

News and Views

Evolution of pedal grasping in Primates

Eric J. Sargis^{a,*}, Doug M. Boyer^b, Jonathan I. Bloch^c, Mary T. Silcox^d

^a Department of Anthropology, Yale University; Division of Vertebrate Zoology, Peabody Museum of Natural History, USA

^b Department of Anatomical Science, Stony Brook University, Stony Brook, NY 11794-8081, USA

^c Florida Museum of Natural History, University of Florida, P.O. Box 117800, Gainesville, FL 32611, USA

^d Department of Anthropology, University of Winnipeg, 515 Portage Avenue, Winnipeg, MB R3B 2E9, Canada

Received 27 June 2006; accepted 29 January 2007

Keywords: *Carpolestes*; *Ptilocercus*; *Caluromys*; Euprimates; Plesiadapiforms; Euarchonta

Grasping extremities have long been associated with the origin and diagnosis of Primates (Mivart, 1873; Le Gros Clark, 1959). The evolution of pedal grasping in euarchontan mammals (Primates, Scandentia, Dermoptera) has recently received a great deal of attention, in part because it has implications for the adaptive significance of specialized grasping in primates. Building on Szalay and Dagosto's (1988) assessment of primate pedal grasping, additional contributions include information on didelphid marsupials (Lemelin, 1999; Argot, 2002), treeshrews (Scandentia; Sargis, 2001, 2002a,b, 2004), and carpolestid plesiadapiforms (Primates, *sensu lato*; Bloch and Boyer, 2002). In a recent synthesis of some of this information, Gebo (2004) proposed the following six-stage sequence for the evolution of primate characteristics, including pedal grasping: (1) a small, insectivorous, scansorial, clawed, non-grasping mammal like the extant shrew *Sylvisorex*; (2) an arboreal, clawed mammal with non-powerful pedal grasping and a non-opposable hallux without a nail, such as the extant tree-shrew *Ptilocercus*; (3) a terminal branch feeder, characterized by "non-powerful" pedal grasping and an opposable hallux that has a nail, such as the extant didelphid marsupial *Caluromys* (but see below); (4) a primate with grasping hands, nails on all digits, orbital convergence, and a powerfully grasping, opposable hallux with a large peroneal process on the first metatarsal, such as might be assumed to be the primitive

condition for extant primates; (5) a primate with leaping adaptations of the hind limb; and (6) a larger primate similar to early Eocene euprimates (see Table 1). Although we agree on many points, we disagree with several premises in his argument for this suggested "sequence of 'preprimate to primate' evolutionary stages" (Gebo, 2004:55). These differences in interpretation, coupled with new data not available to Gebo (2004), lead us to a different interpretation of the evolution of pedal grasping in primates and their euarchontan relatives.

Pedal grasping in extant *Caluromys*

Gebo (2004:55) claimed that the opposable grasping hallux of *Caluromys*, a didelphid marsupial, represents an appropriate extant analog ("*Caluromys* model") for a stage in the evolution of primates, resulting from "an ecological shift toward terminal branches in the canopy as well as a change in quadrupedal gait mechanics and an opposable big toe (nonpowerful)." Although an explicit quantification of grasping power is not available at this time, we accept the definition by Gebo (2004) of euprimate pedal grasping as "powerful" even though it is qualitative. While we also agree that an argument can be made for the grasping complex of *Caluromys* being similar to a stage that preceded the euprimate condition (Gebo's stage 4; see Table 1) in primate evolution (e.g., Bloch and Boyer, 2002), the claim that the opposable grasping hallux of *Caluromys* is "non-powerful" is not supported by either behavioral or morphological evidence.

Caluromys employs hind limb suspension and cantilevering postures as effectively as cheirogaleid euprimates (Lemelin,

* Corresponding author. Department of Anthropology, Yale University, P.O. Box 208277, New Haven, CT 06520, USA. Tel.: +1 203 432 6140; fax: +1 203 432 3669.

E-mail address: eric.sargis@yale.edu (E.J. Sargis).

Table 1
Comparison of Gebo's (2004) scenario with the one proposed here

Six stage sequence (Gebo, 2004)	Ancestral morphotypes (this study)
(1) scansorial, clawed, non-grasping mammal like <i>Sylvisorex</i> (shrew)	(1) Euarchontoglires ancestor: clawed, non-grasping mammal
(2) arboreal, clawed mammal with non-powerful and non-opposable pedal grasping like <i>Ptilocercus</i> (treeshrew). <i>Carpolestes</i> fits this stage	(2) Euarchontan ancestor: arboreal, clawed mammal with <i>Ptilocercus</i> -like pedal grasping mechanism. Micromomyids and paromomyids retain this condition
(3) terminal branch feeder, characterized by “non-powerful” pedal grasping and opposable hallux with a nail, like <i>Caluromys</i> (didelphid marsupial)	(3) Plesiadapoid-euprimate (Euprimateform) ancestor: terminal branch feeder characterized by powerful pedal grasping and opposable hallux with a nail, like <i>Caluromys</i> . <i>Carpolestes</i> retains this condition
(4) primate with grasping hands, orbital convergence, nails on all digits, and powerful, opposable hallux with large peroneal process on first metatarsal	(4–6) Euprimate ancestor: nails on all digits, leaping adaptations of hind limb and large peroneal process on first metatarsal, similar to early Eocene euprimates.
(5) primate with leaping adaptations of hind limb	The fossil record as it currently stands does not provide evidence on the order of acquisition of these traits.
(6) larger primate similar to early Eocene euprimates	

1999). Both of these behaviors require a firm hold on a substrate by the foot and they demonstrate that this arboreal marsupial is capable of “powerful” pedal grasping. Furthermore, *Caluromys* differs from more terrestrial didelphids in having longer digits, a more widely divergent hallux, and a better developed hallucal eminence and pad (Argot, 2002; Lemelin et al., 2003), all of which contribute to its grasping capability. Gebo (2004) classified the grasping hallux of *Caluromys* as

“non-powerful” simply because it lacks a large peroneal process on the first metatarsal (Fig. 1). However, there is mounting morphological and experimental evidence that the size of the peroneal process is not a good indicator of grasping abilities in marsupials or primates (Gebo, 1987; Szalay and Dagosto, 1988; Boyer et al., 2006, in press).

Gebo (2004: 55) correlated a powerful, opposable, grasping hallux with “a long and robust peroneal tubercle on the first metatarsal as in prosimian primates (living and extinct) to maintain contact with branches while the hands manipulate insects.” There are several problems with this correlation. First, experimental evidence from non-human primates suggests that the peroneus longus muscle, the tendon of which attaches to the peroneal tubercle, is not important for grasping (Stern and Susman, 1983; Boyer et al., 2006, in press).

Second, there is not a consistent relationship between powerful grasping and a large peroneus longus muscle in primates. Gebo (1987) himself demonstrated that a small peroneus longus muscle in tarsiers is associated with a large peroneal process that is similar to that of strepsirhines (Szalay and Dagosto, 1988). He suggested powerful grasping is still possible via the intrinsic foot musculature. Lorises are exceptional for their pedal grasping specialization, even among strepsirhines, yet their peroneus longus is not remarkable in its relative mass (Gebo, 1989). If peroneus longus is not critical for hallucal grasping, then it is unclear how an enlarged peroneal process could have any bearing on grasping power.

Third, even if the peroneus longus muscle is important for grasping in some taxa, there are multiple lines of evidence indicating that its size is not correlated with the size of the peroneal process in a predictable way. In addition to the tarsier example above, the muscle is “enormous” in *Caluromys* and other powerfully grasping arboreal marsupials, even though they have a relatively small peroneal process on the first

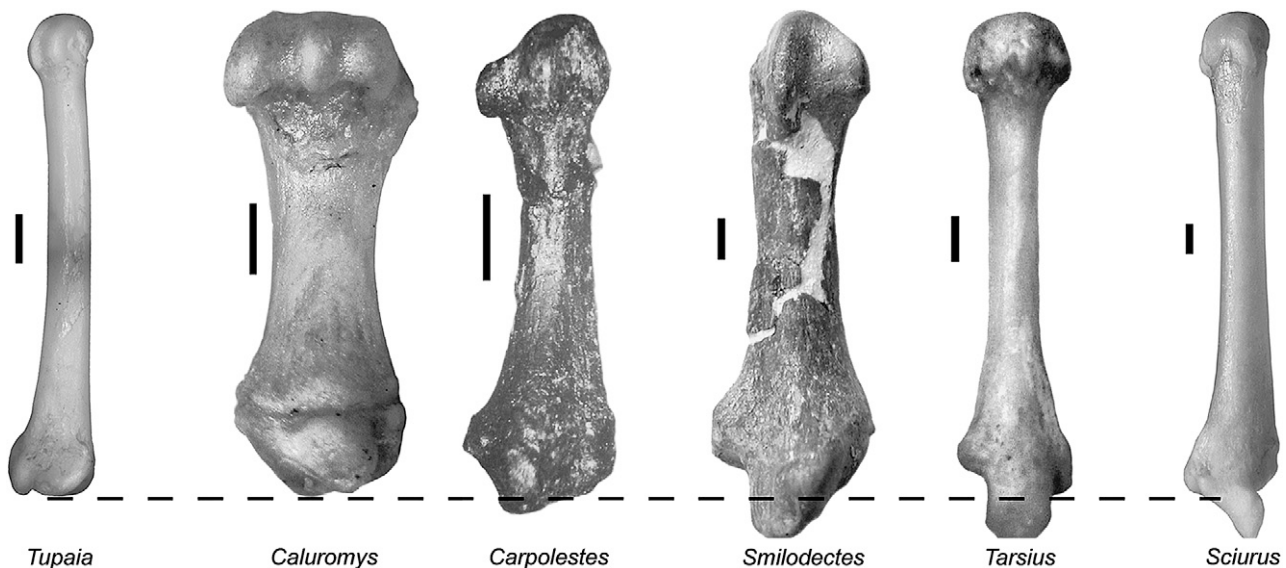


Fig. 1. Left first metatarsals of *Tupaia glis* (SBU specimen), *Caluromys philander* (AMNH 234979), *Carpolestes simpsoni* (UM 101963), *Smilodectes mcgrewi* (UM 95526), *Tarsius syrichta* (UM 139), and *Sciurus carolinensis* (SBU-Mrd10) in lateral view. The line represents the dorsal margin of the articular facet for the entocuneiform. Note the small peroneal processes in *Carpolestes*, *Caluromys*, and *Tupaia*. Also note torsion of the first metatarsal in *Carpolestes*, *Caluromys*, *Smilodectes*, and *Tarsius*. Scale = 1 mm.

metatarsal (Szalay and Dagosto, 1988; also see Argot, 2002). The large size of this muscle in *Caluromys* may help explain how this arboreal marsupial engages in powerful grasping (Lemelin, 1999). However, Argot (2002) has demonstrated that *Caluromys* also has a well-developed flexor fibularis muscle (which is used in grasping), leaving open the possibility that peroneus longus could be enlarged for some other function (Boyer et al., in press). The correlation between a large peroneal process and powerful grasping is also weakened by the presence of a large process in mammals that do not powerfully grasp. Specifically, sciurid rodents have a relatively large first metatarsal, and although their hallux is neither divergent nor opposable, it has a large peroneal process (Fig. 1) similar in proportional size to that of primitive euprimates (Rose, 1999). Thus, the presence of a large peroneal process on the first metatarsal and powerful pedal grasping can be dissociated in a number of ways, such that the former does not predict the latter (Rose, 1999). Based on this dissociation, Szalay and Dagosto (1988) hypothesized that the hypertrophied peroneal process in adapids, omomyids, and lemuriforms may serve a buttressing function in leaping and landing, rather than being strictly associated with grasping power.

Pedal grasping in Paleogene plesiadapiforms

Gebo (2004) described all known non-carpolestid plesiadapiforms as lacking an opposable grasping hallux. Although non-carpolestid plesiadapiforms for which the relevant morphology is known lack an opposable hallux that is rotated toward the other digits, this does not mean that they did not have a grasping (prehensile) hallux. Others who have studied

this joint in non-carpolestid plesiadapiforms have concluded that it was prehensile, mobile, and slightly divergent. For example, Szalay and Dagosto (1988) concluded that the grasping capabilities of *Plesiadapis* were similar to those of *Ptilocercus*, in which the hallux is divergent but non-opposable, and grasping is possible but less powerful than in euprimates (also see Sargis, 2001, 2002a,b,c, 2004, on *Ptilocercus* and *Plesiadapis*; and Boyer et al., 2004, on *Nannodectes*). Additionally, Bloch and Boyer (2007) concluded that the pedal grasping mechanism of micromomyid and paromomyid plesiadapiforms is also similar to that of *Ptilocercus*, but not euprimates (also see Bloch et al., 2003; Sargis et al., 2005). This conclusion was based on similarities in entocuneiform-first metatarsal morphology shared by these plesiadapiforms and *Ptilocercus*, such as an entocuneiform with a distal facet that is mediolaterally wide on its dorsal aspect, a large plantar process, and a long body (Fig. 2). The entocuneiform of *Plesiadapis* also has a distal facet that is wide on its dorsal aspect and a large plantar process (Szalay and Dagosto, 1988; Sargis, 2002b,c).

Although the morphology of the hallucal tarsometatarsal joint in non-carpolestid plesiadapiforms is similar to that of *Ptilocercus*, the morphology of *Carpolestes* differs drastically from this pattern (Fig. 2; Bloch and Boyer, 2002; Sargis, 2002a, 2004; Sargis et al., 2005). This is contrary to the claim of Gebo (2004) that carpolestids fit the “*Ptilocercus* stage” in his sequence of primate evolution. Rather, *Carpolestes* and *Caluromys* are similar in a number of features of their entocuneiform and hallux, which indicate similar grasping abilities. Specifically, *Carpolestes* and *Caluromys* share a number of features of the entocuneiform that are lacking in *Ptilocercus* and non-carpolestid plesiadapiforms, including a short body and a distal facet with

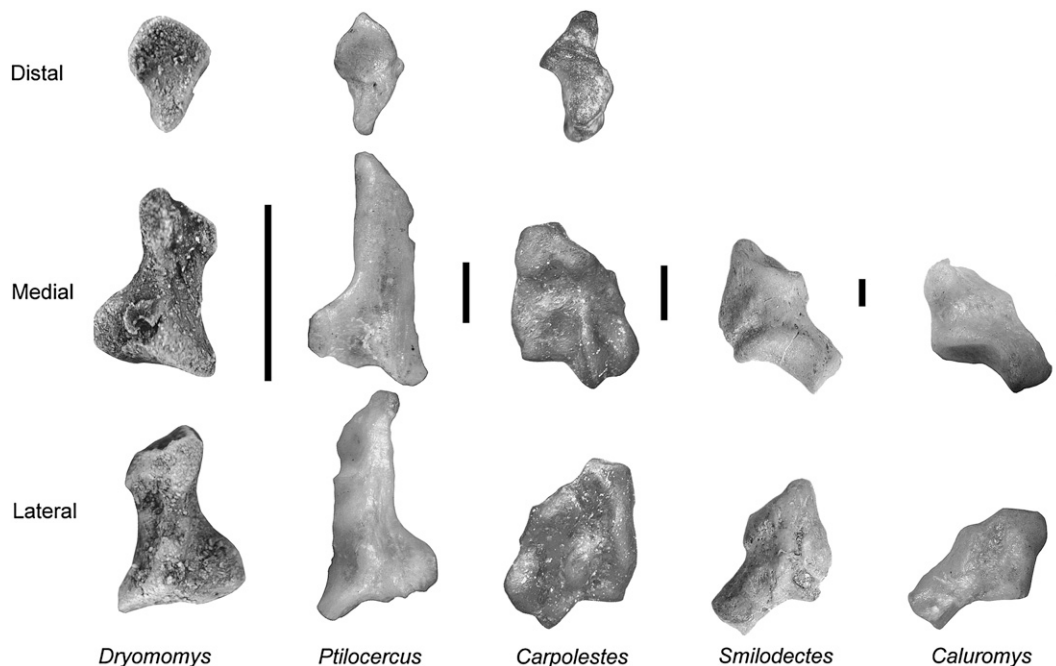


Fig. 2. Left entocuneiforms of *Dryomomys szalayi* (UM 41870), *Ptilocercus lowii* (YPM 4999), *Carpolestes simpsoni* (UM 101963), *Smilodectes mcgrewi* (UM 95526), and *Caluromys philander* (AMNH 234979). Note the wide distal facet (on the dorsal side), large plantar process, and long body in *Ptilocercus* and *Dryomomys*. Also note the saddle-shaped distal facet in *Carpolestes*, *Smilodectes*, and *Caluromys*. Scale = 1 mm.

a dorsal margin that extends farther distally than the plantar margin (making the joint face plantar and giving the hallux some plantar divergence), and that is mediolaterally narrow and saddle-shaped (Fig. 2), permitting a large degree of abduction-adduction. Furthermore, *Carpolestes* differs not only from *Ptilocercus* and other plesiadapiforms but also from *Caluromys* in having a proximally expanded medial surface of the distal facet, which makes it distinctly euprimate-like (Fig. 2; also see Szalay and Dagosto, 1988, for the euprimate condition). Regarding the hallucal metatarsal, both *Carpolestes* and *Caluromys* differ from *Ptilocercus* in that the shaft is more robust and longer compared to the non-hallucal metatarsals. Also, the distal end is rotated laterally to a greater degree so that the shaft exhibits more torsion and the plantar surface of the hallux permanently opposes that of the non-hallucal digits (Fig. 1; Bloch and Boyer, 2002). In both *Carpolestes* and *Caluromys*, the hallucal proximal phalanx is mediolaterally broad and dorsopalmarly flattened, unlike the opposite condition found in *Ptilocercus* (Bloch and Boyer, 2002). Although *Carpolestes* and *Caluromys* both have non-hallucal terminal phalanges with claws, their hallucal terminal phalanges reflect the presence of nails (Bloch and Boyer, 2002). This differs from the condition of the few non-carpolestid plesiadapiforms for which this morphology is known, as they have hallucal terminal phalanges with claws like those of *Ptilocercus*. Based on their similar morphologies, *Carpolestes* was likely capable of opposable pedal grasping in a manner similar to *Caluromys* and euprimates, which behavioral evidence suggests is “powerful”.

The extent to which functionally relevant similarities exist between *Carpolestes* and *Caluromys* contradicts the placement of *Carpolestes* in a “*Ptilocercus* stage.” Gebo (2004) cited the lack of a large peroneal process on the first metatarsal in *Carpolestes* as a distinguishing feature from early Eocene euprimates, but this does not separate *Carpolestes* from *Caluromys* (see above; Fig. 1). Gebo (2004: 56) further cited “other features in the structure of its big toe’s grasping mechanism” to differentiate *Carpolestes* from euprimates, but in the absence of specific morphological features this argument is difficult to assess and does not address his grounds for analogizing *Carpolestes* with *Ptilocercus* rather than *Caluromys*.

To summarize, the pedal grasping mechanism of micromomyid and paromomyid plesiadapiforms is similar to that of *Ptilocercus*, whereas carpolestids have a *Caluromys*-like pedal grasping mechanism. In at least one feature relating to the grasping mechanism, *Carpolestes* differs from other plesiadapiforms and *Caluromys*, such that it is more similar to euprimates. Thus, carpolestids fit the “*Caluromys* stage” (#3) in Gebo’s (2004) sequence (i.e., terminal branch feeders, characterized by an opposable hallux with a nail), not the “*Ptilocercus* stage” (#2).

Grasping in Primate evolution

Here we present an alternative scenario for the evolution of grasping in primates. First, it seems likely that the ancestral euarchontan was similar to *Ptilocercus* in having a capacity for non-opposable pedal grasping (Fig. 3; Table 1; Szalay and Dagosto, 1988; Sargis, 2001, 2002a,b, 2004; Sargis et al.,

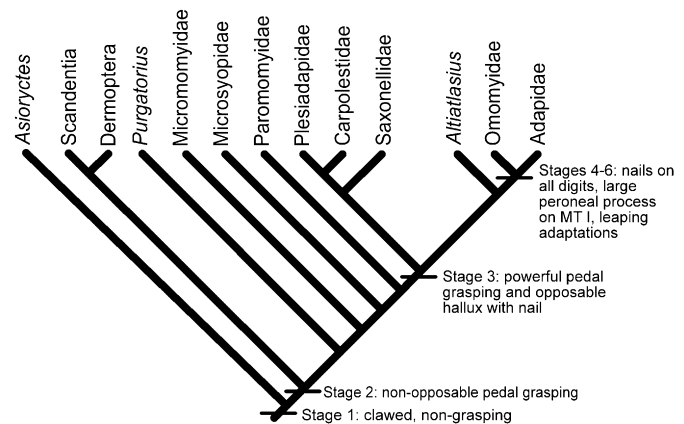


Fig. 3. Hypothesis of relationships for key euarchontan groups taken from the results of an analysis of 173 dental, cranial, and postcranial characters by Bloch et al. (2007), with stages from the right column of Table 1 mapped on. Stem primates like micromomyids and paromomyids are similar to *Ptilocercus*, whereas carpolestids are similar to euprimates and *Caluromys*.

2005). This was probably retained in the ancestor of the Scandentia-Dermoptera clade (Sundatheria; Olson et al., 2005), as well as the ancestral scandentian (Sargis, 2001, 2002b, 2004; Sargis et al., 2005). The morphology of known non-carpolestid plesiadapiforms indicates that a pedal grasping mechanism like that of *Ptilocercus* was also retained in the ancestral primate and earliest stem primates (Table 1; Szalay and Dagosto, 1988; Sargis, 2001, 2002a,b,c, 2004; Bloch and Boyer, 2002, 2007; Bloch et al., 2003; Boyer et al., 2004; Sargis et al., 2005). More powerful pedal grasping, like that of *Caluromys* or euprimates, can be reconstructed as having evolved in the ancestor of the plesiadapoid-euprimate clade (Fig. 3; Table 1; Bloch and Boyer, 2003; Sargis et al., 2005). As detailed above, this condition is present in *Carpolestes* (Table 1; Bloch and Boyer, 2002; Sargis, 2002a, 2004). The small peroneal process of *Carpolestes* likely indicates that it was not a leaper (Bloch and Boyer, 2002), whereas the hypertrophied peroneal process of early Eocene euprimates is probably related to leaping and landing (Szalay and Dagosto, 1988). Finally, the ancestral euprimate may have been characterized by nails on all its digits, leaping adaptations of the hind limb (Fig. 3), and a large peroneal process on its first metatarsal, similar to the conditions found among early Eocene euprimates (Table 1; Szalay and Dagosto, 1988). Although these features may have evolved together as a single complex, there is no evidence contradicting the possibility that they were accrued in a step-like fashion.

In summary, the scenario we propose above differs from Gebo’s (2004) six stage sequence in that our scenario: (1) does not recognize a functional relationship between peroneal process size and powerful grasping, (2) is inferred from a sequence of character acquisition explicitly placed in a phylogenetic context based on recently published analyses (Fig. 3; Table 1; see Springer et al., 2004; Bloch et al., 2007), and (3) relies on detailed comparisons of new plesiadapiform fossils with their extant analogs (e.g., *Ptilocercus* and *Caluromys*). These differences have led us to a different conclusion regarding the evolution of

primate pedal grasping. We expect that future fossil discoveries will allow these alternative scenarios to be further tested.

Acknowledgements

We thank F. S. Szalay, P. Lemelin, and C.J. Terranova for their insights on marsupial and primate grasping, as well as two anonymous reviewers and S.C. Antón for comments that improved the manuscript. Research was funded by grants from NSF (BCS-0129601) to G.F. Gunnell, P.D. Gingerich, and J.I.B.; the Yale University Social Science Faculty Research Fund to E.J.S.; and NSERC to M.T.S.

References

- Argot, C., 2002. Functional-adaptive analysis of the hindlimb anatomy of extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *J. Morphol.* 253, 76–108.
- Bloch, J.I., Boyer, D.M., 2002. Grasping primate origins. *Science* 298, 1606–1610.
- Bloch, J.I., Boyer, D.M., 2003. Response to comment on grasping primate origins. *Science* 300, 741c.
- Bloch, J.I., Boyer, D.M., 2007. New skeletons of Paleocene-Eocene Plesiadapiformes: a diversity of arboreal positional behaviors in early primates. In: Ravosa, M.J., Dagosto, M. (Eds.), *Primate Origins: Adaptations and Evolution*. Springer, New York, pp. 535–581.
- Bloch, J.I., Boyer, D.M., Houde, P., 2003. New skeletons of Paleocene-Eocene micromomyids (Mammalia, Primates): functional morphology and implications for euarchontan relationships. *J. Vert. Paleontol.* 23 (Suppl. to No. 3), 35A.
- Bloch, J.I., Silcox, M.T., Boyer, D.M., Sargis, E.J., 2007. New Paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates. *Proc. Natl. Acad. Sci.* 104, 1159–1164.
- Boyer, D.M., Bloch, J.I., Silcox, M.T., Gingerich, P.D., 2004. New observations on the anatomy of *Nannodectes* (Mammalia, Primates) from the Paleocene of Montana and Colorado. *J. Vert. Paleontol.* 24 (Suppl. to No. 3), 40A.
- Boyer, D.M., Patel, B.A., Larson, S.G., Stern, J.T., 2006. Electromyography of peroneus longus in *Varecia variegata* and *Eulemur rubriventer* helps in grasping primate origins. *Am. J. Phys. Anthropol.* 42 (Suppl.), 68.
- Boyer, D.M., Patel, B.A., Larson, S.G., Stern, J.T. Telemetered electromyography of peroneus longus in *Varecia variegata* and *Eulemur rubriventer*: implications for the functional significance of a large peroneal process. *J. Hum. Evol.*, in press. doi:10.1016/j.jhevol.2006.10.007.
- Gebo, D.L., 1987. Functional anatomy of the tarsier foot. *Am. J. Phys. Anthropol.* 73, 9–31.
- Gebo, D.L., 1989. Postcranial adaptation and evolution in Lorisidae. *Primates* 30, 347–367.
- Gebo, D.L., 2004. A shrew-sized origin for primates. *Yearb. Phys. Anthropol.* 47, 40–62.
- Le Gros Clark, W.E., 1959. *The Antecedents of Man*. Edinburgh University Press, Edinburgh.
- Lemelin, P., 1999. Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. *J. Zool. Lond.* 247, 165–175.
- Lemelin, P., Schmitt, D., Cartmill, M., 2003. Footfall patterns and interlimb co-ordination in opossums (Family Didelphidae): evidence for the evolution of diagonal-sequence walking gaits in primates. *J. Zool. Lond.* 260, 423–429.
- Mivart, St. G., 1873. On *Lepilemur* and *Cheirogaleus*, and on the zoological rank of the Lemuroidea. *Proc. Zool. Soc. Lond.* 1873, 484–510.
- Olson, L.E., Sargis, E.J., Martin, R.D., 2005. Intraordinal phylogenetics of treeshrews (Mammalia: Scandentia) based on evidence from the mitochondrial 12S rRNA gene. *Mol. Phylogenet. Evol.* 35, 656–673.
- Rose, K.D., 1999. Postcranial skeleton of Eocene Leptictidae (Mammalia), and its implications for behavior and relationships. *J. Vert. Paleontol.* 19, 355–372.
- Sargis, E.J., 2001. The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). *J. Zool. Lond.* 253, 485–490.
- Sargis, E.J., 2002a. Primate origins nailed. *Science* 298, 1564–1565.
- Sargis, E.J., 2002b. Functional morphology of the hindlimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. *J. Morphol.* 254, 149–185.
- Sargis, E.J., 2002c. The postcranial morphology of *Ptilocercus lowii* (Scandentia, Tupaiidae): an analysis of primatomorphan and volitantian characters. *J. Mammal. Evol.* 9, 137–160.
- Sargis, E.J., 2004. New views on tree shrews: the role of tupaiids in primate supraordinal relationships. *Evol. Anthropol.* 13, 56–66.
- Sargis, E.J., Bloch, J.I., Boyer, D.M., Silcox, M.T., 2005. Evolution of grasping in Euarchonta. *J. Vert. Paleontol.* 25 (Suppl. to No. 3), 109A.
- Springer, M.S., Stanhope, M.J., Madsen, O., de Jong, W.W., 2004. Molecules consolidate the placental mammal tree. *Tree* 19, 430–438.
- Stern, J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60, 279–317.
- Szalay, F.S., Dagosto, M., 1988. Evolution of hallucial grasping in the primates. *J. Hum. Evol.* 17, 1–33.