New and Views

*Darwinius masillae* is a strepsirrhine—a reply to Franzen et al. (2009)

Blythe A. Williams*, Richard F. Kay, E. Christopher Kirk, Callum F. Ross

* Corresponding author.

E-mail address: blythe.williams@duke.edu (B.A. Williams).

Crown groups include the common ancestor of living representatives of a clade and all descendants (both living and fossil) of that last common ancestor. Stem members of a clade include those taxa that are more closely related to the crown group than they are to its extant sister taxon (Wible and Covert, 1987).

1 In this context, they note that *Darwinius masillae* and adapoids contemporary with early tarsoids, could represent a stem group from which later anthropoid primates evolved, but we are not advocating this here, nor do we consider either *Darwinius* or adapoids to be anthropoids (2009:24).

2 While they are not always consistent in their phylogenetic claims, the suggestion that adapiforms are haplorhine primates is novel (as they note). Our review of the available evidence leads us to conclude that *Darwinius* is not a haplorhine and certainly not an anthropoid.

Because the Franzen et al. paper provided inconsistent and vague phylogenetic inferences, we clarify terminology and identify the nature of several of the features we critique. We discuss the key anatomical features that would allow one to diagnose whether an extinct species is more closely related to living haplorhine or strepsirrhine primates. We also show why *Darwinius*, other cercamoniines, and adapiforms generally are more likely to be basal strepsirrhines, rather than haplorhines as claimed.

The haplorhine-strepsirrhine dichotomy

For more than a century, morphological and molecular evidence has accumulated that supports the monophyly of Haplorhini and Strepsirrhini, as well as an ancient (pre-Eocene) time of divergence for the two clades. Crown haplorhines possess a number of derived anatomical features, as do crown strepsirrhines (Table 1). Until recently, molecular studies have supported a strepsirrhine clade, but the position of *Tarsius* has been ambiguous (Goodman et al., 2005). However, genetic markers called SINEs (‘short interspersed elements’) offer new and more convincing molecular evidence in support of both haplorhine and strepsirrhine monophyly. At present, tarsiers and anthropoids share five SINEs, supporting haplorhine...
Table 1
Synapomorphies of Crown Haplorhini and Crown Strepsirrhini

<table>
<thead>
<tr>
<th>Crown haplorhine features</th>
<th>Feature type</th>
<th>Soft tissue or molecular</th>
<th>Visible in skeleton</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Features associated with loss of a rhinarium</strong> (moist, hairless skin surrounding the nostrils)</td>
<td>Upper lip unattached/not tethered to gum between upper central incisors</td>
<td>Lack of a significant gap between upper central incisor roots (narrow inter-incisal gap)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lack of moist, hairless skin surrounding nostrils (rhinarium absent)</td>
<td>Short, vertically oriented nasolacrimal duct that does not irrigate external nose</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lack of median groove (philtrum) between nostrils</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Features associated with reduction of the sense of smell</strong> (main olfactory system)</td>
<td>Reduced area of olfactory epithelium in nasal cavity</td>
<td>Loss of olfactory recess</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Loss of olfactory recess</td>
<td>Loss of ethmoturbinals III-IV</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Reduced size of paleocortex</td>
<td>Loss of transverse bony lamina separating the airway (nasopharyngeal meatus) from the olfactory recess</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Loss of transverse bony lamina separating the airway (nasopharyngeal meatus) from the olfactory recess</td>
<td>Reduced size of olfactory bulb</td>
<td></td>
</tr>
<tr>
<td><strong>Features associated with improved vision</strong> (particularly high visual acuity)</td>
<td>Presence of a retinal fovea and very high central retinal cone densities (~50,000 cones/mm², or higher)</td>
<td>Presence of a postorbital septum (including zygomatic-alisphenoid contact)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Presence of a perifoveal macula lutea composed of lutein and zeaxanthan</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lack of tapetum lucidum (equivocal—may be primitive for primates)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Increased size of subcortical (e.g., dorsal lateral geniculate nucleus) and cortical (e.g., primary visual cortex) visual structures in forebrain</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Very high visual acuity (~9 cycles/degree, or higher)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pathway of the internal carotid artery</strong></td>
<td>Internal carotid artery enters the posterior carotid foramen anterior to the fenestra cochleae</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Carotid canal travels through a longitudinal septum within the middle ear space (internal carotid artery follows a peri-bullar pathway)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Stapedial branch of the internal carotid artery highly reduced or absent</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pneumatization of the middle ear</strong> (Cartmill and Kay, 1978; MacPhee and Cartmill, 1986)</td>
<td>Presence of an accessory pneumatic space (anterior accessory chamber) anterior to the middle ear space; Both air spaces are continuous through a small foramen (apical aditus) adjacent to the auditory tube</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Attachment point for eardrum</strong> (Cartmill and Kay, 1978; MacPhee and Cartmill, 1986)</td>
<td>Ectotympanic bone fuses with the lateral bullar wall early in ontogeny and is externally visible (phaneric)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Other cranial features</strong> (Cartmill, 1978; Ross, 1994; Rossie, 2006)</td>
<td>Presence of large ethmoidal os planum in medial orbital wall</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Shortened rostrum</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Molecular and physiologic</strong> (Pollock and Mullin, 1987; Kuryshchev et al., 2001; Schmitz et al., 2005; Xing et al., 2007)</td>
<td>Loss of ability to synthesize Vitamin C SINES C7, C9, C12, C14, FLAM-A</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Developmental and life history characteristics</strong> (Hubrecht, 1908; Leutenegger, 1973; Niemitz, 1974; Luckett, 1976; Haring and Wright, 1989; Martin, 1990; Roberts, 1994)</td>
<td>Hemochorial placentation</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Large offspring</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Prolonged postnatal development</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Crown strepsirrhine features</th>
<th>Feature type</th>
<th>Soft tissue only</th>
<th>Visible in skeleton</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dental characters</strong> (Hill, 1953)</td>
<td>Presence of a toothcomb formed by the lower incisors and canines</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Visual characters</strong> (Prie, 1959; Kaas et al., 1978; Nicol, 1981; Kaas and Huerta, 1988)</td>
<td>Presence of a tapetum lucidum composed of crystalline riboflavin (equivocal—may be primitive for primates)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Presence of two distinct koniocellular layers (ipsilateral and contralateral) interposed between the ipsilateral and contralateral parvocellular layers in the dorsal lateral geniculate nucleus</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Features of the hind limb</strong> (Beard et al., 1988; Gebo et al., 2001)</td>
<td>Presence of a grooming claw on the second toe (equivocal—may be primitive for primates)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Talus has a sloping, superiorly-canted facet for the fibula</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
monophyly to the exclusion of strepsirrhines (Kuryshev et al., 2001; Schmitz et al., 2005). Eight SINEs support strepsirrhine monophyly (Roos et al., 2004; Xing et al., 2007). As a result, the molecular and morphological case for a basal split between haplorhines and strepsirrhines in primate evolutionary history is now clearly established.

Identifying stem haplorhines and strepsirrhines

Given that living primates can be confidently classified as either haplorhines or strepsirrhines, the next logical step is to identify members of these clades in the fossil record. It is critical to remember, however, that stem members of these clades may not share all of the features found in living representatives of the group. The haplorhine-strepsirrhine divergence was unquestionably ancient, and early members of the two lineages would be expected to exhibit only minor differences. Indeed, except for a few critical features, the craniodental anatomy and postcranium of primitive omomyiforms and adapiforms (herein considered stem haplorhines and strepsirrhines, respectively—see below) closely resemble one another and differ markedly from early anthropoids (Dagosto and Gebo, 1994; Ross and Covert, 2000).

Table 1 (continued)

<table>
<thead>
<tr>
<th>Crown strepsirrhine features</th>
<th>Soft tissue only</th>
<th>Visible in skeleton</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Molecular</strong> (Roos et al., 2004; Herke et al., 2007; Xing et al., 2007)</td>
<td>SINEs Str-73A, B, C and D; Str-1a, 2, 3</td>
<td>Groove on the talus for the flexor hallucis longus tendon is displaced laterally (equivocal—present in outgroups)</td>
</tr>
</tbody>
</table>

The claim for haplorhine status of Darwinius is graphically demonstrated in Supplementary Figure 7 of Franzen et al. (2009), which is labeled as a cladogram. This figure includes three taxa, Strepsirrhini, Darwinius, and Haplorhini, with Darwinius positioned as the sister taxon to Haplorhini. Six features listed in their Table 3 are keyed onto this figure at the base of a Darwinius-Haplorhini node. Three of these supposed synapomorphies are listed as shared among Darwinius, tarsiers, and anthropoids: (1) cranium with short rostrum, (2) deep mandibular ramus, and (3) relatively small, steep fibular facet on talus. Three other characters are said to be shared exclusively with anthropoids: (1) fused mandibular symphysis, (2) vertical spatulate incisors, and (3) loss of the claw on pedal digit II. Thus, their Table 3 indicates that some synapomorphies are shared with all haplorhines, and some are shared exclusively with anthropoids. However, their Supplementary Figure 7 indicates that all of these synapomorphies are found at the base of Haplorhini. The conflicts between the table and the figure are not clarified in the text. This lack of clarity makes it difficult to

Is Darwinius a strepsirrhine or a haplorhine?

The taxa Anthropoidea, Haplorhini, and Strepsirrhini, as we use them, refer to “closed descent communities” or stem-based clades (Ax, 1985). By definition, Anthropoidea is the stem-based clade of all species, living or extinct, that is more closely related to living platyrhines and catarrhines than to Tarsius. Haplorhini is the clade of all species, living or extinct, that is more closely related to Anthropoidea plus Tarsius than to living strepsirrhines. Strepsirhini is the clade of all species, living or extinct, that is more closely related to extant lemurs and lorises than it is to Tarsius or anthropoids (Kay et al., 1997). Our reading of Franzen et al. is that they would accept these definitions and that their text, Table 3, and Supplementary Figure 7 reflect this agreement.
understand which phylogenetic position Franzen et al. (2009) support, and this resulting uncertainty complicates their discussion.\footnote{Their discussion is further complicated by some conflation of taxonomic definitions versus diagnoses. As described by de Queiroz and Gauthier (1992:401), `Definitions are statements specifying the meanings of taxon names (words); they are stated in terms of ancestry (see footnote 2, for example). Diagnoses are statements specifying how to determine whether a given species or organism is a representative of the taxon (clade) to which a particular name refers: they are most commonly stated in terms of characters.' That is, the diagnosis of a taxon is a `listing of characters that are hypothesized to have been the evolutionary novelties [synapomorphies] in its most recent common ancestor. Both the character and its hypothesized level of generality are stated, and thus diagnoses serve to precisely and testably identify taxa (Rowe, 1987:210).' Franzen et al. (2009) at times conflate the two, as for example, when they state, `Eocene notharctines and adapines have never been considered haplorhines. This is due in part to definitions of Strepsirrhini and Haplorhini that are based on characteristics of the rhinarium that do not preserve in fossils.' (2009:23) and where they note `Defining characters of Darwinius ally it with haplorhines rather than strepsirrhines' (2005:25).}

Regardless, we contend that these features, as well as others that they list in the text, are insufficient to make the case for either haplorhine or anthropoid affinities. Because of the confusion surrounding their phylogenetic claims, we discuss the distribution of these features in living and fossil primate taxa and consider their polarity (Table 2).

**Cranial anatomy**

Although badly crushed, enough of the cranial anatomy of the type specimen is preserved to establish that *Darwinius* is neither a stem nor a crown haplorhine. *Darwinius* possesses a postorbital bar lateral to the orbit as do all other euprimates but lacks the key crown haplorhine synapomorphy of a bony partition behind the orbit (Cartmill, 1980). *Darwinius* has a tympanic ring within the auditory bulla, as in other adapiforms, omomyiforms, and lemuroïds (Ross and Covert, 2000), whereas crown haplorhines and lorisoids have the tympanic ring fused to the lateral edge of the bulla. Franzen et al. (2009) do not report the presence of other diagnostic crown haplorhine features, such as possession of a bony accessory middle ear chamber or an anteromedial position for the internal carotid foramen on the bulla (Kay et al., 1997).

The rostrum of *Darwinius* is short, a trait found in some Eocene adapiforms, such as the North American cercamoniine *Mahgarita* (Rasmussen, 1990) and the notharctine adapiform *Smilodectes* (Gunnell, 1995). However, a short rostrum evolved multiple times in various strepsirrhine and haplorhine taxa and is clearly not a reliable indicator of haplorhine affinities (Ross et al., 1998). Furthermore, a short rostrum is precisely what would be expected in any juvenile primate regardless of its phyletic relationships.

**Dentition**

Franzen et al. (2009) list “vertical spatulate incisors” as a synapomorphy shared with anthropoids (their Table 3). The incisors of *Darwinius* are spatulate and only slightly procumbent (their Fig. 4), as are those of other adapiforms (Rosenberger et al., 1985). Previous researchers have noted this similarity between adapiforms and early anthropoids and have also noted that in both groups the first lower incisor is smaller than the second (Gingerich and Schoenecker, 1977). In contrast, in some omomyiforms the central incisor is enlarged and procumbent (Bown and Rose, 1987). Notably, however, the lower incisors of Eosimia are nearly vertical and I$_1$ to I$_2$ are subequal in size (Beard et al., 1996), as is the case for some omomyiforms (Covert and Williams, 1991). This pattern is also exhibited by *Altaius* (Gingerich et al., 1991), a taxon that is variously considered a plesiadapiform, a basal euprimate, or an omomyiform (Dashezveg and McKenna, 1977; Rose and Krause, 1984; Gingerich et al., 1991; Beard and Wang, 1995; Ni et al., 2005; Bloch et al., 2007).\footnote{\textit{Omomyiforms have unfused symphyses, as does *Tarsius* and most middle and late Eocene anthropoids such as *Catopithecus*, *Protopithecus*, *Bahinia*, and *Eosimia*, indicating that the last common ancestor of living haplorhines did not have a fused mandibular symphysis.}} The pattern of incisor shape and proportions exhibited by *Darwinius* and other adapiforms, eomorphids, and some omomyiforms is likely a symplesiomorphy for Euprimates rather than an adapiform-anthropoid synapomorphy (Cartmill and Kay, 1978; Wible and Covert, 1987; Covert and Williams, 1994).

In some key respects, the molar anatomy of *Darwinius* is more derived than that of most Eocene haplorhines (which retain comparatively primitive molars) and is similar to most other cercopithecoid adapiforms and unlike early crown haplorhines. For example, the mandibular first molar of *Darwinius* lacks a paraconid. By contrast, most omomyiforms (e.g., *Teiellardina*), Eocene tarsiods
(e.g., Tarsius eocaenus, Xanthorhysis), stem anthropoids (e.g., Eosimias, Bahinia), early crown anthropoids (e.g., Catopithecus), and even early Miocene platyrrhines are primitive in retaining paraconids on the lower first molar (Seiffert et al., 2005; Kay et al., 2008). Similarly, the maxillary first molar of Darwinius is quadrate with a relatively large cingular hypocone, while those of many mias, Tarsius eocaenus (e.g., Distributions of the characters discussed by Franzen et al. (2009) in support of a haplorhine affinity for Tarsius extant encountered in non-primate euarchontans (plesiadapiforms, tree accurate, this feature would not provide an exclusive link to hap-
portion of the facet, and this part of the anatomy is not adequately 
exhibits crushing in this area, the fibula conceals the proximal 
this feature as a crown haplorhine synapomorphy. The specimen 
lemurs and lorises with adapiforms from North America, Europe, 
proteopithecids, some patapithecids). 

Conclusions

Franzen et al. (2009) make a strong case that Darwinius is an adapiform, but none of the characters they invoke provide support for the hypothesis that Darwinius (or any other adapiforms) are stem haplorhines. The lack of comparisons with fossil haplorhines, including the contemporaneous and earlier omomyiforms, well-known and universally accepted anthropoids from the African late Eocene (Seiffert et al., 2005), and eosimid anthropoids from the Eocene of Asia (some as old as ~55–54 Ma; Beard et al., 1996; Jaeger et al., 1999; Gebo et al., 2000; Beard and Wang, 2004; Bajpai et al., 2008), poses a large part of the problem. Additionally, their Table 3, in which they list purported synapomorphies linking Darwinius with haplorhines, lumps extant taxa into groups in a manner that disguises critical homoplasies.10 A more detailed comparison of Eocene fossil primates is paramount for understanding the distribution of the relevant anatomical characters, as

---

**Table 2**

Distributions of the characters discussed by Franzen et al. (2009) in support of a haplorhine affinity for Darwinius

<table>
<thead>
<tr>
<th>Character</th>
<th>Presumed condition of ancestral primate</th>
<th>Instances of acquisition of the derived state</th>
<th>Condition in Darwinius (Franzen et al., 2009)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Talofibular joint</td>
<td>Steep, vertical profile: omomyiforms, tarsoiods, anthropoids including eosimids, amphipithecids</td>
<td>Sloping: adapiforms (including Catopithecus, Notharctus, Smilodectes, Adapis, Leptadapis, Genopithecus) &amp; lemuroids and loridos</td>
<td>Deep, vertical profile of talofibular facet b</td>
</tr>
<tr>
<td>Mandibular depth</td>
<td>Shallow mandible: omomyiforms, most adapiforms, tarsoiods, most lemuroids and loridos, some anthropoids (parapithecids, proteopithecids, Bramiella, callitrichines)</td>
<td>Deep: most stem and crown anthropoids, some adapiforms, some lemuroids and loridos</td>
<td>Deep mandible in this juvenile individual</td>
</tr>
<tr>
<td>Fusion of mandibular synphysis</td>
<td>Symphysis fused: most adapiforms, all omomyiforms, omomyiforms, amphipithecids, proteopithecids, some parapithecids.</td>
<td>Fused: some adapiforms (e.g., Adapis, Cercamomius); some lemuroids and loridos (e.g., indris, Archaeolemur, Megaladapis), some stem anthropoids (e.g., Apidium), all crown anthropoids</td>
<td>Partially fused in this juvenile individual</td>
</tr>
<tr>
<td>Incisor morphology</td>
<td>Spatulate incisors with 1 smaller than 2; some omomyiforms, adapiforms, eosimids, amphipithecids, African stem anthropoids, crown anthropoids.</td>
<td>Incisors pointed; Lower first incisor larger than second; Most omomyiforms, tarsoiods.</td>
<td>Spatulate incisors</td>
</tr>
<tr>
<td>Snout length (Ross, 1994)</td>
<td>Long snout: some omomyiforms, some adapiforms, some platyrrhines, some catarrhines</td>
<td>Short snout: some omomyiforms, some adapiforms tarsoiods, most platyrrhines, most catarrhines.</td>
<td>Short snout c</td>
</tr>
<tr>
<td>Pedal terminal digit II</td>
<td>Claw on terminal phalanx II: lemuroids and loridos, tarsoiods, Europolemur (a cercamomine adapiform) (Franzen, 1987).</td>
<td>Nail on terminal phalanx II: crown anthropoids except callitrichine platyrrhines; For omomyiforms and adapiforms, grooming claw absent except (possibly) Europolemur kelleri</td>
<td>Nail on terminal phalanx II</td>
</tr>
</tbody>
</table>

---

* Definitions of the character states given in accompanying citations.
* b We regard the condition in this fossil to be uncertain.
* c Character not quantified by Franzen et al. (2009).
* d Polarity of trait uncertain.
well as their polarities. 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. (2008) have done, that Darwinius and other adapiforms fall within the strepsirrhine radiation.

Using these comparisons we have shown that some of the putative ‘linking’ characters (crista with short rostrum, deep mandibular ramus, partially fused mandibular symphyses) are probably primitive euprimate features. At least one putative stem haplorhine synapomorphy (orientation of spatulate incisors) have evolved multiple times in primates, including in both crown strepsirrhines and anthropoids. Other characters (e.g., vertical spatulate incisors) are probably primitive euprimate features. At least one putative stem haplorhine synapomorphy (orientation of the talofibular facet) cannot be confirmed on the crushed skeleton, while another (loss of grooming claws) may represent the primitive condition for primates. In contrast, numerous derived crown haplorhine features of the orbit, the intracranial vasculature, and the bony middle ear region are absent in Darwinius or its cercamornine close relatives. The lack of clear synapomorphies linking Darwinius to living and fossil haplorhines, the undisputed positive evidence that it is a adapiform, and the detailed evidence that adapiforms are stem strepsirrhines, suggests that Darwinius has little relevance for understanding haplorhine evolution.

Acknowledgements

We thank Dr. Herbert Covert and Dr. Daniel Gebo for helpful discussions. We thank Dr. Mary Silcox, Dr. Chris Beard, and the anonymous reviewers for comments that improved the manuscript. We are grateful to Dr. Erik Seiffert for providing a copy of his paper in press. We extend our heartfelt thanks to Dr. Susan Antón for her assistance with this manuscript and for her years of exceptional service as Editor for the Journal of Human Evolution.

References


Soc. Lond. 1918, 9–53.


