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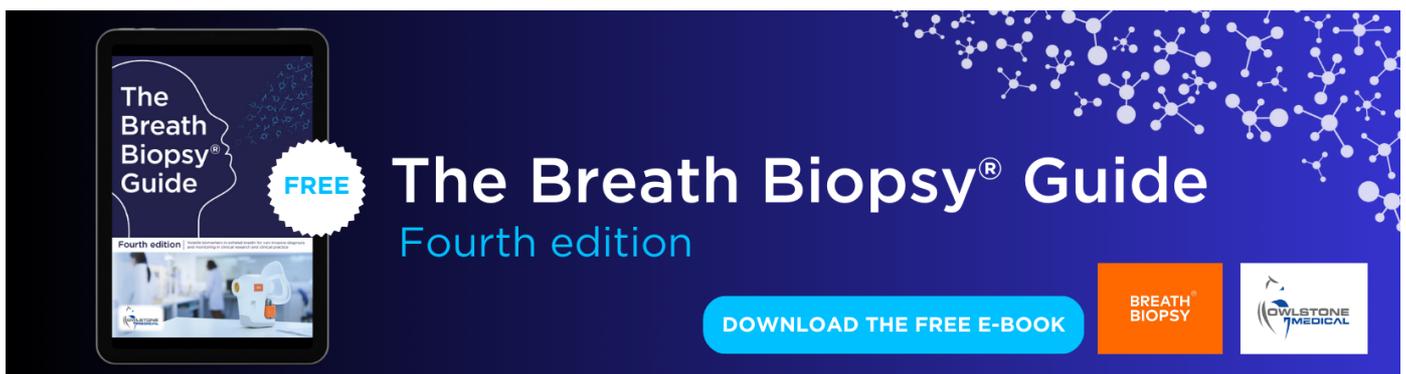
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Hypogean carabid beetles as indicators of global warming?

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Abstract

Climate change has been shown to impact the geographical and altitudinal distribution of animals and plants, and to especially affect range-restricted polar and mountaintop species. However, little is known about the impact on the relict lineages of cave animals. Ground beetles (carabids) show a wide variety of evolutionary pathways, from soil-surface (epigeal) predatory habits to life in caves and in other subterranean (hypogean) compartments. We reconstructed an unprecedented set of species/time accumulation curves of the largest carabid genera in Europe, selected by their degree of 'underground' adaptation, from true epigeal predators to eyeless highly specialized hypogean beetles. The data show that in recent periods an unexpectedly large number of new cave species were found lying in well established European hotspots; the first peak of new species, especially in the most evolved underground taxa, occurred in the 1920–30s and a second burst after the 70s. Temperature data show large warming rates in both periods, suggesting that the temperature increase in the past century might have induced cave species to expand their habitats into large well-aired cavities and superficial underground compartments, where they can be easily sampled. An alternative hypothesis, based on increased sampling intensity, is less supported by available datasets.

Keywords: underground fauna, troglobionts, climate change, Coleoptera, carabidae, biodiversity, caves, MSS

 Online supplementary data available from stacks.iop.org/ERL/8/044047/mmedia



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1. Introduction

Experimental studies on the response to recent climate change of epigeal vascular plants and animals show increasing evidence of a poleward or (in mountain areas) uphill shift

of population and range boundaries [1, 2]. Conversely, little is known about the possible response to climatic changes of the hypogean (or underground) compartment of life, the so called ‘cave animals’ [3], most represented by relict lineages strongly adapted to life in the depths of mountain massifs [4, 5].

The insects of the family carabidae, well known as ground beetles, are inhabitants on the soil surface [6] with various adaptations and modes of life [7]. They may live as arboreal vegetation climbers in the forests [8–10], or as herbaceous plant climbers and seed feeders [11, 12]. In some partitions of the family, especially in the subfamilies Trechinae, Pterostichinae and Platyninae, a remarkable evolutionary trend towards life in underground compartments has been described, and specific adaptations to subterranean life have been recognized since the first half of the 19th century. The characteristics of the hypogean fauna, especially taxonomy, biogeography, morphology and ecology were studied by several authors [13–15].

The habitat of subterranean beetles comprises all types of holes existing below the soil surface, which older authors distinguished as micro- and macrocaves. The former are given by the complex patterns of cracks and fissures existing in the bedrock, especially in calcareous karstic substrates. The latter is the only compartment accessible by humans and in which beetles are actually detected. Only in the last decades the concept of subterranean habitat was extended to the MSS [16], ‘milieu souterrain superficiel’ or ‘mesovoid shallow substrate’, represented by the fissure nets of epikarst, the ground of sinks, rock debris covering mountain slopes, talus, screes, soils rich of stones and blocks, and seepage springs [17].

In this work we aim to demonstrate that underground living beetles are highly sensitive to global warming and that the warming rates of the last century might have impacted the habitat extent of these insects. In the last decades, and especially after 1980, considerable new findings and changes of population sizes in well investigated caves have been recorded [3], and many new species and genera have been detected also in the below ground life hotspots of Europe. Some examples of these findings include (with more cases presented in the supplementary material available at stacks.iop.org/ERL/8/044047/mmedia): the new subspecies *Anopthalmus spectabilis stygius* Drioli in 1980 in the Northern Adriatic mainland, some new species of *Orotrechus*, *O. gigas*, *haraldi*, *schwienbacheri*, *theresiaae*, in the years after 1970 in the Southeastern Alps, the new trechine genus *Lessinodytes* Vigna Taglianti 1982 in caves of the Lessine Prealps near Verona, exhaustively visited by entomologists since 1940; the new genus *Galiciotyphlotus* Assmann 1999, perhaps a Platyninae, in Galicia, Spain; *Dalyat mirabilis* Mateu 2002 in Almería, Southern Spain, assigned [18] to Promecognathinae, a small carabid subfamily with two species in North America and four genera in South Africa.

There is no doubt that the implementation of cave exploring techniques, the use of long term bait traps, as well as the opening of eastern European countries, are reasons for the detection of many new species. Nevertheless, in the last

decades unexpected findings of new subspecies, species or even genera of subterranean carabids progressed at such a rate to warrant at least two main hypotheses.

H1—Global warming hypothesis. Given the strong sensitivity of subterranean ground beetles to climate conditions, among others to low winter temperatures, it is possible that 20th century global warming [19] might have caused these populations to expand their hypogean habitat (or ‘inhabitable volume’) towards the earth’s surface, leading to an increase of findings of new genera/species. We address this question by analyzing the species accumulation curves of representative epigeal and hypogean genera or higher taxa, and by comparing these curves to the progressive increase of temperature observed in the 20th century. The curves were constructed for 12 generic or suprageneric taxa (table A.3 of the appendix) that are representative of European fauna and of the full range of adaptations from the epigeal life to the most specialized troglomorphic habits. Within this context, we hypothesize that the more a group is sensitive to increasing temperatures, the higher will be the number of new species found, especially in the late decades of the 20th century when the surface warming trend is maximum [19]. Basic assumptions are: (a) because of sensitivity to winter frosts, habitat and range extent of hypogean carabid beetles tend to expand if the zone exposed to deep daily/monthly temperatures retreats towards the surface; (b) habitat shifts should have occurred especially after 1970, when the anthropogenic temperature increase was particularly marked [19], inducing for example ‘laurophyllisation’—the spread of evergreen broadleaved species in the submediterranean forests [20]; (c) the warming effects on habitat expansion should be more evident in areas with more continental climate or where the winter frosts are relatively severe, e.g. in Alpine chains and the Balkans compared to Western Europe (Pyrenees); (d) Europe is an especially suitable region to study species accumulation curves because investigations of below ground animals started very early, around the middle of 19th century.

H2—Sampling intensity hypothesis. An alternative explanation to H1 is that the number of biospeologists involved in collecting carabid beetles in subterranean environments may have increased in the last decades in such a way that previously neglected caves and taxa were finally discovered. The systematic use of long-time trapping in the MSS and new cave exploring techniques could have given a substantial ‘speed up’ to new findings, especially by allowing surveys of deeper galleries and shafts. We address this second hypothesis by counting the authors and co-authors of all the descriptions recorded in the crucial taxa of highly evolved cavernicolous carabids, and comparing species/decade statistics with corresponding author numbers, bearing in mind that in most papers (about 70%) collectors and descriptors coincide.

Before addressing these two hypotheses, it is useful to review the ecological classification of hypogean organisms, which has been recently reexamined as follows [15]: (i) troglobionts (strongly bound to hypogean habitats), (ii) eutroglophiles (‘essentially epigeal species able to maintain

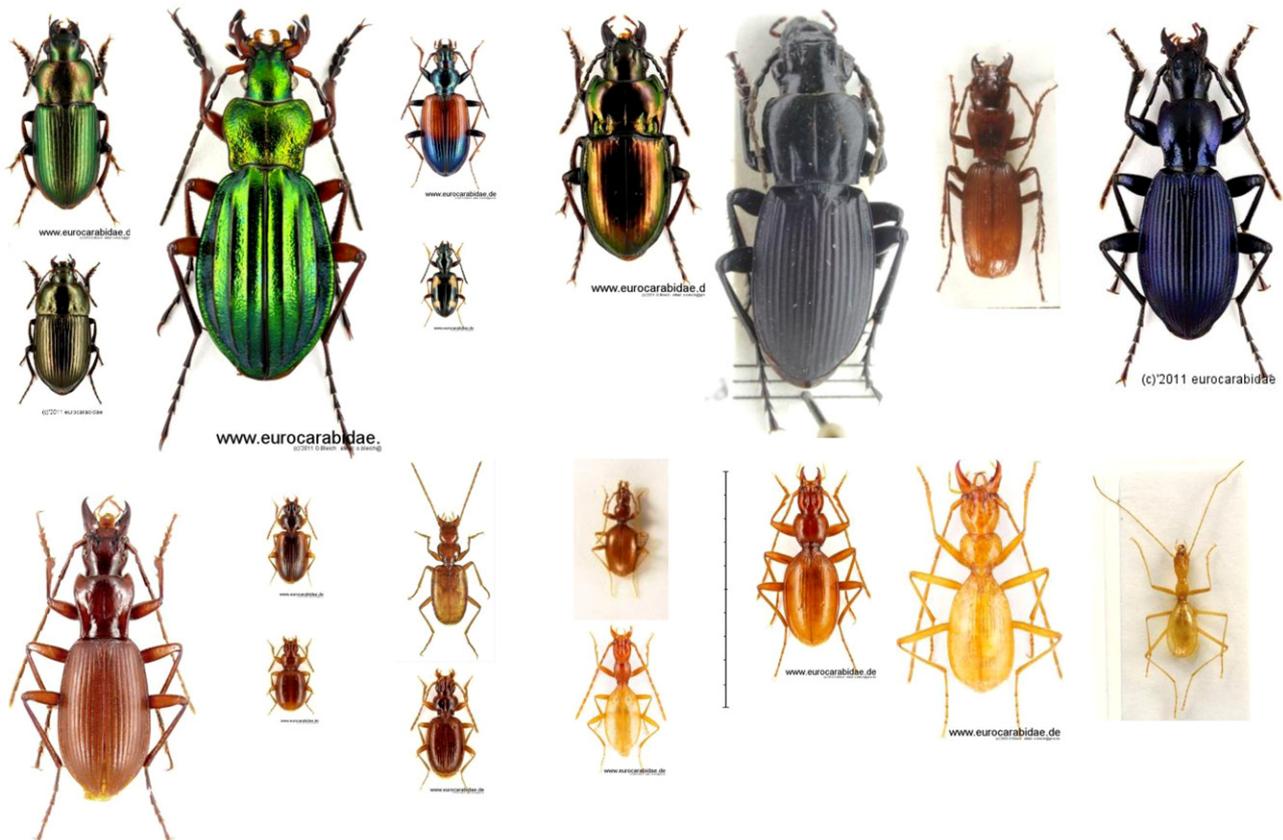


Plate 1. From epigean to hypogean morphs of carabid beetles (hypogean evolution). From left above to right below. *Harpalus distinguendus* and *Amara lunicollis*, Italy, partly seed feeders often found on vegetation. *Carabus auronitens*, Eastern Alps, terricolous predator. *Bembidion eques*, and *B. illigeri*, Germany, river bank dwellers. Pterostichinae genera: *Pterostichus burmeisteri*, Germany; *Percus bilineatus*, Southern Italy, lapidicolous, living in forest soils especially under stones (photo: Brandmayr); *Speomolops sardous*, Sardinia, blind, cave dwelling Pterostichinae (photo: Brandmayr). Sphodrinae: *Laemostenus dalmatinus*, Trieste, karstic soil dweller; *Laemostenus schreibersi*, Eastern Alps, eutroglophile species. Trechine genera: *Trechus quadristriatus*, Italy, soil dweller, *Trechus elegans*, Eastern Alps, several *Trechus* live in the MSS; *Duvalius aliciae* (Sicily, photo from Magrini et al 2007), *Duvalius exaratus*, Eastern Alps, all *Duvalius* species are MSS or cave dwellers. *Orotrechus millerianus*, Karst near Trieste, *O. carinthiacus*, Carinthia, Austria, all *Orotrechus* species are MSS or more or less troglomorph cave dwellers. *Typhlotrechus bilimeki*, Karst near Trieste, stenothermic cave dweller. *Aphaenopidius kannikensis*, Slovenia, highly specialized troglobiont ('aphaenopsian') belonging to the *Anophthalmus* lineage. *Aphaenops cerberus*, Moulis, France, a representative of one the extremely specialized hypogean trechine genera of the European fauna (photo: Brandmayr). All other photographs are courtesy of Mr Ortwin Bleich, Germany, and are taken from the site: www.eurocarabidae.de. Scale: 10 mm.

a permanent subterranean population'), (iii) subtroglaphiles (species inclined to perpetually or temporarily inhabit hypogean habitats but needing epigean environments for some biological functions, e.g. reproduction), (iv) troglonexes (sporadic in caves). A second evolutionary pathway, that of deep soil dwellers (endogenous forms), is not considered in this work, because they are not strictly adapted to life in caves [4] (table A.1 of appendix).

Concerning the adaptation to the hypogean domain, epigean forms of carabid beetles are mostly winged and show well pigmented, metallic, colorful or black-brown bodies, well developed eyes and appendages of normal length. The cave dwelling entities are normally yellow-brownish or pale, the eyes being almost completely or totally reduced (anophthalmic), and are characterized by longer antennae and legs and probably an enhanced tactile-olfactory sensorial set. Common 'troglomorphic' characteristics are found in the specialization of sensory organs (touch chemoreceptors, hygroreceptors, thermoreceptors, pressure

receptors), elongation of appendages and foot modifications, eyes reduction, pigment and wings reduction and increased egg volume [4, 13]. Circadian rhythms of locomotory activity also show a progressive regression in cave beetles [21]. There is a general agreement in defining the status of some extremely specialized taxa as a sort of 'blind end' of subterranean evolution. Their legs and antennae are long, and the swollen elytra form a 'subelytral chamber', perhaps a sort of humid air-volume protecting the animals against rapid desiccation. These extreme specialists are called 'aphaenopsian' and represent the most typical troglobionts.

Hypogean beetles are known to be highly stenothermic and stenohygic, able to react quickly to temperature and/or air humidity variations of their habitats [22]. Most hypogean carabids are adapted to temperatures of 10–12 °C or less, and to relative humidity between 95 and 100% [6]. For example *Typhlotrechus bilimeki* conducts its entire life cycle [23] at a temperature of 4–8 °C, and reproduces [24] during the 'summer' at a stable temperature of 8 ± 1 °C, and air humidity

oscillating between 98 and 100%. Several *Anophthalmus* and *Duvalius* species are bound to even lower temperatures, sometimes demonstrating impressive activity rates in ice dropping caves or in alpine calcareous soils at temperatures of 0–5 °C. Climate changes of the past are thought to be important driving forces of subterranean evolution [17]; for example during the Messinian [25] salinity crisis or the Ice Ages [26] troglophilic populations were forced into even deeper habitats. The Ice Ages appear to be the main causes of the actual relict distribution of hypogean carabid lineages in the mountains of Middle and Southern Europe [3, 27].

2. Methods

In this study only hypogean ‘cavernicolous’ forms [4] are included, as defined in table A.1 of the appendix, i.e. only beetles that are seen as inhabitants of the underground compartment (caves and MSS). Table A.2 of the appendix provides an overview of all hypogean taxa of Europe. To reconstruct the time sequence variations observed in discoveries of epigeal taxa versus hypogean ones, a set of 12 diverse genera or higher taxa was chosen, which are listed and described in table A.3 of the appendix. On the basis of the fauna Europaea database [28] we ordered chronologically all the findings of hypogean carabids starting from 1840. We then compared the species accumulation curve of the western palearctic region [27] (figure 2(a), over 3000 species) with that of the 12 significant carabid genera/taxa groups selected for the European area (figure 2(b)). For each genus or taxa group a chronological list was compiled excluding the nominal forms but including all the subspecies ascertained for any single species. The fauna Europaea database was used for the status of all taxa included in this study, and the decade 2001–2010 was completed by recent descriptions and monographs [29]. The actual discovery dates of type specimens were reconstructed at least for the last decades, and overall more than 2800 taxa were included in the counts (table A.3). For all taxa/groups the discovery dates were ordered chronologically and arranged in: (1) species or subspecies descriptions/decade and (2) cumulated values/decade. An additional set of decadal values were calculated counting the hypogean genera for Europe, (inclusive of endogenous forms), but considering only the date of discovery of the first species.

To obtain a scale of increasing adaptation towards the subterranean environment, the degree of adaptation of the taxa of table A.3 was evaluated and ordered on the basis on their troglomorph evolution using the main behavioral and morphological features listed in table A.4 of the appendix, which presents the results of this evaluation by ranking the twelve genera on a scale from –5 (*Amara*) to 14 (*Aphaenops*). The twelve genera/taxon groups were roughly classified in eight steps: seed eaters, ‘terricolous’, river bank dwellers, ‘lapidicolous’, troglophilous, partly MSS dwellers, MSS or caves, most troglobionts. Two numeric indices were then calculated based on this sequence of genera: (1) the sensitivity index, which quantifies the influence of the last warming phase on the discovery of new taxa (calculated as the

percentage of forms found after 1970 on the total of all species/subspecies known so far); (2) the ‘median decade’, i.e. the decade in which 50% of all forms known for the taxon was reached. This second index provides us with a rough evaluation of the ‘resilience’ to discovery expressed by each taxon/group.

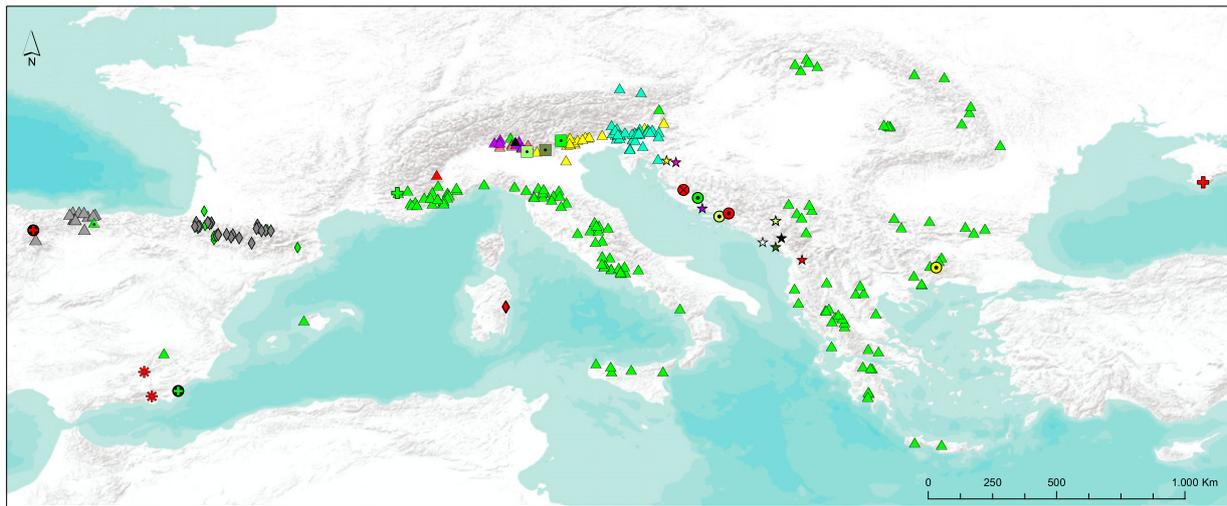
The temperature data used in figures 3(b)–(d) were taken from the half degree resolution dataset produced by the Climatic Research Unit (CRU) of the University of East Anglia (New *et al*, 2000) averaged over the regions shown in figure S1 (supplementary material available at stacks.iop.org/ERL/8/044047/mmedia).

To test the H2 hypothesis, all authors of the descriptions of discoveries were ordered per decade (five year periods for the *Duvalius* species), and the correlation coefficient of authors versus the temporally cumulated taxa was calculated. The number of authors/decade was corrected by adding specialists known to be certainly active in the same period. Furthermore, to test the H1 hypothesis we calculated the correlation coefficient between the cumulated taxa curves of *Duvalius*, *Anophthalmus*, *Aphaenops*, *Orotrechus*, and all European genera, and the decadal variations of the northern hemisphere land-surface temperatures (°C) from 1850 to 2010 relative to the 1961–1990 mean, as expressed by the smoothed curve of CRUTEM4 [30], which are in line with the trends in European temperatures. Figure S2 (available at stacks.iop.org/ERL/8/044047/mmedia) provides a graphic illustration of our temperature hypothesis as applied to a cave rich massif.

3. Results

The geographic distribution of discoveries after 1970 is presented in figure 1. Epigeal taxa (*Amara*, *Harpalus*, *Carabus*, (figures 2(a) and (b))) show regular sigmoid curves, while all true cave dwelling taxa (from *Duvalius* to *Anophthalmus*) show curves far from saturation and in most cases characterized by two peaks in discoveries, the first around the 1920/30s and the second after the 1970/80s (figures 2(c) and (d)). These periods correspond to times of maximum warming rates globally [19]. Mountain dwellers (Pterostichini) or subtroglophile/eutroglophile forms (*Laemostenus*, *Trechus*) show intermediate patterns between the saturation and double peaked ones. Also, the sequence of discoveries of hypogean genera in Europe (figure 3(a)) shows in the past century a first peak in the 20s and a second, impressive burst in the last three decades. In fact, this last period is characterized by the appearance of several ‘aphaenopsian’, highly specialized forms, and by the outbreak of non-trechine troglomorph taxa along with the unexpected new subtribe Lovriciina, with three genera and four species [31]. These peaks in new discoveries also correspond to periods of maximum global warming [19].

To illustrate regional differences observed across the European area, we compare accumulation curves of *Aphaenops* (Pyrenees), *Anophthalmus* (Eastern Alps) and *Duvalius* (European–Mediterranean mountains) with mean annual and winter–spring temperatures over the respective areas (figures 3(b)–(d)). It appears that in Western Europe the



TRECHINE GENERA

- ▲ Allegretta
- ▲ Insubrites
- ▲ Boldoriella
- ★ Tinautius
- ▲ Duvalius
- ◆ Geotrechus
- ▲ Apoduvalius
- ◆ Sardaphaenops
- ▲ Anophthalmus
- ▲ Doderotrechus
- ▲ Orotrechus
- ◆ Aphaenops

- ★ Acheroniotes mlejneki
- ★ Adriaphaenops zupcense
- ★ Adriaph. zupcense tartariensis
- ★ Albanotrechus beroni
- ★ Croatotrechus tvrtkovi
- ★ Dalmataphaenops chiarae
- ★ Derossiella nonveilleri
- ★ Hydrotrechus cantabricus
- ★ Jalzicaphaenops poljaki

- Lessinodytes caoduroi
- Lessinodytes glacialis
- Lessinodytes pivai
- Luraphaenops gionoi
- ★ Minosaphaenops ollivieri
- ★ Scotoplanetes aquacultor
- ★ Taurocimmerites dublanskii
- Velebitaphaenops giganteus

OTHER TRIBES

- Dalyat mirabilis
- Galicityphlotes weberi
- Lovricia jalzici
- Lovricia aenigmatica
- Neolovricia ozimeci
- Paralovricia beroni

Figure 1. Map of new discoveries of hypogean genera and species of carabids recorded after 1970. All taxa show relict distribution in areas of Europe uncovered by Pleistocene ice.

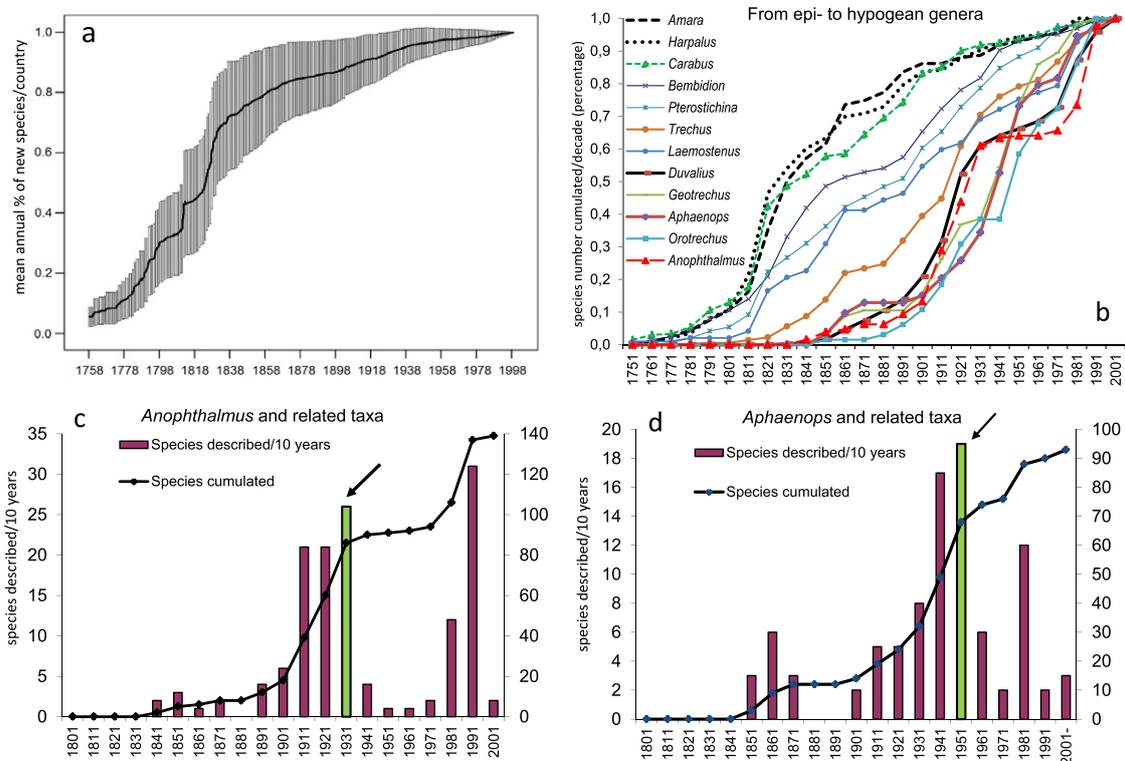


Figure 2. (a) Species accumulation curve of the mean (± 1 SD) annual percentage of newly recorded carabid beetles per country in the western palearctic region. Redrawn from [27]. (b) Species accumulation curves in European carabid genera ranked from true epigeal forms to typical hypogean ones. (c), (d) Species accumulation curves of the pyrenean genus *Aphaenops* and of the eastern alpine genus *Anophthalmus* showing the respective descriptions/decade.

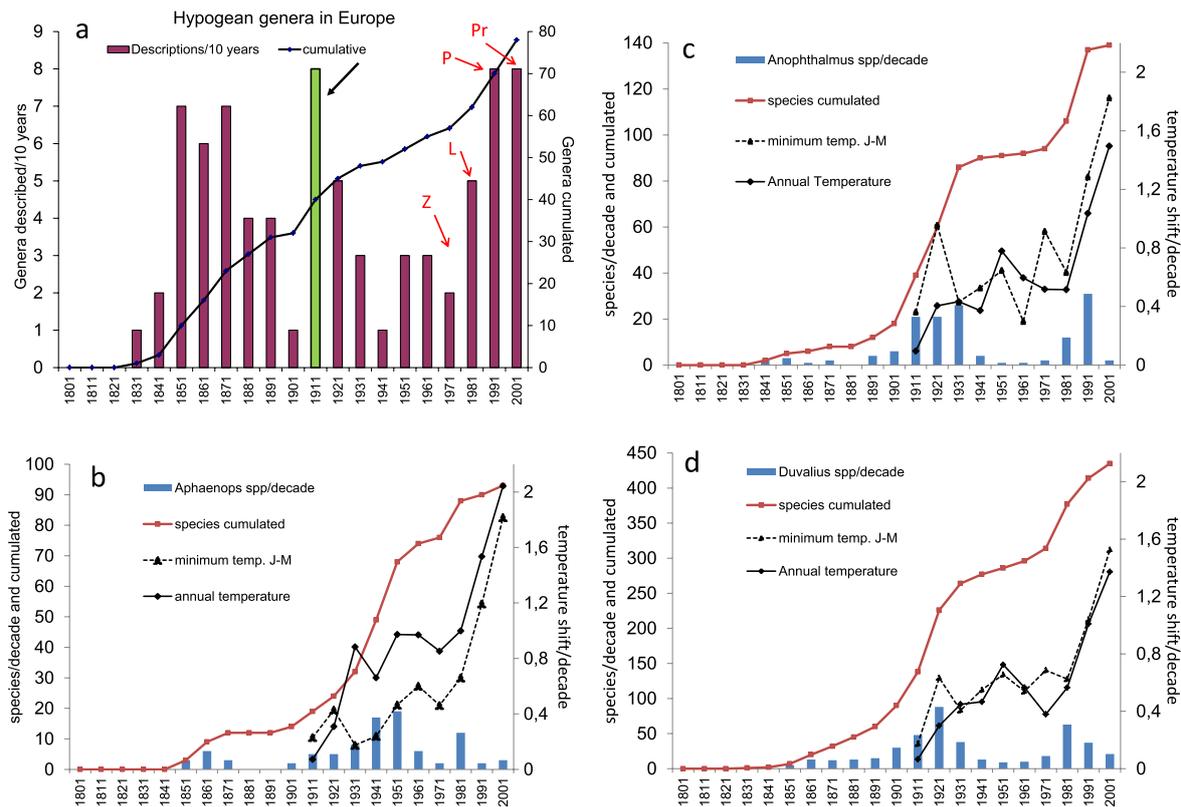


Figure 3. (a) Accumulation curve of the hypogean genera described in Europe. Green bars: decade in which half of the total species/genera was described. Red arrows (d) discovery of unexpected or new taxa belonging to tribes or subtribes so far unknown as troglitic for Europe: Z—Zuphiinae (*Ildobates*); L—Lovriciina (*Lovricia*); P—Platyninae (*Galictyphlotes*); Pr—Promecognathinae (*Dalyat*). (b)–(d) Temperature increase after 1900 and accumulation curves, species descriptions/decade in *Anophthalmus* ((b) Eastern Alps), *Aphaenops* ((c) Pyrenees) and *Duvalius* ((d) southern Europe). In the area of Pyrenees (c) the values of annual mean temperature/decade are distinctly above the mean of minima from January to May, and the decades after 1931 show no decrease. In the *Anophthalmus* and *Duvalius* area after 1931 the temperatures drop markedly, and this seems to ‘stop’ discoveries until the eighties.

warming has been relatively continuous in time, without a plateau in the 50s, whereas in the Eastern regions the warming shows two periods of maxima, the 10–20s and after the 70s, corresponding to peaks of trechine findings, with flat temperatures and low trechine discoveries in 1950–1970.

Thereafter we measure the sensitivity of each taxon/group in two ways: (i) counting the % of new species/subspecies found after 1970 (sensitivity index) and (ii) by recording the medium decade in which each taxon scored 50% of the actually known species. All taxa/groups are ordered on the basis on their troglomorph evolution using main behavioral and morphological features (table A.4 of the appendix), obtaining a scale of 12 levels, roughly classified in eight steps: seed eaters, ‘terricolous’, river bank dwellers, ‘lapidicolous’, troglophilous, partly MSS dwellers, MSS or caves, most troglionts. These two indices are shown in figures 4(a) and (b). The sensitivity index for each level of troglomorph evolution (figure 4(a)) shows that for most cave dwellers about 20% of taxa was found after 1970 (lower values are observed in Pyrenean genera). *Orotrechus*, a genus in which many new highly specialized forms were found in the last decades, shows the most delayed median decade index, but also for other markedly troglomorph groups the median decade index peaks around 1940–50 (figure 4(b)).

Figures 2 and 3 clearly show that in Europe only troglitic carabids (and the eutroglophilous *Laemostenus* species) were increasingly influenced by the pattern of warming periods, suggesting that the rising temperatures may have allowed previously unknown ‘hidden’ species/populations to settle new macrocaves and MSS layers closer to the soil surface, thereby facilitating their discovery by humans. Figure 4 quantifies the sensitivity of each taxon/group to the warming trend and confirms that ‘resilience’ to discovery concentrates in hypogean carabids.

Finally, we compare the correlation coefficients of the cumulated taxa curves of the highly evolved Trechine or European carabid genera versus: (i) the northern hemisphere temperature anomalies based on the 1961–1990 means of CRUTEM4; (ii) the number of authors active/decade in the period 1850–2010 as a quantitative expression of the sampling intensity. The following correlations of taxa versus CRUTEM4 temperatures were found: *Duvalius*, $r = 0.89$; *Anophthalmus*, $r = 0.92$; *Aphaenops*, $r = 0.84$; *Orotrechus*, $r = 0.89$; European genera, $r = 0.87$. The correlation values versus authors/decade were, in the same sequence: $r = 0.61$; 0.15; 0.56; 0.60; 0.65. In figure 5(a) an example is given of the pattern of CRUTEM4 anomalies compared with the species/subspecies cumulated curve of the

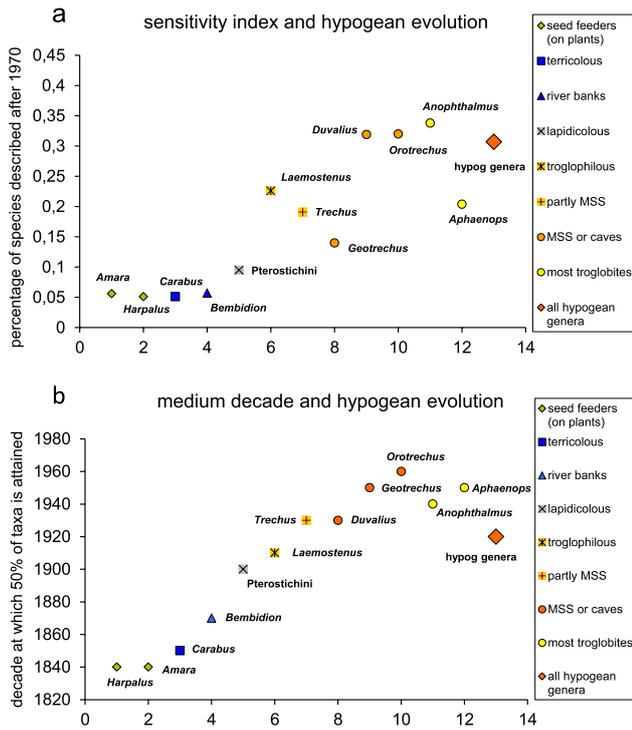


Figure 4. Hypogean evolution degree of large carabid genera or tribes versus sensitivity to global warming and delay in discovery (medium decade). (a) Sensitivity expressed as percentage of species discovered after 1970. (b) Decades in which each taxon (or taxa group) recorded 50% of the species actually known. The position of ‘all hypogean genera’ is arbitrary.

genus *Anophthalmus*, showing a strong correlation between the two curves. By comparison, figure 5(b) presents the authors/decade versus taxa cumulated in time showing that the number of descriptors rises only very weakly in the last three/four decades.

4. Discussion

In this letter we reconstructed a large set of species/time accumulation curves of the largest carabid genera/taxa groups in Europe and attempted to place these curves within the context of recent warming trends globally and over Europe (figures 2(b)–(d)). We found that new discoveries of European cave species are far from saturation, but show peaks in correspondence of periods of maximum warming, in particular in areas that have been explored since many years. Even in the best explored countries of Europe, as in Northeastern Italy or Slovenia, where the Science of Biospeology started [5], and for apparently ‘well known’ genera such as *Orotrechus* and *Anophthalmus*, an increase of more than 30% of taxa was recorded after 1970 (figure 4(a)). Moreover, many of these new findings, especially from the Southern Alpine range and in the Dinaric chains, concern highly evolved trogllobiont or aphaenopsian forms, normally living deep inside and in the more protected portions of the underground compartment. Last but not least, only in the last decades Europe reveals to be a Pandora’s box of

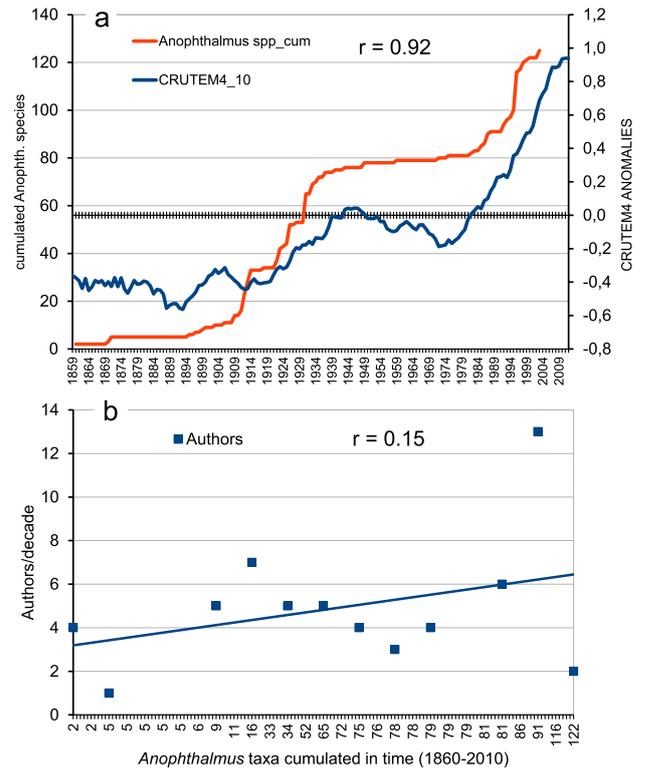


Figure 5. (a) Accumulation curve of *Anophthalmus* species (and related) versus CRUTEM4 temperature anomalies of the northern hemisphere continents (10 y smoothed). Point 0 of the right axis: temperature average of 1961–1990. (b) Authors of the species descriptions (/decade) versus taxa accumulated in time (1860–2010).

carabid (sub)tribes previously unknown from the hypogean environment (Promecognathini, Lovriciina) or shared with other continents (Platynini, Zuphiini). These results suggest that the crowding of highly troglomorph findings in the last decades is not only a consequence of intensified research or technology improvements but also a result of the upward fluctuations of subterranean carabid populations driven by higher temperatures associated with global warming.

In fact, to support this conclusion we quantitatively examined the two hypothesis that the increase in new findings are related to increasing temperatures (hypothesis H1 above) or increasing number of biospeologists and sampling intensity (hypothesis H2 above). We found high correlation coefficients between the species/genera accumulation curves of true cave taxa and decadal temperature anomalies of the northern hemisphere continents, in the range of 0.84–0.92. By comparison, the author numbers are less strongly related to the species curves, with correlation values around 0.60 (0.56–0.65), and even 0.15 (for *Anophthalmus*). This clearly suggests that changes in sampling intensities alone cannot explain the increase in new findings, but that the contribution from rising temperatures might be not only significant, but even dominant.

An alternative explanation for the increase in new findings in the last decades might be related to the fact that small species of insects tend to be discovered later than

medium sized or larger ones, and that many cave dwellers are mostly of small size. In fact, a recent paper [32] demonstrates that in the western Palearctic area the discovery of small species on average started later than that of larger ones, but this conflicts with the fact that in several genera the large size, aphaenopsian forms have been detected only in the last years (*Orotrechus*, *Allegrettia*, *Dalyat*). Moreover, the global warming effect hypothesis is also supported by the fact that a relevant number of new descriptions concerns specimens or populations that appeared suddenly in long-time explored caves (*Lessinodytes*, several *Duvalius*, see supplementary materials available at stacks.iop.org/ERL/8/044047/mmedia).

In conclusion, our results indicate that because of their extremely high sensitivity to abiotic factors, in particular temperature, it is possible that hypogean carabids can be intriguing indicators of climate change, and future work will address the role of possible additional factors acting on more local scales, such as precipitation and cave temperature and humidity. The habitat shifts of these beetles may thus be used as an ecosystem response indicator of global warming, which stresses the importance of a more continuous monitoring of selected cave populations.

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Author contributions

PB and FW planned the study, PB, FG and AC contributed equally to the manuscript, GC constructed most of the species/genera Databases, LM elaborated temperature and climate data at regional scale, RP analyzed species/author/temperature pattern relationships. All authors discussed the analysis and results and commented on the text. Additional information

The authors declare no competing financial interests.

Appendix

A.1. The study object: hypogean carabidae

The first hypogean carabid was described in Italy by Comolli (1837), as *Trechus longhii*, and subsequently assigned to the genus *Duvalius* Delarouzée, 1859. We consider in this work all cave dwelling, ‘cavernicolous’, ground beetles in the latest sense, with exclusion of the endogenous taxa, which are deep soil dwellers bound to the organic layers, but including all taxa found in the MSS (mesovoid shallow substrate, also called: UHZ, upper hypogean zone). This is because only cavernicolous forms are able to colonize the net of macro- and microcaverns of the mountain massifs, reaching

depths of several hundred meters. The adaptive features of cavernicolous and endogenous forms are depicted in table A.1.

A.2. The study area: Europe

Our study area is Europe, in the core of the western Palearctic sub-region. Biospeology started in Slovenia around 1830, but its scientific interest was immediately high among European entomologists (Schjødte, 1851, see also reference list in the supplementary material available at stacks.iop.org/ERL/8/044047/mmedia). The Dinaric karst in the western Balkan Peninsula should be considered a global hotspot of subterranean biodiversity, since from this area more than 900 aquatic and terrestrial subterranean (troglobiotic) species are recorded (Sket, 2005). The structure of this subterranean hotspot is described in Zigmajster *et al* (2008), moreover oromediterranean Europe currently hosts 14 of the 20 richest caves in the world (Culver and Sket [5]). Trechinae and other hypogean carabids crowd in the Southern part of Europe, and old authors (Holdhaus, 1954) demonstrated that in Europe only unglaciated areas were able to preserve relicts of the Tertiary age from extinction. Recent research confirms the ideas of Holdhaus, e. g. Schuldt and Assmann [27] demonstrated that widespread carabid species of western Palearctic are more related to current climate, whereas ‘restricted-range (endemic) species were most notably related to range in elevation and bound to historical factors’.

A.3. Methods

A.3.1. The carabid taxa investigated. The hypogean (anophthalmic) genera so far discovered in Europe and the Canary Islands are 78, as in table A.2.

We reconstructed the species and subspecies descriptions/decade and their cumulated curves in 12 genera or higher groups, selected according to their habitat preferences and adaptation to a subterranean way of life. Starting from the markedly epigeic ones, the taxa groups are listed in table A.3.

A.3.2. Ranking the genera/taxa groups according to their ability to colonize the hypogean domain. Considering behavioral and morpho-ecological characteristics, the genera of table A.3 can be arranged as in table A.4, obtaining a continuous transition from true epigeic forms to the most cavernicolous ones. Each trait found in the taxon/group was assigned a positive or negative value based on the following criteria: a—metallic body (reflection by photonic crystals of the cuticula, well developed in diurnally active sun exposed insects): -1; (b)—plant climbing ability: -1; (c)—vegetal food intake (plant seeds or sprouts): -1; (d)—eyes large or of normal size: -1; (e)—depigmented cuticula: 1; (f)—eyes small in at least some species (but with more than 50 ommatidia): 1; (g)—at least some species microphthalmic: 1; (h)—blind (anophthalmic): 1; (i)—cuticula testaceous (reddish brown): 1; (k)—body entirely yellow: 1, or pale: 2; (l)—elongated appendages: 1, extremely elongated: 2; (m)—specialized trichobothria: 1; n—subelytral chamber: 1,

Table A.1. Adaptive features in endogeous and cave carabids (from [4]).

Endogeous ↓	Common features: depigmented eyeless wingless	Cavernicolous ↓
Small size		Large size
Short appendages		Elongated appendages
Burrower forelegs		Simple forelegs
Moniliform antennae		Filiform antennae
Serrulated shoulders		Not serrulated shoulders

Table A.2. Taxonomic position of the hypogean genera of Europe within the family carabidae.

Subfamily	Tribus	Subtribus	Genera
Scaritinae	Clivinini	Reicheiina (endogeous)	8
Trechinae	Trechini	Trechina	36
		Trechodina	2
	Bembidiini	Anillina (endogeous)	18
		Lovriciina	3
Pterostichinae	Pterostichini	Molopina	6
		Pterostichina	2
Platyninae	Platynini		1
Promecognathinae			1
Dryptinae	Zuphiini		1

Table A.3. The genera/higher taxa for which species/subspecies description and accumulation curves were calculated.

Genus	Notes	Taxa
<i>Amara</i> Bonelli	All subgenera	159
<i>Harpalus</i> Latreille	In the widest sense, including the taxa around <i>Ophonus</i>	196
<i>Carabus</i> Linnaeus	All subgenera + <i>Procerus</i>	331
<i>Bembidion</i> Latreille	In the widest sense, <i>Ocys</i> excluded	329
Pterostichini	Molopina + Pterostichina sensu Vigna Taglianti, 2005, <i>Tapinopterus</i> excluded	482
<i>Laemostenus</i> Bonelli	And other Sphodrina, incl. <i>Sphodrus</i>	97
<i>Trechus</i> Clairville	Sensu stricto, and accepting the synonymy of <i>Hydrotrechus cantabricus</i> proposed by Ortuno and Jiménez-Valverde, 2011	356
<i>Geotrechus</i> Jeannel	A trechine genus limited to French and Spanish Pyrenees	57
<i>Duvalius</i> Delarouzée	All subgenera	435
<i>Orotrechus</i> Müller	A genus of the Southeastern Alps	65
<i>Anopthalmus</i> Sturm	Eastern Alps and Northern Dinarids, + the genus <i>Aphaenopidius</i> Müller	139
<i>Aphaenops</i> Bonvouloir	Pyrenees, all subgenera as in [29]	93
Hypogean genera of Europe	All the genera summarized in table A.2, including the endogeous forms	78
All taxa:		2817

markedly swollen: 2; (o)—open land dwellers in pastures and meadows: -1; (p)—forest dwellers more or less deep in the soil: 1; (q)—life in the MSS: 1, deep in caves also: 2.

The first five groups (*Amara*—Pterostichini) are typical troglaxenes, *Trechus* and *Laemostenus* are often found in caves, especially the *Laemostenus* of the subgenus *Antiphodrus* may be considered eutroglophiles living in the first five/ten meters of the MSS or of the karstic microcaverns. They represent a good example of transition between troglaxene and eutroglophile habits in Europe. The *Duvalius* are in most cases anopthalmic and testaceous or yellow, but many species are microphthalmic and darker. The more evolved forms live in caves, while the less evolved are

frequently found in the MSS, often at very low temperatures. The pyrenean genus *Geotrechus* shows similar features, but all species are blind, the legs are short and the elytrae flat, with no subelytral chamber. In *Orotrechus* the legs vary from short to longer, some late discovered forms are ‘aphaenopsian’, they are found both in the MSS as well as in caves. In *Anopthalmus* there is a clear shift of most species into caves, many species are tied to very low temperatures (life in ‘ice caves’), while in the related genus *Aphaenopidius* a subelytral chamber is somewhat developed. Finally, in *Aphaenops* all species show a more or less pronounced ‘aphaenopsian’ habit, long appendages and subelytral chamber.

Table A.4. Balanced evaluation of the degree of evolution towards subterranean life in representative carabid genera or higher taxa. Monospecific genera or those represented by few species were counted only in 'all hypogean genera', see figure 3(a) in the text.

Taxon	Degree of subterranean evolution	Metallic body	Plant climbing	Plant food		Depigmented cuticula	Eyes small	Microphthalmic	Blind (anophthalmic)	Testaceous	Yellow body	Elongated appendages	Spec. trichobothria	Subelytral chamber	Open land	Forests	MSS or caves
				intake (seeds)	large or normal												
<i>Amara</i>	-5	-1	-1	-1	-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Harpalus</i>	-5	-1	-1	-1	-1	-	-	-	-	-	-	-	-	-	-1	-	-
<i>Carabus</i>	-3	-1	-1	-1	-1	-	-	-	-	-	-	-	-	-	-1	1	-
<i>Bembidion</i>	-2	-1	-1	-1	-1	-	1	-	-	-	-	-	-	-	-	-	-
<i>Pterostichini</i>	-1	-1	-1	-1	-1	-	1	1	-	-	-	-	-	-	-1	1	1
<i>Laemostenus</i>	1	-1	-1	-1	-1	1	1	1	-	-	-	-	-	-	-	1	-
<i>Trechus</i>	3	-	-1	-1	-1	1	1	1	-	-	-	-	-	-	-	1	-
<i>Duvalius</i>	7	-	-	-	-	1	1	1	-	1	1	-	-	-	-	1	1
<i>Geotrechus</i>	8	-	-	-	-	1	-	1	1	1	1	1	-	1	-	1	1
<i>Orotrechus</i>	10	-	-	-	-	1	-	1	1	1	1	1	1	1	-	1	2
<i>Anophthalmus</i>	13	-	-	-	-	1	-	1	1	1	2	2	2	1	-	1	2
<i>Aphaenops</i>	14	-	-	-	-	1	-	1	1	1	2	2	2	2	-	1	2

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