogean carabid beetles of this subgenus, we mention two typical species of the peninsular north: *L. (A.) peleus* (SCHAUFUSS, 1861) (with three subspecies), which is frequent in caves, and widely distributed from Galicia to Biscay, and *L. (A.) navaricus* VUILLEFROY, 1893 (with two subspecies), also of caves but much more located and well-known in the Basque Mountains. In spite of the remarkable number of species, some of them very conspicuous, there is almost no precise data on its biology, although we know that, generally, they are guanophile species, with predatory habits. With respect to *L. (A.) peleus,* concrete data about the morphology of the larva are known (VIVES 1979).

The genus *Platyderus* STEPHENS, 1827, includes near fifty species in the Iberian Peninsula (SERRANO 2003) of which five species are exclusively present in hypogean environments (caves and fissured grounds) because of its geophilic, sciophilic, and hygrophylic behaviour. They are perfectly eyed animals, not or little depigmented, and they do not show any type of corporal stylisation either. Everything aims at them being recent hypogean forced to take refuge in the subsoil because of the xeric conditions in some Andalusian and levantine places (south and east of Spain) (Fig. 27). Their foraging behaviour is based on the depredation of other invertebrates and a complementary saprophytic regime (Ortuño 2007).

Finally, the tribe Zuphiini contributes, in the Ibero-Balearic region, one of the most surprising genera: we refer to *Ildobates* Español, 1966. It has a single species *Ildobates neboti* Español, 1966, that nowadays is known in four caves of the coastal alignments of Castellón (east of Spain) (Ortuño et al. 2006) (Fig. 28). After its description (Español 1966a), its taxonomic location was not solved, since the troglobiomorphic characters it exhibits hide the basic aspects of its morphology that would relate it to its epigean relatives. In spite of this, still without solid arguments, in the last catalogues of the Ibero-Balearic Carabidae (Jeanne & Zaballos 1986; Zaballos & Jeanne 1994; Serrano 2003) it was located among the Zuphiini. Later, it was confirmed by means of a very detailed morphologic and anatomical study (Ortuño et al. 2004) and an molecular analysis (Ribera et al. 2006). It is an active predator that rambles by walls and stalagmitic coladas of the most humid areas of the caves (frequently flooded), and whose atmosphere shows a temperature between 12 and 17 °C (Ortuño 2007). The biocenosis of the caves it inhabits is reasonably well known (Ortuño et al. 2004), nevertheless, concrete aspects of its life cycle are not known.

Sectorisation of the Ibero-Balearic karsts

Of all the Iberian taxa with evident hypogean affiliation, the most widely distributed is the subgenus *Antisphodrus*. As mentioned previously, all species show a weak troglobiomorphism, although evident in all of them is a certain ocular regression accompanied by a depigmentation of the integument. The data we handle suggest that their implantation in hypogean environments (in caves, fissures, and in the MSS) is relatively recent. This fact has caused all Iberian species to extend throughout a "Betic Peri-plateu karstic arc", which includes the Betic Mountains, the Iberian System (although these hypogean are only known in its eastern derivations), the Basque Mountains, and the Cantabrian Cornice.

This peculiar distribution is going to condition and define the regionalization of the Ibero-Balearic biospeleological districts proposed in this article. *Trechus* could also have been employed, as it also shows a wide distribution in the Iberian karsts, but according to our criterion, *Trechus* is only useful to specify regions of smaller geographic scale, since its presence is not exclusive to the hypogean environments and many of the hypogean species have reached this way of life independently of each other. Therefore, the hypogean *Trechus* from the Cantabrian area has little to do with those of the Betic Mountains, for example.

Therefore, the monophyly and hypogean fidelity of the Iberian *Antisphodrus* (moreover, these belonging to the *navaricus* group sensu Casale 1988), in addition to its wide distribution, make them a basic taxon, from which began the regionalization of the Ibero-Balearic karst. Therefore, the **"Betic Peri-plateu karstic arc",** (Fig. 29, area A) that is defined by the presence of *Antisphodrus*, becomes one of the four Iberian districts now set out. The other three districts lack this taxon. The most conspicuous of the rest of the districts is the **"North oriental quadrant"** (Fig. 29, area B) constituted, in the north of the valley of

Fig. 15: Distribution of the *Hypotyphlus* JEANNEL, 1937, found in caves in the Iberian Peninsula and Balearic Islands.

Fig. 16: Distribution of *Iberanillus* ESPAÑOL 1971, in the Iberian Peninsula and Balearic Islands.

Fig. 17: Distribution of *Speleotyphlus* JEANNE, 1973, in the Iberian Peninsula and Balearic Islands.

Fig. 18: Distribution of *Molopidius* JEANNEL, 1942, in the Iberian Peninsula and Balearic Islands.

Ebro, by a great part of the Pyrenees (eastern, central, and most of the western Pyrenees), Catalonian Pre-Pyrenees and Catalonian Coastal ranges. This area is defined by the following hypogean carabid beetle taxa: *Aphaenops, Geotrechus, Oscadytes, Zariquieya,* and *Molopidius*. The third district is the "**Balearic archipelago**" (Fig. 29, area C), exclusively defined by *Henrotius*. And finally, a fourth district, **"Discontinuous Lusitanic karsts"** (Fig. 29, area D) defined by the practical absence of hypogean Carabidae, except a few species of *Trechus* that belong to the "*fulvus* lineage" sensu Ortuño (in REBOLEIRA et al, in press), which are part of a group of Iberian species with greater distribution: the *Trechus fulvus* group sensu JEANNEL (1927).

The district **"Betic Peri-plateu karstic arc"** deserves separate commentary: in spite of the presence of *Antisphodrus*, is quite wide and heterogeneous. This district, as well, requires a subregionalisation into four subdistricts (Fig. 29, areas A1, A2, A3, and A4). The "**Cantabrian**" subdistrict is A1, which is distinguished by the presence of *Apoduvalius*, *Galiciotyphlotes*, *Hydrotrechus,* and *Pterostichus (Lianoe) drescoi*. The subdistrict A2 is the **"Basque mountains**" characterized by the presence of *Troglorites breuili*. A3 is the area of the "**Northern levant"** subdistrict, constituted by the eastern continuations of the Iberian System and associated formations, like the "Alineaciones Costeras" of Castellon. This subdistrict, of little extension and, generally, of small caves, includes a great faunistic diversity, being one of the most surprising biospeleological areas. This is also confirmed by the known data from other faunistic groups. The representative Carabidae of this subsector are: *Ildobates*, *Paraphaenops*, *Aphaenotyphlus*, *Speleotyphlus,* and *Iberanillus*. Finally, the fourth subdistrict, of greater extension, is denominated **"Betic" subdistrict**, which goes along from Cadiz to Alicante and the south of Valencia. This wide area includes several karsts that are characterized by the following taxa: *Trechus* of the *martinezi* lineage sensu ORTUÑO & ARILLO (2005), *Dalyat, Tinautius*, some species of *Platyderus,* and *Thalassophilus breuili*.

It is also necessary to emphasize two taxa that serve as connectors between districts and/or subdistricts. The genus *Duvalius* is present in the "Balearic archipelago" subdistrict and in the south of the "North oriental quadrant" district, which suggests certain bio-karstic relation between these sectors. This could be confirmed by the phylogenetically close relationship between *Henrotius* and other hypogean Molopina of the "North oriental quadrant" like *Zariquieya* and *Oscadytes* (perhaps also with *Molopidius*). Therefore, although geographically the Balearic archipelago is a part of the prolongation of the Betic Chains, its hypogean fauna of Carabidae is much more related to the district of the "North oriental quadrant" than with the "Betic subdistrict" or with the "northern Levant". It is possible to emphasize the controversy that supposes the description of *Duvalius lencinai* that, although it is a hypogean species that characterizes the karst of the Mountain ranges of Alcaraz, might be a *Trechus* and not a *Duvalius* since the main differentiator character of this genus, in this species, is a little confusing. Therefore, we interpreted that the presence of this species in the "Betic" subdistrict does not invalidate the conclusions about the genus *Duvalius* as a connector element between the districts of the "North oriental quadrant" and the "Balearic archipelago."

Another connector element is *Hydraphaenops*, on which there are reasonable doubts about its monophyly, as also happens with other "aphaenopsian" taxa. But accepting the present concept of *Hydraphaenops* we can consider it a connector between the district "North oriental quadrant" and the subdistrict of the "Basque mountains".

Finally, some species present in the listing of hypogean Carabidae have been ruled out for their use in the proposal of regionalization of the Ibero-Balearic districts, because they are taxa that, in our opinion, belong to clearly endogeous lineages, whose presence in the hypogean environments is anecdotal. This hypothesis is reinforced by the low number of specimens collected after their discovery (in some cases only the type of specimens are known). In addition, it is clear that their distribution does not fit into the districts and subdistricts proposed. This is logical if we consider that the endogeous fauna, because of its small size, and its close relation with the horizons A and B of the soil, is influenced by other factors that take part in their distribution, which do not have to take part in the distribution of the hypogean fauna. These taxa are: *Reicheia*, *Hypotyphlus,* and *Microtyphlus* s.str.

Conclusions

1. The terms subterranean and hypogean are not considered synonymous. In this article the division of subterranean environments (and their exclusive faunas) in the following levels is assumed: a) Endogeous environment, consisting of the microspaces generated in horizon B and, sometimes, a deep part of horizon A; b) Hypogean environment, that is the interstices and voids generated in intimate relation with the bedrock. There are two basic hypogean typologies, which have a close relation and connection: Deep Subterranean Environment (MSP) or cavernicolous, and the superficial subterranean environments resulting from the alteration and/or deposit of the bedrock. Only the hypogean fauna has been studied in this article.

2. The strictly hypogean Carabidae of the Ibero-Balearic region consists of more than a hundred species (Table 1); it comprises 15% of the total diversity of Carabidae of the Iberian Peninsula. The most numerously species are represented within the taxon Trechinae. It is necessary to clarify the status of some taxa, for example *Aphaenops*.

3. In light of the information here compiled, the taxonomic and systematic knowledge of the list of hypogean Carabidae is reasonably good, although more studies of molecular biology are still necessary. In addition to taxonomic knowledge, it seems that chorological data are also useful. Nevertheless, our knowledge of the preimaginal stages is extraordinarily poor (almost anecdotal) as well as our knowledge about the biology of the species, which is practically nil. More research is clearly needed in subterranean biology.

4. The first attempt of regionalization of the Ibero-Balearic karst from taxonomic and chorologic knowledge of the Carabidae offers four districts, one of them defined by the taxon *Antisphodrus*, which is divided further into four subdistricts (Fig. 29). The final result is as follows: the Betic Peri-plateu karstic arc (with four subdistricts: "Cantabrian", "Basque mountains", "Northern Levant", and "Betic"), "North oriental quadrant", "Balearic archipelago", and "Discontinuous Lusitanic karsts".

Fig. 19: Distribution of *Henrotius* JEANNEL, 1953, in the Iberian Peninsula and Balearic Islands.

Fig. 20: Distribution of *Zariquieya* JEANNEL, 1924, in the Iberian Peninsula and Balearic Islands.

Fig. 21: Distribution of *Oscadytes* LAGAR, 1975, in the Iberian Peninsula and Balearic Islands.

Fig. 22: Distribution of *Troglorites* JEANNEL, 1919, in the Iberian Peninsula and Balearic Islands.

Fig. 23: Distribution of hypogean *Pterostichus* BONELLI, 1810, in the Iberian Peninsula and Balearic Islands.

Fig. 24: Distribution of *Tinautius* MATEU, 1997, in the Iberian Peninsula and Balearic Islands.

Fig. 25: Distribution of *Galiciotyphlotes* Assmann, 1999, in the Iberian Peninsula and Balearic Islands.

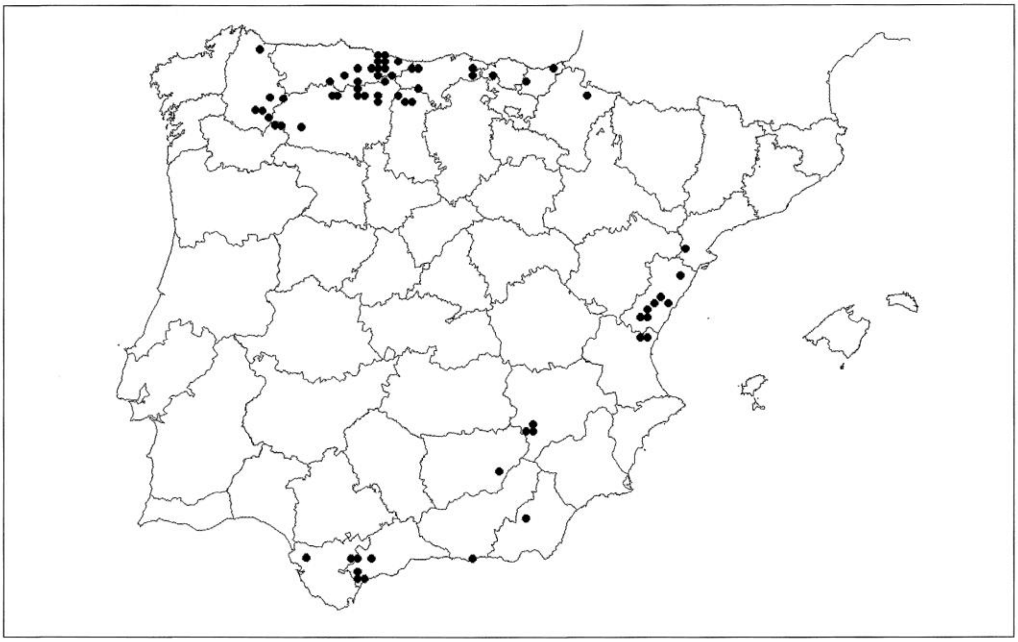


Fig. 26: Distribution of hypogean *Laemostenus* Bonelli, 1810 of the subgenus *Antisphodrus* Schaufuss, 1865, in the Iberian Peninsula and Balearic Islands.

Fig. 27: Distribution of hypogean *Platyderus* STEPHENS, 1827, in the Iberian Peninsula and Balearic Islands.

Fig. 28: Distribution of *Ildobates* ESPAÑOL, 1966, in the Iberian Peninsula and Balearic Islands.

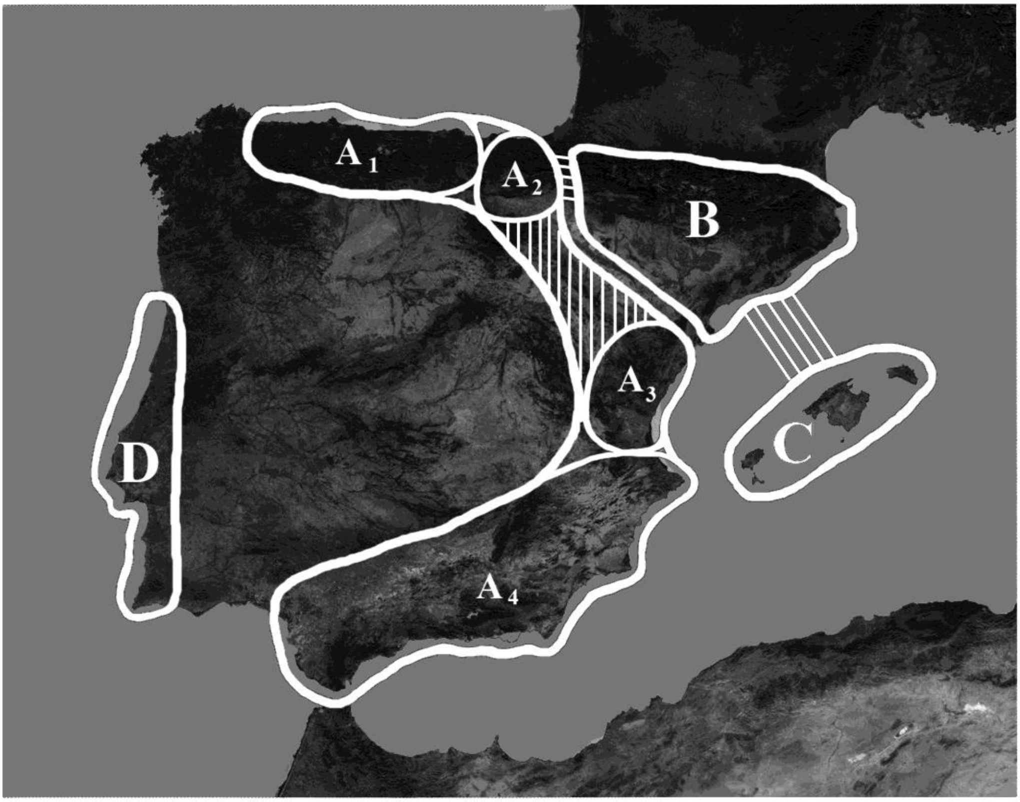


Fig. 29: Biospeleological districts based on the hypogean Carabidae: A – Betic Peri-plateau karstic arc, composed of A1 – Cantabric, A2 – Basque mountains, A3 – Northern levant and A4 – Betic. B – North east quadrant. C – Balearic archipielago. D – Discontinuous Lusitanic karsts.

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