

Clavicle, a Neglected Bone: Morphology and Relation to Arm Movements and Shoulder Architecture in Primates

JEAN-LUC VOISIN

Département de Préhistoire du Muséum National d'Histoire Naturelle, USM 103
and UMR 5198 du CNRS, Institut de Paléontologie Humaine, Paris, France

ABSTRACT

In spite of its importance for movements of the upper limbs, the clavicle is an infrequently studied shoulder bone. The present study compares clavicular morphology among different extant primates. Methods have included the assessment of clavicular curvatures projected on two perpendicular planes that can be assessed overall as cranial and dorsal primary curvatures. Results showed that in cranial view, three morphologies can be defined. One group exhibited an external curvature considerably more pronounced than the internal one (*Gorilla*, *Papio*); a second group was characterized by an internal curvature much more pronounced than the external one (*Hylobates*, *Ateles*); and a third group contained those with the two curvatures equally pronounced (*Pan*, *Homo*, *Pongo*, *Procolobus*, *Colobus*). Clavicle curvatures projected on the dorsal plane could be placed into four groups. The first group is characterized by two curvatures, an inferior and a superior (Apes, Spider monkeys). The second included monkeys, whose clavicles have an inferior curvature much more pronounced than the superior one. The third group includes only *Hylobates*, whose clavicles possess only the superior curvature. The last group includes only modern humans, whose clavicles show only the inferior curvature, which is less pronounced than that which exists in monkeys. Curvatures in cranial view relate information regarding the parameters of arm elevation while those in dorsal view offer insights into the position of the scapula related to the thorax. The use of clavicular curvature analysis offers a new dimension in assessment of the functional morphology of the clavicle and its relationship to the shoulder complex. *Anat Rec Part A*, 288A: 944–953, 2006. © 2006 Wiley-Liss, Inc.

Key words: clavicle; shoulder; locomotion; brachiation; catyrrhine; platyrrhine; hominoid

In Primates, the shoulder complex includes 3 bones (scapula, clavicle, and humerus), more than 20 muscles (the exact number depending on the particular species), and 4 joints working together. Of the bones, the clavicle has been considerably less studied from a comparative perspective than has the humerus and scapula. Although infrequently studied, clavicular morphology may be a crucial element to determining upper limb locomotor behavior, not only among Primates, but among the five orders of Theria (Primates, Chiroptera, Insectivora except Potamogale, Dermoptera, and Tubilidentata) that possess a com-

Correspondence to: Jean-Luc Voisin, Département de Préhistoire du Muséum National d'Histoire Naturelle, USM 103 and UMR 5198 du CNRS, Institut de Paléontologie Humaine, 1 rue René Panhard, 75013 Paris, France. Fax: 00-33-1-43-3122-79. E-mail: jeanlucv@mnhn.fr

Received 12 February 2006; Accepted 27 April 2006
DOI 10.1002/ar.a.20354
Published online 7 August 2006 in Wiley InterScience
(www.interscience.wiley.com).

TABLE 1. Number of clavicles studied*

Species (Abbreviation)	Clavicle
<i>Homo sapiens sapiens</i> ** (Hm)	33
<i>Pan troglodytes</i> (Pt)	26
<i>Pan paniscus</i> (Pp)	19
<i>Gorilla gorilla</i> (Gor)	33
<i>Pongo pygmaeus</i> (Oo)	24
<i>Hylobates</i> sp. (Gb)	22
<i>Ateles</i> sp. (At)	9
<i>Colobus</i> sp. (Cl)	25
<i>Procolobus</i> sp. (Prc)	19
<i>Papio hamadryas</i> (Ba)	28

*Non captive specimens whenever possible.

**Europe 10, Africa 7, North America 5, Asia 7, Unknown 4 (Details in Voisin, 2000b).

plete bone (Lessertisseur and Saban, 1967; Schmidt et al., 2002). In Primates, the clavicle is intimately involved in two very distinctive behaviors: arborialism and/or hand-dling.

Most studies on the clavicle have come from observations on human anatomy (e.g., Broca, 1869; Parson, 1917; Kleiweg de Zwaan, 1931; Terry, 1932, 1934; Apostolakis, 1934; Schultz, 1937; Olivier, 1951b, 1954, 1955; Olivier et al., 1954; Olivier and Capliez, 1957; Ray, 1959; van Dongen, 1963; Longia et al., 1982; Jit and Kaur, 1986) and provide an extensive overview of morphological variation between groups. Some studies are less strictly anthropological and focus on the determination of the age at death of an individual (Szilvássy, 1980; Walker and Lovejoy, 1985; Webb and Suchey, 1985; Stout and Paine, 1992) or the sex through forensic analysis of the clavicle, in whole or in part (Jit and Singh, 1966; Steel, 1966; Kaur and Jit, 1990; Murphy, 1994; Zhang and Han, 1994; Zhang and Tian, 2001). Relatively few studies have approached Primate clavicular morphology from a comparative or functional perspective (e.g., Schultz, 1930; Olivier, 1953; Cave, 1961; Jenkins, 1974; Fleagle, 1978; Jenkins et al., 1978; Ljunggren, 1979; Harrington et al., 1993; Voisin, 2000a, 2000b, 2001, 2004; Voisin and Balzeau, 2004).

The aim of this study was to compare clavicle morphology among different primate species, chosen for differences in their locomotor behavior and/or their phylogenetic relationships. Morphological variations observed among species will be considered from both functional and architectural perspectives and the relationships of the clavicle with the other components of the shoulder complex—humerus, scapula, joints, and contiguous soft tissues—will be considered. The adaptation of the shoulder complex among extant primates, and implications for evolution, will also be discussed.

MATERIALS AND METHODS

Materials

Specimens used in this study included clavicles of humans from various geographic locations, *Gorilla gorilla*, *Pan troglodytes*, *Pan paniscus*, *Pongo pygmaeus*, *Hylobates* sp., *Papio hamadryas*, *Colobus* sp., *Procolobus* sp., and *Ateles* sp. (Table 1). The *Hylobates* sp. material includes clavicles from the two subgenera, *Nomascus* and *Hylobates*, as they have been shown to be sufficiently close for possible hybridization between them (Groves,

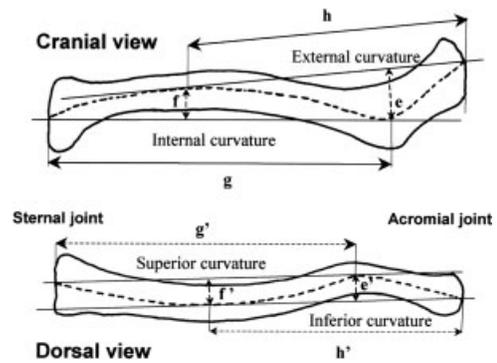


Fig. 1. Determination of the clavicle curvatures (Olivier, 1951a) on a right clavicle of *Pan troglodytes*.

1993). All clavicles were of adults, as determined by complete ossification of the bone (i.e., no cartilage remaining) and dental eruption for comparison. Males were used whenever possible. Specimens are from collections at the Laboratoire d'Anthropologie Biologique du Musée de l'Homme (Paris, France); Laboratoires d'Anatomie comparée et des Mammifères et Oiseaux du Muséum National d'Histoire Naturelle (Paris, France); Musée Royal d'Afrique Centrale (Tervuren, Belgium); and from the Mammals Group, Natural History Museum [London, U.K.; details and collection numbers can be found in Voisin (2000b)].

Methods

Clavicle morphology has been documented via assessment of the bone's curvatures. When projected on two perpendicular planes, cranial and dorsal, curvatures can be visualized in two basic curvatures (Fig. 1).

The middle arc of curvature is estimated according to Olivier's method (1951a) as the proportion between the length of the chord and the height of the curvature (Figs. 1 and 2).

Cranial plane. The acromial (or external) curvature = $e/h \times 100$. The sternal (or internal) curvature = $f/g \times 100$.

Dorsal plane. The acromial (or inferior) curvature = $e'/h' \times 100$. The sternal (or superior) curvature = $f'/g' \times 100$.

Description and distribution of the variables have been computed with Systaw5. The graphic showing the range of variation of each variable is represented by mean \pm two times standard deviation.

RESULTS

Curvatures in Cranial View

Curvature projection, on the cranial plane, distinguished three groups of primates (Figs. 3–5, Table 2).

Group 1. Gorilla and baboons possess asymmetric clavicles. In these species, clavicles are characterized by a pronounced external curvature and a slight, or even absent, internal one (Figs. 5 and 6, Table 2).

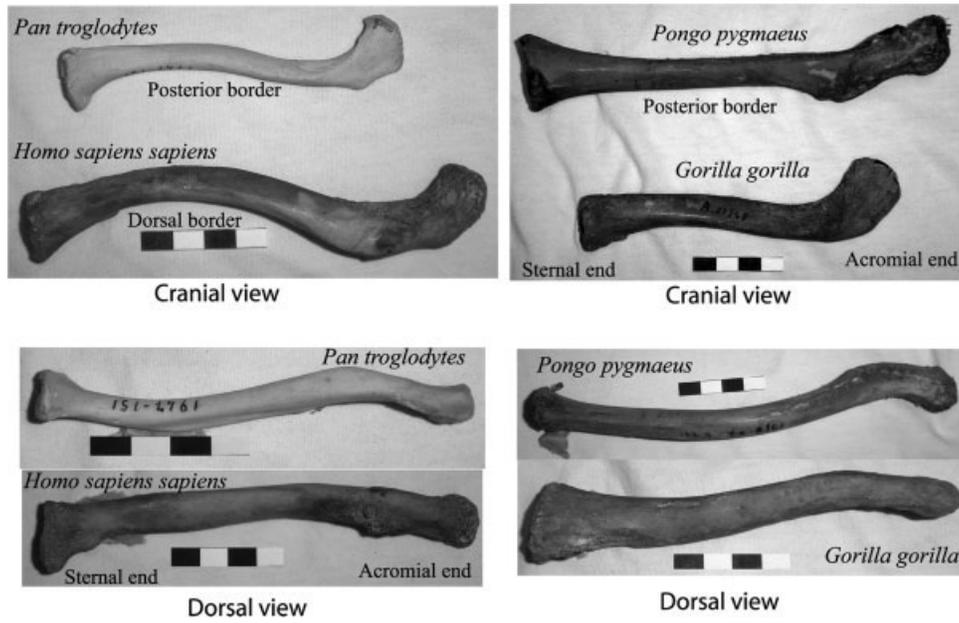


Fig. 2. Right clavicles in cranial and dorsal view.

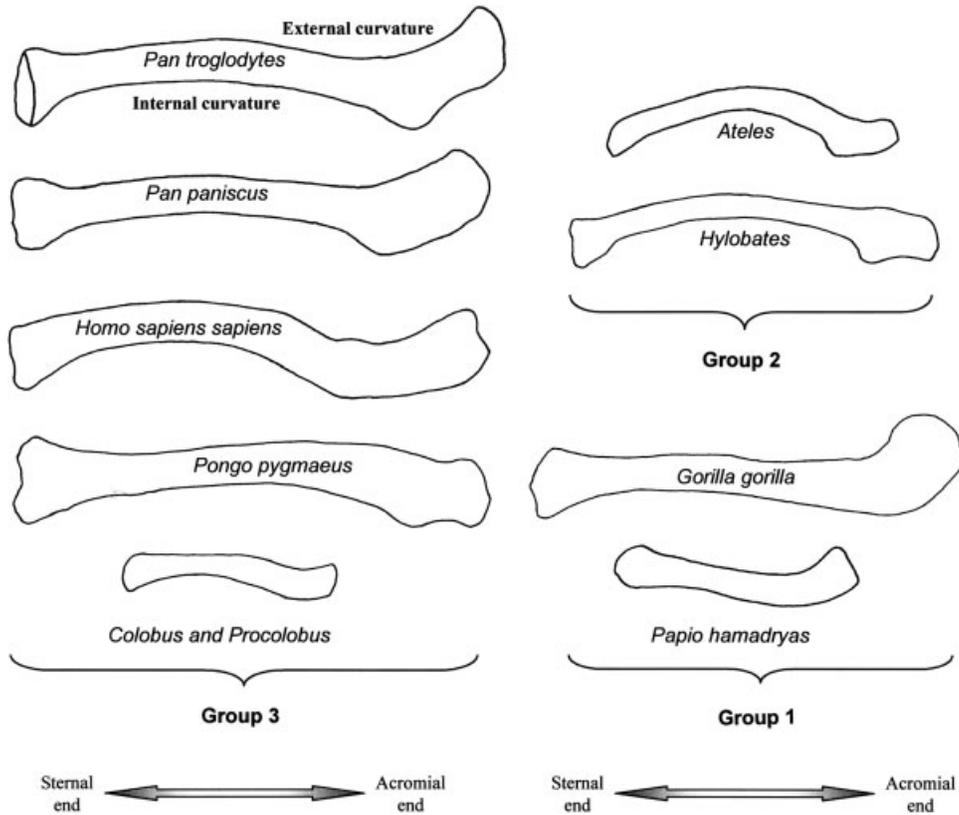


Fig. 3. Right clavicles in cranial view (scale not respected).

Group 2. Gibbons and spider monkey clavicles are characterized by a pronounced internal curvature and a slightly pronounced external one. Their morphology is the opposite of that of the first group (Figs. 5–7, Table 2).

Group 3. Humans, common and pygmy chimpanzees, orangutan, Colobus, and Procolobus monkeys possess clavicles that consistently display both internal and external curvatures, the external one being always slightly

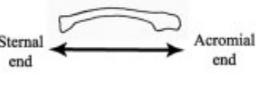
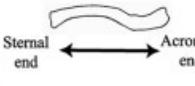
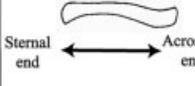
	Group 1	Group 2	Group 3	
Clavicle characteristics	Clavicle with: - a pronounced external curvature - a slight, or absent internal curvature	Clavicle with: - a pronounced internal curvature - a slight, or absent, external curvature	Clavicle with: - an internal curvature - an external curvature	
Diagram				
Primate species	- <i>Gorilla</i> - <i>Papio</i>	- <i>Hylobates</i> - <i>Ateles</i>	- <i>Homo</i> - <i>Pan</i> - <i>Pongo</i>	- <i>Procolobus</i> - <i>Colobus</i>

Fig. 4. Diagram showing the characteristics of each clavicle groups in cranial view.

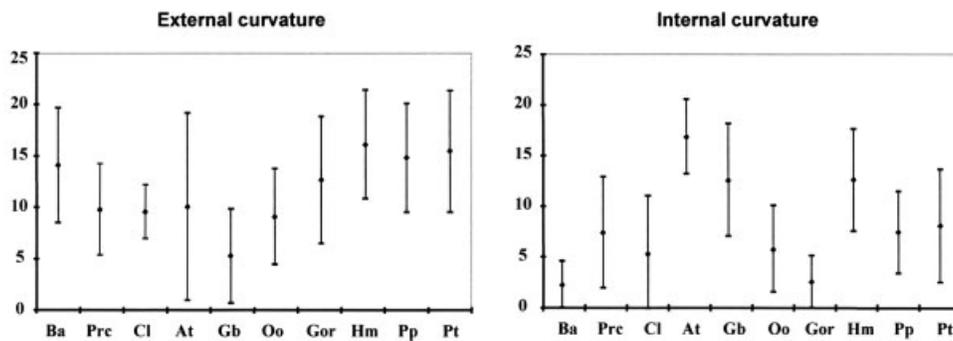


Fig. 5. Mean and range of variation of the internal and external curvatures in Humans, Apes, Baboon, Colobus, and Procolobus monkeys. For Baboon and Gorilla, see footnote to Table 2.

TABLE 2. Characteristics of the clavicle curvatures in superior view*

Species (number of bones)	Internal curvature			External curvature		
	Mean	Standard deviation	Variance	Mean	Standard deviation	Variance
<i>Homo sapiens sapiens</i> (33)	12,6	2,5	6,3	16,1	2,7	7
<i>Pan troglodytes</i> (26)	8,1	2,8	7,8	15,4	3,0	8,8
<i>Pan paniscus</i> (19)	7,5	2,0	4,0	14,8	2,6	7,0
<i>Gorilla gorilla</i> (33)	3,3	1,9	3,6	12,6	3,1	9,6
<i>Pongo pygmaeus</i> (24)	5,8	2,1	4,5	9,1	2,3	5,5
<i>Hylobates sp.</i> (22)	12,6	2,8	7,8	5,3	2,3	5,3
<i>Ateles sp.</i> (9)	16,9	1,9	3,4	10,1	4,5	20,3
<i>Colobus sp.</i> (25)	5,3	2,8	7,8	9,6	1,3	1,7
<i>Procolobus sp.</i> (19)	7,4	2,7	7,3	9,8	2,2	4,8
<i>Papio hamadryas</i> (28)	2,2	1,2	1,4	14,1	2,8	7,8

*For *Gorilla* and *Papio*, we retained only individuals who possess a superior curvature to estimate means and standard deviations.

more pronounced than the internal one. However, this group is heterogeneous and there are great differences between species, and two subgroups may be recognized (Fig. 4): group 3a (*Homo*, *Pan*, and *Pongo*) and group 3b (*Colobus* and *Procolobus*).

The group 3a clavicles are characterized by a positive correlation between the two curves (Fig. 8, Table 3), which is not the case in group 3b clavicles.

Finally, the clavicles of *Homo*, *Pan*, and *Pongo* are not similar. Orangutan clavicles show the least pronounced curvatures among group 3 (Table 2) and appear straighter. On the other hand, human and chimpanzee clavicles show much more pronounced curvatures, but they are not identical; the internal curvature is more pronounced in human than in chimpanzees (Table 4). Unlike *Homo* clavicles, those of *Pan* have a less S-shaped mor-

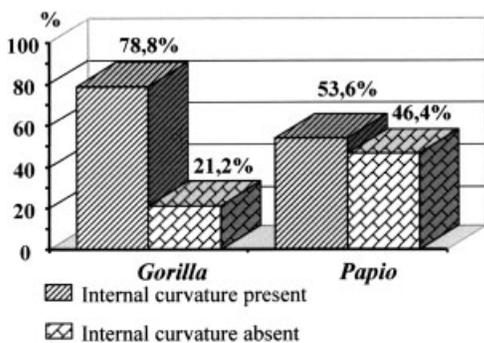


Fig. 6. Proportion of clavicles with an internal curvature in *Gorilla* and *Papio*.

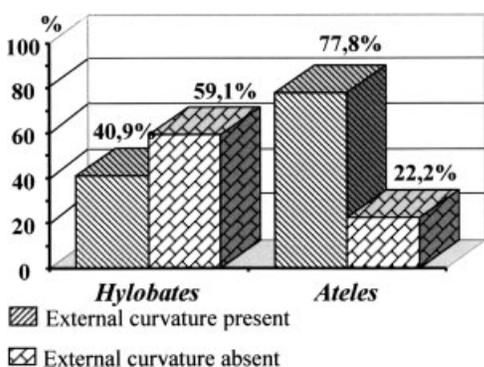


Fig. 7. Proportion of clavicles with an external curvature in *Hylobates* and *Ateles*.

phology, although the latter have been considered historically to be as S-shaped as, or even more so than, those of humans since the work of Schultz (1930). On the other hand, there are no significant differences between the two chimpanzee species (Table 4).

Curvatures in Dorsal View

Clavicle curvatures projected on the dorsal plane distinguish four groups of primates (Figs. 9–12).

Group 1. Great Apes and spider monkeys consistently show clavicles with two curvatures: an inferior one at the lateral end and a superior one at the medial end. There are differences between species, curvatures being more or less pronounced, but never absent (Table 5). Moreover, the inferior curvature is always more pronounced than the superior in the same clavicle.

Group 2. Baboons, Colobus and Procolobus monkeys possess clavicles that always show an inferior curvature and a slightly pronounced or even absent superior one.

Group 3. Gibbons possess clavicles always showing a superior curvature and a slightly pronounced, if not absent, inferior one.

Group 4. Humans possess clavicles showing only the inferior curvature, which is less pronounced than that which exists in monkeys. Sometimes, some individuals show two curvatures in dorsal view, but these curva-

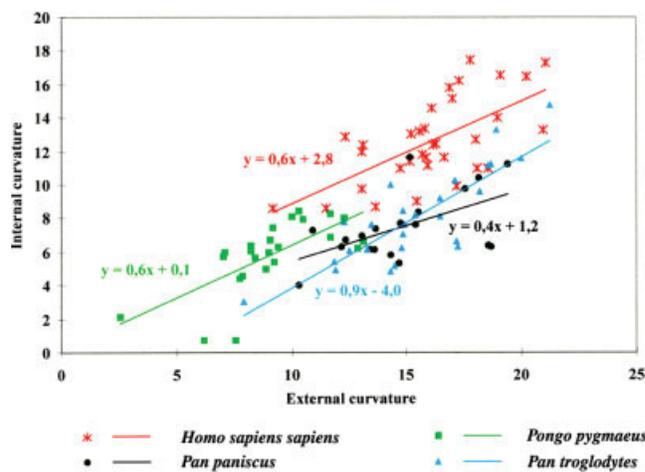


Fig. 8. Regression axes for curvatures in cranial view.

TABLE 3. Pearson coefficient of correlation *r* between internal and external curvatures of group 3 clavicle

Species	<i>r</i>	<i>r</i> ²	<i>P</i>
<i>Homo sapiens sapiens</i>	0,6	0,4	0,0
<i>Pan troglodytes</i>	0,8	0,7	0,0
<i>Pan paniscus</i>	0,6	0,3	0,0
<i>Pongo pygmaeus</i>	0,7	0,5	0,0

tures are slight in regard to the condition exhibited in the great apes.

DISCUSSION

Curvatures in Cranial View

Our results show that clavicle morphology in cranial view is well defined in each species. This strongly suggests that these morphologies may have mechanical and/or architectural explanations other than only allowing arm movement outside the parasagittal plane.

Only a few primate species (*Ateles*, *Hylobates*, *Pan*, *Homo sapiens sapiens*, *Colobus*, and *Procolobus*) possess a clavicle with a marked internal curvature in cranial view. All these primates need powerful and rapid arm elevation.

Among *Hylobates*, *Ateles*, *Pan*, and *Homo*, only *Ateles* does not possess a pectoralis major insertion on the clavicle, contrary to the three other genera (Miller, 1932; Asthon and Oxnard, 1963). This insertion on the clavicle appears to be a unique feature among primates (Stern et al., 1980).

The pectoralis major is very important for arm flexion, especially at the start of the movement, at least in humans (Gagey, 1985) and gibbons (Stern et al., 1980; Jungers and Stern, 1981). The action of this muscle is helped by the pronounced internal curvature that acts as a “crank,” which in turn aids the glenoid cavity of the scapula to rotate cranially. The greater the curvature, the more pronounced the crank effect may be.

Ateles do not have a pectoralis major pars clavicularis, but do exhibit an extended clavicular insertion of the deltoideus (Campbell, 1937; Asthon and Oxnard, 1963;

TABLE 4. T-test between internal and external clavicles curvatures of common and pygmy chimpanzee and human

Internal curvature				External curvature			
Group	n	Mean	SD	Group	n	Mean	SD
<i>Pan troglodytes</i>	26,0	8,1	2,8	<i>Pan troglodytes</i>	26,0	15,4	3,0
<i>Pan paniscus</i>	19,0	7,5	2,0	<i>Pan paniscus</i>	19,0	14,8	2,6
Separate variances	T = 0,9	DF = 43,0	Prob = 0,4	Separate variances	T = 0,7	DF = 41,2	Prob = 0,5
Pooled variances	T = 0,8	DF = 43,0	Prob = 0,4	Pooled variances	T = 0,7	DF = 43,0	Prob = 0,5
Group	n	Mean	SD	Group	n	Mean	SD
<i>Pan troglodytes</i>	26,0	8,1	2,8	<i>Pan troglodytes</i>	26,0	15,4	3,0
<i>Homo sapiens sapiens</i>	33,0	12,6	2,5	<i>Homo sapiens sapiens</i>	33,0	16,1	2,6
Separate variances	T = -6,5	DF = 51,1	Prob = 0,0	Separate variances	T = -0,9	DF = 50,7	Prob = 0,4
Pooled variances	T = -6,5	DF = 57,0	Prob = 0,0	Pooled variances	T = -0,9	DF = 57,0	Prob = 0,4

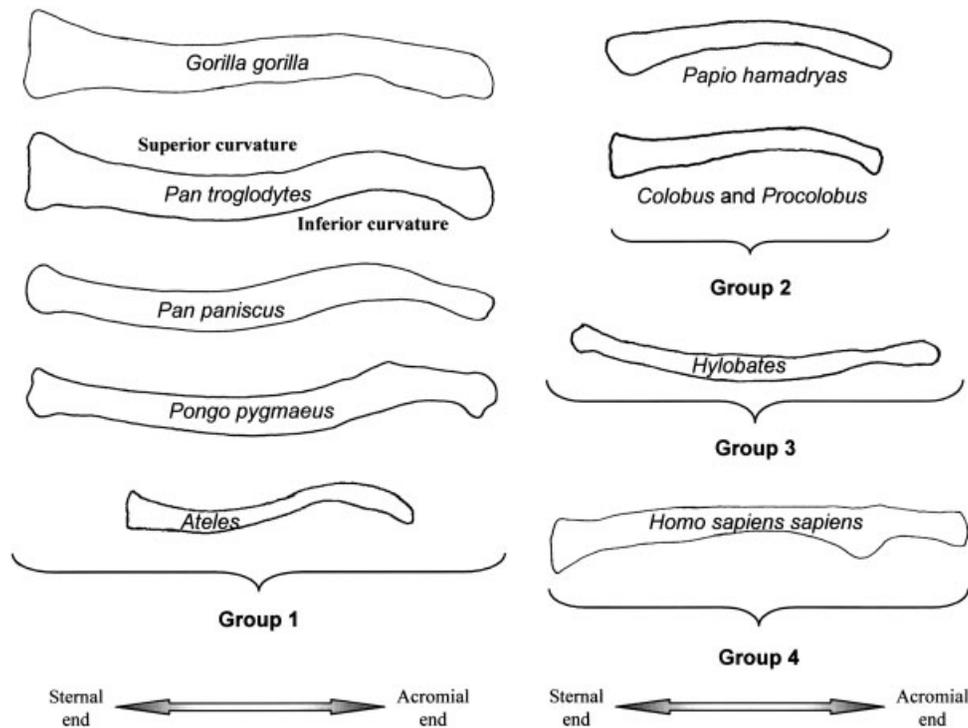


Fig. 9. Right clavicle in dorsal view (scale not respected).

Stern et al., 1980), which takes the place and function of the *pectoralis major* (Stern et al., 1976). The insertion of the *pectoralis major* or *deltoideus* on the clavicle may not reflect locomotor behavior differences (Stern et al., 1980), but may rather reflect different adaptations to similar ecological forces. In other words, *Ateles* and *Hylobates* have both developed brachiation, but in different ways.

Colobus and *Procolobus* clavicle morphology can have the same interpretation as proposed for apes and humans. Both have clavicles with pronounced internal curvatures, but their *pectoralis major* insertion is very small or nearly absent, as is usual in most primates. On the other hand, the *deltoideus* clavicular insertion shows great extension, though smaller than in *Ateles* (Polak, 1908; Ayer, 1948; Asthon and Oxnard, 1963). African Colobinae are arboreal quadrupeds but, unlike baboons, they can hang by one arm. Moreover, they are able, after a jump, to land on

their arms alone, catching branches, while *Macaca* lands on its four limbs (Asthon and Oxnard, 1964). Hence, the action of this muscle is helped by the crank effect made by the S-shaped clavicle.

Primates such as *Papio* and *Gorilla* are less frequently tree-dwelling than *Colobus* or *Pan*. For these primates, a powerful arm elevation, like the one needed by gibbons, is not necessary, and the internal curvature is less pronounced. Clavicle description of other terrestrial primates reveals that the internal curvature is always slightly pronounced or absent (Olivier, 1953; Hill, 1966, 1970, 1974). As we will see below, an internal curvature is not advantageous for terrestrial quadrupeds because it increases the risk of clavicle breakage.

Two other interpretations for the morphology of the primate clavicle have been proposed. According to Olivier (1951a, 1953, 1962, 1965), it is the presence or ab-

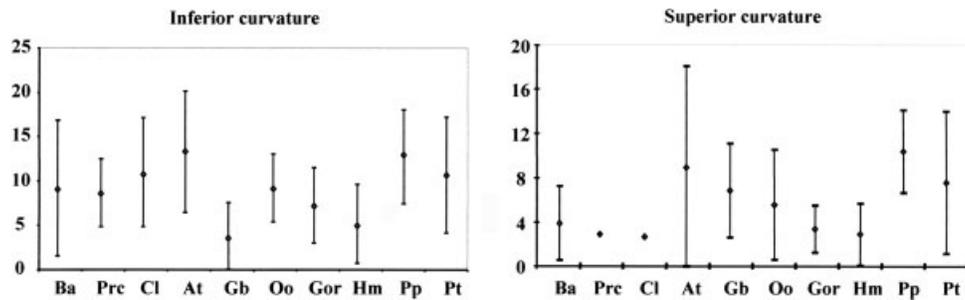


Fig. 10. Means and ranges of variation of the superior and inferior curvatures in Hominoids, African Colobines, and Baboons. In Humans, Baboons, Colobus, and Procolobus monkeys, we considered only individuals that possess a superior curvature to estimate means and standard deviations (see also Table 5).

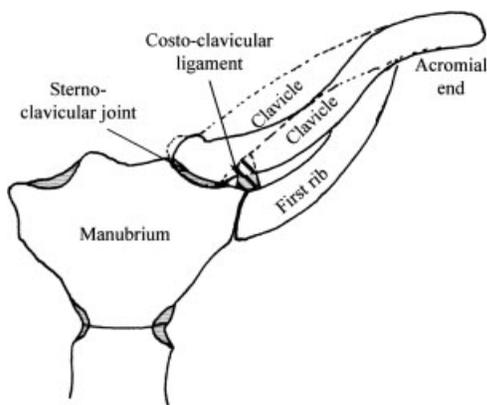


Fig. 11. Clavicles associated with a high scapula in regard to the thorax. Dotted line, human clavicle (with a unique inferior curvature); full line, great ape clavicle (with two curvatures in dorsal view). Note the difference is high in regard to the manubrium between the two clavicular morphologies.

sence of the *pectoralis major pars clavicolaris* that explains clavicle morphology. It has been suggested that the internal curvature appears as a consequence of traction by the *pectoralis major* during intrauterine growth. Two factors, however, speak against such an interpretation. First, young orangutan clavicles are S-shaped (Schultz, 1930), and this species has a very short *pectoralis major* insertion on the clavicle when it is present (Sullivan and Osgood, 1927; Jouffroy, 1962). Two, gorillas possess a long and large insertion of the *pectoralis major pars clavicolaris* (Raven, 1950; Asthon and Oxnard, 1963; Stern et al., 1980), and the internal curvature of their clavicle is only slight or absent.

Jenkins et al. (1978) have proposed that the internal curvature allows the clavicle to join the manubrium and the acromion without crossing the hole (i.e., the thoracic outlet) of the rib cage in those primates, such as hominoids, that have a dorsal scapula. On the other hand, for Cercopithecoids, an internal curvature would not be necessary because their scapula is not dorsal, but lateral, and thus the clavicle does not cross the thoracic outlet. There are two reasons that contradict such an explanation: some *Gorilla* clavicles do not have any internal curvature, and the clavicles of *Colobus* and *Procolobus* possess an internal curvature.

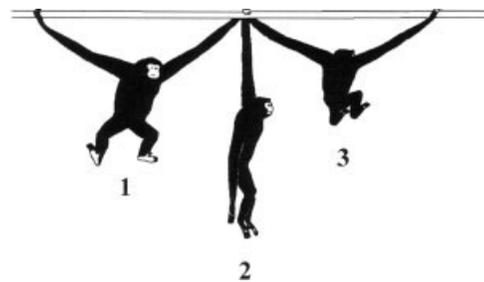


Fig. 12. Gibbon brachiation. 1, start; 2, halfway; the thorax oriented in the way of the pendulum movement; 3, end. After Fleagle (1974). Adapted by permission from McMillan Publications Ltd: Nature, copyright 1974.

The great sinuosity of the human clavicle increases the crank effect as we have noted above, but also the weakness of this bone in regard to flexion and torsion forces (Harrington et al., 1993; Mays et al., 1999). The clavicle allows the transmission of arm weight to the sternum and to the axial skeleton through its major axis (Jenkins, 1974; Harrington et al., 1993; Mays et al., 1999). These compressive forces in conjunction with the S-shaped morphology create torsion and flexion constraints at the junction of the two curvatures (Harrington et al., 1993). In humans, most clavicle fractures appear in the central third of the bone (Harrington et al., 1993; Kamina, 1995). Chimpanzees, which frequently walk on the ground, have a less pronounced internal curvature and thus have a stronger clavicle than humans. This observation is confirmed in both gorillas and baboons, two quadrupedal genera (walking on the knuckle or in the classical way) whose clavicles do not possess well-pronounced internal curvatures. Moreover, the disposition of bony structures of the clavicle show differences between humans, chimpanzees, and gorillas (Voisin and Balzeau, 2004) that confirm greater resistance of the chimpanzee clavicle in comparison to the human one. In short, clavicle morphology influences force diffusion and thus locomotion in each primate species.

Curvatures in Dorsal View

Our results show that clavicle morphology in dorsal view is distinctive in each species. As for the cranial view, it is probable that these morphologies have mechanical and/or architectural explanations.

TABLE 5. Characteristics of clavicle curvatures in dorsal view*

Species (number of bones)	Inferior curvature			Superior curvature		
	Mean	Standard deviation	Variance	Mean	Standard deviation	Variance
<i>Homo sapiens sapiens</i> (33)	5,1	2,3	5,3	2,9	1,5	2,3
<i>Pan troglodytes</i> (26)	10,7	3,3	10,9	7,6	3,2	10,2
<i>Pan paniscus</i> (19)	12,7	3,0	9,0	10,4	1,9	3,6
<i>Gorilla gorilla</i> (33)	7,2	2,2	4,8	3,4	1,1	1,2
<i>Pongo pygmaeus</i> (24)	9,2	1,9	3,6	5,6	2,5	6,3
<i>Hylobates sp.</i> (22)	3,8	1,9	3,6	6,9	2,1	4,4
<i>Ateles sp.</i> (9)	13,3	3,4	11,6	8,9	4,6	21,2
<i>Colobus</i> (25)	10,9	3,1	9,6	2,7	0,0	0,0
<i>Procolobus</i> (19)	8,6	1,9	3,6	2,9	0,0	0,0
<i>Papio hamadryas</i> (28)	9,2	3,8	14,4	3,9	1,7	2,9

*For *Homo*, *Colobus*, *Procolobus* and *Papio*, we retained only individuals who possess a superior curvature to estimate means and standard deviations.

The sternoclavicular joint is supported by the costoclavicular ligament, which exists only in apes and humans (Cave, 1961) and limits horizontal and vertical clavicle movements. In this case, a costoclavicular ligament elongation increases the mobility and weakness of the sternoclavicular joint and involves greater muscular control, exerted by the *subclavius* muscle. In apes, an important superior curvature permits us to associate a high scapula with respect to the thorax and a clavicle with its medial end nearly parallel to the manubrium (Fig. 11). This condition avoids the elongation of the costoclavicular ligament. This interpretation is confirmed by electromyographic studies on spider monkeys, which show that the *subclavius* muscle is not activated when the animal brachiates (Konstant et al., 1982).

In the simplest form of brachiation, “the Ape travels along a branch in a series of swings below alternating handholds. In each swing the animal is suspended by its arm below a single point (its hand)” (Fleagle, 1977). For an efficient brachiation with low energy cost, some constraints are necessary. In particular, during a complete swing, the center of gravity of the individual must remain in the vertical plane, which includes the pendulum center of rotation (Fleagle, 1974; Usherwood and Bertram, 2003; Bertram, 2004; Vereecke et al., 2006). To answer this important constraint, animals can only act on shoulder, elbow, and wrist joints.

When a brachiating primate's back arm releases its handhold, the trunk makes two movements (Fig. 12): a pendulum movement and a rotation under the supporting arm, which directs the thorax in the direction of the pendulum movement. During brachiation, the thorax is able to make a rotation movement under the supporting arm, because the clavicle keeps the acromiomanubrium length constant and thus prevents the scapula from collapsing on the thorax. For this movement, clavicle morphology has no significant importance.

On the other hand, the clavicle morphology in dorsal view appears important for the pendulum movement. Two morphological factors increase the pendulum movement in the gibbon clavicle: a pronounced superior curvature permits association of a high scapula with respect to the thorax without any elongation of the costoclavicular ligament, as we have noted above; and the absence of an inferior curvature, which is present in all other primate clavicles, associated with a high scapula, necessarily involves an acromioclavicular joint (Fig. 13). With this joint, the scapula/clavicle complex becomes more

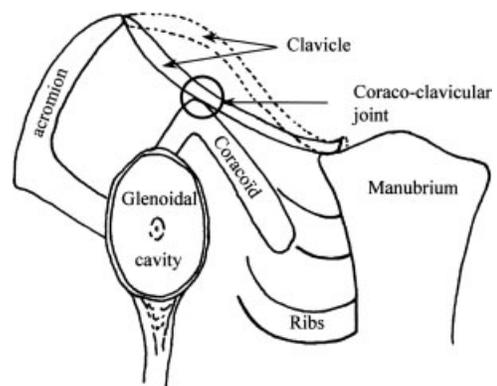


Fig. 13. Relation between scapula, clavicle, and manubrium for a Gibbon clavicle (full line) and that for a great ape (dotted line). After Voisin (2000b).

rigid and thus more efficient for brachiation. This joint, characteristic of gibbon shoulder (Lessertisseur and Saban, 1967), increases force diffusion and limits movement of the center of gravity outside the vertical plane of the supporting hand. This joint is not normally present in other primates that possess one or two ligaments (conoid and trapezoid) between the clavicle and the acromion.

Spider monkeys brachiate slower than gibbons and often help themselves with their tails as a fifth hand (Grassé, 1977; Fleagle, 1998; Cant et al., 2003). Their shoulder does not permit brachiation as in the gibbon, because their scapula/clavicle complex is less rigid. Their clavicle has two pronounced curvatures in dorsal view, and thus they cannot have an acromioclavicular joint as in gibbons. The different types of brachiation of spider monkeys and gibbons do not reflect muscle differences (Stern et al., 1980), but depend on clavicle morphology.

In quadrupedal primates (e.g., baboons, *Colobus* monkeys), the clavicle allows the upper limb to realize movements outside the sagittal plane, but it must not hinder quadrupedal locomotion. A clavicle with a pronounced inferior curvature permits a lateral scapula to have a great swing movement without hitting the clavicle. However, the weak cohesion of the scapula/clavicle complex limits brachiation possibilities and the absence of a superior curvature does not allow the scapula to lie high on the thorax.

In a primate using quadrupedal locomotion, an acromioclavicular joint is not necessary and may even limit its range of movements. Thus, in spider monkeys, which often use quadrupedal locomotion (Asthon and Oxnard, 1964), this joint is not present, which explains differences in clavicle morphology between them and gibbons in posterior view. Although quadrupedal locomotion is not similar in great apes and monkeys, the inferior curvature is also necessary for the clavicle of great apes, as it allows a greater range of movements of the shoulder, and the scapula/clavicle complex does not need to be very rigid.

The neck of humans is longer than that of great apes, so that the human head projects out beyond the shoulder (Sakka, 1985). This phenomenon is due to the low position of the shoulder girdle in regard to the thorax, as shown by the more cranially oriented clavicle in apes (Valois, 1928; Olivier, 1965; Sakka, 1985). The drop of the human shoulder girdle, compared to that of great apes, explains the unique and inferior curvature of the human clavicle. A low shoulder girdle in regard to the thorax does not allow the presence of a pronounced superior curvature because it would involve the dislocation of the sternoclavicular joint.

In sum, clavicle morphology in the dorsal plane allows us to determine the position of the scapula in regards to the thorax: a clavicle with two curvatures, like that of the chimpanzee, is associated in dorsal view with a dorsal and high scapula in regards to the thorax; a clavicle with only a superior curvature, like that of the gibbon, is associated with a dorsal and high scapula; a clavicle with only a pronounced inferior curvature, as in baboons, is associated with a lateral scapula; and a clavicle with a unique, slightly pronounced inferior curvature, as in humans, is associated with a low and dorsal scapula.

Due in considerable part to the inherent difficulty in assessing the clavicle via classic morphometric approaches, the comparative anatomy of the bone has been largely unexplored. Approaches used in this study have employed shape curvature as a vehicle to assess patterns in clavicular morphology among different primate groups that employ differing upper limb locomotor or manipulation behaviors. Findings from this study show that such curvature assessments can indeed shed insight into both the relationship of clavicular morphology to overall shoulder architecture and to dependent locomotor behaviors. The use of curvature assessments may also be of particular value in assessments of fossil primate and hominoid clavicles and provide insight into how this important component of the shoulder complex has changed throughout evolution (Voisin, 2006).

ACKNOWLEDGMENTS

The author thanks all the people at the Institut de Paléontologie Humaine who have helped, and especially S. Condemie and her husband as well as R. Russel for their assistance in correcting the English. He also thanks Professor Jeffrey Laitman for his invitation to publish in the *Anatomical Records*, the time he took for preparing it, and his valuable advice and insightful comments, as well as Professors André Langaney, Daniel Robineau and Christine Lefevre, Michel Tranier, Wim van Neer, and Paula Jenkins who authorized him to work respectively on collections at the Laboratoire d'Anthropologie

Biologique du Musée de l'Homme (Paris, France), Laboratoire d'Anatomie Comparée du Muséum National d'Histoire Naturelle (Paris, France), Laboratoire des Mammifères et Oiseaux du Muséum National d'Histoire Naturelle (Paris, France), Musée Royal d'Afrique Centrale (Tervuren, Belgium), and the Zoological Group from the Natural History Museum (London, U.K.). I also thank Dr. Fleagle, who authorized me to use one of his picture.

LITERATURE CITED

- Apostolakis G. 1934. La clavicle de l'homme. *Arch Anat Histol Embryol* 18:169–180.
- Ashton EH, Oxnard CE. 1963. The musculature of the primate shoulder. *Trans Zool Soc Lond* 29:553–650.
- Ashton EH, Oxnard CE. 1964. Locomotor patterns in primates. *Proc Zool Soc Lond* 142:1–28.
- Ayer AA. 1948. The anatomy of *Semnopithecus entellus*. Madras: India Publishing House.
- Bertram JEA. 2004. New perspectives on brachiation mechanics. *Yearb Phys Anthropol* 47:100–117.
- Broca P. 1869. L'ordre des Primates: parallèle anatomique de l'homme et des singes. *Bull Mém Soc Anthropol* 2:228–401.
- Campbell B. 1937. The shoulder musculature of the platyrrhine monkeys. *J Mammal* 18:66–71.
- Cant JGH, Youlatos D, Rose MD. 2003. Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador. *J Hum Evol* 44:685–699.
- Cave AJE. 1961. Nature and morphology of the costoclavicular ligament. *J Anat* 95:170–179.
- Fleagle JG. 1974. Dynamics of brachiating siamang *Hylobates (Symphalangus) syndactylus*. *Nature* 248:259–260.
- Fleagle JG. 1977. Brachiation as biomechanics: the siamang as example. *Malay Nat J* 30:45–51.
- Fleagle JG. 1978. Mechanical function of primate clavicles. *Am J Phys Anthropol* 48:394.
- Fleagle JG. 1998. Primate adaptation and evolution, 2nd ed. San Diego, CA: Academic Press.
- Gagey O. 1985. Etude de l'élévation du membre supérieur: rôle des ligaments articulaires et des muscles fléchisseurs de l'articulation scapulo-humérale. Paris: Mémoires du Laboratoire d'Anatomie de la Faculté de Médecine de Paris.
- Grassé PP. 1977. Précis de zoologie, vol. 3, reproduction, biologie, évolution et systématique, oiseaux et mammifères, 2nd ed. Paris: Masson.
- Groves CP. 1993. Speciation in living hominoid primates. In: Kimbel WH, Martin LB, editors. Species, species concepts and primate evolution. New York: Plenum Press. p 109–121.
- Harrington MA, Keller TS, Seiler JG, Weikert DR, Moeljanto E, Schwartz HS. 1993. Geometric properties and the predicted mechanical behavior of adult human clavicles. *J Biomechanics* 26:417–426.
- Hill WCO. 1966. Primates comparative anatomy and taxonomy: VI, Catarrhini. Edinburgh: Edinburgh University Press.
- Hill WCO. 1970. Primates comparative anatomy and taxonomy: VIII, Cynopithecinae (Papio, Mandrillus, Theropithecus). Edinburgh: Edinburgh University Press.
- Hill WCO. 1974. Primates comparative anatomy and taxonomy: VII, Cynopithecidae (Cerocebus, Maccaca, Cynopithecus). Edinburgh: Edinburgh University Press.
- Jenkins FA. 1974. The movement of the shoulder in clavicate and a clavicate Mammals. *J Morph* 144:71–84.
- Jenkins FA, Dumbrowski PJ, Gordon EP. 1978. Analysis of the shoulder in brachiating Spider monkeys (*Ateles geoffroyi*). *Am J Phys Anthropol* 48:65–75.
- Jit I, Singh S. 1966. The sexing of adult clavicles. *Ind J Med Res* 54: 551–571.
- Jit I, Kaur H. 1986. Rhomboid fossa in the clavicles of North Indians. *Am J Phys Anthropol* 70:97–103.
- Jouffroy FK. 1962. La musculature des membres chez les Lémuriens de Madagascar: étude descriptive et comparative. *Mammalia* 26(Suppl 2):1–322.

- Jungers WL, Stern JT. 1981. Preliminary electromyographical analysis of brachiation in Gibbon and Spider monkey. *Int J Primatol* 2:19–33.
- Kamina P. 1995. *Ostéologie des membres*, 2nd ed. Paris: Maloine.
- Kaur H, Jit I. 1990. Age estimation from cortical index of the human clavicle in northwest indians. *Am J Phys Anthropol* 83:297–305.
- Kleiweg de Zwaan JP. 1931. La clavicle des javanais de l'est de Java. *Anthropologie (Paris)* 41:273–287.
- Konstant W, Stern JT, Fleagle JG, Jungers WL. 1982. Function of the subclavius muscle in a nonhuman primate, the Spider monkey (Ateles). *Folia Primatol (Basel)* 38:170–182.
- Lessertisseur J, Saban R. 1967. Squelette appendiculaire. In: Grassé P, editor. *Traité de zoologie: anatomie, systématique, biologie*, vol. 16, fasc. 1. Paris: Masson. p 709–1078.
- Ljunggren AE. 1979. Clavicular function. *Acta Orthop Scand* 50:261–268.
- Longia GS, Agarwal AK, Thomas RJ, Jain PN, Saxena SK. 1982. Metrical study of rhomboid fossa of clavicle. *Anthrop Anz* 40:111–115.
- Mays S, Steele J, Ford M. 1999. Directional asymmetry in the human clavicle. *Int J Osteoarchaeol* 9:18–28.
- Miller RA. 1932. Evolution of the pectoral girdle and forelimb in the primate. *Am J Phys Anthropol* 17:2–56.
- Murphy AMC. 1994. Sex determination of prehistoric New Zealand Polynesian clavicles. *N Zealand J Archaeol* 16:85–91.
- Olivier G. 1951a. Technique de mesure des courbures de la clavicle. *CR Ass Anat* 69:753–764.
- Olivier G. 1951b. Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10:67–99,121–157.
- Olivier G. 1953. La clavicle du semnopithèque. *Mammalia* 17:173–186.
- Olivier G. 1954. Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10:144–153.
- Olivier G, Chabeuf M, Laluque P. 1954. Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10:35–46.
- Olivier G. 1955. Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10:282–302.
- Olivier G, Capliez S. 1957. Anthropologie de la clavicle. *Bull Mém Soc Anthropol* 10:225–261.
- Olivier G. 1962. *Formation du squelette du membre chez l'homme*. Paris: Vigot.
- Olivier G. 1965. *Anatomie anthropologique*. Paris: Vigot.
- Parson FG. 1917. On the modern English clavicle. *J Anat Physiol* 51:71–93.
- Polak C. 1908. *Die Anatomie des Genus Colobus*. *Verhandel Konik Ak Wetensch Amsterdam* 14:1–247.
- Ray LJ. 1959. Metrical and non-metrical features of the clavicle of the Australian aboriginal. *Am J Phys Anthropol* 17:217–226.
- Raven MC. 1950. *The anatomy of the gorilla: the raven memorial volume*. New York: Columbia University Press.
- Sakka M. 1985. Morphologie évolutive de la tête et du cou chez l'homme et les Grands Singes: application aux Hominidés fossiles, ensembles anatomiques et cervicaux. Paris: CNRS.
- Schmidt M, Voges D, Fischer MS. 2002. Shoulder movements during quadrupedal locomotion in arboreal primates. *Z Morphol Anthropol* 83:235–242.
- Schultz AH. 1930. The skeleton of the trunk and limbs of higher primates. *Hum Biol* 2:303–438.
- Schultz AH. 1937. Proportion, variability and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Hum Biol* 9:281–328.
- Steel FLD. 1966. Further observations on the osteometric discriminant function, the human clavicle. *Am J Phys Anthropol* 25:319–322.
- Stern JT, Wells JP, Vangor AK, Fleagle JG. 1976. Electromyography of some muscles of the upper limb in Ateles and Lagothrix. *Yrbk Phys Anthropol* 20:498–507.
- Stern JT, Wells JP, Jungers WL, Vangor AK, Fleagle JG. 1980. An electromyographic study of the pectoralis major in Atelines and Hylobates with special references to the evolution of a pars clavicularis. *Am J Phys Anthropol* 52:13–25.
- Stout SD, Paine RR. 1992. Brief communication: histological age estimation using rib and clavicle. *Am J Phys Anthropol* 87:111–115.
- Sullivan WE, Osgood CW. 1927. The musculature of the superior extremity of the Orang-utan. *Anat Rec* 35:193–239.
- Szilvássy J. 1980. Age determination on the sternal articular faces of the clavícula. *J Hum Evol* 9:609–610.
- Terry RJ. 1932. The clavicle of the American Negro. *Am J Phys Anthropol* 16:351–379.
- Terry RJ. 1934. The acromial end of the clavicle in Indians of Illinois. *Am J Phys Anthropol* 18:437–438.
- Usherwood JR, Bertram JEA. 2003. Understanding brachiation: insights from the collisional perspective. *J Exp Biol* 206:364–372.
- Valois HV. 1928. L'omoplate humaine. Etude anatomique et anthropologique. *Bull Mém Soc Anthropol* 7:129–168.
- van Dongen R. 1963. The shoulder girdle and humerus of the Australian aborigine. *Am J Phys Anthropol* 21:469–488.
- Vereecke EE, D'Août K, Aerts P. 2006. Locomotor versatility in the white-handed gibbon (*Hylobates lar*): A spatiotemporal analysis of the bipedal, tripodal, and quadrupedal gaits. *J Hum Evol* 50:552–567.
- Voisin JL. 2000a. La clavicle humaine: adaptation à la station érigée? *Biom Hum et Anthropol* 18:15–22.
- Voisin JL. 2000b. L'épaule des hominidés: aspects architecturaux et fonctionnels, références particulières à la clavicle. PhD thesis. Paris: Thèse du Muséum National d'Histoire Naturelle.
- Voisin JL. 2001. Evolution de la morphologie claviculaire au sein du genre Homo: conséquences architecturales et fonctionnelles sur la ceinture scapulaire. *Anthropologie (Paris)* 105:449–468.
- Voisin JL. 2004. Clavicle: approche architecturale de l'épaule et réflexion sur le statut systématique des néandertaliens. *Comp Rendus Acad Sci Sér Palevol* 3:133–142.
- Voisin JL. 2006. Krapina and other neanderthal clavicles: a peculiar morphology? *Periodicum Biologorum* 108 (in press).
- Voisin JL, Balzeau A. 2004. Internal structures of the clavicle. Method and preliminary results on Pan, Gorilla and Homo. *Bull Mém Soc Anthropol* 16:5–16.
- Walker RA, Lovejoy CO. 1985. Radiographic changes in the clavicle and proximal femur and their use in the determination of skeletal age at death. *Am J Phys Anthropol* 68:67–78.
- Webb PAO, Suchey JM. 1985. Epiphyseal union of the anterior iliac crest and medial clavicle in a modern multiracial sample of American males and females. *Am J Phys Anthropol* 68:457–466.
- Zhang J, Han B. 1994. The sexing of clavicles of Chinese Han. *Acta Anthropol Sin* 13:314–320.
- Zhang J, Tian X. 2001. The sexing of the Chinese Han clavicles with fisher's linear discriminant functions. *Acta Anthropol Sin* 20:209–216.