

CHAPTER SIXTEEN

New Skeletons of Paleocene–Eocene Plesiadapiformes: A Diversity of Arboreal Positional Behaviors in Early Primates

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INTRODUCTION

Knowledge of plesiadapiform skeletal morphology and inferred ecological roles are critical for establishing the evolutionary context that led to the appearance and diversification of Euprimates (see Silcox, this volume). Plesiadapiform dentitions are morphologically diverse, representing over 120 species usually classified in 11 families from the Paleocene and Eocene of North America, Europe, and Asia (Hooker et al., 1999; Silcox, 2001; Silcox and Gunnell, in press). Despite this documented diversity in dentitions,

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implying correlated diversities in diets and positional behaviors, very little is known about postcranial morphology among plesiadapiforms. What is known has been largely inferred from a limited number of plesiadapid specimens, representing only a small sample of the known taxonomic diversity from North America and Europe (Beard, 1989; Gingerich, 1976; Russell, 1964; Simpson, 1935a; Szalay et al., 1975). While it has been suggested that plesiadapids may have been terrestrial, similar to extant *Marmota* (Gingerich, 1976), the consensus in the literature is that they were arboreal (Beard, 1989; Godinot and Beard, 1991; Rose et al., 1994; Russell, 1964; Szalay and Dagosto, 1980; Szalay and Decker, 1974; Szalay and Drawhorn, 1980; Szalay et al., 1975). While it has been further suggested that plesiadapids might have been gliders (Russell, 1964; Walker, 1974) or arboreal quadrupeds (Napier and Walker, 1967), they are now thought to have been more generalized arborealists with some specializations for vertical postures (Beard, 1989; Godinot and Beard, 1991; Gunnell and Gingerich, 1987; Silcox, 2001). Commenting on the need for a taxonomically broader sample of plesiadapiform postcranial skeletons, F. S. Szalay wrote: "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" (Szalay, 1972: 18). In fact, this prediction has been validated in the course of the last 15 years of paleontological field and laboratory research.

Since the early 1980's, field crews and fossil preparation labs of the University of Michigan Museum of Paleontology (UM), New Mexico State University (fossils housed at the U.S. National Museum of Natural History, USNM), and John Hopkins University (fossils also in the USNM) have recovered a number of plesiadapiform skeletons representing groups other than the Plesiadapidae. Several of these specimens with associated dentition and postcrania were collected from mudstones in the Bighorn Basin (Beard, 1989, 1990; Rose, 2001); however, the most complete specimens, including semi- to fully-articulated individuals, are derived from fossiliferous limestones in the Clarks Fork Basin (Bloch, 2001; Bloch and Boyer, 2001; 2002a,b; Bloch et al., 2001, 2003; Boyer and Bloch, 2000, 2002a,b; Boyer et al., 2001).

Beard (1989, 1990, 1993a,b) studied postcranial specimens attributed to paromomyid and micromomyid plesiadapiforms and concluded that these taxa were very different from known plesiadapids in their locomotor repertoire. Specifically, Beard proposed that micromomyids and paromomyids

were mitten-gliders and shared a sister-group relationship with extant dermopterans (=Eudermoptera of Beard, 1993a). Both the mitten-gliding hypothesis and the character support for Eudermoptera have since been questioned both with respect to the original evidence (Hamrick et al., 1999; Krause, 1991; Runestad and Ruff, 1995; Silcox, 2001, 2003; Stafford and Thorington, 1998; Szalay and Lucas, 1993, 1996) and based on new limestone-derived specimens that are far more complete and have more carefully documented dental-postcranial associations (Bloch, 2001; Bloch and Boyer, 2001; 2002a,b; Bloch and Silcox, 2001; Bloch et al., 2001, 2003; Boyer and Bloch, 2000; 2002a,b; Boyer et al., 2001). Despite doubt regarding Beard's original arguments for gliding and a close relationship to Dermoptera, the observation that micromomyids and paromomyids are postcranially distinct from the better known plesiadapids is not disputed. Furthermore, a recent study of a carpolestid plesiadapiform skeleton (Bloch and Boyer, 2002b) indicates 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). Overall, these skeletons confirm the implications of the diverse dental remains by suggesting a commensurate diversity in positional behaviors among plesiadapiforms.

This chapter includes: (1) a review of the methods for documenting postcranial-dental associations in freshwater limestone deposits from which most of the new significant plesiadapiform material is derived, (2) a summary of the postcranial anatomy and inferred positional behaviors of plesiadapiforms based on these new specimens, and (3) a discussion of the implications of the newly discovered postcranial anatomy for phylogenetic reconstructions and understanding primate origins and evolution.

CLARKS FORK BASIN FOSSILIFEROUS FRESHWATER LIMESTONES

Despite the high diversity of mammals known from the Paleocene and Eocene of North America, most species are known only from isolated teeth and jaws. Associations of teeth to postcrania, for many taxa, are unknown (Bown and Beard, 1990; Rose, 2001; Winkler, 1983). This lack of skeletal association, coupled with the fact that most traditional collecting methods are biased against recovery of skeletons of mammal less than 1 kg, partly explains

why an understanding of positional behaviors of most Paleocene–Eocene small mammals has been elusive.

Fossiliferous freshwater limestones are known throughout the Fort Union (Paleocene) and Willwood (Late Paleocene and Early Eocene) formations of the Clarks Fork and Crazy Mountains Basins of Wyoming and Montana (Bloch and Bowen, 2001; Bloch and Boyer, 2001; Bowen and Bloch, 2002; Gingerich et al., 1983; Gunnell and Gingerich, 1987). Through careful application of acid preparation techniques, limestones have yielded many exceptionally preserved skulls and skeletons of Late Paleocene and Early Eocene vertebrates (Beard, 1989, 1990, 1993a,b; Bloch, 2001; Bloch and Boyer, 2001, 2002a,b; Bloch and Gingerich, 1998; Bloch and Silcox, 2001, 2006; Bloch et al., 2001; Boyer and Bloch, 2000, 2003; Boyer et al., 2001; Gunnell and Gingerich, 1987; Houde, 1986, 1988; Kay et al., 1990, 1992).

Fossiliferous freshwater limestones record a complex depositional and diagenetic history, with precipitation of micritic low-Mg calcite and accumulation of bone probably having occurred in low-energy, ponded water (Bloch and Bowen, 2001; Bowen and Bloch, 2002). The fossil assemblages contained within the limestones likely represent faunas derived from rarely sampled floodplain microenvironments (Bloch, 2001; Bloch and Bowen, 2001; Bloch and Boyer, 2001; Bowen and Bloch, 2002). Skeletal element frequencies and occasional preservation of articulated skeletons indicate that mammals likely entered the limestone assemblage as complete skeletons that were subsequently partially disarticulated by bioturbation. It is likely that predation and scavenging, pit-trapping, and normal attritional processes all contributed to the concentration of bone (Bloch, 2001; Bloch and Boyer, 2001).

Documenting Postcranial-Dental Associations

The following is a summary of the method we use for preparation of matrix and documenting association and articulation of skeletons in fossiliferous freshwater limestones (from Bloch and Boyer, 2001). Limestones are usually chosen for study based upon surficial visibility of fossil vertebrates. Once a limestone has been selected, exposed bone is coated with polyvinylacetate (PVA) to protect the bone against etching and breaking. Limestones are dissolved with 7% formic acid buffered with calcium phosphate tribasic. Each acid reduction run lasts from 1 to 3 h, and is followed by a rinse period in running water of 2–6 h.

Documentation of skeletal association is accomplished by careful mapping of bone distributions and, in some cases, through preservation of articulation. When bones are articulated, we try to preserve the articulation by gluing adjacent surfaces together as the bones are exposed. Using this method for preserving articulations for as long as possible during the etching process reveals patterns in the distributions of skeletons that would have otherwise been lost. In order to further illustrate this process, we provide an example of this type of documentation in the following section.

Micromomyid Skeleton: An Example from a Late Paleocene Limestone

We are in the process of preparing a block, originally 20 kg in mass, of fossiliferous limestone from the last zone of the Clarkforkian land-mammal age (Cf-3, locality SC-327; see Bloch and Boyer, 2001 for locality information). One amazing aspect of this rather large block is that all of the exposed skeletons, representing at least 11 individuals, are articulated (80–100% complete; see Bloch and Boyer, 2001, Figure 5). At least one of the individuals is a new genus and species of micromomyid plesiadapiform (Figure 1A). Bone orientations and positions within the block were documented in detail during preparation of the specimen by frequently taking digital photographs of exposed bones and by making drawings that summarized the information in separate photographs with precision on the order of 1 mm or less. The micromomyid skeleton was isolated and not likely to be mixed up with any adjacent skeletons. Our main concern was documenting associations of phalanges to hands or feet, and between individual metacarpals, as persistent functional and phylogenetic questions have gone unanswered simply because cheiridial elements could not be confirmed as belonging to either the hands or feet (Hamrick et al., 1999; Krause, 1991). After extraction, bones were stored with numbers that correspond to the spatial documentation. When dissolution was complete, the photographs and sketches were compiled to produce a map of how the bones were distributed in the limestone (Figures 1B, 2A). The result was recovery of the most complete and clearly dentally associated skeleton of a micromomyid plesiadapiform yet known.

In this specimen, the metacarpals from the left hand (Figure 2A; bone numbers 30, 103–106) were almost perfectly articulated with each other and also closely associated with proximal ends of proximal phalanges 35–38. Furthermore, proximal phalanges 35 and 36, at least, had their distal ends

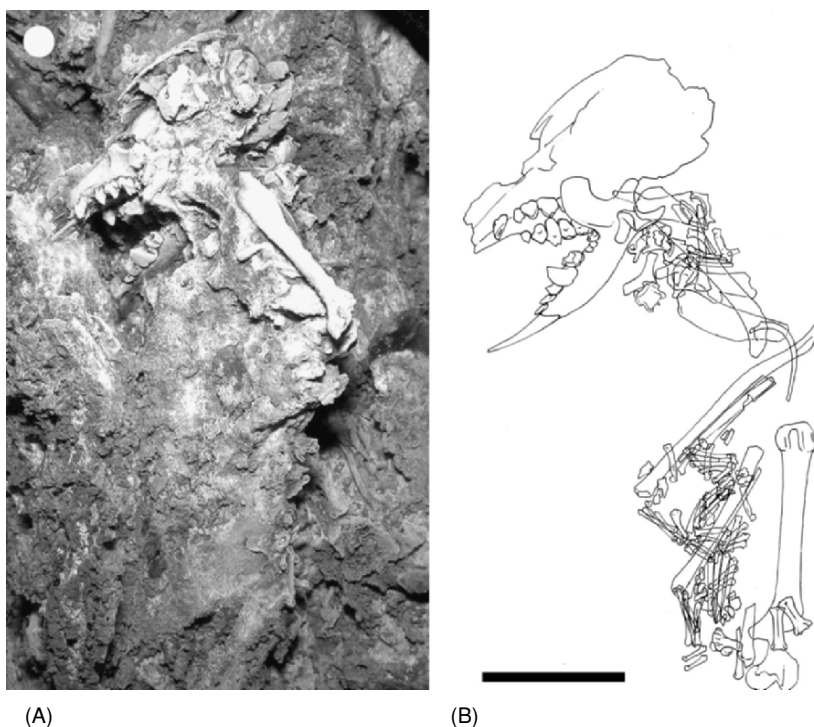


Figure 1. (A) Micromomyid plesiadapiform skull and skeleton (UM 41870) partially prepared from fossiliferous limestone, University of Michigan Locality SC-327, late Clarkforkian (Cf-3) North American Land Mammal Age. (B) Composite map of the bones recovered. Scale = 1 cm.

closely associated with the proximal ends of intermediate phalanges 15 and 16, suggesting that they belong to the same hand. The positional relationships described above make interpretation of metacarpal position relatively certain, and allow for confident attribution of proximal and intermediate phalanges to the left hand. In the foot, metatarsals 72, 74–76 were almost perfectly articulated. The distal ends of metatarsals 74 and 75 were articulated with proximal phalanges 63 and 64. Metatarsal 72 is closely associated with the proximal end of 40. In turn, 40, 63, and 64 had their distal ends associated with the proximal ends of intermediate phalanges 80–83. Based on these associations, we are confident that all these bones belong to the same foot.

None of the ungual phalanges recovered are attributed to the foot. It is possible that some, which were not closely associated with a particular manual or

pedal intermediate phalanx, were wrongly attributed to the hand (i.e., 102, 41, 42, and 44). However, we are prohibited from attributing any to the feet by two factors: (1) no unguals were recovered posterior to the “knuckles” of the flexed toes, instead, all were clustered around the hand and wrist elements; and (2) there are no consistently diagnosable differences between any of the unguals (due at least partly to their small size and variable preservation quality) that could be used to partition them between hand and foot when clear associations were lacking.

Articulations and associations allowed for identification and subsequent morphological differentiation of manual and pedal intermediate and proximal phalanges in this specimen (Figure 2B). Pedal proximal phalanges are longer and have better developed flexor sheath ridges than those of the hand. Pedal intermediate phalanges differ from those of the hand in: (1) being absolutely longer with mediolaterally relatively narrower shafts, (2) having tubercles for the annular ligament of the flexor digitorum profundus and superficialis muscles with relatively more prominent ventral projections, and (3) having a distal trochlea that is dorsoventrally relatively deeper, with a greater proximal extension of the dorsal margin. Such distinctions allowed attribution of other, more ambiguously positioned cheiridial elements to either hand or foot. These associations of manual and pedal phalanges allow functional interpretations that are more valid than those based on phalanges associated through assumptions about what morphological differences between hand and foot are expected to be (e.g., Beard, 1990, 1993).

Newly Discovered Plesiadapiform Skeletons

Using similar techniques to those outlined above, four other fairly complete plesiadapiform skeletons have been recovered from Paleocene limestones (Figure 3). These include the most complete paromomyid and plesiadapid skeletons yet discovered (Bloch and Boyer, 2001; Boyer et al., 2001; Gunnell and Gingerich, 1987) and the only skeleton of a carpolestid yet known (Bloch and Boyer, 2001, 2002a).

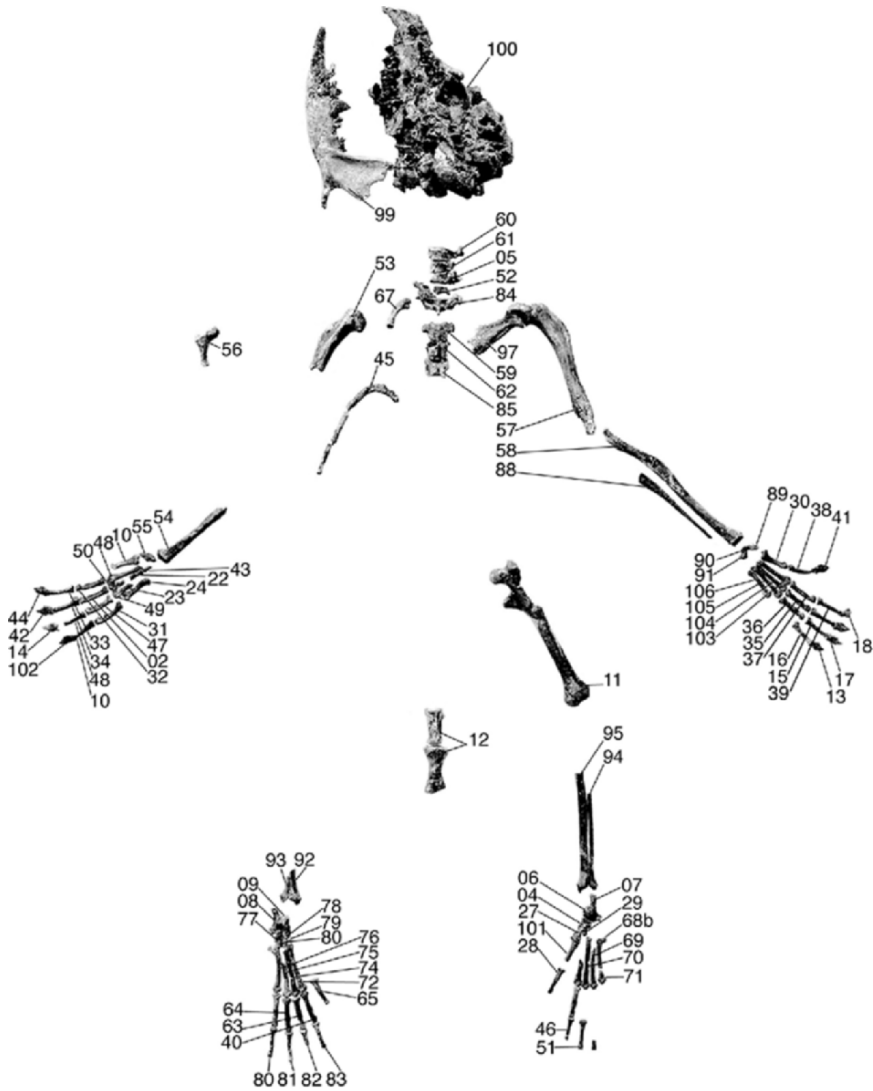
POSTCRANIAL MORPHOLOGY AND INFERRED POSITIONAL BEHAVIORS

Plesiadapiforms as Claw-Climbing Arborealists

Plesiadapiform taxa included in the families Carpolestidae, Micromomyidae, Paromomyidae, and Plesiadapidae are similar to each other in many postcranial



Figure 2. (A) Composite drawing of micromomyid plesiadapiform skull and skeleton (UM 41870) with numbers on bones corresponding to those of anatomical layout. Scale = 1 cm.



(B)

Figure 2. *Continued* (B) Skeleton of micromomyid (UM 41870) laid out in anatomical position with bones attributed to regions based on positional information. Scale = 3 cm. Note that Figure 2B was made before all of the bones were prepared from the rock. As such, not all bones depicted in Figure 2A are laid out in Figure 2B. Furthermore, a few bones attributed to the skeleton are not depicted in either A or B (see Figure 7).

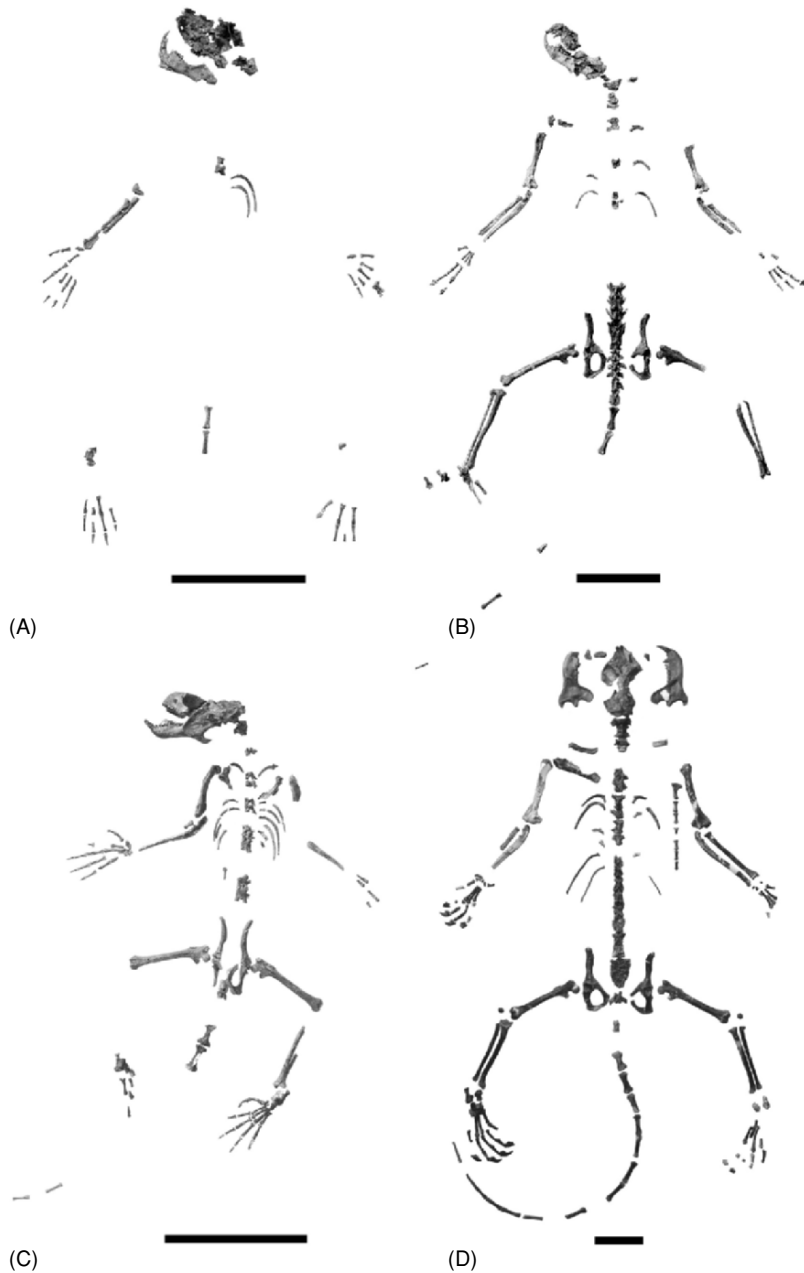


Figure 3. Skeletons representing three plesiadapiform families were recovered from Late Paleocene limestones. Paromomyidae is represented by (A) *Acidomomys hebeticus* (UM 108207) and (B) *Ignacius* cf. *I. graybullianus* (UM 108210 and UM 82606). Carpolestidae is represented by (C) *Carpolestes simpsoni* (UM 101963; figure from Bloch and Boyer, 2002a, Figure 2A). Plesiadapidae is represented by (D) *Plesiadapis cookei* (UM 87990). Scales = 5 cm.

characteristics that are indicative of arboreality. Specifically, plesiadapiforms are inferred to have been capable of clinging and claw climbing on large diameter vertical tree trunks, as well as grasping smaller branches with their hands and feet (Godinot and Beard, 1991; Sargis, 2001a, 2002b,c,d; Szalay and Dagosto, 1988; Szalay et al., 1975, 1987). Callitrichine primates (Bloch and Boyer, 2002a,b; Bloch et al., 2001; Boyer and Bloch, 2002b; Boyer et al., 2001), arboreal phalangerids (Bloch and Boyer, 2002a), and ptilocercine tree shrews (Sargis, 2001a,b, 2002a,b,c,d) have all been cited as close structural analogues to plesiadapiforms. We draw primarily on studies of behavior [Garber, 1992; Kinzey et al., 1975; Sargis, 2001a (see references therein); Sussman and Kinzey, 1984 (see references therein); Youlatos, 1999] and in some cases on understandings of form-function relationships in extant taxa (Godinot and Beard, 1991; Hamrick, 1998, 2001; Sargis, 2001a,b, 2002a,b) to interpret the functional significance of the features shared by all plesiadapiforms that we have studied.

Morphological correlates of vertical clinging and climbing are numerous and easily observed in the appendicular skeleton, as this region is relatively frequently preserved in fossil taxa and thus has been the focus of many studies. Conversely, the vertebral column of plesiadapiforms has received little attention due to the scarce occurrence of skeletons with associated material from this region. However, plesiadapiform vertebral columns are both diagnosably distinctive in their morphology and functionally informative. Distinctive features include: (1) vertebral bodies that increase markedly in size from the cranial to caudal end of the trunk, (2) vertebral bodies of the cervical and lumbar vertebrae that are dorsoventrally shallower than mediolaterally broad, (3) spinous process of the axis caudally oriented, (4) spinous processes of postdiaphragmatic thoracic and lumbar vertebrae cranially oriented, (5) transverse processes of the lumbar vertebrae arise from the pedicle where it contacts the body, (6) postzygapophyses of the postdiaphragmatic thoracic and lumbar vertebrae mediolaterally broadly-spaced, with facets that are craniocaudally short, have a rectangular (rather than elliptical) margin, and face ventrolaterally, (7) a sacrum that has three vertebrae and in which the long axis of the auricular facet is oriented craniocaudally, and (8) a tail that is relatively long.

While the vertebral column varies in functionally significant ways among taxa, our preliminary study suggests that the center of gravity of the plesiadapiform neck and trunk vertebrae was not midway between the pectoral and pelvic girdles as in suspensory taxa and terrestrial cursors, but was caudally shifted, and had more sagittal than lateral flexibility. Morphology of the vertebral column, viewed as an integrated unit, indicates that plesiadapiforms

were capable of bound-galloping in which the brunt of the weight is born on the hindlimbs and flexion and extension of the back contributes to the stride (Gambaryan, 1974). Furthermore, features shared with vertically clinging calitrichine primates (e.g., widely spaced postzygapophyses of lumbar vertebrae that face ventrolaterally), also suggest orthograde postures in plesiadapiforms.

Other plesiadapiform traits that suggest claw climbing on large diameter supports are found mainly in the appendicular skeleton. Many previous studies document and discuss the functional significance of the limb elements in plesiadapiforms (Beard, 1989, 1990, 1991a, 1993a,b; Godinot and Beard, 1991; Sargis, 2002b; Szalay and Dagosto, 1980, 1988; Szalay et al., 1975, 1987). The humerus of plesiadapiforms indicates a mobile forelimb with capabilities for powerful and sustained extension and flexion at the shoulder and elbow joints respectively, as required in vertical clinging postures (Szalay and Dagosto, 1980). The humeral head is spherical and extends superiorly beyond the greater and lesser tuberosities, allowing mobility at the glenohumeral joint (Sargis, 2002a, and references therein) and possibly some stability by providing more room for attachment of the rotator cuff muscles on these tuberosities (Fleagle and Simons, 1982; Grand, 1968; Harrison, 1989). The lesser tuberosity flares medially providing a large insertion site for the subscapularis muscle that extends, adducts, and medially rotates the humerus, making it important during vertical clinging postures and the support phase of vertical climbing (Beard, 1989; Larson, 1993; Sargis, 2002a). The distal humerus has a posterolaterally flaring supinator crest, indicating that plesiadapiforms had a high degree of powerful flexion at the elbow (Dagosto et al., 1999; Gregory, 1920; Szalay and Dagosto, 1980). Presence of a shallow olecranon fossa on the humerus suggests limited extension of the forearm. An extended entepicondyle of the humerus would have provided room for origination of strong flexor muscles of the wrist and fingers, such as flexor carpi radialis and flexor digitorum superficialis muscles (Sargis, 2002a). The capitulum and ulnar trochlea are separated by a deep zona conoidea indicating that the radius and ulna were not highly integrated in their functions (Sargis, 2002a). Instead, the spherical to slightly elliptical capitulum allowed the radius to rotate freely about the ulna (Sargis, 2002a; Szalay and Dagosto, 1980). Therefore, in many regards, the humerus suggests locomotion in an arboreal setting on large diameter supports.

The ulna of plesiadapiforms has a shallow trochlear notch and long, anteriorly inflected olecranon process, indicating habitual flexion as would be used in orthograde clinging and pronograde bounding (Rose, 1987). A flat to slightly

convex proximal articulation with the radius is consistent with independent function of that element in axial rotation. The shaft is medially bowed in cross-section, such that a strong lateral groove, which begins proximally as a deep fossa on the olecranon process, runs along the length of at least its proximal two-thirds. Such a groove expands the area for the origin of extensor muscles of the fingers. The shaft is typically slender without marked expression of an interosseous crest.

The proximal radius of plesiadapiforms typically has a spherical fossa and broad lateral lip that matches the spherical capitulum of the humerus (Beard, 1993a), allowing for a large degree of axial mobility (MacLeod and Rose, 1993; Sargis, 2002a; Szalay and Dagosto, 1980). The bicipital tuberosity of the radius is large and proximally located, indicating the presence of a strong biceps brachii muscle. The shaft of the radius is generally mediolaterally wide and flattens distally in its dorsopalmar aspect. Medial and lateral longitudinal ridges for the deep digital flexor muscles often mark the palmar aspect of the radial shaft. The distal end of the radius supports most of the carpus while the ulna is typically reduced. Because the wrist joint in plesiadapiforms is almost entirely formed by the radius, rotation of this element about the ulna does not compromise stability of the wrist. The distal articular surface of the radius is canted palmarly indicating habitual palmar-flexion of the proximal carpal row.

Though the hand is specialized differently in the four plesiadapiform families considered here, there are several features that are shared and suggest similar functions in an arboreal environment. A divergent pollical metacarpal in all plesiadapiforms indicates that they were capable of effective grasping of small diameter supports. Long proximal phalanges relative to the metacarpals (=prehensile proportions; Bloch and Boyer 2002a; Hamrick, 2001; Lemelin and Grafton, 1998) in non-plesiadapid plesiadapiforms also indicate specialized grasping abilities. The proximal phalanges of all plesiadapiforms have strong ridges for annular ligaments that prevent bowstringing of tendons of the flexor digitorum profundus and superficialis muscles during strong grasping in which the intermediate-proximal phalangeal joint is flexed at a highly acute angle. The distal articular surface of the proximal phalanx is not smooth, but has raised medial and lateral margins that create a broad, central groove into which the grooved proximal articular surface of the intermediate phalanx fits tightly (see description in Godinot and Beard, 1991: 311). Such a grooved surface prevents torsion and mediolateral deviation at this joint. The distal phalanx of plesiadapiforms, like that of *Prilocercus* and other arboreal mammals, is dorsopalmarly deep and mediolaterally narrow providing better resistance against sagittal bending loads

incurred during vertical claw clinging and climbing (Beard, 1989; Hamrick et al., 1999; Sargis, 2002a). The distal phalanx is usually characterized by an articular surface that is ventrally canted, indicating habitual palmar-flexion during clinging. It also has a large flexor tubercle that supported a robust tendon for a powerful flexor digitorum profundus muscle, allowing frequent and sustained use of such claw-clinging postures.

While the innominate of plesiadapiforms varies in functionally significant respects among the taxa considered here, all seem to share characteristics that reflect functions and postures associated with vertical clinging behaviors (Beard, 1991a). In contrast to the acetabulum of cursorial animals and more terrestrial scansorialists (e.g., tupaiine tree shrews), plesiadapiforms have a more elliptical acetabulum, the major axis of which is craniocaudally oriented (e.g., Silcox et al., 2005, Figure 9.5A). This indicates a limited range of sagittal flexion and extension during which the joint surfaces of the femur and acetabulum fit tightly together, and maintain maximal stability. Such morphology suggests a joint that has a large range of stable adduction and abduction (Beard, 1991a). When the femur is articulated with the acetabulum the joint surfaces conform most closely, (fovea capitis femoris aligned with the center of the acetabular fossa), when the femur is flexed and the shaft is abducted by about 45° from the sagittal plane. We infer that this orientation of the femur relative to the innominate represents a component of habitual posture. The acetabulum is cranially buttressed and its axis is dorsally rotated in plesiadapiforms, indicating that this joint was probably subject to caudally directed forces experienced during orthograde postures (Beard, 1991a). The ilium is generally slender and triangular in cross section, much the same as in extant *Prilocercus* (Sargis, 2002b,c). This is in contrast to the condition in euprimates (including extant callitrichines), which are characterized by a hugely expanded dorsolateral face of the ilium, reflecting the origination of hypertrophied gluteal muscles for powerfully extending the femur during leaping or quadrupedal bounding (see Anemone, 1993; Sargis, 2002b; Taylor, 1976).

The femur of plesiadapiforms has been figured for paromomyids, plesiadapids and micromomyids, with its morphology and functional significance discussed many times (Beard, 1991a, 1993b; Sargis, 2002c; Simpson, 1935a; Szalay et al., 1975, 1987). In all plesiadapiforms for which it is known, the posterior margin of the femoral head extends onto a short neck, and farther onto the medial margin of the greater trochanter. This extension gives the articular surface an elliptical or cylindrical form that, in conjunction with a distinct, dorsoposteriorly positioned fovea capitis femoris, indicates abducted limb postures (Beard, 1989;

Sargis, 2002b; Szalay and Sargis, 2001). The femoral neck is typically oriented at a high angle to the femoral shaft and the greater trochanter does not extend beyond the superior margin of the femoral head. Such a configuration allows for mobility at this joint, especially in abduction (Sargis, 2002b), in contrast to taxa that bound-gallop or run using pronograde postures frequently (Gebo and Sargis, 1994; Harrison, 1989; Sargis, 2002b; Szalay and Sargis, 2001). Although the greater trochanter is relatively short, the trochanteric fossa is typically deep and proximodistally oriented, providing ample room for insertion of internal and external obturator and gemelli muscles that serve to abduct or laterally rotate the thigh depending on orientation (Szalay and Schrenk, 2001). In contrast to the condition in cursorial and bounding taxa, the lesser trochanter is medially extended beyond the head, distally positioned on the shaft, and has a large area of attachment for the iliopsoas muscle. This configuration allows the femur to remain somewhat abducted even when the iliopsoas is fully contracted, and hence, when the femur is fully flexed. Furthermore, the distal position of the trochanter gives the iliopsoas muscle a long moment arm for powerful hip flexion (Anemone, 1993) and would have reduced the effort for holding the leg in flexed positions during vertical climbing (Rose, 1987). The third trochanter is relatively small and flares laterally immediately distal to the maximum peak of the lesser trochanter. This is in contrast to the condition in more active, terrestrial tree shrews in which this process flares prominently and is positioned farther distally, allowing the inserting gluteus superficialis muscle to more powerfully extend the thigh (Sargis, 2002b). The femoral shaft is either equal in mediolateral and anteroposterior dimensions or is slightly anteroposteriorly flattened. The distal end is rotated laterally relative to the proximal end, effectively orienting the plane of flexion of the knee mediolaterally. This orientation of the distal femur in plesiadapiforms is similar to that of callitrichines, and differs from leapers and bounders (e.g., *Saimiri* and tupaiids) in which the knees flex in the sagittal plane to accommodate the frequent use of small diameter supports instead of large ones. The medial margin of the patellar groove is buttressed relative to its lateral margin such that, despite the lateral rotation of the distal end, the anterior aspect of the patellar groove lies parallel to the plane defined by the shaft and a transect between the fovea capitis femoris and the tip of the greater trochanter. In extant leaping euprimates and saltatorial lagomorphs, frequent and strong full-extension of the knee is reflected in the distal femur by a deep patellar groove that prevents mediolateral deviation of the patella (Anemone, 1993), a raised patellar groove that increases the moment arm of the quadriceps muscles (Anemone,

1993) and a proximally extended groove that allows the patella to shift high on the thigh during extreme contraction of the quadriceps muscles. In contrast, the patellar groove of plesiadapiforms is shallow, not raised anteriorly above the level of the anterior surface of the shaft, and not extended proximally on the shaft. This form suggests infrequent forceful full-extension of the knee. Notably, the patellar grooves of both *Ptilocercus* and marmosets are nearly identical to those of plesiadapiforms in these respects (Sargis, 2002b,c). Posteriorly, the distal intercondylar area is angled $\sim 10^\circ$ lateral to the shaft, suggesting that the tibia would have rotated laterally, contributing to pedal inversion, during extension of the knee. Medial and lateral margins of the condyles slope away from each other proximally at an angle of $\sim 45^\circ$. This results in the posteroproximal part of the condyles being broader and more robust, again indicating that flexion was the habitual posture with loads being sustained on extended limbs only infrequently. The lateral condyle is generally $\sim 50\%$ wider than the medial condyle.

The morphology of the proximal tibia of plesiadapiforms reflects similar positional behaviors as that of the distal femur. The proximal tibia is antero-posteriorly compressed, unlike that of leapers and runners such as tupaiines (Sargis, 2002b), lagomorphs, tarsiers, and felids. The medial facet is usually smaller than the lateral facet, concave, oriented somewhat posteriorly and sunk below the level of the lateral facet, which is flat to convex and extends higher proximally. Both facets face slightly laterally, rotating the tibial shaft out of the plane of flexion with the knee. The proximal half of the shaft is compressed mediolaterally and triangular in cross section. The posterior and lateral surfaces of the proximal shaft of the tibia are concave in cross section, providing ample room for strong pedal plantar-flexors (soleus and tibialis posterior), and digital flexors (flexor digitorum tibialis), respectively. The distal part of the shaft of the tibia is strongly bowed both in the medial and anterior directions. This makes the foot of plesiadapiforms permanently somewhat inverted when flexed. The medial malleolus on the distal tibia is weaker and more distally restricted than that of other arboreal placentals such as *Ptilocercus* and primitive euprimates. The astragalar facet on the distal tibia is ungrooved, square, angled somewhat posterolaterally, and forms an obtuse angle with its extension on the medial malleolus. With regard to all of these features, the distal tibia of plesiadapiforms is most comparable to that of phalangerid marsupials (e.g., *Petaurus* and *Trichosurus*) in which the distal tibia and fibula have a flexible articulation with each other and the tarsals, allowing for a greater degree of mobility between the tibia and astragalus (the upper ankle joint = UAJ) than is typical for placentals.

Among plesiadapiforms, the proximal articulation of the tibia and fibula is only known in paromomyids and micromomyids. It is transversely oriented and may have been synovial. The distal articulation is known in all four groups discussed here and, except in carpolestids (see the section on Carpolestidae below), appears to have been a flexible syndesmosis (Beard, 1989, 1991a). There are grooves on the posterior surface of the tibia and fibula. On the posterior tibia, such grooves mark the course of the tendons of the tibialis posterior, flexor fibularis, and flexor digitorum tibialis muscles, while on the posterior fibula they mark the course of the tendon of the peroneus brevis muscle. These muscles would have served to resist mediolateral forces at the UAJ, thereby compensating for the stability given up for mobility between joint surfaces, and facilitate inversion and eversion at the lower ankle joint, as they do in arboreal marsupials and some rodents (Gunnell, 1989; Jenkins and McClearn, 1984).

The astragalus, calcaneum, and cuboid of plesiadapiforms have been discussed extensively in terms of their diagnostic and functional features (Beard, 1989, 1993b; Dagosto, 1983; Decker and Szalay, 1974; Gebo, 1988; Gunnell, 1989; Szalay and Decker, 1974; Szalay and Drawhorn, 1980). Plesiadapiforms are limited in the degree of plantar-flexion that can be accomplished at the UAJ by the small arc formed by the tibial facet of the astragalus. A slight amount of pedal inversion, limited by malleoli bracketing the astragalus, results from plantar-flexion at the UAJ (Beard, 1989). The lower ankle joint is axially mobile, the calcaneum being capable of rotating medially and shifting distally to invert the foot (Szalay and Decker, 1974). At the transverse tarsal joint, such rotation is not limited by the calcaneo-cuboid articulation, which is transverse (Beard, 1989; Jenkins and McClearn, 1984). On the cuboid, the orientation of the groove for the tendon of the peroneus longus muscle is transverse, facilitating eversion by this muscle.

Because the distal tarsal rows have rarely been preserved in association, little has been said about them. However, new specimens of micromomyids, paromomyids, and plesiadapids—all show a similar configuration in which the tarsometatarsal articulation faces slightly laterally, causing the foot to be abducted relative to the upper ankle, when dorsiflexed. The mesocuneiform is shorter than the entocuneiform and ectocuneiform such that metatarsal II articulates out of plane with the rest of the metatarsals and is dove-tailed within the distal tarsal row, creating a rigid tarsometatarsal articulation.

The entocuneiform and first metatarsal have been discussed extensively for plesiadapids and paromomyids (Beard 1989, 1993a; Sargis, 2002b,c,d; Szalay

and Dagosto, 1988). These elements are nearly identical among the plesiadapiforms considered here with the exception of those in carpolestids. In plesiadapids, paromomyids, and micromomyids the robust plantar process on the entocuneiform reflects frequent pedal inversion and possibly the presence of powerful pedal and digital flexors (contra Beard, 1993a; but see Sargis, 2002b; Szalay and Dagosto 1988). The hallux is strikingly similar to that of *Ptilocercus* in that the articulation for the hallucal metatarsal on the entocuneiform is dorsally broad and saddle-shaped (Sargis, 2002b,c,d; Szalay and Dagosto, 1988), and the hallucal metatarsal is robust, divergent from the other metatarsals, exhibits slight torsion of the distal end, and has peroneal and medial processes that are reduced such that the entocuneiform joint is open and mobile. These features indicate that the hallux was used in grasping (Sargis, 2002b,c,d; Szalay and Dagosto, 1988), as convincingly demonstrated for that of *Ptilocercus* through behavioral observations (Gould, 1978; Sargis, 2001a and references therein) as well as by myological and osteological studies (e.g., Gregory, 1913, Le Gros Clark, 1926, 1927; Sargis 2002b,c; Szalay and Dagosto, 1988). The hallux seems to have been used primarily as a load-bearing “hook” while the rest of the foot served as a lateral brace during locomotion on subhorizontal supports with relatively small diameters (Sargis, 2002b). Sargis (2001a) considered such grasping to potentially represent the antecedent condition to the powerful grasping of euprimates, as well as the primitive condition in the ancestral archontan or euarchontan (see also Sargis, 2002b,c,d; Szalay and Dagosto, 1988).

Except in carpolestids, the metatarsal/phalangeal proportions of plesiadapiform feet are not as extreme as those of the hands (i.e., the feet do not exhibit prehensile proportions), thus, the feet have proportions unlike those in the feet of specialized slow-moving graspers, and more like those of generalized arborealists that use a bounding gait. This is because the metatarsals are generally relatively long. The long metatarsals that rigidly articulate with the tarsals of plesiadapiforms are similar to those of callitrichine primates, *Ptilocercus*, and many other arboreal and scansorial mammals. These features are indicative of a bounding gait, similar to that usually used on horizontal substrates most frequently by more terrestrial scansorialists such as tupaiine tree shrews (Jenkins, 1974; Sargis, 2002b) and sciurid rodents. Long metatarsals increase the distance that can be covered with each “bound.” The toes are longer than the fingers and thus may have been relied on to support the body weight in clinging and hanging positions more frequently than the fingers.

Overall, the morphology of the appendicular skeleton of plesiadapiforms indicates a mobile forelimb capable of strong flexion at the shoulder and elbow joints that helped keep the body close to the substrate during vertical postures and that assisted the hindlimbs in scrambling up a vertical substrate. The hands could be supinated and pronated freely and were effective at grasping, allowing these animals to move easily through broken substrates on smaller supports. The hindlimbs indicate habitual flexion with a broad foot stance, consistent with habitual use of large diameter supports. Furthermore, the plane of flexion of the hindlimbs is not sagittal, as in terrestrial bounders and runners, but is rotated significantly laterally. Thus, instead of pushing away from a vertical substrate during upward propulsion, the hindlimbs extended more parallel to the substrate. The ankle exhibits axial flexibility and the capability to invert the foot. Such mobility would have allowed the substrate to be grasped from a plantar-flexed position, thereby facilitating head-first descent of tree trunks, as well as moving on small horizontal branches. Although the feet are generally not as committed to grasping as the hands, they too would have been effective on small supports and discontinuous substrates owing to a somewhat divergent, prehensile hallux, like that of *Ptilocercus* and callitrichines.

Plesiadapiform Specializations: A Diversity of Arboreal Behaviors

Despite the large amount of similarity between the four groups of plesiadapiforms considered here, each is also unique in its own way. In some cases, morphological differences are probably engendered by size extremes that change the nature of the arboreal milieu experienced by a given taxon. In other cases, these features truly represent specialized behaviors beyond clinging and claw climbing on large diameter vertical supports and the ability to grasp smaller supports with the hands and feet.

Paromomyidae

New skeletons of Late Paleocene paromomyids *Acidomomys hebeticus* (Bloch et al., 2002a) and a new species of *Ignacius* (Bloch et al., in review) are the most complete known and have clear dental-postcranial associations, allowing for a more refined and better supported understanding of postcranial anatomy and inferred positional behaviors for the group. Elements of the hands and feet have

been recovered for *Acidomomys* (Figure 3A), and nearly the whole skeleton has been recovered for *Ignacius* (albeit a composite of two individuals; Figure 3B). Both paromomyids conform to the general plesiadapiform body plan (described in section on Plesiadapiforms as Claw-Climbing Arborealists above) in most respects. Of all plesiadapiform families considered here, paromomyids are most appropriately described as “callitrichine-like” because of their similar body size of 100–500 g (Fleagle, 1999; Garber, 1992), inferred diet of exudates (Gingerich, 1974; Vinyard et al., 2003) and specific locomotor repertoire that likely included bound-galloping, as well as grasping and foraging on small diameter supports in addition to a large amount of clinging and foraging on large diameter supports. This interpretation is contrary to a previous hypothesis that paromomyids were capable of dermopteran-like mitten-gliding (Beard, 1989, 1991a, 1993b) based on fragmentary, composite specimens with undocumented associations that were proposed to have the hallmark osteological feature of mitten-gliding: elongate intermediate phalanges of the hand. The mitten gliding hypothesis has since been questioned (Hamrick et al., 1999; Krause, 1991; Runestad and Ruff, 1995). Furthermore, the new specimens discussed here do not support the mitten-gliding hypothesis because the intermediate phalanges of the hands in paromomyids are not longer than their proximal phalanges (Figure 4A). Even in the face of such evidence against “mitten-gliding,” one might argue that it is still possible that more general gliding behaviors (e.g., Petauristinae; Thorington and Heaney, 1981) could have been an aspect of the locomotor repertoire of paromomyids. Similar gliding behaviors, with correspondingly similar specialized anatomical structures (but not homologous), have evolved at least four times in mammals (Petauristinae, Anomaluridae, Phalangeridae, Cynocephalidae). Each of these experiments in gliding is also associated with unique aspects of anatomy reflecting very specific differences in behavior and evolutionary history (Essner and Scheibe, 2000; Scheibe and Essner, 2000; Thorington et al., 2005; Thorington and Heaney, 1981). While such differences can be subtle, this is distinctly not the case for dermopterans, which have unique anatomy among gliding animals reflective of the presence of an interdigital patagium and quadrupedal suspensory behaviors (Simmons, 1995; Simmons and Quinn, 1994; Stafford, 1999). Thus, even if evidence for more generalized gliding behaviors were to be found, it would still be inconsistent with Beard’s (1993a,b) hypothesis that paromomyids were mitten-gliding. In fact, paromomyids lack any trace of the osteological correlates for gliding behavior.

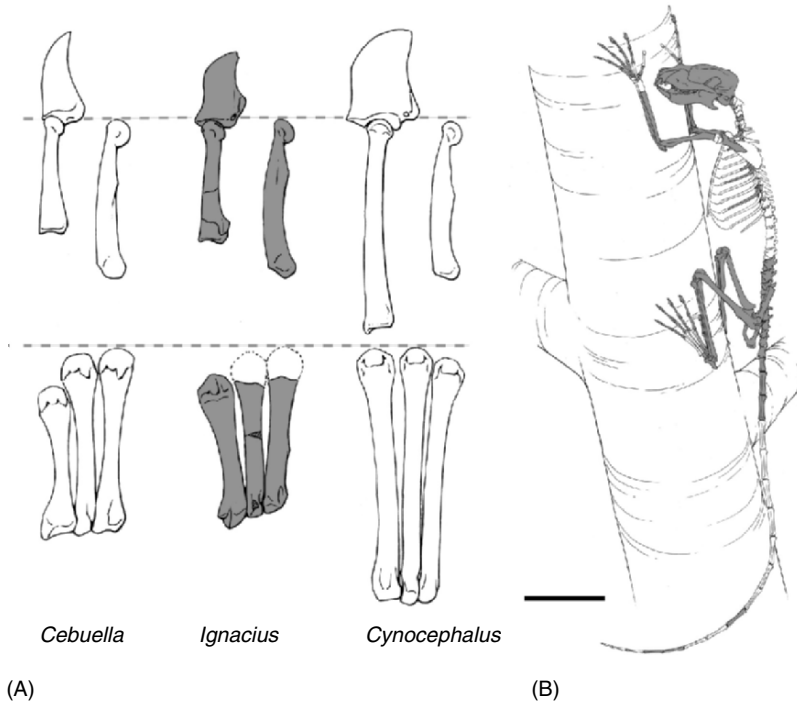


Figure 4. (A) Manual digit rays (top) and metacarpals (bottom) of paromomyid, *Ignacius* cf. *I. graybullianus*, the dermopter, *Cynocephalus volans*, and a callitrichine primate, *Cebuella pygmaea*. Phalanges are in lateral view with distal and intermediate phalanges articulated on the left and proximal phalanx on the right. Below phalanges, from left to right, metacarpals V–III are depicted in palmar view. Note that *Ignacius* lacks the elongate intermediate phalanges and metacarpals of *Cynocephalus* and instead has overall proportions comparable to those of *Cebuella*. In this way, *Ignacius* is similar to euprimates that use their relatively long fingers for grasping (prehensile phalangeal proportions of Hamrick, 2001). (B) Reconstruction of *Ignacius* cf. *I. graybullianus* in a habitual resting or foraging posture on a large diameter trunk. The proportions and morphology of both limbs and vertebrae indicate that it was probably more adept at pronograde bounding than some other plesiadapiforms. Gray areas depict bones present in UM 108210 and another individual (UM 82606) from a different region within the same limestone block. Scale = 5 cm.

Comparative functional studies show that there is a suite of osteological features shared by flying squirrels and dermopterans that appear to be gliding adaptations (e.g., Thorington and Heaney, 1981; Runestad and Ruff, 1995; Stafford, 1999), which are apparently lacking in Paleocene paromomyids (Boyer et al., 2001; Boyer and Bloch, 2002b; Bloch et al., in review). Instead, features uniquely exhibited by paromomyids indicate agile arboreality that involved more frequent use of pronograde bounding and scampering than inferred for plesiadapiforms generally. These tendencies are reflected in the limb proportions, the limb to trunk proportions, and the morphology of the vertebral column, sacrum, and innominate.

Ignacius has an intermembral index of ~80, which is comparable to that of most callitrichine primates except the pygmy marmoset, *Cebuella*, in which it is 82–84 (Fleagle, 1999). Other plesiadapiforms have intermembral indices ranging between ~84 for *Carpolestes* and 89 for *Plesiadapis cookei*. Among clawed agile arborealists, including taxa classified in Rodentia, Scandentia (Sargis, 2002a), and Callitrichinae (Fleagle, 1999), higher intermembral indices may correspond to more frequent and sustained use of vertical clinging postures since the arms take a more active role in supporting and lifting the body, instead of acting as struts that must withstand impacts after propulsion by the hindlimbs, as they do in pronograde bounders (Gambaryan, 1974). Just as relative lengths of hindlimbs and forelimbs are behaviorally indicative, so is overall length of the limbs, relative to the trunk, which increases with frequency of use of vertical clinging postures (Boyer and Bloch, in review). Although trunk length estimates are not yet available for micro-momyids or plesiadapids, comparison of the limb to trunk proportions of *Ignacius* with callitrichines shows *Ignacius* to be similar to tamarins, such as *Saguinus*, which have substantially shorter limbs than the more arboreally committed *Cebuella*.

Vertebral morphology and proportions in *Ignacius* suggest agility and an emphasis on the hindlimb in forward propulsion. It is comparable to other squirrel-like and primate-like taxa in having a narrow atlas and a short neck relative to the trunk. The posterior lumbar vertebrae are larger and more elongate than the thoracic vertebrae. The sacrum is robust and the tail is long and robust. Such a configuration results in a posteriorly shifted center of gravity (COG) of the vertebral column relative to that of a non-bouncer (Shapiro and Simons, 2002) or a quadrupedal runner (Emerson, 1985), thereby reducing the offset between the COG and the pelvic girdle, where the main

propulsive force is applied by the hindlimbs. The morphology of the lumbar vertebrae also indicates the ability to powerfully flex and extend the trunk. These vertebrae have narrow, cranially angled spinous processes and long cranioventrally oriented transverse processes. They are qualitatively similar to those of scansorialists that use a bounding gait and strepsirrhines that leap (Shapiro and Simons, 2002). Furthermore, in bounding taxa, the relationships of the dimensions of these aspects of vertebral morphology to overall body mass are significantly different from those of non-bouncers (Boyer and Bloch, 2002b; in review), with bounding taxa having lumbar spinous processes that are narrower craniocaudally and transverse processes that extend farther ventrally than those of non-bouncers. *Ignacius* fits the scaling relationship characterizing extant bouncers.

The sacrum of paromomyids has a reduced spinous process on its first vertebra and tall, narrow, caudally oriented ones on the second and third vertebrae. Such a configuration is similar to that of hindlimb-propelled taxa in which a large degree of flexibility at the lumbosacral joint is required. Not only does the spinous process of the first sacral vertebra not impede extension, but the supraspinous ligament, which might have spanned two vertebrae instead of one (Gambaryan, 1974), would have allowed a greater range of mobility for the same elastic strain than it would separated into two segments.

The innominate of paromomyids differs from that of other plesiadapiforms in having an ilium with a relatively broader dorsolateral surface, an ischium that is relatively longer and more expanded, and an ischiopubic symphysis that is longer and more cranially positioned (relative to the acetabulum). These features indicate a sturdy pelvic girdle with ample room for origination of the hip extensor muscles. Such a pelvis would be capable of withstanding impacts of a bounding gait and would allow room for the attachment of powerful muscles adequate for the effective use of such an active locomotor style.

In summary, the skeleton of *Ignacius* indicates a versatile locomotor repertoire with no specific features detracting from its ability to use vertical postures (Figure 4B), but with additional features that allowed it to effectively exploit horizontal substrates using above branch postures.

Carpolestidae

Insights into the behavior of the Carpolestidae are derived primarily from a single specimen of the Late Paleocene taxon, *Carpolestes simpsoni* (Bloch and

Gingerich, 1998). The specimen is fairly complete (Figure 3C) and the dental associations are well documented (Bloch and Boyer, 2001, 2002b).

Carpolestes is unique among plesiadapiforms in having a foot that is better adapted for powerfully and precisely grasping small diameter supports, a UAJ that reflects even more freedom of motion, a humerus that suggests relatively stronger grasping, and a vertebral column that indicates only infrequent use of a bounding gait on either vertical or horizontal substrates. In terms of behavior, these features suggest that *Carpolestes* spent relatively little time on large diameter supports, and instead most frequently occupied a small branch niche where grasping is more useful than claw-clinging and bridging is more effective than bounding.

In contrast to the condition in other plesiadapiforms, the feet of *Carpolestes* are similar to the hands in having prehensile proportions, a result of unusually short metatarsals and long toes (Bloch and Boyer, 2002b; Figure 5A). In both the fingers and toes, the proximal phalanges are more curved than those of other plesiadapiforms. The intermediate phalanges are not mediolaterally compressed, but have a more spherical cross section than those of other plesiadapiforms (Bloch and Boyer 2002a). The unguals are relatively smaller and slightly broader than in other plesiadapiforms. The articular surface for the intermediate phalanx has a slight dorsal orientation such that when articulated, it is canted dorsally rather than palmarly on the hands and feet. Furthermore, on the ventral surface of the shaft, distal to the flexor tubercle, there is an expanded area that may reflect the presence of an expanded dermal pad in life, as a similar structure seems to do in the unguals of *Petaurus* as well as in the grooming claws of the euprimate, *Tarsius*. These features, taken together, suggest less frequent use of the hands and feet for claw-clinging and more habitual grasping of small diameter substrates (Figure 5B).

Prehensile proportions and phalangeal morphology in *Carpolestes* are subtle expressions of grasping behavior compared to the condition of the hallux (Figure 6). The structure of the joint between the entocuneiform and the hallucal metatarsal, as well as the structure of both this metatarsal and the hallucal distal phalanx are strikingly similar to those of euprimates, indicating specialized, powerful grasping, beyond that inferred from the usual plesiadapiform condition. The entocuneiform is short with a huge plantar process that would have buttressed hypertrophied pedal flexors and on to which may have inserted the tendon of tibialis anterior, a powerful pedal inverter (Sargis, 2002b;

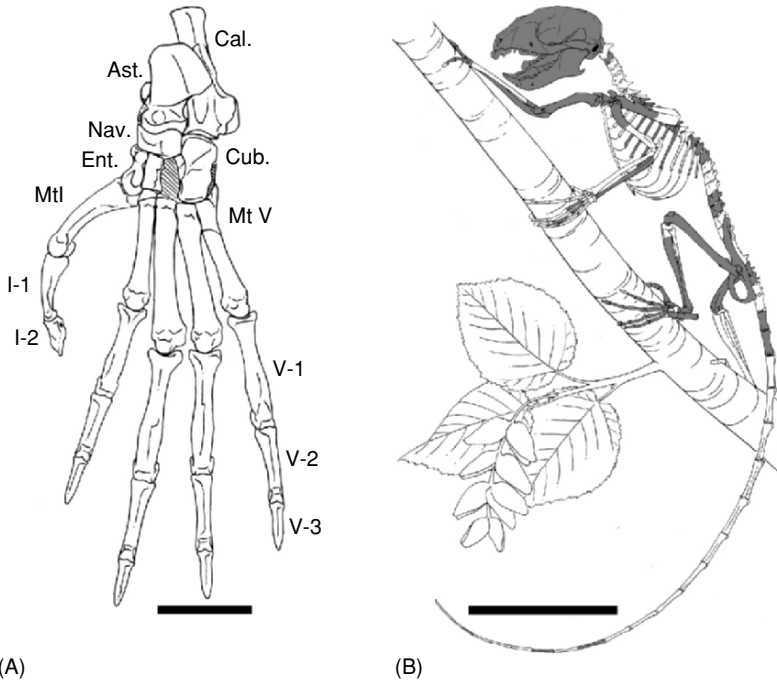


Figure 5. (A) Reconstructed left foot and ankle of *Carpolestes simpsoni* (figure from Bloch and Boyer, 2002a; fig. 4a). Note that the hallux is divergent from and in opposition to the other digits, the metatarsals are short, and the nonhallucal digits are relatively long. All of these features indicate eupriate-like grasping. The foot is unlike that of euprimates, however, in having short tarsals and a diminutive peroneal process on the proximal hallucal metatarsal. Long tarsals and a prominent peroneal process in euprimates are thought to facilitate powerful leaping with stable landings (Szalay and Dagosto, 1988). Abbreviations: *Ast.*, astragalus; *Cal.*, calcaneum; *Cub.*, cuboid; *Ent.*, entocuneiform; *Mt.*, metatarsal; *Nav.*, navicular; *I-1*, proximal phalanx, first digit; *I-2*, distal phalanx, first digit; *V-1*, proximal phalanx, fifth digit; *V-2*, middle phalanx, fifth digit; *V-3*, distal phalanx, fifth digit. (B) Reconstruction of *Carpolestes simpsoni* (figure from Bloch and Boyer, 2002a; fig. 2b). Locomotion on small diameter supports, depicted here, is inferred from the specialized grasping hands and feet; strong, mobile elbow; robust fibula; mobile ankle joints; mobile vertebral column; gracile pelvis; and specialized dentition (Bloch and Boyer, 2002a). Gray areas in B represent bones present in UM 101963. Scale in A = 5 mm. Scale in B = 5 cm.

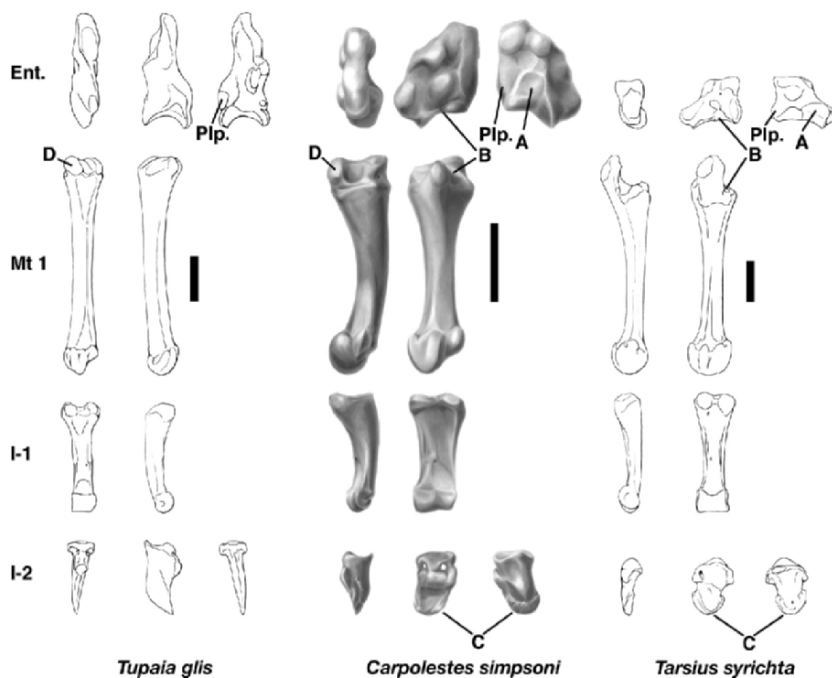


Figure 6. Left hallux of Paleocene plesiadapiform *Carpolestes simpsoni* compared to those of extant euprimate *Tarsius syrichta* and extant tree shrew *Tupaia glis* (figure from Bloch and Boyer, 2002a; fig. 3). The entocuneiform (from left to right) is in ventral, lateral, and medial views, the metatarsal and proximal phalanx are in ventral and lateral views, and the distal phalanx is in ventral, lateral, and medial views. Euprimate traits present in the hallux of *C. simpsoni* include a medial expansion of the distal facet on the entocuneiform (A) for articulation with the first metatarsal that forms a saddle-shaped, or sellar joint (B), and a distal phalanx that supported a nail instead of a claw (C). Primitive traits, also seen in the tree shrew, include a first metatarsal with a peroneal process that is not enlarged (D). Note that the distal, relative to the proximal, end of the hallucal metatarsal of *C. simpsoni* is laterally rotated about 90° compared to the condition in that of tupaiids. Similarities to euprimates are reflective of *C. simpsoni* having a divergent and opposable hallux, while the similarities to tree shrews (and not to euprimates) are reflective of *C. simpsoni* not being a specialized leaper. Size of hallux normalized to the length of the metatarsal. Abbreviations: *Ent.*, entocuneiform; *Plp.*, plantar process of entocuneiform; *Mt 1*, metatarsal, first digit; *I-1*, proximal phalanx, first digit; *I-2*, distal phalanx. Scale = 2 mm.

Szalay and Dagosto 1988). Furthermore, the distal articular surface is saddle-shaped, narrow and cylindrical on its ventral margin, and expanded proximally on its medial side. The articulating metatarsal can rotate medially from its most adducted position by $\sim 60^\circ$, at which point a blunt medial process on the metatarsal meets a correspondingly spherical depression on the medial side of the entocuneiform. Once these surfaces are in contact, there is an increase in the axial mobility of the metatarsal that allows the abducted hallux to form a more stable grip on the substrate than it might be able to achieve otherwise. The metatarsal itself is no more robust than in other plesiadapiforms, but it shows a greater degree of torsion, which makes the hallux more completely oppose the rest of the digits. The proximal hallucal phalanx is flattened with a mediolaterally broad, but proximodistally short distal articular surface that is almost completely plantar-facing. This wide, shallowly dished surface accommodates the distal phalanx that is dorsoplantarly shallow and mediolaterally expanded, distinctly unlike the nonhallucal unguals of this animal and more consistent with morphology that reflects the presence of a large dermal pad and nail in most extant euprimates, as well as some marsupials and rodents.

The ankle of *Carpolestes* differs from other plesiadapiforms in that: (1) the fibula is relatively larger; (2) the groove for the tendon of the tibialis posterior muscle and the groove for the tendon of the peroneous brevis muscle, on the tibia and fibula respectively, are deeper; and (3) the opposing articular facets on both the tibia and fibula are convex indicating increased axial mobility and possibly a synovial articulation. As might be expected, the astragalus reflects this added mobility in lacking the distinct, often acute, ridge marking the boundary between the tibial and fibular facets on the astragalar body, which restricts the UAJ to plantar and dorsiflexion in other plesiadapiforms.

The greater emphasis on grasping behavior in *Carpolestes* is reflected in the forelimb primarily by a relatively large and medially extended entepicondyle. Such medial extension provides relatively more room for the attachment of the flexor muscles of the wrist and digits. Furthermore, the distal articular surface of the humerus suggests even more complete segregation in the function of the radius and ulna. The zona conoidea is so deep that it creates both a lateral keel on the trochlea for articulation with the ulna (on the medial margin of the zona conoidea) and a lateral ridge medial to the capitulum. This condition is otherwise unique to euprimates and microsycopid plesiadapiforms (Beard, 1991b; Silcox, 2001).

Finally, the vertebral column of *Carpolestes* has an anticlinal vertebra positioned within the thoracic region and narrow spinous processes on the lumbar and posterior thoracic vertebrae, indicating that it was capable of sagittal flexion. However, the vertebral column is not particularly suited for the powerful sagittal flexion and extension required in a bounding gait, such as that inferred for paromomyids (Boyer and Bloch, 2002a,b). Such a de-emphasis on features reflective of a bounding gait is expected for an animal that spends the majority of its time in a small branch niche where bridging is safer and more effective than bounding (Sargis, 2001b).

Based on this specimen, carpolestids appear to diverge from the general plesiadapiform body type more than any other group we have studied. Interestingly, many of the deviant aspects in carpolestid morphology and inferred behavior are similar to those observed and/or inferred for early euprimates.

Plesiadapidae

Plesiadapid postcrania are currently known from a wider geographic and temporal range and from a greater diversity of species than are those of any other plesiadapiform group. Not surprisingly, they exhibit greater morphological diversity than seen in any of the other three families considered here. A skeleton of *Plesiadapis cookei* (Figure 3D; Gunnell and Gingerich, 1987; Gunnell, 1989; Gingerich and Gunnell, 1992, 2005; Hamrick, 2001), a large species known exclusively from western North America, is in the process of being described (Boyer, in preparation). Plesiadapids obtain a large size rather early in their evolutionary history, and this may explain many of their characteristic features (Gingerich, 1976).

Clinging and climbing on large diameter substrates appears to be a major feature of the locomotor repertoire of *Plesiadapis* (Gingerich and Gunnell, 1992; Gunnell, 1989). The ability to grasp small-diameter supports with the hands and feet is reduced, and agile pronograde bounding would probably have been infrequent (Gunnell, 1989).

The unguals of plesiadapids differ from those of other plesiadapiforms in having a shaft that is relatively long, an extensor tubercle that is reduced and proximally extended such that the articular surface is more plantarly oriented, and a flexor tubercle that faces plantarly instead of proximally. As a consequence of reduction in the extensor tubercle, the dorsal margin of the ungual shaft is generally convex for its entire length. The digit ray as a whole is most

comparable to that of semi-arboreal new world porcupines such as *Erethizon* and *Sphiggurus* and thus, consistent with the hypothesis of clinging and climbing on large diameter vertical supports. The proximal ends of the unguals of at least *Plesiadapis cookei* are, however, strikingly similar to those of sloths and the pedal unguals of *Pteropus* (Megachiroptera: Pteropodidae), possibly indicating some suspensory behaviors. Godinot and Beard (1991) illustrate the digit ray for *Plesiadapis tricuspiciens* showing it to not have this suspensory feature. Furthermore, Beard (1989) illustrated the phalanges of another plesiadapid, *Nannodectes intermedius* demonstrating that it is more like *P. tricuspiciens* in this regard.

Although the pollex of plesiadapids is divergent and probably fairly mobile (Beard, 1989, 1990), they have been described as lacking prehensile phalangeal proportions (Beard 1990; Hamrick, 2001), suggesting a reduction in their ability to grasp small diameter supports in a euprimate-like way (Beard, 1990; Boyer and Bloch, 2002; Hamrick, 2001). However, Godinot and Beard's (1991) reconstruction of the *P. tricuspiciens* ray shows it to have a short metacarpal, making it more similar to other plesiadapiforms (e.g., different from *P. cookei*) in this respect.

The humerus of *Plesiadapis cookei* suggests less emphasis on euprimate-like grasping (Gunnell and Gingerich, 1987) and might be more similar to that of sloths and dermopterans in features that represent suspensory tendencies. This is distinctly *not* the case for *Nannodectes intermedius* in which the humerus is more like that of other plesiadapiforms (Beard, 1989).

The close similarity of some plesiadapid unguals to those of sloths and bats, the similarity of at least some plesiadapid humeri to sloths and dermopterans, and the lack of prehensile phalangeal proportions, indicate more frequent use of underbranch clinging. Whereas smaller-bodied plesiadapiforms could navigate small branches using strong grasping (similar to extant *Ptilocercus* and callitrichines) and pronograde postures, plesiadapids were also likely capable of some grasping, but may have also relied more on suspensory behaviors to distribute their weight and avoid torques when moving on small branches, as large-bodied platyrrhine and hominoid primates do today.

Micromomyidae

Micromomyids are by far the smallest (30–40 g) plesiadapiforms for which postcrania are known. Postcranial specimens are late Clarkforkian to middle

Wasatchian in age. They represent three genera: *Chalicomomys*, a *Chalicomomys*-like new genus, and *Tinimomys*. Taking all of these specimens into consideration reveals the morphology and inter-element proportions of almost the entire skeleton (Figure 7). While no specific features seem to detract from the ability of these animals to use vertical postures in the man-

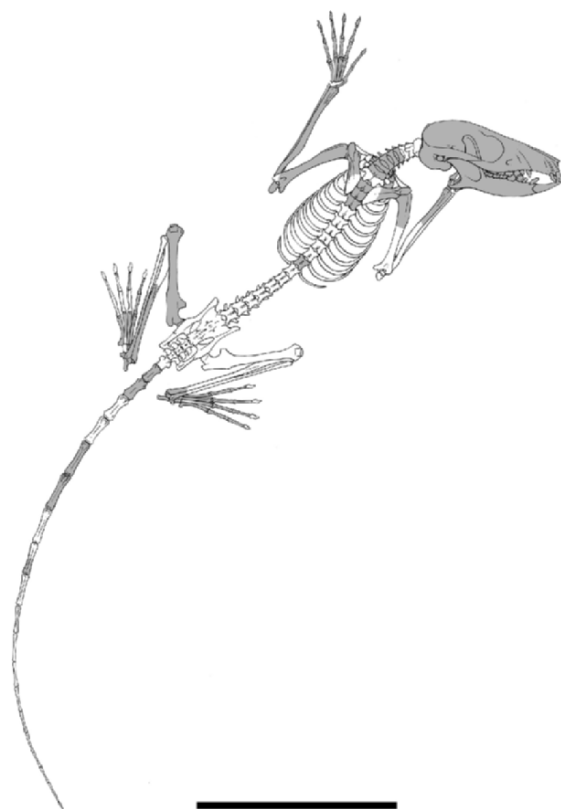


Figure 7. Reconstruction of a micromomyid on a large-diameter support. Features it shares with other plesiadapiforms described here support such a posture. Gray areas depict bones present in one specimen (UM 41870). Note that the posterior three vertebrae and a proximal ulna are not depicted in either Figure 2A or B. These were recently recovered from a block discovered to have broken off from the main limestone (block 821419 from SC-327) early in the preparation process. The association was confirmed by a connection between the broken ulnar shaft and the proximal end of the left ulna. Scale = 3 cm.

ner suggested by the general plesiadapiform morphology, they also exhibit a suite of unique features indicative of some behavioral peculiarities reflected in the morphology and relative length of the radius, the morphology of the innominate, the morphology and relative length of the tibia and fibula, and the morphology of the astragalus.

The radius is unique in having a large, raised area for the origination of the pronator teres muscle on the lateral aspect of the shaft just proximal to its midpoint; a shaft that is mediolaterally expanded starting at the level of the pronator teres muscle (a tuberosity) and continuing to the distal end (providing room for origination of powerful digital flexors and the pronator quadratus muscle, respectively); and a distal articular surface that is deeply cupped, elliptical, and has a distinct dorsal ridge that causes this surface to face palmarly. The form of the distal end is most comparable to that of sloths, dermopterans, and *Ptilocercus* in which it presumably reflects use of suspensory postures wherein the palmar-flexed hand is “hooked” over relatively small-diameter, sub-horizontal supports. Bats have a similar dorsal ridge and palmar-facing articulation, but the shape of the articular surface itself is much different in being almost sloth-like in micromomyids. Taken together, the morphology of the radius seems to indicate sustained use of vertical and underbranch clinging. During underbranch clinging, a strong pronator teres muscle would resist supinatory torque (Miller et al., 1964) produced by gravity, tending to pull the hands out of plane with and away from the substrate.

The fibula and UAJ in micromomyids are substantially different from those of other plesiadapiforms. At such a small body size, micromomyids experienced an arboreal milieu presenting relatively larger diameter supports, and in part these morphological differences seem to reflect that. More specifically, micromomyids appear to have been capable of stronger flexion of the digits and foot, and stronger resistance to pedal inversion than other plesiadapiforms. These inferred functional implications of the ankle morphology are similar to and consistent with those from the forelimb morphology. The proximal end of the fibula flares anteroposteriorly and is blade-like, unlike that known for any other plesiadapiform. The shaft then gradually tapers distally until it obtains a circular cross section. This proximal, blade-like expansion of the shaft provides a large area for origination of pedal plantar-flexor muscles and the pedal evertor muscle, peroneus longus.

The astragalus of micromomyids differs from that of other plesiadapiforms in having, on the body, a relatively high medial ridge that reduces the degree

of natural inversion of the foot; on the tibial facet, a deeper groove that limits the UAJ to sagittal flexibility; and an enormous groove for the tendons of the pedal plantar-flexor muscles (flexor tibialis and fibularis) on its plantar aspect as would be expected from the large area for origination of these muscles on the tibia and fibula. The calcaneum of micromomyids differs from that of other plesiadapiforms [except *Phenacolemur praecox* and some other paromomyids (Beard, 1989; Szalay and Drawhorn, 1980)] in having a longer tuberosity, giving the gastrocnemius and soleus muscles more leverage, and in having a more distally and laterally extended peroneal tuberosity, giving the tendon of peroneous longus an even more transverse line of action and making it a more devoted pedal evertor.

Although leaping between vertical supports is not out of the realm of possibility for micromomyids, given the idiosyncrasies described thus far, pronograde postures and any sort of bounding were probably infrequent. Such obligate arboreality is also probably reflected in the innominate. Unlike in *Ignacius* and bounding taxa generally, the ilium is extremely long and rod-like (Sargis, 2002c), the ischium is relatively short and rod-like; and the ischiopubic symphysis is short and caudally shifted relative to the acetabulum, similar to that of dermopterans (Sargis, 2002c) and lorises, both of which often use suspensory postures and neither of which use pronograde bounding. We note that such features also characterize *Ptilocercus* (Sargis, 2002b,c) and primitive eutherians such as *Ukhaatherium* (Horovitz, 2000, 2003), and may be more reflective of the primitive condition (see Szalay et al., 1975) than a behavioral specialization.

The major differences between micromomyids and other plesiadapiforms reflect the ability of micromomyids to more powerfully flex the digits and manus, to plantarflex the pes, to resist supination and inversion, and to less effectively use pronograde postures. Such adaptations suggest more time spent on the undersides of branches (Bloch et al., 2003), where they would be out of sight of aerial predators.

PHYLOGENETIC IMPLICATIONS: PRIMATE ORIGINS AND ADAPTATIONS

Plesiadapiformes have long been considered an archaic radiation of primates (Gidley, 1923; Gingerich, 1975, 1976; Russell, 1959; Simons, 1972; Simpson, 1935b,c; Szalay, 1968, 1973, 1975; Szalay et al., 1975, 1987). In the last 30+ years, many researchers have questioned a plesiadapiform–euprimate link

and have suggested removing plesiadapiforms from the primate order (Beard, 1989, 1990, 1993a,b; Cartmill, 1972; Gingerich and Gunnell, 2005; Gunnell, 1989; Kay et al., 1990, 1992; Martin, 1972; Wible and Covert, 1987). Discovery of a paromomyid plesiadapiform skull (Kay et al., 1990, 1992) and independent analysis of postcrania referred to Paromomyidae (Beard, 1989, 1990, 1991, 1993a,b) have led some investigators to conclude that micro-momyid and paromomyid plesiadapiforms were mitten-gliders (Beard, 1993b) and shared a closer relationship to extant flying lemurs (classified together in Eudermoptera; Beard, 1993a,b) than Euprimates (Beard, 1989, 1993a,b; Kay et al., 1990, 1992). Despite the fact that this “mitten-gliding hypothesis,” as well as the character support for Eudermoptera, have been strongly challenged in the past 15 years (Bloch and Boyer 2002a,b; Bloch and Silcox, 2001, 2006; Bloch et al., 2001, 2002b; Boyer and Bloch, 2002a,b; Boyer et al., 2001; Hamrick et al., 1999; Krause, 1991; Runestad and Ruff, 1995; Sargis, 2002c; Silcox, 2001, 2003; Stafford and Thorington, 1998; Szalay and Lucas, 1993, 1996), a plesiadapiform–dermopteran relationship has gained currency (e.g., McKenna and Bell, 1997). In contrast, based on a wealth of new postcranial data, we have demonstrated that: (1) no plesiadapiform yet studied shows morphological characteristics reflective of dermopteran-like mitten-gliding (Bloch and Boyer, 2002a,b; Bloch et al., in review; Boyer et al., 2001); (2) many aspects of the generalized plesiadapiform postcranium indicate committed arboreality possibly homologous to that of *Ptilocercus*, which suggests that features related to such a lifestyle, previously thought to uniquely link flying lemurs and paromomyids are, instead, reflective of the primitive condition for Euarchonta (Bloch and Boyer, 2002a,b; Bloch et al., 2001, 2002b, 2003, in review; Boyer and Bloch, 2002a,b; Boyer et al., 2001; Sargis, 2001a,b, 2002a,b,c; Szalay and Lucas, 1993, 1996); and (3) cladistic analyses suggest that some of the more specialized arboreal adaptations of certain plesiadapoid plesiadapiforms (specifically Carpolestidae) are uniquely shared with Euprimates, indicating a closer relationship between these two groups than previously supposed (Bloch and Boyer, 2002a, 2003; Bloch et al., 2002b, in review).

Recent cladistic analyses, drawing on different classes of osteological data and including different groups of taxa, support a monophyletic relationship between Plesiadapiformes and Euprimates (Primates, *sensu lato*; Figure 8). Silcox (2001; also this volume) included dental, cranial, and postcranial data for a large sample of plesiadapiforms, euprimates, scandentians, dermopterans and chiropterans. Her study concluded that plesiadapiforms are the sister

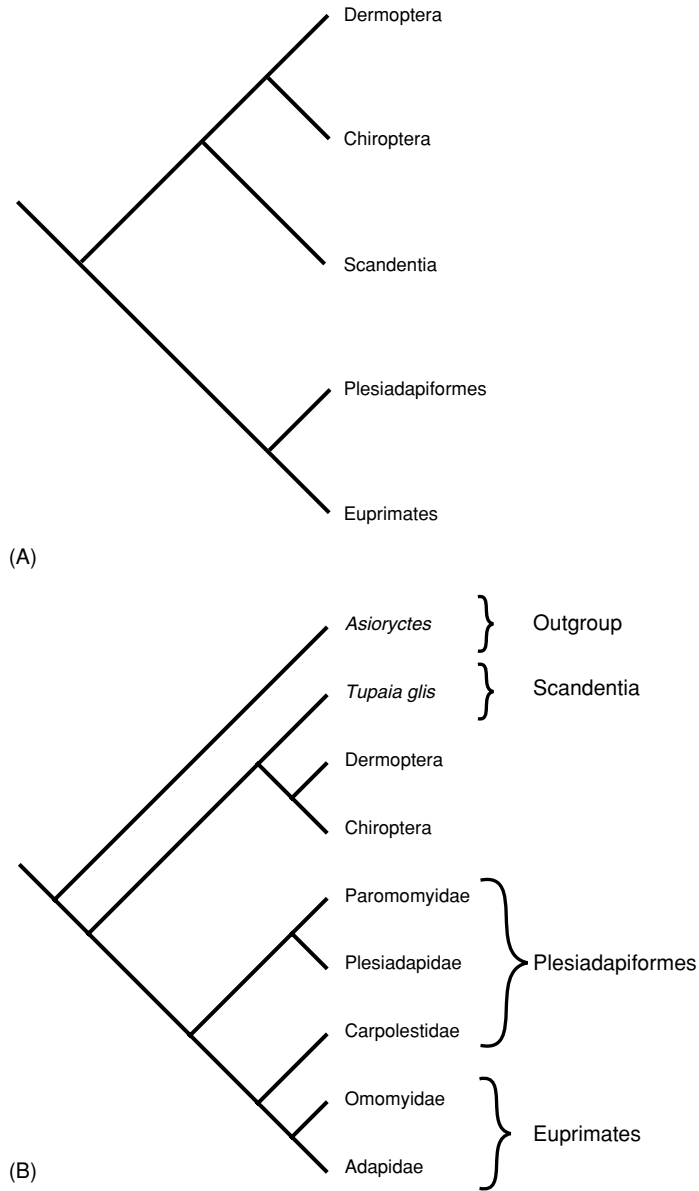


Figure 8. (A) Hypothesis of phylogenetic relationships among archontans that is well supported by dental, cranial, and postcranial evidence presented elsewhere (Silcox, 2001). (B) Hypothesis of phylogenetic relationships among select archontans illustrating phylogenetic position of Carpolestidae based on cladistic analysis of 65 postcranial characters (figure from Bloch and Boyer, 2002a; Figure 1). Note that both topologies support a plesiadapiform-euprimate link, while the cladogram based on new postcranial data presented in Bloch and Boyer (2002a) specifically allies Carpolestidae with Euprimates (Omomyidae + Adapidae).

group to Euprimates to the exclusion of all other included mammals (Figure 8A). Bloch and Boyer (2002a) presented a cladistic analysis of the new postcranial data discussed here. The results of their postcranial analysis are consistent with those of Silcox (2001) in supporting a plesiadapiform-euprimate relationship but, unlike those of Silcox (2001), they suggest that Carpolestidae falls out with Euprimates to the exclusion of other plesiadapiforms (Figure 8B). Analyses that combine new dental, cranial, and postcranial data from these two analyses, as well as that from the work of Sargis (2001b, 2002a,b,c, also this volume), are underway (Bloch et al., in review; but see Bloch and Boyer, 2003; Bloch et al., 2002b). Preliminary results of this project indicate that plesiadapoid plesiadapiforms (including Carpolestidae, Plesiadapidae, Saxonellidae, and Asian *Chronolestes simul*; Silcox, 2001) form a monophyletic clade that is the sister group to Euprimates to the exclusion of all other fossil and living euarchontan mammals (Bloch et al., in review).

This hypothesis of relationships, coupled with new functional interpretations of plesiadapiform skeletons, provides a more resolved picture of the sequence of character acquisitions in early primate evolution than was previously possible through analyses of fragmentary postcrania (e.g., Beard, 1991a, 1993a,b; Szalay and Dagosto, 1980) or through indirect means, such as comparative studies of extant mammals (Cartmill, 1972, 1974; Rasmussen, 1990).

Both arboreal tree shrews (Sargis, 2001a) and didelphid marsupials (Lemelin, 1999) have been presented as living ecological models for plesiadapiforms and the ancestral euprimate, respectively. It is plausible that the earliest primates were capable of grasping in a manner similar to living arboreal tree shrews like *Prilocercus* (Sargis, 2001a, 2002b,c; Szalay and Dagosto, 1988), and in that regard are perhaps best represented in the known postcranial fossil record by micromomyids and paromomyids. The specialized euprimate foot, which includes a divergent and opposable hallux with a nail (see Dagosto, 1988), likely evolved next in a form similar to that of *Carpolestes*, independent of leaping or orbital convergence. This stage of primate evolution might be best modeled by arboreal delphids like *Caluromys* among living mammals (Lemelin, 1999; Rasmussen, 1990).

We acknowledge that plesiadapiform taxa currently known from postcranial material are dentally relatively derived (see Kirk et al., 2003) and are unlikely to represent direct ancestors along a lineage leading to the first euprimates. However, this type of evidence is usually lacking in the fossil record. If paleontologists were to restrict themselves to studying only those species that

were plausibly *directly ancestral* in their studies of the stem lineages of major clades, then we would know very little about the early evolution of, for example, either Hominini (i.e., australopiths) or Cetacea (i.e., archaeocetes). As is the case for these stem taxa and the origin of humans and whales, respectively, we are confident that analyses of plesiadapiform primate skeletons provide useful data in evaluating the competing adaptive scenarios of euprimate origins (Bloch and Boyer, 2003).

At least three possibilities exist concerning the nature of the postcranial similarities between plesiadapiforms and euprimates: (1) plesiadapiforms and euprimates do not share a recent common ancestry, and all of their uniquely shared postcranial similarities are the result of convergence; (2) plesiadapiforms and euprimates do share a recent common ancestry, but all of their uniquely shared postcranial similarities are the result of parallel evolution; or (3) some, or all, of the uniquely shared postcranial similarities are synapomorphies of a clade that either includes carpolestids and euprimates (as suggested by cladistic analysis of only postcranial data; Bloch and Boyer, 2002a), or all plesiadapoid plesiadapiforms (including carpolestids) and euprimates (as suggested by cladistic analysis of dental, cranial, and postcranial data; Bloch and Boyer, 2003; Bloch et al., 2002b, in review). Evidence for and against each of these explanations is outlined below.

It has been suggested that any unique characteristics shared by plesiadapiforms and euprimates must be the result of convergence because the two groups do not share a recent common ancestry (Kay and Cartmill, 1977; Martin, 1990). Evidence for (or against) this interpretation stems from phylogenetic analyses that do not (or do, respectively) support a monophyletic plesiadapiform-euprimate clade. Results of recent phylogenetic analyses unambiguously support a monophyletic plesiadapiform-euprimate clade, based on a larger sample of taxa with more complete morphologic data than ever before analyzed (e.g., Bloch and Boyer, 2003; Bloch et al., 2002b, in review; Silcox, 2001), although these results are not without controversy (Bloch et al., 2003; Kirk et al., 2003). Regardless, there is at least consensus in the literature that plesiadapiforms are euarchontans, and as such, are closer to the origin of euprimates in phylogenetic space and time than are didelphid marsupials (Lemelin, 1999) and arboreal rodents (Kirk et al., 2003) and would be better ecological models and have at least as much, if not more, bearing on the competing adaptive scenarios for euprimate origins as these groups do.

In a similar but not equivalent argument, it is possible that unique similarities between plesiadapiforms and euprimates could have been acquired in parallel from a relatively recent common ancestor (Bloch and Boyer, 2002a, 2003; Kirk et al., 2003). We emphasize that it is implicitly acknowledged in this explanation that plesiadapiforms share a relatively recent common ancestry with euprimates and is thus in broad agreement with recently published phylogenetic hypotheses (Bloch and Boyer, 2003; Bloch et al., 2002b, in review; Silcox, 2001). The most convincing evidence for a “parallel evolution” explanation is that large-bodied plesiadapids, which might share a sister-relationship with carpolestids, lack some of the unique euprimate characters. If *Plesiadapis* represents the primitive condition for Plesiadapoidea, then these characters (e.g., specialized opposable hallux with a nail) would have evolved in parallel. Alternatively, it could be argued that large-bodied species of *Plesiadapis* are derived, and that more primitive, and therefore more phylogenetically relevant, plesiadapids, such as *Nannodectes* (Beard, 1989, 1990), might share more in common with carpolestids than previously recognized. Thus, it is plausible that the primitive plesiadapoid condition is more closely represented by *Carpolestes* (Bloch and Boyer, 2002a) than by *Plesiadapis* (Kirk et al., 2003). However, even if grasping did evolve in parallel from the common ancestor of plesiadapoids and Euprimates, it would represent an example of the parallel evolution of a strikingly euprimate-like mammal from the same arboreal ancestor in potentially identical ecological conditions, and would still be very relevant for assessing hypotheses of euprimate origins (Bloch and Boyer, 2003). Such a scenario would require the common ancestor of euprimates and plesiadapoids to have differed from other euarchontans in having more bunodont teeth and better grasping capabilities. Both of these features are consistent with increased frugivory (Szalay, 1968) and locomotion in terminal branches. In the subsequent hypothetical parallel radiations of euprimates and plesiadapiforms, both could plausibly have evolved more specialized grasping independently, but in similar ways for similar reasons. It is also plausible, although no *direct* evidence supports it yet, that the first euprimates could have then co-opted this initial adaptation to terminal branch frugivory for visually directed predation (Bloch and Boyer, 2003; Ravosa and Savakova, 2004). On the other hand, direct fossil evidence does support the hypothesis that this initial adaptation was co-opted for grasp leaping locomotion in the earliest euprimates (Szalay and Lucas, 1996).

The last argument, and the one preferred here, is that the uniquely shared characteristics of plesiadapoids and euprimates were inherited from a relatively recent common ancestor (Bloch and Boyer, 2003). Arguments against this interpretation are the same as those listed as evidence supporting the convergent and parallel evolution hypothesis outlined above. Furthermore, evidence for this interpretation is the same as that used in the arguments against these two hypotheses: phylogenetic hypotheses that entertain a monophyletic plesiadapoid-euprimate clade (e.g., Bloch and Boyer, 2003; Bloch et al., in review) have greater explanatory power in the face of all of the known dental, cranial, and postcranial data than those based on partitioned data sets (Beard, 1993; Bloch and Boyer, 2002a; Bloch and Silcox, 2006; Kay et al., 1992). If one accepts the hypothesis that Plesiadapoidea are the sister clade to Euprimates, then Euprimates must have originated by around 64 MYA as indicated by the earliest occurrence of a plesiadapoid plesiadapiform (*Pandemonium*; Van Valen, 1994). In this case the first 9 MY of euprimate evolution remains unknown. In this scenario, acquisition of specialized grasping features for terminal branch locomotion would have preceded the evolution of visual specializations in stem-primates and would thus not be considered a specific adaptation for nocturnal, visual predation.

In the words of M. Cartmill (1992: 111) “[w]e can only hope that new fossil finds will help us to tease apart the various strands of the primate story, giving us clearer insights into the evolutionary causes behind the origin of the primate order to which we belong.” Older and more primitive skeletons of plesiadapiforms are needed to test our ideas about the evolution of euprimate-like grasping (Bloch and Boyer, 2002a). Likewise, more complete postcranial fossils of the earliest euprimates, and a better sampling of the Paleocene fossil record of Africa, Asia, and the Indian subcontinent, are needed to address how euprimate-like leaping and forward facing orbits might have evolved from a terminal branch-foraging ancestor.

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