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...
TABLE 1. Number of clavicles studied*

<table>
<thead>
<tr>
<th>Species (Abreviation)</th>
<th>Clavicle</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Homo sapiens sapiens</em>† (Hm)</td>
<td>33</td>
</tr>
<tr>
<td>Pan troglodytes (Pt)</td>
<td>26</td>
</tr>
<tr>
<td>Pan paniscus (Pp)</td>
<td>19</td>
</tr>
<tr>
<td>Gorilla gorilla (Gor)</td>
<td>33</td>
</tr>
<tr>
<td>Pongo pygmaeus (Oo)</td>
<td>24</td>
</tr>
<tr>
<td>Hyllobates sp. (Gb)</td>
<td>22</td>
</tr>
<tr>
<td>Ateles sp. (At)</td>
<td>9</td>
</tr>
<tr>
<td>Colobus sp. (Cl)</td>
<td>25</td>
</tr>
<tr>
<td>Procolobus sp. (Prce)</td>
<td>19</td>
</tr>
<tr>
<td>Papio hamadryas (Ba)</td>
<td>28</td>
</tr>
</tbody>
</table>

*Non captive specimens whenever possible.
**Europe 10, Africa 7, North America 5, Asia 7, Unknown 4

(Details in Voisin, 2000b).

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, Hyllobates sp., Papio hamadryas, Colobus sp., Procolobus sp.,* and *Ateles sp.* (Table 1). The Hyllobates sp. material includes clavicles from the two subgenera, *Nomascus* and *Hyllobates,* as they have been shown to be sufficiently close for possible hybridization between them (Groves, 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 and des Mammifères et Oiseaux du Museum 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 ± 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).
**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...
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-

<table>
<thead>
<tr>
<th>Species (number of bones)</th>
<th>Internal curvature</th>
<th>External curvature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Standard deviation</td>
</tr>
<tr>
<td><em>Homo sapiens sapiens</em> (33)</td>
<td>12.6</td>
<td>2.5</td>
</tr>
<tr>
<td><em>Pan troglodytes</em> (26)</td>
<td>8.1</td>
<td>2.8</td>
</tr>
<tr>
<td><em>Pan paniscus</em> (19)</td>
<td>7.5</td>
<td>2.0</td>
</tr>
<tr>
<td><em>Gorilla gorilla</em> (33)</td>
<td>3.3</td>
<td>1.9</td>
</tr>
<tr>
<td><em>Pongo pygmaeus</em> (24)</td>
<td>5.8</td>
<td>2.1</td>
</tr>
<tr>
<td><em>Hylobates sp.</em> (22)</td>
<td>12.6</td>
<td>2.8</td>
</tr>
<tr>
<td><em>Ateles sp.</em> (9)</td>
<td>16.9</td>
<td>1.9</td>
</tr>
<tr>
<td><em>Colobus sp.</em> (25)</td>
<td>5.3</td>
<td>2.8</td>
</tr>
<tr>
<td><em>Procolobus sp.</em> (19)</td>
<td>7.4</td>
<td>2.7</td>
</tr>
<tr>
<td><em>Papio hamadryas</em> (28)</td>
<td>2.2</td>
<td>1.2</td>
</tr>
</tbody>
</table>

*For *Gorilla* and *Papio*, we retained only individuals who possess a superior curvature to estimate means and standard deviations.*
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 always showing a superior curvature and a slightly pronounced, if not absent, inferior 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 curvatures 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;
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; Ashton 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, 1963; 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-

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

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

Stern et al., 1980)
sence of the pectoralis major pars clavicularis 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 clavicularis (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.

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.
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 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 (Grasse, 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.

### TABLE 5. Characteristics of clavicle curvatures in dorsal view*

<table>
<thead>
<tr>
<th>Species (number of bones)</th>
<th>Mean</th>
<th>Standard deviation</th>
<th>Variance</th>
<th>Mean</th>
<th>Standard deviation</th>
<th>Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Homo sapiens sapiens (33)</td>
<td>5.1</td>
<td>2.3</td>
<td>5.3</td>
<td>2.9</td>
<td>1.5</td>
<td>2.3</td>
</tr>
<tr>
<td>Pan troglodytes (26)</td>
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<td>3.3</td>
<td>10.9</td>
<td>7.6</td>
<td>3.2</td>
<td>10.2</td>
</tr>
<tr>
<td>Pan paniscus (19)</td>
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<td>3.0</td>
<td>10.4</td>
<td>10.4</td>
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<td>3.6</td>
</tr>
<tr>
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<td>7.2</td>
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<td>4.8</td>
<td>3.4</td>
<td>1.1</td>
<td>1.2</td>
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<td>1.9</td>
<td>3.6</td>
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<td>14.4</td>
<td>3.9</td>
<td>1.7</td>
<td>2.9</td>
</tr>
</tbody>
</table>

*For Homo, Colobus, Procolobus and Papio, we retained only individuals who possess a superior curvature to estimate means and standard deviations.
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 Laganey, Daniel Robineau and Christine Lefèvre, Michel Tranier, Vim 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


