

Carpal Development and Morphology in Archontan Mammals

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ABSTRACT Carpal morphology and development in bats, colugos, tree shrews, murids, and sciurids were studied in order to homologize carpal elements. Prenatal coalescence of discrete cartilaginous templates with a loss of a center of ossification appears to be the most common method of reducing carpal elements in these mammals. Only bats and colugos showed postnatal ossification between discrete elements as a method of reducing carpal elements. Carpal morphology of tree shrews is more diverse than previously reported. *Ptilocercus* shows a highly derived carpal morphology that may be related to its relatively greater arboreality. *Dendrogale* exhibits what is most likely the ancestral tupaiid carpal morphology. Carpal morphologies of *Tupaia*, *Urogale*, and *Anathana* are identical to each other. Carpal morphology differs between megachiropterans and microchiropterans. These differences may be related to different aerodynamic constraints between the suborders. The carpal morphology of microchiropterans is diverse and may reflect different adaptive regimes between microchiropteran families. Carpal morphology of the colugos shows both megachiropteran and microchiropteran characters. The function of these characters in colugos and bats (stabilization of the carpus in dorsiflexion) is proposed to be similar, although the locomotor roles may be quite different between these taxa. *J. Morphol.* 235:135–155, 1998. © 1998 Wiley-Liss, Inc.

KEY WORDS: carpal reduction, scapholunate, hands, dermoptera, chiroptera, scandentia, *ptilocercus*, *peromyscus*, sciuridae.

Reduction in the number of proximal and intermediate carpal elements involving the scaphoid, lunate, and centrale is a common condition among mammals. It occurs in marsupials, carnivores, rodents, insectivores, bats, tree shrews, and dermoptera, to name a few. In the case of the scaphoid and lunate, it is usually reported that the radial aspect of the lunate fuses to the ulnar aspect of the scaphoid. If the centrale is absent, it is usually stated to be either lost or fused to the distal aspect of the scaphoid (Leboucq, 1899; Steiner, '22, '42, '65; Schmidt-Ehrenberg, '42; Holmgren '52; Altner, '71). We studied the patterns of carpal element reduction in archontans because the composition and arrangement of elements making up the large proximal carpal element have been proposed as a synapomorphy of a chiropteran-dermopteran clade (the Volitantia Illiger, 1811, see Novacek, '88; Szalay and Lucas, '93, '96; Simmons, '95), or a dermop-

teran-paromomyid-primate clade (the Primatomorpha Beard, 1989, see also Beard, '93). Similarly, fusion of the scaphoid and lunate has been claimed as both a tupaiine and scandentian character. However, there has been some confusion over which scandentians possess which character state (Flower, 1870; Lyon, '13; Clark, '26; Davis, '38; Grassé, '55; Haines, '55; Steiner, '65; Verma, '65; Novacek, '80; Beard, '93; Simmons, '95). Adult morphologies often have been erroneously (Verma, '65) or confusingly (Davis, '38) described, and there is no detailed description of carpal morphology in *Urogale*.

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The Primatomorpha hypothesis proposes that the lunate articulates with the distal aspect of the scaphoid in the paromomyiformes (usually considered to be "archaic" primates) and that it has become fused to the distal scaphoid in colugos (Dermoptera, Cynocephalidae). Under this hypothesis, the scaphoid has expanded ulnarly to articulate with the cuneiform, and the lunate has been displaced to articulate with the distal aspect of the scaphoid. The elements remain unfused in the paromomyiformes but are hypothesized to have fused into a single large element, the scaphocentralolunate, in colugos. Fusion of the scaphoid, centrale, and lunate also has been proposed as a synapomorphy of the Volitantia (Novacek and Wyss, '86; Szalay and Lucas, '93, '96; Simmons, '94, '95). Although the pattern of fusion is not specified in this hypothesis, it is testable. In tree shrews, fusion of the scaphoid and lunate also has been used as a taxonomic character (Novacek, '80; Beard, '93; Simmons, '94).

A central question, then, is how does one determine the homology of carpal elements? If an element is absent, it may have been either lost or fused and an examination of the adult condition is insufficient to distinguish between these two cases. Different ontogenetic pathways can produce similar adult morphologies and the fusion of carpal elements should not be an assumption but an hypothesis to be tested against developmental series.

The literature on carpal development in archontans is extensive (Leboucq, 1899; Steiner, '22, '65; Schmidt-Ehrenberg, '42; Holmgren, '52; Altner, '71), but lacks taxonomic breadth. The carpal elements in ontogenetic series of tree shrews, colugos, and bats were studied in order to determine patterns and processes of carpal fusion in archontan mammals. Ontogenetic series of primates were not examined because primates generally retain unfused carpal elements. Reduction of the scaphoid and lunate to a single element also occurs independently in murids and sciurids, as evidenced by the presence of a free lunate in *Douglassia jeffer-soni* (Emry and Thorington, '82). To see if the process of reduction between these taxa was the same as in archontans, a growth series of *Peromyscus leucopus* and two sciurid specimens, were examined.

MATERIALS AND METHODS

The taxa investigated in this study include members of the Chiroptera, Dermoptera, Rodentia, and Scandentia. Strepsirrhine primates and *Tarsius* were also examined to check specific characters involving the articular relationships of the centrale. The appendix provides a detailed list of specimen numbers, ages, and preparations. Specimens were obtained from the National Museum of Natural History, Smithsonian Institution (USNM), the Field Museum of Natural History (FMNH), and the Department of Zoological Research, National Zoological Park, Smithsonian Institution (DZR-NZP).

Four types of preparations were used for this study: osteological material available at USNM and from FMNH, dissections of fluid-preserved and frozen specimens at USNM and DZR-NZP, cleared and stained specimens provided by USNM and DZR-NZP, and X-rays of USNM and FMNH skins. The tree shrews from DZR-NZP were stained for both cartilage and bone (Dingerkus and Uhler, '77), whereas the *Peromyscus leucopus* were cleared and stained for bone only (Green, '52) at the New England Regional Primate Research Center. Other specimens in the USNM collections had been cleared and stained for bone and cartilage. Cartilaginous templates were easily identifiable in all specimens. The sciurid specimens were not cleared and stained, but were examined grossly. The cartilages were clearly defined. Scanning electron microscope images of selected osteological specimens were enhanced to provide black backgrounds, standard 1 mm scale bars, labels of carpal elements, and to remove extraneous details. In no case was relevant morphology altered, obscured, or deleted.

Many different names have been applied to the different carpal bones. The terminology used in this study follows Romer ('54) as shown in Figure 1. In the primitive mammalian carpus (Fig. 1) the proximal carpal row consists of four elements, the middle row of one element, and the distal row of four elements (see Romer, '54; Lewis, '89). We determined the homology of carpal cartilages and bones by the morphological similarity of these structures and the commonality of their articular relationships. Where the number of carpal elements was reduced, either

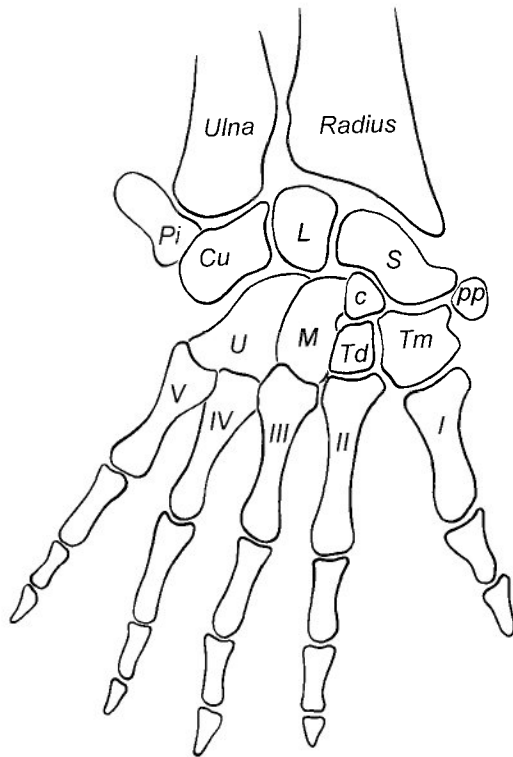


Fig. 1. Hypothesized carpal morphology of an ancestral mammal. Redrawn from Lewis ('89). C, centrale; Cu, cuneiform; L, lunate; M, magnum; Pi, pisiform; pp, prepollex; S, scaphoid; Td, trapezoid; Tm, trapezium; U, unciform.

fusion or loss of primitive elements has occurred. Discrimination of the processes involved in carpal reduction is difficult because reduction of carpal elements can result from nonhomologous processes that produce similar adult conditions (Lewis, '89). These processes include the ossification between discrete cartilaginous templates, the coalescence of cartilaginous templates prior to ossification, or the failure of separate cartilaginous templates to develop. We recognized three different ways in which carpal elements fuse (columns 2-4 of Table 1).

With these factors in mind, the following protocols were used to homologize carpal elements and processes of reduction. A distinct cartilage in a young animal that showed the same position and articular relationships as a primitive carpal (Fig. 1) was considered homologous with that carpal. If all the primitive carpals were present in infant animals, but fewer carpals were seen in adults, then fusion of elements was considered to have occurred during ossification. If there were fewer cartilaginous templates in postnatal animals than in the primitive condition, three possibilities exist: (1) one cartilage may have never developed; (2) it may have developed and then been lost; or (3) it may have coalesced with another cartilage prenatally. If such a cartilage showed multiple centers of ossification, we would presume that it was derived from more than

TABLE 1. Patterns of carpal reduction in some mammals

Taxon ¹	Free scaphoid and lunate in adults	Postnatal ossification between scaphoid and lunate cartilages	Prenatal coalescence of scaphoid and lunate cartilages ²	Two centers of ossification within scapholunate cartilage	Free centrale in adults	Postnatal ossification between scaphoid or lunate and centrale
Megachiroptera	No ³	Yes	No	NA	No	Yes
Microchiroptera	No	Yes	No	NA	No	Yes
Dermoptera	No	No	Yes	No	No	Yes
Prosimians ⁴	Yes	NA	NA	NA	Yes	NA
Rodentia						
<i>Cavia</i>	No	No	Yes	?	Yes	NA
<i>Peromyscus</i>	No	No	?	No	Yes	NA
<i>Callosciurus</i>	No	No	?	?	Yes	NA
<i>Sciurus</i>	No	No	?	?	Yes	NA
Scandentia						
<i>Ptilocercus</i>	Yes	NA	NA	NA	Yes	NA
<i>Dendrogale</i>	Yes	NA	NA	NA	Yes	NA
<i>Tupaia</i>	No	No	Yes	No	Yes	NA
<i>Urogale</i>	No	?	?	?	Yes	NA
<i>Anathana</i>	No	?	?	?	Yes	NA

¹See Appendix for a detailed list of the taxa within each higher taxonomic category used here.

²Prenatal coalescence of the centrale with the scaphoid does not occur in any of the taxa studied here.

³Yes = observed condition, No = condition not present, NA = not applicable, ? = unknown.

⁴Prosimians = strepsirhines + tarsiers, a paraphyletic group.

one cartilage. This latter pattern was not observed in this study. However, if a cartilage of uncertain composition showed a single center of ossification, then it was deduced that one center of ossification has been lost. To distinguish between nondevelopment, loss, and coalescence of prenatal cartilages requires a series of specimens not available for all of the taxa studied here (Leboucq, 1899; Holmgren, '52; Rajtova, '67; Altner, '71).

RESULTS

Ptilocercus: Pen-tailed tree shrew

Ptilocercus (Fig. 2a) possesses four proximal carpal elements: the scaphoid, lunate, cuneiform, and pisiform. They also have a large centrale. All four distal carpal elements are present: trapezium, trapezoid, magnum, and unciform (see Clark, '26; Haines, '55).

In the proximal row, the scaphoid in *Ptilocercus* articulates with the radius proximally, the lunate ulnarly, and the centrale and trapezium distally. The lunate articulates proximally with the radius, ulnarly with the cuneiform, radially with the scaphoid, disto-radially with the centrale, distally with the unciform, and palmarly with the pisiform. The cuneiform articulates proximally with the ulna and pisiform, distally with the unciform, and radially with the lunate. It also may contact the centrale during certain hand positions, but this is unclear. The articulations among cuneiform, pisiform, and the ulnar styloid process are unique. The proximal articular surface of

the cuneiform is concave radio-ulnarly, and there is a dorsal process of the pisiform that forms the ulnar border of the joint. This results in the ulnar styloid process being cupped radio-ulnarly between the cuneiform and pisiform, a condition not seen in the tupaiines.

In the distal carpal row, the articular relationships of magnum, unciform, and centrale further make the carpus of *Ptilocercus* unique. Proximo-radially, the magnum articulates with the centrale, but most of its proximal articular contact is with the unciform, which extends radially to articulate with the ulnar aspect of centrale. This radial extension of the unciform isolates the magnum from the proximal carpal row. Some degree of magnum-lunate contact may be effected in certain hand positions. No developmental series of *Ptilocercus* was available.

Dendrogale: Smooth-tailed tree shrews

Dendrogale (Fig. 2b) has four proximal carpal elements: scaphoid, lunate, cuneiform, and pisiform. They also have a large centrale. All four distal carpal elements are present.

In the proximal row, the scaphoid articulates with the radius proximally, the lunate ulnarly, and a large centrale and the trapezium distally. The lunate articulates proximally with the radius, ulnarly with the cuneiform, radially with the scaphoid, and distally with the magnum. Certain hand positions may elicit lunate-centrale or lunate-unciform contact, but not to any great degree. Cuneiform articulates proximally with the

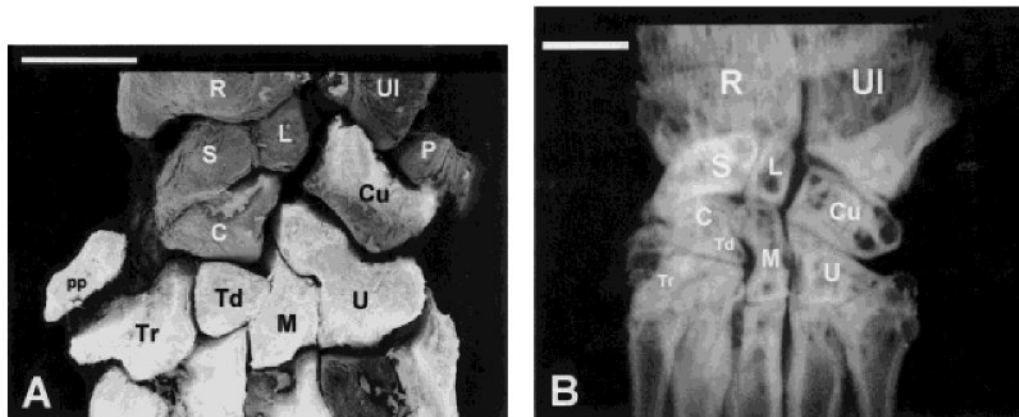


Fig. 2. **A:** Scanning electron micrograph of the dorsal left carpus of USNM 121885 adult *Ptilocercus lowii*. **B:** X-ray of the right carpus of USNM 256752 adult *Dendrogale murina*, image reversed. Scale bars = 1 mm. C,

centrale; Cu, cuneiform; L, lunate; M, magnum; Pi, pisiform; pp, prepollex; R, radius; S, scaphoid; Td, trapezoid; Tr, trapezium; U, unciform; UI, ulna.

ulna and pisiform, disto-radially with the magnum, distally with the unciform, and radially with the lunate. The position of the pisiform is unclear from our X-rays, but there is no indication that it is similar to *Ptilocercus*.

In the distal carpal row, the magnum is not proximo-distally truncated by the unciform as it is in *Ptilocercus*. In *Dendrogale*, the magnum shows the characteristic waisted shape of tupaiane magna, and the unciform does not contact the centrale. With the exception of the unfused lunate, the morphology and articular relationships of the carpus are identical with those of *Tupaia* (Fig. 3), *Urogale* (Fig. 4a), and *Anathana* (Fig. 4b). The specialized articular pattern between magnum, unciform, and centrale seen in *Ptilocercus* is not present in *Dendrogale*.

Tupaia: Tree shrews

Tupaia (Fig. 3) has only three proximal carpal elements: scapholunate, cuneiform, and pisiform. They also have a large cen-

trale. All four distal carpal elements are present.

In the proximal row, the scapholunate articulates with the radius proximally, the cuneiform ulnarly, and the magnum, centrale, and trapezium distally. Cuneiform articulates proximally with the ulna, distally with the unciform, radially with the scapholunate, and palmarly with the pisiform. In *Tupaia*, the pisiform articulates with the palmar aspect of the cuneiform and the ulnar styloid process, and slightly with the scapholunate. It lacks the dorsal process seen in *Ptilocercus*.

In the distal carpal row, the magnum articulates with the centrale on its proximo-radial surface and proximally with the scapholunate; the unciform does not articulate with the centrale. The magnum shows the characteristic waisted shape of tupaianes.

Figure 3a,b illustrates the process of ossification in the carpus of postnatal *Tupaia*. Distinct cartilages are present for all of the carpal elements except the lunate. The scapholunate cartilage ossifies from one cen-

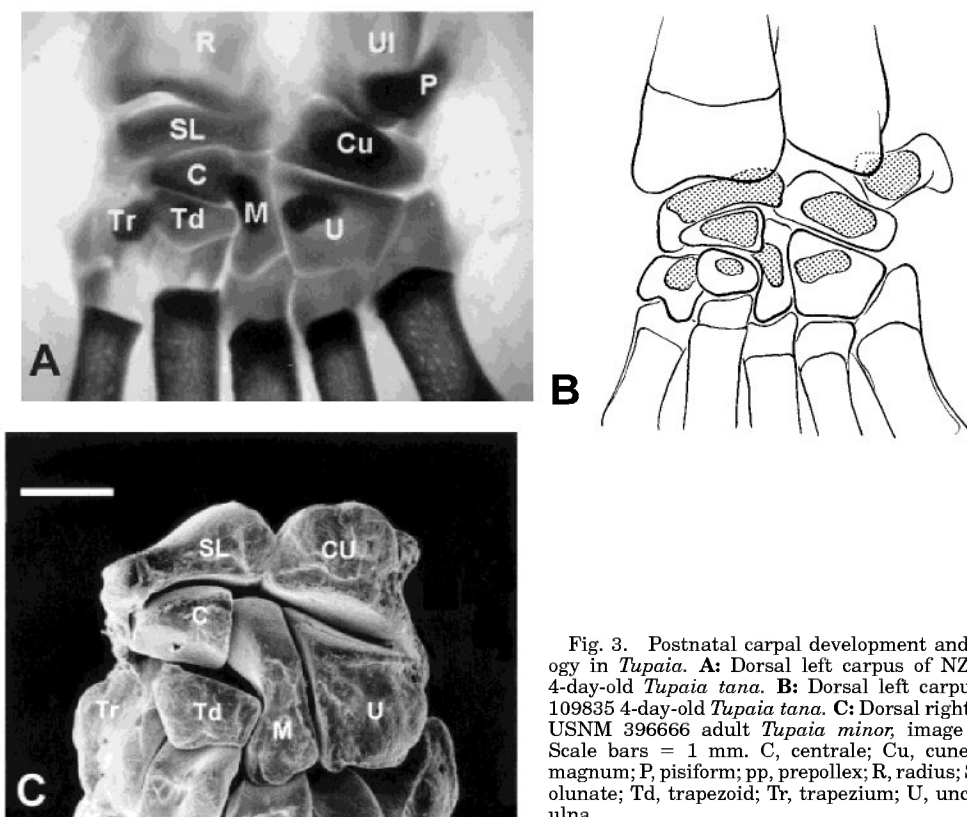


Fig. 3. Postnatal carpal development and morphology in *Tupaia*. **A**: Dorsal left carpus of NZP 109835 4-day-old *Tupaia tana*. **B**: Dorsal left carpus of NZP 109835 4-day-old *Tupaia tana*. **C**: Dorsal right carpus of USNM 396666 adult *Tupaia minor*, image reversed. Scale bars = 1 mm. C, centrale; Cu, cuneiform; M, magnum; P, pisiform; pp, prepollex; R, radius; SL, scapholunate; Td, trapezoid; Tr, trapezium; U, ulna.

ter that appears radially and proceeds ulnarly.

Urogale: Philippine tree shrew

The carpus of *Urogale* (Fig. 4a) is indistinguishable from that of *Tupaia*. It has three proximal carpal elements: scapholunate, cuneiform, and pisiform, and a large centrale. All four distal carpal elements are present. No developmental series of *Urogale* was available.

Anathana: Indian tree shrew

The carpus of *Anathana* (Fig. 4b) is also indistinguishable from that of *Tupaia*. It has three proximal carpal elements: scapholunate, cuneiform, and pisiform, and a large centrale. All four distal carpal elements are present. No developmental series of *Anathana* was available.

Dermoptera: Colugos or "flying lemurs"

The colugos (Fig. 5) also have three proximal carpal elements: scaphocentralolunate, cuneiform, and pisiform. All four distal carpal elements are present.

In the proximal row, the large scaphocentralolunate articulates with the radius and ulna proximally, the cuneiform ulnarly, and the trapezium, trapezoid, magnum, and unciform distally. The scapholunate portion of the scaphocentralolunate articulates proximally with the radius, ulnarly with the cuneiform, and palmarly with the pisiform. The centrale portion of this element articulates with all of the distal carpals and the cuneiform. The articular surface of the centrale

portion that contacts the trapezoid is dorsally oriented. The proximal surface of the cuneiform is concave dorso-ventrally for articulation with the remnant of the ulnar styloid process that is fused to the radius. The pisiform articulates with the palmar portion of the cuneiform and the ulnar styloid process, not with the ulnar side of the process. The ulnar styloid process articulates with the ulnar aspect of the cuneiform, projecting past its proximal border.

In the distal row, the trapezium is large and quadrangular, and possesses a small proximal process that overrides the dorsal surface of the scaphoid portion of the scaphocentralolunate. The scaphocentralolunate-trapezoid articular surface of the scaphocentralolunate is also exposed dorsally. This allows the trapezoid to dorsally override the centrale portion of the scaphocentralolunate.

We found no evidence of a separate lunate cartilage in either fetal or postnatal colugos (see Appendix, Fig. 5a,b,d,e). Our series of specimens (USNM 144374, to USNM 197203, to USNM 317118 and 578084) shows that ossification is complete within the centrale and scapholunate cartilages while fusion between them is incomplete. Fusion between them progresses ulnar to radial.

Chiroptera: Bats

The bats (Figs. 6, 7) also have three elements in the proximal carpal row: large scaphocentralolunate, cuneiform, and pisiform. All four distal carpal elements are present. The position of the pisiform is

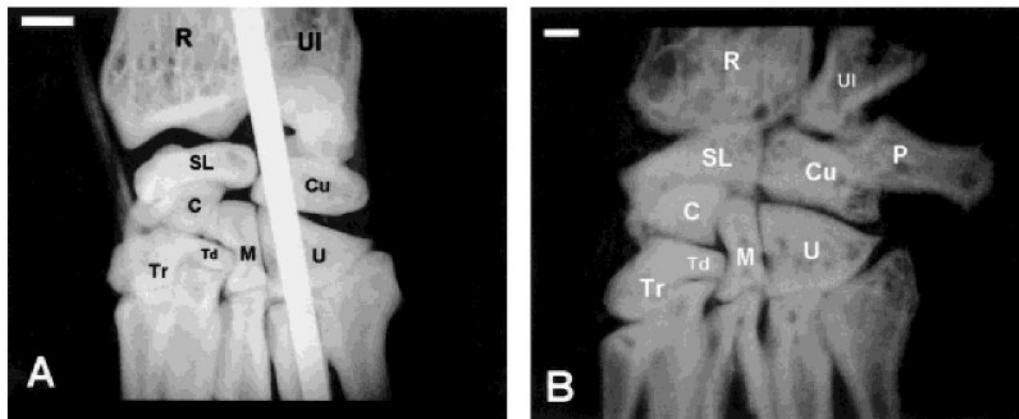


Fig. 4. **A:** X-ray of the left carpus of USNM 292293 *Urogale everetti*. **B:** X-ray of the right carpus of FMNH 91265 *Anathana ellioti*, image reversed. Scale bars = 1 mm. Abbreviations as in Figure 3.

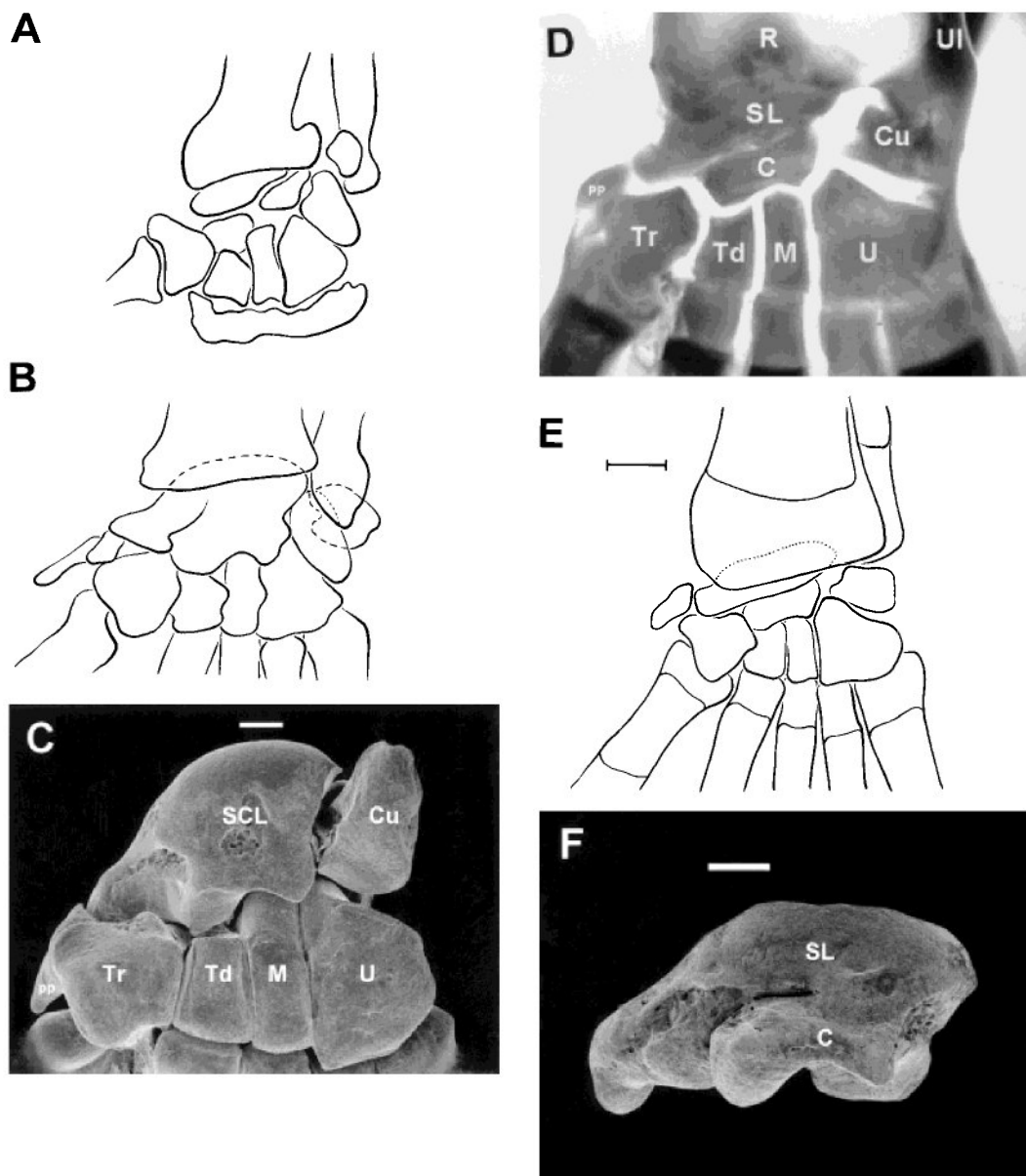


Fig. 5. Carpal development and morphology in colugos. **A:** Dorsal right carpus (reversed) of fetal *Cynocephalus volans*, redrawn from Holmgren ('52). **B:** Dorsal left carpus of fetal *Cynocephalus volans*, redrawn from Holmgren ('52). **C:** Dorsal right carpus (reversed) of USNM 578084 adult *Cynocephalus volans*. **D:** Dorsal left carpus of USNM 144374 fetal *Galeopterus variegatus*.

E: Dorsal left carpus of USNM 144374 fetal *Galeopterus variegatus*. **F:** Dorsal left scaphocentralolunate of USNM 317118 adult *Galeopterus variegatus*. Scale bars = 1 mm. Cu, cuneiform; M, magnum; Pi, pisiform; pp, prepollex; R, radius; SCL, scaphocentralolunate; Td, trapezoid; Tr, trapezium; U, unciform; Ul, ulna.

greatly modified and articulates with the palmar aspect of the magnum (Norberg, '70, '72; Vaughan and Bateman, '70; Altenbach, '79). There are differences between the sub-

orders in the articular relationships of the carpals.

In the Megachiroptera (Fig. 6), the scaphocentralolunate is large and articulates with

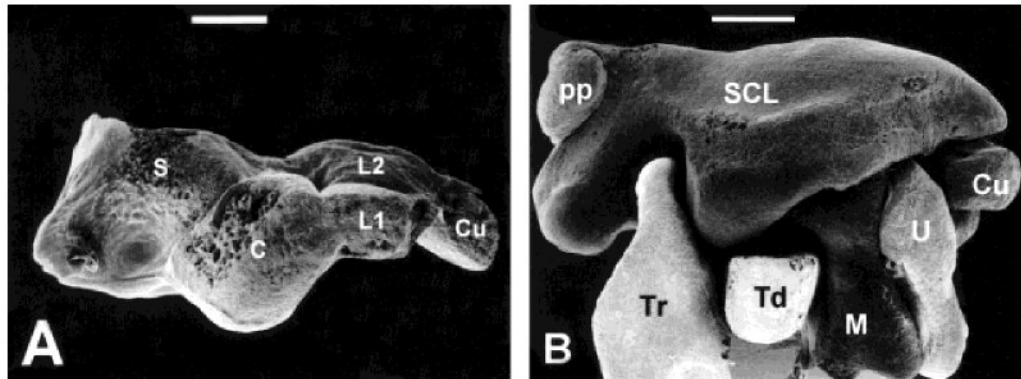


Fig. 6. Carpal development and morphology in megachiropterans. **A:** Dorsal right scaphocentralolunate (reversed) of USNM 448865 juvenile *Hypsignathus monstrosus*. **B:** Dorsal right carpus (reversed) of USNM 543166

adult *Hypsignathus monstrosus*. Scale bars = 1 mm. L1, dorsal component of lunate (centralia 3 of Holmgren, '52); L2, palmar component of lunate (lunate of Holmgren, '52). Other abbreviations as in Figure 5.

the radius proximally. It is expanded ulnarly and interposes between the radioulnar articular surface and the reduced cuneiform. The cuneiform articulates with the palmar radioulnar articular surface when the carpus is flexed. The styloid process of the ulna extends distal to the scaphocentralolunate and articulates with the ulnar aspect of the cuneiform as it does in colugos. Distally, the scaphoid tubercle articulates with the base of metacarpal I. Radial to the line of fusion between the scaphoid and centrale, there is a deep pit on the scaphoid for articulation with a process of the trapezium. The base of metacarpal II is wedged between the trapezium and magnum radio-ulnarly, and articulates with the trapezoid at its base. This pattern is similar to that seen in the colugos, tree shrews, squirrels, and mice examined.

In microchiropterans (Fig. 7), the articular relationships of the carpal elements are generally similar to the megachiropterans, but the articulation of the scaphoid tubercle with the base of metacarpal I is reduced. The scaphoid tubercle forms part of a cup within which the base of metacarpal I fits when it is abducted. The cuneiform is relatively larger in most Microchiroptera than in the Megachiroptera and may extend proximal to the ulnar styloid process. This proximal extension provides part of a grooved passage for the tendon of *M. extensor carpi ulnaris*. The ulnar styloid process does not extend disto-ulnar to the cuneiform. In all microchiropterans, the base of metacarpal II is wedged between the trapezoid and magnum.

The trapezium dorsally overrides the scaphoid when the wrist is dorsiflexed, but there is no trapezial-scaphoid locking mechanism in most microchiropterans. In the Emballonuridae, Nycteridae, Noctilionidae, Mormoopidae, Phyllostomidae, Vespertilionidae, and Natalidae, a proximal process of the trapezoid, rather than the trapezium, articulates with a shallow groove on the dorsal surface of the centrale portion of the scaphocentralolunate.

Artibeus jamaicensis (Fig. 7b) is a good example of this most common microchiropteran condition. There is a high degree of variability in the development and projection of the radial ridge of the centrale groove into the distal carpal row between these families. However, in all of these families the centrale ridge is wedged between the trapezium and the trapezoid.

In the Furipteridae (Fig. 7c), there is a reduced trapezoidal process and a trapezial

Fig. 7. Carpal development and morphology in microchiropterans. **A:** Dorsal left carpus of USNM 103405 juvenile *Phyllonycteris poeyi*. **B:** Dorsal left carpus of USNM 362098 adult *Artibeus jamaicensis*. **C:** Dorsal left carpus of USNM 549510 adult *Furipterus horrens*. **D:** Dorsal right carpus (reversed) of USNM 519701 adult *Thyroptera tricolor*. **E:** Dorsal right carpus (reversed) of USNM 577065 adult *Myzopoda aurita*. **F:** Dorsal right carpus (reversed) of USNM 437362 adult *Otomops martiensseni*. **G:** Dorsal left carpus of USNM 573474 adult *Megaderma spasma*. **H:** Dorsal right carpus (reversed) of USNM 548605 adult *Rhinolophus inops*. Scale bars = 1 mm. Abbreviations as in Figure 5.

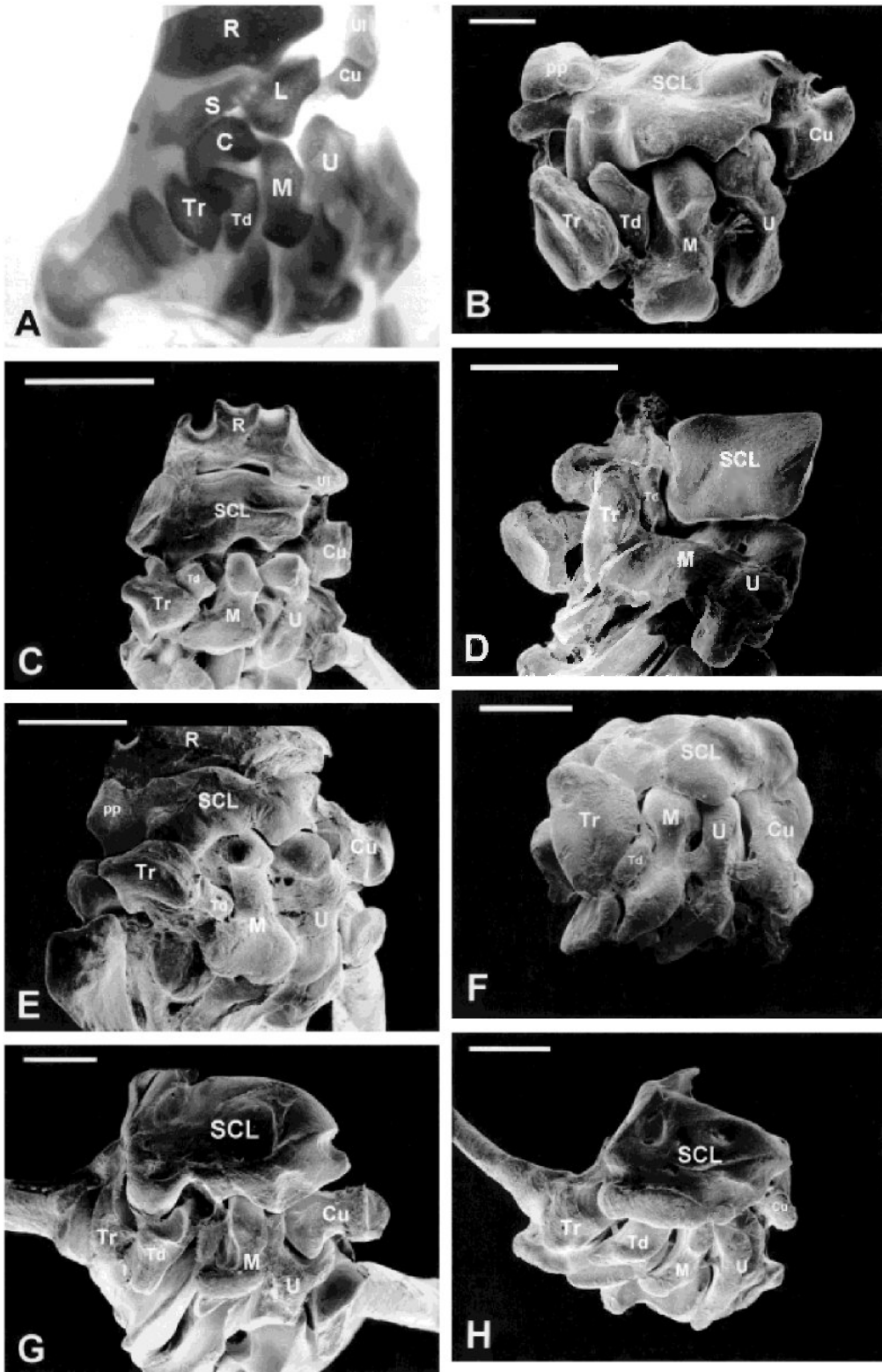


Figure 7

process that articulates with a scaphoid groove. The trapezium overrides the trapezoid to articulate with the magnum dorsally. In the Thyropteridae (Fig. 7d), there is an ulnar expansion of the trapezium over the radial ridge of the centrale groove. Therefore, the trapezium articulates in the centrale groove with the trapezoid. Here also, the trapezium overrides the trapezoid to the extent that it now articulates with the magnum. In both of these families, the trapezoid maintains contact with the centrale groove.

In the Myzopodidae and Molossidae (Fig. 7e,f), the trapezium has expanded ulnarly to articulate with the centrale groove and completely exclude the trapezoid from contact with the proximal carpal row dorsally. In these taxa, there is trapezium-magnum contact proximally, but not dorsally. This arrangement results in a trapezium-centrale locking mechanism with little or no contribution from the trapezoid.

In the Megadermatidae (Fig. 7g), there is no centrale groove, but there is a well-developed centrale tubercle. This tubercle projects distally and is wedged between the trapezium and the trapezoid. The Rhinolophidae (Fig. 7h) and Rhinopomatidae show a similar condition, but here the centrale tubercle is smaller than in megadermatids and does not project between the trapezium and the trapezoid. Instead, the tubercle fits against the deeply concave surface of the trapezium. Both the rhinolophids and rhinopomatids also lack a centrale groove.

In all the bats examined, the scaphocentralunate forms from the fusion of the scaphoid, lunate, and centrale postnatally after the onset of ossification in these cartilages. However, the patterns differ between megachiropterans and microchiropterans. In microchiropterans the scaphoid and lunate fuse medio-laterally and the centrale fuses to the distal aspect of the scaphoid radial to the scapho-lunate border (Fig. 7a). In megachiropterans (Fig. 6a), the centrale is interposed between the scaphoid and lunate and articulates with the radius proximally. In *Hypsignathus monstrosus* and *Pteropus personatus*, the centrale separates the scaphoid from the lunate dorsally. In a juvenile specimen of *Hypsignathus*, the lunate is composed of two distinct elements (Fig. 6a), the more dorsal of which may be the remnant of the 3rd centralia (Holmgren, '52).

Rodentia: Rodents

The carpus of *Peromyscus leucopus* (Fig. 8) has three elements in the proximal carpal row: scapholunate, cuneiform, and pisiform. The centrale is present and unfused. All four distal carpal elements are present. The scapholunate articulates proximally with the radius and ulnarly with the cuneiform. Distally, it articulates with the base of metacarpal I, with the trapezium, trapezoid, centrale, magnum, and unciform, and palmarly with the pisiform. The pisiform has a slight dorsal extension, but this is not nearly as extensive as in *Ptilocercus*, and it does not cup the ulnar styloid process. The base of metacarpal V may articulate with the cuneiform in extreme ulnar deviation or digital abduction.

Peromyscus has a single cartilaginous template for the large proximal carpal element postnatally (Fig. 8a,b) and ossification is complete by about 10 days after birth. Ossification of the single cartilage begins in the radial portion of the cartilage and proceeds ulnarly. There was no evidence of a separate cartilage or center of ossification for the lunate.

Squirrels (Fig. 9) also have three proximal carpal elements: scapholunate, cuneiform, and pisiform, and a free centrale. All four distal carpal elements are present. The articular relationships of the proximal carpal elements are generally similar to *Peromyscus leucopus*. Wrist dissections of one young *Callosciurus finlaysoni*, and one young *Sciurus carolinensis* showed a large cartilage element in the proximal carpal row that had the same shape and articular relationships as the adult element. There is no evidence for a separate lunate cartilage at either about 7 or about 21 days of age.

DISCUSSION

The literature on tupaiine anatomy (Flower, 1885; Lyon, '13; Davis, '38; Holmgren, '52; Haines, '55; Verma, '65; Altner, '71) generally agrees that the Tupaiinae have a fused scaphoid and lunate. Steiner ('65) and Altner ('71) illustrate a separate lunate cartilage in fetal *Tupaia glis*, which coalesces into a single large proximal carpal prenatally. Holmgren ('52) agrees with this interpretation but shows the proximal half of the magnum to be composed of centrale 3. This interpretation agrees with the illustrations in Steiner ('65) and Altner ('71), although these authors do not name this ele-

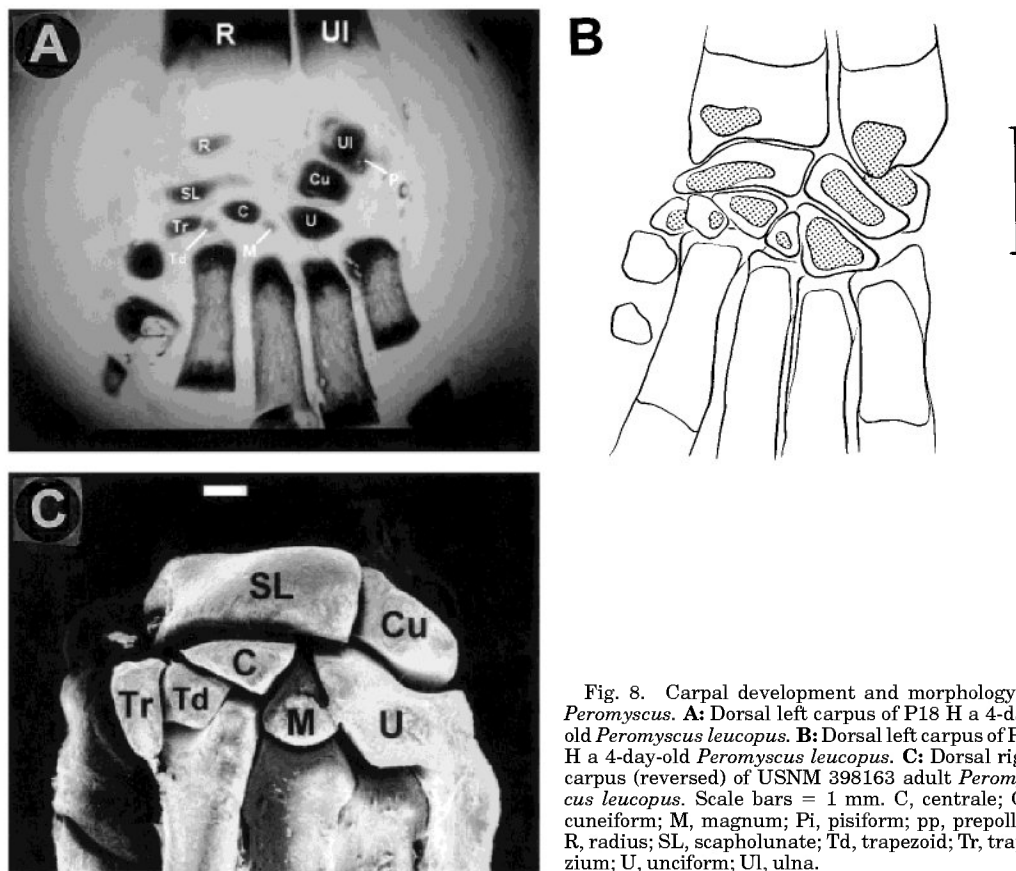


Fig. 8. Carpal development and morphology in *Peromyscus*. **A:** Dorsal left carpus of P18 H a 4-day-old *Peromyscus leucopus*. **B:** Dorsal left carpus of P18 H a 4-day-old *Peromyscus leucopus*. **C:** Dorsal right carpus (reversed) of USNM 398163 adult *Peromyscus leucopus*. Scale bars = 1 mm. C, centrale; Cu, cuneiform; M, magnum; Pi, pisiform; pp, prepollex; R, radius; SL, scapholunate; Td, trapezoid; Tr, trapezium; U, unciform; UI, ulna.

ment. In this study, no evidence of a center of ossification for the lunate in *Tupaia* was found, nor were multiple centers of ossification observed in the magnum (Table 1). This suggests that the loss of an ossification center is not evidence for the loss of an element.

Verma ('65) reports that in *Anathana wroughtoni* not only are the scaphoid and lunate fused, but so are the trapezium and trapezoid, the unciform and magnum, and that the centrale has been lost. This bizarre combination of fusions was not observed in the specimen studied here, which showed the same carpal morphology as *Tupaia* and *Urogale*.

In spite of the general agreement on tupaiine carpal morphology, Novacek ('80) claims the Tupaiidae retain an unfused lunate (pp. 78–79, fig. 23 and table 5, character #11). Simmons ('95) correctly codes this character as polymorphic for the family, but does not discuss its distribution within tree shrews. There is no separate lunate in *Tupaia*, *Uro-*

gale, or *Anathana*, but there is in *Ptilocercus* and *Dendrogale*. Therefore, scapholunate fusion is neither a tupaiid nor a tupaiine character. Davis ('38, p. 386) does note a free lunate for *Dendrogale*, but contradicts himself when he says "The scaphoid and lunar are separate, instead of being fused into a single bone as they are in *Tupaia*," but later that "In keeping with the fused condition of the scaphoid and lunar in *Dendrogale* the magnum articulates with the lunar, rather than with the cuneiform." He also claims that "The carpus is strikingly similar to that of *Ptilocercus*." No especially striking similarities were found in this study between *Dendrogale* and *Ptilocercus*. With the exception of the free lunate, the carpus of *Dendrogale* is very similar to that of *Tupaia*, *Urogale*, and *Anathana*.

Le Gros Clark ('26, p. 1207) notes none of the characters that we found in *Ptilocercus*. He says of the lunate that "On its distal aspect it has a narrow facet for articulation

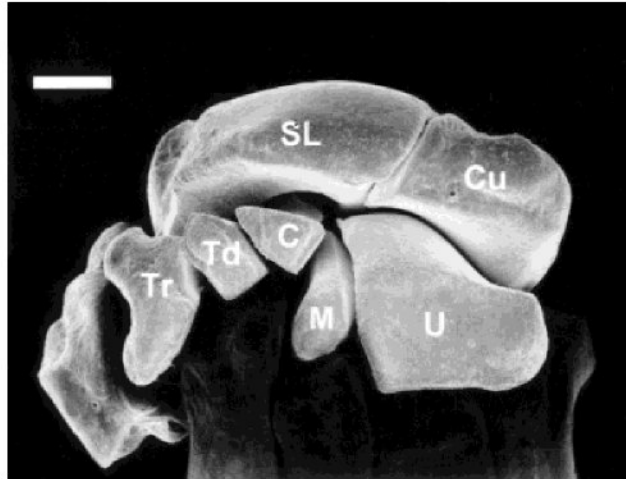


Fig. 9. Dorsal right carpus (reversed) of USNM 396202 adult *Sciurus carolinensis*. Scale bar = 1 mm. C, centrale; Cu, cuneiform; M, magnum; Pi, pisiform; pp, prepollex; R, radius; SL, scapholunate; Td, trapezoid; Tr, trapezium; U, unciform; Ul, ulna.

with the os magnum.”, and that the magnum “. . . has an attenuated head, compressed laterally, which projects proximally to reach and articulate with the lunate.” However, his figure 15 (p. 1207) shows extensive lunate-magnum contact, and no apparent attenuation of the magnum. He makes no special note of any unusual characteristics of the unciform, or of the cuneiform-pisiform-ulna complex. In fact, the condition that Le Gros Clark figures for *Ptilocercus* is what was observed in this study for *Dendrogale*.

The articular patterns between the cuneiform, pisiform, and ulna in *Ptilocercus* are derived, as are the centrale, magnum, and unciform articulations. In *Ptilocercus*, the centrale has expanded ulnarly, articulating with the lunate proximally and almost contacting the cuneiform. Also, the unciform has expanded radially to contact the ulnar aspect of the centrale. The combination of these conditions prevents the magnum from contacting the proximal carpal row. X-rays show that the separation of magnum and lunate is maintained when the carpus is in both radial and ulnar deviation. However, one of the specimens examined (USNM 481105) showed a slight degree of magnum-lunate contact palmarly in the left manus. There was no magnum-lunate contact in the right manus. A similar condition of reduced magnum contact with the proximal carpal row has been noted in living strepsirrhine

primates (Godinot and Beard, '93). It is also present in *Tarsius bancanus*. In the prosimian primates, the centrale extends ulnarly to contact the unciform, but this contact is restricted entirely to the dorsal aspect of the carpus. Magnum-lunate contact is maintained palmarly through a distal extension of the lunate, although the degree of this contact probably varies with hand position. In *Ptilocercus*, however, it is the unciform that is expanded radially and contact between the magnum and the proximal carpal row is completely lost.

The differences in carpal morphology between *Ptilocercus* and the other tree shrews are difficult to interpret due to the lack of information on tree shrew locomotion. Most of what is available is very general in nature (see Banks, '31; Wharton, '50; Davis, '62; Vandenberg, '63; Lim, '67; but also Bishop, '64; and Jenkins, '74 for more detailed treatments). The results of this study suggest that the differences between *Ptilocercus* and the other tree shrews relate to differences in the degrees of ulnar deviation of the manus, to differences in digital abduction, and to differences in the functional axes of the manus. Louise Emmons (pers. comm.) notes that *Ptilocercus* are more arboreal than other sympatric tree shrews in Borneo (see also Payne et al., '85; Corbet and Hill, '92) and that they spend relatively more time on large vertical supports. She has observed that when descending tree trunks head first,

Ptilocercus maximally abducts and pronates the upper extremities in order to grasp the tree trunk. This position produces ulnar deviation of the manus. The derived nature of the cuneiform-pisiform-ulnar complex in *Ptilocercus* (Fig. 2a) would resist dislocation of the carpus ulnarly in this position because the cuneiform and pisiform are effectively wrapped around the ulnar styloid process. The interposition of the pisiform between the cuneiform and the ulnar styloid process would also provide an effective stop to ulnar deviation of the manus. This arrangement would stabilize the ulna as the antebrachium pivots over the manus. *Ptilocercus* appear to use a supinated and ulnarly deviated manus with highly abducted digits to grasp supports (see figures in Le Gros Clark, '26; Napier and Napier, '67; Nowak, '88). The cuneiform-pisiform complex would therefore resist forces generated during plantar flexion of the manus (see Godinot and Beard, '93; Preuschoft *et al.*, '93; but also Hamrick, '97).

Photographs also show that *Ptilocercus* spread their digits widely when grasping a branch. This position would provide a fixed pivot point for the antebrachium. Photographs of tupaiine tree shrews do not show the same manual positioning as *Ptilocercus* (i.e., a supinated, ulnarly deviated manus, with splayed digits). Although Jenkins ('74) notes that in *Tupaia* the deviation between digits I and V may be as large as 150°, Bishop's ('64, table 2, fig. 12) data indicate much less digital divergence. In *Tupaia*, *Urogale*, and *Anathana*, fusion of the lunate would provide stability and prevent the concentration of stresses at the radiocarpal joint at the articulation between the scaphoid and lunate. This fusion and stability may be related to the different degrees of manual mobility in the more terrestrial *Tupaia*, *Urogale*, and *Anathana* compared to *Ptilocercus*. Likewise, the free lunate in *Dendrogale* may also reflect extensive manual mobility. The radial expansion of the unciform in *Ptilocercus* also suggests a pattern of force transmission in which forces from digits IV and V are directed more radially as compared to the pattern in other tree shrews. However, these hypotheses are difficult to evaluate without detailed kinematic and behavioral data.

The Primatomorpha hypothesis proposes that the positioning of carpal elements in colugos and "archaic" primates is homologous. This hypothesis requires that the large

proximal carpal element of colugos be composed of a fused scaphoid, centrale, and lunate and that the lunate be displaced distal to the scaphoid. In the colugos, the cuneiform has developed distinct proximal and distal articular facets on its radial aspect. Beard ('89, '93) proposes that the proximal facet articulates with the scaphoid portion and the distal one articulates with the lunate portion of the scaphocentralolunate (Fig. 5c). This hypothesis parallels Beard's interpretation of the carpals of the plesiadapid *Nannodectes intermedius* (USNM 442229). This specimen includes a scaphoid and a purported lunate, but not a cuneiform. The scaphoid does appear to have two distinct articular facets on its distal face, but most of this surface is broken. Beard ('89, '93) also reports on *Plesiadapis tricuspidens* (MNHM R 5320) and *Phenacolemur* sp. (USGS 17847) that have cuneiforms but lack scaphoid and lunate bones. The cuneiform bones show two articular facets on their radial sides. Beard proposes that the more proximal facet is for articulation with the ulnarly expanded scaphoid and the more distal is for articulation with a distally displaced lunate. Combining these observations and interpretations, Beard proposes that a distally displaced lunate is present in all the taxa just mentioned. However, it seems just as likely that the proximal facet in these specimens could articulate with either the scaphoid or the lunate while the distal facet could articulate with either the centrale, magnum, or unciform. Radial cuneiform-centrale contact occurs in *Ptilocercus* (Fig. 2a), cuneiform-magnum contact in *Dendrogale* (Fig. 2b), and cuneiform-unciform contact in the Chiroptera (Figs. 6, 7). These findings contradict Beard's proposal ('93, p. 137) that the cuneiform only contacts the lunate radially in tree shrews, bats, and primates. Furthermore, Beard's taxonomic assignment of the fossil specimens has been seriously questioned (Krause, '91). Regardless, the proposition that the colugo has a distally displaced lunate, like that proposed for the fossils, is a testable hypothesis.

Prenatally (Fig. 5d,e) the colugo examined in this study had a large proximal cartilage and a large intermediate cartilage. Postnatally (Fig. 5f), fusion between these cartilages proceeds after the onset of ossification within the cartilages (Table 1). There is no evidence for the existence of a separate lunate cartilage in colugos, but *Tupaia* still

retain a distinct lunate cartilage (Steiner, '65) at a comparable stage of development to the youngest colugo (USNM 144374) studied here. However, Holmgren ('52, fig. 33, our Fig. 5b) shows a lunate cartilage fused to the ulnar side of the scaphoid cartilage in *Cynocephalus volans*. This scapholunate element has already coalesced with a distal element composed of the cartilages of centralia 3 and 4. Unfortunately, Holmgren's figure 32 (our Fig. 5a) upon which this interpretation rests is difficult to interpret. This figure shows the lunate cartilage separated from the scaphoid cartilage along an oblique line. It also shows lunate-radius contact and extensive lunate-cuneiform contact. However, there is no cartilage visible for centralia 3.

In colugos, it appears that the large proximal cartilage is the scapholunate, that the lunate cartilage coalesces with the scaphoid cartilage on its ulnar, not distal, aspect, and that the large intermediate cartilage is the centrale. The developmental series examined here (from USNM 144374, to USNM 197203 and 143326, to USNM 578084) shows that ossification is complete within the centrale and scapholunate cartilages, whereas fusion between these elements is still incomplete. This pattern of carpal fusion is a combination of the processes seen in bats and tree shrews. Interestingly, the cleared and stained colugo specimen (USNM 144374, Fig. 5d,e) shows complete separation between the scapholunate and centrale cartilages even though it is significantly older than the specimen reported by Holmgren ('52). This difference may reflect a high degree of variability in the process of carpal reduction in colugos. Clearing and staining further specimens would resolve these questions, but appropriate specimens are not available at this time. Complete ossification within the scapholunate and centrale cartilages prior to ossification between these elements is documented in several colugo specimens, supporting our hypothesis of the homology of these elements. No evidence to support the homology of carpal elements as proposed by Beard ('89, '93) was found. One adult colugo (USNM 317118) does present a defect in the distal face of the centrale. This specimen, although an adult based on complete fusion of all other cranial and postcranial sutures and epiphyses, shows incomplete fusion proximodistally between the centrale and scaphoid. This defect was not interpreted as a suture between the centrale and

a distally displaced lunate because there is no separate lunate cartilage in the fetal colugo (USNM 144374), the juvenile colugos (USNM 197203 and 143326) do not show a similar defect, and this defect is not present in the right scaphocentrale of USNM 317118. Consequently, this defect was interpreted as a postmortem crack in the centrale portion of the scaphocentralolunate of this specimen.

Fusion of the scaphoid, centrale, and lunate also has been used as a taxonomic character of the Chiroptera (Flower, 1885; Grassé, '55; Jepsen, '66, '70; Walton and Walton, '70) and the Volitantia (Novacek, '80; Szalay and Lucas, '93, '96; Simmons, '94, '95). Although the consensus now seems to be that the scaphoid, lunate, and centrale are fused in bats (Novacek, '80; Beard, '89; Szalay and Lucas, '93, '96; Simmons, '94, '95), the *pattern* of fusion in these hypotheses has not been specified. Most studies (Flower, 1885; Allen, 1893; Grassé, '55; Jepsen, '66, '70; Walton and Walton, '70; Szalay and Lucas, '93, '96; Simmons, '94, '95) only mention that the bones fuse and seem to rely on each other for authority. For example, Flower (1885) and Grassé ('55) have been often cited as authorities on the fusion of carpal elements in bats. However, Flower (1870, p. 290) only notes that "In the carpus the scaphoid and lunar are united, and in some genera (as *Pteropus*) the cuneiform is joined with them, so that the proximal bone contains but a single bone. There is no centrale. The pisiform is very small"; and Grassé ('55, p. 1748) cites Leboucq "D'après Leboucq (1899), le centrale au cours de la vie embryonnaire se fusionne rait avec le scaphosemilunaire." It appears that Leboucq (1899), Schmidt-Ehrenberg ('42), and Holmgren ('52) are the primary sources of data on carpal fusion in bats. They show that the scaphoid and lunate fuse mediolaterally, whereas the centrale fuses to the distal aspect of the scaphoid. This study confirms that the patterns described by Leboucq (1899) for *Vespertilio murinus*, by Schmidt-Ehrenberg ('42) for *Molossus*, and by Holmgren ('52) for *Pipistrellus ceylonicus* and *Hipposideros* sp. are also found in five other genera of microchiropterans (see Appendix). Fusion of the scaphoid, centrale, and lunate postnatally after intracartilaginous ossification has commenced is a valid chiropteran character (Table 1). No evidence of postnatal scaphoid-lunate fusion was found in any other taxa

examined, most notably in colugos. However, the colugos do show postnatal fusion between the centrale and scapholunate after intracartilaginous ossification is complete. This process may be homologous between bats and colugos.

The patterns of carpal fusion and articulation between the two chiropteran suborders, however, are difficult to assess and require more detailed study. Different patterns of force transmission related to aerodynamic parameters, wing kinematics, or nonaerial locomotion may be factors in the differences between megachiropterans and microchiropterans. In particular, the development of the trapezium-scaphoid locking mechanism in megachiropterans vs. a trapezoidal-centrale locking mechanism in most microchiropterans may reflect different functional requirements between the two suborders.

In the megachiropterans, the trapezium has a large process. This process dorsally overrides the scaphoid and fits into a deep pit on the dorsal scaphocentralolunate that is radial to the line of scaphoid-centrale fusion (Fig. 6a). This trapezium process is bound to the scaphocentrale pit by a strong ligament. Engagement of the process and pit would stabilize and lock these carpals during dorsiflexion. In megachiropterans the second metacarpal has a large area of articulation with the trapezium, and this would provide support to the leading edge of the wing in flight by resisting dorsiflexion of the second metacarpal. Norberg ('70, '72) discusses the benefits of leading edge rigidity in detail. Megachiropterans also use the pollex in suspensory positional behaviors associated with feeding and roosting. The locking mechanism and its strong ligamentous connection may serve to anchor the trapezium during suspensory positional behaviors where the pollex is dorsiflexed. The locking mechanism would probably not be completely engaged during these behaviors because digits II-V are flexed against the forearm, but the high radial border of the pit would prevent the process from dislocating radially under tension (see Jenkins, '81, figures 5 and 7, that show the separation of carpal elements during suspensory locomotion in spider monkeys and gibbons).

In most microchiropterans, the locking mechanism is located between the trapezoid and the centrale portion of the scaphocentralolunate (Fig. 7). This repositioning of the locking mechanism may reflect differential

mobility of the pollex and thereby the leading edge of the wing between megachiropterans and microchiropterans. The differences in carpal-metacarpal II articulations may also reflect these factors and be functionally linked to the repositioned locking mechanisms. In microchiropterans the second metacarpal is wedged between the trapezoid and magnum and has less contact with the trapezium. This arrangement would still provide a rigid leading edge to the distal wing by stabilizing the second digit. At the same time, it may provide greater mobility of the trapezium and metacarpal I, which would provide greater mobility of the leading edge of the wing. This mobility could enhance control and maneuverability in microchiropterans and be related to the more acrobatic nature of microchiropteran flight (i.e., somersaulting during landing, catching insects "on the wing," etc.).

Most microchiropteran families possess the locking mechanism illustrated by *Phyllonycteris poeyi* and *Artibeus jamaicensis* (Fig. 7a,b). Both the trapezium and trapezoid dorsally override the scaphocentralolunate characterize this mechanism. The trapezium dorsally overrides the trapezoid and articulates with the radial lip of the centrale groove and with the scaphoid portion of the scaphocentralolunate when dorsiflexed. However, it is the proximal process of the trapezoid that articulates with the centrale groove and provides stabilization during dorsiflexion. The height of the radial lip of the groove varies among families. This lip is usually high and sharp, but it can also be low and rounded and more closely resemble the tubercle seen in the megadermatids and rhinolophids.

The Molossidae (Fig. 7f) are characterized by just such low and rounded centrale borders. In this family, the trapezium has expanded ulnarly and reduces trapezoid contact with the centrale portion of the scaphocentralolunate (*Molossus* and *Tadarida*, for example). In other genera (*Otomops*), the trapezoid does not contact the scaphocentralolunate.

The Myzopodidae (Fig. 7e) show a condition similar to that seen in the molossids. Here, the trapezoid still maintains some contact with the dorsal centrale, but the trapezium also has a large degree of articulation with the dorsal aspect of the centrale. In this condition there is no apparent radial lip to the centrale groove. The Furipteridae (Fig.

7c) exhibit still a different condition whereby the carpus shows both trapezium-scaphoid and trapezoid-centrale locking mechanisms.

The Rhinopomatidae and Rhinolophidae (Fig. 7h) also have low rounded centrale tubercles, but are characterized by having no dorsal overlap of the scaphocentralolunate by any of the distal carpals. These families also lack the centrale groove and instead have a transverse (radio-ulnar) ridge across the distal surface of the scaphocentralolunate. These two families do not show any obvious dorsal locking mechanism.

The Megadermatidae (Fig. 7g) exhibit a condition similar to that present in the rhinopomatids and rhinolophids. Megadermatids also show no dorsal overlap of the scaphocentralolunate by the distal carpals, but there is a large centrale tubercle that projects into the distal carpal row dorsally. This distal projection is tightly cupped between the trapezium and trapezoid radio-ulnarly and palmarly. Although very different from any other chiropteran pattern, this pattern would also provide a dorsal locking mechanism.

The conditions seen in the Furipteridae, Thyropteridae, Myzopodidae, and Molossidae may be modifications of the pattern present in *Artibeus jamaicensis* and most other microchiropterans. Because a portion of the centrale is wedged between the trapezium and trapezoid, the megadermatid condition is most similar to the common microchiropteran condition. The condition seen in the rhinolophids and rhinopomatids seems more divergent.

Although the development of these locking mechanism could be related to body size in microchiropterans, there are insufficient data to support the concept that the repositioning of the locking mechanism between megachiropterans and microchiropterans is size related. Small Megachiroptera (i.e., *Micropterus pusillus*) have well-developed trapezium-scaphoid locking mechanisms. The vampire bat *Desmodus rotundus* uses the pollex extensively in locomotion (Altenbach, '79), as do many microchiropterans, but only the Furipteridae (Fig. 7c) show anything resembling a trapezium locking mechanism. Norberg ('70) describes a proximal process of the trapezoid in *Plecotus auritus* as being "... wedged between the lunar, the trapezium, and the magnum . . ." (lunar = scaphocentralolunate). This process may be the

same one described here that articulates with the centrale groove. Norberg notes that this arrangement would act to prevent radio-ulnar movements of the carpus, but does not discuss any restriction of dorsiflexion. She describes no locking mechanism for megachiropterans (Norberg, '72).

Because little is known about the kinematics of the carpus and nonaerial locomotion in bats, functional hypotheses are difficult to evaluate. Altringham ('96, p. 17, citing Pettigrew *et al.*, '89) claims that in microchiropterans the "... thumb and forefinger have minimal independent mobility . . ." while the megachiropterans have an "... opposable thumb and mobile forefinger. . . ." However, Pettigrew *et al.* ('89, p. 492) cite Leen and Novick ('69) as the source of this observation. Leen and Novick ('69, p. 34) simply state that in "All living bats. . . . The thumb bears a claw and is not much modified from the typical mammalian form though it may, as in flying foxes, be rather elongate. The thumb, like that of primates, is also exceptionally mobile." This description does not contradict the morphological evidence of this study that suggests the microchiropterans have a more mobile pollex.

Detailed studies of the kinematics of the chiropteran carpus are needed to fully understand the function and role of the morphological differences between the two suborders. Similar studies on bat and colugo kinematics are also required if we are to evaluate the striking phenetic similarity between the scaphocentralolunates in these taxa.

Although not well developed, the colugos possess a trapezium-scaphoid locking mechanism. Similarly, the trapezoid articulation with the centrale portion of the scaphocentralolunate is oriented dorsally, although there is no hint of a centrale groove. These characters provide a close-packed and stable articulation for the trapezium and trapezoid (and thereby for metacarpals I and II) in dorsiflexion. The significance of this locking complex may relate to the reduction in induced drag imparted by a dorsiflexed wingtip (Thorington *et al.*, '98). In any case, the colugo morphology represents a reasonable analogue for a chiropteran ancestor. The similarity in the function of these characters (i.e., to stabilize the carpus in dorsiflexion) is significant, but whether or not the biological role (*sensu* Bock and von Whalert, '65) of the colugo carpus represents a reasonable ana-

logue for a preflapping bat is difficult to evaluate.

The exact homology of the large proximal carpal element in *Peromyscus* and in *Sciurus* is unclear. A free lunate is found in some rodents (*Bathyergus*, *Ctenodactylus*), and in the fossil tree squirrel *Douglassia* (Emry and Thorington, '82), indicating that reduction of proximal carpal elements is convergent between rodent families. The different morphology of the scapholunate in sciurids and murids also hints at convergence. In the Sciurinae, the large proximal carpal element is universally referred to as a scapholunate (Bryant, '45; Gupta, '66; Emry and Thorington, '82, '84; Thorington, '84), although a separate lunate element has been demonstrated only in *Funambulus* (Holmgren, '52). The scaphoid and lunate cartilages do coalesce prenatally in *Cavia* (Schmidt-Ehrenberg, '42; Holmgren, '52; Rajtova, '67), and *Mus* (Muridae) (Holmgren, '52). Therefore, it appears that the proximal carpal element in *Peromyscus* and *Sciurus* is likely a scapholunate.

CONCLUSIONS

Ptilocercus and *Dendrogale* retain a free lunate, whereas in *Tupaia*, the scaphoid and lunate cartilages coalesce prenatally and ossify from a single center. Adult *Urogale* and *Anathana* have the same morphology as *Tupaia*, and the process of carpal reduction is also assumed to be the same. *Ptilocercus* exhibit a derived carpal morphology, which may be related to a greater reliance on abducted digits and ulnarly deviated hand postures as compared to *Tupaia*, *Urogale*, and *Anathana*. The results of this study suggest that the carpal morphology of *Dendrogale*, not *Ptilocercus*, best represents the ancestral scandentian condition.

The large proximal carpal element in colugos and bats is a scaphocentralolunate. Both colugos and bats show postnatal ossification between discrete carpal elements. However, colugos but not bats show the prenatal coalescence of the scaphoid and lunate cartilages seen in most other mammals. No evidence was found to support Beard's ('93) contention that the lunate fuses to the distal surface of the scaphoid in colugos.

The large proximal carpal element in Chiroptera is a scaphocentralolunate, the discrete elements of which fuse postnatally after the onset of ossification. This character is homologous among the megachiropterans and microchiropterans, but there are unique

articular relationships of the carpals in each suborder. These unique features may reflect different functional-adaptive regimes. Because of the different processes producing scaphocentralolunate fusion in colugos and bats, we cannot unequivocally support the hypothesis of scaphocentralolunate homology among colugos and bats. Nevertheless, similarities in the articular relationships of the carpus and in proposed functional-adaptive scenarios suggest a common evolutionary origin of this character complex in colugos and bats.

Prenatal coalescence of cartilages concomitant with the loss of a center of ossification appears to be the most common pattern of carpal reduction in these mammals. The bats and colugos deviate from this pattern in exhibiting postnatal fusion between elements. This deviation of colugos and bats may be a significant difference with phylogenetic implications. More detailed studies on colugo and chiropteran positional behavior and functional morphology are needed. Detailed descriptions of the kinematics of the carpus during aerial and nonaerial behaviors are needed as well.

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Appendix. Specimens Examined in this Study

Taxon	Number and Ages ¹ of specimens examined	Preparations ²
Chiroptera		
MEGACHIROPTERA		
Pteropodidae		
<i>Acerodon jubatus</i>	3A	SK
<i>Cynopterus brachyotis</i>	3A	SK
<i>Dobsonia crenulata</i>	3A	SK
<i>Eidolon helvum</i>	3A	SK
<i>Eonycteris spelaea</i>	3A	SK
<i>Epomops franqueti</i>	3A	SK
<i>Haplonycteris fisheri</i>	3A	SK
<i>Hypsignathus monstrosus</i>	1J, 8A	SK
<i>Macroglossus minimus</i>	3A	SK
<i>Melonycteris melanops</i>	3A	SK
<i>Micropteropus pusillus</i>	3A	SK
<i>Nyctimene albiventer</i>	3A	SK
<i>Otopterus cartilagonodus</i>	3A	SK
<i>Ptenochirus jagori</i>	3A	SK
<i>Pteropus alecto</i>	3A	SK
<i>Pteropus conspicillatus</i>	3J	SK
<i>Pteropus dasymallus</i>	1J, 3A	AL, SK
<i>Pteropus personatus</i>	1J	SK
<i>Pteropus vampyrus</i>	2A	SK
<i>Rousettus amplexicaudatus</i>	6A	SK
<i>Rousettus madagascarensis</i>	3A	SK
<i>Syconycteris australis</i>	3A	SK

Appendix. Specimens Examined in this Study (continued)

Taxon	Number and Ages ¹ of specimens examined	Preparations ²
MICROCHIROPTERA		
Rhinopomatidae		
<i>Rhinopoma muscatellum</i>	6A	SK
Emballonuridae		
<i>Emballonura semicaudata</i>	6A	SK
<i>Saccopteryx bilineata</i>	5A	SK
<i>Taphozous georgianus</i>	1A	SK
Nycteridae		
<i>Nycteris arge</i>	1A	SK
Megadermatidae		
<i>Lavia frons</i>	1A	SK
<i>Macroderma gigas</i>	2A	SK
<i>Megaderma spasma</i>	5A	SK
Rhinolophidae		
<i>Hipposideros armiger</i>	4A	SK
<i>Rhinolophus inops</i>	6A	SK
<i>Trienops rufus</i>	2A	SK
Noctilionidae		
<i>Noctilio leporinus</i>	6A	SK
Mormoopidae		
<i>Mormoops megalophylla</i>	6A	SK
<i>Pteronotus davyi</i>	4A	SK
Phyllostomidae		
<i>Artibeus jamacensis</i>	1J, 6A	CS, SK
<i>Desmodus rotundus</i>	6A	SK
<i>Erophylla sezekorni</i>	2J, 6A	CS, SK
<i>Phyllonycteris poeyi</i>	4J, 3A	CS, SK
<i>Phyllostomus hastatus</i>	6A	SK
<i>Uroderma bilobatum</i>	1J, 6A	CS, SK
Natalidae		
<i>Natalus stramineus</i>	6A	SK
Furipteridae		
<i>Furipterus horrens</i>	4A	SK
Thyropteridae		
<i>Thyroptera tricolor</i>	2A	SK
Myzopodidae		
<i>Myzopoda aurita</i>	1A	SK
Vespertilionidae		
<i>Antrozous dubiaquercus</i>	5A	SK
<i>Miniopterus minor</i>	6A	SK
<i>Scotophilus kuhlii</i>	6A	SK
Molossidae		
<i>Molossus molossus</i>	7A	SK
<i>Molossus obscurus</i>	1A	SK
<i>Otomops martiensseni</i>	3A	SK
<i>Promops</i> sp.	1J	CS
<i>Tadarida condylura</i>	6A	SK
Dermoptera		
Cynocephalidae ³		
<i>Cynocephalus volans</i>	4A	SK
<i>Galeopterus variegatus</i>	1F, 2J, 4A	CS, AL, and SK
Primates		
Cheirogaleidae		
<i>Cheirogaleus major</i>	1A	SK
Daubentoniidae		
<i>Daubentonia madagascarensis</i>	1A	SK
Galagidae		
<i>Otolemur crassicaudatus</i>	6A	SK
Lemuridae		
<i>Eulemur fulvus</i>	1A	SK
<i>Eulemur macacao</i>	1A	SK
<i>Eulemur mongoz</i>	2A	SK
<i>Hapalemur griseus</i>	3A	SK
<i>Lemur catta</i>	1A	SK
Lorisidae		
<i>Nycticebus coucang</i>	4A	SK
<i>Perodicticus potto</i>	1A	SK

Appendix. Specimens Examined in this Study (continued)

Taxon	Number and Ages ¹ of specimens examined	Preparations ²
Primates (continued)		
Megaladapidae		
<i>Lepilemur mustelinus</i>	1A	SK
Tarsiidae		
<i>Tarsius bancanus</i>	3A	SK
Rodentia		
Muridae		
<i>Peromyscus leucopus</i>	9J, 6A	CS, SK
Sciuridae		
<i>Callosciurus finlaysonii</i>	1J, 2A	AL, SK
<i>Sciurus carolinensis</i>	1J, 6A	AL, SK
Scandentia		
Ptilocercinae ³		
<i>Ptilocercus lowii</i>	1J, 4A	SK, X-ray
Tupaiainae ³		
<i>Anathana ellioti</i>	1A	X-ray
<i>Dendrogale melanura</i>	2A	X-ray
<i>Dendrogale murina</i>	1J	X-ray
<i>Tupaia chinensis</i>	4J	CS
<i>Tupaia glis</i>	6A	SK
<i>Tupaia gracilis</i>	1A	SK
<i>Tupaia minor</i>	1J, 6A	CS
<i>Tupaia montana</i>	1A	SK
<i>Tupaia tana</i>	2J, 6A	CS
<i>Urogale everetti</i>	2A	X-ray

¹A = adult, all epiphyses fused and adult dentition fully erupted. J = juvenile, postnatal, but epiphyses unfused and/or adult dentition not fully erupted. F = fetus, prenatal.

²AL = alcohol preserved specimens used for identifying cartilages via gross dissection. CS = cleared and stained specimens. SK = skeletal material. X-ray = x-rays of museum skins.

³Because our interpretation of the morphology of these taxa differs from that in the literature, we list ages and specimen numbers. Cynocephalidae: *Cynocephalus volans*, FMNH 56442 (A), FMNH 61032 (A), USNM 144662 (A), USNM 578084 (A); *Galeopterus variegatus*, USNM 144374 (F), USNM 143326 (J), USNM 197203 (J), USNM 49470 (A), USNM 49640 (A), USNM 49693 (A), USNM 317118 (A). Ptilocercinae: *Ptilocercus lowii*, USNM 121885 (A). Tupaiainae: *Anathana ellioti*, FMNH 91265 (A); *Dendrogale melanura*, USNM 292544 (A), USNM 300913 (A); *Dendrogale murina*, USNM 256752 (A); *Tupaia chinensis*, USNM 399596 (5 days), USNM 399594 (11 days), USNM (#116)⁴ (15 days), USNM 399591 (20 days); *Tupaia glis*, USNM 320721 (A), USNM 396665 (A), USNM 396666 (A), USNM 396673 (A), USNM 397663 (A), USNM 535137 (A); *Tupaia gracilis*, USNM 578656 (A); *Tupaia minor*, NZP 110705 (32 days), USNM 396668 (A), USNM 396669 (A), USNM 396670 (A), USNM 548410 (A), USNM 574130 (A); *Tupaia montana*, USNM 449964 (A); *Tupaia tana*, NZP 109835 (4 days), NZP 109834 (11 days), USNM 396661 (A), USNM 396663 (A), USNM 449968 (A), USNM 449969 (A), USNM 574901 (A), USNM 579556 (A); *Urogale everetti*, USNM 292292 (A), USNM 292293 (A).

⁴Uncatalogued USNM specimen.