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Re-interpretation of the genus *Parabunodon* (Ypresian, Turkey): implications for the evolution and distribution of pleuraspidotheriid mammals

Grégoire Métais · Emmanuel Gheerbrant · Sevket Sen

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Abstract Early Paleogene mammal faunas from western Asia remain very poorly documented, and the few fossil data currently available raise more issues than they provide answers regarding the palaeobiogeography of the Peri-Tethys area during a key period for the diversification and dispersal of modern group of mammals. *Parabunodon anatolicum* is an ungulate mammal whose both age and taxonomic affinities are disputable. The holotype of this monotypic genus was collected from the early? Eocene Çeltek Formation, Central Anatolia, Amasya Province, and described as a choeropotamid artiodactyl, making it the easternmost occurrence of the family which is mostly restricted to the middle–late Eocene of western Europe. Here, we revisit the relationships of *Parabunodon anatolicum* in the light of recent studies. The reassessment of dental features of this genus as well as of its phylogenetic relationships led us to reconsider the taxonomic assignment of this still enigmatic form. Cladistic analysis was undertaken to understand its relationships with the Pleuraspidotheriidae and the Choeropotamidae, in which *Parabunodon* had earlier been included. Our analysis supports the relationships of *Parabunodon* with other pleuraspidotheriids. It implies an early diversification and a vast geographic distribution from western Europe to Anatolia of pleuraspidotheriid ‘condylarths’ during the early Paleogene.

Keywords *Parabunodon anatolicum* · Çeltek Formation · Choeropotamidae · Pleuraspidotheriidae

Introduction

Fossil mammals from early Paleogene (65–45 million years ago) terrestrial deposits of Anatolia are poorly documented, although they are of utmost significance for understanding the early evolution and distribution of modern faunas during a time marked by strong climatic pulsation. All the palaeogeographic reconstructions place Anatolia at the crossroads between the African and Eurasian landmasses, and thus the most suitable place to explore for both documenting vertebrate assemblages and better constraining the timing of peri or trans-Tethyan dispersal events through various microcontinents of Gondwanan origin that have been accreted to the northern margin of the Neo-Tethys. Because of the collision of continental blocks and volcanism related to the subduction of the Neo-Tethys ocean, the tectonic context of the northern margin of the Neo-Tethys during the Paleocene and Eocene appears a priori unfavourable for deposition of terrestrial units that could preserve fossil mammal assemblages. Also, only two formations of Central Anatolia have so far yielded early Paleogene vertebrates (Fig. 1): the Çeltek Formation which is exposed in several basins of Central Anatolia (Gümüßsu 1984), including the Suluova Basin (Amasya Province), and the Uzunçarşidere Formation which is exposed on the northern margin of the Haymana Basin (Ankara Province). Fossil vertebrates from the Çeltek Formation were all found by miners of the Eski Çeltek coal mine and given to Turkish professional palaeontologists for study. The Çeltek Formation is mostly renowned for having yielded remains of the embrithopod *Palaeoamasia kansui*, which is still the earliest undisputed representative of the order (Sen and Heintz 1979). Another mammal genus was reported

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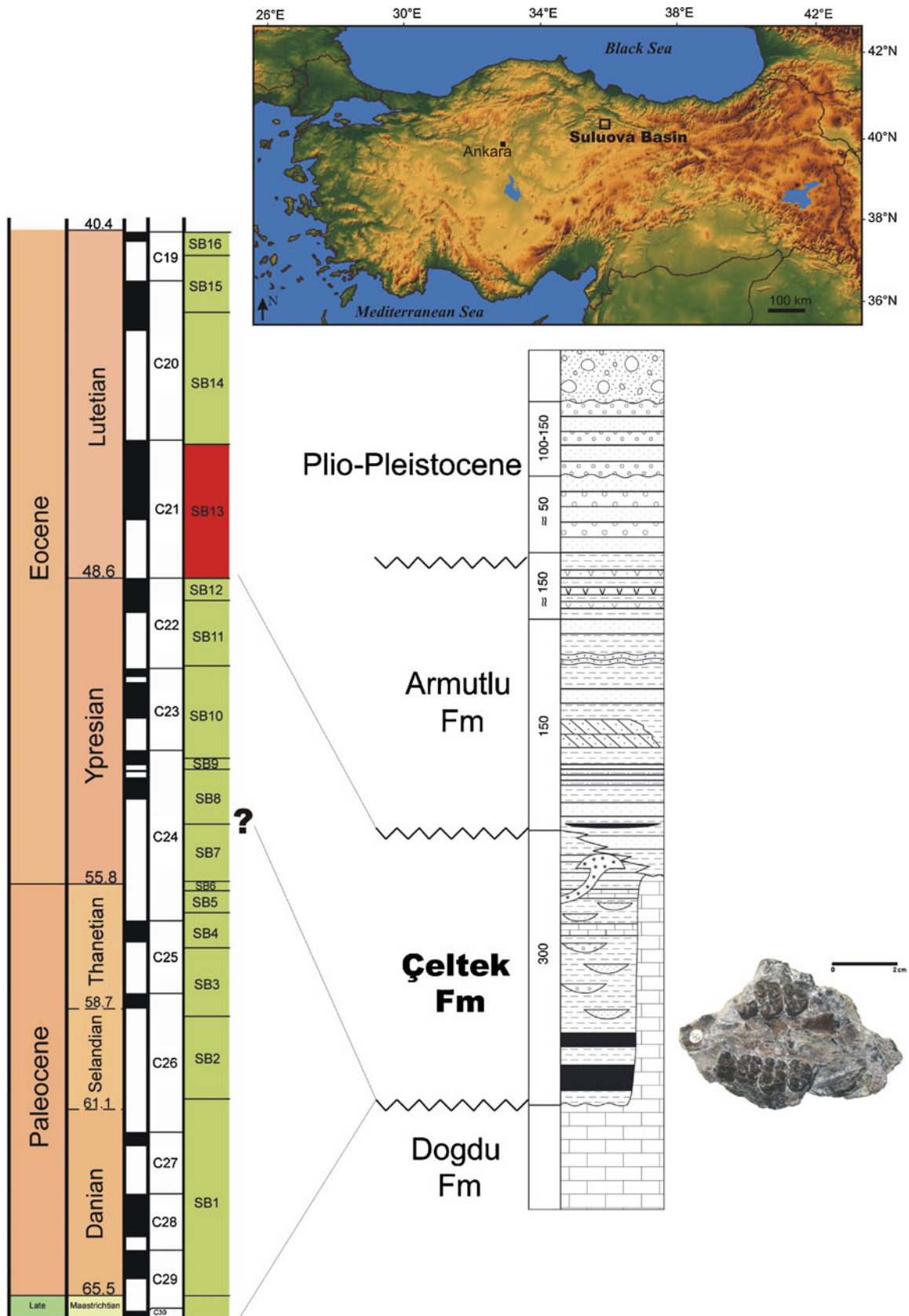


Fig. 1 The Eski Çeltek mine in the Suluova Basin, Central Anatolia, Amasya Province; and raw chronostratigraphic calibration (based on the Geologic time scale of Gradstein et al. 2004) of the Çeltek Formation based on current data

from the same mine by Ducrocq and Sen (1991), *Parabunodon anatolicum*, based on a single palate preserving right P4–M3 and left M1–3 (M3 is partly damaged). Actually, the original specimen, housed in the collections of the Natural History Museum of Ege University (Izmir), consists of a crushed and highly damaged skull preserving the palate and teeth, as well as the frontal and orbital areas, and thus providing additional anatomical features that are here tentatively interpreted. In its initial description, *Parabunodon anatolicum* was referred to a “haplobunodontid” (=choeropotamid) artiodactyl, a family of bunoselenodont artiodactyls showing a trend toward the molarisation of P4/p4, elongation of the snout, and loss of P1/p1 (Erfurt and Métais 2007). Since the revision of the family produced by Gentry and Hooker (1988), haplobunodontids are now included with the genus *Choeropotamus* Cuvier 1822 within the Choeropotamidae. This family of Paleogene artiodactyls first appeared in the Terecina sands (MP 8–9, early Eocene) of the Paris Basin at the site of Avenay with the genus *Cuisitherium* Sudre et al. 1983, and is common in the middle–late Eocene faunas of western Europe. *Parabunodon anatolicum* would be the only choeropotamid genus known outside Western Europe. Here, we review the arguments that led Ducrocq and Sen (1991) to identify *Parabunodon anatolicum* as a choeropotamid, and we propose an alternative taxonomic assignment for this genus based on a phylogenetic analysis stimulated by the recent review of the pleuraspidotheriid condylarths (Ladevèze et al. 2010).

Geochronology and age of the Çeltek Formation

In the Suluova Basin, the Çeltek Formation rests unconformably on the Late Cretaceous marine limestone of the highly folded Lokman Formation. This major regional unconformity corresponds to important tectonic activities related to the closure of the northern branch of the Neotethys Ocean (Keskin et al. 2008). The Çeltek Formation is exposed in several disjunct basins of Central Anatolia, and has yielded fossil vertebrates from different coal mines (Ozansoy 1966). In the Suluova Basin, the Çeltek Formation comprises, from the base upwards, conglomerate, sandstone, marl, a coal seam, bituminous shale, claystone, conglomeratic sandstone, claystone/marl and bituminous shale (Karayığit et al. 1997). According to borehole data, the thickness of the formation ranges from 200 to 500 m, and the vertebrate fossil-bearing coal seam lies at the base of the formation; its thickness does not exceed 8 m (Karayığit et al. 1996). The Çeltek Formation including the coals is thought to have been developed in a fluvial–lacustrine environment (Karayığit et al. 1997). The tectonic setting was that of freshwater lakes developed in a fault-bounded basin, in which the peat-forming swamps probably occurred.

In the Suluova Basin, the Armutlu Formation rests unconformably upon the Çeltek Formation and there is a typical reddish-coloured weathering zone at the unconformable contact. Blumenthal (1937), who formally defined the Çeltek Formation considered it as early Eocene based on the early Lutetian age of the benthic foraminifera of the Armutlu Formation. Akgün (2002) studied the palynomorphs of the early Paleogene sequence in the Basin and proposed a middle–?late Eocene age for the Çeltek and Armutlu Formations, respectively. Koç and Türkmen (2002) found a thin marine horizon above the mammal bearing lignite seam with planktonic foraminifera of Ypresian age, while the overlying marine Armutlu Formation yielded rich benthic and planktonic foraminiferal assemblages suggesting an early Lutetian age for this formation. Further work is needed to better constrain the age of lowermost beds (yielding mammals) of the Çeltek Formation, that are no older than Cretaceous and probably no younger than late? Ypresian (Fig. 1).

Is *Parabunodon* a choeropotamid artiodactyl? Review of available morphological data

Ducrocq and Sen (1991) emphasised close resemblance between *Parabunodon* and western European choeropotamids, such as “*Anthracobunodon*” (= *Amphirhagatherium* Depéret 1908) from the middle Eocene of Geiseltal, and *Massillabune* Tobien 1980 from the middle Eocene of the Messel pit. They suggested that *Parabunodon* was more primitive, with less molariform P4, weaker paraconule and styler cusps, a mesostyle that is not salient buccally and greater bunodonty. They also noticed that the reduced M3 is not known in any choeropotamids, a feature that might well shed some doubts on the familial affinities of their new genus. Ducrocq and Sen (1991) did not extend the comparisons with condylarths (except *Phenacodus*), probably influenced by the supposed middle Eocene age of *Parabunodon anatolicum*. Since the early 1990s, early Paleogene mammals have been reported from the red beds of the Uzunçarşidere Formation exposed on the northern margin of the Haymana Basin near Ankara (Kappelman et al. 1996; Maas et al. 1998, 2001), and an early middle Eocene age was advocated for this mammal assemblage. The fossil fauna includes marsupials, embrithopods, and the genus *Hilalia* Maas et al. 2001, documented by dental and postcranial material, and representing four species of different sizes. First described as a “condylarth” *incertae sedis* (Maas et al. 2001), the taxonomic affinities of *Hilalia* have long remained somewhat problematic, raising more issues (e.g. phylogenetic, biogeographic) than offering answers. Recently, Ladevèze et al. (2010) investigated the phylogenetic relationships of western European pleuraspidotheriids among “condylarths”, and recognised affinities of *Hilalia* with

Pleuraspidotherium Lemoine 1878 and *Orthaspidotherium* Lemoine 1885 from the late Paleocene of western Europe. Although several symplesiomorphic resemblances shared by pleuraspidotheriids and artiodactyls were tentatively discussed, no unambiguous synapomorphy linking these two taxa could be identified based on the available material.

Following Ladevèze et al (2010), we use the term pseudohypocone for the metaconule which has shifted disto-lingually in the place of the classic hypocone. This hypothesis of homology is supported by the primitive upper molar pattern of *Orthaspidotherium*, on which the metaconule is clearly smaller and more labial than it is in *Pleuraspidotherium*. *Parabunodon anatolicum* is characterised by bunolo-phoselenodont cheek teeth, with a W-shaped ectoloph linked to a strong mesostyle that is closer to metacone than to paracone, low and poorly crested paraloph and metaloph, inflated paraconule close to the protocone, well-developed labial and mesial cingula, the presence of an entocingulum between the pseudohypocone and protocone, an absence of postprotocrista, M3 smaller than M2 with a posterior lobe transversely reduced, and submolariform P4 with a small metacone fused to paracone. The upper molars of anthracobunid artiodactyls differ in the shape of the ectoloph: it is straight and the mesostyle is lacking. Moreover, the posthypocrista is always lacking in anthracobunids, giving their upper molar a more bunolophodont morphology by contrast to the bunoselenodont molar pattern of *Parabunodon*. Anthracobunids display lesser transversal development of the upper molar compared to *Parabunodon*, and their cusps are generally more inflated. The W-shaped ectoloph (even if this feature is not marked in *Parabunodon*) differs from anthracobunid artiodactyls. Most of these features are shared with *Hilalia*, suggesting close affinities between *Parabunodon* and *Hilalia*. Some of these dental features are indeed diagnostic of the Pleuraspidotheriidae (e.g. M1–3 with pseudohypocone), or listed as synapomorphies of the Pleuraspidotheriid clade (e.g. P4 with small but distinct metacone fused to paracone; Ladevèze et al. 2010, fig. 11a). *Parabunodon* is, however, clearly distinct from *Hilalia* and other pleuraspidotheriids. Beyond its large size (roughly equal to the largest species of *Hilalia*—*H. robusta*), the most obvious derived character of *Parabunodon* is the marked bunodonty of its upper molars. This is illustrated by the lower cusps, lower and inflated lophs that are obviously less sharp and less functional as illustrated by the absence of an anterior shearing facet. Other derived features include reduced cingula in upper molars (e.g. entocingulum not connected to the precingulum) and on premolars (no ectocingulum or precingulum on P4), reduced parastyle and metastyle, an inflated (neomorphic) “metaconule” that is shifted mesially with respect to the pseudohypocone, and the transversely extended M2. Most of these

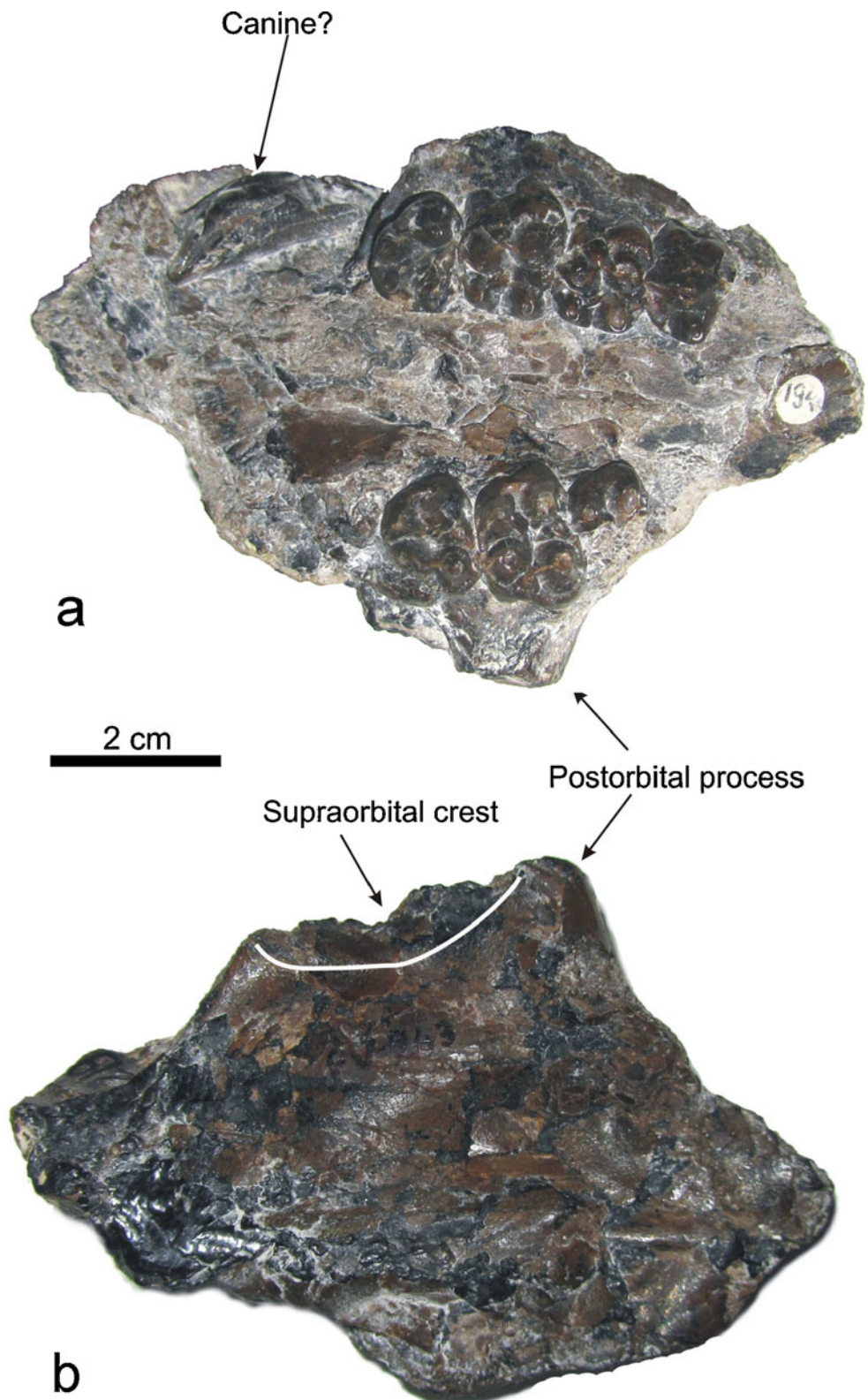
traits are probably autapomorphic in *Parabunodon*. *Parabunodon* and *Hilalia* have a paracone slightly larger than the metacone in contrast to *Orthaspidotherium* and *Pleuraspidotherium*, the only two monotypic genera formerly included within the Pleuraspidotheriidae. Another dental feature shared between *Hilalia* and *Parabunodon* is the mesio-distally compressed protocone and the transverse development of M2. *Pleuraspidotherium* is distinguished by several probably autapomorphic traits (molarized P4 showing full metacone, paracone and paraconule), advanced selenodonty, elongated muzzle and reduced anterior premolar dentition. *Orthaspidotherium* is distinguished by several primitive features (triangular occlusal molar outline, small pseudohypocone, etc.) with respect to other pleuraspidotheres.

Not only is the palate preserved on the holotype, the dorsal part, although heavily crushed, provides interesting anatomical information about cranial architecture around and between the orbits. The cranial roof is too crushed to localise sutures between bones, but the right supraorbital crest is clearly distinct, and it seems to extend distally into a prominent postorbital process (Fig. 2). Considering that, during fossilisation, this supraorbital crest was crushed through a vertical plane and did not undergo any anterior or posterior translation, it is interesting to notice that the postorbital process is localised at the level of M2, which is fairly unusual in ‘ungulate’ mammals. For example, with the exception of *Mixtotherium* Filhol 1880, Eocene artiodactyls display a postorbital process placed at the level of, or posterior to, M3. Likewise, the postorbital process is laterally salient back to M3 in *Orthaspidotherium* and *Pleuraspidotherium* (Ladevèze et al. 2010; Russell 1964). At this point, it is difficult to establish whether or not the anterior position of the orbit observed on the crushed fossil corresponds to its original position, which would make *Parabunodon*, for this character, distinctive from other pleuraspidotheriids. Since this is still uncertain and requires better preserved cranial material, we did not include this observation in the matrix of characters processed below. Another enigmatic element raised by Ducrocq and Sen (1991) is the presence of a large canine-like tooth partly embedded into the palate. This tooth displays a distinct groove on its lingual side, and its root, although damaged, is large and slightly curved posteriorly. The absence of any anatomical relationships between this tooth and the molar row makes any attempt of taxonomical identification highly putative.

Phylogenetic analysis

In order to test the affinities of *Parabunodon*, we have compiled a matrix of 31 dental features known for this genus (no

Fig. 2 *Parabunodon anatolicum* (holotype and unique specimen,) in **a** dorsal, and **b** ventral views. Note the relatively anterior position of the postorbital process, considering that the crushed partial skull roof did not move forward or backward during the fossilisation



postcranial at this point) and scored those in the character-taxon matrix of Ladevèze et al. (2010). The taxa included in the analysis are the 21 genera of Ladevèze et al. (2010) (a large selection of European and North American ‘condylarths,’ as

well as both basal artiodactyls and perissodactyls) plus *Cuisitherium*, because it represents the earliest representative of choeropotamid artiodactyls, and the single occurrence of the family in the early Eocene. In all analyses, Cretaceous

placentals *Zalambdalestes*, *Zhelestes*, and *Asioryctes* were set as the outgroup taxa.

Two separate cladistic analyses were processed. The first based on the 31 dental features of the upper dentition, and the second based on these 31 dental features plus 51 of the 58 cranial and postcranial characters of Ladevèze et al. (2010). Dental characters 27–33 used in Ladevèze et al. (2010) were removed and replaced by 31 characters (see [supplementary information](#)) describing the upper dentition, the only characters that are preserved so far in *Parabunodon*. The matrix of characters was assembled in Mesquite 2.75 (Maddison and Maddison 2010). Most multistate characters were treated as unordered, except for characters 49–51, 61, 64, 65, and 72. The morphology dataset was analysed using collapsing rule 3 in TNT version 1.1 (Goloboff et al. 2000, 2008). Searching was performed with traditional search including 1,000 RAS + TBR. The matrix of 31 dental characters was first run with 4 characters ordered and all of equal weight (see [supplementary information](#); Fig. 3a), whereas on a second occasion

parsimony analysis was conducted under implied weighting method ($k=3$) and a strict consensus tree was generated using the topologies obtained from the implied weights (Fig. 3b). The phylogenetic trees with morphological character state optimizations are generated by Winclada v.1.00. (Nixon 1999). Polymorphic taxa were coded with multiple character state entries. Branch support was assessed by calculating the decay Bremer index (Bremer 1988) with TNT v.1.1.

The character–taxon matrix of 22 taxa and 31 dental characters (4 set as additive) was analysed with the equal weighting search and produced 26 equally parsimonious cladograms of 123 steps. The consistency index of most parsimonious cladograms excluding uninformative characters (CI) is 0.39 and the retention index (RI) is 0.6. The resolution of the strict consensus is relatively low (Fig. 3a), but it shows *Parabunodon* within a distinct clade including pleuraspidotheriids and the North American genus *Mensicotherium* Cope 1874. This clade is supported by 3 non-homoplastic synapomorphies, and 8 homoplastic synapomorphies (Fig. 3a).

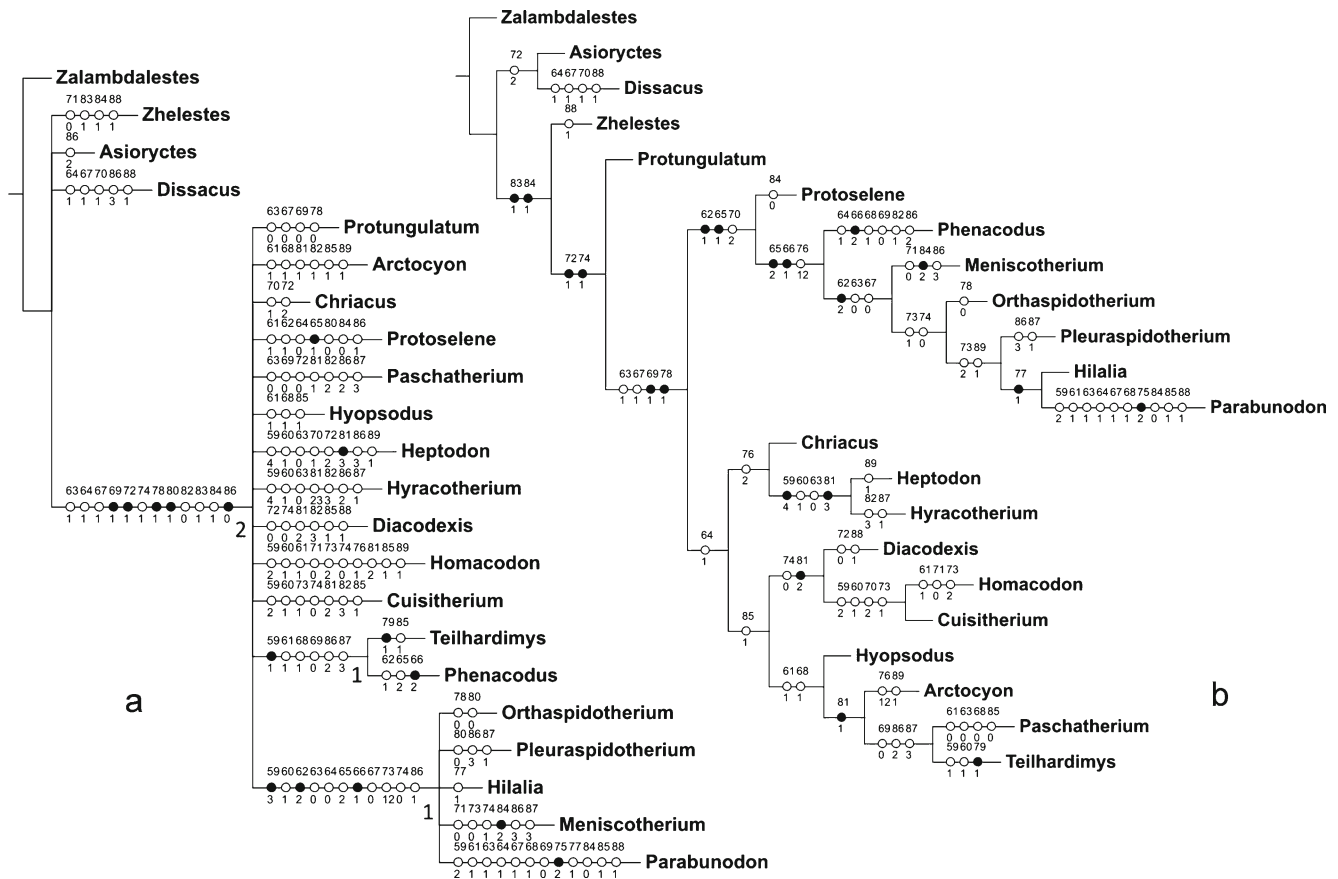


Fig. 3 Trees resulting from the cladistic analysis of 31 dental features (k59–k89 listed in the [supplementary information](#)). Characters 61, 64, 65, and 72 are additive. Taxon-matrix characters were processed with the traditional search on TNT version 1.1 (Goloboff et al. 2008). For each node, the list of the non-ambiguous synapomorphies is given, each synapomorphy being represented by a *black* (strict synapomorphy) or *open white circle* (homoplastic synapomorphy). The *numbers*

above the symbol indicate the character number (see [supplementary information](#)) and the *numbers below the symbol* indicate the state number for this feature. The Bremer index is just below and on the left of the node. **a** Strict consensus tree of 26 most parsimonious trees obtained from the equal weighted search (CI=0.28; RI=0.35). **b** Single most parsimonious tree resulting from the parsimony analysis using implied weighting method ($k=3$) (CI=0.38; RI=0.59)

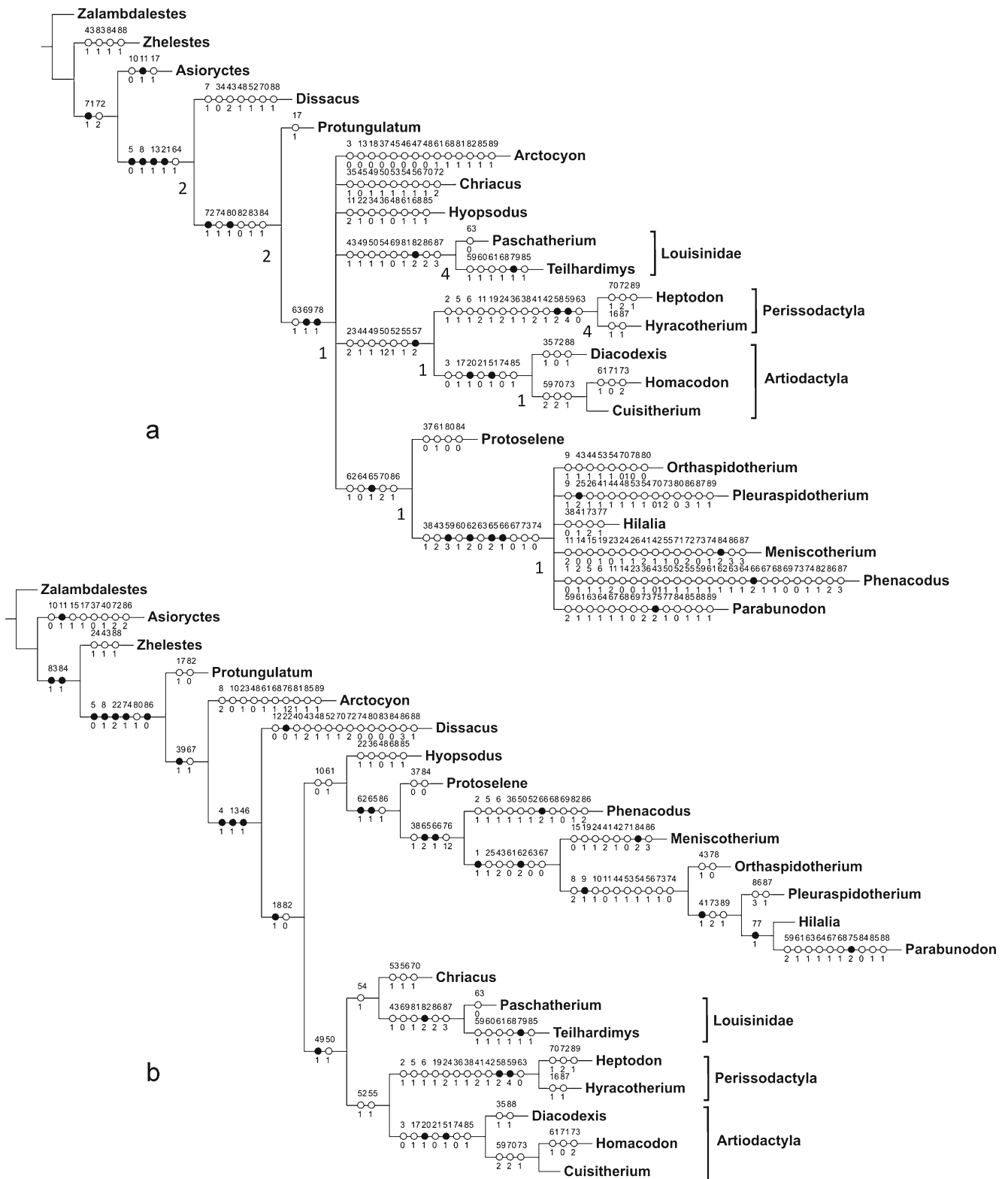


Fig. 4 Trees resulting from the cladistic analysis on 82 morphological features, including 51 characters used in Ladevèze et al. 2010, and 31 dental characters. Taxon-matrix characters were processed with the traditional search (rule 3) on TNT version 1.1 (Goloboff et al. 2008). For each node the list of the non-ambiguous synapomorphies is given, each synapomorphy being represented by a *black* (strict synapomorphy) or *open white circle* (homoplasic synapomorphy). The *upper numbers* indicate

the character number and the *lower numbers* indicating the state number for this feature. The Bremer index is just at the down-left of the node. **a** Strict consensus tree of 9 most parsimonious trees obtained from the equal weighted search (CI=0.36; RI=0.43). **b** Strict consensus of 3 most parsimonious trees resulted from the parsimony using implied weighting method ($k=3$) (CI=0.41; RI=0.53)

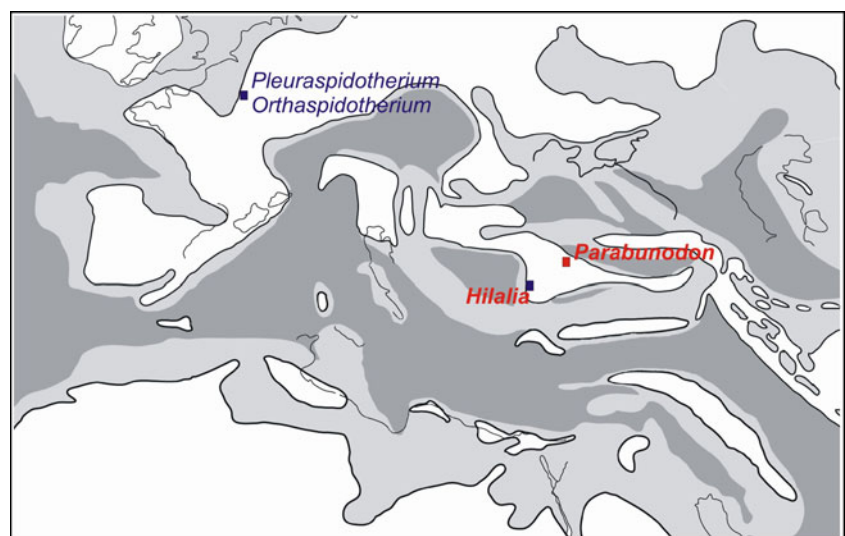
Analyses using implied weighting method ($k=3$) gave a single tree in which the pleuraspidotheriids including *Parabunodon* form a monophyletic group supported by only 2 homoplastic synapomorphies (characters 73 and 74) corresponding to the presence of a pseudohypocone (Fig. 3b). This cusp is not homologous to the hypocone known in most ‘condylarths’, and it is a convergent feature with the metaconule of choeropotamids. Interestingly, *Hilalia* and *Parabunodon* are sister taxa and form a clade of Anatolian pleuraspidotheriids, supported by a unique non-homoplastic synapomorphy (character 77), nested within western European forms. Moreover, this topology is consistent with current stratigraphic ranges of those genera, the Anatolian forms being supposedly early Eocene in age.

The character–taxon matrix consisting of 22 taxa and 82 characters (31 dental characters plus 51 of Ladevèze et al. 2010, and 7 set as additive) was analysed with the equal weighting search and TNT produced only 9 equally parsimonious cladograms of 274 steps. The consistency index excluding uninformative characters (CI) is 0.41 and the retention index (RI) is 0.54. The strict consensus (Fig. 4a) plots *Parabunodon* within a polytomy including pleuraspidotheriids and phenacodontids. This clade is supported by 4 dental non-homoplastic synapomorphies (characters 59, 62, 65, and 66), and 7 optimised features (Fig. 4a). Artiodactyla and Perissodactyla are monophyletic and sister groups; Louisinidae and Perissodactyla are supported by fairly high Bremer values (4).

Analyses under implied weighting method ($k=3$) gave 3 equally parsimonious trees. The strict consensus (Fig. 4b) shows a clade quite similar to that obtained on the sole dental characters (Fig. 3), with phenacodontids forming successive offshoots at the base of pleuraspidotheriids. Therefore, dental features bear sufficient phylogenetic signals to refute affinities between artiodactyls and *Parabunodon* as suggested by Ducrocq and Sen (1991). The pleuraspidotheriid clade is

supported by 8 additional non-dental synapomorphies (1 non-homoplastic and 7 homoplastic synapomorphies). The Anatolian clade occurs again in this analysis, and it appears nested within the monophyletic Pleuraspidotheriidae. In all analyses, *Orthaspidotherium* appears as the first offshoot within pleuraspidotheriids as suggested by Ladevèze et al. (2010). There is a great deal of homoplasy in this tree, few character states being uniquely shared by clades. The intra and interrelationships of the pleuraspidotheriid clade are weakly supported (Bremer index of 1). The most reliable derived character for the Pleuraspidotheriidae is character 9 of Ladevèze et al. (2010): the presence of tympanic aperture of the hiatus fallopii, which is unknown in *Hilalia* and *Parabunodon*. The clade (*Pleuraspidotherium*, (*Parabunodon*, *Hilalia*)) is supported by a single non-homoplastic synapomorphy, and 2 non-homoplastic synapomorphies, which are optimised by TNT for *Hilalia* and *Parabunodon* in the present analysis. The Anatolian clade is united by the shape and relative size of protocone compared to pseudo-hypocone (character 77). However, this remains a rather tenuous morphological support, and the clade clearly needs further testing and support. In that regard, knowledge of the lower dentition of *Parabunodon* would be critical. *Phenacodus* Cope, 1873 and *Meniscotherium* (Cope 1873) appear as successive offshoots at the root of the pleuraspidotheriid clade, and not closely related to perissodactyls as suggested by Ladevèze et al. (2010). In our analysis (Fig. 4b), perissodactyls appear most closely related to artiodactyls, this association being supported by 2 non-homoplastic synapomorphies and a weak Bremer index of 1. In all MP trees, the artiodactyls clade is relatively well supported (Bremer index of 1) by 2 non-homoplastic synapomorphies, and *Diacodexis* Cope 1882 is always the first taxon to split off within this clade. The clade Louisinidae (here represented by *Paschatherium* Russell 1964 and *Teilhardimys* Kretzoi and Kretzoi 2000; see Hooker and Russell 2012) is

Fig. 5 Geographic distribution of pleuraspidotheriid “condylarths” during the late Paleocene and early Eocene (map modified from Barrier and Vrielynck 2008). In western Europe, pleuraspidotheriids are restricted to the late Paleocene while representatives of the family reported so far are probably early Eocene in age in Central Anatolia



also relatively well supported (Bremer index of 4), although its relationships with other taxa varies from one analysis to another (see Hooker and Russell 2012 for an overview). While a thorough assessment of the higher relationships among condylarths is outside the scope of this paper, the question about the affinities of *Parabunodon* is documented and partly answered. Most parsimonious trees obtained from different datasets clearly suggest that *Parabunodon* is not closely related to Artiodactyla. Instead, this genus appears to be related to pleuraspidothériids, confirming the occurrence of the family in Anatolia as suggested by Ladevèze et al. (2010). The topology obtained from the most complete dataset (Ladevèze et al. 2010) suggests the bunodont molar pattern of *Parabunodon* to be a derived condition which would have evolved from a lophoselenodont molar pattern characterising the other pleuraspidothériids. Another hypothesis, so far unsupported, would be to consider *Parabunodon* as a representative of a still undocumented lineage of bunodont pleuraspidothériids, but this assumption requires further testing with additional fossil data. This issue, together with the weakness of the links between the major clades can only be resolved when the missing anatomical structures are discovered for the less complete taxa. The enigmatic *Parabunodon* nests with more typical pleuraspidothériids, and is here included in the family Pleuraspidothériidae, although Anatolian forms (*Hilalia* and *Parabunodon*) are still incompletely known.

Conclusions

The reassessment of fossil material referred to *Parabunodon anatolicum* led us to refute affinities with choeropotamid artiodactyls, and to suggest the inclusion of the genus within pleuraspidothériid ‘condylarths’. This study also describes and figures for the first time the crushed inter-orbital part of the cranium preserved on the type specimen, although no significant anatomical information could be evidenced on this highly damaged skull. Phylogenetic analyses based solely on dental features, and on a more extensive anatomical dataset, are all consistent with close affinities between *Hilalia* and *Parabunodon*, suggesting the existence of an Anatolian clade of pleuraspidothériids during the early Eocene. The dental morphology of *Parabunodon* is clearly distinctive within pleuraspidothériids, and additional material of *Parabunodon* is needed to further test its relationships with and within the family.

The occurrence of *Hilalia* and *Parabunodon* in Central Anatolia during the early Paleogene significantly extends the geographical range of pleuraspidothériids, which were long restricted to the late Paleocene of the Paris Basin (Lemoine 1878; Russell 1964). This distribution does not plead for a supposed endemism of Central Anatolia during the early Paleogene as defended by Kappelman et al. (1996)

and Maas et al. (1998) on the basis of the mammal assemblage of the Uzunçarşidere Formation. It actually suggests early Paleogene palaeobiogeographical relations between Anatolia and western Europe. However, the fauna from Eski Çelték remains quite distinct from early Eocene and late Paleocene western European faunas, most noticeably with the presence of embrithopods. The age of pleuraspidothériid yielding localities of Central Anatolia must be refined (especially in regard to the Paleocene–Eocene boundary) to better understand early evolution of these Peri-Tethyan mammal faunas, and their palaeobiogeographic affinities (Fig. 5). The Anatolian Plateau of Turkey lies at the crossroads between Afro-Arabia, Asia, and Europe during the early Paleogene. Although this area figures prominently for a better understanding of the early evolution and dispersals of many groups of extinct and modern mammal orders, its early Paleogene vertebrate fossil record remains very scarce. Further paleontological data from that area should shed new light on the dispersal history and early evolution of several groups of modern mammals around the Paleocene–Eocene Thermal Maximum (PETM).

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