

Primates Linnaeus, 1758

Strepsirhini Geoffroy, 1812

Lorisiformes Gregory, 1915

Karanisia Seiffert et al., 2003

Karanisia arenula, sp. nov. (Fig. 2a-f)

Hypodigm. In addition to the holotype; DT1-37, right M³; DT1-38, right P₃; DT1-39, left P₄; DT1-40, left M₁; DT1-41, left M₁; DT1-43, left M₃.

Description. DT1-38 (Fig. 2b) is interpreted as a right P₃ of *K. arenula*, although the tooth is single-rooted. This apparently conflicts with the condition in *K. clarki*, in which two alveoli have been identified as pertaining to this locus (see figure 1b in reference 22). The crown is simply constructed and mesially canted. The trigonid bears a single cusp, the protoconid, which is a buccolingually compressed cusp that is buccally convex. The lingual surface of the trigonid is unevenly excavated, with two roughly triangular invaginated areas being separated by a vertical ridge running from the lingual side of the protoconid towards the lingual cingulid. A short preprotocristid descends the mesial face of the protoconid. Where the latter structure meets the lingual cingulid, a tiny cusplule is present. The postprotocristid follows a more nearly vertical trajectory as it descends the distal side of the protoconid. It terminates just prior to reaching the short, simple talonid heel.

DT1-39 (Fig. 2c), a left P_4 , is referred to *K. arenula* on the basis of its close morphological similarity to this tooth in *K. clarki*. The crown is double-rooted, and the talonid is longer than that of DT1-38, but otherwise these teeth are very similar (which is the chief reason why the latter tooth is identified as a P_3 of the same taxon). The trigonid is dominated by the buccolingually compressed protoconid, which is convex buccally and unevenly excavated lingually. Pre- and postprotocristids define the leading and distal edges of the trigonid. The more distal excavated area on the lingual surface of the trigonid is continuous with the talonid, which slopes lingually from the postprotocristid and hypoconid to the lingual cingulid, which is complete. Unlike that of *K. clarki*, P_4 in *K. arenula* lacks a complete buccal cingulid.

Aside from being significantly smaller, the lower molars of *K. arenula* generally resemble those of *K. clarki*. Only the holotype is complete and unbroken, so the following description is based on DT1-42, a left M_2 (Fig. 2e). The trigonid is rhomboidal in occlusal view, because the metaconid is shifted distally well beyond the level of the protoconid, giving the protocristid a distinctly oblique orientation. The trigonid as a whole is mesiodistally compressed, and the leading edge of the trigonid runs roughly parallel to the postcristid. The protoconid and metaconid are similar in height, but the paraconid is diminutive (DT1-42) or vestigial (DT1-41). A mesially directed crest defines the buccal margin of the trigonid, connecting the protoconid with the tiny paraconid. The talonid basin is also rhomboidal, because the postcristid runs roughly parallel to the obliquely oriented postvallid. Despite the odd occlusal plan of the talonid, the entoconid is situated directly lingual to the hypoconid,

placing it well mesial of the distolingual corner of the talonid. The entoconid gives rise to mesial (preentocristid) and distal crests. The former of these connects the entoconid with the lingual base of the postvallid, while the latter becomes confluent with the lingual end of the postcristid. The cristid obliqua is relatively straight, running mesially and lingually from the hypoconid to join the postvallid just lingual to the protoconid (in the holotype M_2). In DT1-41 the cristid obliqua climbs the postvallid to join the protocristid near its flexure, about midway between the protoconid and metaconid. The buccal cingulid is continuous on all lower molars, to the extent that the relevant anatomy is preserved.

M_3 is documented only by DT1-43 (Fig. 2f), the trigonid of which is missing. It has a distally extensive hypoconulid lobe, but otherwise resembles the more mesial molars in comparable parts.

The only upper tooth locus currently recognized for *K. arenula* is M^3 , represented by DT1-37 (Fig. 2a). The crown as a whole is rhomboidal in occlusal outline, with relatively straight buccal and lingual margins matched by mesial and distal margins that are angled distolingually rather than being transverse. The paracone is significantly larger than the metacone, which is the chief reason why this tooth is identified as an M^3 . The centrocrista is straight and mesiodistally oriented. Much shorter preparacrista and postmetacrista follow the same trajectory as the centrocrista. A small parastyle is present, and the buccal cingulum is continuous. The protocone is canted mesially. The pre- and postprotocristae are well-defined. The former structure runs from the protocone to the mesiobuccal corner of the tooth, being confluent with the precingulum. The postprotocrista runs buccally from the protocone up the

lingual face of the metacone. Conules are absent. There is a complete distal cingulum that is particularly extensive lingually, forming a small talon shelf. There is no appreciable development of a hypocone. Unlike the condition in *K. clarki*, the distal margin of the crown of M³ is not invaginated.

Anthropoidea Mivart, 1864

Afrotarsiidae Ginsburg and Mein, 1987

Afrotarsius Simons and Bown, 1985

Afrotarsius libycus, sp. nov. (Fig. 2g-m)

Hypodigm. In addition to the holotype; DT1-31, right P³; DT1-32, left P³; DT1-33, left M²; DT1-34, right M²; DT1-36, right M₃.

Description. The holotype M₁ or M₂ (DT1-35) (Fig. 2k-l) cannot reliably be assigned to either tooth locus because these loci are virtually identical in the holotype lower jaw of *Afrotarsius chatrathi*²⁴. The trigonid is appreciably narrower than the talonid. All three trigonid cusps are present, although the paraconid is shelf-like and integrated within its associated paracristid. The protoconid was apparently taller and more voluminous than the metaconid, although the apices of both the latter cusps are significantly worn. In occlusal view, the apices of the three trigonid cusps approximate the corners of an equilateral triangle. The metaconid is fully lingual in position, being situated slightly distally in relation to the protoconid. The buccal side of the protoconid is not perfectly vertical, so that the protoconid

occupies a less peripheral position on the trigonid than the metaconid. Although it is slightly obscured by wear, both of the latter cusps were connected by a protocristid that traversed the crown at a slightly oblique angle because of the relatively distal location of the metaconid noted earlier. The shelf-like paraconid is not fully lingual in position, but it is widely splayed with respect to the metaconid. The trigonid is broadly open lingually as a result. The talonid is evenly excavated and surrounded on all sides by cusps and crests. The hypoconid is the tallest talonid cusp, being situated at the distal end of the cristid obliqua. The latter structure is trenchant, running mesially and slightly lingually from the hypoconid to join the postvallid near the base of the protoconid. The entoconid lies directly lingual to the hypoconid, and an elevated preentocristid runs mesially from it to join the postvallid near the base of the metaconid. A small hypoconulid occurs midway between the hypoconid and entoconid, although it projects slightly distally in relation to both of the latter cusps. All three talonid cusps are joined by a well-developed postcristid that defines the distal extent of the talonid. A continuous cingulid lines the entire buccal margin of the tooth, extending distally from just below the paraconid to the buccal side of the hypoconulid.

M₃ (DT1-36) (Fig. 2m) bears the same basic molar morphology as the holotype, differing chiefly from it in the anatomy of the distolingual margin of the talonid. In contrast to the condition seen in the holotype M₁ or M₂, the entoconid of M₃ is reduced in size and its position is shifted somewhat buccally. The preentocristid is also less trenchant on M₃, so that the talonid is not as evenly excavated as it is in the holotype (being more nearly open lingually). As a result of the relatively buccal location of the entoconid, the highly reduced hypoconulid is located immediately adjacent to it. A similar condition occurs in the holotype of *Afrotarsius chatrathi*.

Two diminutive upper premolars are tentatively identified as left (DT1-32) (Fig. 2j) and right (DT1-31) P³ (Fig. 2i) of *Afrotarsius libycus*. Of the two specimens at hand, DT1-32 (Fig. 2j) is less worn, and the following description is based on this specimen. The buccal side of the tooth is dominated by the paracone, the apex of which is tilted slightly distally. The mesial side of the paracone is smoothly rounded and convex, while the distal side of the cusp bears a trenchant postparacrista that arcs distally and buccally before terminating at the distobuccal base of the crown. Minor breakage on the mesiobuccal margins of both specimens precludes determination of whether a small parastyle may have been present. The conical protocone is much smaller than the paracone and located near the center of the crown's lingual lobe. Pre- and postcingula frame the mesial and distal margins of the crown, but there is no lingual cingulum. A small postprotocrista runs distally from the apex of the protocone before becoming confluent with the postcingulum.

Two well-preserved upper molars are identified as left (DT1-33) (Fig. 2g) and right (DT1-34) (Fig. 2h) M² of *Afrotarsius libycus*. Although upper molars of *Afrotarsius* have not been described previously, we refer these specimens to *A. libycus* with confidence because they are appropriate in size and morphology to occlude with the holotype lower molar, and because they cannot be referred to any of the other primate taxa known from Dur At-Talah, each of which is also documented by upper molars that differ appreciably in morphology from that which is found here. DT1-33 is less worn than DT1-34, and the former specimen forms the basis for the following description. However, only minor morphological differences occur in the two specimens. Notable among these, DT1-34 has a more prominently invaginated ectoflexus and a more nearly continuous lingual cingulum than DT1-33. The buccal side of M² in *Afrotarsius* bears several features in common with Asian eosimiids, which is a primary

reason we assign *Afrotarsius* to the Anthroidea. For example, both the paracone and metacone are located somewhat internally on the crown, because a well-developed buccal cingulum expands distally into a full-fledged shelf of enamel buccal to the metacone. The preparacrista and centrocrista are trenchant and oriented mesiodistally. In contrast, the postmetacrista forms an arcuate crest that runs distally and buccally from the metacone to terminate at a small metastyle near the distobuccal corner of the tooth. A minor swelling of enamel buccal to the mesial end of the preparacrista appears to mark the presence of a small parastyle. In addition to the mesial and distal crests that typically adorn the paracone and metacone on upper molars of Eocene primates, in *Afrotarsius* these cusps bear variably developed lingual crests that connect the apices of the paracone and metacone with their associated conules. Together with the relatively trenchant centrocrista and pre- and postprotocristae, these lingual crests from the paracone and metacone effectively surround the trigon with a virtually continuous series of crests. A very similar condition occurs on upper molars of Asian eosimiids, particularly *Bahinia pondaungensis*⁵. Conules are present, although these cusps appear to be somewhat reduced in *Afrotarsius*. The paraconule is integrated into the preprotocrista, as is the metaconule with respect to the postprotocrista. Both conules give rise to pre- and postconule cristae. The preparaconule crista is confluent with the precingulum, while the postparaconule crista is confluent with the lingual crest from the paracone. A similar situation describes the relationships of the metaconule crista: the premetaconule crista is confluent with the lingual crest from the metacone, while the postmetaconule crista is confluent with the postcingulum. The protocone is tilted mesially, so that its apex lies nearer the paracone than the metacone. There is no development of a postprotocingulum. The mesial and distal margins of the protocone are lined by moderately developed cingula, but these structures fail to merge lingually.

Parapithecidae Schlosser, 1911

Biretia piveteaui de Bonis et al., 1988 (Fig. 2q-w)

Description. DT2-24 (Fig. 2u-v) is identified as M_2 rather than M_1 on the basis of its mesiodistally constricted trigonid and reduced paraconid, both of which are characters that distinguish these tooth loci in *Biretia fayumensis* and *B. megalopsis*⁷. DT2-24 is virtually identical to the holotype of *Biretia piveteaui* from Bir El Ater, Algeria⁶. The trigonid is dominated by the protoconid, which is substantially taller and more voluminous than the metaconid, as is typical in basal anthropoids¹². The preprotocristid is poorly developed, extending a short distance down the mesial face of the protoconid before angling sharply lingually to merge with the paracristid. The diminutive paraconid is integrated within the weak paracristid. The paraconid is not fully lingual in position, being located mesially and slightly buccally with respect to the metaconid. A minor difference between DT2-24 and the holotype of *Biretia piveteaui* concerns the relationship between the paraconid and metaconid on M_2 . In DT2-24 these two cusps are separated by a tiny furrow, while in the holotype of *Biretia piveteaui* they are connected by a weak premetacristid that is lacking in DT2-24. The protocristid is obliquely oriented because the metaconid is situated slightly distally with respect to the protoconid. All three talonid cusps are well defined and relatively bulbous, with the hypoconid being the largest. The hypoconulid is central in position, and the entoconid is located slightly forward of the distolingual corner of the talonid, leaving space for a tiny distolingual fovea. The cristid obliqua is not particularly trenchant, but it is present, in contrast to the condition in *Qatrania* (including *Abuqatrania*), in which this crest is greatly reduced or even lost. Likewise, a short preentocristid connects the entoconid with the base of the postvallid, and minor crests connect the entoconid and hypoconid with the hypoconulid. All of these talonid crests are more or less suppressed in *Qatrania*. *Biretia fayumensis* and *B.*

megalopsis from the BQ-2 locality in the Fayum⁷ resemble *Qatrania* and differ from *Biretia piveteaui* in having weaker (or even lacking altogether) talonid crests linking the hypoconulid with the entoconid and hypoconid. As a result, the distolingual fovea is larger in Fayum species of *Biretia* (particularly *B. megalopsis*) than is the case in *B. piveteaui*.

DT1-29 (Fig. 2w) is a left M₃. It bears the same general molar morphology as DT2-24, with the most important differences being talonid structure. The talonid of M₃ is narrower than the trigonid, which is not the case for M₂. The hypoconulid extends somewhat distally beyond the remainder of the talonid, as is typical for early primates. However, this distal extension is much less than that which typically occurs among Eocene primates other than anthropoids. The hypoconulid of M₃ is slightly larger and more distally extensive in *Biretia piveteaui* than it is in *B. megalopsis*. In this respect, *B. piveteaui* more closely resembles *B. fayumensis*.

DT1-26 (Fig. 2t) is a left M¹ of *B. piveteaui*. Its crown is bunodont and the major cusps are inflated. The paracone and metacone are similar in size and situated near the buccal margin of the crown. There is no buccal cingulum. The preparacrista, centrocrista, and postmetacrista are aligned mesiodistally. A tiny parastyle occurs at the mesial end of the preparacrista, but there is no metastyle. The protocone and hypocone are similar in size, and these lingual cusps are situated almost directly opposite the paracone and metacone, respectively. As a result, the crown has a very quadrate appearance in occlusal view. The hypocone is considerably larger and more inflated than is the case in *B. fayumensis*. A very short, poorly developed preprotocrista unites the apex of the protocone with the well-developed, bulbous paraconule. A weak preparaconule crista continues mesiobuccally from the paraconule to become confluent with the precingulum. There is no postparaconule crista. The bulbous metaconule lacks any associated cristae, and it is not connected to the protocone because of the absence of a postprotocrista. As a result, both upper molar conules, particularly

the metaconule, are relatively isolated in *B. piveteaui*. In Fayum species of *Biretia* the upper molar metaconules are less isolated, because the postprotocrista and postmetaconule crista are retained, yet weakly developed. A small mesial cingulum runs from below the paraconule to the base of the protocone. A much broader distolingual cingulum supports the massive hypocone, but the mesial and distal cingula fail to unite lingual to the protocone.

DT1-27 (Fig. 2s) is a right M^2 of *B. piveteaui* missing the distobuccal part of the crown. It is virtually identical in morphology to M^1 , differing chiefly in being relatively shorter and broader (i.e., more transverse) in occlusal outline. It also differs from M^1 in having a complete lingual cingulum. *B. piveteaui* lacks any development of a pericone on M^{1-2} .

Two examples of M^3 are available, DT1-28 (Fig. 2r) and DT2-23 (Fig. 2q), both of which come from the right side. DT2-23 is virtually pristine, while much of the enamel has been etched away from DT1-28. Accordingly, the following description is based on the former specimen. The crown as a whole is oval in occlusal outline, being much broader transversely than it is long. The paracone is significantly larger than the vestigial metacone. The buccal crests run mesiodistally, although the postmetacrista is absent owing to the extreme reduction of the metacone. A mesial cingulum is well-developed, being confluent buccally with the preprotocrista. Conules are absent. A lingual crest arises from the apex of the paracone, connecting that cusp with the protocone on its way to join the complete lingual cingulum. The postcingulum forms a shelf-like structure that is buccally continuous with the reduced metacone. The trigon as a whole is reduced, sloping distally.

Oligopithecidae Simons, 1989

Talahpithecus parvus, gen. et sp. nov. (Fig. 2n-p)

Hypodigm. In addition to the holotype; DT1-30, right P⁴; DT1-32, right M₁ or M₂.

Description. DT1-32 (Fig. 2p) is a right M₁ or M₂ that unfortunately is missing the mesial part of its trigonid. The poorly preserved postcrisid appears to have been oriented almost directly transversely. If so, this tooth more likely represents M₂ than M₁, because the postvallid is more obliquely oriented on M₁ in *Catopithecus*. The trigonid is relatively taller and the postvallid is more nearly vertical in *Talahpithecus* than is the case in *Catopithecus* and *Oligopithecus*. Talonid proportions are also longer and narrower than in younger oligopithecids. As a result, the talonid basin in *Talahpithecus* is clearly longer than it is wide, whereas the reverse is true in *Catopithecus* and *Oligopithecus*. The entoconid in DT1-32 is elevated above the adjacent part of the talonid, and a distinct preentocrisid connects the entoconid to the lingual base of the postvallid. This condition differs from that which occurs in lower molars of *Catopithecus* and *Oligopithecus*, in which the preentocrisid is greatly reduced or absent, yielding a talonid that is nearly open lingually between the entoconid and postvallid. The hypoconulid is smaller than either the entoconid or the hypoconid, and it is situated near the distolingual corner of the talonid, immediately adjacent to the entoconid (as is typical of oligopithecids). The hypoconid is large and angular. The cristid obliqua is trenchant, and it runs straight from the hypoconid to the base of the protoconid. As a result, the hypoflexid is very shallow. A weak postcrisid connects the hypoconid with the hypoconulid, but this crest is so low that the talonid is nearly open distally.

DT1-30 (Fig. 2o), a fragmentary right P⁴, is broken distolingually. The buccal margin of the tooth is dominated by the tall, distally tilted paracone. Well-defined pre- and postparacristae emerge from the apex of the paracone, and these are mesiodistally aligned. The preparacrista is noticeably longer than the postparacrista owing to the distal orientation of the paracone noted earlier, as well as the elevated distobuccal corner of the crown. A buccal cingulum is present and continuous. The much smaller protocone lies near the mesiolingual

margin of the crown. Weak crests run mesiobuccally and distally from the apex of the protocone to join the continuous pre- and postcingulum, respectively.

The holotype left M^1 or M^2 (DT1-31) (Fig. 2n) is well-preserved aside from minor damage to the paracone and the distolingual cingulum. The crown bears three main cusps that are similar in size. The paracone and metacone are located near the buccal periphery of the crown. There is no buccal cingulum. The centrocrista is straight, mesiodistally oriented, and trenchant. Much shorter preparacrista and postmetacrista follow the same general trajectory as the centrocrista, although the postmetacrista deviates slightly buccally as it approaches the distobuccal margin of the crown. A small parastyle occurs at the mesiobuccal margin of the crown, but there is no clear metastyle. The protocone is tall and mesially canted, so that its apex lies nearer the paracone than the metacone. Trenchant pre- and postprotocristae delimit the lingual margin of the trigon. These crests continue buccally beyond the location where conules would normally occur (these are absent) to merge with lingual crests that arise from the apices of the paracone and metacone. As a result, the trigon is completely surrounded by trenchant crests. Where a paraconule would normally occur, the preprotocrista divides into two branches. The more mesial branch continues mesiobuccally to form a short precingulum, whereas the other branch climbs the lingual face of the paracone as noted earlier. The lingual cingulum is complete and well-defined. A tiny swelling of enamel marks an incipient pericone located directly lingual to the protocone. A tiny crest runs from the pericone part way up the lingual face of the protocone. There is no clear evidence of a distinct hypocone, although minor damage to the distolingual cingulum may have obscured the presence of this structure. The lingual cingulum is continuous on either side with mesial and distal cingula, the latter of which is more buccally extensive.

Supplementary Table 1. Metric data (in mm) for fossil primate teeth from the Dur At-Talah fauna of central Libya. For lower molars, “width” corresponds to trigonid width. Asterisks indicate estimated measurements of fragmentary specimens.

Taxon	Specimen #	Tooth locus	Length	Width	Talonid width
<i>Karanisia arenula</i>	DT1-37	M ³	1.97	2.70	
<i>Karanisia arenula</i>	DT1-38	P ₃	1.63	1.19	
<i>Karanisia arenula</i>	DT1-39	P ₄	2.46		1.31
<i>Karanisia arenula</i>	DT1-40	M ₁	2.48	1.53	
<i>Karanisia arenula</i>	DT1-41	M ₁	2.52	1.44	
<i>Karanisia arenula</i>	DT1-42	M ₂	2.48	1.74	1.57
<i>Karanisia arenula</i>	DT1-43	M ₃	2.98*		1.60
<i>Afrotarsius libycus</i>	DT1-31	P ³	1.07	1.64	
<i>Afrotarsius libycus</i>	DT1-32	P ³	1.12	1.62	
<i>Afrotarsius libycus</i>	DT1-33	M ²	2.25	3.26	
<i>Afrotarsius libycus</i>	DT1-34	M ²	2.32	3.26	
<i>Afrotarsius libycus</i>	DT1-35	M ₁ or M ₂	2.22	1.50	1.66
<i>Afrotarsius libycus</i>	DT1-36	M ₃	2.27	1.34	1.27
<i>Biretia piveteaui</i>	DT1-26	M ¹	2.65	3.36	
<i>Biretia piveteaui</i>	DT1-27	M ²	2.50	3.68	
<i>Biretia piveteaui</i>	DT1-28	M ³	1.53	3.17	
<i>Biretia piveteaui</i>	DT2-23	M ³	1.40	2.65	
<i>Biretia piveteaui</i>	DT2-24	M ₂	2.66	2.18	1.97
<i>Biretia piveteaui</i>	DT1-29	M ₃	2.49	1.65	1.36
<i>Talahpithecus parvus</i>	DT1-30	P ⁴	2.15	2.72	

<i>Talahpithecus parvus</i>	DT1-31	M ¹ or M ²	2.82	3.40	
<i>Talahpithecus parvus</i>	DT1-32	M ₁ or M ₂	2.59*	1.94	1.92