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The place and the value of phylogeny in paleoanthropology: just talking or nevermind?

Valery Zeitoun

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EDITOR

Marta Arzarello

Università degli Studi di Ferrara, Dipartimento Studi Umanistici, C.so Ercole I d'Este 32 – 44121 Ferrara (IT)

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Marta Arzarello

THE PLACE AND THE VALUE OF PHYLOGENY IN PALEOANTHROPOLOGY: JUST TALKING OR NEVER MIND?

Valéry ZEITOUN

UMR 7207-CR2PCnrs-Mnhn-Sorbonne Université, Alliance Sorbonne Université, Université Pierre et Marie Curie, 4 place Jussieu 75252, Paris, France

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ABSTRACT

The diffusion of sensational and incomplete analyses, as well as the misinterpretation of data, has led to a series of paleoanthropological paradigms which are, for the most part, purely speculative. These practices result from a lack of knowledge of the basic rules of classification, resulting in phylogenetic paleoanthropological discourses that are usually decoupled from the rules of systematics. Since the 1960s paleoanthropological research has focused on the nomenclature and taxonomy of the Hominidae, reporting on the work of Dobzhansky and Mayr. Today, the paleoanthropological discourse incorporates phylogenetic ideas but paleoanthropologists neither use the tools nor the methods of phylogeny, or the rules of systematics. This issue was described by Bonde (1977) at a time when the cladist school was beginning to influence some paleoanthropologists. In subsequent years, discussions on the value and polarity of observed characteristics arose, replacing earlier debates based on overall similarity. Authors proposed species lists based on the presence of autapomorphic characters, and finally, cladograms were produced. However, after two decades, discussions on the constitution of OTU (Operational Taxonomic Unit), the definition of characteristics, variability, and over-representation or redundancy of certain characteristics led to the rejection of cladistics in paleoanthropology. Despite the fact that Barriol (1994) and Tassy (1996) responded to these objections in the 1990s, their points were ignored or misunderstood by paleoanthropologists and, in the 2000s, cladistics was almost completely abandoned in favor of a return to classical evolutionary systematics or the new craze for phenetics; two quantitative approaches. This paper investigates Niels Bonde's long-standing question and concludes that this question is still relevant today: "Is it really impossible to transmit such a simple and logical method (phylogenetic systematics) to anthropologists or do they not care about it? (Bonde 2012).

INTRODUCTION

In current paleoanthropological practice it is important to identify specimens and state the various mechanisms of evolution that were involved in the appearance of modern man. In doing so, paleoanthropologists evade the question of “patterns” and it is acknowledgment of basic knowledge in systematics, and even classification, is largely lacking in this discipline. The observation made by Campbell (1962, p.225) more than fifty years ago remains valid today:

“Human taxonomy is a more difficult science than most, and the difficulties have been enormously accentuated by the fact that some of those who have received little scientific training, let alone taxonomic training...”

Another flaw is criticized by Campbell (1962, p.228):

“The difficulty of being objective in this branch of zoology has already been stressed. Each discovery is attended with so much publicity for the discoverer that he frequently becomes emotionally involved with the precious fossils and is unable to evaluate them in a rational manner. It is for this reason among others that the aim of paleoanthropologists today is to develop an objective methodology in taxonomic work”.

In paleoanthropology the discipline of superlatives, as reflected in the titles of numerous scientific articles announcing the discovery of the oldest or most recent, the southernmost or the most oriental of such or such a taxon? For a long time, epistemology focused on the content of science, and the scientific investigation of humans was left to other disciplines, such as sociology. Following the example of Kuhn (1962), particular attention must be made to the concrete dimensions of scientific activity insofar as this influences the procedures implemented. In his introduction to the study of experimental medicine Claude Bernard (1865, p.10) states that: “the reasoning is always the same, both in the sciences that study living beings and those that deal with the raw bodies”. But phenomena vary across scientific domains, and each domain has its own complexity and investigation limitations. How does the subject of human paleontology justify its special treatment, exempting it from following the rules of systematics? This refers us to the question: Where do paleoanthropologists discuss the place of humans, considering that any discourse is impacted by culture and traditions? Without referring back to the ancient philosophers who helped forge the Western scientific approach, it is recognized that Charles Darwin was part of the Scottish Enlightenment, to which the work of David Hume is linked. Support of Darwin's ideas and the perception of Darwinism differed from one country to another, as Darwin himself mentioned in a letter to the anthropologist Armand de Quatrefages (Darwin, 1887):

“It is curious how nationality influences opinion; a week hardly passes without my hearing of some naturalist in Germany who supports my views, and often puts an exaggerated value on my works; whilst in France I have not heard of a single zoologist, except M. Gaudry (and he only partially) who support my views”.

In one of their papers on the theory of punctuated equilibria, Gould and Eldredge (1977, p. 145) affirm the Western propensity for gradualism:

“The general preference that so many of us hold for gradualism is a metaphysical stance

embedded in the history of western cultures: It is not a high-order empirical observation induced from the objective study of nature..."

However, on the following page they recognize their own influences: "it may also not be irrelevant to our personal preferences that one of us learned his Marxism literally at his daddy's knee". The historical influences of paleoanthropology are understood by analyzing the position of humans in the evolutionary tree and the construction of the tree.

THE TREE OF LIFE: FROM THE ORIGIN OF SPECIES TO HUMAN ANCESTRY

Humans have not always been recognized as belonging to an animal category despite the fact that Charles Linnaeus classified them with monkeys, as Anthropomorpha, in his work Systema Naturae. The concept that established this relationship is based on phenetic similarity, a method Aristotle used two thousand years earlier by classifying humans with other mammals. The systematized preoccupation with the course of evolution and ancestral human forms only really began, however, with Charles Darwin's Origin of Species in 1859, and this is only briefly apparent at the end of his work:

"Light will be thrown on the origin of man and his history (1859, p.488)". As Brace (1981) points out, although human fossil specimens are considered by Huxley, Lyell and later by Darwin in 1871 in the Ascendancy of Man, these authors avoided arranging them into lines to show the course of evolution. Only contemporary authors went much further. Although Gaudry (1866) was one of the first to arrange tree phylogenies by linking fossil and current forms, it is the comparable approach by Haeckel (1866) that is the most significant in paleoanthropology, due to the unequivocal positioning of modern human in the evolutionary tree (Haeckel, 1874).

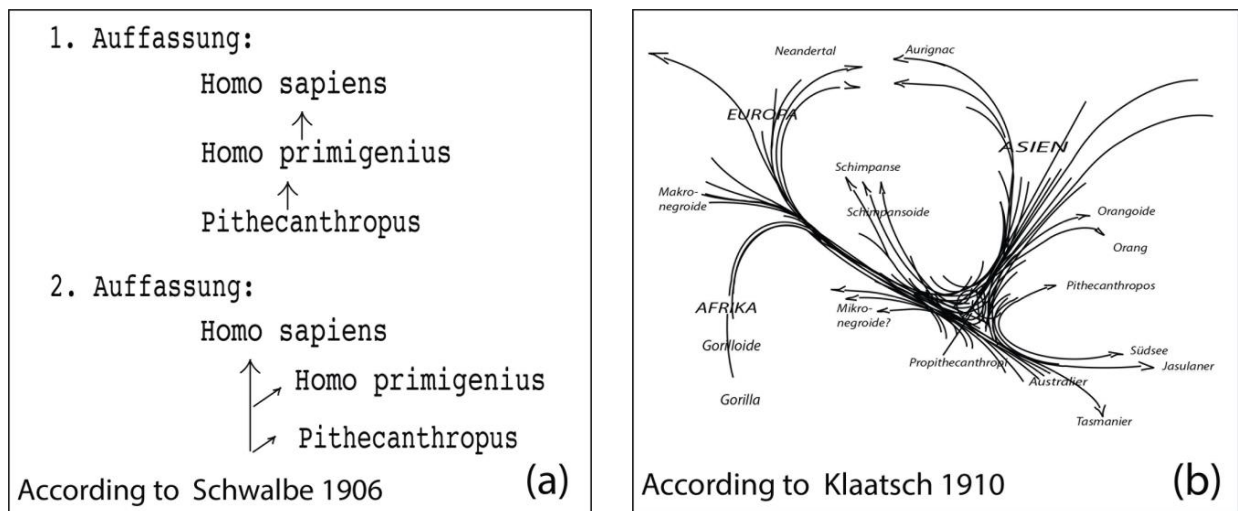


Fig. 1: a) The two hypotheses proposed by Schwalbe (1906) to describe the line of fossil humans known at the time (NB: *Homo primigenius* = *Homo neanderthalensis*). b) Theoretical schematic representation of the arrangement of human populations and fossil humans proposed by Klaatsch (1910).

This documentation was even used in field work, as Eugène Dubois used the theoretical terms proposed by Haeckel to name his discovery of Trinil: *Anthropopithecus alalus* becoming *Anthropopithecus erectus* then *Pithecanthropus erectus* (Dubois, 1893, 1894). The presence of human species in phylogenetic trees then became more common, although trees took different forms. However, this was short-lived, and it was not until 1906 when the

representation of a phylogenetic hypothesis was developed by the anatomist Schwalbe (Fig. 1a). Indeed, in the colonial context of the interwar period with a centre of racial interest in anthropology, the phylogenetic scheme used was that of the anatomist Klaatsch (1910, p. 567) (Fig. 1b), who developed the principle of hypothetical organization associating modern and fossil specimens.

THE FRENCH TOUCH

Anglo-Saxon researchers proposed phylogenies for humans, inspired by Arthur Keith, but French researchers seem to have been slower in their acceptance of this study. This delay could be related to their rejection of Darwinian evolutionary mechanisms, a long-standing French palaeontological tradition, especially since the founder of physical anthropology in France. Paul Broca was a polygenist and not very favorable to Darwinism (Broca, 1870, 1872). However, introduced by Bergson's *Creative Evolution* (1907), a mystical evolutionism developed through the work of Teilhard de Chardin, notably in his posthumous work *Human Phenomenon* after 1956. A French influence in palaeoanthropology appeared after numerous prehistoric discoveries of fossils were made in France, and a more sustained paleoanthropological debate arose following the French anthropological tradition.

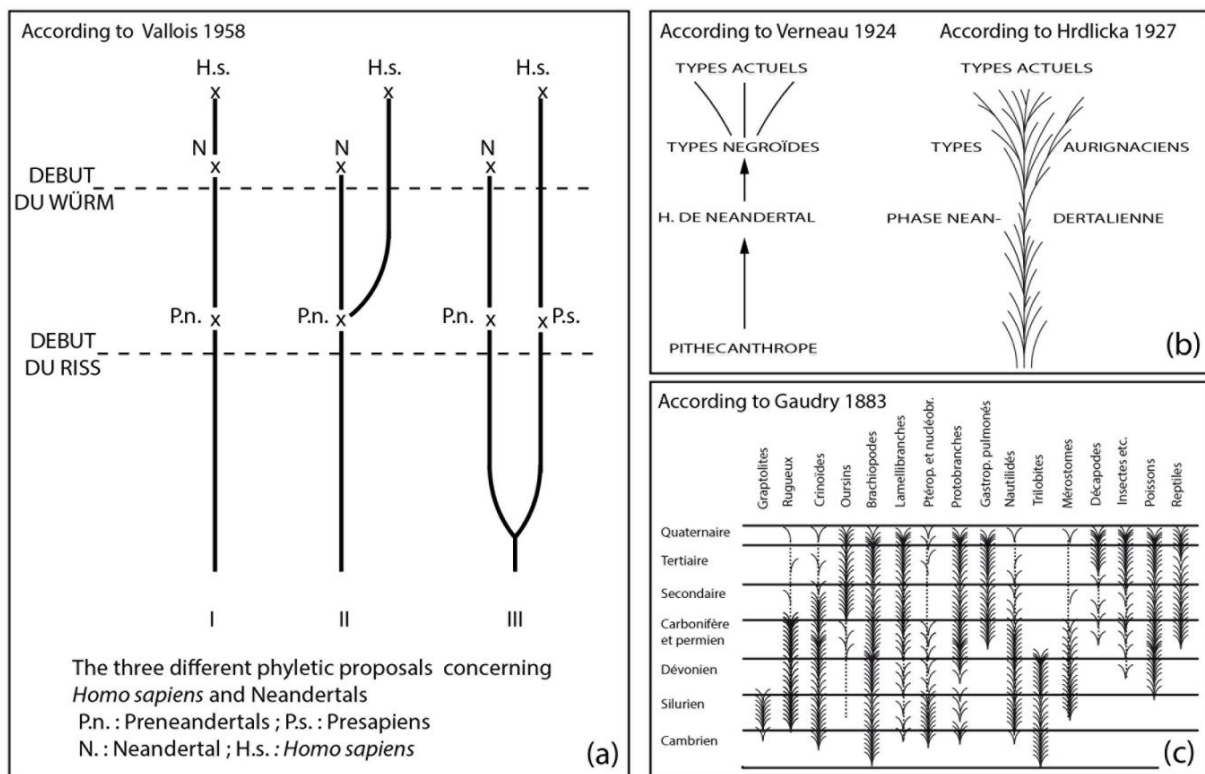
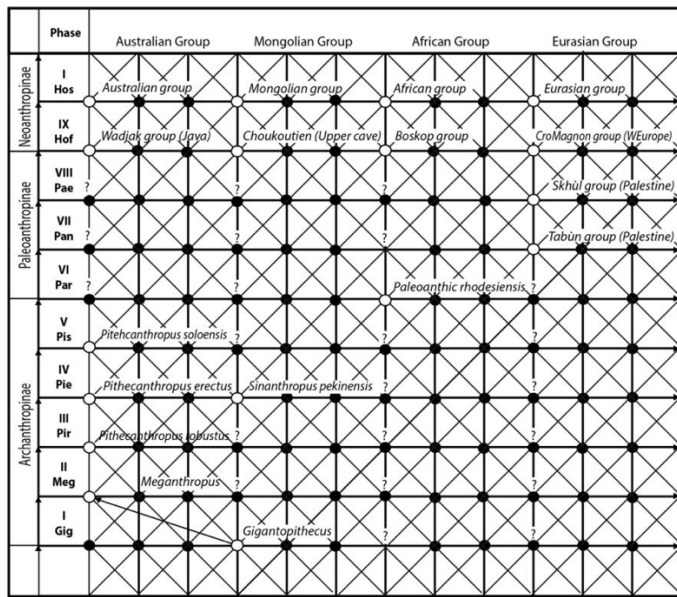


Fig. 2: a) Vallois's presentation (1958) of the three hypotheses on the origin of modern humans according to contemporary authors, the so-called pre-sapiens and/or pre-Neanderthal hypothesis. b) Representation of the pre-sapiens hypothesis by Verneau (1924) and Hrdlicka (1927). c) Parallel representation of the primary animals according to Gaudry (1883).

Vallois (1958) discussed the three hypotheses of the time in his monograph devoted to the cave of Fontéchevade (Fig. 2a). A linear gradualist approach known as the Neanderthal hypothesis proposes a direct *Pithecanthropus*-modern human lineage that Verneau (1924) and Hrdlicka (1927) (Fig. 2b) advocated; the latter borrowing the style of illustration proposed by Gaudry (1883) (Fig. 2c). This hypothesis was transformed by Weidenreich (1947) (Fig. 3)

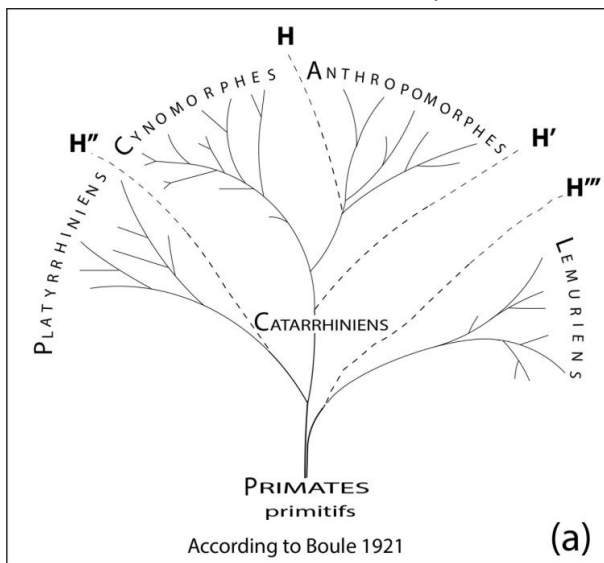
who suggested that evolution in several stages, from *Pithecanthropus* to modern man via Neanderthals, occurs everywhere but with a tempo according to the geographical area.



According to Weidenreich 1947

Fig. 3: The ten intermediate human stages from *Gigantopithecus* to modern humans with geographical variables according to Weidenreich (1947).

Boule produced a phylogenetic tree in his general work of 1921 (Fig. 4a), and he developed a competing hypothesis called the pre-Neanderthal hypothesis. This hypothesis is based on his study of the Chappelle-aux-Saints fossils, in which he noted the presence of intermediate characters between Pithecanthropus and modern humans, and the presence of characters



specific to Neanderthals. Along this line of thinking, Sergi (1953) considered that the oldest Neanderthals was closer to modern humans because they have “not yet reached” the specialization of Neanderthals (Fig. 4b). This was also illustrated by Howell (1951) in a different graphic form (Fig. 4c). Supported by Vallois and generalized by Heberer (1950), the pre-sapiens hypothesis took different forms before and after the Piltdown case. Although cases of fake fossils had already occurred in the second half of the 19th century, such as those of Savona, Castenedolo, and Arezzo in Italy, or Clichy, Grenelle, and Moulin-Quignon in France, Galey Hill in Great Britain, the Piltdown case is a paleoanthropological psychodrama that can be interpreted as a trauma or symptom.

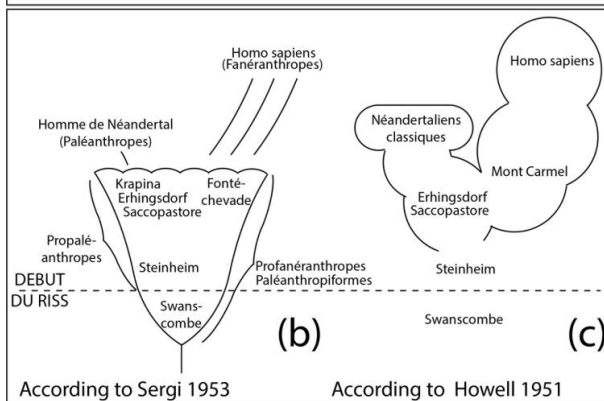


Fig. 4: a) Hypotheses on the genealogical relationships of Hominidae with other primate groups, according to Boule (1921). b) The pre-Neanderthal hypothesis according to Sergi (1953). c) The pre-Neanderthal hypothesis according to Howell (1951).

FROM DOUBLE DISCOURSES TO THE FIRST STEPS TO REASON

In his commentary on the pre-Neanderthal hypothesis, Vallois (1958, p.139) borrows a formulation that supports orthogenetic evolution advanced by Teilhard in the 1950s: “[...] they (the pre-Neanderthals) found themselves to have, in a prophetic state, a certain number of provisions found in *Homo sapiens*”. As Tassy (2007) mentions, if Teilhard grafts metaphysical concerns independent of his construction onto the tree by searching for an arrow (the meaning of life), he theorizes about man in general works decoupled from his paleontological works. From then on, in this double discourse, he forgot his classical paleontological phonetic trees and borrowed the tree representation of Cuénot (1940) when he discussed humans. Teilhard's scaly stem (1949) (Fig. 5a) and the cladogram have a point in common: no taxon appears in the ancestor position. But this impossibility to recognize ancestors was also pointed out by Vallois (1958, p.147): “All the phyletic trees thus imagined have a logical basis. All are possible. All, however, are justifiable from the same criticism: the arbitrary part of wanting, with the few fossil men we have, to trace complete phyletic trees and continuous lines”, and illustrated by Vallois (1952) (Fig. 5b) and Boule (1921). The duality of paleoanthropological discourse seems common at this time.

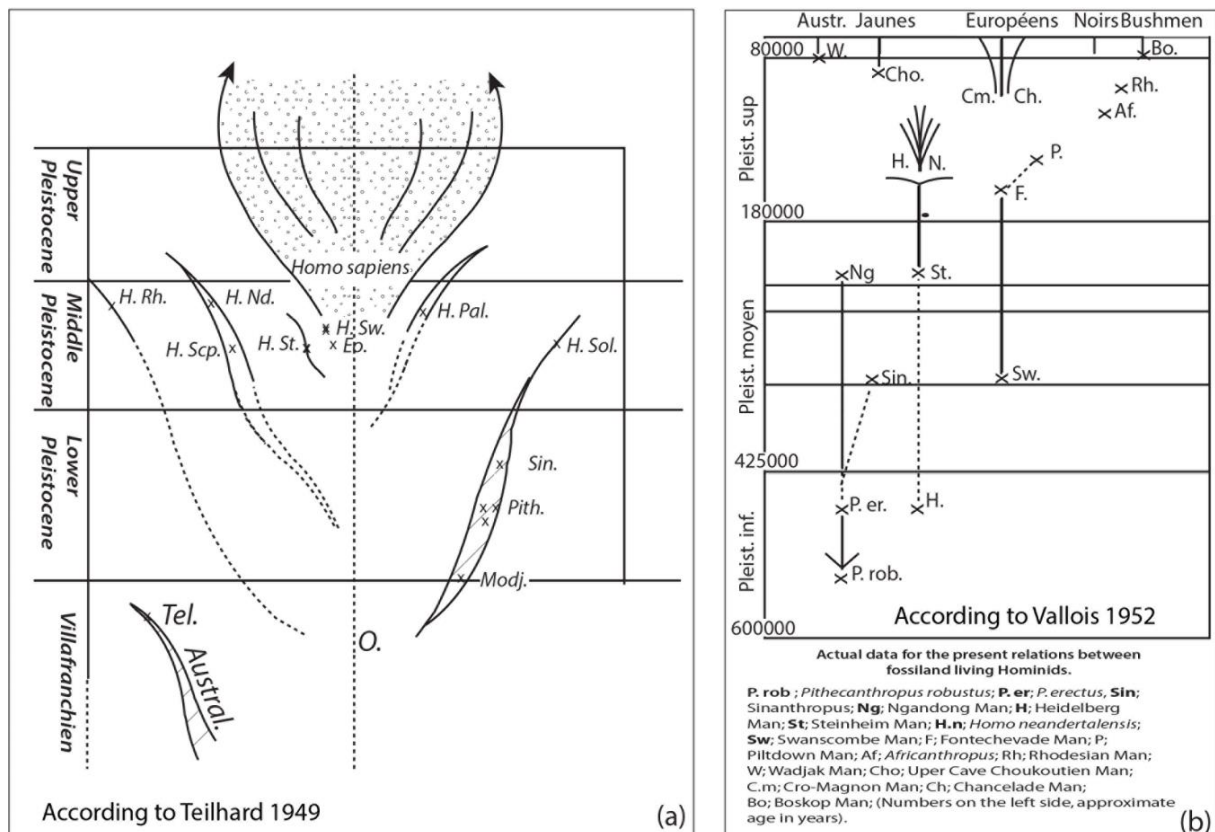


Fig. 5: a) The relationship between hominid fossils without direct ancestors according to Teilhard de Chardin (1949). b) The different lines of Hominidae without common ancestors according to Vallois (1952).

Thus, although a multiregional version of the various stages of human evolution were proposed by several researchers, Weidenreich (1947) had previously made a revolutionary proposal (1943, p.215):

“[...] neither space nor time can play any role in the zoological classification of human types. It is certainly not permissible to consider a form ‘primitive’ only because it is geologically more ancient than some other nor may it be considered more advanced because it is geologically more recent.”

This proposal remained unknown even after its publication (Zeitoun, 1996). In the 1960s, paleoanthropological work followed the general trend of the palaeontology inspired by Simpson (1961), focusing on the nomenclature and taxonomy of the Hominids, reporting on the work of Dobzhansky (1944) and Mayr (1950). Refined identifications were then presented, particularly in the publication of the Wartenstein Colloquium (Campbell, 1963). The genera *Telanthropus*, *Pithecanthropus*, *Sinanthropus*, and *Atlanthropus* were thus abandoned in favor of the single genus *Homo*. At this stage in our historical review, perhaps we should characterize paleoanthropology as a discipline that makes rules that it does not like not to follow. Indeed, Wartenstein's recommendations were not followed, but in an effort to evaluate evolutionary relationships more objectively, in the following decade, some members of the anthropological community did accept to use cladistics. Thus, a first publication concerning primates was produced by Robert Hoffstetter in 1974, followed by the first analyses applied to humans (Eldredge & Tattersall, 1975; Delson, Eldredge & Tattersall 1977; Olson, 1978; Johanson & White, 1979). From then on, discussions of diagnoses based on what was in fact the total morphological pattern of the phenologists (see the diagnoses proposed by Le Gros Clark (1964) and Howell (1978) was gradually replaced by a discussion on the value and polarity of observed characteristics in order to define a hypodigm. In the 1980s, discussions based on the presence of exclusive derived characters were followed by the publication of cladograms. For example, authors influenced by the cladistic approach (Santa-Luca, 1980; Andrews, 1984; Stringer, 1984; Wood, 1984; Andrews & Martin, 1987; Stringer, 1987; Chamberlain & Wood, 1987; Groves, 1989) propose lists of characters derived and specific to *Homo erectus* and attempt to clarify both the taxonomic status and phylogenetic position of the species *Homo erectus*, or of humans previously classified under this name.

RENOUNCEMENT OF THE NEW SUBJECTIVE DISCOURSE

In the 1990s, in parallel with the production of cladograms (Barriel & Darlu, 1990; Liebermann, Wood & Pilbeam 1996; Strait, Grine & Moniz 1997; Skelton & McHenry, 1992; Wood & Collard, 1999, Wood, 1992a,b), discussions emerged on issues of character variability, overrepresentation, and redundancy (Habgood, 1989; Bräuer & Mbua, 1992). These questions led to the rejection of cladistics after two decades. Even if, from the systematics point of view, there is no justification for treating humans differently from other taxa (Bonde, 1977; Stringer, 1987; Tassy, 1996), there were insurmountable pitfalls (time and mosaic evolution), and anthropologists objected at the arrival of cladistics (Brace, 1981). The most illustrative text is undoubtedly that of Trinkaus (1990), reviewed in an article in *Integrative Biology* (Hlusko, 2004). What hinders paleoanthropologists in their search for the truth is, on the one hand, the lack of standardized analyses and, on the other hand, the failure to take time into account a priori. Cladistics is thus judged by its ability to reproduce and thus "demonstrate" the anthropological preconceptions of classical evolutionary systematics. Despite the answers given by Bonde (1977, 1981), Tassy (1991, 1996) and Groves (1989), the problem of a lack of listening (or disappointment) is certainly due to the propensity of anthropologists to prefer stable quantitative approaches. The classical evolutionary approach tends to group finite numbers of species into a given genus. The phenetic approach considers that phylogeny is out of objective reach and that it can only be approached by multiplying analyses with mathematical tools.

For historical reasons, paleoanthropology is at the confluence of two opposing strategies ; one is typological, derived from palaeontology, the other is "population-based", derived from physical anthropology that is resolved by statistical approaches. The latter approach claims to

be closer to “biological reality” because it takes variability into account. However, when distinctive traits are fixed in terminal taxa, even if the traits are polymorphic to account for variability, a hierarchy and story can emerge from the study of polymorphism variation (Darlu & Tassy, 1993). Fossils refer to a typological approach, in the sense of Nelson and Platnick (1981), since it is not possible to escape a typological classification, i.e. one based on an analysis of characters, particularly when it is a question of alpha-taxonomy. Indeed, to speak about variation or polymorphism assumes that the limits of the study group are defined. Contestation of the typological approach is by the systematical schools which deal with current populations composed of species, and not species themselves (Mayr 1974, 1981). In paleoanthropology, the hypodigm is most commonly used to define a species as a whole, but the “population” analysis method, which consists of studying a phenotypic set of characteristics, does not necessarily allow the degree of a phylogenetic relationship to be measured. In quantitative approaches (classical evolutionist or phenetic), it is common to use coefficients of variation to check whether hypodigms contain a priori more than one species. Miller (1991) has shown that this “population-based” approach is inadequate for fossil taxa that are poorly represented.

Nevertheless, current paleoanthropologists undertake taxonomic and phylogenetic research using tools such as scanners and DNA analyses; phylogenetic analysis is no longer appropriate despite the considerable contribution that these tools could have in the search for relevant traits. We are even witnessing a “semantic” shift in the logic of the phenetic approach since, at its origin, phenetic approach admitted the impossibility of being able to objectively reconstruct all phylogenies, and only objectified to achieve them by using mathematical techniques. Today, UPGMA clusters are directly assimilated to phylograms (see Perez & Rosenberger, 2014).

CONCLUSION

Although present-day paleoanthropologists are unlikely to have heard of Gaudry's work (1891), they have made a motto from his writings: "One should not take too much trouble to set the limits of these species because they are only subjective; they do not exist in nature". Is it then so difficult for humans to examine humans, or their remains, in the same impartial and objective way that they give to non-living matter or tries to give to living matter? Anthropological literature shows us some common-sense recommendations (cf Vallois 1958, p.156) :

"To think that the present Man was the result of a single phylum which, from the beginning, would have been modified and in this sense alone, as by a kind of predestination which could only lead him to what he is, was to want to make man a being apart... the hominids differentiated themselves according to a process identical to that which we note for the other groups of mammals, the other groups of primates, as well of course, they put human evolution in its true place"

These recommendations are even revolutionary, as shown by the rejection of the paleontological criterion to guide the states of characters drafted by Weidenreich in 1943, predating Hennig's work. But in conclusion we should reply to Niels Bonde that paleoanthropologists do not undertake rigorous systematic studies. An observation which leads to one last question: Are paleoanthropologists ahead of the scientists? The answer depends on whether we consider this advancement in terms of progress (cf. derived state compared to a primitive state) or as a simple qualifier relating to chronology.

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