

Morphology and evolution of the distal phalanges in primates

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Flat nails and scutiform distal phalanges characterize the hands and feet of primates. However, these display a variety of forms and combinations: Lemuroidea and Lorisioidea have a distinct pedal grooming claw; *Daubentonia* has additional claws; *Tarsius* has two pedal grooming claws; Callithrichidae have claws on fingers and most toes. The adapoid primates *Darwinius* and *Europolemur* from Messel have been interpreted both to have and to lack a grooming claw (Koenigswald, 1979; Franzen, 1994; Franzen et al., 2009).

A single two-state character, “presence or absence of claws or grooming claws,” was used to represent claws in the cladistic analyses of Seiffert et al. (2009), Williams et al. (2010), and Gingerich et al. (2010). However, the distal phalanges in primates are quite diverse, and the claws or claw-like structures of primates may not be adequately represented by a single two-state character. In a detailed survey we provisionally distinguished 11 morphological types of distal phalanges in primates. Some are shown in Figs. 1–11. In the course of this survey, we realized that it is not sufficient to simply note the presence or absence of particular types of distal phalanges, their occurrence on specific fingers or toes having great significance as well. Many primate taxa have distal phalanges of different forms on different digits of the hands and feet. Thus in addition to characterizing the form of individual phalanges, the position and combination with other types of phalanges has to be recognized.

Positions and combinations are especially important when isolated distal phalanges of fossils are discussed (Godinot 1992; Bloch et al., 2010) because their positions and combinations are unknowable. Very few skeletons of fossil primates are known that allow an unquestionable assignment of distal phalanges to specific fingers or toes. Messel in Germany is one of the few localities where such assignments are possible because the fossils are preserved in oil shale as partial or complete articulated skeletons.

To better understand *Europolemur* and *Darwinius*, we started a survey comparing the morphology of distal phalanges across primates. We included *Tupaia* as an outgroup. Zoological collections often have distal phalanges retained in skin preparations or, in articulated skeletons, partially hidden by ligaments. For this reason, it has been advantageous to use high-resolution virtual reconstructions from micro-CT scans.

Our preliminary results show some basic differences in different primates that will enable a more detailed characterization of their distal phalanges

(DP), and also of their positions and combinations on various digits of the hands and feet. Here we denote distal phalanges of the manus as M_I, M_{II}, M_{III}, M_{IV}, and M_V; and distal phalanges of the pes as P_I, P_{II}, P_{III}, P_{IV}, and P_V.

Scandentia, represented by *Tupaia* (Fig. 7), are characterized by laterally compressed claws with large tubercles for the insertion of the flexor tendon in all rays (M_I–M_V and P_I–P_V). The claws of *Tupaia*, in contrast to those of *Callithrix* (Fig. 11), have no lateral furrows (Le Gros Clark, 1936; Godinot, 1992).

Lemuroidea and Lorisioidea, represented by *Indri*, *Microcebus*, *Lemur* (Figs. 1, 2, 8), *Varecia* (Fig. 9), *Cheirogaleus* (Fig. 12), and others, have scutiform DPs on all digits of the hand. The shaft is well separated from the shield, which is pointed. M_I is of variable size but never prominent, in contrast to the enlarged and widened DP of P_I. The characteristic grooming claw, P_{II}, is elongated and slender. There is variability within Lemuroidea, but several characteristics were found that distinguish the grooming claws of lemurs, including *Daubentonia*, from claws of *Tupaia*. The remaining DPs (P_{III}–P_V) are typically scutiform. The only lemur known to lack grooming claws is *Archaeolemur*, which has no grooming claw in the reconstruction of Jungers et al. (2005).

Tarsioida, represented by *Tarsius* (Fig. 10, 13), has scutiform DPs on all fingers. The opposable P_I is scutiform, as are those of P_{IV} and P_V. P_{II} and P_{III} are commonly classified as “grooming claws”. However, they differ from lemuroid and lorisoid grooming claws not only in number and position, but also in their morphology. The grooming claws of *Tarsius* are short and have a triangular cross-section. A large attachment for the flexor tendon is present, well separated from the plantar side. Thus they are not a duplication of the lemuroid P_{II} but seemingly a similar but independent adaptation. The scutiform DPs of *Tarsius* are more similar to those of lemuroids and lorisoids than are the grooming claws.

Ceboidea, Cercopithecoidea, and Hominoidea have similar DPs on fingers and toes, and share the enlarged, widened, more or less scutiform DP of P_I. The pattern of the remaining digits does not show any differentiation of P_{II} or P_{III}. The morphology of these DPs seems to be basically different from that of lemuroids, lorisoids, and tarsioids. The DPs have a large articular facet, and the distal part is more columnar and rounded without being pointed (Fig. 4). Some genera show a tendency to develop some rugosity near the distal end (Fig. 5). This pattern was found, e.g., in *Cebus*, *Macaca*, *Mandrillus*, and *Pan*. Only a few genera developed properly scutiform DPs, best

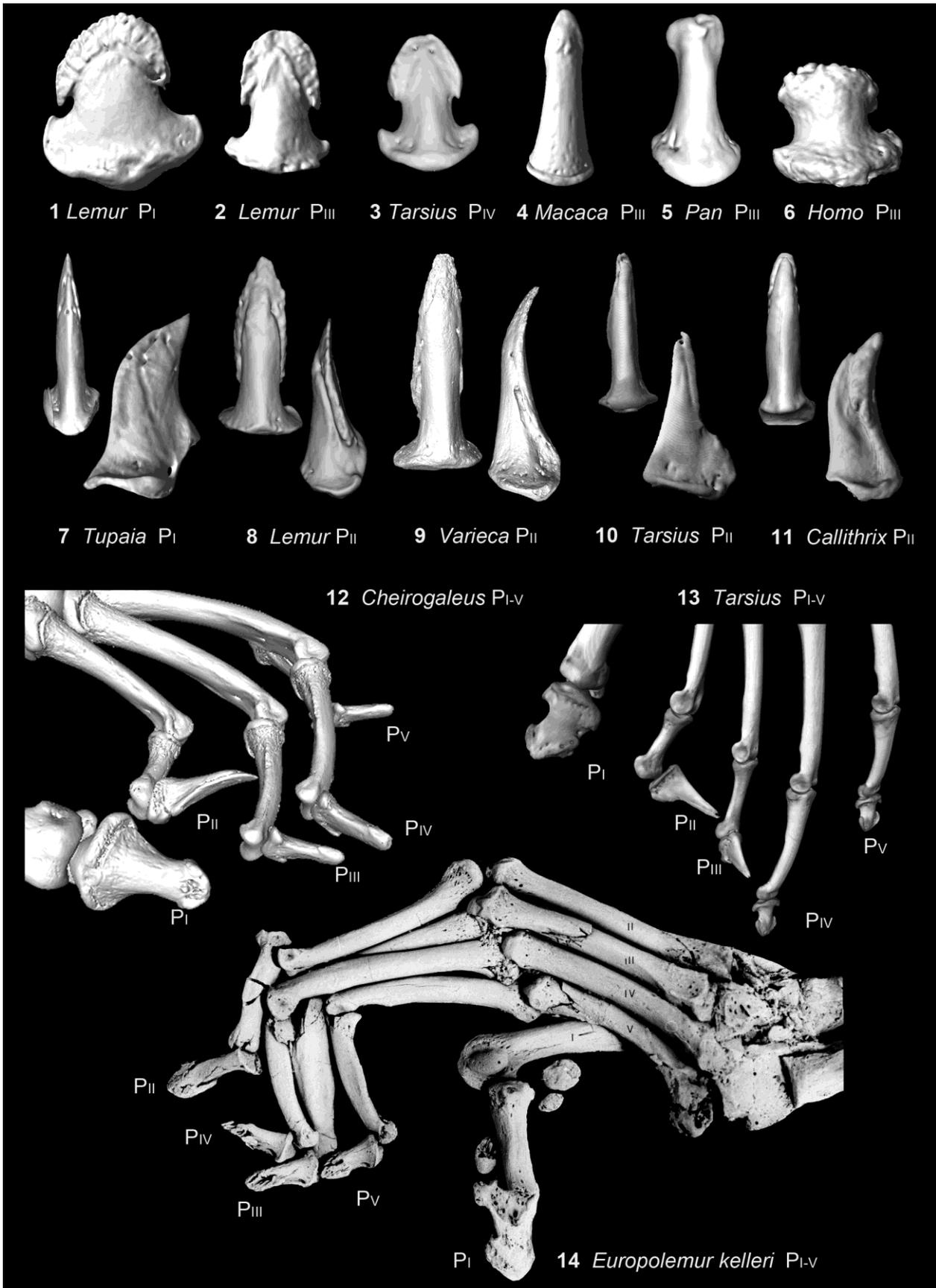


Figure 1-14. Morphological diversity of distal phalanges in the feet of primates and *Tupaia* in high-resolution images reconstructed from micro-CT scans (not to scale). 1-3: scutiform distal phalange (DP); 4: columnar DP; 5-6: columnar DP with terminal rugosity; 7: tupaïoid claw (in dorsal and lateral aspect); 8-9: lemuroïd grooming claw; 10: tarsioid grooming claw; 11: callithrichine claw; 12: lemuroïd foot pattern; 13: tarsioid foot patter; 14: adapoid foot pattern (*Europolemur kelleri* HLMD Me 7430).

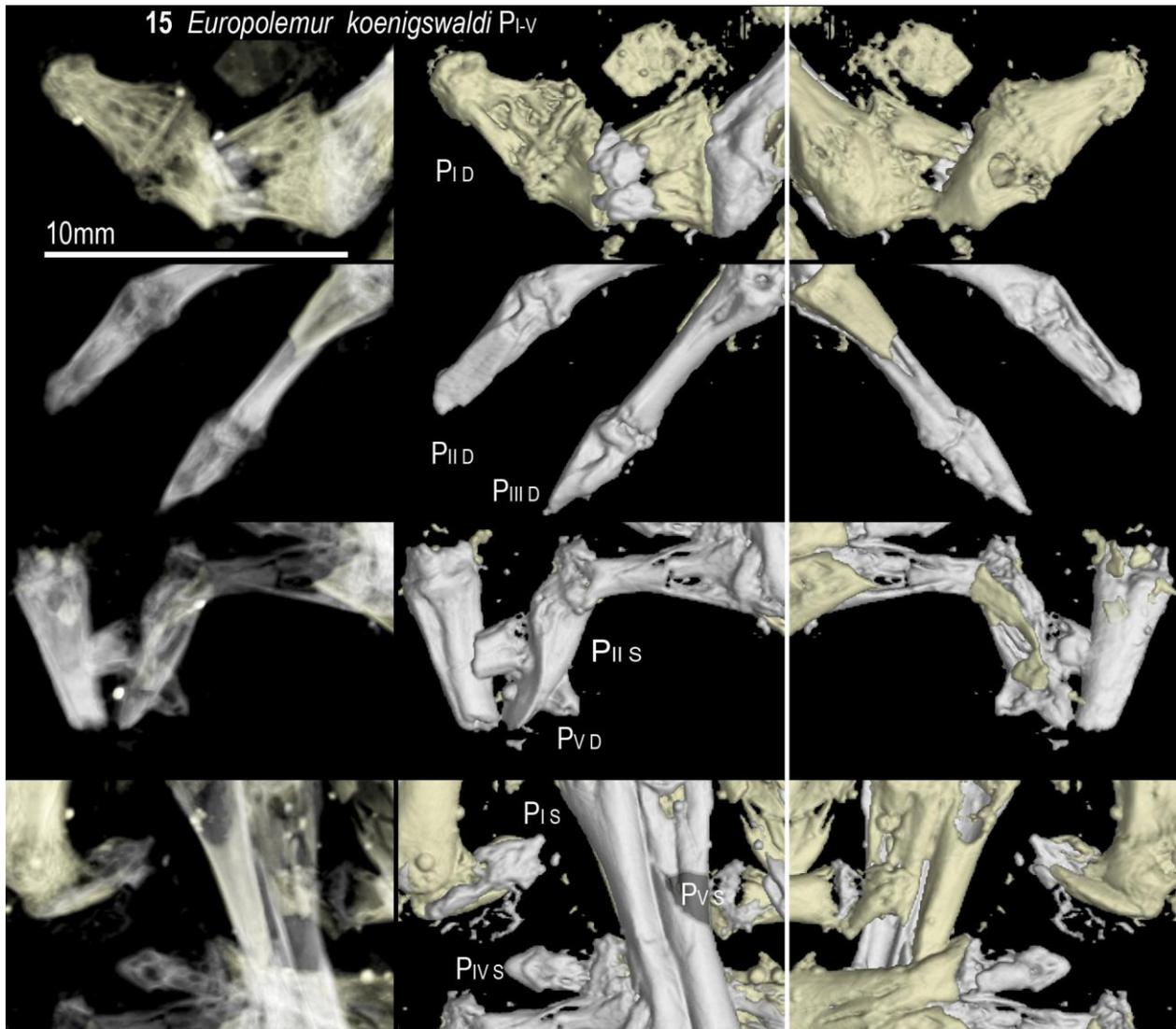


Figure 15. Adapoid foot pattern and distal phalanges of *Europolemur koenigswaldi* (SMNK-Me1125). Left and right foot are partially preserved on plate A (white color) and plate B (yellow-grey color). Micro-CT scans of both plates A and B are superimposed. Distal Pi–Pv are indicated with D for the right foot and S for the left foot. Frontal views (referring to plate A) are shown for X-rays in the left column, 3D surfaces in the middle column, and views from the back-side (referring to plate B) are shown in the right column.

seen in the hands of *Homo*. Most human pedal DPs (except Pi) are better described as rugose than as scutiform (Fig. 6). *Callithrix* has a clawlike development of manual and pedal DPs. Pi is scutiform as usual, but Mi–Mv and Pii–Pv are clawlike. These differ from claws of *Tupaia* in having a distinct lateral furrow (Godinot 1992).

Results of this preliminary survey of the DPs of extant primates enable the following comments on fossil proprimates and euprimates. *Plesiadapis* shows, as far as is known, claws without any differentiation of the various digits (Gingerich, 1976; Godinot and Beard, 1991; Boyer, 2009). *Carpolestes* has a widened, slightly scutiform Pi, other DP as far as is known seem to be clawlike (Bloch and Boyer, 2002). Adapoidea: *Europolemur kelleri* has a scutiform Pi; the Pii has distinct similarities to a lemuroid grooming claw, e.g., the exclusive differentiation of the Pii, the elongated Pii with a

distinct shaft, the low cross-section of the shield, the expanded lateral rims of the shield that extend to the plantar surface, and the flat and slightly concave plantar surface (Koenigswald, 1979). The remaining DPs (Piii–Pv) are scutiform as in lemuroids (Fig. 14). Similar morphology is found in *Europolemur koenigswaldi* (Fig. 15). The DPs differ from lemuroid DPs in having a distinct groove or foramen in the lateral side of the shaft. This foramen is found in other isolated DPs attributed to *Notharctus tenebrosus* (Bloch *et al.*, 2010). In *Darwinius masillae* the DPs of the hand are scutiform (Franzen *et al.*, 2009). The Pi is enlarged, the Pii slightly elongated. In Piv and Pv the scutiform outline can be recognized. However, it appears that parts of the DPs may have been brushed away during preparation and, in contrast to *Europolemur kelleri*, few anatomical details are discernable, especially on Pii. The claimed absence of a grooming claw in *Darwinius* is a subject of ongoing interpretation.

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