

## Comment to “Primates in the Eocene” by Gingerich (2012)

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In his recent article “Primates in the Eocene”, Gingerich (2012) presented a broad review of Eocene primate radiations and their place in the primate evolutionary tree, with a particular focus on Adapoidea. While synthetic reviews of early primate evolution are always welcome additions to the literature, within his larger analysis Gingerich (2012) specifically discussed two issues that deserve special comment, the first relating to the evolution of grooming claws within Adapoidea and the second relating to his phylogenetic interpretation of *Darwinius* and Adapoidea within the order Primates, which was supposedly based on a modification of our own final matrix in Maiolino et al. (2012).

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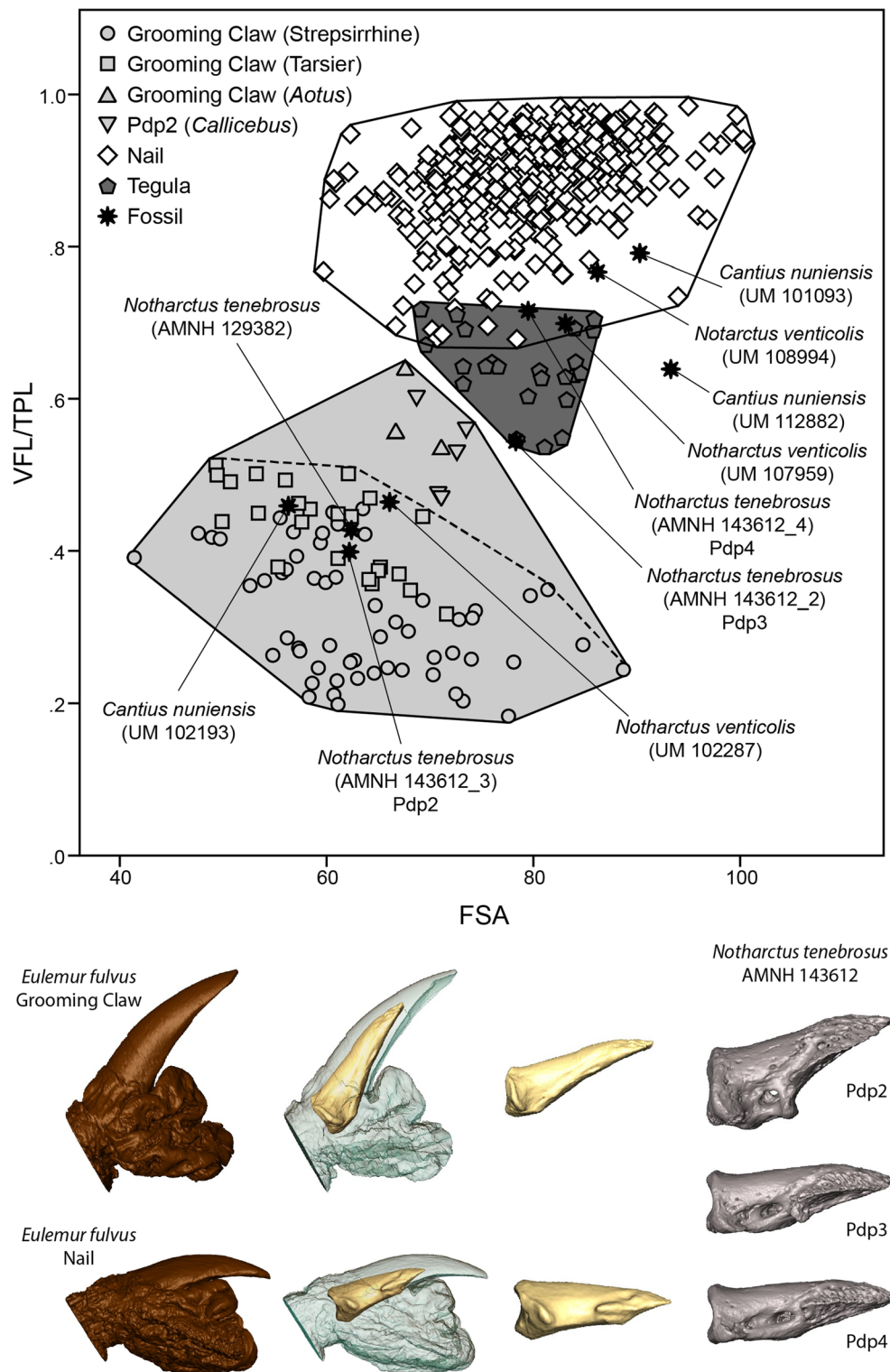
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Unfortunately, as we will demonstrate below, in both cases the interpretations of Gingerich (2012) are unlikely to be correct.

First, Gingerich (2012) characterises the morphology of *Notharctus* pedal distal phalanges as “ambiguous”. In fact, there is very little ambiguity involved. The analyses provided in Maiolino et al. (2012) demonstrate quite conclusively, both metrically and visually, that pedal distal phalanges bearing grooming claws are readily separated from other unguis forms (ungulae=nails, falculae=non-primate claws, and tegulae=claw-like unguis of callitrichins and aye-ayes) on the basis of facet-shaft angle (FSA), volar feature length (VFL), and other distinctive measures. Univariate and multivariate analyses including FSA and VFL clearly indicate that *Notharctus tenebrosus* possessed a grooming claw on pedal digit II (Maiolino et al. 2012). To illustrate this point further, a simple bivariate plot of FSA and VFL divided by total phalanx length (TPL) from 512 primate pedal distal phalanges shows the stark distinction between grooming claw and ungula-bearing distal phalanges (Fig. 1). Strepsirrhine and tarsier phalanges that bear grooming claws are well-separated from ungula- and tegula-bearing forms (Fig. 1, dotted line within convex hull surrounding all grooming claws).

On the basis of FSA and VFL/TPL, Fig. 1 indicates that *Notharctus venticolis* (UM 102287), *Cantius nuniensis* (UM 102193), and *Notharctus tenebrosus* (AMNH 143612\_3 and AMNH 129382) bore grooming claws, confirming the results of Maiolino et al. (2012) for *Notharctus tenebrosus* and extending them to notharctid pedal morphology, more generally. We note that Gingerich (2012) provides no compelling evidence to the contrary, and the discriminant analyses mentioned by Gingerich (2012) (see also von Koenigswald et al. (2012)) exclude FSA, VFL, VFL/TPL, and other distinctive measures. Until our results are contradicted by a proper study including diagnostic features such as FSA, VFL, and VFL/TPL, the analyses in Maiolino et al. (2012) remain the most comprehensive performed thus far and strongly



support our interpretation. Furthermore, given that multiple species of *Euromur* also had grooming claws on pedal digit II (von Koenigswald 1979; von Koenigswald et al. 2012), it seems quite likely that most adapoids, including *Darwinius*, possessed grooming claws, an obvious

similarity with living strepsirrhines. To definitively assess the presence or absence of a grooming claw in *Darwinius* moving forward, an undistorted lateral view of the pedal distal phalanges illustrating FSA and other features will be necessary.

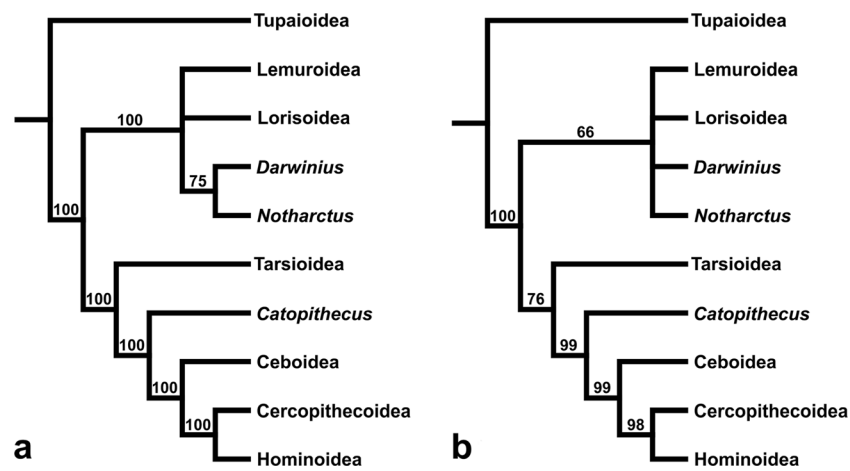
**Fig. 1** *Top*: bivariate plot of facet-shaft angle (FSA) and volar feature length divided by total phalanx length (VFL/TPL) for 512 pedal distal phalanges from extant primates bearing grooming claws, ungulae, or tegulae (58 strepsirrhine grooming claws, 24 tarsier grooming claws, 3 *Aotus* grooming claws, 5 grooming claw-like phalanges from pedal ray 2 of *Callicebus*, 400 ungulae from pedal rays 2–5, and 23 tegulae), representing 61 of the 73 extant primate genera currently recognised by the IUCN. Note the discriminatory power of these variables in distinguishing distal phalanges that bear grooming claws from those that bear nails or tegulae. Ten fossil adapoid specimens are also included: the non-hallucal pedal phalanges from AMNH 143612 (*Notharctus tenebrosus*) and AMNH 129382 (*Notharctus tenebrosus*) and the measureable non-hallucal specimens from fig. 12 of von Koenigswald et al. (2012). Some von Koenigswald et al. 2012 specimens appear to be damaged around the articular facet (*N. venticolis* UM 107959, UM 108994; *Cantius nuniensis* UM 101093, also damaged distally), so we urge caution when assessing these specimens if they are, in fact, damaged. UM 84780 was excluded from the analysis for two reasons: (1) it appears to lack a proximal epiphysis and (2) its primate affinities are uncertain. *Bottom left*: lateral views of microCT reconstructions of a grooming claw-bearing and a nail-bearing digit of *Eulemur fulvus* demonstrating the relationship of external tissue to the distal phalanx. Most grooming claws project far above and beyond the apical pad. Our measurements FSA and VFL are designed to reflect this configuration (Maiolino et al. 2011). Low FSA indicates a distal phalanx whose shaft projects dorsally with respect to its articular facet; such a configuration likely helps to contribute to the dorsal projection of the grooming claw. VFL is a measure that visually appears to be related to the portion of the phalanx that lies embedded in the apical pad (the rest projecting above and beyond it). Grooming claw-bearing distal phalanges with low values of FSA and VFL/TPL project dorsally above and distally beyond the apical pad while nail-bearing distal phalanges with high values of FSA and VFL/TPL show less dorsal and distal projection beyond the apical pad. *Bottom right*: lateral views of *Notharctus tenebrosus* (AMNH 143612) distal phalanges from the second, third, and fourth pedal rays demonstrating a second pedal distal phalanx that strongly resembles extant grooming claw-bearing phalanges and third and fourth pedal distal phalanges that more closely resemble extant nail-bearing distal phalanges. *N. tenebrosus* (AMNH 143612, 3, AMNH 129382), *N. venticolis* (UM 102287), and *C. nuniensis* (UM 102193) all possess the grooming claw morphology that projects above and beyond the boundaries of the apical pad. The third and fourth pedal distal phalanges of *Notharctus tenebrosus* lack this configuration and, rather, bear stronger resemblance to ungula-bearing distal phalanges. We do emphasise, however, that adapoid distal phalanges do not look exactly like those of extant primates. This has long been noted and has even been suggested by Godinot (1992) to reflect morphology that is reminiscent of an ancestral falcular-bearing phalanx. An in-depth analysis of the significance of this morphology is currently underway

Second, and most importantly, Gingerich's cladistic interpretation of *Darwinius masillae* is demonstrably false and, as it is based on our own dataset, demands a strong response. In his paper, Gingerich (2012) stated that after modifying only one of the codings in our final data set (blood supply to the brain in *Notharctus* from “complex” to “promontory dominant”), he produced a most parsimonious phylogenetic tree with *Notharctus* and *Darwinius* reconstructed as stem haplorhines (see his fig. 6). This is, in fact, not true. If one takes the final 39 character matrix in Maiolino et al. (2012) and makes the change Gingerich (2012) advocates to the cranial blood supply character, the four most parsimonious phylogenetic trees produced are exactly the same as originally

reported, with *Notharctus* and *Darwinius* unambiguously reconstructed as strepsirrhines (see Figs. 2 and 3; matrix provided in supporting online information).

Therefore, even using Gingerich's own preferred codings, the most parsimonious interpretation of the data is that *Notharctus* and *Darwinius* are strepsirrhines, not haplorhines. We would also like to point out that ongoing research supports our original coding of “complex” for *Notharctus* cranial blood supply, as both the promontory and stapelial branches of the internal carotid can be enlarged in the specimens we have examined (Welch et al. 2014). Using our final data matrix, the only way one can produce a tree where *Notharctus* and *Darwinius* are reconstructed as stem haplorhines, as reported by Gingerich (2012), is to eliminate a number of characters from the analysis. In other words, the hypothesis that *Notharctus* and *Darwinius* are haplorhines is only tenable if one willingly excludes relevant anatomy and phylogenetic information.

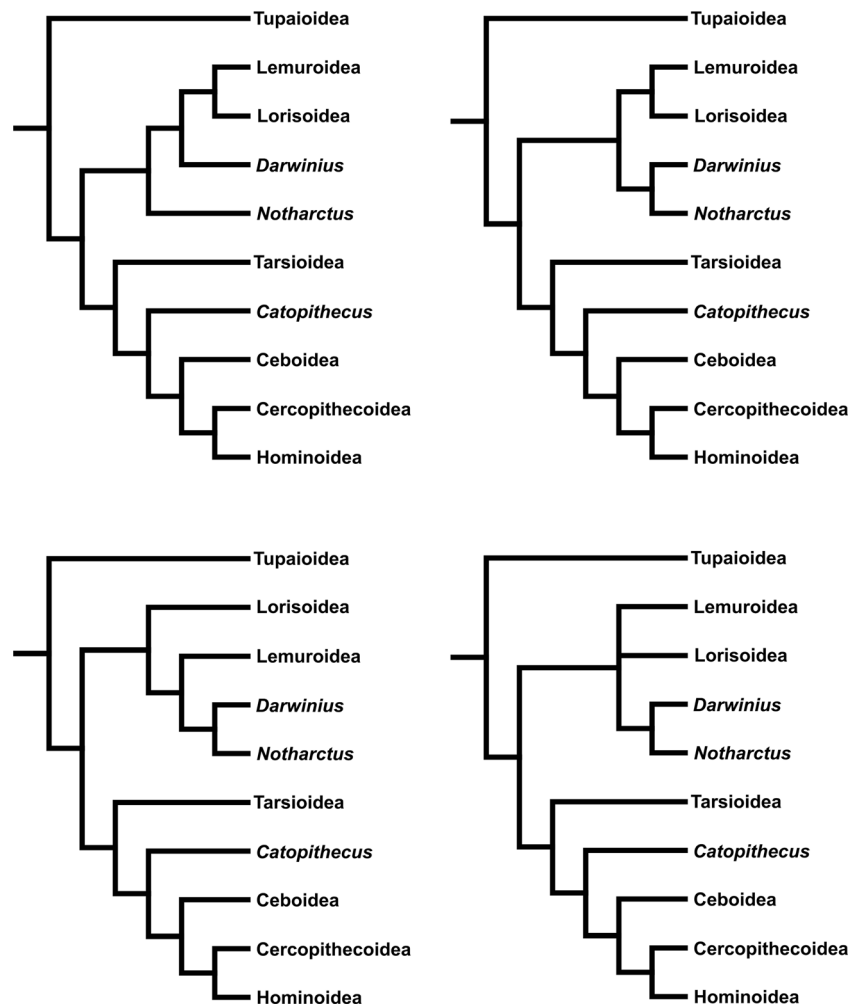
More broadly, we would like to stress the importance of considering multiple fossil taxa and large numbers of morphological characters when assessing primate phylogenetic relationships. For the sake of argument, the phylogenetic analysis here and those in Maiolino et al. (2012) were intentionally restricted to a relatively small number of characters and only a few fossil taxa with fairly complete skulls and associated postcrania, as advocated by Gingerich et al. (2010) and Gingerich (2012). Although our results demonstrate that even an abbreviated morphological analysis and cursory examination of the fossil record leads one to consider a position within Strepsirrhini as the most likely phylogenetic hypothesis for *Notharctus* and *Darwinius* (see Figs. 2 and 3), this limited approach largely ignores the broader Eocene fossil record outside of *Darwinius*, *Notharctus*, and *Catopithecus* and effectively excludes large pieces of phylogenetic information. While Gingerich et al. (2010) and Gingerich (2012) argue against the inclusion of many fossil taxa and characters on the basis that they are typically too incomplete, the inclusion of fossil taxa has been empirically demonstrated to be crucial in phylogenetic analyses because fossil taxa extend taxon sampling (e.g. Gauthier et al. 1988; Donoghue et al. 1989; Huelsenbeck 1991; Wiens 1998; Strait and Grine 2004), provide unique morphologies that help to refine assessments of character transformation (e.g. Gatesy and O'Leary 2001; Springer et al. 2001; Gatesy et al. 2003), and increase overall phylogenetic accuracy (e.g. Gauthier et al. 1988; Wheeler 1992; Zwickl and Hillis 2002). In addition, multiple studies have demonstrated that increasing the number of characters in an analysis generally increases phylogenetic accuracy (e.g. Wiens 2003a; 2003b; 2006; Gilbert et al. 2009) and that missing data is not a serious problem as long as character sampling is sufficiently robust (Wiens 1998; 2003a; 2003b; 2006; Wiens and Morrill 2011; Pattinson et al. 2014). No serious modern phylogenetic analysis denies these facts, and to argue otherwise is philosophically unsound, flying in the face of the past 25 years of research (e.g. Gauthier et al. 1988; Donoghue et al. 1989; Huelsenbeck 1991; Wheeler 1992;



**Fig. 2** Consensus trees resulting from the analysis of 39 cranial and postcranial characters deemed important in separating extant strepsirrhines and haplorhines by Maiolino et al. (2012), modified as suggested by Gingerich (2012). Analysis was run in PAUP 4.10b with an exhaustive search to find the most parsimonious trees (MPTs) followed by a 10,000 replication, branch and bound bootstrap analysis with replacement for clade support. **a** Majority-rule consensus tree of 4

MPTs. Numbers above branches indicate the percentage of MPTs supporting each given clade. **b** Strict consensus tree of 4 MPTs. Numbers above branches indicate bootstrap support for each given clade. Note that *Darwinius* and *Notharctus* are reconstructed as strepsirrhines in all MPTs and that a monophyletic Strepsirrhini including *Notharctus* and *Darwinius* is supported by bootstrap values as well. See also Fig. 3 for individual MPTs and tree statistics

**Fig. 3** The 4 MPTs resulting from the analysis of 39 cranial and postcranial characters deemed important in separating extant strepsirrhines and haplorhines by Maiolino et al. (2012), modified as suggested by Gingerich (2012). Analysis was run in PAUP 4.10b with an exhaustive search to find the MPTs with Tupaioidea assigned as the outgroup. Tree statistics for each MPT are as follows: Tree Length=64, CI=0.7344, HI=0.2656, RI=0.8247, RC=0.6057





Gatesy and O’Leary 2001; Springer et al. 2001; Zwickl and Hillis 2002; Gatesy et al. 2003; Wiens 1998; Wiens 2003a; Wiens 2003b; Wiens 2006; Gilbert et al. 2009; Wiens and Morrill 2011). Not surprisingly, more comprehensive and inclusive studies following rigorous cladistic methodology confirm our narrow results and strongly refute Gingerich’s (2012) hypothesis (e.g. Boyer et al. 2010; Seiffert et al. 2010; Williams et al. 2010; Pattinson et al. 2014). Again, the only way that one can reconstruct *Darwinius* as a haplorhine, even using Gingerich’s own preferred codings, is to effectively ignore relevant phylogenetic information by unjustifiably excluding a number of important characters and taxa because they are “incomplete”. To us, this seems a poor way to conduct a phylogenetic study, particularly if the overall goal is phylogenetic accuracy. Therefore, while we can never know the true phylogeny of any group of extinct taxa, a full consideration of all available evidence at this time strongly suggests that *Notharctus* and *Darwinius* (and adapoids more broadly) are strepsirrhines and, *contra* Gingerich (2012), the data in Maiolino et al. (2012) have never supported any other alternative hypothesis.

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