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## Abstract

“Carpus” is derived from the Greek word *karphoo*, meaning “to shrink together”. This is an appropriate name as the carpus, or wrist, is arguably one of the most complex joint systems in the mammalian body, incorporating some 15–17 bones interconnected by at least 20 articulations and bound together by numerous ligaments and tendons. Wood Jones (1942) considered learning the identity and laterality of the human carpal bones to be minutiae not worth the time of modern-day medical students. However, the carpal bones together function to transfer loads between the hand and forearm (radius and ulna) and permit the mobility of the hand in multiple planes. The study of variation in carpal morphology across primates since Owen (1866), Mivart (1867, 1869) and Leboucq’s (1884) first comparative descriptions not only has provided unique insight into the primate wrist evolution, hand use and hand mobility but also has played an important role in hypotheses regarding primate origins (e.g. Godinot and Beard 1991; Boyer et al. 2013), hominoid origins (e.g. Cartmill and Milton 1977; Beard et al. 1986) and particularly human evolutionary history (e.g. Marzke 1971; Begun 1992; Richmond et al. 2001; Tocheri et al. 2008; Kivell and Schmitt 2009). A history of detailed morphological descriptions by a select few (e.g. Lewis 1989 and references therein; Ziemer 1978; Sarmiento 1988; Hamrick 1996a, b, 1997; Richmond et al. 2001; Daver et al. 2012) and recent advancements in 3D (Tocheri 2007; Tocheri et al. 2003, 2005; Orr et al. 2013) and in vivo/in vitro imaging (e.g. Neu et al. 2001; Crisco et al. 2005; Moritomo et al. 2006; Pillai et al. 2007; Orr et al. 2010; see Chap. 9) have provided insight into the complexities of carpal movement and a better understanding of the implications of what subtle variation in carpal morphology may mean with regard to overall wrist function. Thus, the tiny, irregular-shaped bones of the wrist often considered a tedious nightmare by biological anthropology or medical students hold important insight into our own evolution.

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**Chapter 3** 1  
**The Primate Wrist** 2

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**1 Introduction** 4

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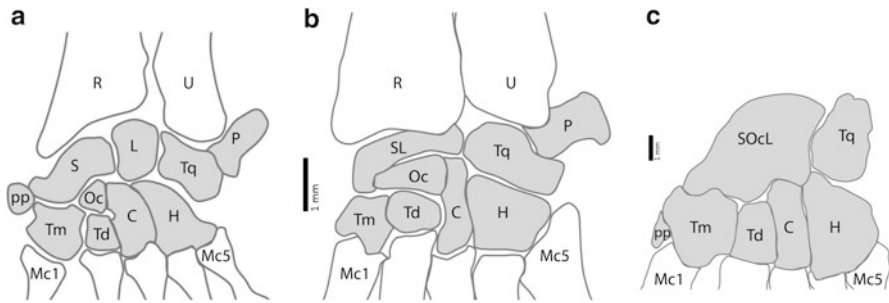
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27 what subtle variation in carpal morphology may mean with regard to overall wrist  
28 function. Thus, the tiny, irregular-shaped bones of the wrist often considered a  
29 tedious nightmare by biological anthropology or medical students hold important  
30 insight into our own evolution.

31 This chapter will review the functional morphology of the carpus across major  
32 primate clades (strepsirrhines, New and Old World monkeys and hominoids, includ-  
33 ing humans), with reference to morphology in other, closely related mammals. Much  
34 of this review is based on the tome of work by Lewis (1965; 1969; 1970; 1971a, b;  
35 1972a, b; 1974; 1977; 1985a, b; Lewis et al. 1970), which is summarized in Lewis  
36 (1989). Although many researchers have disagreed with Lewis's functional interpre-  
37 tations (e.g. Jenkins and Fleagle 1975; Cartmill and Milton 1977; Sarmiento 1988;  
38 Hamrick 1997; Orr et al. 2010), his detailed comparative morphological descriptions  
39 of the primate wrist (and hand) have provided an invaluable foundation for much of  
40 the work that has been done since on the extant and fossil primate wrist.

41 The bones of the primate carpus can be organized into four main joint com-  
42 plexes: (1) **antebrachiocarpal** (between the forearm and carpus), (2) **radial carpo-**  
43 **metacarpal** (between scaphoid/os centrale, trapezium, trapezoid and first and  
44 second metacarpals), (3) **midcarpal** (between the proximal and distal carpal rows)  
45 and (4) **ulnar carpometacarpal joints** (between the trapezoid, capitate, hamate and  
46 second to fifth metacarpals). This chapter is organized by joint complex, with varia-  
47 tion in carpal morphology across primates depicted graphically rather than  
48 described. Given the complexity of carpal shapes, the function of the multiple inter-  
49 carpal joints and the morphological variation across primates, this chapter is by no  
50 means exhaustive. Furthermore, this chapter focuses on the bony morphology only  
51 and generally ignores soft tissues, as the network of interosseous ligaments that is  
52 critical for stabilization of the carpus is too complex to discuss in detail here.  
53 Readers interested in more detailed functional morphology (both bony and soft tis-  
54 sue) are referred to Lewis (1989) for a comprehensive review of the primate carpus  
55 across all clades with comparisons to other mammals; Hamrick (1996a, b, 1997) for  
56 strepsirrhines; O'Connor (1975), Ziemer (1978), Youlatos (1996) and Daver et al.  
57 (2012) for Old and New World monkeys; and Corruccini (1978), Sarmiento (1988),  
58 Richmond et al. (2001), Begun (2004), Richmond (2006), Tocheri (2007) and Orr  
59 et al (2010) for hominoids and references therein.

## 60 2 The Primitive Primate Carpus

61 In most primates, the carpus is composed of nine bones, which have been given  
62 various names since they were first named by Lyser in 1653 (the most common  
63 alternative names are listed below; see also Playfair McMurrich 1914). The carpals  
64 can be divided into three functional columns (most often used in reference to  
65 humans only; Taleisnik 1985; Fisk 1981; Feipel et al. 1994) or in two radioulnar



**Fig. 3.1** The non-primate mammalian carpus. (a) A hypothetical generalized ancestral mammal, redrawn from Lewis (1989); (b) a tree shrew (*Tupaia tana*); and (c) a colugo (*Cynocephalus volans*), both adapted from Stafford and Thorington (1998). The primate carpus is most similar to the hypothesized ancestral mammalian condition. Mammals closely related to primates show more carpal fusions (i.e. a more derived carpus) than most primates; tree shrews have a fused scaphoid-lunate (SL) and colugos have fused scaphoid-os centrale-lunate (SOcL). Note that the prepollex is missing in (b) and the pisiform is missing in (c). Abbreviations: *R* radius, *U* ulna, *S* scaphoid, *Oc* os centrale, *L* lunate, *Tq* triquetrum, *P* pisiform, *pp* prepollex, *Tm* trapezium, *Td* trapezoid, *C* capitate, *H* hamate, *Mc1* first metacarpal, *Mc5* fifth metacarpal

rows; the latter is more common in comparative primate and mammalian studies (e.g. Lewis 1989; Stafford and Thorington 1998) and is used here. The proximal row is comprised of (from radial to ulnar) the **scaphoid** (or radiale), **os centrale**, **lunate** (semilunar or intermedium), **triquetrum** (cuneiforme or ulnare) and **pisiform**. The distal row is made up of the **trapezium** (greater multangular), **trapezoid** (lesser multangular), **capitate** (os magnum) and **hamate** (unciforme) (Fig. 3.1). In humans, African apes and some strepsirrhines, the os centrale is fused to the scaphoid, and thus the carpus is composed of only eight bones in these taxa (see below and Kivell and Begun 2007). The retention of eight or nine carpal bones in primates represents a primitive pattern compared with many other mammals. A reduction in the number of carpal bones—either via fusion or loss of the bone—is common in marsupials, cetaceans, carnivores, rodents, bats, tree shrews and dermopterans (colugos or “flying lemurs”) (Flower 1885; Yalden 1970, 1971; Stafford and Thorington 1998). For example, among the taxa, those that are most closely related to Primates, Tupaiidae (tree shrews) and Rodentia (e.g. squirrels, mice) have a fused scaphoid and lunate (i.e. scapholunate), and Dermoptera show further fusion with the os centrale (i.e. scaphocentralolunate) (Stafford and Thorington 1998; Fig. 3.1) [For a discussion of the homology of different carpal elements throughout tetrapod evolution, see Čihák (1972) and Lewis (1989).] Given the diversity of locomotor, postural and manipulative behaviours, typical of the primate clade, the retention of more separate elements within the carpus may allow for more versatility in wrist function, which is particularly useful for navigating arboreal environments. For example, increased arboreality has been suggested as the functional explanation for why pen-tailed tree shrews (*Ptilocercus*) retain nine carpals compared with other tree shrews, which have seven (Stafford and Thorington 1998).

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### 91 3 Primate Carpal Ossification

92 Chapter 5 focuses on how the bones of the wrist and hand develop up to the point of  
93 ossification. The degree of carpal (and hand bone) ossification is commonly used to  
94 estimate skeletal maturity and age in humans (Greulich and Pyle 1959; Tanner et al.  
95 1983), while variation in skeletal growth in general has been used as a proxy for  
96 assessing differences in life history across primates (e.g. Cheverud 1981; Glassman  
97 1983; Winkler 1996; Zihlman et al. 2007). Within primates, however, there is strong  
98 variation in both the timing and sequence of carpal ossification (Table 3.1). The  
99 capitate, hamate and triquetrum are typically among the first carpal bones to ossify  
100 across primates, while the pisiform is usually among the last. In humans, the capi-  
101 tate and hamate begin ossifying between 2 and 5 months postnatally (Scheuer and  
102 Black 2000). In contrast, the capitate and hamate begin ossifying prenatally in other  
103 apes (*Pan*, *Pongo*, *Hylobates*) (Schultz 1944; Nissen and Riesen 1949; Winkler  
104 1996; Marzke et al. 1987), and in Old and New World monkeys, most carpal ossifi-  
105 cation centres are present at birth (Phillips 1976; Sirianni and Swindler 1985;  
106 Galliari 1988). In humans, the carpus is fully ossified by 12.5 years in females and  
107 15 years in males, while most carpals in great apes are fully ossified by approxi-  
108 mately 10–12 years of age (when the third molar is freshly erupted, but not in occlu-  
109 sion) (Kivell 2007). Winkler (1996) found a positive relationship between the  
110 individual body mass and number of carpals present at birth in *Pongo*, which may  
111 help to explain some of the variation in carpal ossification. However, there is a great  
112 deal of variation in timing and sequence of carpal ossification, both intra- and inter-  
113 specifically (Newell-Morris et al. 1980; Winkler, 1996; Kivell 2007).

### 114 4 General Carpal Function

115 Compared with most other mammals, primates have a diverse repertoire of posi-  
116 tional behaviours, and, particularly in arboreal environments, the wrist and hand  
117 must deal with a variety of irregular and discontinuous supports. Primates are  
118 capable of using a wide range of hand postures to accommodate variation in sub-  
119 strate size and orientation, which require compromises in carpal joint mobility and  
120 stability and diverse mechanical demands on carpal morphology (e.g. Yalden 1972;  
121 Jenkins and Fleagle 1975; Fleagle and Meldrum 1988; Lewis 1989; Hamrick 1996a;  
122 Daver et al. 2012; see also Chaps. 12 and 13). For these reasons, primates retain the  
123 versatility of a primitive mammalian carpal *bauplan*, but also show variations in  
124 carpal morphology that reflect differences in the functional demands placed on the  
125 wrist and hand during locomotion and manipulation.

126 Most primates are pronograde quadrupeds; thus, the wrist assumes an extended  
127 and pronated (i.e. palmigrade or digitigrade) posture during the support phase of qua-  
128 drupedal walking or running (e.g. Jenkins and Fleagle 1975; O'Connor 1975;  
129 Whitehead 1993; Schmitt 1994; Hamrick 1996a; Lemelin and Schmitt 1998; Patel

**Table 3.1** Most common carpal ossification sequence in different primates and other mammals

Taxon	Carpal sequence	Reference
<i>Homo</i>	<b>CAP, HAM, TRIQ, LUN, TRPZM, TRPZD, SCAPH, PISI</b>	Scheuer and Black (2000)
<i>Pan</i>	<b>CAP, HAM, TRIQ, TRPZM, LUN, SCAPH, PISI, TRPZD</b>	Nissen and Riesen (1949), Marzke et al. (1987), Winkler (1996)
<i>Gorilla</i>	( <b>CAP, HAM</b> ) (TRPZM, <b>TRIQ</b> ) SCAPH (TRPZD, LUN, PISI)	Nobaek (1930)
<i>Pongo</i>	<b>CAP, HAM, SCAPH, TRPZM, LUN, (TRPZD, CENT) TRIQ, PISI</b>	Winkler (1996)
<i>Hylobates</i>	( <b>CAP, HAM</b> ) (SCAPH, TRPZM) ( <b>TRIQ, LUN, TRPZD, PISI, CENT</b> )	Schultz (1944)
<i>Macaca nemestrina</i>	<b>CAP, HAM, TRIQ, PISI, SCAPH, TRPZM, TRPZD, LUN, CENT</b>	Newell-Morris et al. (1980), Sirrianni and Swindler (1985)
<i>Macaca mulatta</i>	<b>TRIQ, HAM, SCAPH, CAP, PISI (LUN, TRPZM) TRPZD, CENT</b>	van Wagenen and Asling (1964), Mischejda and Bacher (1980)
<i>Saimiri boliviensis</i>	<b>CAP, TRIQ, HAM, TRPZM, LUN, CENT, TRPZD, PISI, SCAPH</b>	Galliari (1988)
<i>Cebus albifrons</i>	<b>TRIQ, HAM, CENT, CAP, TRPZD, SCAPH, PISI, LUN, TRPZD</b>	Thurm et al. (1975)
<i>Cebus apella</i>	( <b>TRIQ, SCAPH</b> ) <b>HAM (CAP, LUN, TRPZM, TRPZD, PISI, CENT)</b>	Watts (1990)
<i>Callithrix jacchus</i>	(CENT, TRPZM, <b>CAP, HAM</b> ) (SCAPH, LUN, <b>TRIQ, TRPZD</b> ) PISI	Phillips (1976)
<i>Tarsius</i>	( <b>CAP, HAM</b> ) (PISI, TRPZM, <b>TRIQ</b> ) (SCAPH, LUN, TRPZD, CENT)	Kindahl (1944)
<i>Rattus</i>	(SCAPH, LUN) ( <b>TRIQ, CENT</b> ) <b>HAM, CENT, CAP, TRPZM, TRPZD</b>	Strong (1925)
<i>Canis</i>	PISI, LUN, <b>HAM, TRPZM, CAP, TRPZD, SCAPH, CENT, TRIQ</b>	Curgy (1965)
<i>Felis</i>	PISI, CENT, <b>HAM, LUN, CAP, TRPZM, SCAPH, TRPZD, TRIQ</b>	Curgy (1965)

The capitate (CAP), hamate (HAM) and triquetrum (TRIQ) are typically the first carpal bones to ossify in primates and are shown in bold to help visualize this compared with other mammals. Carpal bones in parentheses reflect ossification at the same time or in an unknown sequence. *LUN* lunare, *TRPZM* trapezium, *TRPZD* trapezoid, *SCAPH* scaph, *CENT* os centrale, *PISI* pisiform

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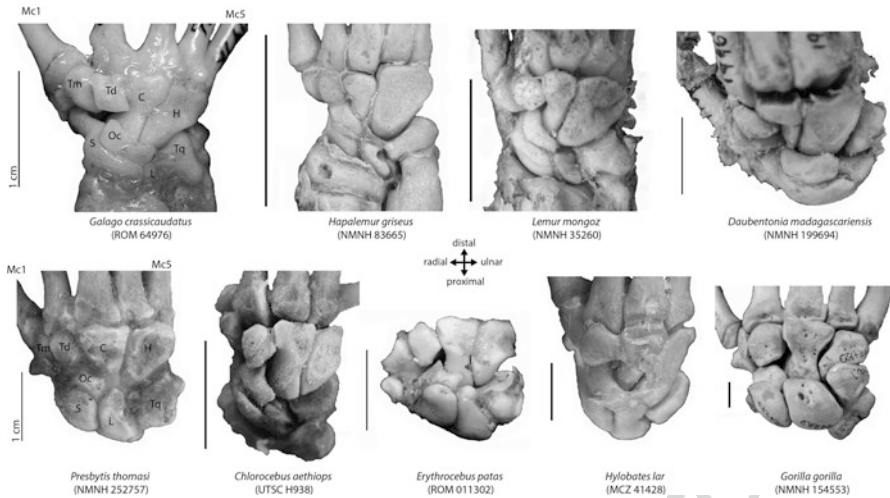
130 2010; Patel and Wunderlich 2010). During terrestrial quadrupedalism, the wrist and  
131 hand tend to be more in line with the forearm (i.e. more neutral posture) (Lemelin and  
132 Schmitt 1998), while during arboreal quadrupedalism, the hand is more ulnarly devi-  
133 ated. These hand postures generally hold true of quadrupedal primates with mesax-  
134 onic (i.e. third digit is the longest) and ectaxonic (i.e. fourth digit is the longest) hands,  
135 though there are several exceptions (e.g. callitrichids and spider monkeys, see Lemelin  
136 and Schmitt 1998). Thus, quadrupedal primates share several morphological features  
137 related to stabilizing the wrist during compression in an extended, pronated posture.  
138 The articulation between the radius and carpus is relatively flat to resist unidirectional  
139 weight-bearing loads (Jenkins and Fleagle 1975; Sarmiento 1988; Hamrick 1996a).  
140 Furthermore, the antebrachio-carpal and midcarpal joints are close packed—meaning  
141 the joint surfaces are in maximum congruency—in an extended, pronated and ulnarly  
142 deviated posture. This means that the antebrachio-carpal and midcarpal wrist joints are  
143 in their most stable position during the support phase of the typical quadrupedal hand  
144 posture. In this close-packed position, radioulnar deviation and rotation are not pos-  
145 sible and the wrist can only flex (O'Connor 1975).

146 Primates that regularly engage in vertical clinging or suspensory behaviours use  
147 a variety of hand postures that place different functional demands on the wrist than  
148 the typical quadrupedal primate. Vertical clinging strepsirrhines (e.g. *Propithecus*,  
149 *Avahi*, *Lepilemur*) use a flexed and partly supinated posture during vertical clinging  
150 and suspension (Hamrick 1996a, b). Their wrists, in turn, show morphological fea-  
151 tures, such as a deeply curved radiocarpal joint or dorsally constricted embrasure  
152 between the capitate and trapezoid (see below), that allow more mobility than quad-  
153 rupeds, but also stabilize the wrist during flexion at the antebrachio-carpal joint and  
154 supination at the midcarpal joint (Hamrick 1996a, b).

155 During suspension or brachiation (i.e. *Ateles*, *Lagothrix* and hylobatids), the  
156 grasping fingers are fixed to the substrate while the body rotates below (e.g. approxi-  
157 mately 90° during brachiation in spider monkeys) through the swing (Jenkins 1981).  
158 The wrist accommodates most of this rotation (i.e. supination; ~70° vs. ~20° by  
159 supination of the radius) by having a midcarpal configuration that acts as a highly  
160 mobile ball-and-socket joint. The wrist is capable of high degree of supination, but  
161 has limited mobility in the opposite direction (hyperpronation, beyond a neutral pro-  
162 nated posture) (Jenkins 1981). This motion and mobility is essentially the opposite of  
163 what we see in quadrupedal, palmigrade taxa (e.g. *Macaca*), which are capable of  
164 very limited supination, but a high degree of hyperpronation (Jenkins 1981).

165 Variation in carpal morphology is largely responsible for differences in the range  
166 of motion at the wrist and hand (Fig. 3.2). For example, in most primates (Old and  
167 New World monkeys and most strepsirrhines), the radius and ulna both articulate  
168 with the carpus, making the antebrachio-carpal joint relatively stable, and therefore  
169 ulnar deviation occurs mainly at the midcarpal joint (Jouffroy and Medina 2002;  
170 Daver et al. 2012; see below). In contrast, in hominoids (including humans), for  
171 which contact of the ulna with the carpus has been lost, ulnar deviation occurs pri-  
172 marily at the antebrachio-carpal joint (Jouffroy and Medina 2002; Crisco et al. 2005).  
173 Furthermore, the degree of curvature of the facets (e.g. the proximal facets of the  
174 capitate and hamate) and relative size of the articular areas (e.g. dorsally extended  
175 proximal facets of the capitate and hamate in some primate taxa) is a good indication  
176 of the range of movement at a particular joint (Sarmiento 1988; Hamrick 1996b;





**Fig. 3.2** Dorsal view of articulated wrists in a sample of primates. Note the relative variation in size between the capitate and hamate. In strepsirrhines and hylobatids, the hamate is much larger than the capitate. In strepsirrhines, the os centrale often articulates with the hamate, cutting off the articulation between the capitate and lunate. In contrast, the capitate of most catarrhines is equal to or larger in size than the hamate, and the hamate does not articulate with the os centrale or scaphoid. Also, note the large size of the triquetrum in most strepsirrhines and Old World monkeys, compared with hominoids. The pisiform is missing for most specimens. All wrists are shown from the right side and scaled to roughly the same size (scale represents 1 cm for each taxon)

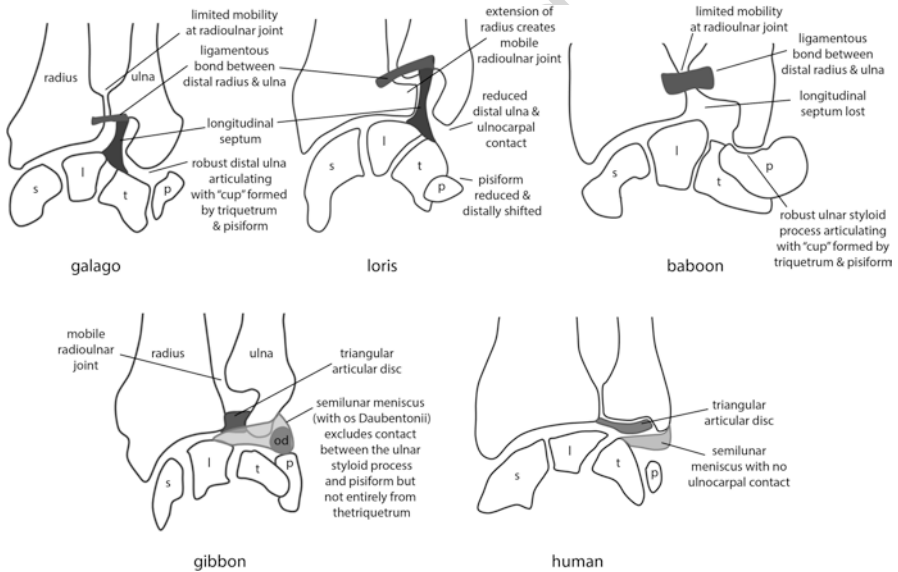
Richmond 2006). However, it is important to note that the interosseous ligamentous network also plays a critical role in carpal mobility/stability (Martin et al. 1998). As such, in vivo mobility can be more limited than might be predicted from bony morphology alone (Richmond 2006; see below).

Given the complexity of the wrist, understanding the movement or kinematics of specific joints or carpal bones is particularly challenging (see Chap. 9). Kinematic studies of humans are most common. They show that the distal carpal row functions essentially as a single unit during wrist motion, but the carpals of the proximal row have more functional independence from one another because they are more loosely tethered by ligaments (Garcia-Elias et al. 1994; Wolfe et al. 2000; Moojen et al. 2003). However, for decades, much of what we understood about the nonhuman primate carpal movement stemmed largely from two in vivo cineradiographic studies: one of a juvenile chimpanzee knuckle-walking (Jenkins and Fleagle 1975) and another of spider monkeys brachiating (Jenkins 1981). Most movements of the wrist and hand require simultaneously combining the flexion or extension with radial deviation or ulnar deviation, making the kinematics of particular bones difficult to visualize and understand. Furthermore, since most of the extrinsic forearm muscles bridge, rather than insert onto, the wrist, the carpals move largely via indirect forces from the activation of muscles inserting on other bones of the hand and forces on the metacarpals and phalanges (Jouffroy and Medina 2002). Finally, the ligaments play an important but rather poorly understood functional role within the wrist. For example, when the wrist is not in an close-packed extended and pronated posture, such as during suspension, vertical clinging or climbing, the articular surfaces may not be in close contact, and thus the ligaments help resist tensile stress

200 and allow individual carpal elements to move while maintaining overall integrity of the  
 201 wrist (Lovejoy et al. 2001; Jouffroy and Medina 2002). New in vivo cineradiography  
 202 imaging techniques (e.g. Crisco et al. 2005, see below) or 3D computed tomography  
 203 (CT) of cadavers that provide 3D models or movies of the movement, such as those  
 204 provided by Orr et al. (2010), represent some of the best ways to better understand the  
 205 complexity of movement in the wrist (see Chap. 9).

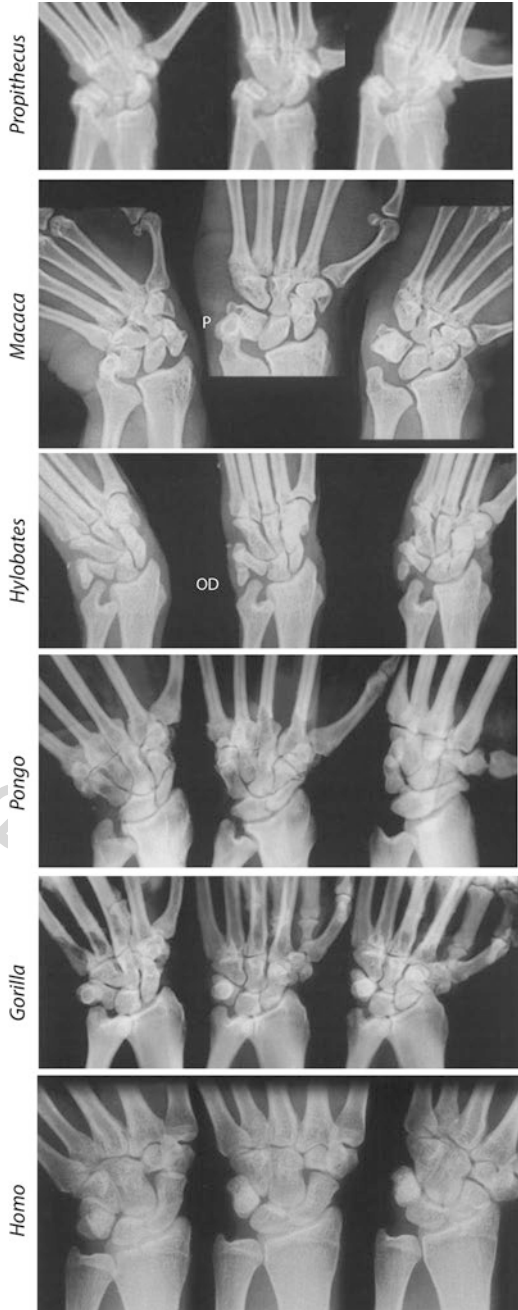
206 **5 The Antebrachiocarpal Joint**

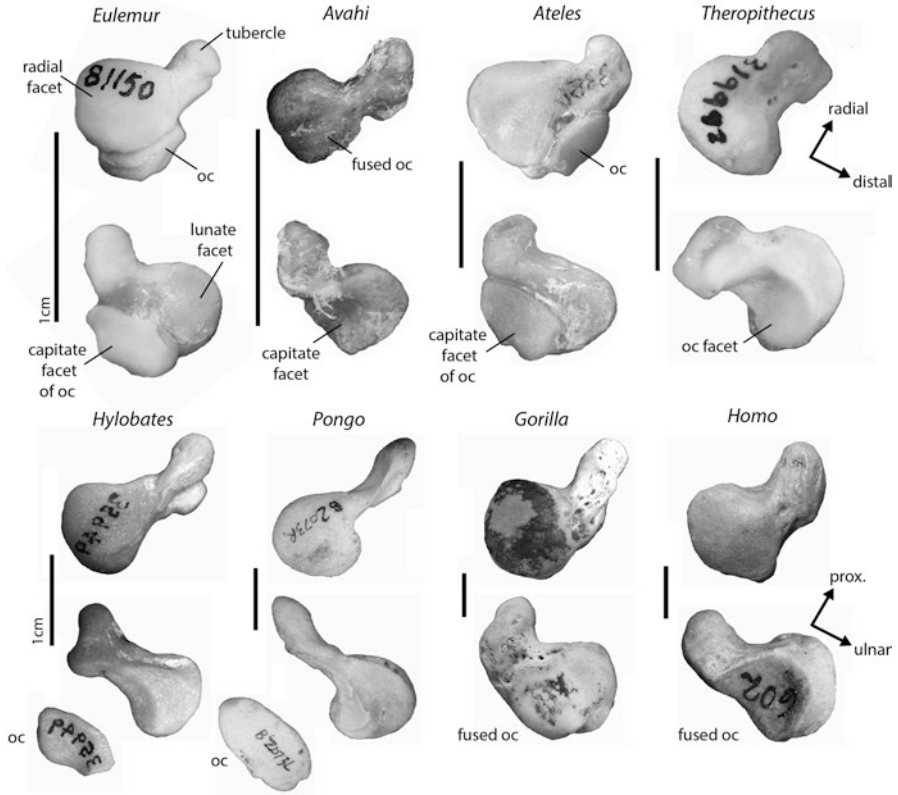
207 The **antebrachiocarpal joint** refers to the articulation between the forearm and  
 208 wrist (Fig. 3.3). In most non-hominoid primates, this joint is composed of a  
 209 radial and ulnar portion, both of which are weight bearing. In all primates, the  
 210 radial portion is formed by the articulation between the radioulnarly and dorso-  
 211 palmarly concave distal radius and the correspondingly convex articular surfaces  
 212 of the scaphoid and lunate (Figs. 3.4 and 3.5). However, modifications to the  
 213 ulnar portion of the antebrachiocarpal joint, particularly in hominoids and



**Fig. 3.3** Schematic of variation in antebrachiocarpal joint morphology across primates. The galago represents the typical strepsirrhine morphology, which is similar to primitive mammals. Lorisids represent a derived condition among strepsirrhines that is convergent in many ways on the hominoid morphology. The baboon is representative of the typical Old World monkey morphology (many New World monkeys still retain a longitudinal septum). The gibbon demonstrates the derived hominoid morphology, including the triangular articular disc and semilunar meniscus that partially (gibbons and chimpanzees) or fully blocks (orangutan, gorilla, human) contact between the ulna and carpus. The os Daubentonii is only consistently found in hylobatids. In the humans, the ulnar styloid process and semilunar meniscus are further reduced than that of other hominoids. See also Lewis et al. (1970)

**Fig. 3.4** Carpal movement at the antebrachiocarpal and midcarpal joints. Radiographs showing the wrist in ulnar deviation (*left*), neutral posture (*middle*) and radial deviation (*right*), adapted from Jouffroy and Medina (2002). Movement during radioulnar deviation stems primarily from the midcarpal joint in *Propithecus*, *Macaca* and *Hylobates*, because there is full or at least partial (in the case of *Hylobates*) contact between the ulnar styloid process and the carpus. In contrast, in *Pongo*, *Gorilla* and humans, there is greater movement at the antebrachiocarpal due to loss of the ulnocarpal articulation. However, note that there is greater ulnar-radial deviation in this particular *Macaca* specimen [species not provided by Jouffroy and Medina (2002)] compared with humans, despite differences in the antebrachiocarpal articulation. *P pisiform*, *OD* os Daubentonii. For additional informative radiographic images of hominoid and macaque wrists, see Jenkins and Fleagle (1975)





**Fig. 3.5** Variation in primate scaphoid and os centrale morphology. *Top* row for each taxon shows the roughly proximoradial view of the scaphoid, featuring the radial facet. *Bottom* row for each taxon shows the distomedial view of the scaphoid [and os centrale (oc)], featuring the lunate and os centrale/capitate articular areas. In *Eulemur* and *Ateles*, the os centrale is independent, but still articulated with the scaphoid via its strong ligamentous attachment. In *Avahi*, *Gorilla* and *Homo*, the os centrale is fused early in ontogeny to become part of the scaphoid. All specimens are shown as the right side and scaled to approximately the same size (scale represents 1 cm for each taxon)

214 lorisids, are arguably the most significant evolutionary changes in the primate  
 215 wrist compared with other mammals (Mivart 1867; Lewis 1969, 1985a, 1989;  
 216 Cartmill and Milton 1977).

217 Most strepsirrhines (e.g. *lemur*, *galago*, but see lorisids below) have an ulno-  
 218 carpal (and antebrachiocarpal overall) joint that is similar to the typical mamma-  
 219 lian pattern (Cartmill and Milton 1977; Lewis 1989). The pisiform is elongated  
 220 and projects proximally to act as a supporting “heel” of the hand (Cartmill and  
 221 Milton 1977; Lewis 1989). The pisiform and triquetrum combine to form a cup-  
 222 shaped facet that articulates with a spindle-shaped extension of the distal ulna  
 223 (homologous to the narrower and more projecting ulnar styloid process in homi-  
 224 noids). Like other mammals, most strepsirrhines retain a thick, fibrous longitudi-  
 225 nal septum that divides the antebrachiocarpal joint into two compartments: an

ulnocarpal portion and radiocarpal portion (Fig. 3.3). This septum links several ligaments together: the lunatotriquetrum ligament distally, the ulnocarpal ligament palmarly and a proximal ligament that unites the distal portions of the radius and ulna (Cartmill and Milton 1977; Lewis 1989). Thus, the septum prevents the proximal carpal row from sliding either radially or ulnarly across the distal radius, thereby limiting radioulnar deviation (Cartmill and Milton 1977; Hamrick 1996a). Therefore, in taxa with a longitudinal septum, the majority of radioulnar deviation occurs at the midcarpal joint (Hamrick 1996a). There is no true synovial joint between the radius and ulna (Lewis 1989). Instead, the radial portion of the distal ulna is more like a small projection, jutting out radially to articulate with the radius, which limits pronation and supination more so than in hominoids or lorises (Cartmill and Milton 1977; see below) (Fig. 3.3).

The antebrachiocarpal joint of most Old and New World monkeys (e.g. *Colobus*, *Cebus*, *Alouatta*; but see *Ateles* below), particularly palmigrade monkeys, is overall quite similar to that the general mammalian and strepsirrhine morphology described above (Lewis 1971b, 1989; Youlatos 1996; Daver et al. 2012; Fig. 3.3). The distal articulation between the radius and ulna is typically a syndesmosis, with a firm ligamentous bond and minimal mobility (Lewis 1965; Cartmill and Milton 1977), although some taxa have an incipient synovial articulation with slightly more mobility (e.g. *Cercopithecus*, *Ateles* and *Lagothrix*; Lewis 1989). The pisiform is rod-like and robust and projects proximally into the heel of the hand. The distal end of the ulna articulates with the concave facet formed by the triquetrum and pisiform and is weight bearing as in strepsirrhines. However, the projecting articulating portion of the ulna has a constricted neck and thus resembles more the ulnar styloid process of hominoids than the morphology of strepsirrhines (O'Connor 1975; Lewis 1989; Hamrick 1996a). Furthermore, there is usually no longitudinal septum separating the radiocarpal and ulnocarpal compartments of the antebrachiocarpal joint in Old World monkeys, though a septum is still found in most New World monkeys (Lewis 1989; Youlatos 1996; Daver et al. 2012; but see Cartmill and Milton 1977).

In hominoids, the distal articulation between the radius and the head of the ulna is a fully elaborated synovial joint, which provides greater mobility (pronation and supination) of the wrist and hand than most other primates. A **triangular articular disc**, which is strongly connected to the palmar ulnocarpal ligament running from the ulnar styloid process to the lunate, separates the ulnar head joint cavity from the remainder of the antebrachiocarpal joint (Fig. 3.3). The pisiform is smaller compared with strepsirrhines and monkeys and projects palmarly and distally into the palm, rather than proximally (except in hylobatids), and does not articulate with the ulna. The ulnar styloid process is reduced, and, instead, a fibrocartilaginous, intra-articular meniscus fills this space and wraps around the ulnar side of the antebrachiocarpal joint from the lunate palmarly to the radius dorsally (Cartmill and Milton 1977; Lewis 1989). Hylobatids are distinct in the presence of an ossified sesamoid-like bone (a lunula), called an os Daubentonii, within the thick, ulnar portion of meniscus [although a small lunula can occasionally be found in *Gorilla*; Lewis (1989); see Sarmiento (1988) for a different interpretation]. The presence of a small aperture in the meniscus in hylobatids and sometimes in *Pan* allows the

271 ulnar styloid process to articulate with the triquetrum. However, in *Gorilla* and  
272 *Pongo*, the meniscus blends with the triangular articular disc, thus completely  
273 excluding the ulnar styloid process from articulating with the carpus (Lewis 1989).  
274 In humans, the ulnocarpal joint is further modified, such that there is no longer a  
275 discrete meniscus, but instead it merges with the remainder of the proximal articular  
276 surface of the radiocarpal joint (Lewis et al. 1970; Cartmill and Milton 1977; Lewis  
277 1989). Altogether, the derived hominoid morphology allows the radius and ulna to  
278 still be held together, but to rotate freely around each other (Sarmiento 1985). Thus,  
279 in hominoids (and lorises; see below), the antebrachiocarpal joint largely consists  
280 of a radiocarpal articulation only, which is why this joint is often referred to simply  
281 as the **radiocarpal joint** in humans and other apes.

282 Lorises and spider monkeys, as well as sloths (Mendel 1979), show some convergent  
283 morphology with hominoids related to greater mobility, particularly ulnar  
284 deviation and rotation, of the wrist needed for the climbing, bridging or suspensory  
285 behaviours common to all of these taxa. Lorises (e.g. *Loris*, *Nycticebus*, *Arctocebus*)  
286 have a derived antebrachiocarpal joint compared with other strepsirrhines (Nayak  
287 1933; Cartmill and Milton 1977). The pisiform is slightly smaller and displaced  
288 distally (along with the triquetrum) and does not articulate with the ulna. The distal  
289 end of the ulna has a narrow projection, which is similar in shape to the ulnar styloid  
290 process of hominoids (Cartmill and Milton 1977). The radioulnar articulation is  
291 also derived such that the radial portion of the distal ulna no longer projects radially,  
292 but instead articulates with an ulnarly extended “shelf” of the radius (Fig. 3.3). This  
293 configuration expands the articulation with the radius, creating an “ulnar head”  
294 morphology, similar to that of hominoids, enhancing pronation and supination  
295 (Cartmill and Milton 1977). However, a longitudinal septum is still present and is  
296 similar in morphology to that of other strepsirrhines, and there is no meniscus like  
297 in hominoids (Cartmill and Milton 1977).

298 Spider monkeys have an intermediate morphology; they have also lost the articula-  
299 tion between the ulnar and pisiform and have a small, distopalmarly positioned pisi-  
300 form compared with other New World monkeys (e.g. *Alouatta*, *Lagothrix*) (Youlatos  
301 1996; but see Lewis 1971b). This morphology is consistent with their increased sus-  
302 pensory, climbing and clambering locomotion (Cant et al. 2001). However, spider  
303 monkeys also retain a large distal ulna that articulates with the triquetrum, providing  
304 support on the ulnar carpus during pronograde quadrupedalism.

305 The functional implications of the derived morphology of the antebrachiocarpal  
306 joint in hominoids, and the convergent development of some of these features in  
307 lorises and spider monkeys, were traditionally thought to allow for greater supina-  
308 tion and ulnar deviation at the wrist, common to the habitual wrist postures used  
309 during climbing, vertical clinging or suspension. However, Jouffroy and Medina  
310 (2002) show that some taxa (e.g. *Macaca*<sup>1</sup>) with a fully elaborated ulnocarpal articula-  
311 tion have greater ulnar deviation than those without (e.g. humans), highlighting the

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<sup>1</sup>Note that the particular *Macaca* specimen depicted in Fig. 3.6 and adapted from Jouffroy and Medina (2002) seems to display an unusual carpal placement that may suggest a greater degree of ulnar deviation (measured as 56°) than is typical for *Macaca*. Jouffroy and Medina (2002) do not

importance of ligaments and tendons in overall wrist mobility. That being said, loss of ulnocarpal articulation does allow for greater mobility at the antebrachio-carpal joint, such that radioulnar deviation in humans and great apes derives primarily from the antebrachio-carpal joint, while Old and New World monkeys, strepsirrhines and hylobatids have greater midcarpal mobility (Jouffroy and Medina 2002; Fig. 3.4).

The other half of the antebrachio-carpal joint—the **radiocarpal articulation**—has received comparatively much less attention, likely because the morphology does not vary substantially across primates (e.g. Jenkins and Fleagle 1975; Ziemer 1978; Lewis 1989). For example, slow-climbing strepsirrhines have more radioulnarly curved radiocarpal (and midcarpal) joint surfaces compared with vertical clinging and arboreal quadrupedal strepsirrhines (Hamrick 1996b). However, the latter two locomotor groups do not differ significantly in radiocarpal curvatures despite loading their forelimbs quite differently (Hamrick 1996b). Most of the discussion about the radiocarpal articulation has focused on extension-limiting mechanisms in terrestrial taxa, such as African apes and digitigrade monkeys (e.g. Jenkins and Fleagle 1975; Corruccini 1978; Zylstra 1999; Richmond and Strait 2000; Richmond et al. 2001; Begun 2004). In African apes, the radiocarpal joint is stabilized in the weight-bearing, slightly extended wrist posture in part by two osteological features of the distal radius: (1) a distal extension of the dorsal margin—called the dorsal ridge (Richmond and Strait 2000)—that buttresses the scaphoid as it rotates during extension and (2) a large scaphoid notch along the dorsolateral margin that contacts a concavity on the dorsal surface of the scaphoid that limits further extension [Tuttle 1967, 1969; see Richmond and Strait (2000) for images]. In addition, the scaphoid has a larger articulation with the radius than that of the lunate (the opposite condition to that of *Pongo*; Zylstra 1999), and the scaphoid and lunate articular surfaces share a similar distoulnar orientation (i.e. they are roughly coplanar). Together, these features are thought to better resist stress during weight bearing, particularly on the radial side of the wrist, and prevent the wrist joint from collapsing into extension (Richmond and Strait 2000; Richmond et al. 2001; Begun 2004).

Terrestrial digitigrade Old World monkeys, such as baboons and patas monkeys, also have limited extension (and ulnar deviation) at the antebrachio-carpal joint compared with palmigrade monkeys (Tuttle 1969; Lemelin and Schmitt 1998; Richmond 2006). Like African apes, they have a similar projecting dorsal ridge of the distal radius (Richmond and Strait 2000). However, the scaphoid notch is much larger and deeper, thus allowing for a greater degree of extension before the radius contacts the scaphoid (Whitehead 1993; Richmond and Strait 2000; Richmond et al. 2001). These more terrestrial primates also have a meniscus in between the dorsal articular areas of the radius and scaphoid that further helps to limit extension (Daver et al. 2012).

In contrast, suspensory apes typically have a much smaller dorsal projection of the distal radius, a smaller scaphoid notch and scaphoid-lunate articular surfaces that are more angled relative to each other, all of which contribute to a much greater range of extension at the antebrachio-carpal joint (Tuttle 1967, 1969; Richmond 2006).

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provide information on the species or sample size. For comparison, Richmond (2006), using different methods, reports 45° ulnar deviation in *Erythrocebus* and 61° ulnar deviation in *Papio*.

354 **6 Scaphoid-Os Centrale Fusion**

355 Scaphoid-os centrale fusion is one of the most discussed features of the primate  
356 wrist (e.g. Mivart 1867; Schultz 1936; Marzke 1971; Jenkins and Fleagle 1975;  
357 Sarmiento 1988; Begun 1992, 1994; Gebo 1996; Richmond et al. 2001; Fig. 3.5). [AU6]  
358 Many of the initial morphological descriptions of the primate carpus in the late  
359 nineteenth century have all discussed fusion of the scaphoid with the os centrale  
360 (Lucae 1865; Mivart 1867, 1869; Giebel 1879; see Kivell and Begun 2007 for  
361 historical review). For example, Huxley (1863) noted that African apes and humans  
362 have eight carpals, compared with nine in most other primates. In spite of all of  
363 these observations, there has been confusion over which taxa have consistent  
364 scaphoid-os centrale fusion (*versus* fusion later in life due to, for example, ossified [AU7]  
365 ligaments or osteophytic growth) and the functional reasons behind this fusion  
366 (e.g. Schultz 1936; Yalden 1972; Jouffroy 1975; Tuttle 1975; Sarmiento 1985;  
367 Schwartz and Yamada 1988; Whitehead 1993; Hamrick 1996a; Begun 2004; [AU8]  
368 Richmond et al. 2001). [AU9]

369 Kivell and Begun (2007) undertook the first systematic study of scaphoid-os  
370 centrale fusion across a broad sample of primates and found consistent fusion  
371 (>95 %) in *Pan*, *Gorilla* and humans that occurred early in ontogeny, compared with  
372 rare fusion in Asian apes (~7%) that occurred only in adulthood. In the smaller  
373 samples of strepsirrhines they examined, they found consistent scaphoid-os centrale  
374 fusion in two extant species of Indriidae (*Indri* and *Avahi*), one species of  
375 Megaladapidae (*Lepilemur*) and one species of the subfossil Palaeopropithecidae  
376 (*Babakotia*) (see Chap. 15). Wood Jones (1942) related scaphoid-os centrale fusion  
377 to the importance of the index finger and the need for stability at the base of the  
378 second digit in African apes and, particularly, humans. Most researchers today,  
379 however, suggest that scaphoid-os centrale fusion in African apes is a functional  
380 adaptation to the increased shear stress on this joint during knuckle-walking  
381 (Marzke 1971; Tuttle 1975; Corruccini 1978; Sarmiento 1994; Gebo 1996;  
382 Richmond et al. 2001; Begun 2004) and that its presence in humans is due to phy-  
383 logenetic “lag” (Richmond et al. 2001) or is an exaptation to shear stress during  
384 power-grip postures (Marzke 1971). Fusion in particular species of strepsirrhines  
385 has been considered advantageous for having a large and divergent thumb (Begun  
386 2004) along with increased loading of the radial side during vertical climbing and  
387 quadrupedalism (Sarmiento 1994). However, there are several reasons why such  
388 functional hypotheses are not consistent with the sporadic occurrence of fusion  
389 across strepsirrhines (e.g. the absence of fusion in lorises, who have the most diver-  
390 gent thumbs among strepsirrhines and engaged in substantial quadrumanous climb-  
391 ing), and there is a strong heterochronic and genetic underpinning to fusion in  
392 hominines that can make functional explanations more challenging (Kivell and  
393 Begun 2007). Furthermore, roughly half the individuals (58 % of  $n=12$ ) of the  
394 highly suspensory subfossil lemur *Palaeopropithecus* shows fusion, suggesting that  
395 we have much to learn about the interplay of genetics, development and function  
396 when it comes to this feature (Kivell and Begun 2007).



## 7 The Pisiform: It Is Not a Sesamoid!

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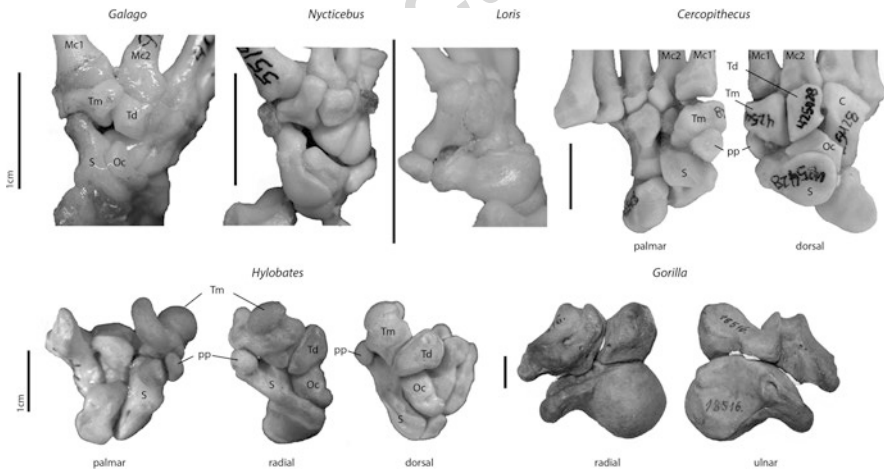
The pisiform is often described as a sesamoid bone and distinguished from the remaining “true” carpal bones (e.g. Flower 1885; Belliappa and Burke 1992; Scheuer and Black 2000). This description reflects the bias towards human morphology, where the pisiform is tiny and “pea-shaped” (hence, the name “pisiform”) bone, developing from a single ossification centre within the tendon of the flexor carpi ulnaris muscle (FCU) (Scheuer and Black 2000) and articulating solely with the triquetrum (Fig. 3.3). However, in other primates and mammals, the pisiform is a much larger, elongated bone that articulates with the distal ulna and, in some taxa, the hamate (Gillies 1929; Etter 1974; Cartmill and Milton 1977) or even the radius (*Daubentonia*; Mivart 1867; Flower 1885; Nayak 1933). The pisiform develops from two ossification centres (Eckstein 1944; Lewis 1989; Jouffroy 1991) that are divided by a palmar epiphyseal or growth plate (Harris 1944; Kjosness et al. 2014). Thus, the primate pisiform does not follow a sesamoid developmental pattern, and, because it articulates with more than one bone, it cannot be considered a true sesamoid (Gillies 1929, but see Flower 1885).

The large pisiform of most nonhuman primates functions as a “heel” for the hand. It is usually considered not to be weight bearing (Lewis 1989; Whitehead 1993), although this should be experimentally tested (see Patel and Wunderlich 2010). The pisiform projects proximopalmarly to provide bony origin for some of the hypothenar muscular and forms a cup-like articulation (with the triquetrum) for the distal ulna, which together stabilize the ulnar side of the wrist during the compressive loading of quadrupedal locomotion (Lewis 1989; Youlatos 1996). The pisiform defines the medial “wall” of the carpal tunnel with the hamate’s hamulus and serves as the attachment for the FCU and the abductor digiti minimi tendons (Diogo and Wood 2011 and references therein, but see Jouffroy 1975; see Chap. 7).

An elongated pisiform appears to be more functionally important for increasing the moment arm of the FCU rather than carpal tunnel depth (Sarmiento 1988; Lewis 1989; Hamrick 1997). For example, in humans, the planar joint between the pisiform and triquetrum allows for approximately 1 cm of movement, and thus contraction of the FCU is necessary to stabilize the pisiform for effective action of the abductor digiti minimi muscle (Brand and Hollister 1993; Marzke et al. 1998). The pisiform is especially long and palmarly projecting in pronograde quadrupedal taxa where the FCU acts to flex the wrist from an extended posture (Sarmiento 1988; Whitehead 1993; Hamrick 1997; Patel et al. 2012). In arboreal climbing primates, particularly lorises, spider monkeys and hominoids, the pisiform is relatively short (compared with the hamate hamulus) and more distopalmarly positioned in the palm (Lewis 1989; Youlatos 1996; Hamrick 1997). This morphology is thought to reflect a decreased commitment to quadrupedalism (i.e. less wrist flexion from an extended wrist posture) (Hamrick 1997) and, along with other derived features of the ulnocarpal region (see above), enhance pronation-supination and ulnar deviation (Sarmiento 1988). In African apes, it has also been proposed that the elongated pisiform plays a role in forelimb propulsion during knuckle-walking, especially at high speeds (Sarmiento 1985).

441 **8 Radial Carpometacarpal Joints**

442 The radial carpometacarpal (CM) joints include the complex articulations  
 443 between the scaphoid, trapezium, trapezoid and the first and second metacarpals.  
 444 In primates, the distolateral portion of the scaphoid body, often including its  
 445 tubercle, and os centrale (or the os centrale portion of the scaphoid when fused)  
 446 articulate with the trapezium and trapezoid (Fig. 3.6). The trapezoid also articu-  
 447 lates with the radiodorsal portion of the capitate (except in the gorilla for which  
 448 there is often no articulation at all; Lewis 1989; Tocheri et al. 2005). This region  
 449 is further complicated by the tendon of flexor carpi radialis, which runs palmarly  
 450 around the base of the trapezium's tubercle, and the trapezium also serves as  
 451 the origin for some the thenar muscles (see Chap. 7). The first metacarpal articulates  
 452 solely with the trapezium (the first CM joint), and the second metacarpal articu-  
 453 lates proximally with the trapezoid, laterally with the trapezium and medially  
 454 with the capitate. The **prepollex**, meaning "before the thumb", is greatly reduced  
 455 in primates compared with other mammals and appears, if at all, at the base of  
 456 the thumb, articulating with (or fused to, which is common in gorillas) to the  
 457 scaphoid tubercle and trapezium (Lewis 1989). The prepollux is thought to have  
 458 little influence on the mechanics of the radial CM joints, though it can serve as  
 459 an attachment site for the abductor pollicis longus and abductor pollicis brevis  
 460 muscles (Howell and Straus 1933). Within the radial CM joint, the trapezium-  
 461 Mc1 joint (Tm-Mc1) has received the most attention, both with regard to primate



**Fig. 3.6** Radial carpal-metacarpal joints. *Top* row showing the articulated radial carpometacarpal joints in some strepsirrhines (radial view) and *Cercopithecus* (palmar and dorsal views). *Bottom* row showing articulated radial carpal joints in *Hylobates* (palmar, radial and dorsal views), and re-articulated carpals in *Gorilla* (radial and ulnar views). Carpal bones included in radial carpal joints are labelled. Abbreviations: *Tm* trapezium, *Td* trapezoid, *S* scaphoid, *Oc* os centrale, *pp* prepollux, *C* capitate, *Mc1* first metacarpal, *Mc2* second metacarpal. All specimens are shown as the right side and scaled to approximately the same size (scale represents 1 cm for each taxon)

[AU10] morphology and in clinical studies (e.g. Haines 1944; Napier 1955; Tuttle 1969b; 462  
Kuczynski 1974; Cooney and Chao 1977; Lewis 1977, 1989; Rafferty 1990; 463  
Rose 1992). 464

Primates differ from tree shrews and other mammals in having a thumb complex 465  
that is relatively independent and more divergent from the remainder of the hand, 466  
which is likely related to more efficient manual grasping (Altner 1971; Boyer et al. 467  
2013; see Chap. 14). The opposable thumb is a functionally important feature of 468  
many, but not all, primate hands. Napier was the first to put forth classifications of 469  
thumb opposability in primates (Napier 1955, 1961; Napier and Napier 1967). 470  
Napier (1961: 119) defined opposition as “a compound movement of abduction, 471  
flexion and medial rotation” that is made possible by a saddle-shaped Tm-Mc1 472  
articulation. Thus, “true opposability” generally applies to the thumbs of catarrhines 473  
(e.g. Napier 1961; Rose 1992). In contrast, New World monkeys and strepsirrhines 474  
are often considered to have “pseudo-opposable” thumbs because the Tm-Mc1 joint 475  
is cylindrical or relatively flat, rather than saddle shaped (Napier 1961; Jouffroy and 476  
Lessertisseur 1979; Ziemer 1978). Thus, the joint acts more like a hinge and does 477  
not allow rotation (Napier 1961). Although these taxa can converge their thumb 478  
towards the fingers, this ability is due partly to a deep carpal arch (i.e. such that the 479  
trapezium is more in-turned relative to the other carpals) and flexion-extension, 480  
with only limited abduction-adduction, at the Tm-Mc1 joint (Napier 1961). 481

However, the terms “opposable” and “pseudo-opposable” are poorly defined and 482  
understood. Many since Napier have shown that a saddle-shaped Tm-Mc1 joint 483  
(implying both flexion-extension and abduction-adduction movements are possible) 484  
is common in most platyrrhines (Rafferty 1990), many strepsirrhines (Etter 485  
1974; Jouffroy and Lessertisseur 1979; Boyer et al. 2013) and some marsupials and 486  
carnivorans (Haines 1958; Lewis 1977, 1989). Indeed, Lewis (1977) suggested that 487  
a saddle-shaped joint Tm-Mc1 may be the primitive condition for mammals. The 488  
more limited opposability in platyrrhines (and likely strepsirrhines) stems from hav- 489  
ing more congruent axes of the saddle joint, such that conjunct axial rotation during 490  
flexion of the thumb is limited or absent (Rafferty 1990; Rose 1992). In addition, 491  
there are certainly muscular and neurological adaptations (e.g. more efficient digital 492  
coordination) that can have a strong influence on opposability, but may not be 493  
reflected in the bony morphology (Costello and Fragaszy 1988; Spinozzi et al. 494  
2004; see Chap. 12), further complicating how we define these terms functionally 495  
and how we might identify such abilities in the fossil record. 496

Across cercopithecoids, the Tm-Mc1 joint is generally saddle-shaped with little 497  
variation in bony morphology (Rafferty 1990). Even in colobines that have a dimin- 498  
utive thumb, the Tm-Mc1 joint is saddle shaped, although the curvature of the con- 499  
cavity is less developed than that of the convexity at this joint (Rafferty 1990). In 500  
contrast to cercopithecoids, there is much more variability in the New World mon- 501  
key trapezium-Mc1 joint (Mivart 1867; Lewis 1977; Rafferty 1990). For example, 502  
in callitrichids, one of the few primates considered to have little thumb opposabil- 503  
ity, the trapezium’s Mc1 facet is usually flat and is positioned distally and palmarly 504  
such that the Mc1 is less divergent and in the same plane as the other metacarpals 505  
(and even articulates with the Mc2) (Rafferty 1990; Boyer et al. 2013). Capuchin 506

507 monkeys, for which some species are known for their dexterity (i.e. *Sapajus*), have  
508 a saddle-shaped Tm-Mc1 facet with a deeper concavity-convexity that is more simi-  
509 lar to that of catarrhines than other ceboids (e.g. *Aotus*). Squirrel monkeys (*Saimiri*)  
510 have a small and relatively flat trapezium-Mc1 facet (Mivart 1867; Lewis 1977;  
511 Rafferty 1990), while still other species (i.e. *Pithecia*, *Chiropotes*) have a pro-  
512 nounced groove (on the trapezium) and keel (on the Mc1) across the dorsopalmar  
513 surface of the Tm-Mc1 joint that makes the joint surfaces highly congruent and  
514 limited in their mobility (Rafferty 1990). In *Ateles*, in which the thumb is extremely  
515 reduced, the trapezium shows no reduction relative to other carpals, but the Tm-Mc1  
516 facet is small and flat (as in *Lagothrix* and *Alouatta*) (Rafferty 1990; contra Lewis  
517 1977; Ziemer 1978).

518 Finally, all great apes have a well-developed saddle-shaped Tm-Mc1 joint and  
519 differ from non-hominoid primates in having much greater abduction-adduction  
520 mobility (Rose 1992). Hylobatids are unusual among primates in that the Mc1 facet  
521 on the trapezium is convex half sphere, rather than saddle shaped, and fits with a  
522 concave trapezium facet on the Mc1 (Lorenz 1971; Lewis 1977, 1989; Rafferty  
523 1990; Fig. 3.6). This morphology creates a distinctive ball-and-socket Tm-Mc1  
524 joint that allows for greater mobility in hylobatids compare with other primates,  
525 although the large tubercle of the trapezium limits abduction and flexion of the  
526 thumb (Lorenz 1971; Lewis 1977, 1989; Rafferty 1990).

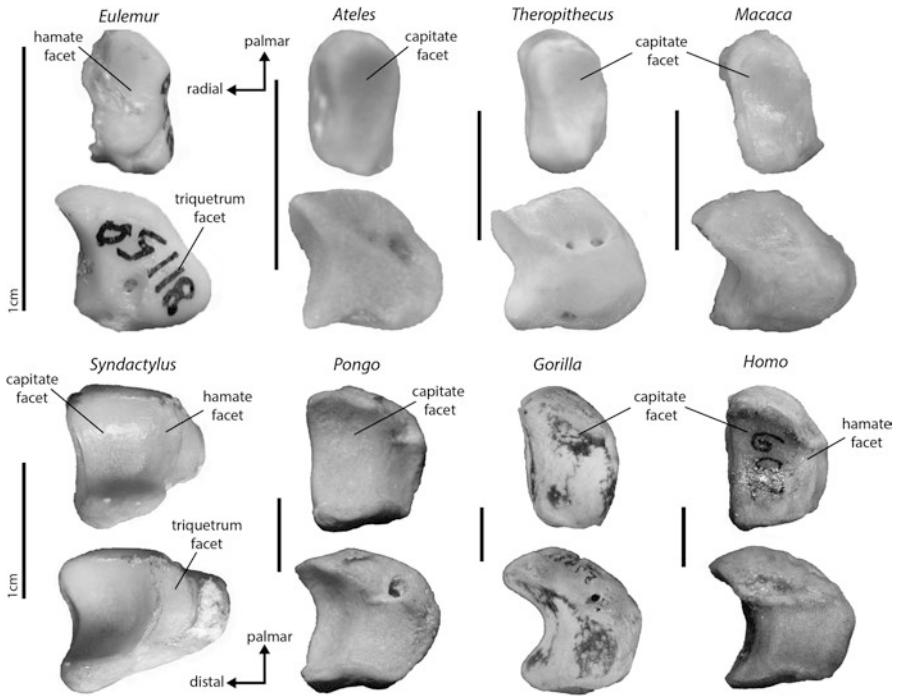
527 The articulations between the scaphoid/os centrale-trapezium-trapezoid (STT)  
528 and the second metacarpal have received much less attention than the Tm-Mc1 joint  
529 (Kauer 1986; Moritomo et al. 2000a, b; Tocheri et al. 2003, 2005; Begun 2004;  
530 Sonenblum et al. 2004; Tocheri 2007). Most studies limit discussion of this region  
531 to the variation in the capitate-trapezoid embrasure (i.e. v-shaped gap) for the os  
532 centrale (or scaphoid, when the os centrale is fused) during midcarpal joint rotation  
533 (e.g. Jenkins 1981; Lewis 1989; Hamrick 1996a; Schwartz and Yamada 1998; see  
534 below). For example, in arboreal quadrupedal strepsirrhines, the embrasure is wid-  
535 est on the dorsal surface, which facilitates palmar rotation (pronation) of the  
536 proximal carpals into the capitate-trapezoid embrasure. In contrast, in vertical cling-  
537 ing and leaping strepsirrhines, the embrasure is wider on the palmar side (and con-  
538 stricted dorsally), thus facilitating dorsal rotation (supination) of the proximal  
539 carpals at the midcarpal joint (Hamrick 1996a). Hylobatids and *Ateles* also have a  
540 dorsally constricted capitate-trapezoid embrasure, allowing for a greater range of  
541 midcarpal supination (Jenkins 1981; see below). These differences in morphology  
542 stem largely from variation in the shape of the capitate and variation in how the  
543 trapezoid is oriented within the carpus. For example, the scaphoid-trapezoid articu-  
544 lation is more proximodistally oriented in vertical clinging and suspensory primates  
545 to enhance mobility, while in quadrupeds the scaphoid-trapezoid articulation is  
546 more radioulnarly oriented to better resist compression (Hamrick 1996a; Richmond  
547 et al. 2001; Begun 2004). However, there is substantial morphological variation in  
548 the orientation of the scaphoid-trapezoid articulation that does not always correlate  
549 well with locomotor strategy [e.g. Figs. 3.2 and 3.6; see also Fig. 7 in Hamrick  
550 (1996a) and Fig. 9 in Richmond et al. (2001)].

The articulations across the STT joint have only been well studied in extant 551  
hominids by Tocheri and colleagues (Tocheri et al. 2003, 2005; Tocheri 2007). The 552  
trapezoid in most primates can be described as wedge shaped with a narrow palmar 553  
non-articular surface and broad dorsal non-articular surface. In most Old World 554  
monkeys and African apes, the Mc2 articulation is strongly keeled (rather than 555  
relatively flat as in Asian apes) to provide a more stable CM joint (Fig. 3.2, see 556  
below). Furthermore, the human trapezoid is derived in having a radioulnarly- 557  
expanded non-articular palmar surface, which gives it its characteristic “boot- 558  
shape” appearance and promotes reorientation of the radial carpals and thumb into 559  
a more supinated position (Lewis 1989; Tocheri et al. 2003, 2005). In most pri- 560  
mates, the scaphoid’s articulation with the trapezoid is larger than that with the 561  
trapezium, while the opposite pattern is true for humans (Marzke et al. 1992; 562  
Tocheri et al. 2005). Humans also have a larger trapezoid-capitate articulation that 563  
is positioned more palmarly rather than dorsally as in other primates. These differ- 564  
ences in the radial CM joints across apes are functionally consistent with how the 565  
hands are used during positional behaviour. In knuckle-walking or suspension, 566  
loading is transmitted distoproximally through the Mc2-trapezoid-scaphoid. In 567  
contrast, forceful precision and power grips load this region of the human hand 568  
more transversely (radioulnarly), mainly via the Mc1-trapezium-scaphoid (Lewis 569  
1989; Tocheri et al. 2005; Tocheri 2007). Thus, reorientation of the radial CM 570  
articulations in humans is thought to better accommodate compressive loading 571  
from the thumb towards the palm (Lewis 1989; Tocheri et al. 2003; Tocheri 2007). 572

## 9 The Midcarpal Joints 573

The **midcarpal joint** refers to the articulation between the proximal and distal rows of 574  
the carpus. It is a complex joint that varies strongly in the relative contributions and 575  
orientations of particular bones and joint surfaces, but generally can be described 576  
broadly as a ball-and-socket-type articulation: the mainly distally oriented facets of the 577  
scaphoid/os centrale, lunate and triquetrum in the proximal carpal row form a radioulnarly 578  
and dorsopalmarly concave “socket”, and the proximal facets of the capitate and 579  
hamate in the distal carpal row form the correspondingly convex “ball” (Figs. 3.2, 3.4, 580  
3.7, 3.8). The capitate and hamate are firmly bound together by interosseous ligaments 581  
and essentially function as a unit in all primates. In most strepsirrhines and tarsiers, the 582  
hamate is much larger than the capitate; the os centrale is ulnarly extended such that it 583  
articulates with the hamate, cutting off the articulation between capitate and lunate 584  
(Jouffroy 1975; Godinot and Beard 1993; Schwartz and Yamada 1998; Stafford and 585  
Thorington 1998; Fig. 3.2). This is thought to be functionally related to the frequent 586  
ulnar deviation at the midcarpal joint common in strepsirrhines (Hamrick 1997; 587  
Lemelin and Schmitt 1998). In contrast, in most anthropoids (although hylobatids are 588  
a notable exception), the capitate is larger than the hamate, such that the midcarpal 589  
articular configuration is primarily between the capitate-os centrale/scaphoid-lunate 590  
and between the hamate-triquetrum (Figs. 3.2 and 3.4). The radial articulations between 591

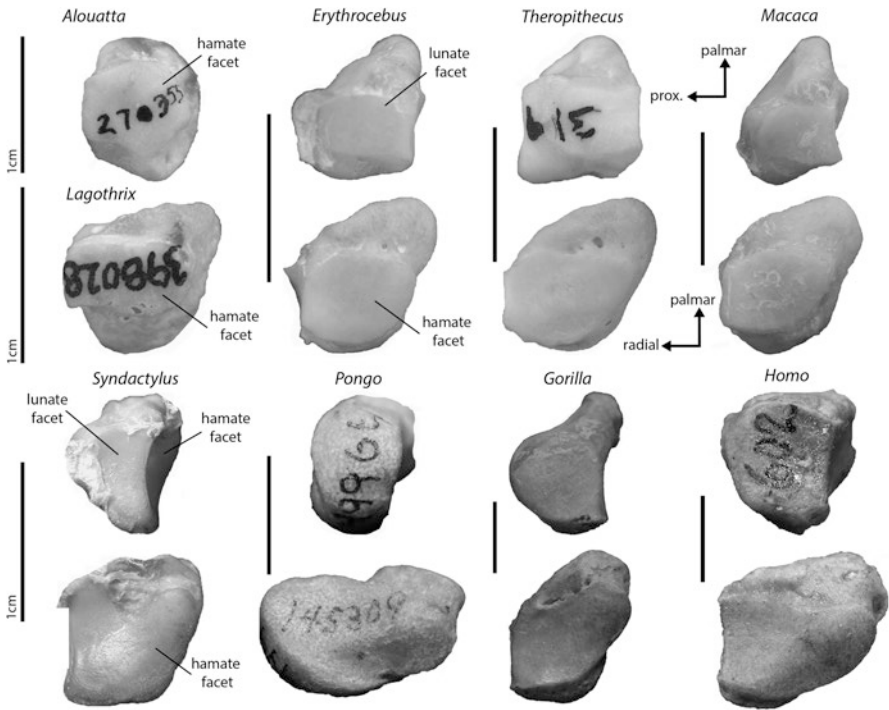
[AU11]



**Fig. 3.7** Variation in primate lunule morphology. *Top* row for each taxon shows the distal view of the lunule, featuring the midcarpal articulation with either the hamate, capitate or both. *Bottom* row for each taxon shows the ulnar view of the lunule, featuring the triquetrum facet. All specimens are shown as the right side and scaled to approximately the same size (scale represents 1 cm for each taxon)

592 the scaphoid, trapezium and trapezoid discussed above also can be strictly considered  
 593 the “midcarpal joint”, but are usually considered as a somewhat separate functional  
 594 unit and not included in discussions of mobility/stability of the primate midcarpal joint  
 595 (e.g. Lewis 1985a, b; Lemelin and Schmitt 1998; Begun 2004; Richmond 2006; but  
 596 see Jenkins 1981 and Richmond et al. 2001).

597 The midcarpal joint permits movement of the hand relative to the forearm in  
 598 three planes: flexion/extension, radial/ulnar deviation and pronation/supination.  
 599 Combinations of movements in these planes in which the proximal carpal row  
 600 moves into a stabilized or “close-packed” position on the distal carpal row is  
 601 referred to as a “screw-clamp” mechanism (MacConaill 1941; Lewis 1989; Orr  
 602 et al. 2010; Fig. 3.9). In quadrupedal primates and humans, movement at the mid-  
 603 carpal joint into a close-packed position is achieved via a combination of exten-  
 604 sion, ulnar deviation and pronation (i.e. rotation) (Lewis 1989). This combined  
 605 movement appears to be primitive, shared with other mammals such as opossums  
 606 (Jenkins 1971; Lewis 1989). Supination at the midcarpal joint in quadrupedal pri-  
 607 mates is relatively limited (Jenkins 1981). In contrast, the screw-clamp mechanism  
 608 in suspensory primates seems not to be as effective as in quadrupeds (at least in the

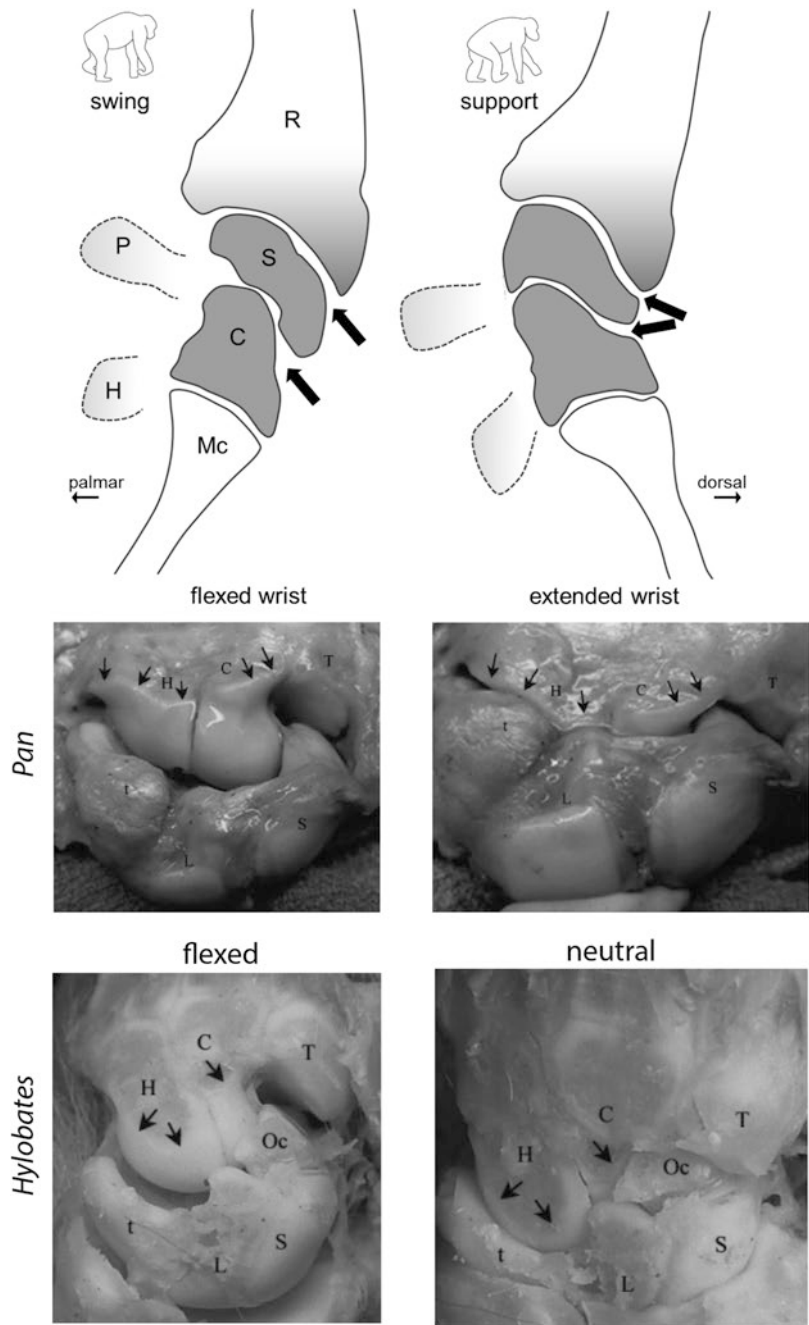


**Fig. 3.8** Variation in primate triquetrum morphology. *Top* row for each taxon (except for *Alouatta*) shows the radial view of the triquetrum, featuring the lunate facet. *Bottom* row for each taxon shows the distoradial view of the triquetrum, featuring the hamate facet. Only distoradial views are shown for *Alouatta* and *Lagothrix*. All specimens are shown as the right side and scaled to approximately the same size (scale represents 1 cm for each taxon)

taxa that it has been studied *in vitro*); close packing occurs at a much higher degree of extension in *Pongo* compared with *Pan* (Orr et al. 2010; see Chap. 9). In brachiators (*Ateles*, *Lagothrix* and hylobatids), the midcarpal joint undergoes a high degree of supination, with limited mobility in terms of pronation (Jenkins 1981); the opposite pattern of quadrupeds (Fig. 3.10).

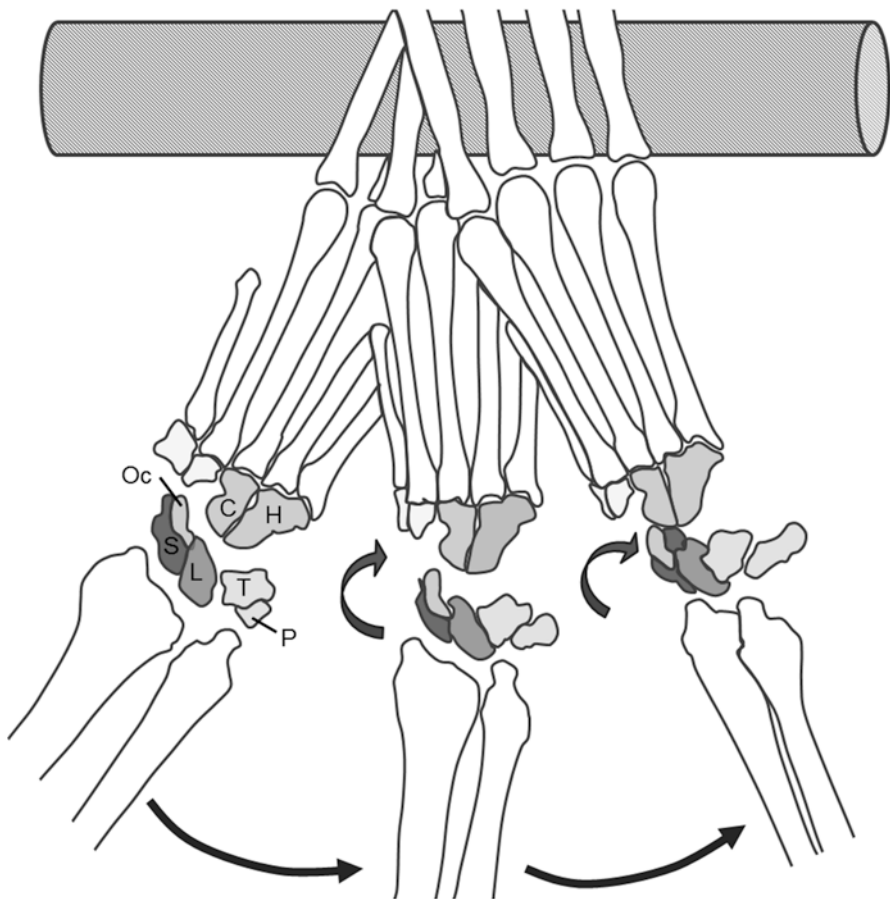
The degree of midcarpal joint curvature is correlated with the range of radioulnar deviation and midcarpal rotation of the hand (Jenkins and Fleagle 1975; Jenkins 1981; Sarmiento 1988; Hamrick 1996a, b). Arboreal or terrestrial quadrupedal primates have flatter midcarpal joint surfaces (i.e. larger radius of curvature) than those of suspensory (e.g. Asian apes, spider monkeys) or climbing/bridging primates (e.g. lorises). The scaphoid-os centrale-capitate and triquetrum-hamate articulations are more proximally oriented compared with suspensory primates, and in terrestrially-adapted quadrupedal taxa [e.g. baboons, patas monkeys, African apes (but also humans)], the proximal capitate and hamate facets are also radioulnarly broader (relative to carpal length) (Yalden 1972; O'Connor 1975; Jenkins 1981; Lewis 1985b; Sarmiento 1988; Richmond 2006; Lemelin et al. 2008).

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**Fig. 3.9** “Close packing” of the midcarpal joint. Schematic *above* shows wrist posture during knuckle-walking swing phase and support phase. In swing phase the wrist is flexed, and there is space between the articulations of the radius-scaphoid-capitate when viewed dorsally (*block arrows*). In the support or weight-bearing phase, the wrist is extended the radius-scaphoid-capitate achieve a “close-packed” articulation. The palmarly projecting pisiform (P) and hamate hamulus (H) are also depicted. *Middle*, dorsal views of a *Pan* cadaveric wrist shown in a flexed and extended “close-packed” postures. *Below*, dorsal views of *Hylobates* cadaveric wrist in a flexed and neutral posture. R radius, S scaphoid, C capitate, Mc metacarpal. All images adapted from Richmond et al. (2001)





**Fig. 3.10** Rotation at the midcarpal joint during brachiation in a spider monkey. “Exploded” dorsal view of the hand at the beginning (*left*), middle and end (*right*) of swing, demonstrating how the proximal carpal row, with the forearm, supinates around the “ball” formed by the capitate and hamate proximal facets. Image adapted from Jenkins (1981)

Together, this morphology limits radioulnar deviation and supination, creating greater stability during the extended wrist postures typically used during palmigrade or digitigrade locomotion. However, it is interesting to note that baboons and patas monkeys have more distally extended dorsal joint surfaces on the capitate and hamate than in hylobatids and yet have much more limited extension, showing that bony morphology is not always necessarily indicative of mobility (Lovejoy et al. 2001; Richmond 2006); instead, joint curvature appears to be more closely linked to mobility (Chap. 9).

During brachiation the majority of rotation in the hand occurs at the midcarpal joint (Jenkins 1981; Fig. 3.10). Thus, brachiators such as spider monkeys and hylobatids, as well as suspensory primates (e.g. orangutans), share similar, highly curved midcarpal joint morphology. The scaphoid-os centrale-capitate articulation is more radially oriented, and the hamate-triquetrum articulation is more ulnarly oriented,

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638 which allows for considerable radioulnar deviation. The more distally extended  
639 (both dorsally and palmarly) proximal facets on the capitate and hamate allow for  
640 increased flexion-extension (Richmond 2006). Together, this morphology allows  
641 for a much larger degree of supination at the midcarpal joint than is typically found  
642 in pronograde quadrupedal primates (Fig. 3.10).

643 Lorisids converge on the suspensory morphotype with proximal facets of capi-  
644 tate and hamate that are more curved and a hamate-triquetrum facet that is oriented  
645 more dorsally compared with other quadrupedal strepsirrhines (Lewis 1985a;  
646 Hamrick 1996b). This morphology, in addition to the reduced ulnar-carpal articula-  
647 tion described above, promotes pronation and extreme ulnar deviation of the hand  
648 (Hamrick 1996b; Lewis 1985a), as well as supination (Lemelin and Schmitt 1998),  
649 required for frequent climbing and bridging.

650 There has been much discussion about the midcarpal joint of African apes and  
651 humans (e.g. Tuttle 1967; Jenkins and Fleagle 1975; Corruccini et al 1975; Corruccini  
652 1978; Sarmiento 1994; Dainton and Macho 1999; Richmond and Strait 2000;  
653 Richmond et al. 2001; Begun 2004; Kivell and Schmitt 2009; Williams 2010).  
654 Because the triquetrum is reduced in size and os centrale is fused, the scaphoid's capi-  
655 tate facet (the os centrale portion) contributes more to the midcarpal joint than in other  
656 anthropoids, in which the os centrale, lunate and triquetrum contribute roughly equally  
657 to the "socket" of the midcarpal joint (Richmond et al. 2001; Begun 2004; Figs. 3.2,  
658 3.5, 3.8). There are several aspects of the African ape midcarpal joint that are consid-  
659 ered advantageous for limiting extension and making the wrist more stable during the  
660 knuckle-walking [the retention of some of these features in humans may suggest  
661 hominins evolved from a knuckle-walking ancestor; see Richmond et al. (2001) for a  
662 review]. On the capitate, the concave distal portion of the scaphoid facet is expanded  
663 in African apes compared with the solely convex articular surface in Asian apes or the  
664 smaller concave portion in macaques (Jenkins and Fleagle 1975). The convex-con-  
665 cave midcarpal articulation on the capitate contributes to the "waisting" or narrowing  
666 of the capitate body, which allows the scaphoid to wedge firmly into the capitate-  
667 trapezoid embrasure during extension (Figs. 3.2 and 3.9). The hamate-triquetrum  
668 facet is described as a spiraling, concavo-convex articulation, with the most distal  
669 portion of this articulation facing nearly proximally, to provide additional stability.  
670 Dorsal ridges at the most distal extent of the capitate and hamate midcarpal articula-  
671 tions also help to limit extension and provide stability during compression in a slightly  
672 extended wrist posture typical during knuckle-walking (Jenkins and Fleagle 1975;  
673 Richmond et al. 2001). Many or all of these traits have been considered specific adap-  
674 tations to knuckle-walking (e.g. Tuttle 1967, 1969; Corruccini 1978; Zylstra 1999;  
675 Begun 2004; Richmond et al. 2001). However, many of these features (e.g. spiral tri-  
676 quetrum-hamate facet and dorsal ridges) are also found in Old World monkeys and,  
677 thus, likely reflect quadrupedal adaptations more generally (Jenkins and Fleagle 1975;  
678 Richmond et al. 2001; Richmond 2006, but see Lewis 1989). Furthermore, there is  
679 substantial variation in degree of expression or even presence of these "knuckle-walk-  
680 ing" features across African apes (Sarmiento 1994; Richmond 2006; Kivell and  
681 Schmitt 2009). For example, capitate waisting and dorsal ridges of the capitate and  
682 hamate proximal facets are less pronounced in *Gorilla* than in *Pan*, despite their more  
683 frequent terrestrial knuckle-walking (Richmond 2006; Kivell and Schmitt 2009).

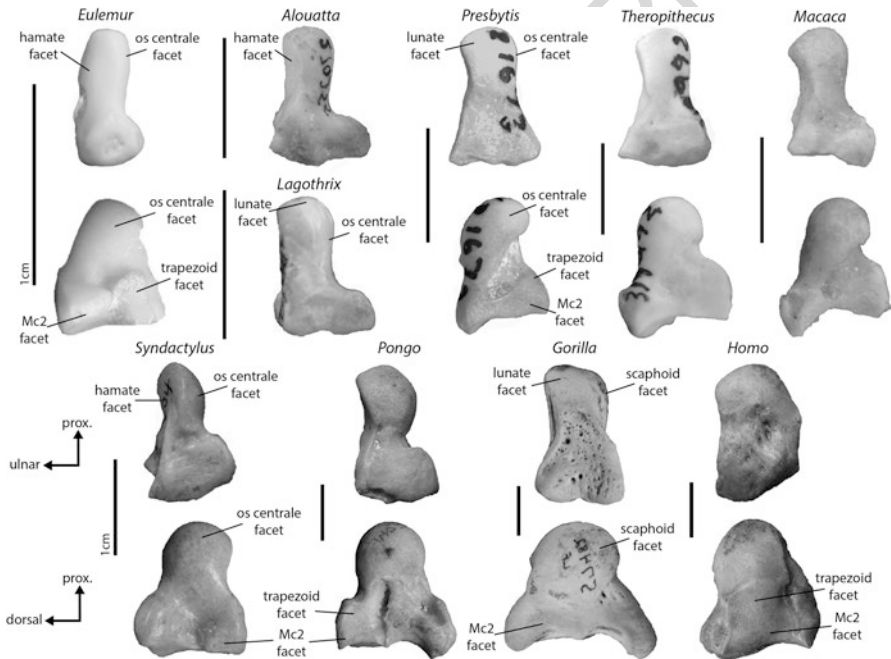
### 10 The Ulnar Carpometacarpal Joints

The ulnar carpometacarpal (CM) joints refer to the articulations between the trapezoid, capitate and hamate and ulnar metacarpals (Mc2-Mc5) (see also Sect. 8 above for discussion on the trapezoid-Mc2 articulation) (Figs. 3.11 and 3.12). These articulations take on various forms depending on the taxon, but are usually much more stable, planar joints in contrast to the mobile, often saddle-shaped, first CM joint.

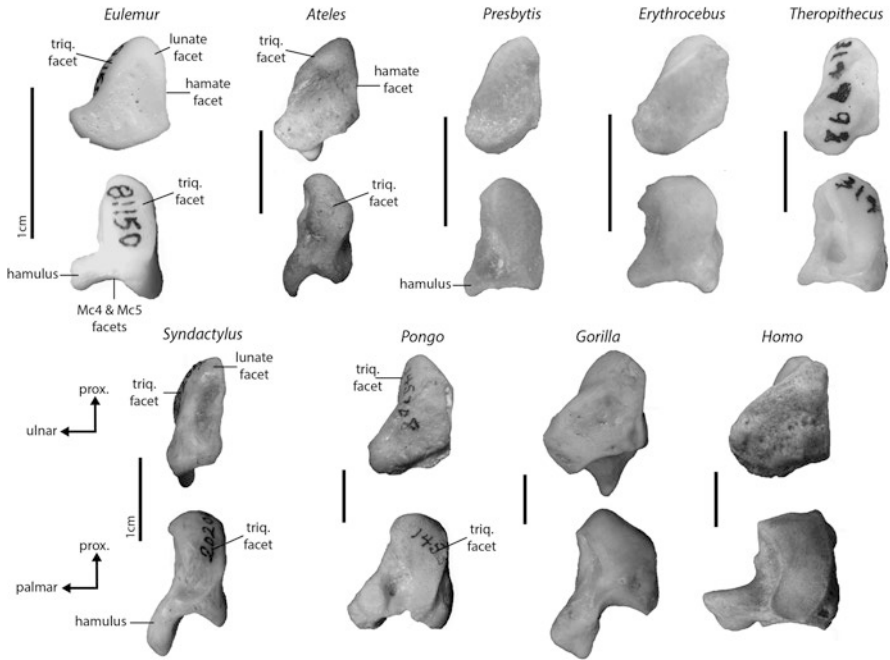
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Primates retain a primitive mammalian condition of a “stepped” configuration across the ulnar CM joints: the Mc2 extends proximally on its ulnar side to articulate primarily with trapezoid, but also the capitate and Mc3 ulnarly and the trapezium radially (Lewis 1989; Figs. 3.1 and 3.2). The Mc3 also extends slightly proximally to articulate with hamate ulnarly. The Mc5-hamate articulation is usually oriented more ulnarly than the remaining ulnar CM articulations. There is a complex network of CM and intermetacarpal ligaments that help stabilize the

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**Fig. 3.11** Variation in primate capitate morphology. *Top* row for each taxon (except for *Lagothrix*) shows the dorsal view of the capitate, featuring the dorsal portion of the proximal facet. *Bottom* row for each taxon shows the radial view of the capitate, featuring the os centrale facet (or scaphoid facet in *Gorilla* and *Homo*), second metacarpal (Mc2) facet and trapezoid facet. Note that the capitate-trapezoid articulation in *Gorilla* is variable, ranging from absent to being palmarly positioned, like in humans (Lewis 1989). Only dorsal views are shown for *Alouatta* and *Lagothrix*. All specimens are shown as the right side and scaled to approximately the same size (scale represents 1 cm for each taxon)



**Fig. 3.12** Variation in primate hamate morphology. *Top* row for each taxon shows the dorsal view of the hamate. *Bottom* row for each taxon shows the ulnar view of the hamate, featuring the triquetrum facet and variation in the size and orientation of the hamulus. Note that the proximal hamate in *Eulemur* and *Symphalangus* also articulates with the lunate (because the capitate is comparatively small) at the midcarpal joint, while in most other anthropoids the hamate articulates only with the triquetrum (apart from occasional hamate-lunate articulation in African apes and humans; see Marzke et al. 1994). The distal articular surface of the hamate articulates with the Mc4 and Mc5 in all taxa. All specimens are shown as the right side and scaled to approximately the same size (scale represents 1 cm for each taxon)

698 joints between the distal carpals and Mc2-Mc5 (while the Tm-Mc1 is notably separated from this ligamentous network, emphasizing its distinctive functional role for  
 699 movement of the thumb) (Lewis 1989). Tree shrews, some insectivorous eutherians  
 700 (e.g. tenrecs) and some marsupials (e.g. opossums) also retain a stepped configuration  
 701 of the ulnar CM joints, but show more derived osteological and soft tissues morphologies  
 702 than most primates (Lewis 1989). For example, in some marsupials, a convex Mc2-capitate  
 703 articulation and loss of the CM ligament permits more mobility of the Mc2, while the  
 704 extensor carpi ulnaris tendon not only attaches on the Mc5 (as in primates) but also  
 705 crosses the palm all the way to the Mc2 (Lewis 1989), possibly enhancing the mobility  
 706 of the ulnar metacarpals at their base. Furthermore, while many primates (particularly  
 707 strepsirrhines and hominoids) have a well-developed and projecting hamate hamulus,  
 708 the hamate of tree shrews and squirrels has only a small palmar protuberance (Lewis  
 709 1989; Hamrick 1997, see his Fig. 3; Fig. 3.12).  
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Most strepsirrhines display the stepped configuration of ulnar CM joints described above; however, in some taxa (e.g. *lemur*), the articulation between the hamate and Mc3 is reduced (Fig. 3.2). The capitate and hamate metacarpal articulations are generally planar, with limited mobility. The hamate hamulus is more well developed than in Old and New World monkeys (Hamrick 1997), creating a deeper carpal tunnel (in conjunction with a well-developed scaphoid tubercle) (Fig. 3.12).

Old and New World monkeys share similar ulnar CM articulations as in strepsirrhines, except that an articulation between the hamate and Mc3 is typically lacking and the Mc4 also articulates with the capitate (Lewis 1989; Marzke et al. 1994; Figs. 3.2 and 3.4). The metacarpal articulations of the capitate and hamate tend to be smooth and dorsopalmarly concave to match dorsopalmarly convex facets on the proximal metacarpals. As such, there is some degree of movement at these joints. For example, the Mc3 is capable of some flexion and combined extension-supination movement (Marzke and Marzke 1987). Furthermore, when the Mc4 and Mc5 extend, this movement is combined with slight pronation. These combined movements bring the metacarpals inline transversely and provide stability during the extended posture of palmigrade or digitigrade locomotion (Marzke 1983; Marzke and Marzke 1987). However, there is subtle variation in the morphology of these CM joints across cercopithecoids, which translates into slight variations in mobility. For example, *Papio* has a more complex concavo-convex capitate-Mc3 articulation, reminiscent of the morphology found in *Pan* (see below), which provides greater stability during digitigrade (Marzke and Marzke 1987). Although the hamate hamulus is usually small (i.e. beak-like process) as in other mammals (Lewis 1989; Hamrick 1997), the metacarpal articular surfaces extend onto the hamulus. The short hamulus of *Papio* reflects a shallow carpal tunnel compared to strepsirrhines and hominoids (Hamrick 1997), likely reflecting a de-emphasis of the digital flexor musculature used during climbing or suspensory activities.

Hominoids also display a stepped configuration, although the Mc4-capitate articulation is reduced relative to Old and New World monkeys, articulating only at the dorsal corner, if at all (Lewis 1989; Marzke et al. 1994). The Mc4 and Mc5 facets extend onto a well-developed hamulus in all hominoids (except humans). However, the hamulus varies in its angulation: Asian apes tend to have a hamulus that is more distally extended; the *Pan* hamulus is best described as being equally distally and palmarly extended; the *Gorilla* and humans hamuli primarily project palmarly [see Orr et al. (2013) for a quantification of hamulus shape and angle]. A well-developed hamulus is most clearly associated with a deep carpal tunnel and a strong digital flexor musculature (Hamrick 1997; Ward et al. 1999; Ward 2002). There have been various functional explanations provided for a more distally projecting versus a more palmarly projecting hamulus. A more distally extended hamulus, like that of *Pan*, obstructs the amount of flexion at the Mc5-hamate joint (Ward et al. 1999; Ward 2002), while a more palmarly projecting hamulus would increase the mechanical advantage of the opponens digiti minimi and flexor digiti minimi muscles (Ward et al. 1999). It has also been suggested that variation in the orientation of the hamulus would enhance the ability of the FCU to act as a wrist adductor or wrist flexor, respectively (Sarmiento 1988; Ward et al. 1999). However, Ward (2002)

757 noted importantly that the FCU attaches (via the pisohamate ligament) to the base  
758 of the hamulus, not its tip, and thus its extension and orientation likely have little  
759 effect on FCU function.

760 In Asian apes, the capitate and hamate metacarpal articulations are smooth and  
761 slightly dorsopalmarly concave, and the Mc5 articulation is more proximally oriented,  
762 falling more in line with the remaining ulnar CM facets compared with other  
763 haplorhines. In contrast, the African ape capitate and hamate metacarpal articular  
764 areas, particularly in *Pan*, are concavo-convex, creating a more complex and stable  
765 articulation that limits sliding and rotation at these joints (Marzke and Marzke 1987;  
766 Begun 2004). The trapezoid-Mc2 articulation has also been described as more  
767 keeled than that of other primates (Begun 2004), although this is debatable as  
768 hylobatids and many Old World monkeys also show similar keeling. Altogether, the  
769 complexity of the ulnar CM articulations in African apes has been functionally  
770 associated with increasing stability needed to resist compressive or shear forces  
771 during knuckle-walking (Richmond et al. 2001; Begun 2004).

772 Humans arguably have the most derived ulnar CM condition among primates. In  
773 humans, the trapezoid-Mc2 articulation is oriented in more of a radioulnar plane,  
774 rather than sagittal (proximodistal) plane, as in other apes (Lewis 1989; Tocheri  
775 et al. 2005; Tocheri 2007). The proximal Mc3 displays a distinct styloid process at  
776 its radiodorsal corner, and the corresponding portion of the capitate is bevelled. The  
777 styloid process is considered to be the result of a separate ossification centre fusing,  
778 via an embryonic migration, to the base of the Mc3 instead of the dorsoradial corner  
779 of the capitate as in other primates (Marzke and Marzke 1987; Lewis 1989; Lovejoy  
780 et al. 2009). A separate “os styloideum” is found in about 6 % of humans (O’Rahilly [AU12]  
781 1953) and rarely in other primates (Marzke and Marzke 1987). Because a styloid  
782 process is found consistently only in humans and Neanderthals (i.e. committed tool-  
783 using hominins), it is thought to help stabilize the intercarpal joints during forceful  
784 and complex manipulative tasks and is associated with the suite of changes that  
785 evolved in the human radial CM joints described above (Marzke and Marzke 1987,  
786 2000; Marzke 2013).

787 The human hamate-Mc4/Mc5 articulation is much flatter than the more complex  
788 articulation of African apes, with only a slight dorsopalmar concavity on the hamate.  
789 However, the hamate facet for the Mc5 is often described as saddle shaped, with a  
790 slightly radioulnar convexity as well (Lewis 1989; Marzke and Marzke 2000). The  
791 Mc4 and Mc5 facets do not extend onto the hamulus. Furthermore, the hamate facet  
792 of the Mc5 is proportionately larger than that of the Mc4, while the opposite is true  
793 in African apes (Marzke et al. 1992; Orr et al. 2013). Together, the relatively  
794 enlarged and saddle-shaped Mc5 facet have been hypothesized to be related to  
795 greater loading of the ulnar digits and allowing slight rotation during flexion of the  
796 fifth digit during forceful precision and power-squeeze grips (Marzke et al. 1992).  
797 However, the relatively larger Mc5 facet in humans likely reflects a reduction in the  
798 Mc4 facet rather than enlargement of the Mc5 itself. Orr et al. (2013) suggested that  
799 reduction of the Mc4 is related biomechanically to reducing obstruction for Mc5  
800 movement, more specifically, for increasing rotation of the Mc5 during flexion as it  
801 opposes the thumb.

## 11 Conclusions

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Just as Wood Jones (1916) and Napier (1961) described the human hand as generalized and primitive compared with most mammals, the primate carpus also can be considered as such. The retention of eight or nine wrist bones, like the retention of five digits, is primitive among mammals and differs from the more derived occurrence of carpal fusions in many mammal orders, including those closely related to primates. But the primitiveness of the primate carpus stems from more than just having retained independent carpal bones; the conjunct movement of the carpal bones (i.e. close packing in extension, ulnar deviation and pronation) is a primitive condition among mammals as well. Even the saddle-shaped trapezium-Mc1 joint that permits the opposability of thumb—a defining feature of the primate hand—is considered primitive among mammals. Primates likely retain this primitiveness because it allows for a greater degree of versatility in wrist (and hand) function necessary for the complex, three-dimensional locomotor and manipulative environments they inhabit.

That being said, there have been some changes in wrist morphology from this primitive condition across primates: some subtle and some not so subtle. The more subtle differences in carpal structure, such as relative sizes of particular carpal bones, slight changes in orientation or size of facets or development of ridges or more complex articular morphology, translate into slight variations in mobility that are generally consistent with differences in locomotor behaviour and habitual hand use. Not-so-subtle changes include convergent changes in the antebrachiocarpal joint, such that hominoids, lorises and, to a lesser extent, spider monkeys have reduced or no contact between the ulna and carpus. Similar derived morphology across other mammals is only known in highly suspensory two-toed sloths (Mendel 1979). Scaphoid-os centrale fusion in African apes, humans and a few strepsirrhine taxa is also a derived feature of the carpus, reminiscent of carpal fusions that are found in closely related mammals, though the development, functional or phylogenetic reasons for this fusion across different primate clades is still unclear.

It is interesting to note that across primates, taxa with extremely specialized hands, such as aye-ayes (elongated third and fourth digits), colobines and spider monkeys (reduced thumbs) or lorises (highly divergent thumb and reduced index finger for pincer-like grasping) could be described as showing relatively limited change in their carpal morphology. In other words, the derived changes appear more so in the digits rather than the carpus. Somewhat ironically, the taxon with the most derived changes to the carpus is arguably humans, which shows scaphoid-os centrale fusion, reorientation of the radial carpals, development of a styloid process and extreme reduction in the pisiform (see Chap. 18). However, despite these changes, Wood Jones and Napier's description of the human hand as primitive is still a valid assessment for the human and nonhuman primate carpus within the broader context of mammals.

843

844 **12 Future Directions**

845 There is still much to be learned about the basic morphology of the carpal bones,  
846 particularly the lunate, triquetrum and trapezoid, that remains relatively understud-  
847 ied across all primates compared with other carpals. There has been a historical  
848 focus on the great ape carpus given their close phylogenetic relationship to that of  
849 humans. Still, we have a comparatively poor understanding about the intraspecific  
850 variation within each taxon, or how subspecies might differ based on variation in  
851 ecology or frequency of locomotor behaviours (e.g. Tocheri et al. 2011). A common  
852 caveat of functional analyses is that morphological variability *within* extant species  
853 may hinder our ability to use living species as models for the functional interpreta-  
854 tion of morphology in fossils (Marzke et al. 1994). Given the particular importance  
855 African ape morphology plays in the functional interpretation of fossil hominin and  
856 hominoid morphology (e.g. Beard et al. 1986; Ward et al. 1999; Tocheri et al. 2007;  
857 Kivell and Begun 2009; Lovejoy et al. 2009; Begun and Kivell 2011; Kivell 2011;  
858 Kivell et al. 2011; see Chap. 18), understanding both intraspecific and interspecific  
859 variation in these taxa is especially important.

860 Furthermore, it is commonly stated or assumed that Old World monkey carpal  
861 morphology is generally similar across the clade (e.g. Corruccini 1978; Lewis 1989;  
862 Rafferty 1990). Further research is needed to determine if this representation holds  
863 true for all Old World monkey wrists, given the extensive variation in (1) arboreal/  
864 terrestrial locomotor behaviours (including high frequencies of bridging and sus-  
865 pensory behaviours in some taxa), (2) ecology (e.g. highly terrestrial macaques  
866 versus cliff-climbing langurs), (3) hand postures [e.g. palmigrade, graspwalk or  
867 digitigrade (Hunt et al. 1996)] or (4) autapomorphic hand morphologies (e.g. reduc-  
868 tion in the thumb in colobines) throughout the clade. This would provide a better  
869 comparative context for understanding the variation in hominoid morphology,  
870 particularly when Miocene fossils are considered (Chap. 17), and the seemingly  
871 greater variation in New World monkey carpal morphology (Rafferty 1990), though  
872 the latter is also relatively understudied.

873 Four recent methodological advancements (see Chap. 9) are ideal for analyzing  
874 the complex and irregular shape of carpal bones. Firstly, 3D analysis of external  
875 morphology (e.g. via surface scanning) has proven to be a much more objective and  
876 informative method for quantifying and comparing morphology across taxa than  
877 traditional 2D measures or qualitative descriptions (e.g. Tocheri et al. 2003, 2005;  
878 Orr et al. 2013). Secondly, analyses of the internal bone structure, including cortical  
879 and trabecular bone distribution, may help to reveal variation in how individual  
880 carpal bones are habitually loaded during life. Initial analyses of trabecular bone in  
881 the primate carpal bones using traditional volume-of-interest-based methods have  
882 proven functionally uninformative (Schilling et al. 2014). However, new methods  
883 of analyzing the distribution of cortical thickness and trabecular structure through-  
884 out the bone promise to reveal greater functional information (Gross et al. 2014;  
885 Skinner et al. 2015).



Thirdly, although single-plane cineradiography (e.g. Jenkins and Fleagle 1975) offers in vivo information on carpal movement during “natural” behaviour, in vitro 3D kinematic studies, like that of Orr et al.(2010) are able to provide a much greater understanding of the complexity of carpal movement, particularly of individual bones. Finally, MRI or X-ray Reconstruction of Moving Morphology (X-ROMM) 3D imaging technology allows one to visualize and quantify skeletal movement in vivo. This has been applied successfully to the human carpus (e.g. Crisco et al. 2005; Moritomo et al. 2006; Pillai et al. 2007). Ideally, application of such methods to nonhuman primates (although not without its ethical challenges) would provide the much-needed information on individual carpal movements and range of motion during “natural” locomotor or manipulative behaviours (compared to “imposed” postures on cadaveric or sedated specimens). Application of these methods, particularly to understudied Old and New World monkeys and most strepsirrhines, will greatly improve our understanding of the morphology and subsequent functional interpretations of both extant and fossil carpal bones.

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