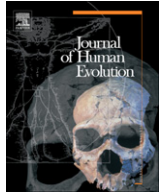




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## News and Views

*Darwinius masillae* is a strepsirrhine—a reply to Franzen et al. (2009)Blythe A. Williams<sup>a,\*</sup>, Richard F. Kay<sup>a</sup>, E. Christopher Kirk<sup>b</sup>, Callum F. Ross<sup>c</sup><sup>a</sup> Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, USA<sup>b</sup> Department of Anthropology University of Texas, Austin, TX 78712, USA<sup>c</sup> Department of Organismal Biology & Anatomy, University of Chicago, Chicago, IL 60637, USA

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## Introduction

The recent publication of a 47 million year old primate, *Darwinius masillae* (Franzen et al., 2009), from Grube Messel, Germany, received a tremendous amount of attention in the popular press (see Gibbons, 2009) mostly because it was heralded as the ‘missing link’ between humans and earlier primates (see the website [revealingthelink.com](http://revealingthelink.com), the book *The Link: Uncovering our earliest ancestor*, and the documentary on the History Channel *The Link* [Atlantic Productions]). Franzen et al. (2009) assign *Darwinius* to the Adapoidea, subfamily Cercamoniinae, an attribution that we accept. However, the authors make further claims about the higher-level evolutionary relationships of *Darwinius* (and other cercamoniine adapiforms by extension) with which we take issue.

Franzen et al. (2009:1) state: “*Darwinius masillae* is not simply a fossil lemur, but part of a larger group of primates, Adapoidea, representative of the early haplorhine diversification.” We interpret this statement to mean that they consider *Darwinius* more closely related to the Haplorhini (tarsiers and anthropoids) than to the Strepsirrhini (lemurs and lorises). At other points in their paper (including their Table 3), the authors propose that *Darwinius* shares synapomorphies with stem<sup>1</sup> or even crown anthropoids.<sup>2</sup> While

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<sup>1</sup> 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).

<sup>2</sup> In this context, they note that “*Darwinius masillae*, and adapoids contemporary with early tarsioids, 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). We are not exactly sure what position Franzen et al. are advocating with this statement, but it does confuse the discussion.

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.<sup>3</sup> 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.<sup>4</sup> At present, tarsiers and anthropoids share five SINEs, supporting haplorhine

<sup>3</sup> There has been a longstanding debate in primate phylogenetic studies as to whether living tarsiers (genus *Tarsius*) are most closely related to anthropoid primates in the clade Haplorhini (Simpson, 1945; Cartmill and Kay, 1978; Rosenberger and Szalay, 1980; Luckett and Maier, 1982; Rasmussen, 1994; Ross, 1994; Kay et al., 1997). If so, the living lemurs and lorises constitute a second major clade of primates—the Strepsirrhini. Alternatively, tarsiers could be more closely related to strepsirrhines, with the two groups together comprising the clade Prosimii.

<sup>4</sup> SINEs are short segments of self-replicating DNA that insert into the genome at apparently random positions. As such, SINEs are excellent phylogenetic markers with an extraordinarily low probability of convergent evolution (Hedges and Batzer, 2005). Because there are billions of potential insertion sites in any primate genome, the probability of a SINE inserting precisely in the same locus in two separate evolutionary lineages is “exceedingly minute, and for all practical purposes, can be ignored” (Shedlock and Okada, 2000:151).

**Table 1**  
Synapomorphies of Crown Haplorhini and Crown Strepsirrhini

Crown haplorhine features		
Feature type	Soft tissue or molecular	Visible in skeleton
<b>Features associated with loss of a rhinarium</b> (moist, hairless skin surrounding the nostrils) (Pocock, 1918; Boyd, 1932; Beard, 1988; Rossie and Smith, 2007)	Upper lip unattached/not tethered to gum between upper central incisors Lack of moist, hairless skin surrounding nostrils (rhinarium absent) Lack of median groove (philtrum) between nostrils	Lack of a significant gap between upper central incisor roots (narrow inter-incisal gap) Short, vertically oriented nasolacrimal duct that does not irrigate external nose
<b>Features associated with reduction of the sense of smell</b> (main olfactory system) (Cave, 1973; Baron et al., 1983, 1987; Stark, 1984; Joffe and Dunbar, 1998)	Reduced area of olfactory epithelium in nasal cavity Reduced size of paleocortex	Loss of olfactory recess Loss of ethmoturbinals III-IV Loss of transverse bony lamina separating the airway (nasopharyngeal meatus) from the olfactory recess Reduced size of olfactory bulb
<b>Features associated with improved vision</b> (particularly high visual acuity) (Cartmill, 1980; Frahm et al., 1984; Stephan et al., 1984; Hendrickson et al., 2000; Kirk, 2004; Kirk and Kay, 2004; The evolution of high visual acuity in the Anthropoidea. In: C. F. Ross & R. F. Kay (eds.) <i>Anthropoid Origins: New Visions</i> . Kluwer Academic /Plenum Publishers, New York. p. 539–602. Collins et al., 2005; Veilleux and Kirk, 2009)	Presence of a retinal fovea and very high central retinal cone densities (~50,000 cones/mm <sup>2</sup> , or higher) Presence of a perifoveal macula lutea composed of lutein and zeaxanthan Lack of tapetum lucidum (equivocal—may be primitive for primates) Increased size of subcortical (e.g., dorsal lateral geniculate nucleus) and cortical (e.g., primary visual cortex) visual structures in forebrain Very high visual acuity (~9 cycles/degree, or higher)	Presence of a postorbital septum (including zygomatic-alisphenoid contact)
<b>Pathway of the internal carotid artery</b> (Cartmill and Kay, 1978; MacPhee and Cartmill, 1986; Ross, 1994)		Internal carotid artery enters the posterior carotid foramen anterior to the fenestra cochlea Carotid canal travels through a longitudinal septum within the middle ear space (internal carotid artery follows a perbullar pathway) Stapedial branch of the internal carotid artery highly reduced or absent
<b>Pneumatization of the middle ear</b> (Cartmill and Kay, 1978; MacPhee and Cartmill, 1986)		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
<b>Attachment point for eardrum</b> (tympanic membrane) (Cartmill and Kay, 1978; MacPhee and Cartmill, 1986).		Ectotympanic bone fuses with the lateral bullar wall early in ontogeny and is externally visible (phaneric) Subtympanic recess and annular bridge absent (equivocal—may be primitive for primates)
<b>Other cranial features</b> (Cartmill, 1978; Ross, 1994; Rossie, 2006)		Presence of large ethmoidal os planum in medial orbital wall Shortened rostrum
<b>Molecular and physiologic</b> (Pollock and Mullin, 1987; Kuryshv et al., 2001; Schmitz et al., 2005; Xing et al., 2007)	Loss of ability to synthesize Vitamin C SINEs C7, C9, C12, C14, FLAM-A	
<b>Developmental and life history characteristics</b> (Hubrecht, 1908; Leutenegger, 1973; Niemitz, 1974; Luckett, 1976; Haring and Wright, 1989; Martin, 1990; Roberts, 1994)	Hemochorial placentation Large offspring Prolonged postnatal development	
Crown strepsirrhine features		
Feature type	Soft tissue only	Visible in skeleton
<b>Dental characters</b> (Hill, 1953)		Presence of a toothcomb formed by the lower incisors and canines
<b>Visual characters</b> (Pirie, 1959; Kaas et al., 1978; Nicol, 1981; Kaas and Huerta, 1988)	Presence of a tapetum lucidum composed of crystalline riboflavin (equivocal—may be primitive for primates) Presence of two distinct koniocellular layers (ipsilateral and contralateral) interposed between the ipsilateral and contralateral parvocellular layers in the dorsal lateral geniculate nucleus	
<b>Features of the hind limb</b> (Beard et al., 1988; Gebo et al., 2001)		Presence of a grooming claw on the second toe (equivocal - may be primitive for primates) Talus has a sloping, superiorly-canted facet for the fibula

**Table 1** (continued)

Crown strepsirrhine features		
Feature type	Soft tissue only	Visible in skeleton
		Groove on the talus for the flexor hallucis longus tendon is displaced laterally (equivocal—present in outgroups) Talus has a large posterior trochlear shelf On the navicular bone, the facet for the cuboid contacts both the facets for the entocuneiform and mesocuneiform
<b>Molecular</b> (Roos et al., 2004; Herke et al., 2007; Xing et al., 2007)	SINEs Str-73A, B, C and D; Str-1a, 2, 3	

monophyly to the exclusion of strepsirrhines (Kuryshv 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).

Total evidence cladistic analyses (ignored by Franzen et al., 2009) combining hundreds of dental, skull, limb-bone, embryological, physiological, and molecular characters of living and fossil primates agree that the Eocene Adapiformes are stem strepsirrhines, that the Eocene Omomyiformes are haplorhines, and that the Eosimiidae are stem anthropoids (Kay et al., 1997, 2004; Ross et al., 1998; Ni et al., 2004; Marivaux et al., 2005; Seiffert et al., 2005, 2009; Bajpai et al., 2008). While some researchers have argued that adapiforms gave rise to extant anthropoids (Gingerich and Schoeninger, 1977; Rasmussen, 1990), there is growing acceptance that adapiforms are stem strepsirrhines, as indicated in each of the phylogenetic studies cited above. The case for omomyiforms as haplorhines is supported even by researchers who disagree on some other aspects of the phylogeny advocated here. While some researchers support a link between tarsiers and omomyiforms to the exclusion of anthropoids (Szalay and Delson, 1979; Rosenberger and Szalay, 1980; Gingerich, 1981; Beard and MacPhee, 1994), others consider omomyiforms to be stem haplorhines (Kay et al., 1997; Ross et al., 1998; Ross and Kay, 2004; Seiffert et al., 2005; Bajpai et al., 2008; Rose et al., 2009). Indeed, *Tarsius* and anthropoids share many critical morphological features not shared with omomyiforms such as postorbital closure, a perbullar pathway for the internal carotid artery, and an anterior accessory cavity in the ear region. However, tarsiers and omomyiforms share several cranial features, such as a basioccipital flange on the bulla and the lateral pterygoid plate overlapping the lateral aspect of the bulla, that are of uncertain polarity (Beard and MacPhee, 1994; Ross and Covert, 2000; Rossie et al., 2006).

Gebo et al. (2001) note that omomyiforms show additional postcranial similarities to eosimiids and later anthropoids, although the polarity of these features is also unclear. In contrast, adapiforms share several derived postcranial features with crown strepsirrhines (Gebo et al., 2001). Most recent phylogenetic interpretations favor a link between adapiforms and extant strepsirrhines (see above references and Gebo et al., 2001; Rose et al., 2009), while a minority question it (Miller et al., 2005; Franzen et al., 2009).

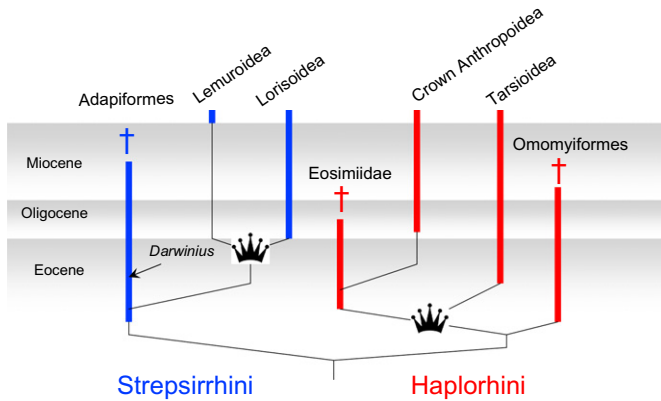
In light of the consistent results of all total evidence cladistic analyses (cited above), we advocate the position that adapiforms are strepsirrhines and omomyiforms are haplorhines (Fig. 1). Table 1 offers hard and soft tissue features that can be used to identify crown members of these clades.

#### Is *Darwinius* a strepsirrhine or a haplorhine?

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,<sup>5</sup> with *Darwinius* positioned as the sister taxon to Haplorhini.<sup>6</sup> 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

<sup>5</sup> The taxa Anthropeida, Haplorhini, and Strepsirrhini, as we use them, refer to “closed descent communities” or stem-based clades (Ax, 1985). By definition, Anthropeida is the stem-based clade of all species, living or extinct, that is more closely related to living platyrrhines and catarrhines than to *Tarsius*. Haplorhini is the clade of all species, living or extinct, that is more closely related to Anthropeida plus *Tarsius* than to living strepsirrhines. Strepsirrhini 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.

<sup>6</sup> As depicted in Franzen et al. Supplementary Figure 7, *Darwinius* would be a stem haplorhine, sister taxon to fossil and living haplorhine primates.



**Fig. 1.** Diagram of cladistic relationships of taxa discussed in text. Daggert refer to extinct taxa; crowns represent crown strepsirrhine and haplorhine clades. Position of *Darwinius* discussed in this paper is consistent with a fuller phylogenetic analysis by Seiffert et al. (2009). Position of all other major groups based on phylogenetic analysis of Bajpai et al. (2008).

understand which phylogenetic position Franzen et al. (2009) support, and this resulting uncertainty complicates their discussion.<sup>7</sup>

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 lemuroids (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*

<sup>7</sup> Their discussion is further complicated by some conflation of taxonomic definitions versus diagnoses. As described by de Queiroz and Gautier (1992:461), "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" (2009:25).

(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.

#### Mandibular anatomy

Franzen et al. (2009) claim that the partially fused mandibular symphysis and the deep mandibular ramus of *Darwinius* are synapomorphies shared with Anthropoidea. Although the symphysis is said to be fused ventrally but open dorsally in the juvenile type specimen, Franzen et al. (2009) hypothesize that such a condition will lead to full fusion in the adult. Even if this is correct, having a deep mandible and fused symphysis does not indicate haplorhine affinities because most stem and early crown haplorhines lack these traits.<sup>8</sup> Additionally, symphyseal fusion has evolved multiple times in primates (e.g., in some adapiforms, some subfossil lemurs, and several stem anthropoids; Ravosa, 1999). Jaw depth is also quite labile evolutionarily. The mandible is shallow in *Tarsius* (contra Table 3, character 9 of Franzen et al., 2009) and in some early anthropoids (parapithecids and proteopithecids) but deep in others (eosimiids, oligopithecids, and amphipithecids).

#### 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 Schoeninger, 1977). In contrast, in some omomyiforms the central incisor is enlarged and procumbent (Bown and Rose, 1987). Notably, however, the lower incisors of Eosimiidae are nearly vertical and I<sub>1-2</sub> 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 *Altanius* (Gingerich et al., 1991), a taxon that is variously considered a plesiadapiform, a basal euprimate, or an omomyiform (Dashzeveg and McKenna, 1977; Rose and Krause, 1984; Gingerich et al., 1991; Beard and Wang, 1995; Ni et al., 2005; Bloch et al., 2007).<sup>9</sup> The pattern of incisor shape and proportions exhibited by *Darwinius* and other adapiforms, eosimiids, and some omomyiforms is likely a sympleisomorphy 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 cercamoniine adapiforms and unlike early crown haplorhines. For example, the mandibular first molar of *Darwinius* lacks a paraconid. By contrast, most omomyiforms (e.g., *Teilhardina*), Eocene tarsioids

<sup>8</sup> Omomyiforms have unfused symphyses, as does *Tarsius* and most middle and late Eocene anthropoids such as *Catopithecus*, *Proteopithecus*, *Bahinia*, and *Eosimias*, indicating that the last common ancestor of living haplorhines did not have a fused mandibular symphysis.

<sup>9</sup> The polarity of this trait is open to some debate because plesiadapiforms (probable euarchontans and possibly the sister taxon of euprimates [Bloch et al., 2007]) commonly have an enlarged and procumbent central incisor. However, many plesiadapiforms are clearly quite derived in having lost the lateral incisor and developed a diastema between I<sub>1</sub> and the premolars. We interpret the great enlargement of I<sub>1</sub> in many plesiadapiforms and some omomyiforms as an independently derived condition in each group.



**Table 2**  
Distributions of the characters discussed by Franzen et al. (2009) in support of a haplorhine affinity for *Darwinius*<sup>a</sup>

Character	Presumed condition of ancestral primate	Instances of acquisition of the derived state	Condition in <i>Darwinius</i> (Franzen et al., 2009)
Talofibular joint (Beard et al., 1988)	Steep, vertical profile: omomyiforms, tarsioids, anthropoids including eosimiids, amphipithecids	Sloping: adapiforms (including <i>Cantius</i> , <i>Notharctus</i> , <i>Smilodectes</i> , <i>Adapis</i> , <i>Leptadapis</i> , <i>Caenopithecus</i> ) & lemuroids and lorisooids	Steep, vertical profile of talofibular facet <sup>b</sup>
Mandibular depth (Ravosa, 1996, 1999)	Shallow mandible: omomyiforms, most adapiforms, tarsioids, most lemuroids and lorisooids, some anthropoids (parapithecoids, proteopithecids, <i>Branisella</i> , callitrichines)	Deep: most stem and crown anthropoids, some adapiforms, some lemuroids and lorisooids	Deep mandible in this juvenile individual <sup>c</sup>
Fusion of mandibular symphysis (Ravosa, 1996, 1999)	Symphysis unfused: most adapiforms, all omomyiforms, eosimiids, amphipithecids, proteopithecids, some parapithecoids.	Fused: some adapiforms (e. g., <i>Adapis</i> , <i>Cercamoni</i> ); some lemuroids and lorisooids (e. g., indriids, <i>Archaeolemur</i> , <i>Megaladapis</i> ), some stem anthropoids (e. g., <i>Apidium</i> ), all crown anthropoids	Partially fused in this juvenile individual
Incisor morphology (Kay and Williams, 1994)	Spatulate incisors with i1 smaller than i2: some omomyiforms, adapiforms, eosimiids, amphipithecids, African stem anthropoids, crown anthropoids.	Incisors pointed; Lower first incisor larger than second; Most omomyiforms, tarsioids	Spatulate incisors
Snout length (Ross, 1994)	Long snout: some omomyiforms, some adapiforms, some platyrrhines, some catarrhines.	Short snout: some omomyiforms, some adapiforms tarsioids, most platyrrhines, most catarrhines.	Short snout <sup>c</sup>
Pedal terminal digit II	Claw on terminal phalanx II: lemuroids and lorisooids, tarsioids, <i>Europolemur</i> (a cercamoniine adapiform) <sup>b</sup> (Franzen, 1987).	Nail on terminal phalanx II: crown anthropoids except callitrichine platyrrhines; For omomyiforms and adapiforms, grooming claw absent except (possibly) <i>Europolemur kelleri</i>	Nail on terminal phalanx II <sup>d</sup>

<sup>a</sup> Definitions of the character states given in accompanying citations.

<sup>b</sup> We regard the condition in this fossil to be uncertain.

<sup>c</sup> Character not quantified by Franzen et al. (2009).

<sup>d</sup> Polarity of trait uncertain.

(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 paracoids 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 Eocene anthropoids (e.g., *Eosimias*, *Bahinia*, *Phenacopithecus*) and extant *Tarsius* lack a hypocone (Seiffert et al., 2005).

### Limb skeleton

In *Darwinius*, the talofibular (lateral fibular) facet of the talus is reported to be vertically oriented, and Franzen et al. (2009) count this feature as a crown haplorhine synapomorphy. The specimen exhibits crushing in this area, the fibula conceals the proximal portion of the facet, and this part of the anatomy is not adequately illustrated to support this claim. However, even if the description is accurate, this feature would not provide an exclusive link to haplorhines. A vertical orientation of the talofibular facet is also encountered in non-primate euarchontans (plesiadapiforms, tree shrews, and colugos), while a sloping facet is known to be present in extant strepsirrhines and adapiforms (except, possibly, *Darwinius*). As a result, a laterally sloping orientation of the facet is most parsimoniously interpreted as a synapomorphy linking living lemurs and lorises with adapiforms from North America, Europe, and Asia, including *Europolemur* and other cercamoniines (Beard et al., 1988; Gebo et al., 2008). Similarly, a vertically oriented talofibular facet appears to be primitive for euprimates and retained in stem haplorhines. If *Darwinius* also had a vertically oriented talofibular facet, then this characteristic must represent a secondary reversion to the primitive euprimate condition.

Franzen et al. (2009) consider the nail rather than a claw on digit II of the *Darwinius* foot as another synapomorphy shared with anthropoids (their Table 3) or with haplorhines (their Supplementary Figure 7). However, the polarity of this feature is unclear. Extant lemurs, lorises, and *Tarsius* have a claw on the distal phalanx of digit II of the foot, whereas non-callitrichine anthropoids do not

(Soligo and Muller, 1999). Tarsiers also have an additional claw on digit III of the foot. Gunnell and Rose (2002) note that there is no clear evidence for the presence of a digit II claw in adapiforms and omomyiforms. A toilet claw has been reported for *Europolemur kelleri* (van Koenigswald, 1979; Franzen, 1994), although from our own observations of high-resolution casts of the specimen in question (HLD-Me7430) we remain unsure. Its congener *Europolemur koenigswaldi* lacks a toilet claw (Franzen et al., 2009). Thus, it is plausible that the presence of flattened nails on all digits is the primitive condition for euprimates and that toilet claws evolved independently in extant strepsirrhines, tarsioids, and callitrichines. Accordingly, the presence of a nail on digit II supports neither haplorhine nor anthropoid status for *Darwinius*.

### 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 eosimiid 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.<sup>10</sup> A more detailed comparison of Eocene fossil primates is paramount for understanding the distribution of the relevant anatomical characters, as

<sup>10</sup> Table 3 includes a longer list of features found in extant strepsirrhines and haplorhines but *Darwinius* is the only extinct species listed. The table includes lemurs and lorises (the strepsirrhines) and tarsioids, ceboids, cercopithecoids, and hominoids (the haplorhines).

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. (2009) 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 (cranium with short rostrum, deep mandibular ramus, partially fused mandibular symphysis, loss of molar paraconids, and presence of an enlarged cingular hypocone) 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 cercamoniine close relatives. The lack of clear synapomorphies linking *Darwinius* to living and fossil haplorhines, the undisputed positive evidence that it is an adapiform, and the detailed evidence that adapiforms are stem strepsirrhines, suggests that *Darwinius* has little relevance for understanding haplorhine evolution.

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