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Late Middle and Early Late Pleistocene Hominin Systematics

Links in the Chain: Lessons on Dealing With Evolving Lineages from the Bighorn Basin, Wyoming, and the Problem of *Homo heidelbergensis*

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ABSTRACT

Species identification in fossils often implicitly makes use of geographic and temporal gaps in the record to help bolster arguments distinguishing one species from another. As these gaps start to be filled paleontologists are faced with the problem of what to do with intermediate forms that bridge the gaps between samples that had previously seemed distinct and well defined. This paper will discuss how this problem has been tackled by researchers working in the early Eocene (Wasatchian North American Land Mammal Age) of the Southern Bighorn Basin (SBHB) of Wyoming—a locale where an excellent, temporally continuous fossil record stretching ~2.5 million years has led to the identification of numerous temporal and morphological intermediates. Three primate examples are discussed: the *Tetonius matthewi-Pseudotetonius ambiguus* lineage of omomyoids, the *Phenacolemur praecox-Phenacolemur fortior* lineage of paromomyids, and the *Arctodontomys nuptus-Microsyops angustidens* lineage of microsyopids. In all three cases, specimens that were intermediate both temporally and in terms of morphology were identified in the context of large alpha taxonomic revisions of the SBHB collections for each group. Arguments are made for retaining the end members of these lineages as distinct taxa and distinguishing intermediates from the other members of the lineages. Based on the lessons learned from those examples it is argued that using *Homo heidelbergensis* as a taxonomic name to encompass members of multiple lineages has the potential to obscure and obfuscate important questions in paleoanthropology. It remains unclear, however, how many of the potentially valid taxonomic names for Middle Pleistocene hominins are diagnosable, a question that will require a temporally informed alpha taxonomic revision of this record.

> "Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps, is the most obvious and gravest objection which can be urged against my theory."
> Darwin (1859: 280)

INTRODUCTION

Darwin (1859) considered the lack of transitional fossils known in the fossil record to be one of the key criticisms of the theory of evolution by natural selection. However, it was also one of its key testable hypotheses, reflected in the importance of the description of the skeleton of *Archaeopteryx* (Owen 1863) only four years after the publication of *On the Origin of Species* for supporting Darwin's framework. Since then, transitional fossils between major evolutionary stages such as *Tiktaalik* (Daeschler et al. 2006), pakicetid whales (e.g., Madar 2007), and australopith hominins (Dart 1925) have helped to demonstrate the fact of evolution. Although perhaps not as emotionally stirring as such landmark discoveries, fossil intermediates at the genus and species levels are also critical for demonstrating the reality of evolution, and for allowing the testing of

ideas about evolutionary process and tempo on a shorter timescale. The Bighorn Basin of Wyoming holds a special place in the terrestrial fossil record as providing one of the few contexts where a "finely graduated organic chain" of the type that Darwin envisioned has been well documented (e.g., Bown et al. 1994a, b; Gingerich 1976a). Students of the Bighorn Basin have long had to face the problem of trying to fit a taxonomic framework erected more than a hundred years before Darwin (Linnaeus 1758) to the complexities of a fossil record rich in intermediate forms (e.g., see discussion in Rose and Bown 1993).

The Middle to Late Pleistocene fossil record of the genus *Homo* may seem like it shares few characteristics of relevance to the fossil record of the Bighorn Basin, encompassing as it does fossils from across several continents (e.g., Bae et al. 2024: Figure 1), many of which are accompanied by uncertain dates. However, as this record includes the likely intermediate forms between *Homo erectus* and later *Homo* (including *Homo sapiens sapiens*, *Homo sapiens neanderthalensis*, and the Denisovans) there are perhaps lessons to be learned from the Bighorn Basin record that are of relevance to the so-called "Muddle in the Middle" (Isaac 1975). Like the record in the Bighorn Basin, workers struggling with this taxonomic problem are faced with transitional fossils that are not conveniently separated by gaps in space and time. The result with respect to the mid-late Pleistocene fossil hominin record is a taxonomic cacophony, with our recent paper (Bae et al. 2024) recognizing 23 taxa that were potentially valid. The alternative approach to dealing with this problem has been to use *Homo heidelbergensis* as a catch-all for all archaic hominins that do not meet some boundary of primitiveness (and so could be considered *Homo erectus*) or derivedness (and so would belong in *Homo sapiens sapiens* or *Homo sapiens neaderthalensis*) (e.g., Martin et al. 2024; Mournier 2009; Stringer 2012). The purpose of the current paper is not to rehash all the complexities of this debate from the perspective of the larger context of the hominin fossil record—other workers are certainly more capable of doing that than myself (e.g., see Roksandic et al. 2022). Instead, I will discuss some primate examples from the Bighorn Basin record and consider if the lessons they teach have any relevance to attempts to resolve the "Muddle in the Middle." More specifically, I consider their bearing on the question of what "*Homo heidelbergensis*" should mean.

BACKGROUND INFORMATION ON THE BIGHORN BASIN

The first mammalian fossils to be found in the Bighorn Basin were described by Cope (1880), so there is a very long history of paleontological research in this area (see summary in Gingerich 1980). Although there are both older and younger deposits in the basin, the bulk of the mammalian fossils date to the Paleocene and early Eocene. Starting in 1974, Philip Gingerich and his collaborators have extensively documented the fossil record of the more northern part, termed the Clarks Fork Basin. In particular, work at Polecat Bench and the surrounding Sand Coulee area has produced fossils from thirteen mammalian faunal zones (i.e., subdivisions of the Tiffanian, Clarkforkian, and Wasatchian North American Land Mammal Ages [NALMA], recording in detail the transition across the Paleocene-Eocene boundary (Gingerich 2001). This work has documented numerous examples of gradual evolution, which have been fuel to the debate over which evolutionary mechanisms predominate (i.e., phyletic gradualism or punctuated equilibrium; e.g., Gingerich 1984; Gould and Eldredge 1977).

Also in the early-mid 1970s, Kenneth Rose and Thomas Bown began intensive collecting efforts (co-led in recent years by Amy Chew) in the more southern part of the Bighorn Basin. Fossils from this area are placed into a stratigraphic framework that stretches much of the length of the Wasatchian (i.e., early Eocene; Bown et al. 1994b). This project has yielded over 50,000 fossil mammal specimens tied into a composite stratigraphy that stretches approximately 650m and covers perhaps 2.5 million years (Chew 2006).

For Primates specifically, there are extensive records from the Bighorn Basin (BHB) of both stem primates (i.e., plesiadapiforms; Silcox et al. 2017) and probable crown primates (i.e., euprimates). With respect to the former, the BHB has produced some of the best records for the families Plesiadapidae (Gingerich 1976b), Carpolestidae (Bloch et al. 2001; Rose 1975), Paromomyidae (Silcox et al. 2008), and Microsyopidae (Gunnell 1989). The euprimates from the BHB can be divided into two superfamilies—Adapoidea and Omomyoidea, both of which are very diverse groups (over 100 species each) whose relationships to modern primates are debated (Silcox and López-Torres 2023). In large scale phylogenetic analyses adapoids usually fall out as stem strepsirrhines and omomyoids as some kind of haplorrhines (e.g., Kay et al. 1997; Ni et al. 2004, 2013), but this perspective has been critiqued by those who would consider adapoids of relevance to anthropoid evolution (e.g., Franzen et al. 2009).

I will focus here on examples from three primate groups, emphasizing collections from the southern part of the BHB. This focus is based on the expertise of the current author, not any implicit statement of the relative importance of the different BHB collections.

Institutional Abbreviations. DPC: Duke Fossil Primate Centre, Durham North Carolina; USGS: United States Geological Survey (mentioned specimens are in the care of the USNM); USNM: United States National Museum, Smithsonian Institutions, Washington, D.C.

OMOMYOIDS

One of the clearest examples of gradual evolution in the fossil record comes from the record of omomyoid primates, specifically the *Tetonius matthewi-Pseudotetonius ambiguus* lineage, which is documented over 200 metres of the Willwood formation in the Southern Bighorn Basin (Bown and Rose 1987; Rose and Bown 1984). As part of a large scale alpha taxonomic revision of the anaptomorphine omomyoids from the BHB (Bown and Rose 1987) specimens were found that bridged the morphological gap between the two end members. Specifically, *Tetonius matthewi* retained a very tiny p2, had a fairly large canine and p3, and a short-

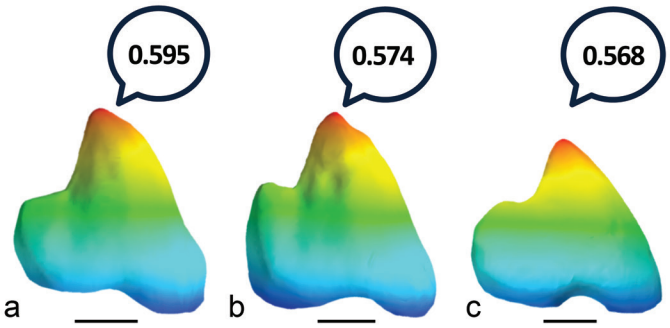

Figure 1. (a) Left p4 (reversed) of Phenacolemur praecox *(USNM 538053); (b) left p4 (reversed) of* Phenacolemur fortior-praecox intermediate *(USGS 12883); (c) right p4 of* Phenacolemur fortior *(USNM 521810). The values in the call-outs are Relief Indices (RFI; a measure of crown height) for the three teeth, (see López-Torres et al. 2018 for more details). The intermediate nature of the specimen in (b) is reflected in its intermediate RFI value (scale bars=1mm; original version of the figure created by S. López-Torres, used with permission).*

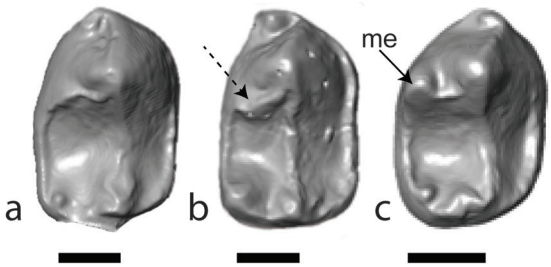

Figure 2. (a) Right p4 of Arctodontomys nuptus *(USNM 521438); (b) right p4 of an intermediate (USNM 540280) between* A. nuptus *and* Microsyops angustidens*; (c) left p4 (reversed) of* Microsyops angustidens *(DPC 1392); me=metaconid. The dashed arrow indicates the fold of enamel that is almost, but not quite, a cuspidate metaconid in the intermediate. Teeth scaled to same length (scale bars=1mm).*

er p4. Over the course of five stages the p2 was lost completely, the canine became smaller, the p3 reduced in size and became single rooted, with the p4 becoming larger and particularly taller. These five stages occur successively in the stratigraphic section, although with some overlap. The authors decided to retain both of the end species as distinct; for the intermediate specimens they identified them as pertaining to numbered stages in the evolutionary sequence. Schottenstein et al. (2020) later translated those stages into Operational Taxonomic Units (OTUs) for their analysis of evolutionary rates. Sinking the full range of variation that occurs along the lineage into a single taxon would have meant that the named species represented much more variation than is typical of other anaptomorphine omomyoid species (or even genera). Additionally, the two end taxa, and their various intermediates, are important as biostratigraphic indicators. So, while certain species concepts (e.g., Wiley's 1978 version of the Evolutionary Species Concept; Ridley's 1989 Cladistic species concept; see also Martin et al. 2024) would suggest that as a single evolving lineage all of the relevant material should be sunk into a single taxon, Bown and Rose (1987) made the decision to preserve the information on morphological variation in the taxonomic schema that they used.

PAROMOMYIDS

As part of a revision of the alpha taxonomy of paromomyid specimens from the Southern Bighorn Basin Silcox et al. (2008) identified three specimens that were both morphologically and stratigraphically intermediate between two previously identified species, *Phenacolemur praecox* and *Phenacolemur fortior*. The critical diagnostic differences between these two taxa are in the p4, with that tooth in *P. praecox* being tall and sharply pointed, while it is shorter and more bulbous in *P. fortior*. The intermediates have a p4 that is taller and more pointed than is observed in *P. fortior*, but shorter and more bulbous than in *P. praecox*. This contrast was demonstrated with linear measurements (Silcox et al. 2008) and later with dental topographic metrics (Figure 1; López-Torres et al. 2017). The decision to retain both of the original species rather than sink the entire lineage into *P. praecox* largely stemmed from the fact that the evolutionary events represented line up with major periods of faunal interchange (i.e., Biohorizons), a nuance that would be lost if a more lumped taxonomy were to be adopted.

MICROSYOPIDS

In the context of an on-going alpha taxonomic revision of Southern BHB microsyopids (Silcox et al. 2014), Silcox and colleagues (2021) identified a specimen that was morphologically and stratigraphically intermediate between the previously identified *Arctodontomys nuptus* and *Microsyops angustidens*. The key difference between these taxa is in the presence or absence of a metaconid cusp on the p4, with it being absent in *Arctodontomys* and present in *Microsyops* (Gunnell 1985; Figure 2). In microsyopine evolution there is a general trend of molarization of the p4 (Gunnell 1989; Szalay 1969), of which the addition of the metaconid is a key component, making the recognition of *Arctodontomys* an important distinction in representing change in the group. At a single locality that straddles 3m of section (locality USGS D-1297, 260–262m from the base of the Willwood formation) specimens of both species are known, as is a specimen (USNM 540280; see Figure 2b) that preserves a strong wrinkle of enamel in the position of the metaconid, which is just short of cuspidate. The latter was identified as an intermediate specimen. Unlike the situation with the paromomyids, in which *P. praecox* goes extinct as it evolves into *P. fortior*, a few specimens of *A. nuptus* re-occur higher in the section after a ~60m gap. Although this gap in the record could be a product of sampling, there are decent quality collections of small mammal teeth from the inter-

val when *A. nuptus* is unknown, suggesting that this absence may be real. This pattern was interpreted as evidence of cladogenetic speciation, with *M. angustidens* evolving from a population of *A. nuptus*, but the latter taxon persisting, presumably re-invading from another area when it re-occurs later in time. Choosing to combine the two taxa (which would necessitate making *Arctodontomys* invalid) would obfuscate one of the key events in microsyopid evolutionary history and generally make the systematics of the group more opaque.

LESSONS ABOUT IDENTIFYING INTERMEDIATES

A common feature of all three examples detailed above is that the identification of lineages including intermediate taxa came as part of an overall alpha taxonomic revision that was being performed in the context of a very well-studied stratigraphic/temporal framework (Bown et al. 1994b). It was possible to clearly delimit which specimens were intermediates and (perhaps most critically) make a compelling argument for such an identification because of an understanding of the *rest* of the record and how it is patterned through time. In all three cases it was argued that taxonomic simplification (i.e., placing all members of a lineage into a single species) would obfuscate temporal or morphological patterns. Although it is certainly fair to acknowledge that these three studies are not independent of one another (i.e., they include many of the same authors), the point still holds that if the three lineages had been sunk into one species each the results would have been OTUs for cladistic analyses that would have been atypically variable and a taxonomic schema that would have failed to represent the true situation for biostratigraphic analyses. As I argued previously (Silcox 2014), there is no universal scientific opinion about how to define a fossil species, so a certain pragmatism should inform the decisions made. Or to put it in the terms used by Bae et al. (2024: 1), "the [species] concept used will depend on the type of data and the analysis conducted."

Having said that, one element common to the omomyoid and paromomyid analyses (which will also be true of the microsyopid study once it is completed) is that the species named were tied to very explicit, updated differential diagnoses. This forms a very important part of retaining the end members of a lineage as distinct taxa; without those diagnoses the names would be meaningless. Along the same lines, OTUs based on intermediates need to be clearly morphologically distinct both from the parent taxa and from one another or else they become effectively meaningless as named entities and (perhaps more to the point) not useful.

Maybe the key lesson from the Bighorn Basin is that more data do not necessarily make matters easier. The more specimens you have from a particular taxonomic group, the more likely you are that gaps in time and morphology are going to become filled. As discussed (Silcox 2014), there is no theoretical consensus about how to deal with the practical problem of recognizing species in the fossil record when they are not conveniently divided by spatial or temporal gaps; after decades of arguing it seems unlikely that there ever will be such a consensus. So, the fond hope, expressed at the end of many paleontological papers, that more specimens are needed to resolve some taxonomic question is often a false hope. More specimens do not necessarily make things easier, although they will of course make our understanding more true.

SO WHAT ABOUT *HOMO HEIDELBERGENSIS*?

Taking an outsider's perspective, informed by the BHB examples, the first issue with *Homo heidelbergensis* as it is often used (i.e., a taxon that includes all fossil specimens of large, advanced hominins that are not *Homo erectus*, *Homo sapiens sapiens*, *Homo sapiens neanderthalensis* or Denisovans; Mounier et al. 2009; Stringer 2012; etc.) is that it mixes members of multiple evolving lineages. Maybe this is not a problem if you want a very "zoomed out" view of recent human evolution (e.g., Martin et al. 2024), but it is a problem if you want to understand the evolutionary process by which our species, and Neanderthals and Denisovans, evolved, and to consider questions such as why we survived and they did not. The taxonomic framework does not work in service of the evolutionary questions that are most interesting. In a sense, the taxon is more of a problem than (for example) combining *Phenacolemur praecox* and *P. fortior* into a single taxon would be—at least the paromomyids are members of the same (single) lineage.

It also does not make a lot of sense to sink specimens from Asia and Africa into that name when they (presumably) do not have anything to do with the immediate ancestry of Neanderthals. The highly lumped approach also does not speak to the problem of how to taxonomically recognize specimens from Europe that do not show Neanderthal traits (e.g., Mala Balanica; Roksandic et al. 2011). The naming of *Homo bodoensis*; Roksandic et al. 2021 is perhaps helpful, inasmuch as those authors suggest that it may be an appropriate name for some European material, but in the absence of a full hypodigm it is difficult to know how to practically apply the name.

With respect to Asia, Ni et al.'s (2021) phylogenetic analysis shows that there is a clade of Asian fossils that does not include the holotype of *Homo heidelbergensis*; as such, surely those specimens must be excluded from *H. heidelbergensis*, representing as they do a further distinct lineage of hominins. In a somewhat parallel scenario, the European record for paromomyids is placed in a distinct genus (*Arcius*; Godinot 1984), supported by its identity as a monophyletic group (López-Torres and Silcox 2018). Bae et al. (2023) make the case that there are multiple distinct morphotypes that exist within the cluster of Middle Pleistocene hominins from Asia; more work is clearly needed to provide diagnoses and hypodigms for subsets of that sample.

CONCLUSIONS

In conclusion, coming from the perspective of the excellent fossil record of the Southern Bighorn Basin, the approach of sinking the huge diversity of variation represented by the Middle Pleistocene record of hominins, including mem-

bers of at least three lineages, into *Homo heidelbergensis* is honestly a bit bewildering. Surely a more "split" taxonomy would make it easier to express the patterns that workers are seeing in the morphology. Having said that, it seems unlikely that all 23 potentially valid taxa listed by Bae et al. (2024) are going to be clearly diagnosable. It is worth noting that all three BHB examples arose out of basic alpha taxonomic work, which involved revising historical diagnoses to better represent the material known at the time. Although it is a daunting task, it is hard to imagine how to move forward with a better understanding of the Middle Pleistocene hominin record in the absence of a similar type of undertaking. The alternatives seem to be using a non-diagnosable wastebasket taxon (*Homo heidelbergensis*) that includes parts of multiple distinct lineages, or to be faced with such a diversity of potentially valid names used in such a variety of different ways that the work is paralyzed. The approach taken in Ni et al.'s (2021) detailed phylogenetic analysis, of starting by mapping patterns of primitive and derived traits at the specimen level, may offer a hopeful first step in identifying clusters that can be the basis for such a revision.

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DATA AVAILABILITY STATEMENT

All the data referred to in the paper is published and available.

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