

# Hands of Early Primates

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**KEY WORDS** primate origins; nocturnal visual predation; vertical clinging and leaping; prosimian; grasping; omomyiform; adapiform; manual; Paleogene

**ABSTRACT** Questions surrounding the origin and early evolution of primates continue to be the subject of debate. Though anatomy of the skull and inferred dietary shifts are often the focus, detailed studies of post-crania and inferred locomotor capabilities can also provide crucial data that advance understanding of transitions in early primate evolution. In particular, the hand skeleton includes characteristics thought to reflect foraging, locomotion, and posture. Here we review what is known about the early evolution of primate hands from a comparative perspective that incorporates data from the fossil record. Additionally, we provide new comparative data and documentation of skeletal morphology for Paleogene plesiadapiforms, notharctines, cercamoniines, adapines, and omomyiforms. Finally, we discuss implications of these data for understanding locomotor transitions during the origin and early evolutionary history of primates. Known plesiadapiform species cannot be differentiated from extant primates based on either

intrinsic hand proportions or hand-to-body size proportions. Nonetheless, the presence of claws and a different carpometacarpal joint form in plesiadapiforms indicate different grasping mechanics. Notharctines and cercamoniines have intrinsic hand proportions with extremely elongated proximal phalanges and digit rays relative to metacarpals, resembling tarsiers and galagos. But their hand-to-body size proportions are typical of many extant primates (unlike those of tarsiers, and possibly *Teilhardina*, which have extremely large hands). Non-adapine adapiforms and omomyids exhibit additional carpal features suggesting more limited dorsiflexion, greater ulnar deviation, and a more habitually divergent pollex than observed plesiadapiforms. Together, features differentiating adapiforms and omomyiforms from plesiadapiforms indicate increased reliance on vertical prehensile-clinging and grasp-leaping, possibly in combination with predatory behaviors in ancestral euprimates. *Am J Phys Anthropol* 57:33–78, 2013. © 2013 Wiley Periodicals, Inc.

## INTRODUCTION

Morphological specializations that allow one-handed grasping (prehension) and object manipulation are thought to be key adaptations in primate evolution (Jones, 1916; Haines, 1955; Napier, 1960, 1961; Cartmill, 1974a,b; Godinot and Beard, 1991, 1993; Jouffroy et al., 1991; Godinot, 1992; Lemelin, 1996; Hamrick, 2001, 2007; Bloch and Boyer, 2002; Kirk et al., 2008). However, the distribution of these specializations, their functional significance, and their novelty relative to other arboreal mammals is poorly understood. For example, “Opposable thumbs” are often viewed by non-specialists, outside of the field of physical anthropology, as a defining feature of primates. However, authorities rarely, if ever, include it on the list of synapomorphies appearing in the common ancestor of all living primates (e.g., Le Gros Clark, 1971; Cartmill, 1972, Martin, 1986). Napier (1961), in a canonical work, found that “true opposability” was only present in catarrhine primates. Napier described “opposition” as the capacity to (1) rotate the thumb so that its ventral surface is at 90–180° to the ventral surfaces of the other digits, and (2) sweep the thumb ulnarly (medially) and ventrally toward the more ulnar (medial) digits (i.e., across the palm toward the pinky). Opposition was defined as a compound motion including sequential “flexion, abduc-

tion, and medial rotation” at the metacarpal-trapezium joint. Napier (1961) suggested that the ability for opposition in catarrhines is associated with a particular “sellar” (=saddle-shaped) morphology of the trapezium and a “misfit” between the metacarpal and trapezium facets that allowed a rocking motion at the joint. He argued that the sellar morphology of the trapezium is lacking in other primates, which instead exhibit more simple curvatures (cylindrical or flat) on their trapezia. Therefore, Napier’s findings imply that an opposable thumb was not a “key innovation” for the adaptive radiation of euprimates. He also suggested that “true

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opposability” is a necessary condition for effective use of a *precision grip* (Napier, 1960) that allows for easy “pulp-to-pulp” contact between the tip of the thumb and other digits in humans (as well as papionines) that have appropriate pollex/non-pollical digit proportions (i.e., the thumb is long enough relative to the other digits so that their tips can easily meet). Napier’s work thus leads to a different perspective on the adaptive significance of opposability in primate evolution: the restriction to catarrhines of features allowing opposition helps explain why platyrrhines or strepsirrhines have never developed a human- or gelada-like grasp pattern, or the ecological benefits it bestows.

While this scenario is elegant, it does not appear to be entirely accurate. Documentation of a sellar-shaped metacarpal facet on the trapezium in indriids (Jouffroy and Lessertisseur, 1959; Etter, 1974) and loriforms (Etter, 1978) contrasts with Napier’s (1961) characterization of these taxa as having a “pseudo-opposable” pollex (see definitions below). Furthermore, careful study of hand postures in *Cebus* suggest it also frequently uses effective precision grips (Spinozzi et al., 2004; Pouydebat et al., 2006, 2009), though these are probably not accomplished through “opposition movements” at the carpometacarpal joint as defined by Napier (1961), given that there is not enough rotation to allow full pad-to-pad contact between thumb and index finger (Spinozzi et al., 2004). Better documentation of the distribution of various specializations in the primate hand (both morphological and functional) remains essential for establishing the hand’s pattern of morphological change through time and the functional/adaptive consequences of such change. The fossil record provides the only direct evidence that allows for testing specific hypotheses focused on the evolution of unique and functionally significant suites of skeletal specializations that characterize the hands of the earliest primates and their descendants.

If the last common ancestor of all extant primates lacked opposable thumbs, then a question remains as to whether other characteristics of the hand of this form differed enough to set it apart from that of its ancestors. Hamrick (2001) hypothesized that increased elongation of the fingers (represented by the intermediate and proximal phalanges) relative to the palm (the metacarpals) represented such a key transformation in the last common ancestor of extant primates. This transformation was linked to the ecological exploitation of a “small branch milieu” and the subsequent adaptive radiation in that newly accessible niche. However, building on Hamrick’s work by incorporating more data on critical fossils and additional extant euarchontans, some researchers (Bloch and Boyer, 2002; Kirk et al., 2008) have shown that increased elongation of the fingers may have occurred earlier in the evolution of euarchontans and stem primates than proposed by Hamrick (2001). Other characteristics, previously described as innovations for the ancestor of extant primates, should be re-evaluated with a similar level of detail.

Ultimately, functional implications of hand morphology in early primates can influence competing hypotheses addressing the nature of adaptive transition(s) in the evolution and radiation of stem- and crown-primates. Here, we review the evidence from the hands of early fossil primates and their close relatives and discuss alternative ideas for some of the ecological transitions that occurred during early primate evolution. In particular, it has been suggested that hand morphology reflects increasing specialization for either a) locomotion and

foraging in a fine-branch niche (Hamrick, 2001, 2007; Bloch and Boyer, 2002; Bloch et al., 2007; Kirk et al., 2008); b) prehensile clinging on relatively “large” and often vertical supports (e.g., Napier and Walker, 1967; Godinot, 1991), c) manual predation in the fine branch niche in certain lineages derived from a clade of terrestrial/scansorial “olfactory-guided” insectivores (e.g., Cartmill, 1972, 1974a,b, 1992; Lemelin, 1996); or d) a “lunging grasp” (Godinot, 2007) predation style similar to that often used by galagos and tarsiers, in which the animal “almost leaps” by rapidly extending its hind limbs while reaching out and grabbing at prey but never disengaging from the substrate.

We begin by detailing functional attributes of primate hands and corresponding patterns of morphological variation reflecting these attributes. This section explains the current evidential and conceptual context in which the form–function relationships of early primate hands are understood, while also pointing out potential shortcomings. We then provide a summary of information currently available for early fossil primates, focusing primarily on plesiadapiforms, adapiforms, and omomyiforms. This section also includes new fossil and comparative data on hand anatomy for plesiadapiforms, early adapiforms and omomyiforms, and non-catarrhine primates. While such a review would ideally consider fossil hands of stem-anthropoids as well, the only such materials currently available are two isolated proximal phalanges assigned to the hand of *Apidium* (Hamrick et al. 1995). We include brief consideration of these bones as well as two manual phalanges assigned to *Aegyptopithecus* by Hamrick et al. (1995). Although *Aegyptopithecus* is a stem-catarrhine, its phalanges represent the only other remains of a Paleogene anthropoid, which is why we include it in our discussion. Finally we attempt some synthesis of these data in terms of the functional–adaptive transitions during early primate evolution. In summary, we hope to provide a clearer view of what is known of the hands of early fossil primates (Fig. 1, Tables 1 and 2), the transitions they underwent, and the functional and adaptive significance of these changes that will be helpful for future studies.

### Fossil taxa reviewed: Systematic considerations

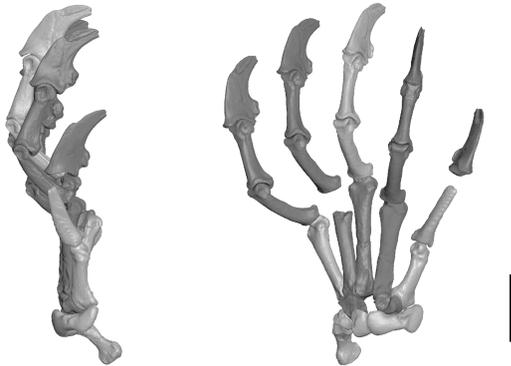
We are most interested in identifying key innovations in the hand skeleton that contributed to, or were perpetuated by, the radiation of extant primates from their common ancestor. This means examining morphological patterns in taxa that are phylogenetically basal to the ancestor of extant primates, but closer to extant primates than to other extant taxa. Animals that meet these criteria can be considered “stem primates.” We are also interested in the earliest members of “crown primates,” the clade including extant primates and their common ancestor. Essentially, if we want to know what the common ancestor of extant primates looked like and what evolutionary steps occurred to make it that way, it is important to document as many stem primates and early members of crown primates as possible. Plesiadapiforms, a geographically widespread radiation of Paleogene mammals (Silcox et al., 2007), are the only group of fossils widely regarded as probable stem primates (Simpson, 1935; Gingerich, 1976; Szalay and Delson, 1979; Szalay et al., 1987; Bloch and Boyer, 2002; Bloch et al., 2007; Janecka et al., 2007). Though various researchers remain skeptical about plesiadapiforms as stem primates [see Godinot (2007)]

and some well-sampled cladistic analyses contradict this idea (e.g., Ni et al., 2013), plesiadapiforms are universally regarded as members of Euarchonta, a group whose extant members include primates, dermopterans (*Cynocephalus* and *Galeopterus*, the “flying lemurs”), and scandentians (Tupaïidae and Ptilocercidae, the tree shrews) (Szalay and Decker, 1974; Szalay and Delson, 1979; Szalay and Dagosto, 1980; Szalay and Drawhorn, 1980; Sza-

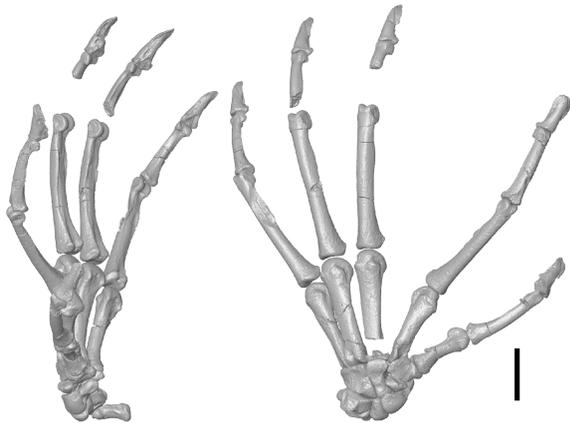
lay et al., 1987; Bloch and Boyer, 2002; Bloch et al., 2007; Cartmill, 2012). At the very least, plesiadapiforms are the only euarchontans with a sampled postcranial fossil record just prior to the appearance of taxa usually assumed to be members of euprimates. As such, they can help evaluate hypotheses for morphological and ecological transitions involved in primate origins (Bloch and Boyer, 2002). They can help provide an understanding of what aspects of euprimate hands are primitive, as well as what features are more likely to be innovations within a lineage close to the common ancestor of euprimates.

While plesiadapiforms may represent primates of the Paleocene, at the beginning of the Eocene (55.8 million years ago), a new kind of primate appeared (Gingerich, 1986; Smith et al., 2006; Rose et al., 2011). These “new primates” are typically referable to either the Omomyiformes or Adapiformes, the two principal Eocene radiations of primates. They are often assumed to be part of the crown clade (Wible and Covert, 1987): the former is assigned to haplorhines, whereas the latter is frequently aligned with extant strepsirrhines (Szalay and Delson, 1979; Beard et al., 1988; Dagosto, 1990; Kay et al., 1997, 2004; Godinot, 1998; Seiffert et al., 2009). However, debate continues about the validity of the adapiform–strepsirrhine relationship (Franzen et al., 2009; Seiffert et al., 2009; Boyer et al., 2010b; Gingerich et al., 2010; Williams et al., 2010; Gingerich, 2012; Maiolino et al., 2012), as some researchers have suggested anthropoid or haplorhine affinities for adapiforms. Hoffstetter (1977) used the term “Euprimates” in reference to a specific formulation of crown primates that includes omomyiforms and adapiforms as stem-haplorhines and stem-strepsirrhines, respectively. However, it is important to keep in mind the possibility that the Eocene radiations also represent stem groups (like plesiadapiforms) given that they do maintain significant differences from all modern radiations and remain under-sampled. The likelihood of this possibility should not be underestimated, as new data continue to change perspectives. For instance, though most postcranial materials known for omomyiforms reveal no features contradicting a “prosimian-like” morphotype for the ancestor of living primates, and suggest that omomyiforms were

*Plesiadapis cookei* (UM 87990\*)



*Notharctus tenebrosus* (AMNH 127167)



*Adapis parisiensis* (RD 311\*)

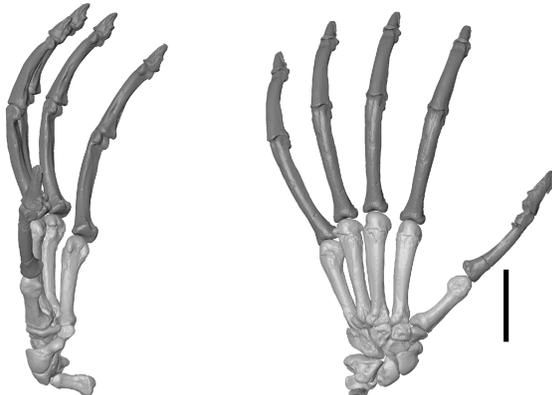


Fig. 1.

**Fig. 1.** Three fossil primate hand reconstructions (*Plesiadapis*, *Adapis*, *Notharctus*). Reconstructed hands depicted in radial (left) and dorsal views. Both *Plesiadapis* and *Adapis* represent composites (\*). The *Plesiadapis* reconstruction is based on UM 87990 from Clarks Fork Basin locality SC-117. The dark gray bones are tentatively assigned to the specimen (see text). Phalanges on all non-pollical digit rays represent the same three bones, replicated to give a more complete (if hypothetical) view of the hand. The *Notharctus* reconstruction is based on AMNH 127167 (Hamrick and Alexander, 1996). Note that lengths of intermediate phalanges (IP) 3-4, and metacarpal (MC) 3 are not known. The *Adapis* reconstruction is primarily based on Rosières 311 (e.g., Godinot and Beard, 1991). Three isolated phalanges from the Phosphorites de Quercy were scaled to represent locality mean proportions of MC3, proximal phalanges (PP), IPs, and distal phalanges (DP). All proximal phalanges illustrated are AMNH 140719, intermediate phalanges are an un-numbered specimen from the Montauban Quercy collection (MaPhQ), and distal phalanges are UM ECA 1400 (Godinot, 1992). Note the hyperextension of the metacarpophalangeal joints on clawed *Plesiadapis*, the wide divergence between both MC1-2 and MC2-3 in *Notharctus*, and that MC2 is relatively much shorter in *Notharctus* compared to *Adapis*. Scale bar is 10 mm in length.

TABLE 1. *Plesiadapiform Fossil Material*

Taxon	Specimen/s	Elements represented	Publications	Summary
<i>Plesiadapis cookei</i>	UM 87990	R, U, Sc, Ln, Tr, Ps, MC1,5; PP, IP, DP	Hamrick 2001 Bloch & Boyer, 2002; 2007; Bloch et al., 2007; Boyer & Bloch, 2008 Kirk et al., 2008	Treeshrew-like digit proportions Claw-clinging arborealism with sensory tendencies. Less prehensility than other plesiadapiforms Proportions similar to <i>Arctictis</i> . Less prehensile than other plesiadapiforms Ambiguity in carpal and metacarpal associations. Low pollical divergence and more prehensility than previously recognized Composite digit ray showed hyperextended metacarpophalangeal joint, and palmar-flexed interphalangeal joints. Reconstructed as a claw-clinging arborealism Arboreal quadruped
<i>Plesiadapis tricuspidens</i>	MNHN R (550, 597), BR (11399, 5440) MNHN BR-07-L, BR 70713, R (411, 546, 443, 452, 1521, 5196) MNHN R 5321 MNHN R 5320 MNHN R 5295 (and 3 un-numbered) MNHN R 5364 (and 1 un-numbered) MNHN R 5305, MNHN R 5373 MNHN R (503, 5303, 5297, 5315), Divers Coll. No#, BR 14538 MNHN R (5296, 5363, 5324, 5341, 5360, 5330, 5346, 5342, 5369), BR 14536, plus 11 un-numbered MNHN R (5344, 539, 5379, 613, 612, 5361, 5309, 5313) MNHN coll. Menat specimen	R U Hm Tr MC3 MC4 MC5 PP IP DP	Godinot & Beard, 1991, 1993  Beard, 1989, 1993a,b  Youlatos & Godinot, 2004  Boyer 2009  Russell, 1967; Gingerich, 1976; Boyer, 2009 Beard, 1989, 1990; 1993ab  Boyer & Bloch, 2008; Kirk et al., 2008 Boyer, 2009; Boyer et al., 2010a  Simpson, 1935 Beard, 1989 Boyer & Bloch 2008; Kirk et al. 2008; Boyer 2009 Bloch & Boyer, 2007; Bloch et al., 2007; Kirk et al., 2008; Boyer & Bloch, 2008	Arboreal quadruped with quantitative similarities to <i>Ratufa</i> noted  Arboreal quadruped; more generalized behavior and more robust than slender bodied, suspensory specialized taxon of similar size <i>P. cookei</i>
<i>Plesiadapis insignis</i>	USNM 442229	Articulated hand/forelimb R, U, Sc, Hm, Cp, Ps, MC1,3,5; PP, IP, DP	Russell, 1967; Gingerich, 1976; Boyer, 2009 Beard, 1989, 1990; 1993ab	Squirrel-like body plan; arboreal to scansorial behavior Arboreal quadruped, high pollical divergence, dermopteran synapomorphies
<i>Nannodectes intermedius</i>	AMNH 17379	R, U, MC1,3; PP, IP, DP	Boyer & Bloch, 2008; Kirk et al., 2008 Boyer, 2009; Boyer et al., 2010a  Simpson, 1935 Beard, 1989	Arboreal quadruped, no valid Arboreal quadruped, similar to <i>N. intermedius</i> Dermopteran synapomorphies Claw-clinging arborealism with euprimates synapomorphies Arboreal quadruped, similar to <i>N. intermedius</i>
<i>Dryomomys szalayii</i>	UM 41870	R, U, Carp, MC1-5; PP, IP, DP	Boyer & Bloch 2008; Kirk et al. 2008; Boyer 2009 Bloch & Boyer, 2007; Bloch et al., 2007; Kirk et al., 2008; Boyer & Bloch, 2008	Arboreal quadruped, similar to <i>N. intermedius</i> Arborealism with specializations for sensory activities. Fingers shorter than toes. IPs shorter than PPs. No evidence for gliding

TABLE 1. Continued

Taxon	Specimen/s	Elements represented	Publications	Summary
<i>Tinimomys graybullianus</i>	UM 85176 USNM 461201	R, U Forelimb	Beard, 1989; 1993a,b Boyer & Bloch, 2008 Beard, 1989; 1993a,b Boyer et al., 2010a	Dermopteran-like morphology Similar to suspensory taxa and <i>Philocercus lowii</i> Includes elongated dermopteran-like IP MC5 is similar to MC of USNM 442229
<i>Ignacius graybullianus</i>	USNM 530203 (B&B2008-Fig. 11.7) USNM 442232 USNM 442256	R, MC1-3,5; PP,IP, DP R PP	Boyer & Bloch, 2008 Beard, 1989; 1990; 1993a,b Krause, 1991	Similar to <i>Dryomomys szalayii</i> in hand proportions Dermopteran-like IP & PP suggesting mitten-gliding Taxon & ray attributions of Beard (1990) not reliable. Dermopteran-like IP/PP ratio questionable Do not exhibit elongation similar to dermopterans
<i>Ignacius clarkforkensis</i>	USNM 442253 USNM 442255	IP IP	Runestad & Ruff, 1995 Hamrick, 1999	IPs most similar to pedal elements of bats, not dermopterans
<i>Phenacolemur jepseni</i>	UM 108210	R, U, MC1, 3-4, PP, IP, DP	Bloch & Boyer, 2007; Bloch et al., 2007; Kirk et al., 2008; Boyer & Bloch, 2008	Lacks dermopteran-like IP/PP ratio as well as other "dermopteran" features. Primate-like prehensility.
<i>Phenacolemur praecox</i>	UM 82606 UM 39926 USGS 17847 UM 86440; 86352	MC5 Sc Tr PP, IP	Beard, 1989; 1990 Beard, 1989; 1990 Boyer & Bloch, 2008	Triangular dermopteran-like shape.
<i>Phenacolemur simonsi</i>	USNM 442261-64 USNM 442265, 442268 USNM 445258 USNM 442247-49 USNM 442250-52, 442254 UM 101963	R U MC1 PPs IPs R, U, Carp, MC1-5, PP, IP, DP	Beard, 1989; 1990; 1993a,b; Krause, 1991; Runestad & Ruff, 1995; Hamrick et al., 1999 Bloch & Boyer, 2002; Bloch & Boyer, 2007; Bloch et al., 2007; Boyer & Bloch, 2008; Kirk et al., 2008	Dermopteran-like morphology. No uniquely dermopteran-like morphology. Same as <i>I. graybullianus</i> .
<i>Carpolestes simpsoni</i>				Grasping extremities. Distal phalanges suggest better developed pads than other plesiadapiforms. Terminal branch niche.

Abbreviations: R, radius; U, ulna; Cp, capitate; Ce, centrale; Ln, lunate; Tr, trapezoid; Trp, trapezium; Trm, trapezium; Hm, hamate; Ps, pisiform; MC, metacarpal;  
PP, proximal phalanx; IP, intermediate phalanx; DP, distal phalanx.

TABLE 2. *Adapiform* & *Omomyiform* Fossil Material

Taxon	Specimen/s	Elements represented	Publications	Summary
<i>Europolemur koenigswaldi</i>	SMF-ME 1228	R, U, MC1-5, PP1-5, IP3-4, DP2-3	Franzen, 1987; 1988; 1993; Franzen & Frey, 1993; Godinot & Beard, 1991; 1993	Arboreal quadruped with some ability for vertical clinging and leaping, most comparable to extant callitrichids in limb proportions.
<i>Europolemur kelleri</i> (Mesel adapid)	SMF-ME 1683	R, U, Carp., MC1-5, PP1,2,4,5, IP2 & 5, DP1-2	Franzen, 1988; 1993; Godinot & Beard, 1991; 1993; Hamrick, 1996; 2001	More similar to <i>Notharctus</i> and <i>Smilodectes</i> than to <i>Adapis</i> , long digits and reduced metacarpals may in ancestral condition for euprimates. Some similarities to grasp-leapers.
<i>Godinotia neglecta</i>	GMH L-2	R, U, Carp., MC1-5, PP1-5, IP3-5, DP1,4,5	Godinot, 1992; Thalmann et al., 1989; Thalmann, 1994	Features of both vertical clinging and leaping and above-branch quadrupedalism are present. More similar to other cercamonines, <i>Notharctus</i> , and <i>Smilodectes</i> than to adapines.
<i>Darwinius masillae</i>	PMO 214.214	R, U, Carp., MC1 and 5 (full), MC3 and 4 (partial), PP1-5, IP 2-5, DP1-5	Franzen et al., 2009	Generalized above-branch quadruped similar to galagids
<i>Notharctus tenebrosus</i>	AMNH 127167	R, U, Sc, Ln, Tr, Ps, Hm, Cp, Ce, Trp, Trm, Px, MC1,2,4,5 (full), MC3 (partial), PP1-5, IP2 and 5 (full), IP3-4 (partial), DP1-5	Hamrick, 1996; 2001; Hamrick & Alexander, 1996; Kirk et al., 2008	Similar to pronograde lemurids and platyrrhines. Digit proportions similar to <i>Tarsius</i> and <i>Daubentonia</i> . Hand morphology suggests the euprimate common ancestor was arboreal, pronograde, and grasp-leaping.
	AMNH 11474	R, U, Hm, Cp, Tr, Ps, MC1 and 4, PP2 and 3 (full), PP4 (partial), IP2-4	Godinot, 1992; Godinot & Beard, 1991; 1993; Gregory, 1920; Jouffroy et al., 1991	Gregory: Manus of <i>Notharctus</i> more similar to <i>Lemur</i> than to <i>Cebus</i> , perhaps some leaping specializations.
	AMNH 11478	R, U, Hm, MC2-5, PP3-4 (full), PP2 and 5 (partial), IP3 and 5 (full), IP4 (partial), DP		Godinot and colleagues: Greater emphasis on palmigrady in <i>Notharctus</i> than <i>Smilodectes</i> . Short metacarpus and long digits not likely to be indicative of grasp-leaping.
<i>Smilodectes gracilis</i>	USNM 21932 USNM 21951 USNM 22009-11 CM 11910 USNM 13251A/B	Cp Hm Sc Sc, Ln, Tr, Ps, Cp, Ce, Trm	Beard & Godinot, 1988	Carpus of <i>Notharctus</i> intermediate between <i>Smilodectes</i> and <i>Adapis</i> . Likely an arboreal quadruped with some leaping.
	USNM 21815 USNM 21954 USNM 21964 USNM 256745 RD 311	Tr, Hm, Cp Sc, Ln, Hm, Cp Hm, Tr, Cp Ln, Pi R, U, Sc, Ln, Tr, Ps, Hm, Cp, Ce, Trp, Trm, Px, MC1-5	Beard & Godinot, 1988; Godinot & Beard, 1991; 1993; Hamrick, 1996c	Beard and Godinot: Broad locomotor repertoire that includes leaping and occasional use of vertical substrates.
<i>Adapis parisiensis</i>	MC: NMB QL 460, QD 60, QL 462 (PP unnumbered)	MC2-4, three PP	Beard & Godinot, 1988; Dagosto, 1983; Godinot, 1991; 1992; Godinot & Beard, 1991, 1993; Godinot & Jouffroy, 1984; Hamrick, 1996c; Jouffroy et al., 1991; Dagosto, 1988	Hamrick: Shares carpal features with extant arboreal quadrupeds Likely an arboreal quadruped with a mobile wrist perhaps indicating increased climbing.
				An agile arboreal quadruped. No osteological indicators for grasp-leaping present in the hand, but still a capable climber.

TABLE 2. Continued

Taxon	Specimen/s	Elements represented	Publications	Summary
<i>Leptadapis magnus</i>	MC: NMB QL 425, WL 900, QF 799, QF 791; PP: QD 495, QL 271, QD 735; IP: QG 382	MC2-5, three PP, one IP	Dagosto, 1983	Similar to <i>Adapis</i> , but perhaps a slower and more cautious climber. Hands prehensile with no osteological indicators for leaping.
<i>Omomys carteri</i>	UM 32306	Hm	Hamrick, 1999	Resembles small-bodied pronograde arboreal primates such as <i>Cheirogaleus</i> and <i>Microcebus</i> .
<i>Teilhardina belgica</i>	UM 32319a, b	Hm, Ps	Gebo et al., 2012	Elongate relative to proximal phalanges, similar to <i>Tarsius</i>
<i>Aegyptopithecus</i>	IRNSB M1266, IRNSB Vert 26857-04	IP3/4 (full), IP3/4 (partial)	Hamrick et al., 1995	PP strongly curved with strong proximally positioned flexor sheath ridges, and dorsal tilt of proximal articular surface, suggesting hyper extension of metacarpophalangeal joints. Similar to <i>Alouatta</i> , <i>Lagothrix</i> , and <i>Colobus</i> . Consistent with arboreal quadrupedalism and powerful grasping, with frequent flexion of interphalangeal joints.
<i>Apidium</i>	DPC 1005, DPC 1650	PP	Hamrick et al., 1995	PP straight with weak flexor sheath ridges and shallow distal condyles. Greatest similarity to <i>Cebus</i> , <i>Cercopithecus</i> , and <i>Presbytis</i> . More emphasis on extension of interphalangeal joints; arboreal quadruped analogous to <i>Saimiri</i> .

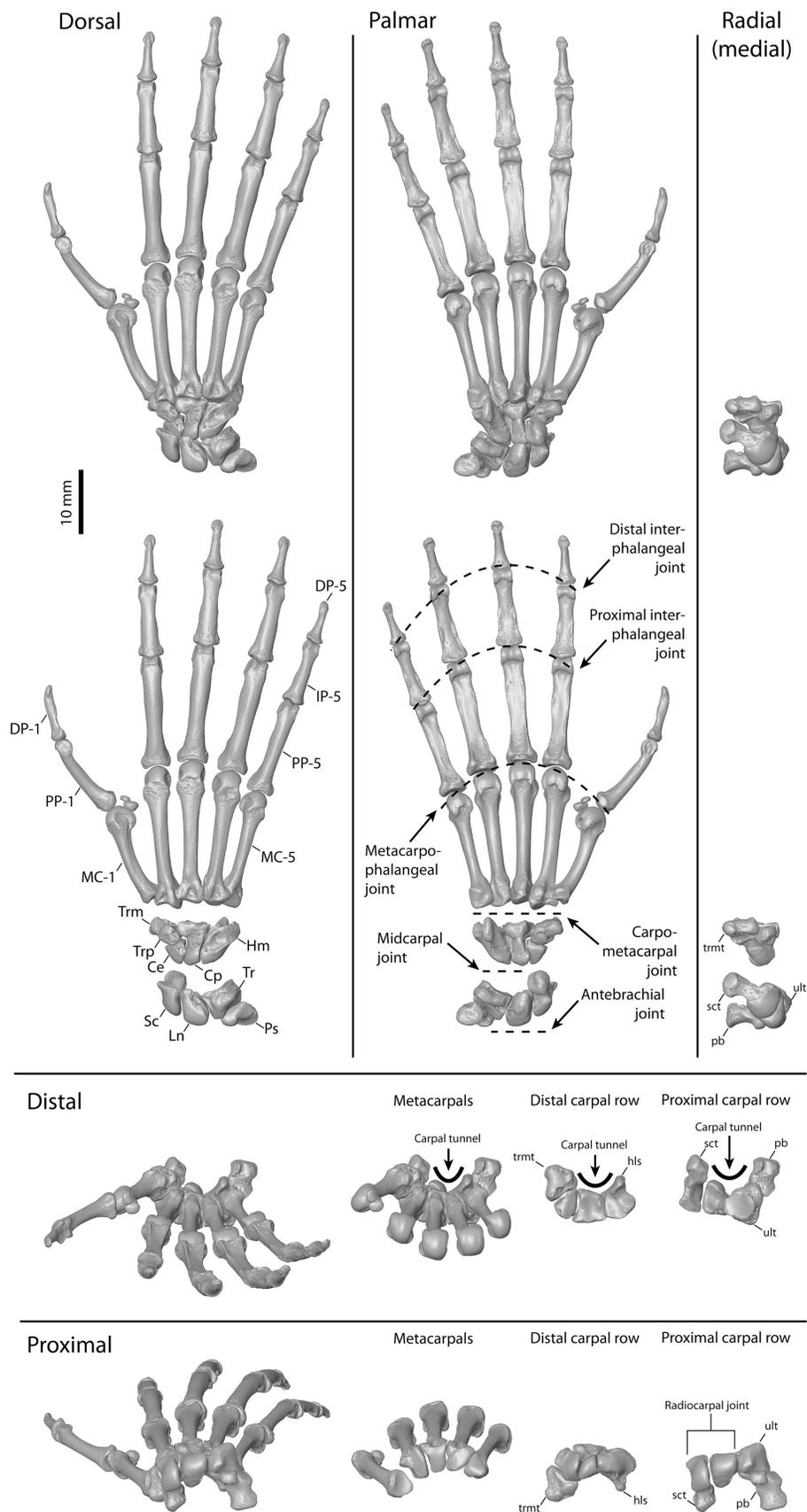
Abbreviations: R, radius; U, ulna; Cp, capitate; Ce, centrale; Sc, scaphoid; Ln, lunate; Tr, triquetrum; Trp, trapezoid; Trm, trapezium; Hm, hamate; Ps, pisiform; Px, prepollex; MC, metacarpal; PP, proximal phalanx; IP, intermediate phalanx; DP, distal phalanx.

adaptively analogous to various living prosimians (Gebo, 1988; Dagosto, 1993; Boyer et al., 2013), recent findings challenge this perspective. The articulated partial skeleton of *Archicebus achilles* (Ni et al., 2013) reveals long metatarsals (unlike tarsiers or strepsirrhines) and a long tibia, giving it more tree-shrew-like (or platyrrhine-like) foot and hind limb proportions.

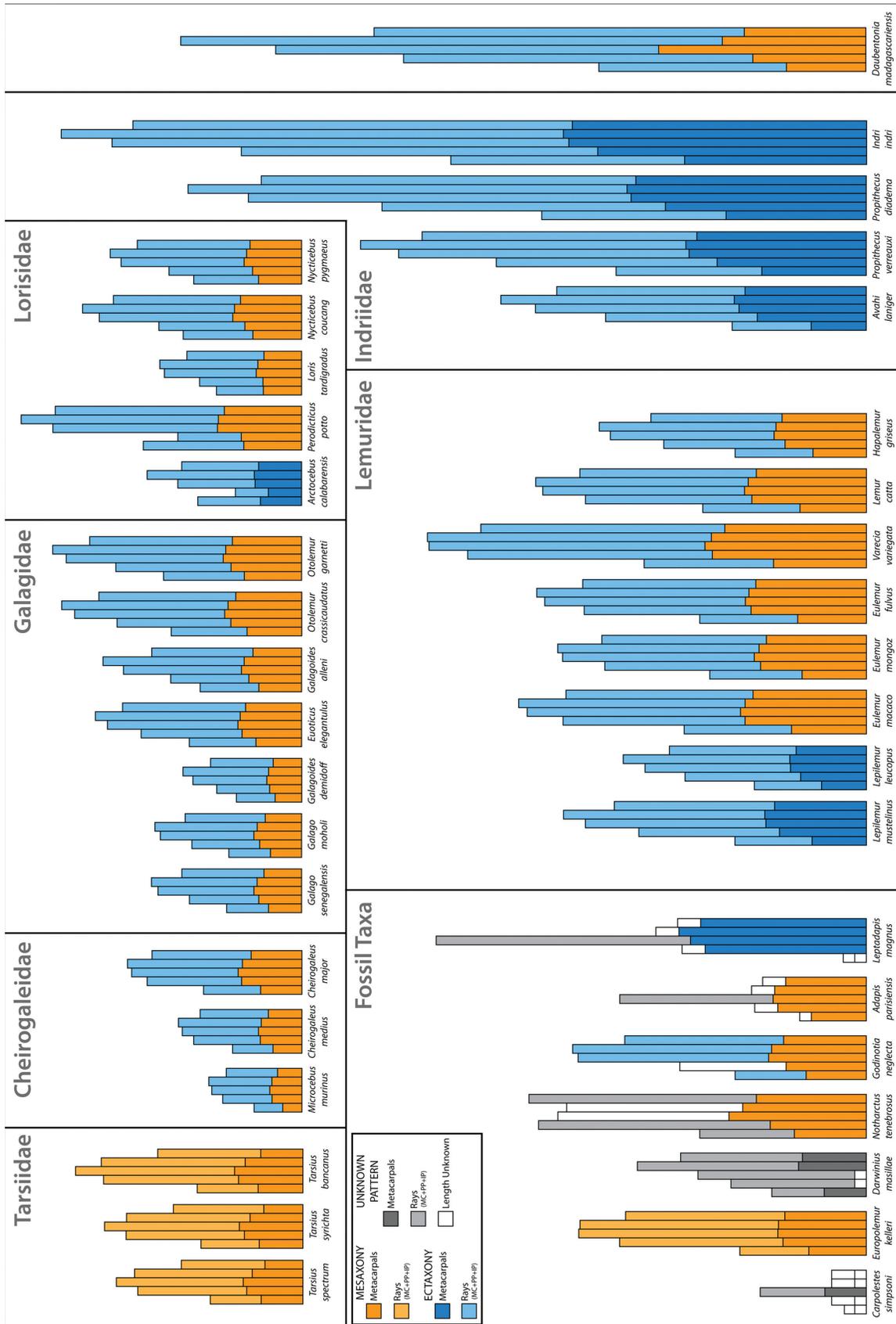
Simons (1972) used the term “primates of modern aspect” with less presumption about the phylogenetic relationships of omomyiforms and adapiforms. Wible and Covert (1987) suggested that referral of omomyiforms and adapiforms to “primates of modern aspect” is justified since the overwhelming majority of cladistic synapomorphies optimized for the crown primate ancestral node in their review are also present in these groups. If any omomyiforms or adapiforms are actually stem primates, we feel Wible and Covert’s (1987) criterion for assessing the validity of the term “primates of modern aspect” is still somewhat arbitrary. We also are slightly uncomfortable with Simons’ term as it implies that extant taxa are “modern” in some phylogenetically important sense as compared to extinct ones, though this is not necessarily so. Despite some uncertainty about the position of omomyiforms and adapiforms, we think the term “Euprimates” (Hoffstetter, 1977) retains utility given that 1) the best-supported hypotheses of primate supraordinal relationships continue to place omomyiforms and adapiforms as members of the crown group (e.g., Seiffert et al., 2009; Gladman et al., 2013) and 2) omomyiforms and adapiforms are likely close to the base of the crown group even if they are not all technically members of it.

### Anatomical correlates for functional attributes among early primates

Wrist joints in primates include the articulation between the carpals and forearm bones (radiocarpal and ulnocarpal, or antebrachial joint), the articulations between the proximal and distal carpal rows (midcarpal joint), and the articulations of the carpals and metacarpals (carpo-metacarpal joints) (Fig. 2). They have been well studied in both “prosimian” and platyrrhine primates (Beard and Godinot, 1988; Whitehead, 1993; Hamrick, 1996a,b,c, 1997; Hamrick and Alexander, 1996; Schwartz and Yamada, 1998) as well as in catarrhines, though the latter is not a focus of this review. The form of these bones has been linked to various functional attributes of the wrist, including its degree of mobility in flexion and extension, as well as abduction and adduction (Godinot and Jouffroy, 1984; Preuschoft et al., 1993; Hamrick, 1996b,c, 1997; Hamrick and Alexander, 1996). The morphology of wrist bones can also reflect habitual position and direction of greatest mobility (i.e., palmar-flexed, dorsiflexed, ulnar-deviated; Preuschoft et al., 1993). Finally, wrist bones can reveal stable hand positions, the directions in which forces can be effectively transmitted and sustained (Hamrick, 1996b,c, 1997; Hamrick and Alexander 1996), and the relative development of the extrinsic digital flexors (Hamrick, 1997). These form–function relationships must be taken with a grain of salt, however, as some predictions of morphological variation based on biomechanical principles (Preuschoft et al., 1993) have not been upheld in comparative studies (Hamrick, 1997). In fact, experimental work has shown that hand postures can be quite variable relative to expectations based on comparative morphology and behavioral categorization (Lemelin and Schmitt, 1998).



**Fig. 2.** Anatomical features and terminology for the hand illustrated using *Cebus apella* (EA 054, Duke Univ. Coll.). Abbreviations: Ce, centrale; Cp, capitate; DP, distal phalanx; hls, hamate hamulus; Hm, hamate; IP, intermediate phalanx; Ln, lunate; MC, metacarpal; PP, proximal phalanx; pb, pisiform body; Ps, pisiform; Sc, scaphoid; sct, scaphoid tubercle; Tr, triquetrum; Trm, trapezium; trmt, trapezium tubercle; Trp, trapezoid; ult, tubercle for ulnarisiform ligament.



**Fig. 3.** Axonic patterning of extant and fossil primate hands. Relative lengths of all five metacarpals and digit rays (from left to right). Mesaxonic and ectaxonic patterning are indicated for both metacarpals and digits. For clarity, paraxonic patterning is not considered. All lengths are proportionally displayed and generated from species means. Note that most strepsirrhines have mesaxonic metacarpals within ectaxonic hands (with the exceptions of indrids, *Lepilemur*, and *Arctocebus*). Fossil taxa, with the exception of *Leptadapis*, have mesaxonic metacarpals. *Godinotia* follows the strepsirrhine pattern of ectaxonic digits, while *Europolemur* displays slight mesaxony.

Typical hand postures may be strongly contingent on substrate size and orientation, as has recently been demonstrated for *Microcebus* (Reghem et al., 2012).

When evaluating the degree and nature of wrist mobility (at both the proximal and distal carpal rows), facet shape is an important consideration. Highly curved facets should permit a greater amount of mobility while maintaining stability (Hamrick, 1996a,b). Typically, a greater degree of curvature at carpometacarpal joints is thought to allow more flexion and extension of the metacarpals (Godinot and Beard, 1991). As noted above, the shape of the trapeziometacarpal joint has been assigned great significance for allowing pollical opposition. In prosimians, the triquetral facet of the hamate is described as a “spiral” that leads to pronation during ulnar deviation at the midcarpal joint (Jouffroy and Lessertisseur, 1959; Jouffroy, 1975; Hamrick, 1996b,c). As the same facet becomes more convex and forms a more pronounced arc with the articulating capitate (the midcarpal joint), a greater degree of stable mobility becomes possible (Hamrick, 1996a,b,c). Furthermore, a greater distal extent of the triquetrohamate facet should allow greater ulnar deviation (Hamrick, 1996b).

The orientations of facets also have functional implications. On the scaphoid and lunate, dorsally oriented facets for the radius indicate habitually dorsiflexed postures, whereas proximally oriented ones suggest more neutral or palmiflexed postures (Godinot and Beard, 1991; Godinot, 1992). The hamate’s facet for the triquetrum is strongly proximodistally aligned in some taxa (likely in part related to a greater distal extent of the facet) such that the metacarpals are more strongly ulnarly deviated with respect to the forearm during closest-packed postures (Godinot and Beard, 1991, 1993; Godinot, 1992; Hamrick, 1996b,c, 1997; Hamrick and Alexander, 1996). Furthermore, a dorsal exposure of the triquetral facet may allow greater force transmission through a partially supinated midcarpal joint (Hamrick, 1996c). The orientation of the metacarpal facet on the trapezium correlates with the degree of pollical divergence.

Fit between facets is another an important indicator of mobility. Napier (1961) notes that for those primates with an opposable pollex, the radii of curvature of the articular surfaces differ, allowing the pollex to rock on the trapezium. Hamrick (1996a) found that increasing convexity of “male” (convex) facets correlates with increased mobility, while female facets show the reverse trend. This implies that increased joint mobility will be achieved in the context of either 1) increased misfit between male and female articulating facets, as suggested by Napier (1961) for the thumb or 2) an increasing ratio of male facet area to female facet area.

Relative carpal size can also be informative about wrist mobility and hand postures. The relative size of the triquetrum compared to hamate may correlate with degree of ulnar deviation of hand (Hamrick, 1996a). Both an enlarged pisiform (Hamrick, 1996b,c, 1997) and a non-articular tubercle on the triquetrum for the ulnospisiform ligament (Godinot and Beard, 1991; Hamrick, 1996b) correlate with habitual dorsiflexion and pronograde body postures. An enlarged trapezium and/or trapezoid correlates with the size and robusticity of the thumb and/or the amount of force habitually transmitted through the radial side of the hand (Godinot and Beard, 1991; Hamrick, 1996c). Variation in the scaphoid tubercle and hamate hamulus reflect the size of the carpal tunnel and strength of the extrinsic flexors (Napier and Davis, 1959; Preu-

schoft et al., 1993; Hamrick, 1997). Finally, carpus length can have consequences on mobility for at least two mechanical reasons: 1) A given angular displacement at the midcarpal joint will result in greater absolute displacements for a longer carpus than a shorter carpus; 2) in a longer carpus, there is more room for development of curvature in the mid-carpal joint. Jouffroy et al. (1991) noted that carpus length is relatively uniform (and relatively short) among primates. Salton and Sargis (2008) suggested that a short carpus is expected in arboreal mammals, whereas long carpals are expected in terrestrial mammals. However, the functional logic behind this statement is undefined and it is not clear whether carpus length should be considered relative to body mass, arm length, hand length, or some other feature.

The functional capacities indicated by carpal features may be further enhanced by patterns in the metacarpus and cheiridia (fingers), inasmuch as they reflect similar functional requirements. Our definitions for hand and grasp types follow Cartmill (1974a), Napier (1960, 1961), Preuschoft et al. (1993), and Reghem et al. (2012). Hand types generally refer to the pattern of differential length and robustness of digits. A *mesaxonic* hand, found in treeshrews and most haplorhines, has the third digit the longest and is assumed to be the primitive condition for primates. The fourth digit is longest in *ectaxonic* hands, often seen in strepsirrhines. Some platyrrhines and colobines have *paraxonic* hands, in which the third and fourth digits are of nearly equal length (Gebo, 2011). Ectaxonic hands are usually associated with ulnarly deviated postures (Preuschoft et al., 1993), whereas mesaxonic hands are associated with postures in which the hand is aligned with the axes of the limb and body. It should be noted that the relative length pattern of any given segment of the digit does not generally correlate with the overall pattern of relative digit length (Fig. 3). Thus, axonic patterning and hand type cannot be reliably inferred from the length of metacarpals alone.

Hand and grasp types have been variously defined. Napier (1961) uses a morphofunctional definition of hand types. In his definition of *convergent hand*, the contrahens muscles pull all the digits together toward a midline raphe (flexing and adducting the digits). Most marsupials and some primates reflect this pattern osteologically via metacarpophalangeal joint axes that converge toward each other. *Prehensile hands* are those that can subtend a large enough angle to retain an object single-handedly. They may or may not be convergent as well. Fingers that are long relative to the palm and have the ability for tight flexion at the metacarpophalangeal and interphalangeal joints promote prehensility. Absolutely long fingers that can be strongly abducted may help in arboreal settings regardless of prehensile grasping ability in a strict sense, as they allow the tips of the claws to be distributed over a larger substrate area and may thereby form a more stable anchor during climbing. A *pseudo-opposable hand* is one in which the thumb can achieve some degree of opposition with the palmar surface of the other digits. As described by Napier (1961), strepsirrhines, tarsiers, platyrrhines, and treeshrews all have pseudo-opposable hands. However, they were said to achieve this capacity through different morphological mechanisms. Strepsirrhines were described as exhibiting a combination of pollical divergence and physiologic rotation of the axis of flexion relative to the other digits. Tarsiers, platyrrhines, and treeshrews were described as exhibiting enhanced

rotational mobility at the pollical metacarpophalangeal joint (Napier, 1961; Sargis, 2001). Napier's *true opposable hand* has already been defined above. In a *schizodactylous hand*, digits II and III are divergent and may grasp the object or substrate (rather than digits I and II).

Then there are grasp/grip types: in a *telaxonic* grasp, the support is gripped with the first digit applying pressure in opposition to all others. *Entaxonic* grips place the second digit along the midline while the thumb opposes the third through fifth digits. In a *schizaxonic* grasp, the first and second digits oppose the third through fifth. A *mesaxonic* grip places the third digit on the midline while the first and second rays oppose the fourth and fifth. Less ulnar deviation is required as the axis of the grip is moved laterally from telaxonic to mesaxonic (Reghem et al., 2011).

It has been argued that arboreal quadrupedalism, vertical clinging, and loris-like slow-climbing each demand different and consistent functions from the wrist and hand, leading to tendencies for standard suites of morphological characteristics (Hamrick, 1996a,b,c, 1997). These form–function relationships should allow behavioral inferences in fossil taxa for which the wrist bones have been recovered. Arboreal quadrupeds are expected to use dorsiflexed, pronated hand postures, to require little ulnar deviation due to use of pronograde rather than orthograde postures, and to transmit greater compressive forces through the wrist and hands than other primates. Therefore, they are expected to have facets oriented in a way to permit stability during dorsiflexion. In order to promote pronation instead of supination, to reduce mobility and thereby require less muscular effort to maintain stability, arboreal quadrupeds should exhibit a broader carpus and flatter carpal joints (particularly a radioulnarly oriented midcarpal joint) compared to other functional groups. They are expected to have a more enlarged pisiform to enable propulsion from a dorsiflexed posture. Finally, arboreal quadrupeds are expected to have only a moderately developed carpal tunnel.

Vertical clingers are expected to use more neutral or palmiflexed wrists and ulnar-deviated, supinated hand postures, and to stress their joints in tension more than pronograde quadrupeds. They are also expected to generate higher normal forces during grasping. These functional demands explain the presence of proximally facing and deeply cupped radiocarpal facets, a strongly convex midcarpal joint, a proximodistally oriented triquetrohamate facet that is also dorsally exposed and distally extended, and a small pisiform. The use of ulnar-deviated postures also explains the presence of a strongly divergent thumb and an ectaxonic hand. Finally, long fingers (if not long arms) and a large thumb (and a corresponding large trapezium) relative to body size are expected in vertically clinging animals to aid in subtending sufficient arcs over a greater range of support diameters (Cartmill, 1974a).

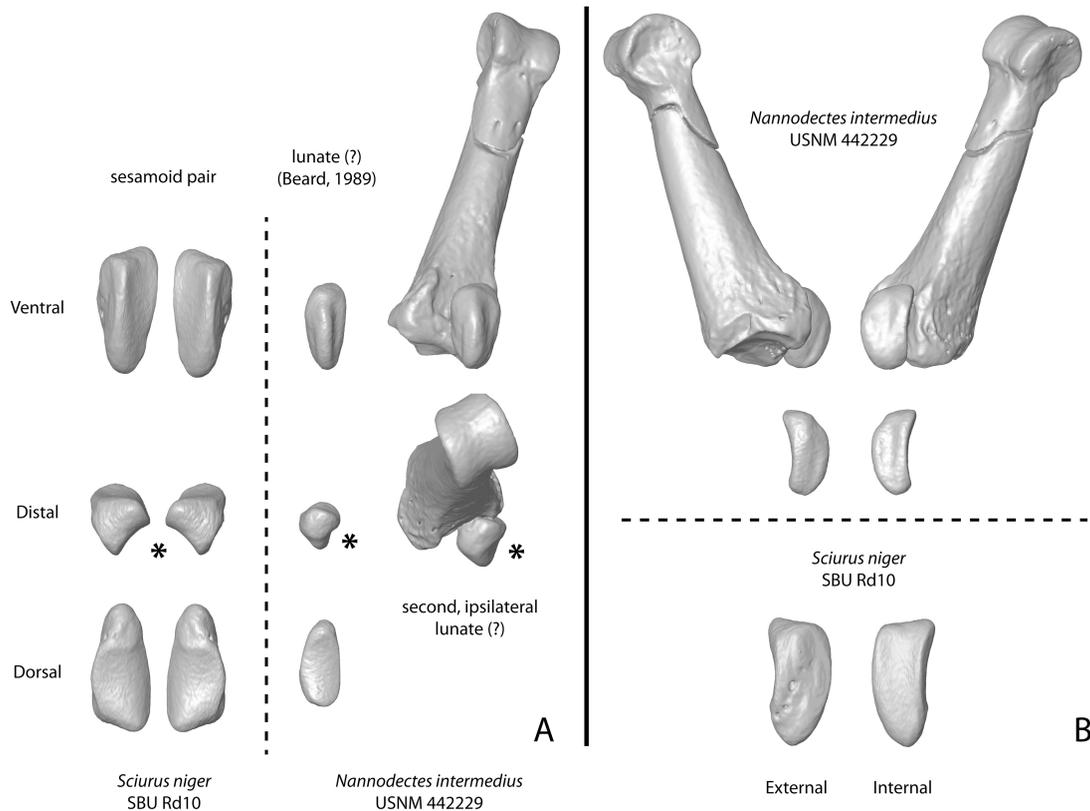
As small branch specialists, lorises are also expected to use ulnarly-deviated hand postures. As a result, they have the most prominently developed ectaxonic hands among primates, including the relatively largest and most divergent pollices, the most reduced second digit rays, and the longest fourth digit rays. However, because they do not typically use vertical supports, their fingers are not as long relative to body size. Requiring more mobility at the wrist joint, they also have a greater degree of curvature at the midcarpal joint and greater reduction of the pisiform (Hamrick, 1996c).

As a group, strepsirrhines have a more reduced pisiform and more enlarged carpal tunnel (with a large scaphoid tubercle and hamate hamulus) than do haplorhines. Hamrick (1997) argued these morphological differences extend back to different ancestral adaptive strategies for the two clades. The strepsirrhine ancestor was argued to have been specialized for vertical clinging and ulnar deviation at the midcarpal joint, whereas ancestral haplorhines were argued to use more pronograde postures as arboreal quadrupeds (Hamrick, 1997). *Tarsius*, despite its vertical clinging and leaping specializations, is somewhat more anthropoid-like in having a reduced hamulus and enlarged pisiform tubercle (Hamrick, 1997). Importantly, *Tarsius* shows that the lack of carpal correlates of vertical postures cannot be used to definitively rule out the use of such postures in a fossil.

In summary, suites of functionally relevant hand features have been recognized in order to characterize taxa in particular behavioral categories (Jouffroy et al., 1991; Godinot and Beard, 1993; Preuschoft et al., 1993; Hamrick, b,c,1997; Lemelin and Jungers, 2007). These can help retrodict locomotor behavior in fossil primates. However, Eocene primates often exhibit a more mosaic morphological suite than extant primates. This may indicate that these taxa sample a volatile point during the initial radiation of euprimates in which the morphological patterns that were developed in previous ecological niches were retained even as novel adaptive features important in the species' immediate ecological context began to appear. To put it more classically, the mix of features reflecting "recent habitus" (i.e., "heritage") vs. "current habitus" (e.g., Gregory, 1936; Szalay, 1981a,b) may be more difficult to disentangle during an adaptive radiation. Various researchers have objected to such treatment of fossil taxa (Kay and Cartmill, 1977; Anthony and Kay, 1993). Whether this is a valid model would depend on 1) how much phylogenetic correlation is apparent in any given character complex, and 2) whether the "lengths" of the phylogenetic branches separating a fossil taxon under consideration from the euprimate common ancestor or other similarly mosaic fossils are "shorter" than the branches separating extant taxa in distinct locomotor categories. Some support for the interpretation that fossil primates have a mosaic of functional characteristics reflecting in part their recent branching history comes from the observation that *Hapalemur* has wrist morphology matching expectations for an arboreal quadruped, while typically utilizing vertical clinging postures (Hamrick, 1996b). Of all the taxa Hamrick studied, *Hapalemur* is most recently diverged from arboreal quadrupedal ancestors, splitting from other lemurids only nine million years ago (Springer et al., 2012). Boyer et al. (2013) found statistical support for similar effects in the tarsus: despite a significant association between variation in behavior and calcaneal elongation, there is also a strong phylogenetic signal suggesting a relatively slow morphological response to changes in behavior, as compared to other ecomorphological indicators of behavior such as, for instance, probably intermembral index.

### Institutional Abbreviations

AMNH, American Museum of Natural History, New York, NY; CM, Carnegie Museum of Natural History, Pittsburgh, PA; DPC, Duke Lemur Center, Division of Fossil Primates, Durham, NC; GMH, Geiseltalmuseum



**Fig. 4.** Lunates and sesamoids. Beard (1989, 1990) identified a lunate bone for the carpus of *N. intermedius* (USNM 442229). Boyer (2009) reidentified this element as a cheiridial sesamoid [labeled as “lunate (?) (Beard, 1989)” in part A] and identified a second similar element attached to an intermediate phalanx of the same specimen (labeled “second, ipsilateral lunate (?)”). Comparisons to hand skeletons of extant taxa reveal that these elements are most likely sesamoid bones of the metacarpophalangeal joint.

Halle, Martin-Luther-Universität, Halle-Wittenberg, Germany; IRNSB, Institut Royal de Sciences Naturelles de Belgique, Brussels, Belgium; MaPhQ, Montauban Musée d'Histoire Naturelle Victor-Brun, Phosphorites de Quercy locality, Montauban, France; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMB, Naturhistorisches Museum Basel, Basel, Switzerland; PMO, Geological Museum, Natural History Museum, University of Oslo, Norway; RD, private collection of A. Collier; Ros, Rosieres locality, France; SMF-ME, Messel collection, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; UM, University of Michigan, Ann Arbor, MI; USGS, United States Geological Survey, Denver, CO; USNM, United States National Museum, Smithsonian Institute, Washington, DC.

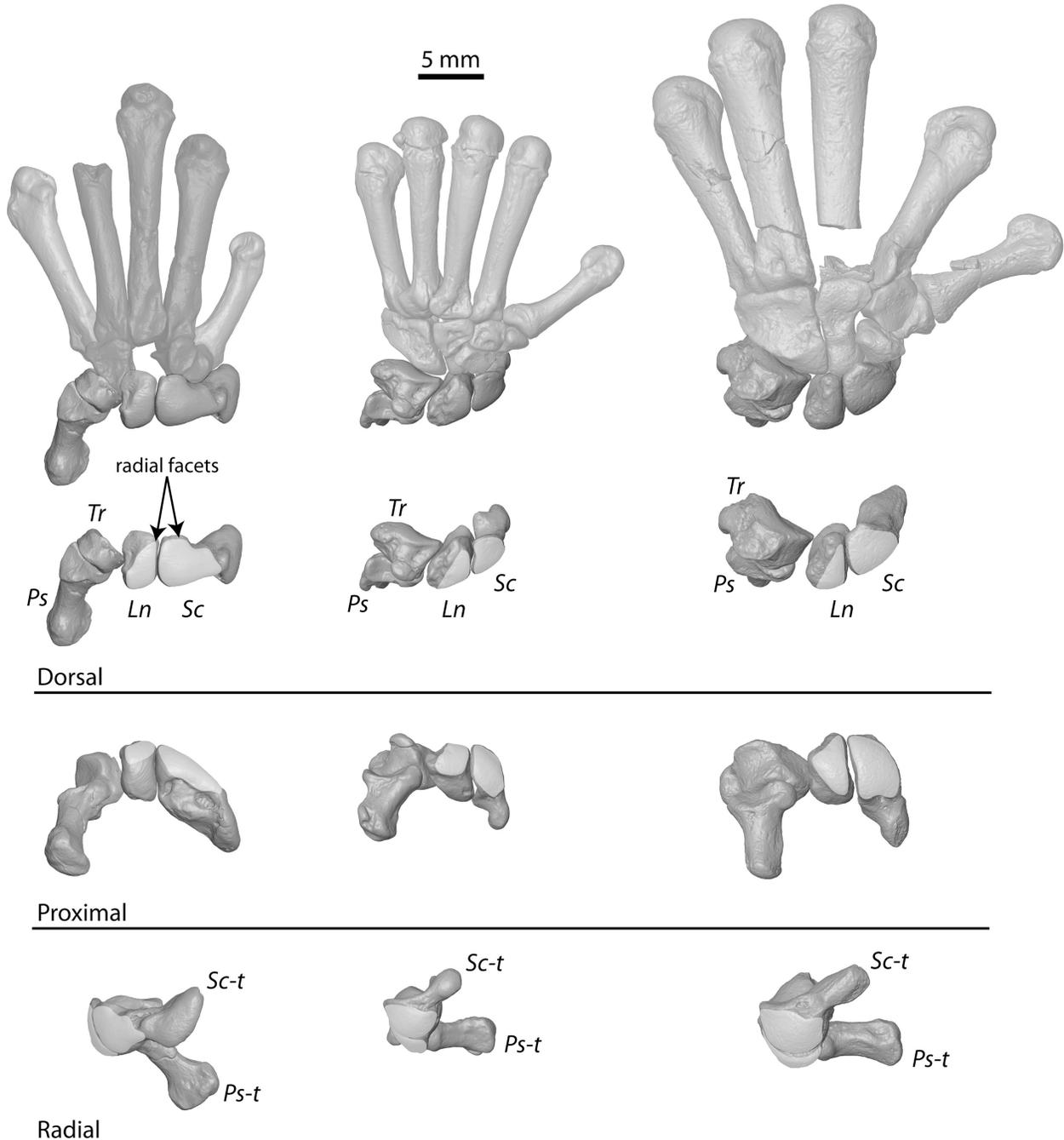
#### THE EARLIEST EUARCHONTANS (PLESIADAPIFORMS)

When Godinot (1992) and Godinot and Beard (1991, 1993) reviewed fossil hands, they figured a composite ray attributed to the plesiadapid *Plesiadapis tricuspidens* from the Cernaysian quarries near Mont de Berru, France. This digit showed a large, mediolaterally compressed, hook-like claw; long, straight intermediate, and proximal phalanges; and a relatively short metacarpal. Godinot and Beard (1991, 1993) identified the metacarpal as belonging to the second ray. However, in their figure they compare it to a fifth metacarpal of *Daubentonia* and indicate that they changed their mind about the

digit attribution shortly before publication. The digit was reconstructed as having a habitually hyper-extended metacarpophalangeal joint and flexed interphalangeal joints. They interpreted the long fingers and claws as correlates of an arboreal habitus in which squirrel-like clinging and climbing was practiced.

Beard (1990) presented a reconstruction of a partial hand of *Nannodectes intermedius*, a plesiadapid that is smaller and more basal than *P. tricuspidens* (Gingerich, 1976; Boyer et al., 2012), based on a relatively complete skeleton from the beginning of the late Paleocene in South Central Montana [Bangtail Plateau, western Crazy Mountains Basin; see Gingerich et al. (1983)]. Recovered with the hand were several carpals (scaphoid, capitate, and hamate) and three metacarpals (MC) assigned to digits I, II, and III. Beard (1990) argued that the corresponding morphologies on the bases of MCI and MCII indicated a habitual articulation between them, and dictated a high degree of divergence between the digits ( $\sim 75^\circ$ ). Beard (1989, 1990) suggested this feature could indicate functional similarities to lorises, the only extant primates exhibiting such high divergence (Beard 1989).

Finally, Beard (1990, 1993a,b) presented data on phalanges of paromomyids, another family of plesiadapi-forms, that revealed apparently dermopteran-like proportions. This was treated as evidence of 1) dermopteran-like mitten-gliding in this fossil taxon and 2) a monophyletic relationship between extant dermopteran and all known plesiadapi-forms, with the

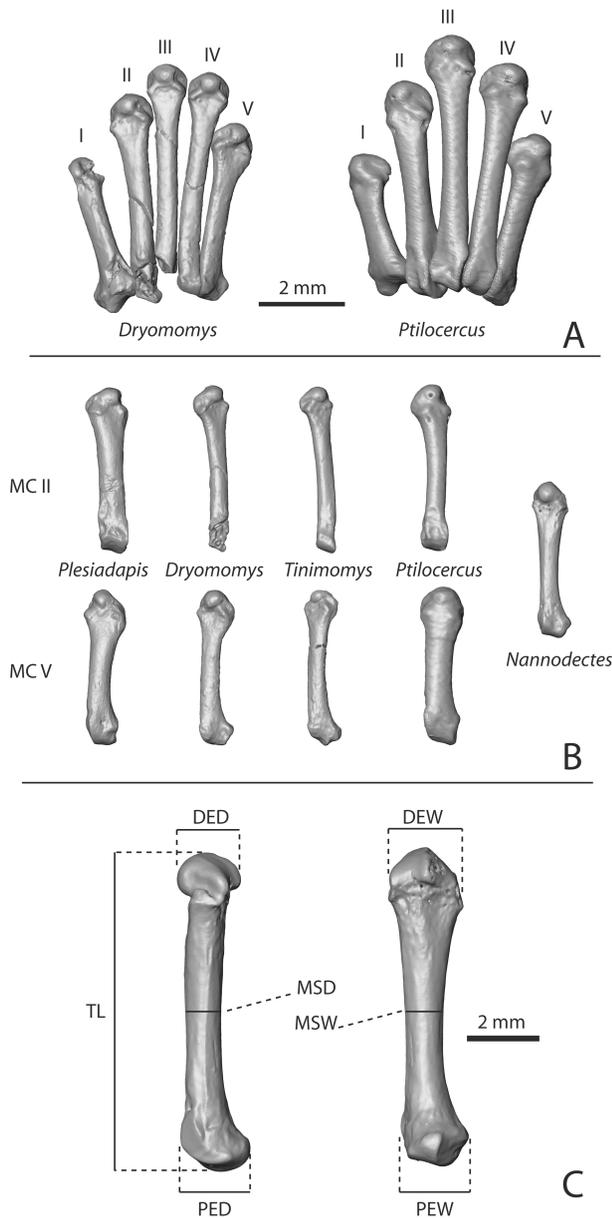
*Plesiadapis* UM 87990*Adapis* Rosieres 311*Notharctus* AMNH 127167

**Fig. 5.** Proximal carpal rows. *Plesiadapis* (UM 87990), *Adapis* (RD 311), and *Notharctus* (AMNH 127167) exhibit differences in pisiform size, radiocarpal facet orientation, and scaphoid tubercle size. Radial facets are highlighted in light gray. Abbreviations: Ln, lunate; Ps, pisiform; Ps-t, pisiform tubercle; Sc, scaphoid; Sc-t, scaphoid tubercle; Tr, triquetrum. Note that *Plesiadapis* and *Adapis* have more dorsal and less proximal exposure of the facet for the radius on the lunate than *Notharctus*. Additionally, *Plesiadapis* has restricted proximal exposure of the radius facet on the scaphoid. Note that all three have large scaphoid tubercles, while *Plesiadapis* has a much larger, and probably more proximally oriented pisiform tubercle.

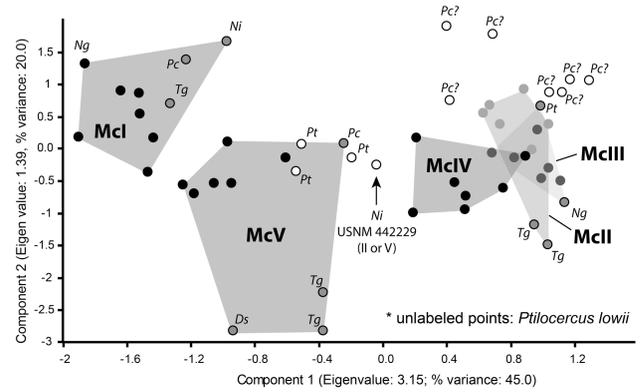
exception of the Microsypidae. Krause (1991) and Runestad and Ruff (1995) questioned the strength of evidence for dermopteran-like proportions in paromomyids. Hamrick et al. (1999) presented a multivariate analysis which showed the phalanges described by Beard to be similar to those of taxa that cling to large diameter

supports (i.e., tree trunks), an attribute that was also consistent with Beard's interpretation.

Starting in the early 2000s, data from new dentally associated skeletons from the Clarks Fork Basin of Wyoming began to surface. Hamrick (2001) published a ternary plot with extant euarchontan metacarpal,



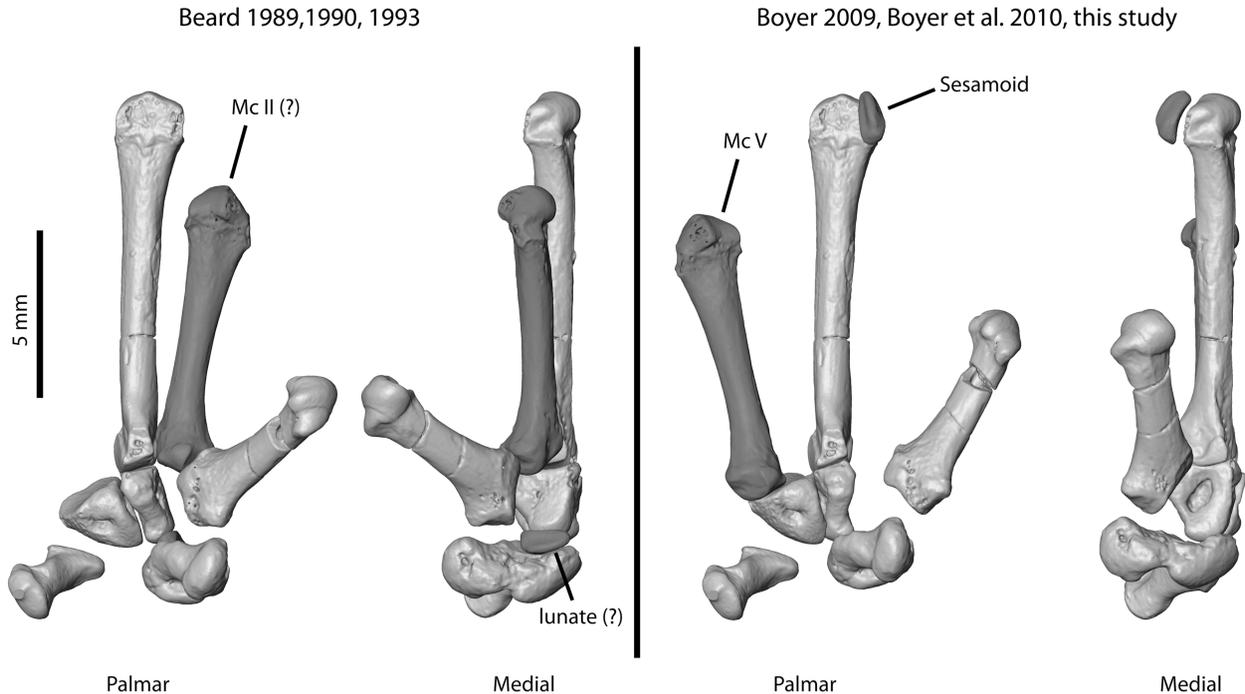
**Fig. 6.** Plesiadapiform metacarpals. **A:** Micromomyid *Dryomomys szalayi* (UM 41870) is the first plesiadapiform specimen to be preserved with metacarpals in anatomical position allowing confident identifications of metacarpal number (Bloch and Boyer, 2007; Bloch et al., 2007). Scanned articulated elements are pictured next to *P. lowii*, the most basal extant treeshrew, showing rough similarity. **B:** metacarpals of different taxa with confirmable associations to digit 2 or 5 compared with an isolated metacarpal of *N. intermedius* USNM 442229, identified as MC2 by Beard (1989, 1990): See Appendix A for specimen information on depicted elements. Qualitatively USNM 442229 looks more like a MC5. Metacarpals standardized to maximum proximodistal length. **C:** Seven measurements designed to assess quantitatively the attribution of USNM 442229 to MC2 using a principle components analysis (Appendix A; Fig. 7). Measurement name abbreviations: DED, distal end depth; DEW, distal end width; DEL, distal end length (not pictured or included in PCA of Fig. 7); MSD, mid-shaft depth; MSW, mid-shaft width; PED, proximal end depth; PEW, proximal end width; TL, total length.



**Fig. 7.** Principal components plot of metacarpal measurements. Results of principle components analysis (PCA) of data from Appendix A. Seven linear measurements were size-standardized using the geometric mean of all measurements on each specimen (see Fig. 6c for measurement illustrations). Geometric mean ratios were then transformed to natural logarithms and the analysis was run on the correlation matrix of these data in the program PAST (Hammer et al., 2001). Minimum area polygons encompass points representing bones that have confirmable attributions to particular digit rays. Black-rimmed, white-filled points represent metacarpals that either have uncertain digit ray assignments [as in the case for bones of *P. tricuspoidens* (*Pt*) and *N. intermedius* (*Ni*)] or uncertainty in both digit ray assignment and taxonomic assignments [as in the case for *P. cookei* (*Pc*)]. Black-rimmed, gray-filled points represent metacarpals for which reasonable evidence of digit ray attribution is available. Solid points are *Ptilocercus*. Note that the bones of *Pt* and *Ni* assigned to MC2 by Godinot and Beard (1991) and Beard (1989, 1990) plot closest to confirmable MC5s of *Ptilocercus*, micromomyids, and *P. cookei*. We suggest these bones are from the fifth digit ray, contra Godinot and Beard (1991) and Beard (1989, 1990).

proximal phalanx, and intermediate phalanx proportions, and included data on an unpublished skeleton of *Plesiadapis cookei* (UM 87990) from the Clarks Fork Basin. The plot showed that extant primates occupied a unique part of the morphospace, whereas *P. cookei* had proportions similar to tupaiid treeshrews. From these data, he argued that there was a developmental change in digit ray patterning in the ancestral crown primate that allowed the evolution of longer fingers and the more effective exploitation of the small branch niche.

Bloch and Boyer (2002) published a description and analysis of the first known skeleton of *Carpolestes simpsoni* [a plesiadapiform in the family Carpolestidae; Bloch and Gingerich (1998)]. Carpolestids have historically been noted for their tarsiiform-like molars (Rose, 1975; Gingerich, 1976; Gingerich et al., 1991) and have even been classified as such in relatively recent taxonomies (McKenna and Bell, 1997), though cladistic support for such a relationship is lacking. The partial skeleton of *C. simpsoni* (UM 101963) includes a skull, jaw, vertebrae, and upper and lower limb bones including girdles. Bloch and Boyer (2002) attributed a number of bones to the hand specifically, even though the specimen's hand was not preserved in articulation. Kirk et al. (2008) give a more detailed account of how digit attributions were determined for this specimen. Bloch and Boyer (2002) refigured the ternary diagram from Hamrick (2001) with data for *C. simpsoni* and other plesiadapiform skeletons that were unpublished at the time. All included plesiadapiforms, except *P. cookei*, plot directly within the morphospace also occupied by euprimates. The digit ray of



**Fig. 8.** Alternative reconstructions of the hand of *Nannodectes*. Left, reconstruction of hand skeleton of *N. intermedius* (USNM 442229) based on interpretations by Beard (1989, 1990, 1993a, 1993b). The implication of this reconstruction is a “dermopteran-like” condition of the lunate (excluded from radial contact; but see Stafford and Thorington, 1998) and an autapomorphic condition of strong pollical divergence. Evidence presented by Boyer (2009), Boyer et al. (2010) and in Figs. 4, 6–7 in this review suggest that the reconstruction on the right is more accurate.

*C. simpsoni* was shown to differ further from that of *P. tricuspidens* figured by Godinot and Beard (1991) in having a proximal phalanx with more curvature, proximal, and intermediate phalanges that are more gracile, and distal phalanges that are proportionally shorter, less hook-like, and have a distally extended volar process for an expanded apical pad (Bloch and Boyer, 2002, 2007).

Bloch and Boyer (2007), Bloch and Silcox (2006), Bloch et al. (2007), and Boyer and Bloch (2008) presented additional documentation and analysis of *C. simpsoni* and other recently discovered plesiadapiform skeletons. These new data, including new associated and semi-articulated skeletons of *Ignacius clarkforkensis*, failed to confirm the presence of dermopteran-like hand proportions in at least that paromyid. Additionally, illustrated elements in situ for semi-articulated specimens of yet another plesiadapiform family, the Micromomyidae, provided contextual evidence of metacarpal positions, independent of morphological assessments, as well as clear identification of phalanges as either manual or pedal (Bloch and Boyer, 2007; Boyer and Bloch, 2008).

Bloch et al. (2007) and Kirk et al. (2008) provide the most comprehensive assessments of the adaptive significance of primate hand proportions and implied grasping abilities based on comparisons with outgroups, including plesiadapiforms. They corroborated the patterns illustrated by Bloch and Boyer (2002), showing that at least *C. simpsoni* and *I. clarkforkensis* plot within the range of modern primates for hand proportions which reflect prehensibility. Additionally, they showed that *Ptilocercus lowii*, a treeshrew not sampled in previous analyses, also overlaps extant primates with prehensile hand proportions. Kirk et al. (2008) interpreted this as evidence that no significant clade-level shifts in hand proportions occurred in the primate stem-lineage, or

in the common ancestor of crown primates, and suggested that improved prehensibility was not a novel adaptation leading to the radiation of crown primates. A caveat to this conclusion is the fact that *Notharctus* (the only included adapiform) has proportionately very elongate digits, suggesting a shift if it is considered as reflective of the common ancestor of extant primates as entertained by Godinot (1991). Kirk et al. (2008) preferred to consider the unusual proportions of *Notharctus* as derived within its own lineage. We present more data on this issue in a later section.

Regarding the plesiadapiform carpus, Beard (1989) argued that known plesiadapiform fossils revealed derivation toward the putative dermopteran condition, which—given Beard’s cladistic hypothesis of Primatomorpha (Primates + Dermoptera with plesiadapiforms as dermopterans)—implied that plesiadapiform wrist morphology had little bearing on understanding the wrist of early euprimates. Specifically, in his description of *N. intermedius* (USNM 442229), he argued that the lunate bone was reduced and excluded from the radiocarpal joint by the scaphoid. Boyer (2009) re-analyzed *N. intermedius* and the relatively complete skeleton of *P. cookei* (UM 87990). Unfortunately, the latter specimen was preserved together with a skeleton of *Uintacyon*, an arboreal carnivoran of nearly identical size. Although the skeleton was in semi-articulation, contextual records allowing attribution based on positional information are no longer available, making the attribution of certain carpal, metapodial, tarsal, and vertebral elements especially questionable. In *N. intermedius*, the element Beard (1989) identified as a lunate was re-identified by Boyer (2009) as a cheiridial sesamoid based on contextual evidence and comparison to other mammals (Fig. 4). Additionally, Boyer (2009) was able to identify the

TABLE 3. Measurements Used in Plots and Body Masses

Bone	<i>Carpolestes</i>	<i>P. insignis</i>	<i>N. intermedius</i>	<i>E. kelleri</i>	<i>Darwinius</i>	<i>Notharctus</i>	<i>Godinotia</i>	<i>Adapis</i>	<i>Leptadapis</i>
carpus	--	--	3.77	7.38-	5.49 r	11.58	7.39 l	8.6	16.24+
mc1	--	--	--	9.96	7.30 r	12.48	10.43 l	9.53	--
mc2	--	--	--	14.44	--	16.65	13.90 l	15.34	27.93*
mc3	7.18	11.7	11.51	15.33	--	23.8** ++	16.93 l	16.15	30.47*
mc4	--	--	--	15.23	11.75 r	21.42	16.42 l	15.88	32.47*
mc5	--	--	--	14.12	11.08 r	19.06	14.33 l	13.97	28.71*
pp1	--	--	--	11.96	9.07	16.39	12.31	--	--
pp2	--	--	--	16.56	13.35	23.98	16.41	--	--
pp3	6.61	8.6	7.76	19.97#	15.62	27.66	18.25	15.53##	26.33*
pp4	--	--	--	20.61	15.66	28.51	19.61	--	--
pp5	--	--	--	16.99	11.66	25.47	16.06	--	--
ip2	--	--	--	11.76	8.12	16.08	--	--	--
ip3	4.6	7.8	6.56	14.54#	11.56	--	14.77	11.17##	17.81*
ip4	--	--	--	13.78#	12.27	-- ++	14.87	--	--
ip5	--	--	--	10.61	9.44	13.94	11.47 r	--	--
dp1	--	--	--	6.12	5.59	8.98	6.49 r	--	--
dp2	--	--	--	3.82	4.13 r	8.14	--	--	--
dp3	2.3	--	5.22	4.30#	4.01	9.38	--	3.96 ##	6.5+
dp4	--	--	--	--	4.21	10.44	5.60	--	--
dp5	--	--	--	--	3.13 r	8.96	3.82 r	--	--
digit 3	13.51	--	19.54	38.81	31.19	--	38.62	30.66	50.60
BM(g)	100	--	352	1,485	660	2,305	1,325	1,066	6,425

Individual specimen data from Appendix E were modified to generate composite hands with maximum completeness. A composite for *Europolemur kelleri* was generated using proportional information from *Europolemur koenigswaldi*. A composite for *Darwinius masillae* was generated by averaging measurements from the left and right sides of PMO 214.214. A composite for *Godinotia neglecta* was generated by averaging measurements from left and right sides of GMH L-2 when measurements were close, but primarily the left side (which is more complete and better preserved). A composite for *Notharctus tenebrosus* was generated using AMNH 127167 and proportional information from AMNH 11478. *Adapis parisiensis* was generated using RD 311 and proportionally adjusted based on locality means for the phalanges. *Leptadapis* is represented by species means with some values inferred by assuming proportional equivalence with *Adapis parisiensis*. Values for *Carpolestes* are those reported by Boyer and Bloch (2008) for UM 101963 with the distal phalanx measurements taken on that specimen for this study. Body mass estimates were generated in the following ways: For *Carpolestes*, we used the estimate of Bloch and Gingerich (1998). For *E. kelleri*, we used the dimensions of the calcaneal cuboid facet (5.01 mm and 5.01 mm) preserved in HLD-ME 7430 and the equation published by Boyer et al. (2013). For *Darwinius*, we used the mean estimate based on the postcranium reported by Franzen et al. (2009). For *Godinotia*, we used diameters of the humerus (5.7 mm and 6.13 mm) and femur (5.87 mm and 5.87 mm) to generate a geomean (5.91). This geomean was used in a regression for prosimian body mass based on the geomean of these four measures with data by Lemelin and Jungers (2007) [ $\ln(\text{BM}) = 2.601 \cdot \ln(\text{geomean}) + 2.57$ ]. See Figure 23. Body masses of *Notharctus*, *Adapis*, *Leptadapis*, and *Nannodectes* are based on calcaneal cuboid facet means from Boyer et al. (2013). All measurements in mm.

Symbols in Table 3:

(-- ) No measurement available

(\*) Locality averages

(-) Based on a caliper measurement that appeared more accurate

(#) Estimated lengths for *E. kelleri*, using *E. koenigswaldi*, assuming identical proportions

(##) Locality averages adjusted so that proportion to MC3 of RD 311 matches proportion of raw value to locality average MC3

(\*\*) Estimated length for AMNH 127167 assuming identical proportions to AMNH 11478

(++) Measurements given in Hamrick and Alexander (1996) are unconstrained due to breakage (see Fig. 1)

(+) Estimated by assuming identical proportions between bones of a digit in *Adapis*

(r) From right side

(l) From left side

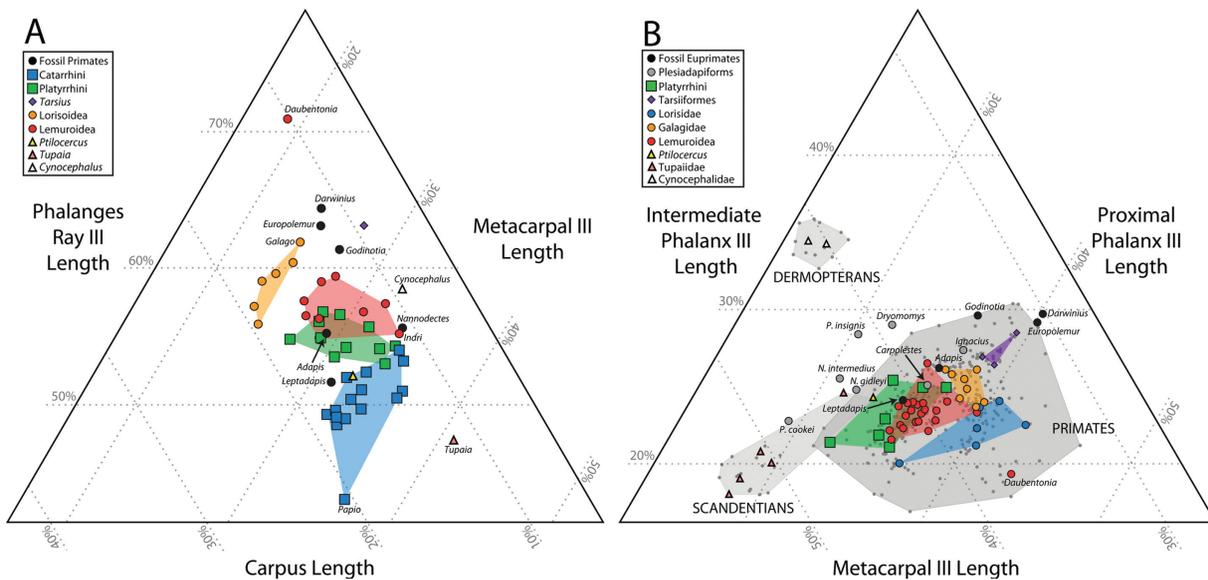
scaphoid of *P. cookei* based on its strong similarities to those attributed to *N. intermedius* and paromomyid pleiadapiforms (Boyer and Bloch, 2008). This attribution is confirmed by comparisons to a scaphoid (UCMP 229399) included among other postcranial bones (e.g., humerus: UCMP 102829) attributed to *Platychoerops*, a close relative of *P. cookei* (Boyer et al., 2012a,b), in the Berkeley UCMP Mutigny collection. Boyer (2009) identified the lunate of *P. cookei* based on its ability to articulate with the scaphoid and comprise a combined joint surface that matched the distal facet of the radius. The morphology of the bone is not strongly specialized in any particular way. However, the radial articular surfaces of both scaphoid and lunate of *P. cookei* seem to be positioned strongly dorsad (Fig. 5), indicating dorsiflexed wrists typical of arboreal quadrupeds and characteristic of the proximal carpal row of the Rosieres hand (RD 311) of *Adapis parisiensis* (Fig. 5) (Godinot, 1992).

Boyer (2009) and Boyer et al. (2010a) also revisited previous metacarpal identifications by Godinot and Beard (1991) and Beard (1990) utilizing new data from Berru *P. tricuspidens* specimens, the new micromomyid skeletons mentioned above, measurements of six specimens of *P. lowii*, and metacarpals associated with UM 87990. Taking seven measurements on each of MCI–MCV (Appendix A; Fig. 6), they evaluated the identifications by Beard (1990) using a principal components analysis (Fig. 7). These analyses show that the bone from USNM 442229, assigned to MCII by Beard, is more similar to MCV of *Ptilocercus* and micromomyids than to the MCII of these taxa. Furthermore, the Berru metacarpal morphs matching that assigned to the second ray of *P. tricuspidens* by Godinot and Beard (1991) are most similar to MCV of *Ptilocercus*.

Unfortunately, distinguishing which metacarpals of UM 87990 belong to *P. cookei* and which to *Uintacyon* remains problematic. Boyer's (2009) reconstruction of

TABLE 4. Proportions Used in Plots Based on Measures in Table 3

Ratio	<i>Carpolestes</i>	<i>P. insignis</i>	<i>N. intermedius</i>	<i>E. kelleri</i>	<i>Darwinius</i>	<i>Notharctus</i>	<i>Godinotia</i>	<i>Adapis</i>	<i>Leptadapis</i>
carp/hnd	na	na	10.83	12.00	11.34	na	11.74	15.55	16.70
mc3/hnd	na	na	33.06	24.92	24.26	na	26.90	29.12	31.30
pp3/hnd	na	na	22.29	32.46	32.25	na	28.74	28.04	27.06
ip3/hnd	na	na	18.84	23.63	23.87	na	23.47	20.16	18.30
dp3/hnd	na	na	14.99	6.99	8.28	na	8.90	7.15	6.64
d3/hnd	na	na	56.12	63.09	64.40	na	61.36	55.35	51.99
carp/mc3	na	na	32.75	48.14	46.72	49-55	43.65	53.32	53.31
mc1/mc3	na	na	na	65.00	na	52-59	61.61	59.01	na
mc2/mc3	na	na	na	94.24	na	70-79	82.10	94.98	91.66
mc4/mc3	na	na	na	99.39	na	90-102	96.99	98.33	106.56
pp3/mc3	92.06	73.50	67.42	130.27	132.94	116-129	107.80	96.30	86.41
ip3/pp3	69.60	90.70	84.54	72.81	73.96	na	90.04	71.90	67.64
dp3/pp3	34.80	na	67.27	21.53	25.67	29.43	30.68	24.55	24.54
pp3/pp4	na	na	na	96.89	99.74	97.02	93.06	na	na



**Fig. 9.** Intrinsic hand proportions. **A:** Lengths of the carpus, third metacarpal, and third digit ray (proximal phalanx + intermediate phalanx + distal phalanx) as percentages of total hand length. Minimum convex hulls bound phylogenetic groups. Data for extant species by Jouffroy et al. (1991). Data for fossil species is presented in Appendix E; Tables 3 and 4. **B:** Length of the third ray metacarpal, proximal phalanx, and intermediate phalanx as percentages of total ray III length. Minimum convex hulls bound phylogenetic groups. Data for extant species is from Kirk et al. (2008). Data for fossil species is presented in Appendix E; Tables 3 and 4.

hand proportions for *P. cookei* (based on what he considered the most plausible element attributions given the data he analyzed) differed from reconstructions previously used to represent this specimen by Hamrick (2001), Bloch and Boyer (2002), Boyer and Bloch (2008), and Kirk et al. (2008): it appeared to Boyer (2009) that previous estimates incorrectly used an MCIII of *Uintacyon*. We wish to take a more conservative position here and acknowledge that currently only MCI and MCV of *P. cookei* can be determined with reasonable certainty, meaning that prehensility remains unknown for *P. cookei*. Likewise, due to inadequate comparative data, we are uncertain of whether Boyer (2009) was correct in his attribution of trapezium, trapezoid, and hamate bones to *P. cookei*. The most important implication of the foregoing analyses is that no MCII, trapezium or trapezoid can yet be identified with certainty for *N. intermedius*, *P. cookei*, or any other described plesiadapiform (Fig. 8). It is therefore premature to estimate degrees of

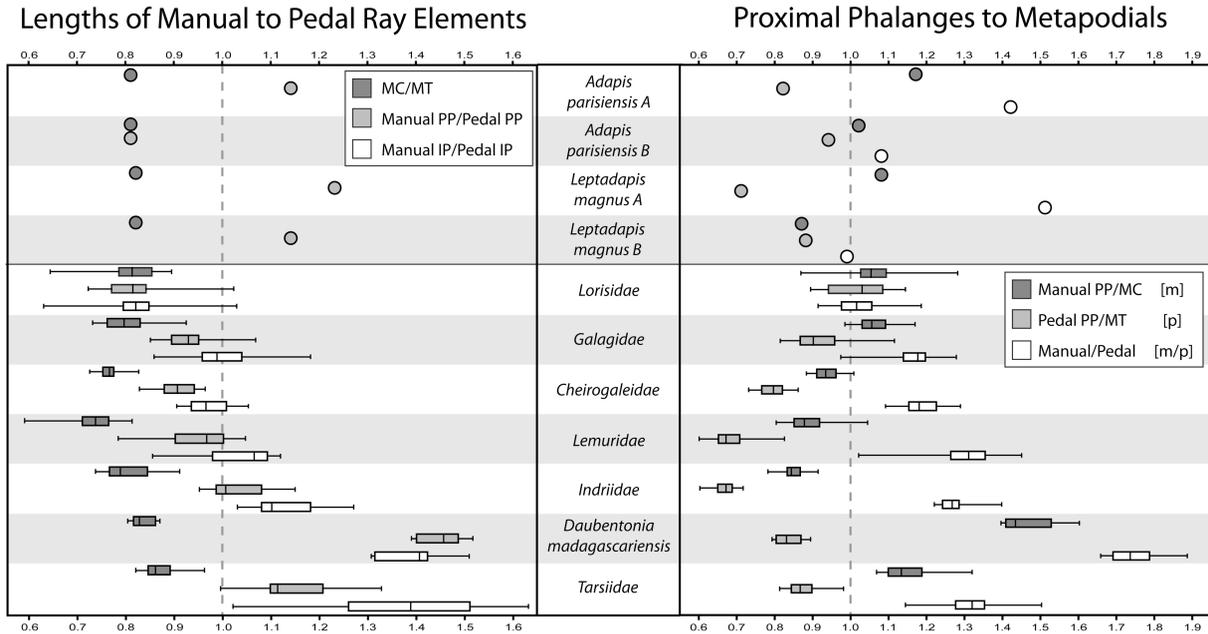
pollical divergence (angle between MCI and MCII) for any plesiadapiform. However, based on the new reconstruction of *N. intermedius* (Fig. 8), it is now possible to estimate intrinsic proportions of the carpus, metacarpus, and third digit ray for this specimen (Tables 3 and 4). This allows a plesiadapiform to be plotted next to extant and fossil euprimates in ternary diagrams by Jouffroy et al. (1991) for the first time. Not surprisingly, the *Nannodectes* specimen plots among the extant radiation of primates (Fig. 9A).

In sum, the last twenty years of collection and study of plesiadapiform fossils have revealed that 1) many of the once perceived autapomorphies (e.g., strong pollical divergence in *Nannodectes*) and non-primate synapomorphies (e.g., dermopteran-like features) of plesiadapiforms are artifacts of incorrect interpretations of fragmentary fossil data; 2) most, if not all, plesiadapiforms have long, primate-like fingers indicative of an arboreal lifestyle; and 3) there is some indication in certain taxa of *Adapis*-like

TABLE 5. Summary Statistics on Cheirida From Phosphorites de Quercy

Variable	L	PEW	PED	MSW	MSD	DEW	DED	DEL <sup>a</sup>	IA
<i>Adapis parisiensis</i> intermediate phalanges									
n	3	3	3	3	3	3	3	3	Na
Mean	12.13	3.39	3.20	2.20	1.77	2.82	1.99	1.88	Na
Sd	1.04	0.11	0.19	0.24	0.08	0.03	0.14	0.19	Na
Range	10.93–12.76	3.31–3.52	3–3.36	1.95–2.43	1.70–1.87	2.8–2.86	1.85–2.13	1.71–2.09	Na
<i>Leptadapis magnus</i> intermediate phalanges									
n	9	7	7	9	9	8	8	7	Na
Mean	17.81	6.04	4.91	4.36	2.73	4.52	2.97	3.09	Na
Sd	1.61	0.44	0.47	0.23	0.22	0.30	0.42	0.35	Na
Range	15.72–20.15	5.35–6.59	4.33–5.6	4.03–4.83	2.29–2.99	4.14–4.87	2.47–3.58	2.63–3.76	Na
<i>Adapis parisiensis</i> manual proximal phalanges									
N	19	19	19	19	19	19	20	20	20
Mean	16.87	4.16	3.18	2.59	2.10	3.20	2.72	2.61	48.32
Sd	0.83	0.19	0.30	0.18	0.13	0.19	0.11	0.18	7.19
Range	15.06–18.22	3.84–4.56	2.75–3.9	2.19–2.89	1.81–2.4	2.9–3.48	2.55–2.97	2.31–2.86	36.22–63.53
<i>Adapis parisiensis</i> pedal proximal phalanges									
n	13	13	13	12	13	13	13	13	13
Mean	19.41	4.45	3.60	2.85	2.30	3.42	2.96	2.78	48.07
Sd	0.82	0.21	0.23	0.24	0.12	0.31	0.28	0.20	6.70
Range	18.52–21.11	4.11–4.71	3.28–3.98	2.57–3.26	2.03–2.49	3.13–4.05	2.5–3.4	2.53–3.08	35.26–58.21
<i>Leptadapis magnus</i> manual proximal phalanges									
n	15	14	14	15	15	14	14	14	15
Mean	26.33	7.22	5.49	5.03	3.24	5.68	4.41	4.31	57.84
Sd	1.57	0.51	0.39	0.61	0.20	0.49	0.27	0.24	6.50
Range	23.17–28.57	6.5–8.2	4.8–5.99	4.01–6.09	2.95–3.64	4.89–6.48	4.01–4.87	3.86–4.7	43.42–68.76
<i>Leptadapis magnus</i> pedal proximal phalanges									
n	22	20	21	22	22	22	22	22	20
Mean	31.76	8.11	6.37	5.44	3.66	6.15	5.06	4.83	53.35
Sd	2.27	0.54	0.46	0.62	0.28	0.60	0.38	0.31	9.06
Range	28.63–38.19	7.29–9.07	5.41–7.42	3.93–6.71	3.2–4.3	5.1–6.94	4.38–5.7	4.22–5.21	39.46–73.2
<i>Adapis parisiensis</i> MC2									
N	5	5	5	5	5	5	5	5	
Mean	15.22	2.52	4.01	2.02	2.00	3.34	3.49		
Sd	0.44	0.14	0.18	0.11	0.14	0.16	0.21		
Range	14.63–15.81	2.35–2.64	3.8–4.17	1.94–2.18	1.87–2.19	3.21–3.6	3.3–3.78		
<i>Adapis parisiensis</i> MC3									
n	5	6	6	6	6	5	5		
Mean	17.54	3.75	3.84	2.35	2.27	3.71	3.74		
Sd	1.26	0.28	0.35	0.26	0.23	0.38	0.39		
Range	16.15–19.3	3.41–4.08	3.39–4.32	2.09–2.77	2.04–2.67	3.26–4.3	3.21–4.26		
<i>Adapis parisiensis</i> MC4									
n	5	6	6	6	6	5	5		
Mean	17.06	3.34	3.87	2.21	2.23	3.65	3.78		
Sd	0.87	0.31	0.25	0.37	0.38	0.27	0.42		
Range	15.88–18.01	2.92–3.76	3.54–4.13	1.67–2.67	1.61–2.6	3.28–4.02	3.3–4.13		
<i>Adapis parisiensis</i> MC5									
n	2	2	2	2	2	2	2		
Mean	14.79	2.91	2.89	2.20	1.96	3.66	3.18		
Range	13.97–15.6	2.76–3.05	2.58–3.19	2.13–2.27	1.89–2.02	3.31–4	3.09–3.27		
<i>Leptadapis magnus</i> MC2									
n	4	4	4	4	4	4	4		
Mean	27.93	4.98	6.98	3.98	3.75	6.27	6.40		
Sd	1.70	0.41	0.58	0.29	0.22	0.25	0.62		
Range	26.33–29.71	4.41–5.39	6.49–7.68	3.6–4.27	3.53–4.04	6–6.59	5.55–6.99		
<i>Leptadapis magnus</i> MC3									
n	3	3	3	3	3	3	3		
Mean	30.47	7.41	7.37	4.25	4.15	7.34	7.25		
Sd	1.20	0.72	0.38	0.43	0.49	0.23	0.39		
Range	29.75–31.86	6.76–8.18	6.94–7.63	3.78–4.62	3.6–4.51	7.15–7.59	6.91–7.68		
<i>Leptadapis magnus</i> MC4									
n	3	3	3	3	3	3	3		
Mean	32.55	7.63	7.43	4.56	4.65	8.18	7.60		
Sd	2.66	0.76	0.78	0.52	0.34	0.62	0.83		
Range	29.5–34.41	6.76–8.13	6.56–8.07	4.17–5.15	4.28–4.96	7.6–8.83	6.65–8.08		
<i>Leptadapis magnus</i> MC5									
N	1	1	1	1	1	1	1		
Value	28.71	6.7	7.46	3.57	4.21	7.41	7.45		

Measurements illustrated in Figure 6C. Raw data provided in Appendices B–D. All measurements in mm.



**Fig. 10.** Manual to pedal elements for assessing autopod attributions in adapines. Measurement of locality samples of adapine MC, proximal phalanges (PP), and intermediate phalanges (IP) (Appendices B–D; Table 5) reveals two distinct size classes representing *Adapis* (small) and *Leptadapis* (large). Additional partitioning can be done within the proximal phalanx samples, as some of the proximal phalanges attributed to *Adapis* are slightly shorter despite overlapping cross-sectional dimensions (i.e., some phalanges are longer and more gracile, while others are shorter and thus more robust). The same is true of the proximal phalanx sample for *Leptadapis*. Comparison to extant prosimian primates suggests these differences are most likely due mainly to some elements being pedal and some being manual. We use somewhat arbitrary cut-off values in proximodistal length for separating the samples into manual and pedal components. Admittedly, the best approach for determining manual/pedal attribution in this sample would be multivariate discriminant function analysis as conducted by Hamrick et al. (1995) with a sample of anthropoids (Table 2). We lacked the necessary comparative sample at the time of publication. However, we note that the highest canonical loading for the DFA in Hamrick et al.’s (1995) study was related to gracility of the phalanx. For researchers who may wish to reassess our attributions more rigorously we provide raw data on proximal phalanges in Appendix D. We assessed two hypotheses on the autopodal attribution of the long and short groups of small and big adapine phalanges using data from other primates and drawing on what has been inferred for adapine locomotion already (e.g., Dagosto, 1983). If one posits longer manual phalanges (“A” in figure), the overall proportions match only tarsiers and are quite unusual. If one posits longer pedal phalanges (“B” in figure), the overall proportions are similar to a number of different strepsirrhines, and best match certain lorises. These data lead us to assign the shorter proximal phalanges of the Quercy sample to the hands. Data are presented in Appendices B–D. It should be noted that the comparative data are processed in a particular way to mimic proportional information available in locality-averaged samples where information on digit rays has been lost. Each individual data point represents a mean across rays 2–5 of a single individual. This gives a different distribution than when only specific rays are plotted.

dorsiflexed hand postures indicative of pronograde locomotion on medium-to-large diameter supports. Based on current evidence, all plesiadapiforms had clawed (falicular) manual distal phalanges. These claws are mediolaterally compressed and dorsoventrally deep, indicating arboreal rather than terrestrial activities in all taxa for which they are known (Bloch and Boyer, 2007). All known plesiadapiform claws exhibit prominent, bilateral nutrient foramina proximal to flexor tubercle and volar process. Furthermore, Godinot and Beard’s (1991) reconstruction of joint angles for a plesiadapiform digit ray remain accurate given low interspecific variation in the corresponding articular surfaces among known plesiadapiforms (see comparisons to extant primates and adapiforms below). Of course, as new and better-preserved fossils are discovered, it is likely that plesiadapiforms will eventually reveal much more about the transition between stem-primates and crown primates. Studies of the most primitive known plesiadapiform hands are currently under way (Chester et al., in preparation), which will certainly modify and enrich the perspective presented here.

## EARLY EUPRIMATES (ADAPIFORMES AND OMOMYIFORMES)

While important questions remain on the broader relationships of adapiforms and omomyiforms as discussed in the introduction, the intra-clade systematics of these groups can be more effectively delineated. The adapiform infraorder is typically divided into three primary families (Godinot, 1998; Gebo, 2002): the early to middle Eocene Notharctidae, the middle Eocene Adapidae, and the Asiatic, Eocene-Miocene family Sivaladapidae. Notharctidae is conventionally split into two subfamilies: the predominantly North American Notharctinae and the predominantly European Cercamoniinae (Gebo, 2002; Gunnell and Silcox, 2010). Recently, a third notharctid subfamily was proposed: the Asiadapinae from the early Eocene of India (Rose et al., 2009). It should also be noted that the inter-relationships among these families is not well-resolved. In particular, it is quite possible that Notharctidae is paraphyletic with cercamoniines more closely related to adapines (e.g., Seiffert et al., 2009; Patel et al., 2012; Gladman et al., 2013).

TABLE 6. Hand Proportions for "Prosimians"

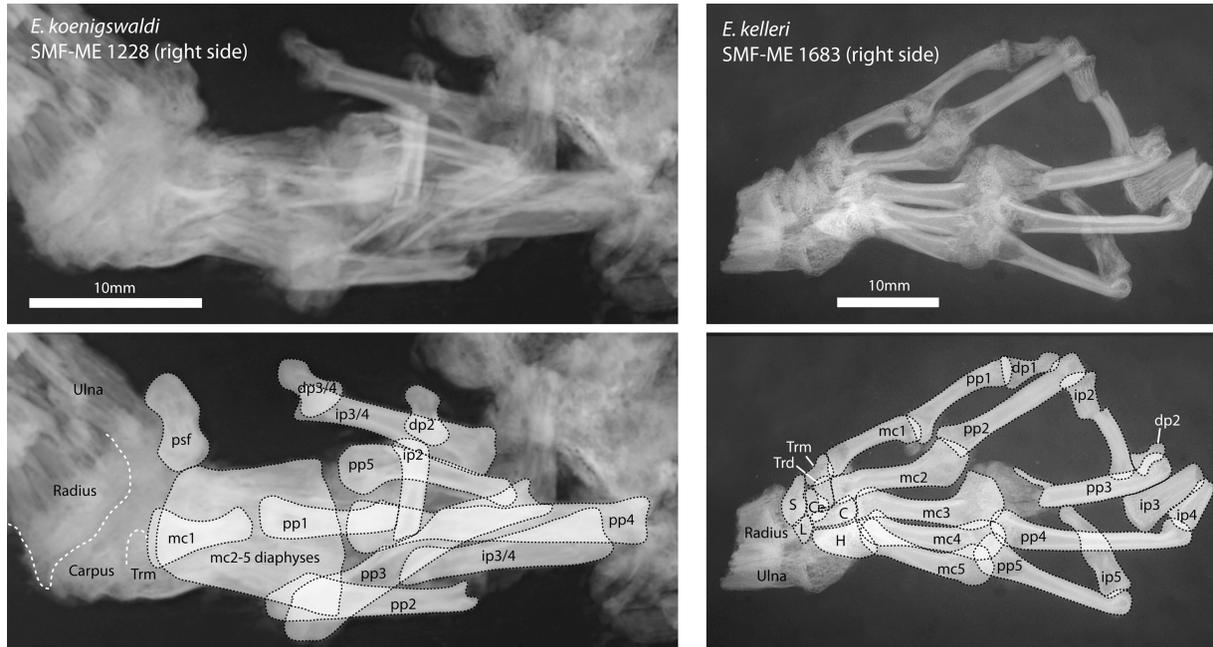
Taxon	Data from Jouffroy et al. 1991			Data from Kirk et al. 2008			Based on unpublished data originally analyzed in Lemelin 1996										Digit Lres.	MC Lres.									
	n	%Carp	%MC3	%D3	n	MC3/D3	PP3/D3	IP3/D3	n	MC1/MC3	s.d.	MC2/MC3	s.d.	MC4/MC3	s.d.	PP3/MC3			s.d.	IP3/PP3	s.d.	DP3/PP3	s.d.	PP3/PP4	s.d.	Digit Lres.	MC Lres.
<i>Arctocebus calabarensis</i>	14	19.1	23.7	57.2	11	43.1	36.9	20.0	11	88.47	3.76	71.39	4.25	101.52	2.50	85.41	4.41	54.09	5.13	40.43	4.09	74.92	3.78	-0.249	-0.115		
<i>Loris tardigradus</i>	10	19.5	24.6	55.9	12	36.8	39.5	23.7	11	84.24	3.64	85.05	2.49	96.39	3.97	107.48	6.48	61.37	5.90	27.06	2.96	96.48	5.24	0.017	-0.023		
<i>Nycticebus couacang</i>	21	16.6	23.8	59.6	17	37.6	40.1	22.3	17	70.74	5.04	82.39	3.71	97.47	4.73	106.75	5.70	55.56	4.27	26.25	2.33	91.74	2.55	-0.111	-0.177		
<i>Nycticebus pygmaeus</i>	7	17.7	23.3	59.1	13	35.4	40.5	24.1	5	74.83	1.98	85.23	4.23	95.66	1.42	113.95	3.77	59.63	1.69	28.16	0.95	93.56	1.41	-0.002	-0.131		
<i>Perodicticus potto</i>	20	15.1	24.5	60.4	11	36.3	39.6	24.0	11	71.74	4.23	93.53	2.52	96.50	2.49	109.16	3.78	60.36	2.41	27.52	3.19	86.38	3.87	-0.140	-0.244		
<i>Eooticus elegantulus</i>	54	13.9	24.2	61.9	7	37.3	36.9	25.8	7	65.40	4.24	87.83	4.37	93.03	2.02	99.03	3.26	69.79	2.07	28.53	3.60	91.05	1.19	0.146	0.048		
<i>Galago moholi</i>																											
<i>Galago senegalensis</i>																											
<i>Galago zanzibaricus</i>																											
<i>Galagoides demidoff</i>																											
<i>Galagoides alleni</i>																											
<i>Otolemur crassicaudatus</i>																											
<i>Otolemur garnetti</i>																											
<i>Cheirogaleus major</i>	7	16.2	27.2	56.4	8	40.9	36.4	22.7	7	64.74	3.44	94.58	1.51	93.27	1.29	87.38	4.13	62.74	3.35	28.45	2.62	94.94	1.58	-0.074	0.033		
<i>Cheirogaleus medius</i>																											
<i>Microcebus murinus</i>	16	14.0	27.0	59	17	38.3	35.2	26.5	14	59.75	2.86	93.18	1.95	93.51	1.86	90.59	3.37	74.71	5.46	25.05	2.58	93.96	5.79	-0.039	0.057		
<i>Mirza coquereli</i>																											
<i>Phaner sp.</i>	2	15.8	26.6	57.6	1	39.3	37.2	23.4																			
<i>Eulemur coronatus</i>																											
<i>Eulemur fulvus</i>																											
<i>Eulemur macaco</i>																											
<i>Eulemur mongoz</i>																											
<i>Eulemur rubriventer</i>																											
<i>Haplelemur griseus</i>	9	15.5	28.2	56.3	12	40.0	36.5	23.5	12	57.82	3.11	88.13	1.75	97.97	2.29	91.55	3.48	64.29	1.89	29.56	2.23	93.58	1.88	0.023	0.038		
<i>Haplelemur simus</i>																											
<i>Lemur catta</i>	39	16.1	29.0	54.9	12	41.3	35.0	23.7	12	54.55	2.45	94.02	1.87	96.93	3.25	84.98	4.05	67.30	19.37	27.65	1.74	94.47	3.23	-0.104	-0.043		
<i>Lepilemur leucopus</i>	11	12.9	27.7	59.4	7	38.4	37.6	24.0	7	59.10	2.16	86.61	1.84	100.90	1.47	98.35	3.65	63.70	4.59	31.10	1.78	88.15	1.51	0.055	0.006		
<i>Lepilemur mustelinus</i>																											
<i>Lepilemur ruficaudatus</i>																											
<i>Varecia variegata</i>	9	16.2	28.9	54.9	10	40.7	36.5	22.8	10	57.53	1.40	95.46	1.38	96.00	1.10	89.58	4.32	62.70	1.95	28.28	1.00	98.07	0.63	0.035	0.013		
<i>Avahi laniger</i>	6	10.8	31.8	57.4	10	42.6	35.3	22.1	10	43.32	2.31	85.61	1.50	103.71	2.04	82.66	2.22	62.34	3.19	31.39	3.14	90.24	1.27	0.119	0.222		
<i>Propithecus verreauxi</i>	6	12.5	30.7	56.8	12	41.8	35.9	22.3	12	58.91	2.35	84.17	6.23	101.74	1.71	85.83	2.88	62.38	1.73	28.66	2.28	90.41	1.82	0.108	0.142		
<i>Propithecus diademata</i>																											
<i>Indri indri</i>	7	11.1	33.7	55.2	8	42.8	35.7	21.6	8	61.11	2.24	90.30	2.51	101.81	0.96	83.27	3.29	60.53	2.54	23.82	3.17	91.90	1.36	0.302	0.393		
<i>D. madagascariensis</i>	9	10.2	18.9	70.9	9	37.1	43.5	19.3	9	38.30	2.99	54.59	4.57	69.29	5.04	117.26	11.29	44.49	2.01	13.27	2.86	90.57	2.79	0.460	0.396		
<i>Tarsius bancanus</i>	10	9.4	27.5	63.1	13	32.3	39.2	28.5	12	65.53	2.32	94.19	2.06	84.42	1.91	120.37	6.57	72.42	22.67	20.96	3.27	112.16	2.27	0.680	0.533		
<i>Tarsius spectrum</i>																											
<i>Tarsius syriaca</i>																											

<sup>a</sup> Digit (D) 3 ratios do not include distal phalanx length.

TABLE 7. Hand Proportions for Anthropoids, Scandentians, and Dermopterans

Taxon	Data from Jouffroy et al. 1991				Data from Kirk et al. 2008				Data from Jouffroy et al. 1991												
	n	%Carp	%MC3	%D3	n	MC3 <sup>a</sup> /D3	PP3 <sup>a</sup> /D3	IP3 <sup>a</sup> /D3	n	MC1/MC3	s.d.	MC2/MC3	s.d.	MC4/MC3	s.d.	PP3/MC3	s.d.	DP3/PP3	s.d.	PP3/PP4	s.d.
<i>Alouatta sp.</i>	8	15.0	28.2	56.8					8	62.3	2.6	88.3	3.6	96.7	7.1						
<i>Aotus sp.</i>	8	16.2	28.9	54.9	5	39.3	35.8	24.9	8	65.5	4.1	90.2	5.8	97.2	5.5						
<i>Atetes sp.</i>	9	13.1	33.9	53.0					9	42.3	4.5	91.1	2.9	98.0	3.5						
<i>Brachyteles sp.</i>	1	11.8	33.9	54.3					1	34.0	--	95.2	--	100.8	--						
<i>Callicebus sp.</i>	3	14.1	29.3	56.6	6	38.0	37.1	24.9	3	67.2	2.3	89.8	3.6	98.0	1.8						
<i>Callithrix sp.</i>	6	12.7	31.6	55.7	8	42.5	34.6	22.9	6	66.8	1.6	92.5	6.2	96.3	5.4						
<i>Cebus sp.</i>	11	16.0	30.5	53.5					11	73.5	5.2	100.2	10.4	97.0	3.1						
<i>Chiropates sp.</i>	2	18.1	27.1	54.8																	
<i>Lagothrix sp.</i>	6	15.6	28.3	56.1	7	46.3	32.3	21.4	6	66.6	5.7	94.1	3.7	99.1	2.6						
<i>Leontopithecus sp.</i>	7	12.9	33.0	54.1					7	67.4	9.8	86.9	4.2	95.9	3.8						
<i>Saguinus midas</i>					8	43.4	34.8	21.8													
<i>Saguinus oedipus</i>					13	43.1	35.8	21.1													
<i>Saimiri sp.</i>	8	14.9	30.9	54.2	5	40.7	33.8	25.4	8	69.7	4.7	93.0	4.8	89.7	5.0						
<i>Cercopithecus sp.</i>	11	18.5	32.2	49.3					11	63.6	2.5	95.1	4.0	95.7	3.1						
<i>Colobus sp.</i>	10	16.5	33.1	50.4					10	44.9	5.0	90.6	7.2	99.0	1.9						
<i>Gorilla sp.</i>	6	16.2	34.1	49.7					6	56.6	6.8	103.6	7.2	95.9	3						
<i>Homo sapiens</i>	3	18.0	32.9	49.1					13	76.3	7.9	111.8	13.0	88.9	10.0						
<i>Hylobates sp.</i>	8	11.7	34.3	54.0					8	61.1	5.0	109.1	4.4	92.0	2.1						
<i>Macaca sp.</i>	12	18.3	33.1	48.5					12	65.7	5.7	98.0	5.4	98.3	5.6						
<i>Miopithecus sp.</i>	7	14.6	33.0	52.4					7	61.2	6.5	92.2	5.8	93.8	3.8						
<i>Pan sp.</i>	14	13.6	35.9	50.5					14	46.8	3.4	100.8	1.8	93.5	2.7						
<i>Papio sp.</i>	10	20.6	36.4	43.0					10	65.5	3.5	98.7	3.8	96.8	2.4						
<i>Pongo sp.</i>	9	13.0	36.0	51.0					9	47.4	3.6	101.5	2.5	95.7	2.7						
<i>Presbytis sp.</i>	10	15.4	33.5	51.1					10	51.6	4.0	94.9	1.3	96.4	1.8						
<i>Rhinopithecus sp.</i>	2	17.6	33.5	48.9					2	44.8	4.3	98.9	3.8	101.0	2.0						
<i>Semnopithecus sp.</i>	5	17.8	32.6	49.6					5	52.0	4.1	96.6	9.1	100.9	4.0						
<i>Synphalangus sp.</i>	3	11.9	34.9	53.2					3	58.5	2.7	106.1	0.6	92.3	2.4						
<i>Trachypithecus sp.</i>	2	15.9	32.1	52.0																	
<i>Ptilocercus lowii</i>	1	15.6	32.4	52.1																	
<i>Tupaia glis</i>	1	11.7	40.9	47.4	1	42.4	33.3	24.3													
<i>Tupaia longipes</i>					10	52.6	28.4	19.0													
<i>Tupaia minor</i>					2	50.5	28.7	20.8													
<i>Tupaia tana</i>					1	44.0	31.4	24.6													
<i>Tupaia gracilis</i>					3	50.3	29.7	20.1													
<i>Galiopterus variegatus</i>					1	53.7	28.3	18.0													
<i>Cynocephalus volans</i>	1	9.3	32.3	58.4	7	41.0	24.6	34.4													
					5	40.1	25.7	34.2													

<sup>a</sup> Digit (D) 3 ratios do not include distal phalanx length.



**Fig. 11.** Hands of *Europolemur koenigswaldi* and *E. kelleri*. Digit proportions were reassessed in *Europolemur* using high-resolution radiographs provided by J. Franzen and casts of original specimens provided by R. F. Kay. Measurements in Appendix E are based directly off the bones as interpreted in this image. Note that metacarpal lengths cannot be constrained in SMF-ME 1228 due to obliterated distal epiphyses, and intermediate phalanges 3–4 are broken and missing in SMF-ME 1683. Thus only a multi-species composite picture of a *Europolemur* hand can be generated (Table 3). Abbreviations: S, scaphoid; L, lunate; H, hamate, C, capitate; Ce, centrale; Trm, trapezium; Trd, trapezoid; psf, pisiform; mc, metacarpal; pp, proximal phalanx; ip, intermediate phalanx; dp, distal phalanx. Radiographs were made by Jörg Habersetzer and the copyright is with Senckenberg Forschungsinstitut Frankfurt am Main, Dr. Jörg Habersetzer.

Six notharctid species are known from hand fossils (Table 2). These include the notharctines *Notharctus tenebrosus* (Gregory, 1920; Hamrick and Alexander, 1996) and *Smilodectes gracilis* (Covert, 1985a,b,1986; Beard and Godinot, 1988; Godinot and Beard, 1991, 1993; Godinot, 1992; Alexander and Burger, 2001) from the Bridger Formation of North America, the cercamoniines (or caenopithecines) *Europolemur kelleri* (Franzen 1988, 1993, 2000; Franzen and Frey, 1993), *Europolemur koenigswaldi* (Franzen, 1987), and *Darwinius masillae* (Franzen et al., 2009) from the Messel oil shale, and *Godinotia neglecta* (Thalmann et al., 1989; Thalmann, 1994) from the Geiseltal lignite beds. Only the first two notharctid species are known from multiple specimens. At least two adapines are known from hand fossils: *A. parisiensis* and *Leptadapis magnus* (Dagosto, 1983; Godinot and Jouffroy, 1984; Godinot and Beard, 1991, 1993; Godinot, 1992). However, only the former includes any articulated remains (RD 311, the Rosieres specimen), and these unfortunately lack associated phalanges.

Much less is known of omomyiform hands and a review of the systematics of the clade is therefore unnecessary. In fact, when Godinot and Beard (1992, 1993) wrote their reviews, no omomyiform hand fossils were known. The first published description of omomyid hand fossils was provided by Hamrick (1999), who described a hamate and pisiform from the Bridger Basin and attributed them to *Omomys* based on linear measures of absolute size. Since then, Gebo et al. (2012) have attributed intermediate phalanges to the “anaptomorphine” *Teilhardina belgica* and tentatively identified two among this sample as pertaining to the manus.

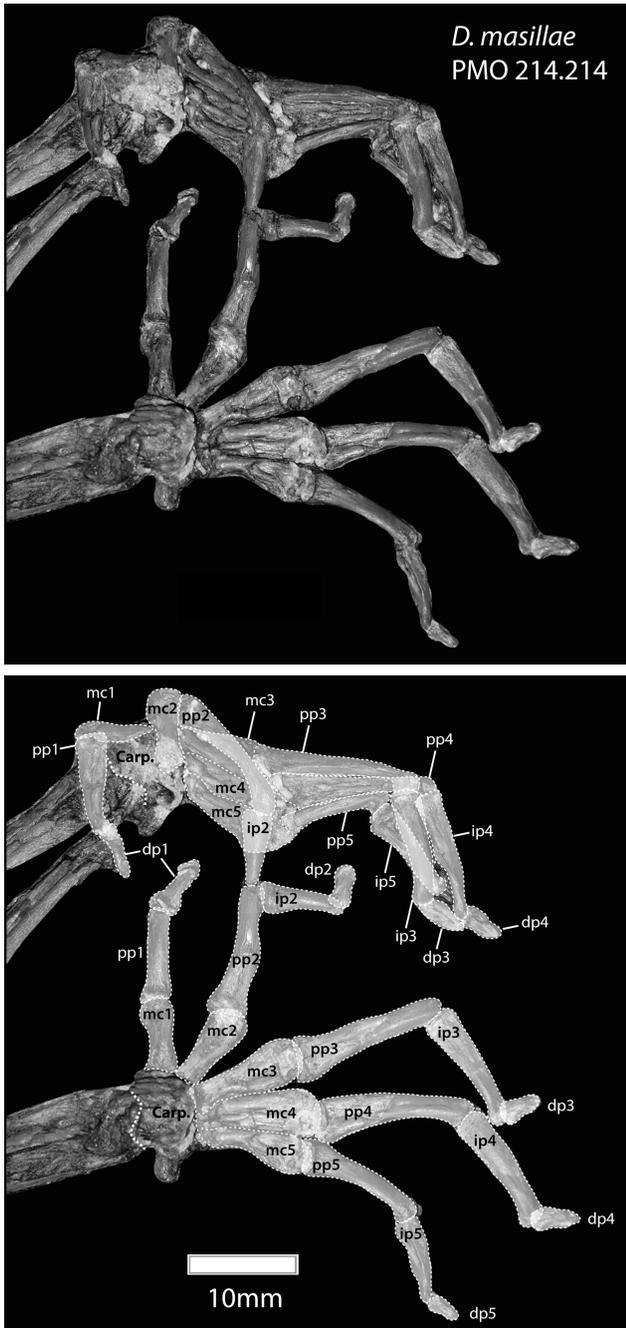
A review of fossil hand specimens representing adapiforms and omomyiforms is provided below. Additionally, Table 2 provides a list of taxa represented by hand fossils,

the manual elements known for these taxa, the major publications describing these specimens and the interpretations given there-in. A reassessment of morphological patterns and discussion of their phylogenetic and evolutionary significance follows this section.

A major goal of this work is to rectify misconceptions about digit proportions that have arisen even for some of the more complete specimens. These stem from 1) the fragmentary nature of intermediate phalanges in *Notharctus* specimens (Fig. 1); 2) inadequate documentation of digit identifications and measurement methods used for the Messel adapiforms, including *Darwinius*; and 3) a tendency to focus on “intrinsic” hand proportions and relative neglect of “extrinsic” proportions. To aid the discussion, we provide new estimates of prehensility and other intrinsic proportions for adapines using recently augmented locality samples (Appendices B–E; Table 5; Fig. 10), and provide new measurements for cercamoniines (*Europolemur*, *Godinotia*, and *Darwinius*) accompanied by detailed identifications on radiographs and specimen photos (Appendix F; Tables 3–7; Figs. 11–13). We also plot digit and metacarpal lengths against estimated body mass (Table 4) and record residuals (Table 6) in order to evaluate extrinsic proportions. Finally, we re-evaluate pollical divergence of fossils in the context of an extant comparative sample and provide the first quantitative estimates of proximal phalanx curvature in *Notharctus*, *Adapis*, *Leptadapis*, and omomyiforms.

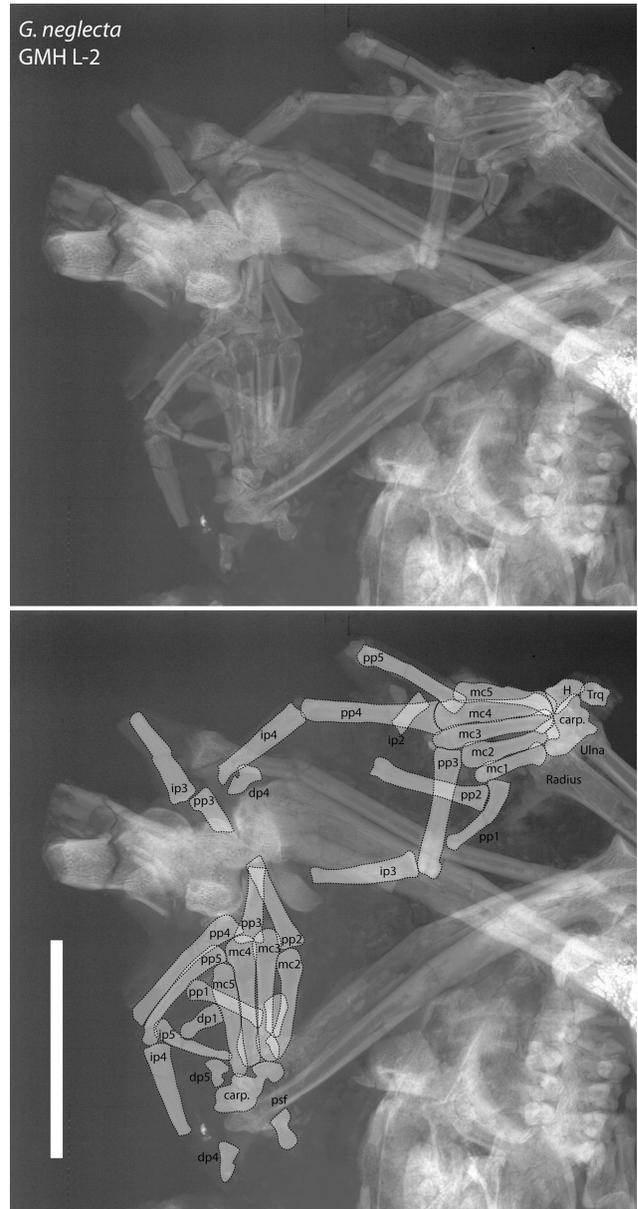
### Carpus

The carpus of adapiforms ranges from 11 to 16% of hand length in taxa for which sufficient fossils are



**Fig. 12.** Hand of *D. masillae*. Images are taken and modified from Franzen et al. (2009). Measurements in Appendix E are based directly off the bones as interpreted in this image. Note that metacarpal lengths cannot be constrained for MC2–3 due to obliterated proximal epiphyses. Lengths are of questionable accuracy for MC4–5 as well. However, it seems likely that MC3 and MC4 were of very similar length. See Figure 10 for abbreviations. Radiographs were made by Jörg Habersetzer and the copyright is with Senckenberg Forschungsinstitut Frankfurt am Main, Dr. Jörg Habersetzer.

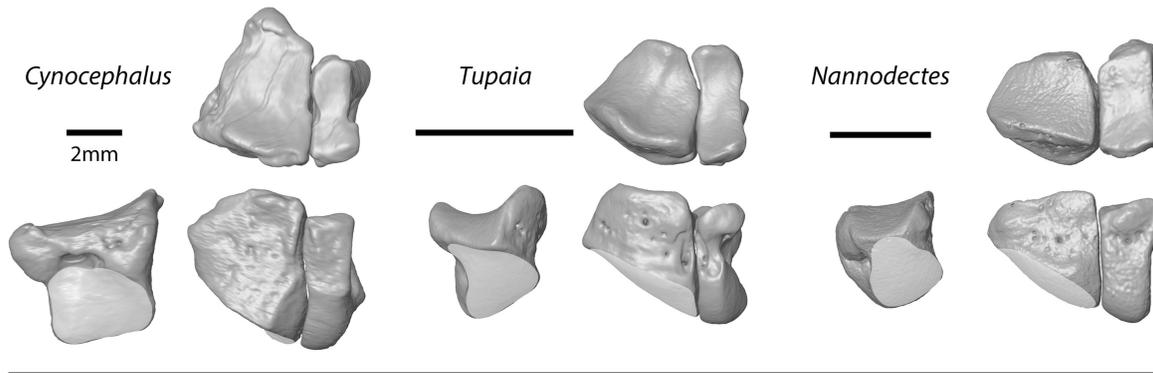
known (Appendix E; Tables 3 and 4; Fig. 9), including various notharctids and *Adapis*. Though estimates of carpus proportions have been previously given for *Notharctus*, even the most complete specimen (AMNH 127167) is too incomplete for an accurate estimate of carpus proportions because MCIII and intermediate pha-



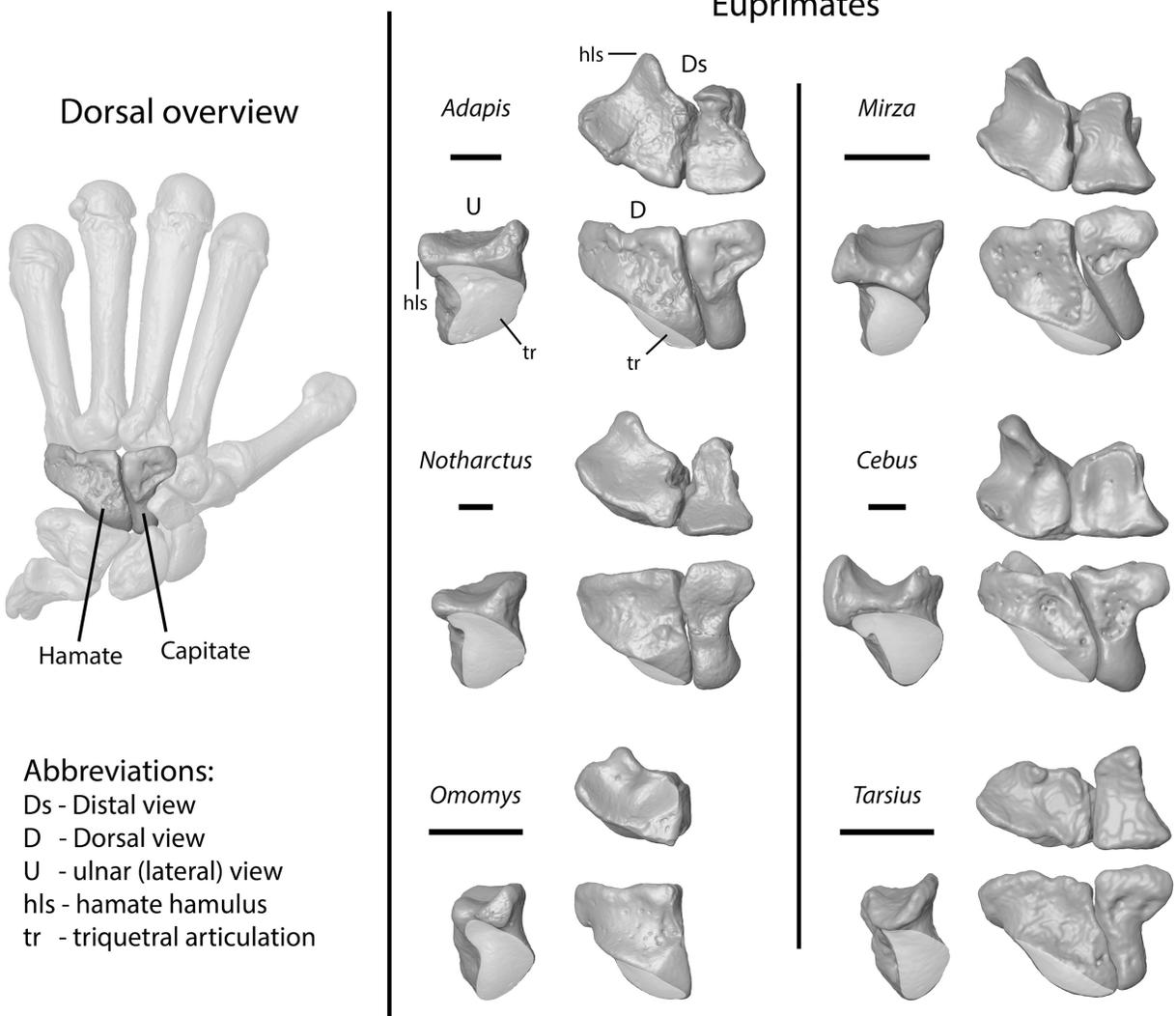
**Fig. 13.** Hand of *G. neglecta*. Original radiographs and photographs used in Thalmann (1994) were provided by U. Thalmann and digitized using an Epson 7100 series transparency scanner. Measurements in Appendix E are based directly off the bones as interpreted in this image. See Figure 10 for abbreviations. Scale bar is 20mm in length.

langes III–IV are broken (Fig. 1). It would be inappropriate to use intermediate phalanx II or V, given that Messel adapiforms show substantial between-digit-ray variation in intermediate phalanx length. However, it seems likely that MCIII–IV would have been extremely close in length. Therefore, the length of the carpus can be compared to the length of MCIV in *Notharctus* and compared to the condition in other early primates (Table 4). All notharctids appear similar in this regard. Hand fossils of *S. gracilis* are too incomplete for any estimate of intrinsic proportions (see Table 2). We provide estimates for *Adapis* in the absence of articulated specimens, but add reliability to these estimates through access to large locality samples (Table 5). However, we

## Nonprimates &amp; Plesiadapiforms



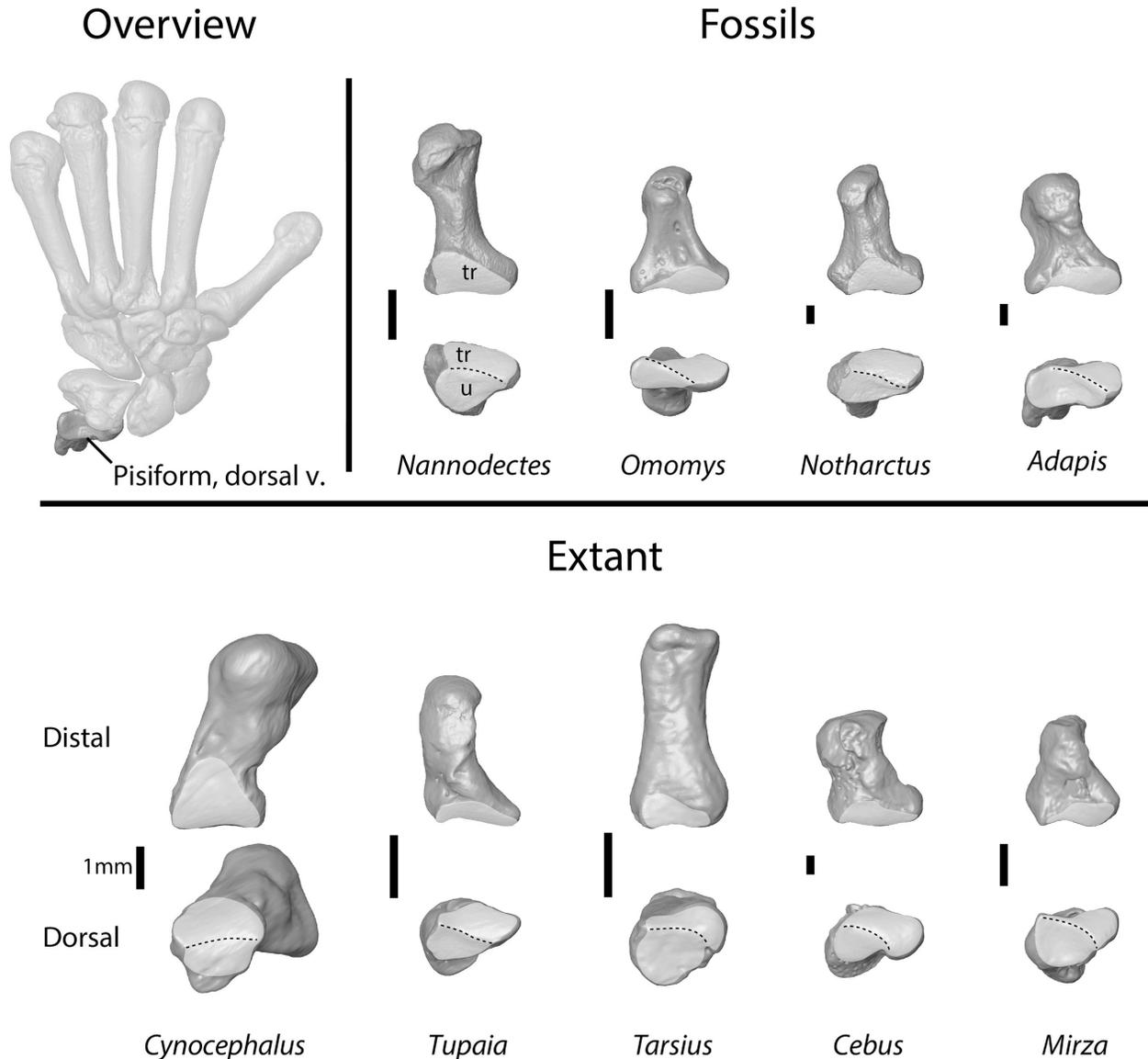
## Euprimates



**Fig. 14.** Hamate and Capitate. Standardized to same proximodistal length. Views for each taxon are distal (top), dorsal (bottom), and ulnar (left). Scale bars equal 2 mm. Overview image is of carpus and metacarpus of *Adapis* RD 311 highlighting position of these carpals in dorsal view. Other views are rotations of 90° from dorsal. Specimens depicted include *Cynocephalus volans* (UNSM 11502), *Tupaia glis* (EA 0174, Duke Univ. Coll.), *N. intermedius* (USNM 442229), *A. parisiensis* (RD 311), *N. tenebrosus* (AMNH 127167), *Omomys carteri* (UM 32319), *Mirza coquereli* (DPC 137), *Cebus* (EA 54, Duke Univ. Coll.), and *Tarsius spectrum* (AMNH 109367).

acknowledge that adapine estimates are more hypothetical than those based on the Messel and Geiseltal adapiform specimens, which are by far the best constrained.

The most broadly represented bones of the wrist are the hamate and pisiform (Figs. 14 and 15). The hamate is similar among all Eocene euprimates for which it is known in



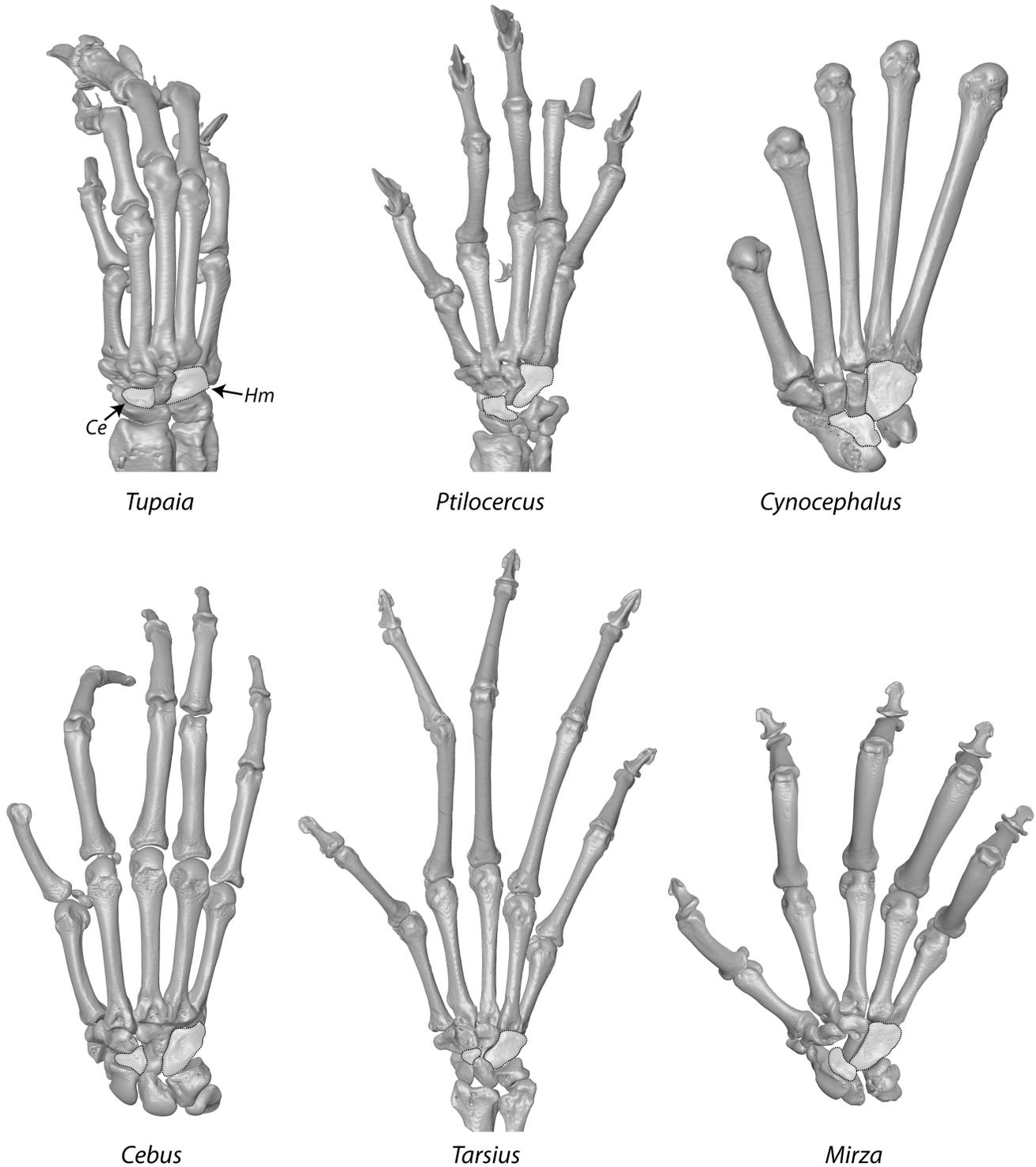
**Fig. 15.** Pisiforms. Standardized to same radioulnar width. Ulnar and triquetral facets highlighted. Views for each taxon are distal with palmar up (top row) and dorsal, with distal toward the top of the page (bottom row), as shown in overview image of carpals and MC of RD 311. A dashed line is used to separate ulnar and triquetral facets. Scale bars equal 1 mm. Specimen information: *N. intermedius* (USNM 442229), *Omomys carteri* (UM 32319), *N. tenebrosus* (AMNH 127167), *A. parisiensis* (RD 311), *Cynocephalus volans* (USNM 11502), *Tupaia glis* (EA 0174, Duke Univ. Coll.), *Tarsius spectrum* (AMNH 109367), *Cebus* (EA 54, Duke Univ. Coll.), *Mirza coquerli* (DPC 137).

having a spiral facet for the triquetrum and a relatively small hamulus (Hamrick, 1997, 1999). The latter feature suggests lesser development of the digital flexors than that of extant strepsirrhines, which have a relatively large hamulus. Notharctines and *Adapis* are said to have a relatively transversely oriented proximal facet similar to that of arboreal quadrupedal lemurs (Hamrick, 1996c), whereas *E. kelleri* and *Omomys* have a more medially (ulnarly) oriented facet also characteristic of extant vertical clingers (Hamrick, 1996c, 1999). Information on more basal omomyiforms and adapiforms (such as *Teilhardina* and *Cantius*, respectively) would help test whether a more ulnar or more transverse proximal facet is primitive for euprimates (though see discussion below).

Hamrick (1997) suggested that the ancestral euprimate differed from tupaiids in having a larger scaphoid

tubercle related to an expanded carpal tunnel, serving as a “windlass mechanism for the pollical branch of the *flexor digitorum profundus*” (p.114). This would aid the powerful pollical adduction needed for clasping onto relatively small-diameter supports. However, we note that plesiadapiforms have a strongly developed scaphoid tubercle as well (Figs. 1, 5, and 8), suggesting pollical adduction was powerful in early stem-primates.

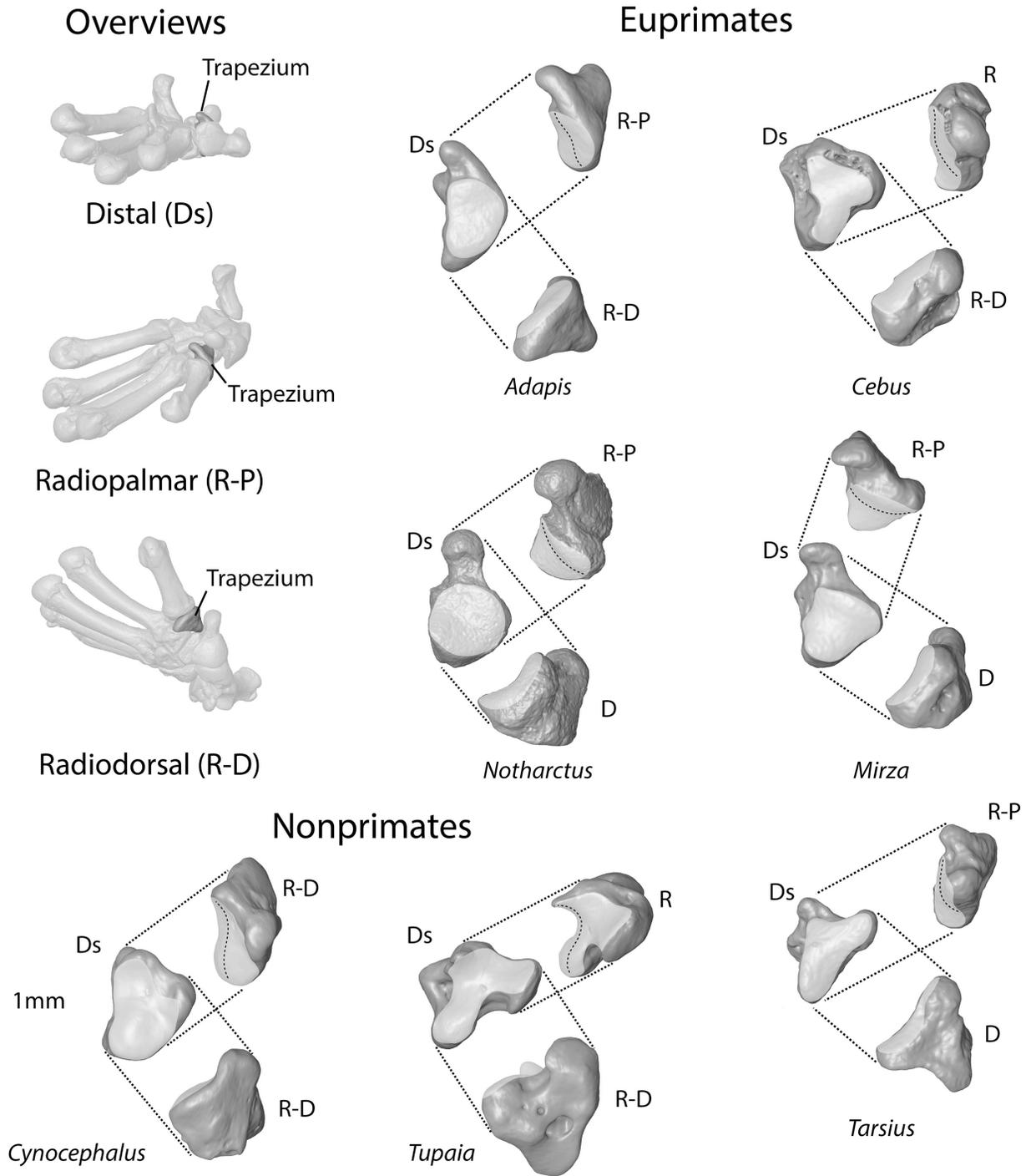
The pisiform is generally proportionally larger in Eocene taxa than in extant lemuriforms, again suggesting a proclivity for arboreal quadrupedal behaviors in which the hands are dorsiflexed (Hamrick, 1996c, 1999). On the other hand, the pisiform in plesiadapiforms is proportionally even bigger (Figs. 1, 5, 8, and 15), suggesting that early euprimates were less specialized for pronograde postures that require a large and



**Fig. 16.** Depiction of skeleton hands showing relationship of centrale to hamate. Though contact of the hamate by the centrale has been treated as a strepsirrhine synapomorphy (Beard and Godinot, 1988), it is also present in some non-primate euarchontans (Stafford and Thorington, 1998; Sargis, 2002). The centrale and hamate are highlighted in light gray. Specimen information: *Tupaia glis* (AMNH 212952), *P. lowii* (USNM 488069), *Cynocephalus volans* (UNSM 11502), *Cebus* (EA 54, Duke Univ. Coll.), *Tarsius pumilus* (AMNH 196477), *Mirza coquerli* (DPC 137).

robust pisiform. It should also be noted that both Hamrick (1997) and Figure 15 show a relatively tall pisiform body in tarsiers, despite their committed use of vertical clinging and leaping. Though differences in pisiform tubercle relative size are not readily apparent

among adapiforms, *Adapis* differs from *Notharctus* in other features suggesting more habitual use of dorsiflexed hand postures and hence pronograde postures. For example, *Adapis* has a dorsally facing radial facet on the lunate similar to *P. cookei* (Boyer, 2009),



**Fig. 17.** Trapezia. Standardized to same articular surface size. Note that saddle-shaped metacarpal facets are quite common. The facet for the pollical metacarpal is highlighted. The main view is distal with palmar toward the top of the page, so that the pollical metacarpal would be pointing out of the page and the pisiform would be pointing toward the top in an articulated specimen, as shown in the overviews using the carpals and metacarpals of *Adapis* RD 311. Other views illustrate principle curvatures of the pollex facet. The dashed black line on the surface in the radial and radiopalmar views shows the arc of the facet surface. No such line is necessary for the dorsal views as the arc is visible in profile if present. Note that *Notharctus*, *Tarsius*, and *Mirza* have two pronounced curvatures that constitute “saddle-shapes” (which are very similar to those of catarrhines) and should permit opposition movements at the carpometacarpal joint. Nonprimate euarchontans have a dorsal “ball-like” facet for unrestricted mobility in rotation, abduction and adduction during dorsiflexed postures, but recurvatures palmarly and radially restricting any mobility in plamarflexed postures. Abbreviations: D, dorsal; Ds, distal; R-D, radiodorsal; R-P, radiopalmar; R, radial. Scale bars equal 1 mm. Specimen information: *A. parisiensis* (RD 311), *Cebus* (EA 54, Duke Univ. Coll.), *N. tenebrosus* (AMNH 127167), *Mirza coquerli* (DPC 137), *Tarsius spectrum* (AMNH 109367) *Tupaia glis* (EA 0174, Duke Univ. Coll.), *Cynocephalus volans* (UNSM 15502).

whereas *Notharctus* has a more proximally facing facet (Fig. 5).

The relative sizes of the triquetral and ulnar facets on the pisiform vary between *Adapis* and those of other fos-

TABLE 8. Pollical Divergence

Taxon	n	Mean	SD
<i>Adapis parisiensis</i>	1	36.18	–
<i>Notharctus tenebrosus</i>	2	34.74	–
<i>Darwinius masillae</i>	1	43.00	–
<i>Tupaia sp.</i>	6	4.36	3.00
<i>Ptilocercus lowii</i>	4	15.07	1.91
<i>Cynocephalus sp.</i>	9	10.66	3.09
<i>Daubentonia madagascar.</i>	4	19.06	3.85
<i>Microcebus griseorufus</i>	4	16.52	2.97
<i>Cheirogaleus sp.</i>	4	27.58	8.07
<i>Mirza coquereli</i>	3	30.03	2.27
<i>Varecia variegata</i>	3	29.32	4.66
<i>Eulemur fulvus</i>	5	28.65	4.82
<i>Hapalemur griseus</i>	3	33.61	9.82
<i>Lemur catta</i>	3	24.60	3.57
<i>Lepilemur mustellinus</i>	6	36.58	10.18
<i>Otolemur crassicaudatus</i>	4	35.31	3.48
<i>Galago senegalensis</i>	4	32.37	6.08
<i>Perodicticus potto</i>	4	71.38	13.11
<i>Nycticebus coucang</i>	3	49.47	3.17
<i>Tarsius sp.</i>	6	18.21	2.75
<i>Cebus sp.</i>	5	13.85	3.76
<i>Saimiri sp.</i>	5	12.07	4.37
<i>Aotus sp.</i>	3	15.19	1.83
<i>Callicebus moloch</i>	3	10.10	2.54
<i>Cebuella pygmaea</i>	2	4.11	–
<i>Callithrix jacchus</i>	5	2.67	1.31
<i>Colobus guereza</i>	1	23.00	–
<i>Macaca mulatta</i>	10	23.23	9.26
<i>Papio sp.</i>	5	21.69	7.12
<i>Homo sapiens</i>	5	33.78	1.67
<i>Pan paniscus</i>	1	33.00	–
<i>Pan troglodytes</i>	8	37.81	5.57
<i>Pongo pygmaeus</i>	5	44.62	8.76

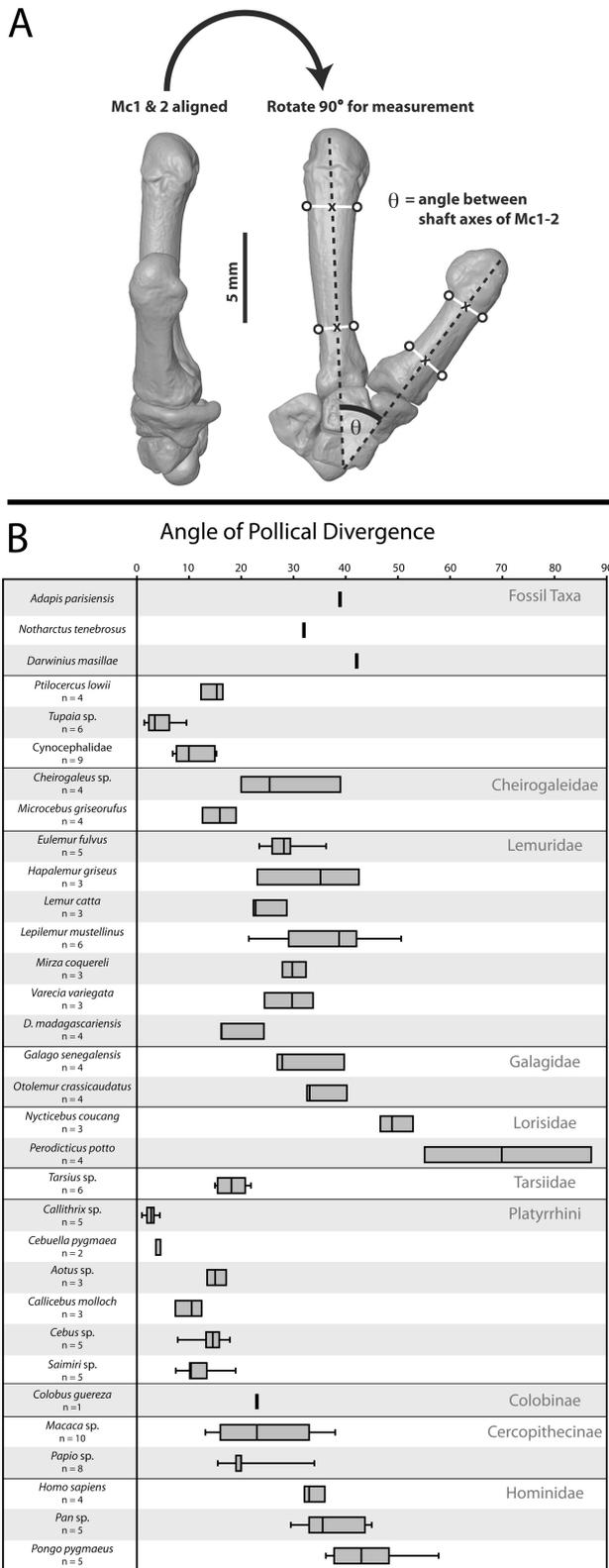


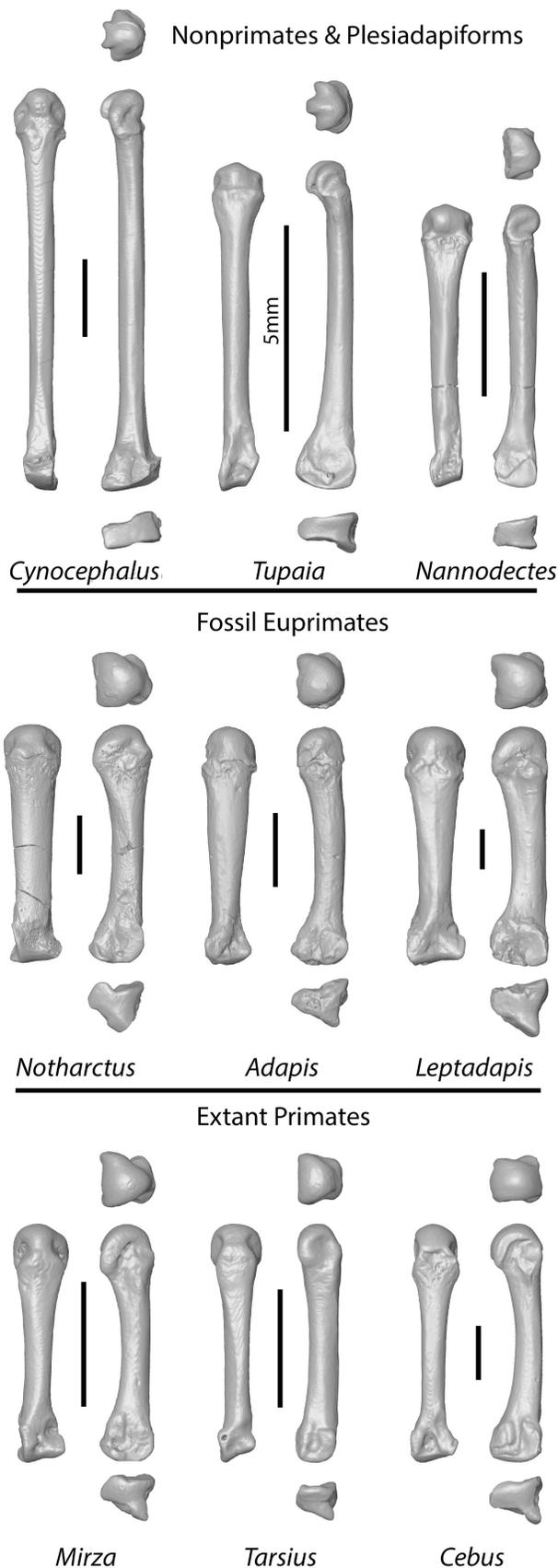
Fig. 18.

See Figure 17 for measurement method. C. Orr provided access to catarrhine scans for these measurements.

sil taxa where the morphology can be observed (e.g., *Notharctus* and *Omomys*) (Fig. 15). In *Adapis*, the pisiform is strepsirrhine-like, with a large, deeply excavated ulnar facet. In *Notharctus* and *Omomys*, the pisiform is more haplorhine-like, with subequal facets (Beard and Godinot, 1988; Hamrick, c,1999). Differences among taxa illustrated in Figure 15 suggest that variation in pisiform morphology must be more carefully studied before systematically informative character states and character-state combinations can be reliably identified.

The presence of extensive centrale-hamate contact (which isolates the capitate from the lunate) is another feature that differentiates modern strepsirrhines, *Ptilocercus*,

**Fig. 18.** Pollical Divergence. **A:** Method for calculating pollical divergence angle. First, it must be verified that corresponding facets on MC1, trapezium, trapezoid, MC2 (and preferably the capitate and centrale) are in closest packed positions. Next, the bones are viewed and photographed (or a screen shot is obtained) with plane of the MC1-2 perpendicular to the viewing plane to ensure that the maximum angle is recorded. Then, the shaft axes are approximated by taking the midpoint of the shaft at two points along its length (“x’s”), and connecting a line through these points. The pollical divergence angle is the angle between the axes of MC1-2 approximated in this way. **B:** Box and whiskers plot for pollical divergence (see Table 8 for sample statistics). Boxes encompass 50% of data, whiskers 75–100%. Horizontal lines represent the median. Note that the pattern of variation in divergence makes it difficult to reconstruct the degree of divergence in the euprimate ancestor. C. Orr provided access to catarrhine scans for these measurements.



and *Cynocephalus* from haplorhines and tupaiids (Beard and Godinot, 1988; Stafford and Thorington, 1998; Sargis, 2002). All Eocene taxa discussed here have a relatively smaller centrale as is also characteristic of extant haplorhines and tupaiids (Fig. 16) (Beard and Godinot, 1988; Godinot, 1992; Hamrick and Alexander, 1996).

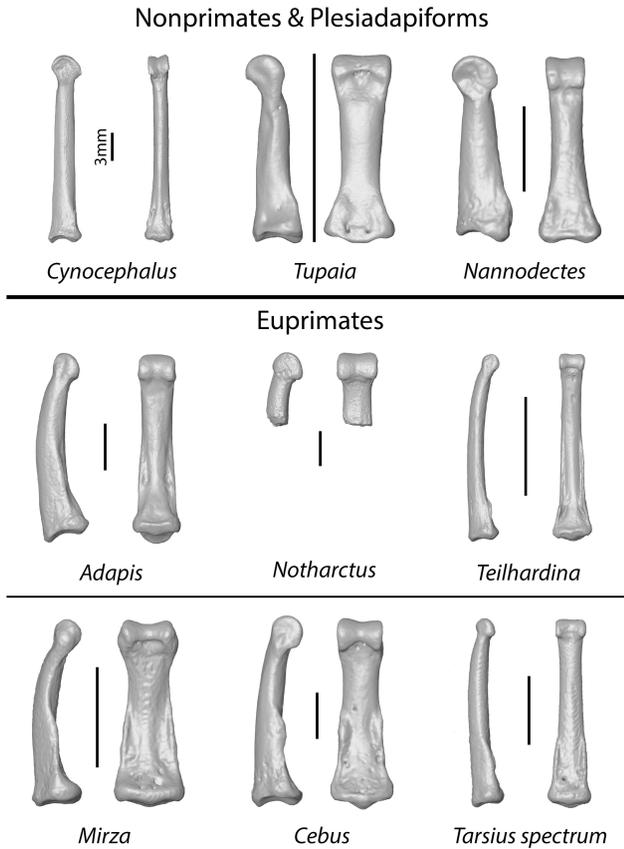
The trapezium exhibits some variation among Eocene taxa. In *Notharctus*, it is relatively large compared to the condition of *Adapis* (Fig. 17) (Hamrick, 1996c). Vertically clinging taxa tend to have a larger trapezium and pollex than do arboreal quadrupeds (Hamrick, 1996c). The MCI facet of the trapezium is sellar-shaped in *Notharctus* (Hamrick and Alexander, 1996). It therefore joins indriids and lorisiforms (Jouffroy and Lessertisseur, 1959; Etter, 1974, 1978) on the list of non-catarrhines that exhibit Napier's (1961) morphological correlates of "true opposability." Furthermore, our inspection of a limited number of extant specimens suggests that a sellar trapezium is also found in *Mirza* and *Tarsius* (Fig. 18). Thus, correlates of "true opposability" can be found in all major primate groups for which data are available except platyrrhines. A quantitative and taxonomically comprehensive study of facet curvatures in the trapezium and pollical metacarpal would provide crucial information for interpreting the evolution of pollical opposability. In contrast to *Notharctus*, *Adapis* appears to have a flat articular MCI surface (Godinot and Beard, 1993) (Fig. 17), as argued to be typical of extant strepsirrhines and platyrrhines (Napier, 1961).

The orientation of the MCI facet on the trapezium can contribute to pollical divergence. *Notharctus*, *Adapis*, and *D. masillae* have around 30°–40° of divergence between first and second digits (though in *D. masillae* this interpretation is based on in situ post-mortem digit postures) (Table 8; Fig. 18B). Modern strepsirrhines and hominoids have a similar degree of divergence as these Eocene forms, whereas tarsiers, platyrrhines, and non-primate euarchontans have less divergence (Table 8; Fig. 18B).

Interestingly, early perspectives on the hand of *Notharctus* (Gregory, 1920; Napier, 1961) suggested its pollex was neither divergent nor "pseudo-opposable." This has likely added to the perception that manual grasping specializations lagged behind pedal grasping specializations in euprimate evolution (Cartmill, 1972, 1974a,b; Bloch and Boyer, 2002). However, the data reviewed here show osteological specializations in *Notharctus* equivalent to that of many modern strepsirrhines (as well as catarrhines), and the potential for pollical mobility and dexterity matching or exceeding that of these extant taxa, depending on the myological and ligamentous limitations/specializations that were also present.

**Fig. 19.** Metacarpal of ray three. Top row is standardized to same mediolateral width of distal end. The bottom two rows are depicted with a similar distal end width, but standardized to same proximodistal length. Note plesiadapiforms and non-primate euarchontans have distal articular surfaces that face primarily dorsad, are dorsoventrally shallower and have more pronounced palmar keels. Scale bars equal 5 mm. Specimen information: *Cynocephalus volans* (UNSM 15502—MCIIV depicted due to image availability), *Tupaia glis* (EA 0174, Duke Univ. Coll.), *N. intermedius* (USNM 442229), *N. tenebrosus* (AMNH 131764), *A. parisiensis* (RD 311), *L. magnus* (MaPhQ no#), *Mirza coquerli* (DPC 137), *Tarsius spectrum* (AMNH 109367), *Cebus* (EA 54, Duke Univ. Coll.).





**Fig. 21.** Intermediate phalanx of digit three. Standardized to same proximodistal length. Scale bars equal 3 mm. Note that plesiadapiforms, dermopterans and treeshrews have mediolaterally narrow, dorsoventrally deep shafts, whereas euprimates exhibit the opposite dimensions. Specimen information: *Cynocephalus volans* (UNSM 15502), *Tupaia glis* (EA 0174, Duke Univ. Coll.), *N. intermedius* (USNM 442229), *A. parisiensis* (MaPhQ no#), *N. tenebrosus* (AMNH 127167), *T. belgica* (IRSMB M 1266), *Mirza coquerli* (DPC 137), *Cebus* (EA 54, Duke Univ. Coll.), *Tarsius spectrum* (AMNH 109367).

### Metacarpus

Detailed morphology, proportions, and articular configurations of the metacarpus of Eocene euprimates can be best assessed in *Notharctus* and *Adapis* (Figs. 1 and 5). Only isolated elements have been recovered for *Smilodectes* (Beard and Godinot, 1988; Godinot, 1991, 1992; Godinot and Beard, 1991). Although the oil shale specimens of cercamoniines usually preserve several metacarpals the epiphyses tend to be obliterated, making assessment of detailed morphology and proportions difficult (Figs. 11–13). The positions of bones in the right hand of the type specimen of *D. masillae* appear to reflect a somewhat natural posture (Fig. 12; Franzen et al., 2009).

Well-preserved metacarpals of Eocene adapiforms look quite similar to those of modern strepsirrhines and platyrrhines (Fig. 18). To our knowledge, no complete metacarpals have yet been figured or described for omomyiforms. Generally speaking, primate metacarpals are distinctive among mammals. So when did this distinctive morphology arise? Compared to known plesiadapiforms, the metacarpals of adapiforms are dissimilar in several respects. First, adapiform metacarpals are relatively shorter and more robust than those of plesiadapiforms.

Additionally, the distal ends are mediolaterally narrower relative to their dorsoplantar depth. Finally, the distal articular surfaces for the proximal phalanges face distally and have a relatively large radius of curvature in adapiforms, whereas in known plesiadapiforms, this articular surface is palmarly restricted and therefore leads to a dorsad-facing articulation (Figs. 1 and 19). The differences in orientation and shape of the phalangeal facets suggest a limited capacity for stable (and probably less frequent) hyperextension of the metacarpophalangeal joint in adapiforms relative to plesiadapiforms. However, palmar-flexion was probably more effective in adapiforms. Furthermore, the larger radius of curvature and greater proportional depth of this surface equate to greater surface area relative to the overall size of the metacarpal, suggesting a greater capacity for transmitting force while maintaining low joint stress (Hamrick, 1996a). Despite these differences, both plesiadapiforms and Eocene euprimates share globular metacarpal heads, suggesting shared capacities for mobility in abduction, adduction, and axial rotation, which are expected to be beneficial in committed arborealists (Figs. 1 and 19).

Metacarpal proportions for available adapiforms show MCII to be shortest, MCIII to be the longest, and MCIV to be second longest [AMNH 127167 has a broken MCIII, so the length reported by Hamrick and Alexander (1996) is an estimate], with the exception of *Leptadapis*, in which MCIV may have been the longest (Appendix B; Table 5). Furthermore, notharctids appear to have a fairly short MCII relative to MCIII, making them similar to lorises, *Daubentonia*, and *Tupaia* (Appendix F; Tables 3 and 4). *Adapis* has a less-reduced MCII and is more typical among euprimates. All taxa that can be reconstructed have high degrees of pollical divergence similar to that of strepsirrhines and hominoids (Fig. 18B). However, *Notharctus* and *Darwinius* appear to have pronounced divergence between the second and third metacarpals as well (Figs. 1, 5, and 12), possibly indicating a habitual schizodactylous grasp in these taxa.

### Phalanges

Though there is important functional information in the detailed morphology of the phalanges, it is the relative proportions (Godinot and Beard, 1991; Jouffroy et al., 1991; Kirk et al., 2008) and degree of curvature (Jungers et al., 1997) that are most frequently discussed. Phalanges are known for most adapiform taxa represented by other hand elements, but no associated accumulations of metacarpals and phalanges have been recovered for adapines. Prehensility has thus been difficult to estimate for these taxa (Godinot and Beard, 1991, 1993; Godinot, 1992). In this section, we begin by discussing morphological details of the phalanges of Eocene euprimates and then consider apparent intrinsic hand proportions.

The proximal phalanges of Eocene adapiforms (Fig. 20) are superficially somewhat similar to those of some large-bodied plesiadapiforms, particularly *P. cookei* (UM 87990; Boyer, 2009), though clearly they are more elongated in adapiforms. They lack the pronounced flexor sheath ridges of paromomyids, micromomyids, and *C. simpsoni* (Bloch and Boyer, 2002; Boyer and Bloch, 2008). *C. simpsoni* also differs from notharctines in the greater curvature of its proximal phalanges (Bloch and Boyer, 2002). The most salient differences in the proximal phalanges of known plesiadapiforms versus those of adapiforms and omomyiforms appear in the morphology

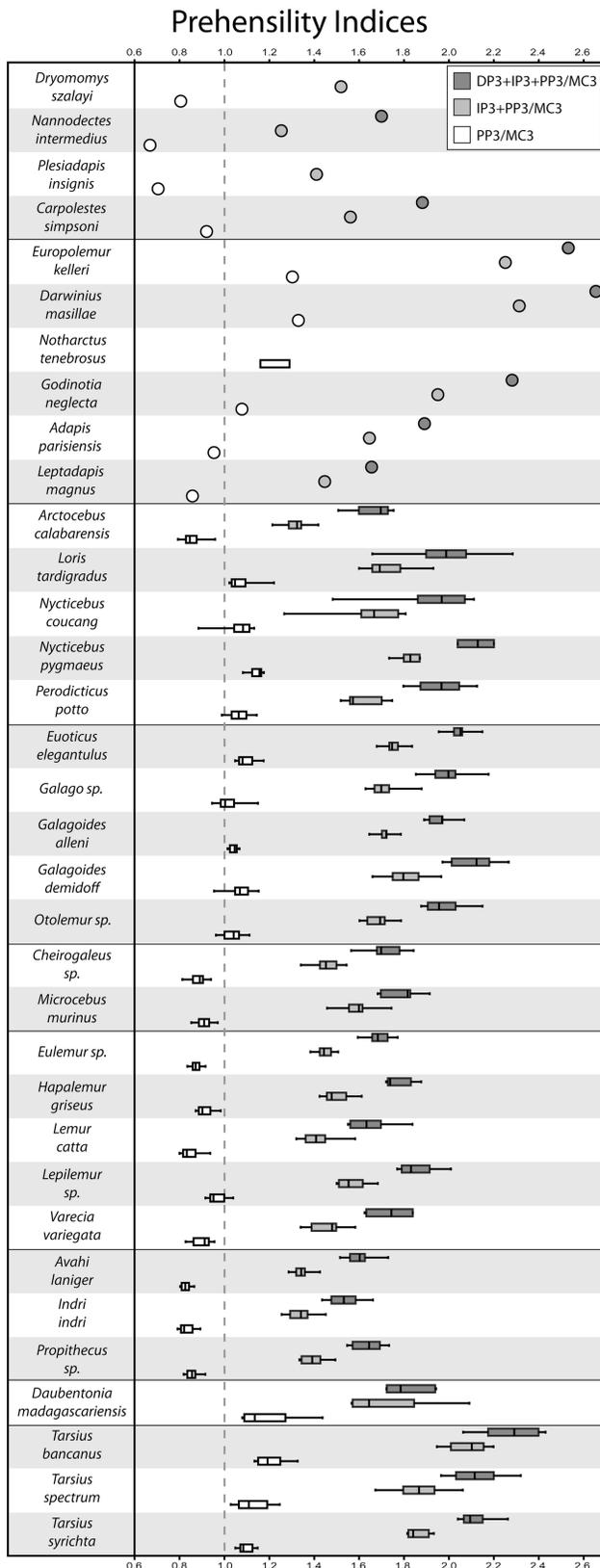
of the proximal end and its metacarpal articular surface. Specifically, in plesiadapiforms, the metacarpal articular surfaces face dorsad due to proximally projecting ventral

tubercles. In contrast, the metacarpal articular surfaces of the proximal phalanges face proximally in notharctines and have both proximal and dorsal facing regions in adapines and omomyiforms (Fig. 20). The morphology of plesiadapiform proximal phalanges enhances the pattern dictated by the distal articular surface of the metacarpals, and promotes hyper-extension of the metacarpophalangeal joint (Fig. 19). These contrasts hold for other Eocene euprimates examined here, except among adapids, which have phalangeal curvature apparently more comparable to that of *C. simpsoni* (see below).

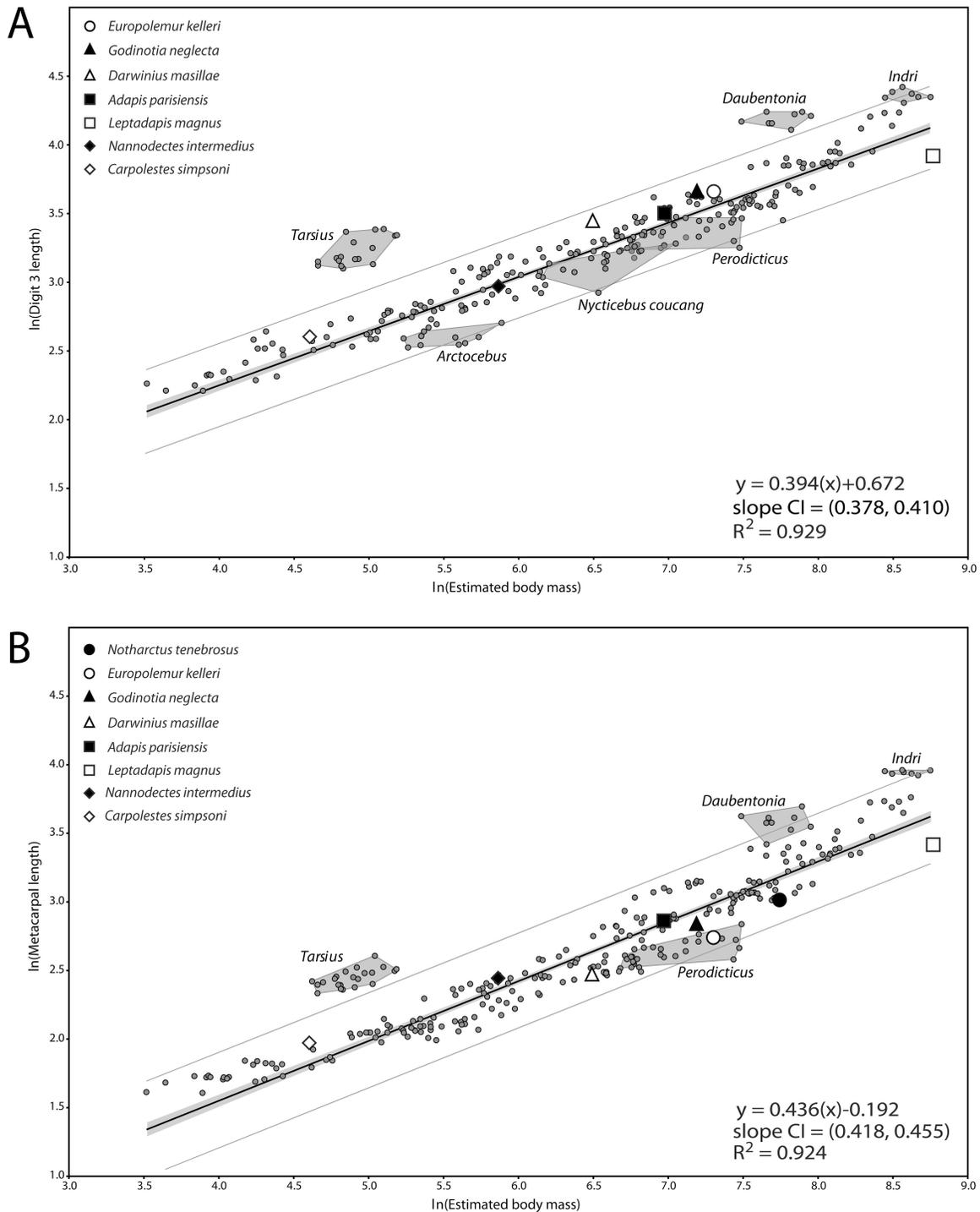
Turning to the only hand material known for Paleogene anthropoids, the proximal phalanges of *Aegyptopithecus* are quite similar to those of *Adapis* and *Leptadapis* in having 1) strong curvature (included angle) that is greatest in the manual elements (Table 9), 2) well-developed flexor sheath ridges, and 3) apparently longer pedal than manual elements (Hamrick et al. 1995). Given these similarities, it would not be surprising if *Leptadapis* and *Aegyptopithecus* had similar locomotor repertoires (probably slow climbing, arboreal quadrupeds with some suspensory tendencies). Hamrick et al. (1995) also note substantial dorsal exposure of the proximal articular facets in *Aegyptopithecus* suggesting frequent hyper-extension at the metacarpophalangeal joints. Future studies should focus on quantifying “dorsal exposure” of the metacarpal facet more systematically. The proximal phalanges of *Apidium*, were described by Hamrick et al. (1995) as *Cebus*- or *Cercopithecus*-like, and suggestive of a *Saimiri*-like arboreal quadrupedal locomotor repertoire in which there was also frequent leaping and the interphalangeal joints were frequently extended. They do not strike us as similar to those of *Cebus* (Fig. 20) or any other taxon considered in this review. The low curvature and reduced flexor sheath ridges are similarities to the condition in omomyids and tarsiers (Table 9; Fig. 20). However, *Apidium* differs from these taxa in having proximal phalanges that are much more robust.

Whereas proximal phalanges of plesiadapiforms and euprimates are superficially similar, there is no mistaking the intermediate phalanges of Eocene euprimates for those of plesiadapiforms (Fig. 21). While plesiadapiform intermediate phalanges are characterized by mediolaterally narrow, dorsoventrally deep articular ends and shafts (Boyer and Bloch, 2008), those of notharctines are typical of extant primates: mediolaterally broad and dorsoventrally flattened. Additionally, plesiadapiforms exhibit relatively straight-shafted intermediate phalanges, whereas those of Eocene euprimates exhibit more dorsal convexity (Boyer and Bloch, 2008). The degree of curvature is difficult to evaluate in cercamoniines due to distortion of the Messel specimens, but these contrasts with plesiadapiforms otherwise hold for all known early euprimates.

When looking at overall hand proportions, it is clear that notharctids have exceptionally long digits, with the third digit phalanges of *Darwinius* and *Europolemur* making up



**Fig. 22.** Prehensility and proximal prehensility of fossil and extant taxa. Box and whisker plots for three different prehensility indices. Boxes encompass 50% of data, whiskers 75–100%. Horizontal lines represent the median. Note increased prehensility by all three measures among most fossil euprimates relative to plesiadapiforms. Dashed line indicates metacarpal length equal to phalangeal length. Data for extant primates by Lemelin and Jungers (2007).

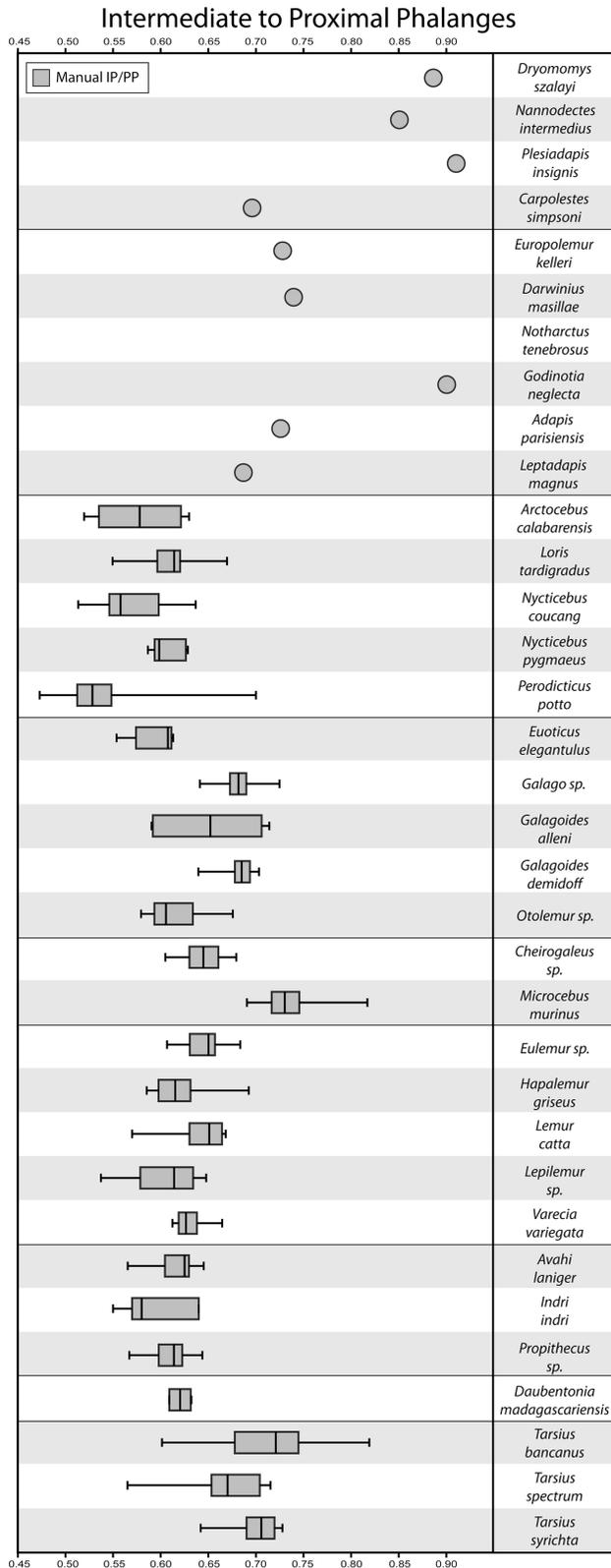


**Fig. 23.** **A:** Digit three length versus body mass and **(B)** Metacarpal three length versus body mass for fossil specimens and extant species. Intrinsic hand proportions of Eocene euprimates are frequently assessed (e.g., Jouffroy et al., 1991), but extrinsic proportions are not. Least squares regression (LSR) analysis was run on log-transformed digit and metacarpal lengths separately against log-transformed body mass estimates generated by the Lemelin and Jungers (2007) data (see Table 3 legend). Mass estimates used to plot fossils here were generated in various ways as described in Table 3. LSR is appropriate (as opposed to reduced major axis) because we are interested in assessing which taxa have longer (or shorter) than expected digits and/or metacarpals for their body masses. *Tarsius* and *Daubentonia* were not included in the regression as Lemelin and Jungers (2007) established that they were outliers to the primate scaling trend. Black lines and shaded areas show ordinary least squares regression and 95% confidence interval; gray lines show 95% prediction intervals. Groups with individuals outside prediction intervals are noted. Note that notharctids have slightly shorter than expected metacarpals, but longer than expected digits, yielding “tarsier-like” manual *intrinsic* proportions without “tarsier-like” *extrinsic* proportions.

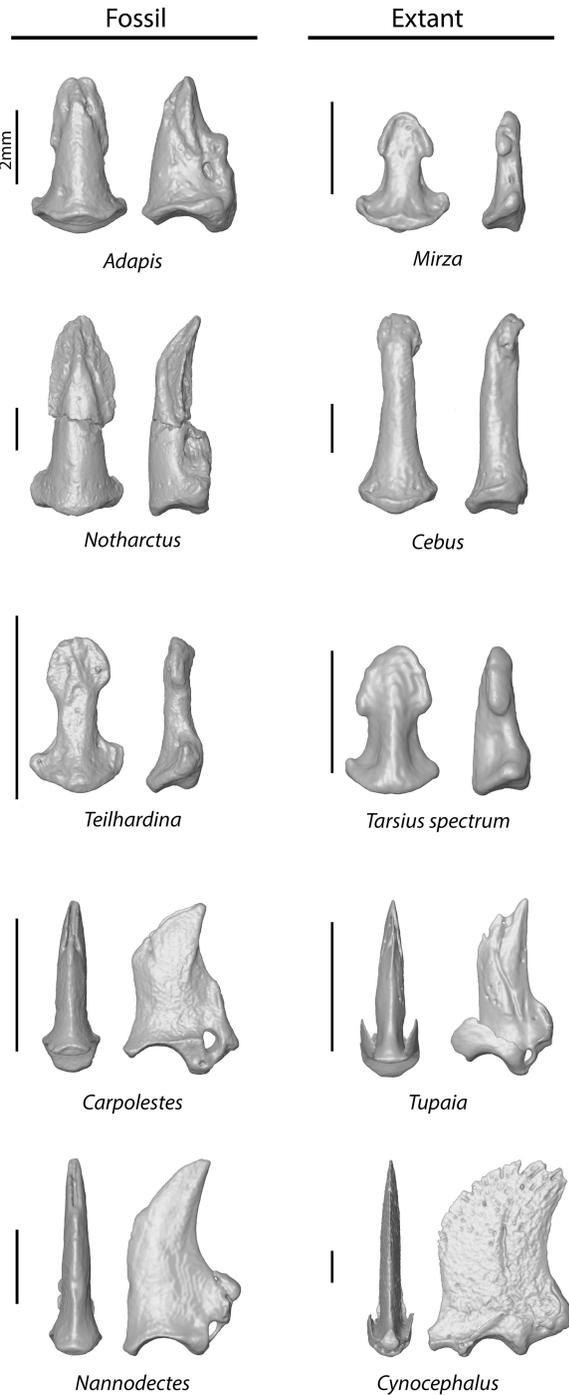
63–64% of the length of the hand (represented by the sum length of carpus, metacarpus, and digit). Among extant primates, only *Tarsius* and *Daubentonia* match these proportions (Tables 3 and 4; Fig. 13; Appendix E), while *Galago* and *Euoticus* come close [species means of 61.2% and

60.4% respectively, as reported by Jouffroy et al. (1991)]. As discussed above, though overall hand proportions have been reported for *Notharctus* (Godinot and Beard, 1991; Godinot, 1992; Hamrick and Alexander, 1996; Kirk et al., 2008), we are hesitant to do so as the third and fourth intermediate phalanges are incomplete in AMNH 127167 [see Fig. 1; Alexander and Burger (2001): their Fig. 6D], and digit ray associations are not documented for AMNH 11478 [described by Gregory (1920)]. Given the great deal of variation in the intermediate phalanges of the Messel adapiforms, it would seem misleading to estimate digit III proportions using intermediate phalanx II. Alexander and Burger (2001) report the existence of many more specimens of *Notharctus* collected for the American Museum of Natural History, and while they may provide information necessary to reconstruct these proportions, they have not yet been studied in detail. Nevertheless, the elements preserved demonstrate distinctive similarities between *Notharctus* and the Messel adapiforms. In particular, the ratio of the third proximal phalanx to the third metacarpal (Tables 6 and 7, Fig. 22) is 1.31 in the Messel species and between ~1.16 and 1.30 in *Notharctus* (uncertainty due to poor preservation in AMNH 127167, but it is probably closer to 1.30). Though values greater than 1.16 are seen in some individuals of *Loris* and *Nycticebus pygmaeus*, the only extant primates with a third digit proximal prehensility index frequently 1.30 or more are *Daubentonia* (species average = 1.18) and *Tarsius bancanus* (species average = 1.21) (Tables 6 and 7; Fig. 22).

Though the Messel adapiforms, *Daubentonia* and *Tarsius*, all have 3rd ray fingers that are unusually long relative to the metacarpus and carpus, the extant taxa differ from the fossils in having fingers that are also unusually long for their body masses (Fig. 23). Notharctid adapiforms examined here appear to have only slightly longer than expected fingers relative to their estimated body masses though admittedly error in body mass estimates renders these residuals non-significant (see Table 3 legend and Figure 23 caption for explanations of body mass estimates used here as well as for regression materials and methods). The unusual, hyper-prehensile intrinsic proportions of the Messel adapiforms appear to stem from a combination of slightly elongated digits, and slightly “shorter than expected” metacarpals relative to their body masses (Fig. 23). Therefore, similar intrinsic ray proportions (Fig. 9) of the Messel adapiforms (and probably *Notharctus*), *T. bancanus*, and *Daubentonia* likely indicate different functional/adaptive properties. Though *Godinotia* shares the pattern of slight digit elongation combined with metacarpal reduction, it is slightly less extreme in many of its intrinsic proportions (Appendix F; Tables 3 and 4, Figs. 9, 22 and 24) than are the Messel adapiforms. Its fingers make up 61.5% of its hand length, and the third digit proximal prehensility index is 1.07. Nonetheless, it is fairly unusual in at least one respect: the intermediate phalanges are closer in length of the proximal phalanges



**Fig. 24.** Intermediate to proximal phalanx ratios in fossil and extant taxa. Box and whisker plots for lengths of intermediate to proximal phalanges. Boxes encompass 50% of data, whiskers 75–100%. Horizontal lines represent the median. Note higher ratios among plesiadapiforms (with the exception of *Carpolestes*) relative to fossil and extant euprimates. Also note high ratio for *Godinotia*, indicating its unusually long intermediate phalanges. Data for extant primates is from Lemelin and Jungers (2007).



**Fig. 25.** Distal phalanges. Standardized to same mediolateral width of the proximal end or proximodistal length. Note plesiadapiforms have mediolaterally narrow, dorsoventrally deep shafts, whereas euprimates exhibit the opposite dimensions. Scale bars equal 2 mm. Specimen information: *A. parisiensis* (UM ECA 1400), *N. tenebrosus* (AMNH 127167), *Teilhardina brandti* (USNM 540587), *C. simpsoni* (UM 101963), *N. intermedius* (USNM 442229), *Mirza coquerli* (DPC 137), *Cebus* (EA 54, Duke Univ. Coll.), *Tarsius spectrum* (AMNH 109367), *Tupaia glis* (EA 0174, Duke Univ. Coll.), *Cynocephalus volans* (USNM 15502).

than is the case for any other extant primates or adapiforms. The intermediate phalanges are 90% the length of their corresponding proximal phalanges (Tables 3–7; Fig. 24). Interestingly, many plesiadapiforms approach

*Godinotia* in this respect (Tables 3–4, Fig. 24). *Adapris* and *Leptadapris* probably had shorter fingers relative to their hands (and body mass), resulting in intrinsic hand proportions most similar to *Perodicticus* and various platyrrhines (Tables 3–4, Figs. 9, and 22–23). The plesiadapiforms *Carpolestes* and *Nannodectes* have digit and metacarpal lengths that are predicted fairly accurately by the regression line based on extant primates using body mass (Tables 3–4; Fig. 23). As for other aspects of anatomy, information on proportions in omomyiforms will help determine the phylogenetic significance of such variation in phalangeal proportions among plesiadapiforms, adapiforms, and extant primates.

Axonic patterns of both metacarpals and digits can be reconstructed for just two adapiforms among known early Eocene forms: *Europolemur* and *Godinotia* (Fig. 3). *Europolemur* has a haplorhine pattern of overall mesaxony (3rd digit longest), and *Godinotia* is like most non-indriid strepsirrhines with overall ectaxony (4th digit longest), but metacarpal mesaxony. It seems likely that *Leptadapris* would have exhibited indriid-like overall ectaxonic proportions. No plesiadapiforms have been preserved with enough completeness or precise enough articulation to estimate overall axony, though micromomyids exhibit metacarpal mesaxony (Fig. 6).

Godinot (1991) noted that curvature is greater in adapines than notharctines though this observation was not quantified. Furthermore, proximal phalangeal curvature is not well studied among small-bodied strepsirrhines and platyrrhines. As a consequence, neither the degree of variation nor its functional correlates are documented for these taxa. We have augmented a comparative data set provided by Jungers et al. (1997) with data on *Tarsius* and the fossils *Notharctus*, *Adapris*, and *Leptadapris* (Table 9). Among extant taxa, vertical clingers and leapers have straighter phalanges, whereas generalists and suspensory taxa have progressively more curved bones. It is not surprising then that *Notharctus* has significantly straighter phalanges than the adapines, given previous ideas about more generalized arboreal quadrupedal or loris-like suspensory behaviors in adapines (Dagosto, 1983; Godinot and Jouffroy, 1984; Godinot, 1991). The Messel adapiforms also appear to have straight phalanges, but the degree to which this feature may have been distorted during preservation is unclear. Recent sorting of skeletal material recovered from the early Eocene of the Washakie basin (Savage and Waters, 1978) has yielded additional bones attributable to omomyiforms. The phalanges of a Washakie Basin omomyid (probably *Anemorhysis* based on small size) and the pedal phalanges of *A. achilles* are straighter than those of *Notharctus*, and similar to those of *Tarsius*. Conceivably, the manual phalanges of *A. achilles* could exhibit greater curvature, but our dataset suggests differences between hands and feet are generally minimal for a given taxon.

Distal phalanges are known for quite a number of Eocene euprimates, but can only be confidently assigned to the hand in *Notharctus*, the Messel adapiforms (Franzen, 1993; Hamrick and Alexander, 1996; Franzen et al., 2009), and *Godinotia* (Thalman et al., 1989; Thalman, 1994). Though all manual distal phalanges identified for Eocene euprimates are unguiform, possessing a flattened apical tuft (which indicates the presence of a flattened nail rather than a claw or falcula), there appears to be substantial variation (Fig. 25) (Gregory, 1920; Dagosto, 1988; Gebo et al., 1991; Godinot, 1991, 1992; Franzen, 1993; Hamrick and Alexander, 1996; Rose et al., 2011; Ni et al., 2013). AMNH 127167 reveals *Notharctus*

TABLE 9. *Phalangeal Curvature*

Taxon	H/F	n	I.A.	S.D.	Source
<i>Notharctus tenebrosus</i>	H	9	34.0	9.0	This study
<i>Notharctus tenebrosus</i>	F	10	25.8	6.2	This study
<i>cf. Adapis sp.</i>	H	19	48.3	7.2	This study
<i>cf. Adapis sp.</i>	F	13	48.1	6.7	This study
<i>cf. Leptadapis magnus</i>	H	15	57.9	6.5	This study
<i>cf. Leptadapis magnus</i>	F	20	53.4	9.0	This study
Omomyid	?	2	25.9	5.8	This study
<i>Aegyptopithecus</i>	H	2	55.5	6.4	H. et al 1995
<i>Aegyptopithecus</i>	F	1	48.7	–	H. et al 1995
<i>Apidium</i>	H	2	27.6	3.5	H. et al 1995
<i>Apidium</i>	F	1	23.5	–	H. et al 1995
<i>Tarsius sp.</i>	H	16	28.3	5.2	This study
<i>Tarsius sp.</i>	F	16	27.3	5.6	This study
<i>Varecia variegata</i>	H	12	51.6	5.4	J. et al 1997
<i>Varecia variegata</i>	F	12	51.2	5.8	J. et al 1997
<i>Propithecus diadema</i>	H	20	35.8	4.4	J. et al 1997
<i>Propithecus diadema</i>	F	28	27.7	6.0	J. et al 1997
<i>Indri indri</i>	H	66	35.0	6.0	J. et al 1997
<i>Indri indri</i>	F	64	31.2	6.5	J. et al 1997
<i>Babakotia radofilai</i>	H	27	58.3	6.3	J. et al 1997
<i>Babakotia radofilai</i>	F	11	60.9	6.4	J. et al 1997
<i>Lagothrix ssp</i>	H	12	62.4	6.0	J. et al 1997
<i>Lagothrix ssp</i>	F	12	53.1	3.2	J. et al 1997
<i>Ateles ssp</i>	H	27	55.2	6.5	J. et al 1997
<i>Ateles ssp</i>	F	28	53.2	5.0	J. et al 1997
<i>Nasalis larvatus</i>	H	12	38.0	5.6	J. et al 1997
<i>Nasalis larvatus</i>	F	14	35.3	3.8	J. et al 1997
<i>Pan paniscus</i>	H	38	44.8	4.2	J. et al 1997
<i>Pan paniscus</i>	F	54	39.2	6.8	J. et al 1997
<i>Pan troglodytes</i>	H	63	42.4	4.8	J. et al 1997
<i>Pan troglodytes</i>	F	37	41.2	6.9	J. et al 1997
<i>Papio ssp</i>	F	19	11.1	6.7	J. et al 1997
<i>Hylobates syndactylus</i>	H	20	53.1	5.6	J. et al 1997
<i>Pongo (both subsp)</i>	H	88	64.9	6.6	J. et al 1997
<i>Pongo (both subsp)</i>	F	24	85.1	7.8	J. et al 1997
<i>Archaeolemur edwardsi</i>	H-F	28	27.9	6.3	J. et al 1997
<i>Palaeopropithecus kelyus</i>	H-F	11	73.3	7.3	J. et al 1997
<i>Palaeopropithecus ingens</i>	H-F	45	60.3	9.9	J. et al 1997
<i>Palaeopropithecus maximus</i>	H-F	13	57.2	9.8	J. et al 1997
<i>Mesopropithecus dolichobrachion</i>	H-F	5	65.8	6.7	J. et al 1997
<i>Megaladapis edwardsi</i>	H-F	18	49.2	7.8	J. et al 1997
<i>Megaladapis madagascariensis</i>	H-F	23	46.1	8.1	J. et al 1997
<i>Gorilla gorilla</i>	H	88	37.2	4.2	J. et al 1997
<i>Gorilla gorilla</i>	F	31	33.0	4.3	J. et al 1997
<i>Hylobates lar</i>	H-F	68	47.8	5.4	J. et al 1997

See Jungers et al. (1997) (“J. et al. 1997” in table) for measurement method. Abbreviations: (H) hand, (H.) Hamrick, (F) foot, (IA) included angle, (SD) standard deviation. T. Clarke generated these data for an independent study project at Brooklyn College.

to have long, narrow, curved manual distal phalanges, possibly suggesting a more claw-like nail or functional tegulae (Godinot, 1991). In contrast, those of *Cantius*, *Smilodectes* (Gebo et al., 1991; Godinot, 1992; Bloch et al., 2010), the Messel adapiforms (Franzen, 1993; Thalmann, 1994; Franzen et al., 2009), and *Godinotia*

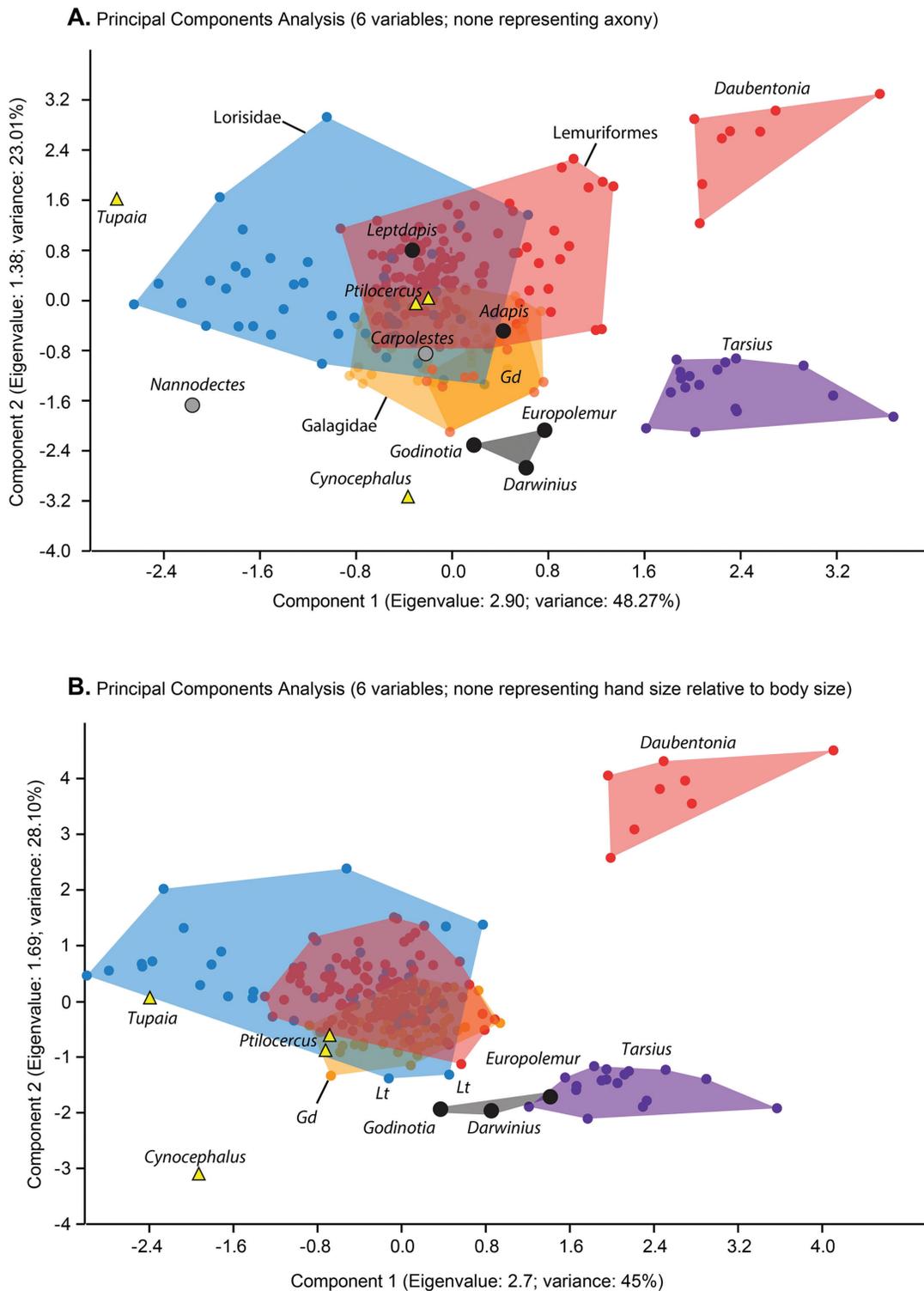
(Thalmann et al., 1989; Thalmann, 1994) appear proportionally shorter, broader, and flatter. Most adapiform distal phalanges retain a feature more typically characteristic of falcular (claw bearing) phalanges: bilateral, well-developed nutrient foramina, as also seen in plesiadapiform distal phalanges, though these foramina face laterally in those of euprimates rather than ventrally as in plesiadapiforms (Maiolino et al., 2012). Known omomyiform distal phalanges are very similar to those of tarsiers and also tend to lack well-developed nutrient foramina (Dagosto, 1988; Rose et al., 2011).

## FUNCTIONAL/ADAPTIVE IMPLICATIONS

New fossils, comparative data sets, and morphometric and phylogenetic analyses have permitted new perspectives on primate hand evolution since published reviews by Godinot and Beard (1991, 1993). It has become clear that plesiadapiforms have hand proportions that overlap with those of modern primates (Figs. 9 and 23). Thus, the hand proportions typical of modern primates do not reflect an ancestral change in developmental patterning allowing exploitation of the fine branch niche (Hamrick, 2001, 2007). There was, however, a change in grasp-mechanics of the hand as evidenced by the metacarpophalangeal joints and the evolution of nails rather than claws in all known early euprimates. Whereas at least some plesiadapiforms were specialized for use of a claw-clinging grasp that entailed hyper-extended metacarpophalangeal joints and palmar-flexed proximal phalangeal joints (convergently similar to callitrichid primates), the earliest known euprimates must have more frequently used grips in which the metacarpophalangeal joints were more palmar-flexed and wrapped around the substrate. This hand posture maximizes contact surface area and potential for points of frictional resistance to torque generated by body mass. However, data reviewed here also show that notharctids (and possibly omomyids) were specialized in several different ways relative to *Adapis*, and the majority of known plesiadapiforms and euprimates. Additionally, there is enough variation in the carpal structure of these groups to make characterization of the ancestral euprimate wrist ambiguous in many respects.

Before delving into these ambiguities, it can be said with some confidence that the ancestral euprimate had a carpus with a large scaphoid tubercle, a reduced hamate hamulus, a spiral facet on the hamate, a small ulnar facet on pisiform, a pisiform body of greater proportional height than in modern strepsirrhines, and prehensile proportions that at least matched those of plesiadapiforms: some of this was already obvious to Hamrick in the mid-1990s (Hamrick, 1996a,b,c, 1997, 1999; Hamrick and Alexander, 1996). Additional features common to all adapiforms known from the relevant anatomy include a strongly divergent pollex, a mesaxonic metacarpal pattern, and the lack of contact between the centrale and hamate. However, it is important to note that none of these features can be confidently inferred for the common euprimate ancestor due to the lack of representation for omomyiforms.

The best modern analogue for notharctines and cercamoniines, taking into account carpal structure (i.e., lack of definitive documented specialization for vertical postures), the intrinsic hand proportions, and the relationship between hand segment lengths and body mass is probably *Galago senegalensis* or *Galagoides demidoff*. Given the two- to sixfold difference in body size between the fossils and the extant taxa with which their hands compare most closely, we wish to emphasize that this



**Fig. 26.** PCA of size standardized hand morphologies. In order to assess to which living primates the fossil primates are most similar, we ran several different PCAs on hand variables using PAST.exe (Hammer et al., 2001). The data on extant prosimians was provided by Lemelin and come from the data set published by Lemelin and Jungers (2007). Analyses were run on the correlation matrix. **A:** Results of including four 3rd ray segment lengths (metacarpal, proximal phalanx, intermediate phalanx, and distal phalanx) per individual standardized to the geometric mean of all measurements, a residual value from the digit length versus body mass regression (Fig. 23A; Table 6); and a residual from the metacarpal versus body mass regression line (Fig. 23B, Table 6),  $n = 265$ . **B:** Results of including four 3rd ray segment lengths (metacarpal, proximal phalanx, intermediate phalanx, and distal phalanx) per individual standardized to the geometric mean of all measurements, the ratio of the third digit to the fourth digit, and the ratio of the third metacarpal to the fourth metacarpal ( $n = 252$  for this analysis). Residuals were not included in this analysis. In (A), notharctids are most similar to *G. demidoff* (highlighted in slightly bolder orange). In (B), *Europolemur* overlaps in morphospace with tarsiers, but notharctids are also close to specimens of *G. demidoff* (*Gd*) and *L. tardigradus* (*Lt*).

analogy is probably most relevant as a description of overlapping functional capacities rather than of ecological or behavioral similarity. Furthermore this analogy is not perfect. Whereas all notharctids appear to have digits slightly longer than expected for their body mass, *G. senegalensis* has a slightly negative digit length residual (Table 6). Though *G. demidoff* is notharctid-like in having a slightly positive digit length residual, it differs from the fossils in also having a positive residual for metacarpal length. *Galago moholi* and *Loris tardigradus* match the notharctids in having a positive digit length residual and negative metacarpal length residual; nonetheless *G. senegalensis* and *G. demidoff* are still more similar to notharctids when also considering intrinsic hand proportions and behavioral implications of carpal structure. Finally, *Notharctus* and the Messel adapids differ from *G. senegalensis* in having long proximal phalanges relative to their metacarpals (i.e., they are more like tarsiers, *Daubentonia*, and *Nycticebus pygmaeus*), and *Godinotia* has relatively long intermediate phalanges similar to those of plesiadapiforms (Boyer and Bloch, 2008). A principal components analysis (PCA) using all discussed proportional variables tends to support our qualitative assessment (Fig. 26A), with *Godinotia*, *Darwinius*, and *Europolemur* plotting closest to *G. demidoff* and other galagids, while occupying a unique morphospace between galagos and tarsiers. When hand-to-body size proportions are discarded, cercamoniines have closer phenetic affinities to tarsiers (Fig. 26B). The functional meaning of these affinities is discussed more thoroughly below.

The observed variation among Eocene adapiforms (between adapines vs. notharctines and cercamoniines) and the lack of comparable data for omomyiforms make it difficult to reconstruct the most likely suite of features present in the last common ancestor of euprimates. The little data that is available for the hands of basal omomyids tentatively suggest highly elongated, tarsier-like fingers (Gebo et al., 2012). Therefore, we suspect hyper-prehensility and long fingers relative to body size separated the ancestral euprimate from the preceding stem taxa.

Previous authors have suggested a connection between long fingers and vertical clinging and leaping (e.g., Napier and Walker, 1967; Godinot, 1991). Our regression of finger length on body mass using data from Lemelin and Jungers (2007) provides some support for this claim, as slight positive residuals in finger length tend to characterize vertical clingers and leapers (Table 6), though we have not yet tested the statistical significance of these patterns, as it is slightly beyond the scope of this review. Nonetheless, *Hapalemur*, *Lepilemur*, and all indriids exhibit higher residuals than similar-sized lemurids. *Microcebus* exhibit higher residuals than cheirogaleids. More acrobatic galagids tend to exhibit higher residuals than lorises. Finally, tarsiers, the most specialized vertical clingers and leapers, also have the longest fingers for their body size [but see Lemelin and Jungers (2007) and discussion below]. Therefore, increased prehensility and longer fingers relative to body size in the ancestral euprimate may reflect increasing specialization to vertical clinging, grasp-leaping, or both (Napier and Walker, 1967; Godinot, 1991). A recent study of evolutionary changes in calcaneal elongation indicate that increasingly effective leaping accompanied primate origins and early euprimate evolution (Boyer et al., 2013), adding weight to this interpretation.

### Implications for dietary hypotheses

The observation that increasingly effective leaping may have played a role in early euprimate evolution does not

resolve competing hypotheses focusing on the diet of the ancestral euprimate. However, it does provide some insights. Primarily, if selection was driving more effective acrobatic behavior, then it is valid to propose that visual system advancements were also a response to such pressures (Szalay and Delson, 1979; Szalay and Dagosto, 1980, 1988; Szalay et al., 1987; Dagosto, 1988). Though it is well established that increased stereoscopic vision is not necessary or beneficial in judging long distance gaps (Cartmill, 1974a, 1992), it can aid in hand-eye (or “foot-eye”) coordination (Crompton, 1995). A small primate ricocheting between shrub-layer branches would benefit from rapid assessment of the position of branches relative to its extremities in the moments before it lands and leaps again.

If the relatively long fingers in the euprimate ancestor do not relate to leaping or acrobatic arboreality, there are other functional-behavioral interpretations of such peculiarities. Godinot (1991, 2007) suggested that long hands in early euprimates may have been related to a mode of predation in which an animal strikes by reaching for prey with the forelimbs while rapidly extending the hind limbs without releasing the support (i.e., lunging at prey with its whole body). It is observed in tarsiers and galagos today. Godinot preferred this explanation because the role of the hind limbs and the acrobaticism of the behavior could potentially explain the adaptive significance of a hypertrophied hallux and claw loss in early euprimates. Others have emphasized that lengthening the fingers improves the potential for success in apprehending rapid prey (like flying insects) as it can be analogized with increasing the size of a “butterfly net” (Lemelin and Jungers, 2007). Lemelin and Jungers (2007) reasoned that as tarsiers are the most committed faunivores that use a two-handed “rapid strike” approach (compared to *Microcebus* and *Galago*), it follows that they exhibit the largest hands in proportion to body mass. Aside from tarsiers, we see no compelling correlation between presence and degree of insectivory and residual finger length in our data (Table 6). However, as discussed above for vertical clinging, these data have not been formally statistically analyzed. Even if the extreme elongation of tarsier fingers is a response to selection for prey capture, Eocene adapiforms lack this trait. Furthermore, the large size of the adapiforms considered here likely precludes against insect-dominated diets. On the other hand, the very long intermediate phalanx of *Teilhardina* suggests a pattern exclusively similar to extant *Tarsius*, which would begin to verify Napier’s (1980) bold suggestion: “We can safely assume that the hands [of omomyiforms] were identical with their modern counterparts [*Tarsius*].” (p.97). If the complete hand of *Teilhardina* or other omomyiforms eventually proves to be extremely tarsier-like, it would be hard to argue against a predatory function. However, critical information on omomyiform hands is still lacking, and if *Teilhardina*’s intermediate phalanges are elongated with respect to the proximal phalanges (as in *Godinotia* and plesiadapiforms), then its overall digit length may still not be tarsier-like with respect to body size.

### Do grasping specializations of the hand lag behind foot specializations?

Despite early views that arboreality and opposable thumbs are primitive for Mammalia (Matthew, 1904) and an emphasis on the importance of manual grasping in primates by Jones (1916), later works began to question these views. Gidley (1919) argued that early mammals were not grasping-specialized, and that the opposable hallux preceded

a specialized pollex. Works by Gregory (1920) and Napier (1961) contributed to the view that foot specializations preceded and were usually more important than hand specializations. Inasmuch as the foot had to be specialized to provide a “stable” anchor point for early primates living in a small branch niche, this may be true. In a certain way, this view is consistent with Jones (1916), who noted that primate hand evolution resulted from an “emancipation of the forelimb,” when the foot took the burden of providing the anchor point in an arboreal setting. Such ideas have been integrated into Cartmill’s (1972, 1974b) definition of primates, can be observed among marsupials (Cartmill, 1974a; Hamrick, 2001), and are apparently supported by the finding that at least one plesiadapiform obtained a specialized grasping hallux with a nail without revealing any “equivalent” specializations of the hand (Bloch and Boyer, 2002). Nonetheless, the data reviewed here suggest that the supposedly limited distribution of morphological correlates for true opposability (*sensu* Napier) is inaccurate. Furthermore, strong divergence of the pollex from the other digits appears to characterize early adapiforms and may be primitive for the euprimate ancestor. A pollex with strong divergence and high carpometacarpal mobility in the euprimate ancestor suggests the hand underwent morphological specializations for effective grasping earlier in primate evolution than previously thought. Though the plesiadapiform *C. simpsoni* clearly has a specialized hallux, the pollex is not as well preserved (the trapezium was not recovered, the MCI is fragmentary, and there is no definitive association of pollical phalanges) leaving open the possibility that it actually did have “equivalent” manual specializations.

Finally, if we consider “grasping specializations” to also include prehensility of the non-pollical digits, then plesiadapiforms and living arboreal non-primate mammals remind us that such features appear more ubiquitously and arguably earlier in the evolution of arboreal specializations than opposable halluces and probably non-hallucal prehensility of the foot (Bloch et al., 2007; Kirk et al., 2008). In this sense, the hand did not lag behind the foot in specializations for arboreality.

### Are platyrrhine hands more primitive?

This review has mainly operated under the premise that features held in common between omomyiforms and adapiforms can be taken as primitive for euprimates, especially if such features are also found in potentially primitive members of other close related groups. This implies that some apparently primitive traits in platyrrhines are reversals from a more “prosimian-like” ancestor (Szalay and Dagosto, 1988; Dagosto, 1990). Not all workers have been willing to accept this assumption (e.g., Ford, 1986, 1988; Godinot, 2007) and have argued that “prosimian” features have been more frequently convergent, while platyrrhines are actually more reflective of the ancestral euprimate. These alternative views could be more effectively tested if more Paleogene anthropoid hand material was available, or if relatively complete material of definitive stem-platyrrhines and catarrhines was available. As it is, the few phalangeal elements of *Aegyptopithecus* and *Apidium* provide little if any additional resolution on features of the ancestral euprimate hand. Regardless of the debate, in this review, extant platyrrhines match our conception of the euprimate ancestor well, based on many features of the carpus also exhibited by adapiforms and omomyiforms. However, we note that platyrrhines look more like scandentians and/or plesiadapiforms in having a relatively smaller scaphoid tubercle, low pollical divergence, a non-sellar trapezium (at least in *Cebus*), and more modest

intrinsic hand proportions, than they look like extant strepsirrhines, adapiforms, or omomyiforms for which the relevant morphology is known. In particular (and relating to the previous section), the unspecialized pollex of platyrrhines has contributed to the perspective that the ancestral euprimate also lacked specializations in this digit despite a divergent pollex in adapiforms, strepsirrhines, and catarrhines (Fig. 18; Godinot and Beard, 1991). Jouffroy and Lessertisseur (1959) argued for convergent acquisition of pollical specializations in lemurs and hominoids based on observations of different degrees and types of mobility. Napier (1961) built on these observations with a morpho-functional explanation for the differences. In this review, we have argued that there is actually little difference in pollical divergence angles (Fig. 18) or carpometacarpal facet shape (Fig. 17) between certain strepsirrhines and hominoids. This tends to weaken the case for convergence. Recent work focused on new descriptions (Gebo et al., 2008) and analyses (Patel et al., 2012) of material attributed to eosimiids and Fayum anthropoids suggest against a platyrrhine morphotype for other traits as well. On the other hand, in *Archicebus*, a taxon argued to be the most basal tarsiiform (Ni et al., 2013), long non-hallucal metatarsals may be indicative of an ancestral euprimate with a foot that was more platyrrhine-like than previously appreciated (Szalay and Dagosto, 1988). In sum, it is not easy to come to a general conclusion on whether platyrrhine hands are more reflective of the ancestral euprimate in functionally critical features: evidence from more fossils is needed.

### What is needed to advance understanding

The most important data needed to evaluate proposed changes in hand proportions and morphology during primate origins are articulated/associated hand fossils of omomyiforms and early anthropoids (such as *Teilhardina* and *Biretia* or *Catopithecus*). More complete and more primitive remains of adapiforms (such as *Cantius* and *Donrussellia*) and eosimiids could also help. Of course, skeletal remains from more proximal stem primates (plesiadapiforms) are also important. Currently, even *Notharctus*, the best-known fossil adapiform, cannot be definitively characterized in terms of many high valence hand features (including metacarpal and digit axony, intrinsic hand proportions, or extrinsic digit proportions).

While comparative data, field studies documenting behavior, and experimental methods will continue to be important tools for evaluating primate origins, the most critical tests of different hypotheses refer to the pattern of change and the pattern of correlation of changes predicted by competing hypotheses as documented in the fossil record. Increased taxonomic sampling will help document the pattern and order of changes during primate origins. Samples of fossils with tight chronostratigraphic control are important for testing predictions about the environmental context of morphological changes. Studies in the spirit of Krause et al. (1986) and Maas et al. (1988) may be able to test whether patterns/rates of change in primate morphology are correlated with increases in abundance and diversity of potential competitors, predators, and prey. The data required by such studies is immense, but the task of gathering it is not impossible, and the potential implications are profound.

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## APPENDIX

### APPENDIX A. MEASUREMENTS FOR PRINCIPLE COMPONENTS ANALYSIS

Taxon	Specimen	Side	Ray	Note	Length	PEW	PED	MSW	MSD	DEW	DED	GM
<i>Plesiadapis cookei</i>	UM 87990	L	II	#2	18.9	2.9	4.2	2.7	2.3	4.3	4.2	4.27
<i>Plesiadapis cookei</i>	UM 87990	L	III	#2	23.2	2.7	4.4	2.3	2.1	4.2	4	4.18
<i>Plesiadapis cookei</i>	UM 87990	R	IV	#2	23.8	3.1	4.4	2.4	2.1	4.3	4.1	4.34
<i>Plesiadapis cookei</i>	UM 87990	L	IV	#2	23.7	3	4.2	2.3	2.1	4.2	4	4.23
<i>Plesiadapis cookei</i>	UM 87990	R	V	#2	17.73	3.86	3.2	1.97	2.17	3.98	3.52	3.87
<i>Plesiadapis cookei</i>	UM 87990	L	II	#1	17	2.7	4	2.5	2.2	3.9	3.5	3.90
<i>Plesiadapis cookei</i>	UM 87990	R	III	#1	20	3	4	2.2	2.2	4	3.5	4.00
<i>Plesiadapis cookei</i>	UM 87990	R	V	#1	15.65	3.32	2.82	2.18	2.1	4.23	3.52	3.73
<i>Nannodectes gidleyi</i>	AMNH 17379	L	III		12.02	1.61	1.88	1.13	1.02	2.14	1.63	2.04
<i>Plesiadapis tricuspiciens</i>	MNHN R 5364	R	IV		24.7	3.2	3.8	2.7	2.4	4.5	3.5	4.37
<i>Plesiadapis tricuspiciens</i>	MNHN R 5305	R	V		15.15	3.3	2.9	2.4	2	4.3	3.4	3.74
<i>Plesiadapis tricuspiciens</i>	MNHN R 5373	L	V		13	3.3	2.7	2.2	1.8	3.6	2.8	3.34
<i>Plesiadapis tricuspiciens</i>	MNHN nm	L	V		15.2	3.4	2.9	2.1	1.8	3.8	3.1	3.52
<i>Plesiadapis tricuspiciens</i>	MNHN R 5295	R	III		21.1	2.7	4.1	2.5	2.3	4.4	3.7	4.17
<i>Nannodectes intermedius</i>	USNM 442229	L	V		8.7	1.93	1.58	1.08	1.01	2.13	1.75	1.95
<i>Dryomomys szalayi</i>	UM 41870	L	V		4.18	0.97	0.62	0.51	0.35	1.04	0.75	0.86
<i>Tinimomys graybulliensis</i>	USNM 461201	L	V		4.79	1.09	0.68	0.56	0.43	1.03	0.7	0.93
<i>Tinimomys graybulliensis</i>	USNM 530203	R	V		4.51	0.90	0.62	0.49	0.37	1.01	0.70	0.85
<i>Tinimomys graybulliensis</i>	USNM 530203		II		5.15	0.56	0.85	0.55	0.44	1.01	0.71	0.89
<i>Tinimomys graybulliensis</i>	USNM 530203		II		5.07	0.61	0.88	0.57	0.45	1.01	0.72	0.91
<i>Ptilocercus lowii</i>	USNM 488055	L	II		5.14	0.74	1.08	0.61	0.62	1.21	0.97	1.09
<i>Ptilocercus lowii</i>	USNM 488055	L	III		6.02	0.95	1.03	0.6	0.6	1.18	0.88	1.12
<i>Ptilocercus lowii</i>	USNM 488055	L	IV		5.49	0.86	0.9	0.58	0.58	1.17	0.89	1.06
<i>Ptilocercus lowii</i>	USNM 488055	L	V		4.15	1.07	0.71	0.7	0.55	1.17	0.91	1.04
<i>Ptilocercus lowii</i>	USNM 488069	R	II		5.42	0.87	1.18	0.7	0.65	1.28	0.94	1.17
<i>Ptilocercus lowii</i>	USNM 488069	R	III		6.09	1.01	1.15	0.66	0.63	1.28	0.95	1.20
<i>Ptilocercus lowii</i>	USNM 488069	R	IV		5.71	0.93	0.96	0.67	0.6	1.25	0.9	1.13
<i>Ptilocercus lowii</i>	USNM 488069	R	V		4.39	1	0.77	0.73	0.62	1.2	0.91	1.08
<i>Ptilocercus lowii</i>	USNM 488058	L	II		4.98	0.82	1.08	0.69	0.64	1.2	0.96	1.12
<i>Ptilocercus lowii</i>	USNM 488058	L	III		5.57	0.97	1.13	0.68	0.64	1.18	0.89	1.16
<i>Ptilocercus lowii</i>	USNM 488058	L	IV		5.04	0.82	0.86	0.69	0.62	1.16	0.91	1.07
<i>Ptilocercus lowii</i>	USNM 488058	L	V		3.86	1.08	0.76	0.69	0.54	1.1	0.89	1.02
<i>Ptilocercus lowii</i>	USNM 488072	R	II		4.71	0.84	1.07	0.7	0.64	1.18	0.89	1.10
<i>Ptilocercus lowii</i>	USNM 488072	R	III		5.47	0.96	1.07	0.65	0.59	1.16	0.87	1.12
<i>Ptilocercus lowii</i>	USNM 488072	R	IV		5.12	0.85	0.97	0.67	0.56	1.16	0.85	1.07
<i>Ptilocercus lowii</i>	USNM 488072	R	V		3.89	1.1	0.7	0.73	0.54	1.13	0.84	1.02
<i>Ptilocercus lowii</i>	USNM 488067	R	II		5	0.82	1.11	0.65	0.65	1.2	0.99	1.13
<i>Ptilocercus lowii</i>	USNM 488067	R	III		5.82	0.99	1.12	0.63	0.6	1.2	0.9	1.15
<i>Ptilocercus lowii</i>	USNM 488067	R	IV		5.21	0.85	0.92	0.64	0.6	1.22	0.88	1.08
<i>Ptilocercus lowii</i>	USNM 488067	R	V		4.02	1.19	0.73	0.71	0.54	1.16	0.87	1.04
<i>Ptilocercus lowii</i>	USNM 481106	L	II		4.99	0.75	1.11	0.68	0.58	1.17	0.93	1.09
<i>Ptilocercus lowii</i>	USNM 481106	L	III		5.59	0.98	1.03	0.67	0.59	1.14	0.87	1.12
<i>Ptilocercus lowii</i>	USNM 481106	L	IV		5.16	0.85	0.87	0.68	0.55	1.16	0.82	1.04
<i>Ptilocercus lowii</i>	USNM 481106	L	V		3.92	1.1	0.8	0.69	0.52	1.15	0.88	1.03
<i>Plesiadapis cookei</i>	UM 87990	L	I	#1	11.4	4.8	3.1	2.5	1.8	3.4	3	3.60
<i>Nannodectes gidleyi</i>	AMNH 17379	L	I		6.92	2.89	1.57	1.54	1.08	2.13	2.02	2.17
<i>Nannodectes intermedius</i>	USNM 442229	R	I		6.64	2.54	1.61	1.27	1.03	1.84	1.71	1.96
<i>Tinimomys graybulliensis</i>	USNM 530203	?	I		3.64	1.37	0.77	0.66	0.46	0.94	0.84	0.99
<i>Ptilocercus lowii</i>	USNM 488055	L	I		3.22	1.29	0.81	0.75	0.49	1.15	0.99	1.05
<i>Ptilocercus lowii</i>	USNM 488069	R	I		3.37	1.44	0.89	0.71	0.56	1.24	1.1	1.13
<i>Ptilocercus lowii</i>	USNM 488058	L	I		2.98	1.36	0.8	0.69	0.53	1.09	0.96	1.03
<i>Ptilocercus lowii</i>	USNM 488072	R	I		2.99	1.33	0.81	0.68	0.54	1.11	0.97	1.04
<i>Ptilocercus lowii</i>	USNM 488067	R	I		3.24	1.42	0.8	0.64	0.53	1.21	0.97	1.06
<i>Ptilocercus lowii</i>	USNM 481106	L	I		3.1	1.35	0.8	0.64	0.52	1.14	0.95	1.03

See Figure 6C for measurement illustration. In “notes” field, #1 and #2 refer to two different “morphs” of metapodials preserved with UM 87990. All measurements in mm.

## APPENDIX B. MEASUREMENTS ON METACARPALS FROM PHOSPHORITES DE QUERCY

Specimen	Species	r/l	d#	L	PEW	PED	MSW	MSD	DEW	DED
RD 311	<i>Adapis sp.</i>	l	1	9.53	3.34	3.36	2.17	1.64	3.36	2.98
Ros2	<i>Adapis sp.</i>	r	1	9.31	3.67	3.32	2.23	1.85	3.70	3.20
MaPhQ no-## AX	<i>Adapis sp.</i>	-	2	14.63	2.35	3.80	1.94	1.87	3.37	3.45
NMB Q.L. 460	<i>Adapis parisiensis</i>	R	2	15.00	2.64	4.09	1.99	1.88	3.60	3.30
RD 311	<i>Adapis sp.</i>	L	2	15.34	2.59	3.82	1.97	1.98	3.26	3.30
MaPhQ no-## BB	<i>Adapis sp.</i>	R	2	15.81	2.64	4.16	-	2.19	3.21	3.78
MaPhQ no-## BC	<i>Adapis sp.</i>	L	2	15.31	2.39	4.17	2.18	2.09	3.24	3.64
MaPhQ no-## AV	<i>Adapis sp.</i>	L	3	-	4.01	3.83	2.09	2.04	-	-
NMB Q.D. 66	<i>Adapis parisiensis</i>	R	3	19.30	4.08	4.32	2.77	2.67	4.30	4.26
NMB Q.M. 8	<i>Adapis parisiensis</i>	L	3	16.49	3.48	3.39	2.30	2.25	3.58	3.76
NMB Q.L. 708	<i>Adapis parisiensis</i>	L	3	17.90	3.65	4.00	2.49	2.36	3.70	3.93
RD 311	<i>Adapis sp.</i>	L	3	16.15	3.41	3.99	2.10	2.16	3.26	3.21
MaPhQ no-## BE	<i>Adapis sp.</i>	R	3	17.85	3.88	3.49	2.37	2.11	3.69	3.55
MaPhQ no-## AW	<i>Adapis sp.</i>	R	4	-	3.76	3.54	1.67	1.61	-	-
NMB Q.L. 642	<i>Adapis parisiensis</i>	R	4	17.61	3.29	3.99	2.67	2.53	4.02	4.11
NMB Q.U. 874	<i>Adapis parisiensis</i>	L	4	18.01	3.45	4.13	2.43	2.60	3.72	4.13
RD 311	<i>Adapis sp.</i>	L	4	15.88	2.92	3.68	1.91	1.97	3.28	3.35
MaPhQ no-## BF	<i>Adapis sp.</i>	R	4	17.33	3.55	4.12	2.41	2.39	3.72	4.00
Ros2	<i>Adapis sp.</i>	R	4	16.49	3.06	3.74	2.18	2.25	3.53	3.30
RD 311	<i>Adapis sp.</i>	L	5	13.97	2.76	2.58	2.13	1.89	3.31	3.09
MaPhQ no-## BD	<i>Adapis sp.</i>	R	5	15.60	3.05	3.19	2.27	2.02	4.00	3.27
NMB Q.F. 896	<i>Leptadapis magnus</i>	L	2	29.04	5.39	6.49	3.93	3.76	6.31	6.69
NMB Q.L. 210	<i>Leptadapis magnus</i>	L	2	29.71	5.09	7.68	4.27	4.04	6.59	6.99
NMB Q.L. 425	<i>Leptadapis magnus</i>	R	2	26.33	5.02	7.23	4.10	3.53	6.17	6.35
MaPhQ no-## BA	<i>Leptadapis magnus</i>	L	2	26.64	4.41	6.53	3.60	3.67	6.00	5.55
NMB Q.L. 664	<i>Leptadapis magnus</i>	L	3	29.75	7.29	6.94	3.78	3.60	7.15	6.91
NMB Q.L. 900	<i>Leptadapis magnus</i>	R	3	31.86	8.18	7.54	4.36	4.51	7.59	7.68
MaPhQ no-## AZ	<i>Leptadapis sp.</i>	R	3	29.80	6.76	7.63	4.62	4.35	7.28	7.16
NMB Q.F. 812	<i>Leptadapis magnus</i>	L	4	33.74	8.13	7.66	4.36	4.70	8.10	8.08
NMB Q.F. 799	<i>Leptadapis magnus</i>	R	4	34.41	8.00	8.07	5.15	4.96	8.83	8.08
MaPhQ no-## AY	<i>Leptadapis sp.</i>	L	4	29.50	6.76	6.56	4.17	4.28	7.60	6.65
NMB Q.F. 791	<i>Leptadapis magnus</i>	L	5	28.71	6.70	7.46	3.57	4.21	7.41	7.45

Measurements illustrated in Figure 6C. All measurements in mm.

## APPENDIX C. MEASUREMENTS ON METATARSALS FROM PHOSPHORITES DE QUERCY

Specimen	Species	r/l	d#	L	PEW	PED	MSW	MSD	DEW	DED
MaPhQ no-## AJ	<i>Adapis sp.</i>	l	1	17.37	5.65	5.87	2.79	2.69	5.05	4.81
MaPhQ no-## AK	<i>Adapis sp.</i>	l	1	15.35	5.52	-	2.44	2.31	5.14	4.86
NMB Q.W. 357	<i>Adapis sp.</i>	r	2	21.25	3.42	4.46	2.42	2.47	3.99	4.29
NMB Q.M. 18	<i>Adapis parisiensis</i>	r	2	19.56	3.25	-	2.27	2.60	3.80	4.31
MaPhQ no-## AT	<i>Adapis sp.</i>	r	2	20.48	3.32	4.56	2.18	2.45	3.82	4.41
MaPhQ no-## AU	<i>Adapis sp.</i>	l	2	18.65	3.29	3.97	2.19	2.43	3.61	4.39
Ros2	<i>Adapis sp.</i>	r	2	20.39	3.16	4.08	2.28	2.58	3.60	4.23
Ros2	<i>Adapis sp.</i>	r	2	18.87	2.96	3.85	1.99	2.00	3.50	4.03
MaPhQ no-## AF	<i>Adapis sp.</i>	l	3	20.06	3.43	3.76	1.93	2.32	3.10	4.00
MaPhQ no-## AG	<i>Adapis sp.</i>	r	3	21.97	3.98	4.10	2.07	2.42	3.45	4.48
MaPhQ no-## AH	<i>Adapis sp.</i>	l	3	20.65	3.93	4.52	2.62	3.02	3.65	4.54
MaPhQ no-## AI	<i>Adapis sp.</i>	l	3	19.59	3.74	4.56	2.28	2.43	3.38	5.06
NMB Q.L. 580	<i>Adapis parisiensis</i>	r	4	21.34	3.96	4.63	2.41	2.53	4.07	4.68
NMB Q.W. 356	<i>Adapis parisiensis</i>	l	4	23.11	-	-	-	-	-	-
NMB Q.L. 519	<i>Adapis parisiensis</i>	l	4	21.50	3.61	4.73	2.59	3.00	4.07	4.95
MaPhQ no-## AO	<i>Adapis sp.</i>	l	4	22.14	3.79	4.45	2.41	2.47	4.05	4.67
MaPhQ no-## AP	<i>Adapis sp.</i>	l	4	21.76	3.99	4.36	2.50	2.64	4.06	4.82
MaPhQ no-## AQ	<i>Adapis sp.</i>	r	4	20.81	3.26	4.14	2.40	2.42	3.79	4.49
MaPhQ no-## AR	<i>Adapis sp.</i>	l	4	18.58	3.29	3.78	2.07	2.32	3.43	4.20
MaPhQ no-## AS	<i>Adapis sp.</i>	l	4	21.09	3.24	3.91	2.38	2.55	3.74	4.48
NMB Q.I. 647	<i>Adapis parisiensis</i>	r	5	18.19	4.91	3.90	1.85	2.48	4.30	4.26
MaPhQ no-## AM	<i>Leptadapis magnus</i>	r	1	29.72	10.23	9.49	5.37	4.87	9.82	8.47
MaPhQ no-## AN	<i>Leptadapis magnus</i>	r	1	27.10	8.39	8.91	4.20	3.74	8.05	7.05
NMB Q.F. 794	<i>Leptadapis magnus</i>	r	1	33.55	9.77	9.30	5.06	4.24	8.83	7.26
NMB Q.L. 299	<i>Leptadapis magnus</i>	l	2	38.43	6.09	8.01	4.29	4.38	6.64	8.40
NMB Q.W. 307	<i>Leptadapis sp.</i>	-	2	36.53	5.59	7.40	3.83	3.78	6.41	7.46
NMB Q.L. 544	<i>Leptadapis sp.</i>	-	3	39.74	6.67	7.85	4.36	5.36	7.25	8.41
NMB Q.L. 283	<i>Leptadapis sp.</i>	-	4	33.88	10.16	6.22	3.70	4.42	7.40	7.53
MaPhQ no-## AL	<i>Leptadapis magnus</i>	r	5	33.30	9.42	5.95	3.08	4.41	6.53	7.79
NMB Q.L. 168	<i>Leptadapis sp.</i>	-	5	38.36	7.00	8.22	4.51	5.01	6.81	8.55

Measurements illustrated in Figure 6C. All measurements in mm.

APPENDIX D. MEASUREMENTS ON PROXIMAL PHALANGES FROM PHOSPHORITES DE QUERCY

Specimen	species	h/f	d#	L	PEW	PED	MSW	MSD	DEW	DED	DEL	IA
NMB Q.L. 643	<i>Adapis parisiensis</i>	h	?	16.86	4.13	2.95	2.68	2.24	3.26	2.74	2.76	47.8
NMB Q.U. 953	<i>Adapis parisiensis</i>	h	?	16.71	4.04	3.90	2.48	1.81	2.91	2.57	2.39	45.8
NMB Q.V. 24	<i>Adapis parisiensis</i>	h	?	17.63	4.06	2.96	2.45	2.10	2.98	2.59	2.48	48.2
NMB Q.G. 324	<i>Adapis parisiensis</i>	h	?	16.67	4.10	2.98	2.75	2.10	3.28	2.74	2.77	52.5
NMB QH 6992	<i>Adapis parisiensis</i>	h	?	16.91	4.23	3.00	2.71	2.13	3.42	2.76	2.83	45.7
NMB Q.O. 242	<i>Adapis parisiensis</i>	h	?	18.22	4.34	3.33	2.44	2.01	3.01	2.83	2.76	39.9
NMB Q.O. 254	<i>Adapis parisiensis</i>	h	?	16.61	4.36	3.02	2.84	2.04	3.33	2.75	2.85	46.1
NMB Q.O. 270	<i>Adapis parisiensis</i>	h	?	15.06	4.15	2.96	2.78	1.97	3.18	2.60	2.86	54.8
MaPhQ no-## R	<i>Adapis sp.</i>	h	?	17.60	4.34	3.60	2.89	2.40	3.39	2.86	2.58	63.5
MaPhQ no-## S	<i>Adapis sp.</i>	h	?	16.10	4.21	3.43	2.56	2.24	3.18	2.83	2.70	44.9
MaPhQ no-## T	<i>Adapis sp.</i>	h	?	16.54	3.84	3.39	2.19	2.15	3.22	2.60	2.31	36.2
MaPhQ no-## U	<i>Adapis sp.</i>	h	?	15.93	3.85	2.94	2.65	1.99	2.90	2.68	2.63	56.6
MaPhQ no-## Z	<i>Adapis sp.</i>	h	?	17.16	4.56	3.40	2.73	2.16	3.44	2.73	2.60	50.7
MaPhQ no-## AA	<i>Adapis sp.</i>	h	?	15.28	3.98	2.75	2.57	1.95	2.90	2.55	2.51	62.7
MaPhQ no-## AB	<i>Adapis sp.</i>	h	?	17.34	4.03	3.50	2.45	2.11	3.36	2.71	2.49	45.2
MaPhQ no-## AD	<i>Adapis sp.</i>	h	?	17.68	3.94	2.94	2.37	2.03	3.11	2.66	2.32	48.5
AMNH 140719	<i>Adapis sp.</i>	h	?	17.5	4.27	3.23	2.57	2.19	3.09	2.80	2.68	45.7
AMNH 140719	<i>Adapis sp.</i>	h	?	17.63	4.43	2.98	2.48	2.13	3.48	2.97	2.70	40.1
AMNH 140719	<i>Adapis sp.</i>	h	?	17.15	4.18	3.11	2.58	2.16	3.28	2.81	2.37	43.1
NMB Q.L. 338	<i>Adapis parisiensis</i>	f	4	18.73	4.24	3.63	3.09	2.35	3.13	2.92	2.71	52.1
NMB Q.U. 558	<i>Adapis parisiensis</i>	f	?	19.03	4.63	3.28	2.95	2.30	3.73	3.06	3.08	35.3
NMB Q.O. 228	<i>Adapis parisiensis</i>	f	?	21.11	4.59	3.73	2.59	2.27	3.37	2.89	2.96	45.9
MaPhQ no-## N	<i>Adapis sp.</i>	f	?	19.59	4.71	3.99	2.81	2.39	3.80	3.29	2.96	54.5
MaPhQ no-## O	<i>Adapis sp.</i>	f	?	20.13	4.59	3.74	2.93	2.40	3.30	3.20	2.72	47.2
MaPhQ no-## P	<i>Adapis sp.</i>	f	?	20.44	4.58	3.56	3.26	2.31	4.05	3.40	2.94	49.6
MaPhQ no-## Q	<i>Adapis sp.</i>	f	?	19.10	4.71	3.87	3.14	2.40	3.63	3.09	2.97	48.7
MaPhQ no-## X	<i>Adapis sp.</i>	f	?	18.65	4.28	3.52	2.69	2.49	3.15	2.99	2.53	42.7
MaPhQ no-## Y	<i>Adapis sp.</i>	f	?	18.65	4.23	3.32	2.65	2.16	3.15	2.63	2.55	58.2
MaPhQ no-## AC	<i>Adapis sp.</i>	f	?	18.52	4.11	3.43	2.57	2.03	3.20	2.58	2.57	38.9
MaPhQ no-## AE	<i>Adapis sp.</i>	f	?	19.15	4.36	3.36	—	2.28	3.15	2.50	2.55	55.1
AMNH 140719	<i>Adapis sp.</i>	f	?	19.8	4.35	3.77	2.61	2.20	3.40	2.96	2.77	48.6
NMB Q.L. 602	<i>Leptadapis magnus</i>	h	?	26.39	7.21	5.02	5.65	3.20	5.93	4.42	4.51	53.8
NMB Q.L. 269	<i>Leptadapis magnus</i>	h	?	26.71	7.09	5.32	5.18	3.18	5.54	4.58	4.29	53.2
NMB Q.M. 748	<i>Leptadapis magnus</i>	h	?	26.51	7.61	5.80	5.22	3.22	5.91	4.46	4.40	55.5
NMB Q.L. 216	<i>Leptadapis magnus</i>	h	?	23.91	6.56	4.93	4.68	2.96	5.06	4.01	3.86	65.5
NMB Q.L. 630	<i>Leptadapis magnus</i>	h	?	26.97	7.18	5.19	4.95	3.05	5.69	4.32	4.33	57.9
NMB Q.L. 454	<i>Leptadapis magnus</i>	h	?	24.08	6.66	4.80	5.22	3.14	—	—	—	68.8
NMB Q.O. 187	<i>Leptadapis magnus</i>	h	?	28.51	6.87	5.80	4.28	3.08	5.29	4.12	4.02	54.6
NMB Q.M. 588	<i>Leptadapis magnus</i>	h	?	27.25	7.92	5.89	6.09	3.64	6.48	4.87	4.70	55.2
NMB Q.N. 578	<i>Leptadapis magnus</i>	h	?	27.26	7.51	5.67	5.21	3.58	5.67	4.56	4.36	64.4
NMB Q.L. 581	<i>Leptadapis magnus</i>	h	?	>23.17	—	—	4.55	2.95	5.41	4.07	4.15	66.0
NMB Q.D. 735	<i>Leptadapis magnus</i>	h	5	26.33	7.62	5.49	5.36	3.21	6.21	4.57	4.47	43.4
NMB Q.L. 495	<i>Leptadapis magnus</i>	h	3	27.30	8.20	5.91	6.03	3.35	6.47	4.87	4.65	59.3
MaPhQ no-## G	<i>Leptadapis magnus</i>	h	?	26.46	6.50	5.99	4.01	3.28	4.89	4.20	4.36	56.1
MaPhQ no-## H	<i>Leptadapis magnus</i>	h	?	25.52	6.92	5.59	4.40	3.33	5.25	4.30	4.04	53.2
MaPhQ no-## I	<i>Leptadapis magnus</i>	h	?	28.57	7.16	5.46	4.63	3.36	5.68	4.35	4.25	60.6
MaPhQ no-## F	<i>Leptadapis magnus</i>	f	?	28.88	7.66	6.13	4.42	3.51	5.28	4.47	4.32	49.5
NMB Q.M. 559	<i>Leptadapis magnus</i>	f	?	28.79	7.67	5.41	5.44	3.86	6.34	4.60	4.46	59.6
NMB Q.L. 558	<i>Leptadapis magnus</i>	f	?	33.61	7.81	7.20	5.44	3.78	5.77	5.02	5.00	49.5
NMB Q.L. 331	<i>Leptadapis magnus</i>	f	?	>31.48	—	—	4.97	3.32	6.06	4.89	4.65	—
NMB Q.M. 749	<i>Leptadapis magnus</i>	f	?	31.67	—	6.01	5.84	3.53	6.74	5.32	4.95	63.5
NMB Q.L. 629	<i>Leptadapis magnus</i>	f	?	32.86	7.59	6.54	5.70	3.58	6.30	4.80	4.90	44.8
NMB Q.M. 210	<i>Leptadapis magnus</i>	f	?	28.63	7.44	6.29	3.93	3.23	5.10	4.71	4.50	39.5
NMB Q.L. 604	<i>Leptadapis magnus</i>	f	?	28.72	7.57	6.48	5.00	3.25	5.26	4.38	4.22	40.1
NMB Q.L. 186	<i>Leptadapis magnus</i>	f	?	29.21	7.85	5.83	5.37	3.20	6.08	4.86	4.40	40.7
NMB Q.L. 255	<i>Leptadapis magnus</i>	f	?	31.90	7.64	6.09	5.48	3.85	6.49	5.53	5.10	—
NMB Q.M. 168	<i>Leptadapis magnus</i>	f	?	32.27	7.94	6.24	5.89	3.57	6.27	5.30	5.01	50.4
NMB Q.L. 401	<i>Leptadapis magnus</i>	f	?	32.25	8.20	6.59	5.25	3.61	5.72	4.97	4.87	48.1
NMB Q.L. 271	<i>Leptadapis magnus</i>	f	4	31.33	8.44	6.29	5.86	3.75	6.94	5.24	5.14	47.5
MNHN Q.U. 10995	<i>Leptadapis magnus</i>	f	?	33.20	8.53	6.93	5.12	3.92	6.30	5.25	4.86	53.4
MNHN Q.U. 11011	<i>Leptadapis magnus</i>	f	?	38.19	8.86	7.42	6.24	4.30	6.71	5.70	5.17	57.8
MNHN Q.U. 11009	<i>Leptadapis magnus</i>	f	?	31.98	8.89	6.19	6.05	4.01	6.91	5.30	5.05	73.2
MNHN Q.U. 10996	<i>Leptadapis magnus</i>	f	?	32.06	9.07	6.13	6.08	4.01	6.83	5.25	5.16	66.7
MaPhQ no-## A	<i>Leptadapis magnus</i>	f	?	31.91	7.96	6.70	5.45	3.52	5.56	5.30	4.89	58.2
MaPhQ no-## B	<i>Leptadapis magnus</i>	f	?	33.46	8.58	6.80	5.40	3.47	6.49	5.08	5.08	52.4
MaPhQ no-## C	<i>Leptadapis magnus</i>	f	?	31.10	8.48	6.29	5.13	3.65	6.14	5.05	4.94	57.1
MaPhQ no-## D	<i>Leptadapis magnus</i>	f	?	35.01	8.70	6.29	6.71	3.91	6.87	5.70	5.21	62.5
MaPhQ no-## E	<i>Leptadapis magnus</i>	f	?	30.11	7.29	5.93	4.83	3.60	5.10	4.52	4.40	52.7

All measurements, except DEL (distal end articular surface proximodistal length) and IA (Included Angle) illustrated in Figure 6C. All measurements in mm.

## APPENDIX E. MEASUREMENTS ON INTERMEDIATE PHALANGES FROM PHOSPHORITES DE QUERCY

Specimen	Species	L	PEW	PED	MSW	MSD	DEW	DED	DEL
NMB Q.V. 36	<i>Adapis parisiensis</i>	12.69	3.31	3.00	2.43	1.75	2.80	1.85	2.09
MaPhQ no-## V	<i>Adapis sp.</i>	12.76	3.52	3.37	2.24	1.87	2.82	2.13	1.71
MaPhQ no-## W	<i>Adapis sp.</i>	10.93	3.35	3.24	1.95	1.70	2.86	2.00	1.83
NMB Q.D. 909	<i>Leptadapis magnus</i>	>18.06	–	–	4.44	2.95	4.63	2.56	–
NMB Q.D. 929	<i>Leptadapis magnus</i>	>17.59	–	–	4.46	2.77	4.83	3.19	3.06
NMB Q.L. 266	<i>Leptadapis magnus</i>	19.04	5.86	5.01	4.40	2.67	–	–	–
NMB Q.M. 840	<i>Leptadapis magnus</i>	16.09	5.35	4.33	4.03	2.29	4.14	2.49	2.63
NMB Q.G. 149	<i>Leptadapis magnus</i>	15.72	6.14	5.23	4.37	2.63	4.87	3.58	3.76
MaPhQ no-## J	<i>Leptadapis magnus</i>	19.13	6.47	4.75	4.36	2.70	4.35	2.98	3.06
MaPhQ no-## K	<i>Leptadapis magnus</i>	18.68	6.19	4.34	4.15	2.61	4.28	2.47	2.81
MaPhQ no-## L	<i>Leptadapis magnus</i>	15.87	5.66	5.12	4.16	2.99	4.24	3.37	3.18
MaPhQ no-## M	<i>Leptadapis magnus</i>	20.15	6.59	5.60	4.83	2.93	4.84	3.12	3.16

Measurements illustrated in Figure 6C or defined in Appendix D. All measurements in mm.

## APPENDIX F. NEW MEASUREMENTS ON PREVIOUSLY PUBLISHED ASSOCIATED EUPRIMATE HANDS

	<i>Europolemur</i>		<i>Darwinius masillae</i>		<i>Godinotia neglecta</i>		<i>Notharctus</i>	<i>Notharctus</i>	<i>Adapis</i>	<i>Leptadapis</i>
Bone	<i>E. kelleri</i> (1)	(2)	(3) L	(3) R	(4) R	(4) L	(5)	(6)	(7) & mean	mean
Carp.	7.38-	–	5.12+	5.49	–	7.39	11.58	–	8.6	–
mc1	9.96	5.91	–	7.30	–	10.43	12.48	–	9.53	–
mc2	14.44	–	–	–	15.39	13.99	16.65	13.50	15.34	27.93*
mc3	15.33	–	–	~11.57**	18.34	16.93	–	20.50	16.15	30.47*
mc4	15.23	–	–	~11.75**	18.04	16.34	21.42	18.00	15.88	32.47*
mc5	14.12	–	–	11.08	15.80	14.07	19.06	14.30	13.97	28.71*
pp1	11.96	7.63	9.54	8.61	11.22	12.31	16.39	–	–	–
pp2	16.56	11.70	13.97	12.73	–	16.41	23.98	–	–	–
pp3	–	16.20	15.90	15.35	–	18.25	27.66	~25.5	15.53 #	26.33*
pp4	20.61	16.73	16.00	15.32	–	19.61	28.51	27.30	–	–
pp5	16.99	9.99	10.63	12.68	16.53	16.06	25.47	–	–	–
ip2	11.76	–	–	8.12	–	–	16.08	–	–	–
ip3	–	11.79	11.00	12.12	–	14.77	–	–	11.17 #	17.81*
ip4	–	11.18	12.42	12.13	–	14.87	–	–	–	–
ip5	10.61	–	9.90	8.98	11.47	–	13.94	–	–	–
dp1	6.12	–	5.04	6.13	6.49	–	8.98	–	–	–
dp2	3.82	3.31	–	4.13	–	–	8.14	–	–	–
dp3	–	3.73	4.04	3.98	–	–	9.38	–	3.96 ##	–
dp4	–	–	3.69	4.73	5.70	5.50	10.44	–	–	–
dp5	–	–	–	3.13	3.82	–	8.96	–	–	–

See Figures 11–13 for documentation. Specimens included: (1) *Europolemur kelleri*, SMF-ME 1683; (2) *Europolemur koenigswaldi*, SMF-ME 1228; (3) *Darwinius masillae*, PMO 214.214; (4) *Godinotia neglecta*, GMH L-2; (5) *Notharctus tenebrosus*, AMNH 127167 with distal phalanx measurements from Alexander and Hamrick (1996); (6) AMNH 11478, with all measurements from Gregory (1920); (7) *Adapis parisiensis*, RD 311. All measurements in mm.

Symbols in Appendix F:

(\*) Average of samples from Phosphorites de Quercy

(#) Locality averages adjusted so that proportion to MC3 of Rosieres 2 matches proportion of raw value to locality average MC3

(\*\*) MC4 length can be used as proxy for MC3 length in digit 3 proportion plots

(##) Based on a single specimen

(+) Not accurate enough to use in "average hand estimate" (use value for other hand instead).

## LITERATURE CITED

- Alexander JP, Burger BJ. 2001. Stratigraphy and taphonomy of Grizzly Buttes, Bridger Formation, and the Middle Eocene of Wyoming. In: Gunnell GF, editor. Eocene biodiversity: unusual occurrences and rarely sampled habitats. New York: Plenum Publishers. p 165–196.
- Anthony MRL, Kay RF. 1993. Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. *Am J Sci A* 293:356–382.
- Beard KC. 1989. Postcranial anatomy, locomotor adaptations, and palaeoecology of early Cenozoic Plesiadapidae, Paromomyidae, and Micromomyidae (Eutheria, Dermoptera). Ph.D. Dissertation. Baltimore: Johns Hopkins University. 660 p.
- Beard KC. 1990. Gliding behavior and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). *Nature* 345:340–341.
- Beard KC. 1993a. Origin and evolution of gliding in Early Cenozoic Dermoptera (Mammalia, Primatomorpha). In: MacPhee RDE, editor. Primates and their relatives in phylogenetic perspective. New York: Plenum Press. p 63–90.
- Beard KC. 1993b. Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In: Szalay FS, McKenna MC, and Novacek MJ, editors. Mammal phylogeny: placentals. New York: Springer-Verlag. p 129–150.
- Beard KC, Dagosto M, Gebo DL, Godinot M. 1988. Interrelationships among Primate Taxa. *Nature* 331:712–714.

- Beard KC, Godinot M. 1988. Carpal anatomy of *Smilodectes gracilis* (Adapiformes, Notharctinae) and its significance for lemuriform phylogeny. *J Hum Evol* 17:71–92.
- Bloch JI, Boyer DM. 2002. Grasping primate origins. *Science* 298:1606–1610.
- Bloch JI, Boyer DM. 2007. New skeletons of Paleocene-Eocene Plesiadapiformes: a diversity of arboreal positional behaviors in early primates. In: Dagosto M, Ravosa MJ, editors. *Primate origins: adaptations and evolution*. New York: Plenum Press. p 535–582.
- Bloch JI, Gingerich PD. 1998. *Carpolestes simpsoni*, new species (Mammalia, Proprimates) from the late Paleocene of the Clarks Fork Basin, Wyoming. *Contrib Mus Paleontol Univ Michigan* 30:131–162.
- Bloch JI, Randall Z, Silcox MT, Chester S, Boyer DM. 2010. Distal phalanges of Eocene North American notharctines (Mammalia, Primates): implications for primate and anthropoid origins. *J Vertebr Paleontol Suppl* 30:60A.
- Bloch JI, Silcox MT. 2006. Cranial anatomy of the Paleocene plesiadapiform *Carpolestes simpsoni* (Mammalia, Primates) using ultra high-resolution X-ray computed tomography, and the relationships of plesiadapiforms to Euprimates. *J Hum Evol* 50:1–35.
- Bloch JI, Silcox MT, Boyer DM, Sargis EJ. 2007. New Paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates. *Proc Natl Acad Sci USA* 104:1159–1164.
- Boyer DM. 2009. New cranial and postcranial remains of late Paleocene Plesiadapidae (“Plesiadapiformes,” Mammalia) from North America and Europe: description and evolutionary implications. *Stony Brook: Stony Brook University*. 569 p.
- Boyer DM, Bloch JI. 2008. Evaluating the mitten-gliding hypothesis for Paromomyidae and Micromomyidae (Mammalia, “Plesiadapiformes”) using comparative functional morphology of new Paleogene skeletons. In: Sargis EJ, and Dagosto M, editors. *Mammalian evolutionary morphology: a tribute to Frederick S Szalay*. New York: Kluwer. p 233–284.
- Boyer DM, Chester SGB, Bloch JI. 2010a. New fossil evidence on the structure of the plesiadapiform hand skeleton: implications for the evolution of grasping in primates. *Am J Phys Anthropol* 143(Suppl 51):34A.
- Boyer DM, Costeur L, Lipman Y. 2012a. Earliest record of Platychoerops (Primates, Plesiadapidae), a new species from Mouras Quarry, Mont de Berru, France. *Am J Phys Anthropol* 149:329–346.
- Boyer DM, Scott CS, Fox RC. 2012b. New craniodental material of *Pronothodectes gaoi* Fox (Mammalia, “Plesiadapiformes”) and relationships among members of Plesiadapidae. *Am J Phys Anthropol* 147:511–550.
- Boyer DM, Seiffert ER, Gladman JT, Bloch JI. 2013. Evolution and allometry of calcaneal elongation in living and extinct primates. *PLoS One* 8:e67792
- Boyer DM, Seiffert ER, Simons EL. 2010b. Astragalar morphology of *Afradapis*, a large adapiform primate from the earliest late Eocene of Egypt. *Am J Phys Anthropol* 143:383–402.
- Cartmill M. 1972. Arboreal adaptations and the origin of the order Primates. In: Tuttle R, editor. *The functional and evolutionary biology of primates*. Chicago: Aldine. p 97–122.
- Cartmill M. 1974a. Pads and claws in arboreal locomotion. In: Jenkins FA, editor. *Primate locomotion*. New York: Academic Press. p 45–83.
- Cartmill M. 1974b. Rethinking primate origins. *Science* 184: 436–443.
- Cartmill M. 1992. New views on primate origins. *Evolutionary Anthropology* 1:105–111.
- Cartmill M. 2012. Primate origins, human origins, and the end of higher taxa. *Evolutionary Anthropology* 21:208–220.
- Covert HH. 1985a. Adaptations and evolutionary relationships of the Eocene primate family Notharctidae, Ph.D. dissertation, Duke University.
- Covert HH. 1985b. The skeleton of *Smilodectes gracilis*. *Am J Phys Anthropol* 66:159A.
- Covert HH. 1986. Biology of early Cenozoic primates. In: Swindler DR, and Erwin J, editors. *Comparative primate biology*. New York: Alan R Liss, Inc. p 335–359.
- Crompton RH. 1995. “Visual predation,” habitat structure, and the ancestral primate niche. In: Alterman L, Doyle GA, Izard MK, editors. *Creatures of the dark: the nocturnal prosimians*. New York: Plenum Press. p 11–30.
- Dagosto M. 1983. Postcranium of *Adapis parisiensis* and *Leptadapis magnus* (Adapiformes, Primates). *Folia Primatol* 41:49–101.
- Dagosto M. 1988. Implications of postcranial evidence for the origin of euprimates. *J Hum Evol* 17:35–56.
- Dagosto M. 1990. Models for the origin of the anthropoid postcranium. *J Hum Evol* 19:121–139.
- Dagosto M. 1993. Postcranial anatomy and locomotor behavior in Eocene primates. In: Gebo DL, editor. *Postcranial adaptations in nonhuman primates*. DeKalb, Illinois: Northern Illinois University Press. p 199–219.
- Etter HF. 1974. Morphologisch- und metrisch-vergleichende untersuchung am handskelet rezenter Primaten. *Gegenbaurs Morphologisches Jahrbuch (Leipzig)* 120:1–484.
- Etter HF. 1978. Lorisiform hands and their phylogenetic implications: a preliminary report. In: Chivers DH, Joysey KA, editors. *Recent advances in primatology*. London: Academic Press. p 161–170.
- Ford SM. 1986. Systematics of the New World monkeys. *Comparative primate biology*, Vol. 1: Systematics, evolution and anatomy. New York: Alan R Liss, Inc. p 73–135.
- Ford SM. 1988. Postcranial adaptations of the earliest platyrrhine. *Journal Human Evolution* 17:155–192.
- Franzen J. 1993. The oldest primate hands: Additional remarks and observations. In: Preuschoft H, and Chivers DJ, editors. *Hands of Primates*. New York: Springer-Verlag. p 379–386.
- Franzen JL. 1987. Ein neuer Primate aus dem mittelozan der Grube Messel (Deutschland, S-Hessen). *Courier Forschungs-Institut Senckenberg* 91:151–187.
- Franzen JL. 1988. Ein weiterer primatenfund aus der grube messel bei darmstadt. *Courier Forschungs-Institut Senckenberg* 107:275–289.
- Franzen JL. 2000. *Europolemur kelleri* n. sp. von Messel und ein nachtrag zu *Europolemur koenigswaldi* (Mammalia, Primates, Notharctidae, Cercamoniinae). *Senckenbergiana lethaea* 80:275–287.
- Franzen JL, Frey CJ. 1993. *Europolemur* completed. *Kaupia Darmstadter Beitrage zur Naturgeschichte* 3:113–130.
- Franzen JL, Gingerich PD, Habersetzer J, Hurum JH, von Koenigswald W, Smith BH. 2009. Complete primate skeleton from the middle Eocene of Messel in Germany: morphology and paleobiology. *PLoS One* 4:e5723.
- Gebo DL. 1988. Foot morphology and locomotor adaptation in Eocene primates. *Folia Primatol* 50:3–41.
- Gebo DL. 2002. Adapiformes: Phylogeny and adaptation. In: Hartwig WC, editor. *The Primate Fossil Record*. New York: Cambridge University Press. p 21–82.
- Gebo DL. 2011. Vertical clinging and leaping revisited: vertical support use as the ancestral condition of strepsirrhine primates. *Am J Phys Anthropol* 146:323–345.
- Gebo DL, Dagosto M, Beard KC, Ni X, Qi T. 2008. A haplorhine first metatarsal from the Middle Eocene of China. In: Fleagle JG, Gilbert CC, editors. *Elwyn Simons: a search for origins*. New York, NY: Springer. p 229–242.
- Gebo DL, Dagosto M, Rose KD. 1991. Foot morphology and evolution in early Eocene *Cantius*. *Am J Phys Anthropol* 86:51–73.
- Gebo DL, Smith T, Dagosto M. 2012. New postcranial elements for the earliest Eocene fossil primate *Teilhardina belgica*. *J Hum Evol* 65:305–218.
- Gidley JW. 1919. Significance of divergence of the first digit in the primitive mammalian foot. *J Washington Acad Sci* 9:273–280.
- Gingerich PD. 1976. Cranial anatomy and evolution of Early Tertiary Plesiadapidae (Mammalia, Primates). *Univ Michigan Pap Paleontol* 15:1–141.

- Gingerich PD. 1986. Early Eocene *Cantius torresi*—oldest primate of modern aspect from North America. *Nature* 319:319–321.
- Gingerich PD. 2012. Primates in the Eocene. *Palaeobiodiversity and Palaeoenvironments* 92:649–663.
- Gingerich PD, Dashzeveg D, Russell DE. 1991. Dentition and systematic relationships of *Altanius orlovi* (Mammalia, Primates) from the Early Eocene of Mongolia. *Geobios* 24:637–646.
- Gingerich PD, Franzen JL, Habersetzer J, Hurum JH, Smith BH. 2010. *Darwinius masillae* is a haplorhine—reply to Williams et al. (2010). *J Hum Evol* 59:574–579.
- Gingerich PD, Houde P, Krause DW. 1983. A new Earliest Tiffanian (Late Paleocene) mammalian fauna from Bangtail Plateau, western Crazy Mountain Basin, Montana. *J Paleontol* 57:957–970.
- Gladman JT, Boyer DM, Simons EL, Seiffert ER. 2013. A Calcaneus attributable to the primitive Late Eocene Anthropoid *Proteopithecus sylviae*: phenetic affinities and phylogenetic implications. *Am J Phys Anthropol* 151:372–397.
- Godinot M. 1991. Approches fonctionnelles des mains de primates Paléogènes. *Geobios* 13:161–173.
- Godinot M. 1992. Early euprimate hands in evolutionary perspective. *J Hum Evol* 22:267–283.
- Godinot M. 1998. A summary of adapiform systematics and phylogeny. *Folia Primatol* 69 (Suppl 1):218–249.
- Godinot M. 2007. Primate origins: a reappraisal of historical data favoring tupaiid affinities. In: Dagosto M, Ravosa MJ, editors. *Primate origins: adaptations and evolution*. New York: Plenum Press. p 83–142.
- Godinot M, Beard KC. 1991. Fossil primate hands: a review and an evolutionary inquiry emphasizing early forms. *Hum Evol* 6:307–354.
- Godinot M, Beard KC. 1993. A survey of fossil primate hands. In: Preuschoft H, Chivers DJ, editors. *Hands of primates*. New York: Springer-Verlag. p 335–377.
- Godinot M, Jouffroy F. 1984. La main d'Adapis (Primates, Adapidae). In: Buffetaut E, Mazin JM, and Salmion E, editors. *Actes du Symposium Palaeontologique G Cuvier*. Paris: Montbeliard. p 221–242.
- Gregory WK. 1920. On the structure and relations of *Notharctus*, an American Eocene primate. *Mem Am Mus Nat Hist* 3: 45–243.
- Gregory WK. 1936. Habitus factors in the skeleton of fossil and recent mammals. *Proc Am Philos Soc* 56:429–444.
- Gunnell GF, Silcox MT. 2010. Primate origins: the early Cenozoic fossil record. In: Larsen CS, editor. *A companion to biological anthropology*. New York: Blackwell. p 275–289.
- Haines RW. 1955. The anatomy of the hand of certain insectivores. *Proc Zool Soc London* 125:761–776.
- Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol Electron* 4:9. [http://palaeo-electronica.org/2001\\_2001/past/issue2001\\_2001.htm](http://palaeo-electronica.org/2001_2001/past/issue2001_2001.htm).
- Hamrick MW. 1996a. Articular size and curvature as determinants of carpal joint mobility and stability in strepsirhine primates. *J Morphol* 230:113–127.
- Hamrick MW. 1996b. Functional morphology of the lemuriform wrist joints and the relationship between wrist morphology and positional behavior in arboreal primates. *Am J Phys Anthropol* 99:319–344.
- Hamrick MW. 1996c. Locomotor adaptations reflected in the wrist joints of early Tertiary primates (Adapiformes). *Am J Phys Anthropol* 100:585–604.
- Hamrick MW. 1997. Functional osteology of the primate carpus with special reference to Strepsirhini. *Am J Phys Anthropol* 104:105–116.
- Hamrick MW. 1999. First carpals of the Eocene primates family Omomyidae. *Contrib Mus Paleontol Univ Michigan* 30:191–198.
- Hamrick MW. 2001. Primate origins: evolutionary change in digit ray patterning and segmentation. *J Hum Evol* 40:339–351.
- Hamrick M. 2007. Evolvability, limb morphology, and primate origins. In: Dagosto M, Ravosa MJ, editors. *Primate origins: adaptations and evolution*. New York: Plenum Press. p 381–401.
- Hamrick MW, Alexander JP. 1996. The hand skeleton of *Notharctus tenebrosus* (Primates, Notharctidae) and its significance for the origin of the primate hand. *Am Mus Novitates* 3182:1–20.
- Hamrick MJ, Meldrum JD, Simons EL. 1995. Anthropoid phalanges from the Oligocene of Egypt. *J Hum Evol* 28:121–145.
- Hamrick MW, Rosenman BA, Brush JA. 1999. Phalangeal morphology of the Paromomyidae (Primates, Plesiadapiformes): the evidence for gliding behavior reconsidered. *Am J Phys Anthropol* 109:397–413.
- Hoffstetter R. 1977. Phylogénie des primates. Confrontation des résultats obtenus par les diverses voies d'approche du problème. *Bull Mém Soc Anthropol Paris* t.4, série XIII:327–346.
- Janecka JE, Miller W, Pringle TH, Wiens F, Zitzmann A, Helgen KM, Springer MS, Murphy WJ. 2007. Molecular and genomic data identify the closest living relative of primates. *Science* 318:792–794.
- Jones FW. 1916. *Arboreal man*. London: Arnold. 230p.
- Jouffroy FK. 1975. Osteology and myology of the Lemuriform postcranial skeleton. In: Tattersall I, Sussman RW, editors. *Lemur biology*. New York: Plenum Press. p 149–192.
- Jouffroy FK, Godinot M, Nakano Y. 1991. Biometrical characteristics of primate hands. *J Hum Evol* 6:269–306.
- Jouffroy FK, Lessertisseur J. 1959. La main des Lémuriens malgaches comparée à celle des autres primates. *Mém Inst Sci Madagascar Sér A* 13:195–219.
- Jungers WL, Godfrey LR, Simons EL, Chatrath PS. 1997. Phalangeal curvature and positional behavior in extinct sloth lemurs (Primates, Palaeopropithecidae). *Proc Natl Acad Sci USA* 94:11998–12001.
- Kay RF, Cartmill M. 1977. Cranial morphology and adaptations of *Palaeochthon nacimienti* and other Paromomyidae (Plesiadapoidea, Primates), with a description of a new genus and species. *J Hum Evol* 6:19–35.
- Kay RF, Ross C, Williams BA. 1997. Anthropoid origins. *Science* 275:797–804.
- Kay RF, Williams BA, Ross CF, Takai M, Shigehara N. 2004. Anthropoid origins—a phylogenetic analysis. In: Ross CF, Kay RF, editors. *Anthropoid origins: new visions*. New York: Kluwer Academic/Plenum Publishers. p 91–135.
- Kirk EC, Lemelin P, Hamrick MW, Boyer DM, Bloch JI. 2008. Intrinsic hand proportions of euarchontans and other mammals: implications for the locomotor behavior of plesiadapiforms. *J Hum Evol* 55:278–299.
- Krause DW. 1986. Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America. *Rocky Mountain Geology* 24(special paper 3): 95–117.
- Krause DW. 1991. Were paromomyids gliders? Maybe, maybe not. *J Hum Evol* 21:177–188.
- Lemelin P. 1996. The evolution of manual prehensibility in primates, Ph.D. Dissertation. Stony Brook: State University of New York at Stony Brook.
- Lemelin P, Jungers WL. 2007. Body size and scaling of the hands and feet of prosimian primates. *Am J Phys Anthropol* 133:828–840.
- Lemelin P, Schmitt D. 1998. The relation between hand morphology and quadrupedalism in primates. *Am J Phys Anthropol* 105:185–197.
- Le Gros Clark WE. 1971. *The antecedents of man*. New York: Quadrangle/New York Times Book Co. 394 p.
- Maas MC, Krause DW, Strait SG. 1988. The decline and extinction of Plesiadapiformes (Mammalia: Primates) in North America: displacement or replacement? *Paleobiology* 14:410–431.
- Maiolino S, Boyer DM, Bloch JI, Gilbert CS, Groenke J. 2012. Evidence for a grooming claw in a north American adapiform primate: implications for anthropoid origins. *PLoS One* 7: e29136.

- Martin RD. 1986. Primates: a definition. In: Wood BA, Martin LB, Andrews PJ, editors. Major topics in primate and human evolution. New York: Cambridge University Press. p 1–31.
- Matthew WD. 1904. The arboreal ancestry of the mammalia. *Am Naturalist* 38:811–818.
- McKenna MC, Bell SK. 1997. Classification of mammals above the species level. New York: Columbia University Press. 631 p.
- Napier JR. 1960. Studies of the hands of living primates. *Proc Zool Soc London* 134:647–656.
- Napier JR. 1961. Prehensility and opposability in the hands of primates. *Symposia Zool Soc London* 5:115–132.
- Napier JR. 1980. Hands. Princeton, New Jersey: Princeton University Press. 176 p.
- Napier JR, Davis PR. 1959. The fore-limb skeleton and associated remains of *Proconsul africanus*. *Br Mus (Nat History) Fossil Mammals Afr* 16:1–69.
- Napier JR, Walker AC. 1967. Vertical clinging and leaping—a newly recognized category of primate locomotion. *Folia Primatol* 6:204–219.
- Ni X, Gebo D, Dagosto M, Meng J, Tafforeau P, Flynn JJ, Beard KC. 2013. The oldest known primate skeleton and early haplorhine evolution. *Nature* 498(7452):60–64.
- Patel BA, Seiffert ER, Boyer DM, Jacobs RL, St Clair EM, Simons EL. 2012. New primate first metatarsals from the Paleogene of Egypt and the origin of the anthropoid big toe. *J Hum Evol* 63:99–120.
- Pouydebat E, Coppens Y, Gorce P. 2006. Évolution de la préhension chez les primates humains et non humains : la précision et l'utilisation d'outils revisités. *L'anthropologie* 110:687–697.
- Pouydebat E, Gorce P, Coppens Y, Bels V. 2009. Biomechanical study of grasping according to the volume of the object: Human versus non-human primates. *J Biomech* 42:266–272.
- Preuschoft H, Godinot M, Beard C, Nieschalk U, Jouffroy FK. 1993. Biomechanical considerations to explain important morphological characters of primate hands. In: Preuschoft H, Chivers DJ, editors. Hands of primates. New York: Springer Verlag. p 245–256.
- Reghem E, Byron C, Bels V, Pouydebat E. 2012. Hand posture in the grey mouse lemur during arboreal locomotion on narrow branches. *J Zool* 288:76–81.
- Reghem E, Tia B, Bels V, Pouydebat E. 2011. Food prehension and manipulation in *Microcebus murinus* (Prosimii, Cheirogaleidae). *Folia Primatol* 82:177–188.
- Rose KD. 1975. The Carpolestidae, early tertiary primates from North America. *Bull Mus Comp Zool Harvard Univ* 147:1–74.
- Rose KD, Chester SGB, Dunn RH, Boyer DM, Chew AE, Bloch JI. 2011. New fossils of the oldest north American Euprimates *Teilhardina brandti* (Omomyidae) from the Paleocene-Eocene thermal maximum. *Am J Phys Anthropol* 146:281–305.
- Rose KD, Rana RS, Sahni A, Kumar K, Missiaen P, Singh L, Smith T. 2009. Early Eocene Primates from Gujarat, India. *J Hum Evol* 56:366–404.
- Runestad JA, Ruff CB. 1995. Structure adaptations for gliding in mammals with implications for locomotor behavior in paromomyids. *Am J Phys Anthropol* 98:101–119.
- Russell DE. 1967. Sur *Menatherium* et l'âge Paleocene du gisement de menat (Puy-de-dome). *Probl Act de Paleont, Coll Inter Cent. Nat Recherche Sci* 163:483–490.
- Salton JA, Sargis EJ. 2008. Evolutionary morphology of the Tenrecoidea (Mammalia) carpal complex. *Biological Journal of Linnean Society* 93:267–288.
- Sargis EJ. 2001. The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T-tana* (Mammalia, Scandentia). *J Zool* 253:485–490.
- Sargis EJ. 2002. Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *J Morphol* 253:10–42.
- Savage DE, Waters BT. 1978. A new omomyid primate from the Wasatch Formation of southern Wyoming. *Folia Primatol* 30:1–29.
- Schwartz JH, Yamada TK. 1998. Carpal anatomy and primate relationships. *Anthropol Sci* 106:47–65.
- Seiffert ER, Perry JMG, Simons EL, Boyer DM. 2009. Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates. *Nature* 461:1118–1121.
- Silcox MT, Sargis EJ, Bloch JI, Boyer DM. 2007. Primate origins and supraordinal relationships: morphological evidence. In: Henke W, Rothe H, Tattersall I, editors. Handbook of paleoanthropology, Vol 2: Primate evolution and human origins. Germany: Springer: Heidelberg. p 831–859.
- Simons EL. 1972. Primate evolution, an introduction to man's place in nature. New York: Macmillan. 322 p.
- Simpson GG. 1935. The Tiffany fauna, upper Paleocene. III. Primates, Carnivora, Condylarthra, and Amblypoda. *Am Mus Novitates* 816:1–28.
- Smith T, Rose KD, Gingerich PD. 2006. Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene thermal maximum. *Proc Natl Acad Sci USA* 103:11223–11227.
- Spinozzi G, Truppa V, Lagana T. 2004. Grasping behavior in Tufted Capuchin monkeys (*Cebus apella*): grip types and manual laterality for picking up a small food item. *Am J Phys Anthropol* 125:30–41.
- Springer MS, Meredith RW, Gatesy J, Emerling CA, Park J, Rabosky DL, Stadler T, Steiner C, Ryder OA, Janečka JE, Fisher CA, Murphy WJ. 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLoS One* 7(11):e49521.
- Stafford BJ, Thorington RWJ. 1998. Carpal development and morphology in archontan mammals. *J Morphol* 235:135–155.
- Szalay FS. 1981a. Functional analysis and the practice of the phylogenetic method as reflected by some mammalian studies. *Am Zoologist* 21:37–45.
- Szalay FS. 1981b. Phylogeny and the problem of adaptive significance: the case of the earliest primates. *Folia Primatol* 36:157–182.
- Szalay FS, Dagosto M. 1980. Locomotor adaptations as reflected on the humerus of Paleogene primates. *Folia Primatol* 34:1–45.
- Szalay FS, Dagosto M. 1988. Evolution of hallucial grasping in the primates. *J Hum Evol* 17:1–33.
- Szalay FS, Decker RL. 1974. Origins, evolution, and function of the tarsus in late Cretaceous Eutheria and Paleocene primates. In: Jenkins FA, Jr editor. Primate locomotion. New York: Academic Press. p 239–259.
- Szalay FS, Delson E. 1979. Evolutionary history of the primates. San Diego: Academic Press. 580 p.
- Szalay FS, Drawhorn G. 1980. Evolution and diversification of the Archonta in an arboreal milieu. In: Luckett WP, editor. Comparative biology and evolutionary relationships of tree shrews. New York: Plenum Press. p 133–169.
- Szalay FS, Rosenberger AL, Dagosto M. 1987. Diagnosis and differentiation of the order Primates. *Yearbook Phys Anthropol* 30:75–105.
- Thalmann U. 1994. Die Primaten aus dem eozänen Geiseltal bei Halle/Saale (Deutschland). *Courier Forsch-Inst Senckenberg* 175:121–123.
- Thalmann U, Haubold H, Martin RD. 1989. *Pronycticebus neglectus*, an almost complete adapid primate specimen from the Geiseltal (GDR). *Palaeovertebrata* 19:115–130.
- Whitehead PF. 1993. Aspects of the anthropoid wrist and hand. In: Gebo DL, editor. Postcranial adaptation in nonhuman primates. DeKalb: Northern Illinois University Press. p 96–120.
- Wible JR, Covert HH. 1987. Primates: cladistic diagnosis and relationships. *J Hum Evol* 16:1–22.
- Williams BA, Kay RF, Kirk EC, Ross CF. 2010. *Darwinius masillae* is a strepsirrhine—a reply to Franzen et al. (2009). *J Hum Evol* 59(5):567–573.
- Youlatos D, Godinot M. 2004. Locomotor adaptations of *Plesiadapis tricuspidens* and *Plesiadapis n. sp.* (Mammalia, Plesiadapiformes) as reflected in selected parts of the postcranium. *Anthropol Sci* 82:103–118.