11. Evaluating the Mitten-Gliding Hypothesis for Paromomyidae and Micromomyidae (Mammalia, "Plesiadapiformes") Using Comparative Functional Morphology of New Paleogene Skeletons

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11.1 Introduction

11.1.1 Plesiadapiformes: Historical Perspective

Teeth of primate-like mammals from the Paleogene ("plesiadapiforms") have been known for at least 130 years (Gervais, 1877). These fossil taxa are generally recognized as being closely related, but not monophyletic (e.g., Gingerich, 1976; Szalay et al., 1987; Beard, 1993a; Silcox, 2001; Bloch and Boyer, 2002a; Bloch et al., 2007) and we maintain that view here. Thus "plesiadapiforms" are referred to with quotation marks throughout the text to reflect that status. Vertebrate paleontologists have struggled to understand the nature of the phylogenetic relationship of "plesiadapiforms" to the extant and extinct members of crown group Primates [= Euprimates (Hoffstetter, 1977)], since *Plesiadapis* was first described by Gervais in 1877 (e.g., Lemoine, 1887; Stehlin, 1916; Teilhard-de-Chardin, 1922; Gidley, 1923; Simpson, 1935; Russell,

1959; Simons, 1972; Szalay, 1973; Gingerich, 1975, 1976; Szalay et al., 1975; MacPhee et al., 1983; Gunnell, 1989; Kay et al., 1990; Beard, 1993a; Silcox, 2001; Bloch and Boyer, 2002a). The strongest support for a close relationship between "plesiadapiforms" and Euprimates, specifically, has historically come from the excellent fossil record of teeth known for "plesiadapiforms," first in Europe and then in North America (e.g., Gidley, 1923). Cranial and postcranial fossils were relatively rare and fragmentary initially, such that the first researchers were unable to evaluate the presence of non-dental euprimate features in "plesiadapiforms." As non-dental fossils of "plesiadapiforms" were recovered there was some disagreement as to whether they suggested treeshrew or euprimate affinities. A humerus from the San Juan Basin (at the time attributed to *Nothodectes*) was figured by Gregory (1920) and interpreted to fit the "tupaioid" pattern. Later, a crushed skull and additional postcranial material associated with that specimen (and now referred to *Nannodectes gidleyi* Gingerich) was interpreted by Simpson (1935) as being similar to both lemurs and treeshrews. An implication of this acknowledged similarity was that *Nannodectes* spent time in the trees, as expected for the early forebears of

the euprimate clade. However, Simpson (1935) discounted the similarities to treeshrews as being primitive (plesiomorphic), while he emphasized perceived shared-derived (synapomorphic) characters with lemurs as supporting a relationship with Euprimates. At the same time, he rejected any special relationship to *Daubentonia*, an idea that had been seriously considered based on the shared presence of procumbent incisors (Stehlin, 1916; Teilhard-de-Chardin, 1922). Instead, Simpson (1935) attributed this similarity to convergence. He interpreted the procumbent incisors of *Nannodectes* as feeding specializations for a way of life that likely differed in significant respects from that of the euprimates to which he had compared it (*Lemur* and *Notharctus*). He also interpreted the differences between *Nannodectes* and euprimates in other parts of the skeleton to reflect differing ecological specializations. These differences indicated to Simpson that *Nannodectes* could not be the direct ancestor to later occurring euprimates. Description of two skulls of *Plesiadapis tricuspidens*, from Cernay and Berru, France, appeared to support a euprimate relationship in certain characteristics. These included a bony auditory bulla continuous with the petrosal bone, and a thin, ring-like intrabullar component to the ectotympanic bone (Russell, 1959, 1964; Szalay, 1971; Gingerich, 1976; Szalay et al., 1987). Additional cranial material also supported a "plesiadapiform"-euprimate link. Szalay (1972b) described *Phenacolemur jepseni*, and found that it too had a petrosal bulla (although, see MacPhee et al., 1983; Bloch and Silcox, 2001), and additionally, that it had a large posterior carotid canal for the internal carotid artery. He concluded that it would have had a transpromontorial bony tube for this vessel, as in many early Eocene adapoid and omomyoid euprimates. Additional evidence for an arboreal lifestyle began to accumulate with fragmentary postcranials (e.g., Szalay and Decker, 1974).

Even as these specimens were described, providing limited evidence of euprimate features in some "plesiadapiforms," the primate status of the group was being even more seriously questioned by a few influential researchers. Cartmill (1972) provided a definition of Primates, requiring members of the group to possess the full suite of features interpreted by him to reflect the ancestral primate innovation of nocturnal, arboreal, visual predation. These included a postorbital bar with forward facing orbits, petrosal bulla, and a divergent, opposable hallux and pollex bearing a flattened nail (Cartmill, 1972). Martin (1972, 1979) and Cartmill (1972, 1974) noted that plesiadapiforms lacked most of these key "adaptive" features. Szalay (1975) objected to this particular adaptive definition of Primates. He maintained that the more general adaptive similarities (arboreality), and clear evidence for a close phylogenetic relationship required that meaningful definitions of Primates include "plesiadapiforms." Gingerich (1976) supported a primate relationship for "plesiadapiforms," but determined that *Plesiadapis* was likely predominantly terrestrial (but see below), further bolstering Martin and Cartmill's case for removing "plesiadapiforms" from Primates. Later, the existing cranial evidence was challenged by MacPhee et al. (1983) who noted that all known "plesiadapiform" skulls

(1) lacked substantial carotid supply to the forebrain, or even any remnant of the artery (contrary to Szalay, 1972b); and (2) could not be shown to have a petrosally-derived bulla without developmental evidence. Furthermore, MacPhee and Cartmill (1986) argued that extant chinchillids among other rodents (Rodentia; *Lagostomus maximus*) have an ear convergent on that of *Plesiadapis tricuspidens*, including apparent continuity of the bulla and petrosal, and an intrabullar ring-like component to the ectotympanic bone. As a result, the consensus in the field became that "plesiadapiforms" were both adaptively different and phylogenetically disparate (Martin, 1986) from Euprimates. To what group(s) "plesiadapiforms" could be related became the most pressing question surrounding them.

Throughout this "dark" period in understanding, Szalay, his students and collaborators (e.g., Szalay, 1975; Szalay et al., 1975; Szalay and Dagosto, 1980; Szalay et al., 1987; Szalay and Dagosto, 1988) continued to support a euprimate relationship for "plesiadapiforms" based on cranial and postcranial anatomy. They developed adaptive scenarios leading from claw-climbing "plesiadapiforms" (or stem-primates) to grasp-leaping euprimates (e.g., Szalay and Dagosto, 1980).

Given the "lost-sibling" status the anthropological community had assigned to "plesiadapiforms," it is not surprising that new affinities were soon suggested and embraced. A skull of a paromomyid, by far the best-preserved skull ever recovered for any "plesiadapiform" group, was described and analyzed by Kay et al. (1990, 1992). Their cladistic analyses of 33 cranial characters supported a special relationship with Dermoptera (flying lemurs – also known as colugos), a strange order of gliding mammals from Southeast Asia, represented today by two species of a single family (*Cynocephalus volans* and *Galeopterus variegatus*) (Stafford and Szalay, 2000). Among extant mammals, dermopterans have been considered close relatives of euprimates, treeshrews, and bats (e.g., Gregory, 1910). In an independant study of postcranial material, then known for "plesiadapiforms," Beard (1990, 1993a, b) added substantial support to the hypothesis of dermopteran relationships. Furthermore, Beard concluded that certain paromomyid and micromomyid plesiadapiforms were "mitten-gliders" like modern dermopterans. These studies were influential, leading to the widespread acceptance of the phylogenetic hypothesis with some (or all) "plesiadapiforms" classified as dermopterans (e.g., McKenna and Bell, 1997). Certain scientists have remained skeptical of both the cranial support (Wible and Martin, 1993) and postcranial interpretations (Krause, 1991; Szalay and Lucas, 1996; Sargis, 2002c).

Now, over a decade after this view was presented and so convincingly argued, new evidence coming from (1) discovery of new fossils, and (2) new methods for accessing morphological information contained within fossils [e.g., Ultra High Resolution X-Ray Computed Tomography (UhrCT)] suggests that some aspects of original interpretations were in fact *not* wrong, and that some "plesiadapiforms" possess more euprimate-like features than imagined (except possibly by F.S. Szalay), making their primate status harder to dismiss on

both adaptive and phylogenetic grounds. Specifically, in the cranium, an additional "plesiadapiform" (beyond *Plesiadapis tricuspidens*) is now interpreted to be euprimate-like in having a bulla continuous with the petrosal (*Carpolestes simpsoni*; Bloch and Silcox, 2006). Further analysis of the same *Ignacius* skull studied by Kay and others (1990, 1992) with UhrCT showed it to have a bony tube enclosing the internal carotid system (Silcox, 2003). Finally, new carpolestid specimens clearly had an unreduced internal carotid artery with promontory and stapedial branches, based on grooves crossing the promontorium (Bloch and Silcox, 2006). It has also been demonstrated that carpolestids are unique among known "plesiadapiforms" in having a foot with a divergent, opposable hallux tipped with a nail like that of euprimates (Bloch and Boyer, 2002a).

It is notable that, following descriptions of this new material, the original proponents of the "plesiadapiform"-dermopteran link have referred to "plesiadapiforms" as likely "stem-primates" (Kay, 2003: 840), and "primates" (Beard, 2006). It seems reasonable to assume that these changes in view are due largely to the fact that previous characterizations of "plesiadapiforms" could not consider the extent to which the morphologies of *Plesiadapis* (and *Nannodectes*) and paromomyids were different from those of other "plesiadapiforms" because the relevant fossil material was not available. Given the dental diversity of "plesiadapiforms," with remains known for over 120 species classified into 11 or 12 families from the Paleocene and Eocene of North America, Europe, Asia, and possibly Africa (Silcox, 2001), it would not be surprising if there existed a commensurate skeletal diversity yet to be discovered. Szalay (1972a, p.18) recognized this and commented on the need for a taxonomically broader sample of "plesiadapiform" postcranial skeletons, writing:

> "It may be that once postcranial elements of the Paleocene primate radiation become more common, *Plesiadapis* might become recognized as a relatively more aberrant form than the majority of early primates."

In fact, the last 15 years of paleontological research, has validated this prediction (Beard, 1989, 1990, 1993a, b; Bloch and Boyer, 2002a, 2007; Bloch et al., 2007). Various *Plesiadapis* species are currently understood to be generalized arborealists with specializations for vertical clinging and climbing (Gunnell and Gingerich, 1987; Beard, 1989, 1991; Gunnell, 1989; Youlatos and Godinot, 2004). Beard's (1989, 1990, 1993a, b) studies of postcranial elements attributed to paromomyid and micromomyid "plesiadapiforms," led him to conclude that they were mitten-gliders. Recent work on a new carpolestid plesiadapiform skeleton indicated that these animals were different from plesiadapids, paromomyids, and micromomyids in exhibiting capabilities for strong pedal grasping in a manner similar to euprimates (Bloch and Boyer, 2002a; Sargis et al., 2007). While the mitten-gliding hypothesis for paromomyids and/or micromomyids is seriously questioned here and elsewhere (Krause, 1991; Runestad and Ruff, 1995; Szalay and Lucas, 1996; Stafford and Thorington, 1998; Hamrick et al., 1999; Bloch et al., 2001a, 2002b, 2007;

Bloch and Silcox, 2001; Boyer et al., 2001; Bloch and Boyer, 2002b, 2007; Boyer and Bloch, 2002a, b), it is still notable that micromomyids, paromomyids and carpolestids are postcranially distinct from each other and plesiadapids. Moreover, it appears that there is diversity even within Plesiadapidae (Boyer et al., 2004; Bloch and Boyer, 2007).

Even with these new finds, it is likely that we are barely scratching the surface of the full skeletal diversity that existed in either "plesiadapiforms" or basal euprimates. As more and better fossils are recovered, they are bound to influence and change our views of phylogenetic relationships. Thus, whether "plesiadapiforms" share a special relationship with dermopterans, euprimates, or neither will be debated far into the foreseeable future. We do not address that subject in this paper. Szalay has emphasized what is generally recognized by paleobiologists, that:

> "…one can often corroborate far better the adaptive strategies of fossil species than their phylogenetic affinities" (Szalay and Sargis, 2001: p.153).

While we do not claim to evaluate "adaptations," exclusively, we *do* evaluate functional morphology to address a more immediately testable hypothesis regarding inferred postional behaviors of some "plesiadapiforms." Simply, we ask the question: ***Do new skeletons of micromomyid and paromomyid "plesiadapiforms" support the hypothesis of "mitten-gliding" proposed by Beard (1989, 1990, 1991, 1993b)?*** We acknowledge that, while we certainly think we can shed some light on this particular subject, the answers to this question will not resolve the phylogeny of the group. Instead, we sincerely hope that this study will be of some interest to those of you interested in the paleoecology of Paleogene mammals, and who "just want to know."

11.1.2 Conceptual Framework

We use comparative functional morphology to address the question presented above within the conceptual framework (as we understand it) carefully outlined by Szalay for analyzing fossil taxa (e.g., Szalay and Drawhorn, 1980; Szalay and Dagosto, 1988; Szalay and Sargis, 2001). Szalay has derived justification for form-function relationships from John Stuart Mill (1872) and referred extensively to the writings of Bock (1977, 1981, 1988, 1991, 1993, 1999; Szalay and Bock, 1991) and Bock and von Wahlert (1965) to define his approach to functional-adaptive analyses. He championed the tenet that elucidating aspects of functional morphology and phylogeny are not separate endeavors, and one should not precede the other in reconstructing the evolutionary history of a group of animals (e.g., Szalay, 1977, 1981; Szalay and Lucas, 1996; Szalay, 1998, 2000; Szalay and Sargis, 2001). He contended that they are "temporally looped" (Szalay and Sargis, 2001, p. 152).

He emphasized that cladistic analyses lack the power to reveal adaptive trends (Szalay, 1981; Szalay and Bock, 1991; Szalay, 2000). On the other hand, he stressed that biological roles and adaptive significance of skeletal features in fossils cannot be

inferred without a thorough appreciation of the evolutionary history of the clade to which the fossil under study belongs. He continually stressed the fact that organisms are comprised of features related to heritage and habitus (e.g., Szalay, 1981; Szalay and Sargis, 2001), those related to habitus being of most value for reconstructing biological roles, yet ineluctable without the context of the features of heritage (those reflecting previous biological roles of ancestral lineages). While he recognized the existence of "heritage" features, he did not believe in "phylogenetic baggage", or non-functional skeletal features. He saw natural selection's effect on morphology as powerful and capable of keeping pace with environmental change in most situations (Szalay and Sargis, 2001) such that the morphology of an organism should, at the very least, not contradict its ability to engage in its observed postional behaviors, if not support those observations (based on mechanical predictions or comparative observations). He took the historic observation of striking convergence among distantly phylogenetically separated mammalian groups as evidence for his view of the interaction between evolving populations, environmental change and natural selection. Ultimately, he endorsed the comparative method, in which observation of similar osteological forms among a diversity of mammals also characterized by similar functions (*sensu* Plotnick and Baumiller, 2000) or faculties, (*sensu* Bock and von Wahlert, 1965) establishes a form-function relationship that can be used to infer the presence of function and faculty in extinct forms (what he referred to as a "model-based approach" Szalay and Sargis, 2001).

He spurned the superficially similar practice of associating morphological features with particular biological roles without consideration of their adaptive (versus exaptive) status (Szalay, 1981), and emphasized that different characters and character complexes had different relative importance for reconstructing certain biological roles (Szalay, 1981). For instance, it had been suggested that dental and cranial features suggesting faunivory in the "plesiadapiform" *Palaechthon* also implied that this animal was a terrestrialist who spent its life "nosing" its way through the leaf litter (Kay and Cartmill, 1977). But Szalay (1981) saw craniodental features as basically irrelevant to the question of substrate preference in this case. Evidence from the postcranium, indicating arboreality in other "plesiadapiforms" suggested more strongly to him that *Palaechthon* was likely arboreal as well (Szalay, 1981).

In this study, we focus on evaluating positional (locomotor and postural) behaviors of paromomyids and micromomyids. Ultimately, we speculate about biological roles (Bock and von Wahlert, 1965) of inferred positional behaviors, but only after also considering what craniodental morphology suggests about food preferences and feeding behaviors.

A given positional behavior is characterized by various static and dynamic functions (*sensu* Plotnick and Baumiller, 2000) or faculties (*sensu* Bock and von Wahlert, 1965). Functions often have osteological correlates identifiable through mechanical modeling and the comparative method. However, identification of a correlate to a particular function in a fossil does not

typically go very far towards elucidating positional behaviors because most functions are required by more than one positional behavior. For instance, taxa that utilize two very different positional behaviors, "quadrumanus suspension" and "terrestrial quadrupedal cursoriality" are characterized by elbow joints that share a static function: the capacity for full extension. But this is not to say these two groups are identical in their functional requirements: for example, unlike suspensory taxa, cursors are also characterized by the capacity for fast, sagittal extension of the femur, a dynamic function.

Thus, a hypothesis of positional behavior can be tested effectively by examining the skeleton for the presence of osteological correlates to a *suite* of functions that characterize the proposed behavior. The lack of osteological correlates of a function rules out its presence in a fossil. Likewise, positional behaviors that require those functions will also be refuted. From the example above, if, in a fossil taxon of interest, the elbow joint had features suggesting that it could be fully extended and the femur lacked osteological correlates of fast powerful extension, we could fairly confidently refute use of cursorial behaviors, but not suspensory ones.

Thus, summarizing various functional features in a fossil generates a limiting hypothesis regarding its positional behaviors. That is, some positional behaviors will be refuted while others will remain plausible, if not specifically supported. The discovery of additional functional attributes not predicted for the un-refuted positional behaviors does not then rule out those behaviors as well, unless such attributes somehow compromise one of the other required functions. Such "extra" features likely correspond to "adaptive" traits of an organism and thus may help elucidate the biological roles of these un-refuted positional behaviors (Szalay, 1981). For instance, if the fossil taxon under consideration had selenodont teeth indicating folivory and postcranial features indicating suspensory postures, we might speculate that the biological role of suspensory postures was to allow access to leaves on terminal branches.

Finally, the functional demands and morphological correlates of some positional behaviors may be poorly understood, as in the case of "mitten-gliding," the subject of focus in this study. However, such positional behaviors may be associated with others, the morphological indications of which are better understood [in this case quadrumanus suspensory behaviors are associated with mitten-gliding (Pocock, 1926; Beard, 1989)]. The presence of suspensory features in a fossil taxon would not positively support mitten-gliding, but the lack of them would definitely refute it.

11.1.3 Main Objectives and Summary of Findings to be Demonstrated

As indicated above, our main objective is to test Beard's (1989, 1990, 1991, 1993b) hypothesis of mitten-gliding for paromomyid and micromomyid "plesiadapiforms." While others have carried out studies with the same goal (Krause, 1991; Runestad and Ruff, 1995; Hamrick et al., 1999), this is the first such

study that applies new postcranial material with documented craniodental associations (see below). The only extant mammal currently referred to as a "mitten-glider" is the dermopteran *Cynocephalus*. Unlike other gliding mammals (but similar to bats), dermopterans possess an inter-digital patagium, which gives their digits the appearance of being united, roughly similar in form to the hand of a person wearing a mitten. Beard (1993b) argued that this "mitten" has a critical role in adjusting the aerodynamic properties of the animal during gliding. Specifically, the mitten's most critical function was said to be its affect on billowing of the patagium. Thus, Beard suggested that the unique termination point for the patagium in *Cynocephalus*, compared to other gliders, had influenced the morphology of the phalanges by placing unusual mechanical demands on them. When it is not gliding, *Cynocephalus* utilizes quadrumanus suspension to forage for leaves or to rest, and bimanual suspension while urinating or defecating (Wharton, 1950). Beard further suggested that the mechanical demands of these suspensory resting/foraging postures had also influenced the phalangeal morphology, resulting in a functional complex of features relating to mitten-gliding and suspension that is unique to dermopterans among extant mammals. As Beard explained:

"Some of the unusual features of the manus of extant *Cynocephalus* are clearly functionally related to the mode of attachment of the patagium to the manus in this genus" (Beard, 1989, p.441)

"…some of the unusual features of the hand skeleton of this genus also appear to reflect its emphasis on suspensory postures and locomotion" (Beard, 1989, p.442)

"…the total morphology of the hands of *Cynocephalus* is an anatomical compromise that in several ways is unique among extant mammals." (Beard, 1989, p.442).

While Beard's explanation is plausible and accepted by us in general, Runestad and Ruff (1995) demonstrated that *Cynocephalus* is also similar to other gliding mammals (regardless of attachment point of the patagium) in having elongate limb bones. Stafford (1999) supported this conclusion and observed more points of similarity between dermopterans and other gliding mammals. In this study, we present evidence that agrees with the observations of these authors, showing that *Cynocephalus* and other gliding eutherian mammals are morphologically similar in many respects. Thus, we would modify Beard's functional explanation of dermopteran morphology by adding that much of the skeleton has additionally been influenced by the mechanical demands for gliding, despite differences in patagial attachment points.

Beard (1989, 1990, 1993b) observed that a number of otherwise rare morphological features of dermopterans potentially unite them with fossil paromomyids and micromomyids. He argued that these shared features reflected the shared presence of the dermopteran functional complex.

The new paromomyid skeletons presented here indicate that these mammals were drastically different from *Cynocephalus* in their positional behavior. Specifically, we demonstrate that (1) they are distinctly unlike living dermopterans in lacking all osteological correlates specific to gliding with an interdigital patagium or associated quadrupedal suspension (Pocock, 1926; Beard, 1993b), and (2) they lack more general osteological correlates to gliding found in *Cynocephalus*, as well as gliding rodents and in some cases gliding marsupials. Likewise, new skeletons of micromomyids lack mitten-gliding features and features unambiguously suggestive of dermopteran-like quadrupedal suspension. While micromomyids are similar to dermopterans and gliding sciurids in some other respects, many of these features are also found in the extant, primitive treeshrew *Ptilocercus lowii* (Sargis, 2002a, b, c), primitive euprimates, and taxa likely to represent euarchontan outgroups (Hooker, 2001; Meng et al., 2004; Rose and Chinnery 2004). Thus, in the context of still other features that appear inconsistent with a capacity for gliding, we are unable to entertain the possibility that micromomyids were gliders of any sort.

11.1.4 Institutional Abbreviations

AMNH	American Museum of Natural History, New York
CR	Cernay-lès-Reims (for MNHN specimens from that locality)
MNHN	Muséum Nationale d'Histoire Naturelle, Paris
UA	University of Alberta Laboratory or Vertebrate Paleontology, Edmonton
UCMP	University of California at Berkeley, Museum of Paleontology, Berkeley
UF	University of Florida Museum of Natural History, Gainesville
UKMNH	University of Kansas Museum of Natural History, Lawrence
UM	University of Michigan Museum of Paleontology, Ann Arbor (specimen reference)
UMMP	University of Michigan Museum of Paleontology, Ann Arbor (institution reference)
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum Department of Paleobiology (Smithsonian Institution), Washington, DC
UW	University of Wyoming, Laramie
YPM	Peabody Museum of Natural History, Yale University, New Haven
YPM-PU	Princeton University collections at the Peabody Museum of Natural History, Princeton

11.2 Materials

In this study we observed and measured a number of fossil and extant mammalian osteological specimens, mainly from the UMMP and UMMZ collections respectively, however, other specimens from institutions given in the abbreviations were also examined. New fossil material focused on here includes *Ignacius clarkforkensis* UM 108210, 82606, *Acidomomys hebeticus* UM

108207 [all from UM locality SC-62 (1335 m above Cretaceous-Tertiary boundary in the Clarks Fork Basin): Clarkforkian (Cf)-2, North American Land Mammal Age (NALMA)], *Dryomomys szalayi* UM 41870 [from UM locality SC-327 (1420 m), Cf-3], and a currently uncatalogued cf. *Tinimomys graybulliensis* specimen from a Wasatchian-1 aged locality in the Clarks Fork Basin. Detailed locality information for these specimens is archived with the UMMP. Additionally, Appendix I provides a list of all known paromomyid and micromomyid postcranial material, some of which is also focused on here. Specifically, we also incorporate information from dentally-associated remains of *Phenacolemur praecox* (UM 66440, 86352), *Phenacolemur jepseni* (USGS 17847), and *Tinimomys graybulliensis* (UM 85176); and some isolated remains attributed to *Phenacolemur simonsi* (USNM 442260, 62) and *Ignacius graybullianus* (USNM 442259) (Beard, 1989). Fossil specimens used for comparative purposes include plesiadapiforms (*Carpolestes simpsoni* UM 101963, *Nannodectes gidleyi* AMNH 17379, *Nannodectes intermedius* USNM 442229, *Plesiadapis cookei* UM 87990), euprimates (*Smilodectes mcgrewi* UM 95526, *Omomys carteri* UM 14134, *Omomys sp*. UM 98604), and dentally-associated postcranial material from an uncatalogued nyctitheriid insectivoran from UM locality SC-327.

Appendix II, Table 1 is a comprehensive list of all specimens measured, observed or figured in the course of this study, including those listed above. All quantitative analyses and all figures with more than four specimens are represented by a column in this table. If a specimen was included in a given analysis or figure, this is indicated by an "x" in the row corresponding to that specimen in the appropriate column.

11.3   Methods

11.3.1   Documentation Of Association in New Specimens

Fossils were extracted from limestone nodules of the Clarks fork basin using acid reduction. The protocol by which this process was carried out and that by which dental, cranial and postcranial associations were documented is described in Bloch and Boyer (2001, 2007).

11.3.2   Functional Analysis: Evaluation of the Gliding Hypothesis

We carried out functional analyses using the comparative method (Bock, 1977; Szalay and Sargis, 2001) and with analytical and statistical techniques including regression, ANOVA, students t-tests and principal components analysis (Sokal and Rohlf, 1997). Morphology was quantified and compared using indices in many cases (e.g., intermembral index). For statistical comparisons, such indices were logged, because this transformation tended to make the distributions of these data normal. We used the software PAST and SPSS

11.0 to carry out statistical analyses, for which the accepted level of significance was 95% or better.

Other comparisons were made based on qualitative morphology or with too few specimens to assign a level of statistical significance to our observations. However, in such cases, the differences between gliding and/or suspensory taxa and those taxa that lack these locomotor repertoires were substantial.

Throughout the text we provide tables that list the key functional characters evaluated in each region of the skeleton. The state of each character is coded for a number of different generalized "locomotor/behavior categories" of modern mammals in each table. Character states that are shared by different locomotor/behavioral groups are inferred to reflect common functions among those groups (if not shared behaviors). With this method we draw conclusions such as the following: elongate intermediate phalanges and restricted mobility at the proximal interphalangeal joint in *Cynocephalus* are likely correlates of suspensory behaviors, not mitten gliding, because the two other taxa that share such features suspend themselves from their hands and/or feet, but are not mitten-gliders (see Table 11.4).

11.4   Results and Discussion

11.4.1   Documentation of Association in New Specimens

11.4.1.1   *Acidomomys hebeticus*

UM 108207. We began preparation of the cranium of *Acidomomys hebeticus* from limestone in 1999 (Bloch and Boyer, 2001: Figures 11.8, 11.11). The preparation took roughly a year and revealed other individuals of *Acidomomys hebeticus*, as well as craniodentally associated postcrania for several other taxa, including *Carpolestes simpsoni* (UM 101963; Bloch and Boyer, 2002a). Initially, it was difficult to identify postcrania for *A. hebeticus* because of its proximity with several animals of similar size (Figures 11.1 and 11.2). Fortunately, parts of the *A. hebeticus* skeleton were in semi-articulation and associated with cranial remains (Figure 11.1A). Having a portion of the skeleton articulated and associated allowed for identification of form, ontogenetic stage and preservational quality of the postcranials. With this information we were able to identify other less well-associated postcranials. *A. hebeticus* is represented by at least three individuals in the accumulation (Bloch et al., 2002a). All are juveniles in various stages of erupting their adult dentitions (UM 108206-8). UM 108207 is represented by a skull and dentaries; distal, intermediate and proximal phalanges of the hand and foot; metacarpals I and V; right and left scaphoids; astragalus; right radius, ulna and distal humeral fragment. Of these elements, the radius, ulna, scaphoids, metacarpals, four proximal phalanges, and three intermediate phalanges are confidently attributed to a single individual (Figures 11.1 and 11.2). Other phalanges, not associated with forelimb

TABLE 11.1. Measurements of "plesiadapiform" proximal phalanges, proximal phalanx length (PPL); intermediate phalanges, intermediate phalanx length (IPL) and mid-shaft area (MSA); and metapodials, metapodial length (MPL) are given in this table. Bold lettering indicates that the measurements are analyzed or plotted in one of the figures. Columns titled "Fig" give the figure number showing a particular specimen with its original skeletal associations, as well as the label or location of that specimen in the figure. Only paromomyids and the micromomyid have information recorded in these columns. For the micromomyid all specimens are shown in Figure 11.6c. The side of the body to which the element was attributed is also given (left-L or right-R). Raw measurements include precisely measured length on pristine specimens, approximately (~) measured length on badly damaged specimens, or estimated {est} length of incomplete specimens. Part of the identification criteria for *Acidomomys hebeticus* was the juvenile status of the elements attributed to it. As such, most measurements do not include proximal end epiphyses. The proximal phalanx epiphyses add from 0.51–0.68 mm to the proximodistal length of these elements. The intermediate phalanx proximal epiphyses are shorter ranging from 0.4–0.51 mm. If a measurement on a particular specimen was not taken, because it was not possible due to breakage), this is indicated by "nm" (not measured). The "autopod" column is coded to indicate whether a specimen is attributed to hand (1) or foot (2). "Ray" gives the digit ray to which an element belongs. In most cases, associations and morphology are not distinctive enough to give a position, and a "?" is put here. First digits and metapodials are exceptions. In Figure 11.8, intermediate phalanx lengths are compared to proximal phalanx lengths to evaluate the probable interphalangeal proportions of these specimens. Intermediate-proximal phalanx pairs used in that analysis occupy single rows in the table.

Catalogue number	Family	Taxon	Figure	Autopod	Ray	PPL	Figure	Autopod	Ray	IPL	MSA	Figure	Autopod	Ray	MPL
UM 101963 **7.18**	**Carpolestidae**	**Carpolestes simpsoni**		**1**	**3**	**6.61**		**1**	**3**	**4.60**	**0.42**		**1**	**3**	
UM 101963	**Carpolestidae**	**Carpolestes simpsoni**		2	5	**6.60**		2	5	**5.05**	**0.41**		2	3	7.40
UM 101963	Carpolestidae	Carpolestes simpsoni		2	3	5.82		2	3	3.88	nm				
UM 101963	Carpolestidae	Carpolestes simpsoni		2	4	5.62		2	4	3.80	nm				
UM 101963	Carpolestidae	Carpolestes simpsoni		2	2	6.26		2	2	4.00	nm				
UM 101963	Carpolestidae	Carpolestes simpsoni		2	1	4.85		2	1	3.24	nm				
UM 41870	**Micromomyidae**	**Dryomomys szalayi**	**R (Fig. 6)**	**1**	**?**	**2.91**	**L (Fig. 6)**	**1**	**?**	**2.56**	**0.10**	**m-1 (Fig. 6)**	**1**	**3**	**3.73**
UM 41870	**Micromomyidae**	**Dryomomys szalayi**	**L (Fig. 6)**	**1**	**?**	**3.03**	**L (Fig. 6)**	**1**	**?**	**2.70**	**0.09**				
UM 41870	Micromomyidae	Dryomomys szalayi	L (Fig. 6)	1	?	3.07	L (Fig. 6)	1	?	2.72	0.09				
UM 41870	**Micromomyidae**	**Dryomomys szalayi**	**R (Fig. 6)**	**1**	**?**	**2.97**	**R (Fig. 6)**	**1**	**?**	**2.61**	**0.09**				
UM 41870	**Micromomyidae**	**Dryomomys szalayi**	**R (Fig. 6)**	**1**	**?**	**2.88**	**R (Fig. 6)**	**1**	**?**	**2.53**	**0.11**				
UM 41870	**Micromomyidae**	**Dryomomys szalayi**	**L (Fig. 6)**	**1**	**?**	**3.07**	**L (Fig. 6)**	**1**	**?**	**2.74**	**0.09**				
UM 41870	**Micromomyidae**	**Dryomomys szalayi**	**R (Fig. 6)**	**1**	**?**	**3.10**	**R (Fig. 6)**	**1**	**?**	**2.78**	**0.09**				
UM 41870	Micromomyidae	Dryomomys szalayi	L (Fig. 6)	1	1	2.84				nm	nm				
UM 41870	Micromomyidae	Dryomomys szalayi	R (Fig. 6)	2	?	3.17	R (Fig. 6)	2	?	2.79	nm	p-1 (Fig. 6)	2	3	5.09
UM 41870	Micromomyidae	Dryomomys szalayi	R (Fig. 6)	2	?	3.18	R (Fig. 6)	2	?	2.82	nm				
UM 41870	Micromomyidae	Dryomomys szalayi	R (Fig. 6)	2	?	3.11	R (Fig. 6)	2	?	nm	nm				
UM 41870	Micromomyidae	Dryomomys szalayi	R (Fig. 6)	2	?	3.00	R (Fig. 6)	2	?	nm	nm				
UM 41870	Micromomyidae	Dryomomys szalayi	L (Fig. 6)	2	?	2.97	L (Fig. 6)	2	?	2.73	nm				
UM 41870	Micromomyidae	Dryomomys szalayi	L (Fig. 6)	2	1	2.70				nm	nm				
UM 41870	Micromomyidae	Dryomomys szalayi	R (Fig. 6)	2	1	2.70				nm	nm				
UM 108207	**Paromomyidae**	**Acidomomys hebeticus**	**12 (Fig. 1)**	**1**	**?**	**{est} 6.27**	**1 (Fig. 1)**	**1**	**?**	**4.82**	**0.43**				
UM 108207	**Paromomyidae**	**Acidomomys hebeticus**	**6 (Fig. 1)**	**1**	**?**	**{est} 6.75**	**2 (Fig. 1)**	**1**	**?**	**~6.12**	**nm**				
UM 108207	**Paromomyidae**	**Acidomomys hebeticus**	**7 (Fig. 1)**	**1**	**?**	**5.90**	**3 (Fig. 1)**	**1**	**?**	**~4.80**	**0.52**				
UM 108207	**Paromomyidae**	**Acidomomys hebeticus**	**5 (Fig. 1)**	**1**	**?**	**{est} 6.3**	**11 (Fig. 1)**	**1**	**4**	**5.50**	**0.44**				
UM 108207	**Paromomyidae**	**Acidomomys hebeticus**	**9 (Fig. 1)**	**1**	**?**	**{est} 6.3**	**13 (Fig. 1)**	**1**	**5**	**5.30**	**0.43**				
UM 108207	Paromomyidae	Acidomomys hebeticus	8 (Fig. 1)	1	1	5.5									
UM 108207	Paromomyidae	Acidomomys hebeticus	15 (Fig. 2)	2	?	6.69	16 (Fig. 2)	2	2	6.51	nm				
UM 108207	Paromomyidae	Acidomomys hebeticus	17 (Fig. 2)	2	?	{est} 7.3	18 (Fig. 2)	2	4	~6.3	nm				
UM 108207	Paromomyidae	Acidomomys hebeticus	19 (Fig. 2)	2	1	5.21	20 (Fig. 2)	2	3	6.48	nm				
UM 108207	Paromomyidae	Acidomomys hebeticus	20 (Fig. 2)	2	?	6.84	21 (Fig. 2)	2	5	6.5	nm				
UM 108207	Paromomyidae	Acidomomys hebeticus	22 (Fig. 2)	2	?	6.77		2	?		nm				
UM 108210	Paromomyidae	Ignacius clarkforkensis	5 (Figs. 3, 5)	1	?	10.30	1 (Figs. 3, 5)	1	?	nm		Figs. 3, 5	1	3	{est} 10.30

(continued)

TABLE 11.1. (continued)

| Catalogue number	Family	Taxon	Figure	Autopod	Ray	PPL	Figure	Autopod	Ray	IPL	MSA	Figure	Autopod	Ray	MPL
UM 108210	**Paromomyidae**	***Ignacius clarkforkensis***	**4 (Figs. 3, 5)**	**1**	**?**	**10.80**	**2 (Figs. 3, 5)**	**1**	**?**	**~7.95**	**0.77**				
UM 108210	**Paromomyidae**	***Ignacius clarkforkensis***	**8 (Figs. 3, 5)**	**1**	**?**	**10.70**	**7 (Figs. 3, 5)**	**1**	**?**	**7.80**	**0.78**				
UM 108210	Paromomyidae	*Ignacius clarkforkensis*	6 (Figs. 3, 5)	1	5	8.30	3 (Figs. 3, 5)	1	?	nm					
UM 82606	Paromomyidae	*Ignacius clarkforkensis*	Figs. 3, 5	1								Figs. 3, 5	2	2	15.3
UM 87990	**Plesiadapidae**	***Plesiadapis cookei***		**1**	**?**	**15.22**		**1**	**?**	**12.11**	4.37		1	3	23.54
UM 87990	**Plesiadapidae**	***Plesiadapis cookei***		**1**	**?**	**12.70**		**1**	**?**	**10.30**	3.55				
UM 87990	Plesiadapidae	*Plesiadapis cookei*		1	?	15.17		1	?						
UM 87990	Plesiadapidae	*Plesiadapis cookei*		2	?	17.27		2	?	13.39	nm		2	3	31.10
UM 87990	Plesiadapidae	*Plesiadapis cookei*		2	?	17.27		2	?	13.39	nm		2	3	31.10
UM 87990	Plesiadapidae	*Plesiadapis cookei*		2	?	17.64		2	?	13.80	nm				
USNM 442229	Plesiadapidae	*Nannodectes intermedius*		1	1	6.95		1	1						
USNM 442229	Plesiadapidae	*Nannodectes intermedius*		1	1	6.95		1	1						
USNM 442229	**Plesiadapidae**	***Nannodectes intermedius***		**1**	**?**	**8.59**		**1**	**?**	**6.72**	**1.22**		1	3	11.50
USNM 442229	Plesiadapidae	*Nannodectes intermedius*		1	?	8.09		1	?	7.18					
USNM 442229	Plesiadapidae	*Nannodectes intermedius*		1	?	7.63		1	?						
USNM 442229	Plesiadapidae	*Nannodectes intermedius*		2	?	9.11		2	?						
USNM 442229	**Plesiadapidae**	***Nannodectes intermedius***						**2**	**?**	**7.10**	**0.95**				
USNM 442229	Plesiadapidae	*Nannodectes intermedius*						2	?	7.39	nm				
AMNH 17379	**Plesiadapidae**	***Nannodectes gidleyi***		**1**	**?**	**9.17**		**1**	**?**	**6.88**	**0.91**		1	3	12.02
AMNH 17379	Plesiadapidae	*Nannodectes gidleyi*		1	?	8.63									
AMNH 17379	**Plesiadapidae**	***Nannodectes gidleyi***		**2**	**?**			**2**	**?**	**8.26**	**1.03**				
AMNH 17379	**Plesiadapidae**	***Nannodectes gidleyi***		**2**	**?**			**2**	**?**	**7.19**	**0.84**				
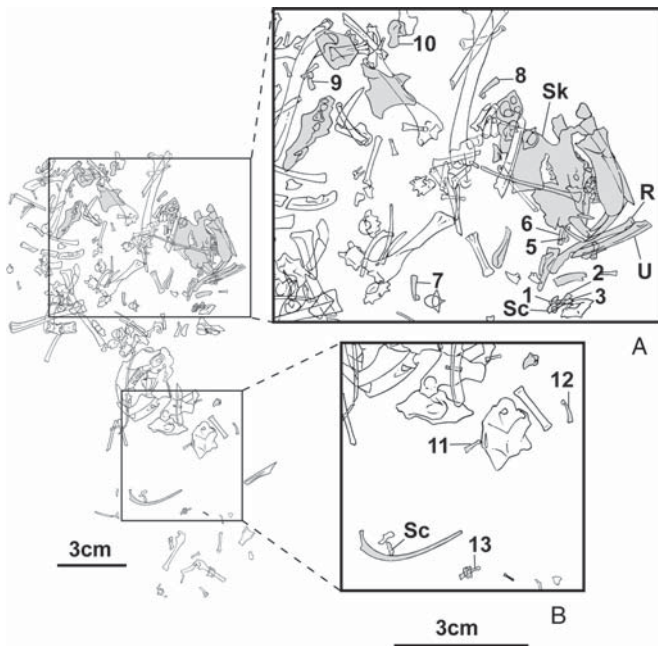
FIGURE 11.1. Documentation of association of *Acidomomys hebeticus* skeleton. Map of bones in upper layer of limestone "Block M," from the Clarks Fork Basin locality SC-62. Elements identified as *Acidomomys hebeticus* (UM 108207) are depicted in gray. A, Enlarged view to show articulated radius (R) and ulna (U) in association with proximal phalanges 5 and 6, intermediate phalanges 1–3 and a scaphoid (Sc), below the crushed skull (Sk). *A. hebeticus* was distinguished from other animals in the accumulation on the basis of associations, size, age and taphonomic state. *A. hebeticus* is a juvenile with porous bone, while the other taxa are adults. Bones not attributed to *A. hebeticus* are attributed to two or more individual paramyid rodents. Lengths and length estimates of phalanges are reported in Table 11.1. Scale = 3 cm.

FIGURE 11.2. Documentation of association of *Acidomomys hebeticus* skeleton. Map of bones in lower layer of limestone "Block M" (see Figure 11.1). Elements identified as *Acidomomys hebeticus* (UM 108207) are depicted in gray. Bones not attributed to *A. hebeticus* belong to a large rodent, an erinaceomorph insectivore, a carpolestid plesiadapiform, or a small marsupial. Lengths and length estimates of phalanges are reported in Table 11.1. Scale = 3 cm.

elements and with consistently different proportions than those that were associated with the forelimb (although still clearly belonging to *A. hebeticus*), are interpreted as pedal phalanges (Figures 11.1 and 11.2). The pedal elements are longer than the manual ones. Table 11.1 gives measurements of phalanges attributed to UM 108207, depicted and labeled in Figures 11.1 and 11.2.

11.4.1.2 Ignacius clarkforkensis

UM 108210. (Holotype; Bloch et al., 2007) Associated dentitions and postcranium were preserved in their original positions in a freshwater limestone from University of Michigan locality SC-62 (Figure 11.3A).

UM 82606. This specimen is also from SC-62. While relative locations of UM 108210 to UM 82606 are undocumented, these specimens cannot represent the same individual, because each preserves an astragalus from the same side of the body (right side). In fact UM 82606 lacks association with teeth (Figure 11.3B), and was identified as
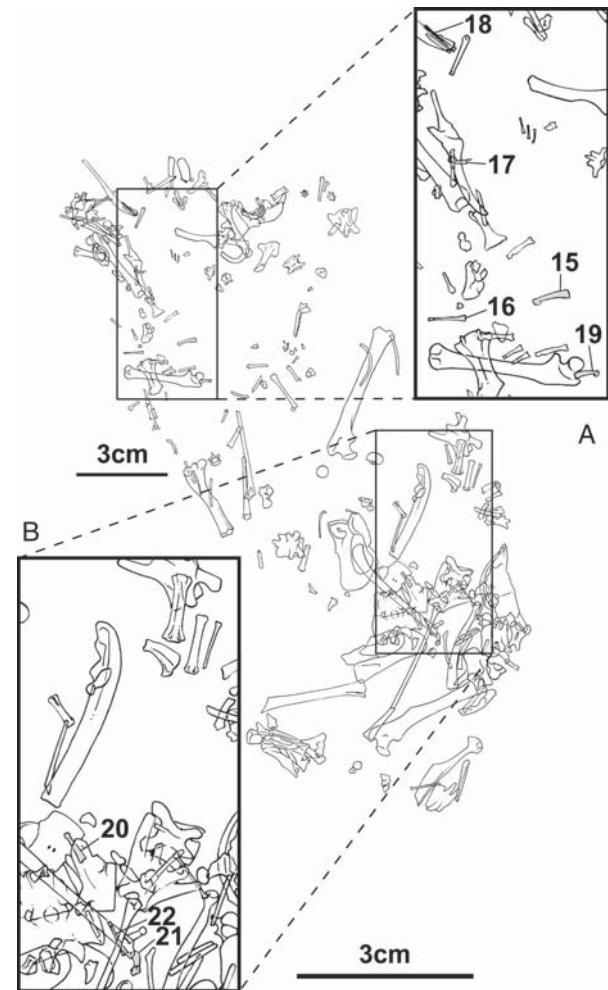
belonging to *Ignacius clarkforkensis* based on (1) size and form of the astragalus (Figure 11.4) and calcaneum, which are nearly identical to those of UM 108210, and (2) by the similarity in hind limb morphology to that of previously described paromomyids (Beard, 1989).

Analysis of this specimen combined with UM 108210 allowed estimates of interlimb and inter body-segment proportions. We justify the use of these specimens as a composite based on the similar astragalus size and the fact that different long bones from each specimen yield overlapping body mass estimates. Together, these two specimens allow analysis of nearly the entire morphology and proportions of a composite individual of *Ignacius clarkforkensis* (Figure 11.5).
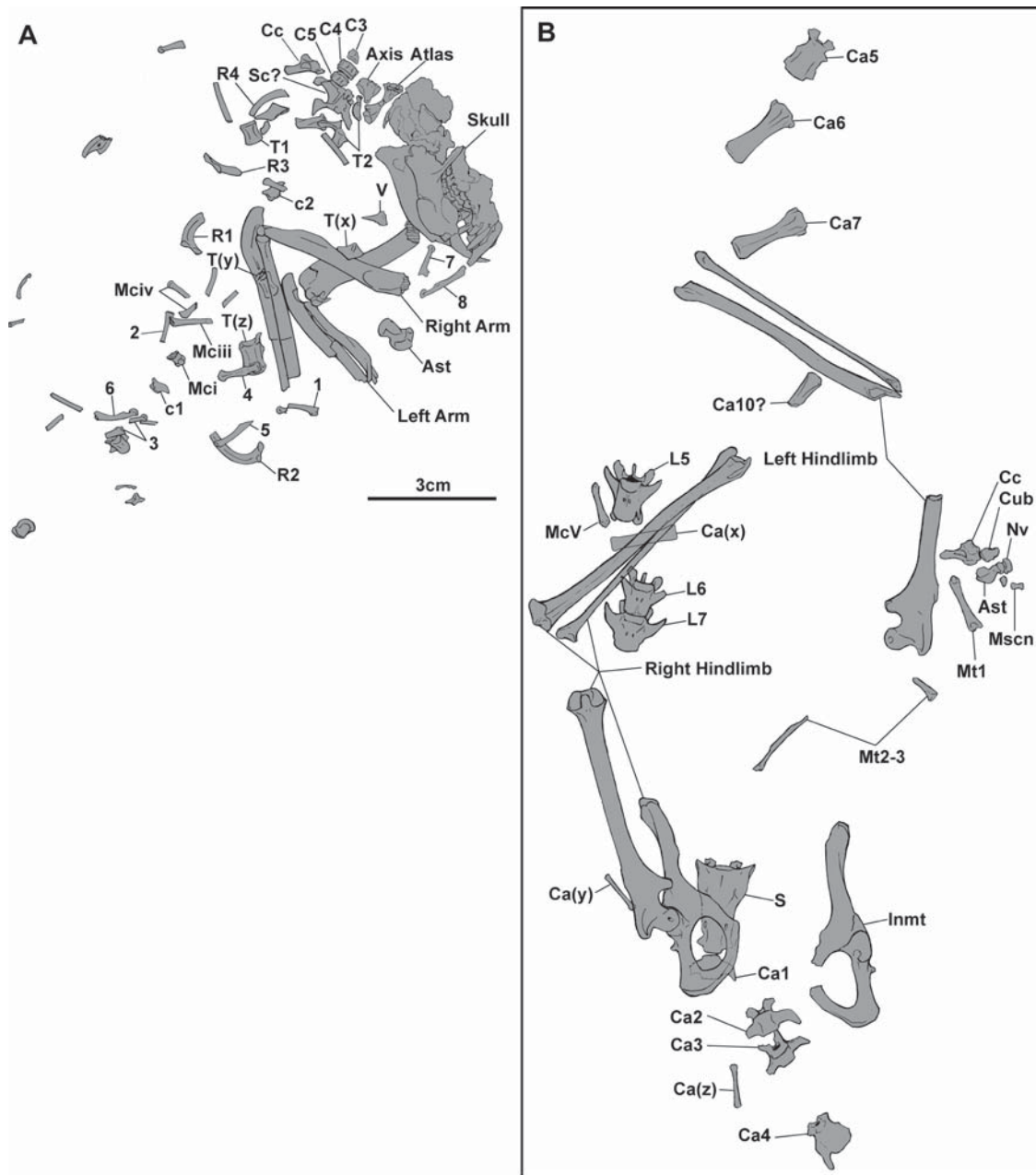
FIGURE 11.3. Documentation of association of *Ignacius clarkforkensis* skeletons. A, Map of semi-articulated skeleton of *Ignacius clarkfork-ensis* (UM 108210) prepared from a limestone from SC-62. The skull has been described by Bloch and Silcox (2001). B, Map of second semi-articulated skeleton of *Ignacius clarkforkensis* (UM 82606) prepared from a limestone from SC-62. See Figure 11.4 for a key to abbre-viated labels on these diagrams. Scale = 3 cm.

11.4.1.3 Dryomomys szalayi

UM 41870. (Holotype; Bloch et al., 2007). In late 2000, we recognized the semi-articulated remains of a micromomyid plesiadapiform, preserved in a richly fossiliferous block of limestone collected by University of Michigan field crews in 1982 from locality SC-327 of the Clarks Fork Basin, Wyoming (Figure 11.6). Through methods described in Bloch and Boyer (2001) and, with regard to this particular

specimen (Bloch and Boyer, 2007), we extracted the bones from their calcite tomb, while preserving critical information on the original position of each bone (Figure 11.6B). The speci-men is the most complete and best articulated "plesiadapiform" yet recovered, and is represented by much of a skull (includ-ing auditory region and perfectly preserved premaxillae) and dentaries (with all tooth positions represented); cervical, thoracic, and caudal vertebrae (but no lumbars or sacrum);
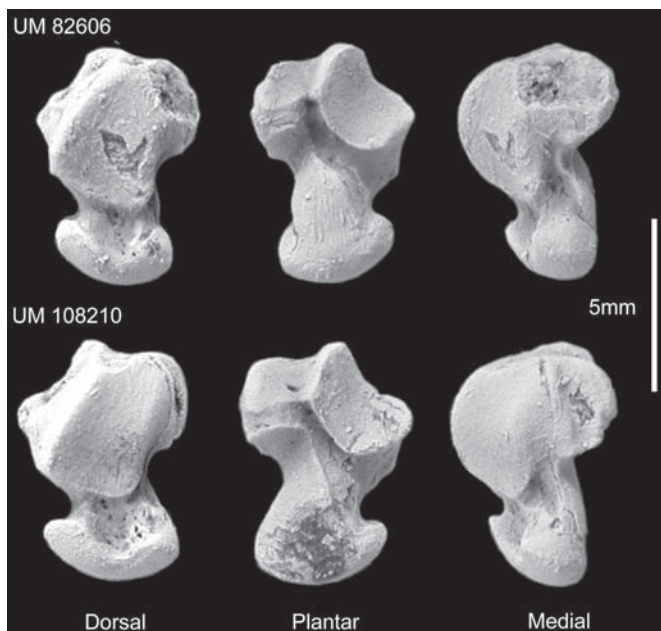
FIGURE 11.4. Right astragali of UM 82606 (top) and UM 108210 (bottom). While these elements differ in subtle respects, they clearly represent the same taxon, *Ignacius clarkforkensis* Scale = 5 mm.

several ribs; manubrium sternae; both scapulae; both humeri and radii; the left ulna; both scaphoids, trapezoids and a triquetrum; metacarpals of both hands (left hand preserved with the metacarpals in almost perfect articulation; Figure 11.6B); many proximal, intermediate and distal phalanges of the hands and feet; a left femur; the distal ends of the left tibia and fibula; both astragali, calcanea, naviculars, and mesocuneiforms; right ectocuneiform and cuboid; left ento-cuneiform; and metatarsals.

Bloch et al. (2003) explored the adaptive morphology of the euarchontan morphotype by comparing micromomyid morphology (reconstructed from this specimen and the one depicted in Figure 11.7) with that of *Ptilocercus lowii* and a possible stem-euarchontan, *Leptacodon* (Nyctitheriidae; see Hooker, 2001). They found a surprising degree of similarity between the micromomyid and *Ptilocercus* in morphology associated with committed arboreality in *Ptilocercus*. Thus, their results supported the hypothesis that the ancestral euarchontan was a committed arborealist (Szalay and Decker, 1974; Szalay and Drawhorn, 1980; Sargis, 2001b, 2002c). Furthermore, the retention of scansorial features in *Leptacodon*, considered to be a euarchontan outgroup by them, suggested an adaptive shift to committed arboreality at the base of the euarchontan radiation (Szalay and Drawhorn, 1980).

Another micromomyid was recently recognized from UM Locality SC-26 (Wa-1, early Eocene) and prepared beginning in 2002 (Figure 11.7). Although no teeth have been recovered, postcranial morphology and stratigraphic position make it attributable to *Tinimomys graybulliensis*. The limestone was recovered in the early 1980s by Dr. Peter Houde during
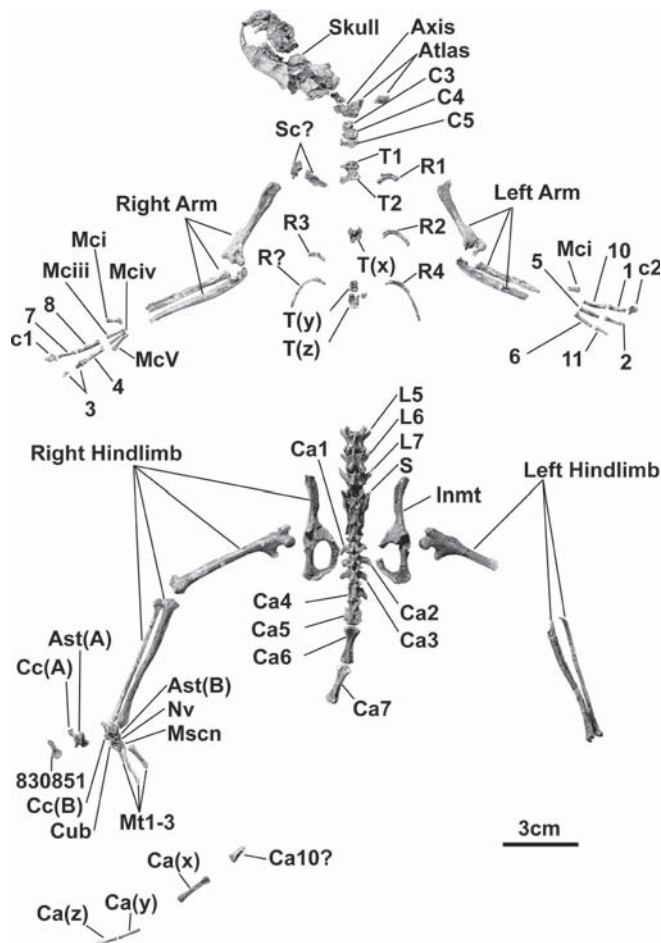

FIGURE 11.5. Composite layout of *Ignacius clarkforkensis* (UM 108210 and UM 82606) in rough anatomical position. Abbreviations: Ast – astragalus; C# – cervical vertebra; c# – claw; Ca# – caudal vertebra; Cc – calcaneum; Cub – cuboid; Inmt – innominate; L# – lumbar vertebra; Mc – metacarpal; Mscn – mesocuneiform; Mt – metatarsal; Nv – navicular; S – sacrum; Sc? – scapula?; T# – thoracic vertebra; R# – rib; "4" and "8" – left proximal phalanges; "6" and "10" – left proximal phalanges; "1", "2", "3", "7", and "11" – right intermediate phalanges. The right "Mci", "10", and "11" were recovered in the screen during preparation, thus their exact positions in the deposit is unknown. Scale = 3 cm.

Smithsonian sponsored field expeditions in the Clarks Fork Basin. The specimen is semi-articulated (Figure 11.7). It includes vertebrae from all anatomical regions of the spine; a left radius; many ribs; both innominates; parts of both femora; both tibiae and fibulae; the right wrist (scaphoid, capitate, lunate, hamate, triquetrum and centrale); the right hand (metacarpals and proximal, intermediate and distal phalanges); the left foot (distal tarsal row); and the right foot (navicular and third metatarsal).

The total lengths of the tibiae and radii can be measured in this Wasatchian specimen, and the total lengths of the femur, radius and humerus are measurable in the Clarkforkian specimen (UM 41870). Thus, by scaling one skeleton or the other
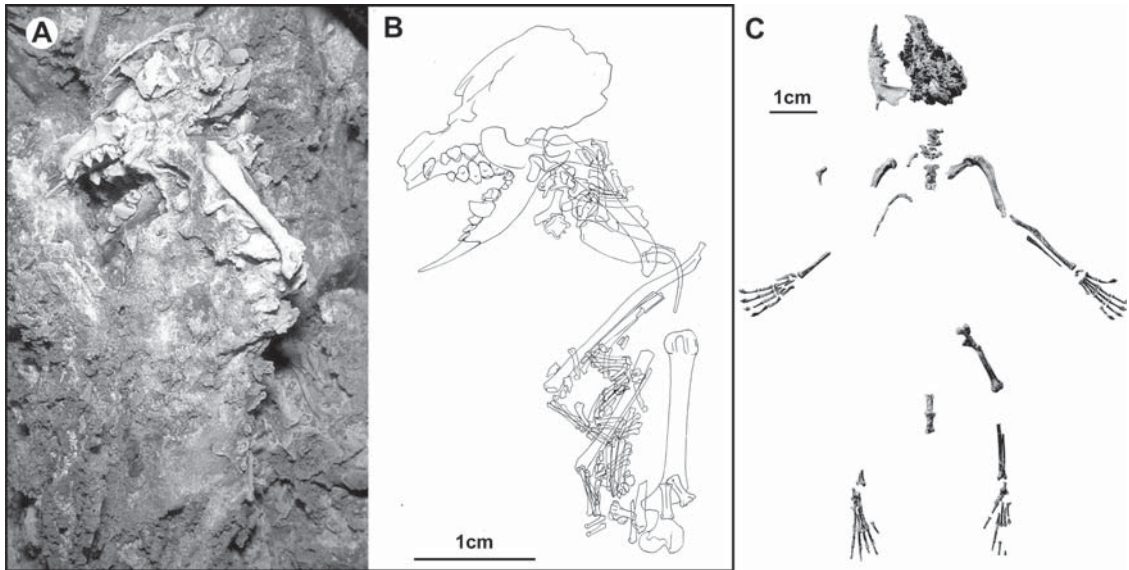
FIGURE 11.6. Documentation of association of micromomyid skeleton, *Dryomomys szalayi* (UM 41870). A, skull and skeleton partially prepared from fossiliferous limestone, University of Michigan Locality SC-327, late Clarkforkian (Cf-3) North American Land Mammal Age. B, Composite map of skull and skeleton with numbers on bones. C, Skull and skeleton in anatomical position. Note that C was made before all of the bones were prepared from the limestone and that not all bones depicted in B are in C. See Bloch and Boyer (2007) for (1) a similar figure that differs in providing numbers on all bones to show the exact correspondence between elements in B and C, and (2) a more detailed discussion of the preparation of this skeleton. Scale in A and B = 1 cm; Scale in C = 1 cm.
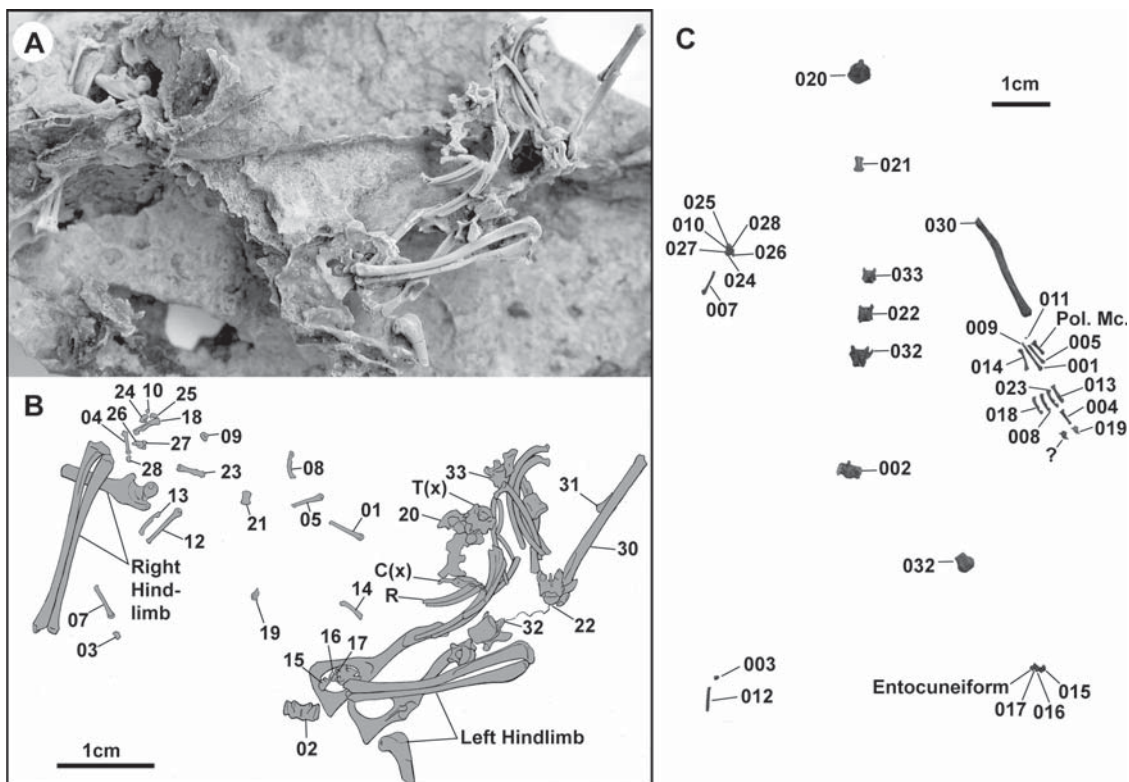

FIGURE 11.7. Documentation of association of micromomyid skeleton, cf. *Tinimomys graybulliensis* from UM locality SC-026 (currently uncatalogued). A, Photograph of a partly prepared limestone yielding a Wasatchian-aged micromomyid skeleton. B, Map of distribution of the bones in the limestone. Although it lacks craniodental remains, this specimen does preserve many of the same elements as that in Figure 11.6, so we can confidently identify it to the familial level, given its age, we tentatively refer to *Tinimomys graybulliensis*. The specimen includes complete tibiae, fibulae, innominates, and a complete radius. C, Some of the fully removed and prepared bones from this specimen in rough anatomical position. Note that most of the right wrist, the left hand, many vertebrae, and the left distal tarsal row are preserved. Scale = 1 cm.

so that radius lengths are equal between the two, the relative lengths of all limb segments of a hypothetical, composite micromomyid can be estimated.

11.4.2 Functional Analysis: Evaluation of the Gliding Hypothesis

11.4.2.1 Features Originally Marshaled to Support Mitten-Gliding

Beard (1990, 1993b) used similarity in morphological and proportional features of the digits of paromomyids, micromomyids and *Cynocephalus* to provide evidence for mitten-gliding in the fossil taxa. This morphology and behavior was inferred to have been present in the common ancestor of the three groups (Beard, 1993a, b). The following is a list of features discussed by Beard (1993b) in his latest comprehensive treatment of the issue, in sections titled "Anatomical Evidence for Gliding in Paromomyids" and "Anatomical Evidence for Gliding in Micromomyids." He argued that at least dermopterans and paromomyids, and in some cases micromomyids exhibited these features to the exclusion of most other mammals. While he did not argue that all of these features were immediate adaptations to the act of mitten-gliding, it was implied that they were at least consistent with and possibly expected in a mitten gliding mammal. Features hypothesized to be adaptations for mitten-gliding, specifically, are listed in bold. All listed features are addressed in functional analyses presented below:

Intermediate Phalanges
1. **Longer than proximal phalanges, as in *Cynocephalus***
2. **High elongation index, as in *Cynocephalus*.**
3. Proximal ends deeper (dorsopalmarly) than wide (mediolaterally), as in *Cynocephalus*.
4. Shafts straight, without dorsal recurvature at distal end, as in *Cynocephalus*

Proximal Phalanges
5. **Shorter than intermediate phalanges, as in *Cynocephalus*.**
6. Morphology of corresponding joint surfaces of the proximal interphalangeal (pip) joint limits extension and flexion, as in *Cynocephalus*.

Beard (1989) argued that additional features suggest a *Cynocephalus*-like habitus for the both paromomyids and micromomyids. We address these as well.

11.4.2.2 Morphological Evidence of Positional Behavior in Paromomyidae and Micromomyidae

Intermediate and Proximal Phalanges. The original evidence for mitten-gliding in paromomyids was based on the observation that their intermediate phalanges were similar to those of dermopterans in being longer than the proximal phalanges (Beard, 1990), extraordinarily gracile, and dorsoventrally

deep at the proximal end (Beard, 1993b). In a paper titled "Were paromomyids gliders? Maybe, maybe not," Krause (1991) warned that these observations were based on unassociated postcranial elements that were not necessarily from single individuals or even the same species, bringing into question the true proportional relationship between the proximal and intermediate phalanges of paromomyids. In fact, the new specimens of *Ignacius* (UM 108210) and *Acidomomys* (UM 108207) presented here (Table 11.1), have exactly the opposite phalangeal proportions as those proposed by Beard (1990), with the intermediate phalanges shorter than the proximal phalanges. Interestingly, in the context of better-established associations and a larger sample size, regression analysis (Figure 11.8A) shows that paromomyids and other "plesiadapiforms" have intermediate phalanx to proximal phalanx proportions comparable to a sample of non-gliding extant eutherian mammals. While some extant taxa in the sample, as well as some "plesiadapiforms," fall slightly above the upper confidence interval for this regression, the only substantial outlier is *Cynocephalus*. In fact, it is the only taxon in the plots of Figure 11.8 with intermediate phalanges that are actually longer than the proximal phalanges (above the x = y line). The fact that the pedal digits of some fruit bats and all digits of clawed suspensory sloths share this feature with *Cynocephalus*, suggest that it may actually reflect suspensory postures (Table 11.4).

Analysis of this relationship in another way (Figure 11.8B) also shows that both paromomyids (as a group) and micromomyids differ substantially from dermopterans. Specifically, Model I ANOVA of natural log interphalangeal ratios showed significant variance (at $P < 0.05$) among "terrestrial," "arboreal," "other plesiadapiform," "paromomyid," "micromomyid," and "*Cynocephalus*" groups (Figure 11.8B). Unlike in the regression, in this analysis our arboreal group included gliding squirrels because the average ratio for these taxa was not actually higher than that of non-gliding tree squirrels (i.e., *Sciurus* has a mean ratio of 0.80, while *Glaucomys*, a glider, has 0.76). Subsequent comparisons of these groups using t-tests (Table 11.2) showed *Cynocephalus* to be significantly higher than the other two extant behavioral groups, which did not differ from one another. Micromomyids, paromomyids and other "plesiadapiforms" were significantly lower than *Cynocephalus*, but higher than extant terrestrialists. Micromomyids were indistinguishable from paromomyids, but had a higher ratio than other "plesiadapiforms" and arborealists. On the other hand, paromomyids were not distinguishable from other "plesiadapiforms" (including micromomyids) but did have a higher average ratio than extant arborealists. Finally, non-micromomyid and non-paromomyid "plesiadapiforms" were indistinguishable from extant arborealists. While the average ratio for paromomyids is slightly higher than for other plesiadapiforms and significantly higher than for extant arborealists, careful inspection shows that these differences are probably artifactual. Adult and juvenile paromomyid specimens have different indices. *Ignacius* has
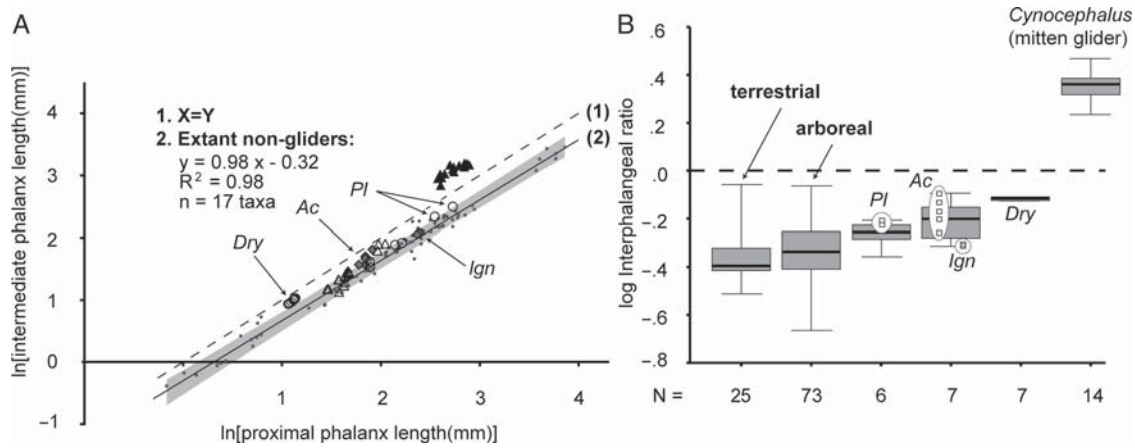
FIGURE 11.8. A, Reduced Major Axis (RMA) regression of intermediate phalanx on proximal phalanx length (solid line; 2) for select non-gliding mammals (small gray circles). Light gray area encompasses the 95% confidence limits for the relationship (y = 0.98 x − 0.32, R^2 = 0.98, n = 18 taxa). The slope is indistinguishable from that expected for an isometric relationship between the two variables (1). Mitten-gliding dermopterans (closed black triangles) have relatively much longer intermediate phalanges than do paromomyids (large gray diamonds), other plesiadapiforms (unfilled circles), and "mittenless" gliders (unfilled triangles). B, Box plots of logged interphalangeal ratios for a sample (same as for A) extant mammals and plesiadapiforms. Boxes encompass 50% of data points with medians depicted as a horizontal line within them. Whiskers encompass all data. Numbers below boxes represent the sample size for data points comprising it. *Ac = Acidomomys hebeticus, Ign = Ignacius clarkforkensis, Dry = Dryomomys szalayi, Pl = Plesiadapis cookei*. Dashed lines in A and B represent position of proximal and intermediate phalanges of equal length. See Table 11.1 for measurements of fossil specimens. See Table 11.2 for group means, t-values, and p-values of t-tests. See Appendix II, Table 1 for all specimens included in these plots.

TABLE 11.2. t-values and p-values of independent t-tests of natural log interphalangeal ratios of various extant behavioral and fossil taxonomic groups. In the right hand column, the group mean is given below its name. Significant p-values are in bold. In the top row, the number in parentheses after the group name is sample size for the group. Blank cells represent comparisons made elsewhere in the table. See Figure 11.8B for a plot of the samples analyzed here. See Appendix II, Table 1 for the specimens included.

	Ln(interphalangeal ratio) (Figure 11.8B)					
Group/mean	Terrestrial (25)	Arboreal (73)	Plesiadapiforms (6)	Paromomyidae (9)	Micromomyidae (4)	*Cynocephalus* (14)
Terrestrial	t = 0					
−0.35	p = 1					
Arboreal	t = 0.630	t = 0				
−0.33	p = 0.0530	p = 1				
Plesiadapiforms	t = 1.644	t = 1.454	t = 0			
−0.27	p = 0.111	p = **0.150**	p = 1			
Paromomyidae	t = 2.790	t = 2.761	t = 1.318	t = 0		
−0.21	p = **0.010**	p = **0.007**	p = 0.214	p = 1		
Micromomyidae	t = 9.405	t = 15.80	t = 6.533	t = 2.913	t = 0	
−0.12	p = **0.000**	p = **0.000**	p = **0.001**	p = **0.026**	p = 1	
Cynocephalus	t = 24.11	t = 32.40	t = 21.57	t = 17.76	t = 28.69	t = 0
0.35	p = **0.000**	p = **0.000**	p = **0.000**	p = **0.000**	p = **0.000**	p = 1

an average ratio of 0.73, while the average for *Acidomomys* is 0.84, with some *Acidomomys* as high as 0.91. The high value for *Acidomomys* cannot be interpreted with too much confidence because it is a juvenile. The fact that the adult *Ignacius* has lower values suggests that an older *Acidomomys* would also be lower. The average for *Ignacius* is actually lower than that reconstructed for at least two species of *Plesiadapis (P.*

cookei = 0.81: see Figure 11.8b, *P. tricuspidens* ~ 0.82 based on MNHN R 5341 and 5305: see Godinot and Beard, 1991) a large bodied "plesiadapiform."

The finding that paromomyids do not really differ from other "plesiadapiforms" in the interphalangeal ratio is inconsistent with predictions of the mitten-gliding hypothesis. While the micromomyid *Dryomomys* is higher than all other

"groups" in the analysis, it certainly does not share a position with *Cynocephalus*. Furthermore, both arboreal and terrestrial groups include taxa with average ratios that are actually as high as those of the micromomyid: if these had been analyzed separately they would have been indistinguishable from the micromomyid. Specifically, terrestrial *Gerbillus* has a mean interphalangeal ratio identical to that of *Dryomomys* (0.89). Anomalurids and some of the digit rays of the arboreal sciurids in the sample also share this value. A qualitative comparison of typical manual digit rays of a callitrichine euprimate, *Cynocephalus volans, Ignacius* and *Dryomomys* shows that the former extant taxon makes a better morphological analogue for both fossils, even though its claws evolved from an ancestor with euprimate-like nails (Figure 11.9).

Responding to critical questioning about the validity of conclusions drawn from comparisons using interphalangeal proportions of unassociated fossils (Krause, 1991), Beard (1993b) devised an index for evaluating elongation and gracility of intermediate phalanges that does not refer to the proximal elements. Based on this elongation index (shaft length divided by the square-root of the cross-sectional area at the mid-shaft) he again concluded that paromomyids, micromomyids and *Cynocephalus* were uniquely similar. Runestad and Ruff (1995), who rejected Beard's gliding interpretation of paromomyids based on evidence from the long bones, showed that the intermediate phalangeal length to square root cross-sectional area ratios for paromomyids (9–10) are more similar to those of non-gliding euprimates *Avahi* (8), *Tarsius* (8.5) and *Microcebus* (9) than to dermopterans (15–17). Hamrick et al. (1999) analyzed elongation in a different way (principal components and discriminant function analyses) and determined that dermopterans are unique among all the taxa included in their study (including paromomyids) in having extreme elongation. They concluded that paromomyids were probably not gliders. They did, however, conclude that dermopteran and paromomyid intermediate phalanges are similar to each other and those of bats in having a dorsoventrally deep proximal end. Hamrick et al. (1999) concluded that this was not a mitten-gliding feature, but potentially a dermopteran or volitantian synapomorphy, based on their use of galagonid and tupaiid morphology as reflective of the primitive archontan state. They did not consider this feature to reflect vertical-clinging with claws on large diameter supports.

We present results of analyses that support the findings of both Runestad and Ruff (1995) (Figure 11.10) and, in some respects, Hamrick et al. (1999) (Figures 11.11 and 11.12). Further, we use regression analysis to address a potential problem with all previous analyses of "elongation": that they have not been performed in an allometric context (Figure 11.14).

Analysis of the elongation index using a sample increased beyond that used by Beard (1993b) or Runestad and Ruff (1995) shows unambiguously (Figure 11.10) that dermopterans have significantly more elongate intermediate phalanges than either paromomyids or micromomyids. More specifically, Model I ANOVA

of elongation indices revealed significant variance (at $P < 0.05$) among the "terrestrial," "arboreal," "other plesiadapiform," "paromomyid," "micromomyid," "gliding squirrel," and "*Cynocephalus*" groups. In this case gliding squirrels were kept as a separate group because their average elongation indices are substantially higher than those of non-gliding sciurids (gliding squirrels range from 9.3–11.4, *Sciurus* has a mean of 7.4). Comparison of these groups using t-tests showed
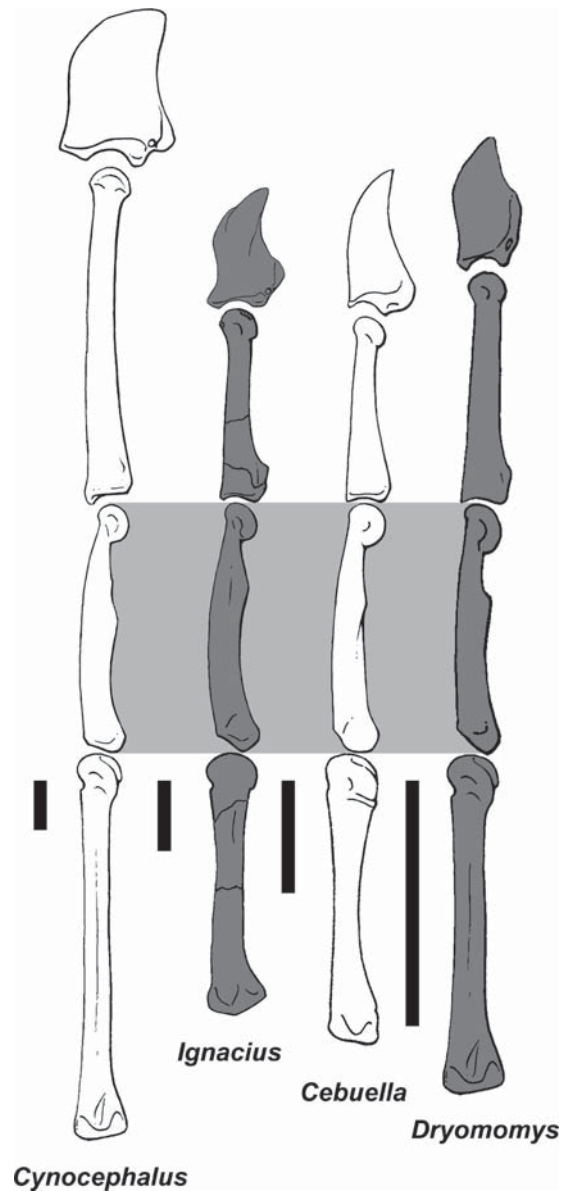

FIGURE 11.9. Comparison of phalangeal proportions in the manual third digit ray, normalized to the length of the proximal phalanx, for a dermopteran *Cynocephalus* (USNM 56530), a paromomyid, *Ignacius clarkforkensis* (UM 108210), a callitrichine euprimate *Cebuella* (UM 160146), and a micromomyid, *Dryomomys szalayi* (UM 41870). Rows from bottom-to-top are: metacarpal III, proximal phalanx, intermediate phalanx, and distal phalanx, respectively. Scales = 3 mm.

TABLE 11.3. t-values and p-values of independent t-tests of natural log elongation indices of various extant behavioral and fossil taxonomic groups. In the right hand column, the group mean is given below its name. Significant p-values are in bold. In the top row, the number in parentheses after the group name is sample size for the group. Blank cells represent comparisons made elsewhere in the table. See Figure 11.10 for a plot of the samples analyzed here. See Appendix II, Table 1 for specimens included.

| Group/mean	Ln(elongation Index) (Figure 11.10)						
	Terrestrial (37)	Plesiadapiforms (9)	Arboreal (62)	Paromomyidae (6)	Micromomyidae (7)	Gliding squirrel (20)	*Cynocephalus* (18)
Terrestrial	t = 0						
1.59	p = 1						
Plesiadapiforms	t = 4.904	t = 0					
1.93	p = **0.000**	p = 1					
Arboreal	t = 9.022	t = 1.105	t = 0				
2.02	p = **0.000**	p = 0.273	p = 1				
Paromomyidae	t = 5.952	t = 2.060	t = 0.508	t = 0			
2.08	p = **0.000**	p = 0.060	p = 0.613	p = 1			
Micromomyidae	t = 14.16	t = 3.861	t = 1.435	t = 1.650	t = 0		
2.16	p = **0.000**	p = **0.002**	p = 0.156	p = 0.127	p = 1		
Gliding squirrel	t = 17.63	t = 7.498	t = 4.586	t = 4.221	t = 2.980	t = 0	
2.29	p = **0.000**	p = **0.000**	p = **0.000**	p = **0.000**	p = **0.006**	p = 1	
Cynocephalus	t = 20.39	t = 12.28	t = 13.33	t = 8.900	t = 11.52	t = 8.261	t = 0
2.63	p = **0.000**	p = **0.000**	p = **0.000**	p = **0.000**	p = **0.000**	p = **0.000**	p = 1
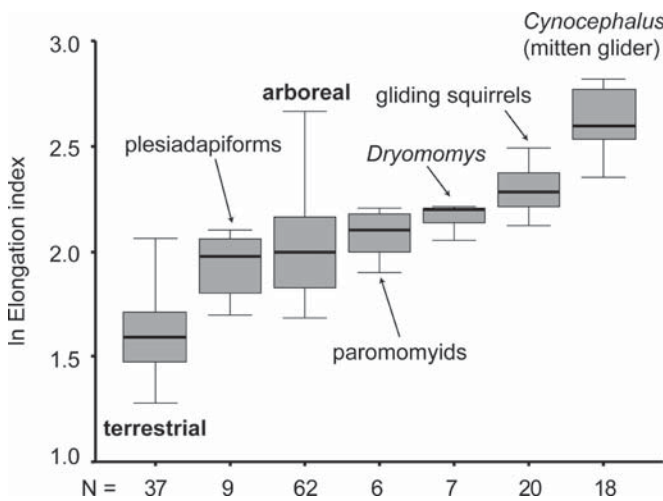
FIGURE 11.10. Elongation index of intermediate phalanx. Box plots of logged elongation indices for a sample of extant mammals and "plesiadapiforms". Boxes encompass 50% of data points with medians depicted as a horizontal line within them. Whiskers encompass all data. Numbers below boxes represent the sample size for data points comprising it. See Table 11.1 for a list of fossil specimens and measurements used in this analysis. See Table 11.3 for group means, t-values, and p-values of t-tests. See Appendix II, Table 1 for specimens included.

FIGURE 11.11. (continued) 2 represents 27.1% and PC 3 represents 12.9%. PC 1 is most strongly correlated to increasing mediolateral breadth of the distal trochlea (articular surface), decreasing dorsopalmar depth of the proximal articular surface, and decreasing total length. Thus, narrow, deep, long phalanges have low PC 1 scores. PC 2 is most strongly correlated to increasing shaft and proximal end dimensions, decreasing breadth of dorsal margin of distal trochlea and decreasing length. Thus, phalanges that are relatively elongate with gracile shafts and ends have low PC 2 scores. See Appendix II, Table 1 for a list of specimens.
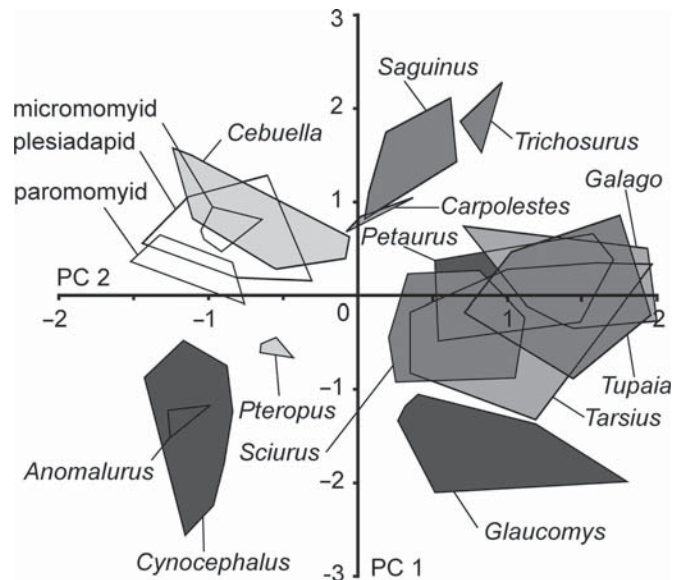

FIGURE 11.11. Principal Components (PC) Analysis (PCA) of manual intermediate phalangeal morphology. Data are derived from nine different measurements taken on 147 manual intermediate phalanges representing 18 genera and 22 species. Taxa are color-coded by functional group: darkest gray = gliders; lightest gray = vertical clinging arborealists; dark gray = clawed, pronograde quadrupeds; light gray = non-clawed, specialized grasping arborealists; and open = fossil. We controlled for body size by running the analysis on variables that were the logged ratio of the value of each raw measurement to the value of the geometric mean of all measurements on each specimen. Much of the comparative extant sample was provided by M. W. Hamrick and was originally used in Hamrick et al. (1999). Eight "plesiadapiform" species are plotted including the following: *Carpolestes simpsoni, Nannodectes intermedius, N. gidleyi, Plesiadapis cookei, Acidomomys hebeticus, Ignacius clarkforkensis*, and *Dryomomys szalayi*. For descriptions and illustrations of measurements taken see Hamrick et al. (1999). PC 1 represents 33.7% of the variance in the dataset, PC

Cynocephalus to be significantly higher than the others (Table 11.3). Gliding squirrels were significantly higher than more generalized arborealists, which were higher than terrestrialists. All "plesiadapiforms," including paromomyids and micromomyids, were significantly higher than the terrestrial group, yet significantly lower than gliding squirrels and *Cynocephalus*. Paromomyids and the arboreal group were not distinguishable from one another or any of the other "plesiadapiform" groups. However, the micromomyid was found to be higher than non-paromomyid "plesiadapiforms".

These results strongly contradict either "mitten" or "mittenless" gliding in either paromomyids or micromomyids.

A principal components (PC) analysis (PCA) of manual intermediate phalanx shape based on data from Hamrick et al. (1999), but with an increased sample of extant mammals and fossil "plesiadapiforms", agrees with Hamrick et al.'s results in showing that *Cynocephalus* and *Anomalurus* are separated from most other extant mammals in the sample (including primates, treeshrews, rodents and marsupials) by having mediolaterally narrow shafts and trochleae (low PC 1 scores). However, restricting the analysis to manual elements *only* and adding callitrichine euprimates and other plesiadapiforms (including micromomyid UM 41870) shows the following: (1) dermopteran manual intermediate phalanges are unique among all extant and extinct taxa (except *Anomalurus*) in being extremely elongate (low PC 1 and PC 2 scores), and (2) the added taxa have manual intermediate phalanx shapes similar to those of paromomyids (UM 108210 and 108207) and dermopterans in being mediolaterally narrow and dorsoventrally deep (low PC 1 scores), but are separated from dermopterans in being relatively shorter (higher PC 2 scores) (Figure 11.11). Looking at this result from a functional perspective, we note that low PC 1 scores characterize extant taxa that use their digits for clinging and/or climbing on large diameter vertical supports (*Anomalurus*, the callitrichine euprimate (*Cebuella pygmaea*), *Pteropus* and *Cynocephalus*), while higher PC 1 scores characterize arboreal primates that predominately grasp small diameter supports, or terrestrial taxa that do not subject their phalanges to tensile forces, but load them in compression, instead. Based on these results, we agree with Hamrick et al. (1999), that narrow trochleae and shafts in intermediate phalanges are strongly linked to frequent exposure to tensile loads and sagittal bending moments associated with vertical clinging on large diameter supports and/or suspending with claws.

This comprehensive PCA of overall intermediate phalanx shape is not entirely sufficient to evaluate Beard's (1993b) suggestion that similarity in the shape of the intermediate phalanx proximal end, specifically, links paromomyids and dermopterans, or Hamrick et al.'s suggestion that this morphology, being additionally found in bats, is a character supporting Volitantia (now typically recognized as polyphyletic; e.g., Murphy et al., 2001b). Thus, we note that in making the foregoing suggestion, Beard did not mention the fact that he had illustrated another
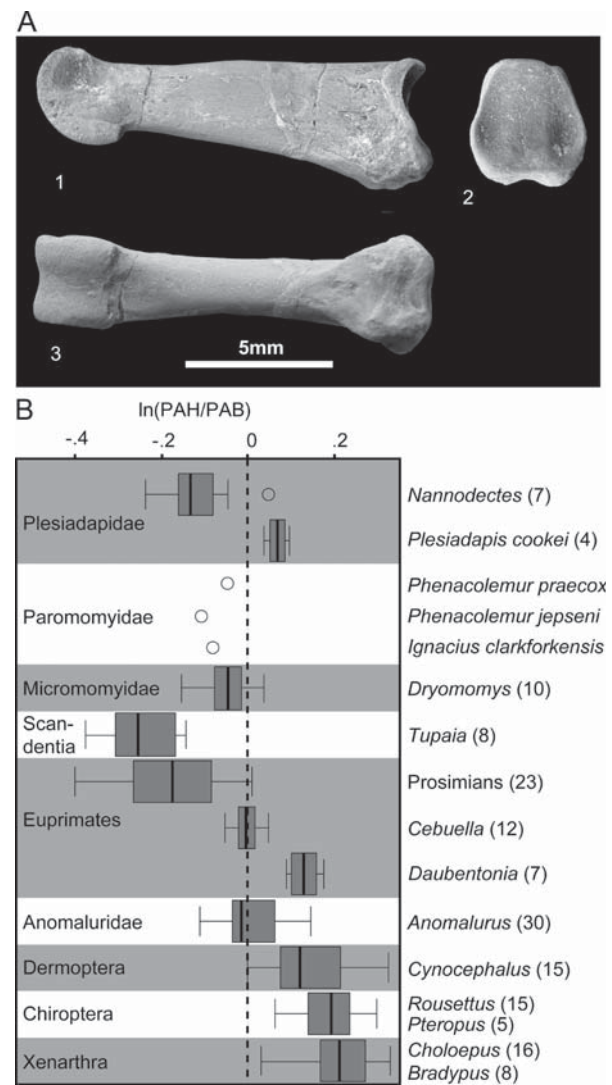

FIGURE 11.12. A, *Plesiadapis cookei* (UM 87990) intermediate phalanx. 1, lateral; 2, proximal; and 3, volar view. *P. cookei* has a proximal articular surface that is dorsoventrally taller than it is mediolaterally wide. The shaft is straight, or slightly dorsally convex (depending on how the central axis is defined) with no dorsal re-curvature at the distal end. Contrary to what this specimen shows, these features (and others) were said to be uniquely shared by paromomyids and dermopterans among "plesiadapiforms," primates, treeshrews and most other mammals (Beard, 1993b). Scale = 5 mm. B, Plot of natural log ratio of dorsoventral height of the proximal articular surface (PAH) to mediolateral breadth of surface (PAB) of intermediate phalanges. Alternating gray and white bars demarcate higher-level taxa. Contrary to previous claims paromomyids, dermopterans and bats are not uniquely characterized by a high value of this ratio (plotting right of the dashed line). *Plesiadapis* (as shown qualitatively in A), *Daubentonia*, and sloths plot in this realm, but paromomyids do not. Intermediate phalanges of *Acidomomys hebeticus* were not included here because none were preserved with their proximal epiphyses solidly attached. Sample sizes are given after taxon names in parentheses. See Appendix II, Table 1 for specimens included.

"plesiadapiform" *Plesiadapis tricuspidens* (MNHN R 5341: Godinot and Beard, 1991: Figures 11.1F, 11.2) such that it appeared to have this morphology. Given that another species of *Plesiadapis, P. cookei* (UM 87990) is also shown (Figure 11.12A) to have an intermediate phalanx with a dorsoventrally deep proximal end, it seems likely that at least this genus of "plesiadapiform" shares this feature with paromomyids and dermopterans. Importantly, the fact that more primitive plesiadapids lack this morphology (Figure 11.12B; Beard, 1993b), suggests that it is adaptive in *Plesiadapis* and does not reflect the probable close relationship between paromomyids and plesiadapids. *Plesiadapis* has never been seriously regarded as a glider by those who have studied it from a functional perspective (including Beard), throwing into further doubt the possibility that dorsoventral depth of the intermediate phalanx proximal end, has a special association with a lifestyle that includes mitten-gliding. Hamrick et al. (1999) never evaluated this feature from a univariate quantitative perspective. They appraised it qualitatively, as did Beard (1993b). However, we plot the ratio of the dorsoventral height of the proximal articular surface (PAH) to its mediolateral breadth (PAB) for a broader sample of mammals which shows (Figure 11.12B) that (1) dermopterans and paromomyids are not necessarily similar to one another, as paromomyids actually have a lower ratio (even those specimens available to Beard); and (2) the condition of having a dorsoventrally deep proximal end is distributed like other features linking together extant taxa that put tensile loads on their digits (i.e., it is present in bats, dermopterans, anomalurids, callitrichines, *Daubentonia* and sloths). Therefore, we interpret this feature to also reflect vertical clinging and/or suspending with claws. It may be that the extremely high ratio of bats, *Cynocephalus*, sloths and possibly even *Plesiadapis* can be specifically linked to use of suspensory behaviors.

Other paromomyids and *Dryomomys* have lower ratios suggesting against frequent quadrumanus suspension. Other features of the intermediate phalanges of paromomyids and micromomyids also suggest against this behavior: Compared to sloths and the pedal intermediate phalanges of bats, they have distal trochleae that face more distally (less ventrally). Compared to sloths, bats and *Cynocephalus* they have tubercles for annular ligaments that are more distinctly flaring, and more distally positioned (Figure 11.13). A ventrally facing trochlea appears to indicate a habitually ventriflexed distal interphalangeal (dip) joint, and reduction of tubercles for annular ligaments appears to reflect a habitually extended pip joint in the phalanges of bats (Simmons and Quinn, 1994) and sloths (Mendel, 1985). While dermopterans are noted for their inability to completely extend the pip joint (Pocock, 1926; Beard, 1993b), they are similar to other clawed-suspensory animals in also being incapable of tight flexion at these joints (Mendel, 1985; Simmons and Quinn, 1994). The inability for tight flexion as a reflection of suspensory behavior is a salient point. Micromomyids and paromomyids have a joint that indicates a capacity for relatively tight flexion in

FIGURE 11.13. Intermediate and proximal phalanges of various taxa. A, *Ignacius clarkforkensis*; B, *Cebuella pygmaea*; C, *Dryomomys szalayi*; D, *Pteropus pumillio*; E, *Cynocephalus volans*; F, *Choloepus hoffmani*. Ventrolateral view of intermediate phalanx (on the left) and proximal phalanx (on the right). Manual elements are represented except in the case of *Pteropus*, for which toe bones are shown. Functionally, its toes are more comparable to the fingers of the other taxa shown, than are its own fingers, which are modified as wings. Phalanges are normalized to length of the proximal phalanx to show variation in intermediate phalanx length, except for F, which is normalized to the length of intermediate phalanx in E. Note that suspensory taxa D–F differ from fossils (A and C) and vertical clinger and climber (B) in having intermediate phalanges that are relatively longer, with more ventrally facing distal articular surfaces and less distinct flexor sheath tubercles. The proximal phalanges of the suspensory taxa have more deeply trochleated distal articular surfaces. See Appendix II, Table 1 for specimen numbers. Scale bars = 3 mm.

so much as they have morphology that is similar to callitrichines that evidently habitually tightly flex the pip joint of their digits because they frequently locomote on small diameter supports even though they forage predominately on large diameter vertical supports (Youlatos, 1999). This morphology is illustrated in Figure 11.13.

Finally, regression analysis using a reduced major axis (RMA) method (Figure 11.14) shows a pattern consistent with previous modes of analysis. "Plesiadapiforms," including paromomyids and micromomyids, have intermediate phalanges that are not significantly different from those of euprimates in their length (y-axis) to midshaft diameter (x-axis) proportions, whereas dermopterans and gliding squirrels differ in being more elongate. More specifically, gliders plot outside the confidence interval of a regression generated using non-gliding eutherian mammals. In contrast, all
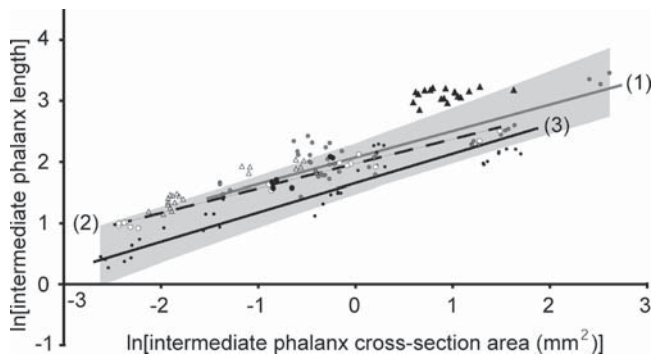
FIGURE 11.14. Intermediate phalanx elongation. Intermediate phalanx length vs. cross-section at midshaft – Solid lines are RMA regressions of the natural log of intermediate phalanx length on the natural log of the mid-shaft area for a sample of non-gliding primates [small gray circles (1) with gray line], "plesiadapiforms" [large white and black circles (2) with dashed line], and other extant non-gliding mammals [small black circles (3) with black line]. A composite "non-gliding mammals regression" is illustrated by a shaded gray area that encompasses the 95% confidence limits for the isometric relationship ($y = 0.54 x + 1.88$, $R^2 = 0.83$). Gliders, including dermopterans (black, filled-in triangles) and flying squirrels (open triangles), have more elongate intermediate phalanges than non-gliders, generally falling outside of the 95% confidence limits. Among non-gliders, euprimates (1) and plesiadapiforms (2) have more elongate intermediate phalanges than do other non-gliding mammals (3). Note that paromomyids (large black circles) lack the elongation characteristic of mitten-gliding dermopterans and are in the range of other plesiadapiforms (2). Equations for the regressions are the following: (1) $y = 0.43 x + 2.07$, $R^2 = 0.71$, n = 8 taxa; (2) $y = 0.40 x + 1.94$, $R^2 = 0.98$, n = 6 taxa; and (3) $y = 0.48x + 1.645$, $R^2 = 0.94$, n = 10 taxa. See Table 11.1 for list of fossil specimens and measurements used in this analysis. See Appendix II, Table 1 for all specimens included.

plesiadapiforms plot within the confidence interval and have intermediate phalanges that fall on the same regression line as those of euprimates. Thus, the relatively high elongation indices of *Dryomomys* can be most easily explained as a consequence of extending a more general scaling relationship between intermediate phalanx length and cross-sectional area to a very small size.

Beard (1993b) stated that both *Cynocephalus* and paromomyids had straight intermediate phalanx shafts that lacked dorsal recurvature at the distal end. He associated these features with the presence of elongated volar pads in *Cynocephalus*. However, his own figures seem to contradict this observation. Beard (1993b: Figure 11.5) illustrates a phalanx attributed to *Ignacius graybullianus* that actually has slight dorsal recurvature, similar to the pronograde creatures with which he contrasted it. Furthermore, *Cynocephalus* actually possesses intermediate phalanx shafts that are dorsally convex, not perfectly straight (Figure 11.9 and 11.13E). The intermediate phalanx of *Ignacius* (UM 108210) has notable dorsal recurvature at the distal end of the shaft (Figure 11.13A). *Dryomomys* possesses straight-to-convex

shafts, but this trait is not otherwise unique to *Cynocephalus*. Notably, it is also found in *P. tricuspidens* (Godinot and Beard, 1991), *P. cookei* (Figure 11.12A) and many euprimates (Stern et al., 1995).

As suggested by Beard (1989), and demonstrated by Hamrick et al. (1999), we also found that different gliders are not consistently distinguishable from non-gliders with regard to the morphology of the proximal phalanges (Table 11.5). For example, in gliding anomalurids (Hamrick et al., 1999) the proximal phalanges have shafts that are straight and relatively short, are deep dorsoventrally, and have flexor sheath ridges that are extended proximally and flare ventrally. On the other hand, the gliding squirrel *Glaucomys* has proximal phalanges that are slender, elongate and have dorsally curved shafts. *Cynocephalus* has proximal phalanx morphology extremely similar to that of anomalurids (Hamrick et al, 1999). This last fact had not yet been documented when Beard explained the "unusual" morphology of the proximal phalanges of *Cynocephalus* as relating to other idiosyncrasies of a mitten-glider in the following way:

"because of elongation of its intermediate phalanges, the proximal phalanges are subjected to relatively higher bending moments in the anteroposterior plane during suspensory postures involving the hands than would otherwise be the case if the intermediate phalanges were more typical (i.e., shorter) in length." (Beard, 1989:p.453)

In *Ignacius* and the micromomyid, but not in *Acidomomys*, the proximal phalanges have a triangular cross-sectional shape and extended flexor sheath ridges somewhat similar to those in *Cynocephalus* (the difference between different paromomyids is very likely an ontogenetic artifact, as noted previously) (Figure 11.13). It seems likely that Beard's explanation for such morphology is correct with regard to the resistance of bending moments during postures in which the digits are loaded in tension (e.g., suspensory postures). However, such stresses appear to select for dermopteran-like proximal phalanges even if the intermediate phalanges are relatively short: Anomalurids, paromomyids and micromomyids lack intermediate phalanges that are "greatly elongated" relative to the proximal phalanges (Figure 11.8) but have proximal phalanx morphology similar to that of *Cynocephalus* in most respects. Furthermore, a number of euprimates have flexor sheath ridges similar to those of *Cynocephalus*, anomalurids, paromomyids, and micromomyids; including spider monkeys, gibbons, and some callitrichines, but (again) do not have elongated intermediate phalanges. Thus, the proximal phalanx morphology characterizing *Cynocephalus*, appears broadly associated with antipronograde behaviors (not just suspension) including clinging to large vertical supports with claws and/or with strong grasping as suggested by Hamrick et al. (1999).

Metapodials. Metacarpal proportions are distinctive for gliders that include the metacarpus in their patagium (Beard, 1993b) (Table 11.6). In *Cynocephalus volans* and *Petaurus breviceps*, metacarpal V is longer than metacarpal III and it is also longer than any metatarsal [in *C. volans* the ratio of metacarpal V to

TABLE 11.4. Comparative morphology of intermediate phalanges of fossil "plesiadapiforms" and extant arboreal mammals. The following explanation applies to this and (in most respects) the remaining tables: Columns represent different "positional behavior groups". Rows represent morphological features of the intermediate phalanges (or other skeletal elements). Gray shading in a box indicates that a feature is present in the corresponding behavior group. Letter codes are sometimes included in gray-shaded boxes to specify the functional significance of the feature. Functions include mitten-gliding (mg), suspension (s), gliding (g), vertical clinging (vc), grasping-clinging (g-c), and pronograde postures (p). Extant taxa used to represent behavioral groups in this table include: (1) *Cynocephalus volans* (mitten-glider); (2) *Choloepus hoffmanni* and *Pteropus pumilio* (non-gliding, clawed suspensory mammals); (3) *Cebuella pygmaea* (non-gliding vertical clinger and climber); (4) *Glaucomys volans* and *G. sabrinus* (rodent gliders); (5) *Petaurus breviceps* (marsupial glider); and (6) *Sciurus niger* and *S. carolinensis* (non-gliding clawed scansorialists). We tried to determine the functional significance of the coded features by (1) noting which behavioral groups exhibited a particular feature, (2) noting what functions were shared by those same behavioral groups, and (3) linking the shared features and shared functions. In some cases we were unable to identify a function distributed among behavior groups in the same way as a particular feature. We took this to mean that the feature had different functions in different behavioral groups. An example of how these tables can be used to determine a feature's functional significance is given in the methods section of the main text. Fossil taxa can be linked to extant behavioral groups by noting with which of those groups they share the most features. *Ignacius*, the paromomid, and the micromomyid have a suite of features most similar to non-gliding vertical clingers and climbers and non-gliding clawed scansorialists. They lack features that uniquely characterize mitten-gliders, as well as those that characterize mitten-gliders and quadrupedal suspensory taxa, together. They exhibit features lacking in rodent and marsupial gliders. Thus, the intermediate phalanges suggest these taxa were non-gliding vertical clingers and climbers in life. For this and the remaining tables, codings are based on observations of specimens listed in Appendix II, Table 1.

Intermediate Phalanges	Extant mammalian behavioral groups						Fossil plesiadapiforms	
	Mitten glider	Non-gliding clawed suspensory mammal	Non-gliding vertical clingers and climbers	Rodent gliders	Marsupial gliders	Non-gliding clawed scansorialist	micromomyid	paromomyid
Extremely gracile (high elongation index)	g			g				
Longer than proximal phalanges	s	s						
Distinct, distally positioned tubercles for annular ligaments			g-c			g-c	g-c	g-c
Deeply trochleated proximal articular surface	s	s						
Proximal articular surface relatively deep dorsopalmarly	vc	vc	vc				vc	vc
Ventrally facing distal articular surface		s						
Trochleated distal articular surfaces		s						
Dorsally recurved shaft at distal end					p	p		p

metacarpal III is 1.03 (Figure 11.15); that of metacarpal V to metatarsal III is 1.16 (Figure 11.16)]. In contrast to that of *C. volans*, metacarpal V of *Ignacius* and *Dryomomys* appears to have been shorter than metacarpal III-IV (Figure 11.15).

Furthermore, the metacarpals are roughly two-thirds the length of the second metatarsal (the only one for which the full length is preserved) in *Ignacius* (the ratio of metacarpal V to metatarsal II

is 0.67 in UM 82606). The same is true for *Dryomomys* (the ratio of metacarpal III to metatarsal III is 0.73; Figure 11.16).

Not only are the metacarpals shorter than the metatarsals in the micromomyid, but the manual digits are shorter than the pedal digits (Figure 11.16). This also seems to have been true for *Acidomomys* UM 108207 (see above): phalanges attributed to its hands are shorter than those attributed to its feet (Table

TABLE 11.5. Comparative morphology of proximal phalanges. Non-gliding suspensory mammals include *Hylobates* and *Ateles*, as well as those listed for the suspensory group in Table 11.4. Functional categories include suspension (s), and vertical clinging (vc)

Proximal Phalanges	Extant mammalian behavioral groups						Fossil plesiadapiforms	
	Mitten glider	Non-gliding suspensory mammal	Non-gliding vertical clingers and climbers	Rodent gliders	Marsupial gliders	Non-gliding clawed scansorialist	micromomyid	paromomyid
Deeply trochleated distal articular surface	s	s						
Extensive, ventrally projecting flexor sheath ridges	vc	vc	vc				vc	vc
Dorsally convex shaft								

TABLE 11.6. Comparative morphology of metapodials. Functional categories include gliding (g). The distribution of "**Metacarpals longer than Metatarsals**" has an ambiguous functional significance. For gliders that include the metacarpus in the patagium (*Cynocephalus* and *Petaurus*), it likely serves to increase patagial area.

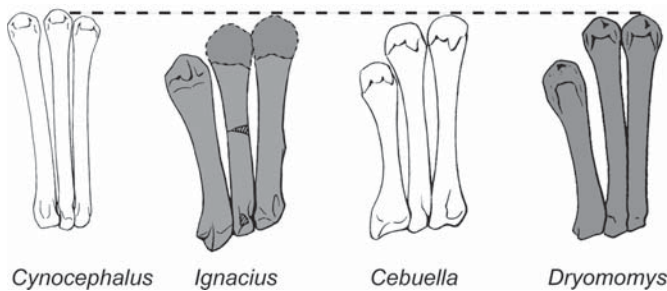| Metapodials	Extant mammalian behavioral groups						Fossil plesiadapiforms	
	Mitten glider	Non-gliding clawed suspensory mammal	Non-gliding vertical clingers and climbers	Rodent gliders	Marsupial gliders	Non-gliding clawed scansorialist	micromomyid	paromomyid
Metacarpal V ≥ length of Metacarpal IV	g				g			
Metacarpals longer than Metatarsals								

FIGURE 11.15. Comparison of relative lengths of metacarpals. Right metacarpals V-III (left to right) in palmar view. *Cynocephalus volans* (USNM 56530) *Ignacius clarkforkensis* (metacarpal V – UM 82606; metacarpal IV-III – UM 108210); *Cebuella pygmaea* (UM 160146); *Dryomomys szalayi* (UM 41870). Elements are standardized to the length of the third metacarpal. Note that *Cynocephalus volans* is unique in having a fourth and fifth metacarpal that extend distally beyond the third metacarpal.

11.1). This is an important point because the gliding hypothesis predicts an elongate manus relative to the pes (Beard, 1993b).

Finally, even though the manual proximal phalanges are shorter than the pedal elements in paromomyids and micromomyids, they are long relative to the metacarpals (Figure 11.9). This likely indicates effective grasping, as in euprimates (e.g., *Tarsius*) and some marsupials (e.g., *Caluromys*) (Lemelin, 1999; Hamrick, 2001; Bloch and Boyer, 2002).

Forelimb. The ability of a mammal to glide and/or use suspensory postures appears to be reflected in the relative lengths and morphology of its limb bones (Thorington and Heaney, 1981; Runestad and Ruff, 1995; Thorington et al., 2005). *Ignacius clarkforkensis* UM 108210 and *Dryomomys szalayi* UM 41870 preserve the first known articulated to semi-articulated forelimbs for their respective families (Figure 11.17, Figure 11.7c), allowing us to assess positional behavior by looking at relative lengths of elements for the first time.

With regard to the radius, Thorington and Heaney (1981) found that all gliding squirrels, regardless of body size, exhibit elongation of this element relative to the humerus. Furthermore, Runestad and Ruff (1995) examined the scaling relationship between radius length and humerus length in non-gliding and gliding mammals. They were able to generalize Thorington and Heaney's conclusion, by finding that gliders with patagia terminating on the wrist or digits (including *Cynocephalus*) have significantly longer radii relative to their humeri (higher brachial index), than non-gliders (Figure 11.18). We further note that suspensory taxa are also characterized by a high brachial index (Godfrey, 1988). Thus, whether a high brachial index is reflective of gliding or suspension in *Cynocephalus volans* (brachial index = 116) it should be present in other mitten-gliders as well. In this context, it is important to note that while a high brachial index is probably required for animals that exhibit these behaviors, it often present without gliding and suspensory behaviors in other extant euarchontan mammals. Specifically, the arboreal treeshrew *Ptilocercus lowii* and the vertically clinging and leaping euprimate *Tarsius* have elongate radii, with brachial indices of 107 and 127, respectively.

While distal radius morphology is not generally distinctive for gliders as a group, *C. volans*, sloths (e.g., *Choloepus*), and gibbons share a number of features in this region, which appear to reflect their use of suspensory behaviors. Specifically, the carpal articular surface of the radius is deeply cupped, faces palmarly and ulnarly, and is marked by a prominent ridge on its dorsal margin (Figure 11.19). Again, however, these traits are also present in *Ptilocercus* (Figure 11.20A), which is not committed to using suspensory postures, and is probably best characterized more generally, as a committed arborealist (e.g., Sargis, 2001a).

Morphological traits of the forearm that may relate to gliding in squirrels (Sciuridae: Pteromyini) include an ulna that has a relatively short olecranon process (Thorington et al., 2005); a deep trochlear notch (Figure 11.18); and a shaft that
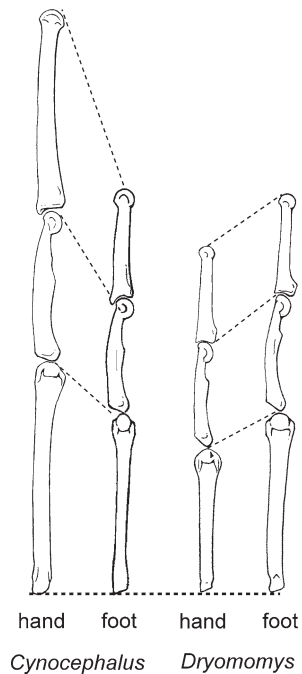

FIGURE 11.16. Comparison of relative lengths of metacarpals and metatarsals of a dermopteran and a micromomyid. Third digit rays of hands and feet of *Cynocephalus* (USNM 56530 – left) and *Dryomomys szalayi* (UM 41870 – right). Digit rays are standardized to the lengths of the metatarsals. Note that manual elements are longer than pedal elements in *Cynocephalus*, while the reverse is true of the micromomyid.

FIGURE 11.17. Forelimb elements of *Ignacius* (UM 108210). A, right humerus in (1) anterior and (2) posterior views. B, right radius in (1) posterior and (2) lateral views. C, right ulna in (1) medial, and (2) lateral views. Note that the proximal-most part of humerus is not preserved, nor are the distal tips of the radius and ulna. Scale bar = 5 mm.
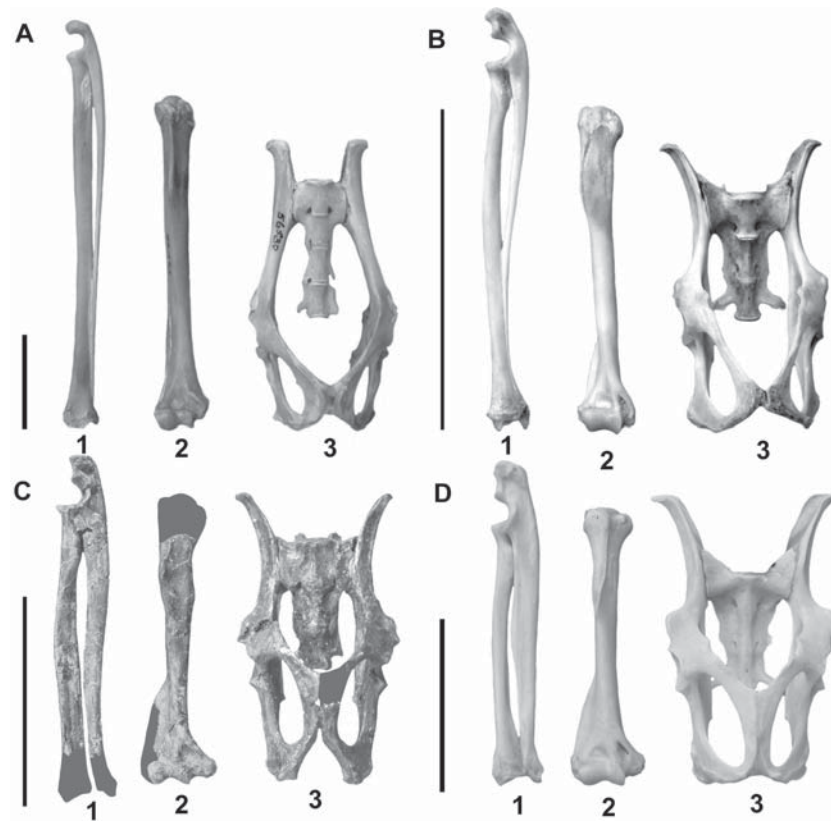
FIGURE 11.18. Proportions of select elements among different gliding and non-gliding taxa. For each lettered specimen, there are three numbered elements, or sets of elements: (1) right ulna and radius in medial view, (2) right humerus in anterior view, (3) articulated sacrum and innominates in ventral view. Elements are standardized to innominate length. A, *Cynocephalus volans* (USNM 56530); B, *Glaucomys sp.* (UMMZ 168356 – flying squirrel); C, *Ignacius clarkforkensis* (UM 108210 and UM 82606); D, *Sciurus niger* (UMMZ 3959 – gray squirrel). Gliding features present in A and B were most likely independently-evolved. Some of these features include a deep trochlear notch on the ulna; an ulnar shaft that is distally reduced and fused to radius; a radius that is substantially longer than the humerus; a humerus that has a proximally-restricted, anteriorly-oriented deltopectoral crest, a mediolaterally narrow distal end, a large capitular area on its distal articular surface, and a total length greater than that of the innominate; an innominate with narrow iliac crests, a long ilium relative to ischium, and a craniocaudally short caudally situated pubic symphysis. *Ignacius* (C) shares more features in common with *Sciurus* (D) than it does with either of the two gliding taxa. Scale bar = 3 cm.

is distally reduced (or synostosed to the radius), lacks ridges for the pronator quadratus muscle, and lacks a longitudinal groove along its lateral surface for the extensor carpi ulnaris muscle (Thorington et al., 2005). Additionally, gliding squirrels are said to have a distal radius with a large tubercle separating the first and second extensor compartments of the wrist, and a shaft with a more circular cross-section than non-gliders (Thorington et al., 2005). Like gliders, suspensory taxa are also typically characterized by a short olecranon process (Godfrey, 1988). Furthermore, Mendel (1979) related a reduced distal ulna in sloths (*Choloepus*) and gibbons to suspensory behaviors. We again note that many of these features are found in *Cynocephalus* (Figures 11.18, 11.19, Table 11.7), and should be present in a mitten-glider whether they reflect gliding or suspensory behaviors.

With regard to the arm, or humerus specifically, gliders have been shown to have a shaft that is relatively gracile (Runestad and Ruff, 1995), a distal end that is mediolater-ally narrow (Thorington et al., 2005), and a deltopectoral crest (DPC) that is proximally restricted (Runestad and Ruff, 1995; Thorington et al., 2005) and anteriorly (versus laterally) oriented (Thorington et al., 2005). The first three features probably reflect elongation of the shaft relative to body mass, which functions to increase the surface area of the patagium (Beard, 1993b; Runestad and Ruff, 1995). The anterior orientation of the DPC in suspensory and gliding taxa may allow the arms to be abducted and flexed to a greater degree, while still maintaining mechanical efficiency of the attaching muscles.

In summary, there are many forelimb traits that characterize *C. volans*, suspensory taxa, and eutherian gliders, reflecting the functional demands they have in common. Thus the fossil forms considered here should also exhibit such features if we are to entertain a gliding hypothesis for them. However, in most cases these traits are not *exclusive* to gliders and their presence would not be sufficient to infer
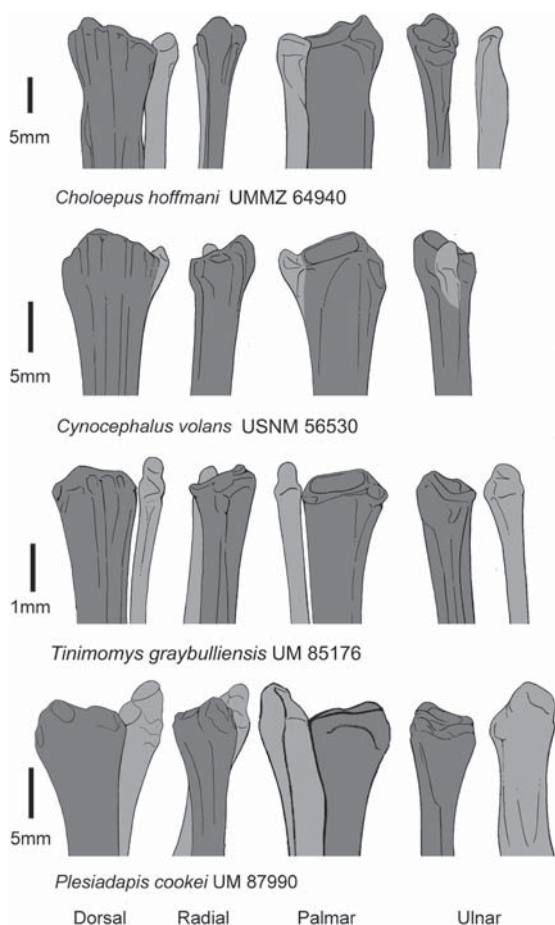
FIGURE 11.19. Right distal radii (dark gray shading) and ulnae (light gray shading) of select taxa (see labels in figure). *Choloepus* and *Cynocephalus* exhibit suspensory features shared by the micromomyid, but not by the larger plesiadapid. Note that *Plesiadapis* differs from the other three taxa in having a distal radius articular surface that is not as concave and is more distally oriented (compare elements in "palmar" and "ulnar" views), and an ulna that is relatively much larger. Scales on *Choloepus*, *Cynocephalus*, and *Plesiadapis* = 5 mm. Scale on *Tinimomys* = 1 mm.
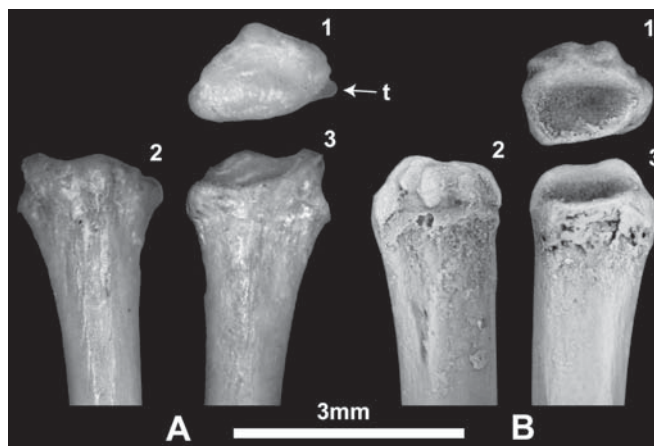

FIGURE 11.20. Comparison of distal radii of *Ptilocercus lowii* and micromomyid. (1) Distal, (2) ventral, and (3) dorsal views of the radii of A, primitive euarchontan mammal, *Ptilocercus lowii* (YPM 10179), and (B) a cf. *Tinimomys graybulliensis* (un-numbered, semi-articulated specimen from SC-26). Note that they are similar in having a ventrally oriented distal articular surface for the proximal carpal row that is also deeply cupped and marked by a prominent ridge projecting from the extensor surface. Note also in A1, a prominent tubercle (t) in *P. lowii*. This may be homologous to that discussed by Thorington et al. (2005) for sciurids, which separates the 1st from the 2nd extensor compartments. If so prominence of this feature is clearly not an indicator of gliding in euarchontans, as it is in squirrels. Scale = 3 mm.

gliding in a fossil. Given the similarities of *Ptilocercus* and *Tarsius* to sloths, gibbons and *Cynocephalus*, such a finding *could*, however, be confidently used to infer anti-pronograde behaviors in a fossil.

We began our evaluation of the paromomyid and micromomyid forelimb material by estimating the lengths of the forelimb bones of *Ignacius* (Figures 11.17 and 11.18). We were able to make well-constrained estimates of total shaft length for the humerus of *Ignacius* based on comparison to isolated elements of other paromomyids (Beard, 1989). Specifically, proportional scaling based on a humerus attributed to *Phenacolemur simonsi* USNM 442260 and one attributed to *Ignacius graybullianus* USNM 442259 allowed estimation of humerus length in UM 108210 (~42.02 mm). Radius length regressed on radial head area for a sample (n = 39) of extant archontans and rodents (gliding taxa included)

yielded a high correlation ($r^2 = 0.953$) and allowed an estimate of the total shaft length of the radius of *Ignacius* UM 108210 (42.2 ± 1.4 mm). Reconstructions based on these estimates are shown in Figure 11.18. Our results indicate that the radius length of *Ignacius* was between 0.97 and 1.04 times the humerus length. This is identical to the proportion seen in the large-bodied, late-Paleocene plesiadapiform, *Plesiadapis cookei* (Brachial index = 101). On the other hand, the brachial index of the micromomyid *Dryomomys* is quite high (117).

Although the distal radius is not preserved for new specimens of paromomyids, one has been described previously for Eocene *Phenacolemur simonsi* (USNM 442262 – see Beard, 1989). It is unlike that of *Cynocephalus*, suspensory taxa or *Ptilocercus*, but is fairly similar to those of plesiadapids such as *P. cookei* in having a shallower, distally oriented, distal articular surface. On the other hand, *Dryomomys* is most similar to *Cynocephalus* and *Ptilocercus* in having a deeply cupped distal articular surface that faces palmarly and ulnarly, and has a prominent ridge on its dorsal margin (Figures 11.19, 11.20A; Table 11.7).

With regard to other forearm features, *Ignacius* and *Dryomomys* differ from gliding squirrels and suspensory taxa in having an ulna with a relatively long anteriorly inflected olecranon process, which would seem to limit full-extension of the forearm (Figures 11.17 and 11.18). They differ from gliders specifically, in having a shallow trochlear notch. *Ignacius* differs further from gliders in the morphology of

its ulna by having a ridge for the pronator quadratus muscle and a longitudinal groove along its lateral surface for the extensor carpi ulnaris muscle (Figures 11.17 and 11.18). Unlike both suspensory taxa and gliders, its distal ulna is fairly robust. (Figures 11.17, 11.18, Table 11.7). On the other hand, *Dryomomys* and *Tinimomys* are characterized by a reduced distal ulna that lacks ridges for pronator quadratus (see Figures 11.6C and 11.19). In the arm, both *Ignacius* and known micromomyids are unlike gliders in having a laterally-oriented deltopectoral crest (e.g., Beard, 1993a; Sargis, 2002c)

TABLE 11.7. Comparative morphology of forelimb. Functional categories include antipronograde (ap) suspension (s), gliding (g), forearm extension (fe) and hand ventriflexion (hv). The forelimb shows a number of features that appear to be related to gliding, one of which is shared by mitten-gliders, marsupial gliders and rodent gliders. The distribution of the presence of a deep trochlear notch on the ulna suggests a function held in common between gliders and "non-clawed suspensory taxa." This similarity is probably related to the common need of both groups to have full arm extension (ae) at the elbow joint. The fact that clawed suspensory taxa tend to lack this feature suggests that in the mitten-glider, *Cynocephalus volans*, which has claws, the trochlear notch depth reflects its gliding behaviors. The forelimb of *C. volans* exhibits a number of features only explainable by its use of suspensory behaviors, given that it shares these features with suspensory taxa only. A deeply cupped radius with a dorsal ridge seems to be related to a habitually ventriflexed hand as used in suspensory postures (Figure 11.19). In the case of the arboreal treeshrew (*Ptilocercus*), it may reflect the use of under-branch clinging (Figure 11.20). The last feature, "long forearm relative to arm," is only lacking in the clawed vertical clinger and climber, *Cebuella pygmaea*, among extant taxa in this table. This is probably due to the fact that *C. pygmaea* has an arboreal quadrupedal component to its locomotor repertoire (Youlatos, 1999; see Jouffroy et al., 1973, for a study on the functional significance of the distribution of euprimate forelimb proportions).

Forelimb	Extant mammalian behavioral groups							Fossil plesiadapiforms	
	Mitten glider	Rodent gliders	Non-gliding suspensory mammal	Non-gliding clawed suspensory mammal	Marsupial gliders	Clawed committed arborealist	Non-gliding clawed vertical clingers and climbers	micromomyid	paromomyid
Ulna distally reduced or synostosed	ap	ap	ap	ap		ap		ap	
Narrow distal humerus	g	g							
Radial shaft narrow and sub-isometric in x-sec dimensions	g	g							
Proximally restricted deltopectoral crest on humerus	g	g			g				
Anteriorly projecting deltopectoral crest	g	g							
Deep trochlear notch of ulna	fe	fe	fe						
Short olecranon process of ulna	fe	fe	fe	fe					
Base of capitulum most inferior surface on humerus	s			s					
Deeply cupped, ventrolateral facing articular surface of radius	hv		hv	hv		hv		hv	
Antebrachium much longer than humerus	ap	ap	ap	ap	ap	ap		ap	

that extends almost as far distally as it does in non-gliding sciurids, and a mediolaterally broad distal end (Figure 11.18). Runestad and Ruff (1995) previously showed paromomyids to differ further from gliders in having humeri with relatively robust shafts, using a regression analysis where the dependent variable was humerus length and the independent variable was humeral TA (cross-sectional area at midshaft, calculated using the formula for the area of an ellipse). The humerus of UM 108210 has a cross-sectional area and reconstructed length (TA = 11.03 mm², L ~ 42.02 mm) that put it closer to the regression line describing the scaling of these dimensions in non-gliding mammals (Runestad and Ruff, 1995: Figure 11.3a) than that describing gliders; however, this result is clearly not independent of Runestad and Ruff's because the humeri they analyzed were the same as those used to generate a length estimate for UM 108210 (see above). Micromomyids are outside the range of the data used to generate Runestad and Ruff's regressions. We note, however, that the dimensions of the humerus of UM 41870 (TA = 1.34 mm², L = 14.58 mm), put it below both glider and non-glider lines of Runestad and Ruff (1995), indicating that it is fairly robust, unlike the humeri of extant gliding mammals.

In contrast to the features of suspensory taxa and gliders, the majority of traits of both paromomyids and micromomyids suggest habitually flexed forearms and adducted arms, characteristic of taxa that locomote using pronograde and/or orthograde postures (Bloch and Boyer, 2007). Additionally, a spherical capitulum and mediolaterally broad distal humerus in *Ignacius* and micromomyids (Beard, 1989) indicate axial mobility of the forearm, similar to that of arboreal euprimates that frequently incorporate manual grasping into locomotor and foraging activities. Features shared by micromomyids, *Cynocephalus*, gliders, suspensory taxa and *Ptilocercus* to the exclusion of *Ignacius*, may represent retentions from an ancestor shared by the micromomyid, *Cynocephalus*, and *Ptilocercus*, and/or frequent use of under-branch clinging and anti-pronograde behaviors by micromomyids (Bloch et al., 2003; Bloch and Boyer, 2007).

Axial Skeleton. The fact that different gliders have different means of locomotion when they are not gliding [e.g., *Cynocephalus volans* is suspensory, whereas *Glaucomys* locomotes above branches using an asymmetrical bounding gait (Thorington and Heaney, 1981)] results in vertebral columns that lack gliding-specific characteristics with regard to morphology or intrinsic proportions. However, all
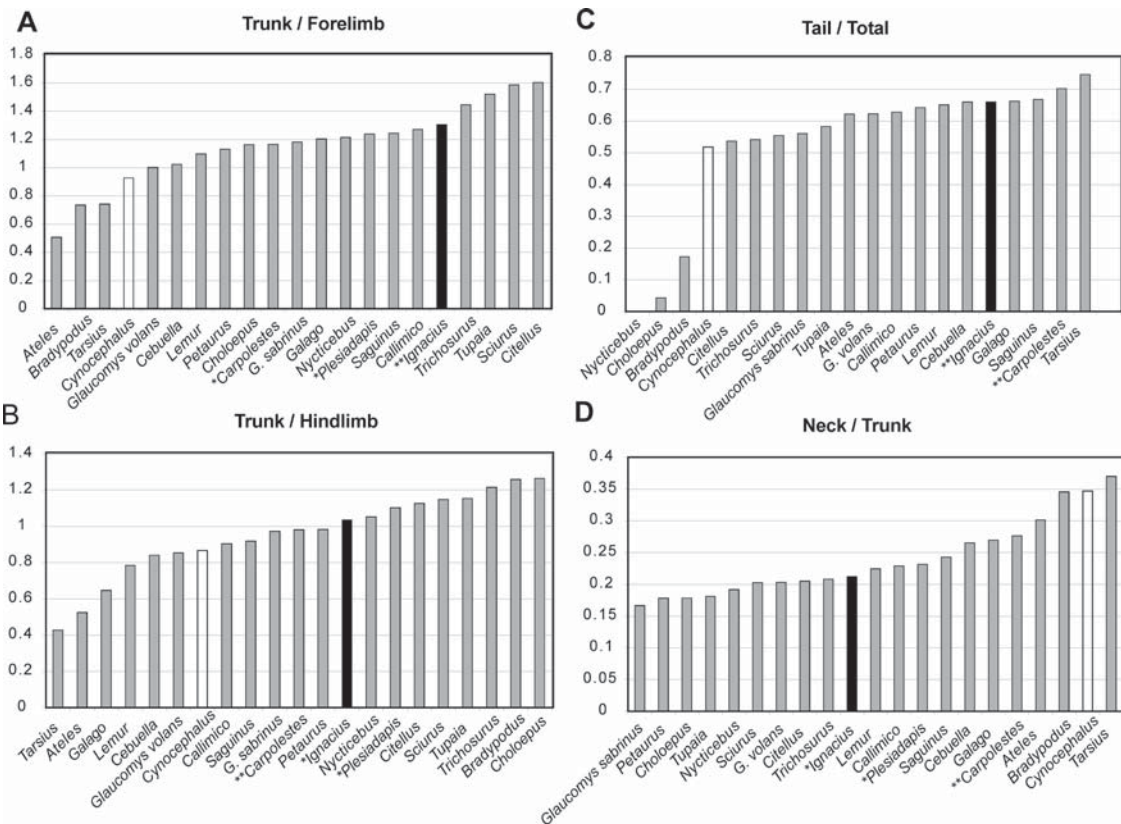
FIGURE 11.21. Selected trunk indices comparing *Ignacius* and *Cynocephalus*. Vertebral column and limb indices for a subset of the comparative sample of extant taxa used in this study are presented with individuals placed in order of increasing index to aid in identification of functional trends. *Ignacius clarkforkensis* (UM 108210 and UM 82606) is represented by a black bar in each plot, while *Cynocephalus volans* is represented by an unfilled bar. *Ignacius clarkforkensis* has indices that, in general, are separated from those of gliders and suspensory taxa by intermediate index values of agile arborealists and scansorialists. One asterisk by a taxon name indicates one parameter in the index has been estimated. Two asterisks by a taxon name indicate that both parameters were estimated. See Appendix II, Table 1 for specimens included.

extant gliding mammals have a short trunk (thoracic, lumbar and sacral regions) relative to the length of their limbs (Figures 11.21A, B), which actually reflects elongated limbs and is probably related to increasing the surface area for the patagium as mentioned previously (Thorington and Heaney, 1981; Beard, 1993b). Furthermore, gliding squirrels have been shown to possess relatively shorter tails than non-gliders (Thorington and Heaney, 1981). *C. volans* was also noted as having a short tail by Pocock (1926). Our data show its tail to be similar to that of non-primates in relative length, whereas quadrupedal arboreal euprimates (not

including slow climbing lorisines) typically have longer tails (Figure 11.21C; see also Stafford, 1999). The short tail of *C. volans* appears to be a result of a reduced number (~20) of caudal vertebrae that are relatively small.

New specimens of *Ignacius* preserve many vertebrae, which allow estimates of neck, trunk, and tail length for the first time (Figures 11.21–11.23). In UM 108210, parts of six of its seven cervical vertebrae are preserved. For our calculations, we assumed it had 12 thoracic vertebrae (four preserved in UM 108210), and 7 lumbars (three preserved in UM 82606). It has three sacral vertebrae. We estimate there were
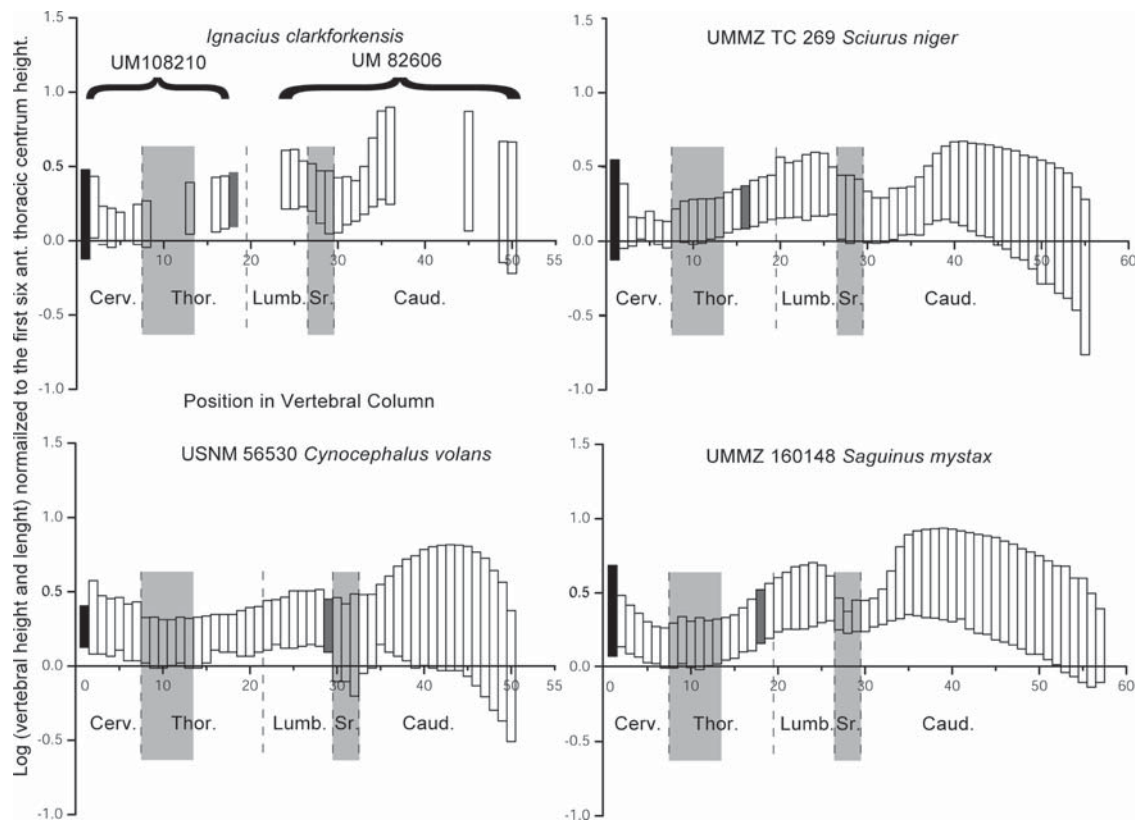

FIGURE 11.22. Comparison of vertebral profiles of *Ignacius* and *Cynocephalus*. Comparison of vertebral proportions following the method of Gingerich (1998). Y-axis depicts the logged value of two separate measurements, (1) vertebral body height and (2) vertebral body length: both are normalized to the average height of the first six anterior thoracic centra. Thus, if the boundary of a bar (vertebral body measurement) is positive, it is greater than the average height of the first six thoracics, whereas if it is negative it is lower. In white bars, the upper boundary represents the length (craniocaudal) of the body, while the base of the bar represents the height (dorsoventral). For black bars, the reverse is true (note that in all taxa depicted, it is only the atlas that has such proportions). Thus, the shorter the bar, the closer the vertebral body is to being square in lateral view. The gray areas depict those vertebrae most closely associated with pectoral (anterior thoracics) and pelvic (sacral) girdles. The gray bar represents the anticlinal vertebra, the boundary between vertebrae with caudally projecting spinous processes (vertebral positions to the left of the gray bar) and cranially projecting ones (vertebral positions to the right of the gray bar). In *Ignacius clarkforkensis* (UM 108210 and UM 82606) the neck is short, trunk vertebrae increase in height and length posteriorly, the sacrum is robust and the tail is long and robust. Such features suggest a relatively posteriorly shifted center of mass of the axial skeleton. Arborealists, *Sciurus* and *Saguinus*, depicted on the right have proportions similar to each other and *Ignacius. Cynocephalus volans*, on the other hand, exhibits a different pattern of vertebral proportions. In *C. volans*, the neck is long, trunk vertebrae remain roughly constant in size throughout the column, the sacrum is gracile, and the tail is shorter and more slender. Such features suggest a more anteriorly positioned center of gravity. We interpret proportional features in the paromomyid to be reflective of hind limb dominance in forward locomotion, while those of *C. volans* reflect a need for maneuverability while gliding, and equal emphasis on the fore and hindlimbs in suspensory locomotion. See Appendix II, Table 2 for measurements used to construct these plots.

TABLE 11.8. Comparative morphology of vertebral column. Functional categories include suspension (s), gliding (g), and bound galloping (bg). Note that long limbs relative to the trunk is a feature shared among all types of gliders. This feature may function to increase the area of the patagium in these taxa relative to their body mass. Features shared by *Cynocephalus volans* and suspensory taxa reflect vertebral columns that ventriflex with moderate, equivalent angular deviations among all intervertebral joints, producing a symmetrical arch. Taxa with such a configuration to the spine do not use pronograde bound-galloping behaviors in which extensive, powerful flexion and extension of the column is required (Slijper, 1946; Gambaryan, 1974). In bound-gallopers the back is rigid between most sets of vertebrae and there are just a few positions [e.g., T11–T12 and sacrolumbar joint in a treeshrew (see Jenkins, 1974)] where most of the flexion occurs.

Vertebral Column	Extant mammalian behavioral groups						Fossil plesiadapiforms	
	Mitten glider	Non-gliding clawed suspensory mammal	Non-gliding vertical clingers and climbers	Rodent gliders	Marsupial gliders	Non-gliding clawed scansorialist	micromomyid	paromomyid
Short trunk relative to limbs	g			g	g		?	
Long neck relative to trunk	s	s					?	
Caudally oriented lumbar spinous processes	s	s						
Craniocaudally deep lumbar spinous processes	s	s						
Short, laterally projecting transverse processes	s	s						
Four or more sacral vertebrae	s	s						
Ribs craniocaudally broad	s	s						
Longest sacral spinous process is 2nd or 3rd sacral vertebra						bg	?	bg
Short tail relative to trunk and neck								

~26 caudal vertebrae (10 preserved in UM 82606), which is the median from counts in 14 other arboreal and scansorial mammals from the UMMZ collection (including primates, rodents, treeshrews and marsupials) that have caudal vertebrae morphologies similar to those preserved in *Ignacius*. The length of the neck was obtained by adding the mean length of the third through sixth cervical bodies (representing the probable length of the seventh cervical body) to the sum of the lengths of the first through 6th cervical bodies. We obtained estimates of the total length of the trunk by estimating lengths of missing vertebrae. This was done by extrapolating trends of change in length along the column from preserved vertebral bodies into regions of the column for which vertebrae were not preserved (see Figure 11.22 for a graphic representation of the dimensions of vertebrae preserved for *Ignacius*). The same method was used to estimate tail length. The estimate of tail length is poorly constrained due to the greater variability in vertebral number in this region among mammals

(e.g., Shapiro, 1993). Even though these methods are far more likely to underestimate total trunk length than to overestimate it, our calculations indicate that *Ignacius* had a longer trunk relative to its limbs than any mammalian glider in our sample (Figure 11.21A, B). Shorter limbs in *Ignacius* make it more similar to scansorial mammals such as tree squirrels and tupaiid treeshrews. Furthermore, the estimated tail length in *Ignacius* is relatively greater than that for gliders including *C. volans*, but is in the range exhibited by euprimates (Figure 11.21C).

In contrast to the vertebral columns of gliders, the trunks of suspensory taxa are not distinctive in their length relative to that of their limbs. They are, however, distinctive in morphological and proportional features (Table 11.8), differing from agile arboreal primates and scansorial rodents in having a thoracic region with an increased number of vertebrae and a lumbar region with fewer elements comprising it (Sargis, 2001a; Shapiro and Simons, 2002). Furthermore, their verte-

bral centra are short and roughly the same size throughout the trunk (as illustrated by *C. volans*, Figure 11.22). In the lumbar region, the transverse processes are reduced and oriented laterally, the spinous processes are wide craniocaudally and oriented caudally, the vertebral body articulations are oriented perpendicular to the body's long axis, and the zygapophyseal articulations are oriented nearly perpendicular to the sagittal plane or are revolute (Shapiro, 1993; Sargis, 2001a). In some cases, the sacrum is shallow and elongate, and includes extra caudal vertebrae, beyond the standard count of three seen in many agile arborealists and scansorialists. Finally, the tail tends to be reduced as dramatically illustrated by sloths, lorises and hominoids.

C. volans exhibits characteristic features of both gliders and suspensory taxa, while also exhibiting some features that do not typically characterize either of these groups. These unique features include a craniocaudally wide atlas (Sargis, 2001a) and a long neck relative to the trunk [Figures 11.21D and 11.22; (Pocock, 1926)]. In contrast, the morphology and proportions of the vertebrae of *Ignacius* suggest agility, as well as an emphasis on the hindlimb in forward propulsion. *Ignacius* is comparable to primates and squirrels in having a narrow atlas and a short neck relative to the trunk (Figures 11.21 and 11.22).

The lumbar vertebrae of *Ignacius* differ from those of *C. volans* in having narrow, cranially angled spinous processes (Figures 11.23 and 11.24). Furthermore, long, cranioventrally oriented lumbar transverse processes that extend below the level of the centrum in *Ignacius* provide a dorsoventrally deep trough for the erector spinae muscles
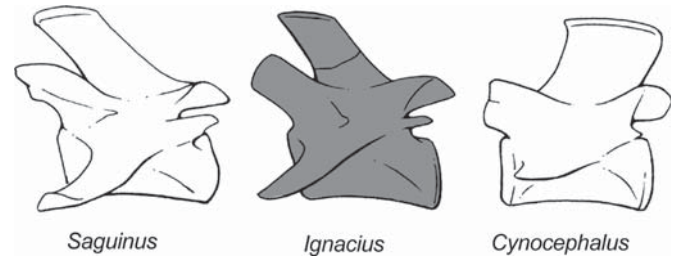
FIGURE 11.23. Comparison of antepenultimate lumbar vertebra of *Ignacius* and *Cynocephalus*. Antepenultimate lumbar vertebrae in lateral view of A, *Saguinus mystax* (UMMZ 160148), B, *Ignacius clarkforkensis* UM 82606 and C, *Cynocephalus volans* (USNM 56530). A and B have longer, more ventrally canted transverse processes, more cranially extended zygapophyses, and narrower, more cranially angled spinous processes than *C. volans*. The suite of features characterizing A and B reflects use of pronograde postures with a habitually ventriflexed back, in which a large range of powerful flexion and extension in the lumbus is possible compared to the condition of *C. volans*.
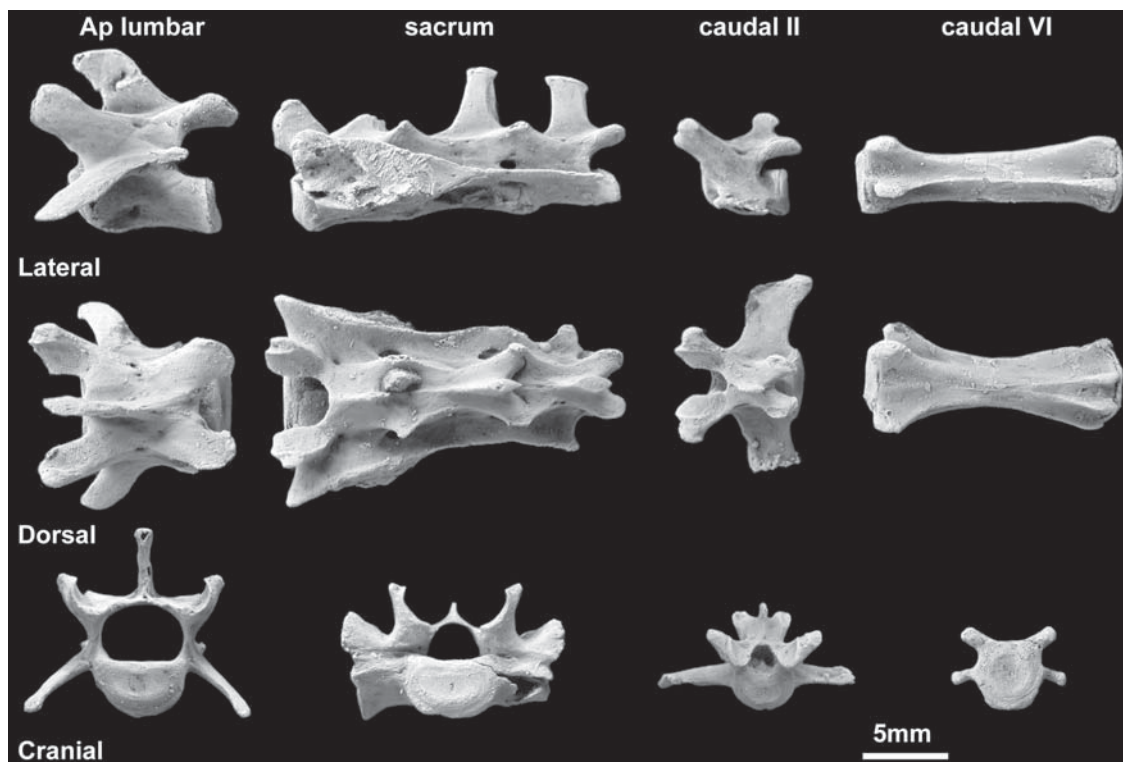
FIGURE 11.24. Vertebral elements from different regions of *Ignacius*. Representative vertebrae of *Ignacius clarkforkensis* (UM 82606). Note the cranioventrally oriented transverse processes in the antepenultimate (Ap) lumbar vertebra; the lack of a well-developed spinous process on the first sacral vertebra (which is unbroken) and large vertebral canal in the sacrum; the large vertebral canal in caudal II; and the robusticity and length of caudal VI. These features are not expected for an animal predominately using suspensory or gliding behaviors. Scale bar = 5 mm.

that extend the back (Benton, 1967; Shapiro, 1995; Sargis, 2001a).

We undertook two regression analyses to illustrate functional trends in lumbar vertebral morphology. These included (1) regression of body size on the dorsoventral depth of the trough formed by transverse processes and anterior zygapophyses of the posterior three lumbar vertebrae (Figure 11.25A), and (2) regression of lumbar spinous process shape (Figure 11.25B). These analyses successfully differentiated taxa that use asymmetrical bounding gaits from those that do not and allow us to comment on the locomotion of *Ignacius*. In the first analysis (Figure 11.25A), body size was represented by femoral cross-sectional area at mid-shaft (TA: x-axis) (see Runestad and Ruff, 1995). "Depth" (y-axis) was represented by the dorsoventral distance between the tip of the mammillary process on the prezygapophysis (dorsal) and the tip of the transverse process (ventral). The dorsoventral dimensions of the erector spinae and the dorsoventral distance of their attachments from the vertebral body should at least partly determine the strength of these muscles and the leverage they have on the intervertebral joints in the sagittal plane. These dimensions are captured by our measurements. We found the measurements from bounding taxa and non-bounding taxa to follow different regression lines. Both lines show slight positive allometry (Because TA [x-axis] is an area and the y-value is a length, isometry would be represented by a slope of 0.5 in log-log space). Taxa that leap and bound have deeper vertebrae (high y-value) for a given femur area, probably because they incorporate forceful flexion and extension of the back into their gaits and require better leverage and more force out of their erector spinae muscles than taxa that do not. *Ignacius* (large

black circle in Figure 11.25A) falls in with bounding taxa. *Cynocephalus* (black triangle), as well as some other plesiadapiforms, plots with non-bounders. In the second regression (Figure 11.25B), lumbar spinous process axial (Ax) length (x-axis) is plotted against its craniocaudal (CC) length (y-axis). Again, bounders are separated from non-bounders. In this case, the bounder regression line is lower because the spinous processes of the posterior three lumber vertebrae of most bounders are smaller in their craniocaudal dimensions relative to their axial (dorsoventral) length compared to those of non-bounders. Narrower spinous processes result in more sagittally mobile backs, required for a bounding gait, which utilizes substantial flexion and extension of the vertebral column to increase the stride length. Again, *Ignacius* clearly falls with bounding taxa in having very narrow lumbar spinous processes, while *Cynocephalus* (black triangle) falls with the other group. Interestingly, other plesiadapiforms plot with *Ignacius* in this feature.

Finally, the posterior lumbar vertebrae are larger and more elongate than the thoracic vertebrae (Figure 11.22) in *Ignacius* and bounding taxa, compared to those of suspensory taxa. Together, these features provide strong evidence for utilization of bounding and leaping that incorporates sagittal flexion and extension of the trunk into the gait (Slijper, 1946; Jenkins, 1974; Shapiro and Simons, 2002). Unlike suspensory taxa, the paromomyid sacrum has only three vertebrae (Figure 11.24), which form a large vertebral canal. *Cynocephalus* has three to four sacrals, with the first one or two caudal vertebrae incorporated by fusion of the bodies and transverse processes into the sacrum in some individuals (Figure 11.18), making it similar to suspensory taxa. Furthermore, in *Ignacius* the spinous process on the first sacral vertebra is short (Figure
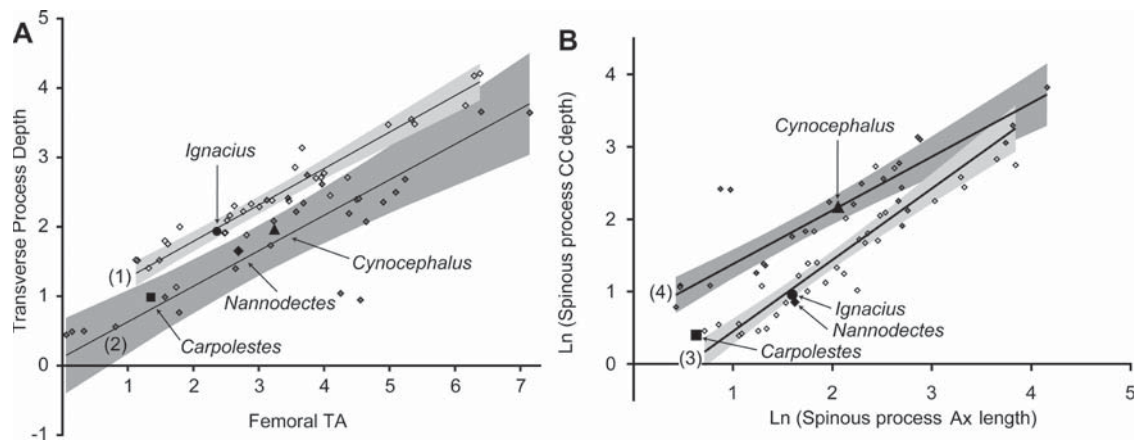
FIGURE 11.25. Regression of lumbar vertebrae against body mass proxies. A, Natural log femoral TA (transverse area) vs average depth of the posterior three lumbar vertebrae in bounding (open diamonds) and non-bounding/ambulatory (gray diamonds) taxa.. See Appendix II, Table 1 for specific taxa included in this analysis. (1) Bounder line: y = 0.524x + 0.74, R2 = 0.93. (2) Non bounder line: y = 0.512x + 0.12 R2 = 0.73. Sample includes 37 taxa. B, Natural log average spinous process length vs. depth for the posterior 3 lumbar vertebrae of bounding (open diamonds) and non-bounding/ambulatory (gray diamonds) taxa. (3) Bounder line: y = 0.91x − 0.45 R2 = 0.92. (4) Non-bounder line: y = 0.79 x + 0.6 R2 = 0.77. Sample includes 37 taxa. See Appendix II, Table 1 for specimens included in this analysis. Specimens marked with a "1" in the table were considered "bounders" for this analysis. Those marked with "0" were considered "non-bounders."

11.24). Such a configuration is similar to that in hindlimb-propelled taxa in which a large degree of flexibility at the lumbosacral joint is required, including scansorial tupaiid treeshrews (Jenkins, 1974) and squirrels. Not only does the spinous process of the first sacral vertebra not impede extension at this joint, but the supraspinous ligament, which spans two vertebrae instead of one, permits more mobility than it does when separated more distinctly into two segments (Gambaryan, 1974).

Morphology of the rib cage of both *Ignacius* and the *Dryomomys* suggests against the suspensory slow-climbing and bridging used by *C. volans*, suspensory taxa and *Ptilocercus lowii* (Sargis, 2001a) (Table 11.8). Whereas the ribs of suspensory or bridging taxa are craniocaudally broad,

Ignacius and the *Dryomomys* have narrow ribs like those of scansorial tree squirrels and tupaiid treeshrews (Sargis, 2001a). Broad ribs may serve to increase rigidity of the thorax (Jenkins, 1970; Sargis, 2001a) and/or result in a more powerful forelimb by providing larger areas of attachment for muscles of the abdomen and shoulder girdle (e.g., serratus, pectoralis and obliquus abdominus muscles).

Innominate. The innominate of paromomyids is unlike that of either extant eutherian gliders or suspensory taxa. In these living forms, the innominate is distinctive in having a relatively long, narrow ilium (Walker, 1974) with a long post-auricular shaft; a short ischium; and a narrow pubic symphysis (Figures 11.18, 11.26; Table 11.9). Furthermore, in suspensory taxa the acetabulae are dorsolaterally oriented.

TABLE 11.9. Comparative morphology of innominate. Functional categories include suspension (s), gliding (g), bound-galloping (bg), and vertical clinging (vc). In the far left column (feature names), the first three features are separated from others by a gray background and a thicker line. This is to indicate that they are different states of the same feature. The only feature that seems to relate to suspensory behaviors is dorsolateral orientation of the acetabulum, although *C. volans* does not exhibit it. A ventrolaterally oriented acetabulum is found only in the most terrestrially-adapted rodents, among extant behavior groups in this table. The fourth and fifth features are present in taxa that hold the thigh in a flexed, abducted position while utilizing orthograde postures on vertical supports (Jenkins and Camazine, 1977; Beard, 1991). In these taxa, a large range of flexion-extension is sacrificed for mobility in abduction-adduction.

Innominate	Extant mammalian functional groups							Fossil plesiadapiforms	
	Mitten glider	Non-gliding clawed suspensory mammal	Non-gliding vertical clingers and climbers	Rodent gliders	Clawed committed arborealist	Marsupial gliders	Non-gliding clawed scansorialist	micromomyid	paromomyid
Acetabulum faces dorsolaterally		s							
Acetabulum faces laterally									
Acetabulum faces ventrolaterally							bg		
Craniocaudally elliptical acetabulum	vc	vc	vc		vc	vc		vc	vc
* Cranially buttressed acetabulum	vc	vc	vc		vc	vc		vc	vc
** Long ilium relative to ischium									
Narrow ilium		***							
Caudally positioned, narrow pubic symphysis									

[a]This feature is better referred to as "caudally-reduced" rather than "cranially buttressed," as it is seems to be the reduction of the caudal part of the acetabular lip that affects the apparent cranial buttressing. Such reduction also results in a shallower acetabulum and more mobile hip joint in these taxa.

[b]This feature does not seem to distinguish sloths or large bodied suspensory euprimates from vertical clinging and leaping euprimates, like *Tarsius*. Given that it is also seen in primitive "plesiadapiforms" (i.e., the micromomyid exhibits it, but *Ignacius* does not), there may be some phylogenetic valence to it. In fact, retention of primitive eutherian (or therian) morphology is a likely explanation for all gray features without functional codes in this table as they are present in *Ukhaatherium* (Horovitz, 2003).

[c]Neither sloths nor suspensory euprimates have a narrow ilium, but bats and the slow climbing euprimate, *Nycticebus*, do.
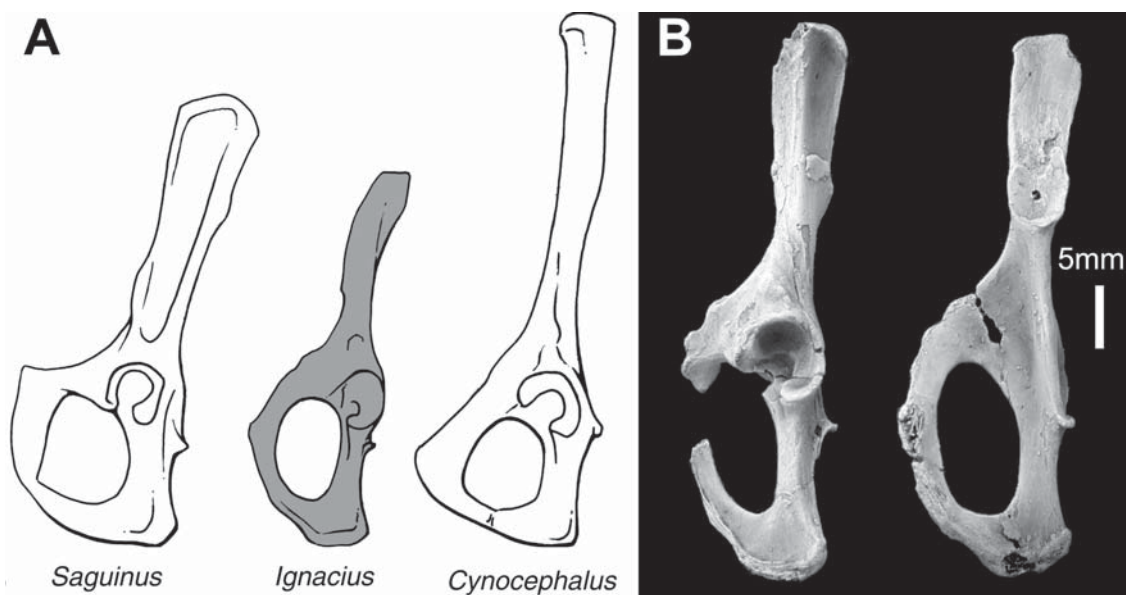
FIGURE 11.26. A, Left innominates in lateral view: *Saguinus mystax* (UMMZ 160148); *Ignacius clarkforkensis* (UM 82606); *Cynocephalus volans* (USNM 56530). Elements are standardized to ischium length. B, Left innominate in lateral view (on left) and medial view (on right) *Ignacius clarkforkensis* (UM 82606). Note the relatively shorter and more flaring ilia, the longer and/or more superiorly extended pubic symphysis, the larger ischial tuberosity and the inferiorly positioned ischial spines in both *Ignacius* and *Saguinus*. Scale bar in B = 5 mm.

Overall, both gliders and suspensory taxa have an elongate, gracile innominate with limited areas for attachment of muscles associated with hip flexion and extension during hindlimb-powered locomotion.

A gracile innominate with a relatively small pubic symphysis does not seem well-suited to resist strains experienced in pronograde postures that result from transmission of the animal's weight through this element. While these features characterize gliders, they are not necessarily exclusive to gliders, as was the case for many of the forelimb features. Specifically, didelphid marsupials, *Ptilocercus lowii* (Sargis, 2002a, b, c), and the proteutherian, *Ukhaatherium* (Horovitz, 2003) are characterized by narrow ilia. The latter two taxa are further characterized by a craniocaudally narrow, caudally positioned pubic symphysis, and a short ischium.

In general, *Ignacius* differs from gliding and suspensory taxa in having a robust innominate, with large areas of attachment for flexors and extensors of the hip (Figure 11.26). In this way, it is similar to other taxa that use an asymmetrical, hindlimb-propelled, bounding gait (e.g., tree and ground squirrels, and tupaiids). Specifically, *Ignacius* has a short ilium relative to its ischium, as well as a flaring dorsal iliac blade (visible in Figure 11.26B), allowing room for attachment of thigh extensors (gluteal muscles) and on its anterior aspect, thigh flexors (iliacus muscle). Its long ischium and large ischial tuberosity provide a long lever arm for other thigh extensors (hamstring muscles). There is a robust anterior inferior iliac spine for the origin of the rectus femoris muscle, a flexor of the hip joint and extensor of the knee joint. The extensive pubic symphy-

sis provides stability and a large area of attachment for the adductor muscles. Finally, the acetabulum in *Ignacius* is more laterally directed than it is in suspensory taxa, indicating that habitual postures and stress orientations were different. In summary, the innominate of *Ignacius* is different from that of gliding and suspensory mammals in nearly every functionally salient respect identified by us.

Micromomyids actually appear quite similar to *Cynocephalus volans* and *Ptilocercus lowii* in the morphology of their innominate, having narrow ilia, a long post-auricular segment of the blade, a short ischium and a craniocaudally narrow, distally-positioned pubic symphysis (Figure 11.7A, B). However, given the distribution of these features outside of gliders and suspensory taxa, it is tenuous to argue that they offer support for gliding or suspension in this group. It is more likely that these reflect antipronograde behaviors more generally and/or are primitive euarchontan features (Sargis, 2002a), as we suggested for some of the forelimb features.

Hind limb. Paromomyids and micromomyids lack hind limb features that generally characterize gliders and suspensory taxa. With regard to interlimb proportions Thorington and Heaney (1981) demonstrated that the intermembral index is higher in gliding rodents (generally greater than 80) than non-gliders. The index of suspensory taxa is also high, generally over 100 (Godfrey, 1988) (Figure 11.27). *Cynocephalus* has an index of 93. Thus, we expect a similarly high index in fossil mitten-gliders, whether it reflects gliding or suspension. However, we note that among clawed euarchontans and marsupials, many generalized arborealists and vertical
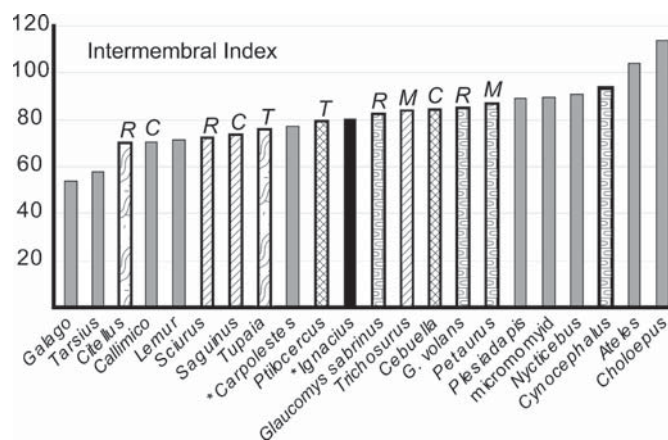
FIGURE 11.27. Intermembral indices of select taxa, presented in order of increasing index to aid in identification of functional trends. Taxa from a given higher-level clade are designated by a unique letter above the bars representing them. "R" = Rodentia; "C" = Callitrichinae; "T" = [treeshrew] Scandentia; "M" = marsupial. *Ignacius* is in black to highlight its position. An asterisk in front of a taxon name indicates that one of the parameters of the index was estimated. Note that in each clade of mammals the most terrestrial members (wavy lines) have the lowest intermembral indices, the more arboreal ones (diagonal lines) and those that spend time on large diameter vertical supports (cross-hatched) have successively higher indices; the gliders (closely packed horizontal lines) and suspensory taxa have the highest. For instance, among Callitrichinae, *Saguinus* is more pronograde and scansorial than *Cebuella* (e.g., Youlatos, 1999). Furthermore, *Callimico goeldii* has the shortest intermembral index of any callitrichine and is not known to utilize large diameter vertical supports or the exudate resources procurable there. Note that the ground squirrel *Citellus* has shorter forelimbs than the tree squirrel *Sciurus*. Both have shorter forelimbs than the gliding squirrels *Glaucomys sabrinus* and *volans*. This trend holds for marsupials as well, with the locomotor generalist *Trichosurus* exhibiting shorter forelimbs than the glider, *Petaurus*. Behavioral overlap occurs in the region of high indices, such that a high intermembral index is not evidence of gliding by itself; however, there seems to be a lower limit to the intermembral indices exhibited by gliders. That limit appears to be somewhere around 80 [although out of eight species of flying squirrels, one (*Eoglaucomys*) has an index below 80 (Thorington and Heaney, 1981)]. Thus, although a strong case for gliding in a fossil taxon cannot be made on the basis of a high index alone, a strong argument against it can be made on the basis of a low index. Almost no extant gliders have an index as low as that of *Ignacius*. See Appendix II, Table 1 for included specimens. If more than one individual is marked per taxon, the intermembral index shown represents an average of those individuals.
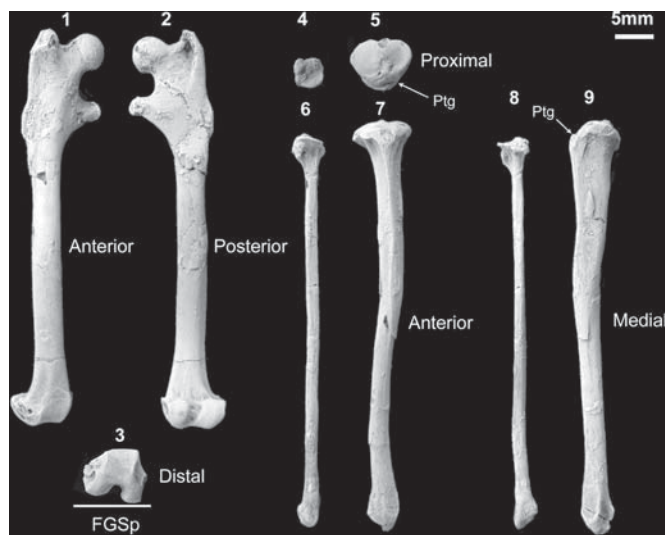
FIGURE 11.28. Illustration of hindlimb elements of UM 82606. Right femur of *Ignacius* in (1) anterior, (2) posterior and (3) distal views. View (3) is oriented so that the greater trochanter and fovea capitis femoris form a horizontal line (FGSp) on the page. Note that the condyles face posterolaterally and would have facilitated postures in which the feet were widely spaced (abducted). The right tibia of *Ignacius* is depicted in (5) proximal, (7) anterior and (9) medial views. The right fibula is shown in (4) proximal, (6) anterior, and (8) medial views. The broad shelf on the proximal fibula (4), oriented perpendicular to the shaft axis, gives it mobility with respect to the tibia. On the distal tibia (7), lateral inclination of the astragalar facet presumably accommodates asymmetry of margins of tibial facets on the astragalus when the foot is dorsiflexed at the crurotarsal joint. On (9), note that the patellar tendon groove (Ptg) is located distal to the tibial plateau. FGSp – Plane defined by Fovea capitis femoris-Greater trochanter-Shaft. Scale = 5 mm.

TABLE 11.10. Comparative morphology of hindlimb. Functional categories include mitten-gliding (mg), suspension (s), gliding (g), bound-galloping (bg), pronograde (p), vertical clinging (vc). The second and third features are considered to characterize eutherian suspensory taxa, as these states are rare among eutherians otherwise, especially primitive ones. These features are more common in phalangerid marsupials, and likely relate to function differently. For example they are present in *Petaurus*, but do not seem to reflect suspensory behaviors in it, because it is a glider and agile pronograde arborealist. For the feature "**Proximal insertion of patellar tendon on tibia,**" the present state signifies a tendon that inserts at the level of the tibial plateau, while the absent state signifies a tendon that inserts distal to the plateau. Paromomyids, micromomyids, sciurids and *Petaurus* have a groove positioned distal to the plateau by a proportionally similar distance. In vertically clinging and leaping euprimates, the groove is much more distally positioned. Taxa that exhibit the present state for the feature "**Proximal tibial shaft lacks cnemial crest**" include *Nycticebus, C. volans*, and *Choloepus*, but not hylobatids. Euprimates and tree squirrels have the most prominently developed crests, among those with the absent state for this feature. The lack of features 17 through 20 probably reflects more active, agile pronograde locomotion in rodent gliders and scansorialists.

Hindlimb	Extant mammalian functional groups							Fossil plesiadapiforms	
	Mitten glider	Non-gliding suspensory mammal	Non-gliding vertical clingers and climbers	Rodent gliders	Clawed committed arborealist	Marsupial gliders	Non-gliding clawed scansorialist (rodent)	micromomyid	paromomyid
Proximal fibula, reduced or fused to tibia	*s	*s							
Short femoral neck	s	s							
Femur lacking third trochanter	s	s							
Femoral condyles broadest distally	s	s							
Concave lateral tibial condyle	s	**s							
Tibial condyles perpendicular to tibial shaft	s	***s							
Proximal insertion of patellar tendon on tibia	s	***s							
Proximal tibial shaft lacks cnemial crest	ap	***ap		ap					
Shallow to absent fovea capitis femoris	s	s							
Distally facing femoral articular surface for tibia	s	s							
Reduced greater trochanter	s	s							
Superiorly extended greater trochanter			p	p		p			p
Reduced lesser trochanter	s	s							
lesser trochanter distally positioned and medially projecting			vc		vc			vc	vc
Femoral condyles face posteromedially	s	s							
Femoral condyles face posterolaterally			vc		vc			vc	vc

(continued)

TABLE 11.10. (continued)

Straight femoral shaft										
Distally restricted, shallow patellar groove										
Shallowly-grooved distal tibial facet										
Shallow femoral condyles (AP)										

[a]A reduced proximal fibula, specifically, only characterizes bats and *Cynocephalus volans*, among taxa that utilize suspension. Sloths fuse their proximal fibulae, as do arboreal porcupines. The common functional trend may be the reduction in number of independent bones that reach the knee. We therefore recognize these morphologically different states as functionally equivalent.

[b]The feature **"Concave lateral tibial condyle"** is not exhibited by the sloth, but characterizes the gibbon and other suspensory taxa. Its absence in the sloth is taken as a primitive retention.

[c]These features do not characterize *Hylobates*. Most features of the hindlimb that otherwise reflect suspensory postures are absent from gibbons, probably because they mainly use bimanual suspension which does not involve the hindlimbs.

clingers and climbers have an intermembral index between 80 and 100, such that this ratio does not distinguish them from gliders (Sussman and Kinzey, 1984; Godfrey, 1988; Fleagle, 1999; Sargis, 2002b) (Figure 11.27).

Ignacius appears to have an intermembral index of ~80, which is comparable to that of most callitrichines except *Cebuella*, for which it is ~84 (Fleagle, 1999). Other plesiadapi-forms have indices that range between ~77 (for *Carpolestes*) and 89 (for *Plesiadapis cookei*) and 93 (for micromomyids). Such proportions argue strongly against use of gliding or suspensory behaviors by *Ignacius*, because its index is below the typical ranges of extant mammals that use such behaviors.

In addition to other findings reviewed by us above, Runestad and Ruff (1995) also found that gliders are characterized by a gracile femur and tibia. They evaluated gracility in hind limb by regressing cross-sectional area on length for each element, as they did for the forelimb elements. Plotting dimensions of known paromomyid and micromomyid material suggested against gliding for the former; however, they did not interpret the position of micromomyids, which have limbs that are beyond the limits of their regression because they are too small, as for the forelimb regression. Out of curiosity we plotted some euprimate postcranial material with Runestad and Ruff's data and found that *Saguinus mystax* (UMMZ 160148) plotted very close to the glider line for both femur and tibia dimensions, while *Smilodectes mcgrewi* (UM 95526), plotted with gliders for femur dimensions. This further supports Runestad and Ruff's (1995) warning that many non-gliders also have gracile limbs such that even this feature cannot be used on its own to infer gliding in a fossil. Nonetheless, we evaluated the gracility of the hind limb elements of *Ignacius*, UM 82606 (Figure 11.28), using the regressions of Runestad and Ruff (1995). Its femur plots midway between the glider and non-glider regressions (length = 53 mm, TA = 10.59 mm). However, the tibia has proportions that put it substantially closer to their non-glider regression line (length = 55 mm, TA = 7.70 mm). We take these

results as consistent with those from our other analyses that suggest against a gliding habitus.

As for the forelimb, Thorington et al. (2005) noted a number of morphological features of the hind limb distinguishing arboreal sciurids from gliding sciurids, including a lesser trochanter that may extend medial to the femoral head; and a third trochanter that is more pronounced and positioned distal to the lesser trochanter in non-gliders. Gliding squirrels were proposed to also differ from non-gliding squirrels in having a rod-like tibia, a characteristically long distal tibia-fibula articulation and a sharply grooved tibial articular surface on the astragalus (Thorington et al., 2005). While some of these features may be useful indicators of gliding in euarchontans, as with the forelimb, others have a distribution among extant members showing that they do not necessarily reflect gliding (Table 11.10). Specifically, a proximally positioned third trochanter does not always indicate gliding because it characterizes many euprimates (e.g., Dagosto et al., 1999). Furthermore, the last two features of the leg and ankle cited by Thorington et al. (2005) to characterize gliding squirrels, while generally lacking in extant euarchontans and fossil "plesiadapiforms," are present in proposed euarchontan outgroups, Nyctitheriidae (Hooker, 2001) and basal gliroids (Murphy et al., 2001b; Meng et al, 2004; Rose and Chinnery, 2004). These outgroups have been reconstructed as more scansorial than most "plesiadapiforms" (Hooker, 2001; Bloch et al., 2003; Rose and Chinnery, 2004), and the ways in which they differ from "plesiadapiforms" in the distal crus and ankle likely represent a less axially mobile crurotarsal joint, corresponding to more frequent use of scansorial locomotion (Szalay 1984).

Both *Ignacius* and micromomyids differ from rodent gliders in having a femur with a lesser trochanter that extends medial to the femoral head, and a tibia with a prominent cnemial crest. *Ignacius* and other paromomyids differ further in having a femur with a distinct third trochanter that arises from the shaft distal to the lesser trochanter (Figure 11.28), a short distal tibia-fibula articulation, and a

shallowly grooved tibial articular surface of the astragalus. On the other hand, micromomyids appear to have a third trochanter that arises lateral to the lesser trochanter (Figure 11.7B; Beard, 1993a: Figure 10.10), a longer distal tibia-fibula articulation (Figure 11.7A, B) and a more sharply grooved tibial articular surface on the astragalus, suggesting they retain the primitive condition for Euarchonta (Szalay and Drawhorn, 1980; Bloch et al., 2003; Bloch and Boyer, 2007).

Suspensory taxa and *Cynocephalus* exhibit features associated with habitually extended limbs that bear tensile (not compressive) loads, frequent use of small diameter supports, and infrequent reliance on the hind limbs in powerful propulsion. The hind limbs of *Ignacius* and micromomyids differ in having features that suggest habitual flexion at the hip and knee joints, use of large diameter supports instead of small diameter ones, and the capacity for powerful flexion and extension of the hind limb.

Features that suggest habitual flexion at the hip and knee of paromomyids and micromomyids are seen in the femoral head, and the femoral condyles and tibia, respectively. First, the articular surface of the femoral head extends onto the posterolateral part of the neck (Figure 11.28), which gives it a somewhat oval shape. Thus, the closest packed

articulation between the head and elliptical acetabulum is achieved when the femur is in a flexed, abducted position (Jenkins and Camazine, 1977; Beard, 1991), as shown in Figure 11.32.

Second, in paromomyids and micromomyids, buttressing of the medial margin of the patellar groove relative to its lateral margin also reflects use of postures in which the thigh was flexed and abducted, and the knee joints were flexed. In such a posture, medial buttressing of the patellar groove would help prevent medial and ventral dislocation of the patella. Such dislocation would otherwise tend to occur in this posture, because the line of action of the quadriceps muscles (predominantly rectus femoris), which runs from the patellar groove on the tibia to the anterior inferior iliac spine on the innominate, is located medial and ventral to the anteroproximal aspect of the patellar groove of the femur, where the patella sits.

Third, the femoral condyles of *Ignacius* and the micromomyid are anteriorly restricted, posteriorly extensive, and broadest at their posteroproximal margin. These features result in a knee that is more stable when tightly flexed, because the tibia articulates with the posteroproximal part of the femoral condyles where they are broadest. Thus forces transmitted through the knee in a flexed position would be distributed over a greater area of articulation than positions in which the knee was extended. In contrast, suspensory taxa that utilize postures
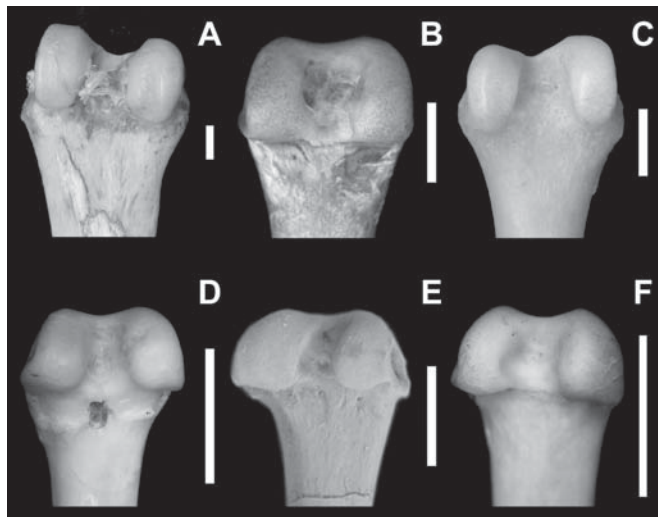
FIGURE 11.29. Comparison of femoral condyles of *Ignacius* to pronograde and antipronograde mammals. Distal femora in posterior view with the distal end pointing up. A, *Choloepus hoffmani* (left); B, *Cynocephalus volans* (right); C, *Nycticebus coucang* (right); D, *Tupaia glis* (right); E, *Ignacius clarkforkensis* (right); F, *Cebuella pygmaea* (right). Outer margins of the condyles on A–C are parallel to one another, reflecting the capacity for extreme knee extension (used during under-branch suspension), and postures that require variable degrees of knee flexion. The condyles of D–F appear wedge-shaped in this view because the outer margins of the condyles converge distally. These taxa use scansorial locomotion, resting postures in which the knees are flexed, and infrequently suspend below branches with extended limbs. See Appendix II, Table 1 for specimen numbers. Scale = 5 mm.
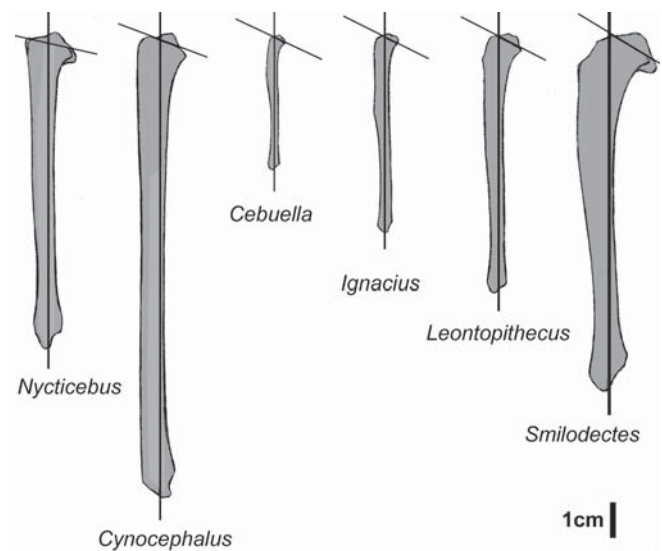
FIGURE 11.30. Right tibiae in medial view showing angle formed between shaft and medial facet of tibial plateau. From left to right, taxa depicted (and the angle formed) are the following: *Nycticebus coucang* (73); *Cynocephalus volans* (69); *Cebuella pygmaea* (65); *Ignacius clarkforkensis* (64); *Leontopithecus sp.* (62); *Smilodectes mcgrewi* (60). *Nycticebus* and *Cynocephalus*, which frequently use extended limb postures, have medial facets at more of an angle to the shaft (they approach perpendicular). Taxa that are more pronograde, or interpreted to have been leapers, have medial facets at less of an angle to the shaft (closer to parallel). See Appendix II, Table 1 for specimen numbers. Scale bar = 1 cm.

with varying degrees of knee flexure (including full extension) tend to have more anteriorly extensive condyles that are equal in mediolateral breadth along their circumference.

Looking at a posterior view of the distal femur (Figure 11.29), it is seen that the paromomyid and micromomyid condition is reflected by condyles that appear wedge-shaped because their outer margins "converge" distally. Such a form also characterizes other scansorial mammals, including some treeshrews and callitrichines. In contrast, Gebo (1989) noted that lorisines were characterized by "parallel" condyles and differed from galagos in this regard. We agree with this assessment by Gebo, and note that sloths and *Cynocephalus* also exhibit "parallel" condyles.

Yet another feature that suggests a flexed knee joint is the angle formed between the tibial shaft and the posteriorly tilted medial tibial condyle (Figure 11.30). *Ignacius* and the *Dryomomys* have more acute angles than *Cynocephalus* and *Nycticebus*. That is, in the former taxa, the medial facet faces more posteriorly than proximally, such that shear forces experienced across the knee joint when flexed, would be reduced.

Features indicating a wide foot stance, and thus large diameter support use in *Ignacius* include femoral condyles that face laterally with respect to the femoral neck and shaft (Figure 11.28, view 3), and tibial condyles that are oriented slightly laterally relative to the tibial shaft (the micromomyid specimens could not be evaluated for these features). As a result of these features a flush articulation between the posterior aspect of the femoral condyles and tibial plateau results in a laterally projecting tibial shaft.

Finally, paromomyid and micromomyid hind limbs appear to be suited for powerful flexion and extension relative to suspensory taxa. Features indicating this include a greater trochanter that extends superiorly above the femoral head in *Ignacius*, although not to the degree exhibited by tupaiid treeshrews (Sargis, 2002a); and a lesser trochanter that is distally positioned and medially extended in both *Ignacius* and the micromomyid (Figure 11.28). An extended greater trochanter increases the leverage that the gluteal muscles attaching to it have in thigh extension (e.g., Rose, 1999). The medial extension of the lesser trochanter allows the femur to remain somewhat abducted even when the iliopsoas muscles are fully contracted and the femur is fully flexed. Furthermore, the distal position of the lesser trochanter gives the iliopsoas muscles a long lever arm that would have made them effective at holding the thigh in flexed positions and capable of easily flexing the thigh during vertical climbing (Rose, 1987). Such prominent trochanters flanking the femoral head, while providing leverage for muscles, consequently also reduce mobility at the hip joint, which further suggests against suspensory behaviors. Unlike the fossil taxa, *C. volans* and tree sloths both have a femoral neck with a central axis nearly in line with that of the femoral shaft, and greatly reduced greater and lesser trochanters (White, 1993). The former two features have been directly related to hip joint mobility and suspensory behaviors in both primates and xenarthrans (White, 1993).
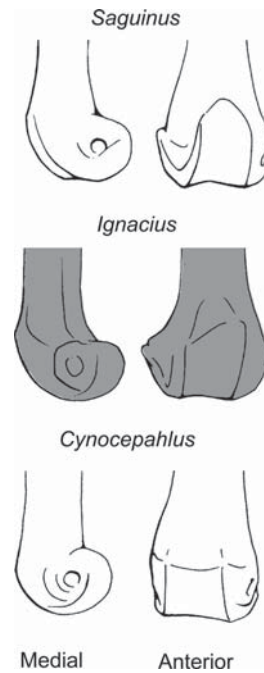
FIGURE 11.31. Distal femora showing patellar morphology. From top to bottom is *Saguinus mystax* (UMMZ 160148), *Ignacius clark-forkensis* (UM 82606), and *Cynocephalus volans* (USNM 56530) in medial and anterior view. Note that despite being an agile arborealist the distal femur in *Saguinus* is nearly identical to that in *Ignacius*. Both of these taxa differ only slightly from the condition in *C. volans* with respect to patellar groove morphology. However, other features discussed and figured in this chapter differentiate the fossil and *Saguinus* from *C. volans*, showing the former two taxa to be capable of pronograde postures and to be more agile than the latter. Images are standardized to distal femur mediolateral breadth.

Finally, features of the tibiae also suggest hind limbs used for quick forward propulsion in orthograde or pronograde postures in both the paromomyid and micromomyid. First, the tibiae are relatively long, with crural indices of the paromomyid and micromomyid being 104 and 127, respectively. Furthermore the tibiae of the paromomyid and micromomyid have a distally positioned groove for the patellar tendon (Figure 11.28: view 5 and 9), a prominent cnemial crest (as mentioned above) that provides room for extensors of the toes and foot, and deep popliteal fossa that provides room for pedal and digital flexor muscles (Figure 11.28: view 9). *C. volans*, suspensory, and slow climbing taxa have a more proximal attachment of the patellar tendon, and a reduced cnemial crest and popliteal fossa (consequently, the tibia is "rodlike").

We note that this view of paromomyid and micromomyid hind limbs as suggesting agile arboreality is slightly different than that previously supported (e.g., Beard, 1989; 1991). One feature frequently cited by Beard (1989, 1990,1991) as limiting "plesiadapiforms" in their agility is a proximodistally short patellar groove (Figure 11.31). It is characteristic of all known plesiadapiforms (e.g., Beard, 1993a). However,

we note that callitrichine euprimates, many agile marsupials (e.g., *Petaurus breviceps*) and *Ptilocercus lowii* (e.g., Sargis, 2002b) have patellar grooves similar in shape to those of known "plesiadapiforms." While animals with narrow, proximally extended grooves, like tupaiid treeshrews and prosimian euprimates, are usually extremely agile and capable of acrobatic behaviors, the lack of this morphology in "plesiadapiforms" does not necessarily require a loris-like speed of progression, or severe limits on agility.

11.5   Summary and Conclusions

In summary, the features forwarded by Beard (1990, 1993b) as uniquely characterizing *Cynocephalus* and paromomyids are either not present in paromomyids or are present in other non-mitten-gliding taxa. Specifically: (1) Paromomyids and micromomyids do *not* have intermediate phalanges that are longer than the proximal phalanges. Furthermore, this proportional relationship is likely to reflect suspensory behaviors and thus would not be definitive evidence of mitten-gliding in the fossil taxa even if it had been substantiated. (2) Elongation of the intermediate phalanges does *not* group paromomyids and micromomyids with *Cynocephalus* to the exclusion of most arborealists including euprimates and other "plesiadapiforms." (3) Relatively great dorsopalmar depth of the proximal end and shaft of the intermediate phalanx does *not* uniquely group *Cynocephalus* with paromomyids and micromomyids, among "plesiadapiforms." It additionally characterizes *Plesiadapis*. Furthermore, callitrichine euprimates, distinctive for their use of vertical clinging and climbing, are actually more similar to "plesiadapiforms" than to typical euprimates in this regard. (4) An intermediate phalanx with a straight shaft that lacks dorsal recurvature of the distal end, does *not* characterize known paromomyids or unite them with *Cynocephalus*, although it does characterize micromomyids. However, it also characterizes *Plesiadapis*, which is traditionally thought to be a non-glider (Gingerich, 1976; Gunnell and Gingerich, 1987; Beard, 1989; Youlatos and Godinot, 2004; Bloch and Boyer, 2007), and at least some extant callitrichines.

These findings refute the gliding hypothesis as proposed by Beard (1993b) inasmuch as they contradict observations he made in the sections "Anatomical Evidence for Gliding in Paromomyids" and "Anatomical Evidence for Gliding in Micromomyids" which indicated that dermopterans, paromomyids, and in some cases micromomyids were uniquely similar. Given the nature of Beard's evidence we considered some of it to be invalidated by the previously unmentioned fact that large plesiadapids are also morphologically similar to dermopterans and paromomyids. While we (and others who have studied plesiadapid functional morphology) see gliding in plesiadapids as extremely unlikely, we feel it is important to acknowledge that if evidence were ever marshalled for gliding in *Plesiadapis*, from other (non-phalanx) regions of the skeleton, then Beard's observations regarding the functional significance of the phalangeal morphology

would regain some validity. However, even in this unlikely scenario, our conclusions regarding paromomyids and micromomyids would probably still stand because analysis of the rest of the skeleton appears to further refute the possibility of *Cynocephalus*-like mitten-gliding, associated suspensory behaviors and squirrel-like gliding (although the functional significance of micromomyid morphology is admittedly ambiguous in several regions). Specifically: (1) The phalangeal morphology of paromomyids and micromomyids does not reflect functions characterizing suspensory behaviors, but suggests the ability for tight flexion of the digits, as is characteristic of euprimate-like grasping. (2) The finger-toe proportions, and the metapodial proportions of paromomyids and micromomyids do not reflect those expected for gliders incorporating the manus into the patagium. Instead, these features are more generalized and fit the pattern of many scansorial mammals (i.e., the fingers and metacarpals are short compared to the toes and metatarsals). (3) Features of eutherian gliders are absent from the forelimb of paromomyids, as are features usually associated with suspensory behaviors. Micromomyids possess some features that may reflect functions required in suspension and gliding, but are not exclusively associated with those behaviors. (4) The axial skeleton of paromomyids lacks features of *Cynocephalus*, more generalized gliders, and suspensory taxa. Specifically, it lacks the long neck and morphological traits of the lumbar vertebrae characterizing *Cynocephalus* and suspensory taxa, as well as the relatively short trunk and tail characterizing gliding taxa. Instead, the vertebrae are similar to those of extant sciurids and tupaiids that do not glide, but *do* utilize bounding gaits in which extensive sagittal flexion and extension of the trunk increases the stride length. (5) The ribs of both paromomyids and micromomyids are unlike those of *Cynocephalus*, sloths and *Ptilocercus*. This suggests against suspension or slow-climbing and bridging behaviors. (6) The innominate of gliders and suspensory taxa is quite distinctive from that of bound-galloping scansorialists or active arborealists. The innominate morphology of *Ignacius* is clearly similar to that of bound-gallopers. The morphology of micromomyids actually appears more similar to that of *Cynocephalus*, but it is also similar to that of some euprimates, *Ptilocercus lowii* and the basal eutherian mammal, *Ukhaatherium*. Thus, although the innominate characters strongly suggest against gliding and suspension in *Ignacius*, their functional significance is not clear, and the reverse cannot be argued for the case of micromomyids, especially in the face of many other characters that clearly suggest against gliding behaviors in micromomyids. (7) The proportion of the forelimb to hind limb (intermembral index) is distinctively different from that for specialized suspensory taxa. While not substantially different from some gliding taxa, it is not exclusively similar to any gliding taxa for either *Ignacius* or the micromomyid. Neither are the intermembral indices in these fossils outside the range of other known "plesiadapiforms," or extant, pronograde to orthograde arborealists. (8) The
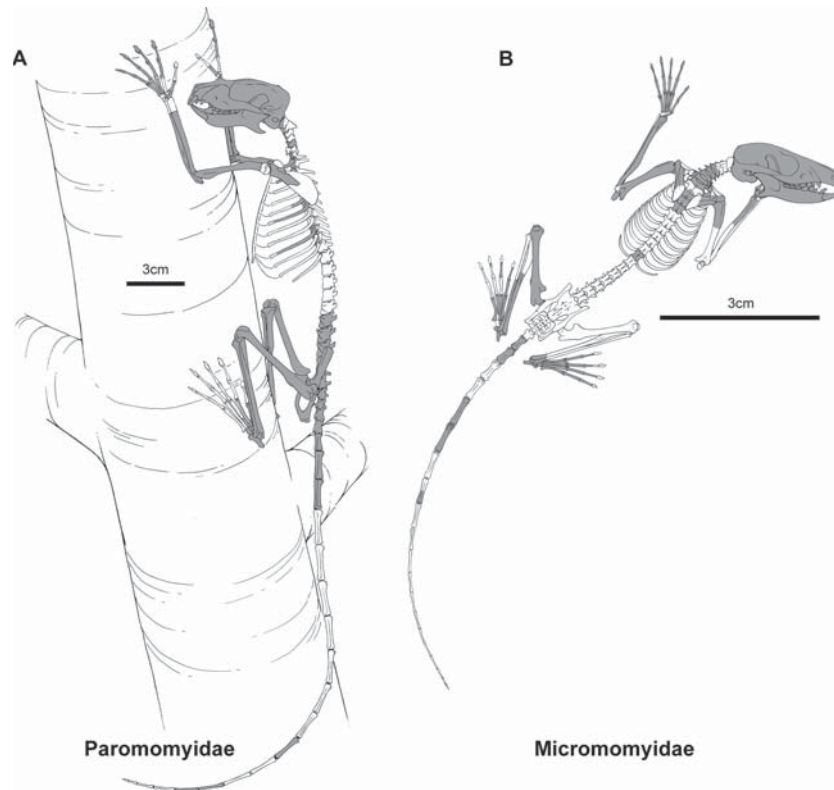
FIGURE 11.32. Reconstruction of paromomyid and micromomyid "plesiadapiforms" in typical postures. Reconstructions are based off of allavailable material for these animals, but skeletons are shaded to show bones present in *Ignacius clarkforkensis* (UM 108210 and UM 82606) and *Dryomomys szalayi* (UM 41870). Scales = 3 cm.

femur and tibia of paromomyids and micromomyids indicate habitually flexed, abducted thighs, flexed knee joints, a wide foot stance, and the capacity for relatively powerful extension and flexion of the thigh and leg, contrary to the expectations for suspensory taxa. Paromomyids also lack features of femur and tibia that characterize gliding squirrels and distinguish them from arboreal ones. Although the micromomyid has some features seen in gliding squirrels (if not in *Cynocephalus*), these features also characterize other non-gliding euarchontans (euprimates) and more basal, non-gliding taxa (nyctitheriids).

In summary, functional features expected for a mitten-glider are essentially absent from new paromomyid and micromomyid skeletons in every region analyzed. Therefore, the mitten-gliding hypothesis is confidently rejected for Paleogene paromomyids and micromomyids. Furthermore, habitual use of suspensory behaviors and more generalized gliding are also rejected for both paromomyids and micromomyids. The postcranial proportions and morphology of paromomyids are strikingly similar to those of callitrichine euprimates in features that signify the use of vertical clinging postures (Figure 11.32A) and more generalized agile arboreal activity (Bloch and Boyer, 2007). Micromomyids likely differed from paromomyids and callitrichines in being slightly less agile, and in utilizing antipronograde under-branch clinging postures more frequently

(Figure 11.32B). Given these inferred behavioral differences, the arboreal treeshrew *Ptilocercus lowii* may make a slightly more appropriate model for the micromomyid (Bloch et al., 2003; Bloch and Boyer 2007; Bloch et al., 2007).

Given the fact that at least paromomyid dentitions suggest exudate-eating (Gingerich, 1974: but see Godinot, 1984), it is not outlandish to speculate that similarities between the functional skeletal and dental attributes of paromomyids and callitrichines reflect the presence of the same biological role. In other words, features reflecting vertical clinging and climbing in paromomyids and micromomyids may be part of an adaptive complex allowing access to exudates. This characterization matches paromomyids and micromomyids with Beard's (1991) view of the "Primatomorpha" morphotype. Thus, if vertical clinging in euarchontans can always be associated with the biorole of specialized exudativory, it is possible that evolutionary origins of Euprimates and Dermoptera were marked by a dietary shift to eating exudates. However, if this is true, Scandentia should also be primitively characterized by an exudate-eating phase, because recent phylogenetic analyses are overwhelmingly consistent in recovering it as the sister-group of Dermoptera (e.g., Liu and Miyamoto, 1999; Liu et al., 2001; Madsen et al., 2001; Murphy et al., 2001a, b; Sargis, 2004, 2007; Van Den Bussche and Hoofer, 2004 Bloch and Silcox, 2006; Bloch et al., 2007). This is to say

that the common ancestor of dermopterans and euprimates also represents the common ancestor of Euarchonta (Sargis, 2002c; Silcox et al., 2005), which includes primates, dermopterans, and scandentians, but excludes chiropterans.

There are several problems with extending the exudate-eating, vertical clinging hypothesis to the base of a Euarchonta: (1) The basal euarchontan was likely characterized by features suggesting improved grasping abilities (i.e., long fingers relative to metacarpals, and incipiently divergent and mobile first digits (Sargis et al., 2005; Sargis et al., 2007, Bloch et al., 2007), not necessarily expected for an animal specialized for clinging to large-diameter supports, exclusively. (2) The dentitions of basal euarchontans and the earliest "plesiadapiforms," while consistent with de-emphasis on faunivory (Szalay, 1968), provide little evidence for initial specializations towards exudativory [i.e., teeth of early members of most "plesiadapiform" groups retain high shearing quotients (Kay and Cartmill, 1977; Biknevicius, 1986) and have relatively smaller central incisors (e.g., Gingerich, 1976; Bloch et al., 2001b)]. (3) Robust, procumbent incisors are also employed to access other types of angiosperm products, such as nuts, specifically (i.e., as in rodents and *Daubentonia*).

Given these caveats and new fossil data that have accumulated in the last 15 years, it now seems more likely that the dietary shift marking the origin of Euarchonta was one towards inclusion of more angiosperm products generally. Such a dietary shift also requires movement into an arboreal setting (Szalay, 1968; Sussman and Raven, 1978; Szalay, 1981). The *heritage* feature of *claws*, characterizing all euarchontans, probably necessitated a claw-climbing phase to this shift (Haines, 1958). Acquisition of claw-climbing, callitrichine-like arboreality (Szalay and Dagosto, 1988) would have opened an adaptive route towards specialization on exudates, which was apparently followed in paromomyid and possibly micromomyid evolution (Figure 11.32).

However, the innovation of an incipiently developed, divergent, opposable grasping hallux in basal Euarchonta also opened the way towards specialized manual and pedal grasping seen in carpolestids (Bloch and Boyer, 2002a) and Euprimates. Other taxa, such as plesiadapids (*Plesiadapis* and *Platychoerops*) evolved large body sizes [an order of magnitude greater than other plesiadapoid or paromomyoid "plesiadapiforms" (Gingerich and Gunnell, 2005)] that allowed utilization of foliage as a protein source, as suggested further by possible suspensory innovations in the postcranium and more selenodont dentitions in late occurring members (Gingerich, 1976; Bloch and Boyer, 2007). It would not be very surprising if evidence for gliding in this arboreal radiation of "plesiadapiforms" were to be eventually found, given that it is likely that much of its skeletal diversity still remains undocumented. However, as we have shown, evidence for such gliding remains elusive. Given the findings presented here and in light of current phylogenetic reconstructions (Bloch and Silcox, 2006; Bloch et al., 2007), if gliding is eventually demonstrated for some "plesiadapiform" group it is unlikely that it will also be demonstrably homologous to dermopteran mitten-gliding.

Appendix I

Postcranial specimens of Paromomyidae and Micromomyidae

Family Paromomyidae

Acidomomys hebeticus

UM 108207 Partial skeleton with associated skull and dentaries. Illustrated in Bloch and Boyer (2001) and Bloch et al. (2002a), and in Figures 11.1 and 11.2.

Ignacius graybullianus

USNM 442233 Damaged left humerus lacking its distal end. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen briefly described, but not illustrated, by Beard (1989).

USNM 442259 Nearly complete left humerus. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described and illustrated by Beard (1989, Figure 50).

USNM 442232 Right proximal radius. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described and illustrated by Beard (1989, Figure 51).

USNM 442256 Proximal phalanx. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early

Eocene) in the Clarks Fork Basin. Specimen illustrated (but not described) by Beard (1989, Figure 52). Identified as *I. graybullianus* based on size and similarity to dentally associated specimens of *Phenacolemur* (Beard, 1989). Identified as belonging to the manus (rather than the pes) based on elongation and "robusticity" (Beard, 1989; see Hamrick et al., 1999, for a different interpretation).

USNM 442253 Intermediate phalanx. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen illustrated (but not described) by Beard (1989, Figure 53). Identified as *I. graybullianus* based on similarity to dentally associated specimens of *Phenacolemur* (Beard, 1989). Identified as belonging to the manus (rather than the pes) based on "robusticity" (Beard, 1989; see Hamrick et al., 1999, for a different interpretation).

USNM 442255 Intermediate phalanx. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen discussed and illustrated by Beard (1989, Figure 53). Identified as possibly belonging to the pes based on lack of elongation (Beard, 1989; see Hamrick et al., 1999, for a different interpretation).

USNM 442284 Pelvic fragment. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen mentioned, but not described or illustrated, by Beard (1989).

USNM 442285 Pelvic fragment. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen mentioned, but not described or illustrated, by Beard (1989).

USNM 442286 Pelvic fragment. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described and illustrated by Beard (1989, Figure 35).

USNM 442245 Femur missing the femoral head. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described and illustrated by Beard (1989, Figure 54).

USNM 442246 Proximal femur. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described and illustrated by Beard (1989, Figure 54).

USNM 442234 Astragalus. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen mentioned, but not illustrated, by Beard (1989).

USNM 442235 Right astragalus. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described and illustrated by Beard (1989, Figure 55).

USNM 442239 Calcaneum. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described, but not illustrated, by Beard (1989).

USNM 442240 Calcaneum. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described, but not illustrated, by Beard (1989).

USNM 442241 Calcaneum. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen described, but not illustrated, by Beard (1989).

Ignacius clarkforkensis

UM 39893 Femur. Specimen prepared out of a Limestone from UM locality SC-117 (Cf-2, late Paleocene) in the Clarks Fork Basin. Specimen listed, but not described or illustrated, by Bloch (2001).

UM 39897 Astragalus. Specimen prepared out of a Limestone from UM locality SC-117 (Cf-2, late Paleocene) in the Clarks Fork Basin. Specimen listed, but not described or illustrated, by Bloch (2001).

UM 39926 Scaphoid. Specimen prepared out of a Limestone from UM locality SC-117 (Cf-2, late Paleocene) in the Clarks Fork Basin. Specimen listed, but not described or illustrated, by Bloch (2001).

UM 108210 Represented by skull and dentaries; distal, intermediate and proximal phalanges of the manus; metacarpals I, III and IV of the right hand and I of the left hand; left and right radius, ulna and humerus; cervical vertebrae I-V, VII; thoracic vertebrae I and three others; parts of the scapula; right astragalus; right and left calcanea. Specimens were retrieved from the same limestone lens as *A. hebeticus* but from a different area within it. See following section Figures 11.3 and 11.4 for documented association.

UM 82606 From the same locality, but from a separate nodule, as UM 108210. It includes metacarpal V; the last three lumbar vertebrae; sacrum; caudal vertebrae I-VII, and three others; left and right innominates; left and right femora, tibiae and fibulae; right astragalus, calcaneum, cuboid, navicular, ectocuneiform, mesocuneiform, and metatarsals I-III. See following section Figures 11.3 and 11.4 on documenting association.

Phenacolemur praecox

UM 37497 Femur. Specimen prepared out of a Limestone from UM locality SC-210 (Wa-1, early Eocene) in the Clarks Fork Basin. Specimen listed, but not described or illustrated, by Bloch (2001).

UM 86440 Dentally associated partial skeleton. Collected from UM locality SC-46 (Wa-2, early Eocene) of the Clarks Fork Basin and thought to be part of the same individual as UM 86352 (Beard, 1989, 1990). Discussed and described by Beard (1989). Partially illustrated by Beard (1989, Figures 32, 33, 41).

UM 86352 Dentally associated partial skeleton. Collected from UM locality SC-46 (Wa-2, early Eocene) of the Clarks Fork Basin and thought to be part of the same individual as UM 86440 (Beard, 1989, 1990). Discussed and

described by Beard (1989). Partially illustrated by Beard (1989, Figures 31, 32, 43, 46).

Phenacolemur jepseni

USGS 17847 Dentally associated partial skeleton. Collected from USGS locality D-1651 (Wa-7, early Eocene) of the Bighorn Basin. Discussed and described by Beard (1989). Partially illustrated by Beard (1989, Figures 23, 24, 32, 33, 48). Also mentioned by Beard (1990).

Phenacolemur simonsi

The following specimens were partially discussed and figured by Beard (1989, 1990; also listed in Bloch, 2001). All are isolated elements prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin: USNM 442230, right tibia; USNM 442231, tibia; USNM 442236, right astragalus; USNM 442237, astragalus; USNM 442238, right calcaneum; USNM 442242, proximal femur; USNM 442243, proximal femur; USNM 442244, proximal femur; USNM 442247, proximal phalanx, missing distal end; USNM 442248, proximal phalanx; USNM 442249, proximal phalanx; USNM 442250, intermediate phalanx; USNM 442251, intermediate phalanx; USNM 442252, intermediate phalanx; USNM 442254, intermediate phalanx; USNM 442257, left hallucal metatarsal; USNM 442258, left pollical metacarpal; USNM 442260, complete left humerus; USNM 442261, nearly complete left radius; USNM 442262, right proximal radius; USNM 442263, left radius lacking distal end; USNM 442264, fragment of left radial shaft; USNM 442265, right proximal ulna; USNM 442266, humerus; USNM 442267, left proximal ulna; USNM 442268, humerus; USNM 442287, right pelvic fragment.

Family Micromomyidae

Chalicomomys antelucanus

USNM 442282 Distal left humerus. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Described by Beard (1989).

USNM 442283 Nearly complete right humerus. Specimen prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin. Described by Beard (1989).

Tinimomys graybulliensis

USNM 461201 Partial skeleton and skull from UM locality SC-26 (Wa-1, early Eocene). Illustrated in limestone (not fully prepared) by Beard (1993b, Figure 11.6). Briefly discussed, but largely undescribed, by Beard (1993b).

USNM 461202 Associated forelimb elements from UM locality SC-26 (Wa-1, early Eocene). Mentioned, but not described or illustrated, by Beard (1993b).

UM 85176 Distal radius and ulna from UM locality SC-327 (Cf-3, late Paleocene), discussed by Beard (1989). Associated with a petrosal fragment, mandible, and two isolated upper teeth, described and illustrated by Gunnell (1989, Figure 11.28).

The following specimens were partially discussed and figured by Beard (1989; also listed in Bloch, 2001). All are isolated elements prepared out of the 8ABC Limestone from UM locality SC-4 (Wa-1, early Eocene) in the Clarks Fork Basin:

USNM 442269, left proximal humerus; USNM 442270, distal humerus; USNM 442271, distal humerus; USNM 442272, distal humerus; USNM 442273, distal humerus; USNM 442274, distal humerus; USNM 442275, left proximal radius; USNM 442276, nearly complete right ulna; USNM 442277, right pelvic fragment; USNM 442278, right pelvic fragment; USNM 442279, left femur; USNM 442280, left femur; USNM 442281, right femur.

Dryomomys szalayi

UM 41870 Partial skeleton and skull from UM locality SC-327 (Cf-3, late Paleocene). Skull and jaws illustrated in Bloch (2001). Briefly discussed in Bloch (2001) and Bloch et al. (2003). See Figure 11.6 section for documented association.

Appendix II

Extant specimens used in comparative analyses

TABLE 1. This table gives all specimens measured or observed in detail in undertaking this research. Each figure depicting more than four specimens is included as a column. An "x" is placed in the row representing each specimen included in a particular figure. If the specimen has a letter label in the figure, that letter indicates its presence, rather than an "x". Some specimens are represented by more than one datum in the phalangeal analyses (if we measured more than one of their digits/phalanges). For such specimens, the number of digit rays representing them is given in the column titled "n phalanges."

Taxon	Museum #	N phalanges	Figure 11.8	Figure 11.10	Figure 11.11	Figure 11.12	Figure 11.13	Figure 11.14	Figure 11.21	Figure 11.25	Figure 11.27	Figure 11.29	Figure 11.30
Artiodactyla													
Bison bison	UMMZ 114227	na								0			
Ovis aries	UMMZ 123400	na								0			
Ovis aries	UMMZ 125084	na								0			
Sus scrofa	UMMZ 167210	na								0			
Carnivora													
Canis lupus	UMMZ 38960	na								1			
Canis lupus	UMMZ 103506	na								1			
Canis lupus	UMMZ 115800	na								1			
Panthera tigris	UMMZ 160141	na								1			
Lynx rufus	UMMZ 157258	na								1			
Panthera pardus	UMMZ 102451	na								1			
Paradoxurus hermaphroditus	UMMZ 157016	na								1			
Paradoxurus hermaphroditus	UMMZ 157019	na								1			
Potos flavus modestus	UMMZ 107906	na								0			
Potos flavus modestus	UMMZ 158610	na								0			
Procyon lotor	UMMZ 65802	na								1			
Procyon lotor hirtus	UMMZ 168355	na								1			
Ursus sp	UMMZ 103537	na								1			
Chiroptera													
Myotis	UMR 1504	na											
Pteropus pumilio	UMMZ 57081	4			x	x	D						
Pteropus pumilio	YPM 133	1				x							
Rousettus aegyptiacus	YPM 5086	5				x							
Rousettus aegyptiacus	YPM 5087	5				x							
Rousettus aegyptiacus	YPM 5088	5				x							
Dermoptera													
Galeopterus variegatus	Hamrick et al. (1999)	4	x	x	x	x		x					
Cynocephalus volans	Hamrick et al. (1999)	4	x	x	x	x		x					
Cynocephalus volans	Hamrick et al. (1999)	4	x	x	x	x		x					
Cynocephalus volans	Hamrick et al. (1999)	2	x	x	x	x		x					
Cynocephalus volans	USNM 56530	4		x	x	x	E	x					
Cynocephalus volans	UF 5969								x	x	x	B	
Lagomorpha													
Lepus crawshayi	UMMZ 123226	na								1			
Lepus sp	UMMZ x	na								1			
Lipotyphla													
Sorex sp.	UMMZ 157176	4		x				x					
Sorex sp.	UMMZ 165481	2	x	x				x					

(continued)

TABLE 1. (continued)

Taxon	Museum #	N phalanges	Figure 11.8	Figure 11.10	Figure 11.11	Figure 11.12	Figure 11.13	Figure 11.14	Figure 11.21	Figure 11.25	Figure 11.27	Figure 11.29	Figure 11.30
Marsupalia													
Didelphis virginianus	RD154	na								0			
Petaurus breviceps	Hamrick et al. (1999)	4			x								
Petaurus breviceps	Hamrick et al. (1999)	4			x								
Petaurus breviceps	Hamrick et al. (1999)	1			x								
Petaurus breviceps	UMMZ 158619	na								1			
Petaurus breviceps	UMMZ 160143	na							x	1	x		
Phalanger sp	UMMZ 159321	na								0			
Trichosurus vulpecula	UMMZ 157192	2	x		x				x	0	x		
Primates													
Alouatta caraya	UMMZ 12489	na											
Alouatta palliata aequatorialis	UMMZ 77300	na								0			
Alouatta palliata mexicana	UMMZ 116300	na											
Alouatta palliata pigra	UMMZ 63503	na								0			
Alouatta pigra	UMMZ 63511	na											
Ateles geoffroyi	UMMZ 63171	na							x		x		
Ateles geoffroyi	UMMZ 63165	na									x		
Callimico goeldii	UMMZ 160149	na							x		x		
Callithrix jacchus	UMMZ 91119	na											
Cebuella pygmaea	UMMZ 160146	4	x	x	x	x		x	x	1	x		x
Cebuella pygmaea	SBU NC-01	8		x	x	x	B	x	x		x	F	
Cebus apella paraguayanus	UMMZ 126129	na								1			
Cebus apella paraguayanus	UMMZ 126131	na								1			
Cebus sp.	UMMZ 126130	4	x	x				x					
Cercopithecus sp.	UMMZ 107905	4		x				x					
Daubentonia madagascariensis	AMNH 185643	7				x							
Eulemur fulvus	UMMZ 160910	na				x		x	x	1	x		
Galago senegalensis	Hamrick et al. (1999)	2	x	x	x	x		x					
Galago senegalensis	Hamrick et al. (1999)	2	x	x	x	x		x					
Galago senegalensis	Hamrick et al. (1999)	2	x	x	x	x		x					
Galago senegalensis	Hamrick et al. (1999)	3	x	x	x	x		x					
Galago senegalensis	UMMZ 113349	na									x		
Galago senegalensis	UMMZ 113350	na									x		
Galago senegalensis	UMMZ 113351	na							x	1	x		
Galago senegalensis	UMMZ 113352	na											
Galagoides demidovii	SBU PGa-02	na											
Hylobates hoolock	UMMZ 160909	3	x					x		0			
Hylobates hoolock	UMMZ 160908	3	x	x						1			
Leontopithecus rosallia	UMMZ 97464	na	x							1			x
Nycticebus coucang	UMMZ 113356	4								0	x		x
Nycticebus coucang	UMMZ 113353	na								0	x		
Nycticebus coucang	UMMZ 113354	na								0			
Nycticebus coucang	UMMZ 113355	na									x	C	
Nycticebus coucang	SBU PNc-01	na											
Otolemur crassicaudatus	UMMZ 113345	na											
Otolemur crassicaudatus	UMMZ 113347	na											
Otolemur crassicaudatus	UMMZ 113344	na											
Saguinus mystax	UMMZ 160148	4	x	x	x			x	x	1	x		

Taxon	Specimen	N									
Saguinus oedipus	UMMZ 157195	na								1	x
Saguinus oedipus	UMMZ 156437	na									
Saguinus oedipus	UMMZ 160147	na			x			x			x
Saguinus sp.	SBU NSg06	8			x						
Saimiri sciureus	UMMZ 113357	na					x			1	
Saimiri sciureus	UMMZ 46415	3	x								
Saimiri sciureus	UMMZ 113358	na									
Saimiri sciureus	UMMZ 120304	na									
Tarsius bancanus	Hamrick et al. (1999)	3	x	x	x	x	x	x			
Tarsius bancanus	Hamrick et al. (1999)	4	x	x	x	x	x	x			
Tarsius spectrum	Hamrick et al. (1999)	4	x	x	x	x	x	x			
Tarsius syrichta	Hamrick et al. (1999)	3	x	x	x	x	x	x			
Tarsius syrichta	UMMZ 95741	na							x		x
Tarsius syrichta	UMR 139	na							x	1	x
Varecia variegata	UMMZ 172669	na									
Rodentia											
Anomalurus beecrofti	Hamrick et al. (1999)	3	x	x	x	x	x	x			
Anomalurus beecrofti	AMNH coll.	4	x	x			x	x			
Anomalurus derbianus beecroftii	AMNH 52100	4					x				
Anomalurus derbianus beecroftii	AMNH 52101	8					x				
Anomalurus derbianus	AMNH 241147	3					x				
Anomalurus derbianus nicrensis	AMNH 89389	3					x				
Anomalurus sp.	AMNH 5101	6					x				
Calomyscus sp.	UMMZ 167176	4	x		x		x			1	
Cavia porcellus	UMMZ 86465	na								1	
Cavia porcellus	UMMZ 88422	na								1	
Erethizon dorsatum bruneri	UMMZ 39970	na								0	
Erethizon dorsatum dorsatum	UMMZ 53682	na								0	
Erethizon sp.	UMMZ 116343	4			x		x				
Gerbillus sp.	UMMZ 117669	3	x		x		x				
Glaucomys sabrinus	UMMZ 113398	na							x		x
Glaucomys volans	Hamrick et al. (1999)	4	x		x		x				
Glaucomys volans	Hamrick et al. (1999)	2	x		x		x				
Glaucomys volans	Hamrick et al. (1999)	3	x		x		x				
Glaucomys volans	Hamrick et al. (1999)	4	x		x		x				
Glaucomys volans	UMMZ 168356	na							x		x
Marmota monax	UMMZ 166225	4			x		x				
Marmota monax	UMMZ 170527	na								0	
Mesocricetus auratus	UMMZ 86440	na								0	
Mesocricetus auratus	UMMZ 121017	na								0	
Phodopus sungorus	UMMZ 168149	na								0	
Phodopus sungorus	UMMZ 168150	na								0	
Rattus sp.	SBU MRD-28	na									
Sciurus carolinensis	SBU MRd10	na							x		x
Sciurus niger	UMMZ TC 269	3	x		x		x		x		x
Sciurus niger	Hamrick et al. (1999)	2	x		x		x				
Sciurus niger	Hamrick et al. (1999)	2	x		x		x				
Sciurus niger	UMMZ 3959	na								1	
Sciurus niger	UMMZ 5195	na								1	
Citellus mexicanus	UMR 1716	na							x		x
Citellus mexicanus	UMMZ 126129	na								1	
Synaptomys cooperi cooperi	UMMZ 146833	na								0	
Synaptomys cooperi cooperi	UMMZ 160087	na								0	

TABLE 1. (continued)

Taxon	Museum #	N phalanges	Figure 11.8	Figure 11.10	Figure 11.11	Figure 11.12	Figure 11.13	Figure 11.14	Figure 11.21	Figure 11.25	Figure 11.27	Figure 11.29	Figure 11.30
Tamias striatus rufescens	UMMZ 165187	na								1			
Tamias striatus rufescens	UMMZ 165188	4						x		1			
Scandentia													
Ptilocercus lowii	BMNH[a]	na									x		
Ptilocercus lowii	YPM 10179	na											
Tupaia glis	UMMZ 118389	na							x		x		
Tupaia glis	SBU collection	na								1		D	
Tupaia tana	Hamrick et al. (1999)	1	x	x	x	x		x					
Tupaia tana	Hamrick et al. (1999)	2	x	x	x	x		x					
Tupaia tana	Hamrick et al. (1999)	2	x	x	x	x		x					
Tupaia tana	Hamrick et al. (1999)	3	x	x	x	x		x					
Xenarthra													
Bradypus tridactylus	UMMZ 64943	na							x				
Bradypus tridactylus	SBU MEd-01	3				x							
Bradypus tridactylus	SBU MEd-02	3				x							
Choloepus hoffmanni	UMMZ 64944	na								0			
Choloepus hoffmanni	UMMZ 64940	na							x	0	x		
Choloepus hoffmanni	AMNH 15960	na					F					A	
Choloepus hoffmanni	SBU MEd-03	3				x							
Choloepus hoffmanni	YPM 268	8				x							
Choloepus hoffmanni	YPM 282	6				x							
Fossil specimens													
Carpolestes simpsoni	UM 101963	3	2	2				2					
Dryomomys szalayi	UM 41870	7	x	x				x	x	x	x		
Tininomys graybulliensis	SC-026 specimen	na			x	x	C						
Tininomys graybulliensis	UM 85176	na											
Acidomomys hebeticus	UM 108207	5	x	4	4			4					
Acidomomys hebeticus	UM 108208	na											
Acidomomys hebeticus	UM 108209	na											
Ignacius clarkforkensis	UM 108210	2	x	x	1	x	A	x					
Ignacius clarkforkensis	UM 82606	na							x	x	x	E	x
Ignacius graybullianus	USNM 442259	na											
Phenacolemur praecox	UM 66440	1				x							
Phenacolemur praecox	UM 86352	4				x							
Phenacolemur jepseni	USGS 17847[b]	1				x							
Phenacolemur simonsi	USNM 442260[b]	na											
Phenacolemur simonsi	USNM 442262	na											
Nannodectes gidleyi	AMNH 17379	3	1	x	x	x		x					
Nannodectes intermedius	USNM 442229	4	1	2	x	x		2		x			
Plesiadapis cookei	UM 87990	4	2	2	x	x		2	x		x		
Plesiadapis tricuspidens	MNHN CR 448	na											
Plesiadapis tricuspidens	MNHN CR 450	na											
Plesiadapis tricuspidens	MNHN CR 546	na											
Plesiadapis tricuspidens	MNHN CR 550	na											
Plesiadapis tricuspidens	MNHN CR 611	na											
Notharctus tenebrosus	UM 99999	na											
Omomys sp.	UM 98604	na											
Omomys carteri	UM 14134	na											
Smilodectes mcgrewi	UM 95526	na											x

[a]Measurements taken on photograph provided by Le Gros Clark (1927)

[b]Measurements taken from illustration in Beard (1989)

TABLE 2. This table gives raw measurements (mm) for vertebrae of the four specimens in Figure 11.22.

Ignacius clarkforkensis			*Saguinus mystax* UMMZ 160148			*Scuirus niger* UMMZ TC 269			*Cynocephalus volans*		
Vert level	Height	Length	Vert level	Height	Length	Vert level	Height	Length	Vert level	Height	Length
C1	6.0	1.5	C1	10.3	2.5	C1	10.3	2.2	C1	9.7	5.1
C2	2.1	5.4	C2	2.9	6.5	C2	2.6	7.1	C2	4.6	14.3
C3	1.9	3.4	C3	2.6	5.6	C3	2.7	4.2	C3	4.6	11.3
C4	1.8	3.3	C4	2.5	4.9	C4	3.0	4.2	C4	4.4	10.9
C5	2.0	3.1	C5	2.3	4.3	C5	2.9	4.6	C5	4.9	11.0
C6	-	-	C6	2.3	4.0	C6	2.8	4.0	C6	4.1	10.0
C7	1.9	3.5	C7	2.1	3.9	C7	2.6	3.9	C7	4.1	10.4
T1	1.8	3.7	T1	2.1	4.2	T1	2.9	4.8	T1	4.0	8.1
T2	-	-	T2	2.3	4.7	T2	2.9	5.4	T2	3.7	8.1
T3	-	-	T3	2.1	4.3	T3	2.8	5.6	T3	3.7	7.9
T4(?)	2.2	4.9	T4	2.1	4.6	T4	2.8	5.6	T4	3.9	7.9
T5	-	-	T5	2.2	4.4	T5	3.0	5.6	T5	4.0	8.1
T6	-	-	T6	2.2	4.5	T6	3.1	5.7	T6	3.7	8.0
T7(?)	2.3	5.3	T7	2.4	4.6	T7	3.3	6.2	T7	3.7	8.1
T8	-	-	T8	2.4	4.8	T8	3.5	6.5	T8	4.0	8.3
T9	-	-	T9	2.7	5.3	T9*	3.5	6.9	T9	4.9	8.5
T10(?)	2.4	5.4	T10*	2.7	6.1	T10	3.7	7.5	T10	4.7	8.5
T11*	-	-	T11	3.1	7.1	T11	3.9	7.9	T11	4.7	8.5
T12	-	-	T12	3.3	7.8	T12	4.1	8.1	T12	4.4	9.0
									T13	4.4	9.5
									T14	4.7	9.6
L1	-	-	L1	3.7	8.5	L1	4.2	10.7	L1	4.9	10.6
L2	-	-	L2	3.8	9.3	L2	4.2	9.8	L2	5.3	10.7
L3	-	-	L3	3.8	10.1	L3	4.2	10.1	L3	5.0	11.1
L4	-	-	L4	3.8	10.3	L4	4.0	11.1	L4	5.0	12.3
L5	3.3	8.1	L5	4.0	10.7	L5	4.3	11.5	L5	5.2	12.3
L6	3.3	8.2	L6	4.3	10.3	L6	4.3	11.4	L6	5.3	12.3
L7	3.4	6.9	L7	4.4	8.8	L7	4.4	9.2	L7	5.2	12.5
									L8*	4.7	10.8
S1	3.2	6.6	S1	3.8	6.2	S1	3.0	8.1	S1	3.0	11.0
S2	2.6	5.9	S2	3.6	5.1	S2	2.2	8.1	S2	3.0	10.0
S3	2.2	5.9	S3	3.7	6.0	S3	2.9	7.6	S3	2.4	11.7
Ca1	2.3	5.3	Ca1	3.7	6.0	Ca1	2.8	6.3	Ca1	3.4	11.6
Ca2	2.6	5.4	Ca2	4.0	6.2	Ca2	2.8	5.7	Ca2	3.7	11.6
Ca3	2.7	5.1	Ca3	4.1	7.1	Ca3	2.9	5.7	Ca3	5.3	13.5
Ca4	3.0	6.3	Ca4	4.4	9.4	Ca4	3.0	6.6	Ca4	4.7	15.4
Ca5	3.4	9.8	Ca5	4.5	13.8	Ca5	3.2	6.6	Ca5	4.4	17.9
Ca6	3.8	14.9	Ca6	4.8	16.6	Ca6	3.2	6.8	Ca6	4.1	20.0
Ca7	3.5	15.8	Ca7	4.7	17.6	Ca7	3.2	7.9	Ca7	3.7	21.1
Ca8	-	-	Ca8	4.6	18.0	Ca8	3.8	9.4	Ca8	3.9	23.2

(continued)

TABLE 2. (continued)

Ca9	2.3	14.8	Ca9	4.6	18.2	Ca9	4.0	11.3	Ca9	3.7	24.3
Ca10	-	-	Ca10	4.4	18.3	Ca10	4.1	12.7	Ca10	3.6	24.8
Ca11	-	-	Ca11	4.3	18.1	Ca11	3.9	13.6	Ca11	3.6	25.1
Ca12	1.4	9.3	Ca12	4.5	17.6	Ca12	3.7	13.7	Ca12	3.6	24.9
Ca13	1.2	9.2	Ca13	3.8	17.1	Ca13	3.4	13.3	Ca13	3.3	24.4
-	-	-	Ca14	3.6	16.7	Ca14	3.2	13.1	Ca14	2.8	22.3
-	-	-	Ca15	3.5	16.3	Ca15	3.1	12.9	Ca15	2.4	20.3
-	-	-	Ca16	3.3	15.9	Ca16	2.7	12.5	Ca16	1.9	16.8
-	-	-	Ca17	3.1	15.0	Ca17	2.6	12.1	Ca17	1.6	14.0
-	-	-	Ca18	3.0	14.3	Ca18	2.3	11.8	Ca18	1.2	9.0
-	-	-	Ca19	2.8	13.4	Ca19	2.2	11.0			
-	-	-	Ca20	2.6	12.7	Ca20	1.9	10.7			
-	-	-	Ca21	2.6	12.0	Ca21	1.5	10.2			
-	-	-	Ca22	2.4	11.1	Ca22	1.5	9.7			
-	-	-	Ca23	2.2	10.2	Ca23	1.3	9.1			
-	-	-	Ca24	2.0	10.2	Ca24	1.2	8.4			
-	-	-	Ca25	1.8	8.5	Ca25	1.0	6.7			
-	-	-	Ca26	1.7	8.5	Ca26	0.5	5.6			
-	-	-	Ca27	1.6	6.7						
-	-	-	Ca28	1.7	5.3						

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