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# Amphipithecine primates are stem anthropoids: cranial and postcranial evidence

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## Abstract

Since their discovery in 1927, the phylogenetic status of the Myanmar amphipithecines has been highly debated. These fossil primates are recognized either as anthropoids or as adapiform strepsirrhines. This uncertainty was largely the consequence of a limited fossil record consisting mostly of jaw fragments but lacking the critical cranial elements that might resolve this debate. We report here cranial remains associated with an ulna from a single individual pertaining to the amphipithecine *Ganlea megacanina*. In addition to anthropoid-like dentognathic characters, *Ganlea* displays several ulna and skull features that testify to its anthropoid affinities (e.g., short subvertically-oriented lacrimal duct, lacrimal foramen and bone inside the orbit, maxillary contribution to the lower orbital rim, fused metopic suture). In contrast to crown anthropoids, however, *Ganlea* lacks postorbital closure, confirming that postorbital closure appeared later than many anthropoid dentognathic characters and evolved convergently in extant tarsiers and anthropoids. Thus, amphipithecines must now be recognized as stem anthropoids offering a unique window on the early evolution of cranial and skeletal features in anthropoids and reinforcing the hypothesis of an origin and early diversification of anthropoids in Asia.

## Introduction

The amphipithecine primates correspond to a monophyletic group of endemic primates documented from the Pondaung Formation of late middle Eocene in Central Myanmar and placed in the Asian family Amphipithecidae [1]. They are represented by three genera, *Pondaungia* [2] (including *Amphipithecus*), *Myanmarpithecus* [3] and *Ganlea* [1]. The phylogenetic affinities of the Amphipithecidae, and more particularly of Myanmar amphipithecines, have been debated for nearly a century [2,4-8] although critical diagnostic skull features have been unavailable until now. Recent workers have supported anthropoid affinities for amphipithecines [9-20]. Other workers maintain that the dentognathic similarities between amphipithecines and anthropoids reflect convergent dietary adaptations to durophagy, thereby obscuring what they consider to be adapiform affinities [21-25]. This last interpretation was additionally supported by the discovery of postcranial bones matching in size with *Pondaungia* and sharing characters with notharctids [22,26]. These undisputed adapiform bones were assigned to amphipithecines without associated dental remains supporting this attribution and without taking into account two isolated tali showing typical anthropoid characters [18,19]. Therefore, the absence of cranial remains and firmly attributed postcranial bones has allowed the debate concerning higher-level relationships of amphipithecines to remain open. Our new discoveries illuminate this long-standing debate.

The new remains (NMMP 101-104, 106) consist of a skull fragment with I<sup>1</sup>-M<sup>3</sup>, anterior part of lower orbital margin and root of zygomatic, a right maxilla fragment with M<sup>1</sup>-M<sup>3</sup>, a fronto-parietal fragment preserving the antero-superior parts of the orbits (Fig. 1), a partial left mandible (Fig. 2, Supplementary note 1, Table S1) with C-M<sub>3</sub> preserved but missing the incisor region, the ascending ramus and the angular region, and an ulna missing its distal extremity (Fig. 3). All these

remains were found scattered on a surface of about 1 m<sup>2</sup> in Than-U-Daw locality (Myaing Township, Central Myanmar) of Pondaung Formation [27] (Fig. S1) and belong to the same individual. According to their dental features and measurements, these remains belong to an adult male of *Ganlea megacanina* (see Methods section).

## Results

### Partial skull description

The skull bones (Fig. 1, Fig. S2) are massive while the rostrum is short and elevated (Fig. S3). The left premaxilla and maxilla are nearly complete. The premaxilla is high and preserves I<sup>1</sup>-I<sup>2</sup>. It displays a large and broad ascending wing, like in *Catopithecus* and *Aegyptopithecus* [28]. The premaxilla separates anteriorly the maxilla from the nasal bone, which is partly preserved. The orbit is small (see Material and Methods, Figs. S4 and S5), testifying to a diurnal activity pattern. It is placed in a very anterior position, its anterior border reaching the level of P<sup>2</sup>. Estimated orbit convergence suggests a high value falling in the range of anthropoids (Methods). The maxilla is longer (27 mm) than high (22.9 mm) but its ascending process is broken so that its height is underestimated. Maxilla shape is deeply influenced by a hypertrophied canine, whose root extends nearly to the summit of the ascending wing and induces a significant canine jugum and a deep postcanine fossa. The zygomatic/maxilla suture is clearly visible and extends obliquely from the lower orbital rim to the basal part of the zygoma. The maxilla constitutes a large part of the lower orbital rim. In the upper part of the preserved orbit, a small rounded lacrimal foramen opens at the inner part of the orbit rim. It is surrounded by a lacrimal bone inside the orbit. The orientation of the lacrimal canal relative to the tooth row indicates an angle of 74°, slightly less than in *Parapithecus grangeri* (77°) and *Aegyptopithecus zeuxis* (85°) but significantly more than the extant strepsirrhines (range: 10-52°) and the adapiform *Notharctus venticolus* (32°) [29]. The zygomatic is high (11 mm). On the distal wall of the preserved zygoma, a concave notch corresponds to the separation between the postorbital bar and the zygomatic arcade. The postorbital bar is broken slightly above the level of the orbital floor and has a triangular section. In superior view, the orbit floor is smooth, wide and long, extending distally behind the M<sup>3</sup> level. Its distal extremity is missing but a small area, internal to the postorbital bar root, is smooth and rounded, indicating a large and open inferior orbital fissure. A large and distally expanded orbital floor is considered as an anthropoid character in contrast to the usually short orbital floor displayed by extant strepsirrhines, adapids (*Adapis*, *Leptadapis*) and notharctids (*Notharctus*, *Smilodectes*) [30, 31].

In anterior view, the nasal opening displays a rather narrow oval outline. I<sup>1</sup> root orientations are less parallel than in crown anthropoids (*Catopithecus browni* DPC 11594 [32], *Aegyptopithecus* CGM 40237 [33]) but less oblique than in some extant and fossil strepsirrhines that possess non-reduced central incisors (e.g., *Adapis*, *Notharctus*, *Smilodectes*, *Mesopropithecus*, *Indri*, *Propithecus*), suggesting an intermediate orientation. Despite the absence of contact facet between I<sup>1</sup>s, the interincisal diastema was probably reduced, unlike in most extant strepsirrhines

[34]. In internal view, the maxilla displays deep depressions corresponding to the maxillary sinuses. The main depression develops just above  $C^1$ . Above it, two smaller depressions occur. A third smaller depression develops behind the main sinus, below the lacrimal foramen and above  $P^4$ .

In occlusal view, the outline of the dental row and of the palate is marked by the impressive size of the canine. Incisors are slightly procumbent but not staggered as in *Notharctus* and *Lemur* [35].  $I^1$  has an asymmetrical shovel-like crown slightly longer buccolingually than mesiodistally (MD:BL ratio = 1.12; Table 1), proportions closer to those of *Pondaungia* (1.3) and anthropoids (range of extant platyrrhines 1.0-1.3; *Parapithecus grangeri* 1.1 [36]) than to those of strepsirrhines which possess proportionally buccolingually much thinner  $I^1$ s (range of Adapidae 1.9-2.2, range of lemuriformes 1.7-3.3 [36]). The lingual wall is concave, inclined, and presents a small basal cusp from which two cingula diverge towards the occlusal surface whose wear facet is horizontal. There is no mesial prong unlike in some adapiforms such as *Notharctus* [35,37]. The morphology of  $I^1$  is more similar to those of *Catopithecus* [32] and *Aegyptopithecus* CGM 40237 [33] than to any adapiform in sharing with the Fayum anthropoids a shovel-like crown with a similar outline, a horizontal apical wear facet, two enamel ridges delimiting the crown mesially and distally and a basal lingual cusp (*Catopithecus*) (see also supplementary note 2). The  $I^1$  crown is not oriented transversely to the tooth row but slightly obliquely.  $I^2$  is smaller, not shovel-like as  $I^1$ , and displays an apical horizontal wear facet. Its lingual part displays a central enamel ridge separating two depressions and its base displays a vertical wear facet with  $C_1$ . An enamel ridge limits its mesiolingual edge. The canine section is huge (Table 1) and oval, wider distally than anteriorly and distally truncated transversely.  $P^2$  is only represented by a buccally shifted tiny root section and circular alveolus.  $P^3$  crown preserves only a distinct lingual lobe bearing a low protocone.  $P^4$  and  $M^1$  crowns are broken. The right  $M^1$  displays a triangular occlusal outline with two sharp crests joining protocone to the buccal main cusps, a complete lingual cingulum with a tiny distolingual true hypocone.  $M^2$ - $M^3$  are also triangular, with a strong and continuous lingual cingulum, a weak and variably developed buccal cingulum, a small parastyle, and a protocone connected to paracone and metacone by complete crests. Small paraconule and metaconule are sometimes developed on these crests and located very close to the main buccal cusps. The hypocone is, as on  $M^1$ , a small cusp emanating from the distolingual cingulum and separated from the postprotocrista by a shallow groove, like in *Myanmarpithecus* [3]. These molars are different from those of *Pondaungia* in being less bunodont, having a triangular trigone basin, and lacking a connection between the distolingual cusp and the metacone and a connection between the lingual cusps, and are similar to those expected from the archetype of crown anthropoids [38]. The zygomatic arcade starts at the level of  $M^1$ - $M^2$  contact and determines an angle of  $45^\circ$ - $50^\circ$  with the molar row. Its base is located 4 mm above the  $M^2$ - $M^3$  contact and marked by important muscle insertion scars including a rounded pit for the superficial masseter muscle ligament.

A fragment uniting parts of the frontal and parietal bones measures 35.4 mm in length and has a maximum width of 15.6 mm. It is very thick dorsally (>4 mm) and displays a very characteristic concave frontal trigone, which is limited laterally by two well-defined frontal ridges converging posteriorly into a sagittal crest. This frontal trigone shows a completely fused metopic

suture, an additional anthropoid character. At the widest preserved parts of the trigone, two expansions of the zygomatic process of the frontal, representing the departures of the postorbital bar, are broken and display a triangular section. The interorbital distance, which is located under the olfactory chamber as in all haplorhines [39,40], measures 9 mm. On its anterosuperior flanges, small parts of the orbits are preserved, displaying a venous foramen located very high in the orbit. Slightly anteriorly to this foramen, there is a distinct dorsoventrally oriented suture representing the frontolacrimal suture. Slightly distal, a low, narrow and rounded bony ridge develops in a distoventral orientation in continuity with the postorbital bar section. This sectional anatomy demonstrates that there was no postorbital closure. The postorbital constriction measures 11.2 mm and is therefore wider than the interorbital distance. A dorsoventral frontoparietal suture can be observed. Two frontal bones (NMMP 19 and 27) have been attributed to large-sized amphipithecines from the Pondaung Formation [41,42] but their characteristics do not match those usually found in primates [12]. The new frontoparietal NMMP 104 confirms this interpretation as it displays typical primate anatomical characters such as a depressed frontal trigone, a completely fused metopic suture, none of the ridges on the frontal trigone visible on NMMP 19, no W-shaped frontoparietal suture, no deep groove for the superior sagittal sinus, and lacks the enigmatic large descending process described for one of these frontals (NMMP 19). On the ventral side of the frontal-parietal fragment, the olfactory chamber and the depressions corresponding to the frontal lobes of the brain are evident. A coronally oriented bridge partially separates the olfactory chambers from the frontal lobes. A small rounded venous sinus opens into this ridge. The superior sagittal venous sinus separates the frontal lobes and is included into a moderately salient bony tube. The large olfactory lobes of *Ganlea*, proportionally larger than those of *Parapithecus grangeri* DPC 1865 [43] and *Aegyptopithecus zeuxis* (YPM 23979, CGM 40237) [44], indicate a developed olfaction and are not divergent as in some adapiforms (*Adapis*, *Smilodectes*) [31]. The frontal lobes are largely incomplete and show a smooth surface without any trace of a coronolateral sulcus [45].

## Ulna

NMMP 106 (Fig. 3, Table 2) corresponds to an incomplete ulna (length= 64.2 mm), with about one quarter to one third of its overall length missing. Its size is similar in terms of its trochlear joint to that of a male *Cebus olivaceus*, with a mean body size of ~3 kg [46]. The radial notch is long and oval in shape along the lateral side. There is a weak supinator crest extending distally from this lateral joint surface. The groove for the abductor pollicis longus is more pronounced relative to the crest of the lateral side. Given the shape of the radial notch, it is most similar to *Aegyptopithecus* (YPM 23940), relative to the shorter and taller facet found in *Apidium phiomense* (DPC 1295, 1131) or *Cebupithecia sarmientoi* (UCMP 38762). The width of the coronoid process appears narrower, being more similar in its medial extension to anthropoid ulnae relative to lemurs, indriids or adapiforms. The olecranon process is long, being of similar length to that of *Aegyptopithecus* and relatively longer than in *Cebus* or *Cercopithecus*. One original feature

concerns the extent of the proximal curvature along the medial side of the trochlear notch for this joint. It extends well back toward the proximal end of the ulna and is more extended than in the ulnae of *Aegyptopithecus*, *Apidium* or *Cebupithecia*. The two fragmentary ulnae described previously [26] from the Pondaung Formation share a narrow mid-facet region within the trochlear notch, a wide coronoid process and more pronounced grooving along the medial ulnar shaft, characters which suggest an adapiform attribution. Their estimated body weight (4-9 kg) is larger than NMMP 106.

NMMP 106 appears to belong to an arboreal quadrupedal anthropoid weighing about 3 kg, looking quite similar to the ulna attributed to *Aegyptopithecus*. It differs in a few minor ways from ulnae attributed to *Apidium* in having greater bony height in the shaft below the trochlear notch, a feature more similar to that of *Aegyptopithecus*. The olecranon process also appears to be relatively longer relative to ulnae attributed to *Apidium*. Given its overall anatomical shape and the shape of the trochlear notch in particular, NMMP 106 clearly suggests an allocation with an anthropoid primate, rather than being associated with any fossil adapiform.

## Discussion

The new specimens provide rich insights not only into *Ganlea*'s anatomy but also into that of the whole amphipithecines considering their phylogenetic proximity [1] and morphological homogeneity. Most of *Ganlea*'s dentognathic characters, with the exception of its autapomorphies (hypertrophied canines, small distobuccal tubercle on C<sub>1</sub>, P<sub>3</sub>-P<sub>4</sub> with elevated and mesially oriented preprotocristids) [1], are indeed shared with all other amphipithecines.

A suite of dentognathic characteristics that strongly resembled those of anthropoids has been established in amphipithecines and largely agreed upon by the field [1,3,14,16,17,36,47-49]. The new remains bring several additional phylogenetically important cranial and postcranial characters that further demonstrate the anthropoid status of *Ganlea*, and by extension, of all amphipithecines: the rostrum is short and high. The lacrimal foramen is situated on the orbit rim and lacrimal duct is subvertical. The lacrimal bone is entirely located inside the orbit. The maxilla contributes significantly to the lower orbital rim, precluding a zygomatic-lacrimal contact. The orbital floor is wide and distally expanded and the interorbital distance is located below the olfactory chamber. The metopic suture is fused. The mandible (deep corpus, subvertical symphysis, mesial roots of P<sub>3</sub>-P<sub>4</sub> shifted buccally) and ulna also display diagnostic anthropoid characters.

Considered separately, some of these characters may be observed on non-anthropoid primates but such a combination of diagnostic features for anthropoids [16,39,50,51] clearly characterizes *Ganlea* as an anthropoid. In contrast to crown anthropoid characteristics, the new skull remains clearly demonstrate that the postorbital septum was absent in *Ganlea*. This allows us to conclude that amphipithecines are in fact stem anthropoids and are certainly not related to adapiforms. When compared with omomyids and tarsiids, it appears that *Ganlea* possesses several characters found in non-anthropoid haplorhines (e.g., vertical lacrimal duct, contribution of the maxilla to the lower orbital rim) but can be distinguished from them by a suite of anthropoid

features: high mandibular corpus, subvertical symphysis, obliquely oriented P<sub>3</sub>-P<sub>4</sub>, deep maxilla under the orbit, lacrimal foramen inside the orbit, and spatulate upper incisors ([52]; see also supplementary note 3).

A maximum parsimony analysis has been performed in order to investigate the phylogenetic position of *Ganlea*. A data matrix of 38 primate taxa and 326 morphological characters (Data S1) was used based on that used in [16]. Anthropoid taxa with uncertain familial status (*Phileosimias*, *Bugtipithecus*, *Aseanpithecus*) and/or only known from scarce material (*Krabia*, *Talahpithecus*, *Afrotarsius*, *Afrasia*) were discarded. Three most parsimonious trees have been obtained by a heuristic search (1000 replications of random addition sequence of taxa) performed with PAUP 4.0b10 [53] (Fig. 4). *Ganlea* and all Amphipithecidae are strongly supported as anthropoids (Bremer index=5, bootstrap frequency=82% for the anthropoid clade). Amphipithecidae are positioned crownward of Eosimiidae (robust clade with Bremer index=10 and bootstrap frequency=97%). However, Amphipithecidae are found to be stem anthropoids, being positioned stemward of the clade composed of all Paleogene Afro-Arabian anthropoids (Propliopithecidae, Oligopithecidae, Proteopithecidae, Parapithecidae) and platyrrhines. This phylogenetic position for Amphipithecidae, which rules out a relationship between amphipithecids and adapiforms, is similar to those of refs. [54,55] and with our new morphological interpretation of *Ganlea*. In addition, the two deepest divergences within total-clade Anthrogoidea involve taxa from Asia, reinforcing the hypothesis of an Asian origin and initial diversification of the anthropoids.

The new *Ganlea* remains from Myanmar indicate that amphipithecines must be definitively recognized as a highly specialized group of stem anthropoids and not as adapiforms. They shed new light on the early evolution of anthropoids for whose skulls were not documented and offer a unique perspective on the character evolution in this group. The features shown by *Ganlea* demonstrate that stem anthropoids lack a postorbital closure and that several skull characters evolved later than the dental ones [56]. Moreover, the subvertical lacrimal duct and the position of lacrimal bone inside the orbit on the skull of *Ganlea* indicate that the oro-nasal complex evolved before the postorbital septum [29]. Another implication of the absence of postorbital closure in *Ganlea* is that it brings crucial new paleontological evidence by a stem anthropoid that this character has evolved convergently in tarsiids and anthropoids. This new evidence reinforces previous claims of a convergence of the postorbital closure in haplorhines proposed by comparative anatomy of the orbital region between tarsiids and omomyids [57,58], between tarsiids and crown anthropoids [58,59], and with developmental data in extant haplorhines [60]. The scenario of a secondary loss of the postorbital closure in amphipithecines appears much less parsimonious.



## Methods

### Taxonomic attribution of the new material

The new Than-U-Daw remains were identified as an amphipithecine after comparisons with known Paleogene anthropoids from the Pondaung Formation of Myanmar and from Afro-Arabia (Supplementary note 2). They share with all amphipithecine genera (*Pondaungia*, *Myanmarpithecus*, *Ganlea*) a peculiar lower premolar structure with an asymmetrical crown displaying a basal expansion distolingually and mesial and trenchant preprotocristid connecting a high paraconid to the protoconid. On lower molars, the trigonid is narrow relative to the talonid and the paraconid is absent. The hypoconulid is also absent on M<sub>1</sub>-M<sub>2</sub>. The entoconid is low. The upper molars show strong resemblance to those of *Myanmarpithecus* but not to the isolated upper M<sup>1</sup> or M<sup>2</sup> (NMMP 75) initially assigned to *Ganlea megacanina*. This doubtfully attributed tooth does not bear like *Myanmarpithecus* and the new remains a small true hypocone, a strong and complete lingual cingulum, developed crests enclosing a trigone basin (fused preprotocrista and hypoparacrista, fused postprotocrista and hypometacrista), variously developed buccal cingulum, more buccally positioned paracone and metacone.

The new mandible NMMP 101 and the holotype of *Ganlea megacanina* NMMP 70 are nearly identical in terms of size, proportions, and morphological characters. Both show hypertrophied canines, subvertical symphysis, deep jaw and similar M<sub>2</sub> morphology. In addition, the size and morphology of the P<sub>3</sub>-P<sub>4</sub> are very close to those of NMMP 74, except for a slightly less developed distolingual crest on P<sub>3</sub> and a squarer outline. NMMP 101 belongs to an adult individual, judging by its completely erupted M<sub>3</sub>. Owing to its greatly enlarged canine, NMMP 70 was considered as a male individual [1]. Thus, the same sexing is proposed for NMMP 101. A body mass of ~2.5 kg for NMMP 101, corresponding well to the 2.4 kg mean body mass estimated for *Ganlea megacanina* [1], is obtained by using a regression equation for anthropoids based on M<sub>1</sub> size [61].

### μCT-scanning and 3D reconstruction

Because of the impossibility of performing micro-computed tomography (μCT) on the original specimens, the casts of NMMP 101, 103 and 104 were scanned at the University of Poitiers (Platina Platform of laboratory IC2MP) using an EasyTom CTscan (voxel size=22.4 μm). The 3D reconstruction of the skull of *Ganlea* was obtained by combining and orienting virtual models of these specimens preliminary extracted from the μCT image stacks with Geomagic Studio 2012 after a symmetrization of NMMP 101 and 103. The symmetrization of NMMP 103 was constrained by the presence of a part of the nasal bone and, therefore, the proximity of the sagittal axis of the skull. It was additionally constrained by the configuration of the I<sup>1</sup>, which was positioned so that its apical wear facet is subhorizontal rather than markedly oblique and so that its crown possesses a medially pointing apex. A small space was conserved on the reconstruction between the apices of the central incisors, owing to the absence of a medial contact facet on the I<sup>1</sup> of NMMP 103. The

frontoparietal NMMP 104 was positioned very close to the maxillae, owing to the presence on this specimen of a part of the lacrimal bone and of the lacrimal-frontal suture inside the preserved part of the orbit. The frontoparietal was also positioned relative to the maxillae so that, in lateral perspective, the slope between the frontal trigone and the nasal varies gently, as in most Paleogene primates, rather than abruptly. The lower jaw was symmetrized, oriented, and positioned relative to NMMP 103 to keep a coherent occlusion between lower and upper teeth, respect the fact the lower jaw is broken near the symphysis, and leave sufficient space for the lower incisors.

### **Orbit size, convergence, and activity pattern of *Ganlea***

The diameter of the orbit of NMMP 103 was estimated using the methodology of [62]. This methodology is using 3 points of the orbit plane (X, Y, Z) to calculate the orbit radius. The original methodology for point selection is using the inferiormost point of the orbit (Y) and two other points along the orbit (X and Z) equally distant from Y. Because the preserved portion of the orbit accessible on NMMP 103 does not allow such a positioning of the points, we have placed X and Z at the two extremities of the preserved rim to maximize the length of orbit rim used. Y was placed at equal distance from X and Z and its position had to be estimated, the central part of the preserved orbit rim being broken (Fig. S4).

NMMP 103 preserves a total length of orbit rim of 14 mm (when reconstructing the central portion), which is sufficient to obtain a reasonably good estimate of the orbit diameter but not an optimal one [53]. The coordinates of X, Y and Z have been determined with Avizo 7.0, and the WY and WZ distances were computed subsequently. The formula used to calculate the orbit diameter D was  $D=2OY=(WY^2+WZ^2)/WY$ .

An estimated diameter of 15.56 mm was found for the orbit *Ganlea megacanina*. This orbit diameter is proportionally small relative to tooth size and better fits with the values displayed the diurnal primates, likely indicating a diurnal activity pattern for *Ganlea* (Fig. S5).

The convergence of the orbit was also estimated using the reconstruction of the skull of *Ganlea*. Three points were taken to estimate the position of the sagittal plane (two along the sagittal crest and a third one on the medial most point of the jaw). Three points along the orbit rim have been selected to obtain an estimation of the orbit plane (Fig. S6). We obtain an estimated value of 72.7° for the orbit convergence of *Ganlea*, a high value of convergence falling into the range of extant anthropoids (58-85°) [63] and Fayum anthropoids (53-96°) [64] but higher than those of extant strepsirrhines (34-68°), adapids (57-66.5°) and extant *Tarsius* (45-54°) [63].

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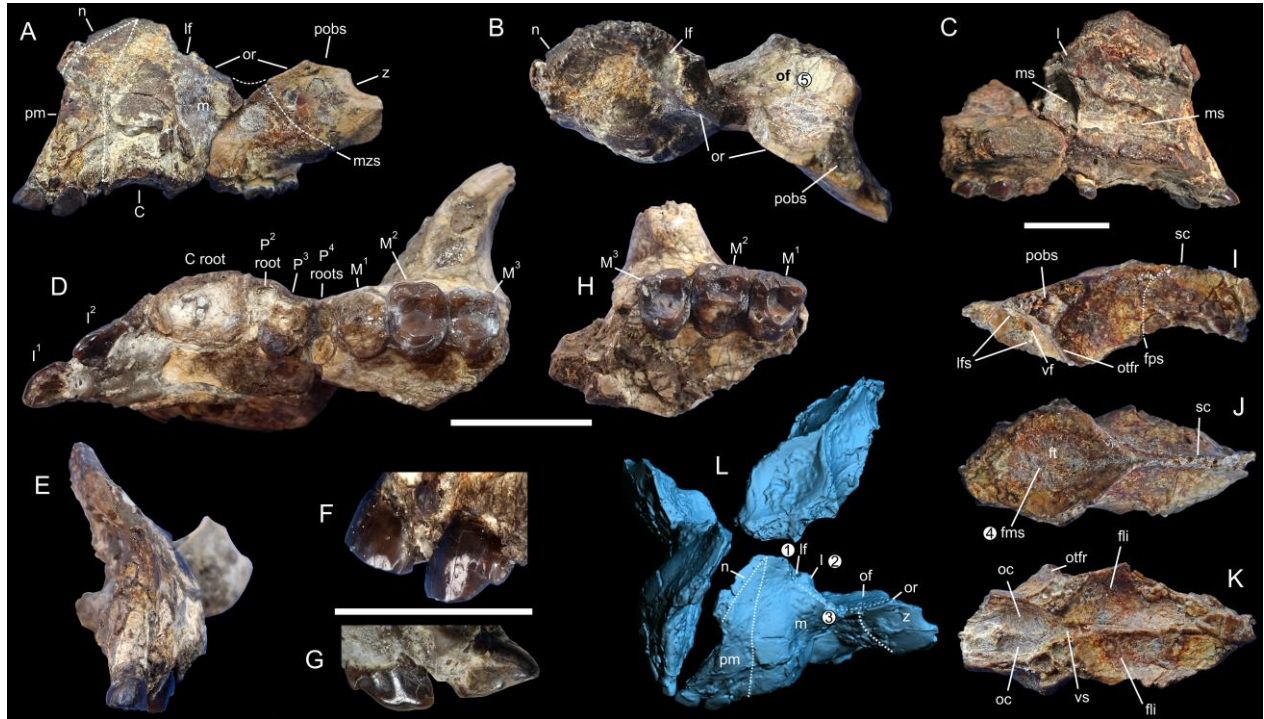
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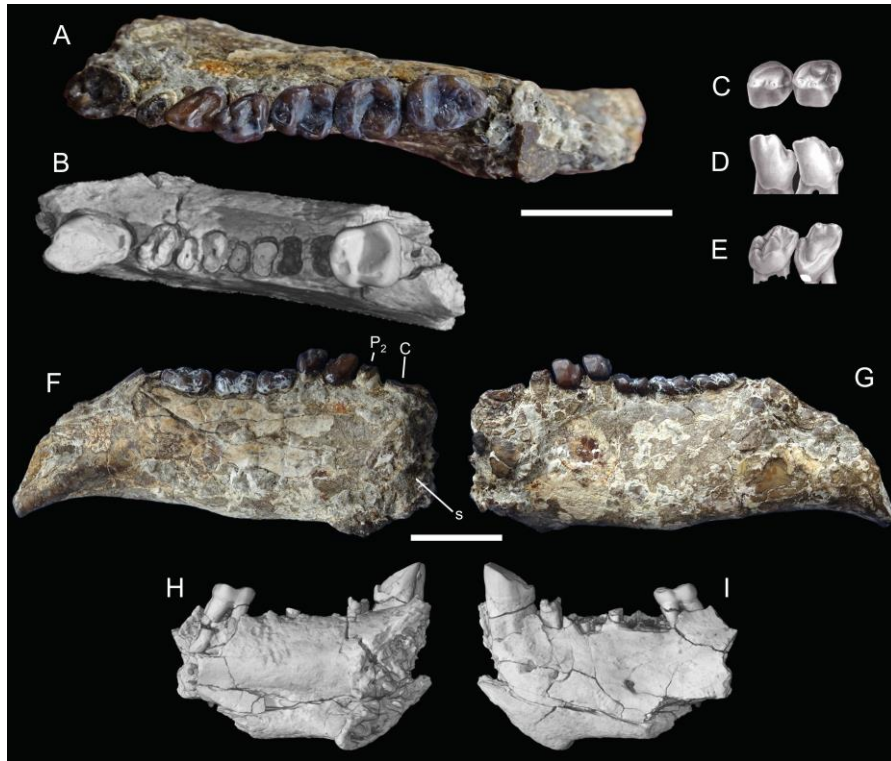
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## Figures captions and Tables

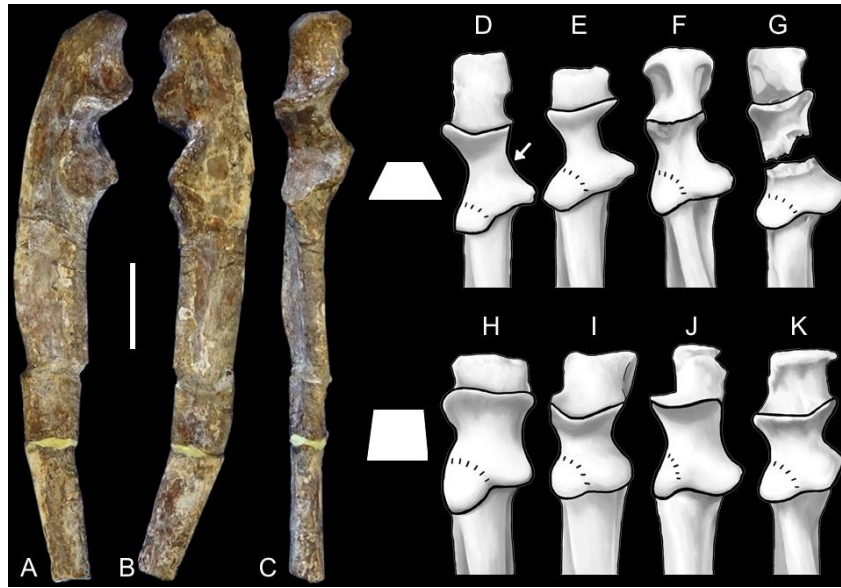


**Fig. 1.** New cranial remains of *Ganlea megacanina* from Than-U-Daw locality. **A-G**, NMMP 103 left skull fragment with I<sup>1</sup>-I<sup>2</sup>, roots of C<sup>1</sup>-P<sup>2</sup> and P<sup>4</sup>, lingual fragment of P<sup>3</sup> and M<sup>1</sup>, and M<sup>2</sup>-M<sup>3</sup>. **A**, buccal view. **B**, dorsal-oblique view. **C**, lingual view. **D**, occlusal view. **E**, anterior view. **F**, buccal view of I<sup>1</sup>-I<sup>2</sup>. **G**, lingual view of I<sup>1</sup>-I<sup>2</sup>. **H**, NMMP 102 right maxilla with M<sup>1</sup>-M<sup>3</sup> in occlusal view. **I-K**, NMMP 104 frontoparietal in left lateral (**I**), dorsal (**J**), and ventral (**K**) views. **L**, 3D reconstruction of NMMP 103 and NMMP 104 in left anterior oblique view. Scale bars, 10 mm (**A-C**, **E**, **I-K**), 10 mm (**D**, **H**), 10 mm (**F**, **G**). Numbers indicate some key anthropoid features of *Ganlea*: **1**, lacrimal foramen not located outside the orbit and subvertical lacrimal duct. **2**, lacrimal bone entirely inside the orbit. **3**, important maxillary contribution to the lower orbital rim. **4**, fused metopic suture. **5**, expanded orbital floor. Abbreviations: **f** frontal, **fli** frontal lobe imprint, **fms** fused metopic suture, **fps** frontoparietal suture, **ft** frontal trigone, **l** lacrimal bone, **lf** lacrimal foramen, **ifs** lacrimal-frontal suture, **m** maxilla, **ms** maxillary sinus, **mzs** maxillo-zygomatic suture, **n** nasal, **oc** olfactory chamber, **of** orbital floor, **or** orbit rim, **otfr** orbit-temporal fossa ridge, **pm** premaxilla, **pobs** post-orbital bar section, **sc** sagittal crest, **vf** venous foramen, **vs** venous sinus, **z** zygomatic.

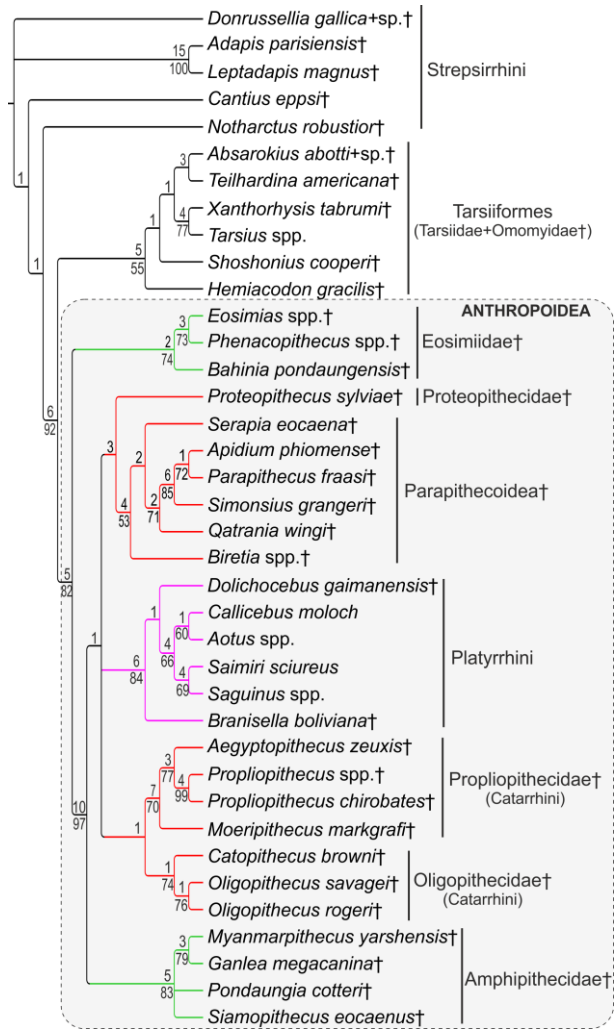


**Fig. 2. Lower jaw remains of *Ganlea megacanina*.** A, F, G, new left mandible with P<sub>2</sub>-M<sub>3</sub> and root fragment of canine from Than-U-Daw locality (NMMP 101) in occlusal (A), lingual (F) and buccal (G) views. B, H, I, holotype right mandible with canine, M<sub>2</sub> and roots of P<sub>2</sub>-M<sub>1</sub> NMMP 70 (mirrored). C-E, right lower jaw fragment with P<sub>3</sub>-P<sub>4</sub> NMMP 74 (mirrored). Abbreviations. s near-symphyseal mandibular section. Scale bars, A-E, 10 mm, F-I, 10 mm. C-E and B, H, I after [1].





**Fig. 3. Right proximal ulna of *Ganlea megacanina* (NMMP 106) from Than-U-Daw locality.** **A**, lateral view. **B**, medial view. **C**, anterior view. Scale bar, 10 mm. **D-K**, right proximal ulnae of living and fossil primates illustrating the proximal joint surface (i.e., the trochlear notch). **D**, *Eulemur fulvus* (NIU 03-1-1). **E**, *Propithecus verreauxi* (NIU 03-1-3). **F**, *Notharctus tenebrosus* (AMNH 11478). **G**, NMMP 20 from PK2 locality (most proximal ulnar element reversed). The arrow points to the narrow mid-joint region of the trochlear notch relative to the widened proximal joint length for taxa in strepsirrhines. **H**, *Ateles paniscus* (NIU 10-1-1). **I**, *Apidium phiomense* (DPC 1295). **J**, *Aegyptopithecus zeuxis* (YPM 23940). **K**, NMMP 106. Anthropoids (**H-K**) (with the exception of Old World monkeys) illustrate a wider mid-joint region with more similar mid to distal widths in trochlear joint proportions compared to strepsirrhine primates (with the exception of lorises) (**D-G**). The shaded quadrilateral polygons on the far left reflect the two trochlear joint shapes of each row. **D-K** are not to scale and are represented with similar ulna breadths to facilitate comparisons. The specimens are drawn in a view orthogonal to the trochlear notch.



**Fig. 4. Phylogenetic position of *Ganlea* among the primates.** Strict consensus tree of three most parsimonious trees (length = 1424, CI = 0.3413, RI = 0.6587). Branch colors for the main anthropoid clades denote the geographic provenance of the taxa (red: Afro-Arabia; green: Asia; magenta: South America). Bremer support values and bootstrap frequencies are indicated above and below the nodes, respectively.

**Table 1. Dental measurements of the new right maxilla (NMMP 102) and left skull fragment (NMMP 103) of *Ganlea megacanina* (in mm). MD, mesiodistal. BL, buccolingual. Parentheses show the estimated values because of partial broken teeth.**

	NMMP 102		NMMP 103	
	MD	BL	MD	BL
I <sup>1</sup>	-	-	3.97	3.56
I <sup>2</sup>	-	-	4.44	2.45
C	-	-	8.24	6.11
M <sup>1</sup>	4.07	5.13	(3.75)	(4.78)
M <sup>2</sup>	4.37	5.64	4.35	5.48
M <sup>3</sup>	3.75	5.40	3.89	5.32
C-M <sup>3</sup> length	-	-	25.83	-
M <sup>1</sup> -M <sup>3</sup> length	12.51	-	12.63	-

**Table 2. Ulna measurements of *Ganlea megacanina* (NMMP 106) in millimeters.**

Length of olecranon process	8.56
Width of olecranon process	7.21
Length of trochlear joint	12.31
Proximal width of the trochlear joint	8.55
Mid-width of the trochlear joint	5.78
Trochlear joint depth	4.00
Length of radial facet	6.23
Height of radial facet	4.55
Height of ulnar shaft	7.20
Width of ulnar shaft	5.38

## Electronic Supplementary Material for

### Amphipithecine primates are stem anthropoids: cranial and postcranial evidence

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#### Content

Supplementary note 1: description of the new lower jaw of *Ganlea* (NMMP 101)

Table S1. Measurements of the new lower jaw NMMP 101 and of previously found lower jaw/teeth of *Ganlea megacanina*

Fig. S1. Location of the *Ganlea*-bearing localities from the Pondaung Formation in Myaing Township, Central Myanmar.

Fig. S2. Comparison between the skull *Ganlea* and those of extant strepsirrhines and anthropoids.

Fig. S3. Bivariate plot of log-transformed maxillary depth versus preorbital rostrum length

Fig. S4. Estimation of the orbit size of *Ganlea*

Fig. S5. Bivariate plot of log-transformed M<sup>1</sup> length versus orbit diameter

Fig. S6. Estimation of the orbital convergence in *Ganlea*

Supplementary note 2: comparisons between *Ganlea* and other Paleogene anthropoids

Supplementary note 3. Comparisons between *Ganlea* and haplorhines

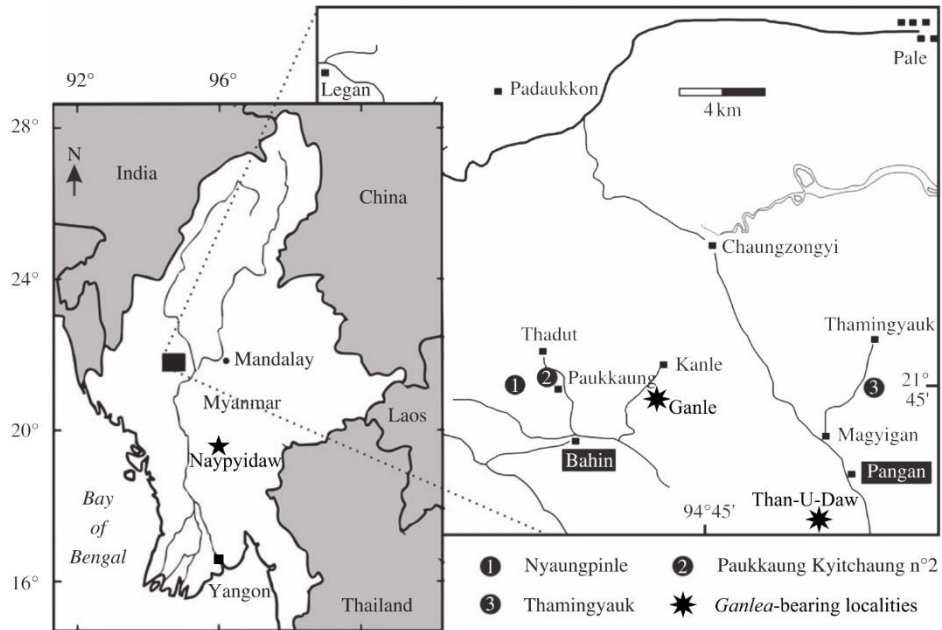
Supplementary references

**Supplementary note 1. Description of the new lower jaw of *Ganlea* (NMMP 101)**

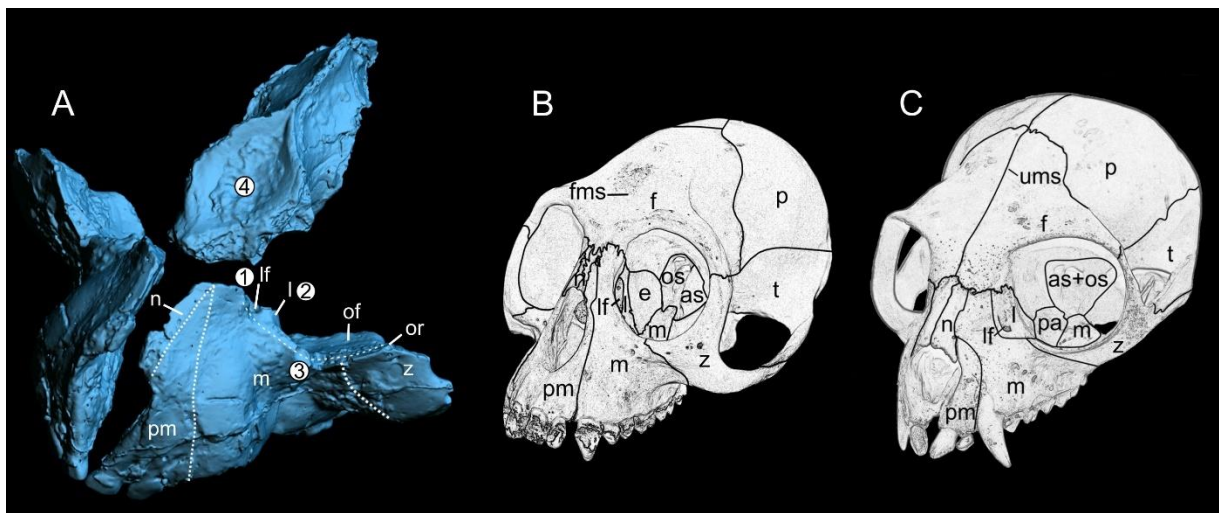
The left lower jaw fragment (Fig. 2, Table S1) has a total length of 47.5 mm. The corpus height is considerable, corresponding to 3.3 times the length of M1. The tooth row between canine and M<sub>3</sub> measures 30.3 mm. The canine is very large, but its crown is missing. The canine displays an oval section oriented antero-posteriorly. All premolars and molars are preserved (except P<sub>2</sub> crown), the premolar length representing 191% of that of M<sub>2</sub> length versus 197% on the holotype [1]. P<sub>2</sub> is single rooted and its root is oriented obliquely in the jaw in regard of the tooth row, not quite as transverse as that of the holotype. P<sub>3</sub> is slightly larger than P<sub>4</sub> and its crown is more elevated. On their lingual side, these two premolars display all the morphological characteristics described for *Ganlea* [1]. Lower molars are similar to those described with the holotype. M<sub>3</sub> trigonid is slightly less wide buccolingually than that of M<sub>2</sub>. The mesial part of the talonid on M<sub>3</sub> is similar to that of M<sub>2</sub> but its talonid basin, which shows fine enamel crenulations, is terminated by a short heel. In buccal view, at its distal extremity, the corpus shows a slightly projecting angular process. No foramen mentale can be observed but the corpus is recovered by several patches of carbonate concretions, which may fill and hide this foramen. In lingual view, the projecting angular process shows a distinct groove for the insertion of the pterygoid muscle. The symphysis is unfused and its surface displays a rugose pattern. Its structure is identical to that described for the holotype.

**Table S1. Measurements of the new lower jaw NMMP 101 and of previously found lower jaw/teeth of *Ganlea megacanina* (in mm).** Abbreviations similar to those of table 1. When available, molar BL values are given as trigonid/talonid.

	NMMP 101		NMMP 70 (holotype)		NMMP 74		NMMP 69		NMMP 73		NMMP 72	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
C	(5.38)	(3.75)	5.90	4.30	-	-	-	-	-	-	-	-
P <sub>2</sub>	(2.32)	(2.72)	(3.46)	(2.50)	-	-	-	-	-	-	-	-
P <sub>3</sub>	3.24	3.30	-	-	2.80	2.90	-	-	-	-	-	-
P <sub>4</sub>	3.29	3.49	-	-	3.05	3.10	-	-	-	-	-	-
M <sub>1</sub>	4.23	3.47/3.98	-	-	-	-	4.30	3.90	4.20	3.80	-	-
M <sub>2</sub>	4.64	4.16/4.32	4.70	4.25/4.50	-	-	-	-	-	-	4.45	-
M <sub>3</sub>	5.32	3.88/3.74	-	-	-	-	-	-	-	-	-	-
P <sub>2</sub> -P <sub>4</sub> length	9.36		9.25		-	-	-	-	-	-	-	-
P <sub>2</sub> -M <sub>3</sub> length	23.62		-		-	-	-	-	-	-	-	-
P <sub>3</sub> -M <sub>3</sub> length	21.22		-		-	-	-	-	-	-	-	-
M <sub>1</sub> -M <sub>3</sub> length	14.03		-		-	-	-	-	-	-	-	-
Corpus depth at P <sub>2</sub>	15.29		15.42		-	-	-	-	-	-	-	-
Corpus depth at M <sub>1</sub>	14.73		14.46		-	-	-	-	-	-	-	-
Corpus depth at M <sub>3</sub>	14.46		-		-	-	-	-	-	-	-	-

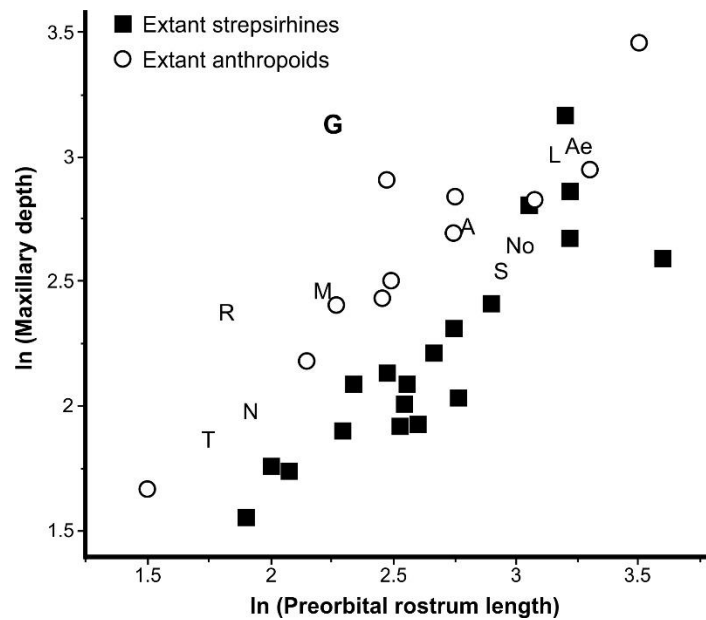


**Fig. S1. Location of the *Ganlea*-bearing localities from the Pondaung Formation in Myaing Township, Central Myanmar. Modified from [1].**

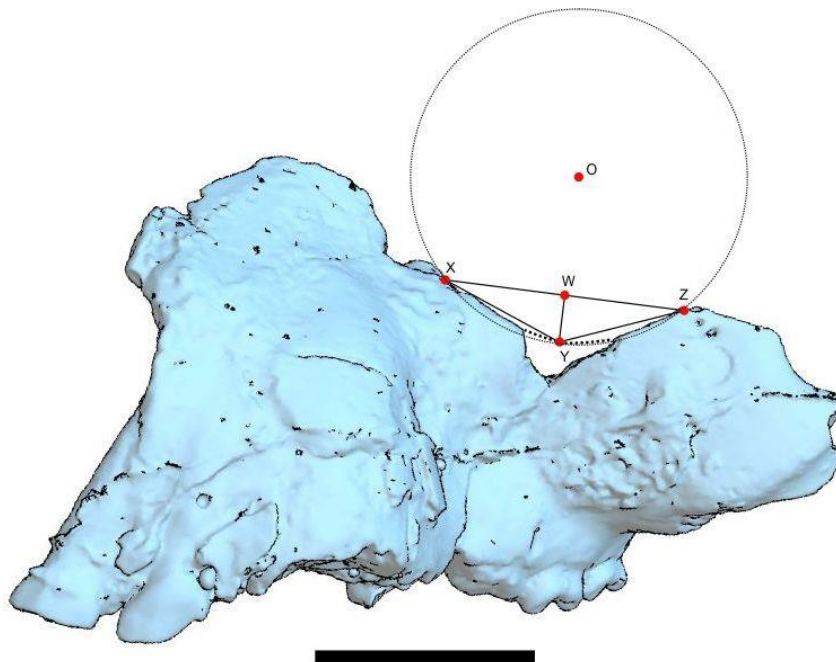


**Fig. S2. Comparison between the skull *Ganlea* and those extant strepsirrhines and anthropoids. A, 3D reconstruction of *Ganlea* in left anterior oblique view. B, skull of *Piliocolobus* in left anterior oblique view showing the anthropoid cranial organization. C, skull of the *Propithecus* in left anterior oblique view showing the strepsirrhine cranial organization. The skulls**

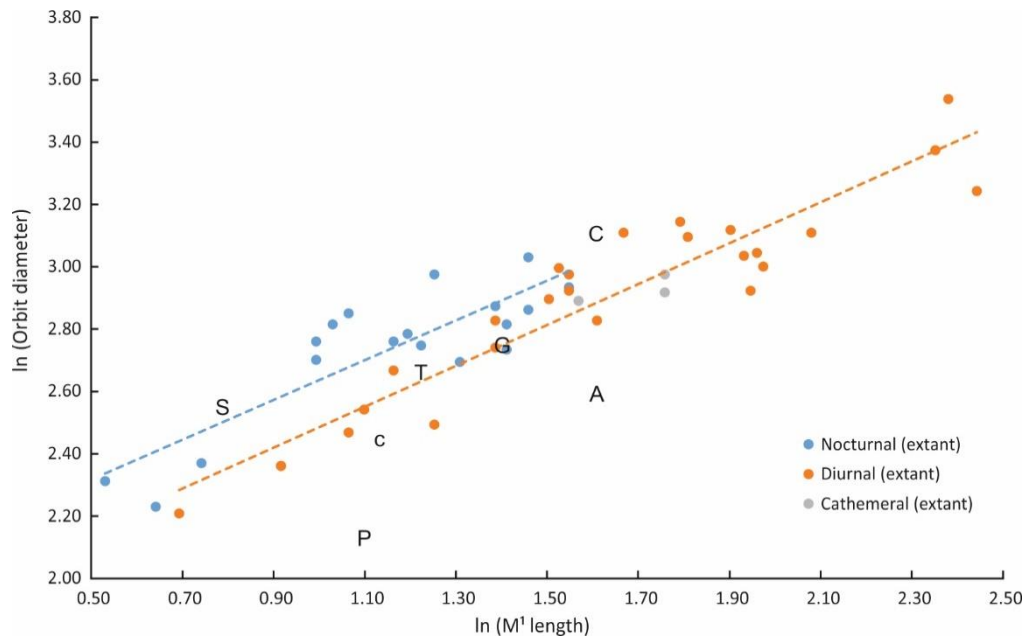
are not on scale. Numbered characters as on Fig. 1. Abbreviations: as on fig. 1 plus **as** alisphenoid, **e** ethmoid, **os** orbitosphenoid, **p** parietal, **pa** palatine, **t** temporal, **ums** unfused metopic suture.



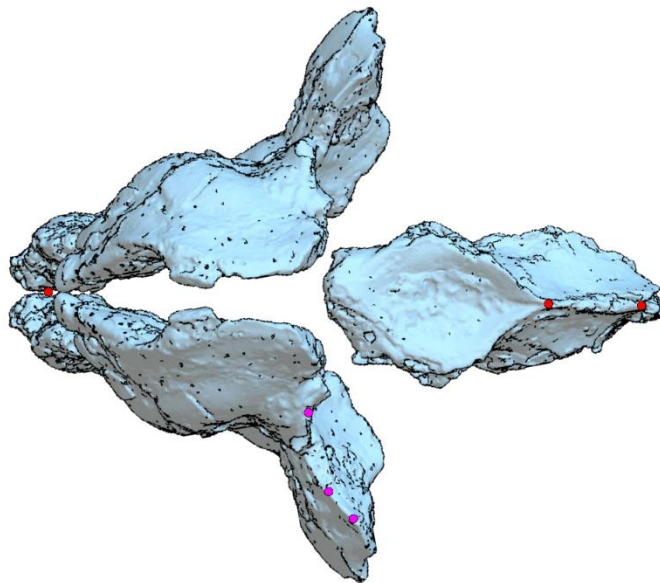
**Fig. S3. Bivariate plot of log-transformed maxillary depth versus preorbital rostrum length (in mm).** Labels for fossil taxa: A, *Adapis*. Ae, *Aegyptopithecus*. G, *Ganlea*. L, *Leptadapis*. M, *Mahgarita*. N, *Necrolemur*. No, *Notharctus*. R, *Rooneyia*. S, *Smilodectes*. T, *Tarsius*. Data from ref. [2]. The preorbital rostrum length is measured between the anterior orbital margin and the anterior margin of the upper canine alveolus, thus excluding the length of the premaxilla. Note that the maxillary depth of *Ganlea* is a minimum value.



**Fig. S4. Estimation of the orbit size of *Ganlea*.** Position of the points X, Y and Z along the orbital rim of NMMP 103. Scale bar, 10 mm.



**Fig. S5. Bivariate plot of log-transformed  $M^1$  length versus orbit diameter (in mm).** The sample includes 47 extant primates and 7 fossil primates including *Ganlea*. The orbit diameter corresponds to the measurement of the mediolateral diameter of the orbit except for *Ganlea* and *Aseanpithecus* for whose orbit diameters were estimated. Linear regressions for extant diurnal and nocturnal primates are shown. All data from [3] except for *Aseanpithecus* from [4] and *Ganlea* (this work,  $M^1$  length from NMMP 102). Labels for fossil taxa: A, *Aseanpithecus*. C, *Cantius*. c, *Catopithecus*. G, *Ganlea*. P, *Proteopithecus*. S, *Shoshonius*. T, *Tremacebus*.





**Fig. S6. Estimation of the orbital convergence in *Ganlea*.** Position of the points selected to estimate the orientation of the sagittal (red dots) and orbital (purple dots) planes.

## **Supplementary note 2. Comparisons between *Ganlea* and other Paleogene anthropoids**

### Comparisons between *Ganlea* and Eocene Asian anthropoids

According to the scarcity of primates cranial remains in the Eocene of Southeast Asia, there are very few comparisons possible. One main comparison can be made with the two maxillae of *Pondaungia cotteri* [5-7], a large sized amphipithecine sympatric with *Ganlea*. NMMP 12 (= NMMP-KU 0003) is slightly larger than NMMP 18 (= NMMP-KU 0228) and differs from it by several characters, demonstrating the variability existing among this population. The best-preserved *Pondaungia* maxilla is NMMP 18, which shares several characters with the new specimens of *Ganlea* (NMMP 102 and 103) but also presents several differences which are listed hereby. Concerning the similarities, both display a similar outline with a wide inferior orbital fissure, a flat and extended orbital floor, a distal position of the robust zygomatic root at the level of M<sup>3</sup>, a strong insertion for the ligament of the superficial masseter muscle masseter, which is located dorsolaterally above the occlusal plane. The orbital floor of both specimens is significantly expanded distally and rather thick, the molar roots being not exposed to the inferior orbital surface. However, several other characters observed in NMMP 18 are not present in *Ganlea*. For instance, the orbital floor of *Ganlea* displays a smooth surface without trace of a shallow groove adjacent to the inner wall of the zygomatic arch as described in both *Pondaungia* specimens. Also, the parazygomatic groove, which is strong on NMMP 12 and weaker in NMMP 18 is nearly not expressed in NMMP 102. Another difference concerns the external surface of the maxilla, which displays a deep canine fossa in NMMP 103 but a shallower one on NMMP 18 and NMMP 12 due to the much smaller size of the canines of *Pondaungia*. In conclusion, these maxillae share some similarities, but they do not appear to display any major shared derived character. The differences in the shape of these maxilla indicate that the skull of *Pondaungia* must have been quite different from that, highly specialized, of *Ganlea*.

Another comparison can be made with the maxilla of *Siamopithecus eocaenus* [8,9]. Unfortunately, there are few common anatomical structures preserved between the specimens. NMMP 103 displays the anterior part of the orbital rim whereas *Siamopithecus* has preserved only the distal orbital rim and a significative part of the postorbital bar, which is missing in NMMP 103. Both maxillae share a high elevation between the occlusal level and the lower orbit rim and an insertion for the superficial masseter muscle situated dorsolaterally above the occlusal plane. On the contrary, the zygomatic part of the postorbital bar of *Siamopithecus* is very distinct from that of NMMP 103, which displays a triangular basal section. In *Siamopithecus*, it is considerably mesiodistally extended, suggesting the development of a postorbital closure. The orbital surface of these maxillae is also very different. While this surface is nearly flat in NMMP 102 and 103, it

presents an oval and rather deep depression in *Siamopithecus*. This depression is separated by a bony crest from a rather large distal part, which is less elevated, and which displays some eminences made by molar roots. There is no distinctive and rounded inferior orbital fissure as can be observed in NMMP 102 and 103.

*Aseanpithecus* [4], also originating from the Pondaung Formation, is represented by a left maxillary fragment with C<sup>1</sup>-M<sup>3</sup> but missing M<sup>1</sup>. The maxilla is slightly smaller than that of NMMP 103 but the molars are of larger size. The dental row displays many differences, especially in the much smaller size of the canine of *Aseanpithecus* and the greater development of its premolar row. Also, it does not display the canine bulge followed by the large canine fossa developed on *Ganlea*. Its canine is subvertical with a long root and its maxilla is high as in *Ganlea*. The orbit of *Aseanpithecus* has a lower convergence and is less anteriorly expanded than in *Ganlea*, reaching the level of P<sup>4</sup> only, instead of the level of C<sup>1</sup>-P<sup>2</sup>. The frontal process of the maxilla is extremely thin in *Aseanpithecus*, having probably lost the lacrimal bone that was located inside the orbit, since there is no trace of lacrimal bone nor lacrimal foramen on the external surface of the maxillary. These main differences confirm that *Aseanpithecus* is not closely related to amphipithecines and confirm that its taxonomic affinities are to be found among other Asian anthropoid groups [4].

*Bahinia*, also from Pondaung Formation, is a much smaller anthropoid which has been attributed to the eosimiids [10]. It is also represented by a maxilla fragment, which, in its anatomical organization, is more similar to that of *Aseanpithecus* than to *Ganlea*. Its canine is strong but not huge, vertically oriented, with also vertically oriented incisors. Its molars are more primitive with developed styles. The maxilla is high, the distance between the lower orbital rim and the occlusal surface being important relative to the molar dimensions. Its orbit extends anteriorly until the level of P<sup>3</sup> indicating a short rostrum. As in *Aseanpithecus*, the canine has a long root but does not modify the morphology of the maxillary as in *Ganlea*.

It appears therefore that most of Pondaung Formation anthropoids had strong canines with long roots, elevated maxilla and rather anteriorly extended orbits in relation with a short snout. These characters, occurring in three distinct families or subfamilies of these Asian early anthropoids (eosimiids, amphipithecines, family indet.) may correspond to general characteristics of these earliest Asian Eocene anthropoids.

#### Comparisons between *Ganlea* and Paleogene anthropoids from Afro-Arabia

*Ganlea* can be compared with African Eocene advanced stem anthropoids (Proteopithecidae, Parapithecidae) such as *Parapithecus grangeri* (DPC 18651) and *Proteopithecus sylviae* (CGM 42214). The skull of *Ganlea* shares with those of *Parapithecus* and *Proteopithecus* a broad interorbital distance and small orbits, related to diurnal activity. However, *Ganlea* differs from these anthropoids by the lack of postorbital closure, a larger snout with a strong postcanine fossa, a higher orbital convergence (72.7° versus 52.5° for DPC 18651), and a larger premaxilla with a higher and broader ascending wing. *Ganlea* shares with *Proteopithecus*

and *Parapithecus* a plesiomorphic dental formula with three premolars but differ from them in several dental features. The dental characteristics of *Parapithecus* are very different from those of *Ganlea*, being characterized by hyperbunodonty and additional cusps on the premolars and molars and by the reduction/absence of lower incisors. *Proteopithecus* CGM 42214 displays very distinctive dental characters absent in *Ganlea*, such as a  $P_2$  larger than  $P_3$ , more transversally elongated upper molars with a stronger hypocone, the development of a hypocone on  $P^4$ , and twinned hypoconid/entoconid on lower molars to mention only the main dental differences.

The Paleogene crown anthropoids (Propliopithecidae, Oligopithecidae) are characterized by their postorbital closure and the lack of  $P^{2/2}$ . Upper incisors have been described for the Fayum genera *Aegyptopithecus zeuxis* and *Catopithecus browni* and can be compared with *Ganlea*. The upper incisors alveoli of these crown anthropoids are closely approximated, with  $I^1$  and  $I^2$  being both spatulated.  $I^1$  of *Catopithecus browni* (DPC 11594; [11]) has an asymmetric crown with a concave lingual wall laterally limited by two cingula originating from a lingual basal cusp, rather similarly to that of *Ganlea*. The  $I^1$  of *Catopithecus* and *Ganlea* also share a horizontal apical wear facet and a concave lingual surface. However, the  $I^1$  of *Catopithecus* displays a small vertical medial contact facet with the other central incisor that is not present in *Ganlea*.

The  $I^2$  of *Ganlea* and *Catopithecus* differ by their proportions, this tooth being proportionally longer mesiodistally than buccolingually in *Ganlea* [11]. The  $I^2$  of *Ganlea* displays a small cusplet at its distal extremity. Its lingual side is not depressed so that it is not spatulated but shows a lingual central ridge separated by two shallow depressions (Fig. 1). In addition, the lingual base of its crown displays a vertical wear facet made by the lower canine that has no equivalent among the  $I^2$  of African crown anthropoids. Its buccal wall is gently convex as in *Catopithecus*. In anterior view, the orientation of the central incisor is more oblique than in *Catopithecus*. Therefore, the midline interincisor diastema at about the alveolar level should have been larger.

*Aegyptopithecus* incisors are similar to those of *Catopithecus* and to those of most catarrhines. Its  $I^1$  (YPM 20932) have a similar outline as that of *Ganlea*, with a shovel-like shape, a horizontal apical wear facet and two enamel ridges delimiting the crown mesially and distally. The  $I^2$  (YPM 23797) is shovel like and is similar in its crown proportions to that of *Catopithecus* but displays a central ridge on its lingual face similar to that of *Ganlea*, separating two adjacent concavities which are deeper than in *Ganlea*. A significative difference between the upper central incisors of *Ganlea* and those of crown anthropoids is that they do not show a contact facet. However, the skull of *Catopithecus* and *Aegyptopithecus* share with *Ganlea* large premaxilla with large ascending wings. In none of them, the canine reaches such a strong development as in *Ganlea*.

To summarize, among the new anthropoid dental characters that were undocumented for the amphipithecines are the shovel like upper central incisors, the closed arc formed by the upper incisors and the small diastema between  $I^2$  and  $C^1$ . These characters complete the true cingulum-derived molar hypocone already observed in *Myanmarpithecus* [12] and that is also present in *Ganlea*. The new anthropoid skull characters documented by *Ganlea* for amphipithecines are the

absence of zygomatic-lacrimal contact, the location of the interorbital constriction below the olfactory tract, the position of lacrimal foramen on the orbit rim, its subvertical orientation, the lacrimal bone location inside the orbit, the high orbital margin convergence and the fusion of the metopic suture. *Ganlea* cumulates so many anthropoid characters that its attribution to strepsirrhines cannot be supported anymore. This suite of characters associated with the lack of postorbital closure allows considering *Ganlea megacanina* and probably also all others amphipithecines as stem anthropoids. However, as several of the previously mentioned anatomical characters are also considered as stem haplorhine characters, it is necessary to compare the new remains of *Ganlea* to omomyids and tarsiids.

### **Supplementary note 3. Comparisons between *Ganlea* and haplorhines**

*Ganlea* shares with all non-anthropoid haplorhines a single rooted p2 [13] and an olfactory tract located above the orbital constriction [14]. However, *Ganlea* differs from non-anthropoid haplorhines by several anthropoid features [15]. The mandible of *Ganlea* is much deeper. It possesses a more vertical symphysis. The maxilla of *Ganlea* is also higher under the orbit than those of tarsiids and omomyids. In *Ganlea*, P<sub>3</sub> and P<sub>4</sub> are oriented obliquely with a mesial root shifted buccally relative to the distal root. The upper incisors are shovel like. The lacrimal foramen is not located outside the orbit like in tarsiids and omomyids.

#### Tarsiidae

The skull of *Ganlea* presents like extant tarsiids a contribution of the maxilla to the lower orbit rim. The lacrimal foramen of extant *Tarsius* is vertical like in all extant haplorhines (*Tarsius bancanus* (90°), range of extant haplorhines = 80-97°; [16]), and slightly more inclined than in Paleogene fossil anthropoids (*Ganlea* =74°, *Parapithecus* = 77° *Aegyptopithecus* =85°; [16]). *Ganlea* differs from extant tarsiids in its short but not peaked rostrum, its lacrimal foramen not located outside the orbit like in extant *Tarsius* [2] and *T. eocaenus* [17], and its much smaller orbit, and the absence of postorbital closure. The dental arcade of *Ganlea* is not bell-shape like those of extant tarsiids and *Tarsius eocaenus* [17]. Dentally, the mandibular anterior teeth of *Ganlea* are more vertically implanted unlike the slightly mesially inclined anterior teeth of extant tarsiids. The anterior dentition of extant *Tarsius* is also extremely different in its reduced and peg-like incisors, the wide diastema between the central incisors, and the smaller upper canine. Additional dental characters observable on *Ganlea* differ strikingly from those of all fossil and extant tarsiids (e.g., ‘spatulate’ lower premolars, much larger canine, marked bunodonty, lower crowned molars, lack of molar paraconid, lack of molar hypoconulid on M<sub>1</sub>-M<sub>2</sub>).

#### Omomyidae

The omomyids, like *Ganlea*, do not possess a postorbital septum. Several omomyids share with *Ganlea* a contribution of the maxilla to the lower orbital rim (*Shoshonius*, *Necrolemur*, *Tetonius*) [2]. However, in comparison with *Ganlea*, this contribution is smaller due to an important medial expansion of the zygomatic that is absent in *Ganlea*. In *Rooneyia*, a zygomatic-lacrimal contact can be observed on one side of the skull [2]. The position of the lacrimal foramen and the lacrimal bone are variable in omomyids and can differ from those seen in *Ganlea*. For instance, *Necrolemur* and *Rooneyia* display a lacrimal bone that expands outside the orbit and a lacrimal foramen located outside the orbit [18].

Several dental features distinguish *Ganlea* from omomyids [18]. *Ganlea* differs from them by the presence of enlarged upper and lower canines and shovel like upper incisors. The lower canine is vertically implanted contrary to anaptomorphine omomyids. The premolars crowns of *Ganlea* are not mesiodistally compressed as frequently in omomyids and show no marked mesial projection as in several omomyids (e.g., *Absarokius*, *Aycrossia*, *Teilhardina*, *Tetonius*) The P<sub>3</sub> and P<sub>4</sub> of *Ganlea* also markedly differ from those found in omomyids in being ‘spatulate’ (asymmetrical crowns developed distolingually and apically thin with a high paraconid connected to the protoconid by a sharp crest). The P<sub>4</sub> of *Ganlea* is not hypertrophied in contrast to several genera of anaptomorphine omomyids (e.g., *Aycrossia*, *Pseudotetonius*, *Strigorhysis*). The lower molars of *Ganlea* share with most omomyids the absence of a hypoconulid on M<sub>1</sub>-M<sub>2</sub> (except Troglolemurini, *Uintanius*, *Necrolemur*, *Microchoerus*, *Hemiacodon*, *Washakius*, *Utahia*) but differ from them by their marked bunodonty, their compressed trigonid lacking a paraconid, a more buccal and mesiodistally oriented cristid obliqua and a talonid basin more enclosed lingually. The upper molars of *Ganlea* share with omomyids cingulum derived hypocone but differ from those of omomyids in their more enclosed trigon basin with more buccally oriented pre- and postprotocrista connected to hypopara- and hypometacrista.

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