Eocene raoellids (Mammalia, Cetartiodactyla) outside the Indian Subcontinent: palaeogeographical implications

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Abstract – Raoellidae are small fossil cetartiodactyls closely related to the Cetacea. Until now undisputable raoellid remains were reported only from the early Middle Eocene of the Indian Subcontinent, although this Indo-Pakistani endemism has been challenged by several recent works describing potential raoellids from Mongolia, Myanmar and China. In this contribution we address the question of raoellid taxonomic content and definition, through a revision of the dental features of the family. This work, which includes a revision of the putative raoellid material from outside Indo-Pakistan, is primarily based on a re-examination of 'suoid' specimens from Shanghuang (Middle Eocene, coastal China). Our results indicate that the Shanghuang material both substantiates the youngest and easternmost occurrence of Raoellidae and represents the only unquestionable record of raoellids outside the Indian Subcontinent at present. This significantly extends the geographical and chronological range of the family. The occurrence of a raoellid species in the Middle Eocene of coastal China implies that raoellids dispersed from the Indian Subcontinent to eastern Asia during Early or Middle Eocene time. This tempers classical hypotheses of Middle Eocene Indian endemism and eastern Asian provincialism.

Keywords: Raoellidae, Shanghuang fissure fillings, coastal China, Greater India.

1. Introduction

Raoellidae form a small group of 'bunolophodont' cetartiodactyls. They have so far been unambiguously reported only from Middle Eocene deposits of the Indian Subcontinent, including localities from India (Kalakot region: Kashmir, Subathu Formation; Sahni *et al*. 1981; Kumar & Sahni, 1985; Thewissen *et al*. 2007) and Pakistan (Ganda Kas area: Kuldana Formation; Thewissen, Williams & Hussain, 2001; Gali Jhagir area: Chorgali Formation; Thewissen, Williams & Hussain, 2001; Chorlakki: Kuldana Formation, 'Mami Khel' Formation; Thewissen, Gingerich & Russell, 1987). Additional to these undisputed reports, some alleged raoellids have also been reported from outside the Indian Subcontinent, in the Middle Eocene of Mongolia (*Haqueina haichinensis*, Khaichin Ula locality; Vislobokova, 2004*a*,*b*), Myanmar ('raoellid indet.', Pondaung Formation; Theodor, Erfurt & Métais, 2007) and China (?*Indohyus yuanchuensis*, Rencun locality; Coombs & Coombs, 1977).

The Raoellidae initially encompassed three genera endemic to the Indian Subcontinent according to Sahni *et al*. (1981), *Raoella*, *Kunmunella* and *Khirtharia*. Subsequent authors have significantly changed the content of the family and included taxa from outside the Indian Subcontinent. For example, Thewissen,

Gingerich & Russell (1987) referred to the Raoellidae *Indohyus* (including *Raoella* and *Kunmunella*), *Khirtharia*, *Bunodentus*, *Metkatius*, all known from the Indian Subcontinent only, and possibly *Haqueina*, a genus initially reported from Middle Eocene deposits of Pakistan (Dehm & Oettingen-Spielberg, 1958) and then described in Mongolia (Vislobokova, 2004*a*,*b*). Later on, Thewissen, Williams & Hussain (2001) identified *Khirtharia* (including *Bunodentus* as proposed by West, 1980), *Metkatius*, *Haqueina*, *Indohyus* and *Kunmunella* as raoellids. More recently, Theodor, Erfurt & Métais (2007) included the genera *Khirtharia*, *Indohyus*, *Kunmunella* and *Metkatius* in the Raoellidae, *Haqueina* being considered as a representative of the Dichobunidae (Table 1). The apparent palaeogeographical extension of the Raoellidae directly depends of the unstable systematic content of the family. This instability is mainly owing to the lack of clear definition of the group. More recently, since they were proposed as sister taxon to Cetacea (Geisler & Uhen, 2003, 2005; Thewissen, Williams & Hussain, 2001), raoellids have become central to questions of cetartiodactyl evolution. However, despite their key position within the Cetartiodactyla, recent large-scale phylogenetic analyses included few raoellid taxa: none in O'Leary & Gatesy (2008); two in Thewissen *et al*. (2007, *Khirtharia* + *Indohyus*); only one in Theodor & Foss (2005, referred to as 'raoellid'); only one in Geisler *et al*. (2007, referred to as 'Raoellidae'); only one

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Table 1. Generic systematics of the Raoellidae according to different authors

Sahni *et al*. (1981)	Thewissen, Gingerich & Russell (1987)	Thewissen, Williams & Hussain (2001)	Theodor, Erfurt & Métais, (2007)
Raoella	*Indohyus* (*Raoella* + *Kunmunella*)	*Indohyus*	*Indohyus*
Kunmunella	*Khirtharia*	*Kunmunella*	*Kunmunella*
Khirtharia	*Bunodentus*	*Khirtharia* (*Bunodentus*)	*Khirtharia* (*Bunodentus*)
	Metkatius	*Metkatius*	*Metkatius*
	Haqueina?*	*Haqueina**	Artiodactyla indet.*

Non-Indo-Pakistani taxa are indicated by a star.

in Spaulding, O'Leary & Gatesy (2009, *Indohyus*), and none of these authors discussed the characters supporting the monophyly of the group.

In this study we address the question of raoellid taxonomic content and definition, through a revision of the dental features of the family, substantiated by a phylogenetic analysis of dental characters. This work is primarily based on a re-examination of some artiodactyl specimens from Shanghuang (Middle Eocene, China) IVPP V12763.1 and IVPP V12764.2, an m3 and a p4, respectively, initially identified as the oldest suoid remains by Métais *et al*. (2008) and here referred to the Raoellidae. The systematic attribution of putative non-endemic raoellid specimens from Mongolia (Vislobokova, 2004*a,b*), Myanmar (Theodor, Erfurt & Métais, 2007) and China (Coombs & Coombs, 1977) is also tested. Dental differences between raoellids and other cetartiodactyls, including dichobunids, suoids, anthracotheriids and basal cetaceans are here discussed and sent back to early cetartiodactylan history.

2. Abbreviations

GSI – Geological Survey of India, Kolkata, India; IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NMMP−KU – National Museum−Myanmar−Paleontology−Kyoto University (stored in the National Museum, Yangon, Myanmar); UM2 – Université de Montpellier 2, Montpellier, France. M/m – upper/lower molars; P/p – upper/lower premolars.

3. Systematic palaeontology

Order CETARTIODACTYLA Montgelard, Catzeflis & Douzery, 1997
Family RAOELLIDAE Sahni *et al*. 1981
Genus ?*Khirtharia* Pilgrim, 1940
?*Khirtharia* cf. *major* (Thewissen, Gingerich & Russell, 1987) comb. nov.
Figure 1

2008 Suoidea indeterminate (1) Métais *et al*., fig. 2e
2008 Suoidea indeterminate (2) Métais *et al*., fig. 2f, g

Differential diagnosis. Differs from other raoellid species by a weaker and more mesially located 'hypolophid'; differs from other *Khirtharia* species
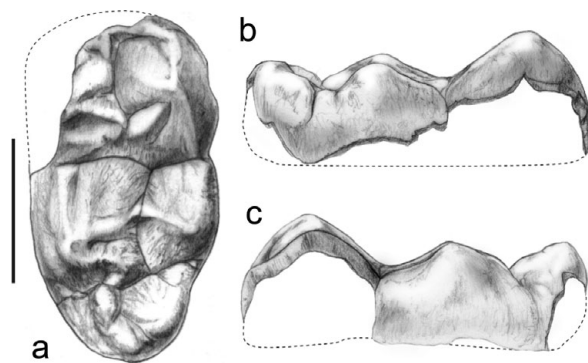

Figure 1. ?*Khirtharia* cf. *major* from Shanghuang (IVPP V12763.1) in (a) occlusal; (b) lingual; (c) labial view. Scale bar = 1 cm.

by more elongated lower m3 with a wider and more massive hypoconulid lobe, a more expressed groove pattern on the mesial lobe (endofossids and postfossids), more pronounced preprotocristid, post-protocristid and metacristids, and an entoconid lacking a postentocristid; differs from *Kunmunella* and from *Indohyus* by lower mesial cuspids deeply separated by a wide longitudinal groove, the presence of a lower prehypocristid (cristid obliqua) and no accessory central cristid.

Stratigraphical and geographical provenance. Middle Eocene Shanghuang fissure filling B (Early Sharamurunian; Métais *et al*. 2008), Jiangsu Province, coastal China.

Description. This material has initially been described by Métais *et al*. (2008). However, some additional features can be added to that primary description. We follow here the nomenclature defined by Boisserie *et al*. (2009) based on dental homologies within 'Suiformes', because it best allows comparison between bunodont to sublophodont forms.

The mesial-most part of the isolated m3 IVPP V12763.1 is broken and the bases of the mesial cuspids, including the labial half of the protoconid, is lacking. The full height of the crown can only be appreciated on the labial wall of the hypoconid (Fig. 1c). The crown of the tooth is low and it bears four blunt cuspids, the two mesial ones being clearly stronger than the distal ones. The thickness of the enamel is visible on the broken parts of the mesial cuspids (Fig. 1b, c); it is 1.3 mm thick at the protoconid tip. Wear is almost absent in this specimen, which leaves the most ephemeral features of the crown visible (Fig. 1a).
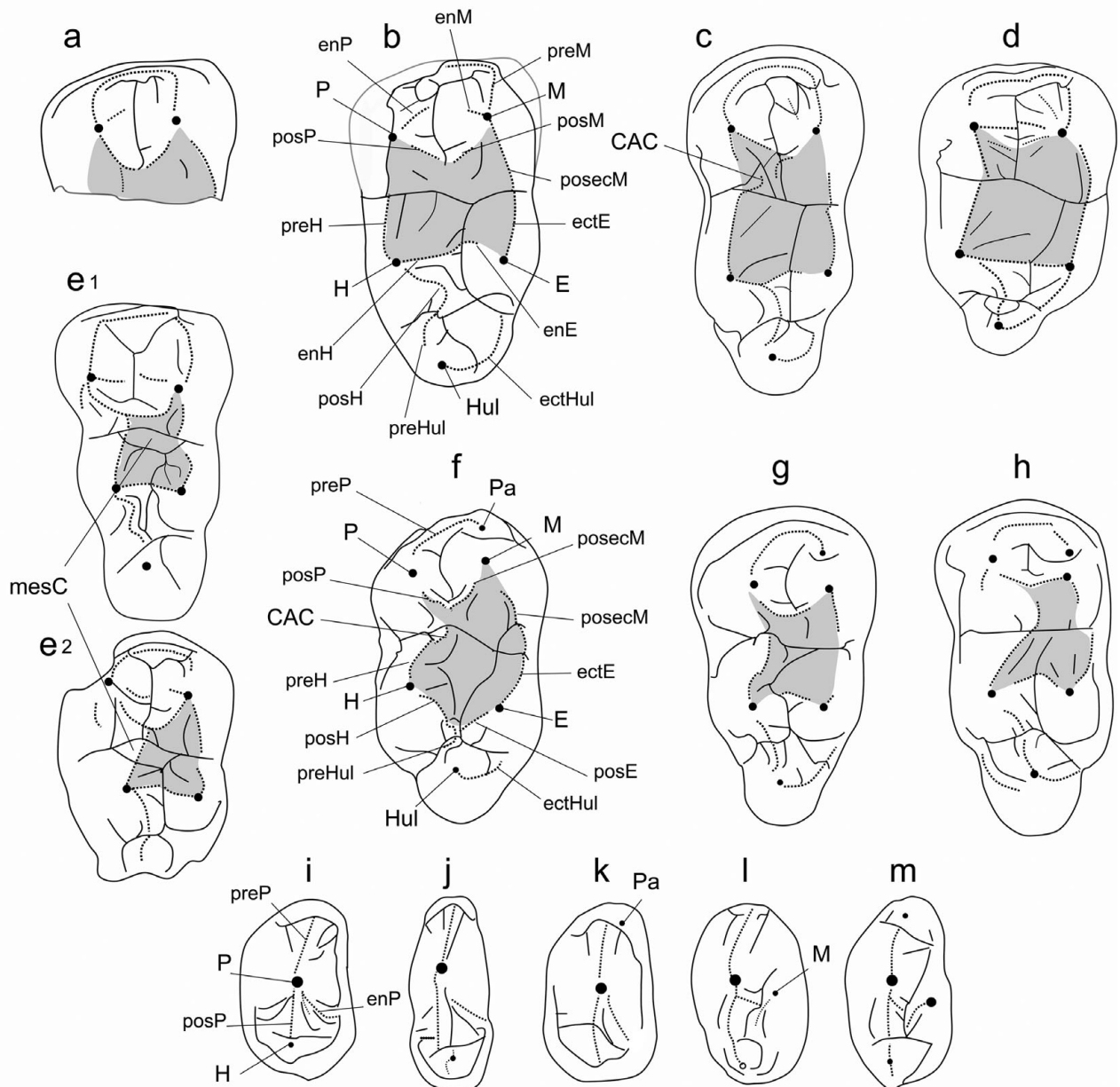
Figure 2. Comparison of lower cheek tooth structure of some Eocene cetartiodactyls. m2–3: (a) *Indohyus major*; (b) ?*Khirtharia* cf. *major*; (c) *Kunmunella transversa*; (d) *Khirtharia dayi*; (e1) *Siamochoerus banmarkensis*; (e2) *Siamochoerus viriosus*; (f) *Gujaratia pakistanensis*; (g) *Dichobune leporina*; (h) *Gobiohyus orientalis*. p4: (i) *Khirtharia dayi*; (j) *Indohyus indirae*; (k) IVPP V12764.2; (l) *Siamochoerus*; (m) *Palaeochoerus quercyi*. Abbreviations: CAC – central accessory cristid; E – entoconid; ectHul – ectohypocristulid; ectE – ectoentocristid; enE – endoentocristid; enH – endohypocristid; enP – endoprotocristid; enM – endometacristid; H – hypoconid; Hul – hypoconulid; mesC – mesoconulid; P – protoconid; Pa – paraconid; posH – posthypocristid; preHul – prehypocristulid; posecM – postectometacristid; posM – postmetacristid; posP – postprotocristid; posE – postentocristid; preH – prehypocristid; preM – premetacristid; preP – preprotocristid. Grey areas indicate the surfaces corresponding to the crushing basin.

The preserved part of the protoconid bears small and blunt endo- and postprotocristids. The metaconid bears sharp pre- and postectometacristids and a short postmetacristid. A very light endometacristid might also be present. The premetacristid is labially lined by a clear groove and the postmetacristid is well delimited by two deep grooves (Fig. 2b). The postectometacristid connects distally to the mesial end of the ectoentocristid to form a continuous mesio-distal structure that constitutes the lingual wall of the tooth. The transverse valley separating the mesial and distal cusps is widely open; it is almost straight and it joins the buccal and lingual walls of the tooth. The centre of the tooth is occupied by a flat and low surface with slightly wrinkled enamel. There is no trace of an accessory cusplet that could be recognized as a mesoconulid. The hypoconid is very wide and it bears a sharp prehypocristid (cristid obliqua) that might be connected to the very base of the postectoprotocristid (not observable on this broken part of the specimen). This structure forms the buccal wall of the tooth. A very low endohypocristid is identifiable; its lingual-most extremity is thin and sharp

(Figs 1a, 2b). This small crest most probably would be obliterated in early wear. The endohypocristid is distally separated from the posthypocristid by a deep groove. The posthypocristid is robust and enlarged distally. The latter, lingually shifted at its distal end and labially lined by a posthypofossid, runs towards the prehypocristulid. Both crests are clearly separated by a deep groove. The entoconid is labio-lingually slender and separated from the hypoconid by a deep groove. It only displays a smooth crest oriented towards the internal part of the tooth, which could be interpreted as the preentocristid or as the endoentocristid. We name this crest endoentocristid because of its connection to the endohypocristid. The lingual wall is delimited by a sharp ectoentocristid. The hypoconulid is strong and as high as other distal cuspids. It is divided by an oblique groove, almost separating it into two equal parts.

4. Systematic reattribution of the 'suoid' material from Shanghuang

4.a. Rejection of IVPP V12763.1 as a suoid

The specimen IVPP V12763.1 was initially considered a suoid by Métais *et al.* (2008) based on the overall bunodonty, the cusped hypoconulid and the system of grooves and bulbous crests interpreted as an incipient 'furchenplan' (Métais *et al.* 2008, p. 1127). According to the same authors, IVPP V12763.1 compares most closely with the earliest suoids known from the Late Eocene of Asia, especially *Siamochoerus*, in the general arrangement of its cuspids and crests, the trigonid transversely wider than the talonid and by the duplicated hypoconulid on the m3. Another important character supporting the suoid affinities of IVPP V12763.1 would be the swelling of enamel linking the hypoconid and the entoconid, which might be interpreted as incipient massive crests.

The systematic attribution of Eocene artiodactyls is often problematic because of the uncertain phylogenetic relationships within the Cetartiodactyla, generating obvious problems of character polarization. The Diacodexeinae are represented in the Holarctic Province and might represent a paraphyletic assemblage. Although they share the same basic structure, regarded as the primitive condition among the Cetartiodactyla, Early Eocene Diacodexeinae already present a complicated molar pattern, with several accessory structures (Fig. 2f). A rudimentary 'furchenplan' is present, with endo- and postfossids on mesial cuspids. The crest pattern is also well developed with postcristids and postectocristids on mesial cuspids. The distal cuspids bear two cristids that could be interpreted as the prehypocristid (cristid obliqua) and posthypocristid on the hypoconid and ectoentocristid and postentocristid on the entoconid, respectively (Fig. 2f), according to the dental nomenclature proposed by Boisserie *et al.* (2009). On the m3, the posthypocristid joins the hypoconulid via a small crest located on the mesio-labial corner of the conule, here recognized as

the prehypocristulid. This cristid pattern appears as symplesiomorphic among cetartiodactyls (Fig. 2f).

Bunodont cusps and a trigonid wider than the talonid are observed in various ungulate groups and, as such, cannot be advocated as diagnostic characters for suoids. The same remark can be expressed for the double hypoconulid, which corresponds to the presence of a lingual groove cutting the hypoconulid lobe, observed in several other cetartiodactyl groups such as the Raoellidae, Diacodexeidae and Dichobunidae. Figure 2 exemplifies the latter lower molar pattern. The swelling of enamel linking the hypoconid to the entoconid corresponds to the 'hypolophid' described in basal artiodactyls, and is also present in most 'non-diacodexeine' Eocene families (Fig. 2b–d, g–h). These characters common to suoids and specimen IVPP V12763.1 are also shared by other cetartiodactyls and might be symplesiomorphies (for discussion of these characters see the phylogenetic analysis in Section 5).

Suoids differ from the primitive artiodactyl lower molar pattern by: (i) the absence of a paraconulid; (ii) the presence of a precristid on the mesial cuspids; (iii) the presence of internal cristids on the distal cuspids (hypolophid), recognized as the endohypocristid and endo- or preentocristid; (iv) a larger entoconid; and (v) a more reduced central part of the molars, occupied by a central accessory cusp (Fig. 2e v. 2f; Orliac, Antoine & Ducrocq, 2010; Orliac *et al.* in press). The specimen IVPP V12763.1 from Shanghuang only shares with suoids the absence of paraconulid, internal cristids on the distal cuspids and rudimentary endocristids on the mesial cuspids. The proportion, height and disposition of the cuspids greatly differ from those of suoids (Fig. 2b v. 2e). The crest and groove pattern of IVPP V12763.1 is not consistent with that of suoids, including Eocene forms like *Siamochoerus* (Fig. 2b v. 2e). Compared to suoids, the groove pattern of IVPP V12763.1 is reduced (no groove on the entoconid) and shallower; there is neither trace of a central accessory cristid (termed CAC in Fig. 2) nor a mesoconulid. The longitudinal groove separates the mesial cuspids, interrupting the postcristids, whereas in suoids the groove network is interrupted by postcristids of the mesial lobe and by the central accessory cusps. The lingual wall of IVPP V12763.1 is bounded at the level of the occlusal surface by the postectometacristid and ectoentocristid, connected to each other. This morphology is never observed in suoids. In suoids, these two lingual cristids are separated by the median groove and the lingual flank of the cuspids does not form the lingual wall of the tooth (Fig. 2b v. 2e). All these differences support exclusion of IVPP V12763.1 from the Suoidea.

4.b. Referral of IVPP V12763.1 from Shanghuang to the Raoellidae

Métais *et al.* (2008, p. 1127) noticed the morphological similarity between IVPP V12763.1 and *Khirtharia* but rejected the attribution of the former to the Raoellidae

because a longitudinally wider trigonid, more reduced hypoconulid lobe on m3, more developed transverse crests and absence of accessory grooves on lower molars characterize raoellids. However, a narrow trigonid can be observed in raoellids such as *Kunmunella* and *Indohyus*, which also exhibit a large hypoconulid lobe on m3 (Fig. 2c). The groove pattern of the lower molars of raoellids is shallow but can be seen in unworn specimens of *Khirtharia* and *Kunmunella* (cf. Fig. 2c–d). The general structure of IVPP V12763.1 is similar to that of some raoellid species in terms of crests and grooves (Fig. 2b v. 2c–d). The most distinctive feature of IVPP V12763.1 is the wide and flat area occupying the centre of the tooth (coloured in grey in Fig. 2). This morphology is observable in raoellids and recognized as the 'crushing basin' (Thewissen *et al*. 2007). The crushing basin is a concave surface receiving a cusp of the opposing cheek tooth during occlusion. In raoellids, this basin is very wide and the four cuspids of the lower molars are far apart. The basin is delimited by labial, lingual, mesial and distal 'lophids' composed of the postcristids of the mesial cuspids, the postectoprotocristid and the prehypocristid on the labial side, the two endofossids of the distal cuspids and the ectoentocristid and postectometacristids on the lingual side. The internal part of the hypoconid is flattened and stretched and it lodges against most of the protocone during occlusion. A deep crushing basin is also observed in the Diacodexeinae. It is, however, smaller than that of raoellids as the prehypocristid (cristid obliqua) points towards the centre of the tooth. There are no endocristids (hypolophid) bordering the crushing basin distally in the Diacodexeinae. All these characters substantiate the referral of IVPP V12763.1 from Shanghuang to the Raoellidae.

Among raoellids, the m3 from Shanghuang is strongly reminiscent of *Indohyus major* from Chorlakki (Fig 2a v. 2b), although it is known by an m2 trigonid only (Thewissen, Gingerich & Russell, 1987). Both specimens are of comparable size. The labio-lingual width of IVPP V12763.1 can only be estimated because the base of the crown is broken but it might not have been much wider than 10 mm, which is the width of the specimen of *I. major* (Thewissen, Gingerich & Russell, 1987, table 3). Both specimens further present the same mesial cuspid structure. The premetacristid of both taxa presents a sharp angle at the metaconid level. The mesial cuspids bear clear postcristids. Mesial to their contact, the protoconid and the metaconid are separated by a wide valley, which is much wider than in *Kunmunella* and *Indohyus*, and deeper than in *Khirtharia inflata* and *K. dayi*. Both specimens show an important enamel crenulation. The specimen from Shanghuang is here referred questionably to *Khirtharia* as the specimen shares the following features: low molar crown, large groove separating the mesial cuspids, presence of a low prehypocristid and no accessory central cristid (based on the results of the phylogenetic analysis in Section 5.a). It is referred to ?*K*. cf. *major* because of the scarcity of

available material from Chorlakki and Shanghuang, and because the specimens differ slightly in the trigonid grooves, which seem to be deeper in the specimen from Shanghuang.

Thewissen, Gingerich & Russell (1987) differentiate *I. major* from *I. indirae* by its larger size only. However, the mesial cuspids of *I. major* are more inflated and less acute than those of *I. indirae* (Thewissen *et al*. 1987, fig. 6e v. 6f). By these characters, *I. major* is of intermediate morphology between the type species *I. indirae* and *Khirtharia*. The lower molar from Shanghuang differs from those of *K. inflata* and *K. dayi* by a deeper groove pattern on the mesial lobe, endofossids and postfossids. The preprotocristid, postprotocristid and metacristids are also sharper. The prehypocristid is lingually lined by a deep groove that is absent in other *Khirtharia* species. The 'hypolophid', particularly the endoentocristid, is reduced and more mesially located compared to that of other raoellids. The lower molar of ?*K*. cf. *major* from Shanghuang is also more elongated than that of other *Khirtharia* species and it bears a wider and more massive hypoconulid lobe, which recalls that of both *Indohyus* and *Kunmunella*. The postentocristid present in *Khirtharia* species is not observed in IVPP V12763.1. The latter differs from the m3 of *Kunmunella* by its lower mesial cuspids, whereas *Kunmunella* presents high mesial cuspids with almost vertical distal walls. Its mesial 'lophid' is constituted by the endocristids, the postcristids lying in a distal position. In ?*K*. cf. *major*, like in *Khirtharia*, the protoconid and the metaconid are more deeply separated by the wide longitudinal groove. The prehypocristid (cristid obliqua) is sharper in *Kunmunella*. The hypoconulid lobe of ?*K*. cf. *major* consists of two distinct cusps, whereas only one cusp occurs on this part of the third molar in *Kunmunella*. However, a labial groove is present in the latter and a small accessory cusplet is observed on the hypoconulid of *Indohyus indirae* (Kumar & Sahni, 1985, fig. 7a).

A p4 from Shanghuang (IVPP V12764.2), found in the fissure filling D (Irdinmanhan, Middle Eocene), has also been referred to the Suoidea by Métais *et al*. (2008). While no character clearly indicates that this specimen is a raoellid, its simple structure would be compatible with the raoellid family. As stated by Métais *et al*. (2008), the material is too scarce to allow association of the m3 from fissure B with the p4 from fissure D (no connection, no comparison, no occlusion). The size difference between the two specimens is noticeable and might prevent referring the teeth to a single taxon. However, the species *K. dayi* from Lammidhan (Pakistan, M15796 and M15797; Thewissen, Williams & Hussain, 2001) presents a similar p4 v. m3 size difference (M15796 and M15797: p4 length 7.0 mm; m3 length 11.3 mm). The p4 IVPP V12764.2 bears a small paraconid (= mesiostylid). This stylid is not observed in *Siamochoerus* (Fig. 2l) but is present in suoids such as *Palaeochoerus* (Fig. 2m). The structure of the tooth deeply differs from that of basal suoids by its cingulid, crest and groove pattern

Table 2. Character list

1. *Enamel crenulation*: **(0)** absence; **(1)** presence.
2. *Lower molars, paraconid*: **(0)** absence; **(1)** presence (modified after Gentry & Hooker, 1988).
3. *Lower molars, entoconid height*: **(0)** greatly reduced compared to hypoconid; **(1)** similar to hypoconid.
4. *Lower molars, entoconid surface*: **(0)** reduced compared to hypoconid; **(1)** only slightly smaller or same size.
5. *Lower molars, endoentocristids*: **(0)** absence; **(1)** presence (with character 7, corresponds to the presence of the hypolophid of Gentry & Hooker, 1988).
6. *Lower molars, orientation of the endoentocristid*: **(0)** forward; **(1)** transversal.
7. *Lower molars, endohypocristid*: **(0)** absence; **(1)** presence.
8. *Lower molars, cristid obliqua*: **(0)** mesially pointed towards the centre of the tooth; **(1)** mesially pointed towards the postectoprotocristid.
9. *Lower molars, accessory internal cristid*: **(0)** absence; **(1)** presence.
10. *Lower molars, postfossids on the mesial cupids*: **(0)** absent or greatly reduced; **(1)** present and deep.
11. *Lower molars, lingual cuspids*: **(0)** connexion between postectometacristid and ectoentocristid; **(1)** no connection between postectometacristid and ectoentocristid.
12. *Lower molars, mesoconulid*: **(0)** absence; **(1)** presence.
13. *m2 hypoconulid*: **(0)** absence; **(1)** presence (Thewissen, Hussain & Arif, 1994).
14. *m3 hypoconulid ectohypoconulid*: **(0)** absence; **(1)** presence.
15. *Lower molar crown height*: **(0)** high (deep transverse valley in lateral view); **(1)** low (wide and shallow transverse valley in lateral view).
16. *p4, mesiostylid (paraconid)*: **(0)** absence; **(1)** presence (Gentry & Hooker, 1988).
17. *p4, lingual face inflexion of the basis of the crown*: **(0)** absence; **(1)** presence.
18. *p4, metaconid*: **(0)** absence; **(1)** presence (Gentry & Hooker, 1988).
19. *p4, hypoconulid*: **(0)** absence; **(1)** presence.
20. *Upper molars, parastyle*: **(0)** absence; **(1)** presence (modified after Gentry & Hooker, 1988).
21. *Upper molars, endoparacrista*: **(0)** absence; **(1)** presence.
22. *Upper molars, hypocone*: **(0)** absence; **(1)** presence (might be present on M1 only).
23. *Upper molars, endometacrista and endometacristule forming a transverse crest*: **(0)** absence; **(1)** presence.
24. *Upper molars, ectometacristule connected to lingual cingulum*: **(0)** absence; **(1)** presence.
25. *Upper molars, labial wall of the cusps of the upper molars*: **(0)** with two wide fossae; **(1)** about rounded (modified after Theodor & Foss, 2005).
26. *Upper molars, connection of labial cristae with labial cingulum*: **(0)** absence; **(1)** presence.
27. *Upper molar, position of the metaconule*: **(0)** located on the labial side of the protocone; **(1)** located on the distal side of the protocone.
28. *Upper molars, lingual roots*: **(0)** one pillar; **(1)** two pillars (may be joined, clear distal pillar).
29. *P4, postprotocrista*: **(0)** absence; **(1)** presence.
30. *P4, endocristae forming an anterior loph*: **(0)** absence; **(1)** presence.
31. *P4, endoparacrista*: **(0)** absence; **(1)** presence.
32. *P4, paracone height/protocone*: **(0)** slightly higher than protocone; **(1)** much higher than protocone.
33. *P4, paracone height/molar*: **(0)** same height as paracones on the molars; **(1)** much higher than paracones on the molars (Thewissen, Hussain & Arif, 1994).
34. *P4, asymmetry of the paracone*: **(0)** absence; **(1)** presence.
35. *P4, constriction between protocone and paracone*: **(0)** absence; **(1)** presence.
36. *P3, protocone*: **(0)** absence; **(1)** presence.
37. *P3, number of roots*: **(0)** three; **(1)** two (Zhou *et al*. 1995).

(Fig. 2k v. 2l–m). However, the differences observed in terms of crests and groove location may be mainly owing to the lack of a metaconid on the specimen IVPP V12764.2. The p4 IVPP V12764.2 is close in shape to what is observed in the raoellid *Khirtharia*, but with a simpler structure (Fig. 2k v. 2l). *Khirtharia* is devoid of a parastyle. However, this structure is present but small in *Kunmunella* (H-GSP 97187; Thewissen, Williams & Hussain, 2001, fig. 5e–f).

5. Raoellidae definition and systematic content

Raoellid species were successively considered as choeropotamids (Ranga Rao, 1971), dichobunids (Ranga Rao, 1972), anthracotheriids (Sahni & Kumar, 1971; West, 1980) or heloyids (Pilgrim, 1940; Coombs & Coombs, 1977) before they were given a familial status by Sahni *et al.* (1981). In order to provide a clear diagnosis of the family based upon synapomorphies, and to formally test the systematic content of the Raoellidae, we performed a phylogenetic analysis based on the available dental characters. Testing the phylogenetic relationships of the Cetartiodactyla is

well beyond the scope here, and the taxa included have been chosen regarding their implication for raoellid systematics. Four taxa have been included for character polarization: the arctocyonid 'condylarths' *Protungulatum* and *Hyopsodus*, and the diacodexeid cetartiodactyls *Diacodexis* and *Gujaratia*. The dichobunid *Dichobune*, the heloyid *Gobiohyus*, and the hippopotamoids *Siamotherium* and *Choeropotamus* (*sensu* Orliac *et al.* 2010), have been included to test previous attribution of raoellid species proposed in the literature (Pilgrim, 1940; Ranga Rao, 1971, 1972; Coombs & Coombs, 1977; Thewissen, Gingerich & Russell, 1987). As raoellids were more recently proposed as the sister taxon of cetaceans within the Cetartiodactyla (Thewissen *et al.* 2007), the basal archaeocete *Pakicetus* was also included.

5.a. Phylogenetic analysis of dental characters

The data matrix composed of 37 characters (Table 2) controlled for 18 taxa (the data matrix and a detailed list of the material controlled are given in online Appendix 1 at http://journals.cambridge.org/geo) was
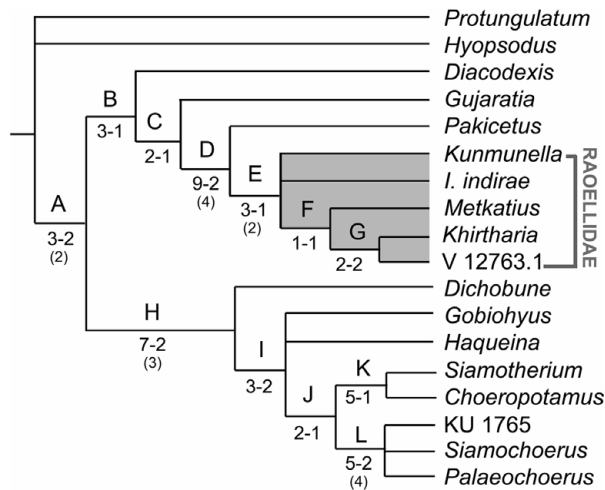
Figure 3. Phylogenetic relationships of raoellid genera: strict consensus of the 18 parsimonious trees (L = 67; CI = 0.55; RI = 0.77). Below the branches are the number of unambiguous synapomorphies on the left and the Bremer support on the right (Bremer, 1994). The numbers in parentheses indicate the Bremer support when the specimen from Pondaung, which introduces a large amount of missing data, is excluded. V 12763.1 – specimen from Shanghuang described in this paper; KU 1765 – 'Artiodactyla indeterminate' from Pondaung; *I. indirae* – *Indohyus indirae*.

treated under the assumption of the minimal model of unweighted parsimony, using PAUP 3.1 (Swofford, 1993), with a branch and bound search. Eighteen parsimonious trees (L = 67; CI = 0.55; RI = 0.77) were obtained. In the consensus tree (Fig. 3), two major clades of the Cetartiodactyla are supported: (a) a clade uniting the dichobunid *Dichobune*, the helohyid *Gobiohyus*, *Haqueina* of problematic affinities, the choeropotamid *Choeropotamus*, the anthracotheriid *Siamotherium* and the suoids *Palaeochoerus* and *Siamochoerus*; and (b) a clade gathering *Pakicetus* and the Raoellidae with *Diacodexis* and *Gujaratia* as early successive offshoots. The raoellid/cetacean relationship retrieved by Thewissen *et al*. (2007) from multiple sources of morphological characters (dental, cranial and postcranial) is supported by our results based on dental characters only. The raoellid/cetacean clade is supported by nine unambiguous synapomorphies, among which two are not homoplastic: prehypocristid (cristid obliqua) labially oriented (8^1) and biradiculated P3 (37^1; this character was proposed as a cetacean synapomorphy by Thewissen *et al*. 2007). Basal cetaceans and raoellids further share wrinkled enamel (1^1; RI = 0.66), the presence of an endohypocristid (7^1; RI = 0.60), the absence of a mesiostylid on p4 (16^0; RI = 0.25), the absence of a parastyle on upper molars (20^0; RI = 0.66), labial walls of upper molar cusps rounded (25^1; RI = 0.80), the paracone of P4 higher than that of the molars (33^1; RI = 0.66) and the absence of a protocone on P3 (36^0; RI = 0.50). Raoellidae are unambiguously defined by the absence of a paraconid (2^0; RI = 0.85), a metaconule of the upper molars located distally to the paracone

(27^1; RI = 0.66, convergently present at node I) and the endocristae of the P4 forming an anterior loph (30^1; RI = 0.50). The presence of an endoentocristid (5^1; RI = 0.66) and the loss of the hypoconid on m1–2 (13^0; RI = 1.00) are potential synapomorphies of the Raoellidae (DELTRAN optimization), but the distribution of these characters is ambiguous because of nonapplicable character states in *Pakicetus*. The Raoellidae form a pectinate clade with *Kunmunella* and *Indohyus* as first offshoots. *Metkatius*, *Khirtharia* and ?*K.* cf. *major* share a low molar crown (15^0; RI = 1.00). ?*Khirtharia* cf. *major* is closely related to *Khirtharia*; both taxa share an entoconid almost as high as the hypoconid (3^1; RI = 0.83, convergently observed at node F) and the loss of the central accessory cristid (9^0; RI = 1.00). IVPP V12763.1 from Shanghuang is the sister taxon to *Khirtharia*.

5.b. What is a raoellid?

Raoellids were recently defined as 'extremely bunodont forms showing various degrees of lophodonty; the premolars are generally simple and trenchant; molars with reduced or absent paraconules on uppers, loss of the paraconid on lowers' (Theodor, Erfurt & Métais, 2007, p. 56). Based on our phylogenetic analysis, the Raoellidae present a reduction of accessory structures in lower and upper molars (paraconid (2^0), hypoconulid (13^0), parastyle (20^0)) and construction of a wide crushing basin by labial displacement of the prehypocristid of the lower molars (8^1, Fig. 2c–e, observed in both 'sublophodont' and 'hyperbunodont' species). Raoellids also present a specialization of their upper and lower premolars to form a complementary shearing device. The lower premolars are very trenchant and the strictly mesio-distal P3 is simplified by the loss of the paracone (36^0) and of the lingual root (37^1). The P4 is highly derived: the endocristae that are primitively present in the Cetartiodactyla (Fig. 4f, i–l) are mesial and high to form a transverse loph (30^1, Fig. 4i), and its paracone with sharp mesial and distal edges is high compared to the protocone (32^1).

Raoellids and cetaceans share high crowns in the posterior premolars (Thewissen *et al*. 2007). Indeed, our results indicate that raoellids and early cetaceans share derived characters corresponding to the development of prominent longitudinal cutting edges: sharp, biradiculated P3 lacking the protocone, a paracone of the P4 higher than that of the molars and a labial orientation of the prehypocristid (cristid obliqua) on the lower molars (corresponding to the opening of the crushing basin, completely open in pakicetids). Raoellids exhibit transverse structures on molars and premolars: a metaconule of the upper molars distal to the paracone (27^1) and the endocristae of the P4 forming an anterior loph (30^1), whereas basal cetaceans developed mesio-distal shearing structures, with an extreme modification of the molars with all transversal structures reduced. The Raoellidae and *Pakicetus* share
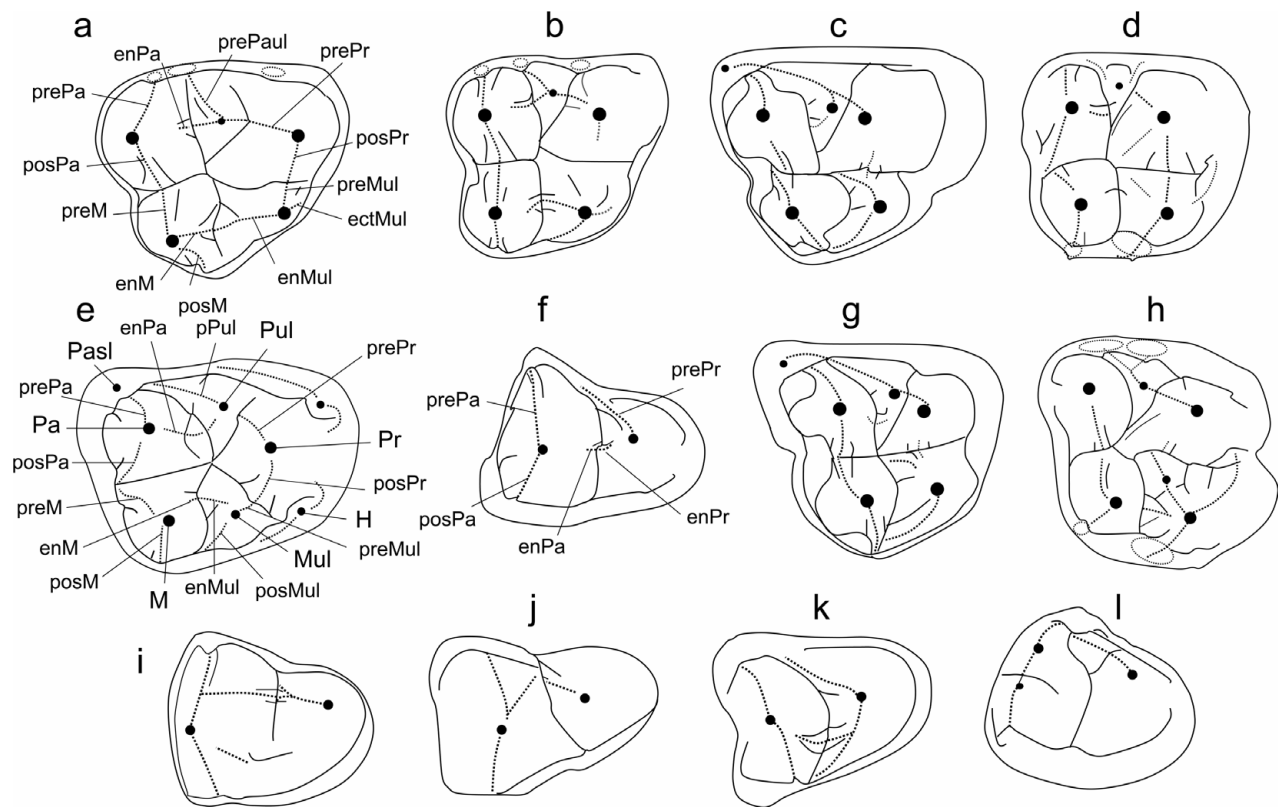
Figure 4. Comparison of upper cheek tooth structure of some Eocene cetartiodactyls. Upper molar: (a) *Kunmunella transversa*; (b) *Khirtharia inflata*; (c) *Haqueina haichinensis*; (d) 'artiodactyla indeterminate' (NMMP−KU 1765, Tsubamoto *et al.* 2005, fig. 2B); (e) *Gujaratia pakistanensis*; (g) *Gobiohyus orientalis*; (h) *Palaeochoerus quercyi*. P4: (f) *Diacodexis secans*; (i) *Kunmunella transversa*; (j) ?*Indohyus yuanchuensis* (after Young, 1937, fig 13); (k) *Gobiohyus orientalis*; (l) *Palaeochoerus quercyi*. Abbreviations: ectMul – ectometacristule; enM – endometacrista; enMul – endometacristule; enPa – endoparacrista; enPr – endoprotocrista; H – hypocone; M – metacone; Mul – metaconule; Pa – paracone; Pasl – parastyle; prePa – preparacrista; posM – postmetacrista; posMul – postmetacristule; posPa – postparacrista; pPul – preparacristule; prePaul – preparacristule; posPr – postprotocrista; Pr – protocone; preM – premetacrista; preMul – premetacristule; prePr – preprotocrista; Pul – paraconule.

several dental characters that can be correlated to a functional adaptation to shearing. Cetaceans can be defined by major changes in dental functions related to dietary changes (O'Leary & Uhen, 1999). According to our results, the 'hyperbunodont' molar morphology is derived among raoellids, indicating that, from a common shearing cheek tooth pattern, raoellids and cetaceans specialized in two different ways, raoellids shifting to a derived 'omnivorous' diet (shearing premolars associated with crushing molars). Isotopes indeed indicate different diet for raoellids and pakicetids (Thewissen *et al.* 2007).

The results of our phylogenetic analysis highlight that raoellids and suoids share numerous dental features. These similarities are here interpreted as convergences: the loss of the parastyle in the upper molars (20^0) and the rounded labial wall of the upper molars (25^1, both convergently present at the nodes B and J), and the loss of the paraconid (2^0, convergently occurring at the nodes B and H). These characters, together with symplesiomorphies explain the overall similarity between suoids and raoellids. This could as well explain why raoellids have been often referred to the Suiformes (e.g. Ranga Rao, 1971, 1972; Sahni & Kumar, 1971; Vislobokova, 2004*a*).

5.c. Systematic content of the Raoellidae

According to our results, the Raoellidae is comprised of the genera *Kunmunella*, *Indohyus*, *Metkatius* and *Khirtharia*. This generic content of the family is congruent with that proposed by Theodor, Erfurt & Métais (2007). The close affinities of the specimen from Shanghuang (morphologically similar to the only specimen known of '*I. major*') with *Khirtharia*, triggers the question of its generic attribution. Based on the results of our phylogenetic analysis, we chose to refer this material to ?*Khirtharia*, as it consists of very poor material.

In agreement with Theodor, Erfurt & Métais (2007), the genus *Haqueina* is not part of the raoellid clade *contra* Vislobokova (2004*a,b*). This result is congruent with the deep morphological differences observed between *Haqueina* and raoellid species for lower and upper molars (Fig. 2h v. 2c–e; Fig. 4c v. 4a–b), *Haqueina* being morphologically very close to *Gobiohyus* (Fig. 4c v. 4g). Theodor, Erfurt & Métais (2007) suggest that the isolated right M2 and M3 from Pondaung referred to as 'Artiodactyla indeterminate 2' (NMMP−KU 1765, 1742; Tsubamoto *et al.* 2005, fig. 2b–c) could be raoellids. The teeth are bunodont

and quadricuspidate as in raoellids, but their structure and crest pattern differ deeply from the latter (Fig. 4d v. 4a–b). On the M2, the paraconule is small and mesially located; it is strongly connected to the mesial cingulum by two small crests. In all raoellids, the crushing basin is mesially delimited by a transversal crest formed by a small endoparacrista connected to the paraconule and to the preprotocrista, and distally, it is delimited by the 'hypoloph' that corresponds to the junction of the endocristae of the distal cusps. The specimens from Pondaung do not present such transversal structures. Upper molars of raoellids exhibit a clear endometacrista, a structure that is not present in the specimens from Pondaung. According to our results, 'Artiodactyla indeterminate 2' from Pondaung is not part of the raoellid clade (Fig. 3).

Coombs & Coombs (1977) assigned *Gobiohyus yuanchuensis* Young, 1937 from Rencun (late Middle Eocene, China; Tsubamoto, Takai & Egi, 2004) to ?*Indohyus* on the basis of the P4 morphology, the lack of a paraconule and a strong parastyle on M1–2, as well as lack of a paraconid on m3. Thewissen, Gingerich & Russell (1987) rejected the attribution of the specimen from Rencun to the Raoellidae on the basis of the bunodont cusps and the lack of transverse crests. The specimens of ?*Indohyus yuanchuensis* have been figured only in the original description of the species (Young, 1937). The drawings are unfortunately not very clear and wear has removed detailed structures of the cheek teeth. As stated by Coombs & Coombs (1977), the P4 is morphologically similar to that of raoellids (Fig. 4j), with a paracone bigger than the protocone (unfortunately the relative height of these cusps cannot be controlled), no postprotocrista (contrary to *Gobiohyus*) and no prominent parastyle. The presence of an endoparacrista cannot be verified from the drawing (Young, 1937, fig.13). The M2 has no paracone and the labial cusps have rounded labial flanks, as in raoellids (Fig. 4a–b). However, the 'selenodont' wear pattern of the M1 is clearly different from that of raoellids, and there is no trace of the crushing basin, or of the endometacrista, forming the distal loph (hypoloph) in Raoellidae. The M2 seems to exhibit a crushing basin, but the distal part of the tooth is broken and the presence of the hypoloph cannot be ascertained. On the left lower jaw fragment of ?*I. yuanchuensis* much of the structure of the m3 (only preserved tooth) is eroded or broken and no diagnostic character can be observed. Because of the difficulty in interpreting the drawings provided by Young (1937, figs 13–14), we chose not to code ?*I. yuanchuensis* in our analysis. To conclude on the familial status of the material from Rencun, the material illustrated by Young (1937) does not allow unambiguous referral to the Raoellidae. However, the morphology of the P4 could be compatible with an attribution to the raoellids, in agreement with Coombs & Coombs (1977). It is also noteworthy that the size of ?*I. yuanchüensis* is similar to that of ?*K. major*.

5.d. The sister taxon of the Raoellidae

In the original description of the family Raoellidae, Sahni *et al*. (1981) rejected their affinities with the coeval Heloyidae from Mongolia, or with the later Eocene Anthracotheriidae of Myanmar. Theodor, Erfurt & Métais (2007) rather suggested a local radiation of raoellids in the Indian Subcontinent, from an ancestry close to *Gujaratia*. Based on additional material, including cranial and postcranial remains, Thewissen *et al*. (2007) advocated the Raoellidae as the sister taxon to the cetaceans. Our results, though based on a reduced number of characters and taxa, clearly discard close affinities with heloyids or with anthracotheriids and support Thewissen *et al*.'s (2007) hypothesis of a sister taxon relationship between raoellids and cetaceans, both being nested within 'diacodexeids'. *Gujaratia* is the sister taxon to the raoellid/*Pakicetus* clade. This relationship, previously proposed partly on geographical grounds (Theodor, Erfurt & Métais, 2007), is here unambiguously supported by the presence of a paracone much higher than the protocone on P4 (32^1; RI = 1.00). Like other recent morphological analyses (e.g. Spaulding, O'Leary & Gatesy, 2009; Thewissen *et al*. 2007), our results support a 'Suiformes' clade, i.e. grouping hippopotamoids (*Choeropotamus* and *Siamotherium*) and suoids (*Siamochoerus*, *Palaeochoerus*), instead of a Whippomorpha clade (i.e. grouping hippopotamoids and cetaceans; = Cetancodontamorpha *sensu* Spaulding, O'Leary & Gatesy, 2009) so far chiefly supported by molecular data (e.g. Montgelard, Catzeflis & Douzery, 1997; Waddell, Okada, & Hasegawa, 1999; Marcot, 2007). However, our taxonomic sampling cannot assess hippopotamid/cetacean relationship.

6. Biostratigraphical and palaeogeographical implications

The endemism of the Raoellidae has been challenged by several recent works describing raoellids from outside the Indian Subcontinent: i.e. in Mongolia (*Haqueina haichinensis*, Khaichin Ula, early to middle Middle Eocene; Vislobokova 2004*a,b*), in Myanmar ('Artiodactyla indeterminate', Pondaung, early Late Eocene; Theodor, Erfurt & Métais, 2007) and in China (?*Indohyus yuanchuensis*, Rencun, late Middle Eocene; Coombs & Coombs, 1977). Our results reject the attribution of the specimens from Mongolia and Myanmar to the Raoellidae, and the referral of '?*Indohyus yuanchuensis*' from the late Middle Eocene site of China (Rencun, Sharamurunian ALMA; Tsubamoto, Takai & Egi, 2004) is still dubious. On the other hand, the attribution of the m3 IVPP V12763.1 from Shanghuang to the Raoellidae documents the presence of the family outside the Indian Subcontinent and substantiates the easternmost occurrence of the Raoellidae. The remaining indisputable reports of the family are limited to the early Middle Eocene of Pakistan and India (Fig. 5).
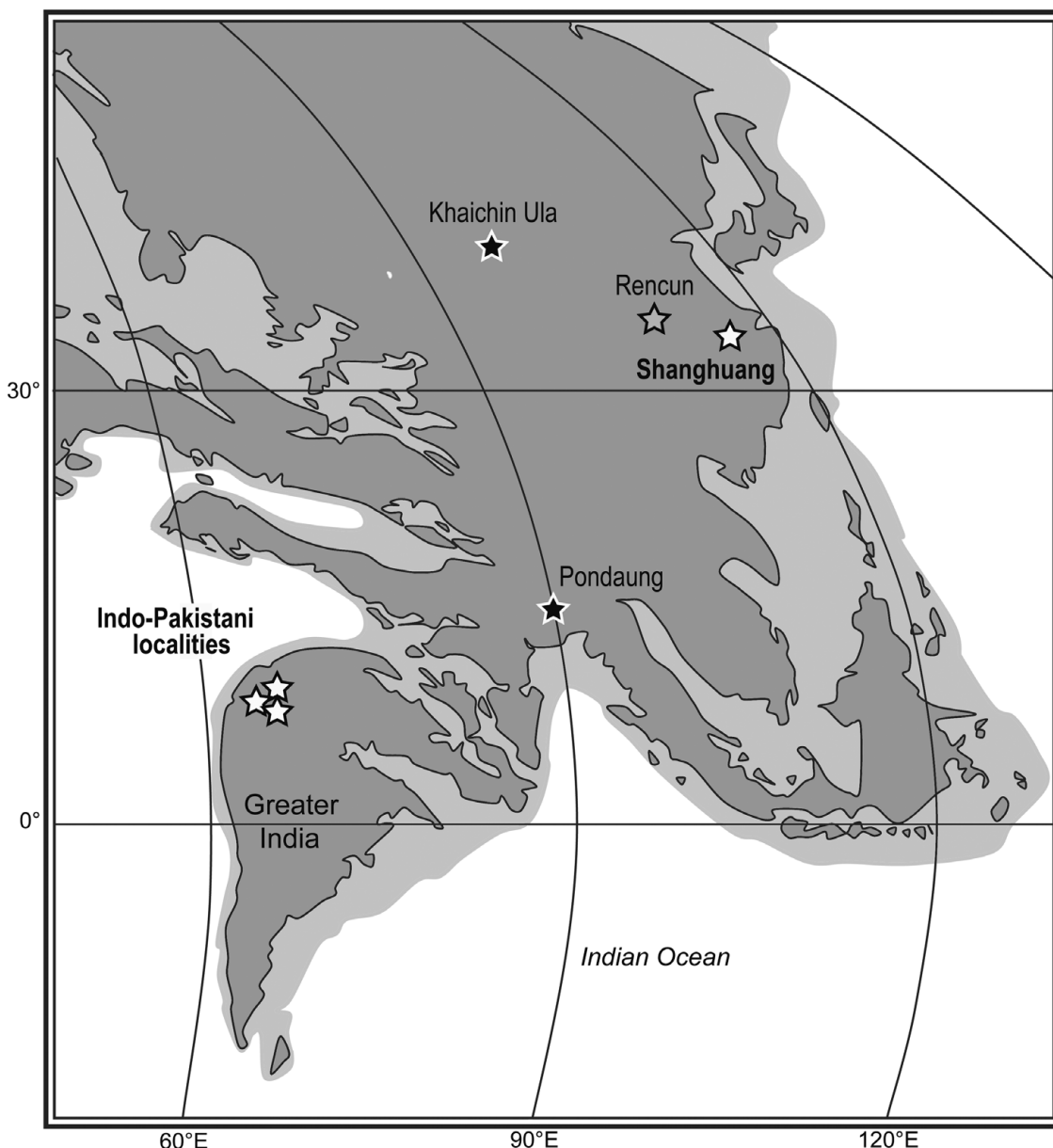
Figure 5. Palaeogeographical reconstruction of South and South-East Asia at *c*. 50 Ma showing localities where raoellids were mentioned. Black stars – raoellid occurrences rejected in the present work; white stars – raoellid occurrences confirmed in the present work; grey star – dubious raoellid occurrence. The map is modified from R. Blakey (available at http://jan.ucc.nau.edu/~rcb7/RCB.html).

The fossil locality of Shanghuang (Jiangsu Province, coastal China) consists of five distinctive karstic infillings, Middle Eocene in age based on mammalian biochronology (Wang & Dawson, 1994; Dawson & Wang, 2001; Dawson, Huang & Wang, 2003). The five fissures are considered to span a short interval of time (*c*. 1–2 Ma) of the Irdinmanhan ALMA (middle Middle Eocene, *c*. 45 Ma), with the fissure D being slightly older than the others (Beard *et al*. 1994; Wang & Dawson, 1994; MacPhee, Beard & Qi, 1995; Qi *et al*. 1996; Métais, Guo & Beard, 2004; Gebo *et al*. 2008). However, a late Middle Eocene age (Sharamurunian ALMA) has also been proposed for the fissures A, B and C (Dawson, Huang & Wang, 2003; Métais *et al*. 2008). The raoellid specimen from Shanghuang fissure filling B represents the youngest occurrence of the

family, so far restricted to the early Middle Eocene in Indo-Pakistan. This species is also among the most derived raoellids according to the results of our analysis. The raoellid specimen from Shanghuang fissure filling B is morphologically very close to the fragmentary m2 described from Chorlakki, Pakistan (Figs 2a, b, 5; Thewissen, Gingerich & Russell, 1987) and, as such, is designated ?*Khirtharia* cf. *major*. The Chorlakki fauna originates from a single locality, late Early or early Middle Eocene in age (Gingerich, 2003), which would be slightly older than the Shanghuang karstic infillings if we consider them to span a short interval of the middle Middle Eocene (Irdinmanhan, Beard *et al*. 1994; Gebo *et al*. 2008). The presence of ?*K*. cf. *major* in fissure B of Shanghuang (very close or conspecific to ?*K. major* from the early Middle

Eocene locality of Chorlakki, Pakistan), would be more consistent with an Irdinmanhan age than with the Sharamurunian age proposed by Dawson, Huang & Wang (2003).

Clyde, Khan & Gingerich (2003) proposed that modern orders of mammals dispersed into India during the initial collision with Asia, rather than from India (*contra* Krause & Maas, 1990). They propose that the endemism of the early Middle Eocene faunas of the Indian Subcontinent (e.g. artiodactyls of the Kuldana and Kalakot formations) would indicate that early dispersal corridors were temporary, and that India was partially isolated by marine incursions during early Middle Eocene times, thus enhancing allopatric speciation (and endemic differentiation). Our results, although based on a reduced sample, would fit this scenario, with the differentiation of the cetacean/raoellid clade in India from a dichobunid-like ancestor of Holarctic origin close to *Gujaratia pakistanensis*. However, the earliest cetaceans (Pakicetidae) have been recovered from Lower Eocene sediments of India and Pakistan (West, 1980; Gingerich & Russell, 1990; Thewissen & Hussain, 1998; Thewissen, William & Hussain, 2001). This, in turn, implies, given this scenario, that the differentiation of endemic Indian Cetartiodactyla occurred well before early Middle Eocene time. The occurrence of the Raoellidae in South-East China, outside the Indian Subcontinent, during Middle Eocene time suggests that dispersal events occurred between the Indian Subcontinent and eastern Asia at the latest by Middle Eocene time. Two other small cetartiodactyls, *Haqueina* and *Chorlakkia*, are known both from the late Early Eocene or early Middle Eocene of Pakistan (*H. haquei*, Gandas Kas, Kuldana Formation; Dehm & Oettingen-Spielberg, 1958; *C. hassani*, Chorlakki, Kuldana Formation; Gingerich *et al.* 1979) and from the Middle Eocene deposits of Mongolia (*H. haichinensis* and *C. valerii*, Khaichin Ula II; Vislobokova, 2004*a*). They further provide evidence of early Middle Eocene faunal dispersals between India and eastern Asia.

Among the small artiodactyls from Shanghuang, three diacodexeids have been described from Shanghuang, from fissures A (*Jiangsudon shanghuangensis*, Métais *et al.* 2008) and D ('cf. *Diacodexis*' and 'Diacodexeidae indet.', Métais *et al.* 2008). The occurrence of diacodexeids in Shanghuang is noteworthy because this family has an Early Eocene to early Middle Eocene stratigraphical range in Europe and North America (Theodor, Erfurt & Métais, 2007), while the raoellid record is restricted to the early Middle Eocene of Indo-Pakistan (Thewissen *et al.* 1983; Thewissen, Williams & Hussain, 2001). Metais *et al.* (2008) suggested that the presence of diacodexeids in Shanghuang points to the persistence of very stable ecological conditions in coastal China during Early to Middle Eocene time, allowing notably the survival of forest-dwelling artiodactyls otherwise extinct elsewhere. During that period (*c.* 45 Ma ago), the palaeolatitude of India was ∼ 20° farther south than today (10° N instead of 30° N), i.e. close to

the equatorial humid belt (i.e. ∼ 15° N; Mattauer, 2002; Kent & Muttoni, 2008), which implies that the latitudinal difference with Shanghuang (∼ 35° N through Cenozoic times) was much more important than it is in present times (Fig. 5). However, global climate was much warmer during Middle Eocene time than today (Mid-Eocene climatic optimum; Zachos, Dickens & Zeebe, 2008) and it is likely that warm and humid conditions (subtropical to tropical) occurred in coastal China, in contrast to the arid to semi-arid vegetation zone that extended at similar latitudes in China throughout Eocene time (Sun & Wang, 2005, fig. 7b). There were neither significant climatic nor paleoenvironmental discrepancies between coastal Northern India and Shanghuang (coastal China) during Middle Eocene (Irdinmanhan) time, which allowed the dispersal/survival of ecologically exigent mammals such as the Raoellidae (aquatic waders; Thewissen *et al.* 2007) in Eastern Asia.

7. Conclusions

Métais *et al.* (2008) tentatively identified an isolated m3 (specimen IVPP V12763.1) from the Middle Eocene of China as an indeterminate suoid, which implied that it was the earliest record of the superfamily. Our analysis and revision of this material led us to challenge this interpretation and we suggest instead that the Shanghuang specimen rather belongs to the Raoellidae. This is the only unquestionable record of raoellids outside the Indian Subcontinent so far, which significantly extends the geographical and chronological range of the family: this specimen represents the youngest and easternmost occurrence of the family. According to the results of our phylogenetic analysis, the Raoellidae include *Kunmunella*, *Indohyus*, *Metkatius* and *Khirtharia*. *Haqueina* from Mongolia and the 'indeterminate artiodactyl' from Pondaung previously tentatively referred to as raoellids (Theodor *et al.* 2007) are excluded from the raoellid clade.

The occurrence of a raoellid species in Shanghuang implies that raoellids dispersed from the Indian Subcontinent to eastern Asia during late Early Eocene or Middle Eocene time. This somewhat tempers the hypothesis of Middle Eocene Indian endemism as well as that of eastern Asia provincialism.

References

BEARD, K. C, QI, T., DAWSON, M. R., WANG, B. & LI, C. 1994. A diverse new primate fauna from Middle Eocene

fissure-fillings in southeastern China. *Nature* **368**, 604–9.

BOISSERIE, J.-R., LIHOREAU, F., ORLIAC, M. J., FISHER, R., WESTON, E. & DUCROCQ, S. 2009. Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae). *Zoological Journal of the Linnean Society* **158**, 325–67.

BREMER, K. 1994. Branch support and tree stability. *Cladistics* **12**, 177–81.

CLYDE, W. C., KHAN, I. H & GINGERICH, P. D. 2003. Stratigraphic response and mammalian dispersal during initial India-Asia collision: Evidence from the Ghazij Formation, Balochistan, Pakistan. *Geology* **31**, 1097–100.

COOMBS, W. P. JR., & COOMBS, M. C. 1977. Dentition of *Gobiohyus* and the reevaluation of the Heloyidae (Artiodactyla). *Journal of Mammalogy* **58**, 291–308.

DAWSON, M. R. & WANG, B. 2001. Middle Eocene Ischyromyidae (Mammalia: Rodentia) from the Shanghuang fissures, southeastern China. *Annals of the Carnegie Museum of Natural History* **70**, 221–30.

DAWSON, M. R., HUANG, X., LI, C. & WANG, B. 2003. Zelomyidae, a new family of Rodentia (Mammalia) from the Eocene of Asia. *Vertebrata PalAsiatica* **41**, 249–70.

DEHM, R. & OETTINGEN-SPIELBERG, T. 1958. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. *Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen* **91**, 1–54.

GEBO, D. L., DAGOSTO, M., BEARD, K. C. & NI, X. 2008. New primate hind limb elements from the Middle Eocene of China. *Journal of Human Evolution* **55**, 999–1014.

GEISLER, J. H., THEODOR, J. M., UHEN, M. D. & FOSS, S. E. 2007. Phylogenetic relationships of cetaceans to terrestrial artiodactyls. In *The Evolution of Artiodactyls* (eds D. R. Prothero & S. E. Foss), pp. 19–31. Baltimore: Johns Hopkins University Press.

GEISLER, J. H. & UHEN, M. 2003. Morphological support for a close relationship between hippos and whales. *Journal of Vertebrate Paleontology* **23**, 991–6.

GEISLER, J. H. & UHEN, M. D. 2005. Phylogenetic relationships of extinct cetartiodactyls: results of simultaneous analyses of molecular, morphological, and stratigraphic data. *Journal of Mammalian Evolution* **12**, 145–60.

GENTRY, A. W. & HOOKER, J. J. 1988. The phylogeny of the Artiodactyla. In *The phylogeny and classification of the tetrapods, vol 2: mammals* (ed. M. J. Benton), pp 235–72. Oxford: Clarendon Press.

GINGERICH, P. D. 2003. Stratigraphic and micropaleontological constraints on the Middle Eocene age of the mammal-bearing Kuldana Formation of Pakistan. *Journal of Vertebrate Paleontology* **23**, 643–51.

GINGERICH, P. D. & RUSSELL, D. E. 1990. Dentition of early Eocene *Pakicetus* (Mammalia, Cetacea). *Contributions from the Museum of Paleontology, University of Michigan* **28**, 1–20.

GINGERICH, P. D., RUSSELL, D. E., SIGOGNEAU-RUSSELL, D. & HARTENBERGER, J.-L. 1979 Chorlakkia hasani, a new Middle Eocene dichobunid (Mallalia, Artiodactyla) from the Kuldana Formation of Kohat, Pakistan. *Contribution from the Museum of Paleontology, University of Michigan* **25**(6), 117–24.

KENT, D. V. & MUTTONI, G. 2008. Equatorial convergence of India and early Cenozoic climate trends. *Proceedings of the National Academy of Sciences* **105**, 16065–70.

KRAUSE, D. W. & MAAS, M. C. 1990. The biogeographic origins of the late Paleocene–Early Eocene mammalian immigrants to the Western Interior of North America. In *Dawn of the age of mammals in the northern part of the Rocky Mountain interior, North America* (eds T. M Bown & K. D. Rose), pp. 71–105. Geological Society of America Special Paper 243.

KUMAR, K. & SAHNI, A. 1985. Eocene mammals from the Upper Subathu Group, Kashmir Himalaya, India. *Journal of Vertebrate Paleontology* **5**, 153–68.

MACPHEE, R. D. E., BEARD, K. C. & QI, T. 1995. Significance of primate petrosal from Middle Eocene fissure-fillings at Shanghuang, Jiangsu Province, People's Republic of China. *Journal of Human Evolution* **29**, 501–14.

MARCOT, J. D. 2007. Molecular phylogeny of terrestrial artiodactyls. In *The evolution of artiodactyls* (eds D. R. Prothero & S. E. Foss), pp. 4–18. Baltimore: The Johns Hopkins University Press.

MATTAUER, M. 2002. New GPS data in China: a key for a better understanding of the Cainozoic tectonics of Asia. *Comptes Rendus Geoscience* **334**, 809–10.

MÉTAIS, G., GUO, J. & BEARD, K. C. 2004. A new small dichobunid artiodactyl from Shanghuang (Middle Eocene, eastern China): implications for the early evolution of proto-selenodonts in Asia. In *Fanfare for an uncommon paleontologist: papers in honor of Malcom C. McKenna* (eds M. R. Dawson & J. A. Lillegraven), pp. 177–197. Bulletin of the Carnegie Museum of Natural History 25.

MÉTAIS, G., QI, T., GUO, J. & BEARD, K. C. 2008. Middle-Eocene artiodactyls from Shanghuang Jiangsu province, Coastal China) and the diversity of basal dichobunoids in Asia. *Naturwissenschaften* **95**, 1121–35.

MONTGELARD, C., CATZEFLIS, F. M. & DOUZERY, E. 1997. Phylogenetic relationships of artiodactyls and cetaceans as deduced from the comparison of cytochrome *b* and 12S RNA mitochondrial sequences. *Molecular Biology and Evolution* **14**, 550–9.

O'LEARY, M. A. & GATESY, J. 2008. Impact of increased character sampling on the phylogeny of Cetartiodactyla (Mammalia): combined analysis including fossils. *Cladistics* **24**, 397–442.

O'LEARY, M. A. & UHEN, M. D. 1999. The time of origin of whales and the role of behavioural changes in the terrestrial aquatic transition. *Paleobiology* **25**, 534–56.

ORLIAC, M. J., ANTOINE, P.-O. & DUCROCQ, S. 2010. Phylogenetic relationships of the family Suidae, new insights on the relationships among Suoidea. *Zoologica Scripta* **39**, 315–30.

ORLIAC, M. J., BOISSERIE, J.-R., MACLATCHY, L. & LIHOREAU, F. 2010. The earliest Hippopotamidae unveiled, new insights into hippopotamid time and place of origin. *Proceedings of the National Academy of Science* **107**, 11871–6.

ORLIAC, M. J., GUY, F., CHAIMANEE, Y., JAEGER, J.-J. & DUCROCQ, S. In press. New remains of *Egatochoerus jaegeri* (Cetartiodactyla, Mammalia) from the late Eocene of Thailand. *Palaeontology*.

PILGRIM, G. E. 1940. Middle Eocene mammals from North-West India. *Proceedings of the Zoological Society of London-B* **110**, 127–52.

QI, T., BEARD, K. C., WANG, B., DAWSON, M. R., GUO, J. & LI, C. 1996. The Shanghuang mammalian fauna, Middle Eocene of Jiangsu: history of discovery and significance. *Vertebrata PalAsiatica* **34**, 202–14.

RANGA RAO, A. 1971. New mammals from the Murree (Kalakot zone) of the Himalayan foot hills near

Kalakot, Jammu & Kashmir state, India. *Journal of the Geological Society of India* **12**(2), 124–34.

RANGA RAO, A. 1972. New mammalian genera and species from the Kalakot zone of the Himalayan foot hills near Kalakot, Jammu & Kashmir state, India. In *Further studies on the vertebrate fauna of Kalakot, India*, pp. 1–19. Special paper of the Directorate of Geology, Oil and Natural Gas Commission, Dehra Dun, India.

SAHNI, A. & KUMAR, S. K. 1971. Three new Eocene mammals from the Rajauri District, Jammu and Kashmir. *Journal of the Palaeontological Society of India* **16**, 41–53.

SAHNI, A., BHATIA, S. B., HARTENBERGER, J.-L, JAEGER, J.-J., KUMAR, K., SUDRE, J. & VIANEY-LIAUD, M. 1981. Vertebrates from the Subathu formation and comments on the biogeography of Indian subcontinent during the Early Paleogene. *Bulletin de la Société géologique de France* **23**, 689–95.

SPAULDING, M., O'LEARY, M. A. & GATESY, J. 2009. Relationships of Cetacea (Artiodactyla) among mammals: increased taxon sampling alters interpretations of key fossils and character evolution. *PLoS ONE* **4**(9), e7062, doi:10.1371/journal.pone.0007062, 14 pp.

SUN, X. & WANG, P. 2005. How old is the Asian monsoon system? – palaeobotanical records from China. *Palaeogeography, Palaeoclimatology, Palaeoecology* **222**, 181–222.

SWOFFORD, D. 1993. *Phylogenetic analysis using parsimony (PAUP), version 3.1.1*. Champaign, IL: Illinois Natural History Survey.

THEODOR, J. M., ERFURT, J. & MÉTAIS, G. 2007. The earliest artiodactyls. In *The evolution of Artiodactyla* (eds D. R. Prothero & S. E. Foss), pp. 32–58. Baltimore: John Hopkins University Press.

THEODOR, J. M. & FOSS, S. E. 2005. Deciduous dentitions of Eocene cebochoerid artiodactyls and cetartiodactyl relationships. *Journal of Mammal Evolution* **12**, 161–81.

THEWISSEN, J. G. M., COOPER, L. N., CLEMENTZ, M. T., BAJPAI, S. & TIWARI, B. N. 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. *Nature* **450**, 1190–5.

THEWISSEN, J. G. M., GINGERICH, P. D. & RUSSELL, D. E. 1987. Artiodactyla and perissodactyla (Mammalia) from the Early-Middle Eocene Kuldana formation of Kohat (Pakistan). *Contribution from the Museum of Paleontology, University of Michigan* **27**(10), 247–74.

THEWISSEN, J. G. M. & HUSSAIN, S. T. 1998. Systematic review of the Pakicetidae, Early and Middle Eocene Cetacea (Mammalia) from Pakistan and India. *Bulletin of the Carnegie Museum of Natural History* **34**, 220–38.

THEWISSEN, J. G. M., HUSSAIN, S. T. & ARIF, M. 1994. Fossil evidence for the origin of aquatic locomotion in Archaeocete whales. *Science* **263**, 210–12.

THEWISSEN, J. G. M., RUSSELL, D. E., GINGERICH, P. D. & HUSSAIN, S. T. 1983. A new dichobunid artiodactyl (Mammalia) from the Eocene of north-west Pakistan. Dentition and classification. *Proceedings Koninklijke Nederlandse Academie van Wetenschappen B* **86**,153–80.

THEWISSEN, J. G. M., WILLIAMS, E. M. & HUSSAIN, S. T. 2001. Eocene mammal faunas from northern Indo-Pakistan. *Journal of Vertebrate Paleontology* **21**, 347–66.

TSUBAMOTO, T., EGI, N., TAKAI, M., SEIN, C. & MAUNG, M. 2005. Middle Eocene ungulate mammals from Myanmar: A review with description of new specimens. *Acta Palaeontologica Polonica* **50**, 117–38.

TSUBAMOTO, T., TAKAI, M. & EGI, N. 2004. Quantitative analyses of biogeography and faunal evolution of Middle to Late Eocene mammals in East Asia. *Journal of Vertebrate Paleontology* **24**, 657–67.

VISLOBOKOVA, I. A. 2004*a*. A new representative of the family Raoellidae (Suiformes) from the Middle Eocene of Khaichin-Ula 2, Mongolia. *Paleontological Journal* **38**, 220–6.

VISLOBOKOVA, I. A. 2004*b*. Artiodactyls from the Middle Eocene of Khaichin Ula II, Mongolia.*Paleontological Journal* **38**, 90–6.

WADDELL, P. J., OKADA, N. & HASEGAWA, M. 1999. Towards resolving the interordinal relationships of placental mammals. *Systematic Biology* **48**, 1–5.

WANG, B. & DAWSON, M. R. 1994. A primitive cricetid (Mammalia, Rodentia) from the Middle Eocene of Jiangsu Province, China. *Annals of the Carnegie Museum of Natural History* **63**, 239–56.

WEST, R. M. 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas Region, Pakistan. *Journal of Paleontology* **54**, 508–33.

YOUNG, C. 1937. An early Tertiary vertebrate fauna from Yuanchü. *Bulletin of the Geological Society of China* **17**(3–4), 413–38.

ZACHOS, J. C., Dickens, G. R. & Zeebe, R. E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–83.

ZHOU, X., ZHAI, R., GINGERICH, P. D. & CHEN, L. 1995. Skull of a new mesonychid (Mammalia, Mesonychia) from the Late Paleocene of China. *Journal of Vertebrate Paleontology* **15**, 387–400.