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## A new orang-utan relative from the Late Miocene of Thailand

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The fossil record of the living great apes is poor. New fossils from undocumented areas, particularly the equatorial forested habitats of extant hominoids, are therefore crucial for understanding their origins and evolution<sup>1</sup>. Two main competing hypotheses have been proposed for orang-utan origins: dental similarities<sup>2,3</sup> support an origin from *Lufengpithecus*, a South Chinese<sup>4</sup> and Thai Middle Miocene hominoid<sup>2</sup>; facial and palatal similarities<sup>5</sup> support an origin from *Sivapithecus*, a Miocene hominoid from the Siwaliks of Indo-Pakistan<sup>4,6</sup>. However, materials other than teeth and faces do not support these hypotheses<sup>7,8</sup>. Here we describe the lower jaw of a new hominoid from the Late Miocene

of Thailand, *Khoratpithecus piriyai* gen. et sp. nov., which shares unique derived characters with orang-utans and supports a hypothesis of closer relationships with orang-utans than other known Miocene hominoids. It can therefore be considered as the closest known relative of orang-utans. Ancestors of this great ape were therefore evolving in Thailand under tropical conditions similar to those of today, in contrast with Southern China and Pakistan, where temperate<sup>9</sup> or more seasonal<sup>10</sup> climates appeared during the Late Miocene.

*Khoratpithecus piriyai* gen. et sp. nov. corresponds to undistorted mandibular corpora, lacking part of the left side inferiorly and also right and left rami, preserving roots of left canine–right I<sub>2</sub> as well as the rest of the dentition. It originates from a sand pit in Chalerm Prakieat District, Nakorn Ratchasima Province (Khorat) of Northeastern Thailand (15° 01' 35" N, 102° 16' 50" E). Sediments correspond to large meandering channels with many tree trunks identified as cf. *Corypha* (palm), cf. *Terminalia*, cf. *Parashorea* and Dipterocarps (C. Vozenin-Serra, personal communication). Large mammals including proboscidians (*Deinotherium indicum*, *Gomphotherium* sp., *Stegolophodon* sp. and primitive *Stegodon*), anthracothere, pig (*Hippopotamodon sivalensis*), rhinos (*Chilotherium palaeosinense*, *Brachypotherium perimense* and *Alicornops complanatum*), bovids, giraffids (*Sivatherium* sp.) and rare hipparions are present. The faunal assemblage corresponds to Upper Nagri and Lower Dhok Pathan Formations of Siwaliks and indicates an early Late Miocene age, between 9 and 7 Myr (million years)<sup>11</sup>.

**Systematics.** Order Primates Linnaeus 1758; suborder Anthropoidea Mivart 1864; superfamily Hominoidea Gray 1825; family Hominidae Gray 1825; subfamily Ponginae Elliot 1913; *Khoratpithecus* gen. nov.

**Type species.** *Khoratpithecus piriyai* sp. nov.

**Referred species.** cf. *Lufengpithecus chiangmuanensis* Chaimanee *et al.* 2003, Middle Miocene of Thailand.

**Etymology.** *Khoratpithecus* means ape from Khorat.

**Diagnosis.** Large hominoid of the size of *Lufengpithecus*, with a high and very thick lower jaw corpus bearing a strong lateral eminence at M<sub>3</sub> level, broad canine–incisor area, U-shaped dental arcade. Symphysis long and proclined with weak upper transverse torus, shallow posteriorly oriented genial fossa and strong inferior transverse torus. Absence of anterior digastric muscle impressions. Canine buccolingually compressed with flat lingual surface, distal groove and shallow lingual cingulum. Procumbent and large lateral incisor roots. Sectorial P<sub>3</sub> without metaconid cusp. P<sub>4</sub> with high talonid bearing strong cusps. M<sub>3</sub> large with discontinuous buccal cingulid, buccally located hypoconulid and large distal fovea. Its original character association distinguishes it from other Miocene hominoids. Differs also from *Lufengpithecus* by its larger anterior dentition, canine structure and larger M<sub>3</sub>. From *Gigantopithecus* by its less distally extended symphysis, larger canine, sectorial P<sub>3</sub>, less elongated molars and less distally divergent tooth rows. From *Ouranopithecus* by its sectorial P<sub>3</sub> and thinner enamel. From *Pongo* by its thicker symphysis with less distally elongated lower transverse torus, smaller incisor alveola, shorter P<sub>4</sub>, less peripheralized molar cusps, M<sub>3</sub>/M<sub>2</sub> proportions, less wrinkled enamel and stronger lateral eminence.

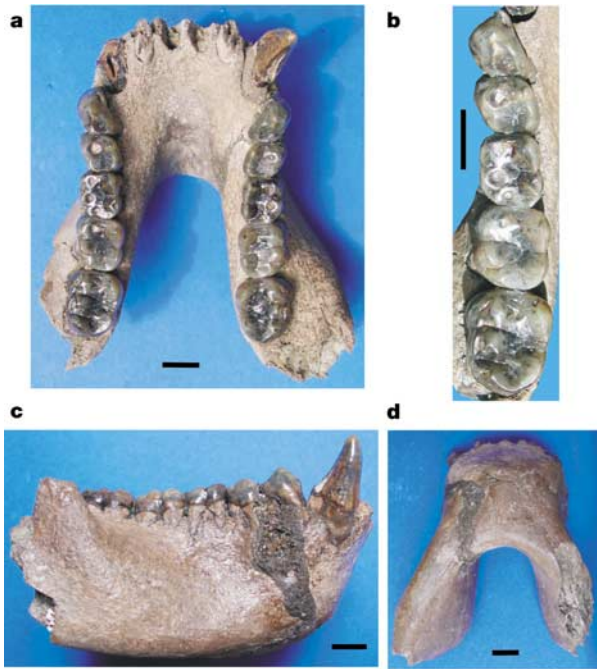
*Khoratpithecus piriyai* sp. nov.

**Etymology.** In honour of Piriya Vachajitpan, who played a critical part in recovering the fossil.

**Holotype.** Incomplete mandibular corpora, RIN 765 (Rajabhat Institute, Nakorn Ratchasima) (Fig. 1, Table 1).

**Locality and age.** Sand pit in Nakorn Ratchasima Province (Khorat), Northeastern Thailand, Late Miocene age.

**Diagnosis.** Differs from *Khoratpithecus chiangmuanensis* (Chaimanee *et al.* 2003) by its buccolingually compressed canine with flat lingual surface, larger lower incisors roots and enlarged M<sub>3</sub>.



**Figure 1** Mandible of *Khoratpithecus piriyai* gen. et sp. nov. holotype (RIN 765). **a, b**, Occlusal view. **c**, Lateral view. **d**, Inferior view. Scale bar, 1 cm.

**Description.** In occlusal view, the mandible displays a broad U-shaped dental arcade, widest at the level of canines and  $M_3$ , with buccally concave tooth rows. Procumbent incisor roots are arranged on a slightly convex arcade and occupy a wide area (27 mm). Left canine section has a triangular outline with rounded corners. The right canine crown has a length/breadth ratio of 1.49, higher than in most other Miocene and extant apes excluding *Dryopithecus* and *Ouranopithecus*<sup>12</sup>. Its relative height index is 1.48, less than that of *Kenyapithecus wickeri* (1.62), *Dryopithecus* (1.54–1.61) and *Lufengpithecus* (1.56–1.85), falling into the range of *Proconsul* and great apes (1.42–1.58) (ref. 13). The short and weak anterior ridge curves lingually into the cingulid and the posterior ridge ends into a talonid cusp. A wide groove develops buccally to the distal ridge. Lingual wall is flattened, as in *Griphopithecus*<sup>14</sup>, and bears two furrows bounding a medial ridge. A shallow lingual cingulid is present above the enamel–dentine junction. Canines of *K. chiangmuanensis* and *L. lufengensis* display rounded/oval sections at the dentine–enamel junction and *L. lufengensis* has a stronger lingual cingulid. The canine of *Sivapithecus* is less outwardly oriented, with more rounded crown and stronger lingual cingulid<sup>15</sup>. *K. piriyai* canine resembles those of some Pleistocene *Pongo*<sup>16</sup>, sharing flat lingual walls, wide distal grooves and shallow lingual cingulids. Premolars and  $M_1$ – $M_2$  are similar to those of *K. chiangmuanensis* but molars differ from those of *L. lufengensis* by  $M_2/M_1$  crown surface ratio (135% on *K. piriyai* and 172% on *L. lufengensis*). Regression of  $M_1$  dimensions on body mass in extant primates<sup>17–19</sup> indicates a body weight of approximately 70–80 kg.  $M_2$  is broad, having a mesiodistal length/mesial width index of 108.5 ( $N = 2$ ) that falls into the range of *Sivapithecus*<sup>20</sup>.  $M_3$  is very large, differing from *Lufengpithecus* by its  $M_3/M_1$  crown surface ratio (196.5% for *K. piriyai*, 142% for male *L. lufengensis*, 128% for *L. keiyuanensis*) and bears a discontinuous buccal cingulid. Its central fovea is deep and displays enamel wrinkles. Talonid and distal fovea are large. It resembles *Ouranopithecus* by its buccal cingulid and on-line positioned buccal cusps.  $M_3$  of *Gigantopithecus giganteus* has shallow central fovea and more elongated outline. Inferiorly, the mandible displays a long and wide symphyseal region. Medially, facets for the geniohyoid muscles are well expressed. Laterally to them, the basal

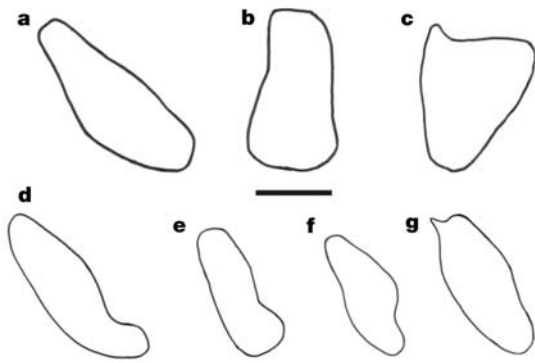
**Table 1** Measurements of *Khoratpithecus piriyai* gen. et sp. nov. (RIN 765)

	Buccolingual		
	Mesiodistal (mm)	Trigonid (mm)	Talonid (mm)
$C_R$	13.71	9.33	
$C_L$	(13.78)	(10.11)	
$P_{3L}$	13.79	8.51	
$P_{3R}$	14.57	8.53	
$P_{4L}$	9.61	10.63	10.53
$P_{4R}$	9.24	10.65	10.23
$M_{1L}$	12.88	10.53	11.30
$M_{1R}$	12.38	10.69	11.34
$M_{2L}$	13.76	12.86	12.88
$M_{2R}$	13.77	12.68	12.72
$M_{3L}$	17.73	14.68	13.16
$M_{3R}$	17.63	14.71	13.12
C– $M_3$ length			78.90
$P_3$ – $M_3$ length			64.30
$M_1$ – $M_3$ length			42.97
C crown height (buccal)	20.40		
Corpus at $P_4$ height	38.88		
Corpus at $P_4$ thickness	21.23		
Corpus at $M_3$ height	36.33		
Corpus at $M_3$ thickness	31.43		
Symphysis height	47.14		
Symphysis thickness	21.00		
Maximal symphyseal length (infradentale–gnathion)	54.40		
Minimum symphyseal length (horizontal projection)	45.65		
External bi- $P_3$ breadth	54.42		
External bi- $M_1$ breadth	52.28		
External bi- $M_3$ breadth	58.95		
Breadth across incisor region	27.03		
Inter canine breadth	31.35		
Depth of mental foramen below alveolar margin	24.20		

R, right; L, left. Measurements in parentheses are estimated values.

symphyseal surface displays no impression of muscle insertion that could correspond to the anterior digastric muscles<sup>7,21</sup>. Other Miocene hominoids display impressions of these muscles and their absence is considered as an exclusive specialization of extant *Pongo*, in relation to the development of laryngeal air sac<sup>7,21</sup>. Laterally, the corpus is deep, with thickness/height index of 55% at  $P_4$  and 87% at  $M_3$ . Depth is nearly constant from symphysis to  $M_3$ . Corpus shows a deep post- $CP_3$  depression, and an extreme thickness with strong lateral eminence at the  $M_3$  level. The foramen mentale is located below mesio-buccal  $P_3$  root, in a low position. The symphysis is strongly proclined (Fig. 2). In mid-sagittal cross-section, its long axis forms an angle of 42° to the alveolar margin of  $P_3$ – $M_3$ , which is less than in other Miocene hominoids except *Equatorius* and *Kenyapithecus wickeri*<sup>20</sup>. It falls in the range of extant large-bodied apes, but at the uppermost limit of adult *Pongo*<sup>20</sup>. Its morphology and forward inclination are similar to those of *Griphopithecus*<sup>14</sup>, whose symphysis extends further distally with a deeper genial fossa. Internally, there is a long planum alveolare sloping at about 35° on the alveolar plane to a weak superior transverse torus. A shallow genial fossa, oriented distally, lies below the superior transverse torus, above a thick, rounded, inferior transverse torus that projects until the level of  $M_1$  trigonid. The buccal symphyseal surface is wide and flat. The symphysis of *Ankarapithecus*<sup>12</sup>, *Sivapithecus*<sup>21</sup>, *Gigantopithecus giganteus*, *Ouranopithecus*<sup>22</sup> and *Lufengpithecus*<sup>21</sup> are more vertically oriented (Fig. 2). *G. giganteus* and *Lufengpithecus* have no strongly developed inferior transverse tori, and *Sivapithecus* displays tori of relatively equal prominence<sup>7,21</sup>. *Equatorius* displays a thicker symphysis section, with a stronger superior torus<sup>20</sup>. *Pongo* shows stronger superior transverse torus, thinner section and more distally extended lower torus<sup>21,23,24</sup>. However, some variants of extant orang-utan symphysis<sup>21</sup> are similar to that of *Khoratpithecus*.

Several Miocene Asian hominoids have been proposed as potential ancestors of orang-utans. On the basis of its facial and palatal similarities<sup>5</sup>, *Sivapithecus* was considered as the best candidate. However, its lower jaw anatomy has been considered markedly dissimilar in all essential components to the *Pongo* mandible<sup>6,21</sup>.



**Figure 2** Mandibular section of *Khoratpithecus piriyai*. **a**, Symphyseal section. **b**, Coronal section at the middle of M<sub>1</sub>. **c**, Coronal section at the middle of M<sub>3</sub>. Scale bar, 2 cm. **d–g**, Symphyseal sections of *Pongo* (**d**), *Lufengpithecus* (**e**), *Sivapithecus* (**f**) and *Gigantopithecus* (**g**), not to scale<sup>21</sup>.

*Lufengpithecus*, from the Late Miocene of South China, displays greater tooth resemblances to *Pongo* than *Sivapithecus*<sup>4,25</sup>, but it has been excluded from *Pongo* ancestry because of its different face and periorbital region structures. It has been allocated, like *Ankarapithecus*<sup>26</sup>, to the sister taxon of the Ponginae + Homininae<sup>26</sup> or to a primitive sister taxon of the Ponginae<sup>4,27</sup>. *K. chiangmuanensis*, from the Middle Miocene of Thailand<sup>2</sup>, shares similar premolar and molar characters and large incisor roots with *K. piriyai*. Therefore we refer the Middle Miocene Thai species to the same new genus. Both species nevertheless differ significantly enough to be distinguished at specific level. *Ankarapithecus*, *Sivapithecus*, *Lufengpithecus* and *Gigantopithecus* are united as members of the *Pongo* clade<sup>26,27</sup>. *Khoratpithecus* displays all characters that distinguish the members of that clade and an original character assemblage that occurs in none of the known Miocene hominoids, justifying its allocation to a new genus. Resemblance of *Khoratpithecus* premolars and molars to those of *Lufengpithecus* are interpreted as shared primitive characters of the orang-utan clade. *Khoratpithecus* jaw shares several derived characters with Pleistocene and extant orang-utans; among them, the absence of anterior digastric muscles represents an exclusive synapomorphy<sup>7,21</sup> demonstrating that it corresponds to orang-utan's closest related fossil hominoid. Both *Khoratpithecus* species are found in association with tropical floras, indicating that extant apes were differentiating in areas where tropical conditions have prevailed from Middle to Late Miocene. In Southern China, Late Miocene *Lufengpithecus*<sup>4</sup> are associated with a more temperate flora<sup>9</sup>. In Pakistan, Late Miocene *Sivapithecus* remains belong to mammal communities, indicating more open environments and increasing seasonality<sup>10,11</sup>. Further discoveries in yet undocumented tropical areas seem to be crucial to an understanding of the origins and evolution of both orang-utans and African great apes. □

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## The strict anaerobe *Bacteroides fragilis* grows in and benefits from nanomolar concentrations of oxygen

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Strict anaerobes cannot grow in the presence of greater than 5 μM dissolved oxygen<sup>1</sup>. Despite this growth inhibition, many strict anaerobes of the *Bacteroides* class of eubacteria can survive in oxygenated environments until the partial pressure of O<sub>2</sub> (P<sub>O<sub>2</sub></sub>) is sufficiently reduced. For example, the periodontal pathogens *Porphyromonas gingivalis* and *Tannerella forsythensis* colonize subgingival plaques of mammals, whereas several other *Bacteroides* species colonize the gastrointestinal tract of animals. It has been suggested that pre-colonization of these sites by facultative anaerobes is essential for reduction of the P<sub>O<sub>2</sub></sub> and subsequent colonization by strict anaerobes<sup>2</sup>. However, this model is inconsistent with the observation that *Bacteroides fragilis* can colonize the colon in the absence of facultative anaerobes<sup>3</sup>. Thus, this