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Ozan Erdal, Pierre-Olivier Antoine, Sevket Sen

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3 **NEW REMAINS OF *PALAEOAMASIA KANSUI* (EMBRITHOPODA, MAMMALIA)**
4
5 **FROM THE EOCENE OF TURKEY AND A PHYLOGENETIC ANALYSIS OF**
6
7 **EMBRITHOPODA AT THE SPECIES LEVEL**
8
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10
11 *by* OZAN ERDAL¹, PIERRE-OLIVIER ANTOINE² *and* SEVKET SEN³
12

13
14 ¹Eurasia Institute of Earth Sciences, Istanbul Technical University, 34469 Maslak, Istanbul,
15
16 Turkey, erdalo@itu.edu.tr
17

18
19 ²Institut des Sciences de l'Evolution, UMR 5554 CNRS, Université de Montpellier, EPHE,
20
21 UR 226 IRD, Place Eugène Bataillon, F-34095 Montpellier cedex 5, France, pierre-
22
23 olivier.antoine@umontpellier.fr
24

25
26 ³Sorbonne Universités, Centre de recherches sur la Paléobiodiversité et les
27
28 Paléoenvironnements, UMR 7207 CNRS, UPMC, MNHN, 8 rue Buffon, 75005, Paris,
29
30 France, sen@mnhn.fr
31

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35
36 **Abstract:** Since the discovery of the megaherbivore *Arsinoitherium zitteli* Beadnell (early
37
38 Oligocene of Egypt), the extinct order Embrithopoda has remained an enigmatic group, with
39
40 disputed affinities among ungulates. In this study, new specimens of *Palaeoamasia kansui*
41
42 from the early Palaeogene of Turkey are described and a synthetic dental terminology is
43
44 proposed for embrithopods. Based on 130 cranial-mandibular and dental characters, the first
45
46 phylogenetic analysis of embrithopods is carried out in aim to enhance the position of
47
48 *Palaeoamasia* within embrithopods. The monophyly of Embrithopoda is confirmed,
49
50 following the topology [*Phenacolophus*, [*Namatherium*, [*Arsinoitheriinae*, *Palaeamasiinae*]]].
51
52 However, phylogenetic relationships between Eurasian embrithopods (*Palaeoamasiinae*:
53
54 *Palaeoamasia*, *Crivadiatherium*, and *Hypsamasia*) remain unresolved. The integration of all
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1
2
3 embrithopod genera within a cladistic analysis encompassing a wider taxonomic sample
4
5 (Condylarthra, Afrotheria/Paenungulata, and Laurasiatheria) also supports Embrithopoda as
6
7 being monophyletic, but questions both the position of *Phenacolophus* and *Namatherium*
8
9 within Embrithopoda. This latter analysis points to palaeobiogeography and the occurrence of
10
11 a single/two distinct dispersal event(s) for embrithopods between Eurasia and Africa during
12
13 the early Palaeogene.
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16
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18 **Key words:** Embrithopoda, *Palaeoamasia*, Palaeogene, systematics, phylogeny,
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20 palaeobiogeography.
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28 **SINCE** the discovery of *Arsinoitherium* Beadnell, 1902 in Fayum (Egypt) and its detailed
29
30 description by Andrews (1906), who provided the general definition of the order
31
32 Embrithopoda, many other remains were found in Africa, the Arabian Peninsula, and Eurasia
33
34 (Fig.1). However, these extinct megaherbivores are mostly represented by cranial-dental
35
36 specimens, except for *Arsinoitherium zitteli*. Hence, the order is still considered one of the
37
38 most enigmatic groups within mammals in terms of systematics and phylogenetic
39
40 relationships. As well, some disagreements endure on their origin, palaeoenvironment or
41
42 lifestyle and dispersal routes that are paradoxical to palaeogeographic maps (Sen 2013;
43
44 Sanders *et al.* 2014 and references therein).
45
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47

48
49 All embrithopods with corresponding localities, time interval and authors are summarised in
50
51 Table 1 and illustrated in Figure 1 in stratigraphical order.
52

53
54 In the Afro-Arabian fossil record, embrithopods are described under two genera,
55
56 *Arsinoitherium* and *Namatherium*, ranging from the middle Eocene up to the latest Oligocene.

57
58 The former genus is better documented from dozen localities and only two species are
59
60

1
2
3 considered valid (*A. zitteli* and *A. giganteum*) whereas *Arsinoitherium andrewsi* is accepted as
4 a synonym of *A. zitteli* (Andrews 1906; Sanders *et al.* 2004; Al-Sayigh *et al.* 2008).

5
6
7 *Arsinoitherium giganteum* is greater than other embrithopods in molar size (Sanders *et al.*
8
9 2004). *Namatherium blackcrowense* is more primitive than *Arsinoitherium* based on its upper
10 molar and palatal morphology and it represents the oldest embrithopod in Afro-Arabia
11
12 (Pickford *et al.* 2008).

13
14
15 Although fossil finds of embrithopods are more abundant in Afro-Arabia, the oldest described
16
17 representatives appear so far in Eurasia from the middle-late Eocene of Romania with
18
19 *Crivadiatherium mackennai* and *C. iliescui* (Radulesco *et al.* 1976; Radulesco & Sudre 1985;
20
21 Radulesco & Samson 1987) and from the early to late Eocene of Turkey with *Palaeoamasia*
22
23 *kansui* (Ozansoy 1966; Sen & Heintz 1979), *Palaeoamasia cf. kansui* (A. Gül, unpub. data,
24
25 2003) and *Hypsamasia seni* (Maas *et al.* 1998; see Sen 2013 for detailed stratigraphic
26
27 discussion).

28
29
30 Recently, Sanders *et al.* (2014) recorded remains of a possible new species of *Palaeoamasia*
31
32 in the Boyabat Basin (north-central Turkey). These authors claim that it extends the upper
33
34 limit of Eurasian embrithopods up to Eocene–Oligocene boundary with a robust stratigraphic
35
36 sampling. Besides, they consider, based on the M3 features, that the Boyabat form is
37
38 intermediate between *P. kansui* from Turkey and *Namatherium* and *Arsinoitherium* from Afro-
39
40 Arabia (Sanders *et al.* 2014, p.1159).

41
42
43 Among Embrithopoda, Sen & Heintz (1979) regrouped *Crivadiatherium* and *Palaeoamasia* in
44
45 the new subfamily Palaeoamasiinae in order to distinguish them from the African
46
47 *Arsinoitherium* (Arsinoitheriinae), both in the family Arsinoitheriidae Andrews, 1906 (Sen &
48
49 Heintz 1979; Radulesco & Sudre 1985; Radulesco & Samson 1987; McKenna & Bell 1997).
50
51 The last member of that family *Namatherium blackcrowense* was added by Pickford *et al.*
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53 (2008)
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3 Thereafter, Kaya (1995) elevated Palaeoamasiinae to family rank, Palaeoamasiidae. This
4
5 statement was also supported by several authors: Maas *et al.* (1998) with inclusion of
6
7 *Hypsamasia seni*; Gheerbrant *et al.* (2005a), according to their phylogenetic analysis and
8
9 Sanders *et al.* (2014) with the recent discovery of the latest *Palaeoamasia* specimen from the
10
11 Eocene–Oligocene transition in Turkey.

12
13 *Phenacolophus fallax* Matthew & Granger 1925 from the late Paleocene – early Eocene of
14
15 Gashato Formation (Mongolia) has disputed affinities, being considered either as a basal
16
17 embrithopod (McKenna & Manning 1977), sister group to them (Gheerbrant *et al.* 2005a,
18
19 2014) or not closely related to them (Sen & Heintz 1979; Radulesco & Sudre 1985; Radulesco
20
21 & Samson 1987; Court 1992c; Kaya 1995; Koenigswald 2012; Sanders *et al.* 2014; Mao *et al.*
22
23 2015). For instance, Novacek and Wyss (1986) mentioned a possible close relationship
24
25 between *Phenacolophus* and Tethytheria; McKenna & Bell (1997) regrouped
26
27 Phenacolophidae (*Phenacolophus* + *Minchenella*) and Arsinoitheriidae within Embrithopoda;
28
29 Sen (2013) considered that ‘phenacolophids remain the most likely stem-group for
30
31 embrithopods, if not for all paenungulates’.

32
33 The name Embrithopoda was originally designated to distinguish *Arsinoitherium* from other
34
35 ungulates, and originally as a suborder and it is thought to be derived from a hyracoid stock
36
37 (Andrews 1906, p. xiv). Since then, embrithopods have undergone several systematic
38
39 revisions and their interordinal relationships remain widely unresolved (see Table 2;
40
41 Gheerbrant & Tassy 2009; Sanders *et al.* 2010; Sen 2013).

42
43 Although embrithopods were thought to be endemic to Africa, discoveries of early
44
45 embrithopods with more primitive features in the 1970s from older Palaeogene Eurasian
46
47 deposits onward enhanced their possible Eurasian origin (Radulesco *et al.* 1976; McKenna &
48
49 Manning 1977; Sen & Heintz 1979; Radulesco & Samson 1985; Gheerbrant *et al.* 2005b).
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3 In addition, conflicting ideas about their palaeoenvironment and lifestyle, which would favour
4 our understanding of their dispersals on both sides of Neo-Tethys, remain unresolved (Sen
5 2013). According to some authors, embrithopods were land-dwellers (Andrews 1906; Thenius
6 1969; C. Delmer, unpub. data 2005; Clementz *et al.* 2008) or they had a semi-aquatic lifestyle
7 for others (Moustapha 1955; Sen & Heintz 1979; Court 1993; Rose 2006; Hutchinson *et al.*
8 2011). However, Sanders *et al.* (2004) refused rigorously that embrithopods were semi-
9 aquatic considering their ability to disperse to highland terrestrial habitats in Ethiopia.

10
11 In this paper, we describe a new material of *Palaeoamasia kansui* from the type locality Eski-
12 Çeltek (Amasya, Turkey) and propose a coherent and neat dental terminology for all
13 embrithopods (Fig. 2). We also provide the first exhaustive phylogenetic analysis of
14 embrithopods at the species level with a relatively restricted taxonomic sample in order to
15 improve the position of *Palaeoamasia* within Embrithopoda, based on cranial, mandibular,
16 and dental characters. In addition, we tentatively reinvestigate the supraordinal phylogenetic
17 position of embrithopods among fossil ungulates. For this, we include all embrithopod species
18 to the data matrix of Tabuce *et al.* (2007) wherein *Arsinoitherium zitteli* was the only
19 representative of the order. Finally, we question their origin and dispersal modalities in the
20 light of phylogenetic results obtained.

21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 **MATERIAL AND METHODS**

44 45 *Comparison material*

46
47 The new material of *Palaeoamasia kansui* from Eski-Çeltek (Amasya, Turkey) is directly
48 compared to published material of the same species by Ozansoy (1966, fig. 3–4) and Sen &
49 Heintz (1979) (MNHN-EÇ-1, left mandibular fragment bearing highly damaged trigonid of
50 m1, m2 and m3; MNHN-EÇ-4, palate fragment bearing left P3–M3 and right P4–M1; MTA-
51 1770, right maxillary with P4–M2; MTA-1771, left mandibular with m1–m3; MNHN-EÇ-3,
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3 left mandibular with m2–m3 of which crowns are broken; MNHN-EÇ-2, left mandibular with
4
5 m3) stored in Muséum National d’Histoire Naturelle, Paris (France) and Mineral Research
6
7 and Exploration Institute, Ankara (Turkey). We followed the descriptions of Kaya (1995), A.
8
9 Gül, unpub. data (2003) and Sanders *et al.* (2014) for the material of *Palaeoamasia* stored in
10
11 Museum of Natural History of Ege University (Turkey), Ankara University (Turkey) and
12
13 University of Michigan, respectively.

14
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16 The new material is also compared to casts of (1) *Hypsamasia seni* Maas, Thewissen &
17
18 Kappelman, 1998 from the late Paleocene – early Eocene of Haymana-Polatlı Basin, Turkey
19
20 (right P2–P3, fragments of right P4 and M1, central portion of left M1, mesial half of M2;
21
22 fragment of M3 in eruption; Maas *et al.* 1998); (2) *Crivadiatherium mackennai* Radulesco,
23
24 Iliesco & Iliesco, 1976 from the middle Eocene of Hateg depression, Romania (isolated left
25
26 p4–m1; Radulesco *et al.* 1976); (3) *Crivadiatherium iliescui* Radulesco & Sudre, 1985 from
27
28 the same locality and age as *C. mackennai* (right m2–m3, left p2–p4, left m2–m3; Radulesco
29
30 & Sudre 1985; Radulesco & Samson 1987); (4) *Arsinoitherium zitteli* Beadnell, 1902 from the
31
32 early Oligocene of Fayum, Egypt (left P2–4 and p2–4; Andrews 1906; Court 1992b).

33
34
35 Based on the descriptions and illustrations available in literature, new material is compared to
36
37
38 (4) the skull and complete dentition of *Arsinoitherium zitteli* (Andrews 1906; Court 1992b,
39
40 1992c), (5) M2–M3, p4 and m2–m3 of *Arsinoitherium giganteum* Sanders, Kappelman &
41
42 Rasmussen, 2004 from the late Oligocene of Ethiopia (Sanders *et al.* 2004), (6) the
43
44 fragmented skull bearing right P3–M3 and left M1–M3 of *Namatherium blackcrowense*
45
46 Pickford, Senut, Morales, Mein & Sanchez, 2008 from the middle Eocene of Namibia
47
48 (Pickford *et al.* 2008) and (7) right maxillary fragment with M2–M3 of the youngest
49
50 *Palaeoamasia* from the Eocene–Oligocene transition of Boyabat Basin, Turkey (Sanders *et al.*
51
52 2014). P2–P4 and p2–m3 of a putative embrithopod (*sensu* McKenna & Manning 1977)
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54
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56 *Phenacolophus fallax* Matthew & Granger, 1925 from the late Paleocene – early Eocene of
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3 Mongolia is also included in this study (Matthew & Granger 1925; McKenna & Manning
4
5 1977).

6
7 The earliest known proboscideans *Phosphatherium escuilliei* Gheerbrant, Sudre & Cappetta,
8
9 1996 (earliest Eocene of Morocco; Gheerbrant *et al.* 1996, 1998, 2005a; stem proboscidean
10
11 *sensu* Benoit *et al.* 2016 and Cooper *et al.* 2014) and *Eritherium azzouzorom* Gheerbrant,
12
13 2009 (late Paleocene of Morocco; Gheerbrant 2009; stem paenungulate *sensu* Cooper *et al.*
14
15 2014), and a hyracoid, *Seggeurius amourensis* Crochet, 1986 (early Eocene of El-Kohol,
16
17 Algeria; Court & Mahboubi 1993) were added in our cladistic analyses as ‘branching group’
18
19 (*sensu* Antoine 2002 and Orliac *et al.* 2010). *Arsinoitherium andrewsi* Lankester, 1903 is
20
21 considered as a synonym of *A. zitteli*, the differences between them being due to sexual
22
23 dimorphism or intraspecific variation (Andrews 1906; Sanders *et al.* 2004; Al-Sayigh *et al.*
24
25 2008). Three genera of Perissodactyla are chosen for the outgroup, namely *Xenicohippus* (*X.*
26
27 *grangeri* Bown & Kihm, 1981; *X. craspedotum* Cope, 1880; *X. osborni* Bown & Kihm, 1981
28
29 from the early Eocene of United States), *Arenahippus* (*A. grangeri* Kitts, 1956; *A. aemulor*
30
31 Gingerich, 1991; *A. pernix* Marsh, 1876 from the early Eocene of United States) and
32
33 *Radinskya* McKenna, Chow, Ting & Luo, 1989 from the late Paleocene of China.
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40 41 *Methods*

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43 In association with detailed observations on specimens and bibliographical researches, 130
44
45 morphological characters (10 cranial-mandibular, 120 dental; see Appendix 1) were coded for
46
47 14 terminal taxa and a data matrix was generated using Nexus Data Editor v.0.5.0 software
48
49 (Page 2001; see Appendix 2). Among characters, 81 were chosen from the literature and either
50
51 used directly or modified for coding. Each character unused in previous phylogenetic analyses
52
53 is considered new and mentioned with an asterisk in character listing. Within terminal taxa,
54
55 *Xenicohippus*, *Arenahippus*, and *Radinskya* constitute the outgroup, *Seggeurius amourensis*,
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3 *Eritherium azzouzorum*, *Phosphatherium escuilliei*, and *Phenacolophus fallax* form the
4
5 ‘branching group’, and seven undisputable embrithopod taxa form the in-group. Cladistic
6
7 analyses are fulfilled via PAUP 3.1.1 (Swofford 1993) and Winclada v.1.00.08 (Nixon 1999)
8
9 softwares.

10
11 A new and neat dental terminology is proposed and illustrated in Figure 2 for upper/lower
12
13 premolars and molars of embrithopods by combining descriptions in previous works of
14
15 McKenna & Manning (1977), Sen & Heintz (1979), Iliescu & Sudre (1985), Court (1992b),
16
17 Maas *et al.* (1998), Sanders *et al.* (2004), and Pickford *et al.* (2008).
18
19

20 21 22 23 *Abbreviations*

24
25 *Institutional abbreviations.* ITU, Istanbul Technical University (Turkey); MNHI, Museum of
26
27 Natural History of Ege University, Izmir (Turkey); MNHN, Muséum National d’Histoire
28
29 Naturelle, Paris (France); MTA, Mineral Research and Exploration Institute, Ankara (Turkey);
30
31 UM2, Université Montpellier 2 (France); ISEM, Institut des Sciences de l’Evolution de
32
33 Montpellier (France).
34
35

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37
38 *Anatomical abbreviations.* L, length (mesio-distal); mes. W, mesial width; dis. W, distal
39
40 width. Upper/lower teeth are mentioned in capital/lower-case letters, respectively: I/i, incisor;
41
42 C/c, canine; P/p, premolar; M/m, molar; D/d, deciduous tooth.
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49 50 **SYSTEMATIC PALAEONTOLOGY**

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52 The supraspecific systematic here below follows the results of the current phylogenetic
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54 analyses.
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3 Unranked clade PAENUNGULATA Simpson, 1945

4
5 Order EMBRITHOPODA Andrews, 1906

6
7 Family ARSINOITHERIIDAE Andrews, 1904

8
9 Subfamily PALAEOAMASIINAE Sen & Heintz, 1979

10
11
12
13 Genus PALAEOAMASIA Ozansoy, 1966

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17
18 *Type species.* *Palaeoamasia kansui* Ozansoy, 1966; the only species of the genus from the
19 type locality, Eocene lignites of Eski-Çeltek, Amasya, Turkey.
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23
24
25 *Palaeoamasia kansui* Ozansoy, 1966

26
27 (Fig. 3)

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31
32 *Type material.* MNHN-EÇ-1, a left mandibular fragment bearing m1 with highly damaged
33 trigonid, better preserved m2 and m3 which is assigned as holotype by Sen & Heintz 1979.

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35
36 *Remarks.* The m3 of the holotype lacks the talonid today but it was illustrated by Ozansoy
37 (1966, figs 3–4).
38
39

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42
43 *New material.* From the type locality, fragment of palate with left P2–P3 (ITU-EÇ-8); right
44 P4–M2 (ITU-EÇ-7); isolated M3 (MNHN-EÇ-6); mandibular fragment with left p2–m1
45 (ITU-EÇ-9); mandibular fragment with right p4–m1 (MNHN-EÇ-5) (Fig. 3C–L).
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51
52 *Occurrence.* Between the late Paleocene and the Eocene–Oligocene transition in Turkey for
53 the genus *Palaeoamasia* (Ozansoy 1966; Sen & Heintz 1979; Kazanci & Gökten 1986; Kaya
54 1995; Koc & Türkmen 2002; Ladevèze *et al.* 2010; Métais *et al.* 2012; Sanders *et al.* 2014).
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DESCRIPTIONS

The dentition of the new material of *Palaeoamasia kansui* is mesodont with cusps, lophs and lophids are broad and transversally arranged. The enamel is corrugated and moderately thick (1.6 mm). See Figure 2 for dental terminology and Table 3 for dental measurements.

Upper dentition

Upper premolars. Lack of wear on the mesial side of P2 might indicate the presence of a diastema between P1 and P2 (as in the lower dentition) or the absence of P1. P2–P4 have at least three roots. The size of premolars increases from P2 to P4. The occlusal outline of P2 is triangular while P3 and P4 are squarish. Hence, the preprotocrista of P2 is more distolingually slanting and the protocone has a much more backward position. Premolars are tribosphenic with a strong ectoloph. The hypocone is absent on all premolars although P3 and P4 have an entoloph formed by the postprotocrista (*sensu* Court 1992b). The tooth wear is more pronounced distally. The paracone is higher than the other cusps on P2 and P3. On the other hand, the apex of the crown on P4 is located in the middle of the ectoloph. The protocone on P2 is lower than the paracone, which is less clear on P3–P4. The preprotocrista is interrupted on the lingual base of the paracone on all premolars and it represents the mesial end of the mesio-distal valley, which is followed up to the distal cingulum. This valley (less pronounced on P2) divides P3–P4 into labial and lingual lophs. In mesial view on P2 and P3, the mesial cingulum is sinuous and gets lower at the level of incomplete junction between the preprotocrista and the paracone, which is not the case on P4.

On P2 (ITU-EÇ-8), the mesial cingulum continues distolingually, parallel to the preprotocrista and it disappears on the lingual face of protocone (Fig. 3C). In occlusal view, this cingulum seems to be weak and very close to the mesial wall. At the connection between the parastyle

1
2
3 and the mesial cingulum, the wall is lightly deflected. The parastyle is individualised by a
4
5 small groove in front of the paracone. The labial wall is weakly convex mesio-distally. The
6
7 distal cingulum was probably continuous (one available P2, this part is overlapped by P3).
8
9 On P3 (ITU-EÇ-8), the mesial cingulum merging from the parastyle is stronger and less
10
11 sinuous than that of P2 (Fig. 3C). It forms a fossette on the mesio-lingual side of the
12
13 protocone, which is different from P2. A subvertical and quite deep mesio-labial fossette can
14
15 be observed at the mesio-lingual junction between the parastyle and paracone. It is much more
16
17 distinct than on P2. At the disto-lingual angle, the distal cingulum is strong and labio-distally
18
19 oriented. It is fused with the postprotocrista and continues buccally to form the distal wall.
20
21 P4 (ITU-EÇ-7) is like an enlarged version of P3 (Fig. 3E). However, in occlusal view, it is
22
23 more developed labiolingually compared to P3, although it does not show a trend to
24
25 molarization. The parastyle and metacone are fully joined to the paracone to form a strong
26
27 ectoloph. The parastyle is mesio-labially elongated and reinforces the depth of the labial
28
29 groove. Finally, the labial wall is slightly more undulated than on the more anterior premolars.
30
31 The mesial cingulum connects with the parastyle, and it is more robust and stronger than on
32
33 P3, particularly at the mesio-lingual angle (mesio-lingual fossette).
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40
41 *Upper molars.* Each molar has four roots and is bilophodont: The paracone is fused with the
42
43 parastyle forming a protoloph, and the metacone is fused with the metastyle forming a
44
45 metaloph. The protocone and hypocone are isolated from the other cusps on unworn teeth.
46
47 The ectoloph is absent on all molars. M1 is much smaller than M2 and M3 (Table 3). M3 is
48
49 slightly larger than M2 although both have a metaloph similar in size because of distal
50
51 narrowing of M3. In occlusal view, the lophs are oblique mesiolabially. In labial view, the
52
53 lophs are inclined mesially from the basis towards the apex. In relation to occlusal wear, the
54
55 distal wall of each loph is much higher than the mesial walls. In occlusal and labial view, the
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2
3 mesial loph is thicker than the distal one on M2 and especially remarkable on M3. On M1,
4
5 high wear degree makes it difficult to observe. Due to tooth wear, the postprotocrista appears
6
7 to run in a distolabial direction. The mesial and distal cingulums are strong. The labial
8
9 cingulum is absent and the lingual cingulum is poorly developed, interrupted on the lingual
10
11 face of each cusps. On M2 and M3, a crista obliqua ('centrocrista' *sensu* Maas *et al.* 1998;
12
13 'postparacrista' *sensu* Court 1992b; 'premesostylecrista' *sensu* Pickford *et al.* 2008; we follow
14
15 in this study the term "postparacrista" for upper molars) links the middle of distal face of the
16
17 protoloph to one third of the labial side of mesostyle. This crista separates the strong lingual
18
19 groove from the labial groove.
20
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22
23 M1 (ITU-EÇ-7) is partially damaged and has a very advanced wear level (Fig. 3E). The
24
25 postprotocrista is very large and reaches the metaloph. A short cingulum leads to the
26
27 hypocone (shattered) and disappears on the distal wall basis of the protocone. The metastyle is
28
29 preserved despite of strong wear, just as a relic of the cingulum on the mesiolingual angle.
30

31
32 On M2 (ITU-EÇ-7), the postparacrista connecting the two lophs reaches the occlusal surface
33
34 of the protoloph (Fig. 3E). This crest is worn revealing a dentine strip. The distolingual angle
35
36 of the tooth is broken and it is interrupted at the base of the metastyle, preventing observation
37
38 of the distal cingulum and whether it continues up to the hypocone or not. The lingual
39
40 cingulum descends from the hypocone and continues toward the flank of the protocone.
41

42
43 Following an interruption, this cingulum reappears on the mesiolingual angle of the protocone
44
45 and becomes labially more marked as a strong mesial cingulum and joins the parastyle. In this
46
47 configuration it forms a deep fossette.
48

49
50 M3 (MNHN-EÇ-6), less worn than M1 and M2, is well preserved although the parastyle and
51
52 the apex of the metastyle are damaged (Fig. 3G). It exhibits the same features as M2, though
53
54 the M3 is distally narrower. A strong and broad mesial cingulum is present between the
55
56 lingual edge of the protocone and parastyle. On its lingual third, this cingulum becomes
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3 broader with wear. The boundary of a concave valley is marked by this cingulum and the
4
5 mesial wall of the protocone. The lingual cingulum is continuous between the base of the fold
6
7 of the protocone and mesiolingual side of the hypocone. On the distal side of the tooth, a
8
9 strong postmetacrista joins the thick distal cingulum. The latter surrounds the distolingual
10
11 angle, reaches the lingual side of hypocone, and is buccally interrupted at the level of the
12
13 distal fold of the mesostyle. It forms also a deep distolingual fossette.
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16 17 18 *Mandible* 19

20 The left mandible (ITU-EÇ-9; Fig. 2H–J) bears a p2–m1 series and two distinct alveoli in
21
22 front of p2, which corresponds respectively to a strong canine and to a one-rooted p1. These
23
24 alveoli are separate from each other by a diastema. The canine alveolus is well developed,
25
26 protruding and transversely oblate (approximate length and width are 14.8 mm and 10.7 mm,
27
28 respectively). The canine was probably extending at least until the level of mesial root of p2.
29
30 The distal edge of the canine alveolus is also separate by a 10 mm-long diastema from the
31
32 alveolus of p1. A circular alveolus (width 4.3 mm; depth 6 mm) situated at 8.5 mm mesial to
33
34 p2 root proves unquestionably the presence of a p1.
35
36

37
38 The mandibular symphysis, broken at its rostral part (no incisor alveolus is preserved),
39
40 displays the same obliquity as the canine. The distoventral edge reaches the anterior root of
41
42 p3. In occlusal view, the inter-mandibular angle is very narrow (*c.* 15°). There are two
43
44 depressions, round and superficial, on the buccal side of the mandible: one below the limit of
45
46 p2–p3 and the second straight below the distal lophid of p3. They are bite marks from a
47
48 predator/scavenger. The mental foramen and accessory foramina are not preserved.
49
50

51 52 53 *Lower dentition* 54 55 56 57 58 59 60

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3 *Lower cheek teeth.* ITU-EÇ-9 preserves a p2–m1 series, with a highly worn m1, and MNHN-
4 EÇ-5 (Fig. 3K–L) preserves p4–m1, with a broken talonid of p4. All preserved cheek teeth
5 display unilateral hypsodonty (*sensu* Radulesco *et al.* 1976). The labiolingual width of teeth
6 and the molarization level increase from p2 to m1 ('série oblongue' *sensu* Radulesco & Sudre
7 1985). p3 and p4 are molarized. Due to wear, the trigonid of p2–p3 appears to be greater in
8 dimension and much higher than the talonid in lateral view. On m1, the trigonid and talonid
9 are equally developed. Premolars and molars are two-rooted.
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21 *Lower premolars.* The cristid oblique links the hypolophid to the protolophid and is centered
22 labio-lingually on p3–p4. It becomes more slanting from p2 to p4, with the labiolingual
23 widening of the corresponding teeth. The labial groove arises from the distal part of the
24 crown, just above the distal root; it slants mesiodorsally and reaches the distal side of the
25 metaconid. The width and the depth of that groove increase from p2 to p4, thus, it determines
26 a W-shape in occlusal view, formed by the junction of protolophid, cristid oblique and
27 hypolophid; this W-pattern of the occlusal surface accentuates from p2 to p4. Wear facets are
28 labio-disto-ventrally oriented on premolars. The degree of wear increases from p2 to p4. The
29 lingual or labial cingulids are absent on premolars. On the lingual side, the absolute height of
30 the metaconid increases from p2 to p4, until it exceeds the paraconid level on p4 (ITU-EÇ-9).
31 The mesiolabial side of trigonid is convex and occupies a wider place than the talonid.
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3 contact with paralophid of p3). However, a small distolingual fossettid forms a superficial
4
5 depression, which is homologous to the valley of the talonid on p3–p4. On p2, the protoconid
6
7 is much higher than the metaconid, contrary to what occurs on p3 and p4.
8

9
10 On p3, the occlusal outline is more sinuous. The protolophid connects the protoconid to the
11
12 metaconid. The paraconid is slightly connected to the protoconid by a paralophid that is
13
14 oriented labiodistally. The metaconid and paraconid have equivalent height whereas the
15
16 protoconid, entoconid and hypoconid are much lower. The lophid that connects the hypoconid
17
18 to the entoconid (hypolophid) is projected over by the paralophid of p4. The mesiolingual
19
20 fossettid is as strong as on p2; the distolingual fossettid is much more developed compared
21
22 with p2. The entoconid forms a notch by its ventrolingual elongation (lingual groove of
23
24 angular talonid in occlusal view).
25

26
27 The p4 (ITU-EÇ-9) has clearly individualised cusps, foreshadowing the morphology of
28
29 molars. The paralophid is oriented mesially (Fig. 3H). The mesiolingual fossettid is wider and
30
31 deeper as compared to the previous premolars. As in the molars, the metaconid is very spread
32
33 lingually, pointed mesiodistally and inclined mesiodorsally in lingual view. The distolingual
34
35 fossettid is semi-circular, wide and deep. The mesiolabial side of the protoconid is faintly
36
37 depressed. In lingual view, the distal walls of the metaconid and the mesial wall of the
38
39 entoconid display a symmetric ‘V’ shape, whereas in occlusal view it designs a wide ‘U’. The
40
41 length of the talonid is similar to that of the trigonid in occlusal view. The p4 on the specimen
42
43 MNHN-EÇ-5, although less worn, perfectly matches that of ITU-EÇ-9 (Fig. 3K). The labial
44
45 wall of the protoconid is much convex and depressed on its mesiolabial side. Contrary to ITU-
46
47 EÇ-9, the protoconid is much more elevated than the paraconid and this latter is slightly lower
48
49 than the metaconid (broken). This observation leads us to deduce that wear decreases the size
50
51 of the protoconid more than the other cusps. A narrow postprotocristid continues vertically
52
53 until the middle of the distal side of trigonid, where it joins the rest of the cristid oblique.
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5 *Lower molars.* The m1 (ITU-EÇ-9) is distally broken (talonid), highly worn, and it provides
6
7 less information than the m1 of the specimen MNHN-EÇ-5. This latter specimen is well
8
9 preserved except for the slightly damaged entoconid and distal cingulid. The trigonid and
10
11 talonid are equivalent in size. The labial groove, relatively parallel to the mesial and distal
12
13 lophids, is situated on the middle of the roots in dorsoventral axis. This groove is
14
15 mesiodorsally oblique in labial view. The mesial cingulid is continuous. The distal cingulid is
16
17 restricted on the distal wall and rises labiolingually, parallel to the neck (*cervix dentis*).
18
19 Unilateral hypsodonty of the crown is salient. A very narrow paralophid is oriented
20
21 labiolingually. The metaconid is well defined on the lingual side and, together with the
22
23 metalophid, it surrounds a small superficial mesial fossettid. The cristid oblique rises distally
24
25 to the metaconid and continues distolabially towards the middle of the hypolophid. The
26
27 enamel wear facets are distinguishable on the distal side of the lophids, and are labiolingually
28
29 elongated and nearly vertical. The lingual groove is distolingually oriented in occlusal view
30
31 and 'V' shaped in lingual view. The metaconid, stronger than entoconid in lingual view, is
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33 slightly depressed on the mesiolingual side.
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40 **COMPARISON AND DISCUSSION**

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42 The dental terminology is illustrated in Figure 2, dental measurements of the new material of
43
44 *P. kansui* in addition to *Hypsamasia* and *Crivadiatherium*, are given in Table 3 and mean size
45
46 values distribution of studied taxa in length/width diagrams are available in Figure 4. Mean
47
48 values are in Appendix 3.
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54 **Remark.** Gheerbrant *et al.* (2005a) consider the upper molar lophids not as 'real' lophids. We
55
56 follow the definition of Court (1992b) in considering the upper molar lophids as derived from a
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3 hyper-dilambdodonty on which labial cusps immigrate lingually with the postparacrista *sensu*
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5 Court (1992b) (ectoloph *sensu* Gheerbrant *et al.* 2005; centrocrista *sensu* Maas *et al.* 1998)
6
7 and with the postmetacrista. Therefore, the lophs of embriothopod cheek teeth are named here
8
9 as ‘pseudolophs’ and even the anterior pseudolophs on upper molars are formed with labial
10
11 migration of paracone and thus, should be named as paraloph, we use the term protoloph to
12
13 avoid any nomenclature conflict.
14
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16 17 18 *Comparison with Palaeoamasia kansui*

19
20 The large majority of morphological features studied here are identical to those of the
21
22 holotype and of other specimens of *Palaeoamasia kansui* described by Sen & Heintz (1979):
23
24 presence of an entoloph on P3–P4, parastyle very distinct and more labially located in
25
26 comparison to the rest of the ectoloph, and the presence of a strong mesial cingulum and of a
27
28 preprotocrista having an equivalent length to postprotocrista on P4. Also, on upper molars, the
29
30 mesial cingulum is reduced, the presence of ‘pseudolophs’ coincides with the lingual
31
32 migration of labial cusps (‘hyper-dilambdodonty’ *sensu* Court 1992), the postparacrista is very
33
34 distinct, the lophs are mesio-ventrally inclined, the postparacrista and postmetacrista are
35
36 present on the distal wall of pseudolophs.
37
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39
40 Molarization of p4 is remarkable. Lower premolars lack cingulids, their lophids are separated
41
42 by an oblique labial groove and the lingual fossettid of the talonid is larger and deeper than
43
44 the one on the trigonid. Thus, attribution of the new material to *P. kansui* is well supported.
45
46

47 A few rare differences observed between the new specimens and those previously described
48
49 by Sen & Heintz (1979) are mainly due to different wear stages and on individual variation.
50

51 For instance, the teeth display dimensions comparable or slightly smaller than the previously
52
53 described material of *P. kansui* (Fig. 4A and Appendix 3; Sen & Heintz 1979; Kaya 1995; A.
54
55 Gül, unpub. data, 2003; Sanders *et al.* 2014). P4 of ITU-EÇ-7 (Fig. 3E) displays a large
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3 mesio-distal valley that prevents a connection between paracone and preprotocrista (fused on
4 hypodigm). Labio-lingual width of M1 (ITU-EÇ-7) is greater than P4 while those dimensions
5 are similar on MNHN-EÇ-4 (Sen & Heintz 1979).
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9 On M2, the labial groove is shallower than other *P. kansui*, the crista oblique joins the
10 protoloph, the surface of the loph is wider and the protocone is fused to the protoloph. On
11 M3 (MNHN-EÇ-6; Fig. 3G), the crista oblique and postmetacrista are stronger, the protocone
12 is completely integrated into the protoloph and the postprotocrista is more distinct. The distal
13 cingulum on new specimens connects to the mesostyle fold and the mesial cingulum does not
14 join the lingual cingulum (interruption at lingual level of protocone). The p4 of ITU-EÇ-9
15 (Fig. 3H) differs from other specimens by a larger trigonid than talonid in size (Sen & Heintz
16 1979, plate 3).
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29 *Comparison with a younger Palaeoamasia from Boyabat*

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31 In a recently published paper of Sanders *et al.* (2014), new *Palaeoamasia* remains are
32 reported from the Cemalettin Formation of Boyabat Basin (Turkey). So far, they represent the
33 youngest specimens referable to *Palaeoamasia* (and to an embrithopod outside of Afro-
34 Arabia, in general). As these authors, we agree on highly similar occlusal features of the only
35 available material, M2–M3 (BOY-2) and ?incisor (BOY-1). Also, measurement ranges are
36 very close, especially with that of *P. kansui* specimens from the type locality Eski-Çeltek
37 (Amasya, Turkey; Fig.4A and Appendix 3). However, the specimen BOY-2 is considered as
38 documenting an unnamed new species of *Palaeoamasia*, depending on four M3 features,
39 intermediate between those of *P. kansui* on the one hand and those of *Namatherium* and
40 *Arsinoitherium* on the other hand (Sanders *et al.* 2014, p.1159).
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56 *Comparison with Hypsamasia seni*

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3 Upper premolars and molars of *H. seni* (only known teeth) are 15–30% larger in size (Table 3,
4 Fig. 4) than the ones of new specimens from Eski-Çeltek (*P. kansui*). P2 of *P. kansui* differs
5 from those in *H. seni* in some features, such as: preprotocrista is not curved, the parastyle is
6 smaller and much closer to paracone, the parastylar cingulum (mesial) is less individualised
7 and has a rather triangular shape. The mesio-distal valley seems narrower in premolars of *P.*
8 *kansui*, the ectoloph is larger and the labial wall is not undulated. On P3, *P. kansui* differs
9 from *H. seni* in the lack of a paraconule, the presence of a shallower depression between the
10 paracone and mesial wall of the parastyle and also by the lack of superficial labial groove at
11 the level of the metacone. The preprotocrista and postprotocrista of P3–4 of *P. kansui* have the
12 same length whereas the preprotocrista is longer on *H. seni*. Upper molars of *P. kansui*
13 possess a lingual cingulum as well as a robust postparacrasta on the distal wall of the
14 protoloph in M2. The latter seems to be greater with a fold labio-ventrally oriented.
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32 *Comparison with Crivadiatherium mackennai and C. iliescui*

33 Both *Crivadiatherium* species are known only by lower dentition. The premolar of
34 *Crivadiatherium iliescui* which is described as a p1 by Radulesco & Sudre (1985) and
35 Radulesco & Samson (1987) is considered in this study as a p2, in agreement with Sen (2013)
36 at least for three reasons; (1) the occlusal wear stage seems to be higher for a p1 especially in
37 comparison with p3, (2) despite of the broken small distal part of that tooth, the distal facet at
38 apical level of the entoconid perfectly contacts the mesial facet of the paralophid on p3, and
39 (3) the mesio-distally increasing size of teeth, i.e. from p2 to p4, as observed in other
40 embrithopod species, such as *Palaeoamasia kansui*. Thus, it is possible to compare the p4–m1
41 series of *P. kansui* with that of *C. mackennai* and the p2–m3 series with that of *C. iliescui*.
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52 Lower premolars of *P. kansui* (ITU-EÇ-9, Fig. 3H) are distinguished from those of
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Crivadiatherium by their noticeably smaller size (Table 3, Fig. 4B and Appendix 3) and much

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3 lower crown, by the W-shape of lophids, by the absence of labial and lingual continuous
4
5 cingulids, and by less elongated trigonids and talonids. In labial view, the labial groove is
6
7 slanting mesio-lingually (vertical in *Crivadiatherium*). Cusps of p2 are mesio-distally aligned
8
9 and individualised in *P. kansui* while in *C. iliescui* they are separate both mesio-distally and
10
11 labio-lingually. In the latter, p2 is buccally shifted on the dental series, which probably
12
13 indicates a post-mortem deformation. The p3 of *P. kansui* has mesio-distally flared crista
14
15 oblique; hypolophid at the entoconid level does not seem to be distally curved as seen in
16
17 *Crivadiatherium iliescui*. On p3–p4, the disto-lingual fossa forms an obvious angle in lingual
18
19 view (V-shaped) as in *C. mackennai*; this angle is less marked in *C. iliescui* (U-shaped). The
20
21 metaconid is more mesio-distally pinched in the p4 of *Palaeoamasia*. The entoconid and the
22
23 talonid are lower in height than the metaconid and trigonid, respectively. The m1 of
24
25 *Palaeoamasia* differs from that of *C. mackennai* in the complete lack of the labial cingulid.
26
27 The mesial cingulid is weaker in *C. iliescui* in which it forms a fossa on the mesio-labial
28
29 angle. The lingual cingulid is absent in *P. kansui* and in *C. iliescui* but present in *C.*
30
31 *mackennai*. The lower molars of *P. kansui* differ from those of *Crivadiatherium* in having the
32
33 labial grooves smaller and shallower, a more mesio-distally compressed crista oblique and
34
35 rather lingually oriented, more transversally oriented lophids, a weaker and more transversely
36
37 oriented paralophid, a short trigonid, more convex lingual walls of the metaconid and
38
39 entoconid, an obvious size increase between m1 and m3 (less clear in *C. iliescui*), trigonid and
40
41 talonid equally developed on m1–m2 (the trigonid is larger than the talonid in
42
43 *Crivadiatherium*), an isolated and weakly developed hypoconulid on m3 (connected to the
44
45 entoconid by lingual and labial cristids in *Crivadiatherium*) and distal inclination of the
46
47 hypoconulid in lingual view.
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56 *Comparison with Arabian-African embrithopods*
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3 The most remarkable differences between *P. kansui* and Arabian-African embrithopods
4 (*Arsinoitherium* and *Namatherium*) are in tooth size and degree of hypsodonty. The latter is
5 less pronounced on *Palaeoamasia* and it becomes more apparent with *Namatherium*,
6
7 *Arsinoitherium zitteli* and *A. giganteum* in parallel with increasing dimensions, respectively.
8
9 However, while P3–M1 of *Namatherium* are overlapping more or less with the size range of
10
11 *Palaeoamasia*, M2 and M3 are slightly larger (Fig. 4A). The premolars and molars of
12
13 *Arsinoitherium* are much larger than those of Eurasian embrithopods, and that discrepancy
14
15 greatly increases for *A. giganteum*, which has teeth larger than in any other taxon (Fig. 4,
16
17 Appendix 3).
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23 In addition, Pickford *et al.* (2008) compared M3 of *Namatherium blackcrowense* with those of
24
25 *P. kansui* and *Arsinoitherium*. They assume that the hypocone would reduce to a lingual
26
27 cingulum fused with the metaloph together with a lingual migration of labial cusps, which is
28
29 noticeable when the hypsodonty degree increases from *P. kansui* towards *Arsinoitherium*
30
31 (Pickford *et al.* 2008, fig. 16A).
32
33

34 Nevertheless, we observe that the hypocone on M3 of *P. kansui* still remains individualised at
35
36 early wear stages and it is at the same height as the metaloph. There is a trend to fusion
37
38 between the hypocone and metaloph in more advanced wear stages. Hereby, it would be more
39
40 parsimonious (*a posteriori*) to assume that the hypocone on M3 is already fused to the
41
42 metaloph rather than a reduction into a cingulum, probably due to increase of hypsodonty
43
44 level without any advanced dental wear occurrence in *Arsinoitherium* and *Namatherium*.
45
46 Finally, in their differential diagnosis, Pickford *et al.* (2008, p. 477) mention the lack of an
47
48 ‘interloph’ crest that serves to distinguish *Namatherium* from *Palaeoamasia*. As we discussed
49
50 earlier for the late *Palaeoamasia* specimen from Boyabat, according to our observation, this
51
52 ‘premesostylecrista’ is homologous to the centrocrista (*sensu* Maas *et al.* 1998).
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3 As to other dental features, *P. kansui* differs from *Arsinoitherium* and *Namatherium*
4
5 *blackcrowense* in having a postmetacrista on upper molars and continuous mesial and lingual
6
7 cingula on M3. *P. kansui* differs from *A. zitteli* and *N. blackcrowense* in having a
8
9 postprotocrista on P3–P4 and a divided lingual root (unknown in *A. giganteum*). *P. kansui*
10
11 differs from *Arsinoitherium* by the presence of a distal cingulum on upper molars, mesio-
12
13 dorsally oblique buccal groove on lower premolars (vertical in *Arsinoitherium*), trigonid much
14
15 higher than talonid in lateral view on p2–p3 and lower molars (height is similar in
16
17 *Arsinoitherium*), molarization of p3 and p4, presence of a mesial cingulid, high position of
18
19 distal cingulids and presence of a cristid oblique at a high position in the middle lingual side
20
21 of trigonid by extending towards the apex of metaconid on lower molars (this cristid oblique
22
23 is relatively low and it extends towards the metaconid base in *Arsinoitherium*), and also size
24
25 increase from m1 to m3 (m2 and m3 have fairly comparable dimensions in *Arsinoitherium*,
26
27 see Fig. 4B).

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31 Regarding the lower jaw, *P. kansui* (Fig. 3H–J) differs from *A. zitteli* in possessing a
32
33 mandibular symphysis oblique anteriorly to the distal edge, at the premolar level (sub-vertical
34
35 anterior to a distal edge at the molar level in *A. zitteli*) and no mandible angular discontinuity
36
37 between the premolar and molar series. Upper premolars of *P. kansui* have a distal cingulum
38
39 and roots higher than crowns (unlike the condition in upper premolars of *A. zitteli*). The P2
40
41 has two labial and one lingual roots, a smooth buccal side (two roots with an undulating side
42
43 in *A. zitteli*) and a straight crest which involves the preprotocrista and protocone (this crest is
44
45 more mesio-lingually convex in premolars of *A. zitteli*). The hypocone is absent on P2–P4; in
46
47 contrast, it is robust in *A. zitteli*. Concerning upper molars, *P. kansui* is distinguished by a
48
49 salient postparacrista (absent in *A. zitteli*), the presence of a postprotocrista and M2–M3 larger
50
51 than the rest of the dental series (size progressively increases from P2 to M3 in *A. zitteli*, Fig.
52
53 4A). As regards lower teeth, *P. kansui* has a canine which is probably caniniform and greater
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3 in size than the incisors (incisiform in *A. zitteli*), a post-canine diastema as well as a diastema
4
5 between p1 and p2 (those diastemas are absent in *A. zitteli*), a lingually shifted metaconid
6
7 which forms a notch on p3 (integrated in the mesio-distal series in *A. zitteli*), a V-shaped
8
9 disto-lingual pit (in lingual view) developed more mesio-distally than its mesial homologous
10
11 on p4 (this fossa is U-shaped and less developed than its mesial homolog in *A. zitteli*).

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14 *P. kansui* differs from *A. giganteum* in the zygomatic process position rising at the level of
15
16 distal loph of M3 (instead of rising at the level of mesial loph in *A. giganteum*) and by the
17
18 absence of a buccal cingulid on the lower premolars, but also regarding crown height.

19
20 Finally, *P. kansui* can be distinguished from *Namatherium blackcrowense* in having a less
21
22 divergent zygomatic arch laterally (very divergent in *N. blackcrowense*), which begins at the
23
24 level of the distal loph of M3 (at the level of M2 in *Namatherium*), a reduced tuber maxillae
25
26 (large in *Namatherium*), no lingual or labial cingulae on upper premolars, and a three-rooted
27
28 P3 (two-rooted in *N. blackcrowense*). On upper molars, *P. kansui* is distinguished by features
29
30 such as the presence of a distolingual cingulum which extends under the hypocone but is not
31
32 connected to the lingual cingulum (connected in *Namatherium*), the absence of a labial
33
34 cingulum and of mesio-ventrally inclined 'pseudolophs' (merged with the occlusal plane in
35
36 *Namatherium*) can distinguish *P. kansui* from *N. blackcrowense*. Last, only M3 of *N.*

37
38
39
40
41 *blackcrowense* lingually outflanks from the dental series due to its greater size. Note that both
42
43 M2 and M3 display that feature in *P. kansui*.

44 45 46 47 *Comparison with Phenacolophus*

48
49 *P. kansui* differs from *Phenacolophus fallax* (Paleocene of Mongolia) in having a zygomatic
50
51 process rising at the level of the distal loph of M3 (at the level of M2 in *Ph. fallax*), an oblique
52
53 orientation of the mandibular symphysis (sub-vertical in *Ph. fallax*), no molarisation, in
54
55 possessing a mesial cingulum but no labial cingulum on upper premolars, in having three-

1
2
3 rooted P2 and P3 (one-rooted P2 and two-rooted P3 in *Ph. fallax*), and an ectoloph on P2–P3.

4
5 The upper premolars of *Ph. fallax* are smaller and more brachydont in comparison to those of
6
7 *P. kansui*. However, upper premolars of *Ph. fallax* are described by McKenna & Manning
8
9 (1977) as ‘very simple’ and the incomplete preservation of the premolars does not allow
10
11 ensuring the presence of an ectoloph in that species. Another character that differentiates *P.*
12
13 *kansui* from *Ph. fallax* is the presence of protocones and postprotocrista in the former.

14
15 However, it should be noted that McKenna & Manning (1977) had considered the mesial
16
17 cusps of P3 in *Ph. fallax* as paracones. We follow that opinion. In addition, *P. kansui* has a
18
19 metacone and a paracone equivalent in size in P3 (metacone smaller than paracone in *Ph.*
20
21 *fallax*). Upper molars of *P. kansui* lack a labial cingulum although it is present in *Ph. fallax*.

22
23 As for the distal cingulum, it is lingually elongated under the hypocone but without any
24
25 continuity with the lingual cingulum, whereas in the Mongolian species, this distal cingulum
26
27 connects to the lingual cingulum. Also, *P. kansui* differs from *Ph. fallax* in having a very
28
29 distinct preparacrista on upper molars (reduced in *Ph. fallax*). The postparacrista connects the
30
31 mesostyle and it is lingually migrated towards the paracone and metacone in *P. kansui*.

32
33 Consequently, the occlusal view of upper molars displays a ‘W’ shape; upper teeth are
34
35 hyperdilambdodont (*sensu* Court 1992b). On the other hand, the paracone and the metacone
36
37 are much closer to the labial side in *Ph. fallax*, which is true also for the postparacrista even if
38
39 the latter is completely connected to mesostyle. Therefore, upper molars of *Ph. fallax* are
40
41 considered by Gheerbrant (2009) as being dilambdodont with a selenodont ectoloph. Conules
42
43 are absent in the upper molars of *P. kansui* and the hypsodonty is unilateral (*sensu* Radulesco
44
45 *et al.* 1976), whereas in *Ph. fallax*, those teeth are brachydont. The postmetacrista is reduced
46
47 in *P. kansui* (well developed in *Ph. fallax*) and M2–M3 are greater in size (Fig. 4, Appendix 3)
48
49 with an outflanking lingual edge on the rest of dental series (only M3 shows those characters,
50
51 while other teeth increase in size progressively and mesio-distally in *Ph. fallax*).

1
2
3 On lower teeth row, *P. kansui* differs from *Ph. fallax* by the presence of c-p1 and (d)p1-p2
4 diastema, a paraconid being in a higher position on occlusal surface (lower in *Ph. fallax*) as
5 well as by a labial groove mesio-dorsally oblique (vertical in *Ph. fallax*) and by the absence of
6 a labial cingulid. The p2 of *P. kansui* is two-rooted (one-rooted in *Ph. fallax*). Molarisation of
7 p3-p4 is marked in *P. kansui* and absent in *Ph. fallax* (p3 is triangular; the talonid is very low
8 on p4 and lower premolars dimensions are remarkably smaller than dimensions of the
9 molars). A hypoconid is present on p3 (absent in *Ph. fallax*) and the metaconid of p4 is
10 lingually isolated in *P. kansui* (integrated to the mesio-distal row in *Ph. fallax*). The p4 of *P.*
11 *kansui* can be distinguished from *Ph. fallax* by the absence of mesial and distal cingulids,
12 similar height of trigonid and talonid (talonid is much lower in *Ph. fallax*) and presence of a
13 mesostylid.

14
15
16 Lower molars of *Ph. fallax* are considered here as having a bunodont-lophodont structure, in
17 contrast to those of *P. kansui* (as in Sen & Heintz 1979, *contra* Gheerbrant *et al.* 2005a). *Ph.*
18 *fallax* differs from *P. kansui* in having cusps more distinct (not fused in lophids) together with
19 lower and less lophoid crests. The mesial cingulid of lower molars in *P. kansui* is poorly
20 developed, whereas in *Ph. fallax*, that cingulid is strong and forms a fossa on the mesio-labial
21 angle. Specimens of *Palaeoamasia* from Turkey differ also from *Ph. fallax* by the absence of
22 a labial cingulid and entocristid, a highly reduced postmetacristid (the latter is distinct and
23 more or less convex into metastylid in *Ph. fallax*), by the presence of a mesostylid and of a
24 paraconid fused to paralophid (paraconid well discriminated in *Ph. fallax*). The paralophid of
25 *P. kansui* is situated on a short trigonid and noticeably mesio-distally compressed while in *Ph.*
26 *fallax* that seems to be more developed and functional on a more mesio-distally dilated
27 trigonid. The trigonid and talonid of *P. kansui* have a comparable size in m1-m2 in occlusal
28 view, while in *Ph. fallax*, the talonid, bearing a distal cingulid, is larger than the trigonid. The
29 cristid oblique has a high position in *P. kansui* (low in *Ph. fallax*). It reaches nearly the apex of
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3 the metaconid, while *Ph. fallax* possesses a cristid oblique mesially elongated towards the half
4
5 width on the trigonid distal wall and increasingly more mesially oriented from m1 to m3. We
6
7 note that the height of the trigonid is greater in size in comparison to that of the talonid in *Ph.*
8
9 *fallax*, although this difference is less remarkable in *P. kansui*.
10

11 12 13 14 **PHYLOGENETIC RELATIONSHIPS**

15
16 Cladistic analyses are performed by using two methods; ‘Branch and Bound’ in PAUP 3.1
17
18 (Swofford 1993) and heuristic search in Winclada 1.00.08 (Nixon 1999), both using
19
20 unweighted parsimony, based on 130 cranial-mandibular and dental characters (Appendix 1)
21
22 and 14 terminal taxa (Appendix 2). *Xenicohippus*, *Arenahippus* (Perissodactyla) and
23
24 *Radinskya* (either closely related to perissodactyls or belonging to phenacodontid
25
26 “condylarths”; Rose *et al.* 2014) are considered as outgroups. Also, one hyracoid and two
27
28 proboscideans from the Paleocene–Eocene are added as terminals into the cladistic analysis as
29
30 forming a ‘branching group’ (*sensu* Antoine 2002 and Orliac *et al.* 2010).
31
32

33
34 We obtained in PAUP 3.1.1 ten equally parsimonious phylogenetic trees with a branch length
35
36 (L) of 237 steps, consistency index (CI) = 0.603 and retention index (RI) = 0.612, which
37
38 coincide only with six distinct topologies, all four other trees depicting alternative
39
40 synapomorphy distribution. Winclada 1.00.08 displayed six equally parsimonious topologies
41
42 with same lengths and indices as in PAUP 3.1.1 (L=237, CI=0.60; RI=0.61). The strict
43
44 consensus tree is shown in Figure 5. The list of unambiguous apomorphies (synapomorphies
45
46 and autapomorphies) and their distribution on the nodes of the strict consensus tree are given
47
48 in Table 4. The complete distribution list of phylogenetic character is provided in Appendix 4.
49
50 Most parsimonious topologies are not very contradictory since a single polytomy is observed
51
52 within the in-group, involving embrithopods from Turkey and Romania (node 9:
53
54 [*Palaeoamasia kansui*, *Hypsamasia seni*, *Crivadiatherium iliescui*, *C. mackennai*]).
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3 Since one of the purposes of this paper is to check phylogenetic position of *Palaeoamasia*
4 within other embrithopods, more specifically within Palaeoamasiinae following the consensus
5 tree, five alternative topologies restricted to that group obtained by PAUP 3.1.1 are illustrated
6 in Figure 6 and discussed further.
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11 12 13 14 *Strict consensus tree and character distributions*

15
16 The strict consensus of ten equally parsimonious trees provides a topology with L=243 steps,
17 CI=0.588 and RI=0.587 (Fig. 5). Among 130 characters included into analysis, 20 are not
18 informative: eight autapomorphies are ambiguous (char. 4, 8, 19, 34, 42, 52, 76, 95) and 12
19 are unambiguous (char. 13, 23, 27, 32, 37, 77, 86, 93, 103, 110, 124, 130). Only 44
20 synapomorphies are unambiguous, of which 11 are homoplastic (<RI=1).
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27 The node 2 involves all in-group taxa. It is robust according to Bremer indices [BI=5]
28 (Bremer 1994). The present taxonomic sample allows us to assimilate that node to
29 Paenungulata, as [Embrithopoda, [Hyracoidea, Proboscidea]]. According to some authors, the
30 phylogenetic relationships among living representatives of Paenungulata are [Hyracoidea,
31 [Proboscidea, Sirenia]] (Meredith *et al.* 2011; Springer *et al.* 2011). On the other hand,
32 embrithopods are strictly related to Tethytheria (either to Proboscidea or to [Proboscidea +
33 Sirenia]) and not to hyracoids as a result of previous studies (Court 1992c; Gheerbrant *et al.*
34 2005b; Tabuce *et al.* 2008; Gheerbrant & Tassy 2009). Rose *et al.* (2014) did not include any
35 embrithopod in their phylogenetic analysis, but the interordinal relationships they recovered
36 within “ungulates” are [[Perissodactyla, Cambaytheriidae], [Phenacodontidae, [Hyracoidea,
37 Proboscidea]]], where the clade Hyracoidea + Proboscidea encompasses Afrotheria.
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54 The basal clade within the in-group (node 5) corresponds to [Embrithopoda + *Phenacolophus*
55 *fallax*]. Interestingly, *Phenacolophus* was considered as an embrithopod by McKenna &
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3 Manning (1977) based on one synapomorphy (weakly developed hypoconulid on m3). This
4
5 hypothesis is far to be in agreement for some authors (Sen & Heintz, 1979; Radulesco &
6
7 Sudre, 1985; Radulesco & Samson, 1987; Court, 1992c; Kaya 1995; Koenigswald 2012;
8
9 Sanders *et al.* 2010, 2014 and Mao *et al.* 2015) whereas it is supported in the phylogenetic
10
11 analysis of Gheerbrant *et al.* (2005a; 2014) while the phylogenetic relationships are not
12
13 resolved in Gheerbrant (2009). *Phenacolophus* appears to be related to Tethytheria in Tabuce
14
15 *et al.* (2007) as ([Hyracoidea, [Proboscidea, [*Anthracobune*, [*Phenacolophus*, *Protosiren*]]]),
16
17 after exclusion of only embrithopod included in their analysis, *Arsinoitherium*. The strict
18
19 relationship of *Ph. fallax* with embrithopods is here strongly supported by 10 unambiguous
20
21 synapomorphies and a BI=5, which is in full agreement with the close relationships between
22
23 Phenacodontidae and Afrotheria recovered by Rose *et al.* (2014). Node 6 (Embrithopoda) is
24
25 supported by three unambiguous synapomorphies (BI=3).

26
27
28
29 *Namatherium blackcrowense*, from the Lutetian of Namibia, is sister group (node 6) to
30
31 Arsinoitheriidae at node 7 which corresponds to the dichotomy between an Arabian-African
32
33 clade (*Arsinoitherium*; node 8) and a Eurasian clade (node 9). As to the Eurasian clade, the
34
35 phylogenetic relationships are unresolved (*H. seni*, *P. kansui*, *Crivadiatherium*; node 9) and
36
37 the possible reasons are discussed in further.

38
39
40 According to Pickford *et al.* (2008), *Namatherium* is closer to *Arsinoitherium* in terms of
41
42 dental morphology (despite cranial differences) than to *Palaeoamasia* and is classified within
43
44 Arsinoitheriidae to which Eurasian embrithopods also belong (“Eurasian arsinoitheres” *sensu*
45
46 Pickford *et al.* 2008). Here, the (*Namatherium* + *Arsinoitherium*) group is paraphyletic
47
48 although node 7 is weakly supported ([BI=1]; see devoted section). Accordingly, pending new
49
50 characters or additional remains, likely to change the branching sequence of *Namatherium*
51
52 and in order to favour the use of monophyletic suprageneric taxa within embrithopods, node 7
53
54 will be considered as anchoring the clade Arsinoitheriidae in which subordinated clades are
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3 Arsinoitheriinae Andrews, 1904 with (*A. zitteli* + *A. giganteum*; node 8) and Palaeoamasiinae
4
5 Sen & Heintz, 1979 with (*P. kansui* + *Hypsamasia seni* + *Crivadiatherium mackennai* + *C.*
6
7 *iliescui*; node 9) as two distinct subfamilies.

8
9
10 The subfamily Palaeoamasiinae, represented by a polytomy in the strict consensus tree,
11
12 consists of five alternative topologies (Fig. 6), in which only the position of *H. seni* is
13
14 ambiguous. The lack of phylogenetic resolution within Eurasian embrithopods and the
15
16 occurrence of a polytomy in the strict consensus tree (Fig. 5) is caused by the fact that *P.*
17
18 *kansui* is the only species providing information on upper dentition as well as lower and also
19
20 on mandibular and maxillary fragments. Unfortunately, *Crivadiatherium* is only known by its
21
22 lower dentition whereas *H. seni* is represented by few upper teeth only (heavily damaged and
23
24 incomplete), which prevents any further phylogenetic resolution.

25 26 27 28 29 30 *Distribution of synapomorphies on strict consensus tree*

31
32 For each node, unambiguous synapomorphies appear by increasing degree of homoplasy
33
34 (following Antoine 2002). Corresponding character states are shown in square brackets. The
35
36 complete list of unambiguous apomorphies is available in Table 4; a complete character
37
38 distribution list (including ambiguous synapomorphies) is given in Appendix 4.

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42
43 *Node 2: Paenungulata Simpson, 1945.* The clade Paenungulata (BI=5) is well supported by
44
45 twelve unambiguous synapomorphies among which seven are non-homoplastic:
46
47 postprotocrista mesio-distally oriented on upper premolars (18[1]); absence of metaconule on
48
49 P3 (30[1]) and on P4 (39[1]); absence of paraconule on P4 (38[1]); mesostyle distinct on
50
51 upper molars (54[1]); dilambdodont upper molars (59[1]); lower incisors medium-sized to
52
53 large (75[1]); postparacrista reaching the lingual side of the mesostyle on upper molars (53[1]

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2
3 or 2]); postprotocrista absent on P4 (40[1]); paraconule absent on P3 (29[1]); diastema (d)p1–
4
5 p2 absent (87[0]); post-canine diastema absent (79[0]).
6
7

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9
10 *Node 3: [Hyracoidea + Proboscidea]*. Two unambiguous synapomorphies supporting this
11
12 clade are non-homoplastic: distocrista present at least on M1–M2 (45[1]) and talonid reduced
13
14 on p4 (99[0]). This node is relatively robust (BI=3).
15
16

17
18 *Node 4: Proboscidea Illiger, 1811*. This is the most robust node of the tree (BI=11). Seven out
19
20 of eight unambiguous synapomorphies situated on that node are non-homoplastic::
21
22 preparacrista absent (49[1]) and mesostyle close to paracone and metacone (55[0]) on upper
23
24 molars; paraconid absent or reduced on lower premolars (80[1]); cristid oblique slightly
25
26 oblique with a mesial end reaching the labial half of trigonid (106[3]), premetacristid distinct
27
28 (108[1]), and cristid oblique mesio-distally centered on lower molars (117[1]); labial
29
30 hypoconulid on m1–m2 (127[1]). The distal cingulum joins the hypocone via the distocrista
31
32 (46[0]).
33
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39 *Node 5: [Embrithopoda + Phenacolophus fallax]*. This node is highly robust (BI=5). Nine
40
41 unambiguous synapomorphies (of which seven are non-homoplastic) supporting the close
42
43 relationships of *Phenacolophus fallax* with embrithopods (node 5) are: large dental
44
45 dimensions (consequently body size) (11[1]); preparacrista oriented rather transversally
46
47 (51[0]), labio-lingually oriented postmetacrista (65[0]), absence of prehypocrista (69[0]) and
48
49 metaloph formed by the alignment of hypocone, metaconule and metacone on upper molars
50
51 (70[0]); lophids oblique compared with transversal axis on lower molars (114[0]); absence of
52
53 hypoconulid on m1–m2 (126[1]). Note that in the phylogenetic analyses of Gheerbrant *et al.*
54
55 (2005) and Gheerbrant (2009), the hypoconulid is considered as present in embrithopods
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2
3 whereas it is considered as a strong cingulid on m1 and m2 instead in this analysis. The last
4
5 two characters are: upper cheek tooth size increasing progressively from P2 towards M2, with
6
7 M3 much larger on the dental series (72[1]); hypoconulid weak on m3 (128[1]).
8
9

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11
12 *Node 6: Embrithopoda Andrews, 1906.* Three unambiguous synapomorphies support the
13
14 monophyly of embrithopods (BI=3): upper molars hyper-dilambdodont (59[2]) and hypsodont
15
16 (73[1]); lingual migration of the postparacrista, paracone and metacone on upper molars
17
18 (53[3]). This character is non-applicable in *A. zitteli* (postparacrista absent) and not scored in
19
20 *Crivadiatherium* (upper teeth unknown).
21
22

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24
25 *Node 7: Arsinoitheriidae Andrews, 1904.* This node is the weakest node of the consensus tree
26
27 (BI=1). Only two unambiguous synapomorphies (one of which is homoplastic) are supporting
28
29 the family Arsinoitheriidae as a clade: labial cingulum absent on upper molars (47[1]); distal
30
31 zygomatic process reaching the level of the distal loph of M3 (2[0 or 1]). This character is
32
33 ordered and its ancestral state is 2.
34
35

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37
38 *Node 8: Arsinoitheriinae Andrews, 1904.* All four synapomorphies which characterise
39
40 Arsinoitheriinae are non-homoplastic, hence, this node appears relatively robust (BI=3): distal
41
42 cingulum absent on upper molars (44[1]); trigonid and talonid having the same height on p2
43
44 and p3 (83[1]) as well as on lower molars (116[1]); mesial cingulid absent on lower molars
45
46 (102[1]).
47
48

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50
51 *Node 9: Palaeoamasiinae Sen & Heintz, 1979.* This node is one of the less supported of the
52
53 consensus tree (BI=2). Three unambiguous synapomorphies support Palaeoamasiinae,
54
55 including two non-homoplastic characters: mesial end of the cristid oblique reaching the
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3 lingual middle of trigonid and elongated towards the apex of the metaconid on lower molars
4
5 (106[0]); cristid oblique high and reaching the occlusal surface of the talonid (115[0]); three-
6
7 rooted P2 (20[1]).
8
9

10 11 *Phylogenetic position of Namatherium*

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14 Nodes of the strict consensus tree are more or less well supported as regards BI (Fig. 5). In
15
16 particular, the node 7 [Arsinoitheriinae, Palaeoamasiinae] is the weakest (BI=1) in bearing
17
18 only two synapomorphies of which one is homoplastic (labial cingulum absent on upper
19
20 molars; distal zygomatic process at the distal loph level of M3 [CI=0.66; RI=0.66]). This node
21
22 merits a further explanation since it excludes *Namatherium* from either Arsinoitheriinae
23
24 (Arabian-African) or Palaeoamasiinae (Eurasian).
25
26

27
28 In order to estimate the potential affinity of *Namatherium* within those clades, two alternative
29
30 topologies are forced via the tool ‘Searching under Topological Constraints’ in PAUP 3.1.1.
31
32 Results are strongly significant, as the Arabian-African clade [*Namatherium*, *Arsinoitherium*]
33
34 is then supported by three unambiguous synapomorphies (e.g. absence of postprotocrista on
35
36 P3, absence of postmetacrista on upper molars, mesial and lingual cingula discontinuous on
37
38 M3; Fig. 7A, branch x) with a length of 244 steps. This is definitely more parsimonious
39
40 compared to the topology where the clade [*Namatherium*, Palaeoamasiinae] is supported by
41
42 14 ambiguous synapomorphies, in a longer tree with 247 steps (Fig. 7B, node y). Noteworthy
43
44 is the fact that only one additional step in the strict consensus tree (L=243+1) generates a
45
46 trifurcation (as mentioned above).
47
48

49
50 The problematic position of *Namatherium* and unresolved relationships within
51
52 Palaeoamasiinae arise probably from the sparse material directly comparable among
53
54 embrithopods, which affects also the number of potential unambiguous synapomorphies
55
56 (Table 5). For instance, *Arsinoitherium zitteli* and *Palaeoamasia kansui* are known by
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3 complete dental remains contrary to *Namatherium* and *Hypsamasia*, known only by upper
4
5 teeth and to *Crivadiatherium*, known only by lower teeth.
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10 *Contribution of the new material of Palaeoamasia kansui*

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12 In order to control the possible relation between new specimens, abundance of comparable
13
14 material and resolution of topologies, we tested four different scenarii (Fig. 8) and we
15
16 obtained *a posteriori* (1) a topology where new specimens of *P. kansui* are removed (P2–P3
17
18 and mandible; Fig. 8A), (2) a topology excluding *Hypsamasia* (known by four damaged upper
19
20 teeth; Fig. 8B), (3) a topology hypothesising a priori that *Palaeoamasia* and *Hypsamasia* were
21
22 synonyms (Fig. 8C) and (4) another hypothesis considering the two species of
23
24 *Crivadiatherium* as a single terminal (Fig. 8D).
25
26

27
28 The results seem to be convincing since (i) the embrithopods and the clade Palaeoamasiinae
29
30 are clearly supported through new material of *P. kansui* (Fig. 8A); (ii) the exclusion of
31
32 *Hypsamasia seni* allows for a better phylogenetic resolution (resulting tree: 234 steps; Fig.
33
34 8B) and (iii) that resolution still increases when the hypodigms of both *Crivadiatherium* are
35
36 amalgamated (232 steps; Fig. 8C). Note that whether *Hypsamasia* is excluded or combined
37
38 with *Palaeoamasia*, the monophyly of Palaeoamasiinae and *Crivadiatherium* is retained. On
39
40 the other hand, (iv) the topology of the general strict consensus tree (Fig. 5) is not affected
41
42 when two species of *Crivadiatherium* are regarded as one (shorter tree: 236 steps instead of
43
44 243; Fig. 8D).
45
46

47
48 In any scenario, the node 7 of the general strict consensus tree (which excludes *Namatherium*
49
50 from Palaeoamasiinae and Arsinoitheriinae, in the family Arsinoitheriidae) is as weak as in
51
52 the main analysis (BI=1; Fig. 5).
53

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55 Overall, our phylogenetic results support the monophyly of Embrithopoda with one family,
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57 Arsinoitheriidae and two subfamilies, Palaeoamasiinae and Arsinoitheriinae (*contra* Kaya
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3 1995; Maas *et al.* 1998; Sanders *et al.* 2014) by excluding *Namatherium* from the family,
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5 which may change with a wider taxonomic sample and/or new findings of early
6
7 embrithopods.
8
9

10 11 *Phylogenetic position of embrithopods within Paenungulata*

12
13
14 The phylogenetic position of embrithopods within Paenungulata and their possible affinities
15
16 with Afrotheria are controlled with the inclusion of three genera, *Palaeoamasia*, *Namatherium*
17
18 and *Crivadiatherium*, in the data matrix from Tabuce *et al.* (2007) wherein embrithopods were
19
20 represented only by *Arsinoitherium* and appeared at the base of Paenungulata (Fig. 9A). The
21
22 original matrix underwent some modifications concerning dental characters, with the
23
24 decomposition of some multistate characters into binary characters and a few character state
25
26 changes. By following the same protocols as in Tabuce *et al.* (2007: strict consensus and
27
28 successive weighting), we obtained distinct topologies (Fig. 9B).
29
30

31
32 As to results, embrithopods are monophyletic and they are located at the base of ungulates
33
34 and clearly separate from *Phenacolophus* and from *Protosiren* (Fig. 9B). While the branches
35
36 x, y and z of ungulates are supported by postcranial characters, the branch 't' is eventually
37
38 supported only by molar features (Fig. 9B). Thus, it is clear that postcranial characters
39
40 (unscored for embrithopods except *Arsinoitherium*) appear to be crucial for the resolution of
41
42 interordinal phylogenetic relationships and that the systematic position of *Phenacolophus* is
43
44 subjected to change depending either on the taxonomic sample or the phylogenetic characters
45
46 scored. Also, *Palaeoamasia* is here sister taxon to other embrithopods contrary to the
47
48 topology as illustrated in Figure 5.
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51 52 53 54 **PALAEOBIOGEOGRAPHICAL IMPLICATIONS**

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3 The previous strict consensus tree (Fig. 9B) makes possible to assume dispersal events within
4 Ungulata between Eurasia and Africa (Fig. 10). According to the available taxonomic sample,
5 there would be at least three dispersal events from Eurasia towards Africa (Macroscelidea;
6 Hyracoidea + Tethytheria; Embrithopoda) and one reversal event with *Anthracobune* (Fig.
7 10A).

8
9 Detailed analysis of three equally parsimonious trees concerning embrithopods (Fig. 10B)
10 point to three dispersal hypotheses, such as (1) one event from Eurasia to Africa at the base of
11 the clade [*Arsinoitherium*, *Namatherium*], (2) two events, with the first one from Eurasia to
12 Africa for the clade which excludes *Palaeoamasia* and a second one from Africa to Eurasia
13 for *Crivadiatherium*, (3) two independent dispersal events from Eurasia to Africa for
14 *Namatherium* and *Arsinoitherium*.

15
16 The most parsimonious topology is one with a single dispersal event (Fig. 10B: x).

17
18 This analysis would confirm the Eurasian origin of embrithopods, as proposed formerly by
19 Radulesco *et al.* (1976), McKenna & Manning (1977), Sen & Heintz (1979), and Radulesco
20 & Sudre (1985). Following a more general context, such as palaeogeography, eustatic curves,
21 fossil record and phylogeny, dispersal events took place either in Thanetian times or before
22 the Ypresian–Lutetian transition (Fig. 11). According to Gheerbrant & Rage (2006), two
23 faunal exchange events probably occurred during the Thanetian interval (Fig. 11A). There is a
24 huge gap in the Arabian-African fossil record, between the latest Paleocene and the Lutetian.
25 Future prospects must focus on this time interval in order to shed light on dispersal events of
26 embrithopods. On the other hand, the recent recognition of *Palaeoamasia* around the Eocene–
27 Oligocene transition in Turkey (Sanders *et al.* 2014) illustrates the existence of another ghost
28 lineage encompassing the middle–late Eocene interval (Fig. 11) and would further point to a
29 morphological stasis within *Palaeoamasia*, at least for the available characters. We do agree
30 with Sen (2013) that some possible sweepstake passage of embrithopods existed during the
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3 Palaeogene interval, most probably during the late Paleocene which perhaps allowed Eurasian
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5 embrithopods to disperse to Arabia-Africa.
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7

9 10 **CONCLUSION**

11
12 New material of *Palaeoamasia kansui* from the type locality Eski-Çeltek (Amasya, Turkey)
13
14 enhances our cranial-dental knowledge concerning Eurasian embrithopods. A phylogenetic
15
16 analysis at the species-level demonstrates the monophyly of Embrithopoda. *Namatherium*
17
18 *blackcrowense* Pickford *et al.* 2008, from the middle Eocene of Namibia, is the first offshoot
19
20 within Embrithopoda. It is sister group to the monophyletic family Arsinoitheriidae, divided
21
22 in two subfamilies. Arsinoitheriinae comprise other Arabian-African embrithopods
23
24 (*Arsinotherium zitteli*, *A. giganteum*) and Palaeoamasiinae include all Eurasian embrithopods
25
26 (*Palaeoamasia*, *Hypsamasia*, *Crivadiatherium*). The position of *Namatherium* outside
27
28 Arsinoitheriinae/Arsinoitheriidae is weakly supported. Phylogenetic relationships within
29
30 Palaeoamasiinae are not totally resolved either. *Palaeoamasia* remains from Boyabat (Sanders
31
32 *et al.* 2014) are here conservatively assigned to *P. kansui*. This new evidence is an
33
34 encouraging hint to prospect further in mid-Palaeogene deposits of Turkey and Balkans, in
35
36 order to clarify the phylogenetic affinities of Eurasian embrithopods.
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Figure, table and appendix captions

Fig. 1. Spatial and temporal distribution of embriothopods. Numbers follow the chronological order of localities (see also Table 1). Chronological distribution of localities (A) (modified after International Stratigraphic Chart, 2015/1); geographical distribution of studied specimens on a contemporary map (B); localities of *Palaeoamasia* and *Hypsamasia* on the contemporary map of Turkey (C). Localities are in the same colour as ones of the geological chart. Lowercase letters indicate different localities of *Palaeoamasia kansui*.

Fig. 2. Dental terminology used in this study. A–C, upper left teeth; D–E, lower left teeth. P2 (A); P4 (B); M2 (C); p2 (D); p4 (E); m3 (F). Terminology is combined after descriptions of McKenna & Manning (1977), Sen & Heintz (1979), Iliescu & Sudre (1985), Court (1992b), Maas *et al.* (1998), Sanders *et al.* (2004) and Pickford *et al.* (2008).

Fig. 3. Holotype and new specimens of *Palaeoamasia kansui* Ozansoy, 1966 (from the late Paleocene – early Eocene of Eski-Çeltek, Amasya-Turkey). A–B, holotype, MNHN-EÇ-1, left mandible fragment with highly damaged trigonid of m1, m2 and trigonid of m3. The relatively complete specimen is illustrated by Ozansoy (1966, fig. 3–4). C–D, ITU-EÇ-8, left P2–P3; E–F, ITU-EÇ-7, palate fragment with right P4–M2; G, MNHN-EÇ-6, isolated left M3; H–J, ITU-EÇ-9, mandible fragment with left p2–m1; K–L, MNHN-EÇ-5, mandible fragment with right p4–m1. Views are occlusal (A, C, E, G, H, K), labial (B, D, F, J, L), and lingual (I). Scale bar equals 2 cm. Photographs: Philippe Loubry (MNHN, Paris).

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3 **Fig. 4.** Size distribution of upper (A) and lower (B) premolars and molars of embrithopods by
4 mean values in mm. *Crivadiatherium*, *Hypsamasia*, and new material of *Palaeoamasia kansui*
5 are re-measured by authors. For other measurements see McKenna & Manning (1977), Sen &
6 Heintz (1979), Kaya (1995), A. Gül, unpub. data (2003), Sanders *et al.* (2004, 2014), Pickford
7 *et al.* (2008). Mean values are available in Appendix 3. Colours indicate tooth type, symbols
8 distinguish taxa. Only comparable tooth types are included in this diagram (e.g. incisors of
9 *Crivadiatherium* or p1 of *A. giganteum* are not included). M1–M3 of *Ph. fallax* is highly
10 damaged and lacks the measurements. L, length; W, width.

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22 **Fig. 5.** Strict consensus tree (L=243 steps, CI=0.588 and RI=0.587) of ten shortest trees
23 (L=237 steps, CI=0.603, RI=0.612) obtained with PAUP 3.1.1 based on 130 cranial and dental
24 characters (character list and data matrix supplied in Appendices 1–2). Number of
25 synapomorphies of each node is mentioned in italics, Bremer Indices in bold; node numbers
26 in circle.

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36 **Fig. 6.** Detail of the most parsimonious trees concerning Palaeoamasiinae (L=237 steps,
37 CI=0.603, RI=0.612). Five alternative topologies of Eurasian embrithopods acquired by
38 PAUP 3.1.1. The letters in lowercase indicate nodes. Note that nodes x and w reappear in
39 different trees.

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47 **Fig. 7.** Comparison of alternative topologies implying *Namatherium*. (A) Strict consensus
48 (L=244, CI=0.586, RI=0.583) of ten equally parsimonious trees with the node x
49 (*Namatherium*+*Arsinoitherium*). (B) Strict consensus (L=247, CI=0.579, RI=0.570) of ten
50 equally parsimonious trees with the node y (*Namatherium*+Palaeoamasiinae). L, branch
51 length; x, three unambiguous synapomorphies; y, fourteen ambiguous synapomorphies.

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5 **Fig. 8.** Strict consensus tree topologies obtained by following different scenarii. Topology
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7 acquired (L=243, CI=0.588, RI=0.567) with exclusion of new specimens of *Palaeoamasia*
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9 *kansui* (A); topology acquired (L=234, CI=0.611, RI=0.596) with exclusion of *Hypsamasia*
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11 *seni* (B); topology acquired (L=232, CI=0.612, RI=0.598) under hypothesis of *Palaeoamasia*-
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13 *Hypsamasia* synonymy (C); topology acquired (L=236, CI=0.602, RI=0.593) where
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15 *Crivadiatherium* is terminal taxon (D). Numbers correspond to Bremer indices.
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21 **Fig. 9.** Comparison of strict consensus trees established after successive weighting process
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23 following the data matrix of Tabuce *et al.* (2007). Topology published in Tabuce *et al.* (2007)
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25 (A; L=49166, CI=0.43, RI=0.67). Topology obtained with the same protocol after including
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27 other embrithopods such as *Namatherium*, *Crivadiatherium* and *Palaeoamasia* (B; L=47841,
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29 CI=0.44, RI=0.66). Lowercase letters indicate characters supporting the concerned node: two
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31 unambiguous postcranial characters (x); three unambiguous postcranial characters (y); two
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33 unambiguous postcranial characters (z) and one unambiguous dental character (t) (Tabuce *et*
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35 *al.* 2007).
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41 **Fig. 10.** Dispersal event hypothesis of Ungulata between Eurasia and Arabian-African
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43 continent. Topology displaying four dispersal events within Ungulata (modified after Tabuce
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45 *et al.* 2007) (A); Alternative topology concerning embrithopods illustrates three different
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47 dispersal events hypotheses (B). Green lines, Eurasian origin taxa; orange lines, Arabian-
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49 African origin taxa; grey lines, marine taxa; arrows, direction of migration. Lower case letters
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51 indicate different topologies with one (x, parsimonious) or two dispersal events (y and y').
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3 **Fig. 11.** Stratigraphical and palaeogeographical distribution of embrithopods in a phylogenetic
4 framework (A). Distribution and hypothetical dispersal events for embrithopods (B). Colour
5 codes on the map equal those of the phylogenetic tree in A. Palaeogeographical map at
6 Ypresian times is modified after Barrier & Vrielynck (2008) and Sen (2013). Geological time
7 scale is modified after International Stratigraphic Chart (2015/1). Eustatic curve is modified
8 after Gheerbrant & Rage (2006). Arrows display possible faunal exchange events between
9 Eurasia and Afro-Arabia.
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21 **Table 1.** List of embrithopods (and *Phenacolophus fallax*) in stratigraphical order with
22 corresponding localities, time interval, authors and locality numbers given in Figure 1.
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27 **Table 2.** Interordinal classification of Embrithopoda (parenthetical mode) according to
28 previous authors. Underlined taxon names followed by a colon are for higher-taxa.
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34 **Table 3.** Dental measurements (in mm) of new material of *Palaeoamasia kansui*, and casts of
35 *Hypsamasia seni*, *Crivadiatherium mackennai* and *C. iliescui* specimens.
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40 **Table 4.** List of unambiguous apomorphies on nodes of the strict consensus tree.
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42 Unambiguous and non-homoplastic characters are in bold, unambiguous autapomorphies of
43 which corresponding state is not homoplastic are in italics and unambiguous and weakly
44 homoplastic characters ($0.75 \leq \text{RI} < 1$) are underlined. Homoplastic characters ($\text{RI} < 0.75$) lack
45 any annotations. Each character state is mentioned in brackets. Ambiguous characters are
46 excluded from that list. Complete distribution of characters is in Appendix 4.
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Table 5. Number of characters scored for *Arsinoitherium*, *Palaeoamasia*, *Namatherium*, *Crivadiatherium* and *Hypsamasia* species depending on available specimens.

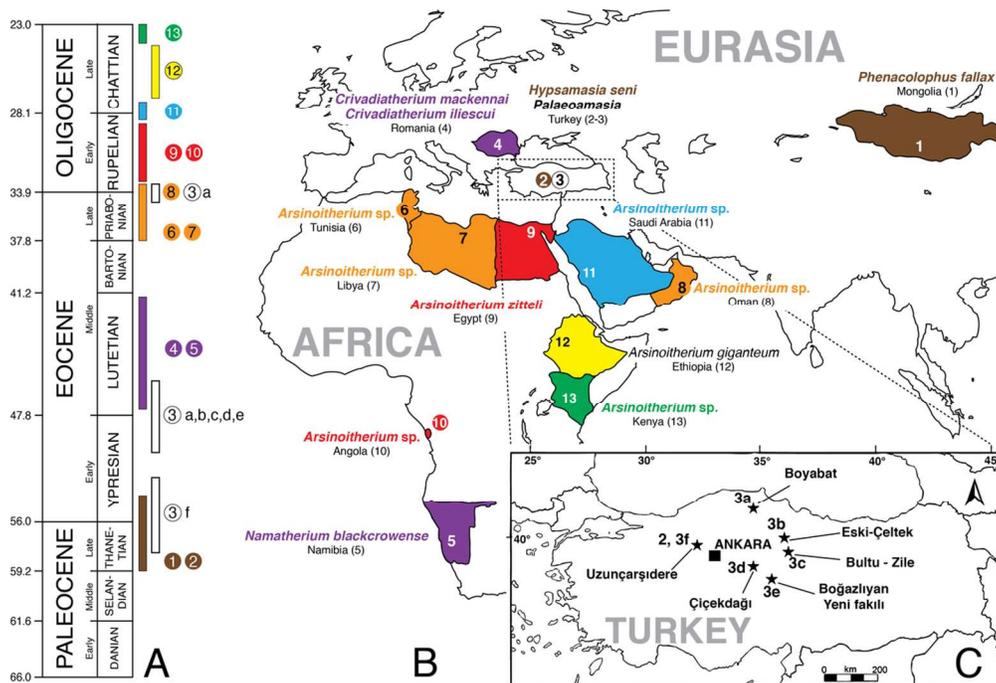


Fig. 1. Spatial and temporal distribution of embrithopods. Numbers follow the chronological order of localities (see also Table 1). Chronological distribution of localities (A) (modified after International Stratigraphic Chart, 2015/1); geographical distribution of studied specimens on a contemporary map (B); localities of *Palaeoamasia* and *Hypsamasia* on the contemporary map of Turkey (C). Localities are in the same colour as ones of the geological chart. Lowercase letters indicate different localities of *Palaeoamasia kansui*.

109x75mm (300 x 300 DPI)

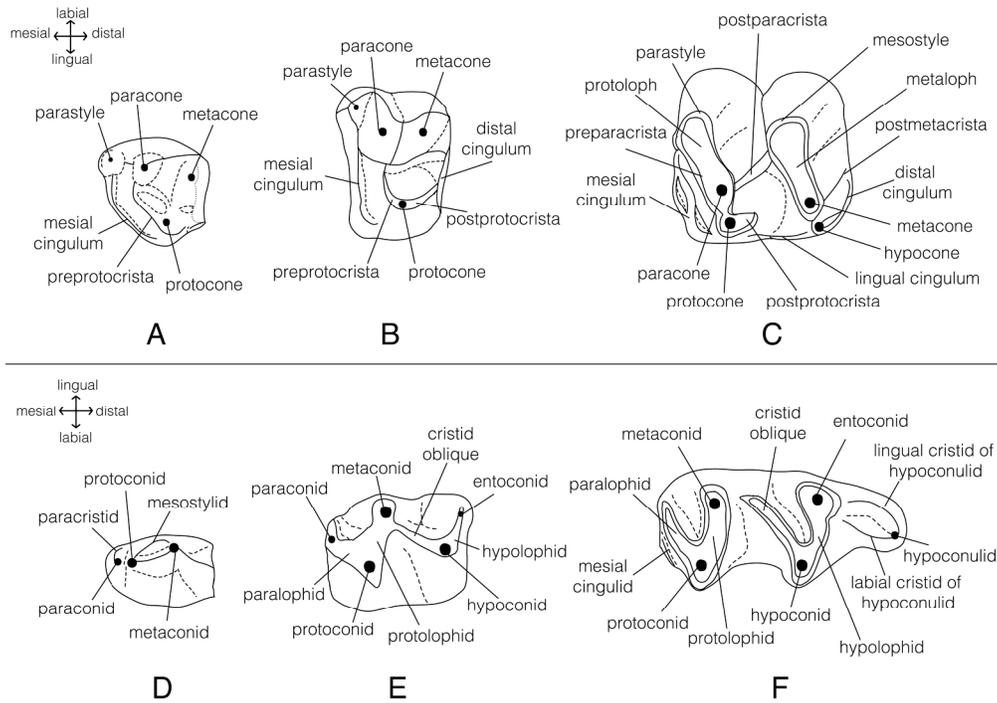


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111x79mm (600 x 600 DPI)

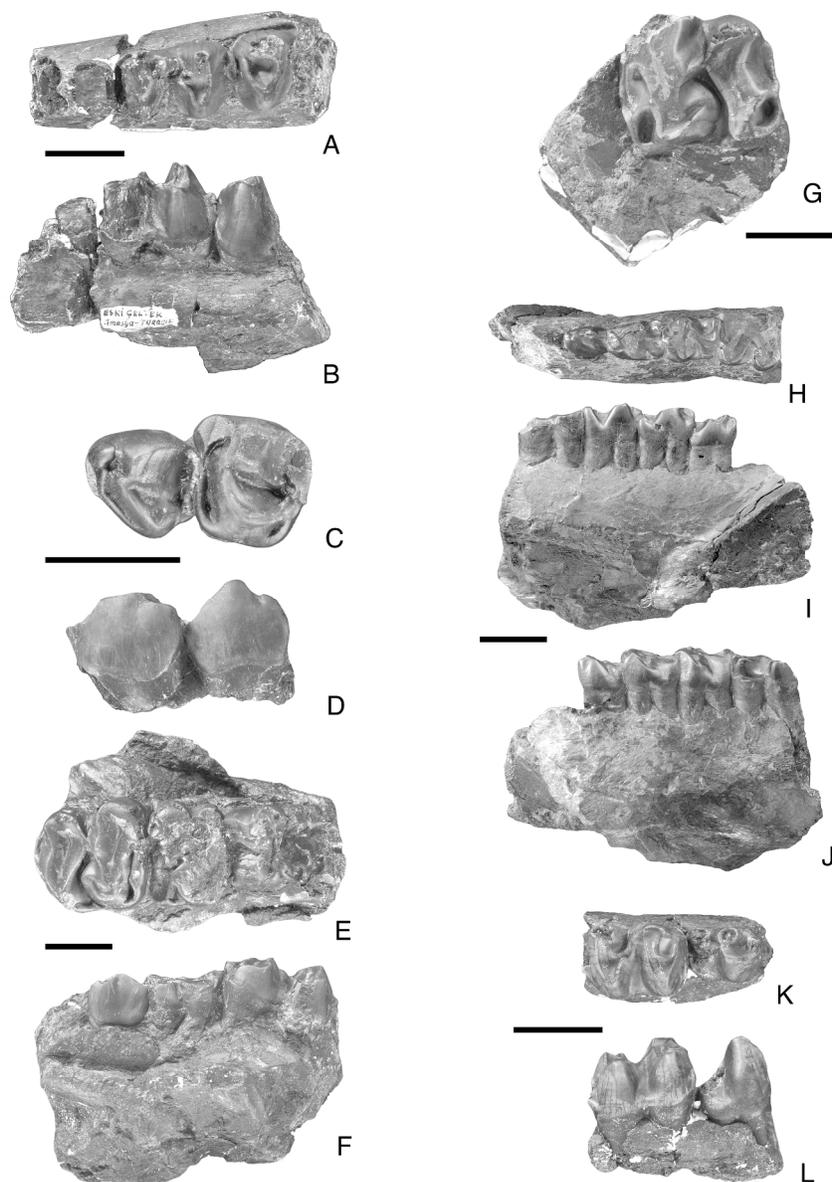


Fig. 3. Holotype and new specimens of *Palaeoamasia kansui* Ozansoy, 1966 (from the late Paleocene – early Eocene of Eski-Çeltek, Amasya-Turkey). A–B, holotype, MNHN-EÇ-1, left mandible fragment with highly damaged trigonid of m1, m2 and trigonid of m3. The relatively complete specimen is illustrated by Ozansoy (1966, fig. 3–4). C–D, ITU-EÇ-8, left P2–P3; E–F, ITU-EÇ-7, palate fragment with right P4–M2; G, MNHN-EÇ-6, isolated left M3; H–J, ITU-EÇ-9, mandible fragment with left p2–m1; K–L, MNHN-EÇ-5, mandible fragment with right p4–m1. Views are occlusal (A, C, E, G, H, K), labial (B, D, F, J, L), and lingual (I). Scale bar equals 2 cm. Photographs: Philippe Loubry (MNHN, Paris).
225x307mm (300 x 300 DPI)

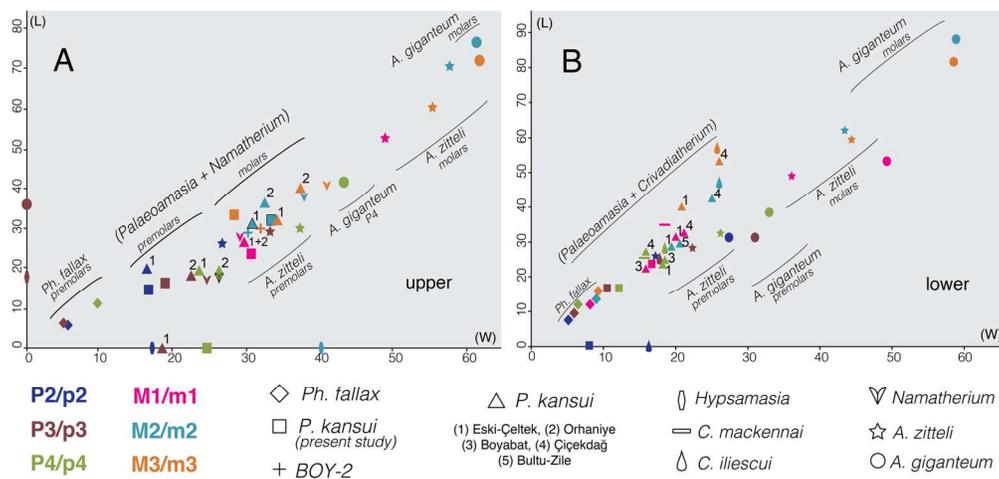


Fig. 4. Size distribution of upper (A) and lower (B) premolars and molars of embrithopods by mean values in mm. *Crivadiatherium*, *Hypsamasia*, and new material of *Palaeoamasia kansui* are re-measured by authors. For other measurements see McKenna & Manning (1977), Sen & Heintz (1979), Kaya (1995), A. Gül, unpub. data (2003), Sanders *et al.* (2004, 2014), Pickford *et al.* (2008). Mean values are available in Appendix 3.

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80x39mm (600 x 600 DPI)

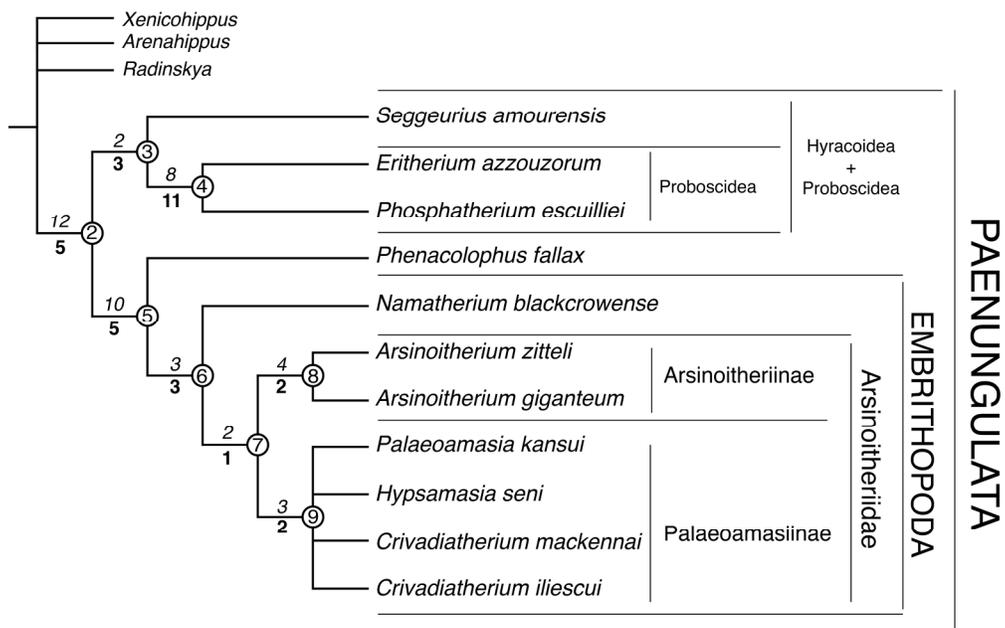
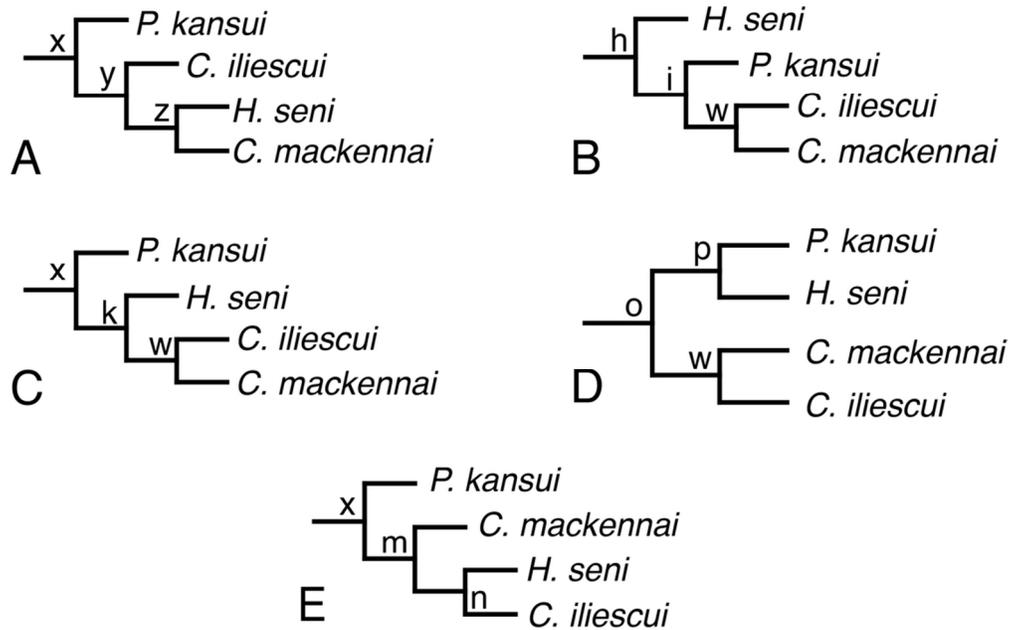


Fig. 5. Strict consensus tree (L=243 steps, CI=0.588 and RI=0.587) of ten shortest trees (L=237 steps, CI=0.603, RI=0.612) obtained with PAUP 3.1.1 based on 130 cranial and dental characters (character list and data matrix supplied in Appendices 1–2). Number of synapomorphies of each node is mentioned in italics, Bremer Indices in bold; node numbers in circle.
 100x62mm (600 x 600 DPI)



29 Fig. 6. Detail of the most parsimonious trees concerning Palaeoamasiinae (L=237 steps, CI=0.603,
30 RI=0.612). Five alternative topologies of Eurasian embrithopods acquired by PAUP 3.1.1. The letters in
31 lowercase indicate nodes. Note that nodes x and w reappear in different trees.
32 48x31mm (600 x 600 DPI)

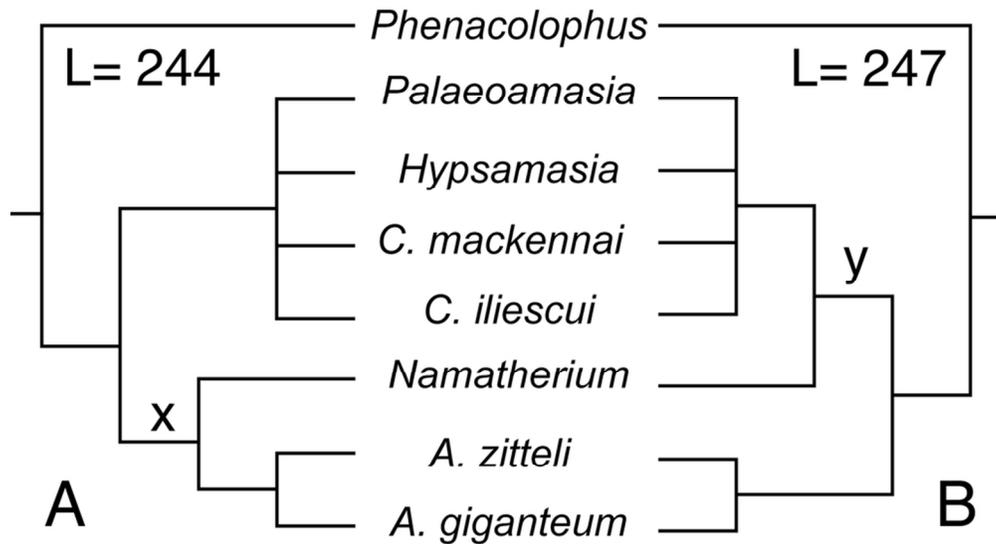


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 43x24mm (600 x 600 DPI)

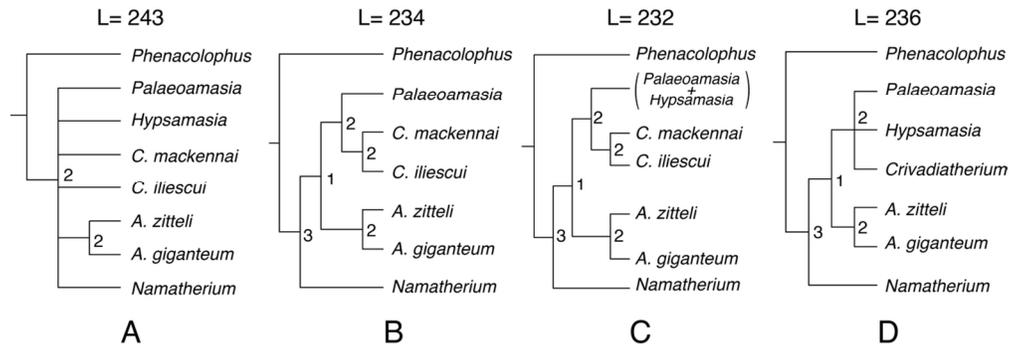


Fig. 8. Strict consensus tree topologies obtained by following different scenarii. Topology acquired (L=243, CI=0.588, RI=0.567) with exclusion of new specimens of *Palaeoamasia kansui* (A); topology acquired (L=234, CI=0.611, RI=0.596) with exclusion of *Hypsamasia seni* (B); topology acquired (L=232, CI=0.612, RI=0.598) under hypothesis of *Palaeoamasia-Hypsamasia* synonymy (C); topology acquired (L=236, CI=0.602, RI=0.593) where *Crivadiatherium* is terminal taxon (D). Numbers correspond to Bremer indices.
57x20mm (600 x 600 DPI)

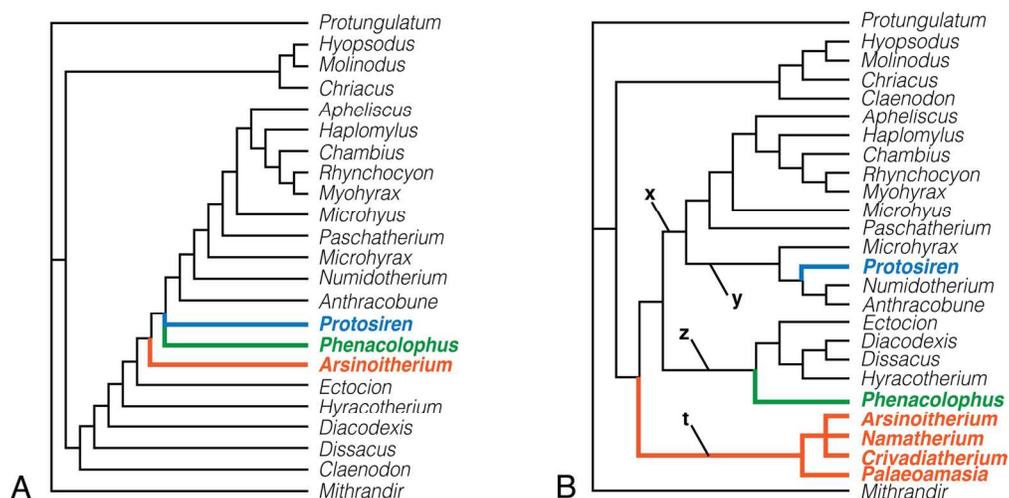


Fig. 9. Comparison of strict consensus trees established after successive weighting process following the data matrix of Tabuce *et al.* (2007). Topology published in Tabuce *et al.* (2007) (A; L=49166, CI=0.43, RI=0.67). Topology obtained with the same protocol after including other embrithopods such as *Namatherium*, *Crivadiatherium* and *Palaeoamasia* (B; L=47841, CI=0.44, RI=0.66). Lowercase letters indicate characters supporting the concerned node: two unambiguous postcranial characters (x); three unambiguous postcranial characters (y); two unambiguous postcranial characters (z) and one unambiguous dental character (t) (Tabuce *et al.* 2007).
78x39mm (600 x 600 DPI)

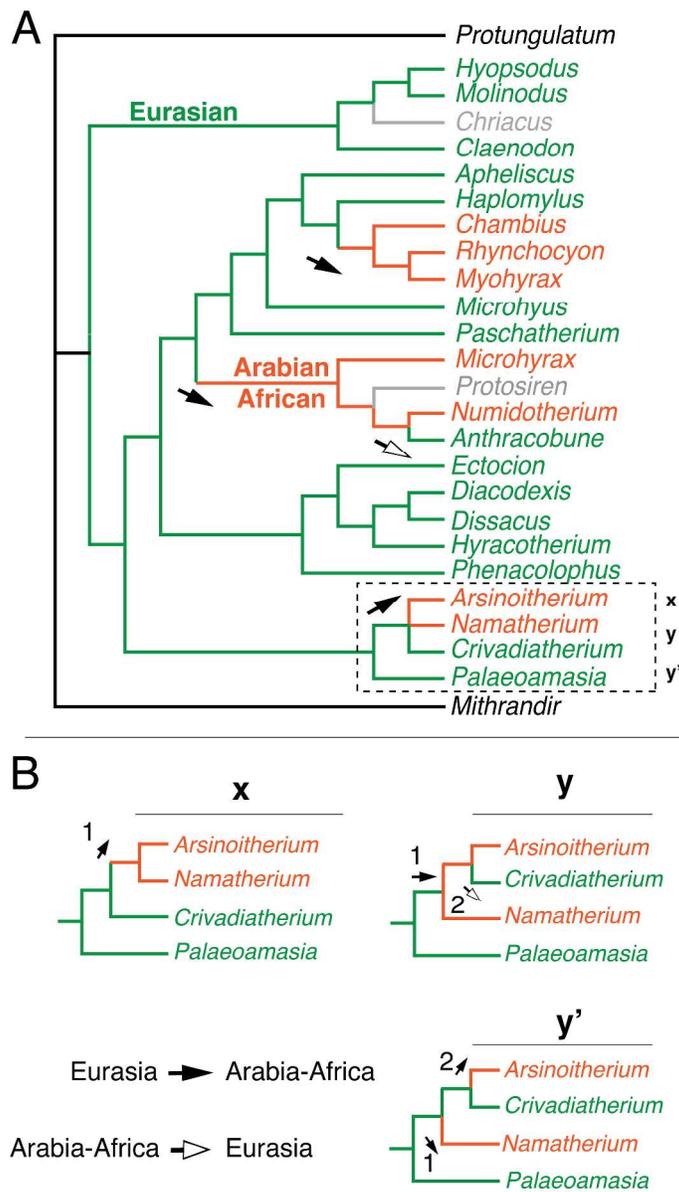


Fig. 10. Dispersal event hypothesis of Ungulata between Eurasia and Arabian-African continent. Topology displaying four dispersal events within Ungulata (modified after Tabuce *et al.* 2007) (A); Alternative topology concerning embrithopods illustrates three different dispersal events hypotheses (B). Green lines, Eurasian origin taxa; orange lines, Arabian-African origin taxa; grey lines, marine taxa; arrows, direction of migration. Lower case letters indicate different topologies with one (x, parsimonious) or two dispersal events (y and y').

130x225mm (600 x 600 DPI)

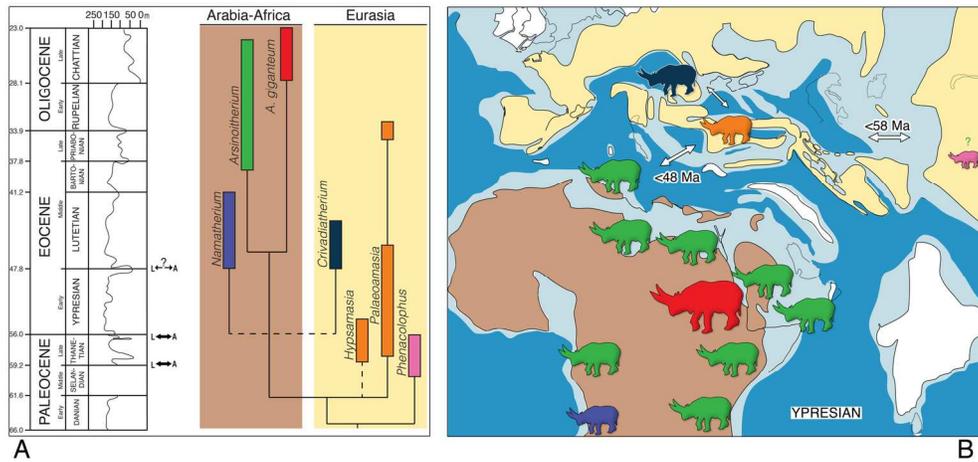


Fig. 11. Stratigraphical and palaeogeographical distribution of embrithopods in a phylogenetic framework (A). Distribution and hypothetical dispersal events for embrithopods (B). Colour codes on the map equal those of the phylogenetic tree in A. Palaeogeographical map at Ypresian times is modified after Barrier & Vrielynck (2008) and Sen (2013). Geological time scale is modified after International Stratigraphic Chart (2015/1). Eustatic curve is modified after Gheerbrant & Rage (2006). Arrows display possible faunal exchange events between Eurasia and Afro-Arabia.

78x36mm (600 x 600 DPI)

Table 1. List of embrithopods (and *Phenacolophus fallax*) in stratigraphical order with corresponding localities, time interval, authors and locality numbers given in Figure 1.

Species	Locality	Age	Authors & Date	Localities in Fig.1
<i>Arsinoitherium</i> sp.	Lothidok (Kenya)	latest Oligocene	Boschetto <i>et al.</i> 1992; Rasmussen & Guterrez 2009	13
<i>Arsinoitherium giganteum</i>	Chilga (Ethiopia)	late Oligocene	Sanders <i>et al.</i> 2004; Kappelman <i>et al.</i> 2003	12
<i>Arsinoitherium</i> cf. <i>zitteli</i>	Shumaysi formation - Harrat Al Ujayfa (Saudi Arabia)	early late Oligocene	Zalmout <i>et al.</i> 2010	11
<i>Arsinoitherium</i> sp.	Malembo - Cabinda (Angola)	early Oligocene	Pickford 1986	10
<i>Arsinoitherium zitteli</i> Beadnell, 1902	Jebel Qatrani Formation - Fayoum (Egypt)	early Oligocene (Seiffert 2006)	Andrews <i>et al.</i> 1906	9
Embrithopoda cf. <i>Arsinoitherium</i>	Ashawq- Taqah Formation - Dhofar (Oman)	early Oligocene (Seiffert 2006)	Thomas <i>et al.</i> 1999	8
<i>Arsinoitherium</i> sp.	Ashawq Formation - Thaytiniti - Dhofar (Oman)	earliest Oligocene (Seiffert 2006)	Thomas <i>et al.</i> 1989	8
<i>Palaeoamasia</i> sp.	Cemalettin Formation, Boyabat-Sinop (Turkey)	Eocene – Oligocene transition	Sanders <i>et al.</i> 2014	3a
<i>Arsinoitherium</i> sp.	Aydim Formation - Dhofar (Oman)	late Eocene (Bartonian-Priabonian)	Al-Sayigh <i>et al.</i> 2007	8
<i>Arsinoitherium</i> sp.	Dor el Talha (Libya)	early Oligocene	Wight 1980; Rasmussen <i>et al.</i> 2008	7
<i>Arsinoitherium</i> sp.	Oued el Grigema (Tunisia)	late Eocene	Vialle <i>et al.</i> 2013	6
<i>Namatherium blackcrowense</i>	Black Crow - Sperrgebiet (Namibia)	middle Eocene (Lutetian)	Pickford <i>et al.</i> 2008	5
<i>Crivadiatherium mackennai</i>	Depression of Hateg (Romania)	middle Eocene (Radulesco & Samson 1987)	Radulesco <i>et al.</i> 1976	4
<i>Crivadiatherium iliescui</i>	Depression of Hateg (Romania)	middle Eocene (Radulesco & Samson 1987)	Radulesco & Sudre 1985	4
<i>Palaeoamasia kansui</i> Ozansoy 1966	Boyabat - Sinop ; Çiçekdağı - Kırşehir ; Bultu-Zile - Tokat; Boğazlıyan-YeniFakili - Yozgat (Turkey)	early Eocene to middle Eocene	Ozansoy 1966; Sen & Heintz 1979; Kaya 1995	3a, c, d, e
<i>Palaeoamasia kansui</i> Ozansoy 1966	Eski-Çeltek - Amasya (Turkey)	early Eocene (Koc & Turkmen 2002; Métais <i>et al.</i> 2012)	Sen & Heintz 1979	3b
<i>Palaeoamasia</i> sp.	Uzunçarşidere Formation - Haymana-Polatlı Bassin (Turkey)	late Paleocene (Kazancı & Gökten 1986; Ladevèze <i>et al.</i> 2010) or early Eocene (Kappelman <i>et al.</i> 1996; Maas <i>et al.</i> 1998; Maas <i>et al.</i> 2001)	Gül 2003	3f
<i>Hypsamasia seni</i>	Uzunçarşidere Formation - Haymana-Polatlı Bassin (Turkey)	late Paleocene (Kazancı & Gökten 1986; Ladevèze <i>et al.</i> 2010) or early Eocene (Maas <i>et al.</i> 1998)	Maas <i>et al.</i> 1998	2
<i>Phenacolophus fallax</i>	Gashato Formation (Mongolia)	late Paleocene - early Eocene	Matthew & Granger 1925; McKenna & Manning 1977	1

Table 2. Interordinal classification of Embrithopoda (parenthetical mode) according to previous authors.

Simpson 1945	<u>Paenungulata</u> : (Proboscidea, Hyracoidea, Embrithopoda , Pantodonta, Pyrotheria, Dinocerata, (Sirenia +Desmostyliiformes))
McKenna 1975	<u>Ungulata</u> : (Arctocyona, Tillodontia, Tubulidentata, Dinocerata, Embrithopoda , Artiodactyla), (Condylarthra, Perissodactyla, Hyracoidea), (<u>Tethytheria</u> : (Proboscidea, Sirenia, Desmostylia))
Novacek 1986	<u>Ungulata</u> : (Arctocyonia, Dinocerata, Embrithopoda , Artiodactyla, Cetacea, Perissodactyla), (<u>Paenungulata</u> : (Hyracoidea, Proboscidea, Sirenia, Desmostylia))
Court 1992b, 1992c	(Sirenia,(Proboscidea, Embrithopoda))
Novacek & Wyss 1986	(Embrithopoda, Paenungulata) or (Embrithopoda , Tethytheria)
McKenna & Bell 1997	<u>Uranotheria</u> : (Hyracoidea, Embrithopoda , <u>Tethytheria</u> : (Sirenia, (Proboscidea + Desmostylia)))
Gheerbrant <i>et al.</i> 2005a	(<i>Phenacolophus</i> , Embrithopoda),(<i>Minchenella</i> , (Anthracobunidae, (Desmostylia, (Sirenia, Proboscidea))))
Tabuce <i>et al.</i> 2007	(<i>Arsinoitherium</i> , (Sirenia + Proboscidea + Hyracoidea))
Seiffert 2007	<u>Paenungulata</u> : (<u>Tethytheria</u> : (Proboscidea, (<i>Arsinoitherium</i> +Sirenia))), Hyracoidea)
Gheerbrant 2009	(Hyracoidea, (<i>Phenacolophus</i> , (Embrithopoda , (<i>Minchenella</i> , (Anthracobunidae, (Desmostylia, Sirenia), Proboscidea))))))
Benoît <i>et al.</i> 2013	(Sirenia, (<i>Desmostylus</i> , (<i>Arsinoitherium</i> , Proboscidea)))
Gheerbrant <i>et al.</i> 2014	((Perissodactyla, <i>Radinskya</i>),(Hyracoidea,(<i>Anthracobunia</i> ,((<i>Eritherium</i> ,(<i>Phosphatherium</i> , <i>Numidoitherium</i>)),(Desmostylia,(Sirenia,(<i>Minchenella</i> ,(<i>Phenacolophus</i> , Embrithopoda))))))
Cooper <i>et al.</i> 2014	((Desmostylia, Anthracobunidae, Perissodactyla), (Afrotheria: (Paenungulata: (((Embrithopoda , Sirenia), <i>Phosphatherium</i> , Proboscidea), <i>Eritherium</i> , Hyracocoidea))))

Underlined taxon names followed by a colon are for higher-taxa. Note that *Arsinoitherium* is displayed in bold as the only representative of embrithopods chosen in the concerning analysis.

Table 3. Dental measurements (in mm) of new material of *Palaeoamasia kansui*, and casts of *Hypsamasia seni*, *Crivadiatherium mackennai* and *C. iliescui* specimens.

	Institution number	Length	Mesial width	Distal width
<i>P. kansui</i>				
Left P2	ITU-EÇ-8	14.7	16.5	–
Left P3	ITU-EÇ-8	16.2	18.7	–
Right P4	ITU-EÇ-7	–	24.5	–
Right M1	ITU-EÇ-7	23.8	30.4	31.4
Right M2	ITU-EÇ-7	32.0	33.2	28.0
Left M3	MNHN-EÇ-6	33.5	–	28.1
Left p2	ITU-EÇ-9	–	8.1	7.8
Left p3	ITU-EÇ-9	16.6	10.7	11.3
Right p4	MNHN-EÇ-5	–	12.3	–
Left p4	ITU-EÇ-9	16.9	12.1	11.5
Left m1	ITU-EÇ-9	–	15.9	17.1
Right m1	MNHN-EÇ-5	24.2	17.8	18.1
<i>H. seni</i>				
Right P2	AK95-52	–	17.0	–
Right P3	AK95-52	18.0	–	–
Right P4	AK95-52	–	–	–
Left M2	AK95-52	–	39.9	–
<i>C. mackennai</i>				
Left p4		26.0	16.1	16.7
Left m1		34.6	18.4	20.6
<i>C. iliescui</i>				
Left p2		–	–	16.1
Left p3		25.3	18.0	18.8
Left p4		28.0	18.5	19.2
Left m2		46.8	25.2	26.9
Right m2		45.9	26.9	26.3
Left m3		>55.0	26.0	26.2

Table 4. List of unambiguous apomorphies on nodes of the strict consensus tree.

Synapomorphies : node 2 (Paenungulata) : **18**(1), 29(1), **30**(1), **38**(1), **39**(1), 40(1), 53(1 or 2), **54**(1), **59**(1), **75**(1), 79(0), 87(0) ; node 3 (Proboscidea + *Seggeurius*) : **45**(1), **99**(0) ; node 4 (Proboscidea) : 46(0), **49**(1), **55**(0), **80**(1), **106**(3), **108**(1), **117**(1), **127**(1) ; node 5 (Embrithopoda *sensu lato*) : **11**(1), **51**(0), **65**(0), **69**(0), **70**(0), 72(1), **114**(0), **126**(1), 128(1) ; node 6 (Embrithopoda *sensu stricto*) : 53(3), **59**(2), **73**(1) ; node 7 (Arsinoitheriidae) : 2(0 or 1), **47**(1) ; node 8 (Arsinoitheriinae) : **44**(1), **83**(1), **102**(1), **116**(1) ; node 9 (Palaeoamasiinae) : 20(1), **106**(0), **115**(0).

Autapomorphies : *Seggeurius amourensis* : 23(0), 86(0) ; *Eritherium azzouzorom* : 32(0) ; *Phosphatherium escuilliei* : 70(2) ; *Phenacolophus fallax* : 27(1), 77(1), 93(0), 110(0) ; *Namatherium blackcrowense* : 13(1) ; *Arsinoitherium zitteli* : not any character unambiguous ; *Arsinoitherium giganteum* : not any character unambiguous ; *Palaeoamasias kansui* : 37(1), 103(1) ; *Hypsamasias seni* : not any character unambiguous ; *Crivadiatherium mackennai* : 124(0) ; *Crivadiatherium iliescui* : 129(0), 130(0).

Unambiguous and non-homoplastic characters are in bold, unambiguous autapomorphies of which corresponding state is not homoplastic are in italics and unambiguous and weakly homoplastic characters ($0.75 \leq RI < 1$) are underlined. Homoplastic characters ($RI < 0.75$) lack any annotations. Each character state is mentioned in brackets. Ambiguous characters are excluded from that list. Complete distribution of characters is in Appendix 4.

Table 5. Number of characters scored for *Arsinoitherium*, *Palaeoamasia*, *Namatherium*, *Crivadiatherium* and *Hypsamasia* species depending on available specimens.

Taxa \ Characters	Cranial- mandibular (/10)	Upper dentition (/63)	Lower dentition (/57)	Total (/130)
<i>A. zitteli</i>	10	55	54	119
<i>P. kansui</i>	6	62	51	119
<i>N. blackcrowense</i>	4	49	0	53
<i>C. iliescui</i>	0	0	51	51
<i>A. giganteum</i>	1	12	36	49
<i>H. seni</i>	0	49	0	49
<i>C. mackennai</i>	0	0	40	40

Numbers in bracket present the total number of characters available on concerning anatomical parts.

1
2
3 **APPENDIX S1. LIST OF CRANIAL AND DENTAL CHARACTERS USED IN THE**
4 **CLADISTIC ANALYSIS**
5
6

7 N.B. Characters chosen from literature are mentioned in brackets; asterisk (*) indicates new
8 characters, not used in any previous phylogenetic analysis; char., characters; (o), ordered
9 character states.
10
11
12

13
14
15
16 *Cranial-mandibular characters*
17

- 18 1- **Zygomatic arch shape** : (0) Poorly divergent laterally ; (1) Widely divergent laterally
19 (char. 21 in Gheerbrant *et al.* 2005 and char. 130 in Gheerbrant 2009)
20
21 2- ***Zygomatic arch, position of zygomatic process (distal side in ventral view) (o)** : (0)
22 Begins at distal loph level of M3 ; (1) Begins at mesial loph level of M3 ; (2) Begins at
23 level of M2-P4. (Sen & Heintz 1979 ; Court 1992c ; Pickford *et al.* 2008)
24
25 3- **Zygomatic process of the squamosal** : (0) Reduced ; (1) Strong (char. 23 of
26 Gheerbrant *et al.* 2005 and char. 132 of Gheerbrant 2009)
27
28 4- **Mandibular symphysis, distal edge** : (0) At level of premolar ; (1) At level of molar
29 (char. 38 modified after Gheerbrant *et al.* 2005 and char. 46 in Gheerbrant, 2009)
30
31 5- **Mandibular symphysis, connection** : (0) Unfused ; (1) Fused (char. 47 in Gheerbrant
32 2009)
33
34 6- **Mandibular symphysis, orientation in lateral view** : (0) Oblique ; (1) (Sub-)vertical
35 (McKenna & Manning 1977)
36
37 7- **Horizontal ramus** : (0) Low; (1) High (char. 40 in Gheerbrant *et al.* 2005 and char. 48
38 in Gheerbrant, 2009)
39
40 8- ***Angular discontinuity of mandible between premolars and molars in lateral view**
41 : (0) Absent ; (1) Present (Court 1992b)
42
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3 9- **Skull shape** : (0) Rostrum > basicranium ; (1) Rostrum ≤ basicranium (Froehlich 2002 ;
4 char. 109 in Gheerbrant 2009)
5
6
7 10- **Tuber maxillae, development**: (0) Reduced or absent ; (1) Wide (char. 122 modified
8 after Gheerbrant 2009)
9
10

11
12
13
14 *Dental characters*

- 15
16 11- **Dental dimensions** : (0) Small ; (1) Large (char. 46 in Gheerbrant *et al.* 2005)
17
18
19

20
21 *Upper teeth*

- 22
23 12- **Upper premolars, molarization** : (0) Absent ; (1) molarized P4 and/or P3 (McKenna
24 & Manning 1977)
25
26
27 13- ***Upper premolars, lingual cingulum** : (0) Absent ; (1) Present
28
29 14- ***Upper premolars, mesial cingulum** : (0) Present; (1) Absent (Sen & Heintz 1979)
30
31 15- ***Upper premolars, distal cingulum** : (0) Present; (1) Absent (Sen & Heintz 1979)
32
33 16- ***Upper premolars, labial cingulum** : (0) Present; (1) Absent
34
35
36 17- ***Upper premolars, junction of postprotocrista/distal cingulum** : (0) Absent ; (1)
37 Present (Maas *et al.*, 1998)
38
39 18- ***Upper premolars, postprotocrista orientation** : (0) Oriented rather disto-labially
40 (towards metacone) ; (1) Oriented rather mesio-distally
41
42
43 19- ***Upper premolars, height of root / crown** : (0) $0 \geq 1$; (1) $0 < 1$ (Sen & Heintz 1979)
44
45
46 20- **P2, number of root** : (0) Two-rooted ; (1) Three-rooted ; (2) One-rooted (char. 99
47 modified after Gheerbrant *et al.* 2005)
48
49
50 21- **P2, protocone** : (0) Present; (1) Absent (char. 100 modified after Gheerbrant *et al.*
51 2005)
52
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3 22- ***P2, preprotocrista and protocone** : (0) Form a mesio-lingually convex crista ; (1)
4 Form a straight crista
5
6
7 23- **P2, metacone** : (0) Absent ; (1) Present (char. 104 modified after Gheerbrant *et al.*
8 2005)
9
10
11 24- ***P2, labial side** : (0) Smooth ; (1) Undulated
12
13 25- ***P2, mesio-distal valley** : (0) Narrow (wide ectoloph) ; (1) Wide (narrow ectoloph)
14
15 26- ***P2-P3, ectoloph** : (0) Present ; (1) Absent (Sen & Heintz 1979)
16
17 27- **P3, protocone** : (0) Present; (1) Absent or reduced (char. 101 in Gheerbrant *et al.* 2005)
18
19 28- ***P3, number of roots** : (0) Two-rooted ; (1) Three-rooted (char. 68 modified after
20 Gheerbrant 2009)
21
22 29- **P3, paraconule** : (0) Present ; (1) Absent (char. 23 in Froehlich 2002)
23
24 30- **P3, metaconule** : (0) Present ; (1) Absent (Maas *et al.* 1998 ; char. 30 in Froehlich
25 2002)
26
27 31- **P3, postprotocrista**: (0) Absent ; (1) Present (char. 27 in Froehlich 2002)
28
29 32- **P3, metacone** : (0) Absent ; (1) Present (char. 70 modified after Gheerbrant, 2009)
30
31 33- **P3, metacone** : (0) Smaller than paracone ; (1) Similar size (char. 70 modified after
32 Gheerbrant 2009)
33
34 34- ***P2-4, hypocone** : (0) Absent ; (1) Present (char. 108 modified after Gheerbrant *et al.*
35 2005)
36
37 35- ***P3-4, paracone and protocone** : (0) Joined by a preprotocrista ; (1) Disjoined (Sen &
38 Heintz 1979)
39
40 36- ***P3, preprotocrista / postprotocrista, length proportion** : (0) Preprotocrista >
41 postprotocrista ; (1) Preprotocrista \leq postprotocrista (Maas *et al.* 1998)
42
43 37- ***P4, preprotocrista / postprotocrista, length proportion** : (0) Preprotocrista >
44 postprotocrista ; (1) Preprotocrista \leq postprotocrista (Maas *et al.* 1998)
45
46
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3 38- **P4, paraconule** : (0) Present ; (1) Absent (Maas *et al.* 1998 ; char. 31 in Froehlich
4
5 2002)
6
7 39- **P4, metaconule** : (0) Present ; (1) Absent (Maas *et al.* 1998 ; char. 33 in Froehlich
8
9 2002)
10
11 40- **P4, postprotocrista** : (0) Present ; (1) Absent (char. 35 in Froehlich 2002)
12
13 41- ***P4/M1, proportion of dimensions** : (0) $P4 \approx M1$; (1) $P4 < M1$ (Sen & Heintz 1979)
14
15 42- ***Upper Molars, root / crown height proportion** : (0) >1 ; (1) <1 (Sen & Heintz 1979)
16
17 43- **Upper Molars, lingual cingulum** : (0) Absent ; (1) Present (char. 121 de Gheerbrant *et*
18
19 *al.* 2005)
20
21 44- ***Upper Molars, distal cingulum**: (0) Present ; (1) Absent (Sen & Heintz 1979)
22
23 45- **Upper Molars, distocrista (=posthypocrista)** : (0) Absent ; (1) Present (at least on M1-
24
25 2) (char. 99 in Gheerbrant 2009)
26
27 46- **Upper Molars, distal cingulum (shape and connection) (o)** : (0) Distal cingulum
28
29 (=postcingulum) in continuity with the hypocone via the distocrista ; (1) Distal
30
31 cingulum extended lingually below the hypocone ; (2) Distal cingulum extended
32
33 lingually below the hypocone and linked to a lingual cingulum (char. 86 in Gheerbrant
34
35 2009)
36
37 47- ***Upper Molars, labial cingulum** (ectocingulum *sensu* Froehlich 2002) : (0) Present ;
38
39 (1) Absent
40
41 48- **Upper Molars, parastyle position** : (0) Labial to the paracone ; (1) Mesial (modified
42
43 after of char. 110 in Gheerbrant *et al.* 2005 and char. 82 in Gheerbrant 2009)
44
45 49- **Upper Molars, preparacrista** : (0) Present ; (1) Absent (char. 93 modified after
46
47 Gheerbrant 2009)
48
49 50- **Upper Molars, preparacrista** : (0) Well developed and distinct ; (1) Small (reduced)
50
51 (char. 93 modified after Gheerbrant 2009)
52
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3 51- **Upper Molars, preparacrista orientation** : (0) Rather transversal ; (1) Rather sagittal
4
5 (char. 93 modified after Gheerbrant 2009)
6
7 52- ***Upper Molars (and dP4), postparacrista** (*sensu* Maas *et al.* 1998) : (0) Distinct ; (1)
8
9 Reduced or absent (char. 112 in Gheerbrant *et al.* 2005)
10
11 53- **Upper Molars, shape of postparacrista (o)** : (0) Rectodont and not linked to
12
13 mesostyle ; (1) Linked to the lingual flank of the mesostyle and nearly rectodont ; (2)
14
15 Extensively linked to the mesostyle and noticeably dilambdodont ; (3) Lingual
16
17 migration of paracone and metacone with the postparacrista hyper-dilambdodont (char.
18
19 91 in Gheerbrant 2009)
20
21
22 54- **Upper Molars, mesostyle development** : (0) Reduced or absent ; (1) Developed and
23
24 well distinct (char. 113 in Gheerbrant *et al.* 2005)
25
26
27 55- **Upper Molars, mesostyle position** : (0) Close to paracone and metacone ; (1) Shifted
28
29 labially (char. 89 modified after Gheerbrant 2009)
30
31
32 56- **Upper Molars, conules** : (0) Present ; (1) Absent or obviously reduced (car. 114 de
33
34 Gheerbrant *et al.* 2005)
35
36
37 57- **Upper Molars, postprotocrista** : (0) Present ; (1) Absent (char. 119 modified after
38
39 Gheerbrant *et al.* 2005)
40
41 58- **Upper Molars, lingual roots** : (0) Endowed with a vertical median groove ; (1)
42
43 Divided (char. 122 modified after Gheerbrant *et al.* 2005)
44
45 59- **Upper Molars, structural plan (o)** : (0) Rectodont ; (1) Dilambdodont ; (2) Hyper-
46
47 dilambdodont ['pseudolophodonty'] (char. 124 in Gheerbrant *et al.* 2005)
48
49 60- **Upper Molars, structural plan** : (0) Bunodont-lophodont ; (1) True lophodont [non-
50
51 applicable on taxa bearing 'pseudolophodonts' teeth] (char. 125 modified after
52
53 Gheerbrant *et al.* 2005 and char. 80 modified after Gheerbrant 2009)
54
55
56 61- ***Upper Molars, ectoloph** : (0) Present ; (1) Absent (Sen & Heintz 1979)
57
58
59
60

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3 62- ***Upper Molars, labial / lingual height proportion** : (0) Higher ; (1) Lower or equal
4
5 (« unilateral hypsodonty » *sensu* Radulesco *et al.* 1976) (Sen & Heintz 1979)
6
7 63- **Upper Molars, postmetacrista** (metastyle *sensu* Froehlich 2002) : (0) Present ; (1)
8
9 Absent (Court 1992b ; char. 92 in Gheerbrant 2009)
10
11 64- **Upper Molars, postmetacrista** : (0) Developed ; (1) Reduced (Court 1992b ; char. 92
12
13 in Gheerbrant 2009)
14
15 65- **Upper Molars, postmetacrista orientation** : (0) Labio-lingual ; (1) Mesio-distal
16
17 (Court 1992b ; char. 92 in Gheerbrant 2009)
18
19 66- **Upper Molars, loph orientation** (or pseudoloph) **in occlusal view** : (0) Disto-
20
21 lingually oblique ; (1) Transverse (Court 1992b ; char. 120 in Gheerbrant *et al.* 2005)
22
23 67- ***Upper Molars, loph wear surfaces** (or pseudoloph) **in lateral view** : (0) Merged
24
25 with occlusal plan ; (1) Mesio-ventrally inclined (Sen & Heintz 1979 ; Pickford *et al.*
26
27 2008)
28
29 68- **Upper Molars, relative size** : (0) $M3 < M2$; (1) $M3 \geq M2$ (Sen & Heintz 1979 ; char.
30
31 123 modified after Gheerbrant *et al.* 2005)
32
33 69- **Upper Molars, prehypocrista** : (0) Absent ; (1) Present (char. 97 in Gheerbrant 2009)
34
35 70- **Upper Molars, metaloph** : (0) Formed by transversal alignment of hypocone,
36
37 metaconule (if present) and metacone ; (1) Formed principally by a prehypocrista which
38
39 joins the metaconule or the base of metacone ; (2) Formed by a prehypocrista which
40
41 joins the apex of metacone (true lophodonty) (char. 97 modified after Gheerbrant 2009)
42
43 71- ***M3, mesio-lingual angle** : (0) Mesial and lingual cingulums continuous ; (1) Mesial
44
45 and lingual cingulums discontinuous
46
47 72- ***Upper teeth row, width (o)** : (0) Increase progressively from P2 to M3 (although M3
48
49 is variable) ; (1) Increase progressively from P2 to M2, M3 is clearly larger ; (2)
50
51
52
53
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55
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2
3 Increase progressively from P2 to M1, M2 and M3 are clearly larger (Pickford *et al.*
4
5 2008)
6

7
8 73- **Crown height** : (0) Crown uniformly brachyodont ; (1) Lingual and/or labial
9
10 hypsodonty (char. 106 in Gheerbrant 2009)
11

12
13
14 *Lower teeth*

15
16 74- **Lower incisors, orientation** : (0) Sub-vertical ; (1) Antero-posteriorly inclined (char.
17
18 48 in Gheerbrant *et al.* 2005)
19

20
21 75- **Lower incisors, absolute size** : (0) Small ; (1) Medium to large (char. 49 in Gheerbrant
22
23 *et al.* 2005)
24

25
26 76- **Lower incisors, relative size of i1** : (0) $i1 \leq i2$; (1) $i1 > i2$ (char. 50 in Gheerbrant *et al.*
27
28 2005 ; char. 3 in Gheerbrant 2009)
29

30
31 77- **Lower incisors, relative size of i3** : (0) $i3 \leq i2$; (1) $i3 > i2$ (char. 5 modified after
32
33 Gheerbrant 2009)
34

35
36 78- **Lower canine** : (0) Incisiform ; (1) Caniniform (Court, 1992b ; McKenna & Manning,
37
38 1977)
39

40
41 79- **Lower dentition, c-p diastema** [(d)p1 or p2] : (0) Absent ; (1) Present (modified after
42
43 char. 55 in Gheerbrant *et al.* 2005 and char. 8 in Gheerbrant 2009)
44

45
46 80- **Lower premolars, paraconid** : (0) Present ; (1) Absent or weak (char. 64 modified
47
48 after Gheerbrant *et al.* 2005)
49

50
51 81- **Lower premolars, paraconid (position)** : (0) Low ; (1) High (char. 63 in Gheerbrant *et*
52
53 *al.* 2005)
54

55
56 82- ***Lower premolars, labial groove in labial view** : (0) Vertical ; (1) Mesio-dorsally
57
58 oblique
59
60

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2
3 83- ***p2-p3, trigonid and talonid (height) in lateral view** : (0) Trigonid > talonid ; (1)
4
5 Trigonid \approx talonid (Radulesco & Sudre 1985)
6
7 84- **Lower premolars, labial cingulid** : (0) Present ; (1) Absent (char. 68 modified after
8
9 Gheerbrant *et al.* 2005)
10
11 85- ***Lower premolars, lingual cingulid** : (0) Present ; (1) Absent (Sen & Heintz 1979)
12
13 86- **(d)p1** : (0) Two-rooted ; (1) One-rooted (char. 57 modified after Gheerbrant *et al.*
14
15 2005 ; char. 10 in Gheerbrant 2009)
16
17 87- ***Diastema between (d)p1 et p2** : (0) Absent ; (1) Present
18
19 88- **p2** : (0) Two-rooted ; (1) One-rooted (char. 59 in Gheerbrant *et al.* 2005)
20
21 89- **p3, molarization** : (0) Absent ; (1) Present (char. 61 modified after Gheerbrant *et al.*
22
23 2005)
24
25 90- **p3, hypoconid** : (0) Absent ; (1) Present (McKenna & Manning 1977)
26
27 91- ***p3, metaconid position** : (0) Integrated into mesio-distal row ; (1) Lingually isolated
28
29 and forms a notch (Court, 1992b)
30
31 92- **p4, molarization** : (0) Absent ; (1) Present (char. 61 modified after Gheerbrant *et al.*
32
33 2005)
34
35 93- ***p4, metaconid position** : (0) Integrated into mesio-distal row ; (1) Lingually isolated
36
37 and forms a notch (Court 1992b)
38
39 94- **p4, mesostylid** : (0) Metaconid lacks mesostylid ; (1) Metaconid possess a mesostylid
40
41 (McKenna & Manning 1977)
42
43 95- ***p4, lingual fossettid in occlusal view** : (0) Distal fossettid more developed mesio-
44
45 distally in comparison to mesial fossettid ; (1) Distal fossettid less developed mesio-
46
47 distally in comparison to mesial fossettid (Radulesco *et al.* 1976 ; Sen & Heintz 1979 ;
48
49 Court 1992b)
50
51 96- ***p4, distal lingual fossettid in lingual view** : (0) in 'V' shape ; (1) in 'U' shape
52
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2
3 97- **p4, mesial cingulid** : (0) Present ; (1) Absent (McKenna & Manning 1977)
4
5 98- ***p4, distal cingulid** : (0) Present ; (1) Absent (McKenna & Manning 1977)
6
7 99- **p4, talonid development** : (0) Reduced ; (1) Enlarged (char. 19 in Gheerbrant 2009)
8
9 100- **p4** : (0) Non-bilophodont (protocristid oblique, hypolophid absent) ; (1) sub-lophodont
10
11 (transversal protocristid, differentiated hypolophid) (char. 65 of Gheerbrant *et al.* 2005)
12
13 101- ***p4, trigonid and talonid (height) lateral view** : (0) Trigonid > talonid ; (1) Trigonid
14
15 \approx talonid (Radulesco & Sudre 1985)
16
17 102- ***Lower molars, mesial cingulid** : (0) Present ; (1) Absent (Radulesco & Sudre 1985)
18
19 103- ***Lower molars, mesial cingulid (development)** : (0) Strong, forms a fossette on
20
21 mesiobuccal angle; (1) Weakly developed
22
23 104- ***Lower molars, distal cingulid (development)** : (0) Not elevated ; (1) Lingually
24
25 elevated
26
27 105- **Lower molars, mesostylid** : (0) Present ; (1) Weak to absent (McKenna & Manning
28
29 1977)
30
31 106- **Lower molars, orientation of cristid oblique in occlusal view (o)** : (0) Noticeably
32
33 oblique, mesial ending in the lingual half of trigonid where it is extended towards apex
34
35 of metaconid ; (1) Cristid oblique is extended towards the base of metaconid ; (2)
36
37 Mesial ending of cristid oblique is at half of width on the distal flank of trigonid ; (3)
38
39 Cristid oblique is weakly oblique, mesial ending at labial half of trigonid (char. 69
40
41 modified after Gheerbrant *et al.* 2005 ; McKenna & Manning 1977)
42
43 107- **Lower molars, entocristid** : (0) Present ; (1) Absent (char. 71 modified after
44
45 Gheerbrant *et al.* 2005)
46
47 108- **Lower molars, premetacristid** : (0) Reduced to absent ; (1) Distinct (char. 72 in
48
49 Gheerbrant *et al.* 2005)
50
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3 109-**Lower molars, postmetacristid** : (0) Absent or well reduced ; (1) Distinct and more or
4
5 less rounded into the metastylid (char. 73 in Gheerbrant *et al.* 2005)
6
7 110-**Lower molars, paraconid** : (0) Present ; (1) Absent (fused into paralophid) (char. 74 in
8
9 Gheerbrant *et al.* 2005)
10
11 111-**Lower molars, trigonid and paracristid** (paralophid) : (0) Trigonid is more or less
12
13 mesio-distally flared with a more developed and functional paracristid ; (1) Trigonid is
14
15 short, noticeably constrict mesio-distally, paracristid reduced (char. 75 in Gheerbrant *et*
16
17 *al.* 2005)
18
19 112-**Lower molars, protocristid** : (0) Protocristid bearing a remarkable median notch ; (1)
20
21 Protocristid lophoid (=protolophid), cristid high and sub-continuous (char. 76 in
22
23 Gheerbrant *et al.* 2005)
24
25 113-**Lower molars, distal lophid** (hypolophid) - **postcristid complex** : Hypolophid
26
27 incomplete or composite, formed by an entolophid in continuity with labial segment of
28
29 postcristid which is shifted anterior to the hypoconulid ; (1) Hypolophid sub-complete
30
31 but bears a strong median notch ; (2) Hypocristid lophoid (high and sub-continuous
32
33 from the apex of entoconid towards hypoconid) (char. 79 modified after Gheerbrant *et*
34
35 *al.* 2005)
36
37 114-**Lower molars, appearance of lophids** : (0) Lophids oblique in comparison to the
38
39 transversal axis ; (1) Lophids obviously transversal (char. 85 in Gheerbrant *et al.* 2005)
40
41 115-***Lower molars, cristid oblique** : (0) High (at the level of occlusal surface of talonid) ;
42
43 (1) Low (Sen & Heintz, 1979)
44
45 116-***Lower molars, height of trigonid/talonid in lateral view** : (0) Trigonid > talonid ;
46
47 (1) Trigonid \approx talonid (Radulesco & Sudre 1985)
48
49 117-***Lower molars, cristid oblique** : (0) Mesio-disto-lingually oriented ; (1) Mesio-
50
51 distally centered (Sen & Heintz 1979)
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3 118-***Lower molars, paralophid development** : (0) Weak ; (1) Well developed (McKenna
4 & Manning 1977 ; Radulesco & Sudre 1985 ; Radulesco & Samson 1987)
5
6
7 119-***Lower molars, paralophid orientation** : (0) Transversal ; (1) Sagittal (McKenna &
8 Manning 1977 ; Radulesco & Sudre 1985 ; Radulesco & Samson 1987)
9
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11 120-**Relative size of low molars** : (0) $m_3 \geq m_2$; (1) $m_3 < m_2$; (2) Size obviously increasing
12 from m_1 to m_3 (char. 86 in Gheerbrant *et al.* 2005)
13
14
15 121-**Lower molars, postentoconulid** : (0) Absent ; (1) Present (char. 82-83-84 modified
16 after Gheerbrant *et al.* 2005)
17
18
19 122-**Lower molars, lophodonty** : (0) Bunodont-lophodont structure ; (1) True lophodonty
20 (char. 126 modified after Gheerbrant *et al.* 2005)
21
22
23 123-**Lower molars, labial cingulid** : (0) Present ; (1) Absent (char. 68 modified after
24 Gheerbrant *et al.* 2005)
25
26
27 124-**Lower molars, lingual cingulid** : (0) Present ; (1) Absent (Sen & Heintz 1979)
28
29
30 125-**m1-2, trigonid/talonid volume in occlusal view** : (0) $\text{Trigonid} \geq \text{talonid}$; (1) Trigonid
31 $< \text{talonid}$ (Sen & Heintz 1979 ; char. 75 modified after Gheerbrant *et al.* 2005)
32
33
34 126-***m1-2, hypoconulid** : (0) Present ; (1) Absent
35
36
37 127-**m1-2, hypoconulid position** : (0) Hypoconulid median ; (1) Hypoconulid labial (char.
38 81 modified after Gheerbrant *et al.* 2005)
39
40
41
42 128-**m3, hypoconulid** : (0) Strong ; (1) Weak (char. 98 in Froehlich 2002)
43
44
45 129-***m3, hypoconulid connection (o)** : (0) Hypoconulid possess at least two crests
46 reaching the distal flank of entoconid ; (1) Only one crest reaches the distal flank of
47 entoconid ; (2) Isolated (with or without crests)
48
49
50 130-***m3, hypoconulid (inclination) in lingual view** : (0) Hypoconulid parallel to the
51 entoconid ; (1) Hypoconulid distally inclined (Sen & Heintz 1979)
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**APPENDIX S2. DATA MATRIX OF 130 CHARACTERS (10 CRANIAL-
MANDIBULAR, 120 DENTAL) APPLIED ON 14 TERMINAL TAXA
(PERISSODACTYLS, HYRACOID, PROBOSCIDEANS, EMBRITHOPODS, AND
PHENACOLOPHUS). THE THREE OUTGROUPS ARE A PRIORI XENICOHIPPIUS,
ARENAHIPPIUS, AND RADINSKYA**

Taxon	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667
<i>Xenicohippus</i>	0200100001	01000000?0	0111100000	1110100000	1?10010000	1000-00000	0000110111
<i>Arenahippus</i>	1?00100011	00????00?2	1?1?000000	11101??000	1?200?0101	1000-00??0	0?00?00011
<i>Radinskya</i>	??0??0000	0?????????	??????0?0?	??????000?	??0?0?0001	1?00-00?01	0?0110?011
<i>Seggeurius amourensis</i>	??????00??	000010-1?0	0?01000?11	110011????	0?10120000	1021111?10	001--10?11
<i>Eritherium azzouzorom</i>	12?00?0?10	000?11--??	?????10111	00-01??111	0?0010011-	-011011010	1101110011
<i>Phosphatherium escuilliei</i>	1210001010	0101??-??0	1?10?10111	01000--111	1?0010011-	-011011011	1101110112
<i>Phenacolophus fallax</i>	??2?0?110??	11?100-??2	??000110??	-100--?1??	??10020001	0021100110	1100001100
<i>Palaeoamasias kansui</i>	00?0?0?0?0	1000011101	0110000111	1110011110	1010011000	003111012-	1001001100
<i>Hypsamasias seni</i>	???????????	10000111?1	0011100101	1110000110	??0??0000	0031110?2-	1001001???
<i>Crivadiatherium mackennai</i>	???????????	???????????	???????????	???????????	???????????	???????????	???????????
<i>Crivadiatherium iliescui</i>	???????????	???????????	???????????	???????????	???????????	???????????	???????????
<i>Arsinoitherium zitteli</i>	0001110100	100011-110	0011000011	01110--111	11110-1000	01-111102-	101--01100
<i>Arsinoitherium giganteum</i>	?1?????????	1? ?????????	????????????	????????????	??110-????	??????????-	?01--01?00
<i>Namatherium blackcrowense</i>	121???????	101000--0?	?????00011	01100--111	1?10020000	003111002-	101--00100

Taxon	0000000000	0000000000	0000000001	1111111111	1111111111	1111111111
<i>Xenicohippus</i>	10010??110	0100011011	1111010010	0000021001	1001100000	0001000011
<i>Arenahippus</i>	??010?010	0????1100	00?00??0?	????12?0?1	100110?000	?0?1?01?
<i>Radinskya</i>	-?0???????	???????????	???????????	???????????	???????????	???????????
<i>Seggeurius amourensis</i>	0?0????100	1??110?00?	00????0000	?001?21011	1011100002	?001000011
<i>Eritherium azzouzorom</i>	0001110001	1001110101	?011??1100	0001130111	10111?1001	1011101011
<i>Phosphatherium escuilliei</i>	000111-?11	-0011--101	-010?-1100	0001130101	11211010?2	1111101021
<i>Phenacolophus fallax</i>	0100111000	0000110100	?0000?0011	0001120010	0120100002	000111-1--
<i>Palaeoamasias kansui</i>	021?????10	1101111011	1111001111	1011001001	1120000002	011101-121
<i>Hypsamasias seni</i>	??1???????	???????????	???????????	???????????	???????????	???????????
<i>Crivadiatherium mackennai</i>	???????????	10000?????	?111001111	0001001001	012000011?	010011-???
<i>Crivadiatherium iliescui</i>	??11110?0?	10000??011	1111011111	0001001001	0120000110	011111-000
<i>Arsinoitherium zitteli</i>	1010100000	1011110001	0011111111	11-0011001	1120110000	011101-12?
<i>Arsinoitherium giganteum</i>	1?1???????	10101??01	?0??????11	11-0011001	1120110000	011?01-???
<i>Namatherium blackcrowense</i>	111???????	???????????	???????????	????0?????	???????????	???????????

APPENDIX S3. TABLE OF MEAN SIZE VALUES OF STUDIED TAXA

N.B. The measurements are given in mm. The talonid width is taken into consideration when trigonid is not accurate. N, numbers of specimens measured; L, length; W, width; P/p and M/m are upper/lower premolars and molars, respectively; ‘-’, specimen not available; ‘?’, measurements not accurate due to possible damage or advanced wear stage. For the length/width diagrams related to that table, see Figure 4 in the main text. The premolars and molars of *Crivadiatherium*, *Hypsamasia* and the new material of *P. kansui* were directly measured by authors. Other measurements are from McKenna & Manning (1977), Sen & Heintz (1979), Kaya (1995), A. Gül, unpub. data (2003), Sanders *et al.* (2004, 2014), Pickford *et al.* (2008).

	P2		P3		P4		M1		M2		M3	
	(N)	L/W	(N)	L/W	(N)	L/W	(N)	L/W	(N)	L/W	(N)	L/W
<i>Hypsamasia</i>	1	?/17	1	18/?	-	-	-	-	1	?/39.9	-	-
<i>P. kansui</i>												
(1) Eski-Çeltek	-	-	1	?/18.4	3	19.3/23.3	3	27.0/29.4	4	31.1/30.5	4/3	31.8/33.5
(2) Orhaniye	2	19.6/16.3	2	18.0/22.3	2	19.5/26.1	2	26.9/29.4	2	36.3/32.2	2/1	40.0/37.2
(3) Boyabat	-	-	-	-	-	-	-	-	-	-	-	-
(4) Cicekdag	-	-	-	-	-	-	-	-	-	-	-	-
(5) Bultu-Zile	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. kansui</i> (present study)	1	14.7/16.5	1	16.2/18.7	1	?/24.5	1	23.8/30.4	1	32.0/33.2	1	33.5/28.1
BOY-2	-	-	-	-	-	-	-	-	1	29.1/30.0	1	30.0/32.0
<i>C. mackennai</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. iliescui</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Namatherium</i>	-	-	1	17.0/24.4	1	19.0/26.1	2	27.7/29.1	2	37.7/37.5	2	40.8/40.7
<i>A. zitteli</i>	2	26.2/26.4	3	29.2/32.9	2	30.10/37.0	1	52.5/48.6	1	70.5/57.4	1	60.5/55.0
<i>A. giganteum</i>	-	-	1	36.0/?	3	42.0/42.9	-	-	2	76.5/61.0	2	71.8/61.2
<i>Ph. fallax</i>	1	5.7/5.4	1	6.1/5.1	1	11.4/9.6	-	-	-	-	-	-
	(N)	p2 L/W	(N)	p3 L/W	(N)	p4 L/W	(N)	m1 L/W	(N)	m2 L/W	(N)	m3 L/W
<i>Hypsamasia</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. kansui</i>												
(1) Eski-Çeltek	-	-	-	-	1	24.7/18.2	2	30.6/20.1	1/2	28.6/19.5	2/3	40.0/20.7
(2) Orhaniye	-	-	-	-	-	-	-	-	-	-	-	-
(3) Boyabat	-	-	-	-	-	-	1	22.2/15.8	-	-	-	-
(4) Cicekdag	-	-	-	-	1	27.0/16.0	1	32.0/21.0	1	42.0/25.0	1	53.0/26.0
(5) Bultu-Zile	-	-	-	-	1	25.5/18.30	-	-	1	29.5/20.5	-	-
<i>P. kansui</i> (this study)	1	?/16.1	1	16.6/10.7	1/2	16.9/12.2	1/2	24.2/16.85	-	-	-	-
BOY-2	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. mackennai</i>	-	-	-	-	1	26.0/16.1	1	34.6/18.4	-	-	-	-

1													
2													
3	<i>C. iliescui</i>	1	7/16.1	1	25.3/18.0	1	28.0/18.5	-		2	46.35/26.05	2	56.5/25.85
4	<i>Namatherium</i>		-		-		-				-		-
5	<i>A. zitteli</i>	3/1	25.9/17.3	4/2	28.2/22.3	4/2	32.4/26.2	11/4	48.8/36.1	13/10	61.9/43.4	8/9	59.3/44.5
6	<i>A. giganteum</i>	1/2	31.2/27.4	2	31.2/31.0	3/2	38.6/33.0	1	53.4/49.3	3/2	88.3/58.9	1	81.6/58.6
7	<i>Ph. fallax</i>	1	7.7/5.1	1	9.7/5.9	1	12.1/6.4	1	12.4/8.2	2	13.2/8.9	2	15.8/9.3

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APPENDIX S4. CHARACTER DISTRIBUTION OF THE STRICT CONSENSUS TREE

N.B. For the strict consensus tree, see main text Figure 5. For some annotations, Antoine (2002) and Gheerbrant *et al.* (2005) are followed. Unambiguous and nonhomoplastic characters are in bold, unambiguous characters displaying an autapomorphy where character state is not homoplastic are in italic, unambiguous and weakly homoplastic characters ($0.75 \leq \text{RI} < 1$) are underlined and character state is in brackets. Unambiguous and strongly homoplastic characters ($\text{RI} < 0.75$) lack any of annotations above, except the character state in brackets. Ambiguous characters are accompanied by an asterisk, related nodes which probably cause the ambiguity mentioned in square brackets and character state indicated in brackets as ‘: (Character state)’ only if it is different from the concerning main node.

Node 1 → *Arenahippus* : 9*(1)[node 3 or 4], 20*(2)[node 5-*Ph. fallax*], 21*(1)[node 4 or 4-*Phosphatherium*], 48*(1)[node 16-15], 90*(0)[node 21-*Ph. fallax*], 94*(0)[node 4-*Eritherium* and node 6 or 7]; **Node 1** → *Radinskya* : 43*(0)[node 4, node 9-*H. seni*], 60*(1)[node 4-*Phosphatherium*], 120*(1)[node 4-*Eritherium*:(1), node 9-*P. kansui*:(2) and node 4:(2), node 6:(0) or node 3:(2), node 5-*Ph. fallax*:(2)]; **Node 2** (Paenungulata) : **18**(1), 29(1), **30**(1), **38**(1), **39**(1), 40(1), 53(1 or 2), **54**(1), **59**(1), **75**(1), 79(0), 87(0); **Node 3** (Proboscidea + *Seggeurius*) : 15*(1)[node 8 or node 8-*A. zitteli*], **45**(1), 57*(1)[node 8-*A. zitteli*], 66*(1)[node 0-*Xenicohippus*], 84*(1)[node 8-*A. zitteli*, node 9-*P. kansui*], **99**(0); *Seggeurius amourensis* : 23(0), 63*(1)[node 6:(1), node 9:(0) or node 6-*N. blackcrowense*:(1), node 8], 78*(1)[node 0-*Xenicohippus*], 86(0), 125*(0)[node 8, node 9-*P. kansui*]; **Node 4** (Proboscidea) : 26*(1)[node 5- *Ph. fallax*], 43*(0)[node 1-*Radinskya*, node 9-*H. seni*], 46(0), 48*(1)[node 1-*Arenahippus*], **49**(1), **55**(0), 62*(1)[node 5-*Ph. fallax*], **80**(1), 98*(1)[node 6 or node 7], **106**(3), 107*(0)[node 5-*Ph. fallax*], **108**(1), **117**(1), 123*(1)[node 9-*C. mackennai* and node 6 or node 7], **127**(1); *Eritherium azzouzorom* : 32(0), 120*(1)[node 1-*Radinskya*, node 9-*P. kansui*:(2) and node 2:(2), node 6:(0) or node 3:(2), node 5-*Ph. fallax*:(2)]; *Phosphatherium escuilliei* : 7*(1)[node 5-*Ph. fallax*], 12*(1)[node 5-*Ph. fallax*], 35*(0)[node 5 or node 6], 60*(1)[node 1-*Radinskya*], 70(2), 79*(1)[node 9 or node 9-*P. kansui*], 112*(1)[node 5], 122*(1)[node 5], 129*(2)[node 9-*C. iliescui*:(0) and node 5, or node 8-*A. zitteli*, node 9-*P. kansui*]. **Node 5** (Embrithopoda *sensu lato*) : **11**(1), **51**(0), **65**(0), **69**(0), **70**(0), 72(1), 112*(1)[node 4-*Phosphatherium*], **114**(0), 122*(1)[node 4-*Phosphatherium*], **126**(1), 128(1); *Phenacolophus fallax* : 7*(1)[node 4-*Phosphatherium*], 12*(1)[node 4-*Phosphatherium*], 14*(1)[node 4 or node 4-*Phosphatherium*], 20*(2)[node 1-*Arenahippus*], 24*(0)[node 9-*P. kansui* and node 4 or node 4-*Phosphatherium*], 26*(1)[node 4], 27(1), 58*(1)[node 9 or node 9-*P. kansui*], 62*(1)[node 4], 77(1), 90*(0)[node 1-*Arenahippus*], 93(0), 107*(0)[node 4], 110(0); **Node 6** (Embrithopoda *sensu stricto*) : 53(3), **59**(2), **73**(1), 105*(0)[node 0-*Xenicohippus*]; *Namatherium blackcrowense* : 13(1); **Node 7**

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 3 (Arsinoitheriidae) : 1*(0), 2(0 or 1), 16*(1)[node 4 or node 4-*Eritherium*], 28*(1)[node 3 or node
 4 4], 33*(1), 47(1) ; **Node 8** (Arsinoitheriinae) : 44(1), 83(1), 101*(1)[node 9-*P. kansui*], 102(1),
 5 104*(0)[node 0-*Xenicohippus*], 116(1), 125*(0)[node 3-*Seggeurius*, node 9-*P. kansui*];
 6 *Arsinoitherium zitteli* : 4*(1)[node 8], 8*(1)[node 8], 19*(1)[node 8], 34*(1)[node 8],
 7 42*(1)[node 8], 52*(1)[node 8], 76*(0)[node 8], 84*(1)[node 3, node 9-*P. kansui*], 95*(1)[node
 8 8] ; *Arsinoitherium giganteum* : 2*(1)[node 7] ; **Node 9** (Palaeoamasiinae) : 20(1), 31*(1)[node
 9 2:(0), node 3-*Seggeurius*:(1) or node 4:(0), node 5:(0)], 40*(0), 89*(1)[node 0-*Xenicohippus*],
 10 91*(1)[node 0-*Xenicohippus*], 92*(1)[node 0-*Xenicohippus*], 106(0), 115(0) ; *Palaeoamasiasia*
 11 *kansui* : 24*(0)[node 5-*Phenacolophus* and node 4 or node 4-*Phosphatherium*], 37(1),
 12 82*(1)[node 0-*Xenicohippus*], 84*(1)[node 3, node 8-*A. zitteli*], 101*(1)[node 8], 103(1),
 13 125*(0)[node 3-*Seggeurius*, node 8] ; *Hypsamasia seni* : 25*(1)[node 0-*Xenicohippus*],
 14 29*(0)[node 3:(1)], 43*(0)[node 1-*Radinskya*, node 4] ; *Crivadiatherium mackennai* :
 15 123*(0)[node 6:(1) or node 7:(1)], 124(0) ; *Crivadiatherium iliescui* : 128*(0)[node 5:(1)],
 16 129(0), 130(0).
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