Taxonomical uses of the species concept in the human lineage

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Abstract

Different species concepts, which broadened the scope of Mayr's Biological Species Concept, have been put forward aiming to produce sound taxonomies of fossil taxa. Here, we propose using a simple one, the Evolutionary Species Concept, on the grounds of considering that separation of populations – disregarding other issues – is enough to describe the evolution of the human lineage. The question of the acceptable number of Middle Pleistocene hominin species is used as an example.

The purpose of grouping organisms in different categories is to order the diversity of living beings using manageable sets. Such a function could be said to be nominal, and its interest only taxonomic. If this were the case, the necessary processes to arrive at this kind of classification would not depend on the fact that they are used to study living beings. They could also be useful to classify ceramics, books or cars. It would be enough to specify the distinctive traits that need to be considered when distributing the units.

Is the concept of species used in a nominal sense by human paleontology to distinguish units in our lineage's fossil record? The introduction to the 4th edition of the International Code of Zoological Nomenclature (ICZN) states: *the Code refrains from infringing upon taxonomic judgements, which must not be made subject to regulation or restraint*. Consequently, scientists are authorized to classify any discovered exemplar within a new species. This complete freedom to establish new species is only limited by the degree of acceptance among specialists in each discipline – botany, zoology, paleontology, and so on. It is, thus, a criterion of pure consensus.

A strictly nominal taxonomy, lacking objective criteria to assign exemplars to each taxon, will always generate great doubts and arguments about definitions. The comparison of several current models of the human lineage attests to this: The status of many hominin taxa is under suspicion. Resolving the doubts will clearly require two conditions. First, that researchers use a concept of species able to go beyond mere nominalism. Second, that researchers have adequate means to decide the species to which a given exemplar belongs.

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Do we have a concept of species capable of going beyond nominalism?

The notion of species is, undoubtedly, one of the Life Sciences' most powerful heuristic tools. Its generalized use, however, in multiple disciplines that have different requirements, use different observation techniques, and rely on different empirical evidence, from microbiology to paleontology, has led to a complete dispersion regarding the kind of *species* concept used in each case. Ramón Rosselló-Mora[1] tallied more than 22 different concepts, which, as argued by the author, can be reduced to a few universal notions. Such a condensation, however, is unattainable unless one is willing to accept a radical kind of reductionism. Rosselló-Mora[1] argued that if we carry out such a reductionist program, the concepts of evolutionary species and phenetic or polyphyletic species have a universal application.

Then again, a *universal purpose species* is of very little use within each particular scientific field. In reference to paleontology, and specifically to paleoanthropology, what is needed is a concept of species (i) that is able to explain the evolution of biological lineages, specifically the human lineage, and (ii) that can be profitably used for any other beings whose reproduction is achieved sexually. This second condition allows not having to take into account *exotic* concepts of species, such as that proposed by DeBach[2] to classify thelytokous organisms.

Several species concepts complying with both conditions have been proposed. The starting point would be the *biological species concept* (hereafter, BSC), which owes to Dobzhansky[3,4] and was developed by Mayr.[5-7] As it is well known, a biological species is *a group of natural populations that interbreed, in reproductive isolation from other similar groups.*[8] However, as noted often, the capacity to interbreed is not a convenient taxonomic tool, particularly when fossil organisms are concerned. In fact, Wu[9] noted that the notions of reproductive isolation and differential adaptation inherent to the BSC have tended to separate as the concept developed in time, and that the focus of the BSC has shifted from whole genome reproductive isolation to genic-level differential adaptation. Under this view, reproductive isolation is regarded as the result of the divergence in organisms' reproductive, developmental or behavioral traits.

Keeping phylogenetic processes in mind, other species concepts are particularly useful for classification. Simpson's concept of *evolutionary species – A lineage (an ancestral-descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies*[10] – is a good example. Aiming to develop Simpson's evolutionary species concept, Leigh Van Valen[11] proposed the *ecological species* – conceptually close to Ernst Mayr's adaptive concept of genus.[12] In this sense, *A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from* *that of any other lineage in its range and which evolves separately from all lineages outside its range*. In Van Valen's concept, a lineage is *a clone or an ancestral-descendent sequence of populations*, and a population is *a group of individuals in which adjacent individuals at least occasionally exchange genes with each other reproductively, and in which adjacent individuals do so more frequently than with individuals outside the population.*

The idea of defining species as lineages, if we agree on the need to adapt taxonomies to the actual process of development of the *Tree of Life*, is sound. Taking phylogenies as the reference model in taxonomy, we quickly arrive at the *phylogenetic species concept* (PSC). However, different PSC have been proposed. For instance, Nelson and Platnick's concept of *the smallest detected samples of self-perpetuating organisms that have unique sets of characters*[13] (p. 12) can be understood as a PSC. Alternatively, Joel Cracraft[14] used the name of Phylogenetic Species Concept to define a species as *an irreducible cluster of organisms, within which there is a parental pattern of ancestry and which is diagnosable distinct from other such clusters.* In Cracraft's terms and aim, a species is *the smallest diagnosable cluster*, *i.e.*, something very similar to Nelson and Platnick's PSC.[13] However, a sharp criticism to any kind of definition implying *species* as *evolutionary units* was expressed prior to Cracraft's PSC definition. Brent Mishler and Michael Donoghue[15] pointed out that no single basal evolutionary unit could be found among all such possible units. In Mishler and Donoghue words – following Hull:[16] *there are* many *evolutionary, genealogical units within a given lineage– a rough hierarchy or network of units, which may be temporally and spatially overlapping*.[15] This criticism led to a different concept of PSC, which was both much more precise and complex: *A species is the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly (usually, but not restricted to, the presence of synapomorphies), that is ranked as a species because it is the smallest important lineage deemed worthy of formal recognition, where* 'important' *refers to the action of those processes that are dominant in producing and maintaining lineages in a particular case.*[17]

With such a complex, detailed description, not only did Mishler and Donoghue define a concept. Their view is actually a developed theory about what a set of collectively evolving organisms is. To call it a *species* is just a question of tradition, since important differences exist between the strategy of Mishler and Donoghue's grouping[17] and that of Mayr's BSC. Let us consider the case of *robust* australopiths. *Paranthropus robustus* and *P. boisei* should be considered, under our current knowledge of their hypodigms, as different species using Mishler and Donoghue's PSC even if a *sorcerer paleoanthropologist*' told us that they actually had the theoretical capacity to interbreed.

Demes or populations can be *species* under Mishler and Donoghue's PSC. But a question arises: Is such a complex concept necessary to go beyond the BSC in order to interpret hominin evolution? Trying to include *all* epistemic details of the evolutionary process in a definition seems a hopeless task. For instance, turning back to Mishler and Brandon's definition,[17] what processes are dominant in producing and maintaining lineages when we are trying to place poorly known specimens in a phylogeny? Alpha-taxonomies can be obviously invoked, and character-based PSC[18] may be useful for any morphometric preliminary approach. However, Mishler and Brandon's demanding PSC concept seems excessive to reach some result faced with taxonomic doubts such as, for instance, whether *Homo habilis* and *Homo rudolfensis* should be integrated or not in a single taxon.

Actually, when trying to classify doubtful specimens we do not have a known cladogram to begin with – necessary to disregard paraphyletic sets – because characterizing that evolutionary episode is actually the final goal to be achieved. What we are lacking is not a theory about how evolution *can* proceed, but how a particular set of organisms can have an unshared history with any other equivalent set.

Let us come back to the evolutionary species concept (ESC), introduced by Edward O. Wiley[19] when reformulating Simpson's[10] proposal: *a species is a lineage of ancestor-descendant populations that retains its identity in relation to other similar lineages and that is characterized by its own evolutionary tendencies and historical destiny*. Invoking *its own evolutionary tendencies and historical destiny* is enough, in our opinion, to disregard any paraphyletic grouping – though whether we have succeeded or not in this task should wait for ex-postfacto procedures. Wiley's ESC, and both Cracraft's and Mishler & Brandon's PSCs, are epistemically useful tools to name fossil specimens that we only suspect constitute a rather homogeneous group. ESC is enough and simpler. Obviously, for theoretical and practical reasons authors disregarding the classes-individuals distinction[20] – such as Mishler and Brandon[17] – would not accept the ESC's *historical destiny* approach.

Since we are talking of organisms, fossil or not, biological laws apply. The members of every ESC would have obeyed, during their extant existence, biological laws belonging to the field of the BSC concept. Actually, this is the grounding of the monophyletic requirement for every alleged lineage. The main discrepancy between BSC and ESC concepts is the inclusion of the *time variable* in the ESC. The ESC allows for chronospecies – as portions of a single anagenetic lineage–, while the BSC would only accept them in hypothetical terms, in the sense that two chronospecies separated in time would have satisfied the reproductive isolation condition if they had been contemporary. This issue has been debated and clarified to satiety by philosophical studies, which have, at least, led to the abandonment of the nominal sense of each of those species concepts, and to the understanding that they constitute entities with a real existence (*individuals*).[21,22] However, the problem that arises when attempting to make the BSC and ESC compatible is not ontological; it is epistemological.

Natural selection only takes place if there is diversity, both in intraspecific cases (the most important, initially) as in interspecific cases (of great transcendence when there is an environmental change and/or a dispersion). The diversity of species owes to the differential accumulation of alterations in two populations, whether sympatric or allopatric. The resulting addition of changes owing to the function of reproductive and inheritance mechanisms would not be shared between the populations, provided there were no interbreeding. This scenario could owe to: (i) the appearance of reproductive isolation mechanisms among sympatric populations, which are the foundation of the BSC, or (ii) their factual separation (whether due to the geographical isolation of allopatric species or the temporal isolation between populations living at different times) implied by the ESC. In the latter case, the fact that these separate populations belongs to the same biological species or not is, indeed, irrelevant. The fact is that they will not hybridize.

Paleontology, and paleoanthropology in particular, has seen thousands of pages devoted to discussions regarding whether two taxa are reducible to the same species or not. This issue is often raised when a new taxon is proposed (for instance, *Australopithecus afarensis vs. Australopithecus africanus*; *Homo habilis vs. Australopithecus africanus*; *Homo floresiensis vs. Homo erectus*). But it is also raised by taxonomic revision studies (for instance, *Homo rudolfensis vs. Homo habilis*; *Homo erectus vs. Homo ergaster*; *Homo neanderthalensis vs. Homo sapiens*). The importance of the phylogenetic process, which lies beyond nominalist approaches, is left aside in many of the discussions about the correct taxonomy. In this sense, it is necessary to understand that the picture would not be altered at all if two taxa really belonged to populations with effective reproductive isolation (being true biological species), or separated by other causes (*i.e.,* species only in terms of the ESC). In fact, a prolonged separation usually leads to speciation, but this matter, as we argue, is secondary to the basic question: two groups remain isolated, for whatever reasons, from each other. As argued by Joel Velasco,[23] the Tree of Life – the schematic representation of phylogenetic processes – has the same shape independently of the species concept one prefers. This may be true, but it is also true that the Tree of Life cannot be dealt with directly. Hence, the way we represent it is not really independent of the concepts we use to construct the scheme. On the other hand, the fossil populations were at some point living populations subjected to biological laws. Even though the scheme for the Tree of Life seeks to narrate a story, it must be respectful with the requirements of reproduction and inheritance mechanisms.

The comparison of fossil species

How can we tell whether two fossil populations remained separate? The first indication is morphological. Other evidences can be obtained by comparing functional traits. If a population P1 exhibits anatomical or functional traits another population, P2, lacks, it can be argued that P1 and P2 did not interbreed, that is, that they remained separate. This is the most relevant circumstance to understand their *own evolutionary tendencies and historical destiny*.

Thus, we can leave aside the discussion about whether the BSC can be applied, even hypothetically, to the fossil record. As noted above, the factual reproductive isolation – due to the species' characteristic isolation mechanisms or otherwise – is the key to the phylogenetic process, which the ESC aims to study. Given that time is a fundamental variable for the ESC, but not very relevant for the BSC, it is clear that there is no sense in discussing the compatibility of the BSC and the ESC. They will be completely compatible when we aim to ascertain the separation of populations, whatever the reason.

Once we have identified a population that has remained separate – which we can consider a *species* –, the extent to which it maintains its identity regarding other similar groups remains to be determined. To put it in another way, whether a species S2 can be reduced to a previously named one, S1, needs to be determined.

It is very common to use morphological measurements of fossils as a taxonomic criterion. Plavcan and Cope,[24] however, examined the criteria used to define species by means of metric features, and they noted the absence of precise means to guide the transition from morphological traits to species. Regarding fossil taxa, one of the main difficulties arises from the variability that might exist within a single species. As argued by Plavcan and Cope,[24] there is no magical number that can be used to determine whether a sample is composed of one or more species.

Leslie Aiello and colleagues[25] examined the application of advanced statistical techniques (exact randomization) that aim to assess the diversity within a specific fossil population based on size or shape affinities – for an overview of other methods see.[26] The techniques examined by Aiello and colleagues[26] usually take the morphological diversity within a given species of current anthropoids and then compare the results with the differences among specific fossil taxa. If the method provided precise conclusions, it would be possible to use them as criteria to decide whether a given fossil specimen should be assigned to existing taxa or whether it is more appropriate to create a new species. The exact randomization technique has been successfully used on several occasions. For instance, Harvati, Frost and McNulty[27] used the procedure to compare the morphological distance between neandertals and modern humans, and concluded that they are in fact two different species. However, Aiello *et al.*'s results[25] revealed that the taxonomic hypotheses produced by these methods are greatly affected by the chosen reference sample, especially because of the overlap in the intra- and interspecific variation ranges in these samples. Some extant species are highly polymorphic, while others exhibit little variation. Given that assessing the possible polymorphism of a fossil population is precisely the aim of the procedure, the chosen starting point has a powerful effect on the results. Aiello and colleagues' study[25] also questioned the sensitivity of the kind of metrical information used in these studies, that is to say, its capacity to reflect taxonomic differences with accuracy.

From phylogenies of genera to phylogenies of characters

The detection of apomorphies, plesiomorphies and homoplasies able to indicate the distance between two specimens provides a qualitative criterion to outline phylogenies. This criterion is applicable to incomplete samples. Hence, to name a species based on few dental traits is not exceptional if conspicuous apomorphies are observed.

The way to determine whether a trait exhibited by fossil exemplars is an apomorphy, a plesiomorphy or a homoplasy, is a long debated issue. David Begun[28] argued that the only safe way to do so is to previously determine the phylogenies of the exemplars whose traits are to be compared. One of the most complete ways to produce such phylogenies is by means of the processual approach. It involves establishing, for each taxon, the mechanisms of development, selection, adaptation, exaptation – traits that evolved under certain conditions that acquire a new functional significance when conditions change – and random changes. Needless to say, such an approach requires much more information that what scarce fossil remains, which often lack an adequate taphonomy, are able to provide. Moreover, determining phylogenies is precisely the objective that we wish to attain by means of the examination of apomorphies, homoplasies and plesiomorphies. Are we not falling into a circular argument?

A possible means to break out of it is to shift the focus level, determining the phylogeny of genera before dealing with the details of character status. The processual approach is comparatively easier to apply to genera. For instance, immunological analyses allowed establishing existing differences between the different hominoids and, thus, producing the most probable phylogeny.[29-31] In fact, the examples provided by Begun[28] refer both to extant and fossil hominoid genera.

An available reference to the phylogeny of genera can be used, on occasions, to detect homologies and analogies relative to species. It can be used to establish lineages as well as variation ranges. The knuckle-walking trait of chimpanzees and gorillas provides a good example of this. Such a trait has to be a plesiomorphy in light of hominoid phylogeny. Otherwise, we would have to regard it as a homoplasy that was acquired separately by *Pan* and *Gorilla*. In the former case, however, the traits related with the locomotion of the first hominins, which were already bipedal, should reflect indications of such a plesiomorphy to some extent. Indeed, the significance of the hands and feet of *Ardipithecus*[32-34] in order to clarify the role of knuckle-walking as a homoplasy in African great apes was possible because the phylogeny of hominoids was previously available.

The processual approach is a comprehensive and valid way of clarifying the status of the observed traits. Its results can aid in the selection of the most informative traits to characterize species, but only if we have previously resolved the phylogenesis of its genera, which, luckily are usually easier to achieve. Mark Collard and Bernard Wood's[35] study on skeletal homoiology constitutes a good example of this approach leading from genus-level phylogenies to character conditions. Although it is commonly believed that homoiologies are abundant in fossil hominins, the results of Collard and Wood's[35] analysis revealed that they do not have a significant impact.

Molecular identification of species

Advances in genetics and genomics have afforded an objective method to identify species: by means of the genetic distance between two taxa. Its comparison with the distance between two closely related species, about whose separate identity there is no doubt – as is the case with chimpanzees and modern humans – could serve as a scale to decide whether two fossil exemplars belong to the same species. This can only be achieved once their genetic material has been retrieved. Occasionally, however, the molecular identification of species paradoxically leads to contradictory results.

Darren Curnoe and Alan Thorne[36] used the genetic distance between chimpanzees and humans to calculate the number of species that the human lineage could accommodate. The condition was that the molecular distances among them were at least equal to that separating *Pan* and *Homo*. They concluded that *Homo sapiens* was the only species existing for the last 1.7 Myr – coinciding with the migration out of Africa. Thus, both African and Asian *Homo erectus*, all *archaic* humans, and *Homo floresiensis* should be regarded as members of our current species.

Aiming to propose a lineage-based approach– explicitly linked to the ESC – Darren Curnoe[37] used the same method for extrapolating genetic distances to establish a phylogenetic tree that included a reduced number of species. Thus, using temporal yardsticks based on molecular clocks (*i.e.*, chronolineages or chronospecies) a test of hominin diversity might be reached. The resulting tree, in fact, coincided with the genera accepted by most lumping authors. These results are contrary to mitochondrial DNA studies, especially those carried out by Pääbo and colleagues,[38-41] which Curnoe and Thorne[36] criticized and rejected as being unreliable indications. The retrieval of Neandertals' genome[42] – though not addressing the question – favors considering *Homo sapiens* and *Homo neanderthalensis* as two distinct species. Thus, it turns out that direct comparison of genomes of fossil taxa – when available – would be a better criterion than measurements of current genetic distances in order to identify ancestral species. Nonetheless, as we mentioned above, genomic approaches can help reaching a sound taxonomy of fossil specimens but is not the central issue. *P. robustus* and *P. boisei* could be considered as different ESC species even if their eventually retrieved genomes were quite similar.

Cladistics

Hennig[43,44] and Mayr's concepts of species both rely on the principle of reproductive isolation to characterize a species. In Mayr's words: *The essence of the biological species concept is discontinuity due to reproductive isolation.*[45] On the other hand, the current interpretation of Hennig's concept of species is of *reproductively isolated natural populations.* [46] Although sporadic hybridization episodes do not contradict the general norm, a consistent concept of species as reproductively isolated groups must include the loss of the potential for cross-fertilization. However, as Kevin de Queiroz pointed out,[47] reproductive isolation might not be very useful for detecting lineage separation, particularly in the early stages of divergence. Instead, geographic information is worth being taken into account, since, as De Queiroz[47] quotes *nearly all species exhibit geographic variation, and it is possible for larger differences to exist between populations within the same old and geographically widespread species than between populations from different but recently separated species.*

This circumstance reflects the fact that isolation can occur even in the absence of mechanisms capable of preventing cross-fertilization. This is the case if populations are geographically or temporally separated. Although geographical separation can be overcome, temporal separation cannot. Two populations from different times cannot interbreed. This trivial fact, taken as a rule, would lead us to place fossils from different periods into different species, even though they might be very similar. But such a classification would be absurd. The issue is, in the absence of a criterion based on the mechanisms of reproductive isolation, how to determine whether two organisms that lived at different times belong to the same species.

Hennig's original cladistics allowed, in certain cases, the reconstruction of phylogenies identifying different species. It is well known, however, that this could not be applied to phyletic lineages. To speak of *species* in that case is the result of applying operational prescriptions upon the fossil record. We have moved from the biological to the evolutionary concept of species: from the BSC to the ESC.

The identification of species, by means of the ESC, in a phyletic lineage is common in paleontology. Evolutionists use a practical criterion to define presumed species in phyletic lineages of organisms that descend from each other. *Chronospecies* are groups of organisms from different periods that seem to be ancestors and descendants that differ morphologically as much as current organisms classified as different species.

Transformed cladistics[48] attempted to keep phyletic lineages as legitimate episodes of speciation. It does so by allowing a daughter species to be considered a different species if it exhibits at least one apomorphy that distinguishes it from the mother species. And the solution adopted by transformed cladistics to admit this simultaneous presence is to consider the mother and daughter species as sister species in the cladogram.

An important consequence of placing the mother and daughter species as sister species is the transformation of the original sense of Hennig's *stem species*. Schaeffer, Hecht and Eldredge[49] had already concluded, before the proposal for the reformation of cladistics, that all taxa, whether fossil or extant, should be placed as terminal taxa in a cladogram. Consequently, only hypothetical ancestors should be placed in the nodes. Once a fossil taxon is correctly identified, it must be placed as a terminal taxon. Thus, not only does the *stem species* disappear as a representation – part of a branch, or as a node – but as a concept in itself. Cladograms lose their meaning as an image of the evolutionary process (in the sense of phylogenetic trees) and are reduced to mere representations of the way in which the lineages diverge into sister species.

The price paid for this transformation in cladistics is the loss of the temporal variable. After the reduction, cladograms were not expressions of ancestor-descendant relations, and speciation processes throughout time could not be established by means of cladistics.

Cladistics, and especially transformed cladistics, only indicates the status of sister groups in lineages that appear from the same node. In this sense, cladograms differ from phylogenetic trees, which are graphic representations of ancestor-descendant relations, collateral relations among taxa, and may even include a temporal scale. But in transformed cladistics ancestor-descendant relations lack any scientific interest, given that the hypothesis that a taxon is ancestral to another cannot be contrasted.[50,51] Siddall boldly expressed the same idea when he referred to the purpose of describing evolutionary relations by searching for ancestors in the fossil record as the reappearance of the cult to the golden calf. [52]

According to Delson, Eldredge and Tattersall,[53] it must be underscored that the concept of *sister species* is a methodological instrument that must be applied even if (i) taxa under consideration are ancestors and descendants – and thus are not true *sister species* – (ii) taxa under consideration have unknown close relatives. Delson and colleagues[53] argued that there is no way of deciding which branches stemming from a given node are sister species and which are mother-daughter species in a cladogram constructed in such a manner.

Transformed cladistics constitutes a useful instrument to reconstruct evolutionary lineages. It has, however, certain serious technical problems that cast doubts on the produced phylogenies. Although it is assumed that cladograms merely order sets of objective data, derived from the morphological examination of fossil exemplars, cladistic analyses require a number of decisions that have the potential to bias the final result. Leaving specific details aside, it is necessary to choose the characters that will be taken into account, the exemplars that will be compared, and to assign these to different taxa. If, for instance, we wish to produce a cladogram for Pliocene humans in Africa, aiming to determine how many species existed at that place and time, we will probably get different distributions of lineages depending on whether we choose to include only metrical characters or if we also take into consideration qualitative traits. Decisions as to whether any given character – say, for instance, the sagittal crest – is present or not in every exemplar can lead to further differences. And, finally, the initial grouping of exemplars into taxa will lead to an unavoidable bias. All these examples have been used to illustrate that creating cladograms is not exempt of aprioristic decisions.[54] The problem, as noted by W. Henry Gilbert, Tim White and Berhane Asfaw,[55] becomes worse when cladograms are used to study the evolution of lineages within the species category based on individual exemplars.

There are procedures designed to minimize these apriorisms when constructing cladograms. Hence, the need to avoid circular arguments recommends not starting by grouping the exemplars whose lineage we are attempting to clarify into species. Alternatives, such as the OTU (Operational Taxonomic Units) have been proposed. An OUT is defined as the smallest taxonomic unit used in a study.[56] Its aim is to afford an objective method of grouping that is not influenced by prior decisions about whether a certain species exists or not.

However, grouping with OTUs is as susceptible to circularity as doing so with species, unless there is a prejudice-free criterion to create OTUs. A useful criterion is that of paleodemes, defined as sets of fossil exemplars that are of *proximate geographic distribution and closely similar age*.[57,58] Although the notions of *proximate geographic distribution* and *closely similar age* might seem somewhat vague, authors such as Eric Trinkaus[59] consider the paleodeme method to be one of the most representative strategies to understand the evolutionary dynamics of fossil populations.

We will not, for lack of space, discuss the criterion of parsimony and the statistical techniques that decide, in a bootstrapping procedure, the degree of admissible consensus (*strict consensus vs. majority rule*, in general). We will turn directly to consider to what extent the usable concepts of species and the identification of lineages can aid in solving the unending controversies, using the number of identifiable species in the hypodigm of *Homo erectus* as a case study.

An ill-defined species?

G. Philippe Rightmire's[60] definition of the hypodigm of the *Homo erectus* taxon rested on the notion that a species' formal diagnostic must be based on its apomorphic or derived traits, and not on plesiomorphies. When Dubois first named the taxon, current requirements of formal description of any taxonomic proposal did not exist. So, in actual fact, *H. erectus* was never adequately defined by indicating its apomorphies *–erect* is, obviously, a plesiomorphy. Numerous subsequent studies, however, noted many of the species' *typical* traits.

G.E. Kennedy[61] analyzed the polarity of 12 traits generally regarded as the taxon's autapomorphies, that is to say, *H. erectus*' own characters, not present in any other prior or later species. Kennedy's[61] results revealed that none of the 12 traits was in actual fact autapomorphic for *Homo erectus*. Eight of the nine non-metrical (qualitative) traits were symplesiomorphies, inherited traits that appeared in the most recent common ancestor. The ninth, the presence of torus occipitalis, is also found in different hominins to *Homo erectus*, including modern humans.

The three remaining traits were: high endocranial volume, remarkable thickness of cranial wall and remarkable thickness of the tympanic plate. The three are metrical traits. Endocranial capacity cannot be regarded as an autapomorphic trait because it is measurable quantitatively. With regards to the second trait, in addition to the same problem just noted, Kennedy[61] showed that, in actual fact, it is constituted by two processes. One of them, lateral expansion of the inferior part of the cranial vault, is primitive, and the other, the thickness of the superior part of the vault, is derived, but shared with Neandertals. Finally, the third trait, the tympanic plate thickness, is also primitive and it is shared with Neandertals.

Kennedy[61] concluded that this absence of autapomorphies meant that *Homo erectus* is an ill-defined species and, thus, invalid. This conclusion was in agreement with Stringer[62] and Hublin's[63] analyses.

In light of these definition problems, the species should be reduced to some other pre-existing taxon because it lacks a distinctive and proper reality. However, Kennedy[61] noted some apomorphies that reveal the derived character of *Homo erectus* in relation to *Australopithecus*. Hence, in this regard, the difference is clear. The apomorphies of *Homo erectus* in relation to *Australopithecus* indicate that a new kind of hominin had appeared. Bernard Wood and Mark Collard[64] argued that *Homo erectus* is in fact the earliest admissible taxon within the genus *Homo*. How can it be, then, that it is an invalid species?

This issue has to do with the possibility that the exemplars that are usually placed within *Homo erectus* might be placed within a previously defined species. *Homo neanderthalensis* and, clearly, *Homo sapiens*, were named before Dubois introduced *Pithecanthropus*. In accordance with the lack of specific distinctive traits that are not present also in modern humans, Hublin[63] argued that the *Homo erectus* exemplars should be included in *Homo sapiens*. However, Kennedy's work[61] rejected the hypothesis that the set of *Homo erectus* exemplars belonged to the same species as modern humans. In fact, only a minority accept Hublin's[63] proposal. Neither Kennedy nor Stringer, to name only to the aforementioned authors, suggested removing the taxon from the list of *Homo* species. *H. erectus* is commonly viewed as member of the human lineage.

Kennedy's[61] analysis revealed the root of the problem. It does not have to do with the biological reality of *Homo erectus*, as much as with its taxonomic consideration. Kennedy[61] admitted the possibility that phylogenetic systematics is not discriminative enough to be useful at levels below the genus. If this were the case, we would have to settle for a phenetic analysis of *Homo erectus* or, at the most, a description of its overall morphological pattern.

Luckily, the pending task of characterizing the phylogenetic process of Pleistocene hominins affords an understanding of the sense of *Homo erectus* quite precisely.

Population consequences of the exodus from Africa

Two different populations can be distinguished after hominins left Africa. If this migration was exceptional and unique, they would have had little relation. But, when did this dispersion occur? The evidence from the Levant Corridor – Jordan Valley – suggests that no less than 5 migrations out of Africa took place between 2.4 and 0.8 Myr.[65,66] This fact raises doubts about what group of hominins might have led to the Asian *Homo erectus* populations. The Levant Corridor sites have not yielded informative enough fossils to characterize the authors of the lithic instruments.

Emiliano Aguirre[67] argued that it is difficult to conceive that *H. georgicus*,[68,69] which exhibits African *H. erectus* traits that are absent in the Asian exemplars, can the considered to be the ancestors of Asian *Homo erectus*, which possibly originated from an earlier migration. Different authors have used a similar argument in reference to *Homo floresiensis*, whose morphology seems to derive from a very early member of the genus *Homo*.[70,71]

Within shared general patterns, the morphological diversity of Middle Pleistocene hominins in Asia and Africa is noteworthy. This has led to different interpretations of how the Lower and Middle Pleistocene members of *Homo* should be classified. Here we will reduce the alternatives to the two most common visions, which are mutually exclusive. The first one posits that all exemplars belong to the same species, *Homo erectus*. The second requires separating them into two different ones: *Homo ergaster*[72] for the African specimens and *Homo erectus* for the Asian ones.

Let us examine one example of each proposal. Berhane Asfaw and colleagues' interpretation of the BOU-VP-2/66 exemplar, from Bouri, Ethiopia (*Daka*), emphasized the similarity between *Daka* and its Asian counterparts, suggesting that African and Eurasian hominin fossils represented populations of an extended paleospecies.[73] The authors reached this conclusion after a cladistic analysis of the 22 most used characters in prior studies of *Homo erectus*, and by dividing the sample by means of operational taxonomic units obtained by means of paleodemes.

The hypothesis of a cladogenesis that would have separated African and Asian *H. ergaster* and *H. erectus* was rejected by Asfaw *et al.*'s[73] analysis. Such a scenario would even be rejected if, as the authors argued, the latest Asian demes were removed from the analysis.

Jeffrey Schwartz[74] put forth a completely opposite opinion to Asfaw *et al.*'s[73] in his analysis of the KNM-OL 45500 exemplar from Olorgesailie, Kenya. Some of its traits are reminiscent of *Homo erectus* traits, and have an even more modern appearance, but its size is very small. After a detailed comparison of KNM-OL 45500 with other *Homo erectus/ergaster* crania, Richard Potts *et al.*[75] argued that KNM-OL 45500 exhibits a distinct set of traits, indicative of the broad variation of hominins between 1.7 and 0.5 Myr. Nevertheless, in the commentary that accompanied the initial description of the exemplar, Jeff Schwartz[74] argued that the task of understanding the relations between the diverse Asian, African and European exemplars would be easier if it were admitted that *Homo erectus* might be more a historical accident than a biological reality. In Schwartz's[74] opinion, the morphology of the exemplars attributed to *Homo erectus* exceeds the limits of individual variation, well documented in the Trinil/Sangiran sample.

What option makes more sense to understand the phylogenesis that leads to the Middle Pleistocene hominins? The possible alternatives are represented in Figure 1. Alternative (A) corresponds to the notion of a single very variable species during the Middle Pleistocene that encompasses African and Asian exemplars, with the intermediate chronospecies *H. georgicus*.

Leaving aside the issue of accepting the possibility of such a large degree of variation or not, there is the added problem of cultural evidence. Mode 2, with its characteristic bifaces that abound in the African Middle Pleistocene, does not appear in Asia to the east of the line of Movius.[76] Given the ease with which culture spreads, the absence of Mode 2 in *Homo erectus* sites is difficult to reconcile with a sufficiently intense population flux to keep the species' unity.

Alternatives (B) and (C) are based on the notion of two species to accommodate African and Asian exemplars. Scheme (B) is based on the Dmanisi evidence, and (C) accounts for the absence of *Homo georgicus* traits in *Homo erectus*.

A separation of species under each of the two alternatives would involve genetic isolation mechanisms that justified the presence of diverse morphological traits, eliminating the difficulties of an excessive variability within the taxon. The cultural differences would also be easy to explain. However, it faces a geographical problem: some African exemplars show a very high morphological similarity with *Homo erectus*, exhibiting some of the traits that even the advocates of *H. ergaster* attribute to the Asian taxon. This is particularly the case with OH 9[77] and the Bouri cranium, *Daka*.[73] If such exemplars are assigned to *Homo erectus*, it must be accepted that this species is also present in Africa.

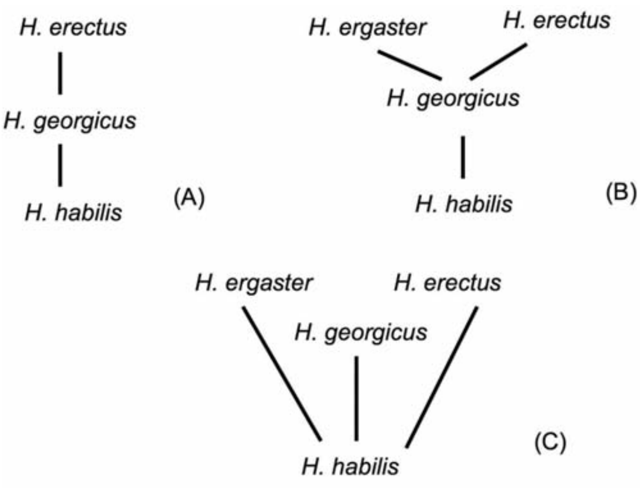

Figure 1. Alternative hypotheses about the evolution from *Homo habilis* to *Homåo erectus*.

Variability in the sample of Homo erectus

The first problem faced by the theory of the single species during the Middle Pleistocene is that of accounting for the range of variability in such a broad hypodigm. The literature on this issue is immense, and we will only be able to refer to some of the studies. The most objective method to understand the implications of morphological difference among diverse exemplars is to perform a statistical analysis that allows comparing them.

James Kidder and Arthur Durband[78] performed a multivariate analysis – canonical correlation – to compare 20 of the most complete crania of the *Homo erectus* hypodigm, including the African exemplars, aiming to determine the degree of specificity of the Zhoukoudian specimens in relation to the rest. The comparisons were carried out based on eight cranial measures, regarded as basic by W.W. Howells.[79,80] The study's results confirmed the Zhoukoudian particularity, but grouped the African, the Java, and the Hexian specimens together. The most logical interpretation for the resulting metrical relations is to admit the particularity of the Zhokoudian crania but, as Kidder and Durband[78] argued, to accept that local variations due to environmental adaptations or genetic drift explain the sample's variation better than a multiple species hypothesis. Consequently, they advocated for the unity of the *Homo erectus* species.

Brian Villmoare[81] carried out a statistical analysis of the African and Asian *Homo erectus* sample, based on 23 metric characters –most of them in agreement with Howells[80] – recreated in a sample of 1000 modern humans. He thereafter established the Euclidean mean between Asian and African exemplars compared with the same mean from 1000 randomly generated samples of current African and Asian humans. A third analysis took into account 10 non-metric characters that covered all the morphological differences observed in the fossil sample and in a sample of 221 current human crania.

The hypothesis of a single *Homo erectus* species was not falsified in either of the first or second analyses (the metrical ones), although the differences were greater than the ones between modern Asian and African humans. Conversely, the analysis performed using non-metric characters revealed notable differences between the Asian and the African fossil samples. The supramastoid crest, the angular torus and the metopic prominence were the characters with the greatest difference between both samples. The discrepancy between the metrical and non-metric analyses is interesting, because, as Villmoare[81] noted, most authors supporting the hypothesis that *Homo erectus* and *Homo ergaster* constitute two different species relied on the morphological study of non-metric characters. Given that non-metric characters are assigned based on their state (present or absent), they result in a gap that is less clear in metric studies. Villmoare noted that it would be interesting to transform non-metric characters into metric parameters using three-dimensional markings capable of defining curved forms.

Claire Terhune, William Kimbel and Charles Lockwood[82] and Karen Baab[83] performed analyses involving quantification of non-metric characters of *Homo erectus* crania. Terhune and colleagues studied the morphology of the temporal bone using 83 three-dimensional markings on 520 extant and fossil species. The distances between current humans were calculated by means of a Generalized Procrustes Analysis,[84] yielding the intraspecific and the interindividual variation within each species and its different groups. Thereafter, Terhune *et al.*[82] obtained the Procrustes distances among the different fossil specimens and among groups of these defined *a priori* (Africa, Eurasia, Indonesia, continental Asia).

The comparison of the distances identified by Terhune *et al.*[82] revealed that the variation of forms in the whole sample of *Homo erectus* was generally greater than in extant species. This finding supports dividing *Homo erectus* and *Homo ergaster* into two different species. The authors, however, stumbled upon the same obstacle that appeared in qualitative analyses: OH 9 and D2280 differ from Koobi Fora *Homo ergaster*. Terhune and colleagues'[82] conclusion was somewhat complex: *Homo erectus* is constituted by multiple species that differentiated in a complex fashion, such that the available samples cannot be grouped geographically or temporally. This is, in fact, not very different from having to admit that an adequate taxonomy cannot be proposed for *Homo erectus*. This realization has led to the use of a different concept to that of species for Middle Pleistocene hominins, and to include them all in an *erectus grade*. Julian Huxley introduced the concept of *grade* in 1958 to refer to a common stage of evolution reached by different taxa.[85] Bernard Wood and Mark Collard[64,86,87] made use of Huxley's grade precisely because of the difficulties inherent to the genus *Homo*.

Karen Baab[83] used the same technique of Generalized Procrustes Analysis to quantify the general variation in the shape of the crania, going beyond the study of a specific region. The sample included 15 Asian and African *Homo erectus* specimens with the necessary anatomical points, 392 current humans from 11 regions in Africa, Eastern Asia/Oceania/North America and Europe/Western Asia, with the addition of fossil modern human crania: Skhul 6 and Qafzeh 6 from the Near East, Abri Pataud from France and Fish Hoek from South Africa. The sample was completed with non-human primates from *Pan*, *Gorilla*, *Pongo*, *Papio, Macaca* and fossil exemplars from *Theropithecus*. Baab's[83] study revealed that the variation within *Homo erectus* is comparable to the variation within each individual species of cercopithecoidea, but also within the genus *Pan*, which includes two species of chimpanzees. Rather than attempting to identify species, the author wishes to establish the patterns of intraspecific variability due to ecological, geographical and temporal factors. According to those patterns, Baab[83] argued that her results favored the consideration of a single *Homo erectus* species. However, Baab[83] also considered other possibilities that are well worth commenting.

What species are we talking about?

The controversy concerning the presence of one or two species in the African and Asian *Homo erectus* seems impossible to resolve if, as Villmoare[81] stressed, the comparative morphometry studies produce different results depending on whether their analyses include quantitative or discrete characters. The difference that emerges from the use of metric and non-metric characters, however, can be interpreted in two different ways. One views two different species that share a similar cranial plane in many aspects, while accepting a variation with regards to the presence or absence of certain traits. This variation would owe to reproductive isolation. This would undoubtedly be the case if they were two sympatric species. However, if we are dealing with species separated in space and time, there is a second possible explanation: a single species showing local adaptations due to differences in the ecological environment. This is the conclusion Karen Baab reached in her doctoral thesis on cranial variations in *Homo erectus*.[83]

In order to derive taxonomy of both possible explanations for the distribution of traits in the set of *Homo erectus* it is necessary to choose what concept of species to use. Part of the controversy about the number of necessary species actually refers to the concept employed. After concluding that the statistical analysis favored the unity of the species, in her 2008 work Karen Baab[83] accepted that, under an evolutionary species concept (ESC), it would be possible to distinguish between to taxa with a strict geographic separation.

The distinction between *Homo ergaster* and *Homo erectus* helps explain the different Middle Pleistocene cultural traditions in Asia and Africa. On the other hand, the existence of very similar specimens to *Homo erectus* in African sites still needs to be explained. This is the case of OH 9 or the Daka cranium.

Karen Baab's[83] study revealed the existence of a greater morphological affinity between OH 9 and the African sample, in contrast with prior morphological analyses,[88,89] as well as Terhune and colleagues',[82] performed with GPA. According to Baab,[83] OH 9 had previously been grouped with the Asian sample because the weight of the geographic variation in the whole *Homo erectus* sample is lower than in current populations, which would make individual differences stand out. Thus, it might be the case that OH 9 shares a general cranial form with other African samples, as Baab's[83] study indicates, while other isolated traits are reminiscent of the Asian sample.

The meaning of two different taxa under the ESC to distinguish between *Homo erectus* and *Homo ergaster* becomes clearer once we leave the taxonomic perspective aside to try to understand the phylogenetic process. After hominins left Africa, the two populations, the African and the Asian one, remained separated to a high degree. It is true that several different dispersions into Asia occurred during the Plio-Pleistocene. They were, however, essentially sporadic.[90] Judging from the stone tools from Gesher Benot Yaaquov and Bizat Ruhama (≈0.8 myr),[65] it seems unlikely that Middle Pleistocene African hominins reached beyond the line of Movius on subsequent dispersions. The absence of Acheulian tools in the Far East indicates so. In light of the evidence, the best scheme suggests a factual separation between Asian and African *Homo erectus* since 1.4 myr. Such a spatial and temporal variation range is more than enough for the appearance of geographical variations, different adaptations, and different ways of life.

A bridge towards the future

The need to identify each group's *own evolutionary tendencies and* *historical destiny*[19] requires the use of a sound, easy and useful species concept. However, any chosen taxonomic tool must be in agreement with the processes leading to the inheritance of biological characteristics. As de Queiroz[47] stated, the notion of a separately evolving metapopulation lineage is the only necessary property of species that we need to achieve operational criteria relevant to assessing lineage separation. Ultimately, retrieving the genomes of fossil populations, crossing this information with the process of development of cultural techniques obtained by means of cladistic studies, like Lycett's work,[91] for instance, would be the best way to falsify any hypothesis. This, unfortunately, is presently out of reach. In any case, with regards to the reconstruction of Lower and Middle Pleistocene hominin phylogenesis – *i.e*., the role of *Homo erectus vs. H. ergaster*, *H. floresiensis*, *H. antecessor*; and *H. neanderthalensis vs. H. sapiens*, it makes little difference to take every alternative as implying two different species or two completely separated populations. Consideration of hominin dispersions under palaeoclimatic and geographic constraints, as Dennell *et al.*[92] did – regarding, particularly, the British case – will be more useful than coming back one more time to the interbreeding issue.

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