A PROPOSAL FOR THE CLASSIFICATION OF THE TERRESTRIAL SUBSOIL FAUNA IN THE CANARY ISLANDS

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In the last decades many of the discoveries affecting the habitat of subsoil species have questioned the suitability of the classifications traditionally used for this fauna. The most usual terms, troglobite, troglophile and trogloxene were first coined at the beginning of the century, at a time when troglobites were thought to be essentially cave-dwelling animals. However, we are certain today that many of these species live preferably in subsoil cracks which are considerably smaller in diameter than any cave accessible to man. Thus, benefiting from the opportunity given by the "Société de Biospéologie" annual meeting, it would not be inappropriate to take the nomenclature of environments, habitats and species into consideration. This presentation only covers the subjects of terrestrial species, and The terminology employed throughout it will be Schiner & Racovitza's, though slight variations are introduced in the concepts being referred to. At the end they will be applied to a practical case in the Canary Islands.

According to the recent "European Community Directive of Habitats", the concept of habitat may be applied to a species as well as to a community. Likewise, the concept of environment may allude both, to a species or to a community. In the first case, it defines the main features of a place where a species lives, usually mankind, i.e. physical environment, ecological environment, etc. The second case refers to a place where a specific animal community establishes itself, differing from others by its exclusive and characteristic species.

Following these statements, the three essential environments can be perfectly distinguished in a hypothetical cutting of the substratum: the epigean, the endogean and the hypogean environments. The first of them extends over the soil -in an edaphic sense-, the second inside it, and the third one under the soil. Crevices and interstices found in the hypogean environment are formed mainly by the retraction of the lava or by holes among the clinker layer interspersed along the various lava flows. They are also produced when fissures result from meteorization of the rock in old areas. Retraction crevices and clinker layers are found at variable depths whereas meteorization chinks are usually located near the surface, right below the endogean environment, in a horizon known by edaphologists as horizon C1.

There are also different compartments at various depths in the hypogean environment: one right below the surface which is characterized by the abundance of roots and also influenced by the surface climate. Another deeper compartment where roots are barely found and there is a higher environmental stability. The former is known as Shallow Subsoil (in Spanish "Subsuelo Superficial"), also as "Milieu Souterrain Superficiel". The latter is termed Deep Subsoil (in Spanish "Subsuelo Profundo") or "Milieu Souterrain Profond". Lava tubes extend along this last one, so that, according to HOWARTH's classification for subsoil areas, it could be said that microcaverns (< 1 mm) and mesocaverns (1 mm to 20 cm) abound in Shallow Subsoil, while the Deep Subsoil includes macrocaverns (> 20 cm) in addition to the former two types.

Each of these three essential environments -epigean, endogean and hypogean-, present a particular common feature: species found here tend to develop into different and characteristic morphological patterns. The species which are best adapted to the hypogean environment are the eyeless, unpigmented and brachypterous, showing spidery body design. Species from the endogean environment share some of the former features, though they are never as slim and often much smaller in size. Finally, epigean species generally display well developed eyes, functional wings and are pigmented. In relation to these features and in a similar manner to CHRISTIANSEN in 1962, three different morphological models can be described: the hypogeomorphic model, the

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endogeomorphic model and the **epigeomorphic** model. Additionally, a species showing combined features from any of the previous models could be termed as ambimorphic or **ambigeomorphic.** This classification refers to the species' body plan regardless of their habitat or physiological conditions, and it is this singularity that differs from CHRISTIANSEN's 1962 proposal. To some extent it could be considered an evolutionary classification but not an ecological one.

The former classification can be complemented by another that takes into account each species' habitat. Thus, epigean species would be **epigeobites**, endogean would be **endogeobites**, and the hypogean as **hypògeobites**, though it would be more appropriate to use the widely accepted term **troglobite**. Anyway, it is seldom an easy task to determine exactly a species' habitat, especially when few specimens are known. Because of this, it is convenient to provide some guidance in order to facilitate the typification process using this terminology. Thus, an epigeobite is a species with a major population in the epigean environment; similarly an endogeobite is a species which is predominant in the endogean environment, and finally, a troglobite in the hypogean environment.

Likewise, species which are capable of spending all of their life in a specific environment where a minor population exists, are named as **epigeophile, endogeophile** and **troglophile** species. Finally, epigeoxene, endogeoxene and trogloxene species are those unable to complete their life history in their corresponding environment, which itself does not house a big population rate. These organisms may be found in their corresponding environment optionally or accidentally, so that it is sometimes interesting to distinguish further between facultative or accidental for trogloxenes, endogeoxenes and epigeoxenes.

This classification only refers to the species' habitat, and not to their morphological or physiological features, other than that, it would be similar to that proposed by Schiner-Racovitza. Thus, it is possible for a troglobite to be an epigeomorph at the same time, or an epigeobite being an ambigeomorph as well.

As the habitats of many species surpass the limits of a single environment, the nomenclature described above can be combined when specifying the distribution of their populations. Any combination between the rows is possible for each species, with the exception that it can only be a "-bite" in a given environment. In this way, an epigeobite can be both an endogeophile and a trogloxene at the same time, and a troglobite can be an epigeoxene simultaneously. Several examples of each can be found in the fauna of the Canary Islands caves:

- *Lymnastis gaudini* is a troglophile endogeobite: that is, it lives commonly in the endogean environment, though sometimes it has been captured in caves as well.
- *Loboptera fortunata* is an epigeoxene troglobite: apart from its abundance in the hypogean environment, it can be occasionally found in moist and unlighted habitats in the epigean environment.

When a species life history has been developed throughout different environments, its classification process can become difficult. In those cases the taken reference is the habitat of the adult individual. The following examples concern Canary fauna:

- Beetles of the family Rhizophagidae can be found both in the epigean environment and in the endogean or hypogean environments, provided that the plant on which their larvae feed is present. Their life history has a larval phase in the endogean environment, as well as another phase supposedly spent out of it when reproduction takes place. Their presence in the hypogean environment may be regarded as accidental, since these animals crawl down attracted by the existence of baited traps. These species are classified accordingly as **epigeobite, endogeophile** and **trogloxene.**

- Fly larvae of the family Phoridae, especially of the genus *Megaselia*, usually grow in decayed heaps of organic matter. They are quite abundant in the endogean environment, though they can also be found in the epigean and hypogean environments. When the adults come out, they move about the surface in order to reproduce themselves. They can also stay in the subsoil and reproduce there provided that they find a suitable place for laying their eggs. They are relatively frequent in some caves where they represent an important energy input. From the habitat view we consider this species of *Megaselia* as **epigeobites, endogeophiles** and **troglophiles.**

In respect of animals which spend part of their lives in forest litter such as many species of springtail, it is difficult to indicate their habitat under the proposed classification. There are epigeobitic collembola, as well as endogeobitic and troglobitic collembola. The former is usually found in the epigean environment, whereas the latter may be located in the hypogean environment. Endogean collembola frequently appear in the forest litter. This is so partly because forest litter is to some extent an ecotonic layer situated between the epigean and endogean environments. We considered it as the deepest layer in the epigean environment, since many species live here and are not related to the endogean environment. Several isopods, chilopods and thysanura are included here. Consequently these animals are considered epigeobites.

Ants and snails are other animal groups which often move about the subsoil and may accidentally be found in caves. However, these are indeed epigeobites instead of endogeobites, since they normally must go outside for food or reproduction.

By means of combining the former two classifications, (ecological classification or by habitats, and evolutionary or morphological classification), and also by accounting the evolution within the hypogean environment of specific characters such as eyes, pigment, wing, etc., a hypothetical evolutionary succession model could be defined for the communities of the subterranean environments.

New subterranean communities like those in an oceanic island which has just emerged, are characterized by housing unadapted species, such as epigeomorphic trogloxenes. The first troglophile species will appear after some time and will be either epigeomorph or ambigeomorph. Later troglobites will appear, at first instance being ambigeomorphs and, later still hypogeomorphs. The more developed the community is, the greater its degree of adaptation and the rate of hypogeomorphic troglobites will grow in comparison to the ambigeomorphic.

In relation to this sequence, in islands belonging to the same archipelago which are geomorphologically similar but different in age, it can be foreseen that these islands will show different evolutionary stages. In the younger islands troglophile species will be dominant over troglobites, and in terms of quantity, ambigeomorphic troglobites will be more important than the hypogeomorphic. The older islands are likely to have more hypogeomorphic troglobites than the younger ones.

Let us consider next a practical case in the Canary islands. This archipelago is formed by a group of seven main islands and several islets. Their origin is oceanic although there is some disagreement expressed by some scientists who tend to consider the easternmost islands of Fuerteventura and Lanzarote of continental origin. Three of these islands, Tenerife, La Palma and El Hierro perfectly meet our requirement in order to relate their fauna with their age.

Tenerife is the greatest and oldest of the three islands studied. Some scientists have dated it more than 15 million years old, but more recent estimats give an age of around 7 million years. El Hierro is the smallest of the three, its age is thought to be a million years. Finally, La Palma island is 1.5 to 2 million years old.

Troglobitic fauna from El Hierro and La Palma is smaller in quantity in comparison to that of Tenerife, likely due to the younger age and more reduced size of the two former islands. An important relation is noticed between the age of the islands and the degree of adaptation shown by their troglobites. Thus, Tenerife has a greater number of hypogeomorphic than ambigeomorphic species, while the opposite occurs in La Palma and El Hierro. In El Hierro, the rate of troglophile species is also greater over troglobitic ones, which are more dominant in Tenerife than in the other two islands.

The development of eyes and pigmentation as well as the lengthening of appendages are different depending on the island considered. Anophthalmous species in Tenerife are more abundant than those with reduced eyes. The opposite occurs in El Hierro and La Palma. However, highly unpigmented species are dominant over the slightly unpigmented in all islands, though in a greater rate in Tenerife and lesser, but similarly, in El Hierro and La Palma. Species with slender, elongated appendages are more abundant than those of normal appendages in the three islands, but especially in Tenerife and El Hierro.

In conclusion, troglobites in younger islands where the local fauna has had less time to develop and specialize, appear in a less adapted stage than those of older Tenerife. The same could be said about the rate of troglobitic and troglophilic species which is higher than in the other two islands.

The convenience or suitability of primary issues within the proposed classification system should be debated as follows:

- 1. Would it be adequate to separate morphological characteristics from the habitat-related ecological features in different classifications?

- 2. Are troglobite, troglophile and trogloxene categories believed to include all of the subsoil fauna, or should they include more? Are the selected terms of troglobite, troglophile and trogloxene, epigeobite, epigeophile and epigeoxene, and endogeobite, endogeophile and endogeoxene accepted?, Is there a more suitable terminology?

- 3. Can we assume from a conceptual point of view the necessity to differentiate between hypogeomorph, endogeomorph, epigeomorph and ambigeomorph? Are the used terms accepted?

- 4. Concerning the environment classification, is it valid to name the Shallow Subsoil and the Deep Subsoil and refer them to the MSS and to the MSP respectively?

- 5. The aquatic habitats may constitute a separate environment; is it equally valid to apply them to the terms troglobite, troglophile and trogloxene?

- 6. With regard to the French term "Milieu souterrain Superficiel" and since the differences between the MSS and MSP and those of the hypogean, endogean and epigean environments do not seem to correspond with one another, would it not be more adequate to use another term, for instance COMPARTMENT or STRATUM instead of ENVIRONMENT, in order to avoid possible confusion? What would be the equivalent French term?