

behaviour from either species. While all its workers died over the next few weeks, the queens of *L. humile* survived for more than 100 days. Figure 1b provides details on worker survival and movement of *L. humile* queens to *T. nigerrimum* nests. Though the figure shows data only for 65 days, we maintained the replicates that showed nest-sharing. In these replicates we found *L. humile* queens surviving for more than 100 days in *T. nigerrimum* nests, even without a single *L. humile* worker.

To the best of our knowledge, there are no previous reports on the non-aggressive, non-evasive, conflict-free coexistence and co-nesting of *L. humile* inside the nest of another ant species. This is in contrast with the characteristic highly aggressive behaviour of *L. humile* workers, which usually leads to them emerging competitively superior against other species<sup>2</sup>. This coexistence is also different from the escape and evasive behaviour shown by *L. humile*, when in small numbers, against other ant species<sup>5</sup>. Results seem to suggest a survival mechanism in an extreme condition when the worker population of *L. humile* had dwindled to a small number. *L. humile* queens that had moved to the *T. nigerrimum* nests survived for several weeks even without a single worker. This is unusual since *L. humile* queens suffer 75–100% mortality without their workers<sup>6</sup>. Co-nesting and coexistence as seen here, therefore, could be a desperate and risky survival strategy on part of *L. humile* queens. Absence of *L. humile* workers indicates that either *L. humile* queens did not reproduce in *T. nigerrimum* nests, or the eggs laid by them did not survive. This also indicates a survival and reproductive dead-end for *L. humile* queens, unless co-habitation was used as a temporary strategy.

The simplest explanation might be that *T. nigerrimum* could not recognize and differentiate between their own and *L. humile* individuals owing to factors such as laboratory conditions and the same diet, which could have led to similar cuticular hydrocarbon profiles. However, lack of nestmate recognition seems a less plausible reason because high aggression was still observed during the first few days in these three replicates. Moreover, in many simultaneously running replicates, species recognition was observed.

Though co-habitation between other ants, as well as ants and invertebrates has been reported before (for example, mixed ant nests, parasitic ants, lycaenid butterflies in ant nests, myrmecomorphic spiders and other myrmecophilous organisms in ant nests)<sup>3</sup>, to the best of our knowledge, coexistence of a global invader such as *L. humile* with other ants has not been reported either in the laboratory or in the field. Detailed investigations into scenarios under which such rare behaviours are displayed should be conducted. More broadly, such studies may give important insights into the novel mechanisms employed by an invasive species to survive under unfavourable conditions.

Our experiments comply with the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research, and with regulations of animal care in France.

The authors declare no conflict of interest.

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## Nine million-year-old ape-like fossils found at Haritalyangar, India

The Middle Siwalik sediments exposed at Haritalyangar (31°32'N, 76°38'E), India are best known for the diversity of fossil primates that no longer inhabit the Sub-Himalaya, including the late surviving<sup>1</sup> large hominoids *Sivapithecus* and *Indopithecus*<sup>1</sup> as well as primitive lemuriform primate, such as *Indraloris* and *Sivaladapis*. However, one poorly known

species of primate from Haritalyangar is represented by an isolated and heavily worn upper third molar found in the 1970s. The specimen was initially identified as *Pliopithecus krishnaii*<sup>2</sup>, but was later transferred to a new genus *Krishnapithecus*<sup>3,4</sup>. No additional finds of this enigmatic primate have been made in the intervening four decades, and as a result

its place in primate evolution has been difficult to determine. Recently, two lower molars, consistent in size and morphology to *Krishnapithecus*, have been discovered at Haritalyangar. If they prove to belong to the same species, they will offer important clues to clarify its taxonomic status and understand its evolutionary relationships. Preliminary

comparisons point to affinities with the pliopithecoids, a group of primitive Old World higher primates that were widespread in Eurasia during the Miocene (from 18 to 7 million years ago), but their fossil record in South Asia is virtually unknown<sup>5-7</sup>.

The fossils come from the middle level of the Haritalyangar stratigraphic section, which has a lithostratigraphic profile typical of the Middle Siwaliks of the Potwar Plateau in Pakistan. The strata at Haritalyangar constitute a 1600 m thick succession of alternating mudstone and sandstone. The fossil-bearing horizon at the discovery site consists of a pale pink mudstone, which was initially correlated with the lithounit 60/61 in Normal Polarity N3 zone<sup>8</sup> in the geomagnetic polarity time scale, but was more recently revised to correlate with the N5 zone<sup>9,10</sup>. In this case, the new primate fossils can be dated to ~9.0 Ma (Figure 1). The specimens were collected in association with *Rhizomyides* spp. and a new rare finding of a chameleon<sup>11</sup>. The composition of the mammalian fauna from Haritalyangar indicates a warm temperate climate at low altitude with a preponderance of mixed forests and patches of woodland and grassland<sup>12</sup>.

The new fossil primate finds consist of two lower molar germs (i.e. permanent teeth that are unerupted and still forming in the lower jaw) from different individuals (Figure 2). The crowns of both molars are fully formed, but there is no root formation. This indicates that they belonged to infants of slightly different ages at the time of their deaths. One specimen (PRS03/12) is a partial right first molar (RM<sub>1</sub>: 8.7 mm in length), and the other is a complete (PRS04/12) left second molar (LM<sub>2</sub>: 9.5 × 7.9 mm). A portion of the M<sub>1</sub> crown got detached from the buccal side and was lost post-fossilization. The teeth are much smaller than those of contemporary *Sivapithecus*, and they probably belonged to a primate that was slightly larger than the living siamang (9–13 kg). In addition, the teeth exhibit a unique and distinctive morphology. Five well-spaced cusps, connected by low, rounded crests, are arranged around a deep central basin. The cusps are tall and conical with deep V-shaped valleys between them. The groove pattern in the central basin is simple and Y-shaped. A shallow triangular fovea on the buccal side of the talonid basin represents a pliopithecine triangle.

The broken face of M<sub>1</sub> exposes a longitudinal section through the crown, which reveals that the enamel was relatively thin. A detailed comparative morphomet-

ric study of the fossil material by the authors is currently underway, which will address more elaborately both the taxonomic assignment of the new specimens

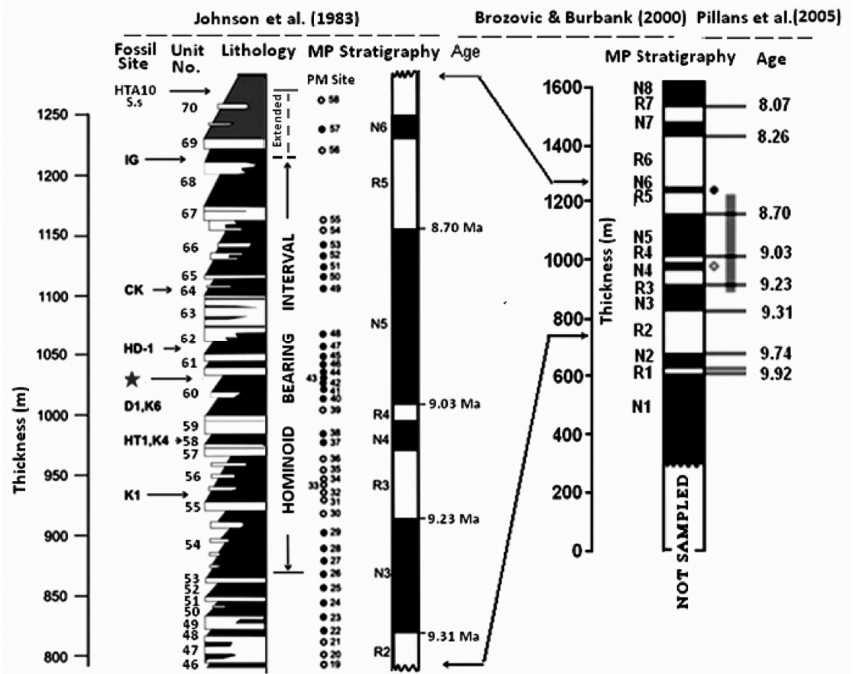


Figure 1. Magnetic polarity stratigraphy of Haritalyangar, India showing the date of the *Krishnapithecus* fossil findings with a star.

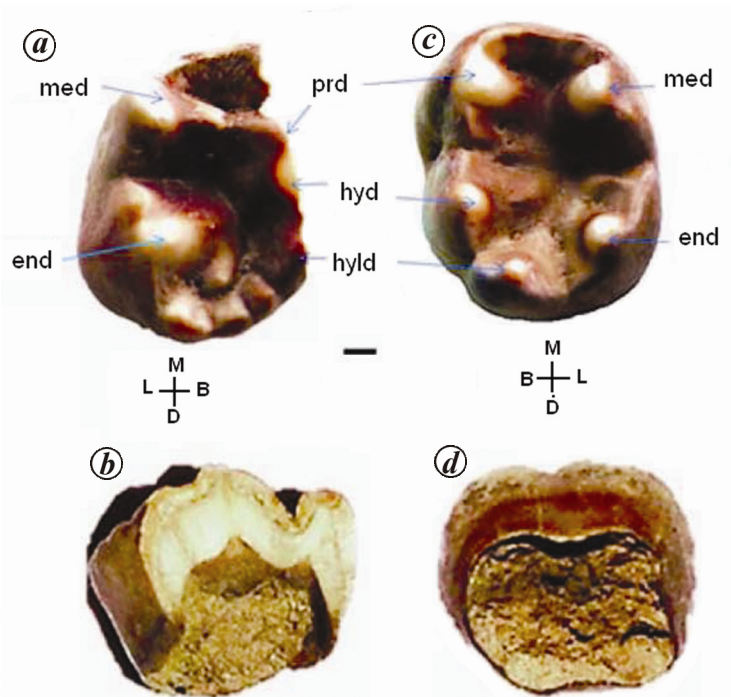


Figure 2. Recently discovered molars from Haritalyangar in different views. *a*, partial RM<sub>1</sub> (PRS03/12) in occlusal view. *b*, Buccal view showing the broken section with the enamel-dentine junction exposed. *c*, LM<sub>2</sub> (PRS04/12) in occlusal view and labelled. *d*, Basal view showing the lack of root formation. Bar scale = 1 mm.

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as well as their phylogenetic relationships.

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