# The Anthropoid-Like Face of *Siamopithecus*: Cherry Picking Trees, Phylogenetic Corroboration, and the Adapiform–Anthropoid Hypothesis

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Zollikofer et al. (2009) digitally reconstructed the damaged and fragmentary remains of the face and mandible of *Siamopithecus eocaenus*, a recently discovered, moderately large primate from the late Eocene of Krabi, Thailand (Chaimanee et al., 1997, 2000a) in order to examine its phylogenetic affinities in greater detail. Opinions differ on the relationships of *Siamopithecus* (Zollikofer et al. enumerate and reference these views) which can be summarized as: (1) *Siamopithecus* is an anthropoid and a member of a monophyletic group that includes two other Eocene Asian genera, *Amphipithecus* and *Pondaungia* (the family-level nomenclature for this taxon has been a source of some confusion—Amphipithecidae Godinot, 1994 has priority; see Holroyd et al., 2002), plus a third that has been described since then (Beard et al., 2009); or (2) *Siamopithecus* and its allies are adapiform strepsirhines and thus are only tangentially related to anthropoids as euprimates. Either way, *Siamopithecus* essentially represents yet another chapter in a decade long debate that revolves around the question of where, if anywhere, do adapiforms fit in the history of anthropoid phylogeny (e.g., Gregory, 1922; Le Gros Clark, 1959; Szalay and Delson, 1979; Gingerich, 1980a,b; Rosenberger and Szalay, 1980; Rosenberger et al., 1985; Kay and Williams, 1994; Fleagle, 1999; Ciochon et al., 2001; Ciochon and Gunnell, 2002; Gebo, 2002; Ross and Kay, 2004; Williams et al., 2010; Gingerich et al., 2010)?

Zollikofer et al. (2009) offer new evidence that, in their view, supports inclusion of *Siamopithecus* within anthropoids. Their approach relies on a three-dimensional geometric morphometric analysis of 15 landmarks drawn from their *in silico* reconstruction, using a broad sampling of genera from most living primate families as well as extinct pliopithecids, archaeolemurids, adapids, and omomyids as a taxonomic framework. The intention to apply a powerful phenetic tool in order to test a phylogenetic hypothesis is appropriate; however, the results of the analysis question the validity of the conclusions. A similar problem is widespread in phylogenetic studies in general—summary trees (i.e., dendrograms), whether explicitly cladistic or phenetic by design, are held to provide robust results for taxa of special interest while the credibility of tree topology is undermined by other branching patterns, which may involve, or even be dominated by, evident phylogenetic errors relating to other included taxa.

Zollikofer et al. (2009) present two phenograms (reproduced here as Fig. 1) summarizing separate analyses of the skull and the cranium (without mandible) based on a UPGMA (unweighted pair group method with arithmatic mean) clustering method. In both phenograms, *Siamopithecus* links to the trees within included anthropoids. However, with regard to established phylogenetic relationships among primates, there is no reason to suppose these analyses produce reliable phylogenetic signals. The broader topologies of the dendrograms are error-filled and inconsistent with well established phylogenetic hypotheses, for the following reasons (see Fleagle, 1999; Delson et al., 2000; Hartwig, 2002):

1. Zollikofer et al. (2009) indicate that lorisids and indriids form a monophyletic group, but this is almost certainly not true. Cladistically, indriids are lemuriforms and lorisids are lorisiforms, hence their union and basal position relative to the remaining modern strepsirhines is a cladistic error (joining galagids with cheirogaleids is also unlikely, but the affinities of the latter *vis a vis* Lorisiformes and Lemuriformes is debatable).

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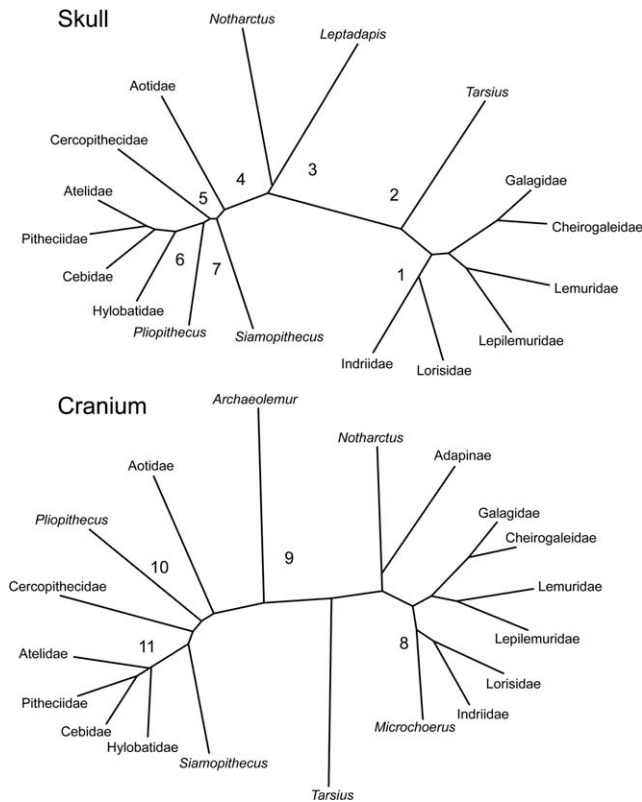
Fig. 1. Dendrograms depicting the alleged phylogenetic position of primate taxa produced by the analyses of Zollikofer et al. (2009)—top (skull) includes both skull and mandibular characteristics; bottom (cranium) includes only cranio-maxillary characteristics. Numbers on dendrograms refer to the enumerated false linkages discussed in the text (figures redrawn from original).

2. The linkage of *Tarsius* with strepsirhines violates the well established strepsirhine–haplorhine dichotomy.
3. The linkage of *Leptadapis* and *Notharctus* is reasonable as both are adapiforms and outside the tooth-combed strepsirhine clade. However, the position of their joint node adjacent to the "anthropoid" group is but a reminder that many of their features are likely convergences shared with anthropoids (e.g., Seiffert et al., 2009).
4. Aotidae (i.e., *Aotus*) falling outside other platyrrhines cannot be reconciled cladistically.
5. The position of Cercopithecidae cannot be reconciled as being outside any form of catarrhine node, which here includes *Pliopithecus* and Hylobatidae.
6. Hylobatids are depicted as being more closely related to platyrrhines than to other catarrhines which is surely incorrect.
7. Pliopithecus is also depicted as being related more closely to a platyrrhine–hylobatid group than to included catarrhines such as cercopithecids.
8. *Microchoerus*, a fossil tarsiiform, is shown to be most closely related to a subgroup of Lemuriformes, indriids, and lorisids, and not to *Tarsius* or other haplorhines, which is problematic.
9. *Archaeolemur*, which is related to indriids, falls outside strepsirhines completely.

10. The catarrhine *Pliopithecus* is inside the *Aotus* node and dissociated from other catarrhines.
11. An unresolved branching sequence fails to distinguish platyrrhines from catarrhines and produces a trichotomy linking gibbons with platyrrhines instead of catarrhines.

With nearly a dozen false phyletic linkages, it is evident that the UPGMA summary is a poor reflection of primate genealogy. The only explicable reason for these numerous discrepancies is that the tree is powerfully driven by phenetic similarity. Thus much of the analysis is likely to cluster taxa based on primitiveness and convergence rather than by exclusive, homologous synapomorphies. Even the position of *Siamopithecus* is inconsistent—in one case falling between *Aotus* and cercopithecids and in the other case between cercopithecids and a grouping consisting of some New World Monkeys (excluding *Aotus*) and hylobatids. The basic question thus becomes: why should we be inclined to accept the alleged phyletic nexus of *Siamopithecus* with anthropoids when so many other linkages in the same study are unfounded and almost certainly false?

Although the broader phylogenetic errors do not immediately disqualify the *Siamopithecus* result, it does mean that the Zollikofer et al. (2009) study has not provided a reliable confirmation of an amphipithecid–anthropoid linkage. Unfortunately, a direct test of the evidence presented in this analysis may be impossible, which casts another, deeper level of doubt. The phenetic basis of the analysis is a synthetic construct, not a feature or character state in the conventional sense. The latter are amenable to homology testing by comparative methods (e.g., morphological detail, correlation, ultrastructure, ontogeny, functional morphology, intertaxon continuity, genes, etc.), but no comparable principles apply to a multivariate compound.

The *Siamopithecus* issue cannot be divorced from ultimate resolution of the adapiform–anthropoid hypothesis. The centrality of this problem is also evident in the recent announcement of yet another Burmese Eocene amphipithecid described as an anthropoid, *Ganlea megacanina* (Beard et al., 2009). Suffice it to say that the characters presented in support of this interpretation are culled from the same list of similarities traditionally used to support the adapiform–anthropoid hypothesis as well as hypotheses favoring the anthropoid affinities of two other Burmese amphipithecid primates in question, *Pondaungia* and *Amphipithecus* (Gingerich et al., 1994; Rasmussen, 1994; Jaeger et al., 1998; Chaimanee et al., 2000b).

Another recent study (Seiffert et al., 2009), based on discovery of *Afradapis longicristatus*, a new Eocene adapiform from the Fayum, Egypt, also addresses the anthropoid–adapiform connection by presenting a broad numerical cladistic phylogenetic analysis under parsimony (PAUP) analysis, which corroborates the notion that adapiforms and anthropoids evolved important features convergently. While welcome, and perhaps expected (see Kay, 2009; Rosenberger, 2009), the Seiffert et al. (2009) contribution is unlikely to resolve the adapiform–anthropoid problem either. In part, this is because research paradigms in primate paleontology have shifted from falsification models based on conjecture and refutation (Popper, 2002) toward a strategy that seeks confirmation by repetitive iteration. Thus, explicitly or

implicitly, Zollikofer et al. (2009) endorse the adapiform–anthropoid hypothesis without consideration of studies that specifically address and counter the proposed homologies and polarities of the dental characters upon which the main hypothesis is based (e.g., Rosenberger and Szalay, 1980; Rosenberger et al., 1985), nor do they consider complementary studies of the postcranium, which also negate it (Dagosto, 1985, 1988; Gebo, 1986). This body of work falsifies the adapiform–anthropoid hypothesis and offers independent sets of derived character states and adaptive complexes that support a sister-group relationship between adapiforms and strepsirhines (including lemuriforms, lorisiforms, and stem strepsirhines; see Seiffert et al., 2003, 2005; Tabuce et al., 2009).

The Zollikofer et al. (2009) dendrograms illustrate phenetic relationships by design. On the other hand, many primate numerical cladistic (PAUP) trees of recent vintage (e.g., Kay and Williams, 1994; Tabuce et al., 2009; Williams et al., 2010) use a common protocol based on massive datasets of characters states without controlling for character redundancy and correlations (e.g., Rosenberger, 2010). Many of these are almost certainly driven by a high phenetic quotient, even though the mathematical models behind them organize data on the basis of trait transformation (i.e., polarity based on algorithmic parsimony) rather than static similarity. As mathematical parsimony is itself an unlikely, never-verifiable, scenario of evolutionary change, analytical models that employ this principle have a status somewhat comparable to phenetics, in contrast to methods based strictly on homology and polarity. Conceptually, the resulting trees are similar to the Zollikofer et al. (2009) dendrograms, because they accept a high degree of within-group homoplasy (i.e., proportionately large "consistency indices"), meaning a combination of error, homology, and analogy reside within them. Therefore, each of these approaches are effectively hybrids, lying somewhere along a phenetic–cladistic continuum, and thus are not strictly cladistic.

The results of Zollikofer et al. (2009) joined with those recently presented by Franzen et al. (2009), Williams et al. (2010), and Gingerich et al. (2010) have served to rekindle the debate over the adapiform–anthropoid hypothesis. Hopefully, this renewed interest will also stimulate efforts to test specific morphological details behind tree topology (i.e., the putative homologies that support nodes) by independent means rather than by reiteration of the same or similar data matrices. All of the relationships embodied in phylograms need to be scrutinized in order to evaluate their overall robusticity before settling on the veracity of any specific node. Cladistic hypotheses need to be confirmed not only by generating more trees using more data having the same properties and consequently producing iterative hypotheses, but also by applying alternative methodologies that employ differing assumptions and adhere to evolutionary models that can be supported empirically.

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