

**ALPINE AND CAVE OR ENDOGEAN HABITATS AS POSTGLACIAL
REFUGIA: EXAMPLES FROM PALEARCTIC GROUND BEETLES, WITH
COMMENTS ON THEIR POSSIBLE ORIGINS (COLEOPTERA: CARABIDAE)**

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Abstract

We detect a common pattern of disjunct distributions of closely related cave or endogean and alpine populations of ground beetles (Coleoptera: Carabidae). This pattern is illustrated with examples from published and unpublished sources from western Europe, northern Africa and central Asia. Many alpine populations have morphological characters similar to those typical of cave or endogean species, and specimens are usually found in sheltered microhabitats, where they may avoid the low humidity and extreme temperatures of alpine environments. We postulate that these factors are similar on the surface in the alpine zone and in subterranean habitats at lower altitude. This may favor the presence of beetles in both habitats, even if they are disconnected and result in disjunct populations. The different degree of morphological divergence between the alpine and subterranean populations (ranging from not appreciable differences to forms considered to be fully separated species) can be taken as a relative indication of the antiquity of their separation. Divergence of alpine populations and their cave or endogean counterparts seems to have occurred at an earlier time in more southern and more recently in the more northern areas of Eurasia.

A classical hypothesis in the biospeleological literature (*e.g.*, Vandel 1964, Barr 1967, Peck 1973, Juberthie 1984, Bellés 1987 and 1991, Chapman 1993, Peck and Finston, 1993) asserts that some cave or soil-inhabiting endogean species originated from cold-adapted populations forced to occupy subterranean habitats because of an inter-glacial or postglacial increase of temperature and dryness in the above-ground habitats. The typical scenario is that of a widespread species living in soil, humus, or other wet microhabitats in periglacial areas during a cold phase, which is forced to track the remnant patches of favourable habitat when general environmental conditions turn warmer and dryer during an interglacial stage. Presumably, this can be achieved by the species either shifting its range to higher altitudes or by entering caves or the endogean medium at low or medium altitudes. This shift would result in separation of contiguous above-ground populations and eventually to speciation (Fig. 1).

This disjunct distributional pattern has been described in different groups of organisms which occur in cold or alpine environments (either at high altitude

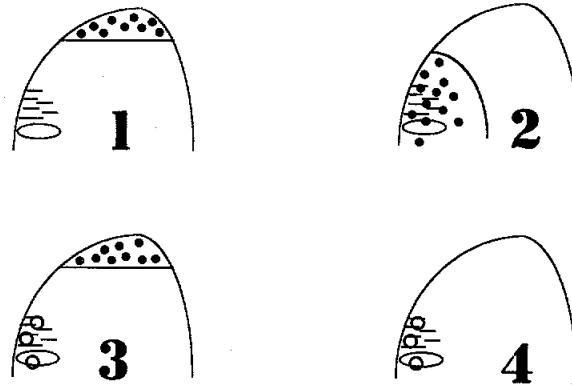


Fig. 1. Schematic representation of the classical hypothesis explaining the colonization of caves by above-ground populations driven by climatic changes (see Introduction) (modified from Juberthie 1984 and Peck 1973). **1)** Alpine ancestor in an interstadial. **2)** Alpine ancestor populations occupy lower altitudinal ranges during a glacial maximum, and colonize underground habitats. **3)** Low altitude above-ground populations disappear with the amelioration of the climate in the following interstadial, and underground populations become genetically isolated by allopatric speciation. **4)** Alpine above-ground populations may disappear, leaving under-ground species without close above-ground relatives.

or latitude), and which have isolated populations in caves at lower altitude or latitude. For example, the Pyrenean newt *Euproctus asper* (Duges) occurs in cold mountain streams at higher altitude, and in caves at lower altitude (Juberthie 1984). The collembolan *Onychiurus schoetti* occurs at sea level in the soil in Norway, but only in caves in Britain and western Europe (Chapman 1993:186). Several species of the alpine tipulid fly genus *Niphadobata* Enderlein, a typical winter inhabitant of snow fields, are regularly found at lower altitudes in caves (Turquin 1973, Bellés 1991; see additional examples in these two papers). Among beetles such patterns have not been clearly recognized, despite the large number of taxa inhabiting caves. Most of these, however, do not have either phylogenetically close surface-dwelling relatives, or the surface populations are not alpine but are typical of the forest litter at medium altitudes (e.g., *Trechus bordei* Peyerimhoff, living in Pyrenean forests between 800–1,000 m, with a close vicariant, *T. navaricus* Vuillefroy, in caves at only 200 m; or the forest species *T. uhagoni despaxi* Jeannel, with a cave population at lower altitude, Juberthie 1984).

In this paper we present several examples of Palearctic Carabidae with a cave or endogean and alpine habitat disjunction (Table 1), and discuss some of the factors that could be implicated in the transition from above-ground to subterranean environments in the evolutionary history of these beetle lineages.

Data

Western Europe. *Oronebria ratzeri ratzeri* Bänninger, a typical alpine taxon, lives in the Swiss Alps on snow fields (Colas 1954). A population of this subspecies occupies a cave in France, in the Jura Bernois, between 5 and 600 m. Another subspecies, *O. ratzeri henroti* Jeannel, also occurs in the Jura

Table 1. Summary data of Alpine and cave or endogean populations of Palearctic carabids.

| Alpine populations | | Cave or endogean populations | |
|---------------------------------------|--------------------------------|-------------------------------------|------------------------------|
| Taxa | Distribution | Taxa | Distribution |
| Europe | | | |
| <i>Oronebria ratzeri ratzeri</i> | Swiss Alps | same | Jura (France) |
| <i>Nebria lafresnayei lafresnayei</i> | Wester Pyrenees | same | Basque Country (Spain) |
| <i>Nebria vuillefroyi</i> | Central Spain | same | Sierra de Ayllon (Spain) |
| <i>Pyreneorites champenoisi</i> | Central Pyrenees | same? | pre-Pyrenees (Spain) |
| <i>Trechus brucki</i> | Pyrenees | <i>Trechus</i> sp. n | pre-Pyrenees (Spain) |
| <i>Apodavallius lecoqi</i> | Cantabrian Mountains (Spain) | <i>Apodavallius</i> spp. | Cantabrian Mountains (Spain) |
| North Africa | | | |
| <i>Nebria exul</i> | Djurdjura (Algeria) | <i>N. nudicollis nudicollis</i> ? | Djurdjura (Algeria) |
| <i>Laenostenus malhommei fongondi</i> | Toubkal, Haute Atlas (Morocco) | <i>N. nudicollis initialis</i> | Haute Atlas |
| Central Asia | | <i>L. malhommei malhommei</i> | |
| <i>Duvalius lindbergi</i> ssp. n | Karakorum (Pakistan) | <i>Duvalius lindbergi lindbergi</i> | Kabul (Afghanistan) |

region in France. The cave population is morphologically indistinguishable from the nominal form of the species, despite being only found about 100 km north of the populations of *O. ratzeri henroti* (Colas 1954). This distribution suggests that the separation of the Jura subspecies predated the separation of the cave-alpine disjunct populations, which should have taken place relatively recently.

Nebria lafresnayeii lafresnayeii Serville lives in the main chain of the Pyrenees in the alpine zone, above 2,000 m, at the edge of snow fields and in sheltered areas with permanent snow. In the Basque country populations of this subspecies live in caves in the Sierras de Aralar and Andía, in an area with humid Atlantic forest (Zaballos and Jeanne 1994, Ramos 1997, and Sierra de Aralar, Navarra, Pagomariko Leizea cave 15.x.1984, O. Escolà leg.). Specimens of *N. lafresnayeii* considered to be a different subspecies are found under stones at lower altitudes (1,700–1,800 m) in the massif Central in France, at a higher latitude (Bonadona 1971). Several subspecies of *N. lafresnayeii* exhibit allopatric distributions, but the populations from caves on the western Pyrenees belong to the same subspecies as the populations living in alpine environments in the area (Zaballos and Jeanne 1994), again an indication of the recent origin of the cave-alpine disjunction.

Nebria vuillefroyi Chaudoir is an Iberian endemic, living in some sierras in Central Spain. It is considered to be an alpine species, typically occurring on snow fields above 2,000 m. Some specimens have recently been found in the Sierra de Guadarrama at lower altitudes, at about 1,700 m, but only along the shore of some mountain streams. In another sierra in central Spain (Sierra de Ayllon, province of Segovia), specimens have also been found below 1,700 m, under the soil surface, in the MSS (“Milieu Souterrain Superficiel”, or superficial underground compartment, Juberthie *et al.* 1980) (Ortuño and Toribio 1994). According to these authors, the limiting factor in the distribution of the species would be the need of a constant high humidity.

Pyreneorites champenoisi Croissandreu is a central Pyrenean endemic living in the alpine zone, above 2,000 m (Zaballos and Jeanne 1994). Populations of the same species, but exhibiting some morphological differences (their taxonomic status is still under study), live in the MSS in some sierras south of the Pyrenees, at about 1,600–1,700 m (Spain, province of Huesca: Sierra de Chía, Chía 21.viii.1996; Macizo del Turbón, Egea 12.viii.1992, C. Hernando and J. Fresneda leg.). The species is closely related to *P. glacialis* Barnecille and *P. amoenus* Dejean, which are also Pyrenean endemics only found above 2,000 m, but which have never been collected in the MSS (see *e.g.*, Bonadona 1971, who treats all three of them as subspecies of *P. amoenus*). All three species exhibit the morphological features of typical cave beetles, being depigmented and having long appendages, flat bodies, and small eyes. At the summit of the southern sierras in which *P. champenoisi* was found in the MSS (all below 2,000 m) there are no species of *Pyreneorites* of the *amoenus* group. The only species of *Pyreneorites* living there is *P. pusillus* Dejean, another central Pyrenean alpine endemic species belonging to another group, with shorter legs and fully pigmented, black bodies.

An undescribed *Trechus* from a cave at 530 m in the Sierra de Lokiz (a mountain system between the Pyrenees and the Cantabrian Mountains, in the province of Navarra) is apparently most closely related to *T. brucki* Fairmaire, an alpine Pyrenean species living between 2,000 and 2,400 m. The two species belong to the *T. uhagoni* group (*sensu* Jeannel 1927), distributed in the Pyre-

nees and the Cantabrian mountains, and including alpine, forest and cave species (see introduction).

All the known species of the genus *Apoduvalius* (endemic to the Cantabrian Mountains in the Iberian peninsula) are troglobitic, with the exception of *A. lecoqi* Deuve, found on the surface of snow at 1,410 m in Covadonga (Zaballos and Jeanne 1994: addenda). Its relationships to the cave *Apoduvalius* are currently unknown.

North Africa. *Nebria (Alpaeus) exul* Peyerimhoff was described from the bottom of a Tessereft in the Algerian Kabyle, at about 2,000 m, in a microhabitat with permanent snow (Peyerimhoff 1910). Tesserefts are holes of karstic origin which retain snow throughout the year (Quinif 1978). The species seems to be most closely related to *Nebria (Spelaeonebria) nudicollis* Peyerimhoff, found in the bottom of a deeper and more "cavern-like" Tessereft at 2,090 m in the Djurdjura (northern Algeria) (two specimens were found, one under a rock, and another upon the snow). *Nebria nudicollis* has some of the morphological features of typical cave beetles (small eyes, long legs, and a depigmented body) and coexists in the same Tessereft with typical troglobitic species of beetles and diplopods (Peyerimhoff 1911). One subspecies, *N. nudicollis initialis* Peyerimhoff, lives in a number of caves in the Djurdjura mountains, at lower altitudes (1,500–1,800 m) (Peyerimhoff 1914).

Laemostenus (Antisphodrus) malhommei (Antoine) is a Moroccan species only known from the Haute Atlas. It has two described subspecies, *L. malhommei malhommei*, living in caves at 1,240 m, and *L. malhommei fongondi* Casale, found near snow fields in an endogean environment at 2,500 m in the Toubkal massif (Casale 1988). The two forms have typical structural features of subterranean species, and the differences between them refer to other kinds of characters (Casale 1988).

Central Asia. *Duvalius lindbergi* Coiffait occurs in two caves about 100 km west of Kabul, at the head of the river Kabul, at 2,240 and 2,180m (Coiffait 1961, Español 1977). A new subspecies was recently described from the Karakorum mountain system in Pakistan, from under rocks at 2,350 m (Hernando 1998). The area is about 700–800 km NE of the previous known sites of the species, in the headwaters of the Indus river. *Duvalius lindbergi* is a depigmented species, with long legs, long antennae, and small eyes. The alpine specimen from the Karakorum is smaller and more slender, and has smaller eyes, than the cave specimens from Kabul (Hernando 1998).

Discussion

A common feature of most examples of cave or endogean and alpine range disjunctions in the Pyrenees and southern France is the absence of morphological differentiation, suggesting a recent origin of the separation. If morphologically differentiated forms can be recognized, most cave and alpine populations are more similar to each other than to allopatric surface populations (as in *Oronebria ratzeri* and *Nebria lafresnayei*). The alpine areas in which these species occur (usually above 2,000 m) were covered by ice in the last glacial cycle, and thus the existence of these alpine populations could not exceed 14,000 to 15,000 years. The extent to which the Younger Dryas cold period (11,000–10,000 years B.P.) affected the mountain systems of some areas in the Pyrenees and central and northern Spain is not well established, although recent studies show that it was similar in its lower temperatures to other more northern areas (Peñalba *et al.* 1997). It may thus be that the occupation of the

alpine habitats is very recent, and possible no older than 10,000 years. It is not possible now to hypothesize the age of the occupation of caves or endogean habitats at low or medium altitudes, but in areas in which the surrounding surface was covered by ice it probably did not predate the last glacial maximum either.

Only in some southern Pyrenean and northwestern Iberian examples do morphological differences suggest an older time of separation of cave or endogean and alpine forms, as in the species of *Apoduvalius*, or the undescribed species of *Trechus* of the *T. uhagoni* group. Due to the lack of available material for study, and despite the clear differences in the external and genital morphology of the endogean and alpine specimens of *Pyreneorites champenoisi*, it is still not possible to decide if these differences represent intra-population variability of the species, or represent diagnostic taxonomic differences separating populations.

The north African and central Asian examples involve morphologically differentiated taxa, generally recognized as subspecies or species (Table 1). For the forms living in Algerian Tesserefts there are different degrees of development of the typical morphology of troglobitic species, involving one recognized species with an apparently less modified morphology (*Nebria exul*) and two subspecies of another with some morphological characters typical of troglobitic species (*N. nudicollis nudicollis* and *N. nudicollis initialis*). The phylogenetic relationships between these three forms and other related species of *Nebria* are, however, not fully understood. They may be the product of independent invasions of the alpine microhabitat of Tesserefts, or they may have a common origin, with subsequent vicariant speciation.

The traditional explanation for the common occurrence of these cave or endogean and alpine disjunctions stresses humidity as the limiting factor favoring the occupation of the subterranean environment, with the subsequent disappearance of intermediate surface populations due to the increased temperature and/or aridity of the above-ground habitats. Typical environmental conditions in caves are high humidity (almost permanently at or near 100%), and fairly constant daily and annual temperature (usually above 0° but less than 15°) (Vandel 1964, Juberthie 1984, Bellés 1987, Chapman 1993, Ramos 1997). However, in alpine environments humidity is often very low (Sømme 1989). The combination of low temperatures and low relative humidity has a strong power for desiccation, which requires special behavioral or physiological adaptations in the species habitually occurring in alpine environments (Sømme 1989, Bale 1996, Danks 1996). Alpine species therefore may search for refugia with higher and more constant humidity, such as endogean microhabitats (crevices, protected areas under stones or amidst dense vegetation, etc.). These refugia also protect against the extremes of low or high temperatures (which are not unusual in alpine environments during the summer), to the extent that some species can survive when surface temperatures are well below their critical point just by seeking protection in the right microhabitats, without further physiological mechanisms (Sømme and Zachariassen 1981, Sømme 1989, Sømme *et al.* 1996). Some tropical alpine carabids, in particular, seem not to have developed specific physiological mechanisms to cope with extreme low temperature and relative humidity. Their survival in high altitude environments depends entirely on particular behaviors, such as the search for suitable refuges during both the driest and coldest or warmest hours, reducing their surface activity to part of the night (Sømme *et al.* 1996). This lack of physiological adaptations in carabids may be related to their predatory behav-

ior, with the need of maintaining high metabolic rates and a high activity level, which are incompatible with most of the frequently observed strategies to resist cold and reduce water loss (*e.g.*, to decrease activity and metabolic rate in desert tenebrionids, Zachariassen 1996).

The search for refugia in sheltered microhabitats in alpine environments may thus be a powerful driving force in the evolution of cold-adapted faunas, resulting in the permanent colonization of subterranean environments. In fact, for some alpine populations general morphological features have a more troglobitic appearance than those of populations inhabiting caves. This is the case of (1) *Duvalius lindbergi*, in which the single specimen found in the Karakorum had smaller eyes, smaller general size, and a more gracile appearance than specimens found in caves. (2) The species found in Tesserefts, which have an alpine microhabitat with permanent snow, and also exhibit many cave-like characteristics; and (3) the single specimen of *Laemostenus malhommei fongondi* found under a stone at 2,500 m in the Haute Atlas. Other known examples of alpine ground beetles exhibit markedly endogean preferences and morphological characters typical of subterranean species, such as *Leistus starkei* Abmann, living in the Cantabrian mountains in an alpine talus under a layer of stones, or the related *L. pyrenaicus* Kraatz (Abmann 1997). The extreme rarity of these forms (many of them known only from a single specimen) poses a limit to conclusions about their autecological preferences. It is interesting in this context that some alpine species, without troglobitic morphological characters, and which are not found in caves or endogean environments (such as *Pyreneorites pusillus*) can be found on lower summits, in habitats in which alpine species with a general troglobitic appearance, and occurring also in the MSS, cannot be found (such as *P. champenoisi*).

Without more comprehensive physiological or experimental data it is not possible to disentangle the requirement for high humidity and the avoidance of temperature extremes as the selective agent in the colonization of cave or endogean environments. The observed correlation provides us with preliminary hypotheses for understanding the evolution of the strikingly species-rich carabid fauna of alpine regions and the subterranean environment, and their way of coping with extreme climatic conditions and changing levels of glaciation. The close link of alpine and endogean or cave populations may hint at evolutionary explanations which are currently unexplored, such as a direct colonization of the subterranean medium by cold-adapted alpine species at low altitudes during glacials, or the colonization (or re-colonization) of alpine environments through direct connections with the MSS during interglacials, with even the possibility that some of the present alpine fauna originated from subterranean populations.

Molecular studies to assess phylogenetic relationships between alpine and cave or endogean populations are needed to test these scenarios, and to address the problem of the apparent differences in time frames for the separation of alpine and cave or endogean forms in different geographical areas and mountain systems.

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