

New hand bones of *Hadropithecus stenognathus*: implications for the paleobiology of the Archaeolemuridae

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Abstract

A partial, associated skeleton of *Hadropithecus stenognathus* (AHA-I) was discovered in 2003 at Andrahomana Cave in southeastern Madagascar. Among the postcranial elements found were the first hand bones (right scaphoid, right hamate, left first metacarpal, and right and left fifth metacarpals) attributed to this rare subfossil lemur. These hand bones were compared to those of extant strepsirrhines and catarrhines in order to infer the positional adaptations of *Hadropithecus*, and they were compared to those of *Archaeolemur* in order to assess variation in hand morphology among archaeolemurids. The scaphoid tubercle does not project palmarly as in suspensory and climbing taxa, and the hamate has no hook at all (just a small tubercle), which also points to a poorly developed carpal tunnel. There is a distinctive, radioulnarly directed “spiral” facet for articulation with the triquetrum that is most similar in orientation to that of more terrestrial primates (i.e., *Lemur catta*, *Papio*, and *Gorilla*). The first metacarpal is very reduced and represents only 48% of the length of metacarpal V, as in *Archaeolemur*, which suggests that pollical grasping of arboreal supports was not important. Compared to *Archaeolemur*, the shaft of metacarpal V is gracile, and the head has no dorsal ridge and lacks characteristics functionally associated with digitigrade, extended metacarpophalangeal joint postures. Proximally, the articular facet for the hamate is oriented more dorsally. Thus, the carpometacarpal joint V appears to have a distinctive hyperextended set, which has no analog among living or extinct primates. The carpals of *Hadropithecus* are diagnostic of a pronograde, arboreal and terrestrial (although not digitigrade) locomotor repertoire that typifies *Lemur catta* and some Old World monkeys. No clinging, suspensory, or climbing specializations that characterize indriids or lorises can be found in the hand of this subfossil lemur. The hand of *Hadropithecus* likely had similar ranges of movement at the radiocarpal and midcarpal joints as of those of pronograde primates, such as lemurids, for which the hand is held in a more extended, pronated, and neutral (i.e., showing less ulnar deviation) position during locomotion in comparison to that of vertical clingers or slow climbers. Although highly autapomorphic, the hand of *Hadropithecus* resembles that of its sister taxon, *Archaeolemur*, in having a very reduced pollex and an articular facet on the scaphoid for a sizeable prepollex. These unusual hand features reinforce the monophyly of the Archaeolemuridae.

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Introduction

Burney and colleagues discovered a partial and associated skeleton of an archaeolemurid, *Hadropithecus stenognathus* at Andrahomana Cave, an eolianite cave and sinkhole complex on the southeast coast of Madagascar (Godfrey et al., 2006; Burney et al., n.d.). The skeleton was discovered in a previously unexcavated area covering several square meter (site AHA-I), and it belonged to a subadult individual as evinced by the state of epiphyseal fusion of the long bones (radius, humerus and femur) and elements of the axial skeleton (Godfrey et al., 2006). It has now been shown by Alan Walker and Tim Ryan to belong to the skull of a subadult that Sikora found in 1899 and Lorenz von Liburnau (1902) described (Burney et al., n.d.; Ryan et al., in press). These are the first associated fore- and hind-limb elements known for *Hadropithecus*, which is generally larger and differs in morphological details from the well-documented and closely related *Archaeolemur* (Godfrey et al., 1997, 2006). Prior misattributions of hind-limb elements of *Hadropithecus* have until recently hampered interpretations of its locomotor behavior (see Godfrey et al., 1997, 2006). Recovered elements of the appendicular skeleton of this individual include the first hand bones attributed to this rare subfossil lemur.

Site AHA-I lies at the northernmost end of the main cave chamber at Andrahomana; it was one of two sites within the cave selected for controlled excavation by Burney and colleagues in July and August 2003 because they appeared to be relatively undisturbed. The skeletal elements of *Hadropithecus* at AHA-I were found in a lower unit generally lacking human artifacts. Dated material from this unit is mid-Holocene but not in consistent stratigraphic order, suggesting some disturbance by extreme marine events, such as tsunami or storm overwashes (Burney et al., n.d.). Despite that disturbance, the skeletal elements of *Hadropithecus* found there are in excellent condition. In addition to the partial skeleton of *Hadropithecus*, bones of other extant and extinct species were found in this deposit (Burney et al., n.d.).

Because several structure-function relationships are well established for the hand of living primates (Napier, 1960, 1961; Tuttle, 1969, 1970; Jenkins and Fleagle, 1975; Susman, 1979; Jenkins, 1981; Hamrick, 1995, 1996a,b; Lemelin, 1996, 2004; Lemelin and Schmitt, 1998; Richmond et al., 2001; Jouffroy and Medina, 2002; Richmond, 2006) and because corresponding elements of the hand also exist for *Archaeolemur*, functional and phylogenetic interpretations of these newly found hand bones of *Hadropithecus* are possible. The goals of this study are to: (1) describe these hand bones, (2) compare them to those of extant strepsirrhines and catarrhines in order to infer hand position during locomotor behavior in *Hadropithecus*, and (3) compare them to elements already known and described for *Archaeolemur edwardsi* (Jungers et al., 2005) in order to assess variation in the hand morphology of the archaeolemurids.

Materials and methods

The five hand bones found in association with the partial skeleton recently recovered at Andrahomana (site AHA-I) and attributed to *Hadropithecus stenognathus* comprise: a right scaphoid (Square D4), right hamate (Squares C3D3), left first metacarpal (Squares C3D3), left fifth metacarpal (Square C3), and right fifth metacarpal (Squares C3D3). All hand bones are complete and show little or no abrasion. These specimens were compared to selected extant strepsirrhines, cercopithecoids, apes, and finally to *Archaeolemur edwardsi* (USNM 447012 and DPC 11823), a close relative of *Hadropithecus* and member of the family Archaeolemuridae. All specimens were examined under a stereoscope and photographed using a digital camera equipped with a macro lens. Selected measurements were taken on elements of the hand of *Hadropithecus* and *Archaeolemur*. Four metric variables were compared between the two archaeolemurid taxa and extant strepsirrhine and catarrhine primates (from an extensive morphometric dataset collected by the authors): (1) relative length of scaphoid tubercle (scaphoid tubercle length/scaphoid breadth \times 100); (2) triquetral-capitate facet angle of hamate (degrees at the intersection of the triquetral facet and capitate facet lines on the hamate in dorsal view); (3) triquetral-metacarpal facet angle of the hamate (degrees at intersection of the triquetral facet and the metacarpal facet lines on the hamate in dorsal view); (4) relative pollical length (length of first metacarpal/length of fifth metacarpal \times 100).

Results

Scaphoid

The overall size of the scaphoid is larger than that of any extant Malagasy lemur. The proximal articular surface for the radius is ovoid and is wide radioulnarly (Figs. 1a,c,d and 2a). On the palmar and proximal side of the scaphoid, a distinctive semilunar articular surface for the lunate can be observed as well (Figs. 1d and 2b). The shape of the scaphoid articular facet for the radius resembles that of quadrupedal lemurids. However, the articular surface for the radius appears slightly more compressed dorsopalmarly. This articular surface extends very much dorsopalmarly and shows a concavity similar to that observed in quadrupedal lemurids, particularly *Lemur catta*, and the presumably quadrupedal archaeolemurid, *Archaeolemur* (Figs. 1a,c,e and 2a). A very shallow, nonarticular surface bound proximally by a small crest meets with the distal articular surface of the scaphoid, which is compressed and convex dorsopalmarly, and concave radioulnarly. This saddle-shaped joint surface likely accommodated the centrale, which is unfused to the scaphoid (Figs. 1 and 2). When viewed dorsally and distally, the contact facets for the centrale and trapezium are distinct (Figs. 1c and 2a). Beard and Godinot (1988) described a similar distinctiveness in those contact facets of the scaphoid of *Smilodectes*. In *Hadropithecus*, the joint surface for the centrale is wide and concave radioulnarly, and extends the entire distal surface of the scaphoid

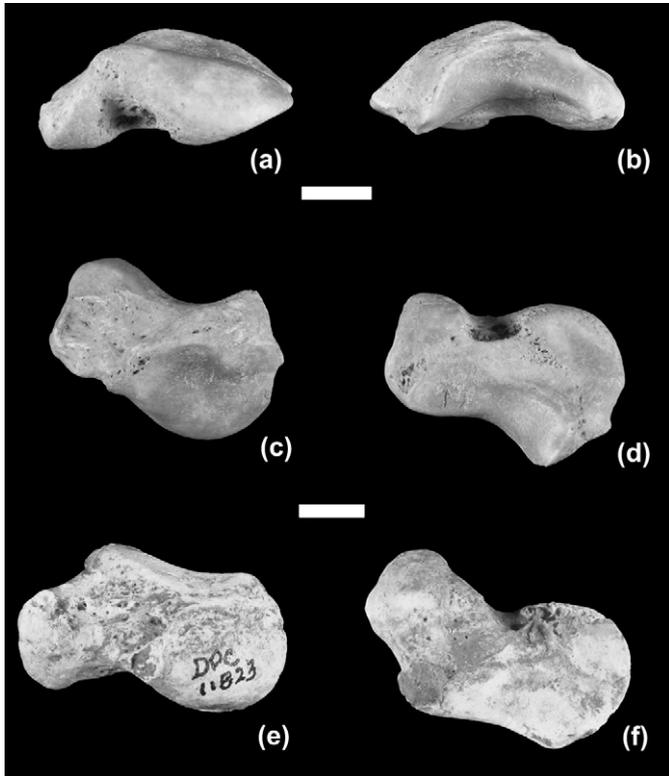


Fig. 1. Right scaphoid of *Hadropithecus stenognathus* (AHA-I; a: proximal, b: distal, c: dorsal, d: palmar) compared to that of *Archaeolemur edwardsi* (DPC 11823; e: dorsal, f: palmar). Scale bar is 5 mm.

(Fig. 2). In contrast, the joint surface for the trapezium is much narrower, flatter and is part of the scaphoid tubercle proper only (Fig. 2a). A distinctive and ovoid articular surface can be observed on the palmar surface of the scaphoid tubercle, which probably accommodated a sizeable prepollex (Figs. 1d and 2b). A large prepollex also typifies the hand of *Archaeolemur* (Jungers et al., 2005).

The tubercle of the scaphoid is relatively short and is most similar to that of *Archaeolemur* and *Lemur catta* (Fig. 3). Nevertheless, the tubercle of the scaphoid of *Archaeolemur*

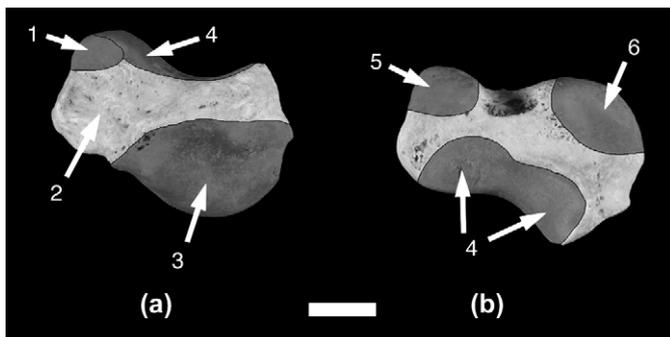


Fig. 2. Key morphological features of the scaphoid of *Hadropithecus stenognathus* (AHA-I; a: dorsal; b: palmar). Shaded areas indicate approximate articular contacts with other carpal bones based on comparisons with extant lemurs (1: contact area for trapezium; 2: scaphoid tubercle; 3: contact for radius; 4: contact for centrale; 5: contact for prepollex; 6: contact for lunate). In (a), top of picture is distal and left is radial, and in (b), top is proximoradial and left is radial. Scale bar is 5 mm.

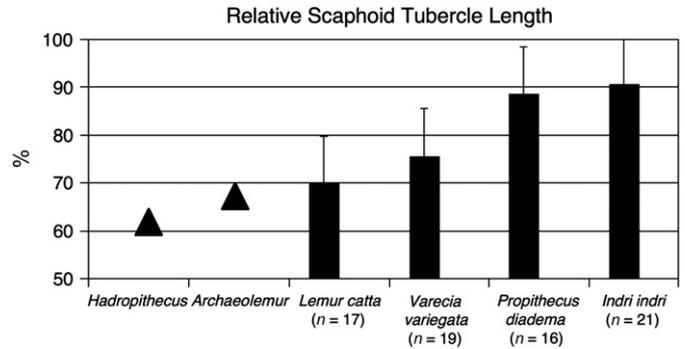


Fig. 3. Relative length of scaphoid tubercle in archaeolemurids and extant lemurs selected for their differences in positional behavior. Both *Archaeolemur* (USNM 447012) and *Hadropithecus* (AHA-I) have a relatively small scaphoid tubercle that more closely resembles the more terrestrial *Lemur catta* than the vertically clinging and more suspensory taxa (indriids). The vertical bar represents the mean and whisker one standard deviation.

is relatively longer and has a more distinctive head (with slight neck) compared to *Hadropithecus* (Fig. 1e,f). Proximally, a deep pit separates the scaphoid tubercle from the proximal radial facet. In the same proximal view, the tubercle and articular surface for the radius are roughly in the same plane (i.e., with a wide angle between them) as in *Babakotia* (Fig. 9 in Hamrick et al., 2000) and *Archaeolemur* (DPC 11823).

Hamate

The right hamate is complete (Figs. 4–7). The hamates of *Archaeolemur* (USNM 447012) and *Hadropithecus* are quite similar in length (12.8 mm vs. 13.7 mm). Radially, the articular facet for the capitate is more developed proximally than distally (Fig. 4b). This is because a large pitted area—probably

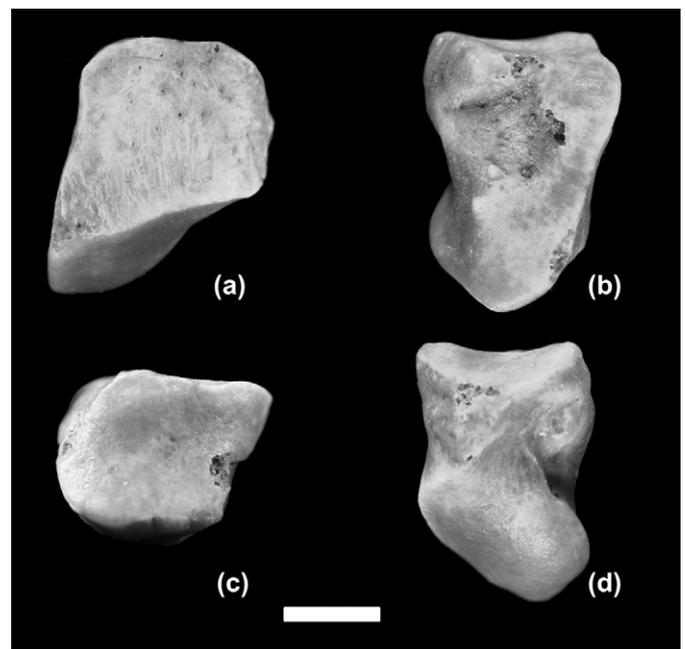


Fig. 4. Right hamate of *Hadropithecus stenognathus* (AHA-I; a: dorsal, b: radial, c: distal, d: ulnar). Scale bar is 5 mm.

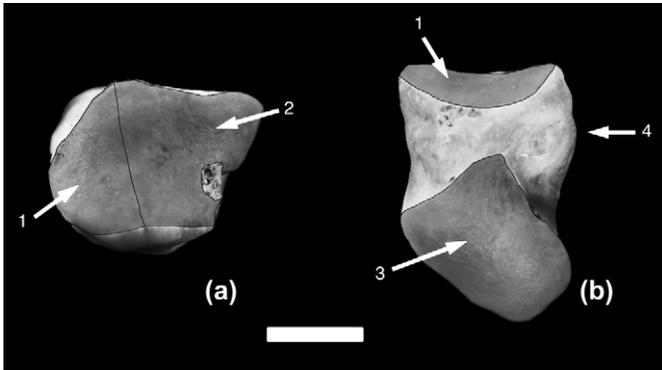


Fig. 5. Key morphological features of the hamate of *Hadropithecus stenognathus* (AHA-I; a: distal; b: ulnar). Shaded areas indicate approximate articular contacts with other hand bones based on associated AHA-I metacarpal V and comparisons with extant lemurs (1: contact area for metacarpal V; 2: contact area for metacarpal IV; 3: contact for triquetrum; 4: bony protuberance equivalent to hamulus of hamate in other primates). In (a), top of picture is dorsal and left is ulnar, and in (b), top is distal and left is dorsal. Scale bar is 5 mm.

for the attachment of the interosseous intercarpal ligament—is present on the palmar half of that radial surface (Fig. 4b). On the same radial view, the hamate shows a small bony protuberance that occupies the distopalmar aspect of the bone and coincides with the palmar edge of the carpometacarpal contact



Fig. 6. (a) Dorsal view of right capitate, hamate and metacarpals III–V of *Archaeolemur edwardsi* (USNM 447012), and (b) right hamate and metacarpal V of *Hadropithecus stenognathus* (AHA-I) in articulated position. Note the radial set of metacarpal V in *Hadropithecus* compared to *Archaeolemur*. The position of metacarpals IV and V of *A. edwardsi* (USNM 447012) shown in Jungers et al. (2005; Fig. 1) was inadvertently reversed (although not in the comparative and morphometric analyses). The current figure shows the correct position of those metacarpals in relation with the hamate for the USNM 447012 specimen.



Fig. 7. Ulnar view of right hamate and right metacarpal V of (a) *Archaeolemur edwardsi* (USNM 447012) and (b) *Hadropithecus stenognathus* (AHA-I) in articulated position. Note the pronounced hyperextended position of carpometacarpal joint V in *Hadropithecus* and the very reduced hamulus of the hamate (arrows) compared to *Archaeolemur*.

for rays IV and V (Figs. 4b and 5b). This bony protuberance is the very reduced hamulus of the hamate (Fig. 5b). In some ways, the diminutive hamulus of the hamate of *Hadropithecus* most resembles the condition reported in adapiform primates (Beard and Godinot, 1988; Hamrick, 1996c). The hamulus of *Archaeolemur*, which is somewhat reduced compared to extant primates we examined, looks well-developed compared to the diminutive process of *Hadropithecus* (Fig. 7). In extant primates, especially lemurs, the hamulus of the hamate extends palmarly, far beyond the carpometacarpal joint surface for rays IV and V (Hamrick, 1996c, 1997).

Distally, the articular surface for the base of metacarpal IV and V is not as concave dorsopalmarly as in extant primates and is somewhat convex radioulnarly (Figs. 4c,d and 5a). In this way, the articular surface for the base of metacarpals IV and V appears slightly saddle-shaped and slopes proximally. In outline, the distal articular surface of the hamate is square like that of some adapiforms (Beard and Godinot, 1988). In most primates, the outline of the same surface is more triangular because of the prominent hook that extends palmarly. Continuous with the deep pit observed on the radial side is a small groove showing slight erosion, which may have transmitted a carpometacarpal ligament attaching onto the radial side of the base of metacarpal IV (Beard and Godinot, 1988). It is worth noting that the distal width of the hamate of *Hadropithecus* (9.8 mm) is smaller than the width of the scaphoid (13.9 mm). In many extant and subfossil lemurs, including *Archaeolemur*, both carpals have similar widths. The narrower distal end of the hamate of *Hadropithecus* is likely associated with the extremely reduced and highly unusual articular contact with the fifth metacarpal, which contrasts dramatically with the morphology observed in *Archaeolemur* and other primates (Figs. 6 and 7). The position of metacarpals IV and

V in relation to the hamate (USNM 447012) shown in Jungers et al. (2005; Fig. 1) in their description of *A. edwardsi* was inadvertently reversed (although not in the comparative and morphometric analyses). Figure 6 shows the correct position of those metacarpals in relation to the hamate for the USNM 447012 specimen.

Most of the dorsal surface of the hamate is nonarticular and is trapezoidal in outline, not unlike that of *Varecia* (Figs. 4a and 6). In contrast, the dorsal surface of the hamate is triangular in cercopithecines and *Archaeolemur* (Fig. 6), or rectangular in *Propithecus* and *Perodicticus*. The proximal surface of the hamate shows a distinctive “spiral” facet for articulation with the triquetrum (Figs. 4d and 5b). This proximal articular surface is extensive and merges with a well-defined and sharp ridge on the dorsal side of the hamate (Fig. 5b). Beard et al. (1986) reported a similar sharp ridge on the dorsal border of the “spiral” facet in *Proconsul* and suggested that it may restrict midcarpal supination when the hand is ulnarly deviated. The “spiral” facet becomes slightly more concave as it turns palmarly and distally. This concave surface is oriented radioulnarly rather than proximodistally, making the midcarpal joint essentially flat. This is especially obvious when examining the angle values for the orientation of the triquetral facet of the hamate (Fig. 8). *Hadropithecus* falls closest to the ranges of variation observed in *Lemur catta*, *Papio anubis*, and *Gorilla gorilla* for the values of those angles (Fig. 8). Overall, the configuration of the proximal articular facet of the hamate is similar to that of pronograde quadrupeds, especially those that are more terrestrial, suggesting a midcarpal joint designed more for stability than mobility (Jenkins and Fleagle, 1975; Hamrick, 1996a; Richmond, 2006).

Metacarpal V

The right and left fifth metacarpals (V) are complete (Fig. 9), with the left metacarpal showing some erosion and wear on the palmar surface of the shaft. The base of metacarpal V has a small tuberosity for the attachment of the extensor carpi ulnaris muscle and possibly the pisometacarpal ligament. On the radial side of the base, the articular facet for metacarpal IV is well defined (Fig. 9b). Just lateral and dorsal to it, the articular surface for the hamate can be found. The joint surface for the hamate is somewhat triangular in shape and is bound radially by a marked, rounded edge and ulnarly by a smaller, sharper edge (Fig. 9b,c). In strepsirrhines, the joint surface of the base is square whereas in some Old World monkeys such as *Papio* and colobines, the same joint facet is more triangular. Although *Hadropithecus* and these Old World monkeys are similar in the overall configuration of this joint surface, the subfossil lemur is different in one very important aspect: the joint surface of the metacarpal base does not extend onto the proximal and palmar surface of the bone (Fig. 9b,c). In all primates we examined, including *Archaeolemur*, the metacarpal facet for the hamate is oriented dorsopalmarly and faces proximally. Although the facet extends dorsally in some Old World monkeys, the articular surface covers the proximal

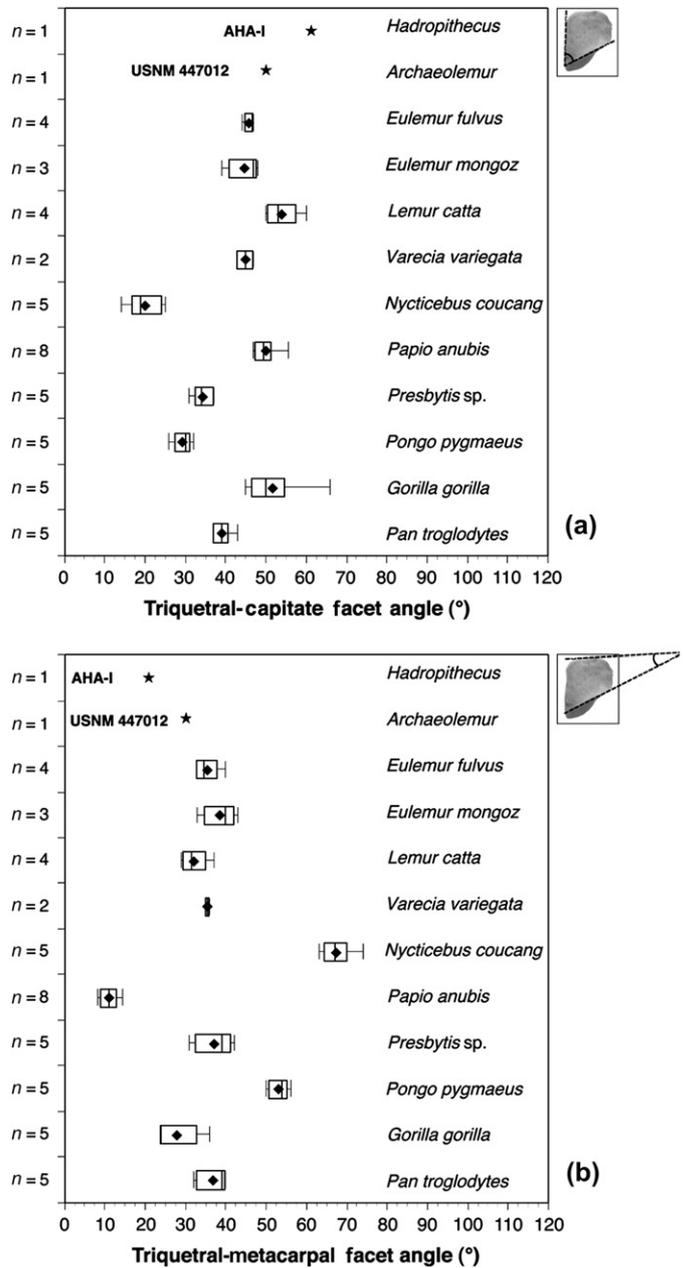


Fig. 8. (a) Box-plots of triquetral-capitate facet angle (°) and (b) triquetral-metacarpal facet angle (°) for selected extant lemurs, Old World monkeys, apes, and archaeolemurids. The diamond represents the mean and the vertical bar is the median (50th percentile). The box includes 50% of the data (25th to 75th percentiles), and the whiskers encompass 80% of the data (10th to 90th percentiles). Note the differences between *Archaeolemur* (USNM 447012) and *Hadropithecus* (AHA-I) in the value of those indices. *Hadropithecus* has a radioulnarly-oriented (i.e., proximally facing) triquetral facet that clusters closer to the range of variation measured for terrestrial primates (*Papio* and *Gorilla*).

and palmar surface of the bone as well. This is not the case in *Hadropithecus*. The articular surface for the hamate is present only on the dorsal side of the base and is tilted obliquely towards the radial side (Fig. 9a left). There is a tight and congruent fit between the right fifth metacarpal and right hamate attributed to that single individual of *Hadropithecus* (Figs. 6 and 7). However, that articular match positions the

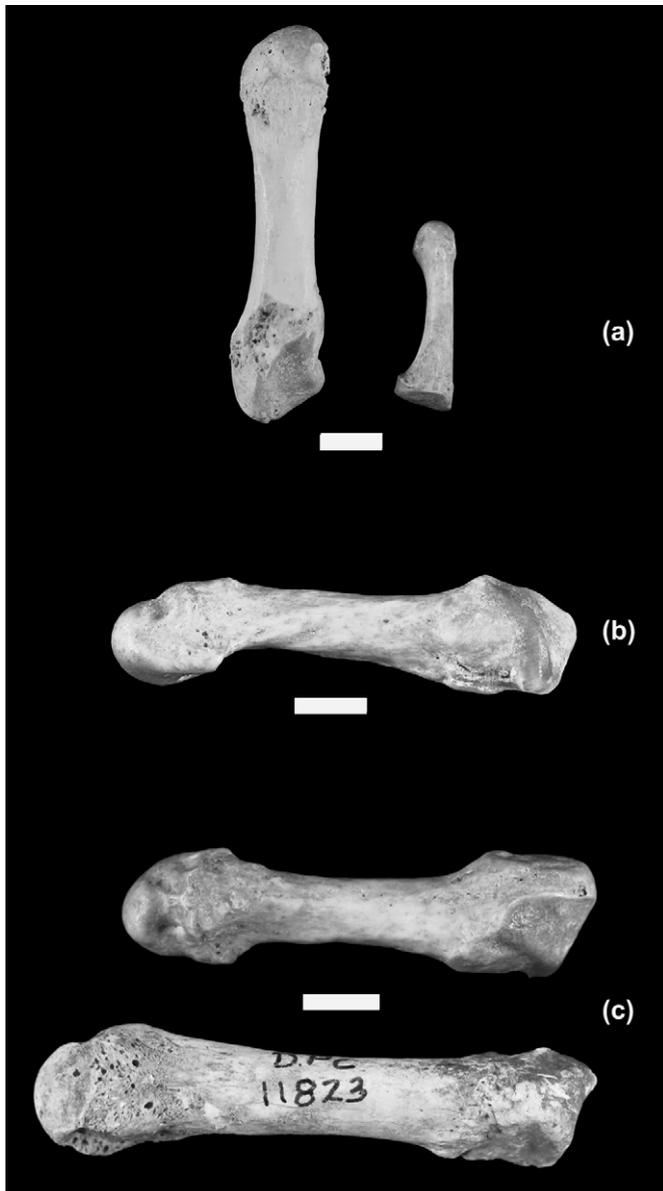


Fig. 9. (a) Dorsal view of left metacarpal V (top left in figure) and left metacarpal I (top right in figure) of *Hadropithecus stenognathus* (AHA-I). (b) Radial view of right metacarpal V of *Hadropithecus stenognathus* (AHA-I). (c) Dorsal views of right metacarpal V of *Hadropithecus stenognathus* (AHA-I) (top) compared to that of *Archaeolemur edwardsi* (DPC 11823) (bottom). Scale bars are 5 mm.

fifth metacarpal with the hamate in such a way that the corresponding carpometacarpal joint has a hyperextended set with the long axis of metacarpal V oriented radially (Figs. 6 and 7). To our knowledge, this very unusual condition for *Hadropithecus* has no analogue among primates, extant or extinct. It is worth pointing out that the shape of the articular base of the fifth metacarpal of *Archaeolemur* is more typical for lemurs (Figs. 6 and 7).

The head of the fifth metacarpal has no distinctive dorsal ridge and the shaft is more gracile compared to *Archaeolemur* (Fig. 9c). The metacarpal head is somewhat pear-shaped when viewed distally and is more similar to that of arboreal, pronograde, primates such as *Varecia* and *Macaca fascicularis*.

Metacarpal I

A complete left pollical metacarpal (I) showing no erosion was recovered as well. The first metacarpal of *Hadropithecus* is very short and gracile compared to the size of the carpals and fifth metacarpal (V) and resembles *Archaeolemur* (Jungers et al., 2005; Fig. 9a right). It represents only 48.4% of the length of metacarpal V, as in *Archaeolemur* (46.5%) and *Avahi* (45.6%; Fig. 10). In other extant lemurs and indriids, the mean value of that index is higher (e.g., 60.4% in *Lemur catta* and 61.7% in *Propithecus verreauxi*; Fig. 10). Among nonhuman primates we sampled, the species mean for the same index ranges between 59.2% (*Lepilemur mustelinus*) and 77.4% (*Theropithecus gelada*; Fig. 10). There is a discrete tuberosity on the radial side of the base as in other strepsirrhines, which is likely to be the attachment site for the abductor pollicis longus muscle (Jouffroy, 1962, 1975; P.L., pers. obs.).

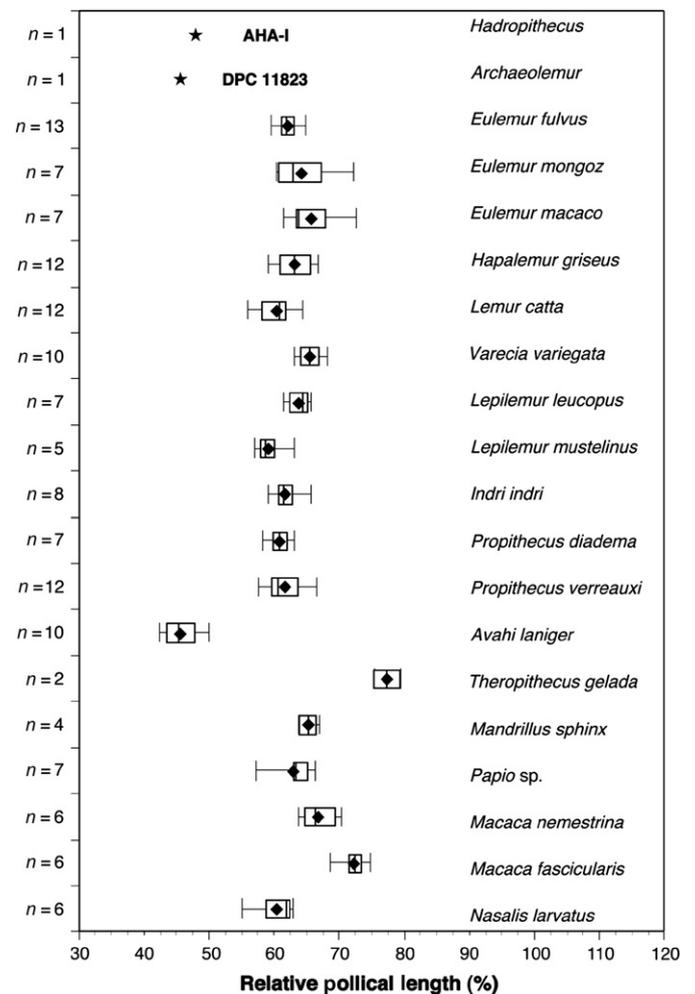


Fig. 10. Box-plots of relative pollical length (%) for selected extant lemurs, Old World monkeys and archaeolemurids. The diamond represents the mean and the vertical bar is the median (50th percentile). The box includes 50% of the data (25th to 75th percentiles), and the whiskers encompass 80% of the data (10th to 90th percentiles). Note the similarities between *Archaeolemur* (DPC 11823) and *Hadropithecus* (AHA-I) in the value of that index, which falls within the range of variation measured for *Avahi laniger*. All other primates compared have a significantly higher index (i.e., relative longer pollex).

The articular surface for the trapezium on the proximal end is round in outline and essentially flat. A distinct ridge is found on the palmar side of the base, giving the impression of a neck. The thin shaft leads distally to a small metacarpal head that is similar in overall shape to that of the fifth metacarpal, only much smaller (Fig. 9a).

Discussion and conclusions

The relative size, morphology, and orientation of the scaphoid tubercle and the virtual absence of a hook on the hamate (only a small bony protuberance) of *Hadropithecus* are indicative of a poorly developed and shallow carpal tunnel. Such features are commonly found in generalized quadrupeds as opposed to more suspensory species that rely more strongly on digital flexion (Napier, 1961). Among subfossil lemurs, the extreme condition seen in *Palaeopropithecus* parallels that of extant sloths (Hamrick et al., 2000), for which the carpal tunnel is well-developed to accommodate powerful extrinsic digital flexor tendons (Mendel, 1979, 1981; Hamrick, 1997), and is far removed from what we observed in *Hadropithecus*.

The proximal articular surfaces of the scaphoid and hamate are similar to those of pronograde primates, implying similar ranges of motion at the radiocarpal and midcarpal joints. The ovoid and radioulnarly broad proximal joint surface of the scaphoid and pitted area on its dorsal, non-articular surface resemble those of lemurids, especially *Lemur catta*. Together, these morphological features of the scaphoid promote extension of the hand at the radiocarpal joint during the support phase of quadrupedal walking, with the joint probably achieving a close-packed configuration during maximal extension (Jenkins and Fleagle, 1975; Hamrick, 1996a,b; Richmond et al., 2001). The lack of convexity on the proximal scaphoid surface indicates that the proximal carpal joint in *Hadropithecus* did not resemble the ‘ball-and-socket’ morphology of more suspensory taxa (Jenkins and Fleagle, 1975; Jenkins, 1981). Instead, it suggests that during locomotion *Hadropithecus* used relatively stereotypical, extended hand postures, unlike the more mobile and more variable hand postures seen in more suspensory primates. The prominent and radioulnarly oriented “spiral” facet on the hamate of *Hadropithecus*, which has a characteristic sharp ridge on its dorsal surface instead of dorsal articular extension as in more suspensory species, very likely indicates a hand that was normally held in pronation during positional behavior compared to the more supinated hand of vertical clingers such as indriids, and slow climbers such as lorises and the sloth-like *Babakotia* and *Palaeopropithecus* (Hamrick, 1996a,b; Hamrick et al., 2000; Lemelin, 2004). Morphometric, behavioral and experimental data all show that the configuration of the proximal articular surface of the hamate is an important determinant of the degree to which ulnar deviation is permitted at the midcarpal joint (Yalden, 1972; Cartmill and Milton, 1977; Jenkins, 1981; Sarmiento, 1988; Whitehead, 1993; Hamrick, 1995, 1996a,c; Lemelin and Schmitt, 1998; Jouffroy and Medina, 2002; Lemelin, 2004). Our comparisons with extant primates

show that the orientation of the triquetral facet of the hamate of *Hadropithecus* is most similar to that of more terrestrial quadrupeds (*Lemur catta*, *Papio*, and *Gorilla*). In these primates, the midcarpal joint shows less mobility in ulnar deviation compared to more suspensory species (Tuttle, 1969, 1970; Jenkins and Fleagle, 1975; Jenkins, 1981; Sarmiento, 1988; Whitehead, 1993; Hamrick, 1996a,b; Lemelin and Schmitt, 1998; Lemelin, 2004; Richmond, 2006).

The metacarpals also provide some information on the positional preferences and hand use of *Hadropithecus*. Clearly, metacarpal V of *Hadropithecus* does not show elongation that characterizes the hands of highly suspensory species. Similarly, the absolutely and relatively short metacarpal I suggests that grasping of arboreal supports was not an important functional role of the pollex. Metacarpal V also lacks the dorsal ridge on the head that is diagnostic of a digitigrade hand posture (Tuttle, 1970; Susman, 1979; Godfrey et al., 1997; Jungers et al., 2005). Taxa that habitually employ extended metacarpophalangeal joint postures, such as *Papio* and African apes, have enlarged dorsal ridges and dorsally expanded joint surfaces that serve to buttress an extended joint (Tuttle, 1970; Susman, 1979). They also have metacarpal heads that are wider dorsally than palmarly, which serves to tighten the collateral ligaments and enhance joint stability in extended metacarpophalangeal joint postures (Susman, 1979). The lack of this morphology in the metacarpal V head of *Hadropithecus* suggests that it did not habitually use extended metacarpophalangeal joint postures during locomotion.

Sorting out a functional signal from the unique configuration of the carpometacarpal joint V of *Hadropithecus* is challenging. It is possible that the carpometacarpal joint between the hamate and the base of the fifth metacarpal had a permanent hyperextended set and that the palmar surface of metacarpal V was rarely or never in contact with the substrate during locomotor behavior. Alternatively, and more likely, the hamate of *Hadropithecus* may have been permanently extended, resulting in habitually extended wrist postures when the palmar surface of metacarpal V contacted the substrate during locomotion. However, without any living primate analog, the meaning of this hyperextended joint configuration and its functional consequences for the hand position of *Hadropithecus* during locomotion and posture remain uncertain. Additional hand specimens, especially carpals and metacarpals, will be needed to test these alternative hypotheses.

The hands of *Hadropithecus* and *Archaeolemur* show morphological features that are diagnostic of pronograde primates without clinging, suspensory, or climbing specializations. This is true despite new molecular confirmation that the Archaeolemuridae are more closely related to lemurs that regularly employ or employed forelimb suspension (the Indriidae and Palaeopropithecidae) than to the quadrupedal Lemuridae (Orlando et al., n.d.). Postcranial convergence between archaeolemurids and more terrestrial quadrupedal primates has been demonstrated (Walker, 1967, 1974; Godfrey, 1988; Godfrey et al., 1997, 2006). As pointed out recently by Godfrey et al., the postcranium *Hadropithecus stenognathus* diverges

from that of most lemurids “in the direction of *Archaeolemur*, but more extremely so” (2006: 408). Indeed, the wrist region of *Hadropithecus* resembles that of more terrestrial primates, particularly *Lemur catta* and some catarrhines, in having a pitted area on the relatively flat dorsal surface of the scaphoid, and a more radioulnarly oriented and proximally facing triquetrotrochamate facet. Moreover, *Hadropithecus* had a shallower carpal tunnel, probably associated with a more reduced extrinsic digital flexor musculature. Thus, it is likely that the locomotor repertoire of *Hadropithecus* included fewer arboreal behaviors and that more time was spent on the ground in comparison to its close relative *Archaeolemur*. Although highly derived, the hand of *Hadropithecus* shares two important similarities with that of its sister taxon, *Archaeolemur*: a very reduced pollex (suggesting that pollical grasping of arboreal supports was unimportant in both taxa) and an enigmatically large prepollex. These two features of the pollical region, which are highly unusual for extant and extinct Malagasy strepsirrhines, underscore the monophyly of the Archaeolemuridae.

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