

## What Are the Odds?

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Evolution is not an exact science—everybody knows that—but just where does the inexactitude lie, and why does it matter? One place is in population genetics, where expectations are based on the average behavior of elements in large samples (whether these are pieces of chromosomes in an individual or variations on the same piece of chromosome in a population). Another is in phylogenetics, the study of how genealogical relationships can be determined from unique morphological similarities that are homologous (features that are the same in two taxa because they descended from the same feature in their last common ancestor). One thing that makes phylogenetics inexact is the inability to distinguish these homologies from homoplasies (sometimes called parallelisms), which are morphological features that became the same in two taxa by independently evolving from a single, different, feature in their last common ancestor. Since in both cases the features are the same, what criteria could distinguish their sources? Well, perhaps an examination of their embryology, which along with some other ideas has been proposed for helping distinguish homologous and homoplastic features in living organisms, but these will not work for fossils. In fact, only a phylogenetic analysis can isolate homoplasies in fossil taxa, and this is by applying the assumption that homologies (similarity by descent) are much more probable than homoplasies (similarity by independent evolution). Once a hypothesis of evolutionary relationships is established, and homologies are identified as the cause of the most common similarities, homoplasy explains the leftovers. By applying a criterion that homologies are much more probable, we are playing the odds when

constructing phylogenetic hypotheses.

The problem of probabilities has been right in the face of paleoanthropologists trying to make sense of Pliocene and early Pleistocene hominid evolution. For instance, look at the results of the several attempts to exam-

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ine the evolutionary trends in the East African robust australopithecine species *Australopithecus boisei*.<sup>1-4</sup> Some prefer to see this species as distinct from the earlier *Australopithecus aethiopicus* and the South African species *Australopithecus robustus*, while others prefer to place these three species in the genus *Paranthropus*.<sup>5,6</sup>

In these studies of evolutionary trends, the *A. boisei* samples were divided into earlier and later groups differently, the analytical techniques vary, and the features examined are not completely the same. Neverthe-

less, they agree in showing that at least some elements of the posterior dentition and mandibular corpus size have increased over time. Most interestingly, however, features of the earliest (about 2.1 million years old) cranium, Omo L 323-896's larger canine size and small cranial capacity (estimated at 490 cc),<sup>1</sup> mark the beginning of other evolutionary trends - decreasing maxillary canine size and increasing cranial capacity in *A. boisei*.

Three of the later-occurring (about 1.5 million years old) partial crania show evidence of significant brain size evolution<sup>7-9</sup>: the Konso-Gardula vault, the Chesowanja juvenile female and the incomplete ER 733 male.<sup>10</sup>

The increases in brain size are marked.<sup>1</sup> The limited data suggest that brain size expansion is disproportionately greater than masticatory apparatus size increases. But in a purely allometric relation we would expect the masticatory apparatus to respond much more strongly to body size increases than brain size does, and larger specimens should have *relatively* larger jaws and teeth. Therefore if the *A. boisei* increases were due to increased body size alone we would expect to have higher cresting frequencies and not lower ones in the later specimens, but the opposite is the case. Thus, body size increases, if there were any—a point that remains unknown—cannot account for the brain size expansion.

Now, the question is whether this is a homology or a homoplasy, because expanding brain size is the hallmark of our lineage, too. What are the odds that it could happen twice, especially in closely-related hominid competitors? Schemes involving the parallel evolution of significant features are generally received poorly.<sup>11</sup> It has been easier to conclude that these are homologies, for if only a single species

was involved, the shared features would be a reflection of conspecificity and no explanation for them would be required. I can already hear the murmuring: is it actually the single species hypothesis that is being unearthed?

However, the relative probabilities that similarities are due to homoplasy are not always the same. Some circumstances provide the potential to elevate these odds, and create the expectation of much more homoplasy than is usual. Closely related species that adapt similarly are a case in point, when homology may not always be the most parsimonious explanation for similarity. When Skelton, McHenry, and Drawhorn attempted their first systematic cladistic analysis of the early hominids,<sup>12</sup> they uncovered numerous homoplasies. Subsequent analysis<sup>5</sup> still resulted in phylogenetic hypotheses that were difficult to choose between because they were close to equal in the amount of data they explained; so close that the authors concluded the differences in consistency index might not be significant. The fact is, as they wrote, all the cladograms and phylogenies presented or discussed here require a large amount of homoplasy.

Where are these homoplasies coming from? There appear to be two sources. One is the group of structural consequences of expanding brain size, including an array of changes from characteristics as minor as the branching pattern of the middle meningeal artery<sup>5</sup> to the increased craniobasal flexion,<sup>13</sup> tucking the face under the vault as in Chesowanja. The second is an independent shared adaptation, one uniting a different group of species - the increasingly powerful masticatory apparatus and all of the features functionally related to it. Analyses assuming homology in brain size evolution would cluster *A. boisei* with *Homo*, while the assumption that the masticatory apparatus expansion is homologous relates *A. boisei* to the other above-mentioned robust australopithecines. The one certain thing is that similarities in both systems cannot reflect homologies, because they result in quite different sets of phylo-

genetic relationships.

The situation is actually more complicated than either of these hypotheses express. There is a unique combination of features and evolutionary trends that shows the expanding brain size in *A. boisei* does not make it *Homo*, and that the single species hypothesis can remain buried. They demonstrate that *A. boisei* fits the description of an evolutionary species with unique evolutionary tendencies and its own historic fate. But the parallelisms it holds with other hominid species are numerous, unexpected, and have been potentially quite confusing because of their effect on the underlying assumptions made about the relative probabilities of the causes of similarities. These many homoplasies give us important information about the evolutionary process because they must come from the combination of similar gene pools (recent divergence for the australopithecine species) and parallelisms in adaptation that lead to comparable genetic responses. But it is also true that these homoplasies really change the underlying probabilities that are important in the assumptions we make. They send a strong signal, that is too easily confused with similarities due to descent for the most parsimonious branching pattern to be much more probable than several others.

Scientists analyzing Pleistocene hominid evolution have not always learned the lessons of these Pliocene analyses, at least insofar as they involve implications following from the inexactness of phylogenetics. In spite of all of the difficulties that homoplasies have created in establishing the pattern of relationship between closely related hominid species, there are paleoanthropologists who insist on using the same cladistic techniques to establish the pattern of relationships of populations within one—ours! But using cladistics within our species is plagued with even more problems than the analysis of closely related species. There are many more sources of similarities than homoplasies that also do not reflect the pattern of descent, because human populations are not isolated and constantly branching, like

species. They are much more like the channels in a river,<sup>14</sup> continuously dividing and merging so that any population may have many ancestors. No cladistic analysis could possibly model such a process, because evolution within a species is not based on branching.<sup>15</sup> The odds that phylogenetic analysis will not accurately reflect population histories are just too great.

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