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# Ancestral radiation of paenungulate mammals (Paenungulatomorpha)-new evidence from the Paleocene of Morocco

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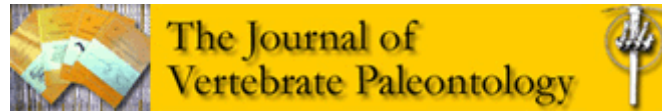
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**ANCESTRAL RADIATION OF PAENUNGULATE MAMMALS  
(PAENUNGULATOMORPHA) - NEW EVIDENCE FROM THE  
PALEOCENE OF MOROCCO**

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ARTICLE

Ancestral radiation of paenungulate mammals (Paenungulatomorpha) - New  
evidence from the Paleocene of Morocco

RH: GHEERBRANT—ANCESTRAL RADIATION OF PAENUNGULATA

1  
2  
3 ABSTRACT—Reported here is the discovery of a new mammal from the middle  
4  
5 Paleocene of the Ouled Abdoun phosphate basin, Morocco. *Hadrogeneios*  
6  
7 *phosphaticus*, gen. et sp. nov., is described based on dental and gnathic specimens.  
8  
9 Comparative dental anatomy and CT scan observations support stem relationships to  
10  
11 paenungulates. The cladistic analysis relates *Hadrogeneios* to paenungulatomorphs,  
12  
13 especially based on the shared morphotypic condition of a dilambdodont ectoloph  
14  
15 linked to inflated styler cusps. Within the Paenungulatomorpha, *Hadrogeneios* is  
16  
17 plesiomorphic not only with respect to crown paenungulates, but also to *Abdounodus*  
18  
19 and *Ocepeia*, making it the basalmost known paenungulatomorph. *Hadrogeneios*, on  
20  
21 the other hand, displays a peculiarly specialized mandibular symphyseal region  
22  
23 (mentum), which is enlarged and raised high above the cheek teeth, and bears at its  
24  
25 apex small incisors that are innervated and vascularized by a peculiar long and thin  
26  
27 dorsal canaliculus. This is tentatively interpreted as a plier-like dental apparatus  
28  
29 specialized for enhanced oral gripping function of the food, with increasing grip  
30  
31 strength or enhanced grip precision. A composite reconstruction of the lower jaw of  
32  
33 *Hadrogeneios phosphaticus*, based on 3D modeling from CT scans, is provided.  
34  
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38  
39 *Hadrogeneios*, *Abdounodus* and *Ocepeia*, all from the same Ouled Abdoun  
40  
41 Paleocene phosphate levels, are the very rare witnesses of the first evolution and  
42  
43 diversification of the endemic African ungulates phylogenetically preceding the  
44  
45 modern paenungulate orders.  
46  
47  
48

49  
50 LSID link: <http://zoobank.org/pub:8A0974FB-6D0D-458C-A756-8D9C21B5AB98>

51  
52 SUPPLEMENTAL DATA—Supplemental materials are available for this article for  
53  
54 free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)  
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## INTRODUCTION

Since the pioneering paleontological work of Camille Arambourg (e.g., Arambourg, 1952), the Ouled Abdoun phosphate basin in Morocco is most renowned for its rich marine vertebrate fauna found in several successive levels, extending from the latest Cretaceous to the early Eocene. Continental vertebrates were first discovered in 1996 in the Ouled Abdoun basin with the primitive proboscidean mammal *Phosphatherium* from Ypresian (early Eocene) phosphate levels (Gheerbrant et al., 1996). Discovery of mammals in the Paleocene levels of the Ouled Abdoun phosphate series was made later in 2001 (Gheerbrant et al., 2001; Gheerbrant, 2010). The Ouled Abdoun Paleocene mammals are the oldest known placentals from Africa, and all belong to African endemic taxa. Whereas the Ypresian phosphate levels yielded early representatives of modern orders of African ungulates (paenungulates), the Paleocene phosphate levels have yielded the first “condylarth-like” mammals, i.e., stem paenungulates, found in Africa, in addition to the earliest proboscidean *Eritherium* (see Gheerbrant, 2009 and Gheerbrant et al., 2012) and the earliest known hyaenodont *Lahimia* (see Solé et al., 2009). Most of these Paleocene mammals come from phosphate levels dated Selandian (Kocsis et al., 2014, 2016, 2021; Yans et al., 2014). The stem paenungulates described from the Paleocene of the Ouled Abdoun basin includes the two genera *Ocepeia* and *Abdounodus*, known by dental and cranial remains (Gheerbrant, 2010; Gheerbrant et al., 2001, 2014, 2016). *Ocepeia* belongs to a specialized lineage of stem paenungulates characterized by some anthropoid-like features such as a shortened and robust dentition (Gheerbrant, 2010; Gheerbrant et al., 2014). *Abdounodus* is

1  
2  
3 closer to the root of crown paenungulates, in particular with an incipiently  
4  
5 quadritubercular upper molar pattern showing a developing metaconular hypocone  
6  
7 (Gheerbrant et al., 2016).  
8  
9

10 Here is reported a new stem paenungulate (Paenungulatomorpha) from the  
11  
12 Selandian phosphate levels, which is well distinct from *Ocepeia* and *Abdounodus*. It  
13  
14 is characterized by very primitive features, but also by a remarkably specialized  
15  
16 mandibular symphyseal region.  
17  
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## 22 MATERIALS AND METHODS

23  
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25  
26

27 **Institutional Abbreviations**—**MHNM.KHG**, Museum d'Histoire Naturelle de  
28  
29 Marrakech (University Cadi Ayyad, Morocco), vertebrate collection from Khouribga  
30  
31 sites (Ouled Abdoun phosphate series), Marrakech; **MHNT PAL**, Museum d'Histoire  
32  
33 Naturelle de Toulouse, collections of paleontology, Toulouse; **MNHN**, Muséum  
34  
35 national d'Histoire naturelle, Paris.  
36  
37

38 **Material Studied**—The holotype MHNM.KHG.227 was donated by N.  
39  
40 Longrich to the collections of the Musée d'Histoire Naturelle de Marrakech (University  
41  
42 Cadi Ayyad, Morocco). Other specimens, MHNM.KHG.224, MHNM.KHG.225 and  
43  
44 MHNM.KHG.226, were donated by F. Escuillié to the same collections.  
45  
46  
47

48 **CT Scan, 3D Modelization, Software**—All specimens studied here were  
49  
50 subjected to X-ray Computed Tomographic (CT) imaging at the AST-RX platform of  
51  
52 the MNHN, using a GE Sensing and Inspection Technologies phoenix|x-ray v|tome|x  
53  
54 L240–180 CT scanner. I used the microfocus RX source 240 kV, detector 400 × 400  
55  
56 mm with a matrix of 2024 pixels (pixel size: 200 × 200 mm). Supplementary Data 1,  
57  
58 Table S1 summarizes the scan parameters of the studied specimens.  
59  
60

1  
2  
3 Data were reconstructed using datovis reconstruction software (Phoenix|x-ray,  
4 release 2.0) and then exported into a 16 bits TIFF image stack of 1537  
5  
6 (MHNM.KHG.225 and MHNM.KHG.226) and 1925 (MHNM.KHG.224 and  
7  
8 MHNM.KHG.227) virtual slices in transversal view. MIMICS Innovation Suite software  
9  
10 (Materialise, Research Edition, release 19–21) was used for the analysis, 3D  
11  
12 modelling, and measurements on the 3D model. Corrections for reconstructions were  
13  
14 also made with the help of the software VG studio Max Cinema 4D (Maxon, release  
15  
16 19–20).  
17  
18  
19  
20  
21

22 The dental nomenclature used here follows Van Valen (1966). The tooth wear  
23  
24 facets nomenclature follows that of Crompton (1971) and Schultz et al. (2018, 2020).  
25  
26 For tooth orientation (anterior and posterior teeth), we use the terms “lingual” (medial  
27  
28 side) and “labial” (lateral side) following classical and widely used comparative dental  
29  
30 anatomical studies of mammals such as Van Valen (1966).  
31  
32  
33

34 **Cladistic Analysis**—The cladistic analysis was made with TNT 1.5 (Goloboff  
35  
36 & Catalano, 2016). The character matrix analyzed, which includes 38 taxa and 209  
37  
38 characters, corresponds to that of Gheerbrant (2009) and Gheerbrant et al. (2021),  
39  
40 with few corrections and additions. The main changes in the matrix analyzed here  
41  
42 correspond to the replacement of the taxon Sirenia by the three following stem  
43  
44 genera: *Prorastomus*, *Pezosiren*, and *Eotheroides*. Their character coding, especially  
45  
46 for *Pezosiren*, is based on Domning (2001, in press) and Domning et al. (2017). The  
47  
48 phylogenetic matrix also includes some suprageneric taxa, the content of which is  
49  
50 explained in Supplementary Data 2. Among them the Eutheria is used as outgroup  
51  
52 taxon in the analyses. The matrix included nine uninformative characters and 48  
53  
54 additive characters that are listed in Supplementary Data 2. The uninformative  
55  
56  
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58  
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1  
2  
3 characters were inactivated before the analyses (xinact command of TNT). The  
4  
5 character numbering scheme used in the description of the resulting most  
6  
7 parsimonious trees (MPTs) starts from 0 (default option in TNT). Several analyses  
8  
9 were developed: standard (unweighted) analysis, and two analyses imposing a  
10  
11 scaffold to constrain the monophyly of the clade Afrotheria, one including the new  
12  
13 species described here in Afrotheria, the other without it (Supplementary Data 2).  
14  
15 We used the TNT command “force” for the constraining analyses (Supplementary  
16  
17 Data 2). All analyses provide congruent results for the relationships of the new  
18  
19 species described here (same topology for the Paenungulatomorpha). The analyses  
20  
21 were made with the Traditional Search command and using the TBR swapping  
22  
23 algorithm (number of replicates 10, tree saved per replicate 100, memory 10000  
24  
25 trees). For these analyses, the default collapsing rule was changed to “max. length =  
26  
27 0”. When some replications overflowed, a second round of TBR was conducted.  
28  
29 Details on phylogenetic analyses are provided in Supplementary Data S1. The  
30  
31 phylogenetic matrix used here is provided as a “NEXUS file” in Supplementary Data  
32  
33  
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37 3.

## 38 39 40 41 42 43 GEOLOGICAL SETTING

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48  
49 The material studied here was collected in the phosphate quarries from the  
50  
51 Ouled Abdoun basin, Morocco. The geographical, geological and stratigraphic  
52  
53 context of the Ouled Abdoun phosphate series and the fossiliferous sites are  
54  
55 described in Gheerbrant et al. (2003), Kocsis et al. (2014), and Yans et al. (2014).  
56  
57 The fossils were collected by local people from unknown exact sites in Ouled Abdoun  
58  
59  
60



1  
2  
3 basin, but mostly from the quarrying area of Sidi Chennane (Yans et al., 2014). Their  
4 stratigraphic provenance is most likely from middle Paleocene phosphate beds. This  
5 is supported by a recent geochemical study by Kocsis et al. (2021) of the phosphate  
6 matrix of the studied mammal specimens, which shows that they have the  
7 chemostratigraphic signature of phosphate levels of the interval between the top of  
8 Bed IIb and the base of Bed IIa (chemostratigraphic Horizons 6–8 in Kocsis et al.,  
9 2021), corresponding to the Selandian–early Thanetian (middle–late Paleocene)  
10 interval. This interval includes the Selandian *Eritherium* bone-bed which has yielded  
11 most of the Paleocene mammal fossils discovered from the Ouled Abdoun  
12 phosphates series (Kocsis et al., 2014, 2021; Yans et al., 2014).  
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## 30 SYSTEMATIC PALEONTOLOGY

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33  
34 AFROTHERIA Stanhope, Waddell, Madsen, De Jong, Hedges, Cleven, Kao,  
35 Springer, 1998  
36  
37  
38

39 PAENUNGULATOMORPHA Gheerbrant, 2016

40  
41  
42 FAMILY INCERTAE SEDIS

43  
44  
45 *HADROGENEIOS*, gen. nov.  
46  
47

48 **Etymology**—From the Greek *hadros*, well-developed, bulky, stout, ripe, large,  
49 strong, great; and *geneion*, chin: literally “strong chin” in reference to the large  
50 anterior part (mandibular symphyseal region and pars incisivus) of the dentary.  
51  
52  
53

54  
55  
56 **ZooBank Life Science Identifier (LSID)**—zoobank.org:act:7AB6F6F4-DCEB-  
57 4678-B74F-1C0831CD39BE  
58  
59  
60

1  
2  
3 **Type [and Only] Species**—*Hadrogeneios phosphaticus*, sp. nov.  
4

5  
6 *HADROGENEIOS PHOSPHATICUS*, sp. nov.  
7

8  
9 (Figs. 1–10; Supplementary Data 7–9)  
10

11  
12 **Etymology**—phosphaticus, in reference to its provenance from the phosphate  
13  
14 beds of the Ouled Abdoun basin, Morocco.  
15

16  
17 **Zoobank Life Science Identifier (LSID)**—zoobank.org:act:0D3F474B-3192-  
18  
19 4902-B7C9-EEC5CF9DB8EB  
20  
21

22  
23 **Type Locality and Age**—Phosphate quarries of the Ouled Abdoun phosphate  
24  
25 basin, Morocco, unknown exact locus. Phosphate Bed IIa, Paleocene, Selandian–  
26  
27 early Thanetian. This age is supported by field data and geochemical analysis of the  
28  
29 matrix of three paratype specimens MHNM.KHG 224, 225, and 226 (see Kocsis et  
30  
31 al., 2021:fig. 6).  
32  
33

34  
35 **Holotype**—MHNM.KHG.227, partial left dentary preserving the mandibular  
36  
37 symphysis, the alveoli for two incisors, c1, and p1–3, and the teeth p4 and m1; in  
38  
39 addition, a broken isolated left m3 is associated with the dentary.  
40  
41

42  
43 **Paratypes**—MHNT PAL 2006.0.19, fragment of right dentary with m3;  
44  
45 MHNM.KHG.223, isolated right M3; MHNM.KHG.224, right dentary broken into three  
46  
47 pieces, including the mandibular symphysis; it preserves p3–4, m2, and the alveoli  
48  
49 for p1, c1, and i1–3; MHNM.KHG.225, fragment of left dentary with m2–3;  
50  
51 MHNM.KHG.226, fragment of right maxillary bearing strongly worn M2–3, and an  
52  
53 associated isolated left M3 of the same individual.  
54  
55

56  
57 **Diagnosis**—Stem paenungulate having an anterior lower dentition elongated  
58  
59 with three distinct diastemata. The morphology of the mandibular symphyseal region  
60

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2  
3 and pars incisiva is distinctive and autapomorphic among Paleogene placentals with  
4  
5 the following features: symphyseal region large, robust and high; pars incisiva and  
6  
7 mandibular symphysis enlarged, forming a prominent antero-dorsal process that is  
8  
9 raised well above the check teeth and bears small incisors and a large canine. Lower  
10  
11 incisors small; p1 single-rooted or partially two-rooted; p3 elongated and sharp; p4  
12  
13 almost fully molariform. Lower molars: bunodont crown, but sharp and crescentiform  
14  
15 crests that outline a selenodont pattern; paraconid inflated and lingual; hypoconulid  
16  
17 cuspidate, shifted lingually close to the entoconid; entolophid and hypolophid absent.  
18  
19 Upper molars: stylar cusps and stylar shelf well developed; ectoloph sharp and  
20  
21 dilambdodont (selenodont), linked labially to a large mesostyle and a large and  
22  
23 bulbous stylocone; protocone large, low, and bunodont, surrounded by a thin lingual  
24  
25 cingulum; conules and hypocone absent.  
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## 35 **Description**

36  
37 **Upper Dentition**—Only M2–3 are known (Fig. 1; Supplementary Data 1, Fig.  
38  
39 S1, Table S2). MHNM.KHG.223 and MHNM.KHG.226 preserve respectively M3 and  
40  
41 M2–3. Upper molars have three simple roots. The occlusal outline of the crown is  
42  
43 triangular and extended transversely. The stylar shelf is wide and more markedly in  
44  
45 the parastylar area. The ectoloph is typically dilambdodont (selenodont pattern), with  
46  
47 a long labially deflected centrocrista that is linked to a large mesostyle. Preparacrista  
48  
49 and postmetacrista (absent in M3) are also long and sharp. The ectoflexus forms a  
50  
51 distinct notch on the labial side. The ectocingulum is present. Large inflated stylar  
52  
53 cusps are present; they are by size order the stylocone, the mesostyle and the cusp  
54  
55 D (variable). The hook-like parastyle is crestiform and mesially protruding (forming  
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3 the parastylar area). It bears on the mesiolabial side a wide parastylar groove (for the  
4 protoconid occlusion) extending transversely along the preparacrista and paracone.  
5  
6 The stylocone is bulbous and it is the largest styler cusp, being only a little smaller  
7  
8 than the metacone. It is linked to the preparacrista. The mesostyle is large and widely  
9  
10 linked to the centrocrista. In labial view, it is located between the paracone and  
11  
12 metacone level, and not transversely aligned with the metacone. A styler cusp D is  
13  
14 distinct and inflated in the M2 of MHN.M.KHG.226. The styler cusp E (metastyle) is  
15  
16 crestiform and small in M2; it is absent in M3. The postmetacrista links the cusp E in  
17  
18 the M2 of MHN.M.KHG.226. Accessory small styler cuspules are present on the labial  
19  
20 cingulum (ectocingulum). A distinct metacingulum extends below the metacone and  
21  
22 postmetacrista in M2 (MHN.M.KHG.226); it is less extended labially in M3  
23  
24 (MHN.M.KHG.223, MHN.M.KHG.226). Paracone and metacone are similar in size and  
25  
26 deeply separated at the base. The conules are weak or absent. Only a tiny  
27  
28 paraconular prominence is seen on the preprotocrista. The protocone is large, low,  
29  
30 and wide mesiodistally. In lingual view it appears slightly canted mesially. The labial  
31  
32 flank (in profossa) of the protocone is flat. The protocone is surrounded by a  
33  
34 precingulum and a postcingulum, which are lingually continuous in MHN.M.KHG.223,  
35  
36 but not in MHN.M.KHG.226. Both end lingual to the paracone and metacone level.  
37  
38 The hypocone is absent. The enamel is wrinkled in MHN.M.KHG.223.  
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47       Wear Pattern (attrition and abrasion). Preparacrista, postparacrista and  
48 premetacrista show well developed crescentiform wear facets (facets 3–4 of  
49 Crompton, 1971), facets Me-M and P-ad of Schultz et al. (2018). They result from a  
50 shearing with labial crests of hypocone and protocone and correspond to a  
51 selenodont pattern. Tooth abrasion is extensively developed in MHN.M.KHG.226 (an  
52 old individual), exposing widely the dentine at the level of the paracone, metacone,  
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3 protocone, centrocrista-mesostyle, and preparacrista. There is a wear facet on the  
4 preparacrista (facet 1 or PA-m), on the postmetacrista (facet 2 or ME-dl), and on the  
5 mesial flank of the protocone (facet 5 or PR-m).  
6  
7  
8  
9

10 The length of M2–3 in MHNM.KHG.226 is 11.96 mm; measurements of  
11 individual teeth are provided in Supplementary Data 1, Table S1.  
12  
13

14 **Lower Tooth Row and Dental Formula**—The tooth row and dental formula  
15 were described and reconstructed with the help of the digital modeling made from the  
16 CT scans of the available material. Measurements are provided in Supplementary  
17 Data 1, Tables S3–4.  
18  
19  
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23

24 The reconstructed lower dental formula is  $3i-c-4p-3m$ , corresponding to the  
25 primitive placental dental formula. One specimen, MHNM.KHG.227, shows the  
26 presence of a small additional alveolus between p2 and p3 (Figs. 2, 6, 7). It is  
27 interpreted as a residual alveolus of a deciduous premolar, probably dp3, in the  
28 course of resorption. The alternative interpretation not retained here would be to  
29 identify this tooth as a remnant of an additional premolar inherited from the ancestral  
30 five premolars eutherian dental formula, i.e. as a dp3 followed by p4–5 (instead of  
31 p3–4), a tooth locus that is thought to be lost in the Placentalia (e.g., O’Leary et al.,  
32 2013). The interdental length between p2 and p3 (2.3 mm) in MHNM.KHG.227  
33 closely matches that of the diastema between these teeth in MHNM.KHG.224 (see  
34 Table S2), supporting that it is the residual alveolus of a deciduous tooth that is  
35 resorbed in MHNM.KHG.224. Specimen MHNM.KHG.227 shows therefore that the  
36 dp3 was probably the last deciduous tooth to be shed in the species. It was lost late,  
37 after all permanent premolars and m1 were erupted, i.e., at the adult or subadult  
38 stage. There are three postcanine diastemata. The longest is between p1 and p2,  
39 followed by the slightly smaller one between p1 and c, and by the shortest between  
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3 p2 and p3. As a result, the anterior lower tooth row is elongated, in sharp contrast to  
4  
5 *Ocepeia*.

6  
7 **Lower Incisors and Canines**—Although not preserved, the incisors are represented  
8  
9 by their alveoli in specimens MHNM.KHG.224 and MHNM.KHG.227 (holotype) (Fig.  
10  
11 7; Supplementary Data 1, Fig. S3). MHNM.KHG.224 shows the presence of three  
12  
13 tiny incisors (Length of i1–3 = 4.4 mm) with short root (alveolus) (Fig. 7D–F). In the  
14  
15 holotype only two incisor alveoli are preserved (Fig. 7A–C); one of the two anterior  
16  
17 incisor alveoli (for i1–2) is broken, corresponding either to i2 or to i1. Judging from the  
18  
19 alveoli, the incisors were closely appressed to each other, anterior to the canine.  
20  
21  
22

23  
24 The CT scans show that the incisors are innervated and vascularized by a  
25  
26 very thin and long dorsal canaliculus that rises very high from the mandibular canal in  
27  
28 the anterior part of the dentary bone with a course parallel to that of the canine root  
29  
30 (Figs. 7–8; Supplementary Data 1, Fig. S3). Although only two incisor alveoli are  
31  
32 preserved in MHNM.KHG.227, three dorsal canaliculi are present, confirming the  
33  
34 presence of three teeth anterior to the canine (Fig. 7A–C). The dorsal canaliculus of  
35  
36 i3 detaches earlier (more distally) from the mandibular canal than those of i1–2, and  
37  
38 the latter separate very high, shortly below the tooth alveolus (Fig. 8); as a result, the  
39  
40 dorsal canaliculus of i3 is much longer than those of i2 and i1. The CT scan section  
41  
42 (Supplementary Data 1, Fig. S3) of MHNM.KHG.224 shows that i3 alveolus is smaller  
43  
44 than that of i1–2, and that it has a subcircular section, whereas i1–2 have a more  
45  
46 laterally compressed alveolus. i3 is located on the labial side of the lower jaw and  
47  
48 closely wedged between the canine and the more lingually placed i2. In addition,  
49  
50 MHNM.KHG.224 shows that i3 has a subvertical root, whereas the roots of i1–2 are  
51  
52 more canted anteriorly.  
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3 A large alveolus indicates the presence of a large canine, which strongly  
4 contrasts with the small size of the incisors (Fig. 8; Supplementary Data 1, Fig. S3).  
5  
6 The root of the canine is very large, deep and anteriorly canted (at about 45°), in a  
7 similar orientation to the incisors. According to the alveolus, it was located anteriorly,  
8 close to the incisors, and very labially. In MHNM.KHG.224, it has the labial border  
9 lower than the lingual border; as a result, the canine might have been asymmetric  
10 and more exposed labially (labially higher crown).  
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19 **Lower Premolars**—There are four premolars (p1 and p2 being known only by  
20 their alveoli).  
21  
22

23 According to its alveolus, p1 is the smallest cheek tooth (Supplementary Data  
24 1, Table S4), but it is larger than the incisors. It is separated from the canine and p2  
25 by diastemata. The p1 is either entirely one-rooted with a simple root  
26 (MHNM.KHG.227) or one-rooted with a bifid root apex (MHNM.KHG.224). The 3D  
27 digital model of the alveolus of p1 in MHNM.KHG.224 (Fig. 7) shows a single main  
28 root which separates in two at its apex. It corresponds either to an intermediate  
29 structural state from an ancestral two-rooted p1 or to a root which is beginning to  
30 divide in this species. In any case, the root of p1 is robust and relatively longer than  
31 those of other premolars (Figs. 6–7).  
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44 According to its alveoli, p2 is only slightly smaller than p3. The latter,  
45 preserved in MHNM.KHG.224, is an elongated, narrow, and high tooth bearing sharp  
46 cusps and crests; its crests are more or less mesiodistally aligned. It has a simple  
47 trigonid and a small unicuspid talonid. It bears a strong and high anterior paraconid,  
48 which is a little higher than the talonid. The main, and by far larger, cusp is the  
49 protoconid. The smallest cusp is the hypoconid, which is located labially.  
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3 The p4, preserved in MHNM.KHG.224, is a nearly fully molariform premolar. It  
4  
5 is larger than p3 and about as long as m1. It bears very small precingulid and  
6  
7 ectocingulid. The trigonid is typically elongated with respect to the molars. It is  
8  
9 narrower than the talonid. It bears a strong and high paraconid that is mesially and  
10  
11 labially located, in front of the protoconid. The paracristid is mostly mesiodistal and  
12  
13 labially placed. The metaconid is well inflated and is located lingually, at a slightly  
14  
15 more distal level than the protoconid. In MHNM.KHG.224, the mesial root of p4 is  
16  
17 longer than the distal one and it is a little canted posteriorly (root apex more anterior).  
18  
19 The talonid is molariform with the presence of a deep basin (postfossid) surrounded  
20  
21 by three well inflated cusps of similar size, the hypoconid, hypoconulid and  
22  
23 entoconid. The postfossid (talonid basin) is widely and deeply open lingually. By  
24  
25 contrast to the molars the three talonid cups in p4 are approximated to each other,  
26  
27 the hypoconulid being distal and slightly closer to the hypoconid. The cristid obliqua  
28  
29 is well developed. It rises lingually on the trigonid, behind the metaconid.  
30  
31  
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34

35 **Lower Molars**—Lower molars have a moderately bunodont crown. The labial  
36  
37 cusps and crests are sharp and bear developed crescentiform shearing wear facets,  
38  
39 drawing a selenodont pattern. The crown is inflated above the roots, especially on  
40  
41 the labial side. The labial cusps, protoconid and hypoconid, are the largest ones;  
42  
43 their lingual flank is convex and bulging as a distinctive vertical carina. The molars  
44  
45 bear a more or less distinct and continuous labial cingulid that extends from the  
46  
47 mesial flank of the trigonid to the distal flank of the talonid. There is a radicular  
48  
49 groove on the internal side of the roots.  
50  
51  
52  
53

54 The trigonid is a little higher than the talonid and of overall comparable width.  
55  
56 It is not compressed but more or less elongated. The precingulid is weak or absent.  
57  
58 The paraconid is well developed, cuspidate, and it is only slightly lower than the  
59  
60



1  
2  
3 metaconid. It has a distinct mesiolingual crest that projects mesially from the trigonid.  
4  
5 This crest links a small but well distinct parastyloid (= "cusp e" in therian terminology)  
6  
7 which is bulging on the mesiolingual angle of the molars. The paracristid and  
8  
9 protocristid are sharp and high and they are arranged in a selenodont pattern. The  
10  
11 paracristid is slightly convex mesially. The protoconid is the largest cusp, but it is low  
12  
13 and only a little higher than the paraconid and metaconid. The metaconid is distally  
14  
15 located with respect to the protoconid, and more so from m1 to m3. The prefossid  
16  
17 (trigonid basin) is widely open lingually. The metaconid bears a distinct  
18  
19 postmetacristid and a metastyloid.  
20  
21  
22

23  
24 The talonid is as long as, or longer than, the trigonid. Its relative length  
25  
26 increases from m1 to m3. The ectoflexid is shallow and wide. The talonid notch is  
27  
28 wide and deep. The cristid obliqua is long and sharp. In most specimens it joins the  
29  
30 trigonid at its mid width, below the protocristid notch, and it does not rise high on it; in  
31  
32 MHNM.KHG.225 it ends slightly more lingually, below the metaconid apex. The  
33  
34 cristid obliqua bears a small mesoconid at its mesial part. The postcristid is also long.  
35  
36 It joins a hypoconulid that is shifted lingually and closely approximated to the  
37  
38 entoconid. As a result, the hypoconid and entoconid are "twinned" and the hypoconid  
39  
40 and hypoconulid are separated by a wide notch on the postcristid. The hypoconulid is  
41  
42 a little smaller than the entoconid. The entoconid lacks an anterior crest (i.e., no  
43  
44 entocristid). When the labial cingulid is distinct, it extends distolingually to the level of  
45  
46 the hypoconulid. There is no entolophid or hypolophid.  
47  
48  
49

50  
51 The m1 is slightly smaller than m2, and m2 is slightly wider than m3  
52  
53 (Supplementary Data 1, Table S4). The paraconid is more lingual on m2 and m3. The  
54  
55 m3 is characterized by a much longer talonid than the trigonid. The distal root of m3  
56  
57 is classically elongated and compressed laterally with respect to the mesial one.  
58  
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3 Individual variation. The most remarkable variable morphological traits are the  
4  
5 p1 that is either one rooted (MHNM.KHG.227) or partially two rooted (roots separated  
6  
7 at apex in MHNM.KHG.224), and the residual dp3 alveolus that is retained in one  
8  
9 specimen (MHNM.KHG.227) at subadult stage. The relative width of the talonid is  
10  
11 variable, especially on m3. A larger talonid than trigonid in m3 is seen on  
12  
13 MHNM.KHG.224, whereas it is subequal to trigonid on MHNM.KHG.227. The  
14  
15 development of the labial cingulid and the ectostylid is variable in the material: it is  
16  
17 absent in MHNM.KHG.225, and present in MHNM.KHG.227 (m3, with ectostylid),  
18  
19 MHNM.KHG.224 (m2), MHNT PAL 2006.0.19 (m3). The m3 of MHNM.KHG.227 has  
20  
21 an inflated ectostylid. m2 and m3 of MHNM.KHG.225 have a cristid obliqua that ends  
22  
23 in the lingual part of the trigonid, whereas the cristid obliqua ends at trigonid mid-  
24  
25 width in other specimens. The m3 of MHNT PAL 2006.0.19 and MHNM.KHG.227  
26  
27 lacks distinct parastylid.  
28  
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33 Wear pattern (attrition). The lower jaw specimens here described belong to  
34  
35 subadult individuals with poorly worn teeth. Attrition wear facets are, however, well  
36  
37 seen. Crescentiform labial shearing wear facets are present on the protocristid (wear  
38  
39 facet 1 of Crompton, 1971, wear facet prod-d of Schultz et al., 2018, 2020) and  
40  
41 paracristid (wear facet 2, pacd-mb). In addition, there are shearing wear facets on the  
42  
43 cristid obliqua (wear facet 3, hy-mb) and the postcristid (wear facet 4, hy-l). Distinct  
44  
45 wear striae are seen especially on wear facets 1 and 2; they are inclined at 40° to 25°  
46  
47 with respect to the horizontal plan. A wear facet is present on the lingual flank of the  
48  
49 twinned hypoconulid and entoconid (facet 6, Ed-Mb). Measurements of lower jaw and  
50  
51 teeth of *Hadrogeneios phosphaticus*, gen. et sp. nov. are provided in Supplementary  
52  
53 Data 1, Tables S2–5.  
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3       **Dentary**—One remarkable feature of the described material is the enlarged  
4 and high mandibular symphysis as shown by the holotype and MHNM.KHG.224, in  
5 which the symphyseal region and the pars incisiva are greatly developed and  
6 expanded high, forming a prominent antero-dorsal process. Between p1 and p2, the  
7 anterior tooth row rises high above the molar occlusal plane at an angle of about 40–  
8 45°. As a result, the incisors are located well above the cheek teeth, at the apex of a  
9 strong and high symphyseal region (Figs. 2B–C, 3B–C, 7, 9; Supplementary Data 1,  
10 Fig. S3A). The pars incisiva and the symphysis are consequently significantly higher  
11 and deeper (mandibular symphysis height: 27 mm from base to apex in  
12 MHNM.KHG.224), by almost twice the height, than the mandibular corpus (height of  
13 corpus = 10–15 mm below m2). A peculiar endostructural feature (CT scan  
14 observation) linked to the enlarged and high symphyseal region is the very long and  
15 thin dorsal canaliculi (Figs. 7–8; Supplementary Data 1, Fig. S3) connecting the  
16 incisors (pars incisiva), which are located high, at the apex of the prominent vertical  
17 process of the mandibular symphysis. The symphysis is flat. There is no evidence of  
18 a fused symphysis in the described material that is represented by subadult  
19 specimens with poorly worn teeth. However, it is not excluded that such a large and  
20 flat mandibular symphysis was fused in older individuals. The structure combining  
21 small incisors (but large canine) with a strong and high mandibular symphyseal  
22 process is remarkable. This morphology indicates a specialized, possibly pliers-like,  
23 anterior dental apparatus that is adapted for a particular oral gripping function of the  
24 food, with increasing grip strength or enhanced grip precision.

25  
26       The mandibular symphysis extends posteriorly to the level of p1  
27 (MHNM.KHG.227) or below the diastema between p1–p2 (MHNM.KHG.224). A  
28 distinct ventrolateral crest (MHNM.KHG.224, MHNM.KHG.227) for strong muscular

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2  
3 attachment runs on the corpus back from the mandibular symphysis to below the  
4  
5 level between p4 and m1 (Figs. 2B, 3C, 7A, D; Supplementary Data 1, Fig. S4). This  
6  
7 is likely the crest for the genioglossus muscle that is involved in the protraction of the  
8  
9 tongue (McClung & Goldberg, 2000). The remarkable development of this bony crest  
10  
11 in the Ouled Abdoun species suggests a long tongue firmly attached anteriorly, in  
12  
13 close relation to the strong mandibular symphysis. The mandibular corpus is not  
14  
15 deep below the teeth (corpus height about three times the molar height), and it is  
16  
17 flattened on the labial side and slightly inflated (convex) on the lingual side. Two  
18  
19 mental foramina of similar size are present. The posterior one is located below the  
20  
21 diastema between p2–p3. The anterior one is just behind the canine. The vertical  
22  
23 ramus, represented by part of masseteric and coronoid crest, rises labial to the m3  
24  
25 talonid (Fig. 3E–F). The masseteric crest is well developed and sharp, and it extends  
26  
27 on the corpus well below the alveolar border. Behind m3, the coronoid crest and the  
28  
29 sharp masseteric crest delimit a coronoid fossa on the ramus. The CT scan  
30  
31 observation confirms that there is no coronoid foramen, unlike paenungulates. The  
32  
33 remnant of the coronoid process seen in MHNM.KHG.225 is slightly canted  
34  
35 posteriorly, in contrast to *Phosphatherium* where it is canted anteriorly. The  
36  
37 subcondylar notch is distinct on MHNM.KHG.225. It is located at a low level of the  
38  
39 mandibular corpus, much lower than in *Ocepeia*. Its position is closer to *Abdounodus*,  
40  
41 but still lower. In addition, the neck of the mandibular condyle diverges from the  
42  
43 ramus below the alveolar plane. This means that the mandibular condyle was low,  
44  
45 close to the tooth row level. The mandibular foramen seen in MHNM.KHG.225 is  
46  
47 located right below the alveolar plane, and 9 mm behind the m3. Mandibular  
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49 measurements are provided in Supplementary Data 1, Table S5.  
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## Comparisons

The new Ouled Abdoun material described here is characterized in this study as belonging to a new genus and species that is named *Hadrogeneios phosphaticus*, gen. et sp. nov. Its comparison with early Paleogene placental mammals shows the closest morphological affinity with the stem paenungulatomorph *Ocepeia daouiensis*, which comes from the same Paleocene levels of the Ouled Abdoun basin (Gheerbrant et al., 2001, 2014; Gheerbrant, 2010). The resemblance in molar morphology is the most noticeable. However, *Hadrogeneios phosphaticus* departs from *Ocepeia* in the derived and likely autapomorphic construction of the strong mandibular symphyseal region (mentum), in which the symphysis and the pars incisiva are enlarged and raised above the cheek tooth row.

This is combined with a suite of other distinct features that are primitive, such as some important molar features and the full placental dental formula with the retention of the two first premolars (p1–2) in contrast to *Ocepeia*.

An enlarged symphyseal region is known in some early Paleogene mammals. This is the case of the arctocyonid “condylarth” *Anacodon ursidens* Matthew and Granger, 1915, from the early Eocene of Wyoming (U.S.A.). However, the construction of the symphyseal region of *Anacodon* is quite different: it is not enlarged in its upper part but in its lower part, forming a mandibular flange similar to the mandibular morphology known in carnivores with large, compressed sabre-like upper canines (e.g., machairodonts). This is not homologous to the morphology of *Hadrogeneios phosphaticus*. In addition, the dental morphology of *Anacodon* is well distinctive from that of *H. phosphaticus*. This is also true for other non-carnassial Paleogene taxa that have a mandibular flange and an enlarged upper canine such as uintatheres (*Bathyopsis* and *Uintatherium*) and astrapotheres (see Kramarz et al.,

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2  
3 2019). Comparisons show that the anterior part of the dentary of *H. phosphaticus* is  
4  
5 instead derived in a specialized functional way for a distinctive mode of ingesting  
6  
7 food.  
8  
9

10 The most remarkable shared dental trait of *Hadrogeneios* and *Ocepeia* is the  
11  
12 incipient but well-distinct selenodont pattern. In the upper molar, the selenodont  
13  
14 pattern is displayed by the dilambdodont ectoloph that is linked to strong stylar cusps  
15  
16 such as the mesostyle and stylocone. In the lower molars, the selenodont pattern is  
17  
18 seen in the sharp and long labial crests (protoconid and hypoconid crests), bearing  
19  
20 crescentiform wear facets. This specialized pattern shared with *Ocepeia* is  
21  
22 associated to a similar general tooth morphology such as the bunodont crown. The  
23  
24 upper molar morphology affinity of *Hadrogeneios* and *Ocepeia* is remarkable not only  
25  
26 in the dilambdodont pattern. It also lies on the occlusal outline, the wide stylar shelf  
27  
28 bearing inflated stylar cusps, the large parastyle, the presence of a metacingulum,  
29  
30 and the massive protocone that is low, bunodont, and surrounded by a well-  
31  
32 developed lingual cingulum. Lower molars of *Hadrogeneios* and *Ocepeia* share other  
33  
34 characters such as a high and cuspidate paraconid, presence of postmetacristid, and  
35  
36 the convex lingual flank of lower cusps. The dentary shares the presence of a lower  
37  
38 bony crest running on the ventral rim of the anterior part of corpus (crest for  
39  
40 genioglossus m.), the masseteric crest extended below the tooth row, and the  
41  
42 presence of a coronoid fossa. The zygomatic apophysis of the maxilla similarly  
43  
44 diverges between M2 and M3.  
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46  
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51 These shared features of *Hadrogeneios* and *Ocepeia* argue for taxonomic  
52  
53 affinity, possibly at the familial level. The cladistic analysis recovers a basal  
54  
55 relationship of *Hadrogeneios* to stem paenungulates such as *Ocepeia*, but in a  
56  
57 paraphyletic position that refutes its familial allocation to the Ocepeiidae (see below).  
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3 *Hadrogeneios* departs indeed from *Ocepeia* in a number of significant features. It  
4  
5 differs most remarkably in the enlarged and robust anterior part of the dentary  
6  
7 (mandibular symphysis and pars incisiva), in the tooth row that is contrastingly  
8  
9 elongated with three distinct anterior diastemata and with a full placental dental  
10  
11 formula (four premolars), and in the much lower bunodonty of p3–4 and molars.  
12  
13 *Ocepeia* has a much less developed chin and shorter dentary and tooth row. It also  
14  
15 has a much higher articular condyle, a wider and rounded angular process, a more  
16  
17 inflated corpus, and a stronger masseteric crest. The cheek teeth of *Hadrogeneios*  
18  
19 are sharper than those of *Ocepeia*. In particular, the crown of lower molars is higher  
20  
21 and raised vertically in contrast to *Ocepeia*, in which the labial flank of the crown is  
22  
23 inflated at the base and lingually inclined. Lower molars of *Hadrogeneios* depart in  
24  
25 many other characters. The most remarkable include the absence of entolophid and  
26  
27 hypolophid, presence of parastyloid, absence of entocristid related to the development  
28  
29 of a wide and deep talonid notch, and the high hypoconulid that is twinned with the  
30  
31 entoconid. Other differences from *Ocepeia* include the trigonid longer (not  
32  
33 compressed), higher, and less canted mesially, the paraconid higher, sharper, and  
34  
35 more lingual (anterior molars), the absence of premetacristid, the postmetacristid and  
36  
37 mesoconid much smaller, the absence of entoconulid, the ectocingulid well  
38  
39 differentiated, the absence of secondary cuspules on the postcristid, and the  
40  
41 proportionally smaller m3, bearing less developed hypoconulid lobe. The premolars  
42  
43 of *Hadrogeneios* are also very different from those of *Ocepeia*; p4 is submolariform in  
44  
45 *Hadrogeneios*, whereas it is simple in *Ocepeia*; it has distinct paraconid, metaconid,  
46  
47 talonid basin, and a large hypoconid. In addition, p3 and p4 are more elongated and  
48  
49 sharper unlike the simple, shorter, and bunodont premolars of *Ocepeia*. The p1–2  
50  
51 are present in *Hadrogeneios* whereas they are lost in *Ocepeia*. Upper molars of  
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3 *Hadrogeneios* depart from *Ocepeia* in the absence of conules, the longer transverse  
4 occlusal outline with narrower protocone, the longer preparacrista, the stylocone  
5 much larger and well separated from the parastyle (fused with parastyle in *Ocepeia*),  
6 the larger and more hook-like parastylar area (M1–3), and the wider interdental  
7 space between molars. *Hadrogeneios phosphaticus* is 80–90% smaller in dental  
8 measurements than *Ocepeia daouiensis*, which is the smallest species of the genus.  
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17 Most of these differences unambiguously relate to the plesiomorphic  
18 morphology of *Hadrogeneios* with respect to *Ocepeia*. A remarkable exception is the  
19 specialized mandibular symphyseal region of *Hadrogeneios* with respect to *Ocepeia*.  
20 The much larger and robust mandibular symphysis and pars incisiva, forming a  
21 prominent high process that is raised well above the cheek tooth row, and bearing  
22 very small and crowded incisors innervated and vascularized by very long and thin  
23 dorsal canaliculus (Figs. 7–8; Supplementary Data 1, Fig. S3), all make a very  
24 peculiar anterior dental apparatus that is most likely autapomorphic in *Hadrogeneios*.  
25 This supports that *Hadrogeneios* documents a distinct new lineage of basal  
26 Paenungulatomorpha.  
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40 *Abdounodus* comes from the same Paleocene phosphate levels of the Ouled  
41 Abdoun basin as *Ocepeia* and *Hadrogeneios* (Gheerbrant, 2010; Gheerbrant et al.,  
42 2001, 2016). It shares with *Hadrogeneios* the presence of a diastema in front of p3,  
43 suggesting a more elongated tooth row in both genera than in *Ocepeia*. Other  
44 resemblances are the strong masseteric crest extending low on the corpus, the  
45 symphysis extended close to p2, the absence of a coronoid foramen (as also in  
46 *Ocepeia*), and the low position of the mandibular condyle with respect to the tooth  
47 row. *Abdounodus*, however, departs from *Hadrogeneios* in several specialized traits,  
48 that are also distinctive with respect to *Ocepeia*. The most noticeable are incipient  
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3 lophodont traits, such as the presence of a small hypolophid and the low cingulid-like  
4  
5 postcristid (Gheerbrant, 2010; Gheerbrant et al., 2001, 2016). Other derived features  
6  
7 of *Abdounodus* are the smaller molar talonid, the hypoconulid located much more  
8  
9 labial, the much more bunodont teeth, and the smaller m3 (reduced in size with  
10  
11 respect to m2). In addition, *Abdounodus* differs from *Hadrogeneios* by the simple  
12  
13 (premolariform) p4 and the narrower mandibular corpus. The upper molars of  
14  
15 *Abdounodus* are well distinctive from those of *Hadrogeneios* in derived traits such as  
16  
17 the large and bulbous metaconule, the smaller parastyle, and the transversely narrow  
18  
19 crown.  
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23  
24 The upper molar pattern of *Hadrogeneios* in styelar area is remarkable. It has  
25  
26 intriguing resemblance with some other taxa, which deserves comments and  
27  
28 comparisons.  
29

30  
31 Outside paenungulatomorphs, it is surprisingly similar to cyriacotheriid  
32  
33 pantodonts from the Paleocene of North America (see Scott, 2010) in the  
34  
35 dilambdodont (= selenodont) ectoloph, which is linked to large and inflated styelar  
36  
37 cusps (stylocone and mesostyle), and the well-developed styelar shelf. This is  
38  
39 associated to a similar transversely extended occlusal outline and to the large and  
40  
41 low protocone that is surrounded by a lingual cingulum. However, *Hadrogeneios* is  
42  
43 well distinctive from the cyriacotheriids *Cyriacotherium* and *Presbyterium* in a  
44  
45 number of important characters such as the absence of conules (present and large in  
46  
47 *Cyriacotherium*), the narrower styelar shelf, the shorter postmetacrasta, the smaller m3,  
48  
49 and the much smaller size. The lower molars of cyriacotheriids have a shorter, more  
50  
51 compressed occlusal outline (shorter and wider), a less bunodont and sharper  
52  
53 morphology with higher crests and cusps, longer cristid obliqua, hypoconulid not  
54  
55 twinned to entoconid, and absence of diastema between p3 and p2. The  
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3 dilambdodont ectoloph connected to stylar cusps is obviously convergent in  
4  
5 *Hadrogeneios* and cyriacotheriids.  
6

7  
8         Comparison of the upper molar pattern of *Hadrogeneios* with advanced  
9  
10 Adapisoriculidae, such as *Garatherium* (Paleocene of Morocco and Ypresian of  
11  
12 Algeria), *Adapisoriculus* and *Remiculus* (Paleocene of France), is more intriguing and  
13  
14 interesting (Supplementary Data 1, Fig. S5). These genera have a remarkably similar  
15  
16 W-like dilambdodont ectoloph that is linked to a cuspsate mesostyle, and they share  
17  
18 some other interesting features such as the inflated stylar cusps, especially the  
19  
20 mesostyle and stylocone, the wide stylar shelf, the large paracingulum, the metacone  
21  
22 as large as the paracone, the occlusal outline wide transversely, and the large and  
23  
24 hook-like parastylar area. In addition, the lower molars strikingly share the  
25  
26 hypoconulid close to entoconid. However, *Hadrogeneios* differs from *Adapisoriculus*  
27  
28 and *Garatherium* in the absence of conules, the lower and larger protocone, the  
29  
30 presence of lingual cingulum, the narrower occlusal outline and stylar shelf, and the  
31  
32 bunodont crown. *Remiculus* shares with *Hadrogeneios* peculiar traits, unknown in  
33  
34 other adapisoriculids, such as an incipiently bunodont crown, the transversely  
35  
36 narrower occlusal outline, the metacingulum present, the large (voluminous)  
37  
38 protocone (unlike *Garatherium*), and the presence of a lingual cingulum.  
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44         The two Paleogene African insectivore-like placentals from the Fayum (Egypt),  
45  
46 *Dilambdogale* (BQ-2, Birket Qarun Formation, late Eocene; Seiffert, 2010), and  
47  
48 *Widanelfarasia* (L41 site, Jebel Qatrani Formation, earliest Oligocene; Seiffert et al.,  
49  
50 2000), share upper molars with a dilambdodont ectoloph and well-developed stylar  
51  
52 cusps. However, their ectoloph morphology is less specialized than in *Hadrogeneios*,  
53  
54 with a much smaller mesostyle that is not linked to the ectoloph. In addition, they are  
55  
56 distinctive in the wider stylar shelf, the mesiodistally narrow protocone, and the larger  
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3 paracone with respect to the metacone. Lower molars of *Dilambdogale* and  
4  
5 *Widanelfarasia* differ in the small talonid basin, the hypoconulid not approximated to  
6  
7 the entoconid, and the (relatively) smaller m3. *Dilambdogale* and *Widanelfarasia*  
8  
9 have in fact a dental morphology that is quite reminiscent of the dilambdodont  
10  
11 adapisoriculids.  
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## 14 15 PHYLOGENETIC ANALYSIS 16 17

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20 The cladistic analysis recovers well-resolved MPTs that support a basal  
21  
22 relationship of *Hadrogeneios* to *Ocepeia*, *Abdounodus*, and crown Paenungulata  
23  
24 (Fig. 10). It indicates that *Hadrogeneios* is the basalmost known paenungulatomorph.  
25  
26 In the standard analysis (Supplementary Data 2, Analysis 1; Supplementary Data 4),  
27  
28 which recovers 180 MPTs (L [length] = 972 steps, RI [Retention index] = 34.8; CI  
29  
30 [Consistency index] = 61.3), *Hadrogeneios* is indeed the sister group of all other  
31  
32 paenungulatomorphs (consensus tree and majority rule tree) (Fig. 10). The node  
33  
34 including *Hadrogeneios* and other paenungulatomorphs is supported by low Bremer  
35  
36 support (BS = 1) and low Bootstrap score; this is related in part to the limited  
37  
38 knowledge of *Hadrogeneios*, which is restricted to dental and mandibular features  
39  
40 representing only 49% of all coded characters in the phylogenetic matrix. In the  
41  
42 cladistic analyses developed here, *Hadrogeneios* is never recovered as sister group  
43  
44 to *Ocepeia*. It belongs to a stem paenungulatomorph lineage that branches earlier  
45  
46 than the Ocepeiidae.  
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51  
52 Another cladistic analysis was developed, in which the monophyly of the clade  
53  
54 Afrotheria is constrained (Supplementary Data 2, Analysis 2; Supplementary Data 5–  
55  
56 6). When the position of *Hadrogeneios* is constrained within the Afrotheria, the  
57  
58 resulting MPTs (30 MPTs found with L = 986) recovers it as the most basal stem  
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3 paenungulate; it is a stem paenungulatomorph, but not a stem afrotherian.

4  
5 Interestingly, the node including *Hadrogeneios* and other paenungulatomorphs is  
6  
7 more robust in this constrained analysis (Bremer support BS = 4) than in the  
8  
9 standard analysis (Supplementary Data 2, Analysis 1). When *Hadrogeneios* position  
10  
11 is not constrained within the Afrotheria (itself constrained), it is recovered at the root  
12  
13 of crown placentals together with *Todralestes* and *Ptolemaia* (Supplementary Data 2,  
14  
15 Analysis 2), with a very low Bremer support.  
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18  
19 The relationships of *Hadrogeneios* with other paenungulatomorphs in the  
20  
21 unconstrained analysis is supported by five synapomorphies. They include a single  
22  
23 exclusive synapomorphy, i.e. the presence of a coronoid (retromolar) fossa  
24  
25 (character 62–1). Other shared features are homoplastic. The most important ones  
26  
27 (i.e., less homoplastic) are the coronoid apophysis rising at m3 level (character 55–1,  
28  
29 RI = 75), the inflated mesostyle (character 104–1, RI = 77), and the centrocrista  
30  
31 strongly dilambdodont and linked to mesostyle (character 113–2, RI = 84). Here also  
32  
33 the dilambdodont ectoloph linked to mesostyle is recovered as a major feature of the  
34  
35 ancestral morphotype of the Paenungulata and Paenungulatomorpha (Gheerbrant et  
36  
37 al., 2016). The resulting MPTs recovered from the cladistic analysis of *Hadrogeneios*  
38  
39 recover a topology for paenungulates congruent with that previously published. In  
40  
41 particular, *Eritherium* is the sister group to Proboscidea (Gheerbrant, 2009), and  
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43 Embrithopoda are the sister group to crown Tethytheria (Gheerbrant et al., 2021).  
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## 52 DISCUSSION AND CONCLUSION

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3           *Hadrogeneios phosphaticus*, gen. et sp. nov. is the third stem paenungulate  
4 lineage found in Africa, along with *Abdounodus* (*A. hamdii*) and *Ocepeia* (*O.*  
5  
6 *daouiensis* and *O. grandis*) from the same Paleocene sites of the Ouled Abdoun  
7 phosphate basin (Morocco). *H. phosphaticus* remains partially known, only by teeth  
8 and jaws. The comparisons and phylogenetic analysis, however, do argue well that  
9  
10 *H. phosphaticus* documents the most basal known paenungulatomorphs. Its dental  
11 morphology is remarkably primitive with respect to crown Paenungulata in the  
12 tritubercular upper molar pattern (no hypocone or pseudohypocone), the upper  
13 molars transversely wide and lacking conules, the retention of a lower molar  
14 paraconid as in *Ocepeia* and *Abdounodus*, the last molar not enlarged, the small  
15 lower incisors, the large lower canine, and the lack of a coronoid foramen. It is more  
16 plesiomorphic than the two other stem paenungulates *Ocepeia* and *Abdounodus* in  
17 the less bunodont teeth, the absence of a hypolophid, and the absence of a  
18 metaconule. Another noticeable distinctive dental trait of *Hadrogeneios* from *Ocepeia*  
19 and *Abdounodus* is the molariform last premolar. It is a possible autapomorphy in the  
20 cladistic analysis (character 22–1). On the other side, *Hadrogeneios* displays the  
21 derived upper molar morphology of stem and crown paenungulates  
22 (Paenungulatomorpha), with the presence of a dilambdodont W-like ectoloph linked  
23 to well-developed styler cusps. This is a plesiomorphic (morphotypic) condition within  
24 Paenungulatomorpha and a derived condition within placentals, i.e., a  
25 paenungulatomorph synapomorphy. Within the Afrotheria, the polarity of the  
26 dilambdodont condition is ambiguous, because extant tenrecoidean insectivores  
27 (tenrecids, potamogalids, and chrysochlorids) are specialized in a divergent molar  
28 zalambdodont condition, in which the centrocrista is reduced. Other insectivore-like  
29 afrotherians, such as early macroscelideans, have a rectodont centrocrista.

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3 Regarding the tubulidentates, the homology of their peculiar molar pattern remains  
4 unclarified. Despite these open questions on the ancestral afrotherian dental  
5 morphotype, when the position of *Hadrogeneios* is constrained to fall within the clade  
6 Afrotheria, it is recovered, with strong support, as a stem paenungulate and not as a  
7 stem afrotherian. Within Afrotheria, the W-like ectoloph linked to an inflated  
8 mesostyle is a key dental feature of the node Paenungulatomorpha, including  
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17 *Hadrogeneios*.

18  
19 As noted above, some adapisoriculids, such as *Garatherium* and *Remiculus*,  
20 share an intriguingly similar dilambdodont upper molar pattern. They also share a  
21 molariform p4 (e.g., *Remiculus*) and the hypoconulid approximated to the entoconid  
22 on lower molars (dilambdodont adapisoriculids; see Gheerbrant, 1995). However, the  
23 significance of this morphological affinity is unknown or uncertain. Recent studies  
24 have excluded the adapisoriculids from the crown group Placentalia, identifying them  
25 as basal eutherians (Goswami et al., 2011). In this hypothesis, the adapisoriculids  
26 are the only stem eutherians displaying dilambdodont molars. This molar morphology  
27 has actually evolved several times in placentals, especially in insectivore-like taxa  
28 (Butler, 1996). Interestingly, within the Afrotheria, it is identified as the ancestral  
29 morphotype of the Paenungulatomorpha (Gheerbrant et al., 2016). The convergence  
30 of the dilambdodont condition in the Paenungulatomorpha and the Adapisoriculidae  
31 is certainly possible or even likely. Nevertheless, most of the differences of  
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*Hadrogeneios* from the adapisoriculids are derived features (including its much larger  
size). They do not a priori conflict with an ancient stem relationship of the  
adapisoriculids to the clade including *Hadrogeneios* (Paenungulatomorpha or  
Afrotheria). We should notice in passing that this is consistent with the distribution of  
the adapisoriculids in time (Late Cretaceous and Paleocene) and space (Africa).

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3 Understanding the significance of the shared derived upper molar traits of  
4  
5 *Hadrogeneios* and adapisoriculids requires additional data. We need more complete  
6  
7 material of these taxa in order to develop further comparisons and significant formal  
8  
9 analysis (e.g., cladistic analysis) of their relationships. Currently, the knowledge of  
10  
11 the adapisoriculids is indeed especially poor, restricted to mostly isolated teeth  
12  
13 (especially for African taxa!) and a few tarsal bones, making any conclusion on their  
14  
15 relationships tentative.  
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18  
19 Besides a basically primitive dental pattern, *Hadrogeneios phosphaticus* is  
20  
21 characterized by a remarkable specialized anterior part of the dentary with an  
22  
23 enlarged and stout mandibular symphysis associated to small incisors. It is  
24  
25 interpreted as corresponding to a peculiar specialization for food acquisition with  
26  
27 increasing grip strength or enhanced grip precision. This is the earliest specialization  
28  
29 evidenced in the evolutionary radiation of the stem paenungulates. It is most likely an  
30  
31 autapomorphy of *Hadrogeneios*; for instance, it is well distinctive from the more  
32  
33 generalized condition seen in *Ocepeia* (Gheerbrant, 2010; Gheerbrant et al., 2014).  
34  
35 However, the morphology of the mandibular symphysis, the pars incisiva, and the  
36  
37 incisors in *Abdounodus* remain unknown, as in the ancestral morphotype of the  
38  
39 Paenungulatomorpha. As a result, the significance of the mandibular symphyseal  
40  
41 pattern seen in *Hadrogeneios* is still unknown in the context of the evolution of the  
42  
43 specialized anterior dental apparatus of the crown paenungulates (e.g., the enlarged  
44  
45 incisors).  
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51 *Hadrogeneios* adds to the genera *Abdounodus* and *Ocepeia* from the same  
52  
53 Ouled Abdoun middle Paleocene phosphate levels, and it further highlights the  
54  
55 diversity of the stem paenungulates (paenungulatomorphs). *Hadrogeneios*,  
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57 *Abdounodus*, and *Ocepeia* belong to three successive stem groups that document a  
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3 basal African radiation preceding that of crown paenungulates. On the other hand,  
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5 *Hadrogeneios* sheds new light on the earliest steps of the evolution of the African  
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7 “ungulates” (i.e., paenungulates); it is probably rooted not far from the origin of  
8  
9 Paenungulatomorpha based on its plesiomorphic dental morphology.  
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12 This new discovery re-emphasizes the importance of the Ouled Abdoun  
13  
14 phosphate deposits in Morocco, which provide the earliest and best fossil evidence  
15  
16 on the origin and early radiation of the African “ungulates”.  
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#### 18 SUPPLEMENTARY INFORMATION

19  
20  
21 Supplementary Data 1.pdf: Tables S1-S5, Figures S1-S5.

22  
23  
24 Supplementary Data 2.pdf: Phylogenetic analysis of *Hadrogeneios phosphaticus*,  
25 gen. et sp. nov.

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29 Supplementary Data 3.nex: Analyzed phylogenetic matrix including *Hadrogeneios*  
30 *phosphaticus*, gen. et sp. nov.

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34 Supplementary Data 4–6.tre: Complete set of # most parsimonious trees obtained in  
35 the parsimony analysis.

36  
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39 Supplementary Data 7–9.pdf: 3D models from CT scans of MHNM.KHG.224  
40 (paratype of *Hadrogeneios phosphaticus*), MHNM.KHG.225 (paratype of  
41 *Hadrogeneios phosphaticus*), MHNM.KHG.225 (paratype of  
42 *Hadrogeneios phosphaticus*), and MHNM.KHG.227 (holotype of *Hadrogeneios*  
43 *phosphaticus*), and MHNM.KHG.227 (holotype of *Hadrogeneios*  
44 *phosphaticus*), and MHNM.KHG.227 (holotype of *Hadrogeneios*  
45 *phosphaticus*).  
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### CAPTION OF FIGURES

FIGURE 1. *Hadrogeneios phosphaticus*, gen. et sp. nov., MHNM.KHG.226. **A**, right M2–3; **B**, associated left M3 of the same individual. **C**. MHNM.KHG.223, right M3. Occlusal views, s.e.m. photographs. [column width]

FIGURE 2. *Hadrogeneios phosphaticus*, gen. et sp. nov. ~~Holotype MHNM.KHG.227, part of left dentary preserving the mandibular symphysis, the alveoli for two incisors, c1 and p1–3 and p4, m1 and m3 that is broken apart. **A–C**, occlusal (stereophotographic views), labial and lingual views of the dentary. **D–F**, details of p4–m1 in occlusal (stereophotographic views), labial and lingual views; **G–E**, the isolated m3, broken from the dentary, in occlusal (stereophotographic views), labial and lingual views.~~ [page width]

FIGURE 3. *Hadrogeneios phosphaticus*, gen. et sp. nov. ~~**A–C**, MHNM.KHG.224, part of right dentary broken in several pieces in occlusal (stereophotographic views), lingual and labial views; it preserves the mandibular symphysis, p3–4, m2, and the alveoli for i1–3, c1, and p1. **D–F**, MHNM.KHG.225, posterior part of a left dentary with m2 and m3, in occlusal (stereophotographic views), lingual and labial views. **G–J**, MHNT PAL 2006.0.19, broken posterior part of right dentary with m3 in occlusal~~

~~view (G: stereophotographic views; J: enlarged view) and lingual and labial views~~ 

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FIGURE 4. *Hadrogeneios phosphaticus*, gen. et sp. nov. Detailed occlusal view of the lower teeth (s.e.m. photographs). **A.** Holotype MHNM.KHG.227, left p4, m1 and m3. **B.** MHNM.KHG.224, right p3–4, and m2. **C.** MHNM.KHG.225, left m2 and m3. **D.** MHNT PAL 2006.0.19, right m3. [page width]

FIGURE 5. *Hadrogeneios phosphaticus*, gen. et sp. nov. Composite reconstruction of the lower cheek-tooth row, occlusal sketches. **A.** p3–4: MHNM.KHG.224 in reversed view; M1: MHNM.KHG.227; m2: MHNM.KHG.224; m3: MHNT PAL 2006.0.19 in reversed view; alveoli of p4 and p3 from MHNM.KHG.224. **B.** p3–4: MHNM.KHG.224 in reversed view; m1: MHNM.KHG.227; m2: MHNM.KHG.225; m3: MHNM.KHG.225; alveoli of p4 and p3 from MHNM.KHG.224. **C.** p4-m1: MHNM.KHG.227; m2: MHNM.KHG.225; m3: MHNM.KHG.227; alveoli of p4, dp3 (annotated “dp”) and p3 from MHNM.KHG.227. [column width]

FIGURE 6. *Hadrogeneios phosphaticus*, gen. et sp. nov. Composite reconstructions of the lower tooth row based on the 3D digital models made from the CT scans of the material. **A.** Occlusal sketch of the left lower tooth row: alveoli of i1–3, c1 and p1–2, and the teeth p3–4; m1–3. **B–C.** 3D digital models in occlusal and lingual views. **B.** alveoli of i1–3, c1, and p1–2, and the teeth p3–4 and m1–3. **C.** alveoli of i1–3, c, p1–3 (dp3 in grey), and p4, m1–3. The specimen numbers for the 3D digital models are indicated below the teeth. [2/3 page width]

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4 views. **E**, same views by transparency of MHNM.KHG.224 showing the mandibular  
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8 canaliculi; **mc**, mandibular canal; **mf**, mental foramen; **symp**, mandibular symphysis.  
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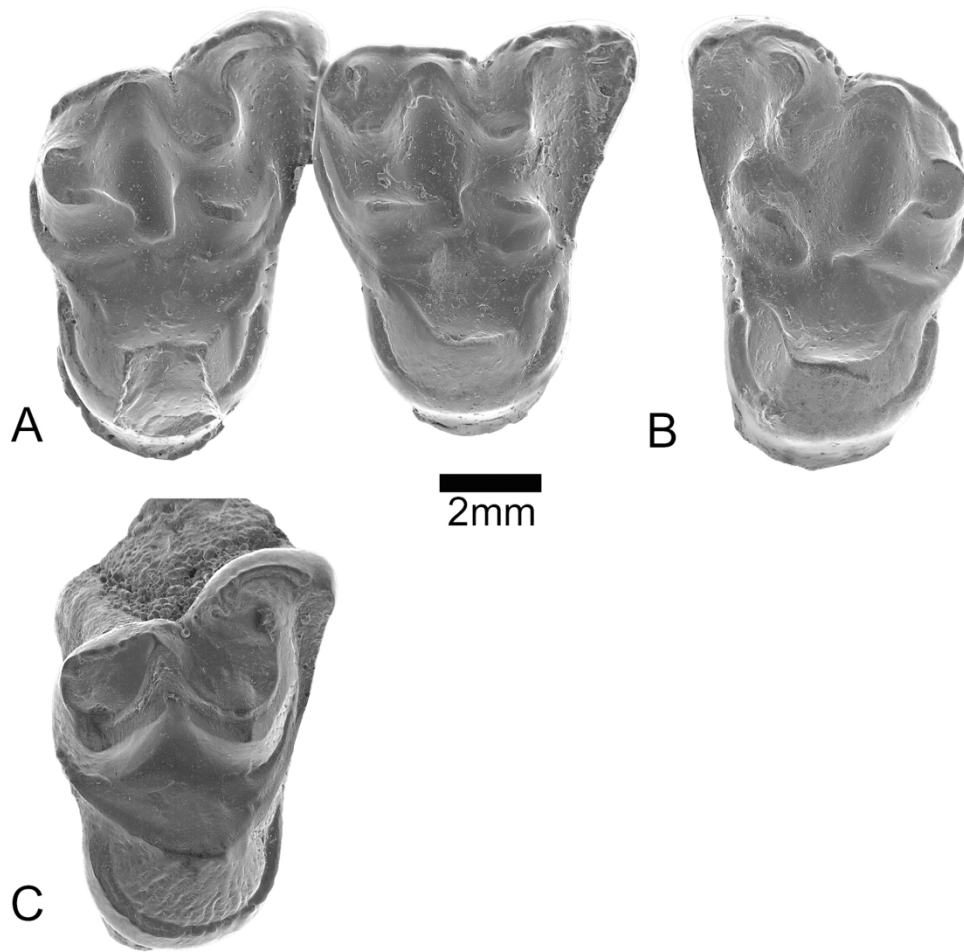
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FIGURE 10. Phylogenetic relationships of *Hadrogeneios phosphaticus*, gen. et sp.  
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5 61.3; Consistency Index (CI)= 34.8. Synapomorphies at the node  
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7 Paenungulatomorpha including *Hadrogeneios*: 38–1, 55–1, 62–1, 104–1, 113–2. See  
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Caption : FIGURE 1. *Hadrogeneios phosphaticus* n. g., n. sp., MHNK.KHG.226. A, right M2-3; B, associated  
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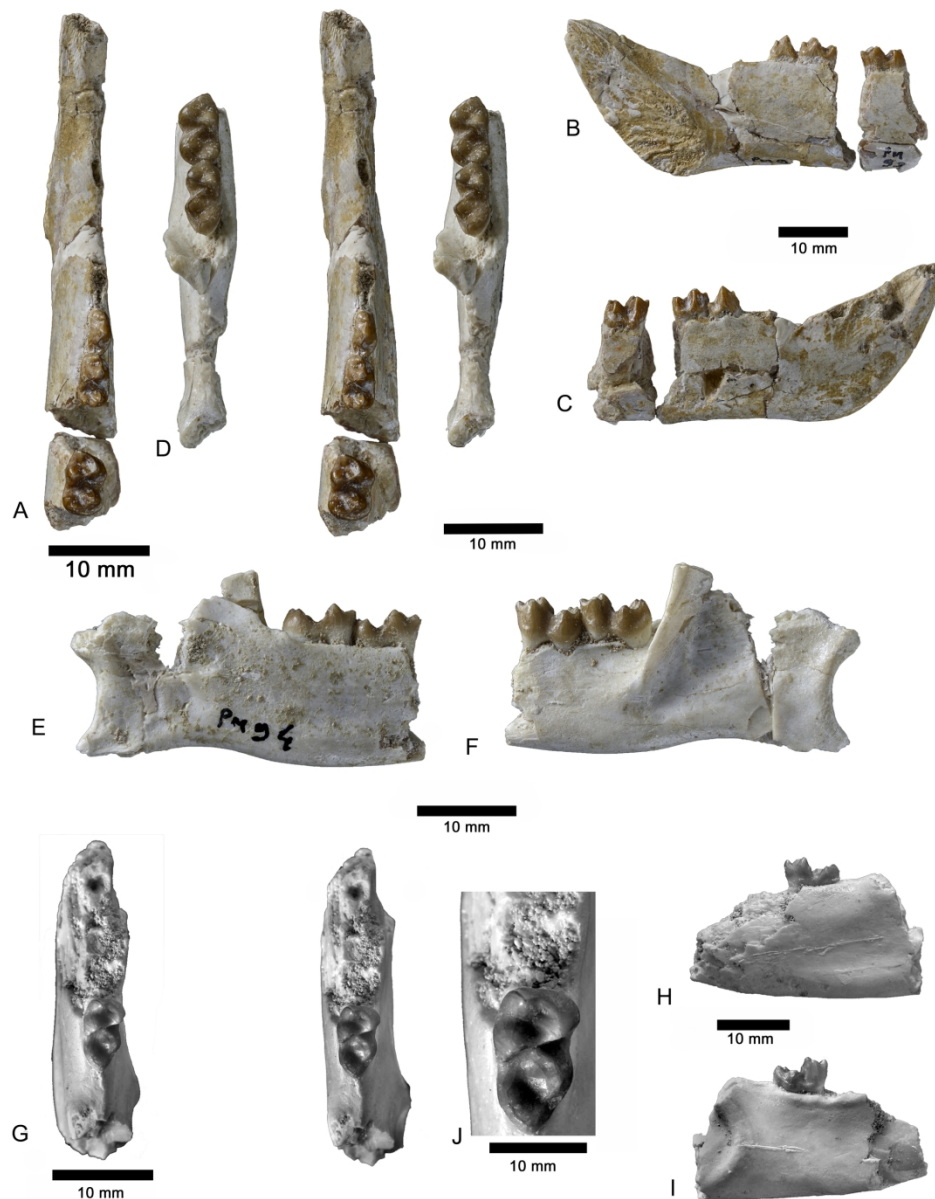


FIGURE 2 (color). *Hadrogeneios phosphaticus* n. g., n. sp. Holotype MHNK.KHG.227, part of left dentary preserving the mandibular symphysis, the alveoli for two incisors, c1 and p1-3 and p4, m1 and m3 that is broken apart. A-C, occlusal (stereophotographic views), labial and lingual views of the dentary. D-F, details of p4-m1 in occlusal (stereophotographic views), labial and lingual views; G-E, the isolated m3, broken from the dentary, in occlusal (stereoviews), labial and lingual views. Scales in millimeters.

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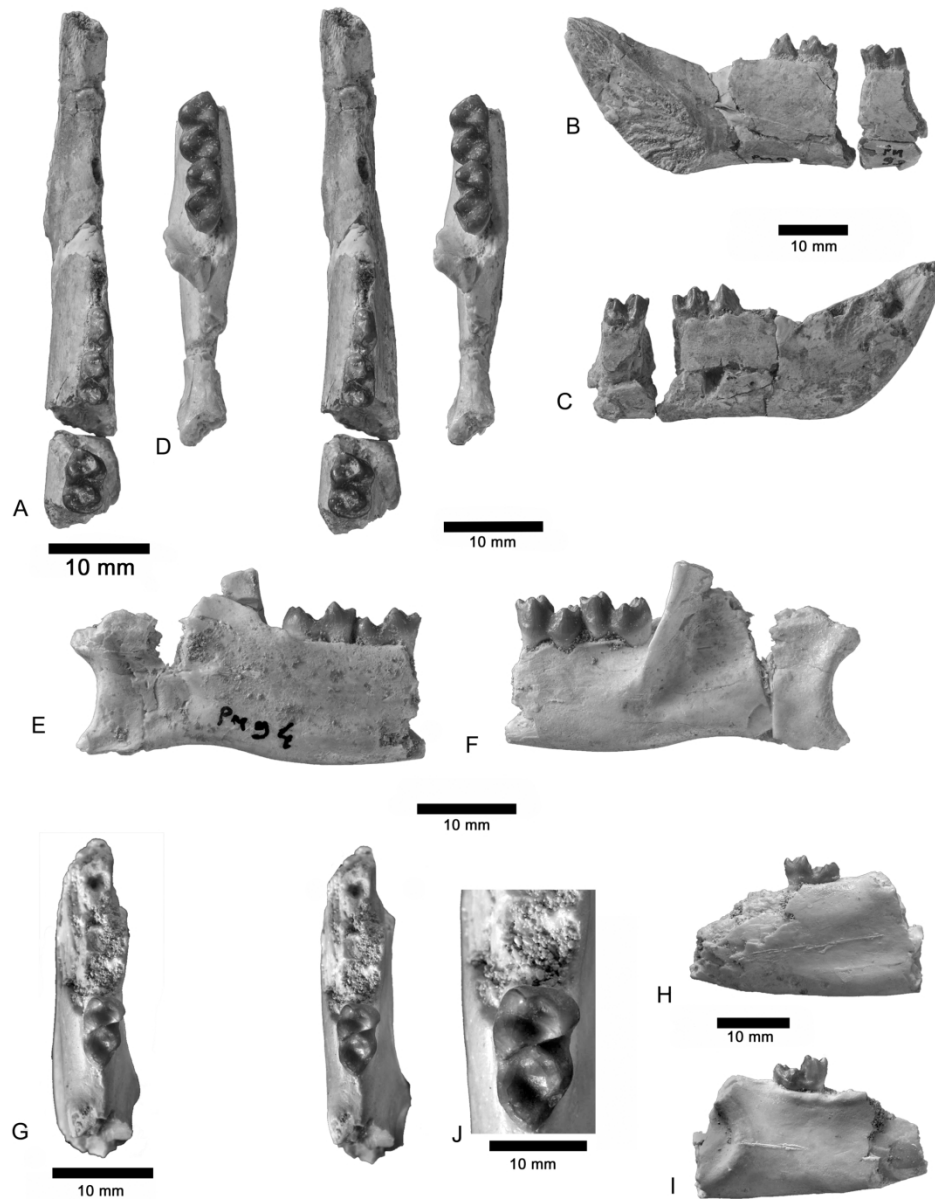


FIGURE 2 (greyscale). *Hadrogeneios phosphaticus* n. g., n. sp. Holotype MHNM.KHG.227, part of left dentary preserving the mandibular symphysis, the alveoli for two incisors, c1 and p1-3 and p4, m1 and m3 that is broken apart. A-C, occlusal (stereophotographic views), labial and lingual views of the dentary. D-F, details of p4-m1 in occlusal (stereophotographic views), labial and lingual views; G-E, the isolated m3, broken from the dentary, in occlusal (stereoviews), labial and lingual views. Scales in millimeters.

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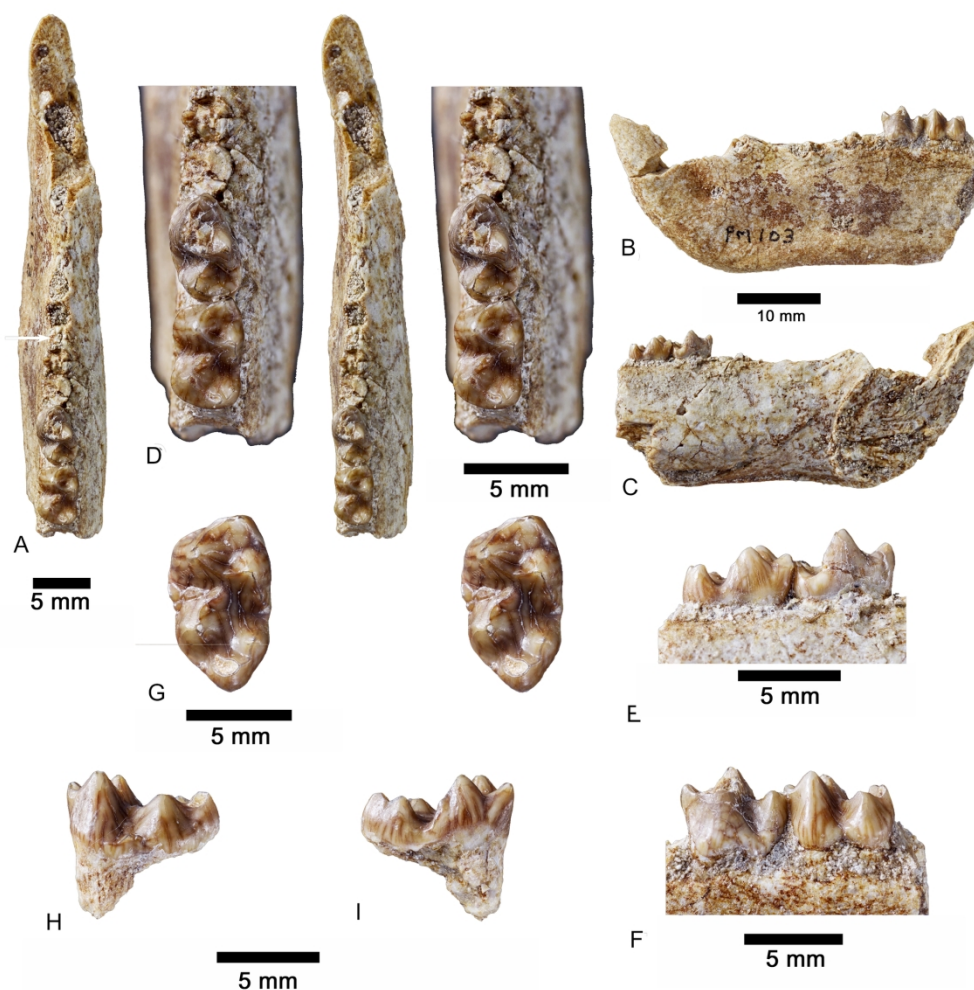


FIGURE 3 (color). *Hadrogoniopsis phosphaticus* n. g., n. sp. A-C, MHNM.KHG.224, part of right dentary broken in several pieces in occlusal (stereophotographic views), lingual and labial views; it preserves the mandibular symphysis, p3-4, m2, and the alveoli for i1-3, c1, and p1. D-F, MHNM.KHG.225, posterior part of a left dentary with m2 and m3, in occlusal (stereophotographic views), lingual and labial views. G-J, MHNT PAL 2006.0.19, broken posterior part of right dentary with m3 in occlusal view (G: stereophotographic views; J: enlarged view) and lingual and labial views. Scales in millimeter.

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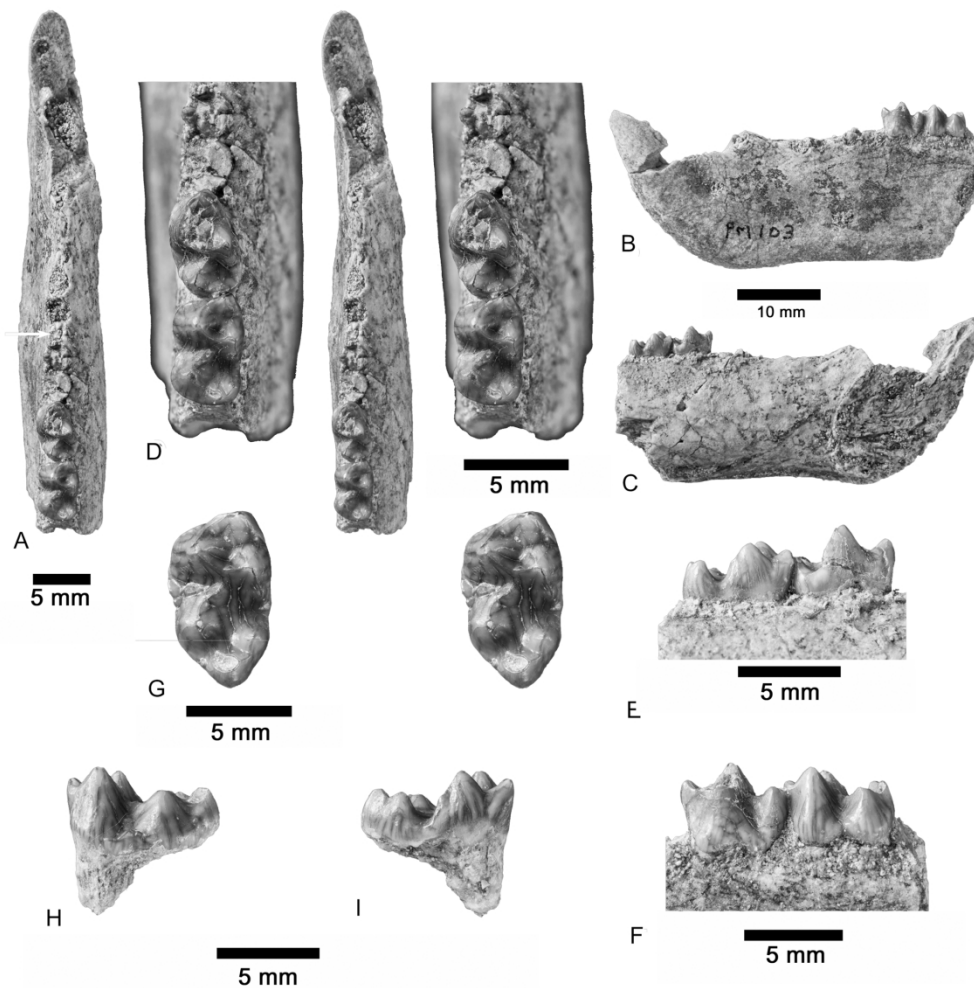


FIGURE 3 (greyscale). *Hadrogonioides phosphaticus* n. g., n. sp. A-C, MHNM.KHG.224, part of right dentary broken in several pieces in occlusal (stereophotographic views), lingual and labial views; it preserves the mandibular symphysis, p3-4, m2, and the alveoli for i1-3, c1, and p1. D-F, MHNM.KHG.225, posterior part of a left dentary with m2 and m3, in occlusal (stereophotographic views), lingual and labial views. G-J, MHNT PAL 2006.0.19, broken posterior part of right dentary with m3 in occlusal view (G: stereophotographic views; J: enlarged view) and lingual and labial views. Scales in millimeters.

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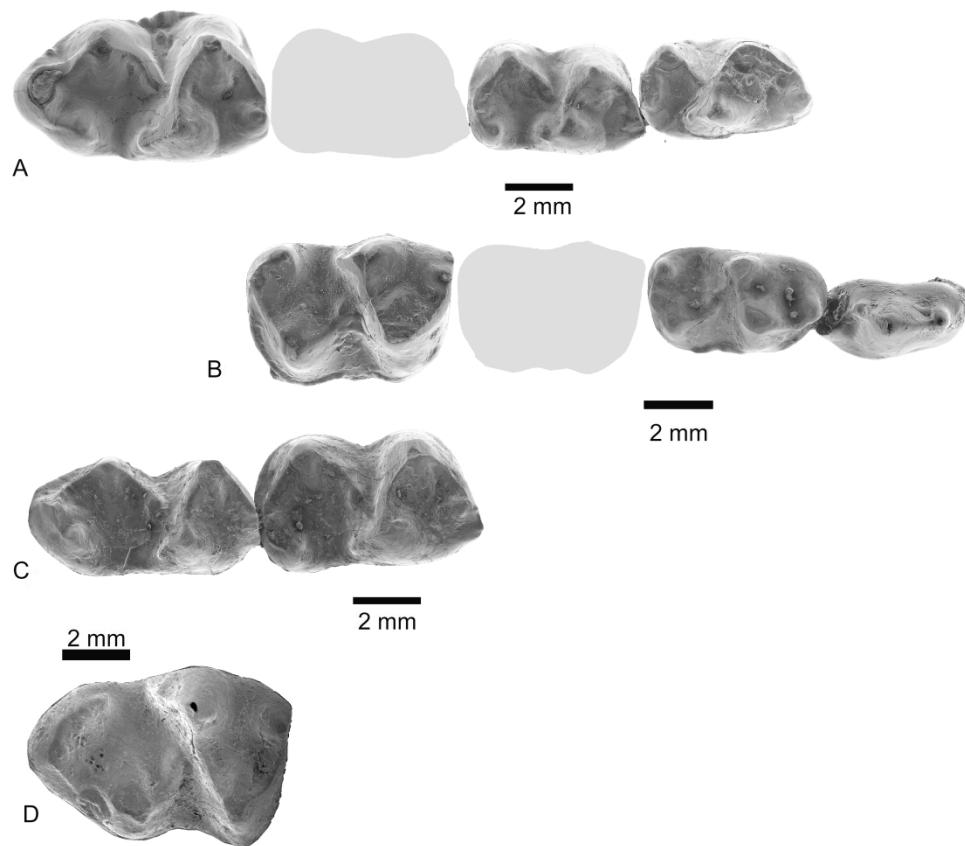


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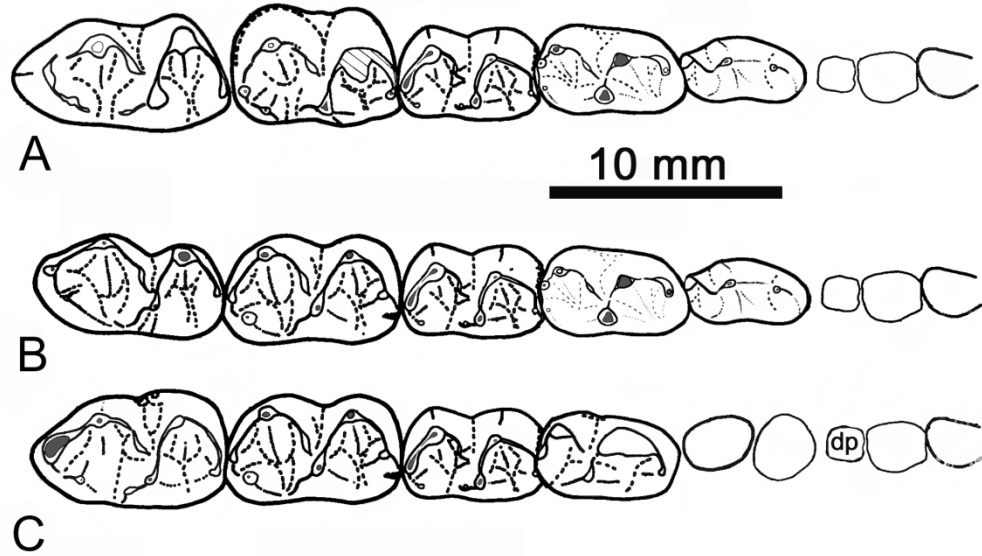


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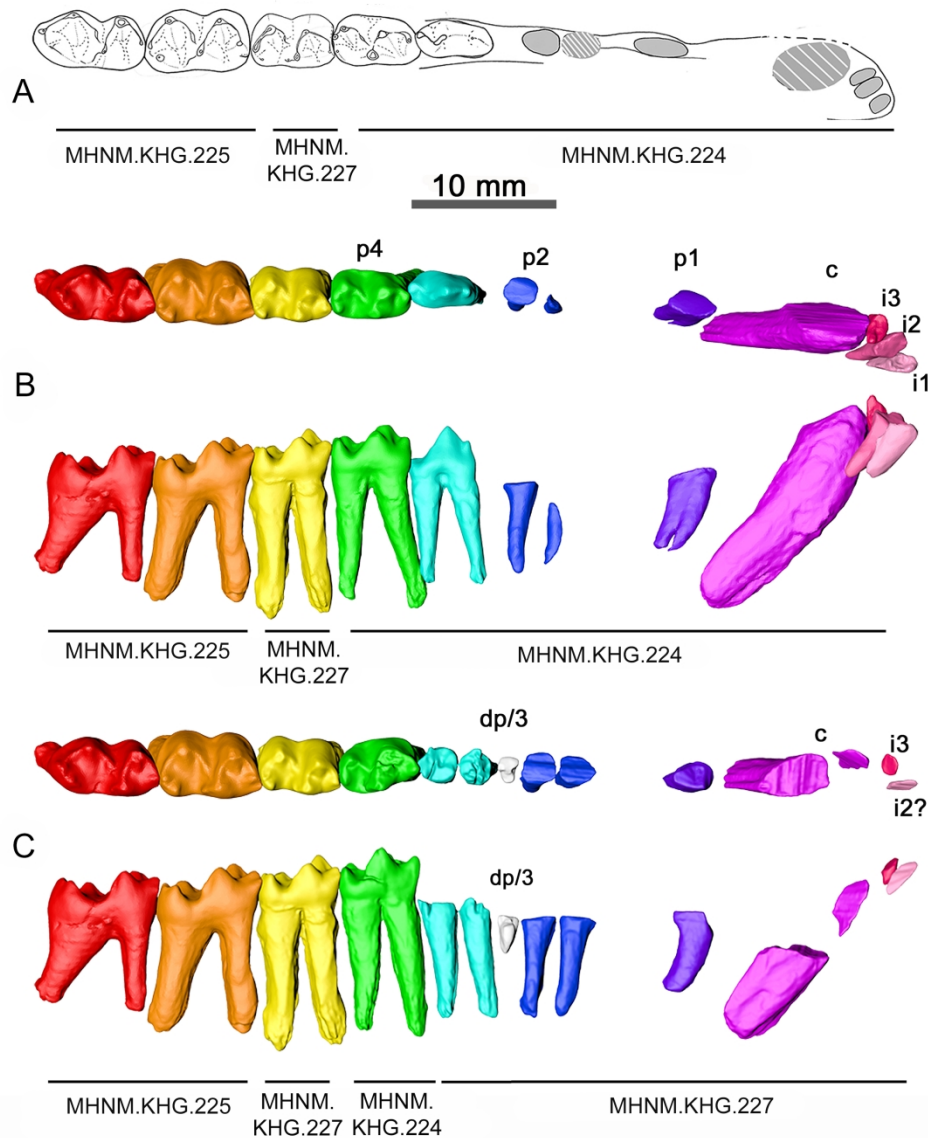


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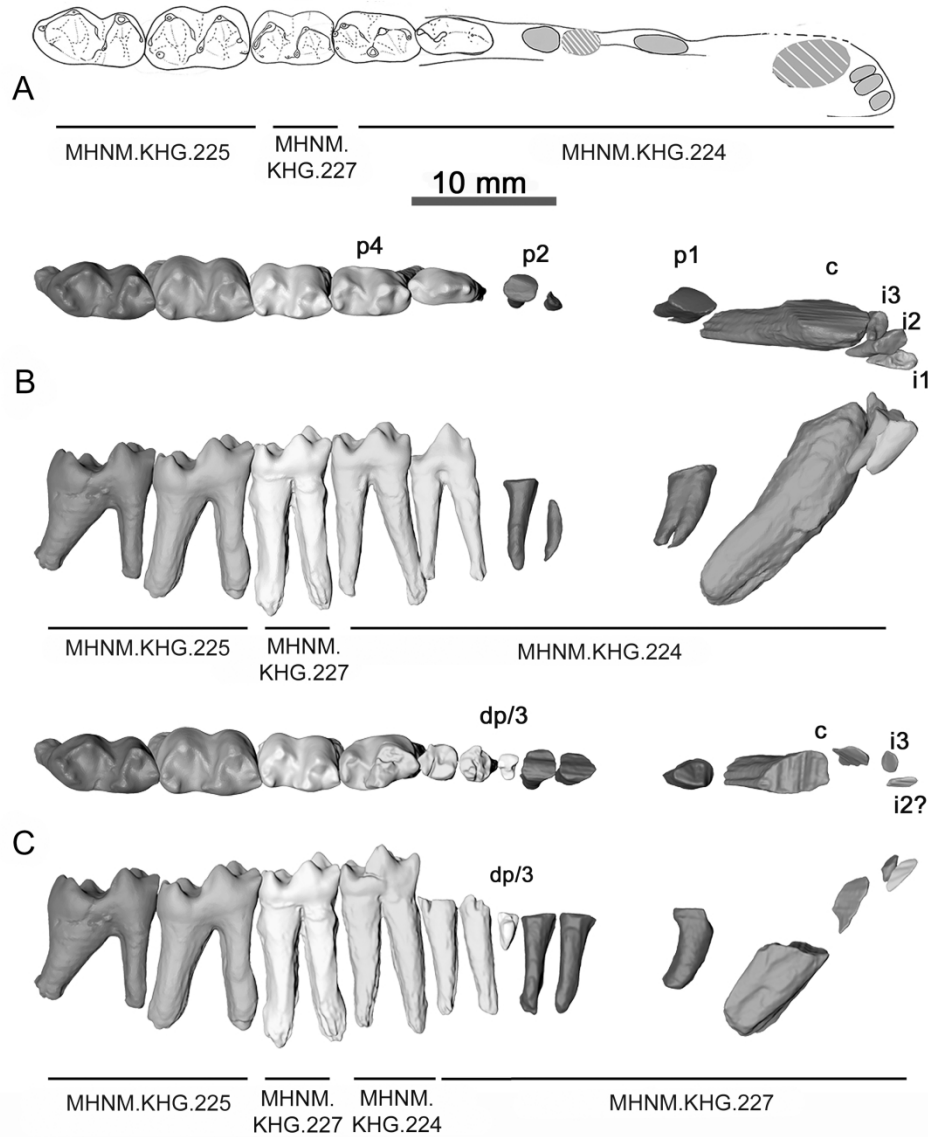


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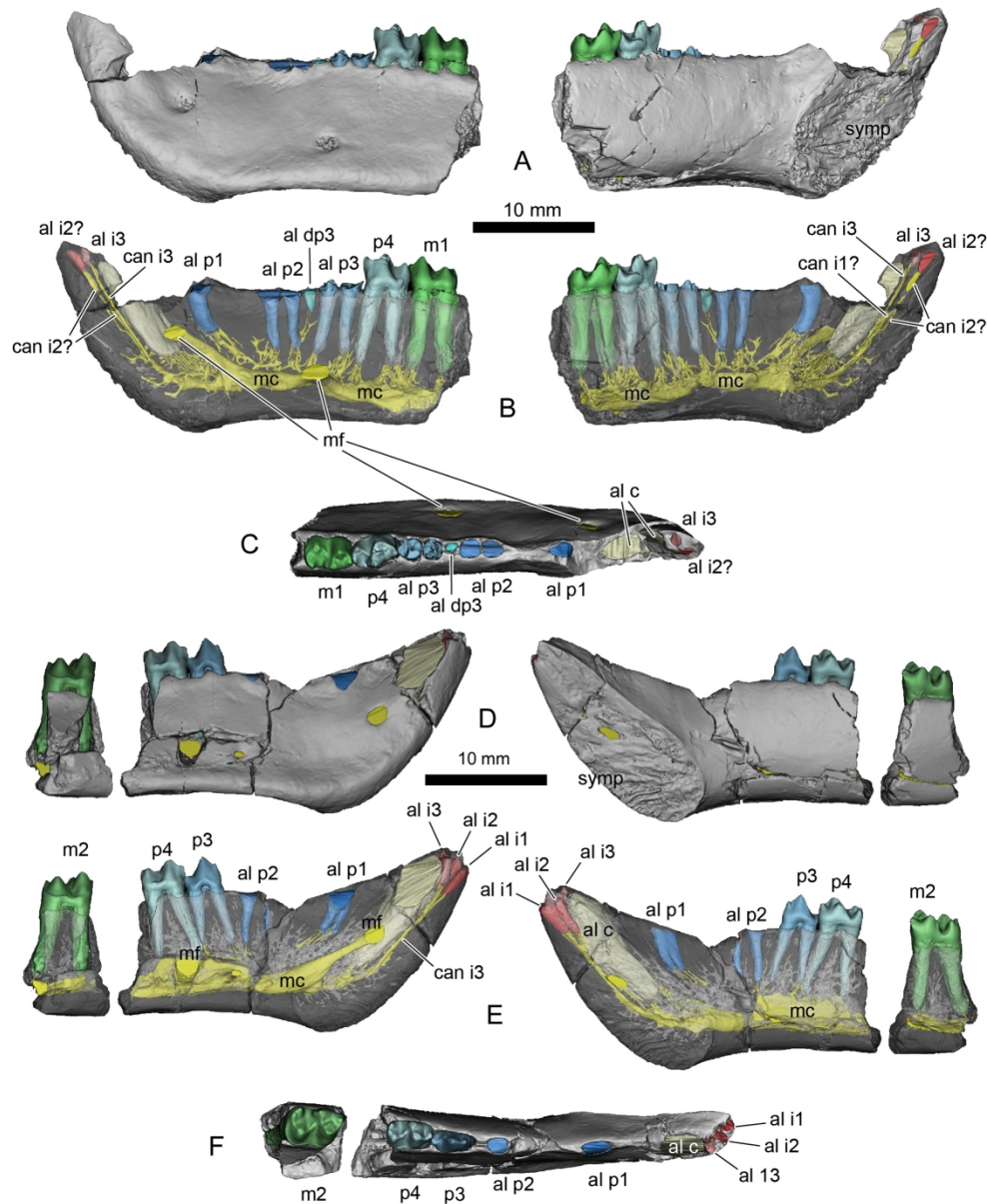


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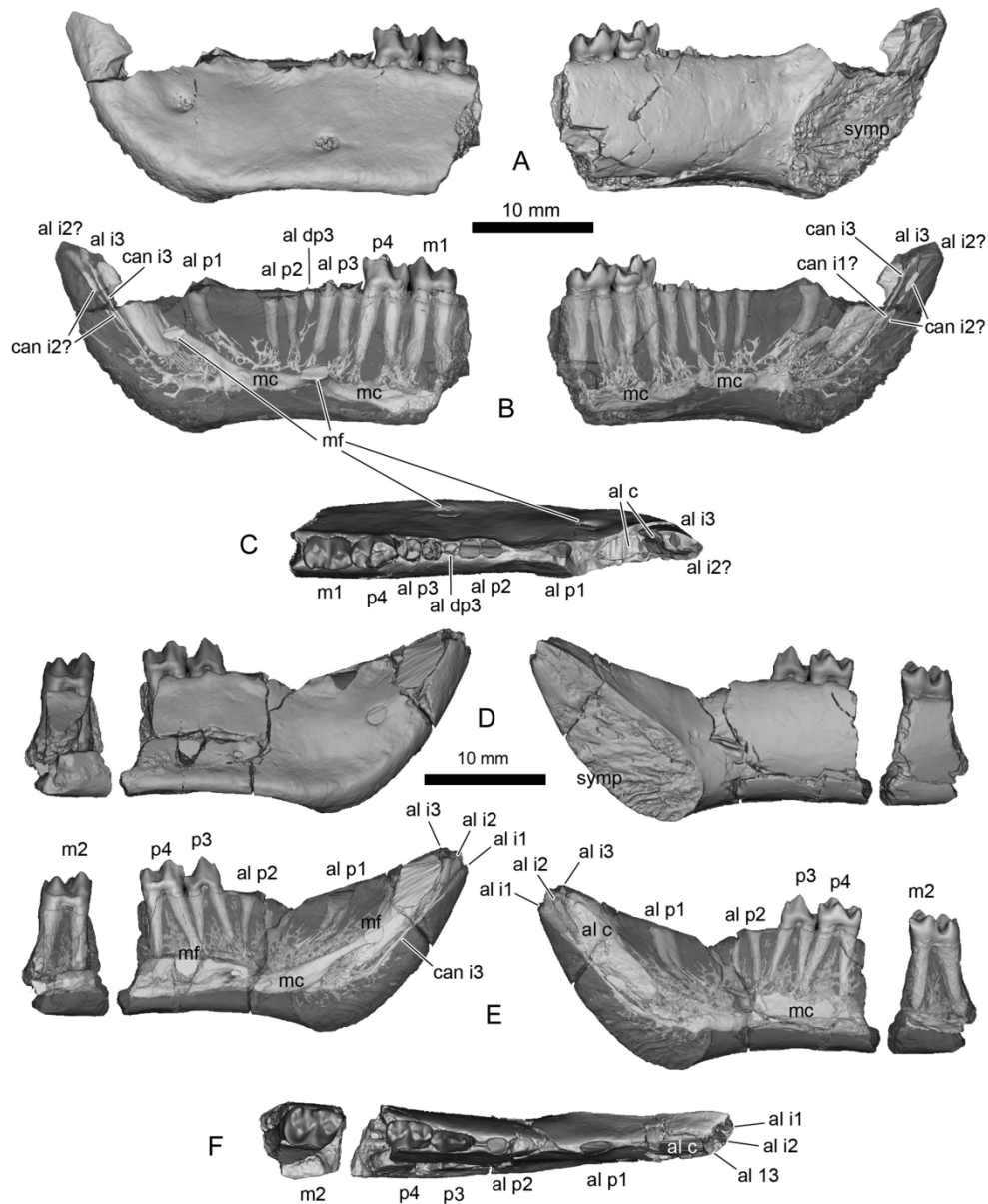


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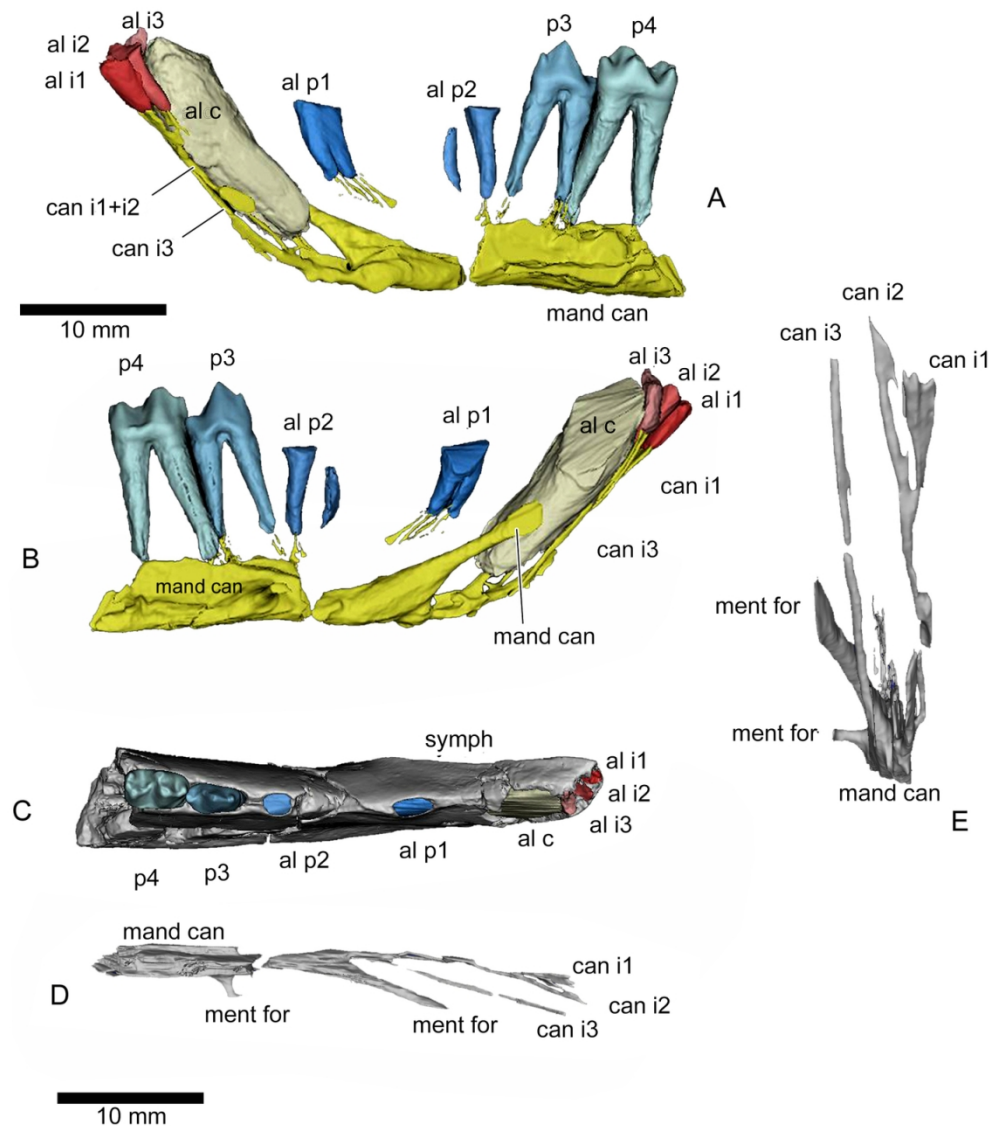


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Link text : Fig. 8

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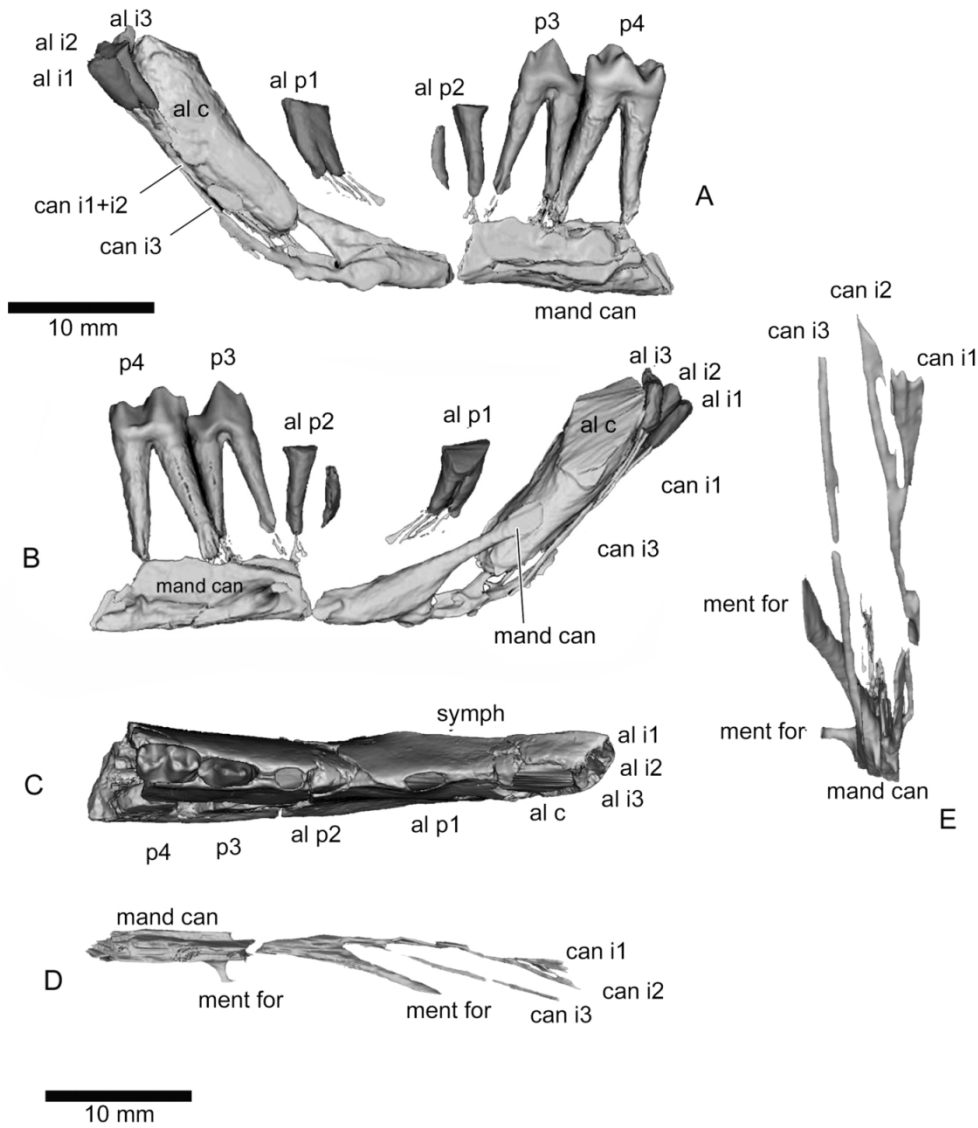


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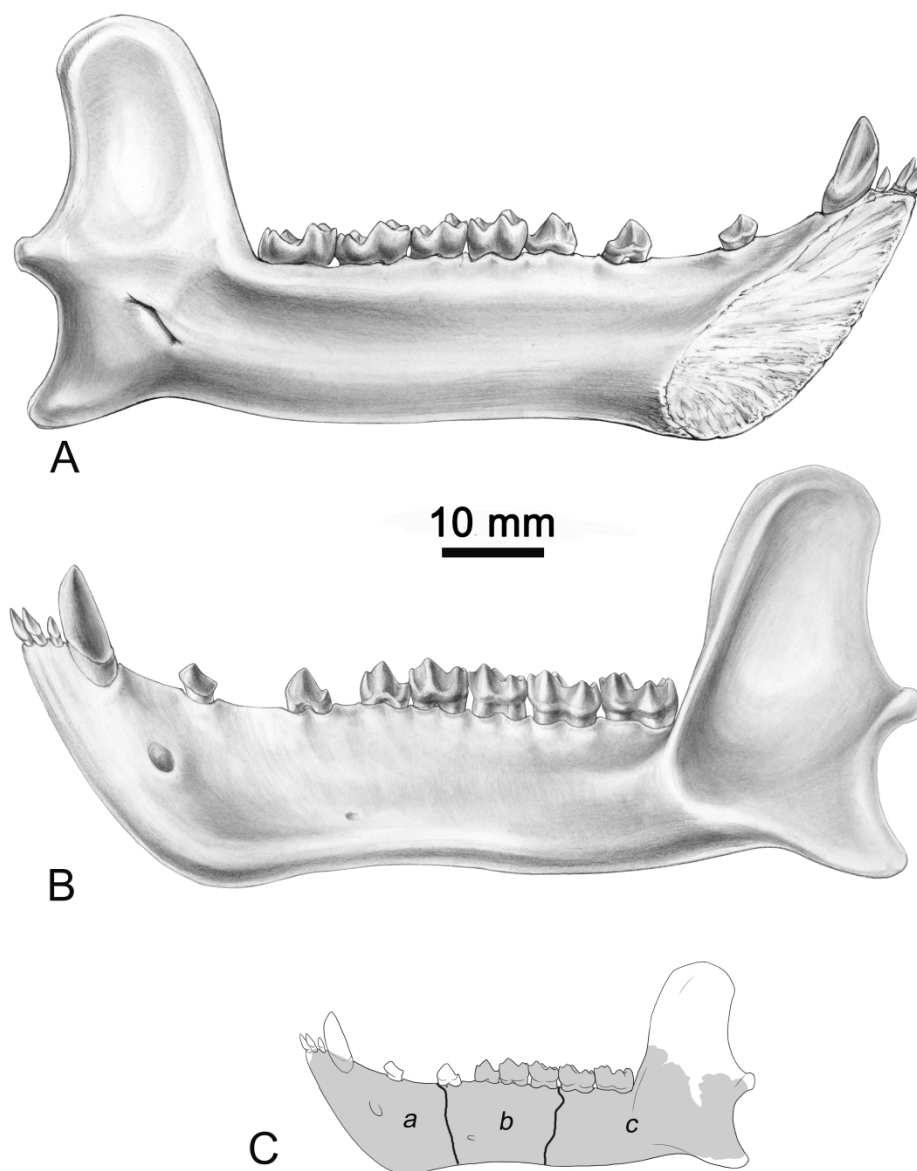


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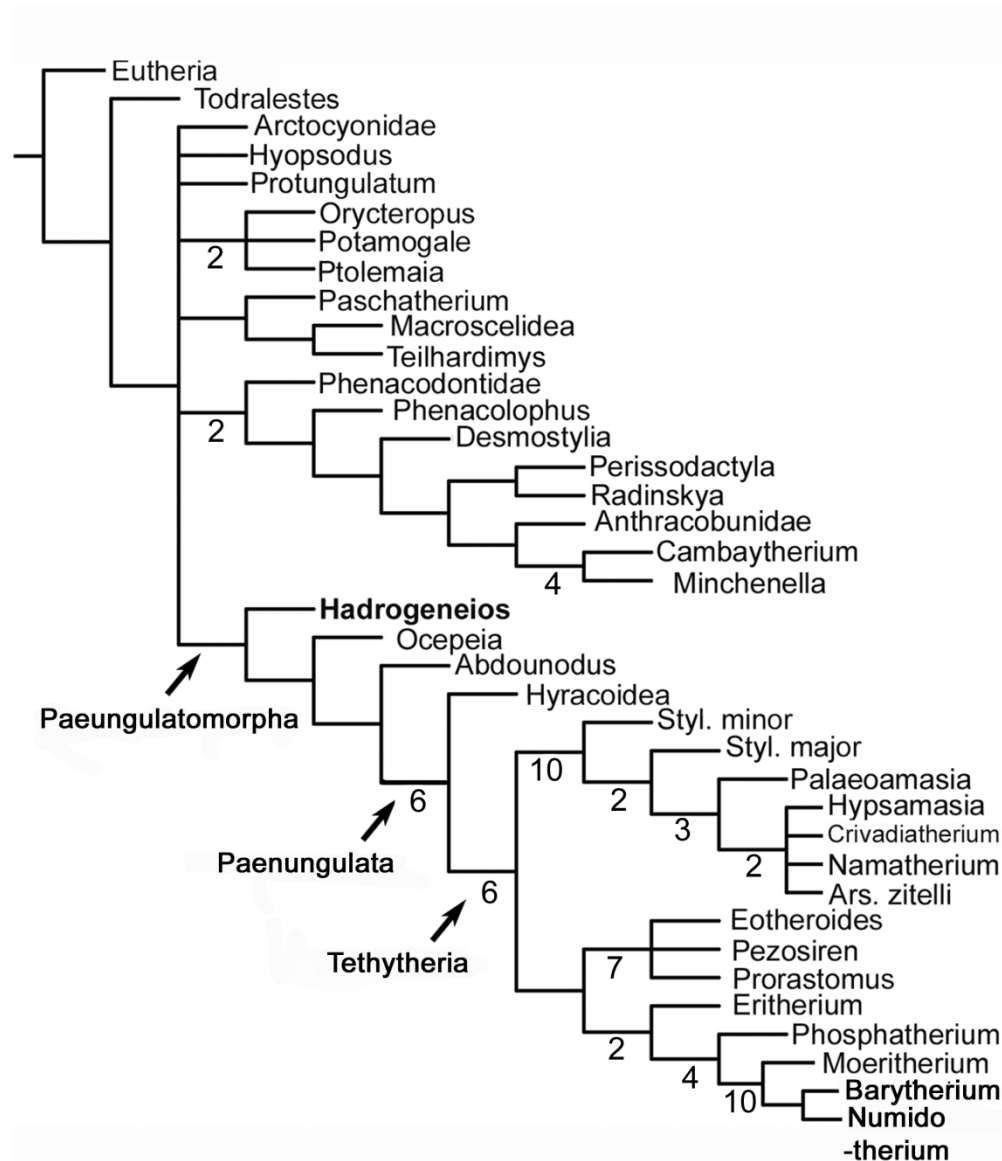


FIGURE 10. Phylogenetic relationships of *Hadrogeneios phosphaticus* gen. et sp. nov. Strict consensus of 130 MPTs from standard analysis with TNT 1.5 and with ordered features. Relative Bremer index >1 (out of 10) is indicated below the nodes. Tree Length (L)= 976 steps; Retention Index (RI)= 61.3; Consistency Index (CI)= 34.9. Synapomorphies at the node Paenungulatomorpha including Hadrogeneios: 38-1, 55-1, 62-1, 104-1, 113-2.

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9 Supplementary data

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15 Ancestral radiation of paenungulate mammals (Paenungulatomorpha) - new  
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## Supplementary Tables S1-5

TABLE S1. Scan parameters of the studied material.

Specimen	Voltage	Current	Filter	Exposure	Voxel size (mm)
MHNM.KHG.225	130 kV	210 $\mu$ A	0.4 mm Cu	1 s	0.02733382
MHNM.KHG.226	130 kV	210 $\mu$ A	0.4 mm Cu	1 s	0.02733382
MHNM.KHG.224	140 kV	270 $\mu$ A	0.5 mm Cu	1 s	0.03821419
MHNM.KHG.227	140 kV	270 $\mu$ A	0.5 mm Cu	1 s	0.03821419

TABLE S2. Measurements (in mm) of upper teeth of *Hadrogeneios phosphaticus* gen. et sp. nov. Abbreviations: L, length; W, width.

Specimen	M1		M2		M3	
	L	W	L	W	L	W
MHNM.KHG.223	?	?	?	?	5.4	7.58
MHNM.KHG.226 R	?	?	6.5	7.6	6.1	8.3
MHNM.KHG.226 L	?	?	?	?	5.86	8.3

TABLE S3. Length of tooth row (in mm) of *Hadrogeneios phosphaticus* gen. et sp. nov.

Abbreviations: L, length; al, alveolus. \*Estimated measurement.

Specimen	MHNM.KHG.225	MHNM.KHG.227	MHNM.KHG.224
L I1 (al)-M1	?	43.35	?
L C (al)-M1	?	36.8	?
L P1 (al)-M1	?	29.3	?
L P2 (al)-M1	?	21.76	?

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2				
3	L P3 (al)-M1	?	14.9	?
4				
5	L P4-P1 (al)	?	25.6	?
6				
7	L P3-4	?	?	9.77
8				
9				
10	L M2-3	13.3	?	?
11				
12	Diastema C-P1	?	3.44	*4.8
13				
14	Diastema P1-2	?	4.9	4.5
15				
16				
17	Diastema P2-3	?	2.13	2.13
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TABLE S4. Measurements (in mm) of lower teeth of *Hadrogeneios phosphaticus* gen. et sp. nov. Abbreviations: L, length; W, width, Meas, measurements. \*Estimated measurement.

Locus Meas.		MHNT	MHNM.	MHNM.	MHNM.
		PAL 2006.0.19	KHG.224	KHG.225	KHG.227
I1	L	?	*1.1	?	?
I1	W	?	*2	?	?
I2	L	?	*1.2	?	?
I2	W	?	*2.4	?	?
I3	L	?	*1	?	*1
I3	W	?	*1.4	?	*1
C	L	?	?	?	*4.1
C	W	?	?	?	*2.9
P1	L	?	3.27	?	2.8
P1	W	?	1.5	?	1.64
P2	L	?	*4.7	?	4.5
P2	W	?	*1.53	?	2
P3	L	?	4.16	?	*4.9 (al)
P3	W	?	2.35	?	*2.5 (al)
P4	L	?	5.44	?	5.16
P4	W	?	3.23	?	3.28
M1	L	?	?	?	5.16
M1	W	?	?	?	3.75
M2	L	?	6.13	6.45	?
M2	W	?	4.24	4.23	?
M3	L	7.6	?	6.85	7.25

1  
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3 M3 W 4.36 ? 3.63 4.3  
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8 TABLE S5. Measurements (in mm) of the dentary of *Hadrogeneios phosphaticus* gen. et sp.  
9

10 nov. \*Estimated measurement.  
11

	MHNM.KHG.2	MHNM.KHG.	MHNM.KHG.2	MHNT PAL
	24	225	27	2006.0.19
Max. Length of symphysis	27.2	?	*23.15	?
Height below M2	*13.8	10.56	15.7	14.9
Transverse width below M1	?	?	7.9	?
Transverse width below M2	?	5.6		7.5

## Supplementary figures S1-5

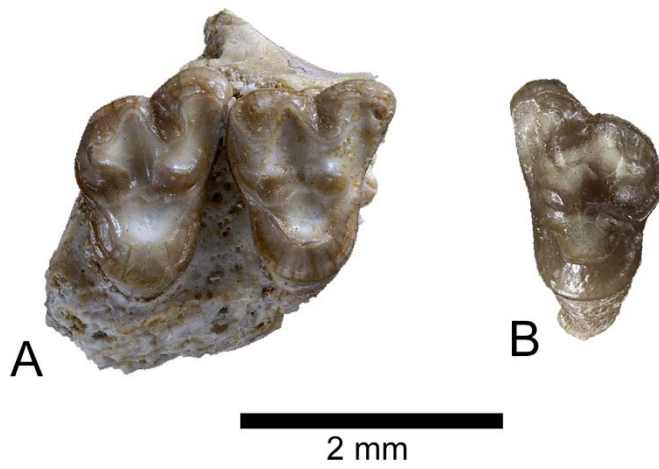


FIGURE S1. *Hadrogeneios phosphaticus* n. g., n. sp. MHNM.KHG.226. **A**, fragment of right maxillary bearing strongly worn M2-3; **B**, isolated left M3 of the same individual. Occlusal views. Scale in millimeters.

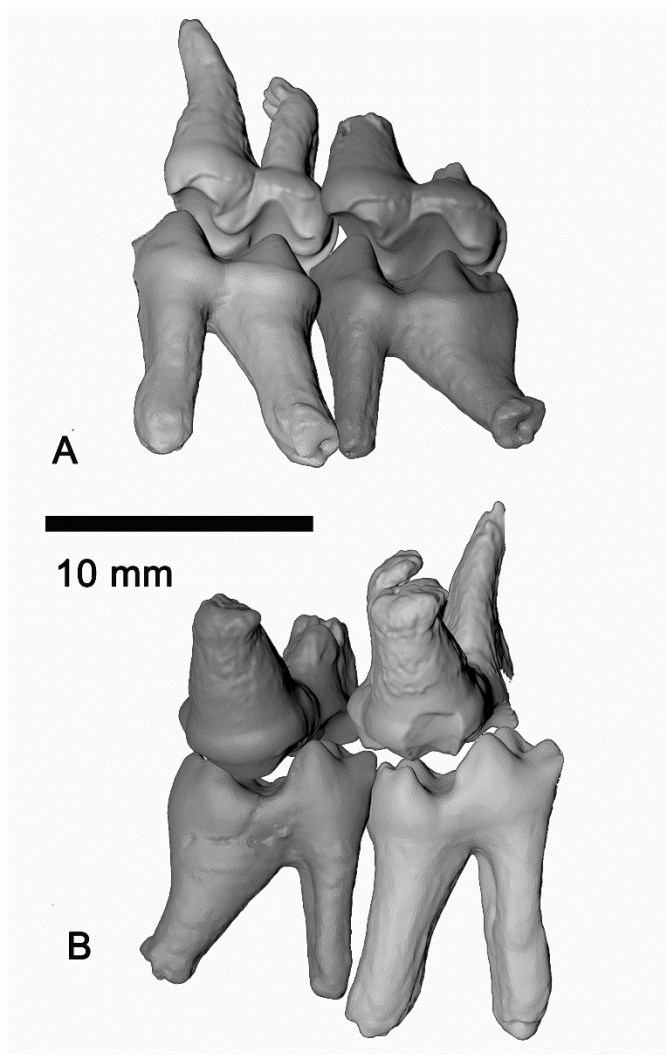


Figure S2. *Hadrogeneios phosphaticus* n. g., n. sp. Reconstruction of the molar occlusion based on the 3D digital models made from the CT scans of specimens MHNM.KHG.226 (right M2-M3 in reversed view) and MHNM.KHG.225 (left m2-3). Ventrolabial and lingual views. The specimen MHNM.KHG.226 is here enlarged by about 10% to adjust the precise molar occlusion with MHNM.KHG.225, which belongs to a slightly larger individual.



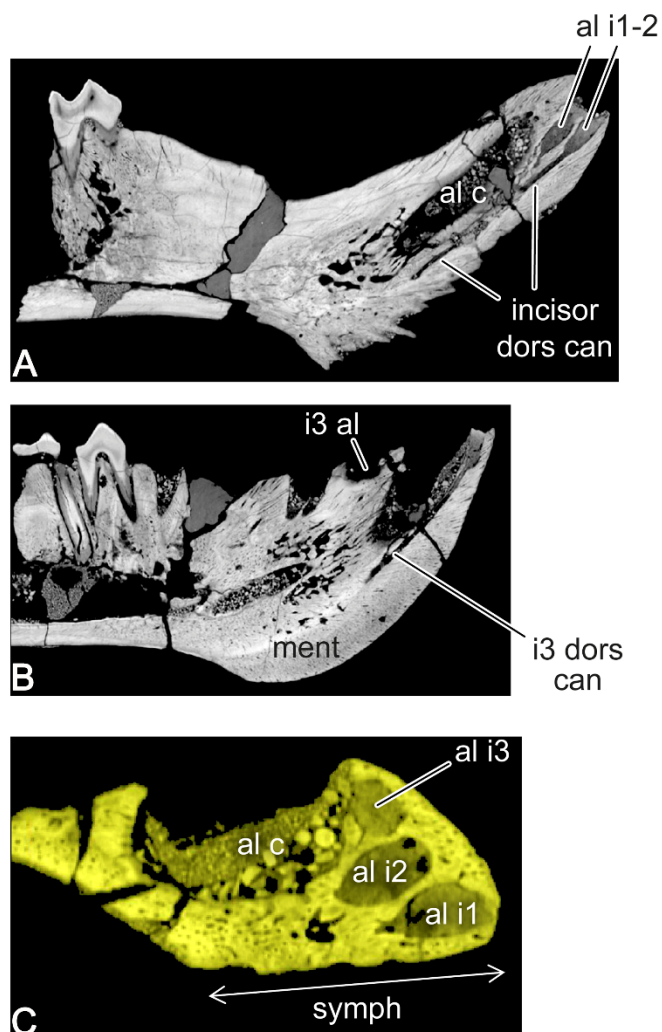


FIGURE S3. *Hadrogeneios phosphaticus* n. g., n. sp. CT scan sections of the dentary MHNM.KHG.224 showing the alveoli of the incisors and their neurovascular canaliculi. **A-B**, longitudinal (sagittal) section showing the alveoli of i1-3 and their thin dorsal canaliculus; **b** also shows the bifid alveolus of p1 (and posteriorly alveoli of p2, and the teeth p3 and p4). **C**, horizontal (axial) section showing the small alveoli of i1-3 and their relative position and development. **Abbreviations:** al: tooth alveolus; dors can: dorsal canaliculus; ment: mentum; symph: mandibular symphysis.

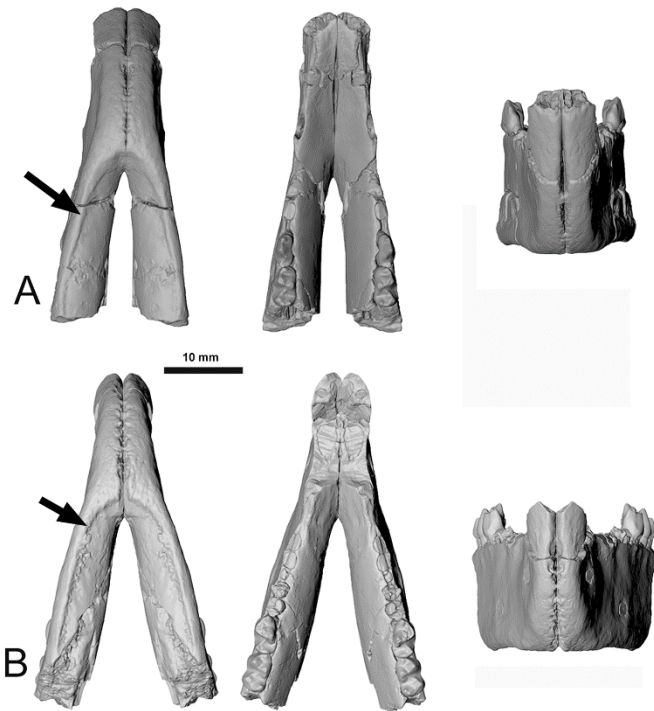


FIGURE S4. *Hadrogeneios phosphaticus* n. g., n. sp. 3D digital reconstruction by symmetrization of the mandibular symphyseal region. **A**, MHNM.KHG.224 in ventral, dorsal and anterior views. **B**, holotype MHNM.KHG.227 in ventral, dorsal and anterior views. The slight difference in the angle of the rami of MHNM.KHG.224 and MHNM.KHG.227 seen here is linked to postmortem deformation (preservation). Arrow: ventral bony crest for muscular attachment, probably for muscle genioglossus of the tongue.

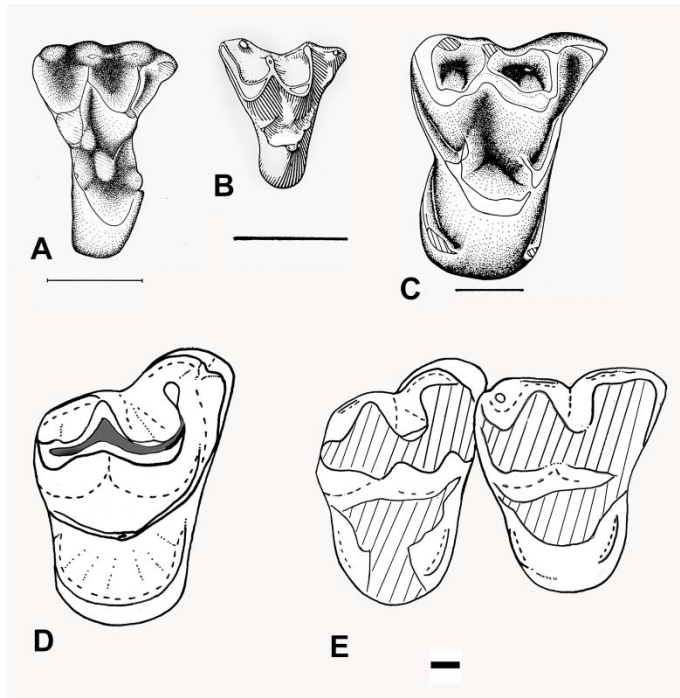


FIGURE S5. Comparison of the upper molar morphology of *Hadrogeneios phosphaticus* n. g., n. sp. with dilambdodont adapisoriculids *Garatherium* and *Remiculus*. **A**, *Garatherium* n. sp. from the Late Paleocene of Adrar Mgorn, Morocco; reversed view of THR362, M1 or M2 (fig. 12-2 in Gheerbrant, 1995). **B**, *Garatherium mahboubi* from the Ypresian of El Kohol, Algeria; holotype, M1 or M2 (fig. 1 in Crochet, 1984). **C**, *Remiculus deutschii* from the late Paleocene of Cernay-Berru, France; reversed view of holotype, M2 (fig. 12-5 in Gheerbrant, 1995). **D-E**, *Hadrogeneios phosphaticus* n. g., n. sp. **D**. Specimen MHNM.KHG.223, right M3. **E**. Specimen MHNM.KHG.226, right M2-3. Occlusal sketches made with camera lucida. Scale bar= 1 mm.

## References

- Crochet, J. Y. 1984. *Garatherium mahboubii* nov. gen., nov. sp., Marsupial de l'Eocène inférieur d'El Kohol (Sud Oranais, Algérie). *Annales de Paléontologie (Vertébrés-Invertébrés)* 70:275–294.

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3 Gheerbrant, E. 1995. Les mammifères paléocènes du Bassin d'Ouarzazate (Maroc). III.  
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5 Adapisoriculidae et autres mammifères (Carnivora, ?Creodonta,  
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7 Condylarthra, ?Ungulata et *incertae sedis*). Palaeontographica A 237:39–132.  
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Journal of Vertebrate Paleontology

Supplementary data

Supplementary Information S1

Ancestral radiation of paenungulate mammals (Paenungulatomorpha) - new evidence from the Paleocene of Morocco

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RH: GHEERBRANT—ANCESTRAL RADIATION OF PAENUNGULATA

## 1. Studied characters

Our character matrix includes 38 taxa and 209 characters numbered starting from 0. It corresponds to that of Gheerbrant, (2009) and Gheerbrant *et al.* (2021) with a few corrections and additions. The main changes with respect to Gheerbrant *et al.* (2021) correspond the replacement of the taxon Sirenia by the following three stem genera: *Prorastomus*, *Pezosiren*, and *Eotheroides*. Their coding, especially for *Pezosiren*, was made from Domning (2001), Domning *et al.* (2017), and Domning (in press).

Other minor changes were made :

- Character 6: state 0 redefined: I/2 “not enlarged” (states for proboscideans recoded 0, except for *Moeritherium*).
- Character 186 (mastoidy/amastoidy): in sirenians there is a mastoid exposure on the occiput, but it is a secondary state (Novacek and Wyss, 1987).
- Character 209 is added to account for the presence of supernumerary premolar (P5 and dP5) in stem sirenians.

The character matrix, including character list and description, is provided in Supplementary File (Nexus file).

## 2. Character matrix for *Hadrogeneios*

### Matrix

The matrix includes 9 characters that are uninformative (4, 5, 63, 73, 102, 132, 178, 190, 199).

1  
2  
3 **Taxa analysed**  
4

5 The basal out-group taxon (Eutheria) corresponds to the generalized eutherian morphotype.  
6

7  
8 38 terminal taxa  
9

10 0 Eutheria (out-group)

- 11 1 *Abdounodus*  
12 2 Anthracobunidae  
13 3 Arctocyonidae  
14 4 *Barytherium*  
15 5 *Cambaytherium*  
16 6 Desmostylia  
17 7 *Eritherium*  
18 8 *Eotherioides*  
19 9 Hyopsodus  
20 10 Hyracoidea  
21 11 Macroscelidea  
22 12 *Minchenella*  
23 13 *Moeritherium*  
24 14 *Numidotherium*  
25 15 *Ocepeia*  
26 16 *Orycteropus*  
27 17 *Paschatherium*  
28 18 Perissodactyla

- 19 *Pezosiren*  
20 Phenacodontidae  
21 *Phenacolophus*  
22 *Phosphatherium*  
23 *Potamogale*  
24 Prorastomus  
25 *Protungulatum*  
26 *Ptolemaia*  
27 *Radinskya*  
28 *Teilhardimys*  
29 *Todralestes*  
30 *S. minor*  
31 *Stylolophus major*  
32 *Palaeoamasia*  
33 *Hypsamasia*  
34 *Crivadiatherium*  
35 *Namatherium*  
36 *Ars zitelli*  
37 *Hadrogeneios*

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3 Suprageneric taxa included in the matrix are coded on the basis of the most plesiomorphic genera included, by reference to the generalized  
4 morphotype of the group (see Gheerbrant, 2009). Their content follows Gheerbrant (2009): Eutheria corresponds to generalized eutherian  
5 morphotype represented by *Acristatherium*, *Prokennalestes*, *Asioryctes*, *Maelestes*, and *Cimolestes*; Arctocyonidae is based on *Loxolophus*,  
6 *Tricentes*, *Lambertocyon*, and *Chriacus*; Perissodactyla was coded based on the primitive perissodactyls *Hyracotherium*, *Cymbalophus*,  
7 *Pachynolophus*; Hyracoidea was coded based on the primitive hyracoids *Seggeurius*, *Microhyrax*, *Dimatherium*, and *Saghatherium*.  
8 Anthracobunidae is based on *Anthracobune*; Desmostylia is based on *Behemetops* and *Ashoroa*; Phenacolophidae is based on *Phenacolophus* and  
9 *Minchenella*; Phenacodontidae is based on *Ectocion* and *Phenacodus*; Macroscelidea is based on primitive herodotine genera *Chambius* and  
10 *Herodotius* and on the extant genera *Petrodromus* and *Rhynchocyon*.  
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### 15 **3. TNT analysis, method, cladograms, and characters at nodes**

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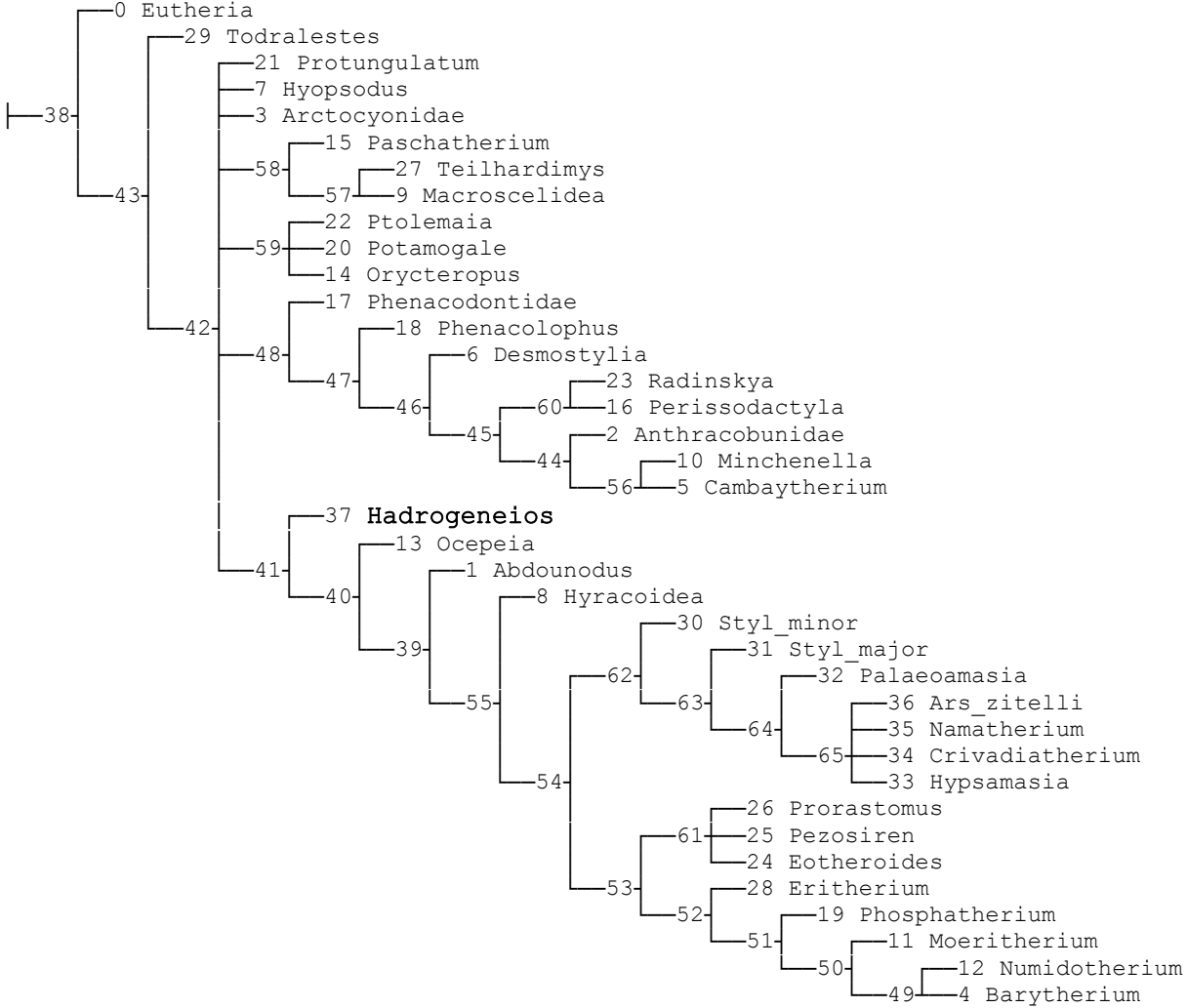
17  
18 The parsimony analysis was developed using TNT 1.5 software. All analyses used the “traditional search” command with the option of  
19 Collapsing Branches with no possible support ("rule 3"). Bremer indices were calculated for 10000 trees with additional 10 steps longer than in  
20 the shortest obtained tree. The nine uninformative characters were made inactive before the analysis (command xinact). The interface  
21 WINCLADA associated with the heuristic algorithm NONA was used in complement of our study, especially for the revision of the matrix, for  
22 the preliminary explorative analysis of tree topology and for examination of character distribution in trees. Characters are numbered starting from  
23 0 (default option of TNT and Winclada).  
24

25 48 characters are treated as additive: 7, 11, 13, 27, 32, 35, 42, 43, 49, 50, 55, 58, 62, 63, 65, 68, 69, 75, 78, 86, 89, 93, 95, 104, 108, 109, 111,  
26 113, 115, 116, 118, 119, 120, 122, 123, 128, 137, 138, 143, 149, 150, 154, 157, 158, 161, 182, 183, 192, 201.  
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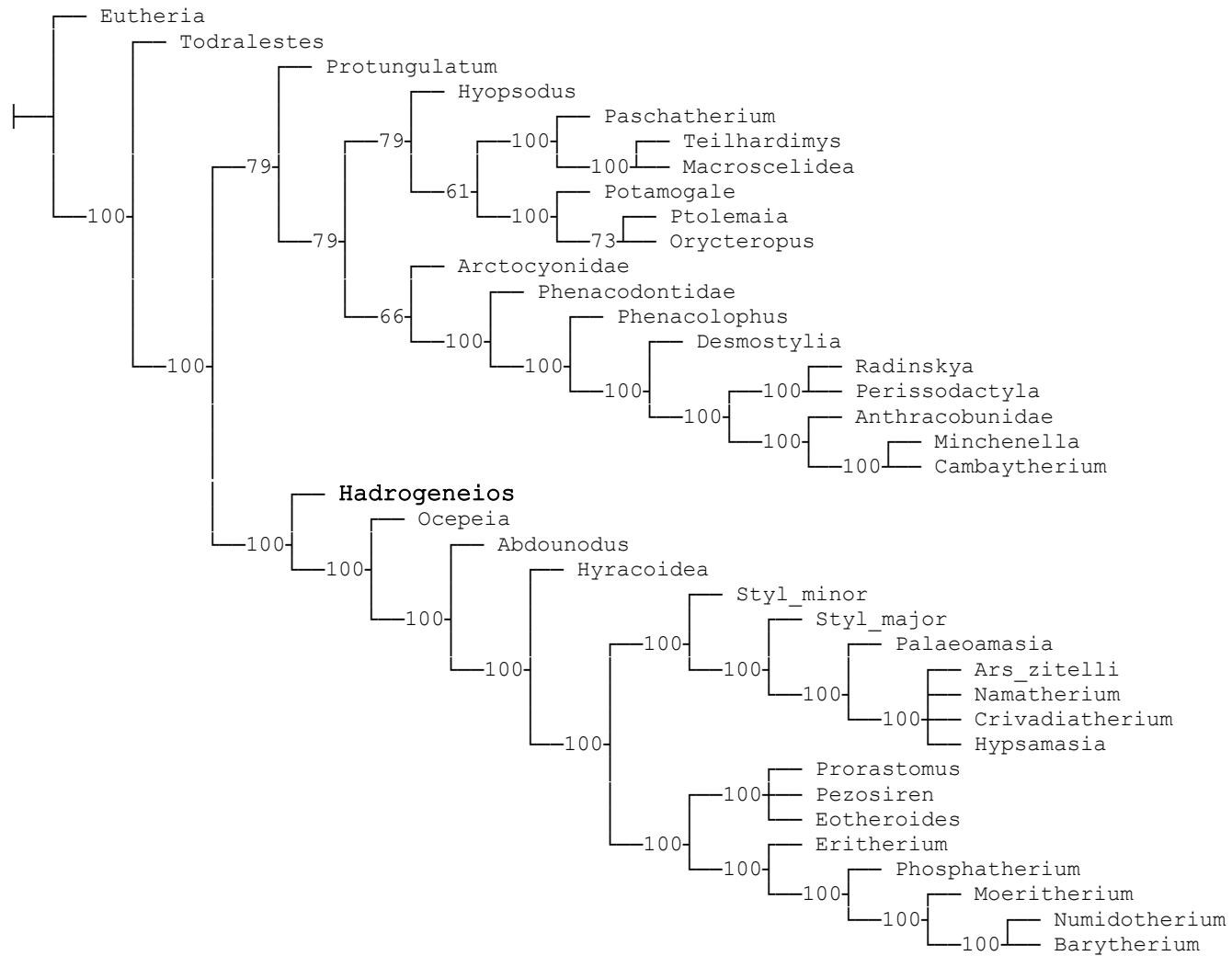
**Analysis 1: standard analysis (unweighted, unconstrained)**

Strict consensus of 180 trees (0 taxa excluded; two rounds of TBR analysis).



Tree lengths: 972. Retention index: 61.3. Consistency Index: 34.8.

## Majority rule tree (from 180 trees, cut 50)



## Synapomorphies common to 180 trees of the standard analysis

(Node numbers refer to nodes in consensus)

9	Eutheria :	Char. 72: 0 --> 1	Char. 21: 0 --> 1	Char. 164: 1 --> 34
10	All trees:	Char. 174: 0 --> 1	Char. 22: 1 --> 0	Char. 181: 0 --> 1
11	No autapomorphies:	Some trees:	Char. 23: 1 --> 0	Some trees:
12		Char. 31: 0 --> 1	Char. 25: 2 --> 1	Char. 58: 2 --> 1
13		Char. 46: 1 --> 2	Char. 39: 0 --> 2	Char. 155: 0 --> 1
14	Abdounodus :	Char. 46: 1 --> 2		
15	All trees:	Char. 155: 0 --> 1		
16	Char. 19: 1 --> 0	Char. 156: 2 --> 1	Desmostylia :	Hyopsodus :
17	Char. 32: 12 --> 0	Char. 180: 0 --> 1	All trees:	All trees:
18	Char. 39: 1 --> 2	Char. 196: 1 --> 0	Char. 0: 0 --> 1	Char. 13: 0 --> 1
19	Char. 41: 0 --> 2	Char. 197: 2 --> 0	Char. 1: 0 --> 1	Char. 176: 0 --> 1
20	Char. 42: 0 --> 1	Char. 204: 0 --> 2	Char. 8: 1 --> 0	Char. 183: 0 --> 1
21	Char. 43: 1 --> 2		Char. 17: 0 --> 1	Char. 188: 0 --> 1
22	Char. 45: 1 --> 0	Barytherium :	Char. 32: 2 --> 0	Char. 193: 0 --> 1
23	Char. 50: 02 --> 1	All trees:	Char. 61: 1 --> 2	Some trees:
24	Char. 98: 0 --> 1	Char. 34: 1 --> 3	Char. 64: 0 --> 1	Char. 6: 0 --> 1
25	Char. 111: 0 --> 1	Char. 55: 1 --> 2	Char. 84: 3 --> 0	Char. 11: 1 --> 2
26	Char. 164: 1 --> 2	Char. 57: 0 --> 2	Char. 91: 0 --> 1	Char. 22: 0 --> 1
27		Char. 63: 0 --> 1	Char. 107: 0 --> 1	Char. 36: 0 --> 1
28		Char. 69: 1 --> 2	Char. 108: 0 --> 3	Char. 39: 1 --> 0
29	Anthracobunidae :	Char. 77: 1 --> 3	Char. 109: 1 --> 3	Char. 41: 0 --> 1
30	All trees:	Char. 79: 1 --> 0	Char. 112: 0 --> 1	Char. 58: 2 --> 1
31	Char. 26: 1 --> 2	Char. 125: 1 --> 0	Char. 115: 12 --> 0	Char. 72: 0 --> 1
32	Char. 165: 1 --> 0	Char. 164: 1 --> 3	Char. 118: 1 --> 2	Char. 115: 1 --> 2
33	Char. 193: 0 --> 1		Char. 145: 0 --> 1	Char. 140: 0 --> 2
34	Some trees:	Cambaytherium :	Char. 147: 0 --> 1	Char. 161: 0 --> 1
35	Char. 58: 2 --> 1	All trees:	Char. 154: 1 --> 23	
36		Char. 16: 1 --> 0	Char. 157: 1 --> 3	Hyracoidea :
37	Arctocyonidae :	Char. 18: 1 --> 0	Char. 161: 0 --> 12	All trees:
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Char. 44: 0 --> 1	Char. 110: 1 --> 0	Char. 164: 1 --> 5	Char. 127: 1 --> 3
Char. 51: 0 --> 1	Char. 111: 1 --> 0	Char. 165: 0 --> 1	Char. 151: 1 --> 0
Char. 74: 0 --> 1	Char. 117: 2 --> 1	Char. 171: 0 --> 1	Char. 154: 1 --> 0
Char. 75: 0 --> 2	Char. 118: 1 --> 0	Char. 172: 0 --> 1	
Char. 88: 0 --> 1	Char. 120: 1 --> 2	Char. 191: 0 --> 1	Orycteropus :
Char. 120: 1 --> 2	Some trees:	Char. 203: 0 --> 1	All trees:
Char. 166: 0 --> 1	Char. 46: 1 --> 0		Char. 10: 0 --> 12
Char. 170: 0 --> 1		Numidotherium :	Char. 13: 0 --> 2
Char. 173: 0 --> 12	Moeritherium :	All trees:	Char. 14: 0 --> 1
Char. 194: 0 --> 2	All trees:	No autapomorphies:	Char. 15: 0 --> 1
Char. 201: 2 --> 1	Char. 2: 0 --> 1		Char. 20: 0 --> 1
	Char. 6: 0 --> 1	Ocepeia :	Char. 57: 0 --> 2
Macroscelidea :	Char. 21: 1 --> 0	All trees:	Char. 63: 0 --> 3
All trees:	Char. 25: 3 --> 4	Char. 7: 0 --> 1	Char. 68: 0 --> 2
Char. 22: 0 --> 1	Char. 27: 0 --> 2	Char. 11: 12 --> 3	Char. 69: 01 --> 2
Char. 24: 0 --> 1	Char. 31: 1 --> 0	Char. 13: 0 --> 3	Char. 74: 0 --> 2
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Char. 84: 2 --> 3	Char. 67: 0 --> 1	Char. 47: 0 --> 1	Char. 135: 0 --> 1
Char. 87: 1 --> 0	Char. 70: 1 --> 0	Char. 51: 0 --> 1	Char. 139: 0 --> 1
Char. 164: 1 --> 2	Char. 76: 0 --> 2	Char. 52: 0 --> 3	Char. 141: 0 --> 1
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Char. 41: 0 --> 1	Char. 145: 0 --> 1	Char. 187: 0 --> 1	Char. 58: 01 --> 2
Char. 54: 0 --> 1	Char. 153: 0 --> 1	Char. 188: 0 --> 1	Char. 61: 0 --> 1
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Char. 179: 1 --> 0	Char. 11: 1 --> 2	Char. 172: 0 --> 1	Char. 127: 1 --> 2
Char. 192: 0 --> 2	Char. 151: 1 --> 0	Char. 184: 0 --> 1	Some trees:
Char. 194: 1 --> 2	Char. 189: 1 --> 0	Some trees:	Char. 8: 3 --> 0
Char. 203: 1 --> 0		Char. 48: 1 --> 0	Char. 17: 1 --> 0
	Phenacolophus :	Char. 53: 0 --> 1	Char. 52: 0 --> 2
Paschatherium :	All trees:	Char. 65: 1 --> 2	Char. 64: 1 --> 0
All trees:	Char. 6: 0 --> 1	Char. 70: 1 --> 0	Char. 69: 01 --> 0
Char. 11: 1 --> 0	Char. 8: 1 --> 3	Char. 92: 1 --> 0	Char. 78: 1 --> 2
Char. 12: 1 --> 0	Char. 21: 0 --> 1	Char. 98: 1 --> 0	Char. 84: 0 --> 1
Char. 25: 1 --> 0	Char. 33: 0 --> 1	Char. 109: 1 --> 0	Char. 171: 1 --> 0
Char. 81: 1 --> 0	Char. 74: 0 --> 2	Char. 110: 1 --> 0	
Char. 92: 1 --> 0	Char. 109: 1 --> 0	Char. 111: 1 --> 0	Radinskya :
Char. 98: 1 --> 0	Char. 110: 1 --> 0	Char. 142: 0 --> 2	All trees:
Some trees:	Char. 113: 01 --> 2	Char. 146: 0 --> 1	Char. 84: 3 --> 1
Char. 39: 1 --> 2	Char. 126: 1 --> 0	Char. 154: 12 --> 3	Char. 164: 1 --> 0
	Char. 204: 1 --> 3	Char. 156: 0 --> 3	
Perissodactyla :	Some trees:	Char. 157: 0 --> 12	Eotheroides :
All trees:	Char. 46: 1 --> 2	Char. 163: 0 --> 1	All trees:
Char. 76: 0 --> 2		Char. 197: 0 --> 1	Char. 140: 0 --> 1
Char. 118: 1 --> 2	Phosphatherium :	Char. 198: 0 --> 1	Char. 179: 1 --> 0
Char. 139: 0 --> 1	All trees:	Char. 202: 0 --> 2	Some trees:
Char. 146: 0 --> 1	Char. 58: 2 --> 1	Char. 203: 01 --> 1	Char. 3: 1 --> 0
Char. 151: 1 --> 0	Char. 134: 0 --> 2		Char. 25: 2 --> 1
Char. 154: 1 --> 0	Char. 140: 0 --> 2	Protungulatum :	Char. 83: 1 --> 3
Char. 180: 0 --> 1		All trees:	Char. 157: 3 --> 5
	Potamogale :	Char. 28: 0 --> 1	Char. 161: 1 --> 2
Phenacodontidae :	All trees:	Char. 46: 1 --> 0	Char. 175: 0 --> 1
All trees:	Char. 46: 1 --> 0	Char. 47: 0 --> 2	
Char. 38: 0 --> 1	Char. 50: 0 --> 2	Char. 61: 1 --> 2	Pezosiren :
Char. 140: 0 --> 2	Char. 114: 0 --> 1		All trees:
Char. 146: 0 --> 1	Char. 153: 0 --> 1	Ptolemaia :	Char. 172: 0 --> 1
Char. 193: 0 --> 1	Char. 158: 0 --> 2	All trees:	Some trees:

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3	Char. 194: 1 --> 2	Char. 192: 1 --> 0	Char. 91: 1 --> 0	Hadrogeneios :
4				All trees:
5	Prorastomus :	Todralestes :	Crivadiatherium :	Char. 11: 1 --> 0
6	All trees:	All trees:	Some trees:	Char. 22: 0 --> 1
7	Char. 9: 1 --> 0	Char. 52: 0 --> 3	Char. 24: 0 --> 1	Char. 41: 0 --> 3
8	Char. 10: 0 --> 1	Char. 53: 0 --> 1	Char. 44: 0 --> 1	Char. 53: 0 --> 3
9	Char. 12: 1 --> 0	Some trees:	Char. 45: 1 --> 0	Char. 114: 0 --> 2
10	Char. 70: 1 --> 0	Char. 10: 0 --> 1		Some trees:
11	Some trees:	Char. 93: 0 --> 1	Namatherium :	Char. 115: 1 --> 0
12	Char. 6: 0 --> 1		Some trees:	Char. 127: 1 --> 0
13	Char. 103: 0 --> 1	Styl_minor :	Char. 88: 0 --> 1	
14		All trees:	Char. 100: 0 --> 1	Node 39 :
15	Teilhardimys :	Char. 31: 1 --> 0	Char. 145: 0 --> 2	All trees:
16	All trees:	Char. 50: 2 --> 1	Char. 164: 0 --> 2	Char. 40: 0 --> 1
17	Char. 21: 0 --> 1	Char. 58: 2 --> 1		Char. 43: 0 --> 1
18	Char. 26: 0 --> 2	Char. 140: 0 --> 2	Ars_zitelli :	Char. 94: 0 --> 1
19	Char. 74: 0 --> 1		Some trees:	Char. 95: 0 --> 1
20	Char. 75: 0 --> 2	Styl_major :	Char. 49: 0 --> 2	Char. 103: 1 --> 0
21	Char. 114: 0 --> 1	All trees:	Char. 83: 1 --> 0	Char. 109: 0 --> 1
22	Char. 120: 01 --> 2	Char. 135: 1 --> 2	Char. 84: 2 --> 3	Char. 110: 0 --> 1
23	Char. 121: 0 --> 1		Char. 89: 0 --> 2	Char. 115: 2 --> 3
24	Char. 135: 0 --> 12	Palaeomasia :	Char. 103: 1 --> 0	Char. 118: 0 --> 1
25	Some trees:	All trees:	Char. 108: 12 --> 3	Char. 120: 0 --> 1
26	Char. 36: 0 --> 1	Char. 10: 0 --> 1	Char. 123: 1 --> 2	Char. 121: 0 --> 1
27		Char. 54: 0 --> 1	Char. 127: 3 --> 0	Char. 157: 0 --> 12
28	Eritherium :	Some trees:	Char. 128: 2 --> 3	
29	All trees:	Char. 87: 0 --> 1	Char. 135: 1 --> 2	Node 40 :
30	Char. 42: 1 --> 2	Char. 91: 1 --> 0	Char. 156: 2 --> 3	All trees:
31	Char. 48: 2 --> 1		Char. 157: 23 --> 01	Char. 31: 0 --> 1
32	Char. 50: 2 --> 0	Hypsamasia :	Char. 160: 01 --> 2	Char. 34: 0 --> 1
33	Char. 100: 0 --> 1	Some trees:	Char. 162: 1 --> 0	Char. 35: 0 --> 1
34	Char. 101: 3 --> 2	Char. 80: 0 --> 1	Char. 205: 1 --> 2	Char. 105: 0 --> 1
35	Char. 127: 3 --> 1	Char. 87: 0 --> 1		Char. 115: 01 --> 2
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Char. 130: 0 --> 1	All trees:	Char. 121: 0 --> 1	Char. 75: 0 --> 1
	Char. 16: 0 --> 1	Char. 165: 0 --> 1	Char. 104: 1 --> 0
<b>Node 41 (<i>Hadrogeneios</i> + <i>Paenungulatomorpha</i>) :</b>	Char. 152: 0 --> 1	Some trees:	Char. 107: 0 --> 1
All trees:	Node 46 :	Char. 22: 0 --> 1	Char. 108: 0 --> 3
Char. 38: 0 --> 1	All trees:	Char. 128: 0 --> 1	Char. 141: 0 --> 1
Char. 55: 0 --> 1	Char. 28: 0 --> 1	Char. 142: 0 --> 2	Char. 148: 0 --> 1
Char. 62: 0 --> 1	Char. 29: 0 --> 1	Char. 204: 0 --> 1	Char. 158: 1 --> 2
Char. 104: 0 --> 1	Char. 30: 0 --> 1	Node 49 :	Char. 175: 0 --> 1
Char. 113: 0 --> 2	Char. 124: 0 --> 1	All trees:	Char. 182: 1 --> 2
Some trees:	Char. 157: 0 --> 1	Char. 13: 2 --> 0	Char. 198: 0 --> 1
Char. 10: 0 --> 1	Some trees:	Char. 38: 1 --> 0	Node 51 :
Node 42 :	Char. 36: 0 --> 1	Char. 39: 2 --> 1	All trees:
All trees:	Node 47 :	Char. 42: 1 --> 0	Char. 3: 1 --> 2
Char. 25: 0 --> 1	All trees:	Char. 43: 12 --> 0	Char. 7: 1 --> 2
Char. 126: 0 --> 1	Char. 26: 0 --> 1	Char. 68: 1 --> 2	Char. 8: 4 --> 5
Some trees:	Char. 34: 0 --> 1	Char. 137: 0 --> 1	Char. 25: 2 --> 3
Char. 32: 0 --> 1	Char. 35: 0 --> 1	Char. 204: 1 --> 2	Char. 32: 1 --> 0
Char. 92: 0 --> 1	Char. 40: 0 --> 2	Char. 207: 2 --> 3	Char. 45: 1 --> 2
Char. 117: 0 --> 1	Char. 78: 1 --> 2	Node 50 :	Char. 46: 1 --> 2
Char. 127: 0 --> 1	Char. 97: 0 --> 2	All trees:	Char. 90: 0 --> 1
Node 43 :	Char. 127: 1 --> 3	Char. 10: 0 --> 3	Char. 95: 1 --> 3
All trees:	Char. 135: 0 --> 2	Char. 11: 2 --> 3	Char. 120: 1 --> 23
No synapomorphies	Node 48 :	Char. 14: 1 --> 0	Char. 135: 1 --> 2
Node 44 :	All trees:	Char. 18: 0 --> 1	Char. 157: 3 --> 4
All trees:	Char. 32: 1 --> 2	Char. 22: 0 --> 1	Char. 162: 0 --> 1
Char. 11: 1 --> 0	Char. 79: 0 --> 2	Char. 51: 0 --> 1	Char. 188: 0 --> 1
Char. 43: 0 --> 2	Char. 82: 0 --> 1	Char. 54: 0 --> 1	Char. 202: 1 --> 0
Node 45 :	Char. 84: 0 --> 3	Char. 56: 0 --> 1	Char. 204: 0 --> 1
	Char. 93: 2 --> 3	Char. 68: 0 --> 1	Char. 207: 0 --> 2
	Char. 120: 0 --> 1	Char. 71: 0 --> 1	Node 52 :
		Char. 74: 0 --> 1	All trees:

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3	Char. 7: 0 --> 1	Char. 58: 1 --> 2	Node 58 :	Char. 135: 2 --> 0
4	Char. 39: 1 --> 2	Char. 79: 0 --> 1	All trees:	Char. 184: 0 --> 1
5	Char. 41: 0 --> 2	Char. 84: 0 --> 2	Char. 79: 0 --> 1	
6		Char. 97: 0 --> 1	Char. 84: 0 --> 2	Node 61 :
7		Char. 115: 3 --> 4	Char. 127: 1 --> 2	All trees:
8	Node 53 :	Char. 116: 1 --> 2	Some trees:	Char. 20: 0 --> 1
9	All trees:	Char. 128: 0 --> 1	Char. 48: 0 --> 1	Char. 51: 0 --> 1
10	Char. 98: 0 --> 1	Char. 131: 0 --> 1	Char. 53: 0 --> 1	Char. 54: 0 --> 1
11	Char. 155: 0 --> 1	Char. 133: 0 --> 1		Char. 148: 0 --> 1
12		Char. 135: 0 --> 1	Node 59 :	Char. 149: 0 --> 2
13	Node 54 :		All trees:	Char. 150: 0 --> 2
14	All trees:	Some trees:	Char. 71: 0 --> 1	Char. 208: 0 --> 1
15	Char. 40: 1 --> 2	Char. 81: 2 --> 1	Char. 155: 0 --> 1	Some trees:
16	Char. 72: 0 --> 1		Some trees:	Char. 15: 0 --> 1
17	Char. 91: 0 --> 1	Node 56 :	Char. 11: 12 --> 3	Char. 61: 1 --> 2
18	Char. 100: 1 --> 0	All trees:	Char. 44: 1 --> 0	Char. 68: 0 --> 1
19	Char. 118: 1 --> 2	Char. 17: 0 --> 1	Char. 59: 0 --> 1	Char. 74: 0 --> 2
20	Char. 157: 12 --> 3	Char. 45: 2 --> 0	Char. 86: 2 --> 1	Char. 77: 1 --> 2
21	Char. 161: 0 --> 1	Char. 124: 1 --> 0	Char. 87: 1 --> 0	Char. 164: 1 --> 2
22	Char. 181: 0 --> 1		Char. 93: 2 --> 0	Char. 194: 0 --> 1
23	Char. 183: 0 --> 12	Node 57 :	Char. 103: 1 --> 0	
24		All trees:	Char. 115: 1 --> 0	Node 62 :
25	Some trees:	Char. 37: 0 --> 1	Char. 140: 0 --> 1	All trees:
26	Char. 127: 1 --> 3	Char. 40: 0 --> 1	Char. 145: 0 --> 1	Char. 25: 2 --> 3
27	Char. 159: 0 --> 1	Char. 78: 1 --> 2	Char. 156: 2 --> 0	Char. 33: 0 --> 1
28		Char. 93: 2 --> 3	Char. 167: 0 --> 1	Char. 35: 1 --> 2
29		Char. 94: 0 --> 1	Char. 175: 0 --> 1	Char. 38: 1 --> 0
30	Node 55 :	Char. 95: 0 --> 1		Char. 39: 1 --> 0
31	All trees:	Char. 128: 0 --> 1	Node 60 :	Char. 41: 0 --> 1
32	Char. 10: 1 --> 0	Char. 134: 0 --> 1	All trees:	Char. 55: 1 --> 0
33	Char. 25: 1 --> 2		Char. 95: 1 --> 2	Char. 67: 0 --> 1
34	Char. 26: 0 --> 2	Some trees:	Char. 120: 1 --> 2	Char. 81: 1 --> 0
35	Char. 28: 0 --> 1	Char. 19: 0 --> 1	Char. 127: 3 --> 1	Char. 96: 0 --> 1
36	Char. 29: 0 --> 1	Char. 27: 0 --> 1		
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Char. 103: 0 --> 1  
Char. 104: 1 --> 2  
Char. 107: 0 --> 2  
Char. 110: 1 --> 0  
Char. 113: 2 --> 3  
Char. 114: 0 --> 2  
Char. 119: 0 --> 1  
Char. 122: 0 --> 1  
Char. 123: 0 --> 1  
Char. 136: 0 --> 1

Char. 143: 0 --> 1  
Node 63 :  
All trees:  
Char. 108: 0 --> 1  
Char. 109: 1 --> 2  
Char. 162: 0 --> 1

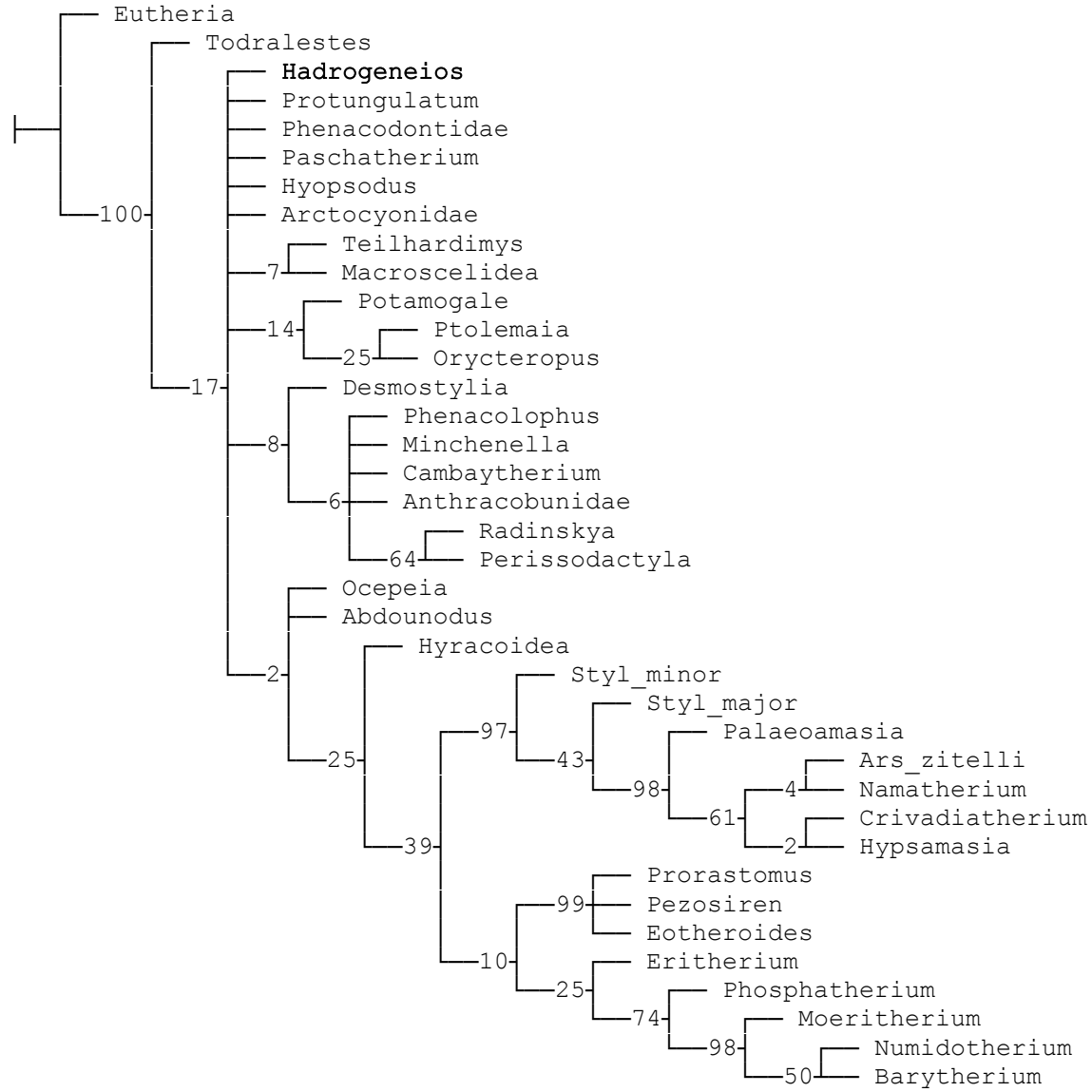
Node 64 :  
All trees:

Char. 74: 0 --> 1  
Char. 75: 0 --> 1  
Char. 76: 0 --> 2  
Char. 128: 1 --> 2  
Char. 129: 0 --> 1  
Char. 164: 1 --> 0

Node 65 :  
Some trees:  
Char. 48: 2 --> 0

Char. 75: 1 --> 2  
Char. 109: 2 --> 3  
Char. 119: 1 --> 2  
Char. 122: 1 --> 2  
Char. 143: 1 --> 2  
Char. 204: 0 --> 1  
Char. 205: 0 --> 1

Standard Bootstrap



## Analysis 2: Clade Afrotheria constrained

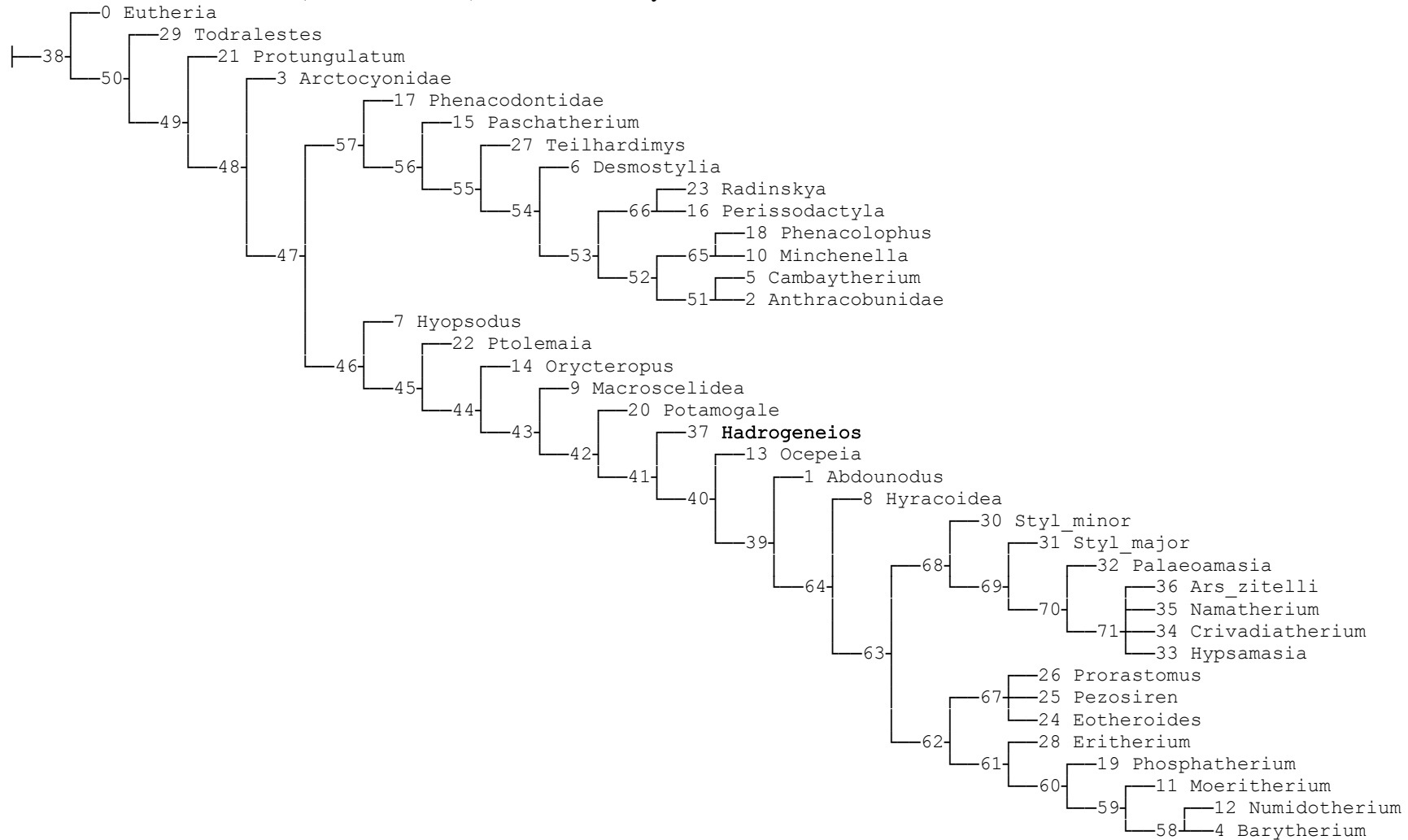
In this analysis the following taxa are constrained to gather in the same clade Afrotheria: 1 *Abdounodus*; 4 *Barytherium*; 8 *Hyracoidea*; 9 *Macroscelidea*; 11 *Moeritherium*; 12 *Numidotherium*; 13 *Ocepeia*; 14 *Orycteropus*; 19 *Phosphatherium*; 20 *Potamogale*; 24 *Eotheroides*; 25 *Pezosiren*; 26 *Prorastomus*; 28 *Eritherium*; 30 *Stylophus\_minor*; 31 *Stylophus\_major*; 32 *Palaeoamasia*; 33 *Hypsamasia*; 34 *Crivadiatherium*; 35 *Namatherium*; 36 *Arsinoitherium zitelli*.

The used TNT command was: force +[1 4 8 9 11 12 13 14 19 20 24 25 26 28 30 31 32 33 34 35 36];constrain =;

1 - *Hadrogeneios* constrained to be included in Afrotheria.

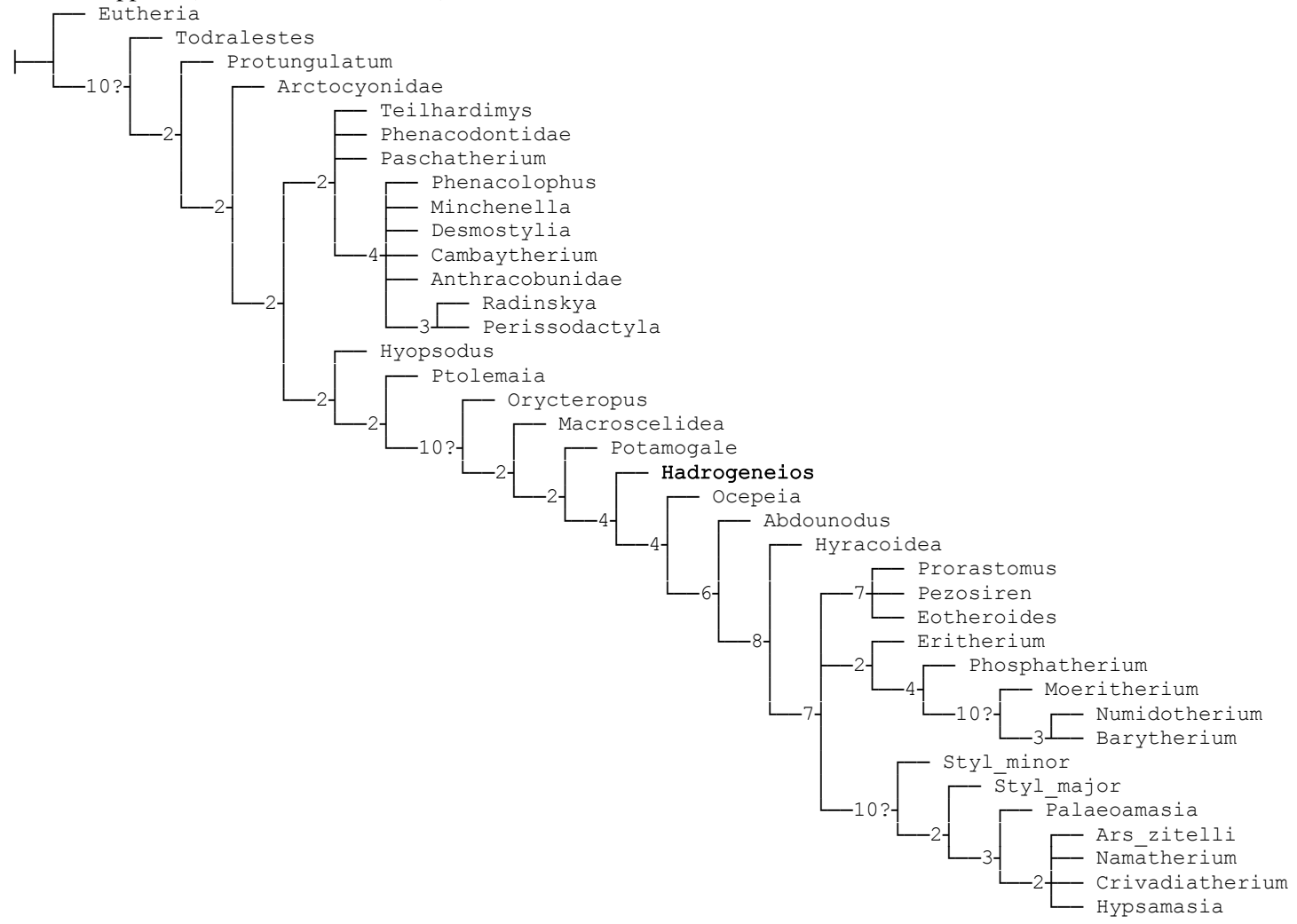
Used TNT command: force +[1 4 8 9 11 12 13 14 19 20 24 25 26 28 30 31 32 33 34 35 36 37]; constrain =;

## Strict consensus of 30 trees (0 taxa excluded), first round analysis



Tree lengths: 986. Retention index: 60.5. Consistency Index: 34.3.

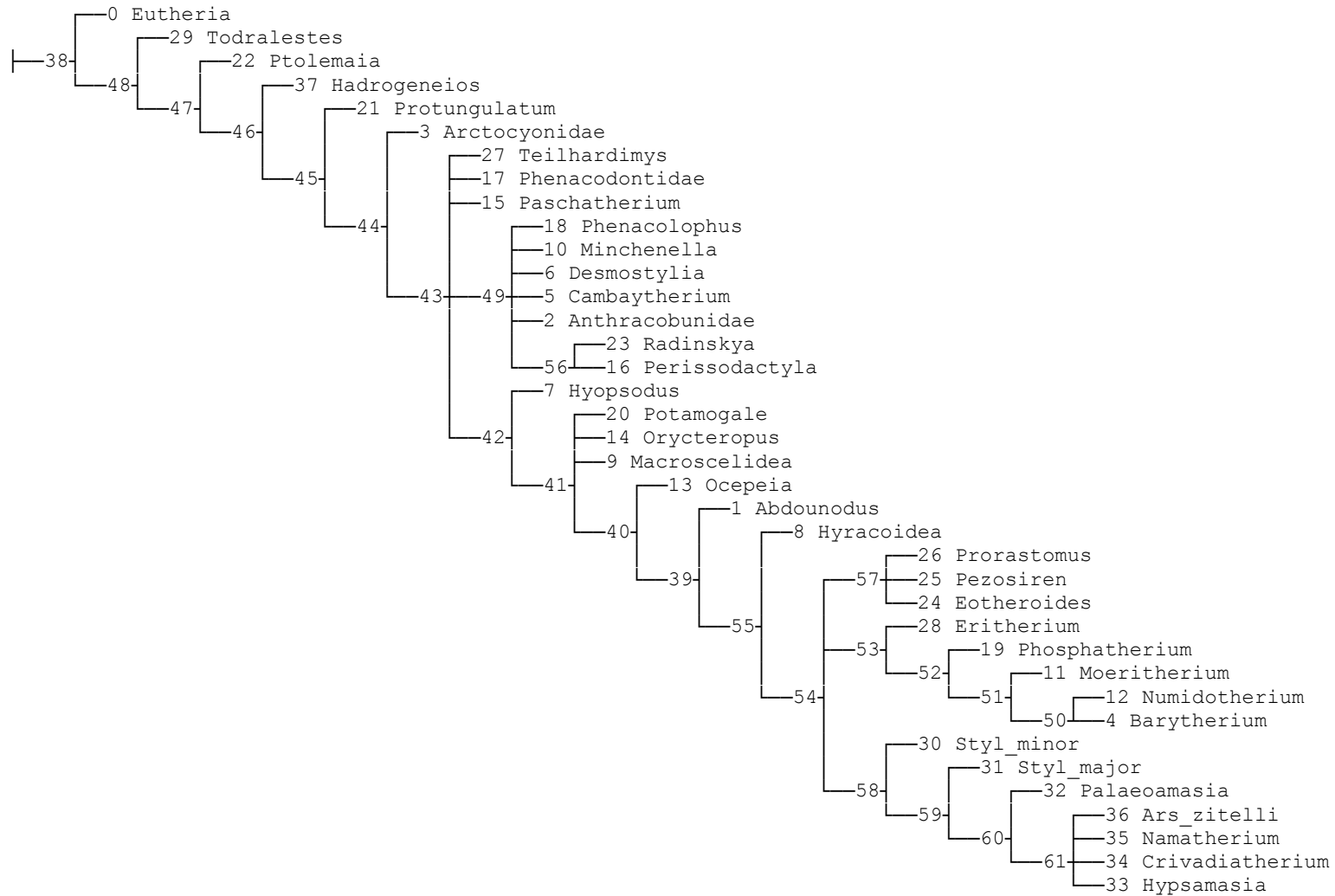
Bremer supports (from 10000 trees, cut 2)



2 - *Hadrogeneios* position not constrained

Used command TNT: force +[1 4 8 9 11 12 13 14 19 20 24 25 26 28 30 31 32 33 34 35 36];constrain =;

## Strict consensus of 530 trees (two rounds of TBR analysis)



Tree lengths: 987. Retention index: 60.5. Consistency Index: 34.2.

Bremer support >2 (from 10000 trees, cut 2)



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