Cladistic Analysis and Anthropoid Origins

Richard F. Kay *et al.* state in their recent article (*1*) that the origin and phylogenetic relationships of Anthropoidea have been resolved by cladistic analysis of 256 dental and osteological attributes in 50 primate taxa, but our analysis of data posted by Kay *et al.* at the time of publication (*2*) indicated that their phylogeny was not the hypothesis best supported by their data. We downloaded the data matrix provided by Kay *et al.* on the Web with the intention of extending their study stratocladistically (*3*). In an attempt to replicate their results, we set all parameters as directed, and performed 30 heuristic searches as they did (*1*). Tree lengths were calculated in PAUP (*4*) with the character weighting scheme used by Kay *et al.* after we removed the 50 artificial characters included to make primates monophyletic. The result we obtained was a set of 39 cladograms of length 98,052 steps, showing relationships compatible with the discussion in the report, a consistency index (CI) of 0.309, and a retention index (RI) of 0.577. However, we then ran the same heuristic search with the same parameters for 1000 replications instead of 30, and obtained 98 cladograms of shorter length (97,977 steps; Fig. 1, A and B).

Comparison of our results with those of Kay *et al.* was complicated because the number of characters in the data then posted (281) was greater than the number in the article (256). Taxa included in the outgroup, as well as those in the ingroup, differed from those described in the article. Kay *et al.* did not provide the number of resulting trees, their lengths, or describe what type of consensus formed the basis for their conclusions. The similarity of our results to those of Kay *et al.*, when we ran the posted data for only 30 replications, is not unexpected because we did not override PAUP's (*4*) random number seed of 1. Our more parsimonious results after 1000 replications probably differed as a result of the greater number of replications with better sampling of possible cladograms.

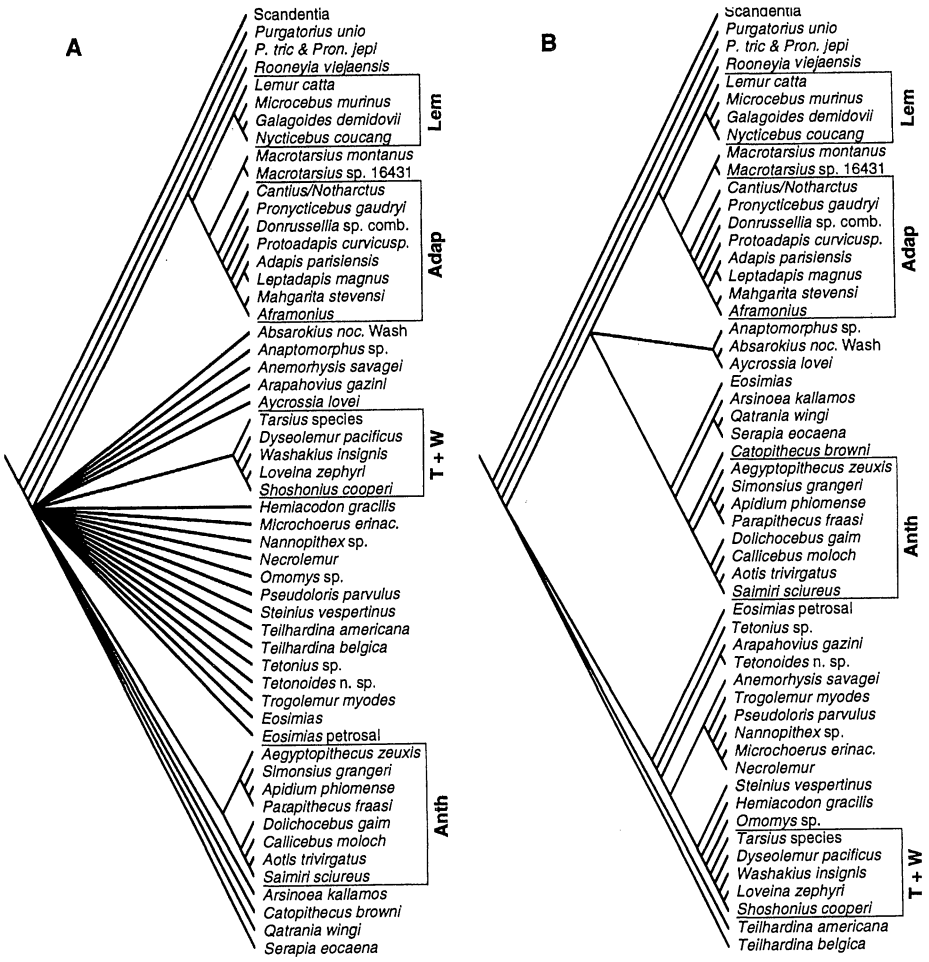

Fig. 1. Strict consensus tree (**A**) and 50% majority rule consensus tree (**B**) of 98 most parsimonious trees of length 97,977 steps, CI = 0.309, and RI = 0.577, obtained after 1000 heuristic search replications. Boxes enclose some traditionally recognized resolved clades. LEM, Lemuriformes; ADAP, Adapiformes; T + W, *Tarsius* + washakiin omomyids; ANTH, Anthropoidea. Strict consensus (A) is dominated by a large polytomy with some resolved clades embedded within it. Fifty percent majority rule tree (B) has a trichotomy with anthropoids (including *Eosimias*, *Arsinoea*, *Catopithecus*, *Qatrania*, and *Serapia*), lemuriformes + adapiformes, and an omomyid clade (*Anaptomorphus*, *Absarokius*, and *Aycrossia*), but all remaining omomyids (except *Teilhardina*) are in a separate clade that includes *Tarsius* as the sister taxon to washakiins. In neither tree is *Tarsius* the sister taxon to anthropoids.

Five conclusions offered by Kay *et al.* form the basis of their scenario of anthropoid origins. Our analysis of the data posted at the time of publication (Fig. 1) found little support for these points: (i) Haplorhine-Strepsirhine dichotomy. The monophyly of Haplorhini was not supported, questioning the usefulness of recognizing this dichotomy. (ii) Adapiformes-Lemuriformes relationships. We found adapiformes to be the sister group of extant lemuriformes, but this clade includes *Macrotarsius* and *Rooneyia*, both traditionally considered omomyids. (iii) Omomyid relationships. No omomyids formed a sister group relationship with anthropoids, and interrelationships among omomyids were essentially unresolved. (iv) Eosimiidae-Anthropoidea relationships. Our strict consensus tree (Fig. 1A) indicated that *Eosimias* and the tentatively assigned "*Eosimias* petrosal" do not share a sister group relationship with anthropoids, but a 50% majority rule consensus of the same results (Fig. 1B) provided limited support for the dentition and jaw (but not the petrosal being anthropoid). (v) *Tarsius* relationships. *Tarsius* is nested within omomyids and is the sister taxon to washakiin omomyids. It did not appear to be the sister taxon of anthropoids in either our strict consensus or our 50% majority rule consensus.

Kay *et al.* changed the Web site data (as is noted on the Web site) since our first analysis. While the ingroup now contains only the taxa cited in their article, the taxa in the outgroup are still different. The number of characters used in the analysis is still 281 (rather than the 256 stated in the article by Kay *et al.*), and at least one coding of morphology has been changed. We now find 21 equally most parsimonious cladograms of length 94,906 steps, and the five conclusions stated by Kay *et al.* appear to have more support. However, a strict consensus of our most parsimonious cladograms is still inconsistent with the phylogeny they described, and neither the data posted at the time of publication nor the data currently posted seem to be identical to those

they describe in their article.

Discovery of more parsimonious interpretations of the data presented originally by Kay *et al.* reopens the issue of primate relationships that Kay *et al.* describe as resolved. Maddison (5) and Templeton (6), analyzing the "Eve Hypothesis," found phylogenetic problems on this scale to require intensive application of computing resources, and a heuristic analysis with 30 replications is not enough. Archiving original data and reporting results in an unambiguous fashion should be the norm for publication in phylogenetics as for other disciplines, especially when they address issues of widely recognized importance.

Jonathan I. Bloch
Daniel C. Fisher
Philip D. Gingerich
Gregg F. Gunnell
Museum of Paleontology and
Department of Geological Sciences,
University of Michigan,
Ann Arbor, MI 48109–1079, USA
Elwyn L. Simons
Department of Biological Anthropology and Anatomy,
Duke University,
Durham, NC 27705, USA
Mark D. Uhen
Cranbrook Institute of Science,
Bloomfield Hills, MI 48303–0801, USA

REFERENCES AND NOTES

1. R. F. Kay, C. Ross, B. A. Williams, *Science* **275**, 797 (1997).
2. Kay *et al.* state [in figure 3 of (*1*) on page 799] that their data are "available at" www.sciencemag.org/feature/data/kay.shl. When we checked this site, it had no data, but instead referred the reader to the personal home page of co-author Callum Ross, at www.informatics.sunysb.edu/anatomy/cross.html. Our first analysis was based on data downloaded from this site on 24 March 1997. These data have been changed subsequently, as stated in a brief note on the C. Ross Web site, at www.informatics.sunysb.edu/anatomicalsci/aboutmx.
3. D. C. Fisher, in *MacClade, Analysis of Phylogeny and Character Evolution*, W. P. Maddison and D. R. Maddison, Eds. (Sinauer, Sunderland, MA, 1992), pp. 124–129; D. C. Fisher, in *Interpreting the Hierarchy of Nature*, L. Grande and O. Rieppel, Eds. (Academic Press, San Diego, CA, 1994), pp. 133–171.
4. D. L. Swofford, *PAUP: Phylogenetic Analysis Using Parsimony*, Version 3.1 (Illinois Natural History Survey, Champaign, IL, 1993). Our tree lengths treat multistate codings as uncertainty.
5. D. R. Maddison, *Syst. Biol.* **40**, 355 (1991).
6. A. R. Templeton, *Science* **255**, 737 (1992).
7. We thank F. Ankel-Simons, W. C. Clyde, D. L. Fox, E. A. Kowalski, and J. A. Trapani for comments and discussion. B. Miljour aided in production of the figure.

28 April 1997; revised 6 October 1997; accepted 25 November 1997

Table 1. Summary of our supplemental phylogenetic analyses. Clade relationships are described in the text and in Figs. 1 and 2. An X indicates that majority-rule consensus supports the proposed clade. Ad, Adapidae; An, Anthropoidea; E, *Eosimias*; H, Haplorhini; O, Omomyidae; S, Strepsirrhini; T, *Tarsius*.

Data set	Number of trees found	Clade relationships				
		(i) H/S	(ii) Ad/S	(iii) O/H	(iv) E/An	(v) T/E/An
1. Table 3 of (*1*)	21	X	X*	X†	X‡	X
2. Web site	1	X	X	X†	--§	X
3. Combined	17	X	X*	X†	X‡	X

**Donrussellia* sister to all Haplorhines. †*Rooneyia* is near base of strepsirrhines. ‡The taxon "*Eosimias* petrosal" falls within Omomyidae. §The position of *Eosimias* is unresolved with respect to the T/An clade: the taxon "*Eosimias* petrosal" is sister to (T/An), whereas the taxon "*Eosimias*" is sister to *Tarsius*.

Response: Our group's cladistic analysis of dental and osteological characters supported the fundamental Haplorhine/Strepsirrhine dichotomy in primate evolution extending back to the early Eocene [figure 1 in (*1*)]. Bloch *et al.* state that our data do not support these results and that we ran an insufficient number of replicates of our analysis. We have performed supplemental phylogenetic analyses, and these support our original conclusions. We are unable to reproduce the results given by Bloch *et al.* either with the data that we originally presented on the World Wide Web or with any other data set.

In our supplemental phylogenetic analyses, we used three data sets (Table 1):

1) Data from table 3 of our article (*1*). Our original analysis [summarized in figure 3 and table 3 of (*1*)] was based on 50 ingroup taxa and three outgroup taxa. We selected the ingroup taxa because they sampled the full phenetic range of the fossil taxa, are relatively complete, and have historic importance in the debates about anthropoid origins. *Eosimias* was represented as two taxa in all analyses; the data on a petrosal bone of uncertain assignment were run separately.

2) Web site data. Bloch *et al.* initially analyzed a data set that we placed on the Web (www.informatics.sunysb.edu/anatomy/cross.html) that inadvertently excluded two of the taxa listed in our report (*Strigorhysis* and *Uintanius*) and included two added taxa not included in the report (a second species of *Macrotarsius* and the early anthropoid *Qatrania*). An equivalent dataset is now archived at www.sciencemag.org/feature/data/46622.shl.

3) Combined data. Data from table 3 in (*1*) with two taxa added (*Macrotarsius* sp. and *Qatrania*).

Bloch *et al.* state that there is a discrepancy in the number of characters in our posted data sets (281), as compared with the number of characters we mentioned in the article (256). This discrepancy is apparent, not real: The posted character list included (and still includes) a number of characters that are invariant in the taxa examined here, but crop up in other taxa analyzed by us in a more exhaustive analysis now in preparation (*2*). Of the 281 characters posted, 256 are "informative" ones [see, for example (*3*), p. 199]. Further, G. F. Gunnell (one of the co-authors of Bloch *et al.*) kindly pointed out to us that the matrix entry for the number of incisors in *Eosimias* was incorrect; this has been rectified in the current analyses.

As in our article (*1*), all analyses used the phylogenetic analysis program PAUP (*4*) with a "proportionate" weighting scheme for multistate characters. This allows us to discern a variety of states for some characters without "penalizing" dual state characters. So as to ensure primate monophyly, 50 two-state "dummy" characters were added, each of which scores the

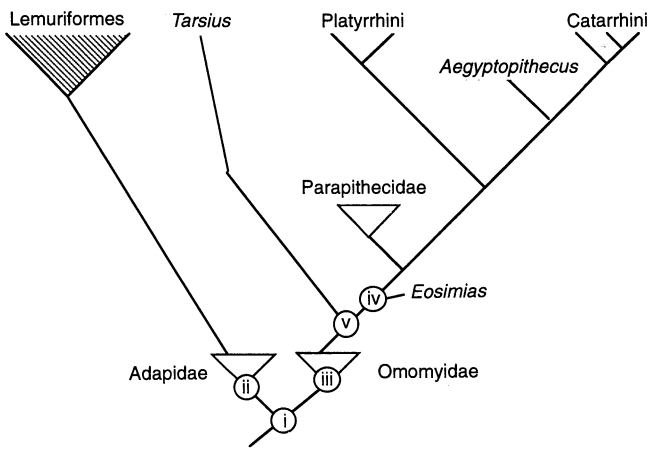

Fig. 1. Summary results of phylogenetic analyses; details in Table 1 and Figs. 1 and 2. Numbers at nodes refer to the list in the text.

outgroups as primitive and the primate taxa as derived. All analyses were undertaken with the use of the "heuristic" search mode, selecting "add-sequence" and "subtree pruning, regrafting" options of PAUP, with 1000 repetitions. Exhaustive searches were not feasible, given the large numbers of characters and taxa. Comparisons between our most parsimonious "Web" tree and the majority consensus found by Bloch *et al.* were undertaken with the use of the MacClade program (*3*).

All of the supplemental analyses (with salient features summarized in Table 1 and Figs. 1 and 2) produce results in agreement with the five main conclusions stated in our article (*1*) and contrary to the trees found by Bloch *et al.* (their figure 1B). All of our trees show that (i) a primary dichotomy exists among living taxa dividing living Haplorhini (*Tarsius*+Anthropoidea) from Strepsirrhini (Lemuriformes); (ii) Adapidae are assignable to the strepsirrhine side of the dichotomy; (iii) Omomyidae are assignable to the haplorhine side of the dichotomy; (iv) Eosimiidae are sister to late Eocene-to-Recent Anthropoidea; and (v) *Tarsius* is either the sister group to (*Eosimias*, Anthropoidea) or nested within omomyids, depending on allocation of a petrosal bone to *Eosimias*.

Bloch *et al.* describe finding 21 trees with the use of data from table 3 in (*1*), presumably the same 21 that we found (*1*), although they have declined our offer to exchange original trees to confirm this point. They state that a "strict consensus" of these 21 trees is "inconsistent" with our conclusions. However, the strict consensus of these 21 trees does support our conclusions (Fig. 2).

We find a single most parsimonious tree with the use of the original Web site data with 1000 repetitions, and the tree supports our original finding. Our tree is about 2% shorter than the majority consensus of 98 trees illustrated by Bloch *et al.*, although without examining the individual trees one cannot calculate precisely how much shorter.

The results of some (not all) of the reanalyses depart from those in figure 3 in our article in that *Rooneyia*, placed by us (with a query) as a haplorhine falling outside of Omomyidae now falls as a basal member of Strepsirrhines. In the original analysis, we depicted the clade [(*Eosimias*, Anthropoidea) *Tarsius*], as always arising out of the Omomyidae and specifically allied with washakiine omomyids. The revised analysis always depicts this clade as arising out of Omomyidae, and sometimes, but not always, supports a sister-group relationship with the Washakiinae.

Bloch *et al.* state that their reanalysis of our data challenges the usefulness of recognizing a haplorhine-strepsirrhine dichotomy of living primates. In this regard, we note that our data set does not include any characters of physiology, development, or soft-tissue anatomy because we were trying to place the Eocene-Oligocene fossil primates, for which such data are unavailable, into phylogenetic context. Many other characters not preservable in the fossil record, as summarized by Martin (*5*), also support the halplorhine-strepsirrhine dichotomy, including loss of the ability to synthesize vitamin C, chromosome morphology, the absence of a rhinarium, the reduced development of the nasal turbinals, several aspects of the organization of the visual cortex, several features of the anatomy of the eye, distinctive features of placentation, and early development. Our findings strengthen this fundamental dichotomy and allow it to be extended to fossils.

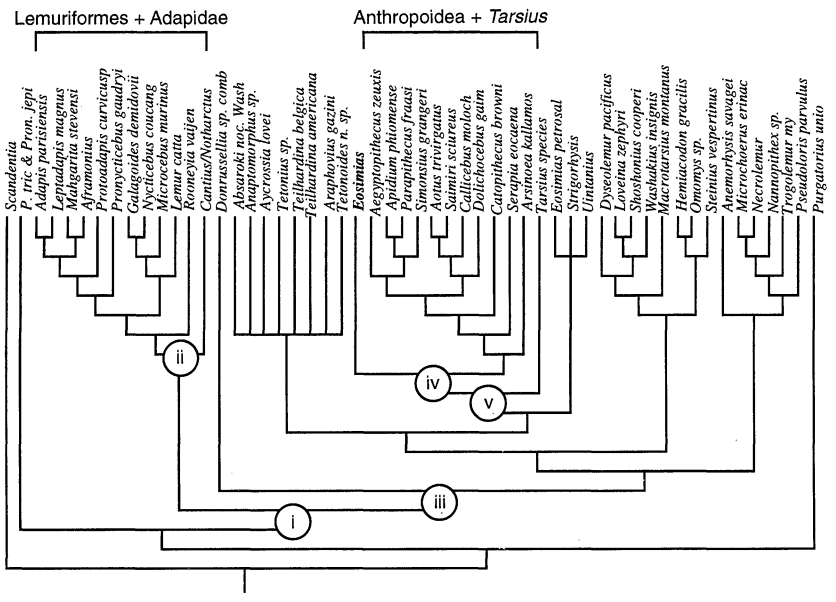

Fig. 2. Strict consensus of 21 trees with the use of taxa in table 3 in (*1*). Numbers at nodes refer to the list in the text.

Richard F. Kay
Department of Biological Anthropology and Anatomy, Duke University, Durham, NC 27710, USA
Callum Ross
Department of Anatomical Sciences, Health Sciences Center, State University of New York, Stony Brook, NY 11794, USA
Blythe A. Williams
Derek Johnson
Department of Biological Anthropology and Anatomy, Duke University

REFERENCES

1. R. F. Kay, C. F. Ross, B. A. Williams, *Science* **275**, 797 (1997).
2. C. Ross, B. A. Williams, R. F. Kay, in preparation.
3. W. P. Maddison and D. R. Maddison, *MacClade Version 3.4 for Macintosh* (Sinauer, Sunderland, MA, 1992).
4. D. L. Swofford, *PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1 and accompanying manual* (Illinois Natural History Survey, Champagne, ed. 3.0, 1993).
5. R. D. Martin, *Primate Origins and Evolution* (Chapman & Hall, London, 1990).

11 June 1997; revised 19 November 1997; accepted 25 November 1997