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Yaowalak Chaimanee, Sasa-On Khansubha, Olivier Chavasseau, Arnaud Mazurier, Jean-Jacques Jaeger. Maxilla of Siamopithecus eocaenus (Anthropoidea, Primates) from the Paleogene of Krabi, Thailand, and its taxonomic status. *Journal of Human Evolution*, 2025, 198, pp.103614. 10.1016/j.jhevol.2024.103614 . hal-04911167

HAL Id: hal-04911167

<https://hal.science/hal-04911167v1>

Submitted on 31 Jan 2025

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Maxilla of *Siamopithecus eocaenus* (Anthropoidea, Primates) from the Paleogene of Krabi, Thailand, and its taxonomic status

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Keywords: Amphipithecidae, Anthropoid, Catarrhine, Primates, Phylogenetic, Southeast Asia

Chaimanee Y, Khansubha S, Chavasseau O, Mazurier A, Jaeger J-J. 2025. Maxilla of *Siamopithecus eocaenus* (Anthropoid, Primates) from the Paleogene of Krabi, Thailand, and its taxonomic status. Journal of Human Evolution 198 (103614):

[DOI:10.1016/j.jhevol.2024.103614](https://doi.org/10.1016/j.jhevol.2024.103614)

Abstract

Detailed descriptions of the maxillae of *Siamopithecus eocaenus*, discovered from the latest Eocene/earliest Oligocene lignite mine in the Krabi basin of Peninsular Thailand are presented. They include the morphology of P³–M³, the palate, a partial orbital region, and the zygomatic root. The specimen exhibits distinctive dental features including a single-rooted P² alveolus, a protocone on P³ and P⁴, and a true hypocone on upper molars, indicating its derived anthropoid dentition. Comparative studies and virtual reconstructions of the facial anatomy reveal close affinities with diurnal anthropoids rather than the notharctid strepsirrhines. The reconstructed facial morphology of *Siamopithecus* displays a short and sub-vertically oriented face, significant orbital convergence (72.1°), and frontation (81.6°), distinguishing it from both fossil and extant strepsirrhines. Moreover, the presence of a thin bony lamina extending from the distal part of the upper preserved area of the zygomatic suggests partial or complete postorbital closure. Phylogenetic analyses suggest an affiliation with amhipithecids, but recent morphological observations challenge this, leading to the proposal of an elevated family-group ranking, Siamopithecidae. Comparison with the most primitive known Afro-Arabian propliopithecid, the Taqah propliopithecid from Oman, reveals similarities in their molar structure but differences in dental formula (retention of P2) and premolar structure. The abrupt appearance of propliopithecids in the early Oligocene of Afro-Arabia, without a local ancestor, contributes to the debate on catarrhine origins, whether from Asia or Africa. However alternative views, based on sister-group relationships with oligopithecids, support an African origin of propliopithecids from an undocumented Afro-Arabian region. This research provides new insights into the evolutionary history of early anthropoids, suggesting a complex biogeographical scenario involving both Asian and African lineages.

1. Introduction

Siamopithecus eocaenus, described by Chaimanee et al. (1997), is a large-bodied primate known exclusively from the Krabi coal mine of Peninsular Thailand, dating from the latest Eocene to the earliest Oligocene (Benammi et al., 2001). Initially, it was considered closely related to late Eocene anthropoids found in the Pondaung Formation of Myanmar, such as *Pondaungia*, *Ganlea*, and *Myanmarpithecus*, as part of the Southeast Asian Amphipithecidae (Jaeger et al., 1998, 2020; Ducrocq, 1999; Chaimanee, 2004; Marivaux et al., 2005; Beard et al., 2009; Seiffert, 2012; Chaimanee et al., 2013). However, subsequent discoveries and detailed studies have led to a reclassification of this family together with *Aseanpithecus* (Jaeger et al., 2019) into three subfamilies: Amphipithecinae (including *Pondaungia*, *Ganlea*, and *Myanmarpithecus*), Aseanpithecinae (*Aseanpithecus*), and Siamopithecinae (*Siamopithecus*) (Chaimanee et al., 2024).

The initial remains of *Siamopithecus* including a maxillary fragment bearing P^3-M^3 (TF 3635) and a mandible fragment preserving the distal part of M_1 , and M_2-M_3 (TF 3634), were described by Chaimanee et al. (1997), with subsequent studies providing further details on these specimens by Ducrocq (1999) and Chaimanee (2004). Additional discoveries include a nearly complete right mandible (TF 7624; Chaimanee et al., 2000) found in occlusion with the maxillofacial components (TF 7625). The mandible exhibits several anthropoid characters, such as a vertical symphysis and an oblique alignment of P_3 and P_4 roots. Distinctive characters also include a significant reduction of the single-rooted P_2 , an elevated corpus, and the presence of a metaconid on the lingual side of P_4 (Chaimanee et al. 2000; Chaimanee, 2004).

Virtual reconstruction analysis of the maxillofacial remains (TF 7625) conducted by Tafforeau (2004), followed by Zollikofer et al. (2009), revealed a short face and highly

convergent and frontated orbits, suggesting greater morphological resemblance to anthropoids than to any known strepsirrhines. Other cranial characters, such as the participation of the maxilla in the lower orbit margin and the absence of an external lacrimal bone, also confirmed its anthropoid affinities.

Nevertheless, several researchers have raised doubts regarding the anthropoid status of *Siamopithecus* (Godinot, 1998, 2015; Gunnell and Miller, 2001; Kirk and Simons, 2001; Gunnell et al., 2002; Kay et al., 2004). Rosenberger et al. (2011) contested the robustness of the dendrograms presented by Zollikofer et al. (2009), arguing that their broader topology contained errors and was inconsistent with well-established phylogenies. However, the phylogenetic status of amhipithecids remained still controversial due to the incompleteness and non-associated dental and postcranial remains (Ciochon et al., 2001). Some authors attributed them to adapiforms and interpreted their shared dental characters as resembling those of anthropoids through homoplasy (Ciochon and Holoyrd, 1994; Ciochon et al. 2001; Gunnell et al., 2002). Nevertheless, the subsequent discovery of cranial, dental, and postcranial remains of *Ganlea megacanina* (Dagosto et al., 2010; Marivaux et al., 2010; Jaeger et al., 2020), demonstrated that *Ganlea*, along with closely related amhipithecine genera, *Pondaungia* and *Myanmarpithecus*, represent stem anthropoids. The cranial anatomy of *Ganlea* displays several anthropoid characters, including fused frontal bones, participation of the maxilla in the lower orbit rim, and an internal lacrimal bone with a sub-vertical lacrimal canal, although *Ganlea* apparently lacks postorbital closure. This phylogenetic interpretation was extended to all Myanmar amhipithecines due to their close phylogenetic relationships. The discovery of the *Ganlea* cranial remain allowed for a precise comparison with *Siamopithecus*, suggesting that in addition to numerous shared dental and cranial anthropoid characters (as presented in Table 3 of Zollikofer et al., 2009), *Siamopithecus* differs from *Ganlea* in most likely possessing partial or complete postorbital closure (Chaimanee et al.,

2024). This, along with differences in dental characters from the Myanmar amhipithecines, raises new questions regarding its phylogenetic position within anthropoid primates and its precise affinities with the Myanmar amhipithecines.

This study aims to provide a comprehensive description and comparative analysis of *Siamopithecus maxillae*, shedding light on its phylogenetic relationships within Asian anthropoid primates and contributing to our understanding of primate diversity during the Paleogene.

2. Materials and methods

2.1. Locality and age

The fossil described here (TF 7625) was recovered from the main lignite bed of the Bang Mark pit, the same layer as the holotype (TF 3635; Chaimanee et al., 1997). These coal pits were developed by the Electricity Generating Authority of Thailand (EGAT), and extend along a 5 km long NNW–SSE axis (Udomkan et al., 2003). Numerous fossils, including large mammals, turtles, and crocodile remains have been discovered from the main lignite bed of the Bang Mark, Wai Lek, and Bang Pu Dam pits (Chaimanee, 2004; Ducrocq et al., 2021) (Fig. 1). The fossil assemblages found in these three coal pits are considered contemporaneous (Ducrocq et al., 1995, 2021). The composition of this fauna and the reverse magnetic polarity (Chron 13r) observed within the fossiliferous sequence indicate an age range spanning from the latest Eocene to the earliest Oligocene, as Chron C13r corresponds to the Eocene/Oligocene transition (EOT) occurring between 35–33 Ma (Benammi et al., 2001). These diverse faunas inhabited a forested area under a tropical climate (Ducrocq et al. 1995).

2.2. Institutional abbreviations

DPC = Duke Primate Center; NMMP = National Museum of Myanmar-Primates; TF = Thai Fossil, the Department of Mineral Resources, Thailand; TQ = Taqah, Oman.

2.3. Measurements

Dental measurements were taken on the 3D digital models, using Avizo 8.

Measurements of mesiodistal length (MD) correspond to the maximum values, and buccolingual width (BL) was measured perpendicular to mesiodistal length taken on upper premolars and molars (Table 1).

2.4. Micro-computed tomography scan imaging

TF 7625 was scanned using an RX-solutions EasyTom XL Duo microtomograph (platform PLATINA of IC2MP, Université de Poitiers, France), which combines a sealed microfocus x-ray source with a flat panel detector. The scanning was conducted according to the following parameters: 4320 projections over 3 turns, a frame rate of 11.5 fps, a frame averaging of 20, a voltage of 90kV, and a current of 240 µA. Reconstruction of the 16-bit TIFF slices stack was performed with the XAct software package (RX-solutions) at a voxel size of 25.25µm. Surface visualization and manipulation were performed with Avizo 3D 2023.2 (Thermo Fisher Scientific, Waltham, Massachusetts, USA) (Figs. 2, 3).

2.5. Estimation of orbit size

The orbit diameter of TF 7625 was estimated using the methodology of Heesy and Ross (2001). This methodology involves using three points positioned along the orbit plane (X, Y, Z) to calculate the orbit radius. The original methodology suggests selecting points along the orbit by using the inferior-most point of the orbit (Y) and two other points (X and Z) equally distant from Y. However, due to limitations in accessing the preserved portion of the orbit in TF 7625, this positioning of points was not feasible. Instead, X and Z were placed at the two extremities of the preserved rim to maximize the length of the orbit rim utilized. The selection of points and the extraction of their coordinates were performed using Avizo 8 software

(ThermoFisher Scientific), which rendered a surface of the maxilla generated from CT-scan data. The formula used to calculate the orbit diameter (D) was $D = 2OY = (WY^2 + WZ^2)/WY$, where O represents the center of the orbit, and W is the midpoint of the XZ segment.

2.6. Body weight estimation

We have estimated the body weight of *Siamopithecus* based on the maxilla TF 7625. We used M^2 , due to the variability observed in M^1 . We applied the regression equations provided by Egi et al. (2004), which were based on the tooth crown area (mesiodistal length, MD, multiplied by buccolingual width, BL). The calculation for body mass estimated was derived from anthropoid models.

2.7. Phylogenetic analysis

The phylogenetic position of *Siamopithecus* was analyzed using PAUP 4.3.99.169.0 (Swofford, 2003). Three maximum parsimony analyses with heuristic search were performed using three different taxon-character matrices based on those of Seiffert et al. (2018), Jaeger et al. (2019), and Jaeger et al. (2020). For full methodological details, see the text and data matrices in the Supplemental Online Material.

3. Systematic Paleontology

Class Mammalia Linnaeus, 1758

Order Primates Linnaeus, 1758

Suborder Haplorhini Pocock, 1918

Infraorder Anthropoidea Mivart, 1864

Family Siamopithecidae Beard et al., 2009 (new rank)

Genus *Siamopithecus* Chaimanee et al., 1997

Type species *Siamopithecus eocaenus* Chaimanee et al., 1997

Siamopithecus eocaenus

3.1. Description

TF 7625 consists of both the left and right maxillae, bearing teeth from P³–M³ (Figs. 2, 3), found associated with the right lower jaw (TF 7624) in occlusion. The left maxilla fragment is more complete and includes a part of the zygomatic bone. It bears the left partial orbital region, the root of the zygomatic arch, a segment of the palate, and the canine and P² alveoli (Fig. 2). The premolars and molars on the left maxilla exhibit heavy wear (Fig. 2D), more pronounced than those observed on the right maxilla, indicating potential asymmetrical chewing patterns (Tafforeau, 2004). The orbital floor, formed by the zygomatic and frontal processes of the maxilla, is also discernible. Post-fossilization damage is evident along the zygomaxillary suture. The palatine is incomplete, missing both proximal and distal parts (Fig. 2D). The right maxilla is less complete and slightly deformed (Fig. 3). The zygomatic bone is broken at its base. Its canine and P² alveoli are also present, and its premolars and molars exhibit less wear than those on the left. In lateral view, the lower part of the premaxilla/maxilla suture is visible and vertically oriented. Although it could be interpreted as a crack, its position and orientation in front of the canine strongly suggest that it corresponds to the premaxilla/maxilla suture. Similar to the left maxilla, the right maxilla also displays the orbital floor. Both fragments display a thick maxillary bone in the vertical section (~14.5 mm), consisting of alveolar bone containing long premolars and molar roots. The dental arcades are curved and parabolic in shape (Zollikofer et al., 2009). The enamel of the teeth

appears relatively thin and prismatic, lacking Hunter-Schreger bands (Tafforeau, 2004).

Detailed measurements are provided in Tables 1 and 2.

Dentition TF 7625 preserves P³–M³ on both the left and right sides (Figs. 2D, 3D). The occlusal surface of the premolars and molars displays a pronounced lingual inclination, with the buccal walls being more elevated than the lingual ones. Moderate wear is observed on the teeth on the right maxilla, whereas those on the left display heavy wear. Additionally, root alveoli of the left and right canine and P² can be observed (Figs. 2D, 3D). The anterior part of the premaxilla, including the incisors, is missing. However, an estimated space suggests a relatively broad area for the incisors, confirmed by the reconstruction of the lower jaws by Tafforeau (2004) and Zollikofer et al. (2009).

Canines Although not preserved, the large root alveoli are present, measuring approximately 7 mm in mesiodistal length and 6 mm in labiolingual width (Fig. 2D). The canines of *Siamopithecus* have a broadly oval cross-section, with a mesiodistal to labiolingual ratio of approximately 1.16, similar to other primates such as *Bahinia* (1.13; Jaeger et al., 1999), *Pondaungia* (1.21; Shigehara et al., 2002), extant *Tarsius*, platyrhines, notharctines, and Fayum anthropoids (e.g., *Aegyptopithecus* 1.19; Kay et al., 1981). This configuration differs from adapines and lemuriformes, which typically have more buccolingually compressed canines, except for *Adapis magnus*, which has a ratio of 1.28 (Gingerich and Martin, 1981).

Premolars There are three premolars. P² has lost its crown, leaving a small, rounded alveolus positioned more buccally than other premolars. Judging from the size of its alveolus, P² must have been greatly reduced and was probably a peg-like tooth. P³ is smaller compared to P⁴, both displaying triangular outlines in occlusal view. The mesiodistal length on the buccal margin is longer than on the lingual margin. The protocone of P³ is broken, but it is visible on the right tooth (Fig. 4A), and on the holotype TF 3635 (Fig. 4B), in which it is small and low. Both teeth are bicuspid with a well-developed paracone, which is higher and larger than the

protocone. However, P^4 has a larger protocone than P^3 . Neither premolar possesses a hypocone, metacone, or conules. The lingual part of the tooth is bordered by the mesial and distal cingula, with a short mesial cingulum present. Neither premolar possesses buccal nor lingual cingulum. P^3 and P^4 have three roots, two buccal and one lingual. The mesiodistal lengths of P^{3-4} represent approximately 35% of the P^3-M^3 length.

Molars The molars decrease in size from M^1 to M^3 . These upper molars are wide buccolingually with well-developed, strongly slanted buccal and lingual walls. M^1 and M^2 display a trapezoidal occlusal outline, whereas M^3 presents a triangular outline. Each molar has four distinct cusps, with the buccal cusps being larger and higher than the lingual cusps. There is no trace of buccal and lingual cingula. The crown height is maximum on M^1 , gradually decreasing on M^2 and M^3 . The upper molars have three roots, two buccal and one lingual.

M^1 is the largest tooth with prominent buccal cusps (paracone and metacone) that are nearly equal in size, connected by short postparacrista and premetacrista. The parastyle and metastyle are weakly developed with a shallow notch in the buccal wall. A hypoparacrista connects the paracone to the protocone, while the crista obliqua connected the metacone to the protocone, forming a small trigone basin. Although the protocone and hypocone are rather worn, the hypocone appears slightly smaller and lower than the protocone. It is clearly derived from the distal cingulum as on *Ganlea* and its interpretation as a displaced metaconule (Coster et al., 2013) is therefore refuted. The preprotocrista extends from the protocone and connects to the preparacrista at a parastyle, creating a small mesial fovea. Additionally, a short mesial cingulum extends from the parastyle to the mesiolingual wall of the protocone. A distal cingulum connects the hypocone to the metastyle.

M^2 displays a molar structure similar to M^1 , but with a smaller and lower metacone, positioned more lingually compared to the paracone. This result makes an oblique orientation

of the buccal wall. The buccal wall displays a shallow notch. A crista obliqua connects the metacone to the protocone, unlike M^2 of the holotype TF 3635, where a crista obliqua connects the metacone to the hypocone (Fig. 4A, B). However, this unique character found in TF 3635 is likely attributed to individual variation. Due to tooth wear, the cusplet initially described as a duplicated protocone (Chaimanee, 2004) cannot be observed as on the holotype TF3635. The enamel on the lingual wall shows a wrinkled appearance, and there is a mesial cingulum and a trace of distal cingulum.

M^3 displays a triangular outline and a highly oblique buccal wall, resulting from a well-developed protocone combined with reduced metacone and hypocone. The paracone is large and exhibits a distinct hypoparacrista. Enamel wrinkles are observed on the lingual wall of M^3 , similar to M^2 , potentially indicating a diminishing lingual cingulum. Ducrocq (1999) previously noted a fragment of M^3 on the holotype TF 3635 as unreduced and considered it a primitive characteristic. However, in this new specimen, M^3 is a complete tooth and appears to exhibit a significant reduction.

Palate and dental arcade The palate of TF 7625 is incomplete, missing its distal part, and is relatively shallow and short compared to its width (Figs. 2D, 3D). The anterior segment is broken at the level of the anterior palatine foramen. The distal end of the anterior palatine foramen is visible, suggesting a short length, reaching the level of the mesial part of the canine. Due to the displacement and lingual bend of the maxillae, a symmetric μ CT image of the right maxilla was used to reconstruct the horizontal palate, revealing a parabolic shape of the dental arcades (Tafforeau, 2004; Zollikofer et al., 2009) (Fig. 5A). Measurements of the distances between the tooth rows were obtained from this μ CT-reconstruction. The dental arcade exhibits a minimum width across the buccal points of P^3 (~ 30.5 mm) and a maximum width across the buccal points of M^2 (~ 42.2 mm). The attachment area for the tendon of the

superficial masseter muscle is well developed and located between M¹ and M². The robust root of the zygomatic process begins at the level of M¹.

Siamopithecus displays a unique combination of characteristics, including a notably short muzzle and strongly parabolic tooth rows. Anteriorly, extending to the distal part of P³, the outer walls of the premaxilla/maxilla bones are parallel but gradually diverge and extend laterally, reaching the root of the zygomatic arch.

Facial morphology On the left maxilla, notable features include a prominent portion of the zygomatic bone, found attached to the maxilla in the current position. The relatively short muzzle suggests a sub-vertical orientation of the face, with a pronounced frontated orbit (Fig. 5E). The reconstructed lower jaw confirms the short muzzle. The left maxilla reveals a lower margin of the left orbit, the broad root of the zygomatic (15.0 mm), and its ramus. The maxilla contributes to the lower rim of the orbit, a consistent trait among anthropoids. The orbit is positioned anteriorly, slightly above M¹, indicating a nearly vertical orientation based on the alignment of its lateral rim. The lateral edge of the orbit may display a slight forward angle, possibly influenced by postmortem deformation during fossilization, which might have increased the observed frontation angle.

The zygomatic is wide at its base with a thin posterior lamina, extending from its base to its preserved apex. This thin posterior lamina is oriented internally and is broken, preserved for about 1 mm at the base of the zygomatic and up to 3 mm at its medial part. In lingual view, a robust, vertical postorbital bar extends distally, featuring a thin posterior lamina separated by a small groove, indicating incipient or complete postorbital closure (Fig. 2F), a characteristic of anthropoids (Cartmill, 1980; Deleon et al., 2016). Near the mesial end of the maxilla, at the lower orbit rim, a small infraorbital foramen is observable. In lateral view, the dental arcade displays a convex shape, with the highest point located on the buccal wall of M¹. The zygomatic-maxillary suture is identified by a fracture zone extending obliquely from

the base of the orbit to the zygomatic point.

In the frontal view, the left maxillary fragment reveals the anterior part of the maxilla, extending from the mesial anterior extremity of the orbital floor, curving toward the interorbital wall (Fig. 2A). It is broken at a point likely corresponding to the suture with the lacrimal bone, suggesting an internal orbit position for the lacrimal bone, similar to that observed in *Ganlea* (NMMP103). Upon symmetrization, a relatively broad nasal opening is apparent, wider at its inferior level than at its superior level (Tafforeau, 2004) (Fig. 5D).

The right maxilla is less complete compared to the left (Fig. 3). It is incomplete both at its mesial extremity and at its upper range. The orbital region has poor preservation, with only a short segment of its lower lateral rim remaining. The sub-vertical orientation of the zygomatic-maxilla suture line appears oblique, potentially due to a single fracture induced during the fossilization process. The right maxillary fragment preserves the lower part of the zygomatic, which forms the lateral boundary of the orbital cavity. This fragment illustrates the involvement of the maxilla in forming the lower margin of the orbital cavity, a common trait among anthropoids. At the anterior section of the lower orbital margin, there is a break that intersects a small infraorbital foramen, partially preserved in its lower half.

Orbital floor The preservation of the left orbital floor is better than that of the right, and the following description is based on its characters (Fig. 2C). The surface displays significant irregularities, making it challenging to accurately assess the impact of post-mortem deformation during fossilization. Primarily, its maxillary bone envelops long premolar and molar roots encased in cancellous bone. This distinctive thickness distinguishes it from strepsirrhines and stands as a defining feature of anthropoids. Furthermore, it is extended distally, forming a substantial surface, a feature absent in strepsirrhines (Shigehara et al., 2002). Towards the lingual aspect and at a lower elevation, an irregular surface emerges,

featuring prominent apices of the molar roots above the surface. Notably, there is an absence of a parzygomatic groove along the base of the postorbital bar.

Orbital size The estimation of orbital size is based on the left maxilla TF 7625, which exhibits better preservation of orbital anatomy compared to the right side. Approximately 18.0 mm of the lower and lateral parts of the orbit rim are preserved on the left maxilla. This length of the preserved orbit rim is sufficient for a reliable estimate of the orbit diameter (Heesy and Ross, 2001). Although the orbit rim is slightly broken in the central part of the preserved portion, the associated missing part and displacement of the rim are minor and thus considered negligible.

An orbit diameter of approximately 15.0 mm was determined for *Siamopithecus*. Relative to the length of its M¹, the estimated orbit diameter of *Siamopithecus* is proportionally small compared to tooth size, confidently indicating a diurnal activity pattern for this anthropoid primate (Fig. 6). This result is consistent with that of Zollikofer et al. (2009), based on virtual reconstructions of TF 7625. These authors compared the bi-orbital width of *Siamopithecus* with two skull measurements (C–M³ length, width between the two M¹s) and inferred a diurnal activity pattern for this anthropoid based on the obtained small relative orbit size.

Orbital frontation According to the virtual reconstruction conducted by Zollikofer et al., (2009), *Siamopithecus* displayed a high frontation angle of 81.6°. It should be noted that this value may be slightly overestimated due to the slight forward orientation of the zygomatic caused by deformation during fossilization. A more accurate estimate might fall within the range of 75°–80°. However, it remains high in any case, indicating a short and sub-vertical facial structure positioned under the orbits.

Orbital convergence According to the virtual reconstruction by Zollikofer et al. (2009), *Siamopithecus* displays an average orbital convergence of 72.1°. Although the orbital morphology of *Siamopithecus* is only partially preserved, it suggests a moderate-size orbit relative to its gnathic dimensions, displaying more convergence and frontation compared to other anthropoids. When considering all available data, including orbit diameter, frontation, and convergence values, they indicate a considerably derived stage of crown anthropoid evolution. This interpretation is further supported by the inferred presence of complete or partial postorbital closure in this fossil, as indicated by the remnants of a thin posterior lamina of the zygomatic.

Mandible The mandible of *Siamopithecus* (TF 7624) has been previously described by Chaimanee et al. (2000) and Chaimanee (2004), and virtually reconstructed by Tafforeau, (2004), and Zollikofer et al. (2009) (Figs. 5B, C and 7). It is massive and strongly elevated with a nearly vertical (70°) but unfused symphysis (Fig. 7A, B). The height of the symphysis (infradental-gnathion) measures 25.7 mm (Zollikofer et al., 2009). The ramus is missing, being broken 1 cm above the occlusal surface of M₃. Its anterior part lies behind the distal end of the M₃ talonid, resulting in a short retromolar space equivalent to the length of M₂.

The canine is robust, with its apex noticeably higher than that of P₃, and it has an oval-shaped crown outline. It displays a clear wear facet on its distolingual crown made by a strong upper canine. P₂ is broken, showing only a small root, indicating a reduced crown size. P₃ is unicuspide and mesiodistally longer than wide, unlike those of *Pondaungia* and *Ganlea*, which are nearly as wide as long. Similarly, P₄ is longer than wide, with a small metaconid slightly distal to the protoconid, and its talonid lacks significant development, reduced to a tiny hypoconid cusp. The molars closely resemble those of the paratype (TF 3634) and display more worn and less distinct characters (Fig. 7D, E). They are characterized by the absence of paraconids which are replaced by a preprotocristid that divides an anterior fovea

while connecting to the metaconid. Similar to P_3 and P_4 , their buccal walls are slightly slanted and lack a buccal cingulid. All three molars, like those of the paratype, are waisted between trigonid and talonid. The hypoconulid is present on all molars, closer to the hypoconid than to the entoconid, and more strongly developed on the paratype M_1 (Fig. 7D). On M_3 , it represents the largest cusps, situated medially. In TF 3634 M_3 , which is only slightly worn, numerous small enamel wrinkling crests develop within the basins.

The reconstruction of the maxillae and the facial features (TF 7625) by Tafforeau (2004) also allowed for the reconstruction of the occlusion between the upper and lower dentitions (Fig. 5). This virtual reconstruction provided visualization of the arrangement of the lower dental rows (TF 7624). These rows display a curved shape, widest around the M_2 metaconids, and narrowing towards the area of the canine (Fig. 5B, C).

Body weight estimation of *Siamopithecus* We estimated the body weight of *Siamopithecus* by examining the maxilla of TF 7625. We employed the surface area of M^2 (mesiodistal length x buccolingual width), due to the variability observed in M^1 within this specimen and applied regression equations provided by Egi et al. (2004). We obtained a predicted body mass for TF 7625 of 7.4 kg. Hence, *Siamopithecus* would have been approximately similar in size to the male white-cheeked gibbon, *Nomascus leucogenys* (Geissmann, 1993).

3.2. Comparison

Siamopithecus displays several anthropoid characters on its upper molars, such as a single-rooted P^2 , bicuspid premolars, and molars with an almost continuous crista obliqua. Its teeth have a greater buccolingual width compared to mesiodistal length, an unwaisted occlusal outline, a short trigon basin, a hypocone derived from the cingulum, and a well-developed hypoparacrista. In the virtual reconstructions, the upper and lower tooth rows of

Siamopithecus present a distinctive parabolic shape unique to this species (Zollikoffer et al., 2009).

Amphipithecids *Pondaungia* reveals some similarities in dentition with *Siamopithecus*, such as a connecting crest between the metacone and the hypocone, although this feature is not consistently present in all upper molars of *Siamopithecus* (exceptional on M² of TF 3635). However, there are several distinguishing differences. *Pondaungia* exhibits more pronounced buccolingual development in its premolars, more bunodont molars with less sharp cristae and small vestigial conules (e.g., NMMP 92; Chaimanee et al., 2024), features that are absent in *Siamopithecus*. Additionally, *Pondaungia* has well-developed lingual and buccal cingula on M¹ and M², and M¹ is smaller than M², unlike *Siamopithecus*.

A left maxilla fragment with P³⁻⁴ and M² of *Pondaungia* (NMMP 87; Chaimanee et al., 2024) provides valuable information for comparison with *Siamopithecus*. It exhibits a distinct infraorbital foramen located above P⁴, whereas in *Siamopithecus*, its position is more anteriorly, above P³. The external surface of *Pondaungia*'s maxilla is smooth without a post-canine fossa. However, the tooth row forms a parabolic shape similar to that of *Siamopithecus*. *Pondaungia*'s orbital floor is flat and inclined medially. The lingual roots of M¹ and M² are salient on the orbital floor but to a lesser degree than those of *Siamopithecus*. In internal view, NMMP 87 displays a notably large, deep, and concave depression, indicating a massive maxillary sinus. This sinus is not observable in *Siamopithecus*. Other maxillary fragments of *Pondaungia* (NMMP 12 and NMMP 18) also display a significant maxillary sinus (Takai and Shigehara, 2004). However, unlike the two other *Pondaungia* maxillae, there is no parzygomatic groove present in NMMP 87.

Ganlea exhibits more primitive dental features than *Pondaungia* (Beard et al., 2009; Jaeger et al., 2020). It has a smaller M¹ compared to M², a prominent hypocone derived from the distolingual cingulum, a small paraconule, and a complete lingual cingulum on its molars.

Its crista obliqua joins the protocone more distally than in *Siamopithecus*. However, unlike in one M² of *Siamopithecus* and most upper molars of *Pondaungia*, it does not connect to the hypocone. *Myanmarpithecus* (Takai et al., 2001) also has molars displaying the same organization as those of *Ganlea*.

A cranial fragment of *Ganlea* (NMMP103; Jaeger et al., 2020) provides valuable insights for comparison with *Siamopithecus*. The *Ganlea* palate shows divergent tooth rows. It also exhibits a high estimated orbit convergence (72.2°), similar to that of *Siamopithecus* (72.1°). The orbit size of *Ganlea* is estimated to be 15.56 mm in diameter (Jaeger et al., 2020) and 15.0 mm in *Siamopithecus*. *Ganlea* has an elongated rostrum that accommodates its very large upper canines, contrasting with *Siamopithecus*. The external surface of the *Ganlea* maxilla is not smooth and displays a post-canine fossa, which may be related to the enlarged canines in *Ganlea*. The frontal bone in *Ganlea* indicates an absence of postorbital closure. The section of the base of its postorbital bar is triangular and mesiodistally short, unlike the flattened and extended posterior lamina seen in *Siamopithecus*, which suggests a partial or complete postorbital closure in the latter. *Ganlea* has an orbital floor that differs noticeably, being flat, shorter and inclined medially, similar to those of *Pondaungia*. Unlike *Siamopithecus*, there is no observable prominent root tip on the *Ganlea* orbital floor.

The similarities between *Ganlea* (NMMP 103) and *Pondaungia* (NMMP 87) align with their close phylogenetic relationships, reflecting common anatomical features among Myanmar Eocene anthropoids. These include short faces and relatively thick maxillae, characters also shared by other Asian anthropoids like *Bahinia*. However, *Siamopithecus* exhibits distinct anatomical features not observed in other known Asian anthropoids. For instance, its molars have root tips protruding noticeably on the orbital floor (Fig. 2C), a feature less prominent in *Ganlea* and *Pondaungia*. Additionally, *Siamopithecus* displays a thin bony lamina on the distal part of its zygomatic bone, indicating the potential presence of

a partial or complete postorbital wall, which is not observed in other Asian Eocene anthropoids. There is no indication of postorbital closure in *Pondaungia*. However, given its close phylogenetic relationships with *Ganlea*, an optimized inference would support a lack of closure as in *Ganlea*.

Aseanpithecus displays several differences. These include a more extensive buccolingual extension of premolars, the presence of both buccal and lingual cingula surrounding the molars, less inclined molar walls, broader and larger trigons, and lack of hypocone. *Aseanpithecus* has been identified as an Asian anthropoid that shares a striking resemblance in its molar anatomy with African oligopithecids (Jaeger et al., 2019).

Propliopithecids The upper molars of Taqah propliopithecid (TQ3), from the early Oligocene of Taqah, Oman, initially described as *Moeripithecus markgrafi* by Thomas et al. (1991), exhibit both similarities and distinctions compared to those of *Siamopithecus*. Significant resemblances include the larger size of M¹ compared to M², reduced bunodonty, conule absence, strong crista obliqua, and weak hypocones. Differences include *Siamopithecus* lacking a prominent lingual cingulum and having more slanted cups. TQ3 displays less developed and elevated hypocones, lacks connection crests between the protocone and hypocone, and has a strong lingual cingulum with a pericone on its molars, contrasting with *Siamopithecus*. Additional differences are observed in premolar morphology. TQ3 lacks P² and displays an enlarged P³, with greater buccolingual extension, with robust protocones. Both P³ and P⁴ exhibit transverse crests connecting the protocone to the paracone, forming anterior, median, and posterior fovea, a feature not found in *Siamopithecus*. Furthermore, TQ3 develops lingual cingula, which are absent in *Siamopithecus*. Notably, P³ is larger than P⁴ in TQ3, contrary to *Siamopithecus*, suggesting a potentially more primitive premolar development for *Siamopithecus*.

The lower tooth row shares many morphological characters with those of the Taqah propliopithecid (TQ4). The molar structure is similar, with differences including the less central position of the hypoconulids, their smaller size on M₂, the absence of buccal cingulids, the less bunodont cusps, and the larger development of the M₃ hypoconulid in *Siamopithecus*. However, as with the upper dentition, the premolars exhibit more significant differences. The P₃ of TQ4 is notably larger than P₄, and its P₄ has a well-defined talonid basin and a stronger metaconid, positioned at the same level as the protoconid rather than distal to it as in *Siamopithecus*. This character has been cited as a synapomorphy of crown anthropoids and is lacking in *Siamopithecus*.

Taqah propliopithecid (TQ3 and TQ4) is generally recognized as the basal sister group of the more derived Fayum propliopithecids (Seiffert, 2012), but its peculiar characters, such as the small size of its molar hypocones, render its phylogenetic position uncertain. However, the resemblance of its dentition to that of *Siamopithecus* raises interesting questions relative to their phylogenetic relationships. *Siamopithecus* appears by some of its characters to be more primitive (premolar structure and retention of P2) and by others more specialized (inclined molar walls and crest linking protocone and hypocone).

Aegyptopithecus is a highly derived anthropoid with a closed postorbital wall. *Siamopithecus* differs from it in several significant aspects. The tooth rows of *Siamopithecus* form a parabolic shape rather than diverging posteriorly, as in *Aegyptopithecus* (Simons, 1987; Leakey et al., 1991). *Siamopithecus* displays a shorter muzzle compared to that of *Aegyptopithecus* (Leakey et al., 1991). *Siamopithecus* exhibits higher frontation (81.2° in *Siamopithecus*; Zollikofer et al., 2009; 69° in *Aegyptopithecus*; Simons, 2004) but a lesser convergence angle (72.1° x 2 in *Siamopithecus*; Zollikofer et al., 2009; 183–192° in *Aegyptopithecus*; Simons, 2008) and displays a smaller orbit (15.0 mm) compared to *Aegyptopithecus* (16.9–18.9 mm; Kay and Kirk, 2000). Another distinguished feature is the

anterior location of the contact point between the zygomatic and maxillary bone on the lower orbit rim in *Siamopithecus*, indicating more anteriorly positioned orbits compared to *Aegyptopithecus*. Furthermore, the zygomatic branch of *Siamopithecus* begins at the level of M¹, whereas in *Aegyptopithecus*, the orbit is located more posteriorly above M², and the elevation of the maxilla is higher (Simons, 1987). The ethmoid region is not preserved in *Siamopithecus* and therefore cannot be compared to that of *Aegyptopithecus* (Rossie et al., 2002; Rossie, 2005).

Pliopithecids Few pliopithecid crania are preserved. Among them, *Epipliopithecus vindobonensis* (Individual II) represents a derived Middle Miocene representative of the pliopithecids (Zapfe, 1960). This specimen shows similarities with *Siamopithecus*, such as orbit size and anterior position, a vertically oriented face, high frontation and convergence values, a short muzzle, a wide base of the zygomatic root, and comparable orbital floor organization. Despite these similarities, the presence of P^{2/2} and the absence of shared derived dental characters does not allow us to consider *Siamopithecus* as a pliopithecid.

Parapithecids The two parapithecid crania from Fayum deposits, *Parapithecus* (DPC 18651) and *Apidium* (DPC 9867), exhibit complete postorbital closure and possess numerous anatomical differences that distinguish them from *Siamopithecus*. For instance, their facial structure is not as short, and their frontation and convergence angles are notably lower. The convergence angle of *Parapithecus* (99-106°) and *Apidium* (105-113°) (Simons, 2008) is less than that of *Siamopithecus* (72.1° x 2 by Zollikofer et al., 2009). Similarly, the frontation angle of *Parapithecus* is 62° (Simons, 2004), lower than that observed in *Siamopithecus* (81.6°; Zollikofer et al., 2009). Additionally, both parapithecids display a prominent zygomasseteric foramen, a characteristic not observed in *Siamopithecus*. In occlusal view, their dental arcade is less parabolic, and the palate length/breath index is considerably larger compared to *Siamopithecus*.

In summary, *Siamopithecus* displays a combination of primitive and derived characters not commonly observed in other anthropoids. Primitive traits include the absence of conules, the presence of P²/₂, and the small sizes of P³ and its protocone. Conversely, more derived features include the inclined orientation of the buccal and lingual walls on the upper molars, the presence of a crest formed by a portion of the postprotocrista and the prehypocrista connecting the two lingual cusps, and the absence of both buccal and lingual cingula on premolars and molars. These characters, associated with their unique facial and orbital morphology, highlight its distinctiveness among anthropoids.

3.3. Phylogenetic affinities

Numerous phylogenetic analyses have suggested that *Siamopithecus* is an amhipithecid, either as a sister group to the Myanmar amhipithecids (*Pondaungia*, *Myanmarpithecus*, and *Ganlea*) or phylogenetically close to this clade (Kay et al., 2004; Seiffert et al. 2005, 2018; Beard et al. 2009; Chaimanee et al., 2012, 2013; Marivaux et al. 2013, 2023; Jaeger et al. 2019). Based on their phylogenetic results and the greater shared morphological features within the Myanmar amhipithecids, Beard et al. (2009) proposed classifying *Siamopithecus* into the subfamily Siamopithecinae and the three Myanmar amhipithecids (*Pondaungia*, *Myanmarpithecus*, and *Ganlea*) into the subfamily Amhipithecinae. However, with the recovery of more complete remains of the amhipithecine *Ganlea* (Jaeger et al., 2020), closer comparisons have revealed numerous differences between *Ganlea* and *Siamopithecus*. The main differences concern molar structure, premolar organization, snout length, and the presence of a postorbital closure. Since no postorbital closure is present in *Ganlea*, the hypothesis of a postorbital reopening among amhipithecines seems very unlikely, as such an evolutionary reversal has never been documented among primates.

Therefore, we reinvestigated the phylogenetic position of *Siamopithecus* using maximum parsimony analysis with PAUP 4.3.99.169.0 (Swofford, 2003) with three different data matrices. In our first analysis, we employed a matrix including 117 taxa and 394 morphological characters based on the data matrix of Seiffert et al. (2018). Conducting a heuristic search in PAUP using the original settings of Seiffert et al. (2018) (utilizing a backbone tree derived from the molecular phylogeny of extant strepsirrhines, weighted characters, and 4 characters with irreversible states), we obtained 20 most parsimonious trees (length = 4727.5, CI = 0.1518, RI = 0.5590). In the strict consensus tree (Fig. 8), *Siamopithecus* is placed within the amhipithecids and is a sister group to the amhipithecines. The amhipithecids are positioned as a sister group to the crown-anthropoids.

In the second analysis, we used the data matrix from Jaeger et al. (2020), enhanced with the new characters for *Siamopithecus*. This data matrix includes 38 taxa and 326 morphological characters (both dental and osteological). Five most parsimonious trees (length = 1425 steps, CI = 0.3411, RI = 0.5581) were obtained after a heuristic search (random addition of taxa, 1000 replications, unweighted characters, no topological constraint). *Siamopithecus* is placed within the amhipithecid clade (see Supplemental Online Material; Fig. S1). In the majority-rule consensus tree, the amhipithecids form a clade of stem anthropoids, similar to the results of Jaeger et al. (2020).

In the third analysis, the data matrix, derived from those of Jaeger et al. (2019, 2020), included a broader sample of fossil anthropoids (45 taxa in total) and a similar set of characters. Twelve most parsimonious trees (length = 1514 steps, CI = 0.3210, RI = 0.5554) were obtained after a heuristic search with the same parameters as in the first analysis. In the strict consensus tree (see Supplemental Online Material; Fig. S2), *Siamopithecus* is part of a poorly resolved clade that included catarrhines, platyrhines, parapithecoidea, oligopithecoidea

and Asian anthropoids commonly classified as amhipithecids (*Pondaungia*, *Ganlea*, *Myanmarpithecus*, *Krabia*). The amhipithecids are not monophyletic in this tree. However, in the 50% majority consensus tree, *Siamopithecus* is again grouped with the amhipithecids clade together with *Pondaungia*, *Ganlea*, *Myanmarpithecus*, and *Krabia*, and amhipithecids are reconstructed as crown anthropoids.

These results are generally inconsistent with our morphological analysis of the skull and dentition of *Siamopithecus*, which suggests that amhipithecids are likely not monophyletic. All of these results also indicate a homoplastic evolution of the postorbital closure in anthropoids, presenting an unparsimonious scenario for this key morphological feature. Additionally, we observe that the phylogenetic position of the amhipithecids varies in our results, similar to previous phylogenetic analyses (see e.g., Seiffert et al. 2005, Beard et al. 2009, Jaeger et al. 2020). The results from the third analysis contradict those of Jaeger et al. (2020), which suggested that the amhipithecids were stem anthropoids with a more basal position than the advanced stem anthropoids (such as parapithecidoids). The results from the first analysis are also improbable, as they imply a loss of the postorbital closure in the amhipithecines.

We believe that the large number of derived (and possibly homoplastic) dental traits observed in amhipithecids compared to cranial/postcranial traits creates a bias in the analysis. Aside from *Aseanpithecus*, only *Ganlea* and *Siamopithecus* are the Paleogene Asian anthropoids with available non-dental-gnathic features, and *Ganlea* is the only taxon with firmly associated postcranial material. Although important, the new cranial features documented for *Siamopithecus* constitute a small fraction of the total number of characters for this anthropoid (less than 2% in the first analysis, and less than 3% in the second and third analyses). As a result, the retained topologies for anthropoids remain inadequately constrained

by the fossil record. Therefore, we believe that our parsimony analyses do not provide reliable affinities for *Siamopithecus*.

4. Discussion and conclusion

The reexamination of *Siamopithecus* maxilla and facial fragment confirms its classification as an anthropoid, supported by numerous cranial and dental characters previously documented by Zollikofer et al. (2009). Newly identified characters, particularly the potential presence of partial or complete postorbital closure, necessitate a reassessment of its phylogenetic affinities. Although its status as an anthropoid is clear, in opposition to Rosenberger et al. (2011) interpretation, its precise phylogenetic position within the anthropoids remains unsolved. Comparative analysis with recently discovered cranial fragments of amhipithecines, particularly *Ganlea* (NMMP103) and *Pondaungia* (NMMP87), reveals notable distinctions despite some shared dental features. These similarities include the connection between the protocone and hypocone on upper molars, weakly developed or absent conules, enamel wrinkling, and thin enamel without Hunter-Schreger bands. Both *Ganlea* and *Pondaungia* also exhibit an elevated mandibular corpus, indicative of a hard-food diet (Smith, 1983; Ramdaswan et al., 2010).

The presence of partial or complete postorbital closure in *Siamopithecus* excluded it from being classified among the amhipithecines. The absence of postorbital closure is a distinguishing feature of amhipithecines, known from *Ganlea* and inferred for other amhipithecines through phylogenetic optimization (Chaimanee et al., 2024). *Siamopithecus* also lacks distinctive shared derived characters typical of amhipithecines, such as the pronounced buccolingual extension of the lower premolars.

In comparison to eosimiids (including *Bahinia*), *Siamopithecus* premolars and molars display more derived characters, including a well-developed cingular-derived hypocone in the

upper molars, the absence of paraconids in the lower molars, and the presence of a metaconid on P₄. Therefore, the establishment of a new family, Siamopithecidae, is justified. In this study, *Siamopithecus* is not considered a basal sister group of amhipithecines due to the probable presence of postorbital closure, challenging the hypothesis that amhipithecines lost their postorbital closure. Such a hypothesis lacks parsimony and is unsupported by evidence from primates. Consequently, shared dental morphology and dietary adaptations between *Siamopithecus* and amhipithecines are interpreted as homoplasies rather than shared derived characters.

Phylogenetic analyses over the past two decades have proposed two main positions for *Siamopithecus*. Initial studies, primarily based on dental characters, placed it within the amhipithecids, often as the basal sister clade of amhipithecines. Amhipithecids were interpreted as members of the crown anthropoids, either as a sister group to catarrhines (Beard et al. 2009; Chaimanee et al., 2012; Jaeger et al., 2019) or sometimes to platyrhines (Seiffert et al., 2010; Marivaux et al. 2023). However, subsequent discoveries of more complete amhipithecines remains (Jaeger et al., 2020) strengthen support for placing amhipithecines as stem anthropoids (Marivaux et al., 2005; Seiffert et al., 2005; Marivaux, 2006; Ni et al., 2013; Jaeger et al., 2020), with *Siamopithecus* sometimes resolved as their closest outgroup (Seiffert et al., 2005, 2018; Seiffert, 2012; Jaeger et al., 2020). One exceptional result placed *Siamopithecus* as a sister group of simiiforms, outside the Amhipithecinae, assigned to a more basal clade (Boyer et al., 2010; Coster et al., 2013).

New data suggest alternative potential phylogenetic relationships for *Siamopithecus*. It shares several characters with the most primitive known Taqah propliopithecid, described by Thomas et al. (1991). In contrast, Taqah propliopithecid has significantly more derived premolars, with P^{3/3} larger than P^{4/4} and a more robust protocone on P³. The primitive structure of *Siamopithecus* premolars and the persistence of small, reduced P^{2/2} suggest that it

has not attained the catarrhine status. Therefore, a hypothesis of a stem catarrhine phylogenetic position for *Siamopithecus* can be proposed. The origin of propliopithecids remains controversial. Most authors suggest that propliopithecids derived from African Eocene anthropoids in an undocumented Afro-Arabian province (Simons, 1990; Seiffert et al., 2004). The absence of African ancestors of propliopithecids in the rich late Eocene Fayum faunas (Seiffert, 2012) and their sudden appearance during the early Oligocene in Afro-Arabia remains an enigma. In Taqah (Oman), the early Oligocene propliopithecid is associated with cricetid rodents (Thomas et al., 1999; Sen, 2012), which are undoubtedly of Asian origin (Rodrigues et al., 2010). This association raises the hypothesis that propliopithecids may have originated in Asia, similar to cricetid rodents. In this context, *Siamopithecus* may document a primitive relative of these unknown Asian propliopithecids. The discovery of Eocene propliopithecids in Afro-Arabia would prompt a reconsideration of this interpretation and encourage the search for new phylogenetic relationships between *Siamopithecus* and African Paleogene anthropoids.

In conclusion, recent discoveries related to Myanmar amhipithecines have allowed more precise comparisons of their maxillae, revealing significant anatomical differences between amhipithecines and *Siamopithecus*. These findings have led to the reinterpretation of shared derived dental and mandibular characters associated with a hard-food diet as homoplasies. Consequently, *Siamopithecus* has been reclassified outside of the amhipithecids and attributed to a new family, the Siamopithecidae. Based on dental similarities between *Siamopithecus* and the most primitive known propliopithecid, from Oman, a phylogenetic position within the stem catarrhines is proposed. This would implicate an Asian origin for propliopithecids rather than deriving from oligopithecid ancestors in an undocumented Afro-Arabian province. However, the status of the Taqah propliopithecid from Oman remains uncertain, and further discoveries should validate or challenge this revised interpretation.

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Acknowledgments

The authors would like to thank Christoph Zollikofer (University of Zurich) for providing the comparative materials. We extend our gratitude to Paul Tafforeau and European Synchrotron Radiation Facility (ESRF) beamlines ID 17 for the CT-scan pictures (Fig. 4, 5, and 7), and ID 19 (Fig. 4B), Sabine Riffaut (PALEVOPRIM) for creating the figures, and the Electricity Generating Authority of Thailand (EGAT) for their scientific assistance and access to the mine. We also thank Mark Grabowski (the editor), the associated editor, and two anonymous reviewers, Laurent Marivaux (ISEM) and K. Christopher Beard (University of Kansas) for their helpful comments and suggestions. This work has been supported by the CNRS-UMR 7262, the University of Poitiers, and the Department of Mineral Resources, Thailand (DMR). Partially funding was provided by the ANR-18-CE92-0029 Project (to O. Chavasseau).

Table 1 Dental measurements of *Siamopithecus eocaenus* (MD, mesiodistal length; BL, buccolingual width; trig, trigonid; tal, talonid). Maxilla (TF 7625) compared with TF 3635* (holotype, Chaimanee et al., 1997) and mandible (TF 7624#, Chaimanee et al., 2000, and TF 3634+, Chaimanee et al., 1997) (in mm).

| | TF 7625 | | TF 7625 | | TF 3635* | | | | TF 7624# | | TF 3634 ⁺ | |
|--------------------------------|-------------|-----|---------|-----|----------|-----|--------------------------------|-------|------------|-----|----------------------|------|
| | Left (worn) | | Right | | Holotype | | | | | | | |
| | MD | BL | MD | BL | MD | BL | | | MD | BL | MD | BL |
| | | | | | | | | | (trig/tal) | | (trig/tal) | |
| | | | | | | | C | 6.46 | 4.96 | - | - | - |
| P ³ | 4.4 | 5.3 | 4.8 | 5.8 | 4.3 | 5.3 | P ₃ | 4.78 | 5.46 | - | - | - |
| P ⁴ | 4.8 | 7.0 | 5.0 | 7.0 | 5.0 | 6.5 | P ₄ | 5.36 | 5.77 | - | - | - |
| M ¹ | 5.7 | 8.6 | 5.8 | 9.0 | 5.4 | 8.1 | M ₁ | 6.37 | 6.12/5.96 | - | - | /5.7 |
| M ² | 5.0 | 8.9 | 5.1 | 9.2 | 4.8 | 8.1 | M ₂ | 6.04 | 5.92/5.32 | 6.5 | 5.7 | |
| M ³ | 4.5 | 7.1 | 4.6 | 7.5 | - | - | M ₃ | 7.97 | 5.22/4.22 | 8.1 | 5.1 | |
| P ³ -M ³ | 22.8 | | 25.0 | | - | | P ₃ -M ₃ | 29.69 | | - | | |
| M ¹ -M ³ | 14.7 | | 15.7 | | - | | M ₁ -M ₃ | 19.32 | | - | | |
| | | | | | | | C-M ₃ | 40.0 | | - | | |

Table 2 Measurements of the cranium of *Siamopithecus eocaenus* (TF 7625).

* Derived from the virtual reconstruction of *Siamopithecus* (Zolikoffer et al., 2009)

| | |
|---|---------|
| Estimated orbit frontation* | 81.6° |
| Estimated orbit convergence* | 72.1° |
| Biorbital width (Bi-frontomolare orbitale)* | 52.9 mm |
| Orbit diameter | 15.0 mm |
| Palate width at M ² (between lingual alveolar borders of M ²)* | 22.9 mm |
| Breadth across P ³ (between buccal alveolar borders of P ³)* | 30.5 mm |
| Breadth across M ² (between buccal alveolar borders of M ²)* | 42.2 mm |
| Breadth across M ³ (between buccal alveolar borders of M ³)* | 40.6 mm |
| Elevation of maxillary bone on vertical section | 14.5 mm |

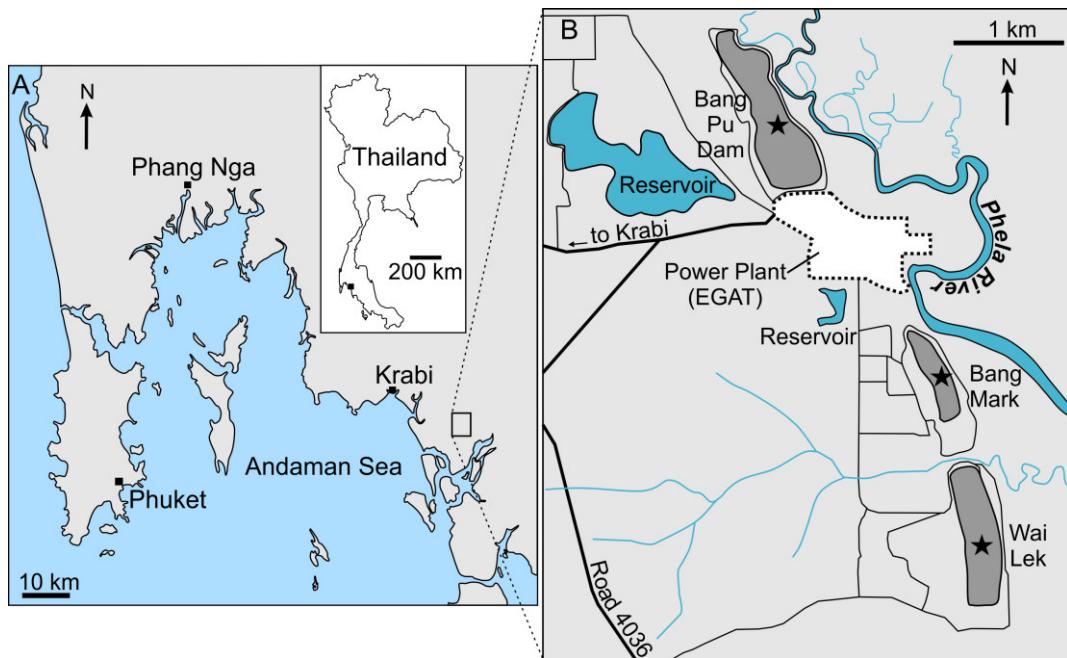


Fig. 1 Map of the Krabi coal mine (Krabi basin, Peninsular Thailand), showing the three coal pits (Bang Pu Dum, Bang Mark, and Wai Lek). Fossils of *Siamopithecus* TF 3635 (maxilla, holotype), TF 7624 (mandible), and TF 7625 (maxilla in this study) were recovered from the Bang Mark pit, while TF 3634 (partial mandible) was recovered from the Wai Lek pit.

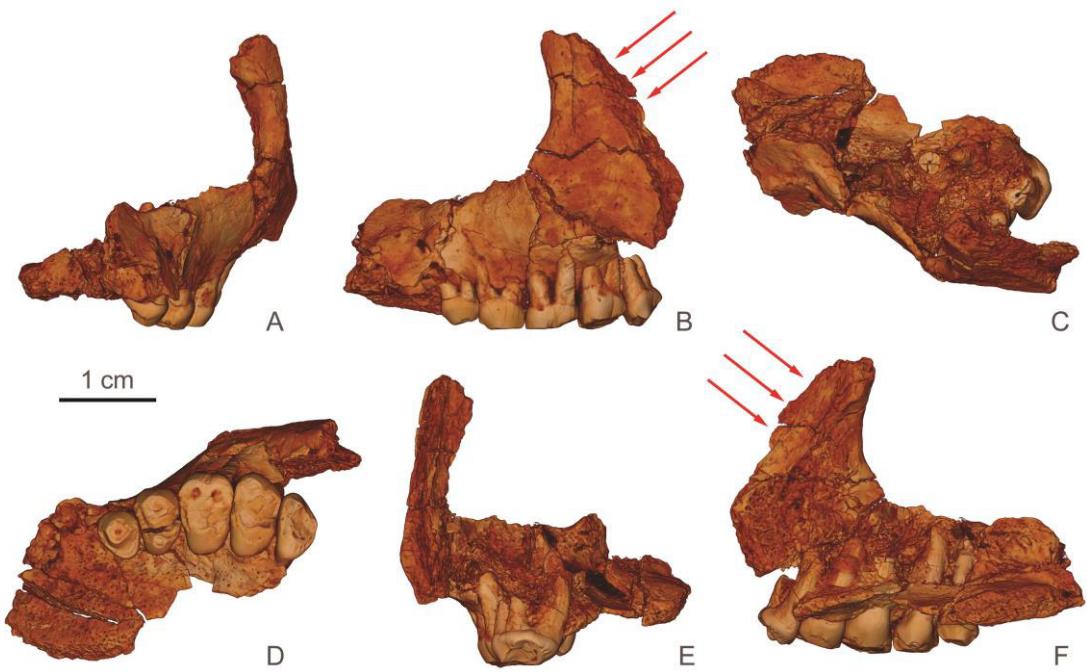


Fig. 2 The left maxilla of *Siamopithecus eocaenus* (TF 7625), rendered from a 3D virtual model generated from μ CT scans, in mesial (A), jugal (B), superior (C), occlusal (D), distal (E), and lingual (F) views. Thin bony lamina on the distal part of its zygomatic, indicating the potential presence of a partial or complete postorbital wall (red arrows).

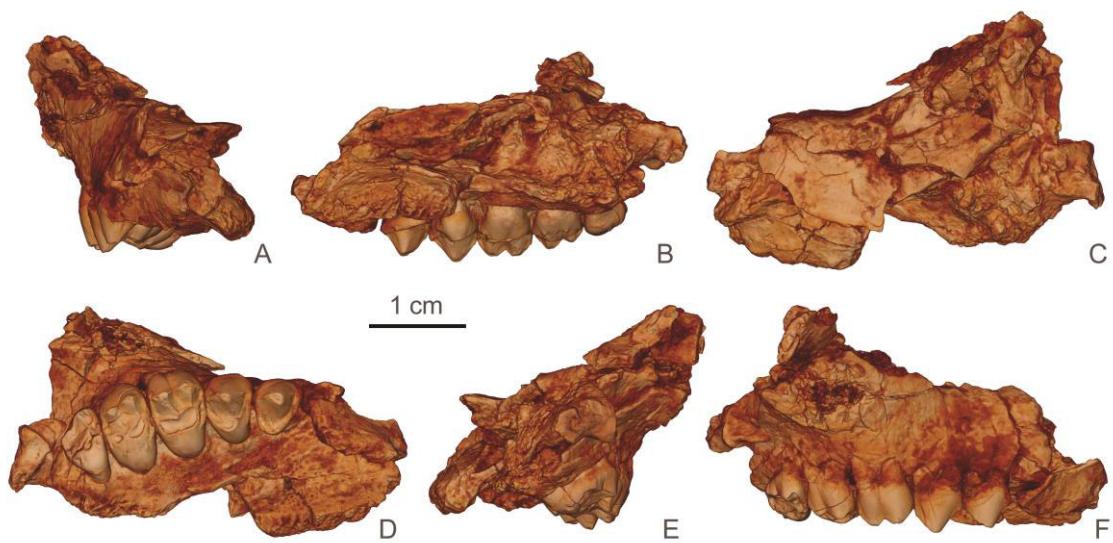


Fig. 3 The right maxilla of *Siamopithecus eocaenus* (TF 7625), rendered from a 3D virtual model generated from μ CT scans, in mesial (A), jugal (B), superior (C), occlusal (D), distal (E), and lingual (F) views.

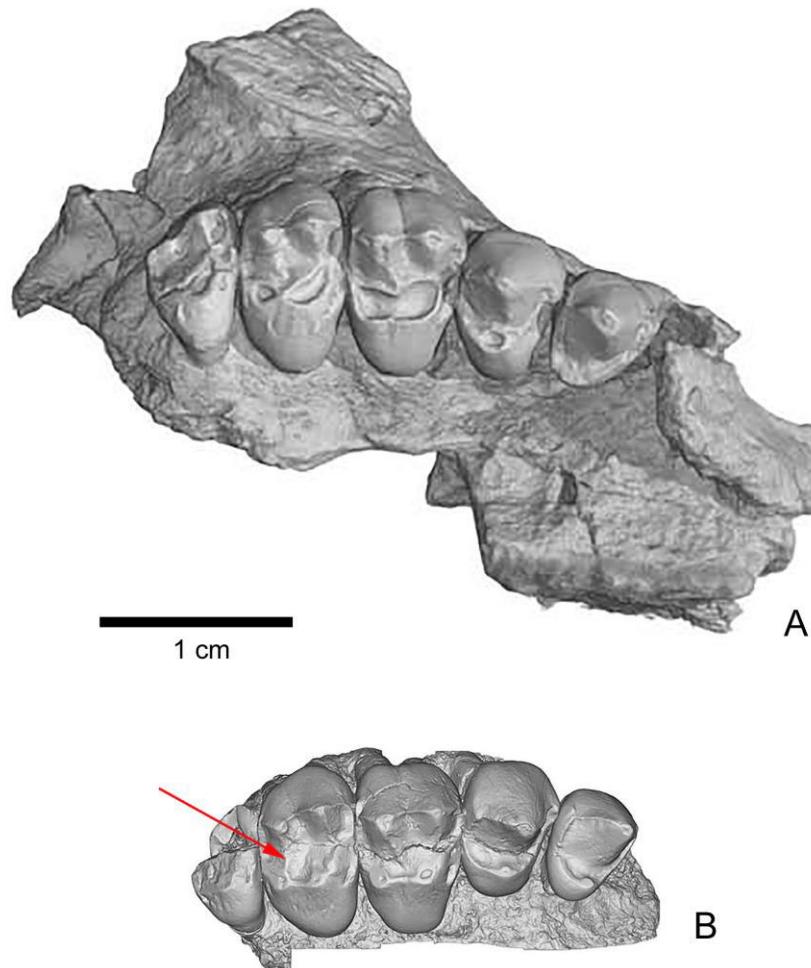


Fig. 4 Comparison of right maxillae of *Siamopithecus eocaenus* (TF 7625) (A) and the TF 3635 (holotype) (B), rendered from a 3D virtual model generated from µCT scans (Tafforeau, 2004; <https://paleoanthro.org/static/dissertations/Paul%20Tafforeau-lowres.pdf>) with the author's authorization). In TF 3635, M² differs by having a transversely oriented hypometacrista that extends lingually from the metacone toward the hypocone (red arrow).

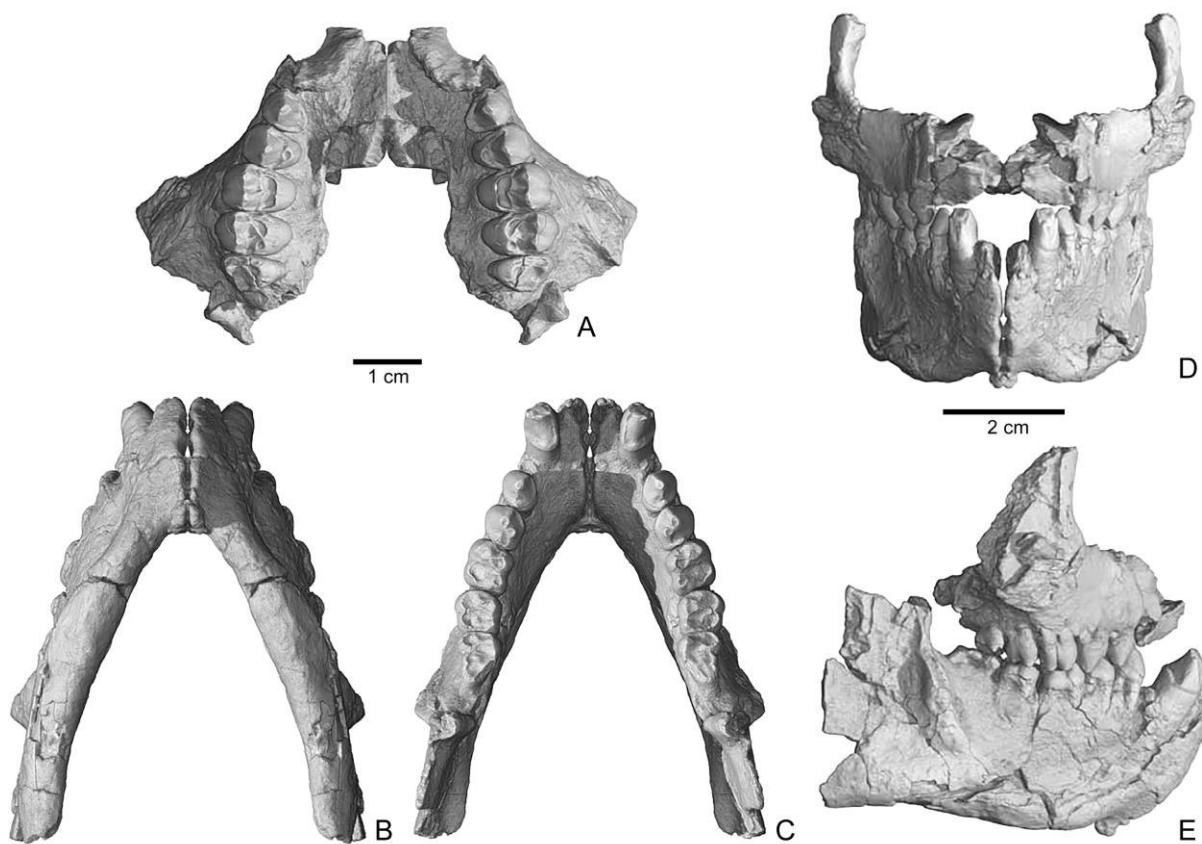


Fig. 5 Virtual reconstitution of the maxilla of *Siamopithecus eocaenus* (TF 7625) using the symmetry of the right maxilla on the horizontal palate in occlusal view (A). The mandible of *Siamopithecus eocaenus* (TF 7624) is reconstructed through the symmetry of the right mandible in the inferior (B) and occlusal (C) views. A virtual reconstitution of the face of *Siamopithecus eocaenus* is achieved by mirroring the left maxilla of TF 7625 and the right mandible of TF 7624, anterior (D), and right lateral (E) views. Images are digital renderings of 3D virtual models generated from μ CT scan data from Tafforeau, 2004; <https://paleoanthro.org/static/dissertations/Paul%20Tafforeau-lowres.pdf> (with the author's authorization).

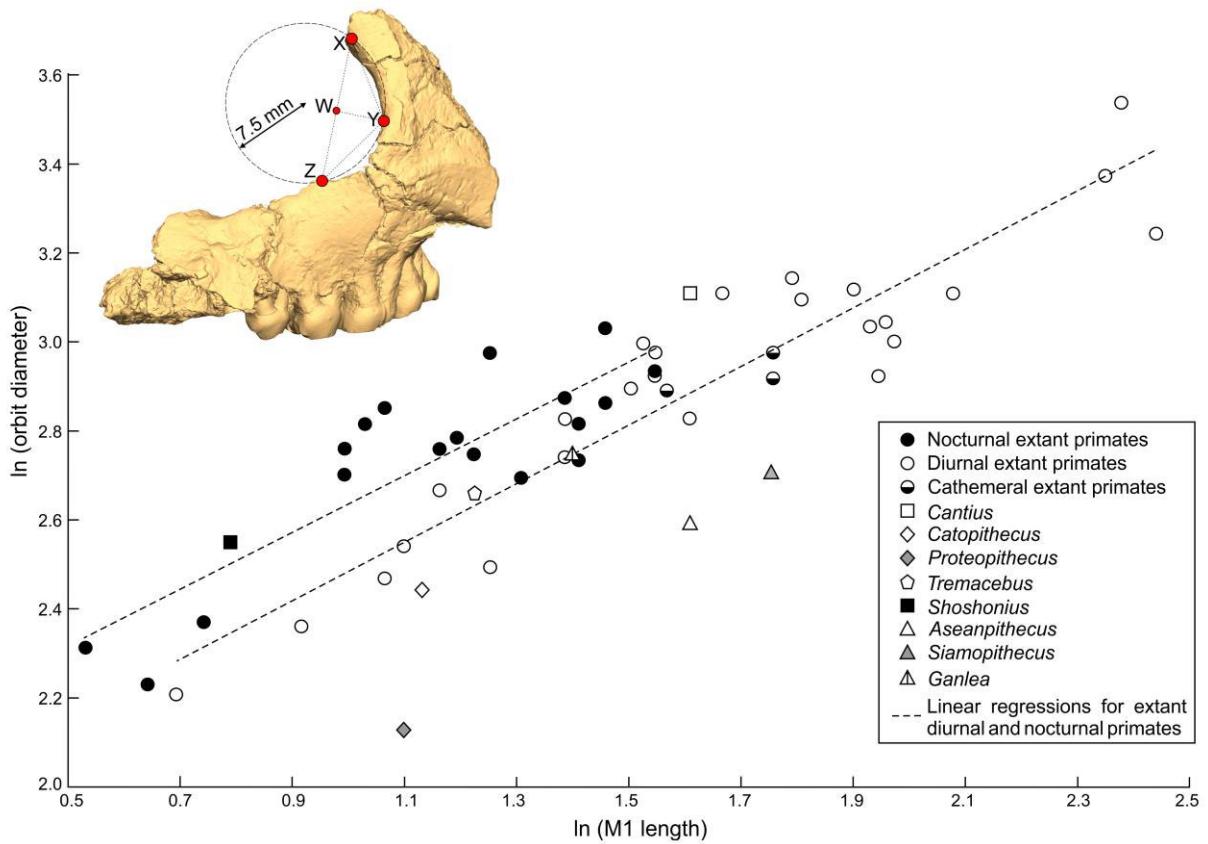


Fig. 6 Bivariate plot of log-transformed orbit diameter versus first molar length in a sample of extant and fossil primates. *Siamopithecus* displays a small orbit diameter relative to molar size, indicating a diurnal activity pattern. Orbit diameters for extant primates are mediolateral diameters. Data sources from Heesy and Ross (2001) and Jaeger et al. (2019, 2020).

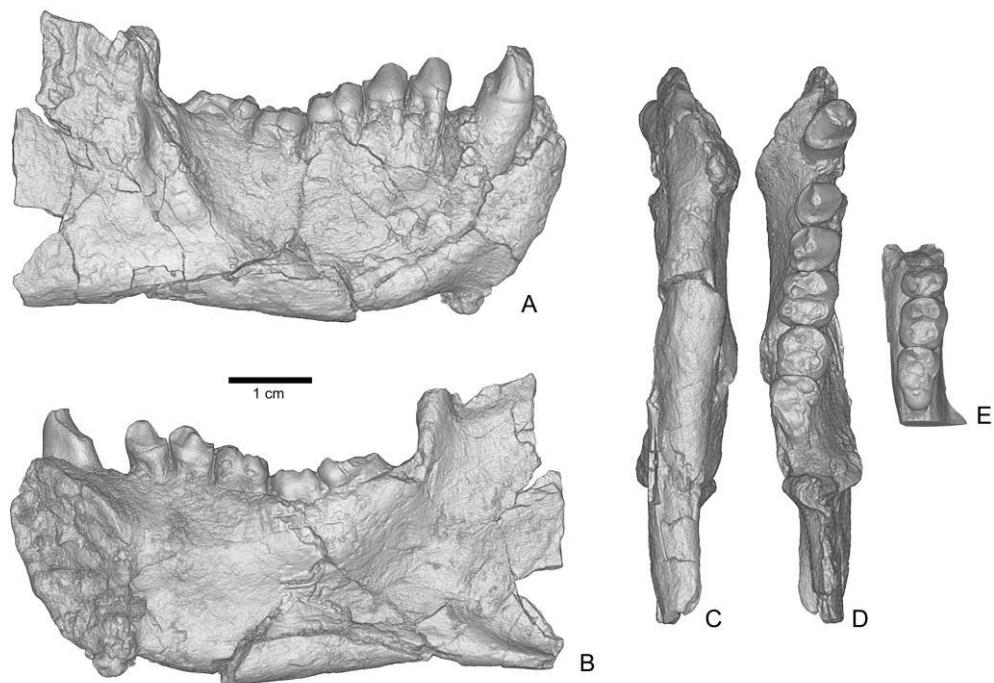


Fig. 7 *Siamopithecus eocaenus* rendered from a 3D virtual model generated from µCT scans (Tafforeau, 2004; <https://paleoanthro.org/static/dissertations/Paul%20Tafforeau-lowres.pdf>) with the author's authorization), right mandible with C-M₃ (TF 7624) in buccal (A), lingual (B), inferior (C), and occlusal (D) views and right mandible with distal M₁-M₃ (TF 3634) in occlusal view (E).

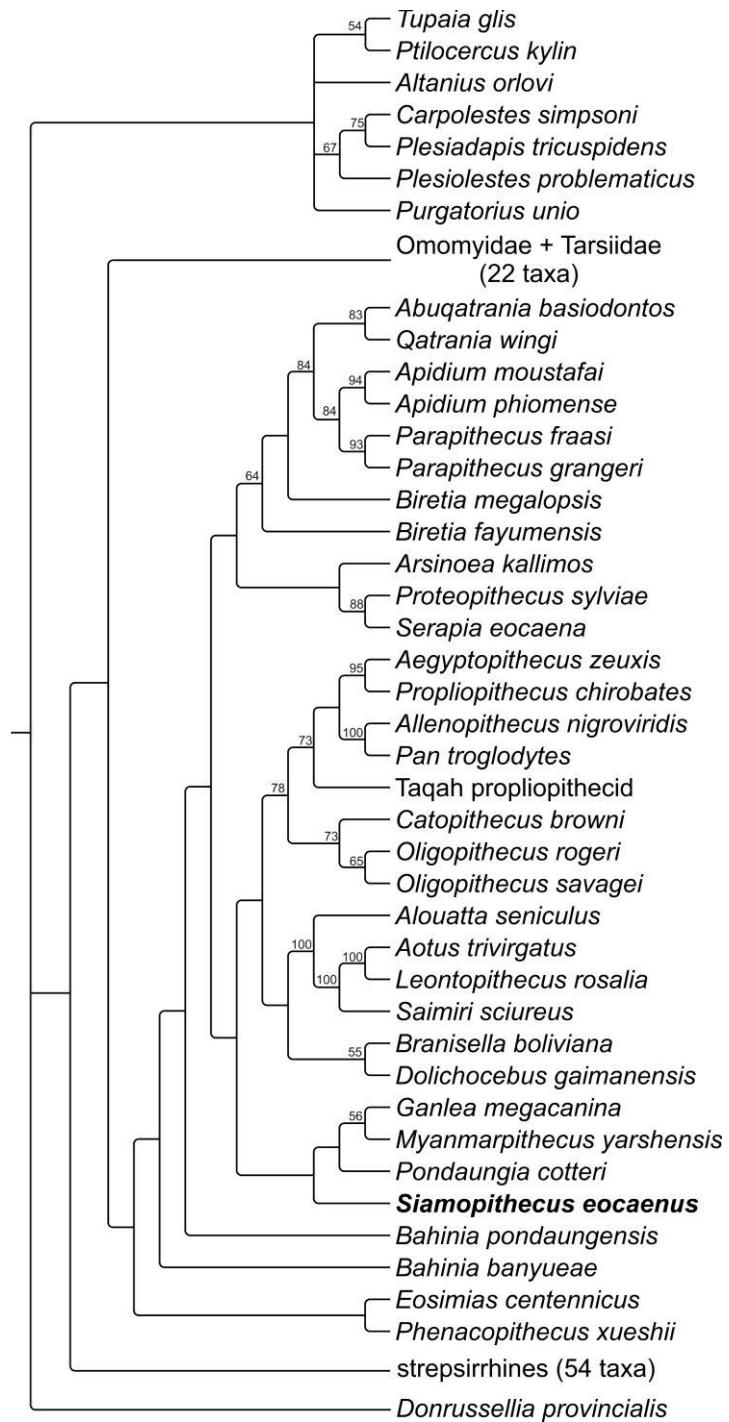


Fig. 8 Phylogenetic position of *Siamopithecus* among the primates. Results of the maximum parsimony analysis based on a taxon-character data matrix of 394 characters and 117 taxa based on the data matrix of Seiffert et al. (2018) (SOM). A Strict consensus tree of 20 most parsimonious trees (length = 4727.5 steps, CI = 0.1518, RI = 0.5590). The numbers above the nodes are the frequencies of the clade among the most parsimonious trees.

Supplementary Online Material (SOM):

Maxilla of *Siamopithecus eocaenus* (Anthropoidea, Primates) from the Paleogene of Krabi,
Thailand, and its taxonomic status

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Phylogenetic analyses

Analysis 1

In this analysis, the data matrix is based on Seiffert et al. (2018), augmented with new coding for *Siamopithecus* (7 new characters). The data matrix includes 117 taxa (33 fossil and living anthropoids, 3 living and fossil tarsiids, 19 omomyids, and 55 fossil and extant strepsirrhines) and 394 morphological characters (see character-taxon-matrix Analysis 1).

A heuristic search was performed in PAUP 4.0a169 using the hsearch command with a random addition sequence of taxa (100 replications), 178 characters were assigned a weight of 1, 216 characters at 0.5, 261 characters were treated as ordered and 4 characters as irreversible. The retrieved topologies were constrained by a backbone tree based on the molecular phylogeny of extant strepsirrhines. All search options follow the protocol used by Seiffert et al. (2018) (Fig. 8).

Analysis 2

In this analysis, the data matrix is based on Jaeger et al. (2020) with the coding of *Siamopithecus* augmented by newly available features (9 new characters states). The data matrix includes 38 primate taxa (27 anthropoids, 2 tarsiids, 4 omomyids, and 5 adapiform strepsirrhines) and 326 cranial, dental, and postcranial characters (see character-taxon-matrix Analysis 2).

A heuristic search was performed in PAUP 4.0a169 using the hsearch command with a random addition sequence of taxa (1000 replications). No character weighting was used, and 144 characters were treated as ordered (Fig. S1).

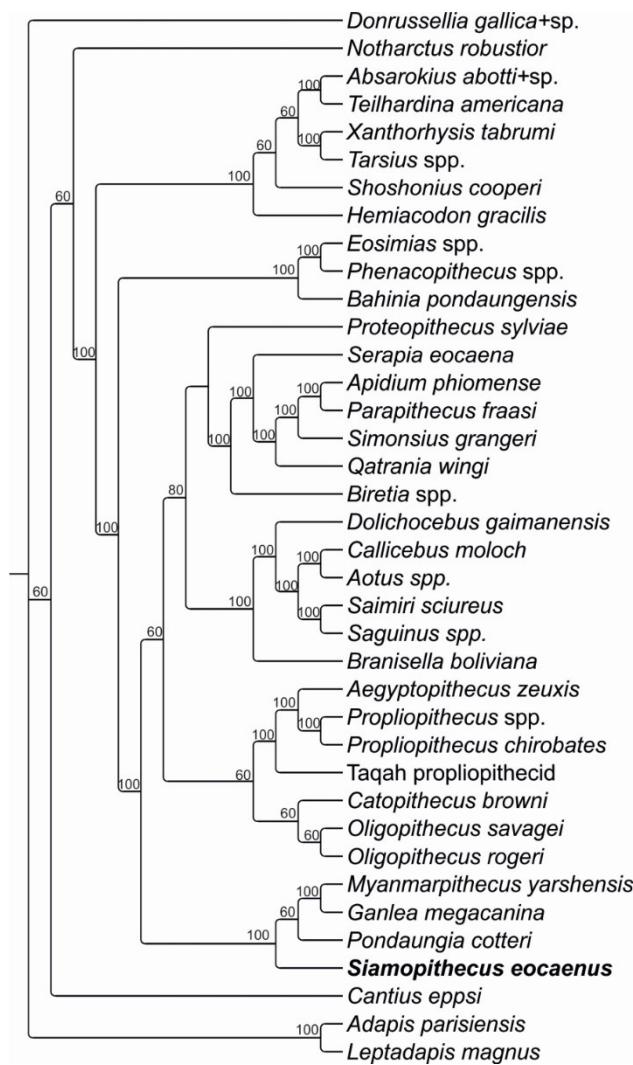


Fig. S1 Majority-rule consensus tree derived from the 5 most parsimonious trees obtained in Analysis 2 (length = 1425 steps, CI = 0.3411, RI = 0.5581). The clade frequencies among the most parsimonious trees are indicated.

Analysis 3

In this analysis, the data matrix is based on those of Jaeger et al. (2019, 2020), incorporating the new coding of *Ganlea* from Jaeger et al. (2020). The data matrix includes 45 primate taxa (34 anthropoids, 2 tarsiids, 4 omomyids, and 5 adapiform strepsirrhines) and 326 cranial, dental, and postcranial characters (see character-taxon-matrix Analysis 3).

A heuristic search was performed in PAUP 4.0a169 with the hsearch command with a random addition sequence of taxa (1000 replications). No character weighting was used and 144 characters were treated as ordered (Fig. S2).

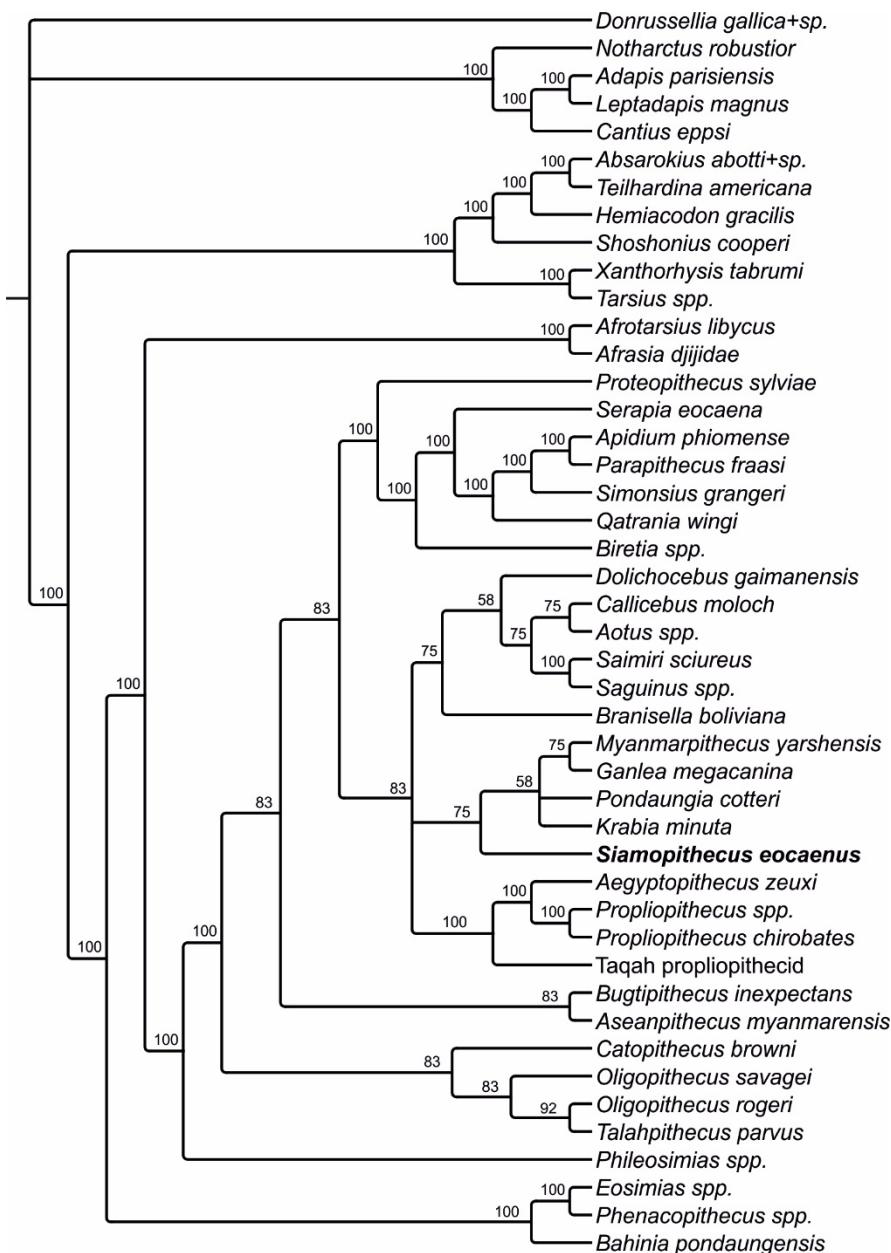


Fig. S2 Majority-rule consensus tree derived from the 12 most parsimonious trees obtained in Analysis 3 (length = 1514 steps, CI = 0.3210, RI = 0.5554). The clade frequencies among the most parsimonious trees are indicated.

Character-taxon-matrix

Analysis 1: We use a matrix with 117 taxa and 394 morphological characters based on Seiffert et al. (2018).

```
#NEXUS
BEGIN TAXA;
DIMENSIONS NTAX=117;
TAXLABELS
    'Tupaia glis'
    'Absarokius sp.'
    'Abuqatrania basiodontos'
    'Adapis parisiensis'
    'Aegyptopithecus zeuxis'
    'Afradapis longicristatus'
    'Aframonijs dieides'
    'Algeripithecus minutus'
    'Allenopithecus nigroviridis'
    'Alouatta seniculus'
    'Altanius orlovi'
    'Anchomomys frontanyensis'
    'Anchomomys gaillardi'
    'Anchomomys milleri'
    'Aotus trivirgatus'
    'Apidium moustafai'
    'Apidium phiomense'
    'Arapahovius gazini'
    'Arctocebus calabarensis'
    'Arsinoea kallimos'
    'Asiadapis cambayensis'
    'Azibius trerki'
    'Bahinia pondaungensis'
    'Bahinia banyueae'
    'Biretia fayumensis'
    'Biretia megalopsis'
    'Branisella boliviiana'
    'Bugtilemur mathesoni'
    'Caenopithecus lemuroides'
    'Cantius abditus'
    'Cantius ralstoni'
    'Carpolestes simpsoni'
    'Catopithecus browni'
    'Cheirogaleus major'
    'Darwinius masillae'
    'Djebelemur martinezii'
    'Dolichocebus gaimanensis'
    'Donrussellia provincialis'
    'Dyseolemur pacificus'
    'Eosimias centennicus'
    'Europolemur dunaifi'
    'Europolemur klatti'
    'Galago demidoff'
    'Galago moholi'
    'Ganlea megacanina'
    'Gatanthropus micros'
    'Hemiacodon gracilis'
    'Hoanghonius stehlini'
```

'Karanisia clarki'
'Komba spp.'
'Laomaki yunnanensis'
'Lemur catta'
'Leontopithecus rosalia'
'Lepilemur mustelinus'
'Leptadapis magnus'
'Leptadapis priscus'
'Leptadapis ruetimeyeri'
'Loris tardigradus'
'Loveina zephryi'
'Macrotarsius montanus'
'Mahgarita stevensi'
'Marcgodinotius indicus'
'Masradapis tahai'
'Mazateronodon endemicus'
'Mescalerolemur horneri'
'Microadapis sciureus'
'Microcebus murinus'
'Microchoerus erinaceus'
'Muangthanhinius siami'
'Myanmarpithecus yarshensis'
'Nannopithex abderhaldeni'
'Nannopithex raabi'
'Necrolemur spp.'
'Nievesia sossisensis'
'Nycticeboides simpsoni'
'Nycticebus coucang'
'Oligopithecus rogeri'
'Oligopithecus savagei'
'Omomys sp.'
'Otolemur crassicaudatus'
'Pan troglodytes'
'Parapithecus fraasi'
'Parapithecus grangeri'
'Perodicticus potto'
'Phenacopithecus xueshii'
'Plesiadapis tricuspidens'
'Plesiolestes problematicus'
'Plesiopithecus teras'
'Pondaungia cotteri'
'Pronycticebus gaudryi'
'Propithecus spp.'
'Propliopithecus chirobates'
'Proteopithecus sylviae'
'Protoadapis curvicuspидens'
'Pseudoloris parvulus'
'Ptilocercus kylin'
'Purgatorius unio'
'Qatrania wingi'
'Rencunius zhoui'
'Saharagalago misrensis'
'Saimiri sciureus'
'Serapia eocaena'
'Shoshonius cooperi'
'Siamopithecus eocaenus'
'Steinius spp.'
'Taqah propliopithecid'
'Tarsius bancanus'
'Tarsius sirindhornae'
'Teilhardina americana'

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'Teilhardina asiatica'
'Teilhardina belgica'
'Tetonius sp.'
'Varecia variegata'
'Wadilemur elegans'
'Washakius insignis'
'Xanthorhysis tabrumi'
'Yunnanadapis folivorus'

;

ENDBLOCK;

BEGIN CHARACTERS;
DIMENSIONS NCHAR=394;
FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = "012345678";
CHARLABELS
[1] 'lower incisor number (modified from Ross et al. 1998 character i1)'
[2] 'lower incisor occlusal arrangement (Ross et al. 1998 character i2)'
[3] 'toothcomb (modified from Ross et al. 1998 character i13)'
[4] 'lower i1-2 area relative to lower m1 area (ratio of i1 + i2 area:m1
area) (Ross et al. 1998 character i5)'
[5] 'i1:i2 proportions (Ross et al. 1998 character i6)'
[6] 'i2 cross-sectional shape (ratio of mesiodistal length to buccolingual
breadth) (Ross et al. 1998 character i8)'
[7] 'lower incisor crown height (Ross et al. 1998 character i9)'
[8] 'lower incisor root orientation (Ross et al. 1998 character i11)'
[9] 'incisor crown orientation (Ross et al. 1998 character i12)'
[10] 'first lower incisor crown shape (Ross et al. 1998 character i14)'
[11] 'i2 heel development (Ross et al. 1998, character i15)'
[12] 'lower first incisor lingual cingulum (Ross et al. 1998 character
i17)'
[13] 'i1 to m1 area (Ross et al. 1998 character i19)'
[14] 'female canine maximum cross-sectional area relative to first lower
molar area (Ross et al. 1998 character c1, modified)'
[15] 'canine dimorphism (square root of male lower canine area:square root
of female lower canine area) (Ross et al. 1998 character c2)'
[16] 'lower canine cross-sectional shape (Ross et al. 1998 character c3)'
[17] 'orientation of lower canine root'
[18] 'lower canine lingual crest development (Ross et al. 1998 character
c4)'
[19] 'lower canine paracristid (Ross et al. 1998 character c5, modified)'
[20] 'lower canine height (Ross et al. 1998 character c6, modified)'
[21] 'p1 presence (Ross et al. 1998 character p1, modified)'
[22] 'p2 roots presence (Ross et al. 1998 character p3, modified)'
[23] 'p2 metaconid (Ross et al. 1998 character p15)'
[24] 'p2 protoconid height and shape (Ross et al. character p13)'
[25] 'p2 buccal cingulum development (Ross et al. character p28)'
[26] 'p3 paraconid (Ross et al. 1998 character p6, modified)'
[27] 'p3 lingual cingulum'
[28] 'p3 metaconid size (Ross et al. 1998 character p16)'
[29] 'p3 lateral protocristid orientation (Ross et al. 1998, character p22,
modified)'
[30] 'p3 roots (Ross et al. 1998 character p4, in part, modified)'
[31] 'p3 root orientation (contains information similar to Ross et al. 1998
character p45)'
[32] 'p3 hypoconid (contains information similar to that of Ross et al.
1998 character p25)'
[33] 'p3 entoconid and lingual talonid crest (Ross et al. 1998 character
p19)'
[34] 'p3-4 protoconid height (Ross et al. 1998 character p41)'
[35] 'p3 area:p4 area (Ross et al. 1998 character p42)'

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[36] 'p4 root number (Ross et al. 1998 character p4, in part)'
[37] 'p4 metaconid size (Ross et al. 1998 character p17)'
[38] 'spacing of p4 metaconid and protoconid (Ross et al. 1998 character p14)'
[39] 'mesiodistal position of p4 metaconid with respect to protoconid'
[40] 'p4 paraconid size (Ross et al. 1998 character p7, modified)'
[41] 'p4 paraconid position (Ross et al. 1998 character p9)'
[42] 'p4 lateral protocristid morphology (contains information similar to Rp21-42 and Rp23-44)'
[43] 'p4 premetacristid (Ross et al. 1998 character p18, modified)'
[44] 'p4 postprotocristid (Ross et al. 1998 character p36)'
[45] 'p4 postmetacristid (contains information similar to Ross et al. 1998 character p37)'
[46] 'p4 entoconid and lingual talonid crest (Ross et al. 1998 character p20)'
[47] 'height of p4 talonid'
[48] 'p4 cristid obliqua development (Ross et al. 1998 character p11)'
[49] 'position of p4 hypoconid or distal terminus of p4 cristid obliqua (Ross et al. 1998 character p26, modified)'
[50] 'p4 hypocristid shearing development (Ross et al. 1998 character p27)'
[51] 'lower premolar crowding (Ross et al. 1998 character p5)'
[52] 'lower premolar inflation (Ross et al. 1998 character p29)'
[53] 'premolar orientation (Ross et al. 1998 character p33)'
[54] 'p4 exodaenodonty (Ross et al. 1998 character p30)'
[55] 'buccal cingulum on p4 (Ross et al. 1998 character p34)'
[56] 'p4 lingual cingulum'
[57] 'p4 md length:bl width (Ross et al. 1998 character p43)'
[58] 'p4 area relative to m1 area (Ross et al. 1998 character p44)'
[59] 'm1 length:m1 width (Ross et al. 1998 character m55)'
[60] 'm1 area (Ross et al. 1998 character m54)'
[61] 'm1 paraconid size (contains information similar to Ross et al. 1998 character m20)'
[62] 'm1 paraconid position (Ross et al. 1998 character m8)'
[63] 'm1 parastylid (Ross et al. 1998 character m11)'
[64] 'm1 premetacristid (contains information similar to Ross et al. 1998 character m18)'
[65] 'm1 metaconid position (Ross et al. 1998 character m19)'
[66] 'm1 trigonid height (ratio of trigonid height to talonid height) (Ross et al. 1998 character m16)'
[67] 'm1 cristid obliqua orientation (Ross et al. 1998 character m32)'
[68] 'm1 cristid obliqua terminus (Ross et al. 1998 character m34)'
[69] 'hypoconulid position on m1 (contains information similar to Ross et al. 1998 character m30)'
[70] 'm1 hypoconulid size (Ross et al. 1998 character m27)'
[71] 'm1 cristid obliqua development (Ross et al. 1998 character m31, in part)'
[72] 'm1-2 hypocristid development (Ross et al. 1998 character m38)'
[73] 'm1-2 buccal cingulum development (Ross et al. 1998 character m45)'
[74] 'm1-2 talonid -- lingual configuration (Ross et al. 1998 character m40)'
[75] 'm2 paraconid size (contains information similar to Ross et al. 1998 character m20)'
[76] 'm2 paraconid position (Ross et al. 1998 character m9)'
[77] 'm2 trigonid width (ratio of buccolingual breadths of trigonid and talonid) (Ross et al. 1998 character m6)'
[78] 'm2 cristid obliqua orientation (Ross et al. 1998 character m33)'
[79] 'm2 cristid obliqua terminus (Ross et al. 1998 character m35)'
[80] 'm2 cristid obliqua development (Ross et al. 1998 character m31, in part)'
[81] 'position of entoconid relative to hypoconid on m2 (contains information similar to Ross et al. 1998 character m57)'

[82] 'hypoconulid position on m2 (contains information similar to Ross et al. 1998 character m30)'
[83] 'm2 hypoconulid size (Ross et al. 1998 character m28)'
[84] 'morphology of distolingual aspect of m2 (contains information similar to Ross et al. 1998 characters m26 and m41)'
[85] 'accessory cusps on distolingual aspect of m2'
[86] 'cusp basal inflation on m1-2 (contains information similar to Ross et al. 1998 character m17 and m44)'
[87] 'm2 length:m3 length (Ross et al. 1998 character m53)'
[88] 'm3 paraconid size'
[89] 'm3 paraconid position (Ross et al. 1998 character m10)'
[90] 'm3 cristid obliqua terminus (Ross et al. 1998 character m36, modified)'
[91] 'm3 trigonid width (based on relative buccolingual breadths) (Ross et al. 1998 character m7)'
[92] 'm3 entoconid'
[93] 'morphology of m3 hypoconulid'
[94] 'position of hypoconulid on m3'
[95] 'm3 hypoconulid (Ross et al. 1998 character m13)'
[96] 'm3 root number (Ross et al. 1998 character m4)'
[97] 'molar centroconids (contains information similar to Ross et al. 1998 character m37)'
[98] 'sulcus between metaconid and protoconid on m1-2 (contains information similar to Ross et al. 1998 character m22 and m23)'
[99] 'lower molar metastylids (Ross et al. 1998 character m12)'
[100] 'molar enamel crenulation (Ross et al. 1998 character m15)'
[101] 'interincisal diastema (RCr42-224)'
[102] 'I1-I2 interstitial contact (RI1-114)'
[103] 'I1:I2 area (RI4-117)'
[104] 'I1-2 lingual cingulum (RI11-124)'
[105] 'I1-I2 buccal cingulum (RI13-126)'
[106] 'I1 occlusal shape (mesiodistal length:buccolingual breadth) (RI6-119)'
[107] 'I1 crown shape (RI8-121)'
[108] 'I1 size (I1 area:M1 area) (RI5-118)'
[109] 'I1 occlusal edge orientation (spatulate incisors only) (RI10-123)'
[110] 'I1 basal lingual cusp (RI12-125)'
[111] 'I2 occlusal shape (mesiodistal length:buccolingual breadth) (RI7-120)'
[112] 'I2-C diastema (RI3-116)'
[113] 'upper incisor number (Y43)'
[114] 'upper canine shape (contains information similar to RC1-127)'
[115] 'rotation of upper canine'
[116] 'C1 mesial groove (females) (RC3-129)'
[117] 'C1 lingual cingulum (RC4-130)'
[118] 'upper canine occlusion (RC2-128)'
[119] 'P1 presence (contains information from Y45)'
[120] 'P2 root number, presence (RP1-131, modified)'
[121] 'P2 occlusal outline (RP6-136)'
[122] 'P2 protocone (RP12-142, modified)'
[123] 'height of P2 relative to P3*'
[124] 'P2 area relative to P3 area (contains information similar to that in RP4-134)'
[125] 'P3 distal crown margin (RP18-148)'
[126] 'P3 protocone (RP9-139, modified)'
[127] 'P3 hypocone (RP13-143, in part)'
[128] 'P3 metacone (RP20-150)'
[129] 'P3 root number (RP2-132)'
[130] 'P4 parastyle (RP15-145, modified)'
[131] 'P4 metastyle (RP16-146, modified)'
[132] 'P3-4 trigon:talon proportions (RP8-138)'

[133] 'P3-4 buccal cingulum development (RP21-151)'
[134] 'upper premolar paraconules (contains information similar to RP14-144)'
[135] 'P4 lingual cingulum (contains information similar to RP19-149)'
[136] 'P4 metacone (RP10-140)'
[137] 'P4 protocone (RP11-141)'
[138] 'P4 hypocone (RP13-143, in part)'
[139] 'P4 pericone'
[140] 'P4 metaconules'
[141] 'P4 postprotocrista (RP17-147, in part)'
[142] 'P4 occlusal outline (RP7-137)'
[143] 'P4 root number (RP3-133)'
[144] 'P4 area:M1 area (RP5-135)'
[145] 'M1 pericone (RM20-170, modified)'
[146] 'M1 area:M2 area (RM4-155)'
[147] 'M1 mesiobuccal fovea delimited by trenchant parahypocrista'
[148] 'M1-2 paraconule size (RM37-180)'
[149] 'M1-2 paraconule position (RM15-165)'
[150] 'M1 hypocone size (RM10-160)'
[151] 'M1-2 hypocone position (RM12-162)'
[152] 'convex distal lobe for M1-2 hypocone'
[153] 'lingual extension of M1 hypocone lobe'
[154] 'M2 prehypocrista development (RM13-163)'
[155] 'M1-2 Nannopithecus fold (RM5-156)'
[156] 'M1-2 postprotocrista development (RM18-168)'
[157] 'M1-2 metaconule size (RM16-166)'
[158] 'M1-2 premetaconule cristae (RM27-173)'
[159] 'M1-2 postmetaconule cristae (RM28-174)*'
[160] 'M1-2 lateral posterior transverse crista development (RM19-169)'
[161] 'shape of M2 centrocrista'
[162] 'buccal cingulum on M1-2 (contains information similar to RM24-172)'
[163] 'M1-2 root number (RM1-152)'
[164] 'M2 shape (bl:md) (RM3-154)'
[165] 'M2 pericone'
[166] 'M2 hypocone size (RM11-161)'
[167] 'M2 postmetacrista'
[168] 'M2 buccal expansion of paracone (RM33-177)'
[169] 'M1-3 lingual cingulum development (RM22-171)'
[170] 'M1-3 anterior cingulum (RM44-181)'
[171] 'molar protocone lingual inflation (RM31-176)'
[172] 'M3 metacone (RM34-178)'
[173] 'M3 paraconule (RM30-175)'
[174] 'M3 hypocone (RM36-179)'
[175] 'M3 size relative to M1 (RM46-182)'
[176] 'M3 root number (RM2-153)'
[177] 'mandibular symphyseal fusion (Y57, RCr39-221)'
[178] 'shape of the mandibular angle (Y40)'
[179] 'shape of masseteric fossa'
[180] 'mandibular depth (Y39, RCr45-227)'
[181] 'height of coronoid process relative to condyle (RCr43-225)'
[182] 'condyle height relative to toothrow (RCr44-226)'
[183] 'scapular morphology (mediolateral width / inferosuperior height)
(contains information similar to that of Y64)'
[184] 'length of scapular coracoid process (coracoid process length /
glenoid fossa height)'
[185] 'relative sizes of infraspinous and supraspinous fossae (Y66)'
[186] 'position of humeral head relative to tubercles'
[187] 'morphology of deltopectoral crest (RH16-247)'
[188] 'shape of intertubercular sulcus (contains information similar to
RH15-246)'
[189] 'teres major insertion'

[190] 'supinator crest (Y76, contains information similar to RH13-244)'
[191] 'brachialis flange (RH14-245)'
[192] 'presence, mediolateral position of entepicondylar foramen (Seiffert et al., 2000)'
[193] 'dorsal placement of medial epicondyle (RH9-240)'
[194] 'medial epicondyle size (RH8-239)'
[195] 'dorsoepitrochlear fossa (RH11-242)'
[196] 'shape of humeral trochlea (contains information similar to RH1-232)'
[197] 'relative heights of medial and lateral edges of the humeral trochlea (RH2-233)'
[198] 'shape of dorsal aspect of distal humeral articulation (contains information similar to that of RH10-241)'
[199] 'trochlear-capitular junction'
[200] 'capitular shape'
[201] 'capitular tail'
[202] 'relative width of capitulum (contains information similar to RH5-236)'
[203] 'olecranon fossa morphology (Y78, contains information similar to RH12-243)'
[204] 'humerofemoral index'
[205] 'size of centrale, orientation of centrale trapezoid facet, and articulation with hamate (modified from RW1-249)'
[206] 'ulnar-pisiform articulation (modified from RW2-250)'
[207] 'styloid process (Y80)'
[208] 'second digit of hand (Y81)'
[209] 'pollical divergence angle (Boyer et al., 2015)'
[210] 'nail / claw on second pedal digit (Y82, RO2-283)'
[211] 'prehallux (RO3-284)'
[212] 'astragalar width:astragalar length (Gebo et al., 2001, character 6)'
[213] 'astragalar body height (lateral body height / mid-trochlear width; Gebo et al., 2001, character 4)'
[214] 'elevated lateral trochlear margin of astragalus (Seiffert & Simons, 2001)'
[215] 'astragalar cotylar fossa (Seiffert & Simons, 2001)'
[216] 'medial tibial facet:ectal facet area ratio (Boyer et al., 2015)'
[217] 'medial tibial facet perimeter:medial tibial facet area (Boyer et al., 2015)'
[218] 'medial tibial facet height ratio (MTH1:MTH2 in Boyer et al., 2015)'
[219] 'astragalar neck length (astragalar neck length / mid-trochlear width; contains information similar to that of RA5-273)'
[220] 'astragalar neck angle (Gebo et al., 2001, character 3)'
[221] 'relative astragalar head width'
[222] 'plantarflexion of astragalar head*'
[223] 'posterior astragalar shelf (D20; contains information similar to RA4-272)'
[224] 'fibular facet angle'
[225] 'size of lateral tubercle buttressing flexor fibularis'
[226] 'position of flexor hallucis longus groove (Yapuncich et al., in press)'
[227] 'depth of flexor hallucis longus groove (Yapuncich et al., in press)'
[228] 'calcaneal width:length'
[229] 'anterior calcaneal elongation (length of calcaneus distal to ectal facet / total calcaneal length x 100) (modified from RC1-275, scoring from D22 addendum)'
[230] 'proximal calcaneal elongation (length from proximal border of ectal facet to proximal end of calcaneus / calcaneus length) from Gebo et al. 2001'
[231] 'relative length of ectal facet (ectal facet width:ectal facet length)'
[232] 'ectal facet radius of curvature'
[233] 'ectal facet flange development'

[234] 'bony distinction between plantar edge of ectal facet and body'
[235] 'size of calcaneal peroneal tubercle (100*widest point on peroneal tubercle to ectal facet, measured perpendicular to long axis of bone / calcaneal width)'
[236] 'peroneal tubercle shape'
[237] 'number of "peaks" on calcaneal peroneal tubercle'
[238] 'position of peroneal process relative to sustentaculum'
[239] 'position of the peroneal tubercle relative to ectal facet (RC2-276)'
[240] 'development of distal plantar tubercle on calcaneus'
[241] 'level of distal plantar tubercle (tubercle to cuboid facet:calcaneal length)'
[242] 'orientation of long axis of calcaneocuboid joint'
[243] 'calcaneocuboid joint shape'
[244] 'concavity of cuboid facet'
[245] 'dorsal extension of bone supporting cuboid facet'
[246] 'posterior (plantar) calcaneal bowing'
[247] 'mediolateral bowing of calcaneal tuber'
[248] 'calcaneal sustentacular facet configuration'
[249] 'form of medial margin between sustentaculum and anterior calcaneal facet (viewed dorsally)'
[250] 'facet anterior to the anterior extension of the sustentacular facet (navicular or otherwise)'
[251] 'angle between sustentaculum and ectal facet'
[252] 'shape of medial edge of sustentaculum in plantar view'
[253] 'morphology of groove for flexor fibularis under sustentaculum'
[254] 'position of distal terminus of ectal facet relative to anterior calcaneal segment'
[255] 'size of tuber calcanei'
[256] 'shape of tuber calcanei'
[257] 'dorsal heel process'
[258] 'navicular length relative to width (contains information similar to RN1-278)'
[259] 'three-pronged' distal navicular articulation'
[260] 'morphology of the naviculocuboid articulation (RN3-279)'
[261] 'MTI relative dorsoplantar diaphysis midshaft breadth'
[262] 'MTI proximal articular surface angle, in dorsolateral view with respect to the proximal end of the bone'
[263] 'MTI proximal articular surface shape in dorsolateral view'
[264] 'MTI proximal articular surface orientation in proximal view (i.e., torsion)'
[265] 'MTI peroneal process proximodistal length in dorsal view with respect to the distal end of the bone'
[266] 'MTI peroneal process dorsoplantar thickness in dorsolateral view with respect to the proximal end of the bone'
[267] 'MTI medial side of proximal articular surface with respect to the proximal end of the bone'
[268] 'MTI dorsal notch located proximal to the distal articular surface in dorsal or lateral view'
[269] 'MTI head distal projection in dorsal view'
[270] 'MTI head shape in distal view'
[271] 'MTI distal epicondyle asymmetry in distal and dorsal views'
[272] 'MTI dorsoplantar axis of head orientation relative to long axis of diaphysis in plantar view, with respect to the distal end of the bone'
[273] 'MTI proximal articular surface notch location'
[274] 'MTI distal articular surface midline keel'
[275] 'MTI medial proximally projecting tubercle size'
[276] 'MTI dorsal extension of proximal articular surface'
[277] 'lateral process of entocuneiform (RE2-281)'
[278] 'foot axis (R01-282)'
[279] 'metatarsus length (MT3 length / proximal phalanx of digit III) (contains information similar to that of R04-285)'

[280] 'length of MT1 relative to MT3 (RMT2)'
[281] 'tibial process for peroneus longus'
[282] 'retroflexion of proximal tibial articulation'
[283] 'fusion of tibia and fibula (RT1-263)'
[284] 'shape of distal surface of tibia (RT3-264)'
[285] 'rotation of the medial malleolus (RT4-265)'
[286] 'shape of the medial malleolar articular surface (RT5-266)'
[287] 'shape of distal tibial shaft (RT6-267)'
[288] 'position of tibialis posterior groove (RT7-268)'
[289] 'fovea capititis (Y75)'
[290] 'femoral head shape (RF6-256)'
[291] 'morphology of femoral head articular surface'
[292] 'femoral neck length'
[293] 'angle of femoral neck (RF2-252)'
[294] 'anteroposterior angulation of proximal femur (contains information similar to RF8-258)'
[295] 'triangular depression on medial side of proximal femur (Dagosto and Schmid, 1996)'
[296] 'greater trochanter shape (Y72)'
[297] 'crista paratrochanterica'
[298] 'relative length of trochanteric fossa (RF9-259)'
[299] 'intertrochanteric crest (RF10-260)'
[300] 'angle of lesser trochanter (RF3-253)'
[301] 'gluteal tuberosity (Y74, contains information similar to RF4-254)'
[302] 'position of gluteal tuberosity'
[303] 'patellar margin asymmetry (raised and sharply defined lateral patellar margin) (contains information similar to RF12-262)'
[304] 'knee index (contains information similar to RF5-255)'
[305] 'shape of manubrium (Y83)'
[306] 'transpedicular foramina (Y85)'
[307] 'number of thoraco-lumbar vertebrae'
[308] 'anterior inferior iliac spine (Y70)'
[309] 'ilium shape (Y67)'
[310] 'ischial flaring (Y69)'
[311] 'ischium:ilium index (Anemone & Covert, 2000)'
[312] 'pubic bone flaring (Y68)'
[313] 'tail length (Y86)'
[314] 'shape of glenoid fossa (RCr40-222)'
[315] 'postglenoid process (Y25)'
[316] 'postglenoid process-auditory bulla relationship (Y26)'
[317] 'postglenoid foramen'
[318] 'position of postglenoid foramen relative to postglenoid process'
[319] 'entoglenoid process (RCr41-223)'
[320] 'position of pyramidal processes (RCr35-217)'
[321] 'position of the anteriormost point on the palatine / maxillary suture of the palate (Y19)'
[322] 'posterior palatine torus (RCr34-216)'
[323] 'maxillary-palatine notch'
[324] 'position of the posteromedial edge of the palate in relation to M3 (Y24)'
[325] 'shape of medial pterygoid plate (RCr36-218, contains information similar to Y22)'
[326] 'lateral pterygoid-bullar overlap (RCr18-200)'
[327] 'extent of contact between the lateral pterygoid plate and the bullar wall (RCr19-201)'
[328] 'position of foramen ovale (Y28)'
[329] 'central stem of basicranium (D47)'
[330] 'choanal shape (D50)'
[331] 'basioccipital flange (contains information similar to RCr20-202)'
[332] 'encroachment of auditory bulla on pterygoid fossa (RCr17-199)'
[333] 'shape of external auditory meatus (D38)'

[334] 'suprameatal foramen (RCr21-203)'
[335] 'ascending pharyngeal artery (Y52)'
[336] 'vascular plexus associated with ascending pharyngeal artery (Y53)'
[337] 'position of chorda tympani relative to m. tensor tympani (Maier, 2008)'
[338] 'relative sizes of stapedial canal (SC) and promontory canal (PC)'
[339] 'mediolateral position of posterior carotid foramen (RCr6-188)'
[340] 'rostrocaudal position of posterior carotid foramen with respect to fenestra cochleae (contains information similar to RCr8-190)'
[341] 'ventrodorsal position of posterior carotid foramen relative to fenestra cochleae (RCr7-189)'
[342] 'position of pathway for internal carotid artery or nerve relative to fenestra cochleae (RCr9-191)'
[343] 'morphology of path for promontory artery and / or internal carotid nerve (RCr12-194)'
[344] 'peribullar pathway for internal carotid artery (RCr4-186)'
[345] 'transverse septum defining caudal wall of anterior accessory cavity (contains information similar to RCr1-183)'
[346] 'trabeculated anterior accessory cavity'
[347] 'number of cochlear turns'
[348] 'composition of bulla'
[349] 'epitympanic crest (RCr48-230)'
[350] 'morphology of annular bridge (RCr16-198)'
[351] 'position of ventral edge of tympanic bone (RCr14-196)'
[352] 'parotic fissure (RCr22-204)'
[353] 'pneumatization of mastoid (from epitympanic recess) (RCr3-185)'
[354] 'paroccipital processes (Y23)'
[355] 'emissary foramina on lateral edge of parietals (Y33)'
[356] 'pattern of sagittal cresting'
[357] 'metopic sutural fusion in adults (RCr31-213)'
[358] 'frontal-maxillary contact'
[359] 'degree of orbital convergence (contains information similar to RCr32-214)'
[360] 'expansion of ethmoturbinals (YIP89)'
[361] 'transverse lamina:ethmoturbinal recess'
[362] 'pronounced interorbital constriction (RCr27-209)'
[363] 'orbit size (contains information similar to RCr23-205)'
[364] 'foramen rotundum (Y12, RCr29-211)'
[365] 'lacrimal foramen morphology (Y11)'
[366] 'position of lacrimal foramen (RCr30-212)'
[367] 'zygomatic-lacrimal contact (Y6, RCr26-208)'
[368] 'lacrimal-palatine contact (RCr28-210)'
[369] 'ethmomaxillary fissure (Y13, modified following Cartmill 1978)'
[370] 'anterior and posterior hiatus of ethmomaxillary fissure (Cartmill, 1978)'
[371] 'frontal-palatine contact (Cartmill, 1978)'
[372] 'position of sphenopalatine foramen'
[373] 'position of infraorbital foramina (contains information similar to Y3)'
[374] 'morphology of zygomatic portion of postorbital bar (Y18, contains information similar to RCr24-25)'
[375] 'morphology of frontal segment of the postorbital bar (Y17, contains information similar to RCr24-25)'
[376] 'zygomatic arch depth'
[377] 'zygomaticofacial foramen (Y16)'
[378] 'snout length (RCr37-219)'
[379] 'maxillary depth (RCr38-220)'
[380] 'facial profile (Masters & Brothers, 2002)*'
[381] 'position of anterior palatine foramina relative to incisors (Masters & Brothers, 2002)*'
[382] 'rostral projection of premaxilla (Masters & Brothers, 2002)*'

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[383] 'ascending wing of premaxilla (RCr49-231)'
[384] 'retia mirabilia of the proximal limb vessels (YIP87)'
[385] 'nasal morphology (Y62, contains information similar to R289)'
[386] 'retinal fovea (Y60, R288)'
[387] 'tapetum lucidum (Y59, R290)'
[388] 'presence-absence of choriovitelline placenta (Y58, KPL4)'
[389] 'epitheliochorial vs. hemochorial placentation (KPL1)'
[390] 'blastocyst attachment (KPL2)'
[391] 'amniotic cavity(KPL3)'
[392] 'embryonic body stalk (KPL5)'
[393] 'allantois development (KPL6)'
[394] 'ascorbic acid synthesis'

;
STATELABELS
1
    'three incisors in each quadrant '
    'two incisors in each quadrant '
    'one incisor in each quadrant '
    'no incisors present ',
2
    'arcuate battery in occlusal view ("U"-shaped arcade) '
    'incisor cusp tips staggered ("V"-shaped arcade) ',
3
    'lower canine is not incorporated into a toothcomb '
    'lower canine is incorporated into a toothcomb ',
4
    'small (=<0.69) '
    'intermediate (=>0.70, =<1.07) '
    'large (>1.07) ',
5
    'i1 / i2 area ratio <0.65 '
    '0 / 2 '
    'i1 / i2 area ratio =>0.65, <0.82 '
    '2 / 4 '
    'i1 / i2 area ratio =>0.83, <1.00 '
    '4 / 6 '
    'i1 / i2 area ratio =>1.01,<1.25 '
    '6 / 8 '
    'i1 / i2 area ratio =>1.25 ',
6
    'ratio =>0.64 '
    'ratio =<0.64 ',
7
    'low-crowned '
    '0 / 2 '
    'moderately highcrowned '
    '2 / 4 '
    'high-crowned ',
8
    'erect or'vertical '
    '0 / 2 '
    'slightly procumbent '
    '2 / 4 '
    'very procumbent ',
9
    'erect or vertical '
    '0 / 2 '
    'procumbent '
    '2 / 4 '
    'very procumbent ',
10

```

```

'spatulate '
'pointed or lanceolate ',
11
'heel absent '
'heel present ',
12
'absent to weak '
'0 / 2 '
'strong but incomplete '
'2 / 4 '
'strong and complete ',
13
'i1 area << m1 area '
'0 / 2 '
'i1 area < or = m1 area '
'2 / 4 '
'i1 > m1 ',
14
'c1 area / m1 area < 0.40 '
'0 / 2 '
'c1 area / m1 area =>0.4, <0.8 '
'2 / 4 '
'c1 area / m1 area =>0.8, <=1.2 ',
15
'<1.07 '
'>=1.07, <1.17 '
'>=1.17 ',
16
'rounded oval '
'mesiodistally compressed '
'buccolingually compressed ',
17
'oriented in line with long axis of crown '
'mesially inflected ',
18
'rounded '
'0 / 2 '
'sharp ',
19
'oblique to occlusal plane '
'nearly horizontal to occlusal plane '
'forms part of cropping mechanism with i1-2 '
'oriented in line with buccal face of adjacent incisor ',
20
'low, squat '
'0 / 2 '
'narrow, short '
'tall, at or above toothrow '
'high crowned but very procumbent ',
21
'present '
'0 / 2 '
'absent ',
22
'two '
'0 / 2 '
'one '
'2 / 4 '
'p2 absent ',
23

```

```

'metaconid absent or indistinct '
'0 / 2 '
'metaconid is small '
'2 / 4 '
'metaconid is large ',
24
'extremely short, shorter than p3 '
'0 / 2 '
'not projecting, in line with p3 '
'2 / 4 '
'slender, projects above protoconids of p3-4 '
'4 / 6 '
'massive, projects above protoconids of p3-4 ',
25
'absent '
'0 / 2 '
'incomplete, broken at protoconid and hypoconid '
'2 / 4 '
'complete ',
26
'present, large '
'0 / 2 '
'present, small '
'2 / 4 '
'negligible or absent ',
27
'present '
'0 / 2 '
'absent ',
28
'absent '
'0 / 2 '
'present, small '
'2 / 4 '
'present, large ',
29
'transversely oriented '
'0 / 2 '
'distally or distolingually oriented '
'2 / 4 '
'absent ',
30
'one '
'0 / 2 '
'two ',
31
'mesial root placed directly mesial to distal root'
'0 / 2 '
'mesial root placed lateral to distal root',
32
'large and well-defined, projects above other talonid cusps'
'0 / 2 '
'very small, absent, or incorporated into talonid as an indistinct
cusp',
33
absent
'0 / 2 '
'lingual talonid crest present but an entoconid does not stand out
above it'
'2 / 4 '

```

```

'entoconid is a small discrete cusp',
34
'p3 much lower than p4'
'0 / 2'
'p3 slightly lower than p4'
'2 / 4'
'p3 equal in height to p4'
'4 / 6'
'p3 higher than p4',
35
'<0.45'
'0 / 2'
'0.45-0.59'
'2 / 4'
'0.60-0.69'
'4 / 6'
'0.70-0.79'
'6 / 8'
'>0.80',
36
one
two,
37
'absent or indistinct'
'0 / 2'
small
'2 / 4'
large,
38
'close to protoconid'
'0 / 2'
'widely spaced from protoconid',
39
'metaconid is distal to protoconid'
'0 / 2'
'metaconid is placed transverse to protoconid',
40
'p4 paraconid is present and large'
'0 / 2'
'p4 paraconid is present and small'
'2 / 4'
'p4 paraconid is very small or absent',
41
'mesial to protoconid'
'mesiolingual, between protoconid and metaconid'
'mesial to metaconid, widely spaced from metaconid',
42
'protocristid poorly developed or absent'
'0 / 2'
'distolingually oriented protocristid present'
'2 / 4'
'trenchant and tranversely oriented protocristid present',
43
'premetacristid absent or poorly developed'
'0 / 2'
'premetacristid present',
44
'weak or absent'
'0 / 2'
moderate
'2 / 4'

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```

    'very strong',
45
    'weak or absent'
    '0 / 2'
    moderate
    '2 / 4'
    'very strong',
46
    'absent or a trace'
    '0 / 2'
    'lingual talonid crest present but an entoconid does not stand out
above it'
    '2 / 4'
    'entoconid is a small discrete cusp',
47
    'no aspect of the talonid is at level of m1 trigonid basin'
    '0 / 2'
    'hypoconid extends to level of m1 trigonid basin'
    '2 / 4'
    'entire talonid basin extends to level of m1 trigonid basin',
48
    absent
    '0 / 2'
    weak
    '2 / 4'
    strong,
49
    'buccal to protoconid'
    '0 / 2'
    'distal to protoconid'
    '2 / 4'
    'between protoconid and metaconid'
    '4 / 6'
    'distal to metaconid',
50
    absent
    '0 / 2'
    weak
    '2 / 4'
    strong,
51
    'no crowding'
    '0 / 2'
    'slightly crowded'
    '2 / 4'
    'very crowded',
52
    'not basally inflated'
    '0 / 2'
    'slightly basally inflated'
    '2 / 4'
    'very basally inflated',
53
    'crown bases vertical in lateral perspective'
    '0 / 2'
    'slightly oblique'
    '2 / 4'
    'strongly oblique',
    'projecting mesially',
54
    'not exodaenodont'

```

```

'slightly exodaenodont'
'very exodaenodont',
55
'absent or indistinct'
'0 / 2'
'present and distinct',
56
'absent or discontinuous'
'0 / 2'
present,
57
'<0.95'
'0 / 2'
'>0.96, <1.14'
'2 / 4'
'>1.15, <1.35'
'4 / 6'
'>1.36, <1.46'
'6 / 8'
'>1.47',
58
'<0.62'
'0 / 2'
'>0.63, <0.72'
'2 / 4'
'>0.73, <0.82'
'4 / 6'
'>0.83, <0.92'
'6 / 8'
'>0.93',
59
'1.0-1.15'
'0 / 2'
'1.16-1.22'
'2 / 4'
'1.23-1.32'
'4 / 6'
'>1.33',
60
'1.10-3.00 mm'
'0 / 2'
'3.10-5.00 mm'
'2 / 4'
'5.10-7.00 mm'
'4 / 6'
'7.10-9.00 mm'
'6 / 8'
'>9.10 mm',
61
'absent or crestiform'
'0 / 2'
'present, small'
'2 / 4'
'present, large',
62
'mesial to protoconid'
'mesiolingual, equidistant between protoconid and metaconid'
'1 / 3'
'mesial to metaconid but widely spaced from it twinned with
metaconid',
63

```

```

absent
'0 / 2'
present,
64
'premetacristid absent or indistinct'
'0 / 2'
'premetacristid present,
65
'approximately transverse to protoconid'
'0 / 2'
'distal to protoconid',
66
'higher than talonid (=>1.20)'
'0 / 2'
'slightly higher than talonid (=>1.10, <1.20)'
'2 / 4'
'trigonid and talonid of similar height',
67
'reaches trigonid wall at a point distal to protoconid'
'0 / 2'
'reaches trigonid wall at a point distolingual to protoconid'
'2 / 4'
'reaches trigonid wall at a point distal to metaconid',
68
'runs to base of trigonid'
'0 / 2'
'runs part way up the distal trigonid wall'
'2 / 4'
'connects with protoconid tip or protocristid'
'4 / 6'
'connects with metaconid',
69
'twinned with, or most closely situated next to, entoconid'
'0 / 2'
central
'2 / 4'
'closer to hypoconid than to entoconid',
70
large
'0 / 2'
moderate
'2 / 4'
small
'4 / 6'
absent,
71
'weak (rounded)'
'0 / 2'
'strong (trenchant)',
72
'absent or indistinct'
'0 / 2'
weak
'2 / 4'
strong,
73
'absent to trace'
'0 / 2'
'partial, discontinuous'
'2 / 4'
complete,

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```

74
open
'0 / 2'
'notched lingually or closed',
75
absent
'0 / 2'
'present, small'
'2 / 4'
'present, large',
76
'mesial to protoconid'
'0 / 2'
'mesiolingual,
'approximately equidistant between protoconid and metaconid'
'2 / 4'
'mesial to metaconid but widely spaced from it twinned with
metaconid',
77
'much wider than talonid (=>1.11)'
'0 / 2'
'width similar (<1.11,>0.90)'
'2 / 4'
'much narrower than talonid (=<0.90)',

78
'reaches trigonid wall at a point distal to protoconid '0 / 2'
'reaches trigonid wall at a point distolingual to protoconid'
'2 / 4'
'reaches trigonid wall at a point distal to metaconid',

79
'runs to base of trigonid'
'0 / 2'
'runs part way up distal trigonid wall'
'connects to protoconid tip or protocristid'
'3 / 5'
'connects with metaconid',

80
'weak (rounded)'
'0 / 2'
'strong (trenchant)',

81
'mesial to hypoconid'
'0 / 2'
'transverse to hypoconid'
'2 / 4'
'distal to hypoconid',

82
'twinned with, or most closely situated next to, entoconid'
'0 / 2'
central
'2 / 4'
'closer to hypoconid than to entoconid',

83
large
'0 / 2'
moderate
'2 / 4'
small
'4 / 6'
absent,

```

```

84
    'no postentoconid sulcus'
    'hypoconulid closely situated next to entoconid and postentoconid
sulcus present, entoconid confluent with distal talonid wall'
    'distolingual fovea present, entoconid confluent with posterior
talonid wall'
    'distolingual fovea present, entoconid mesiodistally abbreviated
and not confluent with posterior talonid wall',
85
    absent
    'variably present',
86
    crestiform
    '0 / 2'
    'moderate basal inflation'
    '2 / 4'
    'cusp bases bulbous',
87
    'm3 much longer than m2 (0.71-0.80)'
    '0 / 2'
    'm3 longer than m2 (0.81-0.90)'
    '2 / 4'
    'm3 slightly longer or equal in length to m2 (0.91-1.00)'
    '4 / 6'
    'm3 slightly shorter than m2 (1.01-1.12)'
    '6 / 8'
    'm3 much shorter than m2 (=>1.13) or absent',
88
    absent
    '0 / 2'
    'present, small'
    '2 / 4'
    'present, large',
89
    'mesial to protoconid'
    '0 / 2'
    'mesiolingual, between protoconid and metaconid'
    '2 / 4'
    'mesial to metaconid but widely spaced from it'
    '4 / 6'
    'twinned with metaconid',
90
    'absent or indistinct'
    'runs to base of trigonid runs part way up distal trigonid wall'
    'connects with protoconid tip or protocristid connects with
metaconid',
91
    '>=1.20'
    '0 / 2'
    '<1.20->1.05'
    '2 / 4'
    '<1.05',
92
    'present and distinct'
    '0 / 2'
    'greatly reduced or absent',
93
    lobate
    '0 / 2'
    'not lobate',
94

```

```

'centrally located'
'twinned with, or situated closest to, entoconid'
'buccally located, closer to hypoconid',
95
absent
'0 / 2'
single
'2 / 4'
'double, or additional cusp distal to entoconid that is independent
of distal lobe',
96
one
two,
97
absent
present,
98
absent
'0 / 2'
'present, protocristids poorly developed or absent',
99
absent
'0 / 2'
'trenchant postmetacristid or incipient metastyloid'
'2 / 4'
'present, large',
100
smooth
'0 / 2'
'slightly crenulated'
'2 / 4'
'highly crenulated',
101
'very broad'
narrow,
102
'absent, teeth widely spaced'
'0 / 2'
'present as a narrow contact'
'2 / 4'
'I2 tightly packed against I1, I1 paracrista abbreviated',
103
'areas approximately equal or I1 smaller than I2 (<=1.00)'
'0 / 2'
'I1 slightly larger than I2 (>1.00,<1.40)'
'2 / 4'
'I1 much larger than I2 (>1.40)',
104
'weak, discontinuous'
'0 / 2'
'moderate, continuous'
'2 / 4'
strong,
105
absent
present,
106
'rounded oval (<1.05)'
'0 / 2'
'buccolingually compressed (>1.05, <1.30)'
'2 / 4'

```

```

    'extremely compressed (>1.30)',

107
    'spatulate (no apparent occlusal cusp, mesial and distal edges
continuous and rounded)'
    '0 / 2'
    'semi-spatulate (central cusp present, but blunt with discernable
mesial and distal occlusal crests)'
    '2 / 4'
    'central occlusal cusp pointed, occlusal edges steep',
108
    'small (=<0.50)'
    'moderate (>0.5, <0.56)'
    'large (>0.56)',

109
    'occlusal edge approximately orthogonal to long axis of root'
    'occlusal edge wears at a steep angle to long axis of root'
    'crown with pronounced mesial asymmetry (=mesial process) in unworn
state',
110
    absent
    present,
111
    'rounded oval (=<1.05)'
    '0 / 2'
    'slightly buccolingually compressed (>1.05, <1.30)'
    '2 / 4'
    'extremely buccolingually compressed (=>1.30)',

112
    present
    '0 / 2'
    absent,
113
    'three in each quadrant'
    'two in each quadrant'
    'one or none in each quadrant',
114
    'round in cross-section'
    '0 / 2'
    oval
    '2 / 4'
    'strongly compressed buccolingually',
115
    'long axis of canine oriented in line with adjacent premolar'
    'canine is slightly rotated internally'
    'canine is strongly rotated internally',
116
    'shallow or absent'
    deep,
117
    'weak or absent'
    '0 / 2'
    strong
    '2 / 4'
    'very strong',
118
    'wears against p1-2'
    '0 / 2'
    'wears against p2'
    '2 / 4'
    'wears against p2-3'
    '4 / 6'

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```

    'wears against p3',
119
    present
    absent,
120
    three
    two
    one
    P2 absent
121
    triangular
    'suboval with the long axis buccolingual'
    'suboval with the long axis mesiodistal'
    round,
122
    present
    absent,
123
    'smaller than, or subequal in height (P2 height / P3 height <=1.1)'
    '0 / 2'
    'P2 slightly taller than P3 (P2 height / P3 height =>1.11, <1.5)'
    '2 / 4'
    'P2 much taller than P3 (P2 height / P3 height >1.51)',
124
    'much smaller than P3 (<=0.85) (if P2 is absent, taxon is assigned
state 0)'
    '0 / 2'
    'approximately the same size, or only slightly smaller, than P3
(>0.85, <0.95)'
    '2 / 4'
    'much larger than P3 (>=.95)',
125
    'smoothly rounded'
    '0 / 2'
    'waisted between buccal and lingual cusps',
126
    absent
    '0 / 2'
    'present, small'
    '2 / 4'
    'present, distinct',
127
    absent
    '0 / 2'
    present,
128
    absent
    '0 / 2'
    present,
129
    one
    '0 / 2'
    two
    '2 / 4'
    three,
130
    present
    '0 / 2'
    absent,
131
    absent

```

```

    '0 / 2'
    present,
132
    'trigon>=talon'
    'trigon<talon',
133
    'absent or weak'
    '0 / 2'
    strong,
134
    'absent or indistinct'
    'transverse crest connecting protocone to paracone'
    present,
135
    absent
    '0 / 2'
    present,
136
    absent
    '0 / 2'
    present,
137
    'low relative to paracone'
    'high relative to paracone',
138
    absent
    '0 / 2'
    present,
139
    absent
    present,
140
    absent
    '0 / 2'
    present,
141
    absent
    '0 / 2'
    'weak, short'
    '2 / 4'
    strong
    '4 / 6'
    'strong, secondary postprotocrista directed toward metacone',
142
    triangular
    suboval
    '1 / 3'
    squared,
143
    one
    two
    three,
144
    'P4<<M1 (<=0.66)'
    '0 / 2'
    'P4<M1 (>0.66, <=0.76)'
    '2 / 4'
    'P4=M1 (0.77-1.05)'
    '4 / 6'
    'P4>M1 (>1.06)',

145

```

```

absent
'0 / 2'
small
'2 / 4'
large,
146
'M1>M2 (<1.40,>1.0)'
'0 / 2'
'M1=<M2 (=<1.0)',

147
absent
'0 / 2'
present,
148
absent
'0 / 2'
'small-moderate (smaller than paracone)'
'2 / 4'
'large (nearly as large as protocone)',

149
'attached to preprotocrista'
'0 / 2'
'not attached to preprotocrista',

150
large
'0 / 2'
small
'2 / 4'
absent,
151
'distal, slightly lingual to protocone'
'0 / 2'
'distal, far lingual to protocone',

152
absent
'0 / 2'
'present, distal crown margin weakly concave'
'2 / 4'
'present, distal crown margin deeply notched',
153
    'lobe does not extend lingually far beyond
protocone'
    '0 / 2'
    'lobe does extend far lingually past protocone',
154
absent
'0 / 2'
weak
'2 / 4'
'strong -- reaches to postprotocrista, encloses the
talon lingually',
155
absent
'0 / 2'
weak
'2 / 4'
'strong ',

156
'strong, runs to base of metaconule or metacone'
'0 / 2'
'strong but short, does not reach to base of
metacone'

```

```

    '2 / 4'
    absent,
157
    absent
    '0 / 2'
    small
    '2 / 4'
    moderate
    '4 / 6'
    large,
158
    'absent or weak '
    '0 / 2'
    'strong ',
159
    'absent or weak'
    '0 / 2'
    strong,
160
    sharp
    '0 / 2'
    indistinct,
161
    'straight, aligned with mesiodistal plane'
    '0 / 2'
    'crests are more buccally oriented, meet at an
angle'
    '2 / 4'
    'crests meet at a sharp angle or form a mesostyle',
162
    absent
    '0 / 2'
    'present but poorly developed'
    '2 / 4'
    'present and distinct'
    '4 / 6'
    'extensive buccal "shelf"',
163
    'three or more, three or more'
    'three, two',
164
    'very broad (>1.65)'
    '0 / 2'
    'broad (<1.65,>1.30)'
    '2 / 4'
    'squared (=<1.30)',
165
    absent
    '0 / 2'
    present,
166
    large
    '0 / 2'
    small
    '2 / 4'
    absent,
167
    'short, indistinct, or absent'
    'long, trenchant, and labially extended',
168
    'no expansion'

```

```

'0 / 2'
'slight expansion'
'2 / 4'
'considerable expansion',
169
absent
'0 / 2'
'weak, broken'
'2 / 4'
'strong, complete ',
170
'strong, complete, long'
'0 / 2'
'strong, short'
'2 / 4'
'weak or absent',
171
'not inflated'
'0 / 2'
'slightly inflated'
'2 / 4'
'very inflated',
172
'absent or very small'
'0 / 2'
'moderate (but smaller than paracone)'
'2 / 4'
'large (equal to paracone)',
173
absent
'0 / 2'
'small-moderate'
'2 / 4'
large,
174
'absent or very small'
'0 / 2'
small
'2 / 4'
large,
175
'very small (half the size of M1 or less)'
'0 / 2'
'small (two thirds)'
'2 / 4'
'large (approximately as large)',

176
three
'0 / 2'
two
'2 / 4'
one,
177
absent
'0 / 2'
present,
178
'sharply hooked '
'0 / 2'
'smoothly rounded '
'2 / 4'

```

```

    'rounded but expanded posteriorly',
179
    shallow
    '0 / 2'
    'deeply excavated',
180
    'shallow (less than 1.8 times as deep @ m2 as md
length of m2)'
    '0 / 2'
    'deep (>1.8 times as deep @ m2 as md length of m2,
<2.19)'
    '2 / 4'
    'very deep (more than 2.2 times as deep @ m2 as md
length of m2)',

181
    'very high above'
    'slightly above or equal',
182
    'at level of toothrow'
    'slightly above'
    'well above toothrow',
183
    '<1.25'
    '0 / 2'
    '<1.5, >1.25'
    '2 / 4'
    '>1.5, <1.75'
    '4 / 6'
    '>1.75',
184
    '<=.90 '
    '0 / 2'
    '>.9, <=1.0'
    '2 / 4'
    '>1.0, <=1.1 '
    '4 / 6'
    '>1.1',
185
    'supraspinous fossa larger than infraspinous fossa '
    '0 / 2'
    'fossae roughly equivalent '
    '2 / 4'
    'infraspinous fossa approximately two times as large
as thesupraspinous fossa '
    '4 / 6'
    'infraspinous fossa approximately three times as
large as thesupraspinous fossa ',
186
    'humeral head is expanded dorsal to tubercles'
    '0 / 2'
    'humeral head and tubercles are approximately equal
in height'
    '2 / 4'
    'tubercles are expanded above humeral head',
187
    prominent
    '0 / 2'
    low,
188
    'narrow and deep'
    '0 / 2'

```

```

'narrow and shallow'
'2 / 4'
'shallow and wide',
189
'absent or poorly defined'
'0 / 2'
'elongate well-defined crest'
'2 / 4'
'well-developed tubercle',
190
prominent
low,
191
broad
'0 / 2'
moderate
'2 / 4'
narrow,
192
'foramen is placed far proximal to trochlea'
'lateral wall of medial strut defining foramen is
confluent with medial edge of the trochlea'
'0 / 2'
'foramen more medial, and lateral wall of medial
strut defining foramen is not confluent with medial edge of the trochlea'
absent,
193
parallel
'0 / 2'
'slight dorsal angle'
'2 / 4'
'large dorsal angle',
194
reduced
'0 / 2'
prominent,
195
present
'0 / 2'
'small, shallow'
'2 / 4'
'absent',
196
'cylindrical, distomedial aspect of trochlea is
straight'
'0 / 2'
'conical, medial aspect of trochlea flares
distally',
197
subequal
'0 / 2'
'medial edge more flared than lateral edge',
198
'no pronounced lips on dorsal trochlear edges'
'0 / 2'
'both medial and lateral edges pronounced'
'very pronounced lateral lip',
199
'trochlea and capitulum are confluent, with no
distinct trochleocapitular ridge'
'0 / 2'

```

'lateral aspect of trochlea is offset from capitulum
 by a weakridge'
 '2 / 4'
 'lateral aspect of trochlea is separated from
 capitulum by a deep gutter',
 200
 globular
 '0 / 2'
 ovoid,
 201
 'elongate and distinct'
 'short or absent'
 '1 / 3'
 'proximodistally tall capitular flange is present',
 202
 'ventral articular width / capitular width >2.5'
 '0 / 2'
 '<2.5, >2.0'
 '2 / 4'
 '<2.0',
 203
 'deep, open and unossified '
 '0 / 2'
 'moderately deep, thinly ossified and nearly
 transparent '
 '2 / 4'
 'shallow, robustly ossified ',
 204
 '<59'
 '0 / 2'
 '60-69'
 '2 / 4'
 '70-79'
 '4 / 6'
 '80-89'
 '6 / 8'
 '90-100',
 205
 'facet faces distally, no articulation with hamate'
 'facet faces distoradially, articulation with
 hamate'
 'centrale not present as an independent element',
 206
 'no ulnar-pisiform articulation'
 'facet on pisiform for ulnar styloid process is
 smaller than, or roughly equal in size to, that for triquetrum'
 'facet on pisiform for ulnar styloid process is much
 enlarged and deeply excavated',
 207
 'no discernable styloid process '
 'present but only moderately developed '
 'long and well-developed ',
 208
 'of normal length '
 'drastically reduced ',
 209
 '0-15 degrees'
 '0 / 2'
 '16-30 degrees'
 '2 / 4'
 '>31 degrees',

```

210
    'nail present'
    'claw present ',
211
    present
    absent,
212
    '<50'
    '0 / 2'
    '>50, <60'
    '2 / 4'
    '>60, <70'
    '4 / 6'
    '>70',
213
    '<100'
    '0 / 2'
    '100-120'
    '2 / 4'
    '>120',
214
    absent
    '0 / 2'
    present,
215
    shallow
    '0 / 2'
    moderate
    '2 / 4'
    'deep, medially projecting',
216
    '< -0.151'
    '0 / 2'
    'between -0.15 and 0'
    '2 / 4'
    'between 0 and 0.15'
    '4 / 6'
    '> 0.16',
217
    '> 1.55'
    '0 / 2'
    'between 1.56 and 1.60'
    '2 / 4'
    '>1.61',
218
    '<-0.151'
    '0 / 2'
    'between -0.15 and 0'
    '2 / 4'
    'between 0 and 0.15'
    '4 / 6'
    'between 0.151 and 0.30'
    '6 / 8'
    '>0.301',
219
    '<100'
    '0 / 2'
    '>100, <120'
    '2 / 4'
    '>120',
220

```

```

'<20 degrees'
'0 / 2'
'20-30 degrees'
'2 / 4'
'>30 degrees',
221
'head width / head height x 100 <115'
'0 / 2'
'head width / head height x 100 >115, <130'
'2 / 4'
'head width / head height x 100 >130',
222
absent
present,
223
absent
'0 / 2'
'present, small'
'2 / 4'
'present, large',
224
'79 degrees or less'
'0 / 2'
'80-89 degrees'
'2 / 4'
'90-99 degrees'
'4 / 6'
'100-109 degrees'
'6 / 8'
'110 degrees or higher,
225
'poorly developed'
'0 / 2'
small
'2 / 4'
large,
226
'> -0.2'
'0 / 2'
'between -0.21 and -0.4'
'2 / 4' 'between -0.41 and -0.6'
'4 / 6'
'> -0.61',
227
'< 1.0'
'0 / 2'
'between 1.01 and 1.25'
'2 / 4'
'between 1.26 and 1.5'
'4 / 6'
'> 1.5',
228
'<35'
'0 / 2'
'>35, <40'
'2 / 4'
'>40, <45'
'4 / 6'
'>45, <50'
'6 / 8'
'>50',

```

229
 '>30,<40'
 '0 / 2'
 '>41,<50'
 '2 / 4'
 '>51,<60'
 '4 / 6'
 '>61,<70'
 '6 / 8'
 '>71',
 230
 '.10-.15'
 '0 / 2'
 '.16-.20'
 '2 / 4'
 '.21-.25'
 '4 / 6'
 '.26-.30'
 '6 / 8'
 '>.31',
 231
 '<50'
 '0 / 2'
 '>50, <60'
 '2 / 4'
 '>60',
 232
 '<120 degrees'
 '>=120 degrees',
 233
 absent
 intermediate
 present,
 234
 'no well-defined border'
 'well-defined border present',
 235
 'massive, extends far laterally (>=21)'
 'medium (<21)'
 'highly reduced or too small to measure',
 236
 'discrete tubercle with clearly defined borders'
 'tubercle gradually slopes into body (substantially
 longer proximodistally relative to mediolateral width)',
 237
 'single tubercle present
 'two "peaks" present',
 238
 'below lower half'
 'upper half',
 239
 'maximum width of peroneal tubercle is placed distal
 to distal terminus of ectal facet
 'maximum width of peroneal tubercle is placed
 approximately at the distal terminus of the ectal facet'
 'maximum width of peroneal tubercle is placed
 proximal to the distal terminus of the ectal facet, closer to the distal
 terminus of the ectal facet than the proximal'
 'maximum width of peroneal tubercle is placed
 proximal to distal terminus of the ectal facet, closer to the proximal
 terminus of the ectal facet than distal',

```

240
    'small, poorly developed'
    '0 / 2'
    'well-developed',
241
    'distal, near cuboid facet (0-0.19)'
    'more proximal (>0.20)',
242
    dorsoventral
    oblique
    mediolateral,
243
    oval
    'fan-shaped, notch is articular'
    'fan-shaped, notch is non-articular'
    'oval but longest in dorsoplantar direction',
244
    'flat (>=160'
    'shallow (>=150, <160'
    'deep (<150)',
245
    absent
    present,
246
    absent
    'present, moderately developed'
    'present, extreme bowing',
247
    absent
    'present, moderate bowing'
    'present, extreme bowing',
248
    'single continuous sustentacular facet present'
    '0 / 2'
    'separate anterior and posterior sustentacular
facets present',
249
    'waisted into body'
    'relatively linear medial margin',
250
    prominent
    'very small or absent',
251
    '<140'
    '140-160'
    '>160-<180'
    '>180',
252
    'triangular or beak-like'
    rounded,
253
    'no noticeable groove present'
    'deep medially with distinct groove or wall',
254
    dorsally positioned on body
    intermediate condition
    sunk into body plantarly,
255
    'relatively small (sliver, oval, no clear insertion
for tendo calcanei)'

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```

        'medium (large in one direction, insertion for tendo
calcanei present but not robust)'
        'relatively large',
256
        oval
        'square / rectangular'
        'uneven walls / trapezoidal'
        'proximally projecting medial wall',
257
        'tucked under ectal facet in lateral view'
        'level with ectal facet in lateral view'
        'projects dorsal to ectal facet',
258
        '<100)'
        '(100-150)'
        '>150% longer than wide)',
259
        absent
        present,
260
        'cuboid facet contacts only the ectocuneiform'
        'cuboid facet contacts the ectocuneiform and the
mesocuneiform',
261
        wide
        narrow,
262
        '<=105 degrees'
        '>105 degrees',
263
        'slight concavity'
        'deep concavity, saddle-shaped',
264
        dorsoventral
        '0 / 2'
        intermediate
        '2 / 4'
        mediolateral,
265
        flat
        short
        intermediate
        long,
266
        flat
        shallow
        deep,
267
        'rounded or weak keel'
        'strong keel',
268
        deep
        intermediate
        shallow,
269
        short
        long,
270
        ovoid
        rectangular,
271

```

'medial epicondyle larger'
 'epicondyles symmetrical'
 'lateral epicondyle larger',
 272
 medial
 intermediate
 lateral,
 273
 absent
 medioplantar
 lateroplantar,
 274
 single
 bifurcate,
 275
 'smaller or equal in size to peroneal process'
 'larger than peroneal process',
 276
 present
 absent,
 277
 'small '
 'hypertrophied ',
 278
 mesaxonic
 paraxonic
 ectaxonic,
 279
 '<1.0'
 '0 / 2'
 '>1.01, <1.5'
 '2 / 4'
 '>1.51, <2.0'
 '4 / 6'
 '>2.01',
 280
 'less than 70% the length of MT3'
 '0 / 2'
 '71-80%'
 '2 / 4'
 '81-90%'
 '4 / 6'
 '91-100%'
 '6 / 8'
 '>100%',
 281
 'absent or poorly developed'
 'present and distinct',
 282
 'absent, articular surface of tibial condyles
 perpendicular to longaxis of tibial shaft'
 'moderate retroflexion present'
 'proximal articular surface is strongly
 retroflexed',
 283
 'absent, small articulation'
 'no fusion, moderate articulation'
 'no fusion but extensive articulation'
 fusion,
 284
 square

| | |
|-----|--|
| | intermediate triangular, |
| 285 | none '0 / 2' slight '2 / 4' strong, |
| 286 | flat '0 / 2' 'anteriorly convex, posteriorly flat' '2 / 4' 'all convex', |
| 287 | 'no compression' 'anteroposteriorly compressed', |
| 288 | 'on medial side of malleolus' '0 / 2' 'on posterior side of malleolus', |
| 289 | 'small and insignificant ' '0 / 2' 'present and well-developed ', |
| 290 | spherical semicylindrical cylindrical, |
| 291 | 'restricted to femoral head' 'extends onto back of femoral neck', |
| 292 | '<=75' '0 / 2' '>75, <120' '2 / 4' '=>120', |
| 293 | '<60' '0 / 2' '60-70' '2 / 4' '>70', |
| 294 | 'bent anteriorly' 'not bent anteriorly', |
| 295 | absent present, |
| 296 | 'hook-shaped ' '0 / 2' 'rounded ', |
| 297 | absent '0 / 2' present, |
| 298 | '>125 (long)' '0 / 2' |

```

'110-125 (moderate)'
'2 / 4'
'<110 (very short)',

299
absent
present,

300
'medial (0-30 degrees)'
'0 / 2'
'posterior (>30 degrees)',

301
'present, large'
'0 / 2'
'present, small and reduced to a thin crest'
'2 / 4'
absent,

302
'proximal to lesser trochanter'
'0 / 2'
'at level of lesser trochanter'
'2 / 4'
'distal to lesser trochanter',

303
absent
present,

304
'100 or higher'
'90-99'
'80-89'
'70-79',

305
'sternal head elongate '
'shortened and triangular in shape ',

306
'absent '
'present ',

307
'17 or fewer'
'18'
'0 / 2'
'19'
'2 / 4'
'20'
'4 / 6'
'21 or more',

308
'tuberosity not expressed'
'small tubercle present along margo acetabuli'
'well-developed tuberosity present',

309
'narrow '
'0 / 2'
'markedly flared ',

310
'absent '
'present ',

311
'60-70'
'0 / 2'
'50-59'
'2 / 4'

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```

        '40-49'
        '4 / 6'
        '30-39 or <',
312
        'absent '
        'present ',
313
        'long tail '
        reduced
        absent,
314
        'wide and biconcave'
        'anteroposteriorly oriented trough',
315
        'present '
        'absent ',
316
        'not confluent '
        '0 / 2'
        'partially fused '
        '2 / 4'
        'postglenoid process fused to lateral aspect of
bulla',
317
        present
        absent,
318
        'posterior to postglenoid process'
        '0 / 2'
        'medial to postglenoid process',
319
        'indistinct or absent'
        '0 / 2'
        robust,
320
        'medially placed'
        '0 / 2'
        'laterally placed',
321
        'medial to space between M1 and M2 or more
posterior'
        '0 / 2'
        'medial to M1'
        '2 / 4'
        'medial to the space between P4 and M1',
322
        present
        '0 / 2'
        absent,
323
        absent
        present,
324
        'anterior to M3 '
        '0 / 2'
        'medial to M3 '
        '2 / 4'
        'posterior to M3 ',
325
        'long medial pterygoid plate extending one-third to
one half of the distance to the anterior surface of the bulla'

```

'0 / 2'
 'short but distinct from lateral pterygoid plate for
 its entiredorsoventral extent'
 '2 / 4'
 'medial pterygoid plate entirely absent, or reduced
 to a low rugosity',
 326
 absent
 '0 / 2'
 abutting
 '2 / 4'
 laminar,
 327
 slight
 'very extensive',
 328
 'lateral side of lateral pterygoid '
 '0 / 2, or posterior to terminus of lateral
 pterygoid'
 329
 narrow
 broad,
 330
 broad
 peaked,
 331
 'absent or minimal'
 'present, extensive',
 332
 absent
 'present and formed by the AAC'
 'present and formed by the tympanic cavity'
 '1 / 2',
 333
 tubular
 '0 / 2'
 'not tubular',
 334
 absent
 'present, small, and in the posterior root of the
 zygomatic arch'
 meatus'
 'present, large, and above the external auditory
 meatus'
 '0 / 2',
 335
 'if present is poorly developed '
 'present and enlarged ',
 336
 'absent '
 'present ',
 337
 'ventral to m. tensor tympani'
 'dorsal to m. tensor tympani'
 'm. tensor tympani absent',
 338
 'LN(PC diameter / SC diameter) <0'
 '0 / 2'
 'LN(PC diameter / SC diameter) >0.01, <1.0 '
 '2 / 4'
 'LN(PC diameter / SC diameter) >1.01, <2.0 '

```

'4 / 6'
'LN(PC diameter / SC diameter) >2.01, <10'
'6 / 8'
'LN(PC diameter / SC diameter) >10',
339
    medial
    'midline of bulla'
    lateral,
340
    'posterior to fenestra cochleae'
    'ventral to fenestra cochleae'
    'anterior to fenestra cochleae',
341
    dorsal
    ventral,
342
    'runs across ventral lip of fenestra cochleae,
shielding it from ventral view'
    'does not shield fenestra cochleae',
343
    'promontorial canal present and fully enclosed in
its course through the middle ear'
    'promontorial canal present but short and continuous
anteriorly with trough / groove'
    'promontorial canal absent, trough or groove present
across entire promontorium',
344
    absent
    present,
345
    absent
    'present, forms lateral wall of AAC pneumatized from
tympanic cavity'
    'present, forms lateral wall of AAC pneumatized from
epitympanic recess',
346
    absent
    present,
347
    '<1.9'
    '0 / 2'
    '2.0-2.49'
    '2 / 4'
    '2.5-2.99'
    '4 / 6'
    '>3',
348
    petrosal
    entotympanic,
349
    absent
    present,
350
    'linea semicircularis or partial anular bridge
formed on anentotympanic bulla'
    'linea semicircularis formed on a petrosal bulla'
    'complete annular bridge',
351
    intrabullar
    extrabullar,
352

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```

        patent
        closed,
353
        absent
        'present, moderately inflated'
        'present, greatly inflated',
354
        absent
        '0 / 2'
        'present, small'
        '2 / 4'
        'present, well-developed',
355
        'present '
        '0 / 2'
        'absent ',
356
        'temporal lines converge on frontal'
        'temporal lines converge on the parietals, forming
short sagittalcrest'
        'temporal lines are not confluent, no sagittal crest
present'
        'sagittal crest is extensive, but temporal lines
converge onparietals that extend far rostrally between frontal bones'
        '0 / 2',
357
        absent
        '0 / 2'
        present,
358
        present
        'absent due to intervening lacrimal '
        'absent due to intervening premaxilla ',
359
        '>89'
        '0 / 2'
        '90-104'
        '2 / 4'
        '105-119'
        '4 / 6'
        '120-134'
        '6 / 8'
        '>135',
360
        'no anteromedial expansion '
        'anterior and medial expansion ',
361
        'extensive transverse lamina and ethmoturbinal
recess present'
        'extensive transverse lamina and ethmoturbinal
recess absent',
362
        absent
        'present below CN I',
363
        small
        large
        hypertrophied,
364
        'confluent with the superior orbital fissure '
        'present ',

```

365
'surrounded by lacrimal bone'
'foramen lies on lacrimal / maxillary suture'
'foramen lies on the lacrimal / maxillary suture but
is primarily surrounded by maxilla',
366
'on rim, or outside of, orbit'
'0 / 2'
'inside the orbit',
367
'present'
'0 / 2'
'absent',
368
'contact present'
'no contact, separated by a large fronto-maxillary
contact (and insome taxa, a small os planum of the ethmoid)'
'no contact, separated by a large os planum',
369
'no complete ethmomaxillary fissure present'
'0 / 2'
'complete ethmomaxillary fissure present',
370
'anterior hiatus variably present'
'0 / 2'
'posterior hiatus at least variably present'
'2 / 4'
'no hiatuses present',
371
present
'0 / 2'
absent,
372
'within palatine'
'0 / 2'
'on ethmopalatine suture',
373
'above P2'
'0 / 2'
'above P3'
'2 / 4'
'above P4'
'4 / 6'
'above M1',
374
'no postorbital bar'
'slender and delicate'
'1 / 3'
'wide and robust'
'contributes to postorbital septum',
375
'partial frontal process but no postorbital bar'
'slender and delicate'
'1 / 3'
'wide and robust'
'incorporated into postorbital septum',
376
slender
'0 / 2'
'dorsoventrally deep',
377

```

'absent '
'0 / 2'
'present, small '
'2 / 4'
'present, large ',
378
'long snout'
'short snout',
379
deep
shallow,
380
straight
'0 / 2'
dished,
381
'foramina sit behind first incisors'
'0 / 2'
'foramina intrude between first incisors',
382
'no extension of premaxilla beyond anterior
incisors'
'mild premaxillary projection'
'considerable projection, forming a tubular anterior
rostrum',
383
narrow
broad,
384
'absent '
'present ',
385
'lateral cleft between medial and lateral nasal
processes '
'lateral cleft fused and rhinarium covered with dry
hairy skin ',
386
'absent '
'present ',
387
'present '
'absent ',
388
'choriovitelline placenta '
'no choriovitelline placenta ',
389
epitheliochorial
'diffuse, hemochorial',
390
invasive
'non-invasive',
391
'primordial cavity absent'
'primordial cavity present',
392
absent
present,
393
'large, vesicular'
rudimentary,
394

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        absent
        present,
;

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MATRIX

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'Tupaia glis'          0000404441 0000000003 2204042022 0202612002
2200120150 0000008066 4300002004 2402442202 1040007441 0020210000 00200240-
0 2012000211 2102-00040 2010000000 00200100-3 00-0020002 4603031004
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 'Masradapis tahai' ??0?00?20 10?????? 22??41022 ?224810--4 -
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 000200? 04?????20 2?????0?20 ???? ?????? ???? ?????? ???? ??????
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 'Microcebus murinus' 1010414241 1200011034 2207040020 -204810--4 -
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 'Nannopithec abderhaldeni' 1102814241 1440?20000 24-0-40020 -200012004 -
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 'Necrolemur spp.' 11028?4241 ?440?00010 24-0-40020 -224814204 -
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 'Nycticebooides simpsoni' ?????????? ?????????? 2208040022 2204610--4 -
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 'Nycticebus coucang' 1010414241 1200011034 2208040022 2204410--4 -
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'Oligopithecus savagei' ?0?????? ????10003 24-0-20022 2206814222
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 0311001101 3102006000 3000000102 42?220-?10 0023001812 110111500-
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 'Serapia eocaena' ??0????????? ???2?10003 2206240022 2204414224 -
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'Siamopithecus eocaenus' ?0?????0?? ??4?00003 22???40022 2204812004 -
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0102440200 0311002001 2210004210 5100000002 4001020010 002000?120
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0222212004 -202220220 4221208462 4100200024 2442422002 2240004421
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;
END;
BEGIN PAUP;
outgroup Tupaia_glis;
ctype ord : 1-4 5 7-9 12-15 18 21 22-28 30-35 37-61 63-67 69-75 77-78 80-84
86-88 91-95 98 99-100 102-104 106-109 111-115 117-118 120 123-131 133 135-
136 138 140-141 143-162 164-166 168-180 182-187 189 191 193-197 199-200
202-204 206-207 209 212-221 223-231 233 235 238-240 242 244 246-248 251
254-255 257-258 264-266 268 271-272 279-280 282-286 288-290 292-293 296-298
300-302 304 307-309 311 313 316 318-322 324-326 328 333 338-339
347 353-355 357 359 363 367 369-373 376-377 380-382;
wts 1 : all;
wts 0.5 : 5 7-9 12-14 18 21-23 24-28 30-35 37-40 42-53 55-61 63-67 69-75 77
78 80-83 86-88 91-93 95 98-100 102-104 106-107 111-112 114 117-118 123-131
133 135-136 138 140-141 144-162 164-166 168-180 183-187 189 191 193-197
199-200 202 -204 209 212 -221 223 -231
240 248 264 279-280 285-286 288-289 292-293 296-298 300-302 307 309 311 316
318-322 324-326 333 338 347 354-355 357 359 367 369-373 376-377 380-381;
ctype irrev : 21;
ctype irrev : 22;
ctype irrev : 119;
ctype irrev : 120;
END;

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Character-taxon-matrix

Analysis 2: We use a matrix with 38 taxa and 326 morphological characters based on Jaeger et al. (2020).

```
#NEXUS  
[ File saved by NDE version 0.5.0, Thu Feb 15 17:53:16 2024 ]  
  
BEGIN TAXA;  
    DIMENSIONS NTAX=38;  
    TAXLABELS  
        'Donrussellia gallica+sp.'  
        'Notharctus robustior'  
        'Adapis parisiensis'  
        'Cantius eppsi'  
        'Leptadapis magnus'  
        'Absarokius abotti+sp.'  
        'Hemiacodon gracilis'  
        'Shoshonius cooperi'  
        'Teilhardina americana'  
        'Xanthorhysis tabrumi'  
        'Tarsius spp.'  
        'Eosimias spp.'  
        'Phenacopithecus spp.'  
        'Bahinia pondaungensis'  
        'Proteopithecus sylviae'  
        'Serapia eocaena'  
        'Apidium phiomense'  
        'Parapithecus fraasi'  
        'Qatrania wingi'  
        'Simonsius grangeri'  
        'Biretia spp.'  
        'Dolichocebus gaimanensis'  
        'Branisella boliviana'  
        'Callicebus moloch'  
        'Saimiri sciureus'  
        'Saguinus spp.'  
        'Aotus spp.'  
        'Myanmarpithecus yarshensis'  
        'Ganlea megacanina'  
        'Pondaungia cotteri'  
        'Siamopithecus eocaenus'  
        'Aegyptopithecus zeuxis'  
        'Taqah propliopithecid'  
        'Catopithecus browni'  
        'Oligopithecus savagei'  
        'Oligopithecus rogeri'  
        'Propriopithecus spp.'  
        'Propriopithecus chiropobates'  
    ;  
ENDBLOCK;  
  
BEGIN CHARACTERS;  
    DIMENSIONS NCHAR=326;  
    FORMAT DATATYPE=STANDARD MISSING=? GAP=- SYMBOLS="012345";  
    CHARLABELS
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[1] 'i1. Lower incisor number'
[2] 'i2. Lower incisor occlusal arrangement'
[3] 'i3. Lower incisor crown spacing'
[4] 'i4. I/2-C diastema'
[5] 'i5. I/1-2 size (ratio of I/1-2 area to M/1 area)'
[6] 'i6. I/1:I/2 proportions (ratio of I/1 area to I/2
area)'
[7] 'i7. I/1 crown width (spatulate incisors only)'
[8] 'i8. I2 crown cross-sectional shape (ratio of m-d length
to b-l breadth)'
[9] 'i9. Lower incisors crown height (crown heights judged
from cementoenamel junction to crown tip on the buccal surface)'
[10] 'i11. Lower incisor roots'
[11] 'i12. Lower incisor crowns'
[12] 'i14. I/1 crown shape'
[13] 'i15. I/2 heel development (a lingual swelling at the
base of crown)'
[14] 'i17. Lower first incisor lingual cingulum.'
[15] 'i19. Relative size of I1 to M1 (based on occlusal
areas).'
[16] 'c1. Female C1 cross-sectional area relative to molar
cross sectional area.'
[17] 'c2. C1/1 dimorphism (square root of male C1
area/square root of female C1 area).'
[18] 'c3. C/1 cross-sectional shape.'
[19] 'c4. C/1 lingual crest development.'
[20] 'c5. Canine paracristid (not scored if species has
canine incorporated into a tooth comb).'
[21] 'c6. Canine height (females).'
[22] 'ML18. Lower canine crown.'
[23] 'ML19. Lower canine root.'
[24] 'p1. P1/1'
[25] 'p2. P/2.'
[26] 'OC1. Relative size (MDxBL) of p2 and p3'
[27] 'OC2. Relative size (MDxBL) of p2 and P2'
[28] 'p3. P/2 roots.'
[29] 'p4''. P/3 roots'
[30] 'p4''. P/4 roots.'
[31] 'p5. Premolar crowding (overlapping of crowns).'
[32] 'p6. P/3 paraconid'
[33] 'OC7. P/3 paraconid height'
[34] 'p7. P/4 paraconid.'
[35] 'p9''. P/4 paraconid position (labiolingually)'
[36] 'p9''''. P/4 paraconid position (mesiodistally) '
[37] 'p11. P/3-4 cristid obliqua'
[38] 'p13. P/2 protoconid height and shape'
[39] 'p14. P/4 metaconid position'
[40] 'p15. P/2 metaconid size'
[41] 'p16. P/3 metaconid size'
[42] 'p17. P/4 metaconid size'
[43] 'p18. P/4 trigonid-configuration of lingual wall'
[44] 'p19. P/3 entoconid and lingual talonid crest'
[45] 'p20. P/4 entoconid and lingual talonid crest: '
[46] 'p21. P/4 lateral and medial protocristid'
[47] 'p22. P/3 lateral protocristid orientation'
[48] 'p23. P/4 lateral protocristid orientation'
[49] 'p24. P/3-4 posterior trigonid wall'
[50] 'p25. P/3-4 hypoconid size'
[51] 'p26. P/3-4 hypoconid (or distal terminus of oblique
cristid) position'
[52] 'p27. P/4 hypocristid shearing development: '

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- [53] 'p28. P/2 buccal cingulum development'
- [54] 'p29. Lower premolar inflation'
- [55] 'p30. P/4 exodaenodonty'
- [56] 'p31. P/4 talonid length (ratio of midline m-d length of trigonid to m-d length of talonid)'
- [57] 'p33. Premolar orientation'
- [58] 'OC 8. Lower premolar crown configuration'
- [59] 'p34. P/4 anterobuccal cingulum development'
- [60] 'p36. P/4 postprotoconid ridge'
- [61] 'p37. P/4 postmetaconid ridge'
- [62] 'p40. P/4 paraconid height'
- [63] 'p41. P3-4 protoconid height'
- [64] 'p42. P/3 to P/4 area'
- [65] 'p43. P/4 m-d L/ b-l W'
- [66] 'p44. Ratio of P/4 area to M/1 area'
- [67] 'p45a. P/3 root orientation'
- [68] 'p45b. P/4 root orientation'
- [69] 'm4. M/3 root number'
- [70] 'm6. M/2 trigonid width (ratio of buccolingual breadths of trigonid and talonid)'
- [71] 'm7. M/3 trigonid width (based on relative buccolingual breadths)'
- [72] 'OC3. M/1 paraconid'
- [73] 'm8'. M/1 paraconid position '
- [74] 'm9''. M/2 paraconid position '
- [75] 'OC4. M/3 paraconid'
- [76] 'm10. M/3 paraconid position '
- [77] 'm8910. M/2-3 paraconid location'
- [78] 'm11. M/1 parastylid (= premetacristid)'
- [79] 'm12. Molar metastylids (postmetacristids)'
- [80] 'm13. M/3 hypoconulid'
- [81] 'm14. M/3 heel'
- [82] 'm15. Molar enamel surface'
- [83] 'm16. M/1 trigonid height (ratio of trigonid height to talonid height measured on the buccal aspect of the crown)'
- [84] 'm17. M/1-2 cusp relief'
- [85] 'm18. M/1 trigonid lingual configuration'
- [86] 'm19. M/1 metaconid position'
- [87] 'm20. M/2 paraconid development'
- [88] 'm21. M/1-2 lateral protocristid orientation'
- [89] 'm22. M/1 distal trigonid wall'
- [90] 'm23. M/2 distal trigonid wall'
- [91] 'm24. M/1-3 wear facet X'
- [92] 'm25. M/1-2 entoconid'
- [93] 'm26. M/1-2 postentoconid sulcus'
- [94] 'm27. M/1 hypoconulid size'
- [95] 'm28. M/2 hypoconulid size'
- [96] 'm29. M/3 hypoconulid size'
- [97] 'm30. M/1-2 hypoconulid position'
- [98] 'm31. M/1-2 cristid obliqua development'
- [99] 'm32. M/1 cristid obliqua orientation'
- [100] 'm33. M/2 cristid obliqua orientation'
- [101] 'm34. M/1 cristid obliqua terminus'
- [102] 'm35. M/2 cristid obliqua terminus'
- [103] 'm36. M/3 cristid obliqua terminus'
- [104] 'm37. M/1-2 centroconid development'
- [105] 'm38. M/1-2 hypocristid development'
- [106] 'm39. M/3 hypocristid development'
- [107] 'm40. Lingual configuration of M/1-2 talonid'
- [108] 'm41. M/1-2 distal fovea'
- [109] 'm42. M/1-2 hypocristid configuration'

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[110] 'm43. M/1-2 cristid obliqua'
[111] 'm44. Molar cusp inflation'
[112] 'm45. M/1-2 buccal cingulum development'
[113] 'm46. M/1 hypoflexid depth'
[114] 'm47. M/2 hypoflexid depth'
[115] 'm53. Ratio of M/2 length to M/3 length'
[116] 'm55. M/1 mesiodistal length/buccolingual breadth'
[117] 'm56. Convergence of buccal and lingual molar cusp
walls'
[118] 'm57. M/1-2 entoconid position relative to hypoconid'
[119] 'ML88. M/1-3 Pre-entocristid'
[120] 'I1. I1/-I2/ interstitial contact'
[121] 'I2. I1/-I1/ interstitial contact'
[122] 'I3. I2/-C diastema'
[123] 'I4. I1/ area:I2/ area'
[124] 'I5. I1/ size (I1/ area: M1/ area)'
[125] 'I6. I1/ occlusal shape (mesiodistal
length/buccolingual breadth)'
[126] 'I7. I2/ occlusal shape (mesiodistal length
/buccolingual breadth)'
[127] 'I10. I1/ occlusal edge orientation (for spatulate
incisors only; all others scored as " ? ")'
[128] 'I11. I1-2/ lingual cingulum'
[129] 'I12. I1/ basal lingual cusp'
[130] 'I13. I1/-I2/ buccal cingulum'
[131] 'C1. C1/ cross-sectional shape'
[132] 'C2. Upper canine occlusion'
[133] 'C3. C1/ mesial groove (females)'
[134] 'C4. C1/ lingual cingulum'
[135] 'OC5. P2/'
[136] 'P1''. P2/ root number'
[137] 'P2. P3/ root number'
[138] 'P3. P4/ root number'
[139] 'P4''. Ratio of P2/ area to P3/ area'
[140] 'P5. Ratio of P4/ area to M1/ area'
[141] 'P6. P2/ occlusal outline'
[142] 'OC6. P3/ occlusal outline'
[143] 'P7''. P4/ occlusal outline'
[144] 'P8. P3-4/ trigon/talon proportions'
[145] 'P9. P3/ protocone'
[146] 'P10. P4/ metacone'
[147] 'P11. P4/ protocone'
[148] 'P12''. P2/ protocone'
[149] 'P13''. P2/ hypocone'
[150] 'P14. P4/ paraconule'
[151] 'P15. P3-4/ parastyles'
[152] 'P16. P3-4/ metastyles'
[153] 'P17. P3-4/ postprotocrista'
[154] 'P18''. P2-4/ distal crown margin'
[155] 'P19. P3-4/ lingual cingulum'
[156] 'P20. P3/ metacone'
[157] 'P21. P3-4/ buccal cingulum development'
[158] 'ML126. P4/ hypocone'
[159] 'ML127. P3/ hypocone'
[160] 'M1. M1-2/ root number'
[161] 'M2. M3/ root number'
[162] 'M3. M2/ shape (bl/md)'
[163] 'M4. Ratio of M1/ area to M2/ area'
[164] 'M7''. M1-2/ metaconule'
[165] 'M9. M1-2/ preprotoconule'
[166] 'M10. M1/ hypocone size'

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[167] 'M11. M2/ hypocone size'
[168] 'M12''. M1-2/ hypocone position'
[169] 'M13. M1-2/ prehypocrista development'
[170] 'M14. M3/ prehypocrista development'
[171] 'M15. M1/ or M2/ paraconule position'
[172] 'M16. M1-2/ metaconule'
[173] 'M17''. M1-2/ mesostyle size'
[174] 'M17''. M1-2/ mesostyle position'
[175] 'M20. P4/-M1/ pericone'
[176] 'M22. M1-3/ lingual cingulum development'
[177] 'M24. M1-2/ buccal cingulum development'
[178] 'M27. M1-2/ pre-metaconule cristae'
[179] 'M28. M1-2/ post-metaconule cristae'
[180] 'M30. M3/ paraconule'
[181] 'M31. Molar protocone lingual inflation'
[182] 'M33. M2/ buccal expansion of paracone (specify which tooth)'
[183] 'M34. M3/ metacone'
[184] 'M36. M3/ hypocone'
[185] 'M37. M1/ paraconule size'
[186] 'M44. M1-3/ anterior cingulum'
[187] 'M46. M3/ size relative to M1/'
[188] 'ML147. M1-2/ metastyle'
[189] 'ML148. M1-2/ parastyle'
[190] 'ML149. M1-2/ parastyle position'
[191] 'ML150. M1-2/ metastyle position'
[192] 'ML151. M1-3/ posterior cingulum'
[193] 'ML152. M1-3/ posterior margin (waisted between buccal and lingual cusps)'
[194] 'ML153. M1-2/ postparacrista'
[195] 'ML154. M1-2/ premetacrista'
[196] 'ML155. M1-3/ protocone arrangement'
[197] 'ML156. M1-2/ postprotocrista development'
[198] 'ML157. M1/ postprotocrista length'
[199] 'ML158. M2/ postprotocrista length'
[200] 'ML159. M1/ postprotocrista direction'
[201] 'ML160. M2/ postprotocrista direction'
[202] 'ML161. M1/ postprotocrista terminus'
[203] 'ML162. M2/ postprotocrista terminus'
[204] 'ML163. M1-2/ preprotocrista'
[205] 'ML164. M1/ preprotocrista connection (buccal side)'
[206] 'ML165. M2/ preprotocrista connection (buccal side)'
[207] 'ML166. M1-2/ postparaconule crista'
[208] 'ML168. M1-2/ hypometacrista'
[209] 'ML169. M1-2/ hypoparacrista'
[210] 'MLN. Hypometaconulecrista'
[211] 'CR1. Transverse septum arising from the cochlear housing'
[212] 'CR2. Extent of pneumatization of anterior accessory cavity'
[213] 'CR3. Pneumatization of mastoid (from epitympanic recess?)'
[214] 'CR4. Presence or absence of perbullar pathway'
[215] 'CR5. Anteroposterior location of posterior carotid foramen in bulla'
[216] 'CR6. Mediolateral position of posterior carotid foramen in bulla'
[217] 'CR7. Ventrodorsal position of the carotid foramen in the bulla'
[218] 'CR8. Position of posterior carotid foramen relative to fenestra cochleae'

- [219] 'CR9. Position of the internal carotid canal relative to the fenestra cochleae'
- [220] 'CR10. Position of the portion of the internal carotid/promontory artery (or its accompanying nerves) lying on the promontorium anterior to the fenestra cochleae'
- [221] 'CR11. Size of stapedial and promontory canals'
- [222] 'CR12. Morphology of promontory canal, when present'
- [223] 'CR14. Position of ventral edge of the tympanic bone'
- [224] 'CR15. The shape of the tympanic bone'
- [225] 'CR16. Morphology of annular bridge'
- [226] 'CR17. Encroachment of the auditory bulla on the pterygoid fossa'
- [227] 'CR18. Nature of contact between the lateral pterygoid plate and the bulla wall'
- [228] 'CR19. Extent of contact between the lateral pterygoid plate and the bulla wall'
- [229] 'CR20. Flange of basioccipital overlapping medial bulla wall'
- [230] 'CR21. Suprameatal foramen'
- [231] 'CR22. Patent parotic fissure'
- [232] 'CR23. Size of orbits'
- [233] 'CR24. Postorbital closure'
- [234] 'CR25. Composition of the postorbital septum'
- [235] 'CR26. Zygomatic-lacrimal contact'
- [236] 'CR27. Pronounced interorbital constriction'
- [237] 'CR28. Contact between lacrimal and palatine'
- [238] 'CR29. Foramen rotundum'
- [239] 'CR30. Position of lacrimal foramen'
- [240] 'CR31. Metopic suture in adult'
- [241] 'CR32. Orbital convergence'
- [242] 'CR33. Posterior nasal spine'
- [243] 'CR34. Posterior palatine torus'
- [244] 'CR35. Pyramidal processes'
- [245] 'CR36. Length of medial pterygoid plate'
- [246] 'CR37. Snout length'
- [247] 'CR38. Maxillary depth'
- [248] 'CR39. Complete symphyseal fusion'
- [249] 'CR40. Temporomandibular joint morphology'
- [250] 'CR41. Entoglenoid process morphology'
- [251] 'CR42. Inter-incisor diastema width'
- [252] 'CR43. Coronoid height relative to condyle'
- [253] 'CR44. Condyle height relative to toothrow'
- [254] 'CR45. Corpus robusticity'
- [255] 'CR46. Zygomatico-parietal contact at pterion'
- [256] 'CR48. Epitympanic crest'
- [257] 'CR49. Broad ascending wing of premaxilla'
- [258] 'CR50. Basioccipital stem'
- [259] 'CR51. Choanal shape'
- [260] 'CR52. Orientation of the mandibular symphysis'
- [261] 'H1. Shape of distal edge of the humeral trochlea'
- [262] 'H2. Relative heights of medial and lateral edges of humeral trochlea'
- [263] 'H3. Trochleocapitular ridge'
- [264] 'H4. Waisted trochlea (Minimum trochlear diameter/maximum trochlear diameter x 100)'
- [265] 'H5. Width of capitulum relative to trochlea (100 x ventral capitulum width/ventral trochlear width)'
- [266] 'H6. Entepicondylar foramen'
- [267] 'H7. Entepicondylar foramen position'
- [268] 'H8. Medial epicondyle size'
- [269] 'H9. Dorsal placement of medial epicondyle'

- [270] 'H10''. Shape of the lateral edge of the dorsal trochlea'
- [271] 'H10". Shape of the medial edge of the dorsal trochlea'
- [272] 'H11. Dorsoepitrochlear fossa'
- [273] 'H12. Olecranon fossa shape'
- [274] 'H14. Brachialis flange'
- [275] 'H15. Bicipital groove morphology'
- [276] 'H18. Capitular tail'
- [277] 'H19. Ratio of humerus length to femur length (H/F)'
- [278] 'W2. Ulnar-pisiform articulation.'
- [279] 'OP1. Gluteal tuberosity'
- [280] 'OP2. Position of posterior gluteal tuberosity'
- [281] 'F1. Length of femoral neck'
- [282] 'F2. Angle of femoral neck'
- [283] 'F3. Angle of lesser trochanter'
- [284] 'F4. Size of third trochanter'
- [285] 'F5. Knee index (Antero-posterior diameter of distal femur/ mediolateral diameter of distal femur).'
- [286] 'F6. Femoral head shape'
- [287] 'F7. Anterior extension of greater trochanter'
- [288] 'F8. Anterior bend of proximal femur'
- [289] 'F9. Relative length of trochanteric fossa'
- [290] 'F10. Presence of intertrochanteric crest'
- [291] 'F11. Size of lesser trochanter'
- [292] 'F12. Lateral rim of knee'
- [293] 'T1''. Fusion of tibia and fibula'
- [294] 'T1". Articulation tibia/fibula'
- [295] 'T3. Shape of distal surface of tibia'
- [296] 'T4. Rotation of the medial malleolus'
- [297] 'T5. Shape of medial malleolar articular surface'
- [298] 'T6. Shape of distal tibial shaft'
- [299] 'T7. Position of tibialis posterior groove'
- [300] 'A1. Position of the flexor hallucis longus groove'
- [301] 'A2''. Shape of talo-fibular facet.'
- [302] 'A4''. Development of the talar posterior trochlear shelf'
- [303] 'A5''. Talar neck length (NL/TL x 100)'
- [304] 'A6. Medial talo-tibial facet'
- [305] 'A7. Lateral talar trochlear asymmetry'
- [306] 'A8. Talar cotylar fossa'
- [307] 'A9. Width of the head of the talus (HW/HHT x 100)'
- [308] 'GEB1. Talar neck angle'
- [309] 'GEB2. Talar body height (HT/MTRW x 100)'
- [310] 'GEB3. TW/TL x 100'
- [311] 'CA1. Anterior calcaneal elongation'
- [312] 'CA2. Position of the peroneal tubercle'
- [313] 'CA3. Posterior calcaneal bowing'
- [314] 'CA4. Calcaneo-cuboid articulation'
- [315] 'N1. Length relative to width'
- [316] 'N3. Morphology of the navicolocuboid articulation'
- [317] 'E1. Shape of Entocuneiform/MT1 articulation'
- [318] 'E2. Lateral process of entocuneiform'
- [319] 'O1. Foot axis'
- [320] 'O2. Toilet claw'
- [321] 'O3. Prehallux'
- [322] 'O4. Metatarsus length'
- [323] 'MT1. Peroneal tubercle of MT1'
- [324] 'MT2. Hallux length'
- [325] 'V1. Optic fovea'
- [326] 'V2. Tapetum lucidum'

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STATELABELS
1
'three '
'two '
'one I/1 present, I/2 absent '
'lower incisors absent ',
2
'Arcuate battery from lateral perspective (U-shape
arcade) ',
3
'cusp tips staggered (V-shaped arcade) ',
4
'No spaces '
'Spaces present between crowns ',
5
'present '
'absent ',
6
'very small (<0.69) '
'moderate sized (<0.70, <1.07) '
'large (>1.07) ',
7
'I/1 much smaller than I/2 (<0.65) '
'I/1 smaller than I/2 (>0.65, <0.82) '
'I/1 almost as large as I/2 (>0.83, <1.00) '
'I/1>I/2 (>1.01, <1.25) '
'I/1>>I/2 (>1.25) ',
8
'consideranly wider (m-d) than root (spatulate) '
'narrow at apex, wider than root '
'"styliform" (crown apex approximately the same
width as the cervical margin)',
9
'rounded oval (> 0.64) '
'mesiodistally compressed (< 0.64) ',
10
'low crowned '
'moderately high crowned '
'high crowned ',
11
'slightly procumbent '
'very procumbent ',
12
'erect or vertical '
'procumbent
'very procumbent ',
13
'erect or vertical'
'procumbent
'very procumbent ',
14
'spatulate
'lanceolate, pointed ',
15
'heel absent '
'heel present ',
16
'absent to weak '
'strong but incomplete '
'strong and complete ',
17
'I/1 very small (I/1 << M/1) '
'moderately enlarged (I/1 < or = M/1) '
'grossly enlarged (I/1 > M/1) ',

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16
    'very small (C1/M1 < 0.40)'
    'moderate (> 0.4, < 0.80)'
    'large (> 0.80, < 1.20); very large (> 1.20) ',

17
    'low (< 1.07)'
    'moderate (> 1.07, < 1.17)'
    'high (>1.17) ',

18
    'rounded oval '
    'mesiodistally compressed '
    'buccolingually compressed ',

19
    'rounded '
    'sharp ',

20
    'oblique to occlusal plane '
    'nearly horizontal to occlusal plane '
    'forms part of cropping mechanism with I/1-2 ',

21
    'low, squat '
    'narrow, short '
    'tall, at or above tooth row ',

22
    'erect or vertical '
    'procumbent '
    'very procumbent',

23
    'erect or vertical '
    'slightly procumbent '
    'very procumbent',

24
    'present '
    'absent ',

25
    'present '
    'absent ',

26
    'p2<<p3 (ratio<0.6)'
    'p2<p3 (0.6<ratio<0.9)'
    'p2> or =p3 (ratio>0.9)',

27
    'P2 larger or equal to p2'
    'P2 smaller than p2',

28
    'single '
    'double ',

29
    'single '
    'double ',

30
    'single '
    'double ',

31
    'no crowding '
    'slightly crowded '
    'very crowded-mesial root positioned buccal to
distal root ',

32
    'large '
    'small '

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    'absent or extremely small ',
33
    Low
    moderate
    'High (nearly as high as the protoconid)',

34
    'large '
    'small '
    'absent or extremely small ',

35
    'mesial to protoconid'
    'mesiolingual, between protoconid and metaconid'
    'mesial to metaconid',

36
    'widely spaced from the metaconid '
    'twinned with metaconid ',

37
    'absent '
    'weak '
    'strong ',

38
    'projects above protoconids of P/3-4 '
    'massive, projects above protoconids of P/3-4 '
    'not projecting, in line with P/3 '
    'extremely short, shorter than P/3 ',

39
    'close to protoconid '
    'widely spaced from protoconid ',

40
    'absent or trace '
    'small ',

41
    'absent or trace '
    'small '
    'large (as big as protoconid) ',

42
    'absent or trace'
    'small '
    'large (as big as protoconid) ',

43
    'closed '
    'open ',

44
    'absent '
    'lingual talonid crest present but an entoconid does
not stand out above it '
    'entoconid forms a small discrete cusp ',

45
    'absent '
    'lingual talonid crest present but an entoconid does
not stand out above it '
    'entoconid forms a small discrete cusp ',

46
    'continuous between metaconid and protoconid '
    'discontinuous between metaconid and protoconid ',

47
    'transversely oriented '
    'distolingually oriented '
    'absent ',

48
    'transversely oriented '

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        'distolingually oriented ',
49
    'complete [taxa without metaconids are assigned this
character state] ',
50
        'deeply notched ',
51
        'large '
        'small or absent ',
52
        'distal to protoconid '
        'distal to metaconid, or between protoconid and
metaconid ',
53
        'absent '
        'weak '
        'strong ',
54
        'absent '
        'incomplete, broken at protoconid and hypoconid '
        'complete ',
55
        'not basally inflated'
        'slightly basally inflated '
        'very basally inflated ',
56
        'not exodaenodont '
        'slightly exodaenodont '
        'very exodaenodont ',
57
        'extremely short or non-existent (tri:tal > 1.61)'
        'short (much shorter than trigonid) (tri:tal >
1.27, < 1.61)'
        'equal or slightly shorter in length to trigonid
(tri:tal > 0.92, < 1.27)'
        'talonid longer than trigonid (tri:tal < 0.91) ',
58
        'Crown bases vertical in lateral perspective '
        'slightly oblique '
        'strongly oblique, projecting medial over the
anterior ',
59
        'Normal
        Spatulate,
60
        'Absent or trace '
        'Strong ',
61
        'Absent or weak '
        'Moderate '
        'Very strong ',
62
        'Absent or weak '
        'Moderate '
        'Very strong ',
63
        'low '
        'moderate '
        'high (nearly as high as protoconid) ',
        'P/3 much lower than P/4 '
        'P/3 slightly lower than P/4 '

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'P/3 equal in height to P/4 '
'P/3 higher than P/4 ',
64
'0.45-0.59 '
'0.60-0.69 '
'0.70-0.79 '
'>0.80 ',  

65
'<0.95 '
'>0.96 <1.14 '
'>1.15 <1.20 '
'>1.21 <1.35 '
'>1.36 <1.46 '
'>1.47 ',  

66
'< 0.62'
'>0.63, < 0.72'
' >0.73, < 0.82'
'>0.83, < 0.92'
'>0.93, < 1.02'
'> 1.03 ',  

67
'Aligned mesiodistally '
'Shifted laterally',  

68
'Aligned mesioditally'
'Mesial root shifted buccally',  

69
'one '
'two ',  

70
'much wider than talonid (> 1.11) '
'widths similar (< 1.11, > 0.90) '
'much narrower than talonid (< 0.90) ',  

71
'much wider than talonid (> 1.20) '
'trigonid and talonid widths similar (< 1.20-1.05) '
'trigonid narrower than talonid (< 1.05) ',  

72
Present  

Absent,  

73
'mesiolingual, between protoconid and metaconid '
'mesial to metaconid ',  

74
'mesiolingual, between protoconid and metaconid '
'mesial to metaconid ',  

75
Present  

Absent,  

76
'mesiolingual, between protoconid and metaconid '
'mesial to metaconid ',  

77
'widely spaced from the metaconid '
'twinned with metaconid ',  

78
'absent '
'present ',  

79
'absent '

```

```

        'small ',
        'large ',
80
        'single ',
        'double ',
81
        'absent '
        'narrower than talonid '
        'approximately equal in width to talonid ',
82
        'smooth '
        'slightly crenulated '
        'highly crenulated ',
83
        'higher than talonid (> 1.20) '
        'slightly higher than talonid (> 1.10, < 1.20) '
        'trigonid and talonid of similar height (< 1.10) ',
84
        'Moderate to high '
        'Low ',
85
        'Open '
        'Closed ',
86
        'transversely aligned-lingual to protoconid '
        'slightly distolingual to protoconid ',
87
        'absent '
        'small '
        'large ',
88
        'runs toward metaconid '
        'runs toward hypoflexid ',
89
        'complete '
        'deeply notched by protoconid/metaconid sulcus '
        'medial and lateral protocristid do not meet but no
sulcus is visible',
90
        'complete '
        'deeply notched by protoconid/ metaconid sulcus '
        'medial and lateral protocristid do not meet but no
sulcus is visible',
91
        'present '
        'absent ',
92
        'barely stands out on lingual talonid marginal crest
'
        'a small discrete cusp '
        'a large cusp ',
93
        'prominent '
        'faintly visible '
        'absent ',
94
        'large '
        'moderate '
        'small '
        'absent ',
95

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```

'large '
'moderate '
'small '
'absent ',
96
'large '
'moderate '
'small '
'absent ',
97
'twinned to entoconid '
'near midline '
'slightly buccal to midline ',
98
'weak (rounded) '
'strong (trenchant) '
'very strong (trenchant) ',
99
'reaches trigonid wall at a point distal to
protoconid '
'reaches trigonid wall at a point distolingual to
protoconid '
'reaches trigonid wall at a point distal to
metaconid ',
100
'reaches trigonid wall at a point distal to
protoconid '
'reaches trigonid wall at a point distolingual to
protoconid '
'reaches trigonid wall at a point distal to
metaconid ',
101
'runs to base of trigonid '
'runs part way up the distal trigonid wall '
'connects with protoconid tip or protocristid '
'connects with metaconid ',
102
'runs to base of trigonid '
'runs part way up the distal trigonid wall '
'connects with protoconid tip or protocristid '
'connects with metaconid ',
103
'runs to base of trigonid '
'runs part way up the distal trigonid wall '
'connects with protoconid tip or protocristid '
'connects with metaconid ',
104
'present '
'absent ',
105
'absent or seen only as a trace '
'weak '
'strong ',
106
'absent or seen only as a trace '
'weak '
'strong ',
107
'open '
'notched lingually but not open '
'closed ',

```

```

108
    'absent '
    'present (weak) '
    'present (large) ',  

109
    'simple '
    'with accessory cusp close to hypoconid ',  

110
    'notched '
    'straight ',  

111
    'cusps not inflated, marginally positioned '
    'slightly inflated '
    'very inflated ',  

112
    'absent to trace '
    'partial, broken at protoconid and hypoconid '
    'complete ',  

113
    'very shallow '
    'moderate '
    'deep ',  

114
    'very shallow '
    'moderate '
    'deep ',  

115
    'M/3 much longer than M/2 (0.71-0.80) '
    'M/3 longer than M/2 (0.81-0.90) '
    'M/3 equal than M/2 (0.91-1.00) '
    'M/3 smaller than M/2 (1.01-1.12) '
    'M/3 much smaller than M/2 (> 1.13) '
    'if M/3 absent',  

116
    '1.0-1.15'
    '1.16-1.22'
    '1.23-1.32'
    ' > 1.33   ',  

117
    'convergent '
    'vertically sided ',  

118
    'transverse to hypoconid '
    'distal to hypoconid ',  

119
    'indistinct to absent '
    'weakly developed (low) '
    'well-developed (strong and high) ',  

120
    'absent; teeth widely spaced '
    'present as narrow contact '
    'I2/ tightly packed against I1/, I1/ preparacrista  

abbreviated ',  

121
    'present '
    'absent: a wide space occurs in the midline between  

these teeth ',  

122
    'present '
    'absent ',  

123

```

```

'areas approximately equal (< 1.00) '
'I1/ slightly larger than I2/ (> 1.00, < 1.40) '
'I1/ much larger than I2/ (> 1.40) ',  

124  

'incisor small (< 0.50) '
'incisor moderate (> 0.50, < 0.56) '
'incisor large (> 0.56) ',  

125  

'rounded oval (< 1.05) '
'buccolingually compressed (> 1.05, < 1.30) '
'extremely compressed (> 1.30) ',  

126  

'rounded oval (< 1.05) '
'slightly buccolingually compressed (> 1.05, < 1.30)  

'extremely buccolingually compressed > 1.30) ',  

127  

'occlusal edge orthogonal to long axis of root '
'occlusal edge wears at a steep angle to long axis  

of root '  

'crown with pronounced mesial asymmetry (= mesial  

process) in unworn state ',  

128  

'Moderate, continuous '
'Strong ',  

129  

'absent '
'present ',  

130  

'absent '
' present',  

131  

'oval '
'rounded ',  

132  

'C1/ wears against P/1-2'
'C1/ wears against P/2 '
'C1/ wears against P/2-3 '
'C1/ wears against P/3 ',  

133  

'shallow or absent '
'deep ',  

134  

'weak or absent '
'strong '
'very strong ',  

135  

present  

absent,  

136  

one  

'two '
'three ',  

137  

'two '
'three ',  

138  

'two '
'three ',  

139  

'P2/ much smaller (< 0.85) '

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```

        'P2/ smaller (> 0.85, < 0.95) '
        'P2/ equal (> 0.95) '
        'Clearly larger',
140
        'P4 << M1 (<0.66) '
        'P4< M1 (> 0.66, < 0.76) '
        'P4 = M1 (0.77-1.05) '
        'P4 > M1 (> 1.06) ',
141
        'triangular '
        'suboval with the long axis b-l '
        'suboval with the long axis m-d '
        'round ',
142
        'Suboval (with roughly mesiodistal long axis) '
        'Triangular (buccal lobe much wider than lingual
lobe) '
        'Trapezoid (tooth buccolingually extended with
buccal lobe wider than lingual lobe) '
        'Rectangular (tooth buccolingually extended with
lingual lobe as wide as buccal lobe) '
        'Squared ( tooth as wide as long with buccal lobe as
wide as lingual lobe) ',
143
        Triangular
        Trapezoid
        Rectangular
        Squared,
144
        'trigon > = talon '
        'trigon < talon ',
145
        'present '
        'absent ',
146
        absent
        present,
147
        'low relative to paracone '
        'high relative to paracone ',
148
        'present '
        absent,
149
        absent
        present,
150
        'large '
        'small '
        'absent ',
151
        'present '
        'absent ',
152
        'absent '
        'present ',
153
        'strong '
        'weak, short ',
154
        'smoothly rounded '

```

```

        'waisted between buccal and lingual cusps ',
155      'absent or weak '
        'strong ',
156      'absent '
        'present ',
157      'absent or weak '
        'strong ',
158      'minute to absent '
        'present but small '
        'strong ',
159      'minute to absent '
        'present but small '
        'strong ',
160      'three, three '
        'three, two '
        'two, two',
161      'three '
        'two '
        'one ',
162      'very transverse (> 1.65) '
        'transverse (< 1.65, > 1.30) '
        'squared (< 1.30) ',
163      'M1 >> M2 (> 1.40) '
        'M1 > M2 (< 1.40, > 1.0) '
        'M1 < M2 (< 1.0) ',
164      'absent '
        'single '
        double,
165      absent
        'weak '
        'strong ',
166      'large '
        'small '
        'minute to absent ',
167      'large '
        small
        'minute to absent ',
168      'distal, far lingual to protocone '
        'distal, slightly lingual to protocone '
        'distal, slightly buccal to protocone ',
169      'absent '
        'weak '
        'strong, reaches to postprotocrista, encloses the
talon lingually. ',
170      absent

```

'strong, reaches to postprotocrista, encloses the
talon lingually',
171
'attached to preprotocrista '
'unattached to preprotocrista ',
172
'absent to indistinct '
'small '
'moderate '
'large ',
173
'absent to indistinct '
moderate
'strong ',
174
'attached to ectocrista '
'present on buccal cingulum ',
175
'absent '
'small '
'large ',
176
'absent to indistinct '
'weak, broken '
'strong, complete ',
177
'absent to indistinct '
'weak '
'strong ',
178
'absent or weak '
'strong ',
179
'absent or weak '
'strong ',
180
'absent '
'small-moderate '
large,
181
'not inflated '
'slightly inflated '
'very inflated ',
182
'no expansion '
'slight expansion '
'considerable expansion ',
183
'absent or very small '
'moderate (but smaller than paracone) '
'large (equal to paracone) ',
184
'absent or very small '
'small '
'large ',
185
'absent '
'small-moderate (smaller than paracone) '
'large (nearly as large as or larger than paracone)
,

186

187 'strong, complete, long (connected to parastyle) '
 'strong, short '
 'weak or absent ',
 187 'very small (half the size of M1/ or less) '
 'small (two thirds) '
 'large (approximately as large) ',
 188 'indistinct to absent '
 'moderate '
 'strong ',
 189 'indistinct to absent '
 'moderate '
 'strong ',
 190 'mesial to paracone '
 'mesiobuccal to paracone ',
 191 'distal to metacone '
 'distobuccal to metacone ',
 192 'moderate, does not reach the metastyle / the
 distobuccal corner of the tooth'
 'connected to metastyle / reaches the distobuccal
 corner of the tooth',
 193 'indistinct to absent '
 'present but shallow '
 'present, deep ',
 194 'indistinct to absent '
 'weakly developed '
 'well developed (but well-marked notch between
 postparacrista and premetacrista) '
 'strongly elevated (weak notch between
 postparacrista and premetacrista)',
 195 'indistinct to absent '
 'weakly developed '
 'well developed (but well-marked notch between
 premetacrista and postparacrista) '
 'strongly elevated (weak notch between premetacrista
 and postparacrista)',
 196 'normal position '
 'oblique ',
 197 'strong '
 'tiny ',
 198 'indistinct to absent '
 'short '
 'long ',
 199 'indistinct to absent '
 'short '
 'long ',
 200 'transverse, directed toward metaconule (or virtual
 metaconule emplacement) '

```

        'lateral, directed toward the lingual posterior
cingulum (post-protocone fold-like) ',
201
        'transverse, directed toward metaconule (or virtual
metaconule emplacement) '
        'lateral, directed toward lingual posterior cingulum
(post-protocone fold-like) ',
202
        'runs to base of metacone (with hypometacrista) '
        'runs to metaconule (at the level of the small or
virtual metaconule) '
        'runs to posterior cingulum '
        'limited at a point distal to protocone ',
203
        'runs to base of metacone (with hypometacrista) '
        'runs to metaconule (at the level of the small or
virtual metaconule) '
        'runs to posterior cingulum '
        'limited at a point distal to protocone ',
204
        'low '
        'elevated ',
205
        'connected to parastyle (by way of preparaconule
crista) '
        'connected to paraconule (or near to it or to a
virtual paraconule) ',
206
        'connected to parastyle (by way of preparaconule
crista) '
        'connected to paraconule (or near to it or to a
virtual paraconule) ',
207
        'indistinct to absent '
        'moderate '
        'well-developed (connected to paracone) ',
208
        'absent '
        'weakly developed (low and short) '
        'well-developed (high) ',
209
        'absent '
        'weakly developed (short) '
        'well-developed (high) ',
210
        'indistinct to absent '
        'moderate (not connected to protocone) '
        'well-developed (connected to protocone or
postprotocrista) ',
211
        Absent
        'present and forming the lateral wall of an anterior
accessory cavity pneumatized from the tympanic cavity'
        'present and forming the lateral wall of an anterior
accessory cavity pneumatized from the epitympanic recess. ',
212
        'Anterior accessory cavity lies anterior to the
tympanic cavity and is not trabeculated '
        'anterior accessory cavity extends medial to the
tympanic cavity, and is trabeculated ',
213

```

214 'Absent '
 214 'Present ',
 214 'Absent '
 214 'Present and formed exclusively by the petrosal bone
 ,
 215 'Posterior to line joining midpoints of tympanic
 bones '
 216 'anterior to this line ',
 216 'medial '
 216 'midline of the bulla '
 216 'lateral ',
 217 'dorsal, adjacent to basioccipital or mastoid bone '
 217 'ventral ',
 218 'posterior '
 218 'ventral '
 218 'anterior ',
 219 'runs across ventral lip of the fenestra cochleae,
 shielding it from ventral view when a canal is present '
 219 'internal carotid canal does not shield the fenestra
 cochleae from ventral view ',
 220 'on ventrolateral surface of promontorium '
 220 'contacting only the cupula of the cochlea ',
 221 'both stapedial and promontory canals are large '
 221 'stapedial slightly smaller than promontory '
 221 'stapedial highly reduced or absent altogether '
 221 'stapedial larger than promontory '
 221 'both promontory and stapedial canals absent ',
 222 'open trough '
 222 'complete canal ',
 223 'intrabullar, or aphaneric '
 223 'extrabullar or phaneric ',
 224 'ribbon-like or only slightly expanded '
 224 'laterally expanded into a collar or tube ',
 225 'Linea semicircularis or partial anular bridge
 formed on a entotympanic bulla '
 225 'linea semicircularis formed on a petrosal bulla '
 225 'a complete annular bridge ',
 226 'Absent '
 226 'Present and formed by anterior accessory cavity '
 226 'Present and formed by the tympanic cavity ',
 227 'absent '
 227 'laminar '
 227 'abutting ',
 228 'slight '
 228 'very extensive ',
 229

230 'Absent or minimal '
 'extensive ',
 zygomatic arch '
 meatus ',
 231 'Present '
 'Absent ',
 232 'Small '
 'Large '
 'Extremely large ',
 233 'None '
 'Postorbital bar present '
 'Postorbital septum present ',
 234 'zygomatic forms most of the septum '
 'frontal forms most of the septum ',
 235 'Present '
 'Absent ',
 236 'absent '
 'resent below olfactory tract ',
 237 'present '
 'separated by a large fronto-maxillary contact (and
 in some taxa, a small os planum of the ethmoid) '
 'separated by a large os planum ',
 238 'Absent '
 'Present ',
 239 'outside orbital margin '
 'within the orbit or on the rim ',
 240 'unfused '
 'fused ',
 241 'low (less convergent than primates)'
 'moderate
 'high
 'Very high',
 242 'Reduced or absent '
 'small but distinct '
 'robust and long ',
 243 'present '
 'absent ',
 244 'Medially placed '
 'Laterally placed ',
 245 'long medial pterygoid plate extending one-third to
 one half of the distance to the anterior surface of the bulla '

'short but distinct from lateral pterygoid plate for its entire dorsoventral extent ',
 'medial pterygoid plate entirely absent, or reduced to a low rugosity ',
 246
 'Long snout ',
 'Short snout ',
 247
 'deep '
 'shallow ',
 248
 'absent '
 'present ',
 249
 'biconcave and transversely wide '
 'anteroposteriorly oriented trough ',
 250
 'weak or absent '
 'strong ',
 251
 'broad and wider than that of extant haplorhines '
 'narrow, haplorhine-like ',
 252
 'very far above '
 'slightly above or equal ',
 253
 'at level of tooth row '
 'slightly above '
 'well above tooth row ',
 254
 'shallow '
 'deep ',
 255
 'no postorbital closure '
 'zygomatico-parietal contact '
 'alisphenoid-frontal contact ',
 256
 'absent '
 'present ',
 257
 'narrow '
 'broad ',
 258
 'narrow '
 'broad ',
 259
 'narrow '
 'broad ',
 260
 'symphysis procumbent '
 'symphysis erect',
 261
 'cylinder, distal edge perpendicular to shaft '
 'distal edge somewhat angled to shaft '
 'distal edge very angled',
 262
 'subequal '
 'medial edge more flared than lateral edge ',
 263
 'absent '
 'weak but distinct '

```

'moderately distinct '
'very distinct ',
264
'> 70 (unwaisted) '
'<= 70 (waisted) ',
265
'< 100 '
'between 100 and 140 '
'140-200 '
'>200 ',
266
'present '
'variable '
'absent ',
267
'above medial epicondyle '
'above ventral trochlea '
'above dorsal trochlea ',
268
'reduced '
'prominent ',
269
'parallel '
'slight dorsal angle'
'large dorsal angle ',
270
'not pronounced '
'moderately pronounced '
'very pronounced',
271
'not pronounced'
'moderately pronounced '
'very pronounced ',
272
'present (strong) '
'small, shallow '
'absent ',
273
'Shallow '
'Moderate '
'Deep,
274
'broad '
'moderate
'narrow ',
275
'shallow '
'deep ',
276
'ventral articular width <2.5 times the ventral
capitular width '
'ventral articular width > 2.5 times the ventral
capitular width ',
277
'100* H/F <= 65 '
'H/F between 65 and 80'
'H/F > 80 ',
278
'Facet on pisiform for ulnar styloid process is
roughly equal in size to that for triquetrum'

```

'Facet on pisiform for ulnar styloid process is much
 enlarged and deeply excavated. ',
 279
 'present '
 'absent ',
 280
 ' Proximal to or level with lesser trochanter'
 'distal to lesser trochanter. ',
 281
 '< 75'
 '75-120'
 '> 120',
 282
 '< 60'
 '60-70'
 '> 70',
 283
 ' medial (0-30°) '
 ' posterior (>30°) ',
 284
 ' large '
 'small '
 'low crest or absent ',
 285
 ' < 90 (shallow knee) '
 ' 90 - 100 '
 ' > 100 (deep knee) ',
 286
 ' spherical '
 ' semicylindrical '
 ' cylindrical ',
 287
 'no extension'
 'extension present',
 288
 'none '
 'bent ',
 289
 ' long (> 125) '
 ' moderate (110-125) '
 ' very short (< 110) ',
 290
 'Crest absent '
 'Crest present ',
 291
 'large '
 'intermediate '
 'small ',
 292
 low
 'high ',
 293
 'absent '
 'present ',
 294
 small
 'moderate '
 'extensive ',
 295
 'square/parallel '
 'triangular ',

```

296
    'none '
    'slight ',
    'strong ',  

297
    flat
    'anteriorly convex, posteriorly flat '
    'all convex ',  

298
    'no compression '
    'anteroposteriorly compressed ',  

299
    'on medial side of malleolus '
    'on posterior side of malleolus ',  

300
    'lateral to trochlea '
    'central to trochlea ',  

301
    'steep-sided'
    'steep-sided with a plantar lip '
    'sloped obliquely ',  

302
    none
    'weakly developed'
    'well developed (prominent) ',  

303
    'short (<50) '
    'long (>50) ',  

304
    'short (does not reach to plantar edge of bone) '
    'long ',  

305
    'absent '
    'present ',  

306
    'shallow '
    'deep, medially projecting ',  

307
    '<120 '
    '>120 ',  

308
    '< 20°'
    '20-30°'
    '> 30°',  

309
    '<100 '
    '100-120 '
    '120-150 ',  

310
    '<60 '
    '>60 ',  

311
    'not elongate (ACL or anterior calcaneal ratio < 40)
        'moderate (ACL >= 40-45) '
        'long (>45) ',  

312
    ' distal to joint'
    'at joint '
    'proximal to joint ',  

313

```

```

    'Absent ',
    'Present ',
314
    ' articular wedge absent (fan-shaped)'
    ' articular wedge present (more circular)',

315
    'Short (<90) '
    'moderate (100-150) '
    'long( >150) ',

316
    'cuboid facet on navicular contacts only the
ectocuneiform'

mesocuneiform facet',
317
    'moiety'
    'dorsally reduced'
    'dorsal moiety of joint enlarged relative to ventral
    'dorsal moiety greatly enlarged',

318
    small
    'hypertrophied ',

319
    'mesaxonic '
    'paraxonic
    'ectaxonic ',

320
    'absent '
    'present ',

321
    'present '
    'absent ',

322
    'short '
    'long ',

323
    'very large '
    'large '
    'small ',

324
    'short '
    'long ',

325
    'absent '
    'present ',

326
    'present '
    'absent ',

;

MATRIX
    'Donrussellia gallica+sp.'      ?1?1?????? ??????????
???00??111 02?1101?1? 011?10?101 02?00{12}0?12 001?530011 1011010010
1000011000 1222202211 3(12)11221001 {01}122{01}{23}101? ??????????
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    'Notharctus robustior'          1001010001 101101?0?0
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1011011{01}1{01} 10{01}0012000 1222202111 3111222001 12220{12}011?
1???0????? ??0?0011{01}1 212-001101 {01}{01}01001000 0221000100

```

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 'Adapis parisiensis' 1001010000 001201?012
 2000020111 02?2--2210 0210201100 022?031?10 0-21430011 11--1--020
 1010010000 121330?111 {23}111220001 1122031101 0?0?222??1 00??011111
 2030111101 1010101000 0220001100 000-022001 0020112110 0102201101
 1331000000 0?10020000 (13)000102000 101?001?0(01) 1101210100 ?011011100
 1011201100 010000?100 1000000010 1100122010 2201011211 1101??00?? 1?2?00
 'Cantius eppsi' ?????????? ???????????
 ???0??111 02?1002?1? 0211101100 01?0020?11 0023420011 10111-0010
 1000012000 1222202111 3011222001 122203011? ?????????? ???0111?1 ?11-
 001??2 0001001000 0121022-00 020-0(12)2101 10101011{01}0 0101100101
 ?330000001 ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
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 2000020111 02?1202200 0210101100 0220010?10 0?23441011 11--1--020
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 2431011102 0010101000 0220001100 000-012001 0021112110 01012011(01)1
 1331000000 0?10020000 300010??00 101?????0? 1??12??100 ????11??0
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 'Absarokius abotti+sp.' 100102???? ????00?0??
 ?001000011 22??2--1300 011(01)102101 100220(12)?00 0-00050011 (01)011011010
 1(01)10012000 122220211(01) 0011112001 122220001? ?????????? ???001103
 341-000102 (01)101000000 0021022-00 010-01210(01) (12)110(01)10010 -
 111101121 1310011001 ?????????? ?????????? ?????????? ??????????0?? ??????????
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 'Hemiacodon gracilis' 110113?0?2 {12}?1{12}10?2??
 {01}00100?011 12??2--2310 02(01)2201001 0100011?11 1023300012
 1011001(01)0(01) (12)210012000 1212201211 {01}111221000 122(12)12101?
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 (01)12112 1(01)20(12)0(12)110 111101111 1320110000 ?????????? ??????????
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 'Shoshonius cooperi' 10?102???? ????00?001
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 002001?101 1111001100 3{12}{12}-100102 (01)101001000 01210{12}{12}100
 0{01}0-02(12)001 00201(01)2010 ?111100220 01110001{01}0 1001121211
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 0200221120 111?011101 100100(01)000 1110201121 101111

'Eosimias spp.' 1001000000 001002?000
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'Phenacopithecus spp.' ??????000 0010?????
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'Bahinia pondaungensis' 1?0?000000 001102?0??
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'Proteopithecus sylviae' 1????????? ??????2???
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 032-000002 0110101100 1011011100 -{01}0-022000 0100010010 0101100220
 0111000?00 1111001210 ?110?00?00 202011??11 2211110001 1020??0101
 110?112111 1011?11?00 221010?0?1 0????????1 0000000221 ?????????? ?????11

'Serapia eocaena' ?????????? ??????1?100
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 ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????
 'Apidium phiomense' 1001010000 0012012000
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 000000 00{01}0000000 0121200010 130-221002 1002211110 010110?00? ???1000010
 1111?0?210 2110?????? 1020?1??11 2????101?? ?1010?0?0 110(01)(12)02111
 1011010?1? 2112200001 0002011011 101000(01)221 01010021?? ???011

'Parapithecus fraasi' ?00101{01}000 001201?000
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 'Qatrania wingi' ?????????? ??????????
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 'Simonsius grangeri' 3----- -----1?000
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 1021110111 0200021100 0001111101 111120001? ?????????? ?1?011101 1?2-
 000000 1000000000 0211000100 120-02(12)001 1100110010 010110?00? ???1000010
 1111001??2 2110?0110? 202011??11 2011010101 1?102?0101 ??????????
 ???1??1? 0????????? 0????????? 0????000??? 0????????? 0????11

'Biretia spp.' ?????????? ??????????
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 132-000002 0110000110 0121000100 020-021001 0110111010 010110100?
 0?110001(01)0 0????????? 0????????? 0????????? 0????????? 0?????????
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'Dolichocebus gaimanensis' 1?????000? 0011?12000
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 'Callicebus moloch' 1001011110 0010010000
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 1111011210 2110-00-00 1020112111 2011210101 1021100101 10{12}{01}22-111
 10120??00? 2012100000 2001011001 1010??1210 110?002110 012011
 'Saimiri sciureus' 1000210000 0012022000
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 132-001102 1000100001 1110000110 -00-12{01}000 0{01}11010110 0101100210
 0111000210 1111011210 2110-00-0{02} 1020112111 2111110100 1121100101
 102{01}{23}001{12}1 10120120{01}0 1{01}12100000 2001011001 1010001110
 21?1002110 012011
 'Saguinus spp.' 1000220000 0012020000
 2001021000 02??2--1110 2201100001 0021121001 1-33{01}2---1 -1----11- -
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 {01}{23}2-000102 101{01}000001 -{01}01022--- 010-02{12}00- 10--12-{01}10
 0101100220 0111000100 1011011110 2110-00-00 1020112111 2111110100
 1121100101 ?????????? ?????????? ?????????? ?????????? ??????????
 ?????????? ??????
 'Aotus spp.' 1001120000 0012010000
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 11010100{12}{01} {01}32-001002 1000000001 22{12}0000121 -00-000000
 011102100- -101100110 0111110220 1111011110 2110-00-00 1120112111
 2111110101 1121101101 {01}01{01}{23}101{01}1 101201?0{01}0 2012100010
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 'Ganlea megacanina' 1??101?010 0?0?02?00?
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 0111000110 ?????????? ?????????? ?01-11?11 2????100?? 1??10?1??1
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 'Pondaungia cotteri' 1?0103?0?0 ????02?0??
 200101?011 02-2--(12)200 1100(12)01000 0101121101 0-2(23)(01)01011 (01)00-
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' Aegyptopithecus zeuxis' 1000010010 0011012000
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32-001--2 1100100220 0121100100 010-021000 1200{01}12010 -101000100
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1010(01)00111 1011012?01 ?0?(12)0?0??? ?00?1????1 1000111211 0101?21??
0?2011
    'Taqah propoliopithecus' ?????????? ?????????? ???11--
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    'Catopithecus browni' 1?0??10010 001??12000 20011-
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0101101000 0120011100 -011022000 10100(01)1110 1111100220 0111000110
??1?001210 ??10????00 10?0?1??11 2?1??10001 1020??1100 101?000111
1011?12?01 1210?00000 0????????1 1010110211 ?????????? ???11
    'Oligopithecus savagei' ?????????? ?????????0?? 20011-
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    'Oligopithecus rogeri' ?????????? ??????2000 20011-
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101110000? ?110022100 -00-020000 1010021{01}10 1121100220 0111000110
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    'Propoliopithecus spp.' 1001110010 0010012000 20011-
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    'Propoliopithecus chiropobates' 1001110010 0010012000 20011-
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ENDBLOCK;

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BEGIN ASSUMPTIONS;
    OPTIONS DEFTYPE=UNORD POLYTCOUNT=MINSTEPS;
    TYPESET * default = ORD: 1 5 - 7 9 - 11 14 - 17 22 - 23 31 - 37 41
- 42 52 - 57 60 - 66 70 - 71 79 81 - 83 87 92 - 100 105 - 107 111 - 116 119
- 120 123 - 126 132 134 136 139 - 140 150 158 - 169 172 - 173 175 - 177 180
- 189 193 - 195 198 - 199 207 - 210 216 218 232 - 233 242 245 253 261 263
265 270 - 274 277 281 - 282 284 - 286 289 291 294 296 - 297 301 - 302 308 -
312 315 317 323;
ENDBLOCK;

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BEGIN NOTES;
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[Taxon comments]  
[Character comments]  
[Character state comments]  
[Attribute comments]  
[Taxon pictures]  
[Character pictures]  
[Character state pictures]  
[Attribute pictures]  
ENDBLOCK;
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Character-taxon-matrix

Analysis 3: We use a matrix with 45 taxa and 326 morphological characters based on Jaeger et al. (2019, 2020).

```
#NEXUS  
[ File saved by NDE version 0.5.0, Thu Feb 15 17:53:16 2024 ]  
  
BEGIN TAXA;  
    DIMENSIONS NTAX=45;  
    TAXLABELS  
        'Donrussellia gallica+sp.'  
        'Notharctus robustior'  
        'Adapis parisiensis'  
        'Cantius eppsi'  
        'Leptadapis magnus'  
        'Absarokius abotti+sp.'  
        'Hemiacodon gracilis'  
        'Shoshonius cooperi'  
        'Teilhardina americana'  
        'Xanthorhysis tabrumi'  
        'Tarsius spp.'  
        'Afrotarsius libycus'  
        'Afrasia djijidae'  
        'Eosimias spp.'  
        'Phenacopithecus spp.'  
        'Bahinia pondaungensis'  
        'Proteopithecus sylviae'  
        'Phileosimias spp.'  
        'Serapia eocaena'  
        'Apidium phiomense'  
        'Parapithecus fraasi'  
        'Qatrania wingi'  
        'Simonsius grangeri'  
        'Biretia spp.'  
        'Bugtipithecus inexpectans'  
        'Dolichocebus gaimanensis'  
        'Branisella boliviana'  
        'Callicebus moloch'  
        'Saimiri sciureus'  
        'Saguinus spp.'  
        'Aotus spp.'  
        'Myanmarpithecus yarshensis'  
        'Ganlea megacanina'  
        'Pondaungia cotteri'  
        'Siamopithecus eocaenus'  
        'Krabia minuta'  
        'Aegyptopithecus zeuxis'  
        'Taqah propliopithecid'  
        'Catopithecus browni'  
        'Oligopithecus savagei'  
        'Oligopithecus rogeri'  
        'Talahpithecus parvus'  
        'Propliopithecus spp.'  
        'Propliopithecus chiropobates'  
        'Aseanpithecus myanmarensis'
```

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ENDBLOCK;

BEGIN CHARACTERS;
  DIMENSIONS NCHAR=326;
  FORMAT DATATYPE=STANDARD MISSING=? GAP=- SYMBOLS="012345";
  CHARLABELS
    [1] 'i1. Lower incisor number'
    [2] 'i2. Lower incisor occlusal arrangement'
    [3] 'i3. Lower incisor crown spacing'
    [4] 'i4. I/2-C diastema'
    [5] 'i5. I/1-2 size (ratio of I/1-2 area to M/1 area)'
    [6] 'i6. I/1:I/2 proportions (ratio of I/1 area to I/2
area)'
    [7] 'i7. I/1 crown width (spatulate incisors only)'
    [8] 'i8. I2 crown cross-sectional shape (ratio of m-d length
to b-l breadth)'
    [9] 'i9. Lower incisors crown height (crown heights judged
from cementoenamel junction to crown tip on the buccal surface)'
    [10] 'i11. Lower incisor roots'
    [11] 'i12. Lower incisor crowns'
    [12] 'i14. I/1 crown shape'
    [13] 'i15. I/2 heel development (a lingual swelling at the
base of crown)'
    [14] 'i17. Lower first incisor lingual cingulum.'
    [15] 'i19. Relative size of I1 to M1 (based on occlusal
areas).'
    [16] 'c1. Female C1 cross-sectional area relative to molar
cross sectional area.'
    [17] 'c2. C1/1 dimorphism (square root of male C1
area/square root of female C1 area).'
    [18] 'c3. C/1 cross-sectional shape.'
    [19] 'c4. C/1 lingual crest development.'
    [20] 'c5. Canine paracristid (not scored if species has
canine incorporated into a tooth comb).'
    [21] 'c6. Canine height (females).'
    [22] 'ML18. Lower canine crown.'
    [23] 'ML19. Lower canine root.'
    [24] 'p1. P1/1'
    [25] 'p2. P/2.'
    [26] 'OC1. Relative size (MDxBL) of p2 and p3'
    [27] 'OC2. Relative size (MDxBL) of p2 and P2'
    [28] 'p3. P/2 roots.'
    [29] 'p4'. P/3 roots'
    [30] 'p4". P/4 roots.'
    [31] 'p5. Premolar crowding (overlapping of crowns).'
    [32] 'p6. P/3 paraconid'
    [33] 'OC7. P/3 paraconid height'
    [34] 'p7. P/4 paraconid.'
    [35] 'p9'. P/4 paraconid position (labiolingually)'
    [36] 'p9'''. P/4 paraconid position (mesiodistally) '
    [37] 'p11. P/3-4 cristid obliqua'
    [38] 'p13. P/2 protoconid height and shape'
    [39] 'p14. P/4 metaconid position'
    [40] 'p15. P/2 metaconid size'
    [41] 'p16. P/3 metaconid size'
    [42] 'p17. P/4 metaconid size'
    [43] 'p18. P/4 trigonid-configuration of lingual wall'
    [44] 'p19. P/3 entoconid and lingual talonid crest'
    [45] 'p20. P/4 entoconid and lingual talonid crest: '
    [46] 'p21. P/4 lateral and medial protocristid'

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[47] 'p22. P/3 lateral protocristid orientation'
 [48] 'p23. P/4 lateral protocristid orientation'
 [49] 'p24. P/3-4 posterior trigonid wall'
 [50] 'p25. P/3-4 hypoconid size'
 [51] 'p26. P/3-4 hypoconid (or distal terminus of oblique cristid) position'
 [52] 'p27. P/4 hypocristid shearing development: '
 [53] 'p28. P/2 buccal cingulum development'
 [54] 'p29. Lower premolar inflation'
 [55] 'p30. P/4 exodaenodonty'
 [56] 'p31. P/4 talonid length (ratio of midline m-d length of trigonid to m-d length of talonid)'
 [57] 'p33. Premolar orientation'
 [58] 'OC 8. Lower premolar crown configuration'
 [59] 'p34. P/4 anterobuccal cingulum development'
 [60] 'p36. P/4 postprotoconid ridge'
 [61] 'p37. P/4 postmetaconid ridge'
 [62] 'p40. P/4 paraconid height'
 [63] 'p41. P3-4 protoconid height'
 [64] 'p42. P/3 to P/4 area'
 [65] 'p43. P/4 m-d L/ b-1 W'
 [66] 'p44. Ratio of P/4 area to M/1 area'
 [67] 'p45a. P/3 root orientation'
 [68] 'p45b. P/4 root orientation'
 [69] 'm4. M/3 root number'
 [70] 'm6. M/2 trigonid width (ratio of buccolingual breadths of trigonid and talonid)'
 [71] 'm7. M/3 trigonid width (based on relative buccolingual breadths)'
 [72] 'OC3. M/1 paraconid'
 [73] 'm8''. M/1 paraconid position '
 [74] 'm9''. M/2 paraconid position '
 [75] 'OC4. M/3 paraconid'
 [76] 'm10. M/3 paraconid position '
 [77] 'm8910. M/2-3 paraconid location'
 [78] 'm11. M/1 parastylid (= premetacristid)'
 [79] 'm12. Molar metastylids (postmetacristids)'
 [80] 'm13. M/3 hypoconulid'
 [81] 'm14. M/3 heel'
 [82] 'm15. Molar enamel surface'
 [83] 'm16. M/1 trigonid height (ratio of trigonid height to talonid height measured on the buccal aspect of the crown)'
 [84] 'm17. M/1-2 cusp relief'
 [85] 'm18. M/1 trigonid lingual configuration'
 [86] 'm19. M/1 metaconid position'
 [87] 'm20. M/2 paraconid development'
 [88] 'm21. M/1-2 lateral protocristid orientation'
 [89] 'm22. M/1 distal trigonid wall'
 [90] 'm23. M/2 distal trigonid wall'
 [91] 'm24. M/1-3 wear facet X'
 [92] 'm25. M/1-2 entoconid'
 [93] 'm26. M/1-2 postentoconid sulcus'
 [94] 'm27. M/1 hypoconulid size'
 [95] 'm28. M/2 hypoconulid size'
 [96] 'm29. M/3 hypoconulid size'
 [97] 'm30. M/1-2 hypoconulid position'
 [98] 'm31. M/1-2 cristid obliqua development'
 [99] 'm32. M/1 cristid obliqua orientation'
 [100] 'm33. M/2 cristid obliqua orientation'
 [101] 'm34. M/1 cristid obliqua terminus'
 [102] 'm35. M/2 cristid obliqua terminus'

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[103] 'm36. M/3 cristid obliqua terminus'
[104] 'm37. M/1-2 centroconid development'
[105] 'm38. M/1-2 hypocristid development'
[106] 'm39. M/3 hypocristid development'
[107] 'm40. Lingual configuration of M/1-2 talonid'
[108] 'm41. M/1-2 distal fovea'
[109] 'm42. M/1-2 hypocristid configuration'
[110] 'm43. M/1-2 cristid obliqua'
[111] 'm44. Molar cusp inflation'
[112] 'm45. M/1-2 buccal cingulum development'
[113] 'm46. M/1 hypoflexid depth'
[114] 'm47. M/2 hypoflexid depth'
[115] 'm53. Ratio of M/2 length to M/3 length'
[116] 'm55. M/1 mesiodistal length/buccolingual breadth'
[117] 'm56. Convergence of buccal and lingual molar cusp
walls'
[118] 'm57. M/1-2 entoconid position relative to hypoconid'
[119] 'ML88. M/1-3 Pre-entocristid'
[120] 'I1. I1/-I2/ interstitial contact'
[121] 'I2. I1/-I1/ interstitial contact'
[122] 'I3. I2/-C diastema'
[123] 'I4. I1/ area:I2/ area'
[124] 'I5. I1/ size (I1/ area: M1/ area)'
[125] 'I6. I1/ occlusal shape (mesiodistal
length/buccolingual breadth)'
[126] 'I7. I2/ occlusal shape (mesiodistal length
/buccolingual breadth)'
[127] 'I10. I1/ occlusal edge orientation (for spatulate
incisors only; all others scored as " ? ")'
[128] 'I11. I1-2/ lingual cingulum'
[129] 'I12. I1/ basal lingual cusp'
[130] 'I13. I1/-I2/ buccal cingulum'
[131] 'C1. C1/ cross-sectional shape'
[132] 'C2. Upper canine occlusion'
[133] 'C3. C1/ mesial groove (females)'
[134] 'C4. C1/ lingual cingulum'
[135] 'OC5. P2/'
[136] 'P1''. P2/ root number'
[137] 'P2. P3/ root number'
[138] 'P3. P4/ root number'
[139] 'P4''. Ratio of P2/ area to P3/ area'
[140] 'P5. Ratio of P4/ area to M1/ area'
[141] 'P6. P2/ occlusal outline'
[142] 'OC6. P3/ occlusal outline'
[143] 'P7''. P4/ occlusal outline'
[144] 'P8. P3-4/ trigon/talon proportions'
[145] 'P9. P3/ protcone'
[146] 'P10. P4/ metacone'
[147] 'P11. P4/ protcone'
[148] 'P12''. P2/ protcone'
[149] 'P13''. P2/ hypocone'
[150] 'P14. P4/ paraconule'
[151] 'P15. P3-4/ parastyles'
[152] 'P16. P3-4/ metastyles'
[153] 'P17. P3-4/ postprotocrista'
[154] 'P18''. P2-4/ distal crown margin'
[155] 'P19. P3-4/ lingual cingulum'
[156] 'P20. P3/ metacone'
[157] 'P21. P3-4/ buccal cingulum development'
[158] 'ML126. P4/ hypocone'
[159] 'ML127. P3/ hypocone'

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[160] 'M1. M1-2/ root number'
[161] 'M2. M3/ root number'
[162] 'M3. M2/ shape (bl/md)'
[163] 'M4. Ratio of M1/ area to M2/ area'
[164] 'M7''. M1-2/ metaconule'
[165] 'M9. M1-2/ preprotoconule'
[166] 'M10. M1/ hypocone size'
[167] 'M11. M2/ hypocone size'
[168] 'M12''. M1-2/ hypocone position'
[169] 'M13. M1-2/ prehypocrista development'
[170] 'M14. M3/ prehypocrista development'
[171] 'M15. M1/ or M2/ paraconule position'
[172] 'M16. M1-2/ metaconule'
[173] 'M17''. M1-2/ mesostyle size'
[174] 'M17''. M1-2/ mesostyle position'
[175] 'M20. P4/-M1/ pericone'
[176] 'M22. M1-3/ lingual cingulum development'
[177] 'M24. M1-2/ buccal cingulum development'
[178] 'M27. M1-2/ pre-metaconule cristae'
[179] 'M28. M1-2/ post-metaconule cristae'
[180] 'M30. M3/ paraconule'
[181] 'M31. Molar protocone lingual inflation'
[182] 'M33. M2/ buccal expansion of paracone (specify which
tooth)'

[183] 'M34. M3/ metacone'
[184] 'M36. M3/ hypocone'
[185] 'M37. M1/ paraconule size'
[186] 'M44. M1-3/ anterior cingulum'
[187] 'M46. M3/ size relative to M1/'
[188] 'ML147. M1-2/ metastyle'
[189] 'ML148. M1-2/ parastyle'
[190] 'ML149. M1-2/ parastyle position'
[191] 'ML150. M1-2/ metastyle position'
[192] 'ML151. M1-3/ posterior cingulum'
[193] 'ML152. M1-3/ posterior margin (waisted between buccal
and lingual cusps)'
[194] 'ML153. M1-2/ postparacrista'
[195] 'ML154. M1-2/ premetacrista'
[196] 'ML155. M1-3/ protocone arrangement'
[197] 'ML156. M1-2/ postprotocrista development'
[198] 'ML157. M1/ postprotocrista length'
[199] 'ML158. M2/ postprotocrista length'
[200] 'ML159. M1/ postprotocrista direction'
[201] 'ML160. M2/ postprotocrista direction'
[202] 'ML161. M1/ postprotocrista terminus'
[203] 'ML162. M2/ postprotocrista terminus'
[204] 'ML163. M1-2/ preprotocrista'
[205] 'ML164. M1/ preprotocrista connection (buccal side)'
[206] 'ML165. M2/ preprotocrista connection (buccal side)'
[207] 'ML166. M1-2/ postparaconule crista'
[208] 'ML168. M1-2/ hypometacrista'
[209] 'ML169. M1-2/ hypoparacrista'
[210] 'MLN. Hypometaconulecrista'
[211] 'CR1. Transverse septum arising from the cochlear
housing'
[212] 'CR2. Extent of pneumatization of anterior accessory
cavity'
[213] 'CR3. Pneumatization of mastoid (from epitympanic
recess?)'
[214] 'CR4. Presence or absence of perbullar pathway'

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- [215] 'CR5. Anteroposterior location of posterior carotid foramen in bulla'
- [216] 'CR6. Mediolateral position of posterior carotid foramen in bulla'
- [217] 'CR7. Ventrodorsal position of the carotid foramen in the bulla'
- [218] 'CR8. Position of posterior carotid foramen relative to fenestra cochleae'
- [219] 'CR9. Position of the internal carotid canal relative to the fenestra cochleae'
- [220] 'CR10. Position of the portion of the internal carotid/promontory artery (or its accompanying nerves) lying on the promontorium anterior to the fenestra cochleae'
- [221] 'CR11. Size of stapedial and promontory canals'
- [222] 'CR12. Morphology of promontory canal, when present'
- [223] 'CR14. Position of ventral edge of the tympanic bone'
- [224] 'CR15. The shape of the tympanic bone'
- [225] 'CR16. Morphology of annular bridge'
- [226] 'CR17. Encroachment of the auditory bulla on the pterygoid fossa'
- [227] 'CR18. Nature of contact between the lateral pterygoid plate and the bulla wall'
- [228] 'CR19. Extent of contact between the lateral pterygoid plate and the bulla wall'
- [229] 'CR20. Flange of basioccipital overlapping medial bulla wall'
- [230] 'CR21. Suprameatal foramen'
- [231] 'CR22. Patent parotic fissure'
- [232] 'CR23. Size of orbits'
- [233] 'CR24. Postorbital closure'
- [234] 'CR25. Composition of the postorbital septum'
- [235] 'CR26. Zygomatic-lacrimal contact'
- [236] 'CR27. Pronounced interorbital constriction'
- [237] 'CR28. Contact between lacrimal and palatine'
- [238] 'CR29. Foramen rotundum'
- [239] 'CR30. Position of lacrimal foramen'
- [240] 'CR31. Metopic suture in adult'
- [241] 'CR32. Orbital convergence'
- [242] 'CR33. Posterior nasal spine'
- [243] 'CR34. Posterior palatine torus'
- [244] 'CR35. Pyramidal processes'
- [245] 'CR36. Length of medial pterygoid plate'
- [246] 'CR37. Snout length'
- [247] 'CR38. Maxillary depth'
- [248] 'CR39. Complete symphyseal fusion'
- [249] 'CR40. Temporomandibular joint morphology'
- [250] 'CR41. Entoglenoid process morphology'
- [251] 'CR42. Inter-incisor diastema width'
- [252] 'CR43. Coronoid height relative to condyle'
- [253] 'CR44. Condyle height relative to toothrow'
- [254] 'CR45. Corpus robusticity'
- [255] 'CR46. Zygomatico-parietal contact at pterion'
- [256] 'CR48. Epitympanic crest'
- [257] 'CR49. Broad ascending wing of premaxilla'
- [258] 'CR50. Basioccipital stem'
- [259] 'CR51. Choanal shape'
- [260] 'CR52. Orientation of the mandibular symphysis'
- [261] 'H1. Shape of distal edge of the humeral trochlea'
- [262] 'H2. Relative heights of medial and lateral edges of humeral trochlea'
- [263] 'H3. Trochleocapitular ridge'

- [264] 'H4. Waisted trochlea (Minimum trochlear diameter/maximum trochlear diameter x 100)'
- [265] 'H5. Width of capitulum relative to trochlea (100 x ventral capitulum width/ventral trochlear width)'
- [266] 'H6. Entepicondylar foramen'
- [267] 'H7. Entepicondylar foramen position'
- [268] 'H8. Medial epicondyle size'
- [269] 'H9. Dorsal placement of medial epicondyle'
- [270] 'H10''. Shape of the lateral edge of the dorsal trochlea'
- [271] 'H10''. Shape of the medial edge of the dorsal trochlea'
- [272] 'H11. Dorsoepitrochlear fossa'
- [273] 'H12. Olecranon fossa shape'
- [274] 'H14. Brachialis flange'
- [275] 'H15. Bicipital groove morphology'
- [276] 'H18. Capitular tail'
- [277] 'H19. Ratio of humerus length to femur length (H/F)'
- [278] 'W2. Ulnar-pisiform articulation.'
- [279] 'OP1. Gluteal tuberosity'
- [280] 'OP2. Position of posterior gluteal tuberosity'
- [281] 'F1. Length of femoral neck'
- [282] 'F2. Angle of femoral neck'
- [283] 'F3. Angle of lesser trochanter'
- [284] 'F4. Size of third trochanter'
- [285] 'F5. Knee index (Antero-posterior diameter of distal femur/ mediolateral diameter of distal femur).'
- [286] 'F6. Femoral head shape'
- [287] 'F7. Anterior extension of greater trochanter'
- [288] 'F8. Anterior bend of proximal femur'
- [289] 'F9. Relative length of trochanteric fossa'
- [290] 'F10. Presence of intertrochanteric crest'
- [291] 'F11. Size of lesser trochanter'
- [292] 'F12. Lateral rim of knee'
- [293] 'T1''. Fusion of tibia and fibula'
- [294] 'T1''. Articulation tibia/fibula'
- [295] 'T3. Shape of distal surface of tibia'
- [296] 'T4. Rotation of the medial malleolus'
- [297] 'T5. Shape of medial malleolar articular surface'
- [298] 'T6. Shape of distal tibial shaft'
- [299] 'T7. Position of tibialis posterior groove'
- [300] 'A1. Position of the flexor hallucis longus groove'
- [301] 'A2''. Shape of talo-fibular facet.'
- [302] 'A4''. Development of the talar posterior trochlear shelf'
- [303] 'A5''. Talar neck length (NL/TL x 100)'
- [304] 'A6. Medial talo-tibial facet'
- [305] 'A7. Lateral talar trochlear asymmetry'
- [306] 'A8. Talar cotylar fossa'
- [307] 'A9. Width of the head of the talus (HW/HHT x 100)'
- [308] 'GEB1. Talar neck angle'
- [309] 'GEB2. Talar body height (HT/MTRW x 100)'
- [310] 'GEB3. TW/TL x 100'
- [311] 'CA1. Anterior calcaneal elongation'
- [312] 'CA2. Position of the peroneal tubercle'
- [313] 'CA3. Posterior calcaneal bowing'
- [314] 'CA4. Calcaneo-cuboid articulation'
- [315] 'N1. Length relative to width'
- [316] 'N3. Morphology of the naviculocuboid articulation'
- [317] 'E1. Shape of Entocuneiform/MT1 articulation'
- [318] 'E2. Lateral process of entocuneiform'

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[319] 'O1. Foot axis'
[320] 'O2. Toilet claw'
[321] 'O3. Prehallux'
[322] 'O4. Metatarsus length'
[323] 'MT1. Peroneal tubercle of MTI'
[324] 'MT2. Hallux length'
[325] 'V1. Optic fovea'
[326] 'V2. Tapetum lucidum'
;

STATELABELS
1
    'three '
    'two '
    'one I/1 present, I/2 absent '
    'lower incisors absent ',
2
    'Arcuate battery from lateral perspective (U-shape
arcade) '
    'cusp tips staggered (V-shaped arcade) ',
3
    'No spaces '
    'Spaces present between crowns ',
4
    'present '
    'absent ',
5
    'very small (<0.69) '
    'moderate sized (<0.70, <1.07) '
    'large (>1.07) ',
6
    'I/1 much smaller than I/2 (<0.65) '
    'I/1 smaller than I/2 (>0.65, <0.82) '
    'I/1 almost as large as I/2 (>0.83, <1.00) '
    'I/1>I/2 (>1.01, <1.25) '
    'I/1>>I/2 (>1.25) ',
7
    'consideranly wider (m-d) than root (spatulate) '
    'narrow at apex, wider than root '
    '"styliform" (crown apex approximately the same
width as the cervical margin) ',
8
    'rounded oval (> 0.64) '
    'mesiodistally compressed (< 0.64) ',
9
    'low crowned '
    'moderately high crowned '
    'high crowned ',
10
    'erect or vertical '
    'slightly procumbent '
    'very procumbent ',
11
    'erect or vertical'
    procumbent
    'very procumbent ',
12
    spatulate
    'lanceolate, pointed ',
13
    'heel absent '
    'heel present ',

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14
    'absent to weak '
    'strong but incomplete '
    'strong and complete ',  

15
    'I/1 very small (I/1 << M/1) '
    'moderately enlarged (I/1 < or = M/1) '
    'grossly enlarged (I/1 > M/1) ',  

16
    'very small (C1/M1 < 0.40)'
    ' moderate (> 0.4, < 0.80)'
    'large (> 0.80, < 1.20); very large (> 1.20) ',  

17
    'low (< 1.07)'
    'moderate (> 1.07, < 1.17)'
    'high (>1.17) ',  

18
    'rounded oval '
    'mesiodistally compressed '
    'buccolingually compressed ',  

19
    'rounded '
    'sharp ',  

20
    'oblique to occlusal plane '
    'nearly horizontal to occlusal plane '
    'forms part of cropping mechanism with I/1-2 ',  

21
    'low, squat '
    'narrow, short '
    'tall, at or above tooth row ',  

22
    'erect or vertical '
    'procumbent '
    'very procumbent',  

23
    'erect or vertical '
    'slightly procumbent '
    'very procumbent',  

24
    'present '
    'absent ',  

25
    'present '
    'absent ',  

26
    'p2<<p3 (ratio<0.6)'
    'p2<p3 (0.6<ratio<0.9)'
    'p2> or =p3 (ratio>0.9)',  

27
    'P2 larger or equal to p2'
    'P2 smaller than p2',  

28
    'single '
    'double ',  

29
    'single '
    'double ',  

30
    'single '
    'double ',

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31
    'no crowding '
    'slightly crowded '
    'very crowded-mesial root positioned buccal to
distal root ',
32
    'large '
    'small '
    'absent or extremely small ',
33
    Low
    moderate
    'High (nearly as high as the protoconid)',
34
    'large '
    'small '
    'absent or extremely small ',
35
    'mesial to protoconid'
    'mesiolingual, between protoconid and metaconid'
    'mesial to metaconid',
36
    'widely spaced from the metaconid '
    'twinned with metaconid ',
37
    'absent '
    'weak '
    'strong ',
38
    'projects above protoconids of P/3-4 '
    'massive, projects above protoconids of P/3-4 '
    'not projecting, in line with P/3 '
    'extremely short, shorter than P/3 ',
39
    'close to protoconid '
    'widely spaced from protoconid ',
40
    'absent or trace '
    'small ',
41
    'absent or trace '
    'small '
    'large (as big as protoconid) ',
42
    'absent or trace'
    'small '
    'large (as big as protoconid) ',
43
    'closed '
    'open ',
44
    'absent '
    'lingual talonid crest present but an entoconid does
not stand out above it '
    'entoconid forms a small discrete cusp ',
45
    'absent '
    'lingual talonid crest present but an entoconid does
not stand out above it '
    'entoconid forms a small discrete cusp ',
46

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'continuous between metaconid and protoconid '
'discontinuous between metaconid and protoconid ',
47
'transversely oriented '
'distolingually oriented '
'absent ',
48
'transversely oriented '
'distolingually oriented ',
49
'complete [taxa without metaconids are assigned this
character state] '
'deeply notched ',
50
'large '
'small or absent ',
51
'distal to protoconid '
'distal to metaconid, or between protoconid and
metaconid ',
52
'absent '
'weak '
'strong ',
53
'absent '
'incomplete, broken at protoconid and hypoconid '
'complete ',
54
'not basally inflated'
'slightly basally inflated '
'very basally inflated ',
55
'not exodaenodont '
'slightly exodaenodont '
'very exodaenodont ',
56
'extremely short or non-existent (tri:tal > 1.61)'
'short (much shorter than trigonid) (tri:tal >
1.27, < 1.61)'
      'equal or slightly shorter in length to trigonid
(tri:tal > 0.92, < 1.27)'
      'talonid longer than trigonid (tri:tal < 0.91) ',
57
'Crown bases vertical in lateral perspective '
'slightly oblique '
'strongly oblique, projecting medial over the
anterior ',
58
Normal
Spatulate,
59
'Absent or trace '
'Strong ',
60
'Absent or weak '
'Moderate '
'Very strong ',
61
'Absent or weak '
'Moderate '

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'Very strong ',
62
'low '
'moderate '
'high (nearly as high as protoconid) ',
63
'P/3 much lower than P/4 '
'P/3 slightly lower than P/4 '
'P/3 equal in height to P/4 '
'P/3 higher than P/4 ',
64
'0.45-0.59 '
'0.60-0.69 '
'0.70-0.79 '
'>0.80 ',
65
'<0.95 '
'>0.96 <1.14 '
'>1.15 <1.20 '
'>1.21 <1.35 '
'>1.36 <1.46 '
'>1.47 ',
66
'< 0.62'
'>0.63, < 0.72'
' >0.73, < 0.82'
'>0.83, < 0.92'
'>0.93, < 1.02'
'> 1.03 ',
67
'Aligned mesiodistally '
'Shifted laterally',
68
'Aligned mesioditally'
'Mesial root shifted buccally',
69
'one '
'two ',
70
'much wider than talonid (> 1.11) '
'widths similar (< 1.11, > 0.90) '
'much narrower than talonid (< 0.90) ',
71
'much wider than talonid (> 1.20) '
'trigonid and talonid widths similar (< 1.20-1.05) '
'trigonid narrower than talonid (< 1.05) ',
72
Present
Absent,
73
'mesiolingual, between protoconid and metaconid '
'mesial to metaconid ',
74
'mesiolingual, between protoconid and metaconid '
'mesial to metaconid ',
75
Present
Absent,
76
'mesiolingual, between protoconid and metaconid '
'mesial to metaconid ',

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77      'widely spaced from the metaconid '
    'twinned with metaconid ',
78      'absent '
    'present ',
79      'absent '
    'small '
    'large ',
80      'single '
    'double ',
81      'absent '
    'narrower than talonid '
    'approximately equal in width to talonid ',
82      'smooth '
    'slightly crenulated '
    'highly crenulated ',
83      'higher than talonid (> 1.20) '
    'slightly higher than talonid (> 1.10, < 1.20) '
    'trigonid and talonid of similar height (< 1.10) ',
84      'Moderate to high '
    'Low ',
85      'Open '
    'Closed ',
86      'transversely aligned-lingual to protoconid '
    'slightly distolingual to protoconid ',
87      'absent '
    'small '
    'large ',
88      'runs toward metaconid '
    'runs toward hypoflexid ',
89      'complete '
    'deeply notched by protoconid/metaconid sulcus '
    'medial and lateral protocristid do not meet but no
sulcus is visible',
90      'complete '
    'deeply notched by protoconid/ metaconid sulcus '
    'medial and lateral protocristid do not meet but no
sulcus is visible',
91      'present '
    'absent ',
92      'barely stands out on lingual talonid marginal crest
    'a small discrete cusp '
    'a large cusp ',
93      'prominent '

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        'faintly visible '
        'absent ',
94      'large '
        'moderate '
        'small '
        'absent ',
95      'large '
        'moderate '
        'small '
        'absent ',
96      'large '
        'moderate '
        'small '
        'absent ',
97      'twinned to entoconid '
        'near midline '
        'slightly buccal to midline ',
98      'weak (rounded) '
        'strong (trenchant) '
        'very strong (trenchant) ',
99      'reaches trigonid wall at a point distal to
protoconid '
        'reaches trigonid wall at a point distolingual to
protoconid '
        'reaches trigonid wall at a point distal to
metaconid ',
100     'reaches trigonid wall at a point distal to
protoconid '
        'reaches trigonid wall at a point distolingual to
protoconid '
        'reaches trigonid wall at a point distal to
metaconid ',
101     'runs to base of trigonid '
        'runs part way up the distal trigonid wall '
        'connects with protoconid tip or protocristid '
        'connects with metaconid ',
102     'runs to base of trigonid '
        'runs part way up the distal trigonid wall '
        'connects with protoconid tip or protocristid '
        'connects with metaconid ',
103     'runs to base of trigonid '
        'runs part way up the distal trigonid wall '
        'connects with protoconid tip or protocristid '
        'connects with metaconid ',
104     'present '
        'absent ',
105     'absent or seen only as a trace '
        'weak '
        'strong ',

```

```

106      'absent or seen only as a trace '
      'weak '
      'strong ',  

107      'open '
      'notched lingually but not open '
      'closed ',  

108      'absent '
      'present (weak) '
      'present (large) ',  

109      'simple '
      'with accessory cusp close to hypoconid ',  

110      'notched '
      'straight ',  

111      'cusps not inflated, marginally positioned '
      'slightly inflated '
      'very inflated ',  

112      'absent to trace '
      'partial, broken at protoconid and hypoconid '
      'complete ',  

113      'very shallow '
      'moderate '
      'deep ',  

114      'very shallow '
      'moderate '
      'deep ',  

115      'M/3 much longer than M/2 (0.71-0.80) '
      'M/3 longer than M/2 (0.81-0.90) '
      'M/3 equal than M/2 (0.91-1.00) '
      'M/3 smaller than M/2 (1.01-1.12) '
      'M/3 much smaller than M/2 (> 1.13) '
      'if M/3 absent',  

116      '1.0-1.15'
      '1.16-1.22'
      '1.23-1.32'
      '> 1.33 ',  

117      'convergent '
      'vertically sided ',  

118      'transverse to hypoconid '
      'distal to hypoconid ',  

119      'indistinct to absent '
      'weakly developed (low) '
      'well-developed (strong and high) ',  

120      'absent; teeth widely spaced '
      'present as narrow contact '
      'I2/ tightly packed against I1/, I1/ preparacrista  

abbreviated ',  


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```

121
      'present '
      'absent: a wide space occurs in the midline between
these teeth ',  

122
      'present '
      'absent ',  

123
      'areas approximately equal (< 1.00) '
      'I1/ slightly larger than I2/ (> 1.00, < 1.40) '
      'I1/ much larger than I2/ (> 1.40 ) ',  

124
      'incisor small (< 0.50) '
      'incisor moderate (> 0.50, < 0.56) '
      'incisor large (> 0.56) ',  

125
      'rounded oval (< 1.05) '
      'buccolingually compressed (> 1.05, < 1.30) '
      'extremely compressed (> 1.30) ',  

126
      'rounded oval (< 1.05) '
      'slightly buccolingually compressed (> 1.05, < 1.30)  

      'extremely buccolingually compressed > 1.30 ) ',  

127
      'occlusal edge orthogonal to long axis of root '
      'occlusal edge wears at a steep angle to long axis
of root '
      'crown with pronounced mesial asymmetry (= mesial
process) in unworn state ',  

128
      'Moderate, continuous '
      'Strong ',  

129
      'absent '
      'present ',  

130
      'absent '
      ' present',  

131
      'oval '
      'rounded ',  

132
      'C1/ wears against P/1-2'
      'C1/ wears against P/2 '
      'C1/ wears against P/2-3 '
      'C1/ wears against P/3 ',  

133
      'shallow or absent '
      'deep ',  

134
      'weak or absent '
      'strong '
      'very strong ',  

135
      present
      absent,  

136
      one
      'two '
      'three ',
```

```

137
    'two ',
    'three ',  

138
    'two '
    'three ',  

139
    'P2/ much smaller (< 0.85) '
    'P2/ smaller (> 0.85, < 0.95) '
    'P2/ equal (> 0.95) '
    'Clearly larger',  

140
    'P4 << M1 (<0.66) '
    'P4< M1 (> 0.66, < 0.76) '
    'P4 = M1 (0.77-1.05) '
    'P4 > M1 (> 1.06) ',  

141
    'triangular '
    'suboval with the long axis b-l '
    'suboval with the long axis m-d '
    'round ',  

142
    'Suboval (with roughly mesiodistal long axis) '
    'Triangular (buccal lobe much wider than lingual
lobe) '
    'Trapezoid (tooth buccolingually extended with
buccal lobe wider than lingual lobe) '
    'Rectangular (tooth buccolingually extended with
lingual lobe as wide as buccal lobe) '
    'Squared ( tooth as wide as long with buccal lobe as
wide as lingual lobe)',  

143
    Triangular
    Trapezoid
    Rectangular
    Squared,  

144
    'trigon > = talon '
    'trigon < talon ',  

145
    'present '
    'absent ',  

146
    absent
    present,  

147
    'low relative to paracone '
    'high relative to paracone ',  

148
    'present '
    absent,  

149
    absent
    present,  

150
    'large '
    'small '
    'absent ',  

151
    'present '
    'absent ',  


```

```

152      'absent',
153      'present',
153      'strong',
153      'weak, short',
154      'smoothly rounded',
154      'waisted between buccal and lingual cusps',
155      'absent or weak',
155      'strong',
156      'absent',
156      'present',
157      'absent or weak',
157      'strong',
158      'minute to absent',
158      'present but small',
158      'strong',
159      'minute to absent',
159      'present but small',
159      'strong',
160      'three, three',
160      'three, two',
160      'two, two',
161      'three',
161      'two',
161      'one',
162      'very transverse (> 1.65)',
162      'transverse (< 1.65, > 1.30)',
162      'squared (< 1.30)',
163      'M1 >> M2 (> 1.40)',
163      'M1 > M2 (< 1.40, > 1.0)',
163      'M1 < M2 (< 1.0)',
164      'absent',
164      'single',
164      'double',
165      absent,
165      'weak',
165      'strong',
166      'large',
166      'small',
166      'minute to absent',
167      'large',
167      'small',
167      'minute to absent',
168      'distal, far lingual to protocone',
168      'distal, slightly lingual to protocone'

```

169 'distal, slightly buccal to protocone ',
talon lingually. ',
170 'absent '
 'weak '
 'strong, reaches to postprotocrista, encloses the
talon lingually',
171 'absent '
 'strong, reaches to postprotocrista, encloses the
talon lingually',
172 'attached to preprotocrista '
 'unattached to preprotocrista ',
173 'absent to indistinct '
 'small '
 'moderate '
 'large ',
174 'absent to indistinct '
 'moderate '
 'strong ',
175 'absent to ectocrista '
 'present on buccal cingulum ',
176 'absent '
 'small '
 'large ',
177 'absent to indistinct '
 'weak '
 'strong ',
178 'absent or weak '
 'strong ',
179 'absent or weak '
 'strong ',
180 'absent '
 'small-moderate '
 'large,
181 'not inflated '
 'slightly inflated '
 'very inflated ',
182 'no expansion '
 'slight expansion '
 'considerable expansion ',
183 'absent or very small '
 'moderate (but smaller than paracone) '
 'large (equal to paracone) ',
184 'absent or very small '

```

'small '
'large ',
185
'absent '
'small-moderate (smaller than paracone) '
'large (nearly as large as or larger than paracone)
',
186
'strong, complete, long (connected to parastyle) '
'strong, short '
'weak or absent ',
187
'very small (half the size of M1/ or less) '
'small (two thirds) '
'large (approximately as large) ',
188
'indistinct to absent '
'moderate '
'strong ',
189
'indistinct to absent '
'moderate '
'strong ',
190
'mesial to paracone '
'mesiobuccal to paracone ',
191
'distal to metacone '
'distobuccal to metacone ',
192
'moderate, does not reach the metastyle / the
distobuccal corner of the tooth'
'connected to metastyle / reaches the distobuccal
corner of the tooth',
193
'indistinct to absent '
'present but shallow '
'present, deep ',
194
'indistinct to absent '
'weakly developed '
'well developed (but well-marked notch between
postparacrista and premetacrista) '
'strongly elevated (weak notch between
postparacrista and premetacrista)',
195
'indistinct to absent '
'weakly developed '
'well developed (but well-marked notch between
premetacrista and postparacrista) '
'strongly elevated (weak notch between premetacrista
and postparacrista)',
196
'normal position '
'oblique ',
197
'strong '
'tiny ',
198
'indistinct to absent '
'short '

```

```

        'long ',
199      'indistinct to absent '
        'short '
        'long ',
200      'transverse, directed toward metaconule (or virtual
metaconule emplacement) '
        'lateral, directed toward the lingual posterior
cingulum (post-protocone fold-like) ',
201      'transverse, directed toward metaconule (or virtual
metaconule emplacement) '
        'lateral, directed toward lingual posterior cingulum
(post-protocone fold-like) ',
202      'runs to base of metacone (with hypometacrista) '
        'runs to metaconule (at the level of the small or
virtual metaconule) '
        'runs to posterior cingulum '
        'limited at a point distal to protocone ',
203      'runs to base of metacone (with hypometacrista) '
        'runs to metaconule (at the level of the small or
virtual metaconule) '
        'runs to posterior cingulum '
        'limited at a point distal to protocone ',
204      'low '
        'elevated ',
205      'connected to parastyle (by way of preparaconule
crista) '
        'connected to paraconule (or near to it or to a
virtual paraconule) ',
206      'connected to parastyle (by way of preparaconule
crista) '
        'connected to paraconule (or near to it or to a
virtual paraconule) ',
207      'indistinct to absent '
        'moderate '
        'well-developed (connected to paracone) ',
208      'absent '
        'weakly developed (low and short) '
        'well-developed (high) ',
209      'absent '
        'weakly developed (short) '
        'well-developed (high) ',
210      'indistinct to absent '
        'moderate (not connected to protocone) '
        'well-developed (connected to protocone or
postprotocrista) ',
211      Absent
        'present and forming the lateral wall of an anterior
accessory cavity pneumatized from the tympanic cavity'

```

'present and forming the lateral wall of an anterior accessory cavity pneumatized from the epitympanic recess. ',
212
'Anterior accessory cavity lies anterior to the tympanic cavity and is not trabeculated '
'anterior accessory cavity extends medial to the tympanic cavity, and is trabeculated ',
213
'Absent '
'Present ',
214
'Absent '
'Present and formed exclusively by the petrosal bone ',
215
'Posterior to line joining midpoints of tympanic bones '
'anterior to this line ',
216
'medial '
'midline of the bulla '
'lateral ',
217
'dorsal, adjacent to basioccipital or mastoid bone '
'ventral ',
218
'posterior '
'ventral '
'anterior ',
219
'runs across ventral lip of the fenestra cochleae, shielding it from ventral view when a canal is present '
'internal carotid canal does not shield the fenestra cochleae from ventral view ',
220
'on ventrolateral surface of promontorium '
'contacting only the cupula of the cochlea ',
221
'both stapedial and promontory canals are large '
'stapedial slightly smaller than promontory '
'stapedial highly reduced or absent altogether '
'stapedial larger than promontory '
'both promontory and stapedial canals absent ',
222
'open trough '
'complete canal ',
223
'intrabullar, or aphaneric '
'extrabullar or phaneric ',
224
'ribbon-like or only slightly expanded '
'laterally expanded into a collar or tube ',
225
'Linea semicircularis or partial annular bridge formed on a entotympanic bulla '
'linea semicircularis formed on a petrosal bulla '
'a complete annular bridge ',
226
'Absent '
'Present and formed by anterior accessory cavity '
'Present and formed by the tympanic cavity ',

```

227
  'absent '
  'laminar '
  'abutting ',
228
  'slight '
  'very extensive ',
229
  'Absent or minimal '
  'extensive ',
230
  'Absent '
  'Present, small and in the posterior root of the
zygomatic arch '
  'Present, large, and above the external auditory
meatus ',
231
  'Present '
  'Absent ',
232
  'Small '
  'Large '
  'Extremely large ',
233
  'None '
  'Postorbital bar present '
  'Postorbital septum present ',
234
  'zygomatic forms most of the septum '
  'frontal forms most of the septum ',
235
  'Present '
  'Absent ',
236
  'absent '
  'resent below olfactory tract ',
237
  'present '
  'separated by a large fronto-maxillary contact (and
in some taxa, a small os planum of the ethmoid) '
  'separated by a large os planum ',
238
  'Absent '
  'Present ',
239
  'outside orbital margin '
  'within the orbit or on the rim ',
240
  'unfused '
  'fused ',
241
  'low (less convergent than primates)'
  'moderate'
  'high'
  'Very high',
242
  'Reduced or absent '
  'small but distinct '
  'robust and long ',
243
  'present '

```

244 'absent ',
244 'Medially placed '
245 'Laterally placed ',
245 'long medial pterygoid plate extending one-third to
one half of the distance to the anterior surface of the bulla '
245 'short but distinct from lateral pterygoid plate for
its entire dorsoventral extent '
246 'medial pterygoid plate entirely absent, or reduced
to a low rugosity ',
246 'Long snout '
247 'Short snout ',
247 'deep '
248 'shallow ',
248 'absent '
249 'present ',
249 'biconcave and transversely wide '
250 'antroposteriorly oriented trough ',
250 'weak or absent '
251 'strong ',
251 'broad and wider than that of extant haplorhines '
252 'narrow, haplorhine-like ',
252 'very far above '
253 'slightly above or equal ',
253 'at level of tooth row '
253 'slightly above '
253 'well above tooth row ',
254 'shallow '
254 'deep ',
255 'no postorbital closure '
255 'zygomatico-parietal contact '
255 'alispfenoid-frontal contact ',
256 'absent '
256 'present ',
257 'narrow '
257 'broad ',
258 'narrow '
258 'broad ',
259 'narrow '
259 'broad ',
260 'symphysis procumbent '
260 'symphysis erect',
261 'cylinder, distal edge perpendicular to shaft '
261 'distal edge somewhat angled to shaft '

```

    'distal edge very angled',
262
    'subequal '
    'medial edge more flared than lateral edge ',
263
    'absent '
    'weak but distinct '
    'moderately distinct '
    'very distinct ',
264
    '> 70 (unwaisted) '
    '<= 70 (waisted) ',
265
    '< 100 '
    'between 100 and 140 '
    '140-200 '
    '>200 ',
266
    'present '
    'variable '
    'absent ',
267
    'above medial epicondyle '
    'above ventral trochlea '
    'above dorsal trochlea ',
268
    'reduced '
    'prominent ',
269
    'parallel '
    'slight dorsal angle'
    'large dorsal angle ',
270
    'not pronounced '
    'moderately pronounced '
    'very pronounced',
271
    'not pronounced'
    'moderately pronounced '
    'very pronounced ',
272
    'present (strong) '
    'small, shallow '
    'absent ',
273
    'Shallow '
    'Moderate '
    Deep,
274
    'broad '
    moderate
    'narrow ',
275
    'shallow '
    'deep ',
276
    'ventral articular width <2.5 times the ventral
capitular width '
    'ventral articular width > 2.5 times the ventral
capitular width ',
277

```

```

'100* H/F <= 65 '
'H/F between 65 and 80'
'H/F > 80 ',
278
'Facet on pisiform for ulnar styloid process is
roughly equal in size to that for triquetrum'
'Facet on pisiform for ulnar styloid process is much
enlarged and deeply excavated. ',
279
'present '
'absent ',
280
' Proximal to or level with lesser trochanter'
'distal to lesser trochanter. ',
281
'< 75'
'75-120'
'> 120',
282
'< 60'
'60-70'
'> 70',
283
' medial (0-30°)'
' posterior (>30°)',

284
' large'
'small'
'low crest or absent ',
285
' < 90 (shallow knee)'
' 90 - 100'
' > 100 (deep knee) ',

286
' spherical'
' semicylindrical'
' cylindrical',

287
'no extension'
'extension present',

288
'none '
'bent ',

289
' long (> 125)'
' moderate (110-125)'
' very short (< 110) ',

290
'Crest absent '
'Crest present ',

291
'large '
'intermediate '
'small ',

292
low
'high ',

293
'absent '
'present ',

294

```

```

        small
        'moderate '
        'extensive ',
295      'square/parallel '
        'triangular ',
296      'none '
        'slight '
        'strong ',
297      flat
        'anteriorly convex, posteriorly flat '
        'all convex ',
298      'no compression '
        'anteroposteriorly compressed ',
299      'on medial side of malleolus '
        'on posterior side of malleolus ',
300      'lateral to trochlea '
        'central to trochlea ',
301      'steep-sided'
        'steep-sided with a platar lip '
        'sloped obliquely ',
302      none
        'weakly developed'
        'well developed (prominent) ',
303      'short (<50) '
        'long (>50) ',
304      'short (does not reach to plantar edge of bone) '
        long,
305      'absent '
        'present ',
306      'shallow '
        'deep, medially projecting ',
307      '<120 '
        '>120 ',
308      '< 20°'
        '20-30°'
        '> 30°',
309      '<100 '
        '100-120 '
        '120-150 ',
310      '<60 '
        '>60 ',
311      'not elongate (ACL or anterior calcaneal ratio < 40)
        'moderate (ACL >= 40-45) '

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```

        'long (>45) ',
312      ' distal to joint'
        'at joint '
        'proximal to joint ',
313      'Absent '
        'Present ',
314      ' articular wedge absent (fan-shaped)'
        ' articular wedge present (more circular)',

315      'Short (<90) '
        'moderate (100-150) '
        'long( >150) ',

316      'cuboid facet on navicular contacts only the
ectocuneiform'
      'cuboid facet contacts the ectocuneiform and
mesocuneiform facet',
317      'dorsally reduced'
      'dorsal moiety of joint enlarged relative to ventral
moiety'
      'dorsal moiety greatly enlarged',
318      small
      'hypertrophied ',

319      'mesaxonic '
      'paraxonic
      'ectaxonic ',

320      'absent '
      'present ',

321      'present '
      'absent ',

322      'short '
      'long ',

323      'very large '
      'large '
      'small ',

324      'short '
      'long ',

325      'absent '
      'present ',

326      'present '
      'absent ',

;
MATRIX
'Donrussellia gallica+sp.'      ?1?1?????? ??????????
???00??111 02?1101?1? 011?10?101 02?00{12}0?12 001?530011 1011010010
1000011000 1222202211 3(12)11221001 {01}122{01}{23}101? ??????????
???????1?1 ?21-000??2 1101001000 012{01}022-00 0{01}0-02{12}000 002?112010
-101111100 -131110000 ?????????? ?????????? ?????????? ??????0??

```

?????1????? ??????????? ??????????? ??????????? ???????????
 ?????????? ????0
 'Notharctus robustior' 1001010001 101101?0?0
 2??00??111 02?1101200 02{01}0101101 0100010?11 001{12}320011
 1011011{01}1{01} 10{01}0012000 1222202111 3111222001 12220{12}011?
 1???0????? ??0?0011{01}1 212-001101 {01}{01}01001000 0221000100
 021002{12}00{01} 1110111221 1102200110 0331110000 0?0020000 301?????0?
 111?????? ????000 2010?11?0 1?3?201?0? ???1?0?0?? 1100100000
 1100022010 2201001020 110?11??0? 1?1?00
 'Adapis parisiensis' 1001010000 001201?012
 2000020111 02?2--2210 0210201100 022?031?10 0-21430011 11--1--020
 1010010000 121330?111 {23}111220001 1122031101 0?0?222??1 00??011111
 2030111101 1010101000 0220001100 000-022001 0020112110 0102201101
 1331000000 0?10020000 (13)000102000 101?001?0(01) 1101210100 ?011011100
 1011201100 010000?100 1000000010 1100122010 2201011211 1101??00?? 1?2?00
 'Cantius eppsi' ?????????? ??????????
 ???0??111 02?1002?1? 0211101100 01?0020?11 0023420011 10111-0010
 1000012000 1222202111 3011222001 122203011? ?????????? ???0111?1 ?11-
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 ?????????? ?????????? ?????????? ?????????? 2201??1020 ?????????? ??????
 'Leptadapis magnus' 1??0?0?00 001201?110
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BEGIN ASSUMPTIONS;

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- 120 123 - 126 132 134 136 139 - 140 150 158 - 169 172 - 173 175 - 177 180
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312 315 317 323;
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BEGIN NOTES;

[Taxon comments]

[Character comments]

[Character state comments]

[Attribute comments]

[Taxon pictures]

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[Character pictures]  
[Character state pictures]  
[Attribute pictures]  
ENDBLOCK;
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SOM References

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