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. Gilley, 1906 and Anchitherium clarencei Simpson, 1932: a heavily worn partial dentition with P2–M4 of A. clarencei: and a partial calcarium of Archaeohippus. Although meager, these fossils appear to represent two distinct taxa of three-toed horses otherwise known 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 clarencei was collected that confirms the fact that the appropriate portion of the facial region may not be preserved. The dental measurements are similar to, if not in-
Anchitherium clarencei — Dental measurements (mm) for UF 236937, 1

|      | LHI  | L CRNHT | L TRN | L APL | RHP* | RCRNHT | RTRN | L PI through M3 and R PI through P3 (and fragment of P4), from the Gaillard Cut L.F., Cucaracha Formation, Miocene of the Panama Canal. Abbreviation: fac, crest.
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*a* Check 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.

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 Holartic 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 Telford 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 oceodont Mercochoerus 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 Re-tallack 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 clarencei 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 (brachydont) 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 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.

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 Holartic distribution, and its closely related genus Kalabatipus 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).
weir 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.

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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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