

Cadernos Lab. Xeolóxico de Laxe
Coruña. 2001. Vol. 26, pp. 349-358

ISSN: 0213-4497

The problem of the species concept in the phylogeny of the cave bears

El problema del concepto de especie en la filogenia del Oso de las Cavernas

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ABSTRACT

This a short review of a series of concepts daily used in palaentology, trying to connect them with their meaning in other fields of study in Biology. Firstly, it should be pointed out if the concept of species comes from an empiric reality or if it has arisen from the scientific need of assembling. The evolutive concept of speciation, as well as its "methods" seem to be based in the term population. Hence, as meaningful discussions on speciation require a common definition of its end result, namely species, a solution to the tricky issue of defining species probably lies in a deeper knowledge of the processes behind speciation itself.

Key words: species, species concept, chronospecies, cave bear phylogeny

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INTRODUCTION

It is well known the complexity of usual phylogenetic discussions in living groups such as Ursidae (panda, polar bear...). But, when fossil taxa are involved, the problem remains in the very concept of species.

It should be wondered whether the concept of species comes from an empiric reality or if it has arisen from the scientific need of sorting out organisms. The evolutive concept of speciation, as well as its "methods" seem to be based in the term *population*. Hence, as meaningful discussions on speciation require a common definition of its end result, namely **species**, a solution to the tricky issue of defining species probably lies in a deeper knowledge of the processes behind speciation itself (ÖDEEN 1996).

HISTORICAL EVOLUTION OF THE SPECIES CONCEPT

Aristotle (384-322 BC)

An animal, an individual, cannot be eternal, because the reality of every being is found in its characters... which is specific (*eidei*). And thus, it always exists a genus (*gênos*) for humans, for animals, for plants.

Linnaeus (1751)

There are many species which the Supreme Being has created with a lot of different forms. They, following the laws

of generation, produce other forms, but always similar to themselves: thus, there are as many forms as number of structures before present.

The Linnaean species concept was that species were static entities of fixed characteristics which defined them as being part of a group. He did not explicitly define "species". Indeed, there is some conflation between the Linnaean category "genus" and what we consider a "species" or a species taxon today.

Lamarck (1802)

Species is every collection of similar individuals which the process of generation perpetuates within the same stage. Thus, the circumstances of their situation do not change enough as to vary their costumes, habits or form.

Darwin (1859)

It is absolutely undefined the number of differences considered as necessary in order to give the category of "species" to two forms (...) I just consider the species concept as something arbitrarily used for a group of individuals with strong similarities, but this concept does not differ of the *variety* term which is given to less different and variable forms.

Ernst Mayr (1942)

Species are groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups.

**Theodosius Dobzhansky (1935).
Dynamic nature of the species concept**

Species is a stage of evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding.

Huxley (1942)

In general, it is becoming clear that we must use a combination of several criteria in defining species. Some of these are of limiting nature. For instance, infertility between groups of obviously distinct mean type is a proof that they are distinct species, although once more the converse is not true. Thus, in most cases, a group can be distinguished as a species on the basis of the following points:

- 1.- a geographical are consonant with a single origin
- 2.- a certain degree of constant morphological and presumedly genetic difference from related groups
- 3.- absence of intergradation with related groups

In most cases a species can thus be regarded as a geographically definable group, whose members actually interbred or are potentially capable of interbreeding in nature, which normally in nature does not interbreed freely or with full fertility with related groups, and is distinguished from them by constant morphological differences. Thus, we must not expect too much of the term species. In the first place, we must not expect a hard-

and-fast definition, for since most evolution is a gradual process, borderline cases must occur. And in the second place, we must not expect a single or a simple basis for definition, since species arise in many different ways.

Smith (1994)

Species are distinguished on phenetic differences, be they morphological, physiological, biochemical, or genetic. All characters that vary among the specimens under study are scored and a taxon-character matrix constructed. This matrix is subjected to multivariate analysis in order to identify discrete clusters of individuals based on total morphological variation. The smallest clusters recognisable then are a species.

**DIFFERENCES AMONG THE
CURRENT SPECIES CONCEPTS**

Biologic

The Biologic Species Concept (BSC) has undergone a number of changes over the years. Du Rietz defined it (1930) as: *the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes*. Barriers to interbreeding are implicit in this definition. Some years later, Dobzhansky defined a species as we have seen above, but later (1951) he relaxed this definition to the point that is substantially agreed with Mayr's (1942), which is the accepted BSC.

Strengths: fits within population genetics. Gives an unambiguous empirical cri-

teria. It provides an important conceptual framework for speciation

Weaknesses: Only really applicable to the present (paleobiological work on evolution cannot use this concept). Doesn't apply to asexual organisms (it is less useful in botany). No evolutionary dimension

Phenetic

Cronquist (1988) proposed an alternative to the BSC that he called a *renewed practical species definition*. "the smallest groups that are consistently and persistently distinct and distinguishable by ordinary means".

Strengths: is in fact the way we recognize species differences. Works well for sexual and asexual organisms. Applies well to past species.

Weaknesses: does not connect with genetics.

Comments: the requirement that species be persistently distinct implies a certain degree of reproductive continuity. This is because phenetic discontinuity between groups cannot persist in the absence of a barrier to interbreeding. This definition places a heavy, though not exclusive, emphasis on morphological characters. It also recognizes phenetic characters such as chromosome number, chromosome morphology, cell ultrastructure, secondary metabolites, habitats and other features.

Recognition

Strengths: Fits within population genetics (it is based on reproduction).

Complements the biological species concept

Mate recognition can be more easily determined than ability to breed (especially in non-living species)

Weaknesses: Isolation mechanisms, which lead to speciation are more difficult to conceptualise. No evolutionary dimension

Ecological

Strengths: it corresponds to the findings of a considerable body of ecological research which suggests that species occupy "adaptative" zones which are determined and reinforced by the resources exploited on the habitats occupied

Weaknesses: Is only loosely connected to genetics Is rigidly tied to ecological niches determining species (consider that even in different life stages an organism will occupy different niches). Perhaps the best that can be said is that ecological processes influence phenetic and genetic aspects of species. Has no evolutionary dimension.

Cladistic/Phylogenetic

There are several definitions. All of them assert that classifications should reflect the best supported hypotheses of the phylogeny of the organisms. There are two types of phylogenetic species concepts:

1.- A species is the smallest cluster of organisms that possesses at least one diagnostic character. This character may be morphological, biochemical or molecular and must be fixed in reproductively cohe-

sive units. it is important to realise that this reproductive continuity is not used in the same way as in the BSC. Phylogenetic species may be reproductive communities. Reproductively compatible individuals need not have the diagnostic character of a species. In this case, the individual need not be conspecific.

2.- A species must be monophyletic and share on or more derived character. There are two meanings to monophyletic: the first defines monophyletic group as all the descendants of a common ancestor and the ancestor. The second defines a monophyletic group as a group of organisms that are more closely related to each other than to any other organism.

Strengths: A clear evolutionary dimension. Establishing phylogenies and, hence branching points uses micro (e.g. DNA) and macro characteristics. It is the richest concept in palaeontological studies.

Weaknesses: Only a very small number of lineages have been uncovered given the detail required for this approach. Disconnected from population genetics

SPECIATION PROCESS

Speciation is a special case in the evolution of biological diversity. Traditionally, we know evolution as the process where new forms of life are shaped through selective screening of biological variation, is this a real concept? How does speciation modify taxa? Is it done by small, almost unnoticeable steps, often called "missing links", as envisioned by gradualists? or is evolution less gradualistic? To the **modern synthesis** it is natural to extrapolate microevolutionary change

to explain evolution on all taxonomic levels. But to "pluralists" like S.J. Gould crossing the level of species requires the postulate of a different process: macroevolution. Macroevolution, as Gould sees it, is signified by large and sudden change, greater than what would be expected from allopatric divergence alone (ÖDEEN, 1996)

It should be reminded, no matter the mode of speciation, the four forces which lead evolution: **mutation, migration, selection** and **genetic drift**. All of them, are finally reduced or constraint by the first one: mutation, its different rates and its relationship with the other.

Mechanisms that prevent gene exchange have been broadly termed **isolating mechanisms**. Some authors include in this category all factors that prevent gene exchange, even geographical and spatial isolation. Such geographically separated, or **allopatric**, populations, obviously do not have the opportunity for gene exchange, and it has been debated whether, given the opportunity, many of them would remain reproductively isolated. Another question related to allopatry is the speciation due to **founder effect** (originated from only a few coloniser individuals) and **bottleneck** (group which has been substantially diminished in size). Other authors have therefore proposed that the term isolating mechanisms be restricted to those that prevent gene exchange among populations in the same geographic locality, that is, mechanisms that isolate **sympatric** populations. The latter have been classified by Mayr into two categories: i) before fertilization (**pre mating**), as seasonal or habitat isolation, behavioural or sexual isolation

and mechanical isolation. ii) after fertilization (*postmating*) as gametic mortality, zygotic mortality or hybrid inviability and hybrid sterility (STRICKBERGER, 1990).

The rate at which new taxa form is difficult to determine, as evolutionary rates differ even within phylogenetic groups. These inconsistencies probably relate to variations in selection pressures on the population at different times. Whether or not microevolutionary forces inducing change within species are identical to macroevolutionary forces generating new species is a matter of contention (STRICKBERGER, 1990).

FOSSILS, URSIDS AND FOSSIL URSIDS

For the Paleontology, the presence of the time dimension makes it impossible to apply the commonly accepted biological species concept. Thus, the Evolutionary Species Concept (ESC) was defined by Simpson as "a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (SIMPSON, 1961).

As fossil material carries the dimension of time, it often shows sequences of species that are obviously related to one another, that follow one another in time, and are generally interpreted as evolutionary lineages. Thus, according KURTÉN (figure 1) it is no doubt that *Ursus savini*-*Ursus deningeri*-*Ursus spelaeus* form a sequence of evolutionary descent as well as a sequence of related species in time.

Evolutionary changes may occur in species even if a speciation event (split) does not occur. This kind of categorization results in naming **chronospecies**. Unlike biological species, chronospecies are arbitrary divisions of a single evolutionary lineage, defined on the basis of morphological change (figure 2).

Although the criteria used to delimit chronospecies boundaries are not described in his formal definition, Simpson suggests that morphologic differences between species should be at least as large as those between living species of the same taxonomic group. In our example, those differences should be similar to these found between the living representants of the genus *Ursus* (*U. arctos*, *U. americanus*, *U. maritimus*...)

But what are, in the cave bears, these morphological differences? Sometimes the difference between *U. deningeri* and *U. spelaeus* is defined by the variation of some continuous features, like the progressive reinforcement and doming of the skull and the jaw, or discrete ones, like the loss of the three anterior upper and lower pre-molars.

Continuous features are often difficult to be used as taxonomic character. The variability of size and morphology is a constant in *U. spelaeus* and *U. deningeri*, even into the same population. This intraspecific variability is increased due to sex dimorphism or the existence of dwarf forms, like in high alpine populations. Moreover, some sites from the Middle Pleistocene show *intermediate* forms between both species, whatever it means (ALTUNA, 1972; RABEDER &

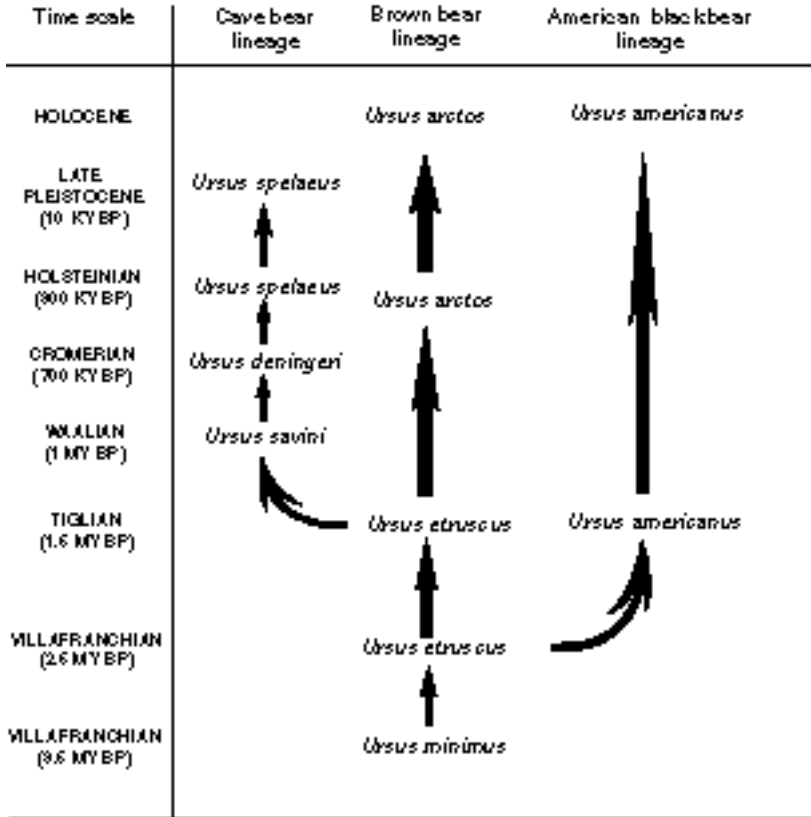


Figure 1. Phylogeny of Ursids. Adapted from KURTÉN (1976). There is a clear difference between *U. deningeri* and *U. spelaeus*.

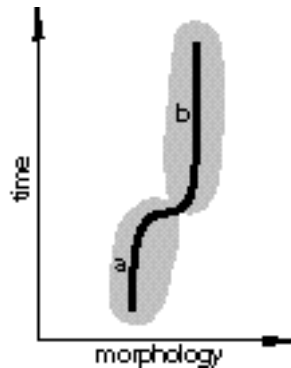


Figure 2. Rapid and large morphological changes in a single evolving lineage may lead to define different species (a and b) in successive geological intervals, which are called chronospecies. The boundary between a and b is often subjective, but in any case it should be well defined.

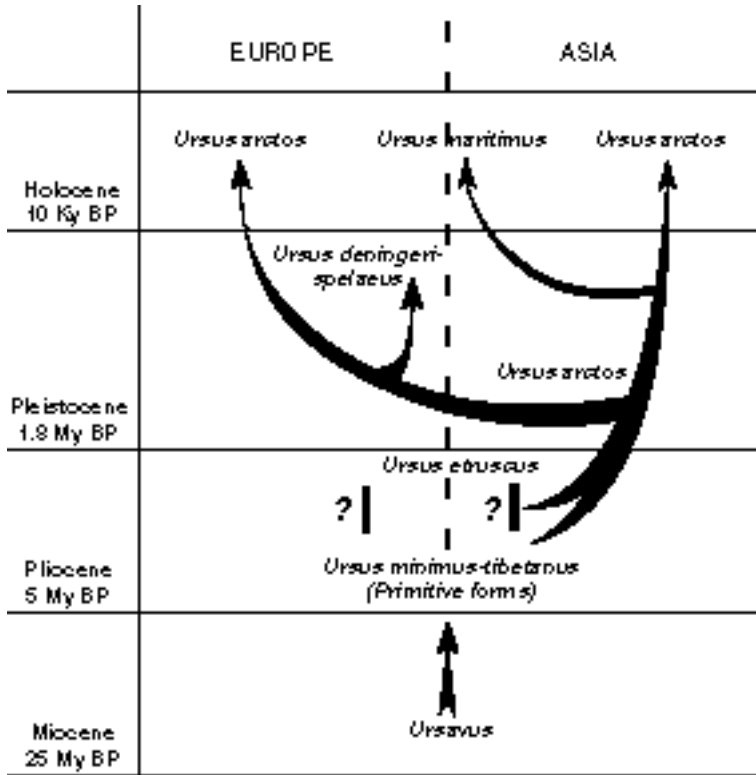


Figure 3. Phylogeny of Ursids. Adapted from MAZZA & RUSTIONI (1994). *U. deningeri* and *U. spelaeus* are considered as a same group.

TSOUKALA, 1990; ARGANT, 1991, AUGUSTE, 1992).

The discrete features could be more conclusive. But the study of the jaws of the Savini's bear from Bacton reveals the lack of the first, second and third premolar as a general feature. And concerning *U. deningeri*, even some Mosbach's skulls and jaws present a long diastema with no anterior premolars. These ones are seldom present and, when present, the percent varies from one population to another.

There is no doubt that the only reliable studies on Cave Bear phylogeny would be

those based on a large number of samples. There is a lack of such studies that should be solved. But, despite of many paleontologists still consider both bears as separated species, there are other well documented papers on Ursidae phylogeny that consider both bears as the same "group", i.e., the same species (MAZZA & RUSTIONI, 1994) as is shown in figure 3.

Taking into account the definition of chronospecies, it is clear that only the morphological differences between two groups from a single lineage are concluding for establish two different species.

The stratigraphic position of the bone remains gives not enough evidence to make a separation. Moreover, the morphological change must be quantified. In this

basis, it is not possible, at present time, to affirm that *U. spelaeus* and *U. deningeri* are different **species**. Even KURTÉN (1976) left room for some doubt on this issue.

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