



The first humans, the second orangutan and the third chimpanzee

Of all the topics in evolutionary biology, it is hard to think of any that is of greater general interest than the topic of where humans arose and from what ancestors. Several decades into the recent renaissance in phylogenetics generated by the advent of molecular methods for determining evolutionary relationships, the prevailing view among anthropologists is that the closest living relatives of humans are the African great apes, with the chimpanzee and bonobo forming the sister-lineage to humans, followed by the gorilla; these species are next joined on the phylogenetic tree by species with Southeast Asian distributions – the orangutan, and then the gibbons and siamangs. This phylogenetic hypothesis – corroborated by multiple independent molecular analyses – is often conveyed to a broader audience [e.g., Jared Diamond's (1992) book *The third chimpanzee: the evolution and future of the human animal*, and Richard Dawkins' (2004) book *The ancestor's tale*] as having been so generally accepted by the scientific community that it is without serious challenge to its veracity.

And so, it may come as a surprise that the *Journal of Biogeography* would choose to publish the paper by Grehan & Schwartz (2009), which challenges this view and provides a detailed account of an alternative evolutionary and biogeographical scenario. In this study, Grehan and Schwartz provide a radically different hypothesis of great ape phylogeny by positing that humans are most closely related to the orangutan rather than to the chimpanzee and bonobo, a view that Schwartz has advocated for a number of years (developed in detail in his book *The red ape: orangutans and human origins*; Schwartz, 2005). Grehan and Schwartz's conclusions in the *Journal of Biogeography* paper are based on four cladistic analyses of up to 64 morphological characters, each analysis comprised of a different array of

living and fossil apes. The authors are quite aware that their hypothesis is in conflict with the consensus hypothesis based on molecular systematics, but argue that this is so because 'Molecular analyses are compromised by phenetic procedures such as alignment and are probably based on primitive retentions' (more on this topic below).

The study becomes relevant for this journal when the phylogenetic conclusions are interpreted in an historical biogeographical framework. The controversial and infrequently used panbiogeographical method of track analysis is their method of choice. This method interprets disjunct (separated) distributions of related taxa as having derived principally through the break-up of the range of an ancestral form by the development of environmental barriers (a process termed vicariance), with subsequent evolution of descendant forms in isolation. And so, by implementing their alternative phylogenetic results in a track analysis, Grehan and Schwartz postulate the equally controversial hypothesis that the ancestors of humans arrived in Africa independently of the other African great apes.

Historical biogeography is a discipline characterized by divergent schools of thought, and in this paper the authors have chosen to rely on two approaches that each are increasingly utilized by a minority of modern practitioners: morphological systematics, with explicit denial of the theoretical underpinnings of molecular systematics; and panbiogeographical track analysis. Within science, being in a minority does not mean that you are wrong of course. Regular readers of this journal will be aware of these differences in perspective, method and interpretation, as we regularly publish papers presenting strongly contrasting perspectives on evolutionary biogeography.

We have chosen to comment on the paper by Grehan and Schwartz not simply because it comes from this minority perspective but because it comments on a topic of such keen general interest and

therefore may well gain wide attention in the scientific and popular press. The main facet of the paper that is worthy of editorial comment is that their analysis challenges, or rather dismisses, a large range of molecular (including modern genomics-based) analyses that support the alternative phylogenetic hypothesis that humans are in fact more closely related to chimpanzees (as reflected in the title of Diamond's book; above). Grehan and Schwartz contend that the morphological data they have selected as the basis for interpreting evolutionary relationships are more robust and reliable for this purpose than the majority of the genetic evidence considered by other authors. Unfortunately, as one of the reviewers of the manuscript pointed out, the identification of characters and the judgement of their significance, is a subjective procedure and depends to a large extent on how the individual worker interprets the characters. The manuscript did not exactly succeed in convincing the journal's reviewers that the 'second orangutan' interpretation is to be preferred over the more popular 'third chimpanzee' scenario, but was felt to be a contribution worth putting out to the test of further scientific scrutiny.

The strength of the paper by Grehan and Schwartz as a contribution to the debate over human origins is, in our view, that the authors have provided a clear account of their hypothesis, the assumptions that have gone into their analysis, the data they have so painstakingly compiled and used, and the relationship of their findings to the existing literature on the topic. While this perspective might superficially appear to be nonsensical to the majority of molecular anthropologists and systematists, we believe that the progress of scientific discourse is served by providing the advocates of this minority view an opportunity to present all of their evidence and assumptions – only then can the scientific community respond in an informed manner.

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