Frequency and timing of scaphoid-centrale fusion in hominoids

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Abstract

Fusion between the os centrale and the scaphoid has played a central role in many functional and phylogenetic interpretations of hominoid evolution. In particular, scaphoid-centrale fusion shared among African apes and humans has been interpreted as an adaptation in knuckle-walkers, an exaptation in hominins, and has been offered as evidence for a knuckle-walking origin of bipedalism. However, discrepancies in the literature concerning the taxa in which this scaphoid-centrale fusion occurs, as well as the timing and/or frequency of this fusion, have confounded the significance of this trait. This study provides an historical review of the literature on scaphoid-centrale fusion in primates and the first formal investigation into the timing and frequency of this character among primates, with a focus on extant hominoids. Results indicate that there is a significant difference in the timing and frequency of scaphoid-centrale fusion in African apes and humans compared to Asian apes, suggesting that prenatal or early postnatal fusion among hominines is a synapomorphy. Scaphoid-centrale fusion does not occur randomly within primates. Instead, only Homininae and some members of Lemuroidea show consistent and ontogenetically early fusion of these carpals. The consistent occurrence of this trait within only two primate clades and a clear heterochronic trend in timing and frequency of scaphoid-centrale fusion among hominines suggest that this character is primarily phylogenetically controlled. We could not falsify the hypothesis that scaphoid-centrale fusion in African apes is indeed related to midcarpal stability in knuckle-walking, but neither were we able to find direct biomechanical or kinematic evidence to support this hypothesis. A more definitive answer to the question of the functional significance of scaphoid-centrale fusion will have to await more detailed analyses of great ape wrist kinematics.
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Introduction

Fusion of the os centrale to the scaphoid is one of the most discussed traits of the hominoid carpus (e.g., Mivart, 1867, 1869; Virchow, 1929; Weinert, 1932; Schultz, 1936; Marzke, 1971; Jenkins and Fleagle, 1975; Lewis, 1974, 1989; Sarmiento, 1988, 1994; Begun, 1992, 2004; Gebo, 1996; Schwartz and Yamada, 1998; Richmond and Strait, 2000; Richmond et al., 2001). The fusion of these bones, a synapomorphy of African apes and humans to the exclusion of Asian apes and most other primates, has received close attention in

discussions of the origin of human bipedalism (Begun, 1992, 2004; Richmond et al., 2001; Orr, 2005). Although this trait has played a key role in many phylogenetic and functional hypotheses, it has yet to be the target of formal study. Little is known about the frequency and timing of scaphoid-centrale fusion or nonfusion in primates. What is known stems largely from studies undertaken during the late nineteenth century to the middle of the twentieth century. This study presents the first formal investigation into scaphoid-centrale fusion in primates, with a particular focus on hominoids.

Historical background

In most primates, including *Pongo* and *Hylobates*, the os centrale is an independent bone that is firmly bound to the scaphoid by strong ligaments (e.g., Lewis, 1989). It articulates

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mainly with the trapezoid distolaterally and the capitate distomedially, thus preventing the scaphoid from participating in the midcarpal joint. This arrangement wedges the os centrale between the trapezoid and capitate during extension. In contrast, in African apes and humans, the os centrale fuses to the distomedial aspect of the scaphoid early in development, allowing the scaphoid to articulate directly with the midcarpal joint (Schultz, 1936; O'Rahilly, 1954) (Fig. 1).

Many workers have interpreted scaphoid-centrale fusion as a functional adaptation to the increased shear stress on this joint during quadrupedal locomotion, particularly knuckle-walking (Marzke, 1971; Tuttle, 1975; Corruccini, 1978; Sarmiento, 1994; Gebo, 1996; Richmond et al., 2001; Begun, 2004). The presence of this trait in humans may be due simply to phylogenetic "lag" (Richmond et al., 2001) or as an exaptation to shear stress during power-grip positions (Marzke, 1971). Such functional hypotheses have recently led to the suggestion that scaphoid-centrale fusion, along with a suite of other synapomorphic forelimb traits, is evidence for a knuckle-walking common ancestor of the hominine clade (Richmond and Strait, 2000, 2001; Richmond et al., 2001; Begun, 2002, 2004).

However, neither the functional nor the phylogenetic significance of scaphoid-centrale fusion is as clear as the above synopsis suggests. Fusion has been noted to occur "rarely" in *Pongo* and *Hylobates* and, usually, only in older individuals (Leboucq, 1884; Mivart, 1867; Schultz, 1936; Schwartz and Yamada, 1998; Lewis, 1989). Conversely, Schultz (1936) is often cited as documenting "rare" occurrences of nonfusion in *Pan*, but the exact frequency of nonfusion in African apes is not known (see below). In *Homo*, nonfusion is rare and is usually associated with congenital pathology (Poznanski et al., 1970; Bergman et al., 1988).

Scaphoid-centrale fusion is said to occur consistently in the Malagasy strepsirrhines *Lepilemur*, *Hapalemur*, *Avahi*, and *Indri*, all of which are vertical clingers and leapers (Jouffroy, 1975; Schwartz, 1992; Schwartz and Yamada, 1988; but see Sarmiento, 1985). Fusion in these strepsirrhines is thought to be adaptive to having a large and divergent thumb (Begun, 2004) along with increased loading of the radial side during vertical climbing and quadrupedalism (Sarmiento, 1994). However, the subfossil lemur taxa *Babakotia* and *Palaeopropithecus* engaged in more suspensory behaviors and show varying frequencies of scaphoid-centrale fusion (Hamrick et al., 2000). Fusion among strepsirrhines appears highly variable and is not clearly correlated with phylogeny or functional requirements.

Fusion of the os centrale to the scaphoid has also been rarely noted in the literature in *Galago* and *Propithecus* (Yalden, 1972; Sarmiento, 1985), *Cebus* and *Macaca* (Sarmiento, 1985), and *Colobus* and *Cercopithecus* (Whitehead, 1993). In all of these species, the timing and/or frequency of os centrale fusion has not been investigated.

Most of the evidence for scaphoid-centrale fusion, or lack thereof, in hominoids comes from a handful of studies completed decades ago on extremely small sample sizes (Mivart, 1867; Weinert, 1932; Schultz, 1936). The most commonly cited reference is that of Schultz (1936) or later publications restating the same conclusions based on the same or larger sample sizes (e.g., Schultz, 1940, 1941, 1944, 1956, 1968). Although Schultz (1936) provided the most detailed description of this carpal trait in nonhuman primates, his conclusions stem
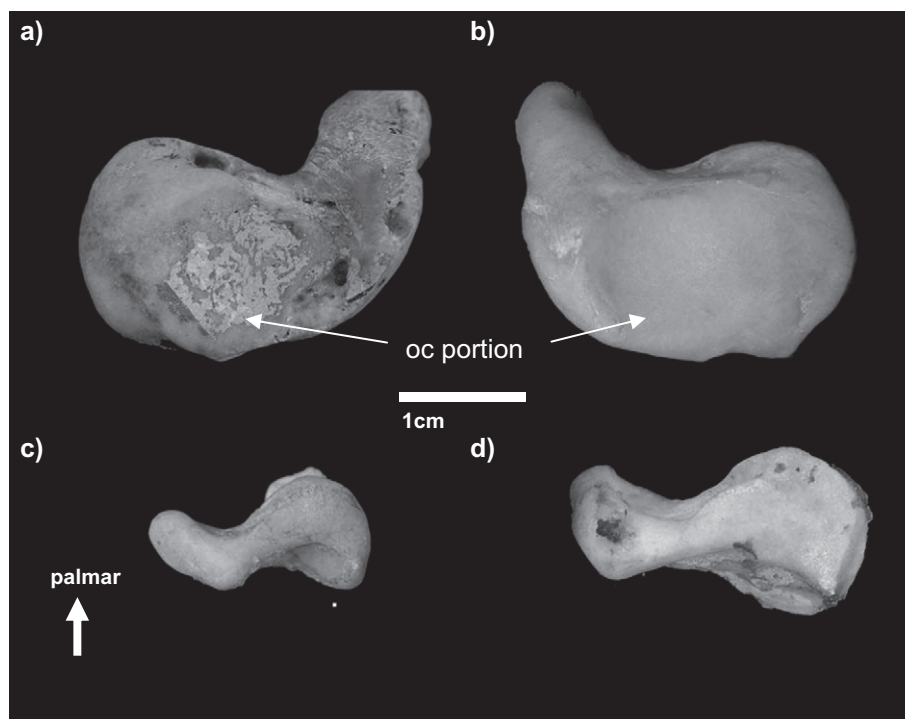

Fig. 1. Typical adult scaphoid morphology in nonhuman hominoids (distomedial view): (a) *Gorilla*, (b) *Pan*, (c) *Hylobates*, (d) *Pongo*. Note the fully fused os centrale (oc) portion in African apes and lack of os centrale in Asian ape specimens.

largely from literature review rather than primary investigation. Although some researchers, particularly in reference to *Pongo* and *Hylobates*, have included discussion of personal observations (Corruccini, 1978: 312; Richmond et al., 2001: 92; Begun, 2004: 18) or informal studies (Sarmiento, 1985; Schwartz and Yamada, 1998), the majority of researchers continue to rely on past studies, the sample sizes of which would be widely viewed as inadequate today.

The lack of formal investigation also generates controversy over why and how often this fusion occurs throughout the primate clade. Most researchers discuss this trait only in relation to its functional or phylogenetic significance among hominoids. However, others have concluded that scaphoid-centrale fusion simply occurs randomly among primates and, therefore, holds little functional or phylogenetic significance (Schwartz and Yamada, 1998; Hamrick et al., 2000). A thorough examination of the frequency and timing of scaphoid-centrale fusion throughout the primate clade will permit a more informed discussion of the significance of this trait.

Our analysis provides the first primary investigation of scaphoid-centrale fusion in nonhuman hominoids. Humans have not been included in this study because an extensive amount of literature is already available on the frequency and timing of scaphoid-centrale fusion in humans (see below). All nonhuman primates for which scaphoid-centrale fusion has been reported in the literature, no matter how rare, are included in this analysis. Since smaller sample sizes prohibit a more in-depth discussion of some taxa (primarily strepsirrhines), a thorough discussion of the frequency and timing of scaphoid-centrale fusion or nonfusion in hominoids is the focus of this paper. We begin with a more in-depth literature review—focusing on Schultz's (1936) study—and a discussion of what is currently known about this character, followed by our investigation into frequency and timing of this character state.

What is known about scaphoid-centrale fusion

Humans

The frequency and timing of scaphoid-centrale fusion in humans has been well documented for over a century. Leboucq (1884) was one of the first researchers to recognize the early presence of an os centrale as part of the scaphoid in embryonic tissue. All carpal mesenchymal and cartilaginous condensations, including that for a separate os centrale, appear around the sixth postovulatory week (O'Rahilly, 1949; Boyes, 1970; O'Rahilly and Gardner, 1975; Scheuer and Black, 2000) (Fig. 2a). The cartilaginous os centrale is incorporated into the scaphoid during the third month of prenatal life in humans (O'Rahilly, 1954; Čihák, 1972) (Fig. 2b). At birth, the human carpus is entirely cartilaginous (Waugh and Sullivan, 1950), with the adult carpal pattern already set (Scheuer and Black, 2000). Therefore, well-before birth, the cartilaginous anlage, essentially adult in form, is that of a scaphoid with a fully fused centrale.

Although developmental variations in the human carpus are relatively rare, one of the most common variations is that of a separate os centrale (Waugh and Sullivan, 1950; but see Louis et al., 1976). Rare occurrences of nonfusion in humans are often associated with either congenital or acute pathology. Holt-Oram and Hand-Foot-Uterus syndromes are associated with the presence of a separate centrale and an abnormally shaped scaphoid (the latter often fused to the trapezium) in children that is retained in adults (Poznanski et al., 1970; Poznanski and Holt, 1971). A separate centrale has also been noted as part of Larsen and Oto-Palato-Digital syndromes (Gerscovich and Greenspan, 1990).

Accessory carpal bones, including the os centrale, are found in approximately 1.6% of the human population (Thijn, 1986). Pfitzner (1895) was one of the first to describe the frequency of a separate os centrale in humans, noting its occurrence in only seven out of 1450 adult dissections (0.48%). Virchow (1929) noted the presence of an independent os centrale in two of 64 individuals (3.13%), plus one individual with partial fusion. A separate os centrale can occur in three ways: (1) as a well-developed, independent bone; (2) as an incompletely separated bony fragment of the scaphoid (or, more rarely, the capitate or trapezoid); or (3) present radiographically as an empty space between the capitate and trapezoid (Wood-Jones, 1942, and references therein). Gerscovich and Greenspan (1990) stated that the os centrale may be unilateral or bilateral, and may exist as an isolated anomaly or in association with pathological syndromes.
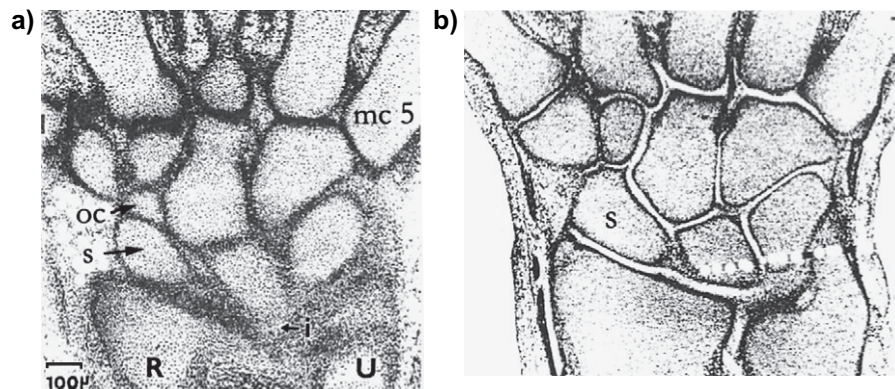

Fig. 2. Embryonic human carpus at (a) 16 mm crown-rump (C-R) length with distinct os centrale (oc) visible (adapted from Čihák, 1972) and at (b) 42 mm C-R length with os centrale fully incorporated into scaphoid (s) (adapted from Garn et al., 1974).

African apes

Weinert (1932) is an oft-cited reference for the synapomorphic fusion of the centrale to the scaphoid in African apes and humans. Although sample sizes are unclear, Weinert (1932) stated that the carpal pattern in *Gorilla* and *Pan* (i.e., eight carpals, fused os centrale) is exactly like that of humans and that he had never observed any variation from this pattern.

Schultz's (1936) discussion of scaphoid-centrale fusion in *Pan* is the most thorough for all nonhuman hominoids, but his discussion of *Gorilla* is extremely limited. Schultz (1936: 272) noted the presence of a small, separate centrale ossification center in two roughly three-year-old (all M1s erupted) *Pan* specimens and that a separate os centrale was not present in "five additional infantile and seven juvenile chimpanzees." In three late-term fetuses, two showed a completely separate cartilaginous os centrale, while the third specimen displayed partial fusion of the centrale portion to the scaphoid. Thus, out of a total sample of 17, three individuals displayed a separate or partially fused os centrale, demonstrating that fusion can occur anywhere between late fetal stages to upwards of three years of age. Schultz provided additional support for his results, citing Hartmann (1883: 127), who found a distinguishable, partially fused os centrale in a "very young" *Pan*.

Schultz (1936) is often cited as documenting "rare" occurrences of nonfusion in *Pan*. However, as just described, Schultz referred only to a separate ossification center for the os centrale during early developmental stages and at no point in any publication did Schultz mention nonfusion in *Pan* later in ontogeny.

Schultz's (1936) discussion of scaphoid-centrale fusion in *Gorilla* consisted solely of a brief reference to Noback (1930). Noback (1930: 129) noted only a separate os centrale in radiographs of a 42-month-old individual. From this analysis, Schultz (1936: 273) concluded that "it appears probable that in chimpanzee (and gorilla?) this fusion between *centrale* and *naviculare* [scaphoid] does not begin until late in fetal life…. The *average* age of complete fusion lies in the infantile period" (emphasis original).

Asian apes

Data on the frequency and timing of scaphoid-centrale fusion in *Hylobates* and *Pongo* comes largely from isolated, brief descriptions of fusion in the literature from the late nineteenth and early twentieth centuries. Schultz (1936: 271) concluded that the os centrale is either fused or lost in *Hylobates* in a "considerable number of cases" based on a literature review and direct examination. Schultz observed six *Hylobates* specimens (two of which were juveniles) and noted in one older siamang specimen complete fusion in one hand and nearly complete fusion in the other. In his review of the literature, Schultz (1936: 271) stated that Lucae (1865) had figured a *Hylobates* without an os centrale. This figure, however, clearly includes an os centrale and it is questionable whether the centrale portion is intentionally drawn as fused to the

scaphoid, or if the drawing is simply incomplete (Fig. 3). Lucae provided little description of the carpal morphology to supplement his figures and sample sizes are not known.

Schultz (1936) cited Giebel (1879) as stating that the os centrale is fused in all hominoids except *Pongo*, which Schultz interpreted as suggesting that the gibbon did not have a separate os centrale. Although Giebel appropriately described hylobatid carpal morphology, he failed to directly mention the presence or absence of an os centrale in this taxon or how many, if any, specimens were examined. Therefore, it is doubtful that Giebel deliberately suggested that *Hylobates* had an absent or fused os centrale.

Leboucq (1884) provided a thorough literature review on scaphoid-centrale fusion in primates, as well as a discussion from direct observation. Leboucq (1884: 68) stated that he had examined two *Hylobates leuciscus* specimens with similar morphology to that seen in Lucae's (1865) "*Hylobates*" figure (Fig. 3). However, Leboucq's statement must be considered with caution for several reasons, the first of which is the ambiguous morphology depicted in Lucae, as described above. The "hooked-shaped extension" (Leboucq, 1884: 68) on the dorsal surface of the scaphoid is characteristic of a fused or firmly bound but separate os centrale in *Hylobates* and *Pongo* (Richmond et al., 2001; Begun, 2004; pers. observation). Leboucq distinguished the morphology of these particular *Hylobates* specimens as being different from the carpal morphology of other, presumably "unfused" *Hylobates* specimens and the fused scaphoid-centrale of African apes and humans. However, the figures of these specimens present ambiguous morphology and mislabeled os centrale portions (Fig. 4).

Leboucq (1884) cited several other authors who reported the presence of an independent os centrale in *Hylobates*. Vrolik (1841) observed a separate os centrale in an unknown number of *Hylobates* specimens, and Hartmann (1876; cited in Leboucq, 1884) recorded this condition in a young adult specimen of
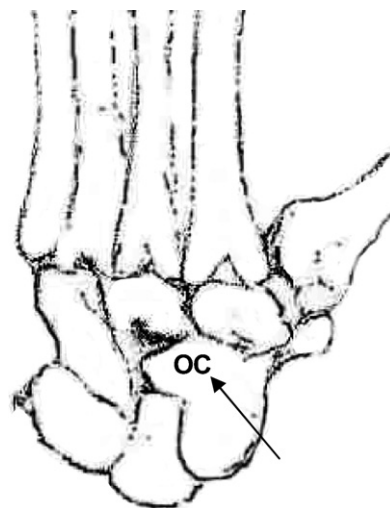

Fig. 3. Carpal drawing of "*Hylobates leuciscus*" adapted from Lucae (1865: 332). Absence of a line between os centrale (oc) and scaphoid (arrow) has been interpreted as fusion between these two bones.
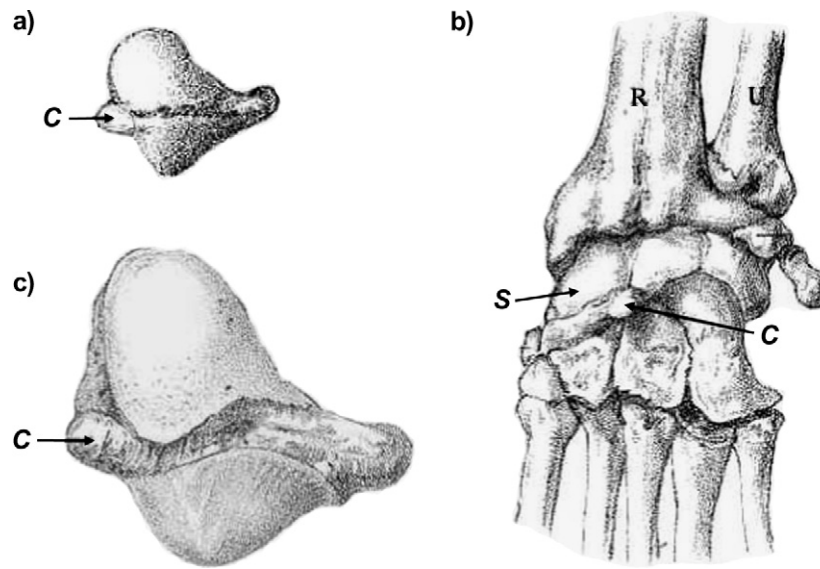
Fig. 4. Figures adapted from Leboucq (1884): (a) a fused scaphoid-centrale of "*Hylobates leuciscus*" but os centrale portion (*c*) is labeled incorrectly; (b) "*Hylobates leuciscus*" carpus (dorsal view) with centrale portion labeled closer to its true anatomical position but fusion is ambiguous; (c) fused scaphoid-centrale of *Pongo* with centrale portion labeled incorrectly.

H. agilis. Gruber (1866) observed nine carpals bones in two *Hylobates lar* and two *Pongo* ("*Pithecus satyrus*"[1]) specimens, as well as several other nonhominoid primates. Rosenberg (1866; cited in Leboucq, 1884) observed a "reduced centrale" in *Hylobates*. However, Rosenberg stated that it is unclear if the "reduced" centrale of *Hylobates* described by Owen had been observed in other specimens or if this perception was simply perpetuated by discussions in the literature (Leboucq, 1884). Finally, Boltze (1926) discovered a fused scaphoid-centrale in one of six adult specimens of *H. leuciscus*, although Schultz (1936) incorrectly reported that the occurrence was one in three specimens. Boltze described the fusion as similar to that observed by Leboucq (1884), but he noted that the os centrale is generally a constant component of the carpus in both *Hylobates* and *Pongo* (Boltze, 1926: 384).

Vrolik (1841) was the first to point out a distinct ninth bone in *Pongo* that differs from the carpal pattern of *Pan*. Mivart (1867, 1869: 188−189) emphasized the independent os centrale ("*os intermedium*") in *Pongo* and made no mention of occasional fusion of these bones in this taxon. It is clear that Mivart's descriptions were based on direct observations, but sample sizes are unknown.

It does not appear that Schultz (1936) observed any *Pongo* specimens directly; he cited only Leboucq (1884) as observing complete scaphoid-centrale fusion in this genus. Leboucq (1884: 68) described anomalous fusion in only one adult *Pongo* specimen (out of an unknown sample size) and, citing Vrolik (1841), considered the os centrale to be a free bone throughout all of life in the orangutan. Leboucq figured a fused

scaphoid-centrale in *Pongo*, but, again, the centrale portion is labeled incorrectly (Fig. 4c).

From the literature described above, and a few direct observations, Schultz (1936: 273) concluded that (1) scaphoid-centrale fusion in African apes probably does not begin until late in fetal life and completes sometime during the infantile period; (2) scaphoid-centrale fusion in *Pongo*, and particularly *Hylobates*, can occur in middle to old age; (3) he had never found or read of reports of fusion in "lower" catarrhines; and (4) all apes share a tendency to fuse their scaphoid and os centrale but differ remarkably in their frequency and timing. Schultz presented his conclusions as tentative. However, over the years these conclusions have been portrayed in the literature as more robust than Schultz intended.

Schultz (1936) provided the most thorough discussion of scaphoid-centrale fusion in nonhuman hominoids and his work has been extremely influential in our understanding of this character. However, the early literature on which Schultz (1936) based many of his conclusions clearly demonstrates confusion over anatomy, repetitious citing of the same references or analysis of identical specimens, and limited, misreported, or unknown sample sizes (Table 1). All of these factors confound frequencies of fusion or nonfusion, particularly in Asian apes.

Schultz discussed scaphoid-centrale morphology in several later publications based on direct observation of much larger samples. Schultz (1944: 83) found complete scaphoid-centrale fusion in four of 26 older *Hylobates lar* individuals (three times bilaterally, one time unilaterally). Schultz (1941: 97) stated that, out of at least 66 complete *Pongo* skeletons, the os centrale had fused to the scaphoid in three older individuals (once bilaterally and twice unilaterally). One of these specimens was the same individual described by Leboucq (1884). Therefore, to date, frequency of scaphoid-centrale fusion occurs, at most, in 4.5% of *Pongo* and 15% of *Hylobates*.

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[1] The genus "*Pithecus*" was originally used by Cuvier (1798, cited in Kretzoi, 2002) to refer to *Pongo*.

Lewis (1989) echoed Schultz's conclusion of rare fusion in older Asian apes. Lewis cited Schultz (1936) and, although Lewis (1989) provided the most extensive discussion of primate carpal morphology to date, he did not disclose how many specimens he examined directly or if his discussion of scaphoid-centrale fusion stemmed solely from Schultz's work. "Rare" fusion in *Pongo* and *Hylobates* has been reaffirmed by Corruccini (1978: 312), who stated: "the fusion … is said to occur only in very old or arthritic Asian apes (I have not seen an instance of fusion in 70 *Pongo* plus *Hylobates* or in 140 cercopithecoids)." Richmond et al. (2001: 92) and Begun (2004: 18) confirmed these conclusions but, again, no formal analysis of frequency, timing, or morphology was completed.

Strepsirrhines

The occurrence of scaphoid-centrale fusion in strepsirrhines is far less well-studied than in hominoids. Mivart (1867) was the first to recognize that some indrids share a fused scaphoid-centrale with hominines, noting the loss of an independent os centrale in *Indri* and *Avahi* ("*Microrhynchus*"[2]) through direct observation. Giebel (1879) also figured the carpus of "*Lichanotus indri*" and *Lepilemur mustelinus* (the latter from Mivart, 1873), both of which lacked an independent os centrale.

The most often cited reference regarding strepsirrhine scaphoid-centrale fusion is Jouffroy (1975), who provided radiographic images of the carpus of several Lemuriformes. However, her discussion of scaphoid-centrale fusion did not extend beyond "the os centrale, free in *Lemur*, *Microcebus*, *Cheirogaleus*, *Propithecus* and *Daubentonia*, is fused with the scaphoid in adults of *Hapalemur*, *Lepilemur*, *Indri*, and *Avahi*" (Jouffroy, 1975: 180). Sample sizes are unknown. Schwartz (1992) also found scaphoid-centrale fusion in *Hapalemur* ($n = 1$). Sarmiento (1985) provided data on scaphoid-centrale fusion in a variety of primates (Table 2). Of particular interest is the frequency of fusion in Indridae and *Lepilemur*. Sarmiento consistently observed fusion in *Indri* and *Avahi* but also in *Propithecus* (contra Jouffroy, 1975). He also noted variation in the occurrence of fusion in *Lepilemur* (again, contra Jouffroy, 1975).

Hamrick et al. (2000) reported on scaphoid-centrale fusion in Malagasy subfossil lemurs. In *Babakotia*, a subfossil lemur displaying a combination of features indicating suspensory positional behavior with vertical clinging and climbing, all five known scaphoids have a fused os centrale. Yet, in *Palaeopropithecus*, a large-bodied, slow-climbing, suspensory subfossil lemur, fusion is reported in seven of nine scaphoids (but see below). Hamrick et al. (2000) stressed not only the randomness of scaphoid-centrale fusion within the Lemuriformes, but also within the genus *Palaeopropithecus*. Therefore, they concluded that, at least among the Malagasy strepsirrhines,

scaphoid-centrale fusion has little functional or phylogenetic significance.

Among strepsirrhines, fusion of the os centrale to the scaphoid is reported to occur consistently in two of three indrid genera, one of four lemurid genera, one of two megaladapid genera, and variably within the genus *Palaeopropithecus*. This is in spite of the fact that the majority of genera within these subfamilies display similar positional behaviors (vertical clinging and leaping) and functional requirements (Tattersall, 1982). Therefore, scaphoid-centrale fusion is not related in an obvious way to a functional constraint, as in the Hominoidea, according to some, nor can it be easily explained by phylogeny.

Schwartz and Yamada (1998) offered one of the only analyses of carpal morphology in a variety of prosimians and anthropoids that included direct examination of scaphoid-centrale fusion. They concluded that the reported distribution of scaphoid-centrale fusion within primates is completely random (Schwartz and Yamada, 1998: 62). The authors figured a young adult *Pongo pygmaeus* with a fused scaphoid-centrale ($n = 1$). However, *Hapalemur* ($n = 1$) is discussed as having scaphoid-centrale fusion, but the figure shows nonfusion (Schwartz and Yamada, 1998) (Fig. 5).

Review of the published literature reveals two main viewpoints. First, some researchers recognize that consistent scaphoid-centrale fusion is generally concentrated within two primate clades—Hominoidea and Lemuroidea[3]—and is explained by phylogenetic and/or functional hypotheses within each clade (Richmond et al., 2001; Begun, 2004). Scaphoid-centrale fusion in both clades is considered to be convergence. The second view is that of those who recognize both consistent and occasional fusion in a variety of primates, suggesting that scaphoid-centrale fusion is random and not correlated with positional behavior (vertical clinging and leaping, suspension, quadrupedalism, and bipedalism), body size (*Lepilemur* to *Gorilla*), or evolutionary relationships (Schwartz and Yamada, 1998; Hamrick et al., 2000).

Our investigation aims to document the timing and frequency of scaphoid-centrale fusion in all nonhuman primate taxa for which this carpal fusion has been noted. An accurate account of the occurrence of this character will provide the foundation needed to understand its functional, phylogenetic, and/or evolutionary significance.

Materials and methods

Both the left and right wrists (when available) were examined to determine if the scaphoid and os centrale were fused or separate. All observations were made by one author (TLK). The taxa included are listed in Table 3. Both juvenile and adult specimens were examined; sample sizes are provided in Tables 3–8. Subadult stages of osteological specimens include the earliest available stage of development at which a sufficient

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[2] The genus "*Microrhynchus*" was originally used by Jourdan (1834, cited in Groves, 2001) to refer to *Avahi*.

[3] Following Groves (2001), the Lemuroidea comprises Lemuridae, Indridae, and Megaladapidae, as well as the subfossil taxa phylogenetically linked to these families (Godfrey and Jungers, 2002).

Table 1
Summary of literature review of scaphoid-centrale fusion in hominoids with sample sizes

Taxon	Author	Sample size	Character state	Total *n*
Pan	Schultz (1936)	*n* = 17 (all juv.)	12 fused	19 juv.
			1 incomplete	4 unfused
			4 unfused	2 incomplete
	→Hartmann (1883)	*n* = min 1 (juv.)	1 incomplete	13 fused
	Lucae (1865)	*n* = min. 1	1 fused	2 adults, fused
	Leboucq (1884)	*n* = min 2 (1 juv.)	2 fused	
	Weinert (1932)	*n* = ?	fused	
Gorilla	Schultz (1936)	0	—	4 adults (?)
	└→Noback (1930)	1 (juv.)	1 unfused	1 unfused
	Lucae (1865)	*n* = min. 1	1 fused	3 fused
	Owen (1866)	*n* = min. 1	1 fused	
	Leboucq (1884)	*n* = min. 1	1 fused	
	Weinert (1932)	*n* = ?	fused	
Pongo	Schultz (1936)	0	—	73 adults (?)
	└→Leboucq (1884)	*n* = min. 1	1 fused	3 fused
	→Vrolik (1841)	*n* = min. 1	1 unfused	70 unfused
	Giebel (1879)	0	—	
	└→Lucae (1865)	*n* = min.2	2 unfused	
	Gruber (1866)	*n* = 2	2 unfused	
	Weinart (1932)	*n* = ?	1 unfused	
	Schultz (1941)	*n* = > 66	3 fused (but one specimen the same as Leboucq, 1884)	
Hylobates	Schultz (1936)	*n* = 6 (2 juv.)	1 fused, 5 unfused	44 adults
	Lucae (1865)	*n* = min. 1	1 fused (?)	11 fused (5 of
	Giebel (1879)	*n* = min 2	2 fused (?)	which may be
	Boltze (1926)	*n* = 6	1 fused, 5 unfused	questionable)
	Leboucq (1884)	*n* = min. 2	2 fused (?)	33 unfused
	Hartmann (1876)	*n* = min. 1	1 unfused	
	Gruber (1866)	*n* = min. 2	2 unfused	2 juv., unfused
	Vrolik (1841)	*n* = ?	unfused	
	Rosenberg (1866)	0		
	Schultz (1944)	*n* = 26	4 fused, 22 unfused	

Abbreviations: "juv.", juvenile; "?", questionable or unknown data; "min.", minimum sample size.

degree of carpal ossification had occurred to (1) identify the scaphoid and (2) identify fusion versus nonfusion with the os centrale. In a small number of specimens, direct dissection or well-preserved earlier stages of development permitted identification of separate versus fused scaphoid-centrale from the cartilaginous anlage. There is much variation in the timing of carpal ossification during ontogeny among primates. For example, *Macaca* is extremely precocious in its carpal development, with most carpal ossification centers appearing during fetal stages (e.g., Newell-Morris et al., 1980; Sirianni and Swindler, 1985), while hominoids show ossification centers for the majority of their carpals between birth and roughly three years of age (Noback, 1930; Marzke and Marzke, 1987; Winkler, 1996). Therefore, an absolute minimum age

Table 2
Sampled ratio of primate genera showing fusion of the os centrale (adapted from Sarmiento, 1985: 388)

Taxon	*n*	Fused	Unfused
Indri	3	3	—
Propithecus	8	8	—
Avahi	2	2	—
Lepilemur	4	2	2
Cebus	15	2	13
Macaca	12	1	11

for the earliest stage of development cannot be given and early ontogenetic stages are subsequently more difficult to come by in primates with precocious growth (e.g., *Macaca*) than those with slower growth (i.e., hominoids).

Given the heterochronic variability in primate development, all taxa were broken down into four age categories based on dental eruption. These categories are:

(a) **Infant**. Ranging from neonate to a fully erupted dP4.
(b) **Juvenile 1**. A fully erupted M1 (ranging from a freshly erupted M1, meaning fully erupted but with no dental attrition, to later stage of M1, with M2 almost, but not fully, erupted).
(c) **Juvenile 2**. A fully erupted M2 (ranging from a freshly erupted M2 to later stage of M2, with M3 almost, but not fully, erupted).
(d) **Adult**. A fully erupted M3 (ranging from a freshly erupted M3, often associated with incomplete epiphyseal union in the postcrania (late juvenile), to older adult, most often defined by significant dental attrition of all molars and/or signs of senescence (e.g., arthritic lipping or osteoporosis).

The specimens examined are housed at the following institutions: The Powell-Cotton Museum (PCM), Musée Royal de l'Afrique Centrale (MRAC), The National Museum of Natural
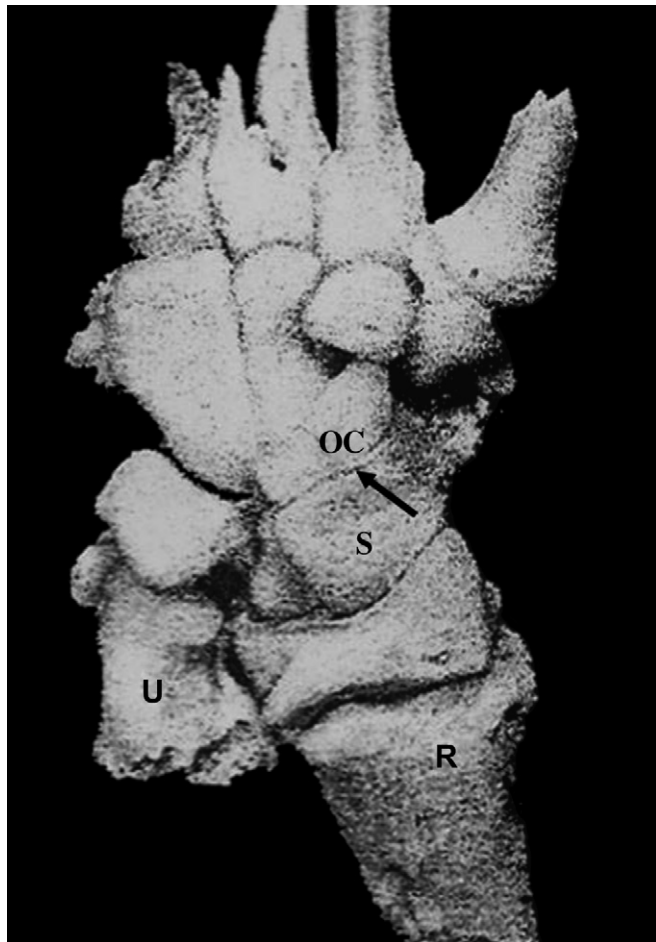
Fig. 5. Adapted from Schwartz and Yamada's (1998: 52) *Hapalemur* specimen with what appears to be a separate os centrale and scaphoid (arrow).

History (NMNH), The Cleveland Museum of Natural History (CMNH), The Duke University Primate Center (DUPC) and Division of Fossil Primates (DFP), State University of New York at Buffalo (SUNY), The Royal Ontario Museum (ROM), The University of Toronto (UT), and University of Toronto, Scarborough Campus (UTSC). Specific specimen numbers are prefixed by the above acronyms.

The misleading perception that carpals are merely indistinguishable nodules of bone until late juvenile stages stems largely from the extensive and dominating literature on hand/wrist radiographic age-determination techniques for humans (e.g., Greulich and Pyle, 1959; Tanner et al., 1983). However, this study and one in preparation demonstrate that the scaphoid and os centrale can be identified in well-preserved osteological specimens with dP3 as the last erupted tooth. The ossification center for the scaphoid can be identified in isolation by the early stages of the Juvenile 1 period in hominines and, with the addition of the os centrale, in Asian apes.

By the late stage of the Juvenile 2 period, the scaphoid and os centrale appear fully formed and adult in all hominoids. Thus, individuals with a fully erupted M3, but lacking complete epiphyseal fusion, are considered "adult."

Table 3
Extant and fossil taxa examined

Taxon	n					
	Total	Adults	Subadults	Male	Female	Sex?
Hominoidea						
*Gorilla gorilla**	96	65	31	46	46	4
*Homo**	41	28	13	19	22	0
*Hylobates**	48	42	6	24	20	4
*Pan paniscus**	41	20	21	18	16	7
*Pan troglodytes**	106	54	52	46	42	18
*Pongo pygmaeus**	59	40	19	22	32	5
Cercopithecidae						
*Cercopithecus**	20	5	15	8	4	8
*Colobus**	20	18	2	9	10	1
Erythrocebus	6	3	3	3	3	—
*Macaca**	82	32	50	34	42	6
Mandrillus	3	2	1	—	3	—
Papio	32	17	15	8	14	10
Colobinae						
Nasalis	4	4	—	3	1	—
Pygathrix	4	1	3	1	3	—
Platyrrhini						
Ateles	4	1	3	3	—	1
*Cebus**	3	3	—	—	3	—
Indridae						
*Avahi laniger**	3	2	1	—	—	3
*Indri indri**	2	2	—	1	—	1
Propithecus	3	3	—	—	2	1
Lemuridae						
*Hapalemur griseus**	8	4	4	—	4	4
Lemur catta	18	18	—	5	4	6
Varecia variegata	3	3	—	1	—	2
Lorisiformes						
*Galago**	51	50	1	29	13	5
Nycticebus	3	2	1	2	1	—
Megaladapidae						
*Lepilemur**	1	1	—	1	—	—
Megaladapis madagascariensis	1	?	?	?	?	?
Palaeopropithecidae						
*Babakotia radofilai**	3	2?	1	?	?	?
*Palaeopropithecus ingens**	10	?	?	?	?	?

*Primates reported as having a fused scaphoid-centrale either consistently or rarely.

At each period, some individuals display delayed development, which may reflect sexual dimorphism. In *Pan*, females are precocious in their development compared to males, based on radiographic studies of the carpus (Nissen and Riesen, 1949; Marzke and Marzke, 1987), while Winkler (1996) remarked on the more advanced development of males compared to females in *Pongo*. In this study it was difficult to attribute the delayed development of some individuals to sexual dimorphism, as sample sizes were limited and many juvenile specimens are of unknown sex. Therefore, the focus is on the average developmental timing and frequency of both sexes in each taxon.

Table 4
Gorilla sample

Age category	Sex	n	Total n	Scaphoid-centrale state		
				Fused	Incomplete	Unfused
Infant	M	2		2*	—	—
	F	—	3	—	—	—
	?	1		1*	—	—
Juvenile 1 (M1)	M	3		1	2	—
	F	12	16	6	3	3[†]
	?	1		1	—	—
Juvenile 2 (M2)	M	6		5	1	—
	F	6	12	2	4	—
	?	—		—	—	—
Adult	M	35		34	—	1
	F	28	65	28	—	—
	?	2		2	—	—
Total sample (%)			96	82 (85.42%)	10 (10.42%)	4 (4.17%)
Total adults (%)			65	64 (96.46%)	0	1 (1.54%)

Notes: Both left and right carpals were observed in 75% of specimens. *Specimens display fused cartilaginous anlages and/or lack a separate ossification center for the os centrale. [†] One specimen (PCM M868) displayed a separate os centrale center on the left, but fused on the right side.

Hominoids

Gorilla

As all hominoids are relatively delayed in their carpal (and general skeletal) development, the earliest stages of development are largely cartilaginous and best observed via direct dissection. Dissection of a neonatal male *Gorilla* revealed a fully cartilaginous carpus, including a scaphoid anlage with a completely fused centrale portion (see Fig. 7a for similar morphology in *Pan*). The scaphoid anlage essentially looks like

Table 5
Pan troglodytes sample

Age category	Sex	n	Total n	Scaphoid-centrale state		
				Fused	Incomplete	Unfused
Infant	M	2		2*	—	—
	F	—	4	—	—	—
	?	2		1*	—	1
Juvenile 1 (M1)	M	11		11	—	—
	F	9	24	9	—	—
	?	4		4	—	—
Juvenile 2 (M2)	M	13		12	1	—
	F	11	28	9	2	—
	?	4		4	—	—
Adult	M	20		20	—	—
	F	24	52	24	—	—
	?	8		8	—	—
Total sample (%)			108	104 (96.30%)	3 (2.78%)	1 (0.93%)
Total adults (%)			52	52 (100.00%)	0	0

Notes: Both left and right carpals were observed in 62% of specimens. *Specimens display a fused cartilaginous anlage.

Table 6
Pan paniscus and total *Pan* sample

Age category	Sex	n	Total n	Scaphoid-centrale state		
				Fused	Incomplete	Unfused
Infant	M	2		2	—	—
	F	—	4	—	—	—
	?	2		1	—	1
Juvenile 1 (M1)	M	3		2	1	—
	F	1	7	1	—	—
	?	3		3	—	—
Juvenile 2 (M2)	M	4		4	—	—
	F	5	11	3	2	—
	?	2		1	1	—
Adult	M	9		9	—	—
	F	10	20	10	—	—
	?	1		—	1	—
Total sample (%)			42	36 (85.71%)	5 (11.90%)	1 (2.38%)
Total adults (%)			20	19 (95.00%)	1 (5.00%)	0
Total *Pan* sample (%)			150	140 (93.33%)	8 (5.33%)	2 (1.33%)
Total *Pan* adults (%)			72	71 (98.61%)	1 (1.39%)	0

Notes: Both left and right carpals were observed in 61% of specimens.

a simplified, smaller version of the adult form. This specimen was no more than two days old at death and had never loaded its carpus. Therefore, the carpal pattern of scaphoid-centrale fusion is set prenatally and prior to loading, regardless of the possible appearance of a separate centrale ossification center later in ontogeny. Of the 14 infant osteological specimens examined, only two preserved a dried but recognizable scaphoid cartilaginous anlage. In both cases, the anlage was

Table 7
Pongo sample

Age category	Sex	n*	Total n*	Scaphoid-centrale state		
				Fused	Incomplete	Unfused
Infant	M	1		—	—	1
	F	1	2	—	—	1
	?	—		—	—	—
Juvenile 1 (M1)	M	1		—	—	1
	F	4	7	—	—	4
	?	2		—	—	2
Juvenile 2 (M2)	M	5		—	—	5
	F	4	10	—	—	4
	?	1		—	—	1
Adult	M	16 (4)		—	—	16 (4)
	F	24 (3)	40 (7)	2 (1)[†]	2	20 (2)
	?	—		—	—	—
Total sample (%)			59	2 (3.39%)	2 (3.39%)	55 (0.93%)
Total adults (%)			40	2 (5.00%)	2 (5.00%)	36 (90.00%)

Notes: Both left and right carpals were observed in 61% of specimens. *Number of older individuals is in parentheses. [†] Of the four specimens showing partial or complete fusion, only one individual is thought to be from an older individual and is also extremely pathological. The remaining specimens appeared to be young adults (minimal dental wear, $n = 2$) or late juvenile (incomplete epiphyseal fusion, $n = 1$).

Table 8
Hylobates sample

Age category	Sex	n*	Total n*	Scaphoid-centrale state		
				Fused	Incomplete	Unfused
Infant	M	—		—	—	—
	F	—0	—	—	—	
	?	—		—	—	—
Juvenile 1 (M1)	M	1		—	—	1
	F	1	3	—	—	1
	?	1		—	—	1
Juvenile 2 (M2)	M	3		—	—	3
	F	1	4	—	—	1
	?	—		—	—	—
Adult	M	20 (2)		—	—	20 (2)
	F	19 (6)	43 (8)	—	—	19 (6)
	?	4		—	—	4
Total sample (%)			50	0	0	50 (100.00%)
Total adults (%)			43	0	0	43 (100.00%)

Notes: Both left and right carpals were observed in 50% of specimens. *Number of older individuals is in parentheses.

characterized by a dorsal extension, indicating that the centrale portion was fully incorporated into the cartilaginous template, similar to that seen in the neonate.

Of the 20 Juvenile 1 specimens examined, three were too young to display identifiable ossification centers of the scaphoid and/or os centrale, eight (40.0%) displayed a single, large ossification center for the scaphoid with a fused centrale portion already incorporated, three (17.7%) displayed a separate ossification center for the os centrale, and six (35.3%) displayed evidence of a separate os centrale ossification center but with varying degrees of fusion to the scaphoid body (Fig. 6a).

Twelve specimens were observed for the Juvenile 2 period, half of which displayed incomplete fusion between the scaphoid and os centrale. Incomplete fusion was usually represented by a cleft along the proximodorsal border of the scaphoid (Fig. 6b). As none of the 65 adult gorillas examined displayed partial fusion, and only one (1.5%) displayed a completely separate os centrale (Fig. 6c), we assume that this cleft represents a final stage of ossification and, had these individuals lived to adulthood, further ossification would have yielded a normal and fully fused scaphoid form.

Throughout the entire *Gorilla* sample, females more commonly displayed a partially fused or unfused scaphoid-centrale (10 of $n = 46$ females, or 21.7%, versus 4 of $n = 46$ males, or 8.7%). This irregular morphology does not appear to be correlated with taxonomy, as partially fused or unfused scaphoids were seen in all three subspecies. Furthermore, as subspecies designations can be suspect in museum collections, this possible correlation was not investigated here.

Pan

Of the 18 specimens of *Pan* (*P. troglodytes*, $n = 13$; *P. paniscus*, $n = 5$) observed for the Infant period, nine individuals were too young for the scaphoid ossification center to be

identified osteologically. Of the remaining specimens, six displayed a cartilaginous anlage with a fused os centrale portion. One specimen displayed a fused yet distinct ossification center for the os centrale, while two individuals showed ambiguous morphology. During the Infant period, scaphoid-centrale fusion occurred in three of four (75%) specimens of *P. troglodytes* (remaining individual was unfused) and three of four (75%) specimens of *P. paniscus* (remaining individual was ambiguous). As seen in *Gorilla*, dissection of an infant (dP3 partially erupted) *P. troglodytes* revealed a fully cartilaginous carpus, including a scaphoid anlage with a completely fused centrale portion (Fig. 7a).

Thirty-seven individuals were observed in the Juvenile 1 stage (*P. troglodytes*, $n = 30$; *P. paniscus*, $n = 7$), of which six were too young to have developed a recognizable scaphoid ossification center. Four (66.67%) of these individuals were male, suggesting that males may be developmentally delayed relative to females. Of the remaining sample, two individuals displayed ambiguous morphology due to limited ossification of the scaphoid body. Of the 29 individuals with a fused scaphoid-centrale, one individual displayed a distinct ossification center along the dorsal edge of the scaphoid body that was in the process of fusion, while three individuals showed an "extension" of the dorsal border or centrale portion (Fig. 7b). Unlike *Gorilla*, none of the individuals displayed a completely independent developmental center for the os centrale.

Thirty-nine *Pan* specimens (*P. troglodytes*, $n = 28$; *P. paniscus*, $n = 11$) were observed in the Juvenile 2 period. None of these individuals displayed a separate os centrale. Thirty-three specimens displayed complete fusion, while six individuals (15.4%) (*P. troglodytes*, $n = 3$; *P. paniscus*, $n = 3$) displayed varying degrees of incomplete fusion. All of the latter individuals are in the earlier stages of the Juvenile 2 period, and thus incomplete fusion probably represents one the final stages of scaphoid ossification in which the proximodorsal border, as in *Gorilla*, is the last portion to ossify.

Seventy-two adult specimens were observed (*P. troglodytes*, $n = 52$; *P. paniscus*, $n = 20$), of which all but one specimen displayed complete scaphoid-centrale fusion (Fig. 7c). This individual has a unique morphology, with a cleft present at both the disto- and proximodorsal borders, demarcating the centrale portion.

Pongo

Of five infant *Pongo* specimens examined, two individuals were old enough to preserve an unfused scaphoid and os centrale, each having its own separate cartilaginous anlage. The separate cartilaginous anlage mimics the adult pattern and is clearly different from the cartilaginous template seen in the African apes.

Seven Juvenile 1 and ten Juvenile 2 specimens were examined. All specimens displayed a completely independent os centrale.

Forty adults were examined, of which seven were determined to be "older" than the remainder of the sample based
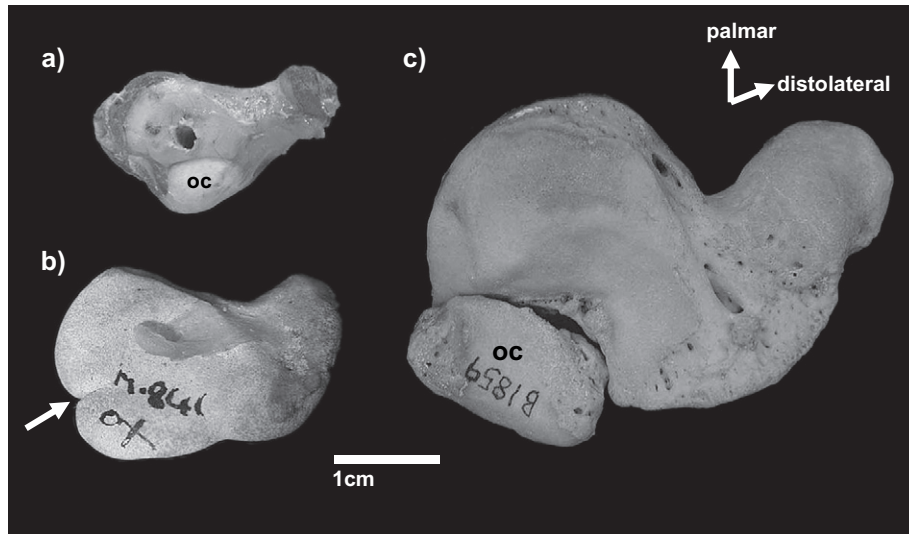
Fig. 6. Various ontogenetic stages of scaphoid and os centrale morphology in *Gorilla* (distomedial view of left scaphoid): (a) early Juvenile 1 period with separate ossification center for the os centrale (oc) (MRAC 808, female); (b) presence of proximodorsal cleft (arrow), partially differentiating the centrale portion at Juvenile 2 stage (PCM M841); (c) sole case of an independent os centrale in an older adult male (CMNH HTB 1859), seen bilaterally.

on a significant amount of dental wear and/or signs of senescence in the postcrania. Four specimens (10%) had a completely fused or partially fused scaphoid-centrale, but only one of these specimens can be regarded conclusively as an "older" individual. Contrary to Schultz (1936, 1941), at least two of the remaining three individuals are young adults (the remaining individual is ambiguous). All four of these individuals are female (females constitute 56% of the entire sample and 60% of the adult sample). One individual showed bilateral fusion. All the other specimens only preserve one scaphoid and/or os centrale, and therefore bilateral versus unilateral fusion cannot be determined.

The older individual with complete scaphoid-centrale fusion has significant dental wear and displays a considerable amount of pathological exostosis (Fig. 8a). Not only is the os centrale fused to the scaphoid, but the trapezium and trapezoid are also fused and all the other carpals have exostoses. Therefore, fusion in this individual appears to be most likely due to pathology.

Two *Pongo* individuals show what we consider to be partial scaphoid-centrale fusion (Fig. 8b, c). Both of these specimens
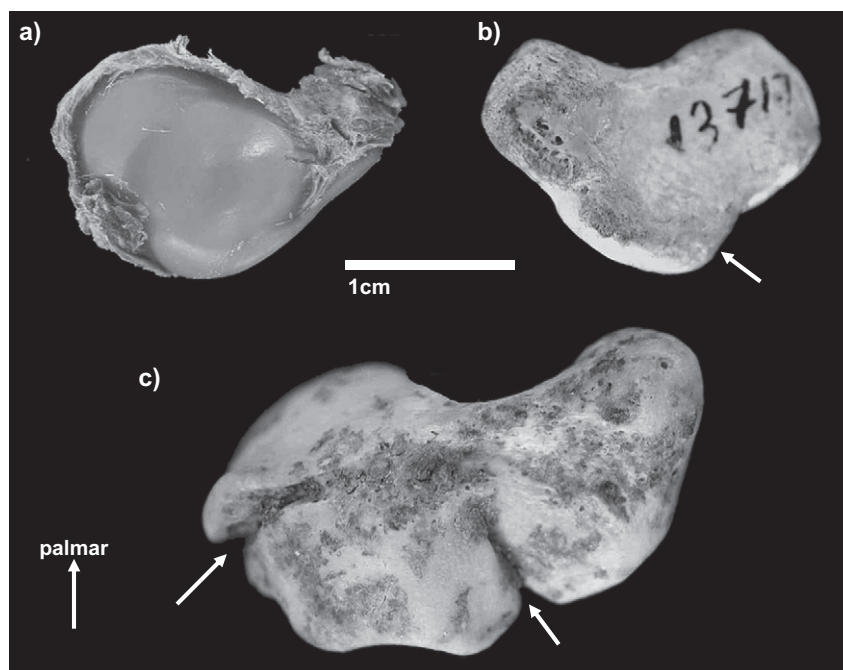

Fig. 7. Ontogenetic stages of scaphoid morphology in *Pan*: (a) distomedial view of cartilaginous scaphoid with os centrale portion fully incorporated into body of the scaphoid in an Infant (dP3 half erupted) *P. troglodytes* (MRAC #?); (b) distomedial view of a midstage Juvenile 1 period female *P. troglodytes* (MRAC 13717) with "dorsal extension" (arrow) of centrale portion; (c) dorsolateral view of unique late juvenile or adult *P. paniscus* (MRAC #?) scaphoid with proximodorsal and dorsodistal clefts (arrows) roughly demarcating the centrale portion.

retain either a distinct line or cleft delimiting the os centrale portion from that of the scaphoid. Both of these individuals also appear to be young adults, as the M3 has only minimal attrition and the iliac crest is not fully fused. Therefore, if these individuals had lived to older adulthood, perhaps this line of division would have been completely obliterated.

The final individual has yet another slightly different type of fusion between these two carpals (Fig. 8d). Despite complete fusion of the os centrale to the scaphoid, the centrale portion can still be identified. Fusion appears irregular due to exostosis and may be the result of injury or pathology as well. The iliac crest is not fully fused in this individual, suggesting that it might be a young adult, but there are no dental remains associated with this specimen to support this. Other

Pongo specimens included in this study have fully erupted and worn dentitions, suggesting adulthood, but the iliac crest remains partially unfused. This indicates that this area of the skeleton may not fully fuse in some *Pongo* individuals, regardless of age, and is probably not a reliable indicator of age. Thus, the age of this individual is unclear.

Scaphoid-centrale fusion in *Pongo* produces a different morphology from that seen in *Pan* or *Gorilla*. As opposed to a centrale that is developmentally incorporated into the scaphoid body as in African apes, in *Pongo*, fusion occurs between a fully developed os centrale and scaphoid. This process produces a more elaborate morphology in that the dorsal portion of the os centrale extends beyond the body of the scaphoid, creating the "dorsal beak" noted by Richmond et al. (2001)
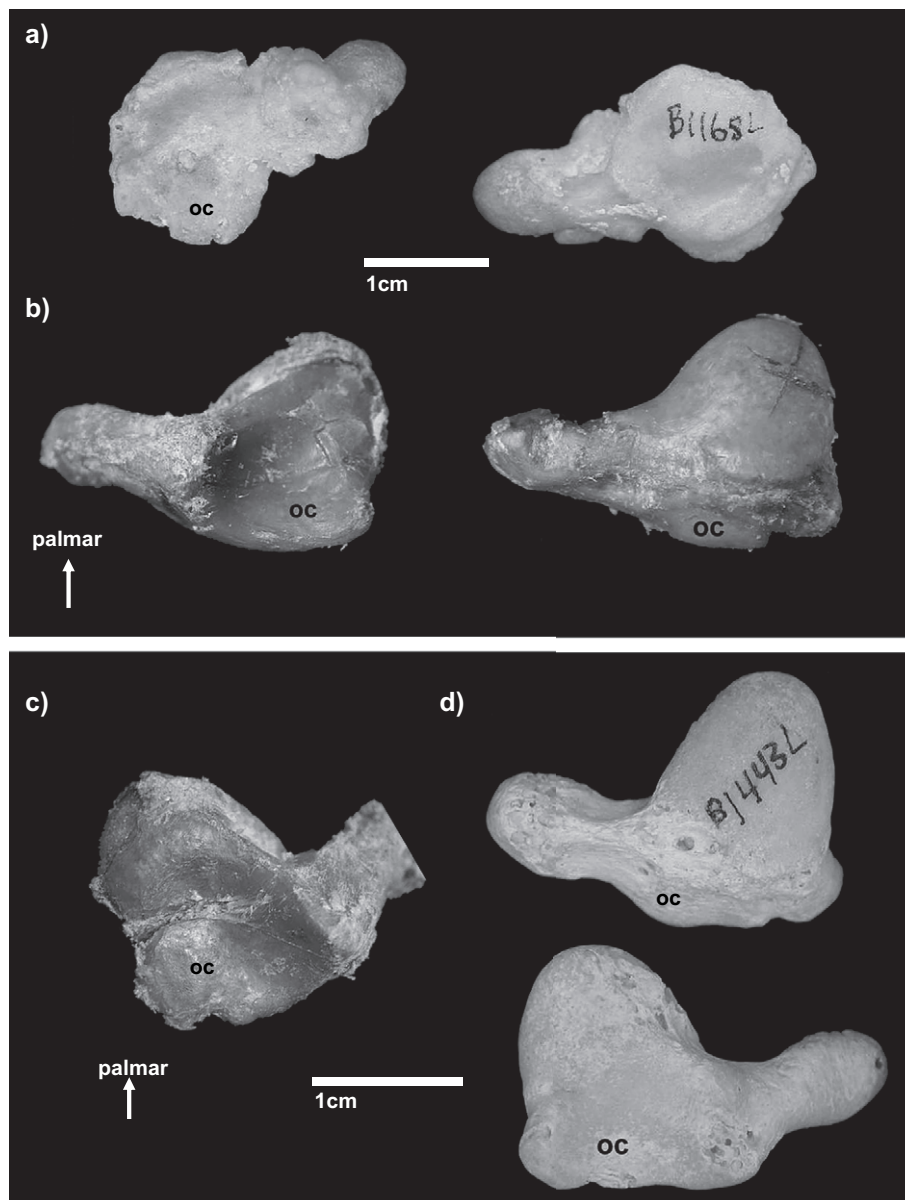

Fig. 8. Scaphoid-centrale fusion in female *Pongo* of various ages: (a) distomedial (left) and proximolateral (right) views of a pathological, older individual (CMNH HTB 1168); (b) distomedial (left) and proximolateral (right) views of bilateral fusion in a young adult (NMNH 143596/A49848); (c) distomedial view in young adult (NMNH 143598/A49851); (d) proximolateral (above) and distomedial (below) views in specimen of unknown age (CMNH HTB 1443).

and Begun (2004). Despite this general *Pongo* morphology, the rare instances of scaphoid-centrale fusion in *Pongo* do not appear to be controlled by a set morphological pattern of fusion, as the resulting morphology differs among all four individuals. Although fusion occurs much later in ontogeny relative to African apes and humans, which is significant in and of itself, it does not appear to be correlated with any particular stage of adulthood, contrary to previous reports (e.g., Schultz, 1936, 1941; Lewis, 1989).

Hylobates

Only one neonatal *Hylobates* was examined; it was too young to preserve any identifiable carpals. Three Juvenile 1 specimens, four Juvenile 2 specimens, and 43 Adult specimens were examined and all displayed an independent os centrale. Eight Adult specimens showed significant dental wear and/or signs of senescence and were considered older adults. Therefore, in contrast to reports of fusion in older *Hylobates* individuals (Schultz, 1936, 1944; Lewis, 1989), there were no incidences of scaphoid-centrale fusion in any ontogenetic stage of *Hylobates* in this study.

Frequency and timing in hominoids

Contrary to past investigations (e.g., Schultz, 1936, 1944; Lewis, 1989), no *Hylobates* specimen examined in this study displayed scaphoid-centrale fusion, even older adults. *Pongo* presented only four (6.8% of total sample) anomalous cases of fusion, all of which occurred in adults and were not associated with any particular stage of adulthood.

When the entire hominine sample is included, results indicate that *P. paniscus* has the highest frequency of an unfused or partially fused scaphoid among African apes. Although this frequency may be a product of the limited *P. paniscus* adult sample size relative to the other African apes, a unique heterochronic shift in this species or other developmental factors cannot be ruled out. When only the juvenile (Infant to Juvenile 2 periods) sample is examined, *Gorilla* displays a much higher frequency of a partially fused or unfused scaphoid than either of the *Pan* species. Of the 31 juvenile *Gorilla*, ten (32.2%) display partial fusion and three (9.7%) display a completely unfused os centrale (total of 13, or 41.9%, of juveniles). This compares to a total of 22 juvenile *P. paniscus* specimens, of which only four (18.2%) display partial fusion and one (4.6%) an unfused scaphoid (total of five or 22.7%). In *P. troglodytes* only three individuals (5.4%) show partial fusion and one (1.8%) out of 56 juveniles has an unfused scaphoid. Therefore, during the juvenile stages, *Gorilla* displays a partially fused or independent os centrale over three times as frequently as in *Pan* (both species combined, 6 of 78, or 7.7%). The persistence of an independent or partially fused os centrale into late juvenile and adult stages is extremely rare among African apes: only two instances, one *Gorilla* (1.5% of 65 adults) and one *Pan* specimen (1.4% of 72 adults), were observed in our sample. Of the 13 juvenile and 28 adult *Homo* specimens, all displayed a fused scaphoid-centrale.

Nonhominoid primates

Strepsirrhines

Although sample sizes for the strepsirrhines examined in this study were limited, a preliminary analysis reveals interesting results. Of the extant strepsirrhines for which scaphoid-centrale fusion has been reported to occur consistently, our analysis confirms fusion in *Indri* ($n = 2$) and *Lepilemur* ($n = 1$) (Fig. 9a, b). However, contrary to previous reports (Jouffroy, 1975; Schwartz, 1992; Schwartz and Yamada, 1998), the os centrale is firmly bound to, but independent from, the scaphoid in all *Hapalemur* specimens examined here ($n = 8$; Fig. 9d). Within the *Hapalemur* sample, four individuals are juveniles and four are adults, at least one of which is an older adult, suggesting that scaphoid-centrale fusion does not occur at any stage of ontogeny in this taxon (contra Schwartz and Yamada, 1998; Schwartz, pers. comm.).

In *Avahi* ($n = 3$), the os centrale is fused to the scaphoid, but a clear fissure on the proximolateral surface delineates the centrale portion from the scaphoid body (Fig. 9c). Sarmiento (1985) reported scaphoid-centrale fusion in *Propithecus*, but the os centrale was unfused in all three specimens we examined. Similarly, the rare fusion that is reported to occur in *Galago* (Yalden, 1972) was not found in any of the 51 specimens examined here. None of the other strepsirrhine taxa examined (Table 3) displayed scaphoid-centrale fusion.

Hamrick et al. (2000) provided detailed descriptions of the fused scaphoid-centrale in the subfossil lemurs *Babakotia* and *Palaeopropithecus*. However, not all *Palaeopropithecus* scaphoids were included in their study. When all the specimens of which we are aware are included, seven of 12 specimens were fused (58.3%). This relatively even distribution of fusion versus nonfusion suggests that scaphoid-centrale fusion is not stablized in *Palaeopropithecus* and may be a neutral character state.

Other catarrhines and platyrrhines

Of the monkeys for which rare scaphoid-centrale fusion has been reported, in our sample, only one *Cercopithecus* ($n = 20$) displayed fusion. This individual evinced significant dental wear and severe arthritis within the carpus and elsewhere in the postcrania. The os centrale was a separate bone earlier in ontogeny, as indicated by a clear separation between the two elements distomedially, but the dorsolateral border is almost fully fused due to hyperostosis. None of the other catarrhine and platyrrhine taxa examined exhibited any cases of scaphoid-centrale fusion.

Discussion

The frequency and timing of scaphoid-centrale fusion within the primate clade suggests that this fusion is not randomly distributed (contra Schwartz and Yamada, 1998; Hamrick et al., 2000). Scaphoid-centrale fusion occurs consistently only within the Homininae and Lemuroidea, suggesting that this character
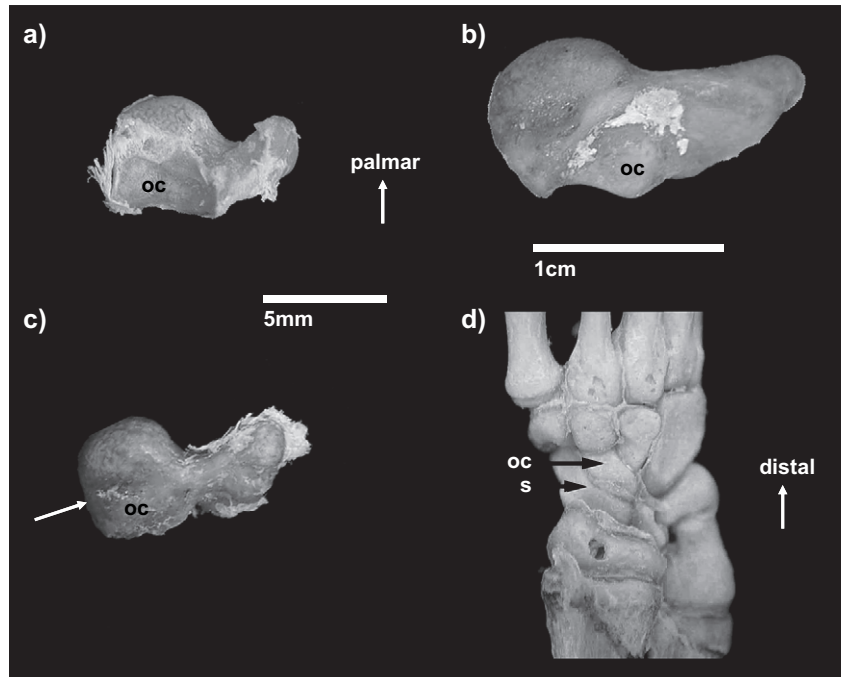
Fig. 9. Scaphoid-centrale fusion and nonfusion in Lemuroidea: (a) distomedial view of *Lepilemur* (NMNH 49668) scaphoid with fused os centrale portion (oc); (b) dorsolateral view of *Indri* (CMNH HTB 1474) with os centrale portion completely fused to scaphoid body (1 cm scale); (c) proximolateral view of *Avahi* (NMNH 83652) with fused scaphoid-centrale but distinct fissure (arrow); (d) dorsal view of *Hapalemur* (NMNH 83665) carpus with a large os centrale firmly articulated but unfused to the scaphoid.

evolved convergently in these two clades. The causes of fusion in each clade, however, are more difficult to elucidate.

Functional and/or phylogenetic hypotheses in strepsirrhines

Among Lemuriformes, consistent fusion occurs only in two of three species of Indridae (*Avahi* and *Indri*), one species of Megaladapidae (*Lepilemur*), and one species of Palaeopropithecidae (*Babakotia*). The varying scaphoid-centrale morphology among these taxa (Kivell, unpublished data) suggests that fusion may occur at different times during ontogeny and/or may be the result of differing ontogenetic processes. Given that most of these strepsirrhine taxa are only broadly characterized as vertical clingers and leapers, or include this locomotor behavior in their positional repertoire, a closer examination of the biomechanics of the postural and locomotor uses of the hands in these taxa is needed to determine the functional implications.

Begun (2004) suggested that fusion has evolved in some strepsirrhines due to loading stresses of a large, divergent pollex while grasping. Compressive forces between the pollex and base of the second metacarpal may cause a more radially oriented trapezoid facet and fusion between the scaphoid and os centrale. This explanation may apply to *Indri*, which has a very elongated and divergent pollex. However, *Propithecus* has almost identical manual morphology yet does not display scaphoid-centrale fusion (contra Sarmiento, 1985). Furthermore, *Hapalemur* and *Lepilemur* have a slightly reduced and less divergent pollex relative to indrids, and yet *Lepilemur* exhibits fusion and *Hapalemur* does not (contra Jouffroy, 1975).

Avahi has a significantly reduced pollex that is less divergent and yet displays scaphoid-centrale fusion (Tattersall, 1982). Thus, scaphoid-centrale fusion does not appear correlated with hand morphology among Lemuriformes.

Hapalemur engages in equal amounts of quadrupedal running and leaping (Jouffroy, 1975). Hamrick (1996) stated that *Hapalemur* is more similar to quadrupedal Lemuriformes in its carpal morphology than it is to other vertical-clinging taxa. This unique difference in the relative components of the *Hapalemur* positional behavior may help clarify the basis for the lack of fusion in this taxon, suggesting that scaphoid-centrale fusion is specifically related to more frequent amounts of vertical clinging and leaping. However, both *Indri* and *Propithecus diadema* (the latter lacking scaphoid-centrale fusion) are of similar body size and engage in frequent vertical clinging and leaping with very similar kinematics (Demes et al., 1996). *Avahi* and *Lepilemur* are of similar body size but *Avahi* is a more committed leaper, while *Lepilemur* climbs more frequently (Warren and Crompton, 1997). Therefore, neither specific positional behavior nor allometry can explain the functional significance of scaphoid-centrale fusion in these taxa.

Palaeopropithecus displays a relatively equal distribution of scaphoid-centrale fusion and nonfusion within a single genus (Hamrick et al., 2000; this study). The wide range of unfused and partially and fully fused scaphoid-centrale morphologies may represent a changing developmental pattern of a perhaps neutral character that had not yet stabilized within the population or may reflect different stages of ontogeny (Fig. 10; Kivell, unpublished data). However, associated skeletal material needed to independently estimate developmental age is not available for *Palaeopropithecus* carpals. Fused versus unfused
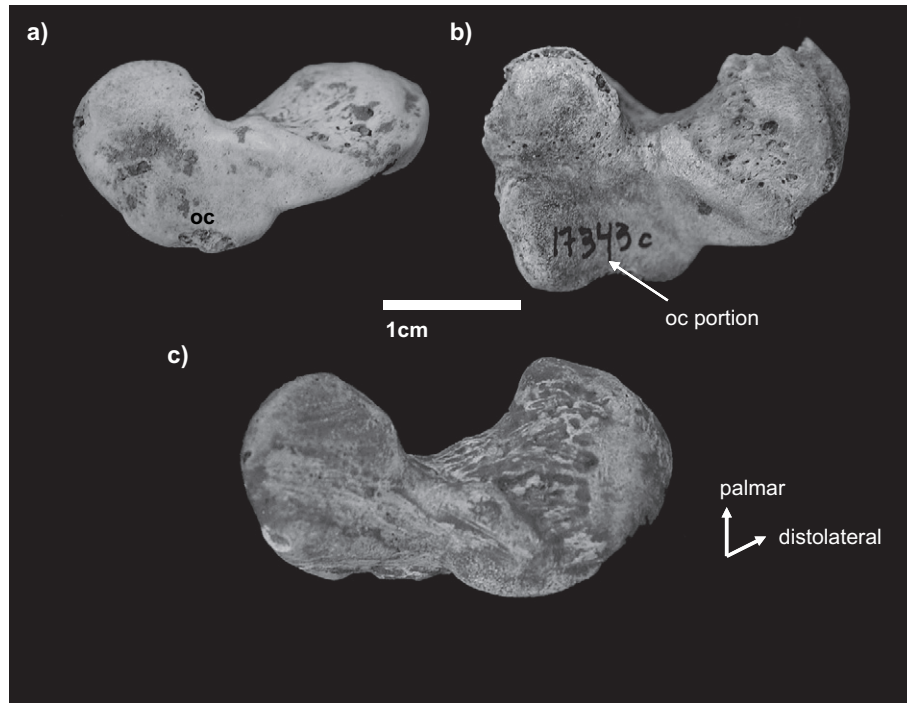
Fig. 10. Variable morphology of scaphoid-centrale fusion and nonfusion in *Palaeopropithecus*. Distomedial view of left scaphoids: (a) fused os centrale (oc) portion (DFP 17345b); (b) fused but os centrale portion more extensive (DFP 17343c); (c) unfused os centrale (DFP 17342).

scaphoids are not correlated with size, suggesting that this variation is not reflective of sexual dimorphism.

Hominoids

Significant differences in frequency and timing of scaphoid-centrale fusion among hominoids suggests that the processes involved in the fusion of these carpals in African apes and humans are not homologous to those responsible for the rare fusion seen in Asian apes. Rare occurrences of fusion in *Pongo* and reported cases in *Hylobates* (e.g., Schultz, 1936, 1944) occur only after functional loading during adulthood and are often associated with pathology and/or exostosis of an already firmly bound scaphoid-centrale articulation. Thus, fusion is not a genetically programmed character in Asian apes that has been selected for and fixed in the population as it has been in hominines.

Given that *Gorilla*, *Pan*, and *Homo* all share (1) early fusion, (2) similar adult scaphoid morphology, (3) a recent common ancestor, and (4) the same morphological pattern of fusion (Kivell, unpublished data), it is most parsimonious to consider scaphoid-centrale fusion as homologous among hominines. Relatively minor differences in frequency and ontogenetic timing are best explained by heterochronic differences within this clade.

Heterochrony in hominoids

The increased frequency and earlier timing of scaphoid-centrale fusion among hominoids follows a heterochronic trend that can best be described by the term "acceleration."

Acceleration is a peramorphic process in which an increased rate of development results in the ancestral adult morphology occurring in the descendant's juvenile stage of growth (Gould, 1977; McNamara, 1986; Godfrey and Sutherland, 1995). When it occurs, the fusion of the os centrale in Asian apes occurs only during adulthood. This timing is in contrast to the much earlier scaphoid-centrale fusion displayed in African apes and humans. Regardless of the occasional appearance of a separate ossification center for the os centrale in *Gorilla* and *Pan*, the cartilaginous anlage form of all hominines is that of scaphoid with a fused centrale. Thus, the carpal template of a fused scaphoid-centrale is set during the fetal period, well before the carpus is subjected to loading. Although in *Gorilla* and *Pan* complete fusion of the centrale portion to the scaphoid body occurs sometime during the Juvenile 2 period at the latest, far more *Gorilla* specimens display this partially fused morphology than *Pan* at this ontogenetic stage. In *Homo*, on the other hand, a separate chondrification center for the os centrale has disappeared by the third to fourth fetal months (O'Rahilly, 1954; Čihák, 1972). The concave dorsal border of the scaphoid or the occasional disappearance of the centrale portion all together (Dwight, 1907) further emphasizes this trend toward earlier fusion and perhaps loss of the os centrale in humans. Sarmiento (1985) stated that the relative overall mass of the scaphoid is smaller in humans compared to other anthropoids, lending support to the hypothesis that the centrale portion of the scaphoid is disappearing in humans.

Schultz (1944) did not recognize the significance of the considerable difference in timing and frequency of scaphoid-centrale fusion among hominoids. We conclude that consistent versus rare fusion and fusion before versus after adult loading

behaviors develop represent significant differences among hominoids. Despite some variation, early ontogenetic fusion of the os centrale to the scaphoid is most likely a synapomorphy of the hominine clade.

Functional and/or phylogenetic hypotheses in hominoids

Despite the hypothesized heterochronic relationship among hominoids, fusion during adulthood in *Pongo* is most likely correlated with function since fusion occurs only after the carpus has been loaded for a considerable period of time. In this study, rare fusion of the os centrale to the scaphoid in *Pongo* stems from varying causes (i.e., pathological in some cases) and produces a variety of morphologies. This inconsistency does not suggest a specific functional explanation for fusion; rather, it implies that fusion occurs simply because of hyperostosis of an already firm and relatively immobile joint. That said, the scaphoid-centrale articulation is a relatively immobile joint in many monkeys as well (Yalden, 1972; pers. observation), yet fusion is less common in these taxa (e.g., *Macaca* or *Cercopithecus*). Therefore, the reasons for the rare but increased occurrence of fusion in Asian apes relative to other monkeys may mean that fusion in the former is related to specific functional requirements. In all incidences of fusion, the centrale portion creates a unique dorsal beak that extends over the capitate neck in midcarpal articulation and may increase stability for different, and still unclear, functional requirements in some individuals. This morphology is not seen in the fused scaphoid-centrale of African apes and humans (Richmond et al., 2001; Begun, 2004; this study).

A fused scaphoid-centrale in African apes creates a broad, flat base along the dorsodistal border that the capitate and trapezoid contact during loading (Richmond et al., 2001; Begun, 2004). Some researchers have suggested that fusion of the scaphoid and os centrale in African apes is an adaptation for increased stability during knuckle-walking (Marzke, 1971; Tuttle, 1975; Sarmiento, 1985; Richmond et al., 2001; Begun, 2004). Specifically, fusion is thought to counter strong shear stress along the scaphoid-centrale joint during loading, particularly as the extended wrist is loaded in compression while rolling from the fourth to second ray during knuckle-walking (Richmond et al., 2001; Begun, 2004). Although this explanation may be theoretically sound, demonstrating it biomechanically is problematic.

Carpal fusions involving the scaphoid and os centrale, as well as the lunate, are very common among mammals (Stafford and Thorington, 1998). Carpal fusions are often linked to a functional need for stability (Wood-Jones, 1942). However, defining a character as "adaptive" is challenging. Adaptation can be defined as "a trait whose *origin* is associated with increased functional efficiency that was favoured by natural selection" (Brooks and McLennan, 2002: 342–343, emphasis original; see also Gould and Vrba, 1982; Coddington, 1994; Lauder, 1996). Therefore, to evaluate a trait as a possible adaptation, we need to extrapolate the current utility of the character from its function at the time of origin (Lauder, 1996). We must investigate the factors that may have been involved in the original success of that trait ideally using fossil evidence.

To convincingly demonstrate that scaphoid-centrale fusion occurred as an adaptation in African apes, we need fossil evidence that the appearance of this trait (i.e., the most parsimonious hypothesis would suggest this character evolved once in the common ancestor of the hominine clade) was coincident with the appearance of knuckle-walking behavior (associated with corroborative evidence in other parts of the postcranial morphology). However, there is no carpal evidence for fossil African apes, and early hominin evidence is meager. Nor have we found a fossil hominoid that is a knuckle-walker. Carpal remains of the Miocene hominoids *Proconsul*, *Equatorius*, *Nacholapithecus*, *Oreopithecus*, and *Dryopithecus* all preserve an unfused scaphoid and os centrale (Begun, 2002; Harrison, 2002). The earliest hominin scaphoids are two *Australopithecus* specimens from Sterkfontein that show scaphoid-centrale fusion (Clarke, pers. comm.). The scaphoid of *Homo habilis* associated with OH 7 resembles that of extant humans in being fused as well (Napier, 1962). Therefore, the fossil record is mute on the issue of when scaphoid-centrale fusion occurred among hominines. We must therefore look to other lines of evidence that may improve our understanding of the function of scaphoid-centrale fusion. Biomechanical, experimental, and comparative data can elucidate the functional significance of a character.

Biomechanical and experimental data on compressive forces in the African ape and human wrist are limited. Patel and Carlson (2006) showed that African apes have a higher subchondral bone density and are thus able to withstand higher compressive forces along the lateral portion of the distal radius compared to a higher medial force concentration in *Pongo*. These data suggest that in *Gorilla* and *Pan*, the lateral portion of the carpus (i.e., the scaphoid) is more heavily loaded, whereas in *Pongo* the medial portion of the radiocarpal articulation (i.e., the lunate) is more heavily loaded. This is compatible with comparative morphology of *Pan*, *Gorilla*, and *Pongo*. African apes have an enlarged scaphoid and larger radioscaphoid articulation, while *Pongo* has an enlarged lunate, the radial facet of which makes a much greater contribution to the antebrachiocarpal joint.

Schuind et al. (1995) provided support for the increased loading of the scaphoid using rigid-body-spring-modeling (RBSM) computer simulation to asses the transmission of force through the human wrist during grasping. The authors found that the majority of forces were dissipated through the scaphoid. Distribution of forces in the antebrachiocarpal joint showed that 61% were transmitted through the radioscaphoid joint, while in the midcarpal joint, 30.7% were distributed through the scaphotrapeziotrapezoidal (STT) joint and 32% through the scaphocapitate joint. Given the integral position of the os centrale amid the scaphoid, trapezoid, and capitate, fusion of this bone to the scaphoid may help to dissipate these forces.

Short et al. (1997) showed that the scaphoid is the most mobile of the proximal carpal bones in humans. The data of Carrigan et al. (2003) support these findings. They used

a three-dimensional finite-element model to simulate load transmission in the human wrist and found that the scaphoid, due to its intrinsic mobility, required the highest amount of constraint force to keep it stable in a computerized carpus model. The scaphoid is the most commonly broken carpal in humans (e.g., Taleisnik, 1985), even with the extra stability created by fusion to the os centrale, suggesting that there are considerable biomechanical forces placed on this carpal.

Comparative data also contribute to understanding the adaptive significance of a character. The "convergence approach" tests the functional significance of a character by analyzing the appearance of that character in unrelated taxa (Coddington, 1994). A character correlated with the same behavior in taxa that do not share a recent common ancestor is statistically more likely to be specifically adapted for that behavior because the effects of phylogeny have been removed. Orr (2005) used the convergence approach to compare the carpal morphology of African apes to a distantly related extant knuckle-walker, the giant anteater (*Myrmecophaga tridactyla*). Early scaphoid-centrale fusion is one of several "knuckle-walking" traits shared between African apes and anteaters. Results from Orr's (2005) study, however, were inconclusive. Scaphoid-centrale fusion in *Myrmecophaga* creates a "dorsal beak" similar to that seen in *Pongo*, a morphology that is distinctly different from that of hominines (described above). Furthermore, all members of Xenarthra (the order to which *Myrmecophaga* belongs) display a fused scaphoid-centrale despite a wide variety of terrestrial and arboreal behaviors (Yalden, 1972; Mendel, 1979; Orr, 2005), suggesting that this trait is plesiomorphic for this clade. Thus, Orr (2005) concluded that this convergence test can neither support nor reject scaphoid-centrale fusion as an adaptation or exaptation for knuckle-walking in these taxa.

Chalicotheres provide another convergence test of the knuckle-walking hypothesis. Chalicotheres are fossil perissodactyls, some of which walked on the intermediate phalanges, as do African apes (Begun, 2004). The functional morphology of the scaphoid in the chalicothere *Macrotherium* is very similar to that seen in African apes in that the dorsal margin contacts that capitate and prevents hyperextension of the midcarpal joint. While all perissodactyls lack a separate os centrale (either through fusion or loss), the scaphoid in *Macrotherium* is modified to support the midcarpal joint dorsally. There are many other striking similarities in the wrists of *Macrotherium* and African apes, as well as other parts of the postcranial skeleton, outlined in more detail in Begun (2004). The convergence test of the relationship between knuckle-walking and scaphoid-centrale fusion in *Macrotherium* is also inconclusive because other perissodactyls, and in fact ungulates generally, also lack the os centrale, but none apart from *Macrotherium* are knuckle-walkers. However, all are digitigrade and place a premium on limiting extension in the wrist. Fusion or loss of the os centrale in digitigrade ungulates is probably convergent on loss of the os centrale in digitigrade (knuckle-walking) African apes, while other similarities in the hands of *Macrotherium* and African apes may be more specifically related to knuckle-walking (Begun, 2004).

If scaphoid-centrale fusion is directly associated with function and increased stability during knuckle-walking, it might be expected that *Gorilla* would experience earlier and more frequent complete fusion than *Pan* for two reasons: (1) *Gorilla* is more terrestrial and engages in more knuckle-walking behavior as a juvenile and adult (Doran, 1997) and (2) *Gorilla* has a significantly larger average body mass (Smith and Jungers, 1997). However, the data presented here do not support this prediction. *Gorilla* demonstrates more frequent non- or partial scaphoid-centrale fusion and similar, if not slightly later, timing of fusion compared to *Pan*.

Hallgrímsson et al. (2002) stated that morphology of early developmental stages, particularly before the occurrence of mechanical loading, is thought to more directly reflect genetic programming and phylogeny rather than function and the environment. Therefore, ontogenetically early and consistent scaphoid-centrale fusion among hominines suggests that this character state carries phylogenetic, more than functional, information in these taxa. However, this conclusion does not help in understanding why this trait evolved in the first place. Scaphoid-centrale fusion may have originally evolved as a functional adaptation to increased shear stress during knuckle-walking in African apes and, because of its functional importance, become part of the phenotype at an increasingly earlier stage. However, the hypothesis remains untested in the absence of fossil evidence directly relating scaphoid-centrale fusion in hominines with other characters associated with knuckle-walking. Biomechanical and experimental data support the hypothesis that fusion of the os centrale to the scaphoid would counteract the significant load sustained by the scaphoid in humans, but this requires further testing in African apes.

As noted above, carpal fusions among mammals are quite common, occurring in marsupials, carnivores, rodents, bats, tree shrews, and dermopterans (Altner, 1971; Stafford and Thorington, 1998; Prochel and Sánchez-Villagra, 2003). However, these fusions usually occur prenatally. There are no reported incidences of postnatal carpal fusion in marsupials (Prochel and Sánchez-Villagra, 2003), and among several species of euarchontans, Stafford and Thorington (1998) found postnatal fusion only in Dermoptera. Primates generally retain the plesiomorphic carpal pattern among mammals in that most taxa lack fusion (Lewis, 1989). Therefore, the appearance of a separate os centrale ossification center in fetal or infant African apes probably reflects this plesiomorphic condition. Scaphoid-centrale fusion in African apes and humans probably reflects peramorphosis in hominines. It is theoretically possible that postnatal fusion of the scaphoid-centrale is a retention of the primitive euarchontan condition. However, the fact that most primates, which are by definition more closely related to hominines then to flying lemurs, fail to fuse these bones and the fact that fusion in primitive euarchontans involves the scaphoid, centrale, *and* lunate strongly suggests that fusion in hominines is a synapomorphy.

Many mammals, particularly digitigrade mammals, such as ungulates, have fused (e.g., scaphoid and lunate) or lost (e.g., trapezium) several carpals (Kent, 1992). It is interesting that the only primates other than humans to show consistent fusion

of the scaphoid and os centrale are also the only truly digitigrade primates, the knuckle-walking African apes. We propose that this is a synapomorphy of the hominine clade functionally associated with digitigrady (knuckle-walking) that is retained in humans as an exaptation for continued stability at the midcarpal and especially lateral carpometacarpal joints. Fossil evidence for the origins of knuckle-walking coinciding with the appearance of scaphoid-centrale fusion will clarify the adaptive significance of this trait. Evidence for knuckle-walking in a fossil taxon lacking a fused os centrale would weaken or falsify this hypothesis.

Conclusion

(1) Our study confirms some, but not all, of Schultz's (1936) conclusions regarding scaphoid-centrale fusion in hominoids. There is an important difference in frequency and the timing of scaphoid-centrale fusion among hominoids; in African apes and humans fusion occurs in almost all individuals (>95%) and early in ontogeny, whereas in Asian apes fusion occurs rarely ($\sim$7%) and only in adulthood.

(2) The data demonstrate a clear heterochronic trend in the frequency and timing of scaphoid-centrale fusion among hominoids. This trend suggests that scaphoid-centrale fusion is primarily under genetic control. The convergent occurrence of this trait in the Homininae and Lemuroidea, compared to its extreme rarity among all other primates, also supports a phylogenetic component within each clade.

(3) The sporadic occurrence of scaphoid-centrale fusion among Lemuroidea is more difficult to interpret, as it is not directly correlated with phylogeny or function. Understanding this convergent character state in Megaladapidae and Indridae requires a more in-depth analysis of positional behaviors, functional morphology, and carpal ontogeny.

(4) The functional basis, if any, of scaphoid-centrale fusion among hominines (and hominoids) remains unclear. That said, there is only one functional hypothesis currently discussed positing that it is an adaptation for stability and compression during knuckle-walking (e.g., Richmond et al., 2001). Some biomechanical data in hominines suggest a concentration of compressive forces on the scaphoid that support this hypothesis. However, convergence tests are inconclusive. Fossil evidence bearing on the origins of knuckle-walking behavior and/or biomechanical analyses of scaphoid-centrale loading are required to further illuminate this hypothesis.

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