Brief Report


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Atelines, Apes and Wrist Joints

Denis Youlatos

Department of Anatomy, University of Puerto Rico School of Medicine, San Juan, P.R., USA

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Introduction

In a series of papers [1–5], as well as a recent synthesis [6], Lewis proposed the synapomorphic nature of the hominoid proximal wrist joint as follows: (a) the distal radioulnar joint is a fully elaborated diarthrodial joint; (b) the distal ulnar extremity reduces in size, forms a styloid process and retracts more or less proximally; (c) the pisiform reduces in size, remains proximal (in gibbons) or migrates disloventrally (in great apes), losing contact with the distal part of the ulna; (d) the ulnar styloid process loses, partly (in Hylobates and Pan) or completely (in Pongo and Gorilla), contact with the proximal facet of the triquetrum, by means of an intra-articular meniscus. According to Lewis, this complex of features is functionally associated with brachiation, which involves not only suspensory locomotion with body rotation of 180° about the grasping hand, but also '... a wide range of versatile arboreal activities, such as climbing, feeding and suspensory posturing in the terminal branches' [6, p. 58]. Such movements require enhanced rotatory capacity of supination and ulnar deviation, accomplished by the combination of the above features [1–6].

Cartmill and Milton [7] however observed that features similar to those of hominoids (excluding a meniscus) were present in lorisines: presence of an ulnar styloid process, reduction and distal migration of the pisiform, loss of the ulnopisiform articulation and also partial loss of the ulnotriquetral articulation. They associated these features with slow climbing, bridging and inverted slow quadrupedalism. Two years later, Mendel [8] showed similar features in the wrist of the slow suspensory two-toed sloth (Choloepus), which further supported the functional associations proposed by Cartmill and Milton [7].

Slow climbing, arm suspension and bridging contribute considerably in the positional behavior of the prehensile-tailed atelines, Alouatta and Ateles [9–12] (classification following Rosenberger and Strier [13]). Thus, these platyrhines might be expected to exhibit features similar to those described above in hominoids and
lorisines. However, neither Lewis [2, 3, 6] nor Corruccini [14] found any particular adaptations in the wrist joints of these primates, although earlier workers such as Parsons and Schwarz (cited in Lewis [2]) had reported the loss of the ulnopalmar articulation in Ateles. More precisely, Lewis [6], after dissection of one Ateles geoffroyi and one Ateles paniscus, found that both specimens retained the ulnopalmar articulation, but he admitted that indeed in some Ateles specimens the pisiform is distally located and it is likely that the contact with the ulnar styloid is lost.

In this report, dissections of the wrist joints of Alouatta seniculus and A. paniscus appear to support in part the hypothesis of Cartmill and Milton and provide evidence contrary to Lewis' views.

Material and Methods

Two adult and 1 subadult males of wild-shot A. seniculus as well as 2 adult females and 1 subadult male of wild-shot A. paniscus were obtained for this study. All 6 specimens come from French Guiana and were preserved in 10% formalin solution. They are in the collections of the Laboratoire d'Anatomie Comparée of the Muséum National d'Histoire Naturelle in Paris, France.

Prior to dissections, radiographs of the region of the wrist were made. This region was then skinned and the joint capsule carefully cut through from either the dorsal or palmar (ventral) side. The articular surfaces of the proximal wrist joint and the intracapsular ligaments were thus exposed and photographs were taken. Findings on the wet specimens were further supplemented by observations on skeletal material from the same laboratory's osteological collections.

Results

Ateles paniscus

In all 3 specimens examined, the pisiform was small in size and positioned disto-ventrally in the palm (fig. 1). Consequently there was no ulnopalmar articulation, contrary to Lewis' observations [2, 6]. The ulnar distal extremity was large, it was not retracted proximally and it articulated with the concave proximal facet of the triquetrum. In all 3 specimens, however, soft tissue covered the ulnar half of the tri-
Fig. 2. a Dorsal view of the opened proximal wrist joint of *A. seniculus*, specimen No. 447. b Palmar view of the *A. seniculus* specimen No. NA179. Abbreviations are as in figure 1; p = pisiform. Here the intra-articular tissue covers parts of both triquetrum and pisiform.

...quetrum, reducing considerably the ulnotriquetral contact (fig. 1). Inside the capsule, and apart from the ulno- and radiocarpal palmar ligaments converging to the lunate, 3 more ligaments were present (fig. 1): (a) a narrow dorsal one connecting the ulnoradial disc with the dorsolateral aspect of the lunate; (b) just palmar to it, lay a large ligament joining the base of the ulnar styloid process with the lunotriquetral interosseous ligament; (c) a third palmar ligament was found between the palmar surface of the distal end of the ulna and the proximomedial surface of the pisiform. There was no synovial septum, as described by Lewis [2].

*Alouatta seniculus*

The wrist joint of the red howling monkey was similar to those of other arboreal quadrupedal monkeys (e.g. *Cebus, Colobus*) described by Lewis [2–4]. Both ulnopisiform and ulnotriquetral articulations were present. The proximal facets of both triquetrum and pisiform were strongly concave and the corresponding ulnar distal facets were well marked and separated (fig. 2a, b). The pisiform was rod-like and robust, projected proximoidemally and bore 2 robust ligaments for the distal carpals and metacarpals. Inside the capsule, only one additional ligament was found, joining the radioulnar disc with the lunotriquetral interosseous ligament (fig. 2a, b). However, in a single specimen (NA179, fig. 2b), soft tissue covered the ulnar third of the triquetral and pisiform proximal facets, hence reducing the ulnocarpal contact surfaces. This tissue was absent in the two other howler specimens, where the ulnocarpal articulation was extensive.

**Discussion**

The findings reported above show that both atelines present, to a certain extent, some of the wrist features seen in hominoids [6], also convergently developed in lorisines and sloths [7, 8]. In fact, only *Ateles* shows a highly modified joint compared...
to other platyrrhines, in contrast to previous reports [2, 6, 14]. The absence of the ulnarisiform contact may be a feature varying within the genus Ateles, but it seems to be constant in A. paniscus (contra [6]). This absence is probably related to enhanced pronation and supination at this level [1–6], as also suggested by Sarmiento [15] (although Yalden [16] denied such an increase). Furthermore, the intra-articular tissue reflects a joint not so well suited for compressive stresses [7]. This distinctive feature of the spider monkey carpus is also mirrored more distally, in the midcarpal joints, which show an enhanced supination ability [17]. Field studies show that A. paniscus is highly suspensory [9, 18] and surely more than its congener A. geoffroyi, which principally climbs and clammers in a pronongrade way [9, 10] (although field studies were conducted in different sites having different forests). These apparently critical differences in percentages of locomotor behavior may be responsible for the morphological differences observed within the genus Ateles. On the other hand, pronograde activities are also important in the positional behavior of Ateles [9, 10, 18]. The large ulnar distum, the concave proximal triquetral facet and other, more distal, carpal features reflect a close-packed condition similar to that of other pronograde primates [2, 6, 19]. Therefore, the spider monkey appears to show a mosaic of features associated with enhanced mobility, as well as stability.

Alouatta’s positional behavior is restricted to more pronograde activities, walking and clambering above substrates, although suspensory modes, such as bridging, are almost exclusively present in moderate proportions [10–12, 20]. Both ulnocarpal articulations persist, and all the facets involved in the ulnocarpal contact are well marked. These features are closely associated with the close-packed weight-bearing condition observed in other pronograde quadrupedal primates, where the robust pisiform plays a very important role [6, 15, 18, 21]. However, the presence of intra-articular tissue in 1 of the 3 howler specimens examined reflects that, at least in some individuals, the wrist joint might not be as extremely adapted to resisting compressive loads and that some mobility does exist. It should be noted that this mobility is compensated more distally, where the midcarpal joints reveal a close-packed condition able to resist compressive forces, also providing limited midcarpal supination [17]. This is interesting because Schön Ybarra [22] postulated that climbing and clambering were the principal activities of ‘proto-howlers’, which later shifted to more pronograde locomotor modes due to their great hyoid development.

In a recent review of atelines, Rosenberger and Strier [13] concluded that the distribution of postcranial characters (carpals excluded) among this subfamily reveals that the last common ancestor of the subfamily was very likely a slow climbing and clambering animal. Intra-articular tissues (in Alouatta and Ateles) and a reduced proximal pisiform facet (in Alouatta, Ateles and Lagothrix [23]) can then be functionally associated with the loss (or at least the considerable reduction) of the ulnocarpal articulations, and to climbing and clambering. Lagothrix and Ateles detached from this stock and evolved more suspensory activities. Their striking similarity in carpal ligaments ([24], contra [2]) and in distal carpal morphology [17] appear to support this hypothesis. However, Lagothrix retains both ulnocarpal articulations [24], as it is more pronograde [25; pers. observ.]. Ateles and Brachyteles further developed more mobile joints (Brachyteles also lacks an ulnocarpal articulation [15, 16, 26]) plausibly related to a more suspensory positional behavior than exhibited by Lagothrix [27].

The similarities in the postcranium of hominoids, lorises, sloths and atelines have been previously well defined [7, 8, 26]. As these similarities convergently
evolved among different groups, it is likely that their common ancestors had similar positional behaviors. Hence it is reasonable to infer that each group derived from climbing and clambering ancestors, as proposed by Cartmill and Milton [7] and certainly not from brachiating ones as first postulated by Lewis [1–5] (although he recently [6] expanded his ‘brachiation’ category to include suspensory feeding and even climbing). This view also seems to be supported by recent functional interpretations of the postcrania of early hominoids, which reflect pronograde climbing and clambering adaptations [28].

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References


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