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## **Evolution, actuality and species concept: a need for a palaeontological tool**

Species concept was developed to fit neontological necessities in ordering biological variability. Transversal (horizontal, synchronic) taxonomy shows hierarchical requirements quite different from those involved in longitudinal (vertical, diachronic) classifications. Furthermore, limitations within the species concept itself make it scarcely available in many paleontological contexts. Classical species definitions are often limited by theoretic and logic constraints, that are seldom available to describe practical situations. Morphology is an uncertain source of phylogenetic information, but it is still the main ground of biological comparison for extinct populations. Therefore, efforts in species recognition should be devoted to making taxonomy a useful tool for communication. First, inferences in systematics have to be led upon the available information about characters and processes. If this information is missing or not developed, no detailed conclusions can be supported. Secondly, definitions should be sufficiently elastic and generalised to allow an adaptation to each different case-study. The final target is to synthesise actual evolutionary histories, and not biological potentialities.

*Keywords: species concept,  
palaeontology, morphology.*

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### **Introduction**

Since classification and Linnean taxonomy were introduced to organise biological variability, one of the main battlefields for naturalists and evolutionary biologists was the "basic unit" of the classification itself, namely the species concept. Probably there are as many species concepts as the number of researchers that have been debating the topic, and the literature is replete with reviews (e.g. Kimbel, 1991, Eldredge, 1993, Rose & Brown, 1993). Clearly, no consensus has been achieved on this matter, and many of the different perspectives about evolutionary theories are the result of misunderstandings due to terminological exactitude. Classification and taxonomy are first of all tools, and secondly operational concepts, yet too many times their role as tools has

been set aside in debates about a theoretic and non-functional approach. Often, this has been one of the greatest obstacles for the evolutionist's work, being the evolution a real (actual) sequence of historical facts, and not a hypothetical expression of potentialities. Anyway, we must admit that the troubles related to a clear and univocal species concept are probably inner to the obscure nature of species itself, represented by a multivariate and complex matrix of factors which are not easily bridled by the rigorous classification of logic. As a tool, the species concept must help to resolve questions pertaining to several and different scientific contexts: it is clear that no species concept will ever meet the needs of all the comparative biologists, and that anyone of them will choose a definition that satisfies their personal hopes, fitting with their everyday problems and solutions. However, evolution and biodiversity are not theoretic proposals, but facts, even if we cannot completely know their history.

In this paper, some aspects concerning the principal approaches on species concept are discussed, which are surely useful to frame the matter of nature of species in a theoretical context, but not quite helpful as a "field tool" to evolutionary biology, and especially to paleontological necessities. Particular attention will be paid to primatology and human palaeontology, with the aim not to define or elaborate some new species concepts, but to propose some approaches to use the existing ones.

### **Species concepts: a light, critical review**

Clearly, a review of the most accepted (and contested) species concepts has to begin with the *Biological Species Concept* (BSC), introduced by Ernst Mayr and Theodosius Dobzhansky during the early '40s, which still is the most widespread definition of species. Following BSC, "... species are groups of actually or potentially interbreeding natural populations reproductively isolated from other such groups" (Mayr, 1942). This kind of approach was developed on a historical background characterised by the novelty of population thinking, and soon became a flagship definition of that new epistemological stage. So, first of all it is a populational concept. Second, it is mainly a relational concept, which ignores morphological characters and phenotypic differences, stressing a reproductive relation between groups of individuals. Third, the BSC is an isolation concept, which sets a genetic isolation as the natural condition of species unity. Discontinuity is then the main product of the evolutionary processes. The BSC has revealed to be quite a useful concept in its general application, but rather incomplete when facing specific arguments.

The principal problem using this concept is its adimensionality: the BSC does not work when applied to populations distant in time or in space and, especially in paleontology, this is a troublesome disadvantage. Simply, the interbreeding faculties of populations which live in different geographical or chronological contexts can not be proved. Simpson first remarked that the BSC was an atemporal concept, and that it sounded strange for an evolutionary definition. While many other authors have stressed the “unsatisfactory nature of the biological concept of species when applied to the past” (Stringer, 1992), others state that in paleontology reproductive inference is still a functional and useful approach (Eldredge, 1995).

Even for sympatric and synchronic population, sometimes the BSC gives problematic results. In primatology, the case-study of *Papio anubis* and *Papio hamadryas* from Middle Awash is well known: two distinct biological models, with different morphology, ecology and social systems, showing a large and growing hybridisation area (Phillips-Conroy & Jolly, 1986; Jolly, 1993). *Macaca* species, biologically well defined and geographically widespread, are genetically not incompatible (Schillaci & Froehlich, 2001). Even comparing *Homo* and *Pan*, it was soon clear that their genetic distance, although they refer to completely different biological systems, is similar to that of two sibling species (King & Wilson, 1975). Speciation processes have been defined “mesoevolution”, standing between population changes and generation of different models (Powell, 1997). The phylogenetic separation between two groups of populations is a complex and unclear stage, where prezygotic and postzygotic barriers interact with biological and environmental schemes that are not at all recognised or interpreted yet (Coyne & Orr, 1989; Powell, 1997). For example the “Haldane rule”, experimentally verified but not yet explained, proposed that infertility or inviability due to early speciation stages are first recorded for the heterogametic sex, and only after a certain development of other genetic barriers the other sex is then affected (Laurie, 1997).

Moreover, many examples in the zoological reign are extremely simple when compared to those found in plant biology, where polyploidy and other genetic “facilities” make the species level a quite permeable concept. Anyway, these unavoidable contrasts make the BSC a useful and powerful theoretical concept, but not a safe operational tool. In 1982 the requirement of “actually or potentially” interbreeding was deleted from the definition of the BSC. Of course, this elimination did not resolve the problem, but simply set it aside.

A particular reformulation of the BSC was the *Recognition Species Concept* (RSC), which defines a species as an inclusive reproductive community, thus a group of populations that share a common fertilization (mating) system (Paterson, 1985). As a specific extension of the BSC, the RSC is an interaction concept: while the previous

stresses on reproductive isolation between populations, the latter remarks the reproductive interaction between populations. The BSC is mainly based on a genetic phenomenon, while the RSC includes a large behavioural component involved in the mating systems (Turner, 1986; Kimbel & Martin, 1993). Moreover, fertilisation is a function (thus an active process) leading to events, while the BSC isolation is an effect (thus, a result), successive to some events (Templeton, 1987). Clearly, they are two faces of the same coin, and the RSC presents the same problems of the biological concept plus others due to the complexity of behaviour and mating systems, which again seldom allow for the use of the RSC in fossil contexts (Tattersall, 1989; Masters, 1993).

The first attempt to introduce time in a definition of species is the *Evolutionary Species Concept* (ESC), which defines an evolutionary species as "... a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson, 1951). Mayr was not very pleased about this endeavour to extend his BSC through time, and stated that the ESC was the definition of an evolutionary lineage, not of a species. Many lineages change biologically during evolutionary processes, and in an anagenetic perspective it is not easy to decide when sequential changes make a species derived enough to be transformed into a different one. Simpson looked at extinction as both the true extinction of a lineage or a complete transformation into a new morph, introducing first the concepts of chronocline subspecies and successional species, and then those of palaeospecies and chronospecies. There is still no agreement about those definitions, and many different concepts are linked to those labels. Often, palaeospecies is regarded as the whole evolutionary lineage, and chronospecies as a specific part of it (Wood, 1993).

One of the operational problems of the ESC is that many authors have always used it to approximate the BSC, forgetting that it was developed exactly to avoid all the limitations of Mayr's definition, and making vain all the efforts to introduce a temporal component in the species concept. It was even suggested that we could single out a new species in an anagenetic lineage when the differences between the more primitive and the more derived morph are enough to make impossible an eventual mating (Raup & Stanley, 1978). Thus, importance is given to some potentialities which exist in a logical formulation but not in nature (mating between two morphs which lived in different evolutionary times!). In a more generalised but more operative characterisation of the ESC, a species is defined as a reproductive lineage, which persists regardless of the amount of phenotypic changes throughout time (Wiley, 1978, 1981). Of course, the ESC was a clear attempt to define a species as the actual product of evolutionary processes and, in its essential definition, it does not take into account any biological constraints, such as reproduction. However, the question about variation of a single, unbranched evolution-

nary lineage must be resolved, for it is clear that a too wide palaeospecies concept can obscure speciation events and evolutionary processes (McHenry, 1994), resulting in an useless tool for both classification and phylogeny.

A further elaboration of the ESC was the *Phylogenetic Species Concept* (PSC) which, integrating the previous formulation with some updated evolutionary concepts such as punctuated equilibria and cladogenesis, explains the species level as "... the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descendant" (Eldredge & Cracraft, 1980). The PSC tries to approach species not as a evolutionary process, but as an evolutionary result. A phylogenetic species approximates extant biological species following three principles: mating system, lineage and discreteness (Kimbel & Martin, 1993; Kimbel & Rak, 1993). The first is the foundation of the BSC and the RSC, describing species as internally cohesive for shared reproduction properties. The second is the conceptual basis of the ESC, placing species between common ancestry and descendant. The third is a consequence of punctuated equilibria and cladogenesis: when a speciation event occurs, the mother species vanishes into its daughters. Species are then an evolutionary entity between phylogeny (branched and sequential history which generated a discrete variability of taxa) and tokogeny (reticulated, non-hierarchical whole of distinct but communicating subgroups). The last principle is the most personal of the PSC, and clearly the most controversial: it is not undoubted that, once a widespread species loses a part of its populations for any zoogeographical reason, then it will be induced to change dramatically its biological model. Wiley's formulation of the ESC states that extinction can be the only conclusion of a species, and that after a splitting (cladogenetic) event the mother species can preserve its original biological structure. Probably this is a more general but safer approach, hypothesising that cladogenetic events do often occur when a lesser variability (population) splits from a wider and widespread area. Genetic inertia is proportional to the dimension of populations and environmental range, and it is possible to suppose that a minor loss of variability could not affect the stability of the mother species. Anyway, this assumption should be tested for any specific situation, and the result must be included into the taxonomic decision.

Extreme approach to the PSC lead to the identification of species by means of their distinction from other biological models, namely their diagnosability (Groves, 2001). This approach, which can be referred to as the "one model one species" approach, can be quite useful in conservation biology, but it can generate confusion and instability due to subjective interpretations or changing knowledge. It probably leads to an equivalence between the concept of "species" and that of "variety".

Maybe, the principal problem with the PSC is that it is an ambitious attempt, based

on the assumption of comprehensive and accurate knowledge of the whole phylogenetic history of a zoological taxon.

It must be stressed that both the ESC and the PSC are anyhow particular formulations of a more general *individualistic thesis*, for which species are approached as “individuals”, with a personal ontogenetic pathway which involves birth, growth, ageing, death and, eventually, genealogy (Ghiselin, 1974; Hull, 1976). This is a rather generalised and theoretical definition, really unpractical to localise a species in palaeontology by an experimental setting, but it represents one of the best conceptual and romantic approaches to the matter, telling exactly what a species is or, better, the way we should have to look at it!

Particular attention must be paid to the *Cladistic Species Concept* (CSC), being the cladistic approach so widely used in evolutionary biology. Based on the Hennigian principle of holophyly and cladistic hierarchical taxonomy, it assumes that a species is an evolutionary entity localised between two cladogenetic events, including all the populations derived by a common ancestor (Ridley, 1989). As in Wiley’s ESC, without cladogenetic events a species remains the same regardless of morphological changes.

The cladistic approach surely has led to a useful formalisation of the evolutionary pathways, and it is as a whole the more complete tool to interpret phylogeny. Anyway, in palaeontology its potentiality is limited by the inevitable morphology-based approach (Trinkaus, 1992; Harrison, 1993; Lieberman, 1999), which is a quite unsafe marker of holophyly. The choice of a set of characters is the first and weaker step in a cladistic analysis in paleontology, being based necessarily only on some osteological remains. Characters must have a biological relevance, not to be intercorrelated and, of course, discrete. Their biological meaning is often not clear, and can be generally only hypothesised by means of inferences with neontological comparisons. Heritability is hardly testable for many structural units, which are determined by pleiotropic and polygenic effects plus several non-genetic influences. It is well clear that anatomical structures are complex, integrated and functional systems in which all parts are related, working as a whole both in ontogeny and phylogeny (Moss & Young, 1960; Enlow, 1990). They constitute a “nexus” of characters which cannot be explained and understood but as a whole (Sneath and Sokal, 1962).

Furthermore, many anatomical traits are often included in a continuous variability, and must be subjectively reduced and coded to discrete units or degrees of expression. Character states should be then weighted, and the difficulties to do it “objectively” in a paleontological context are surely well clear.

Polarity of characters is another major determinant of cladistic approach and, even if it is really a fundamental request to the understanding of evolutionary pattern, it is

nevertheless scarcely determinable on the basis of the scattered fossil record and the frequency of homoplasies and parallelisms during evolution (Wood, 1992). Finally, problems arise when a priori Operational Taxonomic Units (OTUs) must be organised, especially using the few specimens generally available in human palaeontology. Subjective choices based on an heterogeneous and insufficient statistical sample have a determinant influence on the mathematical result.

Homology, polarity and an adequate database are necessary criteria to include a character into a cladistic approach, and many traits classically used in human palaeontology do not satisfy these requests (Lieberman, 1995). Cladistics is a powerful approach to reconstructing evolution, but it requires a developed control on both the characters and OTUs involved, that is scarcely available in palaeontology.

It must be stressed that also in neontological and more heterogeneous applications, attempts to rank taxa by means of a full cladistic approach (i.e. Goodman et al., 2000; Watson et al., 2000) give rise to a number of difficulties that could not satisfy any genetic or morphologic background (Cela-Conde, 2000). Time divergence or number of branching events have been used to homogenise taxonomic scenarios, but this approach leads to a loss of relation between the species concept and the biological model, thus involving an unpractical loss of information. In palaeontology an additional problem is represented by the incomparable variability of species through time and space: fossil species have a realised phylogenetic history, while extant species only have a potential to produce new taxa. This is an insuperable barrier to rank taxa keeping in account cladistic clustering and a functional (operational) variability degree (Harrison, 1993). Moreover, cladograms change rapidly with the addition of new finds to the fossil database, and taxonomy - as an operational tool - should preserve a certain and useful degree of stability (*contra* see Groves, 2000, 2001).

Moreover, it must be kept into account that parsimony is a mathematical trick and clearly a statistical need, but it is not necessarily an evolutionary requirement. Differences in few steps on a computational model can involve a minor loss of parsimony and some major changes in cluster structures, and slight differences in databases or protocols may produce quite different results (e.g. Bloch et al., 1997).

Finally, the *Ecological Species Concept* also has to be mentioned, for which a species is "... a lineage which occupies an adaptive zone minimally different from that of any other lineage" (Van Valen, 1976). It is clear that such an approach is unlikely to offer useful information to the palaeontologist, who often works on just fragments of morphology, but it is fundamental to keep in mind that a species is nothing but the result of a unique interaction between a biological model and its historical environments. Although the economic adaptation of species to the environment are the results of com-

plex interactions involving the whole biota, which can not be isolated or reduced to single individual systems (see Tattersall, 1989), the ecological species concept introduced a basic link between species and niche, which is the real essence of evolution.

### **Species concept in palaeontology and morphology**

A fossil is the anatomical evidence of something (or someone) which once had its own genetic structure, biochemical organisation, ecology, behaviour and emotions. Thus, what is left of a complex biological system is nothing but its morphology. The only questions we could ask the fossil itself are those for which answers are included in its morphology (and, recently, to a few “fossilised” fragments of genome). It is important to keep in mind that fossil records are often a very poor reflection of past biological variability. For primates, it has been hypothesised that the available substantial fossils (thus, remains which are relatively complete to allow some safe assumptions) represent just 1% of the extinct species (Martin, 1990). Furthermore, they report just a small part of the variability of the species they represent. This is a fact, and must be necessarily kept into account when facing taxonomy in palaeontology, and must necessarily influence our choices and strategies.

Could morphology then allow us to approach the species concept and recognise the species level? It is clear that all a palaeontologist can do on this matter is to compare morphological variability of extinct taxa with that of extant ones (Simons & Pilbeam, 1965; Wood, 1993; Plavcan & Cope 2001).

For some primates a marked geographical variability could make morphology a false indication of species level: two different morphologies could then be just the result of a different zoogeographical interaction between individuals (sex and age dependent), populations and environment (Albrecht & Miller, 1993). Bone anatomy is well affected by this sub-specific variability, and there is probably no sure correlation between taxonomic ranks and range of morphological variation, which is often species-specific and influenced by the interactions between polygenic systems and environments. Thus, it could even be unsafe to make inferences on comparisons with ranges of variation in extant taxa (Plavcan & Cope 2001). In this perspective, Subspecies, as ecocline variants, are raised to “real” natural cluster, as suggested by Simpson in 1961, and is defined as a “collection of phenotypically similar demes, inhabiting a geographic subdivision of the range of a species, which differ taxonomically from other such collections of demes within a species” (Albrecht & Miller, 1993).

On the contrary, there are several data suggesting that in primates, morphological variability between close related species shows the same range to that of geographical variants, mainly for common retention of plesiomorphic features and homoplasies, both for bones (Tattersall, 1986) and teeth (Plavcan, 1993). According to this view, morphological differences are not necessarily related to evolutionary differences, and variability could include both morphocryptic and polymorphic species (i.e. different species with a common morphology, and single species with variable and heterogeneous features). Moreover, interspecific differences seldom occur between close phylogenetically related taxa, and they are possibly localised mainly in soft tissues, not in skeletal systems. Two remarks are then based on this assumption. First, fossil species are probably underestimated, for close taxa are not distinguishable on a morphological basis. Second, if an error will be necessarily included in this context, it would be better to work with too many names than with too few, for the sake of an informative communication between evolutionists, and a finer tool to describe evolutionary processes: “if err we must, we err (with reason!) on the side of recognizing too many rather than, as in the tendency, too few species units” (Tattersall, 1986).

Dealing with these two opposite formulations, it must premise that many evolutionary processes such as heterochrony and allometric patterns or pleiotropy can offer a wide range of variability without deep restructuration of the genetic systems (Gould, 1966; Shea, 1992), being also extremely rapid and sensitive to selective pressures as well as to stochastic dynamics. As Simpson stated in 1944, “... pleiotropic genes, polygenic characters, and adaptatively correlated characters form a mesh so intricate that a single change at any point may initiate a series of reactions by which selection eventually produces a change in the whole system”. Following this statement, “morphological potentiality” can be defined as the possible morphological variations based on a common biological model. These conditions are probably the major forces in evolution, and at the same time the major problems in paleontological taxonomy and systematics.

Four operational indications should be taken into account when approaching intraspecific differences in palaeontology. First of all, variability must be interpreted only upon safe knowledge and cognition of apomorphies, sexual dimorphism and population polymorphisms in closely related taxa (Kimbel & Rak, 1993; Lieberman, 1995). Characters should be therefore, tested in their genetic and physiological components (including structural relationships and constraints), by comparison with extant groups and even by available experimental settings. A taxonomy based only on raw morphological aspects, rather than “naming species”, can be reduced to “naming fossils”.

Second, inferences should be suggested only after a multivariate approach to intra and interspecific variability (Sbordoni, 1993; Shea et al., 1993; Wood, 1993; Plavcan &

Cope 2001). It is quite clear that only a multidimensional species concept can allow us to trespass the ambiguous and elusive nature of phylogeny, and help us to identify a correct and operational classification based on “morphologically discrete clusters in the fossil record” (Kimbel, 1991). A “taxonomic species” could be then defined as a character-based multidimensional approximation to the theoretic “biological species” (Szalay, 1993). After all, this is what taxonomy needs: identification of (relatively) isolated biological models and evolutionary histories.

For some databases which are sufficiently complete and developed, a convergence between morphological and molecular results has been reported (Shoshani et al., 1996; Goodman et al., 1998; Groves, 2000). This can reinforce early assumptions of numerical taxonomy which hypothesised that phenetic increase of information (number of characters involved) can be asymptotic, and at the same time a great part of phenetic clusters are monophyletic too (Sneath & Sokal, 1962). Anyway, a comparison between molecular and morphological data can be strongly influenced by the choice of the structures involved, and different indications have been obtained for hard and soft tissues (Collard & Wood, 2000; Gibbs et al., 2000).

Third, it seems unavoidable that a gradistic contribution may help grant stability and biological meaning to taxonomy (Harrison, 1993; *contra* see Tattersall, 1986). As a matter of fact, independently by the biological value of assumptions on grades, anagenesis or clinal variability, a gradistic approach could in some cases increase the available information, making unwise an absolute aprioristic renunciation to this perspective.

Fourth, morphology still remains the principal and most complete tool available to localise species-specific levels in paleontological data, but only through a multidirectional integration with other approaches such as geography, chronology and ecology, it will be possible to reach sufficient cognition on this matter.

When approaching palaeontology and the species concept in human evolution, one more fundamental variable seems to obscure any official definition: the superorganic nature of cultural adaptation.

Culture allows humans to change the environment instead of adapt their own biological parameters, leading all the human systems on a new discrete level of organisation with emergent functions which cannot be interpreted by inference on non-human models. Generally, non-human taxa can only adapt their genetic structures and physiological parameters to interact with the environment. Clearly, biological and environmental systems do interact by means of economical-ecological relations, which are surely indirect and self-organising, but not autonomous and finalised. On the contrary, human systems are less dependent upon their biological models, and they face environment directly changing the environment itself. Tools, fire, clothes and shelter organisa-

tion are all early products of this environmental manipulation. Communication and sociality are dramatically involved in this transition, and they induce a clear de-structuring of all the zoological species concepts, based mainly on relational systems.

In an extreme approach, it has been stated that “our speciation and evolution are different from most of other species’ by virtue of the cultural dimension. This has enabled us to diversify all over the world without speciating, unlike other creatures” (Tobias, 1995). Even if this sounds like a provocation and it does not help to identify some useful operational tools for the palaeontologist, it alerts us to use with some care, inferences from non-human contexts: evolutionists must always work in comparative evidence but, after all, man is not a lemur nor a colobus (primates on which anatomical variability at the species level has been often tested both for “pro- and against morphology” debate).

It has been suggested that the reason mammals have few sibling species is that there is a strong visual component in their mating systems, which does not allow closely related species to overlap morphologically or to reveal an extreme variability (Vrba, 1980). In this context, it is probably possible that, at least from early *Homo*, cultural adaptations such as language (and perhaps even “clothes”) have partially freed human populations from such a bond, shifting social communication towards non-morphological features, and the consequent loss of importance of visual components may have led to an increasing intraspecific variability which confuses phylogenetic inferences (Turner, 1986). Moreover, human evolution occurred on an almost worldwide level, and during a period of marked climatological changes and geographical range fragmentation, which may have increased the expression of variability of human taxa during Pleistocene (Tattersall, 1986; Turner, 1986).

It is clear that, only keeping into account this parameters, we must interpret some unconventional morphotypes such as those often referred to the heterogeneous hypodigm of *Homo heidelbergensis* (*sensu* Rightmire, 1998, 2000), that often includes fossils such as Kabwe, Bodo, Petralona, Arago, Steinheim, Dali and many others (see Wood, 2000). An excessive lumping bent would surely obscure evolutionary patterns and lead to a loss of information and communication, but an anatomical dissection of extinct human variability which does not imply these considerations on peculiar dynamics in human systems should represent, one more time, the misuse of a useless quasi-typological approach, with all the historical criticisms raised by neontologists and zoologist towards palaeontology and anthropology (see Kimbel & Martin, 1993).

### **Some considerations about species concept and evolution**

Some remarks can be suggested to approach a reasonable but useful species concept when working with fossils and evolution. Reasonable, for we must propose only those ideas which can be tested with the available information, avoiding to present romantic and private hypotheses (which anyway have their specific value and dignity!) as scientific assessments. Useful, for what we need is an instrument, that will work on fossil evidence.

First of all, a dichotomy between theoretical and operational needs must be stressed. It is surely useful to idealise a concept by a logical approach and test it by hypothetical arguments: it is necessary to extrapolate the object from its context to study it, and make it available in its pure form to a “mental dissection”. But we must remember that an object exists and works only inside its context, which is real and interactive with the object itself. Thus, evolution is made not by concepts, but by species, and what an evolutionist needs is, after all, not a definition, but a tool. A species concept, before it is complete and conceptually correct, must be operational and usable by a palaeontologist to understand and relate evolution. Theoretical refinement is surely subordinate to applicability. This often involves a generalised and vague definition that could be more useful than a complex and rigorous one, and that any rules introduced to understand a phenomenon could be really helpful only if it is not always applied!

Species concepts arose historically from neontological needs, as classification of extant non-changing varieties. Consequently, palaeontology has always used a tool that was not adapted to a time-dependent system. Fossil species have expressed their evolutionary potential variability, while living ones do not. Fossil species are organised longitudinally, through time (a “vertical phylogeny”), and they have been a part of a dynamic history: variability that has generated variability. On the contrary, we need to order the living species transversally, through space (an “horizontal phylogeny”), representing a photograph standing still (as far as our lives as taxonomists are concerned). The attempt is that of crossing and fusing two different hierarchical organisations, and this dimensional contrast represents surely one of the more marked incompatibility for interpreting and ranking with common rules extinct and extant taxa (Harrison, 1993).

One of the main barriers to the development of an operational species concept was the belief that a “true” species concept must resolve all the related evolutionary situations, included the hypothetical ones: a complete species concept must explain what has occurred and what possibly should have occurred too. Mayr’s BSC includes “actually or potentially interbreeding” populations, and so does the Paterson’s RSC, while

Simpson and students who agree with the ESC try to apply this hypothetical relational potentiality through time, and cladistics invoke the same taxonomic approach for any potential phylogenetic combination. I believe that, if it is rather difficult to find some satisfactory determinants for any real and occurred situation, this purpose becomes uselessly impossible when extended to the non-occurred and hypothetical ones! Moreover, if some potentiality has never been expressed, it clearly does not matter to the evolution itself. Thus, any species concept must be necessarily contextual, aimed to explain the *actuality* of evolution, and not its *potentiality*. Of course, there are some problems due to the scarce power of evolutionary biology in testing some hypotheses: actuality can be only “probable”, and potentiality is still the main inference to understanding evolutionary patterns. Anyway, for an operational efficiency of the whole taxonomic system, we have to keep separated these two conceptual approaches. In this context, a useful case-study in human evolution is represented by the Modern-Neanderthal morphotypes in Europe. Although there are some students who still suggest a certain degree of biological continuity between these two populations ( e.g. Frayer, 1992; Wolpoff et al., 1994, Duarte et al., 1999), it seems quite clear that they represent two different evolutionary models, representing discrete morphological (Stringer & Andrews, 1988; Howells, 1989; Tattersall, 1986; Rak, 1993; Turbòn et al., 1997; Manzi et al., 2000; Schillaci & Froehlich, 2001), genetic (Krings et al., 1997; Ovchinnikov et al., 2000) and cultural (Mellars, 1989, 1992) units. Now, we can never know if Neanderthals and modern humans shared a common fertilisation and mating system. Moreover, if two genera like *Homo* and *Pan* share such a great genetic substratum, we must assume that two human morphs can hardly be assigned to zoological sibling species, and a impermeable genetic barrier is clearly not so probable (Stringer, 1992). But what really matters to evolution (and to evolutionists, of course), is that these two lineages have been kept discrete and separated through their evolutionary pathways. Even if they could have eventually interbred, this seems to have not affected their respective human histories. It is absolutely useless and unhelpful to any epistemological context to state that two species cannot be hypothesised because their biological identities can never be tested. It is not important if two biological models have interbred or if they could eventually interbreed, what it is really meaningful is if this potentiality has changed their evolutionary destinies: “it is also clear that two species may interbreed to some extent without losing their distinction in evolutionary roles” (Simpson., 1961). In the Neanderthal-Modern Humans case-study what really matters to an actual and operational species concept is that they represent the “result of an irreversible genetic and historical process” (Tattersall, 1986), or simply “the result of a long process of independent evolution” (Arsuaga & Martinez, 1998).

A contextual and effective approach could allow palaeontologists to agree at least on three main points that keep the debate on the species concept on a theoretic (non-practical) basis: anagenesis (interpretation of chronospecific variability), cladogenetic events and taxonomic purposes.

First, if an anagenetic lineage can be hypothesised, an evolutionary species concept *sensu* Wiley would be a recommendable characterisation. Anyway, if some particular “phase” can be recognisable inside such a lineage, and if it could represent further biological information, a different specific name should be used to communicate some non-discrete transitional steps. For example, assuming that European *H. heidelbergensis* and *H. neanderthalensis* should belong to a single and continuous evolutionary lineage (Arsuaga & al., 1997), it will be more informative to keep both the specific names, in order to describe two different human populations characterised by different morphological, chronological and environmental contexts (Arsuaga & Martinez, 1998; but see Rightmire, 1998). Again, we never know if this is “biologically correct”, but it could be simply “informative”, and that is what taxonomy needs.

Second, if a cladogenetic branching event can be suggested, taxonomy first should take into account whether or not the “mother species” has been evolutionarily affected by this process, integrating the whole package of information available (biogeography, genetics, culture etc). If the original species does not show marked shifting of (biological) characters after cladogenesis, surely it is not useful to introduce a second name to describe a biological model which already has a definition, just to satisfy a rigorous and univocal cladistic approach. Conversely, if a certain amount of variation occurred after the splitting process in both the derived populations and in the ancestral ones, then it could be necessary to include this information into the taxonomic system. A case-study is represented by the debate about the specific status of African and Asian *Homo erectus*. If some geographical or chronological differences may be described between the early African and late Asian specimen (Wood, 1994; *contra* see Brauer, 1994; Rightmire, 1986, 1998) it may then be useful, lacking some complete evidence or certainty, to introduce a different name for the African group (*Homo ergaster* Groves & Mazak 1975) to indicate some morphological, chronological and ecological characterisation which, even if may have not had importance in reproductive biology of these populations when compared to the later ones, may have had importance in evolution of the subsequent radiation of the genus *Homo*.

The third node is taxonomy itself. If it must represent phylogeny, it has to be surely organised on a cladistic-based hierarchical model describing holophyletic clusters. But if it has to be a useful tool to “tell” phylogeny, it has to include gradistic and phenetic (functional) approaches. Phylogeny represents the evolutionary relationships inside the

biological variability, while taxonomy is an ordering of this variability. If they converge into a same object, clearly a loss of information will be unavoidable.

For example, if a paraphyletic status will be confirmed for the *Australopithecus* group (see Wood & Collard, 1999), it will probably be inconvenient and unhelpful to use a full cladistic approach (quite useful in a conceptual context) and invoke a single genus for almost any *Australopithecus* morphotype, or even include them and the whole *Homo* variability in a single one.

What is really important is that phylogeny reflects the actual history of evolution, while classification is a tool to understand and describe it. We must work to use and improve any species concept and taxonomic descriptions with two principal aims: to optimise the identification of evolutionary pathways and to improve the communication between palaeontologists. Species exist, species concepts do not, and they represent only a mental abstraction that we mould for our contextual purposes.

### Summary

The lack of a general agreement in species definitions is the result of the problematic nature of species themselves, combined with an excessive requirement of theoretical and conceptual approach. Taxonomy is a tool and an operational process, aimed to describe and order actual sequences of facts. The major species concepts have been characterised by attempts to determine unique and rigorous definitions. Regardless, each of them is available only in some specific situations, yet exceptions are so widespread and generalised that they involve a loss of terminological efficacy. In palaeontology, the scarce availability of fossil primates and the biological heterogeneous basis of the “morphological potentiality” lead to the necessity for scientific control of biological factors. Characters should be previously tested, and then organised in a multivariate context to work on species as clustering morphotypes. Every rigorous approach, such as those involved in an extreme cladistic perspective, will probably originate conceptual boundaries forcing evolutionary events into a useless and limited frame. The contribution of integrative information (chronology, ecology, geography) should be improved, with special reference to the cultural context in human evolution case-studies. The dichotomy between theoretical and operational requirements is the principal obstacle to the formalisation of the species concept. Clearly, a fine theoretical background is practically useless if seldom applicable. The second dichotomy is represented by the neontological and paleontological different necessities that can even preclude the use of some common tools. The third node is the dichotomy between potentiality and actuality.

lity that for systematics is a tool to describe what happened, and not what should have happened.

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