The Cranial Anatomy of the Miocene Notoungulate *Hegetotherium mirabile* (Notoungulata, Hegetotheriidae) with Preliminary Observations on Diet and Method of Feeding

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Abstract

The skull and mandible of the Miocene hegetotheriine notoungulate *Hegetotherium mirabile* are described. Although conventional models of hegetothere biology propose that these animals filled a lagomorph-like ecological niche, study of the cranial and dental anatomy of *Hegetotherium* suggests that this extinct South American ungulate may have fed by breaking through wood in order to eat xylophagous grubs and other organisms. This mode of life is seen in two extant mammals, the monotypic Malagasy primate *Daubentonia madagascariensis* and diprotodont marsupials of the genus *Dactylopsila.* It has also been proposed as a feeding mechanism for two extinct groups of mammals: the "proteutherian" apatemyids from the Paleogene of Europe and North America, and the enigmatic marsupial *Yalkaparidon* from the early Miocene of Australia. Collectively, these living and extinct taxa have been proposed as mammalian woodpeckers. They are defined by a suite of morphological characteristics, including unusually developed and continually growing incisors, molars adapted to have a constantly sharp edge, exaggerated klinorhynchy, deep zygomatic arches and a shortened snout. *Hegetotherium mirabile* shares almost all characteristics common to the mammalian woodpeckers, although it lacks several features that are likely to be adaptations for an arboreal, nocturnal lifestyle. This suggests that although the feeding techniques of this species were similar to those of the mammalian woodpeckers, *H. mirabile* occupied a diurnal, cursorial niche, feeding on grubs and insects within fallen trees and logs.

Keywords

Convergence, *Hegetotherium*, *Dactylopsila*, *Daubentonia*, apatemyids, klinorhynchy, mammalian woodpecker

Introduction

The Notoungulata, an extinct group of endemic South American ungulates, were the most diverse and successful archaic order of mammals, with at least 13 families and over 140 genera represented in the fossil record (Simpson 1967; Patterson and Pascual 1968; Cifelli 1993; Croft 1999; Croft and Anaya 2006). They filled a wide variety of evolutionary niches in South America during the early and middle Cenozoic, ranging from the gigantic rhinolike toxodonts to the small, rodentlike interatheres. As described by Patterson and Pascual (1968), the notoungulates underwent an early—Late Paleocene and early Eocene—"adaptational dichotomy" between large ungulates and the smaller rodent- and lagomorph-like forms. Later, post-Oligocene, there were four dominant families of notoungulates: toxodontids, interatheriids, mesotheriids and hegetotheriids (Croft and Anaya 2006).

There are two recognized subfamilies of hegetotheriid: the small Pachyrukhinae and the larger Hegetotheriinae. Although they share certain

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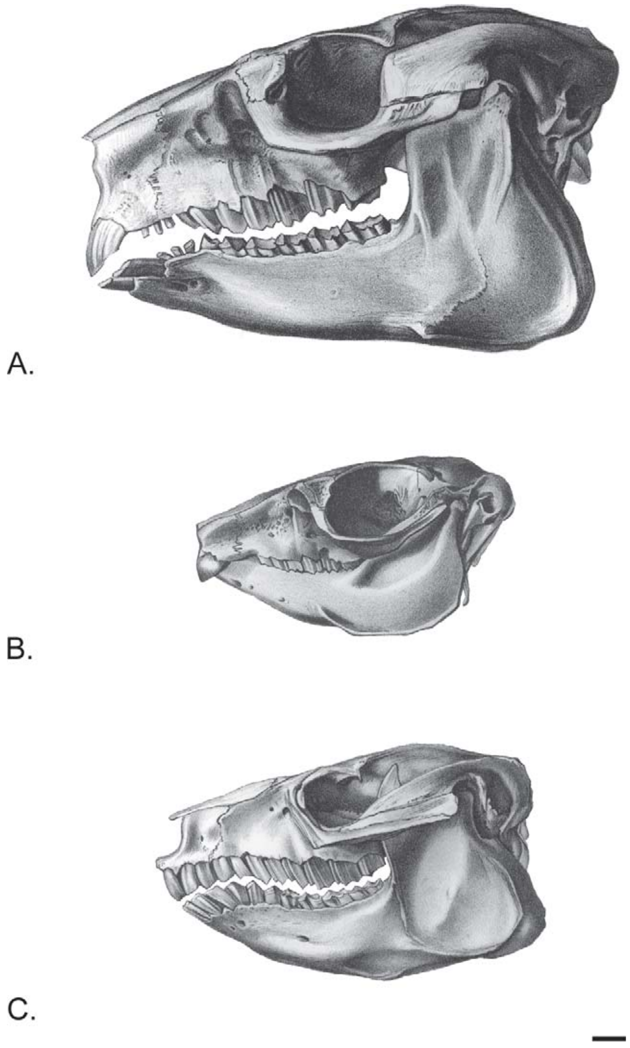

FIGURE 1. Lateral view of the skulls of Miocene notoungulates. **A**, *Hegetotherium mirabile*. **B**, *Pachyrukhos moyani*. **C**, *Protypotherium australe*. Modified from Sinclair 1909. Scale bar equals 10 mm.

similarities with other groups of small to medium-sized notoungulates (Figure 1), such as the mesotheriid typotheres, hegetotheres possess a suite of distinctive morphological synapomorphies (Cifelli 1993; Croft 2000; Croft et al. 2004). These are hypselodont (rodentlike, rootless, and ever-growing) first incisors, premolars and molars; a flattened lingual edge of the molars (which creates a roughly rectangular occlusal surface); the presence of cementum on the roots of the teeth (also present on the crown of *Hegetotherium*); the presence of a deep sulcus on the labial surface of M_1 and M_2; and extended fusion of the tibia and fibula. In hegetotheriines the degree of fusion between the tibia and fibula is much less than in pachyrukhines and the tibia runs parallel to the fibula for much of its length, resulting in a wider distal articular surface (Croft et al. 2004). In addition to these synapomorphic characters, hegetotheres are also characterized, although not distinguished, by a broad and raised zygomatic arch, to which the jugal is entirely restricted; a relatively unspecialized auditory region; and anteroposterial elongation of the basicranium (Simpson 1967).

The distinctive nature of *Hegetotherium* was highlighted in a recent morphometric analysis of notoungulates, which revealed that the taxon occupied an "exclusive" corner of the morphospace separate from its relatives; its feeding methods did not fit well into any classic grazing or browsing niche (Cassini et al. 2011). Hegetotheres have traditionally been compared to rodents and rabbits (e.g., Patterson and Pascual 1968; Simpson 1980; Reguero et al. 2007; Shockey and Anaya 2008). These animals are similar in size, and there are some areas of the postcranium where the convergence in morphology is remarkable; for example, the bowing of the fibula in pachyrukhines closely resembles the condition seen in modern-day leporoids (Sinclair 1909; Croft et al. 2004). The cranial morphology, however, is quite dissimilar in hegetotheres, rodents and rabbits, and the traditional comparison between hegetotheres and these modern groups is based on only superficial similarities. In particular, the morphology of the hypertrophied I^1 in *Hegetotherium*—in which the prognathous upper incisors converge medially onto the midline to form a "pick-axe"-like structure—is very different from the recurved, chisel-like incisors typical of rodents.

The distinctive I^1 morphology of *Hegetotherium* is shared with a small but taxonomically diverse group of otherwise unrelated extant and extinct mammals, including the primate *Daubentonia*, striped possums of the genus *Dactylopsila*, members of the proteutherian family Apatemyidae, and *Yalkaparidon*, a marsupial of uncertain taxonomic affinities from the early Miocene Riversleigh deposits of Australia. These animals, which have been characterized as "mammalian woodpeckers," use their massive incisors to break into wood in search of wood-boring (xylophagous) grubs and other organisms (Cartmill 1976; Beck 2009). Incisor morphology and the presence of other key features identified by Cartmill (1976) and Beck (2009) to be typical of mammalian woodpeckers support the hypothesis that *Hegetotherium* also adopted this mode of feeding, rather than conforming to the established model of a rodentlike herbivore. The few mammalian woodpecker features that *Hegetotherium* lacks are associated with nocturnal activity and an arboreal mode of life, rather than with wood boring. Therefore, *Hegetotherium* may have been ground-dwelling and diurnal, possibly using its teeth to break into fallen logs. Fallen trees and logs provide rich habitat to a variety of species, and animals including salamanders and multiple species of avian woodpeckers feed on wood-boring insects within (e.g., Maser and Trappe 1984; Jackson et al. 2002). The unusual cranial features of *Hegetotherium mirabile* suggest that it filled a similar niche, feeding on wood-boring insects in fallen trees and logs.

Institutional abbreviations are as follows: AMNH, Paleontology Collection, American Museum of Natural History; AMNH M, Mammalogy Collection, American Museum of Natural History; YPM MAM, Mammalogy Collection, Peabody Museum of Natural History, Yale University; YPM VP, Vertebrate Paleontology Collection, Yale Peabody Museum; YPM VPPU, Vertebrate Paleontology (Princeton University) Collection, Yale Peabody Museum.

Materials and Methods

The description of the hegeotheriine cranium is principally based on YPM VPPU 015542, a substantially complete skull and lower jaw of *Hegetotherium mirabile*, with associated postcranial elements from the Miocene Santa Cruz formation of Argentina. Observations were supplemented with reference to other specimens of *Hegetotherium* in the collections of the Peabody Museum of Natural History, Yale University, in New Haven, Connecticut, USA (YPM VPPU 015505, YPM VPPU 015200, YPM VPPU 015298) and the American Museum of Natural History in New York, New York, USA (AMNH 9223, AMNH 9159). Comparisons were made with crania from other notoungulate taxa, including the hegeotheriine hegetotheres *Prohegetotherium caretti* (YPM VPPU 021279, YPM VPPU 021880, YPM VPPU 021882) and *Sallatherium altiplanense* (published description in Reguero and Cerdeño 2005); the pachyrukhine hegetothere *Pachyrukhos moyani* (YPM VPPU 015743, AMNH 9219, AMNH 9525, AMNH 29605, AMNH 29570); the mesotheriid *Trachytherus mendocencis* (YPM VPPU 020687, YPM VPPU 021925, YPM VPPU 021927); the archaeohyracids *Archaeohyrax suniensis* (YPM VPPU 023701, supplemented by the published description in Billet et al. 2009) and *Archaeohyrax patagonicus* (published description in Billet et al. 2009); and the interatheriids *Interatherium robustum* (YPM VPPU 015296, AMNH 9165, AMNH 9483, AMNH 9154, AMNH 9284), *Interatherium excavatum* (YPM VPPU 015043), *Protypotherium praecutilum* (YPM VPPU 015650) and *Protypotherium australe* (AMNH 9565, AMNH 9286, AMNH 9226). Specimens of apatemyid examined included *Apatemys bellulus* (YPM VP 013513), *Labidolemus soricoides* (YMP VPPU 020614) and *Apatemys rodens* (YPM VP 023476), supplemented by Scott and Jepson's (1936) published description of the cranium of *Sinclairella dakotensis* (YPM VPPU 013585—now lost) and the published description of the crania of *Labidolemur kayi* by Silcox et al. (2010). Extant taxa examined were *Daubentonia madagascariensis* (YPM MAM 006801) and *Dactylopsila trivirgata* (AMNH M 105939). Comparisons were also made with published descriptions of the cranium of *Yalkaparidon* (Archer et al. 1988; Beck 2009). Measurements were taken from specimens using a pair of vernier calipers. Klinorhynchy was measured as the angle between the clivus and the palate, following the methodology of Cartmill (1976). Dental terminology follows Cifelli (1993).

Description of the Skull of *Hegetotherium mirabile*

Cranium

The cranium of *Hegetotherium mirabile* was described in detail by Sinclair (1909), and only the main points will be revisited here. YPM VPPU 015542 shows minimal distortion, apart from possible depression or crushing of the nasal bones into the nasal cavity. The maxilla protrudes above the plane of the nasals on either side, creating slight ridges on the upper edges of the snout (Figure 2). Such ridges were not visible in the other specimens of hegetotheres examined, suggesting that they may have been created by postmortem processes rather than being part of the original anatomy. The skull is flattened dorsoventrally and is bent downward so that the ventral–rostral end of the snout is approximately 35 to 40 mm lower than the plane of the cranial base. In profile, the dorsal surface of the cranium curves gently from the rostrum to the occiput. As noted by Sinclair (1909), the braincase is proportionately wider than *Protypotherium* and *Interatherium*, although less so than *Pachyrukhos* (for measurements of the skull, refer to Table 1).

The premaxilla is heavy and short (Sinclair 1909), with no ascending process and little or no nasal retraction, and the nasals are elongated anteroposteriorly. In contrast to the condition seen in *Pachyrukhos,* the rostrum of *Hegetotherium* is proportionately short and deep, and does not taper anteriorly (Figure 3). In YPM VPPU 015542, the maxilla appears to be pinched dorsally when viewed from a rostral aspect (see Figure 2). However, other specimens studied had no such pinching, which suggests that this was due to postmortem forces (similar to the nasal shifting described above). The curving line of the alveoli of the molars and premolars forms the ventral margin of a shallow maxilliary fossa.

The frontals are flared along their lateral margins, where they form the dorsal margins of the orbits. Medially they are flattened and have a slight posterior tilt downward to the frontal–parietal suture. Beyond this, the parietals form a shallow convex dome over the braincase, cresting at the parietal–supraoccipital suture. Farther along the dorsal surface of the cranium dips to the posterior margin of the occiput. The midline of the skull is marked by a very shallow crest. The parietal crests are also shallow, fusing far back on the skull to form a weakly developed sagittal crest.

The anterior base of the zygomatic arch is expanded to form a zygomatic plate analogous to that seen in rodents, which is formed from the jugal and the zygomatic process of the maxilla. The anterior and ventral margins of the orbit are greatly thickened, with the large, wedge-shaped lacrimal making a major contribution to the anterodorsal margin. A well-developed postorbital process of the frontal is present, which closely approaches, but does not fuse with, an equivalent structure on the squamosal portion of the zygomatic arch; this is in contrast to the condition seen in *Pachyrukhos*, where the postorbital process is extremely small. Posterior to the orbit, the zygomatic arch is greatly deepened and composed primarily of the squamosal, with the jugal forming the ventral margin. This structure continues back almost as far as the occiput as a vertical bony lamella, inclining medially to enclose a deep temporal fossa and curving medially toward the midline of the skull. The ventral margin of this lamella is deeply incised by the glenoid fossa.

The palate is not flat; rather, it is somewhat concave so that the snout is deeper at the margins than along the midline. The pterygoid processes are expanded and thickened, and have

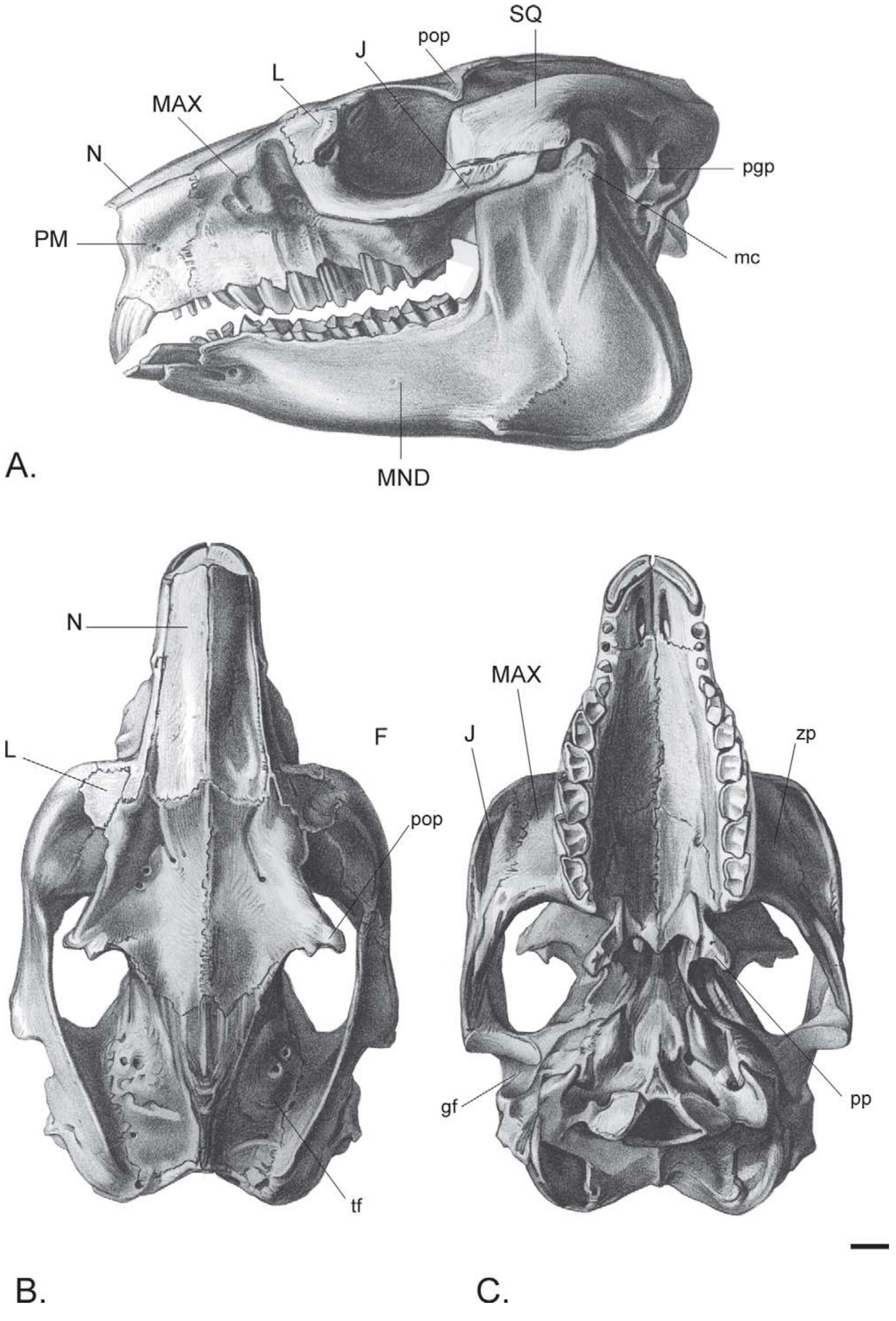

FIGURE 2. Skull of *Hegetotherium mirabile*. **A**, Lateral view. **B**, Dorsal view. **C**, Ventral view. *Abbreviations:* F, frontal; gf, glenoid fossa; J, jugal; L, lacrimal; MAX, maxilla; mc, mandibular condyle; MND, mandible; N, nasal; pgp, postglenoid process of squamosal; PM, premaxilla; pop, postorbital process of frontal; pp, pterygoid process; SQ, squamosal; tf, temporal fossa; zp, zygomatic plate. Modified from Sinclair 1909. Scale bar equals 10 mm.

TABLE 1. Skeletal data for specimens examined. *Hegetotherium mirabile*: YPM VPPU 155342; *Protypotherium praerutilum*: YPM VPPU 015650; *Pachyrukhos moyani*: YPM VPPU 015743. Measurements are in millimeters. N/A indicates that this cranial feature could not be measured, because of damage or incomplete preservation.

	Hegetotherium mirabile	***Protypotherium praerutilum***	***Pachyrukhos moyani***
Skull height (measured from anterior end of cranial base)	40.1	32.0	25.9
Skull length (from median of incisive border to median of occipital crest (Riggs and Patterson 1935)	112.0	89.8	76.0
Skull width (across postorbital processes)	72.2	55.9	N/A
Skull width (across median of anterior root of zygomatic arch)	66.0	51.2	52.0
Skull width (across anterior border of glenoid fossa)	74.0	59.0	N/A
Rostrum length, dorsal (from median of anterior root of zygomatic arch to anterior end of nasals)	47.0	40.1	37.5
Palate length (median line)	61.2	54.2	51.0
Rostrum height, posterior (from anterior root of zygomatic arch to ventral edge of M^2)	42.0	33.5	26.0
Rostrum height, anterior (excluding teeth if no diastemata present)	30.1	26.0	15.5
Breadth of tooth row, posterior (between radial edges of M^3s)	39.1	32.8	28.0
Breadth of tooth row, anterior (just beyond taper after P^2)	28.0	25.0	18.0
Breadth of rostrum, dorsal, posterior (between point just anterior to roots of zygomatic arches)	31.2	28.5	21.0
Breadth of rostrum, dorsal, anterior	22.0	18.1	11.9
Depth of posterior portion of zygomatic arch, maximum	23.7	16.1	N/A
Length of zygomatic arch (from anterior root to median of glenoid fossa)	62.2	46.8	43.0
Angular process of the mandible (extent to which it extends beyond the vertical line through the mandibular condyle)	30.5	N/A	N/A
Mandible length (excluding incisors)	130.0	N/A	N/A
Anterior root of zygomatic arch length	37.5	23.5	26.5
Klinorhynchy angle (measured between clivus and palate)	N/A	Negligible	N/A
Incisor length (from median of emergence point to tip)	19.9	9.9	15.9
Horizontal distance between tip of incisors and vertical plane at anterior end of premaxilla	13.0	Recurved	7.9

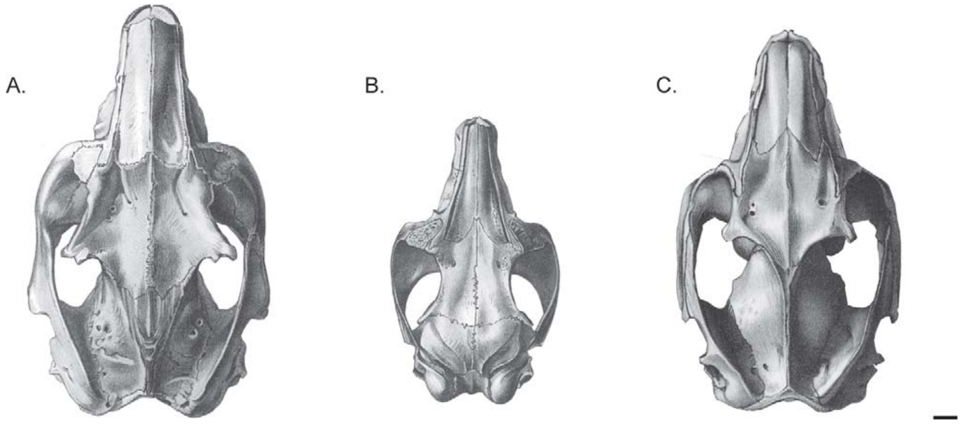

Figure 3. Dorsal view of the skulls. **A,** *Hegetotherium mirabile*. **B,** *Pachyrukhos moyani*. **C,** *Protypotherium australe*. Modified from Sinclair 1909. Scale bar equals 10 mm.

fused with the palatine. The glenoid fossa is deep and concave, and encloses the mandibular condyle anteriorly, medially and posteriorly but still allows for vertical movement of the mandible. The post-tympanic–paraoccipital processes appear to be relatively robust based on the partially complete examples on several specimens.

Mandible

The angular process of the mandible of *Hegetotherium* extends far beyond the mandibular condyle (Gregory 1920). The coronoid process is incomplete in YPM VPPU 015542, but seems to have been quite short, extending only slightly higher than the condyle, which is expanded mesially and laterally. The anterior portion of the condyle is convex and smoothly rounded, whereas the posterior portion has a shallow concavity. The condyle tapers down to a smooth, slightly convex medial surface; the radial surface is marked by shallow fossae and ridges marking the attachment points for the masseter. One such ridge frames the ventral edge, and another originates at the condyle, is directed arteroventrally and disappears in the middle of the angular process on the mandible. The mandible is vertically oriented, with little radial curvature.

Dentition

A remarkable feature of *Hegetotherium mirabile* is the morphology of I^1 (Figure 4), which is massive, curved laterally and enlarged, and has enamel that is restricted to its outer margin, creating a sharp, narrow cutting edge. In contrast to the "chisel-like" I^1 seen in rodents, in which the tooth is recurved, I^1 in *Hegetotherium* is prognathous (projecting at a 45° angle away from the skull), is implanted obliquely and, when viewed rostrally, meets the opposing I^1 to form a point, with the cutting edges positioned along the lateral margins. *Hegetotherium* shows hypselodonty, a derivative of hyposodonty (columnar teeth), in which the teeth are rootless and continue to grow throughout the animal's life (Sinclair 1909; Croft et al. 2004; Billet et al. 2009). I^2 and I^3 are shrunken, peglike and cylindrical with short gaps between each; the third incisor is rooted in the suture between the premaxilla and maxilla. C is peglike, only slightly larger than $I^{2–3}$, angled posteroventrally and similar in morphology to $I^{2–3}$ (see Figure 2). The effect of this reduction of $I^{2–3}$ and C is to create a functional diastema between I^1 and P^1 (the significance of this is discussed below). The premolars and molars are columnar and have enamel that is confined to the outer edge. P^1 is cylindrical, concave posterointernally and heavily imbricate. P^2 is triangular, with the base on the lingual edge; the buccal edge has a single narrow, shallow sulcus at the tip of the triangle. The characteristics of P^3 to M^3 were described by Cifelli (1993). The teeth are all similar in morphology, being (i) roughly rectangular in occlusal view, longer posteroanteriorly than laterally, with a buccal edge that is slightly longer than the lingual edge; (ii) heavily imbricate; (iii) bicuspid, with well-defined paracone and metacone on the

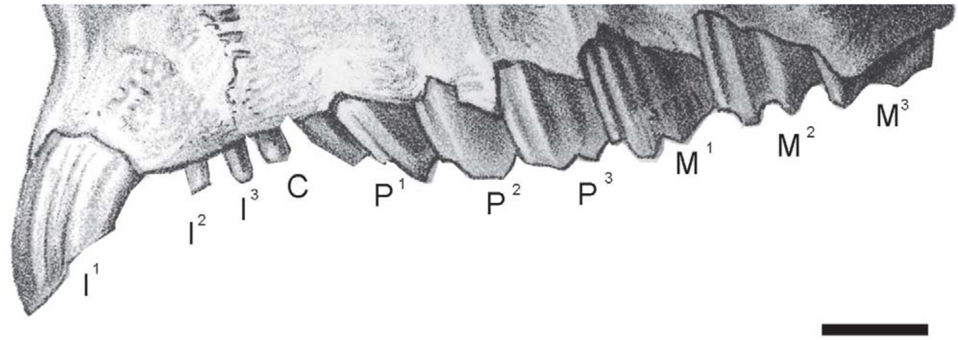

FIGURE 4. Lateral view of upper left dentition of *Hegetotherium* mirabile, showing hypertrophy of I^1. *Abbreviations*: C, canine; I, incisor; M, molar; P, premolar. Modified from Sinclair 1909. Scale bar equals 10 mm.

buccal margin from which lateral lophs emanate; (iv) encased in a thick layer of cementum; (v) without plications of the ectoloph or other complex features on the crowns; (vi) smooth, worn and without plication or cusps on the lingual margin (except for M^3, which has a single lingual plication across from the paracone); (vii) highly emarginated on the buccal surface, with shallow sulci; and (viii) without fossettes. Characters (vi), (vii) and (viii) are diagnostic of the Hegetotheriidae (Cifelli 1993). Characteristic (i) is typical of early Hegetotheriids, whereas later species had molars with a narrower posterior edge of the occlusal surface (Croft et al. 2004). The dental arcade, when viewed laterally, roughly forms a straight line. The paracone is more prominent than the metacone in M^3, they are roughly equal in M^2, and the metacone is prominent in M^1.

I_{1-2} are large and procumbent but do not have the extreme hypertrophy seen in I^1; the two teeth provide a combined occlusal surface for the enlarged I^1. I_3, C and P_1 are small and cylindrical, with P_1 slightly larger than the canine and anteriorly directed. The root of the lower canine is labial to the tooth row, a characteristic that differentiates *Hegetotherium* from the pachyrukhines. P_2 is roughly cylindrical, has a single lingual sulcus, and is oriented posterolabially. P_3–M_3 are fully lophate and imbricate, with overlapping posterointernal corners. P_3–M_2 are bilobate, with deep labial sulci separating the trigonid from the slightly larger talonid, and M_3 is trilobate, with the demarcation between the anterior two lobes consisting of a shallow sulci. P_3–M_3 have a salient and straight lingual margin that is taller than the buccal margin, a single shallow lingual sulci located posteriorly, a taller metalophid than hypolophid, and a protoconid that is more defined than the hypoconid (Patterson 1934; Cifelli 1993). Each of P_2–M_2 has two cusps on the lingual margin, between which is a broad shallow concavity (Sinclair 1909) spanning most of its upper edge, whereas M_3 has three cusps on the lingual margin. The relative wear of the entoconid and metaconid differs among individuals; in some, the metaconid persists in more worn specimens and the entoconid disappears, whereas in others the opposite is true. M_2 has a lingual talonid sulcus, which is shallow in some specimens and well defined in others; this characteristic is widely varied even among specimens of *Hegetotherium* (Croft et al. 2004). As in the upper cheek teeth, all of the lower cheek teeth lack fossettes.

Discussion

Mammalian Woodpecker Characteristics in Hegetotherium

The most striking feature of *Hegetotherium mirabile* is its massive, hypertrophied and prognathous I^1. Similar development of the anterior incisors is seen in a temporally and taxonomically diverse group of mammals that were defined by Cartmill (1976) as "mammalian woodpeckers." Cartmill proposed that in isolated areas where no avian woodpecker exists, mammalian "woodpeckers" fill that niche. He indentified two genera of extant mammal—striped possums of the genus *Dactylopsila* and the nocturnal lemur *Daubentonia*—that fulfill this role in the forests of Australasia and Madagascar, respectively, two regions where avian woodpeckers are absent.

Both groups of mammal feed by tapping and sniffing infested branches and trunks to locate prey, tearing off bark and wood with their enlarged incisors, and inserting an elongated finger into exposed tunnels to snare burrowing larvae (Cartmill 1976). Although only distantly related taxonomically, the two genera share a set of common cranial characteristics that have evolved to facilitate wood boring and reduce the bending forces on the snout brought about by the projected incisors and downward bent facial structure. As Cartmill noted (1976:664), "the amount of force that can be exerted in biting is limited by the capacity of the facial skeleton to withstand these bending stresses."

Koenigswald and Schierning (1987) proposed that the apatemyids, a group of archaic "proteutherian" mammals that lived in Europe and North America during the Paleogene, might be a third group of mammalian woodpeckers. Studies of postcranial material of the Eocene apatemyid *Heterohyus* revealed that, in addition to sharing some of the craniodental features of *Dactylopsila* and *Daubentonia*, the animal was arboreal and also showed extreme elongation of digits II and III (Koenigswald and Schierning 1987). Beck (2009) added a fourth candidate to the list of mammalian woodpeckers with *Yalkaparidon*, a marsupial of enigmatic taxonomic affinities from the early Miocene deposits of Riversleigh, Australia. Although no postcranial material of *Yalkaparidon* is known, it shares many of the craniodental adaptations of the other three taxa. Beck also added characteristics to Cartmill's original list of craniodental characters of mammalian woodpeckers (several are included below).

A synthesis of the relevant characteristics produces the following list: (1) large, forward-projecting incisors; (2) hyposelodont incisors; (3) incisors enameled solely on anterolabial face; (4) procumbent lower incisors; (5) postincisive diastemata; (6) Hunter-Schreger bands (a feature that strengthens enamel); (7) short, narrow dental arcade; (8) self-sharpening postincisive dentition adapted for slicing; (9) tall, anteroposteriorly shortened rostrum; (10) zygomatic arch extended dorsoventrally; (11) tall anterior root of zygomatic arch; (12) large, planar glenoid fossa; (13) reduced postglenoid process; (14) posteriorly extensive pterygoid crests; and (15) klinorhynchy (the distribution of these characters is summarized in Table 2).

Several characteristics chosen by Beck and Cartmill were not included in this study, including wide interorbital breadth and tall braincase, because they were judged to be adaptations to a specifically arboreal and nocturnal lifestyle, not necessarily adaptations related to a wood-boring lifestyle. It is likely that *Daubentonia* and *Dactylopsila* share these characteristics because both taxa are arboreal and nocturnal. Arboreal creatures require excellent depth perception to successfully navigate through the forest canopy, hence the wide interorbital breadth indicative of binocular vision, and nocturnal creatures often have large eyes. Study of the postcranial skeleton of hegetotheres suggests that the group was adapted to a cursorial, saltational mode of locomotion (e.g., Sinclair 1909; Patterson and Pascaul 1968), which seems to be in conflict with the woodpecker analogy. However, this apparent conflict can be resolved by realizing that fallen trees and logs also provide a wealth of grubs and other orgamisms. Thus *Hegetotherium* may have fed by chiseling into and prying wood from fallen trunks rather than from standing trees. Analysis of the cranial anatomy of *Hegetotherium* presents a strong argument in support of this hypothesis.

In the expanded character set for mammalian woodpeckers, *Hegetotherium* shows the upper incisor characters (1) through (3). It has a large, projecting, hypselodont I^1, which creates a beaklike projection that aids in boring through wood to get at the grubs beneath. The teeth have enamel on the outer surface and grow throughout the animal's lifetime, therefore the incisors remain sharp, are resistant to wear, and form a chisel-shaped tip over time. These incisors are thus uniquely suited to boring through wood, a highly abrasive and tough material. Character (4), procumbent lower incisors, is present in *Hegetotherium* and the other mammalian woodpeckers, with the exception of *Daubentonia* (in which the incisors are almost vertical). Once again, the functional importance of this characteristic lies in creating a beaklike projection; the lower incisors must be relatively procumbent and extended to occlude with the greatly hypertrophied upper incisors. Character (5), a postincisor diastema, is not present in *H. mirabile.* However, the postincisor and pre-cheek teeth of *H. mirabile* are all shrunken and peglike, and are thus functionally similar to full diastemata, similarly to the condition

TABLE 2. Characteristics of mammalian woodpeckers, with information gathered from museum specimens and published descriptions. *Hegetotherium mirabile:* YPM VPPU 015542, YPM VPPU 015505, YPM VPPU 015200, YPM VPPU 015298, AMNH 9223, AMNH 9159; *Dactylopsila trivirgata:* AMNH 105939 (Cartmill 1976; Beck 2009); *Daubentonia madagascariensis:* YPM MAM 000680 (Cartmill 1976; Beck 2009); *Yalkaparidon* (Beck 2009); Apatemyids: YPM VP 013513, YPM VPPU 020614, YPM 023476 (Koenigswald and Schierning 1987; Koenigswald et al. 2005; Silcox et al. 2010); *Sinclairella dakotensis:* YPM VPPU 013585 (now lost) (Scott and Jepsen 1936). *Abbreviations:* N, character absent; Y, character present; ?, character state not known.

	Hegetotherium mirabile	***Dactylopsila trivirgata***	***Daubentonia madagascariensis***	***Yalkaparidon***	**Apatemyidae (excluding *S. dakotensis*)**	***Sinclairella dakotensis***
I^1 enlarged and forward projecting	Y	Y	Y	Y	Y	Y
Hyposelodont incisors	Y	N	Y	Y	N	N
Incisors enameled solely on anterolabial face	Y	Y	Y	Y	Y	N
I_1 procumbent	Y	Y	N	Y	Y	Y
Postincisive diastemata	Y	N	Y	Y	N	N
Hunter-Schreger bands	?	?	?	N	?	?
Short, narrow dental arcade	Y	Y	Y	Y	Y	Y
Self-sharpening postincisive dentition adapted for slicing	Y	Y	N	Y	N	N
Tall, anteroposteriorly short rostrum	Y	Y	Y	Y	Y	Y
Zygomatic arch extended dorsoventrally	Y	Y	Y	Y	Y	Y
Tall anterior root of zygomatic arch	Y	Y	Y	N	Y	Y
Large, planar glenoid fossa	N	Y	Y	Y	Y	Y
Reduced postglenoid process	N	Y	Y	Y	Y	Y
Posteriorly extensive pterygoid crests	Y	Y	Y	Y	Y	Y
Klinorhynchy	Y	Y	Y	Y?	Y	Y

seen in *Yalkaparidon* (Beck 2009). Diastema or partial diastema may allow fragments of bark or wood to be expelled rather than swallowed during feeding (Beck 2009). Confirmation of character (6), Hunter-Schreger bands, requires studies of enamel microstructure, which have not yet been performed on *Hegetotherium.* Character (8), self-sharpening post-incisive dentition, is noticeably present in *Hegetotherium*. In contrast to lagomorphs and rodents, which have flattened molars adapted for grinding, *Hegetotherium* has molars adapted for slicing: the upper molars have pronounced cingulae of enamel on the labial face, and the lower molars on the lingual face, which creates precise occlusion and a self-sharpening slicing edge. This morphology is important for the mastication of soft-bodied, xylophagous insect larvae. Characters (9) through (11) are

TABLE 3. Measurements for *Hegetototherium mirabile* (YPM VPPU 155342, AMNH 9223, AMNH 9159) and for *Pachyrukhos moyani* (YPM VPPU 015743, AMNH 9219, AMNH 9525). Rostrum height measurements could not be taken for *Hegetotherium mirabile* (AMNH 9159) and *Pachyrukhos moyani* (AMNH 9525). N/A indicates that measurement could not be taken, because of damage or incomplete preservation.

	Rostrum length (percentage of total skull length)	**Rostrum height (average of two measurements, percentage of total skull height)**	**Percentage decrease in rostrum breadth (posterior to anterior)**
Hegetotherium mirabile			
YPM VPPU 155342	42.0%	90.0%	29.1%
AMNH 9223	38.0	84.4	27.4
AMNH 9159	41.9	N/A	31.1
Pachyrukhos moyani			
YPM VPPU 015743	49.3	80.1	43.0
AMNH 9219	44.4	71.3	30.0
AMNH 9525	47.0	N/A	33.4
Average			
Hegetotherium mirabile	40.4	87.0	29.2
Pachyrukhos moyani	46.9	75.7	35.4

associated with reducing the bending forces on the rostrum, as is character (15), klinorhynchy. A short and thick snout is characteristic of animals that show klinorhynchy, since a bite taken with the incisors results in heightened forces perpendicular to the plane of the nasal, which bends the rostrum (Cartmill 1976). This pressure can be counteracted by having a shorter, denser snout, which provides a biomechanical foundation for the unusual skull structure of *Hegetotherium* and the other mammalian woodpeckers. A high anterior zygomatic root, which is pronounced in *Hegetotherium*, can also effectively counter immense pressures; as Cartmill (1976) shows, the forces applied to the rostrum tend to push the lacrimal back and shift the molar alveoli forward. Having an anteriorly high zygomatic arch creates a thick power arm to resist that torsion. In addition, dense and extensive pterygoid processes (14), as in *Hegetotherium*, absorb the force of a strong bite (Cartmill 1976). Characters (12) and (13), large planar glenoid fossa and reduced postglenoid process, are not as pronounced in *Hegetotherium* as in some of the other mammalian woodpeckers. However, the peculiar posteroventral orientation of the postglenoid process allows for different and freer movement than that of close relatives of *Hegetotherium.* This unusual orientation may have been an adaptation to align the motion of the jaw with the downward-bent snout to create a perpendicular (and thus, maximum) force of occlusion.

Hegetotherium has a much greater degree of klinorhynchy than related species (for a summary of character (15), klinorhynchy, see Table 3). Although klinorhynchy is not always a functional adaptation for wood boring (e.g., DuBrul 1950; Satoh and Iwaku 2008), it is present in all known mammalian woodpeckers. Cartmill (1976) offers a detailed and compelling explanation for the functional importance of a downward-facing snout, which provides resistance to bending pressure. In addition to the characteristics described by Cartmill, *Hegetotherium* has other adaptations that may help absorb forces on the skull, such as the postorbital protrusions and a keystone-shaped lacrimal (Gregory 1920). Further, *Hegetotherium* displays clear evidence of a powerful, elongated masseter muscle, reflected by the deep grooves under and behind its zygomatic arches and the expanded portion of the angular section of the mandible (Gregory 1920). This allows for a more powerful bite, a necessary ability for chipping and prying apart wood.

Most mammalian woodpeckers have planar glenoid fossa and a reduced postglenoid process, characters not shared by *Hegetotherium*. However, the postglenoid process of *Hegetotherium* differs from that of the typotheres in one notable way: it angles posteroventrally, rather than anteroventrally. The difference becomes even more noticeable when one accounts for the klinorhynchy of *Hegetotherium* by comparing the skulls in such a way that the cranial bases are aligned on the same horizontal plane. The functional significance of this difference is that *Hegetotherium* had more freedom of jaw movement. As noted by Sinclair (1909), rodents often have anteroposteriorly elongated mandibular condyles and glenoid fossae aligned so the jaw can move backward and forward; by contrast, typotheres have circular condyles and a flattened glenoid surface, allowing for predominantly lateral movement of the mandible. The sloping anterior margin of the glenoid fossa suggests that the jaw of *Hegetotherium* may have been able to move in a different manner from other typotheres. Also, klinorhynchy changes the slope of the occlusal plane, and this slope is approximately perpendicular to the plane of the anterior margin of the glenoid fossa. This perpendicularity may have allowed for the maximum force to be delivered per bite, so that *Hegetotherium* could puncture the tough shells of wood-dwelling organisms (Beck 2009), or perhaps it provided for some sort of slicing movement as described above. In summary, the remarkable convergence of cranial characters between *Hegetotherium* and the mammalian woodpeckers—with the exception of arboreal characteristics—suggests that *Hegetotherium* fed by breaking through wood of fallen trees and logs.

Additional Evidence for Wood Boring

An interesting addition to these characteristics is the hypselodonty of the cheek teeth of *Hegetotherium*. South American notoungulates were possibly the earliest grazers to develop hypsodont molars; this tooth morphology first appears in South American groups in the late Eocene and Early Oligocene, 36 to 32 million years ago, around 10 to 15 million years earlier than ungulates on any other continent. The trait evolved independently in four or more clades and ultimately led to hypselodont dentitions (Croft and Weinstein 2008). The fact that this character developed independently in several clades, and almost simultaneously, is strongly supportive of some sort of common environmental causal factor (Townsend and Croft 2008). This may imply that the first grasslands appeared in South America, but some argue that notoungulates were simply "precocious" in their acquisition of hyposodonty and that grasslands developed elsewhere simultaneously, with other ungulates taking longer to develop efficient dental structures (Croft and Weinstein 2008; Billet et al. 2009). The ecological paradigm for hyposodonty has generally been grazing accompanied by open habitat feeding (e.g., Patterson and Pascual 1968; Flynn and Wyss 1998), but this has been challenged by recent studies using carbon isotopes (Macfadden et al. 1994; Croft and Weinstein 2008; Townsend and Croft 2008). A more accurate and generalized inference of hypsodonty is that it evolves as an adaptation to counter long-term wear on the tooth due to the presence of abrasive material in the diet (Williams and Kay 2001; MacFadden 2006; Croft and Weinstein 2008; Townsend and Croft 2008; Billet et al. 2009). The nature of this abrasive varies; examples include grass, which because of its high silica content must be chewed extensively to facilitate digestion (Williams and Kay 2001), or "exogenous abrasive particles," such as dust, dirt or ash (Healy and Ludwig 1965; Kay and Covert 1983; Madden 1999). For example, the amount of dirt consumed during feeding may be as significant a factor in the evolution of hypsodonty in grazers as the abrasiveness of the vegetation on which they are feeding (Healy and Ludwig 1965; Damuth and Janis 2011) Thus, hyposodonty in *Hegetotherium* does not preclude a "woodpecker"-type diet; it may be an evolutionary relic from a grazing ancestor that was "co-opted" to resist abrasion from fragments of wood or bark in its diet. Additionally, *Hegetotherium* shows hypselodonty, which is an even more effective and specialized version of hyposodonty in which the teeth are rootless and ever-growing.

Co-option of the dentition of a grazing precursor may explain another difference between the known or postulated mammalian woodpeckers and *Hegetotherium*. Whereas both groups have procumbent lower incisors, those of the mammalian woodpeckers are also strongly recurved, forming a beaklike structure as they occlude with the I^1 pair. This difference may be a reflection of ancestry—whereas the phylogenetic affinities of both *Yalkaparidon* and the apatemyids remain cryptic, both *Dactylopsila* and *Daubentonia* form part of larger evolutionary radiations (petauroid marsupials and strepsirrhine primates) that are dominated by specialist browsers and frugivores. By contrast, the somewhat flattened lower incisors of *Hegetotherium* may reflect ancestors that cropped vegetation.

Non-gliriform Morphology

Traditionally, hegetotheres have been characterized as ecological analogues of lagomorphs and rodents. In fact, the feeding mechanism of *Hegetotherium mirabile*, at least, is likely to have been very different from that of the extant Glires. This can be seen by comparing the mastication of *H. mirabile* to that of lagomorphs and rodents. Although the first incisors of *Hegetotherium* and the Glires both show hypertrophy, they are morphologically and functionally very different. In the Glires, these teeth are recurved; in *Hegetotherium* they are prognathous, suggesting a picklike function as opposed to the chiseling or gnawing action seen in rodents. The cheek teeth of gliriform taxa have flattened occlusal surfaces, suitable for grinding abrasive plant material. By contrast, hegetotheres have a hard enamel layer on the buccal face of the teeth, which forms an edge more suitable for slicing. This disparity in masticatory function is reflected in the structure of the glenoid fossa and its articulation with the mandible. As compared with the typotheres and *Hegetotherium*, rodents and lagomorphs have a poorly developed postglenoid process, and many have anteroposteriorly elongated mandibular condyles (Ellerman 1940). This allows for lateral movement of the jaw; in contrast, the structure of these elements in *Hegetotherium* completely blocks lateral movement of any kind.

The alignment of the masseter in *Hegetotherium* resembles that seen in sciurid rodents, which also have posteriorly elongate pterygoid processes similar to those of *Hegetotherium*. However, in contrast to the condition seen in *Hegetotherium*, there is no lateral flaring of the processes in the sciurid rodents. Also, although sciurids have a well-defined postglenoid process relative to other members of the Glires, the morphology of the postglenoid fossa still allows for much more freedom of movement and dictates a different type of jaw movement than the unique postglenoid morphology of *Hegetotherium*.

Morphological Divergence from Close Relatives

The cranial anatomy of *Hegetotherium* is distinctive among notoungulates, differing significantly even from its closest relatives. Within Hegetotheriidae, *Pachyrukhos* also shows hypertrophy of I[1], similar cheek teeth morphology and development of a diastema. Yet although the overall morphology of the cranium and dentition is strikingly similar, the rostrum of *Pachyrukhos* is longer in respect to the overall skull length and shallower in respect to overall skull height, and decreases sharply in breadth from the posterior end to the anterior (Table 4). The rostrum of *Pachyrukhos* is delicate in comparison to the heavy, short, broad rostrum of *Hegetotherium*. In addition, *Pachyrukhos* lacks several features present in *Hegetotherium* that are indicative of heavy biting musculature: the anterior root of the zygomatic arch is flat and thin and lacks the deep groove evident on *Hegetotherium,* and the temporal fossa is shallow. The differences in rostrum morphology and musculature suggest that the *Pachyrukhos* fed in a way that did not require the ability to exert massive bite forces or adaptations to resist high stresses on the skull. The other hegetotheriid taxa considered during this study, *Prohegetotherium* and *Sallatherium*, also show enlargement of I[1], but the tooth is neither as massive nor as procumbent as the condition in *Hegetotherium*. Development of diastemata is limited. In both taxa the rostrum is relatively longer than that of *Hegetotherium*, tapering gradually in *Prohegetotherium* and showing an abrupt transition from broad to narrow at the junction of the maxilla and premaxilla in *Sallatherium* (Reguero and Cerdeño 2005, fig. 2A).

Both mesotheriid and archaeohyracid notoungulates have been proposed as sister groups of the Hegetotheriidae (Cifelli 1993; Croft et al. 2003; Billet et al. 2009). Comparison of *Hegetotherium* with the mesothere *Trachytherus* revealed some notable similarities: both animals have a relatively massive skull with a tall braincase; short, broad

TABLE 4. Degree of klinorhynchy for specimens examined.

	Degree of klinorhynchy
Hegetotherium mirabile	23.7
Protypotherium praeritulum	10.9
Pachyrukhos moyani	13.7
Interatherium robustum	7.4
Daubentonia madagascarensis	20.3
Dactylopsila trivirgata	23.6

rostrum; postincisive diastema; and large, keystone-shaped lacrimal. Crucially, *Trachytherus* also shows extreme hypertrophy of I^1, with enamel confined to the labial surface. However, the morphology of I^1 is quite different; in *Trachytherus* and other mesothere taxa (e.g., Billet et al. 2008; Townsend and Croft 2010) these teeth are not procumbent but instead are sharply recurved, with the occlusal surface oriented posteriorly. This contrasts sharply with the arrangement of the first incisor pair in *Hegetotherium* and the extant "mammalian woodpeckers." *Archaeohyrax*, like *Pachyrukhos*, has a rostrum that is longer, shallower and narrower than the more robust structure seen in *Hegetotherium* (see Billet et al. 2009, fig. 4), whereas I^1 is neither as large or as procumbent as in the latter taxon.

Within the Interatheriidae, the dentition of *Protypotherium* and *Interatherium* differ markedly from that of *Hegetotherium*, with small, recurved incisors, no functional diastema, and cheek teeth that are not adapted for slicing. Although the temporalis musculature is similar in all species, the anterior root of the zygomatic arch of *Protypotherium* and *Interatherium* limits the area of masseter attachment, whereas the anatomy of *Hegetotherium* provides a long, broad expanse for a powerful masseter. Elongated pterygoid crests have been described as a feature of mammalian woodpeckers, evolved to resist tensile stresses on the rostrum (Cartmill 1976; Beck 2009). The pterygoid crests of *Hegetotherium* are longer than those of *Protypotherium* but are less so than *Interatherium*, which also has a tall, anteroposteriorly short rostrum. When viewed in profile, the tooth row of *Hegetotherium* is horizontally level, with the occlusal surfaces of the teeth lying in roughly the same plane. *Interatherium* and *Protypotherium* do not share this characteristic; rather, in these species the tooth row is bowed ventrally in a shallow, convex curve. It is possible that the level tooth row of *Hegetotherium* allowed it to move its jaws in an anteroposterior slicing motion. Slicing has been previously suggested as a method for the mastication of xylophagus grubs, a hypothesis supported by the self-sharpening molars of *Yalkaparidon* and the bladelike P^2 of apatemyids (Beck 2009). The cheek teeth of *Hegetotherium* occlude in such a way that the lingual edges of the bottom teeth shear against the labial edges of the upper teeth. By contrast, those of *Protypotherium*, and especially *Interatherium*, show a more complex pattern of occlusion that precludes any slicing motion.

In a comprehensive morphometric analysis of the mandibles and crania of Santa Cruz notoungulates, Cassini and colleagues (2011) studied a variety of characteristics to predict feeding methods. *Hegetotherium* was found to occupy an "exclusive" corner of the morphospace separate from its relatives, on the basis of its high level of hypsodonty and unusually short jaw (Cassini et al. 2011). As described above, hypsodonty is a characteristic that would support a wood-boring lifestyle, because it helps teeth resist wear from abrasive particles. Further, as mentioned above, a short jaw is characteristic of mammalian woodpeckers, because it helps reduce bending stresses on the skull during wood boring (Cartmill 1976). Thus, the characters that set *Hegetotherium* apart from its relatives fit the hypothesis of a wood-boring lifestyle. Cassini and colleagues (2011) suggest that *Hegetotherium* may have been a digger, which would explain its unusual position in the morphospace.

Evidence for a Fossorial Mode of Life

A common characteristic of known mammalian woodpeckers is the existence of one or more elongated digits on the manus, which help to probe into the wood to extract grubs (Cartmill 1976; Beck 2009). Confirmation of the presence or absence of such a feature in *Hegetotherium* is not currently possible, because its manus is unknown. The pes, which was described by Sinclair (1909), has a greatly elongated digit III, relative to the other digits. Sinclair hypothesized that the enlarged inner digits of the pes of a related taxon, *Pachyrukhos,* were an adapatation for a hopping, rabbitlike mode of locomotion, which requires large hind feet. However, *Hegetotherium* has only one elongate middle digit of the pes, a condition slightly different from that of the hind feet of lagomorphs, which are enlarged overall with two elongated middle digits, rather than just one (Pocock 1925). There is no reason to assume that this anatomy would be mirrored in the manus of *Hegetotherium,* but the presence of a similarly elongated middle digit would be a characteristic strongly suggestive of a wood-boring lifestyle.

Cassini and colleagues (2011) performed cranial and dental morphometric analyses and found that *Hegetotherium* did not fit neatly within a grazing category. They proposed that its unusual status could be explained if *Hegetotherium* were a digger, a hypothesis supported by Ellissambru's postcranial morphometric analysis of *Hegetotherium* (Elissamburu 2004; Cassini et al. 2011). Elissamburu concluded that *Hegetotherium* had forearms designed for powerful, forceful movements; in contrast, *Pachyrukhos* had forearms adapted for the traditionally proposed locomotion method of lagomorph-like jumping. This combination of cranial and postcranial features in *Hegetotherium* is reminiscent of the Taeniodonta, an extinct group of Early Paleocene and Eocene mammals that evolved enlarged incisors, claws and muscular forearms, commonly interpreted as an adaptation for digging and rooting (Schoch 1986). Possibly *Hegetotherium* was a digger, like the Taeniodonta. However, modern anteaters have enlarged muscular forearms to tear away at wood or termite mounds to expose their prey (e.g., Taylor 2005). *Hegetotherium* may have used its enlarged forearms to tear away wood in a similar way to expose insects. It is certainly possible that *Hegetotherium* supplemented its diet through digging and rooting, like the Taeniodonta; however, it is worth noting that the cranial and incisor morphology of the Taeniodonta is similar to that of Hegetotherium only in that the incisors are enlarged and the skull is robustly constructed (Schoch 1986). Note also that xenarthran-like claws are very rare in notoungulates. Further conjecture about mode of life will remain inconclusive in the absence of a specimen of the manus of *Hegetotherium*.

Potential Niche Competition: Did Avian Woodpeckers Coexist with Hegetotherium?

The modern mammalian woodpeckers, *Dactylopsila* and *Daubentonia*, occupy a woodpecker-like niche in the absence of avian woodpeckers (Picidae). Although *Hegetotherium* was cursorial, multiple woodpecker species also bore through the wood of fallen trees and logs (e.g., Jackson et al. 2002). This raises the question of whether there were avian woodpeckers coexisting with *Hegetotherium* in South America. The occurrence of Picidae in the Neotropics is dominated by the basal picumnine piculets (Short 1982; Benz et al. 2006), and the earliest known New World occurrence of a woodpecker was a feather in amber found in the Dominican Republic (Laybourne et al. 1994). Analysis of the specimen revealed that it was of a species closely related to the Antillean Piculet, *Nesoctites micromegu*, which lived somewhere from the late Eocene to the early Miocene (Laybourne et al. 1994). Woodpeckers in general are characterized by short wings, which lack the power necessary for long-distance dispersal (Benz et al. 2006), and piculets are even more morphologically unsuited to long-distance dispersal, with their small wings and rounded bodies (Fuchs et al. 2006). Piculets also tend to be very philopatric, remaining close to their birthplace, with capture–recapture data showing a very small range of 800 m over several years for a particular individual (Winkler and Christie 2002; Fuchs et al. 2006). The span of ocean between Hispaniola and the South American mainland would represent a formidable barrier to the early piculets, so the presence of piculets in the Greater Antilles during the middle Cenozoic does not imply a similar presence on the mainland. Indeed, the similarity between the feather found in amber and the unique, monophyletic modern Antillean piculet supports this hypothesis of long-term isolation. However, from the late Eocene to the early Miocene, the Antilles arc went through several cycles of paleogeographic change. Although the orientation of the Antilles Arc and its distance from the mainland did not change noticeably, the amount of deep ocean in between the landmasses varied (Iturralde-Vinent and MacPhee 1999). For example, the late Eocene saw the formation of a ridgecrest (or closely spaced large islands) connecting the Greater Antilles Arc to the mainland, whereas the Oligocene saw marine invasions reestablishing oceanic barriers between the Antilles Arc and the mainland (Iturralde-Vinent and MacPhee 1999). Because of these paleogeographic cycles and the uncertain dating of the piculet feather, we cannot be sure that piculets did not disperse to the mainland. Therefore, if piculets were contemporaries of *Hegetotherium*, would there have been direct competition?

Piculets are small, short-tailed and short-billed, feeding mostly on ants, other insects and larvae, and foraging on tree trunks (Fuchs et al. 2006). Their tiny body size makes it unlikely that piculets would be in direct competition with the large and powerful *Hegetotherium.* Further, the

Miocene climatic optimum, a period of hot, humid climate 17 to 15 mya (Zachos et al. 2001), led to the increased diversification of wood peckers, the divergence of the piculets, the formation of more complex ecological niches and a diversification in foraging strategies (Fuchs et al. 2006). This time period of niche diversification is coincident with the appearance of *Hegetotherium*, which may have filled one of the newly formed ecological niches, perhaps by adapting a foraging strategy that the small, short-billed piculets did not use: namely, powerful wood boring of fallen trees and logs.

The Paleoenvironment of Hegetotherium

The Santa Cruz Formation and its associated fauna, of which *Hegetotherium mirabile* is one element, provide a unique window for reconstructing the structure of a South American mammalian palaeocommunity (Vizcaíno et al. 2010). Interpretations of the Santacrucian mammal assemblage have varied. Tauber (1997a), observing the apparent coexistence of the arboreal primate *Homunculus* with many apparently "savannah-adapted" mammals, suggested a mixed habitat of woodlands and more open terrain, driven by a less humid climate that favored open habitats over trees (Tauber 1997b, 1999). By contrast, the analyses of Pascual and Ortiz-Jaureguizar (1990) and Croft (2001) suggest the area was wetter and less open than previously thought. The occurrence of primates and erethizontid rodents may be indicative of forests growing in warm and humid conditions (Vucetich 1986; Pascual and Ortiz-Jaureguizar 1990). Studies of the early Miocene paleoflora of Patagonia suggest that closed and open environments coexisted, with xerophytic shrubby and herbaceous elements gradually increasing over forests as the epoch progressed (Barreda and Palazzesi 2007). By the Santacrucian, the environment of Patagonia was likely to have been comparable to temperate forest and bushland, with less than 1000 mm of rainfall annually. Closed canopy environments would be primarily riparian and gallery forests (Vizcaíno et al. 2010).

Alternative Feeding Strategies

The woodpecker hypothesis explains a number of aspects of *Hegetotherium*'s anatomy, but it is not a perfect fit and there are some significant outstanding issues. First, *Hegetotherium* is a relatively large animal as compared with extant mammalian woodpeckers. For example, *Daubentonia* and *Dactylopsila* have body masses of 2 to 3 kg (Nowak 1999) and 240 to 550 g (Flannery 1995), respectively, whereas the weight of *Hegetotherium* has been estimated at 6 to 8 kg by Elissamburu (2004) and as high as 14 kg (Vizcaíno et al. 2010). Large body size per se is not a barrier to insectivory—the largest extant insectivore (*sensu lato*) is the sloth bear, *Melursus ursinus*, which has a body mass ranging from 55 to 190 kg (McNab 1992), and the weight estimates of *Hegetotherium* compare favorably with those of other extant mammalian insect feeders, including the aardwolf, *Proteles cristata* (9 to 14 kg: Nowak 1999), *Tamandua* (2 to 7 kg: Nowak 1999), and various genera of armadillo, such as *Euphractus* (3.2 to 6.5 kg: Redford and Wetzel 1985), *Cabassous* (2 to 4.8 kg: Redford and Eisenberg 1992) and *Dasypus* (1 to 10 kg: Nowak 1999). Whereas the largest of the insect-feeding mammals, such as the sloth bear, giant anteater and giant armadillo sustain high body mass through feeding primarily on social insects such as ants and termites, medium-sized insectivorous mammals use a diverse range of food sources, including insect larvae from carrion (*Euphractus*: Nowak 1999) and arthropods found in leaf piles, holes and crevices (*Dasypus*: Nowak 1999). One possible dietary analogue for *Hegetotherium* is is the naked-tailed armadillo *Cabassous centralis*, which feeds on insect colonies in dead roots and stumps, although also note that this is by no means a perfect analogy; *Cabassous* is fossorial and, like most xenarthrans, has a simple dentition and relies on a long, sticky tongue and powerful forelimbs to capture its prey (Eisenberg and Redford 1999). Nonetheless, these living analogues show, first, that body size is not necessarily a barrier to insectivory; second, that it can be sustained without recourse to feeding on social insects; and third, that social insect colonies can be found in tree stumps and there is at least one living species of mammal specialized in feeding on them.

Hegetotherium may have fed by boring through wood, but it may also have used additional or alternative feeding strategies to supplement its diet. There is some precedent for mammalian woodpeckers feeding in several different ways. For example, *Daubentonia*'s diet also includes nectar, fungi and seeds (Pollock et al.

1985; Sterling 1993; Beck 2009). In fact, the hypothesized maximum body mass of a true insectivore, calculated as 300 g (Kay and Hylander 1978), is less than the body mass of *Daubentonia* and the hypothesized body mass of *Hegetotherium* (Sinclair 1909; Beck 2009). Even if *Hegetotherium* used wood-boring feeding methods, its diet was probably supplemented by other means. It is possible that *Hegetotherium*'s unique cranial adaptations and powerful bite may have allowed it to crack open the tough outer coatings of fruits and nuts. Janzen and Martin (1982) hypothesized that certain species of South American trees coevolved with the endemic megafauna, growing nuts with thick shells that could only be dispersed by the now-extinct megafauna. Alternatively, as mentioned above, *Hegetotherium* may have been a digger or rooter analogous to the Taeniodonta (Schoch 1986).

However, the combination of prognathous hypertrophied first incisors, enlarged masseter muscles and robust cranium provides strong support for a wood-boring hypothesis. Since *Hegetotherium* was probably cursorial, the most likely scenario is that it fed by boring through the bark of fallen branches or tree trunks to consume xylophagous grubs and other insects. Fallen trees provide a rich and diverse habitat with many trophic levels, ranging from fungi to salamanders (Maser and Trappe 1984). Animals such as millipedes, salamanders and multiple species of woodpeckers feed on animals that dwell within fallen logs (e.g., Maser and Trappe 1984; Jackson et al. 2002). Therefore, it is likely that *Hegetotherium* adopted wood boring of fallen trees and logs, a method probably supplemented by additional modes of feeding.

Conclusion

The cranial anatomy of *Hegetotherium mirabile* is remarkably similar to that of mammalian woodpeckers, a group of phylogenetically distinct mammals that feed by boring through wood to reveal grubs. They each have unique and pronounced incisor development to bore through and pry up wood, self-sharpening molars to masticate xylophagous grubs and other organisms, and highly distinctive cranial reinforcements to absorb the resultant forces on the skull. *Hegetotherium* also has several other cranial characteristics that support the wood-boring hypothesis, such as its hyposelodont cheek teeth—which resist wear—and its keystone-like lacrimal, which absorbs forces on the skull. Since the postcranial anatomy of *Hegetotherium* is suggestive of cursoriality, it may have fed by breaking through the wood of fallen trees and logs, a rich source of habitat and nutrition to many species, including salamanders and multiple species of avian woodpeckers (e.g., Maser and Trappe 1984; Jackson et al. 2002). The manus, as yet unknown for *Hegetotherium*, could provide valuable further evidence for its feeding methods.

It is striking that four different groups of mammals evolved such similar morphological features for a wood-boring method of feeding. If more evidence shows support for the inclusion of *Hegetotherium mirabile* in the small assembly of mammalian woodpeckers, then the number of unrelated groups of mammalian woodpeckers is raised to five. In either case, the uniquely specialized mammalian woodpeckers are a perfect example of convergent evolution.

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