

Carpal Anatomy and Primate Relationships

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Abstract A comparative study of skeletonized and wet specimens of a broad sampling of prosimian as well as anthropoid primates provides evidence for the first time of the diversity of morphology and articular relations of the carpals. Phylogenetically, it appears that derived states within Primates support the monophyly of a cheirogaleine-galagine-lorisine clade (marked contact between the os centrale and the hamate), an Old World monkey clade (lack of a hamate process), and a New World monkey clade (medially truncated, but mediolaterally oriented os centrale with a laterally elongate, horizontally oriented, distal extension that is overlapped extensively dorsally by the trapezoid, and broad contact between the lunate and capitate). The latter features provide the first definitive demonstration of New World monkey monophyly on the basis of easily recognized synapomorphy. Fusion of the os centrale and scaphoid seems to occur randomly among primates. This character is thus best interpreted as autapomorphic for the relevant taxa.

Keywords: carpal anatomy, primate systematics, New World monkeys, prosimians

Introduction

Although studies of the primate postcranial skeleton have been applied for some time now to questions regarding the phylogenetic relationships of fossil and living taxa (for example, see compendium edited by Strasser and Dagosto, 1988, and references therein), few, with the notable exception of Napier and Davis (1959), focused on the carpals. This oversight may be due to taphonomic reasons, such as the infrequency of preservation and subsequent discovery of these remains, as well as to the difficulty of studying these small skeletal elements. Recently, however, Beard and Godinot (1988) and Beard and others (1988) attempted to address this lacuna in their analysis of carpal bones, which yielded features they interpreted as reflecting the monophyly of strepsirhine and anthropoid clades as well as the monophyly of major strepsirhine subclades. Unfortunately, an attempt to replicate the identification of some of the carpal features these authors described failed in the case of various extant prosimian and anthropoid taxa (Schwartz, 1992). In light of

this discrepancy, we undertook a broad survey of primates in order to contribute to a more complete picture of the comparative anatomy and consequent phylogenetic implications of this interesting skeletal region.

Materials and Methods

Seventy-eight specimens, representing a diversity of extant primates, were studied (Table 1). Of these, 69 had been skeletonized and were chosen for this study because one or both wrists and hands were held in anatomical position by desiccated connective tissue. We were able to study right and left sides in 45 individuals, and included information from

Table 1 List of Specimens

Taxon	Catalogue Number	Wet/Skeletonized	Right/Left
<i>Aotus trivirgatus</i>	PRC 2437	s	l
	PRC 2438	s	r
	PRC 2577	s	r, l
<i>Avahi laniger</i>	AMNH 170494	s	r, l
<i>Callithrix jacchus</i>	JMC Pr732	s	r
	JMC 706	s	r
<i>Cebuella pygmaeus</i>	JMC 404	s	r
<i>Cebus apella</i>	PRC 2348	s	l
	AMNH 133817	s	r, l
<i>Cercocebus albigens</i>	PRC 1725	s	r, l
<i>Cercopithecus aethiops</i>	PRC 2453	s	r, l
<i>Cheirogaleus sp.</i>	PRC 7	w	l
<i>Colobus polykomos</i>	PRC (N.C.)	s	r
<i>Daubentonia madagascariensis</i>	AMNH 185643	s	r, l
<i>Erythrocebus patas</i>	JMC Pr1839	s	r
	JMC 3280	s	r, l
	JMC 4104	s	r, l
<i>Galago crassicaudatus</i>	PRC 2439	s	r, l
	PRC unnumbered	w	r
	PRC unnumbered	s	r
<i>G. senegalensis</i>	PRC 16	w	r
	PRC 17	w	r
	PRC 3595	s	l
	PRC 920/21 (no. 4)	s	r, l
	PRC 920/21 (no. 5)	s	l
	PRC 920/21 (no. 6)	s	l
	PRC 920/21 (no. 7)	s	r, l
PRC 920/21 (no. 11)	s	r, l	
<i>Haplemur griseus</i>	AMNH 170687	s	r, l
<i>Hylobates hoolock</i>	AMNH 80068	s	r, l
<i>H. lar</i>	JMC Pr90	s	r
	JMC Pr141	s	l
	JMC Pr633	s	r, l

Table 1 (continued)

Taxon	Catalogue Number	Wet/Skeletonized	Right/Left
<i>Indri indri</i>	AMNH 100504	s	r, l
<i>Lemur catta</i>	PRC 2205	s	r, l
	PRC 2436	s	r, l
	PRC 2576	s	r, l
	AMNH 200881	s	r, l
<i>L. fulvus albifrons</i>	AMNH 170728	s	r, l
<i>L. fulvus fulvus</i>	AMNH 31254	s	r, l
<i>Leontopithecus rosalia</i>	JMC Pr907	s	r, l
<i>Lepilemur mustelinus</i>	AMNH 170556	s	r, l
<i>Loris tardigradus</i>	PRC P030	w	l
	JMC Pr924	s	r, l
	AMNH 22718	s	r, l
<i>Macaca fascicularis</i>	AMNH 103661	s	r, l
<i>M. mulatta</i>	PRC 2654	s	r
	PRC 2675	s	r, l
	PRC 2677	s	r, l
<i>M. nemestrina</i>	PRC 2468	s	r, l
<i>Microcebus murinus</i>	PRC 10	w	r
<i>Nycticebus coucang</i>	PRC 2207	s	r
	PRC 2208	s	r, l
	PRC 2237	s	r, l
	PRC 2353	s	r
	PRC 14	w	r
	AMNH 90381	s	l
	AMNH 16589	s	r
<i>Pan troglodytes</i>	AMNH 201469	s	r, l
<i>Papio anubis</i>	PRC 1626	s	l
<i>P. hamadryas</i>	PRC 2779	s	r, l
	PRC 3388	s	r
<i>Pithecia mona</i>	JMC Pr875	s	r, l
<i>Pongo pygmaeus</i>	AMNH 300900	s	r, l
<i>Presbytis cristatus</i>	PRC 2309	s	r, l
	PRC 1529	s	r
<i>P. entellus</i>	JMC 3249	s	r
<i>Propithecus verreauxi</i>	AMNH 208990	s	r, l
	JMC 3306	s	r
<i>Saguinus oedipus</i>	JMC Pr 839	s	r, l
<i>Saimiri sciureus</i>	PRC 2084	s	r, l
	PRC 2344	s	r, l
	PRC 2580	s	r, l
	PRC 2108	s	r, l
	AMNH 18908	s	r, l
<i>Tarsius syrichta</i>	PRC 140	w	l
	PRC 142	w	r
	AMNH 206757	s	r, l

both sides in our analysis. The intra-individual variation generated by including information from right and left sides would add to the assessment of whether features were, or were not, taxon-specific. In order to double-check our description of the details of radiocarpal, ulnocarpal, carpocarpal, and carpometacarpal articulation in the skeletonized specimens, we dissected the wrists of nine wet specimens. Using wet specimens also gave us the opportunity to move the wrist joint through various excursions in order to observe not only how and/or when various bones might come into contact, but also the angles at which bones crucial to this analysis (especially the os centrale) were oriented and the depths anteroposteriorly (dorsoventrally) to which they extended. Inasmuch as a focus of this study was the morphology and articular relationships of the os centrale, only two of the large-bodied hominoids were included in the analysis.

Specimens for this study are housed at Primate Research Institute, Kyoto University, Inuyama (PRC), the Japan Monkey Center, Inuyama (JMC), and the American Museum of Natural History, New York City (AMNH). Wet specimens were dissected using an Olympus SZH dissecting microscope at variable magnifications of 3.5-20x. The smaller skeletonized specimens were studied at 4-20x using a Nikon SMZ microscope; the larger skeletonized specimens were viewed under a 10x hand-held lens.

Results

Microcebus, *Cheirogaleus*, *Galago*, *Loris*, and *Nycticebus* are similar in various features (Figure 1). For example, the "body" of the os centrale is relatively thick proximodistally and sufficiently distended medially that it may override the head of the capitate completely and make contact with, if not slightly overlap, the hamate. The (distal) portion of the os centrale, which articulates with the relatively broad and shallow embrasure between the trapezoid and capitate, is distended and presents itself as a somewhat "peaked," liplike structure. The facet for the trapezoid lies on the broad distal edge of the os centrale, the lateral corner of which contacts the trapezium. The medial side of the trapezium is elongate; the scaphoid articulates fully along its proximal side. The articular surface on the hamate for the fifth metacarpal is deeply concave and the hamulus (hook) or palmar process of this carpal is typically long proximodistally (in contrast to the drawings in Figure 3 in Hamrick, 1996). (Hamrick (1997) subsequently described the "strepsirhine" hamate hamulus as tending to be long compared to anthropoid primates and various other mammals. However, from his drawings it appears that he was referring to the anteroposterior dimension of this process, whereas our focus was on the proximodistal aspect.) The head and neck of the capitate of the aforementioned prosimians are narrow (see also Figure 3 in Hamrick, 1996). The lunate, which is consistently a mediolaterally narrow bone (contra Beard and Godinot, 1988), cups the head of the hamate; the triquetral is thus positioned more medially along the side of the hamate. As observed at least in *Galago*, the facet on the pisiform for articulation with the ulnar styloid process is small and shallow, whereas the facet for the triquetral is large and convex (contra Beard and Godinot, 1988, and Beard and others' 1988, generalization about the ulnar facet on the

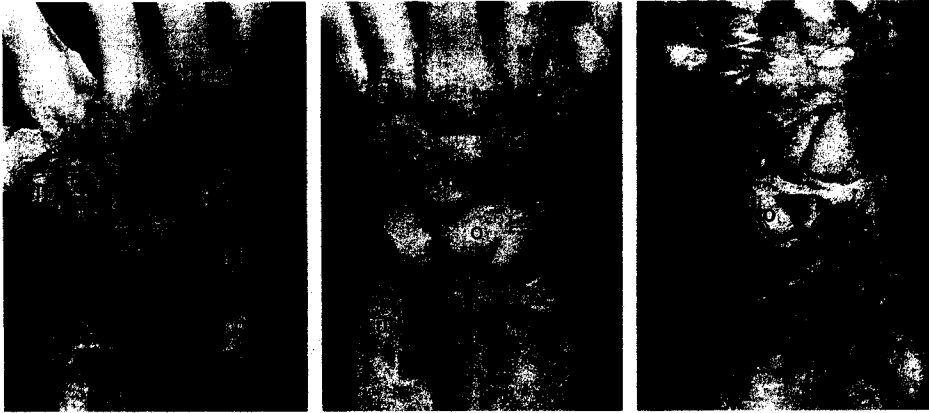


Figure 1 Left: *Galago senegalensis*, right wrist (PRC 11). Middle: *Nycticebus coucang*, left wrist (AMNH 90381). Right: *Loris tardigradus*, right wrist (AMNH 22718). Tm=trapezium; Td=trapezoid; C=capitate; H=hamate; Tr=triquetral; P=pisiform; O=os centrale; S=scaphoid; R=radius; U=ulna. (Dorsal view; not to scale)

pisiform being long in all strepsirhines).

In *Nycticebus* (Figure 1), the bulk of the distal liplike distention of the os centrale is overridden by the trapezoid and is not trapped in the embrasure between the trapezoid and capitate; this liplike distention is oriented horizontally. *Galago* differs from *Nycticebus* in that the peak of the os centrale stays below (that is, articulates proximal to), rather than passes between, the embrasure formed by the trapezoid and capitate. In *Microcebus*, most of the distal portion of the os centrale courses anteriorly underneath the proximal end of the trapezoid. Consequently, and in contrast to *Cheirogaleus*, very little of the distal “peak” of the os centrale of *Microcebus* protrudes into the small, narrow embrasure between the trapezoid and capitate.

Nycticebus is noteworthy in that the os centrale intervenes markedly between the lunate and the capitate, preventing complete contact between the latter two carpals. As in all other extant lorids, the pisiform in *Nycticebus* does not articulate with the ulnar styloid process (also see Cartmill and Milton, 1977).

Proximally, the *Loris* os centrale extends over the capitate head to reach the hamate (Figure 1). The distal end of this bone is blunt and short, rather than peaked, and it articulates with a broad trapezoid-capitate notch. As in other strepsirhines, the *Loris* scaphoid overlaps the lunate considerably on its dorsal surface. The heads of the *Loris* capitate and hamate are cupped by the mediolaterally broad lunate, the only carpal which articulates with the radius and ulna. In *Loris*, the surface of the hamate that articulates with the fifth metacarpal is not as deep as it is in *Nycticebus*, *Galago*, *Cheirogaleus*, and *Microcebus*, and the hamate process is not as long proximodistally. The hamate of *Cheirogaleus* bears a modestly developed process.

In general, the *Lemur* os centrale (Figure 2) can be described as thin and curved. This

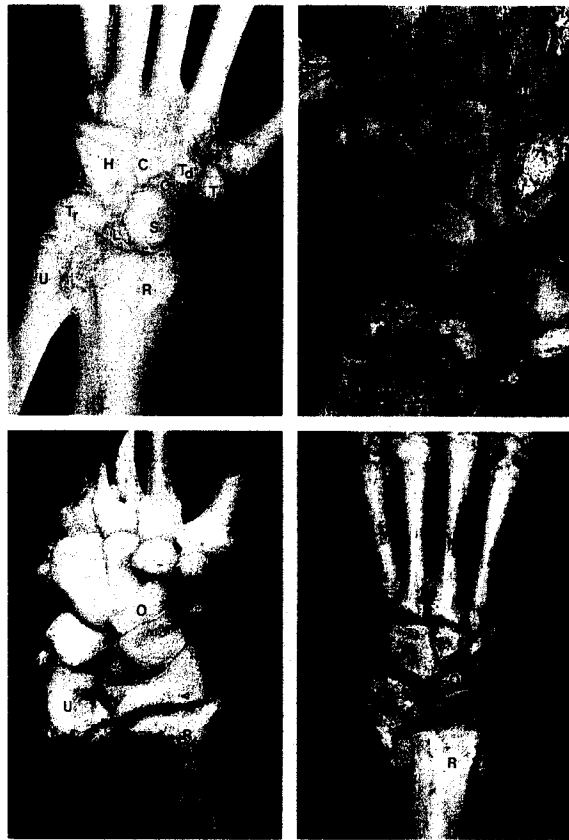


Figure 2 Top left: *Lepilemur mustelinus*, left wrist (AMNH 170556). Top right: *Propithecus verreauxi*, right wrist lacking ulna (AMNH 208990). Bottom left: *Haplemur griseus*, left wrist with broken ulna (AMNH 170687). Bottom right: *Lemur fulvus*, left wrist lacking ulna (AMNH 31254). Abbreviations as in Figure 1. (Dorsal view; not to scale)

bone is steeply faceted on its lateral side in conjunction with the articular surface of the medial face of the trapezoid. Part of the acutely peaked os centrale nestles into a deep and narrow embrasure between the trapezoid and the capitate. Most of the distal liplike portion of the os centrale, which is oriented obliquely rather than horizontally, projects anteriorly beneath the trapezoid. The “body” of the os centrale may taper laterally; it often broadly cups and overlaps the head of the capitate dorsally, but when it extends further toward the proximal end of the hamate, it merely “kisses” the latter carpal (contra Beard and Godinot, 1988, and Beard and others, 1988, who describe a broad overlap of the hamate by the os centrale).

Our study indicates that contact between the os centrale and hamate in desiccated specimens may actually be an artifact caused by shrinkage due to desiccation or removal during specimen preparation of cartilage and periosteum that would otherwise normally be interposed between the articulating bones. These factors might explain why in one

skeletonized specimen of *Tarsius* (see below) the os centrale came to overlap slightly the head of the capitate.

As in other strepsirhines, the neck and head of the *Lemur* capitate are narrow (also see Figure 3 in Hamrick, 1996). Although the trapezium is short and truncated medially, the scaphoid may not make full contact along its proximal surface. The distal surface on the hamate for articulation with the fifth metacarpal is shallow and the hamate process short. The lunate, which is mediolaterally narrow (also see Beard and Godinot, 1988), only cups the head of the hamate. The scaphoid overlaps somewhat the os centrale dorsally, but it does not articulate with the head of the capitate (contra Beard and Godinot, 1988: p. 74). The pisiform contact with the ulnar styloid process is fairly broad (also see Beard and Godinot, 1988; Hamrick, 1996).

Avahi (also see Jouffroy, 1975), *Indri*, and *Lepilemur* are distinguished from other prosimians included in this study in that the os centrale and scaphoid fuse together to form a single, large carpal. In this regard, these three taxa are similar to *Hapalemur* (Jouffroy, 1975; Schwartz, 1992) (Figure 2). In contrast to the os centrale of *Hapalemur* and *Lepilemur*, which terminates medially before reaching the scaphoid tubercle, the os centrale of *Indri* and *Avahi* is quite long, extending medially all the way to the scaphoid tubercle. Unlike other extant indrids, the os centrale and scaphoid of *Propithecus* remain unfused; in addition, the os centrale is short and the scaphoid tubercle is quite long and projecting (Figure 2). *Daubentonia* compares most favorably with *Propithecus* in the morphology and articular relations of its os central and scaphoid. Similar to the condition in *Lemur*, the os centrale of indrids, *Daubentonia*, *Hapalemur*, and *Lepilemur* nestles obliquely into a deep and narrow embrasure between the trapezoid and the capitate. Although it embraces the posterior surface of the head of the capitate, the os centrale of indrids, *Daubentonia*, *Lepilemur*, and *Hapalemur* at most only minimal contacts the proximal end of the hamate. In all of these prosimians, the scaphoid overrides somewhat the proximo-dorsal surface of the os centrale. The indrid and aye-aye pisiform possesses a broad facet for articulation with the ulnar styloid process. The pisiform ulnar styloid facet is less extensive in *Lepilemur* and *Hapalemur* (Schwartz, 1992).

The tarsier's os centrale is acutely peaked distally. This distal "peak" fits tightly and broadly in an anteroposterior direction into a deep, narrow embrasure between the trapezoid and the capitate; this "peak" extends ventrally under the trapezoid. Typically, the body of the os centrale is severely truncated medially; in one specimen (AMNH 206757), however, this carpal is distended sufficiently medially to overlap part of the head of the capitate. *Tarsius*' lunate cups the lateral (ulnar side) half of the capitate's and the medial (radial side) half of the hamate's head. The hamate, which lacks a hook or process altogether, articulates distally with the fourth and fifth metacarpals. The hamate surface that articulates with the fifth metacarpal is shallow and the proximal surface of the fifth metacarpal may extend laterally beyond the articular surface. As in most strepsirhines studied, *Tarsius*' capitate and hamate are subequal in proximodistal length.

The New World monkeys studied are essentially uniform in carpal morphology (Figure



Figure 3 Left: *Cebus apella*, left wrist (AMNH 133817). Middle: *Saimiri sciureus*, left wrist (AMNH 18908). Right: *Pithecia mona*, right wrist (JMC 875). Abbreviations as in Figure 1. (Dorsal view; not to scale)

3). The wedge-shaped os centrale is relatively broad mediolaterally; the trapezoid almost completely covers the dorsal surface of its distended distal moiety. Consequently, the mediolateral breadth of the New World monkey os centrale lies lateral to the capitate and under the trapezoid, rather than being truncated laterally but broad medially due to its extension over the capitate, as is the case in all other primates with the exception of *Tarsius*, which has a narrow os centrale. The articular strip on the distal lip (= the thin edge) of the os centrale is oriented horizontally. The medial side of the os centrale articulates variably with the capitate; only the “corner” of the os centrale contacts or nestles into the embrasure between the trapezoid and capitate. This embrasure is wide in some (for example, *Aotus*, *Saimiri*, *Saguinus*) but not all taxa (for example, *Leontopithecus*, *Pithecia*, *Callithrix*) (contra Beard and Godinot, 1988). Typically among New World monkeys, the lunate articulates broadly with, and overlaps dorsally, the head of the capitate. Although on occasion the lunate may make slight contact with the hamate, the primary articulation of the hamate is with the triquetral. In general among New World monkeys, the capitate is as long as, or longer than, the hamate. The surface on the hamate for articulation with the fifth metacarpal is often deep, although it may be relatively less deep in *Aotus*. The hamate process or hook is well pronounced, being typically long proximodistally and swollen palmar. Rather than bearing a relatively small articulation, the pisiform maintains a mediolaterally long contact with the anterior surface of the ulnar styloid process (contra Beard and Godinot, 1988; Beard and others, 1988). The triquetral articulates distally atop the “platform” created by the distal surfaces of the pisiform and the tip of the ulnar styloid process.

The Old World monkey os centrale (Figure 4) is distended distally into a “peak” or flange that nestles obliquely into a deep and narrow embrasure between the trapezoid and the capitate (contra Beard and Godinot, 1988); the medial portion of this distention is

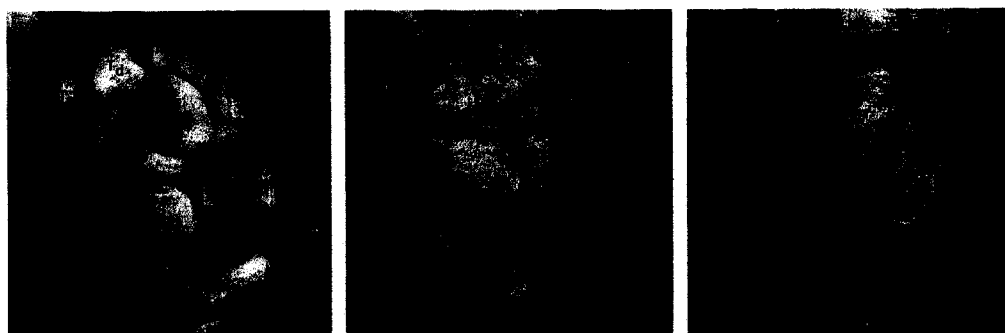


Figure 4 Left: *Macaca nemestrina*, right wrist (PRC 2468). Middle: *Macaca fascicularis*, left wrist (AMNH 103661). Right: *Hylobates hoolock*, right wrist (AMNH 80068). Abbreviations as in Figure 1. (Dorsal view; not to scale)

overridden dorsally by the trapezoid. The body of the os centrale is arcuate and wraps at least partially around the head of the capitate; infrequently, the triquetral may also contact the head of the capitate. The os centrale is not expansive laterally. The scaphoid cups the os centrale proximally and may slightly overlap its dorsal surface. The Old World monkey capitate is longer than the hamate. The latter bone bears a moderately deep articular surface for the fifth metacarpal but it lacks a true process or hook, being merely swollen in that general region (also see O'Connor, 1975). The lunate articulates primarily with the head of the capitate, although it may sometimes also contact the hamate. The facet on the pisiform for the ulnar styloid process is concave and much smaller than the convex facet for the triquetral (also see O'Connor, 1975).

In contrast to the primates so far discussed, *Hylobates* (Figure 4) lacks a prepollex. The os centrale is long and extends ventrally under the length of the trapezoid as well as partly over the dorsal surfaces of the head of the capitate and the distal end of the lunate. The long axis of the os centrale is oriented obliquely along the dorsoventral axis of the wrist. Although not distended distally as in many of the primates described here, the mediolateral corner of the gibbon's os centrale nestles into the essentially right-angled notch between its trapezoid and capitate. The lunate may contact the heads of the capitate and hamate. The latter bone may be longer than the capitate and is relatively narrower than in the other primates studied. The scaphoid cups the os centrale proximally and its radial articular surface is relatively more dorsally reflected than in the other primates studied. As in other extant hominoids, *Hylobates* lacks ulnar-pisiform contact (Lewis, 1969). Schultz (1936) commented that the gibbon os centrale and scaphoid may fuse together in very young as well as older individuals.

The two large-bodied apes in this study, *Pan troglodytes* and *Pongo pygmaeus* (Figure 5), were included primarily to provide information on the shape of the os centrale and its relationship to the capitate alone, or to the capitate and hamate jointly. In both of these large-bodied hominoids, the scaphoid cups the os centrale somewhat dorsally. The os

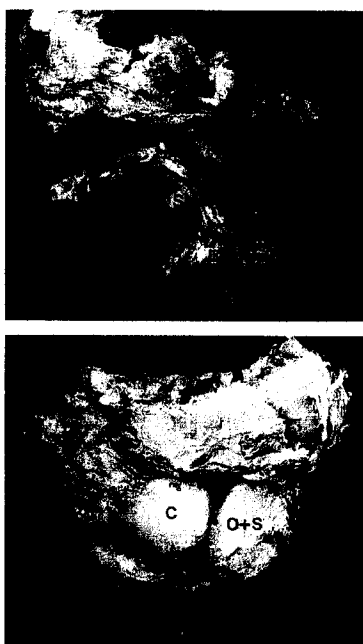


Figure 5 Top: *Pan troglodytes*, right wrist (AMNH 201469). Bottom: *Pongo pygmaeus*, left wrist (AMNH 300900). Abbreviations as in Figure 1. (Dorsal view; not to scale)

centrale, which is relatively thin and arcs partially around the dorsal surface of the head of the capitate, also possesses a distal lip that nestles into a deep and narrow embrasure between the trapezoid and the capitate. In shape and articular relations, the os centrale of these two large-bodied hominoids closely resembles the Old World monkey os centrale. Also as in Old World monkeys, the chimpanzee and orangutan lunate makes partial contact with the head of the capitate. In contrast to Old World monkeys, the os centrale of these large-bodied hominoids is fused to the scaphoid. Such fusion has been cited as occurring earlier in chimpanzees (and gorillas) than in orangutans (for example, Lewis, 1974; Schultz, 1936). Both of our specimens of large-bodied hominoid with os centrale-scaphoid fusion were adult, but, judging by tooth wear and epiphyseal fusion, not very old.

Discussion

The following features emerge as being broadly characteristic of the primates analyzed in this study (see Table 2). 1) The scaphoid cups the os centrale and overrides it somewhat dorsally. 2) The os centrale is distended distally into a peaked or liplike flange. In all primates studied, with the notable exception of the New World monkeys, this distention is oriented obliquely along the dorsoventral axis of the wrist. A portion of this peak or lip is overridden dorsally by the trapezoid. Some small portion of this distal os centrale extension articulates within the embrasure between the trapezoid and the capitate. 3) The embrasure between the trapezoid and capitate is deep and narrow. 4) The capitate and

hamate are subequal in length, with neither bone being disproportionately longer than the other. 5) The surface on the hamate for articulation with the fifth metacarpal is deep. 6) The process or hook of the hamate is pronounced and proximodistally long. 7) The lunate articulates distally primarily with the head of the capitate. 8) The presence of a prepollex. From the literature, we can add that 9) the scaphoid and lunate together articulate with

Table 2 Distribution of characters discussed in text (M = monkeys; Hylo = *Hylobates*)

	Scaphoid/ Os Centrale overlap	Os Centrale distal extension	Os Centrale distal extension orientation	Os Centrale relative to Trapezoid	Os Centrale medial/lateral extension	Os Centrale/ Capitate overlap
<i>Cheirogaleus</i>	dorsally	peak	oblique	slightly under	medial	yes
<i>Microcebus</i>	"	"	"	"	"	"
<i>Loris</i>	"	no peak	"	"	"	"
<i>Nycticebus</i>	"	peak	"	"	"	"
<i>Galago</i>	"	"	horizontal	"	"	"
<i>Lemur</i>	"	"	oblique	"	"	partially/fully
<i>Avahi</i>	"	"	"	"	"	partial
<i>Indri</i>	"	"	"	"	"	"
<i>Propithecus</i>	"	"	"	"	"	"
<i>Lepilemur</i>	"	"	"	"	"	"
<i>Hapalemur</i>	"	"	"	"	"	"
<i>Daubentonia</i>	"	"	"	"	"	"
<i>Tarsius</i>	"	acute peak	"	"	neither	may slightly
New World M	"	peak	horizontal	fully under	lateral	no
Old World M	"	"	oblique	slightly under	medial	partial
<i>Hominoids</i>	"	Hylo-no peak	"	"	"	"

	Os Centrale/ Hamate overlap	Trapezoid/ Capitate Embrasure	Capitate/ Hamate relative length	Hamate/Fifth Metacarpal articular surface	Hamate Hook length	Lunate/ Capitate articulation
<i>Cheirogaleus</i>	strong	broad, shallow	HC	deep	reduced	short
<i>Microcebus</i>	"	"	"	"	long	"
<i>Loris</i>	"	"	"	moderate	reduced	"
<i>Nycticebus</i>	"	"	"	"	long	"
<i>Galago</i>	"	"	"	"	"	"
<i>Lemur</i>	sometimes	deep, narrow	"	"	"	"
<i>Avahi</i>	minimal	"	"	deep	"	"
<i>Indri</i>	"	"	"	"	"	"
<i>Propithecus</i>	"	"	"	"	"	"
<i>Lepilemur</i>	"	"	"	"	"	"
<i>Hapalemur</i>	"	"	"	"	"	"
<i>Daubentonia</i>	"	"	"	"	"	"
<i>Tarsius</i>	no	"	"	shallow	insignificant	"
New World M	"	"	C>H	"	long	broad
Old World M	sometimes	"	"	deep	insignificant	short
<i>Hominoids</i>	no	"	HC	"	long	"

Table 2 (continued)

	Lunate/Hamate contact	Trapezoid/Capitate Embrasure	Articulates with Ulna	Pisiform/Ulnar Styloid Process articulation	Os Central/Scaphoid fusion	Prepollex
<i>Cheirogaleus</i>	slight	broad, shallow	scaphoid/lunate	yes	no	present
<i>Microcebus</i>	"	"	"	"	"	"
<i>Loris</i>	partially cups	"	lunate	no	"	"
<i>Nycticebus</i>	slight	"	scaphoid/lunate	"	"	"
<i>Galago</i>	"	"	"	yes	"	"
<i>Lemur</i>	"	deep, narrow	"	"	"	"
<i>Avahi</i>	"	"	"	"	yes	"
<i>Indri</i>	"	"	"	"	"	"
<i>Propithecus</i>	"	"	"	"	no	"
<i>Lepilemur</i>	"	"	"	"	yes	"
<i>Hapalemur</i>	"	"	"	"	"	"
<i>Daubentonia</i>	"	"	"	"	no	"
<i>Tarsius</i>	partially cups	"	"	"	"	"
New World M	slight	"	"	"	"	"
Old World M	"	"	"	"	"	"
<i>Hominoids</i>	"	"	"	no	yes	absent

the ulna (Cartmill and Milton, 1977; Jouffroy, 1977; Lewis, 1969, 1974; O'Connor, 1975). And, with the exception of New World monkeys and *Tarsius* (see below), 10) mediolateral breadth of the os centrale of all other primates is achieved by a medial extension which overlaps to some degree the dorsal surface of the head of the capitate.

On the basis of commonality, the features enumerated above would seem to be primitive for extant primates. Consequently, character states that are more restrictively distributed among primate taxa can plausibly be interpreted as being derived or apomorphic and would include: 1) in *Loris* and *Hylobates*, a distally non-peaked os centrale; 2) in *Tarsius*, an acutely distally peaked os centrale; 3) in *Lemur* and New World monkeys, a horizontally oriented distal os centrale lip; 4) in New World monkeys, a trapezoid that overrides almost entirely the distal lip of the os centrale; 5) in New World monkeys, a laterally expanded and medially truncated os centrale; 6) in New World monkeys, a broad contact, both proximally and dorsally, between the lunate and head of the capitate; 7) in *Tarsius*, a typically medially truncated os centrale; 8) in many strepsirhine primates, a medially expanded os centrale, which completely overrides the capitate and may come into contact with the hamate; 9) in *Microcebus*, *Cheirogaleus*, *Galago*, *Loris*, and *Nycticebus*, a definitive contact between the os centrale and the hamate; 10) in *Microcebus*, *Cheirogaleus*, *Galago*, *Loris*, and *Nycticebus*, a broad, relatively shallow embrasure between the trapezoid and capitate; 11) in *Galago*, an articular arrangement in which the distal os centrale peak does not project anteriorly through the embrasure between the trapezoid and capitate; 12) in *Loris* and *Cheirogaleus*, a reduced hamate process; 13) in *Tarsius* and Old World monkeys, the lack of a distinct hamate hook or process; 14) in *Tarsius* and

Loris, an articular arrangement in which the lunate cups the lateral half of the capitate head and the medial half of the hamate head; 15) in *Loris*, an enlarged lunate, which alone articulates with the ulna; 16) in *Nycticebus*, the intervention of the os centrale between the lunate and capitate; 17) in lorids and hominoids, lack of articulation between the pisiform and the ulnar styloid process; 18) in *Indri*, *Avahi*, *Hapalemur*, *Lepilemur*, and all hominoids at various ages, fusion of the os centrale and scaphoid; 19) in hominoids, the lack of a prepollex.

Of the above, a feature that is found only in a single taxon would be autapomorphic for that taxon. When a feature occurs in taxa which, on the basis of other features, do not appear to be closely related to one another, it is reasonable to conclude that these apomorphic states developed in parallel. As such, we can suggest that derived character states #1, 3, 13, and 14 were independently attained apomorphies: specifically, for *Loris* and *Hylobates* (#1), *Lemur* and New World monkeys (#3), *Tarsius* and Old World monkeys (#13), and *Tarsius* and *Loris* (#14). None of these sets of groupings emerges as a viable clade (e. g. see review by Schwartz, 1986). However, while neither *Lemur* + New World monkeys nor *Tarsius* + Old World monkeys may constitute a clade, the groups “New World monkeys” and “Old World monkeys” conceivably do. Consequently, character state #3 (a horizontally oriented distal os centrale lip) emerges as a potential apomorphy reflecting the monophyly of New World monkeys, as does character state #13 (lack of a distinct hamate hook) for Old World monkeys. New World monkey monophyly is indicated further by the development of a laterally expanded and medially truncated os centrale (#5) that is overridden dorsally along its lateral length by the trapezoid (#4), and broad distal and dorsal contacts between the lunate and the head of the capitate (#6). Presumably, the broad contact between the lunate and the head of the capitate is possible precisely because the os centrale is not expanded medially.

Although Beard and others (1988; also Beard and Godinot, 1988) argued that a mediolaterally wide os centrale can be counted among the potential synapomorphies uniting extant strepsirhines (Beard and others, “lemuriforms”, 1988), it is important to point out that this can describe the os centrale of New World monkeys, as well. It is, therefore, imperative, as these authors also acknowledged, to specify that mediolateral width of the strepsirhine os centrale (in contrast to New World monkeys) derives specifically from a medially elongate extension that courses dorsally over the capitate and which often makes contact with the hamate. This is not, however, a potential synapomorphy for all strepsirhine primates (contra Beard and Godinot, 1998; Beard and others, 1988) because in some specimens of *Lemur*, *Hapalemur*, *Propithecus*, *Daubentonia*, *Lepilemur*, and *Indri* the os centrale makes little or no contact with the hamate (Etter, 1978; Jouffroy, 1975; Schwartz, 1992). It is unclear whether in *Hapalemur*, *Lepilemur*, *Avahi*, and *Indri* these nuances in carpal associations are correlated with os centrale-scaphoid fusion (Jouffroy, 1975; Schwartz, 1992). However, since two derived character states—broad contact between the os centrale and hamate (apomorphic character state #9) and the presence of a broad, shallow trapezoid-capitate embrasure (apomorphic character state #10)—are consistently

found in *Microcebus*, *Cheirogaleus*, *Galago*, *Loris*, and *Nycticebus*, it is probable that these features reflect the relatedness of cheirogaleines, galagines, and lorisines. Such a clade has been hypothesized on the basis of potential synapomorphies of the carotid circulation and craniodental morphology (for example, Cartmill, 1975; Schwartz, 1986; Schwartz and Tattersall, 1985; Szalay and Katz, 1973; Yoder, 1992).

Inasmuch as all strepsirhines, Old World monkeys, and *Tarsius* (but not New World monkeys) possess an os centrale that is distended into a distal peak (even a blunt one as in *Loris*) with a oblique orientation, we interpret this as a primitive character state within primates. At present, our working hypothesis is that the configuration of the Old World monkey os centrale represents the primitive condition for extant primates. Because the os centrale rarely overlaps the capitata dorsally in *Tarsius*, but it does so to varying degrees in strepsirhines and Old World monkeys, we suggest that the configuration in *Tarsius* is derived among primates. The New World monkey os centrale, which Beard and others (1988; also Beard and Godinot, 1988) illustrate for *Saimiri* but inappropriately globalize as being representative of all anthropoids, does not, as they suggest, reflect the primitive primate configuration. Rather, features of the os centrale of New World monkeys—its truncation medially and its orientation mediolaterally under the trapezoid—emerge in this analysis as being potentially synapomorphic for these primates. The monophyly of New World monkeys is indicated further by the broad contact the lunate makes distally and dorsally with the capitata head.

Although not being in any way similar to the configuration we hypothesize as being primitive for primates, the os centrales that Beard and others (1988; also Beard and Godinot, 1988) illustrate for *Adapis* and *Smilodectes* are of interest. The os centrale of *Adapis* is essentially New World monkey-like in being medially truncated, laterally expanded, and overridden dorsally along much of its distal margin by the trapezoid. We prefer the hypothesis that, if this os centrale and the associated carpal bones are truly those of *Adapis*, the configuration of the os centrale is independently apomorphic for the fossil as well as for New World monkeys.

The os centrale attributed to *Smilodectes* is a small, diamond-shaped bone adhering by matrix to the medial side of a capitata. This supposed os centrale is unmatched morphologically by the os centrale of any extant primate and it is further distinguished from the os centrales of the primates in our study (as well as the os centrale of *Tupaia* illustrated by Hershkovitz, 1977) in that it is nestled into the concavity above (that is, distal to) the head of the capitata rather than articulating with or around the head of the capitata. If it not an os centrale, perhaps this small bone, if it is from the same wrist as the capitata, is a trapezoid that had dropped down alongside and become adherent to the carpal with which it had originally articulated more distally. If, however, additional evidence corroborates the identification of this small, diamond-shaped bone as an os centrale, its unique morphology and articular relations with the capitata probably reflect autapomorphy rather than primitiveness with regard to primates as a clade or strepsirhine/prosimian primates in particular (cf. Beard and Godinot, 1988; Beard and others, 1988). In addition,

if the small facet on a scaphoid that Beard and Godinot (1988) attribute to *Smilodectes* actually did articulate with the head of the capitate (as they suggest based on analogy with *Lemur*), then this feature would be a potential autapomorphy of the fossil taxon inasmuch as scaphoid-capitate articulation does not occur in *Lemur*.

Conclusion

Although carpal morphology and articular relations are potentially revealing of phylogenetic relationships, continued study of species-specific detail is necessary before certain assertions in the literature regarding relationships between fossil and extant primates can be accepted. This is clearly pointed out by the review here of os centrale morphology. Contrary to claims that all anthropoids are similar in os centrale morphology and articulation, it turns out that New World monkey possess a configuration that can be readily distinguished from that of Old World monkeys and hominoids. As to their relative states of primitiveness or derivedness, our broad comparison within primates suggests that the New World monkey configuration is derived—which makes this the first definitive demonstration of platyrrhine monophyly on the basis of unambiguous synapomorphy.

Preliminary observations here, as well as elsewhere (Schwartz, 1992), on pisiform articular facet morphology also indicate that, contrary to previous claims, a broad ulnar styloid facet is neither characteristic of, nor synapomorphic for, all strepsirhines. The finer details of this articulation might prove enlightening upon further investigation. Autapomorphically, lorisids lack ulnar-pisiform contact altogether (see also Cartmill and Milton, 1977). But the presence of a broad ulnar styloid facet on the pisiform of many strepsirhines and some anthropoids (also see Hamrick, 1996, and Schwartz, 1992) can reflect primitiveness for primates as a whole, or a patchy distribution of independently attained apomorphy (that is, synapomorphies of subclades). Consequently, the presence of a broad ulnar styloid facet on the pisiforms attributed to *Adapis* (also see Hamrick, 1996) and *Smilodectes* need not be reflective of a close phylogenetic relationship between these fossils and extant strepsirhines (cf. Beard and Godinot, 1988; Beard and others, 1988). If the development of an anteroposteriorly elongate hamate hamulus is indeed derived within primates (Hamrick, 1997), then at least some prosimians would be united in a clade that also includes *Lemur*, which has a very long process.

Finally, we note, especially in New World monkeys, the apparent lack of correlation between the morphology and articular relationships of the carpals and wrist function, at least with regard to locomotory and positional behavior. First, in spite of the fact that our sample includes some of the smallest taxa (which also are distinguished by the possession of claws) as well as some of the largest platyrrhines (possessing flattened nails), and their modes of locomotion and postures at rest range from varying degrees of quadrupedalism, to semi-brachiation, leaping, climbing, and vertical clinging (for example, Ford, 1992; Sussman and Kinzey, 1984), all are distinguished by the possession of the same broad lunate-capitate articulation. This is certainly impressive and greatly supportive of our interpreting New World monkey os centrale morphology as synapomorphic for the entire

group.

Second, we must note that fusion of the os centrale and scaphoid occurs in only two of the three genera of extant indrids, as well as in *Hapalemur*, *Lepilemur*, and, as has been more widely known, in all extant hominoids, including humans (for example, Sarmiento, 1988; Schultz, 1936). In addition to differing greatly in body size [from the smallest, *Lepilemur* (with its compressed, keeled nails) and *Avahi*, to the largest, *Gorilla*], these primates differ in degree of terrestriality (viz. *Gorilla*) versus arboreality (viz. *Indri*) as well as mode of locomotion (for example, vertical clinging and leaping, quadrupedalism, arm swinging, full brachiation, knuckle walking, bipedalism) (Sarmiento, 1985, 1988; Fleagle, 1988; Tattersall, 1982). When only fusion of the os centrale and the scaphoid in hominoids has been considered, it has been interpreted as being "best suited to forelimb suspension," in spite of the fact that *Pan* and *Gorilla* are the least arboreal of non-human hominoids (Lewis, 1974: p. 159). If we must assume that such fusion is correlated with function, then it becomes unanswerable why, early in human fetal development, either the cartilaginous anlagen of the os centrale and the scaphoid coalesce (Cihák, 1972), or the cartilaginous anlage of the os centrale does not develop at all (cf. Lewis, 1970).

Unlike the case with New World monkeys, in which a diversity of taxa of differing sizes and locomotory and postural preferences share the same lunate-capitate articulation, there is no pattern of os centrale-scaphoid fusion among primates that seems to make any phylogenetic sense. For example, although there might be morphological reasons to suggest that *Hapalemur* and/or *Lepilemur* and/or *Daubentonia* might be closely related to extant indrids (for example, Schwartz and Tattersall, 1985), os centrale-scaphoid fusion does not even characterize all three indrids, which are equally specialized in vertical clinging and leaping (for example, Tattersall, 1982). Even the oft-cited potential synapomorphy of early fusion of the os centrale and scaphoid in African apes and humans (for example, see Andrews, 1992; Lewis, 1974; Tuttle, 1992; and references therein) is difficult to sustain given that, early in prenatal development in humans, the reduction in number of separate carpals occurs either by fusion or absence of the cartilaginous anlage of the os centrale whereas, in the other extant hominoids, it results from postnatal mineralization of soft connective tissue between os centrale and scaphoid. It would seem that, in the broader comparison among primates, fusion of the os centrale and scaphoid has occurred autapomorphically multiple times, and in that context, compared to all other primates, humans are the most autapomorphic.

Clearly, while there is a certain appeal to pursuing questions about carpal anatomy and function (for example, see contributions in Strasser and Dagosto, 1988, as well as Cartmill, and Milton, 1977; Hamrick, 1996; Sarmiento, 1985, 1988), one cannot lose sight of the fact that, until the basic comparative morphology is available and the taxic distribution of features better appreciated, any attempt to generalize about form and function with regard to this anatomical region will be sorely lopsided.

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REFERENCES

- Andrews P. (1992) Evolution and environment in the Hominoidea. *Nature*, vol. 360, pp. 641-646.
- Beard K.C. and Godinot M. (1988) Carpal anatomy of *Smilodectes gracilis* (Adapiformes, Notharctinae) and its significance for lemuriform phylogeny. *Journal of Human Evolution*, vol. 17, pp. 71-92.
- Beard K.C., Dagosto M., Gebo D.L., and Godinot M. (1988) Interrelationships among primate higher taxa. *Nature*, vol. 331, pp. 712-714.
- Cartmill M. (1975) Strepsirhine basicranial structures and the affinities of the Cheirogaleidae. In Szalay F.S. and Luckett W.P. eds., "Phylogeny of the Primates: an interdisciplinary approach", Plenum Press, New York, pp. 313-354.
- Cartmill M. and Milton J. (1977) The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. *American Journal of Physical Anthropology*, vol. 47, pp. 249-272.
- Cihák R. (1972) *Ontogenesis of the Skeleton and Intrinsic Muscle of the Human Hand and Foot*. Springer-Verlag, Berlin.
- Etter H.-U.F. (1978) Lorisiform hands and their phylogenetic implications: a preliminary report. In Chivers D.J. and Joysey K.A. eds., "Recent Advances in Primatology, Vol. 3: Evolution", Academic Press, London, pp. 161-170.
- Fleagle J.G. (1988) *Primate Adaptation and Evolution*. Academic Press, New York.
- Ford S.M. (1992) Systematics and body size: implications for feeding adaptations in New World monkeys. *American Journal of Physical Anthropology*, vol. 88, pp. 415-468.
- Hamrick M.W. (1996) Locomotor adaptations reflects in the wrist joints of early Tertiary primates (Adapiformes). *American Journal of Physical Anthropology*, vol. 47, pp. 585-604.
- Hamrick M.W. (1997) Functional osteology of the primate carpus with special reference to Strepsirhini. *American Journal of Physical Anthropology*, vol. 104, pp. 105-116.
- Hershkovitz P. (1977) *Living New World Monkeys (Platyrrhini)*, Vol. 1. University of Chicago, Chicago.
- Jouffroy F.K. (1975) Osteology and myology of the lemuriform postcranial skeleton. In Tattersall I. and Sussman R.W. eds., "Lemur Biology", Plenum Press, New York, pp.

149-192.

- Lewis O.J. (1969) The hominoid wrist joint. *American Journal of Physical Anthropology*, vol. 30, pp. 251-268.
- Lewis O.J. (1970) The development of the human wrist joint during the fetal period. *Anatomical Record*, vol. 166, pp. 499-516.
- Lewis O.J. (1974) The wrist articulations of the Anthroidea. In Jenkins F.A. Jr. ed., "Primate Locomotion", Academic Press, New York, pp. 143-169.
- Napier J.R. and Davis P.R. (1959) The fore-limb skeleton and associated remains of *Proconsul africanus*. *Fossil Mammals of Africa*, no. 16, British Museum (Natural History), London.
- O'Connor B.L. (1975) The functional morphology of the cercopithecoïd wrist and inferior radioulnar joints, and their bearing on some problems in the evolution of the Hominoidea. *American Journal of Physical Anthropology*, vol. 43, pp. 113-122.
- Sarmiento E. (1985) Functional Differences in the Skeleton of Wild and Captive Orang-utans and Their Adaptive Significance. Ph. D. Thesis, New York University, New York.
- Sarmiento E. (1988) Anatomy of the hominoid wrist joint: its evolutionary and functional implications. *International Journal of Primatology*, vol. 9, pp. 281-345.
- Schultz A.H. (1936) Characters common to higher primates and characters specific for man. *Quarterly Review of Biology*, vol. 11, pp. 259-283.
- Schwartz J.H. (1992) Issues in prosimian phylogeny and systematics. In Matano S., Tuttle R.H., Ishida H., and Goodman M. eds., "Topics in Primatology, Vol. 3: Evolutionary Biology, Reproductive Endocrinology, and Virology", University of Tokyo Press, Tokyo, pp. 23-36.
- Schwartz J.H. (1986) Primate systematics and a classification of the order. In Swindler D.R. and Erwin J. eds., "Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy", Alan R. Liss, New York, pp. 1-41.
- Schwartz J.H. and Tattersall I. (1985) Evolutionary relationships of the living lemurs and lorises and their potential affinities with the European Eocene Adapidae. *Anthropological Papers of the American Museum of Natural History*, vol. 60, pp. 1-100.
- Strasser E. and Dagosto M. eds. (1988) *The Primate Postcranial Skeleton: studies in adaptation and evolution*. Academic Press, New York.
- Sussman R.W. and Kinzey W.G. (1984) The ecological role of Callitrichidae: a review. *American Journal of Physical Anthropology*, vol. 64, pp. 419-449.
- Szalay F.S. and Katz C. (1973) Phylogeny of lemurs, galagos and lorises. *Folia Primatol.*, vol. 19, pp. 88-103.
- Tattersall I. (1982) *The Primates of Madagascar*. Columbia University Press, New York.
- Tuttle R.H. (1992) Hands from newt to Napier. In Matano S., Tuttle R.H., Ishida H., and Goodman M. eds., "Topics in Primatology, Vol. 3: Evolutionary Biology, Reproductive Endocrinology, and Virology", University of Tokyo Press, Tokyo, pp. 3-20.
- Yoder A.D. (1992) The applications and limitations of ontogenetic comparisons for

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