



## News and Views

*Darwinius masillae* is a Haplorhine — Reply to Williams et al. (2010)Philip D. Gingerich<sup>a,\*</sup>, Jens L. Franzen<sup>b,c</sup>, Jörg Habersetzer<sup>b</sup>, Jørn H. Hurum<sup>d</sup>, B. Holly Smith<sup>e</sup><sup>a</sup> Museum of Paleontology and Department of Geological Sciences, University of Michigan, Ann Arbor, Michigan 48109, USA<sup>b</sup> Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, D-60325 Frankfurt, Germany<sup>c</sup> Naturhistorisches Museum, Augustinergasse 2, CH-4001 Basel, Switzerland<sup>d</sup> Naturhistorisk Museum, Universitetet i Oslo, Postboks 1172, Blindern, N-0318 Oslo, Norway<sup>e</sup> Museum of Anthropology, University of Michigan, Ann Arbor, Michigan 48109, USA

## ARTICLE INFO

## Article history:

Received 11 December 2009

Accepted 21 May 2010

## Keywords:

Primate phylogeny

Anthropoid origins

Eocene primates

Haplorhini

## Introduction

A forty-seven-million-year-old primate *Darwinius masillae* from the middle Eocene of Messel in Germany is worthy of attention because it is one of the most complete fossil primates found to date (Franzen et al., 2009). *Darwinius* is exceptional because it demonstrates association of the skull, vertebral column, rib cage, arm, hand, leg, foot, body outline, and gastrointestinal contents of one individual primate in death position on a single plate of shale. Completeness constrains speculation about bones that have not been found, and association constrains conjecture about bones that belong together. Together these enable us to learn things about Eocene primates that cannot be learned from fragmentary remains.

Most primate fossils are isolated teeth, jaw fragments, or individual bones. Fragmentary fossils are important for documenting the distribution and diversity of primates through time, but most provide limited information relevant for higher-level phylogeny. Consequently, higher-level relationships of primates are based largely on neontological comparisons of living lemurs, lorises, tarsiers, ceboids, cercopithecoids, and hominoids, for which we know soft-tissue anatomy, behavior, and complete skeletons. Crown clades are defined by living taxa, and molecular approaches to phylogeny are necessarily focused on living animals.

Fossils are important for primate phylogeny because the origin of each of the major groups involves an evolutionary transition deep in geological time. Fossils calibrate these transitions and often support established relationships to living animals, but fossils may also change our understanding. *Darwinius* is an example of such change.

Williams et al. (2010: 567) describe *Darwinius* as a “crushed skeleton” and question our interpretation of *Darwinius* as a haplorhine primate (Franzen et al., 2009). Inference in our earlier study was based on the relative likelihood of membership in Strepsirrhini or Haplorhini, considered as alternative hypotheses. Here we apply the cladistic methods advocated by Williams et al. (2010), which, with a proper understanding of ‘total evidence,’ reaffirm our earlier interpretation that *Darwinius* is a haplorhine important for understanding the transition to Anthropoidea.

## Preservation at Messel

Messel is a UNESCO World Heritage Site famous for extraordinary preservation of a diverse flora of fossil plants and a diverse fauna of insects, fish, reptiles, birds, and mammals (Schaal and Ziegler, 1992; Koenigswald et al., 1998; Franzen, 2007; Gruber and Micklich, 2007). All, like *Darwinius*, are more or less flat as preserved. Seiffert et al. (2009), Williams et al. (2010), and others infer from *Darwinius*’ flatness that the skeleton must be crushed. Thus it is important to consider how Messel fossils are preserved.

Messel fossils represent Eocene organisms that died and settled to the bottom of an anoxic volcanic lake. All are preserved on bedding planes in oil shale. Fossil mammals at Messel appear to be two-dimensional because they are often whole skeletons, which collapse in thickness when tissues connecting the bones decompose. Bulbous braincases are normally compressed, as are the diaphyses of long bones, especially when they overlie each other. Compact bones of most skeletons retain their three-dimensional shape.

The two-dimensional nature of Messel fossils is exaggerated when they are collected because the fossils are found by separating oil shale along bedding planes. Presence of a fossil makes a bedding plane weaker, and thus separation often preferentially splits a fossil. This divides the fossil, leaving part and counterpart on separate slabs of oil shale, each containing a half-skeleton. In the

\* Corresponding author.

E-mail address: [gingeric@umich.edu](mailto:gingeric@umich.edu) (P.D. Gingerich).

process, individual bones are also split into part and counterpart on the two slabs. Specimens are then preserved by pouring a layer of epoxy resin over the split surface of each slab (polyester resin, used in former times, was banned in 1992). When cured, the resulting plates are turned and the remaining oil shale is removed from each. As a result, one plate preserves the top lateral surface of a skeleton, and a second plate preserves the bottom lateral surface of the same skeleton. In favorable circumstances an entire specimen is preserved. Skeletons are sometimes incomplete because parts were lost due to predation or scavenging before a carcass settled to the bottom of the Messel lake, and bone is sometimes lost when part and counterpart are split during the collecting process.

Williams et al. (2010) state that the ankle of *Darwinius* is too crushed to be certain of talofibular morphology, but there is no crushing and little deformation of these robust bones visible on the surface (Fig. 1). The fibular facet on the talus is partially covered by the distal end of the fibula, but the talus is sufficiently well exposed to show the slope of the lateral surface. The talus does not appear to be broken, let alone crushed.

Two disadvantages of Messel preservation and of the process of preparation of Messel fossils are that bones of a skeleton cannot be removed and handled individually, and the joint surfaces of bones often remain obscured by articulation. However, computerized tomography (CT) now makes it possible, in favorable circumstances, to remove virtual copies of individual bones to expose their joint surfaces. There is a cost, because CT scanning is expensive and interpretation of images is both labor intensive and time-consuming, which explains why our study of *Darwinius* is ongoing. Initial studies of *Darwinius* were focused on the skull and dentition (Franzen, 2000; Franzen et al., 2009) and on the digestive tract (Franzen and Wilde, 2003). Detailed CT studies of the hands and feet of *Darwinius* and contemporary Messel primates are in progress.

### Cladistic analysis

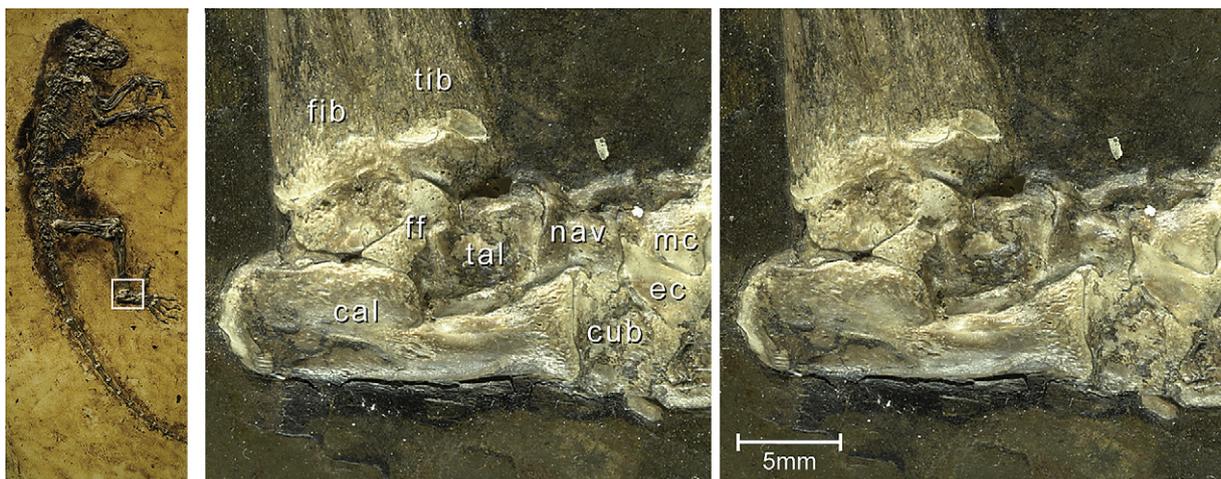
The strepsirrhine-haplorhine dichotomy can be considered from a phylogenetic point of view, and the characteristics distinguishing strepsirrhines and haplorhines can be coded for cladistic analysis. In our earlier study (Franzen et al., 2009), we considered the relationship of *Darwinius* to Strepsirrhini and Haplorhini by compiling

a list of 30 characteristics cited by authors as distinguishing these groups. Most came from the classic monographs on Strepsirrhini and Haplorhini by Hill (1953, 1955) and from the widely-used current primate textbook by Fleagle (1999). The purpose of this compilation was a statistical consideration of relative likelihood at a high taxonomic level. Thus it was important that the characteristics tabulated be (1) representative of the range of characteristics distinguishing high-level taxa, and (2) developmentally, functionally, and evolutionarily as independent of each other as possible. Strepsirrhini and Haplorhini were originally recognized by characteristics of soft anatomy that cannot be studied in fossils (Geoffroy Saint-Hilaire, 1812; Hubrecht, 1897; Pocock, 1918), but ancillary characteristics like a toothcomb in Strepsirrhini or spatulate incisors in Haplorhini can be recognized in fossils.

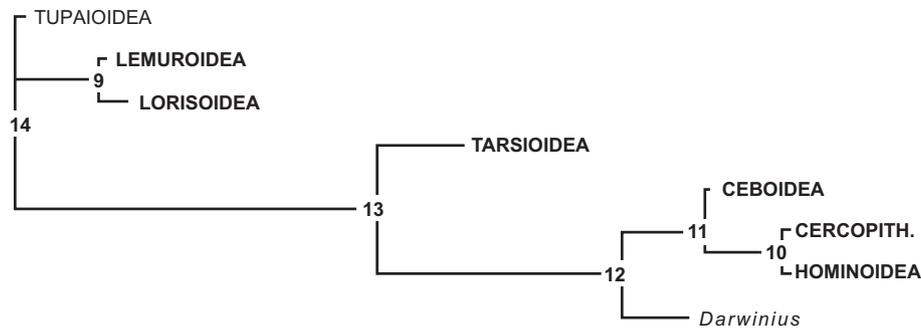
We coded Table 3 of Franzen et al. (2009) as follows: strepsirrhine characteristics were arbitrarily coded '0,' and haplorhine characteristics were coded '1' or sometimes '1' and '2' for two-step characters. We added tree shrews or Tupaioidea, represented by *Tupaia*, as an outgroup. Phylogenetic analysis using parsimony (PAUP; Swofford, 2001) yielded two equally most-parsimonious cladograms of 37 steps. These have a high consistency index (0.84) and high retention index (0.90). The two trees differ only in the monophyly or paraphyly of Strepsirrhini, and the cladogram with Strepsirrhini monophyletic is shown in Figure 2, scaled as a phylogram to represent relative change (character coding and a full log of the analysis are provided in the Supplementary Online Material [SOM] that appears with the online version of this paper).

Strepsirrhini, comprising Lemuroidea and Lorisioidea, is monophyletic at node 9 in Figure 2, and Haplorhini, comprising Tarsioidea, Ceboidea, Cercopithecoidea, and Hominoidea, is monophyletic at node 13 in Figure 2. Most characteristics distinguishing Strepsirrhini and Haplorhini are on the long stem connecting nodes 14 and 13, but many are also on the long stem connecting nodes 13 and 12. Tarsioidea branches at node 13, reflecting its intermediate status in the spectrum of anatomical and morphological changes separating Strepsirrhini and Haplorhini.

Changes in some characteristics such as postorbital closure are ambiguous, with partial closure interpreted as evolving between nodes 14 and 13, before being lost on the branch from node 12 to *Darwinius*. Full closure evolved between nodes 12 and 11. It seems more likely that partial closure evolved independently in *Tarsius*



**Figure 1.** *Darwinius masillae* skeleton, holotype plate A (Paleontological Museum of the University of Oslo no. PMO 214.214), in right lateral view. Inset rectangle (left) shows the location of the stereophotographs of the lateral surface of the right ankle (center and right). The steep part of the fibular facet on the talus (astragalus) is partially covered by the distal fibula, which is compressed onto the distal tibia and talus. However, the talus is neither crushed nor deformed. The talofibular facet is vertical except for the plantar part of the surface where it flares abruptly laterally, resulting in a rather large, pointed plantar process. Note the transversely-broad uncompressed mesocuneiform. Abbreviations: cal, calcaneum; cub, cuboid; ec, ectocuneiform; ff, fibular facet of the talus; fib, distal fibula; mc, mesocuneiform; nav, navicular; tal, talus; and tib, distal tibia.



**Figure 2.** Phylogram showing the position of *Darwinius* relative to major groups of primates, based on data of Franzen et al. (2009). This represents one of two most-parsimonious cladograms in an exhaustive search of 10,395 trees (second cladogram differs only in showing Strepsirrhini as paraphyletic). *Darwinius* falls within crown-group Haplorhini (Tarsiioidea, Ceboidea, Cercopithecoidea, and Hominoidea; node 13) as a stem anthropoid, and it does not group with Strepsirrhini (Lemuroidea and Lorisioidea; node 9). Analysis is based on 30 total-evidence characteristics distinguishing Strepsirrhini and Haplorhini (data from Table 3 of Franzen et al., 2009), with Tupaioidea added as an outgroup. Tree length is 37 steps, consistency index is 0.84, and retention index is 0.90 (see SOM). As expected for characters chosen to distinguish Strepsirrhini and Haplorhini, most change is on the long stem connecting nodes 14 and 13. However, there is also substantial change on the long stem connecting nodes 13 and 12.

(between node 13 and Tarsiioidea) and in Anthropoidea (between nodes 12 and 11; Rosenberger et al., 2008).

The cladogram in Figure 2 places *Darwinius* in Haplorhini and not in Strepsirrhini. Cladistically it is a stem anthropoid because its branch joins the line leading to crown Anthropoidea (Ceboidea, Cercopithecoidea, and Hominoidea) and not the line leading to crown Tarsiioidea. We refrained from calling *Darwinius* an anthropoid in our earlier study (Franzen et al., 2009) because it does not have the morphological features characteristic of Anthropoidea, but *Darwinius* is clearly a stem anthropoid as this designation is used in the literature today.

### Total evidence

Williams et al. (2010) imply that ‘total evidence’ means study of hundreds of characters in a great many taxa. However, total evidence is about combining data before analysis and not about the size of the resulting matrix. Total evidence was introduced in phylogenetic systematics by Kluge (1989) as an alternative to consilience. Kluge reasoned that a single most-parsimonious phylogenetic hypothesis based on all evidence considered together (‘total evidence’) is better than the consilience or taxonomic congruence of multiple phylogenetic hypotheses based on different subsets or partitions of evidence. According to Kluge (1989), the advantages of combining data of different kinds (e.g., morphological and molecular; fossil and living; dental, cranial, and postcranial) are: (1) observations from a spectrum of character systems are more *representative* of all of the available evidence; and (2) observations from a spectrum of character systems are more likely to be *independent* than are observations drawn from the same character system.

Comparisons of phylogenetic trees and comparisons of branch lengths and character distributions in a phylogeny are statistical, and both depend on a balanced representation of taxa and characters. When we play a game of chance with a deck of cards, all players expect that the game will be played with a fair deck, four partitions will be represented (clubs, diamonds, hearts, and spades), and the 13 cards within each partition will be independent (represented once). When we evaluate phylogenetic hypotheses with parsimony we expect that the taxa studied will span the taxa of interest for the scale of our study, and we expect that the characters representing the taxa will be independent. The characteristics we tabulated comparing *Darwinius* to major groups of primates (Franzen et al., 2009: Table 3) were compiled to be representative and independent for a different statistical purpose, but they are also, in Kluge’s sense, ‘total evidence’ for a phylogenetic analysis.

### Many-taxa versus few-taxa matrices

We agree with Seiffert et al. (2009), Williams et al. (2010), and others that there is a strepsirrhine–haplorhine dichotomy in primate evolution. We employ the same cladistic methods. We accept that total evidence drawn from many sources is advantageous. Why then do we reach such a different conclusion about the systematic position of *Darwinius*?

Given that our methods are the same, then our contrasting results can only be explained by differences in the number and balance of taxa chosen for study, the character matrix used to analyze higher-level primate phylogeny, the outgroup chosen to root a phylogenetic network, or some combination of these.

Kay et al. (2004) scored 144 characters for 63 taxa; Bajpai et al. (2008) scored 343 characters for 75 taxa; Seiffert et al. (2009) scored 360 characters for 117 taxa; and we scored 30 characters for 8 taxa. Is a bigger matrix a better matrix? What are the costs and benefits of many-taxa representation? Does adding characters compromise independence? Does adding taxa compromise computation?

Kay et al. (2004) used *Tupaia*, *Ptilocercus*, *Ignaciuss*, *Purgatorius*, *Plesiolestes*, *Plesiadapis*, and *Pronothodectes* as outgroups, and “analyses were constrained to fit this concept of primate monophyly” (Kay et al., 2004: 98). Bajpai et al. (2008) stated that outgroups were not used in their analysis, but Plesiadapiforms were accepted as the sister taxon to Primates (Bajpai et al., 2008: supporting appendix). Seiffert et al. (2009) rooted trees with *Tupaia* spp. We use *Tupaia* as an outgroup for rooting primate trees, so differences in outgroups are not likely to explain contrasting results.

Williams et al. (2010: 567) write “Had Franzen et al. (2009) added the anatomical information on *Darwinius* to published data matrices of extinct and fossil primates they would have found, as Seiffert et al. (2009) did, that *Darwinius* and other adapiforms fall within the strepsirrhine radiation.” Seiffert et al. (2009) already did the experiment that Williams et al. propose, putting *Darwinius* in a many-taxa matrix. So here we have tried the opposite, analyzing *Darwinius* in a few-taxa matrix. We used Seiffert et al.’s characters and scorings for *Darwinius* and other primates but removed all fossils except *Darwinius*.

Surprisingly, in light of Seiffert et al.’s (2009) determination that *Darwinius* is a strepsirrhine, in our experiment *Darwinius* joined Ceboidea as a stem anthropoid (even though anthropoids are poorly represented in the Seiffert et al. [2009] matrix). Details are provided in Figure 3 (and in the SOM). This result indicates that what matters is not the number of characters, the choice and independence of

characters, the outgroup, or who did the scoring. The critical factor seems to be the number of taxa and the representation of characters (or missing data) in the taxa studied.

We have not tried to do a similar test with the Kay et al. (2004) or Bajpai et al. (2008) data, because, in spite of their confidence that *Darwinius* is a strepsirrhine, Williams et al. (2010) have not analyzed *Darwinius* or provided a scoring of its morphology.

We can, however, make one additional comparison. Bajpai et al. (2008) named and analyzed *Anthrasimias gujaratensis*, and concluded that it is a stem anthropoid. Rose et al. (2009), studying the same teeth, synonymized *A. gujaratensis* with another primate, *Marcgodinotius indicus*, which Bajpai et al. (2008) regarded as adapoid. What differences in the Bajpai et al. scoring of *Anthrasimias* and *Marcgodinotius*, arguably synonyms, led them to classify one as a stem anthropoid and the other an adapoid? The characters that show differences are listed in Table 1. All pertain to the morphology of the single lower molar, M<sub>3</sub>, known for *Anthrasimias*. Bajpai et al. recorded five differences from *Marcgodinotius*: a broader trigonid, lack of wear facet 'x,' a larger hypoconulid cusp, a cristid obliqua crest terminating lower on the trigonid, and a stronger hypocristid. Four are differences of degree, and one is related to occlusal tooth wear.

Are the characteristics listed in Table 1 really differences by which haplorhine primates differ from strepsirrhines? Rose et al. (2009: 377) wrote: “the variability of M<sub>3</sub> in our small sample [of *Marcgodinotius*] makes it quite possible that this tooth [M<sub>3</sub> of *Anthrasimias*] is merely a variant of *M. indicus*,” implying that the differences may not distinguish species let alone suborders. The differences in these teeth are trivial compared to the differences observed in a wide range of morphological features across primates.

How can identical methods applied to the many-taxa–many-characters matrix of Seiffert et al. (2009) and to our representative few-taxa–many-characters sample of the same matrix yield opposite results? And, how can straightforward methods yield counter-intuitive results like separation of virtually indistinguishable molars into Strepsirrhini and Haplorhini in the Bajpai et al. (2008) study?

The causes of these capricious results, seemingly linked to character matrices with many taxa, are difficult to understand. It is well known that the number of possible phylogenetic trees for 63, 75, or 117 taxa is literally astronomical, meaning most trees for many-taxa matrices will never be found. Perhaps the many-taxa problem arises in the taxon and character sampling of heuristic search algorithms?

Maybe the many-taxa problem is related to over-representation of particular characteristics in a data matrix? We note that the ‘cristid obliqua’ and cristid obliqua-defined ‘hypoflexid’ are scored 11 times in the Bajpai et al. (2008) matrix, and the cristid obliqua is

**Table 1**

Character-state differences causing *Anthrasimias gujaratensis* ('Anth.') to be interpreted as a stem anthropoid, and probable synonym *Marcgodinotius indicus* ('Marc.') to be interpreted as an adapoid, following Bajpai et al. (2008)

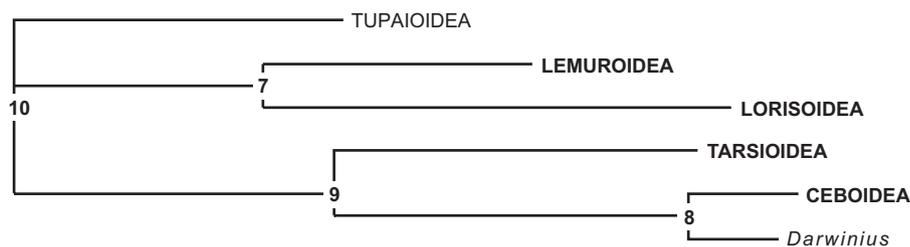
No.	Characters and scored states <sup>a</sup>
70	m7*. M <sub>3</sub> trigonid width (based on relative buccolingual breadths) Anth.: 1 = trigonid and talonid widths similar ( $\leq 1.20-1.05$ ) Marc.: 2 = trigonid narrower than talonid ( $< 1.05$ )
89	m24. M <sub>1-3</sub> wear facet X Anth.: 0 = present Marc.: 1 = absent.
94	m29*. M <sub>3</sub> hypoconulid size Anth.: 0 = large Marc.: 2 = small
101	m36. M <sub>3</sub> cristid obliqua terminus Anth.: 0 = runs to base of trigonid Marc.: 1 = runs part way up the distal trigonid wall
104	m39*. M <sub>3</sub> hypocristid development Anth.: 2 = strong Marc.: 0 = absent or seen only as a trace

<sup>a</sup> Bajpai et al. (2008) character data are available at: <http://www.pnas.org/content/suppl/2008/08/06/0804159105.DCSupplemental>.

scored nine times in the Seiffert et al. (2009) matrix, all on serially homologous mandibular teeth. Eleven and nine are a small proportion of a total matrix of 347 and 360 characters, but eleven and nine are a substantial proportion of characteristics Bajpai et al. (2008) and Seiffert et al. (2009) actually scored for fossils represented principally by teeth.

Maybe the many-taxa problem is related to missing data? Some 11,949 of 25,725 cells (46%) in the Bajpai et al. (2008) matrix are empty, and 22,260 of 42,120 cells (53%) in the Seiffert et al. (2009) matrix are empty. Maybe over-representation of some characters interacts with underrepresentation of others as missing data, with unknown statistical effects?

Or finally, maybe there isn't a problem? Seiffert et al. (2009: 1120 and p. 4 of supplementary information) computed a most-parsimonious tree 'A' with a reported tree length of 2265.671 steps. Seiffert et al. (2009) computed an alternative tree 'B,' with a backbone constraint forcing *Darwinius* (and *Afradapis*) into a stem anthropoid position consistent with our interpretation. This has a tree length of 2268.936 steps. Seiffert et al. (2009) computed a third tree 'C' with a backbone constraint forcing *Darwinius* and relatives into a stem anthropoid position and forcing *Darwinius* to be closer to crown anthropoids than are Eosimiidae or Amphipithecidae. This has a tree length of 2276.247 steps. These differences of 3.265 steps (0.14%) and 10.576 steps (0.46%) distinguishing hypotheses seem negligible. Why postulate that six anthropoid-like features of *Afradapis* are convergent, as Seiffert et al. (2009) proposed, to save three steps in a tree of 2266 steps? It is questionable that there is any signal in these data.



**Figure 3.** Phylogram showing the position of *Darwinius* relative to major groups of primates, based on data of Seiffert et al. (2009). This represents the single most-parsimonious cladogram in an exhaustive search of 105 trees. As in our analysis in Figure 2, *Darwinius* falls within crown-group Haplorhini (Tarsioidae, Ceboidea; node 9) as a stem anthropoid, and it does not group with Strepsirrhini (Lemuroidea and Lorisoidae; node 7). Analysis is based on 360 characteristics representing Tupaioidea (*Tupaia* spp.), Lemuroidea (*Lemur catta*), Lorisoidae (*Loris tardigradus*), Tarsioidae (*Tarsius bancanus*), Ceboidea (*Saimiri sciureus*), and *Darwinius masillae*, as scored by Seiffert et al. (2009: supplemental material). Cercopithecoidea and Hominoidea are not represented in the Seiffert study. Tree length is 580 steps, consistency index is 0.85, and retention index is 0.40 (see SOM). Most character change is on long stems of terminal taxa.

In fact, the Templeton-test probabilities that Seiffert et al. (2009: p. 4 of supplementary information) reported ( $p = 0.66$  for tree A compared to tree B; and  $p = 0.35$  for tree A compared to tree C) show that their favored tree is not significantly different from either of their alternative trees. Significance is normally reserved for probabilities less than 0.05 (Templeton, 1983; Lee, 2000), and 0.66 and 0.35 are each much greater than 0.05. The hypothesis that *Darwinius* is a strepsirrhine cannot be distinguished, in this instance, from our hypothesis that it is a haplorhine.

In the end, parsimony (yes *parsimony*) favors simple comprehensible results like those in Figures 2 and 3, which are based on exhaustive comparison of all possible phylogenetic trees. The results in Figures 2 and 3 involve a manageable number of taxa, more complete specimens, and fewer missing data.

### Polarity of characteristics

Our initial interpretation that *Darwinius* is a haplorhine primate was based on relative likelihood, determined by counting the derived characteristics that *Darwinius* shares with Strepsirrhini and Haplorhini, as listed in Table 3 of Franzen et al. (2009). Polarity of course depends on phylogenetic context, and what is primitive in one context can be derived in another. Here we reconsider each of the six characteristics of *Darwinius* that we initially interpreted as being both shared with Haplorhini and derived.

#### Cranium with short rostrum (character 8)

Rostrum length changes from longer to shorter between nodes 14 and 13 in the phylogram of Figure 2. Thus the relatively short rostrum of *Darwinius* is appropriately counted as a derived characteristic shared with Haplorhini. The short rostrum of *Darwinius* cannot be explained solely as a reflection of subadult age because the number and size of premolar teeth are reduced, and these will not increase with age. Short rostra have evolved in some strepsirrhines and long rostra in some haplorhines, but these are exceptions to the general condition.

#### Mandible with deep ramus (character 9)

Mandibular depth changes from shallower to deeper between nodes 13 and 12 in the phylogram of Figure 2. Thus the relatively deep mandible of *Darwinius* is appropriately counted as a derived characteristic shared with Haplorhini. The contrast of shallow and deep mandibular rami in strepsirrhines and haplorhines, respectively, is again a generalization with exceptions.

#### Mandibular symphysis fused (character 13)

The mandibular symphysis changes from open to fused between nodes 13 and 12 in the phylogram of Figure 2. Thus the partial fusion seen in *Darwinius* is appropriately counted as a derived characteristic shared with Haplorhini. The contrast of open and fused mandibular symphyses in strepsirrhines and haplorhines, respectively, as before, is a generalization with exceptions.

#### Incisors spatulate (character 14)

Incisors change from pointed to spatulate between nodes 13 and 12 in the phylogram of Figure 2. Thus the spatulate incisors of *Darwinius* are appropriately counted as a derived characteristic shared with Haplorhini. The spatulate upper and lower incisors of *Darwinius*, adapoids, and anthropoids are so different from the pointed incisors of other primates (outgroup Tupaioidea, primate Plesiadapoidea and Microsypoidea, Lemuroidea, Lorisioidea,

and Tarsioidea) that, contrary to Williams et al. (2010), we cannot imagine spatulate incisors to be primitive (these are conceivably convergent, but not primitive).

#### Fibular facet on talus steep (character 21)

The fibular facet on the talus (astragalus) changes from steep to sloping between nodes 14 and 9 in the phylogram of Figure 2. Thus the steep fibular facet of *Darwinius* is primitive and we should not have counted it as a derived characteristic shared with Haplorhini (see below). Gebo et al. (2000: 278) considered a steep talofibular facet to be a synapomorphy of Haplorhini, but we now agree with Williams et al. (2010) that this is probably a primitive character of primates.

#### Claws or grooming claws absent (character 25)

Claws or grooming claws on the pes change from present to absent between nodes 13 and 12 in the phylogram of Figure 2. Thus the loss of grooming claws and acquisition of nails on all digits in *Darwinius* is appropriately counted as a derived characteristic shared with Haplorhini. The presence of nails on all pedal digits in all anthropoid families except Callitrichidae contrasts with retention of claws or grooming claws in other primates (outgroup Tupaioidea, primate Plesiadapoidea, Lemuroidea, Lorisioidea, and Tarsioidea). Thus, contrary to Williams et al. (2010), we cannot imagine nails on all digits to be primitive for primates (these are again conceivably convergent, but not primitive).

In addition, two characteristics that we previously scored as indeterminate (Franzen et al., 2009) are better interpreted as derived.

#### Lower molars quadrate (character 19)

Lower molars change from tritubercular to quadrate between nodes 14 and 9 and between nodes 13 and 12 in the phylogram of Figure 2. Thus quadrate lower molars are appropriately counted as a derived characteristic of *Darwinius* shared with Haplorhini.

#### Mesocuneiform uncompressed (character 23)

The mesocuneiform in the foot changes from laterally compressed to uncompressed and broad between nodes 14 and 13 in the phylogram of Figure 2. The laterally expanded mesocuneiform of *Darwinius* is illustrated here in Figure 1. Thus an uncompressed mesocuneiform is appropriately counted as a derived characteristic of *Darwinius* shared with Haplorhini.

As a consequence of these changes, one feature of *Darwinius* that we previously interpreted as a derived characteristic shared with Haplorhini (steep fibular facet on astragalus) is here regarded as a primitive. However, two features of *Darwinius* that we previously interpreted as primitive or indeterminate (lower molars quadrate, and mesocuneiform uncompressed) are now regarded as derived characteristics of Haplorhini. The net result is that derived characteristics of *Darwinius* shared with Haplorhini now outnumber those shared with Strepsirrhini by 7–0, rather than 6–0 as reported by Franzen et al. (2009).

### Discussion

Williams et al. (2010) cite no derived characteristics present in *Darwinius* that are shared with Strepsirrhini, and we cannot find any either. Williams et al. (2010: 567) claim to have found “detailed

evidence that adapiforms are stem strepsirrhines,” but do not substantiate this. We listed six derived characteristics of *Darwinius* shared with Haplorhini in our earlier study (Franzen et al., 2009), which we here revise to seven. Seven is not a large number, but seven is more than zero, and seven is infinitely larger than zero as a proportion.

In conclusion, evidence presented by Franzen et al. (2009) and cladistic analyses here place *D. masillae* in Haplorhini. A central role for Adapoidea in higher primate evolution may be controversial now, but we anticipate that Adapoidea will receive more balanced consideration in the future.

### Acknowledgments

We thank Blythe Williams and co-authors for initiating this exchange, and editor Susan Antón for allowing us to respond. Comments by Williams and co-authors, by Mary Silcox, and by the anonymous reviewers helped focus our response. We thank Alan Templeton for the non-parametric statistical test comparing trees, and Eric Seiffert and co-authors for applying it. Jeffrey A. Wilson read and improved a near-final draft. Wighart von Koenigswald provided critical commentary at all stages. Finally, we thank Per Aas of the Natural History Museum, University of Oslo, for the stereo-photograph in Fig. 1.

### Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jhevol.2010.07.013.

### References

- Bajpai, S., Kay, R.F., Williams, B.A., Das, D.P., Kapur, V.V., Tiwari, B.N., 2008. The oldest Asian record of Anthropoidea. *Proc. Natl. Acad. Sci.* 105, 11093–11098.
- Fleagle, J.G., 1999. *Primate Adaptation and Evolution*, second ed. Academic Press, San Diego.
- Franzen, J.L., 2000. Der sechste Messel-Primate (Mammalia, Primates, Notharctidae, Cercamoniinae). *Senckenberg. Lethaea, Frankfurt* 80, 289–303.
- Franzen, J.L., 2007. Eozäne Equoidea (Mammalia, Perissodactyla) aus der Grube Messel bei Darmstadt (Deutschland): Funde der Jahre 1969–2000. *Schweizer. Paläontol. Abhand.* 127, 1–243.
- Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., Koenigswald, W.v., Smith, B.H., 2009. Complete primate skeleton from the middle Eocene of Messel in Germany: morphology and paleobiology. *PLoS One* 4 (e5723), 1–27.
- Franzen, J.L., Wilde, V., 2003. First gut content of a fossil primate. *J. Hum. Evol.* 44, 373–378.
- Gebo, D.L., Dagosto, M., Beard, K.C., Qi, T., Wang, J., 2000. The oldest known anthropoid postcranial fossils and the early evolution of higher primates. *Nature* 404, 276–278.
- Geoffroy Saint-Hilaire, É., 1812. Suite au tableau des quadrumanes, seconde famille, Lemuriens, Strepsirrhini. *Ann. Mus. Hist. Nat. Paris* 19, 156–170.
- Gruber, G., Micklich, N. (Eds.), 2007. *Messel: Treasures of the Eocene*. Wissenschaftliche Buchgesellschaft, Darmstadt.
- Hill, W.C.O., 1953. *Primates: Comparative Anatomy and Taxonomy. I—Strepsirrhini, a Monograph*. Edinburgh University Press, Edinburgh.
- Hill, W.C.O., 1955. *Primates: Comparative Anatomy and Taxonomy. II—Haplorhini: Tarsiodea, a Monograph*. Edinburgh University Press, Edinburgh.
- Hubrecht, A.A.W., 1897. *The Descent of the Primates: Lectures Delivered on the Occasion of the Sesquicentennial Celebration of Princeton University*. Charles Scribner's Sons, New York.
- Kay, R.F., Williams, B.A., Ross, C.F., Takai, M., Shigehara, N., 2004. Anthropoid origins: a phylogenetic analysis. In: Ross, C.F., Kay, R.F. (Eds.), *Anthropoid Origins: New Visions*. Kluwer Academic/Plenum Publishers, New York, pp. 91–135.
- Kluge, A.G., 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.* 38, 7–25.
- Koenigswald, W.v., Storch, G., Habersetzer, J. (Eds.), 1998. *Messel: Ein Pompeij der Paläontologie*. Jan Thorbecke Verlag, Sigmaringen.
- Lee, M.S.Y., 2000. Tree robustness and clade significance. *Syst. Biol.* 49, 829–836.
- Pocock, R.I., 1918. On the external characters of the lemurs and of *Tarsius*. *Proc. Zool. Soc. London* 3, 19–53.
- Rose, K.D., Rana, R.S., Sahni, A., Kumar, K., Missiaen, P., Singh, L., Smith, T., 2009. Early Eocene primates from Gujarat, India. *J. Hum. Evol.* 56, 366–404.
- Rosenberger, A.L., Hogg, R., Wong, S.M., 2008. *Rooneyia*, postorbital closure, and the beginnings of the age of Anthropoidea. In: Sargis, E.J., Dagosto, M. (Eds.), *Mammalian Evolutionary Morphology: a Tribute to Frederick S. Szalay*. Springer Science, Dordrecht, pp. 325–346.
- Schaal, S., Ziegler, W. (Eds.), 1992. *Messel: An Insight into the History of Life and of the Earth*. Clarendon Press, Oxford.
- Seiffert, E.R., Perry, J.M.G., Simons, E.L., Boyer, D.M., 2009. Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates. *Nature* 461, 1118–1121.
- Swofford, D.L., 2001. *PAUP\*: Phylogenetic Analysis using Parsimony and Other Methods, Version 4.0b10*. Sinauer Associates, Sunderland, Massachusetts.
- Templeton, A.R., 1983. Phylogenetic inference from restriction site endonuclease cleavage site maps with particular reference to the humans and apes. *Evolution* 37, 221–244.
- Williams, B.A., Kay, R.F., Kirk, E.C., Ross, C.F., 2010. *Darwinius masillae* is a strepsirrhine—a reply to Franzen et al. (2009). *J. Hum. Evol.* 59 (5), 567–573.