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Cite this article: Gilbert CC, Ortiz A, Pugh KD, Campisano CJ, Patel BA, Singh NP, Fleagle JG, Patnaik R. 2020 New Middle Miocene Ape (Primates: Hylobatidae) from Ramnagar, India fills major gaps in the hominoid fossil record. *Proc. R. Soc. B* **287**: 20201655. <http://dx.doi.org/10.1098/rspb.2020.1655>

Received: 9 July 2020

Accepted: 13 August 2020

Subject Category:

Palaeobiology

Subject Areas:

palaeontology, taxonomy and systematics, evolution

Keywords:

hylobatid, Asia, biogeography, lower Siwaliks, fossil, gibbon

Author for correspondence:

Christopher C. Gilbert

e-mail: cgilbert@hunter.cuny.edu

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5098945>.

New Middle Miocene Ape (Primates: Hylobatidae) from Ramnagar, India fills major gaps in the hominoid fossil record

Christopher C. Gilbert^{1,2,3,4}, Alejandra Ortiz^{5,7}, Kelsey D. Pugh^{3,6}, Christopher J. Campisano^{7,8}, Biren A. Patel^{9,10}, Ningthoujam Premjit Singh¹¹, John G. Fleagle¹² and Rajeev Patnaik¹¹

¹Department of Anthropology, Hunter College of the City University of New York, 695 Park Avenue, New York, NY 10065, USA

²PhD Program in Anthropology, Graduate Center of the City University of New York, 365 Fifth Avenue, New York, NY 10016, USA

³New York Consortium in Evolutionary Primatology, New York, NY, USA

⁴Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, 10024, USA

⁵Department of Anthropology, New York University, New York, NY 10003, USA

⁶Division of Anthropology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, 10024, USA

⁷Institute of Human Origins, and ⁸School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA

⁹Department of Integrative Anatomical Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA 90033, USA

¹⁰Human and Evolutionary Biology Section, Department of Biological Sciences, University of Southern California, Los Angeles, CA 90089, USA

¹¹Department of Geology, Panjab University, Chandigarh 160 014, India

¹²Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794, USA

id CCG, 0000-0001-8768-3171; AO, 0000-0003-3780-0952; KDP, 0000-0001-8029-0623; CJC, 0000-0001-9530-6130; BAP, 0000-0003-1844-1931; NPS, 0000-0001-9579-1447; JGF, 0000-0003-3162-808X; RP, 0000-0003-2542-7898

The fossil record of ‘lesser apes’ (i.e. hylobatids = gibbons and siamangs) is virtually non-existent before the latest Miocene of East Asia. However, molecular data strongly and consistently suggest that hylobatids should be present by approximately 20 Ma; thus, there are large temporal, geographical, and morphological gaps between early fossil apes in Africa and the earliest fossil hylobatids in China. Here, we describe a new approximately 12.5–13.8 Ma fossil ape from the Lower Siwaliks of Ramnagar, India, that fills in these long-standing gaps with implications for hylobatid origins. This ape represents the first new hominoid species discovered at Ramnagar in nearly a century, the first new Siwalik ape taxon in more than 30 years, and likely extends the hylobatid fossil record by approximately 5 Myr, providing a minimum age for hylobatid dispersal coeval to that of great apes. The presence of crown hylobatid molar features in the new species indicates an adaptive shift to a more frugivorous diet during the Middle Miocene, consistent with other proposed adaptations to frugivory (e.g. uricase gene silencing) during this time period as well.

1. Introduction

Hylobatid origins are shrouded in mystery. Despite being the most speciose group of living apes with a historically large distribution over East and Southeast Asia (figure 1) [1–5], the fossil record of hylobatids (=gibbons and siamangs or ‘lesser apes’) is woefully incomplete, with only a handful of teeth widely recognized as stem hylobatids before the Middle Pleistocene [6,7]. The paucity of fossil lesser apes is particularly vexing given that molecular data consistently estimate their divergence from other primates by at least 20 Ma [8–10], and their sister group,

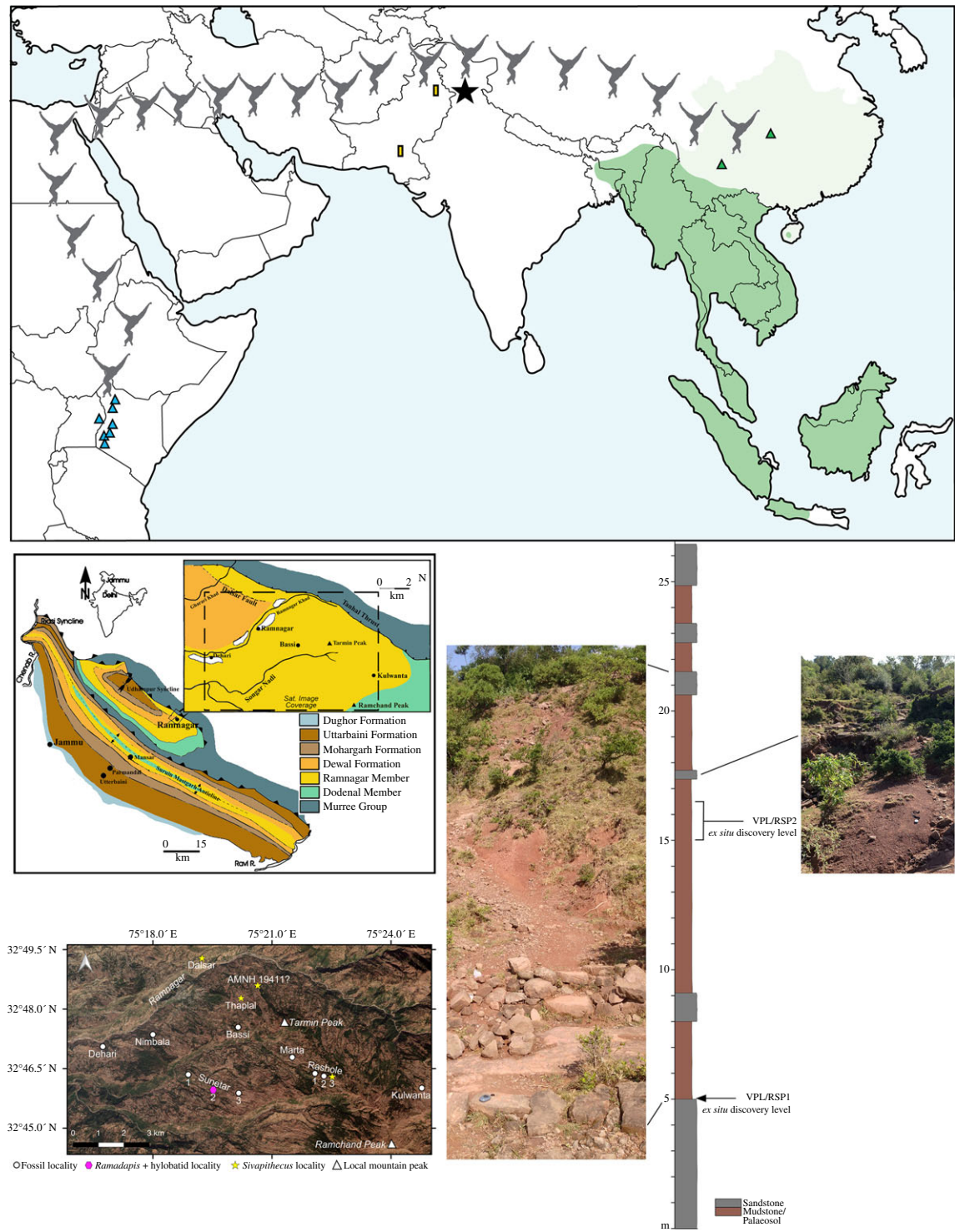


Figure 1. Top: map illustrating the location of *Kapi* (black star) relative to modern (dark green) and historical (light green) populations of hylobatids and the approximate distribution of stem hominoid sites in East Africa (blue triangles). Green triangles mark the location of the hylobatid fossil taxa *Bunopithecus* and *Yuanmoupithecus*; yellow rectangles mark the location of the fossil catarrhine taxon *Dionysopithecus* sp. from Middle Miocene sites in Pakistan (see text). Bottom left: general geological map of the Siwalik Group surrounding Ramnagar with satellite imagery (GeoEye-1) of the Ramnagar region corresponding to the dashed insert of the geological map; bottom right: simplified stratigraphic section and photos of sequence at Sunetar 2 highlighting the *ex situ* discovery levels of primate specimens VPL/RSP1 (*Ramadapis*) and VPL/RSP2 (*Kapi*). Map by Free Vector Maps: <http://freevectormaps.com>.

the great apes, are represented by a large and diverse fossil record in Asia by at least approximately 12.7 Ma [11]. Therefore, fossil hylobatids should be present in the African and/or Asian record well before the first widely recognized fossil taxon, *Yuanmoupithecus*, in the Late Miocene (approx. 7–9 Ma) of Yunnan, China [7,12]. Here, we report a new small-bodied ape specimen from the late Middle Miocene site of Ramnagar (figure 1), a classic locality in the Indian Lower Siwaliks correlating to the middle or lower half of the Chinji Formation on

the Potwar Plateau, Pakistan [13–17]. Specimen VPL/RSP2 is a right lower third molar (M_3) with strong morphological affinities to extant hylobatids, even stronger than *Yuanmoupithecus*, thereby extending the known time range of fossil hylobatids by approximately 5 Myr and providing an updated minimum age for their evolution and dispersal into Asia coeval to that of great apes. As this specimen is distinct from all other known fossil apes, we describe it as a new genus and species below and discuss other Asian Miocene specimens

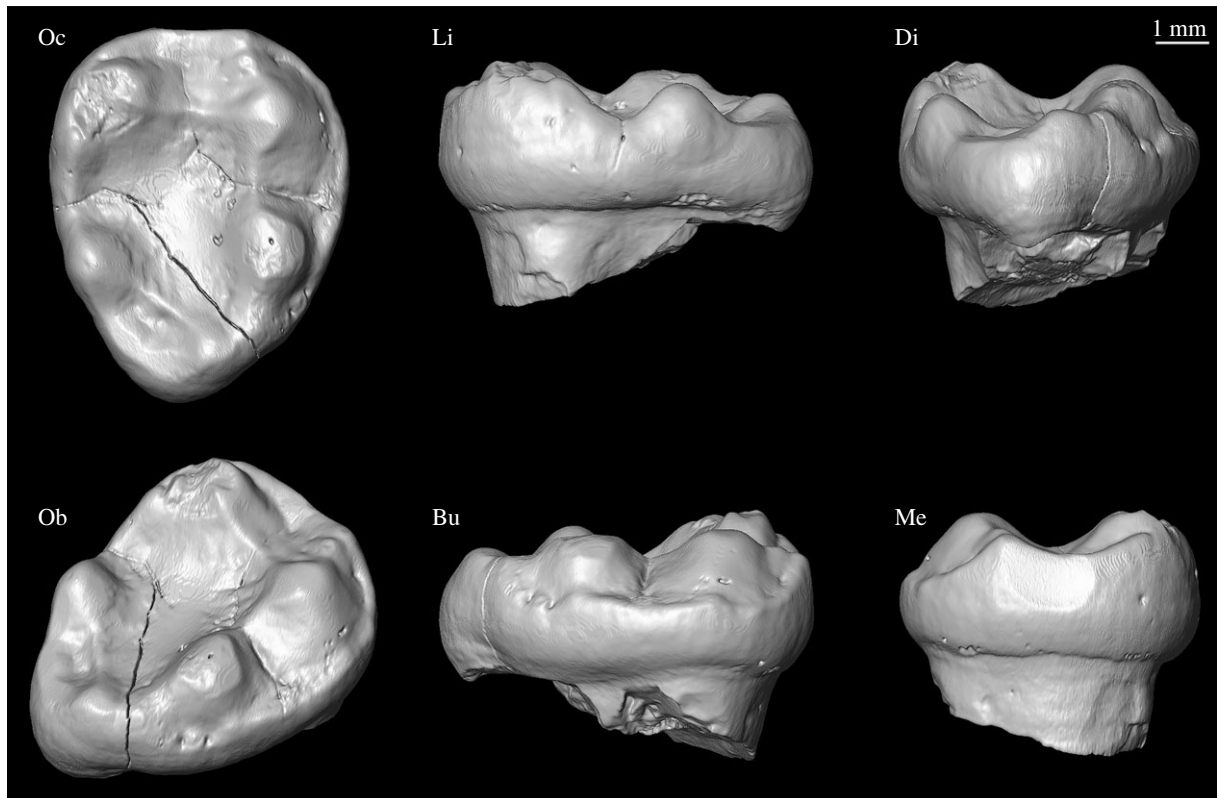


Figure 2. VPL/RSP2 in various views. Clockwise from top left: Oc, Occlusal; Li, Lingual; Di, Distal; Me, Mesial; Bu, Buccal; Ob, Oblique. A three-dimensional surface rendering derived from μ CT scans of the specimen is available at MorphoSource.org (media # M53248-96377; www.morphosource.org/Detail/MediaDetail/Show/media_id/53248).

previously mentioned in the context of catarrhine evolution and hylobatid origins.

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2. Systematic palaeontology

Order Primates Linnaeus, 1758

Suborder Anthropoidea Mivart, 1864

Infraorder Catarrhini Geoffroy St. Hilaire, 1812

Superfamily Hominoidea Gray, 1825

Family Hylobatidae Gray, 1870

Kapi ramnagarensis gen. et sp. nov.

(a) Etymology

Genus name from the Hindi word for a common anthropoid ape or monkey (*kapi*). Species name in reference to Ramnagar (Jammu and Kashmir), India, where the type specimen was found.

(b) Generic diagnosis

Kapi differs from Oligocene and Miocene catarrhine taxa such as propliopithecids, pliopithecids, and dendropithecids in the combination of the following lower molar features: transverse orientation of the mesial cusps with the metaconid even with or slightly mesial to the protoconid, reduced buccal cingulum, peripheral placement of the cusps creating reduced basal crown flare, small entoconid–hypoconulid pair, and a broad, open occlusal basin. Further differs from most pliopithecids in

the mesiodistal orientation of the cristid obliqua (also found in some pliopithecines), the transverse orientation of the hypoconid and entoconid, the more central placement of the hypoconulid on M_3 , and the lack of any crests between the protoconid and hypoconid associated with the pliopithecine triangle. Differs from Oligocene–Miocene proconsulids in the combination of the reduced entoconid–hypoconulid pair, transversely aligned mesial and distal cusps, the more peripheral placement of the cusps on the tooth crown (leading to reduced crown flare), and the reduction of the buccal cingulum (although a reduced cingulum is also present in some proconsulids). Differs from most hominids and hylobatids in the retention of a reduced but moderately developed buccal cingulum and a relatively long, broad mesial fovea. Further differs from hominids in its relatively small size. Further differs from known hylobatid genera in its overall more ovoid and relatively narrower shape (except *Symphalangus*), distal tapering, and less inflated cusps (a more detailed diagnosis of *Kapi* can be found in the electronic supplementary material).

(c) Specific diagnosis

As for genus.

(d) Holotype

VPL/RSP2 (Vertebrate Paleontology Laboratory, Panjab University Department of Geology/Ramnagar Sunetar Primate 2); a complete and slightly worn right M_3 crown (figure 2).

(e) Hypodigm

The holotype is the only known specimen.

(f) Horizon

Lower Siwalik deposits; approximately 12.5–13.8 Ma (see electronic supplementary material, Geological background section).

(g) Localities/sites

Sunetar 2; approximately 4.5 km S/SE of Ramnagar, Jammu and Kashmir, India (figure 1).

(h) Description

VPL/RSP2 corresponds to a low-crowned, bunodont M_3 from a catarrhine slightly smaller than *Hoolock* in molar size (figure 2; mesiodistal (MD) = 7.8 mm; buccolingual (BL) = 6.3 mm). It is mesiodistally longer than broad (breadth–length index of 0.79 calculated from photos; see electronic supplementary material for extended description), indicating proportions most similar to those of typical proconsulids, but considerably broader, on average, than those of pliopithecids, and slightly broader than those of modern *Symphalangus*, propiopithecids, as well as dendropithecids, although much overlap exists between individual specimens. It is relatively narrow compared to many modern gibbons, and slightly narrower than *Yuanmoupithecus* (0.81) and *Bunopithecus* (0.82).

The crown of VPL/RSP2 is ovoid in occlusal outline, tapering distally such that the distal moiety is narrower than the mesial moiety. There are five well-developed cusps, low and conical in shape, arranged around the periphery of the crown. The buccal wall of the crown displays a reduced, semi-continuous cingulum. The metaconid is the most voluminous and highest cusp, followed by the hypoconid and protoconid, which are subequal in elevation. The entoconid is similar in elevation to the hypoconid and protoconid, but relatively smaller in basal area. As is typical for apes, the hypoconulid is the smallest of the five cusps and located slightly towards the buccal side of the crown (figure 2).

The protoconid has a short but well-developed preproto-cristid and postprotocristid. The metaconid is slightly mesial to the protoconid and has a short and rounded premetacristid. The metaconid and entoconid are widely spaced by a long postmetacristid. The hypoconid has a short prehypocristid (cristid obliqua) that is parallel to the long axis of the crown. Both the postentocristid and the posthypoconulid cristid are low and ill-defined. The mesial fovea is broad and rectangular, delimited distally by a well-differentiated mesial transverse crest (hypometacristid and hypoprotocristid). The mesial marginal ridge is relatively sharp and well developed. The distal fovea is intermediate in size, but poorly defined.

The talonid basin is expansive and has a simple Y-shaped groove pattern with no secondary wrinkling. A well-developed postcristid and hypoentocristid link the hypoconulid and entoconid, forming the mesial-most boundary of the distal fovea, separating it from the talonid basin. The metaconid is damaged, but there may be traces of a small mesostylid or tubercle on the postmetacristid. A small tubercle is also present on the preprotocristid. There is no evidence of a pliopithecine triangle and no retention of the paraconid.

3. Morphometric and phylogenetic analyses

Two-dimensional morphometric analyses of M_3 shape as well as a cladistic analysis of 272 craniodental and postcranial features in extant and fossil catarrhine taxa support *Kapi* as a stem

hylobatid. We quantified M_3 crown shape and cusp position as characterized by 14 homologous landmarks (following [18]; see electronic supplementary material, figure S1 and table S1) and conducted a phylogenetic analysis using parsimony inference on a modified version of a recent matrix (electronic supplementary material, datasets S1–S2) [19]. Our comparative morphometric sample includes 166 M_3 specimens: five crown hylobatid genera ($n = 79$), three crown hominid genera ($n = 56$), two propiopithecid genera ($n = 6$), six pliopithecid genera ($n = 9$), four dendropithecid genera ($n = 7$), five proconsulid genera ($n = 7$), the stem hylobatid *Yuanmoupithecus* ($n = 1$), and *Kapi* ($n = 1$) (electronic supplementary material, table S2, figure S2, dataset S3). Landmark data were imported into MorphoJ [20] and Morphologika2 [21] and then subjected to a generalized least-square Procrustes superimposition to focus on size-adjusted shape variables. A Principal Components Analysis (PCA) was performed using Procrustes coordinates and wire-frame models were created to visualize the extreme landmark configurations. Using Discriminant Function Analysis pairwise tests implemented in MorphoJ [20], we also created wireframes and deformation grids to observe shape deformations from the mean shape configuration (reference configuration) of each of our major taxonomic groups to the shape of VPL/RSP2 (M_3) (target configuration; electronic supplementary material, figure S3). Following [18], hierarchical phenetic trees were obtained from Procrustes distances using a neighbour-joining (NJ) cluster analysis with propiopithecids assigned as the outgroup.

Although catarrhine M_3 s are variable in morphology and have been previously discounted in taxonomic identification [22], our multivariate results demonstrate that extant hylobatid M_3 s are distinct from stem catarrhines and stem hominoids, at least at the broad taxonomic levels analysed here (figure 3; electronic supplementary material, tables S3–S4; see also [3]; and [23–26] for other hominoids). These results are in line with recent research suggesting that, while morphologically variable within a taxon, anthropoid M_3 s evolve more quickly and are more distinctive between taxa, thereby making them more taxonomically informative than M_1 s and M_2 s in many cases [27]. VPL/RSP2 falls exclusively within crown hominoid space in the PCA plot, well within the crown hylobatid minimum convex polygon and closest to a number of crown hylobatid specimens on PC1 and PC2. While crown hylobatids do overlap in PC space with crown hominids (great apes), all crown hylobatids are easily differentiated from hominids on the basis of size, which is excluded from the shape analysis presented here (figure 3; see also electronic supplementary material, figure S2). *Yuanmoupithecus* plots within the small area of overlap between crown hylobatid, crown hominid, and stem catarrhine/hominoid taxa, but closest to crown hominoid specimens on PC1 and PC2. The Pleistocene gibbon *Bunopithecus* falls exclusively within crown hylobatid morphospace.

PC1 is most clearly driven by differences in the position of the hypoconulid relative to the protoconid and hypoconid (in a straight line buccally in pliopithecids, more central/slightly buccal in hylobatids), the position of the cusps/width of the occlusal basin relative to the outline of the crown (pliopithecids = internally placed cusps, narrow occlusal basins, increased flare, large cingulum; hylobatids = peripherally placed cusps, wide occlusal basins, reduced flare, reduced cingulum), and the alignment of buccal and lingual cusps (pliopithecids = buccal cusps more mesial than lingual cusps, hylobatids = buccal and lingual cusps aligned transversely). VPL/RSP2 exhibits a negative value on PC1 due to its

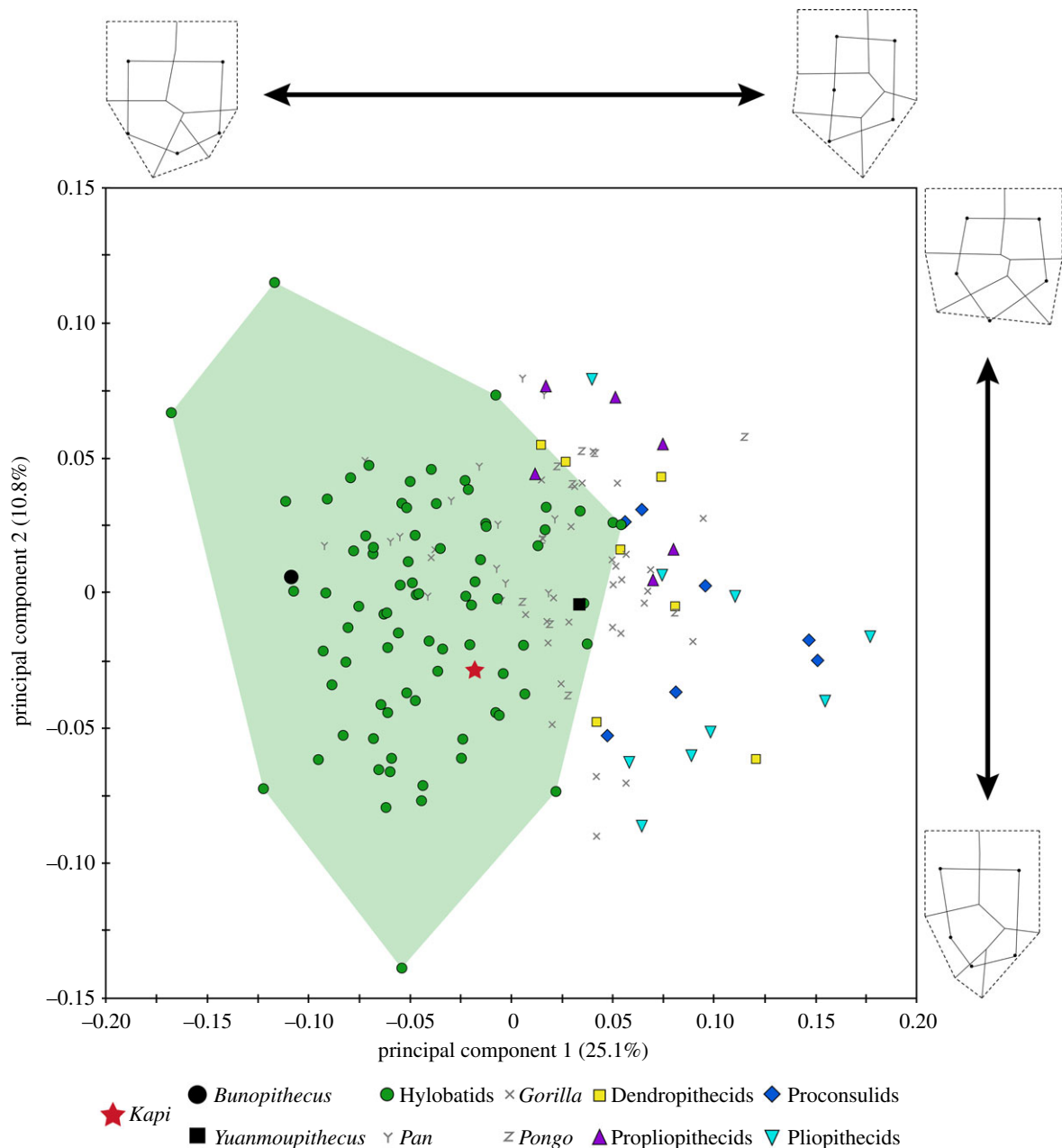


Figure 3. PCA resulting from two-dimensional morphometric analysis of overall M_3 crown shape characterized by 14 homologous landmarks (see wireframes; cusps = black circles). *Kapi* plots comfortably within hylobatid space (=green polygon), and completely outside the sampled distribution of stem catarrhine and stem hominoid taxa. By contrast, *Yuanmoupithecus* plots within the small area of overlap between stem and crown catarrhine/hominoid taxa, including crown hylobatids. (Online version in colour.)

transversely aligned and peripherally placed mesial and distal cusps, wide occlusal basin, reduced cingulum, low degree of flare and more centrally positioned hypoconulid. PC2 does not separate most taxa (except propliopithecids on the positive end), but appears related to crown elongation and distal tapering (negative values = more elongated and tapered, positive values = less elongated and tapered), along with similar features as seen on PC1 including the position of the cusps relative to the crown outline, the position of the hypoconulid, and the alignment of buccal and lingual cusps. VPL/RSP2 exhibits slightly negative values, consistent with its slight distal tapering. The NJ cluster analysis based on the morphometric data places *Yuanmoupithecus* and *Kapi* in a cluster with crown hominoids, with *Yuanmoupithecus* at the base of the cluster and *Kapi* as the sister to hylobatids. Dendropithecids, proconsulids, and pliopithecids are placed in a separate cluster as the sister group to *Yuanmoupithecus* + crown hominoids (figure 4).

The resulting trees from our cladistic analysis are consistent with the morphometric analyses and recover both *Kapi* and *Yuanmoupithecus* as crown hominoids, and both fossil taxa are most parsimoniously reconstructed as stem hylobatids (figure 4; electronic supplementary material, datasets S1–S2 for character list and matrix). In all 18 most parsimonious trees (MPTs), *Yuanmoupithecus* is the sister taxon to a crown hylobatids + *Kapi* clade. Aside from the inclusion of *Yuanmoupithecus* and *Kapi*, the relationships among other catarrhines are broadly the same as those previously presented [19].

4. Discussion

Based on the available evidence of lower molar anatomy, *Kapi ramnagarensis* represents the first new hominoid species discovered at Ramnagar in nearly 100 years. While caution

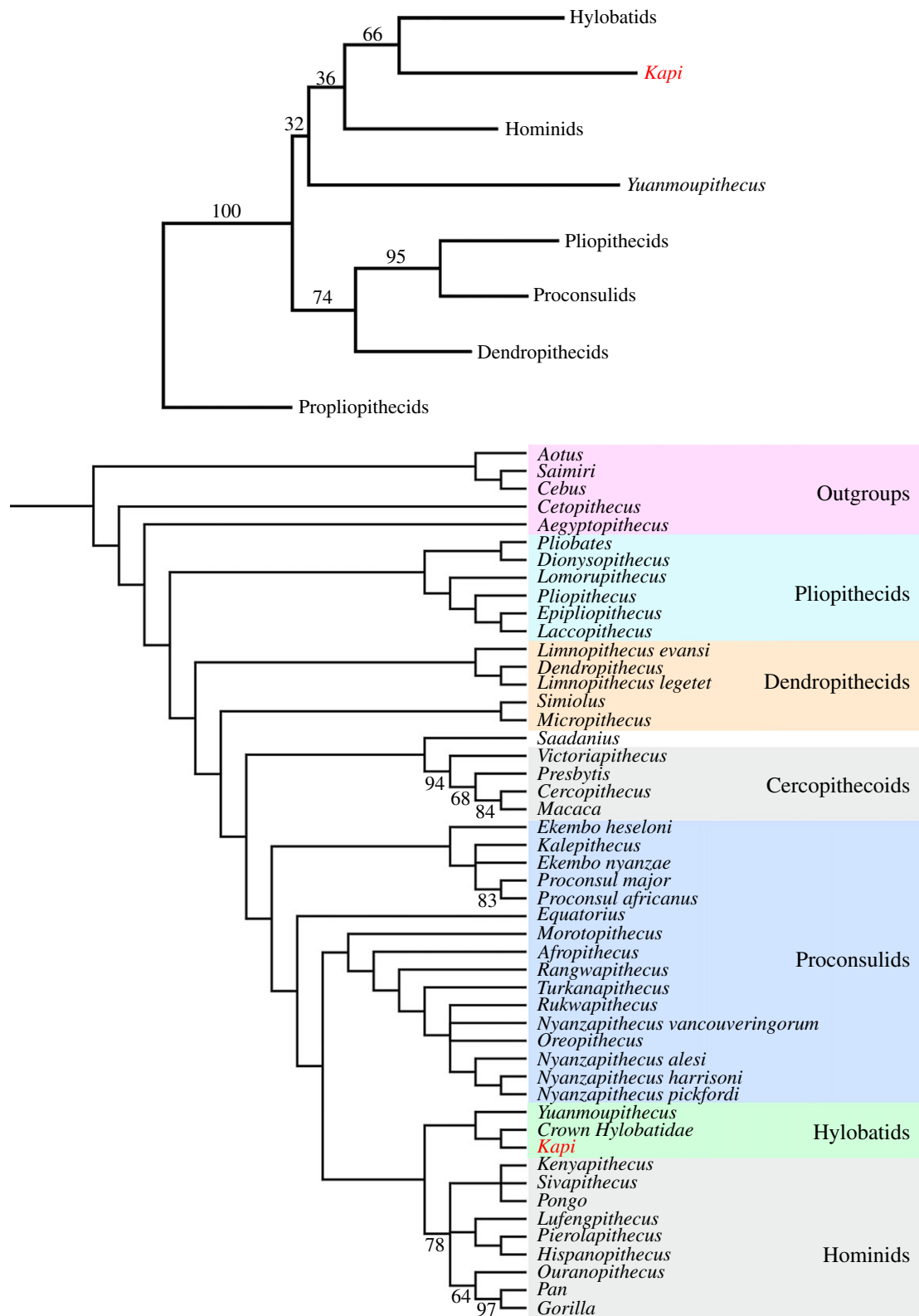


Figure 4. Top: neighbour-joining cluster analysis derived from Procrustes distances of the same 14 landmark morphometric dataset as in figure 3. Numbers above branches indicate bootstrap values based on 10 000 replicates. Bottom: strict consensus of 18 most parsimonious trees (MPTs) resulting from phylogenetic analysis of stem catarrhine taxa including 272 characters (craniodental + postcranial), with outgroups constrained successively. Numbers below branches indicate any bootstrap values over 50%. *Kapi* is reconstructed as a stem hylobatid in both the cluster analysis and all MPTs. Tree length = 1455 steps. (Online version in colour.)

is necessary given that only a single molar is documented, the analyses presented here demonstrate that *Kapi* is more similar to extant hylobatids in its known morphology than the widely accepted stem hylobatid *Yuanmoupithecus*. Thus, if one considers *Yuanmoupithecus* a stem hylobatid, *Kapi* is equally if not more likely to be one as well, making it the earliest known hylobatid in the fossil record (figures 3 and 4).

The phylogenetic placement of these two taxa within hominoids, however, is admittedly difficult to assess in the absence of additional material. Based on shared similarities with extant hylobatids in the premolars and anterior dentition, *Yuanmoupithecus* perhaps represents a slightly different combination of dental morphologies in early hylobatid evolution compared to *Kapi*. Further specimens of both taxa

are necessary to confidently resolve the polarity of stem hylobatid dental features.

The discovery of *Kapi* in approximately 12.5–13.8 Ma Lower Siwalik deposits helps to fill temporal, morphological, and biogeographic gaps in hominoid evolution. While much of hylobatid evolution remains unknown, it is now probable that they dispersed to Asia from Africa by the end of the Middle Miocene, possibly at the same time as great apes such as *Sivapithecus* just after the Middle Miocene Climatic Optimum [28,29]. Judging by the affinities of both *Kapi* and *Yuanmoupithecus* in our analyses, it seems most likely that hylobatids evolved from an African taxon dentally similar to dendropithecids or proconsulids, the two advanced catarrhine groups outside of crown hominoids with specimens closely approaching hylobatids in the multivariate and phylogenetic analyses. Therefore, it is entirely possible that early stem hylobatids are currently represented by some of the fossil material in the extensive East African Early Miocene record, but cannot yet be distinguished based on the lack of clear hylobatid dental synapomorphies among these fragmentary taxa.

In many ways, *Kapi* represents a logical intermediate or mosaic dental morphology between Early Miocene dendropithecids/proconsulids and extant hylobatids; it clearly displays the bunodonty, peripherally placed cusps, expanded basin and transversely aligned cusps as seen in living hylobatids, but also retains primitive features such as a (reduced) buccal cingulum, a relatively long mesial fovea, and possibly a vestigial mesostylid not typically observed in living gibbons and siamangs. It also does not display the expanded cusp areas typical of living hylobatids. Features of extant hylobatid molars, particularly the bunodonty and expansion of the occlusal basin relative to stem catarrhine taxa (figure 3; electronic supplementary material, figures S2–S3), indicate an adaptive shift to a dedicated diet of frugivory. The presence of these characters in *Kapi* suggest that this shift had begun by the end of the Middle Miocene, consistent with the silencing of the uricase gene (another proposed adaptation to frugivory) in hylobatids during this time period as well [30].

While other Eurasian fossils have been advanced as possible hylobatids in the past, none have held up to closer scrutiny and an improved understanding of the catarrhine fossil record. Pliopithecids (i.e. pliopithecoids), a well-represented group of catarrhines found in the Early to Late Miocene of Asia (e.g. *Dionysopithecus*, *Platodontopithecus*, *Pliopithecus*, and *Laccopithecus*), resemble hylobatids in certain cranial features, including a relatively short face, projecting inferior orbital rims, and a broad interorbital distance. However, they also lack a key synapomorphy found in all crown catarrhines, namely a completely ossified tubular ectotympanic (ear tube). In addition, they generally possess a unique combination of primitive features (e.g. very broad upper molars and an entepicondylar foramen in the distal humerus) along with autapomorphic lower molar anatomy (including the pliopithecine triangle), leading most experts to conclude that they are, in fact, late-occurring stem catarrhine taxa (figure 4) [6,7,19,31–33].

A worn M^3 from the Middle Siwalik locality of Haritalyangar, India, was initially referred to as a possible hylobatid ancestor and ultimately placed in its own genus, *Krishnapithecus* [34,35]. However, *Krishnapithecus* has recently been demonstrated to be a late-occurring pliopithecid, with lower molars displaying a distinctive pliopithecine triangle among other pliopithecid features [36]. Notably, our cladistic

analysis reconstructs the recently described and debated *Pliobates* from the Middle/Late Miocene boundary of Spain as a pliopithecid taxon as well (see also [19]).

One other taxon from South Asia, *Dionysopithecus* sp., represented by a handful of isolated teeth from the Lower Siwalik Kamlial Formation and Manchar Formation in Pakistan (approx. 16–17 Ma), has been discussed as a possible dendropithecid, proconsulid, pliopithecid, and even stem hylobatid [7,37–39]. Thus, the affinities of H-GSP 8114/609, the sole lower molar (M_1) assigned to *Dionysopithecus* sp., were re-examined given its proximity in time and space to the M_3 from Ramnagar as well as its possible status as a stem hylobatid or advanced stem catarrhine/hominoid (dendropithecid or proconsulid) in Asia. Although roughly similar in size, GSP 8114/609 is morphologically distinct from *Kapi* in its much higher crown, better developed cingulum, stronger occlusal crests, more restricted occlusal basin, and more centrally located cusps, clearly representing a different taxon. We conducted a separate morphometric analysis on GSP 8114/609 and a large sample of catarrhine M_1 s (electronic supplementary material, figures S4–S5, tables S4–S6, dataset S4). There is more overlap among all groups on the first two components of the M_1 PCA, and GSP 8114/609 falls completely outside hylobatid multivariate space. Instead, it falls within an area of overlap between dendropithecids, pliopithecids, and crown hominids. Thus, while the taxonomic placement of the Manchar/Kamlial specimens is still unclear, they seem unlikely to belong to a fossil hylobatid.

Finally, a proximal humerus (GSP 28062) from site Y499 in the Chinji Formation (approx. 12.05 Ma) [40–42] is the only other small-bodied catarrhine specimen currently known from the Siwaliks close to the likely time range represented at Ramnagar. Interestingly, this specimen displays none of the specializations for extreme mobility present in living hylobatids and great apes, and instead retains a primitive catarrhine morphotype similar to pliopithecids and dendropithecids [42]. While an association with an as yet undiscovered Chinji-level pliopithecid or dendropithecid is perhaps most likely, if this proximal humerus is attributable to a stem hylobatid (e.g. *Kapi*), it would suggest that the suspensory features exhibited by extant hylobatids evolved independently from great apes and within the last around 12.5–13.8 Myr from a more primitive catarrhine morphotype. Such an association would also suggest that the common ancestor of crown apes was not a highly suspensory animal, a hypothesis that we consider likely (see also [43–45]), but that stands in contrast to the consensus view of ape evolution for much of the past century [46–49]. Additional early catarrhine and stem hylobatid fossils such as *Kapi*, particularly with associated postcrania, are necessary to resolve these competing views and gain a clearer insight into the first approximately 6–8 Myr of hylobatid evolution.

Data accessibility. Original raw μ CT image scan data and derived three-dimensional surface rendering of VPL/RSP2 are available on MorphoSource.org (www.morphosource.org/Detail/MediaDetail/Show/media_id/53248; <https://doi.org/10.17602/M2/M96377>). All data used in the morphometric analyses are provided as MorphoJ input files and the matrix used in the cladistic analysis is provided as a text file in the electronic supplementary material associated with this article.

Authors' contributions. C.C.G., A.O., and K.D.P. designed the study. C.C.G., C.J.C., B.A.P., N.P.S., and R.P. did field research. C.C.G., A.O., K.D.P., B.A.P., J.G.F., N.P.S., and R.P. collected and analysed comparative data on primate dental morphology. B.A.P. performed μ CT imaging analyses. C.J.C. and R.P. studied the geological context and provided the geological background. C.C.G., K.D.P., B.A.P., N.P.S., and R.P. identified fauna at Ramnagar. A.O., C.C.G., and

K.D.P. performed morphometric analyses. K.D.P. and C.C.G. performed the phylogenetic analyses. All authors wrote the paper.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by the Leakey Foundation, the PSC-CUNY faculty award programme, Hunter College, the AAPA professional development programme, the University of Southern California, the Institute of Human Origins (ASU), and the National Science Foundation (BCS Award nos. 1945736, 1945618). In addition, R.P. and N.P.S. were supported by MoES/P.O. (Geosci)/46/2015 and SERB-HRR/2018/000063.

Acknowledgements. Terry Harrison provided access to *Yuanmoupithecus* and comments that greatly improved the manuscript. Kai He, Hira

Naseer, and Nastassia Chittumuri assisted with photography and wire-frame representation of the molar specimens. Two anonymous reviewers and an associate editor provided constructive comments that improved the manuscript. We thank Judy Galkin (AMNH), Eric Delson (AMNH), Terry Harrison (NYU), Hannah Taboada (NYU), Eileen Westwig (AMNH), Eleanor Hoeger (AMNH), Bill Kimbel (ASU), Julie Lawrence (ASU), Frieder Mayer (ZMB), Darrin Lunde (NMNH), Mark Omura (Harvard), Jessica Cundiff (Harvard), Larry Flynn (Harvard), and David Pilbeam (Harvard) for access to original specimens and casts in their care. We also thank Morgan Hill and the Microscopy and Imaging Facility at the AMNH for access and assistance with μ CT scanning VPL/RSP2. Luci Betti-Nash prepared the map in figure 1.

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