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Commentary  
[on paper by D. Pilbeam]

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**Species and  
species concepts in  
paleoanthropology**

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Even before Darwin, the "species problem" had been one of the foremost topics for debate in evolutionary biology, including paleoanthropology. Much of the recent literature on species concepts has been ably summarized by Bock (1986 and this volume). I agree with him that the biological species concept is robust and overarching, encompassing such supposedly distinct alternatives as the "evolutionary" species of Simpson (1961) or the "recognition" concept of Paterson (e.g., 1985). However, I strongly disagree with Bock's acceptance of biospecies as theoretically nondimensional, with no time depth, discernible only by comparison to sympatric, contemporaneous populations. Biospecies are multidimensional, theoretically as well as taxonomically, with time as one important aspect of their existence. If species multiply (in Bock's words) through lineage splitting via allopatric isolation, the beginning of a new species *can* be fixed temporally as that time interval (not moment or point) between the first rupture of hereditary continuity and the (often inferred) onset of renewed sympatry. Paleontologists seek to recognize paleospecies that correspond to living biospecies. Even most neontologists do not deal with biospecies as such, but with morphospecies analogized to biospecies through the study of more characters than paleontologists have available. Thus, the problem of central importance today is to develop empirical approaches to delineating species in the fossil record (or in museum collections generally) that correspond to those few that can be defined through direct application of the biological species concept. A paleoanthropological example of the confusion resulting from competing species concepts is offered by the genus *Homo*.

In their symposium papers, Pilbeam and Tattersall both discussed the recent increase in the number of widely ac-

cepted species of *Homo*. By 1970 or so, the three species *H. sapiens*, *H. erectus*, and *H. habilis* were rather firmly entrenched, and for over two decades newly discovered or reinterpreted morphs were allocated to one of them rather than named as distinct species. In the past five years, however, each of these species has been suggested to include two or more similar and broadly contemporaneous species erroneously "lumped" together. The studies of Wood (1985) and colleagues (e.g., Lieberman *et al.*, 1988) and of Stringer (1986, 1987) have led many workers to question the inclusion of all "early *Homo*" in *H. habilis*. Some apparently early fossils may in fact represent *Homo erectus* (see Clarke, 1985), but the range of morphological variation observed in specimens from Olduvai and East Turkana usually allocated to *H. habilis* now is considered at least "disturbing" by a majority of researchers. The situation is even more complex for the two younger species.

*Homo erectus* was first identified in Asia, but various Middle Pleistocene fossils from Africa have been allocated to this species in the past 30 years. Recently, several authors have questioned the inclusion of such specimens in *H. erectus* because they were said to have lacked one or more of the autapomorphies diagnosing the Asian populations (e.g., Andrews, 1984; Stringer, 1984; Wood, 1984; Tattersall, 1986). Others have questioned the formal separation of *H. erectus* from *H. sapiens* on grounds analogous to those invoked by Bock, namely that a continuous lineage should not be arbitrarily divided (e.g., Jelinek, 1981; Hublin, 1986). A third group of researchers (Howells, 1980; Rightmire, 1984, 1987, 1988) has continued to support a broad definition of *H. erectus* as a species distinct from *H. sapiens*. In their review of this situation, Turner and Chamberlain (1989) argue that the purported autapomorphies of Asian *H. erectus* may not be exclusively present in Chinese and Javanese fossils or may be

indeterminate in Africa due to specimen damage. They support, albeit tentatively, retention of a single polytypic (and probably polymorphic) species *Homo erectus*, and I would concur.

Finally, the greatest range of argument rages about the delineation of *Homo sapiens*. Over the past decade, the general consensus has been that early or "archaic" *H. sapiens* evolved either in Europe or Africa from a late regional variant of *H. erectus*. In turn, this group spread broadly over the Old World, replacing the remaining *H. erectus* populations and differentiating into regional variants such as the Neanderthals, eastern Asians and the "Rhodesian" group in sub-Saharan Africa. The origin of modern humans is alternatively suggested to have been from a Neanderthal or Rhodesian/archaic ancestry or simultaneously from several regional variants linked to each other by partial gene flow and to living human variants in similar geographic areas. This pattern has been further complicated by Tattersall (1986, this volume), Pilbeam (this volume), and others who suggest that more than one biospecies may be subsumed in this broadly construed version of *Homo sapiens*. They advocate distinguishing the Neanderthals as a separate species and suggest relegating the "archaic *sapiens*" populations to another one at least. Rightmire (1988) has most recently urged separation of the "archaics" as a distinct species (avoiding comment on the Neanderthals), while Stringer and Andrews (1988a,b) separate the Neanderthals but do not discuss the "archaics" taxonomically. Each of these alternatives conflicts not only with those who would retain the concept of a single broadly defined species developed since 1980, but even more with those who suggest Neanderthal ancestry for some or all living humans (see, e.g., Wolpoff *et al.*, 1988). Which aspects of these conflicting views should be accepted?

Clearly, there must be some morphological or taxonomic baseline employed in any empirical discussion of species recognition. For paleoanthropology, especially in the later phases of human evolution, the obvious standard is variation in living people and the taxonomic level of separation accepted for modern populations. Generally, living human groups are considered to belong to a single polymorphic and "polytypic" (i.e., regionally varying) subspecies. Admittedly, part of this determination is sociopolitical, as distinguishing among living humans at the subspecies level might lead to invidious comparisons and racist inferences by bigots searching for "scientific support" of their prejudices. Yet, there is some systematic basis for such a monolithic view of living humans, given the apparent overall morphological and genetic similarity (and continuity) among moderns and the variation known within subspecies of such wide-ranging primates as *Papio hamadryas*.

If this determination of *H. s. sapiens* for living people is accepted, it then seems to me that Neanderthals can only be classed as a second subspecies of *H. sapiens*. Other populations possibly representing temporal subspecies of this species include: the Arago-Petralona-Heidelberg group (not including Swanscombe and comparable fossils, which would be classed instead as early members of a Neanderthal lineage); the Rhodesian group (Kabwe, Saldhana, Ndutu, possibly Bodo), which might be morphologically similar to the preceding but differentiated geographically; and the more derived African group of Ngaloba, Omo Kibish 2, and Florisbad. Following further study, additional subspecies might be delineated for Asian populations such as those represented by Narmada and the Dali and Jinniushan specimens. Would Tattersall and Pilbeam separate each of these units as a full species, returning to the 1950s' profusion of nomina as mere "handles"; or do I go too far in "lumping" and fall into

Campbell's (1972) trap of naming all variants as subspecies? I suggest it is reasonable to equate temporal and geographic variation and thus apply subspecific names to the relatively distinct groups discerned in any well-documented fossil record where both "axes" of variation are observable.

It would be useful to have a better standard than subjective opinion, and I think that may be possible in the case of the Neanderthals. I suggest that variation among the known specimens be assessed for a variety of characters and compared to that observed in populations of living humans across Eurasia. This is a greater area of distribution than known for Neanderthals, but that would offset the time depth of the fossils. If the variation observed for Neanderthals is comparable to or greater than that seen in living humans, I would accept more readily that the two represent different species; but if the Neanderthals evidence less variation, they might better be included in *Homo sapiens*.

A further factor is archaeological. Where cultural residues are known, the earliest members of *H. s. sapiens* (e.g., Qafzeh, Skhul, perhaps Djebel Irhoud) are associated with Mousterian industries not significantly different from those found with Neanderthals in southern Europe or the Near East. This does not prove that the makers were conspecific, as Acheulean artifacts are associated in Europe with early *H. sapiens* and in Africa with *H. erectus*, but any paleoanthropological "solution" to this question must involve both biological and cultural remains and adaptations.

As Pilbeam said in his symposium paper, paleoanthropology does not usually bring new theory to evolutionary biology, but it is an active area of application of new ideas. Human fossils are often employed as examples of whatever evolutionary pattern or process an author is discussing, as witness Bock (1986 and this volume). The human fossil record, especially for the last few hundred

thousand years, is rather well known and thus open to a variety of interpretations. The evolution of *Homo sapiens* as interpreted here exemplifies rapid diversification and morphological change within the confines of a species delimited by a probable allopatric isolation interval at its origin. It thus serves as a valuable focal point for discussion of the empirical limits of a species-level taxon on the one hand, while demonstrating the temporal aspect of species multidimensionality on the other.

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