Forelimb long bones of *Nacholapithecus* (KNM-BG 35250) from the middle Miocene in Nachola, northern Kenya

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Abstract This paper provides a thorough description of humeral, ulnar, and radial specimens of the *Nacholapithecus* holotype (KNM-BG 35250). A spool-shaped humeral trochlea (and keeled sigmoid notch of the ulna) is a hallmark of elbow joint evolution in hominoids. In lacking this feature, the elbow of *Nacholapithecus* is comparatively primitive, resembling that of proconsulids. However, the humero-ulnar joint in *Nacholapithecus* is specialized for higher stability than that in proconsulids. The humero-radial joint (humeral capitulum) resembles that of extant apes and *Sivapithecus*. This condition may represent an intermediate stage leading to the fully modern elbow in extant apes. If this is the case, specialization of the humero-radial joint preceded that of the humero-ulnar joint. *Nacholapithecus* elbow joint morphology suggests more enhanced forearm rotation compared to proconsulids. This observation accords with the forelimb-dominated positional behavior of *Nacholapithecus* relative to proconsulids, which has been proposed on the grounds of limb proportions and the morphology of the phalanges, shoulder girdle, and vertebrae.

Key words: Hominoid evolution, Miocene, humerus, ulna, radius

Introduction

*Nacholapithecus kerioi* is a middle Miocene hominoid (16–15 Ma) known from the Aka Aiteputh Formation (Iyaya and Sawada, 1987; Sawada et al., 1987, 1998; Ishida et al., 1999) in Nachola, northern Kenya. The holotype specimen KNM-BG 35250 is a partial skeleton that was discovered at the site BG-K during the 1996 and 1997 field seasons (Nakatsukasa et al., 1998; Ishida et al., 2004; Nakatsukasa and Kunimatsu, 2009). KNM-BG 35250 preserves various skeletal elements, such as the maxilla, mandible, vertebrae, and many of the forelimb and hind limb bones, and represents an essential specimen in the study of the morphological evolution of fossil apes (Nakatsukasa et al., 1998; Ishida et al., 2004). Descriptions of KNM-BG 35250 were published by anatomical region (Nakatsukasa et al., 2003, 2007, 2012; Senut et al., 2004; Ogihara et al., 2016) after the preliminary reports. This paper provides a full description of the forelimb long bones of KNM-BG 35250. Previous studies have concluded that *Nacholapithecus* was more specialized for forelimb-dominated behaviors than proconsulids (sensu Alba (2012)) from the early Miocene (Nakatsukasa et al., 2003, 2007; Nakatsukasa and Kunimatsu, 2009; Ishida et al., 2004; Ogihara et al., 2016). We re-examine functional features of the forelimb of *Nacholapithecus*, including comparative fossil specimens not investigated in previous reports. Similarities and dissimilarities with middle–late Miocene Eurasian apes are also discussed.

Materials and Methods

The forelimb long bones described in this paper are listed in Table 1. KNM-BG 35250 was a full adult male with a body mass estimated to be close to 22 kg (Ishida et al., 2004). Most KNM-BG 35250 specimens have suffered erosion, cracking, or plastic distortion. Due to the issues of preservation, the utility of metric data is limited. Ten humeral and nine ulnar lengths were taken, and conventional ratios were calculated (Table 2, Table 3, Table 4, Table 5). We selected these measurements based on previous studies (Richmond et al., 1998; Gebo et al., 2009). The original
specimens were examined in the National Museums of Kenya, Nairobi. Comparative samples of living taxa were examined in the American Museum of Natural History, the National Museums of Kenya, and the Primate Research Institute, Kyoto University. Examined taxa and numbers of examined individuals are listed in Table 4 and Table 5. Linear lengths were measured to the nearest tenth of a millimeter using digital sliding calipers.

Cortical bone distribution and degree of postmortem deformation were evaluated using computed tomography (CT) (X-CT Research SA+; Norland-Stratec Co., Germany). Separation of bone from matrix is clear in the Nachola specimens compared with hominoid fossil specimens from other Miocene localities in Kenya. Pixel size was set at 0.1 mm with a slice thickness of 0.2 mm.

Table 1. Forelimb specimens of KNM-BG 35250 described in this study

| Accession number suffix | Part                              |
|-------------------------|-----------------------------------|
| M                       | Right distal humerus              |
| U                       | Right proximal humerus shaft      |
| N                       | Left distal humerus               |
| BU                      | Left humeral shaft                |
| V                       | Right ulna                        |
| C                       | Left ulna                         |
| V                       | Right ulna                        |
| W                       | Right distal radius               |

Table 2. Humeral measurements

| Measurement                                | Right (KNM-BG 35250M and U) | Left (KNM-BG 35250N and BU) | Definition                          |
|--------------------------------------------|-----------------------------|-----------------------------|-------------------------------------|
| Bicondylar breadth                         | (<53.4)*                    | —                           | (c) in Rose et al. (1992)           |
| Capitular height                           | (<16.9)                     | —                           | (f) in Rose (1988)                 |
| Articular width                            | (<38.7)                     | —                           | (a) in Rose (1988)                 |
| Capitular + zona width                     | 18.9                        | —                           | (d) in Rose (1988)                 |
| Trochlear width (anterior)                 | (<18.9)                     | (17.3)                      | (e) in Rose (1988)                 |
| Capitular width                            | 14.1                        | —                           | (i) in Rose (1988)                 |
| Medial trochlear rim height                | —                           | 15.0                        | (c) in Rose (1988)                 |
| Lateral trochlear rim height               | (13.9)                      | 13.7                        | (j) in Rose (1988)                 |
| Trochlear notch height                     | (11.1)                      | 10.5                        | (k) in Rose (1988)                 |
| Posterior breadth of distal articulation   | (15.8)                      | —                           | (1) in Harrison (1982)             |

* Values in parentheses represent estimates or values affected by deformation.

Table 3. Ulnar measurements

| Measurement*                             | KNM-BG 17824 Nacholapithecus | KNM-BG 35250V Nacholapithecus | KNM-BG 35250C Nacholapithecus | KNM-RU 1786 Ekembo nyanziae | KNM-RU 2036CF Ekembo heseloni | KNM-WK 16950R Turkanapithecus | Definition                          |
|------------------------------------------|------------------------------|-------------------------------|-------------------------------|-----------------------------|-------------------------------|-------------------------------|-------------------------------------|
| Sigmoid notch depth (SND)                | (<16.9)*                     | 17.0                          | (16.2)                        | 20.0                        | 11.5                          | 9.8                           | Begun (1992), Richmond et al. (1998) |
| Anteroposterior thickness at distal beak of trochlear notch (PAAP) | (>27.3)                     | 29.5                          | (28.3)                        | —                           | 19.3                          | 16.2                          | Begun (1992)                       |
| Proximal shaft anteroposterior thickness (PAP) | 20.1                        | (<22.1)                       | (<20.9)                       | 26.5                        | 14.8                          | 11.8                          | Begun (1992), Richmond et al. (1998) |
| Olecranon process mediolateral breadth (OPML) | —                           | (14.9)                        | (14.2)                        | 19.0                        | 11.5                          | 10.5                          | Richmond et al. (1998)           |
| Sigmoid notch mediolateral width (SML)   | —                           | 12.8                          | (10.9)                        | 14.1                        | 9.7                           | 8.5                           | Richmond et al. (1998)           |
| Trochlear articular mediolateral breadth (TAB) | —                           | 17.5                          | —                             | 18.6                        | 11.4                          | 9.9                           | Begun (1992), Richmond et al. (1998) |
| Sigmoid notch proximodistal length (NPD)**| —                           | —                             | (18.6)                        | —                           | 15.0                          | 11.5                          | Richmond et al. (1998)           |

* Values in parentheses represent values affected by damage.
** Distance between tips of the olecranon beak and coronoid process projected to the shaft axis. This definition differs from the original definition by Richmond et al. (1998).
The radial fossa is shallow and indistinct. On the other hand, the coronoid fossa is a deep circular depression (Figure 1f, Figure 2c). The medial epicondyle is robustly built, long, and projects posteromedially. The angle of retroflexion is c. 40°. However, this value must have originally been higher (i.e., stronger retroflexion) before the bone was subjected to anteroposterior compression.

The capitulum is large and globular, being proximodistally taller than wide (Table 2). This height is likely increased from the original dimension due to anteroposterior compression (a thin crack can be observed on the distal surface). In distal view (Figure 1j), the articular surface on the capitulum is wide. The zona conoidea is damaged anteriorly, but the medial part of the capitular surface and the zona are preserved.

The shaft is cracked and widened because of anteroposterior compression. The bi-epicondylar width is 53.4 mm. This value should be regarded as greater than the original one due to the distortion of the medial epicondyle. Above the lateral epicondyle, the brachialis flange is well developed. The margin of this flange shows a weak concave curvature in the anterior view, rather than a convex curvature. In the lateral view (Figure 1e), the most distal part of the supracondylar ridge changes its course distoanteriorly and merges with the lateral epicondyle. The lateral epicondyle is relatively high in position and massive, and shows marked lateral projection (Figure 1f). The proximal border of the lateral epicondyle is c. 24 mm above the distal surface of the capitulum. The radial fossa is shallow and indistinct. On the other hand, the coronoid fossa is a deep circular depression (Figure 1f, Figure 2c). The medial epicondyle is robustly built, long, and projects posteromedially. The angle of retroflexion is c. 40°. However, this value must have originally been higher (i.e., stronger retroflexion) before the bone was subjected to anteroposterior compression.

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**Table 4. Humeral ratios**

| Taxon              | Specimen     | Articular width/bicondylar width | Capitular + zona width/trochlear width | Capitular height/capitular width | Medial trochlear rim height/lateral trochlear rim height |
|--------------------|--------------|----------------------------------|----------------------------------------|---------------------------------|--------------------------------------------------------|
| Nacholapithecus    | KNM-BG 35250M | (0.73)*                          | (1.0)                                  | 1.2                             | (1.09)**                                               |
| ?Rangwapithecus    | KNM-SO 31232  | 0.72                             | 0.98                                   | 1.19                            | 1.14                                                   |
| E. heseloni        | KNM-RU 2036AH | 0.81                             | 0.91                                   | 1.11                            | 1.23                                                   |
| K. wickeri         | KNM-FT 2751   | 0.79                             | 0.97                                   | 1.17                            | 1.25                                                   |
| Pan troglodytes    | n = 11       | 0.73                             | 0.99                                   | 1.14                            | 1.22                                                   |
| range              |              | 0.70–0.76                        | 0.86–1.06                              | 0.92–1.20                       | 1.17–1.39                                              |
| Hylobatids†        | n = 5        | 0.74                             | 1.27                                   | 1.33                            | 1.15                                                   |
| range              |              | 0.72–0.77                        | 1.16–1.34                              | 1.19–1.42                       | 1.08–1.29                                              |
| Cercopithecus mitis| n = 12       | 0.77                             | 1.42                                   | 1.16                            | 1.46                                                   |
| range              |              | 0.74–0.82                        | 1.24–1.60                              | 0.99–1.26                       | 1.28–1.75                                              |
| Colobus guereza    | n = 9        | 0.81                             | 1.76                                   | 0.98                            | 1.33                                                   |
| range              |              | 0.77–0.85                        | 1.58–2.09                              | 0.85–1.07                       | 1.05–1.53                                              |
| Alouatta seniculus | n = 10       | 0.71                             | 1.57                                   | 0.95                            | 1.29                                                   |
| range              |              | 0.65–0.79                        | 1.33–1.89                              | 0.87–1.02                       | 1.04–1.45                                              |

* Values in parentheses are affected by deformation.
** Measured on the opposite (left) side (KNM-BG 35250N).
† Hylobates and Hoolock.

**Table 5. Ulnar ratios**

|                  | PAAP/SND | TAB/SML | TAB/SND |
|------------------|----------|---------|---------|
| Nacholapithecus  | KNM-BG 35250V | 1.73 | 1.37 | 1.03 |
| Nacholapithecus  | KNM-BG 35250C | 1.75 | — | — |
| E. nyanzae       | KNM-RU 1786 | — | 1.30 | 0.93 |
| E. heseloni      | KNM-RU 2036CF | 1.63 | 1.18 | 0.99 |
| ?Rangwapithecus  | KNM-KT 38000B* | 1.63** | — | — |
| Turkanapithecus  | KNM-WK 16950R | 1.65 | 1.16 | 1.01 |
| Pan troglodytes  | (n = 11) | 1.64 | — | (1.20)† |
| range            |          | 1.46–1.73 | — | — |
| Hylobatids       | (n = 5) | 2.18 | — | — |
| range            |          | 2.0–2.39 | — | — |
| Cercopithecus    | (n = 12) | 1.83 | — | — |
| range            |          | 1.68–2.0 | — | — |
| Colobus          | (n = 9) | 1.91 | — | (0.94)† |
| range            |          | 1.81–2.10 | — | — |
| Alouatta         | (n = 10) | 1.74 | — | — |
| range            |          | 1.62–1.85 | — | — |

* Measurements adopted from Gebo et al. (2009).
** Affected by damage.
† Calculated from mean values of TAB and SND in Begun (1992).
most to the proximal break, c. 85 mm from the distal surface of the capitulum. CT of the distal shaft (Figure 2b) reveals that compression caused numerous small fractures in the medial and lateral cortex. Determining the original morphology is thus difficult. The cortex is similarly thick anteriorly and posteriorly.

KNM-BG 35250N (left distal humerus)

This specimen is a distal humeral fragment, preserving the medial epicondyle and medial portion of the humeral trochlea (Figure 3). The anterior surface of the trochlea is flattened due to anteroposterior compression (arrows in Figure 3a).

The lateral trochlear rim is low and blunt (arrow in Figure 3e) and the trochlear groove is shallow. The medial portion of the trochlear articular surface is much wider than the lateral portion (brackets in Figure 3), so the deepest part of the groove lies rather laterally. The medial portion of the trochlear groove is convex mediolaterally in the posterior part of the trochlea, whereas the lateral portion is much narrower. The lateral rim of the trochlea is low and blunt. Distally, this lateral rim disappears near the lateral wall of the olecranon fossa. In the posterior view, the medial border of the trochlear articular surface runs distomedially to proximolaterally. A groove-like depression exists medial to the posterior border of the olecranon fossa. This depression probably represents the area for the attachment of the posterior band of the ulnar collateral ligament.

The olecranon fossa takes a right-angled, triangular form. The lateral border is aligned with the proximodistal direction and forms a prominent keel. The medial border runs distomedially. The posterior surface lateral to the olecranon fossa is wide and flat. The medial border is on a thick pillar leading to the medial epicondyle.

The distal part of the shaft is almost perpendicular to the distal joint axis. The lateral supracondylar ridge reaches almost to the proximal break, c. 85 mm from the distal surface of the capitulum. CT of the distal shaft (Figure 2b) reveals that compression caused numerous small fractures in the medial and lateral cortex. Determining the original morphology is thus difficult. The cortex is similarly thick anteriorly and posteriorly.

KNM-BG 35250U (right humeral shaft fragment)

This is a 45 mm long fragment of the right humeral shaft, preserving the distal part of the deltoid plane (Figure 1a–d). The shaft is flattened. The cortex medial to the deltoid plane is cracked and collapsed toward the posterior cortex (Figure 2a). KNM-BG 35250U does not join the right distal portion KNM-BG 35250M. However, the missing part is probably short, given the similarities in size and shape of the breaks in these pieces (Figure 1d, i). The preserved part of the deltoid plane is flat. The width of the plane is 19.3 mm at the widest part. The deltopectoral crest is sharp. However, this condition is a result of deformation, since the cortex under the crest appears implausibly thin (Figure 2a).

KNM-BG 35250N (left distal humerus)

This specimen is a distal humeral fragment, preserving the medial epicondyle and medial portion of the humeral trochlea (Figure 3). The anterior surface of the trochlea is flattened due to anteroposterior compression (arrows in Figure 3a).

The lateral trochlear rim is low and blunt (arrow in Figure 3e) and the trochlear groove is shallow. The medial portion of the trochlear articular surface is much wider than the lateral portion (brackets in Figure 3), so the deepest part of the groove lies rather laterally. The medial portion of the trochlear groove is convex mediolaterally in the posterior part of the trochlea, whereas the lateral portion is much narrower. The lateral rim of the trochlea is low and blunt. Distally, this lateral rim disappears near the lateral wall of the olecranon fossa. In the posterior view, the medial border of the trochlear articular surface runs distomedially to proximolaterally. A groove-like depression exists medial to the posterior border of the olecranon fossa. This depression probably represents the area for the attachment of the posterior band of the ulnar collateral ligament.

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The distal part of the shaft is almost perpendicular to the distal joint axis. The lateral supracondylar ridge reaches almost to the proximal break, c. 85 mm from the distal surface of the capitulum. CT of the distal shaft (Figure 2b) reveals that compression caused numerous small fractures in the medial and lateral cortex. Determining the original morphology is thus difficult. The cortex is similarly thick anteriorly and posteriorly.
KNM-BG 35250BU (left humeral shaft)

This specimen is a 116 mm long left humeral shaft consisting of a large region of the deltoid plane and a short piece of the mid-shaft portion (Figure 4). The proximal two-thirds of the bone are badly smashed anteroposteriorly. The midshaft portion has not suffered from compression, although some pieces of the cortex are missing. The medullary cavity of the distal portion is filled with siliceous matrix (Figure 4a). At the most distal part of the deltoid plane (arrow ‘d’ in Figure 4b), the mediolateral thickness of the shaft is 17.3 mm and the anteroposterior thickness is 18.9 mm.

The proximal part bearing the deltoid plane is thoroughly flattened. The anterior cortex is entirely collapsed into the medullary cavity (Figure 4f). The deltopectoral crest is sharp, but the shadows (probably microfractures) in the cortex cross-section (arrow in Figure 4f) suggest that this part was subjected to deformation.

Curvature of the anteroposterior shaft is not remarkable (Figure 4c, e). However, the shaft might have undergone lateral bowing, if not strongly (Figure 4b, d), although this observation is not definitive. On the posterior aspect, the cortex just below the proximal break flares posteriorly (Figure 4d). This flaring was probably continuous with the buttress of the humeral head. If this is the case, then this humerus would have lacked strong medial torsion of the head.

KNM-BG 35250BV (right humeral head)

This is a flattened right humeral head, broken below the surgical neck and with loss of the proximal half of the head and most of the greater tuberosity (Figure 5). A short part of the shaft is missing between this specimen and KNM-BG 35250 BU. Otherwise, this specimen is unremarkable due to severe deformation.

Ulna

KNM-BG 35250C (left ulna proximal half)

This is a proximal portion of a left ulna that preserves the olecranon process, a large part of the sigmoid notch, the coronoid process, and the proximal one-third of the shaft (Figure 6). The preserved length is 105 mm. The olecranon was compressed mediolaterally during fossilization, resulting in a parasagittal furrow along the proximal surface of olecranon (Figure 6b). A deep depression posterior to the proximolateral part of the sigmoid articular surface also resulted from this compression (Figure 6c). The anterior tip of the olecranon beak and the distomedial portion of the sig-
A depression is evident anterodistal to the radial notch, for the annular ligament (arrows in Figure 6c). Unlike a previously described ulnar specimen (Rose et al., 1996), the insertion for m. brachialis is not remarkable (Figure 6a). This is probably due to the breakage of the shaft cortex (Figure 6e, ‘3’), since the corresponding insertion site is well developed in the right counterpart (Figure 7a, b).

Near the distal break, the shaft is less severely affected by plastic deformation. However, microcracks in the cortex (Figure 6e, ‘4’) suggest some deformation due to mediolateral compression. The cross-section of the shaft is anteroposteriorly elongated and pear-shaped with the anterior portion wider than the posterior portion. The cortex is thickest posteriorly and then anteriorly.

KNM-BG 35250V (right ulna proximal half)

This is a proximal portion of the right ulna (Figure 7). The preserved length is 122 mm. A large part of the proximal end (anteroproximal part of the olecranon process and proximal part of the sigmoid notch) is broken off. The shaft is heavily squashed mediolaterally. However, the coronoid process appears mostly intact.

The posterior profile of the olecranon process is almost

Figure 4. KNM-BG 35250BU left humeral shaft in (a) distal, (b) anterior, (c) lateral, (d) posterior, and (e) medial views. (f) CT images of the shaft (distal view). In (b), arrow labeled ‘d’ indicates the distal extent of the deltoïd plane, ‘bg’ indicates the medial ridge of the bicipital groove. This position is reflected in the posterior view (d). In (d), a remnant of the head buttress is indicated by a bracket. Bracket in (f) shows the deltoïd plane.

Figure 5. KNM-BG 35250BV left humeral head in (a) posterior, (b) anterior, and (c) distal views.
The coronoid process projects anteriorly, with a weak downward inclination of 22° (Figure 7c). The articular surface on the coronoid process is wide (17.5 mm) and most of the surface is concave (Figure 7b). The articular surface is divided into a narrow, flat, band-like area along the lateral border and a wide, concave area. No distinct border separ-
rates these areas. These areas correspond to the narrow latero-
and much wider medial portions of the articular surface of
the humeral trochlea, respectively (Figure 3c). The lateral
area is slightly higher than the medial one. Anteriorly, the
lateral area ends at a beak-like anterior tip, while the medial
area extends further anteriorly (and distally) (Figure 7b).

The radial notch is elongated anteriorly to posterodistally
(12.4 mm long). Although facing laterally (Figure 7c), this
orientation is altered from the original condition by shaft
fracture (Figure 7e). A distinct depression encroaches on the
radial notch anterodistally (arrow in Figure 7c), representing
an attachment area for the annular ligament. From the pos-
terdistal margin of the radial notch, the supinator crest de-
sends distally and continues to the interosseous crest. On
the medial side, the insertion of m. brachialis forms a deep
groove near the anterior border of the shaft (bracket in Fig-
ure 7a, b). Although the mediolateral compression hampers
determination of the original width of the shaft (Figure 7e),
the proximal part of the shaft is deep anteroposteriorly. The
cortex of the shaft is thick anteriorly and posteriorly.

Radius

KNM-BG 35250W (right radius distal half)

This specimen is a 136 mm long distal portion of the right
radius (Figure 8). The distal portion (c. 4 cm long) is
smashed anteroposteriorly. The distal radioulnar joint and
radiocarpal joint surfaces are crushed, except for the
scaphoid surface on the styloid process. The proximal por-
tion of the shaft bears a flat deltoid plane with a reduced radial
fossa, and this condition is shared with extant great apes and
marked humeral torsion (Rose, 1994), and is shared with the early Miocene
Equatorius heseloni (Napier and Davis, 1959) and the contemporaneous
Equatorius africanus (Le Gros Clark and Leakey, 1951; Sherwood et al., 2002) as well as later Eurasian taxa such as
Griphopithecus (Klein Hadersdorf) and Sivapithecus (GSP
30754) (Zapfe, 1960; Pilbeam et al., 1990; Begun, 1992;
Rose, 1993, 1997).

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Discussion

Humerus

The humerus of Nacholapithecus shows no sign of
marked medial torsion of the head, representing a point of
difference from extant great apes. Marked humeral torsion is
also absent in hylobatids (Larson, 1996). The humeral shaft
bears a flat deltoid plane with a sharp deltopectoral crest.
This condition is regarded as primitive for catarrhines (Rose,
1994), and is shared with the early Miocene
Proconsul heseloni (Senut et al., 2000).

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Griphopithecus (Klein Hadersdorf) and Sivapithecus (GSP
30754) (Zapfe, 1960; Pilbeam et al., 1990; Begun, 1992;
Rose, 1993, 1997).

The brachial flange, from which mm. brachioradialis and extensor carpi radialis longus originate, is well devel-
oped in Nacholapithecus. However, the flange does not flare
out as seen in Pan or some papionins (Fleagle and McGraw,
2002). In this regard, Nacholapithecus resembles
Kenyapithecus wickeri (KNM-FT 2751) and Ekembo
heseloni (KNM-RU 2036, a juvenile). On the other hand, a
recently reported proconsulid (?Rangwapithecus gordonii)
humerus from Lower Kapurtay (KNM-SO 31232) and a
large humerus from Songhor KNM-SO 1007 (Proconsul
major) both show an outward flaring flange (Senut, 1989,
2016; Gebo et al., 2009). The significance of this difference
remains unclear. Of note, Senut (2016) proposed that both
belong to Ugandapithecus major, which was previously in-
cluded within the genus Proconsul (Senut et al., 2000).
While this possibility is worthy of consideration, conclu-
sions must await additional specimens.

The morphologies of the radial and coronoid fossae distin-
guish middle Miocene African hominoids (Nacholapithecus, 
Equatorius, and K. wickeri) from proconsulids (Ward et al.,
1999; Ishida et al., 2004). In proconsulids (and Pliobates
from Spain (11.6 Ma) (Alba et al., 2015)), the radial fossa is
better developed than the coronoid fossa (see Figure 9a, b).
This condition is also common with Dendropithecus and
cercopithecoids, and thus probably represents the primitive
condition for catarrhines. Middle Miocene hominoids dis-
play a deep circular coronoid fossa with a reduced radial
fossa, and this condition is shared with extant great apes and
hylobatids (Ward et al., 1999; Ishida et al., 2004). Although
this characteristic is supposed to reflect structural differenti-
ation of the elbow joint among fossil apes, no hypothesis
appears to have been proposed to explain the meaning of this
difference. One may speculate on a more lateral (rather than

Nacholapithecus (Figure 9c). In Equatorius (KNM-TH 28860G), observation of this trait is impossible due to preservation issues. Although the trochlear groove is very shallow in these early/middle Miocene apes, the humeroulnar joint of Nacholapithecus probably had higher stability against mediolateral shearing forces thanks to a more complex concavoconvexity of the articular surfaces.

The capitulum in Nacholapithecus is distinct from that of the other fossil apes in its marked globularity. In addition, the capitulum is tilted more medially and the groove adjacent to the zona is deep and narrow. This configuration probably entailed greater stability for the radial head during rotation.

The medial epicondyle of Nacholapithecus is moderately long and projects posteromedially with an angle of retroflexion of c. 50°. This angle is close to that of Colobus and higher compared to small catarrhines of the Oligocene and early Miocene, such as Aegyptopithecus, Dendropithecus, and Simiolus (c. 30°: Harrison, 1982; Rose et al., 1992). The angle is higher than that of proconsulid KNM-SO 31232 (40°: this study), but lower than that of K. wickeri (54°: McCrossin, 1994; McCrossin and Benefit, 1997). Strong retroflexion and abbreviation of the medial epicondyle are usually considered as adaptations to habitual use of the forearm in a pronated position and a signal of diminishing wrist and digital flexors in relation to terrestrial locomotor specialization, since a retroflexed medial condyle approximates the line of actions of the pronators and flexor muscles to the axis of the forearm and thus reduces the medial torque exerted to the medial epicondyle (Jolly, 1967; Fleagle and Simons, 1982). McCrossin and Benefit (1997) proposed semiterrestrial adaptation of K. wickeri based on the presence of this feature along with several other postcranial characters, such as a greater tuberosity that projects slightly higher than the anterolateral) position of the radial notch on the ulna, enlargement and globularization of the capitulum (which may cause reduction of the radial fossa), and/or a more anteriorly projecting coronoid process of ulna (leading to emphasis on the coronoid fossa). Although we favor the last interpretation, testing should be performed by morphometric analysis with the accumulation of better-preserved fossil specimens.

Ratios for the distal humeral joints of Nacholapithecus are similar to those of proconsulids (Table 4). In these fossil apes, the humeroradial joint surface (capitulum and zona) takes about half of the whole distal humeral articular surface (anteriorly), as in Pan. This ratio is much higher in Old World monkeys and hylobatids. Conversely, this implies a greater role of the ulna in supporting the elbow in these fossil apes and Pan. Reduced weight-bearing role on the radius may relate to more enhanced rotation of the radial head. The capitulum is proximodistally high, rather than being mediolaterally broad (Table 4).

On the other hand, a difference is evident between Nacholapithecus and other fossil apes. The ratio of trochlear rim heights (medial rim height relative to the lateral rim) is lower in Nacholapithecus than in proconsulids and K. wickeri (Table 4), implying that the medial rim is less salient distally. This index of Nacholapithecus was obtained from a fragmentary but less deformed specimen KNM-BG 35250N and may be variable depending on the definition of the mediolateral orientation of this fragment. However, even at a glance, the medial trochlear keel of the proconsulids is pointing distally, unlike Nacholapithecus (Figure 9). Thus, the most distal portion of the trochlear surface is situated on the medial keel in the proconsulids, whereas it is laterally separate from the medial articular border in Nacholapithecus (Figure 3c, Figure 9). In this regard, K. wickeri resembles Nacholapithecus (Figure 9c). In Equatorius (KNM-TH 28860G), observation of this trait is impossible due to preservation issues. Although the trochlear groove is very shallow in these early/middle Miocene apes, the humeroulnar joint of Nacholapithecus probably had higher stability against mediolateral shearing forces thanks to a more complex concavoconvexity of the articular surfaces.

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humeral head and a relatively long, moderately retroflexed olecranon. However, high dependence on terrestriality is contradictory to the highly developed manual grasping function of *Nacholapithecus* as inferred from the well-developed secondary shaft features of the manual phalanges (Nakatsukasa et al., 2003). In fact, the medial epicondyle is not abbreviated in *Nacholapithecus* (Figure 1j), unlike that in *K. wickeri* (Figure 9c). Mosaicism or multiple functional adaptations are not rare in primate postcranial anatomy. Extant African apes exhibit mosaic adaptations for arboreal and terrestrial locomotion. Whereas chimpanzees (and gorillas to a lesser degree) exhibit elongated forelimbs and medial metacarpals, abbreviated hind limbs, and a proximodistally shortened navicular and cuboid, representing adaptations for vertical climbing and suspension, the wrists and hands are heavily modified for terrestrial knuckle-walking (Lovejoy et al., 2009). Late Miocene *H. laietanus* had very long, curved, non-pollical manual proximal phalanges apparently specialized for suspension, but the proximal joint surface is dorsally canted, which would allow hyperextension of the metacarpophalangeal joints as in *Ekembo/Nacholapithecus* or cercopithecids (Almécija et al., 2007; Nakatsukasa et al., 2016). However, the elbow morphology of *Nacholapithecus* is unlikely to represent an overprint of terrestrial locomotion on primitive arboreal adaptation. As discussed below, the globular capitulum of the humerus and deep zona signify more emphasized rotations of the forearm compared with proconsulids. *Nacholapithecus* optimized efficiency of the pronators and wrist/digital flexor muscle activities in the pronated position for some reason. The meaning behind the retroflexion of the medial epicondyle is not sufficiently understood and warrants functional exploration. For example, *Colobus polykomos* shows a greater angle of retroflexion than *Cercopithecus mitis* (Rose et al., 1992), but this angle is irrelevant to terrestriality.

The olecranon fossa of *Nacholapithecus* is characterized by a prominent lateral wall that projects posteriorly beyond the posterior surface of the shaft. Because of this wall, the olecranon fossa takes a right triangular form. A similar morphology is observed in *K. wickeri*, but not in either *E. heseloni* (KNM-RU 2036) or *Dendropithecus*. This trait was previously posited to represent a derived character that developed in middle Miocene hominoids to elaborate joint stability against mediolateral shear forces (Nakatsukasa and Kunimatsu, 2009). However, a similar condition is also evident in an adult proconsulid humerus (KNM-SO 31232: Gebo et al., 2009). This feature might be common in early-middle Miocene hominoids. If so, the absence in the examined *E. heseloni* specimen may be linked to its immaturity. Additional specimens are necessary to reach a firm conclusion.

At a quick glance, the humerus of *Nacholapithecus* appears to retain a primitive condition as seen in proconsulids. However, the humerus is derived in terms of some elbow joint features, especially of the humeroradial joint, perhaps reflecting more enhanced pronation–supination movements. A truncated ball shape (as opposed to a cone shape) of the medial trochlear portion probably increases the stability of the ulna against mediolateral shearing stress.

**Ulna**

The ulnae of Miocene apes are derived relative to early catarrhines such as *Aegyptopithecus* in terms of increased rotational mobility of the forearm in non-pronated hand postures, but not comparable to more specialized living apes that are adapted for suspension or climbing (Richmond et al., 1998). This generalization also holds for *Nacholapithecus*, which is similar to proconsulids in lacking the distinctive features of living apes such as a reduced olecranon or keeled sigmoid notch (Richmond et al., 1998; Ishida et al., 2004).

On the other hand, the ulna of *Nacholapithecus* displays some derived traits relative to proconsulids. The coronoid...
process slants more distally (Figure 10). Anteroposterior or thickness at the distal beak of the trochlear notch is >170% of the sigmoid notch depth in Nacholapithecus, compared to c. 165% in proconsulids (Table 5), although this index is not useful for comparisons between phylogenetically distant taxa due to the variability of the sigmoid notch depth (SND). The coronoid process is wider in Nacholapithecus. The trocharic articular mediolateral breadth (TAB) is 137% of the mediolateral width of the sigmoid notch (SML) in Nacholapithecus and 116–130% of the SML in proconsulids (Table 5). The superior articular surface of the coronoid process is mediolaterally concave in Nacholapithecus. No such feature is observed in proconsulids or Equatorius. These features correspond to the articular shape of the humeral trochlea (see above) and probably increase the stability of the humero-ulnar joint. Such joint stability permits greater rotational mobility of the radius (Rose, 1988; Richmond et al., 1998). The ulnae of extant apes display a median keel of the sigmoid notch that continues to the anterior beak of the coronoid process, dividing the coronoid surface into a laterally slanted lateral area and a medially slanted medial area. This median keel provides universal stability of the humero-ulnar joint from full extension to flexion of the joints (Rose, 1988). In Nacholapithecus, the coronoid surface corresponding to this lateral area is merely a narrow band, since the anterior beak is positioned quite laterally. However, the coronoid surface must have provided higher stability for the humero-ulnar joint than a less curved surface in proconsulids. In proconsulids (and probably in Equatorius), the medial and lateral areas appear less asymmetric in breadth, although the boundary between them is obscure.

The olecranon process is straight, showing no sign of retroflexion. This condition differs from that in the ulna of E. nyanzae (KNM-RU 1786; Figure 10), which shows retroflexion of the olecranon as in terrestrial cercopithecines (Senut, 1989; Rose, 1993). Olecranon retroflexion in E. nyanzae may be related to elbow-extended quadrupedalism (Senut, 1989) or overuse of the forelimb during arboreal activities (Rose, 1993). However, no olecranon retroflexion is observed in the ulna of Turkanapithecus (KNM-WK 16950R: Rose, 1993) and the condition in E. nyanzae may thus be derived.

### Radius

The large and robust styloid process bearing an anteroposteriorly wide articular surface with dorsal extension suggests that the wrist joint may have experienced radial deviation with quite deep dorsiflexion. Although the condition in KNM-BG 35250W may be affected by plastic deformation, the radii of E. heseloni show a similar condition, even though the styloid process takes varying forms (pyramidal to square-shaped) (Daver and Nakatsukasa, 2015). The dorsal articular extension on the styloid process is observed in both radii of KNM-KPS individual VIII. The distal epiphysis assumes a triangular shape. The distal radii of these Miocene apes seem likely to be principally uniform, enabling very deep dorsiflexion of the wrist.

### Elbow functional adaptation

While the forelimb long bones of Nacholapithecus are generally primitive, resembling those of proconsulids and the proximal humeroulnar joint also shows the primitive cylindrical type rather than the extant hominoid type, the proximal humeroulnar joint of Nacholapithecus exhibits some derived features differing from the condition in proconsulids. The humeroulnar joint appears more stable, owing to a broader coronoid process with a mediolaterally concave articular surface. The medial part of the humeral trochlea exhibits reciprocal morphology to this coronoid articular surface. The coronoid process projects more anteriorly than that in proconsulids. The long, anteriorly projecting coronoid process in extant apes may be associated with the reduction in the olecranon beak that allows full elbow extension. A more anteriorly projecting coronoid process may compensate for this reduction in order to maintain stable articulation with the trochlea. However, since the elbow in Nacholapithecus does not show specialized features for full extension (as the olecranon is straight and high), the deep coronoid in Nacholapithecus probably represents a selection to increase articular contact area through the range of flexion and extension. Although the radial head is not preserved in the KNM-BG 35250 skeleton, the globular and proximodistally deep humeral capitular form strongly suggests enhanced rotation of the radial head. A deep zona contacts with a bevaled area on the proximal surface of the radial head and probably supports effective rotation of the radial head. The deepened area of attachment of the annular ligament may suggest reinforcement of the proximal ulnoradial joint. Elaborated stability of the humero-ulnar joint is probably important to ensure enhanced forearm rotation. The proportionally large forelimb of Nacholapithecus, along with the morphology of the phalanges, shoulder girdle, and vertebrae, suggests that the forelimb played a greater role in supporting the body than seen in proconsulids in relation to a higher frequency of arboreal orthograde behaviors (Ishida et al., 2004; Nakatsukasa and Kunimitsu, 2009).

Since a wide range of pronation and supination is critical to utilizing variously positioned or oriented arboreal supports (twigs, branches, trunks, etc.), it seems reasonable to assume that functional adaptations for more enhanced pronation-supination were selected for in Nacholapithecus (or, more broadly, middle Miocene apes). If some features shared in both Nacholapithecus and extant apes (e.g. reduction of the radial fossa and a more developed coronoid fossa of the humerus) represent synapomorphies, Nacholapithecus might exhibit an early stage in the evolution toward the fully modern elbow joint mechanism seen in extant apes, which are endowed with further stability through the range of full extension to flexion owing to the spared trochlea and keeled sigmoid notch (Rose, 1988). Alternatively, it cannot be precluded that some elbow joint similarities between Nacholapithecus and extant apes represent homoplasy and that the elbow joints of extant apes have evolved through a different course. Current fossil evidence is insufficient to solve this question.
Nacholapithecus and middle-late Miocene Eurasian apes

The higher taxonomy of Nacholapithecus among Miocene apes from Africa and Eurasia remains contentious. While some authors have classified Nacholapithecus as a member of the subfamily Afropithecinae (Proconsulidae), which is confined to the Afro-Arabia (e.g. Fleagle, 2013; Tuttle, 2014), others group it together with Equatorius, Kenyapithecus, and Griphopithecus into the Griphopithecinae (Begun, 2010) or Kenyapithecinae (Alba, 2012) in the Hominoidea (= great apes + humans). Proponents of the latter view (including the authors) regard this group as the ancestral stock from which later Eurasian great apes have evolved. In this sense, contextualizing the results of this study in the evolution of Eurasian apes is interesting.

Nacholapithecus, Kenyapithecus, and Equatorius exhibit similarly derived features in the humerus and ulna. All of these species show a deep circular coronoid fossa with a reduced radial fossa of the humerus. The most distal portion of the humeral trochlear surface is not situated on the medial keel, but laterally apart from the medial articular border (unknown in Equatorius). The coronoid process projects more anteriorly than in proconsulids (unknown in K. wickeri). These features might represent shared derived features of this group. However, additional postcranial specimens are necessary to reach a robust hypothesis regarding this issue. In addition, they also show morphological differences to each other. The medial epicondyle is not extremely reduced in Equatorius (despite being somewhat small) and Nacholapithecus, unlike K. wickeri. Although the estimated body mass of KNM-TH 28860 Equatorius (Ward et al., 1999) considerably exceeds that of KNM-BG 35250, the humerus and ulna are much more robustly built in the latter. Clarifying the evolutionary polarity of these different character states is also important to elucidate relationships between these African and Eurasian fossil apes.

The forelimb bones of Griphopithecus suessi are known from Klein Hadersdorf, Austria, as a humeral shaft and an ulna lacking the distal end (Begun, 1992). These specimens are also referred to as G. darwini (e.g., Alba et al., 2011). However, we follow the taxonomic revision described by Casanovas-Vilar et al. (2011) and consider here G. darwini as a junior subjective synonym of G. suessi. This locality was previously regarded as 14–13 Ma based on the fauna, but a recent chronological revision (Casanovas-Vilar et al., 2011) suggests a considerably younger age (11.6–11.1 Ma). The genus Griphopithecus includes an older species, G. alpani, known from Turkey (14–13 Ma). Postcranial specimens of G. alpani are limited to phalanges, which are generally primitive suggesting primarily pronograde quadrupedal behaviors (Ersoy et al., 2008; Nakatsukasa et al., 2016). While G. alpani is comparable to Nacholapithecus in body size when these phalanges are taken into account (Nakatsukasa et al., 2016), the Klein Hadersdorf humerus is within the size range of Pan (Zapfe, 1960; Aiello, 1981) and much bigger than the humerus of KNM-BG 35250. This humeral specimen preserves only the shaft portion. Humeral shafts of Nacholapithecus and G. suessi share primitive features such as a flat deltoid plane, a sharp deltopectoral crest, and a well-developed brachialis flange. On the other hand, they differ markedly in robustness (less in Nacholapithecus) and cross-sectional shape (oval in Nacholapithecus but sub-triangular with flat posterior surface in G. suessi) (Alba et al., 2011). Whereas the much greater body size in G. suessi is likely to have introduced this difference as an allometric scaling effect, the larger body size might have caused the more stereotypical forelimb use in G. suessi, resulting in less variable stress-loading modes in the humerus. The ulnar specimen from Klein Hadersdorf is similar to (male) Nacholapithecus in overall size (see Zapfe, 1960). Since the proximal epiphysis is completely fused, this ulna is likely to come from an adult female of the highly sexually dimorphic G. suessi. The ulnae of Nacholapithecus and G. suessi are primitive in retaining a non-keeled sigmoid notch. On the other hand, both exhibit derived features such as a more anteriorly projecting coronoid process and a well-developed concavity on the medial part of the coronoid process (see Figure S2 in Alba et al., 2012). The ulna of Nacholapithecus differs from that of G. suessi in that the coronoid process is wider mediolaterally and in the olecranon lacks retroflexion (weakly retroflexed in G. suessi). Surface features of the proximal shaft (e.g. well-developed supinator crest, deep groove-like insertion of m. brachialis) resemble each other. In summary, some of the features that distinguish Nacholapithecus from proconsulids are observed in G. suessi. However, since such features might be obscured by the marked differences in body size, the morphological affinity of the forelimb between Nacholapithecus and Griphopithecus needs to be tested against specimens of G. alpani.

Sivapithecus is currently the earliest documented ape (c. 12.5 Ma) to show the derived spool-shaped humeral trochea (Pilbeam et al., 1980, 1990). The humerus of Sivapithecus exhibits a deep coronoid fossa and reduced radial fossa as in Nacholapithecus and other middle Miocene apes from Africa (Alba et al., 2011). The distal humeral joint is well preserved in Sivapithecus indicus (GSP 30730). Although S. indicus is derived compared to Nacholapithecus in its spool-shaped trochea associated with a deeper zona conoidea, the capitula are similar in the globular and proximodistally tall form (Alba et al., 2011). The primitive shaft morphology, such as lateral bowing and flat deltoid surface (Pilbeam et al., 1990; Richmond and Whalen, 2001), suggests that Sivapithecus was not specialized for suspensory activities, unlike extant apes. Various postcranial elements (including distal humerus) suggest engagement in both pronograde activities and antipronograde activities such as vertical climbing and clambering, with a relatively high frequency of the latter (Rose, 1993; Madar et al., 2002; DeSilva et al., 2010) like Nacholapithecus. The differing elbow anatomies of these species may be explained by differences in body size. Even a smaller species such as S. indicus (male) is chimpanzee-sized (c. 50 kg) (DeSilva et al., 2012), more than double the size of a male Nacholapithecus. As body size increases, arboreal primates need to solve more demanding problems in terms of positional behaviors (Cartmill and Milton, 1977; Cant, 1992). Adaptive changes to the joint surface topology would be effective in preventing ligamentous or muscular injuries even if larger primates stop maintaining functional equivalence as smaller species do when they engage in the same type of arboreal behavior, and adjust kinetic (speed, acceleration) or kinematic (limb posture, excursion range) locomo-
tor characteristics to avoid injuries or reduce the risk of falls. Later large fossil apes (Hispanopithecus laietanus: 11.1–9.5 Ma; Rudapithecus hungaricus: c. 10 Ma; and Oreopithecus bambolii: 8.5–6.5 Ma) in Europe have acquired an extant ape-like humero-ulnar joint (Knaussman, 1967; Morbeck, 1983; Alba et al., 2011, 2012), although the height and sharpness of the median keel of the sigmoid notch vary (Alba et al., 2012). If these functional innovations held a common origin with Sivapithecus, they would have evolved by 12.5 Ma at the latest. Unfortunately, no fossil ape specimen with preservation of the humero-ulnar joint is known from western Eurasia between 14 and 12.5 Ma (even the elbow morphology of Pierolapithecus (12 Ma) is unknown). Additional fossils from western Eurasian middle Miocene and African early late Miocene localities are necessary for a better understanding of the evolutionary history of modern forelimb anatomy in fossil apes.

Conclusion

The morphology of the elbow joint of Nacholapithecus lacks the spool-shaped humeral trochlea (and keeled sigmoid notch of the ulna) that is a hallmark of the elbow joint evolution in hominoids. In this sense, the elbow of Nacholapithecus is comparatively primitive, resembling that of proconsulids. Likewise, the proximal humerus is primitive in retaining only slight medial torsion of the head, a flat deltoïd plane, and possibly lateral bowing of the shaft. However, the elbow of Nacholapithecus exhibits some derived features. Like living apes, the coronoid process is more anteriorly projecting. A deep coronoid fossa of humerus might be related to this feature. The coronoid surface is mediolaterally wide and quite concave, and is distinguished from the narrower, flat surface in proconsulids. Corresponding to this morphology, the medial part of the humeral trochlea takes a truncated, ball-like form rather than the cone-like form seen in proconsulids and primitive catarrhines such as Aegytopithecus. These differences suggest the humero-ulnar joint of Nacholapithecus is modified for greater stability. Although the formation of the lateral trochlear keel (and median keel of the sigmoid notch) creates a strong point of contrast in whole humero-ulnar joint morphology between extant apes and these fossil apes, so far as the medial portion of the joint is concerned, the condition in Nacholapithecus recalls that in extant great apes and hylobatids. The humeroradial joint of Nacholapithecus is characterized by a deep zona conoidea and a taller, more globular capitulum, suggesting enhanced rotations of the radius. As a whole, the elbow of Nacholapithecus is more specialized for pronation–supination than proconsulids. This specialization is more marked in Nacholapithecus than proconsulids. This specialization is more marked in Nacholapithecus is more specialized for pronation–supination enhanced rotations of the radius. As a whole, the elbow morphology of Nacholapithecus (12 Ma) is unknown.

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