Anthracobunids from the Middle Eocene of India and Pakistan Are Stem Perissodactyls

Lisa Noelle Cooper  
*Northeast Ohio Medical University; Kent State University*

Erik R. Seiffert  
*Stony Brook University, Stony Brook, New York*

Mark T. Clementz  
*University of Wyoming, mclemen1@uwyo.edu*

Sandra I. Madar  
*Hiram University, Hiram, Ohio*

Sunil Bajpai  
*Indian Institute of Technology, Roorkee, Uttarakhand, India*

*See next page for additional authors*

Follow this and additional works at: [https://repository.uwyo.edu/geology_facpub](https://repository.uwyo.edu/geology_facpub)

**Publication Information**

Authors
Lisa Noelle Cooper, Erik R. Seiffert, Mark T. Clementz, Sandra I. Madar, Sunil Bajpai, Sofia Taseer Hussain, and Johannes G M Thewissen

This article is available at Wyoming Scholars Repository: https://repository.uwyo.edu/geology_facpub/98
Anthracobunids from the Middle Eocene of India and Pakistan Are Stem Perissodactyls

Lisa Noelle Cooper1,2*, Erik R. Seiffert3, Mark Clementz4, Sandra I. Madar5, Sunil Bajpai6*, S. Taseer Hussain7, J. G. M. Thewissen1,2

1 Department of Anatomy and Neurobiology, Northeast Ohio Medical University, Rootstown, Ohio, United States of America, 2 School of Biomedical Sciences, Kent State University, Kent, Ohio, United States of America, 3 Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York, United States of America, 4 Department of Geology and Geophysics, University of Wyoming, Laramie, Wyoming, United States of America, 5 Department of Biology, Hiram University, Hiram, Ohio, United States of America, 6 Department of Earth Sciences, Indian Institute of Technology, Roorkee, Uttarakhand, India, 7 Department of Anatomy, College of Medicine, Howard University, Washington, District of Columbia, United States of America

Abstract

Anthracobunidae is an Eocene family of large mammals from south Asia that is commonly considered to be part of the radiation that gave rise to elephants (proboscideans) and sea cows (sirenians). We describe a new collection of anthracobunid fossils from Middle Eocene rocks of Indo-Pakistan that more than doubles the number of known anthracobunid fossils and challenges their putative relationships, instead implying that they are stem perissodactyls. Cranial, dental, and postcranial elements allow a revision of species and the recognition of a new anthracobunid genus. Analyses of stable isotopes and long bone geometry together suggest that most anthracobunids fed on land, but spent a considerable amount of time near water. This new evidence expands our understanding of stem perissodactyl diversity and sheds new light on perissodactyl origins.

Citation: Cooper LN, Seiffert ER, Clementz M, Madar S, Bajpai S, et al. (2014) Anthracobunids from the Middle Eocene of India and Pakistan Are Stem Perissodactyls. PLoS ONE 9(10): e109232. doi:10.1371/journal.pone.0109232

Editor: Andrew A. Farke, Raymond M. Alf Museum of Paleontology, United States of America

Received June 19, 2014; Accepted August 20, 2014; Published October 8, 2014

Copyright: © 2014 Cooper et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are within the paper and its Supporting Information files.

Funding: The National Science Foundation is acknowledged for support to M. T. C. (EAR-0847413), E. R. S. (BCS-0819186 and BCS-0416164), and J. G. M. T. (EAR-0207370). Also, S. B. acknowledges financial support received from the Department of Science and Technology, Government of India for field work in the Eocene sections of Gujarat. The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* Email: lcooper@neomed.edu
* Current address: Birbal Sahni Institute of Palaeobotany, Lucknow, Uttar Pradesh, India

Introduction

Anthracobunidae is a family of large mammals that is only known from the middle Eocene of south Asia. Historically, anthracobunids have played a prominent role in debates surrounding the origin of Tethytheria, the group that includes the living and extinct members of the placental mammalian orders Sirenia (sea cows) and Proboscidea (elephants). Anthracobunids are often considered to have branched off near the base of Tethytheria [1–8], sharing most recent common ancestry with either Proboscidea [1,9–13], Sirenia [14,15], or the extinct Desmostylia. However, until now, no cranial parts, only some partial dentitions and two postcranial elements (a scapula associated with a maxilla [11] and an isolated astragalus [13]), were known for the group.

The paucity of fossil evidence has left Anthracobunidae as a phylogenetically and adaptively enigmatic group [2,8,16–20], with little known about their diets, habitats, and time and place of origin. In light of this, anthracobunid genera have also been aligned with two other, non-tethytherian clades, including Artiodactyla [21–23] and Perissodactyla [24], as well as phenacondontids [25,26], one of the extinct families of basal ungulates. The convergent evolution of “ungulate”-like features in Paenungulata (containing Tethytheria) and Laurasiaitheria (containing Artiodactyla and Perissodactyla) revealed by molecular data [27] requires that Anthracobunidae be re-evaluated within this new phylogenetic context.

Here we describe new anthracobunid fossils from the Kuldana and Subathu Formations of the early-middle Eocene of Pakistan and India [28–32]. These new findings more than double the number of anthracobunid fossils, and include cranial and postcranial material. We test the phylogenetic relationships of anthracobunids using a taxonomically rich morphological data set and investigate anthracobunid diet and habitat. Our results have important implications for character transformations near the origins of Perissodactyla, the habitats of stem perissodactyls, and the early biogeography of Paenungulata and Perissodactyla.

Methods and Materials

Osteological Sample

All fossil specimen numbers and identifying information are listed in the Supplementary Information.

Fossils were collected in Punjab Province, Pakistan, under a collaborative agreement of Howard University and the Geological Survey of Pakistan (H-GSP). Localities where fossils were
collected, with topographical coordinates, were described in Thewissen et al. [33]. Specimens were prepared in the U.S.A. at Northeast Ohio Medical University (NEOMED) and are cataloged using the H-GSP acronym and accessioned into the collections of the Geological Survey of Pakistan (GSP). Since the GSP is a branch of the Pakistani government, all collected fossils are the property of the Pakistani state. At present, fossils are for study in the U.S.A., but they will be returned to Pakistan and will be permanently housed at the Natural History Museum of Pakistan, located in Islamabad. GSP geologists are collaborators on all field work as part of their official assignment and all necessary permits were obtained for the described study, which compiled with all relevant regulations.

We also studied fossils from the locality Kalakot in Jammu & Kashmir State, India, the location of which is described by Russell and Zhai [32]. This locality was discovered by A. Ranga Rao, a geologist of the Oil and Natural Gas Commission, and he quarried large quantities of fossiliferous rock matrix from this locality. After his death, we were given access to these by his widow, F. Oberfell. Fossils were prepared at NEOMED in the U.S.A., and are the property of the Rangarao-Oberfell Trust for Geosciences, located in Dehra Dun, India, and are catalogued using the acronym RR. They will be housed on the Trust campus on Rajapur Road in Dehra Dun.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/”.

The LSID for this publication is: urn:lsid:zoobank.org:pub:CD33F507-0D06-4DE1-A3C8-8BF9E7697114. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Phylogenetic Methods

The morphological character matrix is a modified version of that which was most recently employed by Barrow et al. [34], and includes 92 taxa and 403 morphological characters. Extant Canis and Equus, and the following extinct taxa, many of which are of uncertain supraordinal position, were added to the morphological character matrix of Barrow et al. [35] (with references provided for those taxa that were, in whole or in part, scored from the literature): Radinskyya quyngae (Perissodactyla; late Paleocene; China) [36]; Paschatherium dolloë (Louiisiidae; late Paleocene-early Eocene; Belgium, France, England) [37]; Phenacodus intermedius (Phenacodontidae; late Paleocene-early Eocene; U.S.A.); Cambrytherium (Cambrytheriidae; early Eocene; India) [38]; Gaudhieralopus minor (Perissodactyla; early Eocene; Pakistan) [39]; Gyataraya indica (Artiodactyla; early Eocene; India); Gyataraya pakistaniens (Artiodactyla; early Eocene; Pakistan) [40–42]; Homogalax protaprinus (Perissodactyla; early Eocene; U.S.A.) [43–45]; Meniscosorhus chamense (Meniscosorhidae; early Eocene; U.S.A.) [46]; Protomoropus gabunia (Perissodactyla; early Eocene; Mongolia) [47]; Teilhardimys (= Microhyus) reisi (Louiisiidae; early Eocene; Portugal) [48]; Heptodon (Perissodactyla; early-middle Eocene; U.S.A.) [49]; Hyrachyus modestus (Perissodactyla; early-middle Eocene; U.S.A.); Hallassia (?) (Perissodactyla; middle Eocene; France, Germany) [50,51]; Namatherium blackerwense (Embrithopoda; middle Eocene; Namibia) [52]; Mesohippus bairdi (Perissodactyla; late Eocene and early Oligocene; U.S.A.); Behemotoops katsuer (Desmostylia; early Oligocene; Japan) [53]; and Paleoparadoxia (Desmostylia; middle-middle Miocene; Japan, U.S.A.) [54–57].

The matrix analyzed here included a total of 92 taxa and 403 characters (See Suppl. File). Rather than incorporate molecular data directly into the parsimony analysis, we employed molecular “scaffolds” based on the results of Meredith et al. [27] for placental and Smit et al. [68] for relationships within Macro-

Anthracobunids Are Stem Perissodactyls
Anthracobunids Are Stem Perissodactyls

Scleridea. For the primary analysis, the scaffold enforced the monophyly of the following clades: Afrotheria (Chrysochloriformes + Tenrecoidea), Afroinsectivora (Macroscelidea + Afroinsectiphilia), Afroinsectiphilia, Tubulidentata + Afroinsectivora, Paenungulata, Afrotheria, Euarctotheria, Eulipotyphla, and Laurasiatheria. In addition, the Miocene aardvark Myourtheropus was constrained to group with extant Orycteropus; otherwise this taxon tended to form a clade with Dasypus, perhaps because both taxa have a full complement of peg-like featureless teeth, whereas these teeth have been reduced in Orycteropus. As in the original study of Seiffert [69], polymorphisms were scored as an intermediate character state rather than using standard polymorphic scoring (i.e., “0/1”). For analyses in which multistate characters with such intermediate polymorphic states were ordered, they were weighted either as 0.5 or 1.0; analyses were also run with all characters unordered and equally weighted. An additional perturbation that we employed to test for sensitivity of our results was the placement of Xenarthra to fit either the Adaptotheria [Xenarthra + Afrotheria] hypothesis or the Euarctotheria (Xenarthra + (Laurasiatheria + Euarctotheria)) hypothesis. All analyses were run in PAUP 4.0b10 [70], with 10,000 random addition-sequence replicates. Bootstrap support was calculated in PAUP, based on 1000 pseudoreplicates.

Bone Geometric Methods

Midshaft cross-sections of fossil and extant large-bodied ungulate long bones and ribs [71] were visualized via paleontological sections or high resolution micro-CT scans. Bone compactness (total amount of bone per section) was calculated via published methods [72].

Stable Isotope Methods

For the analysis of stable isotopes, three or more specimens of each species were analyzed (when available; see Tables S8 and S9) to provide an estimate of the population mean ± s.d. for carbon and oxygen isotope values [73] http://www.nature.com/nature/journal/v450/n7173/full/nature06343.html - B33. About 5 mg of enamel powder was collected from each specimen, either by drilling directly from the tooth or by grinding enamel chips in an agate mortar and pestle. Before collection, contaminants were removed by abrading the outer surface of the specimen after cleaning the outer surface to a depth of ~0.5 mm using a DREMEL drill with a 1 mm diameter diamond-coated bit.

Preparation of powders for stable isotope analysis followed published methods [74,75]. Powders were first transferred to 1.5 mL microcentrifuge vials and then soaked sequentially overnight in about 0.20 ml of a sodium hypochlorite solution (1–2 g dl-1) and then in about 0.20 ml of calcium acetate buffered acetic acid (pH about 5) following published procedures [31]. On addition of each reagent, samples were agitated for 1 min on a Vortex Genie vortex mixer. After each soak, the supernatant was removed by aspiration and the residual powder was rinsed five times with deionized water. Samples were then freeze-dried into individual test tubes for analysis on a Thermo-Finnigan gas continuous-flow isotope-ratio mass spectrometer at the University of Wyoming Stable Isotope Facility.

All values for stable isotopes are reported in delta (δ) notation, using the equation δ(x‰) = 1,000 x (Rsample/Rstandard - 1), where Rsample is the observed isotope ratio of the sample (13C/12C or 18O/16O) and Rstandard is the accepted ratio for an appropriate international standard (Vienna Pee Dee belemnite for δ13C; Vienna Standard Mean Ocean Water for δ18O). Analytical precision is typically better than 0.1‰ for δ13C values and 0.2‰ for δ18O values (±1σ).

Enamel δ18O values are influenced by the oxygen isotope compositions of oxygen sources (atmospheric O2, food and water ingested by the animal), certain physiological processes that affect intake or loss of oxygen by an animal (sweating, painting, respiration, and elimination of urine and feces), and body temperature [76–78]. For aquatic and semi-aquatic mammals, the flux of environmental water by means of direct ingestion and transcutaneous exchange [79] overwhelms all other oxygen sources, which reduces inter-individual variation [76,80] and causes enamel δ18O values of freshwater taxa (for example Hippopotamus) to be lower than those for terrestrial mammals (~2–3‰); [81–83]. The magnitude of offset between freshwater and terrestrial mammals can vary in response to changes in humidity, such that faunas experiencing drier conditions show a greater offset (~3.0‰) than those living under wetter conditions (~1.0‰) [84].

In combination with enamel δ18O values, we also determined enamel δ13C values of fossil species, which were used to infer diet and past environmental conditions. For herbivorous ungulates, enamel carbon isotopic compositions are enriched in 13C relative to diet by ~14‰ [85]. Variation in enamel δ13C values among ungulate species is most strongly affected by the carbon isotopic composition of the plants they ingest. In the Eocene, terrestrial ecosystems were dominated by plants performing C3 photosynthesis, a process that discriminates against the heavier carbon isotope (12C), causing plant tissue δ13C values to be considerably lower than those of plants exploiting other photosynthetic pathways (C4 plants, CAM plants) [86,87]. The carbon isotopic compositions of C3 plants are more variable than other plant types and are strongly affected by temperature and aridity, causing C3 plants grown under hot dry conditions to have higher δ13C values than those grown in cooler and wetter environments [88,89]. Since enamel δ13C values reflect the carbon isotopic composition of the plants in an animal’s diet, consumer enamel δ13C values can be used to infer past environmental conditions (wet vs. dry) as well as dietary information for extinct species.

Results

Systematic Paleontology

Placentalia Owen, 1837; Order Perissodactyla Owen, 1848. Family Anthracobunidae Wells and Gingerich, 1983.

Type Genus. Anthracobune Pilgrim, 1940.

Included Genera. Josaria Wells and Gingerich, 1983; and Obergellia, new genus.

Diagnosis. Stem perissodactyls with premolars increasing in complexity from anterior to posterior, but never molariform; molars brachydont, but with high cusps and low valleys between cusps; upper molars increasing in size from M1 to M3; lower molars with a distinct trigonid elevated above the talonid; large caudally-projecting angular process of the mandible.

Description. Unlike tethytheres and other paenungulates, anthracobunids have small and simple upper and lower incisors and relatively large canines (Figs. 1, 2). Check teeth are bunodont and brachydont and each cusp has a high apex, but there are deep valleys between cusps. Premolars are never totally molariform, and diastema, if present at all, are short. Upper P3 and P4 are shorter than the molars, and have a paracone, protocone, and metacone, but no hypocone. The M1 and M2 have four well-developed cusps, as well as strong para- and metacones, without lophs. The distance between proto- and paracone is longer than that between the hypo- and metacone, giving the tooth a
posteriorly pinched appearance. Lower molars have a trigonid with two large cusps, and large, sometimes twinned, hypoconulid on the third lobe (Figs. 1G–I, S1).

Partial skulls are known for two anthracobunids (H-GSP 97106 and RR 411), and both show the presence of a very thick bony shelf over the orbits (Fig. 1B, F). The palate is concave mediolaterally, with the areas near the midline much higher than the alveolar processes. The lateral sides of the basiphenoid and basioccipital are reessed; this is particularly true for the basioccipital, which suggests that the petrosal, which is not preserved, was also deeply recessed. The mandibular fossa is concave and is located just lateral to the ear region. The postglenoid process is oval and does not extend along the entire width of the mandibular fossa.

H-GSP 97106 includes, among other elements, metapodials and phalanges (Fig. 1J-O). The heads of most metapodials are wider than deep, strongly convex, and the posterior side bears a strong crest. Proximal phalanges show a broad, oval articular surface for the metapodial and are squat: nearly as wide mediolaterally as they are long proximodistally. Their distal articular facet is rectangular in outline and deeply incised caudally, indicating the presence of a caudal crest on the middle phalanx. Most prominent

Figure 1. Cranial elements of anthracobunids from the middle Eocene of Indo-Pakistan. (A) Crushed skull of A. pinfoldi (H-GSP 97106) in ventro-lateral view (left maxilla detached) and (B) dorsal view; (C) P2 of A. wardi (H-GSP 30229) in lingual view and (D) occlusal view; (E) Skull fragment of A. wardi (RR 411) in occlusal view, and (F) lateral view; (G) Mandible of A. wardi (H-GSP 96434) in occlusal view; (H) Mandible of A. wardi (H-GSP 96258) in lateral view, and (I) occlusal view. (J) Proximal phalanx of A. pinfoldi (H-GSP 97106.105) in dorsal view; (K) Proximal phalanx of A. pinfoldi (H-GSP 97106.101) in ventral view, and (L) lateral view; (M) Head of a metapodial of A. pinfoldi (H-GSP 97106.250) in dorsal view; (N) Phalangeal fragment of A. pinfoldi (H-GSP 97106.257) in dorsal-superior view; (O) Terminal phalanx of A. pinfoldi (H-GSP 97106.302) in dorsal-superior view. Scale bar is 1 cm in length. doi:10.1371/journal.pone.0109232.g001
We restrict the Anthracobune, and we do not include it. Obergfellia occidentalis displays similarities to medium-sized bunodont ungulates. However, it differs from other anthracobunids in exhibiting the following combination of features: (i) lower molars broad, (ii) lower m3 relatively short, and (iii) angular process of the mandible long but shorter than that of Anthracobune (Figs. 1, 2, S1.). The last of these features is not known in Josauria.

We exclude Ishatherium subathanensis from anthracobunids. Its holotype consists of the lingual side of an upper molar, referred originally to Sirenia [15,92]. Wells and Gingerich [1] referred Ishatherium to Anthracobunidae. The holotype and only specimen shares with anthracobunids the strong development of conules and the deep transverse wear along the protocone-paracodon-paracone and along the hypocone-metacodon-metacone. The specimen is decidedly unlike anthracobunids in that the distance between protocone and paracone is similar to that between hypocone and metacone, and in that its cusps are not highly raised. We also exclude Nakusia shahrigensia [6] from anthracobunids (Fig. 2 I,J). Its holotype is a maxilla with P4-M2 and the base of P3. The base of P3 is elongate, the cusps on the relatively un worn M2 are low, and the molars are relatively wide. Anthracobunids have a short P3, high molar cusps, and squarish upper molars. Nakusia is more likely a quettaconyid or cambaythere than an anthracobunid.

The genus Indobune was included in Anthracobunidae [4], but it has low cusps on its teeth and is better classified as a cambaythere. Ducrocq et al. [7] described Hsanotherium parvum on the basis of two specimens with upper molars from Myanmar. These specimens are bunodont, with small conules and lack a hypocone. The transverse wear pattern of anthracobunids is also absent. Hsanotherium displays similarities to medium-sized bunodont artiodactyls, such as Haqueina [22], and we do not include it in anthracobunids.

**Anthracobune** Pilgrim, 1940.

*Type Species.* Anthracobune pinfoldi Pilgrim, 1940.

*Referred species.* Anthracobune wardi (Dehm and Oettingen-Spielberg, 1958).

**Diagnosis.** Anthracobune with narrow lower molars and a very large angular process of the mandible (Fig. 1, Fig. S1).

**Discussion.** We refer to most of the specimens formerly included in Lammidhania and Pilgrimella in the past to Anthracobune. Anthracobune pinfoldi Pilgrim, 1940.

*Holotype.* BMNH M.15792, left m2–3 and right m3, from ‘Lammidhana’ and ‘Planorbis freshwater beds.’ Pilgrim never visited the type region, and the fossils were collected by a geological surveyor (T. G. B. Davies). Lammidhana appears on Davies’ unpublished map and is located on a broad alluvial plain. However, it does not match a modern topographical landmark and its meaning is not known to local people. Eocene deposits occur to the north and south of the plain, with marine limestones and muds forming ledges usually towering over the unconsolidated muds that form the bottoms of valleys. These muds are the “Planorbis freshwater beds,” and it is our contention that the specimen may have been found on these beds, but that it rolled down from overlying marine beds. Gingerich [23] improved the holotype by fitting BMNH M.15794 (the trigonid of the left M2) to it.

**Diagnosis.** Large species of Anthracobune.


**Description.** H-GSP 97106 is the most complete specimen known for any anthracobunid. Upper incisors are similar in size (based on their alveoli); the crown of I3 shows that there is a single, large pointed cusp, with small basal thickening on the cingulum anterior and posterior to it. Canine is long and compressed mediolaterally and P1 is two-rooted, with single cusp. P2 has a small protocone and two cuspules on the posterior crest of the
paraconid. P3 has a protocone, paracone, metacone and two conules, and a strong postprotocrista. Upper molars with four main cusps as well as strong para- and metacristae. In contrast, protocrista-paracone-paraconid have aligned wear surfaces, and similar wear surfaces on hypocone-metacone-metacristae. Tooth wear in anthracobunids tends to be distinct on the protocone and metacone, and to p1 but larger. Lower p3 and p4 are similar with well-developed trigonid and talonid. Protocristae and metacristae on these teeth similar in height and paracone lower, much lower on p4. Talonid of posterior premolars with high hypoconid, and entoconid high or barely distinguishable. Lower molars with distinct trigonid and talonid. Protoconid and metaconid similar in height, paraconid absent, but paraconid well developed. Hypoconid and entoconid similar in height, cristid obliqua strong, hypoconulid weak on m1 and m2, but strong and placed on third lobe in m3, and sometimes twinned. Coronoid process of the mandible small and with steep anterior slope. Length of mandible anterior to anterior edge of coronoid process (to rostral end of the fused synphysis) is approximately two times as long as that posterior from this edge (to the tip of the angular process). This indicates that the angular process is enormous. Lower p3 with three cusps on trigonid, and two on talonid; trigonid long. Lower p4 with shorted trigonid, resembling lower m1 (H-GSP 90532). Mandibular angle of juveniles small (H-GSP 30349, Fig. S1).

Upper dentitions of A. wardi are mostly known from India (LUV 15006, RR 411, WIF/A 616). The P2 is longer than wide, unlike the P3 and P4. P2 has connate paracone and metacone, and a lingual bulge with a small protocone (LUV 15006, H-GSP 30229). P3 and P4 are similar in shape, with connate para- and metacone, and large protocone. Paraconule and metacristae are strong in P3 (LUV 15006), whereas in P4 transverse crests are well developed and conules less so. Upper molars have four strongly developed cusps, with smaller but distinct paraconule and metacristae. Transverse crests are absent, but cusps are lined up in such a way that they form an anteriorly convex arch.

Tooth wear in anthracobunids tends to be distinct on the posterior side of the protoconid-metaconid, and the anterior side of the protocone-paracone-paraconid. Tooth wear pattern is consistent with the large and caudally-projecting angular process of the mandible, the area of insertion for the medial pterygoid and masseter muscles.

Specimen RR 411 reveals some details about the orbit and zygomatic arch. The zygomatic arch has a weak postorbital process and the dorsal part of the zygomatic arch is made up of the maxilla in the orbital rim, but not posterior to the orbit. The ventral edge of the zygomatic arch is made up of the jugal. The morphology of the root of the zygomatic arch, the postorbital process of the frontal, and the mandibular fossa in this specimen resembles that of H-GSP 97106.

The anterior edge of the ascending ramus of the mandible of H-GSP 96259 is vertical, whereas it slopes slightly caudal in H-GSP 96434; the superior part overhanging the inferior part. H-GSP 30349 is a juvenile in which the anterior edge of the ramus slopes slightly rostral. In H-GSP 96149 this ramus is vertical. The mandibular synphysis of all jaws, except H-GSP 30349, is strongly fused, and slopes caudal ending ventral to the premolars.

Discussion. Most specimens of Anthracobunidae and Anthracobunis are known from the lower redbeds of the Subathu Formation of India, where pakicetid cetaceans are common. These are freshwater deposits and the specimens of Anthracobunis found here pertain to A. wardi. Additional specimens of A. wardi are from the freshwater deposits of the Subathu Formation of India.
Anthracobunids Are Stem Perissodactyls

Obergfellia, new genus. urn:lsid:zoobank.org:act:952704F2-F029-4643-B791-B30E7C71AA0A.


Pilgrimella (in part), Wells and Gingerich, 1983; Kumar, 1991.

Type and only species. Obergfellia occidentalis, new species.

Etymology. In honor of the late vertebrate paleontologists Dr. Friedlinde Obergfell and her husband A. Ranga Rao. Both were instrumental in the initial discovery and description of the Kalakot fauna. This fauna became the best-known Eocene land mammal fauna from India, mostly due to the efforts of A. Sahni and K. Kumar.

Distribution. Middle Eocene, northern India and Pakistan.

Diagnosis. As for the type species until other species are described.


Anthracobune pinfoldi (in part), West, 1980, p. 518, Pl. 2.5.

Anthracobune pilgrimi, West, 1981; West, 1983 (in part), p. 367, Fig. 5, Fig. 6; West, 1984 (in part), p. 187, Fig. 4, Fig. 5.

Pilgrimella pilgrimi, Wells and Gingerich, 1983 (in part), p. 122, Fig. 2C–D; Kumar, 1991 (in part), p. 230.

Etymology. Specific epithet is from occidentalis, Latin for west, in honor of Robert M. West, who discovered and described the holotype.

Holotype. H-GSP 1981, mandibles with left p1-m3 and right p4-m3 (Fig. 2P–Q).

Type Locality. H-GSP Locality 62, Ganda Kas Area, Punjab Province, Pakistan.

Formation and Age. Kuldana Formation, Kala Chitta Hills of Northeastern Pakistan, early Lutetian in age (=48 Ma).

Diagnosis. Differs from other anthracobunids in exhibiting the following combination of features: (i) lower molars broad, (ii) lower m3 short, and (iii) angular process of the mandible long but shorter than that of Anthracobune.

Referred Specimens. See Suppl. Info.

Description. The most complete specimen for this species is H-GSP 1981, a left and right mandible not larger than A. wardi (H-GSP 96258 and 96434), but with lower molars much broader than A. wardi. H-GSP 1981 lacks the angular process due to post-mortem damage but it is preserved in H-GSP 96214, a specimen with an erupting m3. In this specimen, the angular process is 80% as long, rostro-caudally, as in A. wardi. The angular process is not preserved in H-GSP 96149, but its root is preserved and the slope thereof indicates that the process is small H-GSP 96149 has extremely worn teeth, but its molars are similar in size to H-GSP 1981 (Fig. S1), premolars and canine are larger and the depth and robusticity of the jaw is much greater than in H-GSP 1981. The wear stage is most consistent with advanced age, and makes it unlikely that the smaller angular process is the result of young age. Eventually this specimen may be shown to pertain to a new species of Obergfellia.

Few upper molars have been discovered for O. occidentalis. H-GSP 538 is a large tooth, and an interstitial facet on its posterior side indicates that it is not an M3. M1 and M2 of P. pilgrimi do not reach this size, and we therefore refer this tooth to P. obergfellii.

Discussion. West [10,93] recognized that his collection of specimens from the Ganda Kas Region of Pakistan contained two species of anthracobunids from the freshwater part of the formation and used the names Anthracobune pilgrimi and Lamnudhania wardi for them. Unfortunately, the type specimen for L. wardi is an isolated trigonid, and pertains to the same species as several large complete lower jaws collected by us (H-GSP 96258 and 96434), and these match upper dentition material referred to Pilgrimella pilgrami (the type of which is an upper molar). Hence a new genus and species name is needed. A specimen described by West, H-GSP 1981, is the most appropriate holotype for this species.

Jozaria Wells and Gingerich, 1983.

Jozaria palustris Wells and Gingerich, 1983.

Discussion. Wells and Gingerich [1] described Jozaria palustris on the basis of a single specimen which shows the diagnostic features of anthracobunids. The lower premolars of this specimen are large compared to the molars, confirming it as distinct from other anthracobunid species and genera.

Phylogenetic Results

 Parsimony analyses were first run to determine the most parsimonious placement of Xenarthra (represented in this analysis by Dasypus) given different placements in placental phylogeny — i.e., as either the sister group either of Afrotheria (the Atlantogenata hypothesis) or of Laurasiatheria + Euarchontoglires (the Exafroplacentalia hypothesis), as this is one of the nodes that was not convincingly resolved by Meredith et al.’s [27] analysis, and continues to be debated in the literature on placental phylogenetics [94]. A placement with Afrotheria was more parsimonious ([3704.5 versus 3716 steps (i.e., constraint A1 versus E1), with 0.0-weighting of ordered multistate characters with intermediate polymorphic states; Fig. S2A versus Fig. S2C) and 5758 versus 5773 steps (A2 versus E2, no weighting of ordered multistate characters with intermediate polymorphic states, Fig. S2B versus Fig. S2D)], and all subsequent alternative constraints accordingly employed an Atlantogenata, rather than an Exafroplacentalia, constraint.

Regardless of whether Atlantogenata or Exafroplacentalia was constrained (assumption sets A1 and A2, and E1 and E2 respectively) anthracobunids and desmostylians were placed as derived stem perissodactyls (Fig. S2). In A1 and E1, desmostylians were joined by Cambytherium and Radinskya as consecutive sister taxa (Fig. S2A and S2C). Anthracobunidae was always monophyletic in A1, A2, E1, and E2, and given the Adams consensus of all trees recovered by these analyses (Fig. 3), 16 character changes emerge as unambiguous synapomorphies of the family (Table S1, e.g., an enlarged p3 paraconid, deep hypoflexids on m2, the presence of two or more cusps on the m3 hypoconulid lobe, and reduction of the P3-4 metacones and metaconules). A placement of Desmostylia outside of Tethytheria and Paenungulata, and within Laurasiatheria, is not unprecedented: in a small number of Asher et al.’s [61] analyses, the desmostylian Paleoparadoxia was placed along the stem lineage leading to Perissodactyla and Cetartiodactyla (see their Table 6). Placements of non-perissodactyl and non-paenungulate fossil taxa were largely stable across all of these analyses, but relationships of stem and crown perissodactyls were not. Bootstrap support along the perissodactyl stem lineage was consistently <50%, but it should be noted that support was also <50% for several clades (e.g., Afroinsectivora, Afrotheria, Paenungulata, Laurasiatheria) that are strongly supported by maximum likelihood and Bayesian analyses of molecular data [27,95–98]. Low support values for several nodes are probably due to dense sampling of incomplete fossil taxa that might decrease stability, but preserve intermediate states that break up long branches [99,100]. Within Afrotheria, embrithopods were always placed as a sister group of Sirenia, while Erthatherium, which has recently been described as a basal proboscidean, never grouped with Proboscidea but rather was placed either as a stem paenungulate (A1 and A2) or as a stem hyraco (E1 and E2). The younger and more derived Phosphatherium was placed as a stem proboscidean in A1 and E1, but as a stem thelytherine in A2.
and E2. The recently described Ocepeia [58] was placed as either a basal atlantogenatan (A1), a stem atlantogenatan (A2), or as a stem paenungulate (E1 and E2).

When anthracobunids were constrained to join Paenungulata and certain multistate characters were ordered (Fig. S3A, Fig. S4A), the group joined Sirenia (along with Desmostylia and Cambaytherium); when all characters were unordered, anthracobunids were placed with Hyracoida (Fig. S5). None of these alternative trees were rejected by non-parametric Templeton tests (Table S4, Table S5, Table S6). Placement with Sirenia required alternative trees were rejected by non-parametric Templeton tests (Fig. S4B). Given this constraint, anthracobunids did not join this desmostylian-sirenia clade, and remained as stem perissodactyls. Constraining Eritherium and Phosphatherium to be stem proboscidians (Fig. S3C, Fig. S4C, Fig. S7B) did not have an effect on the placement of either Anthracobunidae or Desmostylia, both of which formed a clade with Perissodactyla regardless of how characters were weighted. Finally, forcing Cambaytherium to join Anthracobunidae (Figs. S3D and S4D) to the exclusion of hipposorms and tapiromorphs also did not affect the placement of these taxa as perissodactyls.

The Adams consensus of all trees recovered across A1, A2, E1, and E2 (Fig. 3) reveals that two enigmatic Asian taxa, late Paleocene Radinskya [36], and early Eocene Cambaytherium, are consistently situated close to Anthracobunidae as stem perissodactyls. Radinskya has long been an enigmatic figure in the study of perissodactyl origins. The genus was originally identified as a possible phanocorinphid, albeit a "perissodactyl-like" one, by McKenna et al. [36], and was later placed outside of a perissodactyl-paenungulate clade in the phylogenetic analyses of Fischer and Tassy [17]. Both of these studies were undertaken prior to the publication of molecular sequence data that now strongly suggest that "Ungulata" is di- or polyphyletic, and that Paenungulata and Perissodactyla evolved their morphological similarities convergently [101]; Radinskya has not subsequently been included in combined analyses of molecular and morphological data. In our analyses Radinskya was always placed as a perissodactyl, but not in a consistent position relative to other stem and crown perissodactyls -- either as a sister group of desmostylians and Cambaytherium (A1, E1, and E2), or in an unresolved position along the stem lineage of Perissodactyla (A2). The analyses of unordered and unweighted characters recovered hundreds of equally parsimonious trees, the strict consensus of which was poorly resolved, but Radinskya and Cambaytherium occasionally joined Anthracobunidae in some trees.

The placement of Cambaytherium within Perissodactyla is consistent with Bajpai et al.'s [38,91] assessment of the genus. Confusion surrounding the dental similarities that Cambaytherium shares with perissodactyls and anthracobunids [102] is resolved by the placement of cambaytheriids and anthracobunids as closely related sister taxa of crown Perissodactyla, thereby indicating that similarities to tethytheres are entirely due to convergence. Bajpai et al. [38] argued that the middle Eocene European genus Hallensia, which was originally identified as a "condylarth" [50] and later placed within Perissodactyla as either a possible equid [51,103], might be a cambaytheriid. In our analyses Hallensia was usually placed as a stem perissodactyl (A1, E1, E2) or in an unresolved position relative to these taxa (A2). The monophyly of a clade containing Anthracobunidae, Cambaytherium, Hallensia, Radinskya, and "advanced" perissodactyls is supported by 11 unambiguous synapomorphies (Table S2). The clade containing anthracobunids, cambaytheriids, Radinskya, crown Perissodactyla, and Hallensia was reconstructed as having been equivocally of either Asian or European origin (Table S3), while the anthracobunid-desmostyan-hippomorph-tapiriform clade was optimized as having been of Asian origin.

Bone Geometry Results

We quantified the midshaft cross-sectional geometries of limb and rib bones of anthracobunids and other ungulates. Long bone and rib cross-sectional phenotypes are a reliable indicator of vertebrate habitat, with most taxa occupying a shallow-water habitat displaying the greatest amount of bone per cross-section via thickened cortices and/or bone-filled medullary cavities [71,104,105]. In contrast, bones of terrestrial taxa typically display thin cortices and vacant medullary cavities. Bone compactness values, a combined measure of cortical and medullary bone area [72], indicate that Anthracobunia limb bones display values between 0.85–0.96. This range is greater than values observed in a sample of fossil and extant artiodactyls and perissodactyls (0.42–0.83), with the exception of modern Hippopotamus (0.94, 0.96) and Rhinoceros (0.64–0.85), and semi-aquatic pakicetid and rementonocetid Eocene cetaceans (0.93–0.96) (Fig. 4). Similar results were documented in rib elements (Table S7). Stable Isotope Results

We also studied the oxygen and carbon isotope composition of structural carbonate in tooth enamel [75,106] for anthracobunids and coeval taxa from the Early and Middle Eocene of India and Pakistan (Fig. 5, Table S8, Table S9). Mammal fossils sampled from Early Eocene localities (Fig. 5C), including Cambaytherium, spanned a narrow range of δ18O values, and are consistent with occupation of a wet and forested habitat. Enamel δ13C values showed more than 3% range in individual values (~12.4% to ~9.1%), and, when corrected to present-day atmospheric δ13C values [107], suggest foraging in a relatively wet environment. Conversely, taxa sampled from Middle Eocene deposits of Northern Pakistan displayed a much wider range of δ18O values (21 to 27‰) and much higher enamel δ13C values (Fig. 5B,C).

Enamel δ18O values for the anthracobunids Anthracobune pantoldi (23.5±1.2‰), Anthracobune wadi (25.7±1.8‰), and...
Obergfellia occidentalis (24.3%) from the Kuldana Formation fall in between enamel δ18O values for aquatic taxa (archaeocetes, raoellids; 21 to 25%) and terrestrial taxa (Jhagirolophus, 26.8%; undescribed artiodactyl, 27.0 ± 1.0%) (Fig. 5B). These values are suggestive but not conclusive evidence of aquatic habits for these anthracobunids; the small number of terrestrial taxa available from these deposits (n = 2) limits the efficacy of our comparison.

Enamel δ13C values for A. pinfoldi (29.0 ± 0.8%), A. wardi (29.6 ± 0.5%), and O. occidentalis (28.9%) are most similar to values for rhinos, tapirs, and other perissodactyls from these deposits (29.9 to 28.7%), suggesting that like these taxa, anthracobunids browsed on terrestrial C3 foliage. These two groups had much higher enamel δ13C values than freshwater-foraging archaeocetes (214.8 to 29.0%) and showed less variation than artiodactyls (mostly raoellids, 211.4 to −6.9%), which may have had more flexible diets.

Two specimens of A. wardi collected from Middle Eocene deposits of northern India had low enamel δ18O values (21.3% and 21.8%) that approached values for aquatic taxa, but also overlapped with values for terrestrial rhinocerotoids (20.6% to 24.7%) from the same formation. These low enamel δ18O values are more consistent with a freshwater habitat for these individuals, but, again, low sample size complicates differentiating δ18O values for these specimens from δ18O values for taxa assumed to be fully terrestrial.

Discussion

Anthracobunids are Stem Perissodactyls

Anthracobunids have not previously been incorporated into taxonomically broad phylogenetic analyses of morphological data that incorporate the molecular evidence for placental supraordinal relationships. We tested for the possibility that Anthracobunidae and various Laurasian “condylarths” (phenacodontids, louisinids) are not members of Afrotheria by adding a number of living and extinct laurasiatherians to a morphological character matrix that has previously been employed to reconstruct afrotherian phylogeny [19,55,108]. We constrained relationships of extant taxa, based largely on the results of Meredith et al. [27], using the “molecular scaffold” technique proposed by Springer et al. [109]. We also employed several alternative constraints to obtain tree lengths for competing topologies.

Regardless of how ordered multistate characters were weighted, or whether Xenarthra was placed as the sister group of Afrotheria (i.e., the Atlantogenata hypothesis) or of Euarchontoglires + Laurasiatheria (the Exafroplacentalia hypothesis) in the molecular scaffold, parsimony analysis of the morphological data always placed anthracobunids within Laurasiatheria as members of Perissodactyla (Fig. 3). Surprisingly, members of the Order Desmostylia — which, like anthracobunids, have long been placed in Paenungulata — also grouped consistently with laurasiatherian perissodactyls rather than with afrotherian tethytheres, as previously suggested on the basis of similarities in tooth enamel by Ijiri and Kamei [110]. None of these clades were found in more than 50% of the bootstrap replicates, however. Parsimony analysis with all characters unordered and equally weighted consistently placed Anthracobune in Laurasiatheria with Perissodactyla, but the less well-known Obergfellia and Cambyothyrium were “wild-card” taxa that either grouped with Desmostyla and Sirenia (within Afrotheria) or with Perissodactyla (within Laurasiatheria) across 658 equally parsimonious trees.

When continental geography is mapped onto the Adams consensus in Fig. 3, crown and advanced stem perissodactyls (including Cambyothyrium and Radinskya) are optimized as having originated in Asia (Fig. 3), while the perissodactyl stem lineage is of ambiguous (but certainly Laurasian) continental origin. Later
Several studies have identified the early Paleogene Laurasian “condylarths” *Meniscotherium*, *Paschatherium*, *Phenacodus*, and *Teilhardimys* as members of Paenungulata or Macroscelidea [18,60–64]. Some of the authors of these studies have in turn suggested that Afrotheria might not be of Afro-Arabian origin. The reliability of the analyses that place these Laurasian “condylarths” within Afrotheria has been called into question due to concerns that character and taxon sampling has potentially been inadequate for confident supraordinal placement of these and other fossil taxa [69,113]. Our results have an important bearing on this issue, because the matrix analyzed here incorporates denser sampling of taxa (particularly within Afrotheria) than all previous studies. In our more detailed analyses, *Meniscotherium*, *Paschatherium*, *Phenacodus*, and *Teilhardimys* are consistently placed as stem perissodactyls across all assumption sets. This expanded clade of stem and crown perissodactyls was reconstructed as having been of either North American, Asian, or European origin. This biogeographic reconstruction is undoubtedly greatly oversimplified given that numerous allied taxa that were distributed across Laurasia were not included in the analysis, and Carnivora and Artiodactyla are only represented by three taxa. Afrotheria, Paenungulata, Tethytheria, Afroinsectivora, and Afroscordida were reconstructed as having been of Afro-Arabian origin across all assumption sets. Experimental grafting of embrithopod genera from the Eocene of Turkey and Romania [114,115] to the base of Embrithopoda does not alter this biogeographic reconstruction.

Reconstructing the Ancient Habitat and Diet of Anthracobunids

Some early tethytheres are thought to have had a semi-aquatic lifestyle (proboscideans [81,116], desmostylians [117], sirenians [104,118–120]), but no evidence suggests that stem perissodactyls occupied an aquatic habitat. To reconstruct the ancient habitat preferences of anthracobunids, we analyzed bone geometry of the postcranial skeleton as well as stable isotope values within tooth enamel.

We quantified the midshaft cross-sectional geometries of limb and rib bones of anthracobunids and other ungulates. Anthracobunids limb bones displayed bones that were more hyperostotic and therefore more compacted compared to most extant ungulates. Exceptions included extant taxa that are known to frequently swim or wallow in shallow water habitats (i.e., *Hippopotamus* and *Rhinoceros*) [121], and fossil Eocene cetaceans that are thought to be semi-aquatic and also occupy shallow water habitats (i.e., *pikice'id and remingtonocetids*) (Fig. 4). Thus, anthracobunids display a variety of skeletal modifications consistent with taxa that exploit shallow-water habitats, including thickened postcranial elements and widened elements of the autopodium, in addition to large body size.

We also studied the oxygen and carbon isotope composition of structural carbonate in tooth enamel [75,106] for anthracobunids and coeval taxa (Fig. 5). The anthracobunids recovered from the Kuldana formation (*Anthracobune* and *Obergfellia*) displayed enamel δ¹⁸O values suggesting some evidence of aquatic habits, and enamel δ¹³C values showed they fed on land. Anthracobunids recovered from northern India displayed enamel δ¹³C values consistent with occupation of freshwater habitats. Although all sampled anthracobunids may have had some aquatic preferences, stable isotopic evidence alone is inconclusive as there is overlap in range of isotopic values between terrestrial and aquatic taxa.

Taken together, skeletal and isotopic evidence are most consistent with an interpretation of anthracobunids (especially *Anthracobune*) as having had ecological preferences similar to...
those of modern rhinos and tapirs, but not exhibiting the same degree of commitment to aquatic habits as *Hippopotamus* [94,122]. Most rhinos and tapirs have a restricted range near permanent bodies of water in which they frequently wallow and wade [121], and obtain most of their drinking water [94,122]. Modern rhinos may be a good model for the anthracobunid lifestyle as both display thickened limbs and intermediate oxygen isotope values relative to *Hippopotamus* and terrestrial ungulates.

Stable isotopic evidence also showed mammal fossils sampled from Early Eocene localities (Fig. 5C) occupied and foraged within a wet and forested habitat. Conversely, taxa sampled from Middle Eocene deposits of Northern Pakistan (Fig. 5B,C) indicated shifts in the climate toward increased aridity. This climate change was most likely caused by the northward movement of the Indian plate, which pushed these areas out of an equatorial zone of high precipitation in the Middle Eocene [123,124]. Vegetation would have opened up, and shifted to a drier, tropical forest or savanna habitat.

**Conclusions**

Based on new dental, cranial, and postcranial material, our phylogenetic analysis is the first to suggest that anthracobunids are stem members of the laurasiatherian order Perissodactyla, rather than members of the afrotherian clades Tethytheria, Probossicida, or Sirenia. The strictly Asian distribution of anthracobunids is consistent with the isolation of afrotherian and laurasiatherian clades through the early Paleogene [19,113], while the phylogenetic result is consistent with the recent recovery of very primitive basal stem proboscideans such as *Phosphatherium* [125] and *Eritherium* [18], from the early Eocene and Paleocene of Africa. Analyses of postcranial bones and stable isotopes also indicate that anthracobunids were large and lumbering, and suggest at least some taxa spent time in the water similar to modern rhinos, and that all known anthracobunids fed on land. Our results therefore identify an Old World radiation of large, non-cursorial, partly aquatic perissodactyls that convergently came to occupy a basal tethythere-like niche on the northern coast of the Tethys Sea.

One of the more intriguing possibilities raised by our analysis is that the order Desmostylia, which has always been restricted to the Pacific Rim and has never been found in Afro-Arabia, might be aligned with perissodactyls rather than paenungulates, and that this clade might trace its origin back to south Asian anthracobunids, cambaytheres, or both.

This study also provided further resolution as to the placement of Paleocene *Radinskya* [36] [38] and early Eocene *Cambaytherium* as stem perissodactyls. Confusion surrounding dental similarities of *Cambaytherium* with perissodactyls and anthracobunids could be resolved by the placement of cambaytheriids and anthracobunids as closely related sister taxa to crown Perissodactyla, thereby indicating that similarities to tethytheres are entirely due to convergence.

**Supporting Information**

**Figure S1** Mandibles of anthracobunids. (A) *Anthracobune pinfoldi* (HGSP-97106) with p4, m2-3 in lateral view (m3 third lobe is missing). Mandible of *Obergfellia occidentalis* (H-GSP 96149) in (B) lateral view, and (C) superior view. Mandible of a juvenile of *Anthracobune wardi* (H-GSP 30349) with deciduous dp3-m1 in (D) lateral view, and (E) superior view. Scale bar is 1 cm in length.

(PDF)
ordered multistates weighted as 0.5. Constrained topologies: 1) Molecular scaffold alone; 3) Anthracobunidae constrained to join Paenungulata; 4) Desmostylians constrained to join Paenungulata; 5) Eritherium and Phosphatherium constrained to be stem proboscideans (cf. Gheerbrant 2012); and 6) Cambaytherium constrained to join anthracobunids to the exclusion of crown perissodactyls (See Fig. S3 for topologies).

Table S5 Tree lengths for alternative topological hypotheses, number of steps longer than the less constrained topology, and P values from non-parametric Templeton tests (first tree of each tree file only), with steps between ‘fixed’ and ‘polymorphic’ states in ordered multistates weighted as 1.0. Constrained topologies: 1) Molecular scaffold alone; 3) Anthracobunidae constrained to join Paenungulata; 4) Desmostylians constrained to join Paenungulata; 5) Eritherium and Phosphatherium constrained to be stem proboscideans (cf. Gheerbrant 2012); and 6) Cambaytherium constrained to join anthracobunids to the exclusion of crown perissodactyls (See Fig. S4 for topologies).

Table S6 Tree lengths for alternative topological hypotheses, number of steps longer than the less constrained topology, and P values from non-parametric Templeton tests, with all characters unordered and equally weighted. Constrained topologies: 1) Molecular scaffold alone; 3) Anthracobunidae constrained to join Paenungulata; and 5) Eritherium and Phosphatherium constrained to be stem proboscideans (cf. Gheerbrant 2012). (See Fig. S5 for topologies).

Table S7 Taxonomy, specimen number, bone, and bone compactness values for limb and rib bones analyzed in this study.

References


Table S8 Taxonomy, specimen number, tooth identification, and summary statistics of stable isotope values of fossil enamel samples used in this study.

Table S9 Taxonomy, specimen number, tooth identification, and stable isotope values of fossil enamel samples used in this study.

Acknowledgments

The authors thank the reviewers of this manuscript for their constructive comments. Illustrations were provided by Jacqueline Dillard. Assistance in field collection was provided by Dr. A. Friscia and E. Byron. The authors thank Drs. A. Sahni for loan of a cast of *A. wardi* (LUVP 15006), and Drs. B.L. Beatty and D.P. Domning for discussions. Loans of museum specimens were provided by Dr. A. Heinrici and Dr. K.C. Beard (Carnegie Museum of Natural History), and Dr. N. Simmons (American Museum of Natural History). Assistance with CT scans was provided by Dr. S. Ward and S. Usip (NEOMED), B. Labut, L. McCollum (Akron City Hospital), and Dr. J. Maisano and Dr. M. Colbert (University of Texas Computed Tomography facility). G. Styles and Dr. T. Hieronymus are thanked for assistance with photography. Dr. D. Waugh is thanked for comments on this manuscript.

Author Contributions

Conceived and designed the experiments: LNC ERS MTC JGMT. Performed the experiments: LNC ERS MTC. Analyzed the data: LNC ERS. Contributed reagents/materials/analysis tools: LNC MTC SIM SB STH JGMT. Wrote the paper: LNC ERS MTC JGMT.

Table S8 Taxonomy, specimen number, tooth identification, and summary statistics of stable isotope values of fossil enamel samples used in this study.

(PDF)

Table S9 Taxonomy, specimen number, tooth identification, and stable isotope values of fossil enamel samples used in this study.

(PDF)

Table S5 Taxonomy, specimen number, bone, and bone compactness values for limb and rib bones analyzed in this study.

(PDF)

Table S6 Tree lengths for alternative topological hypotheses, number of steps longer than the less constrained topology, and P values from non-parametric Templeton tests, with all characters unordered and equally weighted. Constrained topologies: 1) Molecular scaffold alone; 3) Anthracobunidae constrained to join Paenungulata; and 5) Eritherium and Phosphatherium constrained to be stem proboscideans (cf. Gheerbrant 2012). (See Fig. S5 for topologies).

(PDF)

Table S7 Taxonomy, specimen number, bone, and bone compactness values for limb and rib bones analyzed in this study.

(PDF)


