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Amphipithecine primates are stem anthropoids: cranial and postcranial evidence

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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). By 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.

1. 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

Figure 1. New cranial remains of *Ganlea megacanina* from Than-U-Daw locality. (a–g): NMMP 103 left skull fragment with I^1 – I^2 , roots of C^1 – P^2 and P^4 , lingual fragment of P^3 and M^1 , and M^2 – M^3 . (a) Buccal view, (b) dorsal-oblique view, (c) lingual view, (d) occlusal view, (e) anterior view, (f) buccal view of I^1 – I^2 , (g) lingual view of I^1 – I^2 , (h) NMMP 102 right maxilla with M^1 – M^3 in occlusal view. (i–k): NMMP 104 frontoparietal in left lateral (i), dorsal (j) and ventral (k) views, (l) three-dimensional 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; lfs, lacrimal-frontal suture; m, maxilla; ms, maxillary sinus; mzs, maxillo-zygomatic suture; n, nasal; oc, olfactory chamber; of, orbital floor; or, orbit rim; oftr, orbit-temporal fossa ridge; pm, premaxilla; pobs, post-orbital bar section; sc, sagittal crest; vf, venous foramen; vs, venous sinus; z, zygomatic. (Online version in colour.)

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^1 – M^3 , anterior part of lower orbital margin and root of zygomatic, a right maxilla fragment with M^1 – M^3 , a fronto-parietal fragment preserving the antero-superior parts of the orbits (figure 1), a partial left mandible (figure 2, electronic supplementary material, note 1, table S1) with C – M_3 preserved but missing the incisor region, the ascending ramus and the angular region, and an ulna missing its distal extremity (figure 3). All these remains were found scattered on a surface of about 1 m² in Than-U-Daw locality (Myaing Township, central Myanmar) of Pondaung Formation [27] (electronic supplementary material, figure 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 Material and methods section).

2. Results

(a) Partial skull description

The skull bones (figure 1; electronic supplementary material, figure S2) are massive while the rostrum is short and elevated (electronic supplementary material, figure S3). The left

premaxilla and maxilla are nearly complete. The premaxilla is high and preserves I^1 – I^2 . 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, electronic supplementary material, figures 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^2 . Estimated orbit convergence suggests a high value falling in the range of anthropoids (Material and 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 ventriculus* (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

Figure 2. Lower jaw remains of *Ganlea megacanina*. (a,f,g): new left mandible with P₂–M₃ 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, M₂ and roots of P₂–M₁ NMMP 70 (mirrored). (c–e) Right lower jaw fragment with P₃–P₄ 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]. (Online version in colour.)

Figure 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. (Online version in colour.)

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 M³ 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

Table 1. Dental measurements of the new right maxilla (NMMP 102) and left skull fragment (NMMP 103) of *Ganlea megacantha* (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 ¹	—	—	3.97	3.56
I ²	—	—	4.44	2.45
C	—	—	8.24	6.11
M ¹	4.07	5.13	(3.75)	(4.78)
M ²	4.37	5.64	4.35	5.48
M ³	3.75	5.40	3.89	5.32
C–M ³ length	—	—	25.83	—
M ¹ –M ³ length	12.51	—	12.63	—

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. I¹ 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 I¹s, 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 C¹. Above it, two smaller depressions occur. A third smaller depression develops behind the main sinus, below the lacrimal foramen and above P⁴.

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]. I¹ 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; *P. grangeri* 1.1 [36]) than to those of strepsirrhines which possess proportionally buccolingually much thinner I¹s (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 I¹ 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 the electronic supplementary material, note 2). The I¹ crown is not oriented

transversely to the tooth row but slightly obliquely. I² is smaller, not shovel-like as I¹, 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 C¹. An enamel ridge limits its mesiolingual edge. The canine section is huge (table 1) and oval, wider distally than anteriorly and distally truncated transversely. P² is only represented by a buccally shifted tiny root section and circular alveolus. The P³ crown preserves only a distinct lingual lobe bearing a low protocone. P⁴ and M¹ crowns are broken. The right M¹ 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. M²–M³ 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 paracone and metacone are sometimes developed on these crests and located very close to the main buccal cusps. The hypocone is, as on M¹, a small cusp emanating from the distolingual cingulum and separated from the post-protocrista 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 M¹–M² contact and determines an angle of 45–50° with the molar row. Its base is located 4 mm above the M²–M³ 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 (greater than 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 dorsoventral 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

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

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

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 *P. grangeri* DPC 1865 [43] and *A. zeuxis* (YPM 23979, CGM 40 237) [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].

(b) Ulna

NMMP 106 (figure 3 and 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 approximately 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 *Cebupithecus 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 towards the proximal end of the ulna and is more extended than in the ulnae of *Aegyptopithecus*, *Apidium* or *Cebupithecus*. 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.

3. 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 C₁, P₃–P₄ with elevated and mesially oriented preprotocrists) [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 P₃–P₄ 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. By 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 P₃–P₄, deep maxilla under the orbit, lacrimal foramen inside the orbit and spatulate upper incisors ([52]; see also the electronic supplementary material, 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 (electronic supplementary material, 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*,

Figure 4. Phylogenetic position of *Ganlea* among the primates. Strict consensus tree of three most parsimonious trees (length = 1424, consistency index = 0.3413, retention index = 0.6587). Branch colours for the main anthropoid clades denote the geographical provenance of the taxa (in red: Proteopithecidae, Parapithecoidae, Propithecidae and Oligopithecidae = Afro-Arabia; in green: Eosimiidae and Amphipithecidae = Asia; in magenta: Platyrrhini = South America). Bremer support values and bootstrap frequencies are indicated above and below the nodes, respectively. (Online version in colour.)

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] (figure 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 Palaeogene Afro-Arabian anthropoids (Propithecidae, Oligopithecidae, Proteopithecidae, Parapithecidae) and platyrrhines. This phylogenetic position for Amphipithecidae, which rules out a relationship between amphipithecids and adapiforms, is similar to those of [54,55], and with our new morphological interpretation of *Ganlea*. In addition, the two deepest divergences within total-clade Anthropoidea 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 palaeontological 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.

4. Material and methods

(a) Taxonomic attribution of the new material

The new Than-U-Daw remains were identified as an amphipithecine after comparisons with known Palaeogene anthropoids from the Pondaung Formation of Myanmar and from Afro-Arabia (electronic supplementary material, 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 M₁–M₂. The entoconid is low. The upper molars show strong resemblance to those of *Myanmarpithecus* but not to the isolated upper M¹ or M² (NMMP 75) initially assigned to *G. megacarina*. Unlike *Myanmarpithecus* and the new remains, this doubtfully attributed tooth does not bear 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, and more buccally positioned paracone and metacone.

The new mandible NMMP 101 and the holotype of *G. megacarina* NMMP 70 are nearly identical in terms of size, proportions and morphological characters. Both show hypertrophied canines, subvertical symphysis, deep jaw and similar M₂ morphology. In addition, the size and morphology of the P₃–P₄ are very close to those of NMMP 74, except for a slightly less developed distolingual crest on P₃ and a squarer outline. NMMP 101 belongs to an adult individual, judging by its completely erupted M₃. Owing to its greatly enlarged canine, NMMP 70 was considered a male individual [1]. Thus, the same sexing is proposed for NMMP 101. A body mass of approximately 2.5 kg for NMMP 101, corresponding well to the 2.4 kg mean body mass estimated for *G. megacarina* [1], is obtained by using a regression equation for anthropoids based on M₁ size [61].

(b) Micro-computed tomography-scanning and three-dimensional 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 three-dimensional 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^1 , 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^1 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 Palaeogene primates, rather than abruptly. The lower jaw was symmetrized, oriented and positioned relative to NMMP 103, keeping a coherent occlusion between lower and upper teeth, respecting the fact the lower jaw is broken near the symphysis, and leaving sufficient space for the lower incisors.

(c) 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 three 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 (electronic supplementary material, figure 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 in *G. megacarina*. This orbit diameter is proportionally small relative to tooth size and better fits with the values displayed in the diurnal primates, probably indicating a diurnal activity pattern for *Ganlea* (electronic supplementary material, figure 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 (electronic supplementary material, figure 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].

Data accessibility. The three-dimensional reconstruction of the skull of *Ganlea* based on NMMP 101, 103 and 104 and the data matrix used for the phylogenetic analysis are provided as electronic supplementary material files.

Authors' contributions. J.-J.J., D.G., Y.C. and O.C. wrote the paper. J.-J.J., Y.C. and O.C. designed research. J.-J.J., D.G., Y.C., V.L., O.C. analysed data and performed analyses. J.-J.J., C.S., D.G., Y.C., M.T.N., T.Z.O., M.M.A., K.S., M.R., V.L., A.N.S. and O.C. acquired data.

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