Journal of Human Evolution 59 (2010) 214–217

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

News and Views

Platyrrhines, PAUP, parallelism, and the Long Lineage Hypothesis: A reply to Kay et al. (2008)

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ARTICLE INFO

Article history:
Received 1 October 2008
Accepted 23 September 2009

Keywords:
Fossils
Cladistics
New World monkeys
Primates
Systematics

Kay et al. (2008) presented a parsimony (PAUP) analysis of platyrrhines involving a craniodental database of 268 characters, several targeted Patagonian fossils, *Tarsius*, and 29 anthropoid genera. Their core conclusion challenges a central idea about platyrrhine evolution, but it is flawed by interlocking problems concerning research design, data quality, and methodology. This conclusion rests on a weakly supported cladistic artifact, a purported monophyletic group of southern platyrrhines involving four poorly known, unevenly preserved, barely comparable sets of fossils that emerged by default, juxtaposed against a grouping of essentially modern platyrrhine genera, 94% of which are living forms represented by effectively complete datasets. To rationalize these results, Kay et al. (2008) oddly misconstrue the nature of phylogenetic, functional, and adaptive evidence in historical evolutionary reconstruction, using false analogies. And, their argument ignores the body of evidence supporting the evolutionary model they seek to refute, the Long Lineage Hypothesis (LLH).

The LLH proposes that modern New World monkeys (NWM) are characterized by a relatively large number of long lived genera and subclades (e.g., Rosenberger, 1979, 1992, 2002; Delson and Rosenberger, 1984; Rosenberger et al., 2009). Predicated on an ecophylogenetic study of all platyrrhines known up until 1979 and a major reorganization of NWM systematics, its central hypotheses sought to establish: 1) direct fossil evidence that three of the 16 modern platyrrhine genera, *Saimiri*, *Alouatta*, and later *Aotus* could have arisen within or earlier than the approximately 11–20 Ma time bracket while a fourth, *Cebus*, the living sister-taxon of *Saimiri*, was inferred to be equally as old; 2) generic distinctions between the La Venta fossils *Stirtonia* and *Alouatta* and the modern *Neosaimiri* and *Saimiri*, respectively, were questionable; 3) within-lineage morphological continuity between these sets was evidence for stasis; and, 4) modern NWM differentiation has deeper temporal roots than comparable catarrhine splits. Two Patagonian fossils, *Tremacebus* and *Dolichocebus,* at about 20 Ma, were identified as the oldest affiliates of the modern taxa, related to *Aotus* and *Saimiri*, respectively; the broader affinities of *Dolichocebus* as a cebine (hence the *Cebus-Saimiri* clade) were also explicitly discussed (e.g., Rosenberger et al., 1990). Kay et al. (2008) argued instead that *Tremacebus* and *Dolichocebus* were part of a four-genus, southern "stem platyrrhine" group, proving that NWM evolution unfolded in a more "layered" fashion. A fifth Argentine genus, *Homunculus*, was held to be part of this group but it was not analyzed (see below), while the older Bolivian fossil, *Branisella*, fell outside it.

Although Kay et al. (2008) make no mention that the LLH has been corroborated independently by distinctly different types of data and varied methods of analysis since it was proposed, numerous molecular studies (e.g., references in Opazo et al., 2006) have confirmed the majority of the underlying cladistic hypotheses (e.g., Schneider and Rosenberger, 1997; Schneider et al., 2001; Rosenberger, 2002) and uniformly support the early differentiation model. The median ages (in millions of years) of the divergence of critical genera and subclades calculated from Schrago's (2007) summary of six projects gives the following: *Aotus*, 17.6; *Callicebus*, 15.4; *Alouatta*, 13.7; *Callimico*, 9.7; *Cebus* and *Saimiri,* 16.5; cebines vs. callitrichines, 19.9; cebids vs. atelids, 20.1. A separate study (Opazo et al., 2006), for reference, yields even older divergence dates: *Aotus*, 22; *Callicebus*, 19.3; *Alouatta*, 16.8; *Callimico*, 12.1; *Cebus* vs. *Saimiri*, 19.5; cebines vs. callitrichines, 22.8; cebids vs. atelids, 24.4. Another recent molecular study (Hodgson et al., 2009) inveighed against the LLH, saying "The MRCA [most recent common ancestor] of the living platyrrhines is estimated to have lived 19.5 Ma (95% credibility interval 16.8–23.4 Ma)…" and specifying that *Dolichocebus* and *Tremacebus* thus cannot be

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0047-2484/$ – see front matter
doi:10.1016/j.jhevol.2010.03.003

related closely to modern genera. But the estimated MRCA date is only 0.5 million years prior to the 20 Ma geologically estimated dates for the fossils, which falls well within the wide margins of their confidence limits, and their 14.3 Ma bottom boundary for differentiation of all the major platyrrhine lineages actually conforms with the LLH model.

The pre-Pleistocene fossil record, now comprising over twice as many genera as in 1979, consistently fits LLH predictions. Three examples: 1) The case for fossil-modern congeners was first strengthened in 1987 by discovery of a new large-eyed species at La Venta, Colombia, *Aotus dindensis* (Setoguchi and Rosenberger, 1987), an attribution corroborated in 2001 by new material, also allocated to *A. dindensis* (Takai et al., 2001); 2) An implicit prediction of within-lineage transformational continuity has been confirmed by a detailed micro-CT study (Kay et al., 2004), which shows again that *Tremacebus* shares derived cranial features with *Aotus* pertaining to nocturnality (Fleagle and Rosenberger, 1983), but in more primitive states than in the living owl monkey (e.g., smaller orbits and larger olfactory lobes, in both cases falling between the diurnal *Callicebus* and *Aotus* in their proportions); 3) The recently discovered *Killikaike* (Tejedor et al., 2006), at 16.4 Ma, presents a complete undistorted face that is diagnostically cebine—vaulted anterior braincase, large forebrain, narrow interorbitum, closely appressed medial orbital walls—all derived cebine features securely extending the subfamily's time depth 3–5 millions of years beyond *Neosaimiri*. Indeed, since 1979, 17 new fossil genera have been named (see Hartwig, 2002). Six fossils from mainland South America have been aligned with modern generic lineages and/or low-level clades without evident debate: *Caipora, Acrecebus, Nuciruptor, Patasola, Miocallicebus, Proteropithecia.* The oldest among these is *Proteropithecia*, a 16 Ma pitheciin *from Patagonia* (Kay et al., 1998), that is, within the temporospatial range of the Kay et al. (2008) southern "stem group," thus a strong indicator of historical/faunal continuity between the south and modern Amazonia in the north. The relationships of three others, *Killikaike, Soriacebus,* and *Paralouatta,* have elicited different opinions (e.g., MacPhee and Horovitz, 2002; Kay et al., 2008), but I regard them as securely cebine, pitheciin, and alouattin, respectively. Others, more poorly known, remain difficult to interpret and I ignore them here, taking a conservative stance.

A plethora of issues cast doubt on the reliability of Kay et al.'s (2008) "stem group" hypothesis. Its central tenet, monophyly of *Dolichocebus*, *Tremacebus*, *Carlocebus*, and *Soriacebus,* is weakly supported. It is based on a proportionately small number of features, including states that would appear rather trivial for higher phylogeny studies. Of the final 183 dental features used, only four synapomorphies support this group. Taken verbatim, they are: 1) distolingually oriented P_4 protocristid; 2) mesiodistally reduced P_4 talonid; 3) basally inflated P_4; and, 4) strongly developed P^4 hypocones. How much phylogenetic power should we attribute to this series? How much developmental and taxonomic independence might they have? How confident should we be that these characters properly reflect phylogeny in this case?

These traits represent *one tooth set*, P4. Three are descriptive attributes of one unit from that set, that is, they particularize P_4 shape. The first (#1) is found elsewhere only in *Tarsius*, *Apidium,* and *Simonsius*, where their radically different crown morphologies raise questions about character delineation and coding. Characters #2 and #4 are complex homology and polarity problems involving multi-state characters coded as four and three states, respectively; none of the four "stem platyrrhine" genera mutually share any one of the #2 states. Character #3 is widely distributed within NWM and in the out-groups, occurring in five living platyrrhines plus *Proteropithecia* and among four Fayum genera, which suggests it is primitive and/or prone to analogy. Finally, *none* of the four characters defining the "stem group" are observable in one of its four genera, *Tremacebus,* which is known only by a basically toothless skull.

A variety of researchers working on disparate primate groups, living and extinct—plesiadapiforms, platyrrhines, catarrhines—have shown that the manner in which a PAUP-based study is implemented has profound consequences, and may often lead to unreliable results (e.g., Collard and Wood, 2000; Young, 2005; Sargis, 2007; Silcox, 2007; Matthews and Rosenberger, 2008). In this case, there is no way of objectively quantifying the trustworthiness of the "stem group" hypothesis, specifically, within the context of the supertree. We can only assess *overall tree quality* by metrics like the Consistency Index (CI), which is 0.343 (Kay et al., 2008). Technically, this means the average agreement of each individual character state with the tree as a whole is 34%, that is, two-thirds of the information is spurious. Biologically, it is impossible to determine where in the tree the "good characters" reside, but they are likely to be concentrated among the essentially complete datasets of the modern taxa (plus *Proteropithecia,* well represented by a morphology that is strikingly similar to modern pitheciins). So, some or all of the 34% "positive" results apportioned to the "stem group" is likely due to methodological artifact, error, and chance. The CI is not an empirically proven metric, and there is no agreement as to the biological importance of a CI value of whatever magnitude (unlike Coefficient of Variation). But calculated on a 0.0–1.0 scale, a 0.343 would rate the score of this study at the bottom third of its own internal quality control measure. Does this number represent an adequate level of scientific comfort, credibility, and predictability?

The reliability of parsimony-based cladograms built from morphological information also has a chequered history with regard to modern platyrrhines, and this should be taken into account when evaluating questionable outcomes regarding data-poor fossils. A case in point is *Aotus*, a genus whose cladistic linkage has appeared in fundamentally different positions with nearly every such study that has been conducted. For example, in a comprehensive craniodental and postcranial study, Ford (1986) attached *Aotus* to *Callicebus* but linked both with *Saimiri* (or *Saimiri* and *Cebus*) as the first- or second-branching basal lineage. Kay (1990), in a large study of over 100 dental characters, placed *Aotus* in a triple-junction polytomy which included atelines and callitrichines, nested deep within the NWM cladogram. Kay (1994), in a nine-genus study focusing on the La Venta fossil *Lagonimico*, concluded that *Aotus* was the sister-taxon of *Callicebus* and *Pithecia.* Horovitz (1999), in another comprehensive study, found *Aotus* to be the sister-taxon of Cebidae *sensu* Rosenberger when based on morphology alone. And, Kay et al. (2008:347), when performing their maximum-parsimony analysis of "…the cranial and dental matrix unconstrained by a molecular "backbone"…" found that *Callicebus* and *Aotus* were sister-groups, linked first with *Cebus* and then with a monophyletic group comprised of pitheciins and atelines.

PAUP is programmed to produce (read "force") a result for each taxon in the matrix. There are no fail-safe measures akin to probability statistics, or even empirically derived rules of thumb, to indicate when a specific result falls below a threshold of being realistic; or, what constitutes an adequate sampling of traits needed to characterize an individual taxon or large assemblage of taxa. Even when fossils are notoriously depleted of data PAUP finds a solution, but is it artifact or phylogenetic? Of 286 characters used by Kay et al. (2008: Appendix 4), the total proportion of missing data for the fossils is large: *Dolichocebus*, 20%; *Soriacebus*, 40%; *Carlocebus*, 54%; *Tremacebus*, 73%. By contrast, the average percentage of missing data *in toto* for the living NWM genera is

6.6%. The breakdown for fossils is dramatic for cranial (*Dolichocebus*, 46%; *Soriacebus*, 99%; *Carlocebus*, 99%; *Tremacebus*, 40%) and dental data as well (*Dolichocebus*, 13%; *Soriacebus*, 13%; *Carlocebus*, 33%; *Tremacebus*, 89%). Actually, these figures present an incomplete picture of the nature of the evidence since Kay et al. (2008) did not eliminate redundancies from the input matrix or from the results. For example, of the six derived features said to link the "stem group" with crown platyrrhines (p. 356), the mesial termination point of the cristid obliqua on M_1 and M_2 is counted as two characters, and the root structure of P^3 and P^4 is counted as another two. Surely these traits are better treated as a pair of serial homologs (two traits) rather than four independent characters. Still, the overarching data quality issues are these: *Dolichocebus* and *Tremacebus* are essentially edentulous skulls (a few referred teeth are attributed to the former) with a limited range of well preserved comparable parts or characters; *Soriacebus* and *Carlocebus* are known from teeth, almost all representing lower jaws, without any cranial material; *Carlocebus* lacks anterior teeth, which are often cladistically diagnostic among NWM, and it preserves precious little postcanine occlusal morphology. Given these limitations, it should come as no surprise that PAUP anchored the whole tree by the multiplying effect of the modern taxa with their rich information content, segregating them from the depauperate fossils by the sheer weight of accessible crown-group synapomorphies substantiating its many internal nodes.

These skewed results partly arise from the fact that the taxonomic context of the study is grossly overspecified. Kay et al. (2008:329) curiously exclude the iconic *Homunculus* from the analysis "…because some or all of the pertinent material is undescribed," while criticizing Tejedor et al. (2006), on the very same page, for not making explicit comparisons of the Patagonian *Killikaike blakei* with the "…*abundant* [my italics] comparative material of *Homunculus patagonicus*." This self imposed embargo ostensibly relates to new material under study (Kay et al., 2005) but does not adequately explain why *Homunculus* could not be represented in the matrix by the two other well prepared and published partial, undistorted skulls (e.g., Fleagle and Rosenberger, 1983; Tauber, 1991; Tejedor and Rosenberger, 2008) and the long known dental and mandibular remains, which include many specimens in better condition than the dentitions of *Carlocebus*. Two additional southern cone fossils were also excluded, *Killikaike* and the older *Chilecebus* (Flynn et al., 1995). The latter, at a minimum, provides more occlusal morphology than any Patagonian fossil NWM other than *Killikaike*.

Kay et al. (2008) similarly seek to dismiss or reject cranial information supporting an alternative view of *Dolichocebus*. The most complete statement in this regard, albeit with redundancies and flaws, is from Rosenberger et al. (1990), which proposes features specifically linking the genus to *Saimiri* and, more broadly, to cebines. While the most dramatic character, the interorbital fenestra, Kay et al. (2008) fairly hold in abeyance because its status seems ambiguous, other morphological observations or inferences are negated without due consideration to established norms of paleontological research and comparative anatomy. The presence in *Dolichocebus* of a vaulted frontal region is dismissed because glabella (a poorly chosen term on the part of the Rosenberger et al. [1990] description) is broken away, but the prominent olfactory bulbs and high arc of the frontal lobe—the underlying morphology of import, as stated—are well preserved and clearly show the anterior braincase had a cebine-like, domed shape rather than the flat frontal region which is primitive among NWM. The narrowness of the interorbital pillar is likewise discounted although the circumorbital, intra-orbital, and forebrain morphology can only be interpreted as being cebine-like (i.e., narrow). The inferred lightness of the masticatory apparatus (describing a cebid complex, in opposition to the "robust" pattern of atelids) is ignored because the zygomatic arches are gone. But the gracile pattern is a combination of features involving a flat glenoid fossae, small postglenoid process, shallow temporal fossa, and unremarkable temporal lines. This is a combination eminently observable in *Dolichocebus* and found elsewhere only in cebines and callitrichines (Kay et al., 2008). Kay et al. (2008) concur with Rosenberger and colleagues on these descriptions, except for the temporal fossae, claiming that the latter's size is measured against the zygomatic arch, which is missing, but ignoring that the fossa can also be assessed as a matter of relative postorbital constriction. Kay et al. (2008:348) explain away these features as commonly occurring or body-size related—which is precisely our point: they overlap with cebids, a monophyletic, relatively small-bodied group. Overall, Kay et al.'s (2008) re-description and clarification of *Dolichocebus* morphology utilizing modern technological capabilities is valuable, but their insistence on treating each observable anatomical trait or term as a zero-sum data game obscures the reality that character states evolve inter-connectedly as patterns. This undercuts the validity of observation-based morphological inference as a necessary paleontological research tool.

In conclusion, Kay et al. (2008) do not provide compelling evidence for a monophyletic southern group of "stem platyrrhines" that radiated separately from the modern forms and their other fossil relatives. That specific result is based on only four dental character states—and none go without question. All four appear to be correlated, non-independent traits of a single tooth set, which denigrates their statistical power, and none of them are preserved on the best specimens under study, the edentulous (type specimen) skulls of *Dolichocebus* and *Tremacebus*. Nor do Kay et al. (2008) offer even a single comparative anatomical datum or argument—independent of the tree—that explains the counterintuitive sequelae of their hypothesis (see Rosenberger, 2002): for example, that parallelism is a better explanation than a transformational vector behind the minor adaptive differences separating the nondiurnal *Tremacebus* and *Aotus*; or, that parallelism is a better explanation than ecophylogenetic affinity for the extensive, derived seed-harvesting and -feeding similarities shared by *Soriacebus* and pitheciins in the incisors, canines, and anterior premolars (and likely jaws); or, that ecological parallelism writ large of the Patagonian primate fauna is a better explanation than their primitiveness and older age relative to the anatomically more modern and younger La Venta community. Failing to acknowledge that not all homoplasy is created equal, Kay et al. (2008) instead present a specious plausibility argument by asserting that the parallelisms emerging from their study are as likely to occur as other hypothesized cases of parallelism among NWM, such as the independent evolution of prehensile tails in *Cebus* and atelines, which now appears to be a universally accepted explanation. Left unstated is that an extensive analysis stands behind that hypothesis (Rosenberger, 1983), testing the pros and cons of parallelism by morphologically and functionally deconstructing components of the prehensile tail as a system, from bone to brain to allometric scaling to the biological roles of tail use as informed by fieldwork, and placing this assessment in what was then a new phylogenetic context, which has also been confirmed independently.

Acknowledgements

Several colleagues and reviewers provided very helpful comments on the manuscript, for which I am grateful. The research was partially supported by grants from PSC-CUNY and the Tow Travel Research Fund, Brooklyn College. I thank the authorities at the American Museum of Natural History and the United States National Museum for access to collections, as always.

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