J. Paleont., 83(3), 2009, pp. 489–492

0022-3360/09/0083-489$03.00

THREE-TOED BROWSING HORSE *ANCHITHERIUM* (EQUIDAE) FROM THE MIOCENE OF PANAMA

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INTRODUCTION

DURING THE Cenozoic, the New World tropics supported a rich biodiversity of mammals. However, because of the dense vegetative ground cover, today relatively little is known about extinct mammals from this region (MacFadden, 2006a). In an exception to this generalization, fossil vertebrates have been collected since the second half of the twentieth century from Neogene exposures along the Panama Canal. Whitmore and Stewart (1965) briefly reported on the extinct land mammals collected from the Miocene Cucaracha Formation that crops out in the Gaillard Cut along the southern reaches of the Canal. MacFadden (2006b) formally described this assemblage, referred to as the Gaillard Cut Local Fauna (L.F., e.g., Tedford et al., 2004), which consists of at least 10 species of carnivores, artiodactyls (also see recent addition of peccary in Kirby et al., 2008), perissodactyls, and as described by Slaughter (1981), rodents. Prior to the current report, the horses (Family Equidae) from the Gaillard Cut L.F. consisted of only four fragmentary specimens including: two isolated teeth, i.e., one each of *Archaeohippus* sp. Gidley, 1906 and *Anchitherium clarencei* Simpson, 1932; a heavily worn partial dentition with p2–p4 of *A. clarenci*; and a partial calcaneum of *Archaeohippus*. Although meager, these fossils appear to represent two distinct taxa of three-toed horses otherwise know from the middle Miocene of North America, i.e., the dwarf-horse *Archaeohippus* sp. and the larger *Anchitherium clarencei*.

Over the past decade the government of Panama has undertaken two monumental public works projects, including the construction of the new Centenario Bridge across the Gaillard Cut (completed in 2004) and the most extensive expansion of the Panama Canal since the original excavations by the United States in the early twentieth century, the latter of which is scheduled to continue well into the next decade. Both of these projects have yielded an extensive series of new exposures of the Cucaracha Formation. Consequently, new collections of fossil vertebrates are being made and studied as a result of collaborations between the Smithsonian Tropical Research Institute and the University of Florida. In 2008 a well preserved and relatively complete specimen of *Anchitherium clarenci* was collected that confirms the previous taxonomic identification based on poorly preserved and fragmentary materials (MacFadden, 2006b), while also significantly increasing our understanding of the dental morphology of this species as it is known from Panama. The purpose of this paper, therefore, is to describe this new specimen and discuss its significance with regard to morphology, distribution, and paleoecology of *Anchitherium clarencei* at the extreme southern extent of the known range of this genus, which is otherwise widely distributed throughout Holarctica (occurrence data were downloaded from The Paleobiology Database [www.paleodb.org] on 30 January, 2009, using the genus name "*Anchitherium*").

The following institutional abbreviations are used for specimens described in the text: MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UF, University of Florida Vertebrate Paleontology Collection, Gainesville, Florida; USNM, United States National Museum, Washington, D. C. The following abbreviations are used for morphological descriptions: APL, greatest anterior-posterior length; CRNHT, crown height of enamel measured at mesostyle; HI, hypsodonty index (CRNHT/APL); L, left; M, upper molar; P, upper premolar; R, right; TRN, greatest transverse width.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Genus ANCHITHERIUM Meyer, 1844
ANCHITHERIUM CLARENCI Simpson, 1932
Figures 1, 2, Table 1

Referred specimen.—UF 236937, partial palate (maxilla) with L P1–M3, R P1–P3, and small fragment of anterointernal part of P4 (Fig. 1). Collected by Aldo Rincón of the Smithsonian Tropical Research Institute, Republic of Panama, on 15 May 2008.

Locality and age.—Centenario Bridge locality (UF YPA009), lat. 9°01.741′N, 79°38.164′W, west side of Panama Canal (former Canal Zone), Gaillard Cut, Cucaracha Formation, section 6 (Kirby et al., 2008, fig. 6) in a fossiliferous conglomerate unit 58 m above the base of the local measured section; also above a prominent welded tuff and below the contact with the Pedro Miguel volcanics; middle Miocene, probably either Hemingfordian or early Barstovian North American Land Mammal Age (He1 through Ba1, sensu Tedford et al., 2004), ca. 18 to 15 million years ago.

Description.—UF 236937 preserves the palate and cheek tooth dentition (the symphysial region and its corresponding dentition are not preserved). The cheek region contains a well-developed facial crest that extends anteriorly to above the posterior half of M1 (Figs. 1, 2.1). There is no evidence of a ventrally situated (malar) preorbital facial fossa, but this absence likely results from the fact that the appropriate portion of the facial region may not be preserved. The dental measurements are similar to, if not indistinguishable from, the type of *Anchitherium clarencei* from the Midway L.F. from Florida (Fig. 3, Table 1; also see MacFadden, 2001). Likewise for UF 236937, a P1–M3 tooth row length of 129.3 mm and P2–M3 tooth row length of 118.4 mm are very similar to those same measurements taken from a well preserved dentition (MCZ 3810) of *A. clarencei* from Thomas Farm, Florida (respectively, 126.3 mm and 119.8 mm; MacFadden, 2001). Thus, relative to other middle Miocene horses (e.g., contemporaneous *Parahippus leonensis* and *Archaeohippus blackbergi*), UF 236937 is relatively large, of a size similar to the modern donkey *Equus asinus* (MacFadden, 2001). The HI calculated for each tooth range from 0.39 to 0.51 (Table 1), all indicating a brachyodont (short-crowned) species.

This specimen represents an adult individual in middle wear, and thus preserves many of the essential and diagnostic characters of the dental pattern and full cheek tooth dentition not represented in the previously reported individual tooth (USNM 23156, MacFadden, 2006b). The first premolar, which actually is a deciduous P1 (dP1) retained in the adult dentition (MacFadden, 2001), is longer than it is wide (APL > TRN, Table 1). The ectoloph on the dP1 has a poorly developed, discontinuous cingulum. One principal cusp lies internal to the ectoloph and internal to this cusp is a V-shaped basin. The P2 is the largest of the cheek teeth, with the development of a prominent anterostyle on the anterior part of the ectoloph. The P3–M3 are of generally similar proportions in which the individual teeth are wider than long (TRN > APL, Table 1). P2–M3 all have very well developed

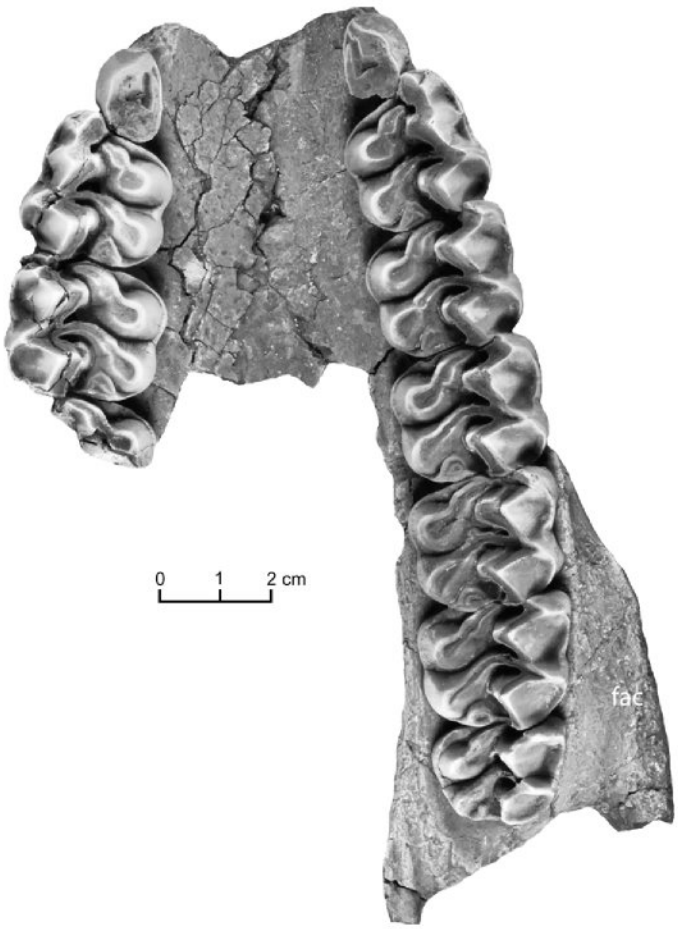

FIGURE 1—*Anchitherium clarencei*, UF 236937, partial palate (maxilla) with L P1 through M3 and R P1 through P3 (and fragment of P4), from the Gaillard Cut L.F., Cucaracha Formation, Miocene of the Panama Canal. Abbreviation: fac, crest.

external cingula that extend ventrally to include the anterior parastyle and medial mesostyle along the ectoloph. The remaining anterior, internal, and posterior perimeters of P2–M3 mostly have well-developed cingula, except along the internal-most portion of the enamel forming the metaloph. The ectoloph on P2–M3 is characteristically W-shaped and in lateral view (Fig. 2.1) forms two prominent dorsoventrally situated enamel ridges (parastyles and mesostyles) on the external face of the tooth. As Stirton (1940) noted, ribs are either poorly developed or absent between the styles on the ectoloph. Internal to the ectoloph, the occlusal surfaces of P3–M3 each demonstrate prominent protolophs and metalophs, and deep basins formed posterior to each of these lophs. A well developed hypostyle lies posterior to the metaloph. There is no evidence of cement having been deposited on the tooth enamel.

TABLE 1— Dental measurements (mm) for UF 236937, *Anchitherium clarencei*, from the Gaillard Cut L.F., middle Miocene of Panama. Abbreviations: APL, greatest anterior-posterior length; CRNHT, greatest crown height taken along enamel (excluding root) of mesostyle; HI, hypsodonty index (CRNHT/APL); M, molar; P, premolar; TRN, greatest transverse width.

	P1	P2	P3	P4	M1	M2	M3*
R APL	15.0	24.1	22.8	—	—	—	—
R TRN	10.5	22.7	25.6	—	—	—	—
R CRNHT	—	9.0	10.0	—	—	—	—
R HI**		0.40	0.39	—	—	—	—
L APL	14.4	24.2	22.6	21.9	21.8	21.2	16.2
L TRN	10.4	22.7	24.7	25.1	24.1	23.8	19.6
L CRNHT	—	10.7	10.4	11.2	9.7	10.1	10.2
L HI	—	0.47	0.42	0.44	0.40	0.42	0.52

* Cheek tooth row lengths, L P1–M3 = 129.3; L P2–M3 = 118.4.
** Mean of eight teeth (2 R and 6 L above) = 0.43.

Taken together, the dental measurements along with the qualitative characters of the upper cheek are indistinguishable from *Anchitherium clarencei* from Florida and other localities in North America (MacFadden, 2001) and therefore unambiguously justify allocation of the Panama specimens (also including the other two specimens described in MacFadden, 2006b) to this species. The species-level systematics of *Anchitherium*, which had a Holarctic distribution, and its closely related genus *Kalobatippus* Osborn, 1915 from North America are in need of a modern revision. Nevertheless, with regard to its apparent closest North American relative, *A. clarencei* differs from *A. navasotae* (Hay, 1924), known from the Texas Gulf Coastal Plain, in that the former species is larger (MacFadden, 2001).

DISCUSSION

Several diagnostic characters of the dental pattern (e.g., development of P1), cheek tooth variation (e.g., relative development of the cingulum), and overall size (e.g., tooth row length) that were not previously represented from the Gaillard Cut L.F. (MacFadden, 2006b) are now known from the specimen described here. These features therefore provide significant new evidence confirming the taxonomic allocation of *Anchitherium clarencei* as it is known from the southern extreme of its biogeographic range. In fact, the presence of *Anchitherium* in Panama extends the range of this previously widespread range of this genus from Holarctica by some 20° of latitude into the ancient Neotropics (in the Old World, this genus is not reported from Africa or other equatorial regions; McKenna and Bell, 1997; http://www.paleodb.org).

The exact biostratigraphic age of the Gaillard Cut L.F. is currently unresolved because this faunal assemblage mixes taxa characteristic of three Miocene North American Land Mammal ages, i.e., the late Arikareean, Hemingfordian, and early Barstovian (sensu Tedford et al., 2004; MacFadden, 2006b). In addition to its presence in Panama, the species *Anchitherium clarencei* is otherwise known from the Hemingfordian and early Barstovian of Florida and similar-aged localities elsewhere in North America, e.g., in the Great Plains (including Nebraska and South Dakota, MacFadden, 2001). This is similar to the biostratigraphic assessment of the age of the Gaillard Cut L.F. for all of the known taxa of mammals except for the oreodont *Merycochoerus matthewi*, the latter of which potentially indicates and older (late Arikareean) age, and may represent a relictual occurrence and biochronological range extension for this artiodactyl in Panama.

As represented by the Gaillard Cut L.F. from the Cucaracha Formation, MacFadden and Higgins (2004) argued for a habitat mosaic during the Miocene of Panama ranging from relatively dense, possibly tropical forest to open woodlands (also see Retallack and Kirby, 2007). With a carbon isotope value of −12.1 per mil (MacFadden and Higgins, 2004), and a hypsodonty index of 0.55 (MacFadden, 2006b), *Anchitherium clarenci* from Panama was interpreted to have been nearer the forest browsing end of the habitat-mosaic spectrum, although based on the single isolated tooth previously available, any such determination is provisional. Nevertheless, this ecological assessment is consistent with the long-held view that *Anchitherium* was primarily a forest-dwelling browser (e.g., Simpson, 1951). The new specimen described here provides additional confirmation of the ecology of *Anchitherium clarencei*. The mean hypsodonty index (N = 8, Table 1) of 0.43 additionally documents the relatively low-crowned (brachyodont) nature of this species and an interpretation of browsing diet (e.g., Janis, 1988; MacFadden, 1992).

In addition to the HI, the dental morphology preserved in the P1–M3 of UF 236937 provides evidence of patterns of occlusal

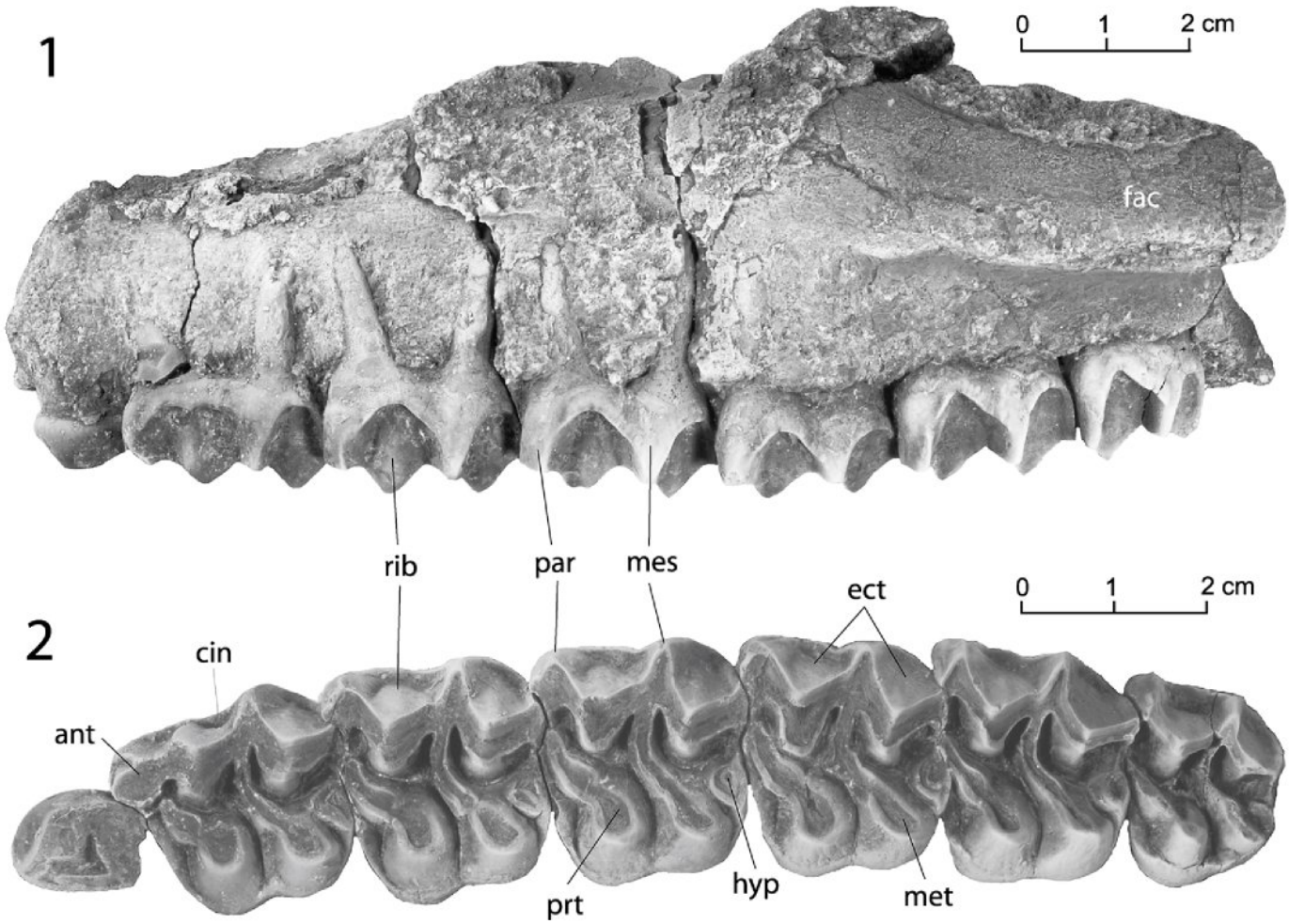

FIGURE 2—*Anchitherium clarencei*, UF 236937, from the Gaillard Cut L.F., Cucaracha Formation, Miocene of the Panama Canal. *1*, Lateral view; *2*, Occlusal view of L P1–M3. Abbreviations: ant, anterostyle; cin, cingulum; ect, ectoloph; fac, facial crest; hyp, hypostyle; mes, mesostyle; met, metaloph; par, parastyle; prt, protoloph; rib, rib.

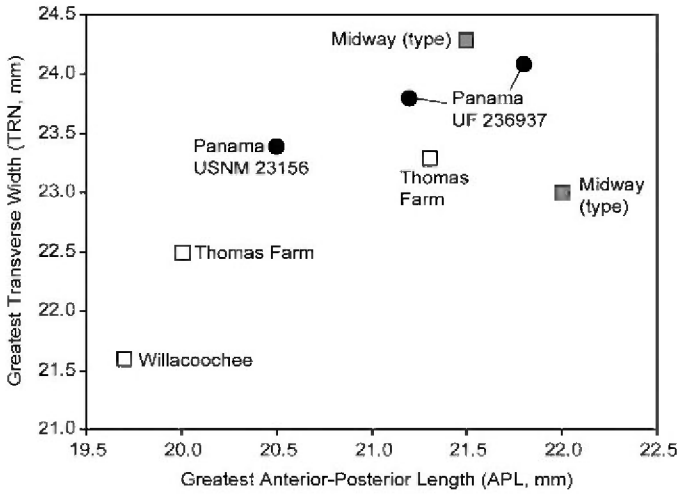

FIGURE 3—Bivariate plot of anterior-posterior length versus transverse width of M1 or M2 (or ?P4, M1, or M2 for USNM 23156) for *Anchitherium clarencei* from Panama and Florida. Measurements taken from Table 1 here and MacFadden (2001; 2006b).

wear indicative of diet, i.e., the mesowear technique proposed by Fortelius and Solounias (2000) that has become widely employed in studies of the paleoecology of mammalian herbivores. The occlusal surface of the ectoloph in this cheek tooth series of UF 236937 is characterized by high relief and sharp cusps (Fig. 1.1), similar to extant herbivores such as the moose, in Europe called elk, (*Alces alces*) known to be principally forest-dwelling browsers. As has also recently been shown for tapirs from the New World, the presence of the three-toed browsing horse *Anchitherium* in extinct faunal assemblages argues for forested habitats in close proximity to the fossil locality (DeSantis and MacFadden, 2007)

CONCLUDING COMMENTS

The current description of the well-preserved maxilla of *Anchitherium clarencei* significantly advances our understanding of the presence of this species at the southern extent of its known biogeographic range. The ongoing excavations along the Panama Canal, which are scheduled to continue well into the next decade, will provide the opportunity for additional important fossil discoveries that will enhance our understanding of the ancient New World tropics during the Miocene.

ACKNOWLEDGMENTS

The author thanks C. Jaramillo and A. Rincon from the Smithsonian Tropical Research Institute for, respectively, logistic support and collecting the specimen described here. J. Mason and J.

Bourque prepared the specimen. J. Bloch and R. Hulbert Jr. provided advice about specimen photography. R. Hulbert Jr. and the anonymous reviewers provided comments and input that improved the manuscript. This research was supported by the 2007 Research Opportunity Fund at the University of Florida and National Science Foundation grants OISE 0638538 and EAR 0751086. This is University of Florida Contribution to Paleobiology number 616.

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ACCEPTED 10 FEBRUARY 2009