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Early anthropoid primates: New data and new questions

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23 **Abstract**

24 Although the evolutionary history of anthropoid primates (monkeys, apes, and humans)
25 appears relatively well-documented, there is limited data available regarding their origins and
26 early evolution. We review and discuss here the earliest records of anthropoid primates from
27 Asia, Africa, and South America. New fossils provide strong support for the Asian origin of
28 anthropoid primates. However, the earliest recorded anthropoids from Africa and South
29 America are still subject to debate, and the early evolution and dispersal of platyrrhines to
30 South America remain unclear. Because of the rarity and incomplete nature of many stem
31 anthropoid taxa, establishing the phylogenetic relationships among the earliest anthropoids
32 remains challenging. Nonetheless, by examining evidence from anthropoids and other
33 mammalian groups, we demonstrate that several dispersal events occurred between South
34 Asia and Afro-Arabia during the middle Eocene to the early Oligocene. It is possible that a
35 microplate situated in the middle of the Neotethys Ocean significantly reduced the distance of
36 overseas dispersal.

37

38 1. Introduction

39 The discovery of numerous late Eocene and early Oligocene anthropoid primates in Fayum,
40 Egypt, initially led to the conclusion that their common ancestor originated in Africa.¹
41 However, exploration of older localities in Afro-Arabia during the early and early middle
42 Eocene revealed the absence of earlier African anthropoids, with only strepsirrhines present.²⁻
43 ⁵ On the other hand, the exploration of middle to late middle Eocene localities in China and
44 Myanmar over the last few decades has challenged this traditional point of view and supports
45 the idea that anthropoids originated in Asia. Subsequently, they dispersed to Africa sometime
46 during the middle Eocene, approximately between 45 and 40 million years ago (Ma).⁶⁻¹⁵ This
47 scenario is further supported by the dispersal of several other mammalian groups with Asian
48 origins to Afro-Arabia.⁹ Asian anthropoids are represented by the most primitive known
49 anthropoids, the Eosimiiformes, as well as a distinctive group of highly derived primates, the
50 amphipithecids. The classification of amphipithecids has been a subject of long-standing
51 debate. Some researchers considered them to be strepsirrhines that have developed
52 anthropoid-like characters, particularly in the dental-gnathic region, through convergence as
53 an adaptation to a hard food diet.¹⁶⁻¹⁸ Others argue that the amphipithecids are
54 anthropoids,^{11,14} as their skull, dentition, and postcranial skeleton display many anthropoid
55 characters. The particular feature, postorbital closure, widely regarded as the most significant
56 character of crown anthropoid, is observed to be absent in *Ganlea*.¹⁴ However, this character
57 might also be present in other taxa within this Asian anthropoid group. Therefore, they are
58 now interpreted as stem anthropoids.^{14,19} Recent fossil discoveries and analyses suggest that
59 certain taxa previously classified as amphipithecids, such as *Siamopithecus* and
60 *Aseanpithecus*, are considered to belong to distinct subfamilies due to the absence of shared
61 derived amphipithecoid characters. Instead, these taxa exhibit dental characters shared with the
62 anthropoids from Afro-Arabia and suggest potential phylogenetic relationships with their

63 Afro-Arabian counterparts. Nevertheless, the incomplete nature of these findings presents
64 challenges for definitive attribution. Regardless of these ongoing problems, the reconstruction
65 of the early stages of Asian anthropoid evolution provides valuable insights into the sequence
66 of anthropoid character acquisition.

67 Regarding the dispersal events from Asia to Africa, various scenarios have been
68 proposed. Among several alternative hypotheses, some authors²⁰⁻²¹ suggest an African
69 anthropoid radiation following the dispersal of a single Asian anthropoid species, possibly a
70 very primitive taxon like an eosimiid. This taxon could serve as the common ancestor of all
71 Afro-Arabian anthropoids. However, we propose an alternative perspective, suggesting
72 multiple dispersals from Asia to Africa. This view is supported by the rapid diversification of
73 African anthropoids in terms of morphology and size during the middle to late Eocene. This
74 diversification occurred within a relatively short time span, especially when compared to the
75 radiation of South American platyrrhines, which followed their supposed late
76 Eocene/Oligocene dispersal out of Africa.²² Nevertheless, new fossil data from the Brazilian
77 Amazonia region suggest a late middle Eocene dispersal from Africa toward South America.²³
78 The study of contemporaneous rodents indicates that these clades repeatedly dispersed
79 between Asia and Afro-Arabia from the late middle Eocene to the early Oligocene.²⁴⁻²⁵ Some
80 authors, based on phylogenetic analyses, propose one to three dispersal events of
81 hystricognathous rodents from Asia to Africa.²⁶ Additionally, the discovery of a newly
82 identified microplate suggests that it may have facilitated dispersal through rafting,
83 connecting Asia with the eastern coasts of Afro-Arabia and bridging the gap of the Neo-
84 Tethys Ocean.

85 Here, we present updated information on Eocene anthropoids in Asia, strengthening
86 support for the hypothesis of an Asian origin for the Afro-Arabian anthropoids. The dispersal
87 events from Asia to Africa and subsequent diversification in Africa and South America are

88 still subjects of ongoing research and discussions. Additionally, we examine the earliest fossil
89 records of anthropoids in Africa and South America in light of recent discoveries to refine our
90 understanding.

91

92 **2. THE EARLY ASIAN ANTHROPOIDS**

93 Asian Eocene and early Oligocene anthropoids have been represented by two distinct
94 groups: the Eosimiiformes, and the Amphipithecidae¹¹ (Table 1). The Eosimiiformes consist
95 of small-sized and very primitive taxa, including Eosimiidae and Afrotarsiidae. Some
96 researchers consider afrotarsiids to be tarsiids, while others view them as an even more
97 primitive group of anthropoids.^{11,19} On the other hand, the amphipithecids are larger in size
98 and display more derived anatomical features when compared to the eosimiiforms.
99 Traditionally, they were considered a monophyletic group based on numerous phylogenetical
100 analyses, which identified several distinct clades within this group. These clades include the
101 amphipithecines and aseanpithecines from the middle Eocene of Myanmar, as well as the
102 siamopithecines from the late Eocene of Thailand. However, a recent review of these taxa in
103 light of the most recent discoveries and studies reported here, raises doubts about the
104 monophyly of the amphipithecids.

105 **2.1 Family Eosimiidae**

106 Asian eosimiids are represented by three genera, *Eosimias* and *Phenacopithecus* from
107 the middle Eocene localities of Shanghuang and Yuanqu in China, and *Bahinia* from the late
108 middle Eocene Pondaung Formation in Myanmar and the early Oligocene Lijiawa locality in
109 South China^{6-7,12,27-28} (Figure 1). The earliest known, *Eosimias*, has a very small body weight
110 (120-160 g). Three species have been described from China: *Eosimias centennicus*, *Eosimias*
111 *dawsonae*, and *Eosimias sinensis*.^{6-7,27} These species share characters observed in other early
112 anthropoids, such as an unfused symphysis, a lower dental formula of 2-1-3-3, small, vertical

113 and spatulated lower incisors, large upper canines with a mesial groove, single-rooted P₂ and
114 a mesiodistally short P₃₋₄ with obliquely oriented roots with respect to the mesiodistal long
115 axis of the tooth row. Additional fragments of two lower jaws, including one with a lower M₃,
116 have been described as a new species, *Eosimias paukkaungensis*, from the Pondaung
117 Formation in Myanmar.²⁹ This species has a larger body weight of approximately 410 g,
118 falling within the range of body weights observed in *Bahinia*. It has been reinterpreted as
119 *Bahinia pondaungensis* based on its molar size and morphology, particularly the organization
120 of cusps, which strongly resemble those of *Bahinia*.¹¹ The M₃ paraconid of *E. paukkaungensis*
121 is less prominent compared to Chinese eosimiids, reflecting the more bunodont cusp
122 morphology observed in *Bahinia*. It can also be distinguished from the Chinese eosimiids
123 *Phenacopithecus*²⁷ which displays a more buccally displaced paraconid. Two species of
124 *Phenacopithecus*, *Phenacopithecus krishtalkai* and *Phenacopithecus xueshii* have been
125 described from China.²⁷ This genus is larger than *Eosimias* but smaller than *Bahinia*.
126 Additionally, the foot bones of eosimiids from China have been described, revealing derived
127 anatomical traits that are typically observed in living and fossil anthropoids, as well as some
128 plesiomorphic characters shared with primitive omomyid haplorrhines.³⁰ These features
129 suggest that eosimiids were primates adapted for leaping and arboreal-quadrupedal
130 locomotion.³¹

131 *B. pondaungensis* was found in the Pondaung Formation, Myanmar dated
132 radiometrically from 40.31 to 40.22 Ma.^{12,32} Its cranial and lower jaw remains were collected
133 from carbonate nodules that formed in a paleosol. The upper molars of *Bahinia* display no
134 conules, prominent buccal and lingual cingula, sharp hypoparacristae and hypometacristae,
135 and the absence of a hypocone (Figures 2f and 5e). Its lower jaw horizontal ramus is deep and
136 exhibits vertical and spatulate incisors, as well as premolar crowns with roots oblique to the
137 tooth row. Its dental characters, such as reduced buccal cingulum and paraconid, wider

138 buccolingual lower premolars, and more bunodont cusps, most closely resemble those of
139 *Eosimias* compared to other more derived anthropoids, although it also appears more
140 advanced than *Eosimias*. Nevertheless, some authors have considered it to be strepsirrhine.³³
141 A small portion of the orbit is also preserved, suggesting a small size and indicating diurnal
142 habits. The preserved inferior orbital ridge indicates the absence of an external lacrimal
143 foramen, suggesting a position inside the orbit of that foramen, representing an additional
144 anthropoid character. Two additional characters found in *Bahinia* help to confirm that
145 eosimiids are anthropoids and not tarsiiforms. One is the spatulate nature of its I² (Figures 2f),
146 similar to those of other Eocene crown anthropoids, and not pointed as in *Tarsius*. The second
147 character concerns its auditory bulla. When discovered, the petrosal of *B. pondaungensis* was
148 exposed, revealing numerous transbullar septa running from the promontory and fossular area
149 to the ectotympanic (Jaeger, personal observation). These septa are similar to those observed
150 in extant callitrichids but slightly more numerous. Unfortunately, this delicate feature was
151 damaged during handling and casting by inexperienced researchers. Transbullar septa have
152 been reported in *Eosimias*, among Fayum anthropoid (YPM 25972)³⁴ and among
153 callitrichids³⁵ suggesting that a pneumatized middle ear is a primitive anthropoid character
154 rather than a derived one as proposed by Horovitz.³⁶ However, they also occur in other
155 primates, such as the strepsirrhine *Allocebus*, the omomyids *Necrolemur* and *Rooneyia*, and
156 even outside of primates, in *Plesiadapis*.³⁷ Therefore, this particular feature alone cannot
157 conclusively support the anthropoid nature of *Bahinia*. However, it does indicate its
158 distinction from tarsiiforms, as this character is absent in the bulla of tarsiids.

159 Another species, *Bahinia banyueae*, has been described based on isolated teeth found
160 in the early Oligocene of China. This species is characterized by a smaller size and less
161 prominent buccal and lingual cingula on the upper molars compared to *B. pondaungensis*.²⁸
162 *Bahinia* can be considered a primitive and generalized anthropoid that is geologically younger

163 than *Eosimias*, representing a slightly more derived archetype in the early differentiation of
164 anthropoids in Asia. *Bahinia* displays only a few derived characters, such as an enlarged P₃
165 and a very short face.

166 *Anthrasimias*, discovered in the early Eocene of India, was initially classified as an
167 eosimiid due to its small size and upper molars with a triangular occlusal outline, cusps
168 hypocone, and less developed buccal and lingual cingulae with a crest-like paraconid.³⁸
169 However, more recently, Rose et al.³⁹ suggested that it might actually be an adapiform and
170 tentatively referred it to *Marcgodinotius*.

171 Recently, an isolated upper molar of a new eosimiid, named *Ashaninkacebus*, has been
172 discovered from the EOT (~34Ma) in Brazilian Amazonia, South America,²³ displaying a
173 morphology closely resembles that of *B. pondaungensis*. This discovery represents the third
174 Asian–African-related anthropoid found in the Eocene/Oligocene deposits of South
175 America.^{22,40} It provides evidence supporting the African origins of South American
176 platyrrhines.

177

178 **2.2 Family Afrotarsiidae**

179 The classification of this family is still a topic of debate regarding its affinities,
180 whether it belongs to the Tarsiiformes or represents a basal anthropoid.^{19,41–44} *Afrotarsius*
181 *chatrathi* was described from late early Oligocene deposits in Quarry M of the Jebel Qatrani
182 Formation, Fayum Province, Egypt.⁴⁵ Its lower molars exhibit a combination of dental
183 similarities to *Tarsius* but are smaller in size. They differ from tarsiids only in the distinct and
184 buccally shifted paraconid, a more distally positioned entoconid that elongates the talonid, a
185 short M₃ with a reduced distal lobe, and a longer M₁ compared to M₂ and M₃. Simons and
186 Bown⁴⁵ initially placed it within tarsiiforms, possibly related to tarsiids. However, Ginsburg
187 and Mein⁴⁶ noticed its anthropoid affinities and proposed a new family, Afrotarsiidae.

188 Nevertheless, some authors still argue that *Afrotarsius* should be classified as a tarsier relative
189 because it shares some characters with a Miocene tarsier, *Tarsius sirindhornae* which are not
190 observed in the most primitive eosimiids.¹⁹ Rasmussen et al.⁴⁷ reported a fused tibiofibular
191 bone, a uniquely derived character of tarsiids. However, this identification was disputed by
192 White and Gebo⁴⁸ who concluded that this bone did not belong to a primate. The definitive
193 identification of this bone is still pending.

194 Two additional taxa have been assigned to this family. One is a new species from Dur
195 At-Talah, Libya, *Afrotarsius libycus*.⁴⁹ The other is a new genus, *Afrasia djijidae*, discovered
196 in the Pondaung Formation in Myanmar¹¹ (Figure 3d). *A. libycus* shares similar characters
197 with *A. chatrathi* but is smaller in size. However, the discovery of a P³ and upper molars of *A.*
198 *libycus* allowed for a reinterpretation of this taxon and its phylogenetic affinities. It bears
199 several features in common with the Asian eosimiids. Apart from the previously mentioned
200 characters related to its lower molars, the P³ differs in shape from tarsiids, being more
201 extended buccolingually than mesiodistally and having a more developed protocone. Its upper
202 molars also differ from tarsiids in the lingual position of the main buccal cusps and the more
203 developed postmetacrista and buccal cingular shelf. Therefore, several important dental
204 features differentiate it from tarsiids and suggest a closer relationship to eosimiids.⁴⁹

205 A small calcaneus discovered in the Pondaung Formation in Myanmar was identified
206 as *Eosimias*-like.⁵⁰ Based on its estimated body size (110.7g), it could potentially belong to *A.*
207 *djijidae* (94–108g), further supporting the anthropoid classification of *Afrasia*. Phylogenetic
208 analysis also suggests a close relationship between *Afrotarsius* and *Afrasia*, with the two taxa
209 representing the sister group of eosimiids.¹¹ The striking morphological similarity between
210 *Afrotarsius* and *Afrasia* indicates that their common ancestor likely colonized Africa before
211 the earliest known record of *Afrotarsius*, providing strong evidence for an early wave of
212 mammalian dispersal from Asia to Afro-Arabia during the middle Eocene.¹¹

213 **2.3 Family Amphipithecidae**

214 Amphipithecids are large-sized primates found in Southeast Asia during the late
215 middle Eocene. Their classification as either anthropoids or adapids has been the subject of a
216 long-standing debate.^{16-17,44} They were regarded as a monophyletic group within the Asian
217 anthropoid clade.^{10,51-52} Currently, amphipithecids are classified into three distinct
218 subfamilies: amphipithecines, siamopithecines, and aseanpithecines.

219 **2.3.1 Subfamily Amphipithecinae**

220 Recent intensive fieldwork conducted in the Pondaung Formation of, Myanmar has
221 contributed to our understanding of amphipithecine diversity. While previously only two
222 genera, *Pondaungia* and *Amphipithecus* were recognized,⁵³⁻⁵⁴ two additional taxa have been
223 identified: *Myanmarpithecus* and *Ganlea*.^{8,14-15} Amphipithecines, in general, exhibit derived
224 features such as short dental rows with a parabolic shape, elevated mandibular corpora,
225 relatively short and broad lower premolars, molars with wrinkled enamel and bulbous cusps,
226 occasional supplementary cusplets, and the presence of an occasional crest between the
227 protocone and the distolingual cusp. They also have invaginated buccal and lingual margins
228 of lower molars, reduced to absent hypoconulid, reduced and mesially displaced entoconids,
229 and reduced to absent lower molar cingulids (Figure 2a–c and 4a–g).⁵⁶ Some of these
230 characters suggest an adaptation to a hard food diet.^{57,58} However, their enamel is also
231 considered to be primitively thin and displays a primitive state, appearing thin with a radial
232 microstructure, lacking well-developed Hunter–Schreger Bands (HSBs) or having very
233 weakly developed ones.⁵⁹

234 Sexual dimorphism within the *Pondaungia-Amphipithecus* complex remains an
235 unresolved issue. As distinct dental characters have not been found to differentiate between
236 *Pondaungia* and *Amphipithecus*, Jaeger et al.⁶⁰ concluded that they likely represent males and
237 females of the same species, displaying sexual dimorphism within the range observed in many

238 anthropoids.⁶¹ Conversely, some authors who supported their attribution to strepsirrhines,
239 interpret these differences as evidence of two separate and sympatric species (*Pondaungia*
240 *savagei/ondaungia. cotteri*). However, there is no compelling dental morphological evidence
241 supporting the recognition of two distinct taxa, aside from variations in overall size that
242 overlap when considering the entire available sample.¹⁷ Therefore, the hypothesis of sexual
243 dimorphism still stands as it can account for the high variability in size and morphology
244 observed within the population. There is an issue regarding *Pondaungia minuta*, which is
245 based on a poorly preserved lower jaw fragment. It is uncertain whether it represents a distinct
246 species⁵⁶ or, simply a pathological individual of *P. cotteri*. Because the genus *Pondaungia*
247 cannot be differentiated from *Amphipithecus*, taxonomic priority is given to the former name.

248 The presence of a true hypocone, derived from the distal cingulum, is considered a
249 basic characteristic of crown anthropoid upper molars.⁶² In *Pondaungia*, the upper molars
250 exhibit bunodont morphology with occasional additional cusplets, making it difficult to
251 determine the true identity of the posterolingual cusp in its molar trigon. This cusp is
252 sometimes located near the protocone and connected to it by a crest, which is likely not a
253 postprotocrista but rather a separate additional crest. Various interpretations have been
254 proposed for the nature of this cusp, including it being a pseudohypocone,^{16-17,63} a true
255 hypocone,^{60,64} or a displaced metaconule.⁶⁵ To gain a better understanding, it is informative to
256 examine the status of this cusp in more basal sister groups of amphipithecines, such as
257 *Myanmarpithecus* and *Ganlea*, as well as their more primitive relatives, the eosimiids.
258 *Bahinia*, like all eosimiiforms, lacks a hypocone. *Myanmarpithecus* and *Ganlea*, on the other
259 hand, exhibit a true hypocone.¹⁴⁻¹⁵ Therefore, it is suggested that regardless of the nature of
260 the distolingual cusp in *Pondaungia*, its ancestor likely developed a true hypocone that either
261 enlarged and shifted closer to the protocone or, alternatively, reduced and disappeared, being
262 replaced by a new cusp or a displaced metaconule.⁶⁵ Notably, the recent discovery of an

263 isolated upper molar of *P. cotteri* displaying a small metaconule adjacent to a hypocone
264 (NMMP 92) supports the interpretation that the distolingual cusp of the upper molars is a true
265 hypocone and not a displaced metaconule (Figure 4g).

266 An unresolved issue concerns the postcranial remains (NMMP 20) discovered at the
267 Sabapondaung locality (PK1) in Myanmar. These bones, including humeri, an ulna fragment,
268 and the distal part of the calcaneus, were initially attributed to a large amphipithecoid taxon.
269 However, they were not associated with dental remains and were allocated to strepsirrhines.⁶⁶
270 Further exploration of the same locality led to the discovery of only one pelvis fragment, also
271 attributed to strepsirrhines.⁶⁷ The strepsirrhine nature of these postcranial remains
272 unchallenged. There is tempting consideration that these postcranial bones belong to
273 amphipithecines based on overlapping size estimates between these bones and the largest
274 dental remains of amphipithecoid. If this were the case, it would suggest that amphipithecines
275 have convergently developed many anthropoid characters in their dentition and jaws.⁶⁶
276 However, the subsequent discovery of two tali (NMMP 39 and NMMP 82) that do not match
277 the previously described calcaneus but display typical anthropoid characters⁶⁸⁻⁷⁰ raises
278 questions about the previous association. The largest talus (NMMP 82) corresponds in size to
279 *Pondaungia* and exhibits clear anthropoid characters, potentially confirming the anthropoid
280 affinities of *Pondaungia* and related amphipithecines. The talus is considered to have high
281 taxonomic value, and these new postcranial remains strengthen support for the hypothesis that
282 medium to large-sized anthropoids were present in the Pondaung fauna. The estimated body
283 size for the medium size NMMP 39 talus is 2.7kg and for the larger size NMMP 82 talus is
284 4.9kg.⁷¹ Therefore, they have been tentatively allocated to *Ganlea* or *Aseanpithecus* for
285 NMMP 39 and *Pondaungia* for NMMP 82. The recent discovery of an ulna attributable to
286 *Ganlea*, exhibiting anthropoid characters and corresponding to a body size estimate of
287 approximately 3 kg, further supports this interpretation.¹⁴ However, further postcranial

288 remains of *Pondaungia* have yet to be discovered to solve this dilemma. In the Pondaung
289 Formation, strepsirrhines are represented by two small-sized sivaladapids,⁷² which are an
290 Asian endemic clade of adapiforms documented in Asia from the Eocene⁷³ to the late
291 Miocene (Lufeng).⁷⁴ Among the screening residue from several localities near Bahin village,
292 several molars have been collected from the same stratigraphic level together with other
293 primate remains, indicating the presence of two additional larger species of sivaladapids, one
294 of which is similar in size to the postcranial remains (NMMP 20) (Figure 4h). Thus, it is
295 highly likely that the postcranial remains (NMMP 20) belong to a large-sized, undescribed
296 sivaladapid strepsirrhine. Indeed, the postcranial anatomy of sivaladapids is still not well
297 understood, and they exhibit many primitive anatomical characters.^{67,75} Further research and
298 comprehensive studies on their anatomy could provide valuable insights and potentially aid in
299 identifying shared derived characters that would help accurately identify the enigmatic
300 postcranial remains from Pondaung. Nonetheless, the resemblance of these remains to
301 postcranial bones of notharctids strepsirrhines from North America warrants further analysis.
302 The interpretation of two isolated cranial fragments that were previously identified as frontal
303 bones of amphipithecines with an unfused metopic suture⁷⁶ has been refuted by Beard et al.⁷⁷
304 who excluded them as belonging to a primate. However, the recent discovery of several skull
305 fragments from a single individual, along with a lower jaw fragment and a partial ulna of
306 *Ganlea megacanina*, provides valuable evidence to challenge the hypothesis of
307 amphipithecines being strepsirrhine¹⁴ (Figure 2a–c). *Ganlea* exhibits cranial features such as a
308 short and broad muzzle, and strongly divergent zygomatic arches, similar to *Pondaungia*
309 (Figure 2a and 4a–d). This newly discovered maxillary fragment, consistent with other
310 described amphipithecine maxilla,⁷⁸ preserves the lower ridge of its orbit, indicating that the
311 jugal bone does not extend to the anterior part of the lower orbit rim to join an external
312 lacrimal bone, a character seen in strepsirrhines, *Tarsius* and most omomyids. Additionally, it

313 displays an intraorbital lacrimal foramen, a lacrimal canal oriented subvertically, completely
314 fused frontal bones, and an ulna with anthropoid characteristics. None of these new skull
315 bones exhibit any strepsirrhine characters. Therefore, considering the presence of the vertical
316 mandibular symphysis, a deep mandibular corpus, high elevation of the orbital lower margin
317 relative to the alveolar level, numerous dental anthropoid characters,¹⁴ and the presence of
318 these new cranial diagnostic anthropoid characters, it is highly unlikely that these similarities
319 are the result of total homoplasy. The absence of postorbital closure in these remains supports
320 the most probable status of *Ganlea* as a stem anthropoid, and by extension, for all other
321 amphipithecines. This finding aligns with the hypothesis that postorbital closure in tarsiers is
322 convergent with anthropoids, as previously suggested.⁷⁹⁻⁸¹ While *Ganlea* may represent a
323 stem haplorrhine displaying a mosaic of derived features seen in crown haplorhines, it is
324 important to note that the postcranial anthropoid characters observed on the talus⁶⁹ and ulna of
325 *Ganlea* do not support the attribution of *Ganlea* to stem haplorrhine. Additionally, the new
326 dental remains of *Ganlea*¹⁴ reveal unexpected similarities with *Myanmarpithecus*, suggesting
327 a close relationship between these two taxa. However, further material on *Myanmarpithecus*
328 is necessary to clarify their relationship.

329 **2.3.2 Subfamily Siamopithecinae**

330 Siamopithecines, represented by the single taxon, *Siamopithecus eoacaenus* (Figure 3a–
331 c), was discovered at the Krabi coal mine in Peninsular Thailand.^{8,10,82,83} The age of this
332 locality was initially determined using magnetostratigraphy, correlating the fossil-bearing
333 level with the Chron 13r,⁸⁴ suggesting an age spanning the latest Eocene to the earliest
334 Oligocene, as C13r spans the Eocene/Oligocene transition (EOT). However, recent findings,
335 identified a normal event (n2) within the former long C13 reverse event, leading to the
336 subdivision of C13r into two reverse events (C13 r1 and C13 r2).⁸⁵ The determination of
337 whether the Krabi fauna is from the latest Eocene or the earliest Oligocene depends on the

338 identification of the specific reverse event in the C13r (r1 or r2). Phylogenetically,
339 *Siamopithecus* is associated with the amphipithecids, sharing characters such as powerful
340 jaws and teeth, as well as molar structure (a crest linking the hypocone to the protocone on
341 upper molars).^{10,52} These features suggest an adaptation to a similar hard food diet.
342 Additionally, the biogeographic proximity of *Siamopithecus* to amphipithecines, along with
343 sharing traits like thin enamel and radial microstructure without HSBs,⁵⁹ further supports its
344 affiliation with this primate group. Tafforeau⁵⁹ proposed a folivorous diet to reconcile the
345 apparent contradiction between a hard food diet and thin molar enamel in *Siamopithecus*. In
346 contrast, Ramdarshan et al.⁵⁸ suggested a frugivorous diet, with a diet including grains similar
347 to other amphipithecids. Recently discovered more complete remains of *Siamopithecus* have led
348 to a reevaluation of its craniofacial characters, revealing a partial face resembling crown
349 anthropoid with strong frontation and high orbital convergence.⁵² Morphometric analyses
350 suggest that the face and lower jaw structures of *Siamopithecus* are more similar to
351 anthropoids than to fossil and extant strepsirrhines, including extinct giant lemurs from
352 Madagascar. A distinctive feature separating strepsirrhines from anthropoids in multivariate
353 analysis is the high elevation of the maxilla below the lower orbital rim. However, upper and
354 lower premolars of *Siamopithecus* exhibit primitive, simple features more similar to
355 eosimiiforms than to *Pondaungia* and other Myanmar amphipithecines.^{8,52,81} *Siamopithecus*
356 presents several distinctive dental characters, setting it apart from other primates. These
357 include the pronounced slanting of the lingual and buccal cusps in the upper molars, a strong
358 crest connecting the hypocone to the protocone, the absence of the lingual cingulum and
359 cingulids on molars, the buccal positioning of hypoconulids, and the presence of a large M₃. If
360 it is with the amphipithecids, as supported by numerous phylogenetic analyses,^{8,13-14,38,86-88}
361 *Siamopithecus* could be considered as an amphipithecids retaining several plesiomorphic
362 premolar characters, potentially inherited from an eosimiids ancestor. However,

363 *Siamopithecus* also shares derived dental characters with the propliopithecids, particularly
364 with the most primitive among them, the Taqah propliopithecid from Oman, described as
365 *Moeripithecus markgrafi*.^{83,89} These shared characters include the buccolingual extension of
366 the upper molars, a small hypocone derived from the cingulum, molar flaring, a larger M¹
367 compared to M², a rounded distal crown margin of P³–P⁴, and invaginated buccal and lingual
368 margins of lower molars.

369 The analysis of *Siamopithecus* and *M. markgrafi* reveals both similarities and
370 differences. Notable distinctions include the presence of a highly reduced P²/₂ in
371 *Siamopithecus*, the absence of a pericone, reduction of lingual cingulae, weak
372 hypometacristae, crests connecting the protocone and hypocone, a smaller and more primitive
373 P³/₃, and a more distal position of the P₄ metaconid. The combination of these derived and
374 primitive characters suggests that *Siamopithecus* might belong to a distinct clade with yet
375 unknown phylogenetic affinities to amphipithecines. Interestingly, *Siamopithecus* appears to
376 be more closely related to a hypothetical and unidentified stem group of Asian
377 “propliopithecid” relatives. This group seemingly did not develop all the necessary characters
378 to attain a catarrhine status. The potential presence of postorbital closure in *Siamopithecus*,
379 indicated by the elongated and flat distal extension of the preserved ascending ramus of its
380 jugal bone (Figure 3a), further supports this interpretation. This differs from *Ganlea*, which
381 has an equilateral triangular section in its postorbital bar root.¹⁴ This interpretation suggests
382 that the limited shared derived tooth characters between *Siamopithecus* and amphipithecines,
383 such as the crest connecting hypocone and protocone and enamel crenulations, may need to be
384 considered as homoplasies. However, this hypothesis raises several intriguing questions,
385 particularly concerning the presence of an advanced anthropoid with a closed postorbital wall
386 in the late Eocene of Southeast Asia. The evolutionary context and relationships of
387 *Siamopithecus* remain subject to further investigation and debate.

388 2.3.3 Subfamily Aseanpithecinæ

389 The discovery of *Aseanpithecus myanmarensis* at Paukkaung 2 (PK 2) locality,
390 Myanmar during the 2015 Myanmar-French Pondaung Expedition adds a new anthropoid
391 taxon to the fossil record¹³. It consists of a maxilla with C/M^3 and a lower jaw fragment with
392 P_2-P_3 (Figure 2d,e). It is characterized by a mix of primitive and derived dental features,
393 making it distinct from eosimiid, amphipithecine, and siamopithecine. *Aseanpithecus* is
394 classified as a medium-sized anthropoid, with an estimated body weight of around 3 kg.
395 Notable features include robust upper canines and a highly elevated maxilla below the lower
396 orbital rim. The absence of evidence for an external lacrimal canal or any extension of the
397 jugal bone beneath the lower orbital rim further confirms its anthropoid nature.

398 *Aseanpithecus* shares several characters with Afro-Arabian anthropoids. Its P_2 is larger
399 than P_3 and wider buccolingually, similar to *Serapia* and *Proteopithecus*. The upper premolars
400 are extended buccolingually and display distinct protocones, while the molars resemble those
401 of *Catopithecus*⁹⁰ (Figure 5a,b). This mosaic of shared characters with late Eocene Afro-
402 Arabian anthropoids suggests close phylogenetic relationships between *Aseanpithecus* and its
403 African relatives, in contrast to amphipithecines. Therefore, *Aseanpithecus* serves as a link
404 bridging the morphological gap between Asian and Afro-Arabian Eocene anthropoids. This
405 finding, along with *Siamopithecus*, demonstrates the presence of taxa in Southeast Asia
406 during the late middle Eocene that exhibits characters previously thought to be restricted to
407 African anthropoids, thereby supporting the notion of an Asian origin for some, if not all,
408 African clades.

409 However, due to the incomplete nature of the new taxa, it is not possible to assign
410 them to African clades or the ancestors of platyrrhines, as they display a unique combination
411 of characters. The mesiodistally broad upper molars with large trigon basins suggest affinities
412 with oligopithecoid, platyrrhine, and propliopithecine lineages. The large P_2 and reduced P_3 as

413 well as the structure of the upper premolars, suggest affinities with proteopithecids and
414 platyrrhines. The bulbous crown of the lower premolar indicates affinities with parapithecoid.
415 However, the orbital orientation of *Aseanpithecus*¹³ corresponds to a rather primitive state
416 compared to the more derived late Eocene African taxa, similar to *Ganlea* and *Parapithecus*
417 *grangeri*.⁹¹ These findings suggest that amphipithecids may not be monophyletic, and other
418 clades were likely present in Southeast Asia during the late middle Eocene, although they
419 remain poorly documented. In contrast, Myanmar amphipithecines appear to be endemic stem
420 anthropoids sharing numerous derived characters, indicating their monophyly.

421 **2.4 Family *incertae sedis***

422 *Bugtipithecus* discovered in the Bugti Hill of Pakistan, is known from isolated teeth
423 and was initially described as a basal Amphipithecidae.⁸⁷ However, its phylogenetic position
424 has been extensively debated as it appears in various positions on phylogenetic
425 trees.^{13,19,38,65,92,93} Importantly, *Bugtipithecus* lacks the previously mentioned synapomorphies
426 with amphipithecines. Its dental characters, such as bunodonty, conules, a strong hypocone,
427 and the absence of a direct connection between hypocone and protocone, a well-defined and
428 complete prehypocrista connected to the postprotocrista suggests an alternative interpretation
429 that *Bugtipithecus* might be an African species that dispersed to the Indian Subcontinent.
430 However, this interpretation is unlikely due to the absence of other African vertebrate groups
431 in the faunal association of the Bugti locality (Paali Nala). An alternative interpretation,
432 supported by Marivaux (personal communication, October 26, 2023), considers *Bugtipithecus*
433 as a member of the Amphipithecinae, having developed distinctive characters. This
434 classification would establish it as a valid Oligocene genus and species within the subfamily,
435 potentially linked to a stem group of African anthropoids.

436 The age of this locality was initially proposed to be early Oligocene, based on the
437 presence of two mammalian groups, rhinocerotids⁹⁴ and cricetid rodent⁹⁵ which successfully

438 dispersed to Europe during the early Oligocene period known as the “Grande Coupure”.
439 However, this argument is weakened by the fact that these taxa have Asian Eocene ancestors.
440 Considering the evolutionary stages of the associated primates and rodents, the strata could
441 potentially be from the latest Eocene age, However, recent paleontological data related to that
442 mammal fauna^{96–99} have further supported the Oligocene age of the locality, potentially
443 situating it close to the Eocene/Oligocene boundary. An earlier argument for an early
444 Oligocene age was based on the presence of specific species of nummulites. However, this
445 group of large benthic foraminifera does not distinctly differentiate between the latest Eocene
446 and lowermost Oligocene levels. Unfortunately, there is a lack of nannoplankton data from
447 these littoral deposits, which could provide further clarity regarding the age assessment.

448 *Phileosimias*, represented by two species, *Phileosimias brahuiorum*, and *Phileosimias*
449 *kamali*, has also been described from the Bugti Hills, Paali Nala locality in Pakistan. Initially,
450 it was attributed to the eosimiid group based on numerous primitive characters, including the
451 strong paraconid and lingually open trigonid.⁸⁷ However, with a better understanding of
452 eosimiiforms, it is now more reasonable to exclude *Phileosimias* from that group, an
453 interpretation recently supported by Marivaux.²³ *Phileosimias* shares several important dental
454 characters with some African anthropoids, such as strong conules, the absence of
455 hypoparacrista and hypometacrista, weak buccal and lingual cingula, and a twinned entoconid
456 and hypoconulid.⁸⁷ This suggests that anthropoids from South Asia (Indo-Pakistan) might
457 display closer morphological similarities to African anthropoids than to their Southeast Asian
458 counterparts. Based on this information, it is proposed that *Phileosimias* should be assigned to
459 a new family.

460 Another primate, *Krabia* is known from the late Eocene/Oligocene Krabi locality in
461 Peninsular Thailand.⁹² It is represented by a partial maxilla with left and right P⁴–M². *Krabia*
462 displays distinctive upper molar characters, including bunodont cusps, pronounced lingual

463 cingula, reduced buccal cingula, and the absence of a hypocone. Initially, assigned to
464 amphipithecids, it does not share derived traits with amphipithecines. Therefore, its
465 classification as an amphipithecid is uncertain. *Krabia* also differs significantly from other
466 known Asian clades, such as eosimiiforms, siamopithecines, and aseanpithecines. The
467 taxonomic status of *Krabia* must remain open until further remains are discovered.

468 The discovery of new Asian Eocene anthropoids has significant implications for our
469 understanding of primate evolution. It challenges along several distinct scenarios,¹⁹⁻²¹ the
470 previous hypothesis of a single mid-Eocene dispersal event from Asia to Africa, followed by
471 the adaptative radiation of African anthropoid clades (proteopithecids, parapithecoids,
472 oligopithecids, propliopithecids + platyrrhines). The presence of derived Eocene Asian taxa
473 with closer affinities to African anthropoids suggests a more complex evolutionary scenario.
474 Eosimiiforms, previously considered a conservative and plesiomorphic clade, originated in
475 Asia and maintained their primitive characters for an extended period. The presence of
476 *Afrotarsius* in the early Oligocene of the Fayum⁴⁵ suggested the persistence of eosimiiforms
477 in Africa. Moreover, eosimiiforms continued to persist in Asia until the early Oligocene,
478 represented by taxa-like *Bahinia* in China. These findings raise questions concerning the
479 transition from eosimiiforms to more derived anthropoids, particularly regarding their
480 geographical distribution and the timing of this shift.

481 Eocene Asian anthropoids are now recognized as a diverse group encompassing
482 various branches. Among them, are the primitive stem group known as eosimiiforms and the
483 endemic stem group, amphipithecines, characterized by highly derived dentognathic
484 characters exclusively found in Myanmar. Additionally, there are siamopithecines, whose
485 affinities remain unresolved but potentially closely related to African anthropoid ancestors,
486 and the aseanpithecines that bridge the dental morphology gap between Asian and African
487 taxa. One notable feature is the postorbital structure, which is lacking in the genus, *Ganlea*, an

488 endemic amphipithecines from Myanmar. This radiation of Southeast Asian anthropoids
489 occurred far from Africa, highlighting the importance of further discoveries from the middle
490 Eocene of South Asia. These findings will contribute significantly to our understanding of the
491 Asian origin of African anthropoids.

492

493 **3. THE EARLY AFRICAN ANTHROPOIDS**

494 Africa has been proposed as the birthplace of anthropoid primates due to the high
495 diversity of anthropoids discovered in the Fayum localities of Egypt over the past 50
496 years^{1,62,100} (Figure 1). The Fayum anthropoids have been recorded from the early late Eocene
497 (37Ma, BQ-2 locality) to the early Oligocene (33Ma, Quarry M locality).¹⁰¹ However, there
498 are very few records of earlier African primates. One such record is the late Paleocene
499 *Altiatlasius koulchii*, found in the Adrar Mgorn 1 locality in Morocco (~57Ma). Initially
500 described as an omomyid,¹⁰² later assigned to stem-anthropoids,^{35,81,103-105} based on a few
501 anthropoid characters, such as bunodonty, the complete lingual cingulum on M², the absence
502 of the nannopithec fold, the enlarged protoconid, the widely splayed paraconid and
503 metaconid, and the distally projected hypoconulid. Nevertheless, some authors attributed it to
504 plesiadapiforms.¹⁰⁶ Due to its classification relying on a few isolated teeth, determining its
505 taxonomic attribution is difficult. Moreover, its primate identity remains unclear as its upper
506 molar morphology lacks a direct connection between the protocone and the hypometacrista,
507 and displays well-developed conules, strong buccal cingulum, and an elevated protocone.

508 In the Western Sahara localities of Glib Zegdou in the Gour Lazib area of Algeria, a
509 few primate molars were initially described as anthropoids, namely *Algeripithecus* and
510 *Tabelia*.¹⁰⁷ However, additional discoveries have clearly demonstrated that these fossils, along
511 with *Azibius*, actually belonged to strepsirrhines (Azibiidae).³ The age of this locality has been
512 estimated to be late early Eocene or early middle Eocene (49-45Ma).¹⁰⁸ Another locality,

513 Chambi in Tunisia, from the early Eocene or early middle Eocene, has so far only yielded
514 remains of strepsirrhines.⁴ In the middle Eocene Aznag locality of southern Morocco, two
515 fragments of primate lower molar were discovered. However, these fragments do not provide
516 enough information to determine their taxonomic identity with certainty.¹⁰⁹ Birket Qarun
517 locality 2 (BQ-2) in Fayum, Egypt,⁸⁸ Bir El Ater locality in Algeria,¹¹⁰ and Dur At-Talah
518 locality in southeast Libya⁴⁹ have documented the oldest unchallenged African primitive
519 anthropoids. These early African anthropoids are all very small in size. They have been
520 attributed to parapithecoids (*Biretia*) and oligopithecids (*Talahpithecus*) and exhibit several
521 diagnostic characters of their respective clades, suggesting that they were already diversified
522 in Africa during that time. At the BQ-2 locality, a still undescribed primitive anthropoid has
523 been found.^{19,111} This taxon exhibits upper molar morphology similar to that of *Bahinia* and
524 *Talahpithecus*, and bears three premolars. Additionally, an enigmatic primate, *Nosmips*
525 *aenigmaticus* was initially considered either a strepsirrhine or anthropoid.¹¹² However, we
526 believe that *Nosmips* exhibits several characters typically found in strepsirrhines, such as a
527 mesostyle on M², waisted P³ and P⁴, and a strongly curved and prominent protocristid on P₃–
528 P₄, indicating its strepsirrhine nature. It may also bear some resemblance to Asian
529 sivaladapids. It is worth noting that a detailed cladistic analysis was unable to resolve the
530 question of its affinities.^{40,112}

531 Although the anthropoid nature of *Biretia* and *Talahpithecus* is undisputed, the age of
532 the Dur At-Talah locality has been consistently challenged by several authors who suggested
533 a younger age than the originally estimated 39–38 Ma, based on magnetostratigraphic and
534 biochronological data.⁴⁹ Some authors argue that rodents, which are often considered reliable
535 biochronological indicators, are younger than 37Ma.¹¹³ On the other hand, Coster et al.²⁵ have
536 demonstrated that the anomalurid species from the Libyan locality is more primitive than the
537 corresponding taxon from BQ-2. *Arcanotherium savagei* represents the most abundant

538 proboscideans at Dur At-Talah.¹¹⁴ However, this taxon has never been found in the Birket
539 Qarun Formation of the Fayum, suggesting it likely became extinct before the deposition of
540 the Birket Qarun Formation or the more recent Eocene fauna of the Fayum, Quarry L-41.
541 Alternatively, it may not have been living in this area, but the similarity between the
542 sediments and the numerous common taxa between these two localities rather supports the
543 former explanation. Two taxa of hyracoids are found in the Libyan locality,¹¹⁵ one identical to
544 *Dimatherium patnaiki*, described from BQ-2,¹¹⁶ and the other similar to *Bunohyrax*
545 *matsumotoi* described from Bir El Ater locality.¹¹⁷ *Witwattia schlosseri*, the largest Eocene
546 fossil bat, was originally described from BQ-2¹¹⁸ but in Dur At-Talah, it is represented by a
547 larger-sized species.¹¹⁹ According to Gunnell et al.¹²⁰ the molar size of this taxon has
548 decreased over time, suggesting an older age for the Libyan locality. The strepsirrhine
549 *Karanisia* found in both Dur At-Talah in Libya and BQ-2 is significantly smaller at Dur At-
550 Talah, suggesting an older age for Dur At-Talah.¹²¹ The relative stratigraphic position of these
551 two localities remains controversial and their absolute ages pose an even greater challenge.¹²²

552 The estimated age interval for these late middle Eocene African localities is between
553 39 and 36Ma. Dur At-Talah corresponds rather to Chron C18 (38–39Ma),⁴⁹ but Chron C17
554 cannot be excluded and BQ-2 corresponds to Chron C17 (37Ma).¹⁰¹ The Bir El Ater locality
555 has limited contribution to this debate. The alleged occurrence of an anthracothere at Bir El
556 Ater has been invalidated, making it impossible to constrain its age based on the presence of
557 that clade.¹²³ Stratigraphically, the fossiliferous layer in Bir El Ater is located at the top of a
558 regressive marine sequence with abundant gypsum, overlying well-dated marine early
559 Lutetian beds.¹²⁴ Considering the anomalurid lineage described by Coster et al.²⁵ a group that
560 displays an increasing number of accessory crests on molar crowns over time, Dur At-Talah
561 appears to be more primitive than BQ-2, suggesting it to be the oldest of the three localities.

562 *Amamria* is represented by a complete upper molar discovered in the late middle
563 Eocene Djebel el Kébar, Central Tunisia, dating back to approximately 39.5Ma.²¹ It has been
564 suggested as a transitional form between Asian Eosimiiformes and Simiiformes. Nevertheless,
565 several distinguishing features, including an enamel swelling possibly corresponding to a
566 small paraconule, a prominent preparaconule crista, a weak hypoparacrista, a relatively low
567 elevation of the hypometacrista-postprotocrista crest, the presence of minute but well-defined
568 hypocone, an incipient pericone, and notably the absence of invagination of the distal crown
569 margin found in all known primitive anthropoids, these collectively present tentative evidence
570 favoring the strepsirrhine interpretation. This fossil record suggests that strepsirrhines
571 developed true hypocones and pericones earlier than anthropoids, further supporting this
572 interpretation.³⁹ However, additional dentognathic material is needed to clarify the precise
573 affinities of this primate from Tunisia, which, like *Anthrasimias* from India,³⁸ also displays
574 eosimiid characters.²¹ Only future discoveries documenting a more comprehensive dental
575 morphology of this intriguing ancient taxon will allow us to either support or reject its
576 anthropoid status.

577 The middle Eocene Black Crow locality in Namibia has yielded an upper maxilla with
578 M²⁻³ of *Notnamaia bogenfelsi*. Initially, it was described as an anthropoid,¹²⁵ but later, it was
579 reattributed to a strepsirrhine primate.^{5,19,126} Similarly, an isolated P₄ from the late Eocene
580 locality of Silica North, originally described as *N. bogenfelsi*,¹²⁵ was later considered as a
581 possible anthropoid (cf. *Proteopithecus*).¹²⁶

582 Therefore, there is currently no documented evidence of an African anthropoid from
583 the early and early Middle Eocene. All primates from that period are now recognized as
584 strepsirrhines, which strongly supports the scenario of one or multiple dispersal events from
585 Asia at the origin of Afro-Arabian anthropoids, in addition to eosimiiforms. The hypothesis of
586 an African radiation stemming from a single eosimiids ancestor would remain the most

587 parsimonious. However, eosimiiforms do not display significant evolutionary dynamics but
588 rather exhibit evolutionary stasis, as seen in species such as *Bahinia* from the early Oligocene
589 of China and *Afrotarsius* from the early Oligocene of Fayum.

590 Furthermore, the estimated time range between the first dispersal of anthropoids to
591 Africa and the late middle Eocene radiation is relatively short, spanning only a few million
592 years, in contrast to the diversification time of platyrrhines in South America. The African
593 fossil record highlights several dispersal events between Asia and Afro-Arabia, occurring
594 during the middle Eocene to the early Oligocene time interval.¹²⁷ These events are
595 documented by the dispersal of *Afrotarsius*, the ancestors of African anthropoids,
596 hystricognaths, and anomalurid rodents during the middle Eocene, anthracotheres during the
597 latest Eocene, and cricetid rodents and propliopithecids during the early Oligocene.¹²⁸⁻¹²⁹
598 Therefore, it is more plausible to consider multiple dispersals of Asian anthropoids to Afro-
599 Arabia originating from a dispersal area that remains undocumented but was geographically
600 closer to Africa than Southeast Asia, even though this hypothesis may appear less
601 parsimonious. Propliopithecids were not documented before the early Oligocene, and their
602 sister group, the oligopithecids, did not show any taxa bridging the gap between the two
603 groups, despite having a good fossil record. An Asian origin can also be considered for other
604 mammal groups that have never been taken into consideration, such as tooth-combed
605 strepsirrhines, which are so far only documented from Africa, and some creodonts.

606 In conclusion, the minimum age of the first middle Eocene dispersal wave from Asia,
607 including anthropoids, can be estimated to have occurred between 45 and 40Ma, as long as we
608 exclude *Altiatlasius* from that scenario. An important dispersal event also occurred in Europe
609 during the MP13 zone, around the same period. This event was marked by the appearance of
610 new adapid primates taxa and many new ungulates, which likely originated from Asia.¹³⁰ It is,

611 therefore tempting to consider these dispersal events as contemporaneous and related to
612 worldwide climatic and paleogeographical changes.¹³¹

613

614 4. EARLIEST ANTHROPOIDS FROM SOUTH AMERICA

615 *Perupithecus*, found in the early Oligocene of Santa Rosa, Peruvian Amazonia, is
616 considered one of the oldest known South American anthropoid primates^{22,132} (Figure 1, 5c).
617 It was associated with other anthropoid molar fragments suggesting that several other taxa
618 were present in this locality. It shares similar molar characters with *Talahpithecus*, an Eocene
619 African anthropoid described as the oldest known oligopithecoid. This raises questions about
620 the nature of the African clade at the origin of platyrrhines. Initially, the Fayum taxon
621 *Proteopithecus* was considered a possible ancestor of platyrrhine,¹³³ but this interpretation has
622 been challenged, leaving the phylogenetic affinities of that genus more open.¹¹² However,
623 *Proteopithecus* is excluded from oligopithecoids, which have never been considered as
624 possible ancestors of South American platyrrhines due to their lack of anterior premolar
625 (P^2/P_2), the presence of a honing facet on P_3 , and their derived postcranial anatomy in well-
626 documented late Eocene representatives.¹³⁴⁻¹³⁵

627 Nevertheless, the available data suggest the possibility that a primitive form of
628 oligopithecoid, retaining three premolars, may have been at the origin of platyrrhines. An
629 undescribed taxon from BQ-2 in Fayum bearing the upper and lower second premolars may
630 correspond to such a primitive oligopithecoid^{19,111} and would support the interpretation that
631 oligopithecoids are the most primitive group of Afro-Arabian anthropoids, implying an
632 independent loss of $P^2/2$ and the development of honing facets from those of
633 propliopithecoids.¹³⁶ Alternatively, if oligopithecoids retain a primitive molar morphology
634 similar to that of the common ancestor of platyrrhines and catarrhines, then oligopithecoids can
635 be viewed as very early catarrhines retaining primitive molar anatomy, with *Perupithecus* as a

636 very early platyrrhine also retaining this anatomy. However, it should be noted that this
637 scenario assumes that *Perupithecus* is a true ancestor of platyrrhines and not just another
638 African Eocene primate that dispersed to South America alongside other primates, including
639 true platyrrhine ancestors. The discovery of parapiithecoid molars from the Santa Rosa locality
640 in Peru, a family previously only documented from Afro-Arabia,⁴⁰ indicates that several Afro-
641 Arabian primitive anthropoids may have dispersed to South America and supports the African
642 origins of *Perupithecus*. In addition, the recent discovery of a new Asian-African eosimiid
643 (*Ashaninkacebus*) in Brazilian Amazonia, near the Eocene-Oligocene boundary,²³ confirms
644 that several distinct African primates lineages were able to colonize South America during
645 that period. Nonetheless, more complete fossils are necessary to fully understand this enigma.

646

647 **5. DISCUSSION**

648 **5.1 Homoplastic evolution of the postorbital septum in tarsiids and anthropoids**

649 The homology of the postorbital septum, a structure previously considered a shared
650 derived character of extant haplorhines, has been a subject of controversy. Early studies pointed
651 to distinct differences in the structures of the postorbital septum in tarsiers and anthropoids,
652 indicating a lack of homology between the two groups.^{79,80} This hypothesis was supported by
653 Beard and MacPhee⁸¹ as well. Recent ontogenetic studies have provided further insights.
654 Investigations into newborn tarsiers revealed their development of partial postorbital closure,
655 unlike that of anthropoids.¹³⁷ Additionally, the partial skull of *Ganlea*, a stem anthropoid from
656 the late middle Eocene, also lacks postorbital closure. This finding suggests that postorbital
657 closure may not have been present in early anthropoids.¹⁴ This supports the suggestion by
658 Rosenberger and Pagano¹³⁸ that frontal fusion may have served as an alternative mechanism for
659 dissipating calvarian strains during mastication, replacing the function previously carried out
660 by an open interfrontal structure.

661

662 **5.2 Sequence of appearance for crown anthropoid characters**

663 The new fossil of *Ganlea* also provides valuable information about the sequence of
664 appearance of anthropoid characters and challenges previous assumptions.¹⁴ Previously, it
665 was thought that many dental and postcranial anthropoid characters emerged early in the
666 evolution of the clades, evidenced by their presence in *Eosimias*, an early middle Eocene
667 Asian primate. *Eosimias* exhibits several anthropoid features including vertically implanted
668 lower incisor crowns with a shovel-like shape, a single-rooted P₂ (also found in the earliest
669 Eocene haplorrhine *Archicebus*),^{6,7,93} obliquely oriented P₃-P₄ in the tooth row, reduction of
670 the M₃ hypoconulid lobe, and a vertical symphysis. *Bahinia*, another middle Eocene Asian
671 primate, displays a short face and elevated mandible ramus and maxilla. Contrarily, *Ganlea*,
672 displays facial anatomical organization similar to crown anthropoids, including the nearly
673 vertical intraorbital lacrimal canal, absence of connection between the jugal and the lacrimal,
674 and strong orbital frontation. However, it notably lacks postorbital closure, which is first
675 documented in anthropoid skulls from the 34Ma L-41 locality in Fayum,^{133,134} and possibly in
676 the contemporaneous *Siamopithecus* in Peninsular Thailand, approximately 6 Ma later than
677 the radiometrically dated Pondaung stem anthropoids (about 40Ma).³²

678

679 **5.3 Ancestral anthropoid dental morphotype**

680 The upper molars of *Aseanpithecus*, *Talahpithecus* (the oldest-known African
681 oligopithecoid), and *Perupithecus* (among the oldest South American anthropoid, along with
682 *Ucayalipithecus* and *Ashaninkacebus*) share several characters, such as peripheralized molar
683 cusps, weak or absent conules, U-shaped protocristae, and strong and united mesial, lingual
684 and distal cingula (Figure 5c–f). These features likely represent the ancestral upper molar
685 morphotype of crown anthropoids.¹³⁹ However, *Aseanpithecus* presents distinct differences in

686 its upper molars compared to the others. These differences include the weakness of the
687 hypoparacrista, the complete absence of hypocone and pericone, a straight distal wall, and
688 more bunodont and lower cusps. It is important to note that the morphological variation
689 observed in the upper molar of *Aseanpithecus* upper molars is known from only one
690 specimen, which limits a more detailed interpretation. Nevertheless, these differences suggest
691 that the pronounced bunodonty observed in propliopithecids and parapithecoids, also present
692 in *Biretia*, likely represents a derived state. This interpretation is supported by the
693 evolutionary sequence of African parapithecoids, which exhibit the development of bunodont,
694 conules, hypocones, and additional cusps on their anterior premolars.⁸⁸ Therefore, the
695 presence of bunodont appears to represent a derived cusp status among the late middle Eocene
696 anthropoids. This contrasts with some previous interpretations,¹⁴⁰ but agrees with Gunnell and
697 Miller.¹³⁹

698 **5.4 Phylogenetic relationships**

699 The phylogenetic trees involving early Asian anthropoids display significant variation,
700 leading to uncertainty in the relationships among different taxa.^{13,14,19,23,40,86} Many Asian taxa
701 rely on limited fossil evidence, mostly comprising isolated teeth, which can lead to instability
702 and potentially modify proposed relationships with the discovery of just a few additional
703 findings. Consequently, these phylogenetic trees are considered provisional and unsettled.
704 Drawing definitive conclusions about biogeography based solely on them would be
705 premature.

706 The phylogenetic position of *Afrotarsius* and *Afrasia*, members of the family
707 Afrotarsiidae, remains a topic of debate. Initially, before their inclusion in anthropoids
708 phylogenetic analyses, Kay et al.⁴³ placed *Afrotarsius* as a basal anthropoid, closely related to
709 the Eosimiidae. However, subsequent analyses have yielded conflicting positions for
710 afrotarsiids. Some studies propose them as basal anthropoids,^{11,23,141} being the sister group of

711 Eosimiidae, and forming a clade named Eosimiiformes.¹¹ On the contrary, other analyses
712 placed afrotarsiids as basal anthropoids where eosimiiforms represent a paraphyletic group,
713 with eosimiids/*Eosimias* considered the most basal anthropoids.^{13,142} Recent studies focusing
714 on the dental features of afrotarsiids indicate closer relationships with anthropoids rather than
715 with tarsiids.^{28,49} Nonetheless, several phylogenies analyses position afrotarsiids within
716 tarsiids^{19,28,38,143,144} or in an uncertain relationship with tarsiids and basal anthropoids.⁸⁸

717 Among Paleogene anthropoids from Asia, the phylogenetic position of the family
718 Eosimiidae stands out as the most consistent and firmly established. They are commonly
719 recognized as basal stem anthropoids in numerous studies.^{8,11,13,14,19,23,28,38,43,87,93,141–146}
720 Eosimiids are frequently recognized as the most basal anthropoids, forming a monophyletic
721 group in various analyses. However, a few analyses suggest eosimiids as a nonmonophyletic
722 group^{87,142,143} or positioned them ambiguously in relation to tarsiids and/or afrotarsiids,
723 although such instances are relatively uncommon.^{87,147} Additionally, in some analyses,
724 eosimiids are not identified as the most basal taxon within the anthropoid clade. Instead, this
725 position is occupied by taxa showing strepsirrhine affinities (such as *Ekgmowechashalidae*),¹⁴⁴
726 omomyid affinities (like *Uintanius*, *Loveina*),¹⁴¹ or taxa with enigmatic affinities (*Altiatlasius*)⁹³
727 which might be considered as outliers.

728 The amphipithecids, including *Pondaungia*, *Ganlea*, *Myanmarpithecus*,
729 *Aseanpithecus*, and *Siamopithecus*, have been the subject of multiple maximum parsimony or
730 Bayesian analyses, suggesting their classification as crown anthropoids.^{8,11,13,23,92} They have
731 been proposed as either the sister group to platyrrhines or to the Fayum anthropoids
732 (*Propliopithecidae*, *Oligopithecidae*). Moreover, many analyses support their relationship as a
733 sister group to crown anthropoids.^{8,19,28,38,87,88,93,143,146} This classification is attributed to the
734 presence of numerous highly distinctive derived dental characters unique to the
735 amphipithecids. However, alternative studies propose a more basal position for

736 amphipithecids among stem anthropoids.^{14,141,144} The discovery of the *Ganlea* partial skull
737 and ulna¹⁴ has notably contributed to enhancing phylogenetic resolution and helped solidify
738 the position of amphipithecines as stem anthropoids.

739 The study of relationships between African and Asian anthropoids is ongoing. If
740 accurate, the phylogenetic tree would display a mixture of both Asian and African clades.
741 However, current phylogenies do not support this scenario, emphasizing the necessity for more
742 complete fossils to establish a stable relationship among Eocene anthropoids. Amphipithecines
743 share certain dental characters with derived African parapithecoids, such as bulbous molar
744 cusps, additional cusps or cusplets, and waisted lower molars. Nevertheless, these shared
745 characters should be considered as potentially homoplastic until further evidence is obtained.
746 Although most phylogenies depict amphipithecids including siamopithecines and
747 amphipithecines, as a monophyletic group,^{11,14,44} the number of shared derived characters
748 supporting this grouping is limited and may be homoplasie. The position of *Siamopithecus* as a
749 stem amphipithecids, as suggested in some analyses, is currently unsupported from current
750 analyses. However, the newly proposed phylogenetic position of *Siamopithecus* remains
751 unformalized.

752 At present, the current view suggests that amphipithecids constitute a varied collection
753 of early Asian anthropoids rather than presenting a unified, cohesive group. Further discoveries
754 of more complete fossils are necessary to better understand and clarify the relationships among
755 these early anthropoids.

756 **5.5 The fate of Eocene Asian anthropoids**

757 Some researchers have suggested that Asian anthropoid lineages may not have
758 survived the Eocene/Oligocene cooling event, unlike their African counterparts.¹⁹ Their
759 argument is due to a lower diversity of anthropoids observed in the Oligocene primate
760 assemblage in China compared to a higher diversity of strepsirrhines.²⁸ This discrepancy leads

761 them to propose the possibility that the extinction of most Asian anthropoids by the end of the
762 Eocene could imply that they were less well-adapted compared to African anthropoids.^{28,139}

763 However, the findings of the current study do not align with this concept. It is
764 important to note that Oligocene mammalian localities in southern Asia are limited. Should
765 recent fossil mammal data confirm the proposed Bugti locality in Pakistan to be of early
766 Oligocene age⁹⁶⁻⁹⁹ would contradict this outdated interpretation. Nevertheless, it is important
767 to acknowledge the incompleteness of our knowledge regarding Oligocene primates in South
768 Asia. Drawing conclusions based on data from a single locality in China is insufficient for
769 making definitive statements about the entire continent. Clearly, further investigations are
770 necessary to obtain a better understanding of the fate of Asian anthropoids during the EOT.

771 **5.6 When, where, and how many dispersal events**

772 During the middle Eocene, paleogeography indicates the isolation of the Afro-Arabian
773 continent and the separation of western Asia from Afro-Arabia by a Neo-Tethys Sea channel.
774 A recently identified Pak-Iran Makran microplate,¹⁴⁸ situated between India and Arabia
775 during this period, may have served as an intermediate landmass connecting the two
776 continents or significantly reduced the width of marine barriers (Figure 6). This emerging
777 platform might have played a role in facilitated dispersal through rafting and acted as a
778 selective filter. We propose a dispersal scenario involving rafting from the delta of a large
779 river located on the Pak–Iran Makran microplate, possibly aided by favorable marine currents.
780 These rafts may have acted as filters, enabling colonization events primarily by small and
781 medium-sized mammals. The presence of unidirectional marine currents might explain the
782 numerous dispersal events observed between Asia and Africa during that time. Previous
783 studies have proposed dispersal events between Asia and Africa for primates, including
784 *Altiatlasius* in the Paleocene, the dispersal of *Afrotarsius*, and a common ancestor of Afro-
785 Arabian anthropoids.^{9,19} Besides *Altiatlasius*, we suggest that at least three dispersal events

786 might have occurred. These events involved the dispersal of *Afrotarsius*, the ancestors of
787 African anthropoids, hystricognaths, and anomalurid rodents during the middle Eocene,
788 followed by the dispersion of anthracotheres in the late Eocene, and finally, during the early
789 Oligocene, the dispersal of cricetid rodents and propliopithecids.^{25,49,113,149} The discovery of
790 undescribed cricetid rodents discovered from the early Oligocene Taqah locality, in
791 Oman,^{128,129} provides strong evidence supporting these later dispersal phases. Cricetids, with
792 their Asian origins, dispersed to Europe during the early Oligocene and likely reached Afro-
793 Arabia (Oman) at the same time.¹⁵⁰ The absence of cricetids from the rich early Oligocene
794 fossil localities of Fayum in Egypt and from the early Oligocene localities in Libya remains
795 unexplained. Possible explanations include limitations to their dispersal out of Oman due to
796 an epicontinental sea barrier isolating Oman¹⁵¹ (although this is not supported by the
797 similarity between Fayum and Oman anthropoids), or the difficulty in discovering them due
798 to their small size.

799 Another striking point is the absence of evidence, within this time interval, supporting
800 dispersal events from Africa to Asia. Some authors^{113,149,152} have proposed that Eocene
801 anomaluroid rodents originated in Africa from zegdomyids ancestors and subsequently
802 dispersed to Asia, evidenced by the presence of *Pondaungimys* from Pondaung Formation
803 (Myanmar).^{153–154} However, there is no other evidence of such a dispersal event in any other
804 vertebrate group. Alternative viewpoints among other authors favor an Asian origin of
805 anomalurids^{25,153} contradicting the proposed African to Asia dispersal hypothesis.

806 The new paradigm corresponds to multiple dispersal events between the middle
807 Eocene and the early Oligocene. In such a scenario involving numerous dispersal events, it is
808 plausible that unexpected mammal clades might have also been involved. Traditionally,
809 Eocene anthropoid primates have been characterized as forest dwellers. However,
810 paleoenvironmental data obtained from the Pondaung Formation suggests that their habitat

811 was more diverse, comprising a mosaic of distinct biotas, ranging from dry dipterocarp forest
812 to riverine forest and open vegetation, existing within a contrasted monsoonal climate with a
813 relatively long dry season.^{155,156} Therefore, some of these eosimiiforms, amphipithecines, and
814 aseanpithecids might have been dwellers of mixed habitats rather than exclusively inhabiting
815 dense tropical forests. This adaptive plasticity may explain the dispersal capabilities of these
816 Asian Eocene anthropoids, enabling their successful colonization of Africa and South
817 America in a relatively short time span.

818

819 6. CONCLUSIONS

820 The discovery of additional Eocene anthropoids remains in Asia has provided a better
821 understanding of the evolution of their anatomical characters. It has been confirmed that the
822 earliest anthropoid taxa were notably small in size and exhibited a crestiform molar structure.
823 The development of bunodonty appeared later as a derived trait. This sequence of anthropoid
824 characters has significantly enriched documented evidence, resolving long-standing debates.
825 Dental and postcranial features of anthropoids appeared earlier than some skull features. In
826 terms of skull characters, the elevation of the maxilla, its contribution to the lower orbit rim,
827 the intraorbital location of the lacrimal canal with its subvertical orientation, and the fusion of
828 the frontal bones appeared before postorbital closure. However, the presence of postorbital
829 closure, previously considered a derived crown haplorhine feature shared between tarsiiiforms
830 and anthropoids, is lacking from the amphipithecine *Ganlea*. *Siamopithecus*, previously
831 classified as an amphipithecid, displays some morphological similarities but likely exhibits
832 postorbital closure, raising questions about its unsolved phylogenetic relationships.

833 The scenario of an Asian origin for Afro-Arabian anthropoids, followed by dispersal
834 across the Trans-Neotethys region, is reinforced by the recognition of a microplate that
835 significantly reduces the oceanic gap between South Asia and the northeastern Afro-Arabian

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865

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1298 **Author Biographies**

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1322 His research also focused on the evolution of mammal faunas and paleoenvironments from
1323 the Paleogene and Neogene of Southeast Asia and Northern Africa.

Table 1 Early anthropoid primates mentioned in the text, including their taxonomy, type specimen, type locality, age, and references.

Suborder Anthropoidea Mivart (1864)

Family Eosimiidae Beard et al. (1994)

Genus *Eosimias* Beard et al. (1994)

<i>E. sinensis</i>	IVPP V10591	Shanghuang fissure-fillings B, Liyang County, Jiangsu Province, China	Middle Eocene	Beard et al. (1994)
<i>E. centennicus</i>	IVPP V11000	Locality 1, Zhaili Member, Heti Formation, Yuanqu Basin, Shanxi Province, China	Late middle Eocene	Beard et al. (1996)
<i>E. dawsonae</i>	IVPP V11999	Locality 11–12, Rencun Member, Heti Formation, Yuanqu Basin, Shanxi Province, China	Late middle Eocene	Beard and Wang (2004)

Genus *Bahinia* Jaeger et al. (1999)

<i>B. pondaungensis</i>	NMMP 14-16	Yashe Kyitchaung, Pondaung Formation, Myanmar	Late middle Eocene (40.31–40.22Ma)	Jaeger et al. (1999)
<i>B. banyueae</i>	IVPP V22730	Lijiawa fossil site, upper part of Caijiachong Formation, Yuezhou Basin, Yunnan Province, China	Early Oligocene	Ni et al. (2016)

Genus *Phenacopithecus* Beard and Wang (2004)

<i>P. krishtalkai</i>	IVPP V11997	Locality 7, Rencun Member, Heti Formation, Yuanqu Basin, Henan Province, China	Late middle Eocene	Beard and Wang (2004)
<i>P. xueshii</i>	IVPP V11998.4	Nanbaotou locality, Zhaili Member, Heti Formation, Yuanqu Basin, Shanxi Province, China	Late middle Eocene	Beard and Wang (2004)

Genus *Ashaninkacebus* Marivaux et al. (2023)

<i>A. simpsoni</i>	UFAC-CS 066	Ponto Rio Juruá, Foz do Breu, Acre, Brazil	Eocene/Oligocene (~ 34Ma)	Marivaux et al. (2023)
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Family Afrotarsiidae Ginsburg and Mein (1987)

Genus *Afrotarsius* Simons and Bown (1985)

<i>A. chatrathi</i>	CGM 42830	Quarry M, Jebel Qatrani Formation, Fayum Province, Egypt	Early Oligocene	Simons and Bown (1985)
<i>A. libycus</i>	DT1-35	DT-Loc.1, Bioturbated Unit, Dur At-Talah escarpment, Libya	Late middle Eocene (39–38Ma)	Jaeger et al. (2010)

Genus *Afrasia* Chaimanee et al. (2012)

<i>A. djijidae</i>	NMMP-81	Nyaungpinle Locality, Pondaung Formation, Myanmar	Late middle Eocene (40.31–40.22Ma)	Chaimanee et al. (2012)
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Family Amphipithecidae

Subfamily Amphipithecinae Godinot (1994)

Genus *Pondaungia* Pilgrim (1927)

<i>P. cotteri</i>	GS1 D201-203	Pangan I Kyitchaung Pondaung Formation, Myanmar	Late middle Eocene (40.31–40.22Ma)	Pilgrim (1927)
<i>P. minuta</i>	NMMP 4	Lema Kyitchaung, Pondaung Formation, Myanmar	Late middle Eocene (40.31–40.22Ma)	Jaeger et al. (1998)
Genus <i>Myanmarpithecus</i> Takai et al. (2001)				
<i>M. yarshensis</i>	NMMP-8-10	Yashe Kyitchaung, Pondaung Formation, Myanmar	Late middle Eocene (40.31–40.22Ma)	Takai et al. (2001)
Genus <i>Ganlea</i> Beard et al. (2009)				
<i>G. megacarina</i>	NMMP 70	Ganle Kyitchaung, Pondaung Formation, Myanmar	Late middle Eocene (40.31–40.22Ma)	Beard et al. (2009)
Subfamily Siamopithecinae Beard et al., 2009				
Genus <i>Siamopithecus</i> Chaimanee et al. (1997)				
<i>S. eoacaenus</i>	TF 3635	Krabi coal mine, Bang Mark pit, Krabi Province, Peninsular Thailand	Late Eocene /early Oligocene (35–33Ma)	Chaimanee et al. (1997)
Subfamily Aseanpithecinae this volume				
Genus <i>Aseanpithecus</i> Jaeger et al. (2019)				
<i>A. myanmarensis</i>	NMMP 93	PK2 locality, Paukkaung village, Myanmar	Late middle Eocene (40.31–40.22Ma)	Jaeger et al. (2019)
Family Parapithecidae Schlosser (1911)				
Genus <i>Biretia</i> de Bonis et al. (1988)				
<i>B. piveteaui</i>	BRT 17-84	Bir El Ater, Algeria	Late middle Eocene	de Bonis et al. (1988)
Genus <i>Ucayalipithecus</i> Seiffert et al. (2020)				
<i>U. perdita</i>	CPI-7936	Santa Rosa, Peru	Early Oligocene	Seiffert et al. (2020)
Family Oligopithecidae Simons, 1989				
Genus <i>Talahpithecus</i> Jaeger et al. (2010)				
<i>T. parvus</i>	DT1-31	DT-loc.1, Bioturbated Unit, Dur At-Talah escarpment, Libya	Late middle Eocene (39–38Ma)	Jaeger et al. (2010)
Genus <i>Perupithecus</i> Bond et al. (2005)				
<i>P. ucayaliensis</i>	CPI-6486	Santa Rosa, Peru	Early Oligocene	Bond et al. (2005)
Family <i>incertae sedis</i>				
Genus <i>Bugtipithecus</i> Marivaux et al. (2005)				
<i>B. inexpectans</i>	UMC-DBC 2174	Paali Nala DBC2, Bugti Hills, Bugti Member, Lower Chitarwata Formation, Pakistan	Latest Eocene /early Oligocene	Marivaux et al. (2005)
Genus <i>Phileosimias</i> Marivaux et al. (2005)				
<i>P. brahuiorum</i>	UMC-DBC 2221	Paali Nala DBC2, Bugti Hills, Bugti Member, Lower Chitarwata Formation, Pakistan	Latest Eocene /early Oligocene	Marivaux et al. (2005)
<i>P. kamali</i>	UMC-DBC 2199	Paali Nala DBC2, Bugti Hills, Bugti Member, Lower Chitarwata Formation, Pakistan	Latest Eocene /early Oligocene	Marivaux et al. (2005)
Genus <i>Krabia</i> Chaimanee et al. (2013)				
<i>K. minuta</i>	MPFT-05-1	Krabi coal mine, Bang Mark pit, Krabi Province, Peninsular Thailand	Late Eocene /early Oligocene (35–33Ma)	Chaimanee et al. (2013)



FIGURE 1 Geographic distribution of early anthropoid localities mentioned in the text.

Paleogene (pink circle), Eocene (red circle), Oligocene (yellow circle), and Eocene/Oligocene (half red half yellow circle). The map was drawn based on the work of C R Scotese, PALEOMAP Project.

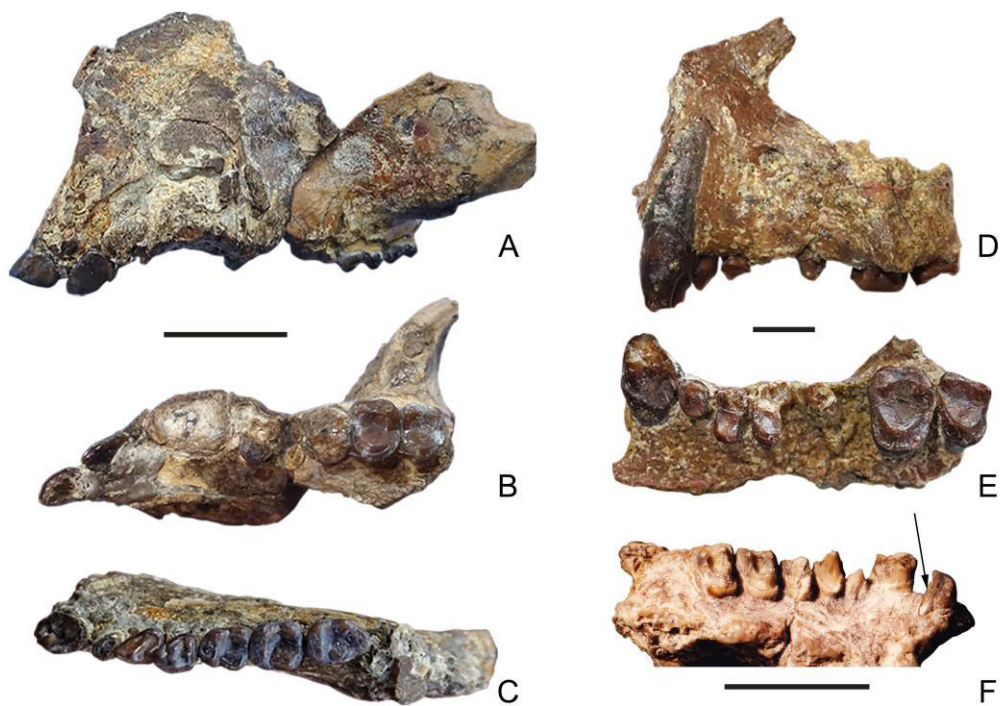


FIGURE 2 *Ganlea megacanina* (a-c) with a scale bar of 1 cm. Left skull fragment (NMMP 103) in buccal (a) and occlusal (b) views, and (c) left mandible (NMMP 101) in occlusal view. *Aseanpithecus myanmarensis* (d, e) with a scale bar of 5 mm. Left maxilla (NMMP 93) in buccal (d) and occlusal (e) views. *Bahinia pondaungensis* (f) with a scale bar of 1 cm. Right maxilla (NMMP 15) in occlusal view, with an arrow indicating the spatulate upper incisor I².

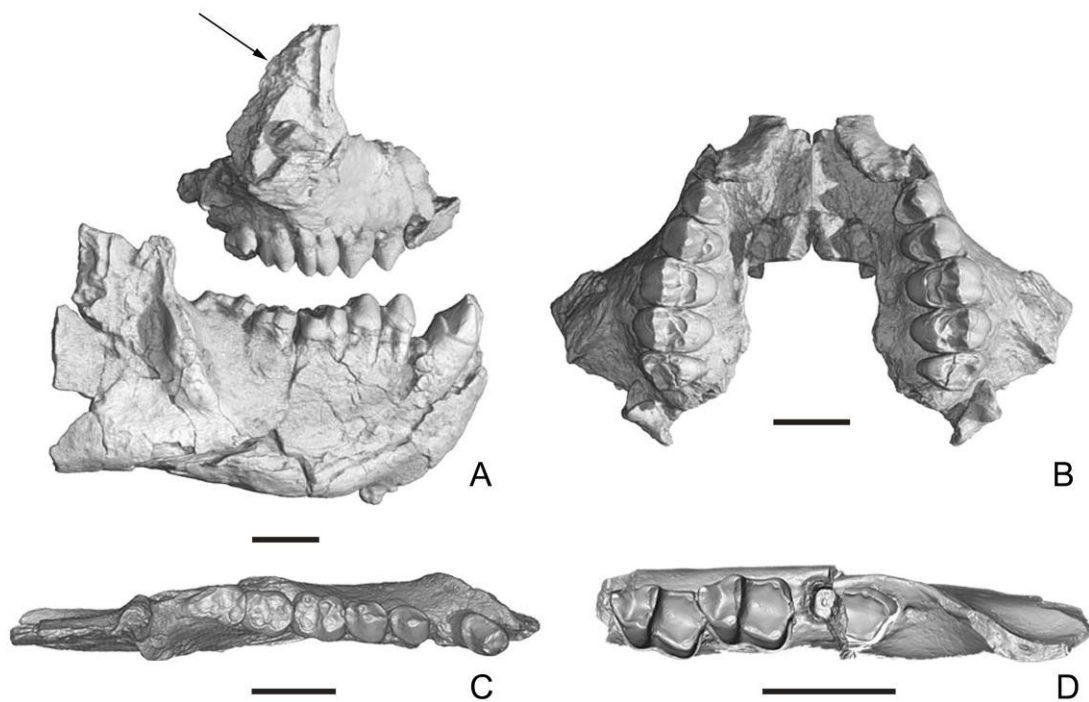


FIGURE 3 *Siamopithecus eocaenus* (a-c) with a scale bar of 1 cm. (a) Right maxilla (TF 7625), and mandible (TF 7624) in buccal view, with an arrow indicating the flattened distal wall of the ascending ramus of the jugal bone. (b) Symmetry of the left maxilla in occlusal view. (c) Right mandible (TF 7624) in occlusal view. *Afrasia djijidae* (d) with a scale bar of 3 mm from PK 2 locality in Myanmar. Mandible with M₁₋₃ in occlusal view, demonstrating the size proportions of M₁/M₂ and the short and narrow hypoconulid lobe on M₃, which are considered as an anthropoid characters.

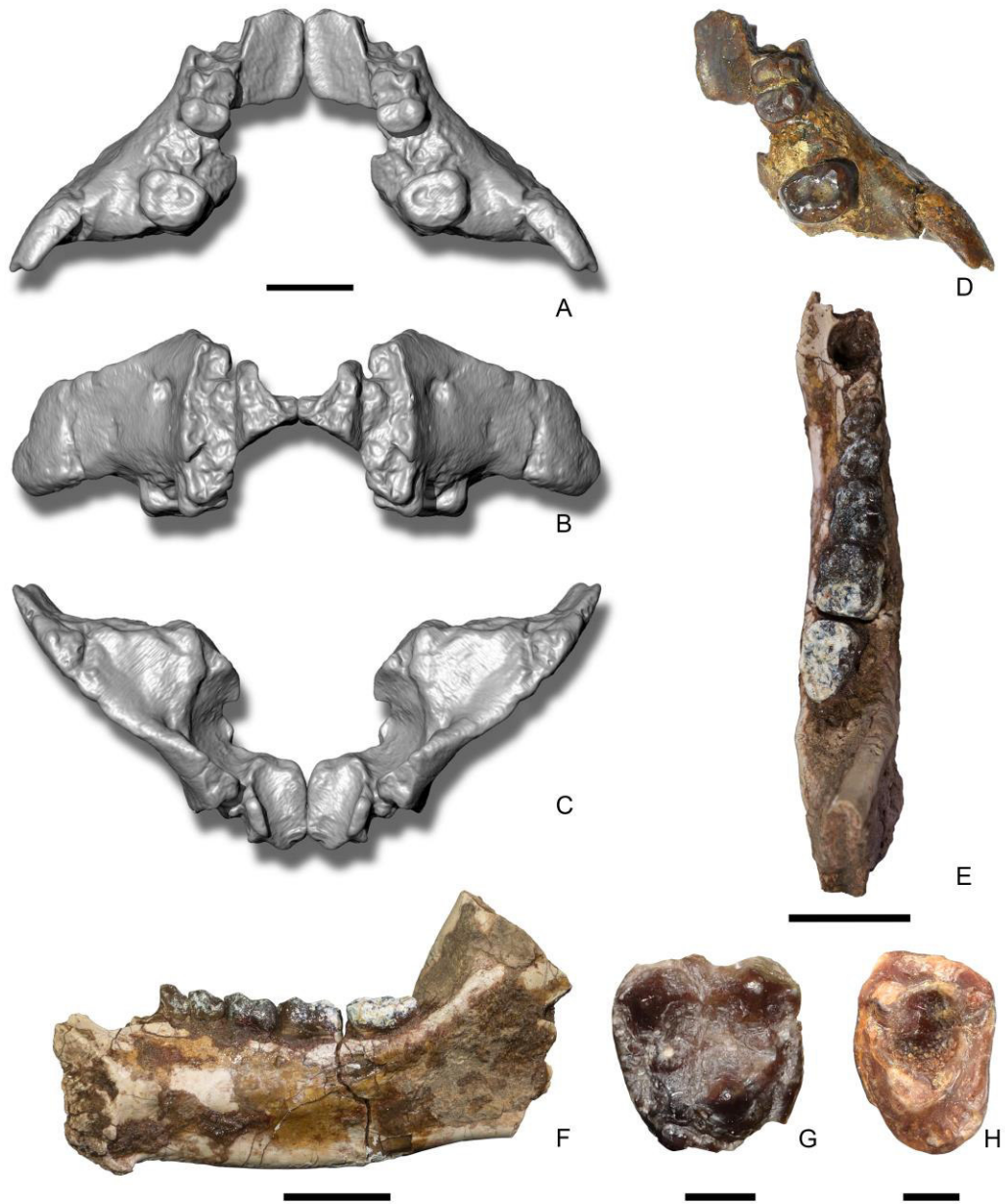


FIGURE 4 *Pondaungia cotteri* (a–f) from the Pangan 1 locality in Myanmar. Scale bar: 1 cm. Virtual reconstruction was achieved by using the mirror image of the left maxilla (NMMP 87) in occlusal (a), anterior (b), and superior (c) views, and d) photographic image in occlusal view. Right mandible (NMMP 94) in occlusal (e) and lingual (f) views, displaying a high horizontal branch, vertical symphysis, and incisors alveoli. (g) Upper molar M² of *Pondaungia cotteri* (NMMP 92) from PK 2 locality in Myanmar, occlusal view. Scale bar: 2

mm. (h) Left upper M^3 of a sivaladapid from the Pondaung Formation in Myanmar in occlusal view. Scale bar=2mm. The estimated body mass of 4.5kg is indicated according to the M^3 regression proposed by Gingerich and Smith.⁵⁵ The absence of the hypocone, the strong development of the lingual cingulum, and the presence of the mesostyle are characteristics of sivaladapids.

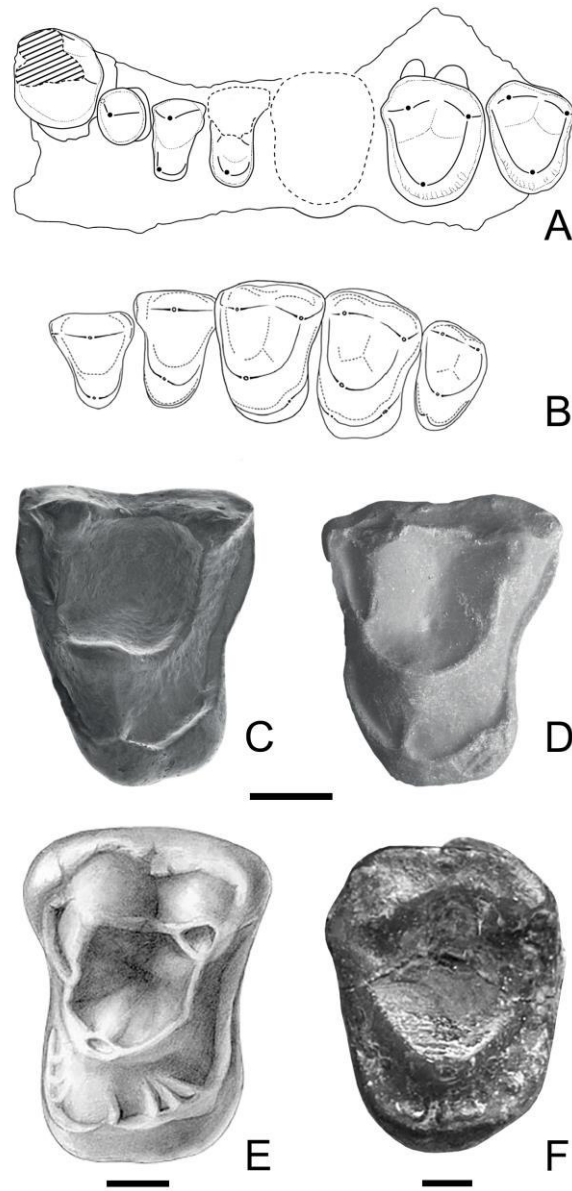


FIGURE 5 There are notable similarities in the morphology and structure of the upper premolars and molars between (a) *Aseanpithecus myanmarensis* (NMMP 93) and (b) *Catopithecus*.⁹⁰ Not to scale. A comparison of the upper molar of (c) *Perupithecus ucayaliensis* (CPI-6486)²², (d) *Talahpithecus parvus* (DT1-31), (e) *Bahinia pondaungensis* (NMMP 14), and (f) *Aseanpithecus myanmarensis* (NMMP 93) in occlusal view. Scale bar=1mm.

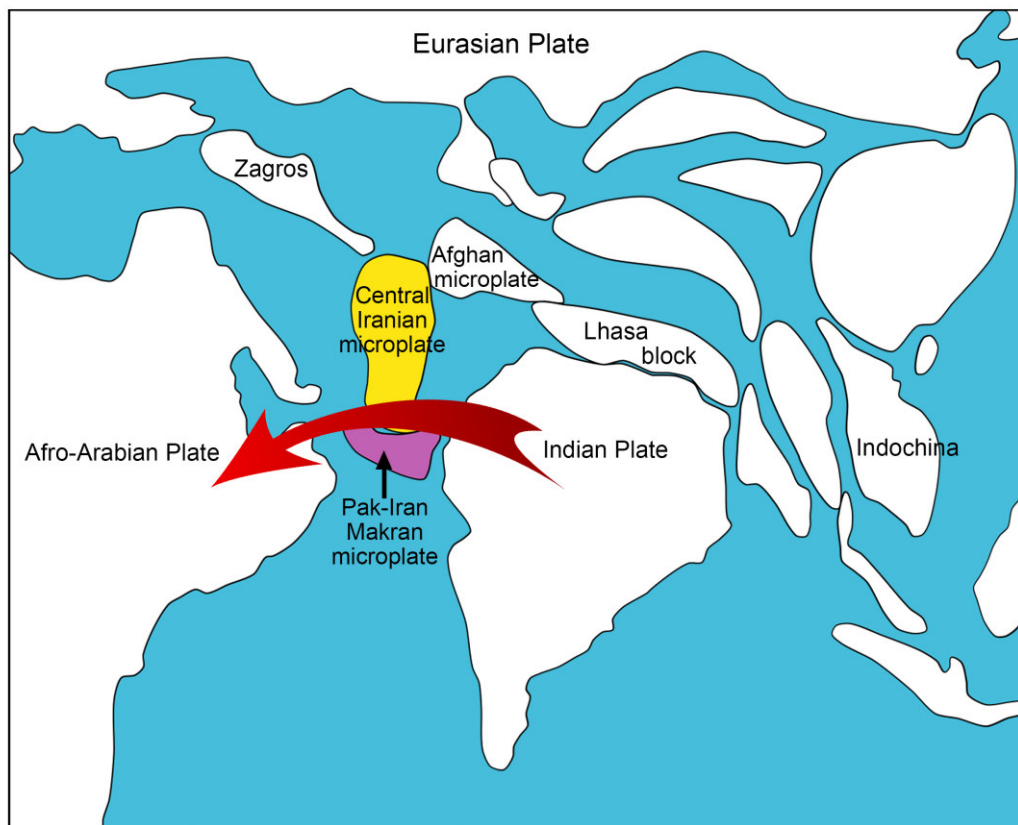


FIGURE 6 Paleogeographic reconstruction of the Neotethys Ocean during the Eocene period reveals the presence of the newly identified Pak–Iran Makran microplate¹⁴⁸ situated between the Indian and Afro-Arabian plates. This microplate’s position has significantly reduced the width of marine barriers, thereby facilitating faunal dispersal events. The red arrow indicates the dispersal route taken by anthropoids, hystricognaths, anomaluroid and cricetid rodents, and anthracotheres during the Eocene and early Oligocene.