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## Oldest evidence for grooming claws in euprimates

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## ABSTRACT

Euprimates are unusual among mammals in having fingers and toes with flat nails. While it seems clear that the ancestral stock from which euprimates evolved had claw-bearing digits, the available fossil record has not yet contributed a detailed understanding of the transition from claws to nails. This study helps clarify the evolutionary history of the second pedal digit with fossils representing the distal phalanx of digit two (dpII), and has broader implications for other digits. Among extant primates, the keratinized structure on the pedal dpII widely varies in form. Extant strepsirrhines and tarsiers have narrow, distally tapering, dorsally inclined nails (termed a ‘grooming claws’ for their use in auto-grooming), while extant anthropoids have more typical nails that are wider and lack distal tapering or dorsal inclination. At least two fossil primate species thought to be stem members of the Strepsirrhini appear to have had grooming claws, yet reconstructions of the ancestral euprimate condition based on direct evidence from the fossil record are ambiguous due to inadequate fossil evidence for the earliest haplorhines. Seven recently discovered, isolated distal phalanges from four early Eocene localities in Wyoming (USA) closely resemble those of the pedal dpII in extant prosimians. On the basis of faunal associations, size, and morphology, these specimens are recognized as the grooming phalanges of five genera of haplorhine primates, including one of the oldest known euprimates (~56 Ma), *Teilhardina brandti*. Both the phylogenetic distribution and antiquity of primate grooming phalanges now strongly suggest that ancestral euprimates had grooming claws, that these structures were modified from a primitive claw rather than a flat nail, and that the evolutionary loss of ‘grooming claws’ represents an apomorphy for crown anthropoids.

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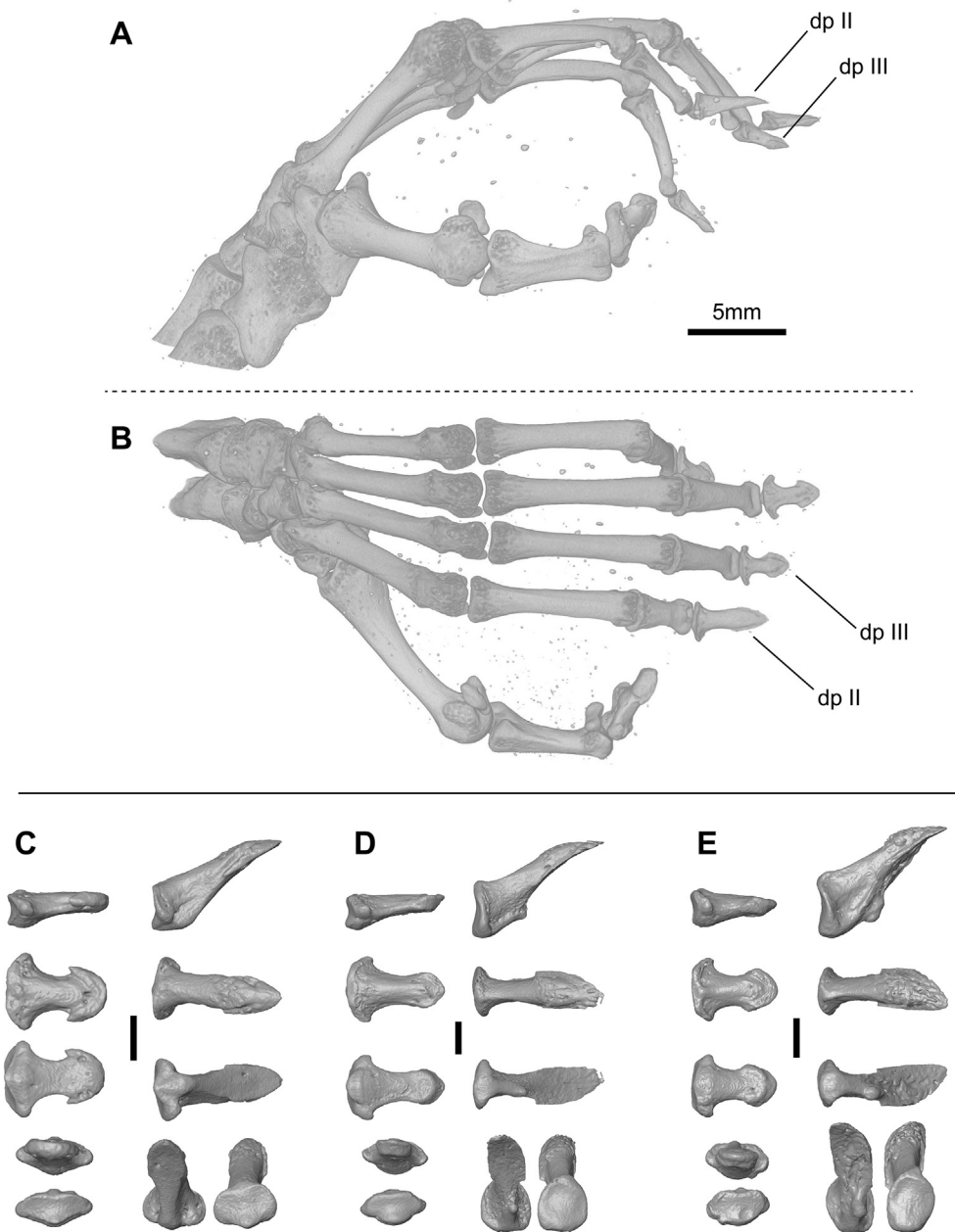
## 1. Introduction

Most extant primates have fleshy-tipped fingers and toes with flattened nails (ungulae) instead of sharp claws (falculae). Indeed, the presence of ungulae is often hypothesized to characterize the common ancestor of extant primates, possibly associated with the evolution of manual dexterity (Jones, 1916; Napier, 1961; Le Gros Clark, 1971; Cartmill, 1974; Soligo and Müller, 1999; Soligo and Martin, 2006; Bloch et al., 2007). Exceptions to the ubiquity of these traits include the presence of tegulae (a falcula-like morphology) found in the aye-aye (*Daubentonia madagascariensis*) and in marmosets and tamarins (Callitrichidae). However, it

is likely that tegulae secondarily evolved from the flattened ungulae more typical among primates (Hamrick, 1998; Soligo and Müller, 1999). Another exception to the ubiquity of ungulae in extant primates is the form of the keratinized structure supported by the distal phalanx of the second digit (dpII) of the foot. In some primates the pedal dpII resembles a dorsally projecting falcula more than a flattened ungula and is referred to as a ‘grooming claw,’ or ‘toilet claw,’ to reflect its observed use in autogrooming and/or scratching (Fig. 1). Groups exhibiting such a ‘grooming claw’ include strepsirrhines (lemurs, lorises, and galagos) and at least the owl monkey (*Aotus*) and titi monkey (*Callicebus*) among New World monkeys. In addition, tarsiers have a similar ‘grooming claw’ on both the second and third pedal digits (Soligo and Müller, 1999; Maiolino et al., 2011; Maiolino et al., 2012; von Koenigswald et al., 2012; Maiolino, 2015).

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**Figure 1.** Examples of 'grooming claw'-bearing distal phalanges and associated ungula-bearing phalanges in strepsirrhine primates. A–B) Foot of *Cheirogaleus major* (AMNH-M-31265) showing 'grooming claw' morphology on dpII next to ungula morphology on dpIII in medial (A) and dorsal (B) views. Image derived from MorphoSource media file #M10879-16410. C–E) Grooming phalanges and associated ungula morphology in several individual strepsirrhines: C) *Cheirogaleus major* (DPC 1285); D) *Galago senegalensis* (DPC 003); E) *Galago senegalensis* (DPC 1063F). Scale bar on C–E is 1 mm. Views from top to bottom are lateral, dorsal, ventral, distal and proximal.

Studies such as those by Maiolino et al. (2011) have shown that ungulae, falculae, tegulae and 'grooming claws' have underlying distal phalanges with distinctive, correlative morphology. Thus, it is possible to infer which type of keratinized structure was present in extinct primates based on fossilized distal phalanges. Primarily, ungular phalanges are distinguished by dorsoventral flattening, mediolateral expansion, and a distally shifted attachment for the long flexor tendon. Falcular phalanges and tegular phalanges tend to be dorsoventrally expanded, mediolaterally narrow and to have a shaft that is plantarly curved and hook-like (Patel and Maiolino, 2016). In addition, ungular and 'grooming claw' phalanges of primates tend to have an 'apical tuft,' a fan- or apron-like sheet of bone that rims the distal tip (Maiolino et al., 2011, 2012).

Debates about the appropriate terminology for the 'grooming claw' stem from different perspectives on (1) the morphological features that distinguish 'grooming claw'-bearing distal phalanges (grooming phalanges) from the bony phalanges underlying more typical falculae (falcular phalanges) and ungulae (ungular phalanges), and (2) the homology of these structures (Maiolino et al., 2011; von Koenigswald et al., 2012; Gebo et al., 2015).

Understanding the functional, developmental and phylogenetic basis of 'grooming claw' morphology contributes to understanding the evolutionary pattern of morphological divergence of euprimates from other euarchontans. More complete understanding of 'grooming claw' taxonomic distribution and morphological variation helps constrain hypotheses on the number of times these

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